WILLIAM F. HUMPHREYS AND JØRGEN LÜTZEN

STUDIES ON PARASITIC GASTROPODS FROM ECHINODERMS L

ON THE STRUCTURE AND BIOLOGY OF THE PARASITIC GASTROPOD MEGADENUS CANTHARELLOIDES N.SP., WITH COMPARISONS ON PARAMEGADENUS N.G.

Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 19,1



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Synopsis

Two specimens, one female and one male, of a new species of Megadenus has been found in the sea cucumber Stichopus chloronotus from Aldabra, Indian Ocean. It is argued that the material was partially displaced when found and that the two gastropods inhabit the intestine of the host, which is pierced by the conspicuous proboscis that is further introduced into the host's body wall. The egg capsules are placed on the shell of the male and the larvae are released continuously into the host's intestine. The morphology of the larvae and the male specimen is described. A comparison with M. holothuricola and M. voeltzkowi, both parasitizing sea cucumbers, shows a close similarity, whereas it is concluded that M. arrhynchus Ivanov, from the sea star Anthenoides rugolosus, should be transferred to a new genus, Paramegadenus n. g.

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Introduction

During phase V of the Royal Society Expedition to Aldabra, Indian Ocean, in 1968 two specimens of the parasitic gastropod Megadenus Rosén were taken from a sea cucumber by one of the authors (W. H.). According to Gruzov (1965) this genus occupies a central position in the phylogeny of the parasitic gastropods grouped in the family "Stiliferidae" and Ivanov (1952) has shown that M. arrhynchus Ivanov 1937, a parasite of sea stars, differs considerably from those species living in sea cucumbers. Owing to the sparsity of material there is little literature on the subject and save for the recent work by Ivanov (l. c.) the descriptions are relatively brief. It was therefore considered of interest to study the present material as extensively as possible, especially as the larval stages of the genus are unknown, and the biology of the parasite has been largely ignored.

The following four species have been referred to Megadenus:

M. holothuricola Rosén 1910, in the water lungs of Ludwigothuria mexicana (Ludwig) (family Holothuriidae) from Bahamas.

M. voeltzkowi Schepman & Nierstrasz 1913 in the oesophageal region of an unidentified sea cucumber (probably Holothuria pardalis Selenka) from Zanzibar, East Africa.

M. cysticola Koehler & Vaney 1925 living in cysts in the spines of the sea urchin Dorocidaris tiara Anderson (family Cidaridae) off Ceylon.

M. arrhynchus Ivanov 1937 from the dorsal surface of the sea star Anthenoides rugulosus Fisher (family Goniasteridae) from the Yellow Sea and, according to personal communication by David Pawson, Curator of Echinoderms, U.S. Nat. Mus., Washington, off the east coast of Mindoro in the Philippines (specimens figured by Fisher, 1919, pl. 85, fig. 4).

Furthermore, an observation by von Martens (1865) of a parasitic gastropod in the respiratory tree of an unidentified holothurian from Luzon, the Philippines, which he referred to the genus Stilifer, could according to his short description very well be a Megadenus.

During the first parts of the present work we have found it necessary to restrict any comparisons made between our material to those species living in sea cucumbers. In a final chapter conclusions are drawn as to the taxonomic and biological affinities between the holothurian-parasites and those described from other echinoderms.

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The separation of the two species of Megadenus which have previously been described to parasitize holothurians is based on rather doubtful characters, *viz.* small and badly defined variations in shell shape and dimensions together with wide geographical separation. Although we recognize that studies on more extensive material when it becomes available may further define the division of the genus, we consider that our material represents a third species. It is distinguished from the other species parasitising holothurians by the unique and extraordinary development of a flange representing an expansion of the proboscis just distal to the pseudopallium. Owing to the likeness of this structure to a chanterelle, the new species is named Megadenus cantharelloides n. sp.

Material and Treatment

Two gastropods, one female and one male, were taken from a single specimen of the aspidochirote sea cucumber Stichopus chloronotus Brandt, collected at low water from the marine angiosperm beds adjacent to the settlement on Ile Picard, Aldabra, British Indian Ocean Territories, on October 16th 1968.

The cucumber was opened about 16 hours after collection when it had relaxed in stale water. It was cut longitudinally along the ventral surface and the intestine was found to have been autotomised at both ends and was lying free in the coelom. The significance of this treatment is discussed later.

The male was found attached by its proboscis to the interior body wall of interradius BC, approximately 1/7 of the distance from the anterior end. The proboscis penetrated about 3 mm into the wall but was withdrawn with only slight resistance. The shell of the male was entirely covered by a helmet of egg-mass substance, to which were attached by thin stalks the globular egg capsules. The female, with the entire proboscis detached, lay free in the coelom adjacent to the male. The animals were removed and fixed in alcoholic Bouin and consequently the calcareous material was lost. After removal of the egg capsules covering the male a perfect protoconch was found whereas this had been broken off in the female specimen.

The male was embedded in tissuemat and cut in 10 μ thick sections parallel to the columellar axis. The section series was stained in tetrachrome (Weigert's iron hematoxyline, Chlorantine fast red, orange G, and Alcian blue). A few were stained with Heidenhain's iron hematoxyline-cosin or Azan. The female was cleared in anise oil and the mantle cavity cut along its upper edge in order to disclose the organs within. A wax reconstruction based on the section series was made on a 75 × scale to show the organization and extent of the main organ systems.

Observations were made on the empty egg capsules and those containing embryos and larvae. Full-grown larvae were studied in entire preparations cleared in anise oil; others were embedded in epon and complete 2 μ sections series prepared and stained in toluidine blue.

All material is being kept at the Institute of comparative anatomy, University of Copenhagen.

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Morphology of the adult Megadenus cantharelloides n.sp.

External appearance. The female and male specimens are broadly similar in that they consist of a body containing several whorls and a proboscis which proximally expands into a large circular flange. Proximal to the flange is a bowl shaped fold of tissue, the pseudopallium of Rosén. Between the flange and the pseudopallium is a deep constriction and the female specimen has broken at this point. The sexes differ in the development of the pseudopallium and it is very much more extensive in the male than the female.

The shell is cyrtoconoid and globose with evenly rounded whorls that show a slight dip at the distinctly double suture lines and increase regularly in height. The shell is smooth and polished save for the presence of multitudinous fine striae, the imprint of which was reproduced on the inner surface of the egg mass helmet. The shell is delicate and transparent so that several organs, especially the dark coloured digestive glands, are clearly visible through it. The protochonch (to be fully described in a later section) forms a fragile mucro of about 2 whorls succeeded by 5 adult whorls in the female and 4 in the male (including the body whorl). There is no operculum. The height and width of the shell in the female was 5.7×4.5 mm and although it was not measured in the male it was only slightly smaller. The colour of the live animal is a pale-cream except for the dark digestive glands.

The head is inconspicuous and carries two equally sized short and blunt tentacles, within the basal part of each an ocellus is located. The foot is broadly divisible into a large, fleshy foremost region of irregular shape, and a posterior semicircular fold inserted along part of the base of the visceral hump and extending to the left opening of the pallial cavity in the female (pl. I, fig. 2, pf), and even further forward in the male (text-fig. 2 B, pf). Whereas this fold is of moderate size in the female, in the male it extends upwards so as to cover the lower (left) parts of the mantle (and the shell). The anterior part of the foot is larger and more elaborate in the male than in the female; the anterior pedal gland has a slit-like opening on an extension of the anterior portion of the foot. This extension is longer in the male than in the female. On that part of the foot opposite the mantle opening, there are numerous wrinkles and deep crevices, into one of which the posterior pedal gland discharges.

In the male a comparatively short penis arises from a point to the right of the tentacles; it is entirely situated outside the pallial cavity

The pseudopallium completely surrounds the base of the proboscis as an extensive fold which is noticeably less developed in both sexes in the areas of the mantle opening. In the male the fold continues half way up the shell and in life must be able to entirely cover the shell and the attached egg capsules (text-fig. 1, ps). In the female where it is proportionally smaller it may possibly be reflected over the lower part of the shell.

The proboscis has the shape of a chanterelle owing to the modification of its proximal portion into a circular flange, the margin of which is thickened and some-

what irregular. In the male the flange envelops part of the pseudopallium. We consider the flange to be a permanent structure which has contracted only slightly during fixation. The distal end of the proboscis is deeply wrinkled and probably strongly contracted. The proboscis is darker coloured and is slightly swollen and heavily pigmented round the mouth opening. The length of the proboscis is 6 mm and the largest diameter of the flange about 7 mm.

The distal part of the proboscis is characteristically curved in relation to the flange in both specimens (text-fig. 1). At a distance of 2–3 mm from the mouth, i.e. at the point where the wrinkled foremost part of the proboscis begins to widen into the smoother surfaced flange, a distinct belt of mucous substance occurs which contains fine rust-brown granules. The belt is incomplete and more pronounced in the female. Its possible significance is discussed later.

As will be shown later, both specimens were wholly or partially displaced when found. In a following chapter we are going to demonstrate that they probably occupied a position similar to that shown in text-fig. 1: the anteriormost part of the proboscis is introduced into the host's body wall and the posterior part of that structure pierces the host's intestine in such a way that the body and pseudopallium lies within the intestine and the remaining part of the proboscis lies in the coelom.

Mantle cavity and pallial complex. The mantle cavity is fairly deep and not very spacious. The general arrangement of the organs associated with it is typical for the Mesogastropoda. Near its left entrance occurs a short osphradium, distinguishable on the sections by its tall, cylindrical and tightly packed cells containing yellowishbrown granules. Dorsal to the osphradium lies the monopectinate ctenidium which in the female carries about 45 triangular leaflets. The right half of the mantle skirt is thickened along most of its length, although separated by a longitudinal groove into two portions, on the right one of which the anus opens fairly far back. The hypobranchial gland occupies most of the thickness of the right half of the mantle roof, opening into the groove just mentioned and overlying the rectum as a single layer of mucous and mucoid cells. Posteriorly, near the floor of the mantle cavity, the gland thickens to overlie the anterior part of the kidney. Two different glandular areas may be distinguished: to the right are cells containing alcian blue-positive granules, and between them, small, distally placed supporting cells; to the left occur glandular cells, containing granules which remain unstained by the constituents of the tetrachrome.

Posteriorly the mantle cavity is much reduced in size, and protrudes back over the heart and kidney; the latter therefore opens on its floor through a simple aperture to the right of the ventricle. In the male the genital duct opens far back and continues as a ciliated gutter, stretching along the edge of the mantle skirt, protected along part of its length by a longitudinal fold.—What is probably the capsule gland extends as a thickening along the right side of the mantle cavity in the female, to open close to the mantle aperture.



Fig. 1. Diagram showing the supposed position of female and male Megadenus cantharelloides n. sp. in the host. bw, body wall of host; c, coelom of host; ec, egg capsules in different stages of development; f, foot; fp, flange of proboscis; h, helmet of mucous substance covering the male shell; i, intestinal lumen of host; iw, intestinal wall of host; l, larvae released into the host intestine; pr, proboscis; ps, pseudopallium; r, ring of slime containing pigment found around the proboscis of female; t, thickening of intestinal tissue from host-parasite response. — The arrow shows the direction of movement of intestinal contents.

The skin and its glands. A ciliated columnar epithelium occurs on the margins of the deep groove marking the opening of the anterior pedal gland, and is present more diffusely on the extension of the foot onto which the gland opens. The epithelium lining all the numerous and complicated crevices of the foot, into one of which the posterior pedal glands opens, is also thickly ciliated. Both the interior and exterior aspects of the pseudopallium are ciliated. Otherwise the epidermis is mostly unciliated.

The basis of the external part of the pseudopallium forms a specialized site of mucus production. The epidermis in this region shows numerous ring-shaped folds with very tall columnar cells arising on connective tissue cores; it produces a secretion

which stains blue with alcian blue and a bright purple with Azan. The abundant supply of mucus formed here considering the morphological relations *in situ* is necessarily conveyed towards the rim of the pseudopallium. All over the pseudopallium unicellular mucous cells produce a similar secretion, which in addition to that just mentioned must aid in protecting the smooth parts from direct contact with the host's gut content (see p. 21).

The epithelium of the proboscis proper, including the flange is neither ciliate nor glandular; its tall columnar cells produce cuticular processes, which are especially long (up to one-third the length of the cells) on that part of the flange facing the pseudopallium. The proboscis, according to our interpretation, is wholly introduced into the body cavity and thus bathed in coelomic fluid, save for the tip which penetrates the body wall of the host.

The pseudopallial epithelium is also ciliated in M. holothuricola, and is secretory in both this species and M. voeltzkowi, although Rosén and Schepman & Nierstrasz were inclined to consider the inclusions found in the epithelial cells to be excretory products. A cuticular surface is present in the proximal part of the proboscis only in M. holothuricola, whereas Schepman & Nierstrasz picture (pl. 27, fig. 7) and describe in a most confusing way the epithelium of the distal part producing a secretion in the form of branched threads, which they claimed to attach to the host's organs, without specifying which organs.

The anterior pedal gland is too big to be accomodated wholly in the tissues of the foot and spreads into the haemocoel of the head as far as the nerve ring. Along its entire length runs a sagittal canal, crescent-shaped in transverse section. It is composed of columnar cells carrying exceptionally long cilia on the convex side, and cubical ciliated cells on the other, between which the gland cells discharge. These cells are arranged in nests within the subepithelial spaces and whereas some of them, especially those occupying a marginal and proximal location, appear to produce a mucous secretion, the staining properties of the majority suggests another production. The gland is very large and in the male occupies an estimated one-third of the portion of the foot in which it is embedded.

The posterior pedal gland is represented by an extremely narrow, unbranched and slightly coiled canal located within the substance of the foot between two major bundles of nerve fibres. Proximally it is lined with a cubical ciliated epithelium forming a non-glandular portion; distally near its opening to the exterior many, very large droplet-shaped gland cells discharge a mucous secretion into its lumen.

A conspicuous anterior pedal gland is also present in M. holothuricola and voeltzkowi, in the latter it even protrudes into the mantle cavity and is larger in the female than in the male. A posterior pedal gland is present in M. holothuricola, but could not be demonstrated with certainty in M. voeltzkowi.

Musculature and connective tissue. The columellar muscle is well-developed and most of the other muscles of the body, except those accompanying the

alimentary canal, are derivatives of it. Its fibres spread into the different part of the foot, the proboscis and the pseudopallium. In the foot and in the proboscis proper, the fibres criss-cross, whereas in the pseudopallium they establish themselves as distinct layers underlying the epithelium and radiating from its base towards the rim. The arrangement of the muscle fibres in the pseudopallium and the proboscis flange is noteworthy: In both structures a conspicuous, concentrated layer of ring muscles underlies the epithelium of the sides directed towards the body whorl, with additional ring fibres scattered in the connective tissues. Contraction of these fibres cause the pseudopallium to close around the shell; and the proboscis flange to be pressed tightly against the outer wall of the host's intestine, thus anchoring it more firmly. These fibres are antagonised in the pseudopallium by layers of radial muscles lying under the epithelium and are much more developed at the side directed away from the body; in the absence of radial muscle layers in the proboscis flange, a system of blood lacunae located there is believed to produce an antagonistic effect, possibly aided by a number of criss-crossing muscles.

It is considered significant that both radial and longitudinal muscle fibres are almost entirely absent in a ring-shaped region of the proboscis, namely at the constriction lying between the flange and the pseudopallium. The conspicuous longitudinal fibres of the columellar muscle running in an anterior direction at that point are abruptly replaced by a very dense connective tissue, except for a very few fibres lining the large blood sinus, surrounding the oesophagus. This discontinuity of the musculature starts exactly at a level where the secretory epithelium of the pseudopallium is replaced by the cuticular epithelium of the proboscis flange. The poor development of musculature here is explained by the supposition that this section is enveloped by the host's intestinal wall.

The connective tissue is vacuolated in the body whorl and vesicular blood spaces occur in the foot, especially in its hind portion. In the remainder of the foot and in the pseudopallium a dense connective tissue occurs whereas that of the proboscis is very loose, and there can be little doubt that this structure is very mobile and capable of rather sophisticated movements produced by the criss-crossing muscle fibres and shifting of the blood in its numerous sinuses. In both specimens the skin of the proboscis was much folded, indicating a state of contraction.

The alimentary canal and proboscis (text-fig. 2 A). The alimentary canal starts with what is probably a buccal cavity, a spacious and very much subdivided space, occupying the central and most of the anterior part of the proboscis. The wall of the foremost part of the buccal cavity is richly folded forming a large number of small and irregularly shaped spaces, lined with a cubical epithelium. Posteriorly the folds increase in size; the subdivisions become much larger and the cells tall and cylindrical with basal nuclei. All the cells lining the buccal cavity discharge a copious mucous secretion, which stains heavily with Alcian blue, into its lumen.

The folds of the buccal cavity are supported by connective tissue cores. Anteriorly their tissue is mainly occupied by true connective tissue, but posteriorly this is gradually replaced by muscle fibres, some of which are in continuity with the sheath of longitudinal muscles enveloping the bulbuous pharynx. Two small and two large retractor muscles accompany the oesophagus and originate among these muscle fibres. A very conspicuous fold containing only a blood sinus, encircles the midportion of the buccal cavity.

An elongate blood sinus containing the pharynx, the oesophagus and the proboscis retractors commences at the posterior margin of the buccal cavity and continues through the stalk separating the true proboscis from the pseudopallium and into the head. The pharynx is bell-shaped with a narrow, slit-like central canal and is about 700 μ in diameter and 800 μ in length; its anterior end projects a little into a particular, cup-shaped region of the buccal cavity. Its structure and possible function will be considered later. On entering the pharynx the epithelium lining the gut becomes very low and squamous. Otherwise its walls consist of radial muscle cells fastened to the under side of the epithelium internally and to a thin sheet of longitudinal muscle fibres and connective tissue externally. These dilator muscles are antagonised by ring muscle fibres, situated mainly on the periphery of the bulb and at regular intervals in the spaces between the radial fibres. The whole structure would form an effective pump to convey fluid from the cup-shaped part of the buccal cavity into the oesophagus.

The oesophagus originates from the inner end of the pharyngeal pump. It is a tube of uniform diameter (ab. 150μ) which coils several times on the way to the visceral hump and forms a particularly close tangle just before reaching the stomach. The constituents of the oesophageal wall are similar throughout its length. It is lined with a columnar epithelium enclosed within a sheath of longitudinal and, to the outside, of circular muscle fibres. The foremost part of the oesophagus is longitudinally folded but further back it becomes smooth-walled. The posterior part of the oesophagus contains an epithelium of cylindrical cells with very many minute granules included in their distal portions.

The small stomach, into which the oesophagus opens receives one major and one minor opening from the digestive gland, the larger draining most of that organ. The intestine arises from the extreme posterior end of the stomach. Typical stomach cells occur almost solely on the dorsal side, between the openings of the oesophagus and intestine; their structure was very badly preserved but they are distinguished

Fig. 2 A and B. Diagram showing the structure of the alimentary canal, peripheral nervous system, anterior pedal gland, and vascular system in male of Megadenus cantharelloides n. sp. a, anus; aa, anterior aorta; af, anterior part of foot; apg, anterior pedal gland; au, auricle; b, buccal ganglion; bc, buccal cavity; dg, digestive gland; eb, efferent branchial vessel; fp, flange of proboscis; g, gills; i, intestine; kv, accessory kidney vein; l, left tentacle; lo, left ocellus; m, mouth; mc, mantle cavity; oe, oesophagus; p, penis with open seminal groove; pa, posterior aorta; pe, pericardial cavity; fp, posterior part of foot; ph, pharynx; ps, pseudopallium; rc, right cerebral ganglion; rt, right tentacle; rv, renal vein; s, stomach; sp, supraoesophageal ganglion; v, visceral ganglion; ve, ventricle; vv, visceral vein; y, opening of anterior pedal gland. Scale represents 2 mm.



Fig. 2 A and B.

by being very tall, vacuolated and probably secretory and, in contrast to those of the oesophagus, provided with very long cilia.

The tubules of the digestive gland are aggregated in distinct groups, most of which discharge into a central tube running up the visceral hump and entering the stomach as the most prominent of the gland's two ducts. The digestive gland and the gonad constitute the major part of the visceral mass.

The posterior part of the stomach is prolonged and penetrates the kidney within which it merges with the intestine. The latter is flung into a U-bend and soon leaves the kidney to open into the anus. Its epithelium is ciliated throughout, and the walls show considerable longitudinal folding.

This description of the alimentary canal agrees well with that of M. holothuricola and voeltzkowi, except that the oesophagus in these species are not as coiled, and are accordingly shorter. Cilia were not described in the stomach cells of M. voeltzkowi; Rosén (1910) considers the stomach to have been completely reduced and its lumen to have been replaced by an enlargement of the combined openings of the two digestive gland ducts into the alimentary canal. Another point of difference is that four proboscis retractors exist in the present species, and only two in M. voeltzkowi; their presence is not mentioned in M. holothuricola, but only two are distinguishable in Rosén's figures (pl. 1, fig. 3; pl. 2, fig. 9).

Rosén described in a confusing manner, which was consequently misunderstood by Schepman & Nierstrasz, the structure of the cup-shaped section of the buccal cavity that is closely associated with the pharynx. Its shape in our species is shown in pl. IV, fig. 7. It is separated from the buccal cavity proper by a narrow duct, the lumen of which can be constricted and dilated respectively by the complex of muscle fibres surrounding it and those connecting its wall with the remainder of the buccal cavity. Dorsally and ventrally the cavity extends posteriorly along the sides of the muscular pharynx, which opens into its centre. Its function is connected with the pumping activity of the pharynx. When the connexion to the buccal cavity is dilated, fluid is sucked into it. With the constriction of this opening, a contraction of the radial fibres of the pharynx will dilate the pharyngeal opening and in addition probably exercise a pressure on the dorsal and ventral extensions resulting in the fluid from the antechamber being pumped through the pharynx and into the oesophagus. If the pharynx opened directly into the buccal cavity its pumping mechanism would be difficult to explain.—A similar structure is present in M. holothuricola, in which it seems to occupy the same position in relation to the pharynx and buccal cavity as in our species, although it is displaced ventrally. It is not reported from M. voeltzkowi, although an equivalent structure is said to be present in the form of a diverticulum arising from the lumen of the pharynx.

The nervous system and sense organs (text-fig. 3 A & B). The ganglia of the nervous system are mainly concentrated into a ring around the oesophagus and in which seven ganglia may be distinguished. In addition to the constituents of

this ring two buccal ganglia, a visceral ganglion and a supra-oesophageal ganglion may be observed. Both cerebral ganglia (lc and rc) are oblong bodies connected by a short commissure. From the anterior part of each cerebral ganglion arises a stout nerve which passes along the oesophagus to the two buccal ganglia (b) and which are mutually connected through a ring-shaped nerve, encircling the posteriormost part of the pharynx bulb. There are no accessory buccal ganglia. Ventro-anteriorly the cerebral ganglia connect to the larger pedal ganglia (lp and rp), which similarly so closely approximate that the commissure is hardly distinguishable. On the posteriordorsal faces of the pedal ganglia lie the statocysts (st), containing a single calcareous statolith. Apart from some minor nerves one prominent nerve leaves the right pedal ganglion and runs along the right side of the anterior pedal gland supplying the right part of the anterior portion of the foot; from the left pedal ganglion arise three conspicuous nerves, the largest of which passes ventral to the columellar muscle to end as a thick and very much twisted bundle, ventral to the anterior pedal gland. A branch from one of the other nerves supplies the posterior folded part of the foot.

From the right cerebral ganglion arises a second connective to a small spherical (right) pleural ganglion (rpl) which connects through a prominent, curved and short nerve to a larger oval ganglion situated just beneath the osphradium, no doubt representing the supra-oesophageal ganglion (sp). No osphradial ganglion could be found. —The left pleural ganglion (lpl) is confluent with the cerebral ganglion; on its left side a stout nerve arises and runs backwards in the body; to the right it is almost confluent with the very elongate sub-oesophageal ganglion (sb); the latter connects with the single visceral ganglion (v) and is located between the stomach and the opening of the vas deferens.

The pseudopallium is entirely supplied by branches of the cerebro-buccal nerves, thus proving its cephalic origin.

The observations on the nervous system of M. holothuricola and voeltzkowi are few and inadequate. They do, however, generally agree with this account of M. can-tharelloides.

The two ocelli are embedded in the connective tissue of the tentacle basis, the least distance from the centre of the lens to the tentacle surface being ab. 100 μ . However, they are orientated so that the distance to that part of the surface from which light may reach the eye is three times this length. The eyes are oval in shape, the right being somewhat larger than the left, at least in the male, on which accurate measurements could be taken; in that sex the maximum width is 65μ and 90μ respectively, the length 92μ and ab. 120μ respectively, and the diameter of the perfectly spherical lens 42μ and 60μ respectively. The epithelium lining the optical vesicle forms a translucent cornea in front of the lens and a normal retina, in which occur pigmented and unpigmented cells. The retina is separated from the lens and the space is occupied by what is probably a small quantity of vitreous.

Rosén and Schepman & Nierstrasz point out that the distal part of the retinal cells are entirely pigmented in M. holothuricola and voeltzkowi, as in our species.



Fig. 3 A and B.

They further claim that no cornea exists, and the lens to be completely surrounded by a pigmented retina; this Rosén considers a sign of reduction and that the eyes do not function in Megadenus. As pl. 4, fig. 6 shows, the presence of a translucent cornea is indisputable in our species and is present in both the eyes of which the histological structure has been examined.

The arrangement of the eyes within the tentacles is similar in our form, in M. holothuricola and in the male of M. voeltzkowi. In the female of the latter species, however, only one tentacle exists, and probably the left, and the right eye has migrated deeper into the tissue than the left.

Vascular system and kidney (text-fig. 2 B). The heart lies in the pericardial cavity at the attachment of the mantle skirt on the left side, immediately proximal to the kidney. The single auricle lies to the left and slightly anterior to the ventricle, from which the anterior and posterior aorta emerge from a short common stem. The anterior aorta (pl. III, fig. 5, aa) runs forward along the left of the stomach and oesophagus and disappears, probably opening into a sinus surrounding the tangle formed by the posterior oesophagus. The posterior aorta ascends the visceral hump, on the concave side of the spiral which rests on the surface of the gonad and opens into the haemocoelic space interpenetrating the lobules of the digestive gland and gonad. This drains into an extremely large vessel running along the inner, convex side of the visceral hump. It is closely wedged between the two ducts of the digestive gland and then turns sharply to enter the kidney as the afferent renal vein; despite the latter giving off a great number of minute vessels on passage through the kidney, it emerges as a tube of almost unaltered diameter to penetrate the posterior part of the hypobranchial gland; here it diminishes in size giving rise to a series of vessels which in the roof of the mantle cavity pass to the left between the lobes of the hypobranchial gland where they ramify and anastomose among themselves. This network is visible from outside (pl. I, fig. 1, and text-fig. 2 B) to the right of the posterior ctenidial region, well in front of the kidney. From it arise the different channels, through which the blood moves to gain the ctenidial leaflets. A prominent efferent branchial vessel (pl. III, fig. 5, eb) returns the blood to the auricle.

A number of sinuses occur, some of which have been mentioned earlier. The most conspicuous of these is a cephalo-proboscideal sinus which extends from in front of the nerve ring to the buccal cavity. Posteriorly it communicates with a spacious sinus which separates the nerve ring and that part of the oesophagus lying behind it from the floor of the mantle cavity. This sinus raises the floor of the mantle cavity so that a long and broad ridge projects into the mantle cavity.

Fig. 3 A and B. Central nervous system of Megadenus cantharelloides n. sp. in dorsal and ventral view. C, same of Paramegadenus arrhynchus n. g. (from Ivanov, 1952, fig. 26 A). ab, accessory buccal ganglion; b, buccal ganglion; lc, left cerebral ganglion; lp, left pedal ganglion; lpl, left pleural ganglion; oe, oesophagus; rc, right cerebral ganglion; ro, right ocellus; rp, right pedal ganglion; rpl, right pleural ganglion; sb, suboesophageal ganglion; sp, supra-oesophageal ganglion; st, statolith; v, visceral ganglion. Scales represent 500μ (A and B) and 1 mm (C).

No comparisons can be made with the vascular system in M. holothuricola and voeltzkowi, since its structure was not investigated in these species.

The kidney is a capacious sac, clearly visible from outside (pl. I, fig. 1, k). It opens into the bottom of the pallial cavity through a simple aperture in which cilia could not be detected and in which sphincters or dilators are obviously absent. The intestine forms a short loop through it. There is no nephridial gland and no renopericardial canal. The kidney is built on a conventional plan: The lumen is finely subdivided by numbers of anastomosing trabeculae, which arise exclusively from its external wall. These often widen internally to form a meshwork of irregularly shaped sinusoids. One cell type dominates, *viz.* a spherical one with a basal nucleus, a minute amount of protoplasm and a vast distal vacuole. In addition, there are scarce cup-shaped cells without vacuoles, with a distal nucleus and a stalk-like connection to the basement membrane; both types were distinguished by Rosén in M. holothuricola, the kidney of which is generally very similar to that of our species.

The vascularization of the kidney in M. cantharelloides is peculiar in that the afferent vein does not break down completely into renal capillaries, but continues through the kidney as a prominent vessel. We have been unable to detect how the blood is collected from the organ and returned to the auricle. A vein leaves either side of the superficial region of the kidney and fuse with one arriving from the intestinal region, but whether these ultimately drain into the heart, and by what course, could not be determined.

The reproductive system. Since the female specimen was left unsectioned we are unable to give any details about the female genital apparatus.—The testis occupies almost all the spaces left in the visceral hump by the digestive glands and blood lacunae, and is displaced preferably to the right sides of the whorls. It consists of numerous lobes, which finally discharge into the vas deferens (text-fig. 4); the latter is fairly long and coiled into a close tangle; its walls are exceedingly flat and covered by an unciliated squamous epithelium; being narrow in its proximal section, the tube gradually widens and terminates in a much enlarged swelling. Tightly packed sperm is stored throughout the vas deferens. It opens via a narrow canal into a short cul-de sac. The cubical epithelium of this blind portion is non-glandular, but the cells of the outer part produce a mucous secretion and become cylindrical. This accessory gland, which probably represents the prostate, opens into the pallial cavity and continues as an open seminal groove (or pallial vas deferens), and still contains a few gland cells in its floor for some distance. The pallial vas deferens runs along the edge of the mantle skirt turning sharply to the left on emerging from the mantle aperture and passes, as a broad, slight depression along the right side of the head to the basis of the penis, where it again becomes grooved and heavily ciliated. It proceeds to the very tip of the penis, which is about 1.2 mm long, and 0.4 mm across, and shows a tendency to spiral. The penis contains a dense connective tissue with muscle fibres



Fig. 4. Vas deferens and accessory gland in the male Megadenus cantharelloides n. sp. The different parts of the coils are drawn somewhat apart. 1 and 2, distal and proximal portion of vas deferens; p, prostate. Scale represents 400 µ.

and vesicular blood sinuses and is certainly capable of extension, since its surface was found to be greatly folded.

The male apparatus is unknown in M. voeltzkowi, except that the presence of a penis was noted. In M. holothuricola the structure of the vas deference was not closely described, although its walls were claimed to be ciliate, which we doubt. A prostate and a penis was also present in that species.

Morphology of the Larva

A few of the ruptured egg capsules contained full-grown larvae, which were seen to rotate. The shell of these larvae (pl. IV, fig. 9) is about 350 μ in height and 200 μ across (after fixation and included in anise oil). The apex is perfectly rounded, and there are only one and a half whorl.

The larva has a well-developed bilobed velum equipped with exceptionally long marginal cilia. The two lobes meet ventrally at the entrance to the mouth. The head carries two pointed tentacles, 35μ long. Two equally large eyes are situated lateral to the tentacle bases. They are not, as in the adult, included within connective tissue, the unpigmented cornea being level with the skin. Almost all available space in the head is occupied by the nervous system, which comprises two fused cerebral, two pleural, two pedal, and supra- and sub-oesophageal ganglia (pl. IV, fig. 8); a small visceral ganglion lies adjacent to the stomach wall. The two statocysts are placed close together between right and left pedal ganglion. The neural mass is penetrated by the oesophagus which is ciliated throughout and connects the mouth with the stomach. The latter is spacious and almost spherical. Two-thirds of its walls is ciliated 2

Biol. Skr. Dan. Vid. Selsk. 19, no. 1.

and secretory, the remaining part secretory only. The stomach receives two outlets from the digestive gland, which is filled with yolk granules and occupies a large part of the first coil of the shell. Yolk granules pass through the two ducts to the stomach to be digested there. A ciliated intestine leads from the stomach to open far back in the mantle cavity. A small sac adjacent to the stomach lined by a squamous epithelium possibly represents the rudiment of the kidney. Neither heart nor a gonad rudiment could be demonstrated.

The foot is pointed, without a creeping sole. The anterior lobular pedal gland opens via a tubular duct on its very tip. The prominent columellar muscle spreads into the posterior part of the foot, which is provided with a shield-shaped operculum.

The mantle cavity contains a comparatively large and much differentiated hypobranchial gland. Neither an osphradium nor rudimentary gills are present.

Rosén (1910) noted that the larva of M. holothuricola possessed a velum, two eyes, and two statocysts. The elaboration of the velum into a powerful swimming organ and the lack of a creeping sole shows that the larvae are planktonic for some time. The apex of the adult (male) is provided with only two embryonic whorls (pl. II, fig. 4). This, in addition to the fact that the last of these suddenly increases in size indicate an early establishment in the host with its resultant ready availability of food. The larvae probably enter the host passively along with the food.

Notes on Biology

The geographical range of Megadenus is noted in the introduction and the present material adds a second locality to the records from the Indian Ocean. It further extends the range of holothurian hosts from the Holothuriidae to the family Stichopodidae and the parasite could perhaps profitably be searched for in all members of the Aspidochirota. Considering the relatively large size of the parasite and the few records, the infestation must be very low. The present material was found in one of 33 aspidochirotes examined of which 18 were S. chloronotus. No specimens were found in 19 aspidochirotes examined at Watamu Kenya. Tikasingh examined 147 individuals of Ludwigothuria mexicana in Curaçao and Bonaire, Netherlands Antilles, but failed to find a single Megadenus (personal communication). Rosén (1910) had five specimens but reported that they always occur in pairs and are exceedingly sparse. Schepman & Nierstrasz (1913) worked on a female and the proboscis of a male and said that they were of rare occurrence.

Reproduction. The female deposits her eggs in capsules which are attached by short delicate stalks to a thick mucous "helmet" almost completely covering the shell of the male (pl. II, fig. 3). A similar habit has been described in M. holothuricola and it probably also occurs in M. voeltzkowi in which species, however, the shell of the male was lost. The pseudopallial fold of the male of our species was considerably

lower on one side, and the capsules were chiefly fastened to that side (pl. II, fig. 3); this is probably the side which in life is adjacent to the female (text-fig. 1). In such a position it is possible that the anterior part of the foot of either sex may manipulate the egg capsules, and the enlarged pedal gland opening on the tip of it could perhaps at the same time produce the helmet to provide a firm attachment for the capsules. It was possible to remove the helmet as a whole together with the capsules; its inner surface showed a perfect moulding of the shell and the occurrence of fine striae perfectly comparable to those found on the fresh shell of the female. The shape of the capsules is similar to those figured by Rosén (1910, fig. I), being somewhat oviform, but their shape varies according to the stage of development of the enclosed young. Newly laid capsules are smooth contoured and the eggs tightly packed. As the embryos develop the capsules become more spacious from ab. 1.5 mm to more than 3 mm in largest diameter, and having attained the final larval stage, the individuals are free to rotate. The larvae escape through random ruptures in the wall of the capsule which then slowly breaks up leaving only the stalks in position.

Twenty-six capsules were attached to the male, of which 10 were empty, 4 were ruptured and partially empty, and 12 were entire; in addition a number of stalks were found in various stages of decay. The capsules showed all the pre-release stages in the development of the young but the contents of each capsule were in a constant stage of development. This indicate a continuous production of eggs and to substantiate this several embryos or larvae from each capsule were sectioned. Since the embryos could be arranged in a fairly continuous series according to their development as evidenced by sectioning, laying seems to be a steady process, obviously not interupted by intervals of non-reproduction.

The contents of the whole capsules were counted, showing an average of 107 larvae or embryos with a range of 85–137.

The location of the present material in the host has been mentioned and comparing this with that of M. holothuricola, the only species in which the location has been described in some detail, we note that our material differs in that no direct connection with the sea existed when the animals were in their observed position According to Rosén (1910) M. holothuricola occupies such a position that the body is located in the lumen of the respiratory tree and so bathed in sea water. The proboscis penetrates the wall of the tree, opens into the coelom and ingests the coelomic fluid. This location is reminiscent of that briefly described by von Martens (1865) on what we suppose is a species belonging to Megadenus. This apparent difference in location has resulted in the following considerations which gives a more meaningful interpretation of both our own and Rosén's observations.

Species so closely related as to be ascribed to the same genus are likely in principle to lead a similar life. Two features are of particular interest here *viz*, the release of the larvae and the nature of nutrition since our observations do not correlate on these points with those of Rosén.

In both species the female deposits her egg capsules on the shell of the male. The position of M. holothuricola within the respiratory tree of the host allows for the release of larvae in the exhalent water. Such a situation did not apparently occur in the male of our species, the body of which including the egg capsules were located within the coelom. It may be argued that in the absence of any coelomoducts in holothurians or other connections between the coelom and the sea the parasite relies for the release of the larvae on periodic evisceration of the host. As with many other tropical aspidochirotes, S. chloronotus may eviscerate under adverse conditions as for instance in stale sea water. Whether this species eviscerates in nature is not known, but it deserves mention that in several other holothurian species belonging to the genera Stichopus, Parastichopus and Actinopyga a seasonal evisceration has been demonstrated (Bertolini (1932); Swan (1961); Mosher (1965), Jespersen & Lützen (1971)). We do not consider, even if seasonal evisceration does occur in S. chloronotus that it may explain the release of the larvae of M. cantharelloides since the production of the larvae has been shown to be a steady process and the opening to the sea following evisceration is of a very transitory nature. We are therefore of the opinion that the reported location of the male in M. cantharelloides only partially corresponds to the natural condition and we will show that the material of M. cantharelloides has been displaced from its original position.

An examination of the egg mass helmet revealed an entire foraminiferan and empty angiosperm mesenchymatous tissue embedded in the substance. The mucus on the distal surface of the female pseudopallium contained assorted unidentifiable debris together with a foraminiferan and a spine probably of a crustacean. No similar material was found on the proximal surface of the proboscis flange despite its close proximity to the pseudopallium. These inclusions would not be expected in the coelom of the host.

The part of the proboscis connecting the pseudopallium and the flange in M. cantharelloides is fairly constricted. In this region an almost complete reduction of the longitudinal musculature was noted. Accompanying this the molluscan epithelium has been sharply disrupted throughout the section series. The nature of this disruption and its restriction to this region illustrates that it is not an artefact of sectioning. It appears that something surrounding the base of the proboscis has been forceably pulled away.

The zone of disruption furthermore marks an abrupt change in the nature of the epithelium lining the proboscis. Posteriorly to the zone occurs a mucus secreting epithelium which becomes increasingly folded towards the boundary to the pseudopallial base. In the section series mucus was seen originating here and produced maximally in the region of the greatest folding. In life there would be an outward flow of mucus from this region (pl. III, fig. 5, large arrows). The proximal surface of the flange, on the contrary, is lined by a cuticularized epithelium. Such an abrupt change in the nature of these adjacent surfaces suggests that they are exposed to different environmental conditions in life.

Throughout the section series an unbroken ring of tissue was found to surround the zone of epithelial disruption (pl. III, fig. 5, iw). Its structure is strongly reminiscent of the connective tissue found in the intestine of a sea cucumber, and a careful examination revealed that it was not derived from the gastropod.

The extent and the development of the intestine and the digestive gland in M. cantharelloides does not suggest an animal living on the very dilute simple organic foods available in the coelomic cavity, such as sugars and aminoacids, as suggested by Rosén (1910) for M. holothuricola. Gastropod parasites feeding on dilute media and simple organic compounds as e.g. nutrients from the coelomic fluid tend to show considerable modification to the digestive system; the endoparasitic family Entocon-chidae provides a classical example of this (Ivanov, 1945).

The evidence presented leads us to the conclusion that the field observations on M. cantharelloides were an artefact of the autotomy of the intestine in the host prior to it being examined. We believe, that the parasite inhabits the intestine of the host, probably, according to the arrangement of the gut in S. chloronotus, in the oesophageal region, although the anterior ventral loop of the large intestine is also adjacent to the area where the male was attached. The entire proboscis lies in the coelom so that the wall of the intestine lies between the pseudopallium and the flange of the proboscis. It is probably partially introduced in the body wall of the host (text-fig. 1) as was actually demonstrated by the male specimen. In this situation the parasite can maintain its position in the alimentary canal without the expendature of much energy, for the flange of the proboscis will prevent the displacement of the animal. The proboscis is now free to attach in different adjacent regions of the body wall without the parasite being displaced. The discontinuity in the musculature referred to above indicates that the proboscis is not functioning as an attachment organ, rather as a food gatherer. The copious mucus production will provide a radial flow of mucus which will clear the area of debris from the host gut content and will provide a degree of protection from digestive fluids of the host in a region where it is particularly vulnerable.

The egg mass on the male must now lie in an exposed position within the lumen of the alimentary canal of the host. The extreme development of the pseudopallium in the male (pl. II, fig. 3) and its position even in the preserved material suggest that in life it covers the egg mass and protects the cocoons from damage. In this position the larvae are able to pass through the gut with the food, or while it is relatively empty in the early morning (Yamanouchi, 1956). That larvae of parasitic gastropods are able to pass the intestine without being digested is well known in members of the family Entoconchidae (Schwanwitsch, 1917).

It follows that although much of the evidence is derived from the male specimen, the female must inhabit the same position as the male so that the egg capsules can be laid on the latter. To support this there is the evidence of the tissue debris restricted to the external side of the pseudopallium and possibly comparable to the ring of tissue around the proboscis of the male. More significant, perhaps, is the earlier mentioned presence of a brownish belt of a mucous substance surrounding the proboscis probably indicating the level at which this structure is introduced in the host's body wall (text-fig. 1, r). Observations on live specimens of S. chloronotus show that the interior body wall is lined by a delicate mucus which is slightly pigmented; it appears dark when concentrated as for example by scraping an instrument across the surface of the coelomic wall.

It is considered that Rosén's observations were correct save that the proboscis of his specimens of M. holothuricola had become detached from the body wall. In the absence of any consideration of the morphology of the alimentary tract he considered that the parasite fed on coelomic fluid.

The observations on the present material in the field are artefacts of the autotomy of the intestine and its subsequent contraction. In this situation with the parasites attached to the body wall a strain would be exerted in a direction opposite to that occurring naturally. The wall of the intestine disrupted leaving the male parasite attached to the body wall and at the same time dislodging the female and breaking her at the base of the proboscis, the weakest point. The subsequent contractions of the intestine expelling the body of the female into the coelom where it was found.

Conclusions

Comparisons between the structure of M. cantharelloides and the two other species known to parasitize sea cucumbers have been given earlier in this account. It is distinguished from both of them by the peculiar flange-like portion of the proboscis, the presence of functional eyes and four, rather than two retractor muscles. It furthermore differs from M. holothuricola in possessing a small, but typical stomach, and from M. voeltzkowi by having two tentacles in the female instead of one. We consider that these differences are sufficient for establishing a new species. On the other hand, it should be emphasized that the three species mentioned are extremely similar in so many fundamental respects that a very close kinship can not be doubted.

It would therefore be of interest to compare the structure of this group of three species with the remaining two species referred to that genus.

Megadenus cysticola Koehler & Vaney, a parasite provoking cysts in the spines of the cidaroid Dorocidaris tiara, was unfortunately described rather briefly and it remains therefore difficult to compare this species with those living in sea cucumbers. It is apparently similar to these in several respects, but the lapidary description does not allow one to decide whether these similarities are real or not. M. cysticola (figured in Grassé, 1968, p. 216) has a mucronate shell, which is whitish, polished, and brittle. Sexual dimorphism is well-expressed, the male being much smaller than the female, both of which live together in the cysts. The egg capsules are deposited within the cysts but it is not known whether they are attached to the male's shell or to the interior of the cyst. There is a well-developed proboscis, from the base of which arises a so-called pseudopallium, which shows greater development in the male than



Fig. 5. Diagram showing the position of Paramegadenus arrhynchus (Ivanov) in the skin of Anthenoides rugulosus. cy, cyst of host's skin plates; m, mouth opening; p, penis; ps, pseudopallium; rcy, rim of cyst enveloping margin of pseudopallium. (From Ivanov, 1952, fig. 4).

in the female. The cephalic region and the foot are said to be reduced, and there is no operculum. Eyes and statocysts are present, and the anterior pedal gland is very prominent.

The most profoundly examined species referred to Megadenus is M. arrhynchus Ivanov, on the structure of which an extensive report has been given (Ivanov, 1952). Ivanov's material consists of two sea stars of Anthenoides rugulosus¹ from the Yellow Sea, each of which were parasitized by three snails and preserved in formalin. The parasites were placed in fairly deep depressions, or cysts, in the skin of the aboral side of the sea star's interradii, the plates of which thereby had become considerably thickened and more or less irregularly deformed (text-fig. 5). The gastropod body

¹ As pointed out by Ivanov, the species was first discovered and pictured by Fisher (1919, pl. 35, fig. 4), although not mentioned in his text. On request, Dr. David Pawson (U.S. Nat. Mus. Wash.) has kindly told us that these gastropods were on the holotype of A. rugulosus (USNM catalogue no. 30561), from 9 miles southeast of Malabrigo Light, east coast of Mindoro, Philippines, 108 faths., mud. Actually the specimen had four gastropods on it, the two shown in Fisher's plate, and two more (also close together) lying near the margin of an arm about two-thirds of the arm length away from the center of the disc. — The Zoological Museum in Copenhagen has one alcohol-fixed specimen of Anthenoides granulosus parasitized by a male and a female of M. arrhynchus, taken on the Th. Mortensen Expedition to Java and S. Africa (Java Sea, 7°35′S, 114°42′E, 200 m), and 3 dried specimens of Anthenoides sp. (according to Dr. F. J. Madsen, Zoological Museum, Copenhagen, these differ from A. rugulosus) with one female, one female, and two pairs respectively, taken by the Th. Mortensen Pacific Expedition (W. of Kyushu, Japan, 32°17′N, 128°11′E, 208 m). Except for one of the pairs, which was placed in the middle of a radius, the others were located interradially and very close to the center of the disc.

is sunk obliquely into the host's skin so that 3 or 4 body whorls may be seen from the outside. In the complete absence of a proboscis, the contact with the host is entirely accomplished by a formation, which Ivanov calls a pseudopallium; all around its margins fit closely into a circular groove formed from the rim of the cyst.

The species is relatively little modified by its parasitic way of life. Besides the presence of a pseudopallium and the absence of a proboscis and an operculum, it is distinguished mostly by specialization of the foot and accompanying structures. The head is small and poorly defined. There are two very large and stout tentacles. An ocellus is included in the base of each. The mouth is a short slit placed accentrically in the pseudopallium.

The pseudopallium is formed from the front part of the head and has the shape of a large fold of skin reflected to form a cavity which is widely open aborally. Owing to the oblique position of the body, it is largest to the right, whereas its lesser development to the left leaves the whorls uncovered and visible at that side.

The foot has obviously lost any locomotory power. Its foremost margin is strongly dislocated and lies adjacent to the right antenna. The foot is subdivided into three parts, the two first of which are shovel-shaped, whereas the third, and posterior one, is a muscular, ciliated fold, that surrounds the base of the visceral mass almost reaching the entrance to the pallial cavity. The two pedal glands open onto the first and second parts respectively. The function of these parts remains somewhat obscure, whereas it is supposed that the third part serves to lead sea water into the mantle cavity, thus forming a specialized siphon of pedal origin.

The shape of the shell appears from Ivanov's fig. 5. It has a well expressed larval shell and 3.5-4 adult whorls. The larval shell is transparent and 400 μ high, whereas the adult whorls are shining, smooth, rather thick and opaque, with almost invisible striae. The sutures are very distinct and whitish. Height and width of shell: 6.4–6.5 and 4.9 mm (females); 1.5 and 1.5 mm (males).

The interrelations between M. arrhynchus and the three other species of that genus (ignoring the poorly described M. cysticola) deserve the closest attention. Gruzov (1965) has provided very convincing evidence that the ancestors of Asterophila japonica Randall & Heath, an internal gastropod parasite of various sea stars were structurally reminiscent of Megadenus. He has proposed an evolutionary trend, which starts with Megadenus (i. e. the species parasitizing sea cucumbers) and ending with Asterophila and in which M. arrhynchus occupies an intermediate position (Gruzov, 1965, fig. 49). We feel that the relations between the forms in question are better expressed when M. arrhynchus is given a generic status of its own.

The general structure of M. arrhynchus is very similar to that of the species of Megadenus living in holothurians. Reliable indications of this relationship are seen in those specializations common to all such as a pseudopallium of purely cephalic origin, the structure and location of the enormously enlarged anterior pedal gland, the reduced size of the posterior pedal gland, and the elaboration of the foot, particularly its posterior, folded portion. To these one may possibly add the similar plan

of the nervous system and reproductive apparatus and the identical histological structure of the eyes. This combination of characters is no doubt expressive of a true affinity. M. arrhynchus, on the other hand, is characterized by a number of peculiarities, which separate it sharply from the other species of that genus to an extent which justifies the raising of a new genus. This we propose to name Paramegadenus n.g., accomodating only one species, P. arrhynchus (Ivanov). The name Megadenus should be restricted to the three species which live in sea cucumbers, *viz.* holothuricola, voeltzkowi, and cantharelloides n. sp.

Among the most distinctive characteristics of Paramegadenus is the complete absence of a proboscis, a feature accompanied by simplification of the buccal cavity, which is lined with a simple, cubical epithelium. Another important distinguishing character is that the males are considerably smaller than the females, although not simple pygmies. Differences also exist in the larval shell which in Paramegadenus has 3 whorls, and, as we shall see, probably in the mode of reproduction. Peculiarities of minor importance are that a posterior pedal gland is found only in the female, and the hind part of the foot is muscular and ciliated.

The position of P. arrhynchus in the phylogenetic scheme was considered by Gruzov (1965) to be one leading from Megadenus towards Asterophila. It might very well be too early to say whether Paramegadenus occupies a more advanced stage than Megadenus. Some of the peculiarities separating it from the latter are obviously directly related to differences in the mode of feeding; thus, the lack of a protruding proboscis and the rudimentary state of the buccal cavity in P. arrhynchus might well be considered original features, and the elaboration of these parts in Megadenus as later aquisitions. The presence of two proboscis retractors in Paramegadenus and Megadenus (four in M. cantharelloides) and the reduced condition of the stomach in both genera do not lend support to either theory.

Perhaps the most conspicuous differences separating Paramegadenus from Megadenus are that the former exhibits a pronounced male-dwarfism. That the number of ctenidial leaflets is smaller in the male than in the female, that no posterior pedal gland exists in the male, and the apparent large size of the penis in Paramegadenus is explained by the great reduction in size of the male. Male dwarfism is often regarded as an indication of an advanced position in an evolutionary series. Among parasites, however, such tendencies usually occur the more intimate the parasitehost relationships become. Since P. arrhynchus depends upon its host no more than does Megadenus, one may just as well turn the problem the other way round and ask why the latter has not aquired this characteristic also. This question may probably, we believe, be related to differences in the mode of reproduction. The fact that there is no information on Paramegadenus' reproduction other than Ivanov's observation of an egg capsule in the capsule gland of a female, may itself offer the most simple explanation. A total of 18 specimens of P. arrhynchus (males and females together) have been observed, compared with half that number, also of both sexes, in the three species of Megadenus. Nevertheless, egg capsules have been commonly observed attached to the male shell in the latter. It is probable that in Paramegadenus the egg capsules are immediately liberated into the sea. Perhaps, supporting this, is the condition prevailing in Asterophila, where the single egg capsule rests unattached in the female pseudopallial cavity (Gruzov, 1965). That the species of Megadenus living in the host's intestine retain their capsules is understandable. If liberated they have to pass the entire alimentary tract of the host unprotected from the digestive juices and attrition. The operculate larvae, on the other hand, able as they are to withdraw into their shell, are excellently equipped for the process of escape. To retain the capsules, however, demands a firm substrate on which to glue them, and in the particular environment which these parasites inhabit, this is provided only by the shells of the adults. For some reason unknown, the female is unable to attach them to its own shell and for that purpose depends upon the male's. The lack of sexual dimorphism in these species could therefore be accounted for by the male requiring a large size in order to anchor and protect the egg capsules. If this is correct then the lack of dwarf males in Megadenus becomes a dubious evolutionary indicator.

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References

- BERTOLINI, F., 1932: L'autotomia dell'apparato dirigente e la sua rigenerazione nelle Oloturie, come fenomeno spontaneo e normale. Atti Accad. naz. Lincei Rc. Classe sci. fis. mat. e nat. 15: 893–896.
- FISHER, W. K., 1919: Starfishes of the Philippine Seas and Adjacent Waters. Bull. U.S. natn. Mus. 100 (3): 1-546, pls.
- GRASSÉ, P.-P., edit. 1968: Traité de Zoologie, V, fasc. III: Mollusques Gastéropodes et Scaphopodes. Paris, 1083 pp.
- GRUZOV, E. N., 1965: The endoparasitic Mollusk Asterophila japonica Randall and Heath (Prosobranchia: Melanellidae) and its relation to the parasitic Gastropods. Malacologia 3: 111–181 (in Russian, with abstracts in English, French, German, and Spanish).
- Ivanov, A. V., 1937: A new ectoparasitic Mollusk of the Genus Megadenus Rosén. Dokl. Akad. Nauk SSSR, N.S. 14 (7): 467–470.
- 1945: Morphological Adaptations in the Intestine of Parasitic Gastropods. Uchen. Zap.
- leningr. gos. Univ., Ser. Biol. Nauk. 15: 112–119 (in Russian, with an English abstract).
 1952: Structure of the parasitic Gastropods Stiliferidae as the result of their mode of life. Trudy leningr. Obshch. Estest, 71 (4): 86–140 (in Russian).
- JESPERSEN, Å. & LÜTZEN, J., 1971: On the ecology of the aspidochirote sea cucumber Stichopus tremulus (Gunnerus). Norw. J. Zool. 19: 117–132.
- KOEHLER, R. & VANEY, C., 1925: Un nouveau Gastropode producteur de galles sur les piquants du Dorocidaris tiara Anderson. C.r. Séanc. Acad. Sci., Paris 180: 1559–1563.
- von Martens, 1865: In: Sber. Ges. naturf. Freunde Berl. 20 Juni 1865, p. 7.
- MOSHER, C., 1965: Notes on natural evisceration of the sea cucumber Actinopyga agassizi Selenka. Bull. mar. Sci. Gulf Caribb. 15: 255–258.
- Rosén, N., 1910: Zur Kenntnis der parasitischen Schnecken. Acta Univ. lund. N.F. Afd. 2, 6 (4): 1–67, pls.
- SCHEPMAN, M. M. & NIERSTRASZ, H. F., 1913: Parasitische und kommensalistische Mollusken aus Holothurien. Reise in Ostafrika in den Jahren 1903–1905 von Professor Dr. Alfred Voeltzkow, 4: 383–416.
- Schwanwitsch, B. N., 1917: Observations sur la femelle et le mâle rudimentaire d'Entocolax ludwigi Voigt. J. russe Zool. 2: 1–147 (in Russian, with a French summary).
- Swan, E. F., 1961: Seasonal Evisceration in the sea cucumber, Parastichopus californicus (Stimpson). Science, N.Y. 133: 1078–1079.
- YAMANOUCHI, T., 1956: The daily activity rhythms of the holothurians in the coral reef of Palao Islands. Publs Seto mar. biol. Lab. 5: 347-362.

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PLATES

PLATE I

Fig. 1 and 2. Female Megadenus cantharelloides n. sp. af, anterior part of foot with opening of anterior pedal gland; cg, capsule gland; dg, digestive gland; g, gills; k, kidney; pf, posterior part of foot; ps, pseudo-pallium; rt, right tentacle. Scale represents 2 mm.



Plate II

Fig. 3 and 4. Male Megadenus cantharelloides n. sp. The mucous helmet and egg capsules have been removed in fig. 4. ec, egg capsules; m, mouth opening; fp, flange of proboscis; pr, proboscis; ps, pseudopallium. Scale represents 2 mm in fig. 3 and 500 μ in fig. 4.



PLATE III

Fig. 5. Section parallel to columellar axis through male Megadenus cantharelloides n. sp. aa, anterior aorta; af, anterior part of foot; bc, buccal cavity; dg, digestive gland; eb, efferent branchial vessel; fp, flange of proboscis; hg, hypobranchial gland (posteriormost part); i, intestine; iw, remains of intestinal wall of host; k, kidney; m, mouth; mc, mantle cavity; oe, oesophagus; pf, posterior part of foot; ph, pharynx (cut tangentially); ps, pseudopallium; r, retractor muscle; t, testis; v, visceral ganglion; vd, vas deferens; x, opening of prostate into mantle cavity; y and z, openings of anterior and posterior pedal glands. — Large arrows illustrate a radial flow of mucus produced by the glandular epithelial folds. The small arrows indicate the discontinuity of the muscle layer and the transition between epithelia of glandular and cuticular nature. Scale represents 500 μ .
Plate III



PLATE IV

Megadenus cantharelloides n. sp.

Fig. 6. Left ocellus in longitudinal section. c, cornea; l, lens; on, optic nerve; re, retina; the arrows mark the boundary between the pigmented cup and the cornea. Scale represents 50 μ . Tetrachrome, 10 μ .

Fig. 7. Slightly oblique longitudinal section through pharynx (ph) and buccal cavity (bc). b, buccal ganglion; iw, remains of intestinal walls of host; oe, oesophagus; r, retractor muscle; the arrows indicate a disruption of the epithelium. Scale represents 500μ . Iron hematoxyline-eosin, 10μ .

Fig. 8. Longitudinal section through larva. cm, columellar muscle; dg, digestive gland; f, muscular portion of foot; lc, left cerebral ganglion; lp, left pedal ganglion; mc, mantle cavity; oe, oesophagus; op, operculum; rp, right pedal ganglion; s, stomach; st, statocyst; x, duct of digestive gland into stomach. Scale represents 100μ . Toluidine blue, 2μ .

Fig. 9. Larval shell. Scale represents 100μ .



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FINN SURLYK

MORPHOLOGICAL ADAPTATIONS AND POPULATION STRUCTURES OF THE DANISH CHALK BRACHIOPODS (MAASTRICHTIAN, UPPER CRETACEOUS)

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Synopsis

The study is based on a large number of 5 or 10 kg samples from all major Danish chalk localities. After washing, the samples yielded a material of about 50.000 brachiopods representing 37 articulate and 6 inarticulate species.

In order to give a comprehensive description of the brachiopod ecology an analysis has been made of spatial and stratigraphical variations, morphological adaptations, population structures, enemies, and interand intraspecific competition of the fauna. Special emphasis has been laid upon comparison between the different types of morphological adaptations and the corresponding population structures as well as comparison with closely related living species.

> BIANCO LUNOS BOGTRYKKERI A/S PRINTED IN DENMARK

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Introduction

In recent years the trend in palaeoecological work has been focused especially on morphological adaptations of the animals to different environments and on fossil communities and evolution at the community level.

Somewhat unexpected, palaeoecological research has concentrated on the evaluation of fossil community successions and parallel communities (sensu THORSON, 1957) mainly in Palaeozoic rocks. Particularly worthy of mention are the studies of early Palaeozoic faunas in North America and Europe by ZIEGLER, 1965, ZIEGLER et. al. 1968, BRETSKY, 1970 a, 1970 b, Fox, 1968, and WALKER & LAPORTE, 1970.

The Upper Cretaceous (topmost Campanian–Maastrichtian) white chalk of Denmark contains a very rich macrofauna dominated by several hundred species of bryozoans associated with bivalves, brachiopods, echinoids, crinoids, ophiuroids, asteroids, belemnites etc.

In the present study the work is concentrated on the brachiopods which comprise 43 species representing 23 genera. In order to give a comprehensive description of the brachiopod ecology, an analysis has been made of spatial and stratigraphical variations, morphological adaptations, population structures, enemies, and inter- and intraspecific competition of the fauna. A special emphasis has been laid upon comparison between the different types of morphological adaptations and the corresponding population structures as well as comparison with closely related living species.

Acknowledgements

The present paper is one of the results of a project concerning the Upper Cretaceous chalk of Denmark initiated by Tove BIRKELUND in 1965.

I am deeply indebted to Tove BIRKELUND for every support and for numerous discussions on all aspects of my work with the Danish Maastrichtian brachiopods during the last 6 years.

N. SPJELDNÆS is thanked for the permission to study his great collections of recent brachiopods, for discussions on brachiopod ecology and for critically reading the manuscript.

The CARLSBERG FOUNDATION supported grants for the field work.

Various aspects of the paper was discussed with Ellinor Bro Larsen, Ulla Asgaard, R. BROMLEY and D. SCHUMANN.

Much of the field work was done in company with my colleagues W. KEGEL CHRISTENSEN and E. HÅKANSSON, who both read the manuscript critically and with whom I have discussed chalk ecology, stratigraphy and palaeontology almost constantly over many years.

The drawings which play an important role in the paper were prepared by H. EGELUND.

ESTHER EBJERG, ERNA NORDMANN, J. AAGAARD, C. HEINBERG, G. JESSEN, and N. SVENDSEN all contributed with highly appreciated help in collecting, washing and sorting the numerous large bulk samples.

Special thanks are directed to ANNELISE NØRGAARD JENSEN who undertook the main part of the sorting and together with J. FUGLSANG NIELSEN assisted in taking the electron micrographs.

R. BROMLEY undertook the great task of improving the English language.

Method

The study is based on a large number of samples or series of samples from all major Danish white chalk localities (fig. 1). The weight of each sample in the more important sections is 5 or 10 kg, but in many cases additional 2.5 kg samples have been collected.

The samples are dried at about 30°, overheating being avoided since this hardens the chalk. The dry samples are weighed out to 5 or 10 kg and poured over with a supersaturated solution of glaubersalt ($Na_2SO_4 \cdot 10H_2O$) with a temperature of 40° . After cooling for some hours the superfluous glaubersalt solution is poured off and the sample deep-frozen. The sample is then reheated until the glaubersalt solution liquifies again (glaubersalt has a maximum solubility at about 40°). This proces is repeated 16–18 times, after which the sample is washed through a 0.25 mm sieve. The residue is then dried and hand-sieved into three fractions: 0.25-0.5 mm, 0.5-1.0 mm and >1.0 mm. The brachiopods are picked only from the two upper fractions, the 0.25-0.5 mm fraction containg practically none. When the brachiopods have been picked out (under binocular microscope at $\times 6$ or $\times 12$ magnification) and determined to species, the number of individuals is estimated by adding whichever the greater number of dorsal or ventral valves to the number of whole shells, thus obtaining the minimal number of individuals. In addition, the number of fragments is counted in order to check if the estimated minimal number of individuals is representative. The term individual is used throughout in this sense to avoid confusion with the term specimen, which is used for any ventral or dorsal valve or whole shell.

A sample weight of 5 kg was found to be ideal. Samples of greater weight only rarely show additional species while the number of individuals seems to vary proportionally with the size of the sample. Nr. 2



Fig. 1. Localities. The signature shows the distribution of the Upper Cretaceous sediments on the Prequarternary map of Denmark. The investigated chalk localities are marked with an asterisk. The positions of the most important localities mentioned in the text are shown.

Material

About 150 samples from 47 localities (13 of which are situated at Møns Klint) have been examined. These have yielded a total of about 50.000 brachiopod individuals representing 37 articulate and 6 inarticulate species. The brachiopod collections of the Mineralogical Museum of the University of Copenhagen have also been examined.

Stratigraphy

Brachiopods have shown themselves to be valuable for the detailed stratigraphical subdivision of the chalk of Rügen, East Germany (STEINICH, 1965) and Denmark (SURLYK, 1970 a, 1970 b). Thus it is possible to divide the Danish Maastrichtian into 10 zones on the basis of the brachiopods (fig. 2). Furthermore, it is possible to correlate precisely the most important Lower Maastrichtian sections in Denmark, north-west Germany and Rügen (SURLYK, 1970 b) by means of the brachiopods.

Besides the zonal stratigraphy, STEINICH (1965, fig. 296) showed that variations in the quantitative distributions of the brachiopods from bed to bed through the chalk sections on Rügen made it possible to correlate neighbouring localities. This is also possible in the Danish chalk, where the glacially folded and faulted chalk of the cliff of Møn can be correlated by means of quantitative brachiopod diagrams.

Sedimentology

The Danish white chalk is a soft, friable, almost pure carbonate sediment of biogenic origin. Although the chalk never has been the subject of a detailed sedimento-logical investigation, its petrographical composition is rather well known. BLACK (1953) showed, that the English Senonian chalk was composed of whole or broken coccoliths in the 5–10 μ fraction and of fragments of molluscs and foraminifera in the sand fraction. The coccoliths of the Danish chalk are well known (PERCH-NIELSEN, 1968, 1969) and constitute the major part of the sediment.

Münzberger (cit. NESTLER, 1965 p. 9) analyzed the quantitative composition of the chalk of Rügen (table 1). His results fit well with those on preliminary work on the Danish chalk. TABLE 1.

Coccoliths	72.0	weigth ⁰ / ₀
Foraminifera	1.0	-
Bryozoans	1.8	—
Ostracods	0.1	-
Non-carbonate	1.2	-
$Carbonate > 0.1 \ mm \ \dots $	5.3	
Carbonate < 0.1 mm	18.0	-

(After Münzberger in Nestler, 1965)

HONJO (1969) classified the Danish chalk as a friable, semiconsolidated nanno-agorite.

The problem of the non-hardening of the chalk has attracted the attention of many authors (e.g. HANCOCK, 1963, TERMIER & TERMIER, 1963, HANCOCK & KENNEDY, 1967, HONJO, 1969), but only in recent years have acceptable explanations been put forward. The lack of hardening of the chalk seems to be due chiefly to the high diagenetic stability of the coccoliths, presumably on account of the persistence of the organic

N	r		9
1.1	Ι.	•	4

Belemnite zones	Localities	Brachiopods						
Belemnella casimirovensis Belemnitella junior	Karlstrup Stevns	aris cula humboldtii Argyrotheca stevensis Thecidea	10	Upper				
		iglobulc Gemmat	9	Upper	Jpper			
Belemnitella junior		Meonia sem	8 -	Lowe				
	Rørdal		7		hian			
Belemnella occidentalis	nella		emnella cidentalis	emnella identalis	lchellus	6	pper	aastrich
		ulina subtilis Trigonosemus pu	5	U	¥			
	σ	s Terebrat	4					
Belemnella lanceolata Belemnella occidentalis	mnella vientalis vientalis	ia spinosa ia acutirostri jasmundi	3	Lower				
		Rug Sis lina	2					

Fig. 2. Stratigraphy. The stratigraphical distribution of the most important brachiopods and the corresponding 10 brachiopod zones shown. The correlation with the belemnite zones used in the European standard Maastrichtian zonation is according to SURLYK (1970b). It must be mentioned that in the *Belemnitella junior* Zone no specimen of the index fossil has been found as this species is extremely rare in Danmark. The stratigraphical positions of some of the sections illustrated in the quantitative diagrams on figs. 3, 14 and 15 are shown.

membranes surrounding the single coccolith plates (HONJO, 1969). Furthermore the shells of almost all the organism groups found in the chalk are composed of the most stable form of CaCO₃, low-Mg-calcite. The only major exceptions are the shells of the

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gastropods, the cephalopods (except belemnite rostra) and some of the bivalves, which were originally composed of aragonite. The shells of the echinoderms are composed of high-Mg-calcite and are well preserved.

Impressions of ammonites are quite common whereas remains of aragonite-shelled bivalves and gastropods are rare except in a few hardgrounds. Therefore the rarity of the bivalves and the gastropods seems in part to be primary and not merely caused by solution of the aragonitic shells. However, borings in shells of brachiopods and bivalves which are attributable to muricid and naticid gastropods are not uncommon. (For details of the mineralogical composition of the shells of the fossils see CLARKE & WHEELER, 1922, CHAVE, 1954 a, 1954 b, SCHOPF & MANHEIM, 1967, RUCKER & CARVER, 1969, LOWENSTAM, 1954).

The non-carbonate content of the Danish chalk normally varies between 0.5 and 5% and consists of clay minerals, dessiminated FeS₂, rare well-rounded æolian quartz grains, and siliceous sponge spicules. The chalk of Zone 8 and 9 (fig. 2) has a higher non-carbonate content (6-12%).

Flint nodules are common in the most horizon of the chalk, especially in Zone 3–5 and 10 (fig. 3). Tabular flint layers occur more rarely. The flint nodules were formed diagenetically under a varying cover of sediment. There is certain evidence that some flint, at least, formed by processes of very early diagenesis (e.g. STEINICH, 1965 p. 205). On the other hand the silicification of fossils after they have been crushed by overburden of sediment, and the existence of oblique to nearly vertical tabular layers following joints shows that flint also formed through processes of late diagenesis (FAIRBRIDGE, 1967).

According to STÖRR, 1966 and ERNST, 1966 flint seems only to be formed in very pure carbonate sediment and that might explain why flint is missing in Zones 8 and 9 where the non-carbonate content is high.

More or less distinct marl layers are common at many horizons. Several 4–5 cm thick, distinct, grey marl layers occur in Zone 2. At the boundary between Zones 7 and 8 two prominent marl layers seem to be good marker horizons for the boundary between Lower and Upper Maastrichtian in Denmark and northern Germany (SURLYK, 1970 b). In Zones 8, 9 and 10 light grey, marly horizons c. 50 cm thick are common (one of the

Fig. 3. Standardsuccession. As the stratigraphy for some parts of the succession is based on numerous small scattered localities and not on borings the correct thicknesses of all the zones are not known. The relative thicknesses of Zones 1–7 and Zone 10 are approximately correct, whereas the relative thicknesses of Zone 8–9 are rough estimates. The samples used in the construction of the three curves were not chosen at random, but it has been attempted to select samples typical for each zone. There is a pronounced parallelism between the washing residue curve (\approx the bryozoa curve) and the curve illustrating the number of brachiopod individuals. The number of species curve follows roughly the two other curves except for the very rich horizons (Zones 4 and 10) where the number of species decreases. The overall trends of the three curves reveal two pronounced maxima of the benthonic fauna (Zones 4 and 10) and a minimum between them (Zones 7–9). HG = hardground. Incip. HG = incipient hardground. M = marl layer. P = platy flintlayer: Black spots indicate flintnodules.

The following samples have been used in the construction of the curves (from bottom to top): Hvide Klint 1, 3, 4. Hvidskud 28, 18, 7, 5, 2. Lille Taler. Rørdal 1, 4, 6. Lindholm 2. Nørre Flødal 1. Linds Kalkværk. Stevns Klint 7, 2, 1. The total thickness increases from c. 350 m to 700 m in the central part of the Danish basin.

Nr. 2





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most important was named the Kjølbygård Marl by TROELSEN, 1955). At some localities (Dania, Limhamn) the marl layers occur very regularly at a distance of a few metres in a somewhat rhytmic manner.

Stratigraphical variations in the sediment

The Danish Maastrichtian is developed as a rather uniform sequence of white chalk with scattered flint nodules arranged in horizontal layers. The regular horisontal layering is however interrupted in Zone 10, where the bryozoans have developed small bioherms (ROSENKRANTZ & RASMUSSEN, 1960) (fig. 3).

The bryozoan bioherms found at several localities in the uppermost part of the chalk have recently been interpreted as the result of wave action, i. e. that they represent a sort of mega ripples (RASMUSSEN, 1971). No arguments are however forwarded to substantiate this hypothesis. The fossils (e.g. the bryozoans and the brachiopods) in the bioherms are extremely well preserved and show absolutely no signs of transport. Furthermore, the bioherms are asymmetrical, the southern flank of each bioherm overlapping the northern flank of the neighbouring bioherm. At Karlstrup (fig. 15) the Maastrichtian chalk bioherms are conformably overlain by Danian bioherms and the same asymmetry and overlapping is found as at Stevns Klint. It is not possible to explain these features as structures produced by wave action.

In addition to the bioherms, many smaller variations in the Maastrichtian sequence occur (fig. 3). 2 m above the boundary between Zones 4 and 5 a thin hardground is developed (fig. 14) (TROELSEN, 1937). It consists of a distinct discontinuity surface beneath which nodules of rather hard, yellow chalk in a softer matrix of only weakly hardened chalk extend downwards for some 10 cm. This nodular hardening is rather common in the Danish chalk and might be considered an initial stage in hardground development (BROMLEY, 1967, 1968). 3.5 m below the Maastrichtian Danian boundary at Stevns Klint (fig. 3) there is a sharp junction between normal white chalk and grey chalk with bryozoan bioherms. This discontinuity surface is developed as the initial stage of formation of a hardground with nodular hardening (SURLYK, 1969).

The Maastrichtian-Danian boundary is at some localities very complex, especially at Stevns Klint (ROSENKRANTZ, 1924, 1940, 1966), but normally the stop in sedimentation is marked by small-scale erosion and nodular hardening of the top 20–30 cm of the Maastrichtian.

Ecology

Stratigraphical variations in the benthonic fauna

The Danish Maastrichtian white chalk can be divided into three ecological units based on the major variations in the richness of the benthonic fauna (fig. 3).

From Zones 1–4 there is a steady increase in the benthonic fauna illustrated by the washing residue curve in fig. 3. The washing residue consists in the main of cyclostome and cheilostome bryozoans with smaller amounts of bivalves, calcareous sponges,

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brachiopods etc. The benthos reaches a clear maximum in Zone 4. A second very pronounced maximum is reached in Zone 10 in the bioherms, where bryozoans comprise almost 20% of the sediment. The chalk between the two maxima (Zones 7–9) is very poor in benthonic organisms.

The variations in the richness of the benthonic fauna are not only illustrated by the weight of the washing residue (approximately equal to the weight of the bryozoans), but are also seen in the number of brachiopod individuals per 10 kg of chalk (fig. 3). The two curves are almost parallel. This feature was previously observed in the Rügen chalk by STEINICH (1965).

The number-of-species curve is in part parallel to the two other curves but in the samples richest in benthos the number of species seems to decrease (this is most characteristic in Zone 4).

This phenomenon is found not only in the samples represented in fig. 3, but it seems to be a general principle that the number-of-species curve is roughly parallel to the number-of-individuals curve except in the samples very rich in benthonic organisms (fig. 14). These samples are dominated by a few species. The exclusion of some of the rare species is presumably due to interspecific competition.

Preservation

All fossils are extremely well preserved. The small fossils, as for instance the bryozoans, are especially well preserved with the most delicate structures and spines intact. Also the brachiopods are preserved with unbroken brachidia, and traces of wear are never found.

It is well known that in recent terebratuloid brachiopods the lophophore is supported by the brachidium and by mesodermal calcite spicules, which sometimes form a nearly coherent endoskeleton (SCHUMANN, 1970). Isolated spicules are described for a few fossil brachiopods (STEINICH, 1965, 1967 b, POPIEL-BARCZYK, 1968) but from the Rügen chalk STEINICH (1963 a, 1965) for the first time succeeded in finding complete spicular skeleton in fossil brachiopods. SURLYK (1970 a) described complete spicular skeletons in *Rugia tegulata* SURLYK, from the Danish chalk. Outside the north European chalk only one fossil brachiopod with complete spicular skeleton is known, viz. *Terebratulina wardenensis* from the Eocene London Clay (ROWELL & RUNDLE, 1967).

Steinich's discovery not only proved that fossil terebratuloids also were provided with spicules, but it permitted detailed description of the structure and form of the lophophore of these chalk brachiopods. Spicular skeletons from three Danish chalk brachiopods are shown on Pl. 1, 2.

In recent *Terebratulina* the spicules are often isolated, but in some species they form a continuous mesh in parts of the lophophore and mantle (SCHUMANN, 1970). When the animal dies the spicules of the mantle, body wall and median sides of the lateral arms of the lophophore disintegrate as the flesh decomposes. It is rare to find spicules at all in dead, dredged specimens of recent brachiopods (Dr. D. SCHUMANN, 1970, personal communication).

Transport

With very few exceptions, signs of current transport of the chalk fossils have not been found. Nevertheless, at two localities in the vicinity of Rørdal (fig. 1) a few specimens of parallel orientated *Baculites* and echinoid spines have been found, which might be referred to current action.

STEINICH (1967 a) showed that at a few horizons in the Rügen chalk very early diagenetic, submarine slides of soft chalk had occurred on the sea-bottom. In the Danish chalk traces of submarine slides can be found on the flanks of the bryozoan bioherms, where breccia-like structures occur.

As the chalk is highly bioturbated, practically all fossils have been shifted or rotated, but the movements seem to be only a matter of a few mm.

The very delicate, coherent spicular skeletons found in the chalk brachiopods described above (pl. 1, 2) indicate that no preburial transport of the brachiopods can have occurred and that the smaller brachiopods must have been buried in the sediment rapidly after or even before death.

The chalk sea bottom as substratum for brachiopods

The existence of brachiopods in a rock which must have accumulated as soft fine grained sediment on the sea bottom has often aroused interest among palaeontologists. Inspired by flume experiments of MENARD & BOUCOT (1951), ELLIOTT (1956) forwarded the hypothesis that these brachiopods might have been transported over rather long distances without being notably worn on the outside of the shell, and used as an example the occurrence of brachiopods in the English chalk.

AGER (1962, 1965) forwarded another hypothesis, namely that many of the small brachiopods found in the chalk could be epiplanktonic forms which lived attached to floating seaweeds of sargasso type.

Both hypotheses may explain isolated occurrences of brachiopods in fine grained sediments, but seem to be of rather limited value in explaining more regular occurrences. RUDWICK (1961), however, pointed out that many recent brachiopods are able to attach themselves to organic materials that will normally escape fossilization. As examples he mentioned ascidians, seaweeds, sponges and horny worm tubes.

The Danish chalk contains a very well preserved brachiopod fauna rich in species as well as individuals. The species composition is almost constant within each zone

Fig. 4. The chalk as substratum for brachiopods. The chalk yielded a number of substrates suitable for the brachiopods. The cocolithic mud in itself was a good substrate for burrowing brachiopods and for free living brachiopods of different shapes corresponding to different adaptive lines.

The numerous small hard objects (bryozoans, serpulids etc.) were excellent substrates for very small brachiopods or for brachiopods with a pedicle split into fine rootlets. Larger hard substrates (echinoids, belemnites etc.) were very rare on the chalk sea bottom and larger brachiopods with a normal functional pedicle are correspondingly extremely rare. Cementing brachiopods with small attachement surface are rather common, whereas forms with a large attachment surface are rare. RUDWICK (1961) mentioned a large variety of substrates which normally would not have been fossilized (e. g. algae, horny worm tubes, ascidians) and some of these have of course also played a role in the chalk sea. The fine grained nature of the chalk as well as the depth of the sea seems, however, to exclude sea-weeds as possible substrates.



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Fig. 4.

(fig. 2) and each species has a characteristic size-frequency distribution whereever it is found in greater numbers. Further the whole fauna is very well adapted to the chalk substratum where practically all the major niches seem to be occupied. Thus the fauna includes burrowing, free-living, cementing and pedunculate brachiopods. Therefore it is not necessary to invoke the hypotheses of ELLIOTT (1956) and of AGER (1962, 1965) to explain the occurrence of brachiopods in the Danish chalk.

In the chalk several major groups of substrates can be distinguished (fig. 4):

1. The fine grained chalk mud.

This substrate would normally be expected to be unsuitable for brachiopods. Nevertheless the chalk contains 1 burrowing species and 9 free living species well adapted to a life directly in or on the coccolithic mud.

2. Hard subjects.

As shown on p. 8 the chalk besides the coccoliths normally contains about 5-10% small bryozoans, bivalves, serpulids and other hard subjects in the size of a few mm. Large hard subjects such as oysters, echinoids and belemnites are much rarer. Correspondingly the chalk contains a great variety of very small brachiopod species which were able to use the small substrates and only a few large pedunculate species which were restricted to the rare large hard subjects.

3. Substrates which will escape fossilization.

This group has of course been of some importance as substrates for the pedunculate brachiopods. In all horizons of the chalk there is a remarkable parallelism between the number of brachiopods and the rest of the benthonic fauna especially the bryozoans. The "soft" substrates have probably followed the numerical variations of the rest of the benthonic fauna, but have presumably always been of minor importance. In this connection it must be mentioned that sea-weeds are unknown from the Danish chalk. The sea-bottom was not ideal for their attachment and the sea was probably too deep in the main part of the Maastrichtian Stage. Finally all accounts from the brachiopod literature as well as inspection of collections of recent brachiopods seem to show that brachiopods absolutely prefer attachment to hard subjects - predominantly stones or the mineral shells of other marine invertebrates.

Ecological groups

Based on their mode of life the chalk brachiopods can be divided into 4 groups (fig. 5):

I. Brachiopods attached to the substrate by means of a pedicle.

This group can be divided into 3 subgroups according to the nature and especially the size of the preferred substrate.

II. Brachiopods living free on the substrate.

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Terebratulina faujasii (Roemer) - 4.6 mm

Terebratulina longicollis Steinich - 5.2 mm

Rugia tenuicostata Steinich - approx. 3 mm

Terebratulina subtilis Steinich - 2.5 mm

Rugia acutirostris Steinich - 2.5 mm

Rugia tegulata Surlyk - 2.5 mm

Rugia spinosa Surlyk - 1.3 mm

Gisilina gisii (Roemer) - 5.5 mm

Gisilina jasmundi Steinich - 4.5 mm Dracius carnifex Steinich-approx. 4 mm

Aemula inusitata Steinich - 3.6 mm Scumulus inopinatus Steinich - 2,5 mm

Argyrotheca bronnii (Roemer) - 5 mm Argyrotheca conjuncta Steinich - 3.7 mm

Argyrotheca hirundo (Hagenow) - 4 mm Argyrotheca obstinata Steinich - 4 mm

Argyrotheca stevensis (Nielsen) - 2.5 mm

Argyrotheca bronnii s.l. (late form) - 5 mm Dalligas nobilis Steinich - approx. 5 mm

hard substrates: 3 species.

Neoliothyring obesg Sahni - 70 mm

Neoliothyrina fittoni (Hagenow) - 15 mm

Kingena pentangulata (Woodward) - 17 mm

Argyrotheca n. sp. aff. conjuncta-approx. 4 mm

I) ATTACHED TO THE SUBSTRATE BY MEANS OF A PEDICLE: 24 species.

a) Minute forms able to use very small substrates: 20 species

II) SECONDARILY FREE-LIVING FORMS, MEDIUM TO LARGE SIZED: 10 species.

Cretirhynchia limbata (Schlottheim) - 12 mm Cretirhynchia retracta (Roemer) - 25 mm Cretirhynchia sp. - approx. 30 mm Carneithyris subcardinalis (Sahni) - 45 mm Terebratulina gracilis (Schlottheim) - 13 mm Trigonosemus pulchellus (Nilsson) - 20 mm Gemmarcula humboldtii (Hagenow) - 20 mm Magas chitoniformis (Schlottheim) - 11 mm Meonia semiglobularis (Posselt) - 4 mm Thecidea pappilata (Schlottheim) - 10 mm

Lingula cretacea Nilsson - 8 mm

Isocrania barbata (Hagenow) - approx. 7 mm

b) Confined to large, hard substrates: 6 species.

Ancistrocrania tubulosa (Nielsen) - 8 mm Crania antiqua Defrance - 14 mm

Crania aff. craniolaris (Linnaeus) - 7 mm

Vermiculothecidea vermicularis (Schlottheim) - 12 mm

Thecidea recurvirostra Defrance - 7 mm

Bifolium wetherelli (Morris) - 4 mm

c) Attached directly to the sediment: 1 species.

b) Medium to very large sized forms confined to large,

Terebratulina chrysalis (Schlottheim) - 22 mm

Fig. 5. All brachiopod species found in the Danish chalk distributed on ecological groups. The approx. maximum length of each species, and a sketch is given together with the species name.

III. Brachiopods burrowing in the substrate.

IV. Brachiopods attached to the substrate by cementation of the ventral valve.

This group can be divided into 2 subgroups according to the size of the substrate. Biol. Skr. Dan. Vid. Selsk. 19, no. 2. $\mathbf{2}$

III) BURROWING FORMS: 1 species.

IV) ATTACHED TO THE SUBSTRATE BY CEMENTATION : 8 species. a) Attached to the very small substrates: 2 species.

Isocrania costata (Sowerby) - approx. 7 mm







I. Brachiopods attached to the substrate by means of a pedicle.

I.a. *Minute forms able to use very small, hard substrates.* Small Cancellothvridid brachiopods.

The following species are only separated by minor differences in shell sculpture and shape of the brachidium. They never reach a length above 5.5 mm and are therefore treated under the same heading. The greatest length of each species in the Danish chalk is added after the name of the species.

Terebratulina faujasii (ROEMER, 1841) – 4.6 mm. Terebratulina longicollis STEINICH, 1965 – 5.2 mm. Terebratulina subtilis STEINICH, 1965 – 3.5 mm. Rugia tenuicostata STEINICH, 1963 – appr. 3 mm. Rugia acutirostris STEINICH, 1965 – 2.5 mm. Rugia tegulata SURLYK, 1970 – 2.5 mm. Rugia spinosa SURLYK, 1970 – 1.3 mm. Gisilina gisii (ROEMER, 1841) – 5.5 mm. Gisilina jasmundi STEINICH, 1965 – 4.5 mm.

Terebratulina subtilis (fig. 6) and the species belonging to the genera *Rugia* and *Gisilina* only rarely dominate the brachiopod assemblages, but are nevertheless almost always found in some quantities.



Fig. 6. Growth stages of *Terebratulina subtilis* STEINICH (sample Hvidskud 9, Zone 4). a: 1.1 mm long, b: 1.7 mm long, c: 2.3 mm long, d: 3.1 mm long. All specimens drawn to scale.

Terebratulina faujasii (fig. 7) appears with a very varying frequency in the chalk. In the most samples it constitutes only a minor part of the brachiopod assemblage, but in the bryozoan rich horizons (Zones 4 and 10) it often occurs in enormous quantities (fig. 15 b, sample no. 3). In this species STEINICH (1965, p. 194) noted common asymmetrical growth combined with displaced spicular skeletons. Asymmetrical lophophores are sometimes met with among recent living brachiopods (e.g. ELLIOTT, 1958), and SCHUMANN (personal communication, 1970) has photographed an asymmetrical

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living brachiopod (*Platidia anomioides*) with displaced lophophore, which was caused by the attachement position close to the commisure of a *Spondylus*.

The distortion in the shell of *Terebratulina faujasii* is also common in the Danish specimens and similar distortions are found in several of the other species, e.g. *Terebratulina subtilis* and *Rugia tenuicostata*. The irregularities are due almost certainly to crowding on the very small available substrates—a theory substantiated by the fact that the distorted shells are in every case most common at the horizons very rich in benthonic life, where small brachiopods occur in thousands in each sample.



Fig. 7. Growth stages of *Terebratulina faujasii* (ROEMER) (sample Hvidskud 7, Zone 4). a: 1.0 mm long, b: 1.4 mm long, c: 2.2 mm long, d: 3.0 mm long. All the specimens are drawn to scale. Note the great similarity between the juveniles of this minute species and the juveniles of the larger *Terebratulina gracilis* (figs. 9 a, b).

Dracius carnifex Steinich, 1967 – approx. 4 mm.

In external appearance this species is very close to the terebratelloid brachiopods *Platidia* and *Megerlia* although as demonstrated by STEINICH (1967 b) it in fact represents a very unusual terebratuloid form. Nevertheless, *Dracius carnifex* seems to be specialized to the same mode of life as these two terebratelloid genera. The very irregular shell and the large amphithyrid foramen show that like e.g. the recent *Platidia anomioides* (see ATKINS, 1959) it lived with the dorsal valve pressed firmly against the substrate.

Aemula inusitata STEINICH, 1968 – 4.6 mm.

The mode of life demonstrated by *Dracius carnifex* is even more obvious in *Aemula inusitata* (Pl. III e, f, h). This species is close to the recent species of *Platidia* and *Amphithyris* and it is very difficult to distinguish between *Aemula inusitata* and the recent *Platidia anomioides*. The major differences are found in the development of the brachidium and the lophophore. In complete spicular skeletons of *Aemula inusitata* it can be seen that the lophophore is of exactly the same type as in *Amphithyris*, viz. a schizolophe (THOMSON, 1927). The lophophore of the recent species belonging to *Platidia* has reached a more complex stage of development. Thus *Platidia anomioides* has an early plectolophe (ATKINS, 1959).

According to ATKINS, living *Platidia* press their dorsal valve firmly against the substrate. Individuals of *P. anomioides* which settle on larger, more even substrates e.g. oysters, have a regular, symmetrical shell in contrary to the individuals that settle on small irregular substrates like e.g. bryozoans and corals. A similar difference in shape is found in specimens of *Aemula inusitata* from the chalk. This species is extremely variable in shape and there is a tendency for the most irregular forms to occur at horizons richest in benthos (Zones 4 and 10), whereas the regular forms dominate in the chalk of Zones 7 and 8, which is poor in small substrates (fig. 3).

Scumulus inopinatus STEINICH, 1968 – 3.5 mm.

Dalligas nobilis STEINICH, 1968 – 5 mm.

These two species are very small and show a remarkable frequency distribution. They are either represented by a few individuals or they dominate the assemblage completely (e.g. Hvidskud samples 7 and 18, fig. 14). Moreover, the two species, which are very much alike morphologically seem to substitute each other. Thus in sample 7 (fig. 14) 442 individuals of *S. inopinatus* were found, comprising 12.7% of the total number of brachiopod individuals, whereas *D. nobilis* was missing. On the other hand, in sample 18 (13 m below sample 7), *D. nobilis* was found in enormous quantities, 886 individuals comprising 73.2% of the total number of brachiopod individuals, whereas only 14 individuals (1.2%) of *S. inopinatus* were found.

D. nobilis is rather constant in shape in contrast to S. inopinatus which displays a considerable morphological variability. This great variability of S. inopinatus together with is amphithyrid foramen suggest a similar mode of life to that of the *Platidia* species i.e. with the dorsal valve pressed against the substrate.

Argyrotheca bronnii (ROEMER, 1841) – 5 mm. Argyrotheca hirundo (HAGENOW, 1842) – 4 mm. Argyrotheca obstinata STEINICH, 1965 – 4 mm. Argyrotheca stevensis (NIELSEN, 1928) – 2.5 mm. Argyrotheca coniuncta STEINICH, 1965 – 3.7 mm. Argyrotheca n. sp. aff. coniuncta – approx. 4 mm. Argyrotheca bronnii s.l. – late form – 5 mm.

The 7 species of *Argyrotheca* found in the chalk are only separated by minor differences in number and shape of the ribs, profile of the median septum, general outline etc. However, they have the same size and general morphology and are considered to have had approximately the same mode of life.

The recent species of *Argyrotheca* are closely related to the chalk species. As they have a short pedicle and sit almost perpendicular to the substrate (Pl. III, a, g) their beaks suffer attrition (ATKINS, 1960). Attrite beaks are common also in the chalk species. The lophophore and the feeding mechanisms of the recent megathirids (to which *Argyrotheca* belongs) are described in detail by ATKINS (1960) and because of the

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great morphological similarity between the fossil and recent *Argyrotheca* there can be little doubt that the two groups lived in the same way.

Substrates used by recent *Argyrotheca* include the ahermatypic corals *Lophelia* and *Dendrophyllia*, solitary coral thecae and crustaceans (ATKINS, 1960), algae (RUD-WICK, 1962), other brachiopods (DAVIDSON, 1880), bryozoans, worm tubes and shell gravel. Recent species of *Argyrotheca* are shallow water forms normally not found below 200 m depth (U. ASGAARD, 1971, personal communication).

Ib. Medium to large sized brachiopods confined to large, hard substrates. Neoliothyrina obesa SAHNI, 1925 – approx. 7 cm.

This species is by far the largest brachiopod in the chalk. The shell is thin and the pedicle opening is labiate and about 3 mm wide, suitable for a normal, functional pedicle. The surroundings of the pedicle opening are often strongly worn showing that the pedicle was short and the shell thus pressed closely against the substrate.

Neoliothyrina fittoni (HAGENOW, 1842) - 1.5 cm.

Kingena pentangulata (WOODWARD, 1833) - 1.7 cm.

These two species are medium sized and are provided with a pedicle opening of "normal" size allowing the passage of a functional pedicle.

All three species belonging to this group are very rare, those of *Neoliothyrina* being the rarest in the Danish chalk. This rarity can no doubt be correlated with the rarity of suitable large hard substrates e.g. echinoids, oysters, belemnites etc.

I.c. Medium sized brachiopods attached directly to the sediment.

The only species which almost certainly has lived attached directly to the sediment by a root-like, divided pedicle is *Terebratulina chrysalis* (SCHLOTTHEIM, 1813) – 2.2 cm. This mode of life is well known from its close recent relatives *Terebratulina retusa* (L_{\cdot}) and Terebratulina septentrionalis Couthoux (Pl. IV, a, d, e, and EKMAN, 1896, SCHUMANN, 1969). In these brachiopods the pedicle is able to etch slender holes or furrows in foraminifera, small fragments of shells, bryozoans etc. This feature of the pedicle of articulate brachiopods has possibly developed independently in different groups (SCHUMANN, 1969), and AGER (1965) proposed this attachment type for Cretaceous terebratulinids. Nevertheless, AGER (1965 p. 160) mentioned a specimen of Terebratulina cf. chrysalis from Czekoslovakia which had a "snowshoe-like" frill comparable to the frill by some Atrypids (COPPER, 1967) indicating a completely different mode of life. As the shell of adult specimens of T. chrysalis is very thin, the species is often found with the anterior part of the shell compressed as a result of compaction under the burden of overlying sediment and in that way a "frill" could be developed diagenetically. Pl. IV b shows a slightly compressed specimen with a thickness of hardly 1 mm where its normal thickness before compression is approximately 3 mm. Thus there



Fig. 8. Variation in the pedicle of recent *Terebratulina relusa* (L.). The specimens are drawn to scale. The length of the largest specimen (d) is 13 mm.

seems to be no evidence of a snowshoe-like frill to suggest a free living mode of life for this species in the Danish chalk.

Two different lines of evidence suggest the mode of life of *T. chrysalis*: Studies of its occurrence in the sediments and comparison with living relatives.

Terebratulina chrysalis is the only Danish chalk brachiopod which was found in all samples from all localities and it is almost the only species which occurs also in marginal facies e.g. the near-shore carbonate sediments in Scania (Sweden). Moreover, the species is a member of a morphologically very stable group which started in Ceno-

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manian and continued through the Tertiary to recent times (*T. retusa* and *T. septentrionalis* are the recent representatives). This indicates that the group is very tolerant and only little specialized compared to the other chalk brachiopods. In detrital carbonate siltstones of Danian (Lower Paleocene) age *T. chrysalis* is found in beds where there are practically no larger fossils as potential substrates. It is also rather common in parts of the Danish chalk which consists almost solely of coccoliths and small foraminifera (Zone 7) and with extremely few larger fossils. These observations indicates that *Terebratulina chrysalis* was able to attach itself to almost all kinds of available substrates.

Comparison with the recent *Terebratulina retusa* (fig. 8 and pl. IV a-e) shows that the two species are very close relatives differing only in minor details of the rib pattern, *T. chrysalis* having coarser and more sculptured ribs. (On pl. IV the ribs of *T. retusa* appear deceptively smooth, because the specimens are overgrown with a thin sponge layer. Thus the difference in morphology is even smaller than indicated by the figure). Apart from the rare *Neoliothyrina obesa*, *N. fittoni* and *Kingena pentangulata*, *Terebratulina chrysalis* is the only larger chalk brachiopod with a normal pedicle opening, which surrounded a functional pedicle. As shown above, the three first mentioned species are extremely rare in the chalk in sharp contrast to *T. chrysalis*. Their pedicles were probably not split up into fine rootlets and they were thus restricted to large substrates, while *T. chrysalis*, on the contrary was able to settle down almost everywhere on the soft Cretaceous sea bottom independant of such restrictions.

Terebratulina chrysalis is not only found in all samples, but is by far the most common brachiopod in the Danish chalk. The sea bottom, sometimes a pure coccolithic mud, at other times rich in a great variety of small shells (bryozoans, foraminifera, serpulids, brachiopods etc.), seems to have been an excellent biotope for *T. chrysalis* due to its low degree of specialization and correspondingly high adaptibility.

The great variability of the pedicle of the recent *T. retusa* is shown in fig. 8. There seems to be a tendency for the pedicle to split up more finely in response to finer substrates. The manner in which it may be split varies more than normally accepted.

The pedicles of the small Cancellothyridid brachiopods (group Ia) were probably also split into fine rootlets, as in recent *Terebratulina*, but this is more difficult to prove than for *T. chrysalis*.

II. Free living brachiopods.

The second group comprises species which, as adults, lie unattached on the sea bottom. All the species belonging to this group, except *Thecidea pappilata*, were attached to the substrate in the young stages by means of a pedicle. At the early ontogenetic stages the brachiopods had the same general shape as the terebratulinid brachiopods of group I a, i.e. longer than wide and biconvex, with normal pedicle openings. But during ontogenetic growth (figs. 9, 10) the pedicle openings were closed by secondary shell or at least narrowed to a "pin hole foramen". Furthermore, in 6 (7) of the species there was a very characteristic tendency towards a hemispherical shape in late ontogenetic stages (fig. 11). This shape is not very common among Mesozoic brachiopods and is

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here developed in a group of species which are not closely related. The hemispherical shape would seem to be ideal for a free-living brachiopod (fig. 4) and it is remarkable that this shape is not found among the brachiopods provided with a functional pedicle (group I and III).

Cretirhynchia limbata (SCHLOTTHEIM, 1813) – 12 mm.

Cretirhynchia retracta (Roemer, 1841) – 25 mm.

Cretirhynchia sp. – 30 mm (figured as Rhynchonella limbata by NIELSEN, 1909 pl. 1, figs. 24, 25).

STEINICH (1963 c) showed that the pedicle opening of *Cretirhynchia retracta* was closed from the inside by a hollow, conical plug. In addition, the pedicle openings of all three species are closed by secondary shell.

Cretirhynchia sp. seems to be especially well adapted to the free living mode of life as the lateral parts of the shell are considerably expanded.

Carneithyris subcardinalis (SAHNI, 1925) – approx. 45 mm.

The pedicle opening of this species is closed during ontogeny by secondary shell. It is the only common large brachiopod in the chalk and morphologically it seems to fit well with one of the ideal shapes of a free living brachiopod i. e. a self-righting "tumbler" (Fig. 4). It is strongly biconvex to almost spherical and thin-shelled except for the posterior part of the shell where the cardinalia are thickened by secondary shell, especially in adult specimens. The thickening is not sufficient to keep the shell in a permanent position on the sea bottom. However, the posterior position of the centre of gravity ensures that the commisure is always kept free of the sediment surface. This inferred mode of life explains the abundance of the species at all horizons of the chalk in spite of its large size, and irrespective of the presence of larger substrates.

Terebratulina gracilis Schlottheim, 1813 – 13 mm.

The juveniles of *T. gracilis* are very difficult to distinguish from juveniles of the small *Terebratulina* species of group I (figs. 6, 7, 9) but at a length of a few mm the shells begin to approach the final hemispherical shape. The pedicle opening is not closed, but very narrow, and this combined with the incurved umbo (figs. 9, 11) would seem to reduce the likelihood of attachment by a pedicle. Stratigraphically slightly older forms of the *Terebratulina gracilis* group (e.g. forms found in the lowermost Maastrichtian and Upper Campanian of England) have a more biconvex shape and the evolution towards a perfectly hemispherical shape does not appear to have been completed until early Maastrichtian time.

Trigonosemus pulchellus (NILSSON, 1827) – 20 mm. Gemmarcula humboldtii (HAGENOW, 1842) – 20 mm.

The pedicle opening in adults of T. pulchellus (figs. 10, 11) and G. humboldtii were closed with secondary shell. The shape is not completely hemispherical in G. hum-



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Fig. 9. Growth stages of Terebratulina gracilis (SCHLOTTHEIM) (sample Rordal 4, Zone 7). a: 1.4 mm long, b: 2.1 mm long, c: 4.8 mm long, d: 10.7 mm long. The specimens are not drawn to scale.



Fig. 10. Growth stages of *Trigonosemus pulchellus* (NILSSON) (sample Hvidskud 5, Zone 5). a: 0.9 mm long, b: 1.5 mm long, c: 2.0 mm long, d: 1.9 mm long, e: 2.9 mm long, f: 5.1 mm long, g: 14.2 mm long. Except f and g, all the specimens are drawn to scale.



Fig. 11. Hemispherical free living brachiopods belonging to group II. a: Meonia semiglobularis (POSSELT), b: Magas chitoniformis (SLOTTHEIM), c: Thecidea pappilata (SCHLOTTHEIM), d: Gemmarcula humboldtii (HAGE-NOW), e: Terebratulina gracilis (SCHLOTTHEIM), f: Trigonosemus pulchellus (NILSSON). The specimens are not drawn to scale.

boldtii, the dorsal valve being flat-convex, but the shape of this species varies considerably. *T. pulchellus* is almost perfectly hemispherical and like *Terebratulina gracilis* its Campanian predecessors have a more biconvex shape (e.g. *Trigonosemus elegans* KOENIG).

Magas chitoniformis (SCHLOTTHEIM, 1813) – 11 mm.

M. chitoniformis is reminiscent of *Terebratulina gracilis* in several ways. Juveniles are extremely difficult to distinguish from small individuals of some of the brachiopods belonging to group I a, viz. *Dalligas nobilis* and *Scumulus inopinatus* and the adults are almost perfectly hemispherical (fig. 11). Furthermore, the pedicle opening is not closed but is narrow and more or less hidden by the umbo which is often strongly incurved (fig. 11).

At horizons where conditions for the small brachiopods (group I) deteriorated, *Magas chitoniformis* and *Terebratulina gracilis* become increasingly dominant (fig. 15 a) and together with *Terebratulina chrysalis* they are in many cases the only species found. This is especially characteristic in the upper part of the section at Hemmoor (north Germany) where the diverse brachiopod fauna gradually disappears upwards corresponding to coarsening of the sediment (F. SCHMID, 1969, written communication) to leave a limited, but individualrich, fauna dominated by *M. chitoniformis* and *T. gracilis*.

Meonia semiglobularis (POSSELT, 1894) – 4 mm.

M. semiglobularis is smaller than the rest of the brachiopods in the group, but nevertheless attains a perfectly hemispherical shape (fig. 11). The pedicle opening is not closed, but extremely narrow and often covered by the incurved umbo. The species is thick-shelled, perhaps for reasons of stability.

Thecidea pappilata (SCHLOTTHEIM, 1813) – 10 mm.

T. pappilata occupies an intermediate position between groups II and IV, since in the young stages it is cemented to the substrate. However, the attachment area is very

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small and impression of small bryozoans are found in only a few cases. Nevertheless, the very small substrates and its hemispherical shape (fig. 11) indicate that the species lived free on the bottom.

III. Burrowing brachiopods.

The third group includes only one species, *Lingula cretacea* LUNDGREN, 1885. The species is small (8 mm in max. length) and very thin-shelled but not uncommon. However, owing to the fragility of its shell, it is found only rarely in the washed samples. There is no direct evidence for the burrowing mode of life in this case, but this seems to have been a characteristic activity of the family since early Palaeozoic time (CRAIG, 1952).

In the palaeoecological literature, lingulids are normally described as near-shore animals capable of surviving occasional brackish conditions, but according to JONES & BARNARD (1963) the recent lingulid brachiopod *Glottidia albida* reaches its peak of abundance at about 34 m depth in a sediment of compact fine sand mixed with coarse silt.

IV. Brachiopods attached by cementation.

This group comprises brachiopods that live attached to the substrate by cementation of the ventral valve. The group can be divided into 2 subgroups based on the size of the substrate.

IV a. Two species, *Isocrania costata* (SOWERBY, 1823) – 7 mm and *Isocrania barbata* (HAGENOW, 1842) – 8 mm have very small attachment surfaces. In *Isocrania costata* this surface is almost invisible and the species in fact occupies a position intermediate between the cemented and the free living forms. Its shape is very close to one of the ideal forms of a free living brachiopod, i. e., discoid (fig. 4). The species is rather common at all horizons, especially where the sediment contains only a few larger substrates e.g. in the Rørdal section (fig. 15 a). Thus the larva seems to have settled on bryozoans and other small objects and as the brachiopod grew, its discoid shape allowed it to become totally independent of this substrate, and to live free on the sea bottom.

Isocrania barbata has a larger attachment surface and is very rare.

IVb. Crania antiqua DEFRANCE, 1818 – 14 mm. Crania aff. craniolaris (L., 1758) – 7 mm. Crania tubulosa NIELSEN, 1909 – 8 mm. Thecidea recurvirostra DEFRANCE, 1828 – 7 mm. Vermiculothecidea vermicularis (SCHLOTTHEIM, 1913) – 12 mm. Bifolium wetherelli (MORRIS, 1851) – 4 mm.

The 6 species belonging to this subgroup are rare and are normally not found in the washing residues, as they are cemented to large, hard substrates, especially irregular echinoids. The size of the attachment surface of *Thecidea recurvirostra*, however, seems



Fig. 12. Lower Maastrichtian brachiopod assemblage.--It has not been attempted to reconstruct the ancient sea bottom, but only to show the morphological adaptations to the different substrates of the brachiopods found in this part of the succession.--The sketches of the substrates here and in fig. 13 are based on actual specimens found in the chalk. 1: Trigonosemus putchellus (NILSSON), 2: Aemula inusitata STEINICH, 3: Draeius carnifex STEINICH, 4: Terebratulina faujasii (ROEMER), 5: Gisilina gisii (ROEMER), 6: Neoliothyrina obesa SAHNI, 7: Bifolium wetherelli (MORRIS), 12: Carneithyris subcardinalis (SAHNI), (shown in one of many possible positions), 13: Argyrotheca bronnii (ROEMER), 14: Tererbatulina chrysalis 8: Terebratulina longicollis STEINICH, 9: Scumulus inopinatus STEINICH, 10: Isocrania costala (SowERBY), 11: Argyrotheca hirundo (HAGENOW), (Schlottheim), 15: Argyrotheca conjuncta Steinich, 16: Vermiculothecidea vermicularis (Schlottheim), 17: Magas chitoniformis (Schlottheim), 18: Rugia tenuicostata Steinich, 19: Lingula cretacea Nilsson, 20: Cretirhynchia retracta (Roemen).—The substrates comprise bryozoans, an is? Rugia tenuicostata Steinice and a siliceous sponge.


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to be variable and in some specimens it is not visible at all. This last variety must have been free living and its dorsal valve is correspondingly flat, giving a hemispherical shape although with a very large incurved umbo (fig. 13).

The 3 *Crania* species are all attached with nearly the whole surface of the ventral valve. All species show a very characteristic geotropic orientation on the substrate (SCHMID, 1949).

Distribution in the sediment

The small brachiopod species dominating the chalk brachiopod fauna seem to have a rather random distribution in the sediment. If a 10 kg chalk sample is divided into smaller samples of very varying size (down to 20–50 g) each partsample normally contains representatives of almost all the species found in the large samples. The number of species decreases markedly in samples of less than 100–200 g. The number of individuals is not so closely correlated with sample size as is the number of species.

Patchy distribution of brachiopods has been described very often in the literature (e.g. HALLAM, 1962, RUDWICK, 1965, 1970); each individual nest of brachiopods is normally comprised of one species. It is remarkable, however, that the small chalk brachiopods are apparently randomly distributed and that local concentrations, correlated with local concentrations of bryozoans and other small potential substrates, are never monospecific but display the same quantitative composition as the whole population contained in the sample.

These features are well documented from washing numerous small samples, e.g. core samples from borings. Another technique is further used in combination with the washing of samples of different size to give a more detailed picture of the spatial distribution of the brachiopods. Small orientated blocks of chalk (e.g. $10 \times 10 \times 10$ cm) are cut out with a saw. As described above the chalk consists of numerous small fossils (bryozoans etc.) embedded in a soft groundmass composed mainly of coccoliths. This groundmass is selectively removed by use of an "Airbrasive unit" (the method is described by Spreng, 1962) with which the block is methodically dissected. When a few mm of groundmass have been removed the remaining harder fossils stand free of sediment. The position of any brachiopods exposed are measured relative to one of the corners of the block and the brachiopod is determined to species. When the positions have been measured the sediment-free fossils are removed and the abrasion is continued. The method is very time consuming, because the speed of the sand-beam must be rather low in order not to damage the larger fossils. Nevertheless, this technique yields so much complementary information on the structure of the chalk that it is much recommended. In thin sections, on ground surfaces, on replicas or on X-radiographs the rock is only seen in two dimensions. From the washing residues the form and size of the larger constituents of the rock are known. But the orientation of these constituents can only be studied by methodical dissection with an "Airbrasive unit".

Throughout most of the Danish Maastrichtian chalk the orientation of the bryozoan stems and other small fossils are almost completely random and they seem to be

preserved very close to the place where they lived. At the most they have been moved only a few mm by bioturbation except those which occur in the fill of larger burrows. Only in Zone 10 in the bryozoan bioherms are the stems of the small bryozoans found to be orientated more or less parallel to the surface of the bioherms. Nevertheless, no signs of wear are found on the fossils in the bioherms and the orientation might be explained by the assumption of a reduced coccolith sedimentation. This is supported by the evidence of total interruption of sedimentation at an initial hardground (fig. 3) immediately below the bioherms and at the complex Maastrichtian-Danian hardground topping the bioherms at Stevns Klint.

The distribution of the brachiopods in the sand-blown blocks confirms the distribution inferred on basis of the washed samples. A statistical treatment is not possible due to the rather limited number of brachiopods contained in each block. (It is not possible to prepare larger samples because of the size of the airbrasive unit).

Contrary to the small brachiopods, the larger brachiopods are sometimes found in small aggregations composed of one to three species. Owing to their rarity, the larger brachiopods are normally collected as isolated specimens, but at some horizons they are found in greater quantities. There is a very pronounced correlation between aggregations of larger brachiopods and absence of potential substrates. The aggregations are thus found almost exclusively in the chalk of Zones 7–9 where the benthonic fauna is reduced (fig. 3). The small brachiopods were well adapted to the bryozoan rich chalk sea bottom and, where the bryozoans were less important or totally absent, the small brachiopods with their great juvenile mortality were not able to survive (figs. 16, 17, 18). The larger brachiopods, dominated by the hemispherical species, all had insignificant juvenile mortality rates (see p. 40) probably due to a rapid initial growth rate. In their early stages they had a functional pedicle, and were thus capable of settling on hard substrates. If only a few larvae succeeded in settling they passed the dangerous juvenile stages rapidly due to high initial growth rate and assumed their free living mode of life and may thus have functioned as substrates for other brachiopods. This may explain the dominance of aggregation of hemispherical brachiopods in environments where the remaining brachiopod fauna has disappeared.

Quantitative variations in the brachiopod fauna

Figs. 14 and 15 a, b show quantitative diagrams for three important Danish chalk sections. Hvidskud (Møns Klint) includes the boundary between the lower and the upper part of Lower Maastrichtian i.e. Zone 4/Zone 5 (BIRKELUND, 1957, SURLYK, 1970 b). Rørdal includes the the Lower-Upper Maastrichtian boundary (SURLYK, 1970 b) and Karlstrup includes the Maastrichtian-Danian boundary. Moreover, the three sections are good representatives for each of the three main ecological units described on p. 12. In Hvidskud the horizons below the hardground are very rich in benthonic animals (fig. 14). Upwards the fauna decreases to reach a pronounced minimum in the Rørdal section (fig. 15 a). At Karlstrup the Maastrichtian is topped by small, slightly asymmetrical bioherms yielding profuse benthonic faunas.







Fig. 15. a: The quantitative distribution of the most important brachiopods in the Rordal section. The lithology is not shown as it comprises uniform white chalk without flint. Only at the top of the section two thin marl layers occur. b: The quantitative distribution of the most important brachiopods in the Karlstrup section.

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The specific composition of the brachiopod fauna is rather constant for each zone, but the abundance of each species is very variable. The quantitative distributions of the most important brachiopods in the Hvidskud section is shown in fig. 14. There is a close agreement between the curve showing the weight of the washing residues (more or less equivalent to the quantity of bryozoans) and the curve illustrating the total number of brachiopod individuals. The number of species is rather constant but follows more or less the two other curves except for the samples richest in individuals, where the number of species decreases (most notably in sample 7). A closer examination

the frequency curves of each species reveals that only a few species follow the "bryozoa-curve". This is the case with *Terebratulina chrysalis, Terebratulina faujasii, Argyrotheca bronnii* and to a smaller degree *Scumulus inopinatus*. On the contrary, *Dalligas nobilis* is rather unimportant in the main part of the section except for sample 26 and especially sample 18 where it outnumbers all the other species.

The correlation between the washing residue curve (i.e. the benthos curve) and the number of individuals curve is remarkable. STEINICH (1965) found a similar accordance in the Rügen chalk.

The parallelism of the curves is mainly primary, the bryozoans and the other small benthonic animals playing the role of substrates for the brachiopods, and is only to a small degree secondary, due to variations in the pelagic sedimentation.

Diversity of the brachiopod fauna

a. Diversity indices.

The concept of diversity and of diversity indices have been much used in ecological studies. Diversity understood as simple species diversity, has been used very often to characterize a fauna or a succession of faunas. The species diversity is sometimes modified so that rare species (e.g. comprising less than 5% of the total number of individuals) are omitted.

As mentioned by AGER (1963 p. 235): "mere numbers of species in themselves are not an adequate ecological guide, however, for obviously a flora of three species may be quite as dense as one of fifty". To compensate for this, different diversity indices have been constructed e.g. $\text{sp}/\sqrt{\text{ind.}}$ (MENHINICK, 1964), sp/\log ind. (ZIEGLER et. al. 1968). In these simple indices the total number of individuals are compared to the number of species, but nothing is inferred about the relative importance of each species. Thus 10 spp totalling 100 individuals, where each species comprises 10 individuals give the same index as where 1 species comprises 91 individuals and the rest of the species are each represented by 1 individual. SIMPSON (1949) suggested the formula $\frac{N(N-1)}{\Sigma n(n-1)}$ where N is the total number of individuals and n is the number of individuals in each species. In this formula the relative frequency of each species is included. Thus the last mentioned example gives $\frac{100 \times 99}{(10 \times 9) \times 10} = 11$ in the first case and $\frac{100 \times 99}{91 \times 90} = 1.2$ in the second. A thorough review of different diversity indices including the so-called FISCHER's α -index was given by MURRAY (1968). The rather teoretical α -index gives good results in recent lagoonal sediments, but seems to be somewhat too elaborate to be used in older rocks.

b. Application to the chalk brachiopod populations.

An important disadvantage of the formula of SIMPSON (1959) and most other comparable formulas is that they are almost impossible to use when the populations are not of approximately the same size. Thus, a sample from Zone 7 with few species each represented by a few individuals will have a greater diversity index than a sample from e.g. Zone 5 with more species many of which are represented by great numbers of individuals, because no species plays a really dominating role in the Zone 7 sample. Formulae of this kind are therefore considered to be of little value in palaeoecological studies based on bulk samples or on square counts.

As it is equally important to know the density as it is the diversity of the fossil fauna, formulae based on counts of equal numbers of specimens must be avoided. We must therefore return to the more simple formulae where the relative importance of the different species is not taken into consideration.

As the total number of species is not usually related linearly to the total number of individuals, but rather, the chance of collecting a new species decreases as sampling increases, MENHINICK (1964) sought a ratio (index) of species to individuals which would be constant for samples of different sizes. He considered sp/\sqrt{ind} . usable while sp/\log ind., $sp-1/\log e$ of ind., and $\log sp/\log$ ind. were considered inappropriate. Nevertheless, for use on the chalk brachiopods the sp/\sqrt{ind} . diversity index was found to be no more useful than MENHINICK's other indices. Thus the very poor faunas from the middle part of the Maastrichtian (Zone 7) e.g. Rørdal (fig. 15 a) give higher diversity indices than the very rich samples from Zone 4 e.g. Hvidskud (fig. 14). The number of species compared to the percent frequency of the most important species gives a more precise picture of the diversity of the investigated fauna and is used here in figs. 14 and 15.

Dominant, accessory and rare species

It is clear from figs. 14, 15 a, b that the different species have different frequency patterns. Some species represented by *Terebratulina chrysalis* and *Argyrotheca bronnii* are present in almost all samples and dominate the fauna. Other species represented by *Terebratulina faujasii* dominate in a few samples but are otherwise rare or totally absent.

A third group of species represented by e.g. *Isocrania costata*, *Carneithyris subcardinalis* and *Aemula inusitata* are present in the majority of samples in small but rather constant numbers and never dominate. Finally, there is a group of species, represented by e.g. *Kingena pentangulata*, which are found in a minority of the samples and always in small numbers. A statistical treatment of this subject would be interesting, but has been avoided since not all samples are comparable from a statistical point of view, and since many of the species only have a limited vertical distribution in the succession.

Size-frequency distribution

a. Premises.

The construction of size-frequency distributions is a mush used technique in palaeoecological studies. Nevertheless the evaluation of the histograms is dubious in many earlier publications. The most common mistake is to compare the size-frequency distribution of a fossil assemblage directly with a survivorship curve. Further, the shape of the histograms is used to determine the nature of the assemblage, that is, if the assemblage is residual or if it is a so-called life assemblage (Boucot, 1953) or fossil community (FAGERSTROM, 1964) etc.

A firm basis for work on size-frequency distributions of fossil assemblages was first established in the very important paper by CRAIG & OERTEL (1966). Here, a clear distinction was drawn between the living and the resulting dead population. These authors emphasized (op. cit. p. 349) that the size-frequency distributions of living and dead populations of organisms in these steady-state experiments depend on five factors. These were: 1) the length of the period(s) of annual recruitment, 2) the growthrate and its coefficient of variation, 3) the period of cessation of growth, 4) the mortality rate and 5), on which the shape of the histograms primarily depends, the interplay between the growth-rate and the mortality rate.

It is therefore evident that the shape of the size-frequency distributions can be used in only a few cases as a criterion of the nature of the investigated population. A strongly right (= positively) skewed curve will normally be indicative of the presence of a fossil community (sensu FAGERSTROM, 1964), but on the other hand a bellshaped curve might equally represent a fossil community.

The use of the shape of the size-frequency distributions as criteria for different kinds of fossil assemblages is a reversal of cause and effect. As a consequence of the results obtained by CRAIG & OERTEL (1966) it is necessary to establish the nature of the fossil assemblage before the size-frequency distribution can be interpreted. The life history of an organism from birth to the time of death and its subsequent burial is ably summarized by HALLAM (1967). Among the most important post mortal factors modifying the structure of the fossil community may be mentioned: sorting by currents, size-selective crushing and diagenetic dissolution of certain size classes. Dissolution of small, thin shells is often mentioned in the literature as an important modifying factor, e.g. FAGERSTROM, 1964, HALLAM, 1967. However, it should be emphasized that in the chalk the shells are better preserved the smaller they are and that dissolution only occurs in very large fossils e.g. the anterior part of the 5–7 cm long *Neoliothyrina obesa*.

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b. Size-frequency distributions of the chalk brachiopods.

Size-frequency histograms are constructed for all species found in three chalk samples (figs. 16, 17, 18). Sample Hvidskud 9 is representative for the lower benthosrich part of the chalk (figs. 3, 14). No samples from Zone 6 and 7 have been investigated because of the small number of individuals found at these horizons. Sample Lindholm 8 belongs to Zone 8 and sample Karlstrup 2 is representative of the upper benthos-rich part of the chalk (figs. 3, 15).

Before the ecological evaluation of the size-frequency distributions can begin, several controls must be made:

1) It is of great importance to determine if any size-selective transport, crushing or solution has taken place. As shown on p. 13, these agents are of no importance in the Danish chalk.

2) It must be ascertained that each sample has been deposited under stable conditions, as the brachiopod population contained in the sample is a sum of many generations. If conditions are stable the shape of the size-frequency distributions will remain constant, irrespective of the number of generations added to the population. From the inspection of the size-frequency distribution of the same species from numerous samples of all sizes from all horizons of the Danish chalk, it is evident that each species has its own distinct size-frequency distribution. Thus the shape of the histograms are results of factors characteristic for the biology of each species and not of changes in sedimentation rate etc.

3) Finally it is of great importance that the taxonomy of the fauna is well known and that it is possible to determine juvenile specimens with absolute certainty. In many ecological papers published in recent years the fossils are only identified to a rather high taxonomical level. This may be useful in the first broad grouping of localities but has only little ecological significance. A detailed and profound knowledge of the taxonomy at species or subspecies level is necessary before a study of size-frequency distributions, species-frequency diagrams and morphological adaptations can be attempted.

c. Types of size-frequency distributions.

In figs. 16, 17 and 18 all species contained in each sample are size-frequency measured to present a view of the whole fauna. Nevertheless, it is evident that only the histograms of the more common species have any value in the population studies.

From only a superficial view of the histograms it is seen that in all the more common species the populations are dominated by large quantities of juvenile individuals. In *Terebratulina faujasii* (fig. 16) only about $3^{0}/_{0}$ of the population exceeds $1/_{2}$ the size of an adult individual. This is even more clearly the case in *Terebratulina chrysalis* (fig. 16). This species reaches an adult length of about 2 cm, but except for one specimen all 235 individuals found in the sample are under 4 mm in length.

This right (= positively) skewed type of distribution is found in all the common species in the three measured samples. Most of the histograms have quite gentle slopes



Fig. 16. Size-frequency diagrams of the species found in sample Hvidskud 9 (Fig. 14, Zone 4). The number of individuals (N) of each species is in some cases somewhat smaller than the corresponding number on fig. 14 as some of the specimens were too damaged to be measured.—*Cretirhynchia* sp. includes all rhynchonelloid specimens found in the sample as it is impossible to distinguish between juveniles belonging to the three *Cretirhynchia* species found in the chalk. They are nevertheless measured to give a clear picture of the size distribution of all brachiopods found in the sample. The following species have been omitted due to small number and bad preservation: *Isocrania costata* (SOWERBY), *Isocrania barbata* (HAGENOW), *Gisilina gisii* (ROEMER) and a dubious *Terebralulina gracilis* (SCHLOTTHEIM). Abscissa is length of pedicle valve in mm, ordinate is number of individuals.

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Fig. 17. Size-frequency diagrams of the species found in sample Lindholm 8 (Zone 8). The remarks in the legend to fig. 16 are also valid here. The following species have been omitted due to small numbers and bad preservation: *Terebratulina gracilis* (SCHLOTTHEIM), *Rugia tegulata* SURLYK, *Scumulus inopinatus* STEINICH, *Vermiculothecidea vermicularis* (SCHLOTTHEIM).

and secondary peaks are only rarely seen. This is of course partly a function of the chosen class-boundaries, but the formation of the fossil populations by summing of many generations will also have a smoothing effect on the distribution. From inspection of the three figured samples and many other samples it is seen that, where they are common, all the small pedunculate brachiopods (group I a, fig. 5) have strongly positively skewed distributions.

The size-frequency distributions of the burrowing and the cemented brachiopods (group III and IV, fig. 5) as well as of the large brachiopods of group I b are unknown because these brachiopods were only rarely found in the samples.

The hemispherical free living brachiopods (group II) are normally quite rare, but where they are common they show a size-frequency distribution quite different from the remarkably uniform, positively skewed histograms of the small pedunculate brachiopods.

The size-frequency curves of the hemispherical brachiopods (notably *Magas* chitoniformis, Terebratulina gracilis and Trigonosemus pulchellus) are in some cases almost bell shaped or in a small number of cases negatively (= left) skewed, but never right skewed with an overweight of juvenile individuals. The most common histograms are those with a concentration of forms which have reached the final adult shape but not the maximum size of the species.

The great difference in size-frequency distributions among two ecologically very different groups of brachiopods makes it possible to draw some important conclusions on the biology of two groups. The species belonging to group II are not taxonomically closely related. On the other hand, juveniles of these hemispherical brachiopods closely resemble juveniles of some of the small brachiopods (group I a). Thus the early ontogenetic stages of *Terebratulina gracilis* are morphologically very similar to *Terebratulina faujasii* of comparable size (figs. 9 a and 7 a) and juveniles of *Magas chitoniformis* are similarly very close to small individuals of *Dalligas nobilis* and *Scumulus inopinatus*.

As no selective removal of certain size classes has occurred and as the juveniles of members of each of the two groups find their counterparts in the other group, the difference in the histograms cannot find its explanation in simple ecological reasons as e.g. different enemies or different feeding habits.

d. Size-frequency distributions compared to the morphological adaptations.

The two types of distribution are due to differences in mortality, growth rate and adult size and must be seen in connection with the different adaptations of the two groups.

The small pedunculate brachiopods are adapted to a life attached to the very small hard substrates on the sea-bottom, i.e. mainly small, delicate bryozoans. This implies that they spend their life very close to the surface of the sediment. This position is dangerous to small, sessile suspension feeders, which are very susceptible of becoming overturned by vagile benthonic animals and more less buried in the uppermost soft



Fig. 18. Size-frequency diagrams of the species found in sample Karlstrup 2 (fig. 15 b, Zone 10). The remarks in the legend to fig. 16 are also valid here.



Fig. 19. Growth curves of the four species shown on figs. 6, 7, 9 and 10 (not the same individuals). In all 4 cases the relation between width and length of the brachial valve starts well below 1.0, corresponding to the very long juvenile shell characteristic of most brachiopods. This relation changes rapidly during growth and at a length of 1-2 mm the width becomes larger than the length. In the two hemispherical species *Terebralulina gracilis* (SCHLOTTHEIM) and *Trigonosemus pulchellus* (NILSSON) the final shape is reached already at about 3–4 mm length and the relation remains constant during the rest of the ontogenetic growth. Only the minute *Terebralulina sublilis* STEINICH never reaches a size where the width becomes greater than the length of the brachial valve. The measurements have been carried out on the basis of growth lines on individual specimens.

layer of the sediment. Furthermore, there must have been considerable competition for space on the small substrates. These factors favour the evolution of small, shortlived forms which become sexually mature at an early age.

RUDWICK (1965, 1970) mentioned that many recent brachiopods are sexually mature when they have reached 2/3 their final size. An early maturity for the small

chalk brachiopods would seem to have been necessary in order to maintain a constant population in an environment which caused high juvenile mortality.

The juveniles of the medium sized, hemispherical free living forms ran the same risk as the juveniles of the minute pedunculate brachiopods as they are in all respects very closely alike (figs. 6, 7, 9). The fact that the free living species had a very low juvenile mortality therefore deserves an explanation.

A rather large size would appear to be necessary for the free living mode of life, and it takes some years to attain this size. It is therefore of great importance that the animals belonging to this group rapidly pass through the vulnerable small growthstages and reach their final size and shape as soon as possible. The initial growth rate of these species must therefore be much greater than that of the small species, a fact that again influences the size-mortality pattern.

It is remarkable that this growth-rate/mortality pattern inferred on theoretical grounds for the two groups is clearly illustrated by the empirical size-frequency diagrams.

e. Growth rates.

In order to substantiate the explanation for the two types of size-frequency distributions an attempt is made to estimate the ontogenetic age of some of the brachiopods. Some authors have used growth rings in age studies (HALLAM, 1967, CRAIG & HALLAM, 1963, VOGEL, 1959) but the growth rings of the chalk brachiopods normally do not occur in regular positions as year-rings or spawning rings. In the majority of species it is not possible to distinguish between year-rings and disturbance rings, and thus the age determination methods of VOGEL (1959) and SHELDON (1965) cannot be used directly. A tendency towards a constant grouping of about 5 growth rings is found only in a few species.

To compensate for the occurrence of disturbance rings the technique used by CRAIG & HALLAM (1963) was followed.

All growth rings were measured and the measurements considered as frequency groups. Compensation of disturbance rings in this way revealed potential year rings as peaks on the histograms.

The position of class boundaries and size of classes has a considerable influence on the position of the peaks. However, the application of several class limits showed that the minima in the histograms corresponding to the position between the year rings are rather regular in distribution. The position of the year rings is interpreted as the mean of the measurements between the minima.

This technique gives a minimum age of adult *Terebratulina gracilis* of 4 years (fig. 20). At greater ages the growth rings become crowded and it is not possible to distinguish isolated peaks on the curve. As the average position of the first three year rings is known the total adult age can then be estimated by aid of the method described by SHELDON (1965). L_t (size at one year) is plotted against L_{t+1} (size the following year) which gives a linear curve, converging on the point $L_t = L_{t+1}$ (= the average maximum



Fig. 20. Frequency distribution of the growth lines of *Terebratulina gracilis* (SCHLOTTHEIM) and *Gisilina gisii* (ROEMER). Due to crowding the last growth rings have only been measured in a few specimens of each species. The growth rings of *Terebratulina gracilis* (SCHLOTTHEIM) show pronounced peaks at about 2.3 mm, 4.0 mm and 6.5 mm length of the brachial valve. At *Gisilina gisii* (ROEMER) there is a pronounced peak at 2.3 mm and a more obscure one at 3.8 mm. The size at each year of ontogenetic growth has been estimated by the method described by SHELDON (1965)—see fig. 21.

size). This method gives for an individual of *Terebratulina gracilis* 1 cm long an age of 10 years. Only a very few age studies on living brachiopods are published (e.g. RUD-WICK, 1962, 1965, PAINE, 1963, 1969) and it is therefore difficult to check the estimated age, but compared with the available data the estimate seems to be rather high.

Several of the small brachiopod species have numerous growth rings (*Argyrotheca*) and seem to be unsuited for age studies, but some of the species have only 1-3 distinct growth rings. This is in good agreement with the theory that the small brachiopods are short-lived and mature early in contrast with the free living brachiopods.

Growth rings were also measured in the small species Gisilina gisii (fig. 20) and the first rings were found to be fairly regularly distributed. As the crowding of growth rings in this small species occurs rather early in the ontogenetic growth compared to *Terebratulina gracilis* the positions of the 2. and 3. maximum do not emerge clearly from the histograms. A closer inspection of the measurements reveals, however, that the 2. maximum is situated at about 3.8 mm length of the brachial valve. By using the technique of SHELDON (1965) the maximum age of *Gisilina gisii* is estimated at 5 years. By plotting the estimated age-sizes of *T. gracilis* and *G. gisii* on an age-length curve (fig. 22) it is clearly revealed that the initial growth rate of *T. gracilis* is much larger than of *G. gisii*, thus substantiating the theory that the low juvenile mortality of the medium







Fig. 22. Age-length curves of *Terebratulina gracilis* (SCHLOTTHEIM) and *Gisilina gisii* (ROEMER) based on fig. 21. It is clearly seen that the initial growth rate of *Terebratulina gracilis* is much greater than of *Gisilina gisii*.

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sized hemispherical, free living species is a result of a high early growth rate of these species allowing a rapid passage of the vulnerable early stages.

f. Comparison with theoretical size-frequency distributions.

To ease comparison with the theoretical size frequency distributions calculated by CRAIG & OERTEL (1966) the population characteristics of the two ecologically different groups are summarized below.

- The free living hemispherical forms (group II): High (or very high) → low growth rate Increasing mortality "Boreal" recruitment.
- 2. The minute pedunculate brachiopods (group I a): High → low growth rate Decreasing mortality "Boreal" recruitment.

The type of recruitment can of course only be roughly estimated, but as the chalk sea is considered to have had a depth varying between about 50 and several hundred meters the "boreal" recruitment type of CRAIG & OERTEL (1966) seems to be the most likely.

In comparison with the experiments of CRAIG & OERTEL the supposed mortality rates, growth rates and recruitment type of the two groups correspond with experiment 38 (possibly 41) and 39 respectively refigured here. Experiment 38 (fig. 23) shows a pronounced left skewed curve with relatively low juvenile mortality and with a maximum in the adult stages corresponding well with all observations on the population structures of the free living hemispherical brachiopods. Experiment 39 (fig. 23) on the contrary is markedly right skewed with high juvenile mortality and only a very few individuals reaching the maximum size. This curve corresponds even better with the size-frequency distributions of the minute pedunculate brachiopods.

Stunting or small brachiopods?

The problems concerning stunting in fossil faunas have attracted many authors (e.g. CLOUD, 1948, HALLAM, 1965, TASCH, 1953).

The numerous 2–5 mm long brachiopod species found in the Danish chalk are naturally suggestive of a stunted fauna. However, this quite conclusively seems not to be the case, for the following reasons:

1. The small species are found in all horizons throughout the Upper Campanian and Maastrichtian Stages of northern Germany and Denmark i.e. through a period of several million years. They are known almost without exception, only from the north European chalk. 2. The maximum adult size of all the species is well known on account of the crowding of growth rings in the largest individuals. This maximum size is about constant throughout the chalk and no localities with individuals of the same species attaining greater sizes are known.

3. The small size, as shown in the foregoing pages, may be considered a positive life adaptation in response to the numerous very small, hard substrates available on the chalk sea bottom.

It is therefore considered that no stunting has occurred and the fauna must be characterized as comprising naturally small-sized species.

Epifauna

In the literature there are numerous accounts of brachiopods more or less covered by a rich epifauna (e.g. RUDWICK, 1970). However, an almost total absence of epifauna is characteristic for the majority of the brachiopod species in the Danish chalk. This absence is easily explained in the case of the small species (group I a) owing to their short life and to rapid burial of the small shells after death. At horizons with a supposed reduced rate of sedimentation, however, (e.g. in the upper part of the succession at Hemmoor in North Germany) epifauna is often found even on the smallest brachiopods.

An epifauna is likewise almost totally absent on the hemispherical free living species (group II). The three *Cretirhynchia* species, *Carneithyris subcardinalis* and the large species belonging to groups I b & c would appear to represent ideal substrates for a rich epifauna. Nevertheless, while an epifauna is only rarely found in *C. subcardinalis, Kingena pentangulata* and *Neoliothyrina fittoni* it is sometimes well-developed on the very large *Neoliothyrina obesa* and especially on the three *Cretirhynchia* species.

The reason for this pronounced difference is not clear, but it might be explained by the past existence of a periostracum of different thickness in the different species (Dr. R. BROMLEY, 1971, in conversation). In species with a thick periostracum the epifauna will be separated from the brachiopod when the periostracum disintegrates. However, the recent species of *Terebratulina* and many terebratelloids have a very thin periostracum.

An examination of the recent brachiopods in the collection of professor N. SPJELD-NÆS showed that even from the same locality some species are almost covered by epifauna while others are completely free of overgrowth. This difference might be due to unknown features of the periostracum.

Recent Terebratulina retusa and Terebratulina septentrionalis are often covered by a thick layer of encrusting sponge. DALL (1920 p. 300) wrote that T. septentrionalis is subject to the (commensal ?) growth of a sponge which when young "appears like a normal pubescence, as in T. retusa, but when full grown becomes a spongy ball in which the brachiopod is entirely concealed".

The spongy layer prevents attachment of other epifaunal organisms. After death it disintegrates rapidly and there is no reason to believe that it would normally be preserved in the fossil state. By analogy this seems to be a reasonable explanation of the almost total absence of epifauna on *Terebratulina chrysalis* in the chalk.

Only in a few cases is it possible to judge if the epifauna was attached to living brachiopods or dead shells. In some examples bryozoans have closely followed the commisure or growth lines. No orientation of epifauna relative to inhalant or exhalant current has been observed. The most common epifaunal organisms are bryozoans, encrusting foraminifera, calcareous sponges, bivalves (*Atreta*), brachiopods (*Crania*) and serpulids.

Borings

Two types of borings have been found in the brachiopods viz. thallophyte and gastropod borings. At some horizons the majority of the specimens are penetrated by thallophyte borings. It is not known if the borings are caused by fungi or algae, but an algal origin seems most likely according to the branching pattern and dimensions of the borings (BROMLEY, 1971, personal communication). There is a pronounced correlation between slow sedimentation and number of thallophyte borings. Thallophyte borings are normally restricted to large disarticulated and broken shells indicating that the borings were not made in the shells of living brachiopods.



Fig. 24. The relative positions of muricid? borings on the outline of: a: a brachial valve of *Trigonosemus* pulchellus (NILSSON) b: a pedicle valve of *Trigonosemus* pulchellus (NILSSON) c: a dorsal valve of *Isocrania* costata (SOWERBY). a and b are based on a population of *Trigonosemus* pulchellus from Dronningestolen, Møns Klint. c is based on a population of *Isocrania* costata from Lindholm.

The gastropod borings are more significant from an ecological point of view, as they must have been made on living brachiopods. STEINICH (1965 p. 196) mentioned that in the Rügen chalk 12% of all specimens of *Terebratulina gracilis* had been bored by gastropods. In the Danish chalk, borings are only found in a few species and not at all horizons. The borings are cylindrical and, by comparison with modern examples, were apparently made by muricid gastropods (BROMLEY, 1971, personal communication) indicating that the brachiopods were attacked at the surface of the sediment and not by burrowing naticid gastropods. Only in *Isocrania costata* and *Trigonosemus* pulchellus are borings common. Thus 20% of a *T. pulchellus* population from Møns Klint were bored by gastropods. In *Isocrania costata* the borings are concentrated in the thick umbonal region (fig. 24 c) where the soft parts of the body were situated. Unfinished borings are very common. In *T. pulchellus* a very characteristic distribution is found of the borings in the dorsal and ventral valves respectively (figs. 24 a, b). In the dorsal valve the borings are concentrated in the umbonal part where the soft parts were situated, but on the ventral valve the borings are found in a ring around the central part of the valve, where borings are absent. This is in good agreement with the supposed mode of life of *T. pulchellus*—lying free on the sea bottom with the ventral valve down.

Fossil communities

PETERSEN (1913, 1918) developed the concept of communities as statistical units based on recurring combination of certain animals (a discussion of PETERSEN's community concept is given by THORSON, 1957 p. 467).

In the present study several of the brachiopod species are found in recurrent combinations. THORSON (1957) noticed that epifaunal organisms were not ideal as "characterizing animals" for a community due to their less constant occurence. Never-theless some of the chalk brachiopods are suitable as characterizing animals as they are found in all samples in the part of the column where they occur. Brachiopods have also been used as such in the Ordovician communities defined by BRETSKY (1970 b). As mentioned by WALKER & LAPORTE (1970 p. 934) it is misleading to name a fossil community after one or more of the type animals as different taxa may be involved at different times when dealing with temporarily separated communities. They therefore chose to name the communities after the presumed biotopes. This is almost impossible in the very monotonous chalk sequence and it seems to be most convenient to delay any designation of fossil communities in the Danish chalk until the taxonomy and stratigraphy of all major fossil groups are known in detail.

Summary

The present study is based on a large number of samples or series of samples from all major Danish chalk localities (fig. 1).

The samples, normally weighing 5 or 10 kg were washed and yielded a total of about 50.000 brachiopods representing 37 articulate and 6 inarticulate species.

The white chalk is a soft, friable, almost pure carbonate sediment of biogenic origin classified as a nannoagorite by Honjo (1969). It consists of coccolith detritus with an admixture of up to 20% smaller macrofossils, chiefly bryozoans.

The brachiopods have shown themselves to be valuable for a detailed stratigraphical subdivision of the Maastrichtian chalk of northern Germany and Denmark

(SURLYK, 1970 b). Thus it is possible to divide the Danish Maastrichtian into 10 zones on the basis of the brachiopods.

The Danish chalk can be divided into three ecological units based on the major variations in the richness of the benthonic fauna (fig. 3). From Zones 1-4 (fig. 2) there is a steady increase in the benthonic fauna with a very pronounced maximum in Zone 4. In Zones 6-7 the benthonic fauna has almost disappeared but upwards the fauna becomes richer again and a second maximum is reached in Zone 10.

All fossils are extremely well preserved. In the brachiopods, mesodermal spicules and even coherent spicular skeletons revealing the whole structure of the mantle, the body wall and the lophophore are commonly found (pl. 1, 2). Furthermore there is a complete mixture of fossils of all size classes. Preburial transport can thus be excluded. Traces of early diagenetic slides have been found only on the flanks of the bryozoan bioherms of Zone 10 (figs. 3, 15).

On the basis of their mode of life, the chalk brachiopods can be divided into 4 groups (fig. 5):

- I. Attached to the substrate by means of a pedicle: 24 spp. This group can be divided into 3 subgroups according to the nature and especially the size of the preferred substrate.
- II. Living free on the surface of the sediment: 10 spp.
- III. Burrowing in the sediment: 1 sp.
- IV. Attached to the substrate by cementation: 8 spp. This group can be divided into 2 subgroups according to the size of the substrate.

Group I is completely dominated by minute brachiopods with a very high juvenile mortality. These brachiopods seem to be well adapted to a life attached to the very small hard substrates, especially bryozoans, available in the chalk.

The brachiopods of group II show several kinds of adaptations to the free living mode of life. Six of the species are hemispherical (fig. 11), one species seems to have functioned like a self-righting "tumbler" (fig. 4), and the three last species are rhynchonelloids with the lateral parts of the shell considerably expanded. The pedicle openings of all the species belonging to this group are closed or at least hidden by the incurved umbo.

The small brachiopods (group I) dominating the chalk brachiopod fauna seem to have a rather random distribution in the sediment. On the contrary, the larger, free living brachiopods (group II) are sometimes found in small aggregations composed of one to three species (pl. 5 c). There is a pronounced correlation between aggregations of the larger brachiopods and absence of potential substrates. The aggregations are thus found almost exclusively in the chalk of Zones 7–9 where the benthonic fauna is very reduced.

The quantitative distribution of the most important brachiopods in three sections is shown on figs. 14 and 15. There is a close agreement between the curve showing the weight of the washing residue (more or less equivalent to the quantity of bryozoans) and the curve illustrating the total number of brachiopod individuals. The parallelism of the curves is mainly primary, the bryozoans playing the role of substrates for the brachiopods, and is only to a small degree secondary, due to variations in the pelagic sedimentation.

Size-frequency diagrams have been constructed for all brachiopods found in three samples (figs. 16, 17 and 18). It is seen that in all the more common species (all belonging to group I) the populations are dominated by large quantities of juvenile individuals. The hemispherical free living brachiopods (group II) are normally quite rare, but where they are common they show a bell-shaped or left (= negatively) skewed size-frequency distribution. The two types of distribution are due to differences in mortality, growth rate and adult size and must be seen in connection with the different adaptations of the two groups.

The small pedunculate brachiopods are adapted to a life attached to the very small hard substrates on the sea bottom, i. e. mainly small, delicate bryozoans. This implies that they spent their life very close to the surface of the sediment. This position is dangerous to small, sessile suspension feeders, which are very susceptible of becoming overturned by vagile benthonic animals and more or less buried in the topmost soft layer of the sediment. The juveniles of the free living larger brachiopods run the same risk as the juveniles of the minute pedunculate brachiopods as they are in all respects very closely alike (figs. 6, 7 and 9). A rather large size would appear to be necessary for the free living mode of life, and it takes some years to attain this size. It was therefore of great importance that the animals belonging to this group rapidly passed through the vulnerable small growth-stages and reached their final size and shape as soon as possible. The initial growth rate of these species must therefore have been much greater than that of the small species, a fact that again influenced the size-mortality pattern. This difference in growth rate is shown for *Gisilina gisii* (group I) and for *Terebratulina gracilis* (group II) in figs. 20, 21 and 22.

There is a good agreement between the actual size-frequency distributions and the theoretical distributions computed by CRAIG & OERTEL (1966).

It is shown that no stunting has occurred and the fauna of minute brachiopods must be characterized as comprising naturally small-sized species.

Thus the Danish chalk contains a rich fauna of brachiopods which were remarkably well adapted to the life on the level, relatively soft and fine grained chalk sea bottom.

References

- AGER, D. V. 1962: The occurrence of pedunculate brachiopods in soft sediments. Geol. Mag., 99, 184–186.
- AGER, D. V. 1963: Principles of paleoecology. McGraw-Hill Book Company, Inc. 371 pp.
- AGER, D. V. 1965: The adaptation of Mesozoic brachiopods to different environments. Palaeogeography, Palaeoclimatol., Palaeoecol., 1, 143–172.
- AGER, D. V. 1967: Brachiopod palaeoecology. Earth-Sci. Rev., 3, 157-179.
- ATKINS, D. 1959: The growth stages of the lophophore of the brachiopods *Platidia davidsoni* (EUDES DESLONGCHAMPS) and *P. anomioides* (PHILIPPI), with notes on the feeding mechanism. J. mar. biol. Ass. U. K. 38, 103–132.
- ATKINS, D. 1960: The ciliary feeding mechanism of the Megathyridae (Brachiopoda), and the growth stages of the lophophore. J. mar. biol. Ass. U. K. 39, 459–479.
- Васкнаиз, E. 1959: Monographie der cretacischen Thecideidae (Brach.). Mitt. geol. Staatsinst. Hamburg. 28, 5–90.
- BIRKELUND, T. 1957: Upper Cretaceous belemnites from Denmark. Biol. Skr. Dan. Vid. Selsk. 9, 1, København. 69 pp.
- BLACK, M. 1953: The Constitution of the Chalk. Proc. geol. Soc. Lond. No. 1499. London. 81–86.
- Boucor, A. J. 1953: Life and death assemblages among fossils. Am. Jour. Sci. 251, 25-40.
- BRETSKY, P. W. 1970a: Upper Ordovician ecology of the central Appalachians. Peabody Museum of Natural History Yale University. Bulletin 34, 150 pp.
- BRETSKY, P. 1970b: Late Ordovician benthic marine communities in North-central New York. New York State Museum and Science Service, Bull. 414, 1–34.
- BROMLEY, R. G. 1967: Some observations on burrows of thalassinidean Crustacea in chalk hardgrounds. Q. Jl. geol. Soc. Lond., 123, 157–182.
- BROMLEY, R. G. 1968: Burrows and boring in hardgrounds. Bull. geol. Soc. Denmark, 18, 2, 247-250.
- CHAVE, K. E. 1954a: Aspect of the biochemistry of magnesium. 1. Calcareous marine organisms. Jour. Geol., 62, 266–283.
- CHAVE, K. E. 1954b: Aspects of the biochemistry of magnesium. 2. Calcareous sediments and rocks. Jour. Geol. 62, 587-599.
- CLARKE, F. W. & WHEELER, W. C. 1922: The inorganic constituents of marine invertebrates. U.S. Geol. Surv. Prof. Paper, 124, 1–62.
- CLOUD, P. E. 1948: Assemblages of diminutive brachiopods and their paleoecological significance. J. sedim. Petrology, 18, 56–60.
- COPPER, P. 1967: Adaptations and life habits of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatol., Palaeoecol., 3, 363-379.
- CRAIG, G. Y. 1952: A comparative study of the ecology and palaeocology of *Lingula*. Trans. Edin. geol. Soc. 15, 110–120.

- CRAIG, G. Y. & HALLAM, A. 1963: Size-frequency and growth-ring analyses of *Mytilus edulis* and *Cardium edule*, and their palaeoecological significance. Palaeontology, 6, 4, 731–750.
- CRAIG, G. Y. & OERTEL, G. 1966: Deterministic models of living and fossil populations of animals. Q. Jl. geol. Soc. Lond. 122, 315–355.
- DALL, W. H. 1920: Annotated list of the recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms. Proceedings U.S. National Museum, 57, 2314, 261–377.
- DAVIDSON, T. 1880: Report on the brachiopoda dredged by H. M. S. Challenger during the years 1873–1876. Zool. Chall. Exp. Part 1, 1–67.
- Екман, T. 1896: Beiträge zur Kenntnis des Stieles der Brachiopoden. Zeitschrift f. Wissensch. Zoologie, 62, 2, 169–249.
- ELLIOTT, G. F. 1956: Post-Palaeozoic brachiopod ecology: A re-assessment. Geol. Mag., 93, 196-200.
- ELLIOTT, G. F. 1958: An abnormal lophophore in *Macandrevia* (Brachiopoda). Universitetet i Bergen Årbok 1958, Naturvitenskabelig rekke Nr. 2, 2–6.
- ERNST, G. 1966: Discussion. In: BROTZEN, F. Faziesveränderungen in der Oberkreide Schwedens. Ber. deutsch. Ges. geol. Wiss. A. Geol. Paläont. 11, 6, 709–719.
- FAGERSTROM, J. A. 1964: Fossil communities in Paleoecology: their recognition and significance. Bull. geol. Soc. Am. 75, 1197–1216.
- FAIRBRIDGE, R. W. 1967: Phases of diagenesis and authigenesis. In: LARSEN, G. & CHILLINGAR, G. V. (editors). Diagenesis in sediments. Developments in Sedimentology 8. 19–89. Elsevier Publishing Company.
- Fox, W. T. 1968: Quantitative paleoecologic analyses of fossil communities in the Richmond Group. Jour. Geol. 76, 613-640.
- HALLAM, A. 1962: Brachiopod life assemblages from the Marlstone Rock-bed of Leicestershire. Palaeontology, 4, 653–659.
- HALLAM, A. 1965: Environmental causes of stunting in living and fossil benthonic invertebrates. Palaeontology, 8, 132–155.
- HALLAM, A. 1967: The interpretation of size-frequency distributions in molluscan death assemblages. Palaeontology, 10, 25-42.
- HANCOCK, J. M. 1963: The hardness of the Irish chalk. Ir. Nat. Jour., 14, 157-164.
- HANCOCK, J. M. & KENNEDY, W. J. 1967: Photographs of hard and soft chalks taken with a scanning electron microscope. Proc. geol. Soc. Lond. 1643, 249–252.
- HONJO, S. 1969: Study of fine grained carbonate matrix: sedimentation and diagenesis of "micrite". In: MATSUMOTO, T. (edit.): Litho- and bio-facies of carbonate sedimentary rocks - a symposium. Palaeontological Society of Japan. Special papers number 14, 67-82.
- JEANS, C. V. 1968: The origin of the montmorillonite of the European chalk with special reference to the Lower Chalk of England. Clay Minerals, 7, 311-329.
- JONES, G. F. & BARNARD, J. L. 1963: The distribution and abundance of the inarticulate brachiopod *Glottidia albida* (HINDS) on the mainland shelf of southern California. Pacific naturalist, 4, 2, 27–52.
- LOWENSTAM, H. A. 1954: Status of invertebrate paleontology, 1953. XI. Systematic, paleoecologic and evolutionary aspects of skeletal building materials. Bull. Mus. comp. Zool. Harvard College, 112, 3, 287–317.
- MENARD, H. W. & BOUCOT, A. J. 1951: Experiments on the movement of shells by water. Am. Jour. Sci. 249, 131-151.
- MENHINICK, E. F. 1964: A comparison of some species-individuals diversity indices applied to samples of field insects. Ecology, 45, 4, 859–861.
- MURRAY, J. W. 1968: Living foraminifers of lagoons and estuaries. Micropaleontology, 14, 4, 435-455.

- NESTLER, H. 1965: Die Rekonstruktion des Lebensraumes der Rügener Schreibkreide-Fauna (Unter-Maastricht) mit Hilfe der Paläoökologie und Paläobiologie. Geologie, Jahrg. 14, Beiheft 49, 147 pp. Berlin.
- NIELSEN, K. B. 1909: Brachiopoderne i Danmarks Kridtaflejringer. D. Kgl. danske Vidensk. Selsk. Skrifter, 7. Række, Naturvidensk. og Mathem. Afd. 6, 4, 52 pp.
- PAINE, R. T. 1963: Ecology of the brachiopod *Glottidia pyramidata*. Ecological Monographs, 33, 255–280.
- PAINE, R. T. 1969: Growth and size distribution of the brachiopod *Terebratalia transversa* SowERBY. Pacific Science, 23, 3, 337–343.
- PAINE, R. T. 1970: The sediment occupied by recent lingulid brachiopods and some paleoecological implications. Paleogeography, Palaeoclimatol., Palaeoecol., 7, 21–31.
- PERCH-NIELSEN, K. 1968: Der Feinbau und die Klassifikation der Coccolithen aus dem Maastrichtien von Dänemark. Biol. Skr. Dan. Vid. Selsk. 16,1, 96 pp.
- PETERSEN, C. G. J. 1913: Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Rep. Danish biol. Stat. 21, 44 pp.
- PETERSEN, C. G. J. 1918: The sea bottom and its production of fish-food. A survey of the work done in connection with the valuation of the Danish waters from 1883–1917. Rep. Danish biol. Stat., 25, 62 pp.
- POPIEL-BARCZYK, E. 1968: Upper Cretaceous terebratulids (Brachiopoda) from the middle Vistula gorge. Prace Muzeum Ziemi, No. 12, 86 pp.
- RASMUSSEN, H. W. 1971: Echinoid and crustacean burrows and their diagenetic significance in the Maastrichtian-Danian of Stevns Klint, Denmark. Lethaia, 4, 191–216.
- ROSENKRANTZ, A. 1924: Nye iagttagelser over Cerithiumkalken i Stevns Klint med bemærkninger om grænsen mellem Kridt og Tertiær. Meddr dansk geol. Foren. 6, 28–31.
- ROSENKRANTZ, A. 1940: Faunaen i Cerithiumkalken og det hærdnede skrivekridt i Stevns Klint. Meddr dansk geol. Foren. 9, 509–514.
- ROSENKRANTZ, A. 1966: Die Senon/Dan Grenze in Dänemark. Ber. deutsch. Ges. geol. Wiss. A. Geol. Paläont. 11, 6, 721–727.
- ROSENKRANTZ, A. & RASMUSSEN, H. W. 1960: South-eastern Sjælland and Mön, Denmark. International Geological Congress. XXI Session, Norden. 1960. Guide to excursions nos A 42 and C 37 Part 1, 1–17.
- ROWELL, A. J. & RUNDLE, A. J. 1967: Lophophore of the Eocene brachiopod *Terebratulina* wardenensis Elliott. The University of Kansas Paleontological contributions, paper 15, 1–8.
- RUCKER, J. B. 1967: Carbonate mineralogy of Recent cheilostome Bryozoa. Geol. Soc. America Program 1967, Ann. Meeting, November 20–22, New Orleans, Louisiana, 191–192.
- RUCKER, J. B. & CARVER, R. E. 1969: A survey of the carbonate mineralogy of cheilostome Bryozoa. Journal of Paleontology, 43, 3, 791–799.
- RUDWICK, M. J. S. 1961: The anchorage of articulate brachiopods on soft substrata. Palaeontology, 4, 475-476.
- RUDWICK, M. J. S. 1962: Notes on the ecology of brachiopods in New Zealand. Trans. Roy. Soc. New Zealand, Zoology, 1, 25, 327–335.
- RUDWICK, M. J. S. 1965: Ecology and paleoecology. In MOORE, R. C. (edit.) 1965: Treatise on invertebrate paleontology, Part H Brachiopoda, 199–214.
- RUDWICK, M. J. S. 1970: Living and fossil brachiopods. Hutchinson University Library, 199 pp.
- SCHMID, F. 1949: Orientierte Anheftung von Ostrea vesicularis LAMARCK, Dimyodon nilssoni HAGENOW und Crania parisiensis DEFRANCE. Mitt. geol. Staatsinstitut Hamburg, 19, 53-56, Hamburg.

- SCHOPF, T. J. M. & MANHEIM, F. T. 1967: Chemical composition of Ectoprocta (Bryozoa). Journal of Paleontology, 41, 5, 1197–1225.
- SCHUMANN, D. 1969: "Byssus"-artige Stielmuskel-Konvergenzen bei artikulaten Brachiopoden. Neues Jb. Geol. Paläont. Abh. 133, 2, 199–210, Stuttgart.
- SCHUMANN, D. 1970: Mesodermale Endoskelette bei Brachiopoden. Naturwissenschaften 57, 124–126.
- SHELDON, R. W. 1965: Fossil communities with multi-modal size-frequency distributions. Nature, 206, 1336–1338.
- SIMPSON, E. H. 1949: Measurement of diversity. Nature, 163, p. 688 only.
- SPRENG, A. C. 1962: Airbrasive cleaning tool. Journal of Paleontology, 36, 1391-1392.
- STEINICH, G. 1963 a: Fossile Spicula bei Brachiopoden der Rügener Schreibkreide. Geologie, Jahrgang 12, 5, 604–610.
- STEINICH, G. 1963 b: Drei neue Brachiopodengattuugen der Subfamilie Cancellothyrinae THOMSON. Geologie, Jahrgang 12, 6, 732–740.
- STEINICH, G. 1963 c: Zur Morphogenese des Foramens der Rhynchonelliden. Geologie, Jahrgang 12, 10, 1204–1209.
- STEINICH, G. 1965: Die artikulaten Brachiopoden der Rügener Schreibkreide (Unter-Maastricht). Paläont. Abh. A. 2, 1, 1–220.
- STEINICH, G. 1967 a: Sedimentstrukturen der Rügener Schreibkreide. Geologie, Jahrgang 16, 5, 570–583.
- STEINICH, G. 1967 b: Neue Brachiopoden aus der Rügener Schreibkreide (Unter-Maastricht). I. Draciinae – eine neue Unterfamilie der Cancellothyrididae THOMSON. Geologie, Jahrgang 16, 10, 1145–1155.
- STEINICH, G. 1968 a: Neue Brachiopoden aus der Rügener Schreibkreide (Unter-Maastricht). II. Die Platidiidae Thomson. Geologie, Jahrgang 17, 2, 192–209.
- STEINICH, G. 1968 b: Neue Brachiopoden aus der Rügener Schreibkreide (Unter-Maastricht).
- III. Dalligas nobilis gen. et. spec. nov. und Kingena sp. Geologie, Jahrgang 17, 3, 336–347. Störr, M. 1966: Discussion In: BROTZEN, F. 1966: Faziesveränderungen in der Oberkreide
- Schwedens. Ber. deutsch. Ges. geol. Wiss. A. Geol. Paläont. 11, 6, 709-719.
- SURLYK, F. 1969: En undersøgelse over de articulate brachiopoder i det danske skrivekridt (ø. campanien og maastrichtien) med en oversigt over skrivekridtets sedimentologi og skrivekridthavets flora og fauna. Unpublished prize dissertation. Københavns Universitet. 319 pp.
- SURLYK, F. 1970 a: Two new brachiopods from the Danish white chalk (Maastrichtian). Bull. geol. Soc. Denmark. 20, 152–161.
- SURLYK, F. 1970 b: Die Stratigraphie des Maastricht von Dänemark und Norddeutschland aufgrund von Brachiopoden. Newsl. Stratigr. 1, 2, 7–16.
- TASCH, P. 1953: Causes and paleoecological significance of dwarfed fossil marine invertebrates. Journal of Paleontology, 27, 356-444.
- TERMIER, H. & TERMIER, G. 1963: Erosion and sedimentation. D. van Nostrand Company, Ltd. London, 433 pp.
- THOMSON, J. A. 1927: Brachiopod morphology and genera (Recent and Tertiary). New Zealand Board of Science and Art. Manual No. 7. 338 pp.
- THORSON, G. 1957: Bottom communities (sublittoral or shallow shelf). In: HEDGPETH, J. (edit.) 1957: Treatise on marine ecology and paleoecology, 1, Geol. Soc. America. Memoir 67, 461-534.
- TROELSEN, J. 1937: Om den stratigrafiske inddeling af skrivekridtet i Danmark. Meddr. dansk geol. Foren. 9, 260–263.
- TROELSEN, J. 1955: *Globotruncana contusa* in the White Chalk of Denmark. Micropaleontology, 1, 1, 76–82.

- VOGEL, K. 1959: Wachstumsunterbrechungen bei Lamellibranchiaten und Brachiopoden. Neues Jb. Geol. Paläont., Abh., 109, 109–129.
- WALKER, K. R. & LAPORTE, L. F. 1970: Congruent fossil communities from Ordovician and Devonian carbonates of New York. Journal of Paleontology, 44, 928-944.
- VINOGRADOV, A. P. 1953: The elementary chemical composition of marine organisms. Sears Foundation for Marine Research, New Haven, Mem. 2, 647 pp.
- ZIEGLER, A. M. 1965: Silurian marine communities and their environmental significance. Nature, 207, 4994, 270–272.
- ZIEGLER, A. M., COCKS, L. R. M. & BAMBACH, R. K. 1968: The composition and structure of Lower Silurian marine communities. Lethaia, 1, 1, 1–27.

PLATES

PLATE I

- a-b: Meonia semiglobularis (Posselt).
- a: Brachial valve. Internal view showing spicular skeleton of anterior body wall. $\times 29$.
- b: Isolated spicular skeleton of the schizolophous lophophore. Anterior downwards. Ventral view. ×72.
 c: Spicular skeleton of left arm of the lophophore. Anterior to the right. Lateral view. Note the strong
- c: Spicular skeleton of left arm of the lophophore. Anterior to the right. Lateral view. Note the strong brachial ridge and the bases of the filaments. \times 72.
- d-e-f: Details of the spicular skeleton of the anterior body wall shown on fig. a.—immediately left of the brachidium. The frontal edge of the brachidium is seen in the upper left corner of d and e. d: ×744, e: ×288, f: ×2940.









Plate II

- a-b: Terebratulina longicollis Steinich.
- a: Ventral valve. Internal view. Spicular skeleton of the plectolophous lophophore showing the lateral arms with long, slender filaments and the recrystalized median spire. $\times 55$.
- b: Ventral valve. Like a, but median spire of plectolophe more strongly recrystalized. $\times 58$.
- с-g: Terebratulina faujasii (Roemer).
- c: Dorsal valve. Internal view showing brachidium. $\times 30$.
- d: Spicular skeleton of plectolophous lophophore. Oblique anterio-lateral view. Note the filament bases along the lateral arm and the partially spiculated median spire. \times 74.
- e: Ventral view of d. Complete spicular skeleton of plectolophous lophophore. Anterior downwards. Mouth opening visible as a white spot at the upper part of the figure. The ventral side of the arms are not spiculated thus making it possible to see the great brachial canal in each arm. ×53.
- f: Lateral view of d. \times 74.
- g: Isolated spicular skeleton of the anterior body wall. Dorsal view. Anterior downwards. Compare with pl. 1 a. $\times 60.$
- d-g are all isolated from the specimen on fig. c.



Plate III

- a: Recent Argyrotheca from Barbados attached to lunulitiform bryozoa. Note the very close attachment. $\times 29.$
- b: Large recent Argyrotheca from Barbados closely attached to lunulitiform bryozoa. $\times 29$.
- c: Recent *Argyrotheca* from Barbados attached to bryozoa. ×36.
- d: As c. $\times 14$.
- e: Aemula inusitata STEINICH from the Danish chalk. $\times 57$.
- f: As e. \times 73.
- g: Lateral view of the specimen on fig. a. $\times 30$.
- h: As e and f. $\times 55.$ e, f and h show the great variability of this species. Note the large amphithyrid foramen.


PLATE IV

- a: Recent *Terebratulina relusa* (L.) attached to bryozoans and shell gravel with a rootlike divided pedicle. $\times 10$.
- b: Terebratulina chrysalis (SCHLOTTHEIM) from the Danish chalk. Note the large foramen and the great similarity to a, e, d. \times 9.
- c: As b. $\times 5.7$.
- d-e: Two specimens of recent *Terebratulina retusa* (L.) with rootlike divided pedicle. a and e are covered with a thin sponge layer. d: $\times 10$. e: $\times 5.5$.
- f: Lunulites sp. from the Danish chalk. ×42. Compare with pl. 3, a, b.
- g: Argyrotheca bronnii (ROEMER) from the Danish chalk. ×25. Compare pl. 3, a, b, c, d, g.
- h: *Terebratulina chrysalis* (SLOTTHEIM) from the Danish chalk with anterior commisure damaged by a bite. $\times 5.5$.



PLATE V

- a: Sand-blown block of uniform white chalk from Hvidskud (Zone 4). Note the wealth of apparently random orientated cheilostome and cyclostome bryozoa. ×8.
- b: Surface of the shell of *Aemula inusitata* (pl. 3, e), showing the thin film of whole and broken coccoliths covering the surface of almost all fossils found in the chalk. $\times 2640$.
- c: Nest of brachiopods from Nørre Flødal (Zone 9). From left to right: 1 specimen of *Carneithyris subcardinalis* (SAHNI), 2 *Terebratulina gracilis* (SCHLOTTHEIM) and 4 *Magas chitoniformis* (SCHLOTTHEIM). All the species are free living and except *C. subcardinalis* of a hemispherical shape. Note the uniform orientation of all the shells. Unfortunately the sample was not collected with upside orientation indicated. Approx. ×3.
- d: Washing residue from Hvidskud (Zone 4) same horizon as fig. a. Approx. ×4.

The figures on pl. I, III, IV f-g and Vb were all taken on a Stereoscan MK Ha scanning electron microscope. The photographic work on pl. IV a-e, h and Va, c-d was carried out by Mr. P. NIELSEN and Mr. J. AAGAARD.









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Synopsis

In the present investigation of Tahitian oribatid fauna, undertaken with the object of perhaps finding species introduced with plant products from Europe, a total of 102 species was found. Of these, 61 species have been described earlier. 41 new species are described, and 5 new genera are established as well as 5 new varieties. 9 species were found which are known from Europe, but which also have a wide distribution over the whole earth. These can have come to Tahiti from any area of land other than Europe, and for this reason a European influence cannot be established.

Subtracting species with a worldwide distribution Tahiti has 40 species in common with Southeast Asia–Indonesia, and only 15 species in common with America. In addition, 6 of the 9 species found on Tahiti that have a worldwide distribution are also found in Southeast Asia–Indonesia, while 8 of these species are found in America. Perhaps the close ties between the fauna of Tahiti and that of Southeast Asia–Indonesia can be explained by an introduction with plant products by the Polynesians during their wanderings, but transport by ocean currents cannot be disproved.

On the atoll Rangiroa 13 species were found, of which 2 were not found on Tahiti.

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Preface

The collection on which the present investigation is based was made in December 1969 and January 1970. The object of the investigation of Tahitian oribatids was if possible to determine if oribatids—perhaps introduced from Europe during the last 200 years with plant products, etc.—could have survived in Tahiti and reproduced under foreign conditions.

I should like to offer my grateful thanks to the Carlsberg Foundation and to the Danish Research Foundation, who paid travelling and other expenses for me and my assistant, cand. scient. BIRGITTE HAMMER. The Carlsberg Foundation have furthermore covered my expenses during the preparation of the collected material. In addition, I am very much indebted to the Royal Danish Academy of Sciences and Letters, who for many years have undertaken the publication of my papers on the distribution of the oribatids. The Rask-Ørsted Foundation have likewise for many years covered the costs of the translation into English of my numerous articles for which once again I wish to offer the Foundation my thanks.

Mrs. JENNIFER DUPUIS-STARCKE has kindly undertaken the translation of part of the manuscript and assisted me with a revision of the remainder.

Fredensborg, March 1971.

MARIE HAMMER

Introduction

For decades it has been a matter of speculation how representatives of the microfauna, among them the oribatids that cannot fly or swim, or even survive transport with ocean currents over longer distances, have been able to populate distant, isolated coral islands or islands of volcanic origin. There is hardly doubt any longer that ocean current must be considered as the means of transport for a part of the fauna. However, is it not possible that some creatures can have been introduced indirectly by humans, i.e. carried in with the many imported materials of plant origin—vegetables, fruit, root crops, etc.? Investigations at plant quarantine stations (HAMMER 1969) have shown that numerous living creatures are carried into every country in the world, but it is not known whether these creatures are able to survive and reproduce under foreign conditions. Tahiti was chosen as a suitable area to investigate this question due to its isolation from all continents and to its 200-year-old trading ties with Europe among other areas. Any introduced European elements of the fauna would easily be distinguished from animals introduced from nearer-lying areas, where the fauna must be supposed partly related to that of Tahiti.

On these grounds I made exhaustive collections of origatids on Tahiti in the autumn of 1969/winter of 1970. Particular weight was laid on making collections from the town of Papeete and its vicinity, as this area must be supposed the easiest in which to find introduced animals. Later on collections were made along large stretches of the coast, particularly the north coast which is most suitable and has rather varied biotopes. Finally collections were made in almost virgin areas in the mountains.

Since it is of no particular significance in this investigation to know in which locality or biotope the individual species were found in so limited an area as Tahiti, and also to avoid the continual repetition of the many sample numbers (114 samples—each of roughly a handful), the material is classified into four groups as follows:

I: Papeete (lawns in the park, garden rubbish, edges of ditches, brooks, private gardens, playgrounds, water reservoirs, etc.). The majority of the samples with scant vegetation and quite without moss.

II: The coast (rocky road sides, slopes with small ferns, low vegetation, moss, moss growing in water trickling down cliff sides, swampy marshes, moss on the foot of coconut palms, rotting leaves, etc.).

III: In the mountains above Papeete along a road leading to the Fare Rau Ape café at a height of 600 m above sea level. Up to this height the mountains are covered with Casuarina and numerous deciduous trees with a rich undergrowth of bushes and plants. In addition collections were made from 600 to 800 m above sea level. Above this stretch the earlier forest has been felled and the mountain crests are now mainly covered with a 1 m height thicket of bracken. In group III collections were made from Casuarina needles, in rotten, deciduous leaves, in bracken litter, sparse moss, lichens and moss on dry bark, bits of crumbling branches, damp leaves under paper sacks, low plants, etc.

IV: This group comprises the atoll Rangiroa, approximately 300 km northeast of Tahiti (rotting leaves between blocks of coral under rather low tree/bush vegetation).

In the following, the locality grouping for each individual species is indicated by the Roman numerals I–IV. The number of individuals found is given in brackets thereafter, while the following number denotes the number of samples in which the species was found. The last number gives an indication of the general distribution of the species. If a species was found in few samples, or only in a single sample, further information is given on the biotope.

There is little information on earlier finds of oribatids on Tahiti. JACOT (1934b) mentions only one species, Austrotritia (Indotritia) lebronneci tahitiana, while SELLNICK (1959) mentions the following six species: Liodes hawaiiensis (Jacot), Humerobates perkinsi (Jacot), Galumna hawaiiensis Jacot, Scheloribates muiri Jacot, Austrotritia lebronneci (Jacot), and Pseudotritia loricata (Rathke) = Rhysotritia ardua (Koch). Of these sic species, only two were found again in this investigation.

List and Descriptions of the Species Found

Palaeacaridae

Andacarus ligamentifer Ham.

– – , 1967, p. 59, fig. 79.

The specimens from Tahiti deviate from the type specimen by having a much shorter f2. The latter is about one half to one third as long as d1. Furthermore f1 and f2 are set very close together. In the type specimen they are situated with a mutual distance as long as f1.

II (1: wet moss and litter), III (3: moist moss; lichens and moss on bark).

Hypochthoniidae

Malacoangelia remigera Berl.

_ _ _ _ _ _ _ _ _ , 1913, p. 101, fig. 86. II (2: low Cyperus vegetation under a hedge).

Hypochthoniella minutissima (Berl.).

Hypochthonius minutissimus Berl., 1903, p. 252. III (4: Leucobryum, moist; thick moss).

Eohypochthonius gracilis (Jacot).

Hypochthonius gracilis – , 1936, p. 251, fig. 9.

The specimens from Tahiti differ from the type in the same way as the specimens found in Viti Levu, the Fiji Islands (HAMMER 1971), i.e. the pseudostigmatic organs have longer branches and the notogastral setae are shorter and do not overlap. II (15: wet Cyperus meadow).

Eohypochthonius gracilis (Jacot) v. crassisetiger Aoki.; fig. 1.

– – , 1959, p. 3, fig. 2.

Length about 0.34 mm. Colour light brown.

The specimens from Tahiti differ from the type from South Japan by the shape of the interlamellar hair, which in most specimens is directed forwards, being long, oval, rounded at the tip and soft as down. The pseudostigmatic organ has 9–11 branches and furthermore some very fine bristles on its posterior border. In one specimen the usually rudimentary setae e1 are present, fig. 1. These two hairs differ from the other notogastral hairs being stiff, slightly uneven, and shorter.

II (5: Cyperus vegetation; met moss).

Phthiracaridae

Hoplophorella rangiroaensis n.sp.; fig. 2.

Length of notogaster about 0.38 mm.

- - aspis - 0.20 - . Colour grey with bluish reticulation.

In the posterior part of the aspis, fig. 2a, there is a broad area with a coarse reticulation consisting of three rows of pits on either side of the carina. The lamellar hairs are lanceolate and hyaline. The interlamellar hairs are missing or not discernible. The curved rostral hairs are directed forwards and situated on either side of the rostral keel. The integument is irregularly pitted. The distal part of the pseudostigmatic organs, which are strongly bent, is directed backwards. This part is uneven or perhaps covered with mucus or minute bristles.

Anteriorly the notogaster has a prominent collar like *H. cucullata* (Ewing), on which the three anterior notogastral hairs are situated. In profile the notogastral hairs are narrow, the tip is spoon-shaped, and the hollow part not much broader than the stalk. In a dorsal view the hairs are lanceolate, from their underside they are broad spoons, fig. 2b. The sculpture of the notogaster consists of strong bluish ribs surrounding angular to round large pits. No punctation.

Ano-genital region. The genital plate has four small hairs, the distance being longest between the third and the fourth. Anteriorly on the anal plate there is a rather short stiff hair, ad 1, and further posteriorly a longer lanceolate hair, ad 2, fig. 2c. Further medially there are three hairs almost equally thick throughout, only slightly thinner at the tip. They represent an 1, an 2, and ad 3. IV (11: moist, rotten leaves).

Hoplophorella glauca n.sp.; fig. 3. Length of notogaster about 0.40 mm.

– – aspis – 0.20 –

Colour grey, when highly magnified showing a bluish-grey reticulation surrounding the light pits.

Seen in a lateral view the aspis has a transverse shallow depression in front of the lamellar hairs. In front of this furrow there is a low aspis keel. The rostral hairs are short, stiff, slightly curved, they are bent forwards, and situated on either side of the keel. The latter is bordered laterally by a broad depression, fig. 3a. The lamellar hairs are lanceolate and hyaline. The interlamellar hairs, also hyaline, are only half as long as the lamellar hairs. Due to their hyaline structure, I am unable to see them in a dorsal view. In the posterior part of the aspis there is a broad area with faint

longitudinal and indistinct transverse stripes together forming an indistinct reticulate pattern. The dorsal carina is shorter than the longitudinal stripes. The pseudostigmatic organs are almost equally thick throughout. They are undulating with the tip bent backwards. The distal end is set with a hyaline uneven structure, fig. 3a. A scale covers the opening of the pseudostigma from above. It has a forwards directed tip.

The notogaster has no prominent collar, on the contrary it slopes forwards. Seen in a dorsal view, fig. 3b, the notogaster is broadest a little in front of the middle line. On either side of the shoulder there is a short backwards directed keel. The posterior end of the notogaster is truncate. There are 15 notogastral hairs, which are shaped as small spoons, the distal end being hollow spoon-shaped, fig. 3c. In a dorsal view the hairs are lanceolate to narrow foliate. The sculpture consists of pits surrounded by bluish-grey ribs forming a distinct reticulation. No punctation.

Ano-genital region. On the genital plate there are four tiny hairs. Due to their hyaline structure they are only just discernible, the shortest distance being between number two and three. Anteriorly in the anal region there is a short, stiff backwards directed hair, ad1, further posteriorly a lanceolate hair, ad2. The anal hairs, which are bent forwards, are rather strong, thinner at the tip and a little shorter than the lanceolate hair. This species can be distinguished from *H. rangiroaensis*, also reticulate, by the absence of a prominent collar, and from *H. scapellata* (see later) by its short rostral hairs and its reticulate structure, *H. scapellata* being densely punctate. I (1: moist to wet Cyperus vegetation).

Hoplophorella scapellata Aoki; fig. 4.

– – , 1965a, p. 131, figs. 2–3.

There can hardly be any doubt that the specimens from Tahiti, shown in fig. 4, belong to AOKI's species from Thailand, although there are small differences concerning the aspis. On the posterior part of the aspis, fig. 4a, there are more stripes than in the type and these are restricted to an area behind the lamellar hairs. I have not been able to see the interlamellar hairs probably due to their minute size. Between the rostral keels there is a deeper incurvation than in the type, but this may be due to the position of the specimen while being drawn. The notogaster is densely punctate and for that reason the pits are rather indistinct as mentioned by AOKI. I (4:3), II (2:2), III (1).

Phthiracarus crispus n.sp.; fig. 5.Length of notogaster about 0.43 mm.---aspis-0.23Colour grevish.

The aspis is highest in its posterior third, in the middle flat or rather slightly hollow, whereafter it bends sharply ventrally. There is a distinct rostral keel. The rostral hairs, which are directed forwards, are short and thin. The very long, extremely thin lamellar hairs are directed forwards and slightly upwards. The interlamellar hairs are also very thin and rather long. The exact length of the lamellar and the interlamellar hairs is difficult to determine, as due to their delicate structure they cannot be seen in a dorsal view, only in profile. They may be equally long. The pseudostigmatic organ is setaceous, thinnest at the tip and directed forwards in a large curve. The exopseudostigmatic hair is distinct.

Notogaster is rounded, highest across its middle. The collar is broad. The notogastral hairs are very thin and difficult to see, the pores, however, are reddish and very distinct in the densely punctate greenish ground. The hairs are curly (hence the specific name). Most of them are directed forwards, the tip often bent backwards. There are several very distinct pores.

Ano-genital region, fig. 5 and 5a. On the genital plate 7 hairs can be seen, viz. five in a marginal row and two further laterally. Not all these hairs have been observed in profile. The adanal hairs are extremely thin decreasing in length towards the posterior end of the plate. The anal hairs, which are much stronger and equally long, are bent forwards and dorsally in a semicircular curve. In fig. 5a it can be seen that the sides of the notogaster are faintly depressed off the genital plates, which may be due to shrinkage although this seems unlikely.

III (6: rotten leaves; moss, Cyperus on moist soil; Oxalis, grass, small ferns on most soil).

Phthiracarus ?insularis Jacot; fig. 6.

– – – , 1934a, p. 233, fig. 4a, b.
Length of notogaster about 0.42 mm.
– aspis – 0.215 –

Colour light grey.

The Tahitian specimens recall *P. insularis* Jacot (1934a) from the Marquesas Islands. *P. insularis* is, however, a little larger, the notogaster measurering about 0.5 mm, while the pseudostigmatic organ is short and oval. Many of the notogastral hairs are not illustrated and for that reason a direct comparison cannot be made.

The Tahitian specimens have a flat aspis with a short posterior carina, fig. 6a. In profile a few light spots or reticulate meshes can be seen laterally to the carina. The rostral hairs are thin and curved upwards and forwards. The lamellar hairs are extremely thin but can be seen because their anterior part is raised above the surface of the aspis. They are approximately as long as their mutual distance. The interlamellar hairs are hardly discernible. The pseudostigmatic organs are short, lanceolate to almost round depending on the view in which they are seen. They consist of an inner transparent part surrounded by a broad hyaline border, fig. 6b. Exopseudostigmatic hair is absent. The integument of the aspis is densely punctate.

The notogaster is evenly rounded, highest at a level from e1 to the border between the genital and the anal plate. The collar is rather broad. There are 14 pairs of very

thin, curved notogastral hairs. In the middle of the notogaster they are bent forwards, on the sides backwards. Several distinct pores can be seen. Ps3 and ps2 are situated rather close together. This is indicated in JACOT's fig. 4a. The integument is densely punctate, the dots being yellow to yellowish-red on a light green ground.

Ano-genital region, fig. 6c. Only 7 pairs of genital hairs have been illustrated, but there may be 9–10, the anterior ones densely crowded on the anterior brim. The anal and adanal hairs are rather long and strong, directed forwards in a faint curve; ad1, however, thinner, shorter, and straight.

II (2: thick, moist moss on the base of a coconut palm; thin layer of moss on bark, III (2: short moss on moist soil).

Phthiracarus tubulus n.sp.; fig. 7.

Length of notogaster about 0.295 mm. - - aspis - 0.113 -

Colour greyish-whitish.

The posterior part of the aspis is rounded; it is more flat in the middle. On the posterior border there in a carina. The rostral hairs, which are almost bent at a right-angle, the two halves being equally long, are slightly rough. The lamellar hairs, which are directed backwards in a curve, are rather strong, distally they are uneven. Their mutual distance is about half as long as the hairs. The interlamellar hairs are hardly discernible. Behind and above the pseudostigma there is a scale covering just a small part of the pseudostigma. The smooth pseudostigmatic organ is long and slender, tapering towards the thin tip. No exopseudostigmatic hair has been observed.

The notogaster is evenly rounded. It is highest in the middle of its length. The collar is broad. There are 14 pairs of notogastral hairs. They are bent near their base, whereafter they form a broad curve. They are almost equally thick throughout, i.e. rather strong and easily seen. Ps3 and ps2 are situated in a deep tube situated ventrally to the line separating the notogaster from the anal plates (hence the specific name).

Ano-genital region, fig. 7a. The border between the genital and the anal plates is very rough with small irregular tongues and laterally on the genital plates with a tooth fitting into a notch in the anal plates. On the anterior part of the anal plates there is a curved line directed backwards and medially meeting the opposite one a short distance in front of an1. There are six genital hairs, of which the posterior one is stronger and longer than the others and separated from the anterior ones by a good distance. In the anal region there are five identical hairs bent and curved like the notogastral hairs. The anal hairs are directed forwards, the adanal hairs backwards. Ad1 and ad2 are situated approximately off the tubes with ps3 and ps2. In fig. 7a the adanal hairs are turned forwards. The left an2 is displaced posteriorly towards ad3, and the right ad3 is removed a little further from the median border than the left ad3.

II (4: Cyperus vegetation).

– – , 1965a, p. 133, figs. 4–6.

This very characteristic mite has been found in many samples. It agrees very well with AOKI'S excellent description and illustrations of the type from Thailand. The pits in the specimens from Tahiti are always very distinct, at a lower level shining gold on a bluish-green ground, which is densely punctate. I (5:2), II (2:2), III (6:4), IV (11:4).

Euphthiracaridae

Microtritia tropica Märkel.

– – – , 1964, p. 48, fig. 11.

III (2: moist moss; moist Leucobryum).

Rhysotritia ardua (C. L. Koch) var. otaheitensis n. var.; fig. 9.

Length of notogaster about 0.545 mm. Length of aspis about 0.240 mm.

The specimens from Tahiti differ from the main form by the shape of the pseudostigmatic organ and by a different number of claws. The pseudostigmatic organ is dilated distally into a flat head set with coarse bristles on its surface, fig. 9a; in a dorsal view bristles can be seen only on its distal border, fig. 9b. Some specimens have one claw only on all tarsi, while others have three claws on all tarsi. The specimen shown in fig. 9 is monodactylous. The ano-genital region is shown in fig. 9c.

Rhysotritia ardua ssp. *penicillata* Pérez-Iñigo (1968, p. 214, fig. 29) differs from the main form almost in the same way as the new variety from Tahiti having a clavate pseudostigmatic organ and two claws on all tarsi.

I (2: moist grass), II (4: moist moss; dead leaves, and rotten twigs), III (9: moist dead leaves; lichens on a tree trunk; moist Casuarina needles).

Indotritia sellnicki Aoki.

– – – , 1965a, p. 137, figs. 14–16.

II (15: wet moss; moist dead leaves), IV (7: moist moss and rotten twigs under shrub).

Austrotritia lebronneci Jacot; fig. 10.

– – , 1934a, p. 234, fig. 4c-h.

Length of notogaster about 0.93 mm. Length of aspis about 0.48 mm. Colour of notogaster black to mahogany red; aspis, legs, and ano-genital region light brown.

The specimens from Tahiti agree with JACOT'S description of the type from the Marquesas Islands apart from a few features. There are two lateral keels separated ny a good distance; the hairs both of the aspis and of the notogaster are rather thick and smooth, most of them directed forwards. Not all the notogastral hairs could be seen. The palps have five segments, not three as mentioned by JACOT. Coxa III has three hairs, Coxa IV five hairs, but I have not ascertained whether the latter is abnormal, fig. 10c. The genital and the aggenital plates are completely fused as also shown by JACOT, fig. 10b.

III (6: moist moss; dead leaves).

Epilohmanniidae

Epilohmannia pallida Wallw. susp. pacifica Aoki.

– , 1965b, p. 312, figs. 4–9.

The only specimen found agrees in every detail with AOKI'S description of the sub-species from Laysan Island, the Hawaiian Islands, apart from its slightly lesser size, measuring about 0,325 mm in length; the material measured from Laysan Island varying from 0.372 to 0.428 mm in length.

I (1: Cyperus vegetation beneath a hedge).

Lohmanniidae

Papillacarus hirsutus (Aoki), fig. 11.Cryptacarus---, 1961, p. 64, fig. 2.Length about 0.37 mm. Colour light brown.

The specimens from Tahiti differ a little from the type from Japan. The hyaline rostrum has an incurvation in the middle (AOKI: vorn fast gerade abgeschnitten). The pseudostigmatic organ has about 10 equally long secondary bristles besides three shorter, proximal ones. On its posterior border a few very fine bristles can be seen. In fig. 2b AOKI shows 14 bristles increasing in length towards the end of the organ, the second and the third distal ones differing by being much shorter.

The notogastral hairs as well as the many neotrichian hairs are much longer in the Tahitian specimens than in the type from Japan.

The ventral side, fig. 11a. In the type most of the genital hairs are branched. I am unable to see the branches.

II (2: Cyperus vegetation beneath a hedge).

Meristacarus tahitiensis n. sp.; fig. 12.

Length about 1.17 mm. Colour reddish brown.

This species agrees in most features with M. madagascarensis Balogh, 1962, p. 121, figs. 1–2, and also with the sub-species M. mad. obscurus Aoki, 1965 a, p. 139, figs. 17–18, from Thailand. The latter differs from the main form only by the absence of distinct fossulae and by having a characteristic indentation in the posterior end of the notogaster.

M. tahitiensis has the same indentation although less pronounced, but it differs in some important characteristics both from the main form and from the sub-species. Only these differences will be mentioned. Fossulae vitiformes are hardly discernible and there may be more than shown in fig. 12. In M. madagascarensis the fossulae are arranged in transverse bands only, in M. tahitiensis some are arranged in a more or less closed ring between d1-d1. The notogastral hair f1 is longer than in M. madagascarensis and in the sub-species obscurus and longer than the other notogastral hairs. The greatest difference is, however, the distance h1-h1, which is longer than e1-e1, almost as long as f1-f1, and almost twice as long as ps1-ps1. In M. madagascarensis the distance h1-h1 is the same as c1-c1 and e1-e1, whereas h1-h1 in *M. mad. obscurus* is the same as c1-c1 and shorter than the distance between any of the other pairs of hairs on the dorsal surface. Fig. 12a shows the hair ps1.

The ventral side, fig. 12b, differs slightly from that of *M. madagascarensis* and its sub-species *obscurus*. Thus the epimeric hairs 3c and 4c are thick and feathered like the notogastral hairs, fig. 12a. 2a and 3a are very short, thin, and finely barbed, the others are longer, thicker and have longer barbs. In *M. madagascarensis* and its sub-species all the epimeric hairs are alike, short and finely barbed. *M. tahitiensis* has only three pairs of adanal hairs. BALOGH mentions four for *M. madagascarensis* and illustrates a specimen with four on the right, five on the left plate. *M. mad. obscurus* has four adanal hairs.

II (3: short moss on a shaded slope).

Nesiacarus granulatus n. sp.; fig. 13.

Length about 0.52 mm. Colour light brown.

In the anterior border of the rostrum there is a low incurvation. The rostral hairs, the lamellar, the anterior exopseudostigmatic, and the posterior exopseudostigmatic hairs are approximately of the same length and alike, being finely feathered for most of their length, the tip smooth. The interlamellar hairs are similar to the others, only shorter. There is a distinct lateral tip or tooth a short distance in front of the hair exa. The pseudostigmatic organ is bent outwards and slightly backwards, its distal end thereafter a little forwards. It has about 12 secondary branches of which the two distal ones are a little shorter than the others. On its posterior border there are some very fine secondary bristles. A broad densely punctate band runs forward in a curve from the latero-posterior corner of the propodosoma almost touching the posterior border of the pseudostigmata. The entire integument is decorated with small granules except on the tip of the rostrum, which is hyaline, and along the lateral border.

The notogaster has two kinds of hairs, those on the dorsal surface being much shorter than those on the borders. The finely barbed dorsal hairs are bent and for that reason they appear too short in fig. 13. The distance d1-d1 is a little longer than f1-f1. E1-e1 is shorter than f1-f1. D2 and h1 are longer than the other hairs of the dorsal surface. The marginal hairs are long, undulating, finely barbed and have a smooth tip. In the posterior part of the notogaster there are some neotrichian hairs, partly a short one laterally to f1, partly 8 long, barbed hairs on the posterior border. Immediately behind c1 and c2 there is a broad punctate band, and in front of these hairs a thin line can be seen. Besides these distinct bands, there are four transversal bands, of which the two anterior ones do not meet in the middle of the dorsum. In the one, between e2-e2, some round spots can be seen, especially between e1-e1. The third fourth band is situated behind h1-h1. The integument is densely granulate.

The ventral side is shown in fig. 13a. The epimeric hair formula is 3:1:3:4. These hairs are short and barbed. The six medial genital hairs are short, the four lateral ones long, undulating, barbed and with a smooth tip. The two anal hairs are

apparently smooth, while the four adanal hairs are long, undulating with a very thin, smooth tip, and barbed for their proximal two thirds.

This species can be distinguished from N. reticulatus Csiszar, 1961, p. 346, figs. 1–2, from Java by its granulate sculpture, (N. reticulatus with a reticulate pattern), by the incurvation at the tip of the rostrum, and by its long undulating hairs, both on the notogaster and on the genital and adamal plates. The neotrichian hairs are in both species similar to the ordinary hairs.

II (1: Cyperus vegetation beneath a hedge).

Javacarus kühnelti Bal. var. foliatus n. var.; fig. 14.

- - , 1961 a, p. 31, figs. 39–40.

Length about 0.65 mm. Colour light brown.

So many features of the specimens from Tahiti agree with those of the type from Java that I do not hesitate in identifying them as *J. kühnelti*. Nevertheless there are differences justifying the establishment of a new variety. Thus the rostrum is hyaline without any sculpture, and the sculpture of the propodosoma consists of much larger spots than in the type. The pseudostigmatic organs have from 8 to 11 secondary branches besides some very short ones distally on the posterior border. In the main form there are 7 secondary branches. Most important are the much longer notogastral hairs, which are foliate. In the main form the hairs are lanceolate without a middle rib. I pay little attention to the difference between the main form and the variety in the pattern of the fossulae vittiformes as it is not even fully symmetric on the two sides of the dorsum in fig. 14. The variety has some undulating chitinized keels along the sides of the dorsum. They are especially well developed anteriorly, but not equally well developed in all specimens. The ventral side (HAMMER 1971 fig. 4a) agrees with that of the main form apart from a more irregular pattern of the sculpture. In the main form there is a linear pattern.

After having studied several specimens from Tahiti, it is evident to me that the only specimen found on Viti Levu, the Fiji Islands (HAMMER 1971, p. 7, fig. 4) also belongs to the new variety with a hyaline rostrum, pseudostigmatic organs with 10 secondary branches and foliate notogastral hairs. The keels along the sides of notogaster are less pronounced, but indicated in fig. 4. The pattern of fossulae vittiformes is a little different from that in fig. 14 from Tahiti. II (27: 10).

Hermanniidae

Phyllhermannia pacifica n. sp.; fig. 15.

Length about 0.57–0.70 mm. Colour light brown.

P. pacifica belongs to a group of *Phyllhermannia* species having two curved ridges in the anterior part of notogaster as is the case with *P. kanoi* Aoki, 1959, from South Japan and *P. gladiata* Aoki, 1965a, Thailand. The present species differs from

these two by having two large oval areas between the pseudostigmata and in the foliate notogastral hairs.

The rostral and lamellar hairs are situated laterally and are short and smooth. The interlamellar hairs, situated on the anterior border of a large, slightly oval area, are broad and leaf-shaped ending in a thin tip. They are directed backwards. The oval areas are surrounded by a ridge, which is indistinct medially. On their posterior border there is a rounded brown lobe. The areas are densely punctate. The pseudostigmatic organs are slightly thicker at the tip, which is covered with minute barbs and secreation. Along the sides of the propodosoma there is a pronounced ridge, ending posterirly in a strong lobe or tooth.

Notogaster. On either side the anterior part of the notogaster is a curved ridge opening medially. In a large specimen this ridge runs backwards to i3. Its anterior end continues medially, but more indistinctly, then it turns backwards thus forming a large framed area on either side of the middle of the dorsum, almost like the two areas between the pseudostigmata. The 16 pairs of notogastral hairs are leaf-shaped and translucent. They are narrowest at their base, then widen slightly towards the end, which tapers into a short thin tip. This is not always easy to see as the end is often bent ventrally. Apparently the hairs have proximally a rib disappearing towards the end of the hair. The dorsal surface of the hairs is set with minute bristles in longitudinal rows. Most of the hairs are of equal length, only those on the posterior border being shorter.

Ventral side, fig. 15a. Epimeres I, II, and III from the two sides are separated by a faintly chitinized sternal plate with a furrow at the middle. The posterior part of Epimeres III is a yellowish brown colour and differs from the anterior part, which is greyish and densely punctate like the other epimeres. Epimeres III and IV are separated by a strongly chitinized ridge, which is curved slightly backwards behind the sternal plate. The epimeric hair formula is 3:1:3(4?):5. The length of the hairs is difficult to see as many are directed ventrally.

On the genital plate there are six short medial hairs and three longer thin lateral hairs, of which the anterior one is much stronger than the two behind it. There are two aggenital hairs, one off either end of the genital field. The two anal hairs and the three adanal hairs are very short, smooth and thin.

The hairs of the legs are mostly thin and smooth, some are broader and more or less shaped like those on the notogaster.

Phyllhermannia species with the curved dorsal ridges mentioned above have so far only been found in Japan, Thailand, and Polynesia.

II (9: wet moss on stone wall; moist moss on foot of coconut palm), III (thin layer of moss on rotten three stump).

Nothridae

Nothrus oceanicus Selln.

– – , 1959, p. 110, fig. 1.

II (49:9), III (24:5).

Allonothrus schuilingi van der Hammen.

_ _ _ _ – , 1953, p. 244, figs. 1–3.

II (246:16), IV (375:5).

Allonothrus russeolus Wallw. var. reticulatus n. var.; fig. 16.

– – , 1960, p. 569, figs. 4–5.

– , Hammer, 1971, p. 10, fig. 9.

Length about 0.56 mm. Colour brown.

The new variety was first found on Viti Levu, the Fiji Islands (HAMMER 1971). It was, however, not established as a new variety, and only few differences from the main form were mentioned. More specimens have now been examined (only one adult was found on Viti Levu) and so many differences from the main form were found during this investigation that they justify the establishment of a new variety.

As already mentioned for the specimen from Viti Levu, the two oblique dark ridges in the middle of the propodosoma meet in a tip. The alveoli on the notogaster are not round or of the same size. They are of different shapes and sizes, very clear, almost luminous and separated from one another by a fine reticulation consisting of thin, white meshes on the brown ground (hence the specific name). Many of the notogastral hairs are rounded distally and not so distinctly truncate as in the main form.

The ventral side, fig. 16. The position of the epimeric hairs differs from that of the main form. Thus 1b is situated almost in the middle of the plate (in the main form further anteriorly), 3b is nearest the anterior border (in the main form near the posterior border). In the main form 1a, 2a, 3a, 3c, 4a, and 4c are setaceous, the remainder smooth. Most of these hairs are very short and furthermore erect for which reason it is almost impossible to see them distinctly and determine their appearance. 1a, 2a, and 3a might be setaceous, 1c and 3c I am unable to see. 4c is distinctly setaceous. The genital field has 13-14 pairs of rather long, apparently smooth hairs lying medially, crossing those from the opposite side. In the main form most of the hairs are setacous and lie laterally. The distance between the genital hairs is shorter at the anterior end of the plates. There are no aggenital hairs. Medially to ps3 a few indistinct alveoli can be seen. The posterior border of the ventral side between ps2-ps2 is rounded. All tarsi are tridactylous.

I (201: grass on dry soil under a tree), II (109: Cyperus vegetation; grass and Cyperus under coconut palms), III (77: moist rotten leaves).

Nanhermannia transversaria n. sp.; fig. 17.

Length about 0.53 mm. Colour clear brown.

The tip of the rostrum forms a small snout, on the lateral sides of which the rostral hairs are situated. They are bent ventrally. The sides of the rostrum form an $\mathbf{2}$

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even cone. The lamellar hairs do not reach beyond the tip of the rostrum. The interlamellar hairs are very long and almost equally thick throughout. The pseudostigmatic organs are distinctly thicker towards the tip where they widen into a small head, the upper surface of which is set with short spines, fig. 17 a. Each of the two crests on the posterior part of the propodosoma have three rounded tubercles, i.e. the medial ones broad, the middle ones narrow, and the lateral ones short and narrow. Further laterally less defined tubercles can be seen. There is no deep or distinct furrow between the interlamellar hairs, nor is the middle field well defined further anterior. The integument is pitted and densely punctate, also outside the middle field.

The hysterosoma is broadest across its posterior half. The 14 pairs of notogastral hairs, are very long, rather broad for most of their length, but the tip is very thin. Some of the hairs of the posterior end lie transversally across the notogaster (hence the specific name). The pits of the notogaster are of different sizes and are arranged more or less in oblique rows.

This species can be distinguished from N. nana (Nic.) (STRENZKE, 1953, p. 73, fig. 4) by the absence of a deep furrow between the interlamellar hairs, by the long distance between the posterior crests, and by the broad pseudostigmatic organs. III (11: thick luxurious moss).

Cyrthermannia luminosa Hammer; figs. 18.

- , 1971, p. 8, fig. 5. Viti Levu, the Fiji Isl.

Length about 0.54 mm.

The specimens from Tahiti differ a little from the type. They are a little longer, the type being 0.50 mm. The pseudostigmatic organs are longer and narrower. In fig. 18a two pseudostigmatic organs are shown, in fig. 18b two from specimens from the Fiji Islands. The latter are shorter and the head round and broad. The backwards directed triangular processes in the posterior part of the propodosoma are closer together than in the specimens from the Fiji Islands and their medial borders are almost parallel, fig. 18c. In specimens from the Fiji Islands, fig. 18d, the processes lie more laterally and proceed for a short distance into the transverse ridge. The furrow between the interlamellar hairs is well defined, deep and with two rows of small pits. In specimens from the Fiji Islands the furrow is less distinct, while its border diverges posteriorly and seems to continue into the medial border of the posterior processes. The propodosoma is decorated with deep regular pits, which are longest in the anterior part of the propodosoma. In specimens from the Fiji Islands the sculpture is irregular, the pits confiuent, separated by thick ribs.

Notogaster. No difference can be seen between the specimens from Tahiti and from the Fiji Islands concerning the notogaster. The notogastral hairs with the basal spur and the peculiar luminous dots in the light spots are alike in both groups, wherefore the differences found are probably only variations not justifying the establishment of a new variety.

This species can be distinguished from other *Cyrthermannia* species by the shape of the notogastral hairs with a spur and by the sculpture with the luminous dots. II (39: wet Cyperus meadow; rotten moist leaves).

Masthermannia mammillaris (Berlese).

- - , 1913, p. 100, fig. 92. II (65: 6), III (1).

Trhypochthoniidae

Trhypochthonius excavatus (Willm.). Camisia excavata – , 1919, p. 552, fig. 3. I (5: in a brook in the park), II (159: wet moss in oozing water).

Afronothrus sulcatus n. sp.; fig. 19.

Length about 0.53 mm. Width about 0.29 mm. Colour pale, the posterior part of the hysterosoma light brown.

This species agrees in most essential features with *A. incisivus* Wallw. 1961, p. 238, figs. 6–7. It differs, however, primarily by having a very distinct transverse furrow (sulcus) between the hairs d2. Laterally to d2 it widens, at the same time becoming more indistinct. There are lesser differences besides this important difference.

The rostrum is rounded. The rostral hairs, situated at some distance behind the tip of the rostrum, are long, smooth, and flexible. The lamellar hairs are situated on a narrow ridge, which apparently continues backwards as a lateral lamella. They are approximately as long as their mutual distance, stiff and erect. The interlamellar hairs are very long, thin, and flexible. The pseudostigmatic organ has a small almost circular, flat head on a short thin stalk. The integument of the propodosoma is densely punctate.

The notogaster is without a lateral incision on each side off cp. The humeral region is rounded and there is no tubercle anteriorly to the incertion of c3. The notogastral hairs are of very different lengths. C2 is very short, d2 about two thirds as long as c1, c3, cp, d1, e1, and e2, and thinner. F1 is absent, f2 is stiff and sickle-shaped. H2 is very long and thin, h3 is also thin, but a little shorter than h2. Ps1 is stiff like a spine, while ps2 is flexible and thinner. The fissure ia is not transveral but situated obliquely behind c3. Im can be seen as a faint indentation in the lateral border off d2, and ip between h1 and h2. The integument is reticulate to foveolate, the pattern being especially distinct at the posterior end of the notogaster. The lateral gland has a short protruding tube.

The ventral side, fig. 19a. The position of the epimeric hairs differs from that of *A. incisivus*. Thus 3b is not situated along the lateral border, but more medially. 4c is situated on the latero-anterior corner of Epimer IV and not in the middle of the lateral border. There are four genital hairs of which the two anterior ones are situated close together at the anterior end, one in the middle of the plate and the fourth between

the third and the posterior border. The anal hair is absent but its pore can be seen between ad3 and ad2. There are two adanal hairs. All the hairs of the ventral side are smooth. The sculpture consists of hexagonal meshes forming a reticulate pattern, which can be seen distinctly laterally to the genital plates.

All the tarsi have three equally thick claws.

IV (13: dead moist leaves).

Trhypochthonius javonicus Csiszar, 1961, p. 349, fig. 10, has long, thin and curved h3 and ps3 corresponding to h2, h3 in fig. 19 and in most features it shows great similarity to Afronothrus sulcatus. Csiszar, however, shows no ventral side, for which reason its relation to the present species cannot be concluded. Trhypochthonius breviclava Hammer, 1958, p. 24, fig. 20, which whole appearance recalls Afronothrus, does not, however, belong to the genus Afronothrus as it has six pairs of genital hairs, two pairs of anal hairs, and three pairs of adanal hairs. Epimeric formula is 3:1:3:2.

Archegozetes longisetosus Aoki.

- - , 1965 a, p. 147, figs. 26-28. II (2: wet Cyperus meadow), III (81: moist rotten leaves).

Malaconothridae

Malaconothrus hexasetosus Hammer.

– – , 1971, p. 9, fig. 7.

II (20:8).

Malaconothrus geminus n. sp.; fig. 20.

Length about 0.425 mm. Colour light to dirty brown.

Propodosoma. The rostral hairs, which are as long as their mutual distance, are very thin, smooth and are directed forwards. The lamellar hairs situated on the end of the lamellae, are thicker than the rostral hairs. They are directed forwards and reach beyond the tip of the rostrum, where they bend ventrally. The interlamellar hairs are very thin, flexible and almost reach the corner of the shoulder. The exopseudostigmatic hair is moderately long. The strongly curved lamellae are posteriorly parallel, then bend slightly medially and are again for some distance parallel, whereafter they turn medially almost at a right angle. They are equally broad for their whole length. Between Leg I and II there is a rather sharp process. The middle field between the lamellae is punctate with coarse, luminous punctures.

Hysterosoma. This is broadest off f2, however, the lateral borders are almost parallel. Behind h2 there is an incurvation followed by a small edge. The posterior end is slightly concave. There are two longitudinal ridges, with distinct lateral border, indistinct medial border, Furthermore there are two lateral ridges which only run to d2. All the ridges are dirty brown. Between the dorsal longitudinal ridges there are

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two indistinct transverse brown bands thus dividing the middle field into three parts. Surrounding the base of e1 there is a light area. The notogastral hairs are very variable both in length and thickness, but all are smooth. C1 and d1 are a little longer than c2, c3, cp, and d2. They are all strong and pointed at the tip. F2, h1, h3, and ps1 are shorter than c2, c3, etc., in addition h1 is besides thinner. E1, e2, and h2 are much longer than the others, flexible and very thin towards the tip. E1 and e2 are directed forwards. No sculpture can be seen.

Ventral side, fig. 20 a. The mentotectum has "nose-like" projections. The epimeric hair formula is 3:1:3:3. Some of the lateral epimeric hairs are rather long. The genital plates are much longer than the anal plates. There are 4(5?) very long, smooth genital hairs situated in the anterior two thirds of the plates. The distance between the anterior hairs is less than between the posterior ones. The three pairs of adanal hairs are almost as long as the genital hairs and also smooth. Anal hairs are absent. Ps3 and ps2 situated close together (geminus), are parallel and directed medially. They are smooth and as strong as the adanal hairs.

II (3: wet moss on stone wall; low vegetation of moss, grass, ferns, Cyperus).

Malaconothrus pachypilus n. sp.; fig. 21.

Length about 0.405 mm. Colour light brown.

Propodosoma. The anterior half of the propodosoma is narrow, the sides rounded, whereafter it suddenly widens forming on either side a strong process between Leg I and II. The rostral hairs, which are almost as long as their mutual distance, are thick and barved (hence the specific name), their tip is thin. The lamellar hairs, situated close behind the rostral hairs, are very thin and twice as long as their mutual distance. The interlamellar hairs are thinner than the lamellar hairs and as long as the latter. There are two short curved posterior lamellar ridges, one on either side and situated laterally to the interlamellar hairs. Their anterior end has apparently no direct connection with the long curved lamellae along the sides of the rostrum. The middle field is densely punctate.

The hysterosoma has parallel sides, and a rounded posterior end with an incurvation behind h2. Its anterior border is slightly convex. There are two distinct longitudinal ridges and more indistinct lines running partly to h3, partly backwards to a short curved transverse ridge situated between ps1. The two posterior fields bordered by these lines are a lighter colour than the three long anterior parts of the notogastral surface. All the notogastral hairs are alike, short, smooth, and thin. Their situation is shown in fig. 21. H1 is situated at the posterior end of the longitudinal ridge, i.e. further medially than found in most species. H2 and h3 are much longer and thinner than the hairs from the dorsal surface. The fissure ia is longitudinal, situated close to c2. Im can be seen in front of e2 and ip in front of h3. The integument is smooth.

Ventral side, fig. 21 a. The mentotectum has "nose-like" projections. The epimeric formula is 3:1:3:3. The genital and anal plates are equally long. There are four pairs of genital hairs situated in the anterior half of the plates. The two posterior hairs are very long and rather broad but tapering towards the tip. The two anterior hairs are apparently much shorter, but their actual length is difficult to see as the tips lie close together. The three pairs of adanal hairs are also very long and broad proximally. Anal hairs are absent. Ps3 is situated on a level with ps2. The latter, which bends outwards, is thinner and longer than ps3. All the hairs are smooth.

I (3: low plant), II (8: moist moss, grass, ferns, Cyperus), IV (1: moist dead leaves).

Trimalaconothrus crassisetosus Willm. var. fijiensis Hammer.

– – – – 1931 a, – – , 1971, p. 10, fig. 8.

II (2: wet moss on stone wall).

Trimalaconothrus albulus n. sp.; fig. 22. Length about 0.60 mm. Colour whitish.

The propodosoma is narrower at its base than the hysterosoma. The rostrum is broad and rounded. The rostral hairs are broad proximally, very thin at the tip. The lamellar hairs are as long as the rostral hairs, and are equally thick throughout. The lamellae are strongly curved being more or less S-shaped. Behind them a straight keel runs obliquely towards the anterior border of the hysterosoma. The interlamellar hairs are curved and extremely thin at the tip. The exopseudostigmatic hair is minute. Between Legs I and II there is a rounded projection. The space between the lamellae is densely punctate.

Hysterosoma. Its anterior border is straight almost forming a right angle to the lateral border. The lateral sides are slightly undulating especially behind e2. The posterior end is slightly pointed, its outline smooth. In the middle of the hysterosoma there is a broad groove bordered by round tubercles covering the whole surface, which can be seen at a deeper level in the groove. Between the tubercles the integument is densely punctate. All the notogastral hairs are thin and smooth; some of them, viz. e2, h1 and h2, are rather long ending in a thin curved thread. The distance c1-c2 is one and a half times longer than c1-c1; c2-c3 less than half c1-c1. C1-c1 and d1-d1 are approximately equal, e1-e1 a little longer. D1-e1 is one and a half times longer than d1-d1. The fissure ia is situated directly behind c2.

Ventral side, fig. 22 a. The mentotectum has "nose-like" projections. The epimeric hair formula is 2:1:2:2. Coxisternum IV from the two sides are separated anteriorly, fused posteriorly. Their posterior border has on either side a deep incurvation. The genital field is longer than the anal field. There are six pairs of genital hairs, all smooth. They are situated in the anterior two thirds of the plates. The adanal hairs are short, the distance ad1-ad2 is very short. The anal hairs are long and hardly discernible. Ps3 is short, ps2 long and curved. Faint tubercles can be seen also on the ventral side. The middle claw is a little thicker than the lateral claws only. This species is viviparous.

II (37: wet moss in oozing water).

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Liodidae

Liodes bataviensis (Selln.). Neoliodes bataviensis – , 1925 a, p. 463, figs. 7–9. II (1: wet Cyperus meadow).

Eremobelbidae

Fosseremus quadripertitus Grandjean.

– , 1965, p. 343, figs. 1–8.

II (7: wet Cyperus meadow).

Eremulus avenifer Berlese; fig. 23.

– – , 1913, p. 96, fig. 77.

Length about 0.395 mm, and thus considerably longer than mentioned by BERLESE (0.32 mm). It is very characteristic with its extremely coarse pseudostigmatic organs, which have several rows of stiff spines in their expanded middle, whereas the distal part is thin with scattered short and thin spines. However, the specimens from Tahiti have much longer rostral and lamellar hairs than shown by BERLESE. The interlamellar hairs are short and situated in the middle of the space behind the longitudinal lamellar ridges and the chitinous band between the pseudostigmata. The notogastral hairs are stiff and strong, slightly curved and unilaterally barbed. They are a dark colour but transparent at their base. The two anterior pairs are thinner than the others. Across the anterior part of the hysterosoma is a chitinous, undulating band, which is not always as distinct as shown in fig. 23. Behind it there are some light pits.

The three aggenital hairs are branched or star-shaped, the adanal hairs are smooth.

II (5: wet Cyperus meadow; wet moss on stone wall).

Eremulus curviseta Hammer.

– – , 1971, p. 15, fig. 14.

Length about 0.34 mm. Colour light brown.

This species can be distinguished by its long, thin interlamellar hairs, its broad band of pits across the anterior part of the notogaster on either end of which there is a hair, and by its slightly curved notogastral hairs. III (1: Oxalis, grass, small ferns on most soil).

Eremulus monstrosus n. sp.; fig. 24.

Length about 0.295 mm. Colour clear light brown.

This small species can be distinguished by its peculiar pseudostigmatic organs, which are very thick proximally and here set with five to six spines of various lengths, the longest distally. After this long spine follows a part without spines, the stalk at the same time becoming much thinner. On the distal half of the organ there are six very thin spines exclusive the long smooth tip.

Nr. 3

Propodosoma. The rostral hairs and the lamellar hairs are both very thin, the latter three times as long as their mutual distance. The distance between the lamellar ridges is longest anteriorly. At the posterior end of the lamellar ridges there is a slightly curved transverse ridge. Laterally to the lamellar ridges there is on either side a strong, curved ridge reaching to the base of the rostral hair. The interlamellar hairs are situated at a good distance behind the transverse ridge. They are very thin and longer than their mutual distance. Between the pseudostigmata can be seen several light spots or pits, and between the interlamellar hairs large polygone meshes.

The hysterosoma is much longer than broad. It is narrow anteriorly, rounded at the posterior end and broadest across the middle. A short distance behind the anterior border there is a transverse, very distinctly undulating, grey line behind which there is a row of light pits. The notogastral hairs are a light colour, and very thin, especially towards the tip. Those on the posterior border are curly. The anterior pairs are shorter than those behind the transverse band.

The ventral side has not been illustrated. It has the same appearance as shown by BALOGH for *E. flagellifer* Berl. in his Synopsis 1965, table 10, fig. 17. The branched, star-shaped and the ordinary smooth hairs are arranged in the same way. III (2: low moss on moist loomy soil beneath bracken).

Liacaridae

Furcoppia cornuta n. sp.; fig. 25.

Length about 0.425 mm. Colour light brown.

The propodosoma is narrow and partly hidden below the lamellae. The latter have cusps, which at their base are as broad as the proximal part of the lamellae. The latter are fused for a length corresponding to the length of the cuspis. On the cuspis there is a short medial tooth. The lamellar hairs are thick, feathered and approximately one and a half times longer than the cuspis. The rostral hairs are situated on short apophyses. They are broad, pointed at the tip and set with long thin bristles, fig. 25 a, b. In a dorsal view they are hidden under the cusps and the lamellar hairs. At the tip of the rostrum three pointed tips can be seen, fig. 25 a. In profile the lateral tips are almost as long as the lamellar hairs, ending in an extremely thin tip, fig. 25b. They are slightly bent at right angles and look like horns (hence the specific name). Their tip is bent ventrally; the right one can be seen behind the rostral hair, fig. 25b. Immediately behind the tip of the rostrum there is a light hole with a forwards directed tip on its posterior border, fig. 25a. The tutorium ends in a thin free tip at the base of the lamellar hair. The interlamellar hairs, situated on low apophyses, cross between the cusps. They are much thinner than the lamellar hairs and densely feathered. The feathered exopseudostigmatic hair is as long as the lamellar hair, but thinner. The pseudostigmata are completely hidden below the proximal part of the lamellae. The pseudostigmatic organs are spindle-shaped and for most of their length set with short upstanding bristles on both edges.

The hysterosoma is longish, oval, apart from the anterior border, which is almost straight. There are short, prominent shoulders. The 11 pairs of notogastral hairs are hardly discernible, two of them are situated on the shoulder.

The ventral side is shown in fig. 25 c. Apodemata II form together with the sejugal apodemata an almost regular broad oval, though faintly developed in its posterior middle border. There is a very faint sternal line. The epimeric hairs are thick and feathered and of different lengths. 3a, the longest, is situated on the anterior border of the fused Epimeres III–IV. 2a is the shortest. There are six genital hairs, viz. three on the anterior border, two near the lateral border, and one on the posterior border. The thick aggenital hair is situated rather laterally. The anal field is very broad, and the anal hairs extremely short and thin. The anterior one is situated close behind the anterior border and off iad, which is a little distance from the anal field. The adanal ahirs, situated with the same mutual distance behind the anal field, are as thin and as short as the notogastral hairs. The legs are rather long and slender with long, soft, densely feathered hairs. Genus I–II have a specially long ventral hair. On its ventral keel Femur II has a strong pointed distal tooth, fig. 25 d. Femora III–IV have a low ventral keel. All the tarsi have three claws of which the lateral one are very thin.

Remarks. F. cornuta is closely related to F. parva, Balogh and Mahunka, 1967, p. 43, figs. 15–16, Vietnam. However, it differs in several features as follows: the hysterosoma is longish, in F. parva almost circular; the tutorium has a free tip off the base of the lamellar hair, in F. parva it is much shorter; the exopseudostigmatic hair is very long and feathered, in F. parva it is a short thick brush; the tip of the rostrum has three long pointed tips, but in F. parva it has three rounded lobes; the aggenital hair is short and apparently smooth, while in F. parva it is thick and feathered; the broad oval between Apodemata II and the sejugal apodemata is not defined in F. parva; F. parva is smaller, being 0.372 mm long.

I (6: moist Cyperus; moist rotten leaves on the lawn in the park).

Carabodidae

Austrocarabodes imperfectus (Selln.). Carabodes imperfecta Sellnick, 1959, p. 119, fig. 4b. III (2: moss; dead leaves beneath shrub).

Carabodes luteo-auratus n. sp.; fig. 26.

Length about 0.35 mm. Colour yellowish-golden.

The rostral and the lamellar hairs are equally long, thin and smooth. The interlamellar hairs are perhaps a little shorter, smooth, and very thin. The lamellae are not distinctly defined medially. Their latero-anterior edge is thickened and gryish with deep pits surrounded by strong ribs. The posterior part of the lamellae has a smooth lateral border, but immediately in front of the pseudostigma there are small tubercles. The head of the pseudostigmatic organ looks like the head of a snake with a large fang. The integument between the lamellae is decorated with low, greyish tubercles on a yellowish-golden ground.

The border between the propodosoma and the hysterosoma is straight and there is no furrow separating the two parts. The shoulder has an undulating lateral border, but immediately behind the shoulder the lateral border is smooth for a very short distance. Then follow numerous round tubercles. The 10 pairs of notogastral hairs are short, foliate and have a middle rib, which is in the bottom of a groove, the sides of the hair being directed upwards, fig. 26 a. The end of those on the posterior border is directed ventrally and these hairs recall short fans, the ribs being very distinct in the hyaline hair and the end of the hairs invisible. Greyish tubercles cover the surface of the notogaster. The ground is yellowish-golden.

The ventral side, fig. 26b. The sternal plate is faintly developed between Epimeres II, otherwise well chitinized. The apodemata are brown bands on a greyishyellowish, reticulate ground. The sejugal apodemata form a brown transverse band, which is broadest in the middle. Apodemata III do not reach the sternal plate. In front of the genital field there is a curved brown band. The epimeric hairs are thin and smooth. The distance between the genital and the anal field is shorter than the length of the genital field. There are two pairs of genital hairs. The aggenital hairs are short and thin. Ad3 is situated off the latero-anterior corner of the anal field; it is thin. Ad1 and ad2, situated in a curve behind the anal field, resemble the notogastral hairs. Also the anal hairs are leaf-shaped. The sculpture of the ventral plate consists of low tubercles resembling those of the dorsal surface.

II (7: moss on coconut palm; moist rotten leaves; Cyperus meadow).

Otocepheidae

Nesotocepheus n. gen.

The lamellae are well developed, but do not extend beyond the insertion of the lamellar hair. There are two pairs of prodorsal and two pairs of notogastral condyles, 10 pairs of notogastral hairs, five pairs of notogastral fissurae, three pairs of genital hairs, one pair of aggenital hairs, three pairs of adanal hairs, and two pairs of anal hairs. The fissure iad is parallel to the sides of the anal field, not preanal. Coxa III has extremely long seta. The ultimate hairs of the tarsi are long, hook-shaped, and thickened at the tip.

Nesotocepheus setiger n. sp.; fig. 27.

Length about 0.73 mm. Colour dirty, light brown.

Propodosoma. The margin of the rostrum is hyaline. The rostral hairs are inserted laterally and cross in front of the tip of the rostrum. They are unilaterally dentate and taper towards the tip. The rostral hairs, situated on the end of the lamellae, are straight, thick, feathered to bushy, at the base less bushy, and reach for half their
length beyond the tip of the rostrum. The lamellae are low, almost parallel keels, which are proximally smooth, distally undulating. Between the lamellar hairs there is a ridge continuing laterally to the lateral border of the rostrum. The interlamellar hairs resemble the lamellar hairs. They are situated at a level a little in front of the pseudostigmata and their base is surrounded by a ring, which is most pronounced laterally. The pseudostigmata are small cups, which open laterally. The pseudostigmatic organs are short, spatulate, broadest distally and the head is set with coarse bristles. On the posterior border of the propodosoma there are four condyles of approximately the same size. The medial condyles are separated by a distance a little longer than the width of the condyles. Their medial border continues forwards as faint keels between which there is a furrow with faint pits. The integument of the propodosoma is decorated with deep round pits, anteriorly arranged in transverse rows, posteriorly in curved rows.

The hysterosoma is broadest across ms-ms. The posterior end is rounded, the anterior border slightly concave and set with four condyles. The two lateral condyles are rounded and protrude only slightly, whereas the two medial ones are short, angular and separated by a distance much shorter than that between the anterior medial condyles, fig. 27 a. There are 10 pairs of notogastral hairs which are stiff, almost smooth in their proximal third, bushy to feathered distally, and equally long. There are five pairs of fissures. Ia is longitudinal, off ta. Im is transversally situated between te and ti but more laterally. Ih can be seen in front of ms, ips between r3 and p3, and ip between p3 and p2. The integument is decorated with small, irregularly scattered luminous dots.

Ventral side, fig. 27 b. The sternum is well developed. Apodemata II and the sejugal apodemata are straight and parallel. Apodemata III do not reach the genital field. The epimeric hair formula is 3:1:4:2. The hairs are smooth; 1b, 1c, and 3b are longer than the others. The integument of the epimeres is pitted, medially with larger grooves. The genital field is separated from the anal field by a distance three and a half times the length of the genital field. It is the same light colour as its surroundings and the plates are smooth. There are three pairs of smooth genital hairs, the two anterior pairs being the longer. Also the aggenital hairs are smooth. The anal plates have parallel sides, the anal hairs being long and slightly barbed distally. The adanal hairs are a little thicker than the anal hairs and distinctly barbed in their distal half. Ad3 are preanal. The two hairs are situated with the same mutual distance as ad2. Ad1 are postanal and their mutual distance is shorter. Iad is almost parallel to the side of the anal field, a little distance from the latter. The integument of the ventral plate is decorated with small light dots between which the integument is densely punctate.

Legs. Coxa III with a feathered hair as long as the coxa and the femur together. Distally all femora have a broad, soft, feathered hair, fig. 27, the genus with a similar but shorter hair. Fig. 27c shows Tibia and Tarsus I. III (4: moss; dead leaves; moist, rotten branches).

Oppiidae

Quadroppia circumita (Hammer).

Oppia – – , 1961, p. 48, fig. 39. II (1: moss on tree trunk), III (1: moist moss on the ground).

Oppiella nova (Oudms.).

Oppia neerlandica (Oudms.), Willmann, 1931 b, p. 128, fig. 132. II (2: 2), III (11: 5).

Oppiella polynesia n. sp.; fig. 28.

Length about 0.205 mm. Colour light brown to brown.

Propodosoma. The rostral hairs are almost smooth, and situated on the dorsal surface but far laterally. In front of them can be seen a faint curved line. The very narrow lamellae converge for most of their length but are parallel in their distal third. There is a translamella and short cusps, which are square. Only the outer border of the lamellae is distinct. The lamellar hairs, which are directed medio-anteriorly, are shorter than their mutual distance. Off the cusps a distinct line runs obliquely forwards disappearing. The integument of the anterior part of the propodosoma is smooth. In the space within the lamellae there are anteriorly four square spots, besides some irregular spots laterally to the latter. In the posterior half there are round light spots arranged round a darker middle area. The interlamellar hairs, that are as long as the lamellar hairs, are situated off the posterior round spots. Behind the interlamellar hairs there are two oblong chitinous projections, almost reaching the anterior border of the hysterosoma. On its posterior border the pseudostigma has a tooth corresponding to a lateral tooth on the hysterosoma. The pseudostigmatic organs are spindle-shaped, the head pointed at the tip and the outer border set with 9-12 bristles as long as the width of the head, the proximal ones shorter.

The hysterosoma. On the anterior border there are two strong teeth, the inner margin of which proceed backwards as faint keels. Ta is situated medially to these teeth. The notogastral hairs are arranged as shown in fig. 28. They are strong, slightly pectinate. Ti, ms, and r2 are directed medially. The distance r1-r1 is only a little longer than p1-p1.

The ventral side is shown in fig. 28 a. It shows no characteristic features.

This species closely resembles Oppia bituberculata Balogh, 1958, p. 15; 1961 b, p. 71, figs. 12–14, Oppiella suramericana (Hammer), 1958, p. 48, fig. 51, and Oppia africana Evans, 1953, p. 260, fig. 2. Both in O. biturberculata and in O. africana the integument in front of the lamellar region is finely pitted, in O. suramericana and in the present species it is smooth. O. suramericana has a semilunar chitinous plate immediately in front of the anterior border of the hysterosoma, but this is absent in O. polynesia. None of the three comparable species has the lines running forwards in front of the lamellae, nor the nicely decorated field between the lamellae. II (9: moss on the trunk of a coconut palm).

Oppia Winkleri Hammer. – – – , 1968, p. 56, fig. 76. I (1: moist rotten leaves in a ditch).

Oppia lanceosetoides Hammer.

- - , 1971, p. 25, fig. 25. II (25: moist moss on dead branches).

Striatoppia opuntiseta Balogh & Mahunka; fig. 29.

, 1968, p. 342, figs. 3-4.

The Tahitian specimen illustrated is 0.235 mm. long. Colour brown.

Although there are small differences between the type specimen from Indonesia and the specimen from Tahiti, especially concerning the development of the lamellae, which are much better developed in the Tahitian specimen, both specimens belong without any doubt to the same species. For this reason only a few features will be mentioned. Besides having stronger lamellae, on either side of the area with the four spots a ridge runs oblique to the lamella reaching the latter a little in front of the pseudostigma. The minute interlamellar hairs are situated between this ridge and the lateral border of the area with the four spots.

On the anterior border of the hysterosoma there are two rounded teeth on which ta is situated. The fissure ia can be seen immediately behind ta.

On the ventral side, fig. 29 a, a longitudinal ridge can be seen running across the fused epimeres III–IV. Medially to this ridge there is a feature resembling a split. The posterior border of the fused Epimeres III–IV partly covers the lateral border of the genital field. The length and the thickness of the hairs of the ventral side differ in the type and in the Tahitian specimen, but this may be due to the position of the hairs, erect or lying appressed. The epimeres are reticulate, the integument of the ventral plate densely punctate between the longitudinal lines running rather symmetrically on the two sides.

II (1: wet Cyperus meadow).

Striatoppia lanceolata n. sp.; fig. 30.

Length about 0.215 mm. Colour yellowish-light brown, usually dirty.

The present species is much like the preceding one and for that reason mainly the differences will be mentioned. The lamellar hairs are lanceolate, narrow at the base, pointed distally. They are set with tiny bristles. The interlamellar hairs are tiny as in the preceding species and are situated similarly. The integument within the space of the lamellae, and on the long keels with the rostral hairs, is longitudinally striated and the lines are set with small dark tubercles.

On either side of the anterior border of the hysterosoma there is a small rounded tubercle on which is situated ta, that is brush-shaped and directed forwards. The remaining notogastral hairs are lanceolate like the lamellar hairs. Those on the posterior border are smaller. Issuing from the anterior border of the hysterosoma, a few lines run backwards for a short distance.

The ventral side is shown in fig. 30 a. Epimeres I are separated by a broad sternal plate, Epimeres II and the fused Epimeres III–IV are separated by a narrow ridge only. Apodemata II are narrow, the sejugal apodemata very broad. The epimeric hairs are short, some of them lanceolate. The epimeres are bordered by lateral ridges as is also the case in the preceding species. The longitudinal ridge in the fused Epimeres III–IV is short. From this ridge a thin line runs backwards to the posterior border of the epimeres. The epimeres are reticulate. The distance ad3–ad3 is much longer than in the preceding species. There are a few lines only on the ventral plate, all of them issuing near the genital field.

This species is related to *S. papillata*, Balogh & Mahunka, 1966, p. 32, figs. 15–16, Brazzaville-Congo. However, the latter does not have the two distinct keels on the propodosoma with the rostral hairs, and the lamellae are only faintly developed. Also the ventral side shows differences. Thus the short longitudinal ridge in Epimeres III–IV is absent and the hair b3, which is lanceolate and situated on this ridge, is displaced laterally and is very thin in *S. papillata*. On the ventral plate there are many irregularly running lines.

I (59:13), II (3:3), III (1).

Multioppia wilsoni Aoki.

- - - , 1964 a, p. 652, figs. 6-8. I (5: moist Cyperus vegetation in the park).

Multioppia gracilis n. sp.; fig. 31.

Length about 0.335 mm. Colour light brown.

The rostral hairs are barbed proximally, the distal part smooth and bent medioventrally. The lamellar hairs are situated on the end of two strongly converging lamellae of which, only the distal part is developed. These hairs are smooth and shorter than their mutual distance. The interlamellar hairs, which are directed upwards, are perhaps a little longer than the lamellar hairs and also smooth. The three pairs of light spots between the interlamellar hairs are of different width, the middle one being broadest, and having the shortest mutual distance. The three from each row are situated closely together. The exopseudostigmatic hairs are slightly barbed and situated on low tubercles. The pseudostigmatic organ differs from that of most other species within the genus by its very long and slender secondary branches on a thin stalk (hence the specific name). From fig. 31 a, b it can be seen that there are four long branches on the posterior border, slightly decreasing in length towards the distal end of the organ and 4–5 short ones on the anterior border. The proximal one is as long as the stalk. The latter is a little broader off the long branches.

The hysterosoma is very broad, almost circular. The 12 pairs of notogastral hairs are arranged as shown in fig. 31, viz. in more or less transverse rows. This is most evident with 1p, dp and h2, h1 from the two sides. H3 is situated unusually far medially and posteriorly, in front of h2. H3, h2, and ps3 are situated on a longitudinal line. Ps3, ps2, and ps1 are situated rather close together, all of them in a line behind h1.

Ventral side, fig. 31 c. The sternum is well developed for its whole length. It is slightly dilated between Apodemata II. On the anterior border of the sejugal apodemata there are two rounded projections near the sternum. The epimeres are faintly reticulate. The epimeric hair formula is 3:1:2:3. Tectopedium IV ends in a short pointed tip. The distance between the genital and the anal field is less than twice the length of the genital field. The genital field is very narrow, the anal field rather broad. There are five pairs of genital hairs, viz. three anterior pairs in two longitudinal rows, one near the latero-posterior border, and one at the posterior border. One pair of aggenital hairs. Three pairs of adanal hairs. Ad3 is preanal and is situated far laterally, ad2 off an1. Ad1 are postanal and are situated rather close together. Iad is parallel to the sides of the anal field. There are two pairs of anal hairs. All the hairs are smooth.

The present species is closely related to *M. pectinata*, Bal. & Mah. 1967, p. 47, figs. 29–30, from Vietnam, and to *M. pectinata*, Aoki, 1967, p. 192, figs. 3–8, from Thailand. Both of them have very long secondary branches on the pseudostigmatic organs, decreasing in length towards the end of the organ. *M. pectinata*, Bal. & Mah., has very long notogastral hairs, while the present species has short notogastral hairs. *M. pectinata*, Aoki, has no knee-bent, barbed rostral hairs as the present species, nor lamellar ridges.

III (2: moist moss on the ground).

Ramusella chulumaniensis (Hammer), var. curtipilus Hammer.

– , 1971, p. 26, fig. 26.

II (13: moss on dead branches).

Machuella ventrisetosa Hammer.

– , 1961, p. 70, fig. 59.

II (6: moss on dead branches; moss on the ground).

Fig. 32 shows a specimen a little smaller (0.19 mm long) than the typical *M. ventrisetosa* (0.20 mm). In addition to this difference in size it differs by having a light, rosetteshaped figure between the pseudostigmata. The lamellar and the interlamellar hairs are apparently absent, the same applies to most of the notogastral hairs. There are no lines on the notogaster issuing from the anterior border of the latter. When laid bare the pseudostigmatic organ is very slender, fig. 32 a. As only one specimen was found, it is doubtful whether it represents a variety or a separate species. II (1).

Suctobelbidae

Suctobelba variosetosa Hammer.

– – – , 1961, p. 43, fig. 35.

I (31: mouldering leaves on a lawn), II (5: 4).

Suctobelba semiplumosa Bal. & Mah., var. tahitiensis n. var.; fig. 33.

– – – , 1967, p. 48, figs. 27–28, Vietnam; o. 1825 mm long. Length about 0.205 mm. Colour very light brown.

The specimens from Tahiti resemble the type from Vietnam in most characteristic, viz. by the proportionately long propodosoma, the long tectopedial field and the space between the latter, the two long projecting rostral teeth (which for the variety can be seen in fig. 33 a), the very coarse proximal part of the rostral hairs, the closed lamellar knob, the large interpseudostigmatic ridges, and the long, barbed pseudostigmatic organs. BALOGH & MAHUNKA neither mention nor illustrate the well developed lamellae.

The variety differs in the shape of the median teeth on the anterior border of the hysterosoma. They are strong, triangular and not "semicircular, short". Of the notogastral hairs only two are feathered, besides the short ones on the posterior border, viz. r2 and r1. R2, which is the thickest, is directed medio-posteriorly. The remaining hairs appear smooth or perhaps slightly uneven. BALOGH & MAHUNKA write "others smooth or hardly ciliate" but ti, ms, and r3 are shown distinctly feathered leaving only ta and te smooth.

The ventral side agrees with that of the main form. All the hairs of the ventral plate are rather long and all except ad1 are directed medially. Ad1 are situated off the latero-posterior corner of the anal field. The two posterior genital hairs are situated closely together.

III (2: moist Leucobryum).

Suctobelba insulana n. sp.; fig. 34.

Length about 0.175 mm. Colour light brown.

The propodosoma is short as compared to the hysterosoma. The rostrum protrudes slightly and appears broad due to the broad apical lobe. There are two almost equally long rostral teeth, separated by an incision, which is rounded at the bottom, fig. 34 a. Behind the teeth there is a slit. The tectopedial field is short, and its outer border is smooth without tubercles. There are no tubercles in the space between the tectopedial fields. The lamellar knob is pointed anteriorly, closed posteriorly. The lamellae are short, not fully reaching the lamellar knob. Each lamella has two small tubercles corresponding to similar tubercles on the posterior border of the tectopedial field. The interpseudostigmatic ridges, situated close to the pseudostigmata, are large, ending posteriorly in a small lobe opposite the medial tooth of the hysterosoma. The pseudostigmatic organs are very long, their end tapering to a thin tip. Most of the head is set with numerous, short bristles. Exopseudostigmatic hair was not observed.

The hysterosoma has four equally strong teeth, all proceeding for some distance backwards as faint keels. The 9 pairs of notogastral hairs are all smooth. Apart from those on the posterior border most are long and strong. Many of them are situated unusually far medially, this applies especially to r3 and r2. The mutual distance of r2 is only a little longer than that of r1.

Ventral side, fig. 34b. The sternal plate is dilated between Apodemata II, and still more between the sejugal apodemata, narrow between the fused Epimeres III–IV. The latter are surrounded by a chitinous ring, which does not reach the sternal plate. There are six genital hairs, of which the two anterior ones are very long and directed forwards. The aggenital hairs, and ad3, ad2 are long and directed medially. Ad1, situated on the latero-posterior corner of the anal field, is directed posteriorly.

II (1: thin moss on the ground in deep shade), III (1: moist moss on the ground).

Suctobelbila dentata (Hammer).

Rhyncobella – – , 1961, p. 46, fig. 37. I (10: dead leaves on a lawn), II (10: wet Cyperus meadow).

Suctobelbila squamosa (Hammer) var. scutata n. var.; fig. 35. Rhyncobella – – , 1961, p. 47, fig. 38. Length about 0.16 mm. Colour light brown.

The variety differs from the main form primarily by the shape of the anterior part of the notogaster being shield-shaped (hence the variety name). Two long keels run from the latero-anterior border of the hysterosoma medio-posteriorly forming faintly protruding shoulders. The variety has, moreover, very distinct notogastral alveoli, surrounded especially laterally by strong ridges. In profile they appear like tubercles or embossments. The notogastral hairs are partly situated within these alveoli. Only 9 pairs could be seen, the anterior one being absent or impossible to see. The sculpture of the hysterosoma consists of irregular scales arranged in irregular rows.

The sculpture of the propodosoma is much like that of the main form, but the dark scales are arranged in regular, transverse rows. No rostral teeth were observed. The lamellar hairs are absent, their pores situated closely together between two dark, rounded scales. The interlamellar hair pores can be seen on the posterior ridge near the pseudostigmata.

Remarks. I am a little in doubt whether the only specimen found represents a separate species or a variety as described above. The notogaster in *S. squamosa* is embossed, which can be seen in HAMMER, 1961, fig. 38, 38 b, although not to the same degree as shown for the variety. BALOGH, 1968, p. 268, figs. 41–44, has established two new species from New Guinea, without teeth on the anterior border of the hysterosoma, based especially on the number of tubercles or embossments on the notogaster, but without showing details of the propodosoma. As long as we do not know how much the structure of the propodosoma and of the notogaster varies it is perhaps too early to establish too many new species.

II (1: Cyperus vegetation beneath a hedge).

Biol.Skr.Dan.Vid.Selsk. 19, no. 3.

Hydrozetidae

Hydrozetes lemnae (de Coggi).

- - - , Grandjean 1948, p. 328, figs. 2-3. I (7: brook in the park), II (128: moss in oozing water).

Tectocepheidae

Tectocepheus velatus (Michael). *Tegeocranus* – – , 1884, p. 313, plate 21, figs. 9–15. I (numerous: 17), II (56: 8), III (11: 7).

Cymbaeremaeidae

Scapheremaeus bicornutus Hammer.

– – , 1971, p. 30, fig. 32.

I (1: rotten leaves on a lawn).

Licneremaeidae

Licneremaeus polygonalis Hammer.

- - , 1971, p. 29, fig. 31. II (1: moss on dead branches), III (2: dead branches), IV (8: rotten leaves).

Eutegaeidae

Eutegaeus biovatus n. sp.; fig. 36.

Length about 0.82 mm. Colour mahogany red.

The cusps project for a good distance beyond the tip of the rostrum. The latter is rounded. The rostral hairs, situated on low apophyses, are short, thick and apparently smooth. They are bent ventrally. The distal fourth of the lamellae bends slightly downwards along a rather sharp crest issuing near the medio anterior border of the lamellae and running obliquely forwards and laterally. The cusps are broader than the lamellae leaving a rather narrow space between them. In this space the tip of the rostrum can be seen. The cusps are evenly rounded laterally, their lateral border ending in a strong tooth, their medial border in a much more pointed tooth, directed medially. The lamellar hairs are thick, serrate and strongly curled into a sling. The interlamellar hairs are situated on the anterior border of two bent ridges forming the anterior end of two ovals. The posterior border of the ovals is composed of two short semilunar ridges. The anterior and the posterior ridges are connected by indistinct lines, thus forming two oval areas (biovatus), which are a slightly lighter colour than the surroundings. The interlamellar hairs are rather short, directed forwards, their tip medially. The pseudostigmatic organ is clavate, broadest distally and set with minute bristles. It almost reaches the lateral border of the forwards directed projection from the hysterosoma.

The hysterosoma is a little broader than long. The forwards directed projections have parallel sides, their tips are rounded although a little flattened laterally. On their ventral border there is a small finger-like distal tip. An indentation can be seen in the lateral border at the transition between the projections and the sides of the hysterosoma. There are five pairs of equally long and thick notogastral hairs situated more or less in two rows parallel to the sides of the hysterosoma. On the posterior border there are three pairs, viz. two stiff hairs, r1 in the middle situated on two small tubercles and on either sides of these two very short and fine hairs, p1 and p2. P3 was not observed. All the hairs are smooth.

The ventral side was not studied as it is in poor condition and most of the hairs are missing.

This species can be distinguished from *E. papuensis* (Aoki 1964b, p. 301, figs. 1-11), with which it is closest related of the species described so far, by its pointed lamellar teeth, its strongly curled lamellar hairs, the narrow space between the cusps, the two ovals behind the interlamellar hairs, and the longer club-shaped pseudostigmatic organ.

III (5: moist moss on the ground; moss on a rotten tree stump).

Microzetidae

Microzetes auxiliaris Grandjean. _

, 1936, p. 138, figs. 1-4.

I (6: rotten leaves), II (1: moss on a coconut palm trunk), III (5: drv moss).

Pelopsidae

Eupelops tahitiensis n. sp.; fig. 37.

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Length about 0.50 mm. Colour brown.

The tip of the rostrum is rounded; the longitudinal furrow in the rostrum widens anteriorly. The lamellae are apparently narrow, vertical blades with a horizontal medial part connecting the lateral parts. I am, however, not sure that the structure has been interpreted correctly. The cusps, which are almost as long as the lamellae, are very narrow and pointed, their tips lying close to the rostrum. The lamellar hairs, situated a good distance behind the tip of the cusps on the ventral side of the latter, are almost as long as the lamellae. They are densely barbed. In front of the indistinct translamellar line there is a forwards directed tip. There is a very long, slightly uneven hair (the rostral hair?) laterally to the interlamellar hair, disappearing under the pseudostigmatic organ. It reaches as far forwards as the lamellar hair. The pseudostigmatic organs are slightly thicker in their distal half. Tectopedium I is dark brown and has a keel on its outer side.

The hysterosoma is seen in an oblique view in fig 37 and for that reason it appears too short. No layer of secretion. The anterior projection between the pseudostigmata is slightly concave at the middle. The notogastral hairs are short, approximately equally long, slightly curved, uneven, and almost equally thick throughout. I2 and s3 are situated close together. Medially to i1 there is a small pore. R2 and r3 cannot be seen due to the oblique position of the mite.

The legs. Tibia I has a lateral, almost smooth, sword-like spine, Tarsus II and Tibia II a similar lateral spine, the largest one on the tarsus. All the tarsi are tridac-tylous.

II (8: wet moss; moist Cyperus vegetation; Cyperus and red clover).

Eupelops crassus n. sp.; fig. 38.

Length about 0.70 mm. Colour mahogany red.

The tip of the rostrum projects as far forwards as the tip of the lamellae. The latter are very broad, strongly chitinized and have broad cusps. The medial border of the cusps is evenly rounded, in its lateral border there is an incurvation thus forming an outwards directed tooth. The lamellar hairs, situated on the ventral side of the cusps at a good distance from the tip, are very coarse, thick, and bushy. They are directed obliquely forwards and medially, fig. 38 a. The rostral hairs, seen in fig. 38 a, are longer than the lamellar hairs, equally thick throughout, and uneven or finely barbed. The translamella is broad. The interlamellar hairs are of the usual shape, hyaline, broad, and set with cilias. The pseudostigmatic organs are fusiform and reach the lamellar hairs.

The hysterosoma. The broad anterior projection is slightly concave, its sides sloping rather steeply to the anterior border of the pteromorphae, but without pronounced lateral lobes. The notogastral hairs are thin, stiff, clear, slightly serrate spines. S1, s2, and s3 are situated along the side near the pteromorphae, s4 in the posterior end. Not all the hairs could be seen.

The legs. Tarsus II has a strong, serrate, lateral spine, Tarsus I a much thinner one. Tibiae I–II have a spine similar to that of Tarsus II. Monodactylous, the claw with a tiny secondary inner tooth near its base. III (30: dead leaves).

Eupelops polynesius n. sp.; fig. 39.

Length about 0.49 mm. Colour mahogany red.

As in the preceding species the lamellae are very strong. The tip of the cusps are bent medially, almost forming a ring round the very narrow rostrum. The latter projects for a good distance beyond the cusps. Its tip is pointed. On the tip of the cusps there is a small clear spine behind which the lamellar hair is inserted, fig. 39a. The latter is equally thick throughout and finely barbed. It is directed straight forwards and reaches almost to the tip of the rostrum. The rostral hairs resemble the lamellar hairs, but are longer, and run parallel to the lamellar hairs. The interlamellar hairs are very short (broken?) and do not reach beyond the cusps. The pseudostigmatic organ is densely set with bristles, and slightly thicker in its distal half.

The hysterosoma. The anterior projection is slightly concave at the middle with low rounded lateral corners. The notogastral hairs are thin, stiff, and hyaline. They are arranged as in the preceding species.

The legs. Tarsus II has a short serrate lateral spine, Tarsus I a much tinner spine. Tibiae I–II have a lateral spine as strong as that of Tarsus II. Tarsus III has two branched spines. Genu and Tibia IV each with a short, almost smooth, distal spine. Monodactylous.

III (3: moss; dead leaves).

Oribatellidae

Lamellobates palustris Hammer.

- - , 1958, p. 100, fig. 124. I (very common: 31), III (8: 4), IV (3: 2).

Eremaeozetes tuberculatus Berlese.

– – – , 1913, p. 92, plate VI, fig. 63.
 I (2: clover, grass in a lawn; dead leaves, bark, branches on a lawn).

Galumnidae

Galumna flabellifera Hammer.

– – – , 1958, p. 93, fig. 116. I (102: 15), II (11: 2), III (10: 2).

Galumna pterolineata n. sp.; fig. 40.

Length about 0.60 mm. Colour light brown (young individual).

The rostrum is rounded distally. The rostral hairs, situated on the ventral surface, fig. 40 a, are straight and barbed. They reach only a little beyond the tip of the rostrum. The lamellar hairs are stronger than the rostral hairs, and are unilaterally barbed. They follow the outline of rostrum and reach the tip of the latter. The interlamellar hairs are as thick and as long as the rostral hairs, but are almost equally thick throughout, not thin at the tip as the lamellar hairs. The lamellae are indistinct, the sublamella well developed. The integument of the propodosoma is very finely wrinkled, but perhaps this pattern can only be seen because a young individual is illustrated. Behind a line a little in front of the interlamellar hairs the wrinkles are less dense. The pseudostigmatic organs are thin setae, densely barbed in their distal two thirds.

The hysterosoma is not separated from the propodosoma by a dorso-sejugal line, not even by a different colour or another pattern as the thin wrinkles can be seen as far as Aa. The pteromorphae have distinct narrow yellow ribs with a rough surface (hence the specific name). The areae porosae are not well defined probably due to the youth of the individual. For this reason it is difficult to see the exact shape of the areae porosae. Aa and A1 are approximately of the same size and round. A2 is absent. A3 is oblong, but as large as Aa and A1. The hair pores are arranged as shown in fig. 40. No hairs were observed.

The ventral side is shown in fig. 40 a. The three anterior apodemata are short chitinous ridges. Apodemata IV are absent. The epimeric hair formula is 1:0:2:2. All the hairs are long and barbed. The hairs issue from a small pore situated in the close vicinity of a much larger pore, fig. 40 b, which shows 4a. Only five pairs of genital hairs can be seen. The two anterior ones are long, thin, and barbed, the others shorter and apparently smooth. The aggenital, anal, and adanal hairs are minute. No area porosa postanalis was observed. All the tarsi are tridactylous, the middle claw being only twice as strong as the lateral claws.

III (9: moist Casuarina needles; moist rotten leaves and grass).

Galumna inperfecta n. sp.; fig. 41.

Length about 0.64 mm. Colour reddish to mahogany red in a broad belt in front of A1. Only one specimen was found of this very characteristic Galumna and unfortunately the left pseudostigmatic organ is missing and the tip of the right one apparently broken. Nevertheless it will be stablished as a new species, as probably it cannot be taken for any other species. The tip of the rostrum is pointed and on either side between the tip of the rostrum and the lamellar hair there is a deep incurvation. The rostral hairs are long, thin, finely serrate, and curved. The lamellar hairs are very thin but can be easily seen. They are situated between lamella and sublamella. The lamella is S-shaped and reaches halfway to the interlamellar hair. The latter is minute. The areae porosae dorso-sejugales are long and narrow. The pseudostigmatic organ bent at right angles a short distance outside the pseudostigma. The stalk is strong becoming a little thicker towards the end, which apparently is missing.

The hysterosoma is separated from the propodosoma by an indistinct dorsosejugal line. The hysterosoma is broadly rounded posteriorly, much narrower at the anterior end. On the pteromorphae, which are light brown, fine ribs can be seen. Aa is very large, T-shaped. Its posterior part along the side of the hysterosoma is long and narrow, its anterior part shorter, irregular and with a dilatation medially. The part directed medially and slightly backwards is shorter than the latero-posterior part. A1 is oblong, A2 also oblong and a little longer than A1. A3 is twice as long as A1. The hair-pores are arranged as shown in fig. 41. Im, which is very indistinct, is situated in front of A1, the gland laterally to r3. P2 and p3 were not observed. There is an indistinct median pore in the notogaster.

Ventral side, fig. 41 a. The three anterior apodemata are narrow ridges. Apodema II is rather short, the sejugal apodema longer and narrower, and Apodema III is angle-bent. Apodema IV is absent. Of the epimeric hairs 1a, 3a, and 4a only were observed. The six pairs of genital hairs, the aggenital hairs, the anal hairs, and the adanal hairs are all minute. Iad is situated in front of ad3 removed from the anal field. All the tarsi are tridactylous, the middle claw only twice as strong as the lateral claws. III (1: moss on dead branches).

38

Galumna sp.; fig. 42.

Length approximately 0.42 mm. Colour light brown.

The only specimen found is subfossil and furthermore crushed. The rostrum is triangular. The rostral hairs, which are situated ventrally and cross in front of the tip of the rostrum, are thin and barbed. The lamellar hairs, situated immediately laterally to the lamellae, have a smooth sharp tooth at their base. They are thinner than the rostral hairs and uneven. The interlamellar hairs, which are equally thick throughout, are short, rather strong and barbed. They are directed medially. The pseudostigmatic organs have a very thin lanceolate head on a very thin stalk.

The hysterosoma and the propodosoma are not separated by a dorso-sejugal line. The hysterosoma is broadly rounded at its posterior end. Aa is situated near the side of the hysterosoma. It is round. A1 and A2 are smaller and round, too; A3 perhaps a little larger than the two former. Im was not observed. The notogastral hair pores are arranged as shown in fig. 42. P1 and p2 could not be seen. In front of the pore of ta there are two smaller pores, fig. 42 a. The same applies to all the notogastral pores.

Ventral side. There are six pairs of genital hairs. Iad is situated close to the anal field. All tarsi are tridactylous, the claws are almost equally strong. I (1: moist bark on the lawn in the park).

Acrogalumna abrupta n. sp.; fig. 43.

Length about 0.395 mm. Colour light brown, being darkest in front of the interlamellar hairs and in a broad belt across the hysterosoma between Aa and A1.

The rostrum projects a little and the strong, barbed rostral hairs do not reach far beyond the tip of the rostrum. The very thin lamellar hairs can be seen in front of the tip of the sublamellae. The interlamellar hairs, which are longer than their mutual distance, the latter being short, are equally thick throughout, barbed, and slightly curved, the tip directed outwards. The interlamellar hairs are situated at the anterior end of a long, light, curved line, the two lines, one from either side, together forming a huge arch, which is broken (abrupta) in the middle between the interlamellar hairs. The pseudostigmatic organs are filiform, finely barbed distally.

The hysterosoma and the propodosoma are not separated by a dorso-sejugal line. The hysterosoma is broadest across the middle, the posterior end being slightly pointed. The fissure on the pteromorphae is very distinct and from its medial end a strong chitinous band runs forwards. Aa is removed from the side of the hysterosoma. It is round or slightly oval. A1 is oblong and situated longitudinally. It is as big as Aa. A3 is narrow and the smallest, A2 being absent. The fissure im, situated immediately in front of A1, is very distinct. The hair pores are arranged as shown in fig. 43. Small dark scales can be seen laterally on the dorsal surface of the anterior part of the hysterosoma.

The ventral side seen slightly obliquely is shown in fig. 43 a. The epimeres are very light, almost whitish. The hair 1a is strong, smooth, and longer than the others. The six genital hairs and the two anal hairs are alike, rather long and smooth. Aggenital

hairs were not observed. The same holds good for ad1 and ad2. Ad3 is minute. All the tarsi are tridactylous with thin lateral claws. III (56: 11, mostly in moss on the ground).

Acrogalumna ventralis (Willmann); fig. 44.

Galumna – , 1931 a, p. 284, figs. 67–68.

Length about 0.36 mm. Colour light brown, darker in a belt across the hysterosoma between Aa and A1.

The rostrum is rounded distally. The rostral hairs are thin and slightly uneven. They almost reach the tip of the rostrum. The lamellar and the interlamellar hairs are hardly discernible, but they can be seen on a sketch, fig. 44 a, of the lateral side of the propodosoma. Lamellae are absent. The area porosa dorso-sejugalis is small, oblong. The pseudostigmatic organ has a broad, greyish fan on the end of a long, thin stalk. The anterior border of the head is rounded, the posterior border straight and its end tapers into a pointed tip, fig. 44 b.

There is no dorso-sejugal line separating the propodosoma and the hysterosoma. The latter is broadest across the middle. The pteromorphae are a lighter colour in their anterior half, a darker in their posterior half. Ta is long. As is oblong and is situated obliquely to the side of the hysterosoma. A1 is round and almost as large as Aa. A2 is only half as large as A1. It is situated within a short distance from A1. A3 is approximately as large as A1. The fissure im is very indistinct, and found at some distance behind Aa. The hair pores are arranged as shown in fig. 44. On the posterior border p1, p2, and p3 can be seen in profile.

Ventral side, fig. 44c. Epimeres I–II are yellow. Apodemata II and the sejugal apodemata are dark ridges, the latter are bent at right angles. Apodemata III–IV are absent. The epimeric hair formula is 1:0:1:1. All hairs are absent on the ventral side. There are six pairs of genital hair pores. Iad is situated rather close to the side of the anal field in front of ad3. There is a small round area porosa postanalis.

All the tarsi are tridactylous. The middle claw is strong, the lateral claws are much thinner.

II (1: crumbling braken), III (1: Casuarina needles).

WILLMANN described this species from Sumatra. He named it *ventralis* due to the coxal region forming a solid plate with a few fainter chitinized holes. In the specimen from Tahiti illustrated in fig. 44 c, the posterior half of the ventral side from the anterior border of the genital field is a darker colour than the coxal region, i.e. the opposite of WILLMANN's observation.

?Pergalumna dubitanda n. sp.; fig. 45.

Length about 0.74 mm. Colour mahogany red.

The rostrum is very broad at the tip. The rostral hairs are situated ventrally. They are as long as the lamellar hairs. Both pairs are strong and unilaterally barbed. They all nearly meet at a short distance in front of the tip of the rostrum. The lamellar

hairs are situated at a short distance medially to the lamellae, which are faint lines seen in a lateral view. The interlamellar hairs, which are about half as long as their mutual distance, are equally thick throughout and serrate or finely barbed. No area porosa dorso-sejugalis was observed. The pseudostigmatic organs are filiform, barbed in their distal two thirds.

The hysterosoma and the propodosoma are not separated by a dorso-sejugal line. The posterior half of the hysterosoma is broad, semicircular. The pteromorphae are a light brown colour and have strong dark ribs. There is no actual fissure, in its place there is only a dark irregular chitinous rib. For this reason I am uncertain where to place this species in the system (dubitanda-doubtful). The areae porosae are very indistinct. Aa is apparently broadest medially. A1 is round and a little smaller than Aa. A3 is oblong and as large as A1. A2 is absent. The arrangement of the hairs can be seen from fig. 45. P1–p3 were not observed.

The ventral side, fig. 45 a. Apodemata II, the sejugal apodemata, and Apodemata III are short undulating ridges. Apodemata IV are absent. The epimeric hair formula is 1:0:2:1, 1a being the longest. They are barbed. Only five genital hairs could be seen on each plate. The two anterior hairs are very long, the others shorter, all are distinctly barbed. The aggenital hairs are as long as the posterior genital hairs, and also barbed.

In fig. 45 a the anal hairs are situated very asymmetrically; on the right plate there is only one hair, on the left two close together. Iad is adjacent to the lateral border of the anal field. No area porosa postanalis was observed. All the tarsi are tridactylous, the middle one being only a little stronger than the lateral ones. III (3: moss on the ground).

Pergalumna bifissurata n. sp.; fig. 46.

Length about 0.62 mm. Colour mahogany red.

The tip of the rostrum is very pointed forming a small sharp point, at the end of which the rostral hairs meet. The latter are rather thin and finely barbed. The lamellar hairs resemble the rostral hairs, fig. 46 a. Interlamellar hairs are absent. The area porosa dorso-sejugalis is a small, bright spot on a dark ground. The pseudostigmatic organs are filiform, strongly barbed in their distal two thirds.

The hysterosoma and the propodosoma are not separated by a dorso-sejugal line. The posterior border of the hysterosoma is slightly undulating. On the pteromorphae there are two large light spots resembling fissures (hence the specific name), i.e. one in continuating of the fissure and another further anteriorly. Both are broadest distally and bordered by darker ridges. Ta is situated between them. Aa is round, removed a good distance from the side of the hysterosoma. A1 is more or less semicircular, rounded medially, and slightly concave or straight laterally. A1 is a little longer than Aa. A3 is round and almost as large as Aa. The notogastral hairs are arranged as shown in fig. 46. In front of Aa 4–6 bright holes can be seen.

The ventral side, fig. 46b. Apodemata II and the sejugal apodemata are rather long, undulating ridges, Apodemata III much shorter and thinner. Apodemata IV are absent. The epimeric hair formula is 1:0:2:1. All the hairs are very short and thin. There are six pairs of genital hairs. The posterior hair and the aggenital hair are not discernible. Ad3 is situated off iad, which is close to the side of the anal field. Ad1 and ad2 are postanal, the distance ad1-ad1 being a little shorter than ad1-ad2. The area porosa postanalis is very indistinct and might be questionable. All the tarsi are tridactylous, the middle claw being much stronger than the lateral ones.

II (14: wet Cyperus meadow; wet moss on a wall; moist leaves in a ditch).

Pergalumna montana n. sp.; fig. 47.

Length about 0.40 mm. Colour light brown, darker in a belt across the hysterosoma between Aa and A1.

The rostrum is conical. Rostral hairs were not observed. The lamellar hairs, situated at a slightly higher level than the tip of the rostrum, almost meet in front of the latter. They are unilaterally barbed. Interlamellar hairs are absent. The lamella and the sublamella are almost parallel, see the sketch, fig. 47 a. The pseudostigmatic organs are filiform and very thin. They are directed backwards in an elegant curve. Their distal half is very finely cilicate. The integument of the propodosoma is smooth. No area porosa dorso-sejugalis.

The propodosoma and the hysterosoma are not separated by a dorso-sejugal suture. The propodosoma is, however, a slightly darker colour than the anterior part of the hysterosoma, which is a yellowish colour. On either side of the hysterosoma there is a thin line running from the anterior gland backwards parallel to the sides of the hysterosoma. From the fissure in the pteromorphae a chitinous band continues forwards disappearing along the anterior border of the pteromorphae. There is no characteristic pattern or ribs on the pteromorphae. Ia is unusually long. Aa is rounded, A1 slightly oblong and considerably larger than Aa. A2 is absent. A3 is the smallest. The arrangement of the hair pores can be seen in fig. 47. P3 was not observed. Im is situated at a short distance in front of A1. In the anterior part of the hysterosoma there are small dark scales, arranged especially round Aa.

The ventral side, fig. 47b, is faintly chitinized. Two pairs of light alveoli can be seen in front of the genital field. Only a few epimeric hairs are present, la being the longest. Apodemata II and the sejugal apodemata are long and narrow; Apodemata III shorter, its medial part situated longitudinally. On either side of the genital field a thin line runs latero-posteriorly to the insertion of Leg IV. There are six pairs of genital hairs. They are bent at right angles outside the pore. Ad3 is situated off the side of the anal field, in front of iad. Ad2 and ad1 are postanal. The adanal hairs are short and apparently finely barbed. No area porosa postanalis. All the tarsi have three claws.

III (1: dead leaves).

Leptogalumna ciliata Balogh; fig. 48.

– – – , 1960, p. 32, figs. 38–40.

Length about 0.32 mm. Colour light brown. The Tahitian specimens differ from the type from Angola in only a few character-

istics, which are of no great importance. Thus it is larger, the type being 0.286 mm long. The cilias of the pseudostigmatic organs are longer, almost as long as the diameter of Aa. Im on the right side is round and as large as A1. The latter is smaller than A2 and A3. In the type A1 is larger than A2 and A3. Furthermore an area porosa dorso-sejugalis can be seen behind the interlamellar hair. On the pteromorphae there is a long V-shaped white spot, on the lateral branch of which ta is situated. The ventral side agrees with that of the type (fig. 40).

II (2: wet Cyperus meadow).

Haplozetidae

Peloribates rangiroaensis n. sp.; fig. 49. Length about 0.375 mm. Colour clear brown.

Apart from the slightly protruding rostrum the propodosoma is triangular. The rostral hairs, situated in front of a sharp free tip of the tutorium, are unilaterally barbed, strong and reach a little beyond the tip of the rostrum. The lamellae are very broad and project beyond the sides of the propodosoma. The lamellar hairs are very long and reach beyond the tip of the rostrum. They are thin and barbed. The interlamellar hairs, situated very close to the anterior border of the hysterosoma, are a little shorter than the lamellar hairs, barbed, and thin. The pseudostigmata are half covered by the border of the hysterosoma. The pseudostigmatic organs are short, club-shaped, the head set with stiff bristles. Their stalk is 3–4 times longer than the head. The sculpture of the propodosoma consists of light pits increasing in size towards the posterior end of the propodosoma. The tip of the rostrum in front of a faint transverse line is smooth.

The anterior margin of the hysterosoma is convex, whereas the anterior border of the pteromorphae is concave with a small swelling immediately behind the pseudostigmata. The 14 pairs of notogastral hairs are alike apart from c2, which is a trifle longer. They are very coarse, equally thick throughout, dull at the tip and all the way set with upstanding stiff bristles, which are shorter at the base of the hair. The distances c1-c1, da-da, h2-h2, and h1-h1 are approximately equally long, dm-dm a little longer. Lm-lm, lp-lp, and h3-h3 are equally long. Ps3, lp, and dp are situated in a broad though slightly irregular curve; h3, h2 form another curve. There are four pairs of sacculi, viz. Sa laterally to lm, S1 medially to lp, S2 laterally to h3, and S3 laterally to h1. The sculpture of the hysterosoma consists of round, regular, light pits, arranged in undulating rows.

The ventral side, fig. 49a. The sternal plate is faintly chitinized, its posterior end clasping the anterior part of the genital field. Apodemata II, the sejugal apodemata,

and Apodemata III are narrow, almost parallel ridges, the anterior with a medial knot. The epimeric hairs are smooth, 1b, 3b, and 4b longer than the others. The genital field is separated from the anal field by a distance twice its length. There are five pairs of genital hairs, all of them situated along the outer border with the same distance between them. One pair of rather long aggenital hairs. Two pairs of anal hairs, and three pairs of adanal hairs. The latter are situated rather close to the anal field, ad3 at the latero-anterior corner, ad2 more or less at the latero-posterior corner, and ad1 postanal. They are apparently smooth. Iad is parallel to the side of the anal field. The sculpture of the ventral plate consists of round, light pits, also seen on the sternal plate. The genital plates are smooth, whereas the anal plates are decorated with very small, irregular dots.

Femur II has a very broad, pitted ventral keel. All the tarsi are tridactylous, the middle claw being the thickest.

IV (21: moist, dead leaves).

Xylobates capucinus (Berlese).

Protoribates – – , 1908, p. 2. I (1: wet Cyperus vegetation), II (11: wet moss and dead leaves).

Xylobates seminudus Hammer.

- - , 1971, p. 38, fig. 44. I (1: Cyperus vegetation on the bank of a brook), II (11: Cyperus vegetation on the road side).

Xylobates bipilus n. sp.; fig. 50.

Length about 0.75 mm. Colour light brown.

The anterior margin of the rostrum is hyaline. It projects beyond a well chitinized border with a short incision in the middle. The rostral hairs, which are as long as their mutual distance, are barbed and directed straight forwards. The lamellar hairs, situated on the rounded tip of the lamellae, are for most of their length very strong, the tip, however, very thin. They are scattered barbed or serrate and appear almost smooth. They cross in front of the rostrum. The interlamellar hairs resemble the lamellar hairs. The lamellae are vertical blades, their tip directed slightly medially. Their medial border seems to proceed to the rostral hair. The pseudostigmatic organs are almost as long as the interlamellar hairs. They are slender, thicker in their posterior third, with a thin tip, and set with cilias on the distal two thirds of their anterior border.

In the anterior border of the hysterosoma there are two incurvations, viz. one behind the pseudostigma and another further laterally. The latero-anterior tip of the pteromorpha projects and its distal triangular tip is bent ventrally. In a dorsal view the pteromorphae are strongly undulating with an anterior incurvation and a posterior bulge, the hysterosoma thus being broadest across Aa–Aa. Notogastral hairs are absent. The arrangement of the hair pores is seen in fig. 50. Ms, which within this genus

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is usually situated close to A1, is displaced more medially. Aa and A3 are larger than A1 and A2, which are situated with almost the same mutual distance, i.e. A1 rather laterally. There are five genital hairs.

Ad1 are seen in a dorsal view and are much longer than ad2, ad1 being the only hairs seen in a dorsal view (hence the specific name). This species can be distinguished by the undulating lateral border of its hysterosoma, the position of the areae porosae, and the two long ad1. Tridactylous.

I (1: Cyperus vegetation in the park).

Xylobates rhomboides n. sp.; fig. 51.

Length about 0.76 mm. Colour light brown.

The tip of the rostrum is more or less truncate. The rostral, the lamellar and the interlamellar hairs are scattered barbed and rather thin. The latter two are equally long. The lamellae are broad; their medial part seems to be at a lower level than their lateral part. The pseudostigmatic organs are very delicate. The stalk is very thin, becoming gradually slightly thicker towards the end, which tapers into a very thin tip, fig. 57 a. On their anterior border there are about 11 to 12 cilias, the distal ones upstanding, the proximal ones appressed.

The hysterosoma. The anterior border of the hysterosoma is almost straight and the pteromorphae do not project beyond this border. The pteromorphae are long and reach im. On either side of the hysterosoma there is a rhomboid spot, situated laterally and in front of Aa. From its border fine lines radiate posterially and laterally but not medially. The spot is a light colour, its border dark. Along the medial border of the pteromorphae the integument is densely punctate. All the areae porosae are surrounded by a very distinct ring. Aa is the largest, A2 and A3 are equally large, and A1 the smallest. The distance A1–A1 is only a little longer than A3–A3. The 10 pairs of notogastral hairs are arranged as shown in fig. 51. Beside each pore there is a long tunnel, fig. 51b. The hairs are extremely small. Im is situated rather far laterally in front of the lateral gland.

The ventral side, fig. 51c. There is no sternal plate, only a short undulating line. Apodemata II are very short brown plates. The sejugal apodemata reach the anterior border of the genital field, Apodemata III are connected with the latter by a thin line. Round light spots can be seen on the epimeres .Not all the epimeric hairs could be seen. The genital plate has five hairs, the two anterior ones being far longer than the others. Ad1 is much longer than ad2 and ad3, as is also the case in *X. bipilus*. *X. rhomboides* can easily be distinguished from *X. bipilus* by its rhomboid spots, its delicate pseudostigmatic organs and by the position of A1 with the hair ms close by. II (1: Cyperus vegetation under a hedge).

Perxylobates n. gen.

In general appearance much like *Xylobates*, but without a dorso-sejugal line between the propodosoma and the hysterosoma. The lamellar hairs are situated me-

dially to the end of the lamellae. Interlamellar hairs removed from lamellae; pseudostigmatic organs filiform, ciliate. Pteromorphae mobile. 10 pairs of notogastral hairs; 3 pairs of areae porosae, A3 being absent. Five pairs of genital hairs, one pair of aggenital hairs, three pairs of adanal hairs, and two pairs of anal hairs. Iad parallel to the side of the anal field. Monodactylous.

A species of this genus was described as ?*Xylobates sinlimes* Hammer, 1961, p. 39, fig. 45. In Tahiti two more species were found.

Perxylobates vermiseta (Balogh & Mahunka); fig. 52. Xylobates – – , 1968, p. 344, figs. 7–8. Length about 0.35 mm. Colour clear light brown.

The rostrum is conical. The rostral hairs, situated on the dorsal side, are thin and slightly barbed. The lamellae, which are only half as long as the propodosoma, are almost parallel, tapering towards their tip. A dark ridge below the lamella continues forwards reaching the rostral hair. The lamellar hairs, situated medially to the tip of the lamellae, are equally thick throughout, smooth and long enough to reach the tip of the rostrum. The interlamellar hairs, situated at some distance from the lateral margin of the lamellae, are thin and slightly barbed, apparently as long as the rostral hairs. The pseudostigmata are hidden below the proximal part of the lamellae. The pseudostigmatic organ is filiform, ciliate, viz. densely set with cilias on its anterior border, more scattered on the posterior border. The pseudostigmatic organs reach far beyond the lateral border of the pteromorphae. The integument of the propodosoma is faintly pitted. Behind the interlamellar hairs there are two long clear yellow glands on a ground lighter than that in front of the interlamellar hairs.

The hysterosoma is not separated from the propodosoma by a dorso-sejugal line. The mobile pteromorphae are short with a convex anterior border. 10 pairs of short and thin notogastral hairs; 3 pairs of areae porosae. Aa is the largest, A1 and A2 are very small. A3 is absent. (In *P. sinlimes*, Hammer 1971, fig. 45, A3 is shown. It appeared, however, to be only an indistinct light spot). Im is situated unusually far anteriorly, at a short distance behind te, and ip is situated between r1 and p2. The integument of the hysterosoma is faintly pitted.

Ventral side, fig. 52a. The whole length of the sternum is broad, but faintly chitinized with deep alveoli cutting into its sides. Apodemata II are short knobs on a very thin ridge, the sejugal apodema and Apodemata III also narrow, the latter being shorter so that they do not meet. The epimeric hairs are all very short and apparently smooth. Light pits can be seen everywhere, also inside the alveoli. The genital field is small and narrow with five pairs of hairs, of which the anterior one is long. The aggenital hairs are short and thin. Compared to the genital field, the anal field is large. Ad3 is preanal, situated immediately in front of the anal field. Ad2 is situated off an2, and ad1 is postanal. The distance ad1-ad1 is the same as ad3-ad3, and shorter than ad1-ad2. Ad1 and ad2 are longer than ad3. The anal hairs are approximately as long as ad2. Iad is situated close to the side of the anal field. As most of the hairs of the

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ventral side are very short and erect, it is extremely difficult to see whether they are barbed or smooth. The ventral plate is faintly pitted. The legs are short. Femora I–II with a broad ventral keel. The tarsi have one claw only.

II (3: Cyperus vegetation beneath a hedge).

Perxylobates barbatus n. sp.; fig. 53.

Length about 0.39 mm. Colour light brown.

This species is slightly larger but otherwise much like the preceding species for which reason only a few features will be mentioned. The lamellar hairs, situated at a good distance medially to the tip of the lamellae, are barbed (hence the specific name); they are shorter than their mutual distance and do not reach the tip of the rostrum. In front of them a faint transverse line can be seen. The pseudostigmatic organs are thinner and denser ciliate than those of the preceding species and the cilias are found only on the posterior border (left side in fig. 53). Behind an imaginary line (dotted) the integument is a yellowish colour, in front of it more brown. The notogastral hairs are a little longer than in the preceding species. The integument is pitted. The pits are especially distinct in the darker integument of the propodosoma in front of the interlamellar hairs. The hysterosoma is densely punctate between the small pits.

Ventral side, fig. 53a. The sternal plate is faintly chitinized and hardly limited from the epimeres. The hairs of Epimeres I are barbed and longer than those of *P. vermiseta*. The ventral side is faintly pitted almost everywhere. Monodactylous. III (3: moss, Cyperus; Oxalis, grass, small ferns on moist soil).

Scheloribatidae

?Scheloribates praeincisus (Berl.) var. interruptus Berlese.

Protoribates (Scheloribates) praeincisus var. interruptus Berl. 1916, p. 315.

I find no differences between the specimens from Tahiti and those described and which I illustrated from Viti Levu, the Fiji Islands, 1971, p. 42, fig. 50, except the considerably larger size of the Tahitian specimens which measure about 0.635 mm in length.

I (extremely common, up to about 200 specimens in one sample: 29), II (common: 13), III (common: 13), IV (many: 4).

Scheloribates praeincisus (Berlese).

Protoribates (Protoribates) praeincisus Berl., 1910, p. 384. Scheloribates praeincisus (Berlese), Hammer 1971, p. 43, fig. 51 a. I (common: 26), II (common: 14), III (common: 17), IV (1).

Scheloribates thermophilus var. corolevuensis Hammer.

- - - , 1971, p. 44, fig. 53. I (26: 6), II (1), IV (1). Scheloribates fimbriatus Thor, var. javensis Willm.

– – – , 1931, p. 273, figs. 46–47.

The specimens from Tahiti agree with WILLMANN's description, although the remains of the translamellar line are rather indistinct. It is tridactylous. I (common: 25).

?Scheloribates imperfectus n. sp.; fig. 54.

Length about 0.32 mm. Colour yellowish-light brown.

This small mite is not a true *Scheloribates* (therefore the questionmark) although very alike. The establishment of a separate genus will have to wait until more species have been found. In most characteristics it is a *Scheloribates*, the species of which are very similar and often difficult to distinguish. Their common features have been repeated so frequently that it is sufficient here to mention only the characteristics of the new species. Like most *Scheloribates* in the Pacific area it has a faint, very short transverse line medially to the lamellar hair, which does not meet the opposite one. The prolamellar ridge is incomplete, the anterior half being very indistinct, fig. 54 a (hence the specific name). Ventrally to the lamella there is an area porosa. The pseudostigmatic organs are short clubs, fig. 54 a.

The hysterosoma, fig. 54. Across the pteromorphae there is a distinct curved line which may indicate mobile pteromorphae. There are 10 pairs of clear bright hair pores. The hairs are absent except p1. There are many cracks in the integument of the dorsal surface. Sa is longer than the other sacculi. Im is very long. It is situated approximately in the middle of the hysterosoma at a short distance in front of S1, i.e. rather medially.

The ventral side, fig. 54b. From the appearance of the ventral side it is evident that this species does not belong to the genus *Scheloribates*, in the species of which the sejugal apodema and Apodema III meet at the latero-anterior border of the genital field. Apodema III is very short and only the sejugal apodema reaches the border of the genital field. The latter has four pairs of short thin hairs, viz. one on the anterior border, one at a good distance more posteriorly, and the third and fourth near the posterior border*. The aggenital hairs are short and thin, the anal hairs, and the adanal hairs longer. Iad is situated close to the side of the anal field.

Femora I–II have a ventral keel. All tarsi with three claws, the lateral ones very thin. Pedotectum I is hyaline.

I (3: pieces of bark on the lawn in the park), II (1: moss on coconut palm trunk), III (14: 8).

Maculobates ventroacutus Hammer.

– – , 1971, p. 41, fig. 47.

II (4: wet moss on a stone wall).

*) By a mistake only three pairs of genital hairs are shown in fig. 54b.

?Reductobates latiohumeralis n. sp.; fig. 55.

Length about 0.43 mm. Colour clear light brown.

Compared with the hysterosoma the propodosoma is narrow. The rostrum is pointed. The rostral hairs, situated at a good distance behind the tip of the rostrum, are longer than their mutual distance, very thin, and distinctly barbed. The lamellae are narrow, slightly converging. The lamellar hairs, situated on the tip of the lamellae, are more than one and a half times longer than their mutual distance, thin and barbed. When laid bare the interlamellar hairs are as long as the lamellar hairs, fig. 55 a. They are situated at the medio-anterior end of the pteromorphae, which reach forwards beyond the proximal free part of the lamellae. A short distance latero-posteriorly to the interlamellar hairs the pteromorphae bend sharply forming a small edge, also seen in fig. 55 a, which shows a lateral view of the lamellar system. There is no accessory ridge. The pseudostigmata are hidden below the anterior border of the pteromorphae. The pseudostigmatic organ is a short club set with minute bristles.

There is no suture between the propodosoma and the hysterosoma. The hysterosoma is very broad compared to the propodosoma. It is especially broad across the shoulder region (hence the specific name). The latero-anterior borders of the pteromorphae run almost transversally, their medial borders reaching the interlamellar hair in a broad curve. The pteromorphae are perhaps mobile. The posterior end of the hysterosoma is semicircular, and apart from the pteromorphae the hysterosoma is globular, although slightly elongated. There are 10 pairs of short, thin, smooth notogastral hairs, ta and te being longer than the others. Three pairs of areae porosae, approximately of the same size. A1 is absent. In front of Aa a small light spot can be seen and medially to A2 there is a further light spot.

Ventral side, fig. 55b. The sternum is faintly chitinized. It is narrow between Epimeres I, widening posteriorly and clasping the anterior part of the genital field. Apodemata II are short, the sejugal apodemata twice as long. Apodemata III are short. Epimeres III–IV are more or less fused. The epimeric hairs are thin, short, and smooth. The discidium, custodium, and circumpedal ridge are absent. The genital field has only two pairs of hairs, viz. one on the anterior border and the other in the middle line in the posterior end of the plate. The aggenital hairs are short and thin. The three pairs of adanal hairs and the two pairs of anal hairs are a little longer than the aggenital hairs. Ad3 is situated off the latero-anterior corner of the anal field, ad2 near the latero-posterior corner, and ad1 behind the anal field. All the hairs of the ventral side are short, thin, smooth, and flexible. Iad is parallel to the side of the anal field.

The legs are short. All tarsi are monodactylous. III (50: moist Casuarina needles).

Subulobates n. gen.

No suture between the propodosoma and the hysterosoma. Lamellae, prolamellae, and interlamellar ridges present. Interlamellar hairs close to the lamellae. Pseudostigmata covered by base of pteromorphae. Pseudostigmatic organs clavate. Ptero-4

Biol.Skr.Dan.Vid.Selsk. 19, no. 3.

morphae not mobile. Areae porosae present. 10 pairs of notogastral hairs. Sternum a straight, narrow ridge widening into a broad, trinangular plate in front of the genital field. Three pairs of genital hairs. From the acetabulum of each leg a pointed chitinization like an awl (subula) is directed forwards. Circumpedal ridge absent. Mono-dactylous.

Subulobates albulus n. sp.; fig. 56.

Length about 0.242 mm. Colour yellowish-white.

The general appearance resembles *Maculobates*. The rostrum is pointed. The rostral hairs situated laterally, are longer than their mutual distance, thin, and barbed. The prolamella does not run to the base of the rostral hair but more medially thus forming together with the lateral border a free tip in front of the base of the rostral hair, fig. 56 a. The lamellae cover the sides of the propodosoma. They converge slightly and are almost equally thick throughout. The lamellar hairs are as long as the rostral hairs, thin, and barbed. The interlamellar hairs are situated close to the medial border of the lamellae. Below the lamella can be seen a curved ridge issuing from the base of the pseudostigma and running to the base of the interlamellar hair, fig. 56 a. Apparently there is also a connection between the medial border of the lamella and the base of the interlamellar hair, fig. 56 a. The interlamellar hairs are almost hidden below the base of the pteromorphae. Only a small part of their broad lateral lobe can be seen in a dorsal view. The pseudostigmatic organs are rough, flat clubs with an undulating outline, apparently set with short scales.

The propodosoma and the hysterosoma are not separated by a dorso-sejugal suture although a very faint line can be seen between the interlamellar hairs. The anterior border of the hysterosoma cannot be seen beyond the pseudostigmata, whereas in i.e. *Maculobates* it proceeds to the base of the interlamellar hair. The pteromorphae are separated from the notogaster by a clear line, but they are apparently not hinged. They are hyaline. On the lateral part of the pteromorphae short white radiating lines can be seen. There are three pairs of areae porosae, A1 being absent. Aa is the largest. 10 pairs of notogastral hairs, all of them short, soft, and thin.

Ventral side, fig. 56b. The sternum is a very narrow ridge, widening into a broad, triangular plate surrounding the anterior part of the genital field. Apodemata II do not reach the sternal ridge. The sejugal apodemata almost reach the sternal triangular plate. Apodemata III are very short. The epimeric hairs are short and thin, 3c and 4c were not observed. The genital field has three pairs of hairs, viz. one on the anterior border, two in the posterior end of the plates situated rather close together. One pair of aggenital hairs, two pairs of anal hairs, and three pairs of adanal hairs. Ad3 is situated at the latero-anterior corner of the anal field, ad2 off the middle of the field, and ad1 at the latero-posterior corner. All these hairs resemble the notogastral hairs, the aggenital hairs although a little shorter. Iad is parallel to the side of the anal field. From the acetabulum of each leg a very pointed chitinized awl apparently proceeds

forwards to the acetabulum immediately in front of it. This can be seen also in a slightly oblique ventral view, fig. 56c. The awls of Leg III have a backwards-directed free dull tip.

The legs are short. Femora I, II and IV with a broad ventral keel. Tarsi bilaterally flattened, especially of Legs I–II. Monodactylous.

II (9: moss on a coconut palm trunk).

Pachygena n.gen.

Sides of propodosoma convex, making the latter appear thick-headed. Lamellae present, translamella absent. Pseudostigmatic organs sickle-shaped. Suture between propodosoma and hysterosoma. 10 pairs of notogastral hairs. Four pairs of sacculi. Glandular funnel behind Sa. Sternum well developed. Apodemata II short, sejugal apodemata and Apodemata III meeting in front of genital field. Four pairs of genital hairs, one pair of aggenital hairs, two pairs of anal hairs, and three pairs of adanal hairs. Iad parallel to side of anal field. Circumpedal ridge absent. Monodactylous.

Pachygena falcata n.sp.; fig. 57.

Length about 0.44 mm. Colour light brown.

Compared to the hysterosoma the propodosoma is narrow and is more or less conical. The rostral hairs, situated laterally on a prolamellar ridge, are very thin and slightly rough. They reach for half their length beyond the tip of the rostrum. The lamellae cover the sides of the propodosoma almost to the rostral hairs. They are apparently erect blades, tapering towards their tip, and are finely longitudinally striped. The lamellar hairs are thinner than the rostral hairs and smooth. The interlamellar hairs, situated near the anterior border of the hysterosoma and at a good distance from the lamellae, are longer than their mutual distance and very thin, smooth, and flexible. The pseudostigmata are hidden below the border of the hysterosoma. Seen in a dorsal view the pseudostimatic organs are spindle-shaped, the end drawn out into a thin tip. In profile they are broad, sickle-shaped with a short thin stalk. They are hyaline, fig. 57 a.

The hysterosoma and the propodosoma are separated by a dorsal suture. The anterior border of the hysterosoma is slightly convex in the middle, laterally concave. The posterior end of the hysterosoma is semicircular. The hysterosoma is broadest across the pteromorphae. The latter are not mobile and only a narrow part of their distal margin is bent ventrally. There are 10 pairs of extremely thin, smooth, and slightly curly hairs. Ta is a little longer than the others. Four pairs of very distinct sacculi. Behind Sa there is apparently a slight depression and here a funnel-shaped gland can be seen. The integument is smooth.

Ventral side, fig. 57b. Between Apodemata II the sternum is expanded into a transverse plate, and in front of the genital field it is dilated again forming a broad plate on the anterior border of which the sejugal apodemata and Apodemata III meet. The two latter are much longer than Apodemata II. The epimeric hairs are thin and

smooth, 1b longer than the others. 3c and 4c were not observed. The genital field, which is much smaller than the anal field, is separated from the latter by a distance twice its length. There are four pairs of genital hairs, viz. two on the anterior border and two much shorter at the posterior end of the plates. The two aggenital hairs are very short. Three pairs of adanal hairs. Ad3 is situated at a short distance in front of the anal field, ad2 at some distance off the sides of the field, and ad1 behind the latero-posterior corner of the anal field. Iad is parallel to the sides of the field. Tecto-pedium I is rounded, almost hyaline, Tecp. III rounded without a projecting tip. The legs are short. Femora II–III with a broad, rounded, ventral keel. Tarsi are bilaterally flattened, short with a concave anterior border set with two rows of hairs between which the claw rests when bent backwards. All tarsi with one strong claw.

II (15: thin moss on dead branches), III (6: lichens and moss on bark; moss on decaying tree stump; moss on the ground).

Rostrozetes foveolatus Sellnick.

– – , 1925b, p. 84, figs. 6–7.

The integument of the specimens found in Tahiti is decorated with small luminous dots, much smaller than illustrated by SELLNICK.

I (common: 12), II (common: 3), III (common: 3).

Tuberemaeus perforatus (Willmann); fig. 58.

Liebstadia perforata – , 1931a, p. 268, fig. 42 a, b.

Length about 0.424 mm. According to WILLMANN it is 0.45 mm long.

There can be no doubt that the specimens from Tahiti are identical with *T. per-foratus* from Java. The interlamellar hairs appear much shorter in the Tahitian specimens, but this is due to their more or less erect position, when laid bare they are longer than the lamellar hairs. WILLMANN does not illustrate the sacculi, which are very small. The sculpture of the propodosoma consists of small round yellow pits, and in the hysterosoma of small, luminous dots, which appear oblong along the lateral and posterior borders.

The ventral side is shown in fig. 58a. WILLMANN describes and illustrates how the proximal part of Trochanter IV in *Tuberemaeus (Liebstadia) thienemanni* issues from a slit or groove, which is bridged by a ridge (1931, p. 268, fig. 41b). The same can be seen in fig. 58a. Only four pairs of genital hairs were observed. Shallow pits can be seen on the anal plates only. All the tarsi with one strong claw. II (9: moss on bark; dead leaves).

Otaheitea n.gen.

Propodosoma with a longitudinal furrow on either side. Lamellar tip ending in front of a furrow. Rostral, lamellar, and interlamellar hairs present. Pseudostigmatic organs club-shaped. Propodosoma and hysterosoma separated. Pteromorphae projecting beyond pseudostigmata, not mobile. Four pairs of sacculi, 10 pairs of noto-

gastral hairs. Ventral side with a deep, longitudinal furrow on either side. Three pairs of genital hairs. On either side of the ventral plate there are two furrows, which fuse off the anal field. Tridactylous.

Otaheitea sulcata n.sp.; fig. 59.

Length about 0.323 mm. Colour light brown.

The tip of the rostrum ends in a well chitinized labium the lateral ends of which apparently proceed for some distance backwards. The rostral hairs, situated laterally, reach for more than half their length beyond the rostrum. They are slightly barbed. This also applies to the lamellar and the interlamellar hairs. The lamellar hairs are a little longer than the interlamellar hairs. The lamellae, situated at some distance from the sides of the propodosoma, are curved, their tip directed medially ending immediately in front of a short, curved slit or furrow. Between the lamellae there is a clear, transverse band; its anterior border is straight, its posterior border with a deep incurvation. Laterally it reaches a longitudinal furrow, which anteriorly apparently runs to the labium, posteriorly disappears under the lamella and reappears medially to the lamella. The pseudostigmata are situated at some distance in front of the anterior border of the hysterosoma. The pseudostigmatic organs are club-shaped, the left one appears much larger than the right one, perhaps due to different views.

The hysterosoma. Its anterior border is almost straight at the middle; laterally it projects as far as the anterior border of the pseudostigmata. At a short distance from the anterior border there is on either side a short transverse ridge towards which the surface seems to be pinched in, forming a groove in front of the ridges. The pteromorphae and the anterior part of the hysterosoma in front of these ridges appear like a "collar" surrounding the posterior part of the propodosoma. There are four pairs of sacculi and 10 pairs of notogastral hair pores. Only the hairs p1 are present. They are almost as long as their mutual distance. No sculpture.

The ventral side, fig. 59a. Apodemata II, the sejugal apodemata, and Apodemata III are present, none of them reaching the sides of the hysterosoma, nor the sternum. The latter is indicated by two grey longitudinal lines, which posteriorly diverge in front of the genital field. The epimeric hair formula is 3:1:3:3. 3a are situated after each other in front of the genital field in a triangular greyish spot. Light alveoli can be seen in the epimeres. On either side of the ventral side there is a deep furrow which runs in a curve forwards to Tectopedium II, then as a straight line proceeds to Acetabulum I. The genital field has three pairs of hairs, viz. two long hairs on the anterior border, two short ones immediately behind the latter, and two short hairs at the posterior end of the plates. The aggenital hairs are very short. The three pairs of adanal hairs are likewise short. Ad3 is preanal; ad2 and ad1 are situated in a curve behind the anal field. The distance ad1-ad1 is twice as long as ad1-ad2. Behind the anal field there is a curved ridge (or furrow?) the ends of which run forwards almost to the aggenital hairs. Anteriorly these ridges are double. Iad is situated near the latero-anterior corner of the anal field.

The legs are slender. Femora I–III with a broad ventral keel. Tibiae I–II have a very long solenidium. All the tarsi are tridactylous, the lateral claws are very thin. III (1: almost dry moss).

Oribatulidae

Zygoribatula oceana n.sp.; fig. 60.

Length about 0.39 mm. Colour light brown.

The sides of the rostrum are rounded, the tip very pointed. The rostral hairs, situated on the dorsal surface immediately behind a curved transverse line, are parallel, about one and a half times longer than their mutual distance, and faintly barbed. The lamellae converge strongly towards their anterior end, which ends in a rounded low cuspis. The distance between the cusps is a little shorter than that between the interlamellar hairs. The lamellar hairs are about twice as long as their mutual distance, thick, and barbed. The interlamellar hairs resemble the lamellar hairs. The exopseudostigmatic hairs are shorter, thinner and slightly barbed. Laterally to the lamellae there is on either side of the propodosoma a narrow furrow bordered on its lateral side by a narrow ridge. Area porosa dorso-sejugalis present.

The hysterosoma is broadest across the middle. The anterior border projects a little, the posterior end is semicircular. The shoulder edge is very small. The 13 pairs of notogastral hairs are stiff, thick, slightly curved, and barbed. Apart from the short hair on the shoulder and those on the posterior border, they are equally long. The integument is faintly pitted. On the sloping sides of the hysterosoma it appears like a faint reticulation. The distance A1-A2 is equal to A2-A3.

The ventral side, fig. 60 a. The sternum is hardly indicated. Apodemata II are very short; the same applies to Apodemata III, whereas the sejugal apodemata form a broad transverse belt immediately in front of the genital field. All the epimeric hairs are smooth, 1a, 2a, and 3a are shorter than the others. Four pairs of genital hairs. From the posterior border of Tectopedium I a line runs backwards crossing the tectopedia of the other legs and ending at the lateral border of the ventral plate. Iad is preanal, situated obliquely and medially to ad3. Ad2 and ad1 are situated on a slightly projecting tongue from the ventral plate behind the anal field. The ventral plate is faintly pitted. Legs II–IV are inserted behind the fold, which is indicated by the above mentioned lateral line issuing from Tectopedium I. There are three claws, the middle a little stronger than the lateral ones.

III (5: moist dead leaves).

Conclusions

Of the 102 species discussed in the preceding pages, 61 have been described earlier and only 41 are new to science. 4 new genera are established.

Had this investigation been undertaken e.g. 20 years ago, the majority of the species would presumably have been considered endemic. In a further 20 to 50 years' time, when thorough investigations of the oribatid fauna have been made on other islands in the Pacific ocean and the surrounding areas of land, it will probably appear that practically all the species on e.g. Tahiti are known in these areas.

In table 1 the 102 species are listed under the locality in which they were found. From this it is seen that in Group I: Papeete, only 30 species were found, while in Group II: the coast, there were 67 species, in Group III: the mountains above Papeete, 47 species, and in Group IV: Rangiroa, 13 species.

In the following table which gives the number of samples (of approx. $1/1000 \text{ m}^2$) etc., the paucity of species of oribatid fauna in Papeete appears even clearer, since only 30 species were found in 44 $^{0}/_{0}$ of the total samples, and in 65 $^{0}/_{0}$ of the total of individuals collected. This paucity of species must be considered in the light of the poor living conditions for oribatids in the town which has only few biotopes and those that exist—lawns with twining grass and practically without other plants—are subjected to burning sun throughout large parts of the year, for which reason there is no moss. With regard to individuals the hardy *Scheloribates* species constitute a very large part of the mites found. Of *Scheloribates praeincisus v. interruptus* 1391 individuals were found, of *Scheloribates praeincisus* 609, and of *Scheloribates fimbriatus* 578 individuals. Together this gives 2578 individuals, or 42 $^{0}/_{0}$ of the total number of oribatids found in Papeete. These 3 species apparently exist for the most part on leaves fallen from the large, spreading Enterolobium trees, on rotten pieces of bark from the same tree (on which they sat thickly), as well as on heaped garden rubbish.

Location	No. of Sampes	No. of Individuals	No. of Species
I	50	6158	30
II	26	1773	67
III	33	984	47
IV	5	639	13
Total	114	9554	102

Much greater possibilities of existence are offered in the many varied biotopes along the coast and in the mountains, where all biotopes are in the shade, even in

TABLE 1 S	howing Dishi	bution of th	e species	found in	Tahiti and	l in	Rangiroa.

	Ι	II	III	IV	I	II	III	IV
Andacarus ligamentifer				Multioppia gracilis				
Malacoanaelia remiaera				Ramusella chulumaniensis				
Hunochthoniella minutissima				v curtinilus		×		
Fohupochthopius aracilis		~		Machuella ventrisetosa		$\hat{\mathbf{v}}$		
Longpoentionitus gracitis				Suctobelha pariosetosa	~	$\hat{\mathbf{v}}$		
				saminlumora y	$^{\circ}$	^		
V. Crussisellyer		×		- semiptumosu v.				
				× iunitiensis				
– glauca	×			- Insuland		×	×	
– scapellata	×	×	×		×	×		
Phthiracarus crispus			×	– squamosa v. sculala		×		
– insularis		×	×	Hydrozetes temnae	×	×		
Hoplophthiracarus tubulus		×		Tectocepheus velatus	×	×	×	
– siamensis	×	×	×	× Scapheremaeus bicornutus	×			
Microtritia tropica			×	Licneremaeus polygonalis		×	×	×
Rhysotritia ardua v. otaheitensis	×	×	×	Eutegaeus biovatus			×	
Indotritia sellnicki		×		× Microzetes auxiliaris	×	×	×	
Austrotritia lebronneci			×	Eupelops tahitiensis		×		
Epilohmannia pallida v. pacifica		×		– crassus			×	
Papillacarus hirsutus		×		– polynesia			×	
Meristacarus tahitiensis		×		Lamellobates palustris	×		×	×
Nesiacarus granulatus		×		Eremaeozetes tuberculatus	×			
Javacarus kühnelti v. foliatus		×		Galumna flabellifera	×	×	×	
Phyllhermannia pacifica		×	×	– pterolineata		×		
Nothrus oceanicus		×	×	– imperfecta			×	
Allonothrus schuilingi		×		× – Sp	×			
– russeolus v. reticulatus	×	×	×	Acrogalumna abrupta			×	
Nanhermannia transpersaria				– pentralis		×	×	
Curthermannia luminosa		×		Peraalumna duhitanda			×	
Maethermannia mammillaris		ÛÛ		- hifissurata		~		
Trhunoahthonius aroanatus		1 Û	^	_ montana			~	
A fronothrue sulcatue				I entogalumna ciliata		~		
A pronountus suiculus				× Leptogatanna cittata		^		~
Archegozetes tongisetostis		×	×	Yulohataa aanuainua		~		^ .
Malaconoinrus nexaselosus		×		A glovales capacinus	×	×		
– geminus		×		- seminuaus	×	×		
– pacnypilus	×	×		\times – $biplius$	×			
1 rimalaconolnrus crassiselosus				- Fhomboldes		×		
v. fijtensis		×		Perxylovales vermisela		×		
Trimalaconothrus albulus		×		– barbalus			×	
Liodes bataviensis		×		Scheloribales praeincisus v.				
Fosseremus quadripertitus		×		interruptus	×	×	×	×
Eremulus avenifer		×		Scheloribales praeincisus	×	×	×	×
– curviseta			X	\times – thermophilus v.				
– monstrosus			×	corolevuensis	×	×		×
Furcoppia cornuta	×			– fimbriatus v. javensis	×			
Austrocarabodes imperfectus			×	?Scheloribates imperfectus	×	×	×	
Carabodes luteoauratus		×		Maculobates ventroacutus		×		
Nesotocepheus setiger			×	Reductobales latiohumeralis			×	
Quadroppia circumita		×	×	Subulobates albulus		×		
Oppiella nova		×	×	Pachygena falcata		×	×	
– polunesia		×		Rostrozetes foveolatus	×	×	×	
Oppia winkleri	×			Tuberemaeus perforatus		×		
 lanceosetoides 		×		Otaheitea sulcata			×	
Striatoppia opuntiseta				Zugoribatula oceana			×	
- lanceolata	~	$\hat{\mathbf{v}}$	×	2990110atata occarta				
Multioppia wilsoni	X			Total 102 species	30	67	47	13

the mountains the bracken shades the sparse moss. Along the coast 67 species were found in 19 $^{0}/_{0}$ of the animals collected, in the mountains 47 species in 13 $^{0}/_{0}$.

Of the 9 species known in Europe (marked with an "asterisk in table 2), 5 were found in Papeete, all 9 along the coast and 5 in the mountains. From table 2, where the earlier described species and their varieties are listed together with a broad outline of their known distribution, it appears that these 9 "European" species are not in fact European or western species, but have a worldwide distribution, with the exception perhaps of *Masthermannia mammillaris* where there is little information on its distribution. Therefore they can just as well have come to Tahiti from any area of land in the vicinity of Tahiti as from Europe. Introduction from Europe seems therefore unlikely, and the many plant products that since the time of Wallis, Bougainville and Cook have been imported from Europe have hardly contributed a European strain to the Tahitian oribatid fauna.

Species from countries having a climate and vegetation similar to that of Tahiti doubtless have greater possibilities of survival than the European species. It appears from table 2 that Tahiti has 32 species (disregarding varieties) common with the Fiji Islands, 15 common with Indonesia, 11 common with Thailand and Vietnam together, 18 with the Pacific area, and 23 with America. Tahiti has comparatively few species common with Japan and Africa from what can be determined from the literature at present. Our almost absolute lack of knowledge of the possible occurence of earlier described oribatids in New Guinea originates from the fact that there is only documentation on new species from this area (BALOGH and MAHUNKA).

Adding up the species that Tahiti has in common with Thailand, Vietnam, Indonesia, New Guinea and the Fiji Islands, we find that Tahiti has 46 species in common with Southeast Asia-Indonesia. On the other hand, Tahiti has 23 species in common with America. 6 of the 9 "European" species found on Tahiti that have a worldwide distribution are also found in Southeast Asia-Indonesia, 8 of these species are found in America. Subtracting these species from the total, it appears that Tahiti has 40 species in common with Southeast Asia–Indonesia, and only 14 in common with America, which lies much closer to Tahiti. The close relationship between the oribatid fauna of Tahiti and of Southeast Asia-Indonesia is thus established. This information tallies with Gressitt 1961, p. 16: "but in the eastern portions [of the Pacific] such as Hawaii and the southeastern extremities of Polynesia, there are varying degrees of American influence, with some Holarctic influence in Hawaii. However, the Oriental influence still dominates". How the species have spread, not only to Tahiti but also to many other islands in the Pacific, is a matter of guesswork —but it cannot be disproved that some of the species may have been introduced by the Polynesians in plant products on their long journey throughout hundreds of years step by step across the Pacific. It seems extremely improbable that transportion by currents of air during violent storms should have contributed to the distribution of these fragile creatures across vast distances. It cannot be disproved, however, that some species may have been brought hither by ocean currents perhaps throughout

	0	T	0 1	
ADIE	•	Distribution	of knowr	1 SDecles
LADLL	4.	Distribution	OI MILOWI	i species.

	Europe	West Africa	East Africa	Thailand	Vietnam	Japan	Indonesia	New Guinea	New Zealand	Fiji Islands	Hawaii	Pacific area	South America	North America
Andacarus ligamentifer									×					
Malacoangelia remigera		×	×				×			×			×	×
*Hypochthoniella minutissima	×								×					×
Eohypochthonius gracilis						×				×			×	×
– – v. crassisetiger						×								
Hoplophorella scapellata				×										
Phthiracarus insularis												×		
Hoplophthiracarus siamensis				×										
Microtrilla tropica												×	×	
* Rhysolfilla aralla V. olanellensis	×					×						~		×
Austratritia labrannasi												~		
Enilohmannia nallida y nacifica				^										
Papillacarus hirsutus						×								
Javacarus kühnelti v. foliatus						^	×			×				
Nothrus oceanicus												×		
Allonothrus schuilingi								×						
– russeolus v. reticulatus		×								×				
Cyrthermannia luminosa										×				
*Masthermannia mammillaris	×									×		×		
*Trhypochthonius excavatus	×								×				×	×
Archegozetes longisetosus				×									×	
Malaconothrus hexasetosus										×				
Trimalaconothrus crassisetosus v. fijiensis							×			×				
Liodes bataviensis							×					×		
*Fosseremus quadripertitus	×			×		×			×	×			×	×
Eremulus avenifer					×	×	×							
- curvisela										×				
Austrocaraboaes imperfectus												×		
*Oppiella popa									LÛ.				LŶ.	
Oppier winkleri	^								LŶ.					
- Innceosetoides										×				
Striatoppia opuntiseta							×							
Multioppia wilsoni											×			
Ramusella chulumaniensis v. curtipilus										×			×	
Machuella ventrisetosa									×	×			×	
Suctobelba variosetosa										×			×	
– semiplumosa v. tahitiensis					×									
Suctobelbila dentata									×	×			×	
– squamosa v. scutata										×			×	
*Hydrozetes lemnae	×								×	×		×	×	
*Tectocepheus velatus	×	×				×			×	×		×	×	×
Scapneremaeus bicornulus										×				
Lichereinaeus polygonalis										×				
I amellohaten paluetrin										X	×	×	Û	×
Energeografes tuberculatus				×			~		×	×				
Galumpa flabellifera							-						×	
Acroadumna ventralis							×							
Lentogalumna ciliata		×												

	Europe	West Africa	East Africa	Thailand	Vietnam	Japan	Indonesia	New Guinea	New Zealand	Fiji Islands	Hawaii	Pacific area	South America	North America
*Xylobates capucinus	×								×	×			×	×
– seminudus										×				
Perxylobates vermiseta							×							
Scheloribates praeincisus v. interruptus							×			×		×		
							×			×		×		
- Inermophilus V. corolebuensis										×	~	~	×	
- punortatus v. juvensis							×			×	~	~		
Rostrozetes foneolatus							×		~	Û.			×	
Tuberemaeus perforatus							Ŷ							
		-	-	<u> </u>							_		<u> </u>	
	9		8	1	1	8	15	1	14	32	1	8	2	3

millions of years. However, it is worth noting in this connection that the earlier known species listed in table 2 have not developed into endemic species on Tahiti—although there would appear to have been ample time for this. JACOT 1934 c, p. 85, states about the origin of oribatid fauna on Hawaii: "It is certain, however, that species originating from east or west are sufficiently modified even after a few decades to be recognized as geographical races". I much doubt that species can alter themselves in the space of a few decades, even though it is only a question of racial difference. On the contrary, it is my impression that it takes millions of years to produce a new species of the oribatids (cp. HAMMER 1965 a regarding *Mucronothrus*, which however is a representative of a very special biotope with a constant, low temperature).

Regarding possible transport by ocean currents it is furthermore worth noting that the ocean currents round Tahiti—the equatorial current—runs from east to west, while the weaker and more irregular counter-current runs from west to east. As a result one would expect a stronger American strain in the fauna, but the opposite is the case.

The spreading of the oribatids across the Pacific is presumably a very complicated matter, where perhaps the geological alterations should be taken into account earlier existing coral and volcanic islands could have constituted "stepping stones" from island to island group (GRESSITT 1961, p. 21).

The atoll Rangiroa presents a striking example of the difficulties that must be overcome by creatures washed ashore: surf thundering against the coral reef, and burning sun and scorching heat on the higher-lying dry blocks of coral. Finally a walk of some 20-50 m over coral rocks only to reach the bone-dry coral sand, where Pandanus and other bushes often with stiff foliage, but also an Abuliton-like bush with soft leaves, form a compact thicket. There is no top soil, but in the withered dead leaves under the thicket animals can find a little nourishment. In such places, but rather further inland, 13 species were found under the Abuliton-like bushes (see table 1). The species could just as well have been introduced by the natives, e.g. with yams which are cultivated by the inhabitants under the mango and breadfruit trees on the lagoon side of the atoll, as by the sea. Of the 13 species found, 11 are common with Tahiti, and thus not endemic indicating a rather recent introduction to the atoll. Neither on Tahiti, nor on Rangiroa, were representatives found of the Brachychthoniidae family, which appears nearly the world over in numerous species. They belong to the smallest and most thin-skinned of all oribatids. In this connection it is interesting that neither were they found in an investigation of oribatids introduced with plant products from the whole world at the plant quarantine stations in the USA (HAMMER 1969). Presumably because of their skin they cannot survive transport over long distances when subjected to dehydration.

Thus the great distance to the islands in the Pacific presumably in itself limits the introduction of oribatids to the hardy and often strongly chitinized species. This must apply to all oribatids regardless of the method of spreading.

Bibliography

Аокі, J.-існі: 1959. Die Moosmilben (Oribatei) aus Südjapan. Bull. Biogeogr. Soc. Japan 21(1). — 1961. Beschreibungen von neuen Oribatiden Japans. Jap. Jour. Appl. Ent. Zool. 5(1).

- 1964a. Some Oribatid Mites (Acarina) from Laysan Island. Pacific Insects 6(4).
- 1964b. Studies on Oribatei (Acarina) from the South Pacific. II. *Eutegaeus papuensis* n. sp. from New Guinea with a Note on the Genus. Pacific Insects 7(2).
- 1965a. Oribatiden (Acarina) Thailands. I. Nature and Life Southeast Asia IV.
- 1965b. Notes on the Species of the Genus *Epilohmannia* from the Hawaiian Islands (Acarina: Oribatei). Pacific Insects 7(2).
- 1966. Oribatid Mites from Bird's Nests on Midway Island (Acari: Cryptostigmata). Pacific Insects 8(3).
- 1967. Oribatiden (Acarina) Thailands. II. Nature and Life Southeast Asia V.
- BALOGH, J.: 1958. Oribatides nouvelles de l'Afrique tropicale. Rev. Zool. Bot. Africaines 58(1-2).
- 1960. Oribates (Acari) nouveaux d'Angola et du Congo Belge (2ème série). "Mus. do Dundo."
- 1961a. An Outline of the Family Lohmanniidae Berl. 1916 (Acari: Oribatei). Acta zool. Acad. Sci. Hung. 7(1–2).
- 1961b. "Descriptions complémentaires d'Oribates (Acari) d'Angola et du Congo" (2ème série). "Mus. do Dundo".
- 1962. Recherches sur la Faune Endogee de Madagascar. VII. Oribtes (Acariens) Nouveaux. Naturaliste malgache 13.
- 1965. A Synopsis of the World Oribatid (Acari) Genera. Acta zool. Acad. Sci. Hung. 11(1–2).
- 1968. New Oribatids (Acari) from New Guinea. Acta zool. Acad. Sci. Hung. 14(3-4).
- and MAHUNKA, S.: 1966. The Scientific Results of the Hungarian Soil Zoological Expedition to the Brazzaville-Congo. Acta zool. Acad. Sc. Hung. 12(1–2).
- 1967. New Oribatids (Acari) from Vietnam. Acta zool. Acad. Sci. Hung. 13(12).
- 1968. Some New Oribatids (Acari) from Indonesian Soils. Opusc. zool. Budapest VIII(2).
- ВЕСК, L.: 1965. Über Variabilität und Wertigkeit morphologischer Merkmale bei adulten Oribatiden (Arachnida, Acari) am Beispiel der Gattung *Rostrozetes* Sellnick 1925. Abh. senckenb. naturf. Ges. 508, Frankfurt a. M.
- BERLESE, A.: 1903. Acari nuovi. Redia I.
- 1908. Elenco di generi e specie nuove di acari. Redia V.
- 1910. Brevi Diagnosi di generi e specie nuovi di acari. Redia VI.
- 1913. Acari nuovi. Redia IX.
- 1916. Centuria terza di acari nuovi. Redia XII.
- CSISZÁR, J.: 1961. New Oribatids from Indonesian Soils (Acari). Acta zool. Acad. Sci. Hung. 7(3-4).
- Evans, O. G.: 1953. On a Collection of Acari from Kilimanjaro (Tanganyika). Ann. & Mag. Nat. Hist. Ser. 12,6.
- GRANDJEAN, F.: 1936. Microzetes auxiliaris n.sp. (Oribates). Bull. Mus. Hist. Nat. (2)8.
- 1948. Sur les *Hydrozetes* (Acariens) de l'Europe Occidentale. Bull. du Muséum, 2e série, 20(4).
- 1965. Fosseremus quadripertius nom. nov. (Oribates). Acarologia 7(2).

- GRESSITT, J. L.: 1961. Problems in the Zoogeography of Pacific and Antarctic Insects. Pacific Insects Monograph 2.
- HAMMEN, VAN DER, L.: 1953. Notes on the Oribatei (Acari) of Dutch New Guinea. I Allonothrus schuilingi Nov. Gen., Nov. Spec., Koninkl. Nederl. Akad. Wetensch. Amsterdam Proceed., Series C, 56(2).
- HAMMER, M.: 1958. Investigations on the Oribatid Fauna of the Andes Mountains. I. The Argentine and Bolivia. Biol. Skr. Dan. Vid. Selsk. 10(1).
- 1961. do. II. Peru. Biol. Skr. Dan. Vid. Selsk. 13(1).
- 1965a. Are Low Temperatures a Species-preserving Factor? Acta Univ. Lund. II(2).
- 1965b. A few Oribatid Mites from Ram, Jordan. Zool. Anz. 177(3-4).
- 1967. Investigations on the Oribatid Fauna of New Zealand. II. Biol. Skr. Dan. Vid. Selsk. 15(4).
- 1968. do. III. Biol. Skr. Dan. Vid. Selsk. 16(2).
- 1969. Oribatids Found at Plant Quarantine Stations in the U.S.A. Vidensk. Meddr. dansk naturh. Foren. 132.
- 1970. A few Oribatid Mites from Easter Island. Pacific Insects 12(2).
- 1971. On some Oribatids from Viti Levu, The Fiji Islands. Biol. Skr. Dan. Vid. Selsk. 16(6).
- JACOT. A. P.: 1934a. Some Tyroglyphina (Sarcoptiformes) of the Marquesas Islands. Bernice P. Bishop Mus.-Bull. 114.
- 1934b. Two Tyroglyphina (Sarcoptiformes) of Tahiti. Bernice P. Bishop Mus.-Bull. 113.
 Pac. Ent. Surv. Publ. 6(23).
- 1934 c. Some Hawaiian Oribatoidea (Acarina). Bernice P. Bishop Mus.-Bull. 121.
- 1936. More Primitive Moss-Mites of North Carolina. Elisha Mitchell Sci. Soc. 52(2).
- MÄRKEL, K.: 1964. Die Euphthiracaridae Jacot, 1930, und ihre Gattungen (Acari, Oribatei). Zool. Verhandelingen 67. Leiden.
- MICHAEL, A. D.: 1884. British Oribatidae. I. London.
- PÉREZ-IÑIGO, C.: 1968. Ácaros Oribátidos de Suelos de España Peninsular e Islas Baleares 1.a Parte) "Graellsia", Revista de Entom. Ibéricos 24.
- SELLNICK, M.: 1925a. Javanische Oribatiden (Acar.). Treubia 6.
- 1925b. Fauna sumatrensis. Suppl. Entomologica 11.
- 1959. Acarina from Southeastern Polynesia II (Oribatidae). Occ. Papers B. P. Bishop Mus. 22(9).
- SENGBUSCH, H. G.: 1957. Checklist of Oribatoid Mites in the Vicinity of Mountain Lake Biological Station Virginia. The Virginia Journ. Sci. 8(2).
- SHEALS, J. G.: 1965. Primitive Cryptostigmatid Mites from Rhododendron Forests in the Nepal Himalaya. Bull. Brit. Mus. (Nat. Hist) Zoology 13(1).
- STRENZKE, K.: 1953. Zwei neue Arten der Oribatiden-Gattung Nanhermannia. Zool. Anz. 150(3-4).
- WALLWORK, J. A.: 1960. Some Oribatei from Ghana. III. Two new Species of the Genus Allonothrus (van der Hammen). Acarologia 2(4).
- 1961. Some Oribatei from Ghana. V. Two Members of the Family Trhypochthoniidae, including a Description of a new Genus. Acarologia 3(2).
- 1962. Some Oribatei from Ghana. XI. The Genus *Epilohmannia* Berlese 1916. Acarologia 4(4).
- WILLMANN, C.: 1919. Diagnosen einiger neuer Oribatiden aus der Umgebung Bremens. Abh. Nat. Ver. Bremen 24(2).
- 1931a. Oribatei (Acari), gesammelt von der Deutschen Limnologischen Sunda-Expedition.
 Archiv f. Hydrobiologie. Suppl. Bd. 9. (Tropische Binnengewässer II.).
- 1931b. Moosmilben oder Oribatiden (Oribatei). Tierwelt Deutschlands 22.
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PLATE VII





PLATE IX







PLATE XII



PLATE XIII



Biol. Skr. Dan. Vid. Selsk. 19, no. 3.

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PLATE XX





PLATE XXII



PLATE XXIII



PLATE XXIV







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COMPARATIVE SPERMATOLOGY OF A PENTASTOMID, *RAILLIETIELLA HEMIDACTYLI*, AND A BRANCHIURAN CRUSTACEAN, *ARGULUS FOLIACEUS*, WITH A DISCUSSION OF PENTASTOMID RELATIONSHIPS

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Synopsis

The structure and development of the spermatozoa of the pentastomid Raillietiella hemidactyli Hett, a lung parasite of lizards, are described on the basis of light and electron microscopical techniques. The mature spermatozoon is 100–130 μ long, and the anterior 35 μ forms a "pseudoacrosome", which differs fundamentally from true acrosomes in its development. The following part, called "body" has a uniform structure throughout its length and contains a filiform nucleus, three filiform mitochondria, and an axonema, all arranged in a strictly symmetrical pattern. Several specialized structures, particularly the pseudoacrosome, some complicated sheaths around the axonema, and details of the latter were believed to be completely unique in the animal kingdom, until an identical pattern was found in the spermatozoa of the branchiuran crustacean *Argulus foliaceus* (L.).

A comparison between the spermatozoa of *Raillietiella* and *Argulus* is presented and shows that identity is extended to surprising details, both in the structure of the mature spermatozoon and in developing spermatids. Comparisons show that most of the specialized features are unknown in other animals. The most prominent difference between *Raillietiella* and *Argulus* is the transient appearance of a true acrosome and an acrosome filament in the latter. These structures are reduced before maturation, but their existence together with the pseudoacrosome shows definitely that the latter is a unique structure without relation to normal acrosomes.

The spermatozoa of *Argulus* and *Raillietiella* share so many specialized features which are unknown in other animals that independent development and evolutional hazards are, in practice, excluded as explanations. It is therefore concluded that the Pentastomida and the Branchiura are more closely related to each other than to other animals, and it is suggested that the Pentastomida be placed as a parasitic and strongly modified sub-group of the Branchiura in the zoological system. Their situation will then be analogous to that of the Rhizocephalia within the crustacean group Cirripedia. The Rhizocephalia, like the Pentastomida, are strongly modified parasites which are difficult to place in the system on the basis of adult morphology, but their spermatozoa are of the same very characteristic type as that of the free-living Cirripedia.

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I. INTRODUCTION

D uring morphological and embryological investigations of Pentastomida, performed in collaboration with Dr. A. Nørrevang (see Nørrevang 1972), it was noticed that pentastomid spermatozoa have a rather exceptional structure. Since this might give a clue to the systematic affinities of this enigmatic group, I undertook a structural and developmental analysis of the spermatozoa in the pentastomid *Raillietiella hemidactyli* Hett, 1934. For a long time these appeared to have a completely unique structure, and comparisons with other animals were not very successful. The theoretical evaluation of the results therefore made little progress until, in the summer of 1971, material of *Argulus foliaceus* (L.) was obtained. The spermatozoa of *Argulus* turned out to be identical with those of *Raillietiella* in general structure and also in many details. Moreover, the spermatogenesis in the two forms proved identical in many important and partly surprising respects.

Since many of the features common to the spermatozoa of *Raillietiella* and *Argulus* are completely unknown in other animals, a close phylogenetic relationship between the two forms is indicated. I realize that many biologists will find it hard to accept a conclusion like this and that substantial documentation is necessary. Therefore, as a basis for the final discussion, the structure and development of the spermatozoa in the two forms is described in great detail in the present paper.

Documentation rests on the electron micrographs reproduced in the Plates 1–23. In order to facilitate comparison, corresponding sections and stages of *Raillietiella* and *Argulus* are shown side by side, when this has been possible. This means that pictures from the two species are completely mixed and could be confused by the reader. Therefore an "R" for *Raillietiella* or an "A" for *Argulus* is added after the number of each figure.

II. MATERIAL AND METHODS

All material of *Raillietiella* was obtained from the lungs of an agamid lizard, *Calotes versicolor* Daudin, imported from Thailand (Bangkok). On an average, one out of five or six lizards contained the parasites, which agree with Hett's (1934) description of *R. hemidactyli* in most respects: Posterior hooks blunt and much larger than anterior ones, head strongly tapering from posterior hooks to mouth segment (Plate 1:1), females 10–16 mm long (Hett: 13–17 mm). But the present females have only 25-27 rather indistinct abdominal rings, not 28–30 as stated by Hett; The mature males are only 3.5-4.0 mm long (hundreds have been seen), not 12–13 mm as stated by Hett. Further, the present animals have double frontal papillae (sensu Heymons 1935) and dorso-lateral papillae (Plate 1:2). Hett does not describe papillae in this species. Identification of the material with Hett's *R. hemidactyli* is supported by the fact that Hett reported the species from the same host, *Calotes versicolor*, from Burma, and that the blunt posterior hooks are regarded as distinctive characters. At any rate, the species belongs to the *R. geckonis* group of Heymons (1935) (See Self 1969).

For fixation, the testicle, vesicula seminalis or receptaculum seminis was removed from the living animal and immersed in cold fixative.

All material of *Argulus* belongs to *A. foliaceus* (L.) (Det. U. Røen), and was obtained from the lake around Frederiksborg castle, Hillerød, Denmark. The living animals were killed by immersion in cold fixative, and the abdominal lobes with testicles or receptacula were immediately cut off. The said organs, sometimes also the vesicula seminalis, were rapidly exposed to the fixative by partial removal of the cuticle.

For electron microscopy, fixation was performed in cold Palade's (1952) osmic, or in cold, phosphate-buffered $2^{0}/_{0}$ glutaraldehyde, followed by washing and post-osmification. Epon sections from a Reichert Om U2 microtome were contrasted with uranyl acetate and lead citrate and were examined in a Zeiss Em 9S-2 microscope. In general, Palade's osmic gave the most reliable pictures of the general morphology. Glutaraldehyde worked well for mature sperm and preserved microtubules best, but caused exaggerated vacuolization and shrinkage of spermatocytes and spermatids in many specimens. These artifacts could not be eliminated by varying the phosphate concentration.

Most light microscopy was performed on thick $(1-2\mu)$ epon sections of the material used for electron microscopy. The sections were stained with toluidine blue – borax. The males of *Raillietiella* were also studied in paraffin sections (fixation:Bouin; staining: Ehrlich's hematoxylin-eosin or Feulgen-light green).

Important observations on whole spermatozoa were made with phase contrast on living sperm, suspended from the receptaculum seminis in mammalian Ringer solution. Osmium-fixed spermatozoa were also spread in distilled water on coated grids and dried to allow EM-observations of intact spermatozoa.

Comparisons were made with material of the tardigrade *Macrobiotus hufelandi* Schultze (testicles, receptaculum), and the thysanurans *Lepisma saccarina* L. (testicles, vesicula seminalis), and *Petrobius brevistylis* Carp. (testicles, vesicula seminalis). This material was examined essentially as the *Raillietiella* and *Argulus* specimens. The results obtained with *Petrobius* are original and will be published in the future.

Im am obliged to several persons who have helped to supply me with material: U. Røen and F. Møller Hansen (Argulus), the Drøbak Station in Norway, particularly Finn Walvig, and also Å. Jespersen and J. Lützen (Petrobius), T. Hallas and B. Theisen (Macrobiotus). The scanning pictures were taken with a Cambridge Stereoscan

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III. RAILLIETIELLA HEMIDACTYLI HETT

V. Haffner (1924) described the development of the sperm cysts in the pentastomid Nettorhynchus (Armillifer) moniliformis (Diesing 1935) and mentions that the mature spermatozoa are filiform as seen with the light microscope (see also v. Haffner 1922). The development of spermatocysts as well as the filiform appearance of the spermatozoa was confirmed by Doucet (1964, 1965) for Nettorhynchus (Armillifer) armillatus (Wyman 1847), Raillietiella boulongeri (Vaney & Sambon 1910) and Sebekia wedli Giglioli 1922. Doucet also published two good EM pictures of cross sections of spermatozoa of Raillietiella boulongeri. These pictures show the interesting structure but were insufficient for a detailed interpretation.

The structure of the testicle

The testicle of *Raillietiella* is an unpaired, thin-walled sac, lying in the posterior half of the abdomen, connected with the dorsal body wall by an unpaired, median ligament (See Heymons 1935, Doucet 1965). Anteriorly it is connected with the large, ovoid vesicula seminalis through a funnel-shaped passage.

The wall of the testicle is a single-layered epithelium, standing on a thick $(0.3-0.5\mu)$ basement membrane, which has the indistinct structure and medium contrast of a mucopolysaccarid coat (Plates 1:3, 3:6,8). In many places this basement membrane projects with tongue-like processes into the intercellular spaces between the epithelial cells.

The testicular epithelium consists of two types of cells: 1) the predominant phagocytic vegetative cells, and 2) the germinal cells (primary spermatogonia). The two types probably correspond to the "nutritive" and "germinative" cells described by v. Haffner (1924) in the testicular wall of *Nettorhynchus*.

The vegetative cells contain few ribosomes, few ergastoplasmic vesicles and a moderate number of mitochondria (Plate 3:6,8). Many of the cells show pronounced indications of phagocytosis and may be more or less filled with large, phagocytotic vesicles. The material taken up by the phagocytes is clearly the cellular debris suspended in the testicular lumen. The newly formed vacuoles often contain recognizable pieces of spermatozoa and sometimes clumps of debris, surrounded by non-nucleated cytoplasm (Plate 3:8). Such clumps are common in the testicular fluid and can sometimes be seen half-engulfed on the surface of vegetative cells. The non-nucleated cytoplasm of these clumps probably derives from the follicular wall of disintegrated sper-

matocysts (see below). V. Haffner (1924) suggested that the vegetative cells in *Nettorhynchus* secrete nutrients into the testicular lumen, to be used by the developing spermatocysts. Such a function is not distinctly reflected in the cytology of the vegetative cells of *Raillietiella*, although some cells contain some empty-looking vacuoles which may be concerned with secretion.

The germinative cells or primary spermatogonia are solitary cells, characterized by a rounded shape, a large nucleus, abundant free ribosomes and many mitochondria, but complete absence of phagocytic vacuoles (Plate 3:6). When typically developed, these germinal cells are always overgrown and separated from the testicular lumen by plasmatic processes from the neighbouring vegetative cells.

The development of the spermatocysts

The solitary germinal cells in the epithelium are the origin of the spermatocysts. Each cell divides into 2, 4, 8, 16, etc., daughter cells, and electron microscopy as well as light microscopy show that all divisions within a cyst are simultaneous. The cell clump thus formed bulges out into the testicular lumen, still covered by a cellular sheath (cyst wall) derived from the vegetative cells (Plate 3:6). About the time maturation begins, the cyst is pinched off from the wall and floats free in the lumen, still surrounded by the thin plasmatic cyst wall (Plates 1:3, 2:4, 3:6–8). Meiotic divisions have only been seen in free-swimming spermatocysts.

The cyst wall is obviously formed by several surrounding vegetative cells, for several cell limits are seen around the periphery of a single cyst. However, I have never seen a nucleus in this sheath, so it must be concluded that only cytoplasmatic parts are detached from the neighbour cells when a cyst is pinched off. The cyst wall is in most places less than 1μ thick and may be as thin as 500Å locally (Plate 3:7). The thicker parts contain some mitochondria, a small number of vacuoles, and rather numerous microtubules, oriented parallel to the outer surface (Fig. 21:106).

The entire spermatogenesis takes place within these cysts. According to v. Haffner (1924), working with *Nettorhynchus*, maturation begins when the 64-cell stage has been reached in the cysts. With two subsequent meiotic divisions this makes 256 spermatozoa in each cyst. Doucet (1965), working with *Raillietiella boulongeri*, states that maturation begins after the 32-cell stage has been reached. This would give 128 spermatozoa in each cyst.

Both possibilities are realized in *R. hemidactyli*. Counting of spermatids is fairly precise in EM-pictures showing cross sections of advanced spermatocysts, because the filiform spermatids are oriented parallel to each other (Plate 3:7). A series of countings gave the following numbers of spermatids for individual cysts:

256, 254, 255, 249, 248, 249, and

128, 128, 128, and 128 + 7 pseudoacrosomes.

Theoretically, only the exact figures 128 and 256 could result from simultaneous divisions of this kind. In the 256 series it is probable, therefore, that some spermatids

have either been dislocated or failed to develop. The 7 extra pseudoacrosomes in the last cyst of the 128-series were situated along the wall of the cyst and had obviously been bent and doubled back.

In cysts with early spermatids there is a narrow cleft-like lumen between the cells in the center of the slightly elongate body. When flagellae appear, these always grow into this central lumen and bend towards the same end of the cyst. This end soon becomes pointed, so the cyst becomes drop-like. Later, when the long pseudoacrosomes grow out from the opposite end of the spermatids, they are directed towards the other end of the cyst, which then becomes spindle-shaped (see Plate 1:3). Inside these more advanced cysts the spermatids are parallel, but the bundle of spermatids is slightly coiled. The spermatids are interconnected by plasmatic bridges until very late stages, i.e., the final separation following meiotic divisions is much retarded.

The cysts finally open and the mature spermatozoa are liberated. Exactly how the spermatozoa were liberated and transferred to the vesicula seminalis was not observed. At any rate, the transfer must be selective, for the vesicula contains no cellular debris or abnormal spermatozoa, only a tangle of non-orientated, normal spermatozoa. The wall of the vesicula is strongly phagocytotic, with many vacuoles containing recognizable remnants of spermatozoa.

The contents of the testicle are rather varied. In addition to spermatocysts and normal spermatozoa there are always some abnormal spermatozoa, cellular debris, and non-nucleated clumps of protoplasm. The non-nucleated plasma balls usually contain large vacuoles with inclusions, and sometimes degenerated spermatozoa. These balls are probably formed by the non-nucleated walls of the cysts when these disintegrate.

For the said reasons, squash preparations of testicles are not very useful in studies of spermatogenesis. The normal spermatids keep together in the spermatocysts and are difficult to spread, so the squash is usually dominated by abnormal spermatozoa and spermatids in addition to undefinable debris.

In some males, the testicle contains mainly normal spermatocysts in different stages of development, and the amount of suspended matter is moderate (Plate 1:3). In other males a great proportion of the spermatocysts show strong vacuolization and atrophy of the spermatids, and the fluid is crowded with abnormal spermatids, plasma balls with large inclusions, and undefinable debris (Plate 2:1). The latter picture is perhaps abnormal, indicating that the hosts were not kept well. On the other hand, such a picture could be a normal physiological condition if the spermatogenesis is under control and is checked when the vesicula seminalis is filled up.

The mature spermatozoa

External features, regional differentiation

The mature spermatozoa from the vesicula seminalis of the male or from the two receptacula of the female are filiform, $100-130 \mu \log (\text{Fig. 1}, \text{Plate 4})$. The thickness is greatest about the middle, ca. 0.8μ , tapering slightly towards both ends. When internal structure is considered, only two regions can be distinguished (Fig. 1): 1) a "pseudoacrosome", occupying the anterior ca. 35μ of the spermatozoon, and 2) a "body" of uniform structure extending from the base of the pseudoacrosome to the posterior end.

The term "*pseudoacrosome*" is introduced here to designate the anterior part of the *Raillietiella* spermatozoon, which could be mistaken for a true acrosome because of its situation and external morphology, but which differs from true acrosomes in internal structure and development. Conditions in *Argulus*, where a similar pseudoacrosome and a true acrosome exist side by side during development, show that this nomenclature is justified.

The pseudoacrosome is thinner than the body, about $0.35 \,\mu$ at the base and $0.15 \,\mu$ at the extreme point. It is stiff and usually arched like the periphery of a half-circle in living material and often preserves this shape in fixed specimens (Fig. 1, Plate 4:10). The transition from the pseudoacrosome to the somewhat thicker body is abrupt and can be seen in living sperm with phase contrast. EM-pictures of intact spermatozoa show this sudden change of thickness distinctly, so measurements of pseudoacrosome and body can be obtained with great accuracy (Plate 4:10).

Internal structure of body

As seen in cross sections, the body is bilaterally symmetrical (Fig. 1:B, Plate 5:16). It contains: 1) a filiform nucleus, cylindrical or slightly flattened in cross section, 2) three mitochondrial rods, arranged symmetrically in relation to the median plane, 3) a typical axonemal complex of the 9+2 type, 4) a system of high-contrast sheaths around axonema and lateral mitochondria, called dorsal and ventral ribbons,

Fig. 1. Raillietiella. Diagram of the mature spermatozoon, based on numerous total preparations and sections like those in Plates 4–7. The scale is 10 μ when used for the intact spermatozoon (A) and 1 μ when used for the details (B–H).

A. Entire spermatozoon. — B. Cross section of body. — C. Median section of body. — D. Median section of transitional region between body and pseudoacrosome. — E. Cross section through anterior end of nucleus. — F. Cross section of pseudoacrosome. — G and H. Cross sections of posterior end.

ax = axonema, dm = dorsal mass of pseudoacrosomal granular matter, investing filaments nos. 9, 1 and 2, dp = dorsal rod of pseudoacrosome, dr = dorsal ribbon, em = posterior end of mitochondria, en = posterior end of nucleus, er = smooth endoplasmic reticulum, g = granulosome, is = inner membranous sac of dorsal ribbon, lc = light core of dorsal ribbon, lp = lump of vesicular plasm, ls = limit of membranous sac on the ventral side of the pseudoacrosome, m = mitochondria, n = nucleus, om = oblique membrane between axonemal doublet 1 and dorsal ribbon, os = outer membranous sac of dorsal ribbon, pa = pseudoacrosome, pc = light core of dorsal rod of pseudoacrosome, ps = pseudoacrosomal membranous sac, td = top of dorsal rod of pseudoacrosome, tv = top of ventral rod of pseudoacrosome, vm = ventral mass of pseudoacrosomal granular matter, investing filaments no. 3-8, vp = ventral rod of pseudoacrosome, vr = ventral ribbon.



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and 5) minimal amounts of cytoplasm with remnants of smooth endoplasmic reticulum and a superficial cell membrane.

For descriptive purposes the axonemal aspect of the spermatozoon is called dorsal, the nuclear aspect ventral (see Folliot and Maillet 1970 p. 297).

The nucleus (Fig. 1:B–E, Plates 5:16, 6:18) has a highly condensed chromatin core, and appears compact black or indistinctly granular in EM-pictures. It is surrounded by the two usual nuclear membranes.

The mitochondria are three filiform, continuous rods, extending throughout the entire body. The median rod lies between axonema and nucleus, the other two form a pair of symmetrical wings in the cross section, closely attached to the median one (Fig. 1:B, Plate 4:16). The mitochondria are bounded by two unit membranes like normal mitochondria, but the cristae are poorly developed. The median mitochondrion has no cristae at all in the mature spermatozoon, whereas one or two folds of the inner membrane are seen in cross sections of the lateral mitochondria (Plate 6:18, Plate 17:83).

The axonema has the 9+2 pattern (Plates 5:16, 17:83). The central pair is always symmetrically placed, one on each side of the median plane, and the peripheral doublet 1 is dorso-median. An astonishing feature, observed by Doucet (1965), is the constant presence of a dark line, connecting the dorsal peripheral doublet (no. 1) with the high-contrast sheaths surrounding the axonema. Since this line is constant in good cross sections, it must represent a continous membrane, extending from the filament no. 1 to the sheath. The membrane is always obliquely oriented, being the only asymmetrical structure in the spermatozoon, if the arms on the axonemal doublets are excepted (Plates 5:16, 17:83). From its attachment to the doublet, the membrane is inclined to that side where the arms of doublet 1 are situated.

The high-contrast sheaths around the axonema have a complex origin, which will be described later. The main components are two half-cylindrical sheaths, which together form a complete, tube-like investment of the axonema (Fig. 1:B). These two half-tubules will be called *dorsal and ventral ribbons* in the subsequent descriptions. The dorsal ribbon covers the dorsal half of the periphery of the axonema. Its free margins are sharp edges, which fit into furrows in the thickened free margins of the ventral ribbon (Fig. 1:B, Plates 5:16, 17:83). The core of the ribbons is a dark-staining granular substance, in which some light areas are found in constant location: One sickle-shaped median area in the dorsal ribbon, and a symmetrical pair of light spots in the ventral ribbon.

The outer surfaces of the dorsal ribbon are formed by double unit membranes, both on the convex and the concave sides (Fig. 1:B). They are the remnants of two flat membrane-bound sacs, which, in spermatids, surround the growing ribbon from the dorsal and ventral sides (Plates 16:80, 17:83). The two membranes are only visible in very thin and fortunate sections of the mature spermatozoon, because the lumen has disappeared and the two membranes are closely attached to each other. The ventral ribbon is not associated with membranes of this kind.

The ventral ribbon is continuous with thin lamellae of dark matter, which cover the dorsal and lateral aspects of the lateral mitochondria (Fig. 1, Plate 5:16). Although these sheaths sometimes can be resolved into two tightly attached dark lines, they are probably not built of unit membranes, for distinct membranous sacs are not observed here during spermatogenesis.

The ventral ribbon is also continuous with the more or less distinct dark matter which fills the narrow space between the lateral and median mitochondria on each side (Plate 17:83, compare Fig. 1:B).

The cytoplasm is not abundant and is covered by a seemingly normal cell membrane, forming the outer surface of the spermatozoon. In cross sections, a few flattened sacs can be seen on each side in the narrow space between lateral mitochondrion and nucleus. These sacs are remnants of the smooth endoplasmic reticulum, which is well developed in spermatids (Plates 5:16, 17:83).

Towards the *posterior end* the body gets thinner, depending on decrease in thickness of nucleus and mitochondria. However, the typical cross section with nucleus, three mitochondria, axonema, ribbons, etc., extends to a point about $4-5\mu$ from the extreme end. At this point the nucleus ends, and the ventral ribbon disappears at about the same level (Fig. 1:A, G, and H, Plates 4:14, 7:29). The mitochondria extend a little further but become very narrow. The filaments of the axonema begin to become irregular and fewer in number from the level where the nucleus ends, but a few axonemal filaments together with the dorsal ribbon form the very tip of the spermatozoon. A free flagellum with normal structure can therefore not be recognized. Irregular clumps of protoplasm, often with some large vacuoles, are regularly seen bulging out from this terminal part of the spermatozoon (Plates 4:14, 7:29).

The anterior end of the body is attached to the long pseudoacrosome. In the transitional region the axonema continues into the base of the pseudoacrosome as a strongly modified centriole (Fig. 1:D,E). The nucleus, at this level very thin and consisting mainly of the narrow tube of nuclear membranes, ends at the level of the pseudoacrosomal base, and the mitochondria reach approximately the same point. The dorsal ribbon is directly continuous with the "dorsal rod" of the pseudoacrosome (see below). The ventral ribbon seems to be continuous with the "ventral rod" of the pseudoacrosome, but development shows that this connection is secondary and is established by the plentiful dark-staining matter, which tends to obscure the region of transition.

The original triplets of the centriole change to doublets at an early stage of spermatogenesis, as will be described in a separate chapter. In cross sections of mature spermatozoa these doublets are seen as pairs of light spots in the plentiful dark matter in which they are embedded (Fig. 1:E, Plate 7:21,22). Although this matter obscures some details, a very constant pattern is repeated in all sections through the transitional region. The three dorsal doublets (nos. 9, 1 and 2) converge and are embedded in a common dorsal mass of the dark pseudoacrosomal matter, continuous with the dorsal rod of the pseudoacrosome. The six ventral doublets (nos. 3–8) are in a similar way cemented together by pseudoacrosomal granular substance continuous with the ventral rod of the pseudoacrosome (see also Plates 6:20, 22:114–116). Details will be described in connection with spermatogenesis.

Internal structure of pseudoacrosome

The long, arched pseudoacrosome is covered by an ordinary cell membrane, immediately followed by two more unit membranes, which are continuous all around the cross section (Fig. 1:F, Plate 7:23–24). The latter are the remnants of a smooth endoplasmic reticular sac, which surrounds the growing pseudoacrosome in the spermatids. The space inside the membranes is occupied by the two pseudoacrosomal rods, a dorsal and a ventral one, which look almost identical in cross sections of mature spermatozoa. Both consist of dark-staining, granular matter which surrounds a lightstaining central area (Fig. 7:24).

Several EM-pictures of total spermatozoa show that the ventral rod, as defined by the proximal attachment to the ventral filaments of the centriole, follows the convex side of the curvature of the pseudoacrosome. At the point, the dorsal rod ends $0.4-0.9\mu$ before the ventral one, so the very tip is supported by the ventral rod alone (Plate 4:12). On the dorsal side of this single rod is a granule of moderate contrast, about 0.2μ in diameter. It has been seen and photographed in five different spermatozoa which had been spread on grids after osmic fixation and had their anterior ends intact (Fig. 1:A, Plate 4:12). Development shows that this granule is a derivative of the so-called granulosome in spermatids (see spermatogenesis).

Movements

Spermatozoa spread in Ringer solution from the receptaculum seminis survive for 15 minutes or more. They swim rapidly by undulating movements of the body, whereas the pseudoacrosome is kept stiff and is bent to one side, usually in the halfcircular fashion seen in Fig. 1:A. This asymmetry results in constant deviation to one side, when the undulations push the spermatozoon forwards. The path described is therefore more or less circular. The spermatozoa were studied with phase contrast. As they were mounted under a cover glass and only had possibilities for movements in two directions, it is unknown how they behave in free liquid.

Spermatogenesis

Spermatogenesis in *Raillietiella* has been analyzed in considerable detail in order to facilitate interpretation and characterization of the many strange structures. The analysis was greatly facilitated by the simultaneous development of all spermatids in each cyst: numerous sections at different levels could be obtained of spermatids of a defined stage. Nevertheless, between 50 and 150 EM-pictures were often necessary to give a reasonably complete picture of a particular stage.

In the following, the general course of spermatogenesis will be described stage by stage with emphasis on features characteristic of *Raillietiella*. At the end of the chapter,

From spermatogonia to early spermatids

This part of spermatogenesis is of an ordinary type. The regular, polygonal cells (Plates 3:6,8, 8:32) reach maximum size with a diameter of ca. 10μ as spermatocytes 1, just before maturation starts. Spermatogonia and early spermatids are smaller, $6-7\mu$. The nuclear diameter is large in spermatogonia and spermatocytes 1 (4.5–5.7 μ) but is reduced to 3–3.9 μ in early spermatids. The cytological picture during this development is characteristic of growth and synthesis: numerous nuclear pores, numerous free ribosomes or polysomes in the plasm, and a large (1.3–1.9 μ) nucleolus.

In early spermatids the nuclear pores and free ribosomes are still abundant, but the nucleolus is smaller, about $0.6-0.7 \mu$.

Two structures are of particular interest for the subsequent development: mitochondria and centriolar structures.

The mitochondria are rod-shaped or tubular in spermatogonia and spermatocytes 1, with a diameter of $0.2-0.3 \mu$ in spermatogonia and $0.3-0.4 \mu$ in spermatocytes (Plate 9:46). The length is difficult to ascertain in sections, but pieces as long as 6μ have been measured. At the end of meiosis the mitochondria change drastically. They become spherical with a diameter of ca. 1μ and are concentrated to a group of eight or more in the neighbourhood of the nuclear membrane of early spermatids (Plate 9:48, Fig. 2). Some mitochondria probably degenerate during this process, but definite proof is difficult to obtain. In spermatocytes and during meiosis dark-staining rods are seen between the scattered, tubular mitochondria. Some of the dark rods have double outer membranes and crista-like folds of the inner membrane, indicating a mitochondrial origin. The majority of these dark bodies have simple membranes and a granular or multivesicular content. In spermatids such bodies are present but lack all mitochondrial characteristics and are seen as a group of dark, membrane-bound bodies, distinctly separated from the group of mitochondria (Figs. 2-5).

The centrioles. Two centrioles, oriented perpendicular to each other, were seen in several spermatocytes 1 (Plate 8:38). This stage could be definitely identified with the help of mitochondrial and cellular size and the presence of well-developed synaptone-mal complexes in the nucleus. Obviously no duplication of the centriole takes place after the 2nd meiotic division, for only one centriole was found in numerous early spermatids 1, which were studied in several spermatocysts. The length of the centriole is $0.8-1.0\mu$ in early spermatids and in 2nd meiotic cells (Plate 8:39,40), whereas shorter centrioles measuring only about 0.6μ were encountered in spermatocytes 1 (Plate 8:38).

The bilateral structure, characteristic of the centriolar complex of spermatids, develops already before the 2nd meiotic division. Cross sections of 2nd meiotic centrioles show two dark outer rods, following one side of the centriole (Plate 8:32). This side is the prospective dorsal side of the centriole, and the rods are the first anlage of the

dorsal ribbon. In early spermatids the two rods are still present and are covered by a dark membrane, formed by a flat membranous sac continuous with the smooth endoplasmic reticulum (Plate 8:33). This sac is the prospective outer sac of the dorsal ribbon. The dark rods and the outer sac are definitely not present in spermatocytes 1, so they must be formed during meiosis.

The characteristic structures at the prospective proximal end of the centriole also appear during or just before meiosis. These structures are: 1) a body of granular substance, here called "granulosome", attached to the proximal end of the centriole, and 2) the "apical membrane", which is a dark, membrane-like condensation of the granular material across the end of the centriole (Figs. 2–4 and 11, Plate 8:41). The granulosome may be traced but is not so well defined during meiosis and in spermatocytes 1 (Plate 8:38,39). The apical membrane is distinctly present in 2nd meiosis centrioles (Plates 8:39), but probably begins to form already in late spermatocytes 1 (Plate 8:38). In these early stages the apical membrane is ring-like, covering only the free edges of the centriolar tube (see also Plate 8:40).

"Granulosome" and "apical membrane" are tentative names, chosen to avoid premature identification with previously described structures such as "centriole adjunct", "acroblast", "acrosome granule", "post-nuclear body", etc.

The granulosome and the apical membrane, from which the pseudoacrosome later develops, as well as the anlage of the dorsal ribbon, are thus present as pericentriolar structures already in meiotic cells. They develop in close contact with the centriole without direct contact or interference of the nucleus. These structures make the centriolar complex bilaterally symmetrical already in late meiosis, so the prospective dorsal and ventral sides, as well as proximal and distal end, can be recognized already at this early stage.

Spermatid 1; with several mitochondria

Sections of early spermatids, often with remnants of meiotic spindles, always show the above-mentioned group of spherical *mitochondria* near the nucleus (Fig. 2, Plate 9:48). Usually a single section shows five to eight mitochondria in the group, so there must obviously be more than eight in many cases.

The centriole in these cells is always in contact with the cell membrane by one end. Usually the membrane is indented to form a pit at the point of contact. A short flagellar rudiment may be formed from the bottom of the pit, but it is purely plasmatic, without axonemal filaments (Fig. 2, Plate 11:56).

As mentioned above, the centriole has developed a distinct granulosome, apical membrane, two dark dorsal fibers and a dorsal, (outer) membranous sac (Plate 8:33, 11:56). The proximal end with the granulosome lies free in the plasm although it sometimes is near the nucleus, as in Plate 11:56. The centriole has thus not established the contact with nucleus and mitochondria so typical of later stages.

The nucleus has many pores and a rather large nucleolus. The cytoplasm contains the above-mentioned group of dark, membranebound bodies (Fig. 2), and is



Fig. 2. *Raillietiella*, spermatid, stage 1. with numerous mitochondria. Fig. 3. *Raillietiella*, spermatid, stage 2. with three mitochondria.

Fig. 4. Raillietiella, spermatid, stage 3. with "Nebenkern". All diagrams based on light microscopical pictures for gross dimensions and on numerous EM pictures like those in Plates 8-11 for details.
am = apical membrane, an = annulus-like thickening around the flagellum in the bottom of the flagellar pit, ce = centriole, cw = wall of spermatocyst, db = dark bodies, perhaps in part degenerating mitochondria, dr = dorsal ribbon, er = smooth endoplasmic reticulum, fr = flagellar rudiment, g = granulosome, m = mitochondria, nk = "Nebenkern".

rich in smooth endoplasmic reticulum, which forms irregular tubules and vesicles. Rough endoplasmic reticulum with ribosomes is very rare and, when seen, of little extension. Stacks of Golgi vesicles have been seen a few times but are rare and very small. They have no relation to the structures described here. Free ribosomes, usually in small clusters, are abundant (Plate 11:56).

Spermatid 2; with three spherical mitochondria

Mitochondria. The three spherical mitochondria of this stage are large, $1.3-1.7 \mu$, and have numerous, distinct cristae (Plates 9:50, 10:54, 11:59). They are arranged in a triangular fashion in contact with the nucleus and touching each other two and two. The contact between the mitochondria is characterized by slight flattening of the membranes and accumulation of medium-contrast matter in the interspace (Plate 9:50).

The final reduction of the spherical mitochondria from more than eight in the preceeding stage to three in the present stage probably takes place by fusion. This is indicated by pictures which are believed to show stages of this process: Two distinctly different, almost spherical mitochondria in contact with each other, with common

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outer membrane but separate inner membranes (Plate 9:47). The other possibility, that some mitochondria degenerate, is practically ruled out by the absence of degenerative symptoms within the group of spherical mitochondria.

The axonema grows out from the centriole into the pre-formed plasmatic flagellum during this stage (Fig. 3, Plate 11:57,59). No transverse disc or similar structure has been seen between the centriole and axonema at any stage of development. This makes the shift from centriole to axonema rather indistinct, so a definition is required. In the following, all parts lying proximal to the point where the central filaments begin are called centriole.

As seen in the figures (Plate 11:57,59), the axonema is restricted to the free flagellum at this stage: The central filaments begin at the level of the bottom of the flagellar pit. Here, around the base of the flagellum, there is a thickening of the cell membrane which probably maintains the shape of the pit. This thickening is called the annulus, although it is associated with very little dark matter in the inside plasm (Plates 11:59, 8:41).

The centriole complex has changed in some important respects. The membranous sac, covering its dorsal aspect, is still present and its inner wall is thickened to form a dark membrane, which arches over the centriole in a cross section (Plate 8:34). But under this membrane there are three dark rods, not two as in previous stages. The change from two to three dark rods during this developmental period is well documented but details are not well understood (compare Plate 8:32–34).

The three dark fibers under the membranous sac correspond to the three dorsal filaments of the axoneme: nos. 9, 1 and 2. Dark outer fibers have also appeared outside the other filaments (Plate 8:34). Of these, nos. 3 and 8 could not be followed further, but nos. 4–7 are often distinct in later stages and are included in the ventral ribbon (Plate 16:76, 80).

During meiosis and in spermatid 1 the filaments of the centricle appear as more or less distinct, obliquely oriented triplets. This picture has changed in spermatids 2, where well-separated doublets are found in cross sections (Plate 8:33,34).

The relation between nucleus, centriole and mitochondria is established during this stage. Early spermatids 2 show nucleus, mitochondria and centriole lying independent of each other (Plate 10:54). In other, more advanced spermatids 2, the granulosome is distinctly attached to the nuclear membrane and the centriole lies in the furrow between two of the mitochondria (Plates 8:34,41, 11:57,59). At the contact point with the granulosome there is an accumulation of dark matter on the inner side of the inner nuclear membrane (Fig. 3, Plate 8:41).

The centriole-axonema always passes from the flagellum to the nucleus in the cleft between two of the mitochondria. In later stages the prospective dorsal ribbon with the endoplasmic membranous sac is always on that side of the axonema which is opposite to the mitochondrial triplet, as seen in Plates 8:34 and 10:52. In the present stage this relation is variable, and the anlage of the dorsal ribbon is sometimes on the side facing the mitochondria. This must mean that the orientation of the centriole

and the dorsal ribbon takes place after the contact with the mitochondria is established.

Other cytoplasmic organelles are not very different from those of spermatids 1.

Spermatid 3; with mitochondrial "Nebenkern"

Mitochondria. The single mitochondrial "Nebenkern" seen with the light microscope in spermatids of this stage consists of the three mitochondria of the previous stage, which have been packed together to form a single body (Fig. 4, Plate 10:52). The Nebenkern is about 2.5μ in diameter and is bilaterally symmetrical in relation to a median plane through the centriole. The limits of the original mitochondria are only faintly indicated as furrows on the outer surface but are distinctly marked by the intact mitochondrial membranes inside the body. Thus, the three giant mitochondria maintain their individuality and never fuse to one body in the way described for many arthropods and molluscs (Favard and André 1970). The space between the mitochondria is filled with a medium-contrast matter, making the attachment desmosome-like (Plate 10:52).

The Nebenkern with its single median and two symmetrical lateral mitochondria has a shallow furrow for the centriole and axonema. In this furrow all three mitochondria face the centriole-axonema with rather sharp, straight edges (Plates 10:52). These edges of all three mitochondria extend from the granulosome to near the annulus, where the axonema enters the free flagellum (Fig. 4).

Centriole-axonema. In earlier stages the centriole entends to the annulus, and the axonema, when it grows out, is restricted to the free flagellum (Fig. 3). In spermatids 3, more and more of the axonema is included in the cell body proper, so the annulus moves away from the end of the centriole, and the posterior part of the cell behind the nucleus is elongated (Fig. 4). This posterior migration of the annulus continues to the end of spermatogenesis. When the axonema inside the cell body grows, the anlages of the dorsal ribbon and the mitochondria grow correspondingly, so their tips keep contact with the annulus but never enter the free flagellum (Figs. 4–10, Plate 11:58).

Spermatid 4; anterior dislocation of centriole

The flagellum grows out from that wall of the cell which faces the inner, cleftlike lumen of the spermatocyst. This end of the cell is the prospective posterior one, whereas the end in contact with the cyst wall is the prospective anterior one. The point of contact of the granulosome-centriole is originally on the posterior surface of the nucleus (Fig. 3). After formation of the "Nebenkern" the point of attachment shifts over to the side and is finally found near the anterior end of the now more elongate nucleus (Fig. 5 and 6, Plate 12:60,61). After this has occurred, the centrioleaxonema, like the dorsal ribbon and mitochondria, extends along one side of the nucleus to reach the anteriorly situated point of attachment.

This dislocation of the centricle could be explained by assuming that the nucleus rotates, as suggested for *Lepisma*, in which a similar dislocation takes place (Werner

1964). Another possibility is that the granulosome-centriole slides along the nuclear surface. Both possibilities are in fact open in *Raillietiella*. Conditions in *Argulus*, where a true acrosome is present as a fixed point on the nuclear surface, are definitely in favour of the sliding alternative.

Mitochondria. During dislocation, the centriole-axonema migrates up along the prospective dorsal side of the nucleus, with the dorsal ribbon on the ab-nuclear side (Fig. 4, 5 and 6). The main bulk of the mitochondrial Nebenkern remains behind the nucleus, but all three mitochondria are extended as narrow tongues between the axonema and the nucleus, their tips remaining in contact with the centriole (Plate 15:72). The mitochondrial tongues are symmetrically situated with one median and a pair of lateral ones like the mitochondria of the Nebenkern (compare Plate 13:65).

The mitochondria are also prolonged as narrow tongues posteriorly, along the ventral aspect of the axonema. These posterior mitochondrial tongues, like the anterior ones, are arranged symmetrically in relation to the median plane (Plates 15:73, 16:76). The posterior tongues grow in proportion to the lengthening of the cell, so the tips remain in the neighbourhood of the flagellar pit.

Dorsal ribbon. During this stage a definite dorsal ribbon begins to form above the centriole and anterior axonema. The three large dark fibers above the flagellum fuse and form a dark plate, covered by the dark sheath formed by the outer membraneous sac of endoplasmic reticulum (Plates 10:52, 16:76, 80. Compare Figs. 11: B, C and 12). A second flat membranous sac appears between the dark core of the dorsal ribbon and the axonema, with lateral connections to the endoplasmic reticulum. One of the walls of this inner sac forms another dark sheath, covering the core of the dorsal ribbon from the ventral side. The growing dorsal ribbon therefore consists of a granular core, formed by the dark outer fibers 9, 1, and 2, delimited by two dark sheaths, formed by the outer and inner membranous sacs (Fig. 12: F).

Differentiation of the dorsal ribbon appears to proceed from the centriole backwards, so very immature stages with three dark fibers can be seen near the flagellar pit. The other outer fibers are also prolonged in a posterior direction to the neighbourhood of the flagellar pit, where particularly the fibers 4–7 can be very distinct (Plate 16:76).

Centriolar apparatus. During dislocation of the centriole the apical membrane appears to be detached, while the granulosome remains attached to its anterior surface (Figs. 5, 6, 11 B, Plate 12:60, 61). The granulosome loses its contact with the nucleus and is seen as a granular pellet on the extreme top of the growing pseudoacrosome of later stages (Figs. 6–10). New granular matter appears behind the apical membrane, in the space delimited by this membrane, the nucleus, the centriole and the mitochondria (pm in Figs. 5–7). This matter plays an important role in the development of the pseudoacrosome, and will therefore be called "pseudoacrosomal granular matter" or PGM. It condenses to form a dark pellet on the posterior side of the apical membrane (pm in Fig. 11), whereas a more diffuse "ventral portion" fills out the space near nucleus and mitochondria (vm in Plate 12:61).

The centriole is covered by a developing dorsal ribbon like the axonema, with inner and outer membranous sacs and granular core. The inner sac, like the granular



Fig. 5. Raillietiella, spermatid stage 4, beginning migration of centriolar complex. Fig. 6. Raillietiella, spermatid, late stage 4.

Fig. 7. Raillietiella, spermatid, early stage 5, development of the nuclear tongue (nt). All diagrams are based on light microscopical sections for gross dimensions and on numerous EM pictures like those on Plates 12, 13, 15 and 16 for details.

am = apical membrane, at = anterior tongues of mitochondria, ax = axonema, ce = centriole, cw = cyst wall, dr = dorsal ribbon, g = granulosome, nk = "Nebenkern", nt = anterior nuclear tongue, pm = pseudoacrosomal granular matter, pt = posterior tongues of mitochondria.

core, ends above the anterior part of the centriole, but the outer sac spreads to cover the anterior surface of the apical membrane (Fig. 11:B). This membranous sac excepted, there is little continuity between the structures of the dorsal ribbon and the apical membrane (Plate 12:61, Fig. 11).

Spermatid 5; formation of nuclear tongue and of pseudoacrosome

After the centriole is dislocated forwards, it is connected with the nucleus by the ventral portion of the PGM (Fig. 6, 11:C). The contact area is situated on a slight elevation of the nuclear membrane. The further development includes excessive growth of this elevation, which develops into an anteriorly directed nuclear tongue, with the contact point at the top (Figs. 7, 8, 11:C–D). The dorsal ribbon, the axonema, and the three mitochondrial tongues follow this elongation, so a narrow rostrum containing all these structures is formed (Figs. 7–8, Plate 13:64,65). The main bulk of the mitochondrial Nebenkern still remains behind the thicker posterior part of the nucleus.

The pseudoacrosome begins to grow out from the anterior rostrum, all the time carrying the granulosome on its top (Figs. 8–9, Plates 13:65, 23:117). The granulosome sits on a transverse membrane, which is identical with all or part of the previously described apical membrane (Figs. 8–10, Plates 12:61, 13:64,65, 23:117). The growing pseudoacrosome is surrounded by a flat membranous sac in communication with the endoplasmic reticulum (Plates 20:99-101, 21:106-107). This sac develops as a forward extension of the outer sac of the dorsal ribbon, which spreads over the apical membrane and down the sides of the growing pseudoacrosome, which finally is completely surrounded (ps in Fig. 12). Below the anterior end of the centriole, this sac fails to fuse ventrally, so there is an opening in the membranes in front of the nucleus (Fig. 12:A,D).

Granular matter (PGM) condenses on the inner side of the pseudoacrosomal sac to form two, eventually half-cylindrical, dark sheaths. These are called *dorsal and ventral sheaths* in the following (Fig. 12:B, C, Plate 20:99–101). The space inside the sheaths is filled with PGM, which is remodelled several times during the subsequent development.

The ventral sheath is directly continuous with the apical membrane. In early stages of pseudoacrosome development, the apical membrane appears to be bent over on the ventral side, and the half-cylindrical ventral sheath seems to grow posteriorly from its ventral margin (Fig. 12:A, Plate 13:64). At the base of the pseudoacrosome the ventral sheath is open in the midline and continues as two wing-like plates to the sides of the centriole (Fig. 12:D, Plate 22:114–116).

The dorsal sheath is originally a narrow, band-like accumulation of granular substance, continuous with the outer dark sheath of the dorsal ribbon (Fig. 12, Plate

Fig. 8. Raillietiella, spermatid stage 5, additional lengthening of nucleus.

Fig. 9. Raillietiella, spermatid, late stage 5, beginning formation of pseudoacrosome.

Fig. 10. Raillietiella, spermatid stage 6. Final elongation of nucleus, pseudoacrosome and mitochondria. All diagrams are based on light microscopical sections for gross dimensions and on numerous EM pictures like those on Plates 13, 17, and 20–23 for details.

am = apical membrane, ax = axonema, ce = centriole, dr = dorsal ribbon, ds = ventral sheath of pseudoacrosome, g = granulosome, m = mitochondria, n = nucleus, nk = "Nebenkern", o = opening between anterior end of nucleus and posterior margin of ventral acrosomal sheath, pm = pseudoacrosomal granularmatter, vs = dorsal sheath of pseudoacrosome.



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20:99–101). Later the dorsal sheath, like the ventral one, grows out to become halfcylindrical (Plate 21:106–107). For a long time it remains somewhat smaller than the ventral one, and thins out before reaching the apical membrane.

The granular matter (PGM) inside the sheaths is condensed to form an irregular tube-like structure in early pseudoacrosomes (Plate 20:99,100). Later the tube collapses and the granular matter typically forms a median lamella, attached to the dorsal sheath and partly stuck in the half-cylindrical ventral sheath (Plate 20:101). In still more advanced pseudoacrosomes of stages 6 and 7 the PGM is divided into two portions, which fill out the dorsal and ventral sheaths, respectively, and are separated by a horizontal cleft (Plate 21:106–107). These sheaths with their contents are then transformed to the dorsal and ventral rods of the mature spermatozoon.

The nucleus still has a small nucleolus when it begins to emit the anterior tongue, and several nuclear pores are present. These structures have not been seen after the pseudoacrosome has begun to grow out. Instead several small, compact accumulations of chromatin are seen as black dots in the nucleoplasm as a first sign of nuclear condensation (Plate 13:64,65, Figs. 8,9).

The cytoplasm of stage 5 spermatids contains numerous small smooth-surfaced vesicles and sacs of endoplasmic reticulum, while rough-surfaced vesicles and Golgistacks are very rare and small, as in earlier stages. Ribosomes and polysomes are still numerous. A system of longitudinal microtubules has developed as an almost continuous layer along the growing pseudoacrosome and, as more scattered tubules, along the elongating anterior end of the nucleus (Plate 20:99–101).

Spermatid 6; elongation of nucleus and mitochondria, formation of ventral ribbon

The nucleus. During previous stages the main bulk of the nucleus is a thick ovoid body, from which the narrow anterior tongue grows out (Figs. 7,8). In the present stage the main body of the nucleus elongates strongly and extends backwards below the axonema (Fig. 10). The Nebenkern remains in the position behind the end of the nucleus and decreases in size, while the mitochondrial rods along the axonema increase in length.

The chromatin of the nucleus is in a state of progressive condensation. The small clumps of chromatin seen in stage 5 grow to large round bodies, which in later stages collapse to form the compact nuclear rod of the mature spermatozoon (Fig. 10, Plate 17:82–83).

The ventral ribbon forms between the axonema and the mitochondria. Differentiation appears to proceed from the centriolar region backwards, for differentiation is generally less advanced near the posterior end. Orginally the outer dark fibers 4-7 are situated in the region where the ribbon develops, whereas fibers 3 and 8 seem to disappear (Plate 16:76). In more advanced stages these dark fibers are less distinct and a dark lamella of unknown origin appears on the ventral aspect of the axonema and extends over the dorsal surface of the lateral mitochondria (Plate 16:80, Fig. 12:F). This lamella together with the outer mitochondrial membranes delimits a space in

which the four dark fibers and an increasing amount of dark-staining matter is present (Fig. 12:F). Finally all these dark-staining components fuse to form the ventral ribbon which, therefore, is supposed to contain the outer dark fibers 4–7 of the axonema. The dark lamella which was mentioned as one of the components is probably not a unit membrane, although it has approximately the same thickness. It is not sharply de-limited as a typical unit membrane, tri-lamination has never been seen, and no connection with endoplasmic reticulum has been observed. The light cores which become visible in the final stages of spermatogenesis could well be the dark outer fibers of doublets 5 and 6, just like the light core of the dorsal ribbon appears to be formed by the fused outer fibers 9, 1 and 2.

The dorsal ribbon extends laterally down the sides of the axonema but final contact with the ventral ribbon is not obtained until very late stages. More dark matter is deposited in contact with the inner and outer sacs, forming the compact dark cortex of the mature ribbon. The granular core, originally formed by outer dark fibers 9, 1 and 2, appears to persist and to change stainability, forming the light core of the mature ribbon (Fig. 12:F, Plates 16:80, 5:16, 22:116).

In the *pseudoacrosome* the granular matter fills the half-tubular sheaths and is divided by a horizontal cleft, so the dorsal and ventral rods are distinctly separated (Plate 21:106–107).

Numerous *microtubules* are seen along all parts of the growing spermatid of this and the following stage.

Spermatid 7; final transformation to mature spermatozoon

The development from stage 6 to mature spermatozoon includes additional elongation of all parts (compare Figs. 10 and 1). At all levels the spermatid is surrounded by numerous microtubules, which must be eliminated before final maturation, for they are absent in the free mature spermatozoa (Plates 21:107, 17:83).

Nucleus, ribbons, and mitochondria extend to near the posterior end of the axonema, and the free flagellum is eliminated. Details of this process have not been studied.

The *pseudoacrosome* is reorganized at the top, so the ventral rod overshoots the dorsal one with a few microns, and the granulosome slides over to the dorsal side of the single terminal rod. That this takes place before liberation of the spermatozoa could be seen in fortunate sections of a nearly mature spermatocyst, in which some granulosomes remained terminal on the top of the rods, whereas others had slid over on the side of one of the rods (Plate 23:118).

Detailed analysis of the pseudoacrosome and of the transitional region between pseudoacrosome and body

The precise derivation of the pseudoacrosome and its relation to other structures is of fundamental interest for comparisons. Its development will therefore be considered separately here. In spermatids 4–5, just before pseudoacrosome development starts, there is an anterior rostrum containing the nuclear tongue, the three mitochondrial tongues, the centriole, and the dorsal ribbon (Fig. 11:C, D). The anterior ends of these structures are at approximately the same level; only the mitochondria are a little shorter. The centriole, the mitochondria, and the nucleus are in contact with the pseudoacrosomal granular matter (PGM), which has condensed to form a dark granule at the end of the centriole, whereas the more scattered ventral portion of PGM is in contact with nucleus and mitochondria (Cf. Plate 12:61). Anteriorly the PGM is covered by the apical membrane, over which the flat membranous sac of the dorsal ribbon extends. The apical membrane carries the granulosome on its anterior surface.

When the pseudoacrosome grows out, it is quite obvious that its dorsal sheath is formed directly as an anterior prolongation of the outer sheath of the dorsal ribbon. The outer endoplasmic reticular sac of the latter grows forwards, and dark matter, continuous with that of the ribbon, accumulates on its inner surface to form the dorsal sheath (Fig. 12: A, C-E).





Originally, the apical membrane is not associated with membranous sacs (Fig. A), but later the outer sac of the dorsal ribbon appears to spread over its surface (Figs. B–D). In Fig. A only the outer sac of the dorsal ribbon is present. In Figs. B–D the inner sac has appeared between the axonema and the dark matter formed by the dark outer fibers.

am = apical membrane, ax = axonema, ce = centriole, cr = granular core of dorsal ribbon, df = dark outer filaments of centriole, er = endoplasmic reticulum, fp = flagellar pit, g = granulosome, is = inner membranous sac of dorsal ribbon, m = mitochondria, n = nucleus, os = outer membranous sac of dorsal ribbon, pm = pseudoacrosomal granular matter.

At an early stage the apical membrane grows out to form a pair of posteriorly directed wing-like flaps on the sides of the centriole. These are also formed on the inner side of membranous sacs, which are connected both with the inner sac of the dorsal ribbon and, anteriorly, with the common sac of the pseudoacrosome (Fig. 12:D, Plate 20:104). When the top of the pseudoacrosome grows forwards, the ventral sheath is formed as a forward continuation of the wing-like flaps and remains in continuity with the apical membrane (Fig. 12:A, B, C).

The PGM appears behind the apical membrane when this is detached from the end of the centriole (Fig. 11:A, B). At this stage a formation of PGM directly from the nucleus could seem possible, but later development makes this interpretation doubtful. During development the acrosome grows out to a 35μ long rod, and the general rule is that the morphological maturation of the PGM is most advanced at the base, whereas it is less advanced just behind the apical membrane. Thus, immediately behind the membrane, there is always an unorganized mass of PGM (Plate 23:117), a little further



Fig. 12. *Raillietiella*, spermatid, stage 6. Diagrams of median section (A) and of cross sections from different regions (B–F). Compare Plates 16 and 20–23. The pseudoacrosome is formed exclusively by the pericentriolar structures shown in Fig. 11.

am = apical membrane, ce = centriole, cr = granular core of dorsal ribbon, df = dark outer fibers of axonema, dm = dorsal extension of the pseudoacrosomal granular matter, ds = dorsal sheath of pseudoacrosome, er = smooth endoplasmic reticulum, g = granulosome, is = inner membranous sac of dorsal ribbon, ls = posterior limit of the membranous sac on the ventral side of the pseudoacrosome, m = mitochondria, mp = membranelike condensation of PGM, mt = longitudinal microtubules, n = nucleus, os = outer membranous sac of dorsal ribbon, pm = pseudoacrosomal granular matter (PGM), ps = membranous sac of pseudoacrosome, vm = ventral extension of the PGM, vr = ventral ribbon, vs = ventral sheath of pseudoacrosome, w = posterior winglike extensions of the ventral sheath on the sides of the centriole. back it may be condensed to a median lamella attached to the dorsal sheath, and at the base the PGM may have formed almost compact rods by filling the dorsal and ventral sheaths. This indicates that addition of new substances takes place from the anterior end, and that the apical membrane or granulosome, perhaps also dorsal and ventral sheaths, constitute the synthetic apparatus.

This means that all structures taking part in the formation of the pseudoacrosome have a peri-centriolar origin: The dorsal ribbon, the granulosome, and the apical membrane are present before the centriole is attached to the nucleus, and the PGM is most probably formed by these structures. The very poorly developed Golgi apparatus has not been observed to have any connection to the developing structures, in contrast to conditions in *Argulus*, in which the Golgi apparatus is better developed.

Since the pseudoacrosome has a purely centriolar origin, it is completely different from typical acrosomes, which form without connection with the centriole, as derivatives of the Golgi apparatus, and in intimate contact with the nucleus, at least in later stages.

The transitional region. When the pseudoacrosome forms, the centriole is directly included in its base. This inclusion of the centriole can be distinctly followed in the sections. Already in stages 5 and 6 some PGM invades the anterior end of the centriole and is condensed to form a dark plate under the dorsal filaments 9, 1 and 2 (Fig. 12: A, C, D). These filaments converge a little and are embedded in additional dark PGM, so a complex dorsal portion of PGM is formed below the inner sac of the dorsal ribbon (Plate 22:115–117). This dorsal portion with the three dorsal centriolar filaments fuses anteriorly with the core of the dorsal rod of the pseudoacrosome.

The six ventral filaments of the centriole are in a similar way surrounded by the more scattered ventral portion of PGM, which tends to condense around the filaments (Plate 22:115–117). This ventral portion fills out the space between the top of the nucleus and the mitochondria and the posterior margin of the ventral sheath, and is covered from the sides by the wing-like posterior extensions of the latter (Fig. 12:A, D). Actually therefore, the six ventral filaments are connected with the ventral rod of the pseudoacrosome.

The gap between the posterior margin of the ventral sheath and the top of the nucleus is preserved also in mature spermatozoa, although the ventral portion of PGM becomes denser (Fig. 1).

IV. ARGULUS FOLIACEUS (L.), COMPARED WITH RAILLIETIELLA

It was Leydig (1850) who discovered the testicles of *Argulus* and described their position in the vestigial, bilobed abdomen. He was also able to see and describe the spermatozoa, although these are only $0.2-0.5 \mu$ thick. He writes that they are filiform, about "0.05" lang". In modern units this corresponds to about 110μ , which is surpris-

ingly accurate, for in the present study values between 110 and 120μ have been obtained both with phase contast and electron microscopy in the same species.

The structure of the testicle was correctly described by Grobben (1908). In his admirable studies of spermatozoa, Retzius (1909) confirmed Leydig's and Grobben's statement that those of *Argulus* are filiform, and could not distinguish any regional differentiation. He demonstrated clearly that the body consists of at least three thin longitudinal fibers. Later light microscopists (Martin 1932, Debaisieux 1953) could, for obvious reasons, get no further.

Recently Brown (1966, 1970) included material of *Argulus* sp. from the garfish *Lepisosteus platyrhinus* Dekay in a combined light- and electron microscopical study of crustacean spermatozoa. He described the body of the spermatozoon and noticed many of the unique features: the three mitochondrial rods, the dorsal ribbon (called U-shaped body), and the symmetrical position of the central filaments of the axonema on each side of the median plane. Several sections of the pseudoacrosome are seen in the pictures in the thesis from 1966. They are correctly marked "sperm ends" but are not further commented on.

Brown's results, which directed my attention to *Argulus*, will be referred to in the following descriptions. These will also include comparisons with *Raillietiella* on all relevant points.

The structure of the testicle and the general course of spermatogenesis

As described by Leydig (1850), Grobben (1908) and Martin (1932), the testicles of *Argulus* are a pair of ovoid bodies, situated in the hemocoelic space of the two lobes of the vestigial abdomen (Plate 2:5). A vas efferens goes from each testicle forwards to the seminal vesicle, which is situated in the posterior part of the cephalothorax.

In a cross section, each testicle is approximately circular, with an external basement membrane and a thick epithelium. This surrounds an internal cavity, which is continuous anteriorly with the lumen of the vas efferens. The epithelium is thinner, 2–3 cell layers only, in the dorsal midline (Plate 2:5). According to Grobben this is the germinal zone, from which spermatogonia are given off to the surrounding walls. Spermatogenesis takes place while the cells move down the walls of the testicles to the ventral midline, where the most advanced spermatids are found. The spermatocytes 1 form very thick layers on the upper part of medial and lateral walls; the zone of spermatocytes 2 is very narrow, and the spermatids occupy a multicellular layer on the lower part of the wall on each side.

About halfway down the walls, some cells with light-staining plasm appear along the basement membrane. These are the prospective Sertoli cells. As soon as a pseudoacrosome is formed in the spermatids it becomes stuck in the plasm of these Sertoli cells. Further down the sides, where the spermatids become filamentous, they are seen in tufts, each associated with one Sertoli cell.

In the electron microscope the long pseudoacrosomal ends of the spermatids are

seen sticking in deep narrow pockets in the distal end of the Sertoli cells (Plate 3:9). These pockets are lined by the plasma membrane of the Sertoli cells, which is separated from that of the spermatids by a narrow cleft, measuring 200–400 Å (Plate 20:102). No membrane fusion between spermatids and Sertoli cells has been observed.

Near the ventral midline the Sertoli cells elongate strongly, standing on the base ment membrane with a narrow stalk, and with their thick distal end with the nucleus just below the center of the testicle (Plate 2:5). These long Sertoli cells bear mature or nearly mature spermatids, which are liberated into the lumen. Actually there are two groups of such high Sertoli cells in a cross section, one derived from the medial side of the testicle and the other from the lateral side. They are separated by degenerating cells which have liberated their spermatozoa.

All this is fundamentally different from the organization of the testicle in *Raillie-tiella*. The most striking differences are:

1. In *Raillietiella* there are typical, free-swimming spermatocysts containing 128 or 256 synchronously developing spermatids and surrounded by a plasmatic cyst wall. In *Argulus* no cysts or cyst walls are formed, only poorly defined groups of synchronously developing cells.

2. In *Argulus* the advanced spermatids develop while their pseudoacrosomes stick deep into the plasm of typical Sertoli cells. No Sertoli cells are present in *Raillie-tiella*. The pseudoacrosomes are free. They may be in contact with the wall of the spermatocyst but this wall is smooth, without pockets for the spermatid ends (Plate 23: 118).

3. The migration along the wall during development, from a relatively small dorsal germinal area to a maturation zone near the ventral mid-line, is peculiar to *Argulus*. In *Raillietiella* no such migration takes place, and proliferation of new cysts is seen from all walls, with the possible exception of a mid-ventral area.

In view of these fundamental differences it may seem astonishing that spermatogenesis and sperm structure is closely related in the two forms. There is, however, one point in which they agree: The sperm is transferred from the vesicula seminalis of the male to the receptaculum seminis of the female in the form of seminal fluid, not as spermatophores, which are common in arthropods. However, Fryer (1958) has found spermatophores in *Dolops ranarum* (Stuhlmann) and *D. geayi* (Bouvier), which are typical branchiurans, placed in the same family as *Argulus*.

The mature spermatozoa

The structure of the mature spermatozoa in *Argulus* is so similar to that of *Raillietiella*, that the same terminology can be used throughout.

External features, regional differentiation

The mature spermatozoa from the female receptaculum or from the vesicula seminalis of the male are filiform, $110-125 \mu$ long (Fig. 13A, Plate 4:11). Four intact spermatozoa, fixed in osmic acid and lying flat on grids were measured with great accuracy, and the figures 110, 119, 121 and 124μ were obtained. Fresh spermatozoa from the receptaculum were photograped in phase contrast, just after the movements had stopped. A slight coiling caused a small degree of uncertainty but values between 110 and 120μ were obtained all the time. These values agree with those obtained by Leyding in 1850.

The diameter (height) of the spermatozoa varies from ca. 0.55μ about the middle of the body to 0.2μ in the anterior part of the pseudoacrosome.

The pseudoacrosome was measured in 13 intact, osmium-fixed specimens, photographed with the electron microscope, and all values fell within the range 27μ to 33μ . The transition from the anterior end of the body, where the height is $4-4.5 \mu$, to the 3μ thick base of the pseudoacrosome is not so distinct as in *Raillietiella* but sudden enough to allow reasonable accuracy when EM-pictures of pseudoacrosomes are measured (Plate 4:11). The pseudoacrosome is stiff in living specimens but is not so regularly arched as in *Raillietiella*. Usually it is almost straight or slightly curved, but half-circular bending has sometimes been seen, both in fresh and in fixed specimens.

The spermatozoa of *Argulus* and *Raillietiella* are thus almost identical with regard to regional differentiation and dimensions:

	Argulus	Raillietiella
Total length	110–124 μ	100–130 μ
Length of pseudoacrosome	$27-~33~\mu$	ca. 35 μ
Maximal diameter	$0.55~\mu$	$0.8~\mu$

The spermatozoa of Argulus are a little thinner (Plate 5:16,17), and there may be a small difference in the average shape of the pseudoacrosome.

In a different (unidentified) Argulus species from Lepisosteus, Brown (1966, 1970) found spermatozoa which are said to be about $350\,\mu$ long, or three times as long as those of Argulus foliaceus. Brown (1966) also describes a spiral structure in the spermatozoa of his Argulus species, and one of his phase contrast pictures shows this coiling distinctly. There are about $5-6\,\mu$ between the coils. In Argulus foliaceus no such dense coiling is present. EM-pictures of whole spermatozoa fixed in different ways show no coiling at all (Plate 4:11). Phase contrast microscopy of fresh sperm of A. foliaceus, studied as soon as movements become slow, show the body bent into three to four coils, but this may as well be an artifact caused by contraction.

Internal structure of body

Cross sections of the body of *Argulus* spermatozoa differ very little from corresponding sections of *Raillietiella* spermatozoa (Figs. 1:B and 13:B, Plate 5:16,17). *Argulus* spermatozoa are more compressed from the sides, but the general pattern is the same.

The nucleus is more flattened dorso-ventrally in Argulus than in Raillietiella. More significant is perhaps, that there are at least one, sometimes more, nuclear membranes inside the two usual ones present in Raillietiella. In Argulus there is also a dark, asymmetrical thickening on one side, associated with the nuclear membranes above the nucleus proper ("af" in Fig. 13:B, Plate 5:17). This structure is discussed in the chapter on spermatogenesis as a probable remnant of the acrosome filament.

The mitochondria are three continuous rods, situated symmetrically between the nucleus and the axonema, as in *Raillietiella*. Typical cristae are present in all three mitochondria, but they are small. This was the case also in Brown's (1966) species of *Argulus*.

The axonema is of the 9+2 pattern and agrees on two very specific points with that of *Raillietiella*: 1) The central filaments are symmetrically situated on each side of the median plane, the peripheral doublet 1 being dorso-median, and 2) the doublet 1 is connected with the dorsal ribbon by an obliquely orinted membrane, which is inclined to the side where the arms of doublet 1 are, just as in *Raillietiella* (Plate 5:16,17).

In addition, the doublets 3 and 7 in *Argulus* are attached to the inner wall of the inner membranous sac of the dorsal ribbon (Fig. 13:B, Plate 5:17). In *Raillietiella* there is no such attachment (Plate 5:16).

Brown noticed the exceptional symmetrical position of the central filaments also in his species of *Argulus* (Brown 1966, 1970).

The dorsal and ventral ribbons are nearly identical with those of *Raillietiella*, and the sharp edges of the dorsal ribbon fit into furrows in the free edge of the ventral ribbon as in this species (Plate 5:16,17). Also the dark but thin lamellae, covering the dorsal and lateral aspects of the lateral mitochondria, are present in *Argulus*. Differences have been found in a few details: 1) The ventral ribbon has tightly set transverse ridges

Fig. 13. Argulus. Diagram of the mature spermatozoon, based on numerous total preparations and sections like those in Plates 4–7. The scale is 10 μ when used for the intact spermatozoon (A) and 1 μ when used for the details (B–H).

A. Total spermatozoon. — B. Cross section of body. — C. Median section of body. — D. Median section of transitional region between body and pseudoacrosome. — E. Cross section through anterior end of nucleus. —
 F. Cross section of the pseudoacrosome, basal part. — G. Cross section of the pseudoacrosome, terminal part. — H. Cross section through posterior end of body.

af = remnants of acrosome filament in the nuclear membranes, ax = axonema, ce = centriole, dl = dorsal lumen of pseudoacrosome, dm = dorsal extension of pseudoacrosomal granular matter, containing axonemal filaments nos. 9, 1, and 2, dp = dorsal rod of pseudoacrosome, dr = dorsal ribbon, en = posterior end of nucleus, is = inner membranous sac of dorsal ribbon, ir = intermitochondrial light rods, ls = limit of pseudoacrosomal membranous sac on the ventral side, m = mitochondria, n = nucleus, o = oblique membrane between axonemal doublet 1 and dorsal sheath, os = outer membranous sac of dorsal ribbon, pa = pseudoacrosome, ps = pseudoacrosomal membranous sac, td = top of dorsal rod of pseudoacrosome, pc = light cores in pseudoacrosome, vm = ventral extension of pseudoacrosomal granular matter, including axonemal filaments 4 and 5, vp = ventral rod of pseudoacrosome, vr = ventrale ribbon.



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on the outer side in *Argulus* but not in *Raillietiella* (Plates 6:18, 19, 18:89, 90). 2) The light cores in the dorsal and ventral ribbons, present in *Raillietiella*, could only be demonstrated in the centriolar region of *Argulus* (Plates 5:16,17, 7:25,26). 3) In *Argulus*, but not in *Raillietiella*, a pair of very distinct light rods with 350 Å diameter are situated in the interspaces between median and lateral mitochondria (Figs. 1:B, 13:B, Plate 5: 16,17). Spermatogenesis indicates that these rods are the homologues of the light cores of the ventral ribbon in *Raillietiella*.

The cytoplasm of the spermatozoon is more reduced in Argulus than in Raillietiella, and remnants of the smooth endoplasmic reticulum, as seen in the latter species, have not been seen in Argulus. Brown (1966, 1970) describes what he calls a lateral organelle in his species of Argulus: a membrane-bound sac with granular content, situated asymmetrically on one side in contact with the lateral mitochondrion. In a few sections this organelle was present on both sides, so Brown suggests that there are two, one on each side, which overlap in a short region. Such lateral organelles are found in nonmature spermatids of A. foliaceus, but they are completely reduced in the mature spermatozoa (Plates 17:86,87, 18:88, 5:17). They will be described in the chapter on spermatogenesis.

The posterior end has some significant features in common in the two forms: There is no free flagellum, and the dorsal ribbon continues into the extreme posterior tip. But constant differences are present in the posterior extension of other components: In *Argulus* the nucleus extends as far as the dorsal ribbon, whereas mitochondria, ventral ribbon and axonema terminate some microns from the end (Fig. 13: A, H, Plates 4:15, 7:30,31). In *Raillietiella* the nucleus is the first structure to end, followed by mitochondria and ventral ribbon, whereas filaments of the axonema can be followed into the very tip (Fig. 1: A, G, H, Plates 4: 14, 7: 29). In *Argulus* the terminal part of the dorsal ribbon often has a remarkable, swollen appearance.

The anterior end of the body carries the long pseudoacrosome, and the transitional area has essentially the same pattern in both forms. In Argulus as in Raillietiella the dorsal ribbon is directly continuous with the dorsal rod of the pseudoacrosome, and its outer membranous sac continues forwards as the pseudoacrosomal sac (Fig. 13:D). The inner sac of the ribbon ends at the level of the anterior end of the centriole (Plate 22:111). The behaviour of the three dorsal centriolar filaments, nos. 9, 1, and 2, is particularly significant. In Argulus as in Raillietiella they converge and are embedded in the dorsal portion of dark PGM, which is continuous with the dorsal rod of the pseudo-acrosome (Plates 22:111, 6:20, 7:21, 22, 25, 26).

The ventral filaments are in both species embedded in the ventral portion of PGM, which connects with the ventral rod of the pseudoacrosome. But in *Argulus* this is true only for the two medioventral ones, for the other four (nos. 3, 4, 7, and 8) disappear in the centriolar region. In *Raillietiella* all six ventral filaments (nos. 3–8) are connected with the ventral rod in this way (Figs. 1 and 13, Plates 7:21,22,25,26, and 22:112–126).

In *Argulus* as in *Raillietiella* there is a deficiency in the ventral pseudoacrosomal wall in front of the nucleus, and the ventral sheath forks posteriorly into a pair of wing-

like plates, which cover the centricle from the sides. This is best seen before final maturation of the spermatids (Plate 22:112–116).

Internal structure of pseudoacrosome

The pseudoacrosome as such, a unique structure not known from other animals, is an important identical feature in *Argulus* and *Raillietiella*. However, its internal structure presents considerable differences in details (Figs. 1:F, 13:F, G).

The cross section of the pseudoacrosome in *Argulus* deviates distinctly from a bilateral symmetry. This asymmetry is constant and is particularly pronounced in the much broader ventral part of the section. Development shows clearly that this ventral part is homologous to the ventral rod in *Raillietiella*, whereas the more narrow dorsal part corresponds to the dorsal rod (Plate 21).

The pseudoacrosome in *Argulus* is surrounded by a flat sac of the endoplasmic reticulum, which is best seen before maturation (Plates 20:102,103, 21:108–110). As in *Raillietiella*, this sac collapses later and forms two closely attached unit membranes all around the pseudoacrosome, but they are often difficult to resolve in the mature sperm.

The dorsal rod has a central lumen, surrounded by dark PGM. This dark substance also forms a transverse bridge, which delimits the dorsal lumen from the central lumen, situated mainly in the ventral rod (Fig. 13:F,G, Plate 7:27,28). In the bridge there is a longitudinal light rod which, near the base of the pseudoacrosome, has an asymmetrical position.

The dark PGM of the ventral rod bulges out into the central lumen as two unequal ridges, which are roughly half-cylindrical and partly fuse when they meet. Each ridge contains a light rod, one thicker than the other. The behaviour of the three light rods at the base of the pseudoacrosome is complicated and has not been followed in detail. It was stated, however, that the dorsal lumen communicates with the central lumen not far from the base, and that the central lumen is continuous with the lumen of the centrile as shown in Fig. 13:D.

The inner structure of the two pseudoacrosomal rods in *Argulus* is thus completely different from the pattern in *Raillietiella*, where the rods are symmetrical, simple, with a light core in the center (Fig. 1:F, Plate 7:23,24).

Intact ends of pseudoacrosomes of Argulus spermatozoa have been seen many times in EM-pictures (Plate 4:13). The terminal part to a point ca. 2μ from the end is extremely narrow, less than 0.1μ , and consists of one rod as in *Raillietiella*. No indication of a granulosome like the one in *Raillietiella* could be found although it is present during development (see Plates 4:12, 23:117–120). The negative statement is perhaps not definite, for technical hazards are difficult to exclude completely.

Movements

Like Brown (1966, 1970), I observed violent movements in sperm suspended from the vesicula seminalis in mammalian Ringer. The movements were so rapid that an analysis was impossible, but came to a sudden stop after a few minutes. Then only abnormal bendings remained.

Spermatogenesis

Spermatogenesis in *Argulus* follows the same general lines as in *Raillietiella*. It is therefore possible to subdivide spermatogenesis into the same stages as those used for *Raillietiella*, with minor modifications. The analysis of spermatogenesis in *Argulus* has only been carried as far as was thought necessary for a comparison with *Raillietiella*, and has been focused on the anterior ends of the spermatids, which contain the most interesting structures.

From spermatogonia to early spermatids

This part of the spermatogenesis is of an ordinary type in *Argulus* as well as in *Raillietiella*. The cells are regular, polygonal, with numerous free ribosomes and polysomes in the plasm. The smooth endoplasmic reticulum is poorly developed in spermatogonia but develops strongly in the spermatids as numerous small sacs and vesicles. Stacks of Golgi vesicles are often seen in the spermatocytes and are in general more numerous and better developed than in *Raillietiella*. This is true also for early spermatids.

The mitochondria are rod-shaped or tubular with a diameter of about 0.5μ in the spermatocytes 1 and during 1st meiotic division. Two anaphase cells with numerous remnants of synaptonemal complexes still had small scattered mitochondria. Late spermatocytes 2, classified on the basis of nuclear size and presence of two centrioles, already had more spherical mitochondria, and cells classified as early spermatids 1 had all mitochondria concentrated into one group.

The centrioles. Four centrioles lying in a group were seen in several spermatocytes 1, and these, like single centrioles seen in cells of this stage, did not show remarkable features. During meiosis two dark outer fibers appear along one side of the centriole, just as in *Raillietiella*. In *Argulus* this must occur already during 1st meiotic division for the above-mentioned cells in 1st anaphase had already two distinct dark rods. Late spermatocytes 2, classified on the basis of nuclear size, rounded and large mitochondria and the presence of two centrioles, always have two distinct outer fibers, covered by a darkened flat sac of endoplasmic reticulum (Plate 8:35,36). Thus in *Argulus* as in *Raillietiella*, the anlages of the dorsal ribbon develop already during meiosis, giving the centriole a bilateral symmetry.

Spermatid 1; with several mitochondria

Very few cells of this stage were seen. The mitochondria form one group near the nucleus and have contracted to irregularly rounded bodies with many cristae and a diameter of more than 1μ (Plate 9:49). The centriole has no contact with the nucleus but in one case was seen attached to the cell membrane and having formed an axonema in a short flagellum.

Spermatid 2; with three spherical mitochondria

The three large, spherical *mitochondria* of this stage are up to 2μ in diameter and have numerous cristae. The mitochondria are in contact with each other in a triangular
fashion (Plate 9:51). The arrangement is strikingly similar to that seen in the corresponding *Raillietiella* spermatids (Plate 9:50).

The centriole at this stage has a distinct granulosome attached to the proximal end of the tube, as in *Raillietiella* (Plate 8:44). A dark, membrane-like condensation seen across the top of the centriole is undoubtedly homologous to the apical membrane in *Raillietiella* (Plate 8:41,45). However, in *Argulus* the dark matter penetrates into the terminal part of the lumen of the centriole, so the "apical membrane" looks more complicated.

A flat sac of endoplasmic reticulum covers the centriole on the prospective dorsal side and is associated with much dark matter. The outer dark fibers under this sac are now three in number. Thus, in *Argulus* as in *Raillietiella* there is a change from two to three dark outer fibers under the membranous sac in the period from meiosis to spermatid 2 (Plate 8:32–37,42,43).

Relation between nucleus, mitochondria and centriole. In spermatids 2 of Argulus I have never seen the granulosome in contact with the nucleus, although many cells have been photographed. This contact appears to be established relatively later in Argulus than in Raillietiella, after the mitochondria have formed a typical Nebenkern. A contact between the mitochondrial triplet and the centriole has been seen in several spermatids 2, the centriole lying in the furrow between two of the mitochondria (Plate 8:37, 45).

In other spermatids 2 such contact has not yet been established; the mitochondria, the nucleus, and the centricle are independent as in corresponding stages of *Raillietiella* (Plate 10:54,55).

The flagellum is well developed and contains a fairly long axonema in all spermatids of this stage, but the distal end of the centriole is still in contact with the flagellar pit, so there is no axonema within the cell body proper.

Spermatid 3; with mitochondrial "Nebenkern"

In spermatids with a Nebenkern, the granulosome has always obtained contact with the nuclear membrane, so a relationship between centriole, mitochondria and nucleus like that in *Raillietiella* is established (Fig. 14, Plate 12:62). In *Argulus* this contact of the granulosome with the nucleus appears to be established late and has never been seen in spermatids 2 with spherical mitochondria. Further, the contact appears to be asymmetrical from the beginning in *Argulus*, as seen in Plate 12:62 and Fig. 14. Attachment to the posterior pole, as seen in *Raillietiella* (Figs. 3, 4, Plate 11:59), was never encountered in *Argulus* although about 20 spermatids 2 and 3 were seen in more or less perfect longitudinal sections.

Mitochondria. The Nebenkern of Argulus is practically identical with that of *Raillie-tiella*: The three large mitochondria do not really fuse, their membranes remaining intact when the spheres are packed together to form a single body (Plate 10:53). All three mitochondria have numerous distinct cristae and are in contact with the ovoid, slightly irregular nucleus (Fig. 14, Plate 12:62,63). Along the prospective dorsal side

of the Nebenkern all three mitochondria are in contact with the centriole with straight, rather sharp edges as in *Raillietiella* (Plates 10:52, 53, 8:42, 43).

The centriole. The original triplets of the centriole probably change to doublets during this stage, for triplets have not been seen in subsequent stages, but documentation is admittedly too poor to allow detailed analysis. The three outer dark fibers 9, 1 and 2 are large and distinct and are covered by the outer sac of the prospective ribbon (Plate 8:42,43). This sac forms a dark outer sheath covering the fibers and bends down to the sides of the centriole. In the anterior direction the sac has covered the apical membrane (Plates 12:63, 20:105). The apical membrane has grown posteriorly as a pair of dark plates, attached to the sides of the centriole (Plate 8:42,43). The granulosome is attached to the apical membrane but is not so well defined as in *Raillietiella* (Plate 12:63, 20:105).

In *Argulus*, the apical membrane is not only detached but is rather far anterior to the end of the centriole in this stage, and plentiful pseudoacrosomal granular matter has appeared (Fig. 14). This matter consists of two portions as in *Raillietiella*, but proportions are a little different. In *Argulus*, the very dark condensation of PGM is shaped like a longitudinal rod between the end of the centriole and the apical membrane, whereas in *Raillietiella* it is an almost isodiametrical pellet (Plates 12:63,61, 20:105). The ventral portion of PGM is less dense and delimited by nucleus, mitochondria, and apical membrane as in *Raillietiella*, but it is located in a distinct pit between nucleus and Nebenkern (vm in Plates 12:63 and 20:105).

If the mentioned differences in proportions are excepted, there is an almost complete identity of details in the centriolar complex of *Raillietiella* and *Argulus* at this stage (Plates 12:60–63, 20:105).

The axonema is no longer restricted to the flagellum proper but has a short inner segment between the flagellar pit and the end of the centriole (Plate 12:62).

The true acrosome begins its development in spermatids of this stage. Stacks of Golgi vesicles are rather common in the anterior end of the spermatids, and some of them form a bowl-shaped body at the anterior end of the nucleus, with the concave side facing the nuclear membrane. The acrosomal rudiment is first seen in the center of this half-spherical Golgi apparatus, in contact with the nuclear membrane (Fig. 14, Plate 14:67–69). When first seen, it consists of a small vesicle, covering a dark granule which is attached to the outer nuclear membrane (Plate 14:67). Later development shows that the vesicle should be regarded as an acrosomal vesicle, and the granule as a post-acrosomal one. The granule soon grows to a short plug, the top of which is covered by the cap-like invaginated acrosomal vesicle (Plate 14:68, 69).

Spermatid 4; anterior migration of centriole, formation of acrosome filament

The migration of the centriolar complex up along the dorsal aspect of the nucleus to a position near its anterior end takes place in the same way as in *Raillietiella* (Figs. 14–15 and 5–7). The three mitochondria of the Nebenkern emit anterior tongues which keep contact with the centriole with their anterior ends (Plate 15:74). The three mito-





Fig. 15. Argulus. Diagram of spermatid, late stage 4. Compare Plates 8, 10, and 12–16. af = acrosome filament, an = annulus-like thickening of cell membrane in the bottom of the flagellar pit, av = acrosome vesicle, ce = centriole, dr = dorsal ribbon, er = smooth endoplasmic reticulum, g = granulosome, go = Golgi apparatus, la = horizontal lamellae, formed by the PGM, n = nucleus, nk = mitochondrial "Nebenkern", p = pseudoacrosomal granular matter (PGM).

chondrial tongues are symmetrically situated between the axonema and the nucleus (Plate 16:78,79). Similar tongues are emitted by the Nebenkern in a posterior direction along the ventral aspect of the axonema (Plate 16:77).

While this dislocation takes place, the shape of the nucleus changes in a characteristic way and is different from that of *Raillietiella*. The anterior end of the nucleus is broad and rounded with the true acrosome planted in a central position (Figs. 14– 15, Plates 14:67–70, 15:74). The posterior end of the nucleus is tapering and projects below the mitochondrial Nebenkern, where finally a posterior nuclear tongue grows out (Plate 15:75). The fact that the true acrosome remains at the anterior end of the nucleus during dislocation of the centriole makes it unlikely that the nucleus rotates during this process, as suggested for *Lepisma* by Werner (1964). It appears more probable that the centriole slides up along the side of the nucleus.

The *centriole* and the pericentriolar structures change considerably during this stage. The apical membrane is still more removed from the end of the centriole, and the dark rod of PGM seen in previous stages elongates and differentiates into several horizontal lamellae in its posterior part (Fig. 16, Plate 19:93–98). There is still no ventral pseudoacrosomal sheath, but a dorsal one developed as an anterior continuation of the dorsal ribbon is present, at least as an anlage. The apical membrane extends posteriorly as two wing-like lateral plates, which are very long and reach the anterior part of the centriole, which is laterally compressed (Plate 19:94). The posterior part of the centriole remains circular in cross sections (Plate 19:93).

In the region of the centriole and axonema an inner sac has appeared between the granular core of the dorsal ribbon and the axonema (Plate 16:77,78, 19:93,94). This sac ends at the anterior end of the centriole, but the sac communicates in a rather complicated way with the pseudoacrosomal sac in this region (Plate 19:95,96).

In most details these centriolar structures are as in *Raillietiella*, but there are a few differences: In *Argulus* the apical membrane is farther away from the centriole, and the horizontal lamellae formed by the PGM are specific to this species (Compare Figs. 11 and 16).

The true acrosome. The acrosomal vesicle remains almost unchanged from the previous stage, but the postacrosomal granule grows out to form an acrosome filament, which penetrates deep into the nucleus, surrounded by a deep, tube-like pocket formed



Fig. 16. Argulus. Diagram showing development of pseudoacrosome in spermatid, early stage 5. Compare Plates 12, 19, 20 and 23. Plate 19 shows cross sections of this particular stage.

am = apical membrane, ax = axonema, ce = centriole, cr = granular core of dorsal ribbon, g = granulosome, is = inner membranous sac of dorsal ribbon, la = horisontal lamellae formed by the PGM, m = mitochondria, n = nucleus, os = outer membranous sac of the dorsal ribbon, pm = pseudoacrosomal granular matter (PGM), vm = ventral extension of loose granular matter between nucleus and pseudoacrosome.

by the nuclear membranes. In spermatids of this stage the acrosome filament does not reach more than halfway through the length of the nucleus (Fig. 15, Plate 14:70).

Spermatid 5; formation of pseudoacrosome

In *Argulus* the pseudoacrosome begins to grow out long before the narrow anterior nuclear tongue is formed; in *Raillietiella* the nuclear tongue develops first (Figs. 17, 8, 9).

The components forming the pseudoacrosome are the same as in *Raillietiella*: The dorsal ribbon and its outer membranous sac, the granulosome, the apical membrane, and the pseudoacrosomal granular matter (PGM). The apical membrane with the granulosome is always on the top of the growing pseudoacrosome, but the granulosome appears to be less compact than in *Raillietiella* (Plate 23:119,120). The dorsal sheath of the pseudoacrosome is a direct anterior prolongation of the outer sheath of the dorsal ribbon and is originally small, half-circular in cross sections (Plate 20:102,103). The ventral sheath is formed in direct continuity with the apical membrane and is U-shaped, rather narrow in cross sections (Plate 20:102,103). The posterior end of the ventral sheath is forked into the two previously mentioned wing-like plates, which extend to the sides of the centriole. This forked posterior part of the ventral sheath appears to be longer than in *Raillietiella*, so a considerable part of the base of the pseudoacrosome is open ventrally (Figs. 17, 18). The growing pseudoacrosome is completely surrounded by the membranous sac ("ps" in Plate 20:102, 103).

At the base the pseudoacrosomal membranous sac is directly continuous with the outer sac of the dorsal ribbon, but it is also connected with the inner sac by two flattened ducts which cover the wing-like plates behind the ventral sheath proper (Plate 19: 94–98). The median, transverse part of the inner sac ends at the level of the anterior end of the centriole, and only its lateral diverticula continue forwards as the mentioned membranes on the wing-like plates.

The PGM behaves rather differently in *Argulus* and *Raillietiella*. In *Argulus* spermatids of stage 5 there is an undifferentiated dark mass just behind the apical membrane, but further back the PGM has condensed to form three horizontal lamellae, which give the cross section a ladder-like appearance (Plates 23:120, 20:102, 103). These lamellae are located in the ventral sheath and between its posterior paired extensions. The most dorsal of these lamellae is fused in a T-shaped fashion to a median lamella which bridges the space between the two sheaths and is surrounded on the dorsal side by the dorsal sheath. This median lamella looks very much like the one seen in corresponding stages of *Raillietiella* (Plate 20:101,102,103).

The Golgi apparatus is still rather well developed at this stage and appears to have a functional connection with the membranous sacs of the dorsal ribbon and pseudoacrosome. As seen in Plate 18:92, the Golgi apparatus is separated by a zone of small vesicles from a sac of endoplasmic reticulum which is directly continuous with the outer sac of the dorsal ribbon. Such connections have also been seen at the level of the pseudoacrosome. In *Raillietiella* no such connections have been seen, and the Golgi apparatus is on the whole very little developed.



Fig. 17. Argulus. Spermatid, stage 5.

Fig. 18. Argulus. Spermatid, stage 6. Compare Plate 13-17, 19, 20, 22 and 23.
af = acrosome filament, am = apical membrane, at = anterior tongues of mitochondria, av = acrosome vesicle, ax = axonema, ce = centriole, ds = dorsal sheath of pseudoacrosome, em = anterior point of median mitochondrion, from which the inner membrane has retracted, er = smooth endoplasmic reticulum, g = granulosome, la = horizontal lamellae formed by the PGM, nk = mitochondrial "Nebenkern", nt = anterior nuclear tongue, o = opening between ventral ribbon and anterior end of nucleus, pb = plasmatic bridge to neighbour cell, indicating very slow separation of cytoplasm after 2nd meiotic division, pm = pseudoacrosome.

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The nucleus. The blunt, originally rounded anterior end of the nucleus grows out to a narrow tongue with the true acrosome on the top (Fig. 18, Plate 14:71). The top remains all the time at the level of the centriole, and the space between nucleus, mitochondrial ends, centriole and ventral sheath of pseudoacrosome is filled with the ventral portion of PGM (Fig. 18).

In *Argulus* but not in *Raillietiella*, the nucleus also develops a posterior tongue along the ventral surface of the mitochondria. This posterior tongue does not, however, reach the flagellar pit but is rather short. The bulk of the Nebenkern is thus not situated behind the nucleus as in *Raillietiella* but lies in a depression of the dorsal surface of the nucleus (Fig. 17, Plate 15:75).

The true acrosome is very close to the base of the pseudoacrosome in this stage, because of the attenuation of the anterior end of the nucleus and its close contact with the centriole (Plate 14:71). The acrosome vesicle is still quite typical, sitting like a cap on and partly surrounding the anterior end of the acrosome filament (Plate 14:71). The filament itself has grown through the entire nucleus to its posterior end, all the way surrounded by a tube of nuclear membranes (Plate 16:79).

The presence of this unmistakable, true acrosome and acrosome filament, separate from the pseudoacrosome, shows of course that the latter has nothing to do with an acrosome in the normal sense.

Longitudinal microtubules are particularly common around the growing pseudoacrosome but are also present along other regions of the spermatid (Plate 20:102,103).

Spermatid 6; elongation of nucleus and mitochondria, formation of ventral ribbon

During this phase of the development the nucleus and the mitochondria are stretched to form long, filamentous structures, and the bulge on the nucleus as well the Nebenkern bulge on the mitochondria disappear. The entire spermatid is greatly elongated. There is still a free flagellum, but it is short compared to the rest of the spermatid.

The nucleus and the acrosome filament change drastically during this development. The nucleus is markedly flattened and is asymmetrically disposed. In a cross section one margin of the flattened body is seen in contact with the median mitochondrion, whereas the other margin is displaced to the lateral part of the cell (Plate 16:81, 17:84). As far as stated, the nucleus is always dislocated to that side of the median plane where the arms on axonemal filament 1 are situated.

Inside this nucleus the greatly swollen membranous tube of the acrosome filament is always asymmetrically situated, near the lateral nuclear margin (Plates 16:81, 17:84,85). The filament itself appears to disappear. It is still visible in Plate 16:81, poorly visible in Plate 17:84 and absent in Plate 17:85.

Chromatin condensation begins and is continued during stage 7. It differs completely from chromatin condensation in *Raillietiella* (Plates 16:81, 17:82–87). In *Argulus* the first signs of condensation are some small threads or lamellae of chromatin, attached like a dark tuft to the medial side of the tube of the acrosome filament (Fig. 16:81). This tuft grows out to form an irregular body of granular or fibrous material (Plate 17:84). It never fills out the fairly voluminous nuclear space. In more advanced spermatids of this stage and stage 7, the chromatin body becomes flattened and the originally rough surface is covered on the dorsal and ventral sides by membrane-like condensations of dark matter, whereas the lateral and medial margins remain "open" for a longer period (Plate 17:85). In more advanced spermatids 7 the dark, compact chromatin body is covered completely by this smooth surface (Plates 17:86,87, 18:88).

When the first signs of chromatin condensation are visible, a row of darker bodies is seen along the inner nuclear membrane all around the nucleus. In more advanced stages a membrane is present here between the original nuclear membranes and the smooth surface of the chromatin body (Plates 16:81, 17:84–87, 18:88). It is probable therefore, that the secondary membrane is formed by the row of dark bodies seen in earlier stages. In some sections, probably from other levels of the spermatozoon, there are several membranes, and probable stages of formation have been seen as concentric rows of dots inside the nuclear membranes in earlier stages (Plates 18:88).

The membranous tube of the acrosome filament remains outside the chromatin body and is probably enclosed between primary and secondary nuclear membranes. The tube does not collapse definitely until stage 7, and details in the degeneration of the acrosome filament tubes have been difficult to follow. It appears probable that the dark body seen in cross sections of mature spermatozoa are remnants of the tube (Plate 5:17). This body, like the acrosome filament tube of later spermatids, is situated on the same side of the median plane as that where the arms on axonemal filament 1 are situated.

The ventral ribbon is formed as in Raillietiella, as an accumulation of dark matter between axonemal doublets 4-7 and mitochondria. As in Raillietiella the surface of the early anlage is marked by a membrane-like condensation of matter, but true unit membranes are probably not present (Plates 16:80, 81, 17:84, 85). It is probable that the dark outer fibers 4-7 are included in this ventral ribbon, but they have been rather indistinct in all sections seen. In Plate 17:84,85 there is a pair of dark dots in the ventral ribbon, probably corresponding to outer dark fibers 5 and 6, but nos. 4 and 7 are indicated only in some sections of the centriole (Plate 8:37,42). Further development including additional accumulation of dark matter, formation of sheaths on the lateral mitochondria, and formation of the furrow in the free margins is as in Raillietiella. Araulus differs only in the development of the light intermitochondrial rods (Plates 17:84-87, 5:17). If the interpretation of the dark spots in the ventral ribbon in Plate 17:84,85 as outer filaments 5 and 6 is correct, it is probable that these filaments form the intermitochondrial rods. In Plate 17:85 the dark spots have moved down into the interspace between the mitochondria, in 17:86 the intermitochondrial rods are formed but are only seen as bulges on the ventral ribbon, and in 17:87 they are in their final location. The rods are dark in relation to their surroundings in early stages. In later stages they loose contrast and are seen as light spots.

If the intermitochondrial rods are formed by outer dense fibers 5 and 6, the ab-

sence of light cores in the ventral ribbon can be understood, for in *Raillietiella* these dense fibers probably form the light cores.

The pseudoacrosome increases in length and develops a distinct asymmetry in spermatids of this stage. The transitional region is still approximately symmetrical, but in front of the centricle the ventral sheath tips over to one side (Plate 21:108–110). The two sheaths are rather far from each other in the earlier stages, connected only by the common flat sac of endoplasmic reticulum. The PGM inside the sheaths is remodelled and the ladder-like pattern of horizontal lamellae is broken down. Instead the dark rods characteristic of the mature stage appear in a strongly asymmetrical way, the asymmetry being most pronounced in the ventral rod (Plate 21:110). Details of this process, which is completed during stage 7, have not been followed.

This asymmetry, and also the type of remodelling of the granular matter, is very different from anything seen in *Raillietiella*. However, Plate 21:106–110 shows that the differences appear at a late stage and that the homologies of the dorsal and ventral rods in the two forms can be established with full certainty in earlier stages.

Spermatid 7; final transformation to mature spermatozoon, transcient appearance of lateral organelles and a row of flat vesicles

As in *Raillietiella* the final development of the spermatozoon includes additional elongation of all structures, elimination of the free flagellum, and reduction of cytoplasm. In *Argulus foliaceus* maturation also includes symmetrization of the nucleus, final reduction of the true acrosome, and appearance of two organelles which soon disappear again: the lateral organelles and the row of flat vesicles.

The elongation of the sperm is accompanied by the appearance of numerous longitudinal microtubules as in *Raillietiella*. These microtubules disappear completely during final maturation, for they are not present in the mature spermatozoa (Plates 18:88, 21:110, 22:112).

The elimination of the free flagellum has not been studied.

The true acrosome. Reduction of the acrosome filament begins already in stage 6 spermatids and is far advanced before the end of this stage. The acrosome vesicle at the anterior pole of the nucleus persists longer. In earlier stage 7 spermatids there is still a doublewalled, i.e., invaginated, vesicle below the tips of the mitochondria (Plate 22:112–113). Longitudinal sections of the anterior nuclear end in late spermatids 7 and mature spermatozoa show only some irregular membranes and nothing like a recognizable acrosome vesicle. This degeration is confirmed by EM pictures of total mature spermatozoa, in which nothing like an acrosomal top or even bulge is seen in the transitional region (Plates 22:111, 4:11).

It must therefore be concluded that the true acrosome and acrosome filament develops progessively from about stage 3 to stage 5 and is established as a rather large and complicated structure, which is reduced to insignificant remnants before final maturation. No trace of a true acrosome or acrosome filament was ever seen in *Raillie-tiella*.

The lateral organelles, described by Brown (1966, 1970) in another Argulus species are present in stage 7 spermatids of Argulus foliaceus. In cross sections they are seen as membrane-bound sacs with medium-contrast, coarsely granular content, in contract with the lateral mitochondrion. Usually the cross sections contain only one lateral organelle, and this is invariably on the side opposite to the one where the dislocated nucleus is situated (Plates 17:86, 87, 18:88). In a few sections lateral organelles are present on both sides, but then the one on the nuclear side is smaller, almost vestigial (Plate 17:86). In longitudinal sections it is seen that the sacs of the lateral organelle are comparatively short, arranged in a row.

The morphological significance of this organelle is uncertain. Its anlage can be seen in some cross sections of late stage 6 and early stage 7 spermatids as empty sacs, communicating with the sacs of endoplasmic reticulum. This communication is seen also later, when the sacs are filled with granular matter, but is so narrow that it is doubtful wether the lumina are in open connection or not.

A lateral organelle of this kind was described by Brown (1966, 1970) in Argulus sp., in which they are said to be present also in the mature spermatozoa. In A. foliaceus there is certainly nothing left of these organelles in mature spermatozoa (Plate 5:17). Brown believed that lateral organelles are developed on both sides, although at different levels, and that they overlap only in a short region. This does not seem probable in A. foliaceus, for in this species the organelle is restricted to, or by far best developed, on the same well-defined side of the spermatozoon. This is the side opposite the one to which the nucleus is dislocated, i.e., the side opposite the arms of axonemal filament 1.

A typical lateral organelle is not present in *Raillietiella*, but membrane-bound vesicles, empty or filled with granular matter, are often seen in cross sections of late spermatids. However, the location and appearance is not constant enough to allow safe comparison with the organelles of *Argulus*.

The row of flat vesicles is a short-lived structure, present only in the stage 7 spermatids. It is a straight rod, consisting of flat circular sacs packed close together like coins in a roll. It is only present during the asymmetrical stage, and is adjacent to the medial margin of the nucleus and to the ventral surface of the lateral mitochondrion on that side where no nucleus is present (Plate 18:88–90). The structure is best seen in longitudinal sections: Numerous, flat, empty vesicles, closely packed but without communication of their lumina. In cross sections the lumen often appears to contain some dense material, but this obviously depends on the almost unavoidable inclusion of one or more of the flat vesicle walls in the section. The organelle disappears completely before final maturation. No structure of this kind was seen in *Raillietiella*.

Ventral ribbon. The annular thickenings of the ventral ribbon are present as fairly independent rods in early stage 7 spermatids (Plate 18:90). Later the rods fuse and are seen as ridges on the ventral ribbon in longitudinal sections (Plate 18:89). The origin of the rods has not been followed.

V. GENERAL COMPARISON WITH OTHER SPERMTOZOA

The descriptive chapters have revealed that the spermatozoa of *Raillietiella* and *Argulus* are closely related with regard to structure and development. In the following, points of identity and difference will be summarized, and a comparison will be made with spermatozoa of other animals, particularly arthropods. The main problem to be solved is whether the mutual similarities between *Raillietiella* and *Argulus* are shared with other animals or not, and if systematic and phylogenetic conclusions are indicated by this material.

General structure of the testicle

With regards to testicular structure and general course of spermatogenesis, *Raillie-tiella* and *Argulus* are different throughout.

In *Raillietiella* the spermatogenesis takes place inside spermatocysts: groups of simultaneously dividing and developing germ cells, surrounded by a plasmatic cyst wall.

Similar spermatocysts are well-known from the majority of insects (Phillips 1970a), including the thysanurans (Werner 1964). In insects, as in *Raillietiella*, the divisions are synchronous and result in a fixed number of spermatids, being a power of 2. In *Raillietiella* the number is either 128 (2^7) or 256 (2^8) . These numbers are not uncommon in insects (Phillips 1970a).

However, a more careful consideration leaves some doubt about the significance of these superficial similarities. That groups of male germ cells divide and develop simultaneously is a wide-spread and common phenomenon in animals and is therefore no significant point of similarity between *Raillietiella* and insects. Actually such groups are present also in *Argulus*, although they are not so distinct because of the absence of cyst walls.

More important is the identity or non-identity of the cyst wall. In *Raillietiella* this is formed by several vegetative wall cells, which extend over the growing group of spermatogonia. The wall of the cyst is therefore a mosaic of non-nucleated plasmatic plates which are pinched off from the wall cells when the cyst becomes free. In insects the cyst wall consists of nucleated cells, regarded as abortive germ cells, which *in toto* attach to the group of spermatogenia (Baccetti and Bairati 1964, Bairati and Baccetti 1964, Phillips 1970b). The structure of the cyst wall is therefore different in insects and *Raillietiella* and the homology is somewhat uncertian.

In chelicerates and crustaceans groups or bundles of simultaneously developing spermatids is a common feature, and in some cases a kind of cyst wall is said to be present, for instance in scorpions (Gilson 1885, Sokolow 1913), pseudoscorpions (Boissin and Manier 1966–67), isopod crustaceans (Fain-Maurel 1970), and, perhaps, araneids and opilionids (Gilson 1885, Bösenberg 1905). Details are poorly known for

many groups. Conditions in isopods, in which plasmatic extensions from large, polyvalent wall cells of the testicle surround the islands of simultaneously developing spermatids, are perhaps more comparable to conditions in *Raillietiella* than are the spermatocyst patterns in insects (Fain-Maurel 1970).

Structure and development of the spermatocysts in *Raillietiella* are therefore hardly decisive with regard to the affinities of the group Pentastomida.

In *Argulus* the clumps of simultaneously developing germinal cells move ventrally along the testicular wall and are not surrounded by cyst walls. They are finally attached in bundles to typical Sertoli cells, the pseudoacrosomes being buried in deep pouches developed from the cell wall of the Sertoli cells. This looks very much like the relation between Sertoli cells and spermatids in the vertebrates, but, of course, in the vertebrates the true acrosomes stick in the depressions of the Sertoli cells.

Nutritive cells similar to Sertoli cells are known from many invertebrates, and are particularly typical in gastropods (Yasuzumi et al. 1960). In arthropods it appears difficult to find unquestioned homologues to the Sertoli cells of *Argulus*. In insects, the anterior ends of the spermatids usually stick in depressions in the large polyvalent cells of the cyst wall (Phillips 1970 a). This could suggest a spermatid-Sertoli cell relationship but occurs inside a spermatocyst. In *Raillietiella* the spermatids remain free inside the cysts; their anterior ends are not surrounded by the protoplasm of the cyst wall. In cirriped crustaceans the bundles of spermatids are attached to the testicle wall, but specialized Sertoli cells do not seem to have been described. In some malacostracans and acarids there are nutritive cells (nurse cells, sustentacular cells) of rather special appearance (Fain-Maurel 1970, Moses 1961, Langreth 1969, Reger 1961).

Altogether the structure of the testicle is specialized in very different ways in *Argulus* and *Raillietiella*, and is little useful in discussions of the phylogeny of these groups within the Arthropoda.

The pseudoacrosome

The pseudoacrosome, occupying the anterior fourth or third of the spermatozoon, is the most outstanding and unique feature in the spermatozoa of *Argulus* and *Raillie-tiella*. The development of the pseudoacrosome is practically identical in the two forms. The structures involved can be readily homologized and are all intimately related to the centriole: The dorsal ribbon, the granulosome, the apical membrane and the pseudo-acrosomal granular matter (PGM).

The development from pericentriolar structures in both forms makes a homology with a true acrosome improbable, and this non-identity is settled in a decisive way in *Argulus*, in which a typical true acrosome and a pseudoacrosome exist side by side during development.

Differences in the structure of the pseudoacrosomes between *Argulus* and *Raillie-tiella* concern the final differentiation of the PGM into rods, particularly its asymmetrical way of condensation in *Argulus foliaceus*. Most differences appear very late during

spermatogenesis, and do not appear to be fundamentally significant. Actually the variation within the genus Argulus appears to be great enough to cover even such differences as those between Argulus foliaceus and Raillietiella, for the Argulus species examined by Brown (1966) appears to have a pseudoacrosome of the *Raillietiella* type. Brown only refers to this structure as "sperm end" in the legends to his Fig. 31, but most probably the sections shown are of symmetrical pseudoacrosomes similar to those of Raillietiella.

A pseudoacrosome of this kind is not known from other animals, and it is even difficult to find homologues to the single components involved in its development. These components will now be considered separately.

The granulosome develops in contact with the centrille in a region where granular bodies have been described in many animal species: Centriole adjunct, post-nuclear body, annexe centriolaire, granular material, juxta-nuclear body, etc. (see Gatenby and Tamishian 1959, Breland et al. 1966, Phillips 1970a, Cantacuzène 1970). The granulosome is hardly homologous with these structures, for it develops in contact with the proximal end of the centriole, not around the centriole as the typical centriole adjunct. Moreover, the typical centricle adjunct is formed after the centricle has obtained contact with the nucleus, whereas the granulosome is present at the end of the centricle long before this has happened, and actually mediates the contact between the centriole and the nuclear membrane in later stages.

The situation and early presence of the granulosome would, perhaps, invite a comparison with the proximal centrille, which is located between flagellar centrille and nucleus in many animals. In some animals, e.g., the spider Pisaurina sp., the proximal centriole appears to lose its characteristic structure early so that it looks like a rather unorganized clump in the figures (Reger 1970b). But no proximal centriole has ever been seen in spermatids of Argulus and Rallietiella, and is certainly not present in the latter species, of which numerous early spermatids have been seen. The early appearance of the granulosome and apical membrane at one end of the centriole before last meiotic division makes such an interpretation completely untenable.

Actually the granulosome could better be compared with the matter forming around the centrioles of certain urodeles before these attain contact with the nucleus (Werner 1970), but criteria for such a homology are weak and the systematic position of the animals makes the comparison purely theoretical.

The best interpretation of the granulosome and the apical membrane is that they are homologues to the "couronne osmophile" attached to the proximal end of the flagellar centriole in the cirriped Trypetesa nassarioides Turquier (Turquier and Pochon-Masson 1969, p. 461). This ring-formed crown of dark matter looks very much like the early anlage of the apical membrane in Raillietiella, but nothing similar to the granulosome proper appears to be present in the cirriped.

The apical membrane is present in Argulus and Raillietiella, and develops during meiosis as a condensation in the granulosome material across the free edges of the centriole. In *Raillietiella* it can be recognized already in late spermatocytes 1. The only 4

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probable homologue is the above-mentioned dark ring at the end of the centriole in the cirriped *Trypetesa*. Although this homology seems reasonable, the differences are considerable. In *Trypetesa* the "couronne osmophile" remains as a dark ring at the end of the centriole in mature spermatozoa, whereas the apical membrane in *Argulus* and *Raillietiella* develops dramatically as one of the constituents of the pseudoacrosome.

Other membranous structures have been described at the proximal end of the centriole in species of arthropods but are more or less clearly derived from the anterior, vestigial end of the nucleus, for instance in the thysanuran *Lepisma saccharina* (Werner 1964), the beetle *Cicindela campestris* (Werner 1965), the mystacocarid *Derocheilocaris typicus* (Brown and Metz 1967, Brown 1970), and cirripeds (Turquier and Pochon-Masson 1969, Pochon-Masson et al. 1970). It is then supposed that the "collar" described by Munn and Barnes (1970) in *Balanus balanus, B. perforatus*, and *B. balanoides* is identical with the flat nuclear diverticulum described by Turquier and Pochon-Masson (1969) and Pochon-Masson et al. (1970).

The pseudoacrosomal granular matter (PGM) is clearly homologous in *Raillietiella* and *Argulus*, being formed in identical areas and subdivided in the same way into a dense dorsal part and a more scattered ventral portion. It is obviously part of the centriolar annexes, for in abnormal spermatids with two centrioles, each is associated with its own portion of PGM (Plate 18:91). I have not been able to find any homologues in other animals.

The dorsal ribbon and its membranous sacs take part in the formation of the pseudoacrosome, but are discussed below.

The general organization of the body

Development of the nucleus and the mitochondria into long, filamentous structures lying parallel with the axonema is in no way a unique feature in Argulus and Raillietiella, for it is a fairly common feature in arthropods (see Baccetti 1968, 1970a, Phillips 1970a). Even dislocation of the centrille to a level near the anterior end of the nucleus, and the filamentous development of the latter, is known in some arthropods, particularly in Lepisma saccharina (Werner 1964), Thermobia domestica (Bawa 1960, 1964 a, b), Cicindela campestris (Werner 1965), Panorpa annexa and P. germanica (Baccetti et al. 1969), Derocheilocaris typicus (Brown 1966, Brown and Metz 1967, Brown 1970), and cirripeds (Brown 1966, 1970, Turquier and Pochon-Masson 1969, Pochon-Masson 1970, Munn and Barnes 1970). Such an anterior dislocation of the centriole is also known from non-articulates, belonging to widely different phyla: some flatworms (Silveria and Porter 1964, Hendelberg 1970), the chaetognath Spadella cephaloptera (v. Deurs 1972), the fish *Polypterus senegalus* (Mattei 1969, 1970), and some amphibians (Austin and Baker 1964). The filamentous shape of nucleus and mitochondria and the anterior dislocation of the centricle are thus far from specific to Argulus and *Raillietiella* and are little useful in discussions on phylogenetic relationships.

The nearly perfect bilateral symmetry of the spermatozoan body is a characteristic feature of Argulus and Raillietiella, although the spermatids of the former pass through an asymmetrical stage before final maturation. Similar symmetry is common in insect spermatozoa, as far as mitochondria and axonema are concerned (Phillips 1970a). In forms with an anteriorly dislocated centriole such as Lepisma, the cross section of the body can be similar to that of Raillietiella and Argulus, with nucleus, mitochondria and axonema symmetrically disposed (Werner 1964). The flagellate crustacean spermatozoa found in the mystacocarids and cirripeds are strongly asymmetrical (Brown and Metz 1967, Brown 1966, 1970, Turquier and Pochon-Masson 1969, Pochon-Masson et al. 1970, Munn and Barnes 1970). The large spermatozoa of ostracods are bilaterally symmetrical but are aflagellate and can hardly be compared to those of Argulus and Raillietiella because of their highly specialized and unique structure (Reger 1970a). A distinctly symmetrical pattern including axonema, filiform mitochondria and a filiform nucleus is not present in chelicerates, myriapods or diplopods (André 1959, 1965, Rosati et al. 1970, Reger 1961, 1962, 1963, 1969, 1970b, Grassé et al. 1965, Reger and Cooper 1968, Horstmann 1968, 1970). It may thus be concluded that Argulus differs strikingly from other crustaceans with regard to the bilateral symmetry of the spermatozoa. However, the presence of similar patterns in some insects makes it difficult to use the strictly identical symmetry of *Raillietiella* and *Argulus* for phylogenetic conclusions.

Complete reduction of the free flagellum is typical of *Raillietiella* and *Argulus* and is possibly a fairly specific feature. In other articulate spermatozoa of filiform type there is a short free flagellum also in the mature spermatozoon, e.g., in *Lepisma* (Werner 1964), *Derocheilocaris* (Brown and Metz 1967) and Cirripeds (Pochon-Masson et al 1970). However, the morphology of this end of the spermatozoon is often incompletely known in the arthropods, so the uniqueness of *Argulus* and *Raillietiella* cannot be regarded as established with regard to this feature.

The axonema

Both in *Argulus* and *Raillietiella* the axonema is of the 9+2 type and presents some very specific features, common to both species: 1) the symmetrical situation of the central filaments on each side of the median plane, 2) the dorso-median situation of peripheral doublet no. 1, 3) the presence of a minute membrane, connecting doublet 1 with the dorsal ribbon, and 4) the oblique situation of this membrane which, in cross sections, is inclined to the side where the arms of doublet 1 are situated.

The constant symmetrical situation of the central filaments on each side of the median plane appears to be a feature restricted to *Argulus* and *Raillietiella*. The plane of the central filaments thus forms an angle of 90° with the median plane in these forms. In other arthropods with symmetrical spermatozoa, i.e., a number of insects, the plane through the central filaments is more or less vertical, forming a small angle with the median plane (Phillips 1970b). Even in the symmetrical spermatozoa of

Lepisma (Werner 1964, own observations) and Petrobius (own observations) the central filaments are oriented as in other insects, i.e., they are nearly but not exactly median. Numerous EM pictures in the literature, particularly in *Comparative Spermatology* (Baccetti 1970b) confirm these statements.

The exceptional orientation of the central filaments may indicate that the bending movements of the spermatozoids of *Argulus* and *Raillietiella* are dorso-ventral, not more or less lateral as is supposed for other arthropods (see Fawcett and Porter 1954, Gibbons and Grimstone 1960, Phillips 1970a).

The orientation of the central filaments has, by definition, the consequence that doublet 1 must be median, but there are two possibilities: dorso-median or ventromedian. Point 2) above says that the first alternative is realized both in *Argulus* and *Raillietiella*.

The small membrane connecting outer doublet 1 with the dorsal ribbon is also a feature restricted to *Argulus* and *Raillietiella*. In cross sections the membrane is inclined to the same side in both species, i.e., the side where the arms of doublet 1 are situated.

Similar membranes, connecting peripheral doublets with surrounding sheaths or fibers, have been described in many different animals, for instance mammals (Fawcett and Phillips 1970), and fish (Mattei 1969). They are probably present in some arthropods (see figures in Phillips 1970b). However, the restriction of this membranous connection to doublet 1, and its very characteristic and constant oblique course, are features only found in *Argulus* and *Raillietiella*. The attachment of the membranous envelopes of the dorsal ribbon to doublets 3 and 8, as seen in *Argulus* only, would appear to be a less unique feature. A (probably analogous) attachment of these doublets to outer fibers and sheaths is seen in some mammals (Fawcett and Phillips 1970, Pedersen 1970).

Altogether, the details in axonemal structure common to *Argulus* and *Raillietiella* are so fundamental and so different from anything known in other animals, that they have to be considered earnestly in phylogenetic discussions.

The dorsal and ventral ribbons

The identical structure and development of the ribbons in *Argulus* and *Raillietiella* was described in pages 32 and 36–44. Identity is extended to numerous details like 1) the sharp lateral edges of the dorsal ribbon, fitting into furrows in the broad margins of the ventral ribbon, 2) the presence of membranous sacs around the dorsal ribbon, not around the ventral one, 3) extension of the ventral ribbon over the dorsal and lateral surfaces of the lateral mitochondria, 4) the early development of the anlage of the dorsal ribbon before 2nd meiotic division in both forms, as a flat membranous sac with underlying dark rods on one side of the centriole, 5) the shift from two to three dark rods in the early anlage of both forms, the latter three rods corresponding to outer dark filaments 9, 1 and 2.

The most astonishing of all these common features is perhaps that the centriole becomes bilaterally symmetrical by the appearance of a rudimental dorsal ribbon long before meiosis is completed.

The only difference of importance between the two forms is the development of a pair of distinct "intermitochondrial rods" in *Argulus*, probably homologous with outer dark fibers nos. 5 and 6. In *Raillietiella* these dark fibers together with nos. 4 and 7 are included in the ventral ribbon and probably form the light cores.

Development of dark outer fibers or outer filaments, peripheral to the doublets, is not rare in arthropods (Baccetti 1970a, Phillips 1970a, b, Rosati et al. 1970), but fusion of such fibers to form something like the dorsal and ventral ribbons of *Argulus* and *Raillietiella* does not appear to have been described.

Other dark-staining rods, situated outside the dark outer fibers along the axonema, have been described in some insects, e.g., culicids (Breland et al. 1966), certain homopterans (Folliot and Maillet 1970), *Lepisma* (Werner 1964) and *Petrobius* (own observations). They are said to be derived from a "centriole adjunct" or "postnukleärer Körper" and may be paired, symmetrically situated as in the homopterans and *Petrobius* or unpaired as in *Lepisma*. Neither the structure nor the development of these bodies supports a homology with the ribbons of *Raillietiella* and *Argulus*, in which no typical centriole adjunct is formed.

The only well-established affinity in the case of dorsal and ventral ribbons was derived from comparisons with the spermatogenesis of cirripeds as described by Bocquet-Védrine and Pochon-Masson (1969) and Pochon-Masson et al. (1970). In cirriped spermatids they found a bilamellar structure, attached to one side of the axonema, often situated between the axonema and the single mitochondrion. They believe that the two lamellae are derivatives of the endoplasmic reticulum. Although the situation on the mitochondrial side of the flagellum is somewhat problematic, the structure looks very much like the endoplasmic sacs of the dorsal ribbon in *Argulus* and *Raillie-tiella*. In the cirripeds this bilamellar structure or "lamelle paraflagellaire" is only present during development and was not seen in mature spermatozoa.

Another possible homologue to the sacs of the dorsal ribbon is the "Lamelle" described by Werner (1965) in spermatids of *Cicindela*. It is a half-cylindrical piece of membrane, situated in the plasm near the centriole, and disappears before maturation. Although a homology is possible, I hesitate to suggest it, because the structure in *Cicindela* has a variable orientation and location.

Thus, with the exception of a possible presence in early spermatids of cirripeds of a homologue of reticular sacs of the dorsal ribbon, this ribbon, like the ventral one, appears to be highly characteristic of *Raillietiella* and *Argulus*, with no real counterparts in other articulates. This is true also of the numerous details of these complicated and composite structures.

The mitochondria

Three mitochondrial rods, with vestigial cristae, situated symmetrically between the ventral ribbon and the nucleus, are typical of the mature spermatozoon of *Argulus* and *Raillietiella*. Development is identical: The tubular mitochondria of the spermatocytes are reduced in number and become spherical. They fuse in early spermatids to form three large spheres in contact with each other. These large, mitochondrial balls are packed together into a single Nebenkern in which the three composite mitochondria remain separated by intact mitochondrial walls. Three mitochondrial tongues are emitted from this Nebenkern along the ventral aspect of the flagellum, first in the anterior direction, a little later also in a posterior direction. When these mitochondrial tongues have attained their definite length the Nebenkern is completely reduced.

The difference between the two forms is inconsiderable: Absence of cristae in the median mitochondrion of *Raillietiella*, and retraction of the inner mitochondrial membrane from the anterior end of the same mitochondrion in *Argulus*.

Long, filamentous mitochondria are common in insects (Baccetti 1968, Phillips 1970a, Favard and André 1970), but the normal number is two or one. Only collembolans have more: in addition to two long ones there may be six to seven small ones in the region of the neck (Dallai 1967). In *Anurida maritima* (Guerin) three long filamentous mitochondria extend along the axonema, the median one being shorter than the other two (Dallai 1970). Cirripeds have only one long mitochondrion (Pochon-Masson et al. 1970). Mystacocarids are not well known but the *Argulus* pattern is certainly not present (Brown and Metz 1967). Other crustaceans have such specialized spermatozoa that a comparison with *Argulus* has little purpose (Brown 1970, Baccetti 1970). Among chelicerates, *Limulus* (= *Xiphosura*) polyphemus has simple mitochondria of the polychaete type (André 1965), and the spermatozoa of other chelicerates and myriapods vary with regard to mitochondria, but nothing like an *Argulus* pattern has been described (Reger 1961, 1962, 1963, 1969, 1970b, Horstmann 1968, Rosati et al. 1970, Baccetti 1970a).

With regard to transformations during development, the mitochondria of Argulus and Raillietiella follow a pattern known mainly from insects and gastropods (André 1962, Favard and André 1970). In insects the large Nebenkern is formed by several mitochondria, which are transformed into a single continuous network of mitochondrial tubes by membrane fusion (de Robertis and Raffo 1957, Favard and André 1970, Pratt 1970). This body may later be subdivided into the two mitochondrial derivatives usually present in mature spermatozoa. Details are known only for few species, but if this description holds for insects in general, it may be concluded that Argulus and Raillietiella are different with regard to the formation of the Nebenkern. In these forms the initial mitochondrial fusion results in formation of three spherical bodies, which remain separated by double membranes in the Nebenkern.

Thus, with regard to the mitochondria, Raillietiella and Argulus follow a pattern

common in arthropods, particularly in insects. The only unique feature is the number of mitochondrial rods, which is three, whereas other filiform arthropod spermatozoa have two or one. Apart from the Branchiura and Pentastomida, three mitochondrial rods are known only from the collembolan *Anurida maritima*. In other respects the collembolan spermatozoa are so different from those of *Argulus* and *Raillietiella* that comparisons are very difficult.

The nucleus

The long, filamentous nucleus is almost identical in mature spermatozoa of Argulus and Raillietiella. The development of the nucleus is, however, different in details. In Argulus both the anterior and the posterior ends of the ovoid nucleus are drawn out to form nuclear tongues, whereas only the anterior end is drawn out in Raillietiella. Eventually the thick part of the nucleus is attenuated in both species, and the final result is the same. Condensation of the chromatin is different: In Raillietiella many small granules grow to large clumps which coalesce, in Argulus there is a rod-like condensation along the acrosome filament. Further, the extra membranes formed inside the original nuclear membranes appear to be peculiar to Argulus.

A long, filamentous nucleus is a common feature in arthropods (Baccetti 1968, Phillips 1970a), but it is rarely extended to the extreme posterior end as in *Argulus* and *Raillietiella* (see also Thompson and Blum 1967). The condensation of chromatin takes place in so many and different ways in different species, that general statements with phylogenetic significance are excluded.

Thus, while the general features of the nucleus are very much the same in *Argulus* and *Raillietiella* and fit well in the phylum Arthropoda, there are no unique features with great significance in phylogenetic discussions as far as the nucleus is concerned.

The true acrosome

With regard to the true acrosome, *Argulus* and *Raillietiella* spermatozoa are nearly identical in the mature state, in which the structure is absent (*Raillietiella*) or present only as an insignificant vestige (*Argulus*). In *Raillietiella* no trace of a true acrosome has been seen during development, whereas spermatids of *Argulus* develop a distinct acrosome vesicle and acrosome filament ("perforatorium"), which eventually disappear.

The acrosome apparatus of *Argulus* spermatids is of a generalized type with a bowl-shaped acrosome vesicle covering the top of an acrosome filament, which extends throughout the long nucleus, lying in a tube-like invagination of the nuclear membranes. Among arthropods, a very similar apparatus is found in *Limulus* (André 1965, Philpott and Shaw 1959), which is supposed to have the most primitive spermatozoa of all arthropods (Baccetti 1970a). In other arthropods there are modifications of the acrosome vesicle or of the acrosome filament or of both. In crustaceans a fairly

typical acrosome vesicle covering a rod-like acrosome filament is found in the cirripeds, but the filament does not penetrate into the nucleus (Pochon-Masson et al, 1970. Munn and Barnes 1970). The acrosome of the mystacocarid *Derocheilocaris* is described as an electron-dense through-like structure, and no acrosome filament is mentioned (Brown and Metz 1967). Other crustaceans are very strongly modified with regard to acrosome development (Yasuzumi 1960, Yasuzumi et al. 1961, Hollande and Fain 1964, Reger 1964a, b, 1966, 1970a, Brown 1966, 1970, Fain-Maurel 1966, 1970, Pochon-Masson 1969).

Chelicerates are not very well known with regard to acrosome development, but the araneids certainly have a fairly compact acrosome vesicle and an acrosome filament (Reger 1970b, Rosati et al. 1970). The chilopod *Geophilus linearis* Koch has a long compact acrosome (Horstmann 1968), whereas pauropods lack an acrosome and the symphylans and diplopods have a strongly modified one (Rosati et al. 1970, Reger and Cooper 1968, Horstmann 1970). No acrosome filament appears to be present in these millipedes and centipedes.

Insect acrosomes are very compact throughout development and there is no acrosome filament penetrating into the nucleus (Phillips 1970a). Interesting exceptions from this rule are found in the collembolan *Anurida maritima* (Dallai 1970) and the thysanur *Petrobius maritimus* (author's unpublished material). In *Anurida* the acrosome filament appears to be permanent. In *Petrobius*, a compact acrosome vesicle and a very large acrosome filament develops during spermatogenesis. The filament penetrates the very long nucleus and ends near the nuclear membrane in the region of the centriole, but disappears completely before final maturation of the spermatozoon. The acrosome vesicle develops into an extremely long and narrow acrosome of the insect type, and persists in the mature spermatozoon.

When the variation of the acrosomal apparatus within the arthropods is taken into consideration, it appears probable that the ancestral arthropods have had an open acrosome vesicle and a long acrosome filament like those seen in spermatozoa of *Limulus* and, in more modified forms, in araneids and in spermatids of *Petrobius* and *Argulus*. This is also the type of acrosomal apparatus found in annelids with fertilization in the water like *Hydroides hexagonus* (Colwin and Colwin 1961a,b) and *Nereis japonica* (Takashima and Takashima 1963).

The transcient appearance of such an apparatus during spermatogenesis in *Argulus* is particularly interesting, since the structures are reduced before final maturation and therefore cannot be used for their original function: to penetrate the egg surface. This reminds strongly of ontogenetical recapitulation, here illustrated on the cytological level. Following this line up, one would assume that the genes regulating the development of the acrosomal apparatus have been partly suppressed in *Argulus* and completely suppressed in *Raillietiella*, in which no trace of a true acrosome has been found. The latter should, therefore, be regarded as more advanced in this respect. The appearance and later reduction of the acrosome filament in *Petrobius* can probably be viewed in a similar way.

The lateral organelles

The lateral organelles are present only in late spermatids of *Argulus* and disappear in *A. foliaceus* before final maturation. In the other *Argulus* species examined by Brown (1966 and 1970) these organelles are said to be present in mature sperm. Membrane-bound vesicles with granular content have been seen in spermatids of *Raillietiella*, but do not have the constant localization typical of lateral organelles. Homologization of these more variable vesicles with the row of elongate sacs in *Argulus* therefore remains uncertain. A possible homologue of the lateral organelles is the "vesicule" in cirriped spermatids, described by Bocquet-Védrine and Pochon-Masson (1969), Turquier and Pochon-Masson (1969) and Pochon-Masson et al. (1970). Like the lateral organelles this "vesicule" is supposed to be developed from the smooth endoplasmic reticulum, but the criteria for a homologization of the two structures are admittedly not very strong.

VI. PHYLOGENETIC AND SYSTEMATIC IMPLICATIONS

Main conclusions

The detailed comparisons in chapter IV show that the spermatozoa of *Raillietiella* and *Argulus* are nearly identical with regard to structure and development. The analysis in chapter V shows that the *Raillietiella-Argulus* type of spermatozoon is highly specialized and represents a type of its own, not encountered in other animals. A long series of fundamental features common to the spermatozoa of *Raillietiella* and *Argulus* has no counterpart in other spermatozoa. This justifies the conclusion that the Pentastomida and the Branchiura are closely related.

The conclusion is of course based on the great over-all similarity between the spermatozoa of the two animals, but is specifically supported by the following features which have only been found in *Raillietiella* and *Argulus*:

1) The presence of a ca. 30μ long pseudoacrosome, developed as two half-tubular sheaths with granular contents and originating in well-defined peri-centriolar structures which can be homologized in the two species: granulosome, apical membrane, dorsal ribbon, and PGM.

2) The very similar structure of the transitional region between pseudoacrosome and body in the two forms: The dorsal rod of the pseudoacrosome is continuous with the dorsal ribbon of the body, and is connected with the centriolar filaments nos. 9, 1, and 2; The ventral rod of the pseudoacrosome is continuous with some of the ventral filaments of the centriole and its outer sheath is forked posteriorly into a pair of winglike flaps which cover the sides of the centriole.

3) The plane of the central filaments of the axonema is perpendicular to the median plane of the body. The peripheral doublet no. 1 is medio-dorsal and differs from the other eight doublets in being connected with the dorsal ribbon by a minute, obliquely oriented membrane. This membrane is inclined to the side where the arms of doublet no. 1 are situated.

4) The presence and structure of the dorsal and ventral ribbons, which together form a tubular investment of the axonema: The dorsal ribbon is half-cylindrical with sharp edges which fit into furrows in the thicker free edges of the ventral ribbon. The latter covers the dorsal aspect of the mitochondria and extends with thin lamellae over the lateral aspects of the lateral mitochondria. The dorsal ribbon, but not the ventral one, is surrounded by narrow membranous sacs, developed from an inner and an outer sac in the spermatids. The dark outer fibers 9, 1, and 2 are included in the dorsal ribbon.

5) The rudiment of the dorsal ribbon is present before the 2nd meiotic division in both species and can be recognized as a pair of dark rods along one side of the centriole, covered by a small sac of smooth endoplasmic reticulum (this sac may be traced also in the Cirripedia). Later, in the early spermatids, there are not two but three dark rods under the endoplasmic reticular sac, and these three rods are the outer dark fibers 9, 1, and 2 of the centriole-axonema. The shift from two to three rods is well documented in both species.

6) The presence of *three* filamentous mitochondria, symmetrically situated between nucleus and axonema. This feature is perhaps not completely unique, for three mitochondrial rods are present in the collembolan *Anurida maritima*.

The most important *difference* between the spermatozoa of *Argulus* and *Raillietiella* is the transient appearance of an acrosome vesicle and an acrosome filament in spermatids of the former. Other differences are hardly greater than what could be expected between different species of a single genus. The most striking ones are found in the pseudoacrosome, which is strongly asymmetrical in *Argulus foliaceus* and strictly symmetrical in *Raillietiella*. However, the *Argulus sp.* studied by Brown (1966) appears to have a symmetrical pseudoacrosome of the same appearance as that of *Raillietiella*, i.e., if my interpretation, that the "sperm ends" in Brown's figures are pseudoacrosomes, is correct.

In view of the numerous points of identity between the spermatozoa of *Raillietiella* and *Argulus*, and the absence of most of these features in other animals, it must be concluded that convergence and evolutional hazards are not good explanations. The identical features must therefore depend on a close phylogenetic relationship in the sense that the Pentastomida and the Branchiura are more closely related to each other than to other animal groups.

It is therefore suggested that the Pentastomida be placed as a sub-group of the Branchiura in the zoological system. The subclass Branchiura can be maintained and can be divided into two orders: The Argulida and the Pentastomida.

It is admitted that adult and larval morphology appear to give little support to such a rearrangement of the system, but negative evidence is of little weight in a case like this, when one of the groups, the Pentastomida, are specialized endoparasites, and

the other, the Argulida, show distinct specializations for an ectoparasitic life. Parallel cases are known, in which the adult morphology of parasites is inconclusive with regard to systematic affinities: e.g., Rhizocephalia among the Cirripedia and the genus *Enteroxenos* among the Gastropoda. In these cases the larval forms finally revealed the true relationships. In the case of *Raillietiella* and *Argulus*, the embryology and internal anatomy of the larval forms is poorly known, and a comparison between the two forms does not seem to have been attempted. This is left for future research.

The present conclusion in the light of crustacean spermatology

Considerable support to the conclusions above can be derived from present knowledge of crustacean spermatozoa. As pointed out particularly by Brown (1970), each major crustacean group is characterized by its own type of spermatozoa, and a classification of the Crustacea based on the spermatozoa alone would fit very well with the system for decapods suggested by Borradaile (1907). Within the Malacostraca, all spermatozoa are non-flagellate, and the group Peracarida stands out beautifully because Isopoda, Amphipoda, Cumacea and Mysidacea have spermatozoa which can be referred to a common type, although there are differences in details between the groups. This indicates strongly that spermatozoan morphology is conservative enough to be a useful diagnostic criterion for the larger systematic units within the crustaceans.

This is also beautifully illustrated by the Cirripedia, which are of interest because they are well investigated, and because they are often believed to be somewhat related to the Branchiura. Both free-living forms such as Balanus, Chthamalus, Lepas and Scalpellum and strongly modified parasites such as the acrothoracid Trypetesa and the rhizocephalian Sacculina have been examined after the electron microscope became available (Brown 1966, 1970, Turquier and Pochon-Masson 1969, Pochon-Masson et al. 1970, Munn and Barnes 1970). It was stated that the spermatozoa of all investigated species were modifications of a characteristic "cirriped type" of spermatozoon, in which the typical relations between acrosome, nucleus, axonema and mitochondrion remained constant (Pochon-Masson et al. 1970). This type is not like any spermatozoa encountered in other crustaceans. It appears that a classification of crustaceans based exclusively on the spermatozoa would include a group Cirripedia, very distinct from other crustaceans, and also containing the strongly modified parasites Trypetesa and Sacculina, which have been difficult to place on the basis of adult morphology. In fact, the situation of Sacculina within the Cirripedia reminds very much of that of Pentastomida within the Branchiura, if the system suggested above is accepted.

The expected similarities between Branchiura and Cirripedia on the spermatological level turned out to be very slight and partly doubtful: 1) Presence in spermatids of cirripeds of a "lamelle paraflagellaire" along the axonema, obviously homologous with the membranous sacs of the dorsal ribbon in the *Argulus-Raillietiella* spermatid (see p. 53), 2) Presence in *Trypetesa* of dark material at the end of the centriole, perhaps homologous with a granulosome or apical membrane (p. 49), and 3) Presence in cirripeds of a "vesicule", perhaps homologous with the lateral organelles in Argulus (p. 57).

Although these similarities between cirripeds and *Argulus-Raillietiella* may seem insignificant, they are the only positive result of the search for homologies of the many unique structures in the spermatozoa of *Raillietiella* and *Argulus*. It is admitted, however, that these similarities to cirripeds are not great enough to be conclusive in systematic discussions.

The present conclusions and general articulate spermatology

All recent investigators of Pentastomida agree that the morphology and larval development definitely show that they are articulates (Heymons 1935, Beklemischev 1958, 1969, Kaestner 1954/55, 1965, Doucet 1965, Legendre 1967, v. Haffner 1971). For this reason, mainly articulate spermatozoa have been considered in the comparative parts of the present work. Actually the Annelida are rarely mentioned, partly because the ultrastructural investigations are few. However, the numerous light microscopical investigations, particularly those of Franzén (1956, 1958, 1962, 1970), show that the majority of polychaete spermatozoa are of the primitive type characteristic of animals with external fertilization in the water. Presence of the advanced pattern characteristic of the Raillietiella-Argulus spermatozoa is therefore excluded. In a few polychaete families, and in the Hirudinea, Oligochaeta and Archiannelida there are more specialized spermatozoa, which in a few cases can be truly filiform. In practically all cases light microscopy has revealed sufficient detail to show that they are fundamentally different from the Raillietiella-Argulus type (see Franzén 1956, 1970). Electron microscopy of the spermatozoa of Hydroides hexagonus (Colwin and Colwin 1961 a, b), Nereis japonica (Takashima and Takashima 1963), Spirorbis moerchi (Postwald 1967), Lumbricus spp. (Gatenby and Dalton 1959, Bradke 1963, Anderson et al. 1967), Enchytraeus albidus (Reger 1967), and Hirudo medicinalis (Pastisson 1966) give no reason to change this statement. The studies of annelid spermatology therefore give us no reason to believe that Argulus and Raillietiella should have inherited their remarkable spermatozoa directly from annelid-like ancestors.

The situation appears to be much the same for arthropods in general. Their sperm structure, which is exceptionally well studied, indicates that specialization of the spermatozoa, perhaps also development of internal fertilization, has taken place independently within several evolutional lines leading up to the major groups of recent arthropods. A striking argument is furnished by Limulus (= Xiphosura) polyphemus, which has external fertilization and a primitive type of spermatozoon (Philpott and Shaw 1959, André 1965). This spermatozoon is almost identical with that found in many polychaetes, molluscs, echinoderms and other animals with external fertilization (Franzén 1956, 1970). This makes it most improbable that Limulus or its ancestors ever had internal fertilization and specialized spermatozoa, for then the "primitive" type of

sperm had to evolve independently. A more probable interpretation is that *Limulus* inherited the mode of fertilization and the primitive spermatozoa directly from the proarticulates. This means that the pro-arthropod (if the group Arthropoda is monophyletic) or at least the pro-chelicerate must have had external fertilization and simple spermatozoa, and that internal fertilization and specialization of the spermatozoa must have evolved independently within several arthropod lines.

Recent chelicerate spermatozoa are also very different from one group to another, and the features common to several groups are seemingly restricted to those present in the primitive spermatozoa of *Limulus* (i.e., symplesiomorphous). This would be expected if specialization for internal fertilization has been largely independent within each evolutional line and has started with a *Limulus* type of sperm. Facts concerning the structure of chelicerate spermatozoa have been supplied for *Limulus* (Philpott and Shaw 1959, André 1965), scorpions (Tuzet 1938, André 1959), araneids (Reger 1970b, Rosati et al. 1970), opilionids (Sotelo et al. 1958, Reger 1969), pseudoscorpions (Boissin and Manier 1966a, b, 1967), and acarids (Reger 1961, 1962, 1963, Breucker and Horstmann 1968).

The very great differences between the spermatozoa of the crustacean groups also support the view that specialization for internal fertilization has been largely independent within each evolutional line (for literature see Brown 1966, 1970, Baccetti 1968, 1970 a). If all crustaceans had started with a specialized spermatozoon in a common ancestor, some of the specializations would be expected to occur in several recent groups, and a kind of "crustacean type" of spermatozoon could be constructed. This is certainly not possible. The round, non-flagellate anostracan spermatozoa, the enormous motile but non-flagellate and complicated ostracod spermatozoa, the ovoid non-flagellate copepod spermatozoa, the flagellate branchiuran spermatozoa with their pseudoacrosome, the flagellate cirriped spermatozoa with true acrosome and anteriorly displaced centriole, and the several types of non-flagellate malacostracan spermatozoa have little in common except features which are present in a primitive cell. Brown (1966, 1970) suggests that the spermatozoids of the cephalocarid Hutchinsoniella macracantha have some features in common with malacostracan spermatozoa, and that those of the mystacocarid Derocheilocaris typicus show affinity to cirriped and branchiuran spermatozoa, but other generalizations are difficult to find.

Insects appear much more uniform with regard to the spermatozoa, and a standard type can be imagined in spite of considerable variations (Baccetti 1968, 1970a, Phillips 1970a).

Very strong specializations are found in the different groups of millipedes and centipedes (Grassé et al. 1965, Horstmann 1968, 1970, Deschamps 1969, Chevallier 1970, Reger and Cooper 1968, Rosati et al. 1970).

Of particular interest are the spermatozoa of Onychophora and Tardigrada, since these animals have played a role as possible relatives of the Pentastomida. Light microscopical investigations of *Peripatus* spermatozoa (Montgomery 1900, Gatenby 1925) indicate that these are almost filiform with "head", "middle-piece" and "tail" after each other in normal sequence. The spermatozoa of the tardigrade *Macrobiotus hufelandi* are comparatively little specialized, with a pointed acrosome, a spiral nucleus, a sheath of metamorphosed mitochondria around the anterior part of the axonema, and a long free flagellum (Baccetti, in print, and author's own material). No pentastomid characters could be discovered.

Although the articulate system and particularly the arthropods are well covered by ultrastructural investigations of spermatozoa, no structures comparable to the specialized features in the spermatozoa of *Raillietiella* and *Argulus* have been found.

It is admitted that the present chapter is theoretical and may be superficial in many respects, but it is supposed to show that placing the Pentastomida outside the Branchiura, e.g., within Chelicerata, or together with Myriapoda, or together with Tardigrada and Onychophora, or deriving them directly from Annelida, is strongly contradicted by the spermatological picture. In these cases, the common ancestor of *Argulus* and *Raillietiella* would be either a pro-articulate, a pro-arthropod, or a promandibulate, hypothetical forms which must be supposed to have had primitive spermatozoa and, most probably, external fertilization. At any rate these hypothetical ancestors cannot have had the specialized *Argulus-Raillietiella* type of spermatozoon, for no trace of such specialized features is found in other descendants of these ancestral forms. Evolution of the highly specialized spermatozoa would therefore have taken place independently within the pentastomid line and the branchiuran line and resulted in the same structure with a long series of identical specialized details. This cannot be accepted as probable.

Comments on previous opinions about pentastomid relationships

Since a relation between pentastomids and branchiuran crustaceans has never been suggested before, the conclusions in this paper must be in conflict with the majority of the numerous ideas published on the pentastomid problem (see reviews in Heymons 1926/27, 1935, Osche 1963, Doucet 1965, Self 1969, v. Haffner 1971).

Among the old ideas, those dealing with affinities to nematodes, trematodes and cestodes did not survive when Leuckart's (1860) admirable monograph appeared. Leuckart himself regarded the pentastomids as related to acarids, particularly eriophyids ("Phytoptus") which have two pairs of anteriorly placed limbs and an annulate body, superficially resembling pentastomid hooks and segmentation.

An affinity of the pentastomids to crustaceans was mainly suggested by v. Beneden (1849), who compared the primary larva with a crustacean nauplius. As probable relatives of the pentastomids he also mentioned the pantopods (pycnogonids), by v. Beneden regarded as crustaceans but now usually placed near the Chelicerata. Although this comes near the conclusions of the present paper it is admitted that v. Beneden's arguments are untenable (see criticism in Leuckart 1860, Osche 1963, v. Haffner 1971).

The more specified ideas from the last few decades may be grouped as follows:

- 1. The Pentastomida are related to the Tardigrada and the Onychophora. The idea originates in a paper on *Myzostoma* by v. Graff (1877), in which myzostomids, tardigrades and pentastomids are compared. Cuenot (1952), Vandel (1949), and Weber (1949) created a particular group including the Pentastomida, the Tardigrada, and the Onychophora and called it Malacopoda, Pararthropoda or Onchopoda. The most important argument for keeping the groups together was the structure of limbs and claws (hooks).
- 2. Most recent authors hesitate with regard to the affinities to tardigrades or directly reject them. It is stated that the pentastomids have a mixture of arthropod and annelid features with some preponderance of the former. Since no distinct and specific relation to any articulate group is found, the pentastomids are derived directly from annelid-like ancestors or pro-arcitulates, independently or in some relation to tardigrades (Kaestner 1954/55, 1965, Beklemischew 1958, 1969, v. Haffner 1971).
- 3. On the basis of new information derived from embryos of the pentastomid *Reighardia sternae*, Osche (1963) concluded that the pentastomids are tracheate arthropods, probably related to myriapods.

It is obvious that all three alternatives are in serious conflict with the conclusions in the preceding pages, for all three will imply that the complicated and distinctly synapomorphous pattern of characters in the spermatozoa of *Argulus* and *Raillietiella* must have arisen independently within the two lines.

The first and second alternatives are not so fundamentally different, for all authors are somewhat hesitant with regard to the significance of those characters which indicate tardigrade relationship (limbs, hooks, nervous system). As stated and documented by v. Haffner (1971) and Osche (1963), this affinity to tardigrades cannot really be regarded as established. Kaestner, Beklemischew and v. Haffner, being unable to accept the affinities to myriapods suggested by Osche, were therefore left with the statement that available knowledge of pentastomids does not reveal distinct and specific affinity to any arthropod or annelid group. The logical consequence is that the pentastomids are regarded as an isolated group and are placed between annelids and arthropods because of their supposed mixture of general characters from both phyla.

When now a specific and obviously synapomorphous set of characters in the spermatozoa indicates a close relation between the pentastomids and the branchiuran crustaceans, there is consequently no alternative theory, and the new findings must be regarded as decisive. Some interesting consequences of the new position of the pentastomids in the system must be discussed, however.

The immediate consequence of the suggested position of the Pentastomida as a subdivision of the Branchiura is that they must have undergone a strong regressive development during their adaption to a parasitic mode of life. Kaestner (1965) admits that such a posibility is open but not proved. V. Haffner (1971) is much more reluctant

with regard to possible reductions in the body of pentastomids. He is of the opinion that the pentastomids never reached the level of fully developed arthropods, mainly because of the presence of a number of characters regarded as specific to annelids. The most important of these are 1) the seemingly unsegmented supraoesophageal ganglion, 2) the non-development of a composite suboesophageal ganglion, 3) the presence of an outer layer of ring muscles in the body wall, and 4) the presence of segmental, paired sensory organs along the body sides ("lateral line organs").

It is obvious that presence of specific and indisputable annelid characters in pentastomids would make it difficult to derive the group from branchiurans, which must be supposed to have lost these characters. The significance of the four points above will therefore be considered critically.

1) The supraoesophageal ganglion. Pentastomids appear to have a simple pair of preoesophageal ganglia like annelids, whereas mandibulate arthropods have a protoand deutocerebrum. Osche (1963), however, on the basis of his observations in *Reighardia* embryos, supposes that the protocerebrum fails to develop in pentastomids, and that the paired preoral ganglion is a deutocerebrum, because it is associated with a pair of appendage-like processes, interpreted as first antennae. Osche refers to the reduction of the protocerebrum which can be seen in blind arthropods, particularly in the blind chilopod *Scolioplanes hirtipes*, which appears to lack the protocerebrum completely (Beklemischew 1969: fig. 54 C). It is possible that a similar reduction of the protocerebrum has taken place in the blind, parasitic pentastomids, for *Argulus* appears to have well-developed proto- and deutocerebrum (Martin 1932). A possible rudiment of the protocerebrum is an ectodermal thickening at the anterior pole of the embryo called "Archicerebrum" in Osche's (1963) figures 12 and 13, but Osche admits that the interpretation of this structure is uncertain.

Von Haffner's interpretation of the single preoral pair of ganglia in pentastomids as an undivided annelid brain has the advantage of being simple and direct. On the other hand, Osche's more circumstantial interpretation is certainly also possible. The former gives a slightly modified annelid type of brain, the latter gives a strongly modified arthropod type of brain. Since both possibilities are open, the structure of the brain cannot be regarded as an absolute annelid character.

2) The suboesophageal ganglion of mandibulate arthropods usually consists of the fused ganglia of the of the mandibular, first maxillular and second maxillular segments, whereas the anterior ganglia of the ventral cord are free in primitive pentastomids and annelids. Failing fusion of the ganglia is not an absolute annelid character, however, for it has been described in several crustaceans, particularly in phyllopods (Horridge 1965). Moreover, the corresponding limbs in pentastomids are certainly strongly modified and reduced, if the animals have evolved from branchiuran crustaceans. This alone could explain why the ganglia fail to fuse into a composite suboesophageal ganglion, which is regarded as a coordinating center for the mouth parts.

3) The ring muscles under the epidermis, present in pentastomids, certainly look like the ring muscles of the annelid body wall (v. Haffner 1971). Their function appears

to be the same in both groups: to exert a pressure on the body fluid so the body can be extended. In other respects, e.g., with regard to cross striation and subdivision of the longitudinal muscles into separate bundles, the musculature of the pentastomids is arthropod-like. The question therefore arises whether the circular muscles could have developed secondarily in connexion with annelid-like movements, when the parasites were adapted to their particular habitat. Parasitic crustaceans often have strongly modified muscles. The most astonishing example is described by Claus (1887) in the copepod *Lerneascus nematoxys*, in which the longitudinal muscles form a layer inside the cuticle as in nematodes. Obvious cases of secondary development of subhypodermal muscles with a circular direction are also known in arthropods. Larval house flies, which move very much like pentastomids, have three pairs of flat muscles in each segment, lying under the hypodermis and probably functioning as the ring muscles of pentastomids (Hewitt 1910). In the Chilopoda epimorpha there is an almost continuous coat of circular muscles under the cuticle in the pleural region (Beklemischew 1969).

It may therefore be concluded that the ring muscles in the body wall of pentastomids are similar to those of annelids, but it cannot be excluded that they are a result of secondary adaptation to a parasitic mode of life.

4) The "lateral line organs" of pentastomids have the same structure as arthropod sense organs. The annelid-like feature is restricted to their situation along the sides of the abdomen, metamerically repeated on each segment, often in a longitudinal pigmented "lateral line". This arrangement has also been observed in several annelids (v. Haffner 1971). But it is possible that incomplete knowledge of this detail of arthropod anatomy is the reason why the arrangement appears to be an annelid feature. In Lepisma saccharina, groups of sensory organs are metamerically repeated on the abdominal segments, forming one ventro-median and a pair of lateral rows on the sternites and a pair of lateral rows on the tergites (K. Birket-Smith, personal communication). Actually it appears quite reasonable that sense organs are metamerically arranged if they are situated on a metameric part of the body. The annelid-like feature is therefore reduced to the presence of sense organs on the sides of the abdomen and their relation to a lateral pigmented zone. It appears to me that independent development of such a sensory system in an endoparasitic group is far from excluded.

In the absence of other arguments, the four characters dealt with above could, with some degree of probability, be interpreted as annelid-like features inherited from some pro-articulates (plesiomorphous, sensu Hennig 1966). On the other hand, it cannot be excluded that these characters could be present in an euarthropod, adapted to an entoparasitic form of life. Placing the pentastomids within the Branchiura as a strongly modified, parasitic sub-group will therefore not meet with serious difficulties. It is in good harmony with the majority of anatomical features in pentastomids, which are distinctly arthropod-like (v. Haffner 1971, p. 92–93), and with the spermatological features which must be regarded as strictly synapomorphous (sensu Hennig 1966): numerous, highly specialized features, identical in detail in the two forms and unknown in other animals.

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Placing the pentastomids outside the Branchiura has the absurd consequence that the spermatozoa must have undergone independent and extreme specialization in each line separately and that they by accident happened to be identical in all the new features evolved, even in minute details. This is certainly excluded on the basis of statistical probability.

Osche (1963), after a step-wise argumentation, partly on the basis of his own findings in embryos, comes to the conclusion that the pentastomids are mandibulate arthropods. This result agrees very well with the present findings. From the view of the conclusions in the present paper, the critical point in Osche's argumentation comes when he has to choose between the crustaceans and the antennates (insects and myriapods) as probable relatives of the pentastomids. Osche prefers the latter alternative, although more or less admitting that the anatomical criteria are not immediately convincing: absence of a digestive gland in pentastomids, poor development of the 2nd antenna in pentastomids, development of a distinct head in pentastomids and antennates, rarely in crustaceans. Osche's main argument is that pentastomids infest the respiratory tract of amniotes and should, therefore, be drived from terrestrial arthropods, not from crustaceans. Although indicative, this argument does not exclude the other possibility, viz., that they have evolved from crustaceans. If, for example, the ancestors were Argulus-like anthropods, infesting gills and perhaps the lung of crossopterygians, they could easily be imagined to evolve into specialized parasites of the lungs, while their hosts developed into terrestrial animals. The absence of pentastomids (as adults) in the small remnants of the amphibian group surviving today is certainly no strong argument against such a possibility.

I have tried not to over-emphasize the importance of the spermatological data in this discussion, for I realize that such data are not more conclusive than other morphological features. On the contrary, I have tried to deal with the spermatological features in the same way as with other morphological arguments used in the phylogenetic discussions. From this point of view, it is obvious that an almost identical set of highly specialized structures in *Argulus* and *Raillietiella*, like that found in the spermatozoa, must be regarded as a decisive argument for a close relationship, when the same features are unknown in other animals. Since no other arguments are in serious conflict with such a conclusion, I do not hesitate to take the consequence and suggest that the pentastomids should be placed within the Branchiura.

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References

ANDERSON, W. A., A. WEISSMAN and R. A. ELLIS, 1967: Cytodifferentiation during spermiogenesis in Lumbricus terrestris. J. Cell Biol. 32: 11–26.

- ANDRÉ, J., 1959: Étude au microscope électronique de l'évolution du chondriome pendant la spermatogénèse du scorpion Euscorpius flavicaudis. J. Ultrastruct. Res. 2: 288–308.
- 1962: Contribution à la connaissance du chondriome. Étude de ses modifications ultrastructurales pendant la spermatogénèse. J. Ultrastruct. Res. Suppl. 3. Academic Press, N. Y. – London.

- 1965: A propos d'une lecon sur la limule. Ann. Fac. Sci., Clermont-Ferrand 26: 27-38.

- AUSTIN, C. R., and C. L. BAKER, 1964: Spermatozoon of Pseudobranchus striatus axanthus. J. Reprod. Fert. 7: 123–125.
- BACCETTI, B., 1968: Spermatologia comparata degli arthropodi. Atti VII. Congresso naz. Ital. di Entomologia, Verona, 1967: 1–32.
- 1970a: The spermatozoon of Arthropoda. IX. The sperm cell as an index of arthropod phylogenesis. In *Comparative spermatology* (ed. B. Baccetti): 169–181. Academic Press, N. Y. – London.
- 1970b (editor): Comparative spermatology. Proc. int. Symp. Rome and Siena, 1–5 July 1969. Academic Press, N. Y. London.
- BACCETTI, B., and A. BAIRATI, 1964: Indagini sull'ultrastruttura delle cellule germinale maschili in Dacus oleae Gmel. *Redia* 49: 1–29.
- BACCETTI, B., R. DALLAI, and F. ROSATI, 1969: The spermatozoon of Arthropoda. III. The lowest holometabolic insects. J. Microscopie 8: 233–248.
- BAIRATI, A., and B. BACCETTI, 1964: Observations on the ultrastructure of the male germ cells of Drosophila melanogaster and Dacus oleae. In *Electron microscopy – Proc. 3rd Europ. reg. Conf., Prague* (ed. M. Titlbach), vol. B: 441–442.
- BAWA, S. R., 1960: Atypical spermiogenesis in Thermobia domestica, a thysanuran insect. *Nature*, *Lond. 188:* 1132.
- 1964a: Electron microscopy of double spermatozoa of an insect, Thermobia domestica Pack. In *Electron microscopy – Proc. 3rd Europ. reg. Conf.*, *Prague* (ed. M. Titlbach), *vol. B*: 445–446.
- 1964b: Electron microscope study of spermiogenesis in a fire-brat insect, Thermobia domestica Pack. I. Mature spermatozoon. J. Cell Biol. 23: 431-446.
- BEKLEMISCHEW, W. N., 1958: Grundlagen der vergleichenden Anatomie der Wirbellosen. Bd. 1. VEB Deutscher Verlag der Wiss., Berlin.
- (1964) 1969: Principles of comparative anatomy of invertebrates. I. Oliver and Boyd, Edinburgh.
- BENEDEN, P. J. VAN, 1849: Recherches sur l'organisation et de développement des Linguatules (Pentastoma Rud.), accompagnées de la description d'une espèce nouvelle provenant d'un mandrill. Mém. Acad. r. Sci. Lett. Belg., Ser. III, Zool., 23: 1–38.
- BOCQUET-VÉDRINE, J., and J. POCHON-MASSON, 1969: Cytodifférenciation d'une vesicule de sécrétion au cours de la speriogenèse chez Balanus perforatus Brug. (Crustacé Cirripède). Archs. Zool. exp. gén. 110: 595-616.

- Bösenberg, H., 1905: Beiträge zur Kenntnis der Spermatogenese bei den Arachnoiden. Zool. Jb., Abt. f. Anat. 21: 515–570.
- BOISSIN, L. and J.-F. MANIER, 1966a: Spermatogenèse d'Hysterochelifer meridianus (L. Koch) (Arachnide, Pseudoscorpion, Cheliferidae). 1. Étude caryologique. Bull. Soc. zool. Fr. 91: 469–476.
- 1966b: Spermatogenèse d'Hysterochelifer meridianus (L. Koch). II. Étude de l'evolution du chondriome. *Bull. Soc. zool. Fr. 91:* 697–706.
- 1967: Spermatogenèse d'Hysterochelifer meridianus (L. Koch) (Arachnide, Pseudoscorpion, Cheliferidae). Bull. Soc. zool. Fr. 92: 705-712.
- BORRADAILE, L. A., 1907: On the classification of the decapod crustaceans. Ann. Mag. nat. Hist. 19: 457-486.
- BRADKE, D. L., 1963: Special features of spermatogenesis in Lumbricus terrestris. Anat. Rec. 145: 360.
- BRELAND, O. P., G. GASSNER, R. W. REISS, and J. J. BIESELE, 1966: Certain aspects of the centriole adjunct, spermiogenesis and the mature sperm of insects. *Can. J. Genet. Cytol.* 8: 759–773.
- BREUCKER, H., and E. HORSTMANN, 1968: Die Spermatozoen der Zecke Ornithodorus moubata (Murr.). Z. Zellforsch. mikrosk. Anat. 88: 1-22.
- BROWN, G. G., 1966: Ultrastructural studies on Grustacean spermatozoa and fertilization. Doctoral thesis, Univ. of Miami. University microfilms, Inc., Ann Arbor, No. 66 12,996.
- 1970: Some comparative aspects of selected crustacean spermatozoa and crustacean phylogeny. In *Comparative Spermatology* (ed. B. Baccetti): 183–203. Academic Press, N. Y. – London.
- BROWN, G. G., and C. B. METZ, 1967: Ultrastructural studies on the two primitive crustaceans Hutchinsoniella macracantha and Derocheilocaris typicus. Z. Zellforsch. mikr. Anat. 80: 78-92.
- CANTACUZÈNE, A.-M., 1970: L'annexe centriolaire du spermatozoide des insectes. In Comparative Spermatology (ed. B. Baccetti): 553-563. Academic Press, N. Y. - London.
- CHEVALLIER, P., 1970: Le noyau du spermatozoide et son évolution au cours de la spermatogenèse. In *Comparative Spermatology* (ed. B. Baccetti): 499–514. Academic Press, N.Y.– London.
- CLAUS C., 1887: Über Lernaeascus nematoxys, Cls, und die Familie der Philichthyiden. Arb. zool. Inst. Wien 9: 55-59 and 71-75.
- COLWIN, A. L., and L. H. COLWIN, 1961a: Fine structure of the spermatozoon of Hydroides hexagonus (Annelida), with special reference to the acrosomal region. J. biophys. biochem. Cytol. 10: 211-230.
- 1961b: Changes in the spermatozoon during fertilization in Hydroides hexagonus (Annelida). J. biophys. biochem. Cytol. 10: 231-274.
- CUENOT, L., 1952: Phylogenèse de rêgne animal. In *Traité de Zoologi* (ed. P.-P. Grassé), *Tome 1:* 1–33. Masson and Cie, Paris.
- DALLAI, R., 1967: Lo spermatozoo degli arthropodi. I. Anurida maritima (Guérin) et Orchesella villosa (Geoffroy) (Insecta, Collembola). Atti Accad. Fisiocr. Siena, Ser. 13, Vol. 16: 468– 476.
- 1970: The spermatozoon of Arthropoda. XI. Further observations on Collembola. In *Comparative Spermatology* (ed. B. Baccetti) 275–279. Academic Press, N. Y. London.
- DEBAISIEUX, P., 1953: Histologie et histogenèse chez Argulus foliaceus L. (Crustacé, Branchiure). Cellule 55: 245-290.
- DESCHAMPS, M., 1969: Étude cytologique de la spermatogenese chez Lithobius forficatus L. (Myriapode chilopode). Archs. Zool. exp. gén. 110: 349-361.
- DEURS, B. VAN, 1972: On the ultrastructure of the mature spermatozoon of a chaetognath, Spadella cephaloptera. Acta zool. Stockh. 53: 93-104.

- DOUCET, J., 1964: Données nouvelles sur l'anatomie et histologie des Pentastomes. Proc. 1st internat. Congr. Parasitology, Roma, Vol. 1: 621. Pergamon Press, Oxford – London.
- 1965: Contributions a l'étude anatomique, histologique et histochimique des pentastomes (Pentastomida). Doctoral thesis, Univ. Paris. Sér. A, No. 4554. No. d'ordre: 5401. Orstom, Paris.
- FAIN-MAUREL, M. A., 1966: Contribution a l'histologie et la caryologie de quelques isopodes. Spermatogenèse et infrastructure du spermatozoide des oniscoidés et cymothoidés. Annls. Sci. nal., Zool. ser. 12, tome 8: 1–188.
- 1970: Le spermatozoide des isopodes. In *Comparative Spermatology* (ed. B. Baccetti): 221–236. Academic Press, N. Y. London.
- FAVARD, P., and J. ANDRÉ, 1970: The mitochondria of spermatozoa. In Comparative Spermatology (ed. B. Baccetti): 415–429. Academic Press, N. Y. – London.
- FAWCETT, D. W., and K. R. PORTER, 1954: A study of the fine structure of ciliated epithelia. J. Morph. 94: 221-282.
- FAWCETT, D. W. and D. M. PHILLIPS, 1970: Recent observations on the ultrastructure and development of the mammalian spermatozoa. In *Comparative Spermatology* (ed. B. Baccetti): 13–28. Academic Press, N. Y. – London.
- FOLLIOT, R., and P.-L. MAILLET, 1970: Ultrastructure de la spermatogénèse et du spermatozoide de divers insectes homoptères. In *Comparative Spermatology* (ed. B. Baccetti): 289– 300. Academic Press, N. Y. – London.
- FRANZÉN, Å., 1956: On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zool. Bidr. Upps. 31: 355–482.
- 1958: On sperm morphology and acrosome filament formation in some Annelida, Echiuroida and Tunicata. Zool. Bidr. Upps. 33: 1-28.
- 1962: Notes on the morphology and histology of Xironogiton instabila (Moore 1893) (Fam. Branchiobdellidae) with special reference to the muscle cells. *Zool. Bidr. Upps. 35:* 369–383.
- 1970: Phylogenetic aspects of the morphology of spermatozoa and spermiogenesis. In *Comparative Spermatology* (ed. B. Baccetti): 29–46. Academic Press, N. Y. London.
- FRYER, G., 1958: Occurrence of spermatophores in the genus Dolops (Crustacea: Branchiura). *Nature, Lond. 181:* 1011–1012.
- GATENBY, J. B., 1925: A reinvestigation of the spermatogenesis of Peripatus. Q. Jl microsc. Sci. 66: 1-48.
- GATENBY, J. B., and J. DALTON, 1959: Spermiogenesis in Lumbricus hercules. An electron microscope study. J. biophys. biochem. Cytol. 6: 45-52.
- GATENBY, J. B., and T. N. TAMISIAN, 1959: Centriole adjunct, centrioles, mitochondria and ergastoplasma in orthopteran spermatogenesis. An electron microscope study. *Cellule 60:* 103–134.
- GIBBONS, I. R., and A. V. GRIMSTONE, 1960: On flagellar structure in certain flagellates. J. biophys. biochem. Cytol. 7: 697-715.
- GILSON, G., 1885–1888: Étude comparée de la spermatogenèse chez les arthropodes. *Cellule 1* (1885): 7–188; 2 (1886): 81–237; 4 (1888): 5–93.
- GRAFF, L. VON, 1877: Das Genus Myzostoma F. S. Leuckart. Engelmann, Leipzig.
- GRASSÉ, P.-P., O. TUZET, and N. CARASSO, 1965: Ultrastructure d'un spermatozoide aberrant d'un Iule, Spirostreptes castaneus Attems (Myriapode, diplopode), avec des remarques sur les chromosomes. C. r. hebd. Séanc. Acad. Sci. Paris 243: 337-343.
- GROBBEN, K., 1908: Beiträge zur Kenntnis des Baues und der systematischen Stellung der Arguliden. Sber. Akad. Wiss. Wien., Math.-naturw. Klasse 117 (1): 191–233.
- HAFFNER, K. von, 1922: Beiträge zur Kenntnis der Linguatuliden II. Zur Eireifung von Porocephalus armillatus (Wyman). Zool. Anz. 54: 170–177.
- 1924: Beiträge zur Kenntnis der Linguatuliden III. Über den Hoden und die Spermatocystenbildung von Porocephalus moniliformis. Zool. Anz. 58: 285–290.

- HAFFNER, K. von, 1971: Das Pentastomidenproblem (Tagmosis, Metamerie, Organisation, Evolution, systematische Stellung). *Mitt. hamb. zool. Mus. Inst.* 67: 53-107.
- HENDELBERG, J., 1970: On the number and ultrastructure of the flagella of flatworm spermatozoa. In *Comparative Spermatology* (ed. B. Baccetti): 367–374. Academic Press, N. Y. – London.
- HENNIG, W., 1966: Phylogenetic systematics. Univ. of Illinois Press, Urbana Chicago London.
- HETT, M. L., 1934: On a collection of linguatulids (Pentastomida) from Burma, with description of a new subgenus. *Proc. R. Soc. London 1934:* 425-431.
- HEWITT, C. G., 1910: The house fly, Musca domestica, Linnaeus. Sherratt and Hughes, Manchester - London.
- HEYMONS, R., 1926/27: Pentastomida. In *Handbuch der Zoologie* (ed. Kükenthal Krumbach), *Bd. 3, 1:* 69–131. Walter de Gruyter, Berlin – Leipzig.
- 1935: Pentastomida. In Bronn's Klassen und Ordnungen des Tierreichs, 5. Bd Arthropoda, IV. Abt. Arachnoidea, 1. Buch Pentastomida. Akademische Verlagsgesellschaft, Leipzig.
- HOLLANDE, A., and M. FAIN, 1964: Structure et ultrastructure du spermatozoide des Cymothoidés. C. r. hebd. Séanc. Acad. Sci. Paris 258: 5063-5066.
- HORRIDGE, G. A., 1965: Arthropoda: General Anatomy. In Structure and Function of the Nervous System of Invertebrates (ed. Th. H. Bullock and G. A. Horridge), vol. 2: 801-964.
 W. H. Freeman, San Francisco London.
- HORSTMANN, E., 1968: Die Spermatozoen von Geophilus linearis Koch (Chilopoda). Z. Zellforsch. mikr. Anat. 89: 410-429.
- 1970: The acrosome complex of the diplopode Spirostreptes sp. In *Comparative Spermatology* (ed. B. Baccetti): 255–262. Academic Press, N. Y. London.
- KAESTNER, A., 1954/1965: Lehrbuch der speziellen Zoologie, Bd. 1:1. 1st ed. 1954, 2nd. ed. 1965. Gustav Fischer, Jena.
- LANGRETH, S. G., 1969: Spermiogenesis in Cancer crabs. J. Cell Biol. 43: 575-603.
- LEGENDRE, R., 1967: Morphologie, histologie er développement des pentastomides. Fortschr. Zool. 18: 337-349.
- LEUCKART, R., 1860: Bau und Entwicklungsgeschichte der Pentastomen nach Untersuchungen besonders von Pent. taenioides und P. denticulatum. C. F. Winter, Leipzig – Heidelberg.
- LEVDIG, F., 1850: Über Argulus foliaceus. Ein Beitrag zur Anatomie, Histologie und Entwicklungsgeschichte dieses Tieres. Z. wiss. Zool. 2: 323–349.
- MARTIN, F. M., 1932: On the morphology and classification of Argulus (Crustacea). Proc. zool. Soc. Lond. 1932: 771-806.
- MATTEI, X., 1969: Contribution à l'etude de la spermiogenèse et des spermatozoides de poissons par les methodes de la microscopie électronique. Doctoral thesis, Univ. Montpellier, Faculté Sci. C. N. R. S., no. A. O. 3263.
- Spermiogénèse comparée des poissons. In *Comparative Spermatology* (ed. B. Baccetti): 57–69. Academic Press, N. Y. London.
- MONTGOMERY, T. H., 1900: The spermatogenesis of Peripatus (Peripatopsis) balfouri up to the formation of the spermatid. Zool. Jb., Abt. fur Anatomie 40: 277-368.
- Moses, M. J., 1961: Spermiogenesis in the crayfish (Procambarus clarkii) II. Description of stages. J. biophys. biochem. Cytol. 10: 301-333.
- MUNN, E. A. and H. BARNES, 1970: The fine structure of the spermatozoa of some cirripeds. J. exp. marine Biol. Ecol. 4: 261–286.

Nørrevang, A., 1972: Oogenesis in Pentastomids. Acta zool., Stockh. 53. In press.

- Nørrevang, A., and K. G. WINGSTRAND, 1970: On the occurrence and structure of choanocytelike cells in some echinoderms. *Acta zool. Stockholm 51:* 249–270.
- OSCHE, G., 1959: »Arthropodencharaktere« bei einem Pentastomiden-embryo (Reighardia sternae). Zool. Anz. 163: 169–178.

- OSCHE, G., 1963: Die systematische Stellung und Phylogenie der Pentastomida. Embryologische und vergleichend-anatomische Studien. Z. Morph. Okol. Tiere 52: 487–596.
- PALADE, G. E., 1952: A study of fixation for electron microscopy. J. exp. Med. 95: 285-298.
- PASTISSON, C., 1966: Anatomie ultrastructurale du spermatozoide du sangsue, Hirudo medicinalis L. Annls Univ. (Reims) et Arers 4: 67-75.
- PEDERSEN, H., 1970: Ultrastructure of the ejaculated human sperm. In Comparative spermatology (ed. B. Baccetti): 133-142. Academic Press, N. Y. - London.
- PHILLIPS, D. M., 1970a: Insect sperm: their structure and morphogenesis. J. Cell Biol. 44: 243-277.
- 1970b: Insect flagellar tubule patterns theme and variations. In *Comparative spermatology* (ed. B. Baccetti): 263–273. Academic Press, N. Y. London.
- PHILPOTT, D. E., and W. N. SHAW, 1959: An electron microscopic study of the sperm of Limulus polyphemus. *Biol. Bull. mar. biol. Lab.*, *Woods Hole*, 117: 423-424.
- Pochon-Masson, J., 1969: Infrastructure de spermatozoide de Palaemon elegans (De Man) (Crustacé décapode). Archs Zool. exp. gén. 110: 363-372.
- POCHON-MASSON, J., J. BOCQUET-VÉDRINE, and Y. TURQUIER, 1970: Contribution à l'étude du spermatozoide des crustacés cirripèdes. In *Comparative Spermatology* (ed. B. Baccetti): 205-219. Academic Press, N. Y. – London.
- POTSWALD, H. E., 1967: An electron microscope study of spermiogenesis in Spirorbis (Laeospira) mörchi Levinsen (Polychaeta). Z. Zellforsch. mikrosk. Anat. 83: 231–298.
- PRATT, S., 1970: Formation and differentiation of the Nebenkern in spermatids of an hemipteran insect, Murgantia histrionica. In *Comparative Spermatology* (ed. B. Baccetti): 301–310. Academic Press, N. Y. – London.
- REGER, J. F., 1961: The fine structure of spermatids from the tick, Amblyomma dissimili. J. Ultrastruct. Res. 5: 584-599.
- 1962: A fine-structure study on spermiogenesis in the tick Amblyomma dissimili, with special reference to the development of motile processes. J. Ultrastr. Res. 7: 550–565.
- 1963: Spermiogenesis in the tick, Amblyomma dissimili, as revealed by electron microscopy. J. Ultrastr. Res. 11: 181–192.
- 1964a: A study on the fine structure of developing spermatozoa from the isopod, Asellus militaris (Hay). J. Microscopie 3: 559–572.
- 1964b: The fine structure of spermatozoa from the isopod Asellus militaris (Hay). J. Ultrastr. Res. 11: 181–192.
- 1966: A comparative study on the fine structure of developing spermatozoa in the isopod, Oniscus asellus, and the amphipod, Orchestia sp. Z. Zellforsch. mikr. Anat. 75: 579– 590.
- 1967: A study on the fine structure of developing spermatozoa from the oligochaete, Enchytraeus albidus. Z. Zellforsch. mikr. Anat. 82: 257–269.
- 1969: A fine structure study on spermiogenesis in the Arachnida, Leiobunum sp. (Phalangida: Harvestmen). J. Ultrastr. Res. 28: 422–434.
- 1970a: Some aspects of the fine structure of filiform spermatozoa (Ostracod, Cypridopsis sp.) lacking tubule sub-structure. In *Comparative Spermatology* (ed. B. Baccetti): 237–245. Academic Press, N. Y. London.
- 1970b: Spermiogenesis in the spider, Pisaurina sp.: A fine structure study. J. Morph. 130: 421–434.
- REGER, J. F., and D. P. COOPER, 1968: Studies on the fine structure of spermatids and spermatozoa from the milliped Polydesmus sp. J. Ultrastr. Res. 23: 60-70.
- RETZIUS, G., 1909: Die Spermien der Crustaceen. In Biologische Untersuchungen von G. Retzius, N. F., 14: 1–54. Gustav Fischer, Jena.
- ROBERTIS, E. DE, and H. F. RAFFO, 1957: Submicroscopic organization of the mitochondrial body and other cytoplasmic structures in the insect testis. *Expl. Cell Res.* 12: 66–79.

- ROSATI, F., B. BACCETTI, and R. DALLAI, 1970: The spermatozoon of Arthropoda. X. Araneids and the lowest myriapods. In *Comparative Spermatology* (ed. B. Baccetti): 247–254. Academic Press, N. Y. – London.
- SELF, J. T., 1969: Biological relationships of the Pentastomida; A biblography on the Pentastomida. *Experiment. Parasitol.* 24: 63–119.
- SILVERIA, M., and K. R. PORTER, 1964: The spermatozoids of flatworms and their microtubular system. Protoplasma 59: 240-265.
- SOKOLOW, S., 1913: Untersuchungen über die Spermatogenese bei den Arachniden. I. Über die Spermatogenese der Skorpione. Arch. Zellforsch. 9: 399–432.
- SOTELO, J. R., and O. TRUJILLO-CENÓZ, 1958: Electron microscope study of the kinetic apparatus in animal sperm cells. Z. Zellforsch. mikr. Anat. 48: 565–601.
- TAKASHIMA, R., and Y. TAKASHIMA, 1963: Electron microscope studies on the fine structure of Nereis spermatozoa before and after the acrosomal reaction. *Tokushima J. exp. Med.* 10: 117–123.
- THOMPSON, T. E., and M. S. BLUM, 1967: Structure and behaviour of spermatozoa of the fire ant Solenopsis saevissima (Hymenoptera: Formicidae). Ann. ent. soc. Am., 60: 632-642.
- TURQUIER, Y., and J. POCHON-MASSON, 1969: L'infrastructure du spermatozoide de Trypetesa (=Alcippe) nassaroides Turquier (Cirripede acrothoracique). Archs Zool. exp. gén. 110: 453-470.
- TUZET, O., 1938: Sur la spermatogénèse de Buthus occitanus (Amor.). Archs Zool. exp. gén. 80: 335-351.
- VANDEL, A., 1949: Généralités Composition de l'embranchement. In Traité de Zoologie (ed. P.-P. Grassé), VI: 79–158. Masson and Cie, Paris.
- WEBER, H., 1949: Grundriss der Insektenkunde. Gustav Fischer, Jena, 1949 and 1954.
- WERNER, G., 1964: Untersuchungen über die Spermatogenese beim Silberfischchen, Lepisma saccharina L. Z. Zellforsch. mikr. Anal. 63: 880-912.
- 1965: Untersuchungen über die Spermatogenese beim Sandläufer, Cicindela campestris L. Z. Zellforsch. mikr. Anat. 66: 255–275.
- 1970: On the development and structure of the neck in urodele sperm. In *Comparative Spermatology* (ed. B. Baccetti): 85-91. Academic Press, N. Y. London.
- YASUZUMI, G., 1960: Spermatogenesis in animals as revealed by electron microscopy. VII. Spermatid differentiation in the crab, Eriocheir japonicus. J. biophys. biochem. Cytol. 7: 73–78.
- YASUZUMI, G., G. I. KAYE, G. D. PAPPAS, H. YAMAMOTO, and I. TSUBO, 1961: Nuclear and cytoplasmic differentiation in the developing sperm of the crayfish, Cambaroides japonicus. Z. Zellforsch. mikr. Anat. 53: 141–158.
- YASUZUMI, G., H. TANAKA, and O. TEZUKA, 1960: Spermatogenesis in animals as revealed by electron microscopy. VIII. Relation between the nutritive cells and the developing spermatids in a pond snail, Cipangopaludina malleata Reeve. J. biophys. biochem. Cytol. 7: 499–504.

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- Fig. 1. Raillietiella ?hemidactyli Hett. Anterior end of ♀ seen from the ventral side. Arrows indicate mouth opening and anterior hooks. Note blunt posterior hooks and tapering anterior end. Scanning microscope picture of specimen from *Caloles versicolor*, fixed in formalin and post-fixed in 1% Osmic over night. Dried with benzene as described in Norrevang and Wingstrand 1970.
- Fig. 2. Same specimen as Fig. 1, seen from the anterior end to show dorso-lateral papillae (dl), frontal papillae (arrow) and mouth opening (arrow). The frontal papillae are in fact double.
- Fig. 3. *Raillietiella*. Light microscopice cross section of testicle. Small, still attached spermatocysts bulge out from the wall at yc, the lumen is filled with free spermatocysts in different stages of development. mc indicates cyst with nearly mature sperm. No degenerative changes.





- Fig. 4. Raillietiella. Thick epon section (2 μ, stained with toluidin blue) of testicle with degenerate features. The lumen is filled with abnormal spermatozoa and debris, some cysts (dc) show abnormal development. A few normal spermatocysts: young, still attached ones at yc, two cysts with stage 4 spermatids at s 4, and one with stage 1 spermatids at sl.
- Fig. 5. Argulus. Transverse section of one testicle (2 μ epon section, stained with toluidin blue). Median plane left. The germinal epithelium is the thin plate above sp, down along median and lateral walls are spermatocytes (spc) and spermatids (spt). Ventrally the large Sertoli cells (sc) are attached, carrying large tufts of advanced spermatids. sp = mature sperm in lumen.

PLATE 2



- Fig. 6. Raillietiella. Part of testicular wall. The basement membrane is black, gc = germinal cell, overgrown by the neighbouring vegetative cells. gs = growing spermatocyst, containing spermatogonia with dark plasm and covered by plasmatic extensions from the vegetative cells.
- Fig. 7. *Raillietiella*. Cross section of free spermatocyst, containing 128 spermatids of stage 6. Note the plasmatic cyst wall.
- Fig. 8. *Raillietiella*. Tangential section of spermatocyst ready to be pinched off from the testicular wall. Four distinct spermatocytes are seen, surrounded by plasm which is continuous with that of vegetative cells at the base. in = large inclusion in vegetative cell. pb = plasmatic balls with cellular debris in the lumen. bm = basement membrane.
- Fig. 9. *Argulus.* Sertoli cells. Three large nuclei are seen. The lower part of the picture shows stalk-like basal parts of the cells, the upper part of the picture shows distal ends with many pseudoacrosomes sticking in the plasm (dark spots). Compare Plate 20: 102.



EM pictures of osmium-fixed, intact spermatozoa, spread on coated grids and dried.

- Fig. 10. Raillietiella. Entire spermatozoon. Transition from body to pseudoacrosome (arrow) is sudden and distinct.
- Fig. 11. Argulus. Transition from body to pseudoacrosome (arrow) is marked by a rather slow decrease in diameter.
- Fig. 12. Raillietiella. Top of pseudoacrosome with granulosome (g). The dorsal rod ends at the arrow.
- Fig. 13. *Argulus.* Top of pseudoacrosome. There is no granulosome. The small granule seen in this picture is not present in other specimens. Dorsal rod ends at the arrow.
- Fig. 14. Raillietiella. Posterior end of spermatozoon. Compare Plate 7.
- Fig. 15. Argulus. Posterior end of spermatozoon. Compare Plate 7.

b = body of spermatozoon, dr = dorsal ribbon, g = granulosome, lp = lump of vesicular plasm near posterior end in *Raillietiella*, n = nucleus, pa = pseudoacrosome.





Fig. 16. Raillietiella. Cross sections of the body and of a pseudoacrosome (pa).

Fig. 17. Argulus. Cross sections of several spermatozoan bodies and of one posterior end (pe).

af = remnant of acrosome filament in the nuclear membranes of Argulus, always asymmetrical, ax = axonemal space, cut just behind the posterior ends of the filaments in Argulus, dr = dorsal ribbon, er = smooth endoplasmic reticulum, ir = intermitochondrial rods in Argulus, is = inner membranous sac of dorsal ribbon, attached to doublets 3 and 8 in Argulus, lc = light core of dorsal ribbon, lv = light rods in ventral ribbon of Raillietiella, m = mitochondria, n = nucleus, om = oblique membrane between axonemal doublet 1 and dorsal ribbon, pa = pseudoacrosome, pe = posterior end of body, pc = light core of dorsal pseudoacrosomal rod in Raillietiella, ps = membranous sac of pseudoacrosome, sm = dark sheath covering lateral mitochondria, vr = ventral ribbon.



Fig. 18. Raillietiella. Seminal vesicle. Median section of body.

- Fig. 19. Argulus. Receptaculum seminis. Median section of body.
- Fig. 20. *Raillietiella*. Seminal vesicle. Median section of transitional region between body and pseudoacrosome. For comparison with *Argulus* see Plate 22: 111, which shows an almost mature spermatid.

cf = central filaments of axonema, dd = dorsal doublets of axonema and centriole, dm = dorsal extension of pseudoacrosomal granular matter including filaments 9, 1, and 2 of centriole, dp = dorsal rod of pseudoacrosome, <math>dr = dorsal ribbon, is = inner membranous sac of dorsal ribbon, lc = light core of dorsal ribbon, m = mitochondria, n = nucleus, vd = ventral doublets of axonema and centriole, vm = ventral extension of pseudoacrosomal granular matter, including ventral filaments of centriole, vr = ventral ribbon, vp = ventral rod of pseudoacrosome.





The acrossomes and the posterior ends of the spermatozoa. Magnification is the same in Figs. 21-28 and 31.

Fig. 21. Raillietiella. Cross section of transitional region between body and pseudoacrosome.

Fig. 22. Raillietiella. Cross section a little in front of the level of Fig. 21.

Fig. 23. Roillietiella. Cross section of basal part of pseudoacrosome.

Fig. 24. Raillietiella. Cross section of terminal region of pseudoacrosome.

Fig. 25. Argulus. Cross section of transitional region between body and pseudoacrosome.

Fig. 26. Argulus. Cross section a little in front of the level of Fig. 25.

Fig. 27. Argulus. Cross section of basal part of the pseudoacrosome.

Fig. 28. Argulus. Cross section of the terminal part of pseudoacrosomes.

Fig. 29. Raillietiella. Median section of posterior end of body.

Fig. 30. Argulus. Median section of posterior end of body.

Fig. 31. Argulus. Cross section of posterior end, at the level of the letters dr and n in Fig. 30.

ax = axonema, cl = central lumen of pseudoacrosome in Argulus, dl = dorsal lumen of pseudoacrosome in Argulus, dm = dorsal extension of pseudoacrosomal granular matter, including doublets 9, 1 and 2 in both species, <math>dr = dorsal ribbon, em = end of mitochondria, en = end of nucleus, lp = lump of vesicular plasm near posterior end in Raillietiella, m = mitochondria, n = nucleus, vm = ventral extension of the pseudo-acrosomal granular matter, including ventral centriole doublets: nos. 3–8 in Raillietiella, nos. 5 and 6 in Argulus.





Development of the centriole complex.

- Fig. 32. *Raillietiella*. Cyst in 2nd meiotic division. Chromosomes (ch) are visible in one cell, a centriole (black arrow) in the other. The centriole with two dark fibers is enlarged in the inset.
- Fig. 33. Raillietiella. Cross section of centriole of early spermatid 1.
- Fig. 34. *Raillietiella*. Cross section of centriole of spermatid 2. With three large dark fibers under the membranous sac (os).
- Fig. 35. *Argulus.* Two centrioles, each with two dark fibers and a flat sac of endoplasmic reticulum, from a spermatocyte 2.
- Fig. 36. Argulus. Spermatocyte 2 with two centrioles, one of which (dark short arrow) is shown enlarged in the inset. The darkened flat sac of endoplasmic reticulum and the two large dark fibers are distinct.
- Fig. 37. Argulus. Spermatid 2. Cross section of centriole with membranous sac (os) and three large dark fibers.
- Fig. 38. *Raillietiella*. Two centrioles from spermatocyte 1, one with a slight condensation at the end, suggestive of an apical membrane.
- Fig. 39. *Raillietiella*. 2nd meiotic cell. Centriole with fairly distinct membrane-like condensations across the edges of the upper end.
- Fig. 40. Raillietiella. Spermatid stage 2. Apical membrane and granulosome rather distinct.
- Fig. 41. *Raillietiella*. Late spermatid 2. Distinct granulosome (g) attached to nucleus (n), apical membrane (am) and membranous sac (os) fully developed, the latter covering dark fibers.
- Fig. 42. *Argulus*. Spermatid 3. Cross section of centriole. The outer membranous sac and three dark fibers distinct.
- Fig. 43. Argulus. Similar stage and section as Fig. 42.
- Fig. 44. Argulus. Spermatid, early stage 2. Membranous sac and its connection with the smooth endoplasmic reticulum distinct.
- Fig. 45. Argulus. Late spermatid 2. Granulosome and apical membrane distinct.

am = apical membrane, an = annulus-like thickening of cell membrane in the bottom of the flagellar pit, ch = chromosomes, g = granulosome, m = mitochondria, n = nucleus, os = flat membranous sac, the prospective outer sac of the dorsal ribbon.



Early development of mitochondria.

- Fig. 46. Raillietiella. Spermatocyte 1 with long, tubular mitochondria.
- Fig. 47. *Raillietiella*. Spermatid 1–2. Picture suggestive of fusion of motochondria: the inner membranes of the presumed partners are separate, the outer membrane is common.
- Fig. 48. Raillietiella. Spermatid 1. The group of spherical mitochondria.
- Fig. 49. Argulus. Spermatid 1. The group of mitochondria before they fuse to three.
- Fig. 50. *Raillietiella*. Spermatid 2. With the three spherical mitochondria. Dark, probably cementing substance is seen in the interspaces between the mitochondria.
- Fig. 51. *Argulus.* Spermatid 2. The three spherical mitochondria appear almost identical to those of *Raillie-tiella* in Fig. 50.

Continued in Plate 10.



- Fig. 52. *Raillietiella*. Spermatid 3. The three mitochondria have formed a common body, the "Nebenkern", and the axonema, covered by a dorsal ribbon, is in contact with all three.
- Fig. 53. Argulus. Spermatid 3. The contour of the mitochondria in the "Nebenkern" appears more irregular than in Raillietiella, but this may be an artifact. The centriole, with outer membranous sac and three dark fibers, is in contact with all three mitochondria.
- Fig. 54. *Raillietiella*. Early spermatid 2. The three mitochondria, the centriole and the nucleus have not yet established the contact typical of later stages. The centriole is attached to the bottom of a very deep flagellar pit.
- Fig. 55. Argulus. Spermatid 2. Still no definite contact between nucleus, mitochondria and centriole. The latter has developed an axonema.
- ce = centriole, m = mitochondria, n = nucleus.



Development of the flagellum in Raillietiella.

- Fig. 56. *Raillietiella*. Spermatid 1. Centriole and first flagellar rudiment without axonema. The white arrow shows a cross section of another flagellar rudiment, in which no axonema is present.
- Fig. 57. *Raillietiella*. Spermatid 2. The granulosome is attached to the nucleus, and the centriole has developed an axonema in the flagellum.
- Fig. 58. *Raillietiella*. Spermatid 4 or 5. Part of the axonema is included in the cell body proper, and the free flagellum remains short. The posterior tongues of the mitochondria (m) and the dorsal ribbon (dr) grow posteriorly so they remain in contact with the annulus-like bottom of the flagellar pit (an).
- Fig. 59. *Raillietiella*. Late spermatid 2. The relations of flagellum, flagellar pit, centriole, apical membrane, granulosome, mitochondria (m) and nucleus are shown. Compare text figures 3 and 11A for explanations.

an = annulus-like thickening of cell membrane in the bottom of the flagellar pit, dr = dorsal ribbon, m = mitochondria, n = nucleus, np = nuclear pores.



Dislocation of the centriole complex.

- Fig. 60. *Raillietiella*. Early spermatid 4. The point of contact of the centriole complex has moved over to the side of the nucleus, and the apical membrane (am) is detached from the end of the centriole (ce). Inset shows magnified centriolar region.
- Fig. 61. *Raillietiella*. Late spermatid 4. Dislocation of the centriolar complex to the anterior end of the nucleus nearly completed. Inset shows magnified centriolar region.
- Fig. 62. Argulus. Early spermatid 4. Similar to corresponding stage of *Raillietiella* (Fig. 60) but the PGM tends to form a long rod (pm) in front of the aperture of the centriole.
- Fig. 63. Argulus. Spermatid 4, a little more advanced than fig. 62.

am = apical membrane, ce = centriole, dr = dorsal ribbon, g = granulosome, m = mitochondria, n = nucleus, nk = mitochondrial "Nebenkern", pm = pseudoacrosomal granular matter (PGM), vm = less compact granular matter in front of mitochondria, later refound as "ventral extension of PGM including the ventral filaments of the centriole" (See text fig. 11 and 12).



Development of anterior end in spermatid 5.

- Fig. 64. *Raillietiella*. Median section of spermatid 5, showing the parallel development of anterior nuclear tongue (n), anterior mitochondrial tongues (m), centriole (ce) and axonema (ax). The pseudoacrosome is still little advanced.
- Fig. 65. *Raillietiella*. Spermatid 5, somewhat more advanced. The pseudoacrosome is growing out, so the apical membrane (am) and granulosome (g) are distinctly separated from the end of nucleus (en) and mitochondria (em). The cross section (cs) shows nucleus, the three anterior mitochondrial rods, axonema and dorsal ribbon.
- Fig. 66. *Argulus.* Spermatid 5. The pseudoacrosome is far developed (pa), but no anterior nuclear tongue is formed. Instead a true acrosome (av) and acrosome filament (af) is present.

af = acrosome filament, am = apical membrane, av = acrosome vesicle, ax = axonema, ce = centriole, cs = cross section of spermatid, dr = dorsal ribbon, em = end of mitochondria, en = end of nucleus, g = granulosome, m = mitochondria, n = nucleus, pa = pseudoacrosome.



Development of the true acrosome in Argulus.

- Fig. 67. Argulus. Spermatid 3-4. Anterior pole of nucleus (n) and the large Golgi complex (go). A dense, post-acrosomal granule covered by a flat acrosomal vesicle is attached to the nuclear membrane (arrow).
- Fig. 68. *Argulus*. Early spermatid 4. Large Golgi complexes (go) surround the developing acrosome, which is attached to the nuclear membrane.
- Fig. 69. *Argulus*. Early spermatid 4. Magnification of acrosome vesicle (av) and postacrosomal granule (gr) at the same stage of development as in Fig. 68.
- Fig. 70. *Argulus.* Spermatid 4. The post-acrosomal granule has grown out to form an acrosome filament (af) inside a tube formed by invagination of nuclear membranes.
- Fig. 71. *Argulus*. Spermatid 6–7. Slightly oblique median section of the anterior end of nucleus (n), showing acrosome vesicle (av) and acrosome filament (af) in relation to the empty anterior end of the median mitochondrion (m), the axonema (ax) and the dorsal ribbon (dr). Compare Plate 13: 66 and text figure 18.

af = acrosome filament, av = acrosome vesicle, ax = axonema, dr = dorsal ribbon, gr = postacrosomal granule, m = mitochondria, n = nucleus.



Transformations of the "Nebenkern" in stages 4 and 5.

- Fig. 72. *Raillietiella*. Late stage 4. The anterior tongues of the mitochondria (at) are distinct along the surface of the nucleus.
- Fig. 73. *Raillietiella*. Late stage 4. The posterior tongues (pt) of the mitochondria along the axonema are distinct.
- Fig. 74. *Argulus*. Late stage 4. Anterior tongues of the mitochondria are thicker than in *Raillietiella* and less sharply demarcated from the "Nebenkern" (nk).
- Fig. 75. *Argulus.* Spermatid 5 with a fairly long pseudoacrosome (pa). The nucleus extends also behind the "Nebenkern" (nk) with a posterior nuclear tongue (pn).

at = anterior tongues of mitochondria, n = nucleus, nk = mitochondrial "Nebenkern", pa = pseudoacrosome, pn = posterior nuclear tongue, pt = posterior mitochondrial tongues.

Plate 15



Development of the body, particularly dorsal and ventral ribbons.

- Fig. 76. Raillietiella. Spermatid 4–5. Cross section behind the "Nebenkern". The granular matter (cr) of dorsal ribbon is located between membranous sacs (os and is) formed by the endoplasmic reticulum. The dark outer filaments 4–7 (df) are believed to be included in the ventral ribbon in later stages.
- Fig. 77. *Argulus*. Spermatid 5. Cross section corresponding to that in Fig. 76, but no outer dark filaments are present.
- Fig. 78. *Argulus.* Cross section through mitochondrial "Nebenkern" (nk) in spermatid 4. The location of the granular matter between the inner and outer sacs of the dorsal ribbon is distinct.
- Fig. 79. *Argulus.* Late spermatid 5. The acrosome filament in the tube formed by the nuclear membranes is visible within the anterior nuclear tongue (nt).
- Fig. 80. *Raillietiella*. Spermatid 6. The two sacs of the dorsal ribbon are still continous with the endoplasmic reticulum (os and is). The ventral ribbon (vr) is being formed and has a membrane-like contour. nuclear condensation has lead to the formation of large chromatin clumps (nc).
- Fig. 81. *Argulus.* Spermatid 6–7. Section and stage corresponding to those in Fig. 80. Section goes through the anterior end of the body, where the median mitochondrion lacks inner membrane. Nuclear condensation has started as seen by the chromatin lamellae (nc) attached to the tube of the acrosome filament (af). Ventral ribbon is little developed: a membrane-like contour is seen below the ventral doublets of the axonema (vr).

af = acrosome filament, at = anterior mitochondrial tongues, er = smooth endoplasmic reticulum, df = dark outer fibres of axonema, is = inner membranous sac of dorsal ribbon, im = intermitochondrial (cementing?) matter, n = nucleus, nc = cromatin condensations in nucleus, nk = mitochondrial "Nebenkern", nm = row of dark bodies, probable precursor of the prospective secondary nuclear membranes, os = outer membranous sac of dorsal ribbon, pt = posterior tongues of mitochondria, vr = ventral ribbon.



Late development of the body in stages 6–7, particularly nuclear condensation.

- Fig. 82. *Raillietiella*. Spermatid 6. Median section of body. Large chromatin clumps (nc) are formed in the nucleus.
- Fig. 83. *Raillietiella*. Spermatid 7. Cross section of nearly mature spermatid. The chromatin clumps in the nucleus have begun to fuse (nc). Numerous microtubules surround dorsal ribbon and mitochondrial rods.
- Fig. 84. *Argulus*. Spermatid 6–7. Ventral ribbon (vr) contains two dark dots, probably corresponding to outer dark fibers 5 and 6. Nucleus asymmetrical, with growing chromatin rod (nc) along axonemal filament tube (af), and indications of a secondary membrane (sm).
- Fig. 85. *Argulus.* Spermatid 7. Sacs of the dorsal ribbon have lost connection with endoplasmic reticulum. The ventral ribbon has two dark centres in the intermitochondrial space. The chromatin rod now has distinct dorsal and ventral walls (nc).
- Fig. 86. *Argulus*. Spermatid 7. Asymmetrical, fully condensed nucleus. Tube of acrosome filament collapsed and probably present between primary and secondary nuclear membranes (af). Large lateral organelles (lo). Oblique membrane of doublet 1(om) is formed. Intermitochondrial rods still closely related to ventral ribbon (ir).
- Fig. 87. *Argulus.* Late spermatid 7. Cross section far anteriorly, where the dorsal ribbon is very high. Remnant of lateral organelle (lo). The intermitochondrial rods (ir) have migrated down in the interspaces between the mitochondria.

af = acrosomal filament or its tube, ax = axonema, dr = dorsal ribbon, er = smooth endoplasmic reticulum, ir = intermitochondrial rods, is = inner membranous sac of dorsal ribbon, lo = lateral organelles, m = mitochondria, mc = mitochondrial cristae, nc = nucleus, particularly chromatin condensations, om = oblique membrane between axonemal doublet 1 and dorsal ribbon, os = outer membranous sac of dorsal ribbon, sm = probable formation of secondary nuclear membranes, vr = ventral ribbon.



- Fig. 88. *Argulus.* Spermatid 7. Cross section of body showing lateral organelles (lo), the one on the same side as the nucleus little developed, and the row of flat vesicles (rv). The nucleus is still strongly asymmetrical.
- Fig. 89. *Argulus*. Spermatid 7. Paramedian section through the row of flat vesicles (rv). The half-circular thickenings of the ventral ribbon (vr) are distinct.
- Fig. 90. Argulus. Spermatid 7, somewhat younger than the one in Fig. 89. The ventral ribbon consists of separate half-rings (vr).
- Fig. 91. *Raillietiella*. Spermatid, late stage 4. Abnormal specimen with two centrioles (ce) and axonemata. Dorsal ribbon (dr), apical membrane (am), pseudoacrosomal granular matter (pm) developed in connection with each centriole.
- Fig. 92. *Argulus.* Spermatid 5. The figure shows that the flat sac of smooth endoplasmic reticulum, which forms the outer sac of the dorsal ribbon (os), is closely related to the Golgi apparatus (go). Many vesicles fill the space between typical Golgi lamellae and the sac, connected with the ribbon.

am = apical membrane, ax = axonema, ce = centriole, dr = dorsal ribbon, er = smooth endoplasmic reticulum, go = Golgi apparatus, is = inner membranous sac of dorsal ribbon, <math>lo = lateral organnelles, m = mitochondria, n = nucleus, os = outer membranous sac of dorsal ribbon, <math>pm = pseudoacrosomal granular matter, rv = row of flat vesicles, vr = ventral ribbon, w = wing-like posterior continuation of ventral sheath of the pseudoacrosome, on each side of the centriole.


Cross section of early pseudoacrosome rudiment in Argulus. Compare text figure 16.

- Fig. 93. *Argulus.* Spermatid 4–5. Cross section of posterior part of centriole (ce), showing the three anterior mitochondrial tongues, the nucleus, and the two membranous sacs of the dorsal ribbon with granular substance (cr) between.
- Fig. 94. *Argulus.* Spermatid 4–5. Cross section through the anterior, laterally compressed end of the centriole (ce), which is covered on each side by the wing-like posterior extensions of the ventral sheath of the pseudoacrosome (w). The median mitochondrion lacks inner membrane in this terminal region. The sac forming the wings is continous with the inner sac of the dorsal ribbon (is).
- Fig. 95. Argulus. Spermatid 4–5. Cross section in front of the mitochondria, through pseudoacrosomal granular matter which forms horizontal lamellae (la) and a more diffuse cloud (vm) down to the wall of the nucleus (n). The lateral plates (w) cover the lamellae from the sides. No inner sac of the dorsal ribbon is present at this level. The sacs forming the lateral wings (w) fuse with the outer sac of the dorsal ribbon (thick arrow).
- Fig. 96. *Argulus.* Spermatid 4–5. Cross section just behind the apical membrane. The thick arrow indicates continuity of the outer sac of the dorsal ribbon with the sac covering the lateral wings, to form the common membranous sac of the pseudoacrosome (ps).
- Fig. 97. *Argulus*. Spermatid 4–5. Cross section through the posterior part of the apical membrane (am), showing the undivided state of the dark pseudoacrosomal matter (pm) at this level.
- Fig. 98. Argulus. Spermatid 4–5. Cross section near the top of the pseudoacrosome. The lateral plates (w) are almost continuous with the apical membrane, which later forms the ventral sheath.

am = apical membrane, ce = centriole, cr = granular core of dorsal ribbon, g = granulosome, is = inner membranous sac of dorsal ribbon, la = lamellae formed by the PGM, m = mitochondria, n = nucleus, os = outer membranous sac of the dorsal ribbon, pm = pseudoacrosomal granular matter (PGM), ps = pseudo-acrosomal membranous sac, vm = ventral, less condensed position of PGM, in contact with nucleus, w = lateral plates; later, when the ventral sheath has been formed, they occur as wing-like extensions of its posterior end.



Early development of the pseudoacrosome.

- Fig. 99. *Raillietiella*. Spermatid 5–6. Cross section through base of early pseudoacrosome, with a large ventral sheath (vs), a small dorsal sheath (ds), and PGM partly shaped as a tube (pm).
- Fig. 100. *Raillietiella*. Spermatid 5–6. Cross section near end of young pseudoacrosome with tube-shaped PGM.
- Fig. 101. *Raillietiella*. Spermatid 6. Cross section near end of pseudoacrosome. Somewhat more advanced than in Fig. 100. The PGM forms a median lemella (pm), attached to the dorsal sheath.
- Fig. 102. Argulus. Spermatid, late stage 5. Cross section of pseudoacrosome and Sertoli cell. Dorsal and ventral sheaths are like those of *Raillietiella* and are surrounded by a membranous sac (ps). The spermatid is separated from the Sertoli cell by a narrow intercellular space (is). The Sertoli cell has large mitoehondria (sm) and granular endoplasmic reticulum (gr).
- Fig. 103. Argulus. Spermatid, late stage 5. More advanced than in Fig. 102. Distinct horizontal lamellae (la) are formed within the ventral sheath, but a median lamella (ml), attached to the dorsal sheath (ds), is very like the one in *Raillietiella*.
- Fig. 104. *Raillietiella*. Spermatid, late stage 5. Horizontal section through a very early pseudoacrosome, protruding very little above the ends of the mitochondria (m). The lateral plates or wing-like extensions of the ventral sheath (w) are distinct.
- Fig. 105. Argulus. Spermatid stage 4. Median section of the rudiment of the pseudoacrosome, showing the membranous sac covering the apical membrane (am), and the plug-like development of the PGM (pm), with a tendency to form lamellae to the right.

am = apical membrane, ax = axonema, ds = dorsal sheath, g = granulosome, gr = endoplasmic reticulum with ribosomes in the Sertoli cell, is = intercellular space between spermatid and Sertoli cell, la = horizontal lamellae of PGM, m = mitochondria, ml = median lamella of PGM, n = nucleus, nk = mitochondrial "Nebenkern", pm = pseudoacrosomal granular matter (PGM), ps = membranous sac around pseudoacrosome, sm = mitochondria of Sertoli cell, vm = ventral, less compact portion of PGM, in contact with the nucleus, vs = ventral sheath of pseudoacrosome, w = lateral plates, later posterior wing-like extensions of the ventral sheath of the pseudoacrosome.



Plate 21

Final development of the pseudoacrosomes.

- Fig. 106. *Raillietiella*. Spermatid 6. Cross sections of pseudoacrosomes and of a single granulosome (g). The ventral and dorsal sheaths (vs and ds) begin to fill with PGM. A distinct membranous sac (ps) surrounds the entire pseudoacrosome.
- Fig. 107. *Raillietiella*. Spermatid 7. Cross sections of pseudoacrosomes, in which dorsal and ventral rods (dp and vp) have been formed by filling of dorsal and ventral sheaths with PGM. A cleft begins to appear between the rods. The membranous sac around the pseudoacrosomes is distinct and is still connected with vesicles of endoplasmic reticulum in the plasm (thick arrow). Numerous micro-tubulus surround the growing pseudoacrosome.
- Fig. 108. Argulus. Spermatid, late stage 6. Cross section of pseudoacrosomal rudiment, still almost symmetrical. Corresponds to the developmental stage in *Raillietiella*, shown in Fig. 106.
- Fig. 109. Argulus. Spermatid, late stage 6. Cross section of pseudoacrosome, in which an asymmetry begins to develop in the contents of the ventral sheath (vs).
- Fig. 110. Argulus. Spermatid 7. Nearly mature pseudoacrosome in cross section. The contents of the ventral sheath have developed the asymmetry typical of the mature stage.

cw = wall of spermatocyst with inclusion body and mitochondrion, dp = dorsal rod of pseudoacrosome, <math>ds = dorsal sheath, g = granulosome, ps = pseudoacrosomal membranous sac, vp = ventral rod of pseudoacrosome, vs = ventral sheath of pseudoacrosome.



Development of transitional region between body and pseudoacrosome.

- Fig. 111. Argulus. Spermatid 7. Median section of nearly mature spermatid. Body to the left, pseudoacrosome with dorsal rod (do) and ventral rod (vp) to the right. The relations of the dorsal ribbon (dr), inner sac of the dorsal ribbon (is), dorsal doublets (dd) and dorsal extension of PGM (dm) are particularly distinct. Compare text figure 13 D.
- Fig. 112. Argulus. Spermatid 7. Cross section through centriole. A vestigial true acrosome is possibly present below (a). The centriole doublets 9, 1, and 2 have converged and are embedded in a dorsal portion of PGM (dd). Ventrally, the doublets 5 and 6 are in the same way embedded in a ventral portion of PGM (vd).
- Fig. 113. Argulus. Spermatid 7, a little younger than in Fig. 112, with a distinct acrosome (a).
- Fig. 114. *Raillietiella*. Cross section of transitional region. All six ventral doublets of the centriole visible (no. 3–8). For explanations see Fig. 116.
- Fig. 115. Raillietiella. Spermatid 6-7. Cross section of transitional region. For explanation see Fig. 116.
- Fig. 116. Raillietiella. Spermatid 6–7. Cross sections through posterior part of centriole (A), through anterior part of centriole (B), and through pseudoacrosomes (C). The constant pattern of the centriolar doublets in this region is evidenced by this figure, Figs. 114–115, and Plate 7: 21–22. The three dorsal doublets (dd) fuse with PGM and are connected with the dorsal rod of the pseudoacrosome, the six ventral doublets (vd) connect with the ventral rod in a similar way. The posterior, wing-like extensions of the ventral sheath (w) are distinct in this figure and in Figs. 112 and 114. The ventral ribbon (vr) in Fig. A appears to contain dark rods, perhaps the outer dark filaments 4–7.

a = acrosome, dd = dorsal doublets of centriole, dm = dorsal portion of PGM with doublets 9, 1 and 2. dp = dorsal rod of pseudoacrosome, dr = dorsal ribbon, en = anterior end of nucleus, is = inner membranous sac of dorsal ribbon, ls = posterior limit of membranous sac on the ventral side of the pseudoacrosome, <math>m = mintochondria, mp = membrane-like condensation in the PGM (see text Fig 12), n = nucleus, os = outer membranous sac of dorsal ribbon, vd = ventral doublets of centriole, vr = ventral ribbon, vp = ventral rod of pseudoacrosome, w = wing-like posterior extensions of the ventral sheath of the pseudoacrosome (to the left and below the w).



Plate 23

Morphology of the top of the growing pseudoacrosome.

- Fig. 117. Raillietiella. Spermatid 6. Note the large granulosomes (g) attached to the apical membranes (am).
- Fig. 118. *Raillietiella*. Spermatid 7. Several pseudoacrosomes with well-filled dorsal and ventral rods (rr) are longitudinally or obliquely cut. The granulosomes (g) are either on the top of the structure or, in one case, by-passed by one rod (arrow). Note also the wall of the cyst in the upper left part of the figure. The growing pseudoacrosomes are not surrounded by Sertoli cells or other plasm.
- Fig. 119. Argulus. Spermatid 6. The top of the pseudoacrosome with apical membrane (am) and granulosome (g), the latter less distinct than in *Raillietiella*. The apical membrane is directly continous with the ventral sheath (vs), less so with the dorsal sheath (ds).
- Fig. 120. Argulus. Spermatid 6. Longitudinal section through the end of the pseudoacrosome, showing particularly the differentiation of the PGM (pm) into longitudinal lamellae (la).

am = apical membrane, ds = dorsal sheath of pseudoacrosome, g = granulosome, la = horizontal lamellae of the PGM, pm = pseudoacrosomal granular matter (PGM), rr = rods of the pseudoacrosome, vs = ventral sheath of the pseudoacrosome.



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TYGE W. BÖCHER & C. A. JØRGENSEN†

JYSKE DVÆRGBUSKHEDER

EKSPERIMENTELLE UNDERSØGELSER AF FORSKELLIGE KULTURINDGREBS INDFLYDELSE PÅ VEGETATIONEN

With an English Summary

Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 19,5



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Synopsis

During the years 1936–1971 a series of experiments were carried out on six different Jutland heath areas with the aim of investigating the influence of various types of heath management on the composition of the vegetation and succession. In each area four (or six) 15×15 m. plots were carefully investigated before any management was undertaken. The main types of management were lea-ploughing, burning off and mowing, and also in two of the areas, peat-removal. One plot was left untreated as a test-plot. The successional stages as well as minor alterations in the composition were followed statistically by measuring shoot density, constancy and coverage of the species. The methods and the main results are summarized in English on pp. 52–55. The six heath areas can be arranged into three groups according to the type of succession:

- (1) the heath develops into grassland and then into woodland,
- (2) the heath develops into grassland or to a dwarf shrub heath where Culluna is scarce,
- (3) the dwarf shrub heath pattern is maintained more or less in its original composition although Calluna becomes more scattered while Empetrum increases its share. The latter type was established on two fluvioglacial areas and in a dune-heath area.

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1. Indledning

rofessor C. A. Jørgensen (1899-1968) havde stor interesse for jyske heder og egekrat. Mens han levede, fik han i samarbejde med K. GRAM og M. KØIE udgivet værket om egekrattene (K. GRAM, C. A. JØRGENSEN & M. KØIE 1944), men han nåede desværre ikke at se afslutningen på hedeforsøgene. Disse blev påbegyndt i 1936 og afsluttedes i 1971. Planerne til forsøgsserien blev udarbejdet i 1935–36 i en periode, hvor T. W. Böcher var i fuld gang med vegetationsundersøgelser på Randbøl Hede og samtidig var assistent hos C. A. Jørgensen på Landbohøjskolens arvelighedslaboratorium. Der var således rige muligheder for forfatterne til nærværende afhandling til at drøfte hedens problemer, og disse diskussioner fortsattes under de følgende års hederejser. På disse undersøgelsesrejser fik vi værdifuld hjælp hos statsskovvæsenet og klitvæsenets personale. De fleste forsøg blev anstillet på statsarealer, hvor der var mandskab til at udføre kulturindgrebene og hvor man var ret sikker på at forsøgsarealerne kunne henligge i fred. Også privatejede fredede arealer blev efter særlig indhentet tilladelse benyttet; men her stødte vi på en del vanskeligheder både med at få udført kulturindgrebene og med at få områderne til at ligge urørt over en lang periode. De forsøg, der f.eks. indledtes på Nørholm Hede, Borris Hede og heden ved Kås i Salling, måtte derfor opgives. Derimod gennemførtes forsøgene i Hammer Bakker i Vendsyssel og på Randbøl Hede. I Hammer Bakker udførtes forsøgene på det område, der ejes af Dansk Botanisk Forening, på Randbøl Hede på et område der tilhører gårdejer HANS HANSEN, Kirstinelyst nær Frederikshåb. Ialt blev der gennemført forsøg på seks forskellige områder, se fig. 1.

Carlsbergfonden bevilgede tilskud til de rejser, der måtte foretages for at anlægge forsøgene og følge dem. Afmærkningen af forsøgsparcellerne og de indledende vegetationsundersøgelser blev foretaget 1936 og 1937 af de to forfattere. Ved flere af de senere undersøgelser, sidst i 1964, deltog C. A. Jørgensen også. Men i et par somre, bl.a. under krigen, hjalp professor M. WESTERGAARD med ved gennemgangen af parcellerne, og i somren 1971 assisterede mag. scient. JENS BÖCHER.

Foruden en tak til Carlsbergfondet er der grund til at takke de mange personer, især knyttet til statsskovene og klitvæsenet, der gennem årene har hjulpet både ved afmærkning og behandling af parcellerne og ved at åbne deres hjem for dem, der arbejdede med vegetationen.

1*



Fig. 1. Beliggenhed af hedeforsøgene. 1. Kronhedeforsøget, 2. Alhedeforsøget, 3. Gludstedforsøget, 4. Randbølforsøget, 5. Forsøget i Hammer Bakker, 6. Østerildforsøget.

Location of experimental areas 1-6 referred to in the text.

2. Metoder

Vi anså det for særdeles vigtigt at udarbejde metoder, hvorved man på den sikreste måde kunne registrere selv meget små ændringer i vegetationens sammensætning.

På hver lokalitet blev der afgrænset et antal kvadratiske parceller, der afmærkedes ved nedgravning af cementpæle i hjørnerne. Parcelstørrelsen var som regel 15×15 m og antallet af parceller på hver lokalitet oftest 4.

Til forsøgene udvalgtes så vidt muligt en hedevegetation med ensartet sammensætning på alle parceller. Disse blev grundigt undersøgt inden behandling af en eller anden art blev foretaget. Ofte blev 3 parceller behandlet, medens den fjerde fik lov at ligge som kontrol. Som standardindgreb valgtes skrælpløjning, svidning og afslåning af lyngen med le. På enkelte lokaliteter foretoges også afskrælning af fladtørv.

Til forundersøgelserne og de senere undersøgelser over regenerationen af lyngheden og successionen som helhed valgtes to metoder.

(1) Skudtætheds- og frekvens-analyser.

Hver parcel blev underafdelt i 36 flader à $2^{1}/_{2} \times 2^{1}/_{2}$ m. Disse flader blev under analysearbejdet afmærket ved snore der blev udspændt over parcellerne. Snorene kom til at krydse hinanden i 25 punkter, og hver af disse blev benyttet som centrum i en kredsrund flade, hvis flora undersøgtes. Cirkelstørrelsen var den sædvanlige af RAUN-KLÆR foreslåede (0,1 m²). Men man benyttede den af Böcher (1935) indførte modifikation af cirklingsmetoden, hvor der opereres med 4 koncentriske cirkler, hvor kun den yderste svarer til den Raunkiærske, der omskriver et areal på 0,1 m² og har en radius på 17,8 cm. En tværpind af denne længde fastgjort til en stok udgør apparaturet (fig. 1). Tværpinden er inddelt i 4 lige lange stykker (mærker sat ved 13.4, 8.9 og 4.5 cm fra centrum).

Under analyserne blev arter, hvis skud (overvintringsknopper) befandt sig inden for inderste cirkel betegnet med 4; de, der kun havde skud inden for næstinderste, fik værdien 3, og videre fik arter, der kun fandtes med skud indenfor den næstyderste og den yderste cirkel, henholdsvis 2 og 1. En art, der på alle 25 krydsningspunkter i kvadratnettet opnåede værdien 4, står naturligvis meget tæt med sine skud. Idet vi følger fremgangsmåden i Böcher & Weis Bentzon (1958 s. 45–46), får den skudtæthedsværdien (ST) 100 (25×4), hvilket svarer til at den er frekvensdominant inden for inderste cirkelstørrelse ($0,006 \text{ m}^2$). En mere spredtstående art får i de 25 skæringspunkter f.eks. 3 4-værdier, 4 3-værdier, 6 2-værdier og 12 1-værdier; den vil da ved simpel addition få ST 48. En meget spredt art vil f.eks kun opnå 3 værdier på 2 og 7 værdier på 1, og den opnår kun 13 i ST. Skudtætheden vil med andre ord kunne udtrykkes i en skala fra 1 til 100.

(2) Konstans- og dækningsgradsanalyser.

De 36 små kvadrater à $2^{1/2} \times 2^{1/2}$ m undersøgtes m.h.t. arternes dækningsgrad. For hver af de små kvadrater udarbejdedes en floraliste idet man samtidig skønnede over arternes dækning. Der benyttedes her HULT-SERNANDERS' skala, hvor 5 angiver at arten dækker mere end halvdelen af fladen, 4 at den dækker mellem 1/4 og 1/2 af



Fig. 2. Professor C. A. Jørgensen under cirklingsarbejdet 1953 i Hammer Bakker. En pind med påsat radius for de fire koncentriske cirkler stikkes ned i vegetationen ved et af de 36 krydsningspunkter i kvadratnettet. Almindelig ulvefod, *Lycopodium clavatum*, nåede i 1953 visse steder op på stor hyppighed og ses stikke op af det lave lyngtæppe. TWB. fot.

The late Professor C. A. Jørgensen during work with determination of shoot density. The short cross-stick works as a radius and when turned around circumscribes a circular area of 0.1 m^2 . The cross-stick is divided into four equally long parts, thus making it possible to distinguish four concentric circular areas. Species having shoots within the innermost and smallest circle (0.006 m^2) are given the value 4, those inside the three other circles – 3, 2, and 1. Very dense species will continuously be given 4 values. With 25 single analyses in each experimental plot, a species of such density will get 100 in ST (shoot density). The picture shows part of the grid of $36 \ 2^{1}_{/2} \times 2^{1}_{/2}$ m squares; the analysis takes place in one of the 25 intersecting points indicated by a knot on the string. *Lycopodium clavatum* abundant in the foreground (exp. area 5).

fladen, 3 at den dækker mellem 1/8 og 1/4, 2 mellem $1/16}$ og 1/8 og 1 at den dækker under $1/16}$ af fladen. Med + angives at arten lige akkurat er til stede, men kun dækker et helt ubetydeligt areal.

Forekomsterne i de 36 kvadrater danner basis for de konstansværdier der anføres (i tabellerne i kolonnen mærket K.). Tallene angiver simpelthen det antal små kvadrater, hvori arten forekom. Skalaen går derfor fra 0 til 36. 36 svarer til en konstansprocent på 100, 18 til en procent på 50 osv.

Variationen i dækningsgrad angives i en særlig kolonne (mærket D). Der er ikke udregnet nogen middeldækningsgrad, idet variationen i dækning indenfor parcellen skønnedes at have særlig interesse.

Der blev de første år taget jordprøver til pH-bestemmelse, men der blev ikke foretaget nogen egentlig kåranalyse på parcellerne. Mosser og lichener blev så vidt muligt bestemt under selve markarbejdet. For slægten Cladonia's vedkommende støttede vi os til den fortræffelige afhandling af Mølholm Hansen & Lund (1929). Medens kun få Cladonia-arter måtte medtages til senere bestemmelse, var det ofte nødvendigt at medtage levermosser, hvoraf der var en del, navnlig i den fugtige hede ved Østerild. Mosprøverne blev venligst bestemt af Aug. Hesselbo, i de senere år af lektor Kjeld HOLMEN og amanuensis KELL DAMSHOLT. I nogle tilfælde var vi ikke under markarbejdet i stand til at skelne visse arter, eller overså at der skjulte sig to arter under det som vi havde betegnet som en enkelt art. Dette har medført, at der i tabellerne nogle steder er slået arter sammen ved klammer. Hvis man sammenligner med de af Mølholm Hansen (1932) udarbejdede vegetationslister fra Nørholm Hede, er det påfaldende, hvor mange levermosser hans lister indeholder sammenlignet med vore. Vi var under arbejdet klare over, at navnlig levermosser blev overset en gang imellem, men i betragtning af den tid det ville tage nøje at eftersøge levermosserne på 4 parceller med 36 kvadrater à $2^{1}_{2} \times 2^{1}_{2}$ m besluttede vi især at lægge vægt på at få levermosserne med under skudtæthedsanalysearbejdet.

3. Beskrivelse af hedeforsøgene

A. To forsøg på hedeslette

Der anstilledes to forsøg på heder, der ligger på typiske fluvioglaciale sandaflejringer, nemlig på Kronhede sydvest for Lemvig og Alheden ved Søndre Feldborg Plantage.

1. Kronhedeforsøget. (Tabel 1 og fig. 1 område 1).

De fire parceller blev lagt i række på plan, tør hedeslette godt 1 km øst for Vilhelmsborg ved vejen fra Lemvig til Ulborg. Et stykke østligere er der et lille vandløb, Risbæk, og her er hedefloraen mere frodig og varieret. Lyngheden, der blev anvendt til forsøget, var artsfattig m.h.t. blomsterplanter, men særdeles rig på lichener. pH i jorden måltes til 3,7–3.9 før behandlingerne der fandt sted i 1936. Jorden i den skrælpløjede parcel havde pH 4.1 året efter behandlingen. Samme værdi fandtes i den parcel, hvor lyngen blev afmejet, medens pH var 4,3 i den afsvedne parcel året efter afbrændingen.

Vegetationens oprindelige sammensætning fremgår af tabel 1 i kolonnerne mærket F (forundersøgelse) og de to kolonner for kontrolparcellen. Den tilhører Arctostaphylos-gruppen af det samfund, der er kaldt Empetrion boreale (smlgn. Böcher 1943: 51–54). Den udmærker sig ikke blot ved stor hyppighed af Arctostaphylos og spredt forekomst af Genista pilosa, der begge er indikatorer for tør bund, men også

TABEL 1. Kronhedeforsøget

Asterisk efter et tal angiver at kimplanter udgør en væsentlig del

				Ski	rælp	løjet	parce	1 (L	.ea plo	oughe	ed p	lot)						А	fsved	en p	arcel	l
År. Year. (F forundersøgelse	F	193	6		1937	7		193	8		194	0		195	3	F	193	6		1937		
forehandinvestigation) Metode. Method. (cp. pp. 52–53)	ST	к	D	ST	К	D	ST	К	D	ST	К	D	ST	К	D	ST	К	D	ST	К	D	
Arctostaphylos uva ursi Calluna vulgaris Empetrum nigrum Genista anglica – pilosa Pinus mugo Salix cinerea – arenaria (repens)	83 99 55 7	36 36 36 6 6 3	$1-3 \\ 4-5 \\ 1-2 \\ 1 \\ 1$	17 33 13 3	$ \begin{array}{r} 36 \\ 36 \\ 36 \\ 4 \\ 2 \\ 2 \end{array} $	+++++++++++++++++++++++++++++++++++++++	$9 \\ 30 \\ 13 \\ 4 \\ 3$	$ \begin{array}{r} 36 \\ 36 \\ 36 \\ 7 \\ 7 \\ 1 \\ 1 \end{array} $	$^{+-1}_{+-2}_{+-1}_{+}_{+}_{+}$	$ \begin{array}{ } 9 \\ 65 \\ 40 \\ 3 \\ 2 \end{array} $	35 36 36 7 8 9	$^{+-2}_{3-4}_{2-3}_{+-1}_{+-1}$	16 90 64 1	$32 \\ 36 \\ 36 \\ 4 \\ 6 \\ 2 \\ 1 \\ 7$	$^{+-3}_{4-5}_{2-4}_{+-1}_{+-1}_{+-1}_{+}_{+-2}$	81 100 51 7	$ \begin{array}{r} 36 \\ 36 \\ 35 \\ 4 \\ 9 \\ 5 \end{array} $	$2 \\ 5 \\ 1 \\ 1 \\ 1 \\ 1$		4 5 10* 6 4	+ + + + +	
Agrostis coarctata ² Aira praecox Carex panicea – pilulifera Deschampsia flexuosa Molinia coerulea Sieglingia decumbens	3 13	10 18 2 2	+-1 1 +-1 +-1	3	5	+	3	12 17	+-1+	12 6 5	$ \begin{array}{r} 16 \\ 6 \\ 17 \\ 2 \\ 2 \\ 1 \end{array} $	$^{+-2}_{+}_{+-2}_{+}_{+}_{+}$	4 6 1	5 14 1 1	+ +-1 + +	. 8	$ \begin{array}{c} 16 \\ 1 \\ 1 \\ 4 \end{array} $	+-1 1 + 1	9	1 21 1 2	+ + + + +	
Arnica montana Euphrasia micrantha Hypochoeris radicata Potentilla erecta Rumex acetosella Scorzonera humilis. Senecio silvaticus Solidago virga-aurea		1 1 1	+-1 1					5 11	+	1 9	$2 \\ 1 \\ 1 \\ 24$	+ + + +		1	+	· · ·	2 1 2	+ 1 1	2	3	+	
Baeomyces sp. Cetraria islandica Cladonia alpestris – chlorophaea – coccifera – crispata	9 5	26 7 6	1 +-1 +					1	+	1	1	+	1 10	3 6	+	1 1	$ \begin{array}{c} 18 \\ 3 \\ 3 \\ 1 \end{array} $	1 1 + +				
 destricta floerkeana furcata. glauca gracilis. impexa mitis-silvatica. rangiferina subulata uncialis verticillata Cornicularia aculeata. Parmelia physodes. 	50 72 9 7 3 10	$ \begin{array}{c} 1 \\ 1 \\ 3 \\ 36 \\ 36 \\ 34 \\ 11 \\ 1 \\ 4 \\ 3 \\ 13 \\ 36 \\ 36 \\ 36 \\ 34 \\ 11 \\ 1 \\ 3 \\ 36 \\ 36 \\ 36 \\ 36 \\ 36 \\ 36 \\ 36 \\ 36 \\ 34 \\ 11 \\ 1 \\ 3 \\ 36 $	$^+$ 1 1 1 2-3 +-1 +-1 + + + +-1 +-1				1) 14)	35	+	4	1	+1	2 34 18 9 2 4 4 21	$ \begin{array}{r} 6 \\ 1 \\ 2 \\ 2 \\ 36 \\ 36 \\ 36 \\ 8 \\ 1 \\ 3 \\ 2 \\ 5 \\ 18 \\ \end{array} $	+ + + + + + + -2 + -2 + -1 + + + + + + + + + + + + + + + + +		2 13 36 36 23 4 15 22 36	+ 1 - 2 2 - 3 + - 1 + 1 + -1 + -1				
Ceratodon purpureus Dicranum scoparium – spurium Hypnum jutlandicum ³ Pleurozium schreberi Pohlia nutans Polytrichum piliferum Ptilidium ciliare	4 95 3 44	$ \begin{array}{c} 4 \\ 1 \\ 36 \\ 2 \\ 36 \\ 36 \end{array} $	$1 \\ 1 \\ 2-3 \\ 1 \\ +-2$					3	+	4	10 4	+-1	9 66 4	3 36 1 20	$^{+-1}_{+-2}$	· · 91 · · · 41	36 36	2-3				

¹ Denne parcel blev ed en misforståelse behandlet inden forundersogelsen var foretaget. I stedet blev der 1937 foretaget en skudtæthedsanalyse i den urørte hede tæt uden for parcellen. ² A. coarctata Ehrh. ex Hoffm., sandsynligvis det samme som A. stricta J. F. Gmel. Tidligere kaldt A. canina var. arida. ³ Hypnum jutlandicum Holmen & Warncke = H. cupressiforme Hedw. var. ericetorum Bruch, Schimp. & Guemb.

(Experimental area 1, cp. Fig. 1)

(Numbers with an asterisk indicate that seedlings form an essential part)

_	(Burned off pl	lot)		Afslå	et parcel (The	mowed plot)	Kontrolparcel (Test plot)
	1938	1940 1953	F1937	1937	1938	1940 1953	1936 1954
	ST K D	ST K D ST K	D ST	ST K D	ST K D	ST K D ST K D	STKD STKD
	36^{*} + $84^{*}36^{*}$ + 5 + 4 9 +	$ \begin{vmatrix} 17 & + & 9 & 27 \\ 100 & 36 & 5 & 100 & 36 \\ 6^* & + & 1 & 7 \\ 3 & + & 1 & 3 \\ 1 & 8 & +-1 & 4 & 10 \end{vmatrix} $	$ \begin{array}{c c c}1 & 78 \\ 5 & 100 \\ + & 42 \\ + \\1 & \end{array} $	$ \begin{vmatrix} 52 & 36 & + \\ 97 & 36 & 1 \\ 8 & 21 & + \\ & 1 & + \end{vmatrix} $	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$
		2 11	2			6 +-2	8 +-3
	6 +-2	$\frac{5 + -2}{$	2 4	5 12 +-1	$\frac{4 \ 10 \ -2}{2 \ 2}$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	1 12 + -2 12 1-3
	+ 6	5 +		1 +	2 6 +	1 + 2 + -1	2 5 +-1 $7 +-1$
	7 21 + -1 2 + 2 + 1 + 4 +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	+ 9 + + 1 + 1	3 16 + 1 + 1	2 22 +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
	1 +	2 +		_			
	1 +	$\begin{vmatrix} 1 & + \\ 1 & + \end{vmatrix}$ 1	+				
	4 +	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	+				
		$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 16 \\ + & 7 \\ + & 3 \\ + & 8 \\ + \\ + \\ + \\ + \\ + \\ + \\ + \\ + \\ + \\$		$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$
	1 +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$+ \\ + \\ 91 \\ 7$			$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$
		$ \begin{vmatrix} 5 & 3 & + \\ 7 & 4 & + \\ & & 4 & 14 \end{vmatrix} $	+ + 35			$\begin{array}{ccccccccc}1&1&+\\19&15&+\end{array}$	$31 \ 36 \ +-1 \ 40 \ 36 \ +-1$

(This plot was unfortunately mowed before the forehand investigation was undertaken, Instead a shootdensity determination was carried out in 1937 in the untreated vegetation just outside the plot).

ved mangel af *Vaccinium vitis idaea*, der åbenbart af ikke klarlagte årsager mangler syd for Lemvig, og i det hele taget er forbløffende sjælden i det vestligste Jylland (se Böcher l.c. fig. 13). Af andre floristiske forhold bør nævnes, at Kronhedeparcellerne havde spredt forekomst af *Cladonia alpestris*, en sub-lavarktisk art der er meget sjælden på den jyske hede. Kun seks lokaliteter kendes, Böcher & SKYTTE CHRISTIANSEN (1941 p. 420). På kontrolparcellen var *Cladonia alpestris* særlig hyppig; den fandtes i ca. 20 af de 36 små kvadrater på $2^{1/2} \times 2^{1/2}$ m.

Den skrælpløjede parcel. Desværre var pløjningen ikke helt godt udført, idet der var gab mellem furerne, og ophøjede morstrimler var skubbet skråt hen over hinanden. Allerede i 1937 fandtes derfor flere steder ret store skud af lyng, revling og melbær i gabene mellem tørvestrimlerne. Lavtæppet begyndte at regenerere i 1938, medens mosset først tog fat i 1940. I de tidligere stadier efter pløjningen var parcellen præget af store mængder af oftest dværgagtige eksemplarer af *Senecio silvaticus*. Ved afslutningen af forsøget i 1953 var ligheden med den oprindelige vegetation stor, om end der var nogen tilbagegang for melbær. På alle parceller var der lidt selvsået bjergfyr. I lavtæppet var *Cladonia impexa* og *C. mitis-silvatica* på vej mod deres oprindelige tæthed, men *C. alpestris* var ikke kommet igen. Det samme var tilfældet i de andre behandlede parceller, medens denne art holdt stillingen i den ubehandlede kontrolparcel.

Den afsvedne parcel. Lyngen var omhyggeligt afsvedet. Ilden havde nået den øverste del af morskjolden og mos og lav var helt bortbrændt. Endnu i 1938 var parcellen dækket af en sort brandskorpe og kun *Salix arenaria* og *Carex panicea* havde evnet at danne større skud. Derimod vrimlede *Calluna*-kimplanter frem og opnåede 84 i skudtæthed. Den videre succession havde et karakteristisk tidligt stadium præget af *Lecidea*-skorper på jorden og lidt *Polytrichum* og *Ceratodon*. Store rensdyrlaver og mos kom først efter 1940, væsentlig senere end på den skrælpløjede parcel. *Senecio silvaticus* spillede her ingen rolle. Ved afslutningen 1953 konstateredes en væsentlig fremgang for *Calluna* på bekostning af de andre hedebuske.

Den afslåede parcel. Lyngtæppet var omhyggeligt afhugget med le. Også alt lav og mos var fjernet. Regenerationen gik her hurtigt, navnlig var lavtæppet i vældig fremgang allerede i 1938. Hele parcellen var dette år grøn af stubskud af *Calluna*, og der sås talrige kimplanter af både *Calluna* og *Arctostaphylos*. Under den videre succession var der intet *Lecidea*-stadium, men derimod et tydeligt *Cladonia clorophaea*maximum i 1940. Denne art dannede da tætte kager på vinderoderet humusbund mellem lyngplanterne. Ved afslutningen i 1953 lå skudtæthedstallene nær ved de samme værdier fra 1937. Imidlertid kan de to sæt tal i dette tilfælde ikke sammenlignes uden videre (se fodnote til tabel 1).

Kontrolparcellen. Vegetationen forekom at være særdeles stabil. Der kunne dog spores en klar, omend ikke meget stor fremgang for *Empetrum nigrum* i de 18 år der var gået mellem de to analyser.



Fig. 3. Kronhedeforsøget 1953. Øverst: I forgrunden ubehandlet hede og til højre en cementpæl i hjørnet af den nordligste (afslåede) parcel, der har ensartet tæt lavt lyngtæppe. De øvrige parceller ligger bagved ned mod den lyse folkevognsbus, der skimtes længst til højre i baggrunden. – Nederst: Parcelrækken set den modsatte vej: Forrest den ubehandlede kontrolparcel, derefter ved de nedstukne tonkinstokke den skrælpløjede parcel og bag den den afbrændte og den afslåede parcel. Enkelte bjergfyrbuske. C. A. Jørgensen fot.

The experimental plots in Kronhede (exp. area 1 in Fig. 1) in 1953. The uppermost picture shows a low, uniform and dense *Calluna* heath vegetation developed on the mowed plot. – Below in the foreground the untreated test plot which is covered by a low *Calluna-Empetrum-Arctostaphylos*-heath rich in lichens, cp. Table 1.

2. Alhedeforsøget. (Tabel 2 og fig. 1 område 2).

Der blev afgrænset 4 parceller på et hedestykke under Søndre Feldborg Plantage i et hjørne, hvor den gamle kommunevej fra Neder Feldborg til Neder Simmelkær krydser plantagevejen til Simmelkærhus. pH i jorden varierede fra 3.2 til 3.9, men efter skrælpløjningen sank surhedsgraden til pH 4.3 og efter svidningen til 4.2. Området blev foruden i de på tab. 2 anførte år også besøgt 1953, hvor der gjordes notater, men ingen mere nøjagtige undersøgelser. På dette tidspunkt havde statsskovvæsenet desværre pløjet uden om parcelrækken og plantet fyr til 3 m fra parcellerne. For at forsøget ikke skulle påvirkes af denne plantning, blev træerne fjernet på de første 10 m fra parcellerne og i området mellem disse og vejen.

Den oprindelige vegetation var også her artsfattig bortset fra lavtæppet; især var der en påfaldende mangel på ikke-græsagtige urter. Jordbunden var mindre tør end på Kronheden, hvilket bl. a. viste sig ved hyppig forekomst af *Carex fusca*. Iøvrigt var denne hede rig på tyttebær og revling. Den kan klassificeres som tilhørende *Empetrum-Vaccinium vitis idaea* gruppen af *Empetrion boreale*, nok den mest udbredte hedetype i Jylland.

Den skrælpløjede parcel. Pløjningen blev udført meget omhyggeligt, således at overfladen i 1937 bestod af hvidt blegsand; der var ingen kimplanter, men mange skud især af *Carex fusca* og *Vaccinium vitis idaea*. Indvandring af lav og mos foregik meget sent. I 1953 var parcellen dækket af 20–35 cm høj lyngvegetation med spredt revling og tyttebær. Der var da en del *Hypnum jutlandicum* og *Dicranum scoparium*, desuden *Cladonia floerkeana* og *glauca*, medens *Cladina*-arterne ikke endnu var af større betydning. Blandt disse var *Cladonia impexa* den første der vandt frem, men slutresultatet i 1964 var en hede, der var mere mosrig end ved starten af forsøget. Navnlig var *Pleurozium schreberis* fremgang særdeles bemærkelsesværdig.

Den afsvedne parcel. Allerede i 1937, kort efter afsvidningen, vrimlede det på parcellen med kimplanter af lyng og revling. De andre arter skød frem fra jorden (*Carex*) eller fra tætte tuer, der havde overlevet branden (*Deschampsia flexuosa, Molinia, Juncus squarrosus, Scirpus caespitosus*). I 1937 ansås de rester af *Cladina*-arterne, der fandtes på parcellen, for døde, men i 1938 blev det klart, at arterne ofte var i stand til at skyde frem fra de halvdøde, gamle dele. I 1940 nåedes et *Lecidea-Cladonia chlorophaea*-stadium, og i 1953 var *Cladina*-arterne (især *C. impexa*) i kraftig vækst, omend tydeligt hæmmet af den unge, tætte lyng. Også *Hypnum jutlandicum* var meget hyppig. Ved afslutningen i 1964 var det klart, at *Calluna* og *Vaccinium vitis idaea* havde forstærket deres position i løbet af forsøget; derimod var det gået noget tilbage for *Carex fusca* og *Deschampsia flexuosa*. I *Cladina*-gruppen var *Cl. mitis-silvatia* blevet svækket i forhold til *C. impexa*.

Den afslåede parcel. Behandlingen medførte fremgang for Vaccinium vitisidaea, sålænge Calluna var ung og lav. Fra 1940 gik det tilbage for tyttebær og i 1953 var tyttebær helt underordnet i en tæt, 10–15 cm høj Calluna-hede, hvori Empetrum tydeligvis var i fremgang. Lavvegetationen gennemløb også her et Lecidea-Cladonia chlorophaea-stadium i 1940. I 1953 var Cladina-arterne dominerende, men C. rangi-





Fig. 4. Alhedeforsøget 1964. På det øverste billede ses kontrolparcellen i forgrunden. Her står lyngbuskene spredt og uensartet, medens de andre parceller har ensartet og tæt lynghede. Grænsen mellem den ubehandlede parcel og de behandlede går tværs over billedet (* - *). – Nederste billede viser den ubehandlede parcel, der er domineret af *Empetrum*. C.A.J. fot.

The experimental plots in Alheden (exp. area 2 in Fig. 1) in 1964. The upper picture shows the test plot in the foreground (below line between the two asterisks). The mowed, the burned off, and the ploughed plots are in the background and appear darker due to the dominance of *Calluna*. – The test plot is also seen in the picture below; it is dominated by *Empetrum* and appears green with scattered patches of flowering *Calluna*.

TABEL 2. Alhedeforsøget

					5	Skræl	lpløje	t pa	arcel (Lea	plou	ghed	plot)							Afbr	ændt
Undersøgelsesår Metode	F ST	1936 K	D	ST	193 K	7 D	ST	19 K	38 D	ST	19 K	40 D	ST	19 K	64 D	ST	F 19 K	36 D	ST	1937 K	7 D
Arctostaphylos uva ursi Calluna vulgaris Empetrum nigrum Genista anglica Populus tremula Vaccinium vitis-idaea	87 71 3 57	9 + - 36 3 - 35 1 - 6 + - 23 1 -	2 -5 -5 -1 -3	7	$3 \\ 5 \\ 2 \\ 22$	+ + + +	24 2 17	35 10 4 24	$^{+-2}_{+-1}$	$56 \\ 5 \\ 4 \\ 25$	$36 \\ 25 \\ 2 \\ 24$	$1-3 \\ +-2 \\ + \\ 1-3$	91 83 60	36 36 5 30	2-4 2-5 +-1 +-2	70* 88 5 14	* 36 36 26 15	$\begin{array}{c}2-4\\2-4\\1\\+-2\end{array}$	63* 25* 8 15	36 31 27 16	+ + + +-3
Carex arenaria – fusca – panicea – pilulifera Deschampsia flexuosa Juncus squarrosus Molinia coerulea Scirpus caespitosus	53 11	35 + - 28 + -	-2	15	33 2 3	+++++	14	33 4 14	+-2 + +-1	35 41	33 1 36	1-2 + +-3	9	34 34 1	+-1 +-1 +	29 3 34 3 6 1	$2 \\ 27 \\ 2 \\ 34 \\ 1 \\ 11 \\ 2$	$1 \\ 1 \\ 1 \\ 1 \\ + \\ 1(2) \\ 1$	35 1 30 4	$ \begin{array}{r} 1 \\ 30 \\ 2 \\ 35 \\ 1 \\ 10 \\ 1 \end{array} $	+ +-1 1 +-1 + + +
Galium saxatile Hypochoeris radicata Rumex acetosella Senecio silvaticus Solidago virga aurea								1	+											1	+
Cetraria glauca Cladonia chlorophaea - coccifera - crispata - floerkeana - floerkeana - floerkeana - glauca - glauca - gracilis - impexa - mitis-silvatica - rangiferina - squamosa - subulata - uncialis Cornicularia aculeata tere	27 5 55 81 11 7 12 18	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	-1 -1 -1 -1 -1 -3 -4 -1 1 -1		1	+	2	6	+		5	+	6 34 4	4 35 6	++1++	27 72 74 9 1 2 7	29 3 1 36 36 36 36 2 1 7 22	+-1 + 1 2-3 2-3 1 1 + 1 1	1	1	+
– granuosa Parmelia physodes – tubulosa	22	35 1	1+					1	+				67	36	1-2	16	$\frac{36}{1}$	+1+		1	+
Marasmius androsaceus Ceratodon pupureus Dicranum polysetum – scoparium Hylocomium splendens Hypnum jutlandicum Pleurozium schreberi Pohlia nutans Polytrichum sp Ptilidium ciliare	11 5 51 3 4	16 + - 12 + - 36 1 - 12 + - 9 + -	-1 -1 -2 -1										19 84 43 2	$ \begin{array}{c} 1 \\ 36 \\ 36 \\ 16 \\ 6 \end{array} $	$^+$ +-1 2-3 +-2 +	47 12 3	7 36 17 7	+ 1(2) 1(2) +	3 2	33	+ +

(Experimental area 2, cp. Fig. 1)

parcel (Burnee	d off plot)	Afslået parc	Kontrolparcel (Test plot)						
1938 ST K D	1940 1964 ST K D ST K D	F 1936 1937 ST K D ST K D	1938 1940 1964 ST K D ST K D	1936 1964 ST K D ST K D					
$82*36 1-2 \\ 10 28 +-1 \\ 9 30 +-1$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$					
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	84 35 +-2 85 36 +-2	94 36 3 92 36 2-3 42 36 +-1	91 36 $+-1$ 64 36 $+-2$					
$egin{array}{ccccc} 1 & + \ 39 & 28 & +-2 \ 6 & 4 & + \end{array}$	$ \begin{vmatrix} 1 & + \\ 40 & 27 & +-2 \\ 4 & 4 & + \end{vmatrix} \ \ \begin{array}{c} 1 & + \\ 3 & 23 & +(1) \\ 1 & + \end{vmatrix} $	$ \begin{vmatrix} 3 & 1 \\ 25 & 21 & 1 \\ 7 & 14 & +-1 \end{vmatrix} \begin{vmatrix} 26 & 20 & +-1 \\ 7 & 15 & +1 \end{vmatrix} $	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$					
$\begin{array}{cccccccc} 40 & 35 & 1{-2} \\ 1 & 1 & 1 \\ 4 & 11 & {+{-4}} \end{array}$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$34 \ 35 \ +-1$ $36 \ 36 \ +-2$					
$\frac{1}{1}$ 3 $+-1$	2 +		1 +						
$\frac{1}{2}$ +			1 +						
	34 36 + 3 14 +	29 26 +	71.36 + 5.5 +						
	1 +	2 + 2 + 2 + 1 + 2 + 1 + 2 + 1 + 2 + 1 + 2 + 1 + 2 + 1 + 2 + 2	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$						
13 29 +	$\begin{bmatrix} 25\\2 \end{bmatrix} 36 +-2 \begin{bmatrix} 75&36&1-3\\17&36&+-1\\1&+\end{bmatrix}$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{cases} 89 & 36 & 1-2 \\ 89 & 36 & 1-2 \\ 2 & 3 & +-1 \\ 2 & 3 & +-1 \\ \end{cases} \begin{array}{c} 97 & 36 & 2-3 \\ 52 & 36 & +-1 \\ 3 & + \\ 3 & + \\ \end{array} $	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$					
	$egin{array}{cccccccccccccccccccccccccccccccccccc$	$egin{array}{cccccccccccccccccccccccccccccccccccc$	$ \left \begin{array}{cccccccccccccccccccccccccccccccccccc$	$egin{array}{cccccccccccccccccccccccccccccccccccc$					
1 +	? 32 36 +-1	$\begin{array}{ cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$					
		3 6 +							
1 +	$ \begin{vmatrix} 5 & 9 & + \\ & & 1 \\ 5 & 19 & +(1) \end{vmatrix} \ \ \begin{array}{c} 1 & + \\ 3 & 2 & + \\ \end{array} $	2 12 1 1 - 1	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	1 9 + 2 10 +					
5 5 +	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$					
	2 + 4 12 + -1	3 +	5 12 +	10 + 4 14 + -1					

ferina kunne åbenbart ikke vinde frem til sin tidligere hyppighed. Dette gjaldt også ved afslutningen, hvor det også var klart at *C. mitis-silvatica* ikke havde nået sin tidligere tæthed. Lavtæppet, med *C. impexa* som dominant, virkede i 1964 lavt og tyndt i forhold til den urørte hede.

Kontrolparcellen. De vigtigste forhold fremgår af Tabel 2. Det kunne fastslås at *Empetrum* langsomt havde forstærket sin position i forhold til *Calluna*. Også *Deschampsia flexuosa, Hypnum jutlandicum* og *Pleurozium schreberi* var tiltaget i betydning i de 28 år, der var forløbet.

B. To forsøg i israndsområdet

Forsøg blev iværksat i nærheden af Kristianshede Station i Gludsted Plantage og på Randbøl Hede nær vejen Frederikshåb-Fitting. Begge steder ligger i randområdet. Det viser sig bl. a. ved jordens store indhold af sten. Begge steder ligger parcellerne på et plant stykke hede i nærheden af lave bakker, der i hvert fald for Randbøl Hedes vedkommende består af flyvesand.

3. Gludstedforsøget. (Tabel 3 og Fig. 1 område 3).

Der blev afmærket fire parceller liggende i række på et større hedestykke under Gludsted skovdistrikt (afdeling 62). I 1937 blev der her undersøgt en jordbundsprofil; den viste følgende lag:

> 0- 8 cm. Sort amorf lyngmor,
> 8-17 cm. Gråligt blegsand med småsten,
> 17-26 cm. Sort-mørkebrun al, ikke stenhård,
> 26-30 (34) cm. Brunligt udfældningslag, herunder groft, stenet, gult sand.

Vegetationen var en mos- og likenrig *Calluna-Vaccinium vitis idaea* hede ofte også med meget *Empetrum*. Den lignede således den lige omtalte hedetype fra Alheden. pH i jorden lå mellem 3.2 og 3.4, efter behandlingen dog mellem 3.7 og 3.9 og i den afsvedne parcel, året efter branden, på 4.0–4.1. Desværre fik arealet ikke lov til at ligge helt uden indgreb. Der blev i vinteren 1939–40 fjernet nogle træplantninger, der ved en misforståelse var anbragt omkring arealet. Der var yderligere på et tidspunkt blevet kørt med tunge vogne over arealet, hvorved der tværs over tre af parcellerne var fremkommet nogle forstyrrende vejspor. På grund af disse indgreb blev det opgivet at analysere heden indgående efter 1940; i stedet blev der gjort notater i 1953 og i 1969 foretaget nogle supplerende dækningsbestemmelser på dele af to af parcellerne.

Den skrælpløjede parcel. I 1937, kort efter pløjningen, lå der løsrevne totter af rensdyrlav over arealet. Disse fik ingen betydning. Den første nykolonisering af rensdyrlav fandt først sted i 1940, men da til gengæld over næsten hele parcellen. *Polytrichum juniperium* spillede også stor rolle i begyndelsen og lige til 1953. Dette år karakteriseredes vegetationen som en 30-40 cm høj *Calluna*-hede med meget *Vaccinium vitis idaea* og spredt *Empetrum*. Lyngplanterne, der da var ca. 25 år gamle, var ved at dø eller helt døde flere steder og overgroet med *Parmelia physodes*. Mos-

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rigdommen (Hypnum, Pleurozium, Ptilidium) var stor, medens kun Cladonia impexa var nået frem til større tæthed. Ellers var der en del C. chlorophaea, glauca og floerkeana. I 1969 var parcellen vestligst bevokset med lynghede af den type som fremgår af Tabel 3. Mod øst var største delen domineret af Deschampsia flexuosa med spredt forekomst af alle tre dværgbuske samt lidt *Vaccinium uliqinosum* på grænsen til den afsvedne parcel.

Den afsvedne parcel. Branden havde ikke forhindret Calluna i allerede 1937 at danne flere skud fra afsvedne stubbe. Imidlertid væltede det op med kimplanter i 1938. Vaccinium vitis idaea var i 1940 meget kraftig, men udviklingen skønnedes at være hæmmet, idet der var dannet en tør, rudret morskorpe med meget Ceratodon purpureus og Cladonia chlorophaea. I 1953 var der en 20-30 cm høj ensartet Callunahede med Vaccinium vitis idaea og rigeligt med mosser, her i mindre grad Pleurozium schreberi og i højere grad Dicranum scoparium og D. polysetum. Cladonia impexa og noget C. mitis stod pletvis tæt. Billedet i 1969 var uensartet. Lidt over halvdelen af parcellen havde Callung-Deschampsig flexuosa-Clading-hede. Midt i parcellen var der en del revling og tyttebær, men ellers var Deschampsia flexuosa den vigtigste art, et sted Carex fusca og ind mod den skrælpløjede parcel Vaccinium uliginosum. I forhold til denne og den afslåede parcel var den afsvedne parcel noget mere græsrig.

Den afslåede parcel. Her regenererede lavvegetationen hurtigere og Vaccinium vitis idaea havde i 1940 talrige bær. I 1953 bar parcellen en 15-25 cm høj Callunaeller Calluna-Empetrum hede med spredte skud af Vaccinium vitis idaea alle vegne. Cladina arterne dannede store tætte måtter, især C. impexa. Mosset var derimod tilbagetrængt. Ligesom i den skrælpløjede parcel var der enkelte døde lyngpletter; bunden var her bevokset med Cladonia glauca og C. chlorophaea. I 1969 bestod vegetationen især af Calluna-Empetrum-Cladonia impexa med spredt Vaccinium vitis idaea, men pletvis dominerede denne art sammen med rensdyrlavet og Carex fusca. Sidstnævnte havde sammen med C. panicea og Cladina erobret et vejspor gennem parcellen. Der noteredes også store pletter af Molinia coerulea, se også Fig. 6.

Kontrolparcellen, der først var hedeklædt (Tabel 3), var i 1953 allerede en mosaik domineret af dels Calluna-Vaccinium vitis idaea, dels Empetrum-Vaccinium vitis idaea-Cladina, dels Vaccinium vitis idaea-Cladina. Mange steder var lyngen død og overgroet med Parmelia physodes. Carex fusca og pletvis C. panicea stod tæt. På tyttebærplanterne var der meget Exobasidium vaccinii. I 1969 var parcellen meget uensartet. Største delen var domineret af Deschampsia flexuosa eller Empetrum med Cladina (smlg. Tabel 3), men der var også kombinationen Carex fusca-Cladina. Set udefra virkede parcellen som en firkantet lysning i heden domineret af græs og lav, se Fig. 5. Udviklingen mindede i flere henseender om den på Randbøl Hede.

4. Randbøl-forsøget (Tabel 4 og Fig. 1 område 4).

Her blev der nord for gården Kirstinelysts dyrkede jorder anlagt 3 parceller i række. I stedet for en afmærket kontrolparcel benyttedes en lille del af den urørte hede udfor den midterste parcel som ubehandlet kontrolområde. Allerede i 1937, hvor 2

Biol, Skr. Dan, Vid. Selsk. 19, no. 5.

TABEL 3. Gludstedforsøget

				Sk	rælp	oløjet	parce	el (I	Lea pl	ough	ed p	lot)					
Undersøgelsesår Metode	F ST	193 K	6 D	ST	193 K	7 D	ST	193 K	8 D	ST	194 K	0 D	19 K º/0	691 D	F ST	193 K	6 D
Calluna vulgaris Empetrum nigrum Vaccinium uliginosum – vitis-idaea	92 19 74	$36 \\ 24 \\ 1 \\ 36$	$4-5 \\ 1-2 \\ 1 \\ 1$	$\begin{vmatrix} 26 \\ 6 \\ 34 \end{vmatrix}$	36 15 36	+ + +(1)	39* 9 43	36 19 36	$1 \\ +-1 \\ +-2$	88 9 62	36 24 36	$3-4 \\ 1-3 \\ 1-3$	100 90 100	2-4 1-3 1-3	95 17 73	$36 \\ 25 \\ 1 \\ 36$	$4-5 \\ 1-2 \\ 1 \\ 1 \\ 1$
Aira praecox Carex fusca – panicea – pilulifera Deschampsia flexuosa Juncus squarrosus Luzula multiflora Molinia coerulea Scirpus caespitosus	8	12 6 2	1(2) 1	3	7 5	+(1)+	2	8 6 3 1	+-2 + +-1 +	8 2 1	$23 \\ 6 \\ 1 \\ 12 \\ 5$	$^{+-4}_{+-2}$ + + + +	50 60	$^{+-2}_{+}_{+-2}$	14 11 3	20 19 16	1 1 1
Rumex acetosella											4	+					
Cetraria glauca Cladonia chlorophaea – fimbriata – floerkeana – glauca – gracilis – impexa – mitis-silvatica – rangiferina – uncialis Cornicularia aculeata Parmelia physodes – tubulosa	17 3 85 56 2 1 28	$ 18 \\ 3 \\ 1 \\ 4 \\ 36 \\ 36 \\ 4 \\ 3 \\ 5 \\ 36 \\ 2 \\ 2 $	+ + + + + 3(2) 2-3 + 1 + + + + + + + +	} ?			} 6	17	+	18 4	2 33 2 2	+ + + +	20 100 80	+ 2-3 + +-1	5 83 62 3 25	21 2 36 36 2 7 36	+ + 2-4 2-3 1 1 +-1
Ceratodon purpureus Dicranum scoparium	11	24	1								3	+	30	1		20	+-1
– spurium Hypnum jutlandicum Lophozia ventricosa Pleurozium schreberi Pohlia nutans	$\begin{array}{c} 61 \\ 1 \\ 47 \end{array}$	36 8 36	$^{1-2}_{+}_{1-2}$							1		+++++	100 10	1-2 1	68 56	36 2 436	$egin{array}{c} 1-2 \\ + \\ 1-2 \end{array}$
Polytrichum juniperinum Ptilidium ciliare	6	10 11	+-1		5	+	3	7	+-1	10	19	+-1			7	4	1 +-1

¹ Konstansprocent på 10 udvalgte kvadrater à $2^{1}/_{2} \times 2^{1}/_{2}$ m, se videre i teksten om parcellen.

forsøget startedes, var der på arealet en del græsrige steder samt områder, hvor *Empetrum* eller *Genista pilosa* var dominanter ligesom *Deschampsia flexuosa*. pH lå inden behandlingerne på 4.0, 4.3 og 5.0 og 5.1. På den urørte kontrol fandtes pH 3.9 og 4.5. En undergrundsprøve havde pH 4.8. Efter behandlingen måltes i den afslåede parcel pH 4.0 og 4.2, i den pløjede 4.3 og 4.6 og i den afsvedne parcel 4.2, 4.6. Forundersøgelsen i 1937 efterfulgtes af analyser i 1938, 1939 og 1971 (det sidste år dog kun i form af skudtæthedsanalyse og dækningsanalyse på udvalgte kvadrater à $2^{1}/_{2} \times 2^{1}/_{2}$ m).

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(experimental area 3 cf. Fig. 1)

Afbrændt	parcel (Burnee	d off plot)		Afslået parcel	(Mowed plot)	Kontrol parce	el (Test plot)
1937 ST K D	1938 ST K D	1940 ST K D	1936 ST K D	1937 ST K D	1938 1940 ST K D ST K D	1936 ST K D	1969 ¹ K ⁰ / ₀ D
$\begin{array}{rrr} 8 & 33{+}{-}(2) \\ & 7 & {+}{-}1 \end{array}$	$ \begin{smallmatrix} 64*36 & 1-2 \\ 2 & 10 & +-1 \\ & 1 & + \end{smallmatrix} $	$ \begin{vmatrix} 83 & 36 & 2{-4} \\ 8 & 8 & +{-2} \end{vmatrix} $	$\left \begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\left \begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$ \begin{array}{ccc} 100 & 1-2 \\ 90 & 1-4 \end{array} $
$54 \ 36 \ +-1$	84 36 1-2	85 36 1-3	75 36 1-2	78 36 +-1	84 36 1-4 87 36 1-3	88 36 2-3	100 1-(2)
$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$ \begin{vmatrix} 1 & + \\ 22 & 20 & +-3 \\ 10 & 24 & +-2 \\ & 1 & + \end{vmatrix} $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccc} 7 & 15 & +-1 \\ 6 & 18 & + \end{array}$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{ccc} 100 & 1{-}2 \\ 10 & + \end{array}$
1 +	1 17 +	24 + 1 + 1	3 8 1	$\begin{array}{ cccccccccccccccccccccccccccccccccccc$	5 + -1 5 6 + -1 1 + 1 +	$\begin{array}{cccc} 3 & 1 & +-1 \\ & 2 & +-1 \end{array}$	100 1-5
		1 +	3 1-2	4 + (3)	3 1-3 1 4 1-3	1 +	
		2 +	-				
		17 17 +	6 36 +-1		5 2 + 47 36 +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	30 +
			$\begin{vmatrix} 2 + \\ 1 + \\ 1 + \\ 3 + -1 \end{vmatrix}$	1 +		$\begin{array}{cccc} 1 & + \\ 1 & + \\ 4 & 5 & + \end{array}$	
4 1 +	6?	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccc} 6 & 13 & + \\ & 1 & + \end{array}$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{ccc}100&2{-}4\\30&+{-}1\end{array}$
		1 +	$\begin{array}{ccc} 4 & +-1 \\ 8 & +-1 \end{array}$	3 +	3 + 3 5 + -1	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	
			$egin{array}{cccc} 2 & + \ 27 & 36 & + -1 \ 2 & 4 & + \end{array}$		$1 + \begin{array}{ccc} 2 & 3 & + \\ & ? & \end{array}$	$egin{array}{cccccccccccccccccccccccccccccccccccc$	20 +
	2 +	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	6 16 + -1 2 +		9 8 +	4 10 +(1)	
	12 7 +	$\begin{array}{ cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		6 8 +	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	70 +
2 +	3 3 +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1 6 +	$6 \ 10 \ + \ 1 \ 9 \ +$	$11 17 +-1 \\ 7 6 +$	

(Constancy percentage (K $^{0}/_{0}$ and coverage D) on 10 selected squares, $2^{1}/_{2}\times2^{1}/_{2}\,m$ large).

Notater om vegetationen blev endvidere gjort i 1940, 1945, 1950, 1953, 1957. Om vegetationen på Randbøl Hede se iøvrigt Böcher 1941 (Tabel 37) 1943 (p. 58-59).

Den skrælpløjede parcel. Efter pløjningen var parcellen meget sparsomt bevokset. Kimplanter af *Genista pilosa* kom allerede i 1938, men lyngkimplanter var meget sjældne, selv i 1940, hvor imidlertid lyngen var i genvækst fra rillerne mellem tørvene. Gyvel var også spiret de første år i stort tal. I 1940 skønnedes vegetationens totaldækning at være ca. ¹/₃. *Deschampsia* var den vigtigste art; ret stor dækning havde 2*



Fig. 5. Gludstedforsøget. Øverst parcelrækken fotograferet 1953 fra et punkt 15 m øst for den østligste parcel (kontrolparcellen) mod V-SV. Hjørnerne af parcellerne afmærket med nedstukne bjergfyrgrene. – Nederst samme område 1969 men med kontrolparcellen i forgrunden (græsvegetation med spredte lyngpletter). Den næste parcel har meget mere lyng og er den afslåede parcel. Denne parcels nordnordvest side markeres af de to lave cementpæle, der stikker op til højre og mere bagtil lidt til højre for midten. C.A.J. og TWB fot.

The experimental plots at Gludsted (exp. area 3 in Fig. 1). The upper picture from 1953 shows the four plots in a row (corners marked by Pinus mugo branches). - Lower picture the same area in 1969. The test plot in the foreground; to the back and between the two concrete posts, is the mowed plot which still has much *Calluna*, while in the test plot *Deschampsia flexuosa* or *Carex fusca* are predominant.


Fig. 6. Øverst: Randbølforsøget 1940. Parcelrækken set mod øst. Forreste parcel med spredte lyngtuer er den afslåede parcel, dernæst følger den afbrændte og den skrælpløjede. Lyse cementpæle i hjørnerne af parcellerne. Nederst t.v. parcelrækken 1950 set mod vest. Parcellerne fremtræder som en lyngklædt rektangel omgivet af gammel hede, meget rig på *Deschampsia flævuosa.* – Nederst t.h. i forgrunden et firkantet område, hvor man under krigen skar fladtørv. 1950 er området tæt, mager *Calluna*-hede med en del *Cladina* i fremvækst. Omkring det kvadratiske lyngområde dominerer *Molinia coerulea* på et område der muligvis dyrkedes endnu for 200 år siden. TWB fot.

Above: The experimental plots in Randbøl Heath 1940. The mowed plot with scattered *Calluna*, the burned off plot, and to the far right the lea-ploughed plot all with concrete posts at the corners. Below on the left: The plots in 1950 covered with uniform *Calluna* heath and surrounded by old heath with abundant *Deschampsia flexuosa*. Below on the right: A quadrate in the heath subject to removal of peat bricks during World War II and covered with uniform low *Calluna* heath. Surrounding areas dominated by *Molinia coerulea* (probably cultivated about 200 years ago).

TABEL 4. Randbøl-forsøget

	Skrælpløjede parcel (Lea ploughed plot)								Afsvedne					
Undersøgelsesår Metode	F ST	1937 K	D	ST	1938 K	D	ST	1939 K	9 D	1 ST	971 D	F ST	1937 K	7 D
Calluna vulgaris Cytisus scoparius Empetrum nigrum Genista anglica – pilosa	100 7 12	$ 36 \\ 8 \\ 5 \\ 36 $	$1-5 \\ 1-2 \\ +-1 \\ +-1$	12 4*	34 4 1 22*	$^{+-1}_{1-3}_{+}$	14 4 4	35 20* 1 17	$^{+-2}_{+-3}_{+}$	87 1 17	3-5 +-1 +-1	98 22 4 15	$36 \\ 4 \\ 21 \\ 14 \\ 36$	4-5 +-1 +-1 + +
Agrostis coarctata ²	10	11	+	6	16	+-1	6	22 1	$^{+-1}_{1}$	10	+-1	7	6	+
 panicea pilulifera Deschampsia flexuosa Festuca ovina Luzula multiflora Sieglingia decumbens 	$32 \\ 74 \\ 11 \\ 2$	$35 \\ 36 \\ 32 \\ 5$	$^{+-2}_{1-4}_{+-1}_{+}$	7 10	$25 \\ 35 \\ 1 \\ 7 \\ 1$	+(1) +-1 + +	$\begin{array}{c} 22\\ 16\\ 5\end{array}$	$34 \\ 36 \\ 24 \\ 12 \\ 1$	$^{+-2}_{-1}_{+-1}_{+(1)}$	$9\\79\\2\\2$	+ 1–3 + +	$\begin{array}{c} 24\\ 55\\ 6\end{array}$	$ \begin{array}{c} 1 \\ 36 \\ 36 \\ 26 \\ 10 \\ 2 \end{array} $	1 + +-1 + + +
Antennaria dioica Arabidopsis thaliana Arnica montana Campanula rotundifolia Chamaenerion angustifolium		6 1	$^{+-2}_{+}$		3 1 2	++++++		1 1 1 1	+++++++++++++++++++++++++++++++++++++++			74	17 7	+(1) +(1)
Chenopodium album Filago minima Galium saxatile Hieracium pilosella – umbellatum	13	34 1	++++++	1	1 22	+ +(1)	4	2 1 33	+ + +-1	9	+-1	18	24	+
Hypochoeris radicata Jasione montana Lotus corniculatus Ornithopus perpusillus Bumex acetosella		5	+		1		3	16 3	+++				1	+
Scorzonera humilis	4	1 9	++++	2	10	+	4	8	+-1				1 11	+ +
Cetraria juniperina Cladonia chlorophaea – coccifera – crispata – furcata	1 19 3	2 15 1	+ +-1 +							12	+	4	8	+
 gratica gracilis impexa mitis-silvatica cfr. pityrea rangiferina 	3 80 30	$ \frac{4}{36} 36 1 $	$^+$ 3-4 1-4 +	}?			2	1	+	$\frac{34}{3}$	$_{+-1}^{1-2}$	85 11	36 36 1	1-4 +-1
– squamosa – uncialis Cornicularia aculeata Lecidea uliginosa	3	8 6	+-1++					1	+			4	3	+
Parmelia physodes – tubulosa	34	36	+							34	+-1	20	17	+
Bryum caespiticum										2	+			
Ceratodon purpureus Dicranum polysetum – scoparium	2	5	+-1							8 10	+	2	1	+-
Hypnum jutlandicum Lophozia barbata Pleurozium schreberi Polytrichum piliferum	88 1	36 8	2-3 +-1	8	3	+	2	1	-+-	64 3	+-1+	96 7	36 27	3-5 +-1
Ptilidium ciliare										3	+			

 1 Se tekst s. 25. 2 A. coarctata Ehrh. ex Hoffm., sandsynligvis det samme som A. stricta J. F. Gmel.

(Experimental area 4, cp. Fig. 1)

pa	rcel (E	Burn	ed off	plot))							Afs	lået	parcel	(Mowe	d plot)			Kontro (Test	lparcel plot)
	ST	193 K	8 D	ST	193 K	9 D	ST	1971 D	F ST	193 K	37 D	ST	193 K	88 D	ST 1	939 D	ST ¹	971 D	1938 ST	1971 ¹ ST
	2*	25* 11	+ +	2* 13*	35* 27*	$^{+(1)}_{+-1}$	67	4-5	91 8	$36\\4\\10$	${3-5\atop +-1\atop +-2}$	45 8	$\begin{array}{c} 36\\ 3\\ 10 \end{array}$	$2-3 \\ + \\ +-1$	60 8	4-5 1 1-2	60 19	$1-5 \\ + \\ 1-5$	95 17	30 30
		21*	+-1	21* 14	* 18* 36	$^{+-1}_{+-1}$	16	+-1	15	$\frac{4}{36}$	$^+_{+-1}$	24	$\frac{7}{31}$	$^+_{+-2}$	3	+-1	16	+-2	29	
	17	20	+-2	24	36	+-3	4	+1++	10 11	9 8	+ +	17 8	17 4	+-1 +	13 6	$^{1-2}_+$	$\begin{array}{c}14\\6\\6\end{array}$	+-1 + +-1	2	10 4
	34 10 10	$ \begin{array}{r} 4 \\ 36 \\ 36 \\ 7 \\ 34 \end{array} $	$^{+-1}_{+-2}$ + 1	$ \begin{array}{r} 4 \\ 34 \\ 35 \\ 1 \\ 29 \end{array} $	$ \begin{array}{r} 4 \\ 36 \\ 36 \\ 25 \\ 36 \\ 2 \end{array} $	$1-2 \\ 1-2 \\ 1-3 \\ +-1 \\ 1-3 \\ +$	$ \begin{array}{c} 2 \\ 19 \\ 73 \\ 2 \\ 6 \end{array} $	+ 1 2 + +	29 64 12	$2 \\ 36 \\ 36 \\ 18 \\ 11 \\ 1$	$^+_{+-2} + -1 + +$	31 83 13 6	$2 \\ 36 \\ 36 \\ 29 \\ 16 \\ 1$	$^+$ 1-2 2-3 +-1 + +	$ \begin{array}{r} 42 \\ 78 \\ 30 \\ 5 \end{array} $	$^+$ 1-2 3-4 +-1 +	$\begin{array}{c} 21 \\ 76 \\ 4 \end{array}$	$^{+-2}_{2-3}$ + +	$\begin{array}{c} 7\\ 86\\ 5\\ 4\end{array}$	$3\\92\\3$
		7	+-1		9	+				7	+		3	+-1		+				
		5	1		6 1	+-1+	2	+								+				
	4 1	16	+- 1 +	3	$1\\13\\1$	+ +- 1 +	4	+	31	$ \begin{array}{c} 36 \\ 1 \\ 1 \end{array} $	+-1 + +	29	36 4	$^{+-2}$	49	+-1	49	+-1	6	35
	1	2 1	+++++	5 3	8 6	$^{+-1}_{+-1}$				6	+		8	+	1	+			1	
	1	1 18	+ +-1	26	29	+-3							1	+						
		1	+		1	+		1		$\frac{1}{3}$	+++++++++++++++++++++++++++++++++++++++		$\frac{1}{4}$	+++++++++++++++++++++++++++++++++++++++		+++++				
	3	$22 \\ 2$	+-1 +	7	19 5	+-1 +-1			1	11	+-1	3	19 1	$^{+-2}_{+}$	3	+-1				16
							20	+	15	12 1	+ +	9	8	+	30	+	19 3	+ +	6	13
					1	+				$\frac{1}{2}$	+++				4	+			7	
				3	1	+	48 9	$^{1}_{+-1}$	84 32	$36 \\ 36$	$\begin{array}{c} +\\ 2-4\\ +-2\end{array}$	83 17	$\frac{36}{19}$	$^{2-3}_{+}$	81 18	$_{1}^{3-4}$	27 22	$\substack{1-3\\2-5}$	99 39	$\begin{array}{c} 60 \\ 26 \end{array}$
									$\begin{array}{c c} 4\\ 4\\ 6\end{array}$	$ \begin{array}{c} 1 \\ 2 \\ 3 \end{array} $	+++++++++++++++++++++++++++++++++++++++					+			3	
					19				3	$\frac{4}{6}$	++++++				$\frac{1}{6}$	++++++			7 1	
				4	12	+	19	+	13 2	15 1	++	2	6	+	4	+	3	+	7	10
							2	+		1	+						2	+		
				4	1 1	+++	4	4.							6		2	+		
					?10	+	4 82	+ +-1	4 82	$\frac{5}{36}$	$^+_{2-4}$	1 83	$\frac{3}{36}$	$^+_{1-2}$	1 84	+ 1	5 35	+++++++	4 66	52
				1	7	+	6	+	3	36	+-2	4	7	+-1			7	+	7	10
								+	5	6	+						6	+		

endvidere Agrostis coarctata, Carex pilulifera og Galium saxatile. Cladonia impexa og mitis-silvatia var tiltagende. Spredt fandtes de to Genista arter, Festuca ovina, Luzula multiflora, Rumex acetosella, Jasione, Hieracium pilosella, Hypochoeris radicata og Viola canina. I 1945 var Deschampsia overvældende og Cladina-planterne endnu ganske små. 1950 karakteriseredes parcellens vegetation som lav græsrig lynghede (Fig. 6) med en del Genista pilosa og Cytisus og lidt Empetrum. I 1953 var der tale om en ujævn, men ofte høj lynghede med meget Genista pilosa, en del Cytisus, Festuca ovina og lidt Empetrum og Galium saxatile. Der var endnu åbne gruspletter med Cladonia floerkeana og glauca. Lyngen var pletvis gået ud. 1957 var vegetationen blevet til en høj Callunahede med spredte strå af Deschampsia og Festuca ovina, flere Cytisus-buske og en del Genista pilosa. Empetrum og Viola canina fandtes spredt. Bunden var nu helt dækket af Cladonia impexa, Hypnum jutlandicum og en del Dicranum. Dette billede ændredes langsomt til det nuværende, hvor lyngen deler herredømmet med Deschampsia og licherne svækkes af græsset.

Den afsvedne parcel. Allerede det første år (1938) spirede ny lyng og begge visse-arter i stort tal, lav- og mosvegetationen var helt undertrykt. Agrostis coarctata var i kraftig fremgang, og i 1940 var dette græs mindst lige så dominerende som Deschampsia. Der var unge Calluna-planter på det meste af arealet og den for afsvedne typiske kryptogam-vegetation: meget Lecidea uliqinosa, Cladonia chlorophaea, C. glauca, Ceratodon purpureus, Bryum caespiticum og Polytrichum piliferum. Dækningen af karplanterne nåede ikke over 1/3 af arealet. Der var meget Carex pilulifera, Luzula multiflora, Rumex acetosella og Viola canina, endvidere en stor plet Carex panicea. Af andre arter bør nævnes begge Genista arter, Cytisus, Antennaria, Galium saxatile, Arnica, Solidago, Hypochoeris radicata, Festuca ovina samt annuelle og bienne arter som Jasione, Viola tricolor og Filago minima. I 1945 var Lecidea-skorperne ved at forsvinde. Agrostis coarctata var stadig dominant, men der var nu lynghede flere steder især med små laver og lidt mos. Selv fem år senere, i 1950, var det de små Cladonia-arter (C. floerkeana, C. glauca, C. chlorophaea) der var fremherskende i en lav Calluna-hede med Genista pilosa og lidt Cytisus. Græsset var nu svækket, men spæde Cladina-planter sås overalt. I 1953 var parcellen dækket af 30 cm høj Calluna. Der var nu temmelig store pletter af Cladina, men også stadig steder hvor Polytrichum piliferum, Cladonia floerkeana og glauca holdt stand. Empetrum, der var ret hyppig før afsvidningen, var ikke genindvandret; der var stadig en del Cytisus og meget Genista pilosa. I 1957 var de små *Cladonia*-arter endelig helt tilbagetrængt, og der var meget *C. impexa* i høj lynghede med begge visse-arter, gyvel og bølget bunke. I 1971 konstateredes en stærk fremgang for sidstnævnte græs, medens sand-hvene (Agrostis coarctata), der før var betydningsfuld, stod meget spredt. Det var endvidere tydeligt, at lyngen var gammel og svækket. Græsset ville derfor nok erobre dens terrain efterhånden som lyngplanterne døde.

Den afslåede parcel. Her genvandt *Calluna* snart en fremtrædende plads, omend *Deschampsia flexuosa* sås mere. *Cladina*-tæppet voksede hurtigt frem. I 1940 var parcellen dækket af en *Calluna-Deschampsia-Cladonia impexa* sociation med en

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del Agrostis coarctata, Carex pilulifera og Empetrum. Fem år efter, i 1945, havde heden en del Cladina-pletter, ofte med Deschampsia, men også med Empetrum og Genista pilosa eller Galium saxatile. I 1950 var de rene Cladina-pletter næsten groet til, og Calluna og Deschampsia delte herredømmet. I 1953 var der tale om en 40–50 cm høj Calluna-hede med lidt Cytisus, men meget Genista pilosa, Carex pilulifera, Deschampsia og Agrostis coarctata. Der var store græspletter uden lyng, men med Cladina og Viola canina. Lyngen var flere steder død. I 1957 blev parcellen stadig karakteriseret som meget kraftig Calluna-hede med meget græs og Cladina. Der var desuden de samme arter som nævnt i tabellen fra 1971, men desuden stadig Viola canina og Hypochoeris radicata. I 1971 var lyngen på tilbagetog, se Fig. 7.

Kontrolområdet ud for den midterste parcel blev undersøgt igen 1971. Desværre var det ikke muligt helt nøjagtigt at fastslå, hvor skudtætheds-cirklerne var lagt i 1938. Derfor kan de to kolonners tal ikke sammenlignes med samme sikkerhed som på de foregående forsøgsområder. Fra iagttagelserne gennem årene er det imidlertid helt klart, at *Calluna* var i jævn tilbagegang medens revling og bølget bunke tog til. Samtidig med at græsset blev tættere, blev lavet svækket. Nytilkommen i 1971 var *Trientalis europaea*, der også gror i heden mellem parcellerne og den lave klitvold langs Kirstinelysts jorder.

C. Forsøg på bakkesand

5. Forsøget i Hammer Bakker (Tabel 5 og Fig. 1 område 5).

Hammer Bakker ligger nordøst for Nørresundby tæt ved Vodskov. En række på fire parceller blev anlagt 1936 på en svagt mod nordøst skrånende hedebakke i det område af Hammer Bakker der tilhører Dansk Botanisk Forening. Dette areal blev i 1911 skænket foreningen af sagfører A. OLESEN, Nørresundby. På initiativ af det daværende udvalg for Naturfredning blev arealet fredet, og det blev overdraget professor A. MENTZ årligt at tilse arealet. Botanisk Forening iværksatte 1915 botaniske undersegelser på det fredede areal. Resultaterne findes samlet i en lille serie afhandlinger i Botanisk Tidsskrift bd. 39, (GRØNTVED 1926, SYRACH LARSEN 1926 og MØL-HOLM HANSEN 1925). Enkelte analyser omtales i Böcher 1943 (pp. 26 og Fig. 9 A).

De fire parceller kom til at ligge sydøst for den bakketop i den nordlige del af det fredede areal, der øverst har en gravhøj med fredningsmærke (smlg. Fig. 8 i baggrunden og Bot. Tidsskrift bd. 39 Tavle 3). I 1936 var der kraftig lynghede på området, hvor parcelrækken blev afmærket, men denne hede var ung, idet den var indvandret på tidligere dyrkede marker. Dette fremgår ikke blot af Mølholm Hansen's bemærkninger (l.c. s. 282) men også af en samtale i august 1937 med fru MAREN NIELSEN, Atterupgård, der fortalte at dyrkningen var fortsat til omkring 1890, hvor Bakkerne erhvervedes af sagfører A. OLESEN. Plantager blev anlagt på en del af arealerne, men sagføreren lod andre dele henligge, således at de sprang i lyng. Oprindelig var der kun hede på de højeste toppe.

De fire parceller blev lagt i række i retningen NV-SØ. Da det skønnedes vigtigt også at kunne vurdere den indflydelse tidligere tiders tørveafgravning kan have haft,



Fig. 7. Randbøl Hede forsøget. Øverst: Parcelrækken 1940 set mod vest. Skaldbakkerne med vindbrud i baggrunden. I forgrunden den skrælpløjede parcel endnu med striber af blotlagt grus og småsten. Dernæst den afbrændte parcel og bagest (henimod hjørnepælen til venstre i baggrunden) den afslåede parcel. – Nederst: Omtrent samme sted i august 1971. Personen står ved samme hjørnepæl som ses på det øverste billede. *Deschampsia flexuosa* dominerer både på parcellerne og på hele den omgivende hede, hvor der også ses spredt opvækst især af bjergfyr. TWB og JB fot.

The experimental plots in Randbøl Hede (exp. area 4) in 1940 (above), and in 1971 (below); view towards the west. On the photo from 1940 the furrows in the ploughed plot are seen in the foreground; there are still many small stones laid bare after the ploughing. Behind is the burned off plot and the mowed plot. The white concrete post is in the northwestern corner of the latter plot. The person in the bottom picture is standing by the same post. The heath has changed into a *Deschampsia flexuosa* community.



Fig. 8. Hammer Bakker forsøget set fra øst mod vest med den skrælpløjede parcel i forgrunden. I 1939 præges parcellen af *Carex pilulifera, Deschampsia flexuosa* og *Rumex acetosella*, i 1953 af *Calluna* (samt *Deschampsia* o.fl. hvilket ikke kan ses) og i 1969 af *Deschampsia* og enorm opvækst af *Juniperus, Sorbus, Pinus* m.m. Drengen sidder ved hjørnepælen lige ved en stor ene uden for parcellen. På det midterste billede er hjørnepælen dækket af en kasket og en mappe. TWB fot.

The experimental plots in the heath in Hammer Bakker (exp. area 5 in Fig. 1). The row of plots is viewed from the east towards the west and the lea-ploughed plot is in the foreground. The boy in the picture from 1969 is sitting by the concrete post at the northeast corner of the plots. A successional grassland stage (1939) is followed by a *Calluna* stage (1953). The final stage may be *Juniperus* thicket with *Deschampsia flexuosa* or a mixed woodland.

blev lyngtørven totalt fjernet på en af parcellerne. De tre øvrige blev behandlet som på de andre arealer, men der blev ikke anlagt nogen permanent ubehandlet parcel.

pH måltes til mellem 4.0 og 4.4 i de fire parceller før behandlingen; der var tale om en tynd, løs morskjold over bakkesandet. I forhold til alle andre hedejorder der undersøgtes, var humusindholdet i prøverne lavt. I 1938, efter behandlingerne, måltes højere pH-værdier, mellem 4.6 og 4.7; pH 5.8 blev målt i det forkullede øvre lag af jorden på den afsvedne parcel. Sandet under det forkullede lag havde pH 4.6. I 1971 lå værdierne gennemgående endnu højere, 5.0, 5.4, 5.6 og 5.7, hvilket dog i nogen grad kan skyldes ændret metodik. Imidlertid havde området nu ofte mere karakter af at være en *Deschampsia*-græsmark end en lynghede.

En cirklingsanalyse foretaget 1915 af A. MENTZ omtrent hvor parcelrækken blev anlagt senere findes gengivet i GRØNTVED (1926 s. 251). Heden var da rig på Hieracium pilosella og Anthoxanthum. Cladonia-arterne dækkede kun ca. 2 %/0 afarealet. De af MENTZ konstaterede frekvenstal fra 1915 bringes her i en særlig kolonne forrest i Tabel 5, idet de giver et interessant sammenligningsgrundlag. På grund af hedens forhistorie (tidligere dyrkning) og ret lave surhedsgrad er artstallet højere end i de øvrige undersøgte heder. Ialt er lidt over 100 arter blevet registreret på parcellerne i årrækken 1936–1971. Man lægger her mærke til den ret sparsomme lavflora, og at arter som *Cladonia scabriuscula* og *C. tenuis* forekommer her, medens de ikke indgår i analyserne fra de andre heder. Begge har imidlertid, om end i forskellig grad, nok større tilknytning til magre græsfælleder end til egentlige lyngheder (smlg. Mølholm HANSEN & LUND 1929). Mossernes dominans i bundlaget er meget udpræget. Det skyldes den svage hældning mod nord. Imidlertid er den overvældende hyppighed for Hylocomium splendens, rigelig forekomst af Lophocoleg bidendata og tilstedeværelsen af Rhytidiadelphus squarrosus og Pseudoscleropodium purum sikkert også udtryk for at jordbunden er relativt rig. Iøvrigt kommer vegetationen nærmest ind i den gruppe af mosrige heder, der er kaldt Myrtillion boreale (Böcher 1943 p. 21).

Den rigere jord må også anses for årsagen til forekomsten af en lang række urter, således Chamaenerion angustifolium, Rubus idaeus, Lotus corniculatus, Achillea millefolium, Veronica chamaedrys, Succisa pratensis o. fl. Hertil må føjes de mange træer og buske, der i løbet af årene gor sig gældende i stigende grad og vil ende med at omskabe området til en slags kratskov af Sorbus aucuparia, Juniperus communis med spredt Pinus silvestris, Picea exelsa og Acer pseudoplatanus (smlg. Fig. 11). I sin beskrivelse af trævæksten på Hammer Bakker omtaler Syrach Larsen (1926) Fagus silvatica, Quercus robur, Populus tremula, Betula pubescens, B. verrucosa, Sorbus aucuparia, Frangula alnus, Pyrus malus, Salix aurita og Juniperus communis. Grøntveds liste (1926) over fanerogamer indeholder desuden Salix repens, tre Ribes-arter samt Picea abies, P. glauca, Pinus silvestris og P. mugo, der alle udtrykkeligt nævnes som plantede, altså dengang endnu ikke, således som nu, forvildede. Acer pseudoplatanus nævnes slet ikke, ej heller Sorbus suecica, og om S. aucuparia, der nu spreder sig i stort tal ud over heden, siges »enkelte eksemplarer spredt i krattene«.

Den skrælpløjede parcel. Pløjningen, der fandt sted sent 1936, var omhyggeligt udført. I 1937 vrimlede kimplanter frem af *Carex pilulifera* og *Rumex actosella*.

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Det tog lang tid for *Calluna* at nå frem til fuld dominans (se Fig. 8). Endnu i 1940 blev parcellens vegetation karakteriseret som en *Carex pilulifera*-sociation med meget *Calluna, Deschampsia, Agrostis* og *Anthoxanthum*. Kun i pløjningsfuren midt ned gennem parcellen var der ren lyngvegetation. I 1940 noteredes allerede stor hyppighed for *Antennaria dioica*, der åbenbart fik særlig gode chancer på denne parcel og beholdt sin stærke position til 1953 og sikkert længere. *Ceratodon purpureus* var også meget vigtig i 1940, men forsvandt igen, fortrængt især af *Hypnum jutlandicum*, der senere måtte vige førerpladsen som en følge af fremtrængen af *Hylocomium splendens* og *Pleurozium schreberi*. *Anthoxanthum*, der sikkert oprindelig spillede stor rolle i den græsvegetation, der sprang i lyng, gik stærkt frem lige til 1953, men rivende tilbage samtidig med at mostæppet blev mægtigere. Endnu i 1969 stod den spredt på parcellen, men i 1971 var den sjælden. Allerede i 1969 karakteriseredes parcel-vegetationen som lynghede rig på *Deschampsia* og *Vaccinium myrtillus* (Fig. 8, 10), men i 1971 var heden her ikke blot rigere på græs og blåbær, den var tillige blevet uensartet med opvækst af ene og gran (Fig. 10, nederst).

Den afsvedne parcel. Det første år efter afsvidningen, der fandt sted 1937, var der rig spiring af *Calluna* og *Genista anglica* samt flere enårige. Blandt disse blev *Filago minima* særlig hyppig i 1939, men forsvandt derefter samtidig med at *Ceratodon* tiltog. Denne mos opnåede sin største tæthed i 1940. *Deschampsia flexuosa* blev meget hurtigt fremtrædende. I 1940 karakteriseredes vegetationen som et *Deschampsia-Agrostis tenuis-Anthoxanthum* stadium med meget *Calluna*, *Lotus*, *Carex pilulifera*, *Antennaria* og *Ceratodon*. Vigtig var endvidere *Hypochoeris radicata* og *Festuca rubra*. I 1953 var der ensartet tæt *Calluna-Deschampsia*-mos-hede (se Tabel 5), hvori *Lotus*, *Antennaria*, *Solidago* og *Anthoxanthum* spillede stor rolle. Dette billede holdt sig imidlertid ikke; i 1969 benævntes vegetationen som en *Deschampsia-Chamaenerion-Pleurozium*sociation med spredt *Calluna* samt *Empetrum*, *Genista anglica*, *Vaccinium myrtillus* og *vitis idaea*, *Sieglingia* o. fl. samt opvækst af røn og ene. I 1971 var *Chamaenerion* noget svækket, men *Deschampsia* endnu mere fremtrædende.

Den afslåede parcel. En enorm spiring af *Carex pilulifera* o.fl. i 1937 efterfulgtes af lyngspiring i 1938. I 1939 var parcellen grøn af *Lotus corniculatus*. Der var desuden en del *Deschampsia* og spredt *Festuca ovina* og *Campanula rotundifolia*. I 1940 var successionen nået frem til et *Calluna-Lotus*-stadium med *Deschampsia* og *Anthoxanthum* som subdominanter, endvidere med meget *Solidago* samt endnu en del pionérplanter som *Rumex actosella*, *Hypochoeris radicata*, *Jasione*, *Ranunculus repens*, *Gnaphalium silvaticum* og *Ceratodon pupureus*. Der var rosetter af en *Cirsium*-art og lidt *Nardus stricta*. Begge forsvandt igen de følgende år. I 1953 var der tæt *Calluna-Deschampsia-Pleurozium*-hede, men den degenererede til en *Deschampsia-Pleurozium*-soc med *Chamaenerion* og meget *Genista anglica* (1969) og med opvækst af *Juniperus*, *Sorbus aucuparia* og *Pinus silvestris* (se Fig. 9). I 1971 opnåede *Calluna* kun ST værdi på 37, medens *Deschampsia* fik 87 og *Pleurozium* 83 og træerne var vokset betydeligt.

Den tørveafskrællede parcel. Her var der i 1937 nærmest tale om en tabula rasa-situation. Tørvene var fuldstændig fjernet, og på den jævne nøgne sandoverflade sås masser af kimplanter, men ingen mosser og laver. Det første stadium prægedes



Fig. 9. Hammer bakker forsøget. Den parcel hvor fladtørv-afgravning havde fundet sted set fra vest mod øst. I 1953 var der endnu lav, græsrig *Calluna*-hede og på visse af de små kvadrater meget tæt *Lycopodium clavatum*, der ses med talrige strobili. I 1969 var der endnu lynghede på parcellen og *Lycopodium*-arten ses endnu. En skovfyr er groet frem nær skellet til den næste parcel (hvor lyngen blev slået af i 1937), men som nu er behersket af *Deschampsia*. TWB fot.

The plot in Hammer Bakker which was subjected to peat cutting and removal of the shallow dry peat layer. In 1953 *Calluna* formed a dense and low vegetation, in some squares with abundant *Lycopodium clavatum*. In 1969 *Lycopodium* was still frequent and the *Calluna* heath coarser. A specimen of *Pinus silvestris* has appeared on the border of the moved plot which is seen behind and is dominated by *Deschampsia flexuosa*.



Fig. 10. Hammer Bakker. Forsøgsområdet 1969 og 1971. Øverst: Udsigt over alle fire parceller 1969. En diagonal fra parcelrækkens sydøsthjørne (ved tasken forrest) til nordvesthjørnet (ved person) skærer næsten lodret gennem billedet. Forrest skrælpløjede parcel, i dens øvre rand en røn og en hvidgran. Lidt til højre for personen i baggrunden en stor ahorn, smlgn. Fig. 11. – Nederst: Omtrent samme udsigt 1971, men fotografiet viser parcelrækkens øvre og sydlige kant. Tonkinstokken står i østranden af den skrælpløjede parcel, $2^{1}/_{2}$ m fra parcelrækkens sydøsthjørne. Personen står i parcelrækkens sydrand mellem den hvidgran, der ses på det øverste billede, og den store skovfyr på den fladtørv-afgravede parcel længst borte, smlgn. Fig. 11. *Deschampsia* er tydeligvis blevet langt mere dominerende i perioden 1969–1971. TWB fot.

The experimental plots in Hammer Bakker. Above, diagonal view (1969) of the four plots (the diagonal runs from the southeast corner at the bag to the northwest corner at the person in the background). Below the same, but looking eastward along the upper and southern border of the row of plots. The lea-ploughed plot is in the foreground. Reproduction of forest trees (*Pinus silvestris, Picea abies, P. glauca, Sorbus aucuparia*), and juniper.

af Rumex acetosella og Carex pilulifera. Disse to arter spillede også ret stor rolle i 1939, men her begyndte mosserne (Ceratodon og Hypnum jutlandicum) at danne bunddækning, og i 1940 kunne parcellen karakteriseres som Calluna-hede med de samme mosser, Polytrichum piliferum og flere Cladonia-arter. Rumex acetosella var omtrent forsvundet og Carex pilulifera gået meget tilbage, til gengæld var Deschampsia og Solidago i klar fremgang. Endnu i 1953 var der stadig lav Calluna-hede, men nu flere steder med store pletter af Lycopodium clavatum (Fig. 9). Blandt laverne var der relativ stor hyppighed af *Cladonia scabriuscula* og *Baeomyces* sp. dannede en del skorper over jorden. I 1969 var vegetationen en Calluna-Deschampsia-Pleurozium hede med en del Lycopodium; i nordvesthjørnet var dominanterne Deschampsia-Chamaenerion samt Pleurozium og Hulocomium splendens. En stor skovfyr var groet op nær parcellens sydøstre hjørne. Der var også opvækst af rødgran og ene. Slutstadiet, der også fremgår af Tabel 5, prægedes af særlig rig træopvækst, af nyindvandret Vaccinium myrtillus og Empetrum (Vaccinium vitis idaea havde indfundet sig før 1969). Lycopodium var gået tilbage, men bregner havde indfundet sig bl.a. i slagskygge-området under den store skovfyr, der ses på Fig. 11. Trientalis var i klar fremgang, men laverne var næsten helt forsvundet. I denne parcel, hvor indgrebet ved fjernelse af tørvene i flere henseende måtte virke særlig radikalt, var Calluna i 1971 stadig så kraftig, at den prægede fladen. Parcellen fremtrådte som en brun firkant overalt omgivet af områder med dominerende Deschampsia flexuosa.

Der var i Hammer Bakker ikke lavet nogen kontrolparcel. Parcelrækken var 1936 omgivet af hede akkurat som den, der fremgår af de fire forundersøgelsesanalyser (F i Tabel 5). I 1971 var næsten hele den skrånende flade, hvor parcellerne var lagt, en stor *Deschampsia*-mos-mark med træopvækst, især af røn, og mængder af enebær (se Fig. 11).

D. Forsøg på flyvesand

6. Forsøget i Østerild Klit (Tabel 6 og Fig. 1 område 6).

I det store klithedeterrain nord for Østerild plantage, ca. 1 km vest for Abildhave, blev der 1936 på klitvæsenets arealer afmærket 6 parceller à 15×15 m. Klitplantør TH. KROGH fandt et ypperligt, relativt plant sted i en stærkt varieret hede, der mod øst, syd og nord var omgivet af en lav parabelklit. Der kom til at ligge fire parceller i række (1-4) fra øst mod vest, men syd for de to vestligste, og stødende lige op til dem, yderligere to parceller (5-6).

pH 1936	(F) p	H 1938
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Parcel	1 (østligst). Skrælpløjedes 1936	3.7	4.4
_	2 (vest for 1). Afsvedet 1936–37	3.6	4.4
	3 (vest for 2). Gravet med spade 1936	3.5	4.6
_	4 (vestligst). Tørv afskåret 1936–37	3.4	4.1
	5 (syd for 3). Lyngen slået med le 1937	_	4.1
	6 (syd for 4). Kontrol	-	4.0



Fig. 11. Hammer Bakker 1971. Parcelrækken set fra dens vestgrænse mod øst. Øverste billede viser et kvadratisk felt med lyng, den sidste rest af den hede der efterulgte kulturindgrebene. Heden holdt sig længst på den fladtørv-afgravede parcel i forgrunden. Tæt ved parcellens nedre, nordlige rand en stor ahorn. Skovfyrren nær grænsen til den afslåede parcel svarer til det træ der ses på Fig. 9 nederst. – Den store skovfyr på det nederste billede står meget nær parcelrækkens vestrand og nær dens øvre, sydlige rand. Billedet er således taget i den stik modsatte retning af billedet nederst på Fig. 10. TWB fot.

The westernmost plot in Hammer Bakker as seen from the west in 1971. The plot was subject to peat layer removal and maintained a *Calluna* heath longer than the other plots. A large specimen of *Pinus silvestris* near the southwest corner has grown up inside the plot (lower picture), while that of *Acer pseudoplatanus* (upper picture) stands a little outside and north of the plot.

Biol. Skr. Dan. Vid. Selsk. 19, no. 5.

Vegetationen er præget af klokkelyng, pors, mosebølle o.fl., og er en typisk fugtig hede tilhørende *Empetrum-Vaccinium uliginosum*-gruppen af *Ulicio-Ericion tetralicis*, cp. Böcher 1943, pp. 85-92.

Jordbunden var temmelig fugtig, og flyvesandet var overlejret af en 1-3 cm tyk mortørv. Denne blev helt fjernet på parcel 4, medens den blev vendt nedad i den håndgravede parcel 3. Også i parcel 1 var tørven godt vendt, således at det hvide sand dækkede parcellen.

Den skrælpløjede parcel (1). I 1937 spirede mange kimplanter af Calluna og Erica, især i pløjefurerne. Derimod skød Salix arenaria og Myrica gale fra de i jorden liggende dele. I 1938 var disse to arter mest fremtrædende, og der var meget få nye lyngkimplanter. I 1939 var der flere lyngkimplanter, og derefter kom der fart i udviklingen. I 1940 var to trediedel af den sydlige del af parcellen dækket især af Calluna, Erica og Murica, medens den nordlige del, der lå lidt højere og havde tørrere bund, var præget af spredt Carex arenaria, Juncus squarrosus og Luzula multiflora. Her var Corynephorus canescens og Deschampsia flexuosa indvandret og Empetrum relativt hyppig. Totaldækningen her lå mellem en trediedel og halvdelen af arealet. I 1953 noteredes på parcellen mager, tør, likenrig *Calluna*-hede med spredt *Empetrum* og Salix samt lidt Erica og Myrica. På de højereliggende dele var der endnu bart sand med likener og tegn på vinderosion (Cladonia destricta-Lecidea- sociation). Også i 1964 var parcellen en likenrig Calluna-hede (se Tabel 6). I 1971 var der i det laveste parti Erica-sociation med bl.a. Scirpus caespitosus, Myrica, Vaccinium uliqinosum og Deschampsia flexuosa, medens den højere del havde Calluna-Empetrum-soc. med Murica, Erica, Salix, Carex arenaria og Deschampsia samt meget Cladonia, især C. impexa og en del C. mitis. Der var stadig lidt C. destricta, men mosserne var trængt stærkt tilbage af rensdyrlaverne.

Den afsvedne parcel. (2). Kort efter afsvidningen i 1937 skød Myrica kraftigt op. I 1938 var der mange lyngkimplanter. I 1939 var Myrica fremherskende med Carex arenaria som co-dominant på tørrere dele og Erica på fugtigere dele. I 1940 var der tæt Carex arenaria-soc. med Myrica og Calluna på den tørrere del og Calluna-Erica-Murica-soc. på den fugtigere. Forskellen mellem de to dele udviskedes noget i 1953, hvor parcellen havde karakter af kraftig Calluna-hede med meget Murica og spredte store Cladina-puder - eller pletvis meget Pleurozium. I 1964 (se Tabel 6) noteredes død Calluna med dækning 1–3 på 15 af de små kvadrater, og levende Calluna opnåede kun beskedne skudtæthedstal. Der havde nu indstillet sig to vidt forskellige vegetationer. På de tørrere dele en Empetrum-hede med Erica, Calluna, Carex arenaria, Salix arenaria og Cladina-arter, og på de fugtigere dele en Erica-Vaccinium uliginosum-soc. også med Cladina. Men der var også små øer f.eks. med Empetrum-Calluna eller Salix-Empetrum, begge ledsaget af Carex arenaria. Antennaria dioica og Carex pilulifera havde holdt sig især på grænsen til parcel 3 (den håndgravede parcel). Myrica, der ved forsøgets begyndelse var meget fremtrædende, var nu ret sparsomt tilstede, sandsynligvis fordi hele området var blevet tørrere og konkurrenceforholdene ændret. Af



Fig. 12. Den skrælpløjede parcel i heden ved Østerild i sept. 1964, 28 år efter pløjningen. De to søndre hjørnesten ses forrest og udfor * til venstre i billedet. Personen i baggrunden står ved den nordvestlige hjørnesten. Heden er meget uensartet. Der ses bl.a. flere pletter med kraftig *Salix arenaria*. TWB fot.

The lea-ploughed plot at Østerild (exp. area 6 in Fig. 1) in 1964, or 28 years after ploughing. The vegetation is heterogeneous with scattered vigorous *Salix arenaria*.

Tabel 6 fremgår det, at *Erica* i perioden 1936–64 aftager, medens *Carex arenaria* tiltager betydeligt i tæthed.

Den håndgravede parcel. (3). På den næsten helt nøgne sandede overflade vrimlede det i 1937 med kimplanter, heriblandt mange af *Juncus squarrosus*. Denne art blev allerede 1938 meget almindelig på den vestlige del af parcellen, og i 1939 blev der her en tæt, høj *Juncus squarrosus*-sociation med *Luzula multiflora* (Fig. 13, Tabel 6). Imidlertid var denne vegetation blot et kort successionsstadium. I 1940 var *Calluna* i kraftig vækst og rigt blomstrende. *Juncus squarrosus* og *Luzula multiflora* var i stærk tilbagegang, men *Carex arenaria* dominerede i det tørre NØ-hjørne af parcellen. I 1953 var *Calluna* og *Myrica* de vigtigste arter. *Juncus squarrosus* fandtes endnu, men blev skygget ihjel af dværgbuskene og var blevet helt underordnet. Men *Carex arenaria* hævdede sig godt. I 1964 var der dels et højnet område med kraftig hede (*Calluna-Empetrum-Erica*), dels et lavere liggende område med tæt *Carex arenaria*. Det tidligere *Carex arenaria*-område var nu blevet til hede, medens hedebuskene var forsvundet fra det lavere område mod sydvest. I 1971 var der stadig to klart adskilte vegetationstyper. Heden var en *Calluna-Salix-Empetrum*-soc. med *Deschampsia flexuosa*, *Carex* arenaria, Cladonia impexa, mitis og silvatica samt en del Dicranum spurium. Græs-starvegetationen var enten helt domineret af Carex arenaria eller Deschampsia og Carex arenaria. På grænsen til hede-delen var der Erica-Vaccinium hede også med Carex arenaria. I græs-star-området var der hverken mosser eller laver, se iøvrigt Fig. 14.

Den fladtørv-afgravede parcel (4). Efter at tørvene var fjernet, fremtrådte parcellen som en sandet, men ikke plan flade. Der var flere lave sænkninger, hvor der kom særlig livlig opvækst af kimplanter af Calluna, Erica og Empetrum. Der var her kun ret få kimplanter af Juncus squarrosus, som var så fremtrædende i naboparcellen (3). Forskellen måtte hidrøre fra, at man på parcel 4 havde fjernet tørven og derved gjort bunden tørrere (ringere vandkapacitet) og fattigere. I 1939 var parcellen koloniseret især af Calluna, som i 1940 dannede en mager, kun 4–5 cm høj hede med Erica og Salix, lidt Myrica og Carex arenaria, panicea, pilulifera, Scirpus caespitosus og Juncus squarrosus samt en del Polytrichum. På de højere partier var dækningen i 1940 kun 30-50 %, medens den var nær 80-90 % i sænkningerne. På de højere dele fandtes bl.a. Hypochoeris radicata og Antennaria samt mange laver især Cornicularia acueleata, Cladonia mitis, C. destricta, C. furcata og C. gracilis samt tætte »kager« af C. chlorophaea og Lecidea uliginosa. Også i 1953 var heden på denne parcel påfaldende mager og lav med laver på de voldagtige forhøjninger gennem parcellen. I 1964 var billedet ændret til en likenrig Calluna-Erica-Salix hede (se Tabel 6). I 1971 havde der i de lavere dele indstillet sig en Erica-hede med Carex arenaria, Myrica og Vaccinium uliqinosum og i bundlaget Cladonia mitis og impexa, Pleurozium, Polytrichum og nogle levermosser. På den voldagtige del var der kommet en likenrig Calluna-Salix-hede med spredt Erica. Her fandtes også lidt Corynephorus, Antennaria dioica, Hieracium umbellatum, Cornicularia, Cetraria islandica, Cladonia destricta o.fl. Empetrum forblev påfaldende sjælden i denne parcel. I den ubehandlede del vest for parcellen og syd for parcel 1 og 2 var der derimod meget revling; det samme gjaldt den ubehandlede parcel nr. 6 (se Tabel 6 og Fig. 15).

Den afslåede parcel (5). Undtagelsesvis foretoges ingen forundersøgelse her, men parcellen afveg oprindeligt ikke på noget væsentligt punkt fra 1-4 og 6. Det første år efter at lyngen var slået af og fjernet (1938) fremkom en *Erica*-hede med en del *Myrica*. Også i 1939 var der tale om en *Erica*-hede, men *Myrica* var mere sparsom, medens *Calluna*-kimplanter sås i stort tal. Imidlertid må et stort antal af disse kimplanter være omkommet, for i 1940 var der stadig ret ensartet *Erica*-hede og ringe kolonisation af *Calluna*. Dette billede forandredes dog; i 1953 kunne man karakterisere parcellens vegetation således: Mod sydvest *Calluna-Myrica*-hede med spredt *Erica* og *Scirpus caespitosus*, mod nordøst likenrig *Calluna-Erica*-hede undertiden *Erica-Cladina*-hede. *Cladina*-arterne var store og fuldt udvoksede, det samme gjaldt *Cetraria islandica*. Undersøgelsen 1964 viser, at *Calluna* ikke beholdt nogen førende stilling, men at *Erica* var den vigtigste art på hele parcellen, samtidig at *Carex arenaria* var blevet påfaldende hyppig. Levermos-floraen var rig, og den indsamlede prøve indeholdt rigeligt af den meget sjældne art *Lophozia atlantica*. I 1971 var parcellen bevokset med en lav, tæt og likenrig *Erica*-hede. Et eksempel er vist i Tabel 7.



Fig. 13. Østerild forsøget. Den håndgravede parcel (3) set mod nordvest fra sydøsthjørnet. Øverst *Juncus squarrosus* stadiet i 1939. – Nederst samme sted i 1953 hvor parcellen præges af *Calluna* og *Myrica gale*. Den skrå cementpæl ved personen kan lige ses nær øvre højre hjørne på det øverste billede. TWB og CAJ fot.

The experimental plot 3 at Østerild (exp. area 6) which was subject to spading. Above, initial stage with dominating *Juncus squarrosus* (1939). Below, later heath stage (1953) with abundant *Calluna and Myrica*.

Tabel 7. Vegetationens dækningsgrader i 1971 på en af de små kvadrater $(2^{1}/_{2} \times 2^{1}/_{2})$ m) indenfor den afslåede parcel ved Østerild.

Table 7. Example of one $2^{1}/_2 \times 2^{1}/_2$ m square from the mowed plot in the dune heath. Final stage 1971. Coverage values.

Calluna vulgaris	1 - 2	Cladonia glauca	+
Empetrum nigrum	2	– impexa	3
Erica tetralix	5	– mitis	3
Salix arenaria	1	– rangiferina	+
Carex arenaria	+	– uncialis	+
Scirpus caespitosus	+	Cornicularia aculeata	+
Cetraria islandica	+	Dicranum spurium	+
Cladonia chlorophaea	+		
– floerkeana	+		

Kontrolparcellen (6). Denne blev analyseret 1938 og 1964 og undersøgt 1971. De to analyser viser, at Calluna er gået stærkt tilbage. Samtidig er de laver, der sædvanligvis breder sig, når lyngen svækkes, taget stærkt til, se således Cladonia chlorophaea, C. floerkeana, C. glauca og Parmelia physodes. Man noterer også at Myrica er gået tilbage, medens Vaccinium uliginosum og navnlig Carex arenaria er tiltaget i hyppighed. Dette kunne, ligesom den aftagende hyppighed for mosset, tyde på noget større udtørring af bunden. I 1971 kunne der på parcel 6 skelnes mellem to samfund. På de tørrere og lidt højnede partier: Empetrum-soc. med Calluna, Erica og lidt Genista anglica, Salix arenaria, Carex arenaria og Deschampsia flexuosa, i bundlaget Cladinaarterne, Pleurozium schreberi og Hypnum jutlandicum. Et enkelt sted Carex pilulifera og Rumex acetosella. På de lavere dele: Vaccinium uliginosum-Erica-soc. med Cladina og Dicranum scoparium, Erica-soc. med lidt Myrica, Vaccinium og Scirpus samt Cladina, Cetraria islandica o.fl., eller Erica-Empetrum-Vaccinium-soc. med Calluna, Carex arenaria, Scirpus, de samme laver og Dicranum scoparium. Dette viser at Calluna - også i klitheder, der ligger hen uden kulturpåvirkning – ikke holder sig som dominant. Når lyngen dør af alder, rykker de mere længelevende arter ind og erobrer i mange tilfælde dens plads.

Fig. 14. Østerild forsøget. Øverst den håndgravede parcel (3) set fra dens sydøsthjørne i 1964. Dominerende *Carex arenaria* og *Deschampsia flexuosa*. Prof. C. A. Jørgensen støtter den nordvestlige hjørnesten der var knækket over og som derfor ikke ses på det midtersted billede. – I midten og nederst den afslåede parcel (5) i forgrunden, og bag denne den fladtørv-afgravede (4, til venstre) og den håndgravede (3, til højre) i 1964 (i midten) og 1971 (nederst). Personen på det midterste billede står ved den skelsten som er sat i hjørnerne af de fire vestligste parceller (3, 4, 5 og 6). Personen med sommerfugleketcheren på nederste billede, står lidt til venstre for den diagonal der går fra den sydøstlige hjørnesten af parcel 5, gennem den skelsten der står i hjørnerne på de fire parceller og til den nordvestlige hjørnesten i parcel 4. Det lyse parti på de to billeder er det græs- og star-rige område på den håndgravede parcel (3). TWB fot.

Part of the experimental area at Østerlid. Above, the spaded plot (3) in 1964 where a large area was covered by *Carex arenaria* and *Deschampsia flexuosa*. In the centre and below the mowed plot is in the foreground 1964 (centre) and 1971 (below). The person in the middle picture stands at the concrete post where plots 3, 4, 5, and 6 meet. The same post is seen on the lower picture as the middle post in the row of three which mark out a diagonal from the southeast corner of plot 5 to the northwest corner of plot 4. The light area corresponds to the area rich in grass and sedge in the upper picture.



Fig. 14.



Fig. 15. Østerild forsøget. Øverst parcel 5 (den afslåede parcel) 1939. Hele feltet bevokset af *Erica tetralix*, idet dog *Cladina*-arterne ikke var blevet totalt ødelagt og var ved at vokse frem igen. Professor Mogens Westergaard står ved skelstenen mellem parcellerne 3, 4, 5 og 6. Bag ham ses parcel 6, til højre for ham parcel 3 (*Juncus*-stadiet) og bag denne skimtes den parcel, hvor fladtørv var blevet skåret og fjernet (4). – Nederst: I forgrunden kontrolparcellen (6) 1971, t.v. parcel 3 (den lyse græs-star-flade), i midten og til højre, bag den hjørnepæl der ses længst til højre, parcel 5. Længst tilbage i midten parcel 2 og 1. TWB fot.

The experimental area at Østerild. Above, the mowed plot in 1939. *Erica tetralix* dominates and *Cladonia sect. Cladina* seems to regenerate. Behind the person is the untreated test plot 6. On the bottom picture plot 6 is in the foreground, and behind plot 3 (light area on the left) and plot 5 (on the right). Farthest away are plots 1-2.

4. Kulturindgrebenes betydning for forståelsen af hedevegationens sammensætning

Det har længe været klart, at jysk hedevegetation – ligesom de fleste andre nordvesteuropæiske lyngheder – måtte karakteriseres som en kalvkultur-vegetation. Heden var, foruden at kræve bestemte jordbundskår, afhængig af en række kulturfaktorer. Hvis kulturindgrebene holdt op, ændredes vegetationen – lyngplanterne døde og erstattedes af græs eller revling og tyttebær, eller også blev lyngen ødelagt ved opvækst især af bjergfyr. Dette blev navnlig klart efter at man begyndte at frede hederne. På flere fredede hedearealer forsvandt lyngen i stor stil. I hvert fald var der forbi med store ensartede lyngflader, som man kendte dem i tidligere tider. Mange fredningsfolk har derfor interesseret sig for, hvordan man bedst kunne bevare lyngheden på de fredede arealer. Sidst har statsskovrider VAGN JOHANSEN (1970) skrevet om emnet og refereret til flere forsøg, som er udført på Ulborg Skovdistrikt med den hensigt, at bevare lyngvegetationen på Urfugle-reservaterne.

Den opgave, som de to forfattere af nærværende afhandling i sin tid stillede sig, var dels at undersøge, hvordan selve vegetationen udviklede sig på heder, der blev udsat for forskellige kulturindgreb, dels at studere de enkelte plantearters reaktion overfor de kårændringer som kulturindgrebene medførte. Det var praktisk muligt at gennemføre forsøg med pløjning, afslåning, afsvidning og tørveafskæring, men desværre ikke med afgræsning.

1. Skrælpløjning. Herunder vil også den håndgravede parcel i Østerild-forsøget blive omtalt.

Pløjningen har ligesom andre indgreb gunstig virkning på *Calluna*, idet en ny generation planter spirer frem og kommer i en årrække til at præge heden. *Empetrum* har efter pløjning fremgang flere steder (se område 3 og 5), ligeledes *Salix arenaria* (område 1 og 4) medens *Arctostaphylos uva ursi* går tilbage i område 1. *Vaccinium myrtillus* har fremgang i område 5. *Deschampsia flexuosa* tager til i hyppighed i område 2, 4, 5 og 6. De vigtigste forskydninger i hyppighed sker dog i lav- og moslaget. Her er det i de fleste områder tydeligt, at mosserne begunstiges, medens visse laver taber terrain efter pløjningen. Det gælder især *Cladonia mitis, silvatica* og *rangiferina*, men ikke *Cladonia impexa*. Denne art er den jyske hedes vigtigste lavart, og dette forhold kan nok i nogen grad tilskrives dens større genindvandrings- og regenerationsevne efter forskellige kulturindgreb. I denne sammenhæng må det også erindres, at den sjældne art *C. alpestris* i område 1 blev udryddet efter skrælpløjningen.

Det er vanskeligt at overskue de ændringer, der sker i økologisk henseende ved en skrælpløjning. Der fjernes ikke stoffer, men det udvaskede sandlag bliver overfladelag, medens mor og døde planterester kommer ned i jorden. Derved kommer der uden tvivl større gennemluftning af jorden, og mange stoffer mobiliseres ved henfald af det gamle vegetationslag. Den løsere jord kunne være årsag til, at arter med underjordiske skud fik bedre kår. Her kan man pege på den fremgang, der kan ses for

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Salix arenaria, Carex arenaria og i område 5 for Chamaenerion angustifolium og Trientalis europaea. Imidlertid tyder den ret betydelige tiltagen af Chamaenerion også på, at jordbunden er blevet mindre oligotrof.

Iøvrigt er det tydeligt, at mange arter efter pløjning får en kortvarig succes og således kommer til at præge de første successionsstadier. Man kan her erindre om Agrostis coarctata på Randbøl Hede (Tabel 4) og Carex pilulifera, Antennaria dioica, Lotus corniculatus og Rumex acetosella i forsøget på Hammer Bakker (Tabel 5).

Juncus squarrosus hører også til de arter, der først breder sig betydeligt, men derefter svækkes stærkt, når lyngen bliver tæt og høj og mos-lichen-laget kraftigt. Den opfører sig ens på den skrælpløjede og den håndgravede parcel i område 6, omend den opnåede de højeste tal i den håndgravede parcel her (se Fig. 13). Denne art er nok en typisk repræsentant for fugtig hede (Erica tetralix-hede), men den bliver kun sjældent dominant, uden hvor de edafiske forhold er særlig gunstige (f.eks. hvor der er trykvand i jorden, se Böcher 1941, s. 180-181). På Ulvshale er arten dominant i fugtig hede uden Erica, men med arter som Molinia, Nardus, Potentilla erecta og Pedicularis silvatica. Denne vegetation er her indskudt som et bælte mellem den tørrere hede og en mesotrof eng (Böcher 1942, s. 21–22), noget der også peger på, at Juncus squarrosus foretrækker steder, hvor forholdene nærmer sig det mesotrofe. På Færøerne indgår J. squarrosus hyppigt i hederne og Nardus-lierne. Den er her fundet som dominant på rig hede på jord med pH 4.7. Juncus squarrosus-moor vegetation på de britiske øer ligger m.h.t. biologisk aktivitet (hvori dyrelivet medregnes) midt mellem græsheden på kalkrig bund og bar tørvejord (KING & NICHOLSON 1964, s. 204–205). Man har måske på grund af J. squarrosus' opførsel på skrælpløjede og gravede parceller lov til at formode, at der her er sket en form for jordforbedring.

2. Afsvidning. Afsvidning af hede er en ældgammel kulturmetode, og den har været genstand for ikke ringe omtale i litteraturen. Der har også været foretaget mange botaniske iagttagelser på afsvedne hedeområder. For skotske heders vedkommende, se GIMMINGHAM 1964. I Danmark har KJELD HANSEN (1964) beskæftiget sig indgående med hedens genindvandring på brændte arealer og sammenfattet den vigtigste litteratur om spørgsmålet. I Randbøl Hede afhandlingen (Böcher 1941, s. 98– 115) er der dels omtalt en del successionsstadier efter hedebrand, dels er de økologiske forhold der skyldes afsvidningen og dens følger omtalt

Ved at sammenligne de seks forsøg med afsvidning af lyngen på i forvejen kendte hedeparceller kan det konstateres, at *Calluna* i hvert fald for en tid genvinder sin dominans, men over en længere periode efter afbrændingen svækkes den, til slut ofte betydeligt (Område 5 og 6). *Empetrum* går ofte stærkt tilbage i forhold til sin oprindelige hyppighed, i område 4 genindvandrede den slet ikke, til gengæld tiltog den i hyppighed i Hammer Bakker (Område 5). Også *Galium saxatile* synes at blive mindre hyppig efter afsvidningen (Område 4–5). En del arter får i begyndelsen af successionen gode kår og breder sig vel sagtens især på grund af askegødningen og den nedsatte konkurrence fra lyng, mos og lav. Det gælder *Carex fusca, C. panicea, C. pilulifera, Luzula multiflora, Agrostis coarctata, Lotus corniculatus, Antennaria dioica, Cytisus sco*

Nr. 5

parius o.fl. De to først nævnte arters skud overlever branden nede i jorden; det samme gælder for Vaccinium vitis idaea, der næppe noget sted taber terrain, men oftest breder sig efter afsvidningen (se således Område 2). Deschampsia flexuosa hører i områderne 2 og 3 til de arter, der først går frem og derefter igen svækkes, medens den i område 4 og 5 kun går frem; det samme gælder i område 5 for Chamaenerion, Hieracium umbellatum, Solidago, Succisa og i område 6 for Carex arenaria, Salix arenaria og Vaccinium uliginosum.

I bundlagets mos of lavflora sker der betydelige ændringer under successionen, især når der som i områderne 1 og 4 kommer en tør skorpe over jorden, der ofte er behersket af *Lecidea* arter, *Cladonia chlorophaea*, evt. *Ceratodon purpureus*. De tørre skorper hæmmer i hvert fald en tid den videre udvikling. Enkelte laver geninvandrer slet ikke (*Cetraria islandica* i område 1). *Cladonia impexa* når som regel op på sin oprindelige tæthedsværdi, men *Cladonia mitis, silvatica*, til tider også *C. uncialis* går tilbage. I modsætning til de skrælpløjede parceller, hvor mosserne oftest tiltager i hyppighed, er der på de afsvedne parceller tegn på det modsatte, især i den fugtige hede (område 6). I Hammer Bakker (område 5) svækkes *Hypnum jutlandicum*, medens *Pleurozium* og *Hylocomium splendens* går betydeligt frem. Her er forholdene imidlertid ganske specielle på grund af jordbundes højere bonitet og den svage hældning mod nord. Det er nok også derfor, at *Empetrum* her undtagelsesvis tiltager i hyppighed. Men også *Vaccinium myrtillus* og *Genista anglica* går frem, og *Vaccinium vitis idaea* indfinder sig på parcellen i den årrække forsøget er gennemløbet.

Et fælles træk for skrælpløjede og afsvedne heder er, at der – for så vidt afsvidningen foretages rigtigt og i en gunstig vejrperiode – ikke ved indgrebene i væsentlig grad fratages hedejorderne plantenæringsstoffer. Ved skrælpløjningen må jordbundens lidt dybere liggende dele nærmest tilføres stoffer. Ved afsvidning omdannes organiske stoffer i væsentlig grad til uorganiske askestoffer. Imidlertid vil asken i tørt og blæsende vejr let blive fraført det område, hvor afbrændingen har fundet sted. Derfor må der ofte regnes med tab af stoffer. Skulle askegødning føre til en virkelig jordforbedring, måtte man derfor i ældre tid bruge furebrændingsmetoden – der imidlertid forudsætter afskrælning og fjernelse af hedetørv (fladtørv), hvilket, hvor det er sket, forringer jordbunden endnu mere. Fælles for de følgende indgreb er netop, at de medfører fjernelse af stof fra heden. Ved afslåning fjernes vegetationen, medens fladtørvafgravningen medfører, at både vegetation og morlag fjernes.

Lyngafslåning. Dette kulturindgreb er uden tvivl meget gammelt og indgik som vigtigt led i hedebruget. Afslået lyng blev brugt til tækning, til at lægge i fårestier, til at bage ved, til koste o.s.v., men frisk ung lyng, d.v.s. lyng i kraftig vækst, blev også slået til kreaturfoder, i foderknappe år i ret stor stil, se videre hos Højrup (1970). og VAGN JOHANSEN (1970, s. 255). Afslåning fandt sted så sent som under sidste krig. På Fig. 16 ses resultatet af denne kulturmetode. Man anvendte da en mejemaskine, ikke, som i gamle dage, le. Resultatet af en regelmæssig og ret ofte udført afslåning var tæt, ensartet lynghede i forskellige højder, som det fremgår af figuren.

De afslåede parceller i de seks forsøg er vanskelige at skrive om. For det første

4*

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mangler forundersøgelser i område 1 og 6, for det andet ser det ud til, at jordbundens forskellig grad af bonitet i de seks områder spiller større rolle. Det i edafisk henseende rigere Hammer Bakker (område 6) opfører sig forskelligt fra de andre. Her er der fremgang for Empetrum, Genista anglica, Vaccinium murtillus, V. vitis idaea (der ikke fandtes i forvejen), Deschampsia, Campanula rotundifolia, Veronica chamaedrus, Hylocomium splendens og Pleurozium schreberi, medens der er tilbagegang for Hupnum *jutlandicum* og til sidst også for *Calluna*. Der er også tiltagende opvækst af træer, men en mængde arter går først frem, dernæst tilbage, af og til meget betydeligt tilbage. Blandt disse kan nævnes Anthoxanthum odoratum, Festuca ovina, Lotus corniculatus, Hieracium umbellatum, også enkelte laver og mosser. Randbøl-parcellerne (område 4) ligner dem i Hammer Bakker ved, at *Empetrum* og *Deschampsia* går frem og *Calluna* sluttelig stærkt tilbage. Derimod er det klart, at Empetrum taber terrain i område 2 og 3. Calluna holder sig i 1, 2 og 3, men ikke i 6. I område 1-2 var Calluna ved afslutningen svagt voksende og lav, antageligt et forhold der hænger sammen med, at jordbunden her er særlig mager. I klitheden (6) får *Erica tetralix* særlig gode kår på den afslåede parcel og danner en lichenrig Erica-hede. Også i de afslåede parceller ses tilbagegang for *Cladonia mitis* og silvatica og af og til totalt bortfald af C. rangiferina, medens C. impexa klarer sig godt. Mærkværdigvis synes Parmelia physodes at forsvinde i område 3, i hvert fald blev den overhovedet ikke noteret ved den sidste undersøgelse. så den må nok have været meget sparsomt repræsenteret på lynggrenene. Imidlertid fandtes den i 1953 rigeligt på de døende lyngbuske i to af naboparcellerne.

Fladtørv-afgravning. Desværre blev dette forhen så vigtige indgreb ikke undersøgt alle steder, men kun i Hammer bakker og Østerild Klithede. Medens tørveskæring næppe har fundet sted som et regelmæssigt led i hedekulturen i Hammer Bakker, var tørveskæring (skæring af fladtørv) meget almindelig i klithederne (Fig. 16) såvelsom på hedeflader og bakkeø-heder i Jylland. Også i Nordtyskland var det et vigtigt led i hedekulturen (Plaggenhieb), se nærmere Böcher 1941, s. 22–23, og det var anset for ødelæggende for de heder det gik ud over. Foranlediget af den tyske værnemagt blev der under krigen skåret mange fladtørv på den fredede Randbøl Hede. Disse arealer blev først bevokset med en mager og spredt vegetation af græsagtige planter, senere af tæt og lav lynghede, der holdt sig lav i mange år efter indgrebet (se Böcher 1970: 161-162). Man kan læse om fladtørvafgravningens enorme omfang i tidligere dage og dens skadelighed bl.a. hos Højrup (1970) og i de fængslende bøger af Hugo Matthiessen (1933 og 1939). I bogen »Viborg-Veje«, 1939, s. 151, skriver sidstnævnte forfatter: »Værst af alt var dog gravningen af hedetørv, som med rette kunne kaldes rovdrift, da den systematisk stjal al saft og marv fra heden og slap den igen som en afskallet ørken. Ved skæringen af disse »fladtørv« gik spaden 16-18 tommer ned i lyngskjolden, således at den muldede skorpe skrælledes bort og kun et magert underlag af sand og flint lodes tilbage i så ørkenagtig en forfatning, at der skulle flere menneskealdre til, før sårene atter lægedes«.

Resultaterne af de to forsøg med fladtørvskæring er omtalt ovenfor s. 29 og 36. I område 5 kom der på en del af parcellen et stadium, hvor *Lycopodium clavatum* var meget almindelig (Fig. 9), senere blev *Calluna* dominerende og holdt sig særlig



Fig. 16. Nær gården Kirstinelyst på Randbøl Hede blev der både før og under krigen slået lyng til foder. Man ser to alderstrin af kraftigt voksende ensartede lyngvegetation. TWB fot. 1938.

Area near the farm of Kirstinelyst on Randbøl Hede where the heath vegetation was mown at rather short intervvals. The heather was cut in order to advance haymaking. Two age-levels of vigorously growing heather are seen on the picture.

stædigt på denne parcel, medens den på de andre parceller blev trængt tilbage af græsser (Fig. 11). Antennaria dioica opnåede stor hyppighed omkring 1953 på den skrælpløjede og den afsvedne parcel, men ikke på den afslåede og den fladtørvafgravede parcel. Lotus corniculatus forholdt sig anderledes; den gik nemlig ikke væsentlig tilbage i de seneste år på den tørve-afgravede parcel, måske fordi den har bakterieknolde. Det bør også her nævnes, at *Genista anglica* på denne parcel i 1971 opnåede ST 35 og på den afslåede 43, medens den på den afsvedne og den skrælpløjede kun fik ST 4. Imidlertid var denne arts udgangsposition i 1936 bedst på den parcel, der blev slået. Chamaenerion angustifolium er som bekendt en art, der optræder med særlig stor hyppighed efter skovrydninger og skovbrand. Dette skyldes de mange næringssalte, der bliver let tilgængelige efter disse indgreb. I forsøget i Hammer Bakker er det påfaldende, at arten først indfinder sig efter, at indgrebene har fundet sted, dernæst at den i alle fire parceller først øger sin skudtæthed væsentligt i perioden 1953–1971, og endelig at denne stigning i tæthed er mindst i den fladtørvafskrællede parcel. Den

pludselige stigning forgår samtidig med at området koloniseres af skovtræer, men kan ikke skyldes øget beskygning.

I klitheden ved Østerild var det tydeligt, at heden var mager og lav og forblev fattig på *Empetrum*, hvor man havde skåret og fjernet fladtørv. *Myrica gale* var i stand til at spire frem og vise sig på 21 af de 36 kvadrater i 1937. I de to følgende år sås den ikke, men en smule *Myrica* noteredes i 1940, og i 1953 står der i noterne: »meget lav og kummerlig *Calluna-Myrica*-hede pletvis med *Salix repens*; meget *Cladonia destricta* og *Cornicularia* på volden gennem parcellen«. Først i 1964 var pors, *Myrica gale*, ved at nå sin oprindelige frekvens. Denne art plejer at ynde relativ næringsrig bund. Den tiltager i hyppighed på den håndgravede parcel, netop hvor *Juncus squarrosus* som omtalt s. 35 en tid fik optimale betingelser. Også på den afslåede parcel går *Myrica* noget tilbage i tæthed.

De ubehandlede parceller. De urørte parceller viser en række bemærkelsesværdige forhold. Medens summen af ST værdier for karplanter holder sig ret konstant, er det påfaldende, at artsantallet for karplanter er relativt højt på Randbøl Hede og fremfor alt i heden på Hammer Bakker. Artstallet synes at være udtryk for, at jordbunden er rigere, men i Hammer Bakker sikkert også for at bunden her ikke er udsat for større grader af udtørring. Dette forhold afspejles også i den fattige lichenflora og det tykke og frodige mostæppe. I Hammer Bakker er der ganske vist ingen kontrolparcel, men det er helt indlysende, at hele området ikke var eller er i ligevægt, men at en hurtig succession finder sted. I virkeligheden ser det ud til, at heden her blot er et stadium under en udvikling hen imod skøvvegetation. Dette er gangske naturligt på jorder, der er relativt rige.

På de andre områder stiller sagen sig væsentlig anderledes. Det er dog i Randbølforsøget tydeligt, at vegetationen på kontrolparcellen har ændret sig støt fra hede til mos- og lichenrig græsmark. På samme hede er der også mange steder tegn på særdeles livlig opvækst af bjergfyr. På Fig. 18 ses et bjergfyrkrat på ca. 20×33 m i størrelse, der havde dannet sig mellem forsøgsparcellerne og Staldbakkerne. Det bestod 1957 af krogede og rankvoksende racer af *Pinus mugo*, en enkelt *Picea glauca* og en *Sorbus aucuparia*, der dog blev holdt nede antagelig af hjorte, der bed dens skud af i 40 cm's højde. Omkring krattet var *Calluna* og navnlig *Cytisus scoparius* i kraftig vækst. Sydligere, nærmere gården Guldbergsminde noteredes 1957 flere steder kraftig opvækst af *Populus tremula* i græsrig hede, der var fulgt efter lynghede på tidligere marker. Nu hvor heden er helt overladt til sig selv bliver den slags opvækst hyppigere (fig. 19), men successionen går sikkert meget langsommere end i Hammer Bakker.

I forsøgene på områderne 1–3 og 6 var der alle steder selvsået bjergfyr, men forholdene her kan ikke sammenlignes med dem på de fredede arealer (4 og 5), idet der alle steder skete regulær plantning af nåletræsplantager i nærheden af parcellerne, hvilket øgede chancen for selvsåning betydeligt. Desuden ændrede læforholdene sig til gunst for eventuel opvækst. Skulle man imidlertid dømme efter den stærke vækst, som selvsåede bjergfyr udviste i nærheden af Gludsted-parcellerne, måtte man tro at forholdene her nærmede sig dem på Randbøl Hedes østlige del. I Gludstedforsøget



Fig. 17. På en stump hede i nærheden af Lunden nord for Byrum på Læsø er der foretaget afgravning af fladtørv. *Calluna* og *Erica* vokser frem igen, men den nøgne sandoverflade ses mellem skuddene. I forgrunden og langs rugmarken ved den lille skov ses ældre hede bl.a. med *Salix arenaria*. TWB fot.

Small heath area in the central part of the island of Læsø in Kattegat. Peat cutting and removal of peat bricks have taken place, and *Calluna* and *Erica* are colonizing on the sandy surface. In the background, a small wood and a field of rye.

viste det sig også, at *Calluna* på kontrolparcellen gik stærkt tilbage, medens bl.a. *Deschampsia* gik voldsomt frem. Pletvis var lyngen helt forsvundet i 1969 (Fig. 5). Det kan således på områderne 3, 4 og 5 konstateres, at heden som vegetationsform ikke er konstant, men ofte afløses af græsrige samfund eller skovagtig bevoksning.

Af en væsentlig interesse er det derfor, at de to fluvioglaciale heder (område 1–2) forholder sig meget anderledes. På Kronheden var vegetationen særdeles stabil; *Calluna* fik i 1936 værdierne 98 (ST) og 36 (K), 3–4 (D) og i 1954 93 (ST) 36 (K), 3–5 (D), hvilket viser, at der ingen ændring er sket i dens hyppighed. Bortset fra nogen fremgang for *Empetrum* og *Cladina* er der tale om en uventet stor stabilitet. På Alheden øgede *Calluna* sin skudtæthed lidt, men den gik noget tilbage i dækning, medens *Empetrum* gik tilsvarende frem (Fig. 4). *Cladina*-arterne gik lidt tilbage, sikkert fordi mosset tog til. *Deschampsia flexuosa* blev også lidt hyppigere, men der var slet ikke tale om, at denne græsart på nogen måde kunne tænkes at true hedebuskenes dominans. På den magre hedeslette ser det således ud til at dværgbuskene er mere stabile. Det er jo dermed



Fig. 18. Lille bjergfyrbevoksning på den fredede Randbøl Hede nær ved forsøgsparcellerne omtalt i tabel 4. Foran fyrrene højtvoksende *Calluna* og den lave jyske race af gyvel. TWB fot. 1957.

Small stand of *Pinus mugo* on the heath reserve of Randbøl Hede near the experimental plots mentioned in Table 4. In the foreground vigorous *Calluna* and abundant, low growing Jutland race of *Cytisus scoparius*.

ikke sagt, at heden her, som flere i ældre tid troede, er en klimaksvegetation, end sige en rest af senglacialtidens »tundra«, men forsøget peger på, at ødelæggelsen af den magre skov, der antagelig stod på hedeslettens tørrere dele, var særlig effektiv, fordi jordbunden her havde så få resourcer. Fjernedes vedmassen, senere eventuelt også fladtørv på heden, var det ikke muligt for skoven at generobre terrainet. Man må her se bort fra bjergfyr, der også gror frem på slette-heder som de foreliggende, og kun tænke på den naturlige skov, der var præget af eg og måske birk (smlg. »Querceto-Betuletum« omtalt fra fluvioglaciale områder i Nordtyskland af bl. a. Tüxen (1937)).

Klitheden slutter sig med hensyn til hedevegetationens stabilitet til de lige omtalte heder på slette-sand. Ganske vist går *Calluna* i kontrolfladen stærkt tilbage fra 1938 til 1964, men i 1971 var *Calluna* pletvis hyppig især på tørrere bund, hvor *Empetrum* dominerede. På de fugtigere dele domineret af *Erica tetralix* og *Vaccinium uliginosum* var der også mange lyngplanter. *Calluna* planterne var i 1964 uden tvivl i stor stil ved at dø af alderdom, men nye planter kunne finde pladser mellem de andre dværgbuske. Samtidig med at *Calluna* døde, blev der som sædvanlig særlig gode muligheder for *Cladonia chlorophaea*, *C. floerkeana* og *C. glauca*.



Fig. 19. Unge bævreaspe på den østlige del af den fredede Randbøl Hede. Den høje græsvegetation (især *Dcschampsia flexuosa*) er fulgt efter kraftig *Calluna*-hede, der i sin tid indvandrede på et lille tidligere opdyrket område. TWB fot. 1963.

Growth of aspen on the eastern part of the heath reserve of Randbol Hede. The vigorous grass vegetation followed a vigorous *Calluna* heath, which had colonized a small formerly cultivated area.

Det er interessant, at *Erica tetralix*, i perioden hvor *Calluna* svækkes, går lidt frem. Samtidig er der tilbagegang for *Myrica* og mosset, og fremgang for *Carex arenaria*, hvilket måske tyder på en vis udtørring af bunden forårsaget af den i området tæt ved parcellerne nyanlagte plantage. Det må imidlertid erindres, at parcellerne i Østerild-forsøget blev anlagt på et forholdsvis fladt område inden for en lav parabelformet klitbræmme (Fig. 15, nederst i baggrunden). Sådanne steder står der meget ofte vand over vegetationen i dele af vinterhalvåret og i alle tilfælde er jordbunden da altid vandmættet, og vandet er stillestående. Under sådanne forhold er det vanskeligt eller umuligt for træer at klare sig over længere perioder. Tüxen (1937) regner *Erica*-heden for at være naturlig – ikke et produkt af skovødelæggelse, men klokkelyngheder kan kunstigt omskabes til skov (plantage), hvis jorden drænes og grøftes. Her skal ikke forsøges ført en videre diskussion af dette emne, men kun peges på at en hede som den foreliggende meget vel kan tænkes at være et klimakssamfund. Undersøgelserne af kontrolparcellen tyder derpå, og beliggenheden bag klitvolden viser, at der er tale om en udblæst klitbund. Jordbunden sådanne steder er ofte relativt gold og er som sagt ofte vandmættet, evt. kortvarigt vanddækket. Sådanne forhold tåles af *Erica tetralix*, men ikke godt af træer. Der kan ganske vist i fugtige klitheder mange steder ses birkeopvækst, men det betyder ikke at alle fugtige klitheder helt naturligt vil udvikle sig til birkeskov, hvis vegetationen overlades til sig selv.

Litteratur

- BORNEBUSCH, C. H., 138: Nørholm Hede. Anden Beretning. Det forstl. forsøgsvæsen i Danmark XV: 33-80.
- Böcher, T. W., 1935: Om en metode til undersøgelse af konstans, skudtæthed og homogenitet. – Bot. Tidsskr. 43: 278–304.
- ,1940: Studies on the Plant-geography of the North-Atlantic heath-formation. I. The heaths of the Faroes. Biol. Medd. Dan. Vid. Selsk. 15.3.1–64.
- , 1941: Vegetationen paa Randbøl Hede med særlig hensyntagen til det fredede Areal. Biol. Skr. Dan. Vid. Selsk. 1.3.1–243.
- , 1942: Vegetationsstudier på halvøen Ulvshale. Bot. Tidsskr. 46: 1–42.
- , 1943: Studies on the Plant-Geography of the North-Atlantic heath formation. II. Danish dwarf-shrub communities in relation to those of Northern Europe. – Biol. Skr. Dan. Vid. Selsk. 2.7.1–130.
- , 1970: Hedens vegetation og flora. Danmarks Natur Bd. 7: 118-191.
- -- & SKYTTE CHRISTIANSEN, M., 1941: Nye Fund af Blad- og Busklikener i Danmark. --Bot. Tidsskr. 45: 415-422.
- & WEIS BENTZON, M., 1958: Density Determination in Plant Communities. Oikos 9: 35–56.
- GIMINGHAM, G. H., 1964: Dwarf-shrub heaths in J. H. Burnett: The vegetation of Scotland: Chapter 7: 232-287.
- GRAM, K., JØRGENSEN, C. A. & KØIE, M., 1944: De jyske egekrat og deres flora. Biol. Skr. Dan. Vid. Selsk. 3.3.1–210.
- GRØNTVED, JOHS., 1926: Hammer Bakker, en botanisk Undersøgelse, iværksat af Dansk Botanisk Forening. – Bot. Tidsskr. 39: 239–298.
- HANSEN, H. Mølholm, 1926: Liken- og mosvegetationen i Hammer Bakker. Bot. Tidsskr. 39: 279–285.
 - , 1932: Nørholm Hede, en formationsstatistisk vegetationsmonografi. Skr. nat.-mat. Dan. Vid. Selsk. 9.3.3.1–190.
- & LUND, MOGENS, 1929: De danske arter af slægten Cladonia. Bot. Tidsskr. 41: 1–80. HANSEN, KJELD, 1964: Studies on the regeneration of heath vegetation after burning-off. –
- Bot. Tidsskr. 60: 1–41.
- , 1971: Heden natur og kultur. Biologisk Orientering. Gyldendal. København.
- Højrup, Ole, 1970: Hedens udnyttelse. Danmarks Natur Bd. 7: 73-106.
- JOHANSEN, VAGN, 1970: Erfaringer med bevarelse af hedearealer på Ulborg statsskovdistrikt. – Dansk Skovforenings Tidsskr. 55: 253–265.
- KING, J. & NICHOLSON, J. A., 1964: Grasslands of the forest and sub-alpine zones in H. Burnett: The vegetation of Scotland: Chapter 6: 168-215.
- MATHIESSEN, HUGO, 1933: Viborg-Veje, studier og vandringer. København.

— , 1939: Den sorte jyde, tværsnit af hedens kulturhistorie. – København.

- SYRACH LARSEN, C., 1926: Trævæksten (Hammer Bakker). Bot. Tidsskr. 39: 260-279.
- TÜXEN, R., 1937: Die Pflanzengesellschaften Nordwestdeutschlands. Mitt. d. florist.-Soziol. Arbeitsgem. Niedersachsen 3: 1–170.

English Summary

Jutland dwarf shrub heaths

Experimental investigations of the influence on the vegetation of various types of heath management

Experiments were carried out in six different heath areas, of which two (1-2 in Fig. 1) were located on fluvioglacial plains, two (3-4 in Fig. 1) near the end moraines of the last Ice Age, one (5 in Fig. 1) in a hilly and sandy area behind the frontier of the last Ice Age, and one (6 in Fig. 1) in a saucer-shaped slack behind a low parabola dune in the wide dune-heath landscape of Northwest Jutland. In the areas 3 and 5 the sand was mixed with gravel and small stones.

In the six experimental areas four (in one case six) quadratic 15×15 m plots were marked out by concrete corner posts. During the analyses a grid was set up by which the plot was divided into 36 squares, each $2^{1}/_{2} \times 2^{1}/_{2}$ m in size. The 25 intersecting points constituted the centres of the concentric circles used during shoot density investigations, while the 36 squares formed the basis for investigations of constancy and coverage.

Shoot density (ST values on the tables). In all the 25 intersecting points four concentric circular areas were investigated according to the modified RAUNKLERfrequency method. The outer circle circumscribes an area of 0.1 m^2 (radius 17.8 cm) and corresponds to the original radius employed by RAUNKLER. The radius is subdivided into four equally long parts, thus, when turned round, making it possible to distinguish between species which are found (have shoots) inside the smallest circular area (0.006 m^2) , and species which similarly are found if the circular area is enlarged to 0.025 m², 0.056 m², or 0.1 m². The four circular areas are designated 4, 3, 2, and 1. A very dense species will have shoots everywhere (hibernating, perennial parts) inside the innermost circle and is given 4-values. By simple addition 25 4-values give a shoot density (ST) of 100. A more scattered species will e.g. be given 3 4-values, 4 3-values, 6 2-values, and 12 1-values and will obtain ST 48. Finally, a very scattered species may not be constant within the 0.1 m^2 circle and is only recorded with 1 4-value, 2 2-values, and 6 1-values, which results in an ST value of 14. With 25 single analyses the shoot density can be expressed in a scale ranging from 0 to 100 (for further details about the method see Böcher 1935, and Böcher & Weiss Bentzon 1958).

Nr. 5

Constancy. (K in the tables). For practical reasons the constancy is expressed simply by the number of occurrences in the 36 squares. The scale thus runs from 0-36.

COVERAGE. (D in the tables). The estimated degree of coverage is expressed by the HULT-SERNANDER Scale in which species covering more than $50 \ {}^0/_0$ of the square are given the value 5, while 4, 3, 2, and 1 indicate that the species in question cover from 25 to $50 \ {}^0/_0$ (4), from 12.5 to $25 \ {}^0/_0$ (3), from 6.25 to $12.5 \ {}^0/_0$ (2), or less than $6.25 \ {}^0/_0$ (1). + means that a species is only just present, but its coverage is very small. The values in the tables express the variation in coverage in those squares where the species is recorded.

In the years of investigation the four (or six) 15×15 m plots were studied carefully and in most cases both ST, K, and D were determined.

Even very small and otherwise hardly observable alterations in the vegetation cover were discovered and established by this combination of methods. In most of the six areas one plot remained untreated as a control or test plot, the other plots were lea ploughed, burned off, or mowed. In two areas the peat was cut and removed in one plot, while in another area one plot was subjected to spading, by which the vegetation cover and the peat were turned over and covered with subsoil sand. This type of management has an effect very similar to that of lea ploughing. When ploughed and spaded almost no substances are removed. On the other hand, the dwarf shrub canopy and most parts of the lower strata are removed by mowing, while peat removal removes both plant cover and peat, implying a considerable loss of substances. Burning off ashes most of the surface humus. The mineral nutrients deposited as ash may or may not improve the soil fertility. Favourable conditions during the period after the burning off may involve a temporary fertilization by ash and a rise in the pH of the soil, but frequently drought and wind remove the ash and bring about some impoverishment of the soil. In any case, the burned off surface often develops into a more or less firm crust very frequently colonized by Lecidea and Cladonia species. This crust seems to have a restrictive influence on the succession and the regeneration of the heath vegetation. A closer study of the influence of the different managements was made possible by comparisons of the vegetation on the plots before they were treated and after a recolonization of heath had taken place. The pre-investigations were undertaken in 1936-1937 (F in the tables), while the final studies of the plots took place in 1953, 1954, or as late as in 1971.

The initial composition of the vegetation in the six areas and the successional as well as final stages appear from the data collected in Tables 1–6 and Figs. 3–15. The table numbers 1–6 correspond to the experimental areas 1–6. After the various forms of management *Calluna* became very abundant and maintained its dominance for a couple of years. Also a species as *Cladonia impexa* usually profited from the managements being able to reach dominance before *Cladonia mitis* and *sylvatica*.

The lea-ploughed (in exp. 6 also the spaded) plots. This type of management very often leads to progress for species like *Empetrum nigrum*, *Salix arenaria*, and *Deschampsia flexuosa*. The ecological conditions seem to be improved for the mosses,

while several lichens are regressive. The rare subarctic-alpine species *Cladonia alpestris* was unable to recolonize in area 1. Many species had a temporary success, thus e.g. *Agrostis coarctata* in area 4, and *Carex pilulifera Antennaria dioica, Lotus corniculatus* in area 5. In the latter area, *Chamaenerion angustifolium* had considerable progress, which may indicate an increase in soil fertility. In the dune-heath (exp. area 6) *Juncus squarrosus* attained higher ST, K, and D values in the first years after ploughing and very high values after spading (Fig. 13). This species is considered particularly common in habitats which are less oligotrophic, and its abundance after spading of the plot is believed to be the result of a low degree of fertilization of the soil.

The burned-off plots. In all the burned-off plots *Calluna* was able to recolonize and attain dominance, but after a number of years it regressed in the exp. areas 4–6. *Empetrum* often reduced in frequency, and in area 4 it did not recolonize at all after burning off. Also *Galium saxatile* seemed to be weakened (exp. area 4–5). In the first years after burning off several species attained higher values, and some which were protected against fire by having buried, perennating organs showed an increased frequency (e.g. *Vaccinium vitis idaea* in area 2). The bryophytes may in many cases be less frequent after burning (e.g. exp. area 6). In area 5 where the soil is more fertile and the ground slopes gently towards the north, *Hypnum jutlandicum* was replaced to a great extent by *Pleurozium schreberi* and *Hylocomium splendens* which have progressed. The same applies to *Empetrum, Vaccinium myrtillus*, and *Genista anglica*, while *Vaccinium vitis idaea* has invaded the plot as a newcomer.

The mowed plots. In the final stages after mowing *Calluna* regressed or, in the areas 1-2, was lower than before mowing. In the dune-heath *Erica tetralix* benefited from the treatment and dominated large parts of the plot (Table 7). *Empetrum* showed progress in the exp. areas 4-5, but disappeared from parts of the plots in the areas 2-3.

The plots where peat was removed. (Only exp. areas 5–6). During the first years *Lycopodium clavatum* became particularly abundant in parts of plot 5 (Fig. 9). Later *Calluna* formed a low canopy and was able to maintain a longer dominance (Fig. 11), probably as a result of the soil impoverishment. *Antennaria dioica* became abundant after ploughing and burning off, but not after mowing or peat removal. Also the progess of *Chamaenerion* is least after this management. On the other hand, *Lotus corniculatus* and *Genista anglica* were able to maintain their position or increase in frequency, perhaps because they have tumours with nitrogen-fixing bacteria. In the dune-heath (exp. area 6) the canopy became lower and poor in *Empetrum. Myrica gale* was able to sprout from the ground after the peat was removed, but it was clearly much weakened in the next years and did not recover and reach its former shoot density until 1964.

The untreated plots. (In the case of exp. areas 4–5 the surrounding area next to the plots). It is possible to arrange the observations and analyses in a series which exhibits decreasing tendency of the dwarf shrub heath to develop into another community not dominated by dwarf shrubs. The contents of soil nutrients may be responsible for the different types of development.

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1) First the heath develops into *Deschampsia flexuosa* grassland, and then into woodland (*Sorbus aucuparia, Pinus silvestris, Picea abies*, etc.), or to *Juniperus* copses. This is clearly what is happening in the hilly exp. area 5. Here the heath had succeeded cultivated land which, after the cultivation had ceased, was transformed into a grassland of *Anthoxanthum-Agrostis tenuis-Hieracium pilosella* (cp. GRØNTVED 1926). The succession from heath to woodland proceeds with increasing speed, cp. Fig. 8, 10, and 11. Although *Calluna* was present in the *Deschampsia* grassland, there were no signs of it regaining its lost sovereignty.

2) The heath develops into *Deschampsia* grassland (exp. area 4) or in area 3 a pattern with a dominance alternating between *Calluna-Vaccinium vitis-idaea*, *Empetrum-Vaccinium vitis idaea-Cladina*, *Vaccinium vitis idaea-Cladina*, *Deschampsia*, or *Carex fusca-panicea*. In both areas which lie on gravelly, marginal morainic soil self sown *Pinus mugo* is capable of forming thickets, and the *Deschampsia* grassland, or heath pattern, does not seem to be short stages or to be replaced by new uniform *Calluna* heath.

3) The dwarf shrub heath vegetation is maintained and stable, although it develops into a pattern in which *Calluna* becomes somewhat more scattered, while *Empetrum* is able to increase its share. *Deschampsia flexuosa* may be without importance or just slightly stronger, but is not able to reach dominance. This type is connected with the heath formed on very leached soils in the fluvioglacial sands (exp. areas 1–2), but a similar development has been noticed in certain protected heath areas where the peat is deep and undisturbed. *Pinus mugo* is able to form low stands also in such areas, but the fact that the dwarf shrub heath persists if *Pinus mugo* is kept away is probably connected with the soil conditions. In the fluvioglacial areas these were poor from the beginning, although probably not inhibitory to oak or birch thickets or low woodlands, but felling or burning of the trees and later burning off and peat removal on the heath has probably further impoverished the soil making impossible any natural development leading to communities other than dwarf shrub heath and low *Pinus mugo* stands.

The dune-heath pattern (exp. area 6) seems to be very constant. Here the heath may represent a paraclimax which is maintained as long as the soil is not drained and is exposed during winter to a high water-table.

Indleveret til Selskabet den 7. april 1972. Færdig fra trykkeriet den 30 november 1972.
TABEL 6. Østerild klithede forsøget	(Experimental area 6, see Fig. 1)
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	Den skrælpløjede parcel (Lea ploughed plot) Den afsvedne parcel (Burned off plot)							Den håndgravede parcel (Spaded plot)									Den fladtørv-afgravede parcel (The plot subject to peat removal)					I	Den afslåede parcel, afslået 1937 (The mowed plot)				Kontrol parcel (Test plot			plot)	-																	
År (Year) Metode (Method)	F 1 ST	.936 K I		19 ST K	37 D	ST	1939 K	D	ST I	64 K D	F ST	1936 K I		193 T K	38 D	ST	1964 K	D	F 19 ST K	36 D	ST	1937 K 1	D 19	38 T	193 ST K	39 D	ST 1	964 K D	F ST	1936 K I	F S	193 ST K	7 D	ST 1	939 K D	ST	1964 K D	F ST	1938 K 1) 193 S	39 T S	196 T K	4 D	ST 1)38 K D	ST	1964 K D	
Calluna vulgaris. Empetrum nigrum. Erica tetralix Genista anglica. Myrica gale. Salix arenaria. Vaccinium uliginosum.	75 57 39 29 12 5	$ \begin{array}{r} 36 & 2 \\ 32 & 1 \\ 35 & 1 \\ 2 \\ 24 & 1 \\ 25 \\ 7 \end{array} $	4 -4 -3 1 -2 1 1	1* 36 ³ 2 30 19* 20 10 2 4 2 1 1	* + 0 + 6^{*} + 2 + 7 +-1 5 + 1 +	26 16 18 26 9 3	36 29 33 2 26 29 7	1-3 +-2 +-2 +-3 +-2 +-1	87 48 19 24 12 7	5 (1)-5 3 1-5 7 +-5 3 +-1 7 1-3 1 +-4 7 1-2	90 36 63 47 5 7	$\begin{array}{cccc} 36 & 2 \\ 33 & 1 \\ 36 & 1 \\ 32 & 1 \\ 24 \\ 13 \end{array}$	-5 -3 -2 -2 1 1	15* 36 3* 18 46 35 49 35 10 31 12 15	+-2 +-1 +-3 1-3 +-2 +-1	21 24 30 47 21 30	31 + 29 + 27 1 33 1 31 20	+-5 +-5 1-5 + 1-3 1-5 1-5	87 3 55 3 70 3 31 2 9 3 7 1	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	24* 1* 29* 14 2 4	29^{*} 7^{*} 36^{*} 1 31 + 22 11	+ 4 + 2 + 1 + 1 + 1 + 1	18 2 22 1* 19 11 +		5 +-4 5 +-1 3 +-2 2 +-1 3 -3 3 +-1 4 +-1	34 20 26 43 20 6	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	93 39 66 29 17 10	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	-5 -3 -3 1 -2 1 -2		+++++++++++++++++++++++++++++++++++++++	89 : 53 : 2 ? 14 :	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	60 7 72 15 30	$\begin{array}{cccccccccccccccccccccccccccccccccccc$		$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	+ 10 + -3 63 -1 -2 2 -2 1 -1 -1	6* 2 4 1 2 8 7* 1 1 7 1		$^{+-3}_{+-4}_{2-5}_{+}_{+-3}_{1-3}_{1-3}_{+-4}$	87 3 62 3 72 3 31 2 23 3 10 3 9 1	$ \begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	9 65 75 20 8 9 20	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	
Carex arenaria - fusca. - panicea. - piblilfera. Corynephorus canescens. Deschampsia flexuosa. Festucar rubra. Juncus atricapillus. - articujatus.	1	14 1 1	1 1 +	4 1	6 + 2 + 1 +	17	29 6 7 6 7	+-2 +-2 + +-1 +	2	7 +-1 1 1 5 +-1 7 +-2	12 3	19 11	1	32 25 15	5 +-3 2 +-1	55	36 + 13 + 13 + 4 +		16 3	0 1	12*	28* 5	+ 1	19 3 +	52 36	5 +-3 0 +-1 3 + 8 +-1 5 +	57 2 6	32 +-5 6 +-1 7 +(1) 18 +-5	6	24 14 1- 8	1-2-1	8* 17' 7* 13'	++-1	5 : 11 : 2	26 + -1 22 + -3 4 + -1 1 +	15	31 + -1 2 1 5 + -1 1 +	1 6 1 5 1	20 2 1 19 + 5	+ 1 -2 -3 +	3 3	$ \begin{array}{r} 33 & 26 \\ 2 & 16 \\ 8 & 22 \\ 2 \\ 2 \end{array} $	+-3 1-2 +-1 +-2 +	2 4 1 2		45 9 2	35 + -3 20 + -4 12 + -1	
– bullosus – squarrosus Luzula multiflora Molinia coerulea Scirpus caespitosus	1	6 7	1	1	1 + 5 + 8 +	15 14	32 28 4	$^{+-2}_{+-2}_{+-1}$	3 7 3	$5 +-1 \\ 9 +-1 \\ 6 +-2$	2	4 12	1	2 14	3 + (1) + (1)	1 2		2 1 +1	6 1	3 1 7 1	2* 21* 2* 1*	1* 33* 7* 4*	+ 3 + +	+ 38 +	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		1 3	$\begin{array}{ccc} 10 & + \\ 26 & +(1) \\ 2 & + \end{array}$	2	10 13 1(1 (2)	5* 18 9* 6 7	+++++	6	$\begin{array}{cccc} 8 & +-1 \\ 12 & +(1) \\ 1 & + \\ 6 & +-1 \end{array}$	1	5 + 5 + 10 +	1 3	3 + 21	-1 +		$\begin{array}{c}1\\2\\3\\3&23\end{array}$	$^+_{\substack{+\\1-2\\+-2}}$	1	1 + 2 + 15 + -1	2	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1
Antennaria dioica	1	4	1		4 +		1 12 4	+ +-1 +	4	$ \begin{array}{ccc} 1 & + \\ 1 & + \\ 4 & + \\ \end{array} $		1	1	3* 8 5 (+ + + + 3 +		1 2 1	+ + +						1	2	+ 3 +1 1 +		1 + 1 + 1 +	1	3	1	3*	+ +		$5 + \frac{1}{4} + \frac{1}{+-1}$ $1 + \frac{1}{+}$		3 +-:	1	8	÷	3						1 +	
Cladonia alcicorrais. – cooccilera . – destricta . – forerkeana . – furerata . – furerata . – mipresa . – mitis-silvatiea . – pityrea . – rangiferina . – f. spimosa . – stepsilia .	1 64 33 7 1	1 5 4 1 35 11 36 2 11 1 1	++++++++++++++++++++++++++++++++++++++						8 46 16	1 + 8 + 2 + 2 + 2 + 2 + 2 + 2 + 2 + 2 + 2	5 5 1 27 63 6 2	7 13 5 1 1 34 1 36 1 20 2 4 $+$	+ + + + + + + + + + + + + + + + + + + +	3 10) +	10 2 21 8 4	6 1 26 23 4	++++++++++++++++++++++++++++++++++++	1 24 2 60 3 2 1	$0 + \frac{7}{2} + \frac{1}{5} + \frac{3}{6} \frac{1}{1-4}$ 2 + -1 $1 + \frac{1}{5} + \frac{3}{5} + \frac{3}{5}$							4 9 4	7 + 1 + 1 14 +-3 9 +-1 2 +	6 6 8 58	$19 + \frac{17}{3} + \frac{17}{3} + \frac{16}{35} + \frac{16}{10} + \frac{17}{7} + \frac{16}{2} + \frac{17}{4} + \frac{16}{4} + \frac{17}{4} + \frac{16}{4} + $	-1 + -1 + -2 -3 1 1 -1			2 } 41	7 +-1 27 +-2	1 14 49 41 5	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	+ + 2 + 1 + + 4 2 + 1 + + 1 + + 1 3	1 ? 4?	+ + } 1	8	2 19 1 7 3 2 4 45 27 31 24 3 17	+-1 + + + + + + +-4 +-2 +-1	3 46 48} 10 1	6 + 1 + 2 + 15 1-5 8 +-1 2 +	24 5 3 1 49 30 5	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	
	8 13 6 2	16 + 2 36 + 22 + 7	-1 + -2 -1 +				1 1	++++	2 7 1 57	4 + -1 4 + -3 36 + -2 1 -2	14 14 1 11	20 + 31 1 19 11 + 1	-2 + -1 +		l +	30	4 4 1 33	+ +-1 + +-2	2 1 34 3 1 5	5 +-1 10 1 1 + 7 + 1 + 1 +							1 60	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	11 8 1 1	$ 17 + - 20 \\ 14 + - 6 +$	-1 1 -1 -1			11 3 4	$\begin{array}{c} 4 & + \\ 2 & + \\ 2 & 1 - 2 \end{array}$	7 6 16 2 24	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 6 + 1 2 1 + 1 1	11 4 2	+ 1 + +	.3	6 18 7 13 5 6 1 20 27	+-1 +-1 + + +-1	1 : 19 : 1 10 :	0 + 0 + 2 + 11 + 1 + 1	1 3 2 40	9 + (1) 1 + 12 + (1) 1 + 2 + (1) 2 + 26 + -3).).+1
Cephaloziella efr. fluitans Frailanda sp (symnosolea influta Lophozia barbata barbata – exectiornia – hatchieri – kunzeana Nardia scalaris.	7	1 6 1 8 4	+ + +						1 4	1 + 2 +	2	1 27 +	+				2	+	11 2	1 +							5	3 +	1	1 1 20 +	+++2					3	11 +-	1	a	,	}	7 8	+ +	12	4 ÷ 36 +-1	5	2 4	+
Dieranum polyselum	60 6	2 3 1 36 12 2	1 + 3 1 +		1 + 2 + 5 +		3	+ +	6 35 21	10 +-1 32 +-5 24 +-5 1 +	<pre>} 10 76 40</pre>	10 36 1 25 1	1 5 3	5 1	2 +-1	3 29 28	9 36 - 32 -	+ }	4 67 3 46 3			1	+		3	1 1	2 68 44	5 +-1 36 +-3 30 +-3	<pre></pre>		1 +-4 -3 +1	5 6 17 10 8 8	+ + +-1	5 } 13 15	2 + 36 + 17 +-3	3 29 12 27	8 - 29 +- 21 +- 14 +-	+ 2 3 19	18 +	-1 2	1	16 4 26 31 21 19 3 9	+-1 +-1 +-2 +-1 +-1	9 89) 67}	9 + 36 2-5 2 +	6 24 35	24 + 28 + 30 + 3	1 1 2 +

TABEL 5. Forsøget i Hammer Bakker. (Experimental area 5, cp. Fig. 1)

	Frekvenspet, 1915 iffg. A. MENTZ	Den skrælpløjede parcel (Lea ploughed plot)									Den afsvedne parcel (1937) (Burned off plot)							Den afslåede parcel (The mowed plot)						Den fladtørv-afgravede parcel (Plot subject to peat removal)														
	Frequency per Cent. 1915 acc. to A. MENTZ	F	1936 K D	ST	1937 ГКД	1938 ST	ST	1939 K D	ST	1953 K D	ST H	71 K D	F 19 ST F	36 5 D	19 ST F	038 K D	19 ST K	53 D	ST 1	971 K D	F 193 ST K	6 D	1937 ST K E	D ST	1938 K D	ST	1953 K D	1971 ST K D	F 1 ST	936 K D	1937 ST K E	s	1938 T K D	1939 ST	ST 1	953 K D	19 ST K	71 D
Acer pseudoplatanus. Crataegus oxyacantha Juniperus communis. – glauca. Pinus ailvestris. Sorhus aucuparia. – scandica. – Imus calabra.	2		8 1 4 1	1	1 +			1 +		5 +-1 1 +	5 1	$\begin{array}{cccccccccccccccccccccccccccccccccccc$		4 1 2 1 1 1		2 +	:	2 + -1 1 1 1 1	12	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1 2 1 2	1 1-2 1	1	+			3 +-1 3 +-1	4 5 1- 4 3 +- 3 4 +-	5 5 1	1 1					1	1	$ \begin{array}{c} 1 \\ 6 \\ 3 \\ 4 \\ 2 \\ 4 \\ 9 \\ 4 \\ 1 \\ 3 \\ \end{array} $	+ +-2 +-2 1-2 1-5 1 1-5 + +
Calluna vulgaris Empetrum nigrum Erice a taralix	97 6	100	35 d 2 3	5 5	i* 22* +	34*	47	36 1-3	100	$\begin{array}{ccc} 36 & 4{-}5 \\ 5 & +{-}2 \end{array}$	80 3 16	8 3-5 8 1-2	100 3 5		31* 3	15* +	100 3 4		86 12	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	100 36 5	5 1	20* 36*	+ 8	1* 36* +-1	97 1	${ \begin{array}{ccc} 36 & 4-5 \\ 4 & +-1 \end{array} }$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5 100 5	$ \begin{array}{ccc} 36 & 5 \\ 3 & 1 \\ 1 \\ 1 \end{array} $	34 36	+ \$	90 36 +	96	100	36 5	95 36 14 9	2-5 +-2
Genista anglica Vaccinium myrtillus – vitis-idaea	7 18 20	1 3	13 20 1(2	1 2)	$\begin{array}{ccc} 9 & + \\ 1 & 11 & + \end{array}$	7+	10 3	$\begin{array}{ccc} 18 & +-1 \\ 10 & +-2 \end{array}$	14 18	$\begin{array}{ccc} 14 & +-1 \\ 18 & +-3 \end{array}$	4 1 39 2	18 1 17 1-4	2		19*	8* + 4 +	9 2 2	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	4 8 2	$\begin{array}{ccc} 20 & +-1 \\ 12 & +-2 \\ 6 & +-3 \end{array}$		1 1	$ \begin{array}{ccc} 17^{*} & 22^{*} \\ 3 & 5 \end{array} $	+ 3:	$ \begin{array}{ccccccccccccccccccccccccccccccccccc$	42 11	$\begin{array}{cccc} 36 & 1-2 \\ 15 & + \\ 2 & + \end{array}$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	2 3 -3 -3	$ \begin{array}{ccc} 10 & 1 \\ 2 & 1 \end{array} $	2 6	+	69-	1	15	24 +-2	35 32 2 2 4	1-2 1 +-2
Agrostis stolonifera – tenuis Anthoxanthum odoratum. Carex arenaria. – pilulifera. Deschampsia flexuosa. Festuca rubra. – ovina. Holcus lamatus.	5 17 7 5 25 8	1 3 29 44		1 + 1 1 1 1 6	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	12 4 82 ? 2 +	25 13 83 56 3	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	32 32 93 2	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	4 7 3 2 70 2 1	$ \begin{array}{ccccccccccccccccccccccccccccccccc$	4 1 32 3 37 5		4 2 26 3 76 3 25 3 8 1	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	<pre> 1 44 3 9 1 92 3 8 3 </pre>	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1 10 71 2 84	$egin{array}{cccc} 2 & + & & & \\ 2 & + - 1 & & & \\ 1 & + & & & & \\ 12 & + & & & & \\ 36 & 2 - 4 & & & & \\ 2 & + & & & & \\ 5 & + - 2 & & & & \end{array}$	5 12 8 7 30 30 43 36 2 4	1 1 1 1	$\begin{array}{cccc} 1 & 2 \\ 8 & 22 \\ 24 & 32 \\ \\ 77^* & 36^* \\ 46 & 36 \\ 3 & 7 \\ 5 \end{array}$	+ + 1 + 3 + 6 + 5 + + + + + + + + + + + + + + + +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 40 30 82 10	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	4 2 2 16 10 87 36 2- 1 3 +- 3 +-	+ + + + + + + + + + + +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccc} 12 & 36 \\ & 9 \\ & 1 \\ 64 & 36 \\ 2 & 7 \end{array}$	+++++	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 37 1 58 14	4 14 12 14 52	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 5 3 18 15 21 7 6 59 36 3 8	+ +-1 +-1 + + -1 -4 -4 -1 -4 -1 -4 -1 -4 -1 -4 -1 -1 -4 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1
— mollis	13?	5	1 1 8	1 1 1	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	+ 8 9	15 12	$\begin{array}{ccc} 2 & +-1 \\ 21 & +-1 \\ 24 & +-2 \end{array}$	2	$\begin{array}{cccc} 1 & + \\ 32 & + \\ 1 & + \end{array}$	1 4	$ \begin{array}{r} 3 & + \\ 1 & + \\ 6 & + \\ \end{array} $			15 :	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	4 2 1	$\begin{array}{c} 0 & + \\ 2 & + \end{array}$	5 19	$\begin{array}{ccc} 3 & + \\ 9 & + -1 \end{array}$	3 6	1 +-1	5^{*} 10* 5 19	+ 1		1	8 +(1) 1 +	5 7 2	++++	$ \begin{array}{cccc} 1 & 1 \\ 1 & + \\ 5 & 1 \end{array} $	3 1	+++++	18 -	- 6	20	31 +(1)	10 8 2 2	+ +
Achillea millefolla Antennaria diolea Arnica montana. Campanula rotundifola. Chemopodium album. Euphrasia micrantha. Filago minima.	6	4	$ \begin{array}{c} 18\\1\\2 \end{array} $	1 1 1	2 + 2 +	+++++		7 + -1 4 + 2 + 2 2 + 2	1 52 - 2 1 5	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	9 :	$5 +-1 \\ 25 +-2$	2	6 1 5 +-1	1	$ \begin{array}{r} 1 & + \\ 18 & + \\ 6 & + \\ 4 & + \\ 2 & + \end{array} $		$ \begin{array}{r} 4 & + \\ 4 & +-2 \\ 4 & +-1 \\ 5 & + \\ 9 & + \end{array} $	5 1 20	$ \begin{array}{c} 6 & + \\ 16 & +(1) \\ 32 & 1-2 \end{array} $	2 7 3 9	1 +-1	2 21 11* 12* 1* 8* 1 1	+ + + + + +	$\begin{array}{cccccccccccccccccccccccccccccccccccc$) 2 17	$\begin{array}{ccc} 6 & +(1) \\ 26 & +-1 \\ 2 & + \\ 1 & + \end{array}$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	-1 -2	5 +-1 12 +-1	2 1 9	++++	1 11 - 2 -	+	9 4 6	26 + 12 + 12 + 11 + 16 + (1)	2 5 10 5 1 18	+ + +(1) +-2
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JØRGEN LÜTZEN

STUDIES ON PARASITIC GASTROPODS FROM ECHINODERMS II.

ON *STILIFER* BRODERIP, WITH SPECIAL REFERENCE TO THE STRUCTURE OF THE SEXUAL APPARATUS AND THE REPRODUCTION

> Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 19,6



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Kommissionær: Munksgaard København 1972

Synopsis

New finds of species of *Stilifer*, a prosobranch gastropod endoparasitic in Indo-pacific starfishes are presented. A study of a collection of *S. linckiae* from Hawaii has revealed that this species is a consecutive hermaphrodite that functions as a male when young and as a female when older. The reproductive system of the male and the female as well as a few transitional stages are described. It is postulated that egg capsules are formed and liberated into the water. The gastropods are usually arranged in groups consisting of two or three individuals of opposite sex; it is concluded that the maintenance of such groups is dependent on the presence of the female preventing the ordinary sex transformation in the males.

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Introduction

As defined by Ivanov (1952), the genus *Stilifer* Broderip includes prosobranch gastropods that live as endoparasites in the skin of starfishes. The body is only slightly modified and bears a small, spiral shell. A cup-shaped (false) mantle or pseudopallium originates at the base of the proboscis and envelops the entire body, thus separating the gastropod from the host tissue. The elongate proboscis is a powerful structure that is introduced deeply into the body or rays of the starfish.

There has been much confusion as to the number of *Stilifer* species. Ivanov (1952) recognizes not more than three, and states that until that time, a total of 23 species have been referred to the genus; I consider even this estimate too moderate. The vague delimitation of the genus is chiefly a result of the inadequate knowledge of the species originally referred to *Stilifer*. This is most regrettable since most authors agree that the genus holds a key position in the phylogeny of the parasitic gastropods grouped in the family "Stiliferidae" (Ivanov, l.c.; Gruzov, 1965), and at the same time are near the base of an evolutionary line leading to the family Entoconchidae (Schiemenz, 1889). The necessity of a modern examination of a species of *Stilifer* has partially been alleviated by Ivanov's study on *S. ovoideus*; but since it is based on a single, immature specimen, it has left many unsolved questions and needs to be amplified.

The present account concentrates on the sexuality and reproduction of one species of *Stilifer*, *S. linckiae*; these subjects have been entirely ignored by earlier students. I have further taken the opportunity to present a number of new finds of various species, since a study of these have partially substantiated the findings on the reproduction.

Examination of valuable material of *Stilifer* in the British Museum (Nat. Hist.), London, was made possible by a grant from the University of Copenhagen. I am greatly indebted to Dr. R. U. Gooding (U. S. Natn. Museum, Washington) and to Mr. Bill Milisen (Pacific Biomedical Research Center, Honolulu), who assisted him, for collecting material of *S. linckiae*.

Synopsis of the Species of Stilifer

To support the separation of the species mentioned in the following, I have cited Habe (1951, 1952) who recognizes six species, based mainly on shell characteristics. New illustrations were deemed unnecessary for the present study, but due references are given for each species.

The known distribution of *Stilifer* is restricted to tropical and subtropical coastal regions of the Indian and Pacific Oceans, extending from Moçambique, E. Africa, to the

Galapagos Islands. The present account extends the number of genera of parasitized starfishes to six (*Ophidiaster, Linckia, Tamaria, Certonardoa*, all of the family Linckii-dae; *Choriaster* of the family Oreasteridae; and *Heliaster* of the family Heliasteridae).

The institutions which have made material of *Stilifer* available to me, are abbreviated as follows: Australian Museum, Sydney: AMS; British Museum (Nat. Hist.), London: BMNH; United States National Museum, Washington, D. C.: USNM; and Zoological Museum, Copenhagen: ZMC.

1. Stilifer astericola Broderip 1832

The original material of this species is in the Mollusk Division and the Echinoderm Division of BMNH. The description of the soft parts given by Broderip (1832: 60, republished and illustrated in Sowerby's Genera of Recent and Fossil Shells, no. 38) is insufficient, and is probably also erroneous as to certain points (for example the structure of the so-called mantle). Since the available material is dried, substantiation of *S. astericola's* relation to the following species relies on similarity in shell structure and mode of life both of which may be dubious characters. Should new material of *S. astericola* become available, it is possible that it will prove to be less related to other species of *Stilifer* than hitherto assumed. This might have nomeclatural implications, *S. astericola* being the first species ever referred to *Stilifer*.

The material consists of (1) an infected specimen of the starfish *Heliaster* sp. from South America (?) with one gastropod, labelled 14.2.1949 and consequently not part of the original material; (2) one infected *Heliaster* (of 6) from the Galapagos Islands, with one gastropod; (3) one gastropod, labelled *S. broderipii*, without further information; (4) three gastropods of different sizes from the Galapagos Islands; and (5) one specimen of *H. cumingi* (Gray) with five gastropods in addition to five gastropods which have been removed (from the same host specimen?). As was noted by Broderip, parasitism occurs only on the oral side, preferably on the rays. Quoting Cuming, who collected the original material and made observations in the field, the gastropods are "almost hidden from sight, so deeply does the animal penetrate into the substance of the Star-fish, in which it makes a comfortable cyst for itself, wherein it most probably turns by the aid of its rudimentary foot" (Broderip, 1832).

2. Stilifer ovoideus H. & A. Adams 1853

The synonymy given by Habe (1952: 80) is adopted here. The species was originally incorrectly identified as *S. astericola* (by Adams & Reeve, 1850: 47), but was later given a status of its own (H. & A. Adams, 1853: 239). Habe (l.c.) identified a gastropod that had earlier been found in Japanese waters in galls in the rays of the starfish *Certonardoa semiregularis* (Müller & Troschel) as *S. ovoideus* while Hirase (1927: (8); 1932: 73), Kuroda (1934: 208), and Ivanov (l.c.: 118) considered it to be *S. celebensis* Kükenthal. The latter author studied the anatomy of an immature female; Hirase examined the histological structure of the pseudopallium (1927), and the penetration of the parasite into the body of its host (1932).

Nr. 6

Along the Japanese coast the species has been taken at Tokioka, Amakusa, Kyushu; Kushimoto, Wakayama Pref., Misaki and Hayama, Kanagawa Pref., Honshu.

The original material in BMNH (taken by the 'Samarang' at Borneo) has been examined by the author. It includes a dried shell, the one figured by Adams & Reeve (l. c., pl. XVII, fig. 5) according to the accompanying label, and two dried starfish, each with one ray parasitized; these were kindly identified by Dr. Ailsa Clark as *Ophidiaster granifer* Lütken. The gastropods seem indistinguishable from those described and illustrated by Habe from *C. semiregularis*.

A dried specimen of the starfish *Tamaria dubiosa* (Koehler) from Cocos Keeling Atoll, E. Indian Ocean (USNM, Moll. Coll. 589237) is parasitized in the basis of a ray by a small gastropod, presumably belonging to *S. ovoideus*.

3. Stilifer linckiae Sarasin & Sarasin 1887

The general organization of the parasite was briefly described by Sarasin & Sarasin (1886: 19; 1887: 21, pls. IV, V) who also illustrated the shell. Davis (1967: 343) showed that the tendency toward spontaneous autotomy in the host, *Linckia multifora* (Lam.), is considerably reduced in parasitized rays.

Originally described from Trincomali, Ceylon, the species has since been found at Inhaca Island, Moçambique (Macnae & Kalk, 1962: 119) and in Kaneohe Bay, Oahu, Hawaii (Davis, l.c.). A few specimens of *L. multifora* from Inhaca Island parasitized by *S. linckiae* are kept in the ZMC (one host with at least three snails) and BMNH (four hosts, of which one had two, or perhaps three infected rays). One dried *L. multifora* from Muscat, Gulf of Oman, Iranian Gulf, had a single gall (BMNH). Another dried *L. multifora* with a gall on one ray is from Lifu, the Loyalty Islands, S. W. Pacific (BMNH); two infected pieces of ray of the same species, one with five gastropods are also from these islands (BMNH). An alcohol preserved specimen of *L. multifora* with a gall derives from Solomon Atoll, Chagos Archipel, Indian Ocean (BMNH).

4. Stilifer celebensis Kükenthal 1897

The species is known from only one specimen, the shell of which was lost at fixation, and, consequently, will be difficult to recognize. Hirase (1918, 1927, 1932), Kuroda (1934) and Ivanov (l.c.) identified their material as *S. celebensis*, but it is more probable, as is stated by Habe (1952), that it belongs to *S. ovoideus*.

The species was found in *Choriaster*, a starfish of the family Oreasteridae, from Celebes.

5. Stilifer utinomii Habe 1951

A shell of this species is illustrated by Habe (1952: 80, pl. VI, fig. 22). The species is said to live in the rays of *Linckia guildingii* Gray at Shirahama, Wakayama Pref., Honshu, Japan.

In the AMS there are four dried specimens of *L. guildingii* parasitized by respectively one, one, and two specimens of *S. utinomii* and taken at Masthead Island, Queensland (C 69680) and Northwest Isle, Capricorn Group, Great Barrier Reef (C 69669 & C 69678). A dried specimen of L. *laevigata* in AMS, also from Masthead Island (C 69676) is parasitized by one snail that obviously belongs to the same species.

Stilifer kochianus Sowerby (1901: 209, pl. XXII, fig. 6), of which I have seen three specimens in BMNH (two of them types, pl. I, fig. 1), seems indistinguishable from the Australian specimens of *S. utinomii. S. kochianus* was collected at Cebú, the Philippines. It was not claimed to be a parasitic species.

6. Stilifer ophidiastericola Habe 1951

The shell is illustrated by Habe (1951: 94; 1952: 80, pl. VI, fig. 19). The species parasitizes the rays of the starfishes *Ophidiaster cribrarium* Lütken and *O. lorioli* Fisher, and is known from Tomioka, Amakusa, Kyushu, and Kushimoto, Wakayama Pref., Honshu, Japan.

A specimen of *O. lorioli* from Queensland, Australia, is parasitized by this species (BMNH). The disk is swollen where two of the rays meet and has an aperture which is slightly ventrally directed. Through it, the top whorls of three snails could be seen. Two dried specimens of *O. confertus* Clark from Masthead Island, Australia (AMS, C 69681) are parasitized by what I consider to be specimens of *S. ophidiastericola*. One of the starfish has a swelling at the base of a ray containing two gastropods. The other is swollen in the mid portion of two rays where one and two gastropods respectively are found.

Stilifer spp.

Two dried specimens of *Ophidiaster* sp. from Northwest Isle, Capricorn Group, Great Barrier Reef (AMS, C 69678) are parasitized respectively on one ray and on two rays.

An alcohol preserved specimen of *Ophidiaster* (?) sp. from N. of Doe Roa, Banda Sea (Dan. Exp. to the Kei Islands, st. 39), 60 m, has swollen galls in the distal part of two rays (ZMC).

The Reproductive System of *Stilifer* with Special Reference to *S. linckiae*

Previous Investigations

Since its discovery, the sexuality of *Stilifer* has remained enigmatic. The earliest investigators (Broderip, 1832; Gray, 1939; and Adams & Reeve, 1850) failed to identify the sex in their material (*S. astericola* and *ovoideus*). Neither did Sarasin & Sarasin (1887) nor Kükenthal (1897) comment on the reproductive organs of the species that they examined (*S. linckiae* and *celebensis*). Hirase (1932) studied the genital organs of twenty specimens of *S. ovoideus*, but noted that they were all females and concluded that the males were free-living. Ivanov (l.c.) had at his disposal only a single specimen

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of the same species, and this proved to be an immature female. Males are, therefore, unknown, and the genital organs of the female remains to be described. Partially as a consequence of this, the method of reproduction is also unknown. Baer (1952: 24) suggested that the species of *Stilifer* will possibly prove to be protandrous hermaphrodites, since "the only species that has been thoroughly investigated, *S. sibogae*, is an hermaphrodite with a well developed male copulatory organ." This suggestion is, however, based on the incorrect premise that "*S. sibogae*" is a true *Stilifer*, which is not the case¹.

Material and Treatment

Davis (1967) has provided detailed information about the occurrence of *S. linckiae* in Kaneohe Bay, Oahu, Hawaii. At my request, Dr. R. U. Gooding, who stayed at Oahu for some time, collected a number of parasitized *Linckia multifora* from a position very close to Davis' locality B8. Sixteen starfish among 40 collected were parasitized. They were taken on 17 June 1971 at a depth of 1.5 m on, in, and under rocks and coral on the reef flat just WNW of Buoy 8 $(21^{\circ}27'11''N, 157^{\circ}47'55''W)$. They were placed in Bouin's fluid, which was changed once, and thereafter transferred to 70% ethyl alcohol.

When received, the material consisted of 1 whole host specimen that was parasitized on the oral side of the disk, and 17 isolated rays, each with a characteristic swelling caused by the gastropods (pl. I, fig. 2). Thirteen of the hosts had one infected ray, whereas two hosts had two rays infected.

The swellings were examined externally and photographed; two specimens were decalcified in HCl in 90% ethyl alcohol and embedded in celloidine for sectioning of the entire ray, while all gastropods were dissected out of the remaining specimens. The majority were embedded in tissuemat and cut into 6 or 8 μ thick sections and stained with H + E, tetrachrome (Weigert's iron hematoxyline, Chlorantine fast red, orange G, and Alcian blue), or Azan. Two small specimens were embedded in epon and cut into 2 μ thick sections which were stained with toluidine blue.

The Swellings or Galls

In the present species these have been illustrated earlier by Sarasin & Sarasin (1887, pl. IV, figs. 1, 2) and Davis (l. c., pl. 48). As observed by the latter author, the gall openings to the exterior occur apparently at random on the oral, lateral, or aboral surface of the rays. My material also supports the information provided by Davis that parasitism may obviously occur everywhere along the ray, from the most basal part to the very tip.

¹ Yet unpublished examinations of the original and new material of "S. sibogae" Schepman & Nierstrasz has convinced me that it actually consists of three species, all of which belong to the sea urchin snails, *Pelsenee*ria Koehler & Vaney. These are unique in several respects and it may be seriously doubted whether they are related to any other parasitic gastropods yet described, except *Parastilifer* Ivanov. They are simultaneous, not protandrous, hermaphrodites.

On one occasion Sarasin & Sarasin (1887: 24) found two gastropods within the same swelling, and they considered the smaller to be an immature. Davis (l.c.) recorded the galls that he examined as containing from one to several (up to five) snails. Although the number of gastropods present may be estimated from the number of apertures to the exterior, it proved necessary to make a careful dissection of the galls to find all gastropods, since the apertures of the smallest individuals may often appear only as extremely minute pores or crevices in the host's skin (pl. I, figs. 2, 6). Among the 17 parasitized rays, one gall contained one snail, twelve galls contained two snails each, three galls contained three snails each, and one gall contained four snails. Three snails were present in the gall of the starfish parasitized on the disk. On an average, therefore, the galls harboured 2.3 snails each.

The apertures in *S. linckiae* may reach a considerably larger size than those of any other species of *Stilifer* (except, perhaps, *S. astericola*), but the variation is great. Through the larger apertures several of the whorls of the snail may be observed from outside, but in most of the smaller apertures this is not possible (pl. I, figs. 2–6). Each snail within a gall is independent and has its own aperture to the exterior.

The Sex in S. linckiae

Of a total of 41 specimens examined by sectioning, 16 were mature females. Nineteen specimens proved to be males; this is, therefore, the first time that the male sex has been demonstrated in a species of *Stilifer*. The remaining 6 specimens are particularly interesting since they show successive stages in the transition from a male to a female phase.

Only the sexual apparatus of *S. linckiae* will be described since the structure of all other organ systems are fundamentally similar to those of *S. ovoideus* as described by Ivanov (l.c.). The two sexes were found to differ only in size, females being substantially larger than males, and in the organization of the reproductive system. In the absence of a shell (which was lost at fixation) the size of any specimen is expressed as the distance separating the apex and the proboscis base (defined by the point marked by two arrows in text-fig. 1) measured on the section series. Sixteen functional females measured from 3.5 to 5.9 mm compared with 0.7 to 2.8 mm in sixteen functional males.

The Male Reproductive System (text-figs. 2 & 3A; pl. I, fig. 8)

The testis occupies the major portion of the upper coils of the visceral mass lying over the lobes of the digestive gland. The testicular duct is very long, and its posterior part is narrow and greatly coiled. More anteriorly it expands enormously, and this section acts as a vesicula seminalis, the walls of which has a very flattened squamous epithelium. The vesicula contains large quantities of sperm. On passing forward it rapidly diminishes in diameter and leads to a small, vesicular prostate gland that has a narrow entrance into the most posterior end of the mantle cavity. From the aperture of the prostate, an open glandular and ciliated seminal groove passes forward along the right side of the body to the base of the penis. In proportion to the size of the animal,



Fig. 1. Diagram showing the position of two specimens, a male and a female, of *Stilifer linckiae* in a gall in the ray of the starfish *Linckia multifora*. Expulsion of egg capsules (1) from the pseudopallial cavity (2) as indicated has actually never been observed. 3, foot; 4, penis; 5, proboscis.

the latter is a large structure, arising from behind the head. When at rest, it lies in a single spiral, folded up in the exterior part of the mantle cavity which is, however, far too small to accomodate it. The penis is entirely ciliated. In transversal section it appears to be flattened, and has a deep seminal groove along its entire length. While the proximal part is predominantly muscular with only a few blood lacunae, vascular spaces are numerous throughout the thickness of its apical half. When extruded and filled with blood, the penis undoubtedly extends considerably, as is indicated by the abundant and closely placed transversal folds seen on its surface.

The Female Reproductive System (pl. I, fig. 7)

The ovary occupies the central and right part of all spire whorls. Dorsally and to the left it is separated from the body surface by a continuous layer of the digestive gland. Numerous haemocoelic spaces issue from the ascending posterior aorta and interpenetrate the ovary lobules. The oviduct emerges far back in the body whorl from the ventral aspect of the ovary, and runs forward along the right side of the main sinus of the digestive gland. Its walls are slightly folded and composed of tall, ciliated cells with

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Fig. 2. Two male *Stilifer linckiae*. The pseudopallium has been removed in A to show animal. Note the open seminal groove on the surface of the penis. The right and, less distinctly, the left eye are seen in front of the penis in A. 6, aperture of pseudopallial cavity; 7, ctenidium; 8, digestive gland; 9, testis. Other symbols as in Fig. 1.

basal nuclei and a plasma that is left almost unstained. Two oviducts were present in two specimens. Anteriorly the oviduct narrows and debouches into the albumen gland. This is a rather conspicuous and subdivided organ that lies to the right of the oviduct and along the surface of the whorl. The gland cells are of two types: large, globular cells with basal nuclei and a plasma that stains intensively with alcian blue, and among them small, slender cells with centrally placed nuclei and short cilia are found. The walls of the next section of the female duct are deeply and heavily folded. This section is far back in the thickened right side of the mantle wall next to the albumen gland on one side and the receptacular pouch and capsule gland on the other. The epithelial cells are small, ciliated, and have relatively large nuclei; much larger goblet cells that stain with alcian blue occur among them, either singly or in groups. Since non-orientated sperm were frequently observed here, this section may be regarded as a bursa copulatrix. It has a narrow connection with the receptaculum seminis, a rather capacious, irregularly shaped sac in which large amounts of sperm are stored; the sperm here are closely packed and orientated with the tips of their heads embedded in the wall cells and with their tails directed into the lumen.

The bursa copulatrix has a fairly wide connection anteriorly with the capsule gland. This is a very large structure which occupies the entire dorsal and right side of the mantle skirt, and opens to the mantle cavity by a ventral slit along the greater part of its length.

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Fig. 3. Stilifer linckiae. Sections through A: male phase (length 1.6 mm, gonad index $68^{\circ}/_{0}$); B: early transitional stage (length 2.3 mm, gonad index $38^{\circ}/_{0}$); and C: late transitional stage (young female, length 2.1 mm, gonad index $20^{\circ}/_{0}$). 10, anus; 11, capsule gland being formed (from seminal groove); 12, heart; 13, kidney; 14, oesophagus; 15, posterior part of seminal groove; 16, posterior part of mantle cavity; 17, rectum; 18, rudimentary ovary; 19, rudiment of oviduct; 20, seminal groove; 21, start of testicular duct; 22, testicular duct; 23, vesicula seminalis, in B and C containing only a few sperm cells and with a tall epithelium. Other symbols as in Figs. 1 and 2.

Transitional Stages from Male to Female Phase (text-fig. 3 B & C)

Functional males and females only occurred in 14 galls (text-fig. 4, nos. 1–14), of which eleven contained one male and one female each (nos. 1–11); in three other there were one female and two males (no. 12), two females and one male (no. 13), and one female and three males (no. 14). Six of the nine individuals in the remaining four galls (nos. 15–18) were clearly undergoing sex transformation. Three were in an early phase, and three were in later phases of the transition from male to female.

The masculine character of the former three specimens (length as earlier defined: 2.1-2.3 mm) is unmistakable, but the testis has atrophied considerably, its volume being 31, 37, and 38% of the combined volume of gonad and digestive gland (calculated

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from the section series) as compared with 59, 68, and 83% in three functional males (chosen at random). Rather few testis lobes showed spermiogenesis; the vesicula seminalis was packed with sperm cells in one specimen, but was largely empty in the other two and had a minute lumen throughout. The epithelial lining of the vesicula differed from that found in the functional males in that the cells were cubical, or even tall and cylindrical. In two specimens sperm cells were noted within the cells of the epithelial lining, and were presumably being digested. The open seminal groove of the specimen with sperm in the vesicle was of normal construction, while the walls had hypertrophied in the other two specimens, especially posteriorly resulting in a deepening of the groove. The penis of all three specimens was of usual size.

The three late transitional stages (length: 1.9–2.6 mm) show further advancements toward a female condition. The volume of the gonad is further reduced since it shows an index of 20, 16, and 9%. The gonad is solid, restricted to the extreme right side of the whorls, and contains oogonia. From the gonad of one of the specimens (gonad index: 20%) two narrow ducts of subequal diameter arise independently (text-fig. 3 C, 19 & 23). One of them is short and curved, whereas the other is rather long, sinuous, and contains some sperm cells throughout; the latter is consequently considered to represent the reduced testis duct including the vesicula seminalis, and its content accordingly autosperm that has escaped digestion; the former is presumably the rudimentary oviduct. The two ducts unite and open by way of a common, narrow aperture into the most posterior part of the open pallial groove, which is unusually deep throughout its length in this specimen. A penis is present, although it is reduced to a vestige. In the two other specimens, an oviduct is clearly distinguishable, but no testis duct could be traced. The pallial groove is very deep, and its posterior part is separated from the mantle cavity by fusion of its walls. The oviduct opens into this portion, which presumably later differentiates into the albumen gland, the bursa copulatrix and the receptacle. A vestigial penis is present in one specimen, but is absent in the other.

The Type of Sexuality in S. linckiae

The findings related above suggest that *S. linckiae* is a consecutive hermaphrodite that functions as a male when young and as a female when older. Cessation of spermiogenesis and resorption of the spermatic tissue initiate the transitory period. At the same time, the cells lining the vesicula seminalis become cubical or cylindrical and start to digest the superfluous sperm cells stored in the vesicle. The testis duct atrophies completely and a new gonadial duct is established at a later stage. In the remainder of the gonad, oogonia appear (by transformation of spermatogonia?) and the gonad resumes growth. It seems fairly certain that the albumen gland, the bursa, and the receptacle are formed by elaboration of the posterior part of the open pallial groove of the male that is partitioned off from the mantle cavity, whereas the section anterior to this area becomes the capsule gland through incomplete fusion of its walls. The penis is reduced, but it may persist as a vestige even in adult females; it was found in two young and two func-



Fig. 4. *Stilifer linckiae*. Diagram showing the sequence of stages found in male phase (A), early and late transitional phases (B and C) and female phase (D), and the distribution of these in the 18 galls examined.

tional females. The fact that more than one oviduct occurred in a few females may indicate that the testis duct is occasionally preserved and transformed into an accessory oviduct.

Although the males of *S. linckiae* possess the ability to undergo sex transformation, it is very interesting to note that this potential is obviously suppressed by the proximity of the female sex. This is apparent upon consideration of the composition of the gall inhabitants (text-fig. 4): With one exception (no. 18), all six gastropods in transitory phases come from the only three galls in which functional females were absent (nos. 15–17); and none of 17 males in 14 galls with functional females (nos. 1–14) had initiated a sex change. Unless two or more gastropods settle on a host at about the same time, this mechanism will ultimately assure the establishment of pairs, trios, or quartets, etc. of gastropods of opposite sex, since those settled first will develop into females (through a male phase) and these will maintain the maleness of individuals settling at a later date. This mechanism could presumably be experimentally tested by studying the effect of extirpation of their female partners on the males.

Consecutive hermaphroditism has been recorded among the Mesogastropoda in the families Ianthinidae (Ankel, 1926), the Scalidae (Ankel, 1936), the Capulidae (Graham, 1954), and the Calyptraeidae (Orton, 1909); the evidence of protandry in the Hipponicidae is not conclusive as is pointed out by Laws (1970). In *Clathrus clathrus* (L.) of the family Scalidae, a sex change is undergone several times throughout life, in species of *Ianthina*, probably only once. In the Capulidae and in *Calyptraea chinensis* (L.), sex change always occurs at a particular stage in the life cycle and appears to be unaffected by external stimuli. Extensive literature on sex reversal in various species of the slipper limpets, *Crepidula* (family Calyptraeidae), summarized by Fretter & Graham (1964), suggests that the sex transformation here is the result of an interaction between the various members of the social group that forms the well known chain. Gould (1919) has proposed that the lower members of the chain, the functional females, secrete a substance into the surrounding water that effects maintenance of the masculinity of the males. It is likely that the sex of the young *Stilifer* may prove to be controlled in a similar way.

Copulation and Oviposition

The *S. linckiae* material examined permits us to draw some conclusions as to how reproduction takes place.

Sperm is stored in the male in the vesicula seminalis. It is then discharged into the final section of the testicular duct and, further on, into the prostate. Here it mingles with the prostatic secretion to form the seminal fluid which is conveyed along the open seminal groove to the tip of the penis.

To reach the female at copulation, the erected penis has to be extended through the male aperture and introduced in the nearest female opening (text-fig. 1). The depth to which the penis penetrates to discharge its contents is open to guesses. It is possible, although hardly likely, that the seminal fluid is simply poured into the pseudopallial cavity, and from there transferred to the female genital opening by the inhalant water current. The penis is more probably introduced into the mantle cavity and the sperm deposited somewhere in the open pallial duct; assuming this, the length to which the penis can extend may be estimated as follows: the greatest distance separating a male and a female pseudopallial aperture was 2.0 mm; the distance from the penis base to the margin of the male aperture was 1.8 mm; and the distance from the margin of the female aperture to the mantle opening, 3.5 mm. Accordingly, the penis would have had to extend at least 7.3 mm should copulation occur; the fact that sperm were found in the receptacle pouch of the female in question proved the penis' ability to do so.

Unorientated sperm were observed in the bursa (and occasionally in the albumen gland), and the eggs are presumably fertilized here after they have been embedded in albumen. As they pass anteriorly they become covered by a secretion from the capsule gland. None of the females examined by sectioning had been preserved at the moment of formation of egg capsules. But since the length of the ventral opening of the capsule



Fig. 5. Relation between body length (as defined in the text), area of pseudopallial aperture, and sexual phase in *Stilifer linckiae* (35 individuals).

gland is undoubtedly correlated with the size of these capsules, we may estimate them to be relative large and to contain several eggs.

Spawning has never been observed in any species of *Stilifer*. The egg capsules of parasitic gastropods are frequently attached to a substrate, as, for example, the skin of the host or the shell of the gastropods; species with a pseudopallial cavity may brood the eggs or capsules. None of the 16 females of *S. linckiae* with sperm in their receptacle were found to contain egg capsules, and Davis (l.c.) did not report any from the many galls which he inspected either. Presumably, therefore, the capsules are expelled directly into the surrounding water through the pseudopallial aperture immediately upon their formation as suggested in text-fig. 1. This would seem advantageous since brooding of the capsules in the incapacious pseudopallial cavity is likely to restrict the number produced at a given time, and further, to function as an obstacle to the respiratory water currents. Hirase (1932: 74) suggests that the foot (in *S. ovoideus*) acts as a type of piston, which together with contraction and expansion of the pseudopallial wall may flush water

in and out through the aperture; Cheng (1968: 679) maintains that the sex products are discharged at the same time. It is unclear whether the latter statement is founded on observations or not. It is apparent from text-fig. 5 that the size of the apertures (measured from close-ups of photographs) increases with the dimensions of the gastropods; as a consequence of this, they are larger in the females (usually 1 to 4 mm²) than in the males. This allows for expulsion of quite large egg capsules.

Comparison with other Species of Stilifer

The salient feature of the galls of *S. linckiae* is that they usually contain two or more gastropods, and that these are most frequently of two different types: small specimens (males or transitional phases) and large specimens (females). The *Stilifer* material at my disposal other than *S. linckiae* has been mainly dried, ill-preserved museum specimens, the sex of which can no longer be determined. The number and size of the gastropods may, however, still be examined.

S. astericola. Of three specimens of *Heliaster* with gastropods still *in situ*, two had one parasite each, and one harboured five. There were probably more parasites at one time in the latter specimen since two or three cystiform deepenings in the starfish skin were now empty, but had probably accomodated some smaller snails.

S. ovoideus. A gall caused by this species in Ophidiaster granifer contained three gastropods: one was comparatively large (length of shell: 5.7 mm) and had been dissected out; the remaining two were still attached to the inner wall of the gall, each located in a shrivelled pseudopallial cover and with the shells, both 1.8 mm long, pointing toward the gall aperture. Through the opening of another gall (in O. granifer), which was not dissected, one snail could be seen. The parasitized specimen of Tamaria dubiosa contained a single gastropod.

S. utinomii. Of the five galls examined, four contained one snail each; the fifth, two snails measuring 4.0 and 5.5 mm in shell length.

S. ophidiastericola. As related above, a gall in the ray of an O. lorioli accomodated three gastropods; since the gall was not opened, however, they could not be measured. Five gastropods in three galls in O. confertus measured as follows: 1) ca. 4 mm; 2) 2.8 and 1.9 mm; 3) ca. 5 mm and 1.5 mm.

Stillifer sp. from Ophidiaster sp. (AMS). One gall was opened from inside, thus exposing one large and one tiny gastropod (length 5.2 and 1.2 mm resp.) placed close together and apparently opening separately to the exterior. Two other galls were left unopened, but from the outside each could be seen to contain one very large and one minute gastropod; the apertures of the latter opened at the margin of the larger's aperture or 1.2 mm from it.

Stilifer sp. from Ophidiaster (?) sp. (ZMC). The two galls on the infected starfish accomodated two and five subequally large gastropods.

We may, therefore, conclude that two or more specimens occur together in a gall more frequently than only a single specimen in other species of *Stilifer* too. The sex of Nr. 6

these could only be determined in one case, *viz.* in the *Ophidiaster* (?) gall taken by the Kei Island Expedition. Although very badly preserved, section series of the five gastropods within a single gall showed that there were one female and four slightly smaller males. It is to be expected, therefore, that the type of sexuality found in *S. linckiae* characterizes all members of the genus.

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References

ADAMS, A. & REEVE, L., 1850: Mollusca, in ADAMS, A., edit.: The Zoology of the Voyage of H. M. S. Samarang. London.

ADAMS, H. & A., 1853: The Genera of Recent Mollusca, I. London.

ANKEL, W. E., 1926: Spermiozeugmenbildung durch atypische (apyrene) und typische Spermien bei *Scala* und *Janthina*. Verh. dt. zool. Ges., Zool. Anz. Suppl. 2: 193–202.

ANKEL, W. E., 1936: Prosobranchia, in GRIMPE, G. & WAGLER, E.: Die Tierwelt der Nord- und Ostsee, IX b I. Leipzig.

BAER, J. G., 1952: Ecology of animal parasites. Urbana, 224 pp.

BRODERIP, W. J., 1832: Characters of New Species of Mollusca and Conchifera, collected by Mr. Cuming. Proc. zool. Soc. Lond. 1832, pt.II: 50–61.

CHENG, T. C., 1968: The Biology of Animal Parasites. Philad. & Lond., 727 pp.

DAVIS, L. V., 1967: The Suppression of Autotomy in *Linckia multifora* (Lamarck) by a Parasitic Gastropod, *Stylifer linckiae* Sarasin. Veliger, 9: 343–346.

FRETTER, V. & GRAHAM, A., 1964: Reproduction, in WILBUR, K. M. & YONGE, C. M., edit.: Physiology of Mollusca, I. N. Y. & Lond., 473 pp.

Gould, H. N., 1919: Studies on sex in the hermaphrodite mollusc *Crepidula plana*. III. Transference of the male-producing stimulus through sea-water. J. exp. Zool. 29: 113–120.

GRAHAM, A., 1954: The anatomy of the prosobranch *Trichotropis borealis* Broderip and Sowerby, and the systematic position of the Capulidae. J. mar. biol. Ass. U.K. 33: 129–144.

GRAY, J. E., 1839: Molluscous Animals, and their Shells, in: The Zoology of Captain Beechey's Voyage, London.

GRUZOV, E. N., 1965: The endoparasitic Mollusk Asterophila japonica Randall and Heath (Prosobranchia: Melanellidae) and its relation to the parasitic Gastropods. Malacologia 3: 111–181 (in Russian, with abstracts in English, French, German, and Spanish).

HABE, T., 1951: New parasitic gastropods. Ill. Cat. Jap. Shells, No. 14: 93-94.

HABE, T., 1952: Parasitic gastropods found in echinoderms from Japan. Publs Seto mar. biol. Lab. 2: 73-85.

HABE, T., 1964: Shells of the Western Pacific in Color, II. Osaka, 233 pp., 66 pls.

HIRASE, S., 1918: On a species of parasitic Gastropod. Zool. Mag. Tokyo, 30: 300–307, 339–345, 451–457, 490–492 (in Japanese).

- HIRASE, S., 1927: On the Structure of a parasitic Gastropod, *Stilifer celebensis* Kükenthal. Jap. J. Zool. 1: (8).
- HIRASE, S., 1932: The adaptive modifications of the gastropod *Stilifer celebensis* Kükenthal, parasitic on the starfish *Certonardoa semiregularis* (Müller & Troschel). Proc. malac. Soc. London, 20: 73–76.
- Ivanov, A. V., 1952: Structure of the parasitic Gastropods Stiliferidae as the result of their mode of life. Trudy leningr. Obshch. Estest, 71 (4): 86–140 (in Russian).
- KÜKENTHAL, W., 1897: Parasitische Schnecken. Abh. senckenb. naturforsch. Ges. 12: 1-14.
- KURODA, T., 1934: On some rare shells from Sagami Bay collected by His Majesty the Emperor of Japan. Venus, 4: 204–208.
- Laws, H. M., 1970: Reproductive Biology and Shell Site Preferences in *Hipponix conicus* (Schumacher) (Gastropoda: Hipponicidae). Veliger, 13: 115–121.
- MACNAE, W. & KALK, M., 1962: The Fauna and Flora of Sand Flats at Inhaca Island, Moçambique. J. Anim. Ecol. 31: 93-128.
- ORTON, J. H., 1909: On the occurrence of protandric hermaphroditism in the mollusc *Crepidula* fornicata. Proc. R. Soc. B. 81: 468–484.
- SARASIN, C. F. & P. B., 1886: Über zwei parasitische Schnecken. Zool. Anz. 9: 19-21.
- SARASIN, P. & F., 1887: Ueber zwei Parasitische Schnecken. Erg. naturw. Forsch. Ceylon 1884– 1886, I (1): 19–32.

SCHIEMENZ, P., 1889: Parasitische Schnecken. Biol. Zbl. 9: 567-574 & 585-594.

- Sowerby, G. B., edit., undated: The Genera of Recent and Fossil Shells. No. XXXVIII, London.
- Sowerby, G. B., 1901: Descriptions of New Species of Marine Mollusca collected by the late Otto Koch at the Island of Cebú, Philippines (second Paper). Proc. malac. Soc. Lond. 4: 208-211.

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PLATE I

Fig. 1. Stilifer kochianus Sowerby, type specimen (cleaned shell), BMNH. Scale 2 mm.

Figs. 2-8. Stilifer linckiae Sarasin & Sarasin.

Figs. 2-6. Position in Linckia mullifora as viewed from outside; the arrows indicate the apertures of the male's pseudopallial cavity. Scales represent 2 mm (Fig. 2) or 1 mm (Figs. 3-6).

Fig. 7. Celloidine section through ray of infected L. multifora (the specimen shown in Fig. 2) containing two gastropods in female and male phase. 20μ , tetrachrome. Scale 1 mm.

Fig. 8. Longitudinal section through male. The arrows indicate open seminal groove. Tissuemat, 8μ , tetrachrome. Scale 200μ .

Symbols

1, albumen gland

2, ambulacral groove

3, ambulacral piece

4. atrium

5, capsule gland

6, coelomic cavity of starfish

7, columellar muscle

8, digestive gland

9, foot

10, kidney

11, oesophagus

12, opening of prostate into mantle cavity

13, ovary

14, pedal gland (anterior)

15, penis, basal part

16, penis, middle section

17, penis, apical section

18, proboscis

19, pseudopallial cavity

20, pseudopallial aperture

21, pseudopallium

22, radial water canal

23, skeletal ossicles

24, strand of connective tissue separating pseudopallium and coelom of host

25, testis

26, testicular duct

Plate I



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H. WIENBERG RASMUSSEN

LOWER TERTIARY CRINOIDEA, ASTEROIDEA AND OPHIUROIDEA FROM NORTHERN EUROPE AND GREENLAND

Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 19,7



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Synopsis

Crinoids, asteroids and ophiuroids are common in the Danian but very seldom in the succeeding Paleocene, Eocene and Oligocene sediments. A review of the species found in northern Europe and Greenland is given. The following species are new to science: Calamocrinus ilimanangei, Amphorometra ornata, Astropecten granulatus, Lophidiaster haunsbergensis, Lophidiaster inversus, Lophidiaster concavus, Ceramaster obtusus, Echinaster jacobseni, Ophiura eachatae, Ophiura furiae, Ophiura bognoriensis, Ophiura costata, Ophiura davisi, Ophiura carpelloides, Ophiura bartonensis and Ophiocoma hessi.

A redefinition of the genus Cainocrinus is given.

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Age and distribution of fauna

The Danian

The Danian originally was established as the uppermost Crétaceous, but is now generally referred to the lowermost Tertiary as a stage, or as a substage of the Paleocene.

The Danian sediments in Denmark, Belgium and the Netherlands contain a rich fauna of crinoids, asteroids and ophiuroids previously described (Rasmussen 1950, 1952, 1961, 1965). There is no new information.

Danian crinoids have been incorrectly recorded from England (Peck 1955). There are however no Danian deposits in England. The specimens belong to *Styraco-crinus peracutus* found in the Albian to Cenomanian. They are found in "chalk detritus" near Charing in Kent. The sample is composed of mixed fragments of white and grey chalk redeposited in fluvial gravel of Pleistocene age. No fossil indicating a Danian age of the components has been found (Rasmussen 1961 p. 384).

From borings through the Upper Maastrichtian or Danian of Pulawy in central Poland Maryańska & Popiel-Barczyk (1969) described remains of the following ophiuroids from presumed Danian sediments: *Ophiura hagenowi*, Rasmussen, 1950, *Ophiomusium subcylindricum* (Hagenow, 1840), *Ophiomusium danicum* Nielsen, 1926, and *Asteronyx ornatus* Rasmussen, 1950. They further recorded the remains of *Astropecten* sp., *Chomataster* sp. cfr. *acules* Spencer, 1913, *Teichaster* sp., *Bourgueticrinus* sp. and *Pentacrinus* sp. The ophiuroids described indicate that Danian as well as Upper Maastrichtian may be present in the samples.

In a sample from the presumed Danian at Boryszew in central Poland I have found a few columnals similar to the Lower Eocene *Cainocrinus tintinnabulum* Forbes, 1852, a few columnals of *Bourgueticrinus* sp. or *Democrinus* sp. and marginals of *Astropecten* cfr. *postornatus* (Rasmussen, 1945) and a few badly preserved marginals of *Chomataster*? sp. and *Teichaster*? sp.

From the Danian near Vienna in Austria Kühn (1930 & 1960) described a *Cyathidium* sp. and recorded the presence of *Isselicrinus paucicirrhus* (Nielsen, 1913), *Metopaster* sp. and presumed ophiuroid remains.

Two small samples, each about 300 g, collected by Professor A. Rosenkrantz in the Danian limesand 2 km ESE of Haidhof, north of Vienna in Austria, have been washed and echinoderm remains picked out. The samples contain several brachials and columnals of crinoids, marginals of asteroids, and arm plates and vertebrae of

1*



Fig. 1. Núgssuaq in West Greenland. Danian localities with echinoderms mentioned in the text. Lower Danian Kangilia Formation: 1, Kangilia. 2, Tunorssuaq. 3, Solemyakløft. 4, Ilugigsoq. 5, Auvfarssuaq. 6, Turritellakløft. Upper Danian Agatdal Formation: 6, Turritellakløft. 7, Agatdal. 8, Marrait kitdlit.

ophiuroids. The following species are identified: *Nielsenicrinus fionicus* (Nielsen, 1913), *Bourgueticrinus* cfr. *danicus* Nielsen, 1913, *Lophidiaster punctatus* Nielsen, 1943, *Teichaster retiformis* Spencer, 1913, *Ophiomusium danicum* Nielsen, 1926, *Ophiacantha danica* Rasmussen, 1951, *Ophiura serrata* Roemer, 1840, and *Asteronyx* sp. All these species are known also from the Danian of Denmark.

From the Danian of Nûgssuaq in West Greenland the crinoid *Isselicrinus groenlandicus* was described by Rasmussen (1961) and a preliminary record of the crinoids and asteroids collected during the Nûgssuaq expeditions by Professor Rosenkrantz and his collaborators was given by Rasmussen in Rosenkrantz (1970). A more detailed study of the Danian species from Nûgssuaq has given the following results:

In the Lower Danian Kangilia Formation only *Isselicrinus groenlandicus* is found. In the Upper Danian Agatdal Formation the following crinoids, asteroids and ophiuroids are found: *Isselicrinus* aff. *paucicirrhus* (Nielsen, 1913), *Calamocrinus ilimanangei* n.sp., *Astropecten postornatus* (Rasmussen, 1945), *Teichaster retiformis* Spencer, 1913, *Ceramaster obtusus* n.sp. and *Ophiura achatae* n.sp. The presence of two Upper Danian species in common with Denmark supports the age determination of the Agatdal Formation and is a remarkable faunal resemblance between Denmark and Greenland in the Danian.

4



Fig. 2. Lower Tertiary localities in Denmark, South Sweden and northernmost Germany. Heersian: 1, Copenhagen. 2, Klagsham. 3, Egsmark. 4, Basballe. 5, Hvalløse. 6, Klintebjerg. Ypresian Mo-Clay Formation:
 7, Isle of Mors. 8, Skærbæk Cliff. 9, Silstrup Cliff. 10, Isle of Fur. 11, Thy. Ypresian Rösnäs Formation: 12, Ulstrup at Rösnäs. 13, Trelde Næs at Lillebælt. 14, Fredericia. 15, Röjle Cliff. 16, Heiligenhafen. 17, Isle of Fehmern. Middle Oligocene (Rupelian) Branden Clay: 18, Branden. 19, Faarup.

The Paleocene

The Danian may be classified as Lower Paleocene. The remaining Paleocene is represented in Denmark by the Selandian greensand and marl with the Lellinge Formation (Heersian) and the Kerteminde Formation (presumably Landenian).

Crinoids, asteroids and ophiuroids are common in the basal conglomerate at Svanemøllen, Vestre Gasværk and other localities in Copenhagen and at Hvalløse in Jutland, Denmark. They belong to Danian species and have been derived from the Danian together with numerous other Upper Danian fossils. They have previously been described in connection with the Danian.

From the Heersian Lellinge Formation of Egsmark and Basballe near Ebeltoft in Denmark are a few remains of crinoids. In these localities the basal conglomerate is not exposed and there is not observed any derived Danian fossils in the rich fauna of molluscs and foraminifera. It is therefore concluded that the echinoderms found here did survive into the Heersian, in spite of the fact that they belong to the most common species in the Danian. At these localities *Isselicrinus paucicirrhus* (Nielsen, 1913), *Bourgueticrinus danicus* Nielsen, 1913, and *Democrinus maximus* (Nielsen, 1915) are found. A column of the Upper Danian *Nielsenicrinus obsoletus* (Nielsen, 1913) is found in erratics of the Heersian Lellinge Formation at Klintebjerg by Mr. P. Graversen.

No crinoids, asteroids or ophiuroids are found in the Kerteminde Formation. In South Sweden minor remains of Paleocene sediments are found in Klagshamn and a few other places. The sediments consist of a basal conglomerate over the Danian limestone and a few meters of glauconitic sand and marl belonging to the Heersian. They are rich in derived Danian fossils including crinoids and asteroids previously recorded.

From the true Montian Calcaire grossier de Mons, described by Cornet & Briart (1865) no echinoderms are recorded, and the sediment has not been exposed for many years. In a very small sample from Mons in the Museum of Brussels a few marginals of Teichaster sp. and Astropecten sp. are observed.

From the Paleocene glauconitic marl at Haunsberg north of Salzburg in Austria Traub (1938) has recorded a *Pentacrinus* sp., here referred to *Isselicrinus subbasaltiformis* (Miller, 1821). This specimen may well belong to the Lower Eocene. In samples collected by Professor A. Rosenkrantz at Kroisbach in the same area and belonging to the Upper Paleocene (Landenian) zone with *Globigerina velascoensis*, the following species are found: Columnals of *Bourgueticrinus* sp. or *Democrinus* sp., marginals of *Lophidiaster haunsbergensis*, n. sp., *Lophidiaster inversus* n. sp., *Lophidiaster* aff. *pygmaeus* Spencer, 1913, and *Teichaster lamberti* Valette, 1925, and a lateral arm plate of *Amphiura senonensis* Valette, 1915.

In samples of glauconitic sand from the Sochaczew boring in central Poland referred to the early Paleocene are several columnals of a crinoid similar to *Cainocrinus tintinnabulum* Forbes, 1852. A few columnals of the same species are found in samples from the underlaying bed referred by Pozaryska (1965) to the Danian.

The British Paleocene consists of the marine Thanet Beds and the partly marine Woolwich Beds and Reeding Beds, all correlated with the Landenian. No echinoderms are found.

The Lower Eocene

The Lower Eocene (Ypresian) is represented in Denmark by the Mo-Clay Formation and the Tuff-Clay Formation succeeded by the Rösnäs Formation.

The Mo-Clay Formation is a marine diatomaceous sediment with some clay and about 200 thin beds of volcanic tuff. Its distribution is restricted to the north-western areas of Denmark around the sound of Limfjorden. The Mo-Clay Formation contains several impressions and a few better preserved specimens of *Ophiura furiae* n.sp. and a few impressions of two asteroids, *Coulonia colei* (Forbes, 1852) and *Echinaster jacobseni* n.sp.

The Tuff-Clay Formation found in other areas with Lower Eocene sediments in Denmark is contemporary with the Mo-Clay Formation and contains the same tuff beds in a marine clay with very few fossils. No echinoderms are found.

The Rösnäs Formation is a very fine-grained, sticky clay of illite and montmorillonite, generally deep red in colour. It succeeds the Tuff-Clay Formation without interruption in the sedimentation. The Rösnäs Formation contains several specimens of the crinoid *Isselicrinus subbasaltiformis* in a few places, specially near Fredericia. The fossils are presumably restricted to a zone in the lower part of the formation. Two specimens of an asteroid, *Teichaster stokesii* (Forbes, 1848) are found in the same area. The fossils are generally preserved in pyrite and liable to decomposition. They have all been found on the beach where the clay is exposed.

In North Germany the Lower Eocene Tuff-Clay Formation and Rösnäs Formation are found with similar sediments as in Denmark. They are recorded as Eocene 1 and Eocene 2–3. There is no distinct limit between Eocene 2 and Eocene 3. Several columnals of *Isselicrinus subbasaltiformis* are found in the clay and referred by Gripp (1964) to Eocene 2.

Much new information on British Eocene echinoderms has been obtained by a review of the collections in the British Museum and the Geological Survey, London, and specially by a study of new large collections made by Mr. Bones, Mr. Rundle and Mr. Cooper, and by sorting of old samples collected by Mr. Davis.

The British Lower Eocene consists of the Oldhaven Beds (= Blackheath Beds) succeeded by the London Clay, Claygate Beds, Bagshot Sands and Lower Bracklesham Beds. The London Clay in the London area is subdivided by Wrigley (1924) into Basement Bed and divisions 1–5, and in Bognor Regis by Venables (1963) into Lower, Middle and Upper Clay. The fauna collected along the cliffs on the Island of Sheppey seems, according to Davis (1936), derived from the middle or upper part of the London Clay, corresponding presumably to division 4 of the London Clay or to division 5 in a less sandy facies of stiff clay.

In the Oldhaven Beds are found several well preserved impressions of an ophiuroid here referred to *Ophiura wetherelli* Forbes, 1852.

The London Clay is correlated with the Rösnäs Formation in Denmark and the Eocene 2–3 in North Germany. Volcanic tuff beds probably corresponding to the

Mo-Clay and Tuff Clay Formation in Denmark and the Eocene 1 in North Germany have recently been found by Elliot (1971) 6–7 m above the base of the London Clay at Harwich. The London Clay is locally rich in fossils, including echinoderms described by Forbes (1848, 1849, 1852). The following crinoids, asteroids and ophiuroids are found: *Isselicrinus subbasaltiformis* (Miller, 1821): London area, division 2. *Cainocrinus tintinnabulum* Forbes, 1852: London area, division 2–4, and Bognor Regis, Middle and Upper Clay. *Democrinus londinensis* (Forbes, 1852): London area, division 2–4, and Isle of Sheppey. *Amphorometra ornata* n.sp.: London area, division 2–3. *Lophidiaster concavus* n.sp.: London area, division 2–3. *Coulonia colei* (Forbes, 1852): London area, division 5, and Isle of Sheppey. *Hippasteria tuberculata* (Forbes, 1852): Isle of Sheppey. *Teichaster stokesii* (Forbes, 1848): Isle of Sheppey, and London area, division 2. *Ophiura bognoriensis* n.sp.: Bognor Regis, Lower Clay. *Ophiura wetherelli* Forbes, 1852: London area, Basement Bed and division 2–5, and Bognor Regis, Middle Clay.

From the Lower Bracklesham Beds at Whitecliff Bay in Sussex, the presence of rare and indeterminable asteroid marginals is recorded by Wrigley & Davis (1937).

The Middle Eocene

The Middle Eocene (Lutetian and Auversian) is apparently represented in Denmark by the Lillebælt Formation of clay similar to the Rösnäs Formation but generally greenish grey and non-calcareous. Fossils are extremely rare, and no echinoderms are found.

In North Germany this sequence is recorded as Eocene 4. No echinoderms are recorded.

In England the upper part of Lower Bracklesham Beds is referred to the Lutetian and the Upper Bracklesham Beds to the Auversian. In the Upper Bracklesham Beds are found several ossicles of *Ophiura bartonensis* n.sp. and some well preserved marginals of *Astropecten granulatus* n.sp.

From Belgium the ophiuroid *Stegophiura eocaenus* (Leriche, 1931) was described from a boulder of "Panisélien" sandstone. The stratigraphical age is recorded as uppermost Ypresian or lower part of Lutetian.

The Upper Eocene

The Upper Eocene (Bartonian) is represented in Denmark by the Søvind Marl. The corresponding clay in North Germany is recorded as Eocene 5. No echinoderms are found.

In England the Barton Beds of sandy clay and fine sands at Higheliff in Hampshire contain well preserved marginals of *Astropecten granulatus* n.sp., an ophiuroid previously referred to *Ophiura wetherelli*, but here described as *Ophiura bartonensis* n.sp. and a few arm fragments of *Ophiocoma hessi* n.sp. In a sample from the Middle Barton Beds (horizon E of Burton 1929) are found several remains of *Ophiura bartonensis*,



Fig. 3. British Eocene localities with echinoderms mentioned in the text. 1, Highcliff and Barton Cliff.
2, Bramshaw. 3, Fawley. 4, Whitecliff Bay. 5, Bracklesham Bay. 6, Selsey Bill. 7, Bognor Regis. 8, Herne Bay. 9, Isle of Sheppey and Warden Point. 10, Sheerness. 11, Friendsburg Extra, Upnor. 12, Clacton. 13, Frinton and Walton-on-the-Naze. 14, Harwich. 15, Oxshott. 16, Talworth. 17, Worchester Park. 18, New Malden. 19, Richmond. 20, Beddington. 21, Waddon. 22, Balham. 23, Clapham South. 24. Battersea. 25, Clapham. 26, Stockwell. 27, Brixton. 28, Elmstead. 29, Poyle. 30, Stanwell. 31. Northwood. 32, Brentford. 33, Kenton. 34, Kensington. 35, Cromwell Road. 36, Imperial College. 37, Besborough Gardens. 38, St. James. 39, U. Thames Street. 40, London Wall. 41, The Minories. 42, Trinity. 43, Bond Street. 44, Baker Street. 45, Islington, Caledonian Road and Copenhagen Fields. 46, Kingsbury. 47, Primrose Hill. 48, Chalk Farm. 49, Haverstock Hill. 50, Hendon. 51, Hampstead Heath. 52, Highgate. 53, Hornsey. 54, Finchley. 55, Cockfort. 56, Seawardstone. 57, Aveley.

	Isselicrinus groenlandicus	I. paucicirrhus	I. aff. paucicirrhus	I. subbasaltiformis	Doreckierinus convexus	D. miliaris	Cainocrinus tintinnabulum	C.? aff. tintinnabulum	Nielsenicrinus fionicus	N. obsoletus	Isocrinus campanularis	I. divergens	I. echinatus	I. longus	Calamocrinus ilimanangei	Bourgueticrinus danicus	B. bruennichinielseni	Bathycrinus windi	Democrinus gisleni	D. maximus	D. londinensis	Monachocrinus regnelli	M. aff. regnelli
Chattian Germany																							
Ruppelian Germany							· · ·																
Denmank							· ·	· · ·					• •	• •	• •		· ·			• •	• •	• •	
-, Denmark		• •					· ·			• •			• •	• •	• •			• •		• •	• •	•••	
Lattorfian		• •	• •	• •	•••					• •		• •	• •	• •	• •	• •	• •	• •		• •	• •	• •	• •
Bartonian, England																							
Auversian, England																							
Lutetian, France					1	1	1	1													x		
Ypresian-Lutetian, Belgium																							
Ypresian, Sheppey Island																					x		
-, Bognor Regis, MU. Clay							x														?		
-, Bognor Regis, L. Clay																							
-, London Clay, div. 5																							
London Clay, div. 4							x														x		
London Clay, div. 3							x														x		
London Clay, div. 2				x			x														x		
London Clay, Basement																							
Germany, Eocene 2				x																			
–. Denmark, Bösnäs Clay				x																			
- Denmark, Mo-Clay				~																			
, Deminiarit, Mo Glay																							
Landenian, Austria				?																			
-, Vincentown, U.S.A																	x					• •	
Heersian, Denmark		х								х						х				х			
Heersian?, Poland								×														• •	
Danian?, Poland								×															
Danian Austria		×						~	×							?							
U - Netherland Belgium		~								x										x			
M - Netherland Belgium																x				x			
L - Netherland Belgium																x				x			
U., Greenland	· · ·	• •	~												×	^							
L Greenland	Y		^												~								
U - Denmark Sweden		~		• •	~				· · ·	~	 v	×	×	×		×	×	×	×	x		x	
M - Denmark Sweden		x	• •		x				x	^	^	x	x			x	~	~	~	x		x	x
L - Denmark Sweden		Ŷ			Ŷ	×			Ŷ		x	x	x			x	x	x		x		x	
I., Dennark Sweden		^		•••	^	^			^		^	~	~			~	~	^		~			
Maastrichtian or older																	×		×			×	

(continued)

NT			-
N	L	•	1

	Cyathidium holopus	Jaekelometra faxensis	Amphorometra bruennichi	A. semiglobularis	A. ornata	Bruennichometra danica	B. granulata	B. parvicava	Himerometra grippae	Palaeocomaster angelini	Hertha mystica	H. plana	Placometra laticirra	Astropecten postornatus	A. granulatus	A.? beyrichi	Coulonia colei	Lophidiaster punctatus	L. haunsbergensis	L. inversus	L. concavus	L. aff. pygmaeus	Hippasteria tuberculata
Chattian Germany									~														
Bunnelian Germany	• •	• •	• •	• •	• •	• •	• •	• •	^	• •	• •	• •	• •	• •	• •			•••	• •		• •	• •	
- Denmark	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	^		• •	• •		• •	• •	
-, Denmark		• •	• •	• •		• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •		• •	• •		• •	• •	
				• •		• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •		• •	• •		• •	• •	
Bartonian, England															x								
Auversian, England															х								
Lutetian, France																?							
Ypresian-Lutetian, Belgium																							
Ypresian, Sheppey Island																	x						х
-, Bognor Regis, MU. Clay																							
-, Bognor Regis, L. Clay																							
-, London Clay, div. 5																	x						
-, London Clay, div. 4																							
-, London Clay, div. 3					x																x		
-, London Clay, div. 2					×																x		
-, London Clay, Basement																							
-, Germany, Eocene 2																							
-, Denmark, Rösnäs Clay																							
-, Denmark, Mo-Clay																	x						
Landenian, Austria																			~	~		~	
- Vincentown USA	1		· ·								• •	• •	• •	• •	• •	• •		• •	^	^	• •	^	
Heersian Denmark			· ·			• •					• •	• •	• •	• •	• •	• •		• •		• •	• •	• •	
Heersian? Poland						• •					• •	• •	• •	• •	• •	• •		• •			• •	• •	
											• •	• •		• •	• •	• •		• •			• •	• •	
Danian?, Poland														?									
Danian, Austria	x																	x					
U, Netherland Belgium																							
M, Netherland Belgium																							
L, Netherland Belgium																							
U, Greenland														x									
L, Greenland																							
U, Denmark Sweden			x	x			x			x	x	x	x	x				x					
M, Denmark Sweden	x	x	x	x		x	x				x	x						x					
L, Denmark Sweden				x				x			x	x	x					x					
Maastrichtian or older	×	• •	• •	• •	• •	• • •	• •	• •	• •	X	x	x	x	• •	• •	• •		• •		• •	• •	• •	

(continued)

11

	Teichaster anchylus	T. retiformis	T. lamberti	T. stokesi	Metopaster kagstrupensis	M. spenceri	M. elevatus	M. planus	M. carinatus	M. maculatus	Ceramaster dividuus	C. granulatus	C. obtusus	C. rabii	C. brandenensis	Recurvaster mammillatus	Stauranderaster miliaris	S. pyramidalis	S. speculum	Valettaster ocellatus	V. granulatus	Pycinaster danicus
Chattian Germany																						
Bunnelian Germany		• •								• •	• •				· · ·			• •	• •		• •	• •
Denmark	• •	• •	• •			• •		• •	• •	• •	• •	• •		^			• •	• •	• •	•••	• •	• •
Lattorfian			•••			•••					•••				×					•••	•••	•••
Bartonian, England																						
Auversian, England																						
Lutetian, France			х																			
Ypresian-Lutetian, Belgium																						
Ypresian, Sheppey Island				x																		
-, Bognor Regis, MU. Clay																						
-, Bognor Regis, L. Clay																						
-, London Clay, div. 5																						
-, London Clay, div. 4																						
-, London Clay, div. 3																						
-, London Clay, div. 2				x																		
-, London Clay, Basement																						
-, Germany, Eocene 2																						
-, Denmark, Rösnäs Clay				x																		
-, Denmark, Mo-Clay																						
Landenian Austria			~																			
Vincentown USA	• •	• •	×	• •	• •	• •	• •	• •	• •	• •	•••	• •	• •	• •	• •		• •	• •	• •	• •	• •	• •
Hearsian Danmark	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	•••	• •	• •	• •	• •	×	• •	• •	• •	• •	• •	•••
Haarsian? Deland	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •
riceisian?, Poland	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	•••	• •
Danian?, Poland																						
Danian, Austria		x																				
U, Netherland Belgium																						
M, Netherland Belgium												x										
L, Netherland Belgium					x	x			x								x				x	
U, Greenland		x											x									
L, Greenland																						
U, Denmark Sweden		x						x	x		x					x	x		x	x	×	×
M, Denmark Sweden		X					x	x		x		x				x	x	x	x	x	x	×
L, Denmark Sweden	x				x	x		x								x	x	x	x	x	x	
maastrichtian or older	• •	• •	• •	• •	• •	• •	• •	• •	• •	•••	• •	• •	• •	• •	• •	• •	• •	• •	• •	×	• • •	• •

(continued)

	1	1	1	1	1		1			1	1		1	1	1	1	1		1	1		
	P. cornutus	P. rosenkrantzi	Chomataster acules	Echinaster jacobseni	Amphiura senonensis	Ophiomusium danicum	0. subcylindricum	Ophiacantha danica	Ophiocoma hessi	Ophiura serrata	0. hagenowi	0. achatae	0. furiae	0. wetherelli	0. bognoriensis	O. bartonensis	O. davisi	0. carpelloides	0. costata	Stegophiura eocaenus	Asteronyx ornatus	A. sp.
Chattian Commons																						
Demosition Commence						• •		• •	• •	• •	• •	• •	• •				• •					• •
Ruppellan, Germany						• •			• •	• •	• •	• •	• •			• •	• •					• •
–, Denmark	· ·					• •		• •	• •	• •	• •	• •	• •				• •	• •		· ·		• •
Lattorfian		···				• •	• •	• •	• •	• •	• •	• •	• •	• •		• •	•••	• •				• •
Bartonian, England									x							x	x	x	x			
Auversian, England															I	x						
Lutetian, France	I																					
Ypresian-Lutetian, Belgium	l																			x		
Ypresian, Sheppey Island														2								
-, Bognor Regis, MU. Clay														×								
-, Bognor Regis, L. Clay															x							
-, London Clay, div. 5														x								
-, London Clay, div. 4														x								
-, London Clay, div. 3																						
-, London Clay, div. 2														×								
-, London Clay, Basement														x								
-, Germany, Eocene 2																						
-, Denmark, Rösnäs Clay																						
-, Denmark, Mo-Clay				x									x									
, , , , , , , , , , , , , , , , , , , ,																						
Landenian, Austria					x																	
-, Vincentown, U.S.A					×	х																
Heersian, Denmark																						
Heersian?, Poland																						
Danian?, Poland			?	• •	• •	×	×	• •	• •	• •	×	• •	• •	• •		• •	• •	• •	• •	• •	×	• •
Danian, Austria					• •	×	• •	x	• •	×	• •	• •	• •	• •		• •	• •	• •	• •	• •	• •	X
U, Netherland Belgium				· ·	• •		• •	• •	• •	• •	• •	• •	• •	• •		• •	• •	• •	• •	• •	• •	• •
M, Netherland Belgium	· ·				• •	• •	• •	• •	• •	x	• •	• •	• •	• •	• •	• •	•••	• •	• •	• •	• •	• •
L, Netherland Belgium			×		• •	• •	• •	• •	• •	• •	• •	· •	• •	• •	• •	• •	٠.	• •	• •	• •	• •	• •
U, Greenland			• •	• •	• •	• •	• •	• •	• •	• •		х	• •	• •			• •	• •	• •	• •	• •	•••
L, Greenland			• •	• •	• •	• •	• •	• •	• •	• •		• •		• •	• •	• •	• •	• •	• •	• •	• •	• •
U, Denmark Sweden	X	X	X	• •	X	х	• •	х	• •	X	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	х
M, Denmark Sweden			X	• •	• •	• •	• •	X	• •	x	•••	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	x
L, Denmark Sweden			X	• •	x	• •	• •	X	• •	x	х	• •	• •	• •		• •	• •	• •	• •	• •	• •	x

... x x ... x x

..|

x

x

Maastrichtian or older....

13

x . .

Nr. 7

Ophiura davisi n.sp., Ophiura carpelloides n.sp. and a few remains of Ophiura costata n.sp. According to Linstow (1912) a specimen of Astropecten crispatus from the Bartonian of Barton in Hampshire is preserved in the collection of Berlin.

Isolated marginals of asteroids are recorded by Linstow (1912) from the Eocene of Hammer, Götzreuther and Rollgraben near Traunstein in Bavaria, Germany.

The Oligocene

In Denmark the Lower Oligocene (Lattorfian) is missing. The Middle Oligocene (Rupelian) is represented by the Branden Clay and the Upper Oligocene (Chattian) by the Cilleborg Clay. A single asteroid, *Ceramaster brandenensis* Rasmussen, 1951, is described from the Branden Clay.

In North Germany the Lower Oligocene is very poor in fossils, and no echinoderms are described. From the Middle Oligocene Septarienton at Mark (Westfalen) Linstow (1912) has described two asteroids, *Goniaster (Goniodiscus) rabii*, here referred to *Ceramaster*, and *Astropecten (?Pentaceros) beyrichi*. The comatulid *Himerometra grippae* is described by Anderson (1967) from the Upper Oligocene Grafenberger Sand near Moers in Niederrhein, Germany.

Asterias propinqua Münster is a nomen nudum introduced by Münster (1835 p. 434) for some undescribed asteroid remains from the Upper Oligocene at Bünde (Westfalen). Philippi (1843) referred marginals from the Upper Oligocene of Freden, Dickholzen and Luithorst (Hannover) to the same species.

Speyer (1864) described asteroid marginals from the Middle Oligocene of Söllingen near Jerxheim (Braunschweig) as *Asterias (Stellaster)* sp. with strongly arched marginals and with irregularly scattered spine pits and slightly concave joint faces.

Several isolated marginals of Tertiary asteroids in German museums are recorded by Linstow (1912) from the Lower Oligocene of Lattorf near Bernburg (Sachsen), Vardeilsen near Einbeck (Hannover), Brandhorst near Bünde (Westfalen), from the Middle Oligocene of Söllingen (Braunschweig), Magdeburg (Sachsen), Kawelwich (Pommern), and from the Upper Oligocene of Astrup near Osnabrück (Hannover), Bünde near Herford (Westfalen), Kassel (Hessen), Krefeld (Nordrhein-Westfalen), Thalsbergsgraben near Siegsdorf and Freden (Hannover). The specimens from the Lower Oligocene of Lattorf are recorded under the name of *Goniaster intistinchus* Semper, a nomen nudum taken from the label of the specimen in the collection.

Hucke and Voigt (1929) recorded the presence of *Ceramaster rabii* in the Middle Oligocene of Steutz (Anhalt) and the remains of *Antedon* and columnals of *Rhizocrinus* in the Middle Oligocene of Joachimsthal (Uckermark, Brandenburg), Germany.

Crinoidea

Isselicrinus groenlandicus Rasmussen, 1961

1961 Isselicrinus groenlandicus.—Rasmussen p. 58 pl. 6 fig. 1-5.

1970 Isselicrinus groenlandicus Rasmussen.-Rasmussen in Rosenkrantz p. 427.

1970 Isselicrinus.—Rasmussen in Rosenkrantz p. 429 (non p. 426, 435).

Isselicrinus from the Maastrichtian and Danian in Greenland

Specimens of *Isselicrinus* are present in the Maastrichtian and Danian of Nûgssuaq in West Greenland, but only specimens from the Lower Danian Kangilia Formation belong to the present species. No other crinoid is found in the Lower Danian of Greenland. Three columns of *Isselicrinus* from the Maastrichtian of Agatdal in Nûgssuaq are referred to *I. buchii* (Roemer, 1840), and columnals from the Upper Danian Agatdal Formation of Nûgssuaq are referred to *Isselicrinus* aff. *paucicirrhus* (Nielsen, 1913).

Material

From the Thyasira Member of the Lower Danian Kangilia Formation at Kangilia are found 26 fragments of columns including the holotype and specimens previously figured.

From the Propeamussium Member of the Lower Danian Kangilia Formation are found 6 fragments of columns at Tunorssuaq, 1 at Solemyakløft, 1 at Ilugigsoq, 1 in a boulder at the southern side of Turritellakløft and 1 in a boulder from Auvfarssuaq near Quvnilik. The specimens are in the collection of the Geological Museum, Copenhagen.

Isselicrinus paucicirrhus (Nielsen, 1913)

1913 Pentacrinus paucicirrhus.—Nielsen p. 81 figs. 9, 10, 24, pl. 6 figs. 39-52, pl. 7 figs. 1-26.

1913 Pentacrinus crassus.—Nielsen p. 84 fig. 29, pl. 7 figs. 27-53. (non Desor 1845).

1913 Pentacrinus Rejstrupianus.--Nielsen p. 94 fig. 21, pl. 9 figs. 32-36.

1913 Pentacrinus Kagstrupianus.—Nielsen p. 96 fig. 22, pl. 9 figs. 37-41.

1960 Balanocrinus paucicirrhus (Nielsen).-Kuehn p. 163.

1961 Isselicrinus paucicirrhus (Nielsen).-Rasmussen p. 61 pl. 5 figs. 1-14.

Previous record

This species has previously been described in details from the Danian. It is a dominant species in the Danian of Denmark and Sweden, and is also recorded from the Danian of Austria.

Material

About 10 columns of *I. paucicirrhus* are found as impressions in the Paleocene (Heersian) glauconitic marl of the Lellinge Formation at Basballe and Egsmark near Ebeltoft in Denmark. At these two localities the basal conglomerate of the Paleocene

is not exposed and there is no indication of derived Danian fossils. It is therefore presumed, that the species did occur in the Heersian fauna. 3 columns are found in erratics of the Lellinge Formation at Klintebjerg near Nykøbing (Sealand) in Denmark. The specimens from the Heersian agree with previous descriptions of the species from the Danian and show no new or uncommon features. The specimens are in the collection of the Geological Museum, Copenhagen.

Isselicrinus aff. paucicirrhus (Nielsen, 1913)

Plate 1 fig. 1.

1970 Isselicrinus.-Rasmussen in Rosenkrantz p. 435.

The specimens here described from the Upper Danian of Nûgssuaq in West Greenland appear intermediate between *I. paucicirrhus* and *I. subbasaltiformis*.

Material

From the Sonja Member of the Upper Danian Agatdal Formation are fragments of 10 columns at Agatdal in Nûgssuaq. From the Turritellakløft Member of the Agatdal Formation are fragments of 1 column at Turritellakløft in Nûgssuaq. The specimens are in the collection of the Geological Museum, Copenhagen.

Dimensions

	Nr. 1	2	3	4	õ	fig.	7	8
Interradius	0.9	1.4	1.5	1.5	2.2	2.2	2.3	2.5
Radius	0.7	1.3	1.4	1.5	1.8	1.9	2.4	2.5
Nodal height	-		-	-	_	1.4		_
Internodal height	1.0	1.6 - 1.7	1.1 - 1.2	1.6 - 1.8	1.0 - 1.3	1.0 - 1.2	1.8	1.4-1.5
Marginal crenellae .	6	6	6	10	10	10	10	_

Description

The column is smooth, pentalobate to cylindrical up to 5 mm in diameter. There is a small alternation in height of columnals. The outline is less lobate than in the majority of specimens from Denmark, and there is no alternation in outline or radial furrows on the surface of some columnals as seen in most specimens from Denmark. The height of columnals is as in the Danish specimens or slightly less.

The articular surface shows a gradual transition of crenellae from marginal to adradial position, and the crenellae reach their maximum length near the transition. The number of crenellae along the margin is as in Danish specimens or slightly greater. There is generally a small, smooth radial area outside the crenellae. The suture is slightly crenulate and there is no radial pore.

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Isselicrinus subbasaltiformis (Miller, 1821)

Plate 1 figs. 2-5, plate 11 fig. 1.

1821 Pentacrinus subbasaltiformis.—Miller p. 142.

1837 Pentaerinus subbasaltiformis Miller.-Wetherell p. 136 pl. 8 fig. 3a (non fig. 3b).

1837 Pentacrinus sowerbii.—Wetherell p. 136 pl. 8 fig. 4.

- 1852 Pentacrinus subbasaltiformis Miller.—Forbes p. 34 pl. 4 figs. 8-10.
- 1852 Pentacrinus sowerbii Wetherell.—Forbes p. 35 fig. 2.

1852 Pentacrinus cingulatus Münster.-Schafhäutl pp. 151, 167.

- 1863 Pentacrinus cingulatus Münster.—Schafhäutl p. 110 pl. 15 fig. 6.
- 1865 Pentacrinus subbasaltiformis Miller.—Gümbel pp. 140, 170.
- 1900 Pentacrinus subbasaltiformis Miller.-Stolley pp. 110, 133.
- 1902 Pentacrinus subbasaltiformis Miller.-Stolley p. 17.
- 1906 Pentacrinus subbasaltiformis Miller.-Gagel pp. 317, 320.
- 1917 Balanocrinus subbasaltiformis (Miller).-Bather pp. 397-404 figs. 6-7.
- 1924 Balanocrinus subbasaltiformis (Miller).-Wrigley pp. 251, 254.
- 1928 Balanocrinus subbasalliformis (Miller).-Davis pp. 339, 340, 347, 349.
- 1936 Balanocrinus subbasaltiformis (Miller).-Davis p. 333.
- 1938 Pentacrinus sp.-Traub p. 39.
- 1940 Balanocrinus subbasaltiformis (Miller).-Wrigley pp. 235, 240.
- 1944 Balanocrinus subbasaltiformis (Miller).—Sieverts-Doreck pp. 141-152 figs. 1-4.
- 1945 Balanocrinus sub-basaltiformis (Miller).—Wrigley p. 217.

1961 Isselicrinus subbasaltiformis (Miller).—Rasmussen p. 46.

1964 Isselicrinus subbasaltiformis (Miller).-Gripp pp. 86, 87, 355.

Synonym

P. sowerbii Wetherell, 1837, is the proximal part of a column belonging to the present species.

Type

The columns studied by Miller (1821) and the column figured by Wetherell (1837, pl. 8 fig. 3 a) are not identified in the collections. The column nr. 57540 in the collection of the British Museum was therefore selected by Bather (1917) as lectotype. It is from the Lower Eocene (Ypresian) London Clay of Hampstead Heath, London. This specimen is among those on which the description by Wetherell (1837) was based. It has not previously been figured, but is shown here pl. 1 fig. 2.

The type specimen of *Pentacrinus sowerbii* figured by Wetherell (1837) pl. 8 fig. 4 from the London Clay of Hampstead Heath, London, is in the collection of the British Museum (E 5888). It is, as demonstrated by Bather (1917), the proximal part of the column of *I. subbasaltiformis*.

Material

This species is recorded from the London Clay as common and characteristic to division 2, 15–30 m above the basement of the London Clay (Wrigley 1924, 1945, Davis 1928, 1936). Two specimens have been recorded from sediments older than the London Clay, but both must be taken with reservation:

Biol. Skr. Dan. Vid. Selsk. 19, no. 7.

In the collection of München (nr. 1943 II. 33) is a column recorded by Traub (1938 p. 39) as *Pentacrinus* sp. from the Upper Paleocene of the old quarry north-east of St. Pankraz near Salzburg. The column is a typical *I. subbasaltiformis*. It shall be remarked, however, that the profile in the quarry reaches from the Upper Paleocene (Landenian) to the upper part of the Lower Eocene (Upper Ypresian).

In the collection of the Geological Survey, London, is a column (nr. 44807) recorded by Sieverts-Doreck (1944) from the Blackheath Beds (Lower Ypresian or "Sparnacian") of the Elmstead Tunnel near Bromley, Kent. It shall be remarked, however, that the London Clay immediately overlies the Blackheath Beds in the railway cutting, and the preservation in pyrite corresponds to fossils from the London Clay, not from the Blackheath Beds (Mr. Rundle, personal communication).

All other British specimens of which the zone is known are from the lower part of the London Clay (division 2 of Wrigley 1924) or from localities where this zone has been exposed. They are found in the London area, Essex, Middlesex, Surrey and Kent. The species is not found in the cliffs of Sheppey Island or in the Hampshire basin. A large number of columns and columnals are preserved in British collections and recorded by Bather (1917), Sieverts-Doreck (1944) and Wrigley (1940).

The specimen figured by Wetherell (1837) pl. 8 fig. 3 b as a cirrus of *P. subbasaltiformis* from the London Clay of Hampstead Heath in London is in the collection of the British Museum (57539). It is, as demonstrated by Bather (1917), the column of *Cainocrinus tintinnabulum*.

In the collection of the British Museum is also a single specimen (E 25023) with theca, arms and a few columnals from the London Clay of Herne Bay, Kent in England. The specimen is described and figured by Sieverts-Doreck (1944).

In North Germany the species is recorded by Gagel (1906), Sieverts-Doreck (1944) and Gripp (1964) from the Lower Eocene clay (Ypresian) of Fehmern, Johannistal near Heiligenhafen and Luisenberg near Kellinghusen in Schleswig-Holstein, from Hemmoor in Hannover and Pisede near Malchin in Mecklenburg. Several specimens from Fehmern and Johannistal are in the collections of Kiel and Copenhagen. The North German specimens are preserved in pyrite. Some are found in erratic boulders, but most specimens are washed out on the coast along cliffs with Eocene clay and referred by Gripp (1964) to the Eocene 2, equivalent to the London Clay.

Columns from the Eocene of Kressenberg in southern Bavaria, Germany, have been referred by Schafhäutl (1852, 1863) to the Jurassic species *Pentacrinus cingulatus*, and by Gümbel (1865) to *P. didactylus* or *P. subbasaltiformis*.

In Denmark several columns preserved in pyrite are found along the coasts of Lillebælt, where the Lower Eocene Rösnäs Formation is exposed. Most of the specimens are found north of Fredericia, but a single column at Rojle Klint. Other columns are found in the Rösnäs Formation near Ulstrup at Rösnäs. A theca with arms and a few proximal columnals preserved in pyrite is found north of Fredericia by Mr. C. Heilmann-Clausen. The Danish specimens are in the collection of the Geological Museum, Copenhagen.



Fig. 4. Columnals of Isselicrinus subbasaltiformis. Mean height and diameter of internodals in the specimens. 1, proximal columnals connected to the theca from Denmark. 2, proximal columnals connected to the theca from England. 3–4, P. sowerbii figured by Forbes. 5–7, P. subbasaltiformis figured by Forbes.

 \bigcirc columns from Denmark. \times columns from England.

Growth and variation of the column

The most proximal columnals seen in connection with the two thecae are deep pentalobate or stellate with extremely low columnals and alternating height. The majority of columnals, however, are subpentagonal to subcircular in section with a height of 1.5–2.5 mm and a diameter of 3–7 mm. There is a gradual morphologic transition from low stellate columnals with alternating height through pentalobate columnals with alternating height to the dominant type of subpentagonal or cylindric columnals with almost uniform height. These forms represent the change from proximal to distal part of the column known in several genera of Isocrinidae. The height of columnals, the alternation in height and the outline depend only on the position within the column, not on the age or size of the animal.

The diameter of the columnals varies from 3 to 7 mm and is independent of their height and form. This indicates that the diameter has been almost uniform in the entire length of the column, dependent mainly on the age and size of the animal, not on the proximal or distal position of the fragment studied. The height and diameter of columnals are therefore not correlated to a single growth function and do not follow a regression line in bivariate analysis.

A study of the variation in specimens from Denmark, North Germany and England indicates that only one species is represented. The type specimen of *P. sowerbii* is a proximal part of the column in a large individual.

Variation in theca and arms

The theca and arms have been known only in a single specimen from the London Clay described and figured by Sieverts-Doreck (1944) and included by her in the diagnosis of the species. The theca with arms now found in Denmark in a similar preservation differs in several details of the arm ramification and also shows differences between the single arms. Only the features common to the two specimens are therefore maintained in the present diagnosis.

There are 2 primibrachials in each arm. I Br 1–2 and II Br 1–2 are synostosial. It was indicated by Sieverts-Doreck, that also succeeding axillaries have a synostoic articulation with the preceeding brachial, but a control has shown, that this articulation is oblique muscular in the British as well as in the Danish specimen. All the brachial articulations except I Br 1–2 and II Br 1–2 are muscular with a regular alternation in the orientation of the articular ridge. There are no third axillaries in the Danish specimen. The first pinnule is seen on the abaxial side of II Br 2, and pinules are placed on alternating side of all succeeding brachials except the axillaries. The number of brachials within each section of the arm shows considerable variation. The ramification of the arms and the number of brachials in each section is shown in a diagram of the British and the Danish specimen.

Ramification of arms in the British specimen:

$$I Br 2 \begin{cases} II Br 12 \\ III Br 12 \\ III Br 11 \\ III Br 9... \\ IV Br 11.. \\ IV Br 11.. \\ IV Br 11.. \\ IV Br 11.. \\ II Br 12 \\ II Br 3... \end{cases}$$

$$I Br 2 \begin{cases} II Br 7... \\ II Br 12 \\ II Br 12 \end{cases} \begin{cases} III Br 12 \\ III Br 12 \\ III Br 10 \end{cases} \begin{cases} IV Br 5... \\ IV Br 4 (+12 reg) \\ IV Br 7... \\ IV Br 8... \\ IV Br 8... \end{cases}$$

$$I Br 2 \begin{cases} II Br 13 \\ III Br 10 \\ III Br 10 \end{cases} \begin{cases} III Br 5 (+10 reg) \\ IV Br 8... \\ IV Br 8... \\ IV Br 3... \\ IV Br 21 \\ III Br 11 \end{cases} \begin{cases} III Br 9 (+10 reg) \\ III Br ... \end{cases}$$

L D 0	II Br 12	<pre>{ III Br 3 (+ ca. 15 partly covered) } III Br 16</pre>
1 Br 2	II Br 11	{ III Br 3 III Br 3
I Br 2	∫ II Br 2 │ II Br 3	
I Br 2	$\left\{\begin{array}{l} H Br 4 \dots \\ H Br 3 \dots \end{array}\right.$	
[Br 9	J II Br 13	∫ III Br ↓ III Br 10
1 01 2	II Br 12	(III Br 2) III Br 2
I Br 9	∫ II Br 10	∫ III Br 16 │ III Br 17
T DI Z	II Br 8) III Br 21

Description

An *Isselicrinus* of moderate size with a low bowl-shaped theca and a smooth surface. The basals are fairly large but surrounded by the radial ring and only just visible in the interradius around the top of the column. The radials are large, almost horizontal with a slightly arched free surface and an outward sloping, almost vertical articular surface for the brachials. There are 2 primibrachials and 8–14 secundibrachials. The number of tertibrachials is 8 or more, and further isotomous branching may occur. Synostosial articulations are found in I Br 1–2 and II Br 1–2. All other articulations are muscular. Pinnules are found on the abaxial side of II Br 2 and on alternating sides of all succeeding brachials except the axillaries.

The proximal part of the column is pentalobate and the columnals here are low with a tumid surface and with alternating height and tumidity. The distal part of the column is rounded subpentagonal to circular in section with cylindric, almost uniform columnals. The diameter is from 3 to 6 mm and the height from 1.7 to 2.3 mm.

The length of an internode may attain 29 internodals. The nodals are slightly higher than the internodals and have 1–4 small, elliptical cirrus sockets at the lower edge, pointing oblique downwards. In most nodals 2 cirri are found.

The articulation between columnals shows a pattern of five petals surrounded by crenellac. There is generally a gradual transition of crenellae along the periphery and radius, and the crenellae near the periphery form an oblique angle with the radius, also in specimens with a rather distinct separation of marginal and adradial crenellae. The number of crenellae along the periphery does not exceed 8 in each of the five lobes of the columnal. The suture is generally straight, seldom undulate except in the interradial area of proximal columnals. The articulation between nodal and infranodal shows a similar or slightly less distinct pattern, and the crenellae may fork near the edge.

Affinity

I. subbasaltiformis differs from the Eocene *I. didactylus* (d'Archiac, 1846) from South Europe in the smaller size of columnals. The articular surface of columnals shows in most specimens a more gradual transition of crenellae from marginal to adradial area and a smaller number of crenellae along the margin. Furthermore a granulation of the surface is never found in the columnals.

The species is more similar in size and form of the columnals to *I. buchii* (Roemer, 1840) from the Maastrichtian, and in size and articular surface of the columnals to *I. paucicirrhus* (Nielsen, 1913) from the Danian. Both of these species have almost smooth articulation between nodal and infranodal and a larger number of crenellae along the margin. Furthermore in *I. buchii* the adradial crenellae are small and perpendicular to the radius, and in *I. paucicirrhus* most columnals are pentalobate, often with sharp radial furrows except on the largest internodals, and the suture is often undulating.

Stratigraphy

I. subbasaltiformis seems a useful index fossil to the Middle Ypresian in North Europe. British specimens are common about 15–30 m above the base of the London Clay (Wrigley division 2). German specimens are found close above the tuff-bearing Eocene 1 and are referred by Gripp to Eocene 2. The stratigraphic level of two specimens from a presumed lower level than the London Clay is uncertain.

Cainocrinus tintinnabulum Forbes, 1852.

Plate 2 figs. 1-20.

1837 Pentacrinus subbasaltiformis Miller.—Sowerby in Wetherell p. 136 pl. 8 fig. 3.

1852 Cainocrinus tintinnabulum.—Forbes p. 33 figs. 1–5.

1852 Pentacrinus oakeshottianus.—Forbes p. 35 fig. 3.

1917 Cainocrinus tintinnabulum Forbes.—Bather p. 405.

1930 Cainocrinus? tintinnabulum Forbes.—Biese p. 716.

1940 Pentacrinus oakeshottianus Forbes.-Wrigley pp. 235, 238, 240.

1945 Isocrinus oakeshottianus (Forbes).—Wrigley p. 217.

1963 Cainocrinus tintinnabulum Forbes.—Venables pp. 253, 255, 258, 263.

1970 Cainocrinus tintinnabulum Forbes.—Rundle & Cooper p. 123.

Type

The theca with primibranchials and a proximal part of the column figured by Forbes (1852) p. 33 figs. 1–2 is holotype. It is from the London Clay (Ypresian) of

Hornsey in London and referred to division 3 of the London Clay (Wrigley). The specimen is in the collection of the Geological Survey, London (99793–99794).

The holotype of *Pentacrinus oakeshottianus* is the specimen figured by Forbes (1852) p. 36 fig. 3 from Primrose Hill near Chalk Farm in London. It belongs to division 3 of the London Clay. The specimen is in the collection of the British Museum (57546).

Material

This species has been recorded by Forbes (1852) from the London Clay of Hornsey (division 3) and Copenhagen House (division 2). *P. oakeshottianus* was recorded from near Chalk Farm (division 3). Wrigley (1940, 1945) has recorded *Isocrinus oakeshottianus* (= tintinnabulum) from Stanwell Reservoir and between Stockwell and Clapham South stations (division 2 or 3). Venables (1963) has recorded the species from Bognor Regis in Sussex, where it is found in the Middle Clay (Beetle Bed and Upper Fish Tooth Bed) and more common in the Upper Clay (Pholadomya Bed and Cainocrinus Bed). Rundle & Cooper (1970) have recorded the species from Trans-World Hotel site, Cromwell Road in London (division 2).

In the collection of the British Museum are several specimens from the London Clay: A column (57539) from Hampstead Heath (division 2) including 2 nodals separated by 15 internodals figured by Sowerby (in Wetherell 1837 pl. 8 fig. 3 b) as a cirrus of *P. subbasaltiformis*, corrected by Bather (1917 p. 405). A theca with primibrachials in pyrite (E 25992) from the Fish Tooth Bed (Middle Clay) of Bognor Regis. A theca and several fragments of columns from the London Clay (division 3) of Staines (E 50358–66). Isolated fragments of columns from the London Clay (division 3) of Haverstock Hill (E 49830) and near Chalk Farm (57545–6), from the London Clay (division 3 or 4) of Worchester Park (E 25921–41, 50406–17), from the London Clay (division 4 or 5) of Highgate (E 430), and from the Upper Clay, Pholadomya Bed of Bognor Regis (E 50375–405).

In the collection of the Geological Survey are columns from the London Clay (division 3) of Hornsey (Zc 4066–4075).

A very large number of specimens has been washed out of the Middle Clay, Craigweil Bed at Bognor Regis in Sussex by Mr. D. A. Bone, who found recently a horizon very rich in these echinoderms. A part of this collection was given by Mr. Rundle and Mr. Cooper to the Geological Museum in Copenhagen. This collection includes several complete thecae with primibranchials and parts of the column, single thecae, and numerous fragments from all parts of the column, theca and arms as well as single ossicles. Mr. Bone's collection contains 91 thecae and numerous fragments and isolated remains from this horizon. In the collection of Rundle and Cooper are also an incomplete theca and a few other remains of the same species from the London Clay (division 3) of Wraysbury Reservoir at Poyle in Buckinghamshire, England.

Diagnosis

A small crinoid belonging to the Isocrinidae. The column is pentalobate and smooth with rounded interradial edges, often with a tubercle. Interradius of column generally about 1.2 mm, height of internodals slightly alternating about 0.8 mm. The suture is undulating, and the edge along the suture may be slightly protruding. Length of internodes often 7 internodals. Articulation between nodal and infranodal almost smooth, cryptosymplectial. Other articulations in the column show five petals of crenellae as in *Isocrinus*. Nodals with 5 cirri. The theca is almost hemispheric with smooth surface. The sutures are entrenched in the lower part of theca. The basals form a contiguous ring, somewhat lobate and with short, rostrate median prolongations downward covering the edges of the uppermost columnal. I Br 1–2 is synostosial. I Br 2 axillary. II Br 1–2 synarthrial. II Br 3–4 symmorphial. II Br 4 axillary. III Br 2–3 symmorphial. Other brachial articulations are muscular. First pinnule is on the abaxial side of II Br 2.

Description

The reconstruction and description of the species is based mainly on the large collection from the Craigweil Bed of Bognor Regis. The theca is small, almost hemi-spherical. Height of theca about 2.8 mm. Height of free surface 2.0 mm. Diameter 3.6 mm. The surface of theca is smooth. There are 5 radials, 5 basals and 5 infrabasals. The small infrabasals are surrounded by the basals, but are seen as a five-rayed star when the radials or the column is removed. Each infrabasal is rod-shaped with a rhombic section.

The basals are seen on the surface of the theca as a complete ring of five-sided plates, slightly wider than high. The basal ring is somewhat lobate in outline with constricted sutures. The lower edge forms a more or less prominent, beak-shaped projection downwards, covering the interradial edges of the uppermost columnal. The joint face against the uppermost columnal is provided with crenellae corresponding to the petaloid pattern of crenellae in the columnals. The surface against the radial ring is roof-shaped, forming two joint faces, and there are two small and narrow faces against the infrabasals. The two nerve canals are seen in the inner end of the basal, running from the radial joint face through the basal to the upper part of the infrabasal joint face. In contrast to other Isocrinidae with infrabasals the nerve canals do not meet and unite inside the basal, although the openings towards the infrabasals almost touch each other. The small surface of infrabasals and basals towards the narrow thecal cavity shows irregular furrows.

The radials are seen on the surface of theca as five-sided plates, almost twice as high and wide as the basals. The outline of the radial ring is almost circular. The articular surface of the radials against primibrachials is outward sloping. It has a deep, concave dorsal ligament fossa and a straight articular ridge. There is a deep median furrow between the ventral muscular fossae. The nerves have formed a ring canal and canals to the basals. There is a narrow radial cavity.

The first primibrachial has a four-sided surface, a little lower than the radial and more curved in the distal than in the proximal end. There is a triangular lateral surface against the neighbouring arm. The proximal articular face is steep, the ventral muscular

fossae almost reaching the distal end of the plate. The distal articular face is flat and smooth corresponding to a synostosial articulation in I Br 1–2. The second primibrachial is axillary. There is a low lateral surface. The two muscular distal articulations meet in an angle of $90^{\circ}-110^{\circ}$.

II Br 1 is wedge-shaped, higher in the abaxial side. The free surface is slightly curved and there is a flat lateral surface on the abaxial side. Both proximal and distal articular surface are outward sloping and there is no pinnule. The distal articular surface has a prominent median ridge corresponding to a synarthrial articulation in II Br 1–2. II Br 2 has a pinnular socket on the abaxial side. The articulation II Br 2–3 is muscular with the dorsal ligament to the abaxial side. There is no pinnule in II Br 3. The articulation II Br 3–4 is symmorphial with a fairly shallow transverse furrow in the distal face of II Br 3. II Br 4 is axillary. The proximal articular face is symmorphial with a pair of lateral teeth united by a transverse ridge and interlocking with II Br 3. There are often faint crenellae along the dorsal edge. The two distal articulations form an angle of 80° – 105° .

III Br 1 is wedge-shaped with a pinnular socket on the abaxial side. The articulation III Br 1–2 is oblique muscular. III Br 2–3 is symmorphial. There is no pinnule on III Br 2, but on the abaxial side of III Br 3. III Br 2 is thus very similar to II Br 3, but is more deep and narrow, and the symmorphial surface is more deeply excavated. The succeeding III Br 4–9 are all wedge-shaped with muscular articulations in both ends and with pinnules alternating adaxial and abaxial. These brachials gradually become more slender, long and rounded.

More distal parts of the arms cannot be correlated to exact number in the succession of brachials, but it is seen that further symmorphy occurs, since there are arm fragments with 4 muscular articulations succeeded by a symmorphy and again 4 muscular articulations or more. Further axillaries are not observed. There are about 125 I Br 2 and a similar number of II Br 4 picked out of the sample. Even considering a collecting failure due to small size, there would be more than 100 third axillaries in the sample if a third arm division occurred. The most distal arm fragments are very slender with long, conical brachials, wider in the distal than in the proximal end. This gives a serrate profile to the distal part of the arms. In these brachials the ventral furrow is very narrow. A single symmorphy was found.

The pinnules consist of long and slender pinnulars. The most proximal pinnular has an almost flat surface, but succeeding pinnulars have a more elliptical section with a rather sharp dorsal edge.

The hour-glass shaped opening of the axial canal in I Br 1-2 and the double opening in II Br 3-4 demonstrate a division of the axial nerve from the base of the first axial plate and before entering the second axial plate. Such features have not been previously observed in any crinoid.

The proximal columnals are low, pentalobate or almost stellate with five concave sides and strongly alternating size. The more distal part of the column is pentalobate with concave sides and rounded internadial edges. The edges often form protruding nodules in some or all columnals of a specimen. The height of the columnals is half the diameter or less. The edge along the suture may be slightly protruding. The sutures undulate corresponding to the crenellae of the articular face. The nodals have five elliptical cirrus sockets on the radial surface near the lower edge. The articulation between nodal and infranodal is almost smooth or has faint crenellae along the margin. The other articulations of the column show a petaloid ornament of crenellae with 5 elliptic petals and 6–8 crenellae along each, 2–4 of which are adradial and do not reach the margin. The crenellae attain their greatest length at the transition from marginal to adradial position.

In the collection of the British Museum a full internode is observed in 2 specimens including 15 and 11 internodals. In the sample from Bognor Regis the number of internodals in a full internode was 9 in 7 specimens, 8 in 10 specimens, 7 in 77 specimens, 6 in 4 specimens and 5 in a proximal fragment of the column. In the most proximal part of the column attached to the theca the number of internodals seen in succeeding internodes was found in one specimen to be 1, 1, 1, 1, 3, 4, and in another specimen 1, 1, 3, 3, 7. The columnals in these specimens are strongly alternating in size.

The cirrals are elliptical in section. They have a transverse articular ridge and a smooth surface. The proximal 6 cirrals are short, width exceeding their length and height. The distal cirrals are long, slender, higher than wide.

Affinity

The present species is remarkable by its small size. No other species of similar size is present in the Eocene except for *P. oakeshottianus*, which seems to be synonymous with the present species. The only other Isocrinidae found in the British Eocene belong to *Isselicrinus*, which differs specially in the form of the nodals. The column of *C. tintinnabulum* is rather similar to the Lower Cretaceous *Isocrinus neocomiensis* (Desor, 1845) but has no sharp interradial edges. The ramification and articulations of the arms differ from other Isocrinidae.

The genus Cainocrinus Forbes, 1852

Type

Cainocrinus tintinnabulum Forbes, 1852, is type of the genus.

History

The genus *Cainocrinus* was established by Forbes (1852) with *C. tintinnabulum* as type and only species recorded. It was characterised as having a contiguous basal ring.

Loriol (1875) established the genus *Picteticrinus* with the type *P. beaugrandi* Loriol, 1875. In 1877 he stated that the generic name was preoccupied by Étallon and that *Picteticrinus* sensu Loriol is identical with *Cainocrinus* Forbes, having the same diagnostic character of the basal ring.

Carpenter (1884) has demonstrated a considerable variation in the size of basals and the form of the basal ring among recent Isocrinidae and rejected any classificatory value of such characters. For this reason Bather (1898) made *Cainocrinus* a junior synonym of *Isocrinus*.

Biese (1930) in obvious disagreement with the international code of zoological nomenclature transferred the generic name *Cainocrinus* to *P. beaugrandi* Loriol, 1873, making this species type of the genus. *P. beaugrandi* is thus the type of two illegitimate genera, *Picticrinus* Loriol non Étallon and *Cainocrinus* sensu Biese non Forbes. The illegitimate genus "*Cainocrinus*" sensu Biese was characterised by irregular arm divisions and based on the irregularity found in one of the arms in the single specimen referred by Biese to the genus.

Redefinition of the genus Cainocrinus Forbes, 1852

The subdivision of Isocrinidae is based on the pattern of ramification in the arms and articulations in column and arms. The type of *Cainocrinus, C. tintinnabulum* Forbes has hitherto been insufficiently known for an adequate definition of the genus comparable with other genera of Isocrinidae, but through the collection and investigation of new material described above, it is now possible to give an exhaustive diagnosis.

Cainocrinus is a genus of Isocrinidae in which the articulations of columnals show 5 petals of distinct crenellae and a gradual transition from marginal to adradial crenellae. The nodals have 5 cirri, circular to elliptical in section. Infrabasals present but not exposed. The articulation I Br 1–2 is flat and smooth, synostosial. I Br 2 is axillary. II Br 1–2 is synarthrial. First pinnule is abaxial on II Br 2. II Br 2–3 is muscular. II Br 3–4 is symmorphial. II Br 4 is axillary. Second pinnule is abaxial on III Br 1–2 is muscular. III Br 2–3 symmorphial. Most succeeding brachials are muscular, but symmorphy does occur. There is no further arm divisions.

Isocrinus (?Cainocrinus) sp. aff. C. tintinnabulum Forbes, 1852

Plate 2 figs. 21-22.

Material

Pozaryska (1965) has described a boring at Sochaczew in central Poland 60 km west of Warsaw, passing through beds of glauconitic sand referred to the presumed Montian Pulawy Beds (191–262 m) and the presumed Danian Sochaczew Beds (262–266 m). In washed samples from the Pulawy Beds are found 69 internodals and 10 nodals of this crinoid. In samples of the Sochaczew Beds are found 5 internodals and 2 nodals of the same species. The specimens are in the collection of the geological institute of Warsaw.

Description

The columnals are very similar to the Lower Eocene *Cainocrinus tintinnabulum* in size and form. They are pentalobate to stellate in outline. Height and interradius

about 1 mm or less. The free surface of the columnals have a low and blunt median ridge or elevation and a slightly protruding edge along the undulating suture. The interradial edges may be gently rounded or form blunt longitudinal ridges. Articulation between internodals with 2–3 crenellae along the periphery on each side of the petals and in some columnals a short one to the radius. Articulation between nodal and infranodal is synostosial. Nodals with 5 elliptical cirrus sockets.

Age of samples

The samples are referred by Pozaryska (1965) to the Danian and to the Montian on a basis of Foraminifera, and by Voigt (1964) to the "Dano-Montian" on a basis of Bryozoa. In the absence of the most characteristic Danian and early Paleocene index fossils, the exact age determination should be taken with some reservation.

Nielsenicrinus fionicus (Nielsen, 1913)

1913 Pentacrinus fionicus.—Nielsen pp. 76, 90, pl. 8 figs. 41–54, pl. 9 figs. 4–7, textfig. 30. 1961 Nielsenicrinus fionicus (Nielsen).—Rasmussen p. 103, pl. 14 figs. 1–11.

Material

Material from the Danian of Denmark and Sweden has previously been described. In two small samples of Danian limesand collected at 2 km ESE of Haidhof, north of Vienna in Austria 10 small internodals and 2 nodals of this species are found. The specimens are in the collection of the Geological Museum, Copenhagen.

Calamocrinus ilimanangei n. sp.

Plate 1 figs. 6-7.

Derivation of name

Ilimanange (Eskimo) the unexpected (or better than expected). Also an Eskimo nickname for Professor A. Rosenkrantz during the expeditions in Greenland.

Holotype

The specimen plate 1 fig. 6 is holotype. It is from the Sonja Member of the Upper Danian Agatdal Formation of Agatdal in Nûgssuaq, West Greenland. The specimen is in the collection of the Geological Museum, Copenhagen (12756).

Material

In the collections of the Geological Museum, Copenhagen are 3 small fragments of columns collected by A. Rosenkrantz among the many thousands of fossils washed out of a loose sandstone ("the Sonja lens") from the type locality. Two of the specimens are slightly curved and their length therefore different in the two sides of the specimens. The area around the axial canal is more or less corroded, specially in the largest specimen, where also the crenellae are rather indistinct.

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Dimensions

		holotype	
Number of internodals	6	6	13
Diameter	1.3	2.0	2.6
Height of specimen	1.2 - 1.6	1.6	3.6 - 4.4
Number of crenellae	28	36	-

Diagnosis

A crinoid with a slender column, circular in outline, straight or slightly curved. Diameter of column 1.3–2.6 mm. Columnals very low, uniform without nodals or cirri in the preserved specimens. Height of columnals 0.2–0.3 mm. Articular face of columnals with numerous straight, uniform, undivided and evenly spaced radiating crenellae reaching from the margin almost to the axial canal. Central area of articular face slightly concave, without crenellae. Axial canal pentagonal, about 0.3–0.6 mm in diameter. Suture crenulate.

Determination of genus and affinity of Hyocrinidae

The columnals of the present species correspond in form to the much larger columnals found in Millericrinidae but are not similar to small or juvenile columnals of Millericrinidae. The Millericrinidae belong to the Jurassic except for a few specimens found in the Lower Cretaceous. Radiating crenellae are also found in some Cyrtocrinidae, but these have high columnals and few crenellae. No fossil crinoid known is similar to the present species.

Among living crinoids radiating crenellae are found only in the columnals of *Proisocrinus* and among Hyocrinidae, both unknown as fossils.

Proisocrinus was described by Clark (1910) and referred to Apiocrinidae or Pentacrinidae. It was interpreted as a possible intermediate form in the evolution from *Millericrinus* d'Orbigny, 1840, to Pentacrinidae (Isocrinidae). The column of *Proisocrinus* is almost 1 m long and 5–11 mm in diameter. The proximal fourth of the column is pentalobate and has nodals alternating with internodes of increasing length downwards. The median part of the column is cylindrical with uniform columnals, 5 mm in diameter and 1.5 mm high with 15 stout, radiating crenellae on the articular face. There are few nodals. The distal part of the column is similar in form, but the diameter gradually increases to 11 mm and the height of columnals to 4 mm. Even in the median part of the column, which best compares with the present species, the columnals are considerably larger and higher and the crenellae are few and larger. Moreover columnals resembling the proximal and distal part of the column are not found in Greenland. The structure of theca and column in *Proisocrinus* indicates, that this genus should be referred to the Holocrinidae.

Hyocrinidae was established as a family by Carpenter (1884). It is an isolated group of recent crinoids without close relation to other living crinoids except perhaps *Proisocrinus*, but with resemblance to early Mesozoic Millericrinida such as the Tri-

assic *Reocarocrinus* Gislén, 1924, and *Dadocrinus* Meyer, 1847. No fossil Hyocrinidae have been described.

The affinity of Hyocrinidae has been discussed since the first species of *Hyocrinus* was described by W. Thomson (1876) and compared with the recent *Rhizocrinus* Sars, 1864 and with Paleozoic Camarata such as *Platycrinus* Agassiz, 1836, and *Dichocrinus* Münster, 1839. Zittel (1882) placed *Hyocrinus* together with the Jurassic *Plicatocrinus* Münster, 1839, in a family Plicatocrinidae. Carpenter (1884) removed *Hyocrinus* from Plicatocrinidae and established the family Hyocrinidae. Jaekel (1892) considered *Hyocrinus* and *Saccocoma* closely related to Plicatocrinidae and descendants from the Palaeozoic Cyathocrinidae (Inadunata). Agassiz (1890, 1892) described the recent genus *Calamocrinus*, which he considered most closely allied to Mesozoic *Encrinus* and Apiocrinidae including by that time *Millericrinus* and in the conception of Agassiz also *Bourgueticrinus* and *Rhizocrinus* and *Millericrinus*, but *Hyocrinus*, *Plicatocrinus* and *Saccocoma* were placed by Bather in his Monocyclica Inadunata and by Jaekel in his Costata. Clark (1912) united *Calamocrinus* with *Hyocrinus* and related genera in the Hyocrinidae.

In a review of the Hyocrinidae Gislén (1939) considered this family related to Eudesicrinidae, a Jurassic family of Cyrtocrinida, but not directly descendant from this group.

The Cyrtocrinida including among others the Jurassic *Plicatocrinus* and *Eudesicrinus* and the recent *Holopus*, is a group specially adapted to reef-environments. The Hyocrinidae is a recent group of deep-sea crinoids. These two groups show similarities in the form of the column, the absence of cirri, the reduced or fused basal ring and the large radial cavity. The common ancestor of these groups and perhaps also *Proisocrinus* may be Triassic Millericrinida such as *Reocarocrinus* or *Dadocrinus*.

Among the Hyocrinidae only the type of *Calamocrinus*, *C. diomedae* Agassiz, 1890, is closely similar to the present species in size, form and articular surface of the columnals. It differs from the fossil species in a generally distinct median ridge on the columnals. *Calamocrinus* is the most primitive among recent Hyocrinidae in the structure of the theca with 5 unfused basals. It is living off Galapagos and Panama at a depth of 705–1410 m.

Bourgueticrinus danicus Nielsen, 1913

Plate 1 fig. 8.

- 1913 Bourgueticrinus danicus.—Nielsen p. 53 pl. 2 figs. 49-51, pl. 3 figs. 1-58.
- 1913 Bourgueticrinus curvatus.—Nielsen p. 55 pl. 3 figs. 59-61.
- 1961 Bourgueticrinus danicus Nielsen.-Rasmussen p. 178 pl. 30 figs. 1-8.
- 1965 Bourgueticrinus danicus Nielsen.—Rasmussen p. 34, 35 pl. 8 figs. 10-11.

Previous record

This species has previously been described in detail from the Danian. It has been recorded from the Danian of Denmark, Sweden, Belgium and the Netherlands. It is one of the dominant species in the Danian of Denmark.

Material

One single theca including the proximale has been found in the Paleocene (Heersian) glauconitic marl of the Lellinge Formation at Egsmark near Ebeltoft in Denmark. This is the first and only documented specimen of a *Bourgueticrinus* from post-Danian deposits. The absence of conglomerate and derived fossils in the other faunal elements at the locality indicates that the presence of *Bourgueticrinus* in the Heersian may be reliable.

Columnals of the *Bourgueticrinus-Democrinus* type found in the Danian near Haidhof north of Vienna in Austria most likely belong to this species, but no theca has been found so far.

The specimens are in the collection of the Geological Museum, Copenhagen.

Democrinus maximus (Nielsen, 1915)

1915 Rhizocrinus maximus.—Nielsen p. 392 fig. 1

1938 Democrinus maximus (Nielsen).-Gislén p. 7 fig. 8.

1961 Democrinus maximus (Nielsen).-Rasmussen p. 207 pl. 31 figs. 1-8.

1965 Democrinus maximus (Nielsen).—Rasmussen p. 34 pl. 8 fig. 12.

Previous record

This species has previously been described from the Danian and recorded from the Danian of Denmark, Sweden, Belgium and the Netherlands. It is common in the uppermost part of the Danian in Denmark and as derived specimens in the conglomerate at the base of the Heersian in Denmark and Sweden.

Material

A few thecae of this species are found in the Paleocene (Heersian) glauconitic marl of the Lellinge Formation at Egsmark near Ebeltoft in Denmark. The specimens are in the collection of the Geological Museum, Copenhagen.

Democrinus londinensis (Forbes, 1852)

Plate 1 fig. 9.

1852 Bourgueticrinus londinensis.—Forbes p. 36 fig. 4.

1884 Rhizocrinus londinensis (Forbes).—Carpenter pp. 257, 259.

1928 Rhizocrinus londinensis (Forbes).-Davis pp. 347, 349.

1937 Rhizocrinus londinensis (Forbes).-Davis p. 79.

1961 Democrinus londinensis (Forbes).-Rasmussen p. 208.

Type

The columnals figured by Forbes (1852) p. 36 figs. 4 a–d are syntypes. They are from the Eocene London Clay (Ypresian) of Copenhagen House in London. The specimens are in the collection of the British Museum (E 22093–22094).

Material

This species has been recorded by Davis (1928, 1937) as characteristic to division 2 of the London Clay together with *Isselicrinus subbasaltiformis* at Copenhagen Fields, Beddington, Clapham, London Wall and The Minories and from Warden Point on the Isle of Sheppey. The London Clay of the Isle of Sheppey was correlated by Davis (1936) with the middle part of the London Clay, presumably division 4. Venables (1963) has recorded "*Rhizocrinus* sp. cf. *londinensis*" from the Craigweil Bed (Middle Clay) of Bognor Regis.

In the collection of the British Museum are isolated columnals from the London Clay (division 2) of Copenhagen Fields (E 38688) and from the London Clay (division 4) of Highgate (E 430, 22119, 38716). In a specimen from Highgate (E 38715) the column and theca are found connected in the clay with slightly displaced brachials. A sample from Highgate includes numerous isolated columnals, fragments of columns and 2 thecae (E 22119).

In the collection of the Geological Survey, London, are isolated columnals from the London Clay (division 2) of Clapham (Zc 4066–4075) and The Minories (61650–1, 98808–15).

In the collection of Valette in Dijon, France, are 4 thecae of this species from the Middle Eocene (Lower Lutetian) of Fontcouverte (Aude) in France.

Dimensions

The specimen figured shows the following dimensions: Height of theca 3.8 mm. Height of basals 3.0 mm. Height of radials 1.0 mm. Diameter of theca at top 3.0 mm. Diameter of theca at its base 1.3 mm. Height of distal columnals 3.0 mm.

Diagnosis

A *Democrinus* with rather high, conic theca. The height of the basals is about three times the height of the radials. The columnals are synarthrial with a single articular ridge with different orientation in the two ends of a columnal. The proximal columnals are short and cylindrical. Their height gradually increases through about thirteen columnals until they reach the same height as width. They have a narrow axial canal. The distal columnals have elliptical articular surfaces with greatest diameter in the direction of the articular ridge. They are slightly higher than the greatest diameter. The axial canal is enlarged at the articular surface. There is often a cirrus socket around the suture at the end of the articular ridge.

Remarks on the identification

Columnals similar to the present species occur in species of *Bourgueticrinus* from the Maastrichtian and Danian and in several members of the family Bathycrinidae including *Democrinus*. A safe determination of the genus and species is not possible on the basis of columnals alone. However no theca of *Bourgueticrinus* has ever been found in Eocene or younger sediments. The presence of *Democrinus* in the London Clay is demonstrated by the three thecae recorded. There is no indication of any other Bathycrinidae or of more than one species with such columnals in the British Eocene.

Affinity

The present species differs from *D. maximus* (Nielsen, 1915) in the simple, conic form of the theca and the smaller height of the basals. It differs from *D. gisleni* Rasmussen, 1961, in the much larger size of the theca and height of basals. No other species of *Democrinus* has been recorded from the Tertiary. The recent species of *Democrinus* have a smaller number of short, proximal columnals and more slender distal columnals or a theca of different form.

Columnals of Bathycrinidae

- 1851 Apiocrinus ellipticus (Miller).-Schafhäutl p. 420 pl. 7 fig. 13.
- 1852 Bourgueticrinus ellipticus cornutus.—Schafhäutl p. 151, 167.
- 1861 Bourgueticrinus goniaster.—Gümbel p. 596, 656.
- 1861 Bourgueticrinus thorenti Archiac.—Gümbel p. 596.
- 1863 Bourgueticrinus ellipticus (Miller).—Schafhäutl p. 110 pl. 15 fig. 7.
- 1863 Bourgueticrinus cornutus Schafhäutl.—Schafhäutl p. 111 (non pl. 24 a fig. 5).
- 1930 Rhizocrinus sp.—Hucke & Voigt p. 160 pl. 6 fig. 11.
- 1938 Rhizocrinus suessi (Munier-Chalmas).—Traub p. 18.

Several records are given on *Bourgueticrinus* sp. or *Rhizocrinus* sp. from the Paleocene of Denmark and Sweden and from Paleocene erratics in Sweden, Denmark and North Germany. *Rhizocrinus* sp. is also recorded from the Middle Oligocene Septarienton at Joachimstal in North Germany. All these records are based on small, slender columnals of a form found among Maastrichtian and Danian species of *Bourgueticrinus* and in fossil and recent genera of Bathycrinidae.

Similar columnals from the Palaeocene and Eocene near Salzburg in Austria and from southern Bavaria in Germany have been referred to the Cretaceous species *Bourgueticrinus ellipticus* (Miller, 1821) and to the Tertiary south European species *Conocrinus thorenti* (Archiac, 1836) and *Conocrinus suessi* (Munier-Chalmas, 1877).

A few columnals have been picked out of a sample from the *Gryphaea*-bed in the uppermost part of the Paleocene (Landenian) section at Kroisbach north of Salzburg in Austria (collection at Copenhagen).

Biol. Skr. Dan. Vid. Selsk. 19, no. 7.

The species *Bourgueticrinus londinensis* was established by Forbes (1852) on such columnals but can now be connected with the theca described above as *Democrinus londinensis* (Forbes, 1852).

Furthermore the two species *Bourgueticrinus cornutus* Schafhäutl, 1852, and *Bourgueticrinus goniaster* Gümbel, 1861, are established for such indeterminable columnals of Bathycrinidae from the Eocene of southern Bavaria. These species have also been referred to the genera *Conocrinus* and *Rhizocrinus*, but a determination of the genus or species is only possible when also the theca is known. A theca belonging to *Conocrinus* was figured by Schafhäutl (1863) and referred to *B. cornutus*.

The few thecae found in the Tertiary show that *Democrinus* lived in the North European Lower Tertiary, and *Conocrinus* in the South European Lower Tertiary. A few specimens of the recent genera *Bathycrinus* and *Monacocrinus* are found in the Danian of Denmark and Sweden. Only one theca of *Bourgueticrinus* has been found in the Paleocene except for the Danian and derived Danian fossils in the conglomerate at the base of the Heersian in Denmark and Sweden.

Amphorometra ornata n. sp.

Plate 1 figs. 10-15.

1928 Antedon n. sp.—Davis pp. 347, 349.

Derivation of name

Ornatum (Latin) ornate, richly decorated. The name is proposed to illustrate the tubercles of the centrodorsal and the thorns of the brachials.

Holotype

The theca with centrodorsal shown plate 1 fig. 10 a-c is holotype. It is from the London Clay (division 3) of Wraysbury Reservoir at Poyle in Buckinghamshire, England. The specimen is collected by Mssrs. Macadie, Rundle and Cooper and transferred to the collection of the British Museum (E 53620).

Material

Davis (1928) has recorded a centrodorsal from the London Clay of Clapham (division 2) and 2 centrodorsals from Worchester Park (division 3). These undescribed specimens have not been found in the collections, but they are the only comatulids recorded from the London Clay. In the collection of the Institute of Geological Sciences, London, are several brachials of the present species collected by Davis from the London Clay of Clapham. In the collection of Mssrs. Rundle and Cooper are, apart from the holotype, an incomplete theca, a centrodorsal, 3 axillary I Br 2 with proximal synarthrial articulation, 1 wedge-shaped II Br 1 with distal synarthrial articulation 21 secundibrachials with muscular articulation and pinnular socket, one of them connected to a hyposyzygial, furthermore 4 hyposyzygial and 19 episyzygial secundi-

brachials. All these specimens are from the type locality, but a few brachials in the same collection are from the London Clay (division 2) of Aveley in Essex, England.

Dimensions

Radius of theca 2.5 mm, internadius 2.2 mm, height 3.6 mm not including the top of the radials which is broken off. Height of centrodorsal 2.0 mm. Diameter of centrodorsal cavity 0.8 mm.

Diagnosis

An Amphorometra with rather low conical centrodorsal covered by 10 radiating rows of cirrus sockets, generally 3 distinct sockets in each row. The sockets are strongly concave with radiating crenellae along the edge and an articular boss on each side of the axial canal. The edges between the sockets form protruding tubercles where they meet. The dorsal pole is slightly protruding and appears rugose due to tubercles and rudiments of juvenile cirrus sockets. There is no dorsal pit or star. The ventral surface of the centrodorsal is slightly concave with 5 lanceolate furrows for rod-shaped basals. Vaults growing out to form new cirrus sockets occur. There are no radial pits. The centrodorsal cavity occupies about one fifth of the centrodorsal diameter. The outline of the centrodorsal is rather irregular, subpentagonal.

The rod-shaped basals are seen in the interradial corners between the radial plates. The radials cover the entire ventral surface of the centrodorsal. There is a free surface of the radials in continuation of the articular surface as a narrow edge or rim with the same orientation and with a strongly irregular outline forming irregular tubercles and blunt thorns. The radial articular surface forms an angle of about 40° with the axis of the theca. The dorsal ligament fossa is semielliptical and separated from the free surface by a regularly curved faint line. There is a deep ligament pit. The articular ridge is straight with a median canal for the brachial nerve. The interarticular ligament fossae are subtriangular and very deeply excavated. The ventral muscular fossae are narrow, subtriangular with the point downwards near the nerve canal. They are less concave than the interarticular ligament fossae and have a rugose bottom. The right and left muscular fossae are separated by a ridge with a median furrow. The top of the radials is broken off, only one of the muscular fossae appearing almost complete. The articular surface in the upper part of the radial, ventral of the articular ridge, does not reach the internadial suture, and the surface of the radial is here exposed as a narrow band sloping towards the suture. The radial cavity is narrow, but may perhaps be enlarged in the missing top.

The brachials have irregular nodules and blunt thorns along the distal edge. The free surface has scattered tubercles in the larger brachials. The axillary primibrachial, presumably I Br 2, has a synarthrial articulation with the preceeding primibrachial. A strongly wedge-shaped secundibrachial with distal synarthrial articulation, flat lateral sides and a dorsal surface with tubercles is obviously II Br 1. The articulations found in other secundibrachials indicate that about every fourth articulation is syzygial corresponding to a syzygial articulation in every second secundibrachial.

Affinity

No other comatulid is known from North European Eocene. The present species differs from other species of *Amphorometra* by the low conical centrodorsal with tubercles, the crenulate cirrus sockets, and the thorns on the brachials. Together with this species in the London Clay are found remains of *Cainocrinus tintinnabulum*, the brachials of which are smooth.

Asteroidea

Astropectinidae

The name Astropecten was introduced as a pre-Linnean name by Linck (1733) and was established as a genus by Gray (1840). Fisher (1908) designated the recent species Asterias aranciaca Linne, 1758, as lectotype of the genus. The name Stellaria proposed by Nardo (1834) is preoccupied by Müller (1832). The pre-Linnean name Crenaster Luidius, 1699, used by d'Orbigny (1850) is in post-Linnean nomenclature a junior synonym.

Pentasteria was established as a genus by Valette (1929) with the type species *P. boisteti* Valette, 1929. It was demonstrated by Hess (1960) that the genus *Archastropecten* Hess, 1955, is a junior synonym of *Pentasteria*. Hess proposed to maintain *Archastropecten* as a subgenus of *Pentasteria*. Considering the close resemblance between this group and *Astropecten*, I prefer to consider *Pentasteria* as a subgenus of *Astropecten*. There is no distinct boundary between the two genera, especially when Tertiary and Recent species are considered.

The genus *Coulonia* was established by Loriol (1873) with the type *C. neocomiensis* Loriol, 1873. Hess (1955) established a genus *Cuneaster* with the type *C. hauteriviensis* Hess, 1955. It was later demonstrated by Hess (1970) that *Cuneaster hauteriviensis* is a junior synonym of *Coulonia neocomiensis*, and *Cuneaster* therefore a synonym of *Coulonia*.

The genus Lophidiaster was established by Spencer (1913). The species L. ornatus Spencer, 1913, was first mentioned as type of the genus by Valette (1915). The genus was distinguished from Astropecten by the absence of dorsal paxillae. Rasmussen (1950) made Lophidiaster a synonym of Astropecten after the observation of typical paxillae in the type species. Hess (1955) separated again the two genera, using as a new characteristic the large, divided or "horseshoe-shaped" tubercles for spines on the inferomarginals, present in Astropecten, but not in Lophidiaster. Following this interpretation, however, L. postornatus is maintained in the genus Astropecten.

36
Astropecten postornatus (Rasmussen, 1945)

Plate 3 figs. 1-4.

1945 Lophidiaster postornatus.—Rasmussen p. 245 pl. 9 fig. 16.

1950 Astropecten postornatus (Rasmussen).-Rasmussen p. 91 pl. 10 fig. 21.

1955 Lophidiaster postornatus Rasmussen.—Hess p. 66.

Material

This species has been described from the Upper Danian of Denmark including the conglomerate at the base of the Heersian. From the Sonja Member of the Upper Danian Agatdal Formation in Agatdal, Nûgssuaq in West Greenland are 12 superomarginals and 13 inferomarginals of this species. In a sample of the presumed Danian beds (193–207 m) in the boring at Boryszew in Poland are a rather worn superomarginal and inferomarginal probably belonging to this species. The specimens from Denmark and Greenland are in the collection of the Geological Museum, Copenhagen, the specimens from Poland are in the collection of the Geological Institute of Warsaw.

Size of marginals

A study of the marginals, the way in which the wedge-shaped marginals fit into a stellate outline and a comparison with other Astropectinidae show that the orientation of the superomarginal and inferomarginal in the original description is incorrect. The contact between superomarginal and inferomarginal was formed by the surface shown to the right in the figure by Rasmussen (1944 pl. 9 fig. 16c and 1950 pl. 10 fig. 21 a). The correct size of the specimens is therefore as follows.

Denmark (1945 fig.):	length	width	height
superomarginal	1.7	2.8	4.0
ridge of superomarginal	0.5	0.7	0.5
inferomarginal	1.6	2.8	3.7
ridge of inferomarginal	0.5	0.4	0.3
Greenland (largest specimen):			
superomarginal	1.2	2.0	3.0
ridge of superomarginal	0.8	0.6	0.6
inferomarginal	1.2	2.3	2.5
ridge of inferomarginal	0.7	0.4	0.5

The marginals from Greenland are slightly smaller than the majority of marginals from Denmark. This, however, is expected as a result of differences in sedimentation and sampling. The majority of specimens from Denmark have been washed out of the Paleocene conglomerate succeeding the Upper Danian limestone, and is primarily sorted according to size. The specimens from Greenland were picked out of a very loose sandstone ("the Sonja lens") and were washed and sorted through a finer mesh than the specimens collected in Denmark.

Description

The superomarginals have a ridge of uniform height. The free surface forms a regular arch. The ornamentation consists of small, uniform, closely placed spine pits, where rudimentary spines or scales were placed. The superomarginals meet in a quarter-elliptical surface.

The inferomarginals are subtriangular in section with a slightly curved free surface. The ridge is almost uniform in height. The ornamentation consists of closely placed granules. Larger granules or tubercles, horseshoe-shaped or incompletely divided by a furrow, form from one to three oblique rows on the ridge of each inferomarginal near the edge against the superomarginal. This, however, is generally obscured by wear of the surface.

Occurrence

This species is found only in the Upper Danian of Denmark and Greenland, but may be present in the presumed Danian of Poland.

Astropecten granulatus n. sp.

Plate 3 figs. 5-8.

? 1937 Asteroid.---Wrigley & Davis p. 208.

Derivation of name

Granulum (Latin) grain. Named after the granulated superomarginals and inferomarginals.

Type

The inferomarginal pl. 3 fig. 6 is holotype. It is from the Upper Eocene (Bartonian) Middle Barton Beds (horizon E of Burton 1929) at Barton Cliff in Hampshire, England. The specimen is from a sample in the British Museum collected by Mr. A. G. Davis (E 53627).

Material

Several isolated ossicles have been picked out from the washed sample collected by Mr. Davis. There are 1963 superomarginals, 2395 inferomarginals, 118 ambulacrals including 23 first ambulacral, 15 adambulacrals and 7 terminals. Other isolated marginals from the type locality are also present in the British Museum (E 52170–52210). Further specimens in the British Museum are from the Middle Eocene (Auversian) Upper Bracklesham Beds (Bed XVII of Fisher 1862 and Wrigley & Davis 1937). These specimens are collected in blue clay on the foreshore opposite Medmerry Farm near Selsey Bill in Sussez (E 13789–13826). Indeterminable asteroid marginals are recorded by Wrigley & Davis (1937) from the Lower Eocene (Ypresian) Lower Bracklesham Beds at Whitecliff Bay, Isle of Wight.

Diagnosis

An *Astropecten* with a granulated narrow ridge on the superomarginals and inferomarginals. There is a variable number of larger, divided tubercles for spines forming oblique rows on the inferomarginals and a few scattered tubercles of similar form on most superomarginals.

Dimensions	height	width	length
superomarginal	1.4 - 1.5	1.2 - 1.3	0.7 - 0.9
superomarginal ridge	0.2	0.2 - 0.3	0.5 - 0.7
inferomarginal	1.4 - 1.5	2.7 - 2.9	0.8
inferomarginal ridge	0.1 - 0.2	0.6 - 0.7	0.6 - 0.7
terminal plate	0.5 - 0.7	0.8 - 1.2	0.7 - 1.0

Description

The marginals and the marginal ridges near the arm base are distinctly wedgeshaped, short near the edge and long near the disc. More distal marginals have almost parallel proximal and distal ends. The inferomarginals are rather high and subtriangular in section. The surface against the superomarginals is very small and forms an obtuse angle with the surface against the body cavity and adambulacrals. The inferomarginals meet in an angular face, intermediate in form between inferomarginals of Astropecten and Coulonia. A low ridge with interruptions bounds this articular face. The free surface is provided with a ridge, which is very low in the ventral part but continues in a slight curve towards the upper edge, where it gradually increases to a considerable size. The sides of the ridge are covered by a faint but distinct, close granulation. The outer surface of the ridge is covered by large granules or tubercles forming one or more rows depending on the size of the surface. In wedge-shaped inferomarginals from near the arm base, the ridge is so narrow, that no distinct arrangement of the tubercles is seen. The smaller, more rectangular plates from the arm show an arrangement of the large tubercles in oblique rows. A variable number of tubercles in the upper part of the ridge are divided by a furrow (horseshoe-shaped) and often slightly larger than other tubercles, but in some inferomarginals such divided tubercles may cover almost the entire surface of the ridge.

The superomarginals are smaller and more quarter-circular in profile or a little higher than wide. The surface against inferomarginals is distinctly concave. The surface against the body cavity is slightly convex. The free surface is provided with a ridge of almost uniform height. The superomarginals meet in a surface quarter-circular in form or slightly pointed towards the dorsal edge. This articular surface is bound by an unbroken low ridge. The ridge of the free surface is slightly granulated on the sides and provided with tubercles on the outer surface. The tubercles are smaller than on the inferomarginals, but a few tubercles (1–3) in varying position may be enlarged and divided or crater-shaped as on the inferomarginals. The adambulacrals have a granulated, almost rectangular ventral surface and a point or vertical ridge towards the ambulacral furrow. They meet in strongly sloping proximal and distal faces. The ambulacrals are rather short, almost flat, with a longitudinal micro-ornament on the surface against the body. The terminal plate is closely granulated and almost divided by a median concavity into a semicylindrical right and left part.

Astropecten? beyrichi Linstow, 1912

1912 Astropecten (? Pentaceros) Beyrichi.—Linstow p. 52 pl. 2 fig. 5–7. 1955 Astropecten (? Pentaceros) beyrichi Linstow.—Hess p. 74.

Type

The arm figured by Linstow is holotype and the only specimen known. It is from the Middle Oligocene (Rupelian) Septarienton of Hermsdorf (Mark) in Germany. Collection, according to Linstow, Museum für Naturkunde, Berlin.

Dimensions

Length of arm fragment 21 mm. Width 17 mm at the base and 5 mm at the end of the preserved fragment. Length of marginals 1-1.5 mm. Height of margin 6-7 mm at the base of the arm.

Description

The arm is slender. There are 12 superomarginals and inferomarginals in each side of the preserved fragment. According to the figure, the specimen will fit a stellate form with interradius 1–1.5 cm and radius at least 3 cm. The marginals are short, wide and apparently low, slightly wedge-shaped at the base of the arm. Inferomarginals along the disc are wider than superomarginals. Width of the arm large at the base of the arm, but decreasing towards the distal end. Length of marginals almost uniform. The free surface of the marginals is regularly arched, slightly tumid, apparently without ridge. It is covered by small, closely placed spine pits. There are no ventral covering plates in the narrow arm. A single row of dorsal plates is possibly present between the superomarginals of the arm.

Affinity

The species is referred by Linstow to "Astropecten sensu lato". The genus is uncertain but the marginals without ridge show that the species does not belong to Astropectinidae. According to Hess it may perhaps belong to the Goniasteridae. It shows some resemblance to the isolated marginals described by Valette (1925) as *Calliderma atagensis* from the Middle Eocene (Lutetian) of France.

Coulonia colei (Forbes, 1852)

Plate 3 figs. 9-15, plate 11 figs. 2-3, plate 12 figs. 1-2.

- ? 1811 Astropecten echinatus minor Linck.—Parkinson p. 4.
- ? 1844 Asteria.—Ansted p. 66 fig.
- ? 1848 Astropecten crispatus.—Forbes p. 479.
- 1848 Astropecten armatus.—Forbes p. 479 (non Gray 1840, nec Müller & Troschel 1842).
- ? 1849 Astropecten crispatus Forbes.—Forbes Dec. 1 pl. 3 fig. 3.
- 1849 Astropecten armatus Forbes.—Forbes Dec. 1 pl. 3 fig. 4.
- ? 1852 Astropecten crispatus Forbes.—Forbes p. 29 pl. 4 fig. 2.
- 1852 Astropecten armatus Forbes.—Forbes p. 29 pl. 4 fig. 1.
- 1852 Astropecten? colei.—Forbes p. 30 pl. 4 fig. 3.
- ? 1909 Astropecten crispatus Forbes.—Linstow p. 57.
- ? 1936 Astropecten crispatus Forbes.—Davis p. 57.
- ? 1955 Archastropecten crispatus (Forbes).—Hess p. 42.
 - 1955 Cuneaster armatus (Forbes).-Hess p. 59.
 - 1955 Cuneaster colei (Forbes).-Hess p. 60.
 - 1963 Archastropecten sp. cf. crispatus (Forbes).-Venables p. 263.

Synonymy

Astropecten echinatus minor Linck, 1733, is a pre-Linnean name for the recent, Mediterranian Astropecten bispinosus Otto. The specimen referred by Parkinson (1811) to Astropecten echinatus minor is preserved in pyrite from the Isle of Sheppey and probably belongs to Coulonia colei, which is rather common on the Isle of Sheppey. Astropecten crispatus Forbes, 1848, is a name used for badly preserved, indeterminable specimens covered by pyrite. They come from the same locality and probably belong to the same species. The name Astropecten armatus Forbes, 1848, is a homonym of A. armatus Gray, 1840 and of A. armatus Müller & Troschel, 1842. It is further a synonym of Astropecten? colei Forbes, 1852. Hess (1955) referred the species to a new genus of Astropectinidae, Cuneaster Hess, 1955. According to Hess (1970) this is a synonym of Coulonia Loriol, 1873.

The type of Astropecten crispatus

In the description of *A. crispatus* Forbes (1848) mentioned a specimen communicated by Mr. Stokes to the Geological Survey and a specimen in Mr. Bowerbank's collection. He further referred to the specimen figured by Ansted (1844). The latter specimen is from Bowerbank's collection and now in the collection of the Institute of Geological Sciences (31439) but now completely decomposed, and only two plaster casts and some not identifiable fragments in paraffin are still preserved.

In 1849 Forbes figured a specimen from Bowerbank's collection but not identical with the specimen figured by Ansted. This specimen, pl. 3 fig. 3 a, is now in the collection of the British Museum (E 57501) but completely decomposed. He further figured a specimen from Mr. Stokes' collection. This specimen, fig. 3 b-c, is now in the Institute of Geological Sciences (49166–49167) but partly decomposed. In 1852 Forbes refigured the specimen previously figured by Ansted. In 1955 Hess selected the speci-

men figured by Forbes 1849 pl. 3 fig. 3 as lectotype without stating which of the two specimens in this figure was meant. According to Hess, the specimen is nr. 31439 in the Geological Survey, which, however, is the specimen figured by Ansted 1844 and Forbes 1852, not by Forbes 1849. There is therefore no unambiguous type of the species.

Identification of Astropecten crispatus

The specimens in the collections referred to this species are from the London Clay of the Isle of Sheppey. All the specimens are more or less completely covered by pyrite and show few or no details. They have in common a stellate form with rapidly tapering arms, very wide near the base, and short, apparently very wide marginals specially in the proximal part of the arm. It is remarkable that no well-preserved specimen shows similar features. The marginals, however, appear double as if divided in an inner and outer part, and in a few specimens it is seen that the outer part is not the marginal but a spine or a group of spines covered by the pyrite. This is seen in the specimen 49166–7 although not indicated in the figure by Forbes, and it corresponds to his indications that a strong spine is attached to each plate in perfect specimens. Interpreted in this way, the actual arm is considerably more narrow in its proximal part, and the specimens may very well belong to *Coulonia colei (= Astropecten armatus)* which is the common species in the London Clay of the Isle of Sheppey.

Other records of Astropecten crispatus

According to Venables (1963) "Archastropecten sp. cf. crispatus" is found in the Lower Eocene (Ypresian) Upper Fish-tooth Bed (Middle Clay) of Bognor Regis. According to Linstow (1909) two specimens from the Upper Eocene (Bartonian) Barton Clay of Barton in Hampshire, England, are in the collection of Museum für Naturkunde, Berlin.

The type of Astropecten armatus Forbes

The specimen described by Forbes (1848), figured by Forbes (1849) and refigured as mirror image by Forbes (1852) is holotype and the only specimen recorded. It is from the Lower Eocene (Ypresian) London Clay of Sheppey in Kent, England. It is the best preserved specimen within this group of British Eocene Astropectinidae, but the name must be rejected as a primary homonym. The specimen is in the collection of British Museum (E 57503).

The type of Astropecten? colei

The specimen figured by Forbes (1852) pl. 4 fig. 3 is holotype and the only specimen recorded. It is from the Lower Eocene (Ypresian) London Clay of the Isle of Sheppey, Kent. Although disturbed, the single plates are rather well preserved without pyrite. The specimen is in the collection of the Institute of Geological Sciences, London (49173). The figure given by Forbes is a mirror image of the specimen.

British specimens

Several specimens preserved in pyrite from the London Clay of the Isle of Sheppey in Kent are in the collections of the British Museum (E 34960, 38490, 52331, 57424, 57503, 75909), and in the collection of the Institute of Geological Sciences (49173, 94302–94304, 99789, 100370). There are further in the British Museum one specimen (E 428) from Highgate, London, and one (E 52164) from Oxshott Brickworks, Surrey, both from the London Clay (division 5). These specimens are preserved in clay and E 428, especially, shows several details of the plates. In the specimen E 75909 three of the terminal plates are preserved. An isolated terminal plate of similar form from the London Clay (division 5) of Highgate is in the Institute of Geological Sciences (5807).

Danish specimens

From the Lower Eocene Mo-Clay Formation of Mors and Fur in Denmark are a few asteroids apparently belonging to this species. One of the specimens from the Mo-Clay of Fur is in the collection of the Institute of Paleontology in Uppsala, Sweden

	Highgate	Isle of Sheppey								
	E. 428	E. 75909	GS. 491	E. 38490	E. 2560	GS. 99789	GS. 94304	Fur		
radius	+60	+40	+30	+18	+25	+17	+30	18	25	45
interradius	± 10	11	-	± 5	± 6	8.5		3.5	± 5	± 8
width of arm near										
base	11	9	± 12	± 5	± 6	8	11	3.5	-	± 7
height of paxillae.	1-2	-	1 - 2	_		-	1.5	-	-	
length of marginal										
spine	2-3	2-3	2 - 3	.5–1	1	-	-	.7	.8	-
length of adambul-										
acral spine	-	1	-	-	-	-	-	.5	-	-
height of supero-										
marginal	2.5	-	$\pm 2.22.5$	÷1	1.0 - 1.2	± 1	2.2	-	$\pm.8$	1.0
width of supero-										
marginal	2.0 - 3.5	-	$\pm 2.5 3.0$.5	± 1	± 1.5	2.5	-	$\pm.8$	-
width of $ridge\ldots$.	1.0-2.0	-	$\pm 1.5 - 2.0$	-	-	-	1.5	-	$\pm .5$	-
height of infero-										
marginal	3.0	-	2.5 - 4.2	± 1	± 1.5	$\div 1.5 - 2.0$	3.0	-	1.2	1.2
width of infero-										
marginal	2.0 - 3.5	± 2	3.5 - 5.5	1.0 - 1.5	$\pm 1.5 - 2.0$	± 2.0	3.2	.8	± 1.4	1.4
length of infero-										
marginal	1.5	±1	1.5 - 2.0	.8	1.0	1.0	1.5	.5	.7	.8
width of marginal										
ridge	1.0-2.0	-	2.0 - 4.0	-	-	-	± 1.5	-	± 1.0	1.0
length of marginal										
ridge	.46	$\pm .5$.6-1.0	.5	.5	.5	1.0	.3	.4	.6

Dimensions

 $+, \pm$ and \pm indicate more than, less than and approximately.

(DM 12). It is preserved as impression in the sediment, showing the dorsal side with distinct paxillae, dorsal and ventral marginals and ambulacrals. Another specimen from Fur is in the collection of Mr. Guldager, Ebeltoft in Denmark. It is preserved as an impression of the dorsal side and embedded dorsal side upwards in the Mo-Clay 35 mm below a 30 mm thick, dark layer of volcanic tuff. The specimen shows the madreporite, ambulacrals, marginals and a few paxillae. In the Geological Museum of Copenhagen is a specimen from the Mo-Clay of Mors, showing the ventral side with distinct ambulacrals, adambulacrals and long adambulacral spines. The inferomarginals are concealed by small spines.

Description

A Coulonia with long, narrow arms, almost uniform in width, and meeting in a short interradial arch near the mouth. The marginals are short with a very prominent ridge and small, elevated articulations of almost rectangular outline between the marginals of each row. The surface of the ridge is covered with tubercles where slender spines are attached. The superomarginals are rather small with a high, lateral ridge or wing curved towards the dorsal side and closely covered on the surface by uniform tubercles for small spines and, near the dorsal end of the surface, one or two larger, crater-shaped tubercles for larger spines. The inferomarginals are larger and wider with a narrow, angular articular surface towards joining inferomarginals. There is a very large lateral ridge or wing with tubercles for small spines and two large, horseshoe -shaped or double tubercles for long spines. The adambulacrals are rather large, fivesided with a prominent edge into the ambulacral furrow near the proximal end. The ventral surface of the adambulacral is granulated with at least 3 long spines. The ambulacrals are rather large, and uniform, accomodated to only one row of podia in each side of the ambulacral furrow. The dorsal surface is covered with high paxillae separating the margins as far as the tip of the narrow arm. There is a small ventral area in each interradius covered by flat, ventral plates with a slightly raised, granulated area forming a low ridge radiating towards the inferomarginals. The terminal plate is almost oviform with a deep ambulacral furrow along the ventral side and distal surface, and on each side is a shallow furrow where small distal superomarginals have met the terminal plate. There is a shallow median embayment in the proximal margin of the plate where it has met the dorsal cover of the arm. The free surface of the terminal plate is closely granulated. The length of the plate is 3-4.5 mm. This terminal plate is very similar in form and size to terminal plates described from the Cretaceous and referred to Asterias (Nielsen 1943, Rasmussen 1950, Müller 1953).

Lophidiaster punctatus Nielsen, 1943

1943 Lophidiaster punctatus.—Nielsen p. 67 pl. 4 fig. 38.

1945 Lophidiaster punctatus Nielsen.—Rasmussen p. 423 pl. 9 fig. 15.

- 1950 Astropecten punctatus (Nielsen).-Rasmussen p. 92 pl. 10 fig. 20.
- 1955 Lophidiaster punctatus Nielsen.—Hess p. 66.

Previous records

This species has been recorded only from the Danian of Denmark.

Material

A single superomarginal and inferomarginal of this species is found in the residue of a small washed sample of the Danian limesand from Haidhof north of Vienna in Austria. The specimens are in the collection of the Geological Museum, Copenhagen.

Lophidiaster haunsbergensis n. sp.

Plate 3 figs. 16-17.

Derivation of name

Haunsbergensis (Latin) from Haunsberg, after the type locality.

Type

The superomarginal pl. 3 fig. 16 is holotype. It is from the Upper Paleocene (Landenian) of Kroisbach at Haunsberg north of Salzburg in Austria (locality Kch 2 of Traub 1938). The specimen is from the biozone with *Globigerina velascoensis*. Collection of the Geological Museum, Copenhagen (12779).

Material

In a sample from the type locality collected by Professor A. Rosenkrantz in 1962, 37 superomarginals and 21 inferomarginals including the type have been found. The specimens are in the collection of the Geological Museum, Copenhagen.

Size of marginals

	length	height	width
superomarginals	1.4	1.5	2.1
	1.3	1.3	1.8
	1.2	1.4	2.1
inferomarginals	1.4	1.4	2.6
	1.3	1.5	2.7
	1.2	1.5	2.6

Diagnosis

The superomarginals are short, slightly wedge-shaped. The free surface has a prominent ridge separated from joining superomarginals and from the dorsal surface of the disc by a narrow, depressed rim. The height of the ridge is almost uniform, only slightly larger near the lower edge. The greatest height of the superomarginal is found at the dorsal end of the ridge. The surface of the ridge is curved but not tumid. The edges of the ridge are rather sharp. The surface is covered by spine pits. The surface against the dorsal cover of the disc forms a large, deep concave furrow along the dorsal edge. The surface against the body cavity is of similar size to the surface against the

disc, but is flat. These two surfaces meet in a sharp angle, where the superomarginals reach their greatest width.

The inferomarginals are subtriangular in profile with a prominent ridge on the free surface separated from joining inferomarginals by a depressed rim. The free surface forms a regular curve. The height of the ridge diminishes towards the ventral side. The edges of the ridge are rather sharp, the surface is curved, not tumid. The surface of the ridge is covered by uniform spine pits. The surface against the superomarginals and the surface against the body cavity and ventral cover of the disc are of equal size. They meet at an angle of about 130° . The surface against the ventral cover or adambulacral plates is not distinctly separated from the surface against the body cavity and is not concave or angulate.

Affinity

This species is similar to *L. punctatus* Nielsen, 1943. It differs through the more prominent ridge of the superomarginals, the sharp edges and never tumid surface of the ridge, the more angulate profile of the superomarginals against the disc and the smaller height of the inferomarginals.

Lophidiaster inversus n. sp.

Plate 3 figs. 18-19.

Derivation of name

Inversus (Latin) inverted, referring to the ornament of superomarginals and inferomarginals.

Type

The superomarginal pl. 3 fig. 18 is holotype. It is from the Upper Paleocene (Landenian) of Kroisbach north of Salzburg in Austria (locality Kch 2 of Traub 1938). The specimen is from the biozone with *Globigerina velascoensis*. Collection of the Geological Museum, Copenhagen (12781).

Material

In a sample from the type locality collected by Professor A. Rosenkrantz 1962, 31 superomarginals and 19 inferomarginals of this species have been found. Collection of the Geological Museum, Copenhagen.

Size of marginals

	length	height	width
superomarginals	1.3	1.2	1.6
	1.2	1.1	1.4
	1.1	1.0	1.5
inferomarginals	1.3	1.4	1.9
	1.3	1.3	1.7
	1.2	1.3	1.6

Diagnosis

The superomarginals are small, rather long with a low ridge or elevated area on the free surface limited by a narrow depressed rim along all the edges. Greatest height of superomarginals is at the dorsal end of the elevated area. The surface of the elevated area is curved but not tumid. It is provided with small, rather prominent, scattered granules. The edges of the elevated area are blunt. There are 3–4 small, slightly concave joint faces towards the dorsal cover of the disc and arm. The lower edge of these facets are not very prominent, and there is a blunt angle with the surface towards the body cavity.

The inferomarginals have a slightly more prominent ridge or elevated area than the superomarginals, at least near the edge against the superomarginals. The depressed rim is very narrow along the upper and lower edges. The elevated area forms a regular curve but is not tumid. The surface of the elevated area is covered by uniform spine pits. The surface against the superomarginals is flat or slightly concave. It forms an angle about 125° with a large surface against the disc. The surface against the disc is flat, often with two indistinct impressions presumably corresponding to the adambulacrals. There is apparently no surface against the body cavity.

Lophidiaster concavus n. sp.

Plate 3 figs. 20-25.

Type

The marginal figured plate 3 fig. 22 is holotype. It is from the Eocene (Ypresian) London Clay of Wraysbury Reservoir in Poyle, Buckinghamshire in England (division 3 of Wrigley 1924). The specimen was collected by Mr. Cooper and Mr. Rundle, and transferred to the collection of the British Museum (E 53632).

Material

In the Institute of Geological Sciences, London, are 8 small marginals (61657) collected by A. G. Davis in the London Clay (division 2) of The Minories in London. In the collection of the British Museum are several small marginals (E 13090–13095) from the London Clay of Hampstead Well, and a single marginal (E 49597) from the London Clay of Islington. There are 9 marginals from a sample of London Clay (division 2) collected by Davis at Aveley in Essex. In the collection of Rundle and Cooper are 14 marginals, 2 ambulacrals and 2 dorsal plates picked out of washed samples from the type locality, and at least 10 marginals and 10 terminals from Aveley. The specimens figured are transferred to the collection of the British Museum.

Diagnosis

A Lophidiaster (?) in which the superomarginals and inferomarginals are long with a narrow depressed margin and a low, narrow ridge with concave surface covered by irregular granules and 0-2 larger crater-shaped tubercles.

Description

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The marginals are small, high, rather long and narrow with a depressed marginal rim and a low ridge with strongly granulated, concave surface. The ridge is more restricted near the outer edge. The granules are large and protruding, some of them elongated in varying direction. There may be 1-2 protruding, crater-shaped tubercles where spines have been attached. The surface of the presumed superomarginals is somewhat curved. The presumed inferomarginals are thin and almost flat. The surface against the body is smooth and flat or may be divided in two faint impressions presumably meeting ossicles of the ventral side.

The terminal plates show a similar ornament of granules with rounded or elongate outline and in some specimens almost connected into a reticulate pattern. There are prominent facets for the attachment of three distal spines, one median and one on each side of the ventral furrow. The length of the plates and the proximal angle is rather variable.

The dorsal plates are stellate at their base, giving room for papulae. There may be 1 or 2 crater-shaped tubercles on the arched surface of the plates. The ambulacrals are rather stout.

Lophidiaster sp. aff. pygmaeus Spencer, 1913

Plate 3 figs. 26-27.

In a sample collected by Professor A. Rosenkrantz in the Upper Paleocene (Landenian) of Kroisbach north of Salzburg in Austria (locality Kch 2 of Traub 1938) are found 9 small marginals of a *Lophidiaster*. The marginals are from the biozone with *Globigerina velascoensis*. They are preserved in the collection of the Geological Museum, Copenhagen.

The marginals are small, higher than wide. Greatest length 1.5 mm, greatest width 1.6 mm, greatest height 1.8 mm. The free surface forms a smooth ridge, which is more narrow and prominent near the outer edge of the margin and becomes low and wide near the disc. Low plates with strongly arched surface may be superomarginals, higher plates with less arched surface and subtriangular profile are presumably inferomarginals. The surface against the body is smooth and flat or may be divided in two faint impressions presumably meeting ossicles of the ventral side.

The marginals are somewhat corroded, but seem to differ from the Upper Senonian *Lophidiaster pygmaeus* in a complete absence of granulation or spine pits. The form of the marginals and marginal ridge shows some resemblance to the Lower Eocene *Lophidiaster concavus*.

Hippasteria tuberculata (Forbes, 1852)

Plate 4 figs. 1-5.

1852 Goniaster tuberculatus.-Forbes p. 31 pl. 4 fig. 5.

Type

The specimen figured by Forbes (1852) is holotype. It is from the Lower Eocene (Ypresian) London Clay of Sheppey Island in Kent, England. The specimen is in the collection of the Institute of Geological Sciences, London (not identified).

Material

The presence of additional specimens was recorded by Forbes. Several specimens from the London Clay of Sheppey are in the collection of the British Museum (E 3818a, 33832, 34961, 35521, 36654, 52242, 53295) and the Institut of Geological Sciences (99787). All the specimens are preserved in pyrite and more or less worn on the surface. There is no specimen from any other locality.

Dimensions

No complete specimen is known. As far as can be seen by fitting the incomplete and disturbed specimens into a five rayed star, the internadius has reached 3–4 cm or more. The narrow part of the arm reaches a length of 3 cm and a width about 1 cm in preserved, incomplete fragments. The height of the margin in the internadial area is about 13 mm and decreases to about 7 mm before reaching the narrow arm. The large conical spine of the internadial superomarginals are about 2.2 mm long and 1.8 mm in diameter at the base.

	disc 99787	disc 53295	arm 33832 a	arm 52242	arm 33832b
superomarginal:					
height	7.0 - 3.5	6.5 - 3.5	3.0-2.5	3.0 - 2.7	2.2 - 1.6
width	ab. 4.0	4.5-4.0	3.5-3.0	3.5-3.0	2.0-1.4
length	4.5 - 5.0	3.0-3.3	4.6-3.1	4.5-4.1	3.5 - 2.6
inferomarginal:					
height	6.0 - 4.5	5.5 - 3.5	3.2 - 2.9	3.0 - 2.8	2.2 - 1.5
width	6.6 - 5.5	5.0-4.0	4.0-2.8	3.0 - 2.8	1.5-1.2
length	4.5 - 5.0	3.0 - 3.4	4.5-3.4	4.5-3.9	3.5 - 2.5
adambulacral:					
width	2.5		1.5	1.5	1.0-0.8
length	2.5	-	2.0 - 1.5	2.0	1.9-1.5

Description

A *Hippasteria* with rather large disc and long, very narrow arms. The dorsal surface of the disc is covered by polygonal plates forming a distinct radial row of rather large plates and a dorsolateral pavement of slightly smaller plates together with much smaller plates. The ventral surface of the disc is covered by polygonal plates forming oblique rows from the adambulacrals towards the marginals. The plates along the adambulacrals are rather large and elongate in the direction of the rows with parallel

Biol. Skr. Dan. Vid. Selsk. 19, no. 7.

sides and oblique cut ends. The long and narrow arms have almost parallel sides and a single row of radial dorsal plates with a row of small dorsolateral plates on each side. There are no ventral plates between marginals and adambulacrals in the arm. Small rudimentary spines are placed in spine pits on the surface of dorsal and ventral plates. There is a row of 5–6 spines on the edge of each adambulacral against the ambulacral furrow, and two rows of smaller spines on the ventral surface.

The margin is high and steep along the disc in the interradial area but rapidly diminishes towards the arm. It is formed by closely granulated superomarginals and inferomarginals. A stout conical spine is attached to each superomarginal and at least to some of the inferomarginals. The granulation of the marginals appears to be primary, but may be due to adhering rudimentary spines.

Affinity

The large disc, stout marginals, large marginal spines and differentiation of the dorsal plates are similar to the genus *Hippasteria*, although the arms are more narrow than in recent species of this genus. The only fossil *Hippasteria* described is *H. antiqua* Fell, 1956, from the Senonian of New Zealand, which seems to have broader arms and larger radial dorsal plates than the present species.

Teichaster retiformis Spencer, 1913

Plate 5 figs. 1-2.

1913 Teichaster favosus var. reliformis.—Spencer p. 122 pl. 12 figs. 17, 19.

1943 Teichaster retiformis Spencer.-Nielsen p. 55, pl. 3 figs. 18-19, textfig. 10.

1950 Teichaster retiformis Spencer.-Rasmussen p. 71 pl. 10 fig. 5, textfig. 6.

Material

From the Sonja Member of the Upper Danian Agatdal Formation in Agatdal, Nûgssuaq in West Greenland are 8 superomarginals, 5 inferomarginals and 3 marginal fragments. A single small inferomarginal is found in a sample of Danian limesand from Haidhof north of Vienna in Austria. The specimens are in the collection of the Geological Museum, Copenhagen.

Occurrence

This species is known only from the Upper Danian of Denmark, Sweden, Austria and West Greenland.

Teichaster lamberti Valette, 1925

Plate 5 figs. 3-6.

1925 Teichaster lamberti.—Valette p. 23 fig. 4. 1966 Teichaster lamberti Valette.—Rasmussen p. 11.

Type

The marginals figured by Valette (1925) are syntypes. They are all inferomarginals although some of them are interpreted by Valette as superomarginals. The inferomarginal fig. 4, 1 is here selected as lectotype.

All the marginals figured by Valette are from the Middle Eocene (Lower Lutetian) of Fontcouverte in Aude, France. They are in the collection of Lambert at the Sorbonne in Paris and in the collection of Valette in Dijon. The type has not been identified in the collections.

Material

This species has been known hitherto only from the type locality. There are several marginals in the collections at Paris and Dijon. In a sample of Upper Paleocene (Landenian) dark clay with glauconite and mica collected by Professor A. Rosenkrantz at Kroisbach north of Salzburg in Austria are found 33 superomarginals and 28 inferomarginals of this species. They are smaller than the largest specimens found in France. These marginals may well belong to a single individual. The sample is from the biozone of *Globigerina velascoensis* (locality 2 m east of Kch 1, Traub 1938). The marginals from Kroisbach are in the collection of the Geological Museum, Copenhagen.



Description

The marginals washed out of the sample from Austria are smaller than at least some of those from France. Most likely they belong to a single, rather small individual.

There is no other *Teichaster* or similar form in the sample, and it is therefore now possible to combine the inferomarginals with superomarginals not previously identified.

The superomarginals are a little higher than long in the margin along the disc, but lower in the more distal, smaller marginals along the arm. They are always very narrow. The joint face against the inferomarginals is extremely narrow, less than a third of the height of the marginal. The free surface is angulate, divided in an almost flat lateral and dorsolateral area. The lateral area is vertical or slightly outward-leaning and united in a short curve with a dorsolateral area of similar size or slightly smaller. The angle between the two areas is about $110^{\circ}-130^{\circ}$. The proximal and distal edges are straight and parallel. The edge against the dorsal surface of the disc is curved in the larger plates along the disc but straight in the smaller, more distal marginals along the dorsal margin. The facets against the dorsal cover of the disc form a deep furrow along the dorsal margin. The surface against the body cavity is flat or slightly concave and very steep, often almost vertical.

The inferomarginals are lower and wider than the superomarginals. The free surface is divided in a lateral and a ventral area meeting in a gentle curve. The lateral area is slightly concave and vertical or leans generally slightly outwards. The ventral area is slightly curved and tumid, more or less horizontal. The surface against the superomarginals is very narrow. The surface against the ventral covering plates is of similar size and often divided in 2–3 joint faces, which have met the covering plates or the adambulacrals. There is a distinctly concave surface against the body cavity even in the small distal inferomarginals.

The free surface of superomarginals and inferomarginals is covered with rather large and shallow, closely spaced, uniform spine pits.

Teichaster stokesii (Forbes, 1848)

Plate 5 figs. 7-10.

1848 Goniaster (Astrogonium) stokesii.—Forbes p. 475.

1848 Goniaster (Astrogonium) marginatus.—Forbes p. 475.

1849 Goniaster stokesii Forbes.-Forbes decade I pl. 3 p. 1 fig. 1.

1849 Goniaster marginatus Forbes.—Forbes decade I pl. 3 p. 2 fig. 2.

1852 Goniaster stokesii Forbes.-Forbes p. 30 pl. 4 fig. 6.

1852 Goniaster marginatus Forbes.—Forbes p. 31 pl. 4 fig. 4.

1928 Goniaster stokesii Forbes.-Davis p. 349.

1928 Goniaster marginatus Forbes.—Davis p. 349.

1936 Astropecten stokesii (Forbes).-Davis p. 340.

1940 Goniaster stokesi Forbes.-Wrigley p. 235.

1963 Goniaster sp. cfr. stokesi Forbes.---Venables p. 263.

Type

The specimens described by Forbes 1848, and redescribed and figured 1849 are syntypes. The specimen shown from the dorsal side pl. 3 fig. 1 d is here selected as lectotype. The specimens were collected by Mr. Stokes in the Lower Eocene (Ypresian)

London Clay of the Isle of Sheppey (Kent) in England. The lectotype is in the collection of the Institute of Geological Sciences, London (49170). The holotype of *Goniaster* marginatus is the specimen figured by Forbes. It is from the same locality. The specimen is in the Institute of Geological Sciences (49165) but is completely decomposed.

Material

Several specimens are recorded by Forbes from the London Clay of the Isle of Sheppey, England. Further specimens are recorded by Davis (1928) from the London Clay (division 2–3) of South London and (1936) of Sheppey, and by Wrigley (1940) from Stockwell. *Goniaster* sp. cf. *stokesi* is recorded by Venables (1963) from the Middle Clay (Beetle Bed and Upper Fish Tooth Bed) of Bognor Regis.

In the collection of the British Museum are 20 specimens (E 3811, 4332a-b, 24625, 28404, 33844, 34486, 38488, 38489a-c, 38587, 38681, 52239 = 1852 fig. 6a, 52240, 52241, 52350, 75842, 75910), and in the Institute of Geological Sciences are 3 specimens (49169 = 1849 fig. 1 a, 49170 = 1849 fig. 1 d, 49171 = 1849 fig. 1 c). All the specimens are from the Isle of Sheppev, and are preserved in pyrite.

In the collection of Mr. Rundle are at least 10 marginals from the London Clay (division 2) of Avely in Essex, England.

In the collection of Copenhagen are 2 specimens (12791, 12792) preserved in pyrite. They were found on the coast north of Fredericia in Denmark, washed out of the Lower Eocene Rösnäs Formation. The Danish specimens show the margin along the disc and a part of the ventral side with covering plates and adambulacrals. A few paxillae from the dorsal side are preserved.

Dimensions

Forbes (1849) indicated a radius from the center of the disc, to the tip of an arm greater than 11 cm and an interradius about 5 cm. A single specimen (E 75910) showing the ventral side is about this size, but the determination of the species is not certain. A reconstruction based on other preserved specimens fit a five-rayed star with a radius about 8 cm and an interradius about 3 cm. There have been 4–5 superomarginals and inferomarginals from the interradius to the base of the arm succeeded by 10–13 superomarginals and inferomarginals in each side of the narrow arm. The length of the marginals along the disc is 3–4 mm. Width of margin along the disc 4–6 mm. Height of margin 6–11 mm.

Description

A rather large *Teichaster* with flat, pentalobate disc and long, narrow arms. The disc is bordered by at least 8 superomarginals and 8 inferomarginals in each side forming a regular curve. The margin is of moderate hight and not very steep. The marginals along the disc are slightly wedge-shaped, almost rectangular with rounded edge against the dorsal and ventral covering plates. The height of the marginals is almost uniform along the disc and arms. The surface is curved and may be slightly

tumid, especially in the superomarginals. It is covered by closely placed, uniform spine pits for rudimentary spines, often preserved on the inferomarginals and giving the surface a granulated appearance. From the base of the arm, the superomarginals meet on the dorsal side, and the inferomarginals are separated only by the adambulacral and ambulacral plates. The inferomarginals are narrower than the superomarginals. The arms are almost parallel-sided and the marginals diminish only slightly up to the obtuse point of the arm, where two smaller superomarginals meet a small, semicircular terminal plate. There are about 10–13 superomarginals and inferomarginals in each side of the narrow arm. The distal superomarginals in the arm are often rather high and the tip of the arm may be recurved. The dorsal surface of the disc is covered by stout, pentagonal, uniform paxillae, the ventral side by flat, polygonal, uniform plates with spine pits. The adambulacrals are almost rectangular with a ridge towards the ambulacral furrow near the proximal end. There is a row of 5–7 small spines on the edge of each adambulacral and two rows of smaller spines on the ventral surface.

"Goniaster marginatus"

The type and only specimen referred by Forbes to *Goniaster marginatus* is a specimen from the London Clay of Sheppey, where *T. stokesii* is common. It consists of 5 superomarginals and 5 inferomarginals preserved in pyrite together with parts of the disc. A row of small plates in the other side of the specimen is the adambulacrals. The marginals preserved are nr. 1-4 from the interradius. The surface is covered by closely placed spine pits.

The specimen is now completely decomposed, but according to the figure it differs from *T. stokesii* only in the elevated rim along the edge of some marginals. This was taken by Forbes as a distinctive character of the species, but is obviously a result of the preservation. The central area of these marginals is depressed and partly exfoliated, leaving the protruding rim along some of the edges. The exfoliation along previous surfaces covered during growth is not uncommon in fossil asteroids and does not change the surface ornament. A similar preservation is seen in 4 of the superomarginals in one of the Danish specimens.

Affinity

The present species may be confused with *Hippasteria tuberculata* from the same locality, but seems to differ in the closely placed spine pits of the marginals. It is, however, very difficult to distinguish a granulation from rudimentary spines preserved in their spine pits on the pyrite fossils. *T. stokesii* further differs in the less steep margin, the absence of large marginal spines and the superomarginals meeting on the dorsal side of the arm.

Ceramaster obtusus n. sp.

Plate 5 figs. 11-13.

Derivation of name

Obtusus (Latin) blunted.

Type

The terminal inferomarginal pl. 5 fig. 12 is holotype. It is from the Sonja Member of sandstone from the Upper Danian Agatdal Formation in Agatdal, Nûgssuaq in West Greenland. The specimen is in the collection of the Geological Museum, Copenhagen (12794).

Material

From the type locality are 23 marginals including a terminal superomarginal and inferomarginal, and from Marrait kitdlît are a terminal superomarginal and inferomarginal and a median marginal found in calcareous and volcanic tuff from the Agatdal Formation. The preservation of the specimens is rather poor, and most of the marginals are exfoliated along growth surfaces, which however does not destroy the form or ornament.

Dimensions	terminal supero- marginal	terminal infero- marginal	I	median supero- narginal	S
length (along margin) width (perpendicular	2.4	3.4	2.8	2.8	4.4
to margin)	2.4	2.9	3.0	4.0	5.6
height	2.5	2.8	3.1	2.9	4.5

The width of the terminal superomarginal shows, that it belongs to a smaller individual than the terminal inferomarginal.

Diagnosis

A *Ceramaster* with equal number of superomarginals and inferomarginals. The marginals have scattered spine pits on the free surface and a depressed border with closely placed, small and shallow spine pits where small, rudimentary spines have been attached. The median superomarginals are evenly arched and a little tumid. The terminal superomarginal is rather large and compact, subtriangular with a rounded free surface indicating an obtuse arm-point. The terminal superomarginal meets the corresponding plate in its entire height along the midline of the arm, leaving no surface against the body cavity. The length of the plate is a little greater than its height and width. The inferior surface of the terminal superomarginal is a single joint face for the inferomarginal. The inferomarginals are less arched and not tumid. The terminal inferomarginal is almost identical in form and size with the terminal superomarginal but less tumid, and it shows faint impressions of adambulacral plates on the otherwise plane surface against the ambulacral system.

Ceramaster rabii (Linstow, 1912)

1912 Goniaster (Goniodiscus) rabii.—Linstow p. 47 pl. 2 figs. 1–4. 1929 Goniodiscus rabii Linstow.—Hucke & Voigt p. 160.

Type

The specimen described and figured by Linstow (1912) pl. 2 figs. 1–3 is here selected as lectotype. It is from the Middle Oligocene (Rupelian) Septarienton of Freienwalde near Mark (Westfalen) in Germany. According to Linstow the specimen is in the collection of Preussische geologische Landesanstalt, Berlin.

Material

The type specimen consists of 4 superomarginals and 4 inferomarginals in natural position corresponding to two incomplete sides of the disc. Another specimen with 3 superomarginals and 3 inferomarginals is described by Linstow from the same locality. Both specimens are preserved in pyrite. The species has further been recorded by Hucke & Voigt (1929) from the Middle Oligocene of Steutz (Anhalt) in Germany.

Dimensions

Length of marginals from 3.5 mm along the margin to 4 mm along the disc. Width of margin 7 mm. Height of marginals estimated about 3.5-4 mm.

Description

The marginals are slightly wedge-shaped, almost rectangular. Superomarginals are placed immediately above inferomarginals. The angle between the two margins of the disc partly preserved in the type indicates that the outline has been slightly stellate, almost pentagonal, and the marginals preserved in the specimen are presumably nr. 1-2 or 2-3 from the interradius. The tip of the arm is not preserved, but the almost uniform marginals indicate a structure as in *Ceramaster* with equal number of superomarginals and inferomarginals. This is also supported by the resemblance to C. brandenensis. It may be expected, that if the species was a Metopaster, the large and robust ultimate superomarginal would be preserved. The length of the marginals is considerably smaller than their width. This is seen from the dimensions and from fig. 3 in Linstow, but not from figs. 1-2 of the same specimen. The contact between superomarginals and inferomarginals in fig. 1 shows that figs. 1 and 2 are not perpendicular to the disc. The joint faces between marginals are smooth and flat. The free surface is arched but apparently not tumid. The surface is covered with large, scattered spine pits and a rather narrow, slightly irregular margin of considerably smaller, closely placed spine pits.

The species differs from *C. brandenensis* in the shorter marginals, the larger spine pits on the central area, the more restricted marginal ornament and the similar ornamentation of the inferomarginals. It differs from *Teichaster stokesii* in the smaller size, pentagonal form, the few and uniform marginals and the larger spine pits.

Ceramaster brandenensis Rasmussen, 1951

1951 Ceramaster brandenensis.—Rasmussen p. 588 fig. 1.

This species has previously been described and figured. It is found in the Middle Oligocene (Rupelian) Branden Clay at Branden and Faarup in Denmark. It differs from other species of *Ceramaster* in the almost squarish median superomarginals, the restricted median ornament of scattered spine pits on the median superomarginals and the absence of a similar ornament on the inferomarginals. There is no new information. The type is in the collection of the Geological Museum, Copenhagen (7639).

Echinaster jacobseni n. sp.

Plate 5 fig. 14, plate 12 fig. 7.

Derivation of name

The species is named in honour of the collector of the type specimen, the Danish writer and botanist J. P. Jacobsen (1847–1885). J. P. Jacobsen is also known as the naturalist who translated the works of Darwin and introduced the theory of evolution to the layman in Denmark.

Type

The specimen figured is holotype. It is from the Lower Eocene (Ypresian) Mo-Clay Formation of diatomaceous clay with volcanic ash layers at Silstrup Cliff near Tisted in Denmark. The specimen is in the collection of the Geological Museum, Copenhagen (12769).

Material

The type specimen is an impression of the ventral side showing a part of the small disc and proximal parts of 3 arms. In the local museum of Fur in Denmark is the impression of the dorsal and ventral side of an asteroid together with some specimens of *Ophiura furiae* from the diatomaceous clay of Fur. The asteroid shows the undisturbed ambulacrals, adambulacrals and adambulacral spines but no covering plates from the disc. There is no indication of marginals, and the asteroid presumably belongs to the present species. In the Geological Museum of Copenhagen are 5 rather poorly preserved asteroids in a calcareous layer (cement-stone) from the Mo-Clay of Skærbæk Cliff on Mors. They show the outline and some of the ambulacrals, but no indication of marginals, and may well belong to the present species.

Dimensions

The length of the arms is unknown in the holotype. They are preserved in a length of 15 mm from the mouth frame without distinctly tapering. Width of the ambulacral furrow is 3.5 mm. The specimen from Fur has arms 11 mm long and tapering through the distal half. The width of the ambulacral furrow is 3 mm. The specimens from Skærbæk Cliff are of similar size.

Diagnosis

An *Echinaster* with rather large, triangular mouth-angle plates with 3 spines along the radial edge, not terminal. Adambulacrals with a transverse row of 2–3 ventral spines and apparently a spine into the furrow. Ventral covering plates rather irregular and with 1 or 2 spines attached to nodules or tubercles on most of the plates. No ventral papulae.

Description

The ambulacrals on each side of the ambulacral furrow are uniform and evenly spaced, not two and two forming symmetrical pairs as in *Asterias*. The adambulacrals are slightly oblique, almost cube-formed with an arched surface and no sharp angle between ventral and adradial area. The proximal and distal edges are sharp and somewhat protruding. The arched median area is provided with 2 tubercles for large spines. A smaller tubercle may be indicated on the adradial side. Spines connected with the large tubercles are slender and reach a length of 1 mm.

The mouth-angle plates are rather large and meet in a sharp edge along the interradius. Their surface is evenly arched and apparently smooth. They are not obtuse, but form a point into the mouth. In 3 of the plates is seen a row of 3 spines decreasing in size towards the mouth, and apparently attached along the rounded edge between ventral and adradial area.

Outside the adambulacral plates there seems to be a row of smaller rounded plates more or less imbricate or raised on edge. In the internadial area between the arm bases are further seen a pavement of rather flat plates with more or less elliptical to rounded subtriangular outline, and some of them with one or two nodules or tubercles where spines have been attached. There is no space for papulae between the plates on the ventral side. The dorsal side is unknown.

Determination of the genus

The Echinasteridae have not previously been recorded as fossil except for a single specimen possibly belonging to *Henricia* according to Durham & Roberts (1948) and the Neocomian *Rhopia prisca* Loriol, 1873, which is now type of the genus *Proto-thyraster* Hess, 1970.

The absence of marginals shows that the species belongs to the group "Cryptozonia". The form of the ambulacrals shows that there have been two rows of podia in the ambulacral furrow opposite Asteriidae, who have four rows of podia and the ambulacrals in each side of the furrow forming symmetrical pairs. The absence of papulae on the ventral side of the disc excludes *Henricia*. The form of mouth-angle plates, the single transverse row of spines on the adambulacrals and the form of ventral plates in the interradial area correspond to the recent genus *Echinaster*. The great similarity was confirmed by a study of the recent *Echinaster sepositus* Retzius after removal of the organic tissue.

Ophiuroidea

Amphiura? senonensis Valette, 1915

Plate 6 fig. 1.

1915 Amphiura senonensis.-Valette p. 16 fig. 6.

1950 Amphiura? senonensis Valette.-Rasmussen p. 118 pl. 15 figs. 6-10.

1951 Amphiura? senonensis Valette.-Rasmussen p. 50 fig. 4.

Previous records

This species has previously been recorded from the Upper Senonian of France, England, Spain, Germany and Denmark, from the Danian of Denmark and South Sweden, and from the Upper Paleocene Vincentown Limesand of New Jersey, U.S.A.

Material

A single but well preserved lateral arm plate of this very characteristic species is found in the Upper Paleocene (Landenian) glauconitic marl of Kroisbach north of Salzburg in Austria. The sample belongs to the biozone with *Globigerina velascoensis* as does the Vincentown Limesand. The specimen is in the collection of the Geological Museum, Copenhagen (12797).

Remark

As mentioned by Rasmussen (1950 p. 119) this species should hardly be referred to *Amphiura*.

Ophiomusium danicum Nielsen, 1926

1926 Ophiomusium danicum.—Nielsen p. 11 figs. 2-4.

1950 Ophiomusium danicum Nielsen.—Rasmussen p. 102 pl. 12 figs. 1-6.

1951 Ophiomusium danicum Nielsen.-Rasmussen p. 56.

1969 Ophiomusium danicum Nielsen.-Maryanska & Popiel-Barczyk p. 135 pl. 2 fig. 2.

Previous records

This species has been recorded by Rasmussen (1950, 1951) from the Upper Danian of Denmark and South Sweden, and by Maryanska & Popiel-Barczyk (1969) from the uppermost Maastrichtian or the Danian of Nasilow near Pulawy in Poland.

Material

5 lateral arm plates of this species were found in the residue after washing a small sample of Danian limesand from Haidhof north of Vienna in Austria. The specimens are in the collection of the Geological Museum, Copenhagen.

Affinity

The species is very similar to *Ophiomusium stephensoni* Berry, 1942, from the Upper Paleocene (Landenian) Vincentown Limesand of New Jersey, U.S.A.

Ophiomusium subcylindricum (Hagenow, 1840)

1840 Ophiura (Aspidura) subcylindrica.—Hagenow p. 661 pl. 9 fig. 7.

1950 Ophiomusium subcylindricum (Hagenow).-Rasmussen p. 108 pl. 14 figs. 4-6.

1951 Ophiomusium subcylindricum (Hagenow).-Rasmussen p. 50.

1965 Ophiomusium subcylindricum (Hagenow).-Rasmussen p. 37.

1969 Ophiomusium subcylindricum (Hagenow).—Maryanska & Popiel-Barczyk p. 135 pl. 2 fig. 3.

Previous records

This species has been recorded by Rasmussen (1950, 1951, 1965) from the Maastrichtian of Denmark, Germany and Limbourg (Netherland-Belgium). It has further been recorded by Maryanska & Popiel-Barczyk (1969) from Upper Maastrichtian and presumed Danian deposits at Nasilow near Pulawy in Poland.

Ophiacantha? danica Rasmussen, 1951

Plate 6 fig. 2.

1950 Ophiacantha? sp.—Rasmussen p. 120 pl. 18 fig. 10. 1951 Ophicantha? danica.—Rasmussen p. 52 fig. 6.

Previous records

This species has been recorded from the Maastrichtian of Denmark and Germany and from the Danian of Denmark and Sweden.

Material

2 lateral arm plates of this species were found in the residue of a small washed sample of the Danian limesand from Haidhof north of Vienna in Austria. The specimens are in the collection of the Geological Museum, Copenhagen (12798).

Ophiura serrata Roemer, 1840

1840 Ophiura serrata.—Roemer p. 28 pl. 6 fig. 23.

1907 Ophiura serrata Roemer.—Spencer p. 102 pl. 27 fig. 3.

1907 Ophiura parvisentis.—Spencer p. 103, 134 pl. 27 fig. 4.

1915 Ophioglypha parvisentis (Spencer).—Valette p. 7 fig. 2.

1950 Ophiura serrata Roemer.—Rasmussen p. 111 pl. 16 figs. 1-8.

1951 Ophiura serrata Roemer.—Rasmussen p. 50, 56.

Previous records

This species has been recorded from the Cenomanian—Lower Senonian of England, the Senonian of France, Spain, Germany and Denmark, from the Danian of Denmark and Sweden, and possibly from the Upper Paleocene (Landenian) Vincentown Limesand of New Jersey, U.S.A.

Material

A lateral arm plate from the Danian limesand of Haidhof north of Vienna in Austria is referred to this species. Collection of the Geological Museum, Copenhagen.

Ophiura? hagenowi Rasmussen, 1950

1950 Ophiura? hagenowi.—Rasmussen p. 114 pl. 17 figs. 1–5.
1951 Ophiura? hagenowi Rasmussen.—Rasmussen p. 51.
1969 Ophiura? hagenowi Rasmussen.—Maryanska & Popiel-Barczyk p. 133.

Previous records

This species has been recorded by Rasmussen (1950, 1951) from the Upper Senonian of England, Germany, Spain and Denmark, and from the Lower Danian of Denmark. It has further been recorded by Maryanska & Popiel-Barczyk (1969) from the Upper Maastrichtian and from presumed Danian samples at Nasilow near Pulawy in Poland.

Ophiura achatae n. sp.

Plate 6 fig. 3.

Derivation of name

Achates (Latin) agate. The species is named after the type locality Agatdal (Agate-valley).

Type

The fragment of an arm figured is holotype and the only specimen known. It is from the Sonja Member of sandstone belonging to the Upper Danian Agatdal Formation in Agatdal, Nûgssuaq in West Greenland. The specimen is in the collection of the Geological Museum, Copenhagen (12799).

Dimensions

The arm fragment consists of 6 joints. Length of the fragment is 3.6 mm. Width tapering from 1.8 to 1.6 mm, height from 1.7 to 1.5 mm, width of dorsal arm plates from 1.4 to 1.2 mm and width of ventral arm plates from 1.2 to 0.8 mm. Length of uppermost lateral spine 0.7 mm.

Diagnosis

An ophiuroid in which the arm is about as high as wide with flattened ventral side and steep lateral sides. Dorsal side evenly arched without ridge. Lateral arm plates thick, short and high with a spine attached near the upper edge, a second below the middle of the frontal edge and a third just above the podial pore. There are no prominent tubercles or pits for the articulation of the spines. The spines are adpressed, the upper one long. Dorsal arm plates imbricate. They are short, wide, evenly arched with regular frontal edge. The ventral arm plates are just in contact along the median line. They are short and wide with a bilobed frontal edge. The surface of the lateral arm plates has an ornament of delicate vertical ridges and furrows. Other plates are smooth. Vertebrae zygospondylous.

Description

The distinctly tapering width of the arm and of the dorsal and ventral arm plates shows that the fragment belongs to the proximal part of an arm. The height of the arm is almost equal to the width. In section the arm is almost subquadrate with flattened ventral side, steep, slightly arched lateral sides and evenly arched dorsal side without median ridge. The joint are short.

The lateral arm plates are thick, high and short with a thick and rounded frontal edge. The surface is covered with delicate ridges and furrows forming a vertical pattern.

At the frontal margin of the lateral arm plate, near the rounded upper end, is a slight elevation to which a long spine is attached. A second, slightly smaller spine is attached to an elevation well below the middle of the frontal edge, and apparently a third has been attached immediately above the podial pore. There are a few papillae on the edge of the podial pore.

The dorsal arm plates are short and wide, evenly arched and with a regular curved frontal edge. There is a short, depressed posterior rim covered by the preceeding plate. The surface is smooth.

The ventral arm plates are rather large, wide and five-sided. They just touch each other along the mid-line of the arm between the lateral arm plates. The frontal margin is slightly bilobate. The surface is smooth.

The vertebral ossicles are large. The proximal end shows a pair of large articular faces for the upper pair of muscles. They form together a little more than half a circle with a shallow embayment for the dorsal furrow. The marginal furrow is distinct and rather deep. There is a zygospondylous articulation.

Affinity

The present species has some resemblance to *Stegophiura eocaenus* (Leriche, 1931), but differs by the short joints and plates of the arm and by the form of the dorsal arm plates. It is distinctly different from other Cretaceous and Tertiary species described.

Ophiura furiae n. sp.

Plate 6 figs. 4-5, plate 13 fig. 1.

Derivation of name

The species is named after the island of Fur in Denmark.

Type

The individual showing the ventral surface in the specimen figured plate 13 fig. 1 (lower part) and plate 6 fig. 4 is holotype. It is from the Lower Eocene (Ypresian) Mo-Clay Formation of diatomaceous clay with tuffit and is preserved in the weathered surface of a calcareous concretion (cement stone) collected by the late schoolmaster

J. P. Andersen in 1948 among removed material from the lower part of the formation in the clay-pit of Fur Molercompany on the Island of Fur in Denmark. The specimen is in the collection of the Geological Museum, Copenhagen (12800).

Material

Together with the holotype in the same concretion are three other individuals, two showing the ventral side and one the dorsal side. The specimen further contains numerous tiny shells of the gastropod *Spiratella mercinensis*.

Several specimens in the collection of the Geological Museum of Copenhagen are found as impressions in the diatomaceous clay from Fur, Mors and Thy in Denmark, but their ossicles are dissolved and very few details are seen. In the local Museum of Fur are a few individuals in a concretion and several specimens as impressions in the diatomaceous clay from Fur. In the collection of Mr. Groes are specimens from cementstone in the diatomaceous clay of Ejerslev.

Dimensions

The diameter of the disc varies from 5 to 8 mm. The preserved parts of the free arms reach a length of 25 mm. The width of the arm basis is in the holotype 1.3 mm.

Diagnosis

An Ophiura with pentagonal disc and large, subtriangular radial shields, apparently separated in the proximal part by a single row of plates. A dorsal arm plate is seen in the small radial embayment of the disc. The oral shields are large, five-sided, the adoral plates are straight. The arms are slender, subtriangular in section, higher than wide. The dorsal arm plates are narrow. They are in contact through about seven proximal arm joints. The ventral arm plates are small, five-sided and separated. The lateral arm plates are thin, adpressed and smooth with short, adpressed spines on the distal edge.

Description

The disc is pentagonal with straight or slightly concave sides. Sutures in the dorsal side of the disc are indistinct in most specimens. The radial shields are rather large and subtriangular, slightly more than half the radius of the disc. Near the margin they meet in the radius, more proximally they seem to be separated by a single row of plates. The rest of the dorsal surface shows no larger plates, but small scales are seen in some of the specimens. In an impression of the dorsal side in the diatomaceous clay the large radial shields are seen, and the rest of the dorsal surface is sunken down, so that only the area of the jaws stands up covered by small scales. There is a small embayment over the arms between the radial shields where a dorsal arm plate is seen.

The ventral side of the disc shows large five-sided oral shields with a convex outer edge evenly connected with concave lateral sides. The adoral plates are straight with no distal curve along the radius. The oral plates are slightly curved and protruding where they meet the jaw plate (torus angularis). There is a single row of teeth and apparently a row of oral papillae along the moth frame. Outside the oral shields the disc is covered by small uniform scales. On each side of the arm is a narrow genital plate. The oral second ventral arm plate at the edge of the mouth is triangular. The five succeeding arm joints are included in the disc and have five-sided, almost rectangular ventral arm plates of similar size or slightly more narrow. The length of these ventral arm plates in the disc is about half the width. Their distal edge is almost straight. They are small and separated by the lateral arm plates. The first tentacle pore seen on the ventral surface of the disc is placed between the first ventral arm plate and the jaw, proximal to the first lateral arm plate and corresponds to the second podia.

The free arms reach a length of twice the diameter of the disc or more. They are subtriangular in section with a rounded dorsal ridge and a flattened ventral side. The dorsal plates in the proximal two free arm joints are slightly wider than long. In the succeeding joints they are narrow and wedge-shaped with strongly curved distal edge. They are in contact with each other in the proximal part of the arm for about 7 joints but separated in the distal part of the arm. The ventral arm plates are small, five-sided with almost straight distal edge. They are completely separated. The lateral arm plates are subcylindrical, thin and adpressed or with slightly protruding distal edge in the proximal part of the arm. The surface is smooth without any ridges or furrows. The distal margin is provided with a row of adpressed spines in a number of three or possibly more. The spines vary in length from one third to two thirds the length of the lateral arm plate.

Affinity

The present species differs from *O. wetherelli* in the smooth lateral arm plates, the five-sided ventral arm plates and the greater number of arm joints included in the disc.

It differs from *O. bognoriensis* in the smaller radial embayment of the disc, the more slender arms and arm joints and the more narrow dorsal arm plates. From *O. bartonensis* it differs in the section of the arms and the smaller dorsal arm plates, and from *Stegophiura eocaenus* in the small dorsal and ventral arm plates.

Ophiura wetherelli Forbes, 1852

Plate 7 figs. 1-5, plate 13 figs. 2-3.

- 1834 Ophiura sp.—Wetherell p. 417.
- 1852 Ophiura wetherelli.—Forbes p. 32 pl. 4 fig. 7.
- 1866 Ophiura wetherelli Forbes.—Busk pl. 12 fig. 4.
- 1923 Ophioglypha wetherelli (Forbes).--Davis p. 113 pl. 3.
- 1928 Ophioglypha sp.—Davis p. 349.
- 1970 Ophioglypha wetherelli (Forbes).--Rundle & Cooper pp. 114, 116, 118, 120.

Type

The specimens figured by Forbes (1852) are syntypes. They are from the Lower Eocene (Ypresian) London Clay of Highgate, London, referred by Wrigley (1924)

to division 5 of the London Clay. The specimens 99786 in the Institute of Geological Sciences and E 2680 in the British Museum are indicated on the labels as types of the figures. The specimen 99786 corresponds to fig. 7b and is here selected as lecto-type. The specimen E 2670 is also figured by Sowerby in Busk (1866).

Material

This species seems to occur from the Oldhaven Beds and Basement Beds below the London Clay at Herne Bay and Lower Upnor near Friendsburg Extra in Kent and Northwood in Middlesex through the London Clay division 2 at Copenhagen Fields, Clapham and Brixton (Victoria Line shaft) in London, division 4 at New Malden in Surrey and division 5 at Oxshott and Talworth in Surrey and at Finchley and Highgate in London. At Bognor Regis the species is found in the Middle Clay (Aldwick Beds). The species is recorded by Forbes (1852) from Hampstead and Highgate in London and Highcliff at Barton, by Davis (1923) from New Malden, Finchley and Copenhagen Fields in London and from the Isle of Sheppey, by Rundle & Cooper (1970) from Bessborough Gardens, Brentford, Brixton and Imperial College in London.

In the Institute of Geological Sciences, London are specimens from Northwood (51231), Talworth (61662, 62106) and Highgate (99786). In the collection of the British Museum are specimens from Herne Bay (E 52343–4, 52358–9), Lower Upnor (E 53229–31, 53233–43), Copenhagen Fields (E 429), New Malden (E 13702), Oxshott (E 52154, 52161–3), Talworth (E 13755, 20639–41, 52155–6, 52167, 52216, 53215–9), Finchley (E 54552), Highgate (E 2650–1, 2670, 13679, 50227) and Bognor Regis (E 20636). In the collection of Mr. Rundle are isolated arm fragments from Brixton (Victoria Line shaft).

The specimens previously recorded from the Isle of Sheppey by Davis (1923, 1936) are covered by pyrite and indeterminable (E 28697). Specimens from the Lower Clay of Bognor Regis referred by Venables (1963) to Ophiura (Ophioglypha) aff. wetherelli are here referred to Ophiura forbesi n.sp. The specimens (E 13702) previously figured by Davis (1923) show the dorsal side of two individuals and the ventral side of three individuals, but the plates of the disc are not distinct. Only the rather small specimens preserved as impressions in clay from Lower Upnor show details of the dorsal surface of the disc. Although in a different preservation and from a deeper level of the clay series than the type, they are referred to the present description is based mainly on these specimens.

Dimensions

Diameter of disc 3.5–9 mm. Length of arms more than twice the diameter of the disc. Width of arm near the disc 1.0–1.5 mm.

Description

The disc is flat, pentagonal in outline. The radial shields are subtriangular, about half the radius of the disc, and separated by two smaller plates along the radius suc-

Biol. Skr. Dan. Vid. Selsk. 19, no. 7.

ceeded by two dorsal arm-plates in the radial embayment limited by the radial shields and genital plates. Between the proximal end of the radial shields are two adradial plates or, in some specimens, possibly a single plate. The interradial areas seen in the specimens from Friendsburg Extra are covered by two interradial plates separated by an interradial pair of plates. Smaller plates may be seen along the radial shields. The central area of the disc is covered by a central plate and alternating circles of interradial plates. There is a thin marginal interradial plate at the edge of the disc of similar size as the dorsal scales or smaller.

The ventral surface of the disc is seen in E 13702. There is in each interradius a rather large, five-sided oral shield with a convex outer edge and concave sides. The adoral plates are straight. There is a single row of teeth on torus angularis. Outside the oral shields are smaller scales, a large interradial marginal plate and along each arm a genital plate. The oral second ventral arm plate at the edge of the mouth is rather large, triangular. The three succeeding arm joints are also included in the disc and have five-sided ventral plates of decreasing size. They are separated by the lateral arm plates. The first tentacle pore visible on the ventral surface is placed between the oral plate and the ventral arm plate proximal to the first lateral arm plate, thus corresponding to the second podium.

The free arms outside the disc are slender and reach a length of at least 2.5 times the diameter of the disc. They are subtriangular to semicircular in section, slightly wider than high, with a flat ventral side. The arm plates are thin. The dorsal arm plates are fairly long and narrow with a slightly trilobate distal edge. In the proximal part of the arm they are in contact with each other, but from about number ten of the free joints they are separated. The ventral arm plates are small, triangular or five-sided, short and wide, and completely separated. The lateral arm plates are thin, ad-pressed, and have a distinct ornament of delicate, slightly irregular vertical ridges and furrows. Close behind the distal edge and above the podial pore are three closely placed, small, adpressed spines, a little shorter than the lateral plates. On the inner side of the lateral arm plate is an oblique ridge from the proximal part of the dorsal edge to the distal part of the ventral edge. The vertebral ossicles are similar to other species of *Ophiura*.

Affinity

O. wetherelli differs from O. bognoriensis in the ornament of the lateral arm plates and the arrangement of their spines, and in the more narrow dorsal arm plates.

Ophiura bognoriensis n. sp.

Plate 8 figs. 1–10, plate 14 fig. 1.

1959 Ophiura wetherelli Forbes.—British Caenozoic Fossils pl. 4 fig. 7. 1963 Ophiura (Ophioglypha) aff. wetherelli Forbes.—Venables p. 248, 264.

Derivation of name

The species is named after the type locality Bognor Regis in Sussex, England.

Type

The specimen figured 1959 in a publication from the British Museum under the title of British Caenozoic Fossils and refigured in the present publication is holotype. It is from the Lower Eocene (Ypresian), Starfish Bed (Lower Clay), London Clay of Bognor Regis in Sussex, England. The specimen is in the collection of the British Museum (E 13761).

Material

This is the only species of Ophiuroidea identified from the Astarte Bed and Starfish Bed (Lower Clay) of Bognor Regis. The holotype is unusually well preserved, but only the arms and the dorsal side of the disc are seen. In the same collection are the remains of three specimens (E 13764–6), an arm (E 13718) and a few isolated arm plates (E 13767–76, 52168) all from the Starfish Bed of Bognor Regis. In the collections of Mr. Rundle, London, and Mr. Gale, Canterbury, are several fragments from the Astarte Bed and Starfish Bed of Bognor Regis.

Dimensions

Diameter of disc 12 mm. Length of arm more than 20 mm. Proximal part of arm about 3.5 mm high and wide. Length of proximal arm joints about 0.8 mm. Width of proximal dorsal arm plate 2.2 mm. Vertebra from proximal part of arm about 1.9 mm high, 1.8 mm wide and 0.7 mm long.

Diagnosis

An Ophiura with flat, subpentagonal disc. Radial shields large, subtriangular, about two thirds of the radius of the disc. The proximal part of the radial shields are separated by a single row of three plates increasing in size towards the center of the disc. On each side of the arm base is seen a genital plate. The embayment over the arm shows four dorsal arm plates, two larger between the genital plates and two smaller between the radial shields. Along the genital plates is an arm-comb with distinct papillae, which do not meet over the arm. The central part of the disc and the narrow interradial areas are covered by smaller scales. There is no large marginal interradial plate. A large, shield-shaped oral shield is found together with other remains in the Starfish Bed.

The arms are subtriangular in section with almost equal height and width. The arm plates are smooth. The dorsal arm plates are very wide in the proximal part of the arm, the exposed part of the imbricating plates about four times as wide as long. The distal margin is regularly curved, not lobate. The dorsal arm plates are in contact with each other in all preserved parts of the arms, including more than 20 joints. The most distal arm plates preserved are about as long as wide. The ventral arm plates are seen in the proximal part of one of the arms and in the distal part of another. They are short, five-sided and completely separated. The thick and stout lateral arm plates are high and short, adpressed and imbricating with a depressed proximal border. There is a very prominent ridge on the inner side of the lateral arm plates. The distal

edge shows three small indentations for three spines, the lower one of which is very small. The upper spine is distinctly separated from the two lower. The spines are adpressed, and the two larger reach a maximal length of two thirds of the joint. The vertebral ossicles are rather short, higher than wide, elliptical with almost parallel sides.

Affinity

The present species differs from *O. wetherelli* by the stout, smooth arm plates, the much wider dorsal arm plates and the arrangement of secondary plates in the dorsal side of the disc. It differs from *Stegophiura eocaenus* in the smaller ventral arm plates.

Ophiura bartonensis n. sp.

Plate 9 figs. 1-9, plate 14 figs. 2-4.

1933 Ophioglypha sp.—Burton p. 152.

Derivation of name

The species is named after the locality Barton in Hampshire, England.

Type

The specimen plate 9 fig. 2 and plate 14 fig. 2 is holotype. It is from the Upper Eocene (Bartonian) Barton Beds of Higheliff, Barton in Hampshire, England. The specimen is in the collection of the British Museum (E 52158).

Material

Several specimens in slightly cemented grey sand are found in the Highcliff Sands (Lower Barton Beds A-3) and in unspecified levels of the Lower Barton Beds at Highcliff. The specimens are in the collection of the British Museum (E 33394, 35263, 49813, 52157–8, 52211–4). There is a small arm fragment from the Middle Eocene (Auversian) Upper Bracklesham Beds at Medmerry Farm, Selsey Bill in Sussex (E 13827–8). Several isolated plates are picked out of samples from the Middle Barton Beds (horizon E) at Barton collected by Mr. Davis (see also p. 71–72). In the collection of Mssrs. Rundle and Cooper are a few fragments from the Lower Bracklesham Beds (Prestwickianus Bed) and the Upper Bracklesham Beds (Brook Beds) of the stream section near Bramshaw in Hampshire, and a large number of specimens from the Highcliff Sands. A single specimen from the Upper Bracklesham Beds (Brook Bed) of Fawley Transmission Tunnel south of Southampton in Hamshire is in the collection of Mr. Stinton. This specimen was taken in Bed L of the profile described by Curry & West (1968). Details of the surface are in most specimens obscured by a thin cover of pyrite, especially along the sutures between the plates and thus no doubt a result of decay in the soft tissue of the dead animal.

Dimensions

The diameter of the disc varies from 7 to 20 mm. In a specimen 9 mm in diameter of the disc, the proximal arm joints are 0.8 mm long, 1.5 mm high and 2.4 mm wide.

Description

An Ophiura with a flat disc, almost circular in outline and covered by a regular pattern of plates. The radial shields are thin, rather large, subtriangular. They cover about half of the radius of the disc and almost touch over the arm base. On the inner side of the radial shield is seen the slightly protruding distal area meeting the genital rod, and a deep pit near the distal end. There is a sloping face meeting the dorsal arm plate in the radial embayment. Outside each radial plate is a genital plate with a few papillae of the arm-comb preserved and not meeting over the arm. The genital plate is subtriangular, strongly curved and smooth. There is only a small radial embayment in the disc with 2 dorsal arm plates and in some specimens a very small proximal third arm plate separating the genital plates and the distal end of the radial shields. The proximal end of the radial shields are separated by 3 plates increasing in size towards the centre of the disc. A few small lateral scales may be intercalated. The central area is covered by a central plate, primary radial and interradial plates and a few secondary scales. The internadial area is covered by a proximal and a distal internadial plate, a median pair of lateral plates and a few smaller scales. There is a very large and stout marginal plate in each interradius. It is elliptical with a lateral and a small ventral area. It covers the entire margin between the genital plates and is seen from the ventral as well as from the dorsal side of the disc. The interradial area of the ventral side is covered by a large oral shield separated by a few scales from the marginal plate. The adoral shields are straight and rod-shaped without distal flap. They meet the first lateral arm plate. There is a single vertical row of teeth on torus angularis. Oral papillae are not preserved. The second podial pore is seen from the ventral side at the edge of the mouth slit.

The arms are slender, elliptical in section, wider than high, with a flattened ventral side. The arm plates are thin. The dorsal arm plates are fairly wide in the proximal part of the arm, somewhat wider than long, but rapidly diminishing in width. Their distal edge is angular. They are in contact with each other in the proximal part of the arm, at least in 10 free joints, but separated in the distal joints. The ventral arm plates are short, rather wide, triangular with an almost straight distal edge. They are separated in the free part of the arm. The two most proximal ventral arm plates in the disc have a pattern of transverse furrows. The lateral arm plates are thin, adpressed with 3 adpressed spines on the distal edge. The median spine is a little shorter than the arm joint, the upper and lower spines are smaller. There is a small separation between the upper and the lower spines. The surface of the lateral arm plates has a pattern of delicate vertical furrows on the lateral part of the surface succeeded by a delicate and irregular granulation along the dorsal, ventral and distal edges. 70

The very large internadial marginal plate and the rather few covering plates of the disc are unusual characteristics except in juvenile specimens of ophiuroids. The present species differs from *O. wetherelli* by the large internadial marginal plate, the low and wide section of the arms and the restriction of the ornament of furrows on the lateral arm plates. It differs from *O. bognoriensis* in the section of the arms, the form and size of arm plates and the ornament of the lateral arm plates. It differs from *Stegophiura eocaenus* in the dorsal side of the disc and the small, separated ventral arm plates.

Ophiura costata n. sp.

Plate 6 figs. 8-9.

Derivation of name

Costatus (Lat.) costate, ribbed. The name refers to the ornament of the lateral arm plates.

Type

The lateral arm plate pl. 6 fig. 8 is holotype. It is from the Upper Eocene (Bartonian) Middle Barton Beds, horizon E of Barton Cliff in Hampshire, England. The specimen is in the collection of the British Museum (E 53637).

Material

29 lateral arm plates are found among the echinoderm remains in a washed sample from the type locality. This sample, collected by Mr. A. G. Davis, also contains numerous remains of other echinoderms recorded on p. 72. 15 vertebra do not belong to other ophiuroids present in this sample and are therefore referred to the present species.

Dimensions

Lateral arm plates: Height 1.6–1.7. Width 0.4–0.6. Length 1.2–1.7. Vertebrae: Height 0.9–1.3. Width 1.0–1.5. Length 0.6–0.9.

Description

An ophiuroid with rather thin, slightly curved almost flat lateral arm plates. The distal edge is provided with a row of 8 rounded tubercles of increasing size towards the ventral edge. There is a row of similar tubercles on the lateral surface close behind the edge. There is no pit or depression on the tubercles and no indication of lateral spines attached to the plates. In the upper part the two rows of tubercles are almost fused, but in the lower part the 4 lateral tubercles are separated by a narrow smooth area from the marginal row. A low ridge divides the lateral surface in a distal and a proximal area, and a high and prominent ridge divides the proximal area in a dorsal

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and a ventral part. The ventral part is cut by a very deep incision for the podium and a small embayment near the proximal ventral angle. The inner surface of the lateral arm plate is almost flat, sloping towards the proximal and distal edges. The dorsal and distal edges meet in a gentle curve where a group of 5 radiating crenellae reach the margin. The flat area along the ventral margin is cut by the deep and narrow podial incision, in front of which an irregular crenulation is seen. A slight depression runs towards the ventral proximal angle.

Other remains referred to O. costata

The sample collected by Davis includes 15 vertebrae distinctly different from other species present in the sample. The low number of these vertebrae agrees with the frequency of lateral arm plates and supports the determination. The vertebrae are zygospondylous, short and disc-shaped, slightly wider than high, almost elliptical with a broad, rounded dorsal edge and a low dorsal furrow. The hinge in the adoral surface is placed in a large, concave, subcircular area with a raised margin, and the dorsal nose is almost divided in two lateral knobs. The lateral surface forms a concave furrow of uniform width along the dorsal muscular faces. The aboral surface has a hinge of two stout knobs and a ventral nose divided by a median furrow.

Ophiura carpelloides n. sp.

Plate 10 figs. 1-9.

Derivation of name

Carpellum (Lat.) a carpel. The species is named after the form of the lateral arm plates, resembling the carpels of an orange.

Type

The lateral arm plate pl. 10 fig. 1 is holotype. It is from the Upper Eocene (Bartonian) Middle Barton Beds (horizon E of Burton 1929) at Barton in Hampshire, England. The specimen is in the collection of the British Museum (E 53658).

Material

In washed samples from the type locality collected by Mr. A. G. Davis are a large number of plates referred to this species together with plates referred to O. davisi, O. bartonensis and O. costata. The specimens are in the collection of the British Museum.

The Middle Barton Bed sample

A large sample of fossils have been washed out of the Middle Barton Clay (horizon E) at Barton by Mr. Davis. Numerous remains of 1 new species of asteroids and 4 new species of ophiuroids have been picked out of the sample. The combination of single ossicles was possible only because one species, *O. costata* is so characteristic in form and ornament of the lateral arm plates, that it cannot be confused with any other

ophiuroid known and also so seldom, that no common remains of the species can be expected in the sample. Furthermore one species, *O. bartonensis*, is found as complete specimens at other localities, so that all types of ossicles belonging to this species can be sorted out from the sample. After comparing size, form and ornament of the common plates, and after several attempts at reconstructing parts of the animals, at least some of the plates have been referred to species.

Astropecten granulatus		
superomarginals	1963	
inferomarginals	2395	
ambulacrals	118	(including 23 first amb.)
adambulacrals	15	
terminals	7	
Ophiura carpelloides		
lateral arm plates	193	(96 right, 97 left)
ventral arm plates	10	
dorsal arm plates	15	
radial shields	204	
oral shields	87	
genital plates	96	
jaws	43	
vertebrae	106	(including 21 first vertebra)
Ophiura davisi		
lateral arm plates	347	(172 right, 175 left)
ventral arm plates	6	
oral shields	45	
vertebrae	247	(no first vertebra)
Ophiura bartonensis		
lateral arm plates	300	(142 right, 158 left)
dorsal arm plates	2	
radial shields	45	
interradial marginal plates	48	
genital plates	32	
vertebrae	35	
Ophiura costata		
lateral arm plates	29	
vertebrae	15	
Not identified ophiuroids, mainly disc plates	58	
Crinoid brachials	4	
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Among the ophiuroid plates remaining after removal of O. bartonensis and lateral arm plates of O. costata are two kinds of lateral arm plates from which the types of O. carpelloides and O. davisi are selected. An uncommon type of vertebrae is referred to O. costata. There are two kinds of common vertebral ossicles not belonging to O. bartonensis. One is very high and narrow with a lateral bead. It fits well between the lateral arm plates of O. davisi. The other is more broad and triangular with a lateral furrow and may fit between the lateral arm plates of O. carpelloides. A few small and very thick dorsal and ventral arm plates are referred to O. carpelloides and may fit the reconstruction of the arm. Thin ventral arm plates with a large podial embayment fit the reconstructed arm of O. davisi. There are several first vertebra of the triangular kind with no lateral bead, indicating a dominant of remains from the disc. The arms of O. carpelloides may therefore have been short and rapidly tapering. There are also two kinds of oral shields not belonging to O. bartonensis. One of them is unusally large and stout, almost hemispheric. It is therefore combined with the unusally large and stout arm plates of O. carpelloides. The other is rather thin and flat, and is referred to O. davisi. The large number of oral shields from O. carpelloides compared with O. davisi is explained by the robustness of the plates and the dominance of remains from the disc in O. carpelloides. There are two kinds of radial shields in the sample, but one of them agrees with the radial shield of O. bartonensis. The other must therefore belong to O. carpelloides or O. davisi or both. They are large, subtriangular, very thick with a broad bevelled edge and a short furrow in the distal edge. Since they cannot be subdivided on a morphologic basis, it is concluded, that large, subtriangular radial shields are present only in one of the species. I have referred these thick radial shields to O. carpelloides. The number of radial shields to oral shields in the animal is 2 to 1, but there is a small overweight of radial shields in the sample. There are also two kinds of genital plates in the sample, one of them corresponding to O. bartonensis. The other is here referred to O. carpelloides. The few unidentified plates are mainly asymmetric plates from the disc. Most of them are rather thick and may well belong to O. carpelloides.

Dimensions	length	width	height
lateral arm plates	0.72 - 1.40	0.94 - 1.57	2.11 - 3.72
ventral arm plates	0.58 - 0.66	1.37 - 1.41	ab. 0.8
radial shields	2.27 - 3.76	1.88 - 2.82	0.78 - 1.10
oral shields	1.56 - 2.04	1.61 - 2.23	0.78 - 1.25
genital plates	2.35 - 2.86	0.94 - 1.06	0.63 - 0.70
jaws	1.25 - 1.84	0.63 - 0.70	1.14 - 1.49
vertebrae	0.74 - 0.86	1.33 - 1.69	1.21 - 1.49
reconstructed arm joint	1.37	3.72	3.84

Diagnosis

An ophiuroid with arms covered by very high and stout but short lateral arm plates. The lateral arm plates are cresentic, slightly more curved towards the ventral side. The outer surface is completely smooth and tapers to a dorsal point. The distal edge is sharp and there is no trace of spines. There is no incision for a podial pore. The proximal margin is somewhat restricted and shows irregular bosses meeting the overlapping plate from the preceeding joint. The plates are triangular in section with proximal and distal sides of similar size as the outer surface. The proximal side is smooth and concave, the distal side is flat or slightly concave with a radiating micro-ornament. The proximal and distal surfaces meet in the upper part of the plate under an angle of $30^{\circ}-40^{\circ}$, but are separated in the lower part of the plate by a small, concave inner surface against the vertebra restricting the width of the distal and specially the proximal side in the lower part of the plate.

Description of other plates referred to O. carpelloides

Among the two kinds of ophiuroid vertebrae common in the sample, those with a subtriangular outline may fit between the lateral arm plates. The vertebrae are zygospondylous, short, disc-shaped, with a narrow lateral furrow along the large dorsal muscular fossae. The dorsal furrow is short and narrow. The adoral hinge is formed by two angular ridges. The dorsal nose is heart-shaped. The aboral hinge is formed by two lateral bosses and there is a prominent ventral nose. The first vertebra differs in having four lateral articular bosses in the proximal surface, and the lateral furrow is restricted to the dorsal end. The lateral arm plates may have met above the vertebra, but are separated by a ventral arm plate below the vertebra. The dorsal arm plate is small, very thick with a sharp distal edge. The distal edge is curved, the sides converge towards the proximal end. Dorsal arm plates from the arm base have a pair of dorsolateral ridges where they meet the radial shields or genital plates. The ventral arm plate is very thick in the proximal part. The distal edge is almost straight and rather sharp. The sides are almost parallel. The ventral surface is four-sided, short and rather wide, and slightly arched. It forms an obtuse angle with the large proximal side of the plate. The inner surface of the plate is divided in a proximal part towards the vertebra and a distal part meeting and slightly overlapping the succeeding plate. The radial shields referred to this species are large, rounded subtriangular in outline, and very thick. There is a broad, gently sloping bevelled margin along the adradial and abradial sides. The rounded distal edge is more steep with a curved, almost horizontal furrow near the underside from the middle of the distal edge towards the presumed adradial side. This furrow may be the joint face towards a disc plate, presumably the genital plate. The underside of the radial shield is slightly concave with a slightly elevated area where it meets the inner genital bar. There is no pit in the underside of the radial shield. The oral shields are large, very thick and turnid, almost circular in outline with curved, sharp lateral edges and in most specimens a short, straight distal edge. The underside shows a steep distal edge and sloping lateral margins forming 3 more or less distinct bosses separated by 2 furrows in each side, and 2 large, flat or concave faces meeting in the proximal point under an angle of 100° -150°. The thick central part of the underside is concave. The genital plates are

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axe-shaped and curved. There is a pair of furrows on the side of the handle, where papillae may have been attached, and one or two ridges separated by furrows on the head. The jaws show the first and second podial pore just above each other. The second pore has opened on the ventral surface behind four small pits where mouth papillae were attached.

Ophiura davisi n. sp.

Plate 10 figs. 10-15.

Derivation of name

The species is named after the British geologist Mr. A. G. Davis, collector of the specimens and of many other fossils from the British Eocene.

Type

The lateral arm plate pl. 10 fig. 11 is holotype. It is from the Upper Eocene (Bartonian) Middle Barton Beds (horizon E of Burton 1929) at Barton in Hampshire, England. The specimen is in the collection of the British Museum (E 53668).

Material

In a washed sample from the type locality are found 347 lateral arm plates together with 247 vertebrae, 6 ventral arm plates and 45 oral shields referred to this species. Remains of other species from the Middle Barton Bed sample are recorded p. 72.

Dimensions	length	width	height	
lateral arm plates	0.94 - 1.18	0.58 - 0.78	1.45 - 2.31	
oral shields	1.76 - 1.96	1.25 - 1.61	0.47 - 0.58	
vertebrae	0.78 - 0.91	0.91 - 1.61	1.25 - 1.71	

Diagnosis

The lateral arm plates are rather large and thick, almost cresentic, slightly arched. The lateral surface is divided in a proximal part with 5-8 large crenellae meeting the overlapping preceeding plate, and a slightly tumid, smooth distal part. The distal edge is sharp with faint traces of pits for the attachment of 4-6 well separated lateral spines increasing in size towards the ventral side. There is a large ventral notch for the podium. The dorsal end of the plate is rounded in the small plates and has a small, inwards sloping median facet above the vertebra, but in most of the larger arm plates is a flat or slightly concave, smooth, outwards sloping dorsolateral facet of variable size. These lateral arm plates may have been included in the disc, the oblique facet meeting the genital bar. The proximal end of the lateral arm plate is rather thick with a high and narrow, concave inner surface towards the vertebra. The distal part of the inner surface is concave, sloping towards the anterior margin, and there are 5-8 crenellae meeting the succeeding plate. There is a large furrow for the podium.

Description of other plates referred to O. davisi

The form of the lateral plates indicates a very narrow vertebra. About 247 vertebrae of this form are found in the sample and referred to this species. The vertebrae are zygospondylous, very narrow, height more than twice their width and very short, disc-shaped. They have always a prominent lateral bead filling out the lateral furrow except in the dorsal end of the vertebra. The dorsal furrow is short and narrow. The edges of the dorsal adoral muscle face form a double median ridge from the dorsal furrow to the V-shaped dorsal nose. The hinge is not very prominent, but there is a distinct ventral nose in the aboral surface. Some of the vertebrae are wider, more triangular in outline and have a restricted lateral bead. They resemble the vertebrae referred to *O. carpelloides*, but may be proximal vertebrae of the present species. Among the numerous plates in the sample are some presumed oral shields referred to this species. They are rather thin, linguiform, pointed towards the proximal end with a rounded central area and a sloping margin towards the straight or curved, sharp distal edge. The inner side of the oral shield is flat or slightly concave with two narrow facets meeting in the proximal point and forming an angle of about 60°.

There are 6 small ventral arm plates obviously belonging to this species as indicated by the size and the podial pore. They are shield-shaped with a wide, bilobate distal edge. Close behind the distal edge is a large lateral embayment corresponding to the podial pore and occupying most of the lateral edge. The ventral surface is flat with a rather wide, bevelled proximal margin divided by a median ridge. The proximal edge is sharp and slightly bilobate. On the inner side the distal margin of the ventral arm plate is bevelled corresponding to the overlap of the plates. When the lateral points of the thin distal edge are broken away, this very small plate will hardly be recognized as an ophiuroid remain, and moreover most of the plates may be lost by washing and sieving of the sample.

Ophiocoma hessi n. sp.

Plate 6 figs. 6-7.

Derivation of name

The species is named after Dr. H. Hess (Basel), student of fossil asteroids and ophiuroids.

Type

The fragment of an arm shown pl. 6 fig. 6 is holotype. It is from the Upper Eocene (Bartonian) Highcliff Sands (Lower Bartonian Beds A-3) at Highcliff in Hampshire. The specimen is transferred from the collection of Mr. Rundle to the collection of the British Museum (E 53635).

Material

There are 6 fragments of arms from the type locality, including the holotype, in the collection of Mr. Rundle.

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Dimensions

Specimen :	1.	2.	3.	4.	5.	Type
number of joints preserved 8	3	6	4	3	6	6
length of joint	.33	0.43	0.50	0.50	0.54	0.58
width of joint 0	.90	1.40	1.64	1.44	1.48	1.55
height of joint ab.	0.49	1.05	0.94	0.94	0.82	1.02
length of ventral plate	-	0.46	0.50	0.50	0.58	0.58
width of ventral plate	-	0.54	0.69	0.66	0.66	0.62
length of dorsal arm plate 0	.39	0.46			0.58	0.54
width of dorsal arm plate 0	.70	1.00	-	_	1.16	1.16

Description

An Ophiocoma in which the arms are low and wide, almost elliptical in section with a flat ventral side. The height of the arm is a little more than the width. The lateral arm plates are short and cresentic, tapering to a narrow dorsal point and forming a more obtuse ventral projection giving plenty of room for the podium without surrounding a distinct podial pore. They are rather thick with somewhat outwards projecting distal edge. There are four well separated, horseshoe-shaped, prominent tubercles immediately behind the edge for the attachment of lateral spines. The lowermost tubercle is above the podial embayment, the uppermost is near the lateral point of the dorsal arm plate. The tubercles are similar in size or the second from the ventral side may be slightly larger. The surface of the lateral arm plates is smooth except for the four tubercles. The ventral arm plates are rather large, flat and smooth, slightly wider than long, almost square with an angular proximal side and a slightly concave distal side. They meet in the midline between the lateral plates. The dorsal arm plates are large, thin, smooth very wide and slightly arched. The proximal edges meet in an obtuse angle. The distal edge forms a gentle curve connected by a short lateral round to the proximal edge. They meet and overlap along the midline at least in the proximal part of the arms. The vertebrae are zygospondylous with thin lateral wings corresponding to the section of the wide and low arm, and with a narrow lateral furrow.

Affinity

The species is similar to *Ophiocoma rasmusseni* Hess, 1960 in the arm section and in the form of lateral arm plates and vertebrae, but differs in the short arm joints and plates.

Stegophiura eocaenus (Leriche, 1931)

1931 Ophiurites eocaenus.--Leriche p. 109 figs. 1-4 pl. 6 figs. 1-3.

Type

The specimen A among the individuals figured by Leriche is here selected as lectotype. It is from a boulder of sandstone collected at the base of the mole in the harbour of Zeebrugge in Belgium. The boulder contains 4 individuals and some fragments of the present species. The sandstone is referred to the Eocene ("Paniselian"), corresponding presumably to the uppermost Ypresian or lower part of the Lutetian. The specimen is in the collection of the museum in Brussels.

Dimensions

Diameter of disc 11–13 mm. Length of free arm more than 35 mm. Width of arm near disc 1 mm.

Description

The disc is almost circular. Dorsal plates of disc rather large. The radial shields are rounded subtriangular and reach about half the radius of the disc. They are separated by a single row of 6 radial plates including dorsal arm plates and increasing towards both ends. The interradial area between the radial shields is covered by two marginal and two interradial plates. At the proximal end of each radial shield is a plate separating the interradial plate from the large plate at the end of the radial row. The central area of the disc is not preserved. The ventral side of the disc shows no details except in connection with the arm. There are 5 brachial joints included in the disc.

The dorsal arm plates are rather large, and contiguous through more than 25 joints. They are wider than long for about 20 free joints. In the distal part of the arm they are longer than wide. The distal edge of the dorsal arm plates is divided in a straight median part, which forms an angle with shorter lateral parts. The ventral arm plates are large, almost square with concave sides against the large podial pores. They are contiguous in the entire length of the arm preserved, including more than 30 free joints. The lateral arm plates are adpressed. No spines are seen

Affinity

The present species was placed by Leriche (1931) under the provisional generic name *Ophiurites*. The very large arm plates are similar to the arm plates of *Stegophiura*. Unfortunately arm spines are not preserved. The species is distinguished from other Tertiary ophiuroids specially by the large ventral arm plates.

Asteronyx? ornatus Rasmussen, 1950

1950 Asteronyx? ornatus.-Rasmussen p. 121 pl. 18 fig. 11.

1950 Asteronyx granulosus.—Müller p. 33 pl. 2 figs. H, 1-5.

1951 Asteronyx? ornatus Rasmussen.—Rasmussen p. 52.

1969 Asteronyx? ornatus Rasmussen.-Maryanska & Popiel-Barczyk p. 136 pl. 1 fig. 4.

Previous records

This species has been recorded by Rasmussen (1950, 1951) from the Maastrichtian of Denmark and Germany, and by Maryanska & Popiel-Barzcyk (1969) from the Upper Maastrichtian and presumed Danian at Nasilow near Pulawy in Poland.

Acknowledgments

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Mr. A. Rundle, London, has offered very valuable information on British localities, and his private collection has been of greatest importance to my study. He has kindly transferred all of his specimens figured in this paper to the collection of the British Museum. He also introduced me to other important collecters including Mr. J. Cooper, London, Mr. D. Bone, Bognor Regis, Mr. F. C. Stinton, Bournemouth, and Mr. A. S. Gale, Canterbury from whom material has been included in the study. Specimens from Poland were offered by Professor K. Pozaryska, specimens from Germany by Professor Gripp. Samples and specimens from Austria were collected and offered by Professor Rosenkrantz.

The drawings are by Mr. C. Rasmussen, photos by the photographic staffs of the British Museum and the Geological Museum in Copenhagen. The manuscript was improved by Dr. R. Bromley.

References

- Agassiz, A. 1890: Ueber einen neuen Tiefsee-Crinoiden aus der Familie der Apiocriniden. Neues Jahrb. Min. Geol. Palaeont. 1890 (1), 94–95. Stuttgart.
- Agassiz, A. 1890: Notice of Calamocrinus diomedae, a new stalked crinoid from the Galapagos. Bull. Mus. Comparative Zool. 20 No. 6. Cambridge Mass. U.S.A.
- Agassiz, A. 1892: Calamocrinus diomedae, a new stalked crinoid. Mem. Mus. Comparative Zool. Harvard. 17 no. 2, 1–95. Cambridge U.S.A.
- Anderson, H.-J. 1967: Himerometra grippae n. sp. (Crinoidea, Articulata), eine freischwimmende Seelilie aus dem niederrheinischen Oberoligocän. Geologica et Palæontologica. 1, 179–182. Marburg.
- Ansted, D. T. 1844: Geology, introductory, descriptive, & practical. 2 part 2, 230 pp.
- Bather, F. A. 1897: On Apiocrinus from the Muschelkalk. Geol. Mag. N. S. Dec. IV. Vol. 4, 116–123. London.
- Bather, F. A. 1898: Pentacrinus, a name and its history. Nat. Sci. 12 no. 74, 245-256.
- Bather, F. A. 1917: British fossil crinoids. XI Balanocrinus of the London Clay. Ann. & Mag. Nat. Hist. Ser. 8, 20, 385-407. London.
- Biese, W. 1930: Über Isocrinus H. v. Meyer und Cainocrinus Forbes. Jahrb. Preuss. Geol. Landesanst. Berlin. 1929. Vol. 50, 2, 702-719. Berlin.
- Biese, W. & Sieverts-Doreck, H. 1939: Fossilium Catalogus I: Animalia. Pars 80: Crinoidea caenozoica. 's-Gravenhage.
- British Museum (Natural History) 1959: British Caenozoic fossils. London.
- Burton, E. S. J. 1929: The horizons of Bryozoa (Polyzoa) in the Upper Eocene Beds of Hampshire. *Quart. Journ. Geol. Soc. London* 85, 223-241. London.
- Burton, E. S. J. 1933: Faunal horizons of the Barton Beds in Hampshire. Proc. Geol. Assoc. 44, 131–167. London.
- Busk, G. 1866: Description of three species of Polyzoa from the London Clay of Highgate in the collection of N. T. Wetherell. *Geol. Mag. 3*, 298-302. London.
- Carpenter, P. H. 1884: Report upon the Crinoidea collected during the voyage of H. M. S. Challenger during the years 1873–1876. 1 Zool. *Challenger Exp. 11 part 32*. 440 pp. Edinburgh.
- Clark, A. H. 1908: Infrabasals in recent genera of the crinoid family Pentacrinitidae. *Proc.* U. S. Nat. Mus. 33, 671–676. Washington D.C.
- CLARK, A. H. 1908: The axial canals of the recent Pentacrinitidae. Proc. U. S. Nat. Mus. 35, 87–91. Washington D. C.
- Clark, A. H. 1910: Proisocrinus, a new genus of recent crinoids. Proc. U. S. Nat. Mus. 38, 387-390. Washington.
- Clark, A. H. 1923: A revision of the recent representatives of the crinoid family Pentacrinitidae, with diagnoses of two new genera. *Journ. Washington Acad. Sci. 13*, 8–12. Washington D.C.
- Curry, F. H. & West, J. M. 1968: The Eocene succession in the Fawley Transmission Tunnel. *Proc. Geol. Assoc.* 79, 179–202. London.
- Davis, A. G. 1923: Note on the occurrence of Ophioglypha wetherelli (Forbes) in the London Clay of New Malden, Surrey. Proc. & Transact. Croydon Nat. Hist. & Sci. Soc. 9, 3, 113-115.

Nr. 7

- Davis, A. G. 1928: The geology of the City and South London Railway, Clapham-Morden Extension. *Proc. Geol. Assoc. 39*, 339–352. London.
- Davis, A. G. 1936: The London Clay of Sheppey and the location of its fossils. *Proc. Geol.* Assoc. 47, 328-345. London.
- Davis, A. G. 1937: Additional notes on the geology of Sheppey. Proc. Geol. Assoc. 48, 77-81. London.
- Davis, A. G. & Elliot, G. F. 1958: The Palaeogeography of the London Clay Sea. Proc. Geol. Assoc. 68, 255–277. Colchester.
- Durham, J. W. & Roberts, W. A. 1948: Cretaceous Asteroids from California. *Journ. Paleont.* 22, 432–439. Tulsa, Okla.
- Elliott, G. F. 1971: Eocene Volcanics in South-east England. Nature Physical Sci. 230, 9. London.
- Fell, H. B. 1956: New Zealand fossil Asterozoa 2. Hippasteria antiqua n.sp. from the Upper Cretaceous. *Rec. Canterbury Mus.* 7 (1). 11–12. Christchurch N. Z.
- Fell, H. B. 1960: Synoptic keys to the genera of Ophiuroidea. Zool. Publ. Victoria Univ. Wellington 26. 44 pp. Wellington N.Z.
- Fisher, O. 1862: On the Bracklesham Beds of the Isle of Wight Basin. *Quart. Journ. 18*, 65–94. London.
- Fisher, W. K. 1911: Asteroidea of the North Pasific and adjacent waters. Part 1, Phanerozonia and Spinulosa. *Smithsonian Inst. U. S. Nat. Mus. Bull.* 76, 406 pp.
- Forbes, E. 1848: On the Asteridae found fossil in British strata. Mem. Geol. Survey Britain 2 part 2, 457–482. London.
- Forbes, E. 1849: Figures and descriptions illustrative of British organic remains. Decade 1. *Mem. Geol. Survey United Kingdom.* London.
- Forbes, E. 1852: Monograph of the Echinodermata of the British Tertiaries. *Palæontogr. Soc.* 36 pp. London.
- Gagel, C. 1906: Über das Vorkommen des Untereocäns (Londontons) in der Uckermark und in Vorpommern. *Monatsber. Deutschen geol. Gesellsch. 1906*, 309–326. Berlin.
- Gislén, T. 1924: Echinoderm studies. Zool. Bidrag Uppsala 9, 1–314. Uppsala.
- Gislén, T. 1938: A revision of the Recent Bathycrinidae. Lunds Univ. Årsskr. N.F. Avd. 2. Vol. 34, Nr. 10 & Kungl. Fysiogr. Sällsk. Handl. N.F. Vol. 49, Nr. 10. 30 pp. Lund & Leipzig.
- Gislén, T. 1939: On the young of a stalked deep-sea crinoid and the affinities of the Hyocrinidae. Lunds Univ. Årsskr. N.F. Avd. 2. Vol. 34, Nr. 17 & Kungl. Fysiogr. Sällsk. Handl. N.F. Vol. 49, Nr. 10. 18 pp. Lund & Leipzig.
- Gripp, K. 1964: Erdgeschichte von Schleswig-Holstein. 411 pp. Neumünster.
- Gümbel, C. W. 1861: Geognostische Beschreibung des bayerischen Alpengebirges und seines Vorlandes. 970 pp. Gotha.
- Gümbel, C. W. 1865: Die Nummuliten-führenden Schichten des Kressenbergs in Bezug auf ihre Darstellung in der Lethaea geognostica von Südbayern. *Neues Jahrb. Min. Geol. Paleont.* 1865, 129–170. Stuttgart.
- Hess, H. 1955: Die fossilen Astropectiniden (Asteroidea). Neue Beobachtungen und Übersicht über die bekannten Arten. Schweitz. Paläont. Abhandl. 71. 113 pp. Basel.
- Hess, H. 1960: Über die Abgrenzung der Astropectiniden-Gattungen Pentasteria Valette und Archastropecten Hess. Bericht Schweiz. Palaeont. Gesellsch. 38 Jahresvers. & Eclogae geol. Helvet. 53, 329–331. Basel.
- Hess, H. 1970: Schlangensterne und Seesterne aus dem oberen Hauterivien "Pierre jaune" von St-Blaise bei Neuchåtel. *Eclogae geol. Helvet. 63*, 1069–1091. Basel.
- Hucke, K. & Voigt, E. 1929: Beiträge zur Kenntnis der Fauna des norddeutschen Septarientones. Zeitschr. Deutschen geol. Gesellsch. 81, 159–168. Berlin.

- Jaekel, O. 1892: Ueber Plicatocriniden, Hyocrinus und Saccocoma. Zeitschr. Deutschen geol. Gesellsch. 44, 619–696. Berlin.
- Kühn, O. 1930: Das Danien der äusseren Klippenzone bei Wien. Geol. Palæont. Abhandl. N.F. 17, 495–576. Jena.
- Kuehn, O. 1960: Neue Untersuchungen über die dänische Stufe in Oesterreich. Repl. Internatl. Geol. Congr. 21. Sess. pt 5, 162–169. Copenhagen.
- Lehner, M. 1937: Fauna und Flora der Frankischen Albüberdechenden Kreide II. Palaeontogr. 87 part A, 158–234. Stuttgart.
- Leriche, M. 1931: Une Ophiure du "Paniselien" de la mer du Nord. Bull. Soc. Belge Géol. 40 (1930), 109–119. Bruxelles.
- Linstow, O. 1912: Zwei Asteriden aus märkischem Septarienton (Rupelton) nebst einer Übersicht über die bisher bekannt gewordenen tertiären Arten. Jahrb. Kgl. Preuss. Geol. Landesanst. Berlin 1909. vol 30, 2. 47–63. Berlin.
- Loriol, P. de 1873: Description de quelques Astérides du terrain neocomien de Neuchâtel. Mem. Soc. Sci. natur. Neuchâtel 4, 2. 1–36. Neuchâtel.
- Loriol, P. de & Pellat, E. 1875: Monographie des étages jurassiques supérieurs de Boulogne-sur-Mer. Mém. Soc. Phys. Hist. Nat. Genève. 24, 1. Genève.
- Loriol, P. de 1878: Monographie des Crinoïdes Fossiles de la Suisse. Mém. Soc. Paléont. Suisse 5, 1–111. Geuève.
- Maryanska, T. & Popiel-Barczyk, E. 1969: On the remains of Ophiuroidea from the uppermost Maastrichtian and Danian deposits of Nasilów near Pulawy, Poland. Prace Museum Zimei 15. Warszawa. Prace Paleozoologiczne. 131–140. Warszawa.

Miller, J. S. 1821: A natural history of the Crinoidea or Lily-shaped animals. 150 pp.

- Müller, A. H. 1950: Die Ophiuroidenreste aus dem Mucronatensenon von Rügen. Geologica 5, 1–35. Berlin.
- Münster, G. 1835: Bemerkungen über einige tertiäre Meerwasser-Gebilde im nordwestlichen Deutschland, zwischen Osnabrück und Cassel. *Neues Jahrb. Min. Geogn. Geol. Petref.* 420– 451. Stuttgart.
- Nielsen, K. B. 1913: Crinoiderne i Danmarks Kridtaflejringer. Danm. Geol. Unders. II række 26. 112 pp. København.
- Nielsen, K. B. 1915: Rhizocrinus maximus n.sp. og nogle Bemærkninger om Bourgueticrinus danicus Br. N. Meddr. dansk geol. Foren. 4, 391–394. København.
- Nielsen, K. B. 1943: The Asteroids of the Senonian and Danian deposits of Denmark. *Biol. Skr. Dan. Vid. Selsk. 2 nr. 5.* 68 pp. København.
- Peck, R. E. 1955: Cretaceous Microcrinoids from England. *Jour. Paleont.* 29, 1019–1029. Tulsa.
- Philippi, R. A. 1843: Beiträge zur Kentniss der Tertiärversteinerungen des nordwestlichen Deutschland. 88 pp. Kassel.
- Pozaryska, K. 1965: Foraminifera and Biostratigraphy of the Danian and Montian in Poland. *Paleontologia Polonica 14*, 1–156. Warszawa.
- Rasmussen, H. W. 1945: Observations on the asteroid fauna of the Danian. *Meddr. dansk geol.* foren. 10, 417–426. København.
- Rasmussen, H. W. 1950: Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. *Danm. geol. unders. 11 række* 77. 134 pp. København.
- Rasmussen, H. W. 1951: An Oligocene asteroid from Denmark. Meddr. dansk geol. foren. 11, 588–589. København.
- Rasmussen, H. W. 1952: Cretaceous Ophiuroidea from Germany, Sweden, Spain and New Jersey. Meddr. dansk geol. foren. 12, 47–57. København.
- Rasmussen, H. W. 1961: A monograph on the Cretaceous Crinoidea. *Biol. Skr. Dan. Vid. Selsk.* 12. 428 pp. København.

Nr. 7

- Rasmussen, H. W. 1965: The Danian affinities of the Tuffeau de Ciply in Belgium and the "Post-Maastrichtian" in the Netherlands. *Meded. Geol. Stichting*, N. S. 17, 33–38. s'Gravenhage.
- Rasmussen, H. W. 1966: Astéroïdes du Tertiaire Inferieur de Libye (Afrique du Nord). Ann. Paléont. Invertébrés 52, 3–15. Paris.
- Roman, J. 1956: Ophiurites (Ophiomusium?) lamberti n.sp. de l'Eocène inférieur de Dahomey. Bull. Museum, 2 sér. 28 no. 4, 428–432.
- Rosenkrantz, A. 1970: Marine Upper Cretaceous and lowermost Tertiary deposits in West Greenland. *Bull. geol. soc. Denmark 19*, 406–453. Copenhagen.
- Rundle, A. J. & Cooper, J. 1970: Some recent temporary exposures of London Clay in the London area. *The London Naturalist* 49, 113–124. London.
- Schafhäutl, K. E. 1851: Über einige neue Petrefakten des Südbayern'schen Vorgebirges. Neues Jahrb. Min. Geogn. Geol. Petref. 407-421. Stuttgart.
- Schafhäutl, K. E. 1852: Der Teisenberg oder Kressenberg in Bayern. Neues Jahrb. Min. Geogn. Geol. Petref. 129–175. Stuttgart.
- Schafhäutl, K. E. 1863: Südbayerns Lethaea geognostica. 487 pp. Leipzig.
- Sieverts-Doreck, H. 1944: Zur Morphologie und systematischen Stellung von Balanocrinus. Neues Jahrb. Min. Geol. Paläont. Abhandl. 88B, 136-155. Stuttgart.
- Sieverts-Doreck, H. 1953: Zur Verbreitung känozoischer Ophiuren. Neues Jahrb. Geol. Paläont. Monatsh. 275–286. Stuttgart.
- Spencer, W. K. 1913: The Evolution of the Cretaceous Asteroidea. Phil. Transact. Royal Soc. London. Ser. B 204, 99–177. London.
- Speyer, O. 1864: Die Tertiärfauna von Söllingen bei Jerxheim in Herzogthum Braunschweig. *Palaeontogr. 9*, 247–337. Stuttgart.
- Stolley, E. 1900: Über Diluvialgeschiebe des Londonthons in Schleswig-Holstein und des Alters der Molerformation Jütlands, sowie das baltische Eocän überhaubt. Archiv Anthrop. Geol. Schleswig 3, 105–146.
- Stolley, E. 1902: Über Eoängeschiebe des Londonclay und ihre Beziehungen zu der jütischen "Moformation". Schr. naturw. Ver. Schleswig-Holstein. 12, 16–19. Kiel.
- Traub, F. 1938: Geologische und palaeontologische Bearbeitung der Kreide und des Tertiärs im östlichen Rupertwinkel, nördlich von Salzburg. *Palaeontogr. 88 A.* 114 pp. Stuttgart.
- Valette, A. 1915: Les Ophiures de la Craie des environs de Sens. Bull. Soc. Sci. hist. nat. Yonne. 26 pp.
- Valette, A. 1925: Note sur les débris de Stellérides fossiles du sud-ouest de la France. Actes Soc. Linn. Bordeaux 76, 167–207.
- Venables, E. M. 1963: The London Clay of Bognor Regis. Proc. Geol. Assoc. 73 (1962), 245–271. London.
- Voigt, E. 1964: A bryozoan fauna of Dano-Montian age from Boryszew and Sochaczew in Central Poland. Acta Palaeont. Polonica 9, 419–498. Warszawa.
- Wetherell, N. T. 1834: On Ophiura found at Child's Hill, to the N.W. of Hampstead. Proc. Geol. Soc. London. 1 no. 29 (1832–1833), 417. London.
- Wetherell, N. T. 1837: Observations on a Well dug on the South Side of Hampstead Heath. Transact. Geol. Soc. London 2. Ser. 5, 131–136. London.
- Wrigley, A. 1924: Faunal Divisions of the London Clay. Proc. Geol. Assoc. 35, 245-259. London.
- Wrigley, A. 1940: The faunal succession in the London Clay, illustrated in some new exposures near London. *Proc. Geol. Assoc.* 51, 230–245. London.
- Wrigley, A. 1945: Some War-time exposures in London of Woolwich Beds and London Clay. Proc. Geol. Assoc. 56, 214–218. London.

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- Fig. 1. Isselicrinus aff. paucicirrhus (Nielsen, 1913), p. 16. Upper Danian sandstone ("Sonja lens"), Sonja Member of the Agatdal Formation. Agatdal in Nûgssûaq, West Greenland. Collection Geological Museum, Copenhagen (12752). Column, × 5; a, lateral; b, articular surface.
- Figs. 2-5. Isselicrinus subbasaltiformis (Miller, 1821), p. 17. Ypresian.
 Fig. 2. London Clay (division 2). Hampstead Heath, London. British Museum (57540). Column, lectotype × 1.4; lateral view.
 Fig. 3. Rösnäs Clay. Røsnæs in Denmark. Geological Museum, Copenhagen (12753). Column, × 5; a, lateral; b, articular surface of nodal.
 Fig. 4. Rösnäs Clay. Røsnæs in Denmark. Geological Museum, Copenhagen (12754). Articular surface of internodal, × 5.
 Fig. 5. Rösnäs Clay. Trelde Næs in Denmark. Geological Museum, Copenhagen (12755). Theca with arms, × 1.8.
- Figs. 6-7. Calamocrinus ilimanangei n.sp., p. 28; × 8.2. Upper Danian sandstone ("Sonja lens"), Sonja Member of the Agatdal Formation. Agatdal in Nûgssuaq, West Greenland.
 Fig. 6. Geological Museum, Copenhagen (12756). Holotype, column; a, lateral; b, articular surface.
 Fig. 7. Geological Museum, Copenhagen (12757). Column.
- Fig. 8. Bourgueticrinus danicus Nielsen, 1913, p. 30; × 5. Heersian glauconitic marl, Lellinge Formation. Egsmark in Denmark. Geological Museum, Copenhagen (12758).
- Fig. 9. Democrinus londinensis (Forbes, 1852), p. 31; × 3.3. Ypresian, London Clay. Highgate in London. British Museum (E 38715).
- Figs. 10-15. Amphorometra ornata n. sp., p. 34; × 12. Ypresian, London Clay. Wraysbury Reservoir at Poyle, England. British Museum.
 - Fig. 10. Theca, holotype (E 53620); a, dordal; b, lateral; c, ventral.
 - Fig. 11. Centrodorsal (E 53621), ventral side.
 - Fig. 12. Primibrachial I Br 2 (E 53622); a, proximal; b, dorsal; c, distal.
 - Fig. 13. Secundibrachial II Br 1 (E 53623); a, proximal; b, dorsal; c, distal.
 - Fig. 14. Muscular secundibrachial (E 53624); a, dorsal; b, distal.
 - Fig. 15. Syzygial secundibrachial (E 53625); a, proximal; b, dorsal; c, distal.



- Figs. 1–20. Cainocrinus tintinnabulum Forbes, 1852, p. 22. Ypresian, Middle Clay (Craigweil Bed). Bognor Regis, England. Collection Geological Museum, Copenhagen.
 - Fig. 1. Reconstruction, $\times 4$.
 - Fig. 2. Diagram of arm.
 - Fig. 3. Theca with column and first primibrachial, $\times 11$. (12759).
 - Fig. 4. Column, $\times 8$. (12760). a, lateral; b, articular surface.
 - Fig. 5. Column, × 7.5. (12761).
 - Fig. 6. Cirrus with first 6 cirrals, $\times 10$. (12762).

Fig. 7. Basals, infrabasals and proximal columnals, $\times 10$. (12763). a, lateral; b, surface against radial ring.

- Fig. 8. Basal showing joint face for infrabasals and column, $\times 10$. (12764).
- Fig. 9. Radial, $\times 10$. (12765). a, dorsal side and brachial articulation; b, lateral.
- Fig. 10. Primibrachial I Br 1, \times 10. (12766). a, proximal; b, dorsal surface and distal articulation.
- Fig. 11. Primibrachial I Br 2, × 10. (12767). a, proximal; b, dorsal; c, distal.
- Fig. 12. Recombined fragment of arm with I Br 1 to III Br 5, $\times 5$. (12768).
- Fig. 13. Secundibrachial II Br 1, × 10. (12769). a, proximal; b, dorsal surface and distal articulation.
- Fig. 14. Secundibrachial II Br 2, \times 10. (12770). a, proximal; b, dorsal; c, distal articulation with pinnular articulation in left side.
- Fig. 15. Secundibrachial II Br 3, \times 10. (12771). a, dorsal; b, lateral; c, distal.
- Fig. 16. Secundibrachial II Br 4, ×10. (12772). a, proximal; b, dorsal; c, lateral; d, distal.
- Fig. 17. Tertibrachial III Br 1, \times 10. (12773). a, dorsal; b, distal.
- Fig. 18. Tertibrachial III Br 2, × 10. (12774). a, dorsal; b, lateral; c, distal.
- Fig. 19. Tertibrachial III Br 3, × 10. (12775). a, proximal; b, dorsal; c, lateral; d, distal.
- Fig. 20. Distal fragment of arm, × 10. (12776). a, dorsal; b, lateral; c, ventral.
- Figs. 21–22. Isocrinus (?Cainocrinus) sp. aff. C. tintinnabulum Forbes, 1852, p. 27. Paleocene, Pulaway Beds in the Sochaczew boring 260–262 m, Poland. Collection Geological Institute, Warsaw. Columnal, × 10. a, lateral; b, articular surface.



- Figs. 1-4. Astropecten postornatus (Rasmussen, 1945), p. 37. Upper Danian. Geological Museum, Copenhagen, Fig. 1. Superomarginal (5184a), × 5. Conglomerate at base of Lellinge Formation. Svanemollen in Copenhagen, Denmark. Fig. 2. Inferomarginal, lectotype (5184b), \times 5. Conglomerate at base of Lellinge Formation. Syanemøllen in Copenhagen, Denmark. Fig. 3. Superomarginal (12777), × 10. Sandstone ("Sonja Lens"), Sonja Member of Agatdal Formation. Agatdalen, Nûgssuaq, West Greenland. Fig. 4. Inferomarginal (12778), ×10. Sandstone ("Sonja Lens"), Sonja Member of Agatdalen Formation, Agatdalen, Núgssuaq, West Greenland.
- Figs. 5-8. Astropecten granulatus n.sp., p. 38. Bartonian, Middle Barton Bed, (Horizon E). Barton Cliff, England. British Museum.
 - Fig. 5. Superomarginal (E 53626), $\times 10$.
 - Fig. 6. Inferomarginal, holotype (E 53627), $\times 10$.
 - Fig. 7. Terminal plate (E 53628), × 20. Fig. 8. Ambulacral (E 53629), × 10.
- Figs. 9-15. Coulonia colei (Forbes, 1852), p. 41. Ypresian.
 - Fig. 9. London Clay (division 5), Highgate in London. British Museum (E 428). Dorsal side of arm, × 5.
 - Fig. 10. Same specimen, superomarginal, $\times 5$.
 - Fig. 11. Same specimen, inferomarginal, $\times 5$.
 - Fig. 12. Same specimen, two paxillae, $\times 5$.
 - Fig. 13. Same specimen, two marginal spines, $\times 5$.
 - Fig. 14. London Clay, Isle of Sheppey, England. British Museum (E 38490). Dorsal side of arm, $\times 3.5.$
 - Fig. 15. London Clay (division 5), Highgate in London. Geological Survey, London (5807). Terminal plate, $\times 6$.
- Figs. 16-17. Lophidiaster haunsbergensis n.sp., p. 45; × 12. Landenian. Kroisbach near Haunsberg, Austria. Geological Museum, Copenhagen.
 - Fig. 16. Superomarginal, holotype (12779).
 - Fig. 17. Inferomarginal, (12780).
- Figs. 18-19. Lophidiaster inversus n.sp., p. 46; × 10. Landenian. Kroisbach near Haunsberg, Austria. Geological Museum, Copenhagen. Fig. 18. Superomarginal, holotype (12781).
 - Fig. 19. Inferomarginal, (12782).
- Figs. 20–25. Lophidiaster concavus n. sp., p. 47. Ypresian, London Clay, British Museum.
 - Fig. 20. Lateral view of reconstructed arm (E 53630), $\times 5$. London Clay (division 3) Wraysbury Reservoir at Poyle, England.
 - Fig. 21. Superomarginal, (E 53631), $\times 10$. Same locality.
 - Fig. 22. Inferomarginal, holotype (E 53632), \times 10. Same locality.
 - Fig. 23. Dorsal plate (E 53633), \times 10. Same locality.
 - Fig. 24. Ambulacral (E 53634), $\times 10$. Same locality.
 - Fig. 25. Terminal plate (E 53675), ×10. London Clay (division 2). Aveley, England.
- Figs. 26-27. Lophidiaster sp.aff. L. pygmaeus Spencer, 1913, p. 48; × 10. Landenian. Kroisbach near Haunsberg, Austria. Geological Museum, Copenhagen.
 - Fig. 26. Superomarginal (12783).
 - Fig. 27. Inferomarginal (12784).



Figs. 1-5. Hippasteria tuberculata (Forbes, 1852), p. 48. Ypresian, London Clay, Isle of Sheppey, England. Fig. 1. Part of disc and arm, × 1.6. Geological Survey, London (99787). a, dorsal; b, ventral. Fig. 2. Part of disc with base of arm w1.6. Particle Museum (E 52205), a, wastral side (second bu)

Fig. 2. Part of disc with base of arm, $\times 1.6$. British Museum (E 53295). a, ventral side (covered by pyrite) and margin; b, profile of margin.

Fig. 3. Distal part of arm, $\times 1.6$. British Museum (E 33832a). a, dorsal; b, lateral; c, ventral; d, proximal section.

Fig. 4. Distal part of arm, $\times 3.2$. British Museum (E 33832b). a, dorsal; b, lateral; c, ventral; d, proximal section.

Fig. 5. Arm, $\times 2.5$. British Museum (E 52242). a, dorsal; b, ventral.



- Figs. 1-2. Teichaster retiformis Spencer, 1913, p. 50. Marginals, × 5. Upper Danian sandstone ("Sonja lens"), Sonja Member of Agatdal Formation. Nugssuaq in West Greenland. Geological Museum, Copenhagen. Fig. 1. Superomarginal (12785).
 - Fig. 2. Inferomarginal (12786).
- Figs. 3-6. Teichaster lamberti Valette, 1925, p. 50. Marginals, × 5. Landenian, glauconitic clay. Kroisbach near Haunsberg, Austria. Geological Museum, Copenhagen.
 - Fig. 3. Superomarginal (12787).
 - Fig. 4. Inferomarginal (12788).
 - Fig. 5. Superomarginal (12789). Fig. 6. Inferomarginal (12790).
- Figs. 7-10. Teichaster stokesii (Forbes, 1848), p. 52. Ypresian. Fig. 7. London Clay. Isle of Sheppey, England. British Museum (E 38587). Arm and part of disc, \times 1.6; a, dorsal; b, ventral; c, profile of margin of disc.

Fig. 8. London Clay. Isle of Sheppey, England. British Museum (E 38489). Distal part of arm, \times 1.6; a, dorsal; b, lateral.

- Fig. 9. Rösnäs Clay. Trelde Næs north of Fredericia, Denmark. Geological Museum, Copenhagen (12791). Part of disc and base of arm, $\times 1.2$; a, dorsal; b, lateral; c, ventral. Fig. 10. Rösnäs Clay. Trelde Næs north of Fredericia, Denmark. Geological Museum, Copenhagen (12792). Part of disc, $\times 1.2$; a, dorsal side and margin; b, ventral.
- Figs. 11-13. Ceramaster obtusus n.sp., p. 54; × 5. Upper Danian sandstone ("Sonja lens"), Sonja Member of Agatdal Formation, Agatdal in Núgssuaq, West Greenland, Geological Museum, Copenhagen. Fig. 11. Terminal superomarginal, (12793); a, lateral; b, profile; c, adradial.
 - Fig. 12. Holotype, terminal inferomarginal, (12794); a, lateral; b, profile; c, adradial; d, ventral. Fig. 13. Median superomarginal, exfoliated, (12795); a, dorsal; b, profile.
- Fig. 14. Echinaster jacobseni n.sp., p. 57. Holotype, ×4. Ypresian, diatomaceous clay, Mo-Clay Formation. Silstrup Cliff south of Tisted, Denmark. Geological Museum, Copenhagen (12796). Ventral side of disc and arms.



- Fig. 1. Amphiura senonensis Valette, 1915, p. 59. Lateral arm plate, \times 10. Landenian, glauconitic marl. Kroisbach at Haunsberg, Austria. Geological Museum, Copenhagen (12797).
- Fig. 2. Ophiacantha danica Rasmussen, 1951, p. 60. Lateral arm plate, × 10. Danian limesand. Haidhof near Vienna, Austria. Geological Museum, Copenhagen (12798).
- Fig. 3. Ophiura achatae n.sp., p. 61. Fragment of arm, × 16. Upper Danian, sandstone ("Sonja lens"), Sonja Member of Agatdal Formation. Agatdal in Nùgssuaq, West Greenland. Geological Museum, Copenhagen (12799). a, ventral; b, lateral; c, dorsal; d, proximal end.
- Figs. 4–5. Ophiura furiae n.sp., p. 62. Ypresian. Calcareous concretion (cement stone) in diatomaceous clay. Mo-Clay Formation. Fur in Denmark. Geological Museum, Copenhagen.
 Fig. 4. Holotype (12800), × 5; a, ventral side; b, section of arm near base.
 Fig. 5. Dorsal side of other specimen in the same sample (12801).
- Figs. 6-7. Ophiocoma hessi n.sp., p. 76. Fragments of arm, × 20. Bartonian Highcliff Sands (Lower Barton Beds, A-3). Highcliff, England. British Museum.
 Fig. 6. Holotype (E 53635); a, ventral; b, lateral; c, dorsal.
 Fig. 7. Distal end of other fragment (E 53636).
- Fig. 8. Ophiura costata n.sp., p. 70. Holotype, lateral arm plate, ×10. Bartonian, Middle Barton Beds. Horizon E of Barton Cliff, England. British Museum (E 53637). a, lateral; b, distal edge; c, inner surface.
- Fig. 9. Ophiura cfr. costata n.sp. Vertebra, × 17. Bartonian, Middle Barton Beds. Horizon E of Barton Cliff, England. British Museum (E 53638). a, proximal end; b, lateral; c, distal end.



Figs. 1-5. Ophiura wetherelli Forbes, 1852, p. 64. Ypresian. British Museum.

Fig. 1. Oldhaven Beds. Lower Upnor near Friendsburg Extra, England. (E 53243), $\times 9$; a, dorsal side; b, reconstruction of dorsal side; c, section of arm.

Fig. 2. London Clay (division 4). New Malden, England. (E 13702), \times 6; a, ventral side; b, reconstruction of ventral side.

Fig. 3. Fragment of arm, \times 20. London Clay (division 2). Victoria Line shaft at Brixton, London. (E 53639); a, dorsal; b, lateral; c, ventral; d, distal end.

Fig. 4. Lateral arm plate, $\times 20$, inner side. London Clay (division 2). Victoria Line shaft at Brixton, London. (E 53640).

Fig. 5. Vertebra, \times 20. London Clay (division 2). Victoria Line shaft at Brixton, London. (E 53641); a, lateral; b, proximal end.



- Figs. 1–10. Ophiura bognoriensis n. sp., p. 66. Ypresian. London Clay (Lower Clay) of Bognor Regis, England. Collection of the British Museum.
 - Fig. 1. Holotype (E 13761). Starfish Bed, $\times 2.7$; a, dorsal side; b, reconstruction of dorsal side.
 - Fig. 2. Proximal arm fragment (E 53642). Astarte Bed, $\times 10$; a, ventral; b, left side; c, dorsal.
 - Fig. 3. Distal arm fragment (E 53643). Astarte Bed, × 10; a, ventral; b, right side; c, dorsal; d, distal
 - end.
 - Fig. 4. Dorsal arm plate (E 53644). Astarte Bed, $\times 10$.

Fig. 5. Inner side of lateral arm plate (E 53645). A starte Bed, $\times\,10.$

- Fig. 6. Lateral view of proximal vertebra (E 53646). A starte Bed, $\times \, 10.$
- Fig. 7. Jaw plate (E 53647). Starfish Bed, ×10; a, adradial; b, internadial; c, ventral surface.
- Fig. 8. Radial shield (E 53648). Starfish Bed, $\times 10$; a, dorsal; b, inner side.
- Fig. 9. Oral shield (E 53649). Starfish Bed, $\times 10$; a, ventral surface; b, inner side.

Fig. 10. Genital plate (E 53650). Starfish Bed, $\times 10$; a, surface; b, adradial side; c, internadial side.





Figs. 1–9. Ophiura bartonensis n.sp., p. 68. Bartonian, near Barton in England. Collection of the British Museum.

Fig. 1. Dorsal side, reconstructed.

Fig. 2. Dorsal side of holotype (E 52158), \times 5. Bartonian, Highcliff Sands. Highcliff near Barton. Fig. 3. Fragment of arm (E 53651), \times 10. Lower Barton Beds (horizon A 3). Highcliff near Barton. a, dorsal; b, right side; c, ventral; d, distal end.

Fig. 4. Internadial edge of disc (E 53652), $\times\,10.$ Lower Barton Beds (horizon A 3). Higheliff near Barton.

Fig. 5. Surface of lateral arm plate (E 53653), $\times 20$. Middle Barton Bed (horizon E) at Barton. Fig. 6. Internadial marginal plate (E 53654), $\times 10$. Middle Barton Bed (horizon E), Barton. a, surface; b, edge; c, inner side.

Fig. 7. Radial shield (E 53655), $\times\,10.$ Middle Barton Bed (horizon E), Barton. a, dorsal surface; b, inner side.

Fig. 8. Genital plate (E 53656), \times 10. Middle Barton Bed (horizon E), Barton. a, surface; b, inner side. Fig. 9. Vertebra (E 53657), \times 20. Middle Barton Bed (horizon E), Barton. a, proximal; b, lateral; c, distal.



- Figs. 1-9. Ophiura carpelloides n. sp., p. 71. Bartonian, Middle Barton Beds (horizon E). Barton in England. \times 10. Collection of the British Museum.
 - Fig. 1. Holotype, lateral arm plate (E 53658); a, proximal; b, inner side; c, anterior; d, lateral.
 - Fig. 2. Arm joint, recombined (E 53659); a, proximal; b, dorsal.
 - Fig. 3. Radial shield (E 53660); a, dorsal; b, inner side; c, distal edge.

 - Fig. 4. Vertebra (E 53661); a, distal; b, lateral.
 Fig. 5. Proximal end of first vertebra (E 53662).
 Fig. 6. Ventral arm plate (E 53663); a, proximal and ventral surface; b, inner side.
 - Fig. 7. Genital plate (E 53664); a, surface; b, inner side.
 - Fig. 8. Oral shield (E 53665); a, surface; b, inner side.
 - Fig. 9. Jaw (E 53666); a, adradial; b, ventral; c, interradial.

Figs. 10-15. Ophiura davisi n.sp., p. 75. Bartonian, Middle Barton Beds (horizon E). Barton in England. \times 10. Collection of the British Museum.

- Fig. 10. Lateral arm plate (E 53667); a, lateral; b, distal; c, inner side.
- Fig. 11. Holotype, lateral arm plate from the disc (E 53668); a, lateral; b, distal; c, inner side.
- Fig. 12. Lateral arm plate from the disc (E 53669); a, lateral; b, distal; c, inner side.
- Fig. 13. Arm joint and lateral arm plate, recombined (E 53670); a, proximal; b, ventral.
 Fig. 14. Vertebra (E 53671); a, distal end; b, lateral.
 Fig. 15. Oral shield (E 53672); a, ventral surface; b, inner side.



- Fig. 1. Isselicrinus subbasaltiformis (Miller, 1821), p. 17. Theca and arms, $\times 1.9$. Ypresian, Rösnäs Clay. Trelde Næs in Denmark. Geological Museum, Copenhagen (12755). Also plate 1 fig. 5.
- Fig. 2. Coulonia colei (Forbes, 1852), p. 41. Cast from impression of ventral side in diatomaceous clay; × 4.5. Ypressian, Mo-Clay Formation. Mors in Denmark. Geological Museum, Copenhagen (12802).
- Fig. 3. Coulonia colei (Forbes, 1852). Cast from impression of dorsal side in diatomaceous clay; × 3.4. Ypresian, Mo-Clay Formation. Fur in Denmark. Palaeontologic Institute, Uppsala (DM 12). Cast in Geological Museum, Copenhagen (12803).



- Fig. 1. Coulonia colei (Forbes, 1852), p. 41. Dorsal side, \times 1.2. Ypresian, London Clay. Highgate in London. British Museum (E 428). Also plate 3 figs. 9–13.
- Fig. 2. Coulonia colei (Forbes, 1852). Holotype, × 1.37. Ypresian, London Clay. Isle of Sheppey, England. Geological Survey, London (49173). Also Forbes (1852) plate 4 fig. 3.
- Fig. 3. Hippasteria tuberculata (Forbes, 1852), p. 48. Dorsal side of arm, × 1.33. Ypresian, London Clay. Isle of Sheppey, England. British Museum (E 52242). Also plate 4 fig. 5.
- Fig. 4. Hippasteria tuberculata (Forbes, 1852). Dorsal side, × 1.6. Ypresian, London Clay. Isle of Sheppey, England. Geological Survey, London (99787). Also plate 4 fig. 1.
- Fig. 5. Teichaster stokesii (Forbes, 1848), p. 52. Dorsal side, × 1.4. Ypresian, London Clay. Isle of Sheppey, England. British Museum (E 38587). Also plate 5 fig. 7.
- Fig. 6. Coulonia colei (Forbes, 1852). \times 0.97. Y
presian, London Clay. Isle of Sheppey, England. British Museum (E
 75909).
- Fig. 7. Echinaster jacobseni n.sp., p. 57. Holotype. Cast from impression of ventral side in diatomaceous clay, × 4.5. Ypresian, Mo-Clay Formation. Silstrup Cliff, Denmark. Geological Museum, Copenhagen (12769). Also plate 5 fig. 14.


PLATE 13

- Fig. 1. Ophiura furiae n.sp., p. 62. Ventral side of holotype (below), and remains of three other specimens in the weathered surface of a calcareous concretion from diatomaceous clay. × 4.25. Mo-Clay Formation, Fur in Denmark. Geological Museum. Copenhagen (12800–12801). Also plate 6 figs. 4–5.
- Fig. 2. Ophiura wetherelli Forbes, 1852, p. 64. Dorsal side of decalcified specimen in Oldhaven Beds. Lower Upnor, Kent in England; × 7.5. British Museum (E 53243). Also plate 7 fig. 1.
- Fig. 3. Ophiura wetherelli Forbes, 1852. Specimens figured by Davis (1923) from the London Clay of New Malden, England; × 3.75. British Museum (E 13702).



PLATE 14

- Fig. 1. Ophiura bognoriensis n.sp., p. 66. Holotype. Ypresian, Lower Clay (Starfish Bed) of Bognor Regis, England. British Museum (E 13761). Also plate 8 fig. 1. a, dorsal side, $\times 2$; b, ventral side of arm, $\times 5$.
- Fig. 2. Ophiura bartonensis n.sp., p. 68. Holotype. Bartonian, Highcliff Sands of Highcliff near Barton. Dorsal side, \times 5. British Museum (E 52158). Also plate 9 fig. 2.
- Fig. 3. Ophiura bartonensis n. sp. Ventral side, \times 9. Bartonian, Lower Barton Beds (horizon A 3) of Highcliff. British Museum (E 53673).
- Fig. 4. Ophiura bartonensis n.sp. Several specimens in Highcliff Sands; \times 1.6. Bartonian, Lower Barton Beds (horizon A 3) of Highcliff. British Museum (E 53674).



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