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SOME REMARKABLE NEW BIRDS FROM DYAUL ISLAND, BISMARCK ARCHIPELAGO, WITH ZOOGEOGRAPHICAL NOTES

BY

FINN SALOMONSEN

NOONA DAN PAPERS NO. 9



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Synopsis

The "Noona Dan Expedition" during its visit to the Bismarck Archipelago in 1962 investigated the fauna and flora of Dyaul Island, which was hitherto unexplored. The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of striking endemic forms, the description of which forms the first part of the present paper.

The second part of the paper deals with various zoogeographical problems in connection with the history of the fauna of Dyaul. The morphological differentiation of the endemic forms must have required a certain amount of time, during which the populations were isolated from those of the neighbouring islands (New Ireland and New Hanover). It is noteworthy that the Gazelle Channel, not broader than 14 km, has been broad enough to form an effective barrier. The length of the period of isolation has been roughly estimated on the basis of a comparison with the faunas of similar tropical islands (Philippine Islands, West Sumatran Islands). It is demonstrated that the populations of the main chain of islands in the Bismarck Archipelago are either identical or only slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is explained as primarily the result of a greater evolutionary rate in the Dyaul populations, but a time factor must be involved also. Evidence is given for the assumption that the main islands were mutually connected, forming one or two big islands, when Dyaul had already received its fauna.

A comparison is made between the faunas of Dyaul and of the Hibernian Islands, which latter differ from Dyaul in having a rather impoverished fauna and only slightly differentiated indigenous subspecies. In order to explain these differences an attempt is made to analyse the factors which control island colonization by birds. According to this analysis Dyaul, evidently, has greater possibilities than the Hibernian Islands for colonization by birds.

New Ireland and New Hanover form the origin of the main part of the land-bird fauna in four zoogeographically different groups of islands: (1) The Admiralty Islands and the St. Matthias Islands, (2) The Hibernian Islands, (3) The Duke of York Islands, and (4) Dyaul Island. The zoogeographical differences between these four categories of islands are due to the unequal possibilities for avian colonization and to the differences in the geological history which have been described in the present paper.

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Dyaul Island in the Bismarck Archipelago was discovered in 1767 by Lieutenant PHILIPP CARTERET during the celebrated voyage of the "Swallow". CARTERET called the island Sandwich Island, and this name was used for more than a hundred years, and was the most common designation even in the German period (REICHENOW 1899, map; PARKINSON 1907, p. 251; SIEVERS 1910, p. 439). During this period, however, the name Djaul or Djaule began to appear, and this name, spelled Dyaul, is now the official designation of the island.

From a natural history point of view Dyaul is quite unexplored. When planning the itinerary of the "Noona Dan Expedition" I, therefore, included a visit to Dyaul during the contemplated investigation of the Bismarck Archipelago. The visit to Dyaul took place in the period in which I served as scientific leader of the expedition. The results of the ornithological investigation proved so interesting that I organized a second visit to the island, but this could not be arranged until I had already left the expedition.

The island of Dyaul is situated due south of the western end of New Ireland, from which island it is separated by the deep Gazelle Channel (fig. 1). The area of Dyaul is 115 sq. km, *i.e.* of the same size as Feni Islands and somewhat smaller than the Lihir group and the Tabar group north of New Ireland. It is of a longitudinal shape, the length being 30.5 km, the greatest breadth 7.1 km. It consists mainly of raised coral rock, which forms a rolling lowland, with hills reaching altitudes of usually about 50–70 meters, in one place (Mt. Bendemann) raising rather abruptly to an altitude of almost 200 meters. The coastal areas are covered with extensive coconut plantations alternating with native gardens and second growth. Further inland there are scattered patches of well developed original forest, and along the coasts there is in most places a broad zone of mangroves; in a few places beach forest is developed. The island is thinly populated; there are only about two hundred inhabitants gathered in four villages, but to this number should be added the imported New Guinea labour on a few big coconut plantations under Australian management.

The "Noona Dan" called at Lamatau Harbour, on the central part of the north coast of Dyaul, on March 1st, 1962. In the following two weeks, until March 13th, I carried out ornithological collecting and investigations with the nearby village Sumuna as camp, in the first days together with Dr. LORENZ FERDINAND, who, how-



Fig. 1. The situation of Dyaul Island, giving all collecting stations of the "Noona Dan Expedition". The broken line designates the 100 meters line of depths.

ever, had to leave the expedition on March 4th, already. An excursion was made to Kollepina Plantation on the western part of the north coast, and Dr. FERDINAND made a boat trip to Mait Island, mainly with the purpose of studying sea birds. During the second visit of "Noona Dan" Mr. IB TRAP-LIND collected birds at Dyaul Plantation, at the eastern end of the island, from May 30th to June 10th 1962, while the main scientific staff of the expedition worked on Mussau Island. All the collecting stations on Dyaul are shown on the map fig. 1.

My thanks are due to Dr. DEAN AMADON, Chief-Curator of Birds, The American Museum of Natural History, New York, for sending me comparative material of *Monarcha hebetior, Monarcha verticalis* and *Lalage leucomela*. I am indebted, further, to Sofus Christiansen, M. Sc. and Viggo Hansen, M. Sc. for various geographical information.

Description of New Forms

The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of endemic forms which strikingly differed from their allies on New Ireland. These new forms are described below, while the main description of the bird life of Dyaul will be published elsewhere.

Dicaeum eximium phaeopygium, new subspecies

Type: 3 ad., Sumuna, Dyaul Island, 3. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 951.

Diagnosis: Differs strikingly from the two other forms of this species (nominate *eximium* Sclater and *layardorum* Salvadori) by having the entire upper parts uniform dark brown without the contrasting bright carmine colour on rump and upper tail-coverts of the two other forms and without the rufous coloration of the head found in nominate *eximium*. The differences hold good of both sexes. In addition the females have a much longer white loral streak, extending on to the sides of nape. The bill is distinctly longer and the wing on an average longer than in nominate *eximium*. Adult males of the three subspecies are illustrated on plate I, fig. 1.

In phaeopygium the entire upper parts are dark and sombre brown, but in most specimens there is a slight dull brownish red tinge on the upper tail-coverts and a slight chestnut tinge on the forehead, but not on the crown and occiput, which are of the same colour as the back and not contrastingly coloured as in nominate eximium. The under parts are nearest to those of eximium, but the grey colour of the sides of head, sides of breast and of the median longitudinal streak on abdomen is more greyish black, distinctly darker than in eximium, and the ear-coverts and sides of throat are uniform dark grey (in eximium rufous), at most with a brownish tinge on the ear-coverts; also, the red pectoral patch in the males is generally of greater extension than in eximium. The adult females differ from those of nominate eximium in the same way as the males and, in addition, in having the white loral streak (which is absent in males), much longer, continuing above the eye onto the sides of the nape, while in *layardorum* and nominate eximium it stops in front of the eye.

In both sexes of nominate *eximium* the upper-side of head and nape, the sides of the throat and the ear-coverts are rufous contrasting with the mantle and back, which are olive-brown, lighter and more bright than the coloration in *phaeopygium*, while the rump and upper tail-coverts are shining carmine red. *D. e. layardorum* differs from *eximium* in having the head and back uniform dark grey, not olive-brown, and without contrastingly coloured head; the grey colour on the sides of breast is lighter than in *eximium*, and the flanks are more brightly coloured, olive-yellow rather than olive-greenish brown. The main differences between the three forms concern the upper parts and can be summarized as follows:

Biol. Skr. Dan. Vid. Selsk. 14, no. 1.

Nr. 1

	eximium	layardorum	phaeopygium
Head Back	rufous olive-brown	dark grey	dark brown
Rump	carmine	carmine	

Measurements: The size differences between the three forms are negligible, but *phaeopygium* has a longer bill than the two other forms and apparently a slightly longer wing, at least than nominate *eximium*.

Length of Wing¹

phaeopygium:	13	33	ad.	53-56,	one	51	(54.1);	2	99	ad.	48, 50	
eximium:	15	33	ad.	50 - 53,	one	55	(52.3);	3	99	ad.	48.5 - 50.5	(49.2)
layardorum:	3	33	ad.	52 - 55	(54.0);		1	Q 8	ad. 4	19	

Length of Bill (from Skull)

phaeopygium:	13	33	ad.	11-12, one 10.5 (11.4);	3	♀♀ ad. 11–11.2 (11.1)
eximium:	15	33	ad.	9.8-11.2 (10.5);	3	♀♀ ad. 10-10.8 (10.4)
layardorum:	3	33	ad.	10-10.8 (10.3);	1	♀ ad. 11

The individual measurements are enumerated in table 1.

TABLE 1

Measurements of *Dicaeum eximium* (All specimens mentioned collected by the "Noona Dan Expedition")

Wing	33 ad.	$\mathcal{Q}\mathcal{Q}$ ad.	33 juv.
Dyaul (phaeopygium)	51, 53, 53, 54, 54, 54, 54,	48, 50, —a	
New Hanover (<i>eximium</i>) New Ireland (<i>eximium</i>)	54, 55, 55, 55, 55, 56 52, 53 50, 51, 52, 52, 52, 52, 52, 52,	50.5 48.5, 49	52
New Britain (layardorum)	52, 53, 53, 53, 53, 53, 55 52, 55, 55	49	
Bill (from skull)			
Dyaul (phaeopygium)	10.5, 11, 11, 11.2, 11.5, 11.8, 11.8, 11.8, 12, 12, 12, 12, 12	11, 11, 11.2	
New Hanover (eximium)	10.5, 11	10.8	11
New Ireland (eximium)	9.8, 10, 10, 10, 10, 10, 10.2, 10.5, 10.8, 11, 11, 11.2, 11.2	10, 10.5	
New Britain (layardorum)	10, 10, 10.8	11	

a Wings in moult, not measured.

Material: 13 33 ad., 3 $\varphi\varphi$ ad.

Range: Restricted to Dyaul Island.

Remarks: The main difference between *phaeopygium* and the two other forms is the loss of the contrasting bright carmine red rump patch in *phaeopygium*. A similar

¹ All measurements given in the present paper are in mm. The figures in brackets are the means.

7

patch, which must be regarded as homologous to that found in *eximium*, is widespread in the genus *Dicaeum*, but its presence or absence is usually a species character, not a subspecific one, and this emphasizes the principal importance of the morphological differentiation in *phaeopyqium*. A contrasting carmine rump patch is present in the Moluccan D. vulneratum Wallace, but not in its ally D. erythrothorax Lesson; it is present in the Papuan D. geelvinkianum A. B. Meyer, but not in the related D. pectorale S. Müller (which I regard as conspecific with D. geelvinkianum owing to the existence of intermediate forms; cf. SALOMONSEN 1960, p. 23). A contrasting carmine rump patch is present also in *D. nehrkorni* Blasius of Celebes and *D. mauqei* Lesson of the Lesser Sunda Islands, but absent in the males of the closely allied D. sanguinolentum Temminck and Laugier (but retained in the females), and absent in both sexes of the superspecies D. hirundinaceum (including D. hirundinaceum (Shaw and Nodder), D. celebicum S. Müller, D. monticolum Sharpe and D. ignipectus (Blvth); cf. SALOMONSEN 1961, p. 10). Even in D. aeneum Pucheran of the Solomon Islands, which is related to geelvinkianum and eximium, the red rump patch has been lost, which indicates that this species and *phaeopygium* have developed in a parallel way.

While *layardorum* is restricted to New Britain nominate *eximium* is found both on New Ireland and New Hanover, and the populations inhabiting these two islands are quite indistinguishable. On a previous occasion I examined very large series from both islands (in the American Museum of Natural History, New York), but could find no differences between them. The Dyaul form is a derivative of nominate *eximium*, not of *layardorum*. The chestnut tinge on the forehead which is usually present in *phaeopygium* is a remnant of the rufous colour found on the head and nape of nominate *eximium*, but absent in *layardorum*. Also, the dark brown colour of the upper parts of *phaeopygium* is closer to the olive-brown of nominate *eximium* than to the dark grey colour of *layardorum*. Evidently, Dyaul has been colonized from New Ireland.

Monarcha chrysomela pulcherrima, new subspecies

Type: 3 ad., Sumuna, Dyaul Island, 7. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 1021.

Diagnosis: Adult males: Differ very strikingly from all subspecies of this species in having the upper parts uniform yellow without any black, in all other particulars indistinguishable from nominate *chrysomela*, except for a slightly smaller wing length.

Adult females: Nearest to nominate *chrysomela*, but differing strikingly in having much more yellow in the plumage. While nominate *chrysomela* has the upper parts and wings uniform dark greenish olive, in some specimens with a yellowish tinge on the head and rump, *pulcherrima* has the forehead and sides of head as well as the rump and upper tail-coverts bright yellow and the lesser and median wing-coverts broadly edged with yellow; the remaining upper parts are distinctly lighter than in nominate *chrysomela*, citrine green, not dark greenish olive.

Immature females¹: Differ from nominate *chrysomela* in the same way as the adult females.

Specimens of both sexes of the new form and of nominate *chrysomela* are illustrated on plate I, fig. 2.

Measurements: The wing-length is slightly smaller than in nominate chrysomela from New Ireland. The specimens from New Hanover appear to bridge the difference between the Dyaul and the New Ireland population. The slightly smaller wing-length of the New Hanover birds in comparison with that of the New Ireland birds is also apparent from the measurements taken by MAYR (1955, p. 32): New Hanover 5 3370-74 (72.3), New Ireland 8 33 71.5-76 (73.1).

Length of Wing

Length of Bill (from Skull)

 pulcherrima (Dyaul):
 5 ♂♂ ad. 14–16.8 (15.6); 3 ♀♀ ad. 15–15.8 (15.4)

 chrysomela (New Hanover):
 6 ♂♂ ad. 15–17 (15.7); 1 ♀ ad. 15.5

 — (New Ireland):
 6 ♂♂ ad. 14–16 (15.2); 2 ♀♀ ad. 16, 16

The individual measurements are enumerated in table 2.

TABLE 2

Measurements of *Monarcha chrysomela* (All specimens mentioned collected by the "Noona Dan Expedition")

Wing Dyaul (<i>pulcherrima</i>) New Hanover (<i>chrysomela</i>) New Ireland (<i>chrysomela</i>)	ినే ad. 69, 69, 70.5, 71, 71 72, 72, 72, 72, —a, —a 73, 73, 74, 74, 75, 76	♀♀ ad. 71, 71, 73 72 73, 73	්් juv. 71	♀♀ juv. 67, 70 68 68
Bill (from skull) Dyaul (<i>pulcherrima</i>) New Hannover (<i>chrysomela</i>) New Ireland (<i>chrysomela</i>)	14, 15, 16, 16, 16.8 15, 15.2, 15.5, 15.5, 16, 17 14, 14,5 15, 15.8, 15,8 16	15, 15.5, 15.8 15.5, 16, 16	16	15.6, 16 16 16.5

^a Wings in moult, not measured.

Material: 5 33 ad., 3 99 ad., 2 99 juv. *Range*: Restricted to Dyaul Island.

Remarks: It is noteworthy that *pulcherrima* has diverged much further than any other subspecies within the species *chrysomela*. Nominate *chrysomela* inhabits New

¹ Immature males: Not examined. In nominate *chrysomela* they are similar to the immature females, but have slightly more yellow on the upper parts.

Hanover and New Ireland. In the Bismarck Archipelago the species inhabits also the Lihir group and the Tabar group, in which areas it has developed local subspecies, whitneyorum Mayr and tabarensis Mayr, respectively. These two forms differ only inconsiderably in colour pattern from nominate chrysomela, the males being lighter yellow, not so orange, the females darker greenish olive on the upper parts; in addition, whitneyorum is distinctly larger (wing-length in 33 ad. 77.5–80), while tabarensis is intermediate in size between whitneyorum and nominate chrysomela (MAYR 1955, p. 31). The extension of the black area on the upper parts in the males of whitneyorum and tabarensis is just as in nominate chrysomela. This holds good also of all the remaining forms of this species, inhabiting the New Guinea area (kordensis, melanonotus, aurantiacus, praerepta and aruensis; cf. MAYR 1941, p. 135), some of them having even more black on the upper parts than nominate chrysomela. This shows how pronounced the differences are which separate palcherrima from the other subspecies of chrysomela. The differences between pulcherrima and the other subspecies in the coloration of the females are almost as striking as in that of the males.

Monarcha ateralba, new species

Type: 3 ad., Sumuna, Dyaul Island, 2. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 923.

Description: Adult males and females: Forehead, forepart of crown, lore, feathers around eye, chin and throat black with a dull gloss, the feathers of forehead and forepart of crown scale-like and stiff and somewhat erect, a narrow transversal band across crown, ear-coverts, temporal region and sides of neck white, posterior part of crown, occiput, neck, mantle, scapulars and anterior part of back bluish black, slightly glossy, posterior part of back, rump and upper tail-coverts as well as the entire under parts below throat pure white, lesser, median and greater wing-coverts, except the outer two-three greater coverts, white, remaining parts of wing, including remiges, black, axillaries white, tail-feathers black, the three outer pairs broadly tipped with white, the apical white band being at least 20 mm broad on the two lateral pairs of tail-feathers, slightly more narrow and sometimes mixed with black on the third pair. Male and female are exactly similar in coloration, but the female is distinctly smaller than the male.

Juveniles: Forehead, forepart of crown, ear-coverts, sides of head, throat and forebreast orange rusty, lower breast, flanks and under tail-coverts lighter, tinged with pale buff, centre of abdomen almost white, upper parts dark grey, on back suffused with brownish olive, rump and upper tail-coverts white tinged with light buff, wings sepia-brown, lesser and median coverts light buff, inner greater coverts pale grey finely tinged with buff, tail-feathers blackish brown, the three outer pairs with about 20 mm broad white tips as in the adult birds.

Specimens of adult males of the new species and of its nearest relative, M. verticalis Sclater, are illustrated in fig. 2.



Fig. 2. Adult males of *Monarcha verticalis* (a-c) and *M. ateralba* (d-f), collected on New Ireland (a, b), New Hanover (c) and Dyaul (d, e, f); a and b belonging to the American Museum of Natural History, New York, c, d, e, and f collected by the "Noona Dan Expedition".

Measurements: A much bigger bird than *M. verticalis*, with longer wings, tail and bill, which appears from the following list of measurements.

Length of Wing

aleralba: $6 \ dallarge d$ $91-95 \ (93.0); 2 \ qq \ ad. 86, 90$ verticalis: $5 \ dallarge d$ $83-88 \ (86.2); 4 \ qq \ ad. 82-85 \ (83.0)$ Length of Tailateralba: $6 \ dallarge d$ $84-87 \ (85.0); 2 \ qq \ ad. 79, 85$ verticalis: $5 \ dallarge d$ $74-79 \ (76.6); 4 \ qq \ ad. 71-75 \ (72.7)$ Length of Bill (from Skull)ateralba: $6 \ dallarge d$ $17-19 \ (18.0); 2 \ qq \ ad. 17.8, 18.2$ verticalis: $5 \ dallarge d$ $5 \ dallarge d$ $15.5-16 \ (15.9); 4 \ qq \ ad. 15-16 \ (15.7)$

Nr. 1

The individual measurements are enumerated in table 3.

The tail is relatively slightly longer than in *M. verticalis*, constituting 91.4 percent of the wing-length, compared with 88.9 percent in verticalis. In addition, the graduation of the tail is stronger, the distance between the shortest (lateral) and the longest (central) tail-feathers being 13-15 mm, compared with 5-8 mm in verticalis.

Material: 6 33 ad., 2 $\varphi \varphi$ ad., 1 φ juv.

Range: Restricted to Dyaul Island.

Remarks: The new species is nearest to *M. verticalis* Sclater, inhabiting Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover, but differs strikingly from this species both in coloration and in proportions. The main differences in coloration between the adult birds of the two species concerns the tail, which is uniform black in *verticalis*, and with the apical parts of the outer three pairs white in ateralba (cf. fig. 2). The white colour of the upper-parts is more extensive in ateralba, in which the lower back, the rump and all the upper tail-coverts are white, while in *verticalis* the lower back is mixed with grey, due to concealed dark feather-bases, and the longest upper tail-coverts are constantly black. In *ateralba* the two sexes are absolutely identical in coloration, but in *verticalis* there is a slight difference, the males having the lower parts of the back white with concealed grev feather-bases, whereas the females have the lower back uniform grey, sometimes mixed with white, but

> TABLE 3 Measurements of Monarcha ateralba and M. verticalis

(The specimens mention w	ned collected by the "Noo hen not otherwise stated)	na Dan Expe	edition"
Wing	ර්් ad.	♀♀ ad.	♀♀ juv.
M. ateralba (Dyaul)	91, 92, 93, 93, 94, 95	86, 90	85
M. verticalis (New Hanover)	86, 87	83	
(New Ireland)	83 ^a , 88 ^a	82 ^a , 85 ^a	78, 78 ^a
— (New Britain)	87	82	
Fail			
M. ateralba (Dyaul)	84, 84, 84, 85, 86, 87	79, 85	82
M. verticalis (New Hanover)	75, 79	71	
— (New Ireland)	74a, 79a	73 ^a , 75 ^a	68, 73 ^a
— (New Britain)	76	72	
Bill (from skull)			
M. ateralba (Dyaul)	17, 17.5, 18, 18.2, 18.5, 19	17.8, 18.2	18
M. verticalis (New Hanover)	16, 16	16	
— (New Ireland)	15.5 ^a , 16 ^a	16 ^a , 16 ^a	15.5,a, l
— (New Britain)	16	15	

^a Belonging to the American Museum of Natural History, New York. ^b Bill broken.



Fig. 3. Juvenile females of *Monarcha verticalis* (a, b) and *M. ateralba* (c), collected on New Ireland (a, b) and Dyaul (c); *a* belonging to the American Museum of Natural History, New York, *b* and *c* collected by the "Noona Dan Expedition". Note big proportions, light wing-coverts and different tail pattern in *ateralba*.

always with more grey than in the males. This sexual difference was pointed out by REICHENOW (1899, p. 85), but wrongly doubted by HARTERT (1925, p. 129).

The differences between the two species in the juvenile dress are even more striking than in the adult birds. The tail is uniform blackish brown in *verticalis*, and the apical parts white for about 20 mm on the three outer tail-feathers in *ateralba*, thus showing the same character as the adult birds. In *verticalis* the crown and nape are dark grey, the mantle, back and wing-coverts olive-brown, while in *ateralba* grey is the predominating colour and the wing-coverts are contrastingly coloured, light buff or pale grey. In *verticalis* the rump and upper tail-coverts are greyish buff and the longest tail-coverts dark slate-grey, in *ateralba* these parts are white with a buffish tinge, the longest upper tail-coverts pure white, and the light colour of the rump extending anteriorly onto the lower back. In *verticalis* the forehead, lore, eye-region, ear-coverts, sides of head and the chin are grey with or without a slight brownish tinge, in *ateralba* these parts are orange rusty, of the same colour as the throat, but strongly contrasting



Fig. 4. Adult males of the four species belonging to the superspecies Monarcha verticalis inhabiting the Bismarck Archipelago; a M. menckei from Mussau in the St. Matthias Islands, b M. infelix from Manus in the Admiralty Islands, c M. verticalis from New Hanover, d M. ateralba from Dyaul; all collected by the "Noona Dan Expedition".

with the dark grey colour of the crown and nape. In *verticalis* the throat and breast are coloured buff or tawny, in *ateralba* bright orange rusty. Cf. also fig. 3 for differences between the two species in the juvenile dress.

The black-and-white Monarch Flycatchers form a complicated group, and the mutual relationship of the different species is still not settled. The division into sections or superspecies has been discussed mainly by MEISE (1929, p. 459), MAYR (1944, p. 162, and 1955, p. 25) and VAN BEMMEL (1948, p. 344). The species inhabiting the Bismarck Archipelago and the Solomon Islands can be united into a superspecies (*verticalis*). MAYR (*loc. cit.*) includes in this superspecies a number of other forms (*manadensis, leucura*, etc.), but this arrangement has not met with general approval.

It is not easy to decide whether *ateralba* should be regarded as a full species or a strongly differentiated subspecies of *verticalis*. The form inhabiting the Admiralty Islands (infelix Sclater) has always been regarded as a full species. It differs, admittedly, much more from *verticalis* than does *ateralba* (cf. fig. 4), but is, on the other hand, similar to *verticalis* in proportions (wing-length of 33 ad. 82–87, \Im ad. 77–83, tail-length in 33 ad. 69–78, in 99 ad. 67–75, according to MAYR 1955, p. 29). As far as the colour pattern of the tail is concerned *ateralba* is intermediate between *verticalis* and *infelix* and approaches very much *menckei* Heinroth from Mussau, which is a very distinct species (cf. fig. 4). Even the pronounced differences between verticalis and *ateralba* in the colour pattern of the juvenile plumage speaks in favour of the view-point that these two taxa are best treated as full species. VAN BEMMEL (loc. cit.) has pointed out that the juvenile plumages in these flycatchers are often suggestive when discussing relationship. Summing up, the distinct differences in colour pattern of both adult and juvenile birds combined with the considerable differences in proportions between verticalis and ateralba make it in my opinion inadvisable to regard these two taxa as conspecific.

I have compared specimens of *verticalis* from New Hanover, New Ireland and New Britain and find them indistinguishable. This has been noticed also by MAYR (1955, p. 28), who adds: "It is rather odd that no subspecies have formed in this species, which belongs to a group elsewhere strongly inclined to geographic variation."

Monarcha hebetior cervinicolor, new subspecies

Type: φ ad., Sumuna, Dyaul Island, 6. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 1013.

Diagnosis: Adult females: Nearest to M. h. eichhorni Hartert, but differ strikingly in having crown pale ash-grey, lores and frontal feathering almost whitish and somewhat contrasting, upper parts much lighter rufous, under parts white, under tailcoverts and lower abdomen tinged with light cinnamon and throat and breast suffused with light grey, but some specimens with under parts almost uniform white, primaries and secondaries blackish brown with whole outer web rufous, tertiaries uniform Nr. 1

rufous only with blackish shaft-streak, tail-feathers rufous, the two central pairs slightly suffused with darker brown.

Juvenile females: Differ from *eichhorni* in the same way as the adult females. Males: Indistinguishable from *eichhorni* in coloration.

In females of *eichhorni* the crown is darker slate-grey, the lores and front of the same colour, not paler, the upper parts chestnut, very much darker and duller than in *cervinicolor*, the under parts slate-grey, lighter on abdomen and suffused with chestnut on flanks, primaries and secondaries blackish brown, with only a narrow chestnut border on outer web, tertiaries blackish brown narrowly edged with chestnut on both webs, tail-feathers blackish brown narrowly edged with fuscous chestnut.

Adult females of the new form and of *eichhorni* are illustrated on plate II, fig. 1.

Measurements: The proportions of *cervinicolor* are slightly larger than those of *eichhorni*. This holds good particularly of the tail, but is apparent also in the measurements of wing and bill. Nominate *hebetior* is in all respects a much smaller bird than the two other subspecies, the tail being particularly short.

Length of Wing

cervinicolor: 5 33 ad. 86-88 (87.4); 6 99 ad. 77-84 (80.2) eichhorni: 4 33 ad. 83-85 (84.0); 7 99 ad. 74-81 (78.7) hebetior: 3 33 ad. 75-77 (76.0); 1 ♀ ad. 69 Length of Tail cervinicolor: 4 33 ad. 75-79 (77.3); 6 ♀♀ ad. 70-77 (72.7) eichhorni: 4 33 ad. 68-75 (71.5); 7 99 ad. 61-69 (66.2) 3 33 ad. 59-62 (60.7) hebetior: Length of Bill (from Skull) cervinicolor: 5 ♂♂ ad. 21-22 (21.6); 6 ♀♀ ad. 20-22 (21.0) 4 ♂♂ ad. 19-22 (20.5); 7 ♀♀ ad. 19-22 (20.3) eichhorni: hebetior: 3 33 ad. all 18; 1 9 ad. 18

The individual measurements are enumerated in table 4. *Material*: 5 $\Im \Im$ ad., 6 $\Im \Im$ ad., 2 $\Im \Im$ juv. *Range*: Restricted to Dyaul Island.

Remarks: The most remarkable character of *cervinicolor* is the rufous colour of tail and wing, which in *eichhorni* and nominate *hebetior* are predominating blackish brown. This is noteworthy, because the closely allied species *Monarcha alecto* also has rufous wings and tail. Even in its whitish under parts with cinnamon under tail-coverts and in its bright rufous upper parts *cervinicolor* approaches or matches *alecto*. It is highly interesting that the isolated form on Mussau (nominate *hebetior*) exhibits a similar resemblance to *alecto* in the white colour of the under parts and in the brightness of the rufous upper parts, while the colour pattern of wings and tail is similar to that in *eichhorni*. On the other hand, females of nominate *hebetior* possess another *alecto* character, namely the black (not grey) crown. Evidently, nominate

hebetior and *cervinicolor* show an almost equal mixture of *alecto* and *eichhorni* characters, although perhaps the *alecto* characters are somewhat more strongly manifested in nominate *hebetior* than in *cervinicolor*.

The relation between the two closely allied species *alecto* and *hebetior* is interesting from an evolutionary point of view. *M. alecto* is a widespread species, inhabiting the Moluccas, the Papuan region and northern Australia, in the Bismarck Archipelago distributed on Umboi, New Britain, New Ireland, New Hanover, Dyaul, Tabar, Tanga, Feni, Vitu Islands and the Admiralty Islands, showing in its huge range only a slight

		TABLE	4			
	Measurem	ents of Mo	onarcha	hebetior		
(The specimens	mentioned	collected 1	by the	"Noona	Dan	Expedition"
	when	not otherw	wise sta	ited)		

Wing	ට ්ට් ad.	$\varphi \varphi$ ad.	♀♀ juv
cervinicolor (Dyaul)	86, 87, 88, 88, 88	77, 80, 80, 80, 80, 84	77, 77
eichhorni (New Hanover)	83a	76, 81, 81, 81, 81	
— (New Ireland)	85 ^a	74 ^a	74a
— (New Britain)	84, 84	77	
hebetior (Mussau)	75, 76, 77	69	67
Tail			
cervinicolor (Dyaul)	75, 77, 78, 79, — ^b	70, 72, 72, 72, 73, 77	66, 67
eichhorni (New Hanover)	69a	62, 68, 68, 69, 69	
— (New Ireland)	68a	61 ^a	66a
— (New Britain)	74, 75	66	
hebetior (Mussau)	59, 61, 62	C	54
Bill (from skull)			
cervinicolor (Dyaul)	21, 21.5, 21.5, 22, 22	20, 20.5, 21, 21, 21.5, 22	21, 21
eichhorni (New Hanover)	22a	20, 20, 20.8, 21, 22	
— (New Ireland)	21 ^a	19a	20 ^a
— (New Britain)	19, 20	19	
hebetior (Mussau)	18, 18, 18	18	18

^a Belonging to the American Museum of Natural History, New York.

^b Tail in growth, not measured.

e Tail damaged, not measured.

geographical variation. *M. hebetior* is restricted to the Bismarck Archipelago, living side by side with *alecto* in New Britain, New Ireland, New Hanover (*eichhorni*) and Dyaul (*cervinicolor*), and inhabiting also Mussau (*hebetior*), where *alecto* does not occur. MAYR (1955, p. 30), who of course did not know the existence of *cervinicolor*, explained this distribution by assuming that *alecto* spread to Mussau, where it was modified and became the present *hebetior*, and that this latter form subsequently, having reached species level, reinvaded the Bismarck Islands, where it became still

more modified, developing into *eichhorni*. The distribution of the two species and the intermediate character of nominate *hebetior* made this theory very plausible. The discovery of *cervinicolor*, however, complicates the situation. It is difficult to understand why *alecto*, which according to MAYR represents an old element, has remained completely unchanged on Dyaul, while the newcomer *hebetior* was able to develop the strikingly different *cervinicolor* in a much shorter period of time. The resemblance between *cervinicolor* and *alecto* is due either to a secondary parallelism or—as in nominate *hebetior*—to an actual retainment of *alecto* characters. Whichever alternative may be the correct one I find it most probable to assume that *alecto* twice invaded the Bismarck Archipelago from New Guinea. The first colonization gave rise to the development of the species *hebetior*, which eventually occupied three separate areas (Mussau, Dyaul, and the main tier of islands), the populations of which diverged and formed the three present subspecies. The second colonization by *alecto* was much more recent and has not resulted in any morphological differentiation.

The coloration of the males in the three forms of *hebetior* is, so far I can see, practically identical, and this species represents a very clear case of heterogynism. The colour of the crown in females of nominate *hebetior* is similar to that in *alecto*, as said above, but is not identical with it. In *alecto* the crown is bright glossy bluish black, while in *hebetior* it is black with only a dull gloss, and the feathers are short and of a soft velvety texture, not scaly and not forming a rounded cap as in *alecto*. This difference is important for a characterization of the species *hebetior* as compared with *alecto*. It has been shown above that the coloration of upper parts, under parts, wings and tail in all these forms is very varying and not suitable to characterize the species. The best distinction marks between the species *hebetior* and *alecto* are the colour and feather texture of the males, which are identical in nominate *hebetior*, *eichhorni* and *cervinicolor* and clearly different from *alecto*, and the colour and feather texture of the females and immature birds, which part is dull black (nominate *hebetior*) or grey (*eichhorni*, *cervinicolor*) in *hebetior*, glossy bluish black in *alecto*.

M. h. eichhorni exhibits some slight geographical variation. MAYR (1955, p. 30) states that New Ireland females are slightly brighter rufous and paler and also slightly smaller than New Britain ones. The single female from New Britain collected by the "Noona Dan Expedition" is not so rufous on the upper parts as New Ireland and New Hanover birds, tending more towards olive-brown, and, in addition, the bill is shorter in both sexes (cf. table 4). The alleged difference in size between the New Britain and New Ireland birds is not apparent in my small series. At any rate, more material is needed to decide whether New Britain birds are separable. During my stay with the "Noona Dan Expedition" I collected a good series of females (five specimens) on New Hanover from which island females were previously unknown. They do not differ from New Ireland females in any respect.

The females of *M. alecto* living sympatrically with *M. hebetior* on many islands in the Bismarck Archipelago and belonging to the subspecies *chalybeocephala* Garnot Biol. Skr. Dan. Vid. Selsk. 14, no. 1. do not show any appreciable variation on New Britain, New Ireland, New Hanover, Dyaul and Credner Islands, in which localities the "Noona Dan Expedition" collected a number of specimens (Credner Islands being a new locality for this species). MAYR (1955, p. 30) states that New Ireland birds are paler than those from New Hanover and New Britain, but I cannot see any difference, but there is some individual variation, however. The birds from Feni Islands, which I have seen in life, but failed to collect, are stated to be slightly darker (MAYR, loc. cit.). The population of the Admiralty Islands, of which I have seen some specimens in the American Museum of Natural History, are much darker rufous on the upper parts than those from all the other islands in the Bismarck Archipelago and appears to form a marked subspecies. This has been noticed already by HARTERT (1930, p. 72) and by MAYR (1941a, p. 3), who both state that the variation in this species is patchy and does not follow any geographical pattern, the New Guinea specimens, particularly those from Biak and Numfor Islands, being as dark as the Admiralty Islands birds, and that it is not possible, therefore, to separate any subspecies. I have not seen any New Guinea specimens and at present cannot add to the discussion, but the fact remains that the Admiralty Islands birds distinctly differ from those of the other islands in the Bismarck Archipelago.

Lalage leucomela sumunae, new subspecies

Type: \bigcirc ad., Sumuna, Dyaul Island, 5. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 989.

Diagnosis: Differs in both sexes from the forms inhabiting the main chain of islands in the Bismarck Archipelago (falsa Hartert, karu (Lesson and Garnot) and albidior Hartert) in having the under parts pure white, completely without rufous, in some specimens (mostly males), however, with a faint yellowish wash on the under tail-coverts; in addition, the females have the upper parts slightly darker grey. The barring on the under parts in both sexes is similar to that in albidior from New Hanover or is slightly paler and the bars slightly narrower. Finally, the bill is slightly longer than in all the other forms of the Bismarck Islands. The new form is more similar in coloration to the forms inhabiting the distant Lihir Island (ottomeyeri Stresemann) and Tabar Island (tabarensis Mayr), which both have white under parts just as sumunae, but, further, in both sexes have much more white on the wing-coverts and secondaries, while the under parts in the males of these two closely allied forms are completely unbarred, being practically pure white (cf. fig. 5), and even in the females the barring on the under parts is much more faint than in sumunae and the other forms of the Bismarck Archipelago. There are also other differences.

Altogether, the differences between most of the forms of the Bismarck Archipelago are more pronounced in the females than in the males, and I have, therefore, chosen a female as the type.



Fig. 5. Adult males of various forms of *Lalage leucomela* from the Bismarck Archipelago; *a-b karu* from New Ireland, *c-d albidior* from New Hanover, *e-f sumunae* from Dyaul, *g-h ottomeyeri* from Lihir; *a, b, c, d, e* and *f* collected by the "Noona Dan Expedition", *g* and *h* belonging to the American Museum of Natural History, New York.

Adult females of the new form and of *karu* are illustrated on plate II, fig. 2, while adult males of *karu*, *albidior*, *sumunae* and *ottomeyeri* are shown in fig. 5.

Measurements: All the forms of the Bismarck Archipelago are evidently of the same size (cf. also the measurements given by MAYR 1955, p. 9), but *sumunae* differs from all the rest by having a slightly longer bill.

Length of Wing

sumunae:	6	33 ad.	98-103	(99.8);	6		ad.	93-	100	(96.5)
albidior:	4	33 ad.	97 - 102	(100.0);	2	99	ad.	96,	102	
karu:	4	33 ad.	98-101	(99.5);	9	99	ad.	93-	101	(96.1)
falsa:					1	Q 8	ad. 9	97		
ottomeyeri:	2	33 ad.	100, 10	2;	2	99	ad.	98,	101	
tabarensis:	1	3 ad.	101;		2	99	ad.	99,	99	

Length of Bill (from Skull)

sumunae:	6	33 ad.	16.5-18.8 (17.4);	6	♀♀ ad.	17-18 (17.2)
albidior:	4	33 ad.	16-17 (16.4);	2	$\begin{array}{c} \mathbb{Q}\mathbb{Q} \\ \mathbf{q} \end{array}$ ad.	15.2, 16
karu:	4	33 ad.	15-17 (16.0);	9	♀♀ ad.	15.2-16.8 (16.0)
falsa:				1	♀ ad. 1	16
ottomeyeri:	2	33 ad.	16, 17;	2	♀♀ ad.	16, 16
tabarensis:	1	3 ad. 1	5.5;	2	$\begin{array}{c} & \bigcirc & \bigcirc & \frown & & \\ & & \bigcirc & & & & \\ & & & & & & & \\ & & & &$	15, 16

3*

The individual measurements are enumerated in table 5.

Material: 6 33 ad., 6 99 ad.

Range: Restricted to Dyaul Island.

Remarks: The "Noona Dan Expedition" collected material of the forms *falsa*, *karu, albidior* and *sumunae*, but failed to find the very rare *conjuncta* Rothschild and Hartert on Mussau, which is known only from the type (\Im ad.). The Tabar and Lihir groups were not visited, but material of the two indigenous forms was kindly supplied by the American Museum of Natural History, New York.

It is noteworthy that the forms inhabiting the islands both south of New Ireland (Dyaul) and north of this island (Tabar, Lihir) have, independently of each other, acquired the same character, the complete loss of rufous on the under parts. All other forms of this widespread species, including those of Australia and the Papuan region, have buffish or partly rufous under parts (MAYR and RIPLEY 1941, p. 13, map). The isolated form of Mussau (conjuncta) has retained the deep rufous colour of abdomen and under tail-coverts, but it differs strikingly from the other forms by the complete absence of barring on the under parts and by lacking the white superciliary streak. Evidently, conjuncta is a very distinct form. Compared with the peripheral forms (sumunae, ottomeyeri, tabarensis, conjuncta) the central populations (falsa, karu, albidior) are much less differentiated. A cline for decreasing amount of rufous on the under parts runs from New Britain (and Umboi) through New Ireland to New Hanover, and the forms with white under parts on Dyaul, Tabar and Lihir may possibly

TABLE 5 Measurements of *Lalage leucomela* (The specimens mentioned collected by the "Noona Dan Expedition" when not otherwise stated)

Wing	33 ad.	우우 ad.
sumunae (Dyaul)	98, 98, 99, 100, 101, 103	93a, 95a, 95a, 97, 99, 100
albidior (New Hanover)	97, 100, 101, 102	96, 102
karu (New Ireland)	98, 99, 100, 101	93 ^a , 94, 95, 96 ^a , 96, 96, 97, 97, 101
falsa (New Britain)		97
ottomeyeri (Lihir)	100 ^b , 102 ^b	98 ^b , 101 ^b
tabarensis (Tabar)	101 ^b	99b, 99b
Bill (from skull)		
sumunae (Dyaul)	16.5, 17, 17, 17, 18, 18.8	17, 17, 17, 17, 17, 18
albidior (New Hanover)	16, 16, 16.8, 17	15.2, 16
karu (New Ireland)	15, 16, 16, 17	15.2, 15.5, 16, 16, 16, 16, 16, 16, 16.2, 16.8
falsa (New Britain)		16
ottomeyeri (Lihir)	16 ^b , 17 ^b	16 ^b , 16 ^b
tabarensis (Tabar)	15.5 ^b	15 ^b , 16 ^b

a Wings immature.

^b Belonging to the American Museum of Natural History, New York.

be regarded as end-links of this cline. Some specimens from neighbouring islands in the main chain are indistinguishable. The darkest females from New Ireland have as much rufous on the under parts as the New Britain specimens, but these latter can be distinguished by their slightly more fuscous, not so greyish upper parts. Similarly, the lightest New Ireland females are quite indistinguishable from New Hanover females. As far as the males are concerned, the differences are still less pronounced. The extension of the rufous colour on the under parts is generally smaller in the males than in the females, and most males of *albidior* and *karu* are very similar, some even indistinguishable on this character, while the females can usually be separated. In the males of *albidior* the barring on the under parts is reduced and more indistinct than in *karu*, and the ground colour of the throat and forebreast is pure white, in *karu* washed with grey (fig. 5), but some males of *karu* are indistinguishable from albidior even in this character. Consequently, I consider *albidior* a rather weak, although acceptable form.

Previous notes on the geographical variation of this species in the Bismarck Archipelago have been given mainly by HARTERT (1925, p. 131), STRESEMANN (1933, p. 114), MAYR and RIPLEY (1941, p. 13) and MAYR (1955, p. 8).

Zoogeographical Remarks

The fauna of Dyaul is noteworthy in many respects. The island has a relatively rich fauna, compared with that of other islands of similar size and situation. Dyaul is not an outlying and remote island, but nevertheless it is characterized by possessing a number of striking endemic forms, which phenomenon is ordinarily characteristic of peripherally isolated faunas. The development of these endemic forms has taken place in spite of the close proximity of Dyaul to New Ireland. These facts call for some zoogeographical comments.

The morphological differentiation of the endemic forms of Dyaul must have required a certain amount of time, during which the populations were isolated from those of New Ireland. The length of this period of isolation is not easy to determine, but a rough estimate can be attempted on the basis of a comparison with other tropical island faunas which have developed under environmental conditions similar to those of the Bismarck Archipelago, *i. e.* exposed to only very slight and negligible differences in the selection pressure due to environmental factors.

The Philippine Islands offer a good example. The islands Negros, Panay and Guimaras form part of the so-called Central or Viscayan Province, a zoogeographical area characterized by many striking endemic species and subspecies. The lowland avifaunas of the said three islands are very similar, and the geographical variation within the populations of the area is very slight and restricted to a few species. The narrow straits separating the three islands are so shallow that the islands must have been broadly connected during the glacial periods. Consequently, the mutual separation and subsequent isolation of the bird populations inhabiting Negros, Panay and Guimaras, respectively, must be a recent phenomenon.

Another example is offered by the West Sumatran Islands. They are even more suitable for a comparison with Dyaul, because they are of about the same size, while the Philippine islands mentioned above are considerably bigger. Among the West Sumatran Islands Nias has a close faunal relationship with Sumatra. It is richer in species than any of the other West Sumatran Islands, but it is poor in endemisms, and the few local subspecies are usually only slightly differentiated from the Sumatran forms. Nias bears all the earmarks of being a very young island. Something similar can be said about the nearby small Batu and Banjak Islands, of which the faunal relationship with Sumatra is even closer. All these islands are situated inside the 100-fathom line, which indicates that they were connected with Sumatra until the late Tertiary and again temporarily in the glacial periods. The other small islands situated on the former Sunda Shelf, even remote ones like the Anambas Islands and the Natuna Islands, resemble Nias in possessing a fauna which is very similar to that of the mainland.

The remaining West Sumatran Islands are all situated outside the 100-fathom line. The island Enggano is a deep-sea island, which has not been in connection with Sumatra for a very long geological period, if ever. The fauna of this island is more divergent than that of any of the other West Sumatran Islands and at the same time the most impoverished. Something similar is the case of the northernmost island, Simalur, also an old oceanic island, although its faunal elements are by no means so differentiated and the fauna is much richer than that of Enggano. The Mentawi Islands possess a still richer fauna, consisting of forms that are generally closer to the Sumatran ones than those inhabiting Enggano and Simalur; cf. also SALOMONSEN 1961, p. 30.

From the description of the insular faunas given above it appears that populations which have been isolated recently, *i. e.* after the last glacial period (about 15,000 years ago) have diverged very little, if at all, while the isolates of greater age have been subject to much greater differentiation. A comparison between the populations of Dyaul and those of the West Sumatran Islands gives the result that the differentiation of the former is of the same order of magnitude as that of the Enggano populations. This indicates a comparatively great age. Dyaul, on the other hand, resembles Nias in having a relatively richer fauna.

It should here be added that, from an evolutionary point of view, it is necessary to distinguish between two fundamentally different categories of insular faunas. The first one comprises those faunas which have been isolated through a segregation of a former continuous range, such as the faunas inhabiting the above-mentioned islands on the former Sunda Shelf. The second category comprises those faunas which have been founded by colonists across the sea. The "founders" of such truly oceanic populations comprise, as a rule, very few individuals or a small flock. For genetical reasons, therefore, the morphological differentiation of the populations takes place at a much greater rate than that in populations on islands separated from a land-mass. These differences must be carefully considered in all zoogeographical studies of island faunas.

The following notes form an attempt to elucidate some of the problems connected with the history and origin of the fauna of Dyaul, based on a comparison with that of the other islands in the Bismarck Archipelago.

Comparison with the Fauna of the Main Chain of Islands

The distribution and differentiation in the Bismarck Archipelago of the species which have developed striking endemic forms on Dyaul have been dealt with above and will be briefly summarized.

Dicaeum eximium: New Britain (layardorum), New Ireland and New Hanover (eximium), Dyaul (phaeopygium). The forms eximium and layardorum are rather similar and have both a bright carmine red rump, while phaeopygium differs strikingly from them by having the rump brownish like the back. The significance of this difference is borne out by the fact that loss of the red rump patch in other groups within the genus Dicaeum serves to distinguish full species (not subspecies).

Monarcha chrysomela: New Ireland and New Hanover (chrysomela), Tabar Island (tabarensis), Lihir Island (whitneyorum), Dyaul (pulcherrima). The three first forms are very similar and, furthermore, do not appreciably differ from the New Guinea forms. The Dyaul form pulcherrima differs strikingly from all other forms within this species by its uniform yellow upper parts in the adult males.

Monarcha verticalis superspecies: In the Bismarck Archipelago four distinct species belong to this superspecies, of which *infelix* from the Admiralty Islands and *menckei* from Mussau in the St. Matthias Islands are the most aberrant. The species *M. verticalis* is found on Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover, without showing any geographical variation. The Dyaul species *ateralba* is strikingly different from *verticalis*.

Monarcha hebetior: New Britain, Duke of York Islands, New Ireland and New Hanover (eichhorni), Mussau (hebetior), Dyaul (cervinicolor). Both the Dyaul and the Mussau form are strikingly different from the form inhabiting the main chain of islands and possess characters which in various ways approach those of the allied species *M. alecto*.

Lalage leucomela: Umboi, New Britain and Duke of York Islands (falsa), New Ireland (karu), New Hanover (albidior), Dyaul (sumunae), Tabar (tabarensis), Lihir (ottomeyeri), Mussau (conjuncta). The first three forms, inhabiting the main chain of islands, are rather similar, having in common rufous colour on the under parts; the Dyaul, Tabar and Lihir forms have white under parts, while conjuncta is very aberrant.

The distribution of these species in the Bismarck Archipelago has been outlined on the map fig. 6. The range given can be divided into three units: (1) Dyaul Island (black on the map) with striking endemic forms in all five species.

(2) The range on the main chain of islands and on the island groups north-east of New Ireland, comprising *Monarcha verticalis*, *Monarcha hebetior eichhorni*, the forms of *Monarcha chrysomela* with black back, the forms of *Dicaeum eximium* with carmine red rump, and the forms of *Lalage leucomela* with rufous colour on the under parts (but including also the distinct forms with white under parts on Tabar and Lihir).

(3) The remaining distribution of the said species and superspecies in the Bismarck Archipelago, including distinct representatives of *Monarcha hebetior*, *Lalage leucomela* and the superspecies *Monarcha verticalis* (*M. menckei*) on Mussau and another distinct species of the *Monarcha verticalis* complex (*M. infelix*) in the Admiralty Islands.

It appears from the summary above that in all five species the populations of the main chain of islands (Umboi, New Britain, Duke of York Islands, New Ireland, New Hanover) are either identical or only comparatively slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is probably to be explained primarily as the result of a greater evolutionary rate in the Dyaul populations, due to their genetic history (change of genetic environment; cf. MAYR 1954, p. 175) as a consequence of their foundation through oversea crossing by a minority of individuals. This is probably not the whole truth, however. Other factors must have been active in order to develop the extraordinary characters of the Dyaul endemics. The time-factor, particularly, has been of importance. I venture to forward the theory that the main chain of islands were mutually connected, forming one or two big islands, in a period when Dyaul had already received its fauna. This land-connection would account for the similarity of the populations inhabiting the main islands. The status of the Duke of York Islands is noteworthy in this respect. This group is even smaller than Dyaul (only 60 sq. km) and situated at a similar distance from the "mainland" (both from New Ireland and New Britain). Consequently, the conditions for morphological differentiation of the local populations should be expected to be just as favourable as on Dyaul, or even more so. Nevertheless, not a single endemic form has developed on the Duke of York Islands. The possibility that an unimpeded gene flow could take place across the straits separating the Duke of York Islands from the neighbouring islands, but not across the narrow channel between Dyaul and New Ireland, is not acceptable. It must be assumed, therefore, that the Duke of York group is much younger than Dyaul, either because it emerged in a more recent period, or because it was connected with New Britain for a long time. The probability speaks for the latter alternative.

Even the island of Umboi, on which only a few weak subspecies have developed, must have been in land connection with New Britain. The islands of New Hanover and New Ireland have definitely been united in the past, at least during the glacial periods. The depths of the strait separating them is less than 30–50 meters and the



Fig. 6. The range in the Bismarck Archipelago of the five species which on Dyaul Island (black on the map) have developed strongly differentiated endemic forms; 1 Monarcha chrysomela, 2 Dicaeum eximium, 3 Monarcha hebetior, 4 Monarcha verticalis (superspecies), 5 Lalage leucomela.

span between them is bridged by many islands. Consequently, the bird fauna is rather similar on the two islands, most species occurring in the same or only slightly different subspecies on New Ireland and New Hanover.

The two former islands (Umboi-New Britain-Duke of York and New Ireland-New Hanover) were undoubtedly in land connection with each other originally, making the whole main chain of islands in the Bismarck Archipelago one big area. The connection between the two islands in question must, however, have been interrupted rather early in order to explain the differences in the composition of the fauna and the development of strikingly different endemic species on the two islands (e. g. in the genera *Micropsitta*, *Ninox*, *Dicrurus*, *Philemon*, *Myzomela*, *Lonchura*), but the faunal colonization of Dyaul must probably date almost as far back in the past.

Admittedly, there is no geological evidence for the assumption that these islands have ever been connected, but the meagre geological information does not contradict it either. I revert to this point below (p. 30).

As mentioned above, the strong differentiation of the Dyaul forms must have required a long time of isolation. It is noteworthy that the Gazelle Channel, not broader than 14 km, in spite of its extreme narrowness has been broad enough to form an effective barrier, preventing gene flow between the populations of New Ireland and Dyaul. Such a situation is extraordinary, but not unique. Even more narrow water gaps are known to separate distinct forms in the Lesser Sunda Islands, in the Western Papuan Islands and in other archipelagos. The gaps between certain islands in the Solomon Islands, which are inhabited by markedly different species belonging to the superspecies *Zosterops rendovae*, are even as narrow as 5–6 km (MAYR 1940, p. 266, and 1942, p. 227), although it appears that the narrowness of these barriers has been exaggerated (GALBRAITH and GALBRAITH 1962, p. 5). The faunal differences between New Britain, New Ireland and New Hanover, which have developed in spite of the narrowness of the water gaps separating these islands, have been emphasized by HEINROTH (1903, p. 99) and HARTERT (1924, p. 194).

Dyaul has undoubtedly received its entire avifauna from New Ireland, apart from a few species which may have immigrated from New Hanover. The morphological characters of the endemic forms on Dyaul are probably in most cases derivative, while those of the forms inhabiting the main island chain represent a more original stage.

Comparison with the Fauna of the Hibernian Islands

It appears from fig. 6 that none of the five species in question have reached the groups of Tanga and Feni and two only have reached Tabar and Lihir, namely *Monarcha chrysomela* and *Lalage leucomela*. Both these species have developed endemic forms on Tabar and Lihir, but in the case of *Monarcha chrysomela* these forms are relatively slightly differentiated, while the *Lalage leucomela* forms have diverged as much as—or even more than—the Dyaul form.

It is a remarkable phenomenon that the five species which have developed Biol. Skr. Dan. Vid. Selsk. 14, no. 1. 4

			0		
	Dyaul	Tabar	Lihir	Tanga	Feni
Passerine Species					
Pitta erythrogaster	*	*			
Hirundo tahitica			*	*	
Lalage leucomela	*	*	*		
Coracina tenuirostris	*		*	*	*
Cisticola exilis		*	*		
Rhipidura leucophrys	*	*	*		
— rufiventris	*	*	*	*	
Monarcha cinerascens	*	*	*	*	*
— ateralba	*				
— chrysomela	*	*	*		
— hebetior	*				
— alecto	*	*		*	*
Pachucephala pectorialis	*	*	*	*	*
Aplonis metallicus	*	*	*	*	*
— cantoroides	*	*	*	*	*
Corvus orru	*				
Dicaeum eximium	*				
Cinnuris sericea	*	*	*		*
— iugularis	*	*	*	*	*
Myzomela cruentata	*	*			
Total number of breeding passerine species	18	14	13	9	8
Total area (in sq. km)	115	251 a	170	99p	115e
Shortest distance from New Ireland (in km)	14.4	23.0	46.8	42.5	48.2

TABLE 6 Breeding passerine species, total area and shortest distance from New Ireland of Dyaul and the Hibernian island groups

^a Simberi 50, Tatau 96, Tabar 105.

^b Boang 22, Malendok 65, Lif 9, Tefa 3.

^c Ambitie 82, Babase 33.

strongly differentiated forms on Dyaul are so poorly represented on the Hibernian Islands¹. Altogether, these islands are much poorer in species than Dyaul. The general distribution of the bird life on these islands is unknown, because the results of the "Whitney South Sea Expedition" (the only expedition which have collected on all four island groups) have not been published, but it is possible to compare the number of passerine species breeding in the different island groups on the basis of the distributional notes published by MAYR (1955, p. 1–46). These species are enumerated in

¹ The islands northeast of New Ireland have no collective name, but in the German period they were often called the "Hibernische Inseln". This designation included not only the four island groups of Tabar, Lihir, Tanga and Feni, but even the remote St. Matthias group and the low atoll Nissan. I have in the present paper retained the name, for lack of any better, but have restricted it to the four first-mentioned island groups, which form a natural geographical unit, being of a similar appearance and structure and having, so far known, a similar geological history.

a list in table 6, which is based on MAYR (*loc. cit.*), HARTERT (1926, p. 33), MEYER (1934, p. 294) and my own investigations.

It appears from table 6 that I found 18 species of passerine birds during my stay on Dyaul, while the corresponding figures for the Hibernian Islands are: Tabar 14, Lihir 13, Tanga 9 and Feni 8. A total of 35 species of breeding passerines is known from New Ireland. Of these species, however, nine are exclusively or predominantly found in the mountains, the number of true lowland species being only 26. This shows that the number of passerine species inhabiting Dyaul rather strongly approaches that found in the lowland of New Ireland, and the same fact holds good of the nonpasseres. The number of species inhabiting Dyaul is probably still slightly greater than mentioned above, because a few species (Cisticola exilis?, Hirundo tahitica?, Lonchura sp.?) may have escaped our notice during the rather short visit of the "Noona Dan Expedition" to the island. As far as the Hibernian Islands are concerned, it should be added that MEYER (1934, p. 299) once professed to hear the call note of Dicaeum eximium on Lihir, but this must be due to some mistake as this species has never been encountered on Lihir. Even more uncertain is MEYER's statement of the occurrence of a Munia sp. (= Lonchura) on Lihir, based solely on a native name, which MEYER, however, admits may also be the name of a quail. There is no evidence for the occurrence of a Lonchura on Lihir.

Within most species the populations of the different Hibernian Islands are very similar. When subspecifically different from the New Ireland population they are either identical on most of the Hibernian Islands or at least very similar, *i. e.* they resemble each other more closely than they resemble the New Ireland population. This may indicate that occasional inter-island crossings take place in the Hibernian Islands resulting in subsequent gene-flow, but the effects of such incidents must be negligible. All evidence, gathered from similar tropical islands, tends to show that invasions of this kind occur as a rule much too rarely to be of any consequence to the genetical constitution of the population. On the other hand, the similarity of the endemic island forms within each species makes it an obvious conclusion that the different islands have been colonized by stray immigrants from the other islands rather than by independent invasions from New Ireland. It is fair to conclude that in each species as a rule only one successful oversea crossing from New Ireland was required. Once established on one island the species managed to colonize one or more of the other Hibernian Islands. This development is not surprising, however, as it forms the normal procedure in island colonization. It is a well-known zoogeographical fact that the potentialities for colonizing small islands are greater in populations of other small islands than in those inhabiting larger land-masses, because the former are already adopted to the insular environment.

It is not easy to decide which one of the four Hibernian island groups originally received the immigrants from New Ireland; the situation differs from one species to another. There are two cases in which a species is restricted to only one island (*Myzomela cruentata*, *Pitta erythrogaster*), and this is in both cases Tabar. In the cases

in which a species is found on only two islands these are usually Tabar and Lihir. This tends to show that Tabar, and perhaps in some cases Lihir, received the colonists from New Ireland. The problem can be further illustrated by a study of the morphological differentiation of the island populations. In Lalage leucomela, Pachycephala pectoralis and Monarcha chrysomela the Lihir form appears to be less modified than that of Tabar, and this indicates that Lihir was first colonized. In the case of *Cinnuris sericea* the Tabar and Lihir populations belong to the same subspecies as that of New Ireland, but in the coloration of the females approach the distinct form (eichhorni) of Feni (MAYR 1955, p. 40). Obviously, this species crossed from New Ireland to Tabar or Lihir and then from one of these islands, subsequently, invaded Feni, but failed to colonize Tanga. In Rhipidura rufiventris the situation is almost the contrary; the Tanga population (tangensis) is less modified than that of Lihir and Tabar (gigantea) and probably constitutes the first colonization, but in this case Feni was not reached. In Coracina tenuirostris the population of Feni belongs to the New Ireland subspecies *remota*, while those of Lihir and Tanga are identical and form the endemic subspecies ultima. Obviously, this species colonized Feni from New Ireland and then, subsequently, spread westwards from Feni to Tanga and Lihir, but has not reached Tabar.

Taking all facts together it appears that the waves of invasions emanating from New Ireland in most cases reached Tabar or Lihir and more rarely Tanga or Feni. Altogether, the passerine fauna of the latter two islands is more impoverished than that of Tabar and Lihir, numbering only 8–9 species, compared with 13–14 in Tabar-Lihir. It is obvious that the general colonization of the islands took place *via* Tabar-Lihir, but that a number of species failed to extend their breeding range from these two islands to Tanga and Feni. It should be added, however, that the absence of a species from one of the islands does not necessarily imply that it never has occurred there; it may have bred there in a former period and was afterwards wiped out.

The situation of the Hibernian Islands on the same arc parallel to New Ireland may be taken as an indication of a former connection between the islands. Nothing is known about it, however, and from a zoogeographical view-point nothing speaks in favour of it. To all appearance, the composition of the bird-fauna of the four island groups makes the impression of being the result of random dispersal across the sea in rather recent time. Any existence of a former land connection between New Ireland and the Hibernian Islands is quite out of the question.

It is noteworthy that all passerine species inhabiting the Hibernian Islands have a wide distribution, ranging well into the Papuan region or even much farther than that. Not a single species endemic to the Bismarck Archipelago have reached the islands, while three of such species (*Dicaeum eximium, Monarcha hebetior* and *Monarcha ateralba*) occur on Dyaul. This is rather puzzling, because the latter species constitute an older fauna element and, therefore, were able to dispose of a longer period of time in which they could make a crossing to the islands. None of these indigenous species can be considered "old relicts" with declining population size and shrinking distribution and it is not probable that they formerly extended their breeding range to the Hibernian Islands, but the widely ranging species, presumably, possess greater colonizing powers and superior competitive capacities.

The development of endemic forms on the Hibernian Islands is not particularly pronounced. Only one form has reached species level (*Accipiter eichhorni* Hartert on Feni¹) and the endemic subspecies are as a rule only comparatively slightly differentiated².

A comparison between the passerine fauna of Dyaul and that of the Hibernian Islands shows that Dyaul is characterized by its greater richness in species and by its high proportions of distinct endemic forms. In order to explain these differences between Dyaul and the Hibernian Islands it is necessary to analyse the factors which control island colonization by birds. An attempt to perform such an analysis is made below.

Factors Controlling Island Colonization

The possibilities available to an island for colonization by land birds across the sea are dependent mainly on:

(1) The age of the island, i. e. the length of time in which the island could have received avian immigrants.

- (2) The size of the island.
- (3) The distance from the area from which immigrants can be expected.
- (4) The direction and strength of the prevailing winds.
- (5) Habitat characters and biotic factors.

These factors are analysed below separately in order to throw some light on the history of the avifauna of Dyaul and the Hibernian Islands.

Age: The Hibernian Islands are partly volcanic in origin and are probably younger than Dyaul (cf. below, p. 31). It is even possible that volcanic activity has destroyed parts of the fauna at a recent date. The relatively low age of the Hibernian Islands may account for their paucity of species and their scarcity of striking endemic forms.

Size: It appears from table 6 that all the satellite islands of New Ireland have an area of about the same order of magnitude. Tanga and Feni are practically the same size as Dyaul, while Lihir is somewhat larger and Tabar more than twice as large. Nevertheless, Dyaul has more species than Tabar and Lihir and even twice the number of that on Tanga and Feni. Consequently, the small differences in size are probably of minor importance only.

Distance: The island groups of Lihir, Tanga and Feni are situated at the same distance from New Ireland, while Tabar is at only half this distance from New Ire-

¹ By MAYR (1957, p. 2) regarded as conspecific with *Accipiter albogularis* of the Solomon Islands. ² The number of endemic subspecies restricted to only one island is 5 on Tabar, 3 on Lihir, one on Tanga and one on Feni.

Biol. Skr. Dan. Vid. Selsk. 14, no. 1.

land, and Dyaul is still closer. These differences may have some bearing on the number of species on the islands. There is a certain correlation between the narrowness of the separating water gap and the number of species, at least as far as Dyaul and Tabar are concerned (cf. table 6).

Wind: The southeastern trade-wind, which is the prevailing wind from May to October blows approximately parallel to the longitudinal direction of New Ireland and does not favour immigration either to Dyaul or to the Hibernian Islands. The monsoon, blowing from November to April, is mostly northern (northeastern-northwestern), and thus favourable for invasions to Dyaul from New Ireland (or from New Hanover), but very unfavourable for the Hibernian Islands.

Habitat: The physical and biotic environment of Dyaul and that of the lowland of New Ireland appear to me to be very similar. The Hibernian Islands differ from Dyaul in being much more mountainous and, if anything, this should result in a more varied environment with a greater number of ecological niches and, consequently, favour the presence of a greater number of species. This difference appears to be of no significance, as the Hibernian Islands are actually poorer in species than Dyaul.

Summing up, Dyaul has evidently greater possibilities than the Hibernian Islands for colonization by New Ireland birds. It is situated closer to New Ireland, is favoured by the direction of the wind and is probably of greater age. These facts may explain the greater richness of the fauna of Dyaul, and its greater antiquity would even satisfactorily explain the stronger development of endemic forms. The assumption concerning the difference in geological age rests on a very slender foundation, however.

Other factors than those mentioned above may have influenced the faunal history of Dyaul and made the situation more complicated. The possibility cannot be ruled out that Dyaul, contrary to the Hibernian Islands, was once in connection with New Ireland. The existence of such a former land bridge would alter the whole picture drastically. If originally being a fraction of New Ireland Dyaul would have taken over the entire lowland fauna of New Ireland, and the richness of its fauna would then be easily explained. Under such circumstances the differentiation of the endemic forms, on the other hand, would have required a much longer period of time than if Dyaul was a truly oceanic island (cf. above, p. 22). The great depth of the Gazelle Channel, amounting to about 1000 meters, is no argument against the land connection; uplifts of this magnitude actually have taken place. A few notes on the geological history are necessary.

Notes on Geology

The geology of New Ireland and its satellite islands is characterized by a violent tectonic and volcanic activity, which gave rise to drastic developments in the later periods of the Tertiary. On both New Ireland and Dyaul wide-spread andesite and tuff layers are evidence of a former very strong volcanic activity. On New Ireland there are extensive layers of oligocene limestone as well as chalk beds with foraminifera belonging to recent species. These cannot, therefore, possibly be older than Pliocene, and are most probably from Pleistocene. Even on Dyaul scattered occurrences of tuffs with foraminifera have been found (SAPPER 1910, p. 22; SIEVERS 1910, p. 439). The chalk beds on New Ireland are found on altitudes up to 1100 meters above sea level, which shows that an enormous upheaval, amounting to at least 1500 meters, has taken place in the recent past. It is evident that the present New Ireland, New Hanover and Dyaul were formed partly by uplift, partly by volcanic extrusion. The volcanic activity, which may have been submarine, cannot be dated, but probably took place in the latest part of the Tertiary. The upheaval is so young that the emergence of the islands above the sea cannot have taken place before Pleistocene. During the latter part of the upheaval, in a period extending into the Quaternary, enormous layers of coral rock were deposited upon the older sediments, adding considerably to the area of the islands (SAPPER 1910, p. 57–60). It is very likely that in a certain period Dyaul was in land connection with New Ireland-New Hanover, but, admittedly, this theory cannot be proved at present. It is noteworthy, however, that the terraced profile of Dyaul and that of the south coast of New Ireland, closely correspond, according to verbal information by SOFUS CHRISTIANSEN, M. Sc., indicating that even during the recent upheaval the two islands are influenced in a parallel way and probably are somehow in connection with each other.

Bearing in mind that the development of the Dyaul endemics must have required a long time of isolation, it is obvious that Dyaul, if it was originally part of New Ireland, was detached from that island rather early, and at any rate earlier than the period in which New Ireland and New Hanover were separated. The great depth of the Gazelle Channel indicates that the age of Dyaul as an independent island cannot possibly be less than 100,000 years, and an estimate of 200,000 years probably comes nearer the truth, but at present this is mere guesswork.

The geological features of the four Hibernian Islands are very similar. They are characterized by a strong volcanic activity, continuing still to-day. Layers of young eruptives are mixed with raised coral beds. There are no signs of older deep sea sediments (SIEVERS 1910, p. 452). This shows that these latter, if present at all, have been completely covered by coral rocks, and this indicates, in my opinion, that the upheaval took place rather slowly and that the islands, consequently, are younger than Dyaul and New Ireland.

New Ireland-New Hanover as Centre of Origin

It has been mentioned above that New Ireland and New Hanover probably formed one island until quite recently. This double-island forms the origin of the main part of the land-bird fauna in a number of islands. These islands belong to four different zoogeographical categories:

(1) The Admiralty Islands and the St. Matthias Islands. These are outlying islands, far removed from New Ireland, characterized by a relative paucity of species and a great percentage of markedly different endemic species and subspecies, char-

acters which are typical of peripherally isolated faunas. Both island groups are inhabited by 15 species of passerine birds (but not necessarily the same species on both groups), *i. e.* only one more species than Tabar, in spite of the very much greater area of both island groups (1950 sq. km in the Admiralty Islands, compared with 251 sq. km in Tabar). There is a slight New Guinea element on the Admiralty Islands, and even on the St. Matthias Islands (*Myzomela nigrita*).

(2) The Hibernian Islands. These islands are situated much nearer to New Ireland than the St. Matthias Islands and the Admiralty Islands. They are poor in species, although relatively richer (in relation to their small area) than the said outlying islands, and the percentage of striking endemics is small. They do not possess a typically peripheral fauna, but like the islands of the first category they are oceanic, in the zoogeographical sense of the word, *i. e.* they have received their fauna across the sea; cf. MAYR 1941b, p. 199. The islands have received faunal elements also from the Solomon Islands, most prominently on Feni, but traceable westwards to Lihir.

(3) The Duke of York Islands. Situated between New Ireland and New Britain, but closest to the latter and with the Credner Islands serving as stepping stones for invading birds. The faunal connection with New Britain is much closer than that with New Ireland; as a matter of fact, there is no proof of a New Ireland origin for any of the species found on Duke of York Islands. They are inhabited by 12 species of passerine birds, none of which have developed endemic forms. The area is somewhat smaller than that of Dyaul. It has probably been in land connection with New Britain until quite recently.

(4) Dyaul Island. This island is situated as near to New Ireland as the Duke of York Islands, but differs by having a much richer fauna (18 passerine species) and by having developed a number of striking endemic forms. The fauna of Dyaul cannot be called peripheral and, as said above, the island is possibly not even oceanic. The relationship of its bird fauna is clearly with New Ireland, but a certain influence from New Hanover is present, however, in spite of the much longer distance from that island (50 km, compared with 14 km from New Ireland). The Dyaul form (sumunae) of Lalage leucomela is obviously an offshoot of the New Hanover form (albidior), which latter is almost intermediate between the New Ireland form (karu) and sumunae. In the case of Monarcha chrysomela the populations of New Ireland and New Hanover are indistinguishable in coloration, but the population of New Hanover is intermediate in proportions between that of New Ireland and that of Dyaul. This may indicate that the Dyaul population originated from New Hanover, but the different proportions may as well express differences in adaptation to some environmental factor; at any rate, similarity in measurements may not necessarily represent any close genotypical agreement, but may be the result of parallel developments. It is more important, however, that a specimen (3 ad.) from New Hanover tends towards the Dyaul form *pulcherrima* in coloration, having the black feathers of the upper parts supplied with broad yellow edges, producing a variegated pattern. This specimen either represents the first step towards the colour pattern of *pulcherrima*
or it constitutes a hybrid between the two forms. If the latter explanation is correct it shows that gene-flow between the populations is possible, but obviously only in exceptional cases and undoubtedly soon being subject to "swamping".

Summary

The "Noona Dan Expedition" during its visit to the Bismarck Archipelago investigated the fauna and flora of Dyaul Island, which hitherto was unexplored. The position of Dyaul, situated due south of the western end of New Ireland, is given on the map fig. 1, on which also all the collecting stations are shown. A short description of the topography and vegetation of Dyaul is given on p. 3.

The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of striking endemic forms, the description of which forms the first part of the present paper. In the following enumeration of the Dyaul endemics the principal importance of the morphological differentiation is emphasized:

Dicaeum eximium phaeopygium, new subspecies (p. 5). Differs strikingly from the two other forms of this species by the loss of the bright carmine red rump patch. A similar evolutionary step has been taken also in other groups within the genus Dicaeum, but then usually serves to distinguish full species (not subspecies). Adult males are illustrated on plate I, fig. 1; measurements are given in table 1.

Monarcha chrysomela pulcherrima, new subspecies (p. 7). Differs strikingly from all other forms of this species by its uniform yellow, not black, upper parts in the adult males. Both sexes are illustrated on plate I, fig. 2; measurements are given in table 2.

Monarcha ateralba, new species (p. 9). Differs from its nearest ally, M. verticalis, so strikingly both in proportions and coloration that it has evidently reached species level. The new species belongs to the superspecies M. verticalis, which is represented in the Bismarck Archipelago by four species (fig. 4). Adult males of the new species are illustrated in fig. 2, juvenile specimens in fig. 3; measurements are given in table 3.

Monarcha hebetior cervinicolor, new subspecies (p. 14). The females differ strikingly from the two other forms of this species by several characters (e. g. rufous, not blackish brown, tail) which approach those of the allied species M. alecto. Adult females are illustrated on plate II, fig. 1; measurements are given in table 4. The relation between the two closely allied species M. hebetior and M. alecto is discussed, and the theory is set forth that alecto twice invaded the Bismarck Archipelago from New Guinea. The first invasion gave rise to the development of hebetior, while the second and more recent colonization has not resulted in any morphological differentiation.

Lalage leucomela sumunae, new subspecies (p. 18). Differs from all the forms inhabiting the main chain of islands in the Bismarck Archipelago (*falsa, karu, albidior*) by having white under parts without rufous. A complete loss of rufous has taken place

also in the forms inhabiting Tabar and Lihir, but all other forms of this widespread species have buffish or partly rufous under parts. Adult females are illustrated on plate II, fig. 2, adult males of various subspecies in fig. 5; measurements are given in table 5.

The morphological differentiation of the endemic forms of Dyaul must have required a certain amount of time, during which the populations were isolated from those of New Ireland. The length of this period of isolation has been roughly estimated on the basis of a comparison with similar tropical islands (Philippine Islands, West Sumatran Islands). Attention is drawn to the fact that, from an evolutionary point of view, it is necessary to distinguish between two categories of insular faunas: (1) Those faunas which have been isolated through segregation of a formerly continuous range, and (2) those faunas which have been founded by colonists across the sea. In the latter category the morphological differentiation of the populations will take place much more rapidly than in the former category.

The distribution of the above-mentioned five species in the Bismarck Archipelago has been outlined on the map fig. 6. In all five species the populations of the main chain of islands (Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover) are either identical or only slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is explained as primarily the resulof a greater evolutionary rate in the Dyaul populations, but a time-factor must have been involved also. Evidence is given for the assumption that the main islands were mutually connected, forming one or two big islands, when Dyaul had already received its fauna. It is noteworthy that the Gazelle Channel, not broader than 14 km, has in spite of its extreme narrowness been broad enough to form an effective barrier, preventing gene-flow between the populations of New Ireland and Dyaul.

A comparison is made between the passerine fauna of Dyaul and the island groups of Tabar, Lihir, Tanga and Feni, for which four groups the collective designation "Hibernian Islands" has been revived. None of the five species which have developed strongly differentiated forms on Dyaul have reached Tanga and Feni, and two only (Monarcha chrysomela and Lalage leucomela) have reached Tabar and Lihir; cf. fig. 6. Altogether the Hibernian Islands are poorer in species than Dyaul. It appears from table 6 that Dyaul is inhabited by 18 species of passerine birds, Tabar by 14, Lihir by 13, Tanga by 9 and Feni by 8. The corresponding figure for the lowland of New Ireland is 26. Within most species the populations of the different Hibernian Islands are very similar, *i. e.* they resemble each other more closely than they resemble the New Ireland population. This similarity makes it obvious that the different islands have been colonized by stray immigrants from the other islands rather than by independent invasions from New Ireland. In each species as a rule only one successful oversea crossing from New Ireland was required. Once established on one island the species managed to colonize one or more of the other Hibernian Islands. The waves of invasions emanating from New Ireland reached in most cases Tabar or Lihir, more rarely Tanga or Feni. A number of species which have colonized Tabar and Lihir failed to extend their breeding range from these two islands to Tanga and Feni, which, consequently, have a more impoverished fauna than Tabar-Lihir. To all appearance, the composition of the bird-fauna of the four Hibernian Islands gives the impression of being the result of random dispersal across the sea in rather recent time, and nothing speaks in favour of the view that a land-connection ever existed between them.

All passerine species inhabiting the Hibernian Islands have a wide distribution outside the Bismarck Archipelago; not a single species endemic to the Bismarck Archipelago has reached the Hibernian Islands. The widely ranging species, therefore, presumably possess greater colonizing powers and superior competitive capacities.

While the Hibernian Islands have a rather impoverished passerine fauna and only slightly differentiated indigenous subspecies, Dyaul differs in having a greater richness in species and a high proportion of distinct endemic forms. In order to explain these differences an attempt is made to analyse the factors which control island colonization by birds. The possibilities available to an island for colonization by land birds across the sea are dependent mainly on: (1) The age of the island, (2) The size of the island, (3) The distance from the area from which immigrants can be expected, (4) The direction and strength of the prevailing winds, and (5) Habitat characters and biotic factors. The total area and the distance from New Ireland of Dyaul and the four Hibernian Islands are given in table 6. A comparison between Dyaul and the Hibernian Islands tends to show that Dyaul evidently has greater possibilities than the Hibernian Islands for colonization by New Ireland birds. It is situated closer to New Ireland, is favoured by the direction of the wind and is probably of greater age. These facts may explain the greater richness of the fauna of Dyaul, and its greater antiquity would even satisfactorily explain the stronger development of endemic forms. It is probable, however, that Dyaul, contrary to the Hibernian Islands, was once in landconnection with New Ireland. In that case Dyaul would have taken over the entire lowland fauna of New Ireland, and the richness of its fauna could then be easily explained. On the other hand, under these circumstances the differentiation of the endemic forms would have required a much longer period of time.

According to the geological features of New Ireland and its satellite islands (briefly described on p. 30–31) the present New Ireland, New Hanover and Dyaul were formed partly by uplift, partly by volcanic extrusion, which took place in the later periods of the Tertiary. The upheaval, which amounted to at least 1500 meters, extended into the Quaternary, and the emergence of the islands above the sea could not possibly have taken place before the Pleistocene. It is obvious, for zoogeographical reasons, that Dyaul, if it was originally a part of New Ireland, must have been detached from that island rather early, and at any rate earlier than the period in which New Ireland and New Hanover were separated. The age of Dyaul as an independent island is estimated to be somewhere between 100,000 and 200,000 years. It is probable that the upheaval took place more slowly in the Hibernian Islands than in Dyaul and New Ireland and that, consequently, the Hibernian Islands are younger, but the geological evidence is insufficient for a satisfactory clarification of the question.

New Ireland and New Hanover form the origin of the main part of the landbird fauna in four zoogeographically different groups of islands: (1) The Admiralty Islands and the St. Matthias Islands, which are outlying islands with a typically peripheral fauna (impoverished, but with a high proportion of strongly modified forms). (2) The Hibernian Islands, which just like (1) are oceanic, but differ in having only slightly differentiated endemic forms. (3) The Duke of York Islands, which are not oceanic and completely lack endemic forms. (4) Dyaul Island, which is possibly not oceanic and has a comparatively rich fauna with many strikingly modified endemic forms. The said zoogeographical differences between the four categories of islands are due to the unequal possibilities for avian colonization and to the differences in the geological history which have been described in the present paper.

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37

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PLATES

PLATE I

Fig. 1. Adult males of the three forms of *Dicaeum eximium*; a-b layardorum from New Britain, $\dot{c}-d$ nominate eximium from New Ireland, e-f phaeopygium from Dyaul; all collected by the "Noona Dan Expedition".

Fig. 2. Adult specimens of *Monarcha chrysomela* from the Bismarck Archipelago, showing differences between nominate *chrysomela* from New Ireland (a-b adult males, e adult female) and *pulcherrima* from Dyaul (c-d) adult males, f adult female); all collected by the "Noona Dan Expedition".





Fig. 2.

PLATE II

Fig. 1. Adult females of *Monarcha hebelior*, showing differences between *cervinicolor* from Dyaul (*a–c*) and *eichhorni* from New Hanover (*d*, *e*) and New Ireland (*f*); *a*, *b*, *c*, *d* and *e* collected by the "Noona Dan Expedition", *f* belonging to the American Museum of Natural History, New York.

Fig. 2. Adult females of Lalage leucomela from the Bismarck Archipelago, showing differences between karu from New Ireland (a-d) and sumunae from Dyaul (e-h); all collected by the "Noona Dan Expedition".





a b c d e f g h Fig. 2.

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BY

GUNNAR NYGAARD



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CONTENTS

1.	Introduction	3
2.	Geology and Morphometry of Grane Langsø	7
3.	On the Water Balance of Grane Langsø	8
4.	The Carbon Dioxide System	16
5.	Analytic Methods	17
6.	The Uncertainty of the Analyses	19
7.	Iron and Phosphate in Grane Langsø	22
8.	The Specific Conductivity of Grane Langsø	31
9.	The Calculation of pH and the HCO3-quantities	44
10.	The Carbon Dioxide	47
11.	The Carbon Dioxide Exchange between the Lake Surface and the Atmosphere	57
12.	The Hydrogen Ion Concentration	63
13.	The Hydrogen-Carbonate Ion	81
14.	The Movement of a Winter Thermocline	83
15.	Summary	89
16.	Acknowledgements	90
17.	Survey of the Analyses	91
18.	Literature	107

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1. Introduction

For anyone who likes nature, the Danish lake Grane Langsø is a remarkable lake. At the shores one may observe how the sundew plants (*Drosera rotundifolia* and *D. intermedia*) catch dragon-flies. In spite of the lime-deficiency of the water the crayfish (*Astacus fluviatilis*) thrives excellently, several of the individuals being remarkable through their blue colour. If these crustaceans in very shallow water are lit up with a hand lamp on a summer night, a bright red light is reflected from their darkadapted eyes. On visiting the lake in May or June one may hear the chinking croaking of the natterjack (*Bufo calamita*) in the afternoon from the sunny shores.

When rowing to the centre of the $11^{1/2}$ metres deep lake, one is surprised to observe the blue-green colour of the water and its great transparency, a white disc being still visible at a depth of $11^{1/2}$ metres in June, July, or August and December. A botanist will be specially interested in e.g. a club-moss as *Lycopodium inundatum*, rare submerged mosses and liverworts (a deep-water modification of *Fontinalis antipyretica*, *Cephaloziella subdentata*, *Chiloscyphus polyanthus*, *Scapania undulata* var. *purpurascens*, and *Riccardia sinuata* var. *submersa*), and in the rare water-wort (*Elatine hexandra*), which forms small submerged meadows in shallow water. In the summer plankton he will find i.a. the indicative and sporadic *Dinobryon bavaricum* var. *Vanhoeffenii*; further *Elakatothrix gelatinosa*, *Stichogloea olivacea*, and many desmids. Besides the indifferent var. *asterionelloides* of the diatom *Tabellaria flocculosa*, the ecologically significant var. *Teilingii*, indicating oligotrophy, also occurs. For an angler, however, there is not much to be got here, perch (*Perca fluviatilis*) being the only fish present.

I think it is worth while to subject this acid *Lobelia-Isoetes-Littorella* lake, unique by Danish standards, to a closer investigation.

JOHS. IVERSEN (1929, p. 311) comments on the lake after a single visit in the summer 1927.

ULRIK RØEN (1954) has given an account of the entomostracan fauna in Grane Langsø, based on collections from 1951–52. Noteworthy are *Eucyclops lilljeborgi*, new to Denmark, and three other species of rare occurrence.

GUNNAR NYGAARD (1955) has published date on the primary production of i.a. Grane Langsø in relation to the Compound Index, on the basis of monthly investigations in 1950–51. In connection with these facts an estimate of the trophic status of the lake is formed, vz. oligotrophy. KAJ HANSEN (1957) has published the results of his many years' work on the bottom deposits of Danish lakes. These sediments are made up of three components: (1) the organic compounds, (2) the minerogenic component, chiefly consisting of quartz, and (3) the inorganic, biogenic substances, predominantly made up of diatom frustules and lime, precipitated by organisms. Out of 14 lakes of various types Grane Langsø has the smallest content, expressed in percentages, of carbon and nitrogen in its gyttja and the smallest loss on ignition. Total SiO₂, however, constitutes no less than about 75 per cent of the deposit, diatom SiO₂ about 2 per cent. The minerogenic component thus 'amounts to more than 70 per cent of the gyttja, a unique quantity within the range of lakes examined. In agreement with the fact the dark greyish sediment from the central part of Grane Langsø feels like fine, sandy mud.

SIGURD OLSEN (1958 and 1958 a) has tried, with the aid of radioactive phosphate, to approach the difficult problem of phosphate ion exchange between lake water and bottom sediment. An experimental method was developed, by with is it possible to measure the two opposite processes. Differences between the experimental conditions and the natural ones are, however, so great that estimating the rate and final result is at present difficult (1958 a, p. 96). During identical experimental conditions, however, the graphs of the net quantities of phosphate adsorbed from the water by the gyttja take a different course in Grane Langsø and the eutrophic Furesø (1958, fig. 7, graph a, and fig. 8, graph a_{ox}).

GUNNAR NYGAARD (1958) has published a bathymetric map of the lake, surveyed by TYGE MØLLER. An account is given for the quantitative benthic distribution of the individual plant species, based upon bottom samples taken by a frogman in 1954 and 1955. The total weights of vegetable dry matter per $\frac{1}{20}$ square meter were deter-

mined for each meter along two section lines from the shore to the deepest part of the lake. Further the productivity of *Nostoc* and *Nitella flexilis* has been determined to about 2.8 and 2 per cent daily increase in July, respectively, indicating the plants of Grane Langsø to be slowly growing.

In his paper of 1961 ULRIK RØEN has correlated the productivity results of NYGAARD (1955) with the quantities of planktonic crustacea of Grane Langsø in 1950–51. Simultaneously with the monthly determination of the gross production below one square metre per day for a vertical column of 10 m length, I took 3 vertical hauls from the 10 m depth to the lake surface by means of a tow-net exclusively used for this purpose. Fig.1 in RØEN'S paper indicates a reasonably good agreement between the two factors in question. Minor discrepancies are explained by the presumption that not all plankton algae are of the same nutritious value for the crustacea.

This agreement between the producers and the consumers of the plankton in Grane Langsø is notable, though the Infusoria and Rotatoria were not considered, and one of the Crustacea is occasionally carnivorous, another exclusively carnivorous (RØEN 1961, p. 19); further some disadvantages by the sampling method may influence the reliability of the number of Crustacea counted. I think that the scarcity of *Leptodora*

Nr. 2

hyalina in Grane Langsø should be explained by the fact that it is a representative of the third link in the food chain: phototrophic algae—herbivorous consumers carnivorous consumers of the first degree. As fig. 1 in Røen's paper of 1961 shows the dependance of the crustacean zooplankton on the primary production of the algae, the conclusion can be drawn that Grane Langsø constitutes a good example of a lake where the grazing of the zooplankton is an important factor in determining the size of the standing stock of phytoplankton. In a contamined and highly productive lake as e.g. the Danish lake Frederiksborg Slotssø, the size of the standing crop of planktonic algae is insignificantly influenced by grazing.

From October 1956 to July 1961 continuous instrument readings of the light climate in $11^{1}/_{4}$ m subsurface depth were plotted automatically by a three colour recorder. The radiant energy can be computed in μ watt per square centimetre from each of three graphs, blue, green, and red, covering the three spectral regions of 400–500 m μ , 500–600 m μ , and 600–700 m μ , respectively. From May 1958 to July 1961 these measurements were extended to include also corresponding registrations of the light climate in $1/_{4}$ m subsurface depth.

In connection with these investigations monthly or fortnightly determinations of the spectral transmission of the individual water layers were carryed out from March 1957 to July 1961, partly by in vitro experiments, partly by the in situ method. Beckmann's spectrophotometer, photoelements furnished with interference filters or the Chance glass filters OB 10, OGr 1, and OR 2 were employed.

The total carbon dioxide has been determined monthly or forthnightly from March 1958 to July 1961 for the subsurface depths of 0, 2, 4, 6, 8, 10, and 11 meters. The oxygen content of the water from the same depths has been measured regularly in the period from March 1958 to March 1959.

Series of temperature measurements have been taken regularly from October 1956 to July 1961. At the same time tow-net samples and quantitative plankton samples have been collected. "Column water" from 0–11 metres was taken by means of a 12 m long and 1 inch thick plastic tube. Moreover, 10 ml samples for counting have been collected from the above mentioned depths since December 1957.

The ¹⁴C-technique was used for determining primary production at the subsurface depths previously mentioned from July 1958 to July 1961. These determinations have been undertaken twice a month since July 1959. Investigations of the respiration of the planktonic algae were started on February 1960, using the method described by STEEMANN NIELSEN and VAGN HANSEN (1959). Coincidently with these investigations the phytoplankton from the corresponding depths has been counted in a living state by means of the counting chamber of Kolkwitz.

Finally the photosynthesis and respiration of *Nitella flexilis* have been determined fortnightly with the light and dark bottles method during one year (July 1959 to July 1960). Carbon dioxide and oxygen as well were analysed.

The subjects of this paper are primarily the yearly fluctuations of carbon dioxide, hydrogen carbonate ion, specific conductivity, and hydrogen ion concentration.



Fig. 1. Bathymetric map of lake Grane Langsø, measured by Tyge Møller in May 1951, when the maximum depth was 11.1 m.

2. Geology and Morphometry of Grane Langsø

The district including Grane Langsø has not been treated in the Danish geological series of D.G.U. (Danish Geological Investigations). KAJ HANSEN (1958, p. 543) has, however, written of the tunnel-valleys in this district and the adjacent ones (cf. also J. HUMLUM and KNUD NYGAARD 1961, map 6).

I am indebted to Dr. HELGE GRY, who is working on the quaternary geology of the district in question, for information on the origin of the lake and its environment.



Fig. 2. The areas of the isobaths plotted against their corresponding depths.

Grane Langsø ($56^{\circ}1'$ N. and $9^{\circ}27'30''$ E.) is situated in a tunnel-valley, formed in stratified drift by a subglacial stream during the Baltic Glaciation. Later on the stagnant ice melted away, but large ice masses remained in the tunnel-valley. Lateglacial sand and gravel were then deposited by more recent glacial streams in the tunnel-valley. Finally the lake appeared as a basin, where a great ice mass had been buried.

Glacial hilly country of diluvial sand lies east of the lake, while late-glacial deposits of sand form still higher hills west of the lake. *The lake basin is thus situated in stratified drift*. The sand is not pure quartz sand, but contain small amounts of other minerals from the Scandinavian bed-rock, especially felspars and ferruginous minerals.

The altitude of Grane Langsø is 74 m, and the lake lies near to the water-shed between Denmark's two largest catchment areas, those of Gudenå and Skernå.

The area of this glacial tunnel-lake is 11.38 ha. The maximum depth is 11.5 m at normal water level (cf. Fig. 3). The lake volume amounts to about 805900 cubic

meters. The areas of the contours on the bathymetric map of Grane Langsø (Fig. 1) are shown relative to their depths on Fig. 2. By means of this figure it is easy to find the volume between two given levels in the lake.

The volume between the 8 m level and the 11 m level is about 119300 cubic meters. The 8 m level has been chosen, because the thermocline normally lies in this depth in June-July (cf. Table 37, p. 88). *The hypolimnic volume thus amounts to 15 per cent of the total lake volume* in the two summer months mentioned.

The mean depth is 7.1 m, consequently no less than 62 per cent of the maximum depth. This percentage indicates that the lake basin of Grane Langsø markedly deviates from a conical depression, which is characterized by the ratio of mean depth to maximum depth = 33 per cent. Fig. 1 and 2 also demonstrates that the lake basin has steep sides, in places very steep indeed, by Danish standards.

Another Danish lake, Gribsø, covers nearly the same area, 10.08 ha, as Grane Langsø and exhibits a similar maximum depth, 11 meters. Its mean depth, is however, only 4.8 meters (BERG and CLEMENS PETERSEN 1956, p. 12). According to LUNDBECK (1926, p. 11) some North German small lakes are recorded to be much deeper than Grane Langsø: Pluss-See has an area of 13.5 ha, and its maximum depth is no less than 26 meters! The area of Kleiner Ukleisee, to which I shall return, is only 2.5 ha, but the depth of this lake is 16 meters.

3. On the Water Balance of Grane Langsø

Grane Langsø has neither a superficial inlet nor a visible outlet. As the precipitation on the lake surpasses the evaporation, however, *the lake must have a sublacustrine run-off*. By means of the following equation I shall try to contribute to methods by which it will be possible to compute the water balance of the lake, provided that better information is available than at present.

$$P + I_s + I_z = O_s + O_z + E + \Delta R \tag{1}$$

P = precipitation

 I_s = superficial inlet, here = 0

 I_z = sub-lacustrine inlet

 O_s = superficial outlet, here = 0

 O_z = sub-lacustrine outlet

E = evaporation from the lake surface

 ΔR = increment of the water volume within a definite period.

For the lake in question the equation (1) can be simplified to

$$P + I_z = O_z + E + \Delta R. \tag{2}$$

On Fig. 3 the monthly precipitation of 1958–61 can be compared with the variations in water level of the lake during the same period. The distance from the meteorological station at Bryrup to Grane Langsø is just under 4 km. Fig. 3 indicates that the water level generally reached its maximum height in April, more rarely in March. In July or August a renewed increase took place; if the precipitation of both months were high, as in 1958, the lake surface even rose to the April-level. A rather low water level could occur in August or July, but the lowest



Fig. 3. The monthly precipitation of Bryrup and the water level of Grane Langsø in the period 1958–61. The small dotted lines in the upper diagram indicate the monthly means of precipitation in 1926–55, while the horizontal dotted line of the lower diagram represents the mean water level, estimated by Mr. NIELS AGERSKOV, who has lived at the lake the last 45 years.

level was observed in October, more rarely in late November. In February to April 1959 the lake surface was unusually high.

The difference between the highest and lowest water level was 28, 36, and 38 cm for the years 1958, 1959, and 1960, respectively. This fluctuation is rather small. The corresponding amplitude of lake Gribsø amounted to 45 cm in 1942 (BERG and CLEMENS PETERSEN 1956, p. 97). This lake, 11 m deep and covering a similar area as that of Grane Langsø, has affluents, but normally no visible outlets.

The evaporation from the surface of Grane Langsø is an unknown quantity. The annual evaporation of the Zealandic lake Søndersø has been measured as about 650 mm in the years 1943–47 and as about 568 mm in 1957 (ASLYNG 1959, Table I, p. 57). According to the paper Danmarks Klima (1933, p. 134), the relative humidity of the winds over Jutland was virtually identical to that measured at Zealandic meteorological stations in the years previous to 1925. Grane Langsø is, however, highly wind-sheltered by coniferous forests on the hills around the lake; therefore the yearly evaporation is roughly estimated as about 450 mm. The monthly values of evaporation in Table 1 consequently have been reduced to about 69 per cent of the Søndersø-values from 1943–47.

The mean precipitation of Bryrup for the period 1886–1925 was 695 mm (Danmarks Klima 1933, p. 140). Mr. INGOLF SESTOFT, State Meteorologist, has kindly informed me that the corresponding value for the period 1926–55 is 772 mm. The precipitation of the four years of investigation amounted to

1958	1959	1960	1961	
887 mm	781 mm	858 mm	836 mm	

In the following calculations the value 770 mm has been used.

An examination of how the surface level of Grane Langsø reacts in relation to the monthly surplus precipitation gave the result that these surpluses, considering the sign, were in fairly good agreement with the corresponding rises and falls of the lake level. By way of example may be cited the figures of 1958 in Table 1.

	Temp. measured	P measured	E estimated	P–E estimated	⊿ R measured
January	- 1.8	78	7	71	40
February	-1.7	115	7	108	90
March	-1.8	24	14	10	130
April	4.1	28	35	- 7	0 (-20)
May	10.2	74	69	5	-10
June	14.3	45	76	-31	- 30
July	16.3	136	86	50	10 (50)
August	15.1	140	69	71	50
September	13.5	59	48	11	-40
October	9.5	60	21	39	10 (30)
November	5.1	37	10	27	- 30
December	1.5	91	7	84	40

TABLE 1. The monthly surplus precipitation (P-E) compared with the corresponding rise of the lake level (ΔR) in 1958, both factors being stated in mm.

This fairly good agreement indicates that the sub-lacustrine outlet of Grane Langso (O_z) probably is small and presumably constant during the year.

At the planter-house, situated in Kongsø plantation about 2 km SE of Grane Langsø and lying in level 86 m, a boring has been performed. The core indicates that

Nr. 2

the soil consists of various thin layers of e.g. moraine clay, coarse sand, loam, sharp gravel, and dark fine sand; it contained several horizons of groundwater. If this section reflects the soil conditions of the tunnel-valley containing Grane Langsø, it is very difficult to make out the groundwater conditions of the environment. The water-table of the Kongsø-boring mentioned possibly lies at level 79 m.

At the farm Højvang, situated 650 m NE of Grane Langsø, a 56 m deep boring has been made. The groundwater table of this well lay at level 67 m on July 29th, 1962; at this time the water level of Grane Langsø was -10 cm.

KAJ HANSEN has performed several borings in the bottom of Grane Langsø. The deepest one went down to well over 18.5 m below the lake surface, i.e. about 7 m below the lake bottom. Dr. HANSEN, whom I thank for information on the cores, estimates the maximum depth of the ancient lake basin to be about 18.5 m. By far the greatest part of most of the cores is gyttja containing fine sand. The cores, all of them, indicate that the *ancient lake basin is covered by a layer of loam*, 20–110 cm thick, which in all cores rests on the substratum of diluvial sand. This loam is rather easily crushed in dry state by the fingers, but the sand is hardly perceptible between the finger tips. HUTCHINSON (1957, p. 248) writes: "Most small lakes not in rock basins are separated from the ground water by a clay seal, formed as an early lake sediment."

Lake Hampen Sø (level about 79 m), lake Torup Sø (level about 78 m), and lake Grane Langsø (level about 74 m) seem to be situated in a rather broad valley of a west-easterly course. The hilly country north and south of this valley exhibits ground levels of a little more than 100 m. The tunnel-valley containing Grane Langsø intersects the broad valley in a northerly direction, and the surface of its 4 lakes, Rævsø, Grane Langsø, Kalgård Sø, and Kongsø, lies at the 74 m level. The two northernmost lakes, Rævsø and Grane Langsø, have no visible inlet or outlet. Kålgård Sø has no superficial affluent, but an insignificant affluent to Kongsø, which has a negligible outlet slightly inclining to the south.

It is conceivable that a stream of groundwater is moving to the eastward from Hampen Sø and Grane Langsø; from there it continues in north-eastern direction to lake Kulsø (level about 54 m), which drain off to the brook Salten Å. If so, the groundwater level is falling downgrade 1 in 93 from Grane Langsø to the Højvang well, and 1 in 100 from this well to Kulsø. These considerations imply a good contact, however, between the lake and the groundwater.

Before passing on to examine whether the water balance of Grane Langsø is determinable by means of the Cl⁻ concentrations of the air, the precipitation, and the lake, I should comment on two possibilities concerning the interaction of the lake water and the groundwater. These possibilities should not be considered as alternatives, as they quite well may be concurrent.

(i) The sides of the lake basin procure a good contact between the lake and its surrounding layers of sand, through which a groundwater stream may be flowing. The accordance between the moments of the highest and lowest level of the groundwater and the lake surface, normally April and October, speaks in favour of this possibility.

(ii) The lake is lying in a basin covered with loam, through which the water slowly, but rather continually, seeps down to a subjacent stream of groundwater. The reaction of the lake soon after the precipitation speaks in favour of this possibility. A further support for this assumption is to be found in the fact that the difference between highest and lowest water level amounted to only 28–38 cm in the three years of investigation. If the lake had received a fairly vigorous sub-lacustrine inlet, the fluctuations of the lake level would undoubtedly have been greater. Finally, the great annual thermal fluctuation of the lake, together with the rather long duration of the ice-cover, is not indicative of a good contact with a groundwater stream flowing into the lake.

Which of the two possibilities mentioned fits the facts cannot be decided on the basis of the available information.

As ΔR in the equation (2) on p. 8 can be neglected, provided that the period considered is long (Lyshede 1959, p. 15), we get when P = 770 mm and E is estimated as 450 mm

$$O_z = I_z + 320. (3)$$

As the lake surface is 113800 square meters, 320 mm correspond to 36416 cubic meters. Therefore the average annual sub-lacustrine run-off is 36416 cubic meters greater than the sub-lacustrine affluent, on condition that the yearly evaporation from the lake surface really is 450 mm.

If the Cl^{-} -content of the rain water over Grane Langsø is estimated to be equal to the average value of the Cl⁻-quantities of the Borris rain and the Ødum rain, the result is 4.6 mg Cl⁻·l⁻¹. According to DRISCHEL'S survey (see HUTCHINSON 1957, p. 545) a quantity of about 5 mg Cl⁻·l⁻¹ should be expected, as the lake is removed about 80 km from the North Sea.

Borris is situated in the westernmost part of Jutland, just E of the large lagoon at Ringkøbing. Ødum lies in eastern Jutland, between Aarhus and Randers (see JENSEN 1962, Fig. 1). Grane Langsø is located halfway between these two stations.

In order to get an idea of the variation in the chloride quantities of rain water from year to year, their values are given in Table 2.

It is evident from Table 2 that the yearly variations from the average value $3.1 \text{ mg Cl}^{-} \cdot \text{l}^{-1}$ at most amount to 2.6 mg Cl $^{-} \cdot \text{l}^{-1}$ within a period of 6 years.

If we imagine the lake lying in a basin covered with loam, through which a slow seepage takes place to an underlying groundwater stream, and being fed nearly exclusively by rainwater, the evaporation E can apparently be calculated from the chloride concentration of the precipitation and the lake water:

4.6 mg Cl⁻·l⁻¹·
$$\frac{770}{770 - E} = 11.3$$
 mg Cl⁻·l⁻¹
 $E = 457$ mm.

	1955	1956	1957	1958	1959	1960	
Borris	_	-	-	5.0	8.5	5.1	
Ødum	3.8	5.7	3.1	2.5	3.7	3.1	
	Chlor 1958-,	Chloride-average of the 1958-, 1959-, 1960- values			Chloride in the accumulated rainfall of 1958, 1959, 1960		
Borris	$6.2 \text{ mg} \cdot l^{-1}$		6.0 mg·l ⁻¹				
Ødum	3.1 mg		$mg \cdot l^{-1}$ 3.1 $mg \cdot l^{-1}$				
Chloride ir	the accum	nulated rain	fall within the	he period			
	1955–1960						
Borris	unknown						
Ødum	3.5 mg · l - 1						

TABLE 2. The quantities of chloride in mg per litre of the Borris rain and the Ødum rain each year.

The precipitation is not the only source, however, that carries Cl^- to the lake; also some dry fallout of airborne chlorides must take place on the lake surface. The rate of the latter process is probably much smaller than the capture by vegetation of condensation nuclei, but it is unknown. The dry fallout has the effect that the true value of E becomes somewhat smaller than 457 mm in the hypothetic case before us.

It is, however, quite conceivable that a good contact between Grane Langsø and the groundwater exists; the lake then receives rainwater (P = 770 mm yearly) and groundwater (I_z), as well. The yearly actual evaporation of great parts of Jutland is about 350 mm (Aslyng 1959, p. 48).

If the chloride content of the precipitation on the lake itself is separately considered, the evaporation 450 mm must alter the concentration in the following way:

4.6 mg Cl⁻ · l⁻¹ ·
$$\frac{770}{770 - 450} = 11.1$$
 mg Cl⁻ · l⁻¹.

This value is believed to be at a lower limit of the true value owing to some dry fallout of airborne chlorides on the lake surface.

The precipitation over the surrounding country with coniferous woods, heaths, and moorland fields must be concentrated by the actual evaporation:

4.6 mg Cl⁻ · l⁻¹ ·
$$\frac{770}{770 - 350} = 8.4$$
 mg Cl⁻ · l⁻¹.

In this case, however, the vegetation capture of sea salt particles must be drawn into the picture. By how much should the value 8.4 be increased owing to this process? ERIKSSON (1960, p. 82) has pointed out that the ratio

$$\frac{\text{precipitation-chloride} \cdot l^{-1}}{\text{riverwater-chloride} \cdot l^{-1}} = \text{about } 0.32$$

for the densely wooded countries Sweden and Finland. "Multiplying rainwater chloride amounts by *three* can therefore be expected to give a fair estimate of the total amount of Cl⁻ brought to the ground" (ERIKSSON loc. cit.).

This rule, applied to the precipitation of the environment of Grane Langsø, yields the result 13.8 mg $\text{Cl}^{-}\cdot\text{l}^{-1}$ for the groundwater. If this value is used for calculating I_z , we get

$$\frac{770 \cdot 4.6 + I_z \cdot 13.8}{(770 - 450) + I_z} = 11.3$$
$$I_z = 30 \text{ mm}$$

According to equation (3) on p. 12 the sub-lacustrine outlet then becomes

$$O_z = 30 + 320 = 350$$
 mm.

As the mean depth of Grane Langsø is 7100 mm, the *water renewal rate should be about 20 years*.

This is a slow rate of replacement. BERG (1938, p. 19) has estimated the water renewal rate of Esrom Sø to 7.5 years on condition that the annual evaporation from the lake surface is 780 mm. If Aslyng's evaporation value of Søndersø, 600 mm, is employed, the renewal rate becomes 8.5 years. A similar renewal rate, about 8 years, was calculated for Cayuga Lake by HENSON, BRADSHAW, and CHANDLER (1961, p. 16– 17). It should be emphazised, however, that Grane Langsø is a typical seepage lake, while Esrom Lake and Cayuga Lake are drainage lakes.

The groundwater from the Højvang well, previously mentioned, has been analysed as to CI^- . According to Mr. HANS MATHIESEN, Master of Science, to whom I am indebted for the analysis, the chloride quantity amounted to 11.6 mg $CI^- \cdot 1^{-1}$.

It may be a matter of chance that this groundwater, removed 650 m from the lake, exhibits the same Cl⁻ concentration as Grane Langsø. The conformity may, however, also be due to a groundwater stream, moving from the environment of Hampen Sø through Grane Langsø and the Højvang well to Kulsø, as mentioned on p. 11.

The reasons why the chloride quantity of the Højvang ground water does not rise to about $3 \times 4.6 \text{ mg} \cdot 1^{-1} = 13.8 \text{ mg} \cdot 1^{-1}$ probably are to be sought for in one fact, that ERIKSSON advanced his rule on the basis of an analytical material originating from a densely forested region. Such areas as stratified drift and sandy moraine covered with heaths, moorland fields, and coniferous plantations must be poorer devices in the capture of airborne salts than densely wooded countries such as Sweden and Finland, as the coniferous forests are able to filter a much greater air-volume per time-unit than the other vegetations mentioned. Nr. 2

It is a fact that the leaves of the plants assimilate Na⁺, Cl⁻, and other ions from the captured sea salt particles, Na⁺ at least being a micronutrient. By harvest of the crops on the fields thus i.a. Cl⁻ quantities are removed (cf. Table 14 bis), which in a natural vegetation would be brought down to the ground water partly by rain, partly by decay. This removal is hardly compensated by the insignificant quantities of Cl⁻ present as impurity in the fertilizers. As is evident from table 14 bis below, the substances removed by wood-felling are quantitatively much smaller than those removed by harvest of the agricultural products. This difference probably also holds good for Cl⁻.

JENSEN has given a summary on the average quantities of airborne salts and the salts of the precipitation from 10 Danish stations (1962, p. 905). His Table 14 is translated and reproduced below.

				kg	pr. ha				
Supply	S	Cl	$NO_3 - N$	$NH_3 - N$	Na	K	Mg	Ca	В
Precipitation	13	26	2	5	16	3	3	7	0.03
Air	25	30	?	8	20	3	3	7	?
total	38	56	?	13	36	6	6	14	?
Removal by an average crop									
Corn	10	15	6	50	5	40	7	15	0.012
Root crops	20	15	12	5	10	150	15	90	0.06
Grass	11	40	11	.0	6	100	12	45	0.012
Spruce forest	2	?	2	20	2	3	2	10	?

TABLE 14 bis (after JENSEN 1962).

"From Swedish investigations on the relation between the content of plant food in the air and the precipitation, the quantities of the atmospheric supply to the crop have been computed . . . It should be strongly emphazised, however, that the values stated represent a rough estimate on the average quantities, from which great deviations can be found in special cases" (JENSEN 1962, p. 905).

According to JENSEN'S calculations the ratio between the total supply of Cl⁻ and the Cl⁻ content of the precipitation is $\frac{56}{26}$. Employing this value on the precipitation over the country around Grane Langsø, where the yearly evaporation is 350 mm, we get 56 - 770

4.6 mg Cl⁻·l⁻¹·
$$\frac{56}{26}$$
· $\frac{770}{770-350}$ = 18.2 mg Cl⁻·l⁻¹.

On condition that this value represent the chloride value of the inflowing groundwater, and the evaporation 450 mm from the lake surface is correct, I_z can be computed:

$$\frac{770 \cdot 4.6 + I_z \cdot 18.2}{(770 - 450) + I_z} = 11.3$$

$$I_z = 11 \text{ mm}; \quad O_z = 11 + 320 = 331 \text{ mm}.$$

Under these conditions the water renewal rate should be about 21 years.

The information given above demonstrates that too many unknown or approximately known factors make the results obtained questionable. The reader is invited to consider this section as a preliminary study on the water balance of a lake, devoid of visible affluents and effluents. The problems may be solved when the composition and succession of the various soil strata are eluciated by borings west and east of the lake, measurements of the water level in these borings are made simultaneously with determinations of the levels of Grane Langsø and its neighbouring lakes, and finally seasonal analyses of chloride are carried out concurrently in the borings and lakes.

4. The Carbon Dioxide System

Some recent investigators, e.g. E. NAUMANN, considered the "N and P standards of the water" as primarily responsible for the rate of organic production in lakes. CO_2 , just as vital as N and P, was hardly realized to be a factor of production. It seemed to be tacitly assumed that the lakes had CO_2 enough for their photosynthetic processes. Grane Langsø represents, however, an example of a lake where the CO_2 factor at any rate occasionally acts as a limiting factor in the primary production.

It is a well-known fact that the carbon dioxide system in water consists of the following components: CO_2 , CO_2 aq, HCO_3^- , and CO_3^{--} . Buch (1917) and FAURHOLT (1924) a.o. have shown that a definite interrelation of these components exists, the equilibrium condition being dependent on p_H , ionic concentration, and temperature. The components occur at any pH value, being present, however, in widely different concentrations. Thus in the case of a pH value smaller than 4 the only component of importance is CO_2 . At the pH value 8.4 the HCO_3^- component constitutes nearly 98 per cent of the total quantity of CO_2 . When pH surpasses 12.5, practically only CO_3^{--} is present. The ratio of the concentrations of CO_2 aq to CO_2 is constant at all pH values, amounting to about 3 thousandths (HUTCHINSON 1957, p. 655). FAURHOLT (1924, p. 56) has published graphs which demonstrate this interrelation.

Normally it is possible to determine the amount of total CO_2 is freshwater, if titration alkalinity, pH, and temperature are known. Alkalinity is often determined by titration of a 100 ml sample with N/10 HCl until the pH has fallen to 4.3. According to RUTTNER (1931, p. 208) a deduction of 0.06 ml must be made. The alkalinity 1 is defined by the hydrogen-carbonate content of 1 litre N/1000 Ca(HCO₃)₂, this being 61 mg HCO₃⁻.

STEEMANN NIELSEN (1944, p. 20) finds this titration method unsatisfying and refers to GRIPENBERG's more exact method (1936), which, however, like other titration methods, is applicable only in the absence of humic compounds.

Nr. 2

In KAJ BERG and IB CLEMENS PEDERSEN'S work of the Danish humic Lake Gribsø (1956, p. 130–131) the results of a usual alkalinity titration have been compared with the results obtained with the aid of KROGH and REHBERG'S method. This comparison clearly demonstrates that the alkalinity titration affords far higher HCO_3^- -values than the latter method, which in all probability is safe.

As far as Grane Langsø is concerned, where the quantity of humic substances must be negligible, an analysis from August 9th, 1950 shoved the following results: pH was 5.5, the temperature was measured as 20° C, and the alkalinity titration value amounted to only 0.05 ml of N/10 HCl per 100 ml lake water. If 0.06 ml of N/10 HCl is deducted, the alkalinity must be $-0.01 \cdot 61 \text{ mg HCO}_3^-$ per litre. According to KROGH and REHBERG's method, however, a content of 1.22 mg total CO₂ per litre was found on august 9th, 1950. Employing the equation (4) (p. 44) on this quantity, a HCO₃⁻ content of 0.2 mg per litre was obtained by the pH value and temperature mentioned.

It only remains to say that water from the 11 m subsurface depth always is pale brown just before the vernal and autumnal turn-overs set in. The analytic results referred to, and the occasional occurrence of brown substances, led to a rejection of the titration method in favour of KROGH and REHBERG's technique, even if a single analysis can hardly be performed in less than half an hour.

5. Analytic Methods

By KROGH and REHBERG's method (1930) the total CO_2 , liberated by adding H_3PO_4 to a given volume of sample water, is distilled off in vacuo into a definite volume of baryta water containing 5 per cent of $BaCl_2$, $2H_2O$. By this procedure a part of the $Ba(OH)_2$ is transformed into $BaCO_3$; the remaining part is then titrated with N HCl. A REHBERG micro-burette was used for this purpose, and the titration was finished at a pH value of 8.6–8.8, thymol blue being added as an indicator.

The result required can be computed from the difference between a standardization value (s cmm N HCl) and an analysis value (a cmm N HCl). The standardization is carried out exactly as an analysis, except that 1 ml CO_2 -free water is distilled off instead of 5 ml from a definite volume of the water sample (v ml). As 1 cmm N HCl is equivalent to 0.022 mg CO_2 , the final result must be

$$\frac{(s-a) \cdot 0.022 \cdot 1000}{v} \text{ mg CO}_2 \text{ per litre.}$$

As the quantity of total CO_2 in Grane Langsø normally lies as low as 1–2 mg per litre, the volume (v) of water to be analysed was always fixed at 100 ml. By all analyses and standardizations 0.5 ml M H₃PO₄ and 1 ml CO₂-free water were injected into the flask (Fig. 4, A). The distillation, performed at a temperature of 95–100° C, was continued until a total of about 5 ml was distilled off into the recipient (Fig. 4, D).

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2

One of the many operations which were to be done during the analysis proved very difficult to carry out in a safe manner, unless one is professor August Krogn or professor BRANDT REHBERG. When the glass apparatus has been filled with CO_2 free air to a pressure slightly above the atmosphere, the recipient should be released so much that the capillary tube of a syringe pipette just can be introduced, in order to empty 0.5 ml of baryta water into the recipient. I therefore let a glass-blower mount



Fig. 4. The glass apparatus used for the determination of total carbon dioxide in water after KROGH and REHBERG' method. The glass container with a 100 ml mark on its lowest tube, which can be connected with the tube of B, is not shown. Half natural size.

a small side tube with glass stopper on to the recipient (Fig. 4, E). In agreement with this improvement the capillary tube of the syringe pipette was drawn out to a thickness of only 1 mm (Fig. 4, F). In order to make the ground joints B, C, and E of Fig. 4 airproof, Dow Corning High Vacuum Grease was employed with a satisfying result.

During each visit at the lake, a 600 ml-sample for determination of total CO_2 , a 300 ml- and a 60 ml-sample for pH measurement and counting of the phytoplankton organisms, were taken from each of the following subsurface depths: 0, 2, 4, 6, 8, 10, and 11 metres. For collecting, the water-sampler described in NYGAARD 1958, p. 151 was employed. This apparatus was improved by replacing the wooden operating rod (7 on fig. 4 loc. cit.) and its two wooden sides serving as a shaft bearing, with Perspex acryl material. The water-sampler fills within 40 seconds.

All these samples were collected between 10 and 12 hrs. in Pyrex glass bottles with glass stoppers, all bottles being completely filled without air-bubbles. They were stored at temperatures approximately the same as those encountered during collecting.

The pH measurements and the counts were undertaken a few hours later, but the CO_2 -determinations were carried out two days later in the laboratory in Hillerød. In order to avoid interference through respiration of the plankton organisms, all the 600 ml-samples were acidified by means of 10 drops of concentrated sulphuric acid. The 100.0 ml glass container, placed with the aid of a small piece of rubber tube on the glass-tube of B on Fig. 4, was flushed out with at least 200 ml of sample water. The slow siphoning was carried out with both glass tubes placed at the bottom of the two vessels.

The pH was measured electrometrically by means of the glass electrode. Attempts were made on October 9th, 1960 to determine pH colorimetrically, but the results deviated highly from those obtained with the aid of electrometrical determinations, the colorimetric values being 0.71 pH-unit lower than the electrometric ones. In agreement with this fact the pH of the indicator itself (brom cresol purple) was determined electrometrically as 3.48. The pH of the water from Grane Langsø, poor in buffer substances, consequently cannot be determined colorimetrically. When determining pH of the lake water, I always allowed 30 seconds for stirring (turning) the small cup with the sample water, and the final reading was undertaken after a further lapse of 60 seconds. Experience has taught me that the water from Grane Langsø can alter in pH appreciably after some extremely small contamination. Suspecting this has happened, one must replace the sample in the small cup with intact water from e.g. one of the other bottles, without adding KCl and without rinsing the electrodes with distilled water. This procedure may have to be repeated. After each series of 7 pH-determinations, the buffer adjustment was controlled by means of the initial buffer solution.

The buffer solutions used have been subjected to careful measurements by RADIOMETER's civil engineers, who employed the method for standardizing the pH scale, used by the National Bureau of Standards, USA. The pH-values of these precision buffers are thus in accordance with pH 4.00 of a 0.05 M potassium hydrogenphthalate, a standard buffer solution used also in e.g. Great Britain and France.

6. The Uncertainty of the Analyses

The material of CO_2 determinations available for a statistical analysis consists of many short measuring series, the parameter values ξ of which are dissimilar. The analyses have been made under approximately similar experimental conditions, the accuracy therefore being virtually identical for all of the series. By the method here employed for estimating the standard deviation σ , the value measured directly has not been conceived as the primary variable. As such, however, is regarded the sample sum of squares, computed from any measuring series: $q = (v^2)$. The distribution of q does not depend on the true mean value ξ . The method thus allows us to determine the standard deviation of different measuring series, ξ being dissimilar for any series (ARLEY and BUCH 1958, p. 109).

The results of the theoretical considerations are as follows. One is given m measuring series, each consisting of $n_1, n_2, n_3, \ldots, n_m$ determinations of CO₂. The *m* sample sums of squares are designed $q_1^2, q_2^2, q_3^2, \ldots, q_m^2$, respectively. The *m* measuring series then furnish the respective estimates

for the parameter σ . As the *m* measuring series must be considered mutually independent, we get the best estimate of σ as follows

$$\sigma \approx s = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2 + (n_3 - 1)s_3^2 \dots (n_m - 1)s_m^2}{(n_1 - 1) + (n_2 - 1) + (n_3 - 1) + \dots (n_m - 1)}}$$
$$= \sqrt{\frac{q_1^2 + q_2^2 + q_3^2 + q_4^2 + \dots q_m^2}{n - m}}$$

where $n = n_1 + n_2 + n_3 + \dots + n_m$ or the total number of analyses. The standard error of the standard deviation is computed by

$$\sigma(s) = \frac{s}{\sqrt{2(n-m)}}.$$

For the determination of the standard deviation σ on the analyses of water from Grane Langsø, two series of figures are available:

(1) a fairly large number of analyses in duplicate, originating from the experiments on the productivity of *Nitella flexilis*;

(2) a rather large number of analyses from the circulation periods, when the lake consequently was uniform throughout all levels as to physical and chemical properties. Samples were taken from subsurface depths of 0, 2, 4, 6, 8, 10, and 11 meters.

(3) For the determination of σ of the standardization values originating from titrations of the baryta water with N HCl, several measuring series, normally including 2-4 titrations, are available.

The results of these calculations are:

(1) from the analyses in duplicate (29 series with a total of 58 analyses) there is obtained

$$\sigma_{\text{water sample}} \approx s = 0.23 \text{ cmm N HCl}$$

Nr. 2

which corresponds to 0.0051 mg CO₂ per 100 ml or 0.051 mg CO₂ per litre. σ (s) = 0.03 cmm N HCl.

(2) the determinations from the circulations periods (11 series with a total of 70 analyses) afford the following estimate

$$\sigma_{\text{water sample}} \approx s = 0.22 \text{ cmm N HCl}$$

 $\sigma(s) = 0.02 \text{ cmm N HCl}$

(3) a total of 56 standardizations distributed in 17 series gives

 $\sigma_{\text{standardization}} \approx s = 0.21 \text{ cmm N HCl}$ $\sigma(s) = 0.03 \text{ cmm N HCl}.$

In order to determine the quantity of CO_2 in a water sample, the difference between the standardization value and the analysis value must be found. The standard deviation on a single determination of total carbon dioxide is then

> $\sigma \approx s = \sqrt{(\sigma_{\text{water sample}})^2 + (\sigma_{\text{standardization}})^2} = \sqrt{0.23^2 + 0.21^2}$ = 0.31 cmm N HCl, corresponding to 0.07 mg CO₂ per litre.

This is the standard deviation on analyses of water samples of which 86 per cent contained only 0.27-1.74 mg total $CO_2 1^{-1}$. The standard error of the standard deviation is 0.03 cmm N HCl, equivalent to 0.007 mg CO_2 per litre. Therefore the final result is stated with 2 decimals.

As the calibration of the REHBERG's microburette may be considered approximate, the capillary glass burette was weighed out with mercury of a definite temperature on a balance with an accuracy of ± 0.1 mg. On the basis of the many figures thus obtained, a correction table was prepared for the individual graduations of this microburette, the deviations at most being 0.05 cmm.

The syringe pipette employed to empty 0.5 ml baryta water into the recipient, gave a fairly good accuracy, the standard deviation on a single discharge being 0.16 cmm (n = 28), and the standard error of the standard deviation is 0.03 cmm; the coefficient of variation consequently amounts to 0.03 per cent. The volume 0.16 cmm baryta water is equivalent to 0.05 cmm N HCl, this being about 16 per cent of the standard deviation on a single determination of total CO₂. The accuracy of KROGH and REHBERG's method may be increased, if one can get a more exact syringe pipette of small size. The 5 ml syringe pipette used for oxygen analyses is of great accuracy, exhibiting a coefficient of variation of only 0.006 per cent. This exactitude in connection with photoelectrically controlled titration gives rise to a standard deviation of only 0.024 mg O₂ per litre on a single oxygen analysis by means of the Winkler method; the standard error of this standard deviation is 0.0015 mg O₂ per litre. The 50 ml syringe pipette used for the ¹⁴C-determinations likewise is very exact, having a coefficient of variation as small as 0.004 per cent.

7. Iron and Phosphate in Grane Langsø

The concentration of the ferrous ions was determined colorimetrically by means of dipyridyl dissolved in N/10 HCl (cf. Standard Methods 1946, p. 51–52). One crystal of Na_2SO_3 and one drop concentrated HCl were then added to the test tubes in order to reduce the ferric ions possibly present to ferrous ions. The colorimetric determination by means of an EEL colorimeter was repeated, and the concentration of the Fe³⁺ was found as the difference between the value last obtained and that of the Fe²⁺.

Phosphate as orthophosphate was determined colorimetrically by DENIGES'S method (Standard Methods 1946, p. 80); the comparison of the samples and standards was made 20 minutes after their preparation, however.

The vertical distribution of the ferrous and ferric ions was determined merely on June 26th, 1951. As shown in Fig. 5 it was not possible to detect any Fe²⁺ in the lake, and the quantity of Fe³⁺ was very small, amounting to $0.005-0.01 \text{ mg} \cdot \text{l}^{-1}$. For the sake of comparison the oxygen graph has been inserted on Fig. 5.

The oxygen saturation was computed on the basis of Table 74 in HUTCHINSON'S great work of 1957 (p. 580). The altitude h of Grane Langsø being 75 m, the pressure P_h at the lake surface has been calculated according to the equation

$$\log P_{h} = \log P_{0} - \frac{273 h}{18421(273 + \theta_{z})}.$$

According to Danmarks Klima (1933, t. I, II, III, and IV) the mean atmospheric pressure, reduced to the sea-level, varied for Grane Langsø between the following values

	January:	761.1 mm
	April:	759.75 mm
	July:	759.35 mm
	October:	759.9 mm
Mean	annual pr	essure $= 759.9$ mm.

 P_0 of the equation mentioned is put equal to 759.9 mm. θ_z stands for the temperatures of the individual water-layers analysed for oxygen. The result required then becomes

$$\frac{[O_2]}{[O_2]_s} \cdot \frac{P_h - p_w}{760 - p_w}$$

where $[O_2]$ is the oxygen quantity, stated as mg l^{-1} , of a given water-layer; $[O_2]_s$ is the oxygen saturation value at the temperature of this water-layer, taken from Table 74 in HUTCHINSON's work, and p_w is the partial pressure of the water vapor at the temperature concerned.

Fig. 5 indicates that Grane Langsø was nearly saturated with oxygen from the surface to a depth of 5 m. A metalimnic oxygen maximum, amounting to about 111
per cent, occurred at a depth of 7 m; the water volume from 7 to 11 m was also supersaturated with oxygen.

As will be shown in a paper to come, the oxygen saturation graphs of Grane Langsø within the period from late May to the beginning of August exhibit a *metalimnic* oxygen maximum in subsurface depths of 8 or 10 m, amounting to 101-126 per cent saturation. The surface water from 0-2 m simultaneously contained quantities of oxygen corresponding to 99-103 per cent saturation, while the hypolimnion usually



Fig. 5. The vertical distribution of the ferrous and ferric ions in Grane Langsø on June 26th, 1951. The other graphs illustrate the variation of temperature, specific conductivity, and oxygen down through the lake.

was supersaturated attaining percentages of saturation from 101 to 117. This oxygen distribution is not identical with what ÅBERG and RODHE call the positive heterograde distribution (1942, p. 192–193), as the hypolimnic saturation values exceed those of the epilimnion.

The large quantities of oxygen in Grane Langso on June 26th, 1951, probably explain why ferrous ions were undetectable on this occasion.

While it was not possible to trace ferrous ions on June 26th 1951, values between 0.01 and 0.03 mg Fe⁺⁺·l⁻¹ were found in the layers from 1 m to 10 m subsurface depths on February 23rd, 1951. At this moment the corresponding oxygen values lay between 73.5 and 93 per cent of saturation (see p. 91).

For the sake of comparison the fluctuations in the vertical distribution of iron in the acid, humic lake Gribsø are given in Table 3. The extremes observed were 0.02 and 2.4 mg total iron $\cdot 1^{-1}$. I made the colorimetric determinations of "total iron"

Nr. 2

by means of ammonium sulphocyanate. The ferrous ions possibly present were beforehand transformed to ferric ions by 30 per cent hydrogen peroxide. The concentration of ferrous ions were afterward determined colorimetrically by means of orthophenantroline-monohydrate and hydroxylamine chloride (Standard Methods 1946, p. 52). The concentrations of Fe^{3+} was found as the difference between the concentrations of "total iron" and Fe^{2+} .

	-	4	- 3	-2		-	1 ci	au + 1
	July 6	August 3	Septe	ember 3	September 17	October 8	Nov. 5	December 3
0 m	0.3	0.02	0.08	(0.05)	0.08 (0.07)	0.14	0.2	0.13 (0.06)
1	0.3	0.02	0.08	(0.05)	0.08(0.07)	0.14	0.2	0.13 (0.06)
2	0.3	0.03	0.09	(0.06)	0.08(0.07)	0.14	0.2	0.13 (0.06)
3	0.3	0.03	0.09	(0.06)	0.08 (0.07)	0.14	0.2	0.13 (0.06)
4	0.3	0.03	0.09	(0.06)	0.08 (0.07)	0.14	0.2	0.13(0.06)
5	0.35	0.15	0.20	(0.15)	0.35(0.25)	0.14	0.2	0.13(0.06)
6	0.35	0.15	0.45	(0.45)	0.75(0.70)	0.14	0.2	0.13 (0.06)
7	0.35	0.25	0.40	(0.40)	0.85(0.85)	0.85	0.2	0.13 (0.06)
8	0.4	0.35	1.0	(1.0)	1.9 (1.9)	2.0	0.2	0.13 (0.06)
9	0.5	0.80	1.8	(1.8)	2.1 (2.1)	2.4	0.2	0.13 (0.06)
10	0.7	1.10	2.1	(2.1)	2.1 (2.1)	2.4	0.23	0.13 (0.06)
11	1.0	1.15	2.2	(2.2)	2.2(2.2)	2.4	0.47	0.13 (0.06)
g iron below one square metre	4.50	3.50	7.	44	9.51	9.76	2.37	1.43
		+2	_	- 1	cive	-	+ 1	+2 $+3$
	Decem 28	ber	January 28	February 25	March 25	April 8	May 4	June 3
0 m	0.09 (0.	.05)	0.15	0.07	0.18	0.15	0.14	0.13
1	0.09 (0.	.05)	0.15	0.15	0.18	0.15	0.14	0.13
2	0.09 (0.	.05)	0.15	0.15	0.18	0.15	0.15	0.13
3	0.09 (0.	.05)	0.15	0.15	0.18	0.15	0.14	0.14
4	0.09 (0.	.05)	0.15	0.16	0.18	0.15	0.15	0.15
5	0.09 (0.	.05)	0.15	0.16	0.18	0.15	0.14	0.18
6	0.09 (0.	.05)	0.15	0.16	0.18	0.15	0.15	0.18
7	0.09 (0.	.05)	0.15	0.16	0.18	0.15	0.14	0.18
8	0.09 (0.	.05)	0.20	0.30	0.18	0.15	0.15	0.19
9	0.09 (0.	.05)	0.25	0.40	0.18	0.15	0.15	0.20
10	0.09 (0.	.05)	0.47	0.45	0.18	0.15	0.15	0.25
11	0.09 (0.	.05)	0.50	0.55	0.18	0.15	0.40	0.34
g iron below one square metre	0.95		2.30	2.55	1.98	1.65	1.73	1.97

TABLE 3. The quantities of iron in lake Gribsø in 1949–50, stated as $mg \cdot l^{-1}$. The values in brackets represent Fe²⁺.

During the stagnation periods an accumulation of iron took place, and analyses in September and October proved this iron to be present principally as ferrous ions, at the end attaining a concentration of 2,4 mg Fe²⁺·l⁻¹. The autumnal circulation, here called *ciau* (cf. p. 50), set in on November 10th, 1949 (\pm 2 days), but the analysis of November 5th indicates a nearly complete circulation before this time. The vernal circulation, here called *cive* (cf. p. 50), occurred on March 12th, 1950, and in the following month the quantities of "total iron" amounted to 0.1–0.2 mg·l⁻¹, just as during the autumnal circulation. *The maxima of Fe²⁺ + Fe³⁺ thus occurred in -1. to* -2. *ciau and -1. cive, while the minima were observed in the circulation periods.*

According to EINSELE's theory (1936) H_2S in the presence of CO_2 is able to reduce some form of precipitated ferric phosphate to ferrous sulphide + ferrous hydrogencarbonate + free, soluble phosphate. This process implies an oxygen-concentration smaller than 0.7 mg $O_2 \cdot l^{-1}$. The quantitative interrelation of the substances mentioned depends i.a. on pH and the H_2S -concentration.

The oxygen-concentration of the bottom layers in eutrophic lakes declines strongly during summer stagnation. Coincidently the quantities of CO_2 and H_2S are rising, although hydrogen sulphide is not necessarily liberated. Conditions are soon established for starting the transformation mentioned, resulting in i. a. an accumulation of phosphate in the bottom layers. Also phosphate ions liberated by decay of the seston under the prevailing anaerobic conditions contribute to the final phosphatequantity just before *ciau*. When circulation sets in, Fe^{2+} is oxidized to Fe^{3+} , which in statu nascendi recombines with phosphate ions to form the nearly insoluble ferric phosphate.

A comparison of Table 3 with Table 4 demonstrates that Gribsø provides a good illustration to EINSELE's theory. This lake is, however, not eutrophic, but mesotrophic in the humic, acid phase.

Lake Gribsø proceeds to phase IV of stagnation (HUTCHINSON 1957, p. 724) as early as -4. *ciau*, as the 11 m water smelled of hydrogen sulphide already on July 15th, 1949. On August 3rd, 1949 the 10 m and 11 m layers contained 0.32 and 0.65 mg H₂S·l⁻¹. In September–October the 8 m and 9 m samples also smelled of H₂S, and even on November 5th, 1949, the 11 m water had a faint smell of hydrogen sulphide.

This gas was determined quantitatively by means of $CdSO_4$, which precipitated the H₂S in the unfiltered water as CdS. After centrifugalization and washing out the cadmium sulphide was treated with a definite volume of "N/100" iodine solution and hydrochloric acid. After reduction of some of the iodine by H₂S to HJ, the remaining iodine was titrated with Na₂S₂O₃ (cf. OHLE 1936, p. 206).

On August 3rd, 1949 the quantity of total CO_2 in the 1 m layer amounted to 2.3 mg·l⁻¹. The 11 m layer contained no less than 21.7 mg total $CO_2 \cdot l^{-1}$, sufficient for the formation of ferrous hydrogen-carbonate. Simultaneously the pH of the 11 m water was 6.25; one month earlier it amounted to only 5.2. The pH of the 11 m layer

increased from 5.15 on June 29th, 1949, to 6.45 on October 29th, 1949 (cf. Table 28 on p. 76). The considerable rise of pH during the summer stagnation period may be a result of the accumulation of ferrous hydrogen-carbonate in the bottom water of lake Gribsø.

The oxygen-content of the 11 m layer had declined to $0.9 \text{ mg} \cdot l^{-1}$ already on June 29th, 1949. On August 3rd, 1949 the 10 m and 11 m layer contained 0.36 and 0.07 mg $O_2 \cdot l^{-1}$, thus less than the critical value 0.7 mg $O_2 \cdot l^{-1}$ (cf. BERG and CLEMENS PETERSEN 1956, p. 127). In the following summer the oxygen was depleted in the bottom layers even as early as July 28th, 1950:

Depth in m	0	1	2	3	4	5	6	7	8	9	10	11
Temperature $\operatorname{mg} O_2 \cdot 1^{-1} \dots$ saturation	20.0 7.97 $90^{\circ}/_{0}$	20.0 8.11 $92^{0}/_{0}$	19.4 8.28 $93^{0}/_{0}$	19.3 8.18 91%	18.5 8.14 89%/0	$ \begin{array}{c c} 11.9\\ 2.34\\ 22^{0}/_{0} \end{array} $	8.6 2.48 $22^{0}/_{0}$	7.3 2.24 19º/0	6.9 0.65 $6^{0}/_{0}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$6.7 \\ 0 \\ 0^0/_0$

The quantity of phosphate in the bottom water of lake Gribso increased concomitantly with the rise of the Fe^{2+} -concentration (cf. Table 3 with Table 4). At the onset of the autumnal circulation the phosphate concentration decreased concurrently with the iron-concentration, no doubt essentially caused by oxidation of Fe^{2+} to Fe^{3+} .

From September 3rd, 1949 to December 3rd, 1949 6.60 g Fe²⁺ per square metre disappeared, being oxidized to ferric compounds. In the same period only 0.458 g PO₄-P per square metre disappeared. Assuming that this phosphorus quantity is transformed into FePO₄, whereby 31 g P is equivalent to 56 g Fe, 0.458 g PO₄-P is able to bind only 0.83 g Fe. By far the greatest part of the 6.60 g Fe²⁺ per square metre consequently was oxidized to $Fe_2O_3 \cdot nH_2O$, which settled on the lake bottom together with a much smaller quantity of $FePO_4$.

Even in very shallow waters the Fe^{2+} concentration can increase and the Fe^{3+} concentration decrease towards the bottom. This is seen from the analyses of July 6th, 1951, from Kattehale Mose, only 1.3 m deep and wind-sheltered:

Analyses of phosphate as orthophosphate were performed monthly in Grane Langsø during one year. Fig. 6 gives an idea of the vertical distribution of phosphate phosphorus during the period from August 1950 to July 1951. The absolute maximum, $7-9 \ \mu g \cdot l^{-1}$, was found in December, at the beginning of the winter stagnation period. As shown in the chapter on the hydrogen ion concentration certain biological processes may take place in Grane Langsø in late November or in the first half of December. The rich bottom vegetation of Nitella is for the most part dying at the end of November or in early December. The release of ions by the decay of this dead material may explain the large phosphate maximum on December 20th, 1951.

One month later the quantities at all levels examined had fallen to the absolute minimum, $1 \ \mu g \ PO_4 - P \cdot l^{-1}$. A re-determination of phosphate in the water samples from January 24th, 1951 yielded the same surprising result. I believe that an uptake of phosphate had occurred by the phytoplankton, the evergreen littoral vegetation of *Littorella*, *Lobelia*, and *Isoetes*, and by the bottom vegetation of *Nitella*, *Drepanocladus* etc.

Surprisingly, relatively large quantities of phosphate, $3-4 \ \mu g \cdot l^{-1}$, were observed at the end of February. Their origin is obscure; it must be admitted, however, that pH behaves similarly. Low pH values were determined only in December and Febru-



Fig. 6. The vertical distribution of phosphate-phosphorus in Grane Langsø during the period August 8th, 1950 to July 20th, 1951.

ary, the two winter months when Grane Langsø contained comparatively large quantities of phosphate.

In late March, when photosynthesis of pelagic algae such as Ankistrodesmus falcatus, and of the benthic charophyte Nitella, had begun in spite of the ice-cover, the phosphate quantity in 1–10 m depth decreased to its autumnal value, $2 \ \mu g \ l^{-1}$. The content of phosphate in the 11 m layer is, however, unknown.

The secondary maximum, $6 \ \mu g \ l^{-1}$, occurred in April, after the vernal overturn. These surprisingly large quantities, present in spite of a strongly increasing photosynthesis implying an uptake of phosphate, may have been supplied by groundwater-streams.

During May and June the phosphate quantities decreased slightly in the intermediate part of the lake and the bottom water, but not in the upper water layers. Productivity determinations by means of the oxygen technique demonstrated the greatest production values of May 23rd and June 26th, 1951 to lie in 7 m and 10 m depth, respectively. The ¹⁴C-determination of the primary production in the same months of 1960 and 1961 likewise indicated the greatest production to take place in either 2–4 m, or 8 m, or 10–11 m, but never in the top layer, depending on the light conditions and the vertical distribution of phytoplankton.

In July the phosphate values have further decreased to $2 \mu g l^{-1}$ in the layers between depths of 1 to 10 m.

In August phosphate increased from $1 \ \mu g \cdot l^{-1}$ in the upper 5 meters to $7 \ \mu g \cdot l^{-1}$ in the 10.8 m layer, in spite of a content of 97 *Uroglena*-colonies $\cdot m l^{-1}$ at this level.

In the circulation period from early September to the beginning of December, about $2 \ \mu g \cdot l^{-1}$ of phosphate was observed throughout the lake.

This review of the phosphate conditions of Grane Langsø suffers from the disadvantage that only a few of the analyses include the 11 m-layer, this layer undoubtedly exhibiting the largest yearly fluctuations of phosphate. On the other hand,

	July 6	Aug. 3	Sept. 3	Oct. 8	Nov. 5	Dec. 3	Dec. 28	Jan. 28	Febr. 25	Mar. 25	Apr. 8	May 4	June 3
0 m	15	3	2	2	7	7	6	6	2	7	1	4	1
1	10	3	1	2	7	6	6	6	3	7	1	2	1
2	9	2	1	2	8	6	6	8	5	6	1	2	1
3	4	2	1	2	9	6	6	8	6	6	1	2	1
4	8	2	2	2	10	6	6	(8)	8	6	1	2	1
5	8	2	4	2	12	6	7	9	10	7	1	2	1
6	10	3	25	2	10	6	7	(10)	10	6	1	2	1
7	10	3	15	50	10	6	7	10	10	7	1	2	1
8	15	25	85	100	10	7	7	(15)	33	7	1	2	1
9	15	70	140	160	10	6	7	20	52	7	1	2	1
10	35	120	160	180	18	6	7	50	82	7	1	2	4
11	70	140	180	210	65	5	7	70	100	7	1	2	9
mg below one square metre	167	304	525	608	140	67	73	182	270	73	11	22	18

TABLE 4. Phosphate-phosphorus of lake Gribsø in 1949–50, stated as $\mu g \cdot l^{-1}$.

	-	1 <i>ci</i>	<i>au</i> +	1 +	2 -	2 -	1 ci	ve +	1 +	2 +	3
	Sept. 12	Oct. 18	Nov. 13	Dec. 12	Jan. 15	Febr. 14	Mar. 8	Apr. 10	May 10	June 11	July 9
0 m	6	6	8	8	4	4	16	11	5	5	8
1	6	6	8	8	7	7	17	11	5	5	8
2	6	6	8	8	7	7	14	11	3	7	7
3	7	5	7	8	10	14	18	12	5	8	11
4	8	5	8	7		(17)		11	5	11	10
5	7		8	8		19		11			(11)
6			7	8		(24)		11			12
7			8	8		28		11			(20)
8			8	7		(49)		11			27
9			8	8		70		11			72
10			9	8		85		11			115
11			8	9		135		11			132
mg below one square metre			87	87		390		121			363

TABLE J. FIIO	sphate	e-phos	phoru	15 01 1	Natien	are m	lose II.	1 1950)-31,	stated	as µ	g·1 .
	. –	1 ci	au +	1 +	2 -	3 -	2 -	1 <i>ci</i>	ve +	1 +	2 +	3
	Aug. 22	Sept. 15	Oct. 13	Nov. 7	Dec. 6	Jan. 9	Febr. 9	Mar. 6	Apr. 7	May 7	June 7	July 6
0 m	3	10	2	2	7	10	1	20	7	1	0	6
$^{1}/_{2}$ m	7	9	2	2	6	10	2	22	7	3	1	6
1 m	12	11	2	2	7	12	1	20	8	12	2	8
mg below one square metre	7.3	9.8	2.0	2.0	6.5	10.5	1.5	21.0	7.3	4.8	1.0	6.5

TABLE 5. Phosphate-phosphorus of Kattehale Mose in 1950–51, stated as $\mu g \cdot l^{-1}$.

the account demonstrates that monthly analyses of Grane Langsø during one year gave values never attaining to $0.01 \text{ mg} \cdot l^{-1}$ of phosphate-phosphorus. This indicates Grane Langsø to be a lake poor in phosphate.

In order to compare the phosphate quantities of Grane Langsø with those of other Danish lakes and ponds, my own analythical *results from lake Gribsø*, *Kattehale Mose, and Frederiksborg Slotssø* have been stated in Tables 4, 5, and 6. The monthly analyses of phosphate in the photosynthetic zone of lake Furesø are published in "Furesøundersøgelser" (KAJ BERG et al. 1958, p. 102).

In Gribsø the greatest quantity of phosphate below one square metre, 608 mg, was measured in October (-2. ciau; probably as a rule in -1. ciau). The second largest, 270 mg, was observed in -1. cive (February). The smallest values, 11 and 18 mg below one square metre, occurred in *cive* +1. (April) and *cive* +3. (June). The fluctuations from year to year can be considerable: in February 1950 270 mg was measured, while in February 1951 390 mg was found; in July 1949 167 mg was observed, in July 1951 no less than 363 mg.

GESSNER (1934, p. 153–154) has demonstrated that humic colloids are able to absorb phosphate ions, a fact which possibly influences the phosphate determinations of Gribsø water by means of DENIGES'S method.

The largest phosphate content of Kattehale Mose, 21 mg below one square metre, occurred in -1. *cive* (March). The largest but one, 10.5 mg, was measured in *ciau* +3. (January). The smallest quantities, 1-1.5 mg, were observed in *cive* +3. (June) and -2. *cive* (February).

Frederiksborg Slotssø exhibited its largest quantities, $2610-2710 \text{ mg PO}_4-P$ below one square metre, in -1. to -2. *cive* (March to April). Great quantities, 2230 mg, were liberated in *ciau* + 3. (November), and, as was the case with Kattehale Mose, also in September: 2460 mg. The minimum, 970 mg, occurred in *cive* +1. (April); the secondary minimum presumably lay in *cive* +3. (June). NYGAARD (1938, t. 7, Abb. 28) pointed out an enormous maximum, 1500 μ g·l⁻¹, in the surface water of Frederiksborg Slotssø on November 16th, 1929. Assuming uniformity of the layers of water on this date, the lake must have contained 7500 mg PO₄–P below one square metre.

29

	с	iau -	- 1 +	2 +	3 +	4 -	- 3 -	2 -	-1 c	ive
	Aug. 18	Sept. 4	Oct. 6	Nov. 3	Dec. 2	Jan. 6	Febr. 6	Mar. 2	Apr. 3	Apr. 14
0.1 m	421	487	312	448	388	305	210	90	220	190
0.5			312	443	388	306	260		219	190
1	420	486	318	440	386	307	315	310	220	192
2	421	487	315	448	389	343	530	525	240	195
3	421	487	315	450	390	457		695	270	198
4	432	502	317	446	387	592		635	695	195
5	429	499	314	449	389	610		1000	2150	192
g below one square metre	2.12	2.46	1.58	2.23	1.94	2.17		2.71	2.61	0.97
			+	1		+2				+
	Ap 2	ril 5	May 3	May 15	N	1ay 26	June 4	Jui 18	ne 3	July 2
0.1 m	1	27	135	130		156	123	18	34	299
0.5	1	27	135	130		161	123	19	90	299
1	1	27	141	130		165	135	21	18	301
2	1	29	151	132		203	207	20	50	310
3	1	42	168	131		267	267	35	50	325
4			425				348			
5			845				920			
g below one square metre			1.38				1.48			

TABLE 6. Phosphate-phosphorus of Frederiksborg Slotssø in 1950–51, stated as $\mu g \cdot l^{-1}$.

NYGAARD (1938, p. 553, 624, and 639) compared his regular investigations on phosphate in 14 North Zealandic ponds both between the ponds and with British, American, German, and Japanese investigations. The result was a jumble of maxima and minima occurring in any month of the year, but in the greatest part of the localities the maximum or maxima lay in the periods November–March or June–September.

In Lyngby Sø, 2.8 m deep and permanently alkaline, SIGURD OLSEN (1955, Fig. 43 on p. 98) demonstrated the greatest quantities of phosphate in the period November-March, amounting to as much as $300 \ \mu g \cdot l^{-1}$ in March.

Summarising the results from Grane Langsø and the Tables 4–6, it is necessary to realize that phosphate in lakes and ponds can be bound and liberated in two quite different ways: (1) by assimilation and decay of hydrophytes and phytoplankton, (2) by transformation to ferric phosphate by means of Fe^{3+} , and liberation when this solid is retransformed to ferrous hydrogenearbonate.

The survey given in Table 7 demonstrates that the phosphate-maxima lay in -1. cive (February and March) and ciau + 3. to + 4. (November, December, and January).

	Maxima	Minima
Gribsø	- 1. cive (February) - 1. to - 2. ciau (October to November)	cive+ 1. (April)cive+ 3. (June)
Kattehale Mose		- 2. cive (February) cive + 3. (June)
Frederiksborg Slotssø		cive 1. (April) cive + 3. (June)
Grane Langsø	$\frac{cive + 1. \text{ (April) !}}{ciau + 4. \text{ (December)}}$	- 3. cive (January)

TABLE 7. The occurrence of maxima and minima of phosphate in four Danish waters.

Gribsø and Kattehale Mose, both rich in iron, normally exhibited one of their maxima in -1. ciau (September and October).

The phosphate minima normally occurred in cive +1. (April) and +3. (June). One more minimum was observed in several of the localities in question: about one month after the maximum within the period November to January the phosphatequantity declined strongly. This decrease was observed in Grane Langsø (1951), Kattehale Mose (1951), Frederiksborg Slotssø (1929), and Lyngby Sø (1945–46, SIGURD OLSEN loc. cit.). The reason is obscure, but may be that the submerged vegetation secures a supply as soon as phosphate is available.

8. The Specific Conductivity of Grane Langsø

The survey below shows that the *values of specific conductivity fluctuate between* 48 and 57, in most cases only between 48 and 51 reciprocal megohms. When water is freezing it liberates its ions to the water below the ice. This fact explains the values of 55 and 54 on January 18th and February 8th, 1959, respectively. In 1958 the lake was ice-covered, however, to the middle of April. The fairly low value of 48 below the ice on April 5th must in this case be due to melting of the underside of the ice.

During winter stagnation a small increase of the ion concentration in the bottom water takes place, especially during a long ice-cover. A similar increase is not observed during the summer stagnation period. On August 24th, the end of the summer stagnation of 1958, the bottom water contained large quantities of CO_2 and HCO_3^- , larger than those at the end of winter stagnation. This increase of HCO_3^- is evidently too small to influence the specific conductivity. The consumption of ions by *Nitella* in the summer months, where its growth is largest, may, however, counteract an accumula-

	5. IV ice	2. V	26. V	18. VI	15. VII	24. VIII	28. IX	23. X	23. X I	29. XII	18. I ice	8. II ice	26. 111
0 m	48	48	48	49	51	51	49	49	50	50	55	54	49
2	51	48	48	49	51	51	49	49	50	50	50	50	49
4	51	48	48	49	51	51	49	49	50	50	50	50	49
6	51	48	48	48	51	51	49	49	50	50	50	50	49
8	51	48	48	48	50	51	49	49	50	50	50	50	49
0	53	48	48	48	49	51	49	49	50	50	52	51	49
11	57	48	48	48	49	51	49	49	50	50	53	52	49

TABLE 8. Specific Conductivity of the water from Grane Langsø, given as $\varkappa_{20} \cdot 10^6$. April 5th, 1958 to March 26th, 1959.

tion of ions in the bottom water, originating from the exchange between water and mud. During winter stagnation the *Nitella* association decays greatly, and no photosynthesis has been observed of the remaining individuals. Consequently an accumulation of ions from mud and decaying *Nitella* material must take place in this period, causing a slight rise in the specific conductivity.

Which ions constitute this specific conductivity of about 50 reciprocal megohms? A quantitative analysis of the most important ions in the lake water was carried out in August 1950 and December 1961. I am indebted to Mr. WERNER CHRISTENSEN, Department Geologist to the Geological Survey of Denmark for the latter analysis.

The quanties of Na⁺, K⁺, Ca⁺⁺, Mg⁺⁺, SO₄⁻⁻, Cl⁻, and PO₄⁻⁻⁻ were determined according to Standard Methods (1946, p. 62, 64, 60, 61, 83, 73, and 80, respectively). $[NH_4^+]$ was measured colorimetrically by the Nessler reagent, $[NO_3^-]$ colorimetrically by diphenylamine dissolved in sulphuric acid, while $[H^+]$ and $[HCO_3^-]$ were calculated from the analyses of total $CO_2 \cdot l^{-1}$. Several litres of unfiltered surface water were concentrated to one tenth by evaporation in a quartz evaporating dish in order to obtain a reasonable concentration of the seven ions first mentioned. The slight discrepancy between the equivalent content of anions and cations is due to uncertainties

	Cations		Anions					
	August 1950	December 1961		August 1950	December 1961			
Na ⁺	6.0 mg·l ⁻¹	6.3 mg·l ⁻¹	$SO_4^2 -$	8.3 mg·l ⁻¹	5.6 mg · l ⁻¹			
K+	0.46 -	0.75 -	Cl-	10.9 –	11.6 –			
Mg^{2+}	1.1 –	0.68 -	HCO ₃	0.2 –	0.2 -			
Ca^{2+}	1.84 -	3.6 –	NO ₃	0 –	0 –			
NH_4^+	0 –	0 –	$PO_A^3 -$	$1 \mu g \cdot l^{-1}$	0 -			
H ⁺	$10^{-5\cdot 5} { m g} \cdot l^{-1}$	$10^{-5.5} \text{ g} \cdot l^{-1}$						

TABLE 9. The most important ions of Grane Langsø.

on the analytic values; further, all the ions present are not included in the investigation. HUTCHINSON (1957, p. 554) thinks that the discrepancy may be due i.a. to cations being held by organic matter.

	Cations		Anions					
	August 1950	December 1961		August 1950	December 1961			
Na ⁺	0.261	0.274	SO ₄ ²⁻	0.174	0.117			
K+	0.012	0.019	C1-	0.307	0.327			
Mg^{2+}	0.090	0.056	HCO ₃	0.003	0.003			
Ca^{2+}	0.092	0.180	NO ₃	0	0			
NH^+_{4}	0	0	PO ³ -	0	0			
H+	0.003	0.003						
Total	0.458	0.532	Total	0.484	0.447			

TABLE 10.	The	most	important	ions	of	Grane	Langsø	given	as	milliequivalents
				p	er l	litre.				

 $\begin{array}{l} \text{August 1950} \left\{ \begin{matrix} 0.458 \text{ millieq. cations} \cdot l^{-1} \\ 0.484 \text{ millieq. anions} \cdot l^{-1} \end{matrix} \right\} 0.94 \text{ millieq. ions } l^{-1} \\ \text{December 1961} \left\{ \begin{matrix} 0.532 \text{ millieq. cations} \cdot l^{-1} \\ 0.447 \text{ millieq. anions} \cdot l^{-1} \end{matrix} \right\} 0.98 \text{ millieq. ions } l^{-1}. \end{array}$

It is possible by a calculation to check the specific conductivity of the lake on the basis of the August analysis from 1950.

The contribution yielded by the individual ion to the specific conductivity can be computed from the equation

$$\varkappa_i = \Lambda^i_{\mathrm{mol}} \cdot \frac{c_i}{1000}$$

where z_i is the contribution of the ion to the specific conductivity, Λ_{mol}^i is the molar conductance of the ion, and c_i the molar concentration of this ion. If the equivalent conductance is employed, defined by

$$\Lambda_{\rm eq}^{i} = \frac{1}{z_{i}} \cdot \Lambda_{\rm mol}^{i}$$

where z_i is the number of positive or negative charges of the ion, the question above gets the form

$$\varkappa_i = \Lambda_{eq}^i \cdot z_i \cdot \frac{c_i}{1000} = \Lambda_{eq}^i \cdot \frac{n_i}{1000}$$

where n_i is the "normality" of the ion in question.

Biol. Skr. Dan. Vid. Selsk. 14, no. 2.

33

3

i	c_i	z_i		
1.84 mg Ca ²⁺ per l	$46 \cdot 10^{-6}$	2	$92 \cdot 10^{-6}$	
1.1 mg Mg ²⁺ per l	$45 \cdot 10^{-6}$	2	$90 \cdot 10^{-6}$	
6 mg Na ⁺ per 1	$261 \cdot 10^{-6}$	1	$261 \cdot 10^{-6}$	
0.46 mg K ⁺ per 1	$ 12 \cdot 10^{-6}$	1	$12 \cdot 10^{-6}$	
10.9 mg Cl ⁻ per l	$ 307 \cdot 10^{-6}$	1	$307 \cdot 10^{-6}$	
8.3 mg SO_4^{2-} per l	$ 87 \cdot 10^{-6}$	2	$174 \cdot 10^{-6}$	
0.2 mg HCO ₃ per l	$3 \cdot 10^{-6}$	1	$3 \cdot 10^{-6}$	
0.003 mg H ⁺ per l	$3 \cdot 10^{-6}$	1	$3 \cdot 10^{-6}$	
$arLapha^i_{ m eq}$ (25° C)	2	κ_i		
Ca ²⁺ 59.5	$59.5 \cdot 10^{-3} \cdot 92$	$10^{-6} = 5.45 \cdot 1$	0-6	
Mg^{2+} 53.0	$53.0 \cdot 10^{-3} \cdot 90 \cdot$	$10^{-6} = 4.77 \cdot 1$	0 - 6	
Na ⁺ 50.1	$50.1 \cdot 10^{-3} \cdot 261 \cdot$	$10^{-6} = 13.00 \cdot 1$	0-6	
K ⁺ 73.5	$73.5 \cdot 10^{-3} \cdot 12$	$10^{-6} = 0.88 \cdot 1$	0 - 6	
Cl – 76.3	$76.3 \cdot 10^{-3} \cdot 307 \cdot$	$10^{-6} = 23.30 \cdot 1$	0 - 6	
SO_4^{2-} 80.0	$80.0 \cdot 10^{-3} \cdot 174$	$10^{-6} = 14.00 \cdot 1$	0-6	
HCO_{3}^{-} 44.5	$44.5 \cdot 10^{-3} \cdot 9 \cdot$	$10^{-6} = 0.13 \cdot 1$	0-6	
H^+ 350.0	$350.0 \cdot 10^{-3} \cdot 3 \cdot$	$10^{-6} = 1.05 \cdot 1$	0 - 6	

TABLE 11. Calculation of the specific conductivity of Grane Langsø on August 1950.

 $\Sigma \varkappa_{25} = 62.6 \cdot 10^{-6}$

The equivalent conductance values of the ions referred to are cited from K. A. JENSEN (1959, p. 682). The specific conductivity of Grane Langsø has thus been calculated to 62.6 reciprocal megohms by a temperature of 25° C.

As the conductivity decreases by about 2 per cent for each degree by which the temperature falls, it amounts to about $56.7 \cdot 10^{-6}$ at 20° C, a value in reasonably good agreement with those commonly measured by means of the Dionic Water Tester. A corresponding calculation, based on the December analysis from 1961, yielded the result \varkappa_{20} = about 58 reciprocal megohms.

As to the diagrams of Fig. 7, I can inform the reader that the ionic diagram representing seawater has been constructed on the basis of Tabelle 14 in MAUCHA's work of 1932 (p. 86). According to this table the HCO_3^- amounts to 0.41 per cent of the total anion quantity in the Adriatic, no CO_3^{--} , however, being stated. Seawater normally contains about 45 ml \cdot l⁻¹ of total CO₂. Provided that the salinity is 3.5 per cent, the temperature 15° C, and pH 8.2, the ratio of HCO_3^- to CO_3^{--} is 85 to 15. Of the 45 ml total $CO_2 \cdot l^{-1}$, 0,3 ml is present as 0.6 mg free $CO_2 + CO_2$ aq, while 38 ml are confined to 103.5 mg HCO_3^- , and 6.7 ml are bound as 17.9 mg CO_3^{--} , cf. STEE-MANN NIELSEN (1944, p. 11). MAUCHA's figure may represent the total CO_2 converted to HCO_3^- .

The analyses of the most important ions demonstrate *Grane Langsø to be a sodium* chloride lake, contrary to most of the Danish lakes, which can be characterized as

34

calcium hydrogen-carbonate lakes (RODHE 1949, p. 378). The ionic diagrams of Grane Langsø (see Fig. 7) exhibit a striking resemblance to that of seawater, the equivalent percentages of K⁺, Na⁺, Mg²⁺, Cl⁻, HCO₃⁻ and CO₃²⁻ being of the same order of size. In two respects there are marked differences, however, the equivalent percentages of SO_4^{--} and especially Ca^{++} in Grane Langsø are far greater than the corresponding ones of seawater.

All the surface water and ground water of the continents have once been rainwater. The aqueous vapours, which become condensed to precipitation, are contained in winds from the oceans and the continents. The evaporation of the oceans is greater than the precipitation over them. In exorheic regions, however, the evaporation is smaller than the precipitation, the surplus of the latter being converted to rivers. As about 70 per cent of the earth surface is covered by the seas, the greatest part of the global precipitation is of oceanic origin.

Besides the aqueous vapours the maritime winds also carry minute, hygroscopic particles of sea salt, called condensation nuclei, over the continents. Breaking waves produce great quantities of air-bubbles in the sea-surface; when these bubbles burst, minute droplets are emitted into the air. Raindrops and snowflakes striking the ocean surface produce very small air-bubbles, which burst and give off extremely small particles. After arriving in the atmosphere the diameter of these particles are reduced by evaporation; the speed of falling is accordingly decreasing.

The Swedish investigator ERIK ERIKSSON, who has made a close study of the subject in question, estimates the airborne salts to be produced over the oceans with a rate of about 1080 mill. tons per years (1959, p. 397). As about 180 mill. tons per year of airborne salts return to the oceans by rivers (ERIKSSON 1960, p. 72, table 4.5) and an unknown quantity by the ground water, at most 80 per cent of the 1080 mill. tons of airborne salts fall out over the oceans themselves.

The sea salt particles are removed from the atmosphere by three processes: deposition by dry fallout, wash-out by rain, and their capture by the vegetation.

ERIKSSON (1959, p. 397) estimates the sinking velocity of the airborne salts to be about 1 cm per second over the seas, and about 2 cm per second over land.

Small obstacles, as e.g. grass-leaves and spruce needles, have proved effective in the capture of condensation nuclei from moving air (ERIKSSON 1955, p. 245). The effectiveness of this capture increases with increasing wind velocity and decreasing radius of the obstacle. The accretion of the hygroscopic airborne salts, which are said to be washed down by rain (see p. 15, however), may be a selective process. ERIKSSON is of the opinion that only giant condensation nuclei, of radii greater than 1μ , are large enough to be captured by pine and spruce needles. These nuclei are mostly NaCl-particles. He admits, however, that ions other than Na⁺ and Cl⁻ are captured by coniferous forests, citing in support TAMM's investigations (1953, p. 88–90). This author found much more Ca⁺⁺ and K⁺, and up to 3 times more Na⁺, in rain water percolating through the outer part of a spruce tree crown than in rain water simultaneously collected in the open. This obvious difference was observed merely at the onset of



Comparing the ion diagrams of Grane Langsø with those of the Borris and Ødum rainwater on Fig. 7, it is evident that the SO_4^{--} mval-percentages of rainwater surpass those of the lake. The chloride percentages are, however, smaller than those found in Grane Langsø. The diagram of the airborne salts from Ødum is markedly dominated by SO_4^{--} .

If the Borris rain and Ødum rain is supplied with Cl⁻, their mval-percentages of Cl⁻ of course will rise, and the SO₄⁻⁻-percentages consequently decrease. According to ERIKSSON (1955, p. 246) the vegetation capture of condensation nuclei is a selective progress, by which essentially NaCl-particles are captured. On condition that especially the airborne chlorides are captured by the coniferous forests, and that a great part of this accretion is washed out into the lake by rain, we have an explanation of the fact, that the chloride percentage of Grane Langsø is greater than that of the rain, and its SO₄⁻⁻-percentage in consequence is smaller than the corresponding one of rainwater.

How much are the individual ion concentrations increased owing to the concentrating effect of the evaporation and the addition of airborne salts and soil substances? In order to get some understanding of this problem, the ion concentrations of two of the British lakes examined by GORHAM (1957, p. 174) are placed in Table 12, together with the ion concentrations of Grane Langsø and the rainwater over these three lakes. Further, the ratios of the individual cations and anions of the lake water to the corresponding ions of the rainwater are given in Table 13.

In Newton Mere an abundant growth of the green alga *Gloeococcus Schroeteri* takes place as in Grane Langsø, whereas Crose Mere, which is mentioned merely as an example of the hydrogen-carbonate type, is characterized by dense water blooms of bluegreen algae.

	K+	Na+	Ca ²⁺	Mg ²⁺	SO_4^{2-}	C1-	HCO ₃	mval- sum	$_{\rm pH}$	$\begin{matrix} \varkappa_{20} \cdot 10^6 \\ (\text{com-} \\ \text{puted}) \end{matrix}$	Ca Mg	$\begin{vmatrix} \mathbf{K} + \mathbf{N}\mathbf{a} \\ \mathbf{C}\mathbf{a} + \mathbf{M}\mathbf{g} \end{vmatrix}$
Lake District												
rain	0.005	0.083	0.015	0.016	0.066	0.092	0	0.309	4.5	27	0.94	2.84
Newton Mere .	0.205	0.360	0.365	0.130	0.325	0.440	0.275	2.100	6.8	121	2.81	1.14
Crose Mere	0.145	0.490	3.400	0.700	1.060	0.580	3.040	9.465	8.1	488	4.86	0.15
Borris rain												
(3 years)	0.013	0.146	0.046	0.044	0.128	0.169	0.0001	0.646	4.6	46	1.04	1.78
Ødum rain												
(6 years)	0.010	0.092	0.047	0.032	0.109	0.099	0.0019	0.480	4.82	33	1.44	1.29
Grane Langsø												
(August and	0.012	0.261	0.092	0.090	0.174	0.307	0.003	0.94	5.5	57	1.02	1.24
December	0.019	0.274	0.180	0.056	0.117	0.327	0.003	0.98	5.5	58	3.21	1.50

TABLE 12. Important ions of three lakes and the rain over them, stated as $mval \cdot l^{-1}$.

	K^+	Na ⁺	Ca ²⁺	Mg ²⁺	SO42-	Cl-	HCO ₃
Newton Mere							
Lake District rain	41	4.3	24.4	8.1	4.9	4.8	∞
Crose Mere							
Lake District rain	29	5.9	226.7	43.8	16.1	6.3	∞
Grane Langsø (average)							
Borris rain	1.2	1.8	3.0	1.7	1.1	1.9	30
Grane Langsø (average)							
Ødum rain	1.6	2.9	2.9	2.3	1.3	3.2	1.7

TABLE 13. The proportions between the ion concentrations, given as $mval \cdot l^{-1}$, of the 3 lakes and their corresponding precipitation.

The specific conductivity values, computed for the British localities, do not include the NH_4^+ and NO_3^- ions; therefore the value of 27 reciprocal megohms is nearly at a lower limit of the true value for the Lake District rain.

It is evident from Table 13 that Grane Langsø is far less changed than is Newton Mere, in comparison with the rain over them. The ion concentrations of the latter (apart from HCO_3^-) are 4.3–41 times as much as those of the Lake District rain, while the ion concentrations of Grane Langsø are only 1.1–3.2 times increased in relation to the corresponding concentrations of the Borris rain and Ødum rain. The ratio of lake- HCO_3^- to rain- HCO_3^- is also much greater for Newton Mere than for Grane Langsø.

The specific conductivity of Newton Mere is 4.5 times as great as that of the Lake District rain, whereas the specific conductivity of Grane Langsø is only increased by the factor 1.25–1.75 in relation to the specific conductivity of the Borris and Ødum rain (see Table 12). The ratio of the alkali metals to the alkaline earths can be influenced by adsoption and ion exchange of the various colloids confined to the bottom sediments. This ratio alters greatly from the Lake District rain to Newton Mere; the values of Grane Langsø and the rain water over Borris and Ødum are, however, of the same order of size.

Table 14 should demonstrate the percentages by which the individual constituents of Grane Langsø have been increased in proportion to the corresponding elements of the Borris and Ødum rain, due to evaporation and addition of airborne salts, atmospheric dust, and soil substances.

It is obvious that the concentrations of K^+ and especially SO_4^{2-} are slightly changed, while those of Na⁺, Cl⁻, Mg²⁺, Ca²⁺ are increased with a factor of about 2–3. These facts prove that the rise in the concentration is not merely a result of evaporation of the rain water in question. Several factors interfere in this evaporation process, e.g.

(1) selection of ions in the rain water by the individual plant communities around the lake,

	A rough estimate of the mean lake-value in proportion to the Borris and Ødum rain-values	Increase expressed in percentages of the concentrations in the Borris and Ødum rain
Na ⁺	2-3 times the amount	$190^{0}/_{0} > increase > 84^{0}/_{0}$
K ⁺	somewhat larger	$57^{0}/_{0} > increase > 17^{0}/_{0}$
$Mg_2^+ \dots$	twice the amount	$125^{0}/_{0} > increase > 66^{0}/_{0}$
Ca ₂ ⁺	threefold the amount .	$198^{0}/_{0} > increase > 191^{0}/_{0}$
SO_4^{2-}	slightly larger	$33^{0}/_{0} > increase > 13^{0}/_{0}$
Cl ⁻	2–3 times the amount	$220^{0}/_{0} > increase > 87^{0}/_{0}$
$HCO_3^- \dots$	multiple amount	$2900^{0}/_{0} > increase > 67^{0}/_{0}$

TABLE 14. The increase of ion concentrations from the Borris and Ødum rain considered as a transformation to Grane Langsø water.

- (2) weathering processes of e.g. FeS_2 and $KAlSi_3O_8$ in the soil,
- (3) influence of the sulphur bacteria and the sulphate-reducing bacteria on the SO_4^{2-} concentration,
- (4) fixation of cations to colloidal clay minerals in about 18 m subsurface depth, by which the affinity is decreasing in the order H⁺, Ca²⁺, Mg²⁺, K⁺, NH₄⁺,
- (5) ion exchange by means of e.g. humic acids in the soil,
- (6) ion adsorption to the neutral humus of the lake sediments,
- (7) selective vegetation capture by impingement of airborne sea salt particles,
- (8) fallout of atmospheric calcareous dust.

The importance of each individual factor is unknown, but Grane Langsø represents the final result of the combined effect of the evaporation of rain water and the factor complex mentioned, in which (7) and (8) are believed to be more important than the other factors.

In order to compare the ionic composition of Grane Langsø with that of softwater lakes other than Newton Mere, the individual quantities have been stated as $mval {}^{0}/_{0}$ in Table 15. The figures from the Wisconsin lakes are cited from HUTCHINson (1957, p. 555), and those from the North German lakes originate from OHLE (1955, p. 243).

Grane Langsø has much in common with the North German lakes, i.a. the high percentages of Na⁺ and Cl⁻. This seems quite natural, as both are lying close to the margin of the Würm (Wisconsin) glaciation. The Wisconsin soft-water lakes are hydrogen-carbonate lakes with high figures for Ca^{2+} and Mg^{2+} . Grane Langsø is probably better characterized, however, by the unusually small quantities of HCO_3^- and free CO_2 than by the great percentage quantities of Na⁺ and Cl⁻, because free CO_2 and HCO_3^- highly determine the production of the lake, while Na⁺ and Cl⁻ are merely micronutrients.

In this connection the question may be put: is the deficiency of CO_2 and $HCO_3^$ in Grane Langsø a result of the CO_2 -consumption by the rich and evergreen submerged vegetation and the phytoplankton, or is it a primary character of the lake? As shown

	Na+	K^+	Mg ²⁺	Ca ²⁺	SO_4^{2-}	Cl-	HCO $\frac{1}{3}$
Wisconsin soft water lakes	10.9	4.8	37.7	46.9	20.5	9.9	69.6
North German soft water lakes	43	6.7	14.3	36	14.1	43.5	42.4
Grane Langsø (August 1950	57.2	2.6	19.8	20.2	36.0	63.4	0.6
and December 1961)	51.8	3.6	10.6	34.0	26.2	73.1	0.7

TABLE 15. The mval-percentages of the major constituents in some soft water lakes.

in section 11 the concentration of free CO_2 during the periods of high productivity is so low (smaller than 0.6 mg·l⁻¹ at 20° C), that atmospheric CO_2 diffuses into the lake; at the same time the HCO_3^- concentration is quite insignificant. In winter, however, when the CO_2 consumption of the phytoplankton and the hydrophytes approaches nil, Grane Langsø must also be characterized as a lake poor in CO_2 and HCO_3^- (see Survey of the Analyses). The deficiency of CO_2 and HCO_3^- consequently cannot be explained as a result of photosynthetic processes.

The ground water inflow contains more CO_2 than the rain water, the CO_2 content of ground air being about 0.3–1 per cent (WERNER CHRISTENSEN 1962, p. 113). Mr. HANS MATHIESEN, who kindly determined the Cl⁻ quantity of the Højvang ground water (see p. 14), also determined its alkalinity as 0.4 mval $\text{HCO}_3^- \cdot \text{l}^{-1}$, and its pH as 6.62. This alkalinity corresponds to 24.4 mg $\text{HCO}_3^- \cdot \text{l}^{-1}$. By means of equation (4) on p. 44 the a_{CO_2} at 10° C has been computed as 0.28. On condition that the ionic strenght is very small, the total CO_2 quantity of the Højvang ground water therefore amounts to 12.3 mg free $\text{CO}_2 \cdot \text{l}^{-1} + 17.6$ mg hydrogen-carbonate- $\text{CO}_2 \cdot \text{l}^{-1} =$ about 29.9 mg·l⁻¹, thus greatly surpassing the largest quantity, 14.89 mg total $\text{CO}_2 \cdot \text{l}^{-1}$, ever measured in the lake. The sub-lacustrine influx of ground water is an unknown quantity, as stated on p. 16, but considering i.a. the deficiency of CO_2 and $\text{HCO}_3^$ in the lake, I think that the influx rate is of secondary importance (cf. p. 14).

There are many indications that the very small quantity of $CO_2 + CO_2aq + HCO_3^$ in Grane Langsø may occasionally be a limiting factor for the production of organic matter. The lake is certainly rich in submerged vegetation (see NYGAARD 1958, Table 1 and Fig. 3), but its hydrophytes are all slowly growing species, and I think that they are obliged to be so.

The ratio Ca to Mg of the rain waters included in Table 12 varies from 0.94 to 1.44 in such a way that the lowest values seem to be confined to coastal rain, and the highest to inland rain. HUTCHINSON writes about this (1957, p. 550): "Both Ca and Mg increase with distance from the sea, but the calcium concentration rises more than that of magnesium." The ratio $\frac{\text{Ca}}{\text{Mg}}$ is lowest for Grane Langsø (average 2.11), greater for Newton Mere (2.81), and greatest, of course, for the hydrogen-carbonate lake Crose Mere.

Low values of the ratio $\frac{Ca}{Mg}$ can also be due to Ca^{2+} adsorption by colloidal

humic acids (OHLE 1955, p. 229), a discovery to be reconsidered in detail. The $\frac{Ca}{Mg}$ values of some North German humic lakes, poor in calcium, amounted to only 0.3–1.2, while the values of the clear water lakes, rich in calcium, lay between 3.6 and 9.8 (OHLE 1955, Tab. 8).

The North German lake Kleiner Ukleisee normally contains

Cations	$mval \cdot l^{-1}$	$mval 1^0/_0$
Na	0.199	63.4
K	0.047	15.0
Са	0.037	11.7
Mg	0.031	9.9

The ratio $\frac{\text{mval Ca}}{\text{mval Mg}} = 1.2$, and the ratio $\frac{\text{mval Na} + \text{K}}{\text{mval Ca} + \text{Mg}} = 3.6$. The latter value is exceptionally high, when one considers that the ratio of alkali metals to alkaline earths amounts to 1.29-2.84 for rain water, according to Table 12.

Professor W. OHLE, to whom I am indebted for this piece of information, further writes in his letter to me that a strong vernal influx of groundwater can change the ionic composition of the lake water considerably. The ratio $\frac{Na + K}{Ca + Mg}$ of the groundwater amounted to 0.69 owing to its great calcium concentration. By admixture to the lake water the analytical values of the litoral water were

Cations	$mval \cdot l^{-1}$	mval ⁰ / ₀
Na	0.221	46.1
K	0.051	10.7
Са	0.185	38.6
Mg	0.022	4.6

These results, partly stated in OHLE's paper from 1955 (Tab. 9), involve the mval-ratios $\frac{Ca}{Mg} = 8.4$ and $\frac{Na + K}{Ca + Mg} = 1.32$. When the increased inflow of groundwater to the lake Kl. Ukleisee has stopped, the ratio $\frac{Ca}{Mg}$ decreases to its normal value of 1.2, and the ratio $\frac{Na + K}{Ca + Mg}$ increases to about 3.6, both changes being the result of the Ca⁺⁺ adsorption by humic acids.

None of the Swedish lakes, investigated by LOHAMMAR, can be described as a sodium chloride lake (LOHAMMAR 1938). Högfjärden and Gärdefjärden certainly contain more Na⁺ than Ca²⁺, but the SO_4^{2-} quantity is three times the chloride-quantity (LOHAMMAR 1938, p. 161–162). RODHE (1949, p. 378) considers these two lakes as representatives of the sulphate type.

There is a possibility, however, that some Swedish lakes examined by QUENNER-STEDT (1955) may be characterized as sodium chloride lakes. Unfortunately QUENNER-STEDT has not quantitatively determined the anions of his lakes, which are extremely poor in ions. The specific conductivity of Resemejaure is 3.7 reciprocal megohms, thus nearly the same as that of distilled water. The Lobelia-Isoetes lake Bergsjön (QUENNERSTEDT 1955, p. 128), with a specific conductivity of nearly 10 reciprocal megohms, contained per litre 1.02 mg Na⁺, 0.16 mg K⁺, 0.38 mg Ca²⁺, and 0.32 mg Mg²⁺. This lake should possibly be classified as a sodium chloride lake like the Danish Lobelia-Isoetes lake Grane Langsø.

Ohle's paper, cited above, on the ion exchange of the bottom sediments of two lakes in North Germany, is instructive and of considerable importance. The *acid "Laubdy*" of Kleiner Ukleisee (pH of the lake water 5.85) contains great quantities of humic acids. Besides being able to liberate H⁺, they possess a *strong and selective capacity for exchanging* H⁺ *with* Ca⁺⁺. Simultaneously with this Ca⁺⁺ adsorption an equivalent quantity of HCO₃⁻ is transformed to $CO_2 + H_2O$ with the aid of H⁺ from the humic acids. The magnesium ions were not affected by this process, in Ohle's opinion because in Kl. Ukleisee they are confined to Cl⁻, perhaps to SO₄⁻⁻. An allochthonous addition of humic acids to a lake consequently results in a decrease of Ca⁺⁺. *The gradual accumulation of "Laubdy" gives rise to an autochthonous deficiency in calcium* (Ohle 1955, p. 240).

The specific conductivity of Kl. Ukleisee is 52 reciprocal megohms (OHLE 1959, p. 21, Tab. 5), thus nearly the same as that of Grane Langsø, but its alkalinity, 0.14 mval $\text{HCO}_3^- \cdot l^{-1}$, is much higher than the alkalinity values of Grane Langsø, 0.002 – 0.01.

Decaying leaves play no part in the bottom sediments of Grane Langsø, which show an ignition loss of only about 10 per cent. According to KAJ HANSEN (1959, p. 40-41) the humus of these sediments is neutral; the calcium content is low, 0.6-0.8 per cent. It would appear that the fixation of Ca⁺⁺ is of minor importance in Grane Langsø itself, but may be significant in the soil of the coniferous plantations and moorland areas around the lake. It is, however, for many reasons impossible to elucidate this influence at present, i.a. because the sublacustrine influent to the lake is an unknown quantity.

The adsorption of Ca^{++} to acid humic compounds is important, however, for the understanding of the changes which took place in the *Danish lake Gribso during the postglacial period*. The qualitative composition of the diatom flora in the Atlantic Period is indicative of an alkaline reaction of the lake water; the finding of leaf-apices of the rapidly growing hydrophyte *Ceratophyllum demersum* supports this assumption (NYGAARD in BERG and CLEMENS PETERSEN 1956, p. 51). Therefore lake Gribsø must have been rich in HCO_3^- in this period, and no doubt an equivalent quantity of Ca^{++} was bound up with the HCO_3^- .

During the first 8 centuries of the Subatlantic Period, which began about 400 B. C., the lake grew more and more acid judging from the pronounced qualitative

alterations of the diatom flora. The presumed deficiency of Ca^{++} in the Sub-atlantic Period was explained by me as a result of a gradual washing-out and an increasing supply of acid humic substances from the raw humus in the forest floor. The investigation by pollen analysis of the core from Gribsø demonstrated that the woods surrounding the lake grew richer in beech at the expense of oak efter 400 B. C.

It is common knowledge that illumination at the beech forest floor is very small, whereas the mixed forests of oak together with other light-demanding trees as e.g. elm and especially ash, give more illumination. The layer of living leaves must consequently be much more compact in the beech forest than in the mixed forest with oak as the characteristic tree. In my opinion, the number of leaves per unit area is increasing as the beech gradually replaces the oak in the mixed forests.

In his brilliant studies on the relation of forest trees to light, BOYSEN JENSEN (1910, p. 21–25) has pointed out that on an average the transmission of light in a beech wood is only 1.8 per cent of the global radiation, whereas an oak wood lets 11 per cent pass through its photosynthetic device. BOYSEN JENSEN writes, in translation (1910, p. 25): "The light quantity absorbed by the tree-top is mainly determined by the quantity of leaves...this quantity being conditioned by their capacity for sustaining shade". The faculty for creating shade-leaves is especially well-developed by the beech.

A woodland lake as Gribsø has, all things considered, probably received a rising quantity of beech leaves when the surrounding forests were increasingly influenced by the beech during the centuries after 400 B. C. The dead leaves on the beech forest floor are presumably more easily carried out in the lake by winds than leaves on the oak forest floor, where the well-developed undergrowth will strongly prevent it (cf. BERG and CLEMENS PETERSEN 1956, p. 13; Figs. 1 and 5).

The intensified formation of "Laubdy" in lake Gribsø contributed in depressing the concentrations of Ca^{++} and HCO_3^- , thus opening the lake for immigration of *Sphagnum*.

One cannot exclude the possibility, however, that the humification of dead beech leaves involves chemical processes which differ essentially from the corresponding processes confined to the humification of leaves from mixed woods.

The decomposition of cellulose in leaves of beech and oak no doubt takes place according to identical chemical patterns. However, the considerable quantities of tannic acid present in oak leaves, as in leaves of heath plants, probably influence the course of the decomposition.

After defoliation the tannic acid and protein combine to form compounds containing nitrogen which is hardly accessible for the soil-microbes. Consequently the bacterial action is highly retarded, and so the formation of raw humus becomes a very slow process. The disintegration of a thick and compact layer of dead beech leaves must, however, also be a very slow process. Whether the decomposition of the leaves of oak and beech takes place similarly in a lake is an open question.

Several Danish woodland lakes situated on sandy morainic deposits have probably

been rich in calcium hydrogen-carbonate at the beginning of the post-glacial period, as the moraine at that time still contained some $CaCO_3$. No doubt the fall of temperature early in the Subatlantic Period intensified the formation of raw humus at the expense of mull formation. The high precipitation, together with atmospheric CO_2 and ground air CO_2 , simultaneously increased the washing-out of lime from the upper layers of the soil, thus preparing the ground for the formation of raised bogs. The concentration of calcium hydrogen-carbonate in the woodland lakes was strongly diminished, partly by washing-out owing to the great precipitation, but especially by ion exchange due to inflow of humic acids from *Sphagnum* bogs near the lakes, and to the increasing quantity of beech leaves in the lakes as the beech spread in the surrounding forests.

9. The Calculation of pH and the HCO_3^- -quantities

As will be seen from sections 12 and 13, pH and $[HCO_3^-]$ have been calculated from the concentrations of total carbon dioxide in Grane Langsø. Referring to HUT-CHINSON's treatment of the chemical equilibria confined to the carbon dioxide system (1957, pp. 655–657), I give the equation which forms the basis of the calculations:

$$\frac{\mathbf{a}_{\mathrm{H}+} \cdot \mathbf{a}_{\mathrm{HCO}_{3}}}{\mathbf{a}_{\mathrm{CO}_{2}}} = \mathbf{K}_{\mathrm{CO}_{2}\mathrm{aq}} \tag{4}$$

(in the following abbreviated to K_{CO_2}), where K_{CO_2} is the product of the hydration constant of carbon dioxide and the first ionization constant of "carbonic acid", and a_{CO_2} is put equal to the activities of CO_2 and CO_2aq . As only about 0.3 per cent of the dissolved CO_2 is present as "H₂CO₃"¹ or rather CO₂aq, the error in setting $a_{CO_2} = a_{CO_2 + CO_2aq}$ at most amounts to about three thousanths within the temperatire interval 0° to 25° C. The standard deviation on total CO_2 values around 1 mg·l⁻¹ amounts to about 7 per cent (cf. p. 21); on values of 10 mg·l⁻¹, very rarely met with in Grane Langsø, it is 0.7 per cent, twice the error in setting $a_{CO_2} = a_{CO_2 + CO_2aq}$.

Concerning the K_{CO_2} -values the reader is referred to the papers of FAURHOLT (1924, p. 55), KURT BUCH et al. (1932, p. 35), SHEDLOWSKY and Mc. INNES (1935, p. 1710), HARNED and DAVIS (1943), HARNED and BONNER (1945, p. 1028), and NÄSÄNEN (1947, p. 208). Table 16 contains the pK_{CO_2} -values within the temperature interval commonly met with in lakes. The calculations in the present paper are based on the averages of the figures in the last three columns of the table.

Shedlowsky and Mc. Innes have given a graph which shows the interrelation of pK_{CO_2} and the temperature (1935, p. 1709). This graph is modified in Fig. 8 in

¹ In this connection I think it is better to talk about the dissociation constants of carbon dioxide water and the hydrogen carbonate ion in preference to the terms first and second dissociation constant of carbonic acid, as H_2CO_3 is probably a paper compound.



Fig. 8. pK_{CO₂} values at various temperatures. The small circles close to HARNED and DAVIS' graph represent Näsänen's values.

such a manner, that $\frac{1000}{T}$ in the abscissa is replaced by t, making it possible to read off $pK_{CO_{\circ}}$ at any temperature between 0° and 25° C.

The problem whether the activities may be replaced by the concentrations can only be solved through a computation of the activity coefficient of HCO_3^- . The activity coefficient of CO_2 is put equal to 1, because CO_2 is a non-electrolyte.

The calculation of the activity coefficient can be based on the August analysis from 1950 of the most important ions of Grane Langsø. The following equation applies to the individual ion

$$a_i = f_i \cdot c_i$$

	SHEDLOVSKY and Mc. Innes, 1935	HARNED and DAVIS, 1943	HARNED and Bonner, 1945	Näsänen 1947
0° C	6.583	6.579	6.577	6.572
5° C		6.517	6.517	6.514
0° C		6.464	6.465	
5° C	6.429	6.419	6.420	6.421
20° C		6.381	6.382	
25° C	6.366	6.352	6.351	6.349

TABLE 16. Values of $pK_{CO_*} = -\log K_{CO_*}$ at $\mu = O$.

Nr. 2

TABLE 17.

i	c_i	z_i^2	$c_i \cdot z_i^2$
0.003 mg H ⁺ /l	3.10-6	1	$3 \cdot 10^{-6}$
1.84 mg Ca ⁺² /l	$46 \cdot 10^{-6}$	4	$184 \cdot 10^{-6}$
1.1 mg Mg ⁺² /l	$45 \cdot 10^{-6}$	4	$180 \cdot 10^{-6}$
6 mg Na ⁺ /1	$261 \cdot 10^{-6}$	1	$261 \cdot 10^{-6}$
0.46 mg K ⁺ /l	$12 \cdot 10^{-6}$	1	$12 \cdot 10^{-6}$
10.9 mg Cl ⁻ /l	$307 \cdot 10^{-6}$	1	$307 \cdot 10^{-6}$
8.3 mg SO $_{4}^{-2}$ /1	$87 \cdot 10^{-6}$	4	$348 \cdot 10^{-6}$
$0.2 \text{ mg HCO}_{2}^{-}/l \dots$	$3 \cdot 10^{-6}$	1	$3 \cdot 10^{-6}$

where a_i is the ionic activity, f_i is the activity coefficient, and c_i the molar concentration of the ion. By infinite dilution the limit of f_i is 1; a_i is then equal to c_i . This means that if the activity coefficient according to calculations lies only slightly below 1, the activity of the ion in question can be replaced by the concentration.

The ionic strength μ can be computed from the equation

$$\mu = \frac{1}{2} \sum c_i \cdot z_i^2$$

where z_i is the charge of the ion considered (c.f. Table 17).

The ionic strenght μ is then

$$\mu = \frac{1}{2} \sum c_i \cdot z_i^2 = 650 \cdot 10^{-6} = 0.00065.$$

According to Debye – Hückel's limiting law the activity coefficient is characterized by

$$-\log f_i = \frac{1}{2} \cdot z_i^2 \cdot \sqrt{\mu}.$$

As the HCO_3^- has the charge 1, we obtain

$$-\log f_{\text{HCO}_{-}} = \frac{1}{2} / 0.00065 = 0.01275; f_{\text{HCO}_{-}} = 0.97.$$

Computing $[\text{HCO}_3^-]$ as $\text{mg} \cdot l^{-1} a_{\text{HCO}_3^-}$ is replaced by $c_{\text{HCO}_3^-}$. The systematic error thus introduced is concequently about 3 per cent. As the electrometrical pH-measurements rather give a_{H^+} than c_{H^+} , and as the activity coefficient of CO₂ is equal to 1, the equation valied for Grane Langsø gets the following form

$$\frac{10^{-\text{paH}} \cdot c_{\text{HCO}_{3}^{-}} \cdot 0.97}{c_{\text{CO}_{2} + \text{CO}_{2}\text{aq}}} = K_{\text{CO}_{2}}.$$

The uncertainty (standard deviation) on the pH-calculations in Grane Langsø probably amounts to ± 0.1 , that is ± 26 per cent on $c_{\rm H}^+$ (10^{0.1} = 1.26). The standard

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47

deviation on the total CO_2 values commonly met with in Grane Langsø, viz. about $1 \text{ mg} \cdot l^{-1}$, is about ± 7 per cent. Assuming that the uncertainties on $c_{\text{CO}_2 + \text{CO}_2 \text{aq}}$ and $c_{\text{total CO}_2}$ are of the same order of magnitude, the uncertainty on the quantity of $\text{HCO}_3^- \cdot l^{-1}$ approaches 35 per cent. This estimate implies a content of about 1 mg total $\text{CO}_2 \cdot l^{-1}$.

The above mentioned analysis from August 1950 was performed on surface water. In the bottom water the CO_2 concentration rises to at most 0.000338 at the end of the summer stagnation. The resulting increase of the HCO_3^- concentration is, however, not accompanied by any appreciable increase of the ionic strenght, since no measurements of the specific conductivity have surpassed the value 57 (see p. 32). This means that the ionic strength of all the water levels examined must lie near to 0.00065 in all seasons, and consequently the activity coefficient of HCO_3^- comes near to 0.97 for the bottom water also.

10. The Carbon Dioxide

Fig. 9 indicates that Grane Langso is a lake poor in CO_2 , as 86 per cent of the total number (477) of CO_2 analyses lay between 0.27 and 1.74 mg total $CO_2 \cdot l^{-1}$. These figures correspond to molar concentrations between $6 \cdot 10^{-6}$ and $4 \cdot 10^{-5}$. The highest value ever measured amounted to 14.89 mg total $CO_2 \cdot l^{-1}$ or the concentration 0.000338. The yearly fluctuations of the CO_2 -quantities measured during three years are outlined in Table 18.

TABLE 18. The yearly fluctuations of the quantities of total CO_2 , as mg·l⁻¹, in Grane Langsø.

Period	Yearly extremes of CO ₂	Fluctuation
March 1958	0.71 (July 2nd, 6 m depth) 9.88 (April 5th 11 m depth)	9.17
August 1958	0.27 (July 21st, 6 m depth)	11 10
- July 1959	11.37 (February 8th, 11 m depth)	11.10
– July 1960	13.07 (August 23rd, 11 m depth)	12.71
August 1960	0.50 (June 15th, 0-2 m depth)	14.39
– July 1961	14.89 (August 28th, 11 m depth)	1100

Apart from the rather short period March–July 1958, the difference between the lowest and highest value of the year fluctuates between 11.10 and 14.39 mg total $CO_2 \cdot l^{-1}$, on an average 12.7 mg.

The difference between the extremes of the individual depth series can rise to at most 14.03 mg \cdot l⁻¹ total CO₂. A difference of this order has only been observed in late August, but considerable differences also occur in February, as shown in Table 19.

	mg total CO ₂ ·l ⁻¹
	0.27 -0.99
	1.00 - 1.74
	1.75 -2.49
	2.50 - 3.24
	3.25 - 3.99
	4.00 - 4.74
	4.75 - 5.49
	5.50 - 6.24
	6.25 - 6.99
	7.00 - 7.74
	7.75 -8.49
	8.50 - 9.24
	9.25 - 9.99
	10.00 - 10.74
	10.75 - 11.49
	11.50 - 12.24
	12.25 - 12.99
	13.00 - 13.74
	13.75 - 14.49
	14.50 - 15.25
Number of CO analyses	1000

Fig. 9. The distribution of the values of total carbon dioxide in Grane Langsø. Note the logarithmic scale of the abscissa.

At the dates mentioned the 11 m layer always exhibited the largest CO_2 -values, and in nearly all other cases this also held true.

In the circulation periods the greatest differences within each vertical CO_2 -series on an average amounts to 0.09 mg·l⁻¹, a quantity of the same order of magnitude as the standard deviation on a single CO_2 -analysis, 0.07 mg·l⁻¹.

A detailed study of the vertical CO_2 -series in Figs. 10–11 indicates that two *distribution patterns* are characteristic for Grane Langsø in the *summer stagnation period*:

Winter stagnation period	Greatest difference	Summer stagnation period	Greatest difference	
April, 5, 1958	9.88 - 1.45 = 8.43	August 24, 1958	11.15 - 1.27 = 9.88	
February 8, 1959,	11.37 - 1.30 = 10.07	August 23, 1959	13.07 - 0.82 = 12.25	
January 31, 1960	5.17 - 1.35 = 3.82	August 28, 1960	14.89 - 0.86 = 14.03	
February 12, 1961	6.92 - 1.15 = 5.77	July 9, 1961	4.14 - 0.64 = 3.50	

TABLE 19. The greatest differences between the extreme values of total CO_2 as $mg \cdot l^{-1}$ within the individual vertical series from 4 years.

(i) The CO_2 -distribution is uniform from the surface to 8 m depth, more rarely to 6 or 10 m depth; the CO_2 -quantities are then increasing in the 10–11 m layers, eventually 8–11 m layers, with the CO_2 -maximum always being placed in the 11 m layer. Examples: August 1, 1958 and August 23, 1959 (cf. Fig. 10).

(ii) The CO_2 -quantities are decreasing from the surface to a minimum at 6 m depth, more rarely at 4 or 8 m depth, after which the quantities are increasing towards the 11 m layer, where the CO_2 -maximum always is found. Examples: July 21, 1959 and June 18, 1958 (cf. Fig. 10).

The occurrence of a CO_2 -minimum in the 11 m layer is a very rare event indeed. Example: May 3, 1958. This minimum is probably a result of the photosynthetic activity of *Nitella* or *Uroglena*, at a moment when inconsiderable quantities of CO_2 are entering the bottom water after the effective stirring of the lake during the vernal circulation in April.

The patterns of the *winter stagnation period* look somewhat different from those of the summer half.

(i) The CO_2 -quantities gradually increase towards a maximum at the subsurface depth of 11 meters. This pattern is rare. Examples: March 9, 1958 and April 5, 1958 (cf. Fig. 11).



Fig. 10. Patterns of the vertical distribution of total carbon dioxide in Grane Langsø during the summer stagnation period of 1959.

Biol. Skr. Dan. Vid. Selsk. 14, no. 2.



50

Fig. 11. Patterns of the vertical distribution of total carbon dioxide in Grane Langsø during the winter stagnation periods of 1958 and 1961.

(ii) A relative CO_2 maximum is present immediately below the ice, while the absolute maximum lies at 11 m depth; a minimum, not very pronounced, is inserted at 4 or 6 m depth. Examples: February 8, 1959 and January 22, 1961 (cf. Fig. 11).

(iii) A uniform distribution to 4 m or 6 m depth, after which the CO_2 quantities rise in the 6 m or 8 m layer; from this level the CO_2 content is either increasing towards the bottom, or it remains nearly constant in the hypolimnion. Examples: February 12, 1961, and March 13, 1960 (cf. Figs. 11 and 23).

In the following descriptions of the temporal variations of total CO_2 , pH, and HCO_3^- , the occasions of the vernal turn-over and the autumnal turn-over have been used as starting-points instead of the calendar. These two events set in at well-defined moments, viz. when the thermocline touches the lake surface and the lake bottom, respectively (see p. 87). I think that the results will appear more clearly when the temporal course of the biological, chemical, and physical fluctuations in a lake is described from these crucial points in the annual cycle of the lake, rather than from the calendar.

In the tables on the temporal variations of CO_2 , pH, phosphate, and iron, the symbol cive stands for the vernal circulation, cive being an abbreviation of circuitus vernales (circuitus here means "Durchwanderungen", which may be translated to transmigration of the water layers). The negative figures before cive denote the number of months of 30 days previous to cive, while the positive ones signify the number of months after cive. The autumnal circulation is symbolized by ciau (from circuitus autumnales), and the meaning of the associated figures is identical with that of the cive figures.

Fig. 12 shows the yearly fluctuations of the quantity of total CO_2 below one square metre in the central part of Grane Langsø during four years. In Table 20 these computed results are arranged in relation to the moments of the two annual turn-overs. Table 21 gives a further account of the length of the circulation and stagnation periods, together with the moments of the turn-overs.



51

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	- 3	-2	-1	cit	ve	-5 + 1		-4 - 3 + 2
1958		28.43	35.	.64			14.45	10.07
1959		24.52	27.	.24	19.05	12.98	13.53	15.21
1960	19.07	20.45 24	19 29.06	25.62	18.15 7.	8.23 02		6.84 11.53
1961			21.07	24.00	18.01	12.54	9.03 8.56	6.74
-	-3 —	2 –	1 ci	au	+ 1	l	+2	+3 +4
1958	10.68 10.93	12.07 11.54	20.71	16.	50	15.79	18.62	19.23
1959	12.49	$9.60 \ \ 6.24$	11.20 18.56	17.39	13.29	12.44 13.13	3 13.90 16.8	81 16.86 16.14
1960	9.44 7.74	11.85	17.15 17.85	11.15	11.55	14.19 12.7	7 14.46 16.0	64 16.99 18.50
1961	8.56 8.56	8.28 6.64	9.30	9.0	01			

TABLE 20. Total CO₂, stated as $g \cdot 11 \text{ m}^{-3}$, in the central part of Grane Langsø.

TABLE 21. The moments of *cive* and *ciau*, and the duration of the four phases in the annual cycle of Grane Langsø.

	Winter stagnation	cive	Spring circulation	Summer stagnation	ciau	Autumn circulation	
1958	100 days	about April 10	15 days	128 days	about Sept. 1	122 days	
1959	58 days	about Febr. 27	32 days	153 days	about Sept. 1	122 days	
1960	86 days	March 26	35 days	122 days	about Sept. 1	122 days	
1961	35 days	Febr. 18	53 days	102 days	about July 23		

(1) The largest quantities of total CO_2 during the winter stagnation periods occur in the month prior to the spring turn-over. If the period is prolonged, as was the case in 1958, the amount was as high as nearly 36 g per 11 cubic meters or 36 g \cdot 11 m⁻³. The quantities occurring in the month before *cive* of the other three years lay between 21 and 29 g \cdot 11 m⁻³. The later CO_2 values of the winter stagnation periods lie, however, between 24 and 27 $\frac{1}{4}$ g \cdot 11 m⁻³. The CO₂ quantity at the end of the short winter stagnation period of 1961 (35 days) was nearly as large as that from the end of the long period of 1960, which lasted for 86 days. The reason for this remarkable result may partly be that the quantity of total CO_2 was no less than 18.5 g \cdot 11 m⁻³ at the end of the end of the corresponding period of 1959. In 1959 the CO_2 quantity just before *cive* attained the value $27 \frac{1}{4}$ g \cdot 11 m⁻³, after a quantity of as much as $19 \frac{1}{4}$ g \cdot 11 m⁻³ at the end of the preceding autumnal circulation period.

In order to examine whether the rise in total CO_2 during the winter stagnation period is constant or irregular, the daily increment has been computed; these average increments are listed in Table 22. The vertical dotted lines indicate the beginning of the winter stagnation periods. The small crosses denote the dates of analyses appro-

-	3		-2		- 1		cive	
1958	?	×	?		×	0.27	×	about April 10
1959			*	0.31	$\times 0.13 \times$			about Febr. 27
1960	 	0.18	× 0.10 ×	0.27 $ imes$	0.35 × -	- 0.25 ×		March 26
1961					$^{ }_{*}$.32 \times	0.14	×	Febr. 18

TABLE 22. The increase, on an average, of g total $CO_3 \cdot 11 \text{ m}^{-3}$. day⁻¹ during the winter stagnation periods of 1958–1961 in the middle of Grane Langsø.

priately arranged relative to *cive*. The value 0.32 of 1961 was computed assuming that the CO₂ quantity of January 14th, 1961 is identical with that of December 28th, 1960, viz. $18^{1/2}$ g·11 m⁻³.

It appears from Table 22 that the daily increase of total CO_2 during the winter stagnation period is irregular, and that the greatest daily increments, more than $0.3 \text{ g} \cdot 11 \text{ m}^{-3}$, occurred in the second month before the vernal turn-over. In the month before *cive* the daily increment decreased, in one case to a negative value. In 1959 and 1961, with short winter stagnation periods, values of $0.31-0.32 \text{ g} \cdot 11 \text{ m}^{-3}$ were found in the first part of the period, whereas the daily increment during the last part was only $0.13-0.14 \text{ g} \cdot 11 \text{ m}^{-3}$. The long winter stagnation period of 1960, however, started with rather small values, $0.18-0.10 \text{ g} \cdot 11 \text{ m}^{-3}$. Nevertheless, in this case also the increment decreased strongly towards the end of the period, even to a negative value of $-0.25 \text{ g} \cdot 11 \text{ m}^{-3}$.

These figures of the daily increment in total CO_2 , mostly computed from time intervals of 14 days, are mentioned here because the CO_2 consumption due to photosynthesis of the algae and submerged vegetation is small during the winter stagnation period. The decreasing values of the last part of the period may be interpreted as a result of increasing photosynthesis, depending on the transparency of the ice-cover and, of course, the rising light intensity.

(2) A remarkable decline in the CO_2 quantity takes place in the first month after the vernal turn-over. The lake now opened for complete circulation of its water volume probably liberates CO_2 to the atmosphere (see p. 59), and the conditions for photosynthesis are growing better. In the spring of 1958 a decline of no less than 21.2 g total $CO_2 \cdot 11 \text{ m}^{-3}$ in 28 days was obtained. In 1959 the decline amounted to 8.2 g $\cdot 11 \text{ m}^{-3}$ in 20 days, whereas in 1960 it was 7.5 g $\cdot 11 \text{ m}^{-3}$ in 14 days, and in 1961 6 g $\cdot 11 \text{ m}^{-3}$ also in 14 days.

(3) During the four summer stagnation periods investigated, the quantities of

total CO_2 always rise. This increase is by no means constant: maxima alternate with minima. The highest values, from 9.3–20.7 g·11 m⁻³, always occurred in the month previous to the autumnal turn-over. In the last part of the second month before *ciau* a minimum was found in 1958, 1959, and 1961; it amounted to 6.2–11.5 g·11 m⁻³. This second minimum of the summer stagnation period was observed in the third month before *ciau* in 1960 (7.7 g·11 m⁻³).

The first minimum of the period mentioned was found in the fourth month before *ciau* in 1958, 1960, and 1961. Quantities of total CO₂ fell to $6.7-10.1 \text{ g} \cdot 11 \text{ m}^{-3}$. In 1959 the first minimum, amounting to $13 \text{ g} \cdot 11 \text{ m}^{-3}$, occurred already in the sixth month before *ciau*, or rather in the first month after the vernal turn-over.

The secondary maxima of total CO_2 occurred in the fourth month before the autumnal turn-overs of 1959 and 1960 (11.5–15.2 g·11 m⁻³), in the second month prior to *ciau*, however, in 1958 (12.1 g·11 m⁻³), and in the third month before *ciau* in 1961 (8.6 g·11 m⁻³).

This alternation of maxima and minima of total CO_2 is closely connected with the alternation of minima and maxima of the phytoplankton productivity. Like many other lakes, Grane Langsø exhibits two production maxima within the summer half. The monthly investigation of the primary production during the period August 1950 to July 1951 demonstrated a small maximum in April and a larger one in July or August (NYGAARD 1955, p. 131). According to Table 20 and Fig. 12, the first CO_2 minimum of Grane Langsø occurred in April or May, while the second one lay in June or July (cf. also the survey of the analyses p. 91–107). These CO_2 minima are reasonably well synchronized with the maxima of productivity, during which a considerable consumption of CO_2 take place.

(4) Shortly after the autumnal turn-over the CO_2 quantities decrease. The fall amounts to 0.3–6.7 g·11 m⁻³, thus being much smaller than that confined to the spring turn-over. In the autumnal circulation period a distinct CO_2 minimum always occurred in October, the second month after *ciau*, where the CO_2 values declined to 12.4–15.8 g ·11 m⁻³. From this moment the quantities of total CO_2 increased to values of 16.9–19.2 g·11 m⁻³ in the fourth month after *ciau*, December.

It will appear from Section 12 that low pH values might have occurred in the time between late November and late December (see p. 68). Within this period of 1950 the phosphate quantity increased fourfold (see Fig. 6 and p. 26). This fact seems to indicate a *strong decomposition of dead plant material in the lake from late November to late December*. This supposition is supported by the result from Table 23, which demonstrates the daily increment of CO_2 during the autumnal circulation periods which were investigated.

It is evident that the daily increments of CO_2 are considerable in the third month after *ciau*. In November decaying organic material no doubt liberates considerable quantities of CO_2 , besides electrolytes such as phosphate.

After beginning in late November, the decay continues during the winter stagnation period, in which the lake cannot be aerated effectively. As photosynthesis of

ciai	<i>u</i> +	1	+2			+ 3		+
1958	×	-0.03	×	0.09	×	1	0.02	×
1959	imes - 0.29 imes - 0.06	× 0.04	× 0.04	×	0.14	×	0.004 ×	-0.05 ×
1960	imes 0.03 $ imes$ (2.19×-0.14	1× 0.09	× 0.1	$6 \times$	0.0	$2 \times$	0.09 ×

TABLE 23. The average increment of total CO_2 , as $g \cdot 11 \text{ m}^{-3} \cdot \text{day}^{-1}$, during the autumnal circulation periods of 1958-60.

the phytoplankton below the ice-cover is very small, and the respiration of Nitella is far greater than its photosynthesis, the absolute CO_2 maximum must consequently occur within the winter stagnation period, as will also appear from Table 20.

The photosynthesis of *Nitella flexilis*, growing in depths of about 11 meters, is undoubtedly affected by variations in the population density of the phytoplankton. As seen from the survey of the analyses on p. 96, the transparency on August 24th, 1958, surpassed 11 meters. This high transparency is due to a marked decrease of the plankton population. The CO₂ quantity coincidently increased from 11.5 g · 11 m⁻³ on August 1st to 20.7 g · 11 m⁻³ on August 24th. This rise is not due merely to the large CO₂ accumulation in the hypolimnion, as the epilimnion also increased its CO₂ content considerably. The epilimnic rise is probably a result of the small CO₂ consumption relative to the quantities of CO₂ liberated by the decay of many dead plankton organisms from the subsiding maximum in early August. A relatively strong photosynthesis of *Nitella* is then conditioned by the improved light-conditions at the lake bottom.

On the contrary, the great *Uroglena*-maximum on July 27th, 1960, when the transparency of 4 meters was exceptionally low, must have inhibited the growth of *Nitella*, causing a smaller CO_2 consumption than usual and consequently a larger content of CO_2 in the bottom water.

It is likely that *Nitella* occasionally is able to counterbalance the changes in CO_2 caused by the phytoplankton.

In the period from April to July, during which light is abundant, *Nitella* and the phytoplankton collaborate effectively in consuming CO_2 from the 11 m layer, as the primary production of the phytoplankton on bright days can attain its greatest values at a subsurface depth of 11 meters.

During the month before *ciau*, as a rule August, when the temperature of the bottom water is rising and light intensities falling, the release of CO_2 from the bottom sediments is evidently far greater than the consumption of CO_2 by *Nitella*. This conclusion is based on the fact that the *secondary* CO_2 -maximum of Grane Langsø always was found in the month before ciau. If this month exceptionally is identical with July, when light conditions for photosynthesis are still optimal, a secondary CO_2 maximum of moderate size will result: only 9.3 g \cdot 11 m⁻³, as in 1961.

The occurrence of two annual CO₂-maxima in the 11 m -water is another matter.

The CO₂-fluctuations of this water-layer are of a great interest for the productivity of the bottomplant Nitella. The absolute CO_2 -maximum (4.14–14.89 mg total $CO_2 \cdot l^{-1}$) usually lay in -1. ciau (late August). In the very windy and cool summer of 1961 it was exceptionally established already in early July, being of a moderate size (4.14 mg·l⁻¹) on account of the vigorous water circulation. The secondary CO_2 -maximum (7.15–11.37 mg total $CO_2 \cdot l^{-1}$) of the 11 m-water occurred in -2. or -1. cive (January-February, rarely in April), apart from the year 1961, when the -1. cive-maximum was greater than the -1. ciau-maximum.

As will be shown in Section 14, the low-lying thermocline is liable to move slowly upwards during the *winter stagnation period*, reaching the lake surface at the onset of the vernal circulation (cf. Fig. 24). Centripetal chemical currents and the heat content of the bottom deposits can probably give rise to convective currents between the bottom and this low-lying thermocline. If so, the *quantity of CO*₂ liberated from the bottom deposits is dispersed in a steadily increasing volume of water, and the CO₂-maximum of the 11 m-water is consequently not observed at the end of this period, but somewhat earlier.

In the summer stagnation period, however, the convection-producing factors act from the lake surface down to the thermocline, which is gradually lowered. Consequently a continuous accumulation of CO_2 takes place in a steadily decreasing volume of hypolimnic water. Under these conditions the CO_2 -maximum of the 11 m-water occurs at the end of the summer stagnation period.

In papers to come dealing with the productivity of *Nitella flexilis*, the oxygen patterns of Grane Langsø, and the phytoplankton productivity, the problems mentioned will be reconsidered.

KROGH und LANGE (1931, p. 33) have determined the quantity of total $CO_2 \cdot l^{-1}$ in the hydrogen-carbonate lake Furesø, probably by the same method as that employed here. They found values fluctuating around 100 mg $\cdot l^{-1}$ for the surface water, which are high values compared with the corresponding ones from Grane Langsø which vary around only 1 mg total $CO_2 \cdot l^{-1}$.

Considering the minimal solubility of calcite, $12.7 \text{ mg } \text{CaCO}_3 \cdot \text{l}^{-1}$ (containing 5.1 mg $\text{Ca}^{++} \cdot \text{l}^{-1}$) at 25° C, in water which is in equilibrium with a CO_2 -pressure of about $5 \cdot 10^{-7}$ atmosphere HUTCHINSON remarks "....that unless at least 5 mg per liter Ca is present in a natural water, calcitic shells will tend to dissolve, whatever the CO_2 -pressure may be." (1957, p. 662). As *Grane Langso* contains only 1.8–3.6 mg $\text{Ca}^{++} \cdot \text{l}^{-1}$, the CO_2 of its water must always be aggressive. The dead calcitic shells of Astacus and Pisidium are consequently liable to dissolve rather quickly. A dead specimen of Astacus lying on shallow water disintegrates within some days.

11. The CO_2 Exchange between the Lake Surface and the Atmosphere

As will be seen from Section 10, CO_2 is a factor exhibiting considerable yearly fluctuations. Now the problem is: does the CO_2 move into the lake surface from the atmosphere, providing an enrichment of the gas in the lake, or is CO_2 lost from the lake, or do both events alternate within a year?

In order to determine the exchange direction at any season, it is first necessary to know the quantities of free CO_2 absorbed in distilled water which is in equilibrium with the atmosphere at the various temperatures met with in nature. These quantities should then be compared with those of free CO_2 in the surface water of the lake.

As the solubility of CO_2 in aqueous solutions of electrolytes must depend on their ionic strength, this question should also be considered before a solution of the problem is possible.

The figures of Table 79 in HUTCHINSON's work (1957, p. 654) have been used for the construction of Fig. 13. These figures are assumed to represent the quantities of total CO_2 in distilled water. It is possible, however, to compute the concentration of free CO_2 on the basis of the Henderson-Hasselbalch equation

$$\frac{\mathbf{c}_{\mathbf{H}^+} \cdot \mathbf{c}_{\mathbf{HCO}_3^-}}{\mathbf{c}_{\mathbf{CO}_3}} = \mathbf{K}_{\mathbf{CO}_2}$$

where c_{CO_3} is the concentration of free CO_2 . The ionization constant of $CO_2aq K_1$ is about 10^{-4} , and so much greater than that of the hydrogen-carbonate ion, K_2 = about 10^{-10} , and the dissociation constant of water, K_w = about 10^{-14} . The increment of $[H^+]$ due to the processes $HCO_3^- \rightleftharpoons H^+ + CO_3^{--}$ and $H_2O \rightleftharpoons H^+ + OH^-$ is consequently negligible and c_{H^+} is practically identical with $c_{HCO_7^-}$. Therefore

$$(c_{H^+})^2 = K_{CO_2} \cdot c_{CO_2} = (c_{HCO_2})^2.$$

As $c_{\text{total CO}_2} = c_{\text{CO}_2} + c_{\text{HCO}^-}$ we get

$$(c_{CO_2})^2 - (2c_{total CO_2} + K_{CO_2}) \cdot c_{CO_2} + (c_{total CO_2})^2 = 0.$$
 (5)

On Fig. 13 total $CO_2 \cdot l^{-1}$, pH, and free $CO_2 \cdot l^{-1}$ can be read for all temperatures between 0° and 25° C and the ionic strength = 0.

In order to approach the next question, the solubility of CO_2 in electrolytes, Fig. 14 has been drawn. It is based on the measurements given by CHR. BOHR (1899, p. 504–505). At the large NaCl concentration of 3.41, the absorption coefficient α of CO_2 is less than 50 per cent of that for destilled water; this also holds true at 0° C and 20° C.

As previously mentioned the ionic strength of Grane Langsø is about 0.00065 (see p. 46). The ionic strength is defined by

$$\mu = \frac{1}{2} \sum c_i \cdot z_i^2$$



Fig. 13. The saturation values of CO_2 in distilled water at various temperatures (thick graph), and the corresponding values of free CO_2 (thin graph) and pH (dotted line). Ordinates: mg $CO_2 \cdot l^{-1}$ and pH-units.



and for a uni-univalent electrolyte such as NaCl μ must be equal to c. A NaCl-solution of identical ionic strength to that of Grane Langsø must consequently be of the concentration 0.00065.

If we make the approximation of assuming linearity of the graphs between c = 0 and c = 1.17, α can be computed for a NaCl-solution of the ionic strength 0.00065.
59

Temp. 0° C. α decreases 1.713 - 1.234 = 0.479 when the concentration increase 1.17. For an alteration in concentration of 0.00065 α must therefore change $\frac{0.479}{1.17}$. 0.00065 \approx 0.0003.

Temp. 20 C. α decreases 0.878 - 0.664 = 0.214 when the concentration increases 1.17. For an alteration in concentration of 0.00065α must concequently change $\frac{0.214}{1.17} \cdot 0.00065 \approx 0.0001$.

Corrections of this order of size are probably much smaller than the uncertainty on the third decimal of α . Therefore we may safely assume that the solubilities of CO₂ in the water of Grane Langsø and in distilled water are virtually identical.

Figs. 15–16 permit a comparison, at intermediate temperatures, of the free CO_2 in surface water of Grane Langsø with that of distilled water in equilibrium with the atmosphere.

In 1958, when normally only monthly analyses were performed, the surface water may have been supersaturated with CO_2 during the whole year.

In 1959, when monthly analyses were made in the first half, but fortnightly ones in the second half, two minima occurred, one in the second month (April) after *cive*, the other in the fifth month (July) after *cive*. The surface water was undersaturated with CO_2 only in July.

In 1960, when analyses were made twice a month, supersaturation likewise prevailed. The surface water exhibited undersaturation in two periods, however: the first and second months (April–May) after *cive*, and the fifth month (July) after *cive*.

In 1961, when two series of CO_2 -analyses were performed monthly until the end of July, the surface water was super-saturated apart from two periods in which undersaturation prevailed: the second and third month (April) after *cive*, and the fourth month (June) after *cive*. The abnormally early time, June, for the second CO_2 minimum may be due to interaction of the mild spring and the windy summer of 1961. Total circulation took place in even July, an exceptional occurrence within the six summers in which vertical temperature distributions of this wind-sheltered lake were followed.

Generally, the surface water of Grane Langsø is supersaturated with CO_2 for the whole year; in two periods, however, the lake can be undersaturated: April with possibly May, and July with possibly June. The lake thus liberates CO_2 to the atmosphere during the greater part of the year.

It is hardly possible to compute how much CO_2 moves into or out from the lake surface within a definite space of time, i.a. because the lake does not make up a closed system. Admission of CO_2 continually takes place, partly direct by precipitation, partly indirect by rain water filting through the soil of the surrounding coniferous plantations.

It is evident that the CO2-fluctuations which are confined to lake surface are



Fig. 15. The thick graphs represent the monthly or fortnightly values of free CO_2 in the surface water of Grane Langso in 1958–59. The thin graphs indicate the saturation values of free CO_2 in distilled water, when in equilibrium with the atmospheric CO_2 pressure under thermal conditions exactly identical to those met with in the lake. Ordinates in mg free $CO_2 \cdot 1^{-1}$.





dependent on biological factors, as well as physical and meteorological ones. Biological processes such as photosynthesis and respiration, decay included, deeply influence the standing stock of CO_2 in the lake. The physically determined and regular change between stagnation periods, when CO_2 is allowed to accumulate in the bottom water, and periods of circulation, when the CO_2 of the bottom water is brought up to i.a. the lake surface, must cause great fluctuations of CO_2 , as shown on Figs. 10–11. Finally, the precipitation yields an irregular CO_2 supply to the lake, but the rain water filtering through the soil of the surrounding plantations must contain much more CO_2 per litre, before it runs into the lake.

A feature common to many temperate lakes is the two yearly maxima in the standing stock of plankton organisms, one in April–May, the other in July–August. On the whole this means that the primary production, and with it the consumption of CO_2 , are largest in the two periods mentioned.

As found earlier by NYGAARD (1955, p. 131), Grane Langsø exhibited two maxima in its gross production within 1950–51, when it was only examined monthly. The first, small maximum occurred in April; the second one, considerably larger, took place in August. I am under the impression that something similar occurred during the three years 1958–61. The matter cannot be decided, however, until the calculations of the 14 C-data are available.

The CO₂-tension of lake Furesø has been determined by KROGH (1904, p. 384) and BRØNDSTED und WESENBERG-LUND (1912, p. 450). According to BRØNDSTED's determinations, the CO₂-tension of the surface water was below the atmospheric value $3.3 \cdot 10^{-4}$ in March–May and July 1909. In the remaining months the CO₂-tension of the surface water lay between 4 and $12.5 \cdot 10^{-4}$.

KROGH and LANGE (1931) determined the CO_2 -tension in lake Furesø at intervals within the years 1929 and 1930. Unfortunately no determinations were made in July and August. Tab. 2 of their paper (1931, p. 33) demonstrates that for surface water an equilibrium with the atmospheric CO_2 or a slight undersaturation of CO_2 was present in March, April, and May, the CO_2 -tension being 0.00024–0.00031 in these spring months. In autumn and winter the surface values surpass the equilibrium value, 0.00033, the CO_2 tension here amounting to 0.00039–0.00060. As will appear from the information given above, the investigation of Grane Langsø has confirmed and extended KROGH and LANGE's results from Furesø.

The two authors write (1931, p. 32) "....CO₂ wird somit gewöhnlich von der Oberfläche abgegeben und ermöglicht eine entsprechende Ablagerung von Calciumkarbonat." In connection with this it may be remarked that any liberation of CaCO₃ is likely to occur only in the spring and high summer, when i.a. the equilibrium-CO₂ of the carbon dioxide system is being exhausted by the vigorous photosynthesis of the phytoplankton; in these two periods the lake probably absorbs CO₂ from the atmosphere.

A hard water lake such as Furesø and a very soft water lake such as Grane Langsø thus seem to behave similarly as regards the CO_2 exchange between lake and

atmosphere. The diffusion of CO_2 from the lake surface to the atmosphere and the supply of CO_2 from the ground water probably balance over a long period. A lake may thus be considered as a device by which CO_2 returns to the atmosphere, after having been fixed photosynthetically by the land vegetation, and gradually liberated by the decay of dead organisms, partly to the atmosphere, partly to the ground water running into the lake.

12. The Hydrogen Ion Concentration

During the period 1950–1961, 545 electrometric pH determinations were carried out on water samples from Grane Langsø. The greatest number of pH measurements lay between 5.6 and 5.7. A critical examination of this material has rendered it probable that some of the pH determinations, expecially those from the bottom water, are not reliable.

The CO₂ content of the lake water from Grane Langsø usually exceeds the quantity of CO₂ (about 0.56–0.59 mg·l⁻¹) of distilled water which is in equilibrium with the atmospheric CO₂ at 18–20° C. The result must be a CO₂ loss by diffusion during some of the pH determinations, which consequently yield values which are too high. Now the question arises whether an essential difference can be ascertained between, on one hand, the pH value computed on the assumption that pH is merely determined by the CO₂ concentration of the lake water markedly poor in electrolytes, and, on the other hand, the corresponding pH value measured electrometrically at about 18–20° C, when the temperature of the lake water itself was about 18–20° C and the CO₂ content was approximately in equilibrium with the atmospheric CO₂. If these two pH values turn out to be nearly identical, the hydrogen ion concentration of Grane Langsø is mainly determined by the CO₂ content of the lake water.

The CO₂ quantities of Table 79 in HUTCHINSON's work of 1957 are assumed to represent mg total CO₂·l⁻¹, thus also including the hydrogen-carbonate CO₂. It is evident that the values of total CO₂·l⁻¹ from Grane Langsø include the hydrogen carbonate CO₂, since the carbon dioxide was distilled off at a pH value far below 4.0.

During the period October 1960 to July 1961 two new glass electrodes were employed, viz. RADIOMETER' G 200 B in a siliconed state in order to obtain a quickly adjustable pH-meter. In the same period precision buffer solutions were used for the adjustment of the instrument (cf. p. 19).

The calculation of pH was made by means of the following equations (cf. p. 57):

$$(c_{\text{free CO}_2})^2 - (2c_{\text{total CO}_2} + K_{\text{CO}_2})c_{\text{free CO}_2} + (c_{\text{total CO}_2})^2 = 0$$

pH = $\frac{1}{2}$ pK_{CO₂} - $\frac{1}{2}$ log c_{free CO₂}. (6)

With the aid of equation (5) on p. 57 it is also possible to compute pH directly from the content of total $CO_2 \cdot l^{-1}$:

Depths	Temp.	pH measured	pH computed	⊿рН	Grane Langsø mg total $CO_2 \cdot l^{-1}$	Distilled water in equilibrium with the atmospheric CO_2 , mg total $CO_2 \cdot l^{-1}$	$\Delta \mathrm{CO}_2$
June 15							
0 m	17.15	5.51	5.71	-0.20	0.50	0.60	-0.10
2 m	17.0	5.50	5.71	-0.21	0.50	0.60	-0.10
4	16.9	5.50	5.70	-0.20	0.57	0.60	-0.03
6	16.0	4.53	5.70	-0.17	0.54	0.62	-0.08
8	15.6	5.63	5.67	-0.04	0.61	0.63	-0.02
10	14.95	5.59	5.61	-0.02	0.78	0.65	+0.13
11	14.85	5.56	5.54	+0.02	1.06	0.65	+0.41
July 9							
0 m	17.2	5.68	5.63	+0.05	0.73	0.60	+0.13
2	17.1	5.69	5.66	+0.03	0.64	0.60	+0.04
4	17.1	5.68	5.63	+0.05	0.72	0.60	+0.12
6	17.1	5.68	5.66	+0.02	0.65	0.60	+0.05
8	17.05	5.68	5.63	+0.05	0.72	0.60	+0.12
10	17.05	5.68	5.64	+0.04	0.69	0.60	+0.09
11	16.3	5.48	5.23	+0.25	4.14	0.62	+3.52
July 23							
0 m	17.65	5.65	5.64	+0.01	0.70	0.59	+0.11
2	17.55	5.64	5.66	-0.02	0.64	0.59	+0.05
4	17.55	5.63	5.66	-0.03	0.64	0.59	+0.05
6	17.55	5.63	5.66	-0.03	0.64	0.59	+0.05
8	17.45	5.65	5.62	+0.03	0.75	0.59	+0.16
10	17.2	5.60	5.49	+0.11	1.42	0.60	+0.82
11	17.2	5.59	5.45	+0.14	1.67	0.60	+1.07

TABLE 24. A comparison of the pH values measured and the corresponding ones computed from Grane Langsø in June–July 1961.

$$\begin{array}{l} (c_{H^{+}})^{2} = K_{CO_{2}} \cdot c_{CO_{2}}; \quad c_{total \ CO_{2}} = c_{H^{+}} + c_{CO_{2}} \\ (c_{H^{+}})^{2} + K_{CO_{2}} \cdot c_{H^{+}} - K_{CO_{2}} \cdot c_{total \ CO_{2}} = 0 \\ c_{H^{+}} = -\frac{1}{2} K_{CO_{2}} + \sqrt{(\frac{1}{2} K_{CO_{2}})^{2} + K_{CO_{2}} \cdot c_{total \ CO_{2}}}. \end{array} \right\}$$
(7)

In the cool and windy summer of 1961 the temperature of the laboratory room used for pH determination was about 18° C, thus nearly identical with that of the lake water. In the following description only the results from water samples measuring at least 16° C are considered.

Table 24 demonstrates that on June 15 the water layers of 0-6 m subsurface depths contained smaller quantities of CO_2 than does distilled water in equilibrium

with the atmosphere at the same temperature. Therefore it is assumed that some CO_2 has diffused from their air into the lake water, thus making it more acid. This assumption fits the facts, the pH values measured being 0.17–0.21 units smaller than the calculated ones.

On July 9 the CO_2 values of Grane Langsø were, on the other hand, slightly higher than the corresponding ones of distilled water in equilibrium with 0.033 per cent CO_2 of the atmosphere. Assuming that the lake water during the pH determination has liberated some CO_2 to the air, the pH must have increased somewhat. There is also in this case accordance between theory and practice, the pH-values measured being 0.02–0.05 units higher than the computed ones.

The bottom water, however, was relatively rich in CO_2 . During the pH determination some loss of CO_2 by diffusion to the air must have taken place. The pH value measured was 0.25 unit higher than the computed one.

Also on July 23 the lake water from 0-8 m subsurface depths contained slightly greater CO_2 concentrations than does distilled water in equilibrium with the atmosphere. In this case the pH values measured lay from -0.03 to +0.03 units higher than the computed ones. The water from 10 m and 11 m subsurface depths was somewhat richer in CO_2 than distilled water in equilibrium with 0.033 per cent CO_2 . The diffusion of CO_2 during the pH determination may have increased pH with 0.11-0.14 units compared to the pH values calculated.

Table 24 thus makes it probable that the diffusion of CO_2 plays a certain part during the pH determination of the very soft water of Grane Langsø. All things considered a good agreement exists under summer conditions between the pH values measured and the computed ones, provided that the pH determinations are made at temperatures nearly identical with those of the lake, and that the CO_2 of the lake water approximately equilibrates with the atmospheric CO_2 .

The conclusion of these comparisons is that pH of Grane Langsø seems in all essentials to be determined by the CO_2 concentration of the lake water.

The calculation of pH implies an ionic strength of the solution approaching nil. The ionic strength of Grane Langsø amounts to about 0.00065, however, and it is possible that i.a. groundwater supply or metabolic products originating from the many organisms of the lake, succeeding each others, may to some degree influence pH. This supposition is founded on the following facts.

During the autumnal circulation of 1960, pH-measurements were undertaken at the temperatures actually met with in the lake. The volumes of the buffer solution and the water samples from Grane Langsø were chosen to be to 60–100 ml instead of the 5 ml normally used, in order to keep their temperatures constant at e.g. $4^{\circ} \pm$ 0.1° C during the standardization and determinations. Correction were made, according to the instruction and operating manual of the pH-meter used, for temperatures deviating from 20° C and for any difference between the reading-pH and buffer-pH.

In the period October 9th to December 28th, the computed pH values fluctuated within the limits 5.50 and 5.56, thus varying at most 0.06 units. The values measured,

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TABLE 25. A comparison of the pH-values measured and computed, their differences $(\Delta \text{ pH})$, the quantity of total $\text{CO}_2 \cdot l^{-1}$ at the various levels of Grane Langsø, the quantity of total CO_2 of distilled water in equilibrium with the atmospheric CO_2 at the corresponding temperatures, and finally the differences (ΔCO_2) between the two last quantities.

Depths	Temp.	pH measured	pH computed	⊿рН	Grane Langsø, mg total $CO_2 \cdot l^{-1}$	Distilled water in equilibrium with the atmospheric CO_2 , mg total $CO_2 \cdot 1^{-1}$	⊿co₂
October 9, 1960							
0 m	13.05	5 79	5 59	+ 0.20	1 98	0.69	0.50
9 _	13.05	5.72	5.51	+0.20 +0.19	1.20	0.69	+0.59
4 -	13.05	5.70	5.52	+0.19	1.30	0.69	+0.01 +0.59
6 -	13.05	5.72	5.52	+0.20	1.20	0.69	+0.59
8 -	13.05	5.72	5.51	+0.20	1.20	0.69	+0.50 +0.61
10 -	13.05	5.70	5.51	+0.20	1.33	0.69	+0.01 +0.64
11	13.05	5.71	5.51	+0.20	1.32	0.69	+0.63
October 19, 1960							
0 m	10.85	5.67	5.55	+0.12	1.17	0.75	+0.42
2	10.75	5.66	5.55	+0.11	1.19	0.75	+0.44
4	10.7	5.68	5.55	+0.13	1.16	0.75	+0.41
6	10.7	5.66	5.56	+0.10	1.14	0.75	+0.39
8	10.7	5.68	5.56	+0.12	1.14	0.75	+0.39
10	10.65	5.69	5.55	+0.14	1.18	0.75	+0.43
11	10.65	5.68	5.55	+0.13	1.15	0.75	+0.40
November 6, 1960)						
0 m	8.45	5.59	5.54	+0.05	1.30	0.80	+0.50
2	8.45	5.60	5.53	+ 0.07	1.35	0.80	+0.55
4	8.45	5.59	5.54	+ 0.05	1.29	0.80	+0.49
6	8.45	5.59	5.53	+ 0.06	1.32	0.80	+0.52
8	8.45	5.60	5.54	+ 0.06	1.29	0.80	+0.49
10	8.45	5.59	5.53	+ 0.06	1.32	0.80	+0.52
11	8.45	5.59	5.53	+ 0.06	1.37	0.60	+0.57
November 20, 196	30						
0 m	6.35	5.44	5.52	-0.08	1.46	0.88	+0.58
2	6.3	5.44	5.52	-0.08	1.49	0.88	+0.61
4	6.2	5.42	5.51	-0.09	1.51	0.88	+0.63
6	6.15	5.43	5.51	-0.08	1.54	0.88	+0.66
8	6.15	5.43	5.51	-0.08	1.51	0.88	+0.63
10	6.15	5.42	5.51	-0.09	1.55	0.88	+0.67
11	6.15	5.42	5.51	-0.09	1.52	0.88	+0.64

TABLE	25 (continued)
LADLL	40 1	commutute.

Depths	Temp.	pH measured	pH computed	⊿рН	Grane Langsø, mg total $CO_2 \cdot l^{-1}$	Distilled water in equilibrium with the atmospheric CO_2 , mg total $CO_2 \cdot l^{-1}$	ΔCO_2
December 11, 19	60						
0 m	4	5.60	5.51	+0.09	1.53	0.94	+0.59
2	4	5.60	5.51	+0.09	1.55	0.94	+0.61
4	4	5.61	5.51	+0.10	1.52	0.94	+0.58
6	4	5.59	5.51	+0.08	1.54	0.94	+0.60
8	4	5.59	5.50	+0.09	1.56	0.94	+0.62
10	4	5.59	5.50	+0.09	1.58	0.94	+0.64
11	4	5.58	5.51	+0.07	1.50	0.94	+0.56
December 28, 19	60						
0 m	3.3	5.63	5.50	+ 0.13	1.70	0.94	+0.76
2	3.3	5.63	5.50	+0.13	1.69	0.94	+0.75
4	3.3	5.62	5.50	+0.12	1.67	0.94	+0.73
6	3.3	5.62	5.50	+0.12	1.70	0.94	+0.76
8	3.3	5.62	5.50	+0.12	1.67	0.94	+0.73
10	3.35	5.63	5.50	+0.13	1.67	0.94	+0.73
11	3.35	5.62	5.50	+0.12	1.67	0.94	+0.73

TABLE 26. Average values of the columns 5 and 8 in the preceding table.

Date	⊿рН	ΔCO_2
October 9	+0.20	+0.60
October 19	+0.12	+ 0.40
November 6	+ 0.06	+0.50
November 20	-0.08	+0.65
December 11	+0.09	+0.60
December 28	+0.12	+ 0.75

on the contrary, fluctuated from 5.42 on November 20th to 5.72 on October 9th, thus varying over 0.30 units.

As the CO_2 values from the autumn of 1960 always surpassed the corresponding ones of distilled water, a CO_2 loss by diffusion to the air is supposed to take place during the pH determinations, ΔCO_2 always being positive. It is consequently to be expected that the pH values measured are higher than the computed ones. According to Table 26, however, the average values measured decreased from October 9th towards a marked pH minimum on November 20th, after which the pH values again increased. This seems to show that *acid-reacting substances*, possibly formed by the dacay of parts of the submerged vegetation, *were liberated during the late autumn of 1960*. Now pH determinations undertaken with water very poor in electrolytes can be rather inaccurate, on account of i.a. the large difference in ionic strength between the lake water and the buffer solution. It is consequently difficult to comment on the pH fluctuations in the autumn of 1960. In this connection I wish to remark, however, that a similar pH minimum, viz. pH 5.44, was measured in late November 1959.

Even if the components of the CO_2 system play an important role in determining pH, other substances such as *ammonia*, formed by decomposition of the proteins contained in dead plankton organisms and hydrophytes, *occasionally must interfere with the CO₂ system*. Even such small NH₃ quantities as 0.01 mg per litre distilled water can raise the pH by a few hundreths, if the quantity of free CO_2 amounts to about 1 mg·l⁻¹.

DOMOGALLA, FRED and PETERSON (1926, p. 371–372, Figs. 1–2) found that the bottom water of Lake Mendota obtained a NH_3 maximum in – 1. to – 2. *cive* and another in – 1. *ciau*. The surface water likewise exhibited two annual NH_3 maxima, one in *cive* + 1. and the other in *ciau* + 1. after admixture with the large quantities of NH_3 in the bottom water introduced by the turnovers.

Similar results were obtained by KUSNEZOW (1959, Abb. 53 p. 163) in Tschornoje See. The two lakes mentioned are eutrophic, the Russian one being very rich in H_2S . Grane Langsø, which may be termed oligotrophic, is an acid lake, however. As extremely few determination of ammonia have been made in this lake (cf. Table 9, p. 32), my own results from the NH_3 measurements in the likewise acid but humic lake *Gribsø*, which may be characterized as mesotrophic, are given in Table 26 bis. The analytic methods for a quantitative determination of NH_3 and NO_3^- are given on p. 32.

In the bottom water of lake Gribsø, also, one NH_3 maximum lay in -1. ciau and the other in -1. to -2. cive, the values being respectively $1.20 \text{ mg} \cdot \text{l}^{-1}$ and $0.6-0.7 \text{ mg} \cdot \text{l}^{-1}$. In Grane Langsø the quantities of ammonia in the bottom water probably never attain these figures, because the rather high oxygen values of its bottom water favour the nitrification of ammonia.

Lake Gribsø. Summer stagnation (August 1949): 0.6 per cent O_2 in 11 m. Winter stagnation (February 1950): 44 per cent O_2 in 11 m.

Grane Langsø. Summer stagnation (August 1958 and 1959): 33-62 per cent oxygen saturation in 11 m. Winter stagnation (February-March 1958, 1959, and 1960): 51-71 per cent oxygen saturation in 11 m.

In Gribsø, however, the oxygen saturation and with it the *nitrification were* extremely small during summer stagnation; during winter stagnation considerable oxygen concentrations in the bottom water favoured a vigorous nitrification at the expense of ammonia, as shown in Table 26 bis.

The rather considerable oxygen saturation values in the bottom water of Grane Langsø make it probable that large quantities of ammonia should not be expected there during the stagnation periods.

TABLE 26	bis.	The	yearly N	y fluc H ₃ – 1	tuation N in th	ns of ne per	amm iod of	onia 1949	and 1 -50.	nitrate	in	lake	Gribsø.
				ci	au				с	ive			
	July 6	Aug.	Sep.	Oct. 8	Nov. 5	Dec. 3	Dec. 28	Jan. 28	Feb. 25	Mar. 25	Apr.	May 4	June 3

	6	3	3	8	5	3	28	28	25	25	8	4	3
0 m	0.15	0.20	0.25	0.24	0.20	0.25	0.29	0.40	0.15	0.23	0.30	0.28	0.25
1	0.15	0.20	0.25	0.24	0.20	0.25	0.29	0.45	0.28	0.23	0.30	0.30	0.24
2	0.15	0.15	0.20	0.24	0.20	0.25	0.29	0.48	0.28	0.23	0.30	0.30	0.23
3	0.10	0.15	0.30	0.24	0.20	0.25	0.29	0.45	0.28	0.23	0.30	0.28	0.22
4	0.10	0.20	0.30	0.24	0.20	0.25	0.29	0.45	0.28	0.23	0.30	0.28	0.21
5	0.10	0.25	0.30	0.24	0.20	0.25	0.29	0.48	0.28	0.23	0.35	0.28	0.20
6	0.10	0.20	0.30	0.24	0.20	0.25	0.29	0.45	0.30	0.23	0.35	0.25	0.22
7	0.10	0.20	0.20	0.27	0.20	0.25	0.29	0.40	0.30	0.23	0.35	0.25	0.22
8	0.10	0.20	0.20	0.30	0.20	0.25	0.29	0.45	0.35	0.23	0.35	0.25	0.22
9	0.10	0.30	0.35	0.85	0.20	0.25	0.29	0.50	0.35	0.23	0.35	0.28	0.22
10	0.20	0.35	0.45	1.00	0.20	0.25	0.29	0.50	0.40	0.23	0.35	0.28	0.22
11	0.20	0.45	0.55	1.20	0.30	0.25	0.29	0.70	0.60	0.23	0.35	0.25	0.25

 $NO_3 - N$ in the period of 1949–50.

				ci	au				cit	<i>ve</i>			
	July 6	Aug. 3	Sep. 3	Oct. 8	Nov. 5	Dec. 3	Dec. 28	Jan. 28	Feb. 25	Mar. 25	Apr. 8	May 4	June 3
0 m	0.005	0.005	0	0.005	0	0.02	0.045	0.045	0.070	0.120	0.03	0	0
1	0.005	0	0	0	0	0.01	0.045	0.040	0.053	0.115	0.02	0	0
2	0.005	0	0	0	0	0.015	0.045	0.035	0.050	0.115	0.02	0	0
3	0.005	0	0	0	0	0.01	0.045	0.032	0.054	0.115	0.01	0	0
4	0.005	0	0	0	0	0.01	0.045	0.040	0.075	0.115	0.02	0	0
5	0.005	0	0.005	0	0.005	0.01	0.045	0.055	0.105	0.115	0.02	0	0
6	0.01	0	0.005	0	0	0.01	0.045	0.060	0.120	0.120	0.02	0	0
7	0.02	0.03	0.005	0	0	0.01	0.045	0.070	0.150	0.120	0.025	0	0.005
8	0.05	0.035	0	0.005	0	0.015	0.045	0.075	0.200	0.115	0.030	0.005	0.005
9	0.04	0.005	0	0	0	0.01	0.045	0.080	0.570	0.115	0.035	0.025	0.02
10	0.02	0	0	0	0	0.01	0.045	0.320	1.00	0.115	0.035	0.04	0.02
11	0.005	0	0	0	0	0.005	0.045	1.70	1.35	0.115	0.035	0.043	0.02
	•												

In order to examine the correctness of this assumption I paid a visit to Grane Langsø on March 27th, 1964, with Mr. Aage Rebsdorf, Master of Science, to whom I am indebted for valuable discussions on the subject in question. At this moment the lake was covered with ice, 11 cm thick. In the Silkeborg Laboratory Mr. Rebsdorf made the analyses of ammonia (cf. MACKERETH 1963) the uncertainty of which does not surpass 0.005 mg $NH_3 - N \cdot l^{-1}$. He further determined pH by means of RADIOMETER'S pH-meter 22, using the precision buffer 6.88 (20° C) for adjustment, while I made the analyses of total carbon dioxide. The following results were obtained.

The quantities of ammonia did not surpass 0.1 mg $NH_3 - N \cdot l^{-1}$, as might have been expected. The pH values, however, turned out surprisingly high.

Grane Langsø.	March	27.	1964.
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Temp.		pH r	neasured	NH	₃ –N	Tota	l CO ₂	Ur am	ogle eric	ena ana
0.1 m	1.0°	6.30	6.18	0.026 n	$ng \cdot l^{-1}$	0.84 m	$g \cdot l^{-1}$	0	per	ml
1 m	4.2°									
2	4.2°	6.32	6.31	0.013	-	1.06	-	0.2	2 -	-
4	4.2°	6.40	6.40	0.020	-	1.10	-	15	-	-
6	4.3°	6.26	6.34	0.015	-	1.17	-	21	-	-
8	4.35°	6.46	6.54	0.018		1.12	-	10	-	-
10	4.35°	6.16	6.15	0.026		1.54		5	-	-
11	4.35°	5.70	5.70	0.091	-	4.97	-	5	-	-

It is not possible to compute the pH of the Grane Langsø water, considering CO_2 and NH_3 as well. It is possible, however, to calculate the pH of distilled water which contains the same quantities of CO_2 and NH_3 as did Grane Langsø on March 27th, 1964. The values obtained in this way lie between 5.48 and 5.83, while the values computed by the CO_2 figures alone, vary between 5.23 and 5.64. At the end of the winter stagnation period the ammonia or rather the concentration of NH_4^+ in Grane Langsø is thus able to increase pH of distilled water with 0.09–0.25 unit. In this connection it should be mentioned, however, that the *nitrification of NH_3 must result in an acidification of the water*. The low pH values measured in late November (cf. p. 66 and 68) may be a result of the nitrification of the quantities of NH_3 liberated during the autumnal decay of the vegetation (cf. p. 26). Only regular determinations of the vertical distribution of NH_3 and NO_3^- in Grane Langsø can decide the matter.

Comparing the calculated and measured pH values from March 27, 1964, it is evident that either the values measured are unreliable, or alkaline substances other than ammonia must have been present in the water. pH determinations in Grane Langsø obviously represent a difficult task. Mr. Rebsdorf has made series of electrometrical pH measurements on distilled water containing much more CO_2 than the water of Grane Langsø ever did. He also made pH determinations on CO_2 water highly undersaturated in relation to the atmospheric CO_2 pressure. These experiments have shown that pH is altered by only a few hundreths during a determination made according to the procedure described on p. 19.

Recalling the standard deviation ± 0.07 per cent on values of total CO₂ lying around 1 mg·l⁻¹ (c.f. p. 21), the uncertainty of pH calculated by the equations (6) or (7) can be determined to a few hundreths. Various metabolic products liberated by the bacterial decomposition of dead organisms in the lake undoubtedly influence the CO₂ system perceptibly on some occasions, as mentioned above. Therefore *pH is stated with one decimal only in the Survey of the Analyses* (p. 91–107). In addition for the period October 1960 to July 1961 the pH values measured by means of precision buffer solutions and two new glass electrodes are given in brackets in the Survey, unless they are stated in the text.

Fig. 17 demonstrates that Grane Langsø is an acid lake, as pH values above 6



Fig. 17. The distribution of the pH values calculated from Grane Langsø. Note the logarithmic scale of the abscissa.

never occurred in the central part of the lake. The extremes are 4.9 and 5.9, computed respectively from August 28th, 1960, at a depth of 11 m, and July 21st, 1959, at a depth of 6 m. The greatest number of pH values lies within the interval of 5.4-5.7, 87 per cent of the 545 calculations falling within this region. The greatest number of pH values measured electrometrically lay within the interval of 5.6-5.7.

As the quantities of HCO_3^- lie between 0.1 and 0.7 mg·l⁻¹, corresponding to HCO_3^- alkalinities of only 0.002–0.01 mval·l⁻¹, Grane Langsø must be characterized as a weakly buffered lake. One would expect a water of this type to exhibit great pH fluctuations. This is, however, not true as evident from Table 27.

The yearly pH fluctuations exhibited identical values in each of the 3 years of investigation, viz. 0.9 pH unit (according to the electrometrical pH measurements 0.87 pH unit). In the very shallow water between the hydrophytes of the littoral zone, the pH fluctuations during the summer half are assumed to be considerably greater.

During the circulation periods the pH differences at the various levels are 0 or a few hundreths. In the stagnation periods considerable differences occur simultaneously within the single vertical pH series. The largest difference was calculated

Periods	Yearly extremes of pH	Fluctuation
August 1958	5.0 (August)	0.9
– July 1959	5.9 (July)	
August 1959	5.0 (August)	0.9
– July 1960	5.9 (July)	
August 1960	4.9 (August)	0.9
- July 1961	5.8 (April and June)	

TABLE 27. The yearly fluctuations of pH in the central part of Grane Langsø.

on July 27th, 1960, when pH was 5.9 and 5.1 in the subsurface depths of 4 m and 11 m, respectively. The hydrogen ion concentration at 11 m was concequently quite 6 times as great as that at 4 m.

A detailed study of the Survey of the Analyses on p. 91 reveals several patterns of the vertical pH distribution in Grane Langsø during the summer and winter stagnation periods.

For the *summer stagnation period* it is possible to distinguish between two types (cf. Fig. 18):

(i) pH is almost constant from the surface to a subsurface depth of 6 m or 8 m, after which pH is falling to a minimum at a depth of 11 meters. *This clinograde pH type always occur at the end of August, just before ciau.* It is, however, also commonly met with in June. Under certain conditions, such as low transparency (July 27th, 1960) or vigorous water circulation due to a windy period (July 9th, 1961), the clinograde pH curve is also found in July.



(ii) pH is nearly constant from the surface to 4 m or 6 m depth, while a pH

Fig. 18. Patterns of the vertical pH distribution in Grane Langsø during the summer stagnation periods of 1958, 1959, and 1960.



Fig. 19. Patterns of the vertical pH distribution in Grane Langso during the winter stagnation period of 1959.

maximum is lying in a subsurface depth of 6 m or 8 m, after which the pH values decrease to a minimum at 11 m. *This positive heterograde pH type is characteristic of July*. It also occurs in the first half of May (May 14th, 1960) and, more rarely, in June.

The vertical pH distribution of the *winter stagnation period* is similar to that of the summer stagnation period, (cf. Fig. 19). The type of February 8th, is very rare, however; only one further example, from January 22nd, 1961, is known. *The pH-type in winter is nearly always clinograde*. The slope of these clinograde hibernal pH graphs is considerably steeper than that of the aestival graphs.

The two patterns of vertical pH distribution are probably due to the interaction of the CO_2 consumers and the ordinary CO_2 producing factors. The CO_2 -consumers are the phytoplankton and the hydrophytes, especially *Nitella* growing at a subsurface depth of 11 meters. The ¹⁴C-determinations of primary production by the plankton algae have shown that within the period March-July the greatest daily photosynthesis can occur at all levels from 0–11 m, depending on the illumination during the experimental day and the quantitative vertical distribution of the plankton-organisms. The maximum productivity is often found in a subsurface depth of 4–6 m. The photosynthesis of *Nitella flexilis* considerably surpasses its respiration already in late March.

The vigorous CO_2 uptake during photosynthesis in the summer stagnation period with intense light must have the effect of increasing pH, especially in the depths of 4–6 m. When covered with ice the lake exhibits an extremely small photosynthesis activity, relatively considerable only in the uppermost water-layers and then only in March.

As it may be difficult from the Survey of the Analyses on p. 91-107 to get an idea of the seasonal pH variations during the three years' investigations, the *average pH* has been computed as a simple arithmetic average of the 7 pH values of each column. pH being a logarithmic function of $[H^+]$, such a calculation is incorrect, of course. A comparison with the results obtained by the adequate method of calculation

$$[\mathrm{H^+}] = \frac{2(\bar{x}_{0-2} + \bar{x}_{2-4} + \bar{x}_{4-6} + \bar{x}_{6-8} + \bar{x}_{8-10}) + \bar{x}_{10-11}}{11}; \quad \mathrm{pH} = -\log[\mathrm{H^+}]$$

where \bar{x}_{0-2} stands for the average of [H⁺] in 0 m and 2 m, etc., demonstrates the differences to be only a few hundreths.

On February 8th, 1959, the mutual differences between the pH values from the various levels amounted to 0.5 pH unit. Only 7 of the 70 vertical pH series exhibit differences as big as 0.5–0.8 units within the single series. The remaining pH series were much more uniform. The arithmetic average of February 8th, 1959, was pH 5.42, thus 0.03 smaller than pH calculated in accordance with the expression above for $[H^+]$, which gave the result pH 5.45. During the circulation periods the differences are smaller than 0.01 pH unit. Therefore Fig. 20 has been drawn on the basis of the arithmetic means of the individual columns.

Fig. 20 shows that *two yearly pH maxima* occur in the central part of Grane Langsø, one with pH values between 5.6 and 5.75 in the *first or second month after cive* (April, rarely in May), the other with pH-values between 5.55 and 5.7 in the *fourth month, rarely the fifth one after cive* (July, exceptionally in June). These maxima are no doubt connected with the photosynthetic activity of the phytoplankton, an assumption to be returned to in a future paper.

The lowest pH values, 5.35-5.45, of the three years' investigations lay in the month before cive, which was normally February and rarely April. The secondary pH minimum, 5.5-5.6, as a rule occurred in the third month after cive (May). During the long period of autumnal circulation, lasting for at least 4 months, pH was rather constant, nearly always fluctuating from about 5.5 to 5.55.

In order to see whether a remarkable lake as Grane Langsø differs from other Danish waters concerning its annual pH fluctuations, monthly electrometrical pH determinations in 1950–51 from lake *Gribsø*, the turf-pit *Kattehale Mose*, and the 5 m deep pond *Frederiksborg Slotssø* are given in the Tables 28, 29, and 30. Lake Gribsø was furthermore subjected to a detailed pH investigation in 1949–50.

It is evident from Figs. 18–19 and the review on p. 72–73 that the pH graphs of the winter stagnation period normally were clinograde in Grane Langsø, whereas positive or alkaline heterograde graphs and clinograde graphs characterized the lake in the summer stagnation period. The likewise acid but humic lake Gribsø exhibits another pH type in both stagnation periods, as demonstrated by Table 28 (cf. ÅBERG and RODHE 1942, p. 192; HUTCHINSON 1957, p. 604).



Fig. 20. The yearly fluctuations of pH in Grane Langsø. An individual pH value represents the arithmetic mean of the 7 calculated values from a vertical series. Circulation periods are indicated by oppositely directed arrows, ice-periods by horizontal hatched columns.

As regards the yearly pH fluctuations of the *bottom water*, lake *Gribso* is characterized by showing its highest pH value, 6.45, in -1. *ciau* (October) and so at the end of summer stagnation. At the autumnal overturn, normally in the first half of November, a marked fall of pH took place, after which pH gradually declined to the smallest value of the year, 4.45, occurring in -1. *cive* (February) and so during winter stagnation. This means an annual pH-amplitude of no less than 2 pH-units. A secondary maximum, pH 6.25, was observed in -4. *ciau* (August), and a secondary minimum, pH 4.85, occurred in *cive* +3. (May–June).

The pH fluctuations of the *surface water of Gribsø*, 0.4 pH units, were far smaller than those of the bottom water. The highest value of 1949–50, pH 5.35, occurred in

-	- 5	-	4 –	3	-	- 2	-	- 1		с	iau	-	+1
	June 29	July 6	Aug. 3	Aug. 15	Sept. 3	Sept. 17	Oct. 8	Oct. 22	Oct. 29	Nov. 5	Nov. 19	Dec. 3	Dec. 17
0 m	5.35	5.35	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
1	5.35	5.35	5.55	5.35	5.40	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
2	5.35	5.35	5.55	5.35	5.35	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
3	5.35	5.30	5.45	5.25	5.35	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
4	5.25	5.25	5.40	5.25	5.35	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
5	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25	5.25
6	5.15	5.25	5.20	5.15	5.25	5.35	5.25	5.25	5.25	5.25	5.25	5.25	5.25
7	5.15	5.20	5.15	5.05	5.10	5.45	5.30	5.25	5.25	5.25	5.25	5.25	5.25
8	5.10	5.15	5.10	5.15	5.55	5.80	5.85	5.95	5.25	5.25	5.25	5.25	5.25
9	5.10	5.15	5.15	5.65	5.95	6.15	6.35	6.30	5.35	5.25	5.25	5.25	5.25
10	5.10	5.15	5.85	5.85	6.05	6.25	6.40	6.40	6.35	5.55	5.25	5.25	5.25
11	5.15	5.20	6.25	6.15	6.15	6.35	6.40	6.45	6.45	6.05	5.25	5.25	5.25
					Tabl	le 28 cc	ontinued	1.					
	+2	2	- 1	L		cit	<i>pe</i>		+ 3	1	+	2	+3
	Dec. 28	Jan. 14	Jan. 28	Feb. 11	Feb. 25	Mar. 11	Mar. 19	Mar. 25	Apr. 8	Apr. 22	May 4	May 20	June 3
0 m	5.20	5.20	5.20	5.00	5.05	5.00	4.95	4.95	5.00	5.05	5.15	5.15	5.20
1 m	5.20	5.20	5.20	5.15	5.15	5.00	4.95	4.95	5.00	5.05	5.15	5.15	5.15
2	5.20	5.20	5.20	5.15	5.15	5.00	4.95	4.95	5.00	5.05	5.15	5.10	5.15
3	5.20	5.20	5.20	5.20	5.15	4.95	4.95	4.95	5.00	5.05	5.15	5.10	5.15
4	5.20	5.20		5.20	5.10	4.95	4.95	4.95	5.00	5.05	5.15	5.00	5.10
5	5.20	5.20	5.15	5.20	4.95	4.95	4.95	4.95	5.00	5.05	5.15	5.00	5.05
6	5.20	5.20		5.15	4.90	4.90	4.95	4.95	5.00	5.05	5.05	5.00	5.00
7	5.20	5.20	5.15	5.15	4.85	4.90	4.95	4.95	5.00	5.05	5.05	5.00	4.95
8	5.20	5.20		5.15	4.80	4.85	4.95	4.95	5.00	5.05	5.00	4.95	4.95
9	5.20	5.20	5.00	5.00	4.55	4.50	4.95	4.95	5.00	5.05	5.00	4.90	4.90
10	5.20	5.20	4.90	4.70	4.45	4.45	4.95	4.95	5.00	5.05	4.95	4.85	4.85
11	5.20	5.00	4.55	4.55	4.45	4.70	4.95	4.95	5.00	5.05	4.95	4.85	4.85

TABLE 28. pH-fluctuations of Lake Gribsø in 1949-50.

	+	4	- 3	-1 ci	au +	1 -	3 –	2 -	1 <i>ci</i>	ve +	1 +	2 +	3 + 4
	June 15	July 28	Aug. 3	Oct. 18	Nov. 13	Dec. 12	Jan. 15	Feb. 14	Mar. 8	Apr. 10	May 10	June 11	July 9
0	5.20	5.25	5.25	5.27	5.26	4.98	4.80	4.92	4.77	4.62	4.68	4.82	4.79
1	5.15	5.25	5.25	5.25	5.23	4.98	4.87	4.93	4.68	4.60	4.71	4.81	4.85
2	5.15	5.25	5.25	5.28	5.20	4.97	4.71	4.72	4.72	4.61	4.72	4.82	4.90
3	5.15	5.15	5.20	5.30	5.20	4.98	4.57	4.54	4.58	4.60	4.63	4.82	4.91
4	5.10	5.15	5.20	5.23	5.21					4.58	4.48	4.59	4.61
5	5.05	4.95	5.10		5.22			4.69		4.59	4.46	4.50	
6	5.00	4.95	5.00		5.21					4.62	4.62	4.49	4.50
7	4.95	5.05	5.10		5.23			4.65		4.60	4.51	4.51	
8	4.90	5.05	5.70		5.23					4.60	4.58	4.53	4.56
9	4.90	5.10	5.70		5.25			4.20		4.61	4.59	4.52	4.70
10	4.90	5.65	5.85		5.24			4.32		4.58	4.56	4.63	4.87
11	5.00	5.95	5.85		5.21			4.44		4.60	4.75	4.67	5.00
average .	5.04	5.23	5.37		5.22			4.60		4.60	4.61	4.64	4.77

TABLE 28 continued (1950-51).

TABLE 29. pH fluctuations of Kattehale Mose in 1950-51.

-	3 –	2 -	1 cie	<i>au</i> +	1 +	2 +	3 -	2 -	1 <i>ci</i>	ve +	1 +	2 +	3 +
	July 27	Aug. 22	Sept. 15	Oct. 13	Nov. 8	Dec. 6	Jan. 9	Feb. 9	Mar. 6	Apr. 7	May 7	June 7	July 6
0.1 m	6.05	6.13	6.43	5.78	5.68	6.11	5.83	5.17	4.72	4.63	4.56	4.87	4.94
0.5		6.07	6.09	5.81	5.62	6.18	5.87	5.03	5.07	4.96	4.64	4.74	5.00
1.0	6.25	5.82	6.03	5.75	5.61	6.38	6.25	4.94	5.10	5.24	5.25	5.49	5.73
average	6.15	6.01	6.18	5.78	5.64	6.22	5.98	5.05	4.96	4.94	4.82	5.03	5.22

-5. ciau (June–July, possibly identical with cive +3. of 1949); the lowest one, pH 4.95, occurred in cive +1. (March).

In the period 1950-51 the absolute pH maximum, 5.25, was observed in the long period from July to November. The secondary maximum, pH 4.82, occurred in *cive* +3. (June). The smallest pH value, 4.62, was measured in *cive* +1. (April) also in 1950-51.

Gribsø grew more and more alkaline from June to October 1949, the arithmetic pH mean increasing from 5.22 to 5.59 (cf. Fig. 21). The average then declined to the absolute minimum, pH 4.85, in March. This arithmic mean is, of course, far more influenced by the pH values of the bottom water than by those of the surface water. Gribsø in its entirety was more acid, pH 4.60–4.77, in spring and early summer of 1951 than in the same period of 1950, when pH varied between 5.0 and 5.2.

The vertical distribution of pH in Gribsø is, during summer stagnation, quite different from that in Grane Langsø. At the beginning of the two stagnation periods

	2 -	-1 ci	au +	-1 +	2 -	- 3 -	+ 4	- 3 -	-2 -1	
	July 31	Aug. 30	Sept. 7	Oct. 6	Nov. 3	Dec. 2	Jan. 6	Feb. 6	Mar. 2	
0.1 m	8.44	8.87	8.46	8.13	8.04	7.91	7.86	7.38	7.13	
0.5				8.25	8.12	7.90	7.86	7.38	7.28	
1 m			8.48	8.23	8.07	7.92	7.86	7.37	7.28	
2			8.43	8.23	8.04	7.90	7.72	7.30	7.30	
3			8.42	8.25	8.05	7.92	7.64			
4			8.42	8.24	8.04	7.90	7.48			
5			8.43	8.25	8.07	7.92	7.38			
				Table 30	continued					
	с	ive		+	+1 +2			+3		
	Apr. 3	Apr. 14	Apr. 25	May 3	May 15	May 26	June 4	June 18	July 2	
0.1 m	7.48	8.37	9.12	8.93	9.01	9.10	9.37	9.55	9.32	
0.5	7.49	8.37	9.11	8.92	9.02	9.10	9.42	9.54	9.32	
1 m	7.48	8.36	9.11	8.87	9.02	9.10	9.32	9.45	9.32	
2	7.42	8.36	9.10	8.78	9.01	8.96	8.56	9.18	9.32	
3	7.32	8.34	8.96	8.67	9.02	8.57	8.22	8.68	9.24	
4	7.09	8.34		7.86			7.88			
5	6.80	8.35		7.57			7.39			

TABLE 30. Frederiksborg Slotssø, pH fluctuations in 1950-51.

the pH graph of Gribsø is always *clinograde*, but then grows gradually *negative or acid heterograde*. It is noteworthy that the *water layer exhibiting the lowest pH value is also shifted upwards during summer and winter stagnation*. ÅBERG and RODHE (1942, p. 223) have pointed out that the smallest value of the vertical pH series from lake Skärshultsjön is shifted upwards during summer stagnation. This slightly acid lake exhibits a specific conductivity nearly identical with that of Grane Langsø, but its water is brown like that of Gribsø. The specific conductivity of the surface water of Gribsø fluctuated around 130 reciprocal megohms (cf. BERG and CLEMENS PETERSEN 1956, p. 139). On January 28th, 1950, it amounted, however, to 273 reciprocal megohms for the 11 m layer.

KROGH and LANGE'S pH determinations from lake Furesø (1931, p. 33) and those made by NYGAARD (cf. BERG et al. 1958, p. 102) do not allow reliable conclusions, either on the shape of the pH graphs in the stagnation periods, or on the occurrence of the maxima and minima of pH.

SIGURD OLSEN made regular pH determinations in the permanently alkaline and large ponds Lyngby Sø and Bagsværd Sø (1955, p. 89–90). The highest values occurred in July or August, whereas somewhat smaller ones were measured in April or June. The deepest pH minimum was observed in November or December; a secondary minimum occurred in March.



Fig. 21. The yearly fluctuations of pH in lake Gribsø. An individual pH value represents the arithmetic mean of the 12 measurements from a vertical series. The onset of the autumnal and vernal circulation is indicated by oppositely directed arrows. The lake was icebound from about January 7th to March 15th, 1950.

NYGAARD examined how pH fluctuated in the surface water of 14 North Zealandic ponds (1938, p. 542). The majority of the alkaline and moderately acid ponds exhibited two annual pH maxima, one in July or August, the other in April or May. The lowest pH values usually were observed in October–November or February– March. A rise of pH occurred in all the ponds except one, shortly after the ice had been broken up.

The results of these two investigations on the yearly pH fluctuations agree very well with the results obtained from Grane Langsø. A pH minimum in late November, due to acid-reacting substances other than CO_2aq , may be proved in Grane Langsø by reliable methods for measuring pH (cf. p. 68).

The results from Grane Langsø, Gribsø, Kattehale Mose, and Frederiksborg Slotssø are outlined in Table 31. Besides the Danish waters, the North American *Lake Mendota*, Wisconsin, is also treated. JUDAY, FRED, and WILSON (1924) made fortnightly pH determinations in this lake by a colorimetric method throughout three years. Considering the measurements from the first two years, where the samples were taken at depths of 0, 5, 10, 15, 20, and 22 m, I suppose that the great majority of the pH graphs may have been clinograde. A positive heterograde vertical distribution of pH seems to be very rare; it occurred on March 14th, 1922.

It seems to be a characteristic feature for Grane Langsø that its surface water

		Surface	Water	Bottom	n Water
		pH-maxima	pH-minima	pH-maxima	pH-minima
	March 1958 – July 1958				- 1. cive (April)
Lake	August 1958 – July 1959	$\frac{-2. \text{ ciau (July)}}{\text{cive } + 1. \text{ (March)}}$		cive + 1. (March)	- 1. ciau (Aug.) - 1. cive (Febr.)
Grane Lang- sø	August 1959 – July 1960	$\begin{tabular}{ c c c c }\hline &-2.ciau(July)\\\hline cive+1.(April)\\\hline \end{tabular}$	$\frac{ \text{cive } + 1. \text{ (March)} }{\text{ciau } + 1. \text{ (Sept.)}}$	cive + 1. (April)	- 1. ciau (Aug.) - 2. to - 1. cive (FebrMarch)
	August 1960 - July 1961	$\boxed{\begin{array}{c} -2. \operatorname{ciau} (\operatorname{June}) \\ \operatorname{cive} +3. (\operatorname{April}) \end{array}}$	cive + 1. (Febr.)	cive +2. (April)	- 1. ciau (Aug.) - 1. cive (JanFebruary)
Lake Grib-	June 1949– June 1950	- 5. ciau = cive+3. (June-July)	cive + 1. (March)	-1. ciau (Oct.); -4. ciau (August)	- 1. cive (Febr.) cive +3. (May- June).
SØ	July 1950– July 1951	cive + 3. (June)	cive + 1. (April)		
	August 1919 –August 1920	 -3. ciau to ciau +3. (Aug. to Febr.); cive +2. and +3. (June and July). 	-1. cive (March); cive +4. (July- August).	ciau + 1. (Nov.); cive + 1. (April)	- 2. and - 1. ciau (Sept. and Oct.) - 4. ciau (August); - 2. and - 1. cive (March)
Lake Men- dota	Sept. 1920 – Oct. 1921	 - 3. ciau to ciau (Aug. to Oct.); - 2. ciau and - 1. ciau (Aug. and Sept.) - 2. cive and -1. cive (Jan. and Febr) 	ciau to ciau + 2. (Nov. to Jan.); cive to cive + 4. (March to July).	ciau + 1. and + 2. (NovJan.); cive + 1. (March- April)	 1. ciau (Sept.) 2. and - 1. cive (February)
Katte- hale Mose	{ July 1950– July 1951	-1. ciau (Sept.); ciau +3. (Dec.).	$\hline \begin{array}{ c c } \hline cive + 1. and + 2. \\ \hline (April and May) \\ \hline ciau + 2. (Nov.). \end{array}$	ciau +3. (Dec.) -3. ciau (July)	-2. cive (Febr.) ciau +2. (Nov.)
Frede- riks- borg Slots- sø	July 1950– July 1951	cive + 3. (June) -1. ciau (August).	- 2. cive (March).		- 1. cive (April)

TABLE 31. The occurrence of maxima and minima of pH in various waters.

usually develops two yearly pH maxima, lying in -2. *ciau* (July or June) and *cive* +1. (March or April). An annual pH-minimum is likewise situated in *cive* +1. (February or March), in which feature it is similar to lake Gribsø. A pH maximum often seems to occur in *cive* +3. In Gribsø; the same is observed in Grane Langsø. In the case of Lake Mendota, it is difficult to recognize general features as to the occurrence of maxima and minima confined to its surface water.

Regarding the *bottom water* Grane Langsø is characterized by having a pH maximum in *cive* +1. (March or April); this also happens in Lake Mendota. The pH minima occurred in -1. *cive* (January-April) and -1. *ciau* (August). In these points Grane Langsø highly resembles Lake Mendota, but also in lake Gribsø, Kattehale Mose, and Frederiksborg Slotssø the minima can occur in -1. *cive*.

It seems to be a recurrent event in the eutrophic and permanently alkaline Lake Mendota for one of the two yearly pH maxima of its bottom water to occur in *ciau* +1. (November), an event never observed in the continuously acid lakes Grane Langsø and Gribsø.

The survey of Table 31 may be simplified as follows:

Surface waters

The *pH-maxima most frequently* occurred in the *second month before ciau*, but also possibly the first one. Maxima were further observed in the *third month after cive*.

The *pH* minima were most often observed in the *first month after cive*.

Bottom waters

The *pH* maxima most frequently lay in the first month after cive.

The *pH* minima generally were found in the *first* month before cive, possibly the second one. Minima were also observed in the *first* month before ciau.

13. The Hydrogen Carbonate Ion

The quantities of $HCO_3^- \cdot l^{-1}$ have been calculated with the aid of the equation on p. 57:

$$\log c_{\mathrm{HCO}\overline{3}} = -\mathrm{pH}$$

If the uncertainty of the pH calculations as estimated is ± 0.1 unit, the uncertainty of the HCO₃⁻ quantities approximates 35 per cent, as shown on p. 47. The HCO₃⁻ values stated in Survey of the Analyses on p. 91 are given with one decimal place.

As pH has not always been measured electrometrically by a safe method I Biol. Skr. Dan. Vid. Selsk. 14, no. 2. 6



Fig. 22. The distribution of the results from the calculation of the hydrogen-carbonate ion in Grane Langsø. Note the logarithmic scale of the abscissa.

think it not being advisable to treat the subject HCO_3^- in such detail as that of carbon dioxide.

As previously mentioned the alkalinity of Grane Langsø must be very small, since the titration values approached nil (cf. p. 17). This conclusions has been entirely confirmed by the results obtained with the aid of KROGH and REHBERG's method for determining total carbon dioxide. About 94 per cent of the total number of $HCO_3^$ calculations (492) from Grane Langsø lay between 0.1 and 0.3 mg $HCO_3^- \cdot l^{-1}$ (cf. Fig. 22), corresponding to alkalinity values between 0.002 and 0.005 mval· l^{-1} . The highest value ever calculated amounted to 0.7 mg· l^{-1} or an alkalinity of 0.01 mval· l^{-1} .

The titration alkalinity of water from the hydrogen-carbonate lake Furesø varies around 2.6 mval·l⁻¹ according to BRØNSTED and WESENBERG-LUND (1912, p. 448). KROGH und LANGE (1931, p. 33) and JONASSON and MATHIESEN (1959, p. 159) found values about 2.3 mval·l⁻¹. The alkalinity values of Grane Langsø, stated as hydrogencarbonate ion concentration, amount to about 0.0025 mval·l⁻¹, thus nearly one thousand times smaller than those of lake Furesø.

The yearly fluctuations of the ion in question during a period of 3 years are given in Table 32.

The difference between the lowest and highest value of the individual years thus fluctuates only between 0.5 and 0.6 mg $HCO_3^- \cdot l^{-1}$, being on an average 0.6 mg.

The greatest difference between the extremes within a single vertical series amounts to about 0.5 mg $HCO_3^- \cdot l^{-1}$, as shown in Table 33. The amplitudes of the various

Period	Yearly extremes of HCO_3^-	Fluctuation
March 1958 – July 1958	$0.1 \begin{cases} (May 26th, 2 m, 6 m, 8 m) \\ (June 18th, 8 m) \\ (July 2nd, 6 m) \\ 0.5 (April 5th, 11 m) \end{cases}$	0.4
August 1958 - July 1959	0.1 (July 21st, 6 m) 0.6 (August 24th, 11 m)	0.5
August 1959	$\begin{array}{l} 0.1 \\ \left\{ \begin{array}{l} ({\rm May \ 14th,\ 6\ m}) \\ ({\rm July \ 27th,\ 4\ m}) \\ 0.7 \end{array} \right. \\ \left. ({\rm August\ 23rd,\ 11\ m}) \end{array} \right. \end{array}$	0.6
August 1960	0.1 {(April 23rd, 8-10 m) (June 15th, 0-6 m) 0.7 (August 28th, 11 m)	0.6

TABLE 32. The yearly fluctuations of the quantities of HCO_3^- , stated as $mg \cdot l^{-1}$, in Grane Langsø.

TABLE 33. The greatest annual amplitudes, stated as mg $HCO_3^- \cdot l^{-1}$, within the single vertical series of Grane Langsø.

Winter stagnation period	Greatest difference	Summer stagnation period	Greatest difference
April 5th, 1958	0.5 - 0.2 = 0.3	August 24th, 1958	0.6 - 0.2 = 0.4
February 8th, 1959	0.5 - 0.2 = 0.3	August 23rd, 1959	0.7 - 0.2 = 0.5
January 31st, 1960	0.3 - 0.2 = 0.1	August 28th, 1960	0.7 - 0.2 = 0.5
February 12th, 1961	0.4 - 0.2 = 0.2	July 9th, 1961	0.4 - 0.1 = 0.3

years are about 0.1 to 0.3 mg \cdot l⁻¹ in the winter stagnation period, and about 0.3 to 0.5 mg \cdot l⁻¹ in the summer stagnation period.

The vertical distribution of HCO_3^- was orthograde, of course, in the circulation periods, and always inverse clinograde in the winter stagnation period. In the summer stagnation period the vertical distribution was either negative heterograde, the minimum occurring in subsurface depths of 4 m, 6 m, or 8 m, or inverse clinograde, the latter being always observed at the end of the period (August). The negative heterograde distribution, often established in June and July, is connected with the relatively strong photosynthetic activity of the plankton algae in the subsurface depths mentioned.

14. The Movement of a Winter Thermocline

After a detailed examination of the thermal conditions and the stratification of total carbon dioxide during the winter stagnation period of 1960 (see p. 101 and Fig. 11), it is suggested that a thermocline has moved upwards to the ice from the deeper levels in Grane Langsø. Fig. 23 should illustrate this assumption.



The lake was nearly homogeneous as to temperature and total CO_2 before the ice-cover. At the beginning of January 1960 the lake had frozen over. On January 17th an upper thermocline, $\frac{d\theta_z}{dz} = 0.65$, between 0 and 2 m, and a lower thermocline, $\frac{d\theta_z}{dz} = 0.50$, between 6 and 8 m, were established.

During the two following months $\frac{d\theta_z}{dz}$ of the upper thermocline steadily increased up to 1.60 on March 13th. Regarding the lower-thermocline, the $\frac{d\theta_z}{dz}$ values of the 6–8 m level decreased to 0 on March 13th, whereas the $\frac{d\theta_z}{dz}$ values of the 4–6 m level were steadily increasing from 0.05 in January to 0.20 on March 13th. These facts demonstrate a shift upwards of the lower thermocline. Unfortunately no observations were possible between March 13th and 26th, when the lake became open. Temperature measurements of previous years seem, however, to indicate a further raising of the lower thermocline at the end of the ice-cover.

Table 34 indicates an increase of the $\frac{d\theta_z}{dz}$ value for the 0–1 m layer from 1.6 to 2.0 in March–April 1958, while the corresponding value for the 1–2 m layer simultaneously decreases from 1.1 to 0.4.

]	March 9, 1958 Ice 10 cm thick			April 5 ce 20 ci	, 1958 n thick	March 29, 1951 Ice 15 cm thick		
2	θ_z	$\frac{d\theta_z}{dz}$	mg HCO₃·l−1	θ_z	$\frac{d\theta_z}{dz}$	mg HCO₃·l−1	θ_z	$\frac{d\theta_z}{dz}$	$\begin{array}{c} \text{mg} \\ \text{HCO}_{3}^{-} \cdot l^{-1} \end{array}$
0 m	0.2°	1.6	0.2	1.1°	2.0	0.2	1.3°	2.9	
1	1.8°	1.0		3.1°	0.4		4.5°	0.2	
2	2.9°	0.2	0.2	3.5°	0.2	0.2	4.5°	0.1	
3	3.1°	0.2		3.7°	0.2		4.4°	0.1	
4	3.3°	0.2	0.2	3.7°	0.1	0.2	4.4°	0	
5		0.1		3.8°	0.1		4.4°	0	unknown
6	3.5°		0.2	4.0°	0.2	0.3		0	
7		0.2			0		4.4°		
8	3.9°		0.3	4.0°		0.3		0	
9		0.1			0.05		4.4°	0	
0	4.1°	0	0.3	4.1°	0.25	0.3	4.4°	0.75	
11	4.1°		0.4	4.35°	0.20	0.5	5.0*)	0.75	

TABLE 34. The position of the thermoclines in Grane Langsø at the end of the winter stagnation period in 1958 and 1951.

*) in 10.8 m depth.

Conditions on March 29th, 1951, represent the final stage just before the tender ice was breaking up. Here the $\frac{d\theta_z}{dz}$ value for the 0–1 m layer is large, 3.2, while the 1–2 m value has decreased to 0, indicating that the lower thermocline has now joined with the upper thermocline.

The solar radiation on March 29th, 1951, and the preceding days contributed to the heating to 4.5° C of the 1–2 m water layer below the ice. Heat given off from the bottom sediments can create vertical currents; how high up in the lake they will reach depends on their densities. The third way in which the water volume below the ice is warmed up is referred to by HUTCHINSON (1957, p. 454 and 456). Centripetal melt water currents from the ice margin run on mild days across the sloping lake bottom, taking up electrolytes and so increasing in density.

On the bright days around March 29th, 1951, a zone about 10 m broad of icefree water was formed each afternoon along the margin of Grane Langsø; next morning this zone had frozen over again. On the data in question the water from 10.8 m measured 5° C. This water from about 0.7 m above the lake bottom must have a greater density than the water from 10 m (4.4° C) , in spite of its higher temperature.

Temperatures of more than 4° C below ice have been observed in the 11 m layer of Grane Langsø in 1951 (5° C), 1958 (4.35° C), 1959 (4.4° C), and 1960 (4.3° C).

As one mg $\text{HCO}_3^- \cdot \text{I}^{-1}$ increases the density of distilled water by 0.000 0018, it is possible to calculate the density changes from distilled water, caused by the HCO_3^- quantities met with on April 5th, 1958 (HUTCHINSON 1957, p. 676 and 204–205).

Table 35 gives the reader an idea of the density changes of the Grane Langsø water, caused exclusively by HCO_3^- at the end of the winter stagnation. It is evident that ions other than HCO_3^- have been liberated from the bottom deposits to the 10 m and 11 m layers in greater quantities than to the other water layers. As the concentrations of the other ions are unknown for the series of April 5th, 1958, it is not possible to comment on the real densities at the various levels of Grane Langsø, except that all the figures must be larger than those stated in Table 35. It is possible that the

depth	temp.	density of pure water	mg $HCO_3 \cdot l^{-1}$	density of pure water $+ \text{HCO}_3^-$		
0 m	1.1	0.999 9315	0.2	0.999 9319		
2	3.5	0.999 9981	0.2	0.999 9985		
4	3.7	0.999 9994	0.2	0.999 9998		
6	4.0	1.000 0000	0.3	1.000 0005		
8	4.0	1.000 0000	0.3	1.000 0005		
0	4.1	0.999 9999	0.3	1.000 0004		
1	4.35	0.999 9989	0.5	0.999 9998		

TABLE 35. The density increase from distilled water, caused by the quantities of HCO_3^- in Grane Langsø on April 5th, 1958.



Fig. 24. The movements of the low-lying thermoclines in Grane Langsø. The pairs of vertical arrows stand for the circulation periods. The short horizontal lines represent the average depths of the thermoclines. The broken lines indicate the probable movements of the thermoclines.

increase of the $\frac{d\theta_z}{dz}$ values for the 10–11 m layer from 0 to 0.75 (see Table 34) are due to "chemical density currents".

The information given above makes it probable, that if the duration of the icecover is 2-4 months, a lower thermocline above the lake bottom will gradually move upwards, finally reaching the primary (upper) thermocline immediately below the ice, and then disappear at the onset of the vernal circulation.

The best possible way to prove the correctness of this hypothesis is to use thermistor thermometers in connection with recorders, which continually register the temperatures of the various levels in a period prior to the breaking up of the ice.

In order to give a survey of the movements of the thermoclines in Grane Langsø, Table 36–37 have been made. Fig. 24 is a diagram based on Table 37, thus demonstrating how, on an average, the lower thermocline behaves during the winter stagnation period, and how the thermocline of the summer stagnation period proceeds.

The preparation of Table 37 and the diagram Fig. 24 presented some problems. The duration of the ice-cover in the five best investigated winters is from about 35 days to about 110 days, on an average about 80 days. In the preparation of Table 36 and 37 the winter stagnation period is considered to last from early January to late March.¹ The vernal circulation normally occurs at the transition from March to April, after which the summer stagnation period extends to the end of August. The exceptional series from April 5th, 1958, when the lake was icebound, is disregarded. Also the temperature series measured in February and March, when the lake was

^{*)} In 1962 the ice broke up about April 6th, and in 1964 about April 1st.

TABLE 36. The depths of the thermoclines in Grane Langsø.

	From January 1st to January 15th: no observations.
January.	17.i.1960: 6-8 m. 18.i.1959: 8-10 m. 22.i.1961: 10-11 m. 26.i.1958: 10-11 m. 31.i.1960: 6-8 m.
February.	8.ii.1959: 6-8 m. 12.ii.1961: 8-10 m. 14.ii.1960: 2-4 m. 23.ii.1951: 1-2 m. 28.ii.1960: 6-8 m.
March.	9.iii.1958: 1-2 m. 13.iii.1960: 4-6 m. 29.iii.1951: 0-1 m. 27.iii.1964: 0-1 m.
April.	5.iv.1953: 2-6 m. 9.iv.1961: 2-4 m. 10.iv.1960: 0 m. 20.iv.1962: 2-4 m. 21.iv.1951: 1-3 m.
	21.iv.1957: 1-2 m. 23.iv.1961: 6-8 m. 24.iv.1960: 0 m. 25.iv.1959: 4-6 m.
May.	3.v.1958: 6-8 m. 6.v.1957: 0 m. 7.v.1961: 8-10 m. 14.v. 1960: 4-6 m. 16.v.1959: 6-8 m.
	17.v.1957: 1-2 m and 5-6 m. 21.v.1961: 8-10 m. 23.v.1951: 6-7 m. 26.v.1958: 8-10 m. 29.v.
	1957: 5–6 m. 29.v.1960: 6–8 m.
June.	4.vi.1961: 10-11 m and 2-4 m. 10.vi.1959: 6-8 m. 15.vi.1960: 6-8 m. 15.vi.1961: 4-6 m and
	8-10 m. 16.vi.1957: 2-3 m and 7-8 m. 18.vi.1958: 6-8 m. 26.vi.1951: 6-7 m. 28.vi.1960: 6-8 m.
July.	2.vii.1958: 6-8 m. 5.vii.1957: 7-8 m. 6.vii.1959: 8-10 m. 9.vii.1961: 10-11 m. 7.vii.1955: 5-6 m
	and 8-9 m. 15.vii.1954: 8-9 m. 15.vii.1958: 6-8 m. 18.vii.1955: 5-6 m. 20.vii.1951: 7-9 m.
	20.vii.1957: 7-8 m. 21.vii.1959: 8-10 m. 23.vii.1961: 8-10 m. 24.vii.1962: 8-10 m. 27.vii.1960:
	8–10 m. 31.vii.1954: 8–9 m.
August.	1.viii.1958: 8-10 m. 4.vii.1957: 10-11 m. 8.vii. 1950: 10-11 m. 9.vii.1960: 8-10 m. 10.viii.
	1959: 8–10 m. 23.viii.1959: 10–11 m. 24.viii.1958: 10–11 m. 28.viii.1960: 10–11 m.

ice-free and isothermal, are left out of account. If two thermoclines occurred simultaneously, only the low-lying one is included in the calculation of the figures in Table 37.

The diagram Fig. 24 indicates a rather rapid shiftning of the lowlying winter thermocline from the bottom water to the lake surface. This movement should ordinarily be finished within about 3 months. The summer thermocline, however, has about 5 months to move from the surface to the lake bottom. The fall of the thermocline is very rapid in April–May, but slow in June-July, after which the fall again becomes rather rapid.

The thermocline of June–July as a rule lies in a subsurface depth of 8 to 8.5 m. In these two summer months a rather stable stratification occurs in the lake. The material is too scanty to decide whether or not a temporary stratification is present at the change from February to March in a subsurface depth of 3.5 to 4 m.

January	First half:	?	latter half:	8.9 m
February	First half:	6.3 m	latter half:	4.3 -
March	First half:	3.3 -	latter half:	0.5 -
April	First half:	2.3 -	latter half:	3.1 -
May	First half:	5.3 -	latter half:	7.1 -
June	First half:	8.4 -	latter half:	7.0 - (?)
July	First half:	8.3 -	latter half:	8.2 -
August	First half:	9.6 -	latter half:	10.5 -

TABLE 37. The average depths of the low-lying thermoclines in Grane Langsø.

15. Summary

The Danish *Lobelia-lake* Grane Langsø, lying on *stratified drift*, covers an area of 11.38 ha and has a maximum depth of 11.5 m. The *transparency* fluctuates between 4 m and at least 11.5 m.

This tunnel-valley lake has no visible affluents and effluents. Section 3 represents a preliminary study of the *water balance* of Grane Langsø. An attempt has been made to determine the flow of the sub-lacustrine inlet by means of the chloride content of the air and precipitation.

With the aid of Krogh and Rehberg' method the total CO_2 quantity has been measured fortnightly or monthly in seven levels of the lake for more than three years. The standard deviation on a single determination is 0.07 mg total $CO_2 \cdot l^{-1}$.

Grane Langsø is poor in CO_2 , values generally varying between 0.27 and 1.71 mg·l⁻¹; the absolute extremes were 0.27 and 14.89 mg·l⁻¹.

The lake is *moderately acid* with pH-values usually fluctuating between 5.4 and 5.7; the absolute pH-extremes were 4.9 and 5.9. Comparisons with pH measurements from Gribsø are made.

A critical examination of the electrometric pH measurements has rendered it probable that some of the determinations are not reliable owing to the loss or uptake of CO_2 by diffusion during the measurement. A comparison between the pH values computed on the assumption that pH is in all essentials determined by the CO_2 concentration of the lake water, and the pH values being measured when the temperature and the CO_2 tension of the lake water correspond to the temperature of the laboratory room and the CO_2 pressure there, revealed a good agreement. The pH values of Grane Langsø, given in this paper, are computed from the quantities of total $CO_2 \cdot l^{-1}$.

As the activity coefficient of HCO_3^- proved to come very close to 0.97, the unmodified HENDERSON-HASSELBALCH equation was employed for *computation of the* HCO_3^- quantities. They normally lay between 0.1 and 0.3 mg·l⁻¹; the absolute extremes were 0.1 and 0.7 mg·l⁻¹. The HCO_3^- alkalinity thus lies as low as 0.002–0.005; the greatest alkalinity ever calculated was 0.01 mval·l⁻¹.

The occurrence of the maxima and minima of these and other factors has been described relative to the *two crucial points in the annual cycle of a lake*: the moments of the vernal turnover (here called *cive*) and the autumnal turn-over (designed *ciau*).

Grane Langsø usually liberates CO_2 to the atmosphere apart from the periods of April–May and July–August, when the lake generally absorbs some CO_2 from the atmosphere.

Phosphate has been determined monthly within one year for five levels of the lake. Grane Langsø also turned out to be poor in phosphate-phosphorus, as no determination attained the value $0.01 \text{ mg} \cdot l^{-1}$.

The results of the *phosphate* and *iron determinations* from Grane Langsø are compared with the corresponding ones from *lake Gribsø* and other Danish waters.

The specific conductivity varied little about 50 reciprocal megohms (extremes 48 and 57), and the ionic strength was as low as about 0.00065; 0.94–0.98 mval ions $\cdot 1^{-1}$ were found. Grane Langsø is a sodium chloride lake, the ionic diagram of which highly resembles that of seawater. The equivalent percentages of SO_4^{--} and especially Ca^{++} is far greater, however, than the corresponding ones of seawater. A comparison between the ionic composition of the lake water and that estimated for the precipitation falling over the lake, renders it probable that Grane Langsø contains rainwater in a somewhat concentrated state, but with an extra supply of chloride, which possibly originates from selective vegetation capture of the large NaCl-condensation nuclei from the air.

The causes of the strongly decreasing Ca⁺⁺ content of *lake Gribso during the Sub*atlantic Period are reconsidered in the light of W. OHLE's discovery of the effect of "Laubdy" in removing Ca⁺⁺ and HCO_3^- from lake water.

The hypothesis is advanced that in Grane Langsø, which normally is ice-covered for a few months, a thermocline is moving upwards during the winter stagnation period from the deepest parts of the lake to the ice-cover. This thermocline reaches the lake surface at the onset of the vernal turn-over.

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17. Survey of the Analyses

August 8, 1950.		•			
0 m	20.6° C	4 m	20.15° C	8 m	19.65° C
1	20.45° C	5	20.1° C	9	19.6° C
2	20.25° C	6	20.0° C	10	18.95° C
3	20.2° C	7	19.9° C	10.8 m	16.6° C
September 27, 1950.					
0 m	14.8° C	5 m	14.8° C	10.8 m	14.9° C
1	14.8° C	7	14.8° C		
3 m	14.8° C	10	14.8° C		
October 26, 1950.					
1 m	9.8° C	5 m	9.8° C	10 m	9.8° C
3	9.8° C	7	9.8° C		
November 26, 1950.					
1 m	4.6° C	5 m	4.6° C	10 m	4.6° C
3	4.6° C	7	4.6° C		
December 20, 1950. Ic	e 11 cm thick !				
0.11 m	1.1° C	3 m	2.9° C	7 m	3.3° C
1 m	2.2° C	4	3.0° C	8	3.4° C
2	2.7° C	5	3.1° C	10	4.0° C
January 24, 1951. Ice	e 21 cm thick.				
0.21 m	0.5° C	3 m	3.0° C	10 m	4.25° C
1	2.0° C	5	3.3° C		
2	2.85° C	7	3.95° C		
February 23, 1951. Ic	e 20 cm thick.				
0.2 m	0.4° C				
1 m	1.75° C	0.01 mg Fe ⁺⁺ ·l ⁻¹	O ₂ -saturation	93°/0	
2	2.7° C				
3	3.2° C	0.01	_	92°/0	
5	3.8° C	0.01		90°/0	
7	4.25° C	0.01		77%/0	
10	4.3° C	0.03		73.5%	

March 29, 1951. Ice 1	15 cm thick.					
0.15 m	1.3° C	4 m		4.4° C	10 m	4.4° C
1 m	4.5° C	5		4.4° C	10.8 m	5.0° C
2	4.5° C	7		4.4° C		
3	4.4° C	9		4.4° C		
April 21, 1951.						
0 m	6.9° C	5 m		6.2° C	11 m	5.8° C
1	7.0° C	7		6.2° C		
3	6.45° C	10		5.8° C		
May 23, 1951.						
1 m	14.45° C	5 m		12.95° C	9 m	7.6° C
2	14.1° C	6		11.65° C	10	7.5° C
3	14.0° C	7		9.05° C	11	7.7° C
4	13.9° C	8		7.9° C		
June 26, 1951. Trans	parency 10.25 m	at 17.30 l	hours.			
1 m	17.5° C	6 m		17.2° C	9 m	11.3° C
3	17.5° C	7		14.5° C	10	11.05° C
5	17.25° C	8		12.4° C	11	10.9° C
July 20, 1951. Transp	parency 10.25 m a	at 17.00 o	n July 26t	h.		
1 m	17.3° C	6 m		17.05° C	9 m	13.4° C
3	17.25° C	7		17.0° C	10	12.9° C
5	17.1° C	8		15.2° C	11	12.8° C
April 5, 1953.						
0 m	6.4° C					
1		oxygen	saturation	97º/0		
2	6.4° C					
3		-	-	96°/0		
4	6.1° C					
5		-		96º/0		
6	5.8° C					
7		-	-	95°/0		
8	5.6° C					
10	5.6° C	-		95°/0		
11	5.6° C					
July 15–19, 1954.						
1 m	17.9° C	oxygen	saturation	$102^{0}/_{0}$		
3	17.8° C					
5	17.6° C					
6	17.4° C					
7	16.7° C	oxygen	saturation	$102^{0}/_{0}$		
8	15.0° C	-	-	1090/0		
9	12.9° C		-	107%/0		
10	12.2° C					
11	11.8° C		-	90%		

July 31, 1954.					
1 m	17.3° C	8 m	16.7° C	10 m	12.9° C
7	16.9° C	9	13.9° C	11	12.4° C
August 3rd, 1954. Tr	ansparency 11 m.				
July 7, 1955. Transp	arency more than	11 m.			
$0\ m\ \ldots\ldots\ldots$	19.1° C	4 m	. 17.3° C	8 m	13.3° C
1	19.2° C	5	16.6° C	9	12.1° C
2	18.8° C	6	. 15.1° C	10	11.7° C
3	18.0° C	7	. 14.4° C	11	11.8° C
July 18, 1955.					
0 m	23.0° C	oxygen saturation	$102^{0}/_{0}$		
1	22.65° C		$101^{0}/_{0}$		
2	22.5° C		101º/o		
3	22.4° C		100%		
4	20.8° C		109%		
5	19.1° C		108%		
6	17.3° C		1110/0		
7	15.9° C		109%		
8	14.6° C		112%		
9	13.45° C		10		
10	13.0° C	_	110%		
11	12.7° C				
11.8 m	12.6° C		100º/ ₀ 75 Urogler	na-col.∙ml ⁻¹ .	
October 20, 1956.		November 11, 1956			
1 m	11.4° C	1 m	6.9° C		
11	11.4° C	11	6.9° C		
December 1, 1956.		December 30, 1956.			
1 m	4° C	1 m	. 1.6° C		
11	4° C	11	2.1° C		
February 3 1057		March 3 1957		April 7 1957	
1 m	2 3° C	1 m	1.4° C	1 m	6 65° C
5	2.5 C	5	. 4.4 C	5	6.3° C
J	2.55 G	J =	. 3.5 C	11	5.1° C
11	2.4 G	Ice 8 cm thick on	March 3, 1957.	11	J.I G
April 21, 1957.					Sec.
1 m	8.1° C	5 m	. 7.5° C	9 m	7.4° C
2	7.7° C	6	. 7.5° C	10	7.2° C
3	$7.6^{\circ} \mathrm{C}$	7	. 7.5° C	11	7.1° C
4	7.5° C	8	. 7.5° C		
May 6, 1957.					
1 m	9 7° C	6 m	. 8.7° C	10 m	8.7° C
	0.7 4	0 m		*** ··· · · · · · · · · · · · · · · · ·	
3	8.7° C	7	. 8.7° C	11	8.7° C
3 4	8.7° C 8.7° C	7 8	. 8.7° C . 8.7° C	11	8.7° C

93

May 17. 1957.					
1 m	13.1° C	5 m	11.1° C	9 m	10.0° C
2	11.9° C	6	10.55° C	10	10.0° C
3	11.7° C	7	10.4° C	11	9.9° C
4	11.6° C	8	10.1° C		
May 29, 1957.					
1 m	13.4° C	5 m	13.4° C	9 m	10.8° C
2	13.4° C	6	12.3° C	10	10.8° C
3	13.4° C	7	11.3° C	11	10.5° C
4	13.4° C	8	11.1° C		
June 16, 1957.					
1 m	19.4° C	5 m	16.7° C	9 m	14.8° C
2	19.0° C	6	16.5° C	10	14.4° C
3	17.45° C	7	16.3° C	11	14.15° C
4	16.95° C	8	15.3° C		
July 5, 1957.					
0 m	19.5° C	4 m	19.6° C	8 m	17.1° C
1	19.5° C	5	18.75° C	9	16.65° C
2	19.6° C	6	18.4° C	10	15.9° C
3	19.4° C	7	18.05° C	11	15.9° C
July 20, 1957.					
1 m	20.0° C	5 m	19.9° C	9 m	17.4° C
2	20.1° C	6	19.7° C	10	17.25° C
3	20.0° C	7	19.5° C	11	17.0° C
4	20.0° C	8	18.1° C		
August 4, 1957.					
1 m	19.3° C	6 m	18.6° C	9 m	18.4° C
3	19.1° C	7	18.6° C	10 m	18.15° C
5	18.8° C	8	18.6° C	11	17.1° C
September 1, 1957.					
1 m	17.2° C	5 m	16.9° C	9 m	16.8° C
2	17.2° C	6	16.9° C	10	16.8° C
3	17.2° C	7	16.85° C	11	16.8° C
4	17.1° C	8	16.8° C		
September 21, 1957.					
1 m	14.6° C	8 m	14.6° C	10 m	14.5° C
5	14.6° C	9	14.5° C	11	14.5° C
7	14.6° C				
October 17, 1957.					
1 m	11.15° C	11 m	11.2° C		
December 29, 1957.					

94
Nr. 2

January 26, 1958. Ice	10 cm thick, co	vered	with 5 cm sn	low.									
0.1 m	0.55° C	4 m			2.4°	С		10 m				. 3.	.3° C
1 m	1.9° C	6 -			2.85	5° C		11 -				. 3.	.9° C
2	2.1° C	8 -			2.9°	С							
March 9, 1958. Ice 10	em thick.												
0.1 m	0.2° C	pH	5.6	1.37	mg	total	CO	1-1		0.2	mg	HCO	$- \cdot l^{-1}$
1 m	1.8° C				0		-				0		3
2	2.9° C	-	5.5	1.41	-	-	-	-		0.2	-	-	· _
3	3.1° C												
4	3.3° C	_	5.5	1.59	-	-	-	-		0.2	-	-	_
6	3.5° C	-	5.4	2.12	_	-	_	-		0.2	-	-	-
8	3.9° C	-	5.3	3.83	-	-	-	_		0.3	_	-	-
10	4.1° C	-	5.3	4.38	_	_	_	_		0.3	_	_	_
11	4.1° C	-	5.2	5.18	-	_	-	_		0.4	_	-	_
				0110									
April 5, 1958. Ice 20	cm thick.												
0.2 m	1.1° C	pH	5.6	1.45	mg	total	CO2.	l – 1		0.2	mg	HCO	l-1
1 m	3.1° C						-						3
2	3.5° C	-	5.5	1.61	-	-	-	-		0.2	_	-	_
3	3.7° C												
4	3.7° C	-	5.4	2.50	_	-	-	-		0.2	_	-	-
5	3.8° C												
6	4.0° C	-	5.3	3.25	-	_	-	2		0.3	_	_	-
8	4.0° C	_	5.3	3.48	_	_	_	_		0.3	_	_	_
10	4.1° C	-	5.2	5.05	_	_	_	-		0.3	_	_	_
11	4.35° C	-	5.1	9.88	_	_		-		0.5	-	_	-
	noo u		011	0.00						0.0			
May 3, 1958.													
0 m	8.7° C	pH	5.5	1.37	mg	total	$CO_2 \cdot$	l- 1		0.2	mg	HCO	$\frac{1}{3} \cdot l^{-1}$
2	8.7° C	-	5.5	1.36	-	-	-	-		0.2	-	-	-
4	8.6° C	-	5.5	1.29	-	-	-	-		0.2	-	-	-
6	8.2° C	-	5.5	1.25	-	-	-	-		0.2	-	-	-
8	7.0° C	-	5.5	1.34	-	-	-	-		0.2	-	-	-
10	6.7° C	-	5.5	1.35	-	-	-	-		0.2	-	-	-
11	6.4° C	-	5.6	1.16	-	-		-		0.2	-	-	-
16													
May 26, 1958.	10 =0.0			0.00			0.0					1100	
0 m	12.7° C	рН	5.6	0.80	mg	total	CO_2 .	I-1		0.1	mg	HCO	3.1-1
2	12.7° C	-	5.6	0.75	-	-	-	-		0.1	-	-	-
4	12.2° C	-	5.6	0.86	-	-	-	-		0.1	-	-	-
6	11.8° C	-	5.6	0.79	-	-	-	-	-	0.1	-	-	-
8	10.6° C	-	5.6	0.84	-	-	-	-		0.1	-	-	-
10	9.0° C	-	5.6	1.10	-	-	-	-		0.2	-	-	-
11	8.3° C	-	5.4	2.28	-	-	-	-		0.2	-	-	-
June 18 1958													
0 m	17.8° C	_	5.5	1.10	mø	total	co	1-1		0.2	mø	HCO	1-1
2 -	17.7° C	_	5.5	1 02		-	-			0.2	- 8		3 -
4 -	17.5° C	_	5.6	0.92		_	_	_		0.2		_	
6	16.0° C	_	5.6	0.88	_	_	_	_		0.2	_	_	_
										· ·			

95

8 m	13.15° C	pH 5.6	0.73 mg total $CO_2 \cdot l^{-1}$	$0.1 \text{ mg HCO}_{2}^{-} \cdot l^{-1}$
10	11.3° C	- 5.5	1.23	0.2
11	10.7° C	- 5.5	1.27	0.2
July 2, 1958.				
0 m	21.2° C	pH 5.6	0.80 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO ₂ ⁻ ·l ⁻¹
2	20.4° C	- 5.6	0.89	0.2
4	18.7° C	- 5.6	0.87	0.2
6	18.0° C	- 5.6	0.71	0.1
8	13.85° C	- 5.5	1.11	0.2
10	13.2° C	- 5.5	1.42	0.2
11	12.6° C	- 5.4	1.69	0.2
July 15, 1958.				
0 m	20.75° C	pH 5.5	1.00 mg total $CO_0 \cdot l^{-1}$	$0.2 \text{ mg} \text{HCO}^{-} \cdot 1^{-1}$
2	19.4° C	- 5.5	0.93	0.2
4	19.25° C	- 5.5	1.03	0.2
6 -	19.1° C	- 5.5	1.01	0.2
8 -	15.2° C	- 5.6	0.86	0.2
10 -	13.0° C	- 5.5	1.48	0.2
11 -	12.8° C	- 5.4	2.39	0.3
	12.0 0	0.1	1.00	0.0
Amanet 1 1958				
August 1, 1990.	17 5° C	pH 5.6	0.82 mg total CO $z = 1$	0.9 mg HCO= 1-1
0 m	17.5 C	5.6	0.83 mg total $CO_2 \cdot 1^{-2}$	$0.2 \text{ mg} \text{ HCO}_3 \cdot 1^{-1}$
4	17.5 C	- 5.0	0.79	0.2
4	17.4 C	- 3.0	0.80	0.2
0	17.3 C	- 3.0	0.79	0.2
7	17.2° C	5.0	0.95	0.0
8	17.15 6	- 3.6	0.85	0.2
9	17.0° C		1 50	0.0
10	15.9° C	- 5.4	1.73	0.2
11	14.7° C	- 5.3	3.32	0.3
	and a second second second			
August 24, 1958. Tra	nsparency more t	han 11 m.		
0 m	17.45° C	pH 5.5	1.35 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg} \text{HCO}_3 \cdot 1^{-1}$
2	17.2° C	- 5.5	1.27	0.2
4	17.2° C	- 5.5	1.34	0.2
6	17.1° C	- 5.5	1.30	0.2
8	17.05° C	- 5.5	1.47	0.2
10	16.85° C	- 5.4	2.02	0.2
11	14.7° C	- 5.0	11.15	0.6
September 28, 1958.				
0 m	15.25° C	pH 5.5	1.47 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg HCO}_{3}^{-} \cdot l^{-1}$
2	15.25° C	- 5.5	1.45	0.2
4	15.25° C	- 5.5	1.50	0.2
6	15.25° C	- 5.5	1.45	0.2
8	15.25° C	- 5.5	1.56	0.2
10	15.25° C	- 5.5	1.58	0.2
11	15.2° C	- 5.5	1.49	0.2

Nr. 2

October 23, 1958.												
0 m	11.1° C	pН	5.5	1.48	mg t	otal ($CO_2 \cdot I$	[- 1	0.2	mg	HCO_3^-	$\cdot l^{-1}$
2	11.1° C	-	5.5	1.45	-	-	-	-	0.2	-	-	-
4	11.1° C	-	5.5	1.43	-	-	-	-	0.2	-	-	-
6	11.1° C	-	5.5	1.40	-	-	-	-	0.2	-	-	-
8	11.1° C	-	5.5	1.44	-	-	-	-	0.2	-	-	-
10	11.05° C	-	5.5	1.45	-	-	-	-	0.2	-	-	-
11	11.05° C	-	5.5	1.39	-	-	-	-	0.2	-	-	-
November 23, 1958.												
0 m	7.35° C	рH	5.5	1.69	mg te	otal (CO.•1	- 1	0.2	mg	HCO-	·]- 1
2	7.3° C	-	5.5	1.68	-	_	-	_	0.2	-	- 3	_
4	7.3° C	_	5.5	1.68	-	_	_	-	0.2	-	-	_
6	7.3° C	_	5.5	1.69	-	_	-	-	0.2	_	_	-
8 -	7.3° C	_	5.5	1.71	_	_	_	-	0.2	_	-	_
10 -	7.3° C	_	5.5	1.67	-	_	_	-	0.2	_	-	-
11 -	7.3° C	_	5.5	1.82	_	-	_	-	0.2	_	_	
	1.0 4		0.0	1.01					0.1			
December 29, 1958. T	ransparency more	tha	n 11.5 m.									
0 m	3.35° C	pН	5.5	1.75	mg t	otal ($CO_2 \cdot I$	l-1	0.2	mg	HCO_3^-	·]- 1
2	3.5° C	-	5.5	1.73	-	-	-	-	0.2	-	-	-
4	3.6° C	-	5.5	1.74	-	-	-	-	0.2	-	-	-
6	$3.7^{\circ} \mathrm{C}$	-	5.5	1.72	-	-	-	-	0.2	-	-	-
8	3.75° C	-	5.5	1.80	-	-	-	-	0.2	-	-	-
10	3.85° C	-	5.5	1.75	-	-	-	-	0.2	-	-	-
11	3.9° C	-	5.5	1.75	-	-	-	-	0.2	-	-	-
January 18, 1959. Ice	10 cm thick.											
0.1 m	0.2° C	pН	5.5	1.79	mg t	otal	CO2.	l- 1	0.2	mg	HCO.	• l ⁻¹
2	2.9° C	-	5.5	1.64	-	-	-	-	0.2	-	-	-
4	3.1° C	-	5.5	1.71	-	-	-	-	0.2	-	-	-
6	3.35° C	-	5.5	1.79	-	-	-	-	0.2	-	-	-
8	3.4° C	-	5.4	2.20	-	-	-	-	0.2	-	-	_
10	3.75° C	-	5.3	3.44	-	-	-	-	0.3	-		_
11	3.9° C	-	5.2	5.78	-	-	-	-	0.4	-	-	_
February 8, 1959. Ice	10 cm thick.				0.04		~ ~					
0.1 m	0.9° C	pH	5.5	1.94	mg t	otal	$CO_2 \cdot$	I-1	0.2	mg	HCO ₃	·1-1
2 m	3.3° C	-	5.5	1.47	-	-	-	-	0.2	-	-	-
4	3.4° C	-	5.6	1.30	-	-	-	-	0.2	-	-	-
6	3.45° C	-	5.5	1.63	-	-	-	-	0.2	-	-	-
8	4.0° C	-	5.4	2.23	-	-	-	-	0.2	-	-	-
10	4.1° C	-	5.3	4.24	-	-	-		0.3	-	-	-
11	4.4° C	-	5.1	11.37	-	-	-	-	0.5	-	-	-
March 1, 1959. The n	orthernmost and	sout	hernmost par	t of th	ne lal	ke co	vered	l with thin	ice.			
0 m	4.2° C	рH	5.5	1.73	mg t	otal	CO.	1-1	0.2	mg	HCO.	-1-1
2	4.2° C	-	5.5	1.71	-	-	-	-	0.2	-	- 3	-
4	4.2° C	-	5.5	1.77	-	-	-		0.2	_	_	-
6	4.2° C	-	5.5	1.70	-	-	-	1	0.2	-	-	-
8	4.2° C	_	5.5	1.73	_	-	-	2	0.2	_	_	-
10	4.2° C	_	5.5	1.77	-	-	-	-	0.2	-	_	-
11	4.2° C	-	5.5	1.69	2	-	-	2	0.2	-	4	_
Biol Skr Dan Vid Sels	k. 14. no. 2.											7

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March 26, 1959.				
0 m	4.85° C	pH 5.6	1.33 mg total $\text{CO}_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2	4.85° C	- 5.6	1.20	0.2
4	4.8° C	- 5.6	1.13	0.2
6	4.75° C	- 5.6	1.15	0.2
8	4.7° C	- 5.6	1.14	0.2
10	4.6° C	- 5.6	1.19	0.2
11	4.6° C	- 5.6	1.26	0.2
April 25, 1959.				
0 m	9.35° C	pH 5.6	1.01 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO. ·1-1
2	9.35° C	- 5.6	1.05	0.2
4	9.15° C	- 5.6	0.99	0.2
6	8.4° C	- 5.6	0.90	0.2
7	8.0° C	- 5.6	0.98	0.2 - '
8	7.25° C	- 5.6	0.96	0.2
10	6.95° C	- 5.5	1.22	0.2
11	6.8° C	- 5.5	1.86	0.2
May 16, 1959.				
0 m	15.7° C	pH 5.5	1.44 mg total $CO_{\circ} \cdot l^{-1}$	$0.2 \text{ mg HCO}_{-}^{-} \cdot l^{-1}$
2	15.25° C	- 5.5	1.43	0.2
4	13.8° C	- 5.5	1.39	0.2
6	12.5° C	- 5.5	1.25	0.2
8	10.1° C	- 5.6	1.19	0.2
10	8.5° C	- 5.5	1.60	0.2
11	8.4° C	- 5.5	1.70	0.2
lune 10 1959 Trans	parency 11 m			
0 m	16 75° C	nH 5 5	1.04 mg total CO $\cdot l^{-1}$	$0.2 \text{ mg} \text{ HCO}^{-1-1}$
9 -	16.75° C	- 5.5		$0.2 \text{ mg} \text{ mGO}_3 \text{ m}$
4 -	16.7° C	- 5.5	1.02	0.2
6 -	16.6° C	- 5.5	1.02	0.2
8 -	12.6° C	- 5.6	0.98	0.2
10 -	12.0°C	- 5.5	1.51	0.2
11 -	10.0° C	- 5.4	2.02	0.2
11	10.5 G	- 0.1	2.02	0.2
1.1. 0. 10.00				
July 6, 1959.	10.10.0		0.50	
0 m	19.4° C	pH 5.6	0.78 mg total $CO_2 I \cdot I$	$0.2 \text{ mg} \text{HCO}_3^- \cdot 1^{-1}$
2	18.6° C	- 5.6	0.73	0.2
4	18.2° C	- 5.6	0.70	0.1
6	18.1° C	- 5.6	0.69	0.1
δ	17.6° C	- 5.6	0.86	0.2
10	14.3° C	- 5.5	1.41	0.2
11	13.8° C	- 5.5	1.49	0.2
July 21, 1959.	00.00.0			Stand Maleria
0 m	22.0° C	pH 5.7	0.49 mg total $CO_2 \cdot l^{-1}$	0.1 mg $HCO_3^{-} \cdot l^{-1}$
2	20.95° C	- 5.7	0.46	0.1
4	20.7° C	- 5.7	0.51	0.1

98

N1. 2					
6 m	20.25° C	pH 5.9	0.27 mg	total CO,	· l ⁻¹
8	19.45° C	- 5.8	0.39 -		-
10	16.5° C	- 5.6	0.76 -		-
11	15.9° C	- 5.3	2.70 -		-
August 10, 1959.					
0 m	21.05° C	pH 5.6	0.61 mg	total CO ₂	·1-1
2	20.6° C	- 5.6	0.63 -		-
4	20.4° C	- 5.6	0.61 -		-
6	20.25° C	- 5.7	0.46 -		-
8	20.1° C	- 5.6	0.68 -		-
10	18.0° C	- 5.4	1.67 -		-
11	16.2° C	- 5.1	6.65 -		-
August 23, 1959.					
0 m	21.35° C	pH 5.6	0.84 mg	total CO ₂	· l- 1
2	21.25° C	- 5.6	0.82 -		-
4	20.95° C	- 5.6	0.82 -		-
6	20.7° C	- 5.6	0.85 -		-
8	20.4° C	- 5.5	1.05 -		-
10	18.8° C	- 5.3	2.74 -		-
11	16.6° C	- 5.0	13.07 -		-
September 6, 1959.					
0 m	19.25° C	pH 5.4	1.53 mg	total CO.	·1-1
2	18.7° C	- 5.4	1.62 -		-
4	18.55° C	- 5.4	1.59 -		-
6	18.45° C	- 5.4	1.53 -		_
8	18.4° C	- 5.4	1.63 -		-
10	18.4° C	- 5.4	1.51 -		-
11	18.35° C	- 5.4	1.71 -		-

September 20, 1959.				
0 m	16.9° C	pH 5.5	1.25 mg total $\rm CO_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2	16.9° C	- 5.5	1.21	0.2
4	16.9° C	- 5.5	1.16	0.2
6	16.9° C	- 5.5	1.22	0.2
8	16.85° C	- 5.5	1.26	0.2
10	16.8° C	- 5.5	1.16	0.2
11	16.8° C	- 5.5	1.20	0.2
October 4, 1959.				
0 m	14.8° C	pH 5.5	1.12 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2	14.75° C	- 5.5	1.08	0.2
4	14.75° C	- 5.5	1.07	0.2
6	14.7° C	- 5.5	1.14	0.2
8	14.7° C	- 5.5	1.14	0.2
10	14.7° C	- 5.5	1.22	0.2
11	14.7° C	- 5.5	1.27	0.2

Nr 9

99

0.1 mg $HCO_3^- \cdot l^{-1}$ 0.1 - - -0.2 - - -0.3 - - -

 $0.1 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$ 0.1 - - -0.1 - - -0.1 - - -0.1 - - -0.2 - - -0.5 - - -

 $0.2 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$ 0.2 - - -0.2 - -

0.2 - - -0.2 - - -0.3 - - -0.7 - - -

 $0.2 \text{ mg } \text{HCO}_3^- \cdot l^{-1}$ 0.2 - - -0.2 - -

0.2 - - -0.2 - - -0.2 - - -0.2 - - -

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October 20, 1959.				
0 m	12.1° C	pH 5.5	1.21 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO ₃ -·l-1
2	12.1° C	- 5.5	1.21	0.2
4	12.1° C	- 5.5	1.18	0.2
6	12.1° C	- 5.5	1.17	0.2
8	12.1° C	- 5.5	1.20	0.2
10	12.1° C	- 5.5	1.21	0.2
11	12.1° C	- 5.5	1.17	0.2
November 8, 1959.				
0 m	8.7° C	pH 5.5	1.25 mg total $\text{CO}_2 \cdot l^{-1}$	0.2 mg HCO ₂ -·l ⁻¹
2	8.7° C	- 5.5	1.21	0.2
4	8.7° C	- 5.5	1.34	0.2
6	8.65° C	- 5.5	1.26	0.2
8	8.6° C	- 5.5	1.25	0.2
10	8.6° C	- 5.5	1.24	0.2
11	8.6° C	- 5.5	1.34	0.2
November 29, 1959.				

November 29, 1959.				
0 m	5.85° C	pH 5.5	1.55 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO ₃ -·l ⁻¹
2	5.85° C	- 5.5	1.51	0.2
4	5.85° C	- 5.5	1.55	0.2
6	5.85° C	- 5.5	1.50	0.2
8	5.85° C	- 5.5	1.52	0.2
10	5.85° C	- 5.5	1.56	0.2
11	5.85° C	- 5.5	1.53	0.2
December 13, 1959.				
0 m	2.65° C	pH 5.5	1.54 mg total $\rm CO_2 \cdot l^{-1}$	0.2 mg HCO ₃ -·l ⁻¹
2	2.85° C	- 5.5	1.48	0.2
4	2.95° C	- 5.5	1.53	0.2
6	3.1° C	- 5.5	1.53	0.2
8	3.15° C	- 5.5	1.54	0.2
10	3.3° C	- 5.5	1.54	0.2
11	3.3° C	- 5.5	1.71	0.2

December 29,	1959. Transparency	more than 11.5 m.	Beginning formation of ice.
0 m	3 25° C	nH 5 5	1.49 mg total CO $\cdot l = 1$

0 m	3.25° C	pH 5.5	1.49 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_3^{-} \cdot l^{-1}$
2	3.4° C	- 5.5	1.46	0.2
4	3.4° C	- 5.5	1.48	0.2
6	3.5° C	- 5.5	1.45	0.2
8	3.6° C	- 5.5	1.48	0.2
10	3.6° C	- 5.5	1.46	0.2
11	3.65° C	- 5.5	1.45	0.2
January 17, 1960. Ice	10 cm thick.			
0.1 m	$0.2^{\circ} \mathrm{C}$	pH 5.5	1.82 mg total $\text{CO}_2 \cdot l^{-1}$	0.2 mg HCO ₃ -·l ⁻¹
2 m	1.5° C	- 5.5	1.65	0.2
4	1.6° C	- 5.5	1.77	0.2
6	1.7° C	- 5.5	1.63	0.2
8	2.7° C	- 5.5	1.73	0.2
10	2.7° C	- 5.5	1.78	0.2
11	2.75° C	- 5.5	2.04	0.2

Nr. 2

January 31, 1960. Ice 10 cm thick.

0.1 m	0.2° C	pH 5.6	1.41 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC	$\binom{-1}{3} \cdot 1^{-1}$
2 m	$1.6^{\circ} C$	- 5.6	1.35	0.2	-
4	1.7° C	- 5.6	1.41	0.2	-
6	1.8° C	- 5.5	1.54	0.2	-
8	2.75° C	- 5.5	1.68	0.2	-
10	2.75° C	- 5.4	3.00	0.3	-
11	2.8° C	- 5.3	5.17	0.3	-
February 14 1960 Ic	e 16 cm thick				
0.16 m	$0.65^{\circ}C$	nH 5 5	1.59 mg total CO $\cdot l^{-1}$	0.2 mg HCC	1-1
9 m	0.00 C	5.5	1.52 mg total 0.02 T	0.2 mg 1100	3 1
4	2.0° C	- 5.5	1.50	0.2	-
4	2.5 C	- 5.5	1.56	0.2	-
0	3.13 G	- 5.5	2.46	0.2	-
0	3.0 C	- 0.4	2.40	0.2	-
10	3.8° C	- 5.5	3.92	0.3	-
11	3.8 6	- 0.3	4.54	0.3	-
February 28, 1960. Ic	e 22 cm thick.				
0.22 m	0.65° C	pH 5.6	1.39 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC	${}_{3}^{-} \cdot l^{-1}$
2 m	3.0° C	- 5.5	1.46	0.2	-
4	3.25° C	- 5.5	1.65	0.2	-
6	3.6° C	- 5.5	1.83	0.2	-
8	4.1° C	- 5.3	4.42	0.3	-
10	4.1° C	- 5.3	4.45	0.3	-
11	4.1° C	- 5.3	4.55	0.3	-
March 12 1060 Loo 1	0 am thial				
March 15, 1900. ICe 1	U CHI UHICK.				
0.1 m	0.7° C	pH 5.6	1.36 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC	[]-1
0.1 m	0.7° C 3.9° C	pH 5.6 - 5.6	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32	0.2 mg HCC 0.2)_3 ·]− 1 3 -
0.1 m 2 m 4	0.7° C 3.9° C 3.9° C	pH 5.6 - 5.6 - 5.6	1.36 mg total CO₂·l ⁻¹ 1.32 1.32	0.2 mg HCC 0.2 0.2	01 - -
March 15, 1900. 100 1 0.1 m	0.7° C 3.9° C 3.9° C 4.3° C	pH 5.6 - 5.6 - 5.6 - 5.3	1.36 mg total CO₂·l ⁻¹ 1.32 1.32 3.14	0.2 mg HCC 0.2 0.2 0.3)l-1 - -
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.6 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19	0.2 mg HCC 0.2 0.2 0.3 0.3	0l-1 - - - -
$\begin{array}{c} \text{March 15, 1500. feel} \\ \text{0.1 m} \\ \text{2 m} \\ \text{-} \\ \-} \\ \begin{array}{-} \\ \begin{array}{-} \\ \end{array} \-} \\ \text{-} \\ \begin{array}{-} \\ \end{array} \-} \\ \begin{array}{-} \\ \end{array}$	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.6 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3)l-1 - - - -
March 15, 1990. Ref 1 0.1 m 2 m 4 - 6 - 8 - 10 - 11 -	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3	01-1 - - - - -
March 15, 1990. Ref 1 0.1 m 2 m 4 6 8 10 11	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 - - - 1.32 - - - 3.14 - - - 3.19 - - - 3.12 - - - 3.29 - - -	0.2 mg HCC 0.2 0.3 0.3 0.3 0.3 0.3	01-1 - - - - -
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960.	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3)
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960. 0 m	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3	[-3, -1] = 1 -3, -1] = 1 -3, -1] = 1
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960. 0 m 2	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.61	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2	$b_{3}^{-}, l = 1$ - - - - - - - - - - - - - - - - - - -
March 15, 1900. Ref 1 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 -	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.61 1.65	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2	$p_3 \cdot l - 1$ - - - - - - - - - - - - - - - - - - -
March 15, 1900. Ref 1 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 11 - 0 m 2 - 4 - 6 - 0 m	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 pH 5.5 - 5.5 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.61 1.65 1.65	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2	$p_{3}^{-}, l = 1$ - - - - - - - - - - - - - - - - - - -
March 15, 1500. Ref 1 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.65	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.2 0.3 0.3 0.2 0.2 0.3 0.3 0.3 0.2 0.2 0.3 0.3 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2	
March 15, 1500. Ref 1 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 10 -	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.2 0.3 0.3 0.2 0.2 0.3 0.2 0.3 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2	
$March 15, 1500.$ Ref $0.1 m$ $2 m$ $4 - \dots$ $6 - \dots$ $8 - \dots$ $10 - \dots$ $11 - \dots$ $March 27, 1960.$ $0 m \dots$ $2 - \dots$ $4 - \dots$ $6 - \dots$ $8 - \dots$ $10 - \dots$ $11 - \dots$ $11 - \dots$ $11 - \dots$	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.61 1.65 1.65 1.65 1.65 1.65 1.65 1.67	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.2 0.2 0.2 0.2 0.2 0.2 0.2	
March 15, 1500. 100 1 0.1 m	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 pH 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.67	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2	$b_3 \cdot l - 1$ - - - - - - - - - - - - - - - - - - -
March 15, 1500. Ref 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 2 - 4 - 6 - 8 - 10 - 11 - A - 10 - 11 - April 10, 1960. 0 m	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 pH 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2	$b_3 \cdot [-1]$
March 15, 1500. Ref 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 2 - 4 - 6 - 8 - 10 - 11 - April 10, 1960. 0 m 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 2 - 0 m 2 - 10 - 2 - 10 - 2 - 10 - 2 - 10 - 11 - 11 - 11 - 11 - 12 -	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 5.7° C 5.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.5	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCC 0.2 0.2 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 -	$b_3 \cdot [-1]$
March 15, 1960. Ref 0.1 m 2 m 4 - 6 - 8 - 10 - 11 - March 27, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 11 - April 10, 1960. 0 m 2 - 4 - 6 - 8 - 10 - 11 - April 10, 1960. 0 m 2 - 4 - 4 - 4 - 2 - 4 - 2 - 4 -	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 5.7° C 5.7° C 5.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.7 - 5.7 - 5.7 - 5.7 - 5.7	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$ 0.67 0.76	0.2 mg HCC 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.1 mg HCC 0.1 0.1	$b_3 \cdot [-1]$
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 6 6 6 6	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 5.7° C 5.7° C 5.7° C 5.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.7 - 5.7 - 5.7 - 5.7 - 5.7 - 5.7	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$ 0.67 0.76 0.71	0.2 mg HCC 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.1 mg HCC 0.1 0.1 0.1	$b_3 \cdot [-1]$
March 15, 1900. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 8 8 8	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 5.7° C 5.7° C 5.7° C 5.7° C 5.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.7 - 5.7	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$ 0.67 0.76 0.71 0.79	0.2 mg HCC 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.1 mg HCC 0.1 0.1 0.1 0.1 0.1	$b_3 \cdot l = 1$ - - - - - - - -
March 15, 1500. Ref 1 0.1 m 2 m 4 6 8 10 11 March 27, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 8 10 11 April 10, 1960. 0 m 2 4 6 8 10 10 10	0.7° C 3.9° C 3.9° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.3° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 4.7° C 5.7° C 5.7° C 5.7° C 5.7° C 5.7° C 5.7° C	pH 5.6 - 5.6 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.3 - 5.5 - 5.7 - 5.7	1.36 mg total $CO_2 \cdot l^{-1}$ 1.32 1.32 3.14 3.19 3.12 3.29 1.65 mg total $CO_2 \cdot l^{-1}$ 1.65 1.65 1.65 1.65 1.65 1.67 0.72 mg total $CO_2 \cdot l^{-1}$ 0.67 0.76 0.71 0.83	0.2 mg HCC 0.2 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.2 mg HCC 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.1 mg HCC 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1	$b_3^- \cdot [-1]$

102				NI. 2
April 24, 1960.				
0 m	7.6° C	pH 5.7	0.64 mg total $\text{CO}_2 \cdot l^{-1}$	0.1 mg $HCO_{3}^{-} \cdot l^{-1}$
2	7.6° C	- 5.7	0.59	0.1
4	7.6° C	- 5.7	0.60	0.1
6	7.6° C	- 5.7	0.60	0.1
8	7.6° C	- 5.7	0.71	0.1
10	7.6° C	- 5.7	0.68	0.1
11	7.6° C	- 5.7	0.73	0.1
May 14, 1960.				
0 m	13.4° C	pH 5.7	0.69 mg total $CO_2 \cdot l^{-1}$	$0.1 \text{ mg HCO}_{3}^{-} \cdot l^{-1}$
2	13.3° C	- 5.7	0.67	0.1
4	12.6° C	- 5.7	0.68	0.1
6	10.5° C	- 5.8	0.42	0.1
8	9.6° C	- 5.7	0.57	0.1
10	9.3° C	- 5.7	0.67	0.1
11	9.3° C	- 5.6	0.93	0.2
May 29, 1960.				
0 m	14.4° C	pH 5.6	0.81 mg total $CO_2 \cdot l^{-1}$	$0.1 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2	14.2° C	- 5.6	0.77	0.1
4	13.9° C	- 5.6	0.83	0.1
6	13.0° C	- 5.6	0.73	0.1
8	11.3° C	- 5.6	1.10	0.2
10	10.3° C	- 5.4	1.90	0.2
11	10.5° C	- 5.4	2.03	0.2
June 15, 1960.				
0 m	16.7° C	pH 5.6	0.78 mg total $CO_2 \cdot l^{-1}$	0.1 mg HCO ₃ ·l ⁻¹
2	16.6° C	- 5.6	0.70	0.1
4	16.4° C	- 5.6	0.68	0.1
6	15.85° C	- 5.7	0.67	0.1
8	13.4° C	- 5.6	0.92	0.2
10	12.1° C	- 5.5	1.32	0.2
11	12.0° C	- 5.5	1.48	0.2

11	12.0° C	- 5.5	1.48 -	-	-	-	0.2 -	-	-
June 28, 1960.									
0 m	17.9° C	pH 5.7	0.65 mg	total	CO_2 .	1-1	0.1 mg	HCO;	l-1
2	17.8° C	- 5.7	0.58 -	-	-	-	0.1 -	-	-
4	17.7° C	- 5.7	0.60 -	-	-	-	0.1 -	-	-
6	17.1° C	- 5.7	0.64 -	-	-		0.1 -	-	-
8	15.1° C	- 5.7	0.65 -	-	-	-	0.1 -	-	-
10	14.5° C	- 5.6	0.84 -	-	-	-	0.2 -	-	-
11	13.3° C	- 5.4	1.79 -	-	-	-	0.2 -	-	-
July 27, 1960. Trans	parency 4 m;	Uroglena-Maximum.							

0.1 m	18.6° C	pH 5.8	0.41 mg total $CO_2 \cdot l^{-1}$	0.1 mg $HCO_3^{-} \cdot l^{-1}$	
2.1	18.4° C	- 5.8	0.39	0.1	
4.1	17.8° C	- 5.8	0.36	0.1	
6.1	17.4° C	- 5.7	0.50	0.1	
8.1	16.5° C	- 5.6	1.00	0.2	
10.1	13.8° C	- 5.4	1.80	0.2	
11.1	13.8° C	- 5.1	8.49	0.5	

Nr. 2

August 9, 1960.				
0.1 m	19.5° C	pH 5.6	0.68 mg total $CO_2 \cdot l^{-1}$	0.1 mg $HCO_{3}^{-} \cdot l^{-1}$
2.1	19.3° C	- 5.6	0.63	0.1
4.1	19.1° C	- 5.6	0.65	0.1
6.1	18.8° C	- 5.6	0.68	0.1
8.1	18.1° C	- 5.5	1.47	0.2
10.1	16.6° C	- 5.4	1.83	0.2
11.1	15.6° C	- 5.0	13.73	0.7
A namet 28 1060				
0.05 m	18.7° C	pH 5.6	0.97 mg total CO $\cdot l^{-1}$	$0.2 \text{ mg} \text{HC} \Omega^{-} \cdot l^{-1}$
2.05 -	18.6° C	- 5.6	0.86	$0.2 \text{ mg} \text{ mGO}_3 \text{ m}$
4.05 -	18.4° C	- 5.6	0.00	0.2
6.05	18.4 C	- 5.6	0.94	0.2
0.05	18.2 C	- 5.0	1.02	0.2
0.00	18.0 C	- 5.5	1.02	0.2
10.05	17.9° C	- 5.5	1.32	0.2
11.05	16.9° C	- 4.9	14.89	0.7
September 11, 1960.				
0.03 m	16.8° C	pH 5.5	1.03 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_3^- \cdot l^{-1}$
2.03	16.8° C	- 5.5	0.98	0.2
4.03	16.75° C	- 5.5	0.98	0.2
6.03	16.7° C	- 5.5	0.93	0.2
8.03	16.7° C	- 5.5	1.03	0.2
10.03	16.65° C	- 5.5	1.05	0.2
11.03	16.6° C	- 5.5	1.42	0.2
September 25, 1960.				
	- Charles State			
0 m	16.1° C	nH 5.5	1.04 mg total CO ₂ ·1 ⁻¹	$0.2 \text{ mg} \text{HCO}^{-} \cdot l^{-1}$
0 m	16.1° C 15.95° C	pH 5.5	1.04 mg total $CO_2 \cdot l^{-1}$	$0.2 \text{ mg } \text{HCO}_3^{-} \cdot l^{-1}$
0 m 2 4 -	16.1° C 15.95° C 15.95° C	pH 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06	0.2 mg $HCO_3^{-} \cdot l^{-1}$ 0.2
0 m 2 4 6 -	16.1° C 15.95° C 15.95° C 15.95° C	pH 5.5 - 5.5 - 5.5	1.04 mg total $CO_2 \cdot 1^{-1}$ 1.06 1.05	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 -	16.1° C 15.95° C 15.95° C 15.95° C 15.95° C	pH 5.5 - 5.5 - 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 5 5	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10 11	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10 11 October 9, 1960.	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10 11 October 9, 1960. 0 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 pH 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10 11 October 9, 1960. 0 m 1.95 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 pH 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 pH 5.5 - 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5 pH 5.5 - 5.5 - 5.5 - 5.5 - 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 7.95	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	pH 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	pH 5.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.28 mg total $CO_2 \cdot l^{-1}$ 1.28 1.28 1.25 1.30 1.33	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 8 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	$pH 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5$	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 October 19, 1960.	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	pH 5.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 October 19, 1960. 0 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C	pH 5.5 - 7.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32 1.32 1.32 1.32	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 0ctober 19, 1960. 0 m 1.96 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 10.85° C 10.75° C	pH 5.5 - 5.5	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32 1.32 1.31 1.32	0.2 mg $HCO_3^{-} \cdot l^{-1}$ 0.2 0.6 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 0.0tober 19, 1960. 0 m 1.96 m 3.96	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 13.05° C 10.85° C 10.75° C	pH 5.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.33 1.32 1.17 mg total $CO_2 \cdot l^{-1}$	0.2 mg $HCO_3^{-} \cdot l^{-1}$ 0.2 0.6 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 0ctober 19, 1960. 0 m 1.96 m 5.96 5.96	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 10.85° C 10.75° C 10.7° C	pH 5.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32 1.17 mg total $CO_2 \cdot l^{-1}$ 1.19 1.16 1.14	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 10.75° C 10.75° C 10.7° C 10.7° C 10.7° C	pH 5.5 -	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.33 1.32 1.14 1.14	0.2 mg $HCO_3^{-} \cdot l^{-1}$ 0.2 0.6 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2 0.2
0 m 2 4 6 10 11 October 9, 1960. 0 m 1.95 m 3.95 5.95 9.95 10.95 0.0tober 19, 1960. 0 m 1.96 m 3.96 9.96 9.96	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 15.9° C 13.05° C 10.75° C 10.75° C 10.7° C 10.7° C 10.65° C	$pH 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5$	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.33 1.32 1.32 1.14 1.14 1.18	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
0 m	16.1° C 15.95° C 15.95° C 15.95° C 15.9° C 15.9° C 15.9° C 13.05° C 10.75° C 10.7° C 10.65° C 10.65° C	$pH 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5.5 \\ - 5$	1.04 mg total $CO_2 \cdot l^{-1}$ 1.06 1.05 1.04 1.06 1.06 1.06 1.28 mg total $CO_2 \cdot l^{-1}$ 1.30 1.28 1.25 1.30 1.30 1.33 1.32 1.32 1.14 1.14 1.18 1.15	0.2 mg $HCO_3^{-}\cdot l^{-1}$ 0.2

104

November 6, 1960.				
0.03 m	8.45° C	pH 5.5	1.30 mg total CO ₂ ·l ⁻¹	0.2 mg HCO_ · l-1
2.03	8.45° C	- 5.5	1.35	0.2
4.03	8.45° C	- 5.5	1.29	0.2
6.03	8.45° C	- 5.5	1.32	0.2
8.03	8.45° C	- 5.5	1.29	0.2
10.03	8.45° C	- 5.5	1.32	0.2
11.03	8.45° C	- 5.5	1.37	0.2
November 20, 1960.				
0.04 m	6.35° C	pH 5.5	1.46 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO·l-1
2.04	6.3° C	- 5.5	1.49	0.2
4.04	6.2° C	- 5.5	1.51	0.2
6.04	6.15° C	- 5.5	1.54	0.2
8.04	6.15° C	- 5.5	1.51	0.2
10.04	6.15° C	- 5.5	1.55	0.2
11.04	6.15° C	- 5.5	1.52	0.2
December 11, 1960.				
0.11 m	4° C	pH 5.5	1.53 mg total CO ₂ ·l ⁻¹	0.2 mg HCO·l-1
2.11	4° C	- 5.5	1.55	0.2
4.11	4° C	- 5.5	1.52	0.2
6.11	4° C	- 5.5	1.54	0.2
8.11	4° C	- 5.5	1.56	0.2
10.11	4° C	- 5.5	1.58	0.2
11.11	4° C	- 5.5	1.50	0.2
December 28 1960				
0.14 m	3.3° C	pH 5.5	1.70 mg total $CO_{\circ} \cdot l^{-1}$	$0.2 \text{ mg} \text{HCO}^{-} \cdot l^{-1}$
2.14 -	3.3° C	- 5.5	1.69	0.2
4.14	3.3° C	- 5.5	1.67	0.2
6.14	3.3° C	- 5.5	1.70	0.2
8.14	3.3° C	- 5.5	1.67	0.2
10.14	3.35° C	- 5.5	1.67	0.2
11.14	3.35° C	- 5.5	1.67	0.2
T	10			
January 22, 1961. Ice	12 cm thick.	pH 5 5 (5 51)	1.52 mg total CO 1=1	0.9 mg HCO=.1=1
0.14 m	0.5 C	pri 5.5 (5,51)	1.55 mg total $CO_2 \cdot 1^{-2}$	$0.2 \text{ mg} \text{ HCO}_3 \cdot 1^{-2}$
4.14	2.0 C	- 5.6 (5,52) 5.6 (5.52)	1.19	0.2
6.14	2.5 C	-5.6(5.53)	1.13	0.2
8 14 -	2.4 C	-5.5(5.51)	1.25	0.2
10.14 -	2.7 C	-5.3(5.51)	3 38	0.3
11.14 -	3.35° C	-5.2(5.42)	7.15	0.4
<i>February 12, 1961.</i> Ice	5 cm thick.	-11 5 6 (5 00)		0.0
0.15 m	1.1° C	pH 5.6 (5.20)	1.19 mg total $CO_2 \cdot 1^{-1}$	$0.2 \text{ mg} \text{HCO}_3 \cdot 1^{-1}$
2.10	3.1° U	- 5.0 (5.45)	1.21	0.2
4.10	3.2° C	- 0.0 (0.47)	1.10	0.2
0.10	3.3 G	- 0.0 (0.40) 5 4 (5 46)	1.40	0.2
0.10	3.4 C	- 0.4 (0.40)	4.20	0.2
10.15	1.0° C	-5.3(0.47)	6.02	0.3
11.10	4.0 0	- 0.2 (0.42)	0.04	0.4

Nr. 2

February 26, 1961.				
0.16 m	3.7° C	pH 5.5 (5.52)	1.68 mg total $CO_2 l \cdot {}^{-1}$	$0.2 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2.16	4° C	- 5.5 (5.51)	1.61	0.2
4.16	4° C	- 5.5 (5.50)	1.61	0.2
6.16	4° C	- 5.5 (5.50)	1.64	0.2
8.16	4° C	- 5.5 (5.50)	1.69	0.2
10.16	4° C	- 5.5 (5.51)	1.62	0.2
11.16	4° C	- 5.5 (5.50)	1.60	0.2
March 12, 1961.				
0.16 m	5.4° C	pH 5.6 (5.49)	1.19 mg total $CO_2 \cdot l^{-1}$	0.2 mg HCO ⁻ .1 ⁻¹
2.16	5.4° C	- 5.6 (5.50)	1.15	0.2
4.16	5.4° C	- 5.6 (5.49)	1.11	0.2
6.16	5.4° C	- 5.6 (5.48)	1.11	0.2
8.16	5.4° C	- 5.6 (5.48)	1.16	0.2
10.16	5.4° C	- 5.6 (5.49)	1.16	0.2
11.16	5.4° C	- 5.6 (5.49)	1.10	0.2
March 26 1961		()		
0.16 m	6.2° C	pH 57 (562)	0.87 mg total CO $\cdot 1^{-1}$	$0.1 \text{ mg} \text{HCO}^{-1}$
2.16 -	6.2° C	-57(564)		$0.1 \text{ mg} 1100_3 \text{ r}$
4.16 -	6.2° C	-5.7(5.63)	0.81	0.1
6.16 -	6.2° C	- 5.7 (5.63)	0.78	0.1
8 16 -	6.2°C	- 5.7 (5.62)	0.81	0.1
10.16	6.2°C	- 5.7 (5.62)	0.84	0.1
11.16	0.2 C	- 5.7 (5.03)	0.84	0.1
11.10	0.2 L	- 5.7 (5.64)	0.80	0.1
April 9, 1961.				
0.19 m	6.85° C	pH 5.7 (5.51)	0.78 mg total $CO_2 \cdot l^{-1}$	0.1 mg $HCO_3^{-} \cdot l^{-1}$
2.19	6.75° C	- 5.7 (5.51)	0.79	0.1
4.19	6.6° C	- 5.7 (5.51)	0.79	0.1
6.19	6.5° C	- 5.7 (5.51)	0.76	0.1
8.19	6.4° C	- 5.7 (5.49)	0.78	0.1
10.19	6.3° C	- 5.7 (5.50)	0.76	0.1
11.19	$6.25^{\circ} \mathrm{C}$	- 5.7 (5.46)	0.80	0.1
April 23, 1961.				
0.16 m	10.15° C	pH 5.7 (5.54)	0.66 mg total $CO_2 \cdot l^{-1}$	0.1 mg HCO ₃ -·l ⁻¹
2.16	10.15° C	- 5.7 (5.52)	0.64	0.1
4.16	10.0° C	- 5.7 (5.51)	0.61	0.1
6.16	9.85° C	- 5.7 (5.53)	0.60	0.1
8.16	8.85° C	- 5.7 (5.55)	0.56	0.1
10.16	8.3° C	- 5.7 (5.52)	0.60	0.1
11.16	8.1° C	- 5.7 (5.48)	0.71	0.1
Mau 7, 1961.				
0.13 m	12.6° C	pH 5.6 (5.50)	0.82 mg total CO ₂ ·1 ⁻¹	$0.1 \text{ mg} \text{HCO}^{-} \cdot l^{-1}$
2.13	12.55° C	- 5.6 (5.50)	0.77	0.1
4.13 -	12.4° C	- 5.7 (5.48)	0.65	0.1
6.13	12.1° C	- 5.7 (5.50)	0.65	0.1
8.13 -	11.5° C	- 5.7 (5.50)	0.69	0.1
10.13 -	10.3° C	- 5.6 (5.46)	1.07	0.2
11.13 -	10.25° C	- 5.5 (5.45)	1 22	0.2
	10.20 0	0.0 (0.10)		

106

May 21, 1961.				
0.1 m	13.6° C	pH 5.6 (5.50)	0.75 mg total $CO_2 \cdot l^{-1}$	$0.1 \text{ mg } \text{HCO}_{3}^{-} \cdot l^{-1}$
2.1	13.5° C	- 5.6 (5.48)	0.73	0.1
4.1	13.4° C	- 5.7 (5.49)	0.69	0.1
6.1	13.4° C	- 5.7 (5.50)	0.71	0.1
8.1	13.0° C	- 5.6 (5.51)	0.86	0.1
10.1	11.25° C	- 5.6 (5.46)	0.82	0.1
11.1	10.95° C	- 5.5 (5.45)	1.20	0.2
June 4, 1961.				
0.07 m	16.2° C	pH 5.6 (5.50)	0.67 mg total $CO_2 \cdot l^{-1}$	0.1 mg HCO ₃ -·l ⁻¹
2.07	16.0° C	- 5.6 (5.51)	0.66	0.1
4.07	14.9° C	- 5.6 (5.51)	0.73	0.1
6.07	14.5° C	- 5.6 (5.53)	0.73	0.1
8.07	14.25° C	- 5.6 (5.53)	0.75	0.1
10.07	13.8° C	- 5.6 (5.51)	0.87	0.2
11.07	13.1° C	- 5.5 (5.47)	1.12	0.2
June 15, 1961.				
0.03 m	17.15° C	pH 5.7	0.50 mg total $CO_{2} \cdot l^{-1}$	$0.1 \text{ mg HCO}_{\circ}^{-} \cdot l^{-1}$
2.03	17.0° C	- 5.7	0.50	0.1
4.03	16.9° C	- 5.7	0.57	0.1
6.03	16.0° C	- 5.7	0.54	0.1
8.03	15.6° C	- 5.7	0.61	0.1
10.03	14.95° C	- 5.6	0.78	0.1
11.03	14.85° C	- 5.5	1.06	0.2
July 9, 1961.				
0 m	17.2° C	pH 5.6	0.73 mg total $CO_2 \cdot l^{-1}$	0.1 mg HCO ₂ ⁻ ·l ⁻¹
2	17.1° C	- 5.6	0.64	0.1
4	17.1° C	- 5.6	0.72	0.1
6	17.1° C	- 5.6	0.65	0.1
8	17.05° C	- 5.6	0.72	0.1
10	17.05° C	- 5.6	0.69	0.1
11	16.3° C	- 5.2	4.14	0.4
Julu 23 1961				
0 m	17.65° C	nH 5.6	0.70 mg total CO ₂ ·l ⁻¹	$0.1 \text{ mg} \text{HCO}^{-} \cdot l^{-1}$
2 -	17.55° C	- 56	0.64	0.1
4 -	17.55° C	- 5.6	0.64	0.1
6	17.55° C	5.6	0.64	0.1
8	17.35 C	- 5.6	0.75	0.1
10	17.40 C	5.5	1.49	0.1
10	17.2° C 17.2° C	- 5.5	1.67	0.2
1				
0.05 m	7.8° C	nH 5.6	1.02 mg total CO $\cdot 1^{-1}$	$0.1 \text{ mg} \text{HCO}^{-} \cdot 1^{-1}$
2.05 -	7.8° C	- 56		0.1
4.05 -	7.0° C	- 56	0.94	01
6.05 -	6.6° C	- 56	0.92	0.1
0.00	0.0 0	- 0.0	0.04	0.1

8.05 m	6.3° C	pH 5.6	0.90 mg total $\mathrm{CO}_2 \cdot \mathbf{l}^{-1}$	$0.1 \text{ mg HCO}_3^- \cdot l^{-1}$
10.05	6.65° C	- 5.6	0.94	0.1
11.05	6.25° C	- 5.6	1.01	0.1

July 24, 1962. Transparency 11.40 m.

0 m	17.5° C	pH	5.7	0.52	mg	total	CO_2	$\cdot l^{-1}$	0.1	mg	HCO_3^-	$\cdot l^{-1}$	O2-saturation	$103^{0}/_{0}$
2	17.3° C	-	5.7	0.56	-	-	-	-	0.1	-	-	-	-	103%/0
4	17.1° C	-	5.7	0.46	-	-	-	-	0.1	-	-	-	-	$103^{0}/_{0}$
6	17.1° C	-	5.7	0.51	-	-	-	-	0.1	-	-	-	-	$103^{0}/_{0}$
8	16.65° C	-	5.7	0.56	-	-	-	-	0.1	-	-	-	-	$105^{0}/_{0}$
10	15.2° C	-	5.6	0.69	-	-	-	-	0.1	-	-	-	-	$126^{0}/_{0}$
11	14.9° C	-	5.5	1.53	-	-	-	-	0.2	-	-	-	-	107°/0
$11^{1}/_{4}$ m	14.9° C	-	5.3	3.66	-	-	-	-	0.3	-	-	-		
11.40 m = bottom														

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BY

KARL GEORG WINGSTRAND AND OLE MUNK



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København 1965 Kommissionær: Ejnar Munksgaard

Synopsis

The pecten of the avian eye was described by OLAUS BORRICHIUS in 1674. The numerous subsequent papers, though mainly morphological, include about 30 different theories on the function of the organ. Some of these theories are examined in the present morphological and experimental investigation of the pigeon's pecten.

The theory that the pecten, like the ciliary body, secretes intra-ocular fluid was mainly founded on the histological and histochemical similarity of the two organs. The similarity was critically re-investigated in the pigeon, but as the structural evidence proved to be short of conclusive, this particular line of approach was abandoned, especially after certain functional differences between the two organs had been brought to light.

Anatomical investigations revealed that it is possible to block the pecten arteries of the pigeon by surgery. The operation stops the pecten circulation and causes slow and progressive degeneration of the organ, until revascularization starts after some weeks. In eyes thus treated the retina shows ophthalmoscopical and histological symptoms of heavy degeneration, particularly in the ganglion cell layer and the layer of optic nerve fibres. In contrast, there was no degeneration in 31 eyes operated upon in the same way but with one or more of the pecten arteries left intact. It is concluded that the pecten is a nutritive organ, necessary for the maintainance of the inner retinal layers.

Investigations of the oxygen pressure in the bulb of normal pigeons by means of oxygen cathodes revealed a fall from about 100 mm Hg near the pecten to about 5 mm Hg near the retina. This shows that oxygen does diffuse from the pecten to the retina, and numerical estimates indicate that the amounts are large enough to be functionally significant. Blocking of the pecten arteries appears to result in almost complete anoxia in the corpus vitreum and the inner retinal layers. It is thus indicated that the inner retinal layers are dependent on the pecten for their oxygen supply.

The results support the theory that the pecten is a substitute for the absent intra-retinal vessels. It cannot be excluded that the pecten may perform other, subsidiary functions in the bulb, but this still remains to be shown.

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CONTENTS

Introduction	5
Historical Note on the Discovery of the Pecten	6
Theories on the Function of the Pecten	8
The Structure of the Pecten in the Pigeon	
Methods	13
External Shape, Orientation	14
The Vessels	15
The Structure of the Folded Part of the Pecten	15
The Bridge of the Pecten	18
The Nature of the Stroma Cells	19
Vessels and Nerves of the Orbital Region of the Pigeon	
Methods	20
The Vascular System of the Pecten	20
Arterial System of the Orbital Region	20
Details of the Arterial Supply of the Bulb Proper	24
The Venous System of the Orbit and the Eye	28
The Nerves of the Orbital Region	32
Comparison between the Pecten and the Ciliary Body	33
Operative Elimination of the Pecten by Coagulation of Its Vessels	
Methods	35
Results	38
The Intra-Ocular Oxygen Pressure of Normal Pigeons	41
Methods	42
Results	44
Quantitative Considerations on the Basis of the Recorded Oxygen Pressure	
The Amounts of Oxygen Supplied to the Retina by the Pecten	47
The Pecten's Role in Oxygen Economy of the Retina	49
The Oxygen Tension in the Bulb after Coagulation of the Pecten Vessels	50
Discussion on the Function of the Pecten	
References	

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Page



Introduction

The pecten oculi is a thin, folded membrane, rich in vessels and pigment, which projects from the papilla of the optic nerve far into the vitreous body of the bird's eye (Pl. I–III). Homologous structures are present in the eye of some reptiles and a few mammals, but these have the shape of a compact cone or are vestigial. Although the pecten has been known and discussed for about 300 years, there is still a great deal of uncertainty about its function. In the majority of papers, the function of the organ was discussed on the basis of morphological data only; this has resulted in about 30 theories, many of which are still accepted by different authors. More direct physiological experimentation with the pecten is difficult because of its inaccessible site, and this explains in part why experimental investigations have been few and insufficient for the making of definite conclusions.

When starting this work, the authors decided upon the classical way of approach. Experiments made by ABELSDORFF and WESSELY (1909) and by SEAMAN et al. (1962, 1963) indicated that the pecten, like the ciliary body, secretes intra-ocular fluid; thus attention was focused on the morphological and histochemical similarities of these organs in the hope of supporting this hypothesis. However, a few primitive experiments soon revealed physiological differences between the organs, and it was realized that the purely morphological way of approach was unlikely to lead to safe conclusions.

Consequently, a more direct way of attacking the problem was sought. To the authors' surprise it was found possible to eliminate the pecten functionally by blocking its vascular supply, and the retinal degeneration observed after such operations showed that the pecten is essential for the maintainance of the retina. In elaborating the method of operation, it was necessary to re-investigate the structure of the pecten in the domestic pigeon (*Columba livia* L.), the species used for the experiments, and to map out the vessels and nerves of the orbital region. Such morphological investigations are summarized in this paper as a basis for the understanding of operational procedure.

The results of the experiments mentioned above directed attention to the widely held idea that the pecten supplies the inner layers of the retina with oxygen by diffusion through the vitreous body (e.g. MANN 1924 a, b). The authors therefore decided to test this hypothesis by recording the oxygen pressure with oxygen cathodes in different parts of the vitreous body. The results obtained in normal eyes, as well as in eyes with blocked pecten vessels, are in good agreement with the theory, and support it to a point not far from definite proof.

The series of investigations could not have been realized without the aid of specialists, who helped with technical problems, and gave advice in their own particular fields: Mr. TH. CHRISTENSEN (Latin text), Dr. E. FOX MAULE (Latin text), Dr. E. GREGERSEN (photo-coagulation), Mr. T. NORMAN and Mr. F. BJERRING (electron microscopy), Mr. H. RASMUSSEN (oxygen cathodes), and Dr. Ry ANDERSEN (eye pathology). The authors are also indebted to the staffs of the Institute for Comparative Anatomy, Copenhagen, and the Institute for General Zoology, Copenhagen, for direct or indirect help. Technical assistance was made possible by a grant from the CARLS-BERG FOUNDATIONS. The authors are aware that this help contributed greatly to the success of the work and wish to express their gratitude to all concerned.

Historical Note on the Discovery of the Pecten

The discovery of the pecten was formerly attributed to PERRAULT (1676), but SEAMAN and STORM (1963), rightly pointed out that STENO had mentioned the organ at an even earlier date. The publication referred to is STENO's famous description of the development of the chick in *Acta Medica Hafniensia*, vol. II for 1673, published in 1675.

This appeared to be the earliest record, but some remarks in the excellent description of the pecten in BLASIUS' "Anatome animalium" (1681, p. 136) indicated that the chapter was based on the work of the Danish scientist, OLAUS BORRICHIUS (OLE BORCH). The paper, copied by BLASIUS, is BORCH'S "Hermetis, AEgyptiorum et Chemicorum Sapientia", printed in Copenhagen in 1674.

In this paper, BORCH criticizes a still older paper by PEIRESC in such a way that one has the impression that the pecten was actually described by PEIRESC. This may be the reason why COLE (1944, p. 322) quite definitely states that PEIRESC knew of the pecten. PEIRESC's investigations were published by the philosopher and physicist GASSENDUS in a book on PEIRESC's life (Latin edition 1641, English edition 1657). In this book, there is a long passage on the structure and function of eyes (pp. 274–283 in the Latin ed. for 1641), but no description of a structure identifiable with the pecten could be found, although remarkable features in the neighbourhood of the lens are mentioned.

The sequence of papers containing the first descriptions of the pecten is as follows, when the reports are arranged after the year of publication:

1674: OLAUS BORRICHIUS, in his "Hermetis, AEgyptiorum et Chemicorum Sapientia", pp. 258–259, describes the pecten of the eagle in a very accurate way and advances the first functional hypothesis: "... Membrana subnigricans et in plicas corrugata, nervoque optico in longum expanso continua, medium digitum lata erat, tota vasis distincta sangvineis secundum longitudinem rugarum. Margo singularis humoris crystallini à *Peirescio* adesse creditus, observari hic nequit. Ex productis jam in medium non difficile, opinor, suerit, rationem reddere, cur oculi aquilae sine noxâ ferre queant solare jubar''.

(... There is a blackish membrane, wrinkled in folds, continuous with the greatly extended optic nerve, as broad as a middle finger, all over distinctly with blood vessels following the longitudinal course of the folds. The remarkable margin of the crystalline humour, which *Peiresc* believed to be present, cannot be observed here. On the basis of the extension (of the membrane) into the middle, I think it will not be difficult, now, to give a reasonable explanation why the eyes of the eagle can withstand the rays of the sun without being damaged).

1675: NICOLAUS STENONIS (STENO), in his article on the development of the chick ("In Ovo et Pullo Observationes") in Acta Medica Hafniensia, vol. II for 1673, described the pecten of the 13 day old chick embryo in the following way: "... Optici nervi filamenta nigra, quae per vitreum pergunt crystallinum ..." (Black fibres of the optic nerve which advance through the vitreus to the crystalline humour ...). Although the volume was printed in 1675, it is the "Acta" for 1673, and STENO'S text was probably written 10 years earlier, in 1665, when he was working with SVAMMERDAM at Iassy (see MAAR 1910, Vol. II, p. 318).

1676: CLAUDE PERRAULT, in the "Mémoires pour servir a l'histoire naturelle des Animaux", described the pecten in several birds (eagles, turkeys, bustards, and ostriches), but believed it was absent in the Numidian crane (Anthropoides virgo). He describes the pecten as a purse ("bourse"), attached to the papilla of the optic nerve. He considered that the "folded appearance" was an illusion, and believed the pecten to consist of a mass of fibres. He suggested that it has the same function as the uvea: "à prèparer la nourriture des humeurs de l'Oeil". This opinion was partly based on the black colour of both organs, and partly on the presumed absence of the pecten in the Numidian crane, which was said to have a particularly dark uvea (p. 334).

1680: PERRAULT, in the "Essais de Physique", repeats some of the earlier statements and his functional theory (1721, pp. 343-345).

1681: GERALDI BLASIUS, in his "Anatome animalium", quotes BORCH's chapter on the anatomy of the eagle (pp. 136–138).

1682: ALLEN MULLEN (MOULIN) reports that he has seen in the chick the "little black bag" which PERRAULT had found in the eye of birds. This is mentioned on p. 63 in the small publication: "An Anatomical Account of the Elephant, Accidentally Burnt in Dublin, on Fryday, June 17. in the Year 1681 (with an Appendix on the Eyes of Animals)".

Of course, the question of the actual discovery of the pecten is not solved by merely filing the published statements after their date of publication. Communication between anatomical schools was very close in those days, as is shown by the almost simultaneous appearance of the pecten in scientific reports from Copenhagen (1674, 1675), from Paris (1676, 1680), from Amsterdam (1681) and from London (1682). It ought

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to be mentioned also, that STENO visited Paris in 1664 and 1665, and may well have received certain hints from anatomists there before he and SVAMMERDAM dissected their chick embryos in 1665. The fact that STENO describes the pecten as "filamenta nigra" is suggestive of the way PERRAULT describes it: "fibres noires". BORCH could well have been inspired by STENO, but his description is entirely independent and actually includes all relevant morphological features which can be seen under low magnification. It is probable, therefore, that BORCH's description is based on very careful dissection. On the other hand, STENO and BORCH often worked together, and the actual dissection may have been performed by either of the two.

Theories on the Function of the Pecten

It is obvious that the beautiful morphological appearance of the pecten has greatly stimulated the imagination of investigators, as about 30 different functional theories have appeared in the pecten literature since the organ was discovered in 1674. In contrast, very few investigators have tried to control the theories experimentally. Consequently, only few theories have been definitely disproved, and none can be said to be so well supported by experimental evidence that it must be preferred to all the others.

This is admirably illustrated by the fact that theories advanced in the 17th century have survived happily to the present day. BORCH (1674) thought that the pecten protected the eye of the eagle from damage from the rays of the sun, and a similar function was accepted as being possible by, e.g., VERRIER (1936) and GRIFFIN (1953). PER-RAULT (1676) suggested that the pecten serves to prepare nourishment for the eye. This basic idea, that the pecten is a kind of nutritive organ, has survived in different variations, including the ideas most widely held at present.

The theories on the function of the pecten have been reviewed more or less extensively by VIRCHOW (1901), WOOD (1917), v. SZILY (1922), KAJIKAWA (1923), MANN (1924 a), FRANZ (1934), WALLS (1942), and DUKE-ELDER (1958). The table below indicates the main lines of thought, together with references to the most important papers in which the theories are mentioned.

- 1. The pecten is a nutritive organ (PERRAULT 1676, 1680).
 - a. It supplies the inner eye in general: MIHALKOWICS (1873), LEUCKART (1875), CARRIÈRE (1885), ABELSDORFF (1910), BLOCHMANN and V. HUSEN (1911), LEPLAT (1912), WOOD (1913, 1914, 1917), SLONAKER (1918), JOKL (1923), PLATE (1924), PASQUINI (1926), DUKE-ELDER (1958). Contender: WIEDERS-HEIM (1909).
 - b. It supplies the vitreous body (and, in some theories, also the lens): Collins (1900), Lindsay-Johnson (1901), Bütschli (1912), Mawas (1913), Strese-MANN (1927–1933).

- c. It secretes the fibrous material of the vitreous body: v. HUSEN (1913), PLATE (1924), MENNER (1938).
- d. It is an enlarged ciliary or choroid process: HOVIUS (1716), HALLER (1768), ROSENTHAL (1811), GIRALDÉS (1836), BRADLEY (1915).
- e. It produces intra-ocular fluid: LEBER (1903), ABELSDORFF and WESSELY (1909), HESS (1913), KAJIKAWA (1923), VERRIER (1936), MENNER (1938), TURCHINI (1933), TANAKA (1960), SEAMAN and STORM (1963), SEAMAN and HIMELFARB (1963).
- f. It supplies the retina (replaces intra-retinal and hyaloid vessels): H. MÜLLER (1872), BEAUREGARD (1876), PARREIDT (1901), ROCHON-DUVIGNEAUD (1920, 1943, 1950), MANN (1924 a, b), WALLS (1942), LEINER (1951), KAUTH and SOMMER (1953), PRINCE (1956), POLYAK (1957), PUMPHREY (1961), O'RA-HILLY and MEYER (1961). Contenders: FRANZ (1909, 1934), GRIFFIN (1953).
- g. It supplies the retina through lymph vessels, supposed to run from the pecten to the retina: DENISSENKO (1881).
- The pecten protects the eye from damage from strong light: BORCH (1674, 1681).
 a. Without specification of mechanisms: BORCH (1674, 1681), DESMOULINS and MAGENDIE (1825), HUSCHKE (1827), V. HUSEN (1913), WOOD (1914). Contenders: LEUCKART (1875), BEAUREGARD (1876), KAJIKAWA (1923), MANN (1924 a).
 - b. Its blood stream carries away heat brought in by sunlight: GRIFFIN (1953).
 - c. It is spread fan-like behind the pupilla and acts as a filter: TREVIRANUS (1820). Contender: TREVIRANUS (1828), BARKOW (1830).
 - d. It is erected by the filling of its blood vessels, to catch the rays of the sun: ZIEM (1891, 1894).
- 3. The pecten absorbs diffuse light in the eye, thereby contributing to a clear image: TREVIRANUS (1828), THOMSON (1929), VERRIER (1936).
- 4. The pecten casts a shadow on the retina, facilitating vision in different ways.
 a. Without specified mechanisms: DESMOULINS and MAGENDIE (1825). Contenders: KAJIKAWA (1923), MANN (1924 a, b).
 - b. It absorbs the rays from lateral and posterior directions in favour of binocular vision: PETIT (1738).
 - c. It absorbs the rays from the dorsal and rostral fields in favour of monocular vision: TREVIRANUS (1820), HUSCHKE (1827), BEAUREGARD (1875). Contender: BEAUREGARD (1876).
 - d. It separates the binocular from the monocular field of vision: SCHLEICH (1896). Contender: RABL (1900).
 - e. The half-shadow cast on the retina increases sensibility: HUSCHKE (1827).
 - f. The grid-like shadow cast on the retina increases resolution of movement: MENNER (1938), CROIZIER and WOLF (1944 a, b). Contender: LEINER (1951).

- g. The increased resolution of movement (point 4:f) is important for registering the sun-arc when the bird determines its latitude and longitude: GRIFFIN (1953), MATTHEWS (1955).
- 5. The pecten is a sensory organ.
 - a. It is a thermoscope which registers radiating heat and prompts the bird when it is time to migrate: TREVIRANUS (1828).
 - b. It registers intra-ocular pressure changes during accomodation, so that distance to objects can be perceived: FRANZ (1908 a, b, 1909, 1910, 1913, 1923, 1934), KALLIUS (1907), WIEDERSHEIM (1909). Contenders: BLOCHMANN and V. HUSEN (1911), TRETJAKOFF (1912), V. HUSEN (1913), BÜTSCHLI (1912), and most later authors.
- 6. The pecten heats the eye, compensating for the cooling effect of air currents in arctic areas and at great altitude: KAJIKAWA (1923), BACSICH and GELLÉRT (1935).
- 7. The pecten is a dark mirror, which casts images on the retina of objects in the sky (e.g. birds of prey): THOMSON (1928, 1929).
- 8. The pecten has an active role in accommodation: Contenders: Leuckart (1875), Th. BEER (1893), ABELSDORFF (1910), WOOD (1914), MANN (1924).
 - a. It is a muscle acting on the lens: de la Hire (1701), Home (1796). Contenders: Home (1822), Leuckart (1875), Carrière (1885), Gadow (1891), Th. Beer (1893).
 - b. It can be erected by blood pressure, thus pushing the lens forwards: OWEN (1866).
 - c. It can be filled with blood and, by increasing intra-ocular pressure, acts hydraulically on the lens: mentioned by DUKE-ELDER (1958), origin not known.
- 9. The pecten smoothes out pressure variations.
 - a. Its vessels are emptied when the pressure rises in connection with accommodation: RABL (1900), HESS (1909), BÜTSCHLI (1912), LEPLAT (1912), v. HUSEN (1913), KAJIKAWA (1923), MANN (1924 a, b), ROCHON-DUVIGNEAUD (1950). Contenders: BEAUREGARD (1876), ABELSDORFF (1910), MENNER (1938).
 - b. It eliminates the pulse shock: Mentioned by DUKE-ELDER (1958).
 - c. It regulates, by means of its blood content, the intra-ocular pressure during changes in altitude: Mentioned by DUKE-ELDER (1958); origin not known (it is not FRANZ (1909) as quoted by DUKE-ELDER).
 - d. Like the corpus ciliare, it regulates the intra-ocular pressure by secretion of fluid (compare point 1:e): Wood (1914), SEAMAN and STORM (1963), SEAMAN and HIMELFARB (1963); compare ABELSDORFF and WESSELY (1909).

Experimental investigations, dealing with the pecten, were introduced by BEAURE-GARD (1875, 1876), who studied the organ with the ophthalmoscope. When the intact eye is stimulated to accommodate the pecten appears to make sudden movements, but as these movements cease when the external eye muscles are removed, BEAURE-GARD concluded that they have no connection with accomodation. In connection with these experiments it is of some interest that HESS (1909) found a small increase of intra-ocular pressure (1 mm. Hg), when the enucleated eye was stimulated to accommodate; he believed that the pressure changes in the intact eye are larger. Such pressure variations could possibly be eliminated by the pecten. ABELSDORFF (1910) re-investigated the problem. He stimulated the iris in situ to contract, after the external eye muscles had been immobilized with curare, and found no pecten movements during accommodation. As a whole, it seems unlikely from these experiments that the pecten has either an active or passive role in accomodation.

The most extensive experiments on the pecten are still those of ABELSDORFF and WESSELY (1909). These authors injected fluorescin into the blood and were able to show that the pecten is readily permeable to this dye and, probably, to other low-molecular substances as well. After extirpation of the ciliary body, the intra-ocular pressure could not be maintained; The bulb collapsed and the pecten was said to hypertrophy. Although crude, and subjected to justified criticism (FRANZ 1934, p. 1175), this experiment might indicate that the pecten helps the ciliary body to maintain intra-ocular pressure by secretion of fluid, and that the reported hypertrophy could be compensatory. ABELSDORFF and WESSELY (1909) also extirpated the pecten in owls, but the results of these experiments are difficult to evaluate, because the optic nerve, parts of the adjacent wall of the bulb, and, probably, the arteries to the choriocapillaris were removed with the pecten.

KAUTH and SOMMER (1953) also experimented along these lines, destroying the pecten by cautherization. Within 8 days of the operation they observed by ophthalmoscope the development of a whitish reflex from the retina, but made no report of histological changes. According to the present authors' experience, rather much heat is needed to destroy the pecten, probably because of its abundant vascular supply. The retinal change could, therefore, perhaps be caused by damage to adjacent structures such as the optic nerve, to which the pecten is attached. On the other hand, the same symptom in the retina was observed by the present authors, after the pecten had been eliminated in a more selective way.

MENNER (1938) used an ophthalmoscopic method to map out the extreme limits of the pecten shadow on the retina in different bird species. In his opinion, the shadow is often complicated and foliated and serves to increase the resolution of movement. The theory was strongly supported by CROIZIER and WOLF (1944 a, b), who investigated the flicker response acuity both in man and in the sparrow. The resolution of small moving objects was much greater in the sparrow, but when a grid-like shadow was cast on the human retina, its resolution rose to a level comparable to that of the sparrow. They concluded that the normal, high resolution of movement in the sparroweye depends on the presence of such a shadow: the foliated pecten-shadow described by MENNER. However, the high resolution of the sparrow retina could also depend on retinal structure, and this explanation is made more attractive by certain doubts expressed about the pecten shadow. Several authors (e.g., KAJIKAWA 1923, MANN 1924 a, b, LEINER 1951) have noticed that the pecten is directed towards the optic centre of the lens and cornea (Pl. I:1, compare Wood 1917, CAMPELL, SMITH, and HARWARD 1962). This means that he pecten shadow is very small under favourable light conditions, when the pupilla is narrow, and falls mainly on the extended papilla of the optic nerve. Although the contours of the shadow can be uneven because of the pecten folds, it is hardly realistic to speak of the "grid pattern" required for the CROIZIER and WOLF theory. Only when the pupilla is wide open can there be a shadow effect on a somewhat wider zone of retina on each side of the pecten, but this zone cannot possibly be sharply contoured and will rapidly fade out to each side. This kind of shadow cannot produce the grid-effect necessary to substantiate the CROIZIER and WOLF theory. As it is realized that MENNER's lines do not represent sharp contours of a dark shadow but only extreme limits of the fading half-shadow under poor light conditions, the grid theory advanced by CROIZIER and WOLF is impossible to uphold.

KAUTH and SOMMER (1953) and LEINER (1951), found great carbonic acid dehydrase activity in the pecten of the fowl, twice as much as in the blood. Their interpretation favoured the hypothesis that the pecten is a respiratory organ for the inner layers of the retina. The enzyme would, in particular, facilitate the removal of CO_2 from the vitreous body.

Histochemical investigations by O'RAHILLY and MEYER (1961) and by SEAMAN and STORM (1963), show the presence of polysaccarid or mucoproteid membranes and alcaline phosphatase in the walls of the pecten vessels. They use these findings to support the theory of active secretion of fluid from the pecten. It is admitted that the said histochemical features indicate active transport through membranes, but it is open to doubt whether they reveal the specific function of the pecten. Positive PAS-reaction and alcaline phosphatase is a common feature in vascular walls, and can be seen in organs with very different functions.

The theory of active transport, particularly that of secretion of intraocular fluid, gains some support from electron microscopical studies (TANAKA 1960, SEAMAN and HIMELFARB 1963, SEAMAN and STORM 1963). It was found that the endothelial cells of the pecten capillaries have strongly folded, brush-border-like cell membranes both on the luminal and on the basal side. Similar membrane structures are familiar from other organs which are known to be concerned with active secretion of fluids, e.g. the ciliary body, the kidney, the choroid plexi, and the salivary glands. Although the analogy with these organs favours the hypothesis that the pecten is a secretory organ, the argument is far from conclusive.

Firstly, the folded membranes of the pecten are found in the endothelial cells of the vessels, whereas in the above-mentioned secretory organs, they are found in the epithelia outside the vessels. The structural similarity is thus restricted to the membrane folds as such and does not include the anatomical arrangement.

Secondly, it cannot be excluded that cell membranes of this type may be correlated with functions other than secretion or absorbtion. This is well illustrated throughout the animal kingdom by the visual sense cells, which have folded membranes of different types, sometimes with the appearance of brush-borders (Röhlich and Törok 1961), sometimes folded into the cell plasm (EAKIN and WESTFALL 1962), and sometimes more elaborate, as in arthropods and vertebrates.

Finally, the brush-borders of actively secreting cells are associated with numerous mitochondria, important for the supply of energy to the transport process. In contrast mitochondria are not exceptionally numerous in the endothelial cells of the pigeon pecten (Pl. VI).

The question of water transport was recently attacked experimentally (SEAMAN and STORM 1963, SEAMAN and HIMELFARB 1963). Injection of the drug Diamox into chickens caused a fall of intra-ocular pressure within an hour and was correlated with great changes of the ultra-structure of the pecten and the ciliary body. In both organs there was a general breakdown of the folded membranes. This was presumed to indicate that the pecten and the ciliary body are both concerned with the secretion of intra-ocular fluid and with the pressure regulation in the bulb. The pecten is believed to come into play only when the regulating mechanism is over-loaded. Although interesting, these experiments are not definitely conclusive, as the effect on the intra-ocular pressure would certainly be obtained after destruction of the ciliary epithelium alone, and the destruction in the pecten may or may not be significant in this respect. Moreover, the doses of Diamox used in these experiments were rather large, 100 times as large as those used for humans. The changes in the cell membranes of the pecten and the ciliary body could, therefore, be interpreted as unspecific destruction and should not necessarily depend on fundamental functional similarities. This possibility is made particularly attractive by the experiments with mammals, performed by TORMEY (1963 a, b). His attempts to correlate the pressure fall after Diamox treatment with ultrastructural changes in the ciliary epithelium gave rather confusing results.

Nevertheless, when all arguments are taken into account, it appears possible and even probable that some fluid escapes from the pecten into the vitreous body. However, it has not been shown that this is an essential function of the pecten, important for the normal function of the eye.

The Structure of the Pecten in the Pigeon

Methods

The species used in the present investigation is the domestic pigeon (Columba livia L.). For light microscopical studies the eye was injected with Bouin's or Zenker's solution, or neutral formalin before dissection and final fixation in the same fluid. 5μ paraffin sections were stained with Azan, hematoxylin-eosin, PAS-hematoxylin, alcian blue, or PAS-alcian blue. For electron microscopy, fixation was performed in ice-cold, collidin-buffered $2^{0}/_{0}$ OsO₄ or in glutaraldehyde, followed by OsO₄. The cold fixative was in 3 cases perfused from the carotis, and fixation was continued in fresh ice-cold solution after the organs had been dissected out on ice. In 2 cases the organs were dissected out immediately after death and were put directly

into the cold fixative. Small pieces were embedded in methacrylate mixture, Westopal or Epon. Sections of about 500 Å were contrasted with uranyl acetate, permanganate or lead hydroxyde (NORMAN 1964) and were examined in a Siemens Elmiskop I.

External Shape, Orientation

In the pigeon, as in the majority of birds, the pecten has the macroscopic appearance described by BORRICHIUS in 1674: It is a thin, pigmented and very vascular membrane, wrinkled into transverse folds, and attached to the elongate, narrow papilla of the optic nerve (Pls. I–III). The folds give it the appearance of a comb, and this impression is strengthened by the thick, compact "bridge", which covers the inner ends of the folds and forms the free margin of the organ (Pl. I:2).

Only few birds differ from this general picture. The Kiwi (*Apteryx*) has instead a solid, pigmented cone resembling that found in lizards (LINDSAY-JOHNSON 1901, KAJIKAWA 1923). In the Ostrich (*Struthio*) and the Rhea, the pecten has the shape of a broad cone with a somewhat elongate base. It consists of branching lamellae, which are radially arranged around the axis of the cone, where they are attached to a more or less distinct central lamella (SOEMMERING 1818, BEAUREGARD 1876, CARRIÈRE 1885, KAJIKAWA 1923, VRABEC 1958). The Cassowary and the Emu have corrugated pecten membranes like the majority of birds, but an intermediate type is found in the Kingfisher (*Alcedo*), in which small supporting lamellae are attached to the normal pecten folds (KOLMER 1924, TANAKA 1938 b).

Variations in relative and absolute size, number of folds, proportions, and site have been reported for about 200 bird species (WAGNER 1837, GIEBEL 1857, BEAURE-GARD 1876, VIRCHOW 1901, FRANZ 1909, 1934, WOOD 1917, ROCHON-DUVIGNEAUD 1920, 1943, 1950, KAJIKAWA 1923, STRESEMANN 1927–33, BACSICH and GELLERT 1935, and TANAKA 1938 a, b).

In the *domestic pigeon* the pecten membrane is wrinkled into 18–19 folds and is covered by a well-developed, compact bridge along the free margin (Pl. I:2). It stands on the narrow, elongate papilla of the optic nerve in the rostro-ventral sector of the bulb, and extends from a point 1.8 mm below the fovea out to a point 3 mm from the ora serrata (Pls. I–III). The maximal height is 3.3–4 mm, the length along the base is about 6 mm, and along the free margin 3–3.7 mm. The thickness between the culmen of the folds is 0.8–0.9 mm. The bridge is somewhat narrower than the folded part.

The pecten is orientated in such a way that its plane cuts the common optic centre of the lens and cornea. This is seen when the pecten is viewed with the ophthalmoscope through the pupilla. The bridge is then seen from the top and a series of low bulges on each side indicate the tops of the folds. The sides of the pecten cannot be seen when the pupilla is normally contracted (cf. figures in WOOD 1917 and in CAMPELL, SMITH, and HARVARD 1962). When the pupilla is wide open after treatment with curare, part of the sides can be seen, although from a very narrow angle. This means that the pecten of the pigeon casts its shadow mainly on its own base, when the pupilla is normally contracted. Under poor conditions of illumination, when the pupilla is wide open, there may be some half-shadow with indistinct contours on a narrow strip of retina along each side of the pecten. For these reasons it is impossible to accept theories founded on the belief that the pecten casts a sharp, grid-like or foliate shadow on the retina (see p. 11). The organ is situated in such a way that it interferes as little as possible with the light coming in through the pupilla.

The Vessels

The folded pecten membrane is only $15-20 \mu$ thick and consists mainly of densely packed capillaries which form two parallel rows in a cross section of the membrane (Pl. X:2, 4). The bridge contains a more irregular net of scattered capillaries. This vascular bed is supplied by 2–4 arteriae pectinis, which enter the bulb through the slit-like opening for the optic nerve, and by a vena pectinis, for which there is a separate foramen in the sclera (Figs. 6, 7, 8, Pl. V:2). After entering, these vessels turn longitudinally under the base of the pecten, emitting arterioles and venules to each fold (Fig. 8, Pl. V:2). Usually there is one arteriole and one venule in each fold. They pass in a fairly straight direction through the basal part of the organ, following the longitudinal course of the folds, and merge with the capillary bed before reaching the bridge. Often, a distinct vessel is seen following the culmen of each fold, whereas another distinct vessel is found in the centre of the organ. However, arterioles and venules and venules may be found in both situations, so the arrangement appears to be very variable.

The Structure of the Folded Part of the Pecten

The thin wall forming the folds is covered on both surfaces by a superficial membrane, which can be identified in electron micrographs (Pls. IV, V:1, VII:1). This membrane is about 300 Å thick and shows the amorphous character and low density typical of basement membranes. The space between this membrane and the vessels is occupied by large intercellular spaces and by the scattered stroma cells and their processes (Fig. 1, Pls. IV, V:1).

The capillaries. As shown by TANAKA (1960), SEAMAN and STORM (1963), and SEAMAN and HIMELFARB (1963), the endothelium cells of typical pecten capillaries are thin plates with brush-border-like fringes on both sides. In most sections the villi are seen as fairly regular, about 1μ long and 4—600 Å thick processes, covered by the unit membrane of the cell surface (Pls. VI, VII:1). Tangential sections of the capillary wall show, however, that the villi are about 1μ broad, tongue-like folds with the said height and thickness. The same sections show that the distal parts of the villi are unbranched and isolated from each other.

The villi on the luminal side of the endothelial cells end freely in the lumen of the vessel. Those on the outer or basal side also have well-defined ends with unbroken

membranes, in contact with and probably adhering to the fibrous perivascular membrane (Pl. VI). The villi are few and low in some of the vessels but are absent only in some of the larger vessels. The authors' methacrylate sections gave a poor picture of the villi on the basal side of the endothelium, particularly when the villi were cut parallel to their flat sides. However, in the Westopal and Epon sections, the villi could be distinctly seen in these places (Pls. VI, VII:1). The use of methacrylate is perhaps the reason why SEAMAN and STORM (1963) describe the basal villi as confluent with the fibrous perivascular membrane in some places in the pecten of the chick.

The cytoplasm of the endothelial cells contains small $(0.3-0.7 \mu)$ mitochondria and some ribosomes, many of which are bound to membranes. Small (200-300 Å) smooth-surfaced vesicles are common in the plasm. SEAMAN and STORM (1963) and SEAMAN and HIMELFARB (1963) observed formation of rows of such vesicles in connection with a general break-down of the villus system in chicks treated with Diamox. In the present material of normal pigeons, this was seen only in parts of a single pecten, which had been poorly fixed with osmic, and was clearly an artefact.

The fibrous perivascular membrane shows up in light microscopical preparations stained with PAS as a sharp, red-violet line, indicating carbohydrate compounds. In the electron micrographs it is seen as a $0.3-0.5\,\mu$ thick zone, consisting of a homogeneous ground substance with low electron density and numerous collagen filaments with distinct periodicity. The inner limit of the zone is undefined and the villi of the endothelium appear to dip into the amorphous ground substance. The outer limit is sharp, formed by a 400 Å thick condensation of amorphous substance, similar to the basement membrane of normal epithelia (Pl. VII:1). This membrane forms the outer surface of the vessels. SEAMAN and STORM interpret the entire fibrous perivascular sheath as being the counterpart of the basement membrane of other capillaries.

Intramural cells are common in light microscopical sections, situated in the thick fibrous perivascular membrane. In electron micrographs they were found in the same site, splitting the perivascular membrane into an inner and an outer lamella (Fig. 1). Their flattened cell body was often seen to contain a well developed endoplasmic reticulum with numerous ribosomes. Parallel filaments, indicating a contractile function, could not be discovered in the pigeon, and SEAMAN and STORM were unable to find them in the chick. The authors also found occasional cells of this type outside the perivascular membrane on the outer surface of the vessel.

The stroma cells are scattered in the space between the vessels and the superficial membrane of the pecten. Their angular, irregular cell body with the large nucleus is often in direct contact with a capillary wall on one or two sides, whereas the major part of the cell membrane is bordered by the intercellular spaces (Fig. 1, Pls. IV–VI). The cell body sends numerous ramified processes out to the superficial membrane and to the walls of the vessels. The finest ramifications of these stroma cells are very numerous in some parts of the intercellular space and may be as thin as 600–700 Å. When reaching the superficial membrane these processes usually end with rounded
tips and do not form a closed plasmatic surface (Pls. V–VII). When ending on the surface of vessels they are often, though not always, inflated to vascular feet (Pl. VI).

The plasm of the stroma cells and their processes is dense in electron micrographs. All stroma cells appear to contain several spherical pigment granules with a diameter



Fig. 1. Diagram showing the folded wall of the pecten in the pigeon, based on an electron micrograph of a cross section. The drawing illustrates the relations of capillaries, stroma cells and the mucopolysaccharid membranes; of the cytoplasmic organellae only pigment granules are shown. — EP = endothelial cell nucleus, ICS = intercellular space, IM = intramural cell nucleus, MUS = superficial mucopolysaccharid membrane, MUV = mucopolysaccharid membrane covering outer surface of capillary, PIG = pigment granules, PM = perivascular membrane of capillary, STR = stroma cell nucleus, STP = stroma cell processes, VI = inner villi of endothelium. VE = outer villi of endothelium.

of $1-2\mu$. The mitochondria of the stroma cells are particularly large $(1.5-2\mu)$ and are usually rounded with beautiful, parallel cristae. There are a few ribosomes and scattered endoplasmic vesicles. Small, smooth-surfaced vesicles and bundles of thin filaments are sometimes seen in the plasm, but these are more typical of the bridge, as described below.

Connective tissue strings, which are fairly few and scattered, are distinct in light microscopical sections, stained in Azan. The counterpart in the electron micrographs Biol. Skr. Dan. Vid. Selsk. 14, no. 3.

is cross sections of tubules, filled with collagen filaments and surrounded by a thin amorphous membrane of the mucopolysaccharid type (Pl. V:1). The collagen is often disposed peripherally within the tube, as was expected from the tube-like appearance of the strings in the light microscope. As there is an almost continuous layer of stroma cell processes outside the membrane, the collagen-filled space is separated from the surrounding intercellular space.

The intercellular space is an important system of cavities and clefts in the pigeon (Fig. 1, Pls. IV, V:1). It forms a continuous cavity under the superficial membrane and extends between the stroma cells and vessels of the interior. The cavity is traversed by the numerous processes of the stroma cells, but as these are slender rods, there is no reason to believe that the intercellular space is divided into separate compartments. The space must therefore be looked upon as a continuous cavity, extending from the superficial membrane to the wall of the vessels and surrounding all stroma cells and their processes. TANAKA (1960) describes this space in different bird species, but SEAMAN and STORM (1963) and SEAMAN and HIMELFARB (1963) did not find intercellular spaces in the chick. It may therefore be of interest that the same general morphology was found in the pigeon both after fixation in OsO₄ and after fixation in glutaraldehyde, and there was no difference between specimens fixed by perfusion from the carotis and those fixed by putting the organ directly into the fixative after dissection. As it is unlikely that the pigeon and the chick are fundamentally different with regard to intercellular spaces, it is probable that the difference rather depends on the method used. It is possible that the fluid in the intercellular space had escaped and that the spaces themselves had collapsed in SEAMAN'S and STORM'S preparations, as these authors cut the fresh organ into small pieces before the fixation.

The superficial membrane, covering the free surface of the wall, may be supposed to have covered a continuous cellular surface on the embryonic pecten as a basement membrane. In adult pigeons, however, the stroma cells have retracted and the large intercellular space begins directly under the membrane. The stroma cells are only in contact with the membrane by means of the tips of the fine processes, which are rather far apart. Large areas of membrane have no contact at all with the stroma cells (Fig. 1, Pls. IV, V:1, VII:1). The amorphous substance of the membrane is often seen to project inwards, between the tips of the stroma cell processes, as strings (Figs. 1, Pls. V: 1, VII:1).

The Bridge of the Pecten

The bridge is a fairly compact structure, consisting mainly of strongly pigmented stroma cells, which give it a black colour. The intercellular spaces are small but fairly numerous, and it has not been possible to ascertain whether they are continuous or not. The surface is covered by the same superficial membrane as that seen on the folded part, but in the bridge it rests on a continuous cellular surface formed by the stroma cells. Capillaries are fairly rare and their endothelium is of the common type, without the brush-borders seen in the folded part of the pecten. The stroma cells are not so extensively ramified as in the folds but often send long processes to the external surface. In addition to pigment granules, large mitochondria and a moderately developed endoplasmic reticulum with ribosomes, the stroma cells contain numerous small, parallel filaments (100 Å thick), plus numerous smooth-surfaced vesicles with ± 500 Å diameter. The bundles of filaments occur regularly in the long processes, but may also be seen in the cell body proper (Pls. VII:2, VIII).

The outer surface of the bridge attaches itself firmly to the vitreous body during dissection, and in electron micrographs the collagen filaments of the vitreus can be seen immediately outside the basement membrane of the surface (Pl. VIII). In light microscopical preparations, stained in Azan, thin strands of blue-staining vitreous substance can be seen penetrating from the surface deep into the tissue of the bridge. This was noted by KAJIKAWA (1923, p. 320). In electron micrographs these narrow, ramified channels, filled with collagen filaments, are seen throughout the tissue of the bridge. They are surrounded by stroma cells and lined by a basement membrane, and are completely separated from the empty intercellular spaces. At the opening on the surface, the basement membrane is continuous with the membrane on the surface of the bridge, and the collagen is continuous with that of the vitreous body.

No distinct nerve fibres or sensory cells could be identified in the bridge or in the folded part, and although the negative statement has a rather limited value, it can be concluded with safety that there is no appreciable innervation. This negative result, which is also supported by SEAMAN and STORM (1963), makes it impossible to accept any theories of the pecten being a sensory organ (FRANZ 1908–1934).

The Nature of the Stroma Cells

Most recent authors agree with BERND (1905), MANN (1921, 1922, 1924 b) and LINDAHL and JOKL (1922 a), who regard the stroma cells as being ectodermal, because the pecten appears to receive contributions from the retina in later embryonic stages. The stroma cells would, then, be a kind of glia cells, but up to now little to support this idea has been gained from morphological studies of the adult pecten.

In the present study two cytological features were revealed which speak in favour of the glial nature of the stroma cells: 1) The way the processes ramify and end with inflated vascular feet on the capillaries in the folded part of the pecten, and 2) The presence of bundles of thin filaments and of numerous small vesicles in the plasm, particularly in the stroma cells of the bridge. Although present in other cell types as well, such vesicles and filaments are typical of the Müller cells in the retina (FINE and ZIMMERMANN 1962, PEDLER 1963, COHEN 1963); the filaments also appear to be typical of fibrous astroglia (LUSE 1956) and of ependyma (FLEISCHAUER 1958). As, moreover, the stroma cells have no significant features in common with fibrocytes, the glial nature appears to be well supported by their cytological appearance.

Vessels and Nerves of the Orbital Region of the Pigeon

The following notes on the vascular supply and innervation of the orbital region in pigeons are reported here because they form the basis of the operational procedure in the following chapter and are necessary for critical evaluation of the results. In many respects, the vessels and nerves of the pigeon eye agree with those of the sparrow, described in detail by SLONAKER (1918), but the differences are large enough to be of essential importance during the operations.

Methods

Routine examination of vessels was made by different methods of injection. In one series of animals, the arteries of the head were injected from the carotis with starch-vermilion, after the animal had been killed with ether (See WINGSTRAND 1951, p. 15); the head was fixed with 80 $^{0}/_{0}$ alcohol, formalin and acetic acid (90:5:5), decalcified in nitric acid (conc. acid, 7 parts : water, 93 parts), bleached in $2^{0}/_{0}$ hydrogen peroxide, and cleared over 96 $^{0}/_{0}$ and absolute alcohol in benzyl benzoate. Another series was, in addition, injected from the v. jugularis with the same starch solution, in which cobalt blue had been substituted for vermilion. Some of these preparations were also used for dissection, and some were cut into smaller pieces or thick sections before being cleared to allow detailed study. A third series of pigeons was injected with Tensol Cement No. 7 (Imp. Chem. Indust. Ltd.). The injection took place from the carotis. First, a thin plastic solution stained with Sudan III was injected until the entire vascular system was filled, followed by plastic with vermilion and cobalt blue, which filled the arteries and could not pass the capillaries. After polymerization, the soft parts of the head were removed with hypochlorite (Bugge 1963), which left the skeleton intact, or with strong hydrochloric acid, which left the plastic clean. Additional information was drawn from some series of celloidin sections through the head of pigeons, injected from the carotis with starch-vermilion or India ink-gelatine.

The Vascular System of the Pecten

As shown already by ANDRE and BEAUREGARD (1874), BEAUREGARD (1876), and DENISSENKO (1881), the vascular bed of the pecten is almost completely isolated from the vessels of the surrounding parts. In the authors' preparations of pigeons, injected with plastic or India ink, there were no vessels connecting the base of the pecten with the choriocapillaris. One or a few small capillaries were usually seen to connect the innermost end of the pecten with the capillary net in the optic nerve. As the pigeon, like other birds, has neither hyaloid nor intra-retinal vessels, the plastic casts of the vascular beds show the pecten vessels entering through a clean opening in the choriocapillaris, through which the optic nerve entered. It thus appeared possible to eliminate the pecten experimentally by blocking its arteries and veins.

Arterial System of the Orbital Region

(Figs. 2-8, Pls. II-III)

1. The *a. ethmoidalis* (Figs. 2, 4) is a branch of the ramus anterior of the carotis cerebralis. It leaves the brain cavity and enters the orbit through a foramen just above the foramen opticum (cf. HOFMANN 1900, HAFFERL 1933, CORNELIAC 1935,



Fig. 2. The arterial system of the pigeon's head, drawn from a cleared specimen, injected with starch-vermilion. — AA = anastomotic arteries in front of the optic nerve, AO = a. antorbitalis, BU = a. buccalis, CCE = a. carotis cerebralis, CCO = a. carotis communis, CE = "a. carotis externa", CIN = a. carotis interna, ET = a. ethmoidalis, F = arteries to frontal skin, IO = a. infraorbitalis, MD = a. mandibularis, MX = a. maxillaris, OI = a. ophthalmica interna, OT = a. ophthalmo-temporalis, RAC = ramus anterior of the carotis cerebralis, RP = ramus posterior of carotis cerebralis, RMO = rete mirabile ophthalmicum, SM =a. spheno-maxillaris, SO = a. supraorbitalis, ST = a. stapedia.



Fig. 3. Superficial arteries of the eye region of a pigeon, drawn from a cleared specimen injected with starchvermilion. — AO = a. antorbitalis, BA, BI and BP = bulbar arteries from the antorbital, the infraorbital, and the postorbital arteries, resp., BU = a. buccalis, F = arteries to the frontal skin, IO = a. infraorbitalis, MEA = meatus acusticus externus, MX = a. maxillaris, OC = arteries to the skin behind the eyes, PI and PS = inferior and superior palpebral arteries coming from the antorbital, PP = palpebral artery coming from the supraorbital, SO = a. supraorbitalis.

WINGSTRAND 1951). The artery passes forwards along the interorbital septum above the optic nerve to the rostro-medial corner of the orbit, where it fuses with the ramus supra-orbitalis of the a. stapedia and passes into the upper beak near the median plane. It is connected with the ramus ophthalmo-temporalis of the a. stapedia by one or, what is more usual, two arteries in front of and one behind the optic nerve. The main branches of the a. ethmoidalis are arteries to the m. rectus superior, the m. quadratus, and the m. obliquus superior. The a. ethmoidalis was called a. ophthalmica interna by SLONAKER (1918), but since a true a. ophthalmica interna does exist, there is no reason to use this name.

2. The *a. maxillaris*, when passing forwards under the orbit, emits a branch, which the present authors call *a. antorbitalis* (Figs. 2–5). This branch passes medial to the jugal arch into the orbit. It follows the anterior margin up to the "lacrymal" (prefontal) bone, which it passes on the posterior side. At the dorsal margin of the lacrymal it leaves the orbit and sends branches to the skin above and in front of the eye. When passing medial to the jugal, it anastomoses with the infra-orbital branch of the a. stapedia and, sometimes, with the small buccal artery described below. In some specimens, the antorbital artery is fed exclusively by the a. maxillaris, in others, by the a. infra-orbitalis, but it is always present and emits the following branches: a) two arteries to the lower beak, b) an a. palpebralis inf. to the lower eyelid, c) an a. palpebralis sup. to the upper eyelid, d) an artery to the dorsal part of the anterior eye segment, and e) skin branches, two of which usually pass backwards to the skin above the orbit, the lateral one following a course lateral to the superior margin of the orbit (Figs. 3, 5).

3. The "*a. buccalis*" is a small artery coming from the carotis externa near the point of division into the a. maxillaris and a. mandibularis (Figs. 2–3). The artery passes out to the skin in front of the meatus acusticus externus and below the lower eyelid. It may communicate with the antorbital artery in some specimens (see above).

4. The small *a. ophthalmica interna* s. str. leaves the carotis cerebralis near the intercarotic anastomosis on each side of the pituitary, passes forwards in the sella turcica and enters the orbit together with a small v. ophthalmica interna below the optic foramen (Fig. 2). The artery joins the a. ophthalmo-temporalis below the optic nerve or connects with the post-optic anastomotic artery (Fig. 8).

5. The *a. stapedia* (HAFFERL 1921), syn. a. ophthalmica externa (SLONAKER 1918) is emitted from the carotis interna in the quadrate region, passes through a canal in the cranial base behind the stapes and emerges through a foramen in the posteroventral wall of the orbit, where a large rete mirabile temporale (ophthalmicum) is formed by this artery and the corresponding veins (Fig. 2). The three main arteries emitted from this rete are:

a) The *a. supraorbitalis*, which passes dorso-lateral to the posterior margin of the orbit (Figs. 3–5). From here, it turns more medially and passes over the dorsal surface of the bulb to fuse with the a. ethmoidalis. The a. supraorbitalis emits branches from behind into the lower and upper eyelid; one branch goes to the temporal sector of the anterior bulb segment, and two or more branches pass out to the skin behind



Fig. 4. Deep arteries of the orbit of the pigeon, seen in the orbit after removal of the bulb. Drawing combined from studies of plastic casts, cleared and injected specimens, and from dissection of injected specimens. — AA = anastomotic arteries in front of the optic nerve, AO = a. antorbitalis, AP = anastomotic artery behind the optic nerve, ET = a. ethmoidalis, HG = arteries to Harderian gland, IO = a. infraorbitalis, LC = a. ciliaris longa, LG = artery to lacrymal gland, OBI = artery to m. obliquus inferior, OI = a. ophthalmica interna, OS = arteries to m. obliquus superior, OT = a. ophthalmo-temporalis, P = pecten arteries PY = arteries to m. pyriformis, Q = arteries to m. quadratus, RA, RI, RP, RS = arteries to mm. recti (anterior, inferior, posterior, and superior, resp.), RMO = rete mirabile ophthalmicum, SO = a. supraorbitalis: "II" marks the entrance of the optic nerve, and the asterisks* mark the short posterior ciliary arteries.



Fig. 5. Arteries of the anterior bulb segment in the pigeon. Combined as fig. 4. — AO = a. antorbitalis, BA, BI, and BP = arteries to the anterior surface of the bulb from the antorbital, the infraorbital, and the supraorbital artery, resp., CI = anterior ciliary arteries, passing round the edge of the ossicular ring, I = iris, IO = a. infraorbitalis, LC = a. ciliaris longa, MX = a. maxillaris, PU = pupilla, RAI = ring artery of iris, RAO = ring artery on the inner side of ossicular ring, RMO = rete mirabile ophthalmicum, SO = a. supraorbitalis, SR = ossicular ring, ST = a. stapedia.

The asterisks* mark arteries, crossing over to the iris in the ligamentum pectinatum.

and above the orbit. These skin branches are usually smaller than those from the antorbital artery.

b) The *a. infraorbitalis* passes forwards from the rete temporale along the bottom of the orbit and fuses with the above-mentioned branch of the a. maxillaris to form the a. antorbitalis (Figs. 2–5). In some specimens it is smaller, and fails to contribute to the a. antorbitalis. On its way it emits two or three smaller branches to the ventral sector of the anterior bulb segment and to the conjunctiva under the lower lid. One or two of these branches are the source of anterior ciliary arteries, whereas one or two additional anterior ciliary arteries are emitted from the branches of the antorbital anterior.

c) The *a. ophthalmo-temporalis* (SLONAKER 1918) is the main artery of the posterior bulb segment and supplies most of the eye muscles and the glands of the orbit (Figs. 2, 4, 6–8). After leaving the rete temporale, the artery passes along the wall of the orbit, making a loop below the optic nerve. From the optic nerve onwards it is attached to the horizontal meridian of the eye, emitting short posterior ciliary arteries to the choriocapillaris. The a. ophthalmo-temporalis anastomoses with the a. ophthalmica interna just below the optic nerve and is connected with the a. ethmoidalis by two or three anastomotic arteries, one of which runs behind the optic nerve, whereas the others run in front of it. Above the nerve the vessels often fuse into two before joining the a. ethmoidalis. In this way, the entrance of the optic nerve into the orbit is surrounded by an arterial ring which often consists of several vessels and is more or less plexus-like (Figs. 6–8, Pl. V:2).

The post-optic part of the a. ophthalmo-temporalis emits arteries to the m. rectus superior, m. quadratus, and 4–5 short posterior ciliary arteries to the bulb (Fig. 4). The m. rectus superior may also receive an artery from the a. ethmoidalis. The infra-optic loop of the a. ophthalmo-temporalis emits branches to the m. rectus posterior and m. r. inferior, and, in addition, the long ciliary artery and 2–3 aa. pectines to the pecten. The pre-optic part of the artery supplies the m. pyriformis, m. obliquus inferior and the Harderian gland, and emits smaller arteries to m. quadratus and m. rectus anterior. The latter muscle also receives an artery from the anastomotic vessel in front of the optic nerve. In addition, the pre-optic part of the a. ophthalmo-temporalis emits about 13 short ciliary arteries, which may branch one or a few times before entering the bulb at approximately the horizontal meridian.

Details of the Arterial Supply of the Bulb Proper

(Figs. 4-8)

In an operation of the kind described in the following pages, it is essential that the pecten arteries should be completely blocked, but it is also essential that vital arteries to other parts of the bulb are not damaged in any way liable to impair the results. For this reason, the vessels of the bulb proper are considered in detail.

The pecten arteries, 2, 3, or even 4 in number, are emitted from the infra-optic



Fig. 6. Variations of the arteries around the entrance of the optic nerve. All figures based on photographs of the orbital bottom in cleared specimens, injected with starch-vermilion, after removal of anterior eye segment. — AA^1 and AA^2 = anastomotic arteries in front of the optic nerve, AP = anastomotic artery behind the nerve, HG = artery to m. obliquus inferior and Harderian gland, LC = a. ciliaris longa, OT = a. ophthalmottemporalis, P = pecten arteries, RI = artery to m. rectus inferior, RP = artery to m. rectus posterior. The asterisks * mark the short ciliary arteries. The anterior (left) artery often sends a small vessel to the pecten.

loop of the a. ophthalmo-temporalis (Figs. 4, 6–8, Pl. V:2). In the pigeon they do not form a rete mirabile pectinis (cf. BARKOW 1829, 1830). They pass along the ventral side of the optic nerve to the bulb and enter it through the elongate, cleft-like opening of the sclera, where the nerve itself enters. Two or three large arteries enter along the posterior aspect of the nerve, but there is a small and variable artery which passes down on the rostral aspect of the nerve. The latter vessel is usually a branch of one of the short ciliary arteries (Fig. 6), but in one pigeon it was emitted by the artery of the pyriform muscle (Fig. 8). Many attempts to eliminate the pecten surgically failed bacause this small anterior artery had been left intact. Although small, it is large enough to prevent degeneration of the pecten even after cautherization of all other pecten arteries. The short posterior ciliary arteries, about 18 in number, are emitted by the a. ophthalmo-temporalis. They often branch a few times before entering through the foramina in the scleral cartilage. They supply the choriocapillaris and are, therefore, of vital importance for the retina, particularly as adult birds lack intra-retinal and hyaloid vessels. Fortunately, as these short arteries are situated far from the exposed area of the bulb, they are never in danger during the operations. In theory, the a. ophthalmotemporalis could be severed, as it passes across the field of operation below the optic nerve. Such accidents are easily discovered, however, because of the uncontrollable bleeding which follows, and because, with the technique used, the pulsations of the artery can be directly checked in the wound. Moreover, the anastomotic arteries in front of the optic nerve will secure the supply of the retina, if accidental blocking of the ophthalmo-temporal artery below the optic nerve should pass unnoticed (Fig. 4).

The supply of the anterior eye segment. The antorbital, infraorbital, and supraorbital arteries emit branches which supply the superficial parts of the anterior eye segment, including the 2–3 anterior ciliary arteries (Figs. 3, 5). The ciliary artery from the infraorbital vessel is the largest, and is present in all investigated specimens. These anterior ciliary arteries pass around the inner margin of the ring of scleral ossicles and enter a ring artery, situated on the inner side of the ossicles, parallel with the canal of Schlemm. One or two rather important arteries branch off from this ring and cross the ligamentum pectinatum to the iris, where they enter a large ring artery in the peripheral part of the stroma iridis (Fig. 5). This annular iris artery also receives the long ciliary artery. The latter leaves the a. ophthalmo-temporalis just behind the pecten arteries, enters the bulb along the postero-ventral aspect of the optic nerve together with the long ciliary nerve, and passes out to the iris in the choroid coat without emitting any branches on the way (Fig. 8).

The annular artery of the iris supplies the abundant capillary plexus of the stroma and sends radial vessels out to the ciliary folds and processes. As the ciliary body is known to be of essential importance in maintaining intraocular pressure, its blood supply via the ring artery of the iris requires particular attention during the operation. One of the affluents to this arterial ring, viz., the long ciliary artery, is often damaged when the pecten vessels are blocked. It is possible, though difficult, to save the long ciliary artery, but in most experiments no attempt was made to keep it intact. The reason for this was that the cutting of this artery in control experiments did not cause damage to the retina or other essential intraocular structures, except for immobilization of the iris caused by the simultaneous cutting of the long ciliary nerve. Obviously, the anterior ciliary arteries and the extensive communications between the ciliary folds and the choriocapillaris are enough to secure sufficient circulation in the region. To ensure that the iris circulation was in order, the iris in pigeons which had been operated upon, was viewed through a dissection microscope. In this way the capillary tufts, which protrude into the anterior eve chamber from the corneal surface of the iris, can be studied in detail through the transparent cornea.



Figs. 7 and 8. The arteries around the entrance of the optic nerve into the left bulb of a pigeon, viewed from the median plane. Anterior direction right. The stippled area is the scleral cartilage, the openings of which are darkly shaded. The zig-zag shadow in fig. 8 is the projection of the base of the pecten. The optic nerve is removed in fig. 8 to show details. Graphic reconstruction from celloidin sections. — AA₁, AA₂ and AP = anastomotic arteries in front of and behind the optic nerve, resp., CH = median section through chiasma, FV = foramen of the ventral posterior ciliary vein and pecten vein, FV_1 = foramina for small veins, F II = foramen for the optic nerve, HG + OI = artery to Harderian gland and m. obliquus inferior, LC = a. ciliaris longa, OI = a. ophthalmica interna, ON = optic nerve extension below the scleral cartilage, OT = a. ophthalmo-temporalis, P = pecten arteries, P_1 = exceptional pecten artery entering in front of the nerve, PY = artery to m. pyriformis, Q = artery to m. quadratus, RA, RI and RP = arteries to mm. recti (anterior, inferior and posterior, resp.), TMN = tendon of the membrana nictitans.

II = nervus opticus. The asterisks* mark the short posterior ciliary arteries.

27

The Venous System of the Orbit and Eye (Figs. 9–11)

Because of the extensive anastomoses in the venous system of the orbit of birds, complications in the drainage of the eye are not anticipated if the operation is performed carefully. The veins are therefore dealt with in a more cursory manner, and for more details the reader is referred to the diagrams (Figs. 9–11). However, the orbital veins of the pigeon differ so much from those of the sparrow (SLONAKER 1918), the turkey, and the duck (NEUGEBAUER 1845), that a few comments are necessary.

A. The inner parts of the orbit are drained by three main outlets: the v. ophthalmica, the rete mirabile temporale (ophthalmicum), and the sinus cavernosus.

1. The v. ophthalmica branches off from the v. facialis interna (NEUGEBAUER 1845) at a point where this vein runs above the pterygoid, behind the palatinum and lateral to the rostrum sphenoidale. The vena ophthalmica follows the medial wall of the orbit upwards, forms the anterior part of the venous ring around the optic nerve and continues upwards to the point where the anterior end of the hemisphere is in contact with the orbital wall (Figs. 9, 10). Here it pierces the bone and communicates with the annulus venosus cerebri antiquus (NEUGEBAUER 1845), which is a venous sinus around the olfactory lobes.

2. The rete mirabile venosum temporale (ophthalmicum) is interdigitated with the rete mirabile arteriosum temporale in the postero-ventral part of the orbit (Figs. 9–11). It is drained by two veins: a laterally situated one which follows the a. stapedia to the v. facialis externa, and a more medial one, which independently passes through the bone to the v. facialis interna (Fig. 9). The rete receives three veins, which follow the branches of the a. stapedia and are named like the arteries:

V. supraorbitalis (v. temporalis, NEUGEBAUER 1845) follows the a. supraorbitalis over the bulb and ends in an anastomosis with the v. ophthalmica at the point where this vein pierces the orbital wall (Figs. 10, 11, Pl. II).

V. infraorbitalis passes below the bulb along the a. infraorbitalis to the rostroventral margin of the orbit, where it communicates with the v. maxillaris (Figs. 10, 11, Pl. III).

V. ophthalmo-temporalis, which is a large vein, following the a. ophthalmo-temporalis from the rete to the optic nerve (Fig. 11, Pl. III). Here it turns dorsally and forms the dorsal part of the venous ring around the nerve before joining the v. ophthalmica. The ventral part of the ring around the optic nerve is formed by rather small vessels.

3. The sinus cavernosus around the pituitary in the sella turcica communicates with the venous ring around the optic nerve by several vessels, of which the "v. nervi III" (WINGSTRAND 1951) is particularly large in the pigeon. The sinus cavernosus is drained by the "v. carotis" which follows the carotis cerebralis through the bone to its junction with the v. facialis externa in the quadrate region.

B. The veins of the anterior eye segment and the eyelids (Fig. 10). The drainage of eyelids, anterior eye segment, and surrounding structures is effected by the v.



Fig. 9. Main veins of the head of a pigeon. Diagram combined from dissection of injected specimens, cleared specimens, and plastic casts. — AO = vena antorbitalis, AVC = annulus venosus cerebri antiquus (NEUGEBAUER), CD and CV = dorsal and ventral posterior ciliary vein, resp., <math>ET = v. ethmoidalis, FC = v. facialis cutanea, FI = v. facialis interna, IO = v. infraorbitalis, MD = v. mandibularis, MX = v. maxillaris, $MX_1 = vein$ along the a. maxillaris, OP = v. ophthalmica, OT = v. ophthalmo-temporalis, SC = sinus cavernosus, SO = v. supraorbitalis, ST = v. stapedia, VJ = v. jugularis, X = vein from the rete mirabile ophthalmicum to v. facialis interna, Y = transverse anastomosis of the jugular vein.





Fig. 10. Veins of anterior bulb segment and superficial parts of eye. Technique as fig. 9. — AO = v. antorbitalis, BA, BI and BP = veins from the anterior bulbar surface to antorbital, infraorbital and supraorbital veins, resp., CUT = veins from the skin behind the eye, F = veins from frontal skin, FC = v. facialis cutanea, I = iris, IO = v. infraorbitalis, MEA = meatus acusticus externus, MX = v. maxillaris, PS, PI, and PP = superior, inferior and posterior palpebral veins, PU = pupilla, RMO = rete mirabile ophthalmicum, RVE = external ring vein of limbus, SO = v. supraorbitalis, ST = v. stapedia, SR = ossicular ring with numerous small anterior ciliary veins passing around the inner margin, <math>X = vein from rete mirabile ophthalmicum to v. facialis interna.

infraorbitalis, the v. supraorbitalis, the v. maxillaris, and the v. facialis cutanea (NEUGEBAUER 1845). The two first-mentioned are described above and their branches follow closely those of the corresponding arteries. The v. maxillaris is the direct forward continuation of the v. facialis interna, from the point where the v. ophthalmica branches off (Fig. 9, P. III). When passing forwards under the orbit, this vein turns laterally, emits a small suprapalatine branch, passes under the rostral end of the jugal arch to a superficial position at the rostro-ventral corner of the orbit, and ends with several branches in the upper and lower beak. One of these branches runs in front of the orbit and supplies approximately the same parts as the antorbital artery (v. antorbitalis, Figs. 9–11). When the maxillary vein emerges under the jugal arch it communicates with three main veins: the v. infraorbitalis, the v. cutanea facialis, and a vein which follows along the a. maxillaris.

The *v. cutanea facialis* (NEUGEBAUER 1845) is a branch of the v. mandibularis. It passes upwards in front of the ear opening just under the skin, and turns rostrally under the orbit to fuse with the v. maxillaris (Fig. 9).

The anterior ciliary veins are branches of the antorbital, supraorbital, and infraorbital veins, which, like the arteries, also supply the eyelids, the conjunctiva, and the surrounding skin. The anterior ciliary veins are very numerous and pass round the inner margin of the ossicular ring (Fig. 10). They drain the ciliary muscle and the canal of Schlemm. The ciliary folds and the iris are probably drained into the large marginal veins of the ora serrata as connections between the iris veins and the anterior ciliary veins are very small and few.

C. Veins of importance for the operation. The drainage of the anterior eye segment cannot be seriously interfered with during the operation. Nor is it necessary to consider in detail the drainage of the eye muscles and glands, which is effected by the extensively anastomozing veins of the orbit (Fig. 11). However, the drainage of the posterior bulb segment with the choriocapillaris and the pecten appears to be more critical, and will therefore be considered separately.

The choriocapillaris is fed by the short posterior ciliary arteries which enter along the horizontal meridian. The drainage takes place through a dorsal and a ventral posterior ciliary vein. The dorsal vein is a branch of the upper part of the v. ophthalmica, whereas the ventral vein bifurcates after leaving the bulb and connects both with the v. ophthalmica and with the venous ring below the optic nerve in somewhat variable ways (Fig. 11). The dorsal vein enters the bulb through a foramen in the scleral cartilage, about half-way between the fundus and the dorsal equator. It passes through the choroid coat to the ora serrata, where it bifurcates into two arms which continue to each side in the large marginal ring sinus of the ora. The ventral vein enters the bulb at the level of the outer part of the pecten, bifurcates early, and the two rami pass out to the ora and continue as the marginal ring sinus (Seen in pl. III). At its entrance into the bulb it receives the veins from the pecten. On their way out to the ora, both the dorsal and the ventral ciliary veins receive numerous small vessels from the cho-



Fig. 11. Veins of the bottom of the orbit, seen from a lateral direction after the bulb had been removed. From plastic casts and dissections of injected specimens. — AO = v. antorbitalis, AVC = anastomosis to the annulus venosus cerebri antiquus (NEUGEBAUER), CD and CV = dorsal and ventral posterior ciliary veins, ET = v. ethmoidalis, FI = v. facialis interna, HA = vein from Harderian gland, IO = v. infraorbitalis, MEA = meatus acusticus externus, MX = v. maxillaris, OI = vein from m. obliquus inferior, OP = v. ophthalmica, OS = vein from m. obliquus superior, OT = v. ophthalmo-temporalis, Q = veins from m. quadratus, RA, RI, RP and RS = veins from mm. recti (anterior, inferior, posterior, and superior, resp.), RMO = rete mirabile ophthalmicum, SO = v. supraorbitalis, VS = v. stapedia, V III = v. nervi III from sinus cavernosus, X = vein from rete mirabile ophthalmicum to v. facialis interna.

II = entrance of n. opticus.

riocapillaris. Other veins from the choriocapillaris connect with the ring sinus along the ora, and are thus indirectly drained by the posterior ciliary veins. The ring sinus also receives radial veins from the ciliary folds and processes.

The operational procedure introduced in the present paper includes blocking of the ventral ciliary vein at the point where this emerges from the bulb at the level of the outer part of the pecten (Figs. 7, 8). This is necessary because its extra-bulbar parts cover the pecten arteries. At the same time, the veins of the pecten are blocked, as they connect with the ciliary vein at its emergence from the bulb. This blocking of the ventral ciliary vein does not appear to cause any severe disturbance of the choroidal circulation, probably because the extensive anastomoses via the ring sinus of the ora offer abundant possibilities for the block to escape. This is shown by the fact that the blocking of the vein alone, in numerous controls, had no significant effect on the retina, as long as one or more of the pecten arteries were left intact.



Fig. 12. Nerves of the left bulb in the pigeon, seen from the median plane. Anterior direction right. Compare fig. 7 and 8. Graphic reconstruction from celloidin sections. — FV = scleral foramen for ventral posterior ciliary vein and pecten vein, F II = foramen for the optic nerve, GC = ganglion ciliare, LC = n. ciliaris longus, RC = n. ciliaris longus, perhaps including radix longa, RS = ramus superior III, RP = nerves to the m. rectus posterior, RI = ramus inferior III, TMN = tendon of the membrana nictitans.
III = n. oculomotorius, V₁ = ramus profundus of n. trigeminus, The asterisks* mark the short ciliary nerves.

The Nerves of the Orbital Region

The nerves of the orbit of the pigeon do not differ very much from those of the sparrow, which were excellently described by SLONAKER (1918). As, moreover, only few nerves need to be safeguarded during surgery, this part of the anatomy is dealt with briefly.

As the branches of the n. trigeminus present in the orbit either pass further to the upper beak or are concerned with the sensorial innervation of eyelids and skin, they are of little interest in the present case. Of these nerves, the ramus infraorbitalis of the n. maxillaris may be damaged in some cases, as it passes across the field of operation together with the a. and v. infraorbitalis, but for the said reasons this cannot interfere with results obtained in the bulb.

Most nerves to eye muscles and glands are never approached. Only the oculomotorius branch to the m. rectus inferior, m. rectus anterior, m. obliquus inferior and the Harderian gland can be damaged in some cases, but this nerve has no connection with the bulb proper (Fig. 12). Nr. 3

The innervation of the bulb proper is effected by the long and short ciliary nerves (Fig. 12). The short ciliary nerves originate in the ciliary ganglion, which is attached to the posterior side of the optic nerve. The ganglion appears to receive a radix longa from the n. profundus V, but in microscopical sections the nerve fibres can be followed as a distinct bundle along the surface of the ganglion into the long ciliary nerve, as shown in fig. 12. The branch from the m. profundus is, therefore, a n. ciliaris longus, perhaps including a radix longa. The short ciliary nerves, about 8 in number, are emitted from the dorsal pole of the ciliary ganglion. They follow the sheaths of the optic nerve to the bulb, where they enter through separate foramina in the scleral cartilage in the region dorsal, or dorso-caudal to the opticus (Fig. 12). In the specimen, reconstructed in fig. 12, one of the short ciliary nerves appears to follow the long ciliary nerve before entering the bulb close to this nerve. The short ciliary nerve in question may be cut together with the long ciliary nerve in operations, but the other nerves and the ciliary ganglion are not in the zone of danger.

The long ciliary nerve follows the long ciliary artery into the bulb just behind the pecten arteries. Inside the choroid coat it divides into 4-6 separate branches, which pass straight out to the iris and ciliary body. Being situated near the pecten arteries, the long ciliary nerve can be damaged during the operation, when the pecten arteries are cautherized. Possible damage to this nerve cannot interfere with the experiments, however, for the cutting of this nerve in numerous control experiments did not cause any visible changes in the eye beyond immobilization of the iris.

Comparison between the Pecten and the Ciliary Body

Originally, the present work was intended to illuminate functional similarities between the pecten and the ciliary body and was inspired by the experiments of ABELSDORFF and WESSELY (1909). These authors showed that the ciliary body secretes intraocular fluid, and as the pecten was said to hypertrophy after extirpation of the ciliary body, there was some reason to believe that it has a similar function. It was hoped that the histological and histochemical properties of the two organs would indicate whether they could have the same function or not.

In some preliminary histological and histochemical studies, the pecten was compared with the ciliary body and with the anterior, vascular surface of the iris. Certain features were common to all three organs: a rich vascularization, strongly PAS-positive perivascular membranes, presence of alcaline phosphatase. Alcaline phosphatase was shown to be abundant in the pecten and the iris, whereas the large amount of pigment made quantitative estimates difficult in the ciliary body.

TANAKA (1960), and SEAMAN and STORM (1963), simultaneously studied the organs in electron microscope and found the remarkable, brush-border-like cellular membranes of the endothelial cells in the pecten. This was compared with the folded cell membranes found in the epithelium of the ciliary folds. Moreover, SEAMAN and STORM 3

Biol. Skr. Dan. Vid. Selsk. 14, no. 3.

(1963) and SEAMAN and HIMELFARB (1963) showed that the drug Diamox caused similar changes in the cell membranes in both organs, and that these changes in structure were simultaneous with a fall of intra-ocular pressure. The pressure change could, of course, depend on interference with one or both of these organs.

It soon became evident, however, that simple comparison of the two organs was not a promising way of approaching the functional problem, as the structural similarities were found to be too little specific (cf. pp. 12–13), and a primitive experiment revealed a distinct functional difference.

This experiment was arranged to check whether the pecten becomes permeable to large molecules when the pressure in the bulb is decreased by corneal puncture. ABELSDORFF and WESSELY (1909) had shown that this is a typical feature of the ciliary body. Four pigeons received 4 subcutaneous injections of 3 ml $0.5 \, {}^{0}/_{0}$ trypan blue with 48 hour intervals. After this treatment, the blood and the urine were distinctly blue-stained, but no trypan blue could be seen ophthalmoscopically in the vitreous body or the camera anterior. This is in accordance with experience in the case of mammals, in which the ciliary body of the normal eye is impermeable to trypan blue. Repeated puncture of the cornea some hours after the last injection resulted in strong blue-staining in the camera anterior and posterior. This was evidently due to leakage through the ciliary body and, perhaps, through the capillary tufts of the iris surface. No staining was seen in the vitreous body or around the pecten, a result confirmed by subsequent fixation and sectioning of the specimens. The pecten thus remains impermeable to the dye, whereas the ciliary body becomes permeable when the pressure is decreased in the bulb.

As the functional properties of the pecten and the ciliary body could be shown to be different, it appeared futile to argue in favour of identity by means of structural comparison.

Operative Elimination of the Pecten by Coagulation of Its Vessels

As the function of the pecten could not be revealed with certainty by histochemical and histological investigations, a more direct experimental approach to the problem had to be found. In many analogous cases, operative elimination of the organ provided valuable information. If such an operation could be performed in the case of the pecten without damage to other relevant structures, the function would, probably, be revealed by the post-operative symptoms.

ABELSDORFF and WESSELY (1909) tried surgical extirpation of the pecten, but since the optic nerve and, probably, the vascular supply of the choroid had been destroyed, the experiments were not very informative. KAUTH and SOMMER (1953) cautherized the pecten, but do not describe the method or the results in detail. The present authors attempted a similar method in collaboration with Dr. E. GREGERSEN, Rigshospitalet, Copenhagen. The light beam from a photo-coagulator, used for coagulation in the human eye, was concentrated on the pecten of an anaesthetized pigeon. Although maximal effect was used, no damage was inflicted on the pecten, probably because the heat of the beam was transported away by the blood of this extraordinarily vascular organ. In contrast, the retina was easily damaged by the light beam. It was realized that coagulation of the pecten would require so much heat that damage to surrounding parts by heat-spreading would be unavoidable. This would ruin the experiments, particularly as heat coagulation by any method would damage the optic nerve head, to which the pecten is attached.

The anatomical analysis of the vessels, briefly summarized in the preceding chapters, gave some hope that coagulation of the pecten vessels at their entrance into the bulb would lead to degeneration of the organ. This finally led to the method employed.

Methods

Operations on domestic pigeons were undertaken on a table covered with plastic which allowed for easy cleaning and firm adherence of plaster tape. Holes were bored for the strings which were to fix wings and legs.

The pigeons (common domestic breed) were placed on the back with wings spread, and fixed by a string between the primaries and secondaries. The wing tips were fixed onto the table by plaster tape, and the legs were held in position by strings. During the whole operation the body of the pigeon was covered with cotton wool to avoid heat loss.

The pigeons were anaesthetized with 6 $^{0}/_{0}$ nembutal in 0.7 $^{0}/_{0}$ NaCl, injected into the vena basilica (NEUGEBAUER 1845) at the point where this runs over the volar side of the elbow joint. The vein is particularly distinct after the skin has been washed with ether. 0.15 ml was given as an introductory dose, and this was slowly increased by 0.02 ml at a time until the animal was completely relaxed. The syringe was fixed with plaster tape to the table with the needle in situ, so that additional injections could be performed without delay. The final dose, necessary for preventing twitches in the neck musculature during operations in the eye region, was between 0.18 and 0.25 ml for normal-sized pigeons.

A glass tube was introduced into the mouth and fixed by plaster tape around the beak. This secured free respiration and facilitated the fixing of the head to the table. The head was turned with the left side up, and attached to the table by plaster tape over the occipital region and the tube (Pl. IX:1).

The area around the eye was washed with 70 $^{0}/_{0}$ alcohol, and the feathers above and below the eye were carefully cut to avoid contamination. It was not possible to perform an aseptic operation, but the wound was rarely infected, probably because the pigeons were treated prophylactically with penicillin.

The operation was performed under a Zeiss binocular operation microscope with illumination through the objective lens. The magnification was varied between 15 and 50 times. An ordinary dissection microscope and a separate spot-light were used in the first experiments but did not operate well, as the incision is deep and narrow.

In the operation proper, the wound was held open with small metal hooks made of fairly large insect needles with a bent tip (Pl. IX:2–3). The needles were connected by a string to a lead load (10–50 g), which was left hanging over the margin of the table and secured a constant pull in the hook. After the first incision had been made, the bulb was pulled dorsally by a broad hook, made by bending a 8 mm metal strip, and connected with a 45 g lead load (Pl. IX:5). During the operation, bleeding must be avoided as much as possible, as even small vessels can fill the narrow wound with blood in a short time. When this occurs, it is very difficult to drain the wound and stop the vessel under the particular conditions of control required by a critical experiment. Therefore, all visible vessels which had to be cut, were first coagulated with a small platinum loop. This was made of 0.15 mm platinum wire, bent to a sharp point, which could be introduced into the narrow wound without touching the walls. The loop was heated to dark red by a controllable current and was applied slowly, so that the vessels were coagulated and not opened.

The operation was performed by the following steps and took about 1.5 to 2 hours. In some cases individual variation made it impossible to block the pecten vessels without extensive bleeding or damage to larger vessels. Such specimens had to be discarded.

1. As the eye fits firmly into the orbit, a piece of the supraorbital crest of the frontal bone must be cut loose to allow the slight upward dislocation of the bulb which is necessary for operations taking place along the bottom of the orbit. The skin incision is made along the edge of the supraorbital crest between the two parallel skin arteries over the eye (Fig. 3). After exposure of the frontal, the supraorbital crest is cut free with iris scissors from a transverse cut behind the lacrymal to another transverse cut in front of the level where the brain cavity begins (Pl. IX:2). No important vessels or nerves are damaged by this operation, but some caution is necessary when cutting longitudinally through the bone to ensure that the a. ethmoidalis in the medial wall of the orbit is not damaged (Fig. 4). The wound is kept moist with saline, and the skin is provisionally closed over it.

2. A skin incision is cut with small scissors along the lower margin of the featherless lower eye-lid as shown in Pl. IX:2–3. The skin flaps are drawn to the side with hooks, whereby the whitish ligamentum orbitale inferius can be seen to extend from the lower margin of the orbit in front of the bulb. If the incision is performed as described, no larger vessels or nerves are cut.

3. The ligamentum orbitale inferius is cut through along the lower margin of the orbit (Pl. IX:3-4). The incision is made cautiously, under careful microscopic control, with small scissors, in order that the branches of the infra-orbital vessels and nerves, some lying directly under the ligament, are not damaged. A hook is attached to the bulbar flap of the ligament and is connected with a 50 g load which pulls the bulb dorsally. A cleft then appears between the bulb and the bottom of the orbit (Pl. IX:4).

4. The musculus depressor palpebrae inferioris, which forms a thin membrane on the ventral surface of the bulb behind the bulbar branches of the infra-orbital vessels, is split (Pl. IX:4–5). The broad metal hook is inserted through the incision to press directly on the bulb and pull it dorsally. The membraneous muscle is freed from the bulb, so that access is obtained to the angle between the inferior and posterior rectus muscles (Pl. IX:5). If necessary, small cotton pellets can be inserted on each side to lift the membrane from the surface of the bulb.

5. Small cotton pellets are carefully inserted under the posterior and inferior rectus muscles in order to elevate the muscles from the bulb. The fat obscuring the vessels under the optic nerve is removed in small pieces with watchmaker's forceps. It often contains small veins, and some caution is necessary to avoid bleeding. The larger vessels first exposed are the ventral ciliary vein and the veins below the optic nerve (Fig. 11). These veins usually cover the pecten arteries and the a. ciliaris longa and n. ciliaris longus, which become visible after the ventral ciliary vein has been blocked. The long ciliary artery and nerve are situated posteriorly, where the tendon of the membrana nictitans disappears between the posterior rectus and the optic nerve.

6. The ventral ciliary vein is coagulated at the point where it emerges from the bulb, and coagulation is continued along the vein, shrinking it up to the neighbourhood of the optic nerve proper. Together with the other sub-optic veins, it is then elevated from the bulb with a needle, thus revealing the underlying arteries and the long ciliary nerve (Pl. IX:6). The two or three pecten arteries are then coagulated and the a. ophthalmo-temporalis is raised from the bulb with a needle, so that the entire ventral and ventro-caudal margin of the optic nerve is exposed, and all vessels passing down here are blocked. As the innermost, often minute, pecten artery may run close to the long ciliary artery and nerve, it is often difficult to save these structures without running the risk that the operation will be incomplete. When the ventral and ventro-caudal border between the whitish optic nerve and the dark bulb is clear of vessels entering the bulb, attention is turned to the anterior side of the optic nerve above the rectus inferior. The a ophthalmo-temporalis is carefully lifted from the bulb and any vessels entering the bulb here are coagulated. Coagulation in front of the nerve must always take place under optic control. If not, the v. ophthalmica will most probably be damaged, and the space filled with blood.

7. The pellets of cotton wool are removed, the wound is filled with 6 $^{0}/_{0}$ penicillin in 0.7 $^{0}/_{0}$ NaCl, the hooks are removed, and the skin incisions are sutured with silk. A compress is fixed over the eye with adhesive plaster.

8. The pigeon is given a prophylactic injection of 1 ml of 6 $^{0}/_{0}$ penicillin in one pectoral muscle and 0.2 ml of 0.2 $^{0}/_{0}$ picrotoxin solution in the other pectoral muscle to counteract the nembutal anaesthetic. The animal is left under a layer of cotton wool until it wakes up.

The pigeons are usually active and have a good appetite 6–12 hours after the operation. They were carefully watched in the following days and conjunctivitis, which was seen in some cases, was treated with penicillin.

Control operations were performed in the same way, but one or two pecten arteries were left intact, whereas the other vessels were blocked.

The right, unoperated eye was always used as a normal reference when the left, operated eye was examined ophthalmoscopically or histologically.

Ophthalmoscopy was performed after mydriasis had been produced with 0.225 $^{0}/_{0}$ tubocurarine chloride in 0.025 $^{0}/_{0}$ benzalkonium chloride, applied directly on the cornea (CAMPELL et al. 1962 a, b). The pupilla of the operated side was often large enough for ophthalmoscopy without treatment because of damage to the long ciliary nerve.

Results

With two exceptions, the first 27 attempts to block the pecten arteries failed. The pecten remained normal ophthalmoscopically as well as histologically, and dissection of some specimens, injected with vermilion-starch from the carotis (p. 20) revealed a fairly large pecten artery. This had probably regenerated from the small and variable vessel to the pecten, which enters in front of the optic nerve (p. 25). As these birds had been operated upon with the same aim in view as the birds with a degenerate pecten, they must be regarded as particularly valuable controls. These 25 birds were grouped with the 4 animals in which one or two pecten arteries had been left intentionally, and the group was later increased by 2 additional, unintentional controls.

After the importance of the small anterior pecten artery had been realized, 11 out of 16 operations were successful. Two of these animals were used for oxygen measurements within the bulb before degenerative symptoms had developed in the pecten, and were then killed. In these cases the oxygen values near the pecten showed that the operation had been successful. The remaining 9 birds, like the first two successful specimens, were allowed to survive for periods varying from 7 to 317 days, and the changes in the bulb were observed ophthalmoscopically until the birds were killed and examined histologically (for technique, see p. 13).

Controls. The intended controls, in which pecten arteries had been purposely left during the operation, did not show any ophthalmoscopic or histological changes in the pecten. The unintentional controls had, by definition, a normal pecten after the operation. In all these controls, a degenerated patch of retina developed just temporal to the base of the pecten. Within a strictly delimited area with a diameter of 2–3 mm, total destruction of the retina followed within a few days of the operation. The fundus, like all other parts of the retina in these controls, remained normal, both as regards the ophthalmoscopical picture and the histological appearance. The patch behind the pecten is, therefore, an effect of the operational technique, and is probably due to prolonged pressure of the broad hook on the bulb during the operation. As the patch is present in all the eyes operated upon, it will not receive special attention in the following.

The degeneration of the pecten could be seen ophthalmoscopically as a slight shrinkage of the folds 2–7 days after a successful operation. The change was often inconspicuous during the first week and could be recognized only after comparison with the normal, right eye. A week or more after the operation, the change could always be distinctly observed in the ophthalmoscope. During the second week, white patches developed and tended to spread over most of the folds, but the bridge remained normal.

When examined *histologically*, the pecten did not show any striking symptoms in animals killed on the 1st and 4th day after the operation, although oxygen records showed that the operation had been successful. The vessels were distended with blood which had been trapped there because the pecten vein was blocked earlier than the pecten arteries.

In 8 animals killed 7–38 days after the operation, different stages of progressive degeneration could be seen. After 7 and 10 days some of the vessels contained many macrophages and small necrotic loci. Macrophages were also seen between the vessels among the stroma cells. Lysis of the endothelial cells was already seen in some speccimens on the 7th day. In specimens killed 15 days or more after the operation, large areas of the folds were reduced to the PAS-positive, perivascular membranes, whereas endothelium cells, intramural cells and stroma cells had disappeared (Pl. X:1–4). These heavily degenerated parts of the folds are probably identical with the white patches seen in the ophthalmoscope. In one specimen, the spaces between the folds were filled with pigmented cells of the retinal type. This tissue had probably invaded the pecten from the retinal pigment layer, which, in this specimen, showed heavy pathological proliferation (Pl. X:6). The bridge did not show any striking changes in any of the pigeons operated upon.

Degeneration of the pecten never led to complete elimination of the organ. It was progressive during the first two or three weeks after the operation, but then came to a stop. Animals fixed 165, 300 and 317 days after the operation, still had a pecten, but this was shrunken and distorted, with large patches consisting of perivascular membranes only. Other parts of these pectens contained scattered vessels with normal blood corpuscles, indicating that some regeneration had taken place (Pl. X:5). The slow degeneration of the devascularized pecten probably depends on its isolated situation in the non-vascular vitreous body. White blood cells can, therefore, only reach the pecten by active migration over large distances. Necrosis develops slowly and is restricted to a few small loci in the larger blood clots. Most parts of the folds break down slowly without formation of necrotic masses.

The revascularization of the pecten probably starts during the second week in most of the pigeons, for some vessels with normal, non-necrotic blood are always found in the pecten, even in birds fixed two weeks or more after the operation. This is borne out also by the oxygen recordings in the bulb (p. 53), which revealed low oxygen values in the neighbourhood of the pecten during a week or more after the operation but indicated some oxygen supply to the organ later. This revascularization will, of course, prevent further degeneration.

The retina of the successfully operated pigeons. Striking symptoms developed in

the retina of all eyes with an atrophic pecten when the animals were kept alive for more than 4 days.

Ophthalmoscopically, the first changes were seen on the 3rd or 4th day as a distinct whitish or yellowish reflex from the entire retina. The choroidal vessels, which can be seen through the retina in the normal eye, were completely hidden. In this respect, the present observations agree with those of KAUTH and SOMMER (1953), who saw a whitish reflex from the retina after they had destroyed the pecten by cautherization.

In three pigeons which were kept alive for 165, 300, and 317 days, this change was found to be transitory. After some months the retina again looked practically normal, the only recognizable difference between the operated and the non-operated eye being the absence of the fine radial striation in the former. Histological examination of these specimens showed strong or almost total reduction of the optic nerve fibre layer and reduction of ganglion cells on the operated side.

The earliest *histological* changes in the retina were noted 7 *days* after the operation, whereas the retina of pigeons killed on the 1st and 4th days appeared to be normal. In the 4 pigeons killed on the 7*th and 10th days*, the retina, particularly the nerve fibre layer along the inner surface, had been invaded by numerous macrophages (Pl. XII:1, 3). A narrow zone along the membrana limitans interna lacked nerve fibres in many places, indicating shrinkage of the nerve fibre layer. No conclusive evidence of oedema was recognized, although the whitish reflex seen in the ophthalmoscope indicated that an oedema had developed.

In the 4 pigeons killed after 15 to 38 days the thickness of the retina was strikingly reduced in comparison with the control eye (Pl. XI and XII). The number of macrophages in the retina was considerable, particularly in the nerve fibre layer. The number of cells in the ganglionic layer was distinctly reduced. Two of the pigeons, killed 2 and 3 weeks after the operation, showed particularly heavy degeneration. The outer and inner segments of the visual cells were atrophic or completely absent, so that the outer surface of the retina resembled that of an ordinary epithelium (Pl. XII:4). The two nuclear layers and the ganglionic layer were strikingly reduced. Local cystoid degeneration and proliferation of the cells of Müller were noted. Needle-shaped pigment granules of the retinal type were found in the retina proper; these were partly free, partly within macrophages. The latter were common also in the layer of rods and cones. The retinal pigment layer was pathologically proliferated locally.

The pigeons killed after 165, 300, and 317 days had obviously recovered from the acute effects of the operation, and the ophthalmoscopic picture of the retina was nearly normal. Histologically, the outer layers including rods and cones, nuclear layers and plexiform layers appeared normal. In one pigeon (165 days), the inner nuclear layer was even thicker than normal in some places. However, in all three specimens, the nerve fibre layer was strongly reduced and was completely absent over large areas of retina (Pl. XII:2). In two of these specimens, the number of cells in the ganglionic layer was strikingly reduced, but changes in this layer were less distinct in the third specimen.

Nr. 3

Conclusion. Complete blocking of the pecten vessels caused progressive degeneration of the organ during the first weeks after the operation, followed by slow and incomplete revascularization. In all eyes with a degenerate pecten the retina developed degenerative symptoms, sometimes restricted to the nerve fibre layer and the ganglionic layer, sometimes including the entire retina. The innermost layers of the retina were the first to show symptoms after the operations. The effect on the retina in 11 experimental animals was not caused by irrelevant factors inherent in the operative technique, as shown by the normal retina in the 31 control eyes. These eyes had a normal pecten and one or two pecten arteries preserved, but had been treated in the same way as those of the experimental animals in all other respects.

It may therefore be concluded that an intact pecten is necessary for the maintainance of a normal retina.

The most simple explanation of this result is that the internal retinal layers are dependent on the pecten for their supply of substances which diffuse through the vitreous body. This is supported by the fact that the innermost layers of the retina, which face the pecten, are the first to degenerate after operations, and may be the only layers which show changes. The old idea that the pecten serves as a nutritive organ for the inner retinal layers and is a substitute for internal retinal vessels is, thus, supported to a point little short of definite proof.

As the distance from the pecten to the retina is considerable, it is plausible that the supply primarily includes easily diffusible substances with small molecules such as oxygen. Removal of carbon dioxyde from the inner parts of the eye may also be an important function of the pecten and is, of course, usually coupled with the oxygen supply. The authors' attention was directed to oxygen supply by the whitish or yellowish colour of the retina in pigeons with degenerate pectens. This could indicate anoxia; it looks very much like the cotton-wool exudate seen in the human retina after occlusion of the arteria centralis (see HOGAN and ZIMMERMANN 1962, p. 495).

The Intra-Ocular Oxygen Pressure of Normal Pigeons

The operations described in the preceding chapter show that the presence of a normal pecten is necessary for the maintainance of the inner layers of the retina. This dependence as such is well established, but the physiological mechanisms responsible for it are not definitely revealed by the post-operative symptoms. For reasons given above, the supply of oxygen from the pecten to the retina may be one of the decisive factors. If this is true, oxygen must diffuse through the vitreous body of normal pigeons, and a gradient in oxygen pressure must be expected from the surface of the pecten to the surface of the retina. A possibility of checking the theory was thus presented, as the oxygen pressure can be measured in different parts of the vitreous body by means of oxygen cathodes.

Methods

The pigeons were fixed to the operating table and anaesthetized as for operations (see p. 35). For recording in one eye only, the head was fixed with one eye facing upwards, but for simultaneous recordings in both eyes it was placed in a holder in a vertical position so that both eyes were accessible. Mydriasis was produced by corneal application of a few drops of $0.225 \, {}^{0}/_{0}$ tubocurarin in $0.025 \, {}^{0}/_{0}$ benzalkonium chloride solution (CAMPELL et al. 1962). The disposition of holders and electrodes must be such as to allow good ophthalmoscopic control of the electrode tip when inserted into the bulb.

Recording of oxygen pressure was made with the oxygen cathodes devised by DAVIES and BRINK (1942, 1957), CONELLY (1957), CATER et al. (1957) and DAVIES (1962). The electrodes were made of 0.1 mm glass-isolated platinum wire and were ground obliquely at the tip like hypodermic needles (Fig. 13). The exposed platinum surface was coated with collodium ad modum CONELLY (1957). The cathode was connected to an amplifier like the one described by CATER et al. (1957) and was given a charge of -0.6 V, as measured against a calomel electrode which was placed in contact with a saline-soaked piece of cotton wool on the head of the pigeon. Under these conditions, the current is roughly proportional to the oxygen pressure around the tip of the electrode (see CONELLY 1957).

The authors made a series of experiments with different types of coated electrodes, but found the syringe-like ones to be most suitable for the purpose; they slide in easily through the wall of the eyeball and the vitreous body and are automatically cleaned of fibres and debris. Conical electrodes with the point formed by platinum are easily inserted, but the coating of the exposed platinum point is easily damaged. Blunt electrodes are difficult to push through the wall of the bulb and tend to collect fibres and membranes on the free platinum surface.

The capillaries for glass isolation were drawn from 5 mm glass tubing; 100 mm of this tubing formed a handle for the electrode, while the platinum wire was melted into the capillary. The handle was mounted in a somewhat shorter piece of thicker tubing, in which the electrode could slide without rocking. This made the forward movement of the electrode precise and stable when inserted.

Before insertion of the electrode, the supraorbital crest of the anaesthetized pigeon was exposed as for operations (p. 36), and the crest was removed. The point of insertion was chosen at the exposed dorsal pole of the bulb, behind the ring of scleral ossicles and approximately in the equator. The main branches of the posterior dorsal ciliary vein, seen with a dissection microscope, were avoided. Under microscopic control a small hole was made with the heated platinum loop described on p. 36. The scleral cartilage and the choroid were perforated and coagulated to avoid bleeding and damage to the coating when the electrode was inserted. The electrode was usually aimed at the pecten, and recordings were made at five different levels on the way down (Figs. 14 and 15), viz.: 1) near the insertion in the dorsal part



Fig. 13. Apparatus for calibration of electrodes. — 1 = shielded wire, 2 = isolation tape, 3 = glass tubing acting as shaft of electrode, 4 = glass tubing acting as holder for electrode, 5 = platinum wire, 0.1 mm, 6 = glass capillary for introduction of air or N₂, 7 = bag of dialysis tubing containing vitreous body, 8 = cotton wool, 9 = calomel electrode.

of the vitreus, 2) behind the upper part of the iris, 3) centrally, 4) behind the lower part of the iris, and 5) close to the pecten. The position of the electrode tip was checked with the ophthalmoscope. In some cases the electrode was re-aimed in order that recordings could be made near the fundus retina or in other parts of the vitreus.

Readings of the current were made 30 and 60 secs after the voltage had been switched on, and the current was interrupted after the second reading to avoid unnecessary polarization of the electrode. After 30 secs the current is approximately stable, and this value was used for calculations. The somewhat lower value at 60 secs was used as a check only.

Calibration of the electrodes was made immediately before and after each series of readings. If the calibration had changed more than $10 \ 0/0$ during the experiments, indicating damage to the coating, only the relative values were of any use, and absolute values were not calculated. Calibration was made in the apparatus shown in

Fig. 13, with the electrode tip in the fresh vitreous body of the pigeon. The vitreous body was saturated first with nitrogen, then with air, and kept at 37°C, the same temperature as that recorded with thermocouples in the vitreous body of ananaesthetized, normal pigeons. The current recorded in nitrogen and air gave the two points on the graph $\mu A/mm O_2$, necessary for calculation of the oxygen pressure.

Whereas the double calibration shows whether the electrodes have operated safely or not, there are a few other sources of error which must be considered and, if possible, avoided, in experiments of this kind. Small air bubbles may be introduced together with the electrode and may spoil the results completely, and a similar effect is produced by bleeding from the point where the electrode penetrates the wall. These complications are avoided by careful coagulation before insertion and by the use of the sharp, syringe-like electrodes, which slide in easily. In spite of all precautions the oxygen pressure is sometimes high near the point of insertion, probably because of diffusion through the opening, but it usually sinks to normal values after some time. The freshly inserted electrodes show too high values during the first few minutes, probably because an amount of atmospheric oxygen is introduced with the coating. Values near the pecten or the retina are dependent on the orientation of the electrode : whether the platinum surface faces the wall or not.

Results

Good *relative values* of oxygen concentration in different parts of the vitreous body were obtained from 15 normal pigeons. In all cases the values from the neighbourhood of the pecten were the highest, and a fall in oxygen pressure was registered when the electrode tip was moved to the dorsal parts of the eye or to the fundus region. The values at the pecten were usually 10–15 times as large as those obtained near the retina of the fundus, and 6–10 times as large as those obtained in the dorsal part of the vitreous body.

An electrode in contact with the pecten always showed regular pulsations of the oxygen pressure, following the rhythm of the respiratory movements. This obviously depends on variations in the oxygen saturation of the arterial blood, caused by the intermittent renewal of air in the air capillaries of the lung.

The *absolute values* of oxygen pressure, obtained from 6 normal pigeon eyes, are given in Table 1. In spite of good calibration there is a good deal of variation from one animal to another, and repeated recordings in the same site during the experiment also gave some rather considerable variations, especially in the neighbourhood of the pecten and the retina. Part of this variation certainly depends on differences in the location of the electrode, as the technique used does not give greater accuracy than 0.5 to 1 mm. However, the main cause of the variation of values, recorded in the same site, is the varying depth of the anaesthesia. This was demonstrated in control experiments, in which the electrode was left with the tip fixed near the pecten of the anaesthetized pigeon, which received an injection of 0.2 ml of $0.2 \ 0/0$ picrotoxin

TABLE 1.

Oxygen pressure in mm Hg, recorded in different parts of the vitreous body of normal pigeons. A-E shows recordings at different levels along a straight line from the pecten to the insertion of the electrode near the dorsal equator. F and G are values in the neighbourhood of or in contact with the retina of the fundus. The asterisk * denotes that the higher values were obtained after picrotoxin injection.

Pigeon nr.	Vitreous body, level of					Fundus retina	
	A Pecten	B Lower iris	C Centre	D Upper iris	E Dorsal bulb	F Ca. 1 mm from	G Contact with
1.	44-94	22-25	14-23	9–18	4-11	6-7	3-7
2.	26-58*	15 - 24	14-17	10	7	4-7	4-7
3.	31-86*	30 - 38	17-30	8	7 - 9	13	-1
4.	49-77	32	16 - 24	12-16	8-14	-	3-12
5.	52 - 70	36-41	14-25	10-13	6-13	-	1-7
6.	70-76	42-51	19-33	14-19	8-13	-	_

in the pectoral muscle. The drug counteracts the nembutal anasthesia and stimulates the pigeon, which has to be killed when it begins to move. In one such experiment the recordings of the fixed electrode rose from 39 to 86 mm Hg in 14 minutes after the injection, in another from 26 to 58 mm Hg in 19 minutes. Thus, the anaesthesia can lower the values to about 50 $^{0}/_{0}$ of the normal ones in the neighbourhood of the pecten, and the higher values recorded here are, therefore, likely to be most reliable.



Figs. 14 and 15. Oxygen pressure in mm O_2 , recorded in different parts of the bulb of two normal pigeons, anaesthetized with nembutal.

The oxygen pressure recorded in the neighbourhood of the pecten varies between 70 and 94 mm Hg, if the lowest values are excluded for reasons given above (see Table 1, Figs. 14, 15). Somewhat lower values were regularly recorded when the electrode surface was facing the bridge, and the highest values were obtained near the folds. In the latter case, the pulsations of the oxygen pressure were most pronounced. This strongly indicates that the oxygen pressure around the pecten of normal, non-anaesthetized pigeons is very close to the arterial oxygen tension, which appears to be about 100 mm Hg in the pigeon (WASTL and LEINER 1931), and in other birds (Duck, WASTL and LEINER 1931, Fowl, MORGAN and CHICHESTER 1935).

As shown in the Table 1 and in the diagrams (Figs. 14–15) the oxygen pressure in the vitreous body of normal pigeons with moderate anaesthesia is 22–51 mm behind the lower iris margin, 14–33 mm in the centre, 9–19 mm behind the upper iris margin, and 4–14 mm in the dorsal part of the bulb near the point of insertion. The variations seen in these figures undoubtedly depend both on the varying position of the electrode and on differences in the anaesthesia. Nevertheless, the fall of oxygen pressure from the pecten up to the dorsal part of the bulb is distinctly shown.

The values at the retinal surface are of particular importance for calculations of diffusion rates. They could not be recorded with the necessary accuracy near the insertion, where contamination with atmospheric oxygen from the wound could be expected. Therefore, in some experiments, the electrode was re-aimed, the tip approaching the wall of the fundus with the platinum surface facing the retina. In all cases values as low as 3 or 4 mm Hg were obtained when the electrode was close enough to the retina (Table 1). Higher values up to 12–13 mm were recorded before it had come close enough. In such cases, the electrode tip could well be 1 mm from the surface as the ophthalmoscopic control did not allow greater accuracy. Thus, the peripheral parts of the vitreous body in contact with the retina have a very low oxygen concentration, about 3–5 mm only. In the authors' calculation of diffusion rates, 5 mm was chosen as a basis to compensate for the effect of the anaesthesia. These values, which must hold good also for the inner layers of the retina, are in good agreement with DAVIES' and BRINK'S (1957) recordings from the cerebral cortex of the cat, where values between 2 and 10 mm Hg were obtained.

A distinct rise up to 25 mm Hg or more was always recorded when the electrode tip was pushed into the retina. In such cases the recording space around the electrode tip obviously included deeper retinal layers, where oxygen diffusion from the choriocapillaris comes into play. The minimum oxygen concentration in the bulb is thus found in the inner layers of the retina. This means that the oxygen coming from the choriocapillaris is consumed in the outer layers and does not reach the inner layers in any significant amounts. The method used is not accurate enough to determine exactly how far into the retina the gradient from the choriocapillaris extends.

A few recordings indicate a slight increase of the oxygen values when the electrode tip is placed close behind the ciliary body (Fig. 15). This probably means that some oxygen is given off from the ciliary folds, but as the gradient system dominated by the pecten is not significantly disturbed, the amounts must be fairly small.

The measurements of oxygen pressure in the vitreous body of normal pigeons thus show that there is a fall of oxygen pressure from about 100 mm around the pecten to about 5 mm along the inner surface of the retina. Such a gradient cannot exist in a homogeneous, non-consuming medium like the vitreous body without diffusion taking place. It is thus shown that oxygen does diffuse from the pecten to the retina. This result satisfies the basic requirement of the theory, according to which the pecten is a substitute for intraretinal vessels and supplies the inner layers of the retina with oxygen.

Quantitative Considerations on the Basis of the Recorded Oxygen Pressure

The oxygen gradient found by recording with oxygen cathodes shows definitely that oxygen diffuses from the pecten out to the retina. However, it still has to be discussed whether the oxygen supply from the pecten is large enough to have a functional significance in the retina, i. e., whether interruption of this supply could have been the reason for degeneration of the retina after the pecten vessels had been blocked. This is not immediately shown by the recorded values, for oxygen gradients will probably be found around many well-vascularized organs and need not necessarily have a specific functional significance. In the present case it is only shown that the pecten is over-supplied with blood with regard to its own oxygen consumption.

The Amounts of Oxygen Supplied to the Retina by the Pecten

In calculating the rate of diffusion of oxygen the folds of the pecten are not taken into consideration, but the organ is regarded as a compact plate with plane, parallel side walls tangential to the folds on each side. The total surface of this organ is around 42 mm², and the oxygen pressure on its surface is about 100 mm Hg. The retina is considered to be a half-sphere with 7 mm radius and an oxygen pressure of 5 mm along the inner surface. The complicated geometrical configuration of the pigeon's eye does not allow simple, exact calculations. Therefore, a few models were introduced which give an idea of the amount of oxygen transferred to unit area of retina per time unit.

1. In the first model, the surface of the pecten (42 mm²) is spread on the surface of a half-sphere (radius 2.58 mm), concentric with another half-sphere with 7 mm radius, representing the retina. The former surface is given the oxygen pressure 100, the latter 5. The amount of oxygen passing half-spherical surfaces concentric with and lying between the two, must obviously always be the same and independent of the radius r. It is proportional to $\frac{dp}{dr} \cdot 2\pi r^2$, where dp is the fall of pressure over

Nr. 3

the thickness dr of the half-sphere. This gives $\frac{dp}{dr} = \frac{k}{r^2}$, and $p = -\frac{k}{r} + a$, where k and a are constants. If the values for the "pecten" (p = 100, r = 0.258 cm) and the "retina" (p = 5, r = 0.70 cm) are inserted, it is found that k = -38.82. The pressure fall/cm at the surface of the retina is then easily found: $\frac{dp}{dr} = -79.22 \text{ mm}$ Hg/cm. This model is presumed to give values which represent conditions in the dorsal parts of the bulb, far from the pecten.

2. The pressure fall at the dorsal retinal surface can be calculated in a second way. If it is assumed that the ventral parts of the vitreous body around the pecten are saturated with oxygen, they may be considered as a "lake" of oxygen with a 70 mm pressure, and with the surface at the level of the bridge of the pecten. The diffusion from this surface along the posterior surface of the lens to the dorsal retina may be considered as diffusion between two parallel surfaces, 9 mm apart (See Fig. 14–15). The fall of pressure will then be linear and its numerical value: $\frac{70-5}{0.0} = 72 \text{ mm Hg/cm}$, which is in reasonable agreement with the above value.

3. Using method 1 for a model, in which the radius of the retina is reduced to 4.5 mm, the value for $\frac{dp}{dr}$ along the retinal surface increases to 283.7 mm Hg/cm. This model will probably fit conditions in the central parts of the fundus, which are less than 4.5 mm from the pecten.

4. The fovea is situated about 1.8 mm from the side of the pecten. A retinal surface here, parallel to the side of the pecten, would receive oxygen corresponding to a fall in pressure at the retinal surface of $\frac{100-5}{0.18} = 530 \text{ mm Hg/cm}$.

A fall of oxygen pressure of 75 mm Hg/cm at the most distant retinal surface in the dorsal part of the bulb, and 300 mm Hg/cm in the central fundus appear, therefore, to be realistic estimates.

The supply of oxygen per unit time to each cm² of retina under these conditions can be calculated approximately by using KROGH'S (1918) "diffusion constant" for oxygen in water: 0.34 ml O₂ passes 1 cm² of surface per minute, if the fall in pressure is 1 athm. per μ and the temperature is 20° C. If it is supposed that the constant increases 1.4 $^{0}/_{0}$ for 1° C increase of temperature, the constant at 37° C, expressed in ml/cm² surface, per hour, and in mm Hg/cm, will be about 0.33 · 10⁻⁵. Diffusion in the eye takes place in the vitreous body, which contains 1–2 $^{0}/_{0}$ of solids. The diffusion constant may therefore be somewhat lower than in pure water, but the difference will probably not be of fundamental importance for the result.

A diffusion constant of $0.33 \cdot 10^{-5}$ gives the following values for the oxygen supply per cm² and hour to the areas of retina dealt with:

The dorsal retina: $0.33 \cdot 10^{-5} \cdot 75 = 2.5 \cdot 10^{-4} \ ml/hour.$ The fundus retina: $0.33 \cdot 10^{-5} \cdot 300 = 9.9 \cdot 10^{-4} \ ml/hour.$

The Pecten's Role in Oxygen Economy of the Retina

A comparison between the amounts of oxygen supplied by the pecten and the total amount of oxygen consumed by the retina would give an idea of the pecten's role in the metabolism of the retina. This comparison can only be made as a rough estimate, however, as the normal oxygen consumption of the retina is unknown in pigeons. Comparisons must therefore be made with values obtained in experiments with the mammalian retina, which is better known in this respect. Another source of error is introduced with the assumption that the percentage of oxygen supplied by the pecten should express its functional importance in the retina. The innermost layers of the retina, which are of interest as potential recipients of the pecten oxygen, probably have a much lower metabolism than the rod and cone layer, which is supplied by the chorio-capillaris. Therefore, the pecten may supply a much thicker layer of tissue than expected from simple calculations on the percentage of retinal oxygen coming from the pecten.

1. In Wahrburg experiments, the mammalian retina consumes 10–20 ml oxygen per g dry weight and hour (SPECTOR 1956). Using the 20.8 ml per g per hour found in dogs as a basis for calculations, the value for 1 cm³ of wet retina will be about 4.2 ml/hour. According to the estimate on p. 48, the oxygen supply from the pecten to each cm² of retina is $2.5 \cdot 10^{-4}$ in the dorsal part of the eye, and $9.9 \cdot 10^{-4}$ in the fundus. If it is assumed that the oxygen consumption is the same throughout the retina, the thickness of the layer, supplied by the pecten, would be:

$$\frac{2.5 \cdot 10^{-4}}{4.2} \text{ cm} = 0.5 \,\mu \text{ in the dorsal part of the bulb, and}$$
$$\frac{9.9 \cdot 10^{-4}}{4.2} \text{ cm} = 2.4 \,\mu \text{ in the fundus.}$$

If reliable, these values would indicate that the oxygen from the pecten plays no particular role in the supply of the ganglion cell layer which lies 10μ (periphery) to 20μ (fundus) from the inner surface of the retina. However, the values are probably much too low for the following reasons: 1) In the Wahrburg experiments, the oxygen consumption of the retina was determined under atmospheric oxygen pressure, and may therefore be much higher than in the living animals, where the oxygen pressure may be as low as 5 mm Hg. 2) The oxygen consumption in the inner retinal layers, which receive the pecten oxygen, is necessarily much lower than in average retinal tissue, as these layers mainly consist of nerve fibres. These two factors taken into consideration it is not excluded that the pecten oxygen may be essential for the innermost $10-20 \mu$ of the retina, which primarily degenerate when the pecten is blocked.

2. The normal brain substance of man consumes 2.1 ml of oxygen per cm³ of tissue under normal conditions of blood supply (LASSEN 1959). If this is assumed also for the internal layers of the pigeon retina, only 1μ (dorsal retina) and 5μ (fundus) deep layers can be supplied by the pecten. However, the nerve fibre layer of the retina

Biol. Skr. Dan. Vid. Selsk. 14, no. 3.

4

probably consumes less oxygen than the average brain substance, so the layer supplied from the pecten may well be much deeper.

3. The following calculation approaches the problem from a quite different angle. The uveal oxygen consumption in the dog was calculated by PILKERTON, BULLE and O'ROURKE (1964 a) to $4 \mu l/g \cdot min$ (cf. also ELGIN 1964). The weight of the uvea is 340 mg (PILKERTON et al. 1964 b), and the radius of the retinal half-sphere is about 10.5 mm. If it is supposed that half of the uveal oxygen is used by the retina, each cm² of retina will consume $59 \cdot 10^{-4}$ ml/hour. In the following calculation it is assumed that the oxygen consumption per cm² retina is of the same order of size in the pigeon. In this animal, the oxygen supply from the pecten was estimated above (p. 48) to be $2.5 \cdot 10^{-4}$ ml/hour in the dorsal part of the bulb and $9.9 \cdot 10^{-4}$ ml/hour in the fundus. This makes about $4 \ 0/0$ and $15 \ 0/0$ of the total retinal supply respectively.

When it is remembered that the optic nerve fibre layer and the ganglion cell layer occupy about $13 \, {}^{0}/{}_{0}$ of the cross section of the pigeon retina, and that $4 - 14.5 \, {}^{0}/{}_{0}$ of the retinal oxygen is supplied from the pecten according to the calculation above, it appears reasonable to assume that the said two layers are supplied mainly by the pecten. The weak points of this calculation are (in addition to the somewhat daring transfer of values from dog to pigeon): 1) The possibility that more than half of the uveal oxygen is used by the retina in the dog, and 2) The presumed lower metabolism of the nerve fibre layer in relation to average retinal tissue. Point 1) will decrease and point 2) will increase the percentage of retinal oxygen coming from the pecten.

All these calculations have been based on the assumption that the fluid in the vitreous body is stationary. If fluid escapes from the pecten and spreads in the bulb, the transport of oxygen will be more efficient.

Although these estimates of the role of the pecten in retinal oxygen supply are very approximate and may be reliable only within a power of ten, they are sufficient to show that the oxygen flow from the pecten is of such an order of size that it may be functionally significant for the inner retinal layers. This is in agreement with the theory that the interruption of the oxygen flow from the pecten caused the degeneration of the retina after the operations. On the other hand, these values are hardly good enough to be regarded as positive proof.

The Oxygen Tension in the Bulb after Coagulation of the Pecten Vessels

The results reported up to now show that the pecten is necessary for the maintainance of a normal retina and have supported the theory that this dependence is a question of oxygen supply. It was shown that oxygen is given off from the pecten to the retina in amounts large enough to have a functional significance. However, it has not been conclusively proved that the degeneration of the retina after pecten operations depends on the interruption of this oxygen supply. It was, therefore,



Fig. 16. Simultaneous recordings of oxygen pressure in the normal ("norm.") and operated ("op.") eye of a pigeon, one and two hours after the pecten vessels of the right eye had been blocked. Oxygen pressure in mm. Hg on the vertical axis, letters on the horizontal axis show sites of the electrode tips. All recorded values fall within the shaded areas.

As the electrode in the operated eye remained constant while the one in the normal eye changed, two graphs were obtained, corresponding to the calibration before and after (upper graph) the experiment. The values from the normal eye are low, probably because of long (5-6 hrs) and deep anaesthesia, but the highest values are similar to those obtained from other normal eyes under deep anaesthesia.

decided to record the oxygen pressure in the bulb after the pecten vessels had been blocked. According to the theory, the oxygen pressure would then be fatally low throughout the corpus vitreum.

Because the absolute values of the oxygen pressure are dependent on the depth of the anaesthesia, simultaneous recordings from the right, unoperated eye were necessary for comparison with the values from the operated eye. The necessity of having reliable calibrations of two electrodes before and after each recording made these experiments rather lengthy, and in the end most of them had to be discarded because the operation, the anaesthesia, or one of the electrodes had failed. However, the few successful experiments are illuminating in several respects.

The first attempts were made with 7 pigeons which had been operated upon 7-27 days earlier, and which showed distinct ophthalmoscopic symptoms of beginning degeneration of the retina. The oxygen pressure was found to be very uniform throughout the corpus vitreum. In three cases somewhat higher values were found near the pecten, indicating beginning revascularization of the organ. In the other cases no distinct increase in the values could be observed when the pecten was approached. The highest values were recorded when the electrode tip was close to or inside the retina, and distinct rhythmic pulsations of the oxygen pressure were seen when the electrode tip reached sufficiently deep into the wall. This showed that the blood supply to the choriocapillaris was functioning normally. All this had been expected, but the absolute values of the oxygen pressure were astonishingly high in all pigeons a week or more after the operation. The values from two cases, when the calibration of the electrodes was satisfactory, indicate about 20-30 mm Hg throughout the bulb. This must mean that the retina was not normal in these eves and that oxygen from the choriocapillaris could pass through and fill the eye interior without being consumed.

It was, therefore, obvious that irreversible changes, which strike the ganglion cells after the pecten operation, must be complete within a week. Retrograde changes in the layer of bipolars and sensory cells probably occur in the same period, causing the inactivity of the entire retina. As shown by the histological examination, this may lead to extensive changes in all layers in some cases, whereas only the inner layers break down in other eyes. The variations from one specimen to another may perhaps depend on differences in the time required for pecten revascularization and also on variations in the size of the regenerated vascular net.

If this interpretation is correct, low and fatal oxygen values in the vitreous body would be expected during the first few days after blockage of the pecten vessels. Consequently, the authors started a series of recordings in the bulb immediately after the operations.

Critical oxygen values were obtained from one newly operated pigeon only, but in this case good recordings were obtained both 1 hour and 2 hours after the pecten vessels were blocked. The electrode on the normal side changed its calibration a little during the experiment, but this is accounted for in the diagram in Fig. 16. One hour after the operation the oxygen pressure had fallen to below 10 mm Hg throughout the vitreous body of the side operated upon. The highest values were recorded in the centre of the eye, where some oxygen still remained. In the dorsal part of the bulb, and near the bridge of the pecten, 2-3 mm only were recorded. These latter values are so close to zero that the difference is hardly significant.
2 hours after the operation some values as high as 7 mm were obtained near the base of the pecten, where oxygen may leak out from the choriocapillaris, and 6 mm was recorded near the lower margin of the iris, where influence from the corpus ciliare is probable. All other values were below 3 mm. This can only mean that the oxygen pressure in the inner retinal layers in contact with the vitreus was between



Fig. 17. Oxygen pressure in mm Hg, recorded in the left bulb of an anaesthetized pigeon, 4 days after the pecten vessels of the eye had been blocked by operation. Note the high values recorded when the recording tip was pushed into the retina of the fundus.

zero and 3 mm, and irreversible changes followed by degeneration would be expected in the ganglion cells, if these behave like ordinary neurons.

Measurements in another pigeon 4 days after the operation showed that the oxygen pressure was still very low in the vitreous body (Fig. 17). Recordings near the surface of the pecten and the retina gave only 3 mm, whereas somewhat higher values were obtained in the central parts of the vitreous body (5–11 mm), probably because of diffusion from the ciliary body. Values higher than 11 mm were obtained only when the electrode tip was pushed into the retina or into the papilla of the optic nerve, so that the recording space came into the diffusion field of the choriocapillaris. When this happened, values as high as 31 mm were recorded, showing that the choriocapillaris supply was intact.

Although few, these experiments show that the operations were efficient in blocking the pecten vessels, and that this results in a drastic decrease of oxygen pressure in the vitreous body within an hour. It is also shown that the choriocapillaris remains intact after the operations. The degeneration of the retina which follows, does, therefore, not depend on interference with the choriocapillaris. This had been predicted on the basis of the morphology of the vessels (p. 26).

The values in the peripheral parts of the vitreous body one and two hours after an operation were below 3 mm Hg, and many of them were, in fact, not significantly different from zero. The oxygen pressure in the inner layers of the retina must have been equally low or probably lower, as these layers consume oxygen. Such low oxygen pressure would be expected to cause irreversible changes and degeneration in the retinal ganglion cells, if these behave as ordinary neurons. Thus, the results support the hypothesis that oxygen supply from the pecten is essential for the inner retinal layers, and that these layers degenerate because of oxygen deficiency after operations. The only point which prevents a definite conclusion is that the minimum oxygen pressure tolerated by the retinal ganglion cells is unknown. It is presumed that the minimum requirements of these cells are similar to those of other ganglion cells, and as this appears to be a realistic postulate, the arguments appear to be rather strong.

Discussion on the Function of the Pecten

The discussion set out step by step in the preceding chapter ended with the conclusion that the pecten is necessary for the maintainance of a normal retina in the pigeon, and that this is so because the pecten supplies the inner layers of the retina with oxygen. The first point is shown by the degeneration of the retina, after the pecten vessels had been surgically blocked (p. 41). No such symptoms were seen in the retina after operations which were performed in the same way, but leaving one or more pecten arteries intact. The conclusion that the pecten is necessary for the maintainance of a normal retina is, therefore, well supported by experimental facts.

The second part of the conclusion, viz., that the oxygen supply from the pecten stands for part of this dependence, is supported by the following points:

1) Measurements of the oxygen pressure in the vitreous body revealed an oxygen gradient, showing that oxygen does diffuse through the vitreous body from the pecten to the retina (p. 47).

2) Numerical calculations on the basis of the recorded oxygen values show that the amount of oxygen transferred from the pecten to 1 cm^2 of retina per hour is about $2.5 \cdot 10^{-4}$ to $9.9 \cdot 10^{-4}$ ml (p. 48). Comparison with the oxygen consumption of the mammalian retina indicates that the said amounts are large enough to be functionally significant in the inner retinal layers (p. 50).

3) After the pecten vessels are surgically blocked, the oxygen pressure in the peripheral parts of the vitreous body falls to values below 3 mm Hg. This is enough to explain why the inner layers of the retina degenerate, if it is presumed that the retinal ganglion cells have the same oxygen requirements as other neurons (p. 54).

The results are thus in agreement with the old idea that the pecten is a nutritive organ, supplying the inner layers of the retina and compensating for the absence of intra-retinal vessels (H. MÜLLER 1872, BEAUREGARD 1876, ROCHON-DUVIGNEAUD 1920, 1943, 1950, MANN 1924 a, b, WALLS 1942, LEINER 1951, and others). The reader is referred to WALLS' (1942) convincing discussion, where he interprets the pecten of birds, the cone of reptiles, and the intra-retinal and hyaloid vessels of other vertebrates as being different solutions to the same functional problem: the supply of the inner layers of the retina. When no such supplying structures are found, the retina is either very thin or is presumed to use less oxygen because it contains fewer cones.

In some teleosts and in Amia, a particularly interesting solution to the problem of retinal supply is found. In these fish, the choriocapillaris is fed by a choroid rete mirabile ("the choroid gland"), which appears to function as a counter-current multiplier for oxygen. This explains why values as high as 250–800 mm Hg were recorded with an oxygen cathode in the vitreous body of fishes with a large rete (J. B. and B. A. WITTENBERG 1962), whereas only 10–20 mm were recorded in fishes without a rete. As the arterial oxygen pressure of fish must be below 160 mm (atmospheric tension), it follows that oxygen is actively secreted into the bulb by the rete-choriocapillaris system. In the pigeon, the vessels of the pecten are not arranged in a way likely to satisfy the requirements of an efficient counter-current system, and the oxygen pressure in the bulb does not exceed that of arterial blood. There is, therefore, no reason to assume that the pecten acts as an oxygen multiplier.

A comparison with the supply system of the human retina is of some interest in the present discussion. According to MICHAELSON (1951) the outer $130\,\mu$ of the human retina are supplied from the choriocapillaris, as this layer is avascular, and because all parts of the retina lying more than $130\,\mu$ from the choroid are supplied by the intraretinal capillaries belonging to the centralis retinae system. MICHAELSON'S view is supported by the fact that the last-mentioned inner layers are the first to degenerate after obstruction of the central retinal vessels. In man, the capillary bed of the a. centralis supplies the nerve fibre layer, the ganglion cell layer, the inner plexiform layer, and the inner nuclear layer. In the pigeon, the supply from the inner side appears to be restricted to the nerve fibre layer and the ganglion cell layer, as these layers may be the only ones which show pathological changes after interruption of supply from the pecten. This seems to indicate that the zone supplied by the choriocapillaris is considerably thicker in the pigeon than in man. In the pigeon, this zone, including all layers from the pigment epithelium to the inner plexiform layer, is about $200\,\mu$ thick in the fundus and $110-180\,\mu$ thick in the peripheral parts of the retina. When this is compared with the $130\,\mu$ supplied from the choriocapillaris in man, it provides some indirect support to the functional interpretation of the pecten: If only $130\,\mu$ of retina can be supplied from the human choriocapillaris, it is improbable that the whole retina in the pigeon could be supplied from this source, for its thickness may exceed $250 \,\mu$ in the fundus part. The suggestion that the inner parts of the retina are supplied from the pecten offers a solution to this problem.

FRANZ (1909) did not believe that the pecten is a nutritive organ because the walls of the capillaries are so thick; he admits, however, that their impermeability remains

to be proved. GRIFFIN (1953) found it unlikely that significant amounts of oxygen can be transferred by diffusion over the fairly large distance from the pecten to the retina. Both objections to the theory of oxygen supply from the pecten are invalidated by the results of the present investigation. Oxygen passes out of the pecten and diffuses to the retina in amounts large enough to be functionally significant (p. 50).

In this paper attention has been exclusively focused on the oxygen supply from the pecten, but it is possible and even probable that removal of carbon dioxide from the inner bulb is an equally important function of the organ. This was suggested by LEINER (1951) and KAUTH and SOMMER (1953), who maintained that the high content of carbonic anhydrase in the pecten facilitates this function. It is certainly probable that oxygen supply and removal of carbon dioxide are combined in the pecten, as in other organs, and diffusion of carbon dioxide in the vitreous body is probably almost as rapid as that of oxygen. However, until quantitative data have been presented, all estimates of the diffusion of carbon dioxide will be little more than guesses, as the absolute concentrations and the hydration to carbonic acid will influence the issue.

Whether other blood-borne substances such as glucose, amino acids, and fatty acids can be transported to the retina from the pecten is still more uncertain. These substances diffuse very slowly, and it appears doubtful whether they could reach the retina in significant amounts without the aid of special transport mechanisms.

Although some problems remain to be solved, they do not interfere with the main result of the present investigation, viz.:

that the pecten is a nutritive organ, necessary for the maintainance of the inner layers of the retina. This must be considered the principal function of the pecten, as structures necessary for vision are seriously damaged when this function fails.

The possibility that the pecten can have other, "subsidiary" functions cannot be excluded, but none of the other potential activities has ever been shown to be so important that its break-down could cause significant deterioration of the eyesight. In the search for subsidiary functions of the pecten, attention is drawn to the numerous theories listed on pp. 8–10. The following activities appear possible or even probable, although their significance in relation to eyesight is unknown:

1. The pecten can take part in the formation of the vitreous body during the embryonic development, as suggested e.g. by v. HUSEN (1913). However, the vitreous body in other animals is formed, whether a pecten homologue is present or not. The root-like fibres of the vitreous body, which penetrate into the bridge of the adult pecten, could indicate formation of vitreous from the bridge in adult birds. However, it appears equally probable that these fibres serve to support the pecten mechanically.

2. As suggested by several authors (pp. 9, 10), the pecten may secrete intraocular fluid. It would hardly be realistic to suggest that the organ is impermeable to water and other low-molecular substances when it is easily permeable to fluorescein (ABELSDORFF and WESSLEY 1909). Absolute proof regarding an active secretion of water from the pecten, and for a significant role in the regulation of intra-ocular pressure, is still wanting, however (pp. 12–13). In the present experiments, pressure on the bulb during operations caused some loss of fluid, with the result that the cornea was soft and uneven when the hooks were removed. An apparently normal, smooth and firm cornea was always reestablished within 5 minutes, probably in part because of hyperaemia of the choroidal vessels. Throughout the post-operative period the cornea remained firm and smooth, and no differences could be felt when control eyes and eyes with degenerated pectens were compared. Therefore, the ciliary body alone must be capable of maintaining a normal or nearly normal pressure in the bulb. According to SEAMAN and collaborators (1963), the pressure-regulating mechanisms of the pecten should come into play when the system is over-loaded, but this appears to be very difficult to prove critically.

3. It is possible that diffusion from the pecten plays some role in the supply of the posterior parts of the lens and the vitreous body. As the vitreous body has a negligible metabolism, and as the ciliary body would appear to be in a better position to cover the comparatively small needs of the lens, it seems improbable that this particular function of the pecten should be decisive. In mammalian eyes the said structures are supplied without the aid of a pecten. The lens and the vitreous body did not show significant changes after the pecten vessels had been blocked.

4. It is probable that the pigmented pecten absorbs some diffuse light in the bulb, as suggested by TREVIRANUS (1828), THOMSON (1929), and VERRIER (1936), but it is an open question whether this can significantly contribute to clearer vision.

5. It appears logical to assume that some heat is given off to the eye from the blood in the pecten (KAJIKAWA 1923), and it is also possible that some heat can be carried off with the blood when the pecten is strongly illuminated (GRIFFIN 1953). Since these problems are solved without a pecten in other vertebrate eyes, it appears less probable that these activities should be a condition for the normal functioning of the avian eye.

A series of other functional theories should be abandoned in view of the fact that they are highly improbable or in direct contradiction to established facts. Some of these theories require no comment, but a few of them will be discussed here:

The theories based on the presence of pecten shadows on the retina cannot be upheld, as these particular kinds of shadow cannot be cast by the pecten in the pigeon's eye (pp. 9–10). The ophthalmoscopic observations supporting this conclusion are found on pp. 10-12 and 14-15.

The theory that the pecten is a dark mirror, reflecting on the dorsal retina images of birds of prey in the sky (p. 10), is unacceptable, as no reflecting surfaces have been found.

All theories that the pecten is a sensory organ meet with the difficulty that nerve fibres have not been found, and, if present, must be very few (p. 19).

All ideas according to which the pecten plays an active role in accomodation appear untenable after it has been shown that the pecten remains unchanged during accommodation (ANDRÉ and BEAUREGARD 1874, ABELSDORFF 1910).

It appears probable that the pecten vessels are partly emptied when intraocular pressure suddenly increases through muscular action or violence, and that the pressure change is somewhat counteracted in this way. However, all vessels tend to empty when exposed to pressure, and it has not been shown that the emptying of pecten vessels under the presumed conditions has any specific significance in the visual organ. The supposition that emptying occurs in connection with accommodation is hardly feasible in view of the experiments referred to above (ANDRÉ and BEAUREGARD 1874, ABELSDORFF 1910).

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1

PLATE I

1. The eye of a pigeon with the pecten (P), cut open by a transverse section through the head. The head was fixed by perfusion with Bouin's fluid and decalcified before being cut. — C = cornea, I = iris, L = lens, P = pecten, PU = pupilla, RSP = rostrum sphenoidale.

2. The pecten, seen from the side. Fundus end to the left. — B = the thickened bridge which covers the folded part.

PLATE I



PLATE II

Horizontal section through a pigeon's head, showing the pecten attached to the papilla of the optic nerve. Fixed in alcohol-formalin-acetic acid, 75μ celloidin section, Mallory's phosphotungstic acid hematoxylin (WINGSTRAND 1951). — CH = chiasma, HG = Harderian gland, LG = lacrymal gland, OI = m. obliquus inferior, OP = v. ophthalmica, OT = a. and v. ophthalmo-temporalis, P = pecten, PY = m. pyriformis, RA = m. rectus anterior, RP = m. rectus posterior, SC = scleral cartilage, SO = a. and v. supra-orbitalis, SR = ossicular ring, TMN = tendon of the membrana nictitans.

 $V_1 =$ ramus profundus trigemini.



Plate III

Transverse section of a pigeons head through the papilla of the optic nerve. Technique as Plate II:1. DPI = m. depressor palpebrae inferioris, FB = os frontale with pneumatic cavities, IO = a. and v. infraorbitalis, LOI = ligamentum orbitale inferius, MX = v. maxillaris, OL = n. olfactorius, ON = n. opticus, OP = vena ophthalmica (cut twice), OT = a. ophthalmo-temporalis, P = pecten, PA = pecten artery, PT = pterygoid bone, Q = m. quadratus, RA = m. rectus anterius, RO = venous ring sinus of the ora serrata, RI = m. rectus inferius, RS = m. rectus superius, RSP = rostrum sphenoidale, TMN = tendon of the membran anictitans.



PLATE IV

Electron micrograph of cross section through the folded wall of the pecten — Perfusion with glutaraldehyde, postfixation in OsO₄, methacrylate, staining with UAc. — ICS = intercellular spaces, MUS = superficial mucopolysaccharid membrane, STR = stroma cells with numerous processes (the one in the middle with damaged pigment granules). X = places where the extension of the intercellular space between the capillary wall and the superficial mucopolysaccharid membrane can be seen.



PLATE V

1. Electron micrograph from the folded part of the pecten, showing three stroma cells, two of which contain pigment granules, and their numerous ramified processes in the intercellular space (ICS). Some of these processes end under the superficial mucopolysaccharid membrane (MUS), some on the outer wall of capillaries (C), and some on the connective tissue string (CTF). Technique as Plate IV:1.

2. Plastic cast of the arteries of the pecten. The camera was focused on the fundus from a lateral direction, after the choriocapillaris, the anterior eye segment, and most veins had been removed. The figure shows the a. ophthalmo-temporalis (OT), which makes a loop below the entrance of the optic nerve (ON). The arteries to the pecten (P) and the long ciliary artery (LC) are emitted from the loop.

PLATE V



PLATE VI

Electron micrograph of a capillary wall in the folded part of the pecten. Mitochondria (M) and some ergastoplasm is seen in the cytoplasm of the endothelial cell (E), which sends inner villi (IV) towards the lumen of the capillary (C) and outer villi (OV) towards the perivascular membrane (PM), in which connective tissue fibrils are visible. The stroma cell (STR) sends dark processes into the intercellular space (ICS) and is attached to the outer mucopolysaccharid membrane of the capillary. — Perfusion with glaturaldehyde, post-fixation in OsO₄, Epon, staining in lead hydroxyde.



PLATE VII

Electron micrograph of the folded part of the pecten, showing the wall of a capillary (C), an endothelium cell with its nucleus (E), the perivascular membrane (PM) with collagen fibrils and the mucopolysaccharid membrane of the vessel (MUV). The intercellular space (ICS), separates the wall of the vessel from the superficial mucopolysaccharid membrane (MUS). Stroma cell processes (STP) are seen in the intercellular space. The outer villi of the endothelial cell are not distinct because they are parallel with the plane of sectioning. — Perfusion with glutaraldehyde, post-fixation in OsO₄, Epon, staining in lead hydroxyde.

2. Electron micrograph from the bridge of the pecten of the pigeon, showing numerous stroma cell processes, some with pigment granules (PIG), separated by fairly narrow intercellular spaces (ICS). "X" marks two processes, in which numerous small vesicles are visible. — Fixation in OsO_4 , Epon, staining in lead hydroxyde.

PLATE VII



PLATE VIII

Electron micrograph of the surface of the bridge of the pecten in a pigeon. Several stroma cell processes pass out to the surface, where a mucopolysaccharide membrane (MUS) delimits the collagen of the corpus vitreum (CVT). One stroma cell nucleus (N), pigment granules (PIG), a large mitochondrion (M), and some ergastoplasm (ER) can be seen. A fairly large intercellular space (ICS) does not reach the surface. All stroma cell processes contain filaments of the glial type, e. g. at "F".



PLATE IX

The operational procedure used when the pecten arteries were approached, demonstrated on a dead pigeon, injected with starch-vermilion in the arteries and with starch-cobalt blue in the veins. For the purpose of illustration, the wound is made much larger than in actual operations.

1. The pigeons head fixed with plaster tape. Note the piece of glass tubing in the bill.

2. A piece of the supraorbital crest of the frontal (FB) has been detached through skin incision above the eye. The stippled line indicates the location of the skin incision below the eye.

3. Skin incision below the eye, exposing the ligamentum orbitale inferius (LI, whitish). The stippled line indicates where the ligament is cut along the lower margin of the orbit.

4. The ligamentum orbitale inferious is cut through, exposing the infraorbital vessels (IO) and the m. depressor palpebrae inferioris (DPI). J = jugal arch. The stippled line indicates where the depressor muscle is split.

5. The m. depressor palpebrae inf. is split, and the broad hook (H) is applied in the opening, pulling the bulb dorsally. The pecten arteries are embedded in veins and fat in the angle between the m. rectus posterior (RP) and m. r. inferior (RI, difficult to discern).

6. Veins and fat removed, the a. ophthalmotemporalis (OT) with the pecten arteries (P) exposed. LC = a. and n. ciliaris long., ON = optic nerve extension, RI = m. rectus inferior, RP = m. rectus posterior.



PLATE X

1 and 2: Sections through the folded part of the pecten of the operated, left eye (1) and the normal, right eye (2) of a pigeon, 15 days after the operation. — 1: Azan staining, 2: hematoxylin-eosin. Magnification same in both figures. N. A. 0.20.

3 and 4: Details of the pectens shown in 1 and 2, resp. - 3: Azan staining, 4: PAS-hematoxylin. N. A. 1.0.

- 5. The pecten of the operated eye 165 days after the blocking of the pecten vessels. Scattered vessels have regenerated. Azan staining, N. A. 0.20.
- 6. The pecten of a pigeon's eye 21 days after the vessels had been blocked. Heavy degeneration and invasion of retinal pigment cells, filling the spaces between the folds. Azan staining, N. A. 0.20.



PLATE XI

1. Normal retina of the right eye of a pigeon. A = pigment layer, B = zone of outer segments, C = zone of inner segments, D = membr. limitans ext., E = outer nuclear layer, F = outer plexiform layer, G = inner nuclear layer, H = inner plexiform layer, I = layer of ganglion cells, K = layer of nerve fibres. — Hematoxylin-cosin, N. A. 0.60.

2. Retina of the left, operated eye of the same pigeon, 15 days after the pecten vessels were blocked. Marked reduction of all layers, particularly of ganglion cells and optic fibres. Numerous macrophages, particularly in inner layers. — Hematoxylin-eosin, N. A. 1.0. Same magnification as 1.



20 µ

PLATE XII

1 and 2: The retina of the right, normal (1) and of the left, operated (2) eye of a pigeon, 165 days after the pecten vessels were blocked in the left eye. Note the total absence of optic nerve fibres and the degenerate ganglion cells.

3. Retina of the operated eye of a pigeon 7 days after the pecten vessels were blocked. Note presence of macrophage cells in the nerve fibre layer (arrows).

4. Retina of the operated eye 15 days after the pecten vessels were blocked.

All figures from the nasal retina near the equator, stained with hematoxylin-eosin. Same magnification in all figures. N. A. 1.0.
PLATE XII



Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter Biol. Skr. Dan. Vid. Selsk.

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København 1965 Kommissionær: Ejnar Munksgaard

Synopsis

Die Arbeit stützt sich wie bei den früher erschienenen Lieferungen der Symbolae Afghanicae auf die Mehrzahl der seit dem Erscheinen von Boissier's Flora Orientalis in Afghanistan zusammengebrachten Sammlungen. Zu den in den früheren Lieferungen bearbeiteten Sammlungen kommen noch mehrere neue, unter anderen die von HEDGE und WENDELBO (1962) und von RECHINGER (1962) angelegten. Die vorliegende Lieferung enthält die Bearbeitung der Cyperaceen durch M. RAYMOND (Montreal) und der Gramineen durch N. C. BOR (Kew) und A. MELDERIS (London).

Die Bearbeitung der Cyperaceen umfasst 95 Arten, darunter vier neue. Der Artenreichtum konzentriert sich besonders auf die vorwiegend dem himalayischen Florengebiet angehörenden Landschaften Nuristan und das zu West-Pakistan gehörige Chitral. Der Formenkreis der Carex stenophylla wird kritisch untersucht und neu gegliedert. Für alle Arten werden Bestimmungsschlüssel gegeben. Die Bearbeitung der Gramineen umfasst 270 Arten, darunter sieben neue. Die Gramineen sind neben den Compositen und Leguminosen eine der artenreichsten Familien der afghanischen Flora. Der Endemismus ist jedoch bei den Gramineen verhältnismässig schwach ausgeprägt.

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Introduction

"Symbolae Afghanicae" was initiated by plant collections made by L. EDELBERG and M. Køie on "The 3rd Danish Expedition to Central Asia".

In addition to these collections there have been included in part I. Labiatae (1954) the following collections: J. L. CHAWORTH-MUSTERS in Herb. of the British Museum, London; J. M. HONIGBERGER in Herb. of the Naturhistorisches Museum, Wien; H. F. NEUBAUER in Herb. of the Naturhistorisches Museum, Wien; W. KOELZ in United States National Herbarium, Washington DC., formerly at the Plant Industry Station, Beltsville, Maryland. Part one contains also a survey of plant-collecting in Afghanistan.

At the time of printing of part II. of the Symbolae Afghanicae, *Compositae* (1955), further collections from Afghanistan were received for determination, namely those of G. KERSTAN and A. SCHEIBE, Deutsche Hindukuschexpedition 1935 in Herb. of the Martin Luther Universität in Halle and O. H. VOLK, private collection, Würzburg. It was, however, too late to include the enumeration of the *Compositae* of these collections in the publication. As to the vast genus *Cousinia*, ALEXANDER GILLI having made extensive collections in Afghanistan (in Herb. of the Naturhistorisches Museum, Wien) between 1949 and 1951 agreed to hand over to me his material of that genus for determination and publication. Most of the results of his activities have been worked out and published separately by himself.

In part III of Symbolae Afghanicae, Leguminosae, all the above mentioned collections are being included. The same is true for part IV, including the following families: Pteridophyta, Cruciferae, Saxifragaceae, Geraniacae, Linaceae, Guttiferae, Onagraceae, Primulaceae, Apocynaceae, Asclepiadaceae, Convolvulaceae, Solanaceae, Scrophulariacae, Rubiaceae, Dipsacaceae, as well as Liliaceae, Amaryllidaceae, Dioscoreaceae, Iridaceae, and Orchidaceae. Among the smaller collections occasionally mentioned in part IV and V, and also now in the present part VI of Symbolae Afghanicae the following should be mentioned: K. LINDBERG, private collection, Lund, R. MEINERTZHAGEN and W. THESIGER, British Museum, London, P. WENDELBO, Herbarium of the University Bergen, and I. HEDGE, Herbarium of the Royal Botanic Garden, Edinburgh.

HONIGBERGER'S specimens collected in 1833 are probably the oldest plant collection from Afghanistan. Most of them have not at all or only provisionally been named and they are inserted since many years in the Vienna Herbarium. Unfortunately their labels do not give any information excepted "Cabul-HonigBerger". Most probably "Cabul" is to be understood in the sense of "Regnum Cabulicum", the plants thus labelled do not necessarily originate from the neighbourhood of Kabul City.

Duplicates of many of the above mentioned collections have been deposited in the Herbarium of the Naturhistorisches Museum, Wien, the Grasses collected by

^{1*}

KØIE and EDELBERG in the Herbarium of the University of Copenhague, in the Herbarium of the Royal Botanic Gardens, Kew, and in British Museum (Natural History), London.

Many of the localities referred to in this work are not shown on any map. Others will be difficult to identify because of the considerable discrepancies in orthography. In the absence of established orthographic rules, we have given the localities in the spelling that has been found on the labels. A complete list of more exact geographical locations cannot be prepared until the treatment has been completed because new material has been coming in all the time. For preliminary orientation we have divided Afghanistan into seven parts: N, NE, E, SE, SW, NW and C as indicated on the map. These geographical abbreviations are placed in front of the localities given. Nuristan has been segregated from the north-east part of the country, mainly because it is a well defined area from which a particularly large number of plants has been collected, but also because the monsoon rain renders the vegetation of Nuristan different from that of most of the other parts of Afghanistan. Otherwise no attempt has been made to divide the country by plant geography.

Data of habitats, etc. have been cited in the language used by the collector on the label.

Whereas in most of the earlier parts of the Symbolae Afghanicae enumerations only of the herbarium material recently obtained have been presented, the treatments published in part V as well as in the present part VI, however, cover all the species reported from Afghanistan. Keys to genera and species have been worked out in *Cyperaceae* by MARCEL RAYMOND. In many cases species reported from neighbouring countries, e. g. from Chitral, Swat, Peshawar and Kurram, as well as Balouchistan in the East, and in Khorasan in the West have been included too because their occurrence in Afghanistan is to be expected.

The names of the collectors are abbreviated as follows; indication of herbaria is given in bracts: AMSEL is H. G. AMSEL (W); B. L. is S. A. BOWES LYON (BM); CH.-M. is J. L. CHAWORTH-MUSTERS (BM); CN is C. DE B. CODRINGTON (BM); E is L. EDELBERG (C, W); G. is A. GILLI (W); H is HONIGBERGER (W); HDG. is I. HEDGE (E, W); K is M. KØIE (C, W); KN is G. KERSTAN (HAL); KZ is W. KOELZ (US); L is K. LINDBERG (W); M. is R. MEINERTZHAGEN (BM); N is H. F. NEUBAUER (W); REPP is G. REEP (W); SCH is A. SCHEIBE (HAL); ST is J. D. A. STAINTON (BM); TH is W. THESIGER (BM); V is O. H. VOLK (W); WDB is P. WENDELBO (BG, E, O, W). The specimens collected by K. H. RECHINGER (RECH, W) in 1962 have been taken up too.

For herbaria the internationally recognized abbreviations as indicated in Index Herbariorum have been used.

Photographs of Grasses have been prepared by Messrs. M. G. SAWYERS and P. GREEN of Photographic Studio, British Museum (Natural History), London.

The plant families will be published in the sequence in which the treatment is completed. It is intended to conclude the work with a survey of Afghanistan's vegetation.

The typescript for the press was prepared by A. PATZAK, Wien.

CYPERACEAE

by MARCEL RAYMOND,¹) Montreal.

The material enumerated below contains 95 species. It includes actual specimens submitted by Dr. K. H. Rechinger, borrowed from several herbaria, as well as reliable records taken in the botanical literature. The loan included the material collected by KERSTAN during the German Hindukush Expedition of 1935, partial results of which only have been published. The Cyperaceae have not appeared in print, though some of them have been determined by the late G. KUEKENTHAL. Present also was a nice set of specimens from Chitral, collected by STAINTON and Bowes Lyon that add considerably to our knowledge of the Cyperaceous flora of that area. In some cases, as several species have been described with immature or fragmentary material, this beautifully prepared collection has given me the opportunity to write more complete descriptions of inadequately understood species. Years ago, my friend PER WENDELBO had given me duplicates of several of his own collection from Tirich Mir, so that I was already familiar with such species as Carex chitralensis NELMES, C. Gilesii NELMES and C. Wendelboi NELMES, to mention only these. Dr. M. KøIE was kind enough to send a very nice set, from various parts of Afghanistan. As several old collections labelled as coming from 'Afghanistan' or 'Kabul' have in fact been collected in Pakistan, the examination of all this material has often allowed me to confirm or reject the actual presence of such species in Afghanistan itself, though several old records have still to be authenticated by new material. GILLI's material, the basis of a recent publication, has also been examined, thanks to Dr. RECHINGER.

The following genera are represented: *Carex* (42 species), *Cyperus* (19 species), *Scirpus* (13 species), *Kobresia* (11 species), *Eleocharis* (6 species), *Bulbostylis* (1 species), *Fimbristylis* (1 species), *Eriophorum* (1 species), *Schoenus* (1 species).

Carex alsia and C. austro-afghanica are described as new, as well as Kobresia afghanica. Carex sanguinea is transferred to the genus Kobresia and Scirpus maritimus var. orientalis LITW. is raised to specifical rank as S. Schmidii. Some minor transfers and taxa are also proposed.

The following enumeration shows that phytogeographically speaking NE. Afghanistan and Chitral, the richest area in species of *Carex* notably, is the western-

¹) Curator, Montreal Botanical Garden, Canada.

most extension of the Himalayan flora, with several endemics of restricted range. The still poorly known Northern district shows floristic affinity with Turkestan and Pamiro-Alaj, whereas the Western district is the continuation of the Iranian flora. *Carex Halleriana*, ranging from Portugal through Iran and Afghanistan (one gathering) to Sind, indicates a faint Mediterranean influence. If Chitral is removed from the picture, the actual Cyperaceous flora of Afghanistan sensu stricto is a relatively poor one.

1a.	Flowers unisexual. Female flowers (nut, achene) enclosed in a more or less
	flask-shaped closed perigynium 2
b.	Flowers hermaphrodite. Female flowers (nut, achene) subtended by a scale 3
2a.	Female flowers enclosed in an incompletely closed perigyniumKobresia
b.	Female flowers enclosed in a completely closed flask-shaped perigynium Carex
3a.	Spikelets flat, the scale distichous Cyperus
b.	Spikelets terete, the scales spirally arranged 4
4a.	Spikelets mostly 1-3-flowered, with several empty basal scales Schoenus
b.	Spikelets several flowered, with 1–2 empty basal scales
5a.	Spikelets solitary, at the end of a leafless culm. Style-base enlarged and
	persistent Eleocharis
b.	Spikelets mostly several, variously grouped. Style-base caducous
6a.	Style-base flattened, often fimbriate Fimbristylis
b.	Style-base not flattened, smooth 7
7a.	Style-base leaving a button-like scar on top of the achene. Plants mostly
	hairy Bulbostylis
b.	Style-base not button-like 8
8a.	Spikelets variously grouped, terminal or pseudolateral, even solitary.
	Bristles several or Ø, shorter than, or as long as, the achene Scirpus
b.	Spikelets small, very numerous, in a terminal compound umbelliform
	panicle. Bristles overtopping the achene Eriophorum

Cypereae

Cyperus L.

1a.	Axis of spikelets continuous	2
b.	Axis of spikelets articulate and broadly winged. Spikes hemispherical.	
	Scales 2,5 mm long, 3-5-nerved. Nutlets oblong. Small tufted annual 2-20	
	cm high C squarrosu	s L
2a.	Stigmas 3. Nutlets trigonous	3
b.	Stigmas 2. Nutlets lenticular compressed or biconvex	15
3a.	Spikelets on a rather long axis, spikelike	4
b.	Spikelets on a very short axis, digitate or fasciculate	10
4a.	Axis of spikelets with margin of scales decurrent at base, conspicuously	
	winged at last. Style long	õ
b.	Axis of spikelets unwinged or narrowly margined. Style short	9

5a.	Spikes cylindrical. Axis broadly winged; wings coloured so often
	C. imbricatus Retz
b.	Spikes broad-ovate or turbinate. Wings of axis hyaline
6a.	Rhizome horizontal with rather long stolons. Scales densely imbricate 7
b.	Rhizome with rather slender stolons or short suckers. Scales elliptical
	obtuse C. eleusinoides Kunth
7a.	Rhizome creeping. Stolons lignescent. Scales keeled, obscurely few-winged 8
b.	Rhizome fibrous. Stolons thin. Scales concave, scarcely keeled, conspi-
	cuously many-nerved C. esculentus L.
8a.	Stolons tuberiferous C. rotundus L.
b.	Rhizome lignescent, creeping; no tuberiferous stolons present C. longus L.
9a.	(4) Spikelets loosely spicate. Scales loosely arranged, broadly obovate or
	ovate, rounded at apex, 5–7-nerved. Nutlets nearly as long as scales C. Iria L.
b.	Spikelets densely spicate. Scales densely imbricate, ovate, cuspidate or
	rounded at apex, 5–13-nerved. Nutlets 1/2 as long as scales C. glaber L.
10a.	Anthela spreading 11
b.	Anthela capitate-contracted 12
11a.	Spikelets 5–15, loosely capitate. Scales ovate, blackish-brownC. fuscus L.
b.	Spikelets numerous, densely capitate. Scales orbicular-obovate, chestnut-
	brown, hyaline at margin C. difformis L.
12a.	Spikelets turgid. Scales inconspicuously carinate towards apex
	C. conglomeratus ROTTB.
b.	Spikelets compressed. Scales conspicuously carinate
13a.	Culms long. Scales muticous obtuse C. niveus RETZ.
D.	Culms very short. Scales ending in a conspicuous mucro C. Michelianus (L) LINK
14a.	(2) Nutlets dorsally compressed, facing the axis
D.	Anthele lagge new pathen long. Scales using the axis
15a.	Anthela loose, rays ramer long. Scales venied C. serotinus Rottis.
D.	Anthela capitale-contracted, not more than 1 mm wide. Scales not venied
169	Outermost cells beyagonal Nutlets reticulate or nunctulate 17
h	Outermost cells rectangular oblong Nutlets undulate or muricate at base
1.	and towards apex
17a.	Scales never sulcate
b.	Scales conspicuously sulcate
18a.	Scales obtuse or acute, never ending in a recurved mucro C. alobosus ALL.
b.	Scales truncate at apex or ending in a recurved mucro

C. conglomeratus ROTTB. - 'Balouchistan' (ELLIOTT).

C. conglomeratus ROTTB. var. Aucheri (JAUB. et SPACH) C. B. CLARKE – Common in nearby Persia and to be expected in SW.-Afghanistan.

7

C. conglomeratus ROTTB. var. effusus (ROTTB.) KUEKENTHAL, – 'Afghanistan' (AITCH. 36). – Pakistan: Balouchistan: Sibi (LACE).

Desert and sandy places of Africa and SW. Asia, eastwards to India. A difficult group to deal with, where BOECKELER recognized 9 species, all treated by KUEKENTHAL as varieties or forms of a single one.

C. difformis L. – E: Prov. Khost: Wuzak (V. 1072). Arghandab bei Kabul (V. 1352). Kabul (Акнтак 422). 'Afghanistan' (GRIFF. 6155 p. p.).

C. eleusinoides KUNTH – E: Kabul (GRIFF. 28, 1267, 6199).

C. esculentus L. – NE: Khanabad, 700 m (Kz. 12201).

C. flavescens L. - 'Afghanistan' (AITCH. 964).

C. fuscus L. – N: Mazar-i Sharif: Aqtscha (N. 1950/131). Kataghan: Pul-e Khomri (N. 1950/239). – SW: Am Hilmend Fluss (V. 1327). – SE: Arghandab bei Kandahar (V. 1356). – E: Khost: Wuzak (V. 1076). Kabul: Sarobi bei Charikar (V. 490). Paghman, Beg-tut, 2300 m (V. 2200). Am Logar Fluss bei Tscharasiah, 1760 m (G. 241). Am Logar Fluss zwischen Tag-i Saidan und Lallandar, 1810 m (G. 242, 243). 'Afghanistan' (GRIFF. 6174, 6175, 6176). – C: Kamard near Doab, 2000 m (Kz. 13591). Doab, 1700 m (Kz. 13517). Pahin Shahr, 2700 m (Kz. 12393).

C. glaber L. – E: Kabul: Paghman, Beg-tut (V. 2208). – 'Afghanistan' (Антсн. 775).

C. globosus ALL. SE: Arghandab-Sümpfe bei Kandahar (V. 1358). – NE: Nuristan: Kamdesh im unteren Baschgal-Tal, 1800 m (KN. 144). – E: Kabul: Sarobi bei Charikar (V. 1392). Lataband (V. 538, 1173). – C: Doab, 1400 m (E. 2882). Kamard, 6000 ft., along stream (Kz. 13604). Rustak, 2000 ft., damp ground (Kz. 13140).

C. imbricatus RETZ. (Syn. C. radiatus VAHL.) – SE: Kandahar: Arghandab (KITAMURA 37).

C. Iria L. - E: 'Afghanistan' (GRIFF. 42, 96, 6177; AITCH. 418).

C. laevigatus L. (Syn. Juncellus laevigatus (L.) C. B. CLARKE). – E: 'Afghanistan' (GRIFF. 6215; AITCH. 778).

C. laevigatus L. var. distachyos (ALL.) Coss. et DURIEU (Syn. C. distachyos ALL., C. junciformis CAV., Acorellus distachyus (ALL.) PALLA). – N: Qataghan (Kataghan): Qunduz (Kunduz), 400 m (RECH. 16057). – SW: Herat, 1000 m (K. 4246). Shin Dand, 1200 m (K. 4245). – SE: Kajkai, 1000 m (K. 2155). – E: Kabul: Sarobi bei Kabul (V. 1214-a). 'Afghanistan' (GRIFF. 6199). – Pakistan: Balouchistan (DUKE 69).

KOYAMA gives 1879 as the date of publication of ALLIONI's classical Auctuarium ad Floram Pedemontanam, instead of 1789. Then, treating var. *distachyos* as a species, he choses *Cyperus junciformis* Cav. (1794) as the oldest name, quite an unusual procedure.

C. longus L. – SE: Arghandab-Sümpfe bei Kandahar (V. 1358-a, KITAMURA 23). Pirzada near Kandahar, 900 m (K. 2132). – E: 'Afghanistan' (N. 1950/437). – NE:

Nuristan: Rustak, 2000 ft., pond edge (Kz. 13142). Takia, 4500 ft., field (Kz. 13113). – Pakistan: Quetta (HAMILTON).

C. longus L. var. pallidior KUEKENTHAL (Syn. C. longus L. var. pallidus (non BOECK.) BOISS.). – NE: Khanabad: Takia, Rustak, 1500 m (Kz. 13113). Rustak, 700 m (Kz. 13142). Nuristan: Arrandz, Waigel-dal, 1800 m (E. 2402). – E: Jallalabad, 580 m (G. 238). 'Afghanistan' (GRIFF. 6145); АІТСН. 624).

Extremely variable. KUEKENTHAL recognizes 19 taxa at various levels.

C. Michelianus (L.) LINK ssp. pygmaeus (ROTTB.) ASCHERS. et GRAEBN. – SW: Am Hilmend Fluss (V. 1326).

C. niveus RETZ. – Pakistan: From Thal to Kurram (AITCH. 438). – Balouchistan (STOCKS 617).

C. pumilus L. – E: Khost (V.). – C: Doab, 2700 m (Kz. 13514).

C. rotundus L. – **NW:** Sangcharak: Tukzar, 1700 m (Kz. 13972). – **N:** Mazar-i Sharif, 400 m (Kz. 13189, КІТАМИВА 47, 48). Kataghan: Baghlan (V. 599, 645-а, 767, 1165, 1385). – **NE:** Kataghan: Qunduz (Kunduz) (RECH. 16028), Bala Hissar, 400 m (Kz. 13189, RECH. 16062). Tagau, 6000 ft., damp ground (Kz. 11805). **Nuristan** Mühlbach bei Barikot, 850 m (G. 239). – **SE:** Kajkai, 1400 m (K. 2882). Zwischen Kandahar und Kushki, Nahod, 1000 m (KN. 310). Kandahar (КІТАМИВА 56). – **SW:** Farah, 600–700 m (Kz. 13253, K. 3906). – **E:** Kabul: Nidjrao, NE Sarobi (V. 2383). Sarobi bei Kabul (V. 1198). Tang-e Gharru, inter Kabul et Jallalabad, 1400–1500 m, substr. Gneiss (RECH. 16938). Jallalabad, Tschardagh, am Alingar Fluss, 600 m (KN. 653). Guzar Gah bei Kabul (N. 1950/670). Garten der Nedjatschule in Kabul, 1770 m (G. 240). 'Afghanistan' (GRIFF. 6179, 6180; АІТСН. 25). – **Pakistan** (KN. 2006).

C. rotundus L. f. latimarginatus KUEKENTHAL. – SE: Zwischen Kandahar und Kuschki Nahod, 1000 m (KN. 310). – E: 'Afghanistan' (Антен. 85). – Pakistan: Chitral: Yarkhun-Tal bei Koghosi, 600 m (KN. 2006).

C. rotundus L. var. salsolus C. B. CLARKE. – E: Jallalabad-Gebiet: Tscharbagh, am unteren Alingar, 600 m (Kn. 653). – Pakistan: Chitral: Mastuj-Tal, 1600 m (Kn. 2006).

C. sanguinolentus VAHL (Syn. Pycreus sanguinolentus (VAHL) NEES, C. Rehmanni BOISS.). – E: 'Afghanistan' (GRIFF. 6188). – Pakistan: Swat: Utror, 2500 (R. 19534).

C. serotinus ROTTB. (Syn. *C. Monti* L. f.). – **NE:** Badakhshan: Jurm, 2300 m (Kz. 12878, 12879). Khanabad, 700 m (Kz. 12208). Between Shinak and Alizai (Антсн. 494). – **E:** 'Afghanistan' (GRIFF. 6188 p. p.). – **Pakistan:** Lutkuh (Lutkho), Tal bei Shoghor (KN. 1601).

C. squarrosus L. (Syn. C. aristatus ROTTB.). – E: Porande-Tal, Seitental des Pandjir (G. 244).

C. squarrosus L. f. **alpinus** (C. B. CLARKE) RAYMOND, comb. nov. (Syn. C. aristatus ROTTB. f. alpinus C. B. CLARKE, JOURN. Linn. Soc. 21: 92 (1884). – **NE: Nuristan:** Tchitur Tal, zwischen Tchitur-Pass und Ramgel-Tal (KN. 1143).

Scirpeae.

Bulbostylis KUNTH.

B. puberula (POIR.) C. B. CLARKE – E: 'Kabul' (fide C. B. CLARKE).

Fimbristylis VAHL.

F. dichotoma (L.) VAHL (Syn. Scirpus dichotomus L., S. diphyllus RETZ., Fimbristylis diphylla (RETZ.) VAHL, F. annua R. et S.). – NE: Nuristan: An der Mündung Kurderbach-Petsch (N. 1951/839). – N: Mazar-i Sharif: Aqtscha (N. 1950/130). – SW: Dilaram, 1100 m (K. 3346). – SE: Kandahar: Arghandab (V. 1357). – E: Sarobi (V. 1184). Nidjrao, NE Sarobi, 2800 m (V. 2310). Am Kabul-Fluss bei Jallalabad, 600 m (G. 285, N. 1949/20).

Eleocharis R. BR.

1a.	Style-base apparently confluent with the summit of the achene, but of a
	different color and texture E. quinqueflora (HARTM.) SCHWZ.
b.	Style-base articulated with the achene 2
2a.	Annual species. Achene deep purple to shining black
b.	Perennial species 4
3a.	Spikelet 1,5–2 mm thick. Achene 0,5 mm long E. atropurpurea (RETZ.) KUNTH
b.	Spikelet 2–3 mm thick. Achene 1 mm long E. geniculata (L.) R. et S.
4a.	Basal scale solitary, spathiform, encircling the base of the spikelet
	E. uniglumis (Link) Schult.
b.	Basal sterile scales usually 2–3 5
5a.	Style-base elongate, longer than broad E. palustris (L.) R. et S.
b.	Style-base mitrate, broader than long E. mitracarpa STEUD.

The genus *Eleocharis* is a difficult one to deal with, and old views on several wide-ranging species have to be revised. The material from Afghanistan is not easy to sort out. Apparently, the most common species is *Eleocharis mitracarpa* STEUD., which turns out either as dwarf rigid plants or as tall plants with spongy wide culms, the spikes varying also in color from white to brown. Yet the mitriform style-base is unmistakable.

The line of demarcation between E. palustris and E. uniglumis is difficult to draw and the characters based on the number and shape of the sterile scales are not always reliable. ZINSERLING's treatment for the Flora URSS includes no less than 21 species in the E. palustrisgroup. One of his names has been retained as variety.

Eleocharis acicularis (L.) R. BR. and E. carniolica KOCH, reported by GILLI, FEDDES Repert. spec. nov. 64:214-215(1962) as occurring in Afghanistan are both based on specimens of E. quinqueflora (HARTM.) SCHWZ., the correct name for the well known E. pauciflora (LIGHTF.) LINK. Of the two specimens of Eleocharis palustris (L.) R. et S. that he mentions, one belongs to it, whereas the other represents E. mitracarpa STEUD., a frequent species in Southwestern Asia.

E. atropurpurea (RETZ.) KUNTH (Syn. Scirpus atropurpureus RETZ.). – Pakistan: Kurram: Shalizan, growing with Scirpus juncoides ROXB., in rice-fields (AITCH. 603).

E. geniculata (L.) R. et S. (Syn. Scirpus geniculatus L., S. caribaeus ROTTB.,

Eleocharis capitata R. BR., E. caribaea (ROTTB.) S. F. BLAKE). – Pakistan: Balouchistan (STOCKS).

E. mitracarpa STEUD. (Syn. E. crassa FISCH. et MEY., E. Kitamurana T. KOYAMA, Act. Phytotax. et Geobot. 17: 48, fig. 1 (1957), E. uniglumis (LINK) SCHULT. var. latior T. KOYAMA, Act. Phytotax. et Geobot. 17: 49, fig. 2 (1957), E. palustris auct. Fl. As. Med. p. p.). – E: Kabul: Lal-i Zarjangel, 2500 m (K. 3344). Sarobi (KITAMURA 61). Darulfanun bei Kabul (V. 2083). Koktscha Mullah bei Kabul (N. 1950/660). Tschaman Wazirabad bei Kabul, 1750 m (G. 276). Wazirabad (N. 1951/123). Zwischen Kabul und Tschaman (N. 1951/56). Kabul, 2000 m (Kz. 11449, KITAMURA 21). – C: Kamard, NW Doab, 2000 m (Kz. 13603). – Pakistan: Kurram Valley (AITCH.).

E. palustris (L.) R. et S. – **E:** Kabul: Aliabad bei Kabul (V. 143). Ghazni: In jugo Sardalu W Qarabagh, 2300–2500 m (RECH. 17324). Ad lacum Djalgah-Shahr-Kawat inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17867). – **C:** Bamian: Ad ripam lacus Band-i Panir prope Band-i Amir, 2800 m (RECH. 18370). Am Bamian-Fluss bei Schar-e Schak, 2320 m (G. 277).

E. quinqueflora (HARTM.) SCHWZ. (Syn. S. quinqueflorus HARTM., S. pauciflorus LIGHTF., E. pauciflora (LIGHTF.) LINK) VAR. meridionalis (ZINSERL.) RAYMOND, comb. nov. (Syn. Heleocharis meridionalis ZINSERL., Fl. URSS. 3: 69, 580 (1935). – NW: Chist, 1600 m (K. 3635). – C: Bamian: Band-i Amir, 2800 m (K. 2844). Band-i Amir, in ripa lacus, 2800 m (RECH. 18319). Farakulum, 2800 m (K. 2577). – E: Kabul: Paghman-Berge oberhalb Beg-tut, 2900 m (G. 284). Porande-Tal, Seitental des Pandschir bei Basarak, 1950 m (G. 283, N. 1950/669). Tscharasiah bei Kabul, 1750 m (G. 282). – Pakistan: Chitral: Im Yarkhun-Tal bei Mastuj, 2040 m (KN. 2047-b).

E. uniglumis (LINK) SCHULT. var. transcaucasica (ZINSERL.) T. KOYAMA, Act. Phytotax. et Geobot. 17: 48 (1957). – NW: Obeh, 1900 m (K. 3648). – SW: Sabst Pass, 10000 ft. (Kz. 13818). – SE: Zwischen Mokor und Kalat-i Ghilzai (KN. 154). – NE: Nuristan: Kulam (Munui), Kulam-Tal, 2200 m (KN. 1069). – E: Ghazni: Dahan-e Barikak, inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17983). Dasht-e Nawar (Naour), 3000 m (RECH. 17805). Kabul: Wiesen zwischen Kartetschar und Aliabad, 1780 m (G. 280). Tschaman Wazirabad, 1750 m (G. 278, N. 1951/124-b). Wazirabad (G. 912, 991). Bala Hissar, 1800 m (RECH. 16003). Zwischen Sarobi und Kabul (KITAMURA 54). Dehrasang bei Kabul, 1770 m (G. 279). W of Kabul (KITAMURA 28). Hauz-i Mahiha, 2500 m (K. 2483). – C: Koh-i Baba, 3100 m (K. 2668). Am Bamian-Fluss bei Schar-e Schak, 2320 m (G. 281). Inter Bulola et jugum Shibar, 2600–2800 m (RECH. 16761). Between Bulola and Doab (KITAMURA 58).

Eriophorum L.

E. comosum (WALL.) WALL. (Syn. Scirpus comosus WALL.). – NE: Nuristan: Wama, Seitental des Petsch, 1380 m (KN. 803). Between Seprigal and Wama (KITAMURA 32). – E: Kabul: In faucibus Tang-e Gharru, inter Kabul et Sarobi, 1100–1300 m (RECH. 16961). – Pakistan: From Thal to Kurram (AITCH. 316). In collibus supra Dargai, 400 m (RECH. 19623). Inter Saidu Sharif et Malakand, 800 m (RECH. 19618).

Scirpus L.

1a.	Spike solitary, terminal, small, 3–4 mm long, few-flowered. In loosely
	stoloniferous small tufts S. pumilus VAHL
b.	Spikelets several, variously arranged 2
2a.	Stem filiform, 3–20 cm high, with 1–3 small spikelets. Hypogynous bristles
	Ø. Annual S. setaceus L.
b.	Stem not filiform
3a.	Inflorescence terminal, subtended by 1 to several bracts
b.	Inflorescence pseudolateral, one of the bract erect as if continuing the stem 8
4a.	Inflorescence distichous, congested, subtended by 1 short bract S. planifolius
	GRIMM.
b.	Inflorescence umbellate, subtended by 1 to several leafy bract. Roots with
	internodes swollen in woody tubers
5a.	Spikelets 1-3 ovoid, straw-coloured, sometimes whitish. Glumes nearly
	glabrous S. af finis Roth
b.	Spikelets pale to deep brown. Glumes minutely pubescent
6a.	Spikelets narrowly cylindrical 1-2 cm long and less than 6 mm thick, in
	dense groups at the end of the rays S. tuberosus DESF.
b.	Spikelets ovoid, more than 6 mm thick 7
7a.	Achene white. Hypogynous bristles Ø S. Schmidii RAYMOND
b.	Achene straw-colored. Hypogynous bristles 3-6 S. maritimus L.
8a.	Spikelets 1–9 aggregated in a dense lateral head located at the middle of the
	often septate stem S. Roylei (NEES) PARKER
b.	Spikelets located below the top of the stem
9a.	Annual, in tufts. Spikelets 8–10 cm long S. juncoides Roxb.
b.	Perennial species 10
10a.	Hypogynous bristles Ø. Spikelets congested into crowded sphaerical heads
	S. Holoschoenus L.
b.	Hypogynous bristles usually present. Spikelets arranged otherwise 11
11a.	Stem triquetrous S. triqueter L.
b.	Stem terete, sometimes triquetrous below the inflorescence 12
12a.	Bristles soft and plumose S. litoralis SCHRAD
b.	Bristles harsh and scabridS. lacustris L. agg.

S. affinis ROTH (Syn. S. strobilinus ROXB., S. maritimus L. var. macer BOECK., S. maritimus L. var. affinis (ROTH) C. B. CLARKE, Bolboschoenus affinis (ROTH) DROBOV). – C: Kamard, 6000 ft. (Kz. 13602). – SW: Dilaram, 1100 m (K. 3345). – SE: 15 km E Kandahar (KITAMURA 36). – E: W of Kabul (KITAMURA 40 p.p.). – C: Doab, 5000 ft. (Kz. 13510, KITAMURA 33). – 'Afghanistan' (AITCH. 421, 788, 868).

S. affinis ROTH f. maritimoides (DROBOV) RAYMOND, comb. nov. (Syn. Bolboschoenus affinis DROBOV var. maritimoides DROBOV, Trav. Mus. Bot. Acad. Petersb. 16: 140 (1916), S. vulpinicolor KOYAMA). – E: W of Kabul (KITAMURA 40 p.p.).

In this form, the rays are elongated and the yellow spikes numerous whereas in Indian and Indo-Chinese specimens, the inflorescence is reduced to 1-2, nearly white, large spikes.

S. Holoschoenus L. – SW: Herat to Shin Dand, 1400 m (K. 3941). 60 km S of Herat, 1600 m (K. 2276). Dilaram, 1100 m (K. 3348). Tuki, 4500 ft., clumps along spring (Kz. 13117). – E: Ghazni: Sang-i Masha, 2500 m (RECH. 17464). Kabul: Zwischen Tang-i Saidan und Lallandar, 1810 m (G. 252). Gulbagh, Kabul, 1800 m (G. 251). – C: Doab (V. 520, KITAMURA 57).

S. juncoides ROXB. (Syn. S. erectus (non POIR.) plurim. auct.). – Pakistan: Kurram, Shalizan, 6000 ft. (AITCH. 420). – C: Kamard, 6000 ft., along stream (Kz. 13587). – E: Zwischen Tang-i Saidan und Lallandar, 1810 m (G. 252, 253). Gulbagh, Kabul, 1800 m (G. 251-b)

S. lacustris L. var. luxurians (MIQ) RAYMOND, comb. nov.

(Syn. S. Tabernaemontani GMEL. f. luxurians MIQUEL, Ann. Mus. Bot. Batav. 2: 143 (1856), S. Hyppoliti V. KRECZ., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS. 7 (I): 28 (1937), S. lacustris L. ssp. validus (VAHL) KOYAMA var. luxurians (MIQ.) KOYAMA, Can. Journ. Bot. 40: 927 (1962), S. Tabernaemontani plurim. auct. asiat.). – EN: Khanabad, 12000 ft., by stream (Kz. 12231). Rustak, 6000 ft. (Kz. 13138). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17907, 17913). Kabul, E Tscharasiah, 1740 m (G. 255, 256). Dehmasang, Dar-ul fanun, Gusargah, 1770–1780 m (G. 257, 158). Jallalabad (КIТА-MURA 59). Between Ghazni and Kabul (КIТАМИRА 25). – C: Doab, 1700 m, in spring stream (Kz. 13534). Kamardtal, am rechten Ufer des Surch, W Doab, 1620 m (G. 254). Kamard, 6000 ft., in stream (Kz. 13593, 13607). – Panjao, 2800 m (K. 2742). – Pakistan: Kurram Valley (AITCH. 312, 465, 689).

Var. *luxurians* seems to link var. *validus* (VAHL) KUEKENTHAL and var. *Tabernaemonlani* (GMEL.) DOELL. Closely related to each other, they more or less intergrade. Together with var. *tenuiculmis* SHELDON (Syn. *S. heterochaetus* CHASE), which is strictly North American, they are at best treated as varieties. KOYAMA (loc. cit. 926–928) has recognized 3 subspecies and 3 varieties in the *Scirpus lacustris* complex.

S. lacustris L. var. Tabernaemontani (GMEL.) DOELL (Syn. S. Tabernaemontani GMEL.). – N: Khanabad, 400 m (Kz. 12231). Rustak, 650 m (Kz. 13138). Kunduz: In paludosis fluvii Kunduz, 400 m (RECH. 16054). In valle fluvii inter Doshi et Doab, 800–1300 m (RECH. 16582). – C: Kamard, NW Doab, 2000 m (Kz. 13593, 13607). Doab, 1700 m (Kz. 13534).

S. litoralis SCHRAD. (Syn. S. subulatus VAHL, S. thermalis TRABUT, S. litoralis SCHRAD. var. subulatus (VAHL) CHIOVENDA (1928), KOYAMA (1958). – SW: Inter Farah et Seistan, 600 m (K. 4345). – SE: Pirzada, nr. Kandahar, 980 m (K. 2185). Zwischen Ghirishk und Hilmend-Fluss, 880 m (G. 259). – Pakistan: From Thal to Kurram (AITCH. 312, 465).

Even if BEETLE (Amer. Journ. Bot. 28:692 (1941) terms *Scirpus subulatus* VAHL "a clear-cut species from Afghanistan", it has been considered by various authors as identical to *S. litoralis* SCHRAD., of which *S. pectinatus* ROXB. is also a synonym. The only difference, if of any importance, resides in the culm, trigonous in *S. litoralis*, terete in *S. subulatus*, though slightly angled below the inflorescence. For another opinion, see TOWNSEND in Kew Bull. 1963: 415–418.

S. maritimus L. – N: Tuloqan (V. 594-a). – C: Kamard, 6000 ft. (Kz. 13602). Wazirabad (N. 1951/124-a). – SE: E von Kandahar, 1100 (Kn. 221). – E: Kabul: Paghman, 6000 ft. (Kz. 11450). Bala Hissar bei Kabul, 1740 m (G. 260). Darulaman bei Kabul (V. 85-a). Pandscheschah bei Kabul (N. 1950/665). Kotsche Mullah bei Kabul (N. 1950/661). Gulbagh bei Kabul, 1800 m (G. 261).

S. maritimus L. f. compactus (HOFFM.) P. JUNGE (Syn. S. maritimus L. var. compactus (HOFFM.) G. F. W. MEYER). – E: Kabul: Paghman, 6000 ft. (Kz. 11450). E von Tscharasiah, 1740 m (G. 264-a). Zwischen Dehmasang und Dar-ul fanun, 1780 m (G. 265). – C: Im Kamardtal W von Doab, 1620 m (G. 266).

S. maritimus L. f. monostachyus (G. F. W. MEYER) P. JUNGE (Syn. S. maritimus L. var. monostachyus G. F. W. MEYER). – E: Kabul: Sumpfwiese bei Dehmasang, 1770 m (G. 267). E von Tscharasiah, 1740 m (G. 264-b).

S. planifolius GRIMM. (Syn. Schoenus compressus L., S. compressus (L.) PERS., S. Caricis RETZ., Blysmus compressus (L.) PANZER, Nomochloa compressa (L.) BEETLE). - NW: Safedsang, 10000 ft., along stream (Kz. 13998). Sabz Pass, 10000 ft., spring trickle (Kz. 13817). – NE: Nuristan: Kulam (Munui), Kulam Tal (Scn. 102). Parun-Tal, zwischen Schtive und Paschki, 2300-2500 m (KN. 1381-b). Porande Tal, Seitental des Pandjir-Flusses bei Basarak, 1950 m (G. 268). - SE: Zwischen Mokor und Kalat-i Ghilzai, 1900 m (Kn. 155-b). - E: Ghazni: Distr. Malestan: Inter jugum Kotal-e Ketschru et pagum Miradina, NW Sang-i Masha, 3200 m (Rech. 17544). Ad lacum Djalgah-Shahr-Kawat inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17871). Okak, NE altoplanitiei Dasht-e Nawar (Naour), 3000 m (Rech. 17682). Ad lacum Sabzabt (RECH. 17918). In montibus Paghman supra Beg-tut, 2900 m (G. 270, 271). In montibus Paghman ad ripam rivuli supra Paghman, 2480 m (G. 269). Paghman, 2500 m (Kz. 12104). Wardak, SW Kabul (V. 828). - C: Bamian: Band- Amir, ad lacum Band-i Gholoman, 2800 m (RECH. 18474). Band-i Amir, in ripa lacus, substr. Sinter, 2800 m (G. 272, 273), 274; RECH. 18303). Inter Bamian et Band-i Amir, 2800-3000 m (Rech. 18176). Bamian (V. 2813). Koh-i Baba, in latere austro-orientali jugi Hadjigak, 3000 m (RECH. 18540). Unai Pass, 2800-3100 m, feuchter Rasen (G., V. 2108). Farakulum (K. 3339). Hauz-i Mahiha, 2900 m (K. 2492). Lal-i Zarjangal, 2500 m (K. 3341). - Pakistan: Chitral: Khot An, N of Mastuj, 1000 ft., between Turikho and Mastuj Rivers (ST. 2858). Mastuj, 2500 m (ST. 2484). Swat: Utror, 2500 m (Rесн. 19563).

S. planifolius GRIMM. var. **tenuis** (GILLI) RAYMOND, comb. nov. (Syn. Blymus tenuis GILLI, FEDDES Repert. spec. nov. 46: 48 (1939). – C: Bamian: Kamard-Tal, rechtes Ufer des Surch, W Doab, 1620 m (G. 275).

Scirpus planifolius is a very variable species. In the Flora of British India (660–661, 1894), C. B. CLARKE, under Scirpus Caricis RETZ., recognized var. brevifolia (DECNE.) C. B. CLARKE, var. sikkimensis C. B. CLARKE and var. dissita (DUTHIE) C. B. CLARKE. These taxa have never been discussed and with such a wide-ranging species, variation is to be expected.

The synonymy of this species is much involved. It was first described as *Schoenus compressus* L., but when transferred to *Scirpus*, the specifical epithet cannot be used, on account of the pre-existence of *Scirpus compressus* MOENCH (1794). See details in Hylander, Upps. Universit. Årsskr. 7: 92 (1945).

Young specimens of this protean species simulate various species of *Carex* Subgenus *Vignea* and are usually found in herbaria with *Carex divisa*. Judging from the specimens that have been turned to me for identification lately, the species is frequent in the Himalaya and extends to Yunnan. The following have been determined (in herb. Univ. Michigan): Kashmir, Ladak (KOELZ 6325, 6345); Lahul (KOELZ 587 p.p., 593, 620, 1029, 1303). Yunnan (these in herb. GRAY). Wei-si Hsien (WANG 67824). Li-kiang Hsien, 2300–2800 m (WANG 70542, 70589, 70892, 70922, 71318).

Nomochloa BEAUV. in LESTIBOUDOIS (1819), has been revived by BEETLE for the present species, whereas KUEKENTHAL cites Nomochloa compressa BEAUV. as a synonym of *Eleocharis* ovala (Bot. Jahrb. 75: 485 (1952).

The correct name of *Scirpus planifolius* MUHLENBERG (1817), an unfortunate later homonym, but a good North American species of Section *Baeothyron*, is *Scirpus verecundus* FERNALD.

S. pumilus VAHL (Syn. S. alpinus SCHLEICH., Trichophorum pumilum (VAHL) SCHINZ et THELL.). – NE: Nuristan: Oberes Ramgel-Tal bei Puschol, 2300 m (KN. 1107). – E: Ghazni: Ad lacum Sabzak, inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17931). Kabul: Paghman, 2500 m (Kz. 12105). – C: Bamian: Band-i Amir, in ripa lacus, 2000–2800 m (RECH. 16321, V. 2847). Farakulum (K. 2613). – Pakistan: Chitral: Prope Mastuj in valle Yarkhun, 2040 m (Kz. 2047-a). Oberes Ramgel-Tal in der Nähe von Puschol, 2300 m, nasse Wiesen (KN. 1107).

S. Roylei (NEES) PARKER (Syn. Isolepis Roylei NEES, I. lupulina NEES, S. quinquefarius Buch-Hamilton, S. lupulinus (NEES) ROSHEV). – E: Kabul (C. B. CLARKE). Scirpus Schmidii RAYMOND, stat. nov.

(Syn. S. compactus HOFFM. var. orientalis LITW. Herb. Fl. Ross. Fasc. 8, n° 2792 (1922) Bolboschoenus compactus (HOFFM.) DROBOV var. orientalis (LITW.)

ROSHEV., non Scirpus orientalis OHWI, Acta Phytotax. et Geobot. 1: 76 (1932).

E grege *Scirpi maritimi* L. – Rhizoma in speciminibus nostris deficiens sed probabiliter durum, lignosum et tuberiferum. Culmi 15–45 cm alti, glaucescentes, striati, trigoni, angulis alato-scabridi. Folia subbasalia 3–4 mm lata, culmo breviora, glaucescentia, vaginis longis brunneis numerosis partem inferiorem culmorum tegentibus. Spiculae numerosae sessiles, ovoideae, 6–8 mm longae, in capitulum hemisphericum 1 cm longum, 2 cm latum dense congestae. Bracteae 2, 3–6 cm longae, basi paulum dilatatae, carinatae, carina et marginibus scabrae, demum deflexae. Squamae concavae, 5 mm longae, late ovatae, dorso et marginibus ciliatae, papyraceae, castaneae, subtiliter rubro-lineatae, nervo medio incrassato praeditae, in aristam recurvam scabram prolongatae. Achenium 3 mm longum, rhomboideum, basi attenuatum, trigonum aut interdum planoconvexum, nitidum, eburneum, demum griseo-album, densissime cellulosum. Stigmata 3 (interdum 2). Styli basis incrassata. Setae hypogynae deficientes.

Afghanistan: E: Kabul: Kabul, Scirpo-Phragmiteta (Volk 69-a, 827, 832). – Persia: E: Khorasan: Bar, 1780–2350 m (Schmid 6288, Typus, G, Isotypus, W).

Scirpus compactus HOFFM. is merely a form of Scirpus maritimus L. with the rays of the normally umbellate inflorescence undeveloped. They often grow in the same colony. All species of section *Bolboschoenus* with a normal umbellate inflorescence exhibit a "congested" phase. On the other hand, S. Schmidii with an inflorescence normally without rays was wrongly associated with S. compactus HOFFM., the correct name of which is S. maritimus L. f. compactus (HOFFM.) P. JUNGE.

Scirpus Schmidii stands apart in the following manner: achene white, 3 mm long, no hypogynous bristles; bracts 2, reflexed; foliage glaucous. Its exact range is not known; it is probably scattered in the mountainous of parts of Southwest and Inner Asia.

S. setaceus L. (Syn. Isolepis setacea (L.) R. Br.). – E: Ghazni: In jugo Sardalu W Qarabagh, 2300–2500 m (RECH. 17321). Kabul: Paghman, Berge oberhalb Beg-tut (G. 249). Paghman, 2500 m (V. 2174, 2316, 2800-a, Акнтак). Im Porande Tal, Seitental des Pandjir, 2200 m (G. 247). Am Kabul Fluss zwischen Tangi Saidan und Lallandar, 1820 m (G. 246). – C: Bamian: Ad ripam fluvii Bamian, 2500 m (G. 248, V. K-236). Im Unai-Tal, 3120 m (G. 250). Koh-i Baba, 3100 m (K. 3342). – Pakistan: Kurram Valley, in glades at Pewarkotal (Агтсн. 965). Swat: Utror, 2500 m (RECH. 19592).

S. triqueter L. – NE: Kataghan: Qunduz, in paludosis fluvii Qunduz, 400 m (RECH. 16056). Qunduz (KITAMURA 29).

S. tuberosus DESF. (Syn. S. corymbosus FORSK., S. maritimus plur. auct. p.p.). – C: Doab, 1700 m (Kz. 13510).

Rhynchosporoideae.

Schoenus

Sch. nigricans L. – SW: Obeh, 1900 m (K. 3649). – E: Kabul: Salangtal N von Djabal Seradj, 1660 m (G. 286). Pandjir-Schlucht bei Gulbahar, 1700 m, feuchte Stelle an einem ENE-Hang, Gneiss (G. 287). In faucibus Tang-e Gharru inter Kabul et Sarobi, 1100–1300 m, substr. conglom. (RECH. 16968). – Pakistan: Kurram Valley (Антсн. 358).

Caricoideae.

Kobresia Willd. (Syn. Elyna Schrad.).

- 1a. Lower leaves of previous years' growth reduced to bladeless, often shining, sheaths

 2
- b. Lower leaves of previous years' growth with conspicuous green or dried up blades 4
- 2a. Inflorescence mostly compound, ovate-elliptic, 5–8 mm wide. Achene ovate, 2–2,5 mm long, beaked, shining. Coarse plant.....K. pamiroalaica Ivanova

b.	Inflorescence mostly spicate, narrow, 3–5 mm wide 3
3a.	Culms robust, rigid. Achene 3 mm longK. tibetica MAXIM.
b.	Culms subrigid. Achene 4 mm long K. capillifolia (DECNE.) C. B. CLARKE
4a.	Densely cespitose. Stigmas short
b.	Loosely cespitose or slightly stoloniferous. Stigmas very long
5a.	Dwarf plants, 2–6 cm high 6
b.	Slender plants up to 50 cm high 7
6a.	Inflorescence oblong, 1 cm long, brown. Perigynium oblong, 2–3 mm long,
	the apex attenuated in a beak K. persica KUEKENTHAL
b.	Inflorescence elliptic, 8-11 cm long. Perigynium oblong, 3 mm long, the
	apex obtuse K. pusilla Ivanova
7a.	Achene oblong, shorter than the perigynium K. stenocarpa (KAR. et KIR.) STEUD.
b.	Achene obovate, as long as the perigynium K. Royleana (NEES) BOECK.
8a.	Small plant. Perigynium split nearly to the base K. afghanica RAYMOND
b.	Taller plants, 40-50 cm high. Perigynium close nearly to the top, utriculi-
	form, scabrous
9a.	Inflorescence short, oblong, subtended by a long bract
	K. curvata (Boott) Kuekenthal
b.	Inflorescence elongate, the bract very short 10
10a.	Leaves 2 mm wide. Achene 5 mm long K. laxa NEES
b.	Leaves 3-6 mm wide. Achene 4 mm long K. sanguinea (BOOTT) RAYMOND

Kobresia afghanica RAYMOND, spec. nov.

Ser. nov. **Longestigmaticae** RAYMOND. – Stigmata longissima, testacea, indurata, persistentia, ad quam K. afghanica, K. laxa et K. sanguinea pertinent.

Planta 6 cm longa, gracilis, tenuiter stolonifera, basi fibrillis stramineis delicatulis praedita. Folia culmo breviora 1 mm lata plus minusve canaliculata. Inflorescentia spicata, 1,5–2 cm longa, oblongo-ovata. Spiculae propriae 5–6 sessiles, basilaribus distantibus, summis coarctatis. Bracteae squamiformes castaneae, late hyalinae, 3-nervis viridibus in aristam usque ad 1 cm longam evanescentibus praeditae. Prophyllum marginibus liberis sed anguste amplectens achenium lineari-oblongum brunneum, 3 mm longum, 0,75 mm latum. Stigmata 3 longissima, testacea, indurata, persistentia. Rhachilla elongata, ad 7 mm.

Afghanistan: E: Panjshir (VOLK 160, Typus, W). Bagrami, Nedjerau-Tal, 2800 m, an schattigen Felswänden und an schattigen Quellen (NEUBAUER 1951/331, VOLK 2346, 2348). Oestlich vom Nedschrabtal, zwischen Sarobi und Gulbahar (GILLI 294, 295).

Looking superficially like K. macrantha BOECK. of western Tibet, that has a crowded inflorescence, 2 stigmas and a lenticular achene loosely invested by the prophyllum. In K. afghanica, the inflorescence is more elongate, the very narrow achene is closely invested by the boat-shaped, open prophyllum and crowned by the three long persistent brick-red stigmas. See note under K. sanguinea (BOOTT) RAYMOND.

Biol.Skr.Dan.Vid.Selsk. 14, no. 4.

K. capillifolia (DECNE.) C. B. CLARKE (SYN. Elyna capillifolia DECNE., Kobresia scirpina (non WILLD.) AITCH., Elyna spicata (non SCHRAD.) BOISS., Kobresia capillifolia (DECNE.) C. B. CLARKE VAR. filifolia (TURCZ.) KUEKENTHAL. – NE: Nuristan: Minjan Pass, 12000 ft., in meadow (Kz. 12677). Auf einem Berg NNW von Kamdesch, 2800 m (G. 291). – Pakistan: Safed-Koh Range, on the tops of the hills from 11000 to 12000 ft. (AITCH. 230). Chitral: Ojhor, 36°04'N, 71°48'E, 12000 ft. (B. L. 863). Kiawas and Shendtoi, 11000 to 12000 ft. (AITCH. 410, 745).

The closely related *K. capilliformis* IVANOVA, with the achenes obovate, instead of elliptic, occurring frequently in the neighbouring Pamiro-Alaj district (sensu Fl. URSS), should be looked for confidently in Afghanistan.

K. curvata (BOOTT) KUEKENTHAL (Syn. Carex curvata BOOTT, Kobresia Royleana (NEES) BOECK. var. bracteata GILLI, FEDDES Repert. spec. nov. 64: 215 (1962).). – NE: Seitental der Pandjir-Schlucht bei Gulbahar, 1700 m (G. 292).

K. laxa NEES. – NE: Shingar, 2200 m, Porande-Tal, Seitental des Pandjir-Tales (G. 293). Nuristan: Kulam (Munui), im Kulam-Tal, 2150 m (KN. 1062-b). Brubruts im oberen Kantivo-Tal, 2500 m (KN. 947). – Pakistan: Chitral: Shokor Shal, 3600 m (WDB.). Drosh Gol, $35^{\circ}33'$ N, $71^{\circ}48'$ E, steep moist bank, 10500 ft. (B. L. 117). Bromboret Gol, $35^{\circ}41'$ N, $71^{\circ}38'$ E, edge of aquaduct, 6800 ft. (B. L. 649). Shishi Gol, E of Drosh, 7000 ft., on marshy ground (ST. 2379). Mastuj, Baroghill Track, Lasam, 9000 ft., at edge of stream (ST. 2951). Chitral, 5500 ft., on boggy ground (ST. 2534, 2536).

K. pamiroalaica IVANOVA (Syn. K. schoenoides (non STEUD.) AITCH.). – NE: Nuristan: Minjan Pass, 13500 ft., clumps (Kz. 12748). Mamgel Pass, Ost-Seite, im oberen Schuk-Tal nach Aterschuker, 3800 m (KN. 987). – Pakistan: Safed Koh Range, 11000–12000 ft. (AITCH. 301). Chitral: Chumarkhan Pass, E of Mastuj, 13000 ft., on open slopes (ST. 2926, 2927, 2928). Zwischen Dorrah Pass und Babur, Pass-Sattel, 4500 m (KN. 1536).

IVANOVA (l. c.) recognizes 5 species in the Kobresia schoenoides complex: K. sibirica TURCZ. (extending from the Urals through Arctic Asia to Olenek River and Tchukh Peninsula, south to Mongolia); K. Smirnovii IVANOVA (alpine regions of Altai, Tarbagatai and Dzungarian Alatau); K. tibetica MAXIM. (Himalaya, Tibet, Nan Mountains in C. China, and W. China); K. pamiroalaica IVANOVA (Pamiro-Alaj, W. Tian-Shan, Himalaya, Chitral, E. Afghanistan and W. Pakistan). The true K. schoenoides (C. A. MEYER) STEUDEL is restricted to the Caucasus and Asia Minor (Cilicia). To which should be added: K. hyperborea A. E. PORSILD (W. Arctic Canada, from the Mackenzie Delta, east to Boothia Peninsula) and K. macrocarpa CLOKEY (Mountains of Colorado, U.S.A.). The exact taxonomical position of the two American species, in regard to the five Asiatic ones, has still to be investigated. The first one seems to be identical to K. sibirica TURCZ.

IVANOVA'S monograph being absent from several botanical libraries, part of her treatment of Series *Sibiricae* is adapted here:

1a.	Mature achene shining	2
b.	Mature achene dull	3

2a.	Inflorescence mostly compound, ovate-elliptical, 5-8 mm wide
	K. pamiroalaica Ivanova
b.	Inflorescence mostly spicate, narrowly elliptical or cylindrical, 3–5 mm wide
	K. tibetica Maxim.
3a.	Female flowers provided with a perianth of small scales falling off with the
	2,5-3 mm long achene K. sibirica Turcz.
b.	Female flowers without a perianth 4
4a.	Achene 2,5-3 mm long; scales mostly oblong-ovate K. Smirnovii Ivanova
b.	Achene 3,5–4 mm long; scales mostly triangular-ovate
	K. schoenoides (C. A. MEYER) STEUDEL

Kobresia pamiroalaica apparently plays quite a part in the composition of pastures at high altitudes. STANIUKOVITCH has described from Eastern Pamir two types of wet association where this Cyperacea is involved. In the first type, Kobresia pamiroalaica and Carex pseudofoetida are dominant, with Poa tibetica, Potentilla multifida, Oxytropis hirsutiuscula, Taraxacum ceratophorum, Primula sibirica and Kobresia stenocarpa. At 4500 m of altitude, Kobresia pamiroalaica and Potentilla pamiroalaica are dominant, the other components of the association being Kobresia stenocarpa, Carex melanantha, Smelowskia calycina, Carex pseudofoetida, Artemisia rupestris, Cerastium cerastioides, Primula sibirica and Roegneria schugnanica. In both cases, Kobresia pamiroalaica occupies $60^{0}/_{0}$ of the space.

K. persica KUEKENTHAL (Syn. Kobresia Royleana (NEES) BOECK. var. humilis KUEKENTHAL, K. humilis SERGIANSKA). – C: Bamian: Koh-i Baba Kette, oberhalb des Sard-darra, 4000 m (G. 2900). Unai, 2900 m, Schneeboden (V. 1635).

K. pusilla Ivanova, Journ. Bot. Russ. 24: 496 (1939). – Pakistan: Chitral: Turikho River, Istar, 10500 ft., on short turf (STAINT. 2496).

A tentative determination, the material being immature.

K. Royleana (NEES) BOECK. (excl. syn. Kobresia stenocarpa C. B. CLARKE p.p. et Elyna stenocarpa KAR. et KIR.). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17918). Inter jugum Kotal-e Ketschru et pagum Miradina, NW Sang-i Masha, 33°25'N, 66°45'E, 3200 m (RECH. 17543). Kabul (fide C. B. CLARKE). – C: Koh-i Baba, 3100 m (K. 2656). Kobresia sanguinea (BOOTT) RAYMOND, comb. nov.

(Syn. Carex sanguinea BOOTT, Trans. Linn. Soc. 20: 137 (1846). - E: 'Afghanistan' (GRIFF. 6094, 6111).

I did not see GRIFFITH'S gatherings, but there is a good set of specimens in the GRAY Herbarium (Cambridge, Mass., U.S.A.) collected by R. R. STEWART at Murree, the only Himalayan locality known. With its very long brick-coloured persistent stigmas, it is closely related to *Kobresia laxa* NEEs and *K. afghanica* RAYMOND, and so aberrant in Subgenus *Indocarex*, that I have no hesitation to bring it into genus *Kobresia* and to create, in conformity with IVANOVA'S monograph, a new series to accommodate them.

K. stenocarpa (KAR. et KIR.) STEUDEL (Syn. Elyna stenocarpa KAR. et KIR., E. kokanica Regel, Carex paniculata (non L.) Regel, Kobresia paniculata MEINSH., K. Royleana KUEKENTHAL). – NE: Nuristan: Sanglich, 11500 ft., along spring (Kz. 12606). In jugo Mrami versus pagum Shtive, 3000 m (Kn. 1412). – C: Sumpfwiese im Sard Darra in der Koh-i Baba, 3350 m (G. 289). Unai-Pass, zwischen Kabul und Bamian, 3120 m (G. 288).

K. tibetica MAXIM. (Syn. K. Littledalei C. B. CLARKE, K. capillifolia (DECNE.) C. B. CLARKE VAR. tibetica KUEKENTHAL, K. schoenoides (non Steudel) auct. p.p.). – **Pakistan: Chitral:** Khot An, N of Mastuj, between Turikho and Mastuj Rivers, on rock ledges, 13000 ft., in tufts (ST. 2844).

Carex L.

1a.	Spikelets single, terminal. Perigynia subulate with an exserted rhachilla. 2
b.	Spikelets several
2a.	Perigynia 3-5 mm long C. microglochin WAHLENB.
b.	Perigynia 7–10 mm long C. parva NEES
3a.	Spikelets all bisexual 4
b.	Spikelets male, female, androgynous or gynaecandrous
4a.	Rhizome long-creeping
b.	Rhizome short-creeping or cespitose 12
5a.	Stem very slender, 1–1,25 mm in diam. Perigynia 4 mm long, barely
	winged, nerveless, castaneous. Achene nearly quadrate C. austro-afghanica
	RAYMOND
b.	Stem coarser. Other characters not linked
6a.	Spikelets few in a dense congested head. Perigynia more or less inflated.
	Sand-binding species with numerous minute rootlets
b.	Spikelets more numerous. Perigynia plano-convex
7a.	Perigynia strongly inflated, reddish, up to 18 mm longC. physodes M.B.
b.	Perigynia subinflated, brown, 3,5 mm long C. maritima GUNNER.
8a.	Perigynia membranaceous, faintly or obsoletely nerved. Spikelets congested
	in a globose head
b.	Perigynia coriaceous, strongly nerved, with the margin thickened. Spikelets
	subcongested in an oblong or oblong-ovate head 10
9a.	Stem 6–20 cm high, subcurved. Spike about 1 cm long. Perigynia with smooth
	margin C. pseudofoetida KUEKENTHAL
b.	Stem 40-60 cm high, erect. Spike 1,5-3 cm long. Perigynia with scabrid
	margin from the middle up to the beak C. vulpinaris NEES
10a.	Rhizome slender, bearing at irregular intervals tufts of sterile leaves and
	floweing stems. Perigynia 3-3,5 mm long, hidden by the scales. Spikelets
	densely congested (laxely in some varieties)C. stenophylla WAHLENB. s. l.
b.	Rhizome coarse. Inflorescence often lobate 11
11a.	Perigynia parchment-like, 3,2–4 mm long, nerved, passing into a scabrous
	short break C. pycnostachya KAR. et KIR.

20

b.	Perigynia coriaceous, 3,5–4 mm long, nerved, contracted into a scabrous
	beak С. coarcta Воотт.
12a.	Perigynia plano-convex, membranaceous, green, often turning brown 13
b.	Perigynia dorsally tuberose-convex, ventrally subconvex, coriaceous 15
13a.	Spikelets small, very numerous in an elongated continuous spike
	C. nubigena D. Don
b.	Spikelets bigger
14a.	Spikelets all simple. Perigynia 5-6 mm long, ovate, contracted at base
	C. polyphylla KAR. et KIR.
b.	Basal spikelets compound. Perigynia 4-4,5 mm long, with a round or
	subcordate base C. subvulpina P. SENAY
15a.	Perigynia ovate-elliptical, plano-convex, 2,5-3 mm long, finely nerved.
	Densely cespitose C. Wendelboi NELMES
b.	Perigynia ovate, dorsally tuberose-convex, 2,5 mm long, striate only at base.
	Laxely cespitose C. diandra Schrank var. major (Koch) Raymond
16a.	Perigynia with a short beak 17
b.	Perigynia with a rather long beak
17a.	Female spikelets densely flowered 18
b.	Female spikelets laxely flowered. Perigynia more or less hairy 25
18a.	Perigynia 2,5 mm long, biconvex, orbicular. Stigmas 2, densely cespitose
	С. orbicularis Воотт
b.	Perigynia trigonous. Stigmas 3 19
19a.	Lower bract foliaceous. Terminal spike often gynaecandrous 20
b.	Lower bract squamiform. Terminal spike male. Perigynia coriaceous,
	glabrous. Scales rufous C. turkestanica REGEL
20a.	Perigynia 3–3,5 mm long. Scales dark, longer than the perigynia. Strongly
	stoloniferous C. melanantha C. A. MEYER
b.	Perigynia less than 3 mm long. Scales shorter than the perigynia. In dense
0.4	tutts, the freely forking rhizome intricate
21a.	Perigynia 2,2 mm long, beakless. Stems 8–12 cm long C. pseudobicolor BOECK.
b.	Perigynia with a short beak
22a.	Culms 40–45 cm long. Leaves 2–3 mm wide. Perigynia 1,75 mm long only,
h	Designing housing to block supple towards head
D. 920	Perigyma brownish to black-purple towards beak
20a.	Beak of the perigyma 0,5 mm long
D. 949	Leaves 2.3 mm wide. Stem 20.45 cm long. Derigunia 3 mm long
44a.	Leaves 2-5 min whee, stem 50-45 cm long, rengyma 5 min long,
h	Leaves 1-1 2 mm wide Stem 3-12 cm long Perigynia 2.75 mm long
D.	C trieniculata Rosev
259	Spikelets subradical Perigynia oboyate-oblong 4-5 mm long shortly
20a.	beaked C Halleriana Asso
	beared internet and Asso

b.	Spikelets not subradical
26a.	Leaves 1 mm wide. Female spikelets 7–14 mm long, subcylindrical.
	Perigynia narrowly ellipsoid, 4,5–5,25 mm long C. chitralensis NELMES
b.	Leaves 1-2 mm wide. Female spikelets 10-20 mm long, cylindrical.
	Perigynia obovate-oblong, 4 mm long C. cardiolepis NEES
27a.	Leaves not septate-nodulose
b.	Leaves septate-nodulose
28a.	Scales dark-coloured 29
b.	Scales not dark-coloured
29a.	Bracts sheathless. Utricles 3,5–4 mm long, yellowish-green, nerved with a
	long bidentate beak. Stoloniferous. Culms 30-60 cm long C. psychrophila NEES
b.	Bracts sheathing
30a.	Leaves narrow. Spikelets 3-6, the 1-3 upper ones male, the lateral one
	female, linear-cylindrical, slender, often pendulous 31
b.	Leaves wider. Phyllopodic species. Spikelets 3-6, the terminal one gynae-
	candrous or more rarely male, all subclavate, rather stout and often
	nodding
31a.	Old sheaths desintegrating into reticulate fibres. Utricles 6-7 mm long,
	hispidulous, plurinerved. Leaves curled at tip C. plectobasis V. KRECZ.
b.	Old sheaths desintegrating into parallel comose fibres. Utricles 4-5 mm
	long, appressed-hispidulous, delicately nerved. Leaves stiffish, not curled at
	tip C. stenocarpa Turcz.
32a.	Spikelets fasciculate, ovate, 0,5-2 cm long, on thick, erect, short peduncles,
	dark-coloured except the tip of the scales and the tip of the partially
	scabrid-margined utricles C. oxyleuca V. KRECZ.
b.	Spikelets subfastigiate on long nodding slender peduncles
33a.	Terminal spike male 34
b.	Terminal spike gynaecandrous 35
34a.	Spikelets 3–5, the female 2–3,5 cm long, 1 cm wide, clavate-cylindrical.
	Perigynia 5–5,5 cm long. Stem 20–60 cm long C. Griffithii BOOTT
b.	Spikelets 4, the female ones 2,5–3,5 cm long, 5 mm wide, cylindrical.
	Perigynia 4 mm long. Stem 50–65 cm long C. Gilesii NELMES
35a.	Spikelets $3-5$, the female ones $2,5-5$ cm long, $0,6-0,8$ mm wide, clavate-
	cylindrical. Perigynia 5 mm long, cinnamon. Stem 60–100 cm long
	C. Oliveri BOECK.
b.	Spikelets $3-5$, subfastigiate, the females $2-3$ cm long, $0,4-0,6$ mm wide,
	clavate-cylindrical. Perigynia 5–6 mm long, dark purple. Stem 20–50 cm
9.0	long C. nivalis Boott
36a.	Perigynia ovate, 2–2,5 mm long, with a short conical beak. Spikelets
	narrowly linear. Leaves narrow. In delicate dense tutts, up to 60 cm high
	Deine in here and the interview of the second secon
b.	Perigynia longer, not ending in a short conical beak

37a.	Perigynia 5–7 mm long, plano-convex, yellowish, ending in a long bidentate
	curved beak, coriaceous, as well as the leaves. Stem 5-7 cm long
	C. secalina Willd. var. alpina Kuekenthal et Bornmueller
b.	Perigynia membranaceous 38
38a.	Spikelets 4-6, congested (sometimes with a distant lower one). Perigynia
	3,5 mm long, yellowish-green. Lower bract much overtopping the inflores-
	cence. Stem 10-30 cm high C. philocrena V. KRECZ.
b.	Spikelets all distant
39a.	Perigynia 3 mm long, glaucous-green, strongly ribbed, ending in a short
	conical beak. Stem 15–60 cm high C. diluta M. B.
b.	Perigynia 4 mm long, yellowish-green, often with darker markings, multi-
	nerved, ending in a short flat scabrous beak. Stem 30-60 cm high C. distans L.
40a.	Perigynia 3,5–4 mm long, densely hirtous, several-nerved, the base
	spongiose, ending upwards in a deeply bidentate beak. Stem 30–60 cm high
	C. fedia NEES
b.	Perigynia glabrous
41a.	Perigynia 5–5,5 mm long. Spikelets 4,5 cm long, 1,5 cm wide
	C. pamirensis C. B. CLARKE
b.	Perigynia 3–4 mm long. Spikelets 2–3 cm long, 0,5 cm wide
	C. songorica KAR. et KIR.

Carex alsia RAYMOND, spec. nov.

Sect. Atratae KUNTH Subsect. Alpinae KALELA – Rhizoma caespitosum, radicibus numerosis, intricatum, breve stoloniferum. Culmi numerosi, 40–45 cm alti, obsolete trigoni, striati, graciles sed rigidi. Folia basalia et subbasalia glaucoviridia culmis breviora, 15–20 cm longa, 2–3 mm lata, longe acuminata, apice margine spinulosa, basi vaginis cinnamomeis mox fibrillosis dense investa. Spiculae 3 sessiles, dense congestae (saepe quarta remotiuscula bracteata), 6–10 mm longae, ovatae, terminali androgyna, lateralibus femineis. Bracteae 6–20 mm longae, spinulosae, ore atratae, aut totae nigrescentes, haud vaginantes. Utriculi 2,5 mm longi, obovati, subinflatotrigoni, celluloso-reticulati, enerves, basi stipitati, in rostrum breve conicum oblique sectum atrum abrupte contracti. Squamae ovatae, atratae, acuminatae, clare carinatae, 2 mm longae. Nux subovata, trigona, stipitata, 1,75 mm longa, dense puncticulata, pallide flava. Basis styli aequalis persistens. Stigmata (3), 2 mm longa.

Pakistan: Chitral: Khotan, N of Mastuj, between Turikho and Mastuj Rivers, alt. 13000 ft., on rock ledges, anno 1958 (STAINTON 2839, Typus, W).

Another apparently good segregate of the 'C. alpina' group, that seems to link the Atratae and the Alpinae and distinct from all its relatives in several minor characters. The whole group, well represented in Western North America and Central Asia, is in need of a serious revision. Examination of several types abroad shows for one thing that most species have been described on very poor material. Working the part of the Cyperaceae for Symbolae Afghanicae has given me the opportunity to write new descriptions of such neglected – but apparently perfectly recognizable species – as C. trispiculata BOECK. and C. pseudobicolor BOECK., to mention only these two. During recent years, I had access to modern and perfectly mature material of several members of this essentially alpigenous group of species, with the hope of eventually revising the whole section.

Carex austro-afghanica RAYMOND, spec. nov.

Sect. Arenariae KUNTH – Affinis C. accrescens OHWI (Syn. C. pallida C. A. MEYER, non SALISB.). – Rhizoma deficiens, sed probabiliter repens. Culmi erecti gracillimi 25–30 cm alti, 1–1,25 mm diam., trigoni, angulis apicem versus scabriusculi. Folia subbasalia, pauca, culmo breviora, 15–25 cm longa, 2 mm lata, glaucescentia, longe vaginantia, vaginis pallide castaneis striatis mox fibrillosis. Spiculae 4–7 ovatae androgynae, 8–10 mm longae, contiguae spicam subcongestam globoso-elongatam 1,5–2,5 cm longam formantes. Bractea amplectens squamiformis scabroso-aristata, ad 7 mm longa. Utriculi squamas aequantes, ovati, 4 mm longi, plano convexi, enervii, vix alati, pallide castanei, basi stipitati, in rostrum ca. 1 mm longum bidentatum spinulosum ore hyalino contracti. Squamae ovatae castaneae acuminatae, carina spinulosa, margine hyalina. Nux fere totum utriculum explans 1 mm longa, quasi quadrata, basi stipitata, luteola, puncticulata, basi styli persistentis coronata.

N. Afghanistan, 6.5.1938 (MEINERTZHAGEN, Typus, BM).

A remarkable plant, yet known only from this gathering and lacking the underground parts, quite important in Subgenus *Vignea*. The slender habit suggests at first look *C. accrescens* OHWI, of Northern and Eastern Asia, but its leaves are narrower and its glabrous perigynia nerveless. The nearly quadrate achene is quite unusual.

C. cardiolepis NEES – NE: Nuristan: Gegenüber Aterschuker, NW-Hang, Horst im Buschwald, 2300 m (KN. 1023). Zwischen Mum und Aspit im Kantiwo-Tal, im lichten Zedernwald, 2400 m (KN. 901). Berg NNE von Kamdesch, 2700–2800 m (G. 334, 335). – E: Waziri, Zedernwald, 2400 m (V. 2533). Pakistan: Kurram Valley (AITCH. 418, 1244). 'Afghanistan' (GRIFF. 6072).

Carex chitralensis NELMES, Nytt Mag. f. Bot. 1: 22, fig. 10 (1952).

Cespitose, the freely stoloniferous horizontal rhizomes very slender, 1 mm in diam., and covered with reddish scales. Stems 15-25 cm long, erect or recurved, the base thickened by fibrous sheaths and reticulate fibrous remains of sheaths. Leaves subbasal, 1 mm wide, mostly shorter than the stems, recurved and circinnate at tips, longly sheathing, the sheaths whitish. Spikes 2-3 (4), the lower one more or less distant; terminal one staminate, 1,25-2 cm long, 2-3 mm wide, cylindrical or subclavate; lateral ones pistillate, 7-14 mm long, 3-5 mm wide, densely flowered, more or less ovoid, the upper ones subsessile. Bract sheathing shorter than the inflorescence. Perigynia 4,5-5,25 mm long, 1-1,5 mm wide, elipsoid, trigonous, densely white-hispidulous, passing into a bidentate barely marginate beak marked on the back by a red patch. Scales 3,75-4,75 mm long, oblong-ovate, cymbiform, transparent, reddish with a wide hyaline margin. Achene 3 mm long, with a definite stipe and a definite beak of same length, 1,25 mm. Stigmas 3.

Pakistan: Chitral: Barum Gol, wet slope above Shokor Shal, E. side of Main Barum Glacier, c. 3600 m, 23.7.1950 (WENDELBO, Typus, OSLO, Isotypus MTJB). Pakistan: Hazara Distr.: Murree Hills, Dsunga Gali, steep slopes along pipe-line trail, c. 8000 ft., locally common in rock crevices (WEBSTER & NAZIR 5710, BM).

C. chitralensis NELMES var. excedens RAYMOND, var. nov.

Pergracilis, ad 50 cm alta, densissime caespitosa; spiculis masculinis saepe rotundatis; ceterum ut in var. *typica*.

Pakistan: Chitral: Shah Jinali Pass, N of Mastuj, 14000 ft., on dry stony rock, 1.8.1958 (STAINTON 3043, Typus, BM). Ziarat, Lowarai Pass, 7000 ft., in tufts on rock ledges (STAINTON 2321). Birir, 35°38'N, 71°44'E, dry cliff facing east, abundant at 10000 ft. (Bowes Lyon 681, BM). Birir, crevices northern slope, 8500 ft. (Bowes Lyon 694, BM).

An interesting species related to *C. cardiolepis* NEES, of a very limited range: Chitral and NW Pakistan, a frequent distributional pattern in the Himalayan flora.

C. coarcta BOOTT (Syn. C. curaica KUNTH var. coarcta BOOTT, C. divisa (non HUDS.) BOISS., C. curaica (non KUNTH) BOISS., C. divisa HUDS. var. coarcta (BOOTT) T. KOYAMA). – NW: Sauzak, 2000 m (K. 2197). Obeh, 1700 m (K. 3785). – E: Laghman: Daulatshah, 2300 m (Kz. 11659). Wazirabad bei Kabul, 1750 m (N. 1951/125-b, G. 311). Aliabad bei Kabul (G. 314, V. 11-a, 896). Zwischen Kartetschar und Aliabad, 1780 m (G. 313). Guzar Gah bei Kabul (N. 1951/156). E von Tscharasiah, 1740 m, Kabul (G. 310). Paghman, W Kabul, 2500 m (Kz. 12073). Kabul (Kz. 11471, V. 146, 450, 1882). 'Afghanistan' (GRIFF. 6079). – C: In valle Kamard W Doab, 1580 m (G. 309).

C. diandra SCHRANK VAR. **major** (KOCH) RAYMOND, comb. nov. (Syn. C. teretiuscula GOOD. VAR. major KOCH, Syn. Fl. Germ. et Helv. 751 (1837), C. diandra SCHRANK f. major (KOCH) KUEKENTHAL). – **NE: Nuristan:** Oberes Ptsigela-Tal, 15 km N Kantivo, zwischen Steinen, 2500 m (KN. 921). Brubruts im oberen Kantivo-Tal, am Bach in dichten Horsten zwischen Steinen, 2500 m (KN. 945).

C. diluta M. B. (Syn. *C. Aitchisonii* ВОЕСК., *C. fissirostris* (non BALL.) АІТСН.). – NW: Obeh, 1700 m (K. 3784). – SW: Herat, 1000 m (K. 3878). – E: Im Panjshir-Tal bei Gulbahar nächst Charikar (G. 341-a, V. 250, 528-c). – C: Am Schumbol-Fluss bei Bulola, 2200–2300 m (G. 342, RECH. 16753). Band-i Amir, 2800–2900 m (G. 343, RECH. 18302). Panjao, 2700 m (K. 2725). Doab: In valle Salang inter Jabal Seradsch et Laghman, 1680 m (G. 340). In valle Kamard W Doab, 1620 m (G. 339). Doab, 1400 m (K. 2883). Ghorat: Qala Qansi (Tschaktscharan), ad ripas fluvii Herirud, 2200 m (RECH. 18843). – Pakistan: Kurram Valley (АІТСН. 313, 508). – Pakistan: Chitral: 5500 ft., damp rocks (ST. 2535).

C. distans L. - North Afghanistan, 2500 ft. (M.).

Specimens of *Carex distans* from Iran and Afghanistan strongly simulate *C. laevigata* J. Sm. More material is needed for a proper appraisal.

C. fedia NEES (Syn. C. Wallichiana PRESC. ex WALL., C. hirta (non L.) Воеск.). - E: Sarobi, Quellsumpf (V. 2604). - Pakistan: Shinnak, Kurram Valley (Антсн. 33).

Carex Gilesii NELMES, Kew Bull. 1939: 306 (1939).

Stoloniferous. Stem 50–65 cm long, triquetrous, leafy at base only, smooth, surrounded by a few leafless sheaths. Sterile leaves bunched 4–7 mm wide, much shorter than the stem, longly attenuate, mostly flat. Spikes 4, the 2 superior ones male, 1,5–2 cm long, the 2 others female, 2,5–3,5 cm long, 5 mm wide, all peduncled, the basal one much more so, the 3 others more or less fastigiate, cylindrical, densiflorous, more laxely flowered at the base, nodding. Inferior bract briefly foliaceous, shorter than the spikes, longly sheathing, the upper ones much reduced. Perigynia 4 mm long, 2 mm wide, elliptic-obovate, papyraceous, whitish at the base and tinged with purple at the tip, compressed, nerveless, passing rapidly to a short whitish slightly bilobed, flexuous, smooth beak. Scales narrowly oblong, 3,5–4 mm long, acuminate, brown purple, the pale midrib excurrent. Achene stipitate, occupying the lower part of the perigynia. Stigmas 3 more or less included.

Pakistan: Chitral: Oihor Gol, 36°04'N, 71°48'E, in running water, 11000 ft. (Bowes Lyon 821). Golen (Krui Ults), 36°01'N, 72°10'E, 13500 ft., moist soil among large boulders (Bowes Lyon 131). Ishporili Gol, S of Mastuj, 14000 ft. (STAINT. 3125). Jamishi Ghochar, 4300 m (WENDELBO). Medial moraine of Main Barum Glacier, 3400 m (WENDELBO). Och Anzog, 3600 m (WENDELBO). Camp 2, 4500 m (WENDELBO).

C. gracilenta BOOTT (Syn. C. alpina SW. var. infuscata (NEES) BOOTT p.p., C. alpina SW. ssp. infuscata (NEES) KUEKENTHAL var. gracilenta (BOOTT) KUEKENTHAL, C. dimorpha BOECK., non BROTERO). – Pakistan: Chitral: Drosh Gol, 35°33'N, 71°48'E, 10000 ft., moist hillside (B. L. 166).

C. Griffithii BOOTT (Syn. C. nivalis BOOTT f. Griffithii (BOOTT) KUEKENTHAL). – NE: Nuristan: Minjan Pass, 13000 ft. (Kz. 12747). Ibidem, 13500 ft. (Kz. 13500). – C: Koh-i Baba (GRIFF. 7814). – Pakistan: Chitral: Golen (Krui Uts), 36°01'N, 72°10'E, moist soil among large boulders, 13500 ft. (B. L. 130).

C. Halleriana Asso (Syn. C. gynobasis VILL).. - E: 'Kabul' (C. B. CLARKE).

Carex infuscata NEES (Syn. C. alpina SW. var. infuscata (NEES) BOOTT p.p., C. alpina SW. var. infuscata (NEES) KUEKENTHAL p.p., excl. syn. C. trispiculata BOECK.), descr. emend.

In dense tufts, the intricate freely forking rhizomes covered with fibrous remains of old sheaths. S tems 30-45 cm high, slender, sharply trigonous, sheathing, the base thickened by accumulated old drab fibrillose sheaths. Leaves basal, much shorter than the stems, glaucous-green, 2-3 mm wide, long acuminate, finely setulose at tip. Spikes 2-3 approximate (or 4 with the lowest one remote), sessile, the terminal one 6-7 mm long, androgynous, the lateral ones slightly smaller, female. Bracts much longer than the spikes, barely sheathing, spinulose, blackish at mouth. Perigynia 3 mm long, ovate, tumid-trigonous, pale yellow, finely cellulose-reticulate, slightly stipitate, the stipe dark red, the two lateral nerves well marked, the others faintly so in the lower half, ending into a conical slightly bidentate, black-girdled beak. Scales

ovate, dark red, the mid-vein paler and spinulose, much shorter than the perigynia. Achene 2 mm long, sharply trigonous, pale yellow, the base of the style persistent. Stigmas 3, slender, exserted.

NE: Nuristan: Im Kantiwo-Tal zwischen den Dörfern Kantiwo und Brubruts, 2200–2460 m (KERSTAN 932). Im Kantiwo-Tal oberhalb Brubruts, 2460 m (KERSTAN 948). Drudo Pass, zwischen Aschkun und Petsch-Tal, 3280 m (KERSTAN 1237-c). Im Kulam-Tal beim Dorf Kulam (Munui), 2200 m, auf nassem Schutt (KERSTAN 1055). Shabul Gul (KITAMURA 40, 46). – E: Kabul: Paghman Tal, am Ufer des Paghman-Flusses, 2540 m (GILLI 329). In den Bergen von Paghman oberhalb Beg-tut, 2900 m (GILLI 331). In Schluchten östlich des Nedschrab-Flusses gegen Schechan, 3100–3200 m (GILLI 330, 332). – Pakistan: Chitral: Chumarkhan Pass, E of Mastuj, on marshy ground, 13000 ft. (STAINTON 2921).

C. Karoi FREYN - NE: Nuristan: Sanglich, Minjan Pass, 3800 m (Kz. 12610). - Pakistan; Chitral: Tirich Gol, 36°25'N, 72°15'E, shady soil beneath willows, 11000 ft. (B. L. 1068).

C. maritima GUNNER. (Syn. C. incurva LIGHTF.). – E: 'Afghanistan' (GRIFF. 89).
C. melanantha C. A. MEYER – NE: Nuristan: Minjan Pass, 12000 ft. (Kz. 12662).
– Pakistan: Chitral: Baroghil Pass, 12500 ft., at edge of marsh (St. 2970).

In addition to *C. melanantha* itself, I have been able, recently, to examine mature material of *Carex praeclara* NELMES, *C. Moorcroftii* FALC., *C. sabulosa* TURCZ. and *C. leiophylla* MACKENZIE, closely-related, mostly sand-binding, species inhabiting high plateaux of Central Asia, except the last one which has been described from Yukon.

Carex praeclara NELMES, of Tibet, with its large scales, stands apart. KUEKENTHAL treated C. Moorcroflii and C. sabulosa as varieties of C. melanantha. On the other hand, KRECZETOWICZ, who wrote the treatment of Carex for the Flora URSS and who, following the Komarovian school, raised most geographical variants of wide-ranging species to specifical rank, recognized C. melanantha C. A. MEYER, a closely-related segregate, C. melanthaeformis LITW., but wrongly considers C. Moorcroftii FALC. a synonym of sabulosa TURCZ. of a much wider range. The three were placed by him in a cycle Orthocranion, a subsectional category, the description of which is written in Russian.

Mr. J. A. CALDER, Ottawa, has provided me, a few years ago, with a good sheet of *Carex leiophylla* MACK. collected at Carcross, the type-locality, cowering large tracts of sand, as well as a photograph of the type (NY). The conclusion of my examination is that *C. praeclara*, *C. melanantha*, *C. Moorcroftii* and *C. sabulosa* are distinct species, but that *C. leiophylla* is identical with *C. sabulosa*.

It is of great phytogeographical interest, that the more we know about the flora of Alaska and Western Canada, the more we find species with a more or less wide area in Asia, transgressing into Western Canada. Outside of *C. sabulosa* TURCZ. (Syn. *C. leiophylla* MACK.), I may add some other examples taken amongst the *Cyperaceae: Carex Franklinii* Boott (Syn. *C. macrogyna* TURCZ., *C. misandroides* FERN.), *C. eleusinoides* TURCZ. (Syn. *C. kokrinensis* A. E. PORSILD) and *Kobresia sibirica* TURCZ. (Syn. *K. hyperborea* A. E. PORSILD). This floristic pattern in our northern flora seems to me more frequent then first suspected.

Several other species of section *Atratae* need revaluation. Essentially alpine species, they are found growing as high as 18000 ft. of alt. in Central Asia. In contrast with Europe, where few species are known to occur, Asia and Western North America harbor a host of them, 30 species alone in America and as many in Asia. Most of these are 'good' species but the problem

with them is that the type is usually poor, either too young or too old, and actual collections are often not better, not mentioning that in herbaria they are, as a rule, wrongly determined.

C. microglochin WAHLENB. - NE: Nuristan: Minjan Pass, 12000 ft., in meadow (Kz. 12676).

C. nivalis BOOTT – NE: Nuristan: Mranu Pass gegen Shtive, 2000 m (KN. 14080. – E: Kabul: Paghman-Berge, N von Kotal-e Kotandar, 4300 m (G. 336). Paghman-Tal (G. 337, N./1950/663). – C: Koh-i Baba, oberhalb Sard Darra, 4320 m (G. 338). – Pakistan: Chitral: Oihor Gol, 11000 ft., $36^{\circ}04'$ N, $71^{\circ}48'$ E (B. L. 821). Baroghil Pass, 12000 ft., on boggy ground (ST. 3025). Rosh Gol, NE of Tirich Mir, 12000 ft., beneath slabs at edge of stream, in tufts (ST. 2830).

C. nubigena D. Don - 'Afghanistan' (fide Fl. URSS., 9: 194 (1946).).

C. Oliveri BOECK. (Syn. C. nivalis BOOTT f. cinnamomea KUEKENTHAL). – NE: Nuristan: Minjan Pass, 13500 ft., clumps (Kz. 12747). – E: Kabul: Paghman, 3500 m, Cousinia-Bestand (V. 932). Mittleres Paghman-Tal, am Bach (N. 1950/663). – Pakistan: Kurram Valley (Алтсн. 1242).

A characteristic species of limited range growing at 3000 m of altitude in Afghanistan and Pamiro-Alaj, Schugan Mountains. In Karakorum, the closely related *C. luteo-brunnea* NELMES (Syn. *C. lepus-aetatis* KOYAMA).

C. orbicularis BOOTT - NW: Sangcharak: Safedsang, 3300 m (Kz. 14013-a). -N: North-Afghanistan (M.). - NE: Nuristan: Mamgel-Pass bei Idsebruts, 3300 m (KN. 986). - E: Ghazni: Ad lacum Djalgah-Shahr-Kawat inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17883). Ad lacum Sabzab inter Okak et Behzud (Diwal Kol), 2800 m (RECH. 17922). Parwan: In declivibus orientalibus jugi Shibar, 2500 m, in prato humido prope pagum Shibar (Rесн. 16876). Kabul: Schakar-darra, Paghman-Berge, 2500-2900 m (G. 323, 327). Paghman-Berge, 2500 m, nasse Wiesen (Kz. 12101, V. 363). Ibidem, 3500 m (V. 932). Paghman, 17 miles W Kabul (CH.-M.). Kalai Surkh (N. 1950/662). Kabul, 7000 ft., swamp (M.). - C: Unai Pass, 2800 m (V. 1656). Bulola, 2200 m (RECH. 16738). Kamard-Tal, W von Doab, 1620 m (G. 326). Am See Band-i Gholaman, Band-i Amir, 2800 m (RECH. 18475). See-Ufer von Band-i Amir, 2800 m (G. 324, 328, Rech. 18300, 18301, V. 2828). Am oberen See von Band-i Amir (N. 1950/476). Sard Darra, Koh-i Baba, 3350 m (G. 325). Montes Koh- Baba, in latere austro-orientali jugi Hadjigak, 3000 m (RECH. 18527). Koh-i Baba, 3100 m (K. 2669). - Pakistan: (GRIFF. 6105). Kurram Valley, 10000 ft. (AITCH. 501). Chitral: Rumbur, 35°46'N, 71°40'E, peaty boggy portion in stream, 9500 ft. (B. L. 668, 670). Partsan, 63°03'N, 71°52'E, wet bank facing south in rich soil, 9700 ft. (B. L. 844). Ojhor, 36°04'N, 71°48'E, damp alpine pasture, steep slope, 12000 ft. (B. L. 864). Mastuj, 7500 ft., in marsh (St. 2482). Agram, Arkari Gol, W of Tirich Mir, 10500 ft., on damp ground (ST. 2643).

C. orbicularis BOOTT var. bulungensis OSTENFELD – NW: Obeh, 1700 m (K. 3724). – C: Hauz-i Mahiha (K. 2406). Farakulum, 2800 m (K. 2605).

In Central Asia, *Carex orbicularis* BOOTT is vegetatively as variable as *C. Bigelowii* TORR. of the arctic zone. In loose soil, the rhizomes are not so tufted and the stolons get longer. Var. *bulugensis* OSTENFELD is a useful name for such specimens reaching 60 cm in length, with wider leaves and bigger spikes.

C. oxyleuca V. KRECZ. (Syn. C. ustulata (non Schkuhr) auct. fl. turkest. – 'Afghanistan' (fide Fl. URSS. 3: 284 (1935).).

C. pamirensis C. B. CLARKE (Syn. C. vesicaria L. var. pamirica O. FEDTSCH., C. pamirica (O. FEDTSCH.) B. FEDTSCH., C. vesicaria L. var. alpigena (non FRIES) B. FEDTSCH., C. ampullacea (non GOOD.) DUTHIE, C. rostrata (non STOKES) O. FEDTSCH., C. obscuriceps KUEKENTHAL var. pamirica (O. FEDTSCH.) KUEKENTHAL). – **NE: Nuristan:** Oberes Kantiwo-Tal oberhalb Brubruts, auf Sumpfwiesen an einem Bach, 2600 m (KN. 957). 'Afghanistan' (fide Fl. URSS. 3: 448 (1935). – **Pakistan: Chitral:** Baroghil Pass, 13000 ft., at edge of lake (St. 2994).

C. parva NEES (Syn. Kobresia Lolonum HAND.-MZT.). – C: Bamian: Sard Darra, Koh-i Baba Kette, 3350 m (G. 296). Koh-i Baba, 3100 m (K. 2657).

C. philocrena V. KRECZ. in Fl. URSS. 3: 393 (1935). (Syn. *C. Oederi* (non RETZ.) auct. var. *philocrena* Коуама in Кітамика, Fl. Afgh. 51 (1960).). – **NE: Nuristan:** Between Chatrass and Kushimaikot (Кітамика 38). – **E:** Im Panjshir-Tal bei Gulbahar, 1700 m (G. 341-b, V. 250 p.p.). Paghman-Tal bei Kabul, 2300–2800 m (RECH. 17193). Paghman, 7500 ft., wet meadow (Kz. 12106). – **C:** Kamard, NW Doab, 2000 m (Kz. 13605). Doab, 1400 m (K. 2883). – **Pakistan: Swat:** Utror, 2500 m (RECH. 19563).

A well-marked species related to *C. demissa* HORNEM. ("*C. Oederi*" *aucl.*, *non* RETZ.) with golden-yellow perigynias gathered in 4-6 spikelets, the lowermost remote, subtended by a bract 3-4 times longer than the inflorescence.

C. physodes M. B. – NW: Hari-rud Valley (Антсн. 1134). – SW: Herat, 1100 m (K. 3541). – E: 'Afghanistan' (GRIFF. 6083).

A typical steppe-plant, well adapted to dry conditions, the numerous minute rootlets covering large tracks of sand (map of distribution in Sov. Bot. 4: 49 (1937).). The enlarged fleshy perigynia are quite unique in the genus *Carex*. The plant is an important fodder for Kara-Kum sheeps in the Kara-Kum region. See KACHKAROV & KOROVINE. La vie dans les déserts, éd. francaise par Théodore Monod (PAYOT, Paris, 1942).

C. plectobasis V. KRECZ. (Syn. C. hirtella DREJER (1844), non F. S. GMEL. (1791). – Pakistan: Kurram Valley, 11000 ft. (Антен. 724, 1007).

C. polyphylla KAR. et KIR. (Syn. C. nemorosa LUMN., non SCHRANK, C. Leersii F. SCHULTZ, C. Pairaei F. SCHULTZ VAR. Leersii (F. SCHULTZ) KUEKENTHAL, C. echinata MURR. VAR. Leersii (F. SCHULTZ) KUEKENTHAL. C. muricata auct. plur., non L.). – Pakistan: Kurram Valley (AITCH. 670).

Carex pseudobicolor BOECK. (Syn. C. alpina SW. var. erostrata BOOTT, C. alpina SW. ssp. infuscata (NEES) KUEKENTHAL var. erostrata (BOOTT) KUEKENTHAL), descr. emend.

In dense tufts; the intricate forking rhizomes covered with fibrous remains of sheaths. Stems 8–12 cm long, filiform, acutely trigonous, scabrous, nodding at tip. Leaves basal, 1–2 mm wide, yellowish-green, the margins scabrous, long acuminate, about half the size of the stems. Spikes 3, approximate, sessile, the central one a little longer, androgynous, the two others female, all densely flowered. Bracts narrow, about equalling the inflorescence, shortly sheathing, the mouth of the sheath blackish. Perigynia 2,2 mm long, obovate, tumid-trigonous, yellow-brick coloured, nerveless, finely cellulose-reticulate, obtuse and beakless, the mouth black-girdled, Scales black, the mid-nerve spinulose, about equalling the perigynium. Achene 1,25 mm long, largely ovate, trigonous, very finely puncticulate, the angles thickened and crowned by the persistent style-base. Stigmas 3, barely exserted.

Pakistan: Chitral: Och Anzog, 3600 m, 19.7.1950 (WENDELBO).

C. pseudofoetida KUEKENTHAL – E: Kabul: Paghman, 17 miles W Kabul, 8000– 9000 ft. (CH.-M.). Kabul (KITAMURA 29, 35). – C: Bamian: Shibar Pass (KITAMURA 44). Sard Darra, Koh-i Baba, 3350–4350 m (G. 316, 317, 318). – Pakistan: Quetta (KITA-MURA 55). Chitral: Lashpur (Ishporill), 26°02'N, 72°27'E, 13600 ft., rich pasture near edge of stream (B. L. 105).

A well-marked species, the Centro-Asiatic representative of *C. foetida* ALL., of the European Alps, and of *C. vernacula* BAILEY, of the Rocky Mountains of North America, an interesting case of parallel evolution.

C. psychrophila NEES – Pakistan: Chitral: Shishi Gol, E of Drosh, 7000 ft., on marshy ground (ST. 2378).

C. pycnostachya KAR. et. KIR. – NW: Qala Nau, 900 m (K. 3693). – E: Darulfanun bei Kabul (N. 1951/22). Kabul (V. 69-b, 827, 834). – C: Panjao, 2800 m (K. 2744).

C. remota L. – Pakistan: Swat: Kulam, 2200 m (RECH. 19455).

C. secalina WILLD. var. alpina KUEKENTHAL et BORNMUELLER – E: Gardez: Sirotai, 9000 ft. (Kz. 11919). Ghazni: Inter jugum Kotal-e Ketschru et pagum Miradina, NW Sang-i Masha, 2700–3200 m (RECH. 17582). In jugo Sardalu W Qarabagh, 2300–2500 m (RECH. 17323).

C. songorica KAR. et KIR. (Syn. C. heterostachya (non BGE.) KUEKENTHAL, C. nutans (non Host) BOECK., C. Fedtschenkoana KUEKENTHAL). – NW: Safedsang, 3300 m (Kz. 14013). – NE: Nuristan: Im Kantiwo-Tal beim Dorf Kantiwo, 2200 m (KN. 910-b). – E: Nidjrao, 2500 m, NE Sarobi (V. 2311). Paghman-Berge, W Kabul, 2500–3000 m (CH.-M., G. 344, V. 980). – C: Bamian: Zwischen Chardeh und Ghorband (V. 2812). Lal-i Zarjangal, 2500 m (K. 2756). Farakulum, 2800 m (K. 2606). Ibidem, 2700 m (K. 2607). Panjao, 2700 m (K. 2726). Am See Band-i Gholaman, Band-i Amir, 2800–2900 m (RECH. 18472, V. 2821). Am See von Band-i Amir, 2800 m (RECH. 18304). – Pakistan: Kurram Valley, Biankhél, common (Airch. 602). Chitral: Khot An, N of Mastuj, between Turikhot and Mastuj Rivers, 13000 ft., on damp shores, at edge of stream (St. 2841). Markhun, between 36°30'N, 72°40'E, and 36°48'N, 73°05'E, alt. 10000 ft., steep moist hillside near stream (B. L. 960).
C. stenocarpa TURCZ. (Syn. C. sempervirens VILL. ssp. tristis (M.B.) KUEKENTHAL) – 'Afghanistan' (fide Fl. URSS. 3: 291 (1935).).

C. stenophylla WAHLENB. var. stenophylla – NE: Nuristan: Brubruts, Mamgel-Pass, 3300 m (KN. 985). Oberhalb Puruns, 2520 m, nasse Wiesen (KN. 1390). Semenek Pass, 3410 m (KN. 1513). Gangallat Gol, Kafiristan, 12000 ft., on damp short turf (ST. 2721). – E: Kabul: Charikar (N. 1950/668). Koh-i Asmai, 17000 m (KN. 4). Kabul, Gulbagh, (N. 1951/24). – C: Bamian: Ufer des Bamian-Flusses bei Schar-e Schak, 2320 m (G. 315). – Pakistan: Khybar Pass, 1200 m (KN. 2142) Chitral: Bogosht, 35°57'N, 71°32'E, well grazed pasture near stream in valley bottom, 8500 ft. (B. L. 772). Barum Gol, Shokov Shal, by a rivulet, 3500 m (WDB.). Mastuj track, 9000 ft., at edge of field (ST. 3519).

C. stenophylla WAHLENB. var. pellucida LITW. – E: Kabul: Bala Hissar, 34°30'N, 69°10'E, in stagno, 1800 m (RECH. 16002).

C. stenophylla WAHLENB. var. planifolia BOISS. – Turcomania: In deserto argilloso prope Aschabad (LITW. 274). - Afghanistan: N: North Afghanistan (M.). - NE: Nuristan: Zwischen Asmar und Barikot, 840 m (G. 297). – E: Ghazni: Ad marginem orientalem altoplanitiei Dasht-e Nawar (Naour), 3000 m (RECH. 17807). Kabul: Unter dem Gipfel des Sebroderakan bei Schewaki im Logartal, 2500 m (G.). Berghang zwischen Tschardeh und dem Logartal, 1840 m (G. 303). Sandfläche W von Darulfanum, 1830 m (G. 302). Westhang des Scher Darwasah, Koh-e Tschelsotun Kette, 1820 m (G. 301). Scher Darwasah, Grabmal Chodsche Safa, 1880 m (G. 304). Sandiger Hügel zwischen Kabul und Tang-i Gharu, 1770 m (G. 298). Aliabader Berg bei Kabul, trockene lössreiche Steppe (V. 11-b). Nordwestlich des Aliabader Berges bei Kabul, 1800 m (G. 300). Aliabad bei Kabul (N. 1951/19). Koh-i Asmai bei Kabul, Süd- und Nordseite, 1700 m (Kn. 4). Pandscheschah bei Kabul (N. 1951/55). An einem trockenen Feldrain bei Gulbagh, nahe Kabul (N. 1951/24 p.p.). In collibus ad septentriones urbis Kabul, 1800 m (RECH. 17042). Kabul, in hills (AKHTAR). Berghang bei Budchak, 1780 m (G. 299). Paghman, 2400 m (G. 306). – C: Bamian (V. 2230). - Pakistan: Khybar Pass (Kn. 2142). Chitral: Mastuj track, 9000 ft., on damp ground at edge of field (Sr. 2518). Gangallat Gol, Kafiristan, SW of Chitral, 12000 ft. (Sr. 2721). Bogosht, 35°57'N, 71°42'E, 8500 ft. (B. L. 772).

C. stenophylla WAHLENB. var. interrupta LITW. – E: Ghazni: In monte ad occidentem jugi Sardalu inter Qarabagh et Sang-i Masha, 2600 m (RECH. 17411). Okak, NE altoplanitiei Dasht-e Nawar (Naour), $33^{\circ}50'$ N, $67^{\circ}55'$ E, 3000 m (RECH. 17759). In jugo Ghoutch Kol, NNE Sang-i Masha, $33^{\circ}40'$ N, $67^{\circ}25'$ E, 3300 (RECH. 17649). Kabul: Dasht-e Tup, S Maidan, inter Kabul et Ghazni, $34^{\circ}10'$ N, $68^{\circ}55'$ E, 2400 m (RECH. 17237). Darulaman-Ebene bei Kabul, an nassen Stellen (V. 85-b). Paghman, 2800 m, feuchter, kiesiger Schwemmkegel (V. 347). Kabul, Cynodon-Rasen (V. 1883), Steppe (V. 1475, 2779). – C: Ghorat: Qala Chahrak (Sharak), 2000 m, $34^{\circ}07'$ N, $64^{\circ}23'$ E (RECH. 19155). Bamian: Koh-i Baba, 2700–2900 m (K. 3337). Ibidem, 2900 m (G. 307). Hauz-i Mahiha, 2600–2700 m (K. 2471, 2472).

It is very difficult to deal with the various biotypes that occur in the *Carex slenophylla* complex. Some of them are apparently quite clear-cut in their extremes, if you do not examine too many specimens of them.

KUEKENTHAL'S treatment is too conservative and a little incoherent in a way, though in later years he had another view on the subject. In 1909, he had in his monograph *C. stenophylla* itself with *f. elata* (SCHUR) KUEKENTHAL and *f. pachystylis* (GAY) ASCHERS. et GRAEBN., and the following varieties: var. *duriuscula* (C. A. MEYER) TRAUTV., var. *exigua* (SCHUR) KUEKEN-THAL, var. *longepedicellata* (BOECK.) KUEKENTHAL, var. *enervis* (C. A. MEYER) KUEKENTHAL and var. *desertorum* LITWINOW.

In 1930, studying SMITH'S Chinese gatherings of sedges, KUEKENTHAL found out that he made a mistake in associating *C. enervis* with *C. stenophylla:* "In meiner Monographie der *Caricoideae* (1909), p. 122, habe ich *C. enervis* C. A. MEYER als Varietät *C. stenophylla* WAHLENB. untergeordnet." Das zahlreiche Material, welches ich seitdem gesehen habe, führt mich zu der Ansicht, das die dort angegebenen Merkmale so konstant und so wesentlich sind, dass sie zur artlichen Trennung drängen". (Acta Horti Gothoburg. 5: 41 (1930).).

In fact, *C. enervis* C. A. MEYER, of which I have examined authentic specimens from Yunnan, Baical and Jacuts, is not related to *C. stenophylla*, but to *C. maritima* GUNN. (Syn. *C. incurva* LIGHTF.).

The North American representative had a poor treatment from the start. It was described as *C. Eleocharis* by BAILEY in 1889, but without any relationship indicated to *C. stenophylla*, instead it was said to be related to *C. disperma*. The type (immature), MACOUN 1665, from Saskatchewan, KUEKENTHAL did not see. In his monograph, he placed *C. Eleocharis* in the same section as *C. disperma*, adapted BAILEY's description to fit his own style, cited MACOUN's specimen with the n.v. that indicated his entire reliance on BAILEY. At the same time, he placed all the North American specimens that he had seen under *C. stenophylla* itself. In the new edition of GRAY'S Manual (1950) FERNALD, unaware of KUEKENTHAL'S second thought on the matter, treated the North American phase as *C. stenophylla* WAHLENB. var. enervis (C. A. MEYER) KUEKENTHAL. In 1931, MACKENZIE had used *C. Eleocharis* BAILEY for the North American plant and had pointed out its relationship with, and its distinction from, typical Eurasiatic *C. stenophylla* WAHLENB.

In 1908, *C. uralensis* C. B. CLARKE was published posthumously, too late to be taken into account by KUEKENTHAL, whose work was already in the printer's hands. C. B. CLARKE was restricting *C. stenophylla* to Europe.

In 1910, LITWINOW had some problems classifying his material from Turkestan and two useful segregates were set out: var. *pellucida* and var. *interrupta*, with reference to a former var. *desertorum*. One finds there a good understanding of the behaviour of the species in the desertic regions of Central Asia.

As early as 1884, FRANCHET had set apart the Far East representative as var. *rigescens*. Examination of various collections, including DAVID's, BUNGE's, FAURIE's, show that, with its hyaline scales and general shape of the aggregated spikes, it is the clearest cut of all the segregates. KUEKENTHAL wrongly placed var. *rigescens* in the synonymy of f. *pachystylis*. C. pachystylis GAY is based on flowering material; GAY states that it is remarkable by its thickened style-base. In a group as difficult as the Vigneae, I would reject this name entirely, though Ascherson and GRAEBNER retained it at formal rank for the European specimens (presumably shade-forms) with wide leaves (not BOISSIER's var. *planifolia*) and in the Flora URSS., it is treated as a species in another section, i.e. the Physodeae, with the well-known C. physodes M.B., characterized by big inflated reddish perigynia, with which it apparently hybridizes. To my mind, C. pachystylis, at least sensu KRECZETOWICZ, is C. physodes with sterile, undeveloped female flowers. The underparts with their innumerable minute rootlets are unmistakable.

The late KRECZETOWICZ wrote the treatment of *Carex* for the monumental Flora URSS. under the editorship of KOMAROV. As everyone knows, the KOMAROVIAN school treats as species every geographical variant, in contrast with the MAXIMOWICZ era, where a sense of synthesis always presided over the setting out of new taxa. So, there is no surprise that in this work *C. stenophylla* itself is not treated, being restricted to Eastern non-Russian Europe. It is replaced by *C. uralensis* C. B. CLARKE. Then *C. stenophylloides*, *C. duriusculiformis*, *C. rigescens* are described. *C. duriuscula*, *C. pachystylis* (in another section) are retained as species. Between this extreme view and KUEKENTHAL's there is an immense gap. Trying to conciliate the two, correcting the first, specially in regard to synonymy, and trying to take the best of the second, I propose here a realignment of the segregates of *Carex stenophylla*.

Pending further investigations, not only in herbaria but in the field, I do not think that any of the so-called species described by V. KRECZETOWICZ can be treated as such, neither as subspecies. At best they can be kept as varieties; though I have no experience with them in the field, they look, as a whole, as accommodates, i.e. seasonal ecotypes. In dry seasons or in dry areas, some plants will have a very short vegetative life, belonging to the ephemeroid type; in better conditions they will grow during all summer. In the first case, the rootstock will become more or less pseudobulbous, through thickening, whereas a luxuriant foliage will develop in the other case, even flat leaves. Examination of a good number of specimens from North America shows that they duplicate several of the variations of the Asiatic population. The adventage of the present grouping is that the names of all the varieties are available as such, so that no transfers are needed. In a difficult group, it is not wise to set up new names; it only adds confusion to chaos.

Dr. TYCHO NORLINDH has recently studied carefully the European population (the type comes from Austria) and concluded that *C. uralensis* C. B. CLARKE is morphologically indistinguishable from *C. stenophylla* WAHLENB., their variation amplitude overlapping greatly. This was a first step towards a better understanding of the Mongolian population. Dr. NOR-LINDH's later opinion may alter the present synopsis:

Carex stenophylla WAHLENB., Vet. Akad. Handl. Stockh. 24: 124 (1803); KUEKENTHAL, Cyper.-Car. 120 (1909), pr. pte. max.; NORLINDH, Bot. Not. 113 (1): 1–19, fig. 1–5 (1960). Syn.: C. juncifolia (non All.) Host, Synops. pl. Austr. 503 (1797), pr. pte.; SCHKUHR, Beschr. u. Abb. d. Riedb. 26, nr. 18, tab. G, fig. 32 (1801). C. glomerata (non THUNB.) Host, Icon. et descr. gram. austr. 1: 34, tab. 44 (1801). C. Hostii SCHKUHR, Nachtr. 7 (1806), pr. pte. C. uralensis C. B. CLARKE, Kew Bull. Add. ser. 8: 76 (1908); V. KRECZETOWICZ, Fl. URSS. 3: 14, tab. 10 a-c (1935).

- - var. stenophylla. - Eastern Europe and Western Sibiria, east to Chitral.

- var. pellucida Litw., Trav. Mus. Bot. St. Pétersb. 7: 84 (1910). Syn.: C. stenophylloides
V. KRECZ., Fl. Turkm. 1 (2): 230, tab. 93 (1932); Fl. URSS. 3: 141, 592, tab. 10, fig. 2a-b (1935); Act. Univ. As. Med. Bot. 20: 22 (1935). - Caucasus, Asia Minor to Central Asia.

- var. planifolia BOISS., Fl. Orient. 5: 400 (1884). Syn.: C. pachystylis GAY, Ann. Sc. Nat. 2nd. sér. 10: 301 (1838); V. KRECZ. in Fl. URSS. 3: 197 (1935); Act. Univ. As. Med. Bot. 20: 23 (1935). C. stenophylla WAHLENB. var. desertorum LITW., Allg. Bot. Zeit. 5, Beih. 1: 56 (1899); KUEKENTHAL, Cyper.-Car. 122 (1909). C. desertorum LITW., Trav. Mus. Bot. St. Pétersb. 1: 19 (1902). C. stenophylla WAHLENB. f. pachystylis KUEKENTHAL, Cyper.-Car. 121 (1909), pr. pte. – The dominant phase in Caucasus, Iraq, Syria, Iran and Afghanistan.

- var. interrupta Litw., Trav. Mus. Bot. St. Pétersb. 7: 85 (1910). Syn.: C. stenophylla
WAHLENB. var. duriuscula (non TRAUTV.) B. FEDTSCH., Act. Hort. Petrop. 38: 189 (1925).
C. duriusculiformis V. KRECZ., Fl. URSS. 3: 142, 591 (1935); Act. Univ. As. Med. Bot. 20: 22 (1935).
- Tian Shan, Pamiro-Alaj, Hindukush, Karakorum, Kuen-Lun, Himalaya and Tibet.

 - var. duriuscula (C. A. MEYER) TRAUTV., Act. Hort. Petrop. 10: 537 (1887–89). Syn.:
 C. duriuscula C. A. MEYER, Mém. Sc. St. Pétersb. Sav. Etrang. 1: 214, tab. 8 (1831). C. steno-Biol. Skr. Dan. Vid. Selsk. 14, no. 4. phylla WAHLENB. var. humilis MEINSH., Act. Hort. Petrop. 18: 316 (1901). – Siberia, Mongolia, and Manshuria.

– – var. longepedicellata (Воеск.) Киекентнаг, Pflanzenr. 4 (20): 121 (1909). Syn.: C. longepedicellata Воеск., Cyper. nov. 1: 41 (1888). – Himalaya and Tibet.

- var. Eleocharis (BAILEY) BREITUNG, Canad. Field. Nat. 71: 48 (1957). Syn.: C. Eleocharis BAILEY, Mem. Torrey Bot. Cl. 1: 6 (1889); KUEKENTHAL, Cyper. - Car. 0): 222 (1909); MACKENZIE, N. American F1. 18 (1): 33 (1931); N. Amer. Car. tab. 16 (1940). C. stenophylla KUEKENTHAL, Cyper.-Car. 120, pr.pte. quoad spec. amer. 1909. C. stenophylla WAHLENB. var. enervis (non C. A. MEYER, nec KUEKENTHAL) FERNALD, GRAY'S Man., 8th. Ed., 302 (1950). C. stenophylla WAHLENB. ssp. Eleocharis (BAILEY) HULTÉN, Fl. Alaska and Yuk. 2: 314 (1942). - Western North America, eastwards to Manitoba.

C. subphysodes M. POPOV ex V. KRECZ., Act. Univ. As. Med. Bot. 20: 23 (1935). E: Kabul, an einem trockenen Feldrain bei Kabul-Gulbagh (N. 1951/24).

Apparently an hybrid between *C. physodes* and *C. slenophylla* var. *planifolia* or, perhaps, a specimen of *C. physodes* with undeveloped utricles.

C. subvulpina P. SENAY, Bull. Mus. Paris, 2e série, 17 (5): 444 (1945). (Syn. C. compacta (non LAM.) V. KRECZ., C. nemorosa REBENT., C. vulpina (non L.) KUEKENTHAL, C. vulpina L. var. nemorosa KOCH, C. vulpina L. var. tenuior TREV., C. vulpinoidea (non MICHX.) BOISS., C. vulpina L. var. pallidior MEINSH., C. vulpina L. var. orientalis PACZ.). – 'Afghanistan' (AITCH. 870).

KRECZETOWICZ was the first to notice that two taxa were involved in *C. vulpina* L. He revived *C. compacta* LAM. (1778) for the second species, but, as the late P. SENAY has demonstrated, in a minutious study of the group (Le *Carex vulpina* et ses alliés, Bull. du Muséum, 1945), LAMARK'S diagnosis applies only to *C. vulpina* s. str.

Carex trispiculata BOECK., Cyper. nov. 1: 45 (1888). (Syn. C. alpina (non Sw.) AITCH., C. Vahlii (non SCHKUHR) BOISS., C. alpina Sw. ssp. infuscata KUEKENTHAL, Cyper.-Car. 386 (1909), pr. pte., quoad spec. AITCHISON, C. alpina Sw. ssp. infuscata (NEES) KUEKENTHAL VAR. humilis GILLI, FEDDES Repert. spec. nov. 64: 217 (1962), descr. emend.

In dense tufts, the intricate freely forking rhizomes covered with fibrous remains of old sheaths. Stem $3-12 \ (-25) \ cm$ long, slender and stiff, sharply trigonous, the base thickened by accumulated old sheaths. Leaves basal, much shorter than the stems, $3-5 \ cm$ long, 1 mm wide, long acuminate, often falcate and involute, the margin finely spinulose. Spikes 2-3, approximate, sessile, the terminal one $4-5 \ mm$ long, androgynous, the lateral ones female, a little shorter and wider. Bracts about equaling the spikes, barely sheathing, spinulose, the mouth black. Perigynia 2,75 mm long, ovate, tumid-trigonous, pale yellow, finely cellulose-reticulate, the two lateral nerves well marked, the others faintly so, ending in a conical slightly bidentate, black girdled beak. Scales dark, red, the mid-vein paler, slightly shorter than the perigynia. Achene 2 mm long, sharply trigonous, rhomboidal, the base-style persistent. Stigmas 3, very slender, exserted.

34

NE: Gomando, Porande valley nr. Basarak, 9000 ft., damp ground (G. 333, Kz. 11712). Pandjshir-Tal bei Ruhka (V. 196). – **E:** Kabul: Bagrami, Nedjerau-Tal, E Kabul, 3000 m (N. 1950/301). Paghman, 2800 m (N. 1950/664, 667, V. 966). – **Pakistan:** Shentoi (AITCH.).

A well-marked species.

C. turkestanica REGEL (Syn. C. orientalis MEINSH., C. nitida HOST var. aspera (BOECK.) KUEKENTHAL, C. heterostachya BGE. f. minor BOOTT). – 'Afghanistan' (fide Fl. URSS. 3: 377 (1935).).

C. vulpinaris NEES – NW: Qala Nau, 900 m (K. 3963). – SW: Herat, 1000 m (K. 3879). – E: Kabul: Paghman, W Kabul, 2500–3000 m, feuchte Geröllhalde (V. 334). Ibidem, 9000 ft., clumps along stream (Kz. 12111, 12142). Ibidem, 3900 m, *Cousinia*-Bestand (V. 926). Paghman-Tal (N. 1950/666). Kurram Valley (GRIFF. 147, AITCH. 818). – C: Band-e Amir, 2900 m, Seeufer (V. 2822).

C. Wendelboi NELMES (Syn. C. nubigena D. DON var. brevi-bracteata GILLI, FEDDES Repert. spec. nov. 64: 216 (1962), syn. nov.) – NE: Nuristan: Shabul Gul (KITAMURA 52). – E: Kabul: Paghman Tal, oberhalb Beg-tut, 2900–3500 m (G. 319, 320). Nedschrab-Tal, zwischen Gulbahar und Sarobi, 3100 m (G. 322). Zwischen Schakar darra und Hauz-e Chas, in einer Schlucht am Fuss einer Felswand, 3250 m (G. 321). Pakistan: Chitral: Oihor Gol, 10500 ft., river bed, $36^{\circ}04'N$, $71^{\circ}48'E$ (B. L. 838). Barum Gol, wet slope, above Shokor Shal, E. side of Main Barum Glacier, 3600 m (WDB.).

GRAMINEAE

By N. L. Bor, Kew

and A. MELDERIS, British Museum, London.

Panicoideae-Andropogoneae

Apluda L.

A. mutica L. – NE: Nuristan: Nishei, ca. 1300 m (E. 825).

Arthraxon P. BEAUV.

A. prionodes (STEUD.) DANDY – NE: Nuristan: Im Tal und um den Ort Kurder, Seitental des Petsch-Tales, 1600–1800 m (N. 1951/754). Darim-Tal ab Ort Darim aufwärts, 1900–2400 m (N. 1951/982).

Bothriochloa O. KTZE.

B. caucasica (TRIN.) C. E. HUBBARD – NE: Nuristan: Kurder-Tal, Seitental des Petsch-Tales (N. 1951/804).

B. Ischaemum (L.) KENG – NE: Badakhshan: Ishkamish, ca. 1200 m, zerstreut in der Löss-Steppe (V. 2657). Kataghan: Taliqan, Khanabad, Grabenränder (V. 608). Nuristan: Aschpi-Pass (N. 1951/1050). Zwischen Kotal-Agok (Agok-Pass) und Alm bis Ort Waigel (N. 1951/867). Porande-Tal, Seitental des Panjshir-Tales bei Basarak, Wiese am rechten Porande-Ufer östlich von Daolana, ca. 2350 m (G. 372). Ort Parigel im Parigel-Tal, linkes Seitenufer des unteren Kulam-Tales, ca. 1800 m, trockener Wiesenhang (Kn. 1167). – E: Ghazni: Inter Miradina et jugum Ghoutch Kol a Sang-i Masha septentriones versus, ca. 3000 m (RECH. 17612). Kabul: Gulbahar bei Charikar (V. 1009). In einer Schlucht zwischen Tschardeh und dem Logar-Tal, ca. 1880 m (G. 371). Guzar Geh, an westoffenem Hang (N. 1950/36). Oberes Paghman-Tal (N. 1950/791). - C: Bamian: In valle Ajar "Königsthal" a Doab occidentem versus, 1400-1500 m (HDG & WDB. 4126, RECH. 16604). - Pakistan: Chitral: Owir, SE of Tirich Mir, 8000 ft., on dry stony ground (St. 2769). Mastuj, Baroghil Track, Bang, ca. 8000 ft., at edge of field (ST. 2935). Beorai Gol, S of Drosh, ca. 5000 ft., at edge of irrigation channel (Sr. 3274). Golen Gol, ca. 7000 ft. (B. L. 24). Dir. Distri.: Panjkora-Tal bei Warai, ca. 1000 m (Kn. 2107).

KERSTAN 2107 is not without interest. The joints and pedicel have a translucent central portion which indicates the genus *Bothriochloa*. – The lower glume of some of the sessile spikelets show a depression like the indication of a pit: also indicating *Bothriochloa*, e.g. *B. pertusa* (L.) A. CAMUS.

Chrysopogon TRIN.

Ch. Aucheri (BOISS.) STAPF – SW: Siason, inter Bakoa et Farah (L. 277). – SE: Kandahar: Am Hilmend bei Germaub, nördlich von Ghirishk, ca. 1200 m (KN. 386). – E: Kabul: Tisin, an der Strasse Kabul nach Jallalabad (KN. 602, SCH. 72). Südöstlich von Sarobi, 1000–1450 m (G. 368, 369). In der Schlucht des Kabul-Flusses bei Tang-i Gharu, 1600–1700 m (KN. 518). Hills 30 miles E of Kabul (M.). – NE: Nuristan: Tshagan Serai, unteres Petsch-Tal, ca. 820 m, Gneiss, Glimmerschiefer (KN. 685). – Pakistan: Quetta: Near Quetta, ca. 1500 m (K. 3060).

Ch. Aucheri (BOISS.) STAPF var. quinqueplumis (A. RICH.) STAPF – SE: Pirzada, near Kandahar, ca. 1000 m (K. 2110). – E: Darunta, Sarobi (V. 1925). An der Strasse von Nimla nach Jallalabad, ca. 600 m, Schotter (SCH. 75-b).

Ch. echinulatus (NEES) W. WATS. – **NE: Nuristan:** Ashpi, ca. 2000 m (E. 1679). Ashpi-Pass (N. 1951/1043). Pashki, ca. 2300 m (E. 552, 1329). Parun-Tal bei Pashki, ca. 2200 m, Wegränder (SCH. 158). Auewiesen oberhalb Pashki, im Parun-Tal zwischen Pashki und Shtive, ca. 2300 m (KN. 1383). East-Nuristan (E. 1677). – **Pakistan: Swat:** Kalam, 35°30'N, 72°30'E, ca. 2200 m, substr. granit. (RECH. 19405).

Ch. serrulatus TRIN. – Pakistan: Dir.: Panjkora-Tal bei Warai, ca. 1000 m (KN. 2118). Peshawar: Inter Saidu Sharif et Malakand, ca. 800 m, substr. granit. (RECH. 19609). Rawalpindi, ca. 550 m (KN. 2267-a).

Cymbopogon Spreng.

C. Olivieri (BOISS.) BOR (Syn. Andropogon Olivieri BOISS.). – NW: Herat: Steppe nördlich von Herat, ca. 940 m (G. 374). – SW: Herat, 900 m (K. 4269). Seistan to Farah (K. 4270). – SE: Germaub am Hilmend, nördlich von Kandahar, ca. 1200 m, Steinsteppe (KN. 383). Kajkai, NNW of Kandahar, ca. 900 m (K. 2127). Pirzada, near Kandahar, ca. 900 m (K. 2091). Baba Wali bei Kandahar, Steppe (V. 229). – E: Kabul: Jallalabad (KN. W-155). Hills 30 miles E of Kabul, ca. 2700 m (M.). Jagdalek, östlich von Kabul (Kz. 8247). – NE: Nuristan: Zwischen Asmar und Barikot, ca. 840 m, Quercus Baloot-Bestand (G. 373). Zwischen Nishei und Ningalam (N. 1951/788). Zwischen Ningalam und Ort Darim, 1300–1900 m (N. 1951/965, 973). Asmar Barikot, ca. 900 m (E. 1615). Kadjahkai, bord de riviere (L. 1958/416). Siakou, champs (L. 284, 304).

C. Parkeri STAPF – NE: Nuristan: Vaigel, ca. 1500 m (E. 886). East-Nuristan (E. 1141). – E: Unteres Kunar-Tal, zwischen Tshagan Serai und Jallalabad oberhalb Nurgel, 600–800 m, Gneiss-Schiefer (KN. 664-b). An der Strasse von Kabul nach Jallalabad in der Gegend des Heiligengrabes Seh Baba, an Sandstellen (KN. 610). In faucibus Tang-e Gharu, inter Kabul et Sarobi, 1100–1300 m, substr. conglom. (RECH. 18977). Von Sarobi bis östlich von Lataband, Steppe (V. 1566). Zwischen Sarobi und Darunta (V. 1955). Auf einem Berg südöstlich von Sarobi, ca. 1100 m, Schutthalde (G. 375). Unter der Kammhöhe eines Berges SE von Sarobi, ca. 1400 m (G. 376). – Pakistan: Quetta: Near Khojak Pass, ca. 1900 m (K. 3046).



Fig. 1. Erianthus kajkaiensis MELDERIS (K. 2159, Holotypus, C).

Dichanthium WILLEMET.

D. annulatum (FORSSK.) STAPF – NE: Nuristan: Unteres Petsch-Tal zwischen Tshaghan und Barkandi, ca. 800 m (KN. 694-a).

Erianthus MICHX.

E. filifolius NEES ex STEUD. (Syn. *Saccharum filifolium* STEUD.) – **NE: Nuristan:** Petsch-Tal, unterhalb Wama, ca. 1200 m (Kn. 1261-b). Petsch-Tal, bei Wama, ca. 1400 m (Kn. 1281). – **Pakistan: Chitral:** Shoghot, N of Chitral, ca. 5500 ft., on stony ground (St. 2734).

E. Griffithii (MUNRO) HOOK. f. (Syn. *Saccharum Griffithii* MUNRO ex AITCH.) – **E:** Sarobi, Talaue (V. 2855, 2856, REGEL). In fauce fluvii Kabul inter Sarobi et Kabul (REGEL). – **NE: Nuristan:** Gusalak, ca. 1000 m (E. 1195).



Fig. 2. Erianthus kajkaiensis MELDERIS, a part of the panicle (K. 2159, Holotypus, C) 4.5/1.

Erianthus kajkaiensis MELDERIS, sp. nov. - Fig. 1, 2.

Gramen perenne, ad 1,25 m altum, erectum, caespitosum. Culmi validiusculi, multinodes, e basi nodisque infimis ramos simplices agentes, teretes, striati, superne et infra paniculam appresse sericeo-longipilosi, ceterum glabri laeves. Nodi longibarbati. Folia viridia; vaginae striatae, glabrae laeves, internodiis saepe longiores; ligulae ad 3,5 mm longae, membranaceae, laceratae, longibarbatae; laminae 10-40 cm longae, 1-2,5 mm latae, rigidae, anguste lineares, planae vel plus minusve convolutae, supra costa media crassiuscula, alba, nervis scabriusculae, marginibus scabrae, subtus glabrae leaves. Panicula erecta, ad 15 cm longa, laxiuscula, sublobata, composita, albo-sericeo-villosa, rhachidi ramulisque appresso-longipilosa. Racemi 1,5-7,5 cm longi, suberecti, laxiflori, articulati, rhachidi fragili; articuli basi subincrassati, villis ipsos paulo superantibus dense vestiti. Spiculae ad rhachidis nodos racemorum binae, altera sessilis, altera pedicellata, lanceolatae, similes, aequilongae vel subaequilongae. Glumae absentes. Lemmata (cum appendice) 5,5–6 mm longa, hyalina, basi lanceolata, apice in appendicem 1,5–2,5 mm longam, tenuem, aristiformem attenuata. Lemma inferum sterile, prope margines 2-nerve, dorso apicem versus brevisetulosum, ad margines longiciliatum; palea absens. Lemma superum infero subaequilongum vel eo leviter longior, 1-nerve, dorso glabrum, ad margines longiciliatum; palea lanceolata, 3–3,5 mm longa, dorso glabra, ad margines longiciliata; stamina 2, antherae 1,8–2 mm longae, purpureo-luteae; ovarium glabrum, stigmatibus plumosis, brunneo-luteis, ex anthoeciis exsertis. Spiculae pedicellatae; pedicellus 2 mm longus, sparse longipilosus. – E. Griffithii (MUNRO) HOOK. f. similis sed ab eo culmis superne, paniculae rhachidi racemorumque rhachidibus appresso-longipilosis, glumis absentibus, lemmatibus basi lanceolatis, apice in appendicem brevem tenuem aristiformem attenuatis, lemmate infero prope margines 2-nervio, lemmate supero 1-nervio, antheris brevioribus, recedit.

SE: Kajkai, ca. 1000 m, 29.5.1948 (Køie 2159, Holotypus, C; Isotypus, BM).

E. Ravennae (L.) P. BEAUV. (Syn. Saccharum Ravennae (L.) MURRAY – SW: Dilaram, östlich von Farah, ca. 1100 m (K. 3036). – E: Sarobi, (V. 2855-b). – C: Doab, ca. 1400 m (V. 2870). Am Fluss zwischen Doab und Doschi nördlich des Schibar-Passes (N. 1950/216). Ghorat: In valle supra Zarni inter Taiwara et Parjuman (Partcheman), ca. 2000 m (RECH. 19008). – NE: Kataghan: In valle fluvii Kunduz (Qunduz) prope Doshi, ca. 850 m (RECH. 16548). Nuristan: Vama, ca. 1300 m (E. 1231, 1237). – Pakistan: Chitral: Drasan, ca. 2080 m, Flusschotter (KN. 2060).

E. Ravennae (L.) P. BEAUV. var. *purpurascens* HACK. – **E:** Kabul: Unterhalb Munar Shakri, in einer Schlucht der Bergkette zwischen Scherwaki im Logar-Tal und Chord-Kabul, ca. 2300 m (G. 366).

E. rufipilus (STEUD.) GRISEB. (Syn. Saccharum rufipilum STEUD.) – Pakistan: Chitral: Urtsun Gol, SW of Drosh, ca. 2000 m (ST. 3197).

Heteropogon PERS.

H. contortus (L.) P. BEAUV. – **NE: Nuristan:** Kurder-Tal, Seitental des Petsch-Tales (N. 1951/809). Zwischen Ningalam und Ort Darim, 1300–1900 m (N. 1949/945, 949).

Hyparrhenia ANDERSS.

H. hirta (L.) STAPF – E: Kabul: Zwischen Sarobi und Darunta, östlich von Kabul (V. 1955). – NE: Nuristan: Unteres Petsch-Tal unterhalb Sinsi, in der Nähe von Retschalam, ca. 900 m (KN. 707). Tshaghan Serai, unteres Petsch-Tal bei der Mündung, ca. 820 m (KN. 677). – Pakistan: Chitral: Arandu, SW of Drosh, ca. 4000 ft., at edge of fields (ST. 2308).

Imperata Cyr.

I. cylindrica (L.) P. BEAUV. – E: Kabul: Jallalabad, östlich von Kabul, ca. 600 m (E. 21). E. Afghanistan (GRIFF. 359). – NE: Nuristan: Gusalak, ca. 1000 m (E. 1193).

Bagrami, Nedjerau-Tal, am Steinrand einer Wiese beim oberen Dorf (N. 1951/249). Baghlan: Pul-e Khomri, Wiese am Fluss (N. 1950/226, 227). – **Pakistan: Chitral:** Im Chitral-Tal zwischen Chitral and Ayum, 1300–1500 m (KN. 2071).

Lasiurus Boiss.

L. hirsutus (FORSSK.) BOISS. – E: Kabul: Jallalabad, östlich von Kabul (V. 2059, 2628).

Phacelurus GRISEB.

Ph. speciosus (STEUD.) C. E. HUBBARD (Syn. Andropogon speciosus STEUD., Ischaemum speciosum NEES ex Steud., Andropogon corollatus NEES ex Steud., Ischaemum corollatum NEES ex Steud., Vossia speciosa (Steud.) Benth., Rottboelia speciosa (STEUD.) HACK., Ischaemum robustum HOOK. f., Pseudophacelurus speciosus (STEUD.) A. CAMUS, Thyrsia viridula OHWI) – E: Kabul: Tang-e Gharu in der Schlucht des Kabul-Flusses, 1600-1800 m (Kn. 503, 504). Nordhang eines Berges am rechten Ufer des Kabul-Flusses in der Tang-e Gharu unweit des Wasserfalles Maipar, ca. 1640 m, senkrechte Kalkfelswände (G. 377, 478). Surkhab-Damm, Artemisia-Steppe (V. 110-b). Kurram: Patan, Kurram-Tal (V. 1133). - NE: Nuristan: Beim Dorfe Wama im oberen Petsch-Tal, ca. 1400 m, auf Felshängen (Kn. 760, Sch. 86). Im unteren Petsch-Tal zwischen Gusalak und der Einmündung des Kurder-Flusses, ca. 1200 m (Kn. 734). Bei Gusalak im Kurder-Tal, Seitental des Petsch-Tales (N. 1951/ 820). Darim-Tal ab Ort Darim aufwärts, 1900–2400 m (N. 1951/994). Im Kulam-Tal bei Kulam (Munui), ca. 2100 m, auf Felshängen (Sch. 111). Westlich des Druda-Passes zwischen Don-Tal und Pischok-Tal, Aschkun-Gebiet, 1900–3000 m (Sch. 140). Ater-Schuker im Schuk-Tal, ca. 2300 m, auf Felsen am Nordhang (KN. 1016). Ahmedi Dewane, oberes Baschgal-Tal, ca. 2600 m (Kn. 1477-b). – Pakistan: Chitral: Shishi Gol, NE of Drosh, ca. 7000 ft., at edge of field (ST. 3143). Madaklasht, NE of Drosh, stony ground (ST. 3137).

Ph. speciosus (STEUD.) C. E. HUBBARD var. afghanicus MELDERIS, var. nov.

A typo in partibus multis (culmis, foliorum vaginisque, rhachidi, pedicellis, glumis) dense brevissime pubescentibus differt.

NE: Nuristan: Vaigel, 31.7.1948 (EDELBERG 2051, Holotypus, C).

Saccharum L.

S. spontaneum L. – NE: Kataghan: In valle fluvii Kunduz prope Doshi, ca. 850 m (RECH. 16544). Badakshan: Faizabad, bord de riviere (L. 1049). – E: Jallalabad, östlich von Kabul, an der Darunta (N. 1951/859). Sarobi, östlich von Kabul, Talaue (V. 2854). – Pakistan: Peshawar: Ad confluentes fluvios Kabul et Indus prope Attok (RECH. 19650).

Sorghum MOENCH

S. bicolor (L.) MOENCH - NE: Nuristan: Vama, ca. 1400 m (E. 1216).

S. halepense (L.) PERS. – NE: Kataghan: In valle fluvii Kunduz inter Pul-i Khumri (Gomri) et Doshi, 700–800 m (RECH. 16527). – E: Kalgani im Nedschrab-Tal,

zwischen Gulbahar und Sarobi, ca. 1700 m (G. 370). – Pakistan: Chitral: Chitral village, ca. 5000 ft., at edge of fields (ST. 3165).

Themeda FORSSK.

Th. anathera (NEES) НАСК. in DC. – NE: Nuristan: Vama, ca. 1300 m (E. 1223). Vaigel, ca. 1650 m (E. 871). Im ganzen Tal und um den Ort Kurder, Seiten-Tal des Petsch-Tales, 1600–1700 m (N. 1951/766). Im Darim-Tal ab Ort Darim aufwärts, 1900–2400 m (N. 1951/996, 1005). – Pakistan: Zambeli, oberhalb Rawalpindi, ca. 600 m (Kn. 276-a).

Th. anathera (NEES) HACK. in DC. var. glabrescens (ANDERSS.) HACK. – NE: Nuristan: Im Kotagel-Tal zwischen Kotagel und der Mündung in das Madschegel-Tal bei Kulatam, 1400–1600 m (KN. 1223-a).

Zea L.

Z. Mays L. – E: Kabul: Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m (G. 345).

Panicoideae-Maudeae

Panicoideae-Paniceae

B. eruciformis (J. E. Sm.) GRISEB. – Afghanistan: (V. 1443). – Pakistan: Chitral: Chitral village, ca. 5000 ft. (St. 3169).

B. ramosa (L.) STAPF in PRAIN – Pakistan: Dir., Panjkova-Tal bei Warai, ca. 1000 m (KN. 2108-a). Peshawar: Inter Saidu Sharif et Malakand, ca. 800 m, substr. granit. (RECH. 19603). Ad confluentes fluviorum Kabul et Indus prope Attok, ca. 200 m (RECH. 19647, 19648).

Cenchrus L.

Brachiaria GRISEB.

C. ciliaris L. – E: Tisin, an der Strasse von Kabul nach Jallalabad (KN. 2185). Dakka, an der Strasse Jallalabad nach Peshawar (KN. 2134). Zwischen Tshagan Serai und Nurgel, unteres Kunar-Tal zwischen Tshagan Serai und Jallalabad, 600– 800 m (KN. 665). – Pakistan: Peshawar: In collibus supra Dargai, ca. 400 m (RECH. 19628). Peshawar, ca. 350 m, Agricult. Res. Farm (KN. 2166). An der Bahn zwischen Lahore und Peshawar, 200–350 m (KN. 2163).

Digitaria HEIST. ex FABRICIUS

D. cruciata (NEES) A. CAMUS in LECOMTE – Pakistan: Chitral: Beorai Gol, S of Drosh, ca. 6000 ft., at edge of irrigation channel (St. 3273).

The spikelets are not so turgid as in typical D. cruciata and the upper glume is larger, but the tip of the upper lemma does project visibly in some spikelets. The inflorescence is typically that of D. cruciata and not D. adscendens.

D. Ischaemum (SCHREB.) SCHREB. ex MUHL. – E: Kabul: Paghman, Begtut, westlich von Kabul, Ackerunkraut (V. 2223).

D. sanguinalis (L.) Scop. – NE: Nuristan: Vama, ca. 1300 m (E. 1234). Zwischen Nischai und Ningalam (N. 1951/800). – Pakistan: Swat: Kalam, ca. 2200 m, substr. granit. (RECH. 19432, 19476).

Echinochloa P. BEAUV.

E. crus-galli (L.) P. BEAUV. – **SW:** Farah: Ad margines deserti Dasht-i Margo prope Khormalik inter Farah et Delaram, ca. 800 m, ad fontem (RECH. 19276). – **C:** Unterhalb Doab, Bewässerungsgraben (V. 504). Ghorband, NNW Kabul, ca. 1700 m (K. 2775). – **NE:** Nuristan: Zwischen Nischai und Ningalam (N. 1951/799). – **Pakistan:** Chitral: Koghosi, ca. 5000 ft., damp shady rich ground (B. L. 8). Chitral village, ca. 5500 ft., at edge of irrigation channel (St. 3166). Swat: Utror, ca. 2500 m, substr. granit. (RECH. 19593).

E. crus-galli (L.) P. BEAUV. var. *brevisetum* DOELL – E: Kabul: Reisfeld bei Gulbagh, ca. 1800 m (G. 350). Ruderal in einem Garten in Kabul, ca. 1780 m (G. 348). Ruderal im Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m (G. 347).

E. crus-galli (L.) P. BEAUV. var. longisetum DOELL – E: Kabul: Reisfeld bei Gulbagh, ca. 1800 m (G. 351).

Panicum L.

P. antidotale RETZ. – SW: Seistan, ca. 500 m, S Farah (K. 3698). – SE: Kajkai, NNW of Kandahar, ca. 1000 m (K. 2172). – E: Kabul-Schlucht bei Sarobi, ca. 1050 m (G. 352, 353). Abhänge bei Sarobi (V. 1895).

P. miliaceum L. – E: Kabul: Tschelsutun (N. 1950/94). – NE: Iamid (Vakhan), cult. (L. s. n.).

P. turgidum FORSSK. – Pakistan: Karachi, Wüste (V. K. 226-b).

Pennisetum RICH. in PERS.

P. divisum (FORSSK.ex GMEL.) HENR. – **SE:** Kandahar: Zwischen Kandahar und Ghirishk am Hilmend, ca. 1000 m (KN. 261). Pirzada, near Kandahar, 900–1000 m (K. 2044, 2074). Tshilsina, bei Kandahar, ca. 1000 m (K. 2241). Yaktchal (L. 411). – **Pakistan:** Karachi, Wüste (V.K.-226).

P. flaccidum GRISEB. – E: Kabul: Schotterbank im Nedschrab-Tal bei Schechan, zwischen Gulbahar und Sarobi, ca. 2200 m (G. 364). – C: Bamian, ca. 1600 m (K. 2896). – NE: Panjshir: Ruka, Panjshir, ca. 2000 m (K. 2932). Nuristan: Vama, ca. 1300 m (E. 1230). Porande-Tal, Seitental des Panjshir-Flusses bei Basarak, ca. 2150 m, Wegränder (G. 363). Zwischen Gusalak und der Einmündung des Kurder-Flusses, unteres Petsch-Tal, ca. 1150 m (Kn. 741). Gusalak, im Kurder-Tal, Seitental des Petsch-Tales (N. 1951/821). Bagrami, im Nedjerau-Tal (N. 1951/252). Gadwol, im oberen Ramgel-Tal, ca. 1970 m, Bachschutt (Kn. 1128). Puschol, im oberen Ramgel-Tal, ca. 2250 m (Kn. 1103-d). – Pakistan: Chitral: Shishi Gol, NE of Drosh, ca. 7000 ft., at edge of fields (St. 3144). Mastuj-Baroghil Track, Bang, ca. 8000 ft., at edge of fields (St. 2932). Lutkuh (Luthko), ca. 8000 ft., at edge of fields (B. L. 796). P. lanatum KLOTZSCH – NE: Nuristan: Ashpi Pass (E. 1770, N. 1951/1052, 1054). Auf dem Wege zwischen Ashpi-Pass und dem Ort Kuschtos, 2500–3500 m (N. 1951/ 725). Darim-Tal ab Ort Darim aufwärts, 1900–2400 m (N. 1951/1016). Pashki, ca. 2300 m (E. 1335). Wama, im oberen Petsch-Tal, ca. 1300 m (Kn. 1290). East-Nuristan (E. 1122). Südlich von Gadwol im Ramgel-Tal, ca. 1900 m (Sch. 133). Bei Puschol im oberen Ramgel-Tal, ca. 2250 m (Kn. 1106-a). Auf einem Berg oberhalb Kamdesch, ca. 2800 m (G. 365). – Pakistan: Chitral: Madaklasht, NE of Drosh, ca. 10000 ft., stony ground (St. 3136). Swat: Kalam, ca. 2200 m, substr. granit. (Rech. 19423, 19437). Ushu, ca. 2400 m, substr. granit. (Rech. 19513).

P. orientale L. C. RICH. - SW: Jija, südlich von Herat, ca. 900 m (K. 4267). -SE: Kajkai, NNW of Kandahar, ca. 1000 m (K. 2143). Germaub am Hilmend nördlich von Kandahar, ca. 1200 m (Kn. 384, 396-b). Kandahar, Steppe (V. K.-228). - E: Zwischen dem Heiligengrab Seh Baba und Dschegdelek, an der Strasse von Kabul nach Jallalabad, Grassteppe (Kn. 614-b). Schutthalde am Fuss einer Felswand südöstlich von Sarobi, ca. 1050 m (G. 360). Zwischen Sarobi und Darunta, Felssteppe (V. 1927). Im Tal des Kabul-Flusses bei Tang-e Gharu, 1600-1800 m, auf Felsschotter (Kn. 562, Sch. 61-a, G. 361, Hdg. & Wdb. 3053). Sher Darwasa near Kabul, ca. 2100 m, steep stony slopes (HDG. & WDB. 3166). In valle Paghman prope Kabul, 2300–2800 m, Gneiss (RECH. 17170), 2700–3000 m (CH-M.). – C: Steiler Berghang im Saighan-Tal, linkes Seitental des Bamian-Flusses zwischen Doab und Bulola, ca. 1820 m (G. 362). – NE: Kataghan: In valle fluvii Kunduz inter Pul-i Khumri et Doshi, 700-800 m (Rech. 16523). Doshi, ca. 3000 m, rocky slopes (M.). Nuristan: Gusalak, ca. 1000 m (E. 1551, 2143). - Pakistan: Chitral: Arandu, SW of Drosh, ca. 4000 ft., on rocky ledges in tufts (ST. 2294). Ghairat, S of Chitral, ca. 4500 ft., on dry stony hillside (St. 3266).

P. triflorum NEES – NE: Nuristan: Zwischen Wama und Tschetras im Petsch-Tal, ca. 1700 m, an Wegränder (KN. 1322).

Setaria P. BEAUV.

S. glauca (L.) P. BEAUV. – N: Mazar-i Sharif: Mazar-i Sharif, Hotelgarten (N. 1950/207). – NE: Pul-e Khomri, Flussufer (N. 1950/223). – Pakistan: Chitral: Chitral village, ca. 5000 ft., at edge of field (ST. 3174).

S. italica (L.) P. BEAUV. - NE: Nuristan: Nuristan (E. 2244).

S. verticillata (L.) P. BEAUV. – C: Ufer des Salatin-Flusses bei Pschang, in der Nähe von Doab, ca. 1700 m (G. 359). – NE: Nuristan: Im Kurder-Tal bei Gusalak, Seitental des Petsch (N. 1951/817).

S. viridis (L.) P. BEAUV. – SE: Ghirishk, ca. 880 m, Wiesen (G. 354). – E: Kabul: Kartetschar, ca. 1780 m (G. 356). Zwischen Kartetschar und Gusargah, ca. 1780 m (G. 357). In collibus ad septentriones urbis Kabul, ca. 1800 m (RECH. 17039). Guzar Geh, bei Kabul (N. 1950/796). Bewässerungsgraben im Garten der Oberrealschule in Kabul, ca. 1770 m (G. 355). – NE: Kataghan: Imam Sayid (V. K-235). Kunduz, in horto inculto (RECH. 16017). – C: Bamian: Shibar Pass, WNW Kabul, ca. 2500 m (K. 2793). Hauz-i Mahiha, SW of Kabul (K. 2469). – **Pakistan: Chitral:** Yarkhun Tal: Zwischen Mastuj und Reshm an der Mündung des Turikho, 1800–2000 m (KN. K-235). Drasan, im unteren Turikho-Tal, ca. 2080 m (KN. 2059). Chitral village, ca. 5000 ft., at edge of fields (ST. 3171).

S. viridis (L.) P. BEAUV. var. maior (GAUD.) KOCH – NE: Nuristan: Baschgal-Tal, zwischen Badamuk und Ningalam (SCH. 165-a).

Tricholaena SCHRAD. ex ROEM. et SCHULT.

T. Teneriffae (L. f.) LINK – **Pakistan: Peshawar:** In collibus supra Dargai, ca. 400 m (RECH. 19625).

Aeluropus TRIN.

Pooideae-Aeluropodeae

Ae. lagopoides (L.) TRIN. var. lagopoides - SW: Hamun, ca. 600 m (K. 3444). - SE: Kandahar (N. 1949/807).

Ae. lagopoides (L.) TRIN. var. mesopotamicus (NáBĚLEK) BOR (Syn. Aeluropus mesopotamicus NáBĚLEK). – SW: Hamun, ca. 500 m (K. 3445).

Ae. littoralis (GOUAN) PARL. - N: Mazar-i Sharif: In limosis salsis 10 km a Shibarghan occidentem versus, ca. 350 m (Rесн. 16120). – NW: Maymana: 5 km outside Maymana, ca. 500 m (Hpg. & Wpb. 3617). - SW: Herat (N. 1950/42). Nördlich des Herat-College (N. 1950/269). - SE: Kajkai, NNW of Kandahar (K. 2179). Tshil-sina, bei Kandahar, ca. 1000 m (Kn. 2238). Bei Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (Kn. 223-a, 225-b, 229-a). – E: Ghazni: Okak, ab altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (Rech. 17752). Kabul: Wazirabad, bei Kabul (N. 1950/41, 1951/165). Scharenau (Tschaman Wazirabad), ca. 1750 m (G. 518). Oestlich von Tscharasiah, ca. 1740 m, sumpfige Ebene (G. 517). In planitie ad orientem urbis Kabul secus viam versus pagum Sarobi ducentem, ca. 1700 m (Rech. 16905). Zwischen Kabul und Aliabad, ca. 1780 m, auf einer Weidewiese (G. 520). Zwischen Kabul und Tang-i Gharu, ca. 1770 m, in der Salzsteppe (G. 519). In collibus a Kabul septentriones versus, ca. 1800 m (RECH. 17041). Bala Hissar, am Beginn des Logar-Tales, südlich von Kabul (N. 1951/36, 134-a, 347). Pandscheschah bei Kabul (N. 1950/818). – C: Bamian: Am Ufer des Kalou-Flusses, Mündungsgebiet bei Schar-e Schak, ca. 2320 m (G. 522). Doab (V. 1752). Zentraler Gebirgsstock bei Bamian (N. 1951/427). Hauz-i Mahiha to Farakulum, ca. 2900 m (K. 3051).

Ae. macrostachyus HACK. – SE: Kandahar: Marja, Boghra distr., S of Ghirishk (V. 1302). Zwischen Kandahar und Ghirishk am Hilmend, 900–1000 m (KN. 251). Pirzada, near Kandahar, ca. 900 m (K. 2120, 2121, 3831). Kandahar, trockener Hang (N. 1949/35).

Agrostis L.

Pooideae-Agrostideae

A. canina L. – E: In feuchten Felsspalten in einer Schlucht oberhalb des Nedschrab-Tales, zwischen Gulbahar und Sarobi, östlich von Kabul, ca. 3100 m (G. 441, 442). Oberhalb Beg tut, im Paghman-Gebirge, westlich von Kabul, feuchte Matten, ca. 2900 m (G. 440). Kotal-i Kotandar, im Paghman-Gebirge, an quelligen Stellen (G. 443 – ad var. *pusillam* Aschers. et GRAEBN. vergens). – C: Bamian: Band-i Amir, Kalktuffe (V. 2266). – NE: Nuristan: Minjan, Ptili, ca. 2700 m (K. 2099). Unterhalb des Semenek-Passes, Westhang, ca. 3400 m (KN. 1498-a, 1511). – Pakistan: Chitral: Shandur Pass, SE of Mastuj, ca. 12000 ft., at edge of streams (ST. 3083).

A. canina L. var. varians Aschers. et GRAEBN. – E: Seitental des Panjshir-Flusses bei Basarak, bewachsener Uferstreifen an einem Nebenfluss des Porande-Flusses, ca. 2800 m (G. 444). – C: Bamian: Obere und mittlere Seen von Band-i Amir, Zentraler Gebirgsstock (N. 1951/457). – NE: Nuristan: Auf dem Wege zwischen Aschpi-Pass, ca. 3500 m, und dem Orte Kuschtos, ca. 2500 m (N. 1951/714). Zwischen Kotal-e Agok (Agok-Pass) und Alm bis Ort Waigel (N. 1951/879, N. 1951/882).

A. gigantea Roth. - SE: Kandahar: Kandahar (V. K-223). - E: Ghazni: In monte ad occidentem jugi Sardalu inter Qarabagh et Sang-i Masha, ca. 2600 m, substr. gyps. (RECH. 17358). Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17935). Kabul: Qala-e Wazir, inter Sar-i Chashma (Tschesch-me) et jugum Unai, ca. 2900 m (RECH. 18092). - C: Ghorat: Qala Shahrak (Sharak), ca. 2000 m (RECH. 19138). Bamian: Band-e Amir, feuchter Moostuff (V. 2279), in ca. 2800 m (RECH. 18306, 18320). Wiesenflächen am Ufer von Band-e Amir, ca. 2900 m (G. 437). Band-e Amir, ca. 2900 m (K. 2840). Sumpfwiese im Sard darra in der Koh-i Baba Kette, ca. 3350 m (G. 438). Panjao, in der Koh-i Baba Kette, ca. 2700 m (K. 2716). Lal-i Zarjangel, ca. 2500 m (K. 3063). Shibar Pass, nordwestlich von Kabul (V. 2799). - NE: Panjshir: Im Porande-Tal, Seitental des Panjshir-Tales, westlich von Daolana, ca. 2350 m (G. 435). Nuristan: Kulam (Munui) im Kulam-Tal, ca. 2150 m, nasse Wiesen (Kn. 1062-a, Sch. 105). Oberes Paschki-Tal bei Wama, Eichenwaldrand, ca. 1400 m (Kn. 1285). Im Parun-Tal bei Paschki, Auewiesen, ca. 2200 m (Kn. 1360). Paschki, ca. 2300 m (E. 1331). – Pakistan: Kalach-Gebiet: Im Brumboret-Tal unterhalb von Darasguru, 1500–1750 m (KN. 2081). Beorai Gol, ca. 6000 ft., at edge of irrigation channel (ST. 3269). Mastuj-Baroghil Track, ca. 8000 ft., at edge of fields (Sr. 2936). Golen Gol, steep moist bank (B. L. 16). Shandur, ca. 12000 ft., at edge of lake (B. L. 87). Swat: Kalam, ca. 2200 m, 35°30'N, 72°30'E (Rech. 19409).

A. hissarica Roshev., Not. Syst. Herb. Hort Petrop. 4: 93 (1923). (Syn. A. Stewartii Bor, Kew Bull. 1956: 255 (1956), syn. nov.). – C: Bamian: Band-i Amir, Kalktuffe (V. 2266). – Pakistan: Kulam (Kalam), ca. 2500 m (STEWART 24733).

A specimen of this species, named by ROSHEVITZ himself, has been seen and matches the type of A. Slewartii Bor: STEWART 24733.

A. Ruprechtii (Nevsкı) Nevsкı – C: Bamian: In latere austro-orientali jugi Hadjigak, in montibus Koh-i Baba, ca. 3000 m (Rech. 18526).

A. stolonifera L. – SE: Kandahar: Kandahar (V.K-223). – C: Hauz-i Mahiha, WSW of Kabul, ca. 2500 m (K. 3062). Band-i Amir, Seeufer, Zentraler Gebirgsstock (N. 1951/440). – E: Kabul: Oberhalb Beg tut, im Paghman-Gebirge, westlich von Kabul, ca. 2900 m (G. 436). Zwischen Tschardeh und dem Logar-Tal, südlich von Kabul,

ca. 1880 m (G. 433). Dehmasang, ca. 1770 m, Sumpfwiese (G. 432). – **NE: Panjshir:** Felswand bei Schingar, Seitental des Panjshir-Tales bei Basarak, ca. 2200 m (G. 434). – **Pakistan: Chitral:** Bang Gol, W of Mastuj, ca. 8000 ft. (St. 3066).

A. subaristata AITCH. et HEMSL. - NE: Nuristan: Gusalak, ca. 1000 m (E. 1190).

A. tenuis Sibth. – NE: Panjshir: Felswand bei Schingar, Seitental des Panjshir-Tales bei Basarak, ca. 2200 m (G. 439).

Rhizocephalus Boiss.

Rh. orientalis Boiss. - SW: Herat, ca. 1000 m (K. 4262).

Alopecurus L.

A. aequalis SOBOL. – NE: Nuristan: Minjan Kalha, ca. 2600 m (E. 2101). – Pakistan: Chitral: Shandur Pass, SE of Mastuj, ca. 12000 ft., on mud at shallow verge of lake (Sr. 3093).

A. apiatus Ovcz. – NE: Panjshir: Panjshir valley, W. side of Anjuman pass, ca. 4100 m (HDG. & WDB. 5448). – C: Bamian: Ad lacum Band-i Zolfikar, prope Band-i Amir, ca. 2900 m (RECH. 18447).

A. arundinaceus POIR. in LAM. - NW: Sauzak pass, ENE of Herat, ca. 2000 m (K. 2201). N of Sauzak pass, ca. 1400 m (K. 3954). - SE: Kandahar: Südlich von Kandahar, ca. 1000 m, Sumpfwiese (G. 389). Kalat-i Ghilzai, zwischen Ghazni und Kandahar, ca. 1000 m (Kn. 188). – E: Ghazni: Okak, ab altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (Rech. 17681, 17727). Dahan-e Barikak, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17976). Kabul: Darul-aman Ebene, östlich von Kabul, ca. 1700 m, Bewässerungsgraben (Kn. 462, Sch. 44). Dehmasang, ca. 1770 m, Sumpfwiese (G. 391). Zwischen der Strasse Dehmasang nach Neu-Delhi und Gusargah, ca. 1770 m, an Entwässerungsgräben der Salzwiesen (G. 390). In einem Garten bei Kabul, ca. 1760 m, an einem Bewässerungsgraben (G. 392). – C: Shibar Pass (V. 2805). Inter pagum Bulola et jugum Shibar, 2600–2800 m (RECH. 16795). Unai Pass, zwischen Kabul und Bamian, ca. 3120 m, quellige Stellen (G. 394). Farakulum, W of Unai Pass, ca. 3000 m (K. 2549). In latere austroorientali jugi Hadjigak montium Koh-i Baba, ca. 3000 m, ad rivulum (RECH. 18528). -**Pakistan:** Chitral: Luthko Bogosht, between 35°55'N, 71°18'E, and 36°06'N, 71°48'E, ca. 8000 ft., at edge of fields (B. L. 773). Oihor Gol, 36°04'N, 71°48'E, ca. 10000 ft., cornfields (B. L. 854). Baroghil Pass, ca. 12500 ft., on open slopes (ST. 2983). Chitral Gol, W of Chitral village, ca. 8000 ft., in tufts (ST. 2685).

A. arundinaceus POIR. in LAM. var. pashkiensis MELDERIS, var. nov.

A typo statura humiliore (10–25 cm alta), rhizomatibus brevirepentibus, caespites densos formantibus, ligulis brevioribus (0,5–1 mm longis), foliorum laminis brevioribus (1,5 cm longis) angustioribusque (1,5–2,5 mm latis), paniculis densis, brevioribus (1–2 cm longis), basi rotundatis vel cuneatis, glumis brevioribus (ad 3,5 mm longis), antheris minoribus (2–2,5 mm longis), bene differt.

NE: Nuristan: Pashki, ca. 2300 m, 9.6.1948 (EDELBERG 916, Holotypus, C). A. glacialis C. Koch – NE: Nuristan: Shtive, ca. 2900 m (E. 1037). A. himalaicus HOOK. f. – NE: Nuristan: Minjan, above Weran, ca. 3800 m (E. 1276). West-Seite des Mrami-Passes in Richtung Schtiwe, ca. 3000 m (KN. 1407-b). Badakhshan: Koul-Choghnan, entre Sangaou et Yeljah, Pam Darreh (L. 1960/901-b). – Pakistan: Chitral: Oihor Gol, $36^{\circ}04'$ N, $71^{\circ}48'$ E, 11000 ft., near or in running water (B. L. 824). Phargam An Gol, Laspur, ca. 14000 ft., $36^{\circ}05'$ N, $72^{\circ}16'$ E, dry steep slope (B. L. 71). Agram, Arkari Gol, W of Tirich Mir, ca. 10500 ft., at edge of stream (ST. 2639). Shera Shing Pass, N of Drosh, ca. 14000 ft., on rocky slopes (ST. 3210). Zwischen Dorah Pass und Baur, 4000–4300 m (KN. 1527-a).

A. mucronatus HACK. – C: Unai Pass (N. 1951/503). Koh-i Baba, ca. 3300 m (K. 3052). Hesaredschad, Baraki Nawor, Zentraler Gebirgsstock (N. 1949/908).

A. myosuroides HUDS. – E: Sarobi, (V. 2573). Kalat Saradj, östlich von Kabul, Ackerrand (V. 1938). – NE: Nuristan: Gusalak, ca. 1000 m (E. 237, 1548). – Pakistan: Peshawar: Agricult. Res. Farm, ca. 350 m (KN. 2172).

A. pratensis L. – NE: Nuristan: Parun-Tal Bei Pashki, Auewiesen in einer Mulde, ca. 2000 m (KN. 1358). Westseite des Semenek-Passes, unterste Steilstufe, flache, steinige Matten, ca. 3400 m (KN. 1507).

A. vaginatus (WILLD.) PALL. – NE: Nuristan: Pashki, ca. 2700 m (E. 991). East-Nuristan (E. 1071, 1093).

Calamagrostis ADANS.

C. dubia BGE. - SE: Pirzada, near Kandahar, ca. 900 m (K. 2096).

C. Epigeios (L.) Roth – C: Bamian: Am Ufer der Seen von Band-i Amir, ca. 2900 m (G. 461). Band-i Amir, ca. 3200 m, feuchter Kalksand (V. 2292).

C. gigantea Rosнev. – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (Recн. 17934).

C. glauca (M. B.) TRIN. - C: Bamian: Lal-i Zarjangel, ca. 2500 m (K. 2772).

C. pseudophragmites (HALL. f.) KOEL. - NW: Ardewan, ca. 1300 m (K. 2256). -SW: Dilaran, ESE of Farah, ca. 1100 m (K. 3065). - E: Kabul: Paghman, W of Kabul, ca. 2100 m (K. 2297, 2299). Sarobi, östlich von Kabul, Bachufer (V. 1224). In planitie ad orientem urbis Kabul secus viam versus Sarobi ducentem, ca. 1700 m (RECH. 16901). Tang-i Gharu, im Tal des Kabul-Flusses, 1600-1700 m (Kn. 550). Kabul gegen Guzar Gah (N. 1950/155). Dehmasang bei Kabul, ca. 1770 m, Sumpfwiesen (G. 459). In einem Garten in Kabul, an Bewässerungsgräben, ca. 1800 m (G. 480, V. 728). - C: Farakulum, ca. 2700 m (K. 3064). Bamian: Sumpfwiese im Kamard-Tal, am rechten Ufer des Surch-Flusses, westlich von Doab, ca. 1620 m (G. 457). Doab, Flussufer (V. 1774, 1776). Inter Bamian et Band-i Amir, 2800-3000 m (Rech. 18178). Near Nayek, on road from Band-e Amir to Panjao, ca. 2600 m, on gravelly streamside (HDG. & WDB. 4822). Ghorat: In faucibus calcareis infra Parjuman (Partcheman), ca. 1850 m (RECH. 19019). - NE: Panjshir: Schutt- und Geröllhalde am Ufer des Porande-Flusses, Seitental des Panjshir-Flusses bei Basarak, ca. 2050 m (G. 458). Nuristan: Vama, ca. 1300 m (E. 1224). Weran, Nau, ca. 3000 m (E. 1472). Minjan Kachari, ca. 2300 m (E. 2085). Minjan Ptili, ca. 2700 m (E. 2098). Gadwol im oberen

Ramgel-Tal, ca. 1970 m (Kn. 1127). Oberhalb Kulam nach dem Pirdum Pass, 2200-2900 m, im Schutt des Bachufers (Kn. 1076). Paschki, im Parun-Tal, ca. 2280 m, Auewiesen (KN. 1361). Mrami- (Papruk-) Pass, 2300-3000 m, Ostseite (KN. 1442). Vom Semenek Pass bis zum Paninger-Tal oberhalb Ahmedi Dewane, 2600-3400 m, Steinfluren (KN. 1503-a). - Pakistan: Chitral: Im Brumboret-Tal, unterhalb von Darasguru, 1500–1700 m, Kalash-Gebiet (Kn. 2080). Yarkhun-Tal bei Mastuj, 2040– 2280 m, Hippophaë-Rosa-Hecken und nasse Wiesen (KN. 2043). Bang Gol, N of Mastuj, ca. 9000 ft., on drv stony slopes (Sr. 3067). Beorai Gol, S of Drosh, ca. 6000 ft., at edge of irrigation channel (ST. 3270). Golen Gol, ca. 6000 ft., 36°01'N, 72°10'E, stream bed (B. L. 5).

Muhlenbergia SCHREB.

M. Huegelii TRIN. – NE: Nuristan: Unteres Baschgal-Tal bei Kamdsch, 1800– 1900 m, nasse Ruderalhänge (Kn. 1454). Unteres Papruk-Tal, zwischen Papruk und der Mündung in den Baschgal-Fluss, 1500-2300 m (Kn. 1428-b).

Phleum L.

Ph. alpinum L. – C: Bamian: Koh-i Baba, ca. 3300 m (K. 2647). – NE: Panjshir: valley, W. side of Anjuman Pass, ca. 3700 m, on wet slopes (HDG. & WDB. 5494). Nuristan: Westseite des Semenek-Passes, unterste Steilstufe, flache, steinige Matten, ca. 3400 m (Kn. 1510). Auf dem Wege zwischen Aschpi-Pass und dem Ort Kuschtos, 2500-3500 m (N. 1951/719). Entrè Sangaou et Yelgah Pam Darreh (L. 901-a). -C: Bamian: Koh-i Baba, in latere austro-orientali jugi Hadjigak, ca. 3800 m (RECH. 18544).

Ph. Boissieri BORNM. - NE: Nuristan: Chetras (E. 856). Gusalak, ca. 1000 m (E. 54, 1583, 2089).

Ph. himalaicum Mez – E: Kabul: Berghang bei Sarobi, östlich von Kabul, ca. 1500 m (G. 397, V. 1894-b). Tang-i Gharu, im Tal des Kabul-Flusses, 1600-1700 m (KN. 543). - NE: Nuristan: Unteres Petsch-Tal zwischen Gusalak und der Mündung des Kurder-Flusses, ca. 1150 m (Kn. 730). Unterhalb Wama, im oberen Petsch-Tal, ca. 1380 m (Kn. 757). Zedernwald bei Kamdesch, ca. 2100 m (G. 388).

Ph. paniculatum Hubs. – N: Danaghosi, swamps, ca. 2400 ft. (M.). – Pakistan: Chitral: Arandu, SW of Drosh, ca. 4000 ft., at edge of fields (ST. 2292).

Polypogon DESF.

P. fugax NEES ex STEUD. - SE: Kandahar: Pirzada, near Kandahar, ca. 980 m (K. 2041). - E: Kabul: Zwischen Tang-i Saidan und Lallandar, Schotterbank am Ufer des Kabul-Flusses, ca. 1810 m (G. 456). Sumpfiger Graben östlich der Strasse Dehmasang nach Dar-ul-fanun, ca. 1780 m (G. 455). In faucibus Tang-e Gharru, inter Kabul et Sarobi, 1400-1500 m, substr. Gneiss (RECH. 16929, 16931). Kotsche Mullah, bei Kabul (N. 1950/156, 798). Munar Schakrie, bei Kabul (N. 1951/441-b). Guzar Gah, bei Kabul (N. 1950/799, 826). Im Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m (G. 454). - C: Kamard-Tal, am rechten Ufer des Surch-Flusses, 4

Biol.Skr.Dan.Vid.Selsk. 14, no. 4.

westlich von Doab, ca. 1620 m (G. 453). Zwischen Bamian und Band-i Amir (V. 2783-a). In faucibus inter Mollah Jakub et Dahan-e Siah Darreh, 4 km E Panjao, ca. 2800 m, Gneiss (RECH. 18726). – NE: Kataghan: Kunduz, in paludosis fluvii Kunduz ca. 400 m (RECH. 16023, 16048). Nuristan: Zwischen Parigel und Waigel, 1700–1800 m (KN. 1193). Am Ufer eines Bächleins bei Eschpuschta, ca. 1500 m (G. 452). – Pakistan: Chitral: Beorai Gol, S of Drosh, ca. 2000 ft., at edge of irrigation channel (ST. 3268). Chitral village, ca. 5000 ft., at edge of fields (ST. 3167).

P. maritimus WILLD. – E: Ghazni: In monte ad occidentem jugi Sardalu inter Qarabagh et Sang-i Masha, ca. 2600 m, substr. gyps. (RECH. 17356). Kabul: Botkhak, 20 km östlich von Kabul (N. 1951/354). – C: Hauz-i Mahiha, WSW of Kabul, ca. 2600 m (K. 2415). Bamian: Zwischen Bamian und Band-i Amir, am Rande der Thermen (V. 2783-b). Band-i Amir, ad lacum Band-i Panir, ca. 2800 m (RECH. 18383). Band-i Amir, Kalksinterterrasse zwischen zwei Seen, ca. 2900 m (G. 451).

P. monspeliensis (L.) DESF. – N: Danaghosi, ca. 2400 ft. (M.). – SE: Kajkai, NNW of Kandahar, ca. 1100 m (K. 3057). Girishk, westlich von Kandahar (L. 1958/ 311). Siason (L. 1958/300). – E: Kabul: Maslakh, am Ufer eines Tümpels (N. 1951/153). Guzar Gah, bei Kabul (N. 1951/159, 173). Kabul (N. 1950/814, 828). – NE: Nuristan: Gusalak, ca. 1000 m (E. 1579).

P. semiverticillatus (FORSSK.) HYLANDER (Syn. Agrostis semiverticillata (FORSSK.) CHRIST.). – SE: Kandahar: Kajkai, NNW of Kandahar, ca. 1000 m (K. 3058). Girishk, westlich von Kandahar (V. 1332). Kandahar, 1000–1200 m, feuchte Gräben (KN. 216, Scн. 73). – E: Ghazni: Inter jugum Kotal-e Ketschru et pagum Miradina, a Sang-i Masha boreo-occidentem versus, 2700-3200 m (RECH. 17581). Ghorband, südlich von Kabul, Tuff-Fels (V. 582-d). Khotsche Mullah bei Kabul, am Rande eines Tümpels, stark versalzen (N. 1951/181). Khotsche Mullah, an trockener Stelle (N. 1951/184-b). Zwischen Tschardeh und dem Logar-Tal, ca. 1840 m, Matte in einer Schlucht (G. 431). Zwischen Tang-i Saidan und Lallandar, ca. 1810 m (G. 430). Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m (G. 429). – C: Hauz-i Mahiha, ca. 2500 m (K. 2487). Hauz-i Mahiha, ca. 2800 m, in rivulo lente fluente (RECH. 18550). Im Kamard-Tal, am rechten Ufer des Surch, westlich von Doab, ca. 1620 m (G. 423). - NE: Kataghan: In valle fluvii Kunduz inter Doshi et Doab, 800-1300 m (Rech. 16589). In paludosis fluvii Kunduz, ca. 400 m (Rech. 16048). Nuristan: Gusalak, ca. 1000 m (E. 1584). - Pakistan: Chitral: Shoghot, N of Chitral, ca. 6000 ft., on marshy ground (St. 2746).

Aristida L.

Pooideae-Aristideae

A. adscensionis L. – E: Unterhalb des Dorfes Nurgel im unteren Kunar-Tal, zwischen Tshagan-Serai und Jallalabad, 600–800 m, Gneiss-Schiefer (KN. 666). Bei Wama im oberen Petsch-Tal, ca. 1380 m, Eichenwald (KN. 1284-a). – NE: Nuristan: Gusalak, im Kurder-Tal, Seitental des Petsch-Tales (N. 1951/836). Darim-Tal ab Ort Darim aufwärts, 1900–2400 m (N. 1951/1006). – Pakistan: Dir.: Distr.: Panj-

kora-Tal bei Warai, ca. 1000 m (Kn. 2106, 2112). Warai, ca. 1200 m (Kn. 2117-a). **Quetta:** Near Quetta, ca. 1100 m (K. 3059).

A. ciliata DESF. in SCHRAD. – E: Jallalabad (V. 2050). Zwischen Nimla und Jallalabad, ca. 600 m (Kn. 630). Nimla, an der Strasse Kabul nach Jallalabad, auf Felsschotter (Sch. 75).

A. cyanantha NEES ex STEUD. – E: Kabul: In glareosis supra Sarobi, ca. 1000 m, ab urbe Kabul orientem versus (RECH. 19347). Im Nedschrab-Tal oberhalb Schechan, zwischen Gulbahar und Sarobi, ca. 2600 m (G. 397). Gulbahar bei Charikar (V. 1020). Oestlich von Istalif, zwischen Kabul und Charikar, Strassenböschung, ca. 1900 m (G. 396). Südhang des Aliabader Berges bei Kabul, ca. 1860 m, in einer Schlucht (G. 395). – C: Ghorband, WNW of Kabul (E. 2910). – NE: Nuristan: Asmar Barikot, ca. 900 m (E. 1611, 1614). Unteres Petsch-Tal bei Sinsi, oberhalb Retschalam, ca. 960 m (KN. 698). Aschkun-Gebiet: Im Kotagel-Tal bei Kulatan, ca. 1500 m (KN. 1223-a). Im Tal und um den Ort Kurder, Seitental des Petsch-Tales, 1600–1700 m (N. 1951/757). – Pakistan: Peshawar: In collibus supra Dargai, ca. 400 m (RECH. 19627). Chitral: Shishi Gol, NE of Drosh, ca. 6000 ft., at edge of fields (ST. 3149).

A. Griffithii HENR. - E: Kabul: Kabul, ca. 1700 m (K. 4006).

A. pennata TRIN. – N: Kataghan: Kunduz, zwischen Hazrat-e Eman und Kunduz (N. 1949/33). Sanddünen bei Karum Kul, nächst Ankhoi (N. 1950/208, 210). Zwischen Ankhoi und Schebergan, auf Sanddünen (N. 1950/211). – NW: Maymana: In arenosis mobilibus ad margines deserti Kara-Kum ca. 15–20 km ab Andkhui austro-occidentem versus, ca. 300 m (RECH. 16129). Halfway between Maymana and Andkhui, ca. 400 m, on sand dunes (HDG. & WDB. 3837).

A. plumosa L. – SE: Kandahar: Pirzada, near Kandahar, ca. 900 m (K. 2099). – E: Inter Jallalabad et Torkhan, in deserto arenoso, ca. 700 m (RECH. 19357). Jallalabad, Gneisshügel (V. 2049). Zwischen Sarobi und Darunta, östlich von Kabul, Steppe (V.). Sarobi (V. 2575). Tang-e Gharu, near Kabul, ca. 1600 m (HDG. & WDB. 5104). – NE: Kataghan: Zwischen Kunduz und Hazrat-e Emen (N. 1949/34).

A. pogonoptila (JAUB. et SPACH) BOISS. – E: Jallalabad, östlich von Kabul, Gneiss-Hügel (V. 2049). Zwischen Sarobi und Darunta, in der Steppe (V. 1966).

A. Raddiana SAVI – SE: Kandahar: In der Schlucht bei Germaub, nördlich von Ghirishk, auf Konglomerat (KN. 413).

Arundo L.

Pooideae-Arundineae

A. Donax L. – SE: Kandahar: Kajkai, N of Kandahar, ca. 1000 m (K. 2171). – E: Kabul: Schlucht Tang-e Gharu, östlich von Kabul, Schutthalde am Ufer des Kabul-Flusses, ca. 1650 m (G. 497). – C: Zwischen Doab und Schibar-Pass, am Fluss (N. 1950/224).

Phragmites TRIN.

Ph. communis TRIN. – N: Mazar-i Sharif: Südlich von Tashkurghan, am Fluss und als Unkraut in einem Baumwollfeld (N. 1950/214, 225). – SW: Herat: Cheshma Obeh, ca. 1800 m, substr. granit. (RECH. 19244). Seistan, ca. 550 m (K. 3463). – E: Kabul: In faucibus Tang-e Gharru, inter Kabul et Sarobi, 1100–1300 m, substr. conglom. (RECH. 16958). In der Salzsteppe zwischen Kabul und Tang-e Gharru, ca. 1770 m (G. 492). Zwischen Kartetschar und Aliabad, auf einer Weidewiese, ca. 1780 m (G. 493). Am Ufer des Logar-Flusses bei Tscharasiah, südlich von Kabul, ca. 1780 m (G. 494). Pandscheschah bei Kabul, Schilfsumpf (N. 1950/37). – C: Am Ufer des Schumbol-Flusses bei Bulola, ca. 2280 m, Wiese (G. 495). Am Ufer des Bamian-Flusses bei Schar-e Schak, ca. 2320 m (G. 496). – NE: Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m (G. 491). Badakhshan: Faizabad, bord de rivière (L.). – Pakistan: Chitral: Im Yarkhun-Tal bei Mastuj, 2040–2280 m, nasse Wiesen, *Hippophaë-Rosa*-Hecken (KN. 2044, 2045). Brumboret, SW of Chitral, ca. 9000 ft., damp meadow (St. 3217).

Pooideae-Aveneae

A. barbata POTT. ex LINK in SCHRAD. – E: Schlucht Tang-e Gharru, östlich von Kabul, 1600–1700 m, sehr steinig (Sch. 59-a).

A. fatua L. – SE: Kandahar: Tshil-sina (SCH. 20). – E: Sarobi (V. 2591). – C: Farakulum, ca. 2700 m (K. 2522). Doab, feuchter Acker (V. 2098). In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m, felsiger Hang (G. 463-a). – NE: Badakhshan: Ishkamish, östlich von Jurm, Löss-Steppe (V. 2655). Jurm, ca. 1500 m (E. 2088). Qazi Deh (L. 1106). – Pakistan: Chitral: Yabur (Sch. 169). Tirich-Mir-Gebiet: Im Ojhor-Tal bei Tsusum, ca. 2800 m (KN. F-134).

A. fatua L. var. glabrata Ретевм. – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (Recн. 17949).

A. ludoviciana DUR. – Pakistan: Chitral: Arandu, SW of Drosh, ca. 4000 ft., a weed in fields of barley (ST. 2291).

A. Wiestii STEUD. – NW: Khwaja, NE of Herat, ca. 700 m (K. 3793). – SE: Kandahar: Nordlich von Ghirishk am Hilmend (KN. 409). Kajkai, NNW of Kandahar, ca. 1000 m (K. 3038). Tshil-sina bei Kandahar (SCH. 20). – NE: Nuristan: Gusalak, ca. 1000 m (E. 1545).

Deschampsia P. BEAUV.

Avena L.

D. caespitosa (L.) P. BEAUV. – Pakistan: Chitral: Baroghil Pass, ca. 12500 ft., at edge of stream (St. 2998).

D. koelerioides REGEL – NE: Minjan, above Weran, ca. 3600 m (E. 1264). – Pakistan: Chitral: Agram, Arkari Gol, W of Tirich Mir, ca. 10500 ft., at edge of stream (ST. 2642). Dorah Pass, Lutko valley, NW of Chitral, ca. 13500 ft., at edge of stream (ST. 3247).

Hierochloe R. BR.

H. laxa R. Br. ex Hook. – NE: Nuristan: Pashki to Atsni Pass, ca. 2800 m (Е. 705).

H. odorata (L.) WAHLENB. – NE: Nuristan: Westseite des Donda-Passes (Sch. 141). Porande-Pass, zwischen Aschkun-Gebiet und Petsch-Tal, ca. 3280 m (Kn. 1237).

Koeleria PERS.

K. cristata (L.) PERS. (Syn. K. gracilis PERS.). - E: Ghazni: In faucibus Say Khoshkak (Nawar Kotal), inter Okak et Behzud (Diwal Kol), ca. 3150 m, in saxosis calcareis (RECH. 17847, 17848). Panjshir valley, westside of Anjuman-Pass, ca. 3700 m, on dry slopes (HDG. & WDB. 5490). - C: Bamian: Kotal-i Reg, ca. 3400 m (K. 3067). - NE: Kataghan: Passhöhe Rabatak, zwischen Haibak und Pul-i Khomri (N. 1950/222). Nuristan: Pashki, ca. 2300 m (E. 905). Shtive, ca. 2800 m (E. 1035). Westseite des Semenek-Passes, ca. 3400 m, flache, steinige Matten der untersten Steilstufe (Kn. 1503). Pitwei-Tal, zwischen Pirdum-Pass und Kulam (Munui), 2200-2900 m, Grashang (Kn. 1080). Mum-Pass, zwischen Parun- und Kantiwo-Fluss, Aufstieg von Gulnischa aus, 2500–2800 m (Kn. 874-a). Dondo-Pass, Aschkun-Gebiet, 2500-3200 m, Matten (Kn. 1251-a). Westseite des Semenek-Passes, ca. 3400 m, flache, steinige Matten der untersten Steilstufe (Kn. 1508). – Pakistan: Chitral: Rosh Gol, NE of Tirich Mir, ca. 9000 ft., on stony ground (Sr. 2809). Chumarkan Pass, E of Mastuj, ca. 12000 ft., on dry open slopes (St. 2900). Rosh Gol, NE of Tirich-Mir, ca. 10000 ft., on stony ground (St. 2805). Baroghil Pass, ca. 12500 ft., on open slopes (Sт. 2985).

Sphenopus TRIN.

S. divaricatus (GOUAN) REICHENB. – SE: Kandahar: Von Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (KN. 224).

Lophochloa REICHENB.

L. phleoides (VILL.) REICHENB. (Syn. Festuca phleoides VILL., Koeleria phleoides (VILL.) PERS.). – N: Mazar- i Sharif: Tacht-e Rustam prope Haibak, ca. 1200 m, in collibus calcareis (RECH. 16378). In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (RECH. 16305). – SE: Kandahar: Nördlich von Arghandab, zwischen Kandahar und Ghirishk, 900–1000 m, Steppe (KN. 315). Im Norden von Kandahar in der Steinsteppe, ca. 1000 m (KN. 373-b, 2218, 2219-b, SCH. 1). Tshil-sina bei Kandahar, ca. 1000 m (KN. 344). – E: Sarobi (V. 1894, 1894-a). Panjshir: Ufer des Panjshir-Flusses bei Gulbahar, nächst Charikar, ca. 1700 m (G. 498-b, N. 1950/827). NE: Kataghan: Inter Haibak et jugum Paigah-Kotal (RECH. 16419). Nuristan: Zwischen Asmar und Barikot, ca. 840 m (G. 498-a). Am Ufer eines Mühlbaches bei Barikot, ca. 850 m (G. 499). – Pakistan: Chitral: Drosh, in running water in ditch (B. L. 700).

L. pumila (DESF.) BOR (Syn. Avena pumila DESF., Koeleria pumila (DESF.) DOMIN). – E: Sarobi (V. 2474). Dakka, an der Strasse von Jallalabad nach Peshawar, ca. 600 m (Kn. 2191).

Trisetaria FORSSK.

T. Cavanillesii (TRIN.) MAIRE (Syn. Trisetum Cavanillesii TRIN.) – SW: Herat: Shin Dand, SSW of Herat, ca. 1200 m (K. 4260). – SE: Kandahar: Zwischen Kalat-i Ghilzai und Kandahar, Steppe (Kn. 209). – E: Kabul: Zwischen Kabul und Tang-i Gharu, sandige Hügel (G. 462). – NE: Nuristan: Gusalak, ca. 1000 m (E. 1534, 2090).

Pooideae-Brachypodieae

T. distachya (L.) LINK (Syn. Brachypodium distachyon (L.) P. BEAUV.). – N: Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (RECH. 16304). – SE: Kandahar: In einer Schlucht bei Germaub, am Hilmend nördlich von Ghirishk, Konglomeratboden (KN. 409-b). Kajkai, NNW of Kandahar (K. 3040). Goldgrube im Nordwesten von Kandahar in der Steinsteppe (Sch. 3). Goldgrube im Norden von Kandahar in der Steinsteppe, ca. 1000 m (KN. 369-a). – E: Kabul: Schutthalde südöstlich von Sarobi, ca. 1100 m (G. 684, 685). Sarobi, Cymbopogon-Steppe (G. 2563-a).

Pooideae-Bromeae

Boissiera Hochst. ex Steud.

Trachynia LINK

B. squarrosa (SOLAND.) NEVSKI (Syn. B. bromoides Hochst. ex Steud., B. pumilio (TRIN.) HACK.). - N: Mazar-i Sharif: Takht-e Rustam prope Haibak, ca. 1200 m, in collibus calcareis (RECH. 16387). - SW: Jija, Shin Dand to Farah, ca. 1100 m (K. 4257). - SE: Kandahar: In einer Schlucht bei Germaub, am Hilmend nördlich von Ghirishk, Konglomerat (Kn. 409-d). Kajkai, NNW of Kandahar, ca. 1000 m (K. 3042). Baba Wali, Argandab-Tal, nordwestlich von Kandahar, auf einem Friedhof (KN. 352, Sch. 8, 10, 11). In der Steinsteppe nordwestlich von Kandahar (Sch. 4). Nördlich von Kandahar, ca. 1070 m (G. 474). Tshil-sina bei Kandahar, ca. 1000 m (Kn. 2234-b, 2235, 2244). Kalat-i Ghilzai, Artemisia-Steppe (Kn. 167-a). Orozgan (L. 937). - E: Ghazni: In monte ad occidentem jugi Sardalu, inter Qarabagh et Sang-i Masha, ca. 2800 m, substr. gyps. (Rech. 17450). Dasht-e Tup, a Maidan meridiem versus, inter Ghazni et Kabul, ca. 2400 m (RECH. 17246). Alischang-Tal bei Jallalabad (Rosenstiel, Kn. F-60). Zwischen Kabul und Tang-e Gharu, ca. 1770 m (G. 475). Darulfanum, südwestlich von Kabul, Steppe (V. 2074). Gipfelfelsen des Koh-i Tschelsotun, ca. 2210 m (G. 384). Zwischen Sher Darwasa und Koh-i Tschelsotun, ca. 2020 m (G. 482). Sher Darwasa bei Kabul, 1800-2000 m (G. 477, 478, 480-b, 481, HDG. & WDB. 2884). Gipfel im Korogh-Massiv, ca. 2800 m (G. 487). Aliabad bei Kabul (N. 1950/820, 833, 1951/147, V. 1556). Bagrami (Bagram) near Charikar, ca. 5000 ft. (Cn. 29, 32). Berg NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 484). In einem Garten in Kabul, ca. 1780 m, ruderal (G. 476). – C: Vorberge der Koh-i Baba Kette bei Bamian, 2600-3000 m (G. 486, 488). Kalkberg nordöstlich von Bamian, ca. 3000 m (G. 489). Im Schutt der Ruinen von Gholgola bei Bamian, ca. 2550 m (G. 485). Band-e Amir, westlich von Bamian, ca. 2900 m (HDG. & WDB. 4794). - NE: Kataghan: In jugo Paigah Kotal inter Haibak et Pul-i Khomri (RECH. 16474). Badakhshan: Faizabad, 110–1900 m (E. 1404). Tang-e Saidan, Steppe (L. 792). Pakistan: In valle Kurram (AITCH. 568). Quetta: Near Khojak Pass, ca. 1900 m (K. 3041).

Bromus L.

B. Danthoniae TRIN. - N: Mazar-i Sharif: In der Steppe zwischen Aqtscha und Mazar-i Sharif (N. 1950/220). Kataghan: Ankhoi, bei Kunduz (N. 1950/219). -SW: Herat, ca. 1100 m (K. 4254-b). Jija, 800–1200 m (K. 4253, 4254, 4255). – SE: Kandahar: In einer Schlucht bei Germaub, am Hilmend nördlich von Ghirishk, Konglomerat (Kn. 409-c). Nördlich von Arghandab, zwischen Ghirishk und Kandahar, 900-1000 m (Kn. 316). Bei der Goldgrube nordwestlich von Kandahar, ca. 1000 m (Kn. 355-c, 2255-c). Nördlich von Kandahar, ca. 1070 m (G. 642). Tshil-sina bei Kandahar, ca. 1000 m (KN. 2234-a, 2244). An Salzstellen bei Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (Kn. 222-b). Orozgan, L. 936). - E: Ghazni: In monte ad occidentem jugi Sardalu inter Qarabagh et Sang-i Masha, ca. 2600 m, substr. gyps. (RECH. 17418). Sang-i Masha, ca. 2500 m (RECH. 17477). Ca. 5 km a Arghandab meridiem versus, inter Ghazni et Kabul, ca. 1900 m, ad versuras et in agris incultis (RECH.). Unter dem Gipfel des Sebroderakan bei Scherwaki im Logar-Tal, ca. 2500 m (G. 655). Zwischen Sarobi und Darunta (V. 1917). Berghang bei Sarobi, ca. 1500 m, Steppe (G. 643, V. 2559). Surkhab-Damm, Kabul-Tal, Artemisia-Steppe (V. 122). Koh-e Tschelsotun, ca. 2200 m (G. 654). Kuh-i Nanagak, S of Gulbagh, ca. 1830 m (HDG. & WDB. 3198). Unter dem Gipfel eines Berges zwischen Koh-e Asmai und dem Aliabader Berg, ca. 1920 m (G. 647). Aliabader Berg, ca. 2070 m (G. 651). Aliabad, bei Kabul (N. 1950/832, 1951/133-a). Tobfels am Scher Darwasah, ca. 1840 m (G. 646). Scher Darwasah, bei Kabul, ca. 2000 m (G. 649). In valle Paghman prope Kabul, ca. 2300 m, substr. Gneiss (RECH. 17126). Beim Königsschloss von Paghman, ca. 2160 m (G. 652, 653). Babur bei Kabul, Abhänge (V. 2024). In einem Garten in Kabul, ruderal (G. 645, N. 1951/133-b). – C: Bamian: Hauz-i Mahiha, WSW of Kabul, ca. 2600 m (K. 2416). Unterhalb des Unai-Passes, ca. 2900 m, steiler Schutthang (G. 658). Unai-Pass ca. 3100 m (G. 660, 661, N. 1951/536, 1951/562). Kalkberg ENE von Bamian, ca. 2800 m (G. 656). Vorberg der Koh-i Baba Kette bei Bamian, ca. 2900 m (G. 657). Auf den Hügeln und an den Ufern der Seen von Band-e Amir (N. 1951/471, 479). Band-e Amir, 2800-2900 m, in declivibus saxosis aridis (RECH. 18234). Band-i Amir, ad lacum Band-i Panir, ca. 2800 m (Rech. 18335). - NE: Badakhshan: Faizabad, 1100-1900 m (E. 2109). Schutthalde im Salang-Tal bei Taghma, ca. 1760 m (G. 644). Pakistan: Kurram Valley (AITCH. 568). Quetta: Near Quetta, ca. 1600 m (K. 3043).

B. fasciculatus PRESL - SW: Jija, Shin Dand to Farah, ca. 900 m (K. 4256).

B. gracillimus BGE. – E: Ghazni: Okak, ab altoplanitie Dasht-e Nawar boreoorientem versus, ca. 3000 m (RECH. 17680). – C: Unai-Pass, 2800–3100 m, an Berghängen und an quelligen Stellen (G. 612, 613, V. 2142). Inter Bulola et jugum Shibar, 2600–2800 m (RECH. 16783). Ibidem, ca. 2200 m (HDG. & WDB. 4184). Band-i Amir, ad lacum Band-i Panir, ca. 2800 m (RECH. 18401). Kalkinterterrasse zwischen zwei Seen von Band-i Amir, ca. 2900 m (G. 611). – NE: Nuristan: Minjan, Miyan Deh, ca. 2550 m (E. 2105). – Pakistan: Chitral: Baroghil Pass, ca. 12500 ft., on open slopes (St. 2981). B. intermedius Guss. – E: In collibus ad septentriones urbis Kabul, ca. 1800 m (RECH. 17057).

B. japonicus THUNB. – SE: Kandahar: In der Steinsteppe nordwestlich von Kandahar, im trockenen Geröll (Sch. 2-b). Bei Sakird südlich von Kandahar, ca. 980 m, Feldrand (G. 669). Bei Kandahar in der Richtung nach Kalat-i Ghilzai, ca. 1100 m (Kn. 237-a). Kandahar, ca. 1000 m (Kn. 2255-a, -b). – E: Unter der Kammhöhe eines Berges südöstlich von Sarobi, ca. 1430 m (G. 663, 675). Schutthalde auf einem Berg bei Sarobi, ca. 1100 m (G. 670). Sarobi, Steppe (V. 2518, 2563, 2564). Zwischen Sarobi und Lataband, Steppe (V. 1867). Kabul: Darulfanun, Weizenfeld (V. 1655). Tisin, an der Strasse von Kabul nach Jallalabad (KN. 2183). Upper part of Tang-i Gharru, very frequent beside the Kabul river, ca. 1700 m (HDG. & WDB. 2758-b). Foot of Sher Darwasah, near Kabul, ca. 1800 m, on stony slopes (HDG. & WDB. 2876). Berg NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 674-b). Scharenao bei Kabul, ruderal in einem Weizenfeld (N. 1951/167). In einem Garten in Kabul, ca. 1780 m, ruderal (G. 667). Panjshir: Panjshir-Tal (V. 254-a). Porande-Tal, Seitental des Panjshir-Tales bei Basarak, Wiese am rechten Porande-Ufer östlich von Daolana, ca. 2350 m (G. 668). - C: Im Kamard-Tal westlich von Doab, ca. 1640 m, Schutthalde am Fuss einer Felswand (G. 665). Doab (V. 1799-a). - Nuristan: Gusalak, ca. 1000 m (E. 1582). Nishei, ca. 1300 m (E. 827). Vama, ca. 1400 m (E. 488). Kulam (Munui), im Kulam-Tal, auf Wiesen (Sch. 98). Parigel-Tal, linkes Seitental des unteren Kulam-Tales beim Dorf Parigel, ca. 1800 m, trockener Hang (Kn. F-75). Parun-Tal, zwischen Schtive und Paschki, 2300-2500 m, auf Felsen (Kn. 1385-b). Oberes Petsch-Tal, Felshänge bei Wama, ca. 1400 m (Kn. 777). An einem Mühlbach bei Barikot, ca. 850 m (G. 662). East-Nuristan (E. 1123). – Pakistan: Chitral: Madakhlasht, NE of Drosh, ca. 10000 ft., on stony ground (Sr. 3141). Bashgalian, Kafiristan, SW of Chitral, ca. 9500 ft. (Sr. 2700).

B. japonicus Thunb. var. acutidens Melderis, var. nov.

A typo spiculis velutinis, glumis 3–5-nerviis, lemmate longiore, 11–12 mm longo, lemmatis lobis acuminatis, differt. – Appropinquat ad *B. oxyodontem* SCHRENK, sed spiculis velutinis, glumis brevioribus, inferioribus 5–7 mm longis, 1–3-nerviis, superioribus 8–10 mm longis, 3–5-nerviis, marginibus non distincte angulatis, diversa.

NE: Nuristan: Kantivo, ca. 2300 m (Edelberg 731, Holotypus, C). Vama, ca. 1400 m (Edelberg 508). Gusalak, ca. 1000 m (Edelberg 1558).

B. japonicus THUNB. var. velutinus (NOCCA et BALBIS) ASCHERS. et GRAEBN. f. humilis GILLI – E: Im Kabul-Tal südöstlich von Sarobi, ca. 1050 m, Schutthalde (G. 673-a). Unter dem Gipfel eines Berges zwischen dem Scher Darwasah bei Kabul und dem Kuh-e Tschelsotun, ca. 2020 m (G. 678). Unter dem Gipfel des Sebroderakan bei Scherwaki im Logar-Tal, südlich von Kabul, ca. 2500 m (G. 680). Gipfelregion eines Berges bei Paghman, westlich von Kabul, ca. 2870 m (G. 672). Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m (G. 676).



Fig. 3. Bromus Koeieanus MELDERIS (K. 2631, Holotypus, C).

Bromus Koeieanus MELDERIS, sp. nov. Fig. 3, 4.

Gramen perenne, 20–35 cm altum, dense caespitosum. Culmi graciles, 2–3-nodi, basi ascendentes vel geniculati, vaginis emarcidis brunneis integris tecti, teretes, striati, glabri, laeves. Folia viridia; vaginae inferiores glabrae vel brevissime setulosae, superiores glabrae laeves; ligulae 1–4 mm longae, hyalinae, laceratae; auriculae absentes; laminae 3–10 cm longae, 1–2 mm latae, planae, tenuiter nerviae, utrinque \pm breviter pubescentes. Panicula 5–8 cm longa, erecta, laxa, effusa, pauci-spiculata, rhachidi scabriuscula, ramis 1,5–4 cm longis, suberectis, solitariis vel binis, scabriusculis, 1–2-spiculatis. Spiculae 1,2–1,8 cm longae, 3–4,5 mm latae, anguste lanceolatae, 5–7-florae, virides vel leviter purpureo-tinctae. Glumae persistentes, leviter carinatae, hyalino-marginatae, nervis glabris, inaequilongae, sensim acuminatae; gluma inferior 5,5 mm longa, linearis, 1–3-nervia, gluma superior 8–12 mm longa, anguste lanceolata,



Fig. 4. Bromus Koeieanus MELDERIS, a part of the panicle (K. 2631, Holotypus, C) 4.5/1.

3–5-nervia, mucronata, mucrone usque ad 1 mm longo. Lemma 8–12 mm longum, firmum, oblongo-lanceolatum, brevissime setulosum, 7-nerve, apice leviter bidentatum, breviaristatum, arista usque ad 4 mm longa, erecta. Palea lemmati subaequilonga, anguste lanceolata, bicarinata, carinis apicem versus breviciliatis. Rhachilla 2 mm longa, strigosa. Antherae 4,5–5 mm longae, luteae. – Affinis *B. tyttholepidi* NEVSKI, a quo statura minore, culmis glabris, foliorum laminis angustioribus, paniculis effusis pauci-spiculatis, rhachidi scabriuscula, spiculis minoribus, lemmate longiore, differt. *B. frigido* BOISS. et HAUSSKN. similis, sed foliorum laminis utrinque vulgo breviter pubescentibus, glumis distincte nervatis, sensim acuminatis, lemmate brevissime setuloso, differt.

C: Bamian: Koh-i Baba, ca. 3600 m (Køre 2631, Holotypus, C). – E: Kabul: Oberes Paghman-Tal (NEUBAUER 1950/789).

B. lanceolatus ROTH – E: Kabul: In valle Paghman, ab urbe Kabul occidentem versus, 2300–2800 m, substr. Gneiss (RECH. 17171). – NE: Kataghan: In jugo Paigah Kotal, inter Haibak et Pul-i Khumri, ca. 1400 m (RECH. 16488). Mirza Abtili Pass, SE of Samangan, ca. 1380 m, roadside (HDG. & WDB. 4037-a). Surkhab-Damm, östlich von Kabul, Artemisia-Steppe (V. 122). – NE: Khanabad: Khanabad (M.). Nuristan: Kulam (Munui) im Kulam-Tal, trockene Wiesen (Sch. 96). Parigel-Tal, Seitental des unteren Kulam-Tales beim Dorf Parigel, ca. 1800 m (KN. W-53).

B. madritensis L. – E: In der Tang-e Gharu, Kabul-Schlucht bei Sarobi, ca. 1050 m (G. 637). Kabul, am Gipfel des Koh-e Tschelsotun, ca. 2210 m, in Felsritzen (G. 640). Im Salang-Tal bei Taghma, ca. 1760 m, Schutthalde (G. 666). Tobfels am Scher Darwasah bei Kabul, ca. 1840 m (G. 677). Im Paghman-Tal, westlich von Kabul, ca. 2750 m, in Felsritzen (G. 679). Berg am linken Ufer des Paghman-Tales, ca. 2750 m (G. 671, 681). Berg NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 674-a). Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m (G. 638). – C: Inter Bulola et jugum Shibar, ab urbe Kabul boreo-occidentem versus, 2600–2800 m (RECH. 16808).

B. madritensis L. var. ciliatus Guss. – SW: Jija, Shin Dand to Farah, ca. 900 m (K. 4257).

B. oxyodon SCHRENK – SE: Kandahar: Von Kandahar in der Richtung nach Kalat-i Ghilzai, ca. 1100 m (KN. 236). – E: In der Schlucht des Kabul-Flusses bei Tang-e Gharu, 1600–1700 m (SCH. 59-b). Tisin, an der Strasse von Kabul nach Jallalabad, in einem Weizenfeld (KN. 592, SCH. 70). Panjshir: Ca. 2 km above Gulbahar, near Charikar, Panjshir valley, ca. 1700 m, stony slopes (HDG. & WDB. W-2980). N: Doshi, ca. 2750 ft. (M.). Nuristan: Pistalik, ca. 1300 m (K. 3866, 3957). Oberes Petsch-Tal, an Felshängen bei Wama, ca. 1400 m, lichter Eichenwald (KN. 776, SCH. 87). Kulam (Munui) im Kulam-Tal, auf Wiesen (SCH. 97). Oberes Ramgel-Tal bei Gadwol, ca. 1970 m, trockene Hänge (KN. F-114).

B. ramosus Hubs. - Pakistan: Chitral: Yarkhun, ca. 8500 ft. (B. L. 943).

B. scoparius L. – SE: Kandahar: Bei Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (Kn. 222-a). – E: Sarobi, Steppe (V. 1915). Kabul, Maslakh, Schlachthaus (N. 1951/141). – NE: Kataghan: Bala Hissar, prope Kunduz, in declivibus siccis, ca. 400 m, substr. Loess (Rech. 16070). Kunduz, in horto inculto (Rech. 16026). – NW: Maymana: 30 km W of Maymana, ca. 500 m, on dry slopes (HDG. & WDB. 3643-b).

B. sericeus DROBOV – SW: Herat, ca. 900 m (K. 3746). – SE: Kandahar: Baba Wali, bei Kandahar, auf einem Friedhof (SCH. 7). Tshil-sina, bei Kandahar, ca. 1000 m, steiniger Felshang (KN. 2236). Am Tschui bei Kalat-i Ghilzai (KN. 199). Kalat-i Ghilzai, Artemisia-Steppe (KN. 152). – E: Koh-i Asmai, nördlich von Kabul, ca. 1700 m (KN. 426). Sandige Hügel zwischen Tang-e Gharu und Kabul, ca. 1770 m (G. 619). SSW-Hang des Scher Darwasah bei Kabul, ca. 1790 m (G. 682). Tobfels am Scher Darwasah, ca. 1840 m (G. 624). Begram, near Charikar (CN. 30). – C: Farakulum, ca. 2700 m (K. 3045). Near Ghorband, ca. 3000 m (E. 2371).

B. stenostachys Boiss. – NE: Nuristan: Mrami- (Papruk-) Pass, Ostseite des Papruk, 3000–3400 m (Kn. 1440). Westseite des Papruk-Passes, in Richtung Shtive, 3000–4200 m (Kn. 1411). – Pakistan: Chitral: Zwischen Dorah-Pass und Gabur, 3300–4000 m (Kn. 1523). Khot An, N of Mastuj, between Turikho and Mastuj River, ca. 10000 ft. (St. 2862). Shah Jinali, Yarkhun River area, 10500 ft. (B. L. 1021). Tirich Gol, ca. 10500 ft. (B. L. 1071). Chumarkhan Pass, E of Mastuj, ca. 12000 ft., dry open slopes (St. 2901).

B. tectorum L. - NW: Nördlich von Herat, Artemisia-Steppe, ca. 940 m (G. 641). Herat (AMSEL). - SE: Kandahar: In der Steinsteppe nordwestlich von Kandahar, trockenes Geröll (Scн. 4). Kalat-i Ghilzai, Steppe (L. 325). – E: Ghazni: Sang-i Masha, ca. 2500 m (RECH. 17469). In monte ad occidentem jugi Sardalu, inter Qarabagh et Sang-i Masha, ca. 2600 m (RECH. 17398). Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17953). Darulaman-Ebene, östlich von Kabul, ca. 1700 m, Bewässerungsfelder (Kn. 453-a, Scn. 40). Sarobi (V. 2020, 2517). Schlucht des Kabul-Flusses bei Tang-i Gharu, 1600–1700 m (Kn. 551). Kabul, Gipfel im Korogh-Massiv, ca. 2800 m (G. 632). Unter dem Gipfel eines Berges zwischen dem Scher Darwasah und dem Koh-e Tschelsotun, ca. 2020 m (G. 630). Unter dem Grabmal Chodsche Safa am Scher Darwasah, 1820–1840 m, (G. 625, 626). Tobfels am Scher Darwasah, ca. 1840 m (G. 623, 624). Am Scher Darwasah bei Kabul, 1900–2000 m (G. 627, 629, N. 1951/68). In valle Paghman ab urbe Kabul occidentem versus, 2300-2800 m (Rect. 17099). Istalif, nördlich von Kabul, ca. 1840 m (G. 621). Berg NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 631). Südhang des Aliabader Berges bei Kabul, ca. 1860 m (G. 622). An einer Berglehne bei Aliabad, nächst Kabul, südexponiert (N. 1951/148). Berg westlich vom Koh-i Asmai, ca. 1920 m (G. 628). Beim Dorf Babur bei Kabul, ca. 1700 m (Kn. 104). W of Kabul, ca. 1800 m, in Medicago field (HDG. & WDB. 3247). Ruderal in einem Garten bei Kabul, ca. 1780 m (G. 620, N. 130-a, 131). - C: Unai-Pass, westlich von Kabul (N. 1951/553, 563). In valle Ajar "Königstal" a Doab occidentem versus, 1400–1500 m (Rech. 16599). Im Kamard-Tal westlich von Doab, ca. 1630 m, auf Kalkschutt am Fuss einer Felswand (G. 616). Im Uferschutt des Salatin-Baches bei Pschang unweit Doab, ca. 1700 m (G. 617). In valle ca. 16 km a Doab meridiem versus, ca. 1600 m (RECH. 16697). In valle Dare Shikar (Darra-i Shikari), inter Doab et Bulola, 1600–2000 m (RECH. 16701). Inter pagum Bulola et jugum Shibar, 2600–2800 m (Rech. 16784). Kalkberg ENE Bamian, ca. 2800 m (G. 633). Gipfelregion eines Kalkberges bei Bamian, ca. 3140 m (G. 636). Vorberg der Koh-i Baba Kette bei Bamian, ca. 2900 m (G. 634). Band-i Amir: Ad lacum Band-i Pamir, prope Band-i Amir, ca. 2800 m (Rech. 18400). Kalksinterterrasse zwischen zwei Seen von Band-i Amir, ca. 2900 m (G. 635-b). Sandbank am Seeufer bei Band-i Amir (G. 635-a). In declivibus saxosis aridis prope Band-i Amir, 2800–2900 m (RECH. 18281). Ghorat: A Naourak austro-occidentem versus, ca. 2480 m (RECH. 18959). - NE: Doshi, ca. 2750 ft. (M.). Nuristan: Oberes Ramgel-Tal bei Gadwol, ca. 1970 m, trockene Hänge (Kn. F-115). Aqtscha, Flussaue (N. 1950/212). Kouh Khvadjah Ghar, coteau (L. 1959/504). – Pakistan: Chitral: Arkari Gol, W of Tirich Mir, ca. 8500 ft., on stony ground (Sr. 2602).

B. tectorum L. var. *hirsutus* REGEL – **NE: Nuristan:** Pashki, ca. 2300 m (E. 1178). – Minjan, Miyan Deh, ca. 2550 m (E. 1450). Minjan, Ptili, ca. 2700 m (E. 2096).

B. tomentosus TRIN. – C: Bamian: Band-i Amir, 2800–2900 m, in declivibus saxosis aridis (RECH. 18237). Band-i Amir, ca. 3200 m, Igelsteppe (V. 2751). – E: Panjshir: Panjshir valley, W. side of Ajuman Pass, ca. 3700 m, on dry stony slopes (HDG. & WDB. W-5499).

B. variegatus M. B. – E: Aufstieg vom Schakhdarre zum Hauz-e chaz, 2800–2900 m im Paghman-Gebirge, westlich von Kabul (G. 610).

Pooideae-Chlorideae

Cynodon RICH. in PERS.

C. Dactylon (L.) PERS. - SE: Kandahar: Pirzada, near Kandahar, ca. 900 m (K. 2001). Kandahar (V. 1347). - E: Schutthalde am Ufer des Kabul-Flusses bei Tang-e Gharru, östlich von Kabul, ca. 1650 m (G. 467). Damm zwischen Reisfeldern bei Gulbagh, ca. 1800 m (G. 469). Oestlich von Tscharasiah, ca. 1740 m (G. 470). Zwischen Kartetschar und Aliabad bei Kabul, ca. 1780 m (G. 468). Aliabad bei Kabul, Salzwiesen (V. 896). Wazirabad bei Kabul, trockener Beckenboden (N. 1950/43), Wardak, südwestlich von Kabul, Wiesen (V. 807). In den Bergen zwischen Tschardeh und dem Logar-Tal, ca. 1880 m (G. 471). Kabul, allgemein verbreitet (N. 1950/810). Panjshir: Gulbahar bei Charikar (V. 205, 258-a). Kataghan: Baghlan, Brache (V. 686). - C: Im Kamard-Tal westlich von Doab, ca. 1550 m, Weideflächen (G. 466). Doab, oberhalb des Hotels, ca. 1500 m (V. 314, 1753). - NE: Taligan, bei Khanabad, Gräben (V. 610). Nuristan: Gusalak, ca. 1000 m (E. 1187). Vaigel, ca. 1500 m (E. 884). Zwischen Asmar und Barikot, ca. 840 m, Quercus Baloot-Bestand (G. 464). Barikot, ca. 850 m (G. 465). Oberes Ramgel-Tal bei Gadwol, ca. 1970 m (Kn. 1129). Unteres Papruk-Tal, zwischen Papruk und der Mündung in den Baschgal, 1500–2300 m (KN. 1429). – Pakistan: Chitral: Shishi Gol, NE of Drosh, ca. 7000 ft., at edge of fields (St. 3155).

Tetrapogon DESF.

T. villosus DESF. (Syn. *Chloris villosa* (DESF.) PERS.). – E: Hills 30 miles E of Kabul, ca. 2800 m (M.). Unteres Kunar-Tal zwischen Tschaghan-Serai und Jallalabad, 600–800 m, Gneiss-Schiefer (KN. 664-a). Jallalabad (SCH. 77-a). Zwischen dem Heiligengrab Seh-Baba und Nimla, an der Strasse von Kabul nach Jallalabad, auf Schotter (KN. 621). Tisin, an der Strasse von Kabul nach Jallalabad (KN. 2188). – **NE: Nuristan:** Zwischen Asmar und Barikot, ca. 840 m, *Quercus Baloot*-Wald (G. 472). Nishei, ca. 1300 m (E. 816, 826). Kulatan im oberen Medschegel-Tal, ca. 1460 m (KN. K-56). Spuk-Pass, Südseite bei Bardadesch, ca. 1700 m (KN. F-88). – **Pakistan: Quetta:** Near Quetta, ca. 1600 m (K. 3068).

Pooideae-Danthonieae

Danthonia DC. in LAM. et DC.

D. cachemyriana JAUB. et SPACH – NE: Nuristan: Pashki, ca. 2300 m (E. 656, 1024). Spuk-Pass, zwischen Parigel und Waigelek, ca. 2760 m (Kn. 1199).

Schismus P. BEAUV.

Sch. arabicus NEES – SW: Shin-Dand, ca. 1200 m (K. 4258). – SE: Kandahar: Ruderal um Ghirishk, ca. 880 m (G. 524). Kajkai, NNW of Kandahar, ca. 1000 m (K. 3050). Pirzada, near Kandahar, ca. 900 m (K. 2015). Goldgrube im Norden von Kandahar in der Steinsteppe, ca. 1000 m (G. 525, KN. 373-a, 2203-a). – E: Ghazni: Zwischen Kabul und Gardez, Brachfeld (V. 100). Dakka, an der Strasse von Jallalabad nach Peshawar, ca. 600 m (KN. 2192). Tisin, an der Strasse von Kabul nach Jallalabad (KN. 597). Im Nedschrab-Tal oberhalb Schechan, zwischen Gulbahar und Sarobi, *Pinus Gerardiana*-Wald, ca. 2580 m (G. 531). Sarobi, Steppe (V. 1908, 2475). Scher Darwasah bei Kabul, 1790–1840 m (G. 528, 529, 530). In einem Garten in Kabul, ruderal (G. 527-a). – C: Am Ufer des Salatin-Baches bei Pschang, unweit Doab, ca. 1700 m (G. 526-a). – NE: Nuristan: Gusalak, ca. 1000 m (E. 135). – Pakistan: Balouchistan: Kila Abdulla (LACE 3006). Balouchistan (STOCKS).

Sch. barbatus (L.) THELL. – E: Kabul: Sarobi, östlich von Kabul, Steppe (V. 1908, 2475). Aliabad bei Kabul (N. 1950/824). Bagrami bei Charikar, nördlich von Kabul, trockener Hang (N. 1951/289). Gulbahar bei Charikar (N. 1950/829). Kabul (N. 1950/834).

Pooideae-Eragrosteae

C. Gatacrei (STAPF) BOR (Syn. Diplachne Gatacrei STAPF) – NE: Nuristan: Kurder-Tal, Seitental des Petsch-Tales (N. 1951/806). – Pakistan: Chitral: (GATACRE 17626). Swat: (STEWART 24516).

Desmostachya STAPF

Cleistogenes KENG

D. bipinnata (L.) STAPF (Syn. Briza bipinnata L., Uniola bipinnata L., Cynosurus durus FORSSK., Poa cynosuroides RETZ., Eragrostis cynosuroides (RETZ.) P. BEAUV.). – SW: Jija inter Shin Dand et Farah, ca. 900 m (K. 4271, L. 111, RECH. 19269). Farah, champs (L. 308). Dahlah, dans sable (L. 344). – SE: Kandahar: Am Hilmend bei Germaub, nördlich von Ghirishk, ca. 1200 m (KN. 399). Ghirishk (V. 1322). Kajkai, NNW of Kandahar, ca. 1000 m (K. 2175). – E: Kabul: Hills 30 miles E of Kabul, 8000 ft. (M.). Jallalabad, ca. 580 m (G. 507). Khost Distr.: Dergai bei Matun (N. 1949/806). Ebene von Khost (V. 1086, 1199). – Pakistan: Peshawar, Agricult. Reserv. Farm, ca. 350 m (KN. 2170).

Eleusine GAERTN.

E. compressa (FORSSK.) ASCHERS. et SCHWEINF. ex C. CHRISTENSEN (Syn. E. flagellifera NEES) – E: Zwischen Nimla und Jallalabad, auf Schotter (Sch. 76). Jallalabad, Geröllhang (V. 2001).

Eragrostis P. BEAUV.

E. Barrelieri DAV. in MOROT – E: Khost Distr.: Jadji (V. 1104-b). – Pakistan: Dir: Panjkova-Tal bei Warai, ca. 1000 m (Kn. 2108-b, 2113).

E. cilianensis (ALL.) VIGN.-LUTAT. – SE: Kandahar: Boghra, südlich von Ghirishk (V. 1344). – E: Kurram: Patan, Kurram-Tal (V. 1124). – N: Kataghan: Baghlan, Brache (V. 686-a).

E. pilosa (L.) P. BEAUV. – **E:** Kabul: Zwischen Kartetschar und Gusargah ca. 1780 m, auf einem Möhrenfeld (G. 506). Kartetschar, ca. 1780 m, Gartenbeet (G. 505). Ad stagnum Band-e Kharghak, inter Kabul et Paghman, ca. 2000 m, in limosis exsiccatis (RECH. 19328).

E. poaeoides P. BEAUV. – N: Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700-800 m (Rech. 16312). Aq Kupruk, ca. 750 m, on cliff ledges (Hbg. & WDB. 3923). Between Samangan (Aybak) and Mirza Abtili Pass, ca. 1250 m, steppic vegetation (HDG. & WDB. 3997). – SE: Kandahar: Boghra, südlich von Girishk (V. 1344). - E: Am Ufer des Kabul-Flusses bei Jallalabad, ca. 600 m (G. 501-a). Am Ufer des Kabul-Flusses zwischen Tang-i Saidan und Lallandar, ca. 1810 m (G. 503). Guzar Gah bei Kabul, Gartenunkraut (N. 1950/830). Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m (G. 502). Kurram: Patan, Kurram Valley (V. 1124). Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak, feuchte Felswände bei Schingar, ca. 2220 m (G. 504). - NE: Kataghan: Inter Haibak et jugum Paigah-Kotal, 1300–1400 m (RECH. 16415). Nuristan: Wama im Petsch-Tal, ca. 1380 m, Stoppelfeld von Winterweizen (KN. 1235). Unteres Papruk-Tal zwischen Papruk und der Mündung in den Baschgal, 1500-2300 m (Kn. 1431). - C: Ufer des Salatin-Flusses bei Pschang, nächst Doab, ca. 1700 m (G. 501). - Pakistan: Chitral: Yarkhun-Tal bei Mastuj, 2040–2280 m, Brachen, Felder, Ruderalstellen (KN. 2042). Chitral village, ca. 5000 ft., at edge of fields (ST. 3173). Swat: Inter Madyan et Kulam, ca. 1700 m, substr. granit. (RECH. 19375). Peshawar: Ad confluentes fluvios Kabul et Indus prope Attok, ca. 200 m (RECH. 19649).

Tripogon ROEM. et SCHULT.

T. Hookerianus BOR (Syn. *T. abyssinicus* Ноок. f., Fl. Brit. Ind. 7 (1896) pr. pte., non NEES ex Steud.). – E: Sarobi, (V. 1912, 2561). – NE: Nuristan: Shtive, ca. 2600 m (E. 1032). Above Derin (E. 1747).

T. purpurascens DUTHIE (Syn. T. abyssinicus HOOK. f., Fl. Brit. Ind. 7 (1896) pr. pte., non NEES ex STEUD.). – E: Kurram: Patan, Kurram Valley, Felsspalten (V. 1287). – NE: Nuristan: Madschegel-Tal, zwischen Gultscheilam und Kulatam, 1500–1600 m, lichter Eichenbusch am Hang (KN. 1269).

Catabrosa P. BEAUV. Pooideae-Festuceae

C. aquatica (L.) P. BEAUV. – SW: Herat: 50 km S of Herat, ca. 1600 m (K. 2281). – E: Ghazni: Ad lacum Sabzab inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17900, 17915). Dahan-e Barikak, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17982). Kabul: Entwässerungsgraben der Salzwiesen zwischen der Strasse Dehmasang nach Darulfanun und Gusargah, ca. 1770 m (G. 500). Unteres Paghman-Tal, nasse Wiese (N. 1950/819). Qala-e Wazir, inter Sar-i Chashma et jugum Unai, ca. 2900 m (RECH. 18075). – C: Bamian: Koh-i Baba, in latere austro-orientali jugi Hadjigak, ca. 3000 m (RECH. 18535). Ghorat: A Naourak austro-occidentem versus, ca. 2480 m, in humidis (RECH. 18957). – Pakistan: Balouchistan: (DUTHIE).

Colpodium TRIN.

C. humile (M. B.) GRISEB. (Syn. Aira humilis M. B., Catabrosa humilis (M. B.) TRIN.). – NW: Sauzak, E of Herat (K. 3970). – NE: Nuristan: Parun to Minjan Pass, ca. 4000 m (E. 1274).

Dactylis L.

D. glomerata L. – NE: Nuristan: Nishei, ca. 1300 m (E. 809). Auf dem Wege zwischen Aschpi-Pass und dem Ort Kuschtos, 2500–3500 m (N. 1951/699).

D. glomerata L. var. himalensis DOMIN – Pakistan: Chitral: Golen Gol, ca. 7000 ft. (B. L. 26).

D. glomerata L. var. hispanica (Roтн) Boiss. – E: Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak, östlich von Daolana, ca. 2350 m (G. 523). Swat: Kalam, ca. 2200 m, substr. granit. (Recн. 19451, 19459).

Eremopoa Roshev.

E. bellula (RGL.) ROSHEV. (Syn. *Festuca bellula* REGEL). – **E:** Ghazni: Ad margine orientalem altoplanitiei Dasht-e Nawar, ca. 3000 m, in limosis salsis exsiccatis (RECH. 17802). – C: Hauz-i Mahiha to Farakulum, ca. 2900 m (K. 2508). Unai-Pass, ca. 3120 m (G. 566, N. 1951/561). Oberhalb Sard-darra in der Koh-i Baba Kette, ca. 4000 m (G. 567). – **NE: Nuristan:** Aoband Kotal, ca. 3000 m (E. 1814).

E. persica (TRIN.) ROSHEV. (Syn. Poa persica TRIN.). – E: Ghazni: In monte ad occidentem jugi Sardalu inter Qarabagh et Sang-i Masha, ca. 2600 m, substr. gyps. (RECH. 17354). Distr. Bezud: Dahan-e Abdila, 35 km a Sar-i Chashma orientem versus, ca. 2800 m, ad rivulum (RECH. 18594). Tisin, an der Strasse von Kabul nach Jallalabad, Felshang (KN. 600). Dar-ul Aman Ebene bei Kabul, ca. 1700 m, Fluss-chotter (KN. 443). Schutthalde in der Tang-e Gharu, 1600–1700 m (G. 559, KN. 502-b). Zwischen Kabul und der Tang-e Gharu, ca. 1770 m (G. 560). Paghman-Tal bei Kabul, 2300–2800 m, substr. Gneiss (G. 564, RECH. 17180-a, -b). Oberhalb Paghman, ca. 2470 m, in Felsspalten (G. 568). Koh-i Asmai bei Kabul, ca. 1700 m (KN. 498). Kabul (V. 1288). – C: Qala-e Wazir inter Sar-i Chashma et jugum Unai, ca. 2900 m (RECH. 18102). Kalkberg ENE von Bamian, ca. 2800 m (G. 570).

E. persica (TRIN.) ROSHEV. VAR. **oxyglumis** (BOISS.) BOR, comb. nov. (Syn. *Poa persica* TRIN. VAR. *oxyglumis* BOISS., Fl. Or. 5: 610 (1884), *E. oxyglumis* (BOISS.) ROSHEV., Fl. SSSR. 2: 430 (1934).). – E: Kabul: Südhang des Aliabader Berges bei Kabul, ca. 1860 m (G. 562). Vorberg des Korogh-Massivs bei Kabul, ca. 1950 m (G. 563). – C: Unai-Pass ca. 3120 m, an quelligen Stellen (G. 565).

E. persica (TRIN.) ROSHEV. var. songarica (SCHRENK) BOR, The Grasses of Burma, Ceylon, India and Pakistan 532 (1960). (Syn. Glyceria songarica SCHRENK, E. songarica (SCHRENK) ROSHEV., Fl. SSSR. 2: 431 (1934).). – E: Kabul: Scher Darwasah bei Kabul,

ca. 1790 m (G. 561). Oberhalb Beg tut, ca. 2900 m, im Paghman-Gebirge, feuchte Matten (G. 574). – C: Hauz-i Mahiha to Farakulum, ca. 2900 m (E. 611). Hauz-i Mahiha, ca. 2600 m (K. 2448). – NE: Nuristan: Netshingel, ca. 3500 m (E. 1564). Pashki, ca. 2350 m (E. 611).

As far as the genus *Eremopoa* ROSHEV. is concerned we are prepared to accept two species only *E. persica* (TRIN.) ROSHEV. and. *E. bellula* (RGL.) ROSHEV. *E. songarica*, *E. multiradiata* and *E. oxyglumis* are in our opinion only worthy of varietal rank.

Festuca L.

F. arundinacea Schreb. – NW: Sauzak, E of Herat, ca. 2000 m (K. 3039).

F. gigantea (L.) VILL. – **NE: Nuristan:** Oberes Petsch-Tal bei Wama, ca. 1380 m (KN. 1324). Oberes Badschingel-Tal (Sadel-Tal) bei Gwarnar, ca. 1900 m, Feldränder (KN. 1201-b). Oberes Petsch-Tal beim Weideplatz Tschetras, ca. 2090 m (KN. 1304). Unteres Paschgal-Tal bei Kamdesch, 1800–1900 m (KN. 1455). – **Pakistan: Swat:** Ushu, ca. 2400 m, substr. granit. (RECH. 19516).

F. ovina L. – E: Oberhalb des Nedschrab-Tales, zwischen Gulbahar und Sarobi, ca. 3310 m, Berghang (G. 590). Aufstieg vom Schakar-darra zum Hauz-e chaz im Paghmangebirge, ca. 3730 m (G. 591). – Pakistan: Chitral: Chumarkhan Pass, ca. 12000 ft., on dry open slopes (ST. 2899). Jingeret Gol, W af Drosh, ca. 12000 ft., on rocky slopes (ST. 3201). Siru Gol, S of Shah Jinali Pass, ca. 14500 ft., on stony slopes (ST. 3056). Golen (Krui Uts), ca. 13500 ft., dry position on cliff (B. L. 120). Ghutbar Gol, ca. 14000 ft., steep slopes (B. L. 46).

F. ovina L. ssp. Kotschyi (НАСК.) St. Yves – C: Bamian: In der Kammregion der Koh-i Baba Kette oberhalb Sard-darra, 4000–4300 m (G. 593, 594). Kammregion der Koh-i Baba, ca. 3780 m (G. 592).

F. ovina L. ssp. sulcata Наск. – C: Bamian: Nil Kotal, ca. 3200 m (К. 2865). Koh-i Baba, ca. 3900 m (К. 2634). – NE: Nuristan: Elasoon (Е. 1683).

F. pratensis HUDS. – E: Kabul: In valle Paghman prope Kabul, 2300–2800 m, substr. Gneiss (G. 598, RECH. 17132). – C: Hauz-i Mahiha, Kabul, ca. 2600 m (K. 2436). Qala-e Wazir inter Sar-i Chashma et jugum Unai, ca. 2900 m (RECH. 18079). Im Kamard-Tal westlich von Doab, Weidewiese, ca. 1580 m (G. 597).

F. rubra L. – C: Unai-Pass, ca. 3120 m, an quelligen Stellen (G. 595). Ad lacum Band-i Panir, prope Band-i Amir, ca. 2800 m (RECH. 18381). Am Seeufer von Band-e Amir, ca. 2800–2900 m (G. 589, RECH. 18317). – E: Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Baserak, ca. 2800 m (G. 595). Nuristan: Kulam, im Kulam-(Munui-) -Tal, ca. 2150 m (KN. 1038, SCH. 108). Oberes Ramgel-Tal in der Nähe von Puschol, ca. 2300 m (KN. 1104-b). – Pakistan: Chitral: Owir, SE of Tirich Mir, ca. 9000 ft., in irrigated meadow (ST. 2770). Baroghil Pass, ca. 12500 ft., at edge of stream (ST. 2997). Shower Shun, E of Baroghil Pass, ca. 13000 ft. (ST. 3007).

F. rubra L. var. *lachnantha* Ovcz. – C: Hauz-i Mahiha to Farakulum, ca. 2900 m (K. 2511). Band-i Amir, ca. 2800 m (K. 2841). – NE: Nuristan: Kantivo, ca. 2200 m (E. 669). Pashki, ca. 2300 m (E. 904). – Minjan, Miyan Deh, ca. 2500 m (E. 2083).

Biol.Skr.Dan.Vid.Selsk. 14, no. 4.

Lamarckia MOENCH

L. aurea (L.) MOENCH – E: Tisin, an der Strasse von Kabul nach Jallalabad, (KN. 2187). Dakka, an der Strasse von Jallalabad nach Peshawar (KN. 2193).

Leucopoa GRISEB.

L. albida (TURCZ.) V. KRECZ. et BORR., Fl. SSSR. 2: 495 (1934). (Syn. Poa albida TURCZ. ex TRIN., Leucopoa sibirica GRISEB., Festuca sibirica HACK. ex BOISS.). – NW: Chrisht, ca. 2100 m (K. 3620). – C: Deh Kundi to Sar-i-Nil, ca. 3000 m (E. 1962). – Pakistan: Chitral: Chumarkhan Pass, E of Mastuj, ca. 13000 ft., on dry open slopes (St. 2896). Ghutbar, ca. 14000 ft., on dry steep slopes (B. L. 51).

L. karatavica (BGE.) V. KRECZ. et BOBR., Fl. SSSR. 2: 496 (1934). (Syn. Poa karatavica BGE., Festuca karatavica (BGE). FEDTSCH., F. subspicata (RGL.) LIPSKY var. griffithiana ST. YVES, Festuca griffithiana (ST. YVES) KRIV., Leucopoa griffithiana (ST. YVES) OVCZ.). - E: Ghazni: Sar-Ab, 40 km a Ghazni boreo-occidentem versus, ca. 2500 m (RECH. 17673). In jugo Kotal Shaghanak, inter Okak et Ghazni, 3400-3500 m (RECH. 17820). Gulbahar bei Charikar (N. 1950/803). Oberhalb Schechan im Nedschrab-Tal, zwischen Gulbahar und Sarobi, ca. 2590 m (G. 599). Gipfel im Korogh-Massiv bei Kabul, ca. 2800 m (G. 601). Mittleres Paghman-Tal, westlich von Kabul (N. 1950/812), 3000-3500 m (N. 1950/239). Ghorband valley, ca. 8900 ft., rocky slopes (M.). Panjshir: Panjshir Valley, W-side of Ajuman pass, ca. 3700 m (HDG. & WDB. 5505). Porande-Tal, Seitental des Panjshir-Tales bei Basarak, ca. 2800 m (G. 602). - C: Hauz-i Mahiha, ca. 2500 m (K. 2400). Qala-e Wazir, inter Sar-i Chashma et jugum Unai, ca. 2900 m (RECH. 18100). Unai-Pass, ca. 3150 m (G. 604, N. 1951/517, 551). Inter Bulola et jugum Shibar, 2600–2800 m (RECH. 16842). Kotal-e Nargiz, inter Panjao et Lal, ca. 3000 m (RECH. 18784). Zwischen Bamian und der Koh-i Baba Kette, ca. 3150 m (G. 603). Sar-i Chashma, Koh-i-Baba Range, ca. 2700 m (E. 1835). Koh-i-Baba, ca. 3400 m (K. 3047). - Nuristan: Pirdum-Tal, nördlich des Pirdum-Passes, zwischen dem Pass und Puschol, 2300-3000 m (KN. 1147). Tschitur-Tal, zwischen dem Tschitur-Pass und dem Ramgel-Tal, 2300-3000 m (KN. 1147).

According to RECHINGER this tufted grass is very common on hillslopes in the high mountain areas of Central Afghanistan, and that it is avoided by cattle in an area where the latter are numerous and every type of vegetable matter is greedily consumed. The dull yellow inflorescences suggested that this grass might be an aluminium-accumulator. Specimens sent to the Government Chemist confirms that this is so and were found to contain 5800 pp. m. aluminium. This is a possible explanation why this grass is not acceptable to grazing animals.

L. Olgae (REGEL) V. KRECZ. et BOBR., Fl. SSSR. 2: 495 (1934). (Syn. Molinia Olgae REGEL, Act. Hort. Petrop. 7, 2: 625 (1881)). – C: In the vicinity of Panjao, ca. 2000 m, limestone slopes (HDG. & WDB. 4925).

Lolium L.

L. perenne L. – C: Doab, Felder (V. K-232). Identification somewhat doubtful (Bor).
Nr. 4

L. persicum BOISS. et HOHEN. – SE: Kandahar, ca. 1020 m (KN. 218). – E: Kabul: Darulfanum, südwestlich von Kabul (V. 326). Scharenau (Tschaman Wasirabad), ca. 1750 m (G. 716). In einem Garten in Kabul, ruderal, ca. 1780 m (G. 717, 718). – C: Bamian: Zwischen Doab und Bulola, Weizenfelder (V. 2097). Doab (V. 1799-b). – NE: Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, ca. 1700 m (G. 715). – Pakistan: Kurram Valley (Агтсн. 280, 1261). Quetta (Stocks). Balouchistan: Balouchistan (MONRO).

L. rigidum GAUD. – C: Doab, Felder (V. K-232). – E: Kotsche Mullah near Kabul (N. 1950/338).

L. temulentum L. – SE: Bei Kandahar in einem Weizenfeld (ScH. 26). – NE: Kataghan: Kunduz, in paludosis fluvii Kunduz, ca. 400 m (RECH. 16043). Kunduz, in declivibus siccis ad aerodromum, ca. 450 m, Loess (RECH. 16085). Doshi, Weizenfelder (V. 547). – N: Mazar-i Sharif: Inter Chashma-e Shafal et Aq Kupruk, ca. 800–1000 m (RECH. 16288). – C: Ghorat: A Naourak austro-occidentem versus, ca. 2480 m (RECH. 18958). – Pakistan: Chitral: Mirkhani, SW of Drosh, ca. 4500 ft., at edge of fields (ST. 2285). Chitral village, ca. 5000 ft., at edge of fields (ST. 2150).

Nardurus (Bluff, Nees et Schau.). REICHENB. ex GODRON

N. Krausei (REGEL) V. KRECZ. et BOBR., Fl. SSSR. 2: 540 (1934). (Syn. Festuca Krausei REGEL). – E: Auf einem Berg am rechten Kabul-Ufer südwestlich von Sarobi, ca. 1100 m (G. 607). – NE: Nuristan: Kammhöhe eines Berges bei Kamdesch, ca. 3300 m (E. PROCHAZKA sub G. 607).

N. maritimus (L.) MURBECK (Syn. Festuca maritima L., Nardurus tenuiflorus (SCHRD.) BOISS.). – Pakistan: Quetta (NORRIS 63).

Nardurus subulatus (BANKS & SOLAND.) BOR, comb. nov. (Syn. Triticum subulatum BANKS et SOLAND. in RUSSELL, Nat. History Aleppo 2: 244 (1794), Loliolum subulatum (BANKS et SOLAND.) EIG, Nardurus orientalis BOISS., Festuca aleppica STEUD., Loliolum orientale (BOISS.) KRECZ. et BOBR.). – SW: Herat: Shin Dand, S of Herat, ca. 1400 m (K. 3585). – SE: Kandahar: Goldgrube im Norden von Kandahar in der Steinsteppe, ca. 1000 m (KN. 2223). – Pakistan: Quetta (NORRIS 63).

Poa L.

P. afghanica BOR, Kew Bull. 1954: 501 (1955). Fig. 5, 6. – NE: Nuristan: Chitras, ca. 3100 m, 30.5.1948 (EDELBERG 851, Holotypus, C).

P. Aitchisonii Boiss. – NE: Nuristan: Above Netshingel (E. 1692). – Pakistan: Kurram Valley (GRIFF. 206, HARSUKH 14934).

P. alpigena (BLYTT) LINDM. (Syn. P. pratensis L. var. alpigena BLYTT). – Pakistan: Chitral: Shost, Mastuj to Baroghil Track, ca. 10000 ft., on stony ground (ST. 2957).

P. alpina L. – **NE: Nuristan:** Auf dem Wege zwischen Aschpi-Pass nach dem Ort Kuschtos, ca. 2500 m (N. 1951/655). – Minjan, above Weran, ca. 3800 m (E.

 5^{*}



Fig. 5. Poa afghanica BOR (E. 851, Holotypus, C).

1255). C: Schutthalde in der Koh-i Baba Kette am Beginn des Sard-darra, ca. 4320 m (G. 541). – Pakistan: Chitral: Rosh Gol, NE of Tirrich Mir, ca. 11000 ft., on stony ground (Sr. 2795). Shah Jinali Pass, N of Mastuj, ca. 14500 ft., on open slopes (Sr. 3044). Oihor Gol, ca. 11000 ft., moist soil among large boulders (B. L. 1054).

P. angustifolia L. (Syn. P. pratensis L. var. angustifolia WAHL. (1812).). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17943). Qala-e Wazir, inter Sar-i Chashma (Tscheschme) et jugum Unai, ca. 2900 m (RECH. 18097). Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak: Ufer eines Nebenflusses des Porande-Flusses, ca. 2800 m (G. 536). – C: Bulola, ca. 2200 m, in pratis humidis (RECH. 16739). – Pakistan: Chitral: Arkari Gol, W of Tirich Mir, ca. 8500 ft., at edge of field (ST. 2611).

P. annua L. – N: Kataghan: Kunduz, in horto inculto (RECH. 16025). – E: Sarobi, Maulbeerhaine (V. 2466). – C: Unai-Pass, westlich von Kabul, ca. 2800 m



Fig. 6. Poa afghanica Bor, a part of the panicle (K. 851, Holotypus, C) 4.5/1.

(V. 2129). – NE: Nuristan: Gusalak, ca. 1000 m (E. 32, 154, 289). – Pakistan: Chitral: Drosh, ca. 4500 ft., at edge of irrigation channel (ST. 2273).

P. araratica TRAUTV. – E: Oberes Nedschrab-Tal, zwischen Gulbahar bei Charikar und Sarobi, ca. 3310 m (G. 554). An einer Dolomitfelswand am Ostabhang des Korogh-Massivs, ca. 2550 m (G. 552). Paghman, W of Kabul, ca. 1900 m (K. 2314). Paghman, ca. 2500 m, an Gräben und auf Feldern (V. 964). In valle Paghman, 2300–2800 m, substr. Gneiss (RECH. 17114). Paghman Valley, ca. 2900 m, streamside (HDG. & WDB. 5059). – C: Qala-e Wazir, inter Sar-i Chashma (Tscheschme) et jugum Unai, ca. 2900 m (RECH. 18078). Shibar Pass (V. 2810). Gipfelregion eines Kalkberges nordöstlich von Bamian, ca. 3140 m (G. 557). Kammregion in der Koh-i Baba Kette, ca. 3780 m (G. 555). Band-i Amir, nördlich der Koh-i Baba Kette, ca. 2800 m (K. 2836). – NE: Nuristan: Parun-Tal bei Pashki, Westhang, ca. 2300 m (Kn. 1337-b). Pashki, ca. 2500 m (K. 738). Unteres Petsch-Tal zwischen Gusalak und der Einmündung des Kurder-Flusses, ca. 1150 m (Kn. 731-a). Oberes Petsch-Tal bei Wama, ca. 1380 m (Kn. 811-b). Beim Ort Kantiwo im Kantiwo-Tal, ca. 2200 m, Westhang, lichter Eichenwald (Kn. 914). – **Pakistan: Chitral:** Chumarkhan Pass, E of Mastuj, ca. 10000 ft., on rock ledges in tufts (Sr. 2893). Chumarkhan Pass, E of Mastuj, ca. 12000 ft., on dry open slopes (Sr. 2904). Ishporili Gol, S of Mastuj, ca. 12500 ft., on stony ground (Sr. 3105). Rumbour, ca. 8500 ft., dry cliff facing South (B. L. 673).

P. bactriana ROSHEV. – E: Kabul: Tang-e Gharu, Schlucht des Kabul-Flusses, östlich von Kabul, 1600–1700 m, sehr steinig (KN. 561). Scher Darwasa bei Kabul, ca. 1700 m, Nordhang (KN. 489). – Pakistan: Chitral: Birmogh Lasht, ca. 8700 ft., moist bank on dry hillside among *Artemisia* (B. L. 722). Mastuj Track, Barenis, ca. 6000 ft., on rock ledges (ST. 2433). Shoghot, N of Chitral, ca. 9500 ft., on stony slopes (ST. 2656).

P. bulbosa L. - N: Ankhoi, Steppe (N. 1950/218). Haibak, ca.3900 ft. (M.). -C: Doshi, ca. 2700 m, rocky slopes (M.). - NW: Chisht, ca. 1900 m (K. 3619). Murghab, ca. 600 m (K. 3517). - SW: Jija, ca. 900 m (K. 4247). Herat, ca. 900 m (AMSEL, K. 3745). - E: Kabul: Surkhab-Damm, Ebene von Darulfanun, E von Kabul, Geröllhang (V. 135). In collibus ad septentriones urbis Kabul, ca. 1800 m (RECH. 17036). Scher Darwasa bei Kabul, 1840–1850 m (G. 542, HDG. & WDB. 2919). Zwischen Dorf Barbur und Barburgarten bei Kabul, ca. 1700 m (Kn. 18). Oberhalb Beg-tut, im Paghman-Gebirge, westlich von Kabul, ca. 2900 m, feuchte Matte (G. 549). Paghman, 17 miles W of Kabul, 8000-9000 ft. (Ch.-M.). Kabul, ca. 7000 ft., rocky hills (M.). - C: Unai-Pass, westlich von Kabul (N. 1951/540). Farakulum, (K. 2560). Bamian: Koh-i Baba Range, ca. 3400 m (K. 2645), 3037). Band-i Amir, nördlich der Koh-i Baba Kette, ca. 3300 m, Igelsteppe (V. 2722). Aoband Kotal, ca. 3000 m (E. 1815). – NE: Nuristan: Gusalak, ca. 1000 m (E. 288, 2091). Vama, ca. 1600 m (E. 636). Pashki, ca. 2300 m (E. 495). Cedrus deodora-Wald bei Kamdesch, ca. 2100 m (G. 545). Mum-Pass, zwischen Parun- und Kantiwo-Fluss, Aufstieg von Gulnischa aus, 2500-2800 m (Kn. 873). - Pakistan: Chitral: Oihor Gol, ca. 10000 ft., cornfields (B. L. 855). Chitral village, ca. 5000 ft., at edge of fields (ST. 2177).

P. bulbosa L. var. vivipara KOEL. – NW: Herat: Nördlich von Herat, ca. 940 m (G. 543). – SE: Kandahar: Kalat-i Ghilzai, Artemisia-Steppe (KN. 146, 153-b). – E: Kabul: Darulaman-Ebene östlich von Kabul, ca. 1700 m (ScH. 61-b). Oberhalb des Nedschrab-Tales bei Schechan, zwischen Gulbahar und Sarobi, östlich von Kabul, ca. 2750 m (G. 547). Pandscheschah bei Kabul, trockene, sandige Berglehne (N. 1951/44). Scher Darwasa bei Kabul, ca. 1700 m (KN. 489-b, 490-b, N. 1950/805, 1951/66). Scher Darwasa, zwischen der Brücke und dem Top-Berg (KN. 96). Oberes Paghman-Tal, westlich von Kabul (N. 1950/794). Paghman, ca. 2470 m, in Felsspalten (G. 546). An der Strasse zwischen der Darulaman- und der Paghman-Ebene, ca. 1700 m (KN. 128, Sch. 32). Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar, 1700–2000 m, am Dorfweg und in Felsen (G. 544, KN. 73). – C: Unai-Pass, ca. 3120 m, an quelligen Stellen (G. 548). Koh-i Baba: In latere austro-orientali jugi Hadjigak, ca. 3000 m (RECH. 18545). – Nuristan: Bagrami, Nedjerau-Tal, 2500–3000 m (N. 1951/203). – Pakistan: Chitral: Shishi Gol, Madaghlasht, E of Drosh, ca. 7000 ft., in tufts on rock ledges (ST. 2351). Bromboret, ca. 8000 ft., dry cliff face (B. L. 655).

P. dzhilgensis ROSHEV., Act. Inst. Bot. Acad. Sc. URSS. 1, 2: 98 (1936). – C: Koh-i-Baba Kette, oberhalb des Sard-Darra, ca. 4000 m (G. 558).

P. glabriflora ROSHEV., Act. Inst. Bot. Acad. Ac. URSS. 1, 2: 99 (1936). – E: Kabul: Lataband-Pass, Berghang, ca. 2030 m (G. 550).

P. nemoralis L. - C: Hauz-i-Mahiha, ca. 2600 m (K. 2434). - NE: Nuristan: Pashki, ca. 2300 m (E. 602). Cedrus deodora-Wald bei Kamdesch, ca. 2100 m (G. 551). Aterschuker im Schuk-Tal, ca. 2300 m, in Felsen (Kn. 1017). East-Nuristan (E. 1132).
- Pakistan: Chitral: Barum, SE of Tirich Mir, ca. 8000 ft., beneath trees (ST. 2771). Swat: Kalam, ca. 2200 m (RECH. 19403).

P. polycolea STAPF - NE: Nuristan: Pashki, 2300-2500 m (E. 559, 629, 741, 750).

P. pratensis L. – C: In declivibus orientalibus jugi Shibar, 2500–2600 m (RECH. 16871). Shibar Pass (V. 2806). – E: Kabul: Darulaman-Ebene, ca. 1700 m, an Bewässerungsgräben (KN. 441). Gulbahar bei Charikar, nördlich von Kabul (V. 201-E). In einem Garten in Kabul, ca. 1780 m, Bewässerungsgräben (G. 535). – NE: Minjan, Miyan Deh, ca. 2550 m (E. 2106). – Nuristan: Gusalak, ca. 1000 m (E. 1546, 1576). Kulam (Munui) im Kulam-Tal, ca. 2200 m, feuchter Schutt (KN. 1048). Inter Kotal-e Agok et pagum Waigel (N. 1951/872, 876, 943). Auf der Westseite des Donda-Passes, Aschkun-Gebiet, 2500–3200 m, auf Matten (KN. 1251-b). – Pakistan: Chitral: Chumarkhan Pass, E of Mastuj, ca. 10000 ft., at edge of stream beneath willows (ST. 2894). Shandur, ca. 12220 ft. (B. L. 84).

P. sinaica STEUD. – **SE:** Kandahar: Nördlich von Arghendab, zwischen Kandahar und Ghirishk am Hilmend, 900–1000 m (Kn. 312). Zwischen Kandahar und Ghirishk am Hilmend, 900–1000 m (Kn. 252). – **SW:** Shin Dand, SSW of Herat, ca. 1220 m (K. 3589, 4248).

P. sterilis М. В. – E: Oberhalb des Nedschrab-Tales bei Schechan, zwischen Charikar und Sarobi, ca. 2580 m, *Pinus Gerardiana*-Wald (G. 553). Paghman-Tal, ca. 2480 m, an einer steilen Felswand (G. 556, V. 964). – C: Inter Bulola et jugum Shibar, 2600–2800 m (RECH. 16766). In valle Darre Shikar, inter Doab et Bulola, 1600–2000 m (RECH. 16723). Kammregion der Koh-i-Baba Kette, ca. 3780 m (G. 555). – **NE: Nuristan:** Oberes Petsch-Tal bei Vama, ca. 1350 m, Flussufer (KN. 747). Zwischen Kotal-e Agok (Agok-Pass) und Alm bis Ort Waigel (N. 1951/938). Bagrami, im Nedjerau-Tal, ca. 2500 m (N. 1951/222). – **Pakistan: Chitral:** Chumarkhan Pass, E of Mastuj, ca. 12000 ft., on dry open slopes (St. 2898). Golen (Krui Uts), ca. 13000 ft., moist soil among large boulders (B. L. 135).

P. supina SCHRAD. – **SE:** Kandahar: In Weizenfeldern bei Kandahar, ca. 1020 m (G. 532). – **E:** Kabul: Zwischen Schakardarra und Hauz-i Chaz, ca. 2850 m, im Paghman-Gebirge (G. 534). Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak, ca. 2800 m (G. 533). – **NE:** Nuristan: Kantivo, ca. 2200 m (E. 686). –

Pakistan: Chitral: Shishi Gol, E of Drosh, ca. 7000 ft., on marshy ground (St. 2380). Owir An, SE of Tirich Mir, ca. 11000 ft., at edge of stream (St. 2764)

P. trivialis L. – NW: Sauzak, NE of Herat (K. 2200). – E: Kabul: Darulaman-Ebene, ca. 1700 m, Bewässerungsfelder (KN. 442). Sumpfwiese bei Dehmasang, ca. 1770 m (G. 538). In valle Paghman, 2300–2800 m, substr. Gneiss (G. 539, 540, RECH. 17137). Im Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m, an Bewässerungsgräben (G. 537). Kabul, ca. 1800 m, side of ditch (HDG. & WDB. 3226). – C: Farakulum, ca. 2800 m (K. 2559). – Pakistan: Chitral: Chitral village, ca. 5000 ft., at edge of irrigation channel (ST. 2393).

P. Vvedenskyi Drob., Fl. Usbekist. 1: 239, 538 (1941). – C: Shibar Pass, sterile slope (М.).

Psilurus TRIN.

P. incurvus (GOUAN) SCHINZ et THELL. – SW: Herat: Jija, Farah to Shin Dand, S of Herat, ca. 900 m (K. 4251). – NE: Nuristan: Gusalak, ca. 1000 m (E. 2093). SE: Kandahar: Goldgrube im Norden von Kandahar in der Steinsteppe, ca. 1000 m (KN. 380).

Puccinellia PARL.

P. gigantea (GROSSH.) GROSSH., Fl. Kauk. 1: 114 (1928). (Syn. Atropis gigantea GROSSH.). – NW: Ghorat: Qala Shahrak, ca. 2000 m (RECH. 19148). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17942). Kabul: Salzwiese hinter Scharenau (Tschaman Wasirabad), ca. 1750 m (G. 580). Bala Hissar prope Kabul, ca. 1800 m, in stagno (RECH. 16008). In planitie ad orientem urbis Kabul secus viam versus Sarobi ducentem, ca. 1700 m (RECH. 16902). – C: Inter Bulola et jugum Shibar, 2600–2800 m (RECH. 16767). Ghorat: Qala Qansi (Tschaktscharan), ad ripas fluvii Hari-rud, ca. 2200 m (RECH. 18835).

P. himalaica Tzvelev, Not. Syst. Inst. Bot. Sc. URSS. 17: 66 (1955).

- - var. scabrida Melderis, var. nov.

A typo ligulis brevioribus (ad 1 mm longis), paniculae ramis scabridis, fructificatione \pm reflexis, glumis brevioribus: gluma inferiore 0,7–0,9 mm, superiore 1,3 mm longa, differt.

C: Hauz-i Mahiha to Farakulum, ca. 2900 m, 17.7.1948 (Køie 2495, Holotypus, C). Panjao, ca. 2700 m (K. 2697).

Puccinellia Koeieana MELDERIS, spec. nov. - Fig. 7, 8.

Gramen perenne, 25–30 cm altum, caespites laxos formans, innovationibus intravaginalibus. Culmi erecti, basi ascendentes vel geniculati, 3–4-nodes, teretes, striati, glabri, laeves. Folia glauco-viridia; vaginae glabrae laeves, infimae luteo-brunnescentes; ligulae 2–2,5 mm longae, acutae, hyalinae; laminae 2–5 cm longae, 1,5-2,5 mm latae, planae vel \pm convolutae, supra nervis scabrae, subtus glabrae laeves. Panicula 7–8 cm longa, basi 5,5 cm lata, anguste ovata, ad temporem florendi



Fig. 7. Puccinellia Koeieana MELDERIS (K. 3061, Holotypus, C).

compacta, demum diffusa, ramis ad rhachidis nodos vulgo binis, ad 3,5 cm longis, tenuibus, scabriusculis, fructificatione saepe reflexis. Spiculae 4–5 mm longae, anguste oblongae, 3–7-florae, saepe purpureo-tinctae. Glumae persistentes, late lanceolatae vel ovatae, acutae vel obtusiusculae, inaequilongae, gluma inferior 0,8–1 mm longa, 1-nervia, gluma superior 1,5–1,6 mm longa, 1–3-nervia, marginibus late scariosae, erose ciliatae. Lemma 1,5–2 mm longum, late oblongum vel ellipticum, apice obtusiusculum, 5-nervium, basi tantum in callo minute pubescens, nervo medio sat prominente et apice plerumque in mucronem brevem abeunte, late hyalinomarginatum, apice aureo-tinctum. Palea lemmati subaequilonga, bicarinata, carinis minute ciliatis, dorso glabra. Antherae 1–1,2 mm longae, ellipticae. – A *P. glauca* (REGEL) KRECZ. in statura minore, paniculis brevioribus, spiculis 4–5 mm longis, saepe variegatis, glumis brevioribus, lemmate late oblongo vel elliptico, basi minute



Fig. 8. Puccinellia Koeieana MELDERIS, a part of the panicle (K. 3061, Holotypus, C) 4.5/1.

pubescenti, antheris longioribus, differt. *P. Hackelianae* KRECZ. affinis, sed paniculis brevioribus, glumis acutis vel obtusiusculis, brevioribus, lemmate late oblongo vel elliptico, breviori, marginibus non ciliolato, differt.

C: Bamian: Lal-i Zarjangel, Koh-i Baba Range, ca. 2500 m, 3.8.1948 (Køie 3061, Holotypus, C).

P. sevangensis GROSSH. (Syn. Atropis sevangensis (GROSSH.) V. KRECZ.). – E: Ghazni: In jugo Sardalu a Qarabagh occidentem versus, 2300–2500 m (RECH. 17340). Okak, a altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (RECH. 17728). Ad lacum Djalgeh-Shahr-Kawat, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17866). – E: Kabul: Salzsteppe zwischen Kabul und Tang-e Gharu, ca. 1770 m (G. 582). Salzwiese westlich von Budchak, ca. 1740 m (G. 579-a). Sumpfwiese bei Dehmasang, ca. 1770 m (G. 581). Weidewiese zwischen Kabul und

Nr. 4

Aliabad, ca. 1780 m (G. 585). Bala Hissar prope Kabul, ca. 1800 m (RECH. 16007). Am Ufer des Logar-Flusses bei Tscharasiah, ca. 1780 m (G. 579-b, 583, 1740). In einem Garten in Kabul, ca. 1780 m (G. 584). – C: Bamian: Am Ufer des Bamian-Flusses bei Schar-e-Schak, ca. 2320 m (G. 586, 587). Inter Bamian et Band-i Amir, 2800–3000 m (RECH. 18198). Band-i Amir, in ripa lacus, ca. 2800 m (RECH. 18318, 18325). Inter jugum Kotal Deraz Kol et Panjao prope pagum Mandigak, 2800–3280 m (RECH. 18721). Ghorat: Qala Sharak, ca. 2000 m (RECH. 19137).

Sclerochloa P. BEAUV.

S. dura (L.) P. BEAUV. – N: Kataghan: Bala Hissar prope Kunduz, in declivibus siccis, ca. 400 m, substr. Loess (RECH. 16074). – E: Kabul: Im Garten der Nedschat-Oberrealschule in Kabul, ca. 1770 m (G. 609).

S. Woronowii (HACK.) TZVELEV, Not. Syst. Herb. Inst. Bot. Acad. Sc. URSS. 18: 27 (1957). – SE: Von Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (KN. 225-a).

Vulpia C. C. GMEL.

V. ciliata Link – N: Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (Rech. 16291). – Pakistan: Quetta (J. J. Norris 45).

V. myurus (L.) C. C. GMEL. – SW: Jija, ca. 1200 m (K. 4248). – E: Panjshir: In der Panjshir-Schlucht bei Gulbahar, nächst Charikar (G. 605). Nuristan: Gusalak, ca. 1000 m (E. 1568). Bagrami, im Nedjerau-Tal, an einer nassen Bachwiese (N. 1951/251). – Pakistan: Chitral: Shishi Gol, E of Drosh, ca. 5500 ft., at edge of fields (ST. 2384). Kaghosi, Chitral-Mastuj track, ca. 5000 ft., on stony ground (ST. 2399).

V. persica (BOISS. et BUHSE) V. KRECZ. et BOBR., Fl. SSSR. 2: 535 (1934). – NW: Qala Nau (K. 3960). – SE: Kandahar: Zwischen Kandahar und Kuschki-Nahod, ca. 1000 m, Steppenrand (KN. 307). – E: Kabul: Tisin, an der Strasse Kabul von nach Jallalabad, Felsrinne (KN. 593). – NE: Nuristan: Gusalak, ca. 1000 m (E. 2092). – N: Mazar-i Sharif: Takht-e Rustam prope Haibak, ca. 1200 m (Rech. 16375).

Glyceria ENDL.

Pooideae-Glycerieae

G. plicata FRIES – E: Ghazni: Bei Gardez, Bewässerungsgräben (V. 1035). Dahan-e Barikak, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17978). Kabul: Zwischen der Strasse von Dehmasang nach Darulfanun und Gusargah, ca. 1770 m (G. 576). In der Sumpfebene östlich von Tscharasiah, an Wassergräben, ca. 1740 m (G. 575). Bala Hissar prope Kabul, ca. 1800 m (RECH. 16010). Wardak, südwestlich von Kabul (V. 823). Versumpftes Ufer eines Bächleins im Paghman-Tal, ca. 2480 m (G. 577). Am Ufer des Paghman-Flusses, ca. 2540 m (G. 578). In valle Paghman, 2300–2800 m, substr. Gneiss (RECH. 17131). – C: Hauz-i Mahiha, W of Kabul, ca. 2500 m (K. 2480).

Pooideae-Melicaeae

Melica L.

M. canescens (REGEL) LAVRENKO, Fl. SSSR. 2: 752 (1934). (Syn. M. Cupani GUSS. var. canescens REGEL). – N: Mazar-i Sharif: In faucibus a Taschkurghan austro-orientem versus, 600–700 m (RECH. 16351). – E: Ghazni: In valle fluvii Arghandab prope Sang-i Masha, ca. 2400 m, in declivibus saxosis gneissaceis (RECH. 17520). Bozghalak, in collibus graniticis prope Shashgao, 24 km a Ghazni boreoorientem versus, ca. 2400 m (RECH. 17293). Scher Darwasa bei Kabul, ca. 1840 m (G. 516). – C: In valle Ajar "Königsthal" a Doab occidentem versus, 1400–1500 m (RECH. 16618). Panjao, ca. 2700 m, on limestone rocks (HDG. & WDB. 4883). – Pakistan: Chitral: Arkari Gol, W of Tirich Mir, ca. 10000 ft., on stony ground in tufts (St. 2618, 2619).

M. Hohenackeri BOISS. (Syn. *M. Cupani* GUSS. var. *Hohenackeri* BOISS.). – **E:** Kabul: Djaouz, in declivibus borealibus montium Kuh Qorogh prope Kabul, ca. 2000 m (RECH. 18014). Afghanistan. (GRIFF. 6676).

M. inaequiglumis Boiss. (Syn. *M. Cupani* Guss. var. *inaequiglumis* Boiss.). – N: Mazar- i Sharif: In faucibus ab Haibak austro-orientem versus, 600–700 m (Rech. 16352). Maymana: Balcheragh, Darrah Balcheragh, ca. 1200 m, on stony slopes (HDG. & WDB. 3775). – E: Ghazni: Sang-i Masha, ca. 2500 m (Rech. 17462). Kabul: Tang-e Gharru bei Kabul, 1600–1700 m (KN.). In faucibus Tang-e Gharru, inter Kabul et Sarobi, 1100–1300 m (Rech. 16934). Sarobi, steinige, Steppe (V. 1612). Koh-i Asmai, Berg im Norden von Kabul, ca. 1700 m (KN. 428, Sch. 56). Felshang am Westhang des Scher Darwasah, ca. 1800 m (G. 510). Berghang am linken Ufer des Paghman-Flusses, ca. 2750 m (G. 513). – C: Unai Pass, ca. 3000 m (HDG. & WDB. 4532). – Pakistan: Chitral: Arandu, SW of Drosh, ca. 4000 ft., on rock ledges in tufts (ST. 2293). Mirjhani, SW of Drosh, ca. 4500 ft., on dry cliffs in tufts (ST. 2282).

M. jacquemontii DECNE. in JACQ. (Syn. *M. Cupani* GUSS. var. *breviflora* BOISS.). – E: Ghazni: Inter Miradina et jugum Ghoutch Kol, a Sang-i Masha septentriones versus, ca. 3300 m (RECH. 17614). Kabul: Schlucht Tang-e Gharu nächst dem Maipar, ca. 1720 m, unter dem Gipfel eines steilen Berges, ca. 1720–1730 m (G. 509). Scher Darwasa bei Kabul, ca. 1700 m, Nordhang (KN. 491). Dolomitfelswand am Osthang des Korogh-Massivs, ca. 2550 m (G. 512). Gipfel im Korogh-Massiv, ca. 2800 m (G. 514). An einer steilen Gneissfelswand im Paghman-Tal, ca. 2480 m (G. 511). In valle Paghman prope Kabul, 2300–2800 m (RECH. 17175). – **Pakistan: Chitral:** Turkho Valley, between 36°25' N, 72'22' E, and 36°45' N, 72°37' E, ca. 9000 ft., dry hillside (B. L. 1057). Tirich Mir Gebiet: Oberhalb von Bomosto, 3100–3500 m (KN. 1566).

M. persica KUNTH (Syn. *M. Cupani* Guss. var. *vestita* BOISS.). – E: Tang-e Saidan, östlich von Kabul, Steppe (L. 778). Bozghalak, Steppe (L. 1960/808). Paghman, 17 miles W of Kabul, 8000–9000 ft. (CH.-M.). – **NE: Nuristan:** Oberhalb Papruk im Papruk-Tal, Ostseite des Mrami- (Papruk-) Passes, 2500–3500 m (KN. K-30).

Pooideae-Monermeae

Parapholis C. E. HUBBARD

P. incurva (L.) C. E. HUBBARD, Blumea, Suppl. 3: 14 (1946). (Syn. Aegilops incurva L., Lepturus incurvatus (L.) TRIN.). – SW: Herat, ca. 900 m (K. 3073). – SE: Kandahar: An nassen Sandstellen bei Kandahar in Richtung Kalat-i Ghilzai, ca. 1100 m (KN. 223-a).

Oryza L.

Pooideae-Oryzeae

O. sativa L. – E: Kabul: Gulbagh bei Kabul, ca. 1800 m (G. 379). – Pakistan: Chitral: Lutkuh- (Lutkho-) Tal bei Shoghor, ca. 1510 m, kultiviert (KN. 1597, 1598). Zwischen Reshun und Koghozi im Yarkhun-Tal, 1650–1800 m, angebaut (KN. 2010-a, -b).

Pooideae-Pappophoreae

Enneapogon DESV. ex P. BEAUV.

E. persicus BOISS. (Syn. Pappophorum persicum (BOISS.) STEUD.). – N: Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (RECH. 16314). Aq Kupruk, in crevices of rocks, ca. 750 m (HDG. & WDB. 3922). Kataghan: In valle fluvii Kunduz inter Doshi et Doab, 800–1300 m (RECH. 16367). E of Pul-i Khomri, limestone rocks, ca. 750 m (HDG. & WDB. 4041). Pul-i Khumri, in valle fluvii Kunduz, ca. 700 m, in collibus aridis calcareis (RECH. 16498). – **SE:** Pirzada, near Kandahar, ca. 1000 m (K. 2092). – **E:** Tisin, an der Strasse von Kabul nach Jallalabad (KN. 2184). Hills 30 miles E of Kabul, ca. 7800 ft. (M.). In der Kabul-Schlucht westlich von Jallalabad, ca. 600 m, Granit (KN. 657-b). Südhang des Aliabader Berges bei Kabul, ca. 1860 m (G. 473-a). Scher Darwasa, Nordhang, ca. 1700 m (KN. 387-a). Berg NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 473-b). In collibus ad septentriones urbis Kabul, ca. 1800 m (RECH. 17085). Fels bei Aliabad (N. 1951/105). – **C:** In valle Ajar "Königsthal" a Doab occidentem versus, 1400–1500 m (RECH. 16616). A Naourak austro-occidentem versus, ca. 2480 m (RECH. 18922). – **Pakistan: Peshawar:** In collibus supra Dargai, ca. 400 m (RECH. 19626).

Phalaris L.

Pooideae-Phalarideae

Ph. arundinacea L. – E: Kabul: Gusargah bei Kabul, an einem Bewässerungsgraben in einem Garten, ca. 1700 m (G. 380). – C: Shibar Pass, ca. 2500 m (K. 3053). Shibar Pass, Wiesengräben (V. 2807).

Ph. minor RETZ. - N: Kataghan: Kunduz, in horto inculto (RECH. 16032). Pul-i Khomri (V. 710, 2048). - NW: Maymana: Between Belcheragh and Maymana, ca. 1000 m, in the side of a ditch (HDG. & WDB. 3800). - SW: Herat, ca. 1000 m (K. 4263). - SE: Kajkai, NNW of Kandahar, ca. 1000 m (K. 3053).

Pooideae-Sporoboleae

Crypsis AIT.

C. aculeata (L.) AITON – E: Ghazni: Ad marginem orientalem altoplanitiei Dasht-e-Nawar (Naour), ca. 3000 m (RECH. 17806). Kabul: Auf einer Weidewiese zwischen Kartetschar und Aliabad bei Kabul, ca. 1780 m (G. 384). Wazirabad, bei Kabul (N. 1950/38, 39).

C. schoenoides (L.) LAM. (Syn. Phleum schoenoides L., Heleochloa schoenoides (L.) Host). – N: Aqtscha, Flussaue (N. 1950/213). – SE: Kandahar: Boghra, südlich von Ghirishk, am Rande salziger Tümpel (V. 1308). – E: Kabul: Schotterbank am Ufer des Kabul-Flusses zwischen Tang-i-Saidan und Lallandar, ca. 1810 m (G. 386). Kartetschar, ca. 1780 m, Graben (G. 381). Pandscheschah bei Kabul (N. 1950/831). Ad stagnum Band-e Kharghak, inter Paghman et Kabul, ca. 2000 m (RECH. 386). In einem Garten in Kabul, ruderal, ca. 1780 m (G. 382, 383).

Oryzopsis MICHX.

Oryzopsis barbellata (MEZ) BOR, comb. nov. (Syn. *Piptatherum barbellatum* MEZ in FEDDES Repert. spec. nov. 17: 211 (1921). – **E:** Sarobi, östlich von Kabul (V. K-231). Berg am linken Ufer des Paghman-Flusses, ca. 2750 m (G. 421). – **C:** Unai-Pass, ca. 3150 m (G. 425). Kalkberg nordöstlich von Bamian, ca. 3000 m (G. 424). Zwischen Bamian und Band-i Amir, Steppe (V. 2785). In der Koh-i Baba Kette oberhalb Sard darra, ca. 4000 m (G. 427-b). An steinigen Hängen bei Band-i Amir, 2800–2900 m (RECH. 18239). Band-i Amir, Igelsteppe (V. 2761). – **Pakistan:** Kurram Valley (GRIFF. 6583).

Pooideae-Stipeae

- - var. effusa Bor, var. nov.

A typo ramis brevibus patentibus recedit.

E: Ghazni: Okak, ab altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (RECH. 17757). – C: Bulola, zwischen Kabul und Bamian, ca. 2780 m (G. 422-a).

The peculiar sausage-shaped hairs at the tip of the lemma distinguish this species from all others, in particular, from *O. songarica* in which the apical tuft consists of silky, narrow, golden hairs.

O. caerulescens (DESF.) RJCHT. (Syn. Milium caerulescens DESF., Piptatherum caerulescens (DESF.) P. BEAUV.). – E: Kabul: Fels bei Aliabad bei Kabul, südexponiert (N. 1951/115).

O. fasciculata Наск. – E: Kabul: Kotal-i Reg, ca. 3400 m (K. 3049). – NE: Nuristan: Gwarnar im oberen Badschaigel-Tal, ca. 1920 m, Feldränder (Kn. 1201-a).

O. gracilis (MEZ) PILGER, Notizbl. Bot. Gart. u. Mus. Berl.-Dahl. 14: 347 (1939). (Syn. Piptatherum gracile MEZ in FEDDE, Repert. spec. nov. 17: 211 (1921).). – Pakistan: Balouchistan (LAGE 3857). Nr. 4

O. holciformis (М. В.) НАСК. (Syn. Agrostis holciformis М. В., Piptatherum holciforme (М. В.) ROEM. et SCHULT.). – E: Kabul: Unter dem Gipfel des Koh Gaworgin, südlich vom Stausee, ca. 2950 m, Artemisia-Stipa-Steppe (G. 423). – C: Ad lacum Band-i Zolfikar prope Band-i Amir, ca. 2900 m (RECH. 18412).

O. lateralis (REGEL) STAPF ap. HOOK. f. (Syn. Milium laterale REGEL, Piptatherum laterale (REGEL) MUNRO ex AITCH.). – E: Ghazni: Inter Miradina et jugum Ghoutch Kol, a Sang-i Masha septentriones versus, ca. 3300 m (RECH. 17608). In jugo Ghoutch Kol, NNE Sang-i Masha, ca. 3300 m (RECH. 17651). Mittleres Paghman-Tal, westlich von Kabul (N. 1950/816). Im Paghman-Gebirge östlich von Kotal-i Kotandar, ca. 3730 m (G. 426). – C: Farakulum, ca. 2700 m (K. 2536). Band-i Amir, Igelsteppe (V. 2761). – NE: Nuristan: Shtive, ca. 2900 m (E. 1042). – Minjan, Miyan Deh, ca. 2850 m (E. 2081). – Pakistan: Chitral: Laspur Gol, SE of Mastuj, ca. 11000 ft., on dry slopes (St. 3103). Rosh Gol, NE of Tirich Mir, 11000–13000 ft., on stony ground (St. 2717, 2791). Baroghil Pass, ca. 12500 ft., on open slopes (St. 2986). Swat: Kalam, ca. 2200 m, substr. granit. (RECH. 19452). Above Ushu, 9000–10000 ft. (Stewart 25326).

O. microcarpa PILGER, Notizbl. Bot. Gart. u. Mus. Berl.-Dahl. 14: 346 (1939). -N: In faucibus a Tashkurghan austro-orientem versus ad Haibak, 600–700 m (RECH. 16350). – NW: Maymana: Darrah Abdullah, ca. 1200 m, dry rocky slopes (Hpg. & WDB. 3712). - E: Baozghalak, 24 km NE Ghazni, ca. 2400 m, in collibus graniticis prope Shashgao (Rech. 17274). Upper part of Tang-i Gharu, Kabul to Sarobi, ca. 1800 m (HDG. & WDB. 3068). Scher Darwasa bei Kabul, Nordhang, ca. 1700 m (KN. 493-b). Tob-Fels am Scher Darwasa, ca. 1840 m (G. 118). Gipfel im Korogh-Massif, ca. 2800 m, auf Schutt zwischen Felsen, Kalk und Hornblendeschiefer (G. 420). Sanglakht supra Jalrez, ca. 2400 m, in saxosis umbrosis cilic. (RECH. 18042). Koh-i Asmai, im Norden von Kabul, ca. 1700 m (Kn. 427, Sch. 55). Zwischen Botkhak und Kord-Kabul (N. 1951/370). Paghman, W of Kabul, ca. 1900 m (K. 2298). In Spalten einer steilen Felswand im Paghman-Tal, ca. 2480 m (G. 419). In valle Paghman prope Kabul, 2300–2800 m (RECH. 17094-a, -b). – C: Bamian: Inter Bulola et jugum Shibar, W Kabul, 2600–2800 m (RECH. 16827). In valle Ajar "Königsthal" a Doab occidentem versus, 1400-1500 m (RECH. 16617). Inter Bamian et Band-i Amir (V. 2785). -NE: Nuristan: Bagrami, im Nedjerau-Tal, ca. 2800 m, über der Baumgrenze (N. 1951/230). – Pakistan: Chitral: Bomboret, dry cliff sandstone, ca. 6800 ft. (B. L. 639). Buni, dry barren steep hillside facing West, ca. 6500 ft. (B. L. 902). Mastuj Track, Barenis, on rock ledges, ca. 6000 ft. (St. 2435). Ziarat (Lowarai Pass), ca. 7000 ft., in tufts (ST. 2549).

O. Munroi STAPF ex HOOK. f. – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17944). – C: Bamian: In declivibus saxosis aridis prope Band-i Amir, 2800–2900 m (RECH. 18299). – NE: Panjshir: Darrah Rastagal, Panjshir Valley, ca. 3200 m (HDG. & WDB. 5226). Nuristan: Ahmedi Dewane im oberen Paschgal-Tal, ca. 2590 m (KN. 1482-b). Mum-Pass, zwischen Parun- und Kantiwo-Fluss, Aufstieg von Gulnischa, 2200–2800 m (KN. 877-a). – Pakistan: Chitral: Beorai Gol, S of Drosh, ca. 5000 ft., at edge of irrigation channel (ST. 3217). W of Gahirat, $35^{\circ}40'$ N, $71^{\circ}46'$ E, ca. 9000 ft., on dry slopes facing South (B. L. 695). Chitral: (HARRIS 16790). Swat: Madian, ca. 4500 ft. (STEWART 24423). Bahrein, ca. 5000 ft. (RAHMAN 220, STEWART 25072). Bishigram, 5000–7000 ft. (STEWART 24919). Inter Madyan et Kalam, ca. 1700 m, substr. granit. (Rech. 19384). Kalam, ca. 2200 m, substr. granit., $35^{\circ} 30'$ N, $72^{\circ}30'$ E (Rech. 19408, 19431, 19452).

O. pamiroalaica GRIGORJ. ex DROBOV, Fl. Uzbekist., ed. SCHREDER, 1: 190 (1941). – NE: Nuristan: Pashki, ca. 2500 m (А. 740). Derin, East-Nuristan (Е. 1721).

O. pubiflora HACK. – SW: Herat: Herat to Shin Dand, ca. 1400 m (К. 3940). – E: Ghazni: Okak, ab altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (RECH. 17758). Panjshir: Darrah Rastagal, Panjshir Valley, ca. 3800 m (HDG. & WDB. 5175). – C: Unai-Pass, ca. 2800 m, felsige Halde (V. 2114). Farakulum, ca. 2700 m (K. 3048). In latere occidentali jugi Unai, 3000–3250 m (RECH. 18108). Bamian: Koh-i-Baba Range, 3400–3600 m (K. 2632, 2644). Kammregion in der Koh-i-Baba Kette, ca. 6780 m (G. 427-a). Panjao, Koh-i Baba Range, ca. 2700 m (K. 2704). – NE: Nuristan: An der Westseite des Semenek-Passes unterhalb der Passhöhe, ca. 3410 m, flache, steinige Matten (KN. 1513-a). Minjan, Miyan Deh, ca. 2550 m (E. 1452).

O. Wendelboi BOR, Nytt. Mag. Bot., Oslo, 1: 16 (1952). – NE: Nuristan: Pashki, 2300–2600 m, 9.10.6.1948 (E. 920, 948). Kantiwo im Kantiwo-Tal, ca. 2200 m, lichter Eichenwald (KN. 912-c). – Pakistan: Chitral: Südabfall des Tirich-Mir oberhalb von Bomosto, 3500–4200 m (KN. 1556).

Stipa L.

St. capensis THUNB. – SW: Jija, between Shin Dand and Farah, ca. 900 m (K. 4265). – SE: Kandahar: Germaub, nördlich von Ghirishk, ca. 1200 m (KN. 385). – E: Nidjrao, nordöstlich von Sarobi, östlich von Kabul, ca. 2500 m (V. 2345). Im Kabul-Tal zwischen Sarobi und Darunta (V. 1967). In der Grassteppe zwischen Nimla und Jallalabad, ca. 600 m, auf Diluvialschotter (KN. 629). Zwischen Tisin und dem Heiligengrab Seh Baba, an der Strasse von Kabul nach Jallalabad, auf Diluvialschotter (SCH. 68). – Pakistan: Waziristan (STEWART).

St. caragana TRIN. (Syn. Lasiagrostis caragana (TRIN.) TRIN.). – Pakistan: Kurram Valley (AITCH. 890).

St. glareosa P. SMIRN. in FEDDES Repert. spec. nov. 26: 266 (1929). – E: Ghazni: In faucibus Say Khoshkak (Nawar Kotal), inter Okak et Behzud, ca. 3150 m (RECH. 17863).

St. Hohenackeriana TRIN. et RUPR. – **SW:** Herat, ca. 1000 m (K. 4268). – **E:** Ghazni: Ghazni, ca. 2400 m (K. 3069). – **Pakistan:** Quetta: Chaman, ca. 1000 m (K. 3070).

St. Jacquemontii JAUB. et SPACH (Syn. Lasiagrostis Jacquemontii (JAUB. et SPACH) MUNRO). – Pakistan: Mount Ilam, ca. 8000 ft. (STEWART 24395). Nr. 4

St. khirghisorum P. SMIRN. in FEDDE, Repert. spec. nov. 21: 232 (1925). – NE: Nuristan: Vaigel (E. 2034).

St. lingua JUNGE – SW: Herat: Zwischen Herat und Farah, ca. 1500 m, Gebirgssteppe (G. 413). – E: Kabul: Logar-Tal, südlich von Kabul, Felssteppe (V. 1726). – C: Ghorat: In jugo Kotal Cherzakh inter Qala Sharak et Chischt, ca. 2450 m (RECH. 19182). Dolaini, Darreh Garmak, inter Qala Shahrak et Naourak, ca. 2540 m (RECH. 18898).

St. munroana BOR, Kew Bull. 1954: 500 (1954). – Pakistan: Siah Kuh (GRIFF. 1066).

St. orientalis TRIN. – E: Oberhalb Schechan im Nedschrab-Tal, ca. 2750 m (G. 412). – C: Bamian: Kalkberg bei Bulola, ca. 2780 m (G. 411, V. 2256, 2257, 2277).

St. pennata L. – N: Kataghan: In jugo Paigah Kotal, inter Haibak et Pul-i Khomri, ca. 1500 m (RECH. 16447). – E: Ghazni: In jugo Kotal-e Ketschru NW Sang-i Masha, Jaghuri Distr., ca. 2880 m, substr. granit. (RECH. 17521). Okak, NE altoplanitiei Dasht-e Nawar (Naour), ca. 3000 m (RECH. 17748). Inter Miradina et jugum Ghoutch Kol, N Sang-i Masha, ca. 3300 m, distr. Malestan (RECH. 17627). – E: Kabul: Aliabad bei Kabul, Felssteppe (V. 1555). – C: Bamian: Band-i Amir, in der Koh-i-Baba Kette, ca. 3200 m, Artemisia-Steppe (V. 2251, 2773). – NE: Nuristan: Zwischen Waigelek und Bardadesch, am Spuk-Pass, Nordseite, ca. 2500 m (Kn. 1197). Westseite des Semenek-Passes, ca. 3410 m, flache steinige Matten (Kn. 1509).

Stipa platypoda Bor, sp. nov.

Ab aliis speciebus huius generis callo glabro, basi expanso distincta. - Gramen perenne usque 60 cm altum. Culmi caespitosi, erecti, teretes, simplices, infra nodos dense puberuli; internodia inferiora retrorse hispida. Foliorum laminae involutae, supra ad nervos marginesque scabrae, infra laeves glabraeque, in apicem pungentem productae; vaginae striatae, laxe pilosae, superiores arcte complectentes, inferne a culmis solutae; ligula ad seriem pilorum redactae. Panicula in vagina superiore abscondita; spiculae superiores demum emergentes. Glumae aequales, ca. 6 cm longae, acuminatissimae, hyalinae, 3-nerviae. Lemma 10-10,5 mm longum, teres, 5-nervium, inter nervos lineari-pilosum, ad marginem usque apicem ciliatum, apice pilis 1,5 mm longis coronatum; callus 1-2 mm longus, glaber, apice in pedem ambitu elliptico expansus; palea lemmati aequilonga, 2-nervia; stamina 3; antherae 6 mm longae, haud barbatae; lodiculae 2, lanceolato-acuminatae, 3 mm longae; styli 2; stigmata plumosa; arista usque 16 cm longa; columna 2 cm longa, glabra vel sparsissime pilis longis obtecta, valde torta; aristula inferne pilis densis 1 mm longis, apicem versus brevioribus instructa.

Afghanistan, Hari-rud valley, profuse over the whole plain, 26.5.1885, (AITCHISON 1137, Holotypus, K).

This species is easily distinguished from all others in the area by the tip of the basal callus of the fruit, being expanded into an easily observed foot.

Biol.Skr.Dan.Vid.Selsk. 14, no. 4.

St. sibirica (L.) LAM. – NW: Maymana: Belcheragh, Darrah Belcheragh, ca. 1200 m, on stony slopes (HDG. & WDB. 3776). – NE: Nuristan: Aschpi-Pass (N. 1951/1042). – Pakistan: Kurram Valley (HARSUKH 15504). Bahrein, ca. 8000 ft. (STEWART 24496).

St. splendens TRIN. in SPRENG. (Syn. Lasiagrostis splendens (TRIN.) TRIN.). – C: Bulola, ca. 2250 m, am Wegrand (G. 414). Inter Bamian et Band-iAmir, 2800–3000 m (RECH. 18157). Bamian, Ackerraine (V. 2243). – Pakistan: Chitral: Mastuj-Baroghil Track, ca. 8000 ft., on river banks and at edge of fields (ST. 2888, 2889). Yarkhun, between $36^{\circ}30'$ N, $72^{\circ}40'$ E, and $36^{\circ}48'$ N, $73^{\circ}05'$ E, ca. 8000 ft., roadside hedgerow (B. L. 83).

St. Szowitsiana Ткім. ex Hohen. – N: Mazar-i Sharif: Inter Chashma-e Shafal et Aq Kupruk, 800–1000 m (Rech. 16285). Maymana: Ca. 5 km outside of Maymana, ca. 500 m (HDG. & WDB. 3598). - E: Ghazni: Bozghalak, in collibus graniticis prope Shashgao, 24 km NE Ghazni, ca. 2400 m (Rech. 17301). Dahan-e Abdila, 35 km E Sar-i Chashma, ca. 2800 m, in saxosis serpentinicis (RECH. 18608). In jugo Ghoutch Kol, NNE Sang-i Masha, ca. 3300 m (RECH. 17650). In monte ad occidentem jugi Sardalu, inter Qarabagh et Sang-i Masha, ca. 2600 m (RECH. 17364). Berg südöstlich von Sarobi, östlich von Kabul, ca. 1430 m (G. 398). Usman Kehl, unfern Sarobi, steinige Steppe (V. 1047, 1604). Tisin, beim Stausee an der Strasse von Kabul nach Jallalabad, Südhang (Kn. 584). Unter einem Berggipfel in der Tang-e Gharu östlich von Kabul, 1600–1700 m (Км. 526, Sсн. 67). In der Tang-e Gharu nächst dem Maipar, ca. 1720 m (G. 399). Scher Darwasa bei Kabul, Nordhang, ca. 1700 m (Kn. 490-a). In declivibus borealibus montis Scher Darwasa, 1800–1900 m, substr. Gneiss (Rech. 17008). Tobfels am Scher Darwasa, ca. 1840 m (G. 400). Grabmoschee Chodsche Safa am Scher Darwasa, ca. 1880 m (G. 401). NNW vom Stausee bei Chord Kabul, ca. 2280 m (G. 402). Gipfel im Korogh-Massif bei Kabul, 2880-2800 m (G. 404, 416). Koh Gaworgin bei Tschakewardak, ca. 2950 m, südlich vom Stausee (G. 405). Wardak, ca. 2800 m, Steinhalde (V. 796). Aliabad bei Kabul (V. 907, 1561). Logar-Tal, südlich von Kabul, ca. 2500 m, Felssteppe (V. 1725). In valle Paghman, W Kabul, 2300-2800 m, substr. Gneiss (G. 403, RECH. 17100). Kabul, ca. 1700 m (К. 4005). - С: Hauz-i Mahiha, ca. 2500 m (K. 2389). Kalkberg nordöstlich von Bamian, ca. 3000 m (G. 408, 409). Oberhalb Doab, Felssteppe (V. 467, 1769). Vorberg der Koh-i Baba Kette, 2600-2800 m (G. 406, 407). Zwischen Bamian und Band-i Amir, Steppe (V. 2786). In declivibus saxosis aridis prope Band-i Amir, 2800-2900 m (RECCH. 18207). Hochfläche oberhalb der Seen von Band-i Amir, ca. 2950 m (G. 410). Ad lacum Band-i Gholoman, prope Band-i Amir, ca. 2800 m (Rech. 18484). Band-i Amir, ca. 2800 m (K. 2851). Ghorat: Qala Sharak, ca. 2000 m (RECH. 19142). Dolaini, Darreh Germak, inter Qala Shahrak et Naourak, ca. 2540 m (RECH. 18899).

St. trichoides P. SMIRN. – E: Kabul: Unter dem Gipfel des Sebroderakan bei Scherwaki im Logar-Tal, ca. 2400 m (G. 415). Gipfel im Korogh-Massif bei Kabul, ca. 2800 m (G. 404, 417). – Pakistan: Chitral: Rosh Gol, NE of Tirich Mir, ca. 10000 ft. (Sr. 2806). Aegilops L.

Pooideae-Triticeae

Ae. Kotschyi BOISS. (Syn. Ae. triuncialis L. var. Kotschyi (BOISS.) BOISS.). – SW: Herat: Herat, ca. 1100 m (K. 4249). – E: Kabul: Sarobi, östlich von Kabul, steinige Steppe (V. 1864 pr. pte.). – Pakistan: (GRIFF. 549).

Ae. Tauschii Coss. – N: Kataghan: In jugo Argana, ca. 20 km W Kunduz, ca. 600 m (RECH. 16112). Kunduz, in declivibus siccis ad aerodromum, ca. 450 m, substr. Loess (RECH. 16084). Pul-e Khomri, in valle fluvii Kunduz, ca. 700 m, in collibus aridis calc. (RECH. 16434, 16497). Inter Haibak et jugum Paigah Kotal, 1300–1500 m (RECH. 16408). Haibak, ca. 3000 ft. (M.). – NW: Khuraja, ca. 700 m (K. 3794). – SW: Herat, ca. 1700 m (K. 3824). Pirzada near Kandahar, ca. 980 m (K. 2072). – E: Kabul: Ca. 5 km S Arghandab, inter Kabul et Ghazni, ca. 1900 m (RECH. 17210). Sarobi, Steppe (V. 2574). Khinjuk-Berg südlich Kabul (N. 1950/811). Schlucht des Kabul-Flusses: Gang-i Gharu, 1600–1700 m (KN. 522-b, SCH. 60). Tisin, an der Strasse von Kabul nach Jallalabad (KN. 591). Beim Königsschloss von Paghman, ca. 2160 m (G. 709).

Ae. triuncialis L. – N: Kataghan: In jugo Argana, ca. 20 km W Qunduz, ca. 600 m (Rech. 16113). In jugo Paigah Kotal inter Haibak et Pul-i Khumri, ca. 1500 m (Rech. 16480). Halfway between Pul-i-Khumri and Samangan (Aybak), ca. 900 m, on low hills (HDG. & WDB. 3522). Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (Rech. 16322). Inter Chashma-e Shafal et Aq Kupruk, 800–1000 m (Rech. 16257). – NW: Maymana: 30 km W Maymana, ca. 500 m, near stream bed (HDG. & WDB. 3644). – SW: Herat, 1100–1600 m (K. 2275, 4250). Herat, Steppe (AMSEL). – E: Lataband, bei Kabul (V. K-224). Sarobi, östlich von Kabul (V. 1864 pr. pte). Jagdalak, ca. 5000 ft. (Kz. 8248). An der Strasse von Kabul nach Jallalabad zwischen dem Heiligengrab Seh-Baba und Nimla (KN. 615, Sch. 69, 77-b). – NE: Badakhshan: Faizabad, 1100–1900 m (E. 2108).

Agropyron GAERTN.

A. afghanicum MELDERIS in BOR, The Grasses of Burma, Ceylon, India, and Pakistan 689 (1960). – Persia: Khorasan (AITCH. 1145 pr. pte.).

A. Borianum MELDERIS in BOR, The Grasses of Burma, Ceylon, India and Pakistan 690 (1960). – Pakistan: Chitral: (TOPPIN 584). Swat: Kalam (RAHMAN 229). Sho Nala (RAHMAN 239).

A. canaliculatum NEVSKI, Bull. Jard. Bot. Acad. Sc. URSS. 30: 509 (1932). (Syn. A. longe-aristatum (BOISS.) BOISS. var. Aitchisonii BOISS.). – NE: Nuristan: Above Netshingel (E. 1691). Auf dem Wege zwischen Aschpi-Pass, ca. 3400 m, und dem Ort Kuschtos, ca. 2500 m (N. 1951/695, 720). Zwischen Kotal-e Agok (Agok-Pass) und Alm bis Ort Waigel (N. 1951/873, 875, 920). W. Nuristan: Pitwei-Tal zwischen Pirdum Pass und Kulam (Munui), ca. 2200–2900 m (KN. 1075). C.-Nuristan: Donda-Pass, Ostseite in Richtung Aschenu, ca. 2000–3000 m (KN. 1241). E.-Nuristan: Mrami- (Papruk-) -Pass, Ostseite bis Papruk, trockene Hänge im Graman-Tal, ca.



Fig. 9. Agropyron colorans Melderis (G. 698, Holotypus, W).

3000–3400 m (Kn. 1439). Westseite des Semenek-Passes, ca. 3400 m (Kn. 1504-a). – E: Nedschrab-Tal, zwischen Gulbahar und Sarobi oberhalb Schechan, östlich von Kabul, 2500–3200 m, feuchter Hang in einer Schlucht bezw. in lichten Wäldern von *Pinus Gerardiana* (G. 686, 687). In der Bergkette oberhalb des Nedschrab-Tales, zwischen Gulbahar und Sarobi, ca. 3300 m (G. 689). – C: Bamian: Band-i Amir, nördlich der Koh-i Baba Kette, Kalktuff (V. 2266-a). – **Pakistan:** Kurram Valley, Segal, and Sikaram (Антсн. 962). N. W.-Frontier Prov. (Hassan-ud-Din 16). Chitral: Urgosh Dhok (Siddiqui et Rahman 26748). Barum Gol, Zapotili (Wendelbo).

The following specimens are characterized by having nearly glabrous lemmas, with a more or less hairy callus:

NE: Nuristan: Zwischen Kantiwo im Kantiwo-Tal und Pirdum-Pass in West-Nuristan (Sch. 109). Spuk-Pass zwischen Waigelek und Bardadesch, Nordseite nach



Fig. 10. Agropyron colorans MELDERIS, a part of the spike (G. 698, Holotypus, W).

Waigelek zu, 2500–2700 m (Kn. 1198-a). – E: Kabul: Oberes Paghman-Tal (N. 1950/792).

Agropyron colorans Melderis, sp. nov. - Fig. 9, 10.

Gramen perenne, 35-60 cm altum, caespitosum. Culmi graciles, 4-5-nodi, basi ascendentes vel geniculati, teretes, striati, sub nodis brevissime pubescentes ceterum glabri laeves. Folia glauco-viridia; vaginae inferiores pilis brevissimis tectae, vaginae superiores glabrae laeves; ligulae ca. 0,2 mm longae, hyalinae, laceratae; auriculae glabrae laeves, breves, angustae, patentes; laminae 5-19 cm longae, 2-6 mm latae, planae, supra nervis marginibusque scabrae, interdum nervis sparse longipilosae, subtus glabrae laeves. Spica 6-8 cm longa, densiuscula, erecta, purpureo-tincta; rhachis glabra laevis, sed marginibus breviciliata. Spiculae 12-13



Fig. 11. Agropyron Edelbergii MELDERIS (E. 1171, Holotypus, C).

mm longae (aristis exclusis), anguste lanceolatae, circiter 3-florae. G1um a e inaequilongae, gluma inferior 6,5–7,5 mm, gluma superior 7,5–9 mm longa, lanceolatae vel anguste oblongae, apicem versus \pm hyalino-marginatae, apice abrupte acuminatae vel breviaristatae, arista usque ad 1,5 mm longa, 3–5-nerviae, leviter scabrae. Lemm a 8,5–10 mm longum, lanceolatum, appresso-pilosum, nervis apicem versus conspicuis, breviaristatum, arista usque usque ad 1,5 mm longa. Palea lemmati subaequilonga, anguste lanceolata, apice acuto-emarginata, bicarinata, carinis brevissime ciliata, dorso brevisetulosa. Rhachilla 1,5–2 mm longa, strigosa. Antherae ca. 2,5 mm longae. – Affinis A. mutabili DROB. sed spiculis non unilateralibus, glumis brevioribus, apicem versus \pm late hyalino-marginatis, apice abrupte acuminatis vel breviaristatis, lemmate appresso-piloso, arista breviore, rhachilla strigosa, differt.

NE: Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak, ca. 2800 m, 25.8.1950 (GILLI 698, Holotypus, W).



Fig. 12. Agropyron Edelbergii MELDERIS, a part of the spike (E. 1171, Holotypus, C) 4.5/1.

A. curvatiforme NEVSKI, Bull. Jard. Bot. Acad. Sc. URSS. 30: 633 (1932), in adnot. – Pakistan: Kurram Valley (AITCH. 903).

Agropyron Edelbergii MELDERIS, sp. nov. - Fig. 11, 12.

Gramen perenne, 30–90 cm altum, caespitosum. Culmi graciles, 3–4-nodi, teretes, striati, sub et in nodis dense brevissime pubescentes ceterum glabri laeves. Folia viridia; vaginae inferiores saepe pilis brevissimis tectae, superiores plerumque glabrae laeves; ligulae 0,2–1 mm longae, hyalinae, apice laceratae; auriculae glabrae laeves, angustae, falcatae; laminae 6,5–11 cm longae, 2,5–4 mm latae, planae, utrinque nervis marginibusque scabrae, supra interdum plerumque nervis marginibusque scabrae, supra interdum plerumque nervis sparse longipilosae. Spica 8–12,5 cm longa (aristis inclusis), erecta vel subnutans; rhachis plerumque costis scabridula, marginibus breviciliata. Spiculae 0,8–1,4 cm longae (aristis exclusis), anguste

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lanceolatae, virides, 3–4-florae. Glumae inaequilongae, gluma inferior 6–8,5 mm, superior 7,5–10 mm longa, lanceolatae vel anguste lanceolatae, hyalino-marginatae, apice sensim acuminatae vel breviaristatae, arista usque ad 3 mm longa, 3–5-nerviae, nervis conspicuis, scabris. Lemma 7–9,5 mm longum, oblongo-lanceolatum, brevisetulosum, nervis apicem versus conspicuis, aristatum, arista 1–3 cm longa, erecta vel leviter curvata. Palea lemmati aequilonga vel subaequilonga, anguste lanceolata, apice obtusa vel emarginata, bicarinata, carinis breviciliata dorso brevisetulosa. Rhachilla strigosa. Antherae ca. 2,5 mm longae, flavae. – Ab *A. kuramensi* MELDERIS foliorum vaginarum marginibus glabris, glumis longioribus, lanceolatis vel anguste lanceolatis, marginibus hyalinis latioribus, apice saepe breviaristatis, lemmate brevisetuloso, arista longiore, differt.

– – var. Edelbergii.

Culmi 60-90 cm alti. Foliorum laminae supra plerumque sparse longipilosae; ligulae ca. 0,2 mm longae; gluma inferior 6-8,5 mm, gluma superior 7,5-10 mm longa, uterque saepe breviaristatae, arista usque ad 1,5 mm longa; lemma 7-8 mm longum, arista 1-2,5 cm longa, erecta vel subcurvata.

NE: Nuristan: Pashki, 25.7.1948 (EDELBERG 1171, Holotypus, C). Ibidem, ca. 2300 m, 25.7.1948 (E. 1179).

– – var. Kerstanii Melderis, var. nov.

Culmi 30–45 cm alti. Foliorum laminae supra non longipilosae; ligulae 0,3–1 mm longae; gluma inferior 6–6,5 mm, gluma superior 7–8 mm longa, utraque saepe breviaristata, arista 1,5–3 mm longa; lemma 9–9,5 mm longum, arista 2,5–3,5 cm longa, curvata.

NE: Nuristan: Aschkun-Gebiet, Donaa-Pass, Matten auf der Westseite des Passes, ca. 2500–3200 m, 20.7.1935 (KERSTAN 1251-b, Holotypus, W, Isotypus, BM).

A. elongatiforme DROB. - NW: Obeh, E of Herat, ca. 1700 m (K. 3773).

 $A. \times interjacens$ Melderis in Bor, The Grasses of Burma, Ceylon, India, and Pakistan 691 (1960). – Pakistan: l'Ishkuman Aghost (Schmid 2430).

A. intermedium (HOST) P. BEAUV. – Pakistan: Balouchistan: Spin Karez (NASIR 28476).

A. kuramense MELDERIS in BOR, The Grasses of Burma, Ceylon, India, and Pakistan 691 (1960). – Pakistan: Kurram Valley, fields near Kaiwas (AITCH. 709).

A. macrolepis DROB. NE: Nuristan: Donda-Pass, Ostseite in der Richtung Atschenu, 2000–3000 m, Felsen in der Hochwaldregion (KN. 1241-a). Aschkun-Gebiet: Donda-Pass, Matten auf der Westseite des Passes, 2500–3200 m (KN. 1251-d).

A. pectiniforme ROEM. et SCHULT. – NW: Ardewan, N of Herat, ca. 1500 m (K. 2248). NW Afghanistan (Антсн. 511).

A. repens (L.) P. BEAUV. – Persia: Khorasan (AITCH. 1145 pr. pte.), Aoi Khurak, ca. 9000 ft. (Kz. 13787-a), Biankhel (AITCH. 886), Zabardastkalla (AITCH. 1259). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17940-a). Scharenau (Tschaman Wazirabad), ca. 1750 m, Weizenfeld (G. 694). Garten der Nedschat-Schule in Kabul, Bewässerungsgraben (G. 695, 696). Beim Königsschloss von Paghman, westlich von Kabul, ca. 2160 m, buschiger Hang (G. 697). - C: Qala-e Wazir, inter Sar-i Chashma et jugum Unai, ca. 2900 m (RECH. 18051). Lal-i Zarjangel, ca. 2500 m (K. 2760). Zwischen Bulola und Doab (V. 433). Ghorat: Qala Sharak, ca. 2000 m (RECH. 19147).

A. semicostatum NEES ex STEUD. (Syn. A. striatum NEES ex STEUD., Roegneria nuristanica OHWI). - NW: Ca. 65 miles NE of Herat, ca. 2500 m (STUTZ 645). - E: Panjshir: Porande-Tal, Seitental des Panjshir-Tales bei Basarak, Wiese am rechten Porande-Ufer östlich von Daolana, ca. 2350 m (G. 691). Nuristan: Gusalak, Kurdertal, Seitental des Petsch (N. 822). Zwischen Kotal-e Agok (Agok-Pass) und Alm bis Ort Waigel (N. 1951/874, 884, 933). Darim-Tal ab Ort Darim aufwärts, ca. 1900-2400 m (N. 1951/1012). East-Nuristan (E. 1157). C.-Nuristan: Oberes Petsch-Tal: Felshänge bei Wama, ca. 1400 m (Kn. 756). W.-Nuristan: Kulam (Munui) im Kulam-Tal, ca. 2150 m (Kn. 1046). Pitwei-Tal zwischen Pirdum-Pass und Kulam (Munui), ca. 2200-2900 m (Kn. 1075). Wurertschitur im Tschitur-Tal, ca. 2000-3000 m (Sch. 130). Im Ramgel-Tal südlich von Gadwol, auf Trockenschotter (Sch. 125). NW.-Nuristan: Oberes Ramgel-Tal oberhalb Puschol, ca. 2250 m (Kn. 1114). - E: Kabul: Zwischen abgestürzten Felsblöcken und in Felsspalten einer steilen Wand im Paghman-Tal, 2500–2560 m (G. 691, 692). Paghman, W of Kabul, ca. 1900 m (K. 2318). - Pakistan: Kurram Valley, near Shalizan, Shendtoi, and Sikaram (AITCH. 803, 903). Chitral: (HASSAN-UD-DIN 36). Brir (SIDDIQUI & RAHMAN 26749, 26758). Swat: Kalam, ca. 2200 m, substr. granit. (RECH. 19430).

× Elyhordeum MANSFELD 1955 (Syn. x Elymordeum Lepage 1957).

× **Elyhordeum** Schmidii (MELDERIS) MELDERIS, comb. nov. (Syn. x *Elymordeum* schmidii MELDERIS in BOR, The Grasses of Burma, Ceylon, India and Pakistan, 696 (1960)). – Pakistan: Chitral: Upper Yarkhun Valley (SCHMID 2334).

Elymus L.

E. dahuricus TURCZ. (Syn. Clinelymus dahuricus (TURCZ.) NEVSKI). – C: Zwischen Bulola et Doab, feuchte Wiesen (V. 2100). – NE: Nuristan: Pashki, ca. 2300 m (E. 1330). Parun-Tal bei Pashki, Aue-Wiesen am Uferrand, ca. 2200 m (KN. 1357-a).

E. dasystachys TRIN. (Syn. Aneurolepidium dasystachys (TRIN.) NEVSKI). – NE: Minjan, Miyan Deh, ca. 2500 m (E. 2082, 2107). – Pakistan: Chitral: Tirich-Mir-Gebiet: Ojhor-Tal bei Tsusum, nach Bomosto zu, ca. 2800 m (KN. 1577).

E. multicaulis KAR. et KIR. (Syn. *Aneurolepidium multicaule* (KAR. et KIR.) NEVSKI). – C: Der-i Shikari, feuchter, ansalziger Boden (V. 2094).

E. nutans GRISEB. (Syn. Clinelymus nutans (GRISEB.) NEVSKI). – NE: Nuristan: Gusalak, ca. 1000 m (E. 1523).

E. Paboanus Claus (Syn. Aneurolepidium Paboanum (Claus) NEVSKI).

– var. **Paboanus** – E: Ghazni: Okak, ab altoplanitiei Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (RECH. 17733). Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17940).

- - var. saxatilis Melderis, var. nov.

A typo rhachidi glabra, sub spiculis strigosa, marginibus longiciliata, spiculis binis, glumis in parte basali glabris laevibus, apice scabris, lemmate sparse appressolongipiloso, palea lemmati vulgo longiore, differt.

C: Bamian: Band-i Amir, in declivibus saxosis aridis, 2800–2900 m (RECHINGER 18244-a, Holotypus, W). Band-i Amir, ca. 2800 m (K. 2849). Band-i Amir, Artemisia-Steppe, an sandigen Stellen, ca. 3200 m (V. 2255). Band-i Amir, Seeufer (N. 1951/439). Obere und mittlere Seen von Band-i Amir (N. 1951/454). Band-i Amir, am untersten See (N. 1951/461).

- - var. scabridus MELDERIS, var. nov.

Affinis *E. paboano* var. *saxatili* sed foliorum vaginarum marginibus non longiciliatis, glumis scabris, lemmate in parte basali et apicem versus scabrido pilis brevissimis tecto, dorso \pm glabro, differt.

C: Bamian: Beim "Kleinen Drachen" (VOLK 2787, Holotypus, W, Isotypus, BM).

Eremopyrum (LEDEB.) JAUB. et SPACH

E. Bonaepartis (SPRENG.) NEVSKI (Syn. Triticum Bonaepartis SPRENG., T. squarrosum ROTH). – SE: Kandahar: Kalat-i Ghilzai, zwischen Kandahar und Kabul, Artemisia-Steppe beim Hotel (KN. 152-a, 169). Artemisia-Papaver-Steppe zwischen Kalat-i Ghilzai und Kandahar (KN. 196-b). Kandahar-Umgebung, in Richtung Kalat-i Ghilzai, ca. 1100 m (KN. 246-a). Goldgrube im Norden von Kandahar in der Steinsteppe, ca. 1000 m (KN. 2225). – E: Ghazni: In monte ad occidentem jugi Sardalu, inter Qarabagh et Sang-i-Masha, ca. 2600 m, substr. gyps. (RECH. 17355). Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17945). Im Kabul-Tal, zwischen Tangi Gharu und Kabul, ca. 1770 m (G. 699, 702). Gulbagh bei Kabul, ca. 1840 m (G. 703). Koh-i Asmai, Berg im Norden von Kabul, ca. 1700 m (KN. 430-a). – C: In valle ca. 16 km a Doab meridiem versus, ca. 1600 m (RECH. 16691). Am Fuss einer steilen Felswand im Kamard-Tal, westlich von Doab, ca. 1630 m (G. 701). – N: Haibak, ca. 3900 ft. (M.). Doshi, ca. 2700 ft. (M.). – Pakistan: Quetta: Quetta (NORRIS 65). Balouchistan: Killa Abdulla (DUTHIE).

E. Bonaepartis (SPRENG.) NEVSKI VAR. sublanuginosum (DROB.) MELDERIS (SYN. Agropyron orientale (L.) JAUB. et SPACH VAR. sublanuginosum DROB,. Hordeum hirsutum BERTOL., Eremopyrum hirsutum (BERTOL.) NEVSKI). – SW: Herat: Jija, between Shin Dand and Farah, ca. 900 m (K. 4266). – SE: Kandahar: Pirzada near Kandahar, ca. 900 m (K. 2014). Goldgrube in der Steinsteppe im Norden von Kandahar, ca. 1000 m (KN. 369-b), 2239 pr. pte.). – C: In den Ruinen von Gholghola bei Bamian, ca. 2550 m (G. 700). – N: Mazar-i Sharif: Haibak, ca. 3900 ft. (M.). – E: Kurram Valley, Alikhel, amongst stones (AITCH. 561). Pakistan: Quetta (DUTHIE 8740). Balouchistan: Killa Abdulla (AITCH. 561).

E. Bonaepartis (SPRENG.) NEVSKI VAR. pakistanicum MELDERIS – Pakistan: Quetta: Quetta (Norris 75-a).

Nr. 4

E. distans (С. КОСН) NEVSKI, Fl. SSSR. 2: 665 (1934). – E: Kabul: Tobfels am Sher Darwasa bei Kabul, ca. 1840 m (G. 704). Schutthalde am Sher Darwasa, ca. 1900 m (G. 705). Berg beim Stausee Chord Kabul, ca. 2280 m (G. 706). Aliabad bei Kabul (N. 1951/102). Koh-i Asmai, Berg im Norden von Kabul, ca. 1700 m (KN. 430-b, SCH. 57). – SE: Kandahar: Goldgrube im Norden von Kandahar, ca. 1000 m (KN. 2239 pr. pte.). Artemisia-Papaver-Steppe zwischen Kalat-i Ghilzai und Kandahar (KN. 197-b). – NE: Badakhshan: Ishkashim (GILES). – Pakistan: Quetta (NORRIS 67). Fort Sandeman (HARSUKH 20672).

Henrardia C. E. HUBBARD

H. persica (BOISS.) C. E. HUBBARD, Blumea, Suppl. 3: 17 (1946).

– var. persica. (Syn. Lepturus persicus (Boiss.). – SW Herat: Herat, ca. 1100 m (K. 4252). "Afghanistan" (Антсн. 409). – Pakistan: Balouchistan (Stocks).

var. glaberrima (HAUSSKN.) C. E. HUBBARD (Syn. Lepturus persicus BOISS.
var. glaberrimus HAUSSKN. ex BORNM.). – E: Sarobi, östlich von Kabul, steinige Steppe (V. 1863). Tobfels am Scher Darwasah bei Kabul, ca. 1840 m (G. 719). Pakistan: (GRIFF. 514 pr. pte.).

Heteranthelium HOCHST.

H. piliferum (BANKS et SOLAND.) HOCHST. ap. KOTSCHY (Syn. Elymus pilifer BANKS et SOLAND. ex RUSSELL). – N: Kataghan: Inter Haibak et jugum Paigah-Kotal, S Kunduz, 1300–1400 m (RECH. 16412). – NW: Herat: Qala Nau to Sauzak, ca. 1400 m (K. 3927). – E: Kabul: Babur bei Kabul (V. 2039). An der Strasse von Kabul nach Jallalabad zwischen dem Heiligengrab Seh-Baba und Nimla (KN. 627). Tal des Kabul-Flusses, in der Tangi Gharu, 1600–1700 m (KN. 548). – SE: Kandahar: In der Steinsteppe nordwestlich von Kandahar (SCH. 5). Baba Wali nordwestlich von Kandahar, auf einem Friedhof (SCH. 9). Schlucht des Hilmend bei Germaub, nördlich von Ghirishk, ca. 1200 m (KN. 405).

Hordeum L.

H. bogdanii WILENSKY, Izv. Saratovsk. Op. Stan. 1: 13 (1918). – E: Ghazni: Ad lacum Sabzab, inter Okak et Behzud (Diwal Kol), ca. 2800 m (RECH. 17902). Kabul: Sumpfwiese bei Dehmasang bei Kabul, ca. 1770 m (G. 726). Darulfanun bei Kabul (V. 994). Am Ufer des Logar-Flusses bei Tscharasiah, südlich von Kabul, ca. 1780 m (G. 724). Guzar Geh bei Kabul, in einem Brachfeld nahe am Flussufer (N. 1951/178). Khotsche Mullah bei Kabul, im Wasser (N. 1951/184-a). Kabul, Allee, nach Darelfanun, in einem Bewässerungsgraben (N. 1950/790). – C: Farakulum, ca. 2800 m (K. 2613). Bamian: Inter Bamian et Band-i Amir, 2800–3000 m (RECH. 18158). Kamard-Tal westlich von Doab, ca. 1550 m (G. 725). Doab (V. 1799-b). Band-i Amir, nasse Kalktuffe (V. 2266-a). Band-i Amir, ca. 3000 m (V. 2784). Panjao, S of Koh-i Baba Range, ca. 2700 m (K. 3077). H. bulbosum L. – NE: Badakhshan: Tschal-Ischkamisch, ca. 1200 m, Löss-Steppe (V. 2653).

H. geniculatum ALL. (Syn. H. Hystrix ROTH, H. Gussoneanum PARL., H. maritimum WITH. ssp. Gussoneanum (PARL.) ASCHERS. et GRAEBN., H. marinum HUDS. ssp. Gussoneanum (PARL.) THELL., H. marinum HUDS. var. Gussoneanum (PARL.) HYL.). – SE: Kandahar: Goldgrube im Norden von Kandahar, in der Steinsteppe, ca. 1000 m (KN. 356-b). – E: Kabul: Maslakh, am Schlachthaus (N. 1951/141-b). – N: Kataghan: In paludosis fluvii Kunduz prope Kunduz, ca. 400 m, in limosis (RECH. 16051).

H. glaucum STEUD. (Syn. H. Stebbinsii COVAS). – SW: Jija, between Shin Dand and Farah, ca. 900 m (K. 4364). – SE: Kajkai, NNW of Kandahar, ca. 1000 m (K. 3078). Kandahar, in Richtung Kalat-i Ghilzai (KN. 247-a). Pirzada near Kandahar, ca. 900 m (K. 2019). In einem Garten in Kandahar, ca. 1020 m (G. 721). – E: Kabul: Sarobi, östlich von Kabul (V. K-269). Kabul, ca. 1780 m, an einem Gartenweg (G. 723). Jallalabad bei Kabul, ca. 600 m (E. 2338). Kabul, Unkraut im Hausgarten (N. 1951/132). Schlucht des Kabul-Flusses Tang-i Gharu, 1600–1700 m (KN. 516-a). Bagram (Begrami) near Charikar, ca. 5000 ft. (CN. 25). Panjshir, ca. 2000 m (K. 3993). Nuristan: Between Parundal and Bashgaldal (E. 1153). Gusalak, ca. 1000 m (E. 1571). Am Ufer eines Mühlbaches bei Barikot, ca. 850 m (G. 720). – Pakistan: Chitral (HARRIS 16830).

H. leporinum LINK – N: Mazar-i Sharif: In faucibus fluvii Balkh supra Aq Kupruk, 700–800 m (RECH. 16630). – E: In einem Garten in Kabul, ca. 1780 m (G. 722). – C: In valle ca. 16 km a Doab meridiem versus, ca. 1600 m (RECH. 16674).

H. spontaneum C. Косн (Syn. H. ithaburense Boiss.). – E: Kabul: Schlucht des Kabul-Flusses Tangi Gharu, 1600–1700 m (Kn. 516-c). – SE: Kandahar, einheimisch auf Feldern (Sch. 73). Kandahar, ca. 1020 m (Kn. 215). Schlucht des Hilmend bei Germaub, nördlich von Ghirishk, ca. 1020 m (Kn. 408). – SW: Herat, ca. 1700 m (K. 3823). – NW: Khwaja, NE of Herat, ca. 700 m (K. 3795). – 'Afghanistan' (Агтсн. 465). – Pakistan: Quetta (Stocks 1062).

H. turkestanicum NEVSKI, Act. Univ. As. Med. Ser. VIII-b, Fasc. 17: 45 (1934) et Act. Inst. Bot. Acad. Sc. URSS. 1, 2: 61 (1936), dign. lat. – NW: Afghanistan (AITCH. 465). – C: Unai-Pass, ca. 3120 m (G. 729). Unai-Pass (N. 1951/544, 550). Inter Bulola et jugum Schibar, 2600–2800 m (RECH. 16782). Am Ufer des Schumbol-Flusses bei Bulola, ca. 2280 m (G. 728). Im Sard-Darra in der Koh-i Baba Kette, ca. 3350 m, Sumpfwiese (G. 730). In latere boreo-occidentali jugi Hadjigak montium Koh-i Baba, 3000–3200 m (RECH. 18496). – NE: Minjan, Miyan Deh, ca. 2500 m (E. 2110). Nuristan: Urura-Passhöhe, beiderseits oberhalb der Waldgrenze, ca. 3900 (N. 1951/586).

H. violaceum Boiss. et Hohen. – **NE: Nuristan:** Mrami- (Papruk-) -Pass, Westseite in Richtung Schtiwe, 3000–4200 m, über der Waldgrenze (Kn. 1407-а).

H. vulgare L. – **SE:** Kandahar: Einheimisch auf Feldern bei Kandahar (Sch. 74). Kandahar, ca. 1020 m (Kn. 214). – **NE:** Nuristan: Parun-Tal, zwischen Schtiweh und Pashki, 2500–2550 m (Kn. 1391). – **N:** Der-i Shikari, kultiviert (V. K-233, 1791).

Nr. 4

Psathyrostachys NEVSKI

Psathyrostachys caduca (BOISS.) MELDERIS, comb. nov. (Syn. Elymus caducus BOISS., Fl. Or. 5: 691 (1884), Hordeum caducum MUNRO ex AITCH. Cat. in Journ. Linn. Soc. 18: 110 (1880), nomen nudum). - Nuristan: Weran, Nau, ca. 3000 m (E. 1473). Nedjerau-Tal, oberhalb der Steinsteppe, ca. 3000 m (N. 1951/207). Oberes Kantiwo-Tal bei Brubruts, ca. 2460 m (Kn. 946). Parun-Tal, oberhalb Schtiwe, ca. 2600 m (Kn. F-108). Ptsigela-Tal, ca. 15 km N von Kantiwo, ca. 2400 m, Ferula-Fluren (Kn. 923). Nordseite des Pirdum-Passes zwischen Puschol und Pirdum-Tal, 2200-2700 m (Sch. 117). W.-Nuristan: Kulam-Tal, trockene Felshänge zwischen Kulam (Munui) und der Mündung des Tales, 1800–2100 m (Scn. 110). E.-Nuristan (E. 1473). - E: Panjshir: Panjshir, ca. 2100 m (K. 4000). Porande-Tal, Seitental des Panjshir-Tales bei Basarak, ca. 2800 m (G. 753). Ghazni: Inter Miradina et jugum Ghoutch Kol, N Sang-i Masha, Malestan distr., ca. 3300 m (Rech. 17632). In jugo Ghoutch Kol NNE Sang-i-Masha, ca. 3300 m (RECH. 17656). Okak, ab altoplanitie Dasht-e Nawar (Naour) boreo-orientem versus, ca. 3000 m (RECH. 17730). Berg oberhalb des Nedschrab-Tales, zwischen Gulbahar und Sarobi, östlich von Kabul, ca. 3310 m (G. 735). Sebroderakan bei Scherwaki im Logar-Tal, ca. 2400 m, Nordhang (G. 731). Berg am linken Ufer des Paghman-Flusses, ca. 2760 m (G. 732). Oberhalb Beg tut, Paghman-Gebirge, Hang unterhalb der Kammhöhe, ca. 3300 m (G. 734). Oestlich von Kotal-i Kotander, Paghman-Gebirge, ca. 3740 m (G. 736). Oberes Paghman Tal (N. 1950/793). - C: Hauz-i Mahiha, ca. 2500 m (K. 2367). Farakulum, ca. 3000 m, (K. 3074). Deh Kundi, ca. 3000 m (E. 1960). In declivibus saxosis aridis montium Koh-i Baba prope Band-i-Amir, 2700–2900 m (RECH. 18243). Koh-i Baba, ca. 3400 m (K. 3075). Kammregion der Koh-i Baba Kette, ca. 3780 m (G. 737). Band-i Amir, Igelsteppe (V. 2739). Band-i Amir (N. 1951/486). Unai-Pass (N. 1951/497).

P. juncea (FISCH.) NEVSKI (Syn. Elymus junceus FISCH.). – C: Bamian: Band-i Amir, ca. 2200 m (V. 2282).

P. lanuginosa (TRIN.) NEVSKI (Syn. Elymus lanuginosus TRIN.). – C: Bamian: Kalkberg nordöstlich von Bamian, ca. 3000 m (G. 741).

Secale L.

S. afghanicum (VAVILOV) ROSHEV., Act. Inst. Bot. Acad. Sc. URSS. 1, 6: 139 (1947). (Syn. S. cereale L. var. afghanicum VAVILOV). – NW: Afghanistan (AITCH. 442). – E: Kabul: Darulaman-Ebene, ca. 1700 m, Bewässerungsfelder (KN. 461-b). – NE: E. Nuristan (E. 1131-a).

S. cereale L. – E: Kabul: Scharenau (Tschaman Wazirabad), ca. 1750 m, Weizenfeld (G. 706). In einem Garten in Kabul, ca. 1800 m, ruderal (G. 708). – NE: Nuristan: Vaigel, ca. 1500 m (E. 889). Im Parigel-Tal, linkes Seitental des unteren Kulam-Tales, ca. 1800 m, verwildert im Bachschutt (KN. 1161).

S. montanum Guss. - Pakistan: Chitral (HARRIS).

S. segetale (ZHUK.) ROSHEV., Act. Inst. Bot. Acad. Sc. URSS. 1, 6: 143 (1947).

(Syn. S. cereale L. ssp. segetale Zник.). – E: Kabul: Darulaman-Ebene, ca. 1700 m, Bewässerungsfelder (Kn. 461-а).

Taeniatherum NEVSKI

T. crinitum (SCHREB.) NEVSKI (Syn. Elymus crinitus SCHREB., Hordeum crinitum (SCHREB.) DESF., Elymus intermedius M. B., E. caput-medusae Boiss., non L.). -N: Takht-e Rustam prope Haibak, in collibus calcareis, ca. 1200 m (RECH. 16397). Doshi, ca. 2750 ft., shingle (M.). – E: Tob-Fels am Scher Darwasah bei Kabul, ca. 2000 m, on stony slopes (HDG. & WDB. 3155). Berg beim Stausee von Chord Kabul, ca. 2280 m (G. 740). Sarobi, Steppe, zwischen Cymbopogon (V. 2563). Tang-i Gharu, Schlucht des Kabul-Flusses, 1600–1700 m (Kn. 504). Ebendort, im Schotter (Sch. 65). Aliabad bei Kabul, auf Felsen, südexponiert (N. 1951/117). Darulfanun, zwischen Felsen (V. 1548). Panjshir: Im Panjshir-Tal zwischen Gulbahar und Anoba, ca. 1720 m, Quercus Baloot-Bestand (G. 738). - SE: Kandahar: Schlucht des Hilmend bei Germaub, nördlich von Ghirishk (Kn. 409-a). – Nuristan: W. Nuristan: Parigel-Tal, linkes Seitental des unteren Kulam-Tales beim Dorf Parigel, aus Samen kult. in Bot. Garten Halle (KN. F-100). Maweni-Tal, rechtes Seitental des unteren Kulam-Tales bei Mawe (Kn. F-201). Oberes Ramgel-Tal zwischen Puschol und Gadwol, Quercus-Wald in einer Seitenschlucht oberhalb von Gadwol, 1900–2000 m (Kn. 1118). Oberes Ramgel-Tal bei Gadwol, ca. 1970 m, an trockenen Hängen (KN. 1125). Im Ramgel-Tal zwischen Gadwol und der Einmündung des Tschitur, ca. 1900 m (Sch. 132). Ramgel-Tal, zwischen Gadwol und der Einmündung des Tschitur, Trockenhänge, 1900-2000 m (Sch. 129). – Pakistan: Quetta: Khojak, ca. 1900 m (K. 3076). Quetta (NORRIS 62).

Triticum L.

Tragus (HALL.) SCOP.

T. aestivum L. (Syn. T. hybernum L., T. compositum L., T. sativum LAM., T. vulgare VILL.). – N: Mazar-i Sharif: Inter Chashma-e Shafal et Aq Kupruk, 800–1000 m (RECH. 16286). – SE: Kandahar: Pirzada near Kandahar, ca. 900 m (K. 2118). – E: Jallalabad, ca. 600 m (E. 13). Scharenau (Tschaman Wazirabad), ca. 1750 m (G. 710). An einem Gartenweg in Kabul, ca. 1780 m (G. 711, 712).

T. compactum Host - E: Kabul: In einem Garten in Kabul, ruderal (G. 712-b).

Pooide a e-Zoysie a e

T. biflorus SCHULT. – Pakistan: Peshawar: Panjkora-Tal bei Warai, Dir Distr., ca. 1000 m (Kn. 2110).

Acknowledgments

We are indebted to Messrs. M. G. SAWYERS and P. GREEN of Photographic Studio, British Museum (Natural History), London, for preparing the photographs of the type specimens.

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BY

SVEND ERIK BENDIX-ALMGREEN



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CONTENTS

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Preface	3
Material and Methods	5
Introduction	6
Review of previous works	9
Review of classification and taxonomy 1	1
Description of the Material 1	4
Helicoprion ferrieri 1	4
Helicoprion ergasaminon n. sp	9
Helicoprion cf. ferrieri 4	5
Helicoprion sp. indt 4	8
Summary and conclusions 4	9
References	3
Plates	5

Synopsis

The treated material comprises 10 specimens of the genus *Helicoprion* representing the species *H. ferrieri* HAY, *H. ergasaminon* n. sp. and *H. cf. ferrieri*, and *H. sp. indt*, preserved in bituminous, phosphatic limestone boulders, and originating from the lower Upper Permian Phosphoria formation in south-east Idaho, U.S.A.

Descriptions are given of some general traits of the anatomy of the foremost part of the cranial capsule, the lower and the upper jaw (*H. jerrieri*, *H. erga*saminon), revealing features not previously known. The compound tooth-spiral, occuring in the symphysis of the lower jaw is described and its function discussed (*H. jerrieri*, *H. ergasaminon*, *H. cf. jerrieri*, *H. sp. indt.*), as is also the remains of a weak dentition situated on the very anterior part of the upper jaw (*H. jerrieri*). The tooth-histology is discussed, bringing out a few new details (*H. jerrieri*).

The new evidence found in the anatomy and the tooth-histology in *Helicoprion* are discussed and compared with the same anatomical and histological features, as they occur in some of the better known forms among the so-called *Bradyodonts*. It is concluded that *Helicoprion* systematically can not be placed close to any of these forms but shows indications of a closer relationship to the *Selachians*.

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Preface

In the autumn of 1961 the material treated in the present paper was handed over to me for investigation by Professor WILLIAM FURNISH, head of the paleontological department at the University of Iowa, Iowa City. For permission to investigate and describe these really valuable finds I wish to express my most sincere thanks to Professor FURNISH.

The material is the property of the University of Idaho and Idaho State College. It was borrowed from these institutions in 1950 and 1951 by Dr. A. K. MILLER and Dr. WALTHER YOUNGQUIST, the latter having himself collected the greater part of it. To both these gentlemen I express my sincere gratitude.

On behalf of Dr. A. K. MILLER, Dr. W. YOUNGQUIST and myself, I would like to take this opportunity to express our grateful thanks to the following persons:

Mr. and Mrs. A. E. THIEL of Montpelier, Idaho, who in different ways have given valuable assistance and also donated one of the specimens investigated.

Professor A. ISOTOFF of Idaho State College, Moscow, Idaho.

Mr. D. L. KING and the authorities of the "San Francisco Chemical Company", Montpelier, Idaho.

Mr. C. W. Sweetwood and the authorities of the "Simplot Fertilizer Company", Pocatello, Idaho.

Mr. J. HAEGELE, Mr. CALDWELL and Mr. B. HAWLEY for their assistance to Dr. W. YOUNGQUIST during the collection of the material.

During a one month stay in Moscow and Leningrad for the purpose of carrying out investigations on fossil elasmobranchs, especially the renowned Russian Helicoprion finds, I made the acquaintance of Professor D. OBRUCHEV of Moscow, and Dr. L. S. GLÜCKMAN of Leningrad. I am greatly indebted to these two gentlemen for their assistance in making the fossil material accessible to me, and for valuable discussions with respect to fossil and recent fishes. My thanks are also due to Mr. RASTA-TUROV, vice-chief of the International Department of the Ministry of Higher and Secondary Education of the U.S.S.R., and to Mr. P. N. VARFOLOMEEV, Director of the Tschernyschev Museum, Leningrad. Financial support for this journey was also received from the Rask-Ørsted Foundation.

The map was drawn by Mrs. E. HANSEN in the Geographical Institute of the University of Copenhagen, and placed at my disposal through lecturer B. FRISTRUP. To both I offer my cordial thanks.

To Dr. EIGIL NIELSEN, head of the Department of Vertebrate Paleontology at the Mineralogical and Geological Institute of the University of Copenhagen, I express my cordial thanks for many discussions on problems related to the subject of the present paper.

To my wife Mrs. BENTE BANG SOLTAU, Conservator in the Department of Vertebrate Paleontology at the Mineralogical Museum, Copenhagen, I am greatly indebted for assistance she has offered me in the preparation of the photographs, and for advice during cleaning and casting of the fossil material.

Mrs. RAGNA LARSEN, artist at the Mineralogical and Geological Institute prepared three of the figures for the text, for which careful work I express my thanks.

I would like, moreover, to thank the authorities of the Mineralogical Museum, Copenhagen, for the excellent working facilities they have afforded me.

Civil engineer V. BUCHWALD, Royal Technical University, Copenhagen and civil engineer BRAM-HANSEN, Danotrix, Copenhagen, are thanked for their considerable technical assistance in the preparation of the thin sections.

Dr. A. K. HIGGINS kindly corrected the English manuscript.

The Mineralogical and Geological Institute of the University of Copenhagen. *February 1965.*

SVEND ERIK BENDIX-ALMGREEN.

Material and Methods

The fossil material is preserved in strongly bituminous and phosphatic limestone boulders which may be parts of limestone bands, but more probably are parts of large concretions.

The vertebrate remains are represented by four kinds of hard tissues i. e. bone, dentine and enamel, all belonging to the preserved teeth-structures, and lime prisms from the endoskeletal cartilage elements belonging to the neurocranium and the jaws. Numerous invertebrates, mainly brachiopods, occur in association with the vertebrate fossils.

The hard tissues have, unfortunately, been subjected to a diagenetic process which particularly affected the prismatic calcifications and the enamel. They are therefore not well suited for detailed microscopic analysis, although attempts have been made.

The preparation of thin-sections for these investigations was first attempted in the normal manner employing the adhesives Lakeside and Canada balsam. However, this method was unsuccessful because of the great friability of the material. A second method described by WEBER (1963) was later adopted in which the crystic resin "Palatal" in polymerised condition was used both as the adhering and the embedding medium.

When the suitable material was too small for the normal preparation of thinsections, the small fossil specimens were first embedded in a clear acrylic resin using a warm pressure agregate manufactured by A. BÜHLER (A. B. Simplimet Press 1303). The block was then cut into slices, using a very thin, absolutely precise diamond saw, a process which yielded as many as eight slices from a tooth-fragment not more than 5 mm long and 3 mm broad.

A Leitz Dialux polarisation microscope was used in the microscopical study, and to take the microphotographs.

Other photographic work was carried out utilising a Sinar 9×12 cm camera equipped with a Schneider Symmar 135 mm objective. Photograph reproductions were made using the same camera and objective, together with a coldlight adaptor of the Graphlarger type. Perutz Silbereosin negative plates were used and reproductions were made on the paper types Umbrano UB 1 SP and UB 1 N manufactured by LEONARD.

The fossil material was photographed both in dry condition, and also in Xylene to take advantage of the refraction between matrix, fossil and liquid. Some of the larger specimens are illustrated on the plates in both conditions in order to give a more detailed impression of the material.

In some cases a positive cast was made of a specimen, using the warm polymerising PVC and Dibuthylphtalate. The casts were coated with graphite to bring out the finer details.

Some preparations were made employing a modified dental mallet, and dental cutting and grinding tools. A stereomicroscope of the Zeiss Jena SM XX type was used in this work and in examinations of the fossils.

An attempt to stain the hard tissues using a $0.1 \ ^0/_0$ solution of alizarine in 96 $\ ^0/_0$ ethylated spirit was unsuccessful, possibly on account of the previously mentioned diagenetic process, which occurred during fossilisation.

Most of the figures were drawn by the author. A Zeiss Jena drawing instrument attached to the stereomicroscope was utilized for some of this work.

The reconstruction of the section through the lower jaw (fig. 7) and the reconstructions of the shape of this jaw in lateral and ventral aspects (figs. 8–11) were achieved by NIELSEN'S method (1952, pp. 13–19).

Introduction

The fossil material comprises ten specimens. All of them originate from the lower part of the Phosphoria formation, and were collected in two localities in south-east Idaho, where the beds of the formation are mined for the contained phosphatic minerals.

All but one of the specimens are from the so-called "Waterloo Mine", which is owned and worked by the "San Francisco Chemical Company". It is situated in the Montpelier Canyon not far from Montpelier (fig. 1).

The "Waterloo Mine" specimens are:

- Idaho no. 1, Idaho no. 2 and Idaho no. 3, which were collected by Dr. W. YOUNGQUIST and Mr. B. HAWLEY in the summer of 1949.
- Idaho no. 4, Idaho no. 6, Idaho no. 7, Idaho no. 8 and Idaho no. 9, which were collected on 11th and 12th july 1950 by Dr. W. YOUNGQUIST and his assistant Mr. J. HAEGELE.

The specimens referred to as Idaho mrk. "Thiel P" and Idaho mrk. "Thiel MP", are counterparts of the same concretion, and were donated by Mrs. A. E. THIEL of Montpelier to the University of Idaho.

Only a single specimen, Idaho no. 5, originates from another locality, and was collected in the so-called "Gay Mine", owned and worked by the "Simplot Fertilizer Company". This mine is situated about 30 miles ESE. of Pocatello at the Fort Hall Reservation (fig. 1). The specimen is the property of Idaho State College, Moscow, Idaho.



7

A number of documents were received with the fossil material. These partially dealt with the collection of the material, but also gave important information of further, still undescribed, *Helicoprion* finds from the Phosphoria beds in south-east Idaho. These additional finds number at least 17 specimens which, with the material already at hand, bring the total number of specimens known from the U.S.A. to at least 27, not including those previously described in the literature.

Of the 17 undescribed specimens, 10 were collected by Mr. J. SMEDLEY and are stored in the collections of the U. S. Geological Survey and the U. S. National Museum in Washington. Of the remaining 7 specimens one is still at the Idaho State College or the University of Idaho, two are in the possession of Mrs. THIEL, two are owned by Mr. F. W. CHRISTENSEN, Lava Hot Springs, Idaho and two specimens, originating from the "Waterloo Mine", have been reported by Mrs. THIEL as disappeared or destroyed. For three of these specimens a few details, given below, are available concerning the preserved part of the tooth-spirals:

- A: Specimen owned by Mrs. A. E. THIEL: Greatest diameter of the symphyseal tooth-spiral: 10 ins. Number of volutions preserved: 2. Locality: "Waterloo Mine", Montpelier Canyon, Idaho.
- B: Specimen owned by Mr. F. W. CHRISTENSEN: Greatest diameter of the symphyseal tooth-spiral: about 115 mm. Number of volutions preserved: 2¹/₂. Locality: "Waterloo Mine", Montpelier Canyon, Idaho.
- C: Specimen owned by Mr. F. W. CHRISTENSEN: Greatest diameter of the symphyseal tooth-spiral: about 142 mm. Number of volutions preserved: 2. Locality: Possibly the "Conda Mine", near Soda Springs (fig. 1).

As far as can be ascertained most of the remaining specimens were obtained from the "Waterloo Mine", and a few from the "Gay Mine".

Only eight specimens have previously been described in the literature. Four of these specimens (HAV 1907, 1909), of lower Upper Permian age, were derived from the "Waterloo Mine", as were most of those described in the present paper. WHEELER described two specimens (WHEELER 1939), of which one was collected from beds of Artinskian or Uralian age in Nevada, and the other, which is of uncertain age (possibly Artinskian or Uralian) was found in California. One other specimen, poorly preserved, is known from Nevada and is said to be of certain Leonardian age (LARSON & SCOTT, 1951).

The best preserved specimen hitherto known of those recorded in the literature, is that dealt with by DUNKLE and WILLIAMS in a short note (DUNKLE & WILLIAMS 1948, p. 1362), and it is reproduced as figure 3 in the present paper. This Helicoprion specimen was collected in the "Gay Mine". One of the documents at my disposal



Fig. 2. Sketch showing the sedimentary sequence of the Phosphoria formation and parts of the adjacent formations, as represented in the "Gay Mine", Fort Hall Reservation, about 30 miles ESE of Pocatello, Idaho. Based on a field sketch by Dr. W. YOUNGQUIST.

deals with its position in the sedimentary sequence and includes several photographs of the specimen¹. According to this document the sedimentary sequence is as shown in fig. 2. The specimen itself was derived from the beds just above, or just below, the "false cap rock", but most probably below such that it represents one of the concretions which are common in the phosphatic shales.

It is worth recording that the sequence of the sediments in the "Waterloo Mine" is almost identical to that shown above. Generally, there are only very small and unimportant variations between the successions at different lower Phosphoria localities in south-east Idaho, and that given in figure 2. It is likely that at least the majority of the finds were derived from the concretions in the phosphatic shales, or from the false cap rock itself.

Review of previous works

The descriptions and reports concerning the genus *Helicoprion* published before 1940 were briefly but excellently reviewed by WHEELER (1939) and TEICHERT (1940) in their papers on North American and Australian finds respectively.

In addition to these works MOY-THOMAS (1939 a & b) and BERG (1940) deal briefly with *Helicoprion*, as will be referred to below in a discussion of the different classification attempts.

¹ To judge from the photographs the specimen is probably of the species Helicoprion ferrieri HAY.



Fig. 3. The *Helicoprion* specimen discovered in 1947 at the "Gay Mine" and briefly discussed by DUNKLE and WILLIAMS in 1948. This exceptionally well preserved specimen shows clearly defined remains of the anterior part of the right lower jaw-branch (calc. r. l. j) and the left lateral wall of the symphyseal cavity, formed by the anterior part of the left lower jaw-branch (calc. l. l. j.). Note the strongly calcified symphyseal crista (calc. cart. sym.), still situated in the groove on the ventral side of the complex root. The oldest part of the tooth-spiral—the juvenile tooth-arch—is preserved. The photograph was donated by Mr. C. Sweetwood. Scale in inches.

The Russian paleontologist OBRUCHEV published in 1952 a work dealing with the elasmobranch *Helicoprion*. He dealt with the problems concerning the orientation of the roots of the teeth forming the symphyseal spiral, comparing them to those of *Edestus*. He concluded that the root in *Helicoprion* was directed backwards, that the forward directed narrowed and pointed bases of the crowns were only of secondary origin, and consequently that there were no fundamental differences between the teeth of *Helicoprion* and *Edestus*.

This publication was followed by a work dealing with the complete *Helicoprion* material collected in Russia (OBRUCHEV 1953), which included new finds and the considerable research done by KARPINSKY on this group. OBRUCHEV here attempted a thorough classification of the *Bradyodonts*, including *Helicoprion*.

Nr. 5

In connection with investigations on *Edestid* material from East Greenland NIELSEN published an excellent reconstruction of the complete tooth spiral (NIELSEN 1952, fig. 21 p. 50). ØRVIG (1951) dealt briefly with the prismatic calcifications of the endoskeleton.

The few and extremely short reports of American finds since WHEELER have been mentioned above (p. 8). A more detailed up to date list of these finds, as given below, may be of some interest in connection with the material at hand:

- Helicoprion ferrieri (Lissoprion f.) HAY 1907 and 1909. Montpelier, Bear Lake County, Idaho. Phosphoria formation, Permian.
- Helicoprion nevadensis, WHEELER 1939.
 U. N. Loc. 28, Rochester district, Lovelock quadrangle, Perking County, Nevada.
 Rochester trachyte, Uralian or Artiskian.
- 3) Helicoprion sierrensis, WHEELER 1939.
 U. N. Loc. 29, Downieville quadrangle, Plumas County, California.
 Boulder from glacial moraine, possibly originating from beds of Uralian or Artinskian age.
- 4) Helicoprion sp.¹, DUNKLE and WILLIAMS 1948.
 "Gay Mine", Fort Hall Reservation, Bingham County, Idaho, Phosphoria formation, Permian.
- 5) *Helicoprion sp. indt.*, LARSON and SCOTT 1951. China Mountain, SSW. of Contact, Nevada. Leonardian age.

Review of classification and taxonomy

A brief review of the classification of the genus *Helicoprion* KARPINSKY was given by TEICHERT (1940, p. 143). TEICHERT, besides supporting the view of KARPINSKY (1924) and BRANSON (1936) that the genus *Campyloprion* EASTMAN (1902) and the genus *Lissoprion* HAY should be regarded as synonymous with the genus *Helicoprion*, also quoted the four more recent attempts then made, by HAY (1929), NIELSEN (1932), ROMER (1933) and WHITE (1936), to classify this unusual elasmobranch. TEICHERT objects to the suggestion of NIELSEN (op. cit.) that the genus *Helicoprion* should be included in the *Bradyodont* group because of the specialisation of the symphyseal row of teeth and the microscopic tooth structure, since this structure, as far as he could determine from the description given by KARPINSKY (1899), differed fundamentally from that described by NIELSEN for the *Edestids* from the Permian of East Greenland.

¹ See footnote p. 9 and fig. 3 p. 10.

In his review of the fossil elasmobranchs MOY-THOMAS (1939 a) supports NIELSEN'S point of view, with some reservations, and classifies the genus *Helicoprion* within the *Bradyodonti* in the following manner:

Subclass: Elasmobranchii.

Division 2: Bradyodonti. Order I: Eubradyodonti. Suborder 6: Edestidi.

e. g. Edestus, Agassizodus, Orodus, ? Helicoprion.

BERG (1940) lists, also with some reservations, *Helicoprion* among the *Holocephali* in the following way:

Class: Holocephali.

Subclass: Chimaerae. Order: Chimaeriformes. Family: Edestidae. Genus: Helicoprion Какрільку 1899 has teeth with an enamel layer and according to Moy-Thomas (1939) may belong to the class Elasmobranchii.

TEICHERT'S statement, mentioned above, was rejected by NIELSEN (1952). The latter stated that the microscopic structure in *Helicoprion* did not in his opinion "differ in any fundamental respect from the tooth structure in other *Bra-dyodonti*" (p. 52).

NIELSEN, in the same publication, summarises his views regarding the main lines of evolution within the family *Edestidae*, and illustrates this with the diagram reproduced here as figure 4.

NIELSEN'S views were supported by OBRUCHEV (1953, pp. 57–59), who published the following systematic division of the *Bradyodonti* as a whole:

Subclass: Holocephali.

Superdivision: Chondrenchelyes.

: Chimaerae.

Division: Cochliodontiformes.

- : Janassiformes (= Petalodontidae).
- : Psammodontiformes.
- : Copodontiformes.
- : Menaspiformes.
- : Edestiformes.
 - Family: Edestidae: Edestus, Protopirata, Edestodus, Lestrodus.
 Family: Helicoprionidae: Campodus, Agassizodus, Fadenia, Parahelicoprion, Helicampodus, Toxoprion, Helicoprion.
 - Family: Orodontidae: Orodus.

Division: Chimaeriformes.



Fig. 4. The main lines of evolution within the family *Edestidae* according to Nielsen (1952).

In the German translation of BERG'S (1940) systematical work, scientifically revised by W. GROSS (BERG 1958), some hesitation is still expressed with regard to the classification of *Helicoprion*.

New investigations in paleohistology (ØRVIG 1965) have revealed facts showing that the microscopic tooth structure, previously regarded as being of some importance in classification within the Elasmobranchs, in this respect is without any significance.

Nevertheless, the present investigations have yielded features of the anatomy of the anterior part of the neurocranium and the mandibular arch. From these features it is evident that *Helicoprion* systematically is not closely related to those Elasmobranchs hitherto grouped as *Bradyodonts* in which corresponding traits of the cranial anatomy are known.

Finally, it should be noted that as a result of new and well preserved finds from Upper Carboniferous limestones in the Moscow region, it has been shown by OBRUCHEV (1964), that *Campyloprion* EASTMAN forms a well defined genus, which is not synonymous with the genus *Helicoprion*; also that *Helicoprion ivanovi* KARPINSKY (1922) is in fact a species of *Campyloprion*.

Description of the Material

Genus Helicoprion KARPINSKY 1899.

Syn. Lissoprion HAY 1907, 1909, 1929.

Helicoprion ferrieri HAY 1907.

Syn. Lissoprion ferrieri HAY 1907, 1909, 1929.

Pl. I–VI, VII fig. 2, VIII, IX fig. 1–3, X–XIII, XIV fig. 1–2. Text-fig. 3, 5, 7–24.

Material: The material representing this species consists of the following specimens: Idaho no. 1, Idaho no. 2, Idaho no. 3, Idaho no. 4, Idaho no. 7, Idaho no. 9 and Idaho mrk. "Thiel P" and "Thiel MP".

Introductory notes on the endoskeleton of the head: Some of the specimens show extensive endoskeletal remains, representing the anterior part of the neurocranium and the upper and lower jaws. This is notably the case with the specimen Idaho no. 4, as may be seen from the illustrations pl. I–IV and fig. 5. They are also present to a lesser extent in specimens Idaho no. 1 (calc. cart.: pl. VIII) and in Idaho mrk. "Thiel P" and "Thiel MP" (r. calc. cart.: pl. X–XII).

The preserved parts are the layers of prismatic calcifications, which were originally located superficially in the cartilage, as can be generally observed both in recent Elasmobranchs and in many well preserved fossil Elasmobranchs. The layers are preserved to some degree in their original positions with regard to each other and to the symphyseal tooth-spiral. These circumstances permit an interpretation of the limitations of the different elements, a reconstruction of the anterior portion of the lower jaw, and an interpretation of the original location of the tooth-spiral.

Unfortunately the layers of calcifications of the neurocranium are so strongly affected by pressure, as seen on pl. IV and fig. 5, that it has proved impossible to make detailed investigations. However, due to a fortunate dorso-ventral section through the preserved parts of specimen Idaho no. 4, which displays a large number of calcification walls (pl. IV & fig. 5), it is possible to give a few general observations on the neurocranium and also the upper jaw. The dislocation which the elements observable in the section have undergone during decay and compaction are shown schematically in figure 6 A, B, C.

Although the calcifications are in close mutual connection, it is possible to distinguish two areas of different complexity. The less complex of these is adjacent to the tooth-spiral. The more complex area is situated partly below some of the younger tooth-crowns of the spiral, partly outside and away from them and has a long extension in a forward direction (calc. cart. n. cr. & r. p. n. cr.: pl. I). These two areas can only be adequately interpreted as representing the lower jaw and the neurocranium



Fig. 5. Helicoprion ferrieri HAY: Transverse section through the anterior part of the neurocranium and the palatoquadrates, and through the lower jaw, just caudally to its symphyseal region, as exposed on Idaho no. 4. Only the sections through the calcification layers are shown on the sketch. $1,1 \times$ nat. size. calc. cr. b.: layers of calcifications from the broken ventral part of the neurocranial capsule. calc. l. l. j. & calc. l. r. j.: layers of calcifications from the left and the right part of the lower jaw respectively. can.: two pair of canals. cav. cr.: the cranial cavity. i. cr. w. & o. cr. w.: layers of calcifications originally lining the inner and the outer surface respectively of the neurocranial capsule. l. & r. pq.: the left and the right palatoquadrate. sym. t.: sections of tooth-crowns belonging to the youngest part of the symphyseal tooth-spiral.

respectively. The area representing the lower jaw exhibits a rather simple pattern with the calcifications concentrated around the tooth-spiral. The area with the remains of the neurocranium shows, as might be expected, a pattern of great complexity.

The neurocranium.

The layers of calcifications representing the neurocranium show clearly in their dorsal parts the presence of an inner and an outer wall of calcifications (l. &r. i. cr. w. and l. &r. o. cr. w.: pl. IV; see also fig. 5: i. cr. w. & o. cr. w. and pl. I: calc. cart. n. cr.). The inner wall, which is comparatively thin, lines the inner surface of the cartilaginous cranial capsule along the cavum cerebrale cranii (cav. cr.: pl. IV and fig. 5), while the outer wall is situated superficially in the cartilage along the outer surface.

Ventrally to these walls are situated a number of broken pieces of calcifications, which clearly represent the lower lateral parts and the floor of the cranial capsule (calc. cr. b: pl. IV and fig. 5). It has not been possible to deduce their original pattern. However, the presence of two pairs of rather prominent canals can be demonstrated (can. l. &r.: pl. IV and fig. 5; can. r.: pl. I). These canals run in a forward direction and may originally have been situated with two canals in each lateral wall of the cranial capsule, possibly at the connection between the walls and the cranial floor. It is not possible to state whether they originally conducted some of the main vessels or the stems of nerves, but their presence does suggest that the mentioned cranial cavity represents a portion of the cavum cerebrale cranii proper.

In lateral view the neurocranium tapers in a forward direction. The most anterior part preserved occurs as a strongly calcified cartilage balk, which represents the rostrum. Because of the incompleteness of the specimen in the area where the rostral element is found, it is not possible to state whether or not the rostrum originally consisted of more rostral elements than that observed (r. p. n. cr.: pl. I–III). On the ventral side of the rostral element is found proximally a broad, evenly rounded tuberosity (art. p.: pl. I). This tuberosity may have acted as the area of attachment for the ligaments running to the anterior part of the palatoquadrates, a suggestion which is supported by the fact that the only traces found of a lateral dentition are situated below the neurocranial remains just caudally to the tuberosity (dnt.: pl. I).

It may be concluded, from the above evidences, that the preserved rostral element corresponds to an unpaired ventral rostral balk, similar to that found in many Selachian skulls e. g. *Mustelus, Isurus*, and *Carcharhinus*.

A rather large foramen (f. o. l.: pl. I) is situated in the calcifications of the left wall in the anterior part of the neurocranial capsule just caudally to the rostrum, and thus at the very anterior end of the ethmoidal region. The foramen is divided into three sections by very delicate bars of calcifications. Outside the foramen there occurs a space surrounded by a layer of calcifications. This space is only partially filled by argillaceous sediment, the remainder, as far as the foramen, being occupied





Fig. 6. Three sketches to show the outlines diagrammatically of the cranial elements seen on the transverse section of Idaho no. 4, fig. 5 and pl. IV. The sketches illustrate the authors opinion of the original mutual position of the elements (A), their mutual position after dislocation during decay (B), and the elements pressed together during fossilisation (C). n. cr.: transverse section of the neurocranial capsule. 1. j.: transverse section of the lower jaw immediately behind the symphyseal region and the tooth-spiral. pq.: transverse section of the palatoquadrates. Red arrows: the directions of the mutual movement of the elements during the decay. Black arrows: direction of the pressure during the compaction of the sediment.

by an accumulation of calcite crystals, which suggest that originally the communication between the space and its surroundings was somewhat restricted.

These facts suggest that the foramen can be regarded as the divided foramen for the nervus olfactorius; outside this is situated the olfactory capsule, the interior of which would be in only restricted communication with the surroundings through the fenestra endonarina communis, if an annular cartilage was originally present.

If these suggestions are correct, the fila olfactoria entered the nasal capsule through a divided olfactory foramen, and therefore through a very simply formed lamina cribrosa.

Biol.Skr.Dan.Vid.Selsk. 14, no. 5.



18



Remarks: – The presence of a type of lamina cribrosa closing the canalis olfactorius toward the nasal capsule is also known in the recent Elasmobranch *Chlamydoselachus anguineus*, although it is here formed by a layer of connective tissue and not by a proper endoskeletal cartilage wall (ALLIS 1923 p. 113). On the other hand a lamina cribrosa formed by proper endoskeletal bony tissue is known in many *Arthrodires* (STENSIÖ 1942; 1963, p. 50, pp. 147–152, fig. 50 A, B, D).

Visceral skeleton.

The palatoquadrates: On the left side of the neurocranium of Idaho no. 4, and situated below it in the matrix are found two nearly oval shaped, but somewhat compressed, walls of calcifications representing sections through two elements, which now lie close together and apparently parallel with the neurocranium (pq. l. & pq. r.: pl. IV; l. & r. pq.: fig. 5).

These two elements, which as can clearly be seen were originally mirror-images of each other, on account of their size and general shape can only be regarded as sections through the palatoquadrates. During decay and compaction these elements



Fig. 8. Helicoprion ferrieri HAY. Attempted restoration of the anterior part of the lower jaw. Lateral view. $0.55 \times$ nat. size.

appear to have loosened and moved out laterally to the neurocranium (fig. 6 A, B, C). If this assumption is correct, the upper jaw would seem to have been very weak in its anterior portion compared to the lower jaw.

The anterior part of the lower jaw: Just behind the symphyseal region the anterior part of the lower jaw is about $1^{1/2}$ times higher than it is wide. Its height increases in the symphyseal region forwards to the midpoint of the symphysis and then gradually decreases, tracing in this distance a circular path along the upper margin of the jaw (fig. 8). The lateral width decreases continuously in a forward direction, although it is always broader ventrally than dorsally (figs. 7, 11).

The prismatic calcifications, which form a continuous layer along and just below the surface of the cartilage, are heavier in the ventral than in the dorsal part of the jaw, except along the symphyseal border (calc. l. l. j. & calc. r. l. j.: pl. IV and fig. 5; r. l. j. & l. l. j.: fig. 7; sym. c.: fig. 9). Here the left and the right branch of the jaw are connected by a strongly calcified cartilage crista (calc. cart. sym.: pl. I; r. calc. cart.: pl. X and XII). This crista runs in a coil forward from the rear point of symphyseal connection of the jaw branches to form a prominent crista—the symphyseal crista—between the two jaw branches along the upper and anterior margin of the symphysis. It then coils backwards and inwards, between the left and the right jaw branches, and terminates at a point just caudally to the vertical diagonal axis of the symphyseal region, leaving an opening on the ventral side between the

19

2*



Fig. 9. *Helicoprion ferrieri* HAY. Attempted restoration of a median section through the symphyseal region of the lower jaw. The strong calcifications of the symphyseal crista (sym. c.) and the rear connection (r. con. j.) between the two jaw branches are indicated by dense shading. $0.55 \times$ nat. size. op. sym.: the opening through which the older parts of the tooth-spiral enter the symphyseal cavity (sym. cav.). pit.: the pit where the new tooth-members are formed. pr. l. j.: the anterior process of the left half of the lower jaw.

termination of the crista and the rear connection of the jaw branches (op. sym.: figs. 9 and 11).

The upper anterior margins of the two jaw branches follow the symphyseal crista to a level just below the middle horizontal plane of the symphyseal region. Ventrally to this plane each jaw branch is prolongated as nearly triangular, broad based, but comparatively thin processes forming the termination of the jaw (pr. l. j.: pl. I, and fig. 9; and fig. 11).

The ventral border of the symphyseal region is formed by the ventral borders of the two jaw branches which are not here in mutual connection (figs. 7, 9, 11).

This unique construction leaves a cavity in the interior of the symphyseal region within the symphyseal crista. This cavity, the lateral walls of which are formed by the left and the right jaw branch (calc. cart. l. l. j. & calc. cart. r. l. j.: pl. I–III, and fig. 3), contains completely enclosed the older volutions of the tooth-spiral (sym. cav.: fig. 9) which entered it through the opening situated on the ventral side (op. sym.: figs. 9 and 11). In fact the tooth-crowns of the older half part of the last formed volution are already, before entering the symphyseal cavity, protected laterally



Fig. 10. Helicoprion ferrieri HAY: Attempted restoration of the anterior part of the lower jaw and the exposed parts of the tooth-spiral. Lateral view. $0.55 \times \text{nat. size.}$

by the anterior processes and the ventral parts of the jaw branches, as shown on fig. 10 and pl. I.

At the lingual end of the symphysis is situated the pit, where the development of the new teeth takes place as normally in the Elasmobranchs.

Remarks: The unusual form of the symphyseal region with the connection between the jaw branches restricted to, and formed by, the symphyseal crista, seems to indicate that the elements present in this region at the embryo stage, during ontogeny developed in a rather special manner.

The symphyseal connection of the Meckelian cartilages is situated caudally to their anterior termination. The connection between them is formed by a coiled, strongly calcified cartilage element which laterally is fused with the Meckelian cartilages. However, it does not fuse their median surfaces completely together but only a part of their dorsal and anterior edges and also a part of their median surfaces, leaving a cavity inside the symphysis. This cavity communicates with the surroundings by an opening on the ventral side of the symphyseal region.



Fig. 11. Helicoprion ferrieri HAY: Attempted restoration of the anterior part of the lower jaw in ventral view. The tooth-spiral is omitted to show the symphyseal crista (sym. c.), and the entrance to the symphyseal cavity (op. sym.). $0.7 \times \text{nat. size. pr. l. j.:}$ the anterior process of the left branch of the lower jaw. r. con. j.: the rear connection of the jaw branches. t. sym. c.: the termination of the symphyseal crista.

These facts seems to suggest that the coiled cartilage element—the symphyseal crista—represents an independently formed cartilage structure, which during the ontogenetic development fused to the Meckelian cartilages.

A similar position in relation to the anterior end of the Meckelian cartilages is characteristic for the Basimandibular element known in the embryos of several recent Elasmobranchs (HOLMGREN 1940, *Etmopterus* 34 mm stage, p. 132 fig. 90; 43 mm



Fig. 12. *Helicoprion ferrieri* HAY: Restoration of the tooth-spiral in Idaho no. 4. The oldest part, the juvenile tooth-arch, is omitted. ro. gr.: the upper limitation of the youngest part of the groove on the underside of the tooth-spiral. 0.7×nat. size.

stage, p. 139 fig. 96. *Squalus* 38 mm stage, p. 106 figs. 56 & 64; 68 mm stage, p. 113 figs. 68 & 78). It is therefore probable that the symphyseal crista as it occurs in Helicoprion represents a special development of the Basimandibular.

With regard to this discussion the conditions found in the recent Elasmobranch *Lamiostoma belyaevi* GLÜCKMAN may be of some value. In this form an elongated visceral element is present, the posterior end of which articulates with the distal end of the Ceratohyals, while its anterior part is located between the anterior ends of the branches of the lower jaw (GLÜCKMAN 1964 p. 105, fig. 32).

It is clear that this element is of compound origin and represents a Basihyal which is fused distally with a well developed Basimandibular, although no observable traces show the original presence of two elements.

Dentition.

The symphyseal tooth-spiral: In the description of the tooth-spiral and the individual tooth-crowns of this species by HAY (1907 p. 22, 109 pp. 52–56) many points concerning the shape, the superficial structure, and their mutual relations are excellently described and discussed. However, the new material treated in this paper contributes further detail and justifies the re-description given below.

The dimensions of the same volution in the tooth-spiral vary to some degree from one specimen to another as shown by a comparison of Idaho no. 4 and Idaho mrk. "Thiel P & MP" (pl. I–III & pl. X–XII). The width of the former at $2^{3}/_{4}$ volution is 16.5 cm against 18.8 cm in the latter. For the most complete specimen available to HAY (1909 pl. 15) the equivalent measurement is 15.6 cm. However, these circumstances do not appear to affect the mutual relative dimensions within different tooth-spirals at particular stages of growth.

With regard to the number of volutions present in a tooth-spiral, this is naturally mainly dependant upon the lifetime of the particular individual concerned, although the possibility of some individuals producing teeth more or less rapidly than others is to be taken into consideration. In the two specimens Idaho no. 4 and Idaho mrk. "Thiel P & MP", which are the best preserved in the collection at hand, there are $3^3/_4$ volutions, although the oldest part of the latter specimen is not preserved. The complete number of tooth-crowns in Idaho no. 4 is 118 plus the juvenile tootharch, and in Idaho mrk. "Thiel P & MP" at least 122, and possibly 124.

The tooth-spiral consists of a number of enamel covered individual parts, which at their bases are attached to a coiled, completely undivided structure. The former has usually been referred to by previous authors as the teeth or the denticles, and the latter has generally been termed the shaft. However, both these terms are in the authors view inadequate, and they have been replaced in the present paper by the terms "the tooth-crowns" and "the compound root".

The oldest part of the tooth-spiral occupies about 1/5 of a volution (pl. V fig. 1–2; pl. VIII: r. em. cr.; fig. 13). It has the form of an enamel covered curved rod and can most adequately be termed "the juvenile tooth-arch". Its crenulation occuring along the upper margin is very delicate but is more coarse in the youngest portion where it to some degree resembles the crenulation on the cutting edge of the smaller tooth-crowns. The juvenile tooth-arch is well preserved in Idaho no. 4, and a part of it is also seen in Idaho no. 1. It is nearly as broad ventrally as it is high, and in section it shows a sigmoidal curving of the surface from the ventral border to the upper cutting edge.

The first formed individual tooth-crowns occur immediately after the juvenile tooth-arch (pl. V fig. 1–2, fig. 13).



Fig. 13. *Helicoprion ferrieri* HAY. The oldest part of the tooth-spiral, the juvenile tooth-arch, in the form of an enamel covered curved rod crenulated along a part of the upper margin, followed by the first formed individual tooth-crowns. $6.3 \times \text{nat. size. Idaho no. 4.}$

In the first 6 tooth-crowns there is a discernable angle between the lower and the upper portion of the front cutting edge, but it becomes rapidly inconspicious in later tooth-crowns, and is not apparent after the first half of the first volution. The rear edge of the cutting blades is slightly concave. The lateral tapering parts, which are only slightly bent forwards, are relative short and strong, and are somewhat concave along the front and rear margins (fig. 13).

The height of the cutting blades increases gradually, and in the middle part of the first volution is nearly half the total height of the tooth-spiral. The cutting edges, which on the first tooth-crowns are smooth, show at this stage of growth a feeble crenulation, and both edges are convex. The lateral tapering parts are slender and directed forwards, and terminate at a point below the centre of the next tooth (fig. 14).



Fig. 14. Helicoprion ferrieri HAY. Three tooth-crowns from the middle part of the first volution of the tooth-spiral. $5.2 \times \text{nat. size. Idaho no. 4.}$

In the second volution the tooth-crowns gradually acquire a shape which can be regarded as the mature form. Here they have strong and pointed cutting blades with crenulated convex cutting edges, and long and slender tapering lateral parts in which





Fig. 15. Helicoprion ferrieri HAY. Two tooth-crowns from the last part of the first half of the second volution of the tooth-spiral. $5 \times$ nat. size. Idaho no. 4.

Fig. 16. Helicoprion ferrieri HAY. Two tooth-crowns from the middle part of the second half of the second volution of the tooth-spiral. $4.5 \times$ nat. size. Idaho no. 4.

"a middle portion" and "a narrowed base" can be distinguished (fig. 15 & 16 and pl. I, V fig. 1, XII, XIII, XV fig. 1–2; terminology after WHEELER 1939). The middle portions posses strongly concave margins in the tooth-crowns of the oldest part of the second volution, while in the younger part the rear margins are almost straight. The narrowed bases become gradually longer and more slender. In the older part of the second volution the narrowed bases terminate at a point below the rear margin of the second tooth-crown in front, but in the younger part the termination point is situated beneath the centre of that tooth-crown (fig. 15 & 16; pls.: op. cit.).

All three portions of the tooth-crowns, i. e. the cutting blade, the middle portion, and the narrowed base, are clearly distinguished in the tooth-crowns of the third volution (fig. 17, pl. I–III). The pointed cutting blades possess convex cutting edges of which the front edge is the most strongly curved, and both edges show a pronounced crenulation. The middle portions have concave margins. The narrowed bases are long and slender, directed towards the older parts of the tooth-spiral and terminate at a point below the centre of the second tooth-crown in front.

The fourth volution of the tooth-spiral is characterised by tooth-crowns with strong and pointed cutting blades with a coarse crenulation along the cutting edges. The front cutting edges are the most strongly convex (fig. 18 & 19; pl. I–III, VIII–X). The middle portions have different characteristics; the front margin is always concave, but the rear margin can in the older parts be slightly concave or straight, and in the younger parts straight or even a little convex. The narrowed bases are long and very



Fig. 17. Helicoprion ferrieri HAY. Two tooth-crowns from the middle part of the second half of the third volution. $5 \times$ nat. size. Idaho no. 4.

slender compared to the other parts of the tooth-crown. Their point of termination is situated below the front margin of the second tooth-crown in front.

The tooth-crowns are only in contact at the base of the cutting blade, where the front lower corner of the cutting edge fits into a small recess at the lower point of the cutting edge of the tooth-crown in front (pl. I; pl. X fig. 1).





Fig. 19. Helicoprion ferrieri HAY. A cutting blade with a rather coarse crenulation from one of the largest tooth-crowns of the fourth volution. $2.1 \times$ nat. size. Idaho no. 4.

Fig. 18. *Helicoprion ferrieri* HAY. Tooth-crown from the middle of the first half part of the fourth volution of the tooth-spiral. $2.4 \times$ nat, size. Idaho no. 4.

Originally the tooth-crowns were covered by a layer of enamel-like hard tissue, but in only one specimen, Idaho no. 4, are a few small traces of this layer still preserved. It is impossible, therefore, to state the nature of the original ornamentation of the surface with any certainty. However, as HAY (1909 p. 55) has observed, there may have been a number of narrow ridges radiating from the apex (pl. I & III). The crenulation on the cutting edges also contributes to the surface sculpture, especially in the larger tooth-crowns (pl. IX fig. 1–2).

The tooth-crowns are supported by the solid, undivided and coiled compound root, which has developed through a complete fusion of the tooth-roots. This fusion is already observable in the development of a new tooth (y. t.: pl. I; y. p. t. sp.:

28



Fig. 20 a. *Helicoprion ferrieri* HAY. Reconstruction of a single complete tooth. in. c. v. t.: inner core of strongly vascular hard tissue of the root. ou. ds. t.: the outer denser hard tissue of the root. o. v. c.: openings for vascular canals on the area exposed between the middle portions and the narrowed bases of successive teeth. $0.7 \times$ nat. size. Based on Idaho no. 4.



Fig. 20 b. *Helicoprion ferrieri* HAY. Reconstruction of the dividing lines between the roots of two successive teeth, to show the limitation between the root-parts. l. l. b.: the green lines show the lower lingual and labial borders of the roots. o. v. c.: openings of vascular canals. ro. gr.: line showing the location of the dorsal wall of the groove on the ventral side of the roots. u. l. b.: the red lines show the upper lingual and labial borders between the successive teeth. v. l. b. r.: ventro-lateral border of the roots. $0.7 \times$ nat. size. Based on Idaho no. 4.

pl. X). The differences which are seen in the structure of the hard tissue below the three last formed tooth-crowns (pl. I), may however, to a certain degree, reflect the original limitation of these members of the tooth-spiral.

These observations, and the fact that the last formed tooth clearly shows the rear border of its root (y. t.: pl. I), have been employed in the reconstruction of a single complete tooth and of two successive teeth (fig. 20 a–b).

The surface of the parts of the compound root situated between the middle portions and the narrowed bases of successive tooth-crowns exhibits a large number of openings of vascular canals (o. v. c.: pl. II–III). These openings are oval and are larger than the openings on the surface of the compound root ventrally to the narrowed bases of the tooth-crowns, where the hard tissue lining them has produced fine ridges running nearly parallel to the lower border of the compound root (a. rdg.: pl. II–III).

On the ventral side of the compound root occurs a prominent longitudinal groove with a smooth surface. The section through the tooth-spiral of fig. 24 b shows the outlines of the groove, which differs in some respects from that figured by H_{AY} (1909, p. 56 fig. 7). In this groove the symphyseal crista of the lower jaw is situated (see pp. 20–21). The lateral parts of the compound root between and below the tooth-crowns were covered only by soft tissue.

A notable feature of the tooth-spirals of this species is that none of the specimens show traces of wear on the tooth-crowns, or other evidence of use or destruction during the life of the animals.

The lateral teeth: In specimen Idaho no. 4 some small tooth-like elements are to be seen. They are located in an area below and just behind the rear part of the rostral region of the neurocranium (dnt.: pl. I; pl. VII fig. 2).

Some of the elements are seen still to be lying in mutual positions and forming parts of rows (r. dnt.: pl. VII fig. 2).

In the present state of preservation the elements are seen in profile or longitudinal section (ct. dnt.: pl. VII fig. 2), except one element which exhibits its lower surface (rt. dnt.: pl. VII fig. 2).

The elements are nearly rectangular in shape as seen in profile or longitudinal section. At the upper and the lower surfaces a layer of dense hard tissue is seen. One of the layers is much heavier than the other, and possibly represents the base of the root. Between these layers the hard tissue is formed as a coarse mesh-work connecting the upper and lower denser layers. The openings in the mesh-work clearly represent openings for the vascular canals (fig. 21 A & B).

It has not been possible to investigate the hard tissue of these elements in thin section, but from the visible structure it may be suggested that the inner part consists of osteodentine, capped by a layer of pallial-dentine and coated by a thin outer layer of an enameloid substance.



Β.

Fig. 21. *Helicoprion ferrieri* HAY. Small lateral teeth from the anterior part of the upper jaw. Lateral view. A: Isolated tooth. B: Two teeth in natural mutual position. $13 \times$ nat. size. Idaho no. 4.

It is not certain whether the elements as seen from above were rectangular or rhombic. The nature of their upper surface is not known in detail, but it may be regarded as a crushing surface.

The small elements are interpreted as part of a dentition situated in the anterior part of the upper jaw. No other traces of a lateral dentition have been found in connection with the remainder of the jaws. This may be due to the fact that only remains of the anterior part of the neurocranium and the jaws are preserved. However, it is more likely that it reflects a strong reduction of all other parts of the dentition.

The smallest of the elements is 4.1 mm in length and 1.2 mm high, and the largest is 5.2 mm long and 2.6 mm high.

Scale covering.

None of the specimens show any traces of a scale covering. Consequently it is proposed that *Helicoprion ferrieri* at least on the anterior part of the head, was completely devoid of scales.

Histological notes on the tooth-spiral.

The histological structure of the hard tissues which compose the tooth-spiral was treated by KARPINSKY (1899 pp. 44–61, pl. III–IV). His observations were completely verified by TEICHERT (1940 pp. 145–147), although the latter was unable to add further detail on account of the state of preservation of the Australian material.

In the present work only very little can be added to the excellent description by KARPINSKY, the principal features of which are as follows:

- 1) An inner core of strongly vascular tissue, the so-called "schwammiges Vasodentin", occupies the central part of the compound root, in the centre of which can be observed one, or a pair, of prominent canals. The canals are not distinguishable in the smaller parts of the spiral. The vascular tissue is devoid of cell-spaces, but is concentrically laminated around the vascular canals and penetrated by dentinal tubes.
- 2) Surrounding the "schwammiges Vasodentin" is a denser type of vascular tissue with smaller vascular canals, termed "faserigen Vasodentin". In its upper part is situated a very prominent longitudinal canal, which runs through the complete extent of the spiral. In polarized light a concentric lamination is observed and dentinal tubes are seen penetrating the surface of the vascular canals at right angles.
- 3) The interior of the tooth-crowns is occupied by strongly vascular tissue, in the centre of which strong nutritive canals run out nearly at right angles to the spiral. These canals send out smaller dichotomously branching canals, which bend towards and nearly at right-angles to the surface of the tooth-crown terminating just below the surface. They form the layer called "Röhrenvasodentin" or "Paral-lelröhrendentin" in the periferal parts of the tooth-crown. Dentinal tubes can be observed, running out nearly at right-angles into the hard tissue surrounding the parallel canals, as well as from their termination below the superficial layer of enamel-like hard tissue.
- 4) An outer layer of comparatively thin enamel-like hard tissue.

This description shows clearly that the tooth-spiral is composed of osteodentine comprising denteons (\emptyset RVIG 1965), penetrated by dentinal tubes, and with an interdenteonal bony substance which lacks bone-cells. Furthermore the tooth-crowns are coated with a thin layer of shiny hard tissue, which, at least in part, may represent an enameloid substance (\emptyset RVIG 1965).

With respect to the observations which can be made on the material of the present study, the histological composition of the tooth-spiral of *Helicoprion ferrieri*





Fig. 22. Helicoprion ferrieri HAY. Simplified sketch of a section through the superficial part of a tooth-crown, showing the thin layer of enameloid substance (en.), the layer of pallial dentine (p. dt.) with dentinal tubes (d. t.), the osteodentine (dti.), and the pulp cavities (p. c.). ×580. Idaho no. 4.



Fig. 23. Helicoprion ferrieri HAY. Simplified sketch of a vertical orientated section through a part of the compound root, showing the circumvascular denteons (cv. dti. o.) and the interdenteonal bone trabecles (int. s.). v. c.: vascular canals. $\times 580$. Idaho no. 4.

Biol.Skr.Dan.Vid.Selsk. 14, no. 5.

is identical in detail with that described for *Helicoprion bessonowi*. The root and the interior of the tooth-crowns show osteodentine (dti.: fig. 22; pl. VI fig. 1–3) with denteons (c. v. dti. o.: fig. 23; pl. VI fig. 4) surrounding the vascular canals and the pulp cavities (v. c. & p. c.: fig. 22 & 23). The interdenteonal bony substance can also be observed (int. s.: fig. 23). The dentinal tubes can be seen penetrating the denteons surrounding the vascular canals of the root; no traces of them are found in the tooth-crowns where the denteons are badly preserved.

The outer layer, coating the osteodentine in the tooth-crowns, is penetrated by very densely set, strongly branching dentinal tubes. These are more widely spaced in their proximal part (d. t.: fig. 22; pl. VI fig. 1–2). A comparatively thin superfical part of the outer layer is devoid of dentinal tubes. This part is thickest in the area around the cutting edges. Thus the outer part of the tooth-crown of *Helicoprion ferrieri*, as is also the case with *Helicoprion bessonowi*, comprises two distinct layers: an inner layer of pallial dentine (p. dt.: fig. 22; pl. VI fig. 1–2) and an outer thinner layer of enameloid substance (en.: ibid).

The pulp cavities in the most superficial parts of the osteodentine are about 0.06 mm wide; the thickness of the layer composed of the enameloid substance and the pallial dentine is 0.09–0.1 mm, and the diameter of the proximal parts of the dentinal tubes situated in the pallial dentine is about 0.003 mm.

Comparisons and affinities.

The tooth-spiral of *Helicoprion ferrieri* has previously been compared with that of *Helicoprion bessonowi*, *Helicoprion nevadensis*, *Helicoprion sierrensis* and *Helicoprion davisii* in the discussions of HAY (1909), KARPINSKY (1912), WHEELER (1939) and TEICHERT (1940).

Their principal conclusions can be summarised as follows:

- 1) The apical angle of the tooth-crowns is smaller in *Helicoprion ferrieri* than in *Helicoprion bessonowi*, *Helicoprion davisii* and *Helicoprion nevadensis*, but about the same as in *Helicoprion sierrensis*.
- 2) The height of the free lateral lower portion of the compound root (= the shaft, WHEELER, TEICHERT) is greater in *Helicoprion ferrieri* than in *Helicoprion bes*sonowi, *Helicoprion nevadensis* and *Helicoprion sierrensis*. In *Helicoprion ferrieri* it is equal to about 1/5 to 1/7 of the total height of a volution, while in *Helicoprion* nevadensis and *Helicoprion sierrensis* it is nearly 1/10 and in *Helicoprion bessonowi* about 1/15 of the total height. It differs also from the equivalent dimension in *Helicoprion davisii*. It most closely resembles the condition found in the Japanese specimen described by YABE (1903) under the name *Helicoprion bessonowi*.
- 3) HAY regarded the American species as representing a particular genus *Lissoprion*, but this was rejected by KARPINSKY whose statement has since been confirmed by other workers.

Nr. 5

4) Helicoprion ferrieri, Helicoprion sierrensis, Helicoprion nevadensis, Helicoprion davisii and Helicoprion bessonowi apparently form one group of closely allied species.

Several further points can be added to these conclusions concerning the toothspiral in *Helicoprion ferrieri* as a result of the present investigation. In *Helicoprion ferrieri* the height of the middle portions of the tooth-crowns is smaller than in *Helicoprion bessonowi* and *Helicoprion nevadensis*, as well as in the new species *Helicoprion ergasaminon* described below. It more closely resembles the dimensions found in *Helicoprion davisii* and *Helicoprion sierrensis*, of which the latter may be rather closely related to *Helicoprion ferrieri*.

The groove on the ventral side of the compound root (fig. 24 b) differs characteristically in shape and in depth from that described and figured for *Helicoprion bes*sonowi (KARPINSKY 1899, pp. 37–38, fig. 30–34) and for *Helicoprion davisii* (TEICHERT 1940, pl. 22 fig. 3).

Concerning the endoskeletal remains found in *Helicoprion ferrieri* and in *Helicoprion ergasaminon* n. sp., as described in the present paper, many details of the structure are readily comparable to those described by KARPINSKY for *Helicoprion bessonowi*, thus representing in this form the remains of the symphyseal region of the lower jaw. The so-called "besondern Gefässes" (KARPINSKY 1899, pp. 76–79, fig. 57) represents cartilage-calcifications, as shown by OBRUCHEV (1952, p. 279). These calcifications are located inside the groove on the ventral side of the tooth-spiral and might be regarded as the remains of the symphyseal crista, as are those found in *Helicoprion ferrieri* and *Helicoprion ergasaminon*.

With regard to the layers of cartilage-calcifications preserved laterally to the tooth-spiral on KARPINSKY'S specimen no. 1 (1899, pp. 65–76, fig. 47), their relation to the spiral is exactly the same as found in the American material, thus representing the calcifications from the walls of the symphyseal cavity formed by the left and the right lower jaw. The suggestion by KARPINSKY and OBRUCHEV that these elements are forward and upward coiled prolongations of the palatoquadrates has thus been proved to be incorrect.

The anterior part of the lower jaw in *Helicoprion ferrieri* differs from that found in *Helicoprion ergasaminon* n. sp. (p. 40) by the presence of prolongations of the two branches of the jaw rostrally to the symphysis.

Diagnosis:

The neurocranium consists of cartilage with an inner and an outer layer of prismatic calcifications lining the cranial cavity and the outer surface. A rostrum consisting of at least one strong rod of cartilage situated ventrally in the median line is present. The palatoquadrates are independent elements attached to the neurocranium, possibly in an amphistylic or a hyostylic manner. The lower jaw, consisting of calcified cartilage, possesses a long, high but narrow symphyseal portion, formed by a spiral-coiled crista lying between the two branches of the jaw which terminates rostrally to the symphysis. Between the branches of the jaw and inside the symphyseal crista is situated a cavity, the symphyseal cavity, which contains the older parts of the symphyseal tooth-spiral. The dentition comprises a strongly developed symphyseal tooth-spiral situated in the lower jaw, and a few rather small crushing teeth in rows on the anterior part of the upper jaw. The symphyseal tooth-spiral is formed in its oldest part as a crenulated curved rod, the juvenile tooth-arch, about 1_{a} of a volution long, while the rest of the tooth-spiral consists of isolated tooth-crowns the root-parts of which are completely fused. On the ventral side of the compound root is situated a broad, deep groove with a smooth surface. The tooth-crowns undergo a gradual change in form from the older to the younger part of the spiral in that their three parts, the proportionally broad cutting blades with crenulated cutting margins, the paired middle portions and the paired narrowed bases, tend gradually to become more clearly defined. Histologically the tooth-spiral consists of a thin outer layer of enameloid substance covering a layer of pallial dentine, both restricted to the toothcrowns, and an inner core of osteodentine composed of denteons and an interdenteonal bony substance. The anterior part of the head is devoid of scales.

Dimensions.

The measurements given in the schedules below were assessed as outlined in fig. 24 a & b, a system based on that used by WHEELER (1939) and TEICHERT (1940), and refined by NIELSEN (1952).

The number of tooth-crowns in the volutions of the tooth-spiral is counted in each case from the oldest to the youngest preserved part of the specimen. It is to be noted that the numbers with which the tooth-crowns are designated refer not to the number of the tooth-crown in question in the originally complete spiral, but to its number in the sequence of preserved or partly preserved tooth-crowns in the tooth-



Fig. 24 a & b. The two sketches show the points between which the measurements of the specimens were made. The sketches are based on Idaho no.4 and Idaho mrk. Thiel "P" and "MP". $0.7 \times$ nat. size.

Nr. 5

spiral. The symbols S. T. 1-2-3-4 and L. T. 1-2-3-4 are employed in the schedules to indicate the smallest and the largest tooth-crown measured in the first, the second, and subsequent volutions of the tooth-spiral. All linear measurements are given in mm.

Idaho no. 1.

The tooth-spiral consists of $3^{1}/_{6}$ volutions, which have the following numbers of tooth-crowns preserved:

1st volution: 26. 2nd volution: 34. 3rd volution: 28. 4th volution: 6.

The greatest width of the preserved part of the spiral measures 170 mm.

	В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
S. T. 1 (no. 16)	—	6.5	1.5	-	—	3.0	_	-
L. T. 1 (no. 26)	—		2.5	-	—	_	_	0.75
S. T. 2 (no. 39)	30°	12.0	3.5	-	—	6.5	—	-
L. T. 2 (no. 58)	35°	20.0	6.5			9.0	_	3.0
S. T. 3 (no. 68)	—	-	-	—	23.0	-	—	3.5
L. T. 3 (no. 86)	40°	55.0	14.5	_	_	21.5	_	6.2
L. T. 4 (no. 94)	45°	56.0	17.0	—	—	21.5	-	-

Idaho no. 2.

Nearly two volutions of the tooth-spiral are preserved, in which the following number of tooth-crowns can be observed:

1st volution: 32. 2nd volution: 28.

The greatest width of the preserved part of the tooth-spiral measures 66 mm.

	В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
S. T. 1 (no. 11)	$\ldots 22^{\circ}$	5.4	1.4	5.8	3.0	2.6	_	-
L. T. 1 (no. 29)	$\ldots 25^{\circ}$	-	3.0	-	6.5	-	-	-
S. T. 2 (no. 43)	33°	17.7	4.4	15.5	10.0	7.2	-	
L. T. 2 (no. 56)	$\dots 30^{\circ}$	_	6.0		6.0	-	-	1.5

Idaho no. 3.

The specimen shows parts of two volutions, probably the second and the third, in which the following numbers of tooth-crowns are present:

Oldest volution: 11. Youngest volution: 3.

The greatest width of the oldest volution measures 52 mm and the part preserved of the youngest measures 45 mm.

Tooth-crown no. 7 in the oldest volution has the following dimensions:

Idaho no. 4.

This specimen is the best preserved in the collection and consists of $3^2/_3$ volutions with a total of 118 tooth-crowns in addition to the juvenile tooth-arch. The latter forms the first $1/_3$ of the oldest volution. The following numbers of tooth-crowns can be observed:

1st volution: 23 + the juvenile tooth-arch. 2nd volution: 35. 3rd volution: 37. 4th volution: 23.

The greatest width of the tooth-spiral measures 221 mm.

The height of the juvenile tooth-arch is at the anterior end 0.75 mm and at the posterior end 1.4 mm.

	В	A-E	C-D	A-E	C-F	A-L	J-K	M-E
S. T. 1 (no. 2)	27°	2.8	1.3	2.2	1.2	1.0	—	-
L. T. 1 (no. 19)	29°	7.4	2.3	6.5	3.5	3.3	—	0.8
S. T. 2 (no. 36)	34°	10.2	3.4	11.5	7.7	5.5	2.2	1.7
L. T. 2 (no. 49)	32°	15.9	4.3	16.8	11.3	7.6	2.4	1.8
S. T. 3 (no. 74)	_	25.8	_	26.5	20.4	11.0	_	2.5
L. T. 3 (no. 84)	32°	31.0	8.5	35.0	27.2	14.0	4.8	2.6
S. T. 4 (no. 102)	40°	49.1	13.7	51.0	38.0	19.1	—	_
L. T. 4 (no. 115)	45°	-	18.8	-	-	24.0	-	_

Idaho no. 7.

A part of a tooth-spiral, probably belonging to the third volution, is preserved and represented by 9 tooth-crowns partially hidden in the matrix.

The greatest width of the part visible measures 63 mm. No other dimensions can be given.

Idaho no. 9.

Parts of $2^{1/2}$ volutions of the tooth-spiral are preserved, mostly as a cast. The following numbers of tooth-crowns can be observed:

1st volution: 12. 2nd volution: 23. 3rd volution: 16.

The greatest width of the preserved parts measures 148 mm.

	В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
S. T. 1 (no. 3)	_	3.5	1.7	_	-	1.5		
L. T. 1 (no. 12)	35°	12.2	-	12.0	8.6	5.0	_	
S. T. 2 (no. 14)	36°	13.5	3.5	12.4	9.0	5.5	_	-
L. T. 2 (no. 35)	35°	32.0	8.5	30.0	21.4	13.2	-	5.0
S. T. 3 (no. 37)	34°	33.0	9.2	31.9	22.3	14.3	—	-
L. T. 3 (no. 50)	34°	44.4	11.6	—	-	16.3	-	-

38
Nr. 5

Idaho mrk. Thiel "P".

The specimen, which is the counterpart to Idaho mrk. Thiel "MP", is represented by $3^{3}/_{4}$ volutions. However, a part of the youngest volution is lacking, and it is therefore not possible to state exactly the original number of tooth-crowns. The number of tooth-crowns present is 122, which are distributed in the volutions in the following manner:

1st volution: 33. 2nd volution: 34. 3rd volution: 35. 4th volution: 20. The greatest width of the tooth-spiral measures 290 mm.

		В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
S. T. 1 (no.	1)	35°	3.7	1.4	_	_	1.5	_	_
L. T. 1 (no. 3	33)	30°	11.0	3.0	-	—	4.8	_	-
S. T. 2 (no. 3	34)	30°	11.2	3.2	_	_	5.0	_	-
L. T. 2 (no. 6	36)	35°	26.4	7.8	—	—	10.5	—	—
S. T. 3 (no. 7	71)	32°	28.4	8.5	_	_	13.8	—	
L. T. 3 (no. §	97)	34°	57.3	14.6	—	—	20.7	—	-
S. T. 4 (no. 11	10)	40°	76.8	22.0	70.8	51.9	30.1	13.8	13.2

Helicoprion ergassaminon n. sp. Pl. XV.

Figs. 25-26.

Material: The new species is represented only by specimen Idaho no. 5, thus being the holotype of this species.

Introductory notes: The specimen possesses a tooth-spiral in which most of the tooth-crowns are fairly completely preserved, with the exception of those in the youngest volution. A large part of this volution is missing and for the most part only impressions are found of the tooth-crowns. In the present state of preservation 107 tooth-crowns can be observed, but this number may have been exceeded by about 50 in the complete spiral, giving an estimated total of 150–160 tooth-crowns.

A large number of the preserved tooth-crowns, especially those in the older volutions, are more or less hidden by layers of calcifications from the cartilage. It was decided to preserve these endoskeletal remains because of their importance as representing the symphyseal portion of the lower jaw, and the form of the older tooth-crowns is thus only partially known.

Most of the compound root of the tooth-spiral is also hidden by the endoskeletal remains, but it has been possible to study some of its youngest part in some detail, although it is preserved in a relatively broken condition. This circumstance, however, made it well-suited for studies of the internal structure.

The endoskeleton.

The anterior part of the lower jaw: This part of the mandibular endoskeleton is represented by layers of prismatic calcifications from the cartilage. The specimen is immediately caudally to the tooth-spiral broken off from the adjoining rock.

The layers of calcification occur laterally to the tooth-spiral on both sides of it and in close connection with it (calc. cart.: pl. XV). Thus the cartilage remains in the anterior part of the jaw show the same pattern as that found in *Helicoprion* ferrieri (pp. 19–22).

The jaw symphysis is formed by a coiled, strongly calcified symphyseal crista (calc. cart. sym.: pl. XV), nearly ${}^{3}/{}_{4}$ of a volution long, which connects the anterior parts of the branches of the lower jaw along their dorsal and anterior margins and parts of their median surfaces; the connection here is situated dorsally to the ventral borders of the jaw branches. Thus a cavity is formed within the symphyseal region. This symphyseal cavity communicates with the surroundings through an opening on the ventral side of the symphyseal region, where it opens into a relatively deep groove. The lateral walls of this groove are formed by the ventral parts of the jaw branches, while its base is formed by the symphyseal crista.

The symphyseal crista supports the tooth-spiral, the older parts of which are stored in the symphyseal cavity and enter it through the opening on the ventral side of the symphyseal region. The tooth-crowns situated in the older half part of the last formed volution of the tooth-spiral are protected by the lateral walls of the groove on the ventral side of the symphyseal region.

The anterior end of the jaw is formed by the anterior margin of the jaw branches and the adjoining part of the symphyseal crista. Thus no anterior processess, such as those characterizing the anterior part of the lower jaw of *Helicoprion ferrieri* (p. 20, figs. 8–11), are present.

Remarks: The symphyseal region of the lower jaw in *Helicoprion ergassaminon*, it can be seen, is formed in the same way as that of *Helicoprion ferrieri*. Although no traces of anterior processes of the jaw branches are present, the shape and location of the symphyseal crista is essentially the same in both species, as is also the formation of the symphyseal cavity.

Thus, there is no evidence against the assumption put forward above (pp. 21-24) that the symphyseal crista represents a fully developed Basimandibular element highly specialized for the support of the immense tooth-spiral, and which during the ontogenetic development fused completely with the anterior parts of the Meckelian cartilages.

Dentition.

The symphyseal tooth-spiral: This consists of a large number of individual tooth-crowns situated on a completely undivided, strongly coiled compound root, as is normal in Helicoprion forms (pl. XV).

Nr. 5

It has already been mentioned that the greater part of the tooth-spiral is hidden below the remains of the jaw and thus a detailed description of the variation of the tooth-crowns in the different parts of the tooth-spiral cannot be given.

Also no description can be given of the oldest part of the tooth-spiral. It seems probable that as in *Helicoprion ferrieri* (p. 24) it has the form of a curved rod—the juvenile tooth-arch. The shape of the oldest tooth-crowns is unknown.

Some of the tooth-crowns at the beginning of the second volution are visible. A notable feature of these is the strongly worn nature of the cutting blades (fig. 25),



Fig. 25. *Helicoprion ergassaminon* n. sp. A part of the beginning of the second volution, showing toothcrowns with strongly worn cutting blades. The very narrow, exposed part of the compound root is seen below the narrowed bases of the tooth-crowns. $3 \times$ nat. size.

as a result of which the original total height and shape is impossible to reconstruct. The middle portions are rather low and broad and have more or less concave margins. The narrowed bases are broad and comparatively short, forming a rather open angle to the middle portions and point rostro-ventrally. Their terminations vary from gently rounded to angular and are situated below the front margin of the tooth-crown in front (fig. 25).

Since these tooth-crowns were observed in their original place in the symphyseal cavity, covered by the compressed but undisturbed calcifications from the cartilage, the wearing marks are of premortal origin.

In the second volution really marked changes occur in the form of the middle portions and the narrowed bases but could not be studied in detail. However, at the beginning of the third volution these parts of the tooth-crowns have a sharper mutual angle and the middle portions are rather high and narrow with both margins concave, the front margin more strongly so. The narrowed bases are comparatively stout, but long and with nearly pointed terminations situated below the front margin of the second tooth-crown in front. The pointed cutting blades have delicately crenulated cutting edges of which the front edges are more strongly curved than the rear. Some of the cutting blades show undoubted wearing marks.

In the last part of the third volution the tooth-crowns are high with relatively narrow cutting blades. These are only a little greater in height than the middle portions. Their crenulated edges are convex with the stronger curving along the front edge (fig. 26). The middle portions have concave margins with the strongest concavity also along the front margin. The narrowed bases are proportionally narrower than in the preceding volutions and sharply pointed at their terminations, which are



Fig. 26. *Helicoprion ergassaminon* n. sp. Tooth-crowns from the middle part of the third volution. The most complete of them shows a gentle rounding of the apex caused by use. The tooth-crown in front has a broken cutting blade, also originating in actual use during the lifetime of the animal. Note the exposed lower lateral surface of the compound root, which is rather narrow in comparison with the proportions within the tooth-spiral. $2.9 \times$ nat. size.

situated anterior to the front margin of the tooth-crown in front. The angle between the middle portions and the narrowed bases is rather acute (fig. 26).

In the last formed part of the tooth-spiral, which amounts to about ${}^{3}/_{4}$ of a volution, the tooth-crowns have nearly the same characteristics as those found in the third volution. The only difference occurs in the form of the narrowed bases, which are somewhat more slender (pl. XV).

The high and narrow tooth-crowns are only in mutual contact at the lower end of the cutting edges. Here the front lower corner of one edge is inserted in a pocket situated at the rear lower corner of the cutting edge of the adjacent tooth-crown.

A very thin layer of enameloid hard tissue originally covered the tooth-crowns, but on the specimen only very small vestiges of this layer are still preserved. From these remains it appears that the surfaces of the tooth-crowns were originally covered all over the surface from the apex to the termination of the narrowed bases by delicate striations.

In cross section the compound root is, like the tooth-crowns, rather narrow. The lateral surfaces of it, exposed below the narrowed bases, exhibit a sculpture of small irregular ridges. The ventral part of this surface is gently curved in a median direction. Moreover, the surface is also exposed in the long and narrow grooves beNr. 5

tween the lower parts of the tooth-crowns i. e. between the middle portions and the narrowed bases. The surface displays here a number of large vascular canals (o. v. c.: pl. XV).

On the ventral surface of the compound root is situated a longitudinal groove (ro. gr.: pl. XV), nearly as deep as the height of the exposed lower lateral surface of the root. The surface of this groove is rough due to small delicate tubercles.

The greatest lateral width of the spiral is situated at the level of the terminations of the narrowed bases.

Histologically the compound root consists of osteodentine. Internally in the median dorsal part occurs the characteristic longitudinal nutritive canal (c. can.: pl. XV), which gives off branches to the tooth-crowns. The last formed part of the root has the rather widely spaced meshwork typical for osteodentine in an early stage of development (y. p. t. sp.: pl. XV).

Remarks: Apart from the symphyseal tooth-spiral no other traces of a dentition appears in the specimen.

Scale-covering:

No traces of placoid scales are found on the preserved part of the lower jaw. As is the case with *Helicoprion ferrieri* and *Helicoprion bessonowi* it appears that *Helicoprion ergasaminon* n. sp. may have been devoid of scales on the anterior part of the head.

Comparisons and affinities.

The tooth-spiral of the new species differs clearly in its habitual appearance from all other hitherto described *Helicoprion* species. This can readily be seen by a comparison of the figures in the present paper with the previously figured specimens of *Helicoprion bessonowi* (KARPINSKY 1899; YABE 1903; OBRUCHEV 1953), *Helicoprion karpinskii* (OBRUCHEV 1953), *Helicoprion ferrieri* (HAY 1907, 1909), *Helicoprion davisii* (WOODWARD 1886; TEICHERT 1940), *Helicoprion nevadensis* (WHEELER 1939) and *Helicoprion sierrensis* (WHEELER 1939).

However, if the different details of the tooth-spiral are compared there are a number of details in which the new species resembles, to a certain degree, some of the species listed above.

The height of the exposed lower lateral part of the compound root is nearly the same as that found in *Helicoprion davisii*, *Helicoprion bessonowi* and especially *Helicoprion nevadensis*. This area is comparatively broad in *Helicoprion ferrieri* and in *Helicoprion sierrensis*.

The height of the cutting blades in relation to the other parts of the tooth-crowns only closely resembles the conditions occurring in *Helicoprion ferrieri*, but in the latter species the tooth-crowns are broader and exhibit a more coarse crenulation.

The height of the middle portions in relation to the other parts of the toothcrowns bears a close resemblance to the conditions in *Helicoprion nevadensis*, especially in the younger volutions, but the interspaces separating the tooth-crowns are much narrower in the new species.

The narrowed bases have a large angle between the upper and lower borders, similar to that in *Helicoprion bessonowi*, but they form a more acute angle to the middle portions in the new species, resembling more closely in this respect *Helicoprion ferrieri*.

The proportions between the middle portions and the narrowed bases are very like those occurring in *Helicoprion nevadensis*, although the angle between the two parts is somewhat more acute in the new species, and in particular the rear corner between the two parts is sharper.

The apical angle $(25^{\circ}-35^{\circ})$ is rather small in comparison to Helicoprion ferrieri and Helicoprion sierrensis $(34^{\circ}-37^{\circ})$, Helicoprion bessonowi (45°) , and also Helicoprion nevadensis $(42^{\circ}-37^{\circ}-45^{\circ})$.

A further notable feature of the new species is the great number of tooth-crowns represented per volution. This amounts to 48–50, while in most other species between 30 and 39 are found. The highest hitherto known number is 43 found in *Helicoprion bessonowi*.

The lower jaw differs from that found in *Helicoprion ferrieri* by the lack of the anterior processess.

It may be said, in conclusion, that the new species is most closely comparable to *Helicoprion nevadensis*, from which, however, it differs essentially in many respects. It forms a well-defined new species.

The specific name proposed, *Helicoprion ergasaminon*, refers to the distinct wearing marks found on the type specimen, and in translation from the Greek Εργασαμινον means "the one, who has done work".

Diagnosis.

The endoskeleton consists of cartilage with a superficially situated laver of prismatic calcifications. The lower jaw has a high and long, but narrow symphyseal region. A spiral-coiled, strongly calcified symphyseal crista connects the two jaw branches, which terminate rostrally along the border of the symphyseal crista. These three elements enclose the symphyseal cavity. The known parts of the dentition are represented by the high, narrow symphyseal tooth-spiral, composed of a large number of separated tooth-crowns placed on a solid, spiral-coiled, undivided compound root, which has on the ventral side a narrow, deep, longitudinal groove with a rough surface. The closely set tooth-crowns are high and narrow, and are proximally separated from each other by shallow grooves. Their cutting blades have crenulated cutting edges and are a little higher than the middle portions. The middle portions have concave margins. The form of the narrowed bases varies from short and stout with angular or evenly rounded terminations, to long and narrow with extremely pointed terminations. Histologically the tooth-spiral is composed of osteodentine covered by a thin layer of enameloid substance below which, it is presumed, a layer of pallial dentine was originally present.

Nr. 5

Dimensions.

Parts of $3^3/_4$ volutions of the tooth-spiral are preserved. The greatest width of the tooth-spiral measures 218 mm.

Due to the conditions of preservation it is impossible to give systematic measurements of the tooth-crowns in the spiral. However, in order to give some idea of the proportions between the different parts of the tooth-crowns, and of tooth-crowns in successive parts of the tooth-spiral, the dimensions of some of the more completely preserved tooth-members are given below. All linear measurements are given in mm.

	В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
I	-	_	2.7	_	5.5	_	_	_
II	-	-	4.7	_	15.0	-	-	—
III	25°	31.8	6.9	29.5	21.0	13.6	_	-
IV	35°	37.3	9.1	-	_	13.0	_	3.8
V	35°	41.9	9.8	_	—	16.2	_	5.0

I: One of the last tooth-crowns in the first volution.

II: One of the early tooth-crowns in the third volution.

III: One of the intermediate tooth-crowns in the third volution.

IV: One of the last tooth-crowns in the third volution.

V: One of the youngest tooth-crowns in the third volution.

Helicoprion cf. ferrieri. Pl. VIII fig. 1. Fig. 27–28.

Material: The material is represented by only a single specimen, Idaho no. 8.

The symphyseal tooth-spiral.

The specimen preserves parts of $3^{1}/_{6}$ volutions of a tooth-spiral, which occurs mainly as impressions of the tooth-crowns and of the compound root (pl. VIII, fig. 1).

All the tooth-crowns, or parts of them preserved, have a more or less prominent long and tapering lower portion, representing the narrowed base. The other parts, the middle portions and the cutting blades, can be observed in detail only in the second, the third and the fourth volutions.

The strong pointed cutting blades are in the younger portions of the tooth-spiral nearly half as high as the complete tooth-crown. The front cutting edges are longer and more strongly convex than the rear edges; both possess a crenulation, which is somewhat coarse in the youngest preserved tooth-crowns.

The tooth-crowns are in mutual contact at the lower part of the cutting edges. This contact is formed by the lower corner of the front cutting edge of one tooth-crown,



Fig. 27. *Helicoprion cf. ferrieri*. Tooth-crowns from the fourth volution showing the mutual dimensions of the three parts of the crown, in particular the short, triangular shaped and strongly pointed narrowed bases. The broad lateral lower part of the compound root is a characteristic feature of the specimen. $1.1 \times$ nat. size.

which fits into a small recess in the lower portion of the rear cutting edge of the preceeding tooth-crown.

The middle portions are more clearly defined in the younger than in the older parts of the tooth-spiral. The front margins are strongly concave, and the rear margins are straight or slightly convex.

The narrowed bases are more prominent in the older than in the younger parts of the tooth-spiral. They are in the oldest tooth-crowns directed nearly vertically, but, after a short distance, they are bent more forward, and in the youngest tooth-crowns they are nearly at right-angles to the axis of the remainder of the tooth-crowns.

In the oldest part of the tooth-spiral the narrowed bases terminate at a point below the middle of the second tooth-crown in front, while in the younger parts they only reach below, or just behind, the front margin of the middle portion of the adjacent tooth-crown. The narrowed bases of the younger tooth-crowns have extremely pointed terminations.

The tooth-crowns were probably originally covered by a layer of enameloid substance, but this layer has completely disappeared and nothing can be stated about the presence or absence of any kind of original surface ornamentation.

Undoubted wearing marks occur on a number of the tooth-crowns belonging to the youngest of the preserved volutions (fig. 28). These wearing marks are found as a series of distinct facets bordering broad shallow depressions on the lateral proximal parts of the cutting blades and on the middle portions. The pattern shown by the marks seems to be a compound of systems of alternating directions. This circum-



Fig. 28. Helicoprion cf. ferrieri. Tooth-crowns from the youngest of the preserved volutions showing distinct wearing marks. Idaho no. 8, Cast in PVC-plastic. $0.7 \times$ nat. size.

stance reflects the change of inclination of the tooth-crowns in relation to the rows of small teeth on the upper jaw, and is a consequence of the gradual movement in a labial direction of the symphyseal tooth-spiral.

The lateral surfaces of the compound root are covered by a fine meshwork formed by the walls of hard tissue surrounding the openings of the small vascular canals. In the areas situated between the middle portions and the narrowed bases of adjacent tooth-crowns the openings are larger and fewer, and oval shaped.

A longitudinal groove is present on the ventral side of the compound root, but nothing is known of its original form, size or surface features.

Remarks: No traces of other teeth, scales or calcifications from the cartilage are found in the specimen.

Discussion.

The tooth-spiral of the described specimen shows in many details a close resemblance to that of *Helicoprion ferrieri* (pp. 24–30). However, there are strong differences with regard to the form and length of the narrowed bases of the tooth-crowns. This is especially the case with the younger tooth-crowns of *Helicoprion ferrieri* in which the narrowed bases reach a point situated below the front margin of the middle portion of the second tooth-crown in front, while in the specimen under discussion they only reach a point below or just behind the front margin of the first adjacent tooth-crown.

Furthermore the shape of the narrowed bases differs in the two species. In *Helicoprion ferrieri* they are long and slender with nearly parallel upper and lower borders, and have a rounded termination (pl. I and fig. 12). In the specimen in question they are rather short and nearly triangular in shape, with a strongly pointed termination.

These differences might be considered as sufficient for the erection of a further new species. This, however, has been rejected on account of the many similarities between the specimen and *Helicoprion ferrieri*, and the possibility that the observed differences are only of secondary origin. They could in this particular individual have been caused by a local destruction or other alteration of the ectomesodermal tissue which took part in the formation of this portion of the tooth-crown. Therefore, until more and better material becomes available, it has been decided to refer to the specimen as *Helicoprion cf. ferrieri*.

Dimensions.

Parts of $3^{1}/_{6}$ volutions are preserved with the following numbers of tooth-crowns occurring in each volution:

1st volution: 30. 2nd volution: 37. 3rd volution: 26. 4th volution: 6.

The greatest width of the preserved part of the spiral measures 181 mm.

The general state of preservation does not permit systematic measurements. No dimensions could be obtained from the first and the fourth volution. For the second and the third volution the following measurements can be stated:

	В	A-E	C-D	A-F	C-F	A-L	J-K	M-E
S. T. 2 (no. 36)	-	_	4.0	-	9.5	-	-	
S. T. 3 (no. 70)	—	—	8.0	-	16.0	-	-	_
L. T. 3 (no. 86)	40°	49.6	15.5	44.2	32.0	20.5	_	-

Helicoprion sp. indt. Pl. XIV fig. 3.

Material: This consists of the specimen Idaho no. 6.

Description: The specimen preserves the remains of 12 tooth-crowns and a part of the compound root. From the size it seems most reasonable to assume that the fragment originally formed a part of a second volution.

Most of the specimen is preserved as a impressions in the matrix. None of the tooth-crowns are complete, and their original form and sculpture cannot be determined. In contrast, the impressions of the middle portions are fairly clearly defined, and show a concave curving along their front margins while the rear margins are straight or slightly convex. The narrowed bases are slender and terminate at a point below the centre of the second tooth-crown in front.

The state of preservation is too poor to permit a specific determination.

Dimensions.

The greatest width measures 57 mm.

Tooth-crown no. 8, counted from the posterior end of the specimen, has the following dimensions:

B A-E C-D A-F C-F A-L J-K M-E - - 6.0 - 15.6 - - -

Summary and conclusions

The treated North American Helicoprion material comprises the species *Helico*prion ferrieri, Hay, *Helicoprion ergasaminon* n.sp. and two other not closely determinable specimens referred to respectively as *Helicoprion cf. ferrieri*, and *Helicoprion sp. indt*.

The investigations have yielded a number of new features in our knowledge of this Elasmobranch.

With respect to the neurocranium details of the rostral and the ethmoidal region are now known.

The rostral region is found to possess one un-paired cartilage rod ventrally. On the posterior part of this rod occurs a smooth rounded, relatively broad tuberosity, to which ligaments apparently have been attached. Because of incompleteness of the material the dorsal part of the rostral region is unknown. However, the presence of a ventrally situated un-paired rod is a character typical of a Selachian skull pattern. Therefore, it is most likely that the rostrum originally has been formed as a basket with a pair of cartilage rods dorsally forming its upper lateral limitation and anteriorly joining the un-paired ventral rod.

The remains of the ethmoidal region of the neurocranium indicate that the nasal capsules are placed at the most anterior part of this region.

Of the visceral skeleton the anterior part of the lower jaw and two dorsal elements are known. The latter are tentatively interpreted as the anterior parts of the palatoquadrates on account of their shape, size and position in relation to the neurocranium, and their relation to the remains of a weak upper dentition. If this interpretation is correct the palatoquadrates are completely independant elements. Consequently they may have been suspended on the neurocranium in an amphistylic or hyostylic manner, both of which characters are typical of the Selachians.

The anterior part of the lower jaw is strongly formed, with an extremely high symphyseal region composed of a strongly developed, coiled Basimandibular element connecting the Meckelian cartilages, and enclosing a cavity in which the older volutions of the symphyseal tooth-spiral are successively stored.

The symphyseal tooth-spiral is described in detail. Its oldest part, not previously known, is found to be a curved rod, which along its dorsal edge is developed as a crenulated cutting crista. The individual tooth-crowns vary to some degree in shape from the oldest part to the youngest part of the tooth-spiral. Considerable but gradual changes are found in the relations between the three principal parts of the tooth-crowns. It has been possible, also, to give an interpretation of the limitations between the roots of the teeth in the youngest portion of the tooth-spiral. This was due to the fact that, although the complete fusion between successive teeth is already at hand at the development of a new tooth, the hard tissue of the compound root in the youngest part of the tooth-spiral exhibits a clear gradual degree of completion of the circumvascular denteons of the vascular canals. On the tooth-spiral of *Helicoprion ergasaminon* n. sp. and *Helicoprion cf. ferrieri* distinct wearing marks are found on the tooth-crowns.

Biol.Skr.Dan.Vid.Selsk. 14, no. 5.

A number of very small crushing teeth form a weak tooth-pavement on the most anterior parts of the upper jaw. Apart from these and the symphyseal toothspiral no other traces of dentition have been found. This circumstance may be due to the fact that only the anterior parts of the jaws are present. However, it is more likely that it reflects a very strong reduction of the lateral dentition.

A reduction seems also to have taken place in the dermal skeleton since no traces of scales are found on the anterior part of the head.

Although KARPINSKY had already, in his admirable monograph (1899), given great attention to the histology of the symphyseal tooth-spiral there were still several obscure points, which led to the discussion of its histology (NIELSEN 1932, 1952; MOY-THOMAS 1939 a; TEICHERT 1940). A re-description, such as that given in the present paper, was therefore highly desirable. This re-description has clearly shown that the tooth-crowns consist of typical osteodentine, composed of denteons arranged at right angles to the tooth-surface in its outer parts. The denteons are separated by an interdenteonal bony substance in which dentinal tubes, issuing from the vascular cavities of the denteons, penetrate to a certain degree. The outer coating of the tooth-crowns consists of two layers, an outer very thin layer of an enameloid substance underlain by a thin layer of pallial dentine with strongly developed, irregular branching dentinal tubes.

The new evidence concerning the anatomy of the anterior part of the neurocranium and the palatoquadrate provides good reasons for a closer determination of the systematical position of *Helicoprion ferrieri* and *Helicoprion ergasaminon* as well as for the other known *Helicoprion* species. It is obvious from these anatomical features that this Elasmobranch may be grouped most adequately close to the Selachian Elasmobranchs. However, because of the restriction of the known features, it is necessary provisionally to establish the genus *Helicoprion* in a separate order within the subclass *Elasmobranchii* as follows:

Class: Elasmobranchiomorphi.

Sub-class: Elasmobranchii. Super-order: Helicoprioni. Order: Helicoprioniformes. Family: Helicoprionidae. Genus: Helicoprion¹.

This is in strong contrast to previous suggestions put forward by most of the authors who have dealt in details with *Helicoprion* or problems related to this form. Only TEICHERT (1940 p. 143) has maintained a corresponding view, while others (NIELSEN 1932, 1952; MOY-THOMAS 1939 a; OBRUCHEV 1953, 1964; BENDIX-ALM-GREEN 1961) have placed *Helicoprion* within the *Edestid* group among the *Bradyodonti*

¹ The genus *Toxoprion* HAY 1909 founded on *Toxoprion lecontei* DEAN 1895 may be regarded as synonymous for *Helicoprion*, as suggested by OBRUCHEV (1953 p. 59).

due to the similar specialisation of the symphyseal tooth-row, and because of the microscopic tooth-structure suggested to be tubular dentine. In this type of dentine the tooth-crowns are composed of denteons clearly separated by an interstitial enameloid substance (NIELSEN 1932 pp. 30, 33; MOY-THOMAS 1939 a pp. 2–3; ØRVIG 1951 pp. 342, 349) thought to be characteristic for all Elasmobranchs grouped as *Bradyodonts*.

However, new investigations in paleohistology (RADINSKY 1961; ØRVIG 1965) have revealed certain features showing that the tubular dentine is without any significance as a systematical character. It is beyond the scope of this paper to consider this problem, which will be dealt with in detail in a forthcoming publication. Nevertheless, it can be stated that the results of these investigations also involve that the osteodentine found in the tooth-crowns of *Helicoprion* does not provide evidence of value with regard to the systematical position of this Elasmobranch.

On the other hand, the anatomical features of the neurocranium and palatoquadrate show clearly the non-existence of a close relationship with the better known *Edestids* i. e. *Sarcoprion edax* (NIELSEN 1952), *Fadenia crenulata* (NIEL-SEN 1952; BENDIX-ALMGREEN 1961; 1962) and *Erikodus groenlandicus* (BENDIX-ALMGREEN 1961). This applies also to the other better known Elasmobranchs hitherto placed as members of the *Bradyodont* group i. e. *Helodus simplex* (MOY-THOMAS 1936; PATTERSON 1965) and *Chondrenchelys problematica* (MOY-THOMAS 1935; PATTERSON 1965). All these forms possess a holostylic jaw suspension and the rostral region has an entirely different configuration.

The facts discussed above show the interesting feature that parallel evolution and specialisation of the teeth in the symphyseal region of the lower jaw has taken place within different Elasmobranch lines during Carboniferous and Permian time. The acme of this form of specialisation was reached in late Carboniferous and Permian time with the complete tooth-spiral found in Helicoprion.

The reasons for the development of such an unusual organ as the *Helicoprion* tooth-spiral are certainly obscure, especially since in all the previously described species no observations of evidence of actual use have been reported. However, during a visit to Moscow and Leningrad, I had the opportunity to study the classical *Helicoprion* material. This study, which also fully confirmed the description of the tooth-histology given above, revealed that some of the specimens of *Helicoprion bessonowi* do, in fact, show weak but clear wearing marks. These occur on the lateral surfaces of the middle portions and on the narrowed bases of the tooth-crowns, and show to some degree a pattern comparable to that found on *Helicoprion cf. ferrieri* described above (pp. 46–47). The strongest wearing marks known from a *Helicoprion specimen remain*, however, those described in the present paper for the specimen known under the new specific name, *Helicoprion ergasaminon*, where they are found, not only on the lateral surfaces of the tooth-crowns, but also on the apex of the cutting blades.

In the past some confusion has prevailed over the question of the original location

of the tooth-spiral in the mouth. The most adequate previous explanation was given by KARPINSKY (1899 p. 107, fig. 72), although it was viewed with great scepticism by many authors (HAY 1909, 1912; WOODWARD 1900 pp. 33–36). OBRUCHEV, in his 1953 work, published a new reconstruction mainly based on Karpinsky's material and original figures, but the tooth-spiral was still placed in the upper jaw symphysis and was thought to have acted as a defence weapon. OBRUCHEV, however, notes, ".... one may hope that new finds will show, how near such a reconstruction is to the truth" (p. 57).

Our present extended knowledge enables us to state with certainty that the toothspiral is, in fact, situated in the symphysis of the lower jaw and that no similar organ was developed in the upper jaw.

With regard to the role and function of the symphyseal tooth-spiral many different opinions have been published, in which it has been suggested as a defence weapon, as a cutting device or as a crushing organ. If it was principally a crushing organ, really strong wearing marks would be expected, as occur, for example, in *Fadenia crenulata*, which it is known from a specimen with preserved stomach contents preyed on Brachiopods (BENDIX-ALMGREEN 1961). The proposal that the tooth-spiral acted as a defence weapon was mostly based on its assumed location in the upper jaw symphysis, a now invalid assumption. The most probable function and use of the tooth-spiral on the evidence of the wearing marks seems to have been as a cutting and, probably to some degree, a tearing device, in combination with the rows of small upper jaw teeth.

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Indleveret til Selskabet den 15. februar 1965. Færdig fra trykkeriet den 2. marts 1966. PLATES

PLATE I Helicoprion ferrieri HAN. Idaho no. 4. 0.5× nat. size. Photographed in Xylene. art. p.: the tuberosity on the proximal part of the rostral element. calc. cart. l. l. j. & calc. cart. r. l. j.: the left and the right branches respectively of the lower jaw. calc. cart. n. cr.: frontal part of the neurocranium. calc. con. j.: calcifications from the rear connection between the two branches of the lower jaw at the lingual end of the symphyseal crista. calc. cart. sym.: the symphyseal crista. The calcifications are enclosed in the ventral groove of the compound root of the tooth-spiral. calc. na. ?: layers of calcifications possibly belonging to the nasal capsula. can. c.: two canals which were possibly originally situated ventrally of the upper jaw. f. o. l.: foramen for the nervus olfactorius. pit.: the cavity where the new tooth-members in the lateral wall of the neurocranial capsule. dnt .: teeth from the tooth-pavement on the anterior part of the spiral are developed. pr.l.j.: the anterior process of the left branch of the lower jaw. r. p. n. cr.: unpaired ventral rostal balk. y. t.: the last formed tooth in the spiral. The large spaces in the hard tissues forming the crown and corresponding root are clearly seen. This circumstance indicates the incompletely developed state of the tissues and is in strong contrast to the condition found in the older parts of the tooth-

spiral.

PLATE I



Helicoprion ferrieri HAY. PLATE II

Photographed dry. Idaho no. 4. $0.5 \times$ nat. size.

a.rdg.: area clearly showing the delicate ridges which characterize the lateral surface of the compound root. cale.cart.r.l.j. & cale.cart.l.l.j.: anterior part of the right and the left branches of the lower jaw forming the lateral walls of the symphyseal cavity. dnt.: teeth from the upper jaw. o. v. c.: fairly widely

spaced vascular canals.

PLATE II



PLATE III Helicoprion ferrieri HAY. Cast in PVC-plastic. Idaho no. 4. 0.5× nat. size.

a. rdg.: area showing the delicate ridges on the lateral surface of the complex root. o. v. c.: vascular canals.



PLATE IV

Helicoprion ferrieri HAY. Idaho no. 4.

$1\times$ nat. size.

Photograph of the specimen submerged in xylene, showing a transverse section through the anterior portion of the neurocranium, the palatoquadrates and the lower jaw.

calc. cr. b.: layers of prismatic calcifications representing the basal part of the neurocranium. calc. l. l. j. & calc. r. l. j.: prismatic calcifications from the left and the right lower jaw. can. l. & can. r.: two pair of canals which possibly originally were situated close to the base in the left and the right side of the neurocranium. cav. cr.: cavum cerebrale cranii. l. i. cr. w. & r. i. cr. w.: calcification layer lining the inner surface of the neurocranium. l. o. cr. w. & r. o. cr. w.: calcification layer lining the outer surface of the neurocranium. pit.: location of the pit where the symphyseal teeth are developed. pq. l. & pq. r.: transverse section through the supposed left and right palatoquadrates. sym. t.: two tooth-crowns from the symphyseal spiral.

PLATE IV



PLATE V.

Helicoprion ferrieri HAY. Idaho no. 4. Fig. 1. 4× nat. size. Fig. 2. 8.2× nat. size. Photographed in Xylene.

Both figures show the oldest part of the tooth-spiral with the juvenile tooth-arch, and the first developed tooth-crowns. These differ somewhat in general shape from the later tooth-crowns. On figure 2 the crenulation on the cutting edge of the juvenile tooth-arch is visible.



Fig.1



Fig.2

PLATE V

PLATE VI

Helicoprion ferrieri HAY. Fig. 1: Idaho no. 4. Fig. 2: Idaho no. 4. Fig. 3: Idaho no. 4. Fig. 4: Idaho no. 1. Enlargement: 483×.

Fig. 1: Thin-section through the area of the cutting edge of a tooth-crown showing the osteodentine (dti.) surrounding the pulp cavities (p. c.), the pallial dentine (p. dt.) with strongly branching, densely set dentinal tubes (d. t.), and the outer layer of enameloid substance (en.). Horizontal section.

Fig. 2: Thin-section through an area of the tooth-crown, showing a thin layer of enameloid substance (en.), the osteodentine (dti.), parts of pulp cavities (p. c.), and the layer of pallial dentine (p. dt.) with dentinal tubes (d. t.). Horizontal section.

Fig. 3: Thin-section of the osteodentine (dti.) of the tooth-crown. The osteodentine shows clearly a fairly eoarse lamination. No traces of the hard tissue of the circumpulpar denteons are preserved. Horizontal section \times Nicols.

Fig. 4: Thin-section through a part of the compound root showing circum-vascular denteons (cv. dti. o.) surrounding the vascular canals (v. c.), and the interosteonal bony substance (int. s.) Vertical section.

PLATE VI







PLATE VII

Fig. 1: Helicoprion cfr. ferrieri. Idaho no. 8. 0.7× nat. size. Photographed dry. can. w.: vascular canals.

Fig. 2: Helicoprion ferrieri HAY. Idaho no. 4. 0.9× nat. size. Photographed in Xylene.

Detail of specimen Idaho no. 4 showing small scattered teeth (dnt.), which represent parts of a strongly reduced tooth-pavement situated on the anterior part of the upper jaw.

ct. dnt.: tooth in lateral view. r. dnt.: teeth forming part of the original rows. rt. dnt. lower surface of the root.

Plate VII



PLATE VIII

Helicoprion ferrieri HAY. Idaho no. 1. $0.6 \times$ nat. size. Photographed dry.

calc.cart.: prismatic calcifications from the cartilage of the lower jaw. c. can.: parts of the central canal which runs through the compound root of the tooth-spiral, and originally contained the main nutritive vessel. r. em. cr.: remains of the juvenile tooth-arch.



PLATE IX

Helicoprion ferrieri HAY. Idaho no. 1. 0.9× nat. size. Photographed dry.

Fig. 1: Impressions of tooth-crowns of the fourth volution. Fig. 2: Cast in PVC-plastic; lateral view from the right. Fig. 3: Same seen from above.

The coarse crenulations along the cutting edges of the cutting blades are clearly seen, as well as the fine striations characterizing the surface of the dentine. The original layer of enameloid substance, which once covered the tooth-crowns, is not preserved.







PLATE X

Helicoprion ferrieri HAY. Idaho mrk. "Thiel P". $0.5 \times$ nat. size. Photographed in Xylene.

r. calc. cart.: calcifications from the cartilage of the symphyseal portion of the lower jaw, corresponding to the symphyseal crista. ro. gr.: the right lateral wall of the groove occuring ventrally on the compound root. y. p. t. sp.: remains of the last formed portion of the compound root.


PLATE XI

Helicoprion ferrieri HAY. Idaho mrk. "Thiel P". 0.5× nat. size. As plate X but photographed dry.

h. v. g.: the lateral wall of the ventral groove.

PLATE XI



PLATE XII

Helicoprion ferrieri HAY. Idaho mrk. "Thiel MP". 0.5× nat. size. Photographed in Xylene.

r. calc. cart.: calcifications from the symphyseal crista.



r. calc. cart.

PLATE XIII Helicoprion ferrieri HAY. Idaho no. 9. nat. size. Photographed dry.

PLATE XIII



PLATE XIV

Helicoprion ferrieri HAY. Fig. 1–2: Idaho no. 2. 0.8× nat. size.

Original specimen and cast in PVC-plastic. The minute, densely set openings for the vascular canals occuring laterally on the compound root can be seen on the cast.

Fig. 4: Idaho no. 3. 0.5× nat. size.

Badly preserved parts of two volutions of a tooth-spiral, possibly the second and the third.

Helicoprion sp. indt.

Fig. 3: Idaho no. 6. 0.7× nat. size.

All specimens photographed dry.



Fig. 1







Fig. 2



Fig. 4

PLATE NV Helicoprion ergasaminon n. sp. 1daho no. 5. 0.6× nat. size.

Photographed in Xylene.

cale, cart :: calcifications from the cartilage of the lower jaw. cale, cart, sym.: calcifications from the symphyseal crista. c. can.: the central canal of the compound root. Some of the branches for the nutritive vessels diverging from the main canal into the tooth-crowns can be seen. o. v. c.: openings for vascular canals. ro. gr.: the groove on the ventral side of the compound root. y. p. t. sp.: the last formed part of the compound root.



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PART I:

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BY

FR. J. MATHIESEN



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PALAEOBOTANICAL INVESTIGATIONS INTO SOME CORMOPHYTIC MACROFOSSILS FROM THE NEOGENE TERTIARY LIGNITES OF CENTRAL JUTLAND

PART I:

INTRODUCTION AND PTERIDOPHYTES

BY

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Synopsis

The discovery of a fossiliferous layer of Neogene-Tertiary age, rich in plant remains, at Moselund (Denmark, Central Jutland) in the year 1916 gave rise to intensified geological investigations of the Danish lignite beds, made accessible during the great brown-coal mining campaign in the years 1917–20. The quarrying favoured an inspection of the layers of clayey soil (hardened "Gyttja"), which, accompanying the coal, according to previous experiences was to be regarded as one of the main localities for determinable plant remains of this geological period.

Besides the find at Moselund, the investigations at Silkeborg Vesterskov and the Fasterholt quarries proved particularly successful; the fossils procured: leaves, twigs, cones, and seeds were in part so well preserved as to make an anatomical study possible; animal remains were scarce.

Gymnospermous wood was very common in the coal layers, sometimes remains of the trees were found on the stumps.

This memoir, the first of the series of papers giving the results of our investigations, contains – besides a geological survey – a systematic account of the ferns and fern allies discovered. An anatomical study of a *Salvinia* from Moselund has yielded details for a closer comparison with the recent species.

The floristic character of the fossils, found in the layers at Moselund, Silkeborg Vesterskov, Fasterholt, and Salten, points towards an "Aquitanian" age, approaching the biological aspect of the lignitic floras of the Upper Oligocene and Lower Miocene from Eastern Central Europe (Hungary, Austria, Bohemia, Switzerland, Germany and Poland) and also exhibiting relations to the flora of the lignites of Bovey-Tracey (Kent).

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Preface

The main material on which this paper is based was procured during the lignite Γ \blacksquare mining campaign in the years 1917–1920 by J. P. J. Ravn, Keeper of the palaeontological Department of the Mineralogical and Geological Museum of the University, V. Milthers, State Geologist, Thorkil Bjerring Pedersen, M. Sc. (all deceased), and the author. It is deposited in the collections of the University and of Danmarks Geologiske Undersøgelse (D.G.U.) and has liberally been placed at my disposal. In the following years supplementary material has become available through excavations made by Professor A. Mentz (†) and Preparator K. Skou (1924 and 1937, respectively). All the material at hand was collected in Jutland, partly from the Tertiary clay (hardened "gyttja") at Moselund and partly from layers of an identical nature accompanying coal-producing layers in Silkeborg Vesterskov and the quarries at Fasterholt (Skibild), and also, though to a somewhat lesser degree, from the coal itself in the quarries west of the Silkeborg-Herning area, mainly near Troldhede, from the Torvig quarry as well as from the state quarry in this locality. The majority of the samples of fossil wood suitable for anatomical investigation, originate from the last-named quarries.

From our Palaeogene Tertiary (the Diatomite on the islands of Mors and Fur in the Limfjord, as well as from the lower Oligocene) no finds of fossil higher plants, save for some pollen, have been described since the publication of N. HARTZ 1909.

The material from the coal layers and accompanying clay is, even if the geological age in some details is still open to discussion, to be referred to the Neogene Tertiary. The floras from the Silkeborg-Herning area are of a rather uniform type, and will be dealt with in the present paper as a palaeontological unit. Previous to the floristical account is given, as a general introduction, a description of the stratigraphy of the fossiliferous layers investigated, with details of the profiles as they appeared in 1920.

The number of the determinable specimens of the Tertiary flora of Denmark has grown considerably as a result of our collections. Besides such ubiquitous types as *Taxodium*, *Glyptostrobus* and *Sequoia*, to mention a few Gymnosperms, we have succeeded in demonstrating the presence of many types (Gymnosperms as well as Ferns and Angiosperms) of a more restricted vertical distribution. In the last section of this paper the age of the floras will be discussed, mainly by comparison with some Neogene Tertiary floras from Europe which through the presence of animal remains

1*

in the plant bearing layer, or-more commonly-by the character of the bordering strata, have been dated rather exactly.

In recent years Mr. P. Ingwersen from the staff of D.G.U. has started an investigation of the pollen types occurring in the lignite. The first very promising results of this work agree with my determinations of macrofossils from the brown-coal "gyttja", but have also shown the existence of types not present in my material.

I started upon these researches, which I regarded as an extension of my former studies in the systematic anatomy of higher plants, mainly because of the interest the late Lecturer in Palaeontology at the University, J.P.J. Ravn, and the Director of Danmarks Geologiske Undersøgelse at that time, Dr. V. Madsen, took in the question of our Tertiary floras. The state of preservation of the material was an invitation to extend the research on anatomical details, in order to supplement determinations based on macroscopic inspection. This method is now in common use and quite indispensable, especially regarding the leaves of Dicotyledons.

In 1921 the Royal Danish Academy of Sciences and Letters proposed as a subject for a prize dissertation: "An investigation of the fossils of higher plants occurring in the Danish Tertiary strata". This gave me the opportunity of preparing a provisional account of my studies, which the Academy considered worthy of the prize. The final publication had to be postponed until now, owing to the pressure of my duties whilst at the Royal School of Pharmacy, Copenhagen. This paper contains the information given in my prize dissertation, but is completed by the results obtained by studying the new supplies of material, and in a good many cases extended by inspection of the literature of recent years.

In the Dansk Geologisk Forening and the Dansk Botanisk Forening I had the opportunity of giving a general review of my studies during the spring session of 1922.

As for the work in the field, Professor A. Mentz and the State Geologists V. Milthers and Dr. V. Nordmann showed the kindest interest, and the local knowledge of Mr. Milthers, in particular, proved invaluable. Mr. K. Skou has been good enough to hand his collections from the Moselund locality over to me for investigation. The Chief Inspector of the Silkeborg forest district, Mr. N. Bojesen, as well as the District Superintendent at the State Railways, Mr. M. J. C. T. Lysholm, Skanderborg, showed their interest in my work by arranging for assistance with excavating. I have very pleasant memories of my stay in the friendly home of Mr. P. C. Christensen, Engesvang, during the work at Moselund. Finally the Carlsberg Foundation awarded me a grant for the completion of this paper.

Danmarks Geologiske Undersøgelse has permitted the completion of field work, and I have had en opportunity of discussing stratigraphical details with the former Director, Dr. H. Ødum, as well as with the staff of D.G.U. This institution has also borne the expense of a rather deep boring at Moselund. Professor A. Rosenkrantz has in many questions of a general geological nature rendered me a most valuable help.

The Botanical Museum and Botanical Garden of the University as well as the Forest Department and the Arboreta of the Royal Veterinary and Agricultural School,

Nr. 6

Copenhagen, has kindly placed material for comparison at my disposal. I am indebted to the Royal Society for Gardening for material of roots and knees of Taxodium. The readiness of our University Libraries in procuring papers not at hand here, e.g. from Kgl. Vetenskaps Acad. in Stockholm, has in many ways been extremely useful. The Mineralogical and Geological Museum as well as the Royal School of Pharmacy, Copenhagen, have kindly placed working facilities at my disposal.

My thanks are due to all these institutions and their staffs for their efforts in making it possible to finish this memoir—a work not without some difficulties, mainly those of procuring material for comparison. Works on these subjects are, after the publications of N. Hartz, rather scarce in our literature.

In rendering my thanks for all the courtesy received and keeping the deceased colleagues in a grateful memory, I would also express the hope that the results of my studies may not prove unworthy of our united efforts, as I, at an advanced age, offer these notes for the kind review of the public.

Dr. B.T. Walton has been good enough to revise my translation into English. My thanks are also due to Mr. P. Ingwersen from the staff of D.G.U. for his kind help in reading a proof.



Introduction

Description of the localities investigated

I. The fossiliferous stratum at Moselund railway station

In the summer of 1916 Thorkil Bjerring Pedersen, M. Sc., discovered a layer of yellowish clayey soil in the gravel pit belonging to the State Railways near the station of Moselund on the Silkeborg-Herning line. This soil proved rich in imprints of leaves and various other parts of plants. At a meeting of the Dansk Geologisk Forening the following winter the Keeper of the palaeontological Department of the University Museum, J. P. J. Ravn, gave an account of the find and exhibited a number of the fossils, the nature of which proved that they belonged to a flora of a Neogene Tertiary character.

Tertiary strata containing such an abundance of well preserved vegetable remains had hitherto been unknown in this country and so the find claimed the greatest interest. In the summer of 1917 an excursion was therefore arranged to the place in question by Mr. J. P. J. Ravn and the present writer in order to make a closer investigation of the locality and, if possible, to collect some more material.

The locality discovered by Mr. Thorkil Bjerring Pedersen is marked + in the map Fig. 1.

At a distance of 10 m from a steep slope about 2 m high that bounds the gravel pit to the south-east, a ochreous layer of the fossiliferous clayey soil came to the surface. This layer extended below the slope. The covering layer had been stripped off and the gravel digging stopped on reaching the clay. By digging a ditch at right angles from the edge of the clay towards the slope it was found that the line of demarcation at this point presumably must be the natural one, the layer tapering very much towards the edge, whereas, only one metre further in, it attained a thickness of about 1 m and retained this thickness for the following 10 m. It was bedded on medium grained, ochreous sand.

We were told by Mr. Lysholm, the District Superintendent of the line at that time, that extensive amounts of clay of a similar kind had been found close to the railway during the building of the line. The rising ground to the north-east of the gravel pit in question and consequently on the other side of the present railway line was cleared away during the building, its gravel furnishing good material for the construction of the railway track. The stripping of this low hill was continued until



Fig. 1. Part of the topographical map M 2409, Kragelund, (Copyright Dansk Geodætisk Institut) including the area at Moselund. Scale 1:20 000. Altitudes in metres.

a level had been reached at which outcrops of the clay mentioned above—which was useless for building purposes—occurred in several places.

North-east of the line, on the almost level site of the formerly rising ground, a small plantation was laid out the circumference of which roughly indicates that of the hill (Fig. 2. A magnified copy of part of an older edition of the map Fig. 1). Where the clay approached the surface, foliiferous trees were planted (alder and ash), but where the substratum of gravel and sand reached some depth, Conifers (Mountain Pine and Silver Fir) were preferred. Three groups of foliiferous trees are indicated on the map Fig. 2. A fourth is not noted in this figure, although, in 1917, it was by far the most important in the plantation. It began just opposite the high south-eastern rim of the present gravel pit and extended towards the south-east for a distance of about 50 m and with a similar width (compare Fig. 2). The recording of the site of the last mentioned area is of importance, as the best preserved fossils of our material originate from this place.

In the autumn of the same year (1917) the locality was again visited by Mr. J. P. J. Ravn, this time accompanied by Mr. V. Milthers. Prior to their visit the Danmarks Geologiske Undersøgelse had caused diggings to be made in the layer. Amongst others, at the suggestion of Mr. V. Milthers, two excavations, each 1.1 m wide, had been sunk in the midst of the largest group of the foliiferous trees. One excavation was dug 20 m north-east to the railway line, the other further in (10 m) to the northeast of the first one. Both excavations were carried through the clay which was over-



Fig. 2. Part of the map Fig. 1. Scale $1:10\ 000$. The + in the eastern corner of the gravel pit marks the protruding margin of the fossiliferous layer, discovered 1917 by Th. Bjerring Pedersen. I, II and III indicate the situation of the wells east of the railway line. Altitudes given in Danish feet (one foot = about 31.4 cm).

lain by about 75 cm of gravel. The first excavation was 2.5 m, the other 3.8 m deep. The layer of clay thus increases considerably in thickness towards the north-east. In both excavations it was bedded on the coarse, ochreous sand, familiar from the excavation in the gravel pit. The situation of the excavations is marked on the map Fig. 2 (I and II); they are to be found near the highest point of the plantation area (83 m in Fig. 1; 263 feet in Fig. 2. One Danish foot is equivalent to 0.314 m).

In the excavation no. I the whole of the clay from top to bottom was of an

ochreous yellow colour, but considerably darker than the clay of the gravel pit. In excavation no. II on the other hand, with the exception of the first 50 cm at the top, the clay was pitch-black as long as it was damp; on drying it turned from a lighter to a darker grey. It was of a far harder and firmer consistence and, as it was transversed by cracks at right angles to the direction of the layer, it proved rather easy to excavate the material in large unbroken pieces, which could be split up very regularly, almost like schist.

The clay brought up from the excavations proved rich in fossils (twigs, leaves, cones and seeds) evenly distributed troughout the layer, but while the ochreous clay of excavation no. I mainly offered imprints of the various plant remains, the black clay of excavation no. II yielded fossils far better preserved; the vegetable substance being only slightly carbonised. The transition from the brownish clay at the top, to the underlaying black clay of excavation no. II, took place by imperceptible degrees and, altogether, the brown and yellow clay is to be regarded as transformation products of the black, due to oxidizing and decomposing agencies.

Some packing cases containing blocks of clay from excavation no. II were, by the care of Mr. Milthers, sent to the museum and a number of excellent fossils was in this way obtained.

In 1919, owing to a grant-in-aid from the Mineralogical and Geological Museum of the University, I was able to spend a fortnight at Moselund. Excavation no. I was found dry, excavation no. II was unfortunately filled with water up to the height of about 1 m. After it had been emptied the water poured in again so briskly that in a quarter of an hour it was too full of water to work in. Through the obliging assistance of Mr. Lysholm the necessary help was, however, obtained, and some cubic metres of the black clay were brought up for examination. From excavation no. I a similar quantity was secured. The material was split up in as thin and regular layers as possible. After drying in the air for a few days, it split very easily and presented in many cases rather perfect, even cleavage surfaces.

The number of species represented in the flora was considerably increased by this inspection, and as the result of this and former investigations abundant material was obtained.

The black clay was in some places, notably in the lower parts of this layer, rich in mica scales. Here and there the cleavage surfaces were quite covered with mica intermixed with vegetable detritus.

What makes the black clay from excavation no. II of special interest is the fact that the tissue of the plant remains, though carbonized, is on the whole well preserved. In several instances it has been possible to obtain anatomical preparations of epidermis, even of the leaves of foliiferous trees, and in one instance also transverse sections. Cones, seeds and twigs were obtained perfectly fitted for anatomical investigation.

Regarding remains of animals I have only found a wing of a dragon-fly, determined by the late Dr. K. Henriksen as belonging to a hitherto unknown species: Oplonaeschna staurophlebioides (A new Tertiary Dragon Fly O. st. n. sp. from Denmark. Medd. fra Dansk Geologisk Forening. Bd. 6. Nr. 9. 1922).

To preserve the excavations for future investigation frames of boards were placed round them at their top edges to prevent loose gravel, overlying the clay, from sliding down and filling them. They were also covered with sleepers.

Little is known about the horizontal extension of the clay outside the plantation as it was not at that time possible to make borings. According to Mr. Lysholm's statement it must be assumed to extend over a larger part of the area along the railway and it is certain that the clay in the gravel pit and that of the excavations forms a continuous layer. The clay increases in thickness towards the north-east, and I came across it again on digging through the gravel about 20 m to the north-east from excavation no. II. Also a third excavation (III), dug by Mr. K. Skou (1937) about 200 m to the north-west of excavation no. I and II, showed the same thickness of the fossiliferous layer as was found in those excavations. Therefore it is to be supposed, that the area covered by the plantation alone is so considerable as to render it improbable that the clay could represent a loose flake carried by the ice from its original bed. It must be assumed to have been originally deposited in its present place.

A statement made by the foreman of the line at the Moselund station would seem to indicate that the clay in question has a still greater extension. An old workman, who was employed in the diggings for the foundation of the water-tower at the station, thought that he recognized in the hard black clay from excavation no. II the "coaly-looking" clay that he remembered coming across on that occasion.

Investigations of the ground sloping towards Bølling bog and on the steep slopes on the opposite side of the bog at Bjeldskov did not give any results.

As regards the nature of the clay it seems beyond doubt that it was deposited as a mud ("gyttja") on the bottom of a freshwater lake and later became hardened and shale-like. It looks exactly like layers found both in this country and elsewhere associated with lignite, either interspersed between coal producing layers or forming the base of the series (HARTZ 1909, p. 71). As mentioned above, gravel overlies the clay, and it is thus impossible to determine how much has disappeared by erosion. Most probably the clay once formed part of a bottom layer in a basin of lignite, and the less resistant, overlying coal succumbed to erosion.

A boring reaching a depth of about 45 m was sunk in 1960 by Danmarks Geologiske Undersøgelse, mainly in the hope of finding layers of marine origin below the clay. Such layers were not found; the underlying stratum proved to consist of yellowish, medium-grained sand, alternating with thin layers of coal, containing fossil wood. The sand is of the same nature as that directly underlying the clay in the excavations in the plantation.

II. The fossiliferous layers of the lignite series

In 1917–1918, when the exploitation of our brown-coals was extended to a hitherto unknown degree owing to the shortage of fuel caused by the war, the possibility

of finding determinable macrofossils greatly increased. With this object in view and at the request of Danmarks Geologiske Undersøgelse I spent about three weeks in the mining district in Jutland in the summer of 1919.

According to experience gained elsewhere it could not be expected to find well preserved plant remains, with the exception of fossil wood, in the coal itself, whereas such remains are frequent in the associated layers of clay and sand. Other Things being equal, the fossils in question are of course the better preserved the finer the material of the surrounding matrix. As pointed out by HARTZ 1909, the comparatively few macrofossils of plants known at that time from our Neogene Tertiary are mainly found in such layers, and it would be, as a first step, convenient to look for the existence of the fine, dense and shale-like clay (hardened "gyttja") in the sections presented in the quarries. Therefore I visited all the localities where lignite had been quarried to any considerable extent during the previous years.

The places were examined in the following order:

1. The district of Troldhede with the large State quarry and the Torvig quarry at Vorgod Å; The Sk(j)ærbæk quarry; the quarry at Torsk(j)eld Bjerg and the quarry at Pøl Mose on the south side of Vonds Å.

2. The district of Fasterholt with the State quarry at Skibildgård (indicated as the State quarry, Fasterholt, in the description of the fossils); the private quarries a little further west near the briquette factory; the three small private quarries to the east of Skibild at Holtum Å, named "Nissen Jøkers quarry", "Harildgårds quarry", both south of the river, and "Skibild eastern quarry" north of the Holtum Å (Fig. 3).

3. The more remote localities at Sandfeldgård, well known from Hartz's description.

4. The district in the neighbourhood of Silkeborg; viz. the quarries at Gammel Ry and those in Silkeborg Sønder- and Vesterskov. Finally some days were spent in investigation of the localities at Bryrup, where brown-coal had been quarried at Vorret and Lystrupsminde. Also an excursion was made to the Salten profile.

As a result of this reconnaissance I decided that work had to be concentrated on the State quarry at Fasterholt and the locality in Silkeborg Vesterskov, these being the only places where clay contained macrofossils of plants in the desirable state of preservation. It was further ascertained that the State quarry and the Torvig quarry at Troldhede deserved attention owing to the admirably well preserved fossil wood occurring there.

Of the time remaining at my disposal I spent another ten days in the State quarry at Fasterholt, five days in the locality in Silkeborg Vesterskov and two days at Troldhede. The results of these investigations may be considered satisfactory as more well preserved specimens of leaves, twigs, cones and seeds were collected and my collections of fossil wood were considerably augmented.

In 1920 I again made an excursion to the mining district, my chief object being to continue the examination of the locality in Silkeborg Vesterskov. I could now put



Fig. 3. Part of the topographical map M 2707, Brande, (Copyright Dansk Geodætisk Institut) showing the position of the quarries at Skibild and along the Holtum Å, marked \bigotimes and \times . Scale 1:20 000. Altitudes given in Danish feet (one foot = about 31.4 cm).

in twelve days at the place, and owing to the kind assistance of Mr. N. Bojesen, the Chief Inspector of the Silkeborg forest district, in obtaining the necessary help with excavation, I obtained a very satisfactory result.

When the work in this place was finished, I made short visits to Fasterholt and Troldhede. In the former locality work in the State quarry had been stopped, and further investigation was consequently not possible. From the quarries at Troldhede a number of fine specimens of wood were again obtained.

Stratigraphical details of the localities visited are given in the following notes.

A. Silkeborg Vesterskov and the other finds in the neighbourhood of Silkeborg.

In the steep slope bordering on the north the bogland which, under the name of Jensk(j)ær, forms a continuation of the Thorsø depression to the west, is situated the

lignite layer first known from C. Ring's excavation in 1861 (HARTZ 1909, p. 22—in the map l.c. fig. 10, p. 51 marked +).

During the Great War 1914–1918 attempts were made to utilize the coal. The gravel and sandy micaceous clay overlying the producing layer were removed and shot down the slope, thus uncovering the lignite for exploitation. When mining stopped in 1918 a semicircular incision with a diameter of about 30 m had been produced; the bottom of which was level and almost horizontal. At the back Ring's old adit could be seen. Its supporting props had almost rotted away, but the ceiling and walls of the gallery had apparently not suffered much, thanks to the considerable stiffness of the strata. A spring had made its way out through the passage.

At the back and on the right hand side of the excavation the overlying moraine gravel had already fallen in to a great extent and quite hidden the lignite layer. However, towards the edge on the left hand side, where the slope was more gradual, and where some beech stumps with their long horizontally extending roots had formed a protecting cover, a profile could be dug out showing a layer of coal about 70 cm thick in which flattened trunks of fossil wood were preserved. Under the coal bed appeared a layer of almost 1 m thickness of a fine and stiff clay, pitch-black in its humid condition and chocolate-brown after drying. The clay was riddled with cracks across the horizontal direction of the laver and for that reason was easily broken out in blocks. The top part of it proved extremely hard, the middle part was softer and richer in mica with coarse mica scales on the cleavage surfaces, whilst the lowest part was of a nature similar to that of the top. The clay was resting on micaceous sand. It abounded in plant remains (leaves, twigs, cones and seeds) for the most part well preserved. Unfortunately it does not split up so regularly in the direction of the layer as does that from Moselund, and consequently it was difficult to extract the larger leaves without damaging them. Some of the cleavage surfaces prove to be almost covered with twigs of *Taxodium*. On fractures at right angles to the layer yellow retinite stripes frequently appear. They indicate the presence of Taxodium cone scales; the fossil Taxodium, like the recent one, encloses resiniferous cysts in the scales. Fruit stones of Nyssa and seeds of Taxodium are frequent; also some curious fossils, referred to the larval tubes of a *Phryganida* species, could be demonstrated. The clay abounded in pyrite, and in some cases small branches of Gymnosperms were found completely replaced by this mineral.

Next to that at Moselund the clay in Silkeborg Vesterskov, owing to its abundance in fossils and its accessibility, is at present the most important place known for the study of our Neogene Tertiary flora.

The layers on the south side of Jensk(j)ær (in the map on pag. 51 of N. HARTZ' paper also marked by a +), in the Gjedsø Skov and at Gjedsø Savmølle, were not accessible during my stay. Most probably they are to be considered as having been formed in connection with those in Silkeborg Vesterskov in order afterwards to be separated from them by the excavation of the depression of Jensk(j)ær, formed during the Ice Age.

Nr. 6

Among the other lignite occurrences in the neighbourhood of Silkeborg, Ring's second locality in Silkeborg Sønderskov at Slåen Sø, might be expected to yield some interesting fossils. Here N. Hartz found a cone referred to *Pinus Laricio Thomasiana* O. Heer and seeds of *Hydrocharis tertiaria* N. Hartz, in a bed of clay under the coal. An excavation, made shortly before my visit to the place, was found to be filled almost entirely with gravel, and without greater means than were at my disposal it would be useless to begin investigations here. However, as the layer in Sønderskov could evidently yield other kinds of fossils than those from Vesterskov, it would be highly desirable if it could be subjected to a closer examination in the future.

In Ry Sønderskov, to the west of Gammel Ry, on the outskirts of the forest south of Knasbjerg, lignite had been quarried to some slight extent in 1917. In 1919 the quarry had almost entirely fallen in, and only from the bottom of a small pool in the middle of it it was possible to obtain samples of coal. They proved to be of a rather peculiar nature, differing from those in the other quarries by their large content of coarse mineral constituents (sand, mica) and by the much less advanced transformation of the plant remains inclosed. On cleavage surfaces were found cones of *Glyptostrobus*, seeds of *Sequoia* and twigs of *Taxodium*.

In the profile at Salten (HARTZ 1909, p. 49, figs. 8 and 9) unmethodical digging and subsequent landslips had made the lignite bed inaccessible. In the layer of clay overlying the coal N. Hartz found badly preserved parts of leaves of Dicotyledones and pinnulae of a Fern, determined as *Pteris parschlugiana* Unger, seeds of *Sequoia* and some carpoliths, together with abundant fossil wood. The only result of my visit here was some samples of fossil wood that lay scattered about. One of the samples proved to be of some interest representing the type of fossil wood designated as *Taxoxylon*.

In the valley of the Lystrup Å at Lystrupsminde brown-coal was extensively quarried during 1917–1918. The producing bed was found on the eastern side of the valley about half way up the steep slope which bounds the river there. Work was stopped in 1919, and the sides had already been greatly affected by slips. The coal layer was about 1 m thick, it was bedded between layers of mica-containing clay and sand, but no macrofossils, except fossil wood, were preserved in such a state that further work was likely to be of any use.

Some of the samples of fossil wood showed anatomical details fairly well and yielded material of much interest.

B. The State quarries at Fasterholt (Skibild) and the other lignite localities in the district of Brande.

About 1.4 km south of Fasterholt station, where a road from Vester Harild to Skibild cuts the railway line from Herning to Brande, and from there southward to Skibildgård (fig. 3), the State began very extensive quarrying in 1917. The ground in this area very much favoured the exploitation of the coal beds, as only comparatively thin layers of gravel were superposed and drainage conditions were favourable, since the ground sloped towards the Holtum Å. Furthermore the beds had considerable horizontal extent.

Two quarries were made, one on either side of, and close to, the railway line. In 1919 the work had resulted in the excavation of a pit east of the line about 200 m in length, 100 m wide and extending to the south almost as far as Skibildgård.

Work in the eastern quarry had been stopped the previous year and its sides had caved in. In the quarry on the western side of the railway some work was still carried on in 1919. The excavation had there attained a length to the south of about 300 m, its breadth varied somewhat (50–100 m), the depth in the eastern half was about 6 m, in the western part only about 4 m.

In the last-mentioned quarry the whole of the western side appeared as an almost clean-cut profile; the two coal beds in the cut running almost parallel and horizontal. Measurements near the middle of the pit showed a sequence of strata as follows:

Gravel the lower 10 cm of which were mixed with particles of coal		
Uppermost coal bed, free from fossil wood, of which the upper 60 cm were		
of a loose, earthy consistence, designated as A-coals	145 cm	
Fine, sharp quartz-sand, with brown stripes of coal	7 cm	
Clay the lower 20 cm of which were fossiliferous	48 cm	
Fine, sharp quartz-sand	15 cm	
Lowermost coal bed, rich in fossil wood, designated as B-coals	80 cm	

390 cm

The bottom of the quarry in this place consisted of a layer of fine, mica-containing quartz-sand.

During the first period of quarrying an underlying layer of coal about 1.5 m in thickness was also exploited; this was designated as C-coals. As the digging proceeded from east to west, this layer was abandoned, and consequently the bottom of the western part of the quarry was higher by the amount of the thickness of the C-coals. At the time of my visit the bottom layer exhibited a profile in a north-south direction almost in the middle of the quarry. This showed that the C-coals were almost of the same vertical extent throughout the area.

The C-coals consisted partly of a substance closely corresponding to the "Brunkul-Gytje fra Sandfeldgård" described and figured by HARTZ 1909, p. 72. fig. 11. On the surface of the flakes there was a thin covering of fine, white micaceous sand and an irregular network of finer and coarser dark lines, no doubt due to cracks in the mass, filled with humus and without direct connection with organisms. The C-coals did not contain enough organic material to be profitable for fuel. The plant remains in them were only present as detritus. The C-coal layer was bedded on very

Nr. 6

fine, sharp, mica-containing sand, which presumably constitutes a deposit of some considerable vertical extent, as a boring with a drill 3 m in length did not reach the bottom of it.

The layers between the A- and B-coals varied slightly in individual thickness in different places of the cut, but their total magnitude was very nearly the same everywhere.

At the south end of the profile the Tertiary deposits had been worn away by erosion almost down to the B-coals. The layer of A-coal disappeared suddenly, the underlying clay had resisted erosion better and formed a southward pointed wedge. As the thickness of the gravel layer increased in the same ratio as the underlying Tertiary decreased, the surface remained almost parallel with the bottom of the pit.

The upper 20 cm of the clay above the B-coals consisted of a more or less fine debris, whilst the lower 28 cm cohered in blocks of various sizes, the clay being divided by cracks (as was also the clay at Moselund and Silkeborg Vesterskov). On the surface of the cracks it was black, whereas the interior of the blocks was of a dark chocolate brown. On drying the clay assumed a lighter or darker grey colour and split readily, though somewhat irregularly, in the horizontal direction of the layer. It contained some mica and abundant pyrits. In the lower part a good many fossils were found but the dicotyledonous leaves were mainly met with in fragments or as imprints.

As already mentioned the B-coals abounded in fossil wood. No stumps of trees could be demonstrated, and, so I was told, none had been found there. The trunks were always pressed flat and the early formed parts of the growth rings (the "spring-wood"), consisting of large and relatively thin-walled elements, folded and destroyed. A determination was consequently difficult, but most of the fossil wood is probably to be referred to *Taxodioxylon*. The trunks were often of considerable dimensions. According to the report of the foreman of the quarry a specimen had been dug up, shortly before my arrival in 1919, that measured 10 m in length and 2 m at its broadest part (i.e. measured along the greater axis of the strongly elliptical transverse section) which may correspond to a thickness of the trunk in an unaltered state of about 1.5 m.

In the private quarry somewhat further to the west (in the map fig. 3 marked \otimes) were also found two coal layers, the lower one with, the top one without fossil wood. They were separated by layers of quartz sand and clay and the entire sequence was of a magnitude similar to that in the State quarry. A certain hesitation on the part of the managers prevented more accurate examination. The clay contained plant remains in the same state of preservation as those found in the State quarry and belonging to the same species.

During my stay only very little of the fossiliferous layer of the private quarry was brought up, the work there consisting mainly in removing the cover of gravel and the upper coal layer over a rather extensive area, in order to lay open the layer of B-coals and thus to procure suitable material for the production of briquettes.

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The three smaller quarries along the Holtum Å valley (marked \times in the map fig. 3) were abandoned and for the most part already filled by landslips. Yet in the eastenmost quarry, on the south side of the river ("Nissen Jökers Brud") one wall remained almost intact. The profile showed the following sequence of strata:

In "Skibild østre Brud" in the bluff north of the river the northern wall showed the following sequence:

Gravel	200	cm
Fine and firm clay. About 1 m at the top of a light brown colour, the lower		
part black	225	cm
Coarse ochreous sand	60	cm
Earthy coal	50	cm
Mica-containing black clay	45	cm
Coal with fossil wood	50	cm
	630	cm

The coal was bedded on mica-containing clay and sand. In the ochreous sand above the upper coal layer were found a couple of flint boulders. None of the clay in these two quarries yielded determinable plant remains.

At Sandfeldgård lignite had been quarried in several places in the bank of the Skjern Å. HARTZ 1909, p. 32 gives a map of the district. The coal beds were, as appears from the borings of 1906, of a rather considerable extension.—They are now completely exhausted. According to the profiles measured and the report on the 30 borings, the sequence of the layers was, at least where the series was more completely developed, very much like that found at Fasterholt. Two producing coal beds, separated by a layer of clay, with a layer of sandy coal at the bottom, correspond to the A-, B- and C-coal layers at the locality formerly mentioned. The largest quarry was found a little to the north-west of the most easterly of the three places marked with a \times in the map cited. Work had been stopped in 1919 and water stood high in the pit, so that the bed of "gyttja" below the coal with its interesting matting of tiny roots (l.c. Fig. 3 and p. 72) was inaccessible. In the coal bed N. Hartz found the stump of a tree in a very perfect state of preservation.

Nr. 6

C. Brown-coal quarries in the Troldhede district.

Whereas at Fasterholt and Sandfeldgård the coal beds as a whole were lying rather near the surface, in the localities around Troldhede station they were covered by layers of gravel of a considerable thickness, which made their exploitation difficult, the mechanical facilities at that time not being so highly developed as subsequently.

In the State quarry the bottom lay much lower than the adjacent river Vorgod Å. This necessitated constant pumping to keep the pit free from water. At the time of my visit 1919 the work there, as well as in the Torvig quarry, had been stopped temporarily. The State quarry appeared in the landscape as a lake surrounded by sand slopes. The Torvig quarry too was for the most part under water, so stratigraphical details were not available.

The coals in these places were rich in fossil wood. On the slopes of both quarries I found numerous pieces scattered on the sand, partly in a very perfect state of preservation. I was told by Mr. V. Milthers, that stumps, standing on the root in these coal beds, were very commonly found, sometimes attaining such a height, that their tops rose above the level of the coal into the overlying layer of gravel.

The wood in such stumps was nearly always well preserved, the pressure perpendicular to the length of the trunk, so destructive to the more thin-walled springwood elements of the growth rings, having been avoided.

An examination of the coal heaps near the branch line from the quarries to Troldhede station on the Herning–Skjern railway line also furnished several good specimens of fossil wood.

On my second visit in 1920 the work in the Torvig quarry had been resumed. I then had an opportunity of seeing 8 basal parts of trees, about 3 m in height and 1-1.5 m in diameter, on the stump. The distance between them was varying from 5 to 8 m. The roots proper had quite disappeared, no doubt the rule in such cases, but the huge root bases indicated that the trees had grown on the same level and consequently belonged to a group of the same geological age. Lignite was also found below the stumps.

Five samples were taken from each of two of the stumps, viz. one from the root base, and one each from the centre and circumference of the trunk at two different heights. The object was to find possible variations in anatomical details of the wood in the various parts; such variations were found to be very slight. The wood of all the stumps examinated could be referred to *Cupressionoxylon sequoianum*, so that the group of trees was most probably composed of individuals of a *Sequoia*. For anatomical details of the fossil wood from Troldhede and elsewhere reference should be made to the systematical description of the flora. All the samples of wood gathered in our Neogene Tertiary originate from Gymnosperms.

The other, rather small quarries in this district (Sk(j)ærbæk, Føvdals Mose south of Bjørslev (Thorsk(j)eld Bjerg), Brunshøj- and Pøl Mose showed nothing of much interest. The coals in the two last-named quarries are rich in fossil wood, but it was always so much decayed and compressed that a closer examination of it was useless. In the coals from Brunshøj were found remains of small globular cones peculiar on account of yellow stripes of retinite, which the cone scales had left in the matrix.

From the above it will appear that it is by no means a hopeless undertaking to look for beds containing well-preserved and consequently determinable macrofossils of plants in our deposits of lignite. As already pointed out by HARTZ 1909 attention should especially be directed towards the accompanying beds of fine clay (hardened mud, "gyttja"), but the fossil wood bedded in the coals themselves should not be neglected. Groups of trees on the stump are particularly important finds, partly because their wood is generally in such perfect state of preservation and partly also because collective occurrences of them—similar to the stump layers in our bogs—would help in the understanding of the character of Tertiary forests.

The systematic description of determinable macrofossils from our Neogene Tertiary now follows. The first section which describes the Pteridophytes, will terminate this part of the paper. The second will be devoted to the Gymnosperms, enclosing the fossil wood, and the third and last part is planned to embrace the angiospermous remains, to be followed by a discussion of the geological age of the fossiliferous layers.

Most of the fossils described have been dealt with in a good many previous publications and their names are consequently cited in numerous papers. A reference to the first adequate diagnosis only is given, together with references to papers of more recent date.

It will be readily understood that in an exposition like this it has not always been possible to distinguish between that which has already been stated in the literature and hitherto unknown facts. Where information of some importance especially concerning details of structure was at hand, references are included in the text.

In many cases, particularly where only an imprint of the fossil in the matrix was available, a photographical reproduction proved unsatisfactory so it was necessary to have recourse to drawings. These were all executed by means of a camera lucida; the real size of the object will be evident from the information given in the text accompanying each figure.

The Flora of the fossileferous layers from Moselund and the lignite series I. Pteridophyta

Osmunda lignitum (Pecopteris lignitum C. Giebel) D. Stur.

An extensive list of the literature dealing with this characteristic Fern, together with a specification of synonyms, is given by P. FRIEDRICH 1883, p. 41.
From the layer of clay at Moselund we have numerous fragments of pinnules of *O. lignitum*, partly with well preserved leaf substance. A number of the finest specimens are shown in fig. 4, A–G, magnified twice.

O. lignitum is a rather variable type, mostly known from isolated pinnules. GIEBEL 1857, p. 303 has, out of 5 fragments, founded no less than 4 species: *Pecopteris leucopetrae, lignitum, angusta* and *crassinervis,* mainly to be distinguished by the shape of the marginal incisions and the somewhat different ramification of the tertiary veinules. The accompanying figures are not convincing and according to the more recent investigators HEER (1862, p. 1047. *Pecopteris lignitum*), as well as GARDNER and ETTINGSHAUSEN (1879–1886, p. 49 and 66) the species of C. GIEBEL are regarded as mere varieties. By the last-named authors the species, as already proposed by STUR 1870, is correctly referred to the recent genus Osmunda.

In the memoir of GARDNER and ETTINGSHAUSEN (vol. I, p. 50) the following, very extensive diagnosis of the pinnules is given: Osmunda fronde pinnata, pinnis elongatolinearibus, subcoriaceis, apice valde attenuatis et acuminatis, basi breviter petiolatis, margine profunde incisio-serratis rarius remote denticulatis vel basi undulatis; nervatione Pecopteridis verae, nervo primario basi valido prominente, subrecto, apicem versus attenuato, indiviso; nervis secundariis numerosis, angulis acutis egredientibus, plus minusve flexuosis sub apicibus loborum plerumque furcatis; nervis tertiariis inferioribus furcatis sub angulis minus acutis orientibus, rarius elongatis convergentiarcuatis, sinum attingentibus; nervis tertiariis superioribus sub angulis acutissimis orientibus, saepe simplicibus subcurvatis flexuosisve — —.

To this diagnosis may be added that the tertiary venation shows catadromy, i.e. the first tertiary vein proceeds from the outward side of the secondary. As can be seen from our figures, the starting point of the lowermost tertiary veinule has often been so much displaced in the proximal direction that it in fact issues from the primary vein of the pinnule. GARDNER and ETTINGSHAUSEN'S figures show similar peculiarities as is also the case with those of HEER.

As already mentioned STUR (1870) was the first to refer the species to the recent genus Osmunda. He compared it with the recent O. Presliana J. Sm. (= O. banksiaefolia (Presl). Kuhn). GARDNER and ETTINGSHAUSEN mention O. javanica Blume as the closest allied, now extant type. Yet the three still existing species of the first section of the genus Osmunda are closely related; HOOKER and BAKER even class them in the same species (Synopsis Filicum. 1874) and consequently retain the oldest specific name O. javanica Blume, while O. Vachelli and O. Presliana are noted as synonyms. L. DIELS in ENGLER und PRANTL 1902, p. 378 characterizes the genus Osmunda. Sect. I. Plenasium as follows: Bl. einfach gefiedert. Fiedern I höchstens gelappt. Aderung nach V. Pecopteridis. — O. javanica Blume is described as a large, rather robust Fern. The sterile pinnules are from 2–2.5 cm broad, linear-lanceolate, petiolate, the margin entire, crenate, serrate or slightly lobed, vide J. MILDE (1868, p. 21 — and Pl. VI, figs. 1–20). O. Presliana J. Sm. = O. banksiaefolia (Presl) Kuhn (CHRISTENSEN: Index Filicum I, p. 4. 1906) and O. Vachelli Hooker are smaller, the pinnules of the last-



Fig. 4. Osmunda lignitum (Giebel) D. Stur. Fragments of pinnules (Moselund) (\times 2).

named, a native of South China, are only 5–6 mm broad with entire margin. O. banksiaefolia is noted from China, South-east Asia, Ceylon, Malaysia, the Philippine Islands and spreads northward to Japan and Kamchatka. The secondary veins of the pinnules of O. banksiaefolia issue at more acute angles than is the case with the two other species and the margin is always serrulate to serrulate-lobate. The displacement of the lowermost tertiary veinule in the proximal direction of the primary vein, and so apparently issuing from this, proved to be a very common feature in material at hand from the Philippine Islands. So a very close agreement between O. lignitum and the recent O. banksiaefolia is beyond doubt. At least it is certain that a species of an Osmunda belonging to the section given, whose habitat is now exclusively limited to the Far East, was widespread in Europe in the Tertiary. It probably formed an important part of the vegetation here, as in the floras where it occurs its remains are often to be found in considerable numbers.

STUR (1870, p. 9) has described and figured an Osmunda of a related type, but differing in certain details which may be of some systematic value and so possiby should allow the constitution of a distinct species, i. e. the author's Osmunda Grutschreiberi. STUR has figured a very beautiful specimen in which some pinnules are found in connection with rachis. The pinnules are sessile and at the outer side of the base widened into a lobe. The type has only been found at Möttnig (Carinthia, the Sotzka-Series) and its specific value is doubted by GARDNER and ETTINGSHAUSEN.

When the leaves wither, the pinnules in the *Osmunda* genus separate from the rachis by a special detachment layer, leaving a regular scar. Fig. 4 E shows the basal part of a pinnule of *O. lignitum*. Judging from the shape of the end of the petiole it is evident that it has separated from the rachis in a similar way.

In the fossil the leaf substance must have been of the same firm, almost coriaceous consistence as is found in the recent *O. banksiaefolia*. The carbonized crust, into which it has been transformed, is unfortunately very brittle and inclined to crumble and scale off. By clearing with a diluted solution of sodium hypochlorite fairly good preparations of the leaf substance could be obtained; fig. 5, A and B, is drawn from such. A shows a portion of the epidermis of the upper side of a pinnule, B a portion of the under side, the latter exhibiting two stomata, while an oval aperture indicates the place of a third one, the guard cells here being dissolved. Stomata are only found on the underside; they are level with the surface.

For comparison the corresponding parts of epidermis of O. banksiaefolia are reproduced at the same magnification (fig. 5, C and D). As might be expected, the fossil also in this respect closely agrees with the recent species. The slighter thickness of the epidermal walls of the fossil may very well be due to a waste of substance caused by the maceration and clearing. Fig. 5 E shows a transverse section of the epidermis from the underside of a pinnule of O. banksiaefolia. The stomata appear to be of an uncomplicated type. The thin ridges terminating the guard cells at the aperture have disappeared in the preparation of the fossil, so that the unnaturally large apertures in the stomata figured (fig. 5 B) are not an original feature.

Fertile pinnules are not yet observed.



Fig. 5. A and B, Osmunda lignitum (Giebel) D. Stur. Epidermis of the upper- and underside of a pinnule. (Moselund). C-E, Osmunda banksiaefolia Presl (recent). C and D, epidermis of the upper- and underside of a pinnule, E, transverse section of epidermis (A-E × 300).

Finds of O. lignitum (Giebel) D. Stur are noted e.g. from the following localities:

Bournemouth (England)	Eocene.
Bovey Tracey (England) (U	Jpper) Oligocene.
Manosque (Switzerland) Aquitanian ((Lower Miocene).
Sotzka (Styria)	Aquitanian.
Zsilthal (Hungary)	Aquitanian.
Münzenberg, Stedten, Segengottesschacht, Runthal b. Weissenfels $\ .$.	(Thuringia,
Germany)	ligocene-Miocene.

Osmunda Heerii Gaudin

In the clay from the State quarry at Fasterholt was found an almost complete pinnule of a species of an *Osmunda* belonging to the section II. Eu-Osmunda Presl.



Fig. 6. A–C, Osmunda Heerii Gaudin. Pinnule and some fragments of pinnules (Fasterholt). D, pinnule of the recent O. regalis L. $(A-D \times 2)$.

The specimen is shown in Fig. 6A; in B and C are figured fragments of pinnules, probably of the same species. DIELS (ENGLER und PRANTL 1902, p. 380) characterizes the section Eu-Osmunda as follows: Blätter doppelt gefiedert. Aderung nach V. Neuropteridis oder V. Sphenopteridis.—The section comprises three species: O. lancea Thunberg, O. bipinnata Hooker and O. regalis L. In the first species the: Fiedern II (i. e. the pinnules of the second order) schmal-lanzettlich—while the other two species have: Fiedern II länglich oder oval.—O. bipinnata is described as having: Fiedern II sitzend—Adern in die Zähnchen auslaufend.—And O. regalis: Fiedern II kurz gestielt—Adern in die Buchten der Zähnchen auslaufend—However, it should be noted, in this connection, that according to MILDE (1868, p. 60), a var. acuminata of O. regalis exists, in which the margin of the pinnules is finely dentate and the veinules run into the denticles. The variety is found "In Wohlau and Bärhaus zugleich mit der Normalform—An ihren Standorten in Wohlau geht sie allmählich in die Stammform über" (1. c.). According to MILDE, O. regalis is an extremely variable species.

A close examination of the material at hand, combined with a study of the

figures given by ETTINGSHAUSEN (1865), showed that the pinnules of *O. regalis* are really so well defined, that a determination of them, even in the isolated condition, is possible. On withering the pinnules detach and it is rare to find specimens of the fossil where pinnules and secondary ribs are still connected. HEER (1859, vol. III, Pl. CXLIII, fig. 1) has figured such a one referred to *O. Heerii* Gaudin.

Fig. 6D shows a pinnule of *O. regalis* L., which resembles the pinnules of *O. Heerii*, and like fig. 6A is magnified twice. They agree so well, that the fossil must be assumed to originate from an *Osmunda* species at least closely related to the recent *O. regalis* L., if not identical with it. Several specimens of such pinnules from the European Tertiary have been figured and described.

The species O. Heerii was first constituted by GAUDIN et DE LA HARPE (1855, p. 423). It is found in the "Molasse" of Switzerland, and noted l.c. without description or figure. It is described by HEER (1859, vol. III, p. 155) as showing a: Fronde bipinnata, pinnulis sessilibus, alternis, oblongo-lanceolatis, basi rotundatis, plerumque inaequilaterales, apice obtusiusculis, subtilissime crenulatis, nervis secundariis dichotomis. Rivaz bei Lausanne—Schimper (1869, vol. I, p. 678) observes about this species: Ressemble à l'Osmunda regalis L., mais les pinnules sont beaucoup plus courtes, en proportion plus larges et moins rétrécies vers le haut.—But as HEER (l.c. p. 156) mentions having seen another specimen from the same locality in which the pinnules were narrower and more elongated, the difference pointed out can hardly be of much significance.

O. schemnitziensis (J. v. РЕТТКО) has been described and figured by STUR (1867, p. 136, Pl. III, fig. 1–3). The name of J. v. РЕТТКО, given in brackets, is according to UNGER (1854, p. 137), referring to an admirably preserved rhizome, discovered in the Tertiary "Süsswasserquarze von Ilia" in Hungary and formerly described by v. РЕТТКО as Asterochlaena schemnicensis. UNGER referred it to Osmunda (Osmundites) and by D. Stur brought in relation to some pinnules found in the same locality. Some rhizones probably appartaining to an Osmunda sp. are figured by Unger (Salzhausen, Austria) (1864), and fossils of the same type are also mentioned from Bovey Tracey (Kent, England).—The Asterochlaena (Osmundites) may, according to the anatomy, which is very exactly figured by UNGER, appertain to an osmundaceous Fern, but it is certainly differing from the extant Osmunda sp. by the development of numerous adventitious roots, very conspicour in the transverse section, and taking their origin as well from the centre as from the outer side of the stele.

About the O. polybotrya (Brongniart) Schimper (fertile pinnules), this last author notes (1869, p. 679): Le *Filicites polybotrya* Brongniart a tous les charactères d'un Osmunda, et paraît même être assez voisine de l'Osmunda Heerii. The specimen is also recorded by SAPORTA (1865, p. 38).

Some intact sterile pinnules of an Osmunda are figured Pl. I, fig. 1 in the memoir of GAUDIN and STROZZI (1862, p. 9, Pl. I, figs. 1–4). These fossils agree very well with O. regalis and are named O. Strozzi by the authors who accompany their description with the following note: Cette espèce ressemble beaucoup à l'O. regia L.; elle paraît en differer par ses pinnules plus larges et toutes dépourvues d'ailerons à la base; ces pinnules sont ègalement plus larges et plus longues que celles de l'*O. Heerii* — Age: Pliocene, Northern Italy.

Some pinnules from the Danian-Paleocene layer of Atanikerdluk (W. Greenland, Nûgssuaq Peninsula) are referred by HEER (1868, p. 88, Pl. I, figs. 6–11, Pl. II, fig. 15b) to *O. Heerii* Gaudin. The determination may be correct.

SAPORTA and MARION (1873, Pl. I, fig. 2) describe a small fragment of a pinnule as *O. eocenica*. The specimen is a rather problematical one, having a finely denticulated margin and showing a venation which is not at all convincing. Age: Eocene.

Whether there is actually any reason to distinguish the European and arctic fossil species (except *O. eocenica*) from each other and from the recent *O. regalis*, seems rather doubtful. But bearing in mind the extreme range of variation of *O. regalis*, and as our knowledge of the fossils of this type is almost exclusively based upon isolated pinnules, it is at present hardly possible to solve this question.

That O. regalis probably represents a very ancient type is not only apparent from the fossil remains mentioned but also from its remarkable geographical distribution. Quoting L. Diels it is: eine sehr verbreitete Art; in verschiedenen Formen durch die borealen Länder Eurasiens, Indien und Ostasien (besonders in den Gebirgen), das atlantische Nordamerika, die Gebirge der Antillen und Südamerikas bis Uruguay, Ostafrika bis zum Cap, Angola, das madagassische Gebiet. Doch ist das Areal durch weite Lücken stark zerklüftet——.

Finds of O. Heerii Gaudin are registered from the following localities:

Atanikerdluk (W. Greenland)	Paleocene.
Rivaz by Lausanne A	Aquitanian (Lower Miocene).
Wiener and ungarisches Becken	Miocene, Pliocene.
Northern Italy	Pliocene.

Lygodium Gaudini O. Heer

In the layer of clay at Moselund were found two small fragments of fern leaves, the nearest living analogue of which must be sought for in the recent genus *Lygodium*.

Sterile leaf segments referred to Lygodium have previously been detected in Tertiary deposits in Europe and North America. In the Eocene and Lower Oligocene L. Kaulfussii Heer is noted from England and Germany. This species is distinguished by its rather large, regularly dissected, palmate segments with rather broad lobes and repeatedly furcated veins. From the "Lower Molasse" of Switzerland, HEER has described and figured four Lygodium species: L. Gaudini, L. acutangulum, L. Laharpii and L. achrostichoides (1855, pp. 41–43, Pl. XIII, figs. 1–15–1859, p. 155, Pl. CXVII, fig. 25 b). L. Gaudini is described as having palmate, 3–4 lobed secondary segments



Fig. 7. A-D, Pteris sp., probably Pt. parschlugiana Fr. Unger. Fragments of pinnules (Fasterholt). E and F, Lygodium Gaudini O. Heer. Fragments of leaf sections (Moselund) (A-F × 2).

of sterile leaves, the lobes of which are 6-8 cm long, 3-6 mm broad, with entire margin. In the figures the venation is only indicated, it appears rather open, as is also the case in the leaves of the three other species. These differ only slightly from *L. Gaudini*, but the figured segments are smaller with partly quite short lobes which are fewer in number.

As for *L. acutangulum*, the specimen figured as Taf. CXVII. Fig. 25 b shows the venation particularly distinct and has thus allowed a correct reproduction of the veinlets. They appear here more close set than in the other figures cited and may represent the typical feature; it agrees closely with our fossils, which also show an

 $\mathbf{28}$

entire margin. The two fragments, reproduced in our fig. 7, E and F, probably represent parts of two-lobed segments.

GARDNER and ETTINGSHAUSEN (1879, p. 48) as well as FRIEDRICH (1883, p. 81) are inclined to unite the four species of HEER under the name of *Lygodium Gaudini*, and so am I. In some recent *Lygodia* a variation of the secondary leaf segments similar to that which has served HEER in establishing his four species, is met with even in the same specimen.

The living Lygodium species have creeping rhizomes from which proceed leaves with a slender rachis with apical growth and which finally attains a considerable length. In section I. of the subgenus Palmatae the sterile leaf segments of the second order show a repeatedly dichotomous venation; mostly they are pedate with lobes of various length and width. In subsection I.B (ENGLER und PRANTL 1902, L. DIELS p. 366) where the segments are almost sessile, is included L. circinnatum (Burm.) Sw., which HEER has regarded as a living analogue of L. Gaudini. Its area of distribution is stated to be: Ceylon, Southeast Asia, Southern China, Malaysia and New Guinea. FRIEDRICH (l.c.) gives expression to some hesitation in respect of its correlation with the fossil. A close examination of the very complete collection of Lygodium in the Botanical Museum of the University, made it seem probable that a living species completely agreeing with the fossil is not really to be found. L. circin*natum* may be an allied type, but the range of variation in shape and size of the secondary leaf segments of the type constituting L. Gaudini is occasionally to be found also in other species. The segments of L. cubense, figured by ETTINGSHAUSEN (1865, Pl. 169, figs. 2 and 7) are very much like some of the specimens reproduced by HEER.

Lygodium Gaudini Heer has previously been noted from the plant-bearing beds at Rochette (near Lausanne), probably of Aquitanian age.

Goniopteris stiriaca (Fr. Unger) A. Braun

A list comprising the main literature of this fossil up to the year 1887 is given by STAUB (1887, p. 232). References to papers of a later date are to be found in the memoir of H. CZECZOTT (1959, part. 2, p. 15).

In the clay at Moselund fragments of pinnules that are to be referred to this Fern are found, but they are rather rare. Fig. 8, A and B, shows such fragments, magnified twice.

GARDNER and ETTINGSHAUSEN (1879–86, vol. I, p. 39) have given an ample diagnosis of the species as follows: *Goniopteris* fronde pinnata. Pinnis linearibus, prælongis, inferioribus grosse crenatis serratisve, superioribus argute serratis vel serrulatis; nervatione Goniopteridis Aspidii, nervo primario valido prominente, recto, nervis secundariis sub angulo $50-60^{\circ}$ orientibus, tenuibus subrectis vel paulo arcuatis, nervis tertiariis in pinnis inferioribus plerumque 6–7, in pinnis superioribus plerumque 4–5, cum vicinis conniventibus, angulis remoto curvatis, subparallelis, angulo acuto egredientibus. Soris rotundatis biseriatis— —.



Fig. 8. Goniopteris stiriaca (Fr. Unger) Alex. Braun. Fragments of pinnules (Moselund) (\times 2).

It is not uncommon to find specimens of this fossil Fern on which pinnules are still in connection with the rachis, thus giving an impression of the very considerable total size of the leaf. HEER has recorded such large fragments (1855, Pl. VIII, figs. 1–2); also other authors e.g. CZECZOTT (1959, Pl. V, fig. 1) and DOTZLER (1937, Pl. I, fig. 1) have had the opportunity of meeting such.

The size of the pinnules may also be considerable. Some dimensions are given by the authors cited. CZECZOTT notes: 79–110 mm length of pinnules on the right side of a rachis, 51 mm on the left side; width 22–24 and 14 mm (ditto); DOTZLER (1937, Pl. II, fig. 1) has figured a pinnule attaining a length of about 200 mm, being about 20 mm broad, but his photo Pl. I, fig. 1 shows pinnules of far more modest dimensions, i.e. 120×10 mm. CZECZOTT emphasizes the great range of variation as regards the marginal incisions: The lobes - - - are essentially subcircular but may taper into sharp points directed towards the apex of the segment (\mathfrak{d} : pinnule). The

Nr. 6

apical segments are almost lobeless but bear sharp teeth along the margin (Pl. V, fig. 2–p. 88 in the English translation accompanying the Polish text). Other details concerning the structure of the margin appear from the excellent photos of DOTZLER. In his Pl. I, fig. 2 the pinnules show at their basal part an entire or only slightly crenated border; the characteristic denticulation is first developed some cm.s from the base and fades out again in the apical part, here—as also noted by CZECZOTT—only represented by small teeth. Here and there a rounded lobe is found intermingled between the pointed ones, but the specimens figured in the photos cited clearly belong to the type with serrate or serrulate margin.

As appears from HEER's figures the rounded lobes may prevail in some specimens (1855, Pl. VII and VIII) which is also in accordance with the diagnosis cited and the notes of CZECZOTT. HEER states (l.c. p. 31): Die Zähne – – – bei den meisten Exemplaren sind sie scharf, bei einzelnen (so figs. 4 und 6) sehr scharf, bei anderen dagegen (figs. 3 und 7) stumpf, so dass die Fieder gekerbt wird – – Our material evidently belongs to the last type.

The arrangement of the veins of the secondary and tertiary order agrees with what is demanded in the diagnosis and what also is shown by the figures given by previous authors, so I have no hesitation in referring our fossil to *G. stiriaca*, so common in the Tertiary floras of Europe, especially those of Aquitanian age.

Fertile pinnules of *G. stiriaca* are met with and are figured e.g. by HEER (1859, Pl. CXLIII, figs. 7 and 8). The sori are placed in the middle of the tertiary veins of the pinnule, one sorus on each; consequently the secondary veins have a row of sori on either side. HEER has also succeeded in demonstrating sporangia and a group of these is figured as l.c. fig. 9, magnified about 50 times.

Some allied fossil species, probably of a somewhat doubtful specific rank, have been described and figured by HEER l.c.: Lastraea (Goniopteris) helvetica, oeningensis and dalmatica. They mainly differ from G. stiriaca and from one another by the shape of the marginal incisions, a character which is shown to be very variable (GARDNER and ETTINGSHAUSEN).

This fossil Fern has been referred to various living species. ZINCKEN (1867, p. 53) considers *Lastrae prolifera* Kaulfuss as being a related type and so does KRäusel (*Phegopteris prolifera* Mettenius). According to CHRISTENSEN (1906, p. 300) this species has to be named provisionally *Dryopteris vivipara* (Raddi), and so as to point out that it belongs to the group of *Dryopteris* characterized by "Venatio Goniopteridis", the prefix *Go*- (in brackets) may be added. The genus name *Goniopteris* may be retained provisionally for the fossil.

According to CZECZOTT (l.c.) the material from Turow (Poland) has yielded remains of about 1 cm thick, branched creeping rhizomes, evidently belonging to a Fern, which may be referred to *G. stiriaca*, the only known and very common Fern from this locality. The rhizomes of some *Dryopteris* (*Goniopteris*) species are in fact of this type (ENGLER und PRANTL 1902, L. DIELS p. 178). Goniopteris stiriaca (Fr. Unger) A. Braun is noted e.g. from the following localities:

Altenrath (Germany) Lower Oligocene.
Zsilthal (Hungary),
Monod, Rivaz, Rochette,
Paudeze, Hohe Rhonen (Switzerland) and
Macedonia (R. Kräusel 1927) Upper Oligocene-Aquitanian.
Eriz, St. Gallen (Switzerland) and
Münzenberg (Germany) Lower Miocene.
Parschlug (Styria),
Rilzing and
Lemnos, Thessalonike Middle Miocene.

A statement of its occurrence in the Lower Pliocene, given by PALIBIN 1937 (The fossil flora of the Goderzhy summit. Acta Instit. Bot. in Acad. Science Ser. I. Fasc. 4. p. 7–92. Moscow-Leningrad) is regarded by CZECZOTT as probably being insufficiently supported, the geological age seems doubtful.

Blechnum dentatum (Goeppert) Ettingshausen

This species is first mentioned by GOEPPERT (1836, pp. 128, 138, 355, Pl. XXI, figs. 7 and 8), under the name of *Aspidites dentatus* then noted by STERNBERG (1838, p. 142) as *Taeniopteris dentata*, and finally by ETTINGSHAUSEN (1854, p. 15, Pl. XIV, fig. 2 and 1867, p. 90, Pl. III, figs. 1, 2 and 4) referred to the genus *Blechnum*.

The clay at Moselund has yielded a considerable number of fragments of pinnules which are to be referred to this interesting and, as it seems, rather rare fossil Fern. In our fig. 9 some of these are reproduced, magnified twice. A–C show fragments of sterile, D and E of fertile pinnules. Both agree very well with the specimens of these types figured by ETTINGSHAUSEN, and they very probably belong to the same species. The specimen figured by GOEPPERT only represents a fragment of a sterile pinnule. The fertile pinnules of some *Blechnum* sp. (sectio Eublechnum) are markedly narrower than the sterile ones and sufficiently characterized by the two anastomoses of veinlets, parallel with and near to the midrib, bearing the sporangia and indusium and forming the sori.

ETTINGSHAUSEN (l.c.) gives the diagnosis as follows: Blechnum fronde pinnata, pennis linearibus vel lineari-lanceolatis, apices versus attenuatis, basi rotundata brevissime petiolatis, margine dentatis, nervatione Taeniopteridis, nervo primario valido, prominente, recto, nervis secundariis angulis acutis vel subacutis egredientibus, creberrimis, tenuissimis, furcatis vel dichotomis, ramis elongatis craspedodromis; soris linearibus continuis, nervo primario utrinque adnatis.

As shown by the figures of ETTINGSHAUSEN as well as by our reproductions, the veinlets part from the midrib at an acute angle and are very closely set, the space between them rarely surpassing 0.5 mm. The portion of the veinlets between the

Nr. 6



Fig. 9. Blechnum dentatum (H. R. Goeppert) C. v. Ettingshausen. A, B and C, fragments of sterile — and D and E, of fertile pinnules (Moselund) ($A-E \times 2$).

sori and the main rib is somewhat difficult to distinguish in the fossil as the leaf substance in this part is a deep black colour. The details figured do, however, conform with what is found in the related living species.

The base of the sterile pinnule shows a slight incision on both sides of the very short stalk, thus being faintly auriculate (Ettingshausen 1867, Pl. III). A complete basal part was not found in our material. Fig. 9B will give an impression of a base conforming to the figures of ETTINGSHAUSEN.

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3

Fertile pinnules of the same shape, denticulation and venation as found in the fossil are met with, as mentioned, in several living species of *Blechnum*. These belong to the section Eublechnum, characterized by L. DIELS (1902, p. 246, ENGLER und PRANTL) as follows: Blätter meist nicht oder schwach dimorph, ungeteilt oder einfach gefiedert. Blattstiel gerade, nicht windend. Sori parallel zur Mittelrippe und ihr dicht anliegend; zwischen Sorus und Rand ein breiter Raum – –

Hence *B. dentatum* comes under this section and is to be referred to its group B: Sori nahe der Mittelrippe. The sub-group Ba is characterized by undivided leaves. Bb and Bc both comprise species with sectioned leaves and the living analogue is consequently to be sought for in one of these two sub-groups. A further approximation is not possible as the characters distinguishing Bb and Bc are such as cannot be demonstrated by isolated pinnules.

B. brasiliense Dev. is, among others, regarded as a living analogue, and certainly there is some resemblance between this species and the fossil, but not to such a degree that one would venture to regard them as closely related or even identical. *B. ser-rulatum* Rech. might also be considered an allied species.

The fact that sterile and fertile pinnules of types agreeing with the corresponding parts of certain *Blechnum* species have been found together in two so widely separated localities as Bohemia and Denmark and of probably almost the same geological age, must strengthen the opinion that they in fact belong to the same species.

Blechnum dentatum (H. R. Goeppert) C. v. Ettingshausen has previously been recorded from Kutterschütz at Teplitz, Priesen and from Bilin, Bohemia, all comprising floras of the Aquitanian type.

Pteris parschlugiana Fr. Unger

A fragment of a pinnule, found at Salten and figured by HARTZ (1909, p. 55, Pl. III, fig. 1) has been referred to this Fern. Remains of it are said to be common in the lignite of this locality but are difficult to secure intact because of the nature of the matrix. The l.c. figured specimen is indeed very incomplete, as both apex, base and margin are damaged, and only the midrib and the inner part of the venation passably preserved. The author refers to the figures published by FRIEDRICH (1883, Pl. VIII, IX and XXIX) who also discusses the relationship of this and some other Tertiary *Pteris* spp.

The diagnoses given by UNGER (1847, p. 122) and O. HEER (1855, p. 38) are completed by P. FRIEDRICH as follows: Folia pinnata, pinnulae alternae, sessiles, lineari-lanceolatae, basi inaequilaterali rotundatae, argute serrulatae; nervus primarius validus, nervi secundarii angulo acuto egredientibus, semel-bi-vel tri-furcati.

FRIEDRICH is inclined to regard *Pt. parschlugiana* as closely related to the Eocene *Pt. Prestwichii* Gardner and ETTINGSHAUSEN (1879, p. 53, Pl. X, fig. 8), but the diagnosis of the last-named species maintains that its pinnules have an entire margin



Fig. 10. A-C, Pteris parschlugiana Fr. Unger. Fragments of pinnules; C shows a part of the margin which probably had carried a sorus (Moselund) (×2). D-E, Pteris longifolia L. (recent). Parts of pinnules. In D the margin has partly been sorus-carrying. E, base of a pinnule (×2).

(margine integerrimis), this being the only real difference between the two species in question. FRIEDRICH has somewhat bridged over the gap by altering the diagnosis of *Pt. Prestwichii* from "margine integerrimis" to "pinnae integerrimis vel crenulate", but a marked point of distinction is at any rate obvious from this term and the note "argute serrulatae", used to characterize the nature of the margin of the pinnules in *Pt. parschlugiana*. Also O. HEER (1.c.) attributes to *Pt. parschlugiana* the character "margine argute serratis". He further adds the rather important information: Fieder am Grunde zugerundet, auf einer Seite etwas breiter – deutlich und scharf, aber sehr fein sägezähnig, nach vorn stehen die Zähne gedrängter –. The statements of FRIED-RICH agree very well with these details.

The specific rank of *Pt. pennaeformis* O. Heer and *Pt. Gaudini* O. HEER is rather doubtful according to the last cited author. The base of the pinnules is not preserved, though in the former species it was probably tapering. The venation is chiefly of the same nature as in *Pt. parschlugiana*, but the veinules are probably more densely set.

On the whole I should be inclined to refer our material to the species described by UNGER, which is a rather widespread type. Pinnules and fragments are common in the clay at Moselund, and some fragments, probably to be referred to the same species, are also found in the State quarry at Fasterholt. Figures 7, A–D, and 10, A–C, show specimens of this fossil; those from Fasterholt are distinguished by having a somewhat more markedly serrulate margin and more close set veinules than those from Moselund, but probably do not surpass the range of variation characteristic of the species. The rounded basal lobes are evident in the specimens from Moselund shown in Fig. 10, A and B. Towards the apex of the pinnules the denticulation grows more marked.

These fossils are very much like the pinnules of some still living *Pteris* species of the section I. Eupteris § 1. Simplicinnatae (L. DIELS). O. HEER states Pt. longifolia L. as an allied species, and indeed the morphological parallelism between Pt. parschlugiana and its probably most nearly related living analogon is very striking. (ETTINGS-HAUSEN 1865, Pl. 52, fig. 15 and Pl. 54, fig. 1, etc.) A serious disadvantage to the determination of the generic relation has hitherto been the lack of demonstration of the linear marginal sori so characteristic in *Pteris*. The sporangia and indusium in the fossils might be destroyed by crumbling away, but their place should always be recognizable by the line of marginal anastomosing veinlets on which the sori develop and by the absence of a marked denticulation of the part of the margin outside the sorus. In some extant species the whole margin is bordered by sori, but often-as just in Pt. longifolia-the sorus line might be interrupted by parts of the margin showing the normal denticulation and the usual ending of the veinlets in the denticles. Fig. 10D shows such a part of the margin from a pinnule of Pt. longifolia (the sorus itself has been removed) and Fig. 10C a corresponding part from the fossil; the similarity of the two parts figured is evident. Fig. 10 C is drawn from a specimen from Moselund, with the leaf substance partly preserved. In the imprints these details are often somewhat obscure, but in many cases at least traceable.

Nr. 6

As for anatomical details only the structure of the mesophyll could be demonstrated. The uppermost layer consists of small, cohesive elements, the lowest of a lacunous tissue, details which are not very characteristic, but which at any rate agree very well with the mesophyll of *Pteris longifolia*.

Pteris longifolia L. is a tropical and subtropical cosmopolite with a very broad range of variation; the apex of the pinnules is mostly tapering, but may exceptionally end bluntly.

Pteris parschlugiana Unger has been recorded from the following localities:

Bornstedt (Saxony)	Lower Oligocene.
Monod, Rochelle, Paudeze (Switzerland)	Aquitanian.
Parschlug, Leoben (Styria)	Middle Miocene.

Salvinia Bjerringii n. sp.

An extensive list of the literature dealing with the morphology, development, systematics, geographical and geological distribution of the known living and fossil *Salvinia* species, is to be found in the papers of FLORIN (1919 and 1940). The references here given to the papers of HOLLICK (1894), HERZOG (1934) and KOPP (1936) are of special importance regarding the comparison of the living *Salvinia* species with the fossils.

In the clay at Moselund the floating leaves of a *Salvinia*, are found rather commonly both as fossils, in which the leaf substance is admirably preserved, and as imprints only. The former occur mainly in the black parts of the layer.

A selection of such leaves is shown in fig. 11, A–D, reproduced double life size; all these figures show the upper side of leaf. Though some of the specimens are somewhat damaged, the figures will give an impression of the range of variation with regard to shape and size. The outline is from oval-cordate to ovoid-cordate, the apex obtuse or slightly incised, and the deep incision at the base is often disguised as the two lobes are partly overlapping. In short and relatively broad leaves the outline can consequently become almost circular. Fig. 11D shows a leaf of an exceptionally large size.

The point where the lamina has been connected with the stalk can be traced in fig. 11, E and F, as the secondary basal veins radiate out from there. In cases where the underside of the leaf presents itself by turning upward (in the imprint fig. 11 H) the scar left by the disintegration of the lamina is very conspicuous. From the base to about the middle of the leaf the midrib on the underside is rather thick and somewhat protruding, but towards the apex, it passes rather suddenly into a slender and low part. A longitudinal marking, not unlike a scar, is often found on the relief of the thickened part. The real length of the stalk could not be ascertained. It is most probably connected with the lamina at an angle of about 120° and thus inclined to be broken off by the horizontal splitting of the matrix. In a few cases the length could be estimated at about 1 cm, for a *Salvinia* consequently rather long.

As is well known, the leaves of Salvinia are arranged in whorls of three, each



Fig. 11. Salvinia Bjerringii n. sp. A–D, outlines of floating leaves, upper side, and H of under side (\times 2). E and F, outlines and venation of floating leaves (\times 4). G, some intervenia with air chambers of the middle layer of äërenchyma, as seen from below, and showing the extension of some black spots of the upper side of meso-phyll (All from Moselund) (\times 20).

whorl consisting of two dorsal floating leaves and a ventral one, submerged and split up in numerous hairlike laciniae. Submerged leaves were not found in the material at hand, but in the figures of FLORIN (1919) leaves of this type are also reproduced (*S. formosa* from the Tertiary of Japan). In several instances the dorsal leaves, as shown in our figures, were found connected in pairs, undoubtedly representing the two floating leaves of the same whorl.

In the outline-figures A–D only the midrib of the leaf is shown in. E and F show details of the venation. The meshes of the network, formed by the anastomoses of the veinlets, are rather regular, exhibiting a system of five- to six-sided polygons, the size of which only slightly diminishes from midrib to margin. The type of venation corresponds to what is known from the fossil species *S. formosa* O. Heer and *S. Mil-deana* Goeppert; see R. FLORIN (1940).

Nr. 6

A character of some importance according to KOPP (1936, p. 19), but rather difficult to ascertain in the fossils, is the pattern formed by the last ramification of the veins. KOPP (l. c.) distinguishes two types in the living species of *Salvinia*: I. Die Seitennerven I. Ordnung werden nach dem Blattrande zu in fortschreitendem Masse vermehrt durch gleichlaufende, jedesmal kürzere Seitennerven höherer Ordnungen, die von den Anastomosenwinkeln entspringen. Die Maschen des Gesamtnetzes werden dadurch nach der Peripherie des Blattes zu kleiner und zahlreicher (wiederholt trichotom-anastomosierend). II. Die Maschen bilden ein annähernd gleichmässiges Netzwerk (gleichmässiger Netztypus) – – The latter group only includes two living species: *S. nigropunctata* A. Braun and *S. oblongifolia* Martius. The two Tertiary *Salvinia* species mentioned above, as well as our fossil, are evidently to be referred to the last group. In the species belonging to the former group, including the rest of the living *Salviniae*, the last ramifications end freely just inside the margin of the leaf. In *S. nigropunctata* A. Braun (= *S. nymphellula* Desveaux) and *S. oblongifolia* Martius they form connecting arches, in *S. nigropunctata* (as shown in the figures Pl. IV. 1 and 2

by KOPP) at least in the apex and at the base of the leaf. Such anastomoses could be demonstrated in our fossils, though of course only where the margin was left intact and the outline of the peripheral meshes could be distinguished (fig. 11, E and F). This is often better to ascertain in the imprints than in cases where the leaf substance is preserved.

In the papers of earlier authors the venation of the Salvinia leaf is generally reproduced in a very diagrammatic way, though UNGER has given a fairly accurate representation of it as to S. Mildeana in his Sylloge Plantarum fossilium (Part I, 1861, Pl. I, fig. 10). According to the venation the Salvinia species of KOPP's group II, as well as the two fossil species mentioned above and also the Salvinia from Moselund, have the lamina divided into a number of polygonal fields corresponding to the meshes of the veins. These fields consequently show a rather regular arrangement in series, in the lower half of the leaf almost transverse or slightly ascending, with a decidedly apically directed curve towards the upper part and a somewhat fanshaped pattern in the basal lobes. In our fossil the middle part of the upper side of the field often shows a darker patch, slightly projecting as a low papilla' and, corresponding to this, an the under side a more or less deep depression. The nature of this last feature is not immediately obvious; as far as I know no recent Salvinia show anything similar, and it is probably caused by the shrinking of the underside mesophyll under decay and fossilization. According to the facts mentioned the extant S. nigropunctata, a West African species, might be a related type and consequently deserves special attention. This view is further strenghtened by the study of the anatomy of the two species. As a preliminary guide the figures of HERZOG and KOPP have served; from the Collections of the Musée d'histoire Naturelle, Brussels, and of Riksmuseet, Stockholm, material of S. nigropunctata for comparison has kindly been placed at my disposal.

Anatomy

The anatomy of the *Salvinia* leaf offers some very peculiar details, which from an early time attracted the attention of botanists. The results of these studies are reviewed in the papers of HERZOG and KOPP, and used recently by FLORIN for palaeobotanical purposes. In our material a good many details are preserved, which can be fairly well demonstrated in reflected light under a low-power objective. If the leaf substance is moistened with xylene or cedar oil the structure becomes more apparent. However, even for these objects I have found it most convenient to reproduce the details by drawings.

On the upper side of the floating leaf the form and size of the epidermal cells are traceable where the side walls locally are left intact; the outer walls seem most often to have vanished; where they are preserved, as is mainly the case in the parts covering the veins, they appear flat or slightly convex; real papillae could not be demonstrated. Fig. 12A shows a group of epidermal elements; lateral walls straight and thin, the size of the cells is varying from $50-80 \ \mu$. The three small elliptical gaps probably represent places of stomata; here, as in the whole genus Salvinia, quite small (14-16 μ); the guard cells are dissolved. The mesophyll is in the intervenia developed as a three-storied aërenchyma, the intercellular spaces (air chambers) of the middle and undermost layer forming penta- to hexagonal polygons, while the smaller ones of the uppermost layer are more rounded in outline. The shape and relative size of the air chambers are exhibited in fig. 12C; the polygons of the undermost layer measure 120–180 μ in diameter, of the middle layer 80–100 μ and of the uppermost only 30– 50 μ . The separating borders are in fact one cell-layer thick, but in the lamellae of the middle and undermost layer of aërenchyma details are not discernible in the fossil. However, those of the uppermost layer are partly better preserved. As can be seen from fig. 12, D and E, the undermost part of their sideward borders, as well as the lamella separating the uppermost layer of aërenchyma from the middle one, is formed by quite small cells, $4-6 \mu$ in diameter. In the uppermost parts of the borders these elements are far less distinct, the lumina being filled with a dark material and also the walls are dark coloured, so that details were not discernible; they are consequently in the figures shown in unbroken lines.

The black spot in the centre of the intervenia is mainly caused by the dark substance here filling the tissue to a higher degree than elsewhere in the leaf. Here and there, especially in the vicinity of the veins, smaller groups of such dark coloured cells also can be found.

In several recent Salvinia spp. (e.g. S. natans and auriculata) the conductive tissue of the veins on the upper side of the floating leaf is accompanied by cells markedly smaller than the surrounding elements each containing a globular or ellipsoidal concretion of silica, with a finely warted surface (Fig. 12F). In S. nigro-punctata such idioblasts are lacking, but a quite small, stellate concretion of silica is to be found at the top of the greatly protruding papilla of every epidermal cell.

Nr. 6



41

Fig. 12. A–E, Salvinia Bjerringii n. sp. A, epidermis from the upper side of floating leaves (×100). B, intervenium with outline of air chambers from upper and middle layer of aërenchyma (×50). C, outline of air chambers from upper, middle and lower layer of aërenchyma (×100). D and E, airchambers from the uppermost layer of aërenchyma, showing the cellular texture of side walls and some cells from the bottom of the intercellular space (×400). F, recent Salvinia auriculata. Part of tissue bordering on a vein from the upper side of a floating leaf showing idioblasts containing silica concretions (×400). G–I, Salvinia Bjerringii n. sp. G, elements of epidermis from the bottom of an underside depression of a leaf, probably indicating the four cells which have carried a "Sockelbüschel" (×100). H, part of epidermis from upper side; three circular cells probably indicating the bases of "Papillenhaare" (×100). I, upperside epidermis from the central part of an intervenium; the four stellately arranged cells in the centre might have carried the four branches of a "Sockelbüschel" (×100).

These features have not previously been recorded. As in our fossil the outer walls of epidermal tissue has almost totally vanished, I had no opportunity of demonstrating the detail last mentioned. The silica concretions would certainly have been dissolved, but the type of the epidermal elements in question should be recognizable.

The epidermis of the underside of the floating leaf had in all specimens been

totally dissolved, so that details such as hair-covering, the occurrence of "hydropotes", etc., were not demonstrable.

As the type of hair-covering, especially that of the upper surface, is to be regarded as being of systematic value, some efforts were made to clear up this feature. Unfortunately this was not thoroughly successful, as the epidermis, as mentioned, is only preserved in small patches and furthermore the outer wall of the elements is mostly dissolved, so that the bases of the trichomes consequently may have disappeared. On the top of the somewhat projecting dark spot in the centre of the intervenia, where bases of larger trichomes pre-eminently might be sought for, in the epidermis in some cases a regular star-shaped group of four cells could be traced. According to their size and outline these groups might be regarded as the place where a four-branched tuft of trichomes, forming what KOPP has termed a "Sockelbüschel", had emerged (fig. 121). Particularly at the bottom of the shallow pits of the imprints (underside of the floating leaf turning upward) which correspond to the somewhat elevated central parts of the intervenia, several epidermal elements are often preserved. Such groups of four, not unlike a clover-leaf with four leaflets, probably representing the base of a "Sockelbüschel" seen from below (Fig. 12 G).

Fig. 12 H show some cells of the common epidermal type surrounding some circular elements, evidently belonging to the same layer. Such cells are not uncommon, their distribution is somewhat irregular but, as far as could be ascertained, mainly occurring in small groups near the veins. Their nature is uncertain, most probably they represent the bases of what KOPP termed "Papillenhaare".

The presence of a "keel", i.e. an on the underside of the floating leaf from the proximal part of the midrib protruding part of tissue connected with the petiole, is not clearly demonstrable from the material at hand, but some facts might be regarded as hints indicating the existence of such a formation. The scar on the underside of the thickened proximal part of the midrib (fig. 11 H), in connection with the relatively long petiole, in a single case found adjoining with remains of tissue which could be referred to a keel, would perhaps point in this direction. As the hypothetic keel would be oriented vertically towards the layers of matrix, it is not likely to be found in situ, and its presence is not noted in any of the fossil species formerly described.

Of fossil Salvinia spp. only the S. formosa O. Heer, S. Mildeana Fr. Goeppert and S. macrophylla Kirchheimer have been studied in such detail that a comparison is of any use for stating the specific value of our fossil.

According to the photos of FLORIN (1940) S. formosa and S. Mildeana exhibit, as mentioned, the type of venation agreeing with the Salvinia from Moselund, the veinlets forming meshes of approximately the same type and—as far as could be ascertained—anastomosing by marginal arches. S. Mildeana is l. c. described as having: zwischen den Sekundärnerven befindlichen Doppelreihen seichter Vertiefungen, die von Haargebilden hervorgerufen sind – The photo Pl. III, Fig. 3 shows this character very distinctly. S. macrophylla, which according to CZECZOTT (1959) might be identical with S. Reussii Ettingshausen, shows, in the photos of FLORIN, the resistant

basal parts of large "Sockelhaare" (KOPP). The markedly protruding papillae on the upper surface of the leaf in the photos of CZECZOTT may be of the same origin. As a closer relative perhaps *S. formosa* may be considered. However, the floating leaves here are much larger than is commonly the case in our specimens and also of a somewhat other shape, i.e. more oblong in outline. As for the number of layers of air chambers in the mesophyll, none of the figures cited offer the details necessary for exact comparison.

O. HEER has noted S. Mildeana in his memoir: Miocene baltische Flora (1869) and has figured two leaves which are referred to this species (Pl. III, figs. 1 and 2). One agrees in outline and size with the main type in our material and also here represents the most common form. The other, of a rarer occurrence, conforms with our leaf pictured as fig. 11 D. These two leaves may belong to the same species, as this is the case according to anatomical details with all the leaves figured by me. The floating leaves of the same Salvinia sp. may, as shown by experiment (Kopp), vary greatly in size and also somewhat in outline according to the nature of environment. The intensity of insolation and abundance or shortage of nutrients in particular play a decisive role. The same types of floating leaves, occurring associated both at Rixhöft in Samland and at Moselund, might suggest that the specimens are identical, in which case the determination of HEER is not correct. Furthermore HEER (l.c. p. 17) notes: In jeder Zelle die so entsteht (i.e. in the meshes of veinlets), bemerkt man einen schwarzen Flecken—which is in accordance with our specimens.

An absolute identity with any of the fossil species considered cannot be demonstrated and it is consequently necessary to constitute the *Salvinia* from Moselund as a new systematic unit: *Salvinia Bjerringii*—the specific name commemorating the discoverer of the fossil flora of this locality.

As for still existing species of Salvinia an uppermost third layer of small air chambers is only recorded in the West African S. nigropunctata Alex Braun. The structure of the mesophyll agrees in the main with that found in our fossil; however, the rings of small, closely set cells forming the undermost part of the top layer of the aërenchyma are in S. nigropunctata crowned by vertically extended, almost palisadelike elements, which cannot be demonstrated in the fossil; the structure of this part must consequently remain obscure, as transverse sections were not available. A marked difference is to be found in the size and structure of the epidermal cells of the upper side of the floating leaves; the elements are in S. nigropunctata much smaller than in our fossil (only $30-40 \ \mu$ in diameter) and, as mentioned, each protruding as a marked papilla. The keel is developed as a 1-2 mm thick, semicircular lamina, built up of exceedingly thin-walled cells and protruding as a continuation of the underside layer of aërenchyma, consequently with very large air chambers. On the upper side of the floating leaves of S. nigropunctata are found "Sockelbüschel", one or two in each intervenium, "Papillenhaare" and "Thurmhaare" (KOPP), the last type not beeing demonstrable in the fossil the reasons advanced.

Considering the limited amount of fossiliferous material examined, the Pterido-

phyte flora of Moselund is to be regarded as astonishingly rich, both concerning the number of species and the abundance of specimens. The locality of Fasterholt has yielded two species, of which *Osmunda Heerii* is only found here. It may be added that at Moselund also some isolated leaf-sheets of an *Equisetum* are found, not unlike the specimen figured by ETTINGSHAUSEN (1867, Pl. II, fig. 15), and that Ferns and Fern Allies were lacking in the fossiliferous layer at Silkeborg Vesterskov.

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BY

TYGE W. BÖCHER



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Synopsis

Comparative cultivations and cytological investigations were carried out on a number of arctic or montane species of the genera Arabis, Draba, Braya and Kernera. New chromosome numbers were recorded in Arabis arenicola (2n = 16), Draba sibirica (2n = 16), D. lanceolata (2n = 32), D. gilliesii (2n = 48), D. aurea (2n = 76), Braya rosea (2n = 42), B. alpina (2n = 42) and Kernera cfr. decipiens (2n = 14). In the Draba cinerea group the three chromosome levels (2n = 48, 64)and 80) are shown to be connected with three taxa for which the names D. cinerea Adams, D. arctica J. Vahl p. p. ssp. groenlandica (Ekm.) comb. nov. and D. arctica J. Vahl p. p. are used. D. arctogena Ekm. is connected with D. norvegica by transitional forms. Both are maintained as species but seem to belong to the same group and not to the *D. cinerea* group. In *D. glabella*, races with 2n = 64 and 80 have been studied, but so far it has not been possible to divide the material taxonomically into two entities corresponding to the two chromosome numbers. D. aurea has a very deviating chromosome number, 2n = 76, or perhaps 2n = 72+4 extra chromosomes. Clear evidence of small supernumerary chromosomes (B-chromosomes) however, was only found in D. norvegica. The material of Braya rosea deviates sharply from the description of the type and deserve a closer taxonomical study. In B. linearis two strains with B-chromosomes occurred and one of them from Junkerdal in Norway deviated morphologically from the other strains. As this race also can be distinguished in herbarium material it has been described as a new variety (var. meizophylla). In B. novae-angliae, strains from Colorado and W. Greenland had the same chromosome number (2n = 56) but deviated morphologically, the American material belonging to ssp. ventosa (Rollins).

In *Draba* there seems to be at least three basic chromosome numbers x = 8, 10, and 12 while in *Braya* all species can be arranged in a series with x = 7. The evolutionary trends in both genera are discussed on the basis of cytological, morphological and plant geographical evidences. Some of the distributional patterns are illustrated by maps.

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1. Introduction

From a taxonomic point of view, some of the most critical genera in the flora of arctic and montane areas are undoubtedly found among the Crucifers. Botanists working in the Arctic agree that the genera *Draba* and *Braya* are particular problematic. In other groups, e.g. the *Arabis holboellii* complex, the situation is complicated by the occurrence of apomixis.

A critical study of arctic Arabis, Draba and Braya was made by GELERT as early as 1898. Draba has been studied thoroughly by EKMAN 1912–1941, Pohle 1925, Schulz 1927, FERNALD 1934, and HITCHCOCK 1941. More important works and papers concerning Braya were published by OSTENFELD 1923, SCHULZ 1924, ABBE 1941, Rollins 1953, Sørensen 1954, and Böcher 1956.

In spite of this extensive taxonomic and cytological literature, our knowledge of these arctic-montane Crucifers is unsatisfactory. We have no real understanding of the micro-evolutionary dynamics which are responsible for the complexity nor the evolutionary trends and the processes leading to species formation. Experimental hybridizations as done by WINGE (1933, 1940) in *Erophila* is one of the most urgent tasks.

The present study is mainly cytotaxonomical. Its purpose is to create a basis for experimental crossings by limiting or elucidating the problems.

The study was considerably faciliated by the improved cultivation possibilities available in the Arctic Greenhouse in the Copenhagen Botanical Garden. This greenhouse was granted by the Carlsberg Foundation and the Rockefeller Foundation.

For material placed at my disposal for the present investigation I wish to express my sincere thanks to Drs. T. T. ELKINGTON, NIELS FOGED, BENT FREDSKILD, KJELD HOLMEN, KNUD JAKOBSEN, MARTIN LEWIS, Professor H. MERXMÜLLER, and Professor TH. SØRENSEN. I am also indebted to the curators of the museums in Bergen, Copenhagen, Stockholm, and Uppsala for loan of important collections of *Draba* and *Braya*. Correction of the english was kindly undertaken by Dr. MARTIN LEWIS, Birmingham.

2. Arabis

Arabis arenicola (Rich.) Gelert and A. petraea (L.) Link

Material of *Arabis arenicola* from two localities in continental West Greenland has been cultivated in the arctic greenhouse and in pots in frames at the experimental field. The species is not easy to cultivate even in the arctic house as the plants sometimes die after luxuriant flowering. In pots at the field the plants form small dense cushions with small leaves and few short flowering stems and are also inclined to die after two or a few years.

Chromosome number. Both strains (Cult. No. 4851 from head of Sdr. Strømfjord and No. 6064 from Nunatarujuk at the head of Arfesiorfikfjord) had 2n = 16or n = 8 and quite normal meiosis. (Figs. 1a-b and 10e). The number is the same as that in *A. petraea* (L.) Link. which has been cultivated simultaneously (No. 28 see below) and was already counted by Böcher & LARSEN (1950).

Variation. The two strains of *A. arenicola* differed from each other and from *A. petraea* in a number of characters which may be summarized as follows.

- No. 4851: First year rosettes vigorous. Second year flowering shoots (5) 8–14 cm long, ascending or \pm upright. Diameter of largest flowers 4–5 mm. Siliques up to 2.1 cm long and 2 mm broad \pm ascending. Leaves \pm entire. 3–5 stem leaves.
- No. 6064: First year rosettes slender, second year flowering shoots 7–13 cm long, prostrate. Diameter of largest flowers 4–4.5 mm. Siliques up to 2.0 cm long and 1.7–2.0 mm broad, spreading. Leaves more light green, smaller and sometimes with few shallow incisions. 2–3 stem leaves.
- A. petraea (No. 28) from Falljökull in Iceland has also \pm prostrate shoots, but the plants are much larger than those of the two strains of A. arenicola and the flowers attain almost double the size. Furthermore the incisions in the rosette leaves are deeper and more numerous. The plants are easy to cultivate.

GELERT (1898) who referred the *Eutrema arenicola* of RICHARDSON, and the *Sisymbrium humifusum* of J. VAHL to the same species of *Arabis*, viz. A. *arenicola*, has discussed the relation between the latter and A. *petraea*. He concludes that the two species replace one another geographically and that A. *arenicola* possibly is a rather young species having evolved from A. *petraea*.

This opinion, however, is not supported by the observations referred to above. Both species are diploids and any estimate of their evolution must therefore at the moment rest upon geographical data.

Arabis petraea is a north-Atlantic European species; it occurs in Iceland, the Faroes, Scotland, Wales, Scandinavia, North shore of lake Onega as well as in the mountains of Central Europe. In Scandinavia its peculiar, disjunct range was studied and mapped by Holmboe (1936: 22–24) who concludes that there is every indication that in Norway it must be considered as an interglacial "winterer". The range of *A. arenicola* is also interesting. It is a NE-American-Greenland endemic (A. E. PORSILD 1964 map 197), today almost exclusively found in areas which previously were glaciated; its present area is also disrupted. Both species are exclusive to open rocks, moraines or sands and show clear preference for basic soils often rich in minerals (serpentine soils, basalt soils etc.). Today in West Greenland *A. arenicola* grows abundantly along the margin of the Inland Ice. It behaves as a glacial plant able to follow retreating ice sheets and fitted for glacial conditions. Similarly *A. petraea* according to Holmboe probably reached its stations in the skerries of Ångermanland by late glacial migration from Trøndelag.

It is a striking feature that there are no records of *Arabis arenicola* on the basaltic East Coast of Greenland opposite Iceland (see map in Böcher 1952 fig. 9) which would probably be the case if this species had developed from *A. petraea*. Although clearly related the two species are very distinct and neither of them probably young species. If they, as is most likely, are perglacial survivors *A petraea* has spread from a refuge of an oceanic type (e.g. in Iceland and in Norway) while *A. arenicola* came from continental refuges in Ellesmere-Greenland; the two species became adapted to very different climatic conditions and are therefore allopatric in our day.

3. Draba

Draba fladnizensis Wulfen and D. lactea Adams

These two species are undoubtedly related. While POHLE (1925: 84) unites them in one species, most recent authors separate them, as did EKMAN 1932. Chromosome investigations clearly show that they are distinct.

Draba fladnizensis seems to be one of the basic diploids within the subsection Euleucodraba. n = 8 has been counted in material from Dovre (Norway), HEILBORN (1927: 60), NE Greenland (Jørgensen et al. 1958: 69), and the Alps (MERXMÜLLER & BUTTLER 1965). The same number also occurs in Spitzbergen. Seeds were collected there by NIELS FOGED 1958 in the Advent Valley (Hotelnæsset 78°15' lat. N. 15°30' E.) and plants were grown in the Arctic Greenhouse (Cult. Dr. 8). They resembled D. lactea in growth habit but had only simple hairs, mainly as marginal cilia on the basal leaves. Jørgensen et al. found some variation in size of the bivalents. The mitotic metaphases studied by the present author (Fig. 10) do not show much variation in chromosome size indicating that the differences found during meiosis may be due to variation in the number of terminalized chiasmata.

Draba lactea is hexaploid (n = 24) according to JØRGENSEN et al. This interesting result based on material from NE Greenland can now be corroborated, again in Spitzbergen material collected by NIELS FOGED. (Two stations in Van Keulenfjord $77^{\circ}37'$ lat. N., $14^{\circ}55'$ E., cult. Nos. Dr. 2 and Dr. 5).

The relation between the two species was discussed by HULTÉN (1958: 226) in connection with his mapping of their world ranges. HULTÉN assumes that the two species cross freely where they are sympatric or rather that *D. lactea* constitues a hybrid series formed by crossings between *D. fladnizensis* and *D. nivalis*. He has seen a complete series of transitional forms between these two species, in which *D. lactea* occupies a central position. HEILBORN (1927) gives an analysis of the hybrid between the two diploids *D. fladnizensis* and *nivalis*. In spite of the fact that the hybrid had entirely abortive seeds, meiosis in the anthers proceeded normally. EKMAN (1932: 440) also refers to this hybrid and says that it is always sterile.

The available evidence therefore makes any explanation of *D. lactea* as a primary hybrid, unlikely. On the other hand much is in favour of the view that it is an allohexaploid and a well established balanced species. Morphologically it is much closer to *D. fladnizensis* than to *D. nivalis*, a fact which suggests that it arose after doubling in a triploid hybrid having two '*fladnizensis*' genomes (from an unreduced gamete) and one '*nivalis*' genome.

In this connection some deviating specimens of *D. lactea* from Niaqorssuaq in Nordre Strømfjord, W. Greenland (Altitude 500 m, TWB 1958 No. 812) deserve mention. The rosette leaves have the same mixed pubescence as in *D. lactea*, but the lower part of the stem has a thin covering of very small stellate hairs. The plants seem to be fertile. Such plants and many others belonging to the transitional series mentioned by HULTÉN may not to be new hybrids (back crossings) but the result of some kind of structural change in the chromosomes of the allohexaploid resulting in the occurrence of stellate hairs on the stem, a character which is usually masked in *D. lactea*.

D. lactea has a circumpolar range similar to that of D. nivalis but unlike D. fladnizensis which is arctic-alpine (montane) and has many disjunct areas. One such area is found in NE Greenland, another in West America. HITCHCOCK (1941) mentions it as a rare plant on the highest peaks of Colorado and Southern Utah and from British Columbia; he adds that the widely separated localities must represent relic stands.

In culture, under uniform conditions, *D. fladnizensis* and *D. lactea* showed clear size differences during flowering (Table 1). The dimensions found in the Arctic Greenhouse were generally smaller than those given by EKMAN (1932) in the diagnose. *D. lactea* flowered a little earlier. Both species produced elongated racemes with short peduncles.

Species	Draba fladnizensis	Draba lactea	
Cult. No.	Dr. 8	Dr. 5	Dr. 2
2n	16	48	48
Height of plants cm	3.0 - 4.0	4.5 - 6.5	5.0-8.0
Length of sepals mm	1.4 - 1.5	1.6 - 2.0	1.6 - 2.0
Length of petals mm	2.0 - 2.2	2.8 - 3.3	2.6 - 3.0
No. of stem leaves	0-1	0	0
Length of rosette leaves mm	9-11	8-10	8-11
Length of longest cilia at leaf margins mm	0.5 - 0.6	0.8 - 1.0	1.0 - 1.1
Stellate hairs on rosette leaves	none	present	present

TABLE 1.

Draba lanceolata Royle

This species seems to be identical with *Draba stylaris* J. Gay and *D. thomasii* Koch, see FERNALD (1934: 359). MERXMÜLLER & BUTTLER (1965), however, still uphold *D. stylaris* and have found 2n = 32 in this taxon from Engadin; this is the
7

same number as found in the closely related *D. incana* L. from localities in Europe and Greenland. Material of *D. lanceolata* from Angujârtorfik in the hinterland at Søndre Strømfjord, W. Greenland, was also tetraploid (n = 16, see Fig. 1c). Thus the entire *D. incana*-complex seems to be tetraploid.

In Greenland *D. incana* and *D. lanceolata* are vicarious, being largely allopatric (BöCHER 1952 fig. 32 and p. 26). *D. incana* has an atlantic subarctic distribution and is very common in South Greenland. *D. lanceolata*, on the other hand, is confined to continental Central W. Greenland and the interior of the Scoresbysund fjord system. It was recently refound there by HOLMEN and LÆGAARD; an older collection from the same area by N. HARTZ (as *D. arctica*, Head of Gåsefjord, June 2nd 1892) belongs to *D. lanceolata*. The locality in question is described by HARTZ (1895: 248–249). It occurred on moraine soil, probably together with *Calamagrostis purpurascens* and *Kobresia myosuroides*, two species which very frequently occur together with *D. lanceolata* in W. Greenland.

The two species *D. incana* and *D. lanceolata* seem to hybridize in the narrow zone where they are sympatric. In Greenland there are a few transitional forms e.g. in the Godthåbsfjord area.

The Greenland material of D. lanceolata (Cult. No. 4884) was grown in the Arctic Greenhouse and in pots at the experimental field together with D. cinera, D. norvegica and D. glabella. The meiosis in D. lanceolata was completely regular. In a young stage there was a good deal of resemblance between D. lanceolata and D. cinera but in a flowering fruiting stage these two species are easily distinguished (Plate IV). D. lanceolata is coarser, with narrower and longer siliques which are often somewhat contorted. The characters of the cultivated plants appear from Table 3a. They deviate in having only 3–6 cauline leaves, while very often 4–10 are found in herbarium material from other places. They have a dense covering of small stellate hairs but also bear unbranched hairs particularly on the petioles and main stems. The morphological resemblance between D. lanceolata and cinerea will be discussed below. It may, however, already be pointed out that they also show clear ecological affinities. Both have a low-arctic continental distribution in Greenland and there occur in steppe-like communities.

Draba norvegica Gunn. and D. arctogena Ekm.

These two species have much in common. Both have a heterotrichous pubescence and broad, rather short siliques and both are hexaploids.

Draba norvegica. Earlier chromosome counts were made by HEILBORN (1927: 61, 1941: 142) who found n = 24 in material with glabrous siliques (Dovre and Jotunheimen, Norway) and in plants with hairy siliques (Scotland, Kisteskarsnuten in Norway, Jämtland in Sweden and Godhavn on Disko, W. Greenland).

Here, material from two West Greenland localities (No. 4772 from Østerlien at Godhavn and No. Dr. 9 from Tupilaq at Egedesminde) has been cultivated and studied cytologically. Both showed n = 24 during meiosis and both had comparatively large flowers (sepals 2.1–2.3 mm, petals 4 mm long, cp. ssp. grandiflora Ekm., see EKMAN 1941: 140) a mixture of hair types on the leaves, and broad siliques with mainly bifid hairs (see further Plate Id and Table 2).

Cytologically Dr. 9 differed from 4772. The latter had a regular meiosis (Fig. 1e-g) although sometimes two pairs were situated so closely together that they might be interpreted as a quadrivalent. One cell had 23 bivalents and 2 univalents (Fig. 1g). Dr. 9 was interesting in the occurrence of two pairs of minute B-chromosomes. They seemed to be heterochromatic in as much as four minute dark bodies were observed in many resting nuclei. However, they were often difficult to detect during meiosis and may be absent from some of the PMCs (e.g. Fig. 1h). Figs. 1i-m show their behaviour at Metaphase I and Telophase I-II. In ana- and telophases the small chromosomes were only seen in cases where they were lagging; Fig. 11 shows that two of them may even occasionally form a bridge-like configuration.

Draba arctogena. Unfortunately no material was available for cultivation but a comparison of two collections of plants with known chromosome number (n = 24) gives some important information.

The material studied cytologically by HEILBORN (1941) was presumably collected by EKMAN at Godhavn (see EKMAN 1929: 490). It corresponds to the type collections kept in the Naturhistoriska Riksmuseet in Stockholm (Plate I a). These consist of two sheets. Those specimens marked on the label as *D. arctogena* sp. n. were collected on July 26th 1923 in Lyngmarksfjeldet, above Godhavn, Disko. The plants are 12-14 cm high with one stem leaf only. The short pedicelled siliques are up to 9 mm long and 2.5-3.5 mm broad, with a pubescence of bifid hairs. In habit, it is very similar to *D. norvegica*, the main difference being the greater density of the hairs on the leaves.

The plants studied by HOLMEN (1952) originate from Peary Land (Brøndlund fjord, HOLMEN No. 6551). It is a high artic "condensed" plant, 3.5 cm high with 0–1 stem leaf. The basal leaves are densely covered with long unbranched hairs hiding the mid-nerves. The stems have a mixed pubescence although simple or bifid hairs predominate, but the hairs on the siliques are stellate. The sepals attain a length of about 2 mm and the petals 3–3.5 mm.

A comparison of all high arctic collections of *D. arctogena*, e.g. those studied by HOLMEN (1957: 55-56), shows that the siliques have a mainly stellate type of pubescence. This is also the case with the specimen collected by FREUCHEN (Plate I b Table 2) which has been determined by EKMAN as *D. arctogena*.

A further examination of hebecarp *D. norvegica* and *D. arctogena* from Greenland shows that the siliques almost always have a mixed pubescence but that the bifid and unbranched hairs predominate in *D. norvegica* and the stellate in *D. arctogena*. There are however, some plants of high-arctic *D. arctogena* (e.g. Rivieradal $80^{\circ}06'$ lat. N., leg. Schwarzenbach) in which the bifid hairs are most common and some



Fig. 1. Chromosomes in Arabis arenicola No. 4851 (a-b) and Draba (c- \ddot{o}). — c: D. lanceolata (No. 4884, n = 16). — d: D. cinerea (No. 4813, first anaphase, n = 24). — e-g: D. norvegica (No. 4772, n = 24 (in fig. g one pair of univalents at *)). — h-m: D. norvegica (No. Dr. 9, n = 24 + 4 B; h and m: first metaphases; i: second metaphase; j-l: telophases I-II showing B-chromosomes; m: the two pairs of B-chromosomes are placed on both sides of the plate of normal bivalents). — n, p-r: D. aurea (n, p-q: Nos. 4883; r: No. 4820; 2n = 76, n = 38; particularly small, possibly extra chromosomes are marked with *). — o: D. fladnizensis (No. Dr. 8, 2n = 16). — s-z: D. glabella; s-t: No. 6325; u: No. 4814; v: No. Dr. 12; all n = 32, in fig. s one pair precociously separated, arrow in fig. u points towards pair displaced from plate; w-z: No. 4788, n = 40, in x two displaced pairs drawn separately, in z first telophase bridge and laggard pair. — w- \ddot{o} : D. arctica (No. Dr. 8b, n = 40, in \ddot{o} first anaphase bridge). — All microtome technique. Scale 10 μ .

J	Ľ	A	в	L	E	2	

	Draba n	norvegica	Draba a	urctogena
	Cult. 4772	Cult. Dr. 9	Type coll.	Vildtland Plate I b
2 n	48	48 + ff	48	-
Height in cm	7-8	7-9	9-14	6
Length of ripe siliques mm Breadth of ripe siliques mm Pubescence of siliques	6–7 3.2–3.5 Dense, bifid (-stellate with few large branches)	6-7 3.3-3.5 Not dense, bifid (-stellate with few large branches) subglabrate	6–9 2.5–3.5 Unbranched- bifid	5.5–6 2.8–3.0 Stellate (-bifid)
Seed length mm	1.1	1.1	1.0-1.1	1.0
Length of lower pedicels mm	3.0	2.0-3.5	2.5	2.0
Leaf pubescence (leaves in all four * examples entire): Marginal cilia	Unbranched	Unbranched- bifid-stellate	Unbranched (-bifid)	Dense and unbranched
Upper surface	Unbranched- bifid	Almost glabrous	Unbranched- bifid, very dense on young leaves	Unbranched (-bifid) very dense
Lower surface	Unbranched- bifid-stellate	Stellate-bifid	Unbranched- bifid-stellate, dense on young leaves	Unbranched (-bifid-stellate) very dense

Draba norvegica	Draba arctogena				
Stem leaves 0–3	$\leftrightarrow \rightarrow$	Stem leaves 0–1			
Rosette leaves often \pm dentate	\longleftrightarrow	Rosette leaves entire			
Pubescence of rosette leaf surface not dense, some leaves with many stellate hairs, some mainly ciliated	\longleftrightarrow	Pubescence of rosette leaf surfaces dense, con- sisting mainly of unbranched hairs, which cover the blades			
Siliques usually with mainly bifid hairs	$\leftrightarrow \rightarrow$	Siliques usually with mainly stellate hairs			
Inflorescence mostly elongated	$\leftrightarrow \rightarrow$	Inflorescence usually only slightly elongated			
Low-arctic oceanic	\longleftrightarrow	High arctic continental			

northern *D. norvegica* plants which also have stellate hairs. According to POHLE (1925: 97) the siliques in *D. norvegica* can have unbranched, bifid or stellate pubescence.

In many respects the transition from *D. norvegica* to *D. arctogena* is clinal, which can be expressed in the scheme following Table 2.

Екмах (1929: 489) in camparing Draba norvegica and D. arctogena remarks the pubescence in the latter is much denser. Moreover Draba norvegica in

summer develops leaves with stellate hairs and has some dentate leaves. In cultivated specimens of D. arctogena only the first eight or nine leaves had stellate hairs and the simple ones appeared already on the tenth or eleventh leaf whereas in D. norvegica they made their first appearance with the 25th leaf. Considering the fact that the appearance of unbranched hairs in D. norvegica varies considerably (this was later shown by EKMAN (1941: 137)), it seems as if D. arctogena might be interpreted as one extreme in a clinal series including both species.

EKMAN (1929) first included D. arctogena within D. groenlandica as a variety of the latter. But D. groenlandica is an octoploid and it belongs clearly to the D. cinerea group to which D. arctogena scarcely belongs. In any case, the type of pubescence and the habit of D. arctogena bears no resemblance with those of hexaploid D. cinerea.

The Greenland distribution of *D. norvegica* and *D. arctogena* is of great interest. A detailed map of the Greenland area of *D. norvegica* is found in Böcher (1963) while Hultén (1958) gives a map of its total range. *D. norvegica* can be classified as north-atlantic low-arctic. In sharp contrast to this *D. arctogena* is higharctic-continental. It is common in the interior of Peary Land (Holmen 1957) and extends south to the nunataks of NE-Greenland (Schwarzenbach 1961). In the west it reaches NW-Greenland and Ellesmereland. There are no records between the Thule district and the two occurrences on Disko and at Holsteinsborg. On the map Fig. 5 these two stations are indicated by a special symbol as the specimens in question (hence even the type collection) are transitional between this species and *D. norvegica*. Both stations lie within the northern part of the range of *D. norvegica* where in all probability typical *D. arctogena* is very rare and high-montane as in NE-Greenland. Altogether it is highly probable that the two species where they are sympatric show signs of hybridization or introgression.

At present I am against a reduction of *D. arctogena* to subspecific level. It differs strongly from *D. norvegica* in ecology (distributional type) and it is most likely a comparatively old species with a total area which is almost identical with that of *Braya thorild-wulffii* (see p. 69) and other high arctic relics. Perhaps it survived the last ice-age in ice-free areas in Ellesmere-North Greenland and has only relatively recently come into contact with its southern relative, *D. norvegica*.

Draba arctogena may have evolved from the same group as *D. norvegica* which in itself is very heterogeneous. A partly independent development, however, is not out of the question. Both species are hexaploids and may have reached that level by allopoloploidy after different crossings of species with n = 8 and 16 (or perhaps after fertilization between cells with n = 16 and 32).

Draba cinerea Adams and D. arctica J. Vahl

The *Draba cinerea* group consists of hexaploids, octoploids and decaploids. One of the main problems concerns the identity of *D. arctica* J. Vahl.

According to Ekman (1912: 3, 1917, 1929: 484) typical D. cinerea Adams is

identical with *D. arctica* J. Vahl, a statement which is not in agreement with POHLE (1925: 71) who like BUSCH (1919) tried to maintain *D. arctica* as a sub-group within *D. cinerea*. SCHULZ (1927) in his monograph even maintains *D. arctica* as a separate species.

POHLE considers *D. cinerea* var. arctica (J. Vahl) Pohle to be distinguished from *D. cinerea* by lower stems with fewer leaves, larger flowers and siliques and not so dense a covering of stellate hairs. POHLE's view agrees with that of GELERT (1898: 306) who pictures a specimen of *D. arctica* which has the distinguishing characters mentioned by POHLE. EKMAN (1929) cites the diagnosis of *D. arctica* in order to show how it fits in with the type specimens of *D. cinerea*. But the diagnosis contains no measurements and includes the words "foliis basi ciliatis" which EKMAN interprets as "a few cilia at their base". EKMAN neglects the treatment of the group in BUSCH (1919: 382) in which ssp. arctica (J. Vahl) Busch is described as follows: "Folia rosularum basi ciliata. Caules ca. 5–7 cm alti, 2–4 phylli, pedunculi fructiferi 2.5–10 mm lg. Siliculae pubescentes, ca. 6 mm lg., ca. 2.75 mm lt." BUSCH clearly puts emphasis, on the cilia and he emends VAHL's description by adding the short length of the stems. BUSCH gives stem length of 14–44 cm for *D. cinerea* ssp. "normalis".

In my opinion the character *foliis basi cilialis* refers to the high arctic type found e.g. in Spitzbergen and collected and mentioned by J. VAHL (see Plate II a-d and Table 4). EKMAN tries to avoid the difficulties by saying that in her view the synonomy of *D. cinerea* and *D. arctica* was confirmed by the specimens collected by VAHL in Greenland and adds: "Those from Svalbard are less typical".

A closer study of *D. arctica* reveals that the description and picture of the species in Flora Danica (39:1840:5, Tabula 2294, see Fig. 2) refer to two widely different plants which are both cited in the description. VAHL mentions in his description first Umanaq in W-Greenland and later Bellsound in Spitzbergen. His collections from both places are found in the Botanical Museums of Copenhagen and Stockholm.

The Umanaq plants (Plate II e, III d) have an elongated inflorescence, short peduncles, short and small siliques, short styles, small dense stellate hairs and (1)-2 stem leaves.

The Bellsound plants (Plate II a) in the Copenhagen herbarium have been severely damaged, probably by the painter who made the plate in the Flora Danica. They have longer pedicels, siliques, styles and the inflorescences have fewer flowers. The stellate hairs are longer and not very dense and the stems are short with few or no leaves. In the Stockholm herbarium there is one low specimen (Plate II b) which corresponds to that in Copenhagen and one 25 cm tall specimen (Plate II d) with an elongated raceme, long pediceles and siliques and one stem leaf only. In all the specimens from Bellsound there are some simple hairs on the pedicels and even along the midribs on the lower surface of the rosette leaves. The cilia on these leaves are far more numerous than in the Umanaq plants, see further Table 4.

The main picture on the plate in Flora Danica (Fig. 2) shows a plant which is intermediate between the two collections. It has stem leaves as in the Umanaq



Fig. 2. Draba arctica J. Vahl. The plate 2294 in Flora Danica. The pubescence consists of rather large and not very dense stellate hairs and the siliques have long pedicels as in the Spitzbergen material but 1–2 stem leaves as in the Umanaq material. — Scale 10 cm.

plant while the peduncles and siliques correspond to the Spitzbergen plants. The stellate pubescence on the enlarged silique is also as in the Spitzbergen plants but the style is short as in the Umanaq plants.

This shows that VAHL'S *D. arctica* is an ambiguous entity. It includes partly material which must be referred to *D. cinerea* Adams, partly a high-arctic taxon, which corresponds to POHLE'S *D. cinerea* var. *arctica* and which in the following will be mentioned as *D. arctica* J. Vahl (p. p.).

Thus *Draba arctica* which will be described in detail below has now to be based on the collections by VAHL from Bellsound in Spitzbergen, all three specimens serving as lectotypes.

In the following, the taxa in the *D. cinerea* group are arranged according to their ploidy-level.

Draba cinerea Adams

Cytological studies. HEILBORN (1927, 1941) counted n = 24 in material from Umanaq and from "Greenland" (without locality, but presumably also from Umanaq). The same number was found in the var. *brachysiliqva* (Mela) Ekm. from the Ladoga area. Concerning the Umanaq material he says that the plants have a few simple hairs on the petioles and somewhat dentate leaf laminae.

The var. *brachysiliqva* (from Mäkisalo, Karelia ladogensis) has a few long and simple hairs on the leaves which otherwise have a very dense covering of small stellate hairs. EKMAN (1917, 1926:42) takes the simple hairs as an indication of some kind of introgression, but HEILBORN (1927) doubts its hybrid nature and suggests it to be a primitive form within the species complex. It has very short siliques while the stems are tall (14–22 cm) with some simple hairs at the base and 2–3 leaves (see Plate III and Table 3b).

Material with the hexaploid number was also collected by the present author at the head of Søndre Strømfjord (Store Saltsø), SW-Greenland and was cultivated in the Arctic Greenhouse over several years (Cult. No. 4813). The meiosis proceeded very regularly (Fig. 1 d). The plants in culture maintain small flowers and short siliques and have a dense covering of small stellate hairs and only very few marginal cilia at the base of the petioles. They have usually two stem leaves, see Plate VIb–c and Table 3c.

JØRGENSEN, SØRENSEN & WESTERGAARD (1958:68) refer to material with n = 24 which they have called *D. ovibovina* and material with n = 40 which they refer to *D. cinerea*. Unfortunately the dried material corresponding to the two fixations had been mixed. It is clearly the hexaploid number which has to be attached to *D. cinerea*. The plants in question are very small (Plate VI, a) but have two stem leaves. They have the dense covering of small stellate hairs and short siliques. Marginal cilia are present on the lower part of the rosette leaves and a few simple hairs also occur on the basal part of the stems, see further Table 3e.

It is very probable that EKMAN's collection from Umanaq W-Greenland (Aug. 1923, Herb. Stockholm) corresponds to the plants which were counted by HEILBORN. The plants resemble VAHL's collection from Umanaq (Plate IIId), the dimensions are given in Table 3d.

Common to all material which has been studied cytologically and shown to be hexaploid, is the dense cover of small stellate hairs (Fig. 3), the short peduncles, the short siliques and the presence of more than one stem leaf.



Fig. 3. On the left three stellate hairs of hexaploid *D. cinerea* (No. 4813); on the right three of octoploid *D. arctica* ssp. groenlandica (K. Holmen No. 6712). — Scale 100 μ .

Typical Draba cinerea. According to EKMAN (1929:484) the type of *D. cinerea* from Schigansk has short oval siliques and a fine pubescence of stellate hairs. She found some needles of *Larix sibirica* between the rosulate leaves. It was collected 1817 by ADAMS in "locis montosis sterilibus". Schigansk is on the Arctic Circle and south of the timber line.

The type specimen which is illustrated in EKMAN 1917 (Plate 3) is 27 cm high with 3 stem leaves and a long raceme. It differs from the material which was counted in having long pedicels and narrow siliques which have a tapering distal part and fairly long styles. It is clearly the same plant which is mentioned by BUSCH (1919:381) as "ssp. normalis". His drawing on p. 383 shows a specimen 16 cm high with 3–4 stem leaves and a raceme of narrow tapering siliques on long pedicels. The diagnosis says "Pili simplices desunt", but a few simple hairs are shown on the drawing.

The Stockholm Herbarium contains several sheets collected by N. H. NILSSON from Asia which resemble the type material in every detail. Some measurements of this material are collected in Table 4. It appears that all the plants have narrow and rather long siliques (4.5–9 mm long, 1.5–2 mm broad) and most often long pedicels and 3–4 stem leaves (Plate IV a–b). They correspond to the material studied cytologically in two respects: The small size of the stellate hairs, the very few cilia and the small flowers and seeds.

 TABLE 3. Draba lanceolata – cinerea – arctica.

Taxon	Reference to text	2 n	Height in cm	Length of rosette leaves mm	No. of stem leaves	Length of longest siliques mm	Length of styles mm	
D. lanceolata	a	32	13-21	10-12	3-6	10.5(9-11)	0.3(0.2-0.4)	
D. cinerea	b	48	14-19	12–15	2 - 3	4.4(4-5)	0.5(0.4 - 0.5)	
D. cinerea	с	48	10-16	5-	2 - 3	4.4(4-5)	0.5(0.3-0.6)	
D. cinerea	d	48	12-20	10-15	(1)-2	5.5(4.5-6)	0.6(0.5-0.7)	
D. cinerea	e	48	5-6	6	2	4.4(4.2–4.5)	0.5(0.4-0.5)	
D. arctica ssp. groenlandica	f	64	4-11	7-10	0-1(2)	7.1(6.3-7.7)	0.3(0.2-0.4)	
D. arctica ssp. groenlandica	g	64	8-10	8-10	0-(1)	6.0(5.3-7.0)	0.4(0.3-0.5)	
D. arctica	i	80	10	12-15	0	7.2(7-7.5)	0.5(0.4 - 0.6)	
D. arctica	j	80	7-8	5-6	0-1	7.3(6.5-8.0)	0.6(0.5-0.7)	
D. arctica	k	80	4	4-5	0	7.4(7-8)	0.7(0.6-0.9)	

In spite of the fact that no chromosome count exists for the Siberian population of typical *D. cinerea*, it is most probable that it is hexaploid too. The small stellate hairs and comparatively many stem leaves (more than one) and the small seeds are probably important characters as indicators of the ploidy-level.

Most of the material which was counted can without difficulty be referred to var. brachysiliqva (Mela) Ekm. EKMAN (1917:35) says that this variety is very closely related to typical *D. cinerea*. As mentioned already she puts forward the hypothesis that the variety is hybridogenous, originating from crosses between *D. cinerea* and *D. norvegica* (coll.), which is not untenable as both species belong to the same ploidy -level. The occurrence of simple hairs in the Finnish material from Kuusamo as well as in the Ladoga plants may indicate this. However, Greenland plants with almost the same habit (Plate III), are without simple hairs apart from a few cilia on the petioles. In my opinion it is impossible to base hybrid origin on small deviations in the hair cover. We must not forget that hexaploids within the *cinerea* group may have evolved from different crosses or that various cytological aberrations may have had the effect of a repatterning of the chromosome set leading e.g. to difference in the proportion of hair types.

HEILBORN (1927:65) holds the view that the series n = 24, 32, 40 has arisen out of two primitive forms, one with 16 and the other with 24 haploid chromosomes. A 16-chromosome form as the hypothetical parental species is, however, as he says, difficult to demonstrate.

As mentioned under *D. norvegica*, plants with 2n = 48 may have arisen by

	Lowest pedicels	Length of	Length of	Length of	s: ste	Pubescence s: stellate, b: bifid, c: cilia or unbranched ↓: occurring mainly downwards						
(shorten or equa (e) silic	shorter (s) • equalling e) siliques	sepala mm	mm	mm	Rosette leaves	Stems	Pedicels	Siliques	Diameter of stellate hairs μ			
	s	2.0	3.5 - 4.0	0.8–1.1	s(c↓)	sc↓	cb(s)	s	225(125-350)	 Plate IVd		
	s	1.5	2.2	0.8 - 1.0	sc↓	sc↓	s(b)	s(b)	230(150-275)	Plate IIIb-c		
	S	1.5 - 2.0	3.0 - 3.5	0.8 - 0.9	s(c↓)	S	S	S	235(175-300)	Plate VIb-c		
	s	2.1 - 2.5	3.5 - 3.6	0.6 - 0.7	$s(c\downarrow)$	$s(cb\!\downarrow)$	S	S	250(200-300)	Plate IIe, IIId		
	s	2.0	3.0 - 4.0	- 1	s(c↓)	s(c↓)	S	S	250(175-300)	Plate VIa		
	s	2.5 - 3.2	4.5 - 5.0	0.9-1.0	s(bc)	sc↓	s(b)	s	310(200-375)	Plate Va-c		
	s	-	-	0.9-1.0	s(c↓)	s(c↓)	S	S	300(200-425)	Plate VIe		
	e	2.3 - 2.5	4.5	1.1	sbc	S	S	s	375(250-500)	Plate VIf		
	s-e	—	-	-	sbc↓	sbc	sc	_	350(150-500)			
	s		-	1.1	sbc	$\mathrm{sbc}\!\!\downarrow$	sbc	S	400(325-550)	Plate VIg		

Measurements of plants with known chromosome number.

doubling the chromosomes in a hybrid $n = 8 \times n = 16$ or by crossing between tetraand octoploids ($n = 16 \times n = 32$). The latter idea has in the case of *D. cinerea* the great advantage that one is dealing with chromosome numbers which are known within the *D. cinerea* group and adjacent groups. POHLE (1925:1) groups *D. incana*, *D. lanceolata* (*-stylaris*) and *D. cinerea* together and in SCHULZ (1927:206), *D. cinerea* and *lanceolata* end up in the same part of the key to *Leucodraba*. As 2n = 32 is found in *D. lanceolata*, we may imagine that typical *D. cinerea* was endowed with erect stems and rather many stem leaves and its dense very small stellate hairs from *D. lanceolata* or its ancestors while other characters were received from the octoploids within the *D. cinerea*-group, e.g. *D. arctica* ssp. groenlandica.

EKMAN (1935:352) states that *D. cinerea* due to its pubescence is closely related to *D. lanceolata*. She discusses also a sterile specimen from Sofia's Harbour in continental W. Greenland which she interprets as *D. cinerea*×*lanceolata*. This hybrid would probably be the result of a fertilization between cells with n = 24 and n = 16.

The geographical distribution of *D. cinerea* s. str. is quite interesting. In Asia it is sub-low-arctic, whilst in N. America A. E. PORSILD (1955:124–125) says that *D. cinerea* s. str. "is a continental, subarctic rather than high-arctic species which, north of the mainland, extends only to the southernmost islands of the Arctic Archipelago." This is in complete agreement with the distribution in Greenland. It is here restricted to the two continental districts CW and CE (cp. Böcher, Holmen & Jakobsen 1966). Most of the material has short siliques, but some specimens, mainly those from Northeast Greenland, closely resemble typical Asiatic or North American *D. cinerea*. Böcher

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(1954: 155, 156, 163) contains some notes about its type of habitats. It is found on dry gravelly slopes together with *Dryopteris fragrans*, *Woodsia ilvensis* and *Saxifraga tricuspidata*. In Greenland typical *D. cinerea* is a low arctic continental species; it seems only to touch higharctic areas and is absent from subarctic—suboceanic environments.

Draba arctica J. Vahl p. p. ssp. groenlandica (Ekm.) comb. nov.

Cytological studies. The first count of *Draba groenlandica* was made by HEIL-BORN (1941: 142). As EKMAN (1929: 487) includes the chromosome number (n = 32)in the diagnosis there is no doubt that this number was found in the type material collected by herself in 1923 at Godhavn, Disko.

The type material (D. groenlandica sp. n.) which is kept in the Stockholm Herbarium was collected on June 23th 1923, other specimens (labelled D. groenlandica mihi) were collected in August (Plate V, a-c). The plants are 4–11 cm high with 1 (rarely 2) stem leaves. Pedicels are short and the seeds larger than in D. cinerea. Some of the rosette leaves are ciliated along their margins and have some simple hairs on the lamina. Usually, there are also simple hairs on the lower part of the stems and on the pedicels. The stellate hairs are larger than in D. cinerea. (Fig. 3), Table 3f.

HOLMEN (1952: 13) also reports n = 32 in material from Peary Land. This material is closely related to *D. groenlandica*. In his later treatise (1957: 59) he transfers the material to *D. cinerea* coll. which is quite understandable as the pubescence differs from the type material of *D. groenlandica* having fewer simple hairs (cp. Plate VI, e and Table 3g).

The very interesting plants counted by HOLMEN have lead me to the conclusion that the octoploids form a series of plants with different density of simple hairs; none of them, however, have as few simple hairs as typical *D. cinerea*. They are distinguished from typical *D. cinerea* by larger stellate hairs and seeds, fewer cauline leaves, coarser and shorter growth, and in many cases the occurrence of unbranched hairs on the basal part of the stem.

As plants belonging to ssp. groenlandica are octoploids they may have reached that level in a less complicated way perhaps more resembling autopolyploid development. We have no knowledge of similar species with 2n = 32, but they may exist e.g. in Siberia. In the Stockholm herbarium one sheet from Irkaj pij (Tjuch peninsula) ($68^{\circ}55'$ N., $179^{\circ}25'$ Long.) collected by KJELLMANN Sept. 1878 was determined by EKMAN as *D. groenlandica*. It has the mixed type of pubescence, short stems and coarse habit, but has small seeds and siliques (see Table 4 No. 6). It is presumably related to *D. parvisiliquosa*. Tolm. from arctic Taymir. According to Tolmatchew (1932: 142) the type of pubescence in this species is mixed and it has thick siliques 3–4 mm long. It is closely related to *D. cinerea* and occurs on dry stony hillslopes and on the edges of large tundra-hummocks.

19

As compared with *D. cinerea* the octoploids within *D. arctica* have a much more arctic distribution and at the same time are not so continental in their climatic requirements. In Greenland they are wide ranging with a montane behaviour in the south (Fig. 5). They grow on Disko Island where no true *D. cinerea* is found. A. E. POR-SILD (1955: 125–126) mentions ssp. groenlandica from the Arctic Canadian Islands from Banks Island to Greenland. His picture (1957: Fig. 40 a–e) agrees with Greenland material of ssp. groenlandica.

The octoploids are difficult to separate from *D. arctica* as defined above and would be covered by POHLE'S *D. cinerea* var. *arctica*.

Taxonomically, the octoploids may best be distinguished from true D. arctica by the shorter pedicels and the shape of siliques. But in many cases the determination will be difficult. In my opinion it is therefore best to treat them as members of a subspecies. In a previous paper (B. 1952) I proposed the combination D. cinerea ssp. groenlandica but as I consider that the octoploids in many respects resemble D. arctica more than D. cinerea I now prefer the new combination D. arctica Vahl (p. p.) ssp. groenlandica (Ekm.).

From the continental area at the head of Søndre Strømfjord and at Arfersiorfikfjord there are a few collections of plants which have a pubescence closely resembling ssp. groenlandica but which differ in habit, having slender, erect stems (Plate V h–i). They have been referred to ssp. groenlandica but may perhaps have resulted from a cross between true ssp. groenlandica and D. lanceolata. In some of the plants the seedfertility seems to be reduced, in others not. A hybrid of this type would be less puzzling if we suppose that e.g. normal pollen of ssp. groenlandica fertilized an unreduced egg cell in D. lanceolata.

On the map Fig. 6 specimens which with regard to type of pubescence, correspond to the type of *D. groenlandica* have been indicated with open circles. The majority of specimens resemble the specimen collected by HOLMEN and counted by him (Plate VI e and Fig. 6 solid circles). They might have been referred to a separate variety with fewer unbranched hairs and broader siliques. However, I am unwilling to erect a new taxon as it would involve an unnecessary complication. On the other hand the present treatment involves an emendation of EKMAN's taxon, amplifying it to cover both types of octoploids.

Draba arctica J. Vahl p.p. ssp. arctica and ssp. ostenfeldii (Ekm.) comb. nov.

Cytological studies. Decaploid plants belonging to the *D. cinerea* group were first found by HEILBORN (1927: 62) working with Spitzbergen material. Morphologically this material differed from typical *D. cinerea* in having simple hairs on the fruiting pedicels. It also had scattered simple hairs on the surface of the leaves as well as stellate hairs. Also FLOVIK (1940: 433) reports 2n = 80 in plants from Spitzbergen, but has no description of their morphology.









A third count (n = 40) was made by the present author in material collected in the Advent Valley on Spitzbergen by NIELS FOGED and cultivated as Dr. 8b. In most PMCs meiosis appeared regular (Fig. 1æ) but in a few cells inversion bridges with fragments occurred at first anaphase (Fig. 1ö). Most loculi had normal tetrads but not infrequently dyads and giant pollen grains were formed, see Fig. 6. Smaller deviations such as elimination of single univalents or exclusion of a single chromosome at Metaphase I occurred occasionally. Also, in a few loculi a degeneration of the PMCs took place. In such loculi, anaphase I cells had sometimes numerous bridges due to stickiness of some kind.

The plants in question have stellate publication on the rosette leaves intermixed with a few simple hairs. They were compared with *D. cinerea* No. 4813 which was cultivated simultaneously:

- No. Dr. 8b: Largest rosette leaves frequently more than 3 mm broad, green; the stellate hairs do not cover the surface and the interstices are often broader than the hairs. The stellate hairs coarser on relatively long and broad hairstalks. Unbranched hairs along leaf margin (cilia) reach middle part of leaf. Young leaves grey, with much denser hair cover. 0–1 stem leaf, large flowerbuds. Difficult to cultivate.
- No. 4813: Largest rosette leaves usually less than 3 mm broad, grey. Almost covered by smaller and more slender stellate hairs with thin and short hairstalks. Marginal cilia on petiole only. Up to 3 stem leaves, small flowerbuds. Easy to cultivate.

The first decaploid material from Greenland was reported by JØRGENSEN et al. from two places on Clavering Island in N.E. Greenland. As mentioned under *D. cinerea* (p. 14) one part of the dried material of the fixed plants had been mixed. Accordingly the decaploid number has almost certainly to be attached to two somewhat different plants, one (k) belonging to EKMAN's taxa. *D. ostenfeldii-ovibovina*, the other (j) to *D. arctica*.

(j) 7–8 cm high with 0–1 stem leaf. Rosette leaves 5–6 mm long with large stellate hairs. Marginal cilia present, which in the upper part are often replaced by bifid hairs. In young leaves cilia also along the upper margin and some bifid hairs between the stellate ones on the laminae. Siliques 7.3 mm. Pedicels with stellate hairs and few simple ones (see Table 3 j).

(k) Plants 4 cm high without stem leaves. Rosette leaves 4–5 mm long covered with large stellate hairs intermixed with a few bifid hairs, cilia along margin and below on midrib. Siliques 7.4 mm long with large stellate hairs. Pedicels also with simple hairs (see Plate VI g and Table 3 k).

The difference between j and k is not striking and can be characterized as a difference in the amount of simple and bifid hairs.

A third fixation of material from Kap Oswald, NE Greenland was made by KJELD HOLMEN who kindly placed imbedded buds and a dried specimen (Plate VI f) at my disposal. Unfortunately most buds were too old, but in one flower some unclear second anaphase plates were studied. They showed that the number was about 40. The dried material has long siliques and cilia (Table 3).

The Spitzbergen material of D. arctica

Three fixations from Spitzbergen all showed the same number 2n = 80. The lectotype collected by VAHL is from Spitzbergen and agrees completely with other material from the Svalbard area. The very comprehensive collections from Spitzbergen kept in the Stockholm herbarium show that the species is particularly uniform in that part of the Arctic. We may therefore use a detailed study of this material as a starting point for a discussion of the decaploid section of the *D. cinerea* group. On the basis of the material in Table 3–4 the following description can be given:



Fig. 6. Two loculi in two adjacent anthers in *Draba arctica* (Dr. 8b) showing giant pollen (on the right) and normal pollen as well as one dwarf grain (on the left). — Scale 100 μ .

3-15 (-25) cm tall with many ascending-erect stems bearing 0-1 (2) leaves. Full-grown rosette leaves greenish, usually 4-6 mm long, covered with large stellate hairs, ciliated at base or up to the middle part of the leaf and sometimes with some few simple or bifid hairs even on the lamina. Stems with stellate pubescence, in the lower part intermixed with simple hairs. Pedicels with stellate hairs usually also with some bifid or simple hairs, the lower pedicels almost as long as the siliques. Sepals 2.5-3 mm, petals 4-5 mm long; large ripe siliques 7-11 mm long, broadest below, tapering; styles 0.5-0.9 mm long. See further Plate VI h-i.

The taxonomic status of D. ostenfeldii Ekm. and ovibovina Ekm.

In high arctic areas some deviating plants occur, which appear to be overnourished, possible by guano (Plate VII). They have broader leaves and the hair cover is more soft and some of them have larger flowers. It is impossible without cultivation experiments to decide whether such plants are modifications due to enriched soil conditions or not. EKMAN (1929) referred them to a new species *D. ostenfeldii* Ekm. with large flowers (Petals 4.5-5.25 mm) and comparatively many simple and bifid hairs on the leaves and to its var. *ovibovina* with predominantly stellate hairs on the leaves and flowers of the same size as in *D. arctica* (see above) This latter

TABLE

Collection	Taxon	Origin and Collector	Height in cm	No. of cauline leaves	Length of longest siliques mm	Length/ Breadth of siliques	Lowest pedicels shorter (s) or equalling (e) siliques	Length of sepala mm
1 2		Jakutsk, Kumach Sur. 71°30' N. H. Nilsson Jakutsk, Balaganach	17–29	2-4	5.5–7.5	3.2 – 3.8	e	1.8 - 2.0
0	D	71°35′ N. H. Nilsson	15	3-4	4.5 - 6.0	3.0 - 4.0	е	2.1 - 2.4
3	var. cinerea	N. H. Nilsson	15–19	1–2	7.5–9.0	3.5 - 4.5	е	-
-		N. H. Nilsson	19–24	3-4	7.0–10.0	4.0 - 4.5	е	
Э		A. Tolmatchev No. 43	ca. 8	2–3	-	-	-	1.5
6	D. cfr. parvisiliquosa	Irkajpij, 68°55′ F. R. Kjellman	6-8	1–2	3.8-4.2	1.8 - 2.9	s	_
7		Kuusamo, Aulaukajoki, A. L. Backman	15–18	2–3	3.3-4.5	1.8 - 2.0	s	1.8
8		Kuusamo, Ruskeakallio, J. Montell	13–23	2-(4)	5.0-5.5	2.0 - 2.5	s	2.0
9	D. cinerea	Ladoga, Mäkisalo A. L. Backman	22	1–3	3.5-4.5	1.8 – 2.0	s	1.3
10	var. brachysiliqva	W. Greenland, Strömfjordshavn, TWB	16 - 25	2	4.0 - 4.5	2.0 – 2.2	s-e	-
11		W. Greenland, Umanaq, J. Vahl	8–12	2–3	4.0-5.5	2.0 – 2.5	s	1.8
12		W. Greenland, Umanaq, Enander	6-13	1-2(3)	4.0-5.5	2.6 – 2.8	s–e	2.0 - 2.5
13		W. Greenland, Godhavn,	- 10					
14	D. arctica ssp. groenlandica	J. Lagerkranz E. Greenland, Skeldal, T. T. Elkington	7–10 7–10	0-1	6.0-7.0	2.5 - 3.0 2.4 - 3.0	s s–e	_
15	D anation	W. Greenland, Tunertoq						
16	ssp. groenlandica	TWB & Lægaard W. Greenland, East of	14	2	7.0-10.0	4.0 - 5.0	S	-
	(deviating)	Mt. Hassel, TWB	10	1	8.0-9.0	4.0-4.3	s	-

¹) s = stellate; b = bifid; u = unbranched; c = marginal cilia; \downarrow means that the hair type occurs downwards

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Length of petala mm	Length of ripe seeds	of Length of Pubescence ¹) m m							Remarks
	mm	Rosette leaves	Main stems	Pedicels	Siliques	Size of stellate hairs			
3.0	-	s c ↓	s	s	s	small			
3.5-3.8	=	s c↓	8	S	s	small			
-	0.7	s c↓	s(u−b ↓)	s	s	small			
	0.7 - 0.8	s c ↓	s	s	s	small	Plate IVa		
2.5	-	s c↓	S	S	s	small			
-	0.6 - 0.7	s, u, b, c ↓	s	5	s	small			
2.5 – 3.0	0.7 - 0.8	s c↓	s(u ↓)	s	s	small			
4.0	0.7	s c↓	s(u ↓)	s	s	small			
2.0 – 2.2	0.7 - 0.8	s c ↓	s(u ↓)	s	s	small			
-	0.6 - 0.8	s c ↓	s	s	s	small	Plate IIIa		
2.0	0.6 - 0.7	s c↓	s	s	s	small	Plate IIId	(Type material)	
3.5 - 3.8	_	s c↓	s	s	s	small			
-	1.0	scb	s(u ↓)	u-b(s)	s	intermediate	Plate Vd–f		
-	1.1	s c↓	s(u ↓)	s(b)	s	intermediate	Plate Vj		
-	-	s c b	s(u ↓)	s(u)	s	intermediate	Plate Vh–i		
_	-	s c ↓	s	s(u)	s	intermediate			

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Collection	Taxon	Origin and Collector	Height in cm	No. of cauline leaves	Length of longest siliques mm	Length/ Breadth of siliques	Lowest pedicels shorter (s) or equalling (e) siliques	Lenght of sepala mm
17	(Spitzbergen, Bell Sound.						
		J. Vahl	8-10(25)	1-2	7.0-8.5	3.0 - 3.7	e	2.0
18		Spitzbergen, Sassenberg,	7.10	0.1	0.0.10.0	90 90		17.00
19		Spitzbergen, Advent Bay,	7-10	0-1	9.0-10.0	2.8-3.0	e	1.7-2.0
		E. Jørgensen	6-10	0-1	7.0-9.0	3.3 - 3.5	s-e	2.5
20	D. arctica	Spitzbergen Isfjord, Advent	10.15	0.1	80.110	2744		2.0
21	ssp. arctica	Spitzbergen, Middlehook,	10-13	0-1	8.0-11.0	5.7-4.4	e	5.0
		I. A. Bjørling	3–5	0-1	6.0 - 7.0	2.4 – 3.0	e	2.5
22		Spitzbergen, Longyearbyen, J. Lagerkranz	6-16	0-1	8.0-10.0	3.8-4.0	e	2.5
23		E. Greenland, Ostenfeld				010 110		
	l	Nunatak, Schwarzenbach	23	0-1(2)	8.0-11.0	3.8-4.0	e	-
24	D. arctica ssp. arctica	W. Greenland, 900 m,						
	(deviating, approach.	Sdr. Strømfjord, Beschel	18-21	1-2(3)	6.5-9.0	3 2-3 4	e	2.2
		W. Crearland Saundara Isl	1 10 21			0.2 0.1		
20	ssp. ostenfeldii	P. Freuchen	4-10	2	8.0-9.0	3.4 - 3.0	s	4.0
26	D. arctica	Spitzbergen, Longyearbyen,						
97	ssp. ostenfeldii	J. Lagerkranz	5-8	0(1)	7.0-8.0	3.2 - 3.4	s–e	-
21	ssp. ostenfeldii	H. G. Simmons	10-15	1-2	7.0-9.0**	2.3 - 3.0	s-e	3.0
	var. ovibovina							
28	D. arctica	Ellesmereland, Fram Hb.	12	0-1	7.5-8.5**	2 5-2.8	е	
	var. ovibovina					210 210		
	(ad groenlandica)							

¹) s = stellate; b = bifid; u = unbranched; c = marginal cilia; $\downarrow = means that the hair type occurs downwards on$

rather doubtful taxon was later promoted to a separate species by EKMAN (1941: 135). Common to both is a soft pubescence of mixed hairs (unbranched, bifid, stellate) on the pedicels.

The chromosome counts of 2n = 80 in very small plants of the *ovibovina* type, which clearly have not been affected by enriched soil (Plate VIg) makes it most probable

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4 (continued).

Length of petala mm	Length of ripe seeds mm			Reference to Figures	Remarks			
		Rosette leaves	Main stems	Pedicels	Siliques	Size of stellate hairs	0	
3.2	1.0	s(u)c↓	s	s(u)	s	large	Plate IIa–d	(Type material)
3.5 - 3.7	1.0 - 1.2	s c \downarrow	s	s	S	large	Plate VI	
4.0	1.0	s(u)c \downarrow	s(u ↓)	s(u)	s b	large	Plate VI	
4.5 - 5.0	1.0 - 1.1	sbc↓	s u(↓)	S	s b u	large		
4.0 - 4.5	1.0	sbuc↓	s(u ↓)	s b	s b	large		
4.0 - 4.5	1.1 - 1.2	sbuc↓	s(u ↓)	s b u	s	large		
-	1.0-1.1	s(b u)c \downarrow	s(u ↓)	s u	S	large	Plate VI d	
3.0	0.9 - 1.0	s(b) c \downarrow	s(u ↓)	S	5	intermlarge		
5.0 - 6.0	-	s*b u c↓	s b u	u s	s b	large	Plate VIIa	(Type material)
-	1.0 - 1.1	$s(c \downarrow)$	s(u ↓)	u s	s	large	Plate VIIb	material)
4.0-4.5	1.0	s b(c \downarrow)	sbuc↓	u s	s b	large	Plate VIIc	(Type material)
	1.0	s u b(c \downarrow)	s(u ↓)	u s	S	large	Plate Vg	

the organ. * stellate hairs with long stalks. ** very short styles.

that genetically deviating decaploids exist which ought to be considered taxonomically. However, the type of pubescence is not widely different from that found in typical *D. arctica*. As long as it is completely obscure whether *D. ostenfeldii* represents a modification of *D. ovibovina*, it may not be practical to abandon it. Therefore, it is proposed provisionally to consider both as was proposed by EKMAN (1929) but at the same time reducing *D. ostenfeldii* to subspecific rank as the new combination, *D. arctica* J. Vahl p. p. subsp. *ostenfeldii* (Ekm.). Var. *ovibovina* Ekm. belongs to this subspecies; see further Plate VII c.

Key to the Greenland taxa of the Draba cinerea group

The key given here summarizes the points made in the preceeding section. Draba arctogena and D. dovrensis Fries which are mentioned in EKMAN's key (1941: 135) are omitted. The former because it is considered to be closely related to D. norvegica, the latter because it is connected with D. glabella, see p. 29.

- A₁ Stem leaves 2–4. Stellate hairs small, about ¹/₄ mm in diameter, always dense, covering leaves and siliques. Very few cilia on petioles. Flowers small, seeds 0.7–0.8 mm long..... D. cinerea Adams.
 B₁ Siliques narrow and tapering towards the apex, lowest pedicels equaling the siliques.... D. cinerea Adams, ssp. cinerea (Plate IV a–c).
 B₂ Siliques short, not tapering, with almost obtuse apices, pedicels short 2n = 48. D. cinerea Adams ssp. brachysiliqva (Mela) Ekm. (Plate III).
 A₂ Stem leaves 0–1 (2). Stellate hairs large, flowers large, seeds about 1–1.1 mm long. Pubescence on siliques (sometimes on leaves) less dense. D. arctica J. Vahl p. p.

D ₁ Many unbranched hairs on the leaves, flowers large	
var. ostenfeldii (Plate VII a, h).
D2 Predominantly stellate hairs on the leaves, flowers of normal si	ze
2n = 80 var. ovibovina Ekm. (Plate VII o).

Draba glabella Pursh

Draba glabella Pursh, which according to FERNALD (1934: 333-334) covers D. hirta of many authors and D. daurica DC., is another very polymorphic species. In many respects, it constitutes a series of forms which is parallel to the D. arctica complex, in that both species include both octoploids and decaploids. The main difference between the two series is difficult to define in as much as D. glabella s. l. also embraces forms with more or less hirtellous siliques. However, D. arctica is a member of a xerophytic group which ecologically differs from the D. glabella group, the latter being mesophytic with greenish leaves and with sparsely pubescent scapes and usually almost glabrous siliques.

Previous chromosome counts. There are many counts of n = 32 in the *D. glabella* complex. HEILBORN (1927: 62, 1941: 142) found this number in "*D. magellanica* ssp. *borea* Ekm." from Swedish Lappland, Umanaq in W. Greenland (two strains, one being a *condensata*-form), Atanikerdluk in W. Greenland (var. *lutescens* Ekm.) and Godhavn, Disko. Also the populations of *D. glabella* in the Søndre Strømfjord area (67° lat. N.) in spite of attaining very different heights (BöCHER 1952 Fig. 10) are octoploids. Three strains were counted by BöCHER & LARSEN (1950: 19). According to Jørgensen et al. (1958: 68) material from NE Greenland studied by Holmen also belongs to the octoploid series.

Draba dovrensis Fries (D. hirta var. dovrensis), which resembles D. dasycarpa Mey. of Altai and seems to be closely related to D. glabella, has n = 32 (HEILBORN 1927 in material from Kongsvold in Dovre). It has hairy siliques and was interpreted as a hybrid between D. cinerea and D. glabella (hirta) by EKMAN (1935), but HEILBORN reports no meiotic irregularities which might indicate hybrid origin and there are no D. cinerea or D. arctica in southern Scandinavia where it occurs.

Also *D. magellanica* Lam. from the straits of Magellan has n = ca. 32 (Heilborn 1941) which agrees with the fact that this species resembles *D. dovrensis* (EKMAN 1933: 479).

Decaploid strains were hitherto only found in Greenland material, i.e. from Godhavn by Heilborn (1927: 62) and Clavering Island, NE. Greenland, by Jør-GENSEN et al. (1958).

Cytological observations. New material of the *D. glabella* complex has been studied from five very different localities. In three of the cases the plants were octoploid, i.e. Cult. No. Dr. 12 from Finland (Turku Bot. Gardens) No. 6325 from rocks at Percé (Gaspé Peninsula, Canada) and No. 4814 from head of Søndre Strømfjord, W. Greenland. One culture No. 4788 from Godhavn was decaploid as was a plant fixed in N.E. Greenland by KJELD HOLMEN (Holmen No. 261, see Fig. 7).

Meiosis was regular in No. 6325 (Figs. 1, s-t). In No. 12 one univalent (and possibly a trivalent) occurred in a very few cells. In No. 4814 one pair was often placed above or below the first metaphase plate. Meiosis proceeded here mostly normally but in

Cult. No.	Origin	2n	Height of plants in cm	Number of stem leaves	Length of ripe siliques, mm	Length of ripe seeds mm	Other characters	
6325	Gaspé Peninsula Canada	64	12(10-16)	2-3(4)	9–10	1.0-1.2	Rosette leaves more narrow mostly with two opposite	
Dr. 12	Turku Bot. Gardens Finland	64	15(9-20)	2-4	7–10	0.9–1.1	teeth, ciliation often restric ted to petiole or as in No 2325, sometimes also reaching	
4814	Søndre Strømfjord W. Greenland	64	11(7–15)	(1)2–3	6–9	0.9–1.0	higher up. Flowering once a year.	
4788	Godhavn, Disko W. Greenland	80	7(6-8)	(0)1-2	5–8.5	0.9–1.0	Rosette leaves rather broad more green almost entire, cili- ated up to middle part. Flow- ering twice a year.	

TABLE 5. Cultivations of Draba glabella.

some of the anther loculi dyad formation occurred indicating apomeiotic development. Some of the dyad cells developed into giant pollen grains. In the decaploid No. 4788 displacement of one or two bivalents from the equatorial plane took place in some PMCs (Fig. 1 x) while in others a pair of univalents were observed outside the plate. Occasionally a quadrivalent configuration occurred. Most anaphases appeared normal but Fig. 1 z shows that laggards and bridges occur although probably rarely.

Morphology of material with known chromosome number. The octoploid strains were all relatively tall with 2–4 cauline leaves and the racemes became elongated at fruiting stage resulting in a rather remote positioning of the siliques (Fig. 7). The decaploid No. 4788 was low in culture with (0) 1–2 leaves and its raceme was denser on a longer peduncle (Table 5). The East Greenland decaploid plant (Holmen No. 261) has also the dense terminal raceme and 0–2 cauline leaves (Fig. 7 on the left).

It proved impossible to demonstrate any distinct differences between octoploids and decaploids with regard to size of stellate hairs and seeds but there seemed to be a slight difference in the shape of the fruits and the breadth of the rosette leaves (Table 5). The siliques are lanceolate, subacute in the octoploids, while they may be elliptic and slightly obtuse in the decaploids (Fig. 7). The longest siliques are 6-8.5 mm in the latter and 9-10 mm in the octoploids. The cauline leaves are broader near the base in the plant from NE. Greenland, and \pm cuneate in most octoploids. The latter distinction corresponds to that used by SCHULZ in his attempt to distinguish



Fig. 7. Draba glabella Pursh. On the left decaploid from Kap Oswald, Ella Ø, East Greenland (leg. K. HOLMEN Aug. 1960), on the right single shoot and new rosette from hexaploid cultivated material (Cult. No. Dr. 12 from Finland). — Scale 10 cm.

between D. hirta and D. daurica and appears also from the pictures of D. hirta and D. daurica in BUSCH (1919: 351 and 357). However, as pointed out by FERNALD (1934 Plate 308) it is impossible to use this difference between two species as the type material of D. daurica has cuneate stem leaves as has that of D. glabella. Although the shape of the stemleaves may be of some importance it is certainly not a reliable character and seems not to be clearly correlated with differences in chromosome number.

The octoploids vary in degree of pubescence. No. 6325 and 4814 have almost glabrous upper stems and leaves and completely glabrous siliques, while in Dr. 12 the siliques have some unbranched or bifid hairs along the margins. Both decaploids have glabrous siliques.

Almost the same pattern of variation in pubescence is found in dried material of plants with unknown chromosome number. Most specimens have completely glabrous siliques and scattered stellate pubescence on pedicels and stems. Deviations from this may be exemplified as follows:

- Scattered unbranched (-bifid) hairs mainly along the margins of the siliques as in Dr. 12. Examples: Spiret, N. Strømfjord (leg. F. Salomonsen 1954), Qapiarfik (leg. TWB 1958), Godhavn (leg. G. Kleist 1904; NB. siliques broad and obtuse, probably var. brachycarpa, see below), Pröven 72°22' (leg. I. A. Bjørling, determined as D. hirta var. hebecarpa Lindbl. but later as D. cinerea×daurica by Екман, Herb. Stockholm).
- 2) More dense pubescence on the siliques of unbranched and bifid hairs. Examples: Upernivik Ø, 71°10' (leg. M. P. & R. T. Porsild 1929, determined as D. cinerea×daurica by EKMAN, Herb. Stockholm), Sermermiut (leg. S. B. 1870, by TOLMATCHEV 1927 determined as D. hirta, by EKMAN as cinerea×daurica and on the label with the remark "corresponds to D. dovrensis", Herb. Stockholm). These two collections are almost identical with plants from Knutshö and Kongsvold in Dovre.
- 3) Glabrous siliques but with long unbranched hairs on the pedicels: Some of the rosette leaves ciliated with unbranched hairs. Type of *D. daurica* var. *rupestriformis* Ekm. (Екман 1930: 286, Umanaq, leg. B. Floderus 1929, Herb. Stockholm). ± Ciliated rosette leaves also seen in Cult, No. 6325 from Gaspé, Canada.

Taxonomical remarks. JØRGENSEN et al. (1958: 68) express the view that "D. hirta perhaps covers two species with n = 32 and 40 respectively, but add that until more material has been collected, it is impossible to settle the discrepancy between chromosome number and taxonomical demarcation". The new material now available has not contributed a great deal to the solution of the problems. The morphological differences found between octo- and decaploids are too vague. FERNALD's treatment (1934: 333) of the polymorphy within D. glabella deserves, however, to be discussed in this connection. FERNALD operates with four varieties arranged into two groups. His var. typica and var. orthocarpa may belong to the octoploid series while var. brachycarpa (Rupr.) Fern. and his var. megasterma are possibly decaploids with n = 40 or in the case of the latter even higher numbers. His pictures of D. glabella var. brachycarpa (Plate 310) from Greenland show plants which resemble the decaploids studied cytologically although the plants chosen by FERNALD have particularly broad and obtuse siliques. On the other hand, his pictures of typical D. glabella from

Labrador (Plate 307) resemble octoploids from Greenland (e. g. as No. 4814) while his var. *orthocarpa* from Quebec (Plate 309) has much in common with the octoploid material from Finland (Dr. 12). FERNALD's distinction between the two groups, however, is based on differences found between morphologically extreme specimens and these also show some difference in the size of the seeds. It must therefore be remembered, that octoploids show clear differences in the size of the seeds (Table 5).

At the present stage of our knowledge it is preferable to refrain from erecting any taxa (e.g. varieties or subspecies) to cover the decaploids. It seems clear that typical *D. glabella* specimens are octoploid and have a relatively southern sub-low arctic distribution. One part of the decaploids, on the other hand, seems to constitute a high arctic group which so far is not found south of Godhavn on Disko.

Relationship between the Draba glabella, the D. cinerea, and the D. norvegica group

Hybrids between D. glabella (daurica) and "D. cinerea" were discussed in EKMAN's earliest papers and in EKMAN (1930). HITCHCOCK (1941) also tackled the problems by saying that he is inclined to consider D. cinerea as merely a very pubescent form of D. glabella. He also mentions D. cinerea var. kamschatica (Regel) Schulz which has glabrescent siliques. In Greenland, however, there is no reason to unite any species of the D. cinerea group with D. glabella s. l. in spite of the existence of some forms considered by some to be intermediate.

Some of the hybrids mentioned by EKMAN (1930) seem from a cytological point of view rather unlikely, e.g. *D. glabella* × norvegica, *D. arctogena*×glabella and *D. cinerea* (typical)×daurica, all of which would involve crossings between plants with n = 24and n = 32. On the other hand are hybrids at the octo- or decaploid level more probable. In fact EKMAN assumes a rather frequent occurrence of the hybrid *D. arctica* ssp. groenlandica×daurica and thinks this hybrid is identical with *D. dovrensis*.

On p. 287 EKMAN expresses the view that it may be difficult to decide whether the other parent plant is *D. arctica* ssp. groenlandica or *D. norvegica* as publicent siliques may have been inherited from either of these species. But in specimens where the rosette leaves are ciliated, she adds "the other parent plant is in most cases *D. norvegica*". This remark is curious as *D. arctica* ssp. groenlandica often has ciliated basal leaves. Obviously plants interpreted as *D. glabella*×*norvegica* are suspect and need a closer study. In fact *D. glabella* s. l. includes an octoploid form with cilia on the rosette leaves (e.g. Cult. No. 6325); this culture originates from a locality outside the known area of *D. norvegica* (A. E. PORSILD 1957: 184, HULTÉN 1958 map 14).

Also the presumed hybrid D. arctica ssp. groenlandica \times glabella needs corroboration. D. dovrensis shows no meiotic irregularities and occurs outside the area of ssp. groenlandica. A striking fact is that D. dovrensis has simple or bifid hairs on the siliques, not stellate as in ssp. groenlandica. If the plants determined by EKMAN are hybrids it is necessary to assume inheritance of hair type from D. glabella and high hair density on the siliques from ssp. groenlandica.

Biol.Skr.Dan.Vid.Selsk. 14, no. 7.

At the head of Søndre Strømfjord where octoploid *D. glabella* is sympatric with hexaploid *D. cinerea* there were no signs of hybridity between these two species. The presumed hybrids are all from areas where octoploids or decaploids within the *glabella*- and *cinerea*-group occur together. This makes introgression a possibility but there is no substantial evidence.

Draba sibirica (Pallas) Thell.

Material of this species was obtained as seeds from the Botanical Gardens of Strassbourg, Halle and Moscow. Unfortunately no seed from nature was available. The plants were easily grown in pots in the Experimental Field and all three samples (Nos. 7647, 7667, 7671) flowered already in the autumn of the first year of cultivation. Morphologically there was no difference between them and all had the chromosome number 2n = 16 (Fig. 10, h–i).

According to SCHULZ (1927: 79) *D. sibirica* belongs to the section *Chrysodraba*, and is the first diploid found in this section. It is an Asiatic-East European subarctic-subalpine species, although extending to low arctic areas, e.g. in Middle East Greenland and also to temperate areas in Middle Russia. All the high arctic representatives of *Crysodraba* are polyploids (see e.g. *D. bellii*).

The material from the Botanical Gardens which is very uniform may have originated from localities of southern type. In Halle *D. sibirica* was observed growing abundantly in the Rock Garden thus certainly not behaving as an arctic species. Morphologically *D. sibirica* deviates from all high arctic species of *Chrysodraba* by being loosely tufted, its vegetative shoots being elongated and stolonlike (GELERT 1898: Fig. 9).

Draba bellii Holm

Material of this species from Spitzbergen (Cult. No. Dr. 1, Kongsfjord, W. Spitzbergen) collected as seeds by Dr. N. FOGED and grown in the Arctic Greenhouse appeared to be 16-ploid with 2n = 128. The root tip mitoses could not be counted with absolute cetainty but the clearest metaphse had $2n = 128 \pm 2$ chromosomes. Holmen (1952) has found a similar high chromosome number in material from Peary Land ($82^{\circ}10'$ lat. N.). He first referred the plant to the closely related taxon *D. macrocarpa* Adams. Later, however, (1957) he expresses doubt about the taxonomical status of his material and is inclined to refer it to *D. bellii*. Dr. Holmen has kindly lent me his pressed material thus enabling me to make a comparison between the two 16ploid plants from Spitzbergen and N. Greenland (Table 6).

According to HOLMEN (1957: 57-58) Draba bellii has a great range of variation. In many ways this variation appears also from a comparison of the two strains which were studied cytologically. The Spitzbergen plants have longer, more numerous, unbranched hairs and have narrower leaves and petals and smaller flowers. In most

TABLE 6.

	Draba bellii from Spitzbergen Kongsfjord (NB. cultivated material; Dr. 1.)	Draba bellii from Peary Land, Holmen No. 6594 (collected in nature)		
Height and habit	3–5 cm, densely caespitose no stem leaves	5–6 cm, densely caespitose no stem leaves		
Basal leaves	Narrowly spatulate, weakly acute marginal cilia 1–1.2 mm. Lamina glabrescent above with few scat- tered bifid and unbranched hairs, below with stellate and bifid hairs	Spatulate, obtuse, marginal cilia 0.6–0.9 mm. Lamina above with mixed pubescence of stellate hairs (near margin) bifid and unbranched hairs, below also mixed but with more stellate hairs		
tems and pedicels Dense covering of ca. 1 mm long unbranched or bifid hairs		Mixed dense pubescence of mainly unbranched-bifid hairs		
Flower	Sepals 2.5 mm, Petals 4 mm rather narrow and emarginate, pale yellow	Sepals 3 mm, petals 5–6 mm broad and emarginate, pale yellow		
Siliques (without style)	8.5 mm long, 2,5 mm broad. Pubescent with ca. 0.4 mm long unbranched hairs which are partic- ularly dense along the margin. Seeds 1.2–1.3 mm long. Siliques sometimes solitary on short peduncles between basal leaves	8–9.2 mm long, 4–5 mm broad. Pubescent with ca. 0.4 mm long unbranched hairs. No seeds available		
Style and stigma	0.5 mm long style and capitate stigma	0.5 mm long style and capitate stigma		

characters this strain corresponds to *D. bellii* var. *svalbardensis* Ekman (see EKMAN 1931: 470), while the material from Peary Land may be referred to "f. *typica*". It differs from the description of *D. macrocarpa* in having emarginate petals and stellate hairs (with more than two-three branches). Considering, however, the great range of variability in *D. bellii* as found in Greenland and Spitzbergen and the slight morphological difference between *D. bellii* and *D. macrocarpa* it seems probable that these two species ought to be united. If so the species has to be called *D. macrocarpa* Adams. From a phytogeographical point of view this *D. macrocarpa* s. lat. would be circumpolar high arctic. The great range of variation in the complex is not surprising as it is composed of 16-ploids and may have been formed as a result of allopolyploid evolution. TOLMATCHEW (1932: 52) has a map of the world range of *D. macrocarpa*. It shows stations for this species in NE. Greenland, NW. Greenland, the American Arctic Archipelago, Arctic Siberia and Novaja Semlja. This shows that TOLMATCHEW included in *D. macrocarpa* specimens which others e.g. A. E. PORSILD (1955: 123–214, 1957: 95) have referred to as *D. bellii* Holm.

Draba aurea M. Vahl

This is a West American species occurring in forests and montane regions from Alaska to New Mexico, Southern Utah and the higher mountains of Arizona. In East America it is confined to a few stations in Northern Labrador and a single one in Ungava (James Bay), see HITCHCOCK (1941: 26), FERNALD (1934 map p.: 299). In East and West Greenland, however, it has a wide range extending to 70–71° n. lat., see Fig. 8. In continental West Greenland it occurs mainly in the lowland and often in connection with dry willow scrubs (BÖCHER: 1954). The type of distribution within Greenland is low-subarctic and subcontinental.

Chromosome number. The first count of this species was made by BÖCHER (1958: 351) in plants from the Botanical Garden in Copenhagen. The material was very small as it was only possible to count one megaspore mothercell at diakinesis. 32 chromosome pairs were found. During examination of the slide the cell was not found again; it is therefore impossible to say more than the haploid number was at least 32 and probably not much higher. This remark is necessary as the new material clearly had more than 32 bivalents.

Two strains from W. Greenland (Fig. 9, Cult. Nos. 4883 and 4820) had the unusual number 2n = 76 or n = 38. While somatic plates distinct enough for safe countings were rare (Fig. 1 n, r), the meiotic metaphases showed clearly that the haploid number was 38, see fig. 1 p-q. According to SCHULZ (1927: 173) *D. aurea* belongs to the section *Phyllodraba* which contains 11 species from mountains of N. America and 17 montane asiatic species but no true arctic species, *D. aurea* being the only one which reaches sub-lowarctic Greenland. The possibility exists, therefore, that the *Phyllodraba* section has another basic number, which may be 19 or perhaps 12, see p. 64. In the latter case *D. aurea* would have 2n = 72 + 4 small extra chromosomes. In fact in two of the plates, fig 1 p-q, two small pairs are seen (\$\xi\$) which supports this explanation without of course giving any kind of proof. With 12 as the basic number *D. aurea* is a type of decaploid with extra-chromosomes whilst with 8 it is a secondary decaploid by loss of two pairs. In this connection it is perhaps of some importance that small extra chromosomes occur in other species in the genus (e.g. *D. norvegica*, Fig, 1 j-m).

Variation. EKMAN (1934) classifies *D. aurea* as perennial and HITCHCOCK (1941) describes it as an erect to decumbent perennial but adds biennial with a questionmark. The material from Greenland cultivated by me was biennial or pauciennial as the plant died after prolific fruiting. HITCHCOCK also makes a remark about the variation which deserves comment. Undoubtedly, he says, *D. aurea* is more variable than any other of our western North American species, but I am convinced that much of this variation is due to local ecological conditions. According to him only one variant deserves taxonomic recognition viz. *D. aurea* var. *leiocarpa* (Payson & St. John) Hitchc. Also FERNALD is of the opinion that the West-American material which customarily is referred to *D. aureiformis* Rydb. is not specifically distinct from *D. aurea*. From the



Fig. 8. Greenland range of Draba aurea.

treatise in SCHULZ 1927 and the discussions in HITCHCOCK and FERNALD, however, it seems quite clear that *D. aurea* is polymorphic in its West-American main area while it is evident that the range of variability in Greenland is much smaller. Decumbent plants have never been found in Greenland while plants with glabrous siliques were interpreted as *D. aurea*×glabella by Ekman (1934: 78). The two strains from West Greenland which were cultivated simultaneously were not morphologically



Fig. 9. Draba aurea from W. Greenland. No. 4883 from N. Isortoq is early flowering with light yellow flowers and many stems while No. 4820 from Søndre Strømfjord is late flowering with ochre-yellow flowers and fewer stems. — 8/5 1959.

identical but deviated from one another in flowering time—one being almost a week earlier (Fig. 9)—in branching and in colour of the petals, one being more deeply yellow than the other.

No. 4883 is from a place not far from the outer coastal mountains while No. 4820 is from the extreme continental inland. Studies in the Greenland herbarium in Copenhagen shows that the plants from the most continental areas, e.g. Scoresbysund and the Strømfjord hinterland all belong to the type with few or no branches on the lower part of the inflorescence and few basal shoots. The branched type however is found in many places in South and West Greenland from N. Isortoq southwards. Very vigorous specimens of both types are shown in Plate VIII. The paler flowers in No. 4883 perhaps deserve attention. If EKMAN is right in her opinion that *D. aurea* can cross with *D. glabella*, such pale plants might be results of some kind of introgression. The cytological observations referred to above, however, do not suggest easy hybridization and there are glabrous fruited specimens found in Western America which are not referred to any hybrid (Hitchcock 1941).

Draba gilliesii Hook. & Arn.

Material of this species collected by Dr. JOSÉ DIEM in Parque Nacional Nahuel Huapi in the provinces Neuquén and Rio Negro in Argentina was cultivated in the Botanical Garden in Copenhagen. The plants were quite typical, 12–13 cm high with 5, remotely dentate cauline leaves, white flowers and 3 mm long styles on the ripe siliques. In all parts the plants were densely covered by stellate hairs. According to SCHULZ (1927: 156–158) the species is polymorphic. The material studied by me belongs clearly to var. *rosulata* (Phil.) Reiche.

Numerous PMCs were studied at diakenesis in orcein squash slides. 24 bivalents were found. One large pair (\Rightarrow in Fig. 10 c) had one terminalized and one non-terminalized chiasma, its two free ends being often less condensed. In root tip squashes 48 chromosomes occurred (Fig. 10 b) among which two were large and showed a high degree of splitting. They may correspond to the deviating pair. The species belongs probably to a series with 12 as basic number (cp. p. 64).

Brava thorild-wulffii Ostf.

4. Braya

This high arctic species was first counted by Holmen (1952) in material from Peary Land and later by K. JAKOBSEN in plants from Nugssuaq, West Greenland (JØRGENSEN et al. 1958: 73). Quite recently 2n = 28 was counted by MulliGan (1965) in plants from Northwest Territories (see Postscript). The present writer received seeds collected in Peary Land by BENT FREDSKILD (Slope at Kedelkrogselven, FREDSKILD No. 2715). The plants were grown as Cult. No. 7327 in the Arctic Greenhouse and counted in root tip squashes. 2n = 28 was found thus corroborating earlier counts.

HOLMEN (1952, Fig. 18) pictures a first metaphase plate in which one large bivalent is seen in the center and another rather large one at the top. In the clearest plate studied by me (Fig. 10 a) there are two particularly large chromosomes with submedian centromeres (marked with black asterisks), about 8 which are intermediate in size and about 18 which are much smaller. It was not possible to detect four large chromosomes with submedian centromeres, a fact which may be of some importance in indicating that the species is not an autotetraploid.

B. thorild-wulffii No. 7327 was grown simultaneously and together with three strains of *B. purpurascens* (see Table 10). The plants appeared to be very clearly separated from the latter species, having i.a. ciliated leaf margins and more greyish green leaves. Most of the plants did not flower but formed cushions of small rosettes at the same time as the strains of *B. purpurascens* were luxuriantly flowering.

One of the plants formed flowers on 0.5–0.8 cm high pubescent stems which were almost hidden among the rosette leaves. These were up to 1.6 cm long. The sepals were 3 mm long, with some few hairs usually near the top. They were spreading and persistent during ripening of the siliques. The petals equalled or were shorter



Fig. 10. — a: Braya thorid-wulffii (No. 7327, 2n = 28). — b-c: Draba gilliesii; b: root tip mitosis, 2n = 24;
c: diakinesis n = 24. — d: Arabis arenicola (No. 6064, 2n = 16). — e: Braya linearis (No. 7388, n = 21). —
f-g: Braya alpina (No. 6988; f: n = 21; g: 2n = 42). — h-i: Draba sibirica Nos. 7647, 7671, root tip mitoses, 2n = 16. — j-k: Braya purpurascens; j: No. 7114, n = 28; k: No. 7368, 2n = 56. — All orcein squashes, the mitotic cells after pretreatment with α monobromnaphthalin. — Scale 10 μ.



Fig. 11. Material of *Braya rosea* grown as Br. 4 in the Arctic Greenhouse. — a-b: Normal appearance at flowering stage. — c-e: Later stage with elongated decumbent stems producing leaf rosettes in leaf axils and ascending sometimes elongated racemes with long siliques (c). In d fusion between proximal part of pedicel and subtending leaf (marked with*). — Scale 10 cm.

than the sepals, 1.6–3 mm long and not rarely fewer than four. The siliques were densely publication up to 8 mm long and 3.2 mm broad, with 0.4 mm long styles and 1.2–1.4 mm long, finely dotted or granulate seeds. In a few flowers the two carpels were not united and of unequal size, the short style being borne on the larger carpel.

Braya rosea (Turcz.) Bunge

According to SCHULZ (1924: 232) this is a central asiatic montane species but belonging to a species aggregate comprising also *B. aenea* Bunge. *B. angustifolia* (N. Busch.) Vass. has also now to be referred to this aggregate (see KOMAROV-BUSCH Flora URSS VIII, 1939).

Chromosome studies. Counts were made in meiotic material of plants raised from seeds obtained from the Botanical Gardens in Leningrad. n = 21 was found in numerous cells (Figs. 12 a–f). Some deviations were noticed such as a pair of univalents (Fig. 12 d), occasional laggard bivalents at first anaphase and bridge formation at second anaphase. Fig. 12 f shows one acentric fragment and a dividing persistent double bridge connecting three of the resulting chromosome groups. The size difference between the bivalents is rather conspicuous.

Cultivation. The plants were cultivated as Br. 4 together with *B. linearis* and *B. novae-angliae*. They showed some resemblance to *B. linearis* but were much coarser with broader siliques and upright-ascending, always entire, rosette leaves, cp. Table 7 and Plate IX d-h. Both species had a clear tendency towards additional rosette formation in the axils of stem leaves, but in *B. rosea* this axillary rosette formation became abnormally prolific late in the year (August) in the batch cultivated in the Arctic Greenhouse (Fig. 11). Some of the rosettes were cut off and planted as cuttings but were unable to produce roots.

Morphology. Table 8 contains a summary of the description given by SCHULZ (1924) compared with measurements of herbarium material from Asia and the Cult. Br. 4. The cultivated plants greatly exceed the dimensions given by SCHULZ and have 2–6 stem leaves. The inflorescence is elongated but terminates in a dense or capitate part. The siliques are 6–12 mm long and the styles are either narrow along their entire length or expanded below the stigma. In some specimens a number of new axillary rosettes were concentrated on the main stem as a new basal rosette separated from the first formed rosette by an elongated internodium (Fig. 11). The difference between such plants and those with many rosettes in stem leaf axils depends only on an elongation of the internodia between the leaves which subtend the short rosette shoots.

Another character which is not mentioned in the description by SCHULZ nor appears from his drawings (Fig. 47 L–N) is the occurrence of fusions between the proximal parts of the pedicel and the subtending leaf.

The degree of pubescence varies within the population. Some plants were completely glabrous (cp. var. *glabra* Regel & Schmalh.).

Taxonomy. Some of the deviations from typical *B. rosea* found in Br. 4 may be due to better growing conditions in culture, but the longer siliques and larger number of stem leaves deserve attention. In height Br. 4 resembles *B. aenea*, but not in the breadth of the rosette leaves and the siliques. It therefore probably represents a new taxon but any description has to be postponed until more information is available.


Fig. 12. Chromosomes in *Braya*. — a-f: *B. rosea* (No. Br. 4, n = 21; a-d: Mataphase I; e: anaphase I; f: anaphase II with dividing bridge and acentric fragment). — g-m, o-x: *B. linearis* (n = 21; g: No. 845 with one ring of four; h-j: No. 4855 in i with precousiously separated pair, in j with one pair of univalents; k-m: No. 4811 with one B, marked $\frac{1}{24}$; k: diakinesis; l: metaphase I; m: prometaphase II; o-x: var. *meizophylla* No. Br. 3; one B chromosome, marked $\frac{1}{24}$; with ordivided during anaphase I in v-w); — n and y: *B. novae-angliae*; n: ssp. *ventosa*, 2n = 56; y: ssp. *novae-angliae* n = 28. — All microtome technique. — Scale 10 μ .

Braya linearis Rouy

This species is restricted to the continental parts of W. and E. Greenland and Scandinavia, where it has a bicentric distribution (HULTÉN 1958: 82).

Chromosome studies. B. linearis is another hexaploid with n = 21 as found in material from two collections from Sdr. Strømfjord (Böcher & LARSEN

Nr. 7

Cult. No.	Taxon	Origin	2 n	Diameter of first year rosettes, cm (Exp.: E*)	Rosette characters (first year)
6788	B. alpina	Gross Glockner, Austria	42	5.6(4.1-6.6)	Adpressed. Leaves entire, lanceolate, hairy
Br. 3	B. linearis var. meizo- phylla	Junkerdal, Nordland, Norway	42 + B	3.5(2.0-6.0)	Adpressed. Leaves variable. Entire-incised, glabrous- hairy, lanceolate to ovate-lanceolate
Br. 7	B. linearis	Sørdal, Troms, Norway	42	5.0(3.0-7.0)	Adpressed. Leaves \pm incised at distal end, lanceolate with marginal hairs
7388	B. linearis	Bøvertun, Oppland, Norway	42	2.8(2.0-4.0)**	Small and adpressed lanceolate, slightly incised; hairy
4811	B. linearis	Store Saltsø, W. Greenland	42 + B	4.6(1.6-7.0)	Adpressed. Leaves \pm incised at distal end, lanceolate with marginal hairs
4855	B. linearis	Lille Saltsø, W. Greenland	42	1.5(0.5–2.5)	Small and adpressed. Leaves entire-slightly incised, lanceolate-ovate lanceolate glabrous
Br. 4	B. rosea	Leningrad, Bot. Gardens	42	7.5(4.0–11.0)	\pm Upright. Leaves entire lanceolate, ciliated at base, shiny

* Experiments: A-D: In pots in frames at the Experimental Field (A 1959, B 1962, C 1964, D 1965). E-G: In pots lowest flower between rosette leaves.

1950), one from Ella Ø, NE. Greenland (Jørgensen et al. 1958) and one from Jotunheimen, Norway (KNABEN in Jørgensen et al.). New material of this species consisted of plants raised from seeds from five places viz.

No. 4811. West Greenland. Shores of Store Saltsö at Sdr. Strømfjord. No. 4855. West Greenland. Shores of Lille Saltsö at Sdr. Strømfjord. No. Br. 3 Norway, Junkerdalen Nordland (see text).

Nr. 7

alpina, B. linearis and B. rosea.

Height of plants with ripe siliques cm, experiments A-G*	Breadth broadest stem leaf mm	Length of ripe raceme cm	Length of ripe siliques mm	Petal size mm L Length B Breadth	Other characters
C: 4 (3–5) D: 5 (4–6)		D: 1.8–2.0	C: 8–9 D: 10–11	L: 0.9–1.2 B: 1.1–1.5	Petals pale lilac, slightly emarginate. Sepals \pm persistent
B: 6 (3-9) C: 7 (5-9) D: 7 (5-9) E: 25 (16-31) F: 16 (11-21) G: 24 (22-27)	D: 2-3.5 E: 2-3.5 G: 2-3	D: 4 (2.5-6) E: 7 (5-10) G: 8 (4-11)	D: 10 (9-11) E: 12 (11-13) G: 11 (11-12)	L: 1.0 B: 1.0	Petals white (-very pale lilac) emarginate. Hairy siliques. Stem leaves long and spreading sometimes subtending small rosettes
C: 7-8 F: 17-18 G: 23	F: 1-1.5 G: 1-1.5	G: 6	G: 11	L: 1.0 B: 1.0	Very slender, greener and later flowering. Weak; few plants reached flowering stage
D: 6 (4–10)	D: 1–1.5	D: 4 (3–5)***	D: 8 (7–9)	L: 1.0 B: 1.0	Stem leaves few and short. Petals white (-very pale lilac) emarginate
A: 3.8 (2-8) C: 6.0 (3-8) D: 5.0 (3-6) E: 18 (14-23) F: 16-20 G: 21 (12-25)	E: 1.3–1.5	E: 7 (5-9) G: 8 (3.5-10)	A: 10 C: 9 (8-11) E: 8 (7-9) G: 11 (8-12)	L: 1.0 B: 1.0	Petals white (-very pale lilac), not or very slightly emarginate. Siliques \pm spreading
$ \begin{array}{c} {\rm A:} \ 2.9 \ (1.5{-}4) \\ {\rm E:} \ 16 \ (13.5{-}18) \\ {\rm F:} \ 16{-}25 \\ {\rm G:} \ 20 \ (11.5{-}26) \end{array} $	E: 1.0-1.5	E: 6 (4–11) G: 6 (4–11)	A: 7 E: 8 (7-9) G: 10 (9-11)	L: 1.0 B: 1.0	As the preceeding but siliques ± upright, curved. Plants more slender
B: 14 (5–17) E: 33 (26–42) F: 12–21		E: 10 (5–17.5)	E: 9 (7-12)	L: 2.0	Petals white, not emarginate. See further Table 8

in the Arctic Greenhouse (E 1961, F 1962a, G 1962b). ** Experiment D. *** Entire stem often occupied by raceme;

No. Br. 7 Norway, Sørdal, Troms (coll. by Dr. G. Halliday).

No. 7388 Norway, Høirokampen, Oppland (seeds from Bergen; probably the same population as studied by Dr. G. KNABEN).

All five had n = 21 (Figs. 10 e, 12 g-m, o-x) but in two, viz. No. 4811 and Br. 3 a supernumerary small chromosome occurred. The difference in size between the bivalents is striking. One bivalent seemed to exceed all the others. Thise size dif-

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	Height in cm	Rosette	No. of		Sepal	Petal	Siliq	nes	Style	Axil- larv
Origin	of plants	leaves	stem leaves	Inflorescence	length mm	length mm	Length mm	Breadth mm	length mm	roset-
B. rosea. Description in Schulz 1924: 231	2-5 (-10)	Lanceolate (obverse lanceolate obtusiuscula), mostly entire, glabrous; peti- oles ciliated	0-1	Capitate with remote flower in stem leaf axil	2.5	.0. 10.	4-6	1.5	0.5–1.0	
 B. rosea f. albiflora Maxim. Valley of Dar river, Margelan Distr. Fergana Prov. N. Dessiatoff, 1913, No. 1368, Bot. Museum, Stockholm 	2-5	Spathulate- lanceolate, 2 cm long, entire $\pm \text{ glabrous}$; petioles ciliated	0-1	Capitate very short	2.0-(2.5)	3-(3.5)	Broad base, rij	est at not pe	I	
 B. rosea. Altai, near glacier, P. Krylow, 1900. Herb. Flor. Russ. Fasc. XXIII No. 1105 (distrib. as B. aenea), Bot. Museum, Copenhagen 	5-9	Spathulate, 1.5 cm long entire, gla- brous; petioles ciliated	1-(2)	Lowest flower removed from capitate inflorescence	2.0-2.5	2.2-3.5	4-6	Above 1.3, below 1.6-1.9	0.4–0.8	+
B. rosea Cult. No. Br. 4 see p. 42 and Fig. 11	5-42 see 7	Lanceolate spathulate glabrous; petioles sparsely ciliated	$(1)^{2-6}$	Raceme capi- tate or with several flowers below. Racemes 5-17.5 cm long	2.5-3.0	3.3-4.0	6-12	Above 1.2, below 2.0	1.0-1.5	+
B. aenea. Description in Schulz 1924: 232	4-10 (-12)	Linear, with narrow petiole	1	E	2-2.5	3.0–3.5	4-6.5	1.2	More slender than in B. rosea	
B. aenea. Jakutsk, Sibiria oblastia, Balaganach. N. H. Nils- son 1898, No. 7135, Bot. Museum, Stockholm	7-17	Almost linear	1-2 very narrow	Lowest flower much removed from capitate inflorescence	2.0	3.0	10–15	$\begin{array}{c} \text{Above} \\ 0.5{-}0.6, \\ \text{below} \\ 0.8{-}1.0 \end{array}$	0.8	
B. aenea. Jakutsk, Sibiria oblastia, Kumach Sur (ca. 71°30'). N. H. Nilsson, 1898, Bot. Museum, Stockholm	11-20	Linear- lanceolate- narrowly, spathulate, dentate, gla- brous; petioles ciliated	2-3	Lowest flower little removed from \pm capi- tate inflore- scence	1.6-2.5	3.0-4.0	7-12	1-1.1	0.4-0.7	+

Table 8. Braya rosea and B. aenea.

46



Fig. 13. Variation in Norwegian *Braya linearis*. Two specimens on the left var. *meizophylla* (Type of the variety) from Junkerdal (leg. Peters & Pettersson July 1904, Bergens Museum). On the right three specimens from Bardu in Troms Fylke. Lundeng in Sørdal (leg. A. Blytt July 1891, Bot. Museum, Copenhagen), cp. Cult. Br. 3 and 7 and Plates IX-X. – Scale 10 cm.

ference was also found by JØRGENSEN et al. It is greater than in *B. rosea* (Br. 4). One possible quadrivalent or association of four was seen in some PMCs of No. 845 which was studied by BÖCHER & LARSEN 1950 (see Fig. 12 g). In No. 4855 two small chromosomes may be precociously separated (Fig. 12 i) but in one cell (Fig. 12 j) behaved as true univalents; two larger univalents were observed occasionally in Br. 3 (Fig. 12 t).

The small extra chromosome in No. 4811 during diakinesis was placed near or in connection with one of the chromosomes of a pair (Fig. 12 k). It was detected in some first metaphase plates (Fig. 12 l) and could be traced through first anaphase to the second prometaphase (Fig. 12 x). Its later fate could not be followed. In Br. 3 from Norway the small extra chromosome was sometimes easy to see during first metaphase (Fig. 12 s–u) but mostly it was impossible to detect and was assumed either to be absent from some of the PMCs or was sticking to one of the chromosome pairs (see e.g. Fig. 12 q below). At first and second anaphase it was sometimes observed dividing or divided and often in connection with a lagging chromosome (Figs. 12 v–x).

47

Origin Norway. Oppland. Bövertun valley Høirokampen, K. Fæg R. Nordhagen 1932, Bot. Museum, Bergen, 6 specimens (and average heights 26 specimens from Bövertun) Norway. Nordland. Junkerdal, scree, Joh. Dyring, July 1893 Bot. Museum, Bergen, 25 specimens Norway. Troms Fylke. Sørdal. Bardudalen, Axel Blytt, July 1891, Bot. Museum, Bergen and Copenhagen, 22 specimens W. Greenland, Store Saltsø near head of Sdr. Strømfjord. T Aug. 1946, Nos. 499–500. Bot. Museum, Copenhagen, 11 specimens W. Greenland. Head of Sdr. Strømfjord, Roadside near Airb TWB. Aug. 1946, No. 493, Plate Xa. Glabrous form	Height in cm of plants	Rosette leaves	Pubescence of stems	No. of stem leaves
Norway. Oppland. Bövertun valley Høirokampen, K. Fægri & R. Nordhagen 1932, Bot. Museum, Bergen, 6 specimens (and for average heights 26 specimens from Bövertun)	9 (5–15)	Narrowly spathulate, entire or with 1 (-2) pair of teeth	Hairy	2–3
Norway. Nordland. Junkerdal, scree, Joh. Dyring, July 1893, Bot. Museum, Bergen, 25 specimens	12 (5-26)	Narrowly spathulate, entire or with few shallow teeth	Hairy	1–3
Norway. Troms Fylke. Sørdal. Bardudalen, Axel Blytt, July 1891, Bot. Museum, Bergen and Copenhagen, 22 specimens	8 (4–14)	Lanceolate entire and short	Hairy	0-2
W. Greenland, Store Saltsø near head of Sdr. Strømfjord. TWB. Aug. 1946, Nos. 499–500. Bot. Museum, Copenhagen, 11 specimens	10 (7–16)	Linear- narrowly lanceolate (-spathulate)	Hairy	1-2 (3)
W. Greenland. Head of Sdr. Strømfjord, Roadside near Airbase, TWB. Aug. 1946, No. 493, Plate Xa. Glabrous form	(10–14)	Linear- lanceolate (-spathulate)	Glabrous	1-2

In Br. 3 a tendency towards a peripheral positioning of the large pairs was particularly pronounced (see e.g. Fig. 12 s).

Cultivation. The four strains cultivated simultaneously exhibited some differences which deserve consideration (cp. Table 7).

The Norwegian strains Br. 3 and 7 were clearly very different, Br. 7 being much more slender and difficult to cultivate (Plate IX a, c, p, q, Plate X e, f). Only a few specimens completed a normal life cycle, and many died as rosette plants. The few specimens with ripe siliques attained similar heights to No. 3 but the stem leaves were much narrower and aggregated towards the base. The first year rosettes, on the other hand, were broader.

The Greenland strains No. 4811 and 4855 closely resembled one another. Some small differences appear from Table 7. In almost all characters No. 4855 is slightly smaller than No. 4811. The largest difference was found in the first year rosette diameters.

In both Norwegian strains the petals were slightly emarginate while they were

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Braya linearis.

Longe le	est stem eaf	Sepal length	Petal length	Longes (withou	t siliques 1t style)	Style	Axillary	Persistance of senals
Length cm	Breadth mm	mm	mm	Length mm	Breadth mm	mm	rosette	and petals
1–3	0.4-1.1	2.0-2.3	3.2–3.4	6.2–7.2	1.1–1.4	0.1-0.3	+	±
2-5.5	1.5–3.0	2.2-2.3	3.5–3.6	8.3–11	1.2–1.5	0.3-0.5	+	+
0.8–1.5	0.2-1.0	1.7–1.8	? 2.5	7.5–9.0	1.1–1.2	0.3–0.5	(+)	÷
2.5-3.0	1.0-1.4	1.7-2.2	2.5–3.5	7.5–11	1.4-1.4	0.2-0.5 (0.6)	(+)	÷
2.5-2.6	1.0–1.5	-		10-12	1.2–1.4	0.4-0.5	+	÷

entire in those from Greenland; otherwise there was no general difference between the plants from the eastern and most western populations of the species.

Taxonomy. The only difference which may deserve taxonomic recognition is that found between Br. 3 and the other strains. The material of Br. 3 was received as seeds in 1959 from the Botanical Gardens of Bergen. Professor KNUT FÆGRI and professor PER WENDELBO have kindly tried to trace the origin of the seeds and came to the conclusion that they were collected on plants either from Jotunheimen (Høyrokampen) or from Nordland (Junkerdalen). A comparison of the material of Br. 3 with a great number of herbarium sheets in the Botanical Museums in Bergen, Oslo and Uppsala revealed that Br. 3 closely resembles plants from Junkerdalen. Likewise a large number of specimens from Sørdal in Troms were very similar to Br. 7 being small and slender. Some of the observations are collected in Table 9. It appears that the specimens from Junkerdalen are larger, with longer and broader stem leaves and often with elongated racemes, just as in Br. 3. The plants from Jotunheimen are small with very narrow leaves, as in the cultivated specimens from that

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locality (Table 7). Almost all plants from Troms, Finmark and Jotunheimen have narrow leaves and are comparatively low as are some from Nordland (e.g. Bindalen, Knurvig, Ravatnet in Vefsen). The broad-leaved type occurs in Junkerdalen and Saltdalen but closely similar specimens were also collected in Lule Lapmark in Sweden more to the east (Aresvare north of Vastenjaure, leg. T. Å. Tengwall 1913). Even specimens from Jukkasjärvi (leg. H. Smith 1920) may be related.

The broad leaved and relatively robust race is concentrated in Junkerdal-Saltdal, but the genes which distinguishes it may be traced as introgressions in some Swedish populations. Not all specimens from Junkerdal-Saltdal correspond to Cult. Br. 3. Some have long erect red peduncles and leaves aggregated below (e.g. specimens collected by Mörner 1885 and E. Jørgensen 1923). Thus the population here is not uniform. In some cases relatively broad and long stem leaves may be found in single specimens from outside Junkerdal-Saltdal (e.g. Troms-Målselven, leg. I. M. Norrman, Bjørkåsen, leg. Andr. Notø; Sørdal: Sørgaard, leg. Andr. Notö and Sørmo, leg. Peter Beum, all Herbarium Oslo). They may represent modified specimens of the normal type or be genetically related to the Junkersdal-Saltdal-race.

In order to stimulate a further study I have chosen to describe the Br. 3 type as var. meizophylla var. nova. Differt a var. lineari foliis caulinis usque ad 3 mm latis, 5.5 cm longis, racemis elongatis. Habitat in vallibus Junkerdalen et Saltdalen, Norvegiae. Typus in valle Junkerdalen Norvegiae a Peters & Petterson lectus in Museo Botanico Bergensi depositus, in Fig. 13 depictus.

The occurrence of var. meizophylla coincides with a number of very rare arctic plants which in Norway has been considered as "interglacial survivals". According to NORDHAGEN (1935: 135) there are here isolated occurrences of Arenaria humifusa, Carex scirpoidea, Saxifraga aizoon (ssp. laestadii, see HOLMBOE 1936 map. Fig. 12), Papaver radicatum ssp. subglobosum, to which may be added Potentilla hyperborea (emarginata), found on the Swedish side, and the southern group of localities of Pedicularis flammea (see NORDHAGEN 1933 Fig. 5). These striking isolated assemblages make the occurrence of var. meizophylla particular interesting as it seems to indicate that it constitutes an old population which perhaps was isolated in an ice-free pocket during the last glaciation.

The scree vegetation on limestone and mica-schists with *Braya linearis* var. *meizophylla* was described by NORDHAGEN (1954: Fig. 3 and Table 2). Fig. 4 in the same paper shows typical specimens of the variety growing in the scree of Baatfjell, Junkerdal.

Braya alpina Sternb. & Hoppe

Braya alpina is an endemic east-alpine species, a character species of calcareous screes (*Leontodontetum montanei*) cfr. GAMS (1936: 49). Material was obtained from the Grossglockner area (seeds kindly collected at "Wasserfallsee" by Dr. Zollitsch and sent by Prof. H. MERXMÜLLER). The plants Cult. No. 6788 were grown together with *B. linearis* (see Table 7).



Fig. 14. Above *Braya alpina* (No. 6788) compared with two specimens of *B. linearis* var. *meizophylla* (Br. 3, middle row) and two of *B. linearis* (No. 7388, below). All cultivated simultaneously in pots at the experimental field. May 1965.

Chromosome number. The old count of 2n = 32 (MANTON 1932: 545) could not be verified, the error being perhaps due to falsely identified plant material. Squashes of PMCs and root tips of No. 6788 showed 21 bivalents or 42 chromosomes (Figs. 10 f-g), the same number as in *B. linearis* which has been considered by some as a variety of *B. alpina* (var. *rivularis* Fries). In the plate pictured by MANTON (1932 Fig. 24) the chromosomes are only slightly different in size almost as in the genus 4^*



Fig. 15. Braya. — a: Metaphase plate in root tips, B. intermedia from NE. Greenland (2n = 70, cp. Böcher 1956). — b-n: PMCs in B. purpurascens; b-f: Cult. No. KJ 54; g-i: Cult. No. KJ 53, both from Nugssuaq, W. Greenland; k-n: Cult. No. 6356 from Spitzbergen; c, g, j, k: first metaphase; d, e, h, i, l, m: first anaphase; b, f: second metaphase; n: restitution nucleus (see text). Inversion bridges and acentric fragments in b, d, e, f and i; bridges due to stickiness in h, i, l, m (see Text). — All microtome technique. Scale 10 μ .

Nr. 7

Draba. According to MANTON the basic number in many other genera of the tribe Alysseae is seven, thus e.g. 2n = 14 in Chorispora tenella which is referred to the sub-tribe Brayinae.

Cultivation. In the first year rosette stage there was a clear difference between *B. alpina* and *B. linearis. B. alpina* had more vigorous rosettes and its leaves were entire and hairy (along the margins and on the lamina) while in *B. linearis* they were often incised, glabrous or if hairy mainly along the margins. Both species had \pm depressed rosettes. The leaves of *B. alpina* are broader and more succulent and anatomically distinguished by a more dorsiventral structure. *B. linearis* has almost isolateral leaves. Second year flowering plants differed from *B. linearis* in the following characters: petals larger and pale lilac, sepals (and some petals) often persisting below ripening siliques which are shorter and a little broader. *B. alpina* is earlier, all plants having ripe siliques by June 5th, while three strains of *B. linearis* still had flowers and unripe fruits. *B. alpina* is lower and its inflorescence more dense and capitate. Finally the styles in *B. alpina* (No. 6788 and herbarium material) are broader and more often tapering.

The comparative cultivation makes it evident that *B. alpina* and *B. linearis* are clearly distinct species. They are obviously related as are *B. linearis* and *B. aenea*, cp. p. 71.

Braya purpurascens (R. Br.) Bunge

This species was studied in the Arctic Greenhouse in plants from East Greenland and Spitzbergen. Additional material from Nugssuaq W. Greenland was kindly placed at my disposal by Dr. KNUD JAKOBSEN. Unfortunately, many plants which were brought into culture in order to compare W. Greenland, East Greenland and Spitzbergen material died early in a rosette stage. A more detailed comparison therefore was made impossible. The general impression, however, is that *B. purpurascens* is a very polymorphic species and this seems to be explained by its meiotic behaviour. Six strains were examined: viz. two cultivated by KNUD JAKOBSEN as KJ 53 (from Store Dal, Nugssuaq) and KJ 54 (Marrait, Nugssuaq), three strains from Mestersvig in NE. Greenland (Nos. 6679 and 7114, seeds collected by Dr. T. T. ELKINGTON, No. 7368 from Central Skeldal at Mestersvig, D. SPEARING and N. LASCA NO. 767), and one strain No. 6356 from W. Spitzbergen, Kongsfjord 78°58' N., 12°10' E. (seeds collected 1958 by Dr. NIELS FOGED).

Cytological observations. B. purpurascens is an octoploid with n = 28. This number was first counted by HOLMEN (1952) in material from Peary Land and later by JØRGENSEN et al. in material from Clavering Island NE. Greenland and by MULLI-GAN (1965) from Northwest Territories, Alaska and British Columbia (see Postscript). The six new strains to be discussed here had also n = 28 (Fig. 10 j-k and 15).

It was particularly interesting that three of them proved to be structurally deviating in various ways.



Fig. 16. Variation in *Braya purpurascens.* — a: NE. Greenland, Nordfjord (P. J. Povelsen June 1949). — b–c: N. Greenland, Peary Land, Brønlund Fjord (K. Holmen Nos. 6757 and 687). — d: NE. Greenland, Strindberg Halvø (Th. Sørensen No. 3566). — e: W. Greenland, Ignerit Fjord, Magdlåq (M. P. & R. T. Porsild July 1929). — f: Baffin Isl. Frobisher Bay (H. A. Senn & I. A. Calder No. 4020). — g: Alaska, Atkasuk 70°28' (K. Holmen & Olle Mårtensson No. 61-1526). — h: Alaska, Utokok River, 68°55' (K. Holmen, August 1960). The latter belongs probably to *B. glabella*, but in shape of the siliques it is approached by the specimens a, and e–g while specimens b–d have siliques which clearly are broadest in the middle part. Specimen d shows an extreme case with headlike inflorescence. — All specimens from the Bot. Museum in Copenhagen. Scale 10 cm.

No. KJ 54 (Figs. 15 b–f). In this strain bridges and acentric fragments occurred with great frequency, the number of bridges per cell at first anaphase often amounting to four. In some cells one bridge persisted until the second metaphase (Figs. 15 b, f) and was in one case (Fig. 15 f) very short almost uniting the two plates. At second telophase two or three bridges were seen with a corresponding number of acentrics. Laggards occurred in a few cells, while 1–2 univalents were not infrequently placed outside the two nuclei in PMCs at interphase.

Nos. KJ 53 (Figs. 15 g–i) and 6356 (Figs. 15 k–n) resembled each other but deviated from the preceeding by the rare occurrence of bridges due to inversions. On the other hand there was sometimes an abundance of bridges which seemed to be due to stickiness, probably mainly localized stickiness resulting from sub-chromatid exchanges (see EVANS 1962, BÖCHER 1964). In Fig. 15 h the bridge on the far right has clearly two side arms as found in plants with localized stickiness. The bridges were often found in a central position in the separating chromosome plates, and the same position was held by some groups of four chromosome at metaphase I (Fig. 15 j–k) which were not assumed to be quadrivalents. In fig. 15 l–m there seemed to be a connection at one end between two of the bridges which makes it probable that the groups of four are held together by sticky connections.

The highly deviating cell fig. 15 n represents probably a rare case. It was found among young pollen tetrads and its chromosome content resembled a giant restitution nucleus. Most chromosomes were dividing (second division). A neighbouring cell had some lagging bivalents surrounded by scattered univalents. Perhaps division into four pollen cells is inhibited in such cells which finally will develop into giant pollen grains, which sometimes are found in *Braya purpurascens*.

It is difficult to estimate to what extent and in which way such cytological disturbances influence the variational pattern. However, it is not too speculative in this case to state that the species as compared with e.g. *B. linearis* is cytologically more unstable and morphologically more variable. In many respects it resembles the high polyploid complex species of *Draba*.

Cultivations. The Spitzbergen strain No. 6356 was slender as compared with the West Greenland plants KJ 53–54 which were cultivated at the same time in the Arctic Greenhouse. Unfortunately all plants of No. 6356 died after having set fruit and could not be compared with the East Greenland plants. In 1965 the two series from Mestersvig (No. 6679 and 7114) were relatively robust and almost identical while No. 7368 from Skeldal was much more slender with smaller flowers. The dimensions appear from Table 10. All three strains had glabrous siliques, while the West Greenland strains KJ 53–54 had hairy siliques and KJ 53 longer siliques (up to 10–11 mm long).

Variation. If taken in a very wide sense this complex would be a species aggregate consisting of the octoploid *B. purpurascens*, the tetraploid *B. thorild-wulffii* (see OSTENFELD 1923) and probably *B. glabella*, *B. pilosa* and *B. henryae* (see RAUP 1934), which are unknown cytologically. Taken in a more restricted sense, however,



Fig. 17. Braya glabella Rich. Authentic, specimen kept in the Naturhistoriches Reichsmuseum in Vienna. The type specimens kept at Kew from the Franklin Expedition correspond to this specimen although in one of the plants there is one large stem leaf in the middle part of the stem subtending a very remote silique. The Copenhagen Herbarium contains two specimens of the type collection, a very small one and a larger which, however, is without the terminal part of the inflorescence.

Cult. No.	Origin	Height cm	Dia- meter of stem mm	Breadth of broadest rosette leaf mm	Dia- meter of flower mm	Length of lowest siliques mm	Breadth of broadest siliques mm	Other characters
6679-7114	Mestersvig Damp soil	9(6-13)	1.5	5-7	(4)5-6	8–9 (Style 1 mm)	3	Siliques glabrous. Not infrequently with one stem leaf subtend- ing remote flower
7368	C. Skeldal Heavily cracked clay mounds	9(6–10)	1.0	3-(4)	(2)3-4	8–9 (Style 0.6–0.9 mm)	2	Siliques glabrous. Very rarely with one stem leaf. Sometimes flowering at the basal rosette

B. purpurascens is very complex in itself (Fig. 16), but it is here, as in Draba glabella and D. arctica, difficult or impossible to find dividing lines enabling a sensible taxonomic subdivision. ABBE (1948) is not inclined to recognize any of the variants which SCHULZ (1924) has accepted. A. E. PORSILD (1955: 133) discusses the badly defined var. dubia (R. Br.) Schulz, which he would like to be able to use as a name for certain high arctic compressed and decumbent forms. Otherwise he describes the variation as very considerable as to stature, shape and degree of pubescence of the siliques, length of style and length of flowering and fruiting axes. Even within the same population, plants with pubescent siliques might be as common as those with perfectly glabrous ones. HOLMEN (1957: 52) on the other hand says that B. purpurascens in Peary Land varies somewhat, but that this variation is due to differences in environmental conditions. B. purpurascens, therefore, may locally appear rather uniform, but studied in its total range, it is clearly polymorphic. This impression is based on studies of the style lengths and shape of the stigma (see BÖCHER 1956 Fig. 8 b-d) and on the preliminary observations of cultivated plants mentioned above.

Braya glabella Rich.

No living plants have been available for study, but in the Vienna Herbarium a specimen was found which most probably is authentic. It is labelled "*B. glabella* North America, Hooker" (see Fig. 17) and it corresponds entirely with the description given by SCHULZ (1924: 230).

ABBE (1948: 9) concludes that *B. glabella* falls in the *B. purpurascens* complex more than it does in the *B. linearis* group and this agrees with the opinion set forth by JØRGENSEN et al. (1958). In BÖCHER (1956: 13) *B. glabella* was assumed to have resulted from a cross between *B. linearis* and *B. purpurascens*, but this idea has now clearly lost much credibility, as the authentic material resembles B. pilosa and B. henryae and also approaches B. rosea-aenea. Furthermore the established localities for B. glabella are West-American and B. linearis is unknown west of West Greenland. B. glabella resembles what ABBE pictures as the "robust phase" of B. purpurascens, but has an elongated inflorescence. It also resembles plants from Southhampton Island collected by MALTE and referred by him to B. glabella but by ABBE to the above mentioned "robust phase". A. E. Porsild, however, referred Malte's plants to B. pilosa (1943: 46). A recent collection by K. HOLMEN from Utokok River in Alaska (68°55' N., 161°10' W., Aug. 1960) and kindly placed at my disposal (Fig. 16 h) was recently determined by A. E. PORSILD as B. glabella. It has 1 mm long styles with capitate stigmas and glabrous 10 mm long siliques. The petals are 3.5-4 mm long and reddish. The stems have scattered hairs and the leaves are narrowly spathulate, glabrous but ciliated on the petioles. The racemes are elongated and the lower siliques are remote from the terminal part as in *B. rosea*. The appearance of this plant as well as of the material from Vienna suggests that it belongs to a separate species closely related to *B. purpurascens*. The identity of *B. glabella*, however, is still problematic and the questions cannot be answered before material has been cultivated along with the "robust phase" of *B. purpurascens* and chromosome studies have been made.

Braya novae-angliae (Rydb.) Th. Sør.

Braya novae-angliae is another polymorphic species. In the previous paper (B. 1956) it was divided into three subspecies and its ssp. novae-angliae into three varieties, this division being partly based on the geographical races mentioned by ABBE (1948).

The chromosome number of *B. novae-angliae* was first counted by BÖCHER & LARSEN (1950) who found 2n = 56 in material from continental West Greenland. In the paper of 1956 this number was corroborated by studies of meiosis where a number of distinct metaphase plates clearly had 28 bivalents. New material from West Greenland collected in 1956 at Tarajonitsup (Salt lake area at Strømfjordshavn) has now been cultivated for several years (No. 4885) including 1962–65 when it was grown together with Br. 6 originating from Colorado.

The material from Colorado was collected in 1960 by Dr. K. HOLMEN on the summit of North Star Mt., Hoosier Pass, 1200', 150 km SW of Denver. It is obviously the type locality for *B. novae angliae* ssp. *ventosa* (Rollins) Böch. cp. ROLLINS (1953: 114) to which taxon the material belongs.

Chromosome number. As might be expected the Greenland plants (No. 4885) had the same number as those counted previously. Much more interesting, however, was that 2n = 56 was established also in the Colorado sample (Fig. 12 n) in spite of the fact that ROLLINS in plants from the same area found n = 32. It is almost impossible to misinterprete a somatic plate like that in fig. 12 n. But according to my experience it is sometimes difficult to count meiotic stages in *Braya* because



Fig. 18. Simultaneously cultivated specimens of *Braya novae-angliae* var. *interior* (Cult. No. 4885, upper row) and ssp. *ventosa* (Cult. No. Br. 6, lower row). Arctic Greenhouse, Copenhagen July 1964. — Scale 10 cm.

so often some of the small chromosome pairs separate precociously (Fig. 12). The fact that ssp. *ventosa* has 2n = 56 removes any doubt about its taxonomical status; it is closely related to ssp. *abbei* Böch. from Newfoundland, but is not an independent species, see remark p. 6 in Böcher 1956.

MULLIGAN (1965, see Postscript) also counted 2n = 56 in plants from North

	Ssp. novae anglica var. interior Cult. No. 4885	Ssp. <i>ventosa</i> Cult. No. Br. 6
First year rosettes	Adpressed, leaf colour variable between green and dark red-green, leaves (anthocyanin) in most cases with few hairs and little toothed. Diameter of rosettes 3.9 cm (2.5-6.0 cm)	Adpressed-ascending, leaves dark red- green, hairy, broadly ovate. First leaves \pm entire, but increase in incision in later leaves which also are more hairy. Diameter of rosettes 4.2 cm (3.0–5.0 cm)
Later rosettes	Leaves lanceolate-narrowly spathulate, entire or with a few, broad and shallow teeth, reddish (or green), almost glabrous. Longest leaf 2–4 cm	Leaves spathulate, entire or rarely with 1–3 small sharp teeth, green, with scattered bifid (2-3- pronged) hairs along margin and unbranched cilia along petiole. Longest leaf 2.5–3.5 cm.
Stems	Stems 5–12(17) cm long, \pm erect with \pm dense pubescence of bifid (2–3-pronged) hairs; 3–11 narrow leaves, the largest being 1.5 cm long and 1.5 mm broad, often with 2 small teeth and scattered bifid hairs	Stems rather coarse 3–10 cm long, \pm ascending with dense pubescence of bifid (2–3 pronged) hairs; 3(–5) leaves, entire, \pm spathulate, the largest being 1.5 cm long and 2 mm broad with very few bifid hairs
Flower: Sepals Petals	2.5 mm long, with red spots 4–5 mm long, white with pink claw	3 mm long, green, persistent 5 mm long, white with pink claw
Pedicels	Obliquely upright, 2–4 mm	Divaricate, slightly curved 2-4 mm
Siliques	Max. length (without style) 13 mm, almost straight or slightly curved. Max. breadth 0.7–1.0 mm. Valves ± tapering above. Style 0.7 mm long, 0.3–0.4 mm broad. Stigma 0.5–0.7 mm broad. Seeds about 1.0 mm long	Max. length (without style) 16–19 mm, more curved than in No. 4885. Max. breadth 0.9–1.2 mm. Valves more rounded above. Style 0.8–1.0 mm long, 0.3–0.5 mm broad. Stigma 0.5–0.7 mm broad. Seeds about 1.0 mm long
Earliness	Much later in flower than Br. 6	Early

Table 11. Braya novae-angliae. Comparative cultivations.

Star Mountain, Colorado. He has not subdivided *B. humilis* coll. and refers the material to this species aggregate. However, there is no doubt, that all specimens from Colorado belong to *B. novae-angliae* ssp. *ventosa*. MULLIGAN also states that the somatic chromosomes in *B. humilis* coll. are smaller than those in e.g. *B. purpurasceus*, a fact which is in accordance with observations made by the present author (cp. Fig 12 y).

Comparison of simultaneously cultivated plants. Table 11 contains a comparison of a number of characters in the two subspecies of *B. novae angliae*. It

appears that the main difference is expressed in the growth habit the leaf shape and colour, and the dimensions of flowers and siliques.

Of particular interest is the relation between ssp. *ventosa* and ssp. *abbei*. From a comparison of the information in Table 11 it appears that there is very little morphological difference between ssp. *abbei* and ssp. *ventosa*. This means that the suggestion expressed earlier (BÖCHER; 1956: 9) that ssp. *abbei* perhaps ought to be considered as a variety of ssp. *ventosa* might be discussed. At the present stage, however, I see



Fig. 19. Braya novae-angliae in full flower. On the left two pots with No. Br. 6 from Colorado, North Star, Mt., on the right two of No. 4885 from W. Greenland, Tarajonitsup. Arctic Greenhouse. 22th of June 1962.

no advantage in reducing ssp. *abbei* to varietal rank as it seems distinguished at least by one character: a higher number of stem leaves. From the picture in BÖCHER 1956 Fig. 3 of the type collection of ssp. *abbei* it appears that even small specimens of ssp. *abbei* may often have more than five leaves while cultivated specimens of ssp. *ventosa* did not have more than 3 leaves. Otherwise the two subspecies are widely separated geographically, ssp. *ventosa* being the only representative of *B. novae-angliae* in Western America.

5. Kernera

Material of *Kernera* collected by Dr. M. LEWIS in the Pyrenees (Garvarnie) was cultivated as No. 7332 and flowered abundantly in the Arctic Greenhouse as well as in pots at the Experimental Field. Root tips were squashed and the chromosome number determined as 2n = 14 (Fig. 20).

The plants resembled K. saxatilis (L.) Rchb. but deviated in some characters from this species, which according to CHIARUGI (1933) has 2n = 16 and perhaps 2n = 32 (MATTICK in TISCHLER 1950). 2n = 14 corresponds to the number found by CHIARUGI (1933) in *Rhizobotrya alpina* Tausch (= Kernera alpina (Tausch) Prantl.), a relic species restricted to the southern Alps (Dolomiti occidentali). CHATER & HEYWOOD (1964) in their treatise of K. saxatilis remark that further investigations especially on plants from the Pyrenees are needed and they discuss the identity of plants from that area which have been referred to K. decipiens (Wilk.) Nym. (Cochlearia decipiens Wilkomm, see WILLKOMM 1852: 12). In such plants the cauline leaves are sagittate and amplexicaule at the base, and the siliques are ellipsoidobovoid, not orbicular. They add that such plants tend to have somewhat showier petals but they do not list K. decipiens as a separate species.



Fig. 20. Kernera; from the left drawings of ripe siliques: two siliques of K. saxatilis (from river Drava at Feistritz, leg. J. Vahl 1824), two of K. cfr. decipiens (Cult. No. 7332) and two of K. boissieri (Sierra Nevada, Mt. Dornajo, leg. Campo 1852). Scale 2 mm. — On the right No. 7332, late prophase and metaphase from mitoses in root tips (orcein squash technique). Scale 10 μ.

The cultivated plants correspond to K. decipiens although the stem leaves are hardly sagittate, but clearly amplexicaul. The flowers are a little larger than most flowers in K. saxatilis, but the latter contains races with different flower size which makes it difficult to distinguish it from plants of the K. decipiens type.

The Copenhagen Museum contains some sheets from the Pyrenees and S. France which closely resemble Cult. No. 7332 (thus Fond des Comps, Pyren. leg. Blytt; St. Guilhem du Desert, leg. Ibérault(?), Inst. Bot. Montpellier; Pic Lhièris, Pyren. Centr. Gall. Sept. 1851 leg. Joh. Lange; Cevennes, Herbar. Liebm.). A comparison of this material with the cultivated plants seems to justify regarding *K. decipiens* as a separate taxon and the deviating chromosome number does not support its reduction to a subspecies of *K. saxatilis*.

It is not easy to distinguish *K*. cfr. *decipiens* from *K*. *saxatilis* morphologically, but two characters which appear from the material mentioned above seem to be important additions to the characters mentioned by WILLKOMM (1852) and WILLKOMM & LANGE (1880). First the number of stem leaves is higher and the internodia shorter

Nr. 7

in K. cfr. decipiens, and the siliques of this taxon have thinner walls and the styles are longer.

With regard to the shape of the fruits *Kernera* cfr. *decipiens* is intermediate between *K. saxatilis* and *K. boissieri* Reuter from Sierra Nevada in Spain (see Fig. 20). Also *Rhizobotrya* (or *Kernera*) *alpina* has longer styles than *K. saxatilis* (CHIARUGI 1933: 70) and its siliques are not orbicular but broadly ovate and the style may be slightly tapering just as in the available material of *K. boissieri* and to some extent also in Cult. 7332 (*K.* cfr. *decipiens*).

The above mentioned herbarium material which probably is referable to K. *decipiens* indicates a certain variability in this species. The plant collected by JOHAN LANGE has broader, nearly spherical siliques and approaches thereby K. *saxatilis*, and the plants from the Cevennes are almost glabrous thus in this respect resembling K. *boissieri* which seems to deserve species rank being characterized by thick rhizomes, spathulate rosulate leaves and glabrous stems and leaves (see description in WILL-KOMM & LANGE 1880: 842).

The discovery of plants with n = 7 in a *Kernera* should prompt further cytotaxonomical studies e.g. of *K. boissieri* and other highly deviating plants. At the same time it has weakened the theories about the evolution of the *Thlapsidinae* mentioned by CHIARUGI and also the justification of maintaining *Rhizobotrya* as a separate genus, the latter being mainly distinguished by having bracteate racemes.

6. Evolutionary trends

Draba

Chromosome numbers

From earlier studies, supplemented by some recent investigations, (e.g. MERX-MÜLLER & BUTTLER 1965) a long series of euploid chromosome numbers is presented, the basic number of which is in most sections clearly 8. Counts have been made within eight of the 17 sections (subgenera) mentioned by SCHULZ 1927. In all, the numbers of 46 species and subspecies are known ranging from diploids (2n = 16) to sixteenploids (2n = c. 128).

In the section Aizopsis (x = 8) 10 species have been counted, of which 8 are diploids and 2 tetraploids (x = 8) (see Skalinska (1964), MERXMÜLLER & BUTTLER (1965)).

The section *Chrysodraba* (x = 8) goes a step further in having a high polyploid level throughout, the only exception being *D. sibirica* which is diploid. There are two species found at the octoploid level, and one sixteen-ploid, while in one complex species, *D. alpina*, different strains have been counted with 2n = 64, 80, and 112. However, the tetraploids in the section *Aizopsis* seem to form a transition between *Aizopsis* and the high polyploid *Chrysodraba* (cp. MERXMÜLLER & BUTTLER 1965).

The large section Leucodraba (x = 8) falls into two subsections which differ cytologically. Euleucodraba behaves almost as Aizopsis in the dominance of diploids

(7 species) but it also contains four hexaploids, of which at least two (*D. norvegica* and *D. arctogena*) are closely related to the species of the other subsection *Holarges*. This section on the other hand has no diploids but four (three) tetraploids, one (or three) hexaploids, six octoploids, 4 decaploids and one duodecaploid (2n = 96).

The three species of the section *Drabella* are diploid, tetraploid and perhaps pentaploid (2n = 40, D. crassifolia, cp. HEILBORN 1941 and below). The diploid and tetraploid species belong to a series with x = 8.

In the Central- and South American yellow-flowering section Adenodraba only one species, *D. jorullensis* H.B. Kth., has been counted. BEAMAN et al. (1962: 43-46) reports n = 12 in material from Mexico (Alt. 3980-4160 m) and they discuss this interesting number saying that it could be interpreted as an additional basic number of x = 6 or 12. They also discuss the possibility of a connection between this new number and arctic *Draba* species with n = 24. However, while the latter might be a stabilized allohexaploid in a series with x = 8, it is difficult to imagine *D. jorullensis* being a triploid. I therefore agree with the opinion that *D. jorullensis* is either a diploid or a tetraploid in a series with x = 6 or 12.

Quite recently 2n = 24 was also reported in one species of the white-flowering section *Rhabdocarpa* (*D. pickeringii* Abray from Peru, FAVARGER & HUYNH in Taxon 14: 88, 1965). *Rhabdocarpa* is also a purely American section with 10 species in the Andes.

Finally the number 2n = 48 found in *Draba gilliesii* (see p. 39) may indicate a further evolution within a series with 12 as basic number. The species in question belongs to the section *Calodraba* which is purely South-American (14 species in Andes-Patagonia).

The question of the occurrence of more than one basic number in *Draba* has further been accentuated from a closer study of *Draba aurea* Vahl. This species belongs to another, mainly yellow-flowering section *Phyllodraba* which according to SCHULZ contains 29 species from East Asiatic and North Pacific American mountains extending southwards to California and Northern Mexico (*D. helleriana*). As mentioned on p. 36 *D. aurea* has either 2n = 76 (x = 19) or perhaps 2n = 72 + 4 small extra chromosomes. *D. aurea* might therefore be interpreted as a secondary hexaploid (perhaps allohexaploid) in a series with x = 12.

As pointed out above *D. crassifolia* may possibly be interpreted as a pentaploid in a series with x = 8; the only reason for this is that two other species of *Drabella* have this same basic number. However, it is more probable that the species is a tetraploid member of a 10-series. This opinion is held by JØRGENSEN et al. (1958: 143).

Most facts point towards the conclusion that in *Draba* there are at least three basic numbers, viz. 8, 10, and 12.

The very specialized dense cushion plant, *Lithodraba mendocinensis*, from the South American Andes has 2n = 64 according to BOELCKE (1951), a fact which is of some interest as its nearest relatives *Eudema* and *Xerodraba* are referred by SCHULZ (1924) to the *Brayinae* which is a group with seven as the basic number (see later).

Species formation

According to SCHULZ (1927: 7) Draba flowers are adapted to cross-pollination. However, there is strong evidence for assuming a high degree of selfing and inbreeding in many arctic species resulting in a number of uniform and true-breeding lines within each species. The many hybrids which are described indicate occassional crosspollination, but as already suggested many specimens which have been interpreted as hybrids might as well be considered as extreme variants within one complex species which owes its complexity to a high degree of structural changes in its chromosome complement.

It became evident from the cytological analysis of a number of *Draba* species with a high ploidy-level that polyvalent chromosome associations are very rare, if present at all. This fact which also appears from Fig. 92–99 in JØRGENSEN et al., strongly suggests alloploid evolution. In the preceeding sections alloploid evolution was suggested in hexaploids, e.g. *D. lactea*, *D. norvegica*, *D. arctogena* and *D. cinerea* $(8 \times 16 \rightarrow 24 \rightarrow 48)$ and it may well also have been involved in the formation of the decaploids $(24 \times 16 \rightarrow 40 \rightarrow 80)$. In the case of octoploids and 16-ploids autopolyploidy is perhaps a little more likely, but octoploid plants also lack polyvalents. What is needed is of course evidence based on experiments and so far we have only one example of known allopolyploid evolution in the closely related genus *Erophila* (WINGE 1933). MANTON (1950: 14), however, suggests that the proportion of allopolyploids in the *Cruciferae* is high.

Now, if we assume alloploid evolution as the most important type we may imagine that the same species arose by chromosome-doubling in various parts of the arctic zone resulting in several different ± sterile primary hybrids. As the parental species themselves often were tetraploid or even of a higher level and already rather complex it seems entirely apprehensible that the resulting high polyploid species became very intricate making the work of taxonomists troublesome and perhaps sometimes impossible. Any deviating type which might owe its origin either to an independent alloploid evolution or to changes in chromosome structure within some of the established allopolyploids would probably in a high arctic environment be maintained for long periods as an independent entity. Its features—e.g. type of pubescence would be maintained because selfpollination was predominant and if cross pollination took place it would most probably be between plants of the same inbreeding line. Isolation in small pockets of vegetation in the high arctic deserts would further favour differentiation into small units which some taxonomists would evaluate as species and others as varieties or perhaps even forms of little taxonomic importance.

The distribution of species belonging to different chromosome levels is interesting. It appears from the work of MERXMÜLLER & BUTTLER (1965) that the majority of alpine species are diploid. Among the arctic species, on the other hand, only four species, *D. fladniensis*, *D. nivalis*, *D. subcapitata* and *D. sibirica*, are diploids. In *Draba*, therefore, the mountains south of the arctic area seem to constitute centers of origin,

Biol.Skr.Dan.Vid.Selsk. 14, no. 7.

5

a view which corresponds with that of SCHULZ who mentions the mountains which surround the Mediterranean Sea as "ein abgeschlossenes Schöpfungszentrum." *Draba* is sub-divided into so many widely different sections, that it seems reasonable to postulate more than one center of origin, and perhaps a polyphyletic origin. In this connection the deviating chromosome numbers of *D. jorullensis*, *D. pickeringii*, *D. gilliesii*, and *D. aurea* are of particular interest.

There is no indication of any area in the Arctic which could have been a center of origin for species with basic or low chromosome numbers. *Draba sibirica* is an Asiatic-East European subalpine species ranging to subarctic or low arctic areas. *Draba fladnizensis* occurs in Eurasian and North American mountains and *D. nivalis* and *D. subcapitata* have close relatives among the species in Central Asia.

Montane North-American species have reached the Arctic areas, e.g. *D. aurea* which has its eastern limit in Scoresbysund (Fig. 8), and *D. crassifolia* which extends across the North Atlantic Ocean and reached Northern Norway (Hultén 1958, map 174). On the other hand, there is no doubt that, in case of the polyploids within the sections *Leucodraba* and *Chrysodraba*, the Arctic zone is a recent center for speciation. The species are all very complex, but the entities are comparatively young and often not yet sufficiantly distinct to deserve species rank. Isolating forces such as self pollination, geographical barriers, and chromosome barriers, however, are clearly operating and will probably gradually lead to better defined demarcations.

Polyploidy and distribution

There has been much discussion about the high frequency of polyploids in the Arctic (e.g. works of HAGERUP, TISCHLER, LÖVE & LÖVE). Recently JOHNSON & PACKER (1965) have made an interesting contribution to our understanding of this phenomenon. They found a particular high frequency of polyploids on cold, wet soils in which frost action plays an important rôle and conclude that newly formed polyploids were successful pioneers on newly exposed glaciated surfaces. This success is explained by assuming that polyploids are at a selective advantage in having a higher genetic variability.

If the taxa treated in the present paper are considered we find some agreement with these ideas as certain of the high polyploids (octoploids or higher levels) are found on solifluction soils (e.g. *Draba alpina*, *D. bellii*) while some of the tetra- and hexaploids are found on stable, dry and warm soils (e.g. *Draba lanceolata*, *D. cinerea*).

What is more striking, however, is the fact that all taxa at the high ploidy-levels (8x or more) have high arctic distributions, while species with sub-low-or medium arctic distribution do not reach more than the hexaploid level. In two groups this trend is very clear as relatively southern taxa or races have lower numbers than the northern ones (*Draba cinerea* \rightarrow *D. arctica*; *Draba glabella* $2n = 64 \rightarrow 2n = 80$). In both these groups a higher chromosome level is correlated with a morphological

Nr. 7

change, the high arctic representatives being more compressed and with fewer stem leaves.

But it should be emphasized that not less than three diploids (*D. subcapitata*, *D. fladnizensis* and *D. nivalis*) and two hexaploids (*D. arctogena* and *D. lactea*) reach the high arctic areas, and that some of them (*D. subcapitata* and *arctogena*) are almost restricted to the northernmost parts of the Arctic. They are therefore probably old species, perhaps tertiary relics; they are certainly what JOHNSON & PACKER regard as "old species sufficiently rich in biotypes to adjust". Such species are relatively important in NW. Alaska which was never glaciated, and they are also present in N. Greenland where the existence of such unglaciated areas is also assumed.

Braya

Chromosome numbers and species formation

A critical summary of *Braya* species with known chromosome numbers is presented in table 12. Apart from some countings of 2n = 32, 40, and 64 which probably are due to various kinds of error (see later), all numbers can be arranged in a series with the basic number of 7. HOLMEN (1952) was the first to find a species at the tetraploid level, viz. *B. thorild-wulffii* with 2n = 28. The hexaploid level is the most common in the material studied at present.

In table 12 the species are arranged in three groups; the first corresponds to Torularia humilis, the second to Braya in Schulz (1924: 223–227). The third group comprises only one decaploid species, B. intermedia Th. Sør., an endemic species of NE. Greenland (cp. SØRENSEN 1954). This species is difficult to place as it combines characters from *B. humilis* and *B. linearis* or *B. purpurascens*, or both, being perhaps a triple-allodecaploid. This latter idea which was proposed by the present author in 1956 presupposes a very intricate process of formation. It is however a fact that B. linearis and B. humilis in NE. Greenland are hexaploids and the easiest way of obtaining a plant with 2n = 70 would be fertilization between an unreduced gamete of a hexaploid and a normal reduced gamete of an octoploid. In NE. Greenland only B. purpurascens is octoploid. B. intermedia resembles B. humilis and linearis but approaches also B. purpurascens and might be interpreted as B. humilis \times linearis (unreduced: 42)×B. purpurascens (reduced: 28). A fact which supports this complicated species formation is that species of *Braya* have similar rather narrow ecological ranges and therefore very often grow together. This is striking e.g. at the saltlakes in continental West Greenland.

The first metaphase plate of *B. intermedia* pictured by JØRGENSEN et al. (1958 fig. 107) contains exclusively bivalents indicating a regular meiosis and no or very few multivalents. Also in the polyploid *Braya* species studied by the present author true associations of more than two chromosomes were very rare if present at all.

These facts and the occurrence of two large chromosomes only in the tetraploid *B. thorild-wulffii* favour the view that alloploid evolution has been as important in *Braya* as it was assumed to be in *Draba*.

Evolution in relation to geographical distribution

In Table 12 and Fig. 21 are summarized the distribution of all known species and subspecies in the genus *Braya* (incl. *B. humilis* and *B. novae-angliae*). Europe is very poor in species while the Central Asiatic mountains harbours 10 species and may constitute the center of origin of the genus.

B. rosea is the only central-asiatic species with known chromosome number; almost nothing therefore can be said about the chromosome level of the asiatic group of species which may contain some relatively ancient diploids. In the case of the B. humilis group, however, measurements of pollen size (ROLLINS 1953: 112 and BÖCHER 1956, Fig. 2) have shown four size classes of pollen grains and here the two largest sizes are connected with the hexaploids and octoploids. The two smallest size classes may therefore correspond to diploids and tetraploids. All three samples of small sized pollen studied by the present author originated from central asiatic plants.

If the central asiatic high mountains are considered as the place of origin we may imagine that some species migrated from the center in various directions. One possible way was towards NE. in the highland east of river Jenisei to Arctic Siberia and further to N. America and Greenland. Another way would perhaps be through the mountain ranges towards the west.

The *B. humilis* group is undoubtedly one phylogenetic line. As illustrated in BÖCHER (1950: 40) and Fig. 21 in the present paper, this species group is found in the unglaciated highland area of Siberia west of river Lena from where it extends to arctic coast. One branch of hexaploids (ssp. *arctica*) continued along the Arctic Sea and reached NE. Greenland while another branch probably of octoploids (*B. novae anglica*) reached southwards to Colorado and eastwards to Hudson Bay, Newfoundland and Continental Middle West Greenland. But the range of *B. novae angliae* is split up into at least 8 disjunct areas. Being almost exclusively found in previously glaciated areas, the disjunctions are most probably due to postglacial extinction in connection with forest expansion and soil leaching.

The other group, the *B. alpina*-group, probably followed the same route towards NE. This is indicated by the distribution of species like *B. aenea* extending from Pamir to Arctic Siberia and *B. siliquosa* which from Altai reaches the Lena-Kolyma river area in the north and Okotsk and westernmost Alaska in the east.

In the case of *Braya* the unglaciated highlands east of Jenisej have undoubtedly served as an important route for migration of high montane asiatic species to Arctic Siberia (cp. the ideas proposed by TOLMATCHEV (1960: 272)). At an early stage the ancestors of the *B. purpurascens* group may have reached the Arctic area and were able to establish a circumpolar range. One ancient tetraploid (*B. thorild-wulffii*) is now connected with the high arctic parts of the American Arctic Archipelago and Greenland. The *B. glabella-pilosa* complex may represent another ancient group.



Fig. 21. World distribution of the genus Braya and border of greatest extension of larger quaternary iceshields (<u>1111111</u>). Areas with horizontal hatching (horizontal short lines) are occupied by the B. humilis-B. novae-angliae complex. The broken line shows the approximate southern limit of the circumpolar B. purpurascens while the dotted area shows the distribution of B. thorild-wulffit. The areas of B. linearis are black while the east-alpine area of B. alpina is cross-hatched. The continous line in Asia shows the limits of the whole genus while the small vertically hatched areas shows that parts where the concentration of species is greatest. Here we have the following endemic species: B. pamirica, B. scharnhorsti and B. brachycarpa. In the Angara-Sajan district the Komarov-expedition has found the endemic B. angustifolia and south of latitude 50° the following wider ranging endemics occur: B. tibelica, B. oxycarpa and B. rosea. In Alaska and Eastern Chuch peninsula there are small areas of B. plosa, B. glabella, B. henryae in British Columbia.

69

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Taxon							(Geog	rapl	hical	l are	a				
	2 n	Ploidy level	Spitzbergen	Scandinavian Mountains	Central European Mountains	Central Asiatic Mountains	Central North Siberia	NE. Asia	W. North America	E. North America	Arctic Alaska	Arctic Canada	Middle W. Greenland	NW. Greenland	N. Greenland	NE. Greenland
Braya humilis (C. A. Mey.) Robins. ssp. humilis Braya humilis (C. A. Mey.) Robins. ssp. arctica (Böch.) Rollins Braya novae-angliae (Rydb.) Th. Sør.	28 ¹ 42	6 x				x	x		x ¹ x ¹		x	x			x	x
ssp. novae-angliae Braya novae-angliae (Rydb.) Th. Sør. ssp. abbei Böch Braya novae-angliae (Rydb.) Th. Sør. ssp. ventosa (Rollins) Böch	56 56	8 x 8 x					х		x	x x			х	x		
Braya alpina Sternb. & Hoppe Braya linearis Rouy Braya glabella Richards Braya pilosa Hook Braya henryae Raup Braya aenea Bge Braya angustifolia (N. Busch) Vass Braya rosea (Turcz.) Bge	42 42 42	6 x 6 x 6 x		x	x	x	x	x x x	x		x x x	xx	x	x ?		x ?
Braya longli FernaldBraya fernaldii AbbeBraya thorild-wulffii OstenfeldBraya purpurascens (R. Br.) BgeBraya siliquosa BgeBraya brachycarpa VassBraya pamirica (Korsh.) FedschBraya tibetica HookBraya oxycarpa HookBraya scharnhorstii Regel & Schmalh(?) Braya limosella Bge. (see Schulz 1924)	28 56	4 x 8 x	x	(x)		X X X X X X X X	x	x x		x	x x	x x		x x	x x	x x
Braya intermedia Th. Sør	70	10 x	İ	İ		İ	Í	İ	İ	İ	İ	1		İ		x
No. of species			1	2	1	10	3	5	2	4	6	5	2	4	3	5

 1 Data from Mulligan (1965, see Postscript), where however B. humilis is treated as a collective species.

In both cases some of the present day stations lie within areas which are believed to have been unglaciated. The successful polymorphic octoploid *B. purpurascens*, however, was able to invade greater parts of the previously glaciated areas.

The most problematic species within the genus are undoubtedly *B. linearis* and B. alpina. As may appear from Fig. 21 the similarity between certain races of B. aenea and B. linearis is great enough so suggest that these two taxa have common ancestors and perhaps it will prove justified to regard, as POLUNIN does (1959), B. glabella, B. pilosa, B. linearis, B. alpina, B. aenea and B. henryae as one huge complex with common origin. If so this complex may have established a circumpolar distribution comparatively early but the area was later disrupted and at the same time the isolation of the separated populations led to speciation. This, however, implies that the present species are largely relics. B. linearis may be connected with the arctic circumpolar branch of the complex while *B. alpina* might be regarded as an isolated westerly survival of an Eurasiatic high montane branch (cp. HULTÉN 1937). GAMS (1933: 29) lists it among the tertiary relics of the Alps as one of the species with south-siberian origin. The relic hypothesis for B. linearis in Norway has been supported by NORD-HAGEN (1935) while the relic nature of its Greenland populations was discussed in BÖCHER (1956). In a case like B. linearis it is certainly impossible to classify it as either west- or east-arctic. Its present day north Atlantic areas are probably to be explained as remains of a more continous area. The species may have arisen as a north Atlantic geographical race within the complex. However, this race was by no means ecologically connected with oceanic climatic conditions. It is a typical member of the genus which in its entirety avoids areas with an oceanic type of climate. This fact also points towards Central Asia as the place of origin.

In several species of *Braya*, isolation in various kinds of refugia has played an important rôle in the formation of species or lower entities. Within *B. linearis*, the Junkerdal race (var. *meizophylla*) may be one such unit which was isolated in an ice age refugium, whilst in the complex octoploid species, *B. novae-angliae*, the various subspecific units were probably isolated later.

Species pairs like *B. glabella-B. pilosa* and *B. aenea-B. linearis* may represent relic populations of extinct species which now as a result of isolation over long periods are just distinct enough to be regarded as separate species.

Postscript

After having finished this work a paper by MULLIGAN (1965) appeared. It has been possible in the first proof to incorporate a number of references to this important contribution by MULLIGAN. Most interesting is his countings of plants belonging to the *Braya humilis* complex. Tetraploids (2 n = 28) were found in Mackenzie District, Alberta and British Columbia, hexaploids in the same areas as well as in Franklin District, Northwest Territories. Finally octoploids occurred from Mackenzie District southwards to Colorado. A taxonomical treatment of the three cytotypes is clearly desirable.

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Nr. 7

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74

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PLATES

PLATE I

a-c: Draba arctogena, d: Draba norvegica. — a: Type of D. arctogena Ekman (Godhavn, W. Greenland leg. Elis. Ekman Aug. 1923, Riksmuseet, Stockholm). — b: Material determined by Mrs. Екмам as D. arctogena (N. Greenland, Navy Cliff Land, Vildtlands western part leg. P. Freuchen, Aug. 1912, Bot. Museum, Copenhagen). — c: D. arctogena from Centrum Lake, NE. Greenland 80°07' leg. Schwarzenbach 1952, Bot. Museum, Copenhagen). — d: Draba norvegica, Cult. No. 4772 (from Godhavn, W. Greenland). — Scale 10 cm.



PLATE II

Draba arctica J. Vahl p. p. Type material from Bell Sund, Spitzbergen and below on the right (e) D. cinerea Adams from Umanaq. W. Greenland collected by J. Vahl and considered by him as identical with his D. arctica. — a: D. arctica mihi (200 feet above the sea, Bell Sund, August 1938, Bot. Museum, Copenhagen). — b, c, d: Bell Sund material of J. Vahl in the Riksmuseum, Stockholm; b: D. arctica, Bell Sund fl. Spitzberg. Vahl jun. scripsit et misit; c: D. arctica Vahl Spitzb. misit auctor. On the label of Elis. Ekman: "This form deviates somewhat from D. arctica Vahl from Greenland by being more pilose and having more simple hairs on the fruit stalks". e: Belongs to the same collection as shown in Plate III d. Note: Many stem leaves, short and short peduncled siliques. — Scale 10 cm.


PLATE III

Draba cinerea Adams ssp. brachysiliqva (Mela) Ekm. — a: At the road between Stromfjordshavn and the Airbase (leg. Aug. TWB. Aug. 1946). — b–c: Karelia Ladogensis, insula Mäkisalo (leg. G. Lång, June 1898, Plantae Finlandiae Exsiccatae No. 244). — d: Part of VAHL's type collection of Draba arctica (corresponding to that in Plate IIe). On the label below is written Draba incana? Linné, but incana is struck out and substituted by arctica. Below, referring to the collection No. 5, is added "in locis subhumidis tam ad pedestum ad latera inferiora alpinum, distr. Colon. Umanaq: 1834 Juli J. Vahl'. All Collections in the Botanical Museum, Copenhagen. — Scale 10 cm.



PLATE III

PLATE IV

Draba cinerea Adams ssp. cinerea. — a-b: Siberia, Jakutsk distr., Bulun 70°43' N. (leg. H. Nilsson, July 1898, Riksmuseet, Stockholm); b: Ignerit Fjord, Magdlaq, West Greenland 71°7' N. c: Nugssuaq, Påtůt 70°15' N. (leg. M. P. & R. T. Porsild, July 1929, Riksmuseet, Stockholm). — d: D. lanceolata Royle from W. Greenland, Cult. No. 4884. — Scale 10 cm.



PLATE V

Draba arctica J. Vahl p. p. ssp. groenlandica (Ekm.) Böch. — a-c: Type material of D. groenlandica Ekm. W. Greenland, Godhavn (leg. Elis. Ekman, Aug. 1923, Riksmuseet, Stockholm). — d-f: Godhavn (leg. J. Lagerkranz 1934). — g: According to determination by Ekman transitional type between D. groenlandica and D. ostenfeldii, Ellesmereland, Fram Harbour (leg. H. G. Simmons July 1899 (No. 1092). — h-i: Deviating type with erect, very slender stems; h: Mountain east of Mt. Hassell, Søndre Strømfjord (leg. T. W. Böcher, Aug. 1946); i: Tunertoq, Arfersiorfik (leg. T. W. Böcher & S. Lægaard Aug. 1961). — j: Sandy bank, Lower E. Skeldal, Kong Oscars Fjord, NE. Greenland (leg. T. T. Elkington July 1962). — d-i: from the Botanical Museum, Copenhagen. — Scale 10 cm.



PLATE VI

Draba cinerea Adams ssp. brachysiliqva (a-c) and Draba arctica J. Vahl p. p. (d-i). — a: Clavering Island NE. Greenland n = 24 (leg. Th. Sørensen). — b-c: Store Saltso, Central West Greenland, cultivated material (No. 4813), n = 24. — d: Vigorous specimen of *D. arctica* from Ostenfeld Nunatak, NE. Greenland, 74°18' N. (leg. F. Schwarzenbach Aug. 1956). — e: *D. arctica* ssp. groenlandica from Jorgen Bronlunds Fjord, Peary Land (leg. K. Holmen No. 6712, 2n = 64 cp. HOLMEN 1952: 13). — f: *D. arctica* from Clavering Island NE. Greenland, n = 40 (leg. Th. Sørensen). — h: *D. arctica* ssp. ostenfeldii var. ovibovina from Clavering Island NE. Greenland, n = 40 (leg. Th. Sørensen). — h: *D. arctica* from Sassenbay, Spitzbergen (leg. E. Jørgensen). — i: *D. arctica* from Adventbay, alt. 400 m, Spitzbergen (leg. E. Jørgensen). d-f, h-i; from the Botanical Museum, Copenhagen. — Scale 10 cm.



PLATE VII

Draba arctica J. Vahl ssp. ostenfeldii (ekm.) Böch. — a: Type of D. ostenfeldii Ekm. Sounders Island, Cape York, NW Greenland, 14. July 1914 (leg. P. Freuchen) first determined by C. H. Ostenfeld as D. hirta ssp. arctica (Vahl) Wats. — b: Isfjorden, Longyearbyen (leg. Lagerkranz 1932, Loco palætræ). — c: Type of var. ovibovina Ekm. Fram Harbour Ellesmereland 20. July (leg. H. G. Simmons, No. 1092). — a and e: Bot. Museum, Copenhagen; b: Riksmuseet, Stockholm.



PLATE VIII

Draba aurea M. Vahl. — a: Unbranched vigorous specimen from continental West Greenland (Søndre Strømfjord, eastern part of Sandflugtsdalen, Southern slope, Aug. 19, 1946 (leg. T. W. Böcher No. 637). — b, c, d: Branched vigorous specimens with broad leaves from Narsarssuaq, Tunugdliarfikfjord, South Greenland, July 13, 1946 (leg. T. W. Böcher No. 621). — Scale 10 cm.



PLATE IX

Experimental cultivations with *Braya linearis* and *B. rosea*. All, except d-e, from the Arctic Greenhouse. — Two specimens of *B. linearis* var. *meizophylla* (Br. 3); b: typical specimen from W. Greenland (No. 4811); c: Troms (Br. 7): Scale 10 cm. — d-e: Two specimens of *B. linearis* (d: Br. 3) compared with *B. rosea* (e: Br. 4); second year plants in their first flowering stage (June 1961, Exp. field). — f-h: One specimen of *B. linearis* from Greenland (f: No. 4811) and two of *B. rosea* (g-h: Br. 4) second flowering (June 1962). — i-k: Two W. Greenland plants of typical *B. linearis* (i: No. 4855, j: No. 4811) compared with var. *meizophylla* (k: Br. 3), the latter being higher with elongated raceme and longer and broader leaves. — 1-m: Two specimens of *B. linearis* var. *meizophylla* (l: Br. 3) and two typical ones of No. 4855 from W. Greenland (m). — n-q: n: No. 4811; o: No. 4855 (both W. Greenland); p: Br. 3 (var. *meizophylla*); and q: Br. 7 from Troms (june 1962).



PLATE IX

PLATE X

a-b: *Braya linearis*; a: Head of Sondre Stromfjord, W. Greenland at the airbase (leg. T. W. Böcher Aug. 1946); b: Store Saltsø near head of Søndre Stromfjord (leg. T. W. Böcher Sept. 1956, Bot. Museum, Copenhagen). — c: *Braya aenea* from Kumach Sur, c. 71°30' Sibiria, oblastia Jakutsk (leg. H. Nilsson, July 1948, Riksmuseet, Stockholm). — d: Specimen of *B. linearis* var. *meizophylla* No. 3 from Junkerdal, Norway. cultivated in the Arctic Greenhouse. — e: Another specimen of this variety cultivated in pots at the experimental field together with the specimens shown in f-g. — f: *B. linearis* No. 7 from Sordal, Troms, Norway. — g: Two specimens of *B. alpina* from the Grossglockner area (No. 6788). — Scale 10 cm.

PLATE X



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