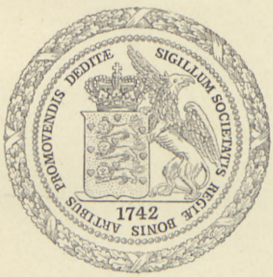
DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB KØBENHAVN.

BIOLOGISKE MEDDELELSER

UDGIVET AF

DET KGL. DANSKE VIDENSKABERNES SELSKAB

BIND XVII



KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942—43

INDHOLD

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 1

THE VENTILATION
OF THE
RESPIRATORY TRACT IN BIRDS

BY

ERIK ZEUTHEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

Printed in Denmark.
Bianco Lunos Bogtrykkeri A/S.

I. EXPERIMENTS ON THE HEN AT REST

A. Earlier investigations on the respiration of birds[1].

a. **Anatomy.** The lung of the bird is a relatively small organ which is confined to the dorsal part of thorax where it is attached to the wall of thorax. The ribs are wedged into the dorsal surface of the lung where they form rather deep furrows. The lungs are ventrally bounded by the pulmonary diaphragm, a formation peculiar to birds. This diaphragm is to be considered as the ventral surface of the lungs themselves. It is a membrane of connective tissue with weak musculature. It arches slightly up into the lungs — hence it must be assumed that the lungs will expand slightly by its contraction. The pulmonary diaphragm is perforated by a number of holes, the ostia. The bronchi of the lung penetrate through these holes and are connected with a number of air sacs which are inserted between the organs of the body cavity. The air sacs frequently also penetrate into the marrow of the bones (being nearly always found, for example, in the humerus and the femur), and they may even extend beneath the skin. Since a diaphragm of the mammalian type is absent, the air sacs lie in one large thoraco-abdominal space. There are 4 air sacs on either side. Named from the front, they are: The interclavicular sac (between the clavicles), the prethoracic sac (level with the lung), the postthoracic sac (at the posterior edge of the lung), and the abdominal sac (filling a large part of the abdomen)[2]. The interclavicular sac is in open connection with the corresponding sac on the other side;

[1] It is not the intention to give a complete review of the literature. Such a review will be found in WINTERSTEIN (1921) and SCHARNKE (1934).

[2] At the very front we find the unpaired cervical sac, but it is very small and unimportant and will not be taken into consideration here.

the other sacs are free. While the air sacs in the duck, for example, constitute about 20 % of the body volume, the lungs are small, as mentioned, and tissue + air of the lung represent only 1—2 % of the body volume. In comparison it may be noted that the air of the lungs in man occupies about 5 % of the body volume.

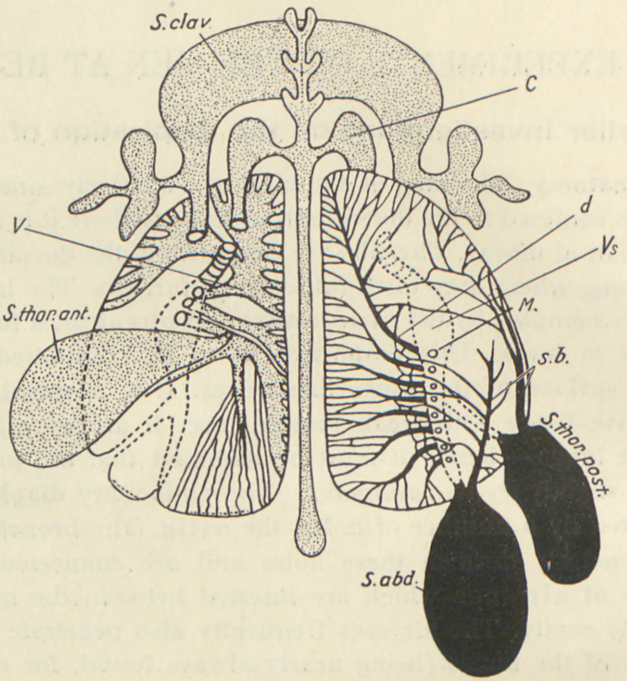


Fig. 1. (From BRANDES)
Lung of a pigeon, seen from the ventral side (left) and from the dorsal side (right).

C:	Cervical sac	*M*:	Mesobronchus
S. clav.:	Interclavicular sac	*V*:	Ventrobronchi
S. thor. ant.:	Prethoracic sac	*d*:	Dorsobronchi
S. thor. post.:	Postthoracic sac	*s. b.*:	Saccobronchi
S. abd.:	Abdominal sac	*Vs*:	Vestibulum

The bronchial system of the lungs is very complicated. Fig. 1 (from BRANDES (1924)) shows, very schematically, the lung of a pigeon, seen from the dorsal side (right) and from the ventral side (left). The trachea and its two branches (the main bronchi) are not shown, but it is seen how the continuation of the main

bronchus, mesobronchus, (*M*) runs through the entire lung, ending, after a single ramification, in the 2 posterior sacs (the abdominal and the postthoracic sac). A number (5—6) of ventrobronchi (*V*) start from the anterior extended part of the mesobronchus, the vestibulum (*Vs*) (fig. 1 left) and branch out on the ventral surface of the lung. 8 to 10 dorsobronchi (*d*) start from the mesobronchus, back of the ventrobronchi (fig. 1 right); their ramifications spread over the dorsal surface of the lung. These two systems of ramified bronchi do not end blindly, but are connected by means of a number of narrow tubes, the air pipes or parabronchi (diameter 0.2—0.5 mm.). The parabronchi run throughout the entire lung tissue in dorsoventral direction. It should also be mentioned that the two anterior air sacs (the interclavicular and the prethoracic sacs) open into the ventrobronchi.

The above mentioned bronchi have been known for a long time. An entirely new system of bronchi, the saccobronchi, was discovered in 1910 by SCHULZE. The saccobronchi form an extra connection between air sacs and lung. The anterior sacs are in this way connected once more directly with the ventrobronchi, but the saccobronchi of the posterior sacs (*s. b.* in fig. 1) are connected with a number of longitudinally running parabronchi in the lateral part of the lung. These parabronchi open towards the front into the ventrobronchi.

The exchange of gases in the lung must be supposed to take place in the air capillaries. These are extremely fine tubes (10—20 μ) which radiate in a very large number from the individual parabronchi. The air capillaries intercommunicate. They are entangled with an equally dense meshwork of blood capillaries, and there is so intimate contact between blood and air capillaries that the question of a common epithelium has been raised.

b. **The mechanics of the respiratory movements and other physiological investigations.** The thorax of birds is very strong. It is cranially and ventrally bounded by the arc consisting of caracoids, clavicles and sternum, on the side by the articulated ribs, and dorsally by the short and rigid vertebral column. In contrast to what is found in man, the respiratory movements in birds are brought about almost exclusively by

means of movements of the ribs. Both inspiration and expiration are active, since we do not find in birds the forces which in man drive the passive expiration, viz., the DONDER pressure and the inspiratory twisting of the costal cartilages. The reason is that costal cartilages are lacking, and the avian lungs are not elastically distended. They may be removed from the body without suffering any essential change of form.

During inspiration, the thorax is expanded in all directions (SOUM (1896), BAER (1896) and ZIMMER (1935)). The ribs move forward and outward, and the arc consisting of caracoids, clavicles, and sternum swings forward and downward with the shoulder as the fixed fulcrum; it follows that the posterior edge of the sternum performs the largest movements during the respiration. Since all the air sacs, as mentioned, are located in one large thoraco-abdominal space, it follows that all sacs, as shown by SOUM, are exposed at the same time to negative pressure and to excess pressure respectively, and hence inspire and expire simultaneously, provided the bronchi leadings to the sacs are open. VOS (1935) tried to form an opinion regarding the participation of the individual air sacs in the ventilation. He let a resting duck inspire pure oxygen, and showed that the increase in the percentage of oxygen was far slower in the anterior than in the posterior sacs. Since moreover the last mentioned sacs are considerably larger than the former, VOS could conclude that the posterior sacs in the duck played a dominating rôle in the respiration at rest. The results of VOS are in harmony with the above mentioned fact, that the amplitude of the respiratory movements is the greatest at the posterior end of sternum.

As mentioned, the lungs are very small in proportion to the sacs, and for this reason alone it does not seem probable that the lungs should be able during inspiration to take up any substantial part of the inspiration volume. That the lungs do expand during inspiration has been shown by SOUM, but the same author also showed that the inspiratory expansion of the lungs was inhibited by the pulmonary diaphragm which contracts during expiration, in direct contrast to the diaphragm in man.

Thus the results of VOS and SOUM point to the air sacs as the parts of the respiratory system which are ventilated by the respiratory volume fluctuations. A question immediately presents

itself. Does a substantial part of the exchange of gases between blood and air take place in the walls of the air sacs? The question must be answered in the negative. The total surface of the air sacs is rather small (of the same of order of magnitude as the surface of the body), and the walls of the air sacs are supplied with blood to an exceedingly slight extent. Moreover, SOUM was able to lead pure CO through an abdominal sac, the ostia of which had been blocked, without obtaining any toxic symptoms in his experimental animal (pigeon); the experiment lasted 15 minutes. Thus the whole exchange of gases must take place in the lungs, and, since the lungs do not undergo any essential fluctuations of volume, air must flow through them in one or in both phases of respiration.

The lungs are inserted between the trachea and the air sacs, and the air sacs have therefore always been considered to be the bellows that ventilate the lungs. It has always been a riddle, however, how the air current could ventilate the respiratory parts of the lung when the air sacs are directly connected with the trachea through the largest bronchi of the lung (mesobronchus and ramifications), while the respiratory sections are connected onto this main line through narrow side channels. First BRANDES (1924) and then BETHE (1925) thought to solve this problem by assuming the presence of a large number (13—15) of valves or muscular sphincters in each lung. These valves should work in time with the respiration and thus force all the air through the parabronchi — according to the theory of BETHE in such a way that the direction of flow in the parabronchi was the same (dorso-ventral) in both phases of respiration.

The theories of BRANDES and BETHE are purely speculative. And the attempts of later authors to substantiate them must be considered to have failed (DOTTERWEICH (1930 1. and 2., 1936), WALTER (1936), SCHARNKE (1934, 1938), VOS (1935)). Thus it has been impossible to demonstrate the presence of valves or sphincters in the lung of the bird. We are therefore still in need of an answer to the question of how the ventilation of the lung is achieved by a flow of air if, as it is generally assumed, the main connection between trachea and air sacs passes by the respiratory parts of the lungs.

B. The author's own investigation.

1. Introduction.

Based on the data of FISCHER (1905) and SCHULZE (1910) the author has been able to draw a highly schematized diagram of the lung of the hen (fig. 2). The 2 anterior air sacs are combined into one, and the same applies to the 2 posterior sacs. The 5 ventrobronchi and the 8 dorsobronchi are represented by one of each. The same applies to the saccobronchi of which each sac actually has several. For the purpose of clearness the drawing shows the medial parabronchial system, the main direction of which is dorso-ventral, turned an angle of 90° so that it is now located in the plane of the paper. FISCHER made a large number of measurements of the diameters of the individual bronchi, and it was possible, on this basis, to calculate the cross sectional areas of the most important bronchi with a fair degree of accuracy. The results are recorded at the extreme right of the figure. The cross section of the mesobronchus has not been measured by FISCHER, but it is narrower than the main bronchus (which has been measured) before its entrance into the lung. The figures show the surprising result that the aggregate cross sectional area of all ventrobronchi as well as all dorsobronchi is definitely larger than the cross sectional area of mesobronchus. Finally, the total cross sectional area of the parabronchi is at least 10 times as large as the cross sectional area of the mesobronchus. The saccobronchi were not known to FISCHER, but their total cross sectional area is (according to SCHARNKE (1938)) of about the same magnitude as the cross sectional area of the mesobronchus.

Until now it has been considered a basic principle of the physiology of the avian lung that the bronchi leading to the respiratory section of the lung should be very narrow in relation to mesobronchus. This idea must be abandoned. Moreover, since there is a distance of about 10 mm. between the points at which a ventrobronchus and its connected dorsobronchus open into the mesobronchus, it follows of necessity that the air which reaches the ventrobronchi from the trachea during the inspiration has two possible paths to follow in its further progress towards the posterior air sacs (these, as it will be shown, being by far the most important of the air sacs), namely, either the short passage

through mesobronchus, or the longer, but wider through ventrobronchi, parabronchi and dorsobronchi (or saccobronchi). The

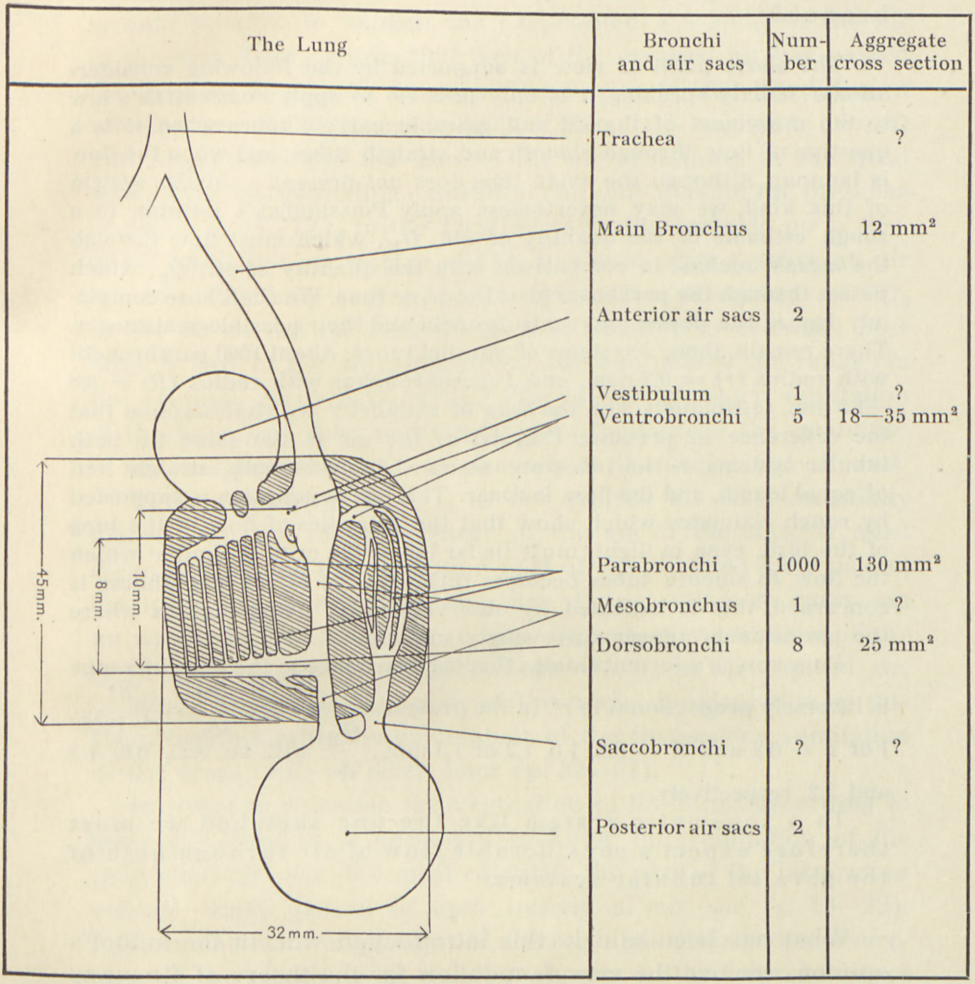


Fig. 2. Diagram of the hen's lung.
For explanation see text.

same passages must be considered to be open for the expiratory air, moving in the opposite direction. The ratio between the quantities of air which pass either way during the inspiration or expiration must be determined by the resistance to the air current of the passages in question. Nothing definite can be said

regarding the resistance of these passages, but it would seem probable that a not unsubstantial part of the air passing to or from the air sacs must pass through the parabronchi.

The above point of view is supported by the following considerations: Strictly speaking, it is only possible to apply POISSEUILLE's law to the movement of liquids and gases in narrow tubes when it is a question of flow through smooth and straigth tubes, and when the flow is laminar. Although the avian lung does not present a tubular system of this kind, we may nevertheless apply POISSEUILLE's formula to a rough estimate of the quantity of air, Q_M, which must flow through the mesobronchus, in comparison with the quantity of air, Q_p, which passes through the parabronchi at the same time. We shall here completely ignore the dorso- and ventrobronchi and their possible resistances. There remain, then, 2 systems of parallel tubes: About 1000 parabronchi with radius (r) = 0.2 mm., and 1 mesobronchus with radius (R) = 0.8 —1.5 mm. (estimated). For the sake of simplicity we shall assume that the difference in pressure that drives the air is the same for both tubular systems — the tubes are assumed to be smooth, straight and of equal length, and the flow laminar. The last assumption is supported by rough estimates which show that the velocities of flow in the lung of the bird, even in flight, must lie far below the critical limit at which the flow in smooth tubes becomes turbulent. As far as smoothness is concerned, this is indicated by observations on living pigeons where the parabronchi appear surprisingly smooth.

POISSEUILLE's formula states that the resistance to the flow in a tube is inversely proportional to r^4. In the present case we find $\frac{Q_M}{Q_p} = \frac{R^4}{r^4 \cdot 1000}$. For r = 0.2 and R = 0.8, 1.0, 1.2 or 1.5 mm., $\frac{Q_M}{Q_p}$ will be 0.25, 0.6, 1.3 and 3.2, respectively.

In a schematic system like the one sketched we must therefore expect a considerable flow of air through both of the parallel tubular systems.

What has been said in this introduction will, in the author's opinion, remove the very foundation for the theory of BRANDES and BETHE.

The purpose of this paper is first of all to ascertain whether the avian lungs are actually ventilated in both inspiration and expiration, and, next, to obtain as far as possible a measure of

the ventilation of the lung in both phases of respiration. The following may be said regarding the principles on which the investigation is based: As already pointed out by Vos (1935) it is only possible to explain the CO_2-content ($> 2\ ^0/_0$) of the air in the sacs if we assume that part of the inspired air has passed the lung on its way to the sacs. The reason is that the diffusion into the sacs of CO_2 from the walls of the sacs is negligible (Soum) and inspiration into the sacs of the air remaining in the dead space from the preceding expiration can only explain the presence of about $0.5\ ^0/_0$ CO_2 in the sacs (see also the footnote on p. 25). If we know the percentage of CO_2 in the air that reaches an air sac from the lung (say $6\ ^0/_0$) as well as the percentage of CO_2 in the air of the sac (say $3\ ^0/_0$), it is possible to calculate how large a part of the air going to the sac has passed the lungs (in the example given it is $50\ ^0/_0$). The total respiratory ventilation of the lungs can then be calculated as the sum of the quantities of air that pass the lungs on the way to the individual air sacs.

If the percentage of CO_2 in the expired air is substantially higher than the CO_2-percentage of the air of the sacs, it must mean that during the expiration part of the air must have passed the lungs on its way from the sacs. It is possible to carry out an approximate calculation of the expiratory ventilation of the lungs on the basis of the percentage of CO_2 in the expired air, in the air sacs, and in the air of the lungs. A calculation of this kind, together with the calculation of the inspiratory ventilation of the lungs, will be given later (p. 33—37).

In order to calculate the ventilation of the lungs according to these principles it is necessary to know the ventilation of the individual air sacs. We must calculate the part of the inspiration volume which passes to each individual air sac (p. 13—22). Experiments with inspiration of a foreign gas (H_2) and measurement of the velocity with which it appears in the individual sacs will form the basis for these calculations.

It will be found (p. 22—26) that the previously mentioned calculation of the ventilation of the lungs is only possible after thorough considerations and calculations on the exchange of gases in the avian lung. These considerations will be outlined on p. 27—33.

regarding the resistance of these passages, but it would seem probable that a not unsubstantial part of the air passing to or from the air sacs must pass through the parabronchi.

The above point of view is supported by the following considerations: Strictly speaking, it is only possible to apply POISSEUILLE's law to the movement of liquids and gases in narrow tubes when it is a question of flow through smooth and straigth tubes, and when the flow is laminar. Although the avian lung does not present a tubular system of this kind, we may nevertheless apply POISSEUILLE's formula to a rough estimate of the quantity of air, Q_M, which must flow through the mesobronchus, in comparison with the quantity of air, Q_p, which passes through the parabronchi at the same time. We shall here completely ignore the dorso- and ventrobronchi and their possible resistances. There remain, then, 2 systems of parallel tubes: About 1000 parabronchi with radius (r) = 0.2 mm., and 1 mesobronchus with radius (R) = 0.8—1.5 mm. (estimated). For the sake of simplicity we shall assume that the difference in pressure that drives the air is the same for both tubular systems — the tubes are assumed to be smooth, straight and of equal length, and the flow laminar. The last assumption is supported by rough estimates which show that the velocities of flow in the lung of the bird, even in flight, must lie far below the critical limit at which the flow in smooth tubes becomes turbulent. As far as smoothness is concerned, this is indicated by observations on living pigeons where the parabronchi appear surprisingly smooth.

POISSEUILLE's formula states that the resistance to the flow in a tube is inversely proportional to r^4. In the present case we find $\frac{Q_M}{Q_p} = \frac{R^4}{r^4 \cdot 1000}$. For r = 0.2 and R = 0.8, 1.0, 1.2 or 1.5 mm., $\frac{Q_M}{Q_p}$ will be 0.25, 0.6, 1.3 and 3.2, respectively.

In a schematic system like the one sketched we must therefore expect a considerable flow of air through both of the parallel tubular systems.

What has been said in this introduction will, in the author's opinion, remove the very foundation for the theory of BRANDES and BETHE.

The purpose of this paper is first of all to ascertain whether the avian lungs are actually ventilated in both inspiration and expiration, and, next, to obtain as far as possible a measure of

the ventilation of the lung in both phases of respiration. The following may be said regarding the principles on which the investigation is based: As already pointed out by Vos (1935) it is only possible to explain the CO_2-content ($> 2\ ^0/_0$) of the air in the sacs if we assume that part of the inspired air has passed the lung on its way to the sacs. The reason is that the diffusion into the sacs of CO_2 from the walls of the sacs is negligible (Soum) and inspiration into the sacs of the air remaining in the dead space from the preceding expiration can only explain the presence of about $0.5\ ^0/_0$ CO_2 in the sacs (see also the footnote on p. 25). If we know the percentage of CO_2 in the air that reaches an air sac from the lung (say $6\ ^0/_0$) as well as the percentage of CO_2 in the air of the sac (say $3\ ^0/_0$), it is possible to calculate how large a part of the air going to the sac has passed the lungs (in the example given it is $50\ ^0/_0$). The total respiratory ventilation of the lungs can then be calculated as the sum of the quantities of air that pass the lungs on the way to the individual air sacs.

If the percentage of CO_2 in the expired air is substantially higher than the CO_2-percentage of the air of the sacs, it must mean that during the expiration part of the air must have passed the lungs on its way from the sacs. It is possible to carry out an approximate calculation of the expiratory ventilation of the lungs on the basis of the percentage of CO_2 in the expired air, in the air sacs, and in the air of the lungs. A calculation of this kind, together with the calculation of the inspiratory ventilation of the lungs, will be given later (p. 33—37).

In order to calculate the ventilation of the lungs according to these principles it is necessary to know the ventilation of the individual air sacs. We must calculate the part of the inspiration volume which passes to each individual air sac (p. 13—22). Experiments with inspiration of a foreign gas (H_2) and measurement of the velocity with which it appears in the individual sacs will form the basis for these calculations.

It will be found (p. 22—26) that the previously mentioned calculation of the ventilation of the lungs is only possible after thorough considerations and calculations on the exchange of gases in the avian lung. These considerations will be outlined on p. 27—33.

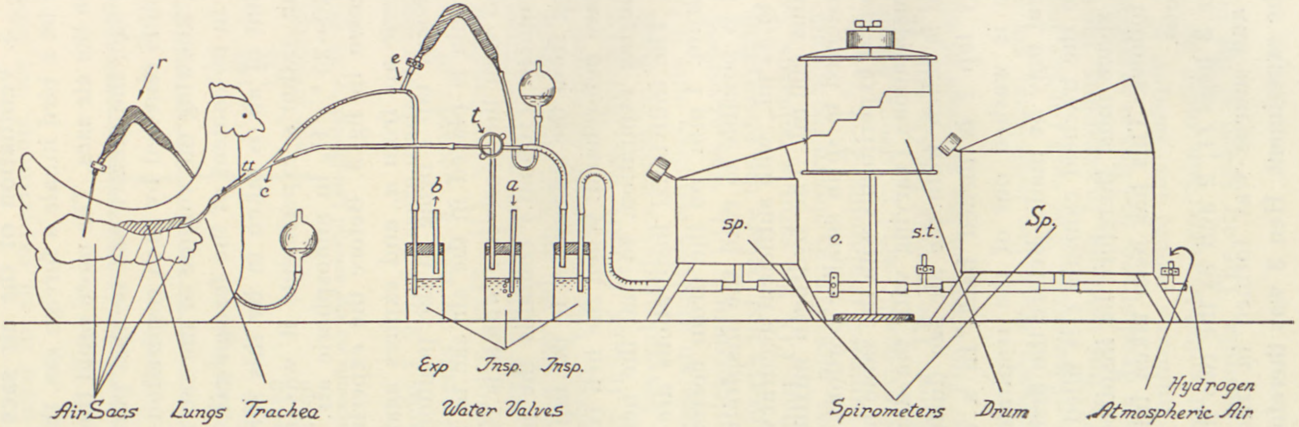


Fig. 3. Apparatus for investigating the ventilation of the air sacs.

t. t. Connection of the tracheal cannula with trachea
c. Ramification of the tracheal cannula
e. Side tube for sampling of the expiration air
t. Three-way tap
sp. and *Sp.* Spirometers with hydrogen mixture
o. Pinchcock for stopping between the spirometers
s. t. Side tube for sampling of the hydrogen mixture
r. Receiver for air samples

but the intact trachea was connected directly with the tubing of the apparatus by means of a curved glass tube which was led from the mouth cavity down through the glottis and fitted closely to the walls of trachea. The formation of mucus was insignificant in this hen since the cannula was removed after each experiment. The coughing reflex was partly inhibited by intramuscular injection of 0.4—0.8 mg. of codein. Hens 1 and 2 sat free and quietly on the table, while hen 3 had to be fixed in a suitable manner.

After the experiments the inspiratory volumes of the air sacs were determined as follows: The hen was strangled in the position of inspiration and was then frozen in this position. Openings were now made into the individual air sacs, and the sacs were filled with melted paraffin (Vos' method). The weight of the paraffin blocks after hardening, and the specific gravity of the paraffin, could then be used in calculation of the volumes, taking into account the contraction of the paraffin upon cooling.

At inspiration the air is heated from room temperature to the body temperature of the hen (about 40°) and is, at the same time, saturated with water vapour at 40°. Correction has been made in the calculations for the expansion due to the increase in temperature, by figuring in the above volume determinations the volume of the sacs at the temperature of the experiment, not at 40°. The expansion caused by the higher vapour pressure at body temperature has not been taken into account. The resulting error is insignificant.

As an example of how the volume of air which is taken up by an air sac per inspiration can be calculated from the increase measured in the H_2-percentage of the sac, we shall here give the calculation of the ventilation of the right abdominal sac in hen 3, in the experiment of 25.I.1941 (see table 4). In the inspiratory position the right abdominal sac holds 28 ml. The hen inspired a mixture containing 12.2 % H_2. After 3 inspirations the air of the sac contained 9.2 % H_2. Trial and error methods were used in the calculations. First, an attempt was made to find out whether inspiration into this sac of 40 or 50 % of the total inspiration volume of the hen in the course of 3 inspirations could bring the H_2-percentage of the sac up to the measured H_2-percentage of the inspired hydrogen mixture. It was found that the assumed

40 % led to a too small, and the 50 % to a too large increase in the H_2-content of the sac. By narrowing this down it was found that 47 % of the inspiration volume of the hen was taken up by the air sac investigated. This final calculation is reported below. In this calculation it has been assumed as reasonable that also 47 % of the dead space air (trachea + mesobronchus = 5.4 ml.),

Calculation.

1st. inspiration: 30 ml.

Dead space + air of the lung:

$$\frac{(5.0+5.4)\cdot 47}{100} + 2.2 = 7.1 \text{ ml.}$$

Hydrogen mixture:

$$\frac{30\cdot 47}{100} - 7.1 = 7.0 \text{ ml. } H_2\text{-mixture}$$

After 1st. inspiration: 7.0 ml., or 25 % of the volume of the air sac (28 ml.).

Expiration:

$$\frac{14.1\cdot 25}{100} = 3.5 \text{ ml.}$$

Residue in sac 3.5 ml. H_2-mixture

2nd. inspiration: 34 ml.

Dead space + air of the lung:

$$\frac{5.4\cdot 47}{100} + 2.2 = 4.7; \quad \frac{4.7\cdot 25}{100} = 1.2 \text{ ml.} \quad —$$

Hydrogen mixture:

$$\frac{34\cdot 47}{100} - 4.7 = 11.3 \text{ ml.} \quad —$$

After 2nd. inspiration: 16.0 ml., or 57 % of the volume of the air sac.

Expiration:

$$\frac{16.0\cdot 47}{100} = 9.2 \text{ ml.}$$

Residue in sac 6.8 ml. H_2-mixture

3rd. inspiration: 34 ml.

Dead space + air of the lung:

$$\frac{5.4\cdot 47}{100} + 2.2 = 4.7; \quad \frac{4.7\cdot 57}{100} = 2.7 \text{ ml.} \quad —$$

Hydrogen mixture:

$$\frac{34\cdot 47}{100} - 4.7 = 11.3 \text{ ml.} \quad —$$

After 3rd. inspiration: 20.8 ml., or 75 % of the volume of the air sac.

and at the 1st inspiration also 47 % of the air standing in the inspiration tubing from *t* to *c* (5 ml.) have been inspired by this sac. In this as in all calculations on the ventilation of the abdominal sacs it has been assumed that 40 % of the air from both lungs pass to each abdominal sac; this corresponds to 2.2 ml. It is moreover assumed that the dead space and the lung before each inspiration contain air of the H_2-percentage which was attained in the sac at the previous inspiration. Finally, it is also assumed that each inspiration is followed by an equally large expiration.

The reliability of this calculation is essentially dependent on the accuracy with which the volumes of the sac and the lung can be determined, and this accuracy is certainly not great. Thus the volume of the lung is simply determined by perfusion of a lung with warm paraffin from the main bronchus, followed by a melting off and weighing of the paraffin. In order to investigate the possible magnitude of the error of calculation, an examination has been made (using the above calculation as example) to determine within what limits the result will vary when we vary the volume of the air sac and the volume of the lung within wide limits. The variations which the author considers possible are shown in braces in table 2. It will be seen from this that the percentage found in the example used may be given as 47 ± 5 %.

In the calculation of the ventilation of the small pre- and postthoracic sacs we encounter the great difficulty that the dead space (trachea + large bronchi) as well as the volume of the lung prove to be large in proportion to the quantity of air taken in by these sacs per inspiration (about 20 % of the inspiration volume). In the calculations, which are therefore subject to a large percentage but a small absolute error, it has been assumed that 10—15 % of the air from the dead space and from the lung are inspired by the prethoracic sacs, and 10—5 % by the postthoracic sacs. The interclavicular sac in the hen is much smaller than in the duck. The author did not succeed in puncturing it, and its ventilation has therefore not been measured. In the calculations based on the experiments by Vos on the duck (to be reported later) it was found that the ventilation of the interclavicular sac is almost zero. The same is probably true in case of the hen.

Table 2.

Air sac volume ml.	air space of the lung ml.	Per cent of inspired air passing to the air sac
22	2.2	40
25	2.2	44
28	2.2	47
31	2.2	52
34	2.2	56
28	0	40
28	1	43
28	2	46
28	3	51
28	4	55

The effect on the calculated result (last column) of (1) varying the volume of the air sac (1st. column) with constant air space of the lung, and (2) varying the air space of the lung (2nd. column) while keeping the air sac volume constant.

Table 3.

The volumes of the different air spaces of the hen's respiratory tract, corrected to the temperature of the experiments (ml.).

Hen No.	Abdominal air sacs	postthor. air sacs	prethor. air sacs	intercl. air sac	Volume of the whole lung	Volume of the air space of lung	Dead space
1	left 25 right 38	6 ..	12 ..	9	.. 8	.. 3	1.1
2	left 32 right 44	2.1 2.0	9 8	..	.. ..	.. ..	1.0
3	left 18 right 28	2 to 3 3 to 4	5 to 6 7 to 8	9	.. 10	.. 2.5	2.7 [1] 5.4 [2]

[1]) Without cannula. [2]) With cannula.

Results: Table 3 records, for the hens employed, the volume determinations of the air sacs, the lungs, and the dead space (mesobronchus and trachea up to the branching out of the tracheal cannula). Table 4 records all experiments and results of calculations dealing with the ventilation of the air sacs. Hen 1 was suffocated by mucus in trachea on the second night after the operation. It probably died in the position of expiration, or

Table 4.

The ventilation of the different air sacs of the hen.

Hen and date	air sac	inspirations		hydrogen in the		a/b	dead space ml.	% of insp. air passing to the air sac
		frequency per min.	depth ml.	air sac a per cent after insp.	insp. air b per cent			
1. 4. XII 1940	right abdom.	16	14.0 15.3 14.7 16.3 16.1 16.4	8.3	14.2	0.58	1.1+5 1.1 1.1 1.1 1.1 1.1	51
1. 4. XII 1940	left abdom.	24	12.3 15.0 12.4 15.7 15.1 13.8	8.3	14.2	0.58	1.1+5 1.1 1.1 1.1 1.1 1.1	46
1. 4. XII 1940	left post-thor.	24	12.8 12.7 13.0 14.2 12 6 14.0	7.2	14.2	0.51	1.1+5 1.1 1.1 1.1 1.1 1.1	6
1. 4. XII 1940	right pre-thor.	18	13.1 13.1 14 4 16.0 14.1 14.8	5.3	14.8	0.36	1.1+5 1.1 1.1 1.1 1.1 1.1	8
2. 18. XII 1940	right abdom.	14	22 8 19.7 28.7 29.0 23.5	9.2	15.6	0.59	1.1+5 1.1 1.1 1.1 1.1	42
2. 18. XII 1940	left abdom.	15	22.9 23.2 26.4 23.7 22.5	10.9	15.6	0.70	1.0+5 1.0 1.0 1.0 1.0	42
2. 18. XII 1940	right post-thor.	21	18.6 17.5 17.3 17.0	7.3	22.0	0.33	1.0+5 1.0 1.0 1.0	1.5

(continued.)

Table 4 (continued).

Hen and date	air sac	inspirations		hydrogen in the		a/b	dead space ml.	% of insp. air passing to the air sac
		frequency per min.	depth ml.	air sac a per cent after insp.	insp. air b per cent			
3. 20. I 1941	left abdom.		37.0 36.0 37.0 34.0	14.6	17.0—18.0	0.81—0.86	5.4+5 5.4 5.4 5.4	31—33
3. 25. I 1941	right abdom.	13	30.0 34.0 34.0	9.2	12.2	0.75	5.4+5 5.4 5.4	47
3. 29. I 1941	left abdom.	15	23.0 20.0 35.0 37.0	19.0	22.8	0.83	5.4+5 5.4 5.4 5.4	34
3. 1. II 1941	right pre-thor.	15	47.0 43.0	2.9	11.8	0.25	5.4+5 5.4	4
3. 4. II 1941	right post-thor.	14	35.0 37.0	4.0	21.4	0.19	5.4+5 5.4	1.5
3. 4. II 1941	right post-thor.	14	36.0 34.0 41.0 32.0	12.6	21.4	0.59	5.4+5 5.4 5.4 5.4	3

The deep inspirations of hen 3 are due to the low temperature (5—10°) of these experiments and the resulting high metabolism. The temperature was about 20° in case of hens 1 and 2.

in the act of expiration. The experiment on this hen is therefore of less value, but it does show the relative ventilation of the individual sacs. It applies to all hens that the increase in H_2-percentage is most rapid in the posterior sacs. The mass of air is here, as in the duck (Vos) renewed more rapidly than in the anterior sacs. The experiments on hens 2 and 3 show that about 80 % (70—90) of the total inspiration volume pass to the abdominal sacs, 8—15 % to the prethoracic sacs, and 3—12 % to the postthoracic sacs. The interclavicular sac presumably takes 0—1 %. Theoretically it should be possible to calculate the inspiratory dilatation of the lungs as the difference between the

total inspiration volume and the sum of the inspiration volumes of the individual sacs, but the figures do not permit a calculation of this kind. Assuming, however, that the percentage expansion of the lungs is of the same magnitude as that of the prethoracic sacs (which lie level with the lungs) we find that the lungs may take up 4 % of the inspiration volume by their increase in volume. Since the pulmonary diaphragm contracts during expiration, it follows that even this figure may be too high.

As a last result we shall emphasize that the percentage participation in the ventilation of the individual sacs is independent of the depth of the inspirations.

4. Ventilation of the air sacs in the duck.

(Calculations based on the experiments by Vos).

As mentioned on page 6 Vos concluded from his oxygen inspiration experiments that the posterior sacs in the duck (the abdominal and postthoracic sacs) play a dominating rôle in the respiration at rest. How dominating a rôle is not apparent until we attempt a calculation of the ventilation of the individual air sacs. Such an attempt is made in table 5. The calculation is

Table 5.

The ventilation of the air sacs of the duck.

air sac	volume determinations ml.	number of experiments	per cent of inspired air passing to the air sac
both abdominal air sacs	65 + 80 = 145	4	49[1])
both postthor. air sacs	27 + 30 = 57	12	23
both prethor. air sacs	11 + 13 = 24	8	3
interclav. air sac	53	11	1
dead space	4		
		Total...	76 per cent

[1]) Vos' experiment No. 3 has not been included in these calculations because it differs distinctly from the other experiments on these air sacs.

based on the principles given above for the hen. Vos did not measure the depth of the individual inspirations, but since he states that the duck was always at rest before and during the experiment, it should be justified to accept a single measurement of the depth of inspiration (35 ml.) as representative of all inspirations. Nor did Vos attempt to measure the volume of the lungs. Hence this volume is not taken into account in the calculations, and the systematic error that follows from this makes the calculated results 10—15 % too low. It is probably because of these sources of errors that we can only account (table 5) for 76 % of the total inspiration volume. Of these 76 %, the 72 % pass to the posterior sacs which are thus playing a very dominating rôle in the respiration at rest. While the postthoracic sacs were of quite secondary importance in the hen, they are essential in the duck. A simple explanation is that the sacs are widely different in size in the two animals (cf. tables 3 and 5).

5. The CO_2-content of the different parts of the respiratory organ.

In continuation of the programme outlined on p. 10—11 we shall now proceed with the measurement of the CO_2 of the air sacs, the expired air, and the air of the lungs, all in the hen at rest.

CO_2-content of the air sacs. At the sampling the hen was partly free and partly connected with the apparatus shown in fig. 3. All air sacs contained CO_2 — frequently a rather large amount. Table 6 shows that the posterior sacs have a CO_2-content which is lower than that of the anterior sacs.

CO_2-content of the expired air (table 6). The hen was connected with the apparatus in fig. 3. Samples were drawn during the whole or a major part of an expiration, from the expiration tube *e*. An exception were the samples from hen 3 on 20.I.1941; they were taken at the close of an expiration. It will be seen that the CO_2-percentage of the first mentioned samples is distinctly lower than that of the latter (20.I.41). This must, at least partly, be attributed to the fact that they also contain CO_2-free air from the dead space.

CO_2-content of the air of the lungs. The hen rested free and quietly on the table. The air of the avian lung cannot be

Table 6.

Carbon dioxide determinations (in per cent) on samples from the air sacs and the expired air. Where also oxygen analyses have been made, the results of these are given in italics below the corresponding carbon dioxide figure.

Hen and date	Abdominal air sacs		Postthoracic air sacs		Prethoracic air sacs		Expired air
	left	right	left	right	left	right	
1. 25. XI. 40	2.1 *18.5*	2.1 *18.3*	..	..	..	..	..
1. 4. XII. 40	3.1	2.6	3.8	..	3.7	..	4.4 5.7 5.8
2. 9. XII. 40	2.0 *19.2*	2.6 *18.4*	4.8 *15.1*	5.8 *14.6*	4.4 *16.7*	5.1 *14.1*	..
2. 18. XII. 40	..	..	..	..	..	..	5.6 *13.3* 5.1 *13.6*
3. 20. I. 41	3.4	..	..	..	..	..	8.1 7.0
3. 22. I. 41	..	..	..	..	..	..	5.9
3. 23. I. 41	..	..	..	..	..	..	5.2
3. 24. I. 41	..	2.7 2.7	..	..	..	..	6.1
3. 28. I. 41	..	..	..	..	..	..	6.6 6.7
3. 29. I. 41	3.4	..	..	..	..	..	..
3. 1. II. 41	..	..	..	..	..	6.4 6.4	..
3. 3. II. 41	..	..	..	..	..	..	5.5
3. 4. II. 41	..	..	6.1 6.6	..	..	..	..
3. 5. II. 41	..	2.9 3.5	..	..	..	..	5.8 6.2 5.9
3. 10. II. 41	..	3.0 3.5	..	..	..	..	..

(continued.)

Table 6 (continued).

Comments:

25. XI: The animal is intact and quiet. Dead space 2.0 ml. Respiration frequency about 20 min.

4. XII: The hen is connected with the apparatus (fig. 3) through a cannula. Dead space 1.1 ml. Frequency about 20 min.

9. XII: The animal is intact and quiet. Dead space 2.0 ml. Frequency about 20 min.

18. XII: Tracheal cannula. Dead space 2.0 ml. Frequency about 20 min.

All experiments on hen 3: Tracheal cannula: Dead space 5.4 ml. Frequency about 12—15 min. All experiments on this hen were carried out at 5—10°. This explains the deep inspirations (30—50 ml.).

All experiments on hen 1 and 2 were carried out at normal temperature (20°). The inspirations of hens 1 and 2 were about 15—20 ml.

20. I: The 2 expiration air samples have been drawn at the end of an expiration. They are accordingly not contaminated with the CO_2-free air of the dead space, and they are not included in the mean value calculated for this hen.

All other expiration samples in hens 1, 2 and 3 were drawn through the whole or most of an expiration.

obtained for analysis, but a priori we may assume that the air which is inspired into the air sacs from the lung, or was intermixed with the expired air, is comparable to the alveolar air in mammals, since it comes rather directly from the respiratory parts of the lung. KROGH (1910) showed that the CO_2-tension of the arterial blood in mammals is identical with that of the alveolar air. It is therefore to be assumed that a determination of the CO_2-tension of the arterial blood of birds should indicate the CO_2-tension of the air of the lung. Evidently a tonometric determination of the CO_2-tension of the arterial blood should be difficult to perform. CAMPBELL (1924) claimed, however, that the CO_2-tensions in tissues and in the alveolar air of mammals are practically identical, even when it is a question of tissues (subcutis) where the O_2-tension is low (3 %). CAMPBELL injected large volumes of air under the skin or into the abdominal cavity in cats and rabbits. The composition of the injected air changed in accordance with the tension of the gases in the tissues investigated. An analysis of the injected air, after equilibrium had been established, gave information regarding the tension of the gases in the tissues.

In birds the marrow in the larger bones usually contain

diverticula from the air sacs. If, for example, the humerus air sac in the hen is not ventilated, its air must be in equilibrium with the CO_2- and O_2-tensions in the surrounding blood and tissue. The following experiment shows clearly that the humerus section is not ventilated: A hen inspired a mixture containing 21.5 % H_2 in 1 minute (22 inspirations). Immediately after, an air sample was taken from the humerus. No trace of H_2 could be found in this sample[1]. Analysis of the humerus air in the hen showed that the composition of this air was very constant, even from animal to animal (table 7). The O_2-content (11—14 %) is far higher than the O_2-tensions normally found in the tissues — so high that we may well maintain that the humerus air must be in diffusion equilibrium with almost pure arterial blood. Thus the CO_2-tension of the humerus air is identical with the CO_2-tension of the arterial blood, and must therefore be assumed to indicate the CO_2-tension of the air of the lung. In the 4 hens investigated this CO_2-tension should then be 6.0, 5.6, 5.8 and 5.4 — mean 5.7 %.

Having now determined the ventilation and CO_2-content of the air sacs, as well as the CO_2-content of the expired air and of the air of the lungs, it seemed reasonable to believe that the road was clear for a calculation of the inspiratory and expiratory ventilation of the lungs according to the principles laid down on p. 11. Tables 6 and 7 show, however, that the expired air frequently contains definitely more CO_2 than the above determined CO_2-percentage of the air of the lungs, particularly so when the expired air is sampled at the close of an expiration. This does not harmonize with the assumption made on p. 24, that the CO_2-content of the air of the lung should be indicated by the CO_2-tension of the arterial blood. The author must here point out that "air of the lung" is understood to mean the air that leaves the parabronchi during the inspiration and expiration. Thus the above mentioned assumption cannot be maintained,

[1] If the air space of the humerus is cleared entirely of CO_2, it will take 15—20 minutes before the diffusion equilibrium with the surrounding tissue is again established. Now, it is known from Baer (1896) that the air sacs of the bones are the only air sac sections which are well supplied with blood capillaries. But if we assume that the ingoing diffusion of CO_2 from the walls of the other air sacs, for a certain difference in pressure, occurs with the same velocity as in the humerus sac, then we find that the ingoing diffusion from the walls of the sac at the most can explain the presence of 0.1—0.2 % in the sac.

Table 7.

Carbon dioxide determinations (in per cent) on samples from the humerus air space. Where also oxygen analyses have been made, the results of these are given in italics below the corresponding carbon dioxide figure.

Hen 1		Hen 2		Hen 3		Hen 4	
4. XII	6.0	9. XII	5.5	21. I	5.7	4. XI	5.0
1940	*11.2*	1940	*13.0*	1941	6.1	1940	5.3
	6.0		5.5		5.6		5.0
			13.0		6.0		5.2
			6.2[1])		5.7		*12.6*
			11.3		5.9	5. XI	5.6
						1940	*13.9*
						6. XI	5.3
						1940	5.4
							11.7
						8. XI	5.5
						1940	*11.4*
							5.4
							12.1
							6.2
							10.6
							5.4
							12.4
Mean: 6.0 % CO_2		Mean: 5.6 % CO_2		Mean: 5.8 % CO_2		Mean: 5.4 % CO_2	
11.2 % O_2		13.0 % O_2				12.7 % O_2	

[1]) The hen was asleep just before the sample was drawn. In mammals the arterial carbon dioxide tension is increased somewhat during sleep. Maybe this is the case also in birds.

but the air which leaves the lungs during expiration (and probably also during inspiration) must be considerably richer in CO_2 than indicated by the CO_2-tension of the arterial blood.

There is here a distinct contrast between birds and mammals, and we are led directly into considerations of the way in which the exchange of gases must be considered to take place in a lung like that of the bird where air flows through the lung. The question will be considered in the following, after which it should be possible to revert to the main question, viz., the determination of the inspiratory and expiratory flow of air through the lungs.

6. The exchange of gases when air flows through the avian lung.

It has previously been mentioned that complete equilibrium between the CO_2-tensions of the alveolar air and of the arterialized blood is obtained in the mammalian lung. No alveoli are found in the avian lung, but the exchange of gases must take place in the air capillaries. However, there is no reason to assume that complete equilibrium between the CO_2-tensions of the air of the air capillaries and of the arterialized blood should not occur in the lung of the bird.

As far as the mammalian lung is concerned, it seems quite clear that the alveolar air under normal conditions has the same composition in the different parts of the lung, and in each individual place shows only a very small variation with the respiratory phase. In case of the avian lung, however, it can be established, as it will be mentioned below, that the composition of the air of the air capillaries varies widely from place to place as well as from time to time during the respiratory cycle. The arterial CO_2-tension is therefore only indicative of the average composition of the air of the air capillaries.

We know that the air flows in the parabronchi, but not whether it also flows in the air capillaries. All we know is that the CO_2 which is given off in the air capillaries (or the O_2 that is consumed) must pass the parabronchi. Moreover, that we have the least favourable conditions for the exchange of gases between parabronchi and air capillaries if the air does not flow, so that all exchange must take place by diffusion in the air capillaries. The maximum difference between the average CO_2-tensions of the air of the air capillaries and of the parabronchial air may be calculated when we assume that the exchange of gases occurs by diffusion in the air capillaries. The calculation is based on KROGH's formula (1920).

$$p - p_1 = \frac{S \cdot l}{k_{CO_2} \cdot a} \qquad (1)$$

where

$p - p_1$ = the difference in pressure to be determined (in atm.),
k_{CO_2} = 0.15,
a = the total cross sectional area of the air capillaries in one lung (sq.cm.),

l = the length of the diffusion path (cm.),

S = the amount of CO_2 to diffuse. Since the calculation here is made for a hen at rest and for one lung, it follows that S is equal to one-half of the metabolism of the hen at rest (ml/sec.).

The figures of FISCHER (1905) permitted an approximate measurement of the total cross sectional area of the air capillaries (a). It was estimated to be equal to one-half of the total surface of the parabronchi. Since one lung of the hen contains about 1000 parabronchi with an average length of about 8 mm. and a diameter of about 0.4 mm., the area wanted is $^1/_2 \cdot 2 \cdot \pi \cdot 0.2 \cdot 8 \cdot 1000 = 5000$ sq.mm. = 50 sq.cm. The length (l) of the diffusion path was estimated to be $^1/_4$ of the distance between the individual parabronchi, or 0.025 cm. S was measured as 0.2 ml/sec. Entering these values in (1) we find $p - p_1 = 0.0007$ atm., or 0.07 % of 1 atmosphere. For a hen at rest the difference between the CO_2-percentages of the parabronchial air and the air of the air capillaries is only 0.07 %, i. e., the percentages are, practically speaking, identical. It follows that the arterial CO_2-tension does not only give the average CO_2-tension of the air of the air capillaries, but also the average CO_2-tension of the parabronchial air.

A few additional remarks will deal with the calculations of the diffusion:

1. The results are valid also for O_2 which in air diffuses with about the same velocity as CO_2 ($k_{O_2} = 0.18$).

2. Ventilation of the air capillaries is superfluous in a hen at rest.

3. It is true that the hen is not a flying bird, but the following example illustrates the tendency in the flying bird: Assuming that the metabolism in the flying bird can rise to a maximum of 25 times the metabolism at rest, it follows that $p - p_1 = 25 \cdot 0.7 = 1.75$ % CO_2. This is thus the maximum difference in pressure between the average contents of CO_2 in the air of the air capillaries and of the parabronchial air in the flying bird. The result indicates that ventilation of the air capillaries will possibly be beneficial in the flying bird, though it is hardly a necessity.

It will be shown later (p. 33—37) that the air actually flows through the parabronchi of the bird's lung in both respiratory phases, and that the direction of flow is reversed when the

respiratory phase changes. During inspiration CO_2-free air flows in at the ventrobronchial end of the parabronchi, and the air becomes gradually richer in CO_2 as it passes through the parabronchi. It is exceedingly difficult, however, to say how high

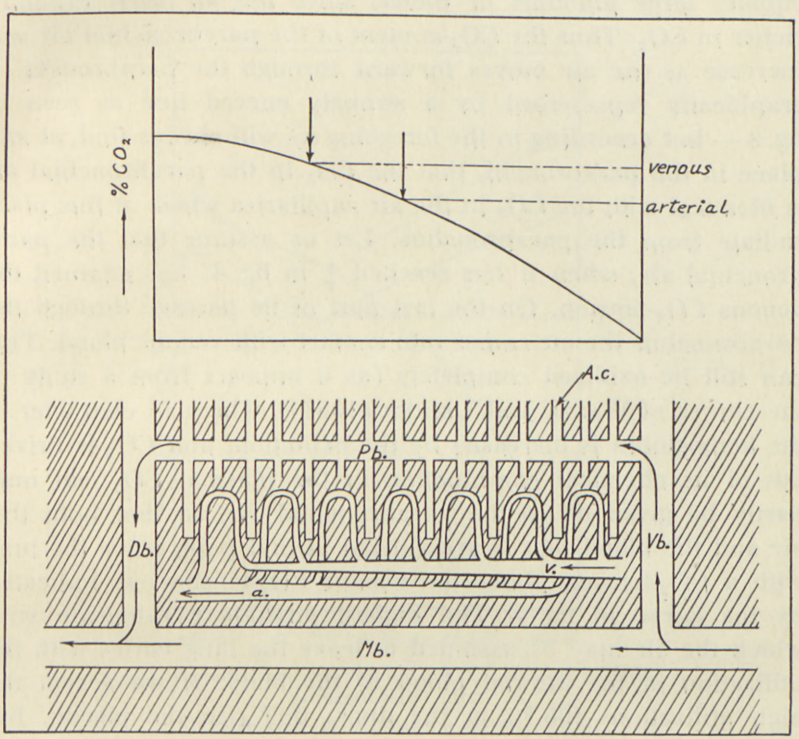


Fig. 4. Below: A parabronchus with blood vessel supply. Above: The CO_2-content of the parabronchial air, arbitrarily drawn.

Mb:	Mesobronchus	*A. c.*:	Air capillaries
Vb:	Ventrobronchus	*a*:	Arterial blood
Db:	Dorsobronchus	*v*:	Venous blood
Pb:	Parabronchus (air-pipe)		

The arrows indicate the direction of flow of air during inspiration.

must be the CO_2-percentage of the air that leaves the parabronchi in both respiratory phases. In the parabronchi we have a system of air flow which is shown schematically in fig. 4 (only the inspiratory phase is considered). The air comes into contact with constantly new blood capillaries which all receive venous blood of the same CO_2-tension from the artery of the lung (*V*). Making

the reasonable assumption that the air, for each millimeter it moves through the parabronchi, comes into contact with equally large, but constantly new amounts of blood, it is apparent that the air will receive constantly smaller amounts of CO_2 from equally large amounts of blood, since the air itself becomes richer in CO_2. Thus the CO_2-content of the parabronchial air will increase as the air moves forward through the parabronchi — graphically represented by a strongly curved line as seen in fig. 4 — but according to the foregoing we will always find, at any place in the parabronchi, that the CO_2 in the parabronchial air is identical with the CO_2 in the air capillaries which at this place radiate from the parabronchus. Let us assume that the parabronchial air, when it has reached ↓ in fig. 4, has attained the venous CO_2-tension. On the last part of its passage through the parabronchus the air comes into contact with venous blood. This can still be oxidized completely (as it appears from a study of the curves of WASTL and LEINER (1931)). The acid character of the hemoglobin is increased by the oxidation, and CO_2 is driven out of its chemical combination in the plasma. CO_2 can only partly be given off to the parabronchial air, so that both this air and the blood that is arterialized at that point leave the lung with a CO_2-tension above the venous CO_2-tension, as indicated by the curve in fig. 4. The highest possible CO_2-tension with which the air may be assumed to leave the lung varies with the utilization of the arterial blood in the body. If we accept the high utilizations (60 % in the duck, 60 % in the pigeon, but only 26 % in the goose!) which have been given by WASTL and LEINER, we must estimate the highest possible CO_2-tension with which the air leaves the parabronchi to be 10—11 %. This tension will (as appears from a study of the curves of WASTL and LEINER) arise when the venous blood is oxidized in such a way that no CO_2 can be given off, and hence the CO_2-tension of the blood is forced up. It should be pointed out that we have as yet said nothing here regarding the question of whether so high CO_2-tensions are actually reached in the air that leaves the parabronchus. Fig. 4 shows that the arterialized blood leaves the lung with widely different CO_2-tensions, all according to the place on the parabronchus where it is oxidized.

The foregoing considerations are of importance if we are now

to attempt more accurately to draw the curves for the CO_2-content of the parabronchial air during inspiration and expiration. Moreover, the curves shall be drawn so that the areas above and below the 5.7 %-level (the average tension) are of about the same size. The 2 fully drawn curves in fig. 5 are traced under

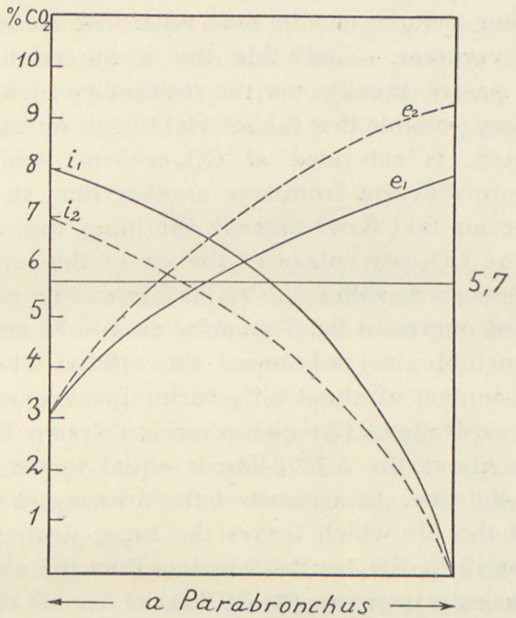


Fig. 5. Hypothetical curves for the CO_2-content of the parabronchial air.
→ Direction of expiratory flow (e_1, e_2)
← Direction of inspiratory flow (i_1, i_2)

the assumption that the composition of the air that leaves the lungs during inspiration and expiration is about the same. At the same time, the areas which are cut off by each curve above and below the 5.7 %-line are about the same, i. e., the CO_2-tensions of the parabronchial air (and hence of the mixed arterial blood) is about 5.7 % during the inspiration as well as during the expiration. Drawing the curves according to the principles outlined here, we obtain the result that the air that leaves the lungs during inspiration and expiration must contain 7—9 % CO_2.

In man, however, the composition of the alveolar air (and hence of the arterial blood) varies with the respiratory phases,

so that the alveolar air contains about 0.2 % more CO_2 at the end of an expiration than at the end of an inspiration. In case of the hen, the author has actually only determined the average arterial CO_2-tension to be 5.7 %. If we assume that the arterial CO_2-tension varies with the respiratory phases it is necessary to draw the curves in fig. 5 in a manner different from that described above. Nothing definite can be said regarding the magnitude of the possible variation — only this, that in the avian lung where the fresh air passes directly over the respiratory surfaces we must consider it very possible that the arterial blood, during inspiration and expiration, is saturated at CO_2-tensions which may be distinctly more different from one another than in man. Since moreover the air that flows through the lungs during expiration starts with the CO_2-percentage of the air of the sacs, while the inspiratory flow starts with 0 % CO_2, it follows that curves shaped like the dotted curves in fig. 5 must be said to be possible. Here the parabronchial air (and hence the arterial blood) has an average CO_2-content of about 5 % during inspiration, and about 7 % during expiration. The curves are so drawn that the sum of the areas above the 5.7 %-line is equal to the sum of the areas below the line. As a result of the drawing of these curves we find that the air which leaves the lungs during inspiration contains about 7 % CO_2, or 2—3 % less than the air that leaves the lungs during expiration (9—10 %).

It is the author's opinion that the 2 types of curves mentioned represent the possible extremes. Which of the 2 possibilities (or which intermediate) should be chosen cannot be decided at present.

The curves in fig. 5 show that the CO_2-content anywhere in the parabronchi, but particularly at their ends, varies with the respiratory phases. In the bird at rest, however, we still find, anywhere in the parabronchi, that the CO_2-percentages of the parabronchial air are identical with those of the air of the air capillaries. It is namely possible to calculate that, following a fall of 5 % in the CO_2-content of the parabronchial air, equilibrium between the parabronchial air and the air of the air capillaries will be reestablished in about $^1/_{50}$ second. The respiratory phases in the hen at rest change each 1 to 2 seconds. It must be emphasized that in the flying bird, where the respiration frequency is greatly increased[1] and where the metabolism is multiplied, the fluctu-

[1] According to ZIMMER (1935) and others the respiration during flight is synchronous with the wing beats.

ations in the composition of the air of the air capillaries will be noticeably damped in relation to the fluctuations in the composition of the parabronchial air.

7. The inspiratory and expiratory flow of air through the lungs.

Inspiration: The inspiratory flow through the lungs is calculated as the sum of the quantities of air passing the lungs on its way to the individual sacs. The amount of air, x, passing the lung on its way to an air sac may be determined from the formula

$$i \cdot \frac{n}{100} \cdot a = s \cdot \frac{n}{100} \cdot e + b \cdot x$$

where

i = the depth of the individual inspiration,
n = the amount of air taken up by the sac per inspiration — in per cent of the total inspiration volume,
a = the CO_2-percentage of the air sac,
s = the dead space (trachea + large bronchi),
e = CO_2-percentage of the expired air,
b = CO_2-percentage of the air coming from the lung.

It is expressed in the formula that the amount of CO_2 which is inspired into the sac in each inspiration is equal to the amount that has its origin in the dead space (which at that time contains expiratory air) plus the amount that has its origin in the lung. Since the air that is already contained in the sac (the residual air) has the same composition as the air mixture which the sac receives by each inspiration, it is possible to ignore the residual air in this formula.

Expiration: The expired air is a mixture of the quantities of air that are expelled from the dead space and from the air sacs. Knowing the CO_2-content of the individual air sacs, and knowing how large a percentage each sac contributes to the expired air, it is possible to calculate the CO_2-percentage, α, which should be expected if all the sacs expired directly through the mesobronchus. α lies at 3—4 % and is thus considerably lower than the CO_2-percentage actually found in the expired air (6 %). This means that part of the air expired from the sacs

must have passed the lungs, and the amount, y, may be calculated from the equation:

$$i \cdot e = (i - (s + y)) \cdot \alpha + b \cdot y,$$

where the symbols have the same meaning as in the foregoing equation. The formula states that the amount of CO_2 in the expired air must be attributed to CO_2 from the air sacs as well as CO_2 from the lungs, while the air from the dead space was free from CO_2.

Results: Since the exact composition of the air that leaves the lungs is unknown it will now be attempted to calculate the inspiratory and expiratory flow of air through the lungs on the basis of the different assumptions that the air leaving the lungs in both respiratory phases contains 7, 8, 9 or 10 % CO_2.

Table 8.

Flow of air through the lungs of the hen during inspiration and during expiration.

	CO_2-percentage of the air that leaves the lungs in inspiration and expiration	Inspiration. Flow through the lungs in % of inspiration volume	Expiration. Flow through the lungs in % of expiration volume
Hen 1+2	7	14 + 24 = 38	64
	8	11 + 21 = 32	52
	9	10 + 19 = 29	44
	10	9 + 17 = 26	38
Hen 3	7	16 + 25 = 41	87
	8	14 + 22 = 36	67
	9	12 + 19 = 31	54
	10	12 + 19 = 31	46

Hen 1+2: i = 20 ml. s = 1.0 ml. α = 2.8 %. CO_2 of the abdominal sacs = 2.4 %. CO_2 of the thoracic sacs = 4.6 %. CO_2 of the expired air = 5.5 %.

Hen 3: i = 35 ml. s = 5.4 ml. α = 3.8 %. CO_2 of the abdominal sacs = 3.1 %. CO_2 of the thoracic sacs = 6.4 %. CO_2 of the expired air = 6.0 %.

Table 8, 3rd column, gives the quantity of air which passes the lungs during inspiration, recorded as the sum of the quantity

of air that passes the lungs on its way to the 4 thoracic sacs (the 1st figure, calculated as average CO_2 for these 4 sacs together), and of the quantity of air that passes the lungs on its way to the 2 abdominal sacs (the 2nd figure, determined analogously). All figures are expressed as percentages of the total inspiration volume of the hen. The quantity of air that flows through the lungs during expiration (4th column) is stated directly in percentage of the expiration volume. Because of insufficient analytical results, one calculation is based on the average figures for the CO_2-percentages (table 6) in hens 1 and 2 (hen 1 + 2 in table 8). The average values for hen 3 permitted a special calculation for this hen.

Discussion: The main result, as clearly seen in table 8, is that the lungs are ventilated quite considerably during both inspiration and expiration, regardless of where within the limits of 7—10 % we estimate the CO_2-content of the air that leaves the lungs during inspiration and expiration. It is not possible at present to establish the absolute magnitude of the ventilation of the lungs, since we (as frequently mentioned) do not know the exact composition of the air that leaves the lungs during inspiration and expiration. For that reason the author must in the following (a and b) confine himself to a discussion of the possibilities at hand.

a) If we assume, in accordance with what was said on p. 31 that the air leaving the lungs during inspiration and expiration contains the same (i. e., 7, 8 or 9 %) CO_2, it will be seen from table 8 that the expiratory flow through the lungs must be about twice as large as the inspiratory flow. With for example 8 % CO_2 in the air that comes from the lung, we find in hen 3 that 36 % of the inspiration volume, but 67 % of the expiration volume must have passed through the lungs. It might be difficult to understand a result like that, from an anatomical point of view, since it would be expected beforehand that the ventilation of the lungs was of about the same magnitude during inspiration and expiration.

It is to be pointed out, however, that the bronchial system of the avian lung is not to be regarded as an entirely rigid tubular system. The lungs expand very slightly during the inspiration, so that the caliber of the individual bronchi in the lung is

increased. Soum has actually observed such a faint inspiratory distension of dorso- and ventrobronchi. If the expansion of the mesobronchus during the inspiration is greater than that of dorso-, ventro- and parabronchi, it should explain why a greater part of the inspiratory, but only a smaller part of the expiratory flow will pass to and from the air sacs by the direct route through the mesobronchus.

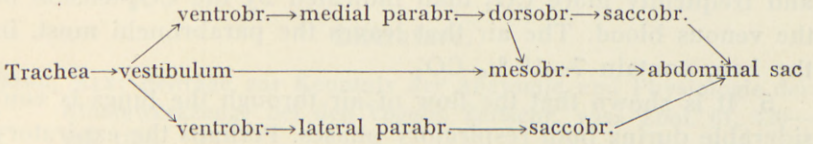
We shall finally mention that, besides the above mentioned passive changes in the calibre of the bronchi of the lung, it is possible that there occur also active changes of the calibre, conditioned upon rhytmical contractions of the musculature of the bronchi. Such active changes of calibre are known from the mammalian bronchioles, the musculature of which is contracted during expiration, and thus narrows the bronchioles — without in any way blocking them, however. The parabronchi of the avian lung are equipped with muscles that strongly resemble the musculature of the mammalian bronchioles. If the ventilation of the avian lung in reality is smaller during inspiration than during expiration, it would be possible to find the explanation in an active inspiratory contraction of the parabronchi. The author does not consider this last theory probable, however, and it is strongly emphasized that it can never be a question of blocking of any bronchial system, but only of a faint — very faint — contraction during one or the other respiratory phase, since it has in fact been demonstrated physiologically that the passage through the parabronchi as well as the passage through the mesobronchus is open in both respiratory phases. Hence we must take exception to any actual valve theory.

b) If we assume, as on p. 32, that the air which leaves the lungs during expiration contains 8—10 % CO_2, or 2—3 % more than the air that leaves the lungs during inspiration, we find that the inspiratory flow of air through the lungs is about the same as the expiratory. If for example the air that leaves the lungs during inspiration contains 7 % CO_2 and the air that leaves the lungs during expiration contains 10 % CO_2, we find in hen 3 that 41 % of the inspiratory and 46 % of the expiratory flow must have passed through the lungs. This result must be said to be in beautiful harmony with the anatomical facts known to date. But as mentioned, it is not possible at present to decide

which one of the two possibilities discussed under a) and b) (or which intermediate) should be given preference.

The following schedule may be drawn for the flow in the bronchi of the avian lung, based on the calculated results. (For the sake of perspicuity only the abdominal sacs are taken into consideration).

Inspiration (cf. diagram in fig. 2).



Expiration: All directions of flow are reversed. Perhaps, for unknown reasons, considerably less air is now passing through the mesobronchus.

8. Summary.

1. The passage through the parabronchi in birds is in parallel as regards the flow of air with the direct connection (mesobronchus) between the trachea and air sacs. The parabronchi represent a larger aggregate cross sectional area than the mesobronchus. It follows that part of the air that passes to or from the air sacs must pass the respiratory sections of the lungs, without it being necessary to assume the presence of any guiding valves (as assumed by Brandes and Bethe).

2. In the hen, 80 (70—90) % of the inspiration volume pass on to the abdominal sacs, 3—12 % to the postthoracic sacs, 8—15 % to the prethoracic sacs, and probably 0—1 % to the interclavicular sac. In the duck (calculations based on experiments by Vos) the corresponding figures were 49, 23, 3 and 1 % respectively. In the duck it was only possible to account for 76 % of the total inspiration volume. This is due to experimental errors. The inspiratory expansion of the lungs is slight. In the hen, the lungs can only take up 4 % (as a maximum) of the inspiration volume and are therefore ventilated almost exclusively by the flowing through of air.

3. It is shown by calculation that the average CO_2-tensions of the parabronchial air and of the air of the air capillaries

must be identical in the bird at rest, and equal to 5.7 %. Both CO_2-tensions vary, however, (parallel) from place to place in the lung, and also, at each individual point, with the respiratory phases.

4. The air flows through the parabronchi and, when leaving these during inspiration and expiration, it always contains more CO_2 than indicated by the tension of this gas in the arterial blood, and frequently more CO_2 than indicated by the CO_2-tension of the venous blood. The air that leaves the parabronchi must, in the hen, contain 7—10 % CO_2.

5. It is shown that the flow of air through the lungs is considerable during both respiratory phases. Perhaps the expiratory flow is stronger than the inspiratory. In that case it is probable that about 35 % of the inspiration volume and about 65 % of the expiration volume have flown through the parabronchi, while the remainder has passed to an from the air sacs through the mesobronchus. It is just as possible, however, that the inspiratory flow through the lungs is about the same as the expiratory. In that case 40—50 % of both the inspiration and expiration volumes must have passed through the parabronchi. At present, no choice can be made between the two possibilities.

6. A diagrammatic representation is given for the probable directions of flow in the bronchi of the avian lung. All directions are reversed when the respiratory phase changes.

Literature.

Baer, Max: Beiträge zur Kenntnis der Anatomie und Physiologie der Athemwerkzeuge bei den Vögeln. Zeitschr. wiss. Zool. 61, 420—498, 1896.

Bethe, A.: Hdbch. der norm. path. Physiol. 2, 20—27, 1925.

Brandes, G.: Beobachtungen und Reflexionen über die Atmung der Vögel. Pflügers Arch. 203, 492—511, 1924.

Campbell, J. A.: Changes in the tensions of CO_2 and O_2 in gases injected under the skin and into the abdominal cavity. Journ. Physiol. 59, 1—16, 1924.

Christensen, E. Hohwü and Dill, D. B.: Oxygen dissociation curves of bird blood. Journ. Biol. Chem. 109, 443—448, 1935.

Dotterweich, H.: Versuche über den Weg der Atemluft in der Vogellunge. Zeitschr. vergl. Physiol. 11, 271—284, 1930.

— Die Bahnhofstauben und die Frage nach dem Weg der Atemluft in der Vogellunge. Zool. Anz. 90, 259—262, 1930.

— Die Atmung der Vögel. Zeitschr. vergl. Physiol., 23, 747—770, 1936.

Fischer, G.: Vergleichend-anatomische Untersuchungen über den Bronchialbaum der Vögel. Zoologica, 19, 1905—07.

Krogh, Aug.: On the mechanism of the gas-exchange in the lungs. Skand. Arch. Physiol. 23, 248—278, 1910.

— Studien über Tracheenrespiration 2. Über Gasdiffusion in den Tracheen. Pflügers Arch. 179, 1920.

Scharnke, H.: Die Bedeutung der Luftsäcke für die Atmung der Vögel. Erg. Biol. 10, 177—206, 1934.

— Experimentelle Beiträge zur Kenntnis der Vogelatmung. Zeitschr. vergl. Physiol. 25, 548—583, 1938.

Schmit-Jensen, H. O.: Determination of carbon dioxide, oxygen and combustible gases by Krogh's method of microanalysis. Biochem. Journ. 14, 4—24, 1920.

Schulze, F. E.: Über die Luftsäcke der Vögel. Verh. des VIII intern. Zool. Kongr. zu Graz 1910, 446—482, 1912.

Soum, M.: Récherches physiologiques sur l'appareil réspiratoire des oiseaux. Thèse à la Fac. Sci. Lyon, Paris 1896.

Walter, W. G.: Beitrage zur Frage über den Weg der Luft in den Atmungsorganen der Vögel. Arch. Neerl. Physiol. 19, 529—537, 1934.

Wastl, H. and Leiner, G.: Beobachtungen über die Blutgase bei Vögeln I—III. Pflügers Arch. 227, 367—474, 1931.

Winterstein, H.: Die physikalisch-chemischen Erscheinungen der Atmung. XI, Vögel. Wintersteins Hdbch. 1_2, 223—235, 1921.

Vos, H. J.: Über den Weg der Atemluft in der Entenlunge. Zeitschr. vergl. Physiol. 21, 552—578, 1935.

Zimmer, K.: Beitrage zur Mechanik der Atmung bei den Vögeln in Stand und Flug. Zoologica, 33, 1935.

II. RESPIRATION AND HEAT REGULATION IN THE BIRD AT REST AT HIGH TEMPERATURE AND IN THE FLYING BIRD

As already suggested by Soum (1896) and Victorow (1909) the respiratory tract of birds has two functions: that of respiration and that of heat regulation. Most often the needs of heat regulation and of respiration vary independently. Since, however, the loss of heat from the body surface of birds (birds possess no sweat glands) must be assumed to be relatively low and only slightly variable, we must suppose the respiratory tract of birds (which perform a very intense work during flight) to be exceedingly well suited for serving at the same time as a tool of respiration and of heat regulation.

In the hen at rest at low temperature, the loss of heat through the respiratory tract must be assumed to be at a minimum. Accordingly, the ventilated air must be supposed to be utilized as well as possible in respiration. How this is accomplished has been outlined in the preceding paper.

In the hen at rest at high temperature we may expect only a relatively small part of the inspired air to ventilate the lungs, whereas much air must be assumed to ventilate non-respiratory parts of the respiratory tract. In this paper this point will be discussed more in detail.

In the bird, flying at a high rate, finally, we may a priori expect all parts of the respiratory tract to be ventilated at a maximum. However, it will be shown that in flying birds the needs of heat regulation are greatly in excess of the needs of respiration and the consequences of this fact will be discussed.

Since any organ must be constructed so as to comply with the demands of a maximum effort, the anatomy of the avian respiratory tract can only be understood if we consider respiration as well as heat regulation during flight of high intensity. Therefore one of the objects of this paper dealing with respiration and heat regulation during flight is to explain why the lungs of birds have developed into such curious organs.

This paper is almost purely speculative, and I am well aware that many points which I deal with are still open to discussion.

1. The ventilation of the respiratory tract in birds at rest at high temperature.

In a bird at rest at low temperature (say, $< 25°$), the loss of heat from the body surface by radiation and conduction is so high that we may expect the loss of heat by evaporation from the respiratory tract to be at a minimum. In fact, in the preceding paper it has been shown that about 75 % of the air either in leaving or in entering the air sacs under these circumstances flows through the lungs. At low temperature, therefore, the air sacs of birds serve only respiratory purposes.

In hot weather, however, birds largely increase the loss of heat by increasing the ventilation of the respiratory tract (v. SAALFELD 1936). In hot weather respiration becomes very frequent but more superficial than at normal temperature. This type of respiration is named "Hackeln". In the hen the arterial carbon dioxide tension does not measurably decrease during "Hackeln" as will appear from the following: In the preceding paper the arterial carbon dioxide tension of the hen was determined. In 4 hens, resting at room temperature (about 20°), this figure averaged 5.7 %. In hen 2 three determinations (5.5, 5.5 and 6.2) averaged also 5.7. In the experiments to be described here hen 2 was transferred to a hot chamber (30°), where it was placed on a hot radiator. "Hackeln" soon began. The hen respired 200—300 times per minute. After prolonged "Hackeln" a sample was drawn from the humerus air space. Two experiments were performed. In the first experiment ($^{12}/_{12}$ 1940) the sample contained 5.3 % CO_2 and 13.5 % O_2, in the second ($^{13}/_{12}$ 1940) 5.6 % CO_2 and 14.0 % O_2. Since, accordingly, in the hen the

arterial carbon dioxide tension does not decrease at high temperature, the ventilation of the lungs themselves is not increased during "Hackeln". Therefore the increase in ventilation must be localized to the dead space and perhaps also to the air sacs. If the ventilation of the air sacs is increased while the ventilation of the lungs remains unaltered — and the theory is supported by the statement of SCHARNKE (1938), that at high temperature when the pigeon respires very frequently, the carbon dioxide per cent of all air sacs of this bird is lower than at normal temperature — the question arises: can the bird regulate the ventilation of the lungs and of the air sacs independently?

From the diagram fig. 2 in the preceding paper it appears, that if the resistance to the air flowing through the lungs could be augmented, the ventilation of the air sacs might be increased relative to the ventilation of the lungs. In this respect the demonstration of FISCHER (1905) quoted also by BRANDES (1924) of the parabronchial muscles of the avian lung is of interest. These plain muscles do not form a uniform layer, but they lie as a coarse network in the parabronchial wall. Just distal to the muscular network lies a distinct and corresponding network of elastic tissue. When the parabronchial muscles contract, they must therefore be assumed to rise a close system of slimy walls, made up of elastic tissue. Do these muscles represent a variable resistance to the air flowing through the avian lungs?

In order to study this point, I operated from the dorsal side into the lung of a pigeon in ether or amytal narcosis. This can be done, because the avian lung is not kept expanded by a Donder's pressure as is the mammalian lung. When, however, the bird was heated and the respiration became frequent (about 300/min.), no contraction of the parabronchial muscles could be observed (2 experiments were carried out), and this was the case also in a pigeon in which the abdominal air sacs were opened and which was brought into apnoea by sucking large quantities of air through the respiratory tract in the antero-posterial direction, in spite of the fact that the lungs were so greatly overventilated, that the bird remained in apnoea for half a minute after the air current had been stopped. In my opinion, however, in experiments of the above type (narcosis, operation) only positive results may be accepted as convincing, and I therefore

still think it possible, that under physiological conditions the parabronchial muscles may act as variable resistances to the air flowing through the lungs.

That the parabronchial muscles can bring about an increased resistance to the air currents in the parabronchi is evident from the following observation: In a pigeon at rest the wall of the parabronchus is quite smooth, but when stimulated with a hair,

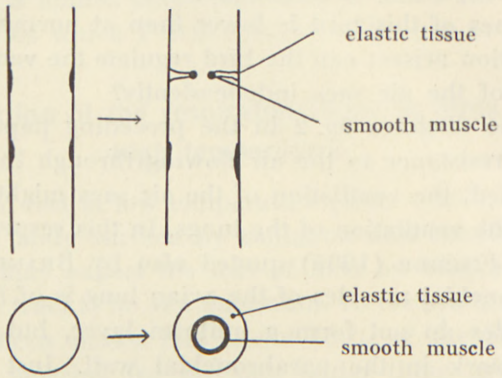


Fig. 1. The parabronchial muscle.
Left: before stimulation.
Right: after stimulation with a hair.

the parabronchial muscles contract after a latency of one or two seconds, and now a slimy wall almost occludes the parabronchus at the stimulated place (fig. 1). This has been observed in both pigeons investigated.

2. The ventilation of the air sacs and of the lungs in birds flying at a high rate.

The metabolism of flight has never been measured, but it is no doubt very high. By calculation carried out in cooperation with the air craft engineer K. G. ZEUTHEN the metabolism of a pigeon weighing 290 gr. and flying at different velocities was found to be of the order indicated in the table 1, column c (the figures are accurate only to $\pm$ 50 per cent). In the calculations, the efficiency of the metabolism of flight has been estimated at 25 per cent. From the table it appears that in the pigeon flying

at the speed of 70 km. per hour (modern measurements indicate the maximum speed of flight in pigeons to be of about 70 to 80 km. per hour), the metabolism is about 27 times the metabolism of rest (the figure of KROGH (1904) for the metabolism of resting pigeons has been made use of). Since in the resting bird at room temperature the expired air contains 5 to 6 per cent carbon dioxide and is saturated with water vapour at about 40°, only 20 per cent (at most) of the heat produced in the metabolism at rest is eliminated by evaporation from the respiratory tract, whereas 80 per cent is lost by convection and radiation from the body surface. Now I do not think it possible for the flying bird to increase the loss of heat from the body surface beyond a certain limit which I estimate to be, say 5 times the loss of heat by the same route in the resting bird[1]. If this is so, an amount of heat equivalent to $0.8 \cdot 5 = 4$ times the metabolism of rest at room temperature represents the maximum of heat which can be eliminated by convection and radiation from the body surface of the bird flying at a high rate at room temperature. But since in the bird flying 70 km. per hour the heat to be eliminated must be of the order $27 \cdot {}^3/_4 = 20$ times[2] the metabolism at rest, this means that an amount of heat equivalent to $20 - 4 = 16$ times the metabolism at rest must be eliminated by evaporation from the respiratory tract. Accordingly, the flying bird must ventilate $5 \cdot 16 = 80$ times as much air as when resting, in spite of the fact that in this example the metabolism is only 27 times the metabolism of rest (more detailed information is given in table 1). In the bird flying at a high rate, therefore, the ventilation of the respiratory tract is about 3 times as high as might be expected when considering the needs of respiration only, and the ventilation of the respiratory tract as a whole must therefore be adjusted in accordance with the needs of heat regulation. These needs are so high, that the ventilation of the lungs should be highly in excess of the needs of the respiration, if the ventilation of the

[1] In duck I observed the bill and the legs to be very warm at high air temperature. KALLIR (1931), however, found the temperature of a bird's skin always to be high and not to be lowered, when an air current was directed against the bird from in front.

[2] Since the efficiency of the metabolism of flight has been estimated at 25 per cent, 25 per cent of the energy evolved during flight is transformed into work and thereupon into heat of friction.

Table 1.

a	b	c	d	e	f	g	h	i
Speed km/ hour	Energy to overcome the resistance Cal/hour	Metabolism Cal/hour	Metabolism of flight × metabolism of rest	Heat to be eliminated Cal/hour	Loss of heat by radiation and conduction Cal/hour	Loss of heat from the respiratory tract Cal/hour	Ventilation during flight × ventilation during rest	$\frac{h}{d}$
0	0	2.3	1	2.3	1.8	0.5	1	1
30	1.2	7.1	3.2	5.9	?	?	?	?
40	2.8	13.5	5.9	10.7	?	?	?	?
50	5.4	23.9	10.4	18.5	9	9.5	19	2.0
60	9.3	39.5	17.2	30.2	9	21.2	42	2.4
70	17.8	61.5	26.8	46.7	9	37.7	76	2.8

respiratory tract was accomplished just as in the bird at rest at low temperature. In all probability, however, the air does not pass to and from the air sacs of the flying bird just as in the bird at rest at low temperature. In fact, the few indications available go to show, that during flight the ventilation of the air sacs is increased relative to the ventilation of the lungs. According to SCHARNKE (1938), for instance, the carbon dioxide per cent of all air sacs is lower in a flapping pigeon than in a pigeon at rest at room temperature and whereas VOS (1935) showed the interclavicular air sac of the duck at rest not to be ventilated at all, SOUM (1896) and SCHARNKE (1938) made it probable, that in the flying pigeon this air sac is intensely ventilated. If the ventilation of the air sacs is increased relative to the ventilation of the lungs of the flying bird, the question (already dealt with when discussing the ventilation of the bird at rest at high temperature) at once arises: do the lungs possess variable resistances? And, if we accept the parabronchial muscles as variable resistances: do they contract during flight? This question can not be settled at present, and here I only refer to the statements on p. 44 of the present paper.

The expired air and the arterial carbon dioxide tension in the flying bird. In the hen at rest, the expired air contains about 6 per cent carbon dioxide. When accepting the above

view point that in the intensely flying bird the ventilation of the respiratory tract is about thrice the ventilation to be expected from the needs of respiration only, this involves the statement that in intensely flying birds the expired air contains only $^6/_3 = 2$ per cent carbon dioxide, and if, moreover, the air runs through the lungs just as in the hen at rest at low temperature, the arterial carbon dioxide tension should be $5.7/3 = 1.9$ per cent or, as a maximum, $1.9 + 1.7 = 3.6$ per cent carbon dioxide (1.7 per cent is the pressure difference necessary to transport by diffusion in the air capillaries the gases involved in metabolism of intense flight). As outlined above, however, during flight the ventilation of the air sacs is most probably increased relative to the ventilation of the lungs. If this is so, the arterial carbon dioxide tension is not so low as calculated above.

Flight at great heights. Many birds are known to fly at great heights. Whereas some of these birds, such as the eagle, (7000 m.), glide in the air without moving the wings, others perform an intense work at great heights, as they move the wings constantly during flight. As an example of this last type I quote *Anas crecca* which has been observed in the Himalayas 5600 m. above the sea (Groebbels, p. 181). When this bird in flight of constant and high intensity ascends from 0 m. to 5600 m. it can not (even at constant temperature) — as mammals do — increase the ventilation of the respiratory tract, since to fulfill the thermoregulatory needs, the ventilation of the respiratory tract must remain constant at all heights. If, however, the lungs of the flying bird is (or can be) highly overventilated in all heights, it is much easier to understand how birds can perform such hard work at great heights. In an overventilated lung, the blood is coming into contact with air of low carbon dioxide content and relatively rich in oxygen. Both circumstances improve the binding of oxygen by the hemoglobin (the oxygen dissociation curve of the avian blood resembles that of human blood, except that it is a little less steep (Wastl and Leiner (1931), Christensen and Dill (1935)).

The capacity of the air sacs as heat regulating organs. From the work of Zimmer (1935) and others it seems probable that during flight the respiratory movements are synchronous with the wing beats, which Marey (1890) in flying pigeons deter-

mined at 8/sec. VICTOROW (1909) and ROCHÉ (1891) determined the volume of all air sacs in the pigeon at 70 and 74 cc., respectively. In pigeons flying 70 km/hour I calculated the ventilation necessary to eliminate all the heat formed in metabolism to be so high that about 50 cc. must be ventilated per respiration. Since 50 cc. must be very near the maximum quantity of air which can be inspired per inspiration by a pigeon, I believe 70 km. per hour to be the maximum speed of flight in pigeons (when critically considering all errors in the calculations the figure may be given as 70 ± 10 km. per hour). Of course other processes may be limiting factors even before this speed has been attained (circulation, capacity of the muscular machine). However, modern measurements of the speed of flight in birds seem to agree well with the above figure.

In my opinion, the above considerations give a clear understanding of the strange anatomy of the avian respiratory tract: The lungs and the air sacs are organs of respiration and of heat regulation, respectively. The air sacs, however, function only as heat regulating organs in the flying bird (and perhaps also in the bird at rest at high temperature), and even during flight as well as during rest the air sacs serve also respiratory purposes, since they ventilate the lungs in both respiratory phases. During flight, the ventilation of the air sacs is most probably in excess of the ventilation of the lungs, and only a minor part of the air entering or leaving the air sacs flows through the lungs. This is why the air sacs directly communicate with the trachea through the wide mesobronchus and why the lungs communicate with the mesobronchus much in the same way as a radiator is connected with the pipe carrying the hot water. Just as the quantity of water which flows through the radiator may be adjusted independently of the flow through the main pipe by simply turning the cock, I advance the theory that the ventilation of the lungs may be regulated independently of the ventilation of the air sac by means of variable resistances in the lungs. Perhaps the parabronchial muscles act as such variable resistances. If this is so, we may assume the parabronchial muscles in the bird at rest at low temperature to be relaxed (and in fact they have

been observed to be so) whereas they must be assumed to contract to some extent in birds flying at a high rate in the lowlands, but again to relax during flight in great heights.

Summary.[1]

1. In the hen at rest at high temperature the ventilation of the lungs remains unaltered as compared with the ventilation of the lungs at low temperature. But the ventilation of the dead space, and in the pigeon most probably also the ventilation of the air sacs, is increased as compared with the ventilation at low temperature. If, in hot weather, the ventilation of the air sacs is increased relative to the ventilation of the lungs, this might be explained by assuming the resistance to the air flowing through the lungs on its way to and from the air sacs to be increased. The possibility of the parabronchial muscles to act as variable resistances is suggested, but direct experimentation, which cannot, however, be considered convincing, failed to demonstrate this. When stimulated mechanically, the parabronchial muscles contract, almost to the point of occluding the parabronchus.

2. In the flying bird, the thermoregulatory needs may become so high that the ventilation of the respiratory tract may be about 3 times as high as to be expected when considering the needs of respiration only. If, therefore, in the flying bird, the air passes to and from the air sacs just as in the hen at rest at low temperature, the arterial carbon dioxide tension should be as low as 1.9 to 3.6 per cent as compared with the tension 5.7 per cent in the hen at rest. However, in the bird flying at a high rate, I assume the parabronchial muscles to be suitably contracted so as to avoid an overventilation of the lungs. Only in the bird flying at great heights, I do not think that these muscles contract.

Most probably pigeons cannot fly faster than 70 ± 10 km. per hour, since at that rate heat regulation becomes a limiting factor. In a pigeon flying at this speed, the air sacs can be calculated to be almost completely emptied during each expiration.

The anatomy of the avian respiratory tract can only be understood, if we consider respiration as well as heat regulation during flight of a maximum intensity.

[1] cf. the summary p. 37—38.

At this place I want to express my thanks to Professor Aug. Krogh for allowing me to undertake this work with the aid of a grant given to him from the Carlsberg Foundation, for directing my interest towards this field, for advice on many points, and for valuable criticism during the preparation of these papers. I also want to express my thanks to Professor J. Lindhard for stimulating discussions.

From the Laboratory of Zoophysiology, Copenhagen University.

Literature.

BRANDES, G.: Beobachtungen und Reflexionen über die Atmung der Vögel. Pflügers Arch. 203, 492—511, 1924.

CHRISTENSEN, E. HOHWÜ and D. B. DILL: Oxygen Dissociation Curves of Bird Blood. Journ. Biol. Chem. 109, 443—448, 1935.

FISCHER, GUIDO: Vergleichend-anatomische Untersuchungen über den Bronchialbaum der Vögel. Zoologica 19, 1905—07.

GROEBBELS, FRANZ: Der Vogel. 1. Atmungswelt und Nahrungswelt. Berlin 1932.

KALLIR, EVA: Temperaturtopographie einiger Vögel. Zeitschr. vergl. Physiol. 12, 231—247, 1931.

KROGH, AUG.: Some Experiments on the cutaneous Respiration of Vertebrate Animals. Skand. Arch. Physiol. 16, 348—57, 1904.

MAREY, E. J.: Le Vol des Oiseaux. Paris 1890.

ROCHÉ, GEORGES: Contributions à l'étude de l'anatomie comparée des reservoirs aériens d'origine pulmonaire des oiseaux. Ann. Sci. Nat. (Zool.) 11, 1—118, 1891.

SAALFELD, E. v.: Untersuchungen über das Hacheln bei Tauben. Zeitschr. vergl. Physiol. 23, 727—43, 1936.

SCHARNKE, HANS: Experimentelle Beiträge zur Kenntniss der Vogelatmung. Zeitschr. vergl. Physiol. 25, 548—83, 1938.

SOUM, MARCEL: Récherches physiologiques sur l'appareil réspiratoire des oiseaux. Thèse à la Fac. Sci. Lyon. Paris 1896.

WASTL, H. and G. LEINER: Beobachtungen über die Blutgase bei Vögeln. I—III. Pflügers Arch. 227, 367—474, 1931.

VICTOROW, CONSTANTIN: Die kühlende Wirkung der Luftsäcke bei Vögeln, Pflügers Arch. 126, 300—322, 1909.

VOS, H. J.: Über den Weg der Atemluft in der Entenlunge. Zeitschr. vergl. Physiol. 21, 552—78, 1935.

ZIMMER, KARL: Beiträge zur Mechanik der Atmung bei den Vögeln in Stand und Flug. Zoologica 33, Heft 88, 1935.

Indleveret til Selskabet den 17. Oktober 1941.
Færdig fra Trykkeriet den 17. Juni 1942.

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 2

THE MECHANICAL PROPERTIES OF THE SINGLE STRIATED MUSCLE FIBRE AT REST AND DURING CONTRACTION AND THEIR STRUCTURAL INTERPRETATION

BY

FRITZ BUCHTHAL

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

Printed in Denmark.
Bianco Lunos Bogtrykkeri A/S.

Introduction.

The mechanical properties of the muscle may primarily be expressed by means of length-tension diagrams registered either statically or dynamically. In static experiments, consolidated tension values are registered as a function of stretch. In dynamic experiments, the simultaneous variations of stretch and tension are recorded. The results obtained are a source of valuable information concerning elasticity, viscosity and plasticity of a muscle as a function of length and time.

The first investigations by E. Weber (1846) deal exclusively with the static properties of the muscle. However, the importance of the dynamic properties was discovered very soon, as may be seen from numerous papers by Ludwig (1858), von Kries (1880), Fick (1882), and Blix (1895).

After a period of rest of about thirty years, these problems were resumed in 1924 by Gasser and Hill who drew our attention to the quantitative relations of the elastic and the viscous phenomena.

Besides Gasser and Hill, also Beck (1923), Steinhausen (1926), Lindhard and Møller (1926), Sulzer (1930), Reichel (1934), and others have been occupied with the study of the static and dynamic mechanical constants of the muscle. At that time, only work on a whole muscle had been found possible, and these investigations in many cases led to ambiguous or contradictory results, presumably because of the heterogeneous structure of the total muscle. As soon as the technique of preparation was sufficiently developed, attempts were made to study the mechanical properties of fibre bundles or of isolated fibres (Sichel (1934), Buchthal, Knappeis and Lindhard (1936), and Asmussen (1936)). The results of these experiments are reported in a summarizing discussion by Buchthal and Lindhard (1939).

The above mentioned investigations deal exclusively with the static mechanical properties of the fibre, such as length-tension diagrams, and the length of the individual components of the fibre as a function of stretch.

The registration apparatus available at that time did not allow a more complete and precise mechanical analysis of the static and dynamic properties of the muscle fibre. It is, therefore, the aim of the present work to study by means of suitable apparatus the elastic properties of an isolated muscle fibre at rest and during contraction. These properties are investigated by means of length-tension diagrams which represent static stiffness, plasticity, and work-capacity. Furthermore, dynamic stiffness and viscosity are investigated by means of periodic and rapid single length alterations as a function of stretch or loading.

The static experiments are carried out both on the whole fibre and on its anisotropic and isotropic parts, while such a differentiation has not yet been possible in dynamic experiments.

Method.

Preparation: The experiments were carried out on isolated fibres of the frog's m. semitendinosus. Both summer frogs and winter frogs were used (and also the two species *Rana esculenta* and *Rana temporaria*). The m. semitendinosus is especially suited for the present experiments, since all the fibres continue through the total length of the muscle from tendon to tendon and are of uniform cross section in the medial portion of the muscle. A number of comparative experiments were performed on small bundles containing 2 to 8 fibres.

It was found to be of great advantage to kill the frog one day before the muscle is to be used in experiments, since irritability fluctuations which always appear in freshly prepared muscles could be avoided in this way. Preparations showing marked fluctuations of irritability at the beginning of the experiment were discarded so that the irritability of the preparations used in the present experiments was constant throughout the whole period of experimenting. The preparation was made in an ice-cooled Ringer solution with constant p_H 7.2—7.3. In some

of the experiments, the temperature of the Ringer bath containing the muscle during the experiment was kept constant by circulation and was continuously thermoelectrically verified. (12—14° C.)

The hydrogen ion concentration of the Ringer solution was found to be of decisive importance for maintaining constant irritability during a long period of time. Therefore, a stream of a CO_2—O_2 mixture was passed through the Ringer solution, the CO_2 together with the bicarbonate of the Ringer solution thus guaranteeing a constant p_H which was checked regularly by means of a glass electrode.

In the first series of experiments, a suitable colloid-osmotic pressure in the Ringer solution was attained by adding dialyzed 6 per cent gum arabic. Since, however, the commercial gum preparations contain varying amounts of K and Ca, and as it is not known how many of the cations can be bound by the gum arabic solution, a dialysis with repeatedly renewed Ringer solution becomes necessary in order to secure the right cation concentration. (Dialysis in cellophane bags, 30 hours, gum concentration 6 per cent, determined refractometrically.) In later experiments, this rather complicated operation was replaced by adding another high molecular substance, chemically well defined, viz. Polyviol Am., 1.35 per cent, osmotic pressure: 110 cm of H_2O, (Polyvinyl alcohol), a substance which in the doses necessary for these experiments does not noticeably affect the irritability or contractility of the fibre.

Stimulation: The stimulation of the preparation was direct or indirect with maximal stimuli and the method of stimulating had no influence on the shape of the length-tension diagrams or the elasticity determinations. The height of the threshold value or application of curarine allows us to differentiate whether the stimulation works directly or through the end plate. As stimulating electrodes, two stainless steel tweezers were applied to hold the tendon ends of the fibre. A few control experiments were carried out with large platinized platinum electrode plates, placed along the fibre (cf. Sichel and Prosser (1940)). In the present experiments where the intensity of the stimulation mostly was considerably above the threshold value, no different effects of the various stimulating electrodes could be observed.

A thyratron arrangement was used for the stimulation; the

shape of the stimulating impulses, their duration, strength, and frequency could be varied. The rectangular current impulse of a duration of 2—4 ms was used most frequently. (For a more detailed description of the stimulation device I refer to a later publication.)

By means of repeated controls it was insured that there was no stimulus escape to the registration device.

Microphotography: The results of tension- and elasticity measurements may be correlated with the mechanical properties of the different elements of the fibre, if the length and the length alterations of the fibre under various exterior influences and during contraction are known. Therefore, the fibres were microphotographed at rest, during contraction at various extents of stretch and during release from isometric contraction to the same tension as at rest ("release contraction"). In all essential points, a similar technique was applied as described formerly by BUCHTHAL, KNAPPEIS and LINDHARD (1936). As the preparation technique has been further developed since that time, it is now possible to take series of microphotographs of the same preparation at rest and during contraction at a continuously varying stretch.

Microscope optics: Objective Apo 70, water immersion, NA. 1.25. Ocular: 10×, Zeiss Focu, magnification 350 times. Film: Ilford Pan Hypersensitive. Time of exposure about $^1/_5$ sec. In some experiments, a water-cooled Philip's Super High pressure Hg lamp (effective intensity 15000 Lumen) was used as a light source; in most registration experiments, however, a Wolfram arc lamp (5 amps.) was applied.

The photographs during isometric contraction or release were not taken before the fibre had become consolidated in the new state (i. e. about 0.3—0.5 sec. after the beginning of the stimulation). As far as possible, double exposures were taken in all experiments. The negatives were measured by means of a measuring microscope. The measurements included the height of the anisotropic (A) and the isotropic (I) substances and of the total height of compartments (A + I) of 10 to 20 compartments of the microphotogram (magnification of the measurements about 10 times).

Condenser arrangement for the registration of the tension: The tendon ends of the muscle fibre were fastened to a pair of micro tweezers each. These micro tweezers (Fig. 1)

were made of phosphor bronze or steel wire, 0.8 mm. in diameter, and their prongs pressed together by moving the ring *a*; the tendon was thus held in the tweezers without danger of displacement.

The micro tweezer (1) (cf. Fig. 2) was in direct contact with the earthed and movable condenser plate (2) whose distance from the other fixed condenser plate (3) was reduced as soon as the fibre was stretched. The tweezer (1) was held by two steel springs (4 and 5), (7.0 mm. broad, 0.11 mm. thick), the stiffness

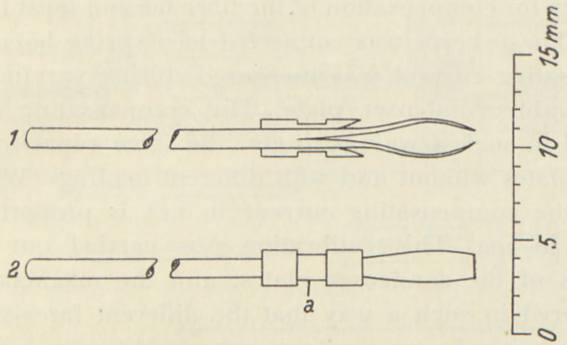


Fig. 1. Micro tweezer to hold the tendon of a muscle fibre. The prongs are pressed together by a movement of (*a*).
(1) side view; (2) viewed from above.

of which may be altered by varying their effective length. These two springs did not only provide the necessary stiffness but they guaranteed furthermore a parallel movement of the tweezer and the condenser plate. The distance between the condenser plates is one of the factors which determine the tension sensitivity of the arrangement and could be varied by moving the slide (6) which served to move forward and backward the micro tweezers, the condenser plate, and the springs. The non-earthed condenser plate was shielded against exterior capacitive disturbances and stimulus escape (7).

During stronger stretching of the fibre, the distance between the condenser plates would be decreased considerably, which might effect the sensitivity of the arrangement. Therefore, it was necessary to maintain a constant distance between the plates by means of a counter-force. The movable condenser plate (2) was provided with a coil (8) (40 windings, wire diameter 0.1 mm.)

which moved in the air gap of a ring-shaped permanent magnet (9) of about 1000 Gauss, the coil and the magnet being arranged similarly to those in a loud-speaker system. By varying the current in the coil, the latter together with the movable condenser plate was drawn with variable force over the centre of the permanent magnet, and in this way we compensated the alterations in the distance between the condenser plates caused by extension or relaxation of the fibre.

As the loading of the fibre was measured in mg., the current necessary for compensation of the fibre tension must be calibrated in mg. The tweezer was connected to a spring balance and the compensating current was measured during varying loading of the movable condenser plate. The compensating current was adjusted in such a way as to give the same capacity of the condenser plates without and with different loadings. Within a wide range, the compensating current in mA is proportional to the loading in mg. This calibration was carried out at different positions of the condenser plates, and the magnetic field must be centered in such a way that the different force-strength constants (in mg/mA) are constant over a wide range (up to 5 mm.). The leads to the coil must be introduced perpendicularly to the direction of the motion as, otherwise, indefinable additional stiffnesses may appear. The magnitude of the compensation current and the impedance of the external circuit did not measurably affect the total stiffness and damping of the system.

The calibration of the spring-balance involved some difficulties, as this should necessarily take place with the spring in the same horizontal position as employed during the loading of the tweezer, without the weight of the spring proper playing any part in the deflection. A calibration by means of a torsion-balance was not feasible, since these instruments can only be used vertically, and a transformation of the loading would introduce essential errors. Therefore, an analytical balance was used for the calibration, the tongue of the balance being connected through a hair with the spring to be calibrated. Under loading of one lever of the balance, the tongue deflects from the equilibrium position and the spring of the spring-balance is spanned until the deflection of the tongue is compensated. The tension of the spring was produced by a side-movement of the

spring-balance which was placed on a movable slide. The position of the spring was read by means of a microscope and an ocular micrometer. In order to calculate the actual loading of the spring P_1, we must know the loading of one lever of the balance P,

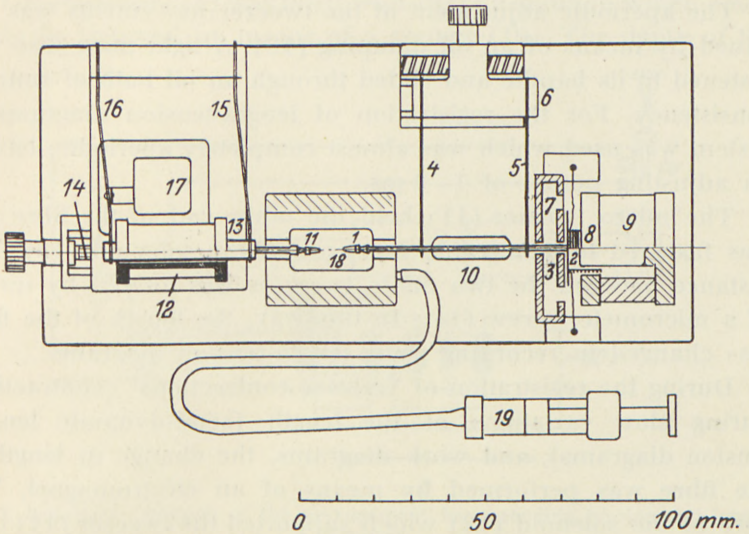


Fig. 2. Apparatus applied to the registration of length-tension diagrams and the measurement of dynamic stiffness.

(1) micro tweezer;
(2) movable condenser plate in connection with (1);
(3) fixed condenser plate connected with the grid of the high frequency circuit;
(4) and (5) steel springs to keep the tweezer (1) in position;
(6) cog-wheel mechanism or micrometer screw to vary the distance between the condenser plates (2) and (3);
(7) screen for the non-earthed condenser plate (3);
(8) coil firmly attached to condenser plate (2);
(9) ring shaped permanent magnet;
(10) variable oil damping for tweezer (1);
(11) micro tweezer to hold the other tendon end of the muscle fibre;
(12) and (13) solenoid with iron core;
(14) micrometer screw to vary the distance between (1) and (11);
(15) and (16) strong steel springs to hold the iron core (12) in the axis of the solenoid (13);
(17) oil bath to damp movements of tweezer (11);
(18) chamber with Ringer solution;
(19) syringe for changing Ringer solution in (18).

the distance between the point of application of the spring and the point of rotation of the balance (a) and the point of application of the weighing pan (b) $P_1 = \frac{P \cdot b}{a}$. The measuring range of the calibrated spring-balance was 1—130 mgm.

Within a small range of loading, a compensation is not necessary, since loading and change in capacity are practically proportional. The stiffness of the system was regulated so that additional contraction tensions could be correctly registered.

The aperiodic adjustment of the tweezer movements was obtained by means of an oil damping (10). A light mica disc was fastened to its handle and slided through an oil bath of suitable consistency. For the registration of length-tension diagrams, a system was used which was almost completely aperiodic, having an adjusting period of 1—2 ms.

The micro tweezer (11) held the other end of the fibre and was fastened to a movable iron core of the solenoid (13). The distance between the two micro tweezers was altered by means of a micrometer screw (14). In this way, the length of the fibre was changed in recording static length-tension diagrams.

During the registration of "release contractions", contractions during slow variations of the length (semi-dynamic length-tension diagrams), and work diagrams, the change in length of the fibre was performed by means of an electromagnet. The core of the solenoid (12) which supported the tweezer (11) consisted of iron from the tweezer to the middle of the solenoid, and the rest of brass. By means of two strong flat springs, the core was kept in the axis of the coil. When the current in the coil (12) was varied, the iron portion of the core was drawn into the middle of the solenoid with a force proportional to the magnitude of the current. This current was calibrated relative to the movements of the tweezer by means of a measuring microscope and hence became a measure of the length alterations. A rheostat served to regulate the movement of the core, and these movements were damped by an oil bath (17). In the present arrangement, the movement of the tweezer was 12 mm. at the most. The length alterations were registered by means of a torsion band oscillograph (Fig. 3).

The original length of the fibre and—in static experiments—the increases in length were measured with a measuring microscope, the tubes of which can be moved horizontally over a range of 20 cm. The accuracy of the measurements is 0.01 mm.

For the measurement of the dynamic stiffness in vibration experiments, practically the same arrangement was used as for

the registration of length-tension diagrams. The springs 4 and 5 were replaced by two very long and soft springs. The period of vibration of the system was further increased by increasing the mass of the registering system.

The chamber (18) was filled with RINGER solution which could easily be renewed by means of a syringe (19). The depth of the

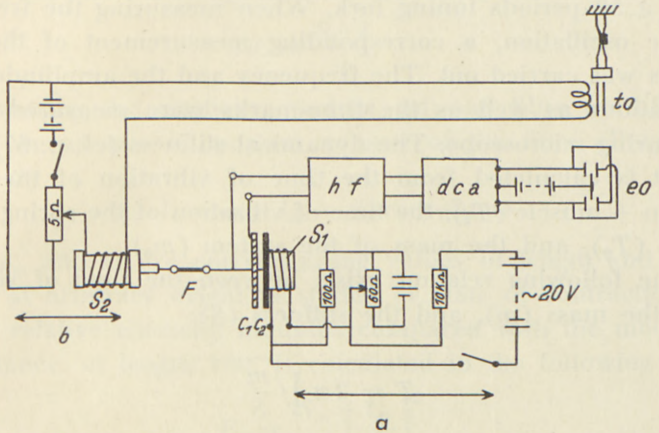


Fig. 3. Schematic diagram of the arrangement for recording tension and length variation.

(*a*) arrangement to compensate mechanical tension by the current in coil S_1 (= (8) of Fig. 2); the same arrangement is used to give a sudden impulse producing vibrations in dynamic elasticity measurements.

F = muscle fibre;
C_1 and C_2 = condenser plates ((2) and (3) of Fig. 2);
h f = high frequency apparatus;
dca = direct current amplifier;
eo = electrostatic oscillograph employed for the measurements of the variations in capacitance between C_1 and C_2;

(*b*) arrangement for varying the fibre length by means of an electromagnetic system ((12) and (13) of Fig. 2).

S_2 = solenoid;
to = torsion oscillograph registering the current in S_2.

chamber was 0.5 cm. and even very markedly relaxed fibres were not in danger of touching the glass on the bottom of the chamber. In vibration experiments, it was found that the friction resistance of the RINGER solution can introduce a considerable error. Therefore, the RINGER solution was removed immediately before the vibration impulse occurred and was replaced later. In order to facilitate the adjustment of the fibre in the tweezer, an object slide was inserted directly beneath the tweezers while preparing took place.

The fibre and the registering arrangement were caused to vibrate by sudden current variations in the solenoid (8) (cf. Fig. 2). The different stretches at rest and during contraction were registered twice with four vibration impulses. The individual values are thus mean values from 8 determinations.

Simultaneously with the vibrations, time-marks were registered from a 50 periods tuning fork. When measuring the frequency of the oscillation, a corresponding measurement of the time-marks was carried out. The frequency and the amplitude of the oscillations as well as the time-marks were measured with a measuring microscope. The dynamical stiffness (cf. p. 67) of the object is calculated from the time of vibration of the spring system + muscle (T_1), the time of vibration of the spring system alone (T_0), and the mass of the system (m_0).

The following relation exists between the time of vibration (T), the mass (m), and the stiffness (S):

$$T = 2\pi \sqrt{\frac{m}{S}}. \tag{1}$$

For the calculation of the muscle stiffness (S_1), the stiffness of the spring system (S_0) and its mass (m_0) must be known. The effective mass of the spring system was determined by measuring its natural time of vibration and the time of vibration (T'_0) with a small additional mass (m'_0).

On the basis of equation (1), we get the following relations:

$$T_0 = 2\pi \sqrt{\frac{m_0}{S_0}} \tag{2}$$

$$T'_0 = 2\pi \sqrt{\frac{m_0 + m'_0}{S_0}} \tag{3}$$

$$T_1 = 2\pi \sqrt{\frac{m_0}{S_0 + S_1}}. \tag{4}$$

Transposing m_0, S_0, and S_1, we get

$$m_0 = m'_0 \frac{T_0^2}{T_0'^2 - T_0^2} \tag{5}$$

$$S_0 = 4\pi^2 \cdot m'_0 \frac{1}{T_0'^2 - T_0^2}. \tag{6}$$

The stiffness of the object (S_1) is found as the additional stiffness of the system

$$S_1 = 4\pi^2 \cdot m_0 \frac{1}{T_1^2} - S_0. \tag{7}$$

If the stiffness of the fibre, its length (l), and cross section (q) are known, the elasticity modulus (E) may be calculated as

$$E = \frac{S_1 \cdot l}{q}. \tag{8}$$

Comparing the elasticity modulus of one fibre at different lengths we assume a constant volume of the fibre (POISSON's ratio = 2)

$$q_1 \cdot l_1 = q_m \cdot l_m = \text{fibre volume} \tag{9}$$

where q_m and l_m are corresponding values of length and cross section at arbitrary extent of stretch or state of contraction.

The relative elasticity modulus compared with the modulus, for instance, at length 100, is calculated in the following way:

$$E_m = \frac{S_m}{S_{100}} \left(\frac{l_m}{100}\right)^2 \tag{10}$$

where l_m is the length of the fibre in per cent of the equilibrium length, S_m the stiffness measured at l_m, S_{100} the stiffness at equilibrium length, and E_m is the required relative elasticity modulus. Equation (10) gives a correction for length alterations and corresponding changes of the cross section during stretch and release contractions.

In every experiment, we register the vibration frequencies of the spring system + the resting fibre, of the spring system + the tetanically contracted fibre, and of the unloaded and the loaded spring system. It is of great importance that the length alterations imposed on the fibre are small (less than 1 per cent of the length of the fibre) and that they do not give rise to a mechanical stimulation. Furthermore, the stiffness of the system and that of the fibre should be of the same order of magnitude so as to enable the highest possible accuracy of the measurements. Working with springs which are very stiff compared with the muscle—as those used by GASSER and HILL (1924)—considerably reduces the difference in the time of vibration of the system with or without the muscle and, consequently, the accuracy of the measurements.

In the present experiments, the period of vibration of the system amounted to 200—300 ms. and its effective mass was 2—3 gm. If the stiffness is measured during contraction, a constant height of contraction during a longer period of time can only be maintained in a tetanus. It has been possible to register tetanic contractions of a single fibre of a duration longer than 40 sec. at practically constant level. In general, however, the shortest

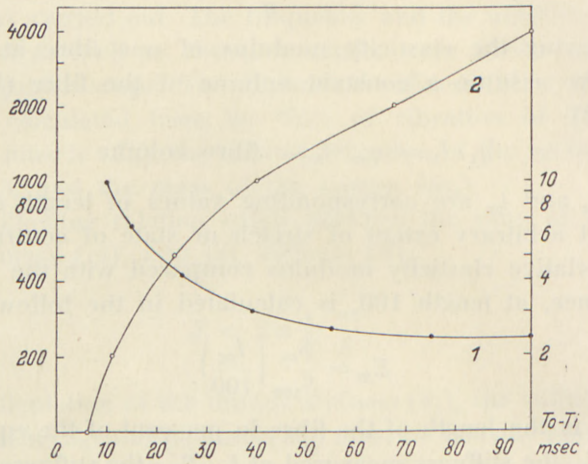


Fig. 4. Curve 1 = standard error in determination of stiffness as a function of oscillation period ($T_0 - T_1$).
Curve 2 = stiffness as a function of variation in the oscillation period.
abscissa = variation of the oscillation period in ms;
ordinate = (to the right belonging to curve 1) percentage error;
(to the left belonging to curve 2) stiffness in dynes cm^{-1}.

possible contractions were applied, i. e. of a duration limited by the consolidation of the fibre. For the registration of the stiffness during release contractions, the fibre was brought to vibrate after being adapted to the release length during contraction.

Accuracy of the measurements: As mentioned before, the stiffness of the object was measured by determining the characteristic period of vibration of the system with and without the object. The uncertainty of the determination of the period of vibration or the variation measured of the system + object without exterior influences was found to be 2.5—3 ms when the period of vibration varied between 270—175 ms. The influence of this uncertainty on the calculation of the stiffness is illustrated

in Fig. 4 which shows the standard error of an individual point determined by seven measurements (Curve 1). It may be concluded from this figure that, at a difference of 10 ms. (stiffness 200 dynes cm^{-1}), the standard error of the stiffness determination amounts to 10 per cent, corresponding to 20 dynes cm^{-1}. The error in per cent decreases with increasing stiffness and amounts to less than 3 per cent if the measured stiffness is above 1000 dynes cm^{-1}. The standard error is then 30 dynes cm^{-1}. In the present experiments, stiffnesses between 400—5000 dynes cm^{-1} are determined, i. e. the experimental error is between 2.5 and 5 per cent.

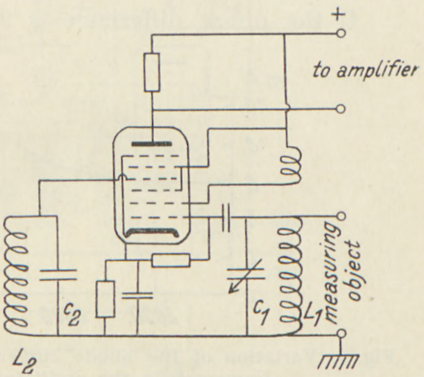


Fig. 5. High frequency circuit for measuring small variations in capacity (explanation, see text, pp. 15—16).

High frequency arrangement for the tension-registration: The changes in tension of the muscle fibre were registered as minute changes in length. These length alterations were measured as variations in the capacity of a plate condenser, the one plate of this condenser being connected with the fibre and, at the same time, electrically connected to earth. The changes in capacity were measured by a high frequency arrangement, the principle of which has been described by ZAKARIÁS (1938) as especially suited for condenser microphones. The scheme of the circuit is given in Fig. 5.

An octode is connected with two tuned circuits. Grid 1 and grid 2 together with the first oscillating circuit which is coupled with the object form an oscillator, the frequency of which is given by the self induction L_1 and the sum of the capacity of the object + the leads and the capacity of the variable condenser c_1. When this circuit is oscillating, the current flowing through the valve oscillates in time with it. Grid 3 and grid 5 behave like screened grids and, hence, do not take part in the process mentioned. Grid 4, however, is influenced capacitively by the current impulses because of space charge capacities and is affected as if a negative capacity was introduced between grid 1 and grid 4. Grid 4 is connected with a circuit L_2c_2 which is

tuned to the same frequency as the oscillator circuit. If the resonance frequency is the same as the oscillator frequency, the circuit L_2c_2 acts as a resistance, the imposed high frequency potential on grid 4 having a phase difference of 90° relative to the potential of the oscillator. The resulting anode current in the valve depends upon the potential of the oscillator grid and grid 4 and, furthermore, on the phase difference between these two potentials.

If the phase difference is 90°, these two grids do not effect

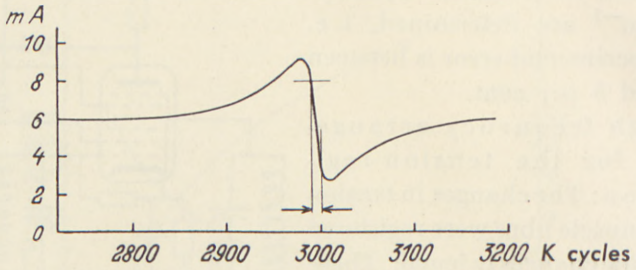


Fig. 6. Variation of the anode current (ordinate in mA) as a function of the frequency in the oscillator (abscissa in frequency/sec.).

the resulting emission of the plate. At a phase difference of 0°, the highest possible emission is attained, and at a phase difference of 180°, the plate emission is at a minimum, the grids counteracting each other. A frequency alteration of the oscillator will cause the circuit L_2c_2 to cease acting as a resistance but as a capacity or an induction and, consequently, the high frequency on grid 4 will be phase-shifted either more or less than 90°, thus resulting in a smaller or greater anode current. The curve of Fig. 6 shows the variation of the anode current as a function of the frequency variation. Hence, the anode current reaches a constant mean value before resonance between the circuits is attained. The very low impedance of the circuit L_2c_2 explains this fact. With the oscillator frequency approaching the resonance frequency of L_2c_2, the anode current increases, reaches a maximum (at a phase difference of 135°), decreases again very rapidly, and passes the mean value (at a phase difference of 90°). The decrease continues to a minimum at a phase difference of 45° and is followed by a slow increase in the anode current to its stationary value. The range between the maximum and the minimum is

especially suited for the measurement of minute changes of capacity, since a frequency variation of about half the resonance range is sufficient for optimum loading of the octode. The accuracy of the measurements with this arrangement is not limited

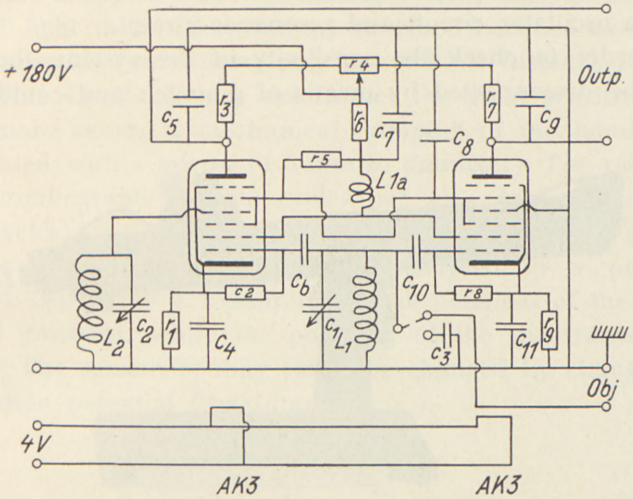


Fig. 7. Balanced high frequency circuit as used in the present investigation.

resistances.

r_1 = 300.
r_2 = 0,2 meg. Ohm.
r_3 = 50 k Ohm.
r_4 = 25 k Ohm (potentiometer).
r_5 = 50 k Ohm.
r_6 = 10 k Ohm.
r_7 = 50 k Ohm.
r_8 = 0.2 meg. Ohm.
r_9 = 300 Ohm.

condensers.

c_1 = 100 $\mu\mu$F.
c_2 = 50 $\mu\mu$F.
c_3 = condenser for comparison.
c_4 = 0.1 μF.
c_5 = 1000 $\mu\mu$F.
c_6 = 100 $\mu\mu$F.
c_7 = 0.1 μF.
c_8 = 0.1 μF.
c_9 = 1000 $\mu\mu$F.
c_{10} = 100 $\mu\mu$F.
c_{11} = 0.1 μF.

Ak_3 = indirectly heated four ray octode.*

* In more recent experiments, a directly heated heptode has been used with satisfactory results. In using this tube, a dry battery placed inside the apparatus may serve as a source of the filament current; one of the output terminals can be connected to earth.

by the electrical properties, but by the purely mechanical vibrations of the movable plates of the measuring condenser.

For the present purpose, the system was built in a balanced circuit, with two octodes and the oscillator parts in parallel (Fig. 7). One of the control grids was connected with the resonance circuit, the other control grids were earthed, the potential difference

between the two anodes thus being the desired measuring voltage. The potential difference is independent of temperature variations of the cathode within a wide range, and is furthermore independent of the anode potential and the high frequency potential of the oscillator. It depends exclusively on the frequency difference between oscillator circuit and resonance circuit.

In order to check the sensitivity of the system, the object could be disconnected by means of a switch and could be re-

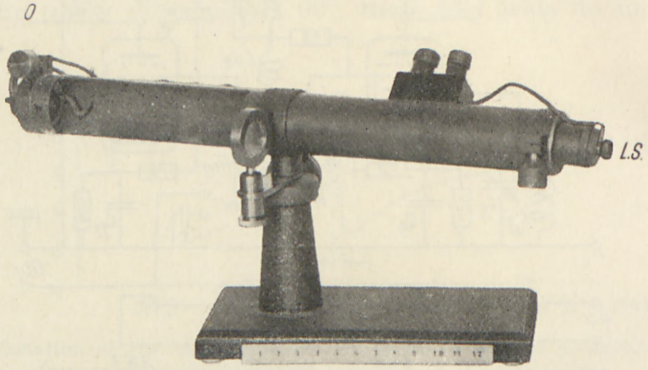


Fig. 8. Electrostatic oscillograph.
L.S. = light source; *O* = oscillograph.

placed by a capacity. Since, however, minute capacity variations have to be measured, great stress must be laid upon keeping the capacity of the leads constant. The leads from the measuring condenser to the high frequency arrangement were placed concentrically into a metal tube and supported at numerous points in order to avoid vibrations and, consequently, capacity variations. The output potential of the high frequency system was led through a 1- or 2-stage d. c.-amplifier (Buchthal and Nielsen, 1936) to the oscillograph described below.

By means of a 1-stage d. c.-amplifier (70 times) the sensitivity can amount to a 1 mm deflection with a condenser movement of $5 \cdot 10^{-3}$ μ. (Distance between oscillograph and camera 60 cm.).

The movement of the condenser plate was registered by means of an electrostatic oscillograph. Originally, this oscillograph has been employed in a somewhat different form for sound-film recording according to Beer. The apparatus was adapted for biophysical application according to our suggestions.

Fig. 8 shows the apparatus in its present form with the light source placed in a fixed position on the stand of the oscillograph. The electrostatic oscillograph is a potential-sensitive mirror oscillograph, a type which is of special advantage for the connection to a valve amplifier. The oscillating system consists of a thin band of light metal (0.0015 mm) stretched between two sets of solid electrodes (quadrants) and at a minute distance from the latter. This small distance determines the great sensitivity and furthermore causes a mechanical damping of the band which is provided with a mirror (1.5 mm in diameter). The resonance of the oscillograph is 3000 cycles per sec. (increasable up to 5000 cycles), its sensitivity at a 60 cm registration distance amounts to 0.5—1 mm/volt. When coupled to a push-pull amplifier—as in the d. c.-amplifiers—the potential of the torsion band is constant, while the potential of the quadrants varies (Fig. 3). The sensitivity may easily be changed by changing the polarization potential (maximum 90 V.).

Length-tension diagrams.

Static length-tension diagrams.

1) Rest.

The curve begins at a point corresponding to the equilibrium length of the fibre (length 100, Fig. 9*a*), i. e. the length where the fibre is just developing tension as a consequence of increased length. The increase in tension (t) following the increase in length (l) $\left(\frac{\Delta t}{\Delta l} = \text{static stiffness}\right)$ increases with the extent of stretch over the whole range of the curve until the fibre is disintegrated. A stretching of the fibre up to a length of 200—220 per cent of the equilibrium length has been observed.

The stiffness measured in the beginning varies and depends —to some extent—on the sensitivity of the registering system, i. e. a more sensitive system would register a somewhat shorter equilibrium length, because an increase in tension would be noticed at an earlier stage. However, the uncertainty originating from this fact does not exceed 5 per cent of the "true" length of the fibre.

The slight incline of the curve in the beginning, at a stretch from about equilibrium length to length 130, must be interpreted as originating partly from a length-orientation of minute structure elements (micellae). This accords with BUCHTHAL and KNAPPEIS' (1939) optical experiments which show an adjustment of the elements up to a stretch of 30 per cent. From that point an

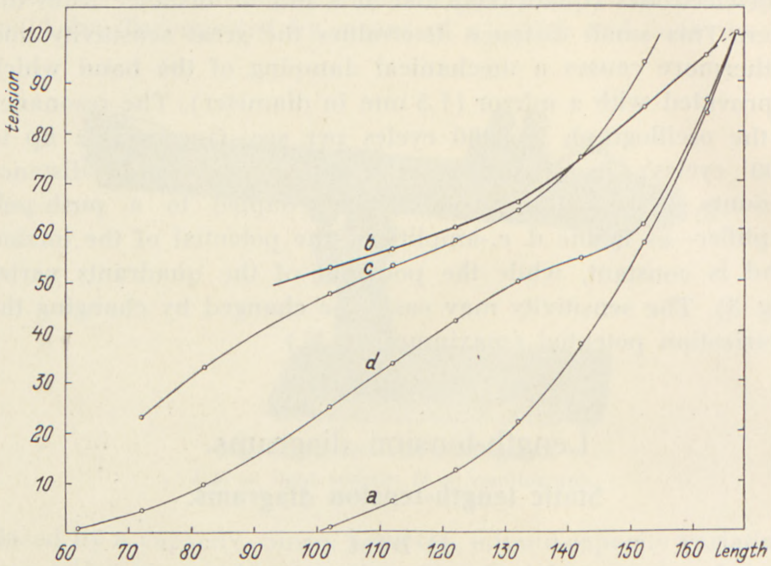


Fig. 9. Length tension diagram of the isolated striated muscle fibre. (*a*) rest; (*b*) tetanic isometric contraction (fibre stretched at rest); (*c*) tetanic isometric contraction (fibre stretched during contraction); (*d*) release contraction (release to the same tension as at rest).
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

obvious gradient increase appears, the micellae are adjusted and they cannot contribute further to the elasticity because of complete orientation. After this stretch, the curve represents the "true" qualities of the elements of the fibre. In agreement with ASMUSSEN's (1936) experiments, stretching up to a length of 150 was found to be reversible. At higher extent of stretch, the increase in length was partly irreversible (plasticity).

2) Isometric tetanic contraction.

The isometrically contracted fibre develops a tension in equilibrium length (length 100) approximately corresponding to the

tension of a resting fibre at length 150 (Fig. 9*b*). With increasing length, the tension of the contracted fibre increases and generally the tension difference between contraction and rest is constant up to a length of about 140. At further stretch, the contraction tension is relatively reduced; rest and contraction curves approach each other and they meet at the length 160—200.

At a length above 160, the isometric length-tension curve exhibits a somewhat irregular course; the total tension changes its rising tendency rather suddenly, becomes constant, and may even be reduced in a range of about 10 per cent of stretch. Later,

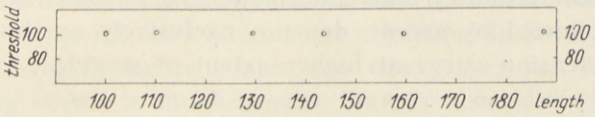


Fig. 10. Irritability of the directly stimulated fibre as a function of stretch. abscissa = length of the fibre (equilibrium length = 100); ordinate = threshold value in relative units (threshold of the non-extended fibre = 100).

the curve inclines rapidly. This deviation from the continuous course may be of different origin. A change in irritability of the fibre has been suggested as the cause (Asmussen 1936). In a number of experiments the threshold value was constant up to lengths of 180—200. This observation proved to be true for directly (in some experiments curarized) as well as indirectly stimulated fibres (Fig. 10). As an indicator of the threshold value, the contraction of the single fibre visible under the microscope or sometimes the tension developed has been applied. The decrease in extra-tension at high extensions can therefore not be due to a change in irritability, as an increase in stimulation intensity, which was maximal at moderate stretch, does not inhibit the decrease in extra-tension during contraction at high extensions. When registering the length-tension diagram, stimuli being considerably above the threshold value were chosen.

The decrease in tension already described by Blix (1892) is scarcely caused by fatigue. As supposed by Blix, it may rather originate from reduced contractility during heavy loading or from reduced stiffness. In the case of the I substance, a reduced stiffness following the contraction could be observed, since under the same loading I is elongated during contraction when a certain

stretch is reached (cf. length-tension diagrams of the I substance, where the rest-curve and the contraction curve have a point of intersection at higher stretch; comp. Fig. 28.).

However, this small change of the length can scarcely explain the disappearance of tension (extra-tension) during contraction. The main cause of the reduced extra-tension must be found in a diminished contractility. A structural interpretation of this behaviour is given in a later section.

The total contraction tension during isometric contraction is = tension at rest + extra tension. Whether the contraction curve shows a continuously increasing course, a constant level, or a decline followed by ascent, depends exclusively on the slope of the extra-tension curve at higher extent of stretch.

3) Stretch of a tetanically contracted fibre.

During stretch of a tetanically contracted fibre, the curve corresponds up to length 160—in all our experiments—to the length-tension diagram of a fibre which is stretched at rest, and contracted isometrically (Fig. 9*c*). In this case, it is furthermore possible to register at a length below the equilibrium length, i. e. at length 80, a tension corresponding to the resting fibre at length 140 can be registered. Of course, the tension 0 must correspond to the shortest contraction length of the fibre.

In BECK's (1923), SULZER's (1930) and ASMUSSEN's (1936) experiments, the muscle or small fibre bundles, respectively, show—when they are stretched during contraction to a length 125—a marked increase in tension, compared with that during isometric contraction at the same length. This difference increases with increasing stretch. In the present experiments, up to a length 150, it has not been possible to observe a difference between these two curves beyond the limits of the uncertainty of the measurements.

ASMUSSEN interprets the deviation as expressing an incomplete consolidation. In our experiments with single fibres, however, the adaptation must have been sufficiently accomplished.

The length-tension diagrams in which the increase in length occurs during the contraction itself do not indicate the above mentioned decrease in tension at higher extent of stretch, as

found in the isometric length-tension diagrams. If the already contracted fibre is stretched, the contractile elements adjust themselves to the maximum extent of contraction in the non-extended state, and they develop the highest possible tension when they are stretched.

For both types of length-tension diagrams during isometric contraction it must be emphasized that the curves are uniform, where the gradient variation is most marked in the curve of the resting fibre, thus indicating an orientation of the elements. This fact is in agreement with the optical experiments on muscle fibres already mentioned (BUCHTHAL and KNAPPEIS, 1939) which proved that the micellae already are orientated in the equilibrium length during isometric contraction where they are exposed to a loading which is much greater than is necessary to orientate the micellae at rest.

Therefore the change in direction of the curve (9*c*) at a length 140—150 cannot originate from a micellar adjustment. The relation between these phenomena and the minute structure will be discussed in a later paragraph (cf. p. 119).

4) Release of the tetanically contracted fibre to the same tension as at rest.

During extension of the contracted fibre, a length-tension diagram is found which corresponds rather well to the length-tension diagrams during isometric contraction of a fibre stretched at rest. After release during contraction, however, quite different corresponding values of length and tension are observed (Fig. 9*d*). The tension developed in the release diagrams is much less than the tension at the same length during isometric contraction and in the stretched contracted fibre. Nevertheless, the tension is always higher than the tension at rest.

In a series of experiments, the length-tension diagram was registered in such a way that the fibre was released during tetanic contraction to the same consolidated tension as at rest. Obviously, this length is of special interest, since it offers the best possibilities of comparing the state of the fibre at rest and during contraction. The exterior mechanical conditions are the same and there is some reason to assume that the interior mechanical

situation of the fibre can best be compared with that of the resting fibre.

By means of the "compensation method" (cf. p. 8), it has been possible to register the shortest length of the fibre during contraction (contraction equilibrium length).

After release from isometric contraction at equilibrium length (rest) to the tension 0 during contraction, the single fibre was found to be shortened on average by 30 per cent. However, this is not the shortest length of the fibre during contraction since, during tensionless contraction, an average shortening of 45 per cent (limits 35—55 per cent) could be measured. This phenomenon has been investigated in greater detail in a special series of experiments in which the fibre was released from isometric contraction to the tension 0, then contracted in completely released state (in order to attain a tensionless contraction) and, finally, stretched until the beginning development of tension. These two lengths—at release contraction, where the tension ceases, and at tensionless contraction, where the developing tension begins—have been determined up to six times on the same fibre in different experiments. The difference is in full agreement with the material available which, at whatever extent of stretch above 100, showed less tension at the same length during release contraction than in any other "type of contraction". The difference may be explained by an "elastic locking" of the fibre at the maximum of the isometric contraction, an effect which will be analyzed more thoroughly in a later paragraph.

In some preliminary experiments on single contractions no similar phenomena could be observed. Also in these experiments, the fibre was released from the equilibrium length to that length where the peak-tension disappears; the completely released fibre was then stimulated and stretched until tension begins to develop. During release contraction a shortening of 33 per cent was found, during tensionsless contraction the shortening amounted to 35 per cent. The explanation of the lack of any difference in the case of single contractions must be found in an interruption of the mentioned "locking" in between every stimulation.

Comparative experiments with fibre bundles (20—30 fibres) did not lead to unambiguous results as regards the difference in the shortening during release contraction and tensionless con-

traction. Here, the shortest length was 45—50 per cent of the original equilibrium length. However, the equilibrium length which was checked in between every experiment showed considerable variations—in contrast to the experiments with single fibres. These variations are presumably caused by deformation of the fibre originating from the connective tissue.

Especially in the older literature, we find some notes on the shortening of the total muscle of up to 85—90 per cent of the length at rest (WEBER 1846). These remarkable shortenings are certainly due to an incorrect definition of the initial length of the muscle. However, it is not improbable that the values found on total muscles can exceed the maximum shortenings found on the single fibre. It is well-known that the muscles most frequently used in physiological investigations contain fibres of considerably differing lengths (cf. LINDHARD's (1926) measurements on m. gastrocnemius with length variations from 1.8 to 5 mm and on m. sartorius varying from 5 to 24 mm). From these facts it can be concluded that the muscle at an arbitrary stretch may contain fibres with far different degrees of stretch. Even at the length 100, it can be assumed that fibres may exist which are held in a stretched position by the supporting tissue of the muscle: e. g. a muscle bundle, 13 mm long, consists, for example, of fibres of an equilibrium length of 10, 13, and 16 mm, respectively. The shortening of the single fibre may amount to 30 per cent, which means that the single fibres are shortened to 7, 9, or 11 mm, respectively. The shortest fibre causes a curling of the others and, consequently, the total muscle is shortened to a length of 7 mm = 46 per cent.

During isotonic contraction with relatively small loading only part of the fibre material (the most stretched fibres) is able to work. Even when contracted, the rest will follow passively the length alterations of the muscle, as these fibres curl as soon as they have reached their shortest contraction length (cf. WEBER, 1846, and the author's own observations). During a higher extent of stretch, however, those fibres which are least stretched have to perform the greatest work, since the extra-tension of the most stretched ones has passed the maximum. In agreement herewith, the extensibility of the total muscle is considerably smaller than the extensibility of a single fibre. This phenomenon is not

only due to the reduced extensibility of the connective tissue but, first of all, to the inhomogeneous state of stretch of the single fibres.

In the first part of the curve (Fig. 9*d*), the shape of the length-tension diagram during release to the same tension as at rest corresponds accurately to the length-tension diagram at rest, apart from a length difference of 30 per cent. At stretch above 150 per cent, the contraction tension approaches the curve at rest (in agreement with the results from isometric curves) and runs parallel with it. At high extent of stretch, this curve and that at rest coincide.

The diagram of release contraction (tension under contraction = tension at rest) cannot be considered reversible, which means that every individual point can only be reached by producing continuous tetanic contraction and then releasing the fibre to the desired length. When the fibre is stretched in this state, the tension will rise above the curve, and on release, the tension will decline to lower values. This indicates: from every point of the isometric length-tension curve proceeds a special length-tension diagram connecting this isometric point with the corresponding release point. Hence, the curves of the isometric maxima and those of the release contractions (release to the same tension as at rest) differ essentially and are not reversible.

The phenomenon here described may be called an elastic "locking" of the fibre. In this state, the fibre follows only one among all possible length-tension diagrams at different release or stretch until the locking is broken off, for instance on account of a further stretch or interruption of the stimulation.

For further illustration of these length-tension diagrams, a number of experiments were carried out in which the tension was measured during isometric contraction, for instance at the length a, then at a length of $(a + 1)$ mm. and released during contraction to the length a. The stimulation was then interrupted for a short time and—as a check measurement—the fibre was restimulated at the length a. The experiments were carried out at various extents of stretch. The release contraction reveals essentially less tension than the isometric contraction at the same length. The control contraction shows thereafter the same length as the contraction in the beginning.

In some cases, the control does not regain the original value, which presumably may be ascribed to fatigue of the fibre. These experiments seem to indicate that release contractions fatigue the fibre more rapidly than ordinary isometric contractions of the same duration.

Thus, the contraction process depends not only upon the stimulation but also on the external conditions under which the contraction occurs. This has already been stated by VON KRIES (1880); later, SEEMANN (1905) came to corresponding conclusions on the basis of experiments with length alterations during contraction.

At sudden release during contraction of the whole muscle, GASSER and HILL (1924) found that the resulting tension after consolidation is only a function of the instantaneous length and independent of the preceding length or of alterations of the loading. The curve of the isometric maxima should then be reversible which, however, is in disagreement with our experiments with release contractions on single fibres where the final tension—in spite of complete consolidation—does not reach the isometric maximum corresponding to this length. The first part of the tension decrease during "quick release" is, of course, caused by "viscosity". However, the viscosity effect cannot explain the continuously lower tension during contraction in relation to the corresponding isometric maximum. Our differing observations on single fibres as compared with those of GASSER and HILL on total muscle might be due to a discontinuous activity of the individual fibre in the muscle. (A fatigued muscle fibre will cease to contract and will after restitution begin again with its isometric maximum). The rapidity of the tension development after release was found to be considerably less in SULZER's (1930) and in our own experiments than found by GASSER and HILL, a fact which might indicate that the majority of fibres were in an unstimulated state in these experiments.

In experiments on total muscle, SULZER (1930) found a reversibility of the length- and tension alterations as long as a certain low loading was not exceeded. According to our interpretation, this observation is due to a tension too low to produce the locking (cf. p. 24); stop-contractions and support-contractions, as described by REICHEL (1934) in his experiments on total muscles, show a length-tension function which indicates clearly that the curve of the isometric maxima is not reversible. However, REICHEL's correlation between the resting curve, the

curve for isotonic maxima, and the curve for isometric maxima is not correct, since it is based on experiments which show rather low extra-tension during contraction; furthermore, REICHEL assumes a linear dependence between isotonic shortening and initial length.

The locking after release from isometric contraction is not identical with the "catch mechanism" which appears in smooth muscle. It has often been attempted to transfer the observations on smooth muscles to cross-striated muscles. BECK (1923), for instance, thought he had demonstrated such a mechanism in cross-striated muscles. It is, however, not admissible to interpret the difference between the curves for the isometric maxima at long-lasting tetanic stimulation and the length-tension diagrams of the stretch of a tetanized muscle at short-lasting (0.1 sec.) tetani as a "catch mechanism" in the tetanic contraction. A tetanus lasting 0.1 sec. does not cause a full development of tension, it must rather be compared with a single contraction, the tension of which may amount to $^1/_3$ of the tension during isometric contraction (cf. p. 33).

In contrast to the "catch mechanism", a "locking" can only be observed during release of a tetanized muscle fibre by a steeper partial length-tension diagram than the curve of the isometric maximum. Certainly, this steep diagram may continue above the curve of the isometric maximum, but only to about 5 per cent of the extra stretch; then, the curve bends sharply—the locking is broken—and the curve proceeds parallel with or overlapping the curve of the isometric maxima. While, in physiological respect, the "catch mechanism" would be a very economical procedure, this is not the case in the above described locking (cf. work diagrams with and without locking, p. 43).

On the basis of these release-length-tension diagrams, it becomes possible to draw some conclusions as regards the largest possible amount of work which a stretched muscle is able to perform during length reduction.

If the length reduction occurs during continuous stimulation, the work performed is but a fraction of the area between the resting curve and the curve of the isometric maxima of the muscle. If, however, the reduction of length occurs during repeated interruption of the stimulation, an isometric maximum

is reached at the start of the stimulation. The tension is then somewhat reduced, the stimulation is interrupted, and a new stimulation begins. In this way, the average tension of the fibre is held on a much higher level in spite of—or rather just because of—the interruptions of the stimulation.

The quantitative conditions are investigated more thoroughly in the registration of work-diagrams (cf. p. 43).

Length-tension diagrams from single contractions.

1) Single contractions at long time intervals.

The diagram of Fig. 11 represents the resting tension, the contraction extra-tension, and the resting tension + extra tension

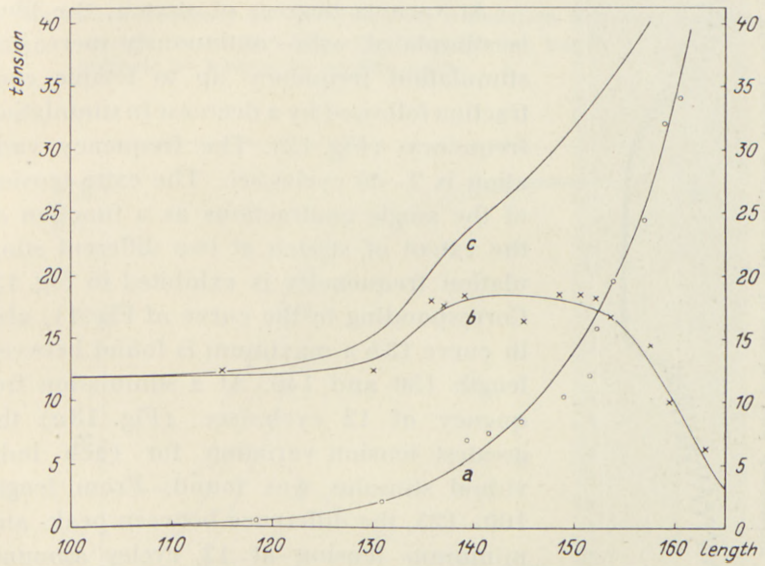


Fig. 11. Length-tension diagram of a single fibre at rest and during isometric contraction (single contractions).

(*a*) length-tension diagram at rest; (*b*) extra-tension produced by contraction; (*c*) initial tension + extra-tension.

abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in mgm.

(peak tension) as a function of length. The curve of the extra-tension is horizontal from length 100—130, then the extra-tension increases, reaches a maximum at about length 140 and

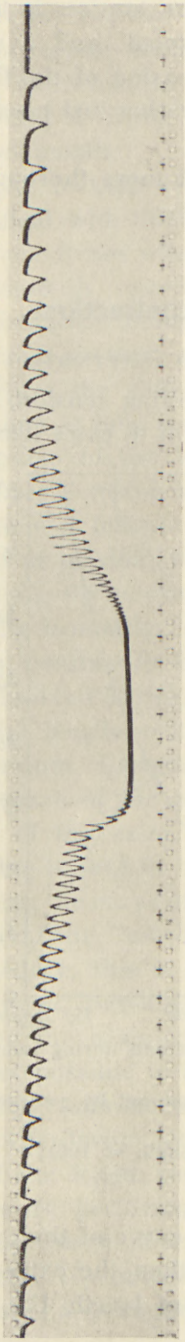


Fig. 12. Isometric tension of a single muscle fibre during continuously increasing and decreasing stimulation frequency (2—50 cycles/sec.) time marks 1/5 sec.

decreases again approximating 0 with increasing stretch. The maximum of the extra-tension indicates that in a single contraction the fibre has the greatest mechanical reaction at moderate stretch. The increase in extra-tension occurs in the same range of stretch where we must assume that the orientation of the elements of the fibre occurs and, thus, greater tension is transmitted to the tendon.

2) Single contractions at varying time intervals.

At various degrees of stretch, the fibre is stimulated with continuously increasing stimulation frequency up to tetanic contraction followed by a decrease in stimulation frequency. (Fig. 12). The frequency variation is 2—50 cycles/sec. The extra-tension of the single contractions as a function of the extent of stretch at two different stimulation frequencies is exhibited in Fig. 13. Corresponding to the curve of Fig. 11, also in curve 13*b* a maximum is found between length 130 and 140. At a stimulation frequency of 12 cycles/sec. (Fig. 13*a*) the greatest tension variation for each individual stimulus was found. From length 100—125, the difference between peak- and minimum tension at 12 cycles amounts to about twice the "pure" single contractions (Fig. 13*b*) with long time intervals. Fig. 14 shows the course of tension of a fibre in equilibrium length as a function of the stimulation frequency. The height of the single contractions (curve *a*) in the first range is equal to peak-tension minus rest tension. Gradually as the stimulating impulses follow more frequently, the fibre

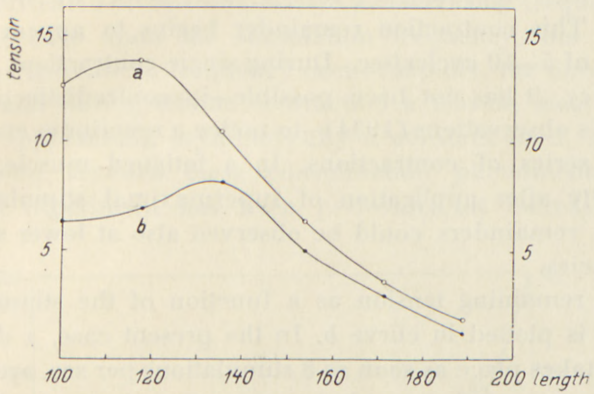


Fig. 13. Extra-tension (peak-tension) produced by single contractions of the isolated fibre as a function of stretch.

(*a*) stimulation frequency 12 cycles/sec.; (*b*) stimulation frequency 2 cycles/sec.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

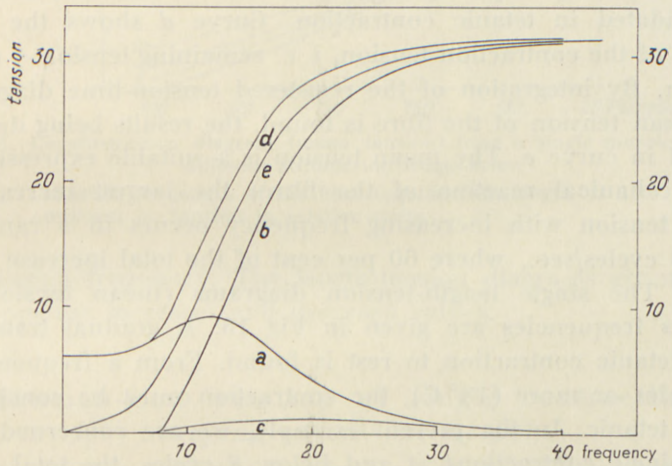


Fig. 14. Tension produced by a single non-extended fibre (length = 100) as a function of the stimulation frequency.

(*a*) height of the single contractions; (*b*) contraction remainder; (*c*) increase in contraction remainder per stimulus; (*d*) peak values of tension during contraction (contraction remainder + extra-tension); (*e*) mean tension.
abscissa = stimulation frequency, cycles/sec.;
ordinate = tension in relative units.

tension does not reach the resting value before the new stimulus begins. This contraction remainder begins to appear at a frequency of 5—10 cycles/sec. During single contractions at a lower frequency, it has not been possible—in contradistinction to ASMUSSEN's observations (1934)—to notice a remainder even in long-lasting series of contractions. In a fatigued muscle, however, especially after application of supermaximal stimulation, contraction remainders could be observed also at lower stimulation frequencies.

The remaining tension as a function of the stimulation frequency is plotted in curve *b*. In the present case, a direct summation takes place as soon as 8 stimulations per sec. are exceeded. The increase of the remainder per stimulus as a function of frequency is shown in curve *c*. As is to be expected, the curve inclines up to 20 cycles, since the relaxation time is shorter at smaller stimulation intervals. However, this increase can only continue up to a certain limit, because the extra-tension is reduced with increasing frequency and becomes = 0 when the fibre is consolidated in tetanic contraction. Curve *d* shows the peak values of the contraction tension, i. e. remaining tension + extra-tension. By integration of the registered tension-time diagrams, the mean tension of the fibre is found, the results being demonstrated in curve *e*. The mean tension is a suitable expression of the mechanical reaction of the fibre; the largest increase in mean tension with increasing frequency occurs in a range of 10—20 cycles/sec., where 60 per cent of the total increase takes place. The single length-tension diagrams (mean tension) at various frequencies are given in Fig. 15. A gradual transition from tetanic contraction to rest is found. From a frequency of 30 cycles or more (18° C), the contraction must be considered to be tetanic. In the present example, we are concerned with pure single contractions at and below 8 cycles, the total mean tension being so low that the yield of work cannot be positive because of viscous loss. The principal variation range is between 10 and 30 cycles. At 8 cycles, where the intervals between the single contractions are so long that the rest tension may just be reached before the following stimulation begins (remainder = 0), the mean extra-tension amounts to $^1/_5$ of the tension in tetanic contraction.

Consolidation: The summation at increasing frequency depends not only upon the stimulation frequency, but also on time. If the increase in frequency occurs rapidly, the fibre cannot "follow" and during tetanic contraction a tension may thus be observed approaching asymptotically a constant level. In order to take into account these consolidation phenomena, every individual experiment has been performed at increasing and

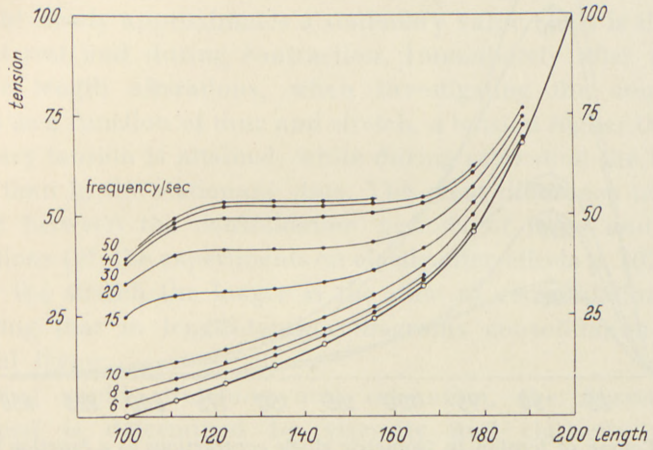


Fig. 15. Length-tension diagram (mean tension) from a single muscle fibre at different stimulation frequencies.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

decreasing frequency. The length-tension diagrams given lie in between the increase- and decrease values.

3) Tension-time relation of single contractions at varying extents of stretch.

Fig. 16 shows the tension during isometric single contraction as a function of time. The peak extra-tension developed is reached 40 ms. after the first noticeable development of tension (temp. 18° C). The duration of the development of tension is not influenced by the extent of stretch as long as the fibre is not fatigued. The course of tension is considerably prolonged in tired fibres. The peak extra-tension is not highest at the equilibrium length (cf. length-tension diagram, Fig. 11), but increases

with increasing extent of stretch reaching a maximum at a length of 120—130.

At length 100, the duration of the relaxation from the peak extra-tension to half of its value lies around 30 ms and increases continuously to 50 ms at a length of 170—180. Correspon-

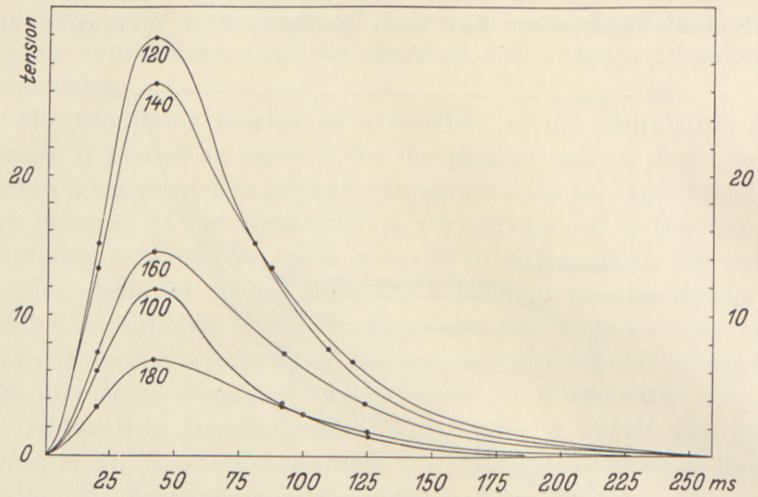


Fig. 16. Course of tension in isometric single contractions as a function of time; different extents of stretch (the figures below the curves indicate the length of the fibre).
abscissa = time in msec.
ordinate = tension in relative units.

dingly, the distance from the peak extra-tension to $^1/_4$ of its value increases from 55 to 80 ms.

Semi-dynamic length-tension diagrams.

In static length-tension diagrams, the elastic properties of the fibre mainly determine the slope of the curves. It must, however, be emphasized that also other physical properties of the fibre are changed proportionally to the stretch and its duration. This may be proved by comparing the equilibrium length of the fibre before and after the experiment. The equilibrium length is generally increased by 10 per cent after stretch above a length 130—150. This change can be partially restored by allowing the

fibre to remain for some time in an unloaded state, but full restoration of the original length is not attained above length 150, which may be ascribed to an irreversible alteration (plasticity).

Hence, the static length-tension diagram does not give full information about the elastic properties of the fibre. By registering the fibre-tension developed simultaneously with the stretch, it was found that the tension does not immediately reach a constant level but slowly approximates a stationary value. This is the case both at rest and during contraction. Immediately after the respective length alterations, when investigating the course of tension as a function of time and stretch, a tension higher than the stationary tension is attained, while during relaxation the tension is less than in the stationary state. The great difference becomes evident between the consolidation periods of large and small elongations (cf. the experiments on elastic after-effects p. 102). The greater the stretch the longer is the time of consolidation, thus indicating that in length-tension diagrams consolidation is an essential factor.

During rapid stretching and relaxation, the fibre-tension developed is determined by viscosity and elasticity of the fibre, while the tension in static length-tension diagrams is given by elasticity and plasticity of the fibre. Hence, the most comprehensive information is derived from static curves combined with length-tension diagrams at varying rates (static, semi-dynamic, and dynamic experiments).

In static length-tension diagrams, the duration of an experiment is about 30 min. In semi-dynamic experiments, the time of duration of stretch for a total length-tension diagram varies from 10 to 1 sec, and in purely dynamic experiments, the duration of a small stretch amounts to 0.1—0.05 sec. On account of the considerably shorter experimental period, the semi-dynamic and dynamic experiments have the advantage of reducing fatigue or other drawbacks conditioned by the duration of the experiment.

Semi-dynamic length-tension diagrams of the whole muscle were investigated by Blix (1892), Fick (1892), and Sulzer (1930). In agreement with the majority of the subsequent investigators, Blix found even in the resting muscle a difference between the

curves at stretch and those during relaxation, this difference increasing with the rate of stretch. He assumed the curve to be reversible, provided that the length alterations occur sufficiently slowly. Employing BLIX' method, FICK investigated the contracted muscle and he found also here a difference between the curve at stretch and the curve during release. In this case, the difference is so remarkable that it cannot be explained by the effect of viscosity alone; FICK, therefore, assumed an increase of irritability occurring during stretch and, consequently, an increase of tension. At stretch followed by release of a muscle during stimulation, SULZER—in agreement with FICK—does not notice any reversibility.

As already mentioned in the description of the experimental method, length and tension of the fibre were registered simultaneously by means of an electrical transmission (p. 10). The experiments may be classified in two groups: one series in which the fibre is stretched about 50—60 per cent in the beginning, is then released, and thereupon stretched again. In some experiments, stretch and release are repeated several times, beginning with small length alterations and continuing with increasing length alterations starting from the same original length. In other experiments, slight stretch and release are performed at different arbitrary lengths of the fibre.

1) Semi-dynamic length-tension diagram of alternating stretch and relaxation at rest.

During stretch (Fig. 17), the tension of the fibre increases with increasing differential quotient. In the beginning, the release curves show a somewhat steeper slope than the stretch curves, a fact which must be ascribed to the viscous resistance of the fibre to length alterations. Completely relaxed fibres exhibit an equilibrium length which is a little greater than that before stretching. This change is reversible, and after a lapse of some time, the fibre will regain its initial length. However, in the present experiments, the intervals are not very long, a new stretch and release following almost immediately. The difference between corresponding stretch- and relaxation-curves and, on the other hand, between the different curves of stretch and relaxation,

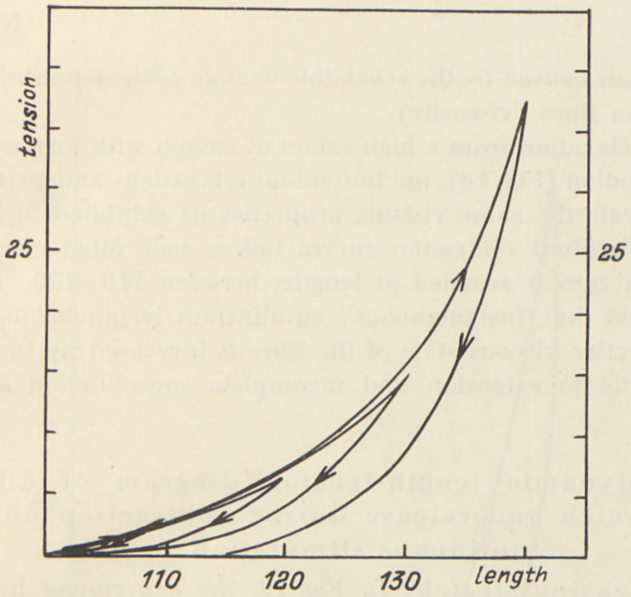


Fig. 17. Semi-dynamic length-tension diagram of the resting fibre; extension with following relaxation starting from length 100.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

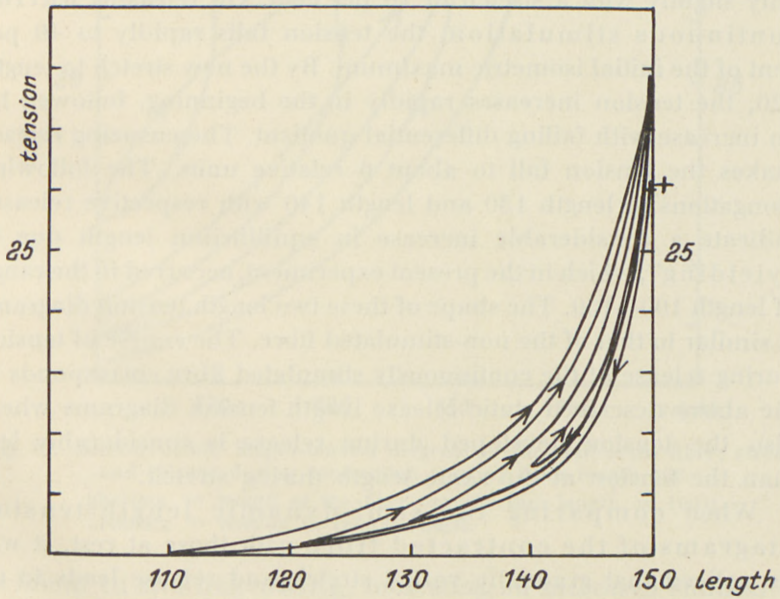


Fig. 18. Semi-dynamic length-tension diagram of the resting fibre; relaxation and extension starting from length 160.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

respectively, is caused by the reversible change of the equilibrium length of the fibre (viscosity).

During relaxation from a high extent of stretch with increasing rate of relaxation (Fig. 18), the individual relaxation- and stretch-curves indicate the same viscous properties as exhibited in Fig. 17. The individual relaxation curves follow each other closely. The tension zero is reached at lengths between 110—120. This indicates that the "instantaneous" equilibrium length belonging to the respective viscous state of the fibre is increased by 10—20 per cent due to extension and incomplete consolidation after relaxation.

2) Semi-dynamic length-tension diagram of alternating stretch and release during contraction under continuous stimulation.

a) Increasing stretch: In Fig. 19, the experiment began from length 100 with a stretch of 10 per cent. The curve is markedly different from that representing stretch of the resting fibre. The tension in isometric contraction amounts to 33 units and increases only slightly with a stretch of 10 per cent. On releasing during continuous stimulation, the tension falls rapidly to 40 per cent of the initial isometric maximum. By the new stretch to length 120, the tension increases rapidly in the beginning, followed by an increase with falling differential quotient. The ensueing release makes the tension fall to about 6 relative units. The following elongations to length 130 and length 140 with respective releases indicate a considerable increase in equilibrium length due to "yielding", which in the present experiment, occurred in the range of length 100—130. The shape of these two length tension diagrams is similar to that of the non-stimulated fibre. The course of tension during release of the continuously stimulated fibre corresponds to the above described static release length-tension diagrams where also the tension developed during release is considerably less than the tension at the same length during stretch.

When comparing the semi-dynamic length-tension diagrams of the contracted fibre with those at rest, it will be noticed that gradually varied stretch and release leads to an essentially different course than do similar conditions at rest. During stretch after release from length 110—115 a steep ascent

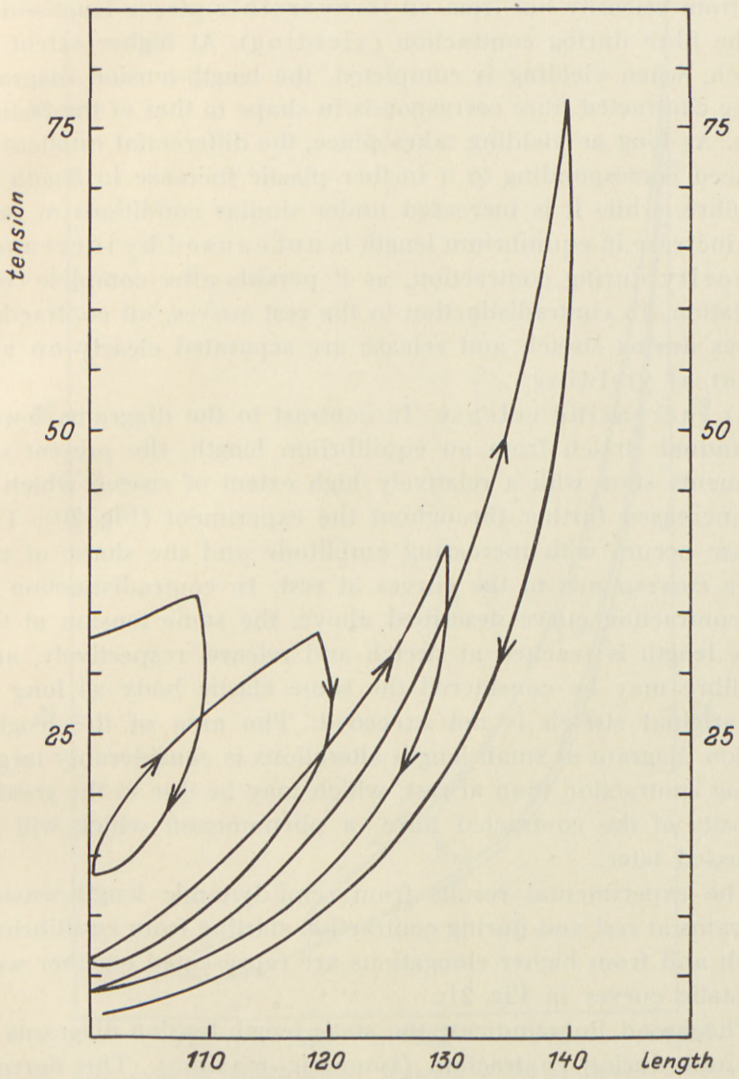


Fig. 19. Semi-dynamic length-tension diagram of the contracted fibre; stretch and release during contraction starting from length 100.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

is found in the beginning, indicating an increased stiffness of the fibre. With further elongation, a reduction of the steepness is observed, in spite of the same rate of extension, originating

not from viscosity but from an irreversible plastic lengthening of the fibre during contraction (yielding). At higher extent of stretch, when yielding is completed, the length-tension diagram of the contracted fibre corresponds in shape to that of the resting fibre. As long as yielding takes place, the differential quotient is reduced corresponding to a further plastic increase in length of the fibre, while it is increased under similar conditions at rest. The increase in equilibrium length is not caused by increased viscosity during contraction, as it persists after complete consolidation. In contradistinction to the rest curves, all contraction curves during stretch and release are separated clearly on account of yielding.

b) Increasing release. In contrast to the diagrams found at gradual stretch from an equilibrium length, the present experiments start with a relatively high extent of stretch which is not increased further throughout the experiment (Fig. 20). The release occurs with increasing amplitude and the shape of the curve corresponds to the curves at rest. In contradistinction to the contraction curve described above, the same tension at the same length is reached at stretch and release, respectively, and the fibre may be considered the same elastic body as long as the original stretch is not exceeded. The area of the length-tension diagram at small length alterations is considerably larger during contraction than at rest, which may be due to the greater viscosity of the contracted fibre, a phenomenon which will be discussed later.

The experimental results from semi-dynamic length-tension diagrams at rest and during contraction starting from equilibrium length and from higher elongations are represented together with the static curves in Fig. 21.

The broad lines indicate the static length-tension diagrams at rest and during contraction (isometric maxima). The narrow lines around the lowest curve show a semi-dynamic length-tension diagram at rest, and the narrow lines of the upper system represent the semi-dynamic curves from a contracted fibre gradually stretched and released at continuously increasing stretch. The arrows denote whether the experiments are carried out starting from equilibrium length or from greater stretch. It is apparent that the release curves during contraction are of a

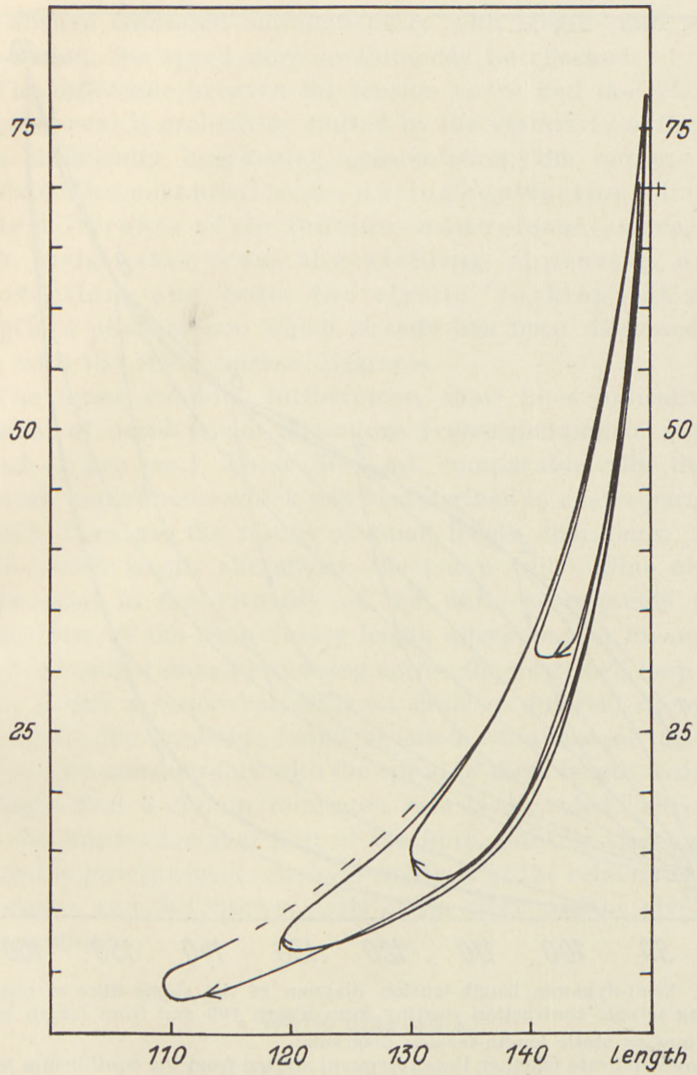


Fig. 20. Semi-dynamic length-tension diagram of the contracted fibre; release and stretch starting from length 150.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.
+ = starting point of the curve.

uniform type, running parallel, their gradient reminding of length-tension diagrams at rest. The curves indicate a considerably lower tension than at a corresponding length during stretch.

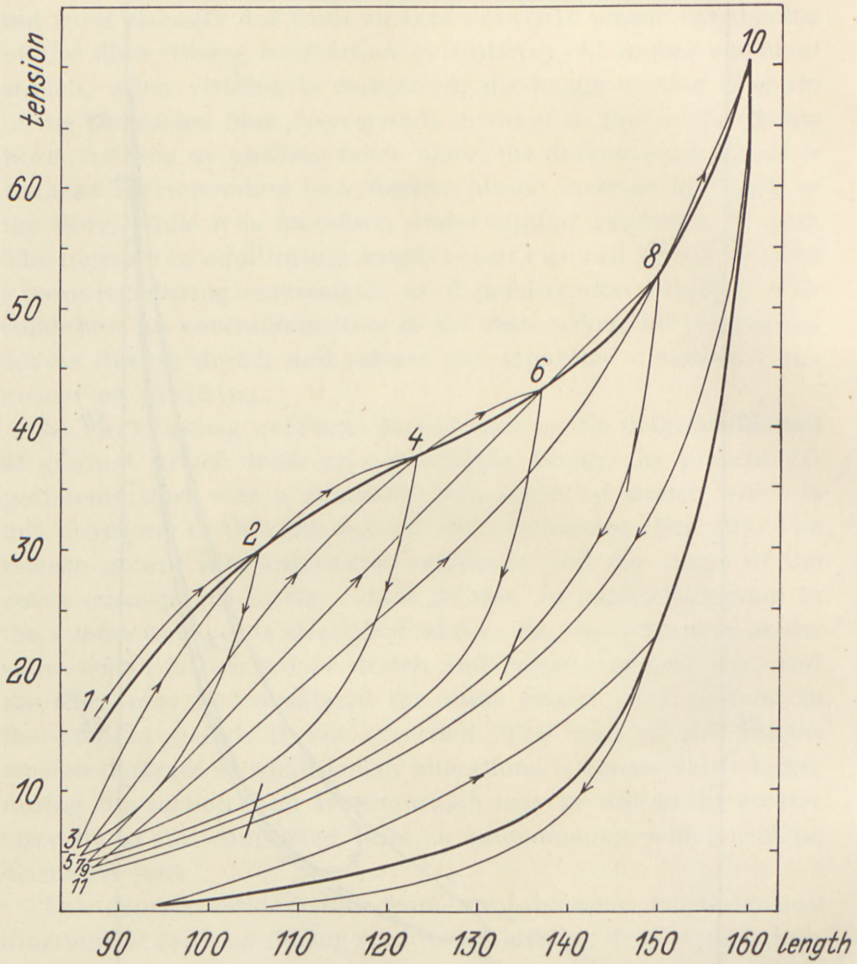


Fig. 21. Semi-dynamic length-tension diagram of the single fibre at rest and during tetanic contraction starting from length 100 and from length 160.
broad lines = static length-tension diagrams;
the arrows indicate whether the experiment started from the equilibrium length or from greater elongations;
the figures on the curves indicate the succession of extensions and releases.
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in relative units.

In the semi-dynamic diagrams, the shape of the curves depends greatly on the rate of the length alterations. In the present mean diagram, only such curves are given which are registered at the same rate and which, therefore, are comparable. Since time marks

are always registered simultaneously with length- and tension registration, the speed may continuously be checked.

The difference between the tension curve and the relaxation curve at rest is exclusively caused by the viscosity of the fibre; with sufficiently long-lasting consolidation, the curves would overlap. The essential and—during contraction—irreversible difference of the tension- and release-curve, however, originates from the yielding appearing during contraction, and from the elastic "locking" at a new length, a phenomenon which already has been discussed together with the static release diagrams.

The figure exhibits, furthermore, short lines indicating the gradient of rapid length alterations (corresponding to a period of 0.2—1 per sec.). These lines are comparable with the true dynamic experiments which will be described in a later paragraph (p. 67). They are the results of small length alterations. During rapid small length alterations, the curve will outline an area which—due to the viscosity of the fibre—corresponds to the energy loss of the fibre during length alterations. A mean curve which we might imagine running across the described loop of the curve shows a somewhat different slope at different stretchings.

Finally, the gradients found at small variations of the length do not vary considerably with the speed of these length variations, provided that a certain minimum rate is exceeded. This might give the impression that part of the fibre, only, is viscous while the rest is purely elastic. A closer analysis of the relation between the elastic and the viscous parts of the fibre will be given in a later section.

Work diagrams.

1) Tetanic contractions.

Using the same experimental procedure as applied to the registration of the above described semi-dynamic length-tension diagrams, work diagrams of isolated single fibres were studied in order to determine the amount of work performed at stretch and following contraction (cf. indicator diagram of, for instance, a steam engine). The fibre was stretched at rest, a process, where energy is externally supplied (compression in the steam engine);

then, it was stimulated tetanically and, finally, allowed to contract and to perform work (expansion). The net work performed (i. e. the amount of work available for exterior purposes) is the difference between contraction work and stretch work. In the length-tension diagram, this magnitude corresponds to the difference in the areas of the contraction curve and the rest curve. All work diagrams were registered with single fibres of known weight (after removal of the tendon tissue which served to fasten the fibre in the tweezers). The work performed is expressed in erg/gm of the fibre substance.

During stretch from length 100 to length 150 and following release, the resulting work performed in a tetanic contraction was almost constant. In all experiments, the stretch- and contraction-period lasted 4 seconds, each. In the case of a non-fatigued fibre, the mean work performed was 10 000 erg/gm of fibre substance.

The difference in the course of the curves of isometric maxima and those of release contractions has been discussed in a former section (p. 23). As a result of this discussion, one might expect a greater energy yield by interrupting the stimulation for a short time during release; on renewed stimulation the curve starts from a new isometric maximum. The influence of an interruption in stimulation is represented in Figs. 22a and b. Fig. 22a exhibits a work diagram without interruption of the stimulation. In the present case, the net work performed by the fibre amounts to 10 erg, the stretch being 40 per cent. Fig. 22b shows a work diagram of the same fibre, indicating the same course at rest and during the first part of release to length 125. The stimulation is then interrupted for a short period (ca. 0.1 sec.) and, when begun anew, a tension is obtained about 2.5 times higher than before the interruption. The tension is then reduced at release during stimulation in the same way as before, but it remains constantly higher than the previous tension. The net work is now 17.7 erg indicating that the interruption of the stimulation brings about a gain of energy of about 80 per cent. The increase in work obtained cannot be interpreted as a consequence of restitution of the fibre during the short period of rest. This could be shown by means of control experiments with long-lasting stimulations and intermittent interruptions without changing the length of the fibre. In general, the short restitution

period within the time of experiment applied here has no discernible influence. As might be expected, the working power of the

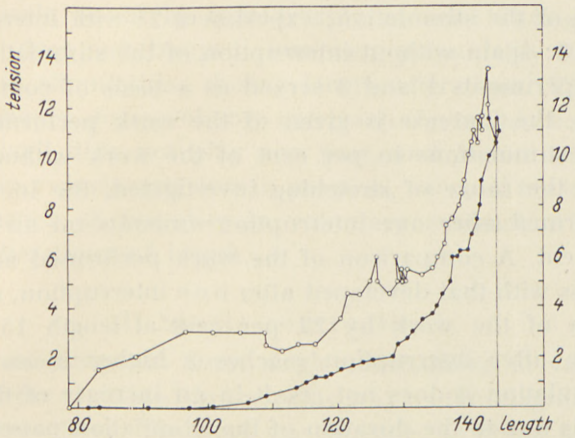


Fig. 22 a. Work diagram of a single fibre. stretch of the resting fibre (lower curve) and release during tetanic contraction (upper curve).

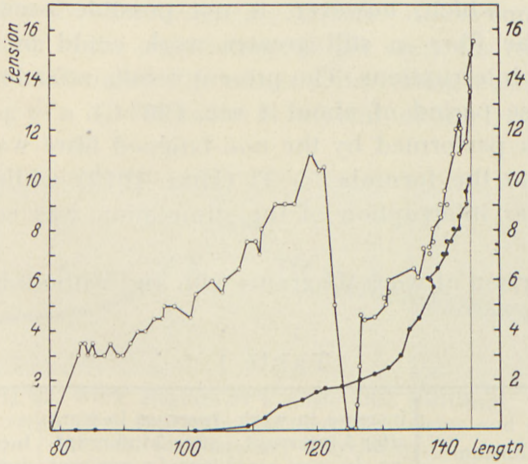


Fig. 22 b. Work diagram of the same fibre as in Fig. 22 a.
stretch of the resting fibre (lower curve) and
release during tetanic contraction with short stop in stimulation (upper curve);
abscissa = length of the fibre (equilibrium length = 100);
ordinate = tension in mgm.

fibre changes from one work experiment to another and, therefore, in every experiment for the determination of the difference

between work with interruption and work without interruption at least three work diagrams were recorded. In most cases, the following procedure was employed: Experiment 1: without interruption of the stimulation; experiment 2: with interruption; experiment 3: again without interruption of the stimulation. The mean of experiments 1 and 3 served as a basis of comparison. In Table 1, the increase is given of the work performed with interrupted stimulations in per cent of the work without interruption. In the range of stretching investigated, the increase in work performed after one interruption amounts on an average to 45 per cent. A comparison of the work performed after two interruptions with that developed after one interruption, revealed a reduction of the work by 22 per cent at length 150. Even if the fibre after interruption reaches a higher mean tension during stimulation it does not result in an increase of the work area. This is due to the duration of the stimulation pause. There is, indeed, not sufficient time for two interruption periods. Only at a higher stretch may further work be obtained after two or more interruptions. If the release could be carried out even more slowly—which, however, is not possible because of the fatigue of the fibre—a still greater work could be performed after several interruptions. The present results refer to a duration of the release period of about 4 sec. (20° C).

The work performed by the non-fatigued fibre was found to correspond to the formula $^1/_6$ Tl (HILL 1913) while the work obtained after interruption of the stimulation was considerably larger.

A comparison of work diagrams with and without interruption

Table 1.

length (equilibrium length = 100)	Increase in work after 1 interruption in per cent of the work without interruption	Increase in work after 2 interruptions in per cent of the work after 1 interruption	Increase between second and third interruption
140	+ 46	..	..
150	+ 52	— 22	..
155	+ 42	— 9	..
165	+ 39	+ 25	+ 6

is of interest also from a practical aspect, as all dynamic work in muscle is accompanied by a length alteration. If the stimulation during dynamic work was continuously tetanic, the tractive force of the muscle would be considerably reduced during contraction. This does not happen, however, presumably due to the intermittent stimulations during length alterations. The stimulation frequency does probably not reach the tetanic level so that the "locking" does not play any part, and higher tensions are attained. In experiments now in progress, we shall try to compare the frequency of impulses in voluntary contraction with and without alterations of length.

2) Single contractions.

The work diagrams from single contractions at various frequencies were registered in the same way as the diagrams during tetanic contractions. The fibre was stretched to about length 140; then, the single stimulations began while the fibre was released from length 140 to its equilibrium length. Fig. 23 exhibits a fibre stretched to length 135. As soon as the increase in length ceases, the fibre tension shows a decreasing tendency due to consolidation. In the beginning of the stimulations (8 per sec.), the length of the fibre is at first unchanged. The values of the resting tension increase corresponding to a consolidation at this stimulation frequency (re-

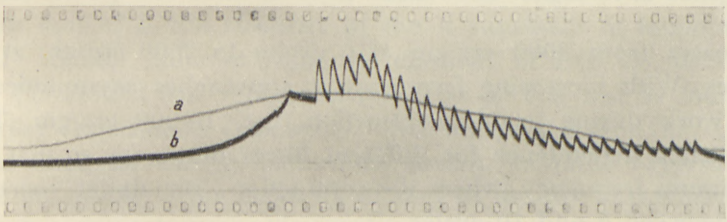


Fig. 23. Work diagram of a single fibre (twitches).
Stretch of the resting fibre to length 135, thereafter release and simultaneous stimulation (frequency 8 cycles/sec.).
Work performed = 15.4 erg = 6420 erg/gm fibre.
(*a*) length recording; (*b*) tension recording.

mainder). Before the final consolidation tension is reached, the relaxation and, consequently, the decrease in tension begins. The mean tension is found by integration of the registered curve.

The area between the length-tension diagram from resting muscle and the contraction diagram of the mean tension is a direct expression of the work performed by the fibre. In the present case, it amounted to 15.4 erg corresponding to 6400 erg per gm fibre. Fig. 24 represents the work performed by the same fibre at different stimulation frequencies. The actual work

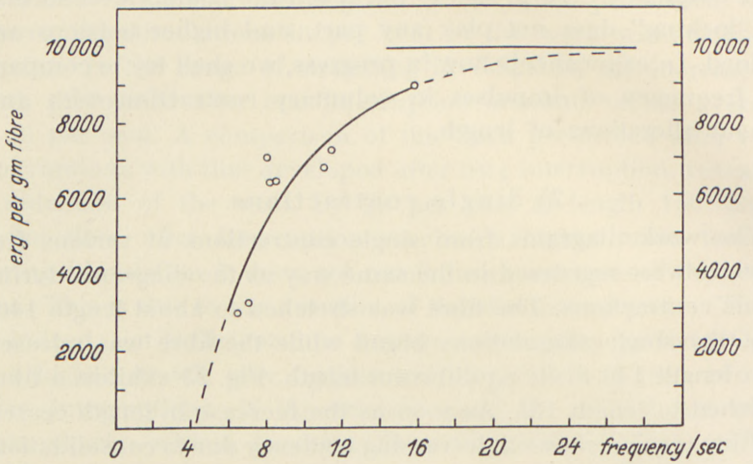


Fig. 24. Work done at different stimulation frequencies of the same fibre. The line at 10000 ergs indicates the work performed in complete tetanus (frequency 30—50 cycles/sec.); release from length 140 to tension 0.
abscissa = frequency in cycles/sec.;
ordinate = erg/gm fibre.

increases from 3000 erg/gm at 6 cycles to 9000 erg/gm at 16 cycles. With increasing frequency it approaches asymptotically the work during tetanic contraction, i. e. 10 000 erg/gm. The frequency dependence for different fibres may vary so that the minimum frequency, where the contraction "remainder" occurs, lies between 5 and 10 cycles.

Length-tension diagrams of the anisotropic (A) and the isotropic (I) substance at rest and during contraction.

Length-tension diagrams of the individual substances (A and I) may be obtained from the tension of A + I as a function of the extension and from the length ratio A : I at different stretchings.

1) The length of A and I at rest as a function of stretch.

When different fibres are examined, a variation is observed of approximately 5 per cent in the ratio A : I, and of approximately 10 per cent in the height of compartments. For our purposes, the height of compartments at rest and at equilibrium length were put at 100, and the mean values of the lengths A and I were calculated relative to A + I. In addition to the earlier material available (Buchthal, Knappeis and Lindhard, 1936), new experiments with continuous stretching of the same fibre served as a basis for these calculations.

At equilibrium length at rest, the mean values of A and of I were found to be 61 per cent and 39 per cent, respectively, of the height of compartments. The fibres were photographed at lengths 70—160 and the lengths of A and I were plotted in a coordinate system (Fig. 25), where the abscissa represents the length A + I in per cent of the equilibrium length, and the ordinate indicates the length of the individual substances in arbitrary units (the height of compartments at equilibrium length is 100 units = 2.2 μ). The mean error of the rest curve is approximately 1 per cent. The curves of A and I at rest are practically linear. The increase in length of A is about twice that of I; that is, A is contributing twice as much to the resulting extensibility as I. However, taking into consideration the greater length of A compared with that of I, the elasticity of the A substance is found to be only slightly different from the elasticity of I (c. 20 per cent).

The dotted line represents the ratio A : I at rest as found in earlier experiments (Buchthal, Knappeis and Lindhard, 1936), not obtained during continuous stretch. In these experiments, the difference of the elasticity moduli of the two substances was greater than in recent experiments, the tendency, however, being the same in both series.

2) The length of A and I during isometric contraction as a function of stretch.

Also at maximum stimulation, different preparations show quantitatively different reactions with respect to changes in the length of the substances at the same stretch. However, it was

observed that changes in length of A and I as a function of stretch vary uniformly and, therefore, it is possible to draw parallel

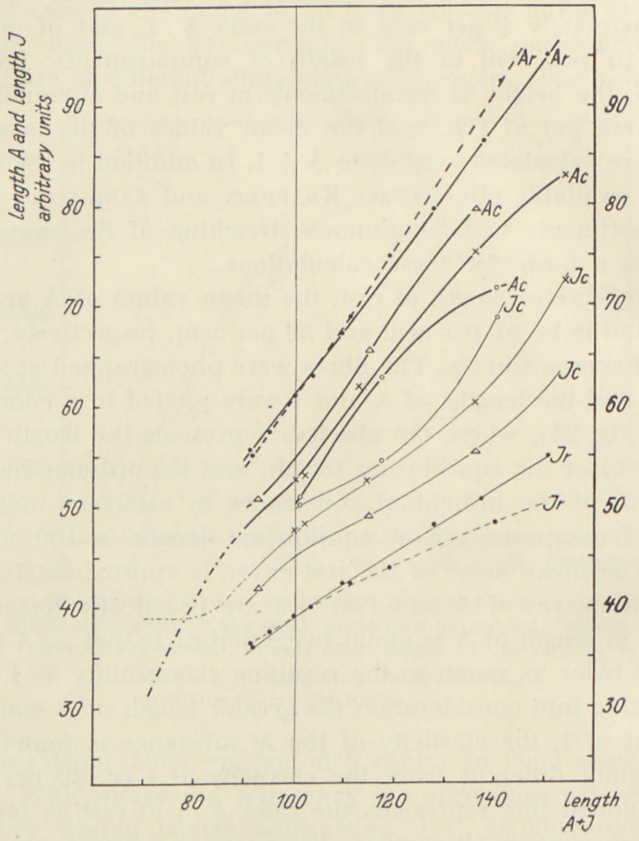


Fig. 25. Length of A and of I substance at rest (*Ar*, *Ir*) and during contraction (*Ac*, *Ic*) as a function of the height of compartment (A + I).

—●—●— = resting fibre, new material;
– – –●– – –● = resting fibre, material BUCHTHAL, KNAPPEIS & LINDHARD (1936);
—+—+—, —o—o—, —△—△— = fibre groups with different ratio A/I.

abscissa = A + I (equilibrium length = 100);
ordinate = length of the individual substances in arbitrary units (100 units = height of compartment in the non-extended fibre = 2.2 μ).

curves corresponding to the different ratio A/I (isometric contraction, equilibrium length) (Fig. 25). These curves cover corresponding points of the different preparations in a satisfactory

way. A comparison of different preparations with approximately the same ratio A/I (isometric contraction, equilibrium length) indicates that the mean scattering in these experiments is not very different from that in the rest curves. The experimental material is classified in three groups according to the extent of contraction during maximum stimulation. The error is largest in experiments below the equilibrium length due to the tendency of the fibre to curl up, and to the displacement of the fibrils in the various planes of the fibre.

The dotted part of the curves below length 90 (Fig. 25) refers not only to the above described continuous measurements but, moreover, to a special series of experiments in which it was found that I preserves its length unchanged during tensionless contraction.

During isometric contraction, A always becomes shorter and, consequently, I becomes longer than when at rest, the length of A and I being almost identical at equilibrium length during isometric contraction. At a stretch of 25 per cent, the difference in length between A and I is somewhat greater while, with augmented stretch, the lengths of the two substances again approach each other. During contraction below the equilibrium length, I comes very near to its resting length[1].

3) Length-tension diagram of A and I at rest and during contraction.

The curves described above show the lengths of A and I relative to the height of compartments at equilibrium length. In order to procure a length-tension diagram of A and I separately, the length-tension diagram of the whole fibre must be known, and it must furthermore be assumed that A and I are arranged as links in a long chain so that each is exposed to the same load. Different extensibilities of A and I at constant fibre volume are only possible if a transfer of fluid takes place between A and I regions. This transport of fluid must occur unhindered in order

[1] Ramsay and Street (1940) describe a histological investigation of fibre shortenings up to 70 per cent of the equilibrium length. These great shortenings, however, are only to some extent due to shortenings of the working substance, part of them being a coarse, mechanical curling up. The microphoto-

to attain uniform loading of A and I. It is finally implied that no other elements of the fibre are exposed to any considerable tension. With regard to the length-tension diagram, it must be

graph of an extremely shortened fibre, reproduced in RAMSAY and STREET's paper, proved to correspond to a resting, possibly slightly stretched fibre. The table given below contains our measurements carried out at four different regions of RAMSAY and STREET's microphotograph, Fig. 10. The last file shows the mean values of a resting living frog muscle fibre determined by BUCHTHAL, KNAPPEIS and LINDHARD (1936) on more than 80 preparations.

Table 2.
Lenght of A and I, and of A + I, at different points of the microphotogram of an "extremely shortened" fibre, according to RAMSAY and STREET.

	A	I	A + I	Point
	1.29	0.98	2.27	I
In per cent. of A + I	57	45		
	1.50	1.01	2.51	II
In per cent. of A + I	59.5	40.5		
	0.40	0.43	0.83	III
In per cent. of A + I	48	52.1		
	1.17	1.11	2.28	IV
In per cent. of A + I	51.5	48.5		
	1.37	0.81	2.18	(± 0.01) mean value of resting fibre (BUCHTHAL, KNAPPEIS and LINDHARD (1936)).
In per cent. of A + I	63	37		

Fig. 26. Correlation between the length-tension diagram of the single fibre and the individual length of A and I as a function of stretch. Mean curves.
(1) length-tension diagram of the resting fibre;
(2) curve of isometric maxima;
d = direction of release length-tension diagrams;
ordinate (short *y* axis) tension in relative units;
(3) length of I at rest as a function of the height of compartment;
(4) length of I during contraction as a function of the height of compartment;
(5) length of A during contraction as a function of the height of compartment;
(6) length of A at rest as a function of the height of compartment;
——●——● = release contraction-curves for A and I, resp., starting from the curve of isometric maxima;
——×——× = stretch during contraction;
abscissa (common for the length-tension diagram and for the diagram of relative lengths of A and I) height of compartment (A + I = 100 = equilibrium length);
ordinate (long *y* axis) length of A and of I in arbitrary units (100 units = height of compartment of the fibre at its equilibrium length = 2.2 μ).

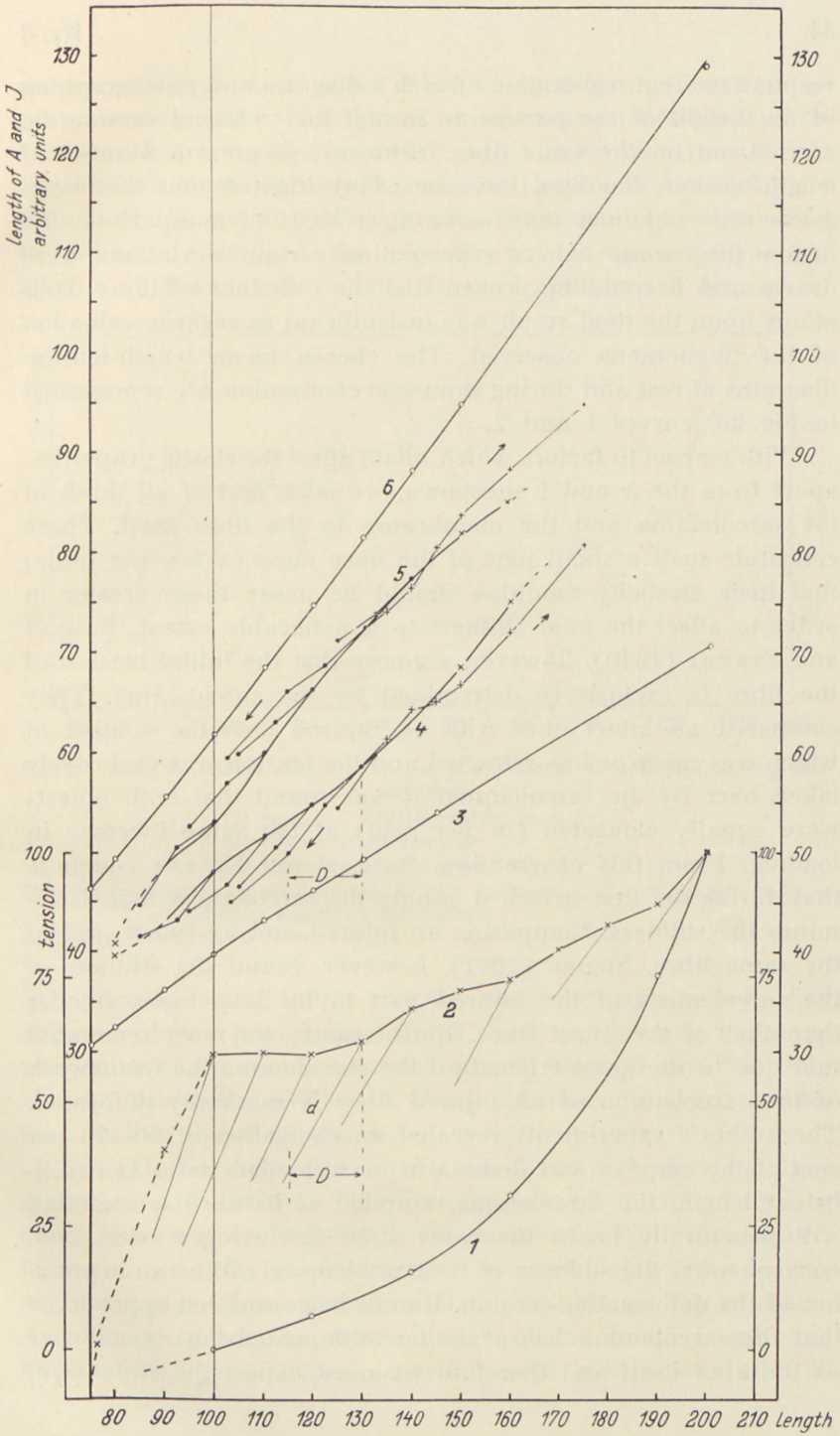


Fig. 26. For explanation, cf. p. 52.

emphasized that registration of such a diagram and photographing of the height of compartments cannot for technical reasons be carried out on the same fibre. However, so great a number of length-tension diagrams have been investigated that the mean curve thus obtained may serve as a basis of comparison. To insure this, some curves representing certain deviations were drawn and it could be proved that the influence of these deviations upon the final result was insignificant as regards valuation of the phenomena observed. The chosen mean length-tension diagrams at rest and during isometric contraction are represented in Fig. 26, curves 1 and 2.

With respect to factors which might affect the elastic properties, apart from the A and I substance, we must first of all think of the sarcolemma and the membranes in the fibre itself. These constitute such a small part of the fibre mass (a few per mille) that their elasticity modulus should be many times greater in order to affect the total stiffness to a noticeable extent. RAMSAY and STREET (1940), however, suppose that the initial tension of the fibre is exclusively determined by the sarcolemma. They compared an intact fibre with an injured one, the content of which was more or less retracted and the tension was exclusively taken over by the sarcolemma. It was found that both objects were equally elongated (in per cent) at the same increase in loading. From this observation, RAMSAY and STREET conclude that during the first stretch it is only the sarcolemma that determines the stiffness. Comparing an injured and an intact part of the same fibre, SICHEL (1941), however, found the stiffness of the sarcolemma of the injured part to be 1—4 times smaller than that of the intact fibre. Furthermore, we must remember that due to the greater length of the sarcolemma the framework of the sarcolemma of an injured fibre is markedly deformed. The author's experiments revealed an elongation of 50—70 per cent of the emptied sarcolemma in an unloaded state. At equilibrium length, the sarcolemma, emptied of its fibrillar material, will structurally be in the same state as during tension and, consequently, the stiffness of the sarcolemma will be an expression of the deformation-tension. It must be considered appropriate that the sarcolemma has a similar stiffness-tension dependence as the fibre itself and therefore we must expect the stiffness of

the sarcolemma of an intact fibre at equilibrium length to be many times smaller than that of an injured and deformed fibre.

Length-tension diagrams of A and I at rest. At equilibrium length at rest, the original lengths of A and I were found to be 60 and 40 arbitrary units, respectively (corresponding to 1.38 μ and 0.88 μ). At the respective tension, the corresponding lengths of A and I are plotted in the length-tension diagram of

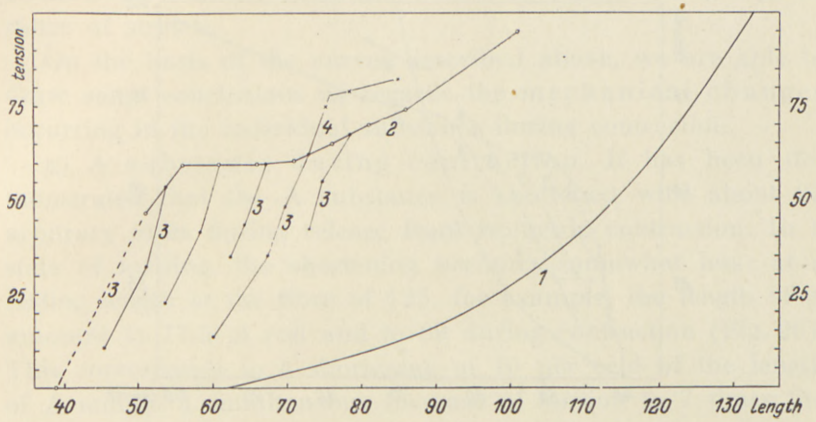


Fig. 27. Length-tension diagram of the A substance at rest and during contraction.

(1) rest; (2) isometric maxima;
(3) release contractions;
(4) stretch during contraction;

abscissa = length in arbitrary units (60 units = 1.32 μ = length of A at equilibrium length of the fibre);
ordinate = tension in relative units.

the resting fibre and, in this way, two curves are obtained showing different slopes but similar shape, and representing the static properties of the two substances at rest (Figs. 27 and 28). Obviously, the static stiffness of the I substance is much greater than that of the A substance.

Length-tension diagrams of A and I during isometric contraction. The investigation of A and I during contraction was carried out in the same way; it must, however, be mentioned that the initial lengths, i. e. the length at the load 0, are not derived from the material represented in Fig. 26 alone. As already stated, the determination of the initial length was based upon special experiments in which a fibre was allowed

to shorten without tension. The shortening of the whole fibre, and as far as possible the lengths of the single substances, were measured photographically. During tensionless contraction, it was observed that the I substance did not change in length and, consequently, the shortening of the fibre must, be ascribed to the A substance. If the length of the I substance is assumed to amount to 40 and that of the A substance to 60 arbitrary units,

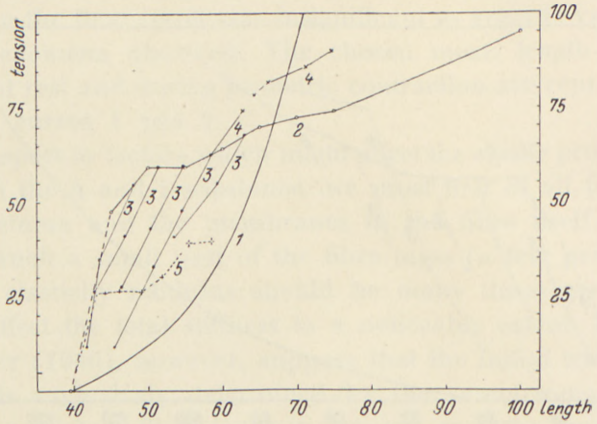


Fig. 28. Length-tension diagram of the I substance at rest and during contraction.
(1) rest; (2) isometric maxima;
(3) release contractions;
(4) stretch during contraction;
(5) "corrected" isometric maxima;
abscissa = length in arbitrary units (40 units = 0.88 μ = length of I at the equilibrium length of the fibre);
ordinate = tension in relative units.

and if the contraction constitutes 30 per cent, A must contract from length 60 to 30. The other points of the curve were obtained in the same way as the length-tension diagram at rest. The ranges below 45 in the case of I and below 50 in the case of A are dotted, as the length during isometric contraction considerably below the equilibrium length is unknown. The dotted line (3) does not represent the isometric maxima but a length-tension diagram of the release of the fibre from isometric contraction to the tension 0 (cf. p. 60).

It is characteristic for both curves that the initial gradient is considerably steeper than when at rest, and that a decrease in slope occurs with increased loading. This reduction of the steep-

ness is usually ended as soon as the tension of isometric contraction at equilibrium length is reached. In the case of the A substance, the curve shows a horizontal region which is followed by a slight ascent, and in the case of the I substance the curve is slightly ascending and approximately linear.

After the first steep part of the length-tension diagram, an irreversible length alteration (yielding) occurs during contraction which limits the tension attainable within a given range of stretch.

On the basis of the curves described above, we are able to draw some conclusions as regards the mechanical changes occurring in the individual substance during contraction.

a) A substance during contraction. It has been demonstrated that the A substance is shortened with about 25 arbitrary units during release from isometric contraction. In a state of loading, the shortening becomes somewhat less; at a resting length of the fibre of 125, for example, the length of A amounts to 77.5 at rest and to 69 during contraction (Fig. 26). This corresponds to a shortening of 10 per cent of the length of A and to a simultaneous increase of tension to 7 times the original value. Also at other stretchings, the mean shortening of A constitutes 10 per cent of the corresponding length at rest. On the basis of a direct comparison of the length of the A substance at rest and during contraction at the same loading (Fig. 27), one might conclude that A has been shortened corresponding to the difference between the lengths of the substances. At a loading 50, for example, the ratio between the lengths at rest and during contraction is equal to 2. Considering the course of the curves it must, however, be taken into account that the length of A during contraction depends not only on the stretch but also on the length alterations which are imposed during contraction (see page 60).

b) I substance during contraction. The course of the I curve is described above (Fig. 28). At rest, I deviates from A, the rest curve and contraction curve having two common points, viz. the starting point at the tension 0 and a point of intersection at the tension 70 (height of compartments 140). When comparing at the same tension, I was found to be shorter during contraction than at rest until a certain loading is reached. At a higher loading,

I becomes longer than at rest for the same tension. The first part of the curve indicates a certain contractility of the I substance. Even if I undergoes an increase in length due to a contraction tension originating from A, this cannot explain the very high tension of the I substance during contraction, relative to the same rest length. At equilibrium length (tension 0), the length of the I substance is 40. During contraction, I is elongated to 50, which causes an increase in tension amounting to 12. In reality, I is loaded with a tension of 60, i. e. the ratio between rest- and contraction tension is 1 : 5.

The length-tension diagram of I—in contrast to that of the whole fibre—cannot be interpreted as a length-tension diagram of isometric contraction, since the I substance is not only stimulated but, furthermore, increased in length. However, we may correct for this increase in length by means of release-contraction diagrams and, hence, an "isometric" length-tension diagram is constructed the points of which lie probably lower than those obtained in true isometric contractions (cf. other release-contractions). Curve 5, Fig. 28, shows the constructed length-tension diagram which is known from length 40 to 52; above this length, this diagram is extrapolated and constructed on the assumption that the gradient of the release diagram is directed towards the starting point of the curve.

This curve indicates that no increase in tension at the length 40 is registered, as this corresponds to the equilibrium length of the I substance which is unchanged. Length 42 to 47 is the range of the maximum working ability of the I substance, the extra-tension being approximately 20, calculated from a rest tension of only 3 to 8. The extra-tension then decreases and presumably becomes 0 before the point of intersection between the rest curve and the contraction curve is reached.

From the constructed "isometric" length-tension diagram of I it is evident that I is able to perform work which exceeds that supplied by the stretch. In the case of the A substance, a stretch is unnecessary for the performance of work because A changes its equilibrium length during stimulation.

During contraction of fibres up to a length of 150 (length of I at rest = 55, and of I during contraction = 68), also an extra-tension of I could be obtained due to the increasing stiffness

Table 3.

Length of A and of I during isometric contractions and during release contractions at various elongations.

Preparation	Isometric contraction			Length (100 = length of equilibrium)	Release contraction			Extent of release in arbitrary units (length of equilibrium = 100 = 2.20 μ)	Δ A μ	Δ I μ	$\frac{\Delta A}{\Delta I}$
	A μ	I μ	A+I μ		A μ	I μ	A+I μ				
166 EIII	1.08	0.97	2.05	93	1.07	0.92	1.99	2.0	0.01	0.05	0.20
166 FIV	1.22	1.10	2.32	105	1.01	0.91	1.92	18.0	0.21	0.19	1.11
220 AIII	1.23	1.02	2.25	102	1.06	0.90	1.96	13.0	0.17	0.12	1.41
207 AI	1.25	1.08	2.13	106	1.16	0.97	2.13	9.0	0.09	0.11	0.82
217 AI	1.34	1.16	2.50	114	1.27	0.96	2.23	13.0	0.07	0.14	0.50
218 AI	1.36	1.18	2.54	115	1.30	1.10	2.40	6.0	0.06	0.08	0.75
217 BI	1.40	1.15	2.55	116	1.32	1.07	2.39	7.0	0.08	0.08	1.00
202 CIII	1.35	1.21	2.56	116	1.09	0.98	2.07	22.0	0.26	0.23	1.13
207 CI	1.37	1.21	2.58	117	1.34	1.12	2.46	5.0	0.03	0.09	0.33
220 BII	1.38	1.21	2.59	118	1.31	1.11	2.42	8.0	0.07	0.10	0.70
166 AI	1.42	1.32	2.74	124	1.33	1.16	2.49	11.0	0.09	0.16	0.56
218 CI	1.47	1.25	2.72	124	1.32	1.14	2.46	12.0	0.15	0.11	1.36
220 BI	1.46	1.28	2.74	125	1.22	1.01	2.23	23.0	0.24	0.27	0.89
220 AII	1.48	1.28	2.76	125	1.45	1.15	2.60	7.0	0.03	6.13	0.23
169 CII	1.49	1.31	2.80	127	1.51	1.27	2.76	2.5	0.02	0.04	0.50
201 CII	1.48	1.34	2.82	128	1.24	0.98	2.22	27.0	0.24	0.36	0.67
159 AI	1.58	1.38	2.96	134	1.43	1.17	2.60	16.0	0.15	0.21	0.72
190 FIII	1.56	1.43	2.99	136	1.45	1.29	2.74	11.0	0.11	0.14	0.79
166 CII	1.61	1.42	3.03	138	1.51	1.35	2.86	8.0	0.10	0.07	1.43
202 IIV	1.62	1.46	3.08	140	1.13	1.07	2.20	40.0	0.49	0.39	1.26
202 DII	1.65	1.50	3.15	143	1.45	1.24	2.69	21.0	0.20	0.36	0.77
218 CII	1.73	1.46	3.19	145	1.64	1.19	2.83	16.0	0.09	0.27	0.33
201 EIII	1.73	1.53	3.26	148	1.45	1.32	2.77	22.0	0.28	0.21	1.33

during contraction. Above 150, I contributes negatively to the contraction. This fact can partly explain the decreasing extra-tension during contraction at high stretchings, which is therefore due partly to a yielding of the I substance (cf. p. 22).

Comparing A and I during contraction, we find that the tension increase in the case of I is due to an alteration of the stiffness; in the case of A it is due not only to a change in stiffness but, furthermore, to a change in equilibrium length.

c) A and I during release contractions. The description of release length-tension diagrams and semi-dynamic length-tension diagrams indicates that the mechanical properties of a fibre contracted at a certain length and then released to a somewhat shorter length are different from those of a fibre which contracts isometrically at a corresponding length. In connection with the elucidation of the properties of A and I during isometric contraction, it was desirable to investigate the corresponding changes of the internal structures during release contraction.

The experiments were carried out in the following way. The fibre was brought to an isometric contraction at a known length and was microphotographed at rest as well as during isometric tetanic contraction. The fibre was then re-stimulated and, immediately after development of tension, released from 4 to 30 per cent of the original length and was photographed during continuous stimulation. The photograph of the release contraction did not require a longer stimulation period than was necessary for the pure isometric contraction.

The material from these experiments which were carried out in cooperation with Mr. G. KNAPPEIS is collected in Table 3 (p. 59). The table contains the lengths of A and I during isometric contraction and during release contraction at various elongations; furthermore, the difference between the length of A—isometric contraction—and A—release contraction—(ΔA), and the corresponding values of I (ΔI). The quotient $\frac{\Delta A}{\Delta I}$ represents the ratio between the static softness[1] of A and I during release. The softness of A is expressed by $\frac{\Delta A}{\Delta P}$ and that of I by $\frac{\Delta I}{\Delta P}$, where P is the change in load due to length variations, a factor which cancels out when comparing the two softnesses. The ratio $\frac{\Delta A}{\Delta I}$ is dependent on the initial length and on the extent of release. The results from 25 different experiments, arranged according to the extent of release, are given in Table 4. Each value in the table was determined by 3 to 6 measurements and the mean error for the ratio $\frac{\Delta A}{\Delta I}$ is $\pm$ 0.2. The table contains A and I as functions of the length of the fibre and of the extent of release.

[1] Here and in the following, softness $= \frac{1}{\text{stiffness (dyne cm}^{-1})}$.

Table 4.

Extent of release in length units					
7.5	99.5	116	123	134	length of the fibre during isometric contraction.
...	0.51	0.82	0.62	0.91	$\frac{\Delta A}{\Delta I}$
15	107*	...	141	...	length of the fibre during isometric contraction.
...	1.00	...	0.60	...	$\frac{\Delta A}{\Delta I}$
26	133	...	...	...	length of the fibre during isometric contraction.
...	0.77	...	...	...	$\frac{\Delta A}{\Delta I}$

* The point marked * shows a relatively large variation in the length of A. This is due to a compression of I which only can decrease in length down to its equilibrium length.

The figures given in Table 4 were evaluated graphically. In this way, the value of $\frac{\Delta A}{\Delta I}$ as a function of the extent of release at the lengths 100, 110, 120, 130, and 140 were obtained (Table 5).

Table 5.

Extent of release in length units	Length of fibre					
	100	110	120	130	140	
7.5	0.50	0.60	0.72	0.85	...	$\frac{\Delta A}{\Delta I}$
15	...	0.90	0.74	0.65	0.60	$\frac{\Delta A}{\Delta I}$
26	...	...	...	1.00	...	$\frac{\Delta A}{\Delta I}$

On the basis of these results (Table 5 and Fig. 26), the individual length-tension diagrams may be calculated, starting from the curve of the isometric maxima in the length-tension

diagram of A and I (Figs. 27 and 28). $\Delta A + \Delta I = D$ = extent of release; $\frac{\Delta A}{\Delta I}$ is obtained from Table 5 and ΔA and ΔI are thus calculated for the respective lengths.

The new lengths of A and I were found by subtracting ΔA and ΔI, respectively, from the original lengths, the mean values of which during isometric contraction are plotted in curves 4 and 5 (Fig. 26).

For example, at the length 130, the release may amount to 15 units. $\frac{\Delta A}{\Delta I}$ is found from the table to be 0.65. Consequently,

$$\Delta I = \frac{15}{1.65} = 9.1.$$

The length of I during release contraction is thus $58.5 - 9.1 = 49.4$, (where 58.5 is the length of I during isometric contraction read from the curve at the length 130, and 9.1 is ΔI). The tension of I during isometric contraction (Fig. 26, curve 2) at the length 130 is found to be 60.8, and the tension of I during release contraction (Fig. 26, curve 2*d*) from the length 130 to the length 115 is approximately 35 In this way, we get two corresponding values of length and tension from the release length-tension diagram of I starting from a fibre length 130. In a similar way, the release length-tension diagrams of A and I represented in Figs. 27 and 28 were procured.

d) Partial release length-tension diagram of A. In the range investigated, the release diagrams of A are of a uniform type (Fig. 27, 3). The shortening during release contraction from an isometrically obtained tension extrapolated to the equilibrium length of the contracted A amounts to 15—20 units, or 25—30 per cent of the length of A. The gradients of the release diagrams decrease somewhat with the extent of release.

e) Partial release length-tension diagrams of I. The initial steepness of the release diagrams is less in the case of I than of A. In contrast to the diagrams of A, those of I are not parallel but are presumably directed towards the equilibrium length of I (Fig. 28, 3). Also this fact indicates that I has the same equilibrium length at rest and during contraction, while the equilibrium length of A changes. The change in steepness of the partial diagrams, furthermore, expresses a decreasing stiffness of I with increasing stretch.

The release lengths of A and I are plotted in Fig. 26, starting

from the contraction curves 4 and 5. During release from the equilibrium length (abscissa 100), the lengths of A and I coincide with the length alterations obtained during isometric contraction. Hence, the curve is reversible in this range. At higher stretch (length 110—130), the course of the curve during contraction is irreversible, corresponding to a yielding followed by a new locking of the fibre. This is evident in the clear distinction between the length of A during isometric contraction and during release contraction when referring to equal lengths of the fibre. The difference between A_{ic} (isometric contraction) and A_{rc} (release contraction) increases continuously in proportion to the extent of release until the equilibrium length is approached. $\frac{\Delta A}{\Delta I}$ is in the mean 0.8 ± 0.1 (cf. Table 3). During release contraction, A is thus on average 20 per cent stiffer than I, in agreement with the fact that the major part of the length variation during release must be ascribed to I.

Each release diagram represents a new elastic body determined by the stretch at the moment of contraction. The deviation of the individual length-tension diagram from the curve of the isometric maxima may be explained as an elastic locking of the A and I substances. This locking is the true cause of the irreversibility of the length-tension curves of isometric maxima.

4) Stretching of the fibre during contraction.

a) The length of A and I at stretch during contraction. A number of experiments were carried out with fibres stretched during contraction. The experimental technique was the same as in all earlier experiments. In the region investigated, the ratio $\frac{\Delta A}{\Delta I}$ was found to be a function of stretch, increasing from 0.25 at a stretch of 7.5 per cent to 1.5 at 20 per cent of elongation; the ratio then decreases and amounts to 1.25 at 45 per cent of stretch. Judging from the material available, the initial length is without any influence on the ratio $\frac{\Delta A}{\Delta I}$. The stretch diagrams of A and I as a function of the length of the fibre were constructed in the same way as the release diagrams

and plotted in the same curve (Fig. 26). Up to 10 per cent elongations, the points fall on the continuation of the release diagram. The curve then bends, intersects the isometric curve, and continues parallel with the latter. The inflection point is an expression of the yielding of the A substance, since the length of the I substance does not vary much at that point.

b) Length-tension diagram of A and I stretched during contraction. Length-tension diagrams from isometric contraction and length-tension diagrams of stretch during contraction indicated that stretch diagrams and release diagrams join each other and show the same gradient in the tension range of the isometric contraction. In the partial length-tension diagrams of the A substance, the same interdependence between length increase and tension increase was found in the beginning (Fig. 27, 4). In the given example, the A substance was able to endure a stretch of 3 per cent during contraction before a yielding occurred. This corresponds to an increase in tension of 15. The gradually decreasing differential quotient of the length-tension diagrams of the I substance (Fig. 28, 4) indicates that a yielding also appears in this case, however later and to a less pronounced extent than in the *A* substance.

Elasticity measurements.

In experiments on single muscle fibres both static and dynamic stiffness have been investigated (method, p. 11). An ideal elastic body will display the same static and dynamic stiffness if only temperature alterations due to deformation are taken into account. Since the deformation energy of this system is small compared with its heat capacity, the adiabatic temperature alterations may be disregarded in this connection.

As well-known, a muscle fibre is no ideal elastic body. Apart from elasticity, we must reckon with viscosity which presumably is not uniformly distributed over the elastic elements of the fibre. Dealing with muscle substance, an agreement between static and dynamic measurements can therefore not be expected. A discussion of the relationship between these properties will be given in a later section (p. 87).

While static measurements are an expression of the total stiffness, dynamic measurements express only part of the stiffness, primarily the stiffness of those elements the length alterations of which are only slightly retarded by viscosity. Static stiffness (criterium: gradient of the curve) is difficult to evaluate due partly to the time of consolidation demanding long-lasting experiments, and partly to fatigue and plastic yielding which require short experiments. On the other hand, dynamic stiffness (criterium: vibration frequency and amplitude) can be investigated under well-defined conditions.

On whole muscle, there exist static as well as dynamic elasticity measurements, the main problem investigated being the changes of elasticity during contraction.

Weber (1846) found the contracted fibre to be statically softer than the resting fibre under the erroneous assumption, however, that static length-tension diagrams of isometric maxima were reversible. These experiments and their interpretation were soon criticized, among others by Wundt (1858) and Enko (1880) who emphasized, further, that the connective tissue was a considerable source of error in Weber's calculation of the elastic constants of muscle substance. Weber's experiments did not contain the first part of the length-tension diagram where there is reversibility, presumably because of a too high initial load. In the first part of the length-tension diagram, Blix (1892—95) observed a greater stiffness of the contracted than of the resting fibre and, in agreement with other investigators, he stated that he had never observed an elongation of the muscle during stimulation at heavy loading (Weber's paradox). At a greater stretch (above 120), Schenck (1899, 1900) and Blix found a higher extensibility during contraction than at rest. On the basis of constructed partial length-tension diagrams, Reichel (1934) concluded that the elastic properties are identical at rest and during contraction and, consequently, he rejected the theory of muscle as a new elastic body during contraction.

Semi-dynamic and dynamic elasticity have been investigated both by means of torsion oscillations (Weber 1846, Wundt 1858, Schenck 1900, Kaiser 1899, Lindhard and Møller 1926 and 1928) and by oscillations longitudinal to the axis of the fibre (Gasser and Hill 1924, Steinhausen 1926, Richter 1928).

In spite of the constant volume, no relation between torsion elasticity and longitudinal elasticity can be expected in muscle due to its anisotropic structure. In this connection, it may be recalled that a simple crystal has numerous independent elasticity moduli (VOIGT 1909). Hence, the torsion elasticity is independent of the elastic properties derived from the length-tension diagram, but may nevertheless express structural peculiarities which are not accessible when longitudinal oscillations are employed.

GASSER and HILL (1924) were the first to introduce a mechanical, periodically vibrating system, the frequency and damping of which were affected by the total stiffness and viscosity of the muscle. Measurements were carried out during practically isometric contraction where the stiffness was found to be many (11) times greater than when at rest. However, the tension developed during contraction was not taken into account in these experiments, although it caused the predominant part of the registered stiffness, as already pointed out by WEBER. STEINHAUSEN (1924—26), and later RICHTER (1928) performed elasticity measurements by means of impulse-period determinations and introduced tension compensation. They found an increase as well as a decrease in stiffness during contraction. Even for the whole muscle, a systematic investigation of the dynamic stiffness at rest and during contraction over a wide range of load does not exist.

Moreover, all experiments on whole muscle involve essential errors. A change in form and a displacement of the fibres take place even during isometric contraction and, further, inhomogeneous states of stretch and contraction in various parts of the muscle and the connective tissue must exercise an uncontrollable influence upon the results.

Static and dynamic measurements of the elasticity of the single muscle fibre at different loading should therefore be of great significance for the elucidation of the elastic and viscous properties of the muscle fibre.

A. Dynamic stiffness.

Comparison of the elastic properties of the fibre at rest and during contraction.

The stiffness, i. e. $\frac{\Delta \text{ force}}{\Delta \text{ length}}$ expressed as dyne/cm, is accessible to direct measurement in vibration experiments. In the case of a homogeneous body, this magnitude will generally be expressed as the elasticity modulus, viz.

$$\frac{\Delta \text{ force} \times \text{length}}{\Delta \text{ length} \times \text{cross section}};$$

in a highly elastic body, however, great changes in the existing length and cross section may occur. The elasticity modulus based upon an arbitrary stretch and a corresponding cross section is less suited for the elucidation of the required properties of the respective substance than is the measured stiffness, especially in the case of anisotropic substances. Stiffness-tension variations must primarily be regarded as determined by structural changes in the molecular or micellar constitution of the fibre and, to a minor extent, as dependent on the inversely proportional changes in length and cross section.

In the evaluation of the measurements, primarily the ratio $\frac{\Delta \text{ force}}{\Delta \text{ length}}$ = stiffness furnished a basis of comparison. Measurements of stiffness at rest and during contraction were performed according to the following aspects.

Method I. Stiffness comparison at the same length of the fibre. This would seem to be the most natural procedure, as it corresponds to a comparison of the moduli at constant cross section area.

Method II. Stiffness at the same tension.

a) At rest and during isometric contraction. On the basis of corresponding values of stiffness and tension, the ratio

$$\frac{\text{Stiffness (contraction)}}{\text{Stiffness (rest)}}$$

is found for equal tension, i. e. we compare fibres the single elements of which are exposed to the same tension but are of different length.

b) The stiffness is compared at rest and during contraction at the same tension obtained by release from isometric contraction to the same tension as at rest. Also in this case, the length of the resting and the contracted fibre is different.

The elasticity moduli may be calculated on the basis of results obtained from these stiffness experiments. Comparing the stiffness at rest and during contraction as found by method I, we arrive at the elasticity constant referring to the same length of the fibre. The difference between these two measured elasticity moduli is due to contraction. During contraction, an increase in tension occurs which is produced by some kind of change in the fibre substance. In a not "highly elastic" substance, the increase in tension would not influence the elasticity modulus to a considerable degree; in a highly elastic body, however, the tension controls decisively the magnitude of the modulus.

The interesting point in stiffness measurements is more the change of the material constant during the contractile process than the change of the elasticity modulus due to tension. A differentiation of these two magnitudes is essential, as the structural changes accompanying contraction are the most interesting problem, while the tension—which may be regulated externally —is of minor interest. Formerly, it was assumed that the increase in stiffness during contraction should be ascribed mainly to the contraction process itself (Gasser and Hill 1924), while the increase in tension was disregarded. The present material, however, makes it quite clear that the increase in stiffness actually due to contraction is very small and may even be negative and, further, that the very marked increase in stiffness formerly observed by Gasser and Hill is mainly due to tension (i. e. structural changes which will appear in the same way at rest under the influence of exterior forces).

When fibres are compared at the same length (method I), a distorted picture is given of the influence of contraction upon the material.

It must, furthermore, be taken into consideration that the individual substances of the fibre change their lengths also during isometric contraction (shortening of A and elongation of I). An isometric contraction of the fibre is thus not synonymous with isometric conditions of the single elements of the fibre.

The true elasticity constant of the total fibre substance is found by a stiffness comparison of fibres at the same tension at rest and during contraction (method II, a and b) corrected for different lengths and cross sections.

A differentiation of the stiffness and elasticity moduli of the total fibre with respect to the individual substances is given in a later section (p. 90).

Elasticity measurements at rest and during contraction.

1) Treatment of the material.

The results from the individual experiments are arranged as stiffness at rest and during contraction and corresponding tension as a function of stretch. The extent of stretch proved not to be the most suitable basis of comparison of elastic properties, since it was found that different fibres were able to endure greatly differing elongations. Some fibres may, for example, be stretched to a length 150, others up to 220, before the extra-tension during contraction becomes zero. In the individual length-stiffness and length-tension diagrams, however, it was observed that a variation of the loading generally led to a corresponding variation in stiffness. This variation of the load need not necessarily be externally caused by a length alteration, but it might originate from a change in contractility of the fibre or by fibre yielding. On plotting the stiffness in the different experiments as a function of the load, the material became practically uniform.

In the present investigation, we have been mostly interested in the interdependence of loading, stiffness, and length at rest and during contraction. Absolute values of elasticity moduli have been determined in a special series of experiments where in addition to the length of the fibre its diameter was measured.

The absolute values of the different experiments vary con-

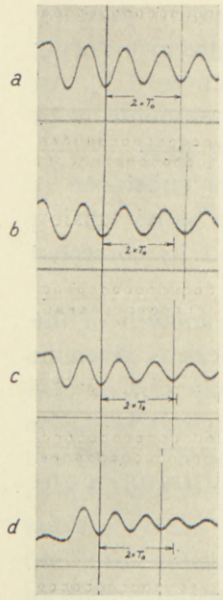


Fig. 29. Determination of dynamic stiffness in vibration experiments.
(*a*) oscillations of the vibrating system without muscle fibre (T_0);
(*b*) oscillations of the system loaded with 0.5 gm (determination of the effective mass of the system);
(*c*) oscillations of the system + resting fibre;
(*d*) oscillations of the system + contracted fibre (release contraction to the same tension as present in the resting fibre).
Time marks = 20 msec.

siderably and it was, therefore, necessary to find a common measure of stiffness and tension for the different fibres. All tension measurements refer to the tension existing in the fibre when the extra-tension during contraction becomes zero due to the stretch. This is a well-defined point on the length-tension diagram and, using it as a basis, the measuring system enables an adequate conformity between the different elastic properties of the fibre.

As a measure of the stretch, the length of the fibre is put = 200, where the extra-tension during contraction becomes zero. This length—twice that at rest—corresponds very closely to the mean value from all experiments with isometric contraction. In a series of experiments on release contractions, however, the measure of length is put = 150, as this is the mean stretch where the extra-tension during contraction is zero. In these latter experiments, the respective fibres showed a maximum extensibility amounting to about half that measured in the first series of experiments with isometric contractions.

The measure of the loading is the same as in the series of experiments during isometric contraction.

As a measure of the stiffness, the stiffness at rest is put = 100 at a stretch where the extra-tension during contraction ceases.

Series I includes measurements of tension and stiffness at rest. Isometric contraction of the fibre followed by release until the contracted fibre shows the same tension as before when at rest (Fig. 29, method IIb, p. 67). Registration of the

corresponding length and stiffness. These measurements were performed at different elongations.

Series II includes determinations of tension and stiffness at rest. Measurements of tension and stiffness at the same length during isometric contraction and, finally, measurements of tension and stiffness during release from isometric contraction to an arbitrary length (and not, as in series I, to the same tension as when the fibre is at rest). The measurements were performed at different elongations.

On the basis of length-stiffness and length-tension diagrams, the respective values of tension and stiffness were corrected to the above described units. From the diagram of the resting fibre, the isometrically contracted fibre and

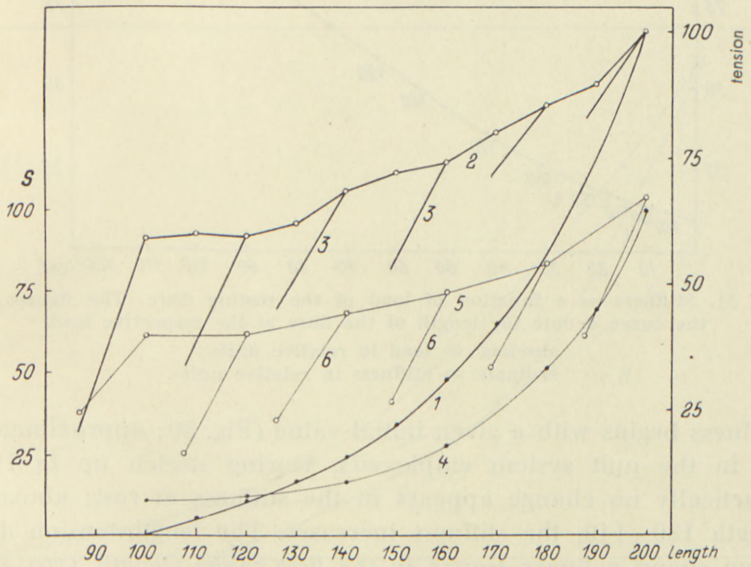


Fig. 30. Length-tension and length-stiffness diagram of the single muscle fibre at rest and during contraction. Mean curve.

(1) length-tension diagram of the resting fibre;
(2) length-tension diagram of isometric maxima;
(3) direction of release contractions, when releasing from the isometric maximum;
(4) length-stiffness diagram of the resting fibre;
(5) length-stiffness diagram of the isometrically contracted fibre;
(6) variation of stiffness in release contractions, when releasing from the isometric maximum;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left) stiffness in relative units;
(right) tension in relative units.

the fibre with release contractions, the ratio $\frac{S_c}{S_r}$ (with uniform load) was determined for every experiment as a function of the load and the extent of stretch.

2) Stiffness at rest.

Length-stiffness diagram. As the fibre has a certain stiffness also at its equilibrium length, the diagram of the dynamic

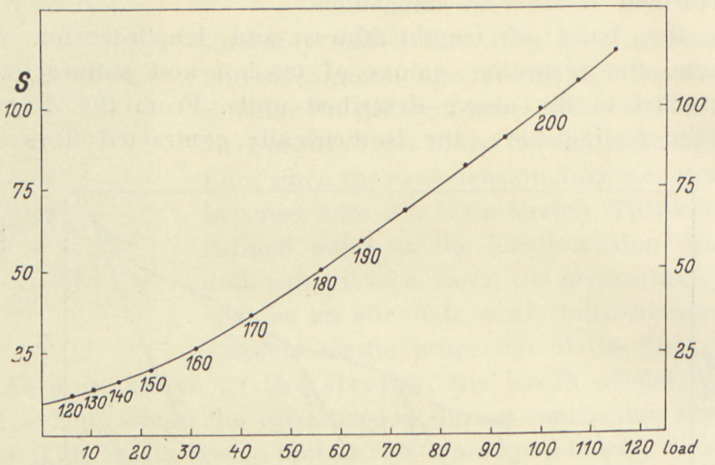


Fig. 31. Stiffness as a function of load of the resting fibre. The figures on the curve denote the length of the fibre at the respective load.
abscissa = load in relative units;
ordinate = stiffness in relative units.

stiffness begins with a given initial value (Fig. 30; approximately 10 in the unit system employed). During stretch up to 120, practically no change appears in the stiffness at rest; above a length 130—140, the stiffness increases. The length-tension diagram shows a linear course in the first range (length 120) and starts bending between length 130—140, then continueing with increasing differential quotient.

Load-stiffness diagram. This diagram naturally begins at the same value as at length 100, since here the load is 0. Apart from a concave bend towards the x axis at a load 15, the stiffness increases proportional to the loading. In the mean diagram, the transition between these two ranges (Fig. 31) is slightly smoothened. Actually, the difference in slope is more pronounced

in the case of the individual fibres (Fig. 34). The interpretation of this characteristic straight course of the curve will be given in a later section (p. 116).

3) Stiffness during contraction.

Release contractions (release to the same tension as when at rest; method II b).

Length-stiffness diagram. The stiffness of the contracted fibre begins at the load 0 (length 75) with a value of about 30, and remains constant up to length 120 (Fig. 32). From length 100—140, it amounts to approximately 15 units above the resting value when comparing fibres of identical lengths. At greater lengths, the stiffness at rest and during contraction approach each other.

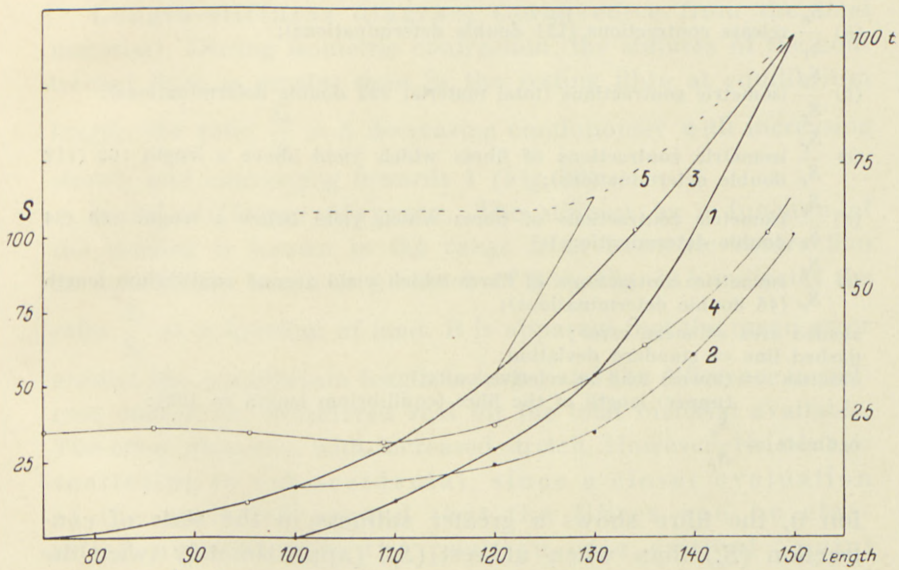


Fig. 32. Length-tension and length-stiffness diagram of fibres at rest and during release contraction.

(1) length-tension diagram of the resting fibre;
(2) length-stiffness diagram of the resting fibre;
(3) length-tension diagram of release contractions (release to the same tension as at rest);
(4) length-stiffness diagram of release contractions;
(5) curve of isometric maxima with partial release diagram;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = (right) tension in relative units;
(left) stiffness in relative units.

Load-stiffness diagram. In order to elucidate the variation in stiffness when a fibre is contracting, the ratio contraction stiffness/rest stiffness at the same load is employed (Fig. 33*a*), as we are mainly interested in a distinction between stiffness during contraction and at rest. After release to the tens-

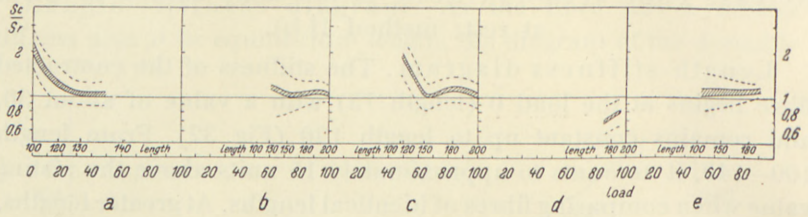


Fig. 33. $\frac{\text{Stiffness during contraction } (S_c)}{\text{Stiffness at rest } (S_r)}$ as a function of loading.

(*a*) $\frac{S_c}{S_r}$ release contractions (131 double determinations);

(*b*) $\frac{S_c}{S_r}$ isometric contractions (total material 242 double determinations);

(*c*) $\frac{S_c}{S_r}$ isometric contractions of fibres which yield above a length 100 (112 double determinations);

(*d*) $\frac{S_c}{S_r}$ isometric contractions of fibres which yield below a length 100 (84 double determinations);

(*e*) $\frac{S_c}{S_r}$ isometric contractions of fibres which yield around equilibrium length (46 double determinations);

shaded area = mean error;
dashed line = standard deviation;
abscissa = (lower) load in relative units;
(upper) length of the fibre (equilibrium length = 100);
ordinate = $\frac{S_c}{S_r}$.

ion 0, the fibre shows a greater stiffness in the state of contraction (S_c) than when at rest (S_r) (approximately twice the resting value). With increasing load, the ratio $\frac{S \text{ release contraction}}{S \text{ rest}}$ decreases converging towards 1. Already at a load of 30 (length 130), the ratio has almost reached the value 1. As the standard deviation is not distributed symmetrically about the mean value, partly because the stiffness cannot attain negative values, the material is unsuited for a graphical representation in linear coordinates. In a logarithmic coordinate system, however,

the individual measurements fall symmetrically around the mean value. For this reason, the ratio $\frac{S_c}{S_r}$ is plotted in a logarithmic system and the mean curve as well as the standard deviations and the mean errors are represented in this coordinate system.

The shaded part of the curve marks the standard error which amounts to approximately 3 per cent. The dashed line above and below the mean curve, respectively, denotes the standard deviation. The mean error at load 0 is 3.5 per cent of the measured difference between the stiffness at rest and during contraction, and up to a load of 20 units (length approx. 120), the difference must be regarded as real.

4) Isometric contractions (method II a).

Length-stiffness diagram (mean curve from the total material). During isometric contraction, the stiffness of the contracted fibre is greater than in the resting fibre at equilibrium length, the ratio $\frac{S_c}{S_r} = 5$ decreasing continuously with increasing stretch and converging towards 1 (Fig. 30).

Load-stiffness diagram. The stiffness as a function of the loading is known in the range from isometric contraction at equilibrium length to a stretch of 200. Fig. 33 *b* indicates the ratio $\frac{S_c}{S_r}$ as a function of load. It is apparent that the mean error around the equilibrium length is large, and the difference in stiffness cannot be considered real for the total material available. The error decreases with increased stretch. However, this large scattering is not accidental, since a closer evaluation of the material proved that the fibres can be classified according to the position of a critical "point of yielding" on the tension-stiffness diagram of the contracted fibre. The course of the loading-stiffness diagram of the individual series of experiments is given in the examples of Fig. 34 *a*. Fig. 34 *b* represents an ideal diagram. The initial stiffness during contraction is somewhat higher than when at rest and increases rapidly with augmented loading. The stiffness shows here a very sharp maximum (the point of yielding) and then decreases rapidly with increased load. At greater loads, the contraction

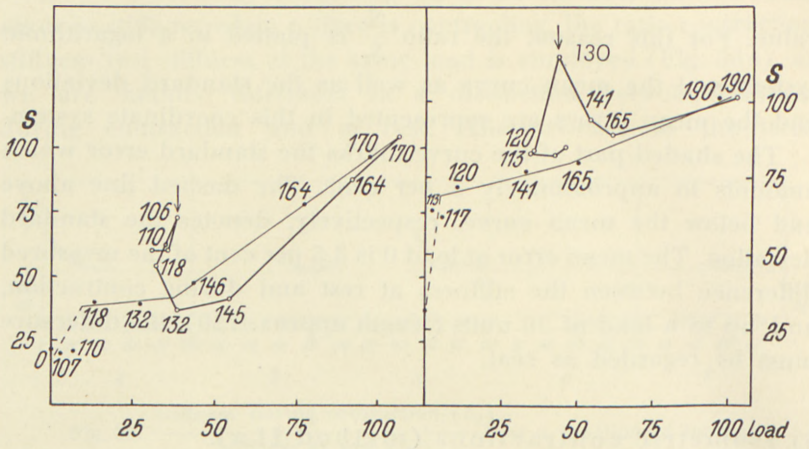


Fig. 34a. Stiffness-load diagram of individual fibres showing yielding at different points of the stretch diagram.

—●—●— = resting fibre;
—o—o— = isometrically contracted fibre.

The figures on the curve denote the fibre length at the resp. loading; the arrows indicate the point of yielding.

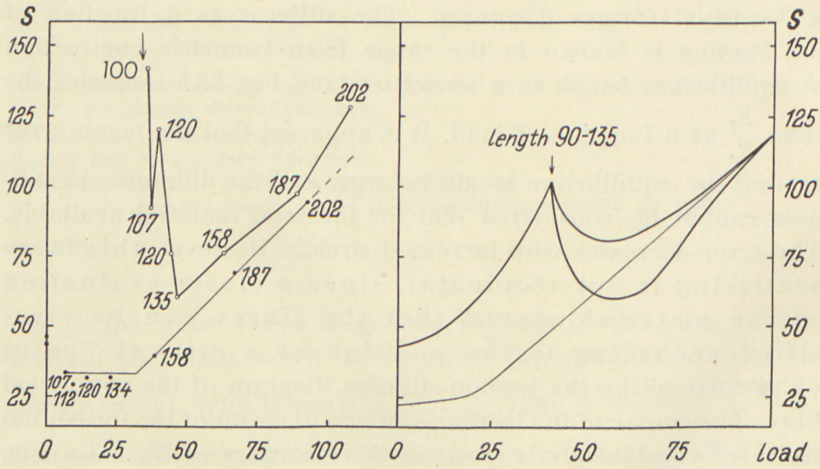


Fig. 34a.

Fig. 34b. Schematic diagram of stiffness as a function of load at rest and during contraction.

abscissa = load in relative units;
ordinate = stiffness in relative units.

curve can fall below the curve of the resting fibre. At maximal elongations, S_c approaches S_r. The point of yielding is situated from below equilibrium length up to length 135.

In all cases, the stiffness during contraction is considerably greater than at rest, as long as the yielding point is not exceeded.

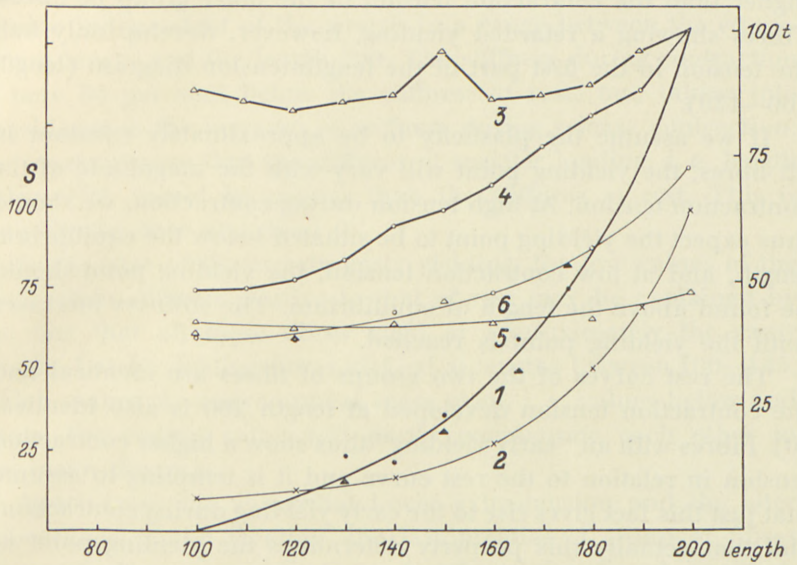


Fig. 35. Length-tension and length-stiffness diagrams of fibres with a yielding below and above length 100, respectively.

(1) common length-tension diagram of the resting fibre;
(2) common length-stiffness diagram of the resting fibre;
(3) length-tension diagram, isometric contraction, yielding below length 100;
(4) length-tension diagram, isometric contraction, yielding above length 100;
(5) length-stiffness diagram, isometric contraction, yielding below length 100;
(6) length-stiffness diagram, isometric contraction, yielding above length 100;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left) stiffness in relative units;
(right) tension in relative units.

Then, the contraction stiffness approaches that of the resting fibre. A uniform treatment of the material is rendered difficult because of the great variation of the yielding point from fibre to fibre. Therefore, we differentiate between fibres having the yielding point below the equilibrium length ("early yielding") and fibres with the yielding point above the length of equilibrium ("late yielding") (Figs. 33*c* and *d*). Between these two groups, all transitory types may naturally be found

(Fig. 33*e*), but when these two characteristic groups are considered separately, the mean length-tension diagrams also reveal typical differences (Fig. 35). Fibres with a yielding point below the equilibrium length develop a contraction tension which is almost constant over the entire range of stretch, and which is much higher than the contraction tension of the other group of fibres. Fibres showing a retarded yielding, however, develop only half the tension in the first part of the length-tension diagram (length 100—130).

If we assume the plasticity to be approximately constant in all fibres, the yielding point will vary with the magnitude of the contraction tension. At high tension during contraction, we should thus expect the yielding point to be situated below the equilibrium length, and at low contraction tension, the yielding point should be found above the length of equilibrium. The stiffness increases until the yielding point is reached.

The rest curves of the two groups of fibres are identical and the contraction tension developed at length 200 is also identical (0). Fibres with an "early yielding" thus show a higher contraction tension in relation to the rest curve and it is tempting to assume that just this fact gives rise to the early yielding during contraction, and that actually this property determines the yielding point of the fibre.

The mean curve of stiffness as a function of load in the late yielding group of fibres indicates the following. (cf. Fig. 33*c*).

At a load 50 (length 100), the stiffness of the contracted fibres is about 80 per cent above the stiffness at rest at the same loading. It must, however, be taken into consideration that the fibres compared are of different lengths (cf. elasticity moduli, p. 80). In the range between the equilibrium length (load 50) and the shortest length during contraction (load 0), the load-stiffness diagram is not known (only a few single observations are available). From the above described determinations during release contractions it is known that the contraction stiffness at load 0 is about twice that at rest. At stretch from load 50 to 65, the mean stiffness approaches that at rest. The slight deviation from the resting value at a load 75—90 cannot be considered real. The fibres which could endure a stretch exceeding a load 100 indicate that stiffness at rest and during contraction at this

elongation are still approximately identical. The yielding load of the fibres described here is presumably on the average 50 units.

On the mean curve of fibres with an early yielding (Fig. 33*d*), the stiffness as a function of the loading indicates the following results. A curve cannot be drawn from the measurements of this group, since the fibre develops almost constant tension independent of the stretch in a range between the equilibrium length and the length 200. The stiffness during contraction is here 30 per cent below the stiffness at rest; but, taking into consideration the increase in stiffness during release contraction, we must suppose that the stiffness at smaller loading, i. e. length below 100, would be greater than the stiffness at rest. This is actually the case at a load 0.

In the case of fibres with early yielding, the low values of the contraction stiffness relative to that at rest may be explained by the fact that all these fibres yield at approximately the same length. Lately yielding fibres yielded at lengths between 100—135, which makes the curve appear more even, i. e. values below and above the resting value will partly compensate each other in the mean diagram.

Apart from the somewhat lower extra-tension and the later appearance of the yielding, the last mentioned group of fibres does not show any indication of reduced functional qualities. Their irritability, stiffness variation, the character of the release diagram, and the endurance of the fibre are not different from fibres with early yielding.

5) Partial release from isometric contraction.

Length-tension diagram. In the case of partial release (Fig. 30, 3), no difference could be found between the above discussed groups of fibres. When a fibre is brought into isometric contraction and then released, the release curve does not follow the curve of the isometric maxima but shows a much steeper course, a phenomenon which has already been described in connection with the semi-dynamic length-tension diagrams (p. 43). The gradient is similar to that at rest with the load 100. The gradient apparently decreases at higher stretch from length 170—200. At these elongations, the curve of isometric maxima and that of release contraction approach each other. Theoretically,

there is no difference between the releases discussed here and the above mentioned semi-dynamic experiments. The semi-dynamic curves show loops due to viscosity (Fig. 20), while linear curves are obtained by the technique employed here. The present release length-tension diagrams must be considered a "mean line" of the loops in semi-dynamic curves.

Length-stiffness diagram. The length-stiffness diagrams of release contractions (Fig. 30, 6) are of the same type as the release length-tension diagrams. It must, however, be emphasized that the stiffness—in contrast to the tension—does not converge towards 0 but towards a given initial value.

Release stiffness relative to rest stiffness. As previously mentioned, the stiffness at rest varies over a wide range (loads 25—100, length 130—200) proportional to the load, $\frac{\Delta S}{\Delta P} = k$. The same was the case in release contractions for the corresponding extensions, since connecting lines between the coordinates of stiffness and tension of isometric contraction and the corresponding coordinates of release contraction are parallel with the rest curve. Consequently, $\frac{\Delta S}{\Delta P}$ (isom.) and $\frac{\Delta S}{\Delta P}$ (release) are approximately equal.

6) Elasticity moduli at rest and during contraction. On the basis of the measured stiffness $\left(\frac{\Delta \text{force}}{\Delta \text{length}}\right)$ and the relative lengths, the relative elasticity moduli could be calculated. It is a supposition of this calculation that the fibre volume remains constant during stretch and isometric contraction. Measuring the fibre at different extensions by means of a Fedoroff microscope stage, where the fibre diameter can be determined in different planes, Buchthal and Knappeis[1] found the fibre volume to be constant within the limits of microscope accuracy. Volume changes found in total muscle by Ernst (1925) and by Meyerhof and collaborators (1933) are considerably smaller than those which are detectable microscopically.

Elasticity modulus $= \frac{\text{stiffness } (S)}{\text{cross section } (q)} \times \text{length } (l)$. For the same fibre at various elongations, the modulus is proportional

[1] Unpublished experiments.

to the product $S \times l^2$, since the cross section is inversely proportional to the length, if the volume is constant (cf. p. 13).

Apart from the modulus as a function of stretch, Fig. 36 exhibits a length-tension diagram where the tension is calculated as

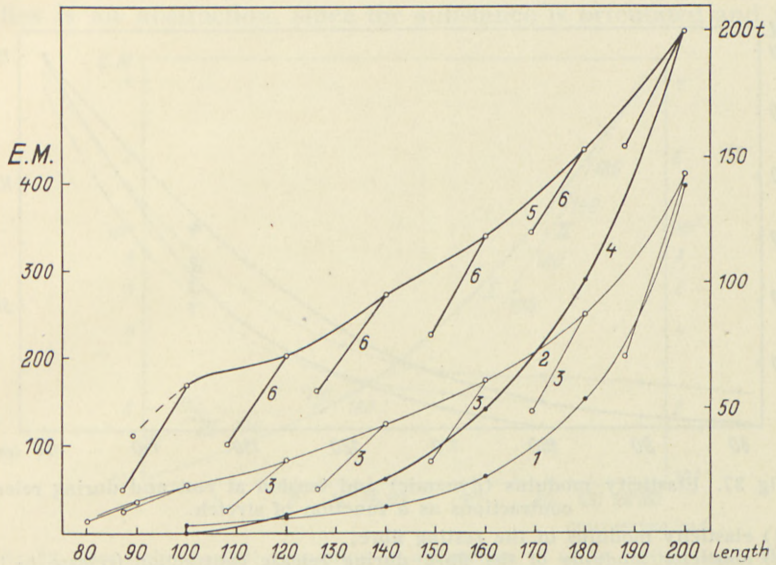


Fig. 36. Elasticity modulus (dynamic) and tension of the single fibre at rest, during isometric contraction, and during release contraction as a function of stretch.
(1) elasticity modulus of the resting fibre;
(2) elasticity modulus of the isometrically contracted fibre;
(3) elasticity modulus of the fibre during partial release contractions;
(4) length-tension diagram of the resting fibre;
(5) length-tension diagram of the isometrically contracted fibre;
(6) length-tension diagram of the fibre during partial release contractions;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left) dynamically determined elasticity modulus in relative units; (right) cross section loading in relative units.

tension per cross section unit, i. e. the figures of the ordinates (right side of the figure) are proportional to the cross section loading.

When calculating the elasticity modulus, the stiffness values are based on those of a "unit body". It is, therefore, reasonable to base the corresponding loadings upon a unit cross section. Figs. 36 and 37 show the elasticity modulus and the cross section loading at rest, during isometric contraction, and during release contraction as a function of the length of the fibre. These curves

do not reveal any fundamental deviation from the above described length-tension and length-stiffness diagrams. In the last region of stretch, however, they show a relatively steeper slope, as the length directly enters the calculation of the cross section loading as l^1 and of the modulus as l^2.

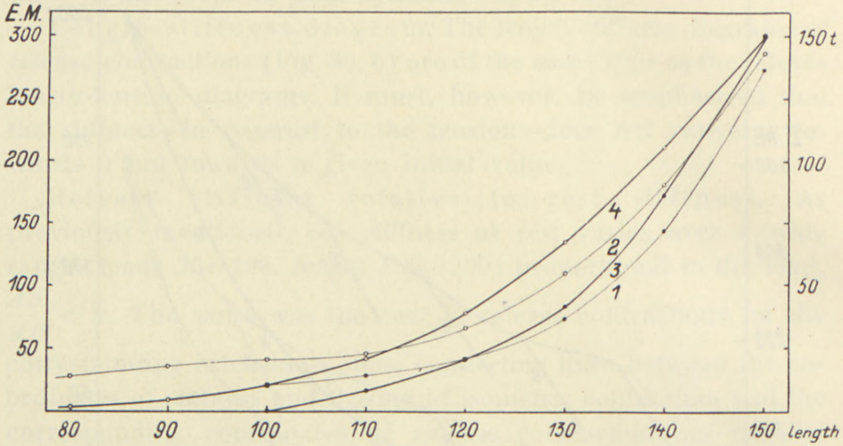


Fig. 37. Elasticity modulus (dynamic) and tension at rest and during release contractions as a function of stretch.

(1) elasticity modulus of the resting fibre;
(2) elasticity modulus of the fibre during release contraction (release to the same tension as at rest);
(3) length-tension diagram, rest;
(4) length-tension diagram, release contractions;

abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left) dynamically determined elasticity modulus in relative units; (right) cross section load in relative units.

The elasticity modulus as a function of the cross section loading is represented in Fig. 38. The difference between the moduli at rest, during isometric contraction, and during release contraction reduced to the same loading is very small. At loads 0—7, the modulus of the contracted fibre (release contraction) is higher than the modulus at rest. At a loading 0—3, the difference amounts to about 30 per cent. In the range 30, the elasticity modulus of the contracted fibre (isometric contraction) is about 25 per cent below the value at rest. The difference decreases at higher loading and becomes zero at the load 100. The measurements of stiffness indicate that scattering in the range 0—3 is relatively low and, in this range, the difference between the elasticity moduli at rest and during contraction

is beyond the limit of error. In the range 30 and at higher load, the scattering is considerable, due to the different position of the yielding point; the latter deviation from rest on the mean curve cannot with certainty be considered real.

As previously emphasized, the modulus of highly elastic bodies is an abstraction, since the substance is orientated and the

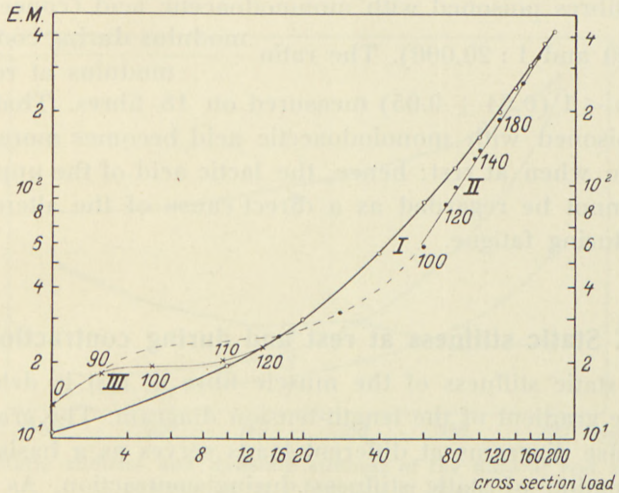


Fig. 38. Dynamic elasticity modulus as a function of cross section load. Mean curve.

I. resting fibre;
II. isometric contraction;
III. release contraction (release to the same tension as at rest).

The figures on the curve denote the length of the fibre at the respective load.
abscissa = cross section load in relative units, log scale;
ordinate = elasticity modulus in relative units, log scale.

degree of orientation becomes greater at higher stretch. Therefore, the elasticity modulus is less suited to characterize the mechanical composition of the substance than the directly measured stiffness.

7) Elasticity modulus during contraction of a fatigued fibre.

The elasticity modulus of a non-fatigued fibre during release contraction from equilibrium length to the tension 0 is considerably larger than that of the resting fibre. The ratio

$$\frac{\text{modulus during contraction}}{\text{modulus at rest}} = 1.97 \pm 0.13$$

(measured on 19 single fibres). In a fibre fatigued by numerous

preceding contractions (up to 50 contractions), the stiffness during contraction increases much less, and the coefficient is 1.13 ± 0.06 (measured on 15 fibres).

In order to investigate whether this change of stiffness is connected with the production of lactic acid in a fibre fatigued by long-lasting series of contractions, the moduli were studied on fatigued muscle fibres poisoned with monoiodoacetic acid (concentration 1 : 10,000 and 1 : 20,000). The ratio $\frac{\text{modulus during contraction}}{\text{modulus at rest}}$ becomes < 1 (0.84 ± 0.05) measured on 18 fibres. That is, the fibre poisoned with monoiodoacetic acid becomes more extensible than when at rest; hence, the lactic acid of the unpoisoned fibre cannot be regarded as a direct cause of the altered coefficient during fatigue.

B. Static stiffness at rest and during contraction.

The static stiffness of the muscle fibre at rest is determined from the gradient of the length-tension diagram. The gradient of the release diagrams at different loads serves as a basis for the determination of static stiffness during contraction. As already discussed, the curve of the isometric maxima is irreversible and therefore unsuited for a calculation of stiffness.

In the following sections, the material from measurements of the statically determined stiffness and of the elasticity modulus is treated in the same way as the dynamically determined material.

1) Static stiffness as a function of stretch.

In analogy to dynamic stiffness, static stiffness at rest increases with increasing elongation and amounts to about half the dynamic stiffness (Fig. 39, 1). During contraction, however, the static stiffness deviates essentially from the dynamic measurements, as static stiffness decreases with increasing stretch.

During contraction at equilibrium length, S_c lies about 10 times above the stiffness at rest (Fig. 39, 2). At length 180, the stiffness at rest is equal to that during contraction, and at length 200, the stiffness during contraction, is only about 50 per cent of the stiffness at rest.

Compared with the shortening in equilibrium length, the change in stiffness during contraction has not been considered an impor-

tant factor for the amount of tension developed by the muscle. However up to length 150 the increase in tension during isometric contraction is predominantly due to the increase in stiffness, as shown by the following example.

When the resting fibre is stretched 30 units (from 100—130), the tension developed amounts to only 15 tension-units. During

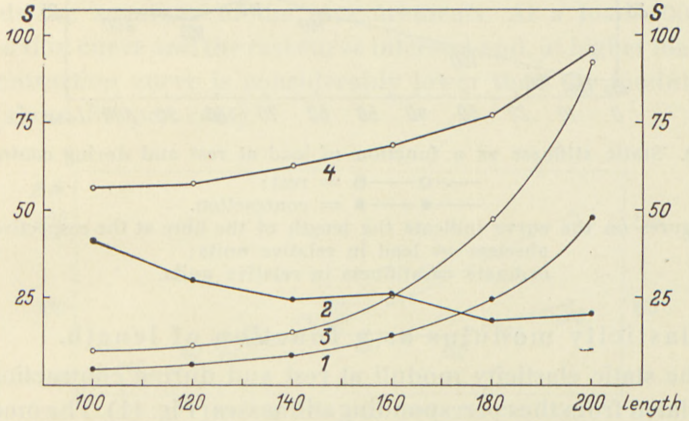


Fig. 39. Static stiffness and dynamic stiffness of the fibre at rest and during contraction as a function of stretch.
(1) static stiffness, rest;
(2) static stiffness, contraction;
(3) dynamic stiffness, rest;
(4) dynamic stiffness, contraction;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = stiffness in relative units.

isometric contraction at length 100, on the other hand, the equilibrium length shortens 30 units to length 70 (cf. release diagram) while the tension amounts here to four times that of the resting fibre, (60 tension-units).

2) Static stiffness as a function of loading.

Static stiffness at rest shows an approximately linear course as a function of load. During contraction, we find corresponding relations, as already described when discussing stiffness-length diagrams (Fig. 40); the stiffness decreases with increasing length and, consequently, also with increasing loading. At a load 60, the stiffness is twice that at rest; at a load 72, the

rest curve and contraction curve intersect and then the contraction stiffness decreases to about half that at rest.

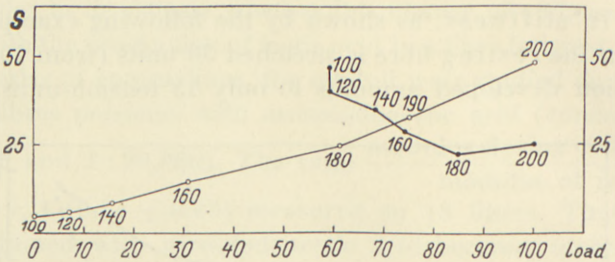


Fig. 40. Static stiffness as a function of load at rest and during contraction.
—o—o— = rest;
—•—• = contraction.
The figures on the curve indicate the length of the fibre at the respective load.
abscissa = load in relative units;
ordinate = stiffness in relative units.

3) Elasticity modulus as a function of length.

The static elasticity moduli at rest and during contraction are calculated from the corresponding stiffnesses (Fig. 41). The modulus

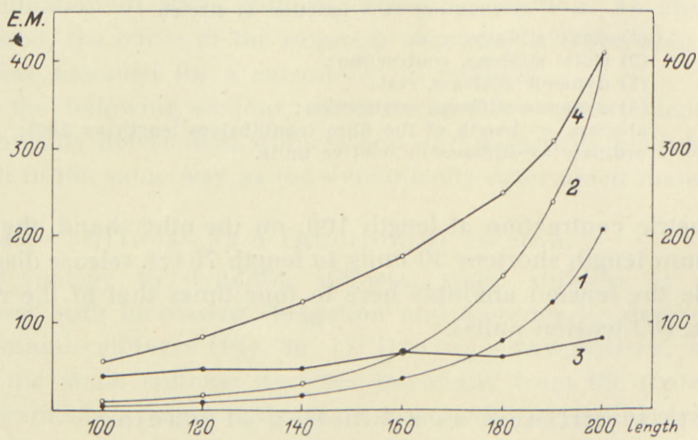


Fig. 41. Static and dynamic elasticity moduli of the fibre at rest and during contraction as a function of stretch.
(1) static elasticity modulus, rest;
(2) dynamic elasticity modulus, rest;
(3) static elasticity modulus, contraction;
(4) dynamic elasticity modulus, contraction;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = elasticity modulus in relative units.

during contraction exceeds the modulus at rest up to a length 175, where the curves intersect each other.

4) Elasticity modulus as a function of cross section load.

With a cross section load 60—80, the static modulus during contraction is somewhat higher than the modulus at rest (Fig. 42) when referred to the same load; however, the difference scarcely exceeds the accuracy of the measurements. At a load 100, the contraction curve and the rest curve intersect and, at higher loading, the contraction curve is considerably lower than the modulus at rest (about 50 per cent).

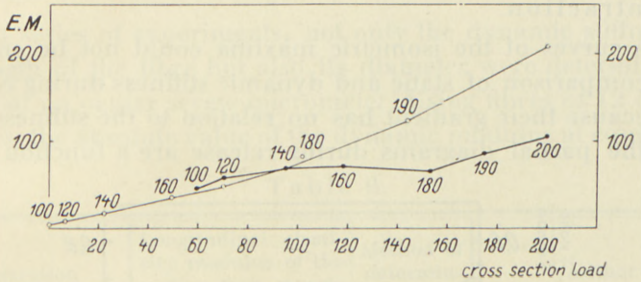


Fig. 42. Static elasticity modulus at rest and during contraction as a function of cross section loading.

—o—o— = rest;
—•—•— = contraction.

The figures on the curve indicate the length of the fibre at the respective loading.

abscissa = cross section load in relative units;
ordinate = elasticity modulus in relative units.

C. Comparison of static and dynamic stiffness.

1) Resting fibre.

A comparison of the gradient of the single length-tension diagrams in dynes/cm with the measured dynamic stiffness in dynes/cm reveals that the dynamic stiffness measured in vibration experiments is about twice the static stiffness. The ratio $\frac{S \text{ static}}{S \text{ dynamic}}$ varies only slightly with stretch and amounts on an average to 0.5 (variation between 0.45 and 0.6; Fig. 43). This means that only approximately half of the extensible material participates in the rapid length alterations produced by vibrations.

Hence, the viscosity is not uniformly distributed over the extensible elements of the fibre and part of this is not hindered by viscosity. (For a more detailed discussion of the viscosity and elasticity distribution see p. 105.)

In a new series of experiments (carried out at another time of the year and on different frogs), we found the ratio $\frac{S \text{ static}}{S \text{ dynamic}} = 0.7$ (variation between 0.6 and 0.8). The deviation from the above described experiments was not surprising, as the first mentioned material showed other elastic properties, especially an inferior extensibility.

2) Contraction.

The curves of the isometric maxima could not be employed for a comparison of static and dynamic stiffness during contraction, because their gradient has no relation to the stiffness. However, the partial diagrams during release are a function of stiff-

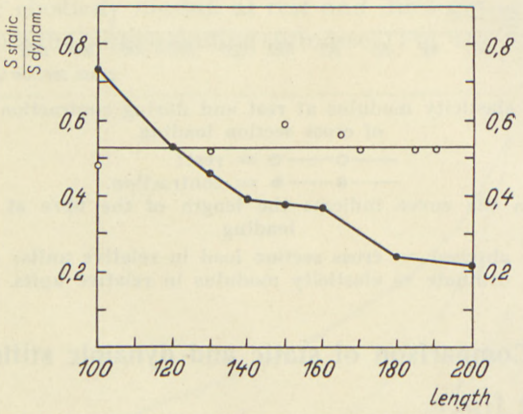


Fig. 43. Relation between static stiffness and dynamic stiffness as a function of stretch, at rest and during contraction.

—o—o— = rest;
—•—• = contraction;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$.

ness, since they are reversible to the same extent as the rest curves. $\frac{S \text{ static}}{S \text{ dynamic}}$ during contraction varies considerably with the stretch (Fig. 43). At equilibrium length, the ratio between static

and dynamic stiffness is highest (0.75), decreasing until the value 0.2 is reached at the length 200. It would be reasonable from this fact to conclude that below the equilibrium length the ratio will approach unity, so that the total elastic mass is uniformly involved in the elastic deformations. At higher stretch, smaller and smaller parts of the fibre participate in the rapid elastic length alterations; at a stretch around 180—200, for example, only $^1/_5$ of the total elasticity of the fibre is at the disposal of the rapid vibrations (5 per sec.) here applied; the rest is blocked by viscosity.

D. Absolute values of the elasticity modulus of the striated muscle fibre.

In a series of experiments, not only the dynamic stiffness and the length of the fibre but also its diameter were determined, by means of an ocular screw micrometer. Using fibres of 12 different muscles, the absolute value of the dynamic modulus at equilibrium

Table 6.

Preparation	Longitudinal elasticity modulus of the resting frog muscle in dynes $\times$ cm^{-2} *	Method of determination	Author
Total muscle.....	0.6×10^6	static	E. Weber (1846)
»	0.94×10^6	static	Wundt (1858)
»	$(0.01 - 1.0) \times 10^6$	static	Triepel (1902)
»	$(2.7 - 3.9) \times 10^6$ **	static	Bouckaert a. o. (1930)
»	$(0.09 - 0.17) \times 10^6$	static	Wöhlisch a. o. (1930)
»	$(0.01 - 0.15) \times 10^6$	static	Wöhlisch and Clamann (1936)
»	0.15×10^6	dynamic	Steinhausen (1926)
0.5 mm part of single fibre	$(0.7 - 2.8) \times 10^6$	static	Sichel (1934)
non-injured single fibre	0.5×10^6	static	Buchthal (1942)
»	$(0.81 \pm 0.11) \times 10^6$	dynamic	Buchthal (1942)
Slightly vulcanized caoutchouc.	10×10^6	static	K. H. Meyer (1940)
Caoutchouc, not specified	0.5×10^6	static	Wöhlisch (1940)
Myosin thread ...	2.0×10^6	static	H. H. Weber

* For the transformation of an elasticity modulus given in kgm/mm^2 into the c.g.s.-system, the first mentioned is multiplied by 1.02×10^7.
** Temperature: 0° C.

length is on an average $(0.81 \pm 0.11) \times 10^6$ dynes $\times$ cm^{-2}. The static modulus is between 75 and 50 per cent of the dynamic modulus and amounts on the average to 0.5×10^6 dynes $\times$ cm^{-2}.

Table 6 shows measurements of elasticity moduli available from total muscles and single fibres at rest. Most of the determinations were carried out at equilibrium length or at a slight initial tension.

E. Static stiffness of A and I at rest and during contraction.

The stiffness at rest is obtained from the curve of the total static softness $(\frac{1}{S} = \frac{1}{S}A + \frac{1}{S}I)$ which is taken from the curve of static stiffness (Fig. 39, 1) and from the ratio $\frac{\text{softness of A}}{\text{softness of I}}$; the latter is identical with the ratio between the increase in length of the two substances at a small elongation of the whole fibre. At rest, the length of A and I as a function of stretch is used to determine the ratio $\frac{\Delta A}{\Delta I}$ (Fig. 26). During contraction, however, the gradient of the curve of isometric contraction is unsuitable for stiffness determinations because of its irreversibility. The ratio $\frac{\Delta A}{\Delta I}$ may be found, however, from release- and stretch contractions. As previously discussed, these curves represent a reversible length-tension alteration. From the ratio $\frac{\Delta A}{\Delta I}$ and the sum of softness A and softness I, the softnesses of both substances may be derived.

1) Static softness of A and I at rest as a function of stretch.

The upper curve of Fig. 44 represents the softness of the whole fibre (A + I), and the distance from the x-axis to the lower curve (Fig. 44, 2) is an expression of the softness of I. The distance between both curves is a measure of the softness of the A substance. The softness of both substances decreases uniformly with increasing stretch. The softness of A is the greater, mainly due to its greater length (cf. the moduli, p. 95). The ratio $\frac{S_A}{S_I}$ (Fig. 45, 1) indicates that the softness of A at equilibrium length is about twice that of I, a ratio which increases to about 2.5 at length 200.

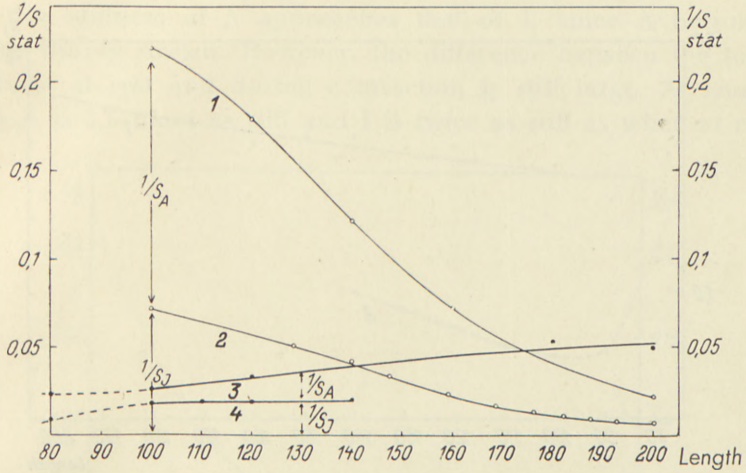


Fig. 44. Static softness $\left(\frac{1}{S}\right)$ of A and I at rest and during contraction as a function of stretch.

(1) $\frac{1}{S}$ of A + I at rest;

(2) $\frac{1}{S}$ of I at rest.

The difference between curve (1) and curve (2) corresponds to $\frac{1}{S}$ of the A substance at rest.

(3) $\frac{1}{S}$ of A + I during contraction;

(4) $\frac{1}{S}$ of I during contraction.

The difference between curve (3) and curve (4) corresponds to $\frac{1}{S}$ of the A substance during contraction.

abscissa = length of the fibre (equilibrium length = 100);

ordinate = $\frac{1}{S}$ (static) in relative units.

2) Static softness of A and I during contraction as a function of stretch.

The ratio $\frac{\Delta A}{\Delta I}$ (release contraction Fig. 45, 2) is known in the range of length 100—140 and, furthermore, at lengths 80—100 from interpolation (determination of the gradients in the length-tension diagram of the single substances, Figs. 27 and 28). The remarkable increase in stiffness during contraction, referring to the same length as when at rest (Fig. 44), originates from a change in stiffness of both substances. At equilibrium length, A becomes 7 times stiffer and I becomes 4 times stiffer than when at rest (Fig. 46). At stretch above equilibrium length, the con-

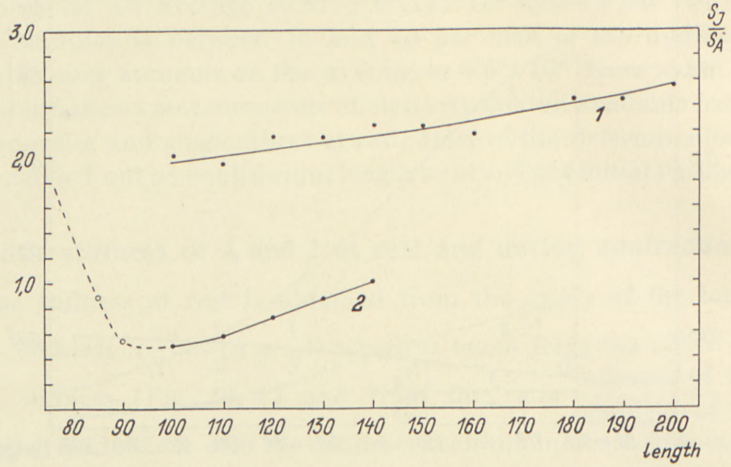


Fig. 45. $\frac{\text{Softness of A}}{\text{Softness of I}}$ at rest and during contraction as a function of stretch.

(1) $\frac{\text{softness A}}{\text{softness I}}$ at rest;

(2) $\frac{\text{softness A}}{\text{softness I}}$ during contraction;

abscissa = length of the fibre (equilibrium length = 100);

ordinate = $\frac{\text{softness A}}{\text{softness I}} = \frac{\text{SI}}{\text{SA}}$.

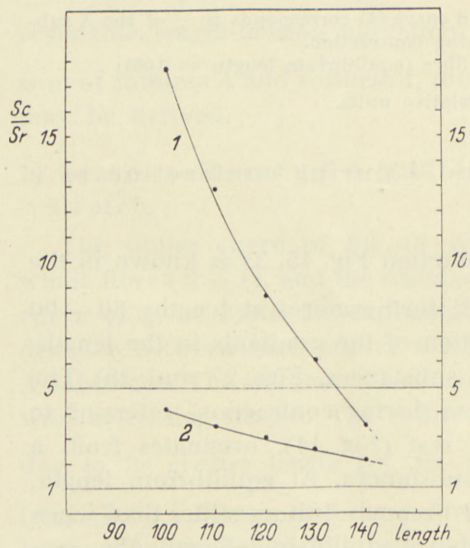


Fig. 46. $\frac{\text{Stiffness during contraction}}{\text{Stiffness at rest}}$ of the A and I substance as a function of stretch of the fibre.

(1) $\frac{Sc}{Sr}$ A substance;

(2) $\frac{Sc}{Sr}$ I substance;

abscissa = length of the fibre (equilibrium length = 100);

ordinate = $\frac{Sc}{Sr}$.

traction stiffness of A approaches that of I, since A becomes softer during stretch. However, the difference between the total stiffness at rest and during contraction is still large. At length 140, A is 3.5 times as stiff and I is twice as stiff as when at rest

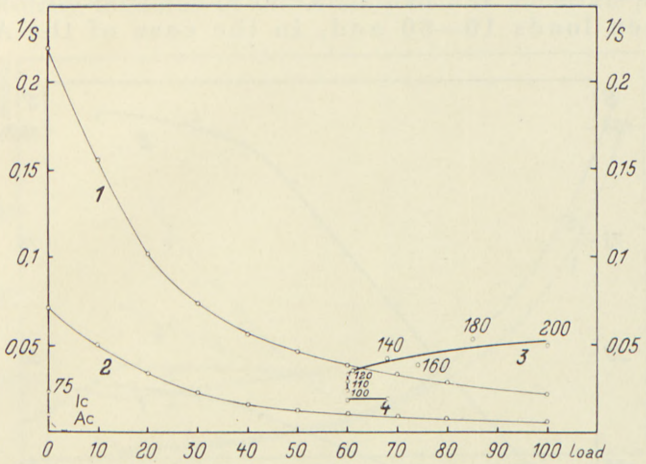


Fig. 47. Static softness $\frac{1}{S}$ of A and I at rest and during contraction as a function of loading.

(1) $\frac{1}{S}$ of A and I at rest;

(2) $\frac{1}{S}$ of I at rest.

The difference between curve (1) and curve (2) corresponds to $\frac{1}{S}$ of A at rest.

(3) $\frac{1}{S}$ of A + I during contraction;

(4) $\frac{1}{S}$ of I during contraction.

The difference between curve (3) and curve (4) corresponds to $\frac{1}{S}$ of A during contraction. The figures on the curve denote the length of the fibre at the respective load.

abscissa = load in relative units;

ordinate = softness $\frac{1}{S}$ in relative units.

(Fig. 46). At lengths below 100, the stiffness of A and I shows a peculiar course, the total stiffness being almost constant; the distribution between A and I, however, being changed (Fig. 44). At length 100, A is almost twice as stiff as I, and at length 80, I is about twice as stiff as A. The large increase in stiffness found from rest to contraction at low loading must first of all be ascribed to the I substance.

3) Static softness of A and I as a function of load.

Resting fibre. The static softness of A and I at rest as a function of load decreases continuously with increasing load (Fig. 47). The curve of stiffness (Fig. 48) as a function of load shows for the I substance a straight course between loads 10—60 and, in the case of the A sub-

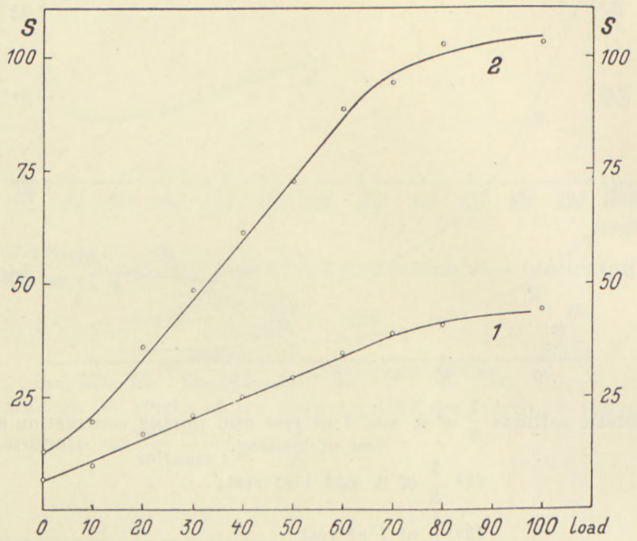


Fig. 48. Static stiffness of A and I at rest as a function of loading
(1) Stiffness of the A substance;
(2) stiffness of the I substance;
abscissa = loading in relative units;
ordinate = stiffness in relative units.

stance, the curve is linear between loads 0—70. This corresponds to the linear interdependence of loading and dynamic stiffness (Fig. 30). The structural interpretation of this course of the curve will be given in a later section.

Contracted fibre. The static softness of the single substances is known from length 100—140, corresponding to a load 60—70 and, further, at a load 0 (Fig. 47). At load 0, I is about twice as stiff as A, and the total stiffness is approximately the same as up to load 60. At load 60, the stiffness of A decreases suddenly (yielding) and then continuously, while the stiffness of I remains constant.

F. Elasticity moduli of A and I.

1) Elasticity moduli of A and I as a function of stretch.

Resting fibre. The moduli of A and I at rest are not markedly different referring to the same fibre length (Fig. 49). On an average, the elasticity modulus of the A substance is about 20 per cent

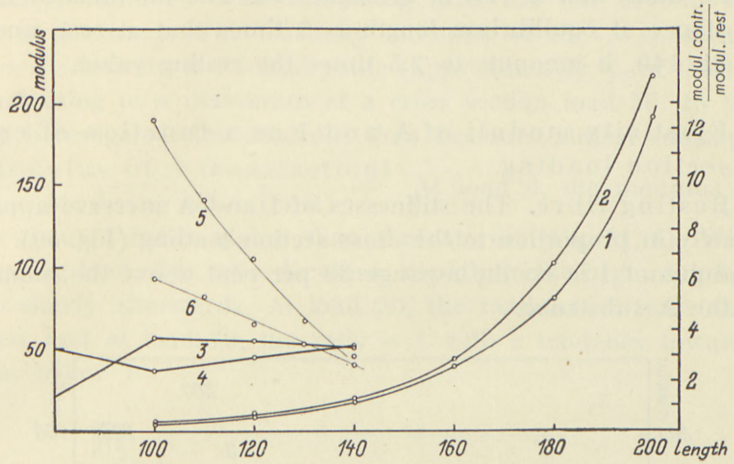


Fig. 49. Static elasticity modulus (*EM*) of A and I at rest and during contraction as a function of stretch.
(1) *EM* of the A substance at rest;
(2) *EM* of the I substance at rest;
(3) *EM* of the A substance during contraction;
(4) *EM* of the I substance during contraction;
(5) $\frac{\text{modulus A contraction}}{\text{modulus A rest}}$;
(6) $\frac{\text{static modulus I contraction}}{\text{static modulus I rest}}$;
abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left) static elasticity modulus in relative units;
(right) $\frac{\text{modulus contraction}}{\text{modulus rest}}$.

below that of I. The moduli increase uniformly with increasing length and at a length 200, they are about 35 times higher than at equilibrium length.

Contracted fibre. At equilibrium length, the elasticity modulus of A is about 50 per cent higher than that of I. The modulus of A decreases with increasing stretch while that of I increases, the moduli becoming equal at a length 140. In the range below the equilibrium length, the ratio $\frac{\text{modulus A}}{\text{modulus I}}$ is

reversed in analogy to the stiffness of the substances; the modulus of the I substance is about 2.5 times that of A. Compared with those at rest, the moduli of both substances are considerably higher (Fig. 49, 5, 6). At equilibrium length, the modulus of the A substance is thus 14 times higher than when at rest, decreasing to 2.5 times that at rest at a length 140. The modulus of the I substance at equilibrium length is 6 times that at rest, and at length 140, it amounts to 2.5 times the resting value.

2) Elasticity moduli of A and I as a function of cross section loading.

Resting fibre. The stiffnesses of I and A increase approximately in proportion to the cross section loading (Fig. 50). The modulus of I is on the average 30 per cent above the modulus of the A substance.

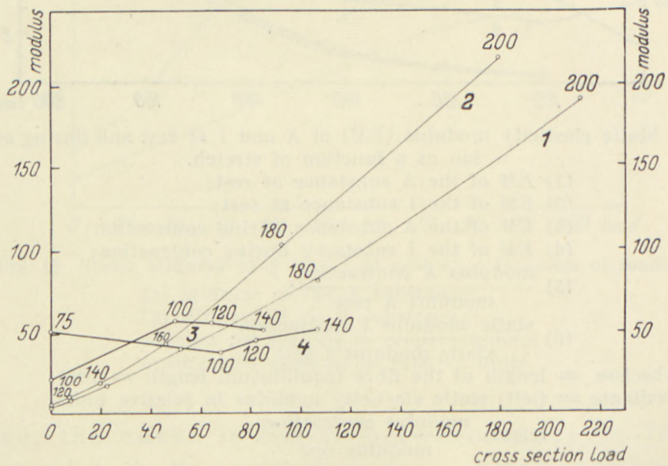


Fig. 50. Static elasticity modulus of A and I at rest and during contraction as a function of cross section loading.
(1) *EM* of the A substance at rest;
(2) *EM* of the I substance at rest;
(3) *EM* of the A substance during contraction;
(4) *EM* of the I substance during contraction.
The figures on the curve denote the length of the fibre at the respective load.
abscissa = cross section load in relative units (load 100 = cross section load 200 = mean length 200);
ordinate = elasticity modulus in relative units.

Contracted fibre. When studying the elasticity moduli at rest and during contraction, the modulus

as a function of the cross section loading represents an elasticity constant which is best suited for comparison.

The modulus of the I substance does not vary considerably and at the load 0, it is 2.5 times above the modulus of A. The variations observed with increasing load are not beyond the limit of accuracy. The elasticity modulus of the A substance shows a relatively low initial value (approximately $^1/_3$ of that of I) increasing to a maximum at a cross section load 50. In the range investigated, the modulus then becomes almost constant.

$\frac{\text{Modulus of A (contraction)}}{\text{Modulus of A (rest)}}$. At load 0, the modulus of A is about 5 times higher than that at rest (Fig. 51, 1). With increasing load, this ratio decreases rapidly in the beginning and more slowly afterwards. At load 30, the modulus is twice that at rest and at load 70, the ratio is 1 with a tendency towards values below 1.

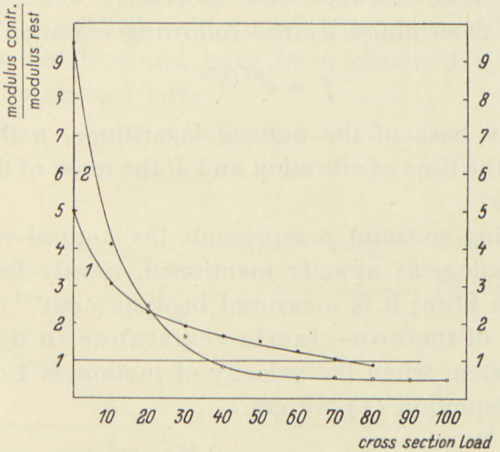


Fig. 51. $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$ as a function of cross section load.

(1) $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$ of the A substance;

(2) $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$ of the I substance;

abscissa = cross section load in relative units;

ordinate = $\frac{\text{modulus contraction}}{\text{modulus rest}}$.

$\frac{\text{Modulus of I (contraction)}}{\text{Modulus of I (rest)}}$. At load 0 (Fig. 51, 2), the ratio is 10, decreasing rapidly with increasing load. At load 35, the ratio is 1, and at load 60—100, the ratio is 0.5.

Determination of the damping constant (viscosity) of the single muscle fibre.

A preceding section (p. 67) dealt with vibration experiments in which the dynamic stiffness was determined from a change in the period of vibration. The same experiments served, further, for the measurement of the vibration amplitude which was found to decrease exponentially with time. Hence, we are here concerned with periodic, damped oscillations. The decrease in vibration energy originates mainly from the muscle fibre itself and is an expression of its viscosity. In a vibrating system, the damping rate, i. e. the ratio between two successive deflections to the same side, is determined by the following equation

$$f = e^{pT/2M} \tag{1}$$

where e is the base of the natural logarithms, p the damping constant, T is the time of vibration and M the mass of the vibrating system in gms.

The damping constant p represents the natural resistance to motion originating, as already mentioned, mostly from internal friction in the fibre; it is measured in dyne $\times$ cm^{-1} $\times$ sec and is an expression of the non-elastic resistance in dynes which retards the system when the velocity of motion is 1 cm per sec.

From the equation (1) we get

$$p = \ln f \frac{2M}{T}. \tag{2}$$

p is independent of the absolute amplitude values of vibration, but depends on the ratio of successive amplitudes and is, thus, proportional to the natural logarithm of this ratio (the logarithmic decrement) and inversely proportional to the period of vibration.

In the previously mentioned vibration experiments, the period of vibration and the single amplitudes were measured. The

amplitudes were plotted as ordinates in a semi-logarithmic coordinate system, the period of vibration being represented as a constant distance on the abscissa. The gradient of these curves is then proportional to the logarithmic decrement. The expression (2) can therefore be written as follows

$$p = \frac{\tan \alpha}{\tan \alpha_e} \times \frac{2\,M}{T} \qquad (3)$$

where tan α is the gradient of the curve between the values of the amplitudes and tan α_e the slope of a line corresponding to the damping rate e. The logarithmic graph of the individual deflections indicates that the damping at rest and during contraction is an exponential function. The value of p found in the single experiments expresses the total damping. In order to find the damping of the fibre, that of the measuring system itself must be subtracted.

Fig. 52 exhibits an example of the course of the amplitude of the vibrating system without muscle fibre (a), of the system + muscle fibre at rest (b), and during contraction (c) and, finally, the gradient which would have been obtained if the damping rate were e (nat. log.) (d).

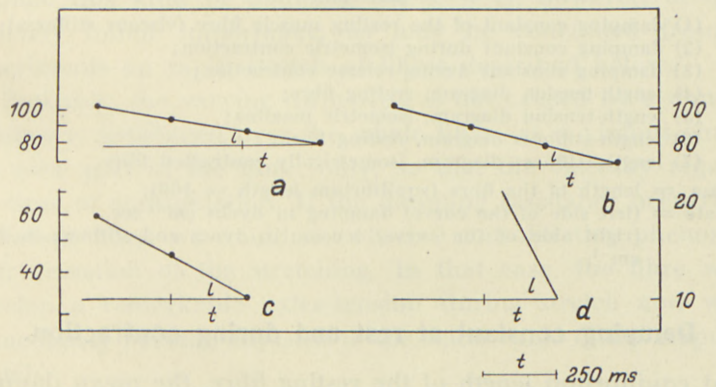


Fig. 52. Amplitude of damped oscillation of
(a) vibrating system without muscle fibre;
(b) vibrating system with muscle fibre at rest;
(c) vibrating system with muscle fibre during isometric contraction;
(d) gradient of $f = e$.
The difference in tan α of curves (b) and (c) is a direct expression of the increase in damping during isometric contraction.
abscissa = time, t = 250 msec;
ordinate = log of successive amplitudes.

All damping constants available from curves of this kind are represented in Fig. 53 as a function of stretch. Besides the damping constant at rest and during contraction, the length-tension diagram is plotted in the same figure.

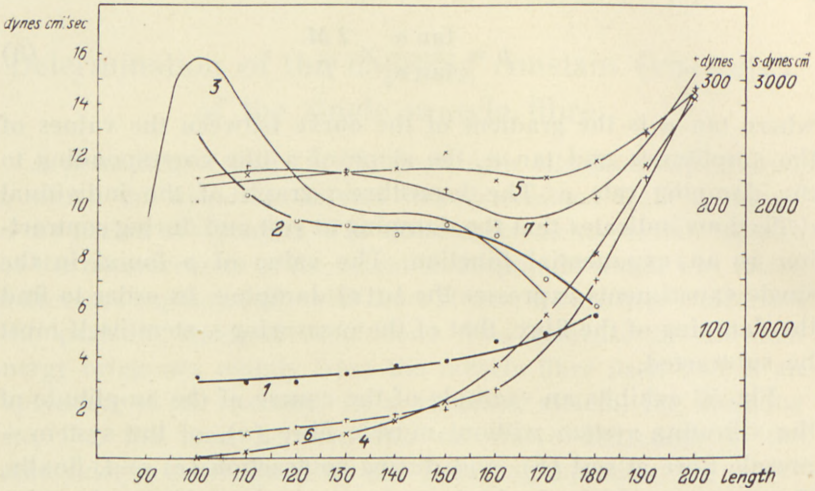


Fig. 53. Mean curve of the damping constant at rest and during contraction as a function of stretch; length-tension and length-stiffness diagrams of the same material.

(1) damping constant of the resting muscle fibre (viscous stiffness);
(2) damping constant during isometric contraction;
(3) damping constant during release contraction;
(4) length-tension diagram, resting fibre;
(5) length-tension diagram, isometric maxima;
(6) length-stiffness diagram, resting fibre;
(7) length-stiffness diagram, isometrically contracted fibre.

abscissa = length of the fibre (equilibrium length = 100);
ordinate = (left side of the curve) damping in dynes cm^{-1} sec.
(right side of the curve) tension in dynes and stiffness in dynes cm^{-1}.

Damping constant at rest and during contraction.

At equilibrium length of the resting fibre, the mean damping is 3 dynes cm^{-1} sec, increasing with augmented stretch to about 6 dynes cm^{-1} sec at a length 180.

During isometric contraction, the damping increases at equilibrium length up to 4 times the initial value, and decreases then with increasing stretch approximating the damping at rest. The curve of the damping constant of release contraction does

not differ considerably from the curve of the isometric contraction. At lengths below 100, lower dampings are found than at equilibrium length.

The increased damping during contraction is due partly to the "contractile changes" and partly to tension. In the case of release contractions, the tension in this state can be compared with that at rest. In spite of an identical tension at rest and during contraction, a contraction damping is found, which is 3 times as high as the damping at rest. For isometric contraction, this comparison cannot be made with the material available, as we do not know the damping of the resting fibre at tensions similar to those developed during isometric contraction.

On total muscle, GASSER and HILL (1924) found an increase of damping during contraction of about 16 times that at rest, while the difference found on single fibres amounts to 4—5 times that at rest. The difference measured by GASSER and HILL must be mainly ascribed to the friction between fibres, caused by their different states of contraction and stretch.

GASSER and HILL explain the main part of this difference in "viscosity" between rest and contraction by a transport of fluid. Though this kind of damping exists, it is, however, of quantitatively minor importance, as may be concluded from the experiments on rapid stretch of fibres described below.

Probably, the varying damping is not caused by a damping resistance distributed over the whole fibre—as a viscous shunt—but over part of the fibre, only, so that the viscosity regulates the time of consolidation. If the damping resistance occurred in the whole fibre, we would not observe consolidation phenomena after cessation of the stretching. In that case, the fibre would develop a remarkable extra-tension during stretch and would immediately become adjusted to the static value of the respective stretch.

In some experiments in which the vibration frequency was approximately 4 times higher than 5 cycles/sec (the frequency used in most experiments), the same fibre showed a damping considerably smaller than at lower frequency (Fig. 54). This frequency dependence indicates that the damping effect of the fibre on the vibrating system must be in series with the main part of the

elastic mass of the fibre. For a system with a damping in parallel, the damping constant would be independent of the vibration frequency.

Apart from the damping, the course of consolidation after a change of length or tension is an expression of the viscous properties of the fibre, and the first investigations of the magnitude of viscosity were thus based upon the study of elastic after-effects. v. KRIES (1880) found elastic after-effects both in the resting fibre and still more pronounced in the contracted muscle. BLIX (1892) made a precise investigation of the course of consolidation at rest and during contraction and he found that the viscous resistance cannot be distributed uniformly over the muscle substance. GASSER and HILL (1924), however, assumed the viscosity to be arranged as a shunt across the whole muscle and—in contradistinction to v. KRIES and BLIX, GASSER and HILL were not able to observe elastic after-effects in the resting muscle. LEVIN and WYMAN (1927) continued GASSER and HILL's experiments and they constructed a mechanical model in agreement with BLIX' interpretation. BOUCKAERT et al. (1930) obtained a purely exponential consolidation curve due to the technique applied which excluded the measurement of rapid variations.

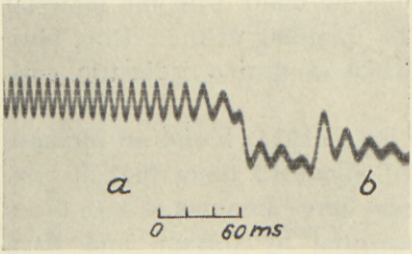


Fig. 54. Vibration experiment at higher frequency of oscillations (Isometric contraction).

At higher frequencies (*a*) in the range 12—6 cycles/sec, the damping is about 1/4 of the damping at 6 cycles (*b*) per sec. Time marks = 20 msec.

For the purpose of comparison between the elastic after-effects of single fibres and total muscle, the friction between the individual fibres diminishes the applicability of results obtained from total muscle.

Experiments with rapid stretches.

In order to study the viscosity of the single fibre at rest and during tetanic contraction, a series of experiments were carried out with instantaneous stretches of 1 mm or approximately

10—20 per cent at various elongations. The ratio between the decrease in tension during consolidation and the increase in tension at this sudden increase in length (elastic after-effect) was found to amount to 0,4 at rest at a length 100. This ratio increased to 0.5 at a length 180. During contraction, the elastic after-effect is 0.3 at equilibrium length, increasing to 0.6 at length 170. At further stretch, the contraction values approach the values found at rest. The variation in the elastic after-effects is complementary to the variation of the ratio $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$ (Fig. 43) which at rest amounts to approximately 0.5. During contraction, the ratio varies between 0.7—0.35 (length 100—160), i. e. an elastic after-effect of 0.3—0.65.

On total muscle, H. H. Weber (1941) found a very slight elastic after-effect at equilibrium length relative to the increase in tension, while the elastic after-effects at moderate and maximum loading corresponded to those measured in the present experiments. The disagreement in the case of the equilibrium length is presumably due to a coarse mechanical adjustment of individual fibres of the muscle, a process which is not accompanied by essential changes of the structure and, therefore, is of a purely elastic type. The elastic after-effect in the myosin thread (which is about 10 per cent higher than in a resting muscle fibre) corresponds better to the results on single fibres, since myosin threads do not show the great change of the after-effect between equilibrium length and moderate loading.

Measurements of the gradient at different points of the tension curve revealed that this curve represents the sum of at least 3 approximately exponential curves with rather different time constants. In the example exhibited in Fig. 55, the gradient is plotted as a function of time in a semi-logarithmic coordinate system. As a basis of calculation, the course of the curve was interpreted in the following way. After a sudden stretch, the tension increases instantaneously and then decreases rapidly, mainly according to the short time constant τ_1. This part of the curve is consolidated very soon, and the following part represents the course of consolidation corresponding to the time constant τ_2. When this region is practically consolidated, the last time constant τ_3 can be observed. Plotted in a logarithmic coordinate system,

a curve of uniform course is found consisting of three almost linear parts. Each of these regions corresponds mainly to the effective range of one time constant, and the magnitude of τ_1, τ_2, and τ_3 may be determined by the gradients of the different parts of the curve.

The lowest time constant τ_1 at rest and during contraction amounts to approximately 10 ms. The constant τ_2 is about 25 ms

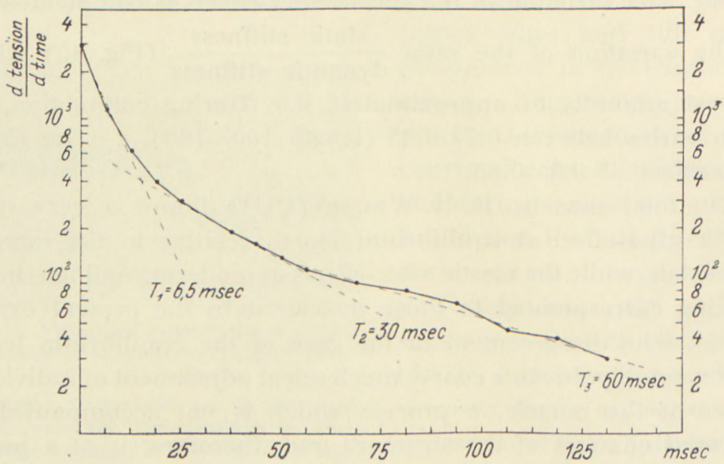


Fig. 55. Logarithm of the rate of change in tension after rapid stretch as a function of time.
abscissa = time in msec.
ordinate = $\log \frac{d \text{ tension}}{d \text{ time}}$.

at rest and 30—35 ms during contraction. τ_1 and τ_2 are independent of the extent of stretch. τ_3 varies with the stretch at rest, from 50 ms at length 100, to 100 ms at length 180. The variation of τ_3 during contraction is less marked with increasing elongation than at rest.

On total muscle, GASSER and HILL (1924) found the time constant of the tension development after release of the contracted muscle to be 150 ms. According to GASSER and HILL, this time constant is very similar to that of the tension development during isometric contraction. Our observations (cf. p. 26) indicate that this is not the case when dealing with single fibres. The development of tension after release occurs considerably more slowly (time constant 200—250 ms) than that during isometric contraction (time constant 50 ms).

At rapid stretching of the contracted fibre, we could only observe a course of tension corresponding to type B of GASSER and HILL's experiments (p. 412, Fig. 9). One might assume that curves of the type D appear after a mechanical stimulation of the muscle during rapid stretching.

BOUCKAERT et al. (1930) found a time constant of 150 ms at rest after rapid stretch, while we find $\tau_3 = 50$ ms. This difference may be due to the lower temperature applied (0°) or to fibre displacements in the total muscle.

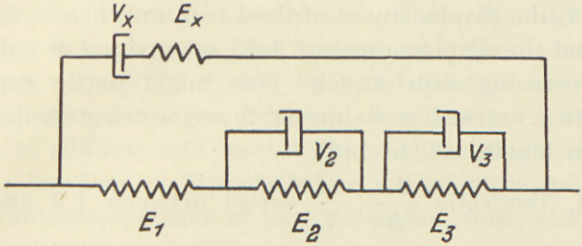


Fig. 56. Equivalent circuit of elasticities (E) and viscosities (V). Explanation see text p. 105.

When testing various combinations of damping and elasticity, the system given in Fig. 56 was derived from all observations available. This system seems to be the best equivalent of the elastic and viscous properties of the fibre, as represented by the three measured time constants.

The mathematical evaluation of elasticity and viscosity was carried out in analogy to the usual treatment of resistance and capacity, respectively, in complex electric systems. The magnitude of the single elasticities of the fibre were obtained by determining the extra-tension due to stretch (difference between initial tension and consolidation tension) in the beginning of the respective parts of the curve. In this way, E_2 and E_3 were found to be equal, while the corresponding viscosities were markedly different (one of them being about 5—10 times greater than the other).

The damping corresponding to τ_1 which is determined from the stiffnesses E_1 and E_2 and the viscosity V_2 is not noticeable in our dynamic experiments, as the vibrations occur so slowly that the fibre is continuously able to consolidate. The system E_2V_2 must be regarded as purely elastic at 5 cycles.

A small part of the increase in the damping constant during

contraction is presumably caused by the exchange of fluid between the different parts of the compartment which are not stretched and released equally (in per cent) during the vibrating loading. If the change in per cent of A and I was the same during a change of length, no displacement of fluid would be necessary. The maximum displacement of fluid between A and I takes place during contraction. Here, the ratio $\frac{\Delta A}{A} : \frac{\Delta I}{I}$ varies between 0.45 and 0.8 at lengths of 100 and 140, respectively. At a ratio 1, the displacement of fluid is 0 and, hence, the results indicate that the displacement of fluid is maximal at equilibrium length, decreasing with stretch. This might partly explain the decrease in contraction damping found during stretch of the fibre (from length 100 to 140).

At rest, the ratio $\frac{\Delta A}{A} : \frac{\Delta I}{I}$ varies between 1.2 and 1.3 at equilibrium length and length 160, respectively. This means that the transport of fluid increases only slightly with the extent of stretch.

The resistance due to fluid displacement between A and I might be placed as a complex shunt across the fibre, consisting of a viscosity V_x and an elasticity E_x in series. These components must be assumed to determine the time constant τ_2. The total stiffness of this shunt is zero if the stiffness of one component becomes zero. E_x depends on the disproportion of the elasticity moduli of the A and I substance. During contraction, E_x amounts to about 10 per cent of the total stiffness of the fibre substance, decreasing with the extent of stretch. At rest, E_x is about 4 per cent of the fibre stiffness. This means that E_x can only be noticed during contraction at equilibrium length.

The time constant τ_3 which is determined by the elasticities E_1, E_2, E_3, and the viscosity V_3 introduces the maximum damping at such frequencies as employed in the present investigations. If τ_3 was 40 ms, we would get the same stiffness in the viscous and the elastic components at vibrations of 5 cycles, i. e. the highest possible damping. If τ_3 is more or less than 40 ms, a smaller damping would be obtained: in the first case, because the main part of the deformation is elastic, in the second case, because the viscosity is reduced.

The damping might be expected to become less at a higher stretch due to an increase of τ_3. However, the total stiffness of the fibre increases, and therefore the damping fails to decrease. This phenomenon presumably explains the rather small increase in total damping of the resting fibre during extension (cf. Fig. 53, 1).

The time constant τ_3 is also essentially determining the course of the damping curve during contraction. In the range of stretch investigated, the stiffness is almost constant and the deviation of τ_3 from the optimum value must be ascribed to the observed damping reduction at a higher stretch. The rather steep increase in damping during contraction around equilibrium length, however, is not caused by τ_3 but by τ_2 (displacement of fluid).

The equivalent system described does not yet permit a distribution of stiffness and viscosity among the single elements of the fibre; however, it represents the most simple model of the observed interdependence of length, tension, time, elasticity, and viscosity. Hence, the difference between static, semi-dynamic, and dynamic stiffness is caused by a different damping in the fibre substances.

The elastic properties of the fibre in relation to its submicroscopic structure.

The present section attempts to correlate results from investigations of the elastic properties of the fibre with its minute structure.

The main points of these results were as follows.

Resting fibre. The elasticity moduli of the A and I substances are only slightly different. The stiffness-loading diagram shows a constant level in the beginning, followed by a linear increase after a short region of transition.

Contracted fibre. The length-tension diagram of the contracted fibre cannot be interpreted as a single reversible curve but as a system of curves the single components of which can be regarded as originating from the isometric maximum and directed towards the tension zero (reached by release contraction). The single curves, however, may be considered reversible. The course of the curve indicates an "elastic locking" at the maximum of the isometric, tetanic contraction at the respective fibre length.

On account of the "locking", the fibre remains at a greater length during release than during isometric contraction producing the same tension. The locking is mainly located in the A substance.

During contraction, the fibres yield at a given tension (on the average the tension which corresponds to the extra-tension at equilibrium length). Before the occurrence of a yielding, the fibre is considerably stiffer during contraction than at rest; after the yielding, the fibre becomes softer, sometimes markedly softer than when at rest at the same loading. At further stretch, the stiffness increases again, approaching the values of the stiffness at rest at maximum stretch.

The "locking" which appears at the maximum of the isometric contraction is not an absolute locking. Release of a fibre which has been stretched above the point of yielding reveals a new locking at a greater length. This displacement of the locking, which is caused by a new small yielding as soon as a given tension is reached, is indicated in the length-tension diagram by a reduced increase in tension.

The modern conception of the minute structure of a muscle fibre is based upon investigations and theories by K. H. Meyer (1929), H. H. Weber (1934), and Astbury (1936). Chains of proteins are assumed to be the active elements. As first pointed out by K. H. Meyer, these chain-molecules can be brought into contraction and out of contraction by chemical changes of the surrounding medium. Although Engelmann (1875), Hermann (1879), and v. Kries (1880) already suggested that molecular changes of the contractile substance occurred during contraction, K. H. Meyer's theory is the basis of further discussions and of our present picture of the minute structure of muscle.

The investigations of the X-ray pattern, the birefringence, and the thermo-elastic properties of the fibre form the fundament of the theory of the submicroscopic structure.

As regards K. H. Meyer's and Astbury's X-ray diagrams of the muscle, it must be emphasized that most of them are performed on dead muscles. Apart from that, they do not permit a closer analysis of the type of linkages, and until now they cannot reveal more than do birefringence measurements, viz. the presence of a certain moderate molecular orientation in the muscle. Further-

more, it seems doubtful whether it is admissible from diagrams of smooth muscles to draw general conclusions applicable to the structure of cross-striated muscle.

The existence of movable chain-molecules was made probable by thermo-elastic experiments carried out by Wöhlisch (1931) and by Meyer and Picken (1937). In a resting muscle, these authors found a negative temperature coefficient at a length 100—130, which indicates an increased orientation of structural elements at stretchings within this range. Part of this negative temperature coefficient may, however, be ascribed to a micellar structure, the orientation of which occurs just at lengths 100—130.

In some essential points, however, K. H. Meyer's interpretation (1940) of the viscous properties is not in agreement with our experimental observations on single fibres.

In analogy to the structure of rubber, the molecules of the fibre substance are assumed to be arranged as a framework with freely movable chains. The framework itself represents the true elastic resistance, and the freely movable chains are thought to slide over one another and form the viscous resistance. At a high stretch, the free chains slide away from each other and, thus, come in a certain state of disorder. This state should be noticeable in birefringence[1] measurements which, however, do not show any decrease until the fibre is stretched so violently that its cross-striation is disintegrated (Buchthal and Knappeis 1938). According to K. H. Meyer's model, we must assume that the dynamic stiffness corresponds to the total stiffness of framework and chains, while the static stiffness is that of the framework, only. In the resting muscle, the ratio $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$ is independent of the extent of stretch and reaches a value considerably below 1 (Fig. 43).

If K. H. Meyer's conception of the framework and the free chains were correct, we should expect a better agreement between static and dynamic stiffness at higher stretchings, since then exclusively the structure of the frame would be involved. Further, we should expect that the viscosity decreases with increasing stretch, as the surface of contact between the free chains is reduced. However, experiments proved that the viscosity increases with

[1] Due to the mutual fibre displacement, changes in birefringence found on total muscle cannot serve as a proof.

increasing stretch, although not quite proportional to the tension developed.

On the basis of his own and ASTBURY's investigations, H. H. WEBER (1934) considered the myosin threads to be the main components of the contractile substance, and he suggested a "zig-zag" molecular structure similar to that discussed by the author in Fig. 57. The forces between the single arms of the molecules should be mass attraction forces. In agreement with SULZER (1930), WEBER assumed two different lengths at which the molecules can develop the same tension and, further, that they can be brought from one length to the other by thermal forces.

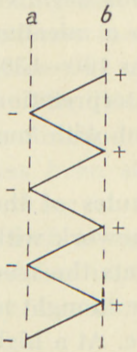


Fig. 57. "Zig-zag" molecule with two series of charges (*a* and *b*).

In this way, it should be possible to explain the viscosity and the irreversible behaviour of the myosin threads. However, it seems difficult to understand that a molecule of this kind—i. e. without electrostatic forces and with pure mass forces, only—shows so strong connective forces that the repulsive effects due to thermal movement are counteracted and that a state of disorder can be avoided. The assumption of electrostatic intermolecular forces is certainly necessary in order to maintain a state of the molecule as described by WEBER.

If we assume the presence of electrostatic forces in a molecule of this type with two series of charges, and furthermore, a mobility of the chain elements, then its elements must necessarily be unstable and will straighten out or possibly carry out a helical movement turning into a space system which consists of an odd number of charge series (cf. p. 113).

WÖHLISCH (1940) made an attempt to symbolize the change in the mechanical properties of the fibre during contraction by a rather primitive spring model. The intramolecular forces are represented by a spring which is somewhat compressed at the equilibrium length of the model. A spring which is slightly extended at equilibrium length represents the normal muscle elasticity. When the first mentioned spring is removed, the model will contract, i. e. the contraction mechanism is symbolized in the removal by a simple extending force. As a support of this

view, WÖHLISCH used the length-tension diagram of the muscle at rest and during isometric contraction. At the point of indifference (where the extra-tension during contraction disappears), no extra-tension appears, since here the extended spring has its natural length. However, the length-tension diagram of the model (showing WEBER's paradox) is not in agreement with experimental observations on the single fibre. The contraction curve and the rest curve overlap from the point of indifference and they have no point of intersection, as claimed for the model, when the stiffness of the extented spring is eliminated. The greater stiffness during contraction at small loading of the fibre is, furthermore, incompatible with the spring model which, therefore, does not seem to be a suitable equivalent for the demonstration of the elementary differences between rest and contraction.

On the basis of their experiments on the electrostatic properties of the fibre, BUCHTHAL and LINDHARD (1939) assumed that the electrostatic energy present in the resting muscle is in equilibrium with the elastic forces. According to this theory, the electrostatic energy is transformed into mechanical energy during contraction. On the basis of this hypothesis and of the observations on the mechanical properties of the fibre as described in the preceding chapters, the author has made an attempt to find the simplest molecular structure which might agree with the observed properties.

In molecular systems which one might imagine as mechanical equivalents of the fibre, the following main forces should be present:

1) Central forces.

a) Electrostatic central forces originating from attraction between charges of opposite sign and from repulsion between charges of the same sign.

b) Central forces originating from mass attraction. These are insignificant in comparison with electrostatic central forces and, therefore, not considered in the calculations.

2) Angular forces between two neighbouring elements of the molecular chain due to the linkage structure located in the electron orbits.

3) Thermal forces in the form of attraction due to "curling"

caused by Brownian movements or as a kind of repulsion caused by collisions between neighbouring chains.

The influence of the respective forces on the equilibrium of the molecule will be discussed in the following.

All calculations were carried out in accordance with the rules of central forces in classical physics. When dealing with molecular magnitudes, the classical interpretation cannot quite satisfactorily describe the phenomena, and quantum mechanical considerations should be applied. Since, however, the present considerations are approximations, only, this omission will not be of essential influence upon the results.

1) Electrostatic central forces in the proposed molecular system.

The simplest type of a molecular chain, where the single elements of the molecule lie in the same plane, is represented in Fig. 57 ("zigzag" molecule). If the vertices of the angles carry alternately positive and negative charges, the same side of the molecules will show a charge of the same sign. The forces between neighbouring vertices must consequently be repulsive forces, giving rise to an orientation effect. Forces between a and b charges cause an attraction and, hence, a certain curling. The calculation of such forces in a system of this kind reveals that the repulsive forces at any stretch are greater than the attractive forces and, hence, this system will endeavour to straighten out as far as possible. While the internal forces of an almost straightened system are small and cause only a negligible deviation of the molecule out of its plane, a molecule with the type of charge distribution described cannot be in equilibrium as a plane system in a somewhat folded state. Neighbouring charges will repulse each other and thus turn the elements of the chain into a three-dimensional system, as shown in Fig. 58. Here, the neighbouring charges are of opposite sign, attracting each other and, therefore, the molecule must exhibit at least three series of charges (a_1, a_2, a_3, a_4, a_5; b_1—b_5; c_1—c_5).

In a molecular chain with four series of charges, the same instability will appear as in system 1, the system either turning into a system with five or with three series of charges. At five

series of charges, we shall again obtain stability against curling. The angular forces discussed on p. 114 determine the number of charge series.

Consequently, the simplest stable system is that with three charge series, and the following calculations are based upon this assumption.

For the calculation of the resulting effect of the electrostatic forces, we consider one single vertex of an angle and the corresponding point of charge a_1 (Fig. 58). This point is affected by all other charged points of the molecular system. We assume the effective charge of the individual points of the molecular system to be equal, but of alternating sign. The point a_1 is thus influenced by potentials originating from the charges of the b as well as the c series. For symmetry reasons, the forces—projected on the longitudinal axis of the fibre—are assumed to be equal in both directions and, therefore, we consider only the forces in one direction of the molecule. a_1 is attracted in a longitudinal direction by a_2, is repulsed by a_3, attracted by a_4 etc., with a force inversely proportional to the square of the distance. Simultaneously, a_1 is repulsed by the charges of c_1 and b_2. These forces do not operate parallel to the longitudinal axis of the fibre, but must be projected on the axis, whereby their components are reduced. The forces originating from b_4 and c_3, however, are attractive forces.

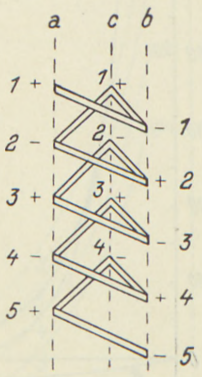


Fig. 58. Molecular chain with three series of charges (a, b, and c).

Vertical to the longitudinal axis of the molecule we find the effect of some forces, the resultant of which tends to increase the cross section of the molecule and thus causes a contracting effect.

A calculation of the resulting central forces in a longitudinal direction, which is based upon the rules of central forces brings out a length-tension dependence as follows: At the shortest lengths, the attractive forces are predominant, but they decrease rapidly during stretch; when the molecule is stretched to about

half the maximum length, these forces are practically negligible (Fig. 59, 1). In the present system—in contrast to the "zigzag" system—the electrostatic forces have a contracting effect.

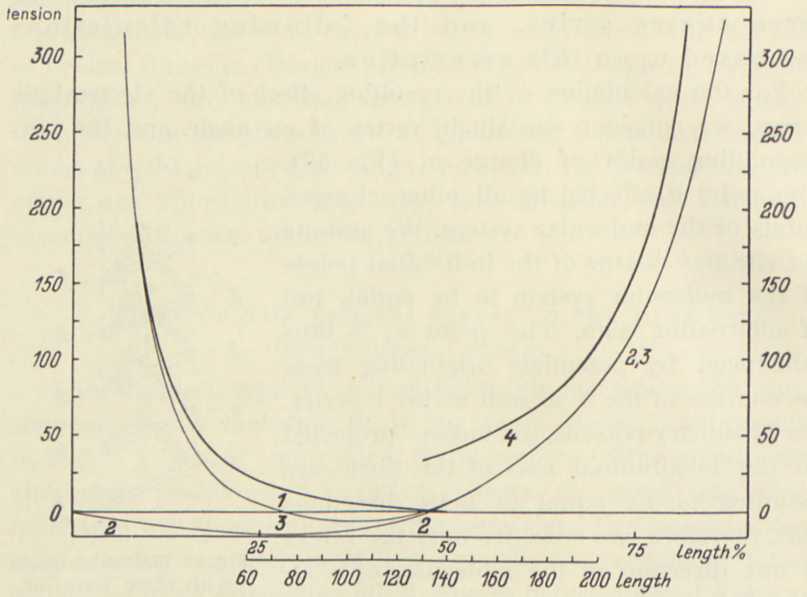


Fig. 59. Intramolecular attractive and repulsive forces as a function of the length of the molecule.

(1) resulting electrostatic central forces;
(2) elastic forces, originating from angular forces, natural angle 80°;
(3) length-tension diagram obtained by summation of curves (1) and (2);
(4) length-stiffness diagram of curve 3;
abscissa = (above) length in per cent of the maximum molecular length;
(below) length in relation to the muscle fibre, equilibrium length = 100;
on account of micellar adjustment, length 100 does not correspond to load 0;
ordinate = tension in relative units.

2) Angular forces.

The angular forces between neighbouring elements of the molecular chain acting on the lines of the angle have a contracting and extending effect, respectively, dependent on whether the angle is larger or smaller than the natural angle. As the natural angle we denote that which is exclusively determined by the atomic forces between two neighbouring arms. Fig. 60 exhibits the calculated relative course of tension corresponding to natural

angles between 60° and 90°. At an angle of 60°, the angular force in the completely contracted system is 0 and the contractive force increases with increasing length. At natural angles above 60°, the force is 0 in the beginning, attaining negative values, passing 0, and reaching positive, i. e. contracting values. Tension

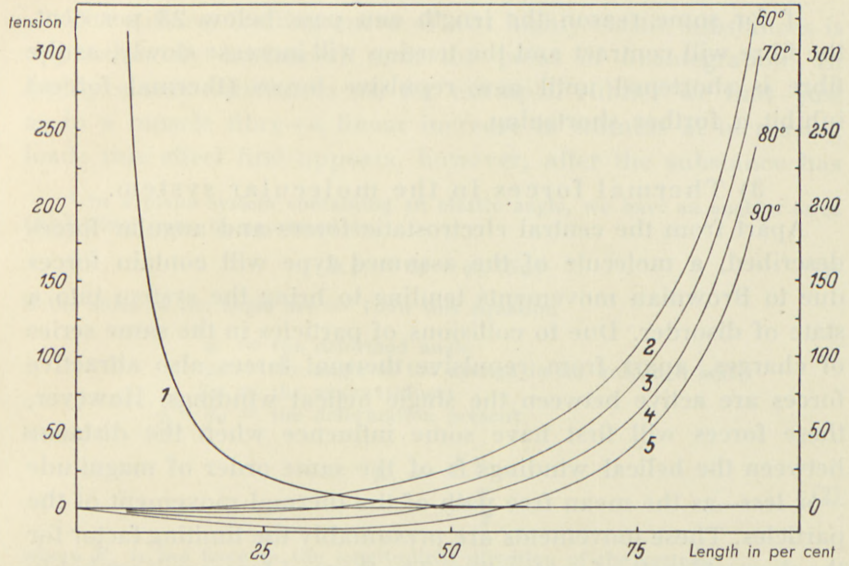


Fig. 60. Length-tension diagram of intramolecular forces of a system with three series of charges.
(1) electrostatic central forces;
(2) angular forces at a natural angle of 60°;
(3) angular forces at a natural angle of 70°;
(4) angular forces at a natural angle of 80°;
(5) angular forces at a natural angle of 90°;
abscissa = length in per cent of the maximum molecular length;
ordinate = tension in relative units.

0 is obtained at a length where the angle is equal to the natural angle. At an angle of 70°, this tension is reached at 33 per cent of the maximum length. At an angle of 90°, the tension 0 is obtained at 57 per cent of the maximum length.

Natural angles above 90° cannot exist in this system, since they would lead to a five-edge system.

Fig. 59, 2 shows the dependence of the elastic forces on the length at a natural angle of 80°.

Fig. 59, 3 shows a resulting length-tension curve of the central

electrostatic forces and of the angular forces with a natural angle of 80°. It is apparent that the forces are in an unstable equilibrium at a length 28 per cent of the maximum length, and in a stable equilibrium at 47 per cent of the maximum length. From length 47 per cent (stable equilibrium length), the tension increases with increasing stretch.

If for some reason the length can pass below 28 per cent, the fibre will contract and the tension will increase slowly, as the fibre is shortened until new repulsive forces (thermal forces) inhibit a further shortening.

3) Thermal forces in the molecular system.

Apart from the central electrostatic forces and angular forces described, a molecule of the assumed type will contain forces due to Brownian movements tending to bring the system into a state of disorder. Due to collisions of particles in the same series of charges, apart from repulsive thermal forces also attractive forces are active between the single helical windings. However, these forces will first have some influence when the distance between the helical windings is of the same order of magnitude —or less—as the mean free path of the thermal movement of the particles. These movements are presumably the limiting factor for the shortest length of contraction. The thermal forces will probably be of secondary influence on the single arms; but the linear tension-temperature dependence found in highly elastic substances indicates that the thermal movements are of great significance for the whole molecule or for molecule aggregates.

Stiffness-loading diagram of the resulting electrostatic and angular forces. From the slopes of the curves of Fig. 59, 3 a stiffness-loading diagram (Fig. 61) of the resulting electrostatic forces and angular forces $\left(\frac{\text{tension}}{\text{length}}\right.$ as a function of tension) was obtained. From the length 100 (stable equilibrium length) to the length 200 (corresponding to a length 130—200 of a muscle fibre) the stiffness-tension curves are linear. Their course thus corresponds to the stiffness-tension curve of the muscle fibre after the micellae being adjusted.

The variation of stiffness with loading indicates

that the fibre structure must include single elements between which angular movements occur[1].

Even if the above considerations on the mutual relation between the internal forces within the molecule are abstractions, the mentioned angular movement between elements of the minute structure is an experimental fact.

The stiffness-loading curve of not highly elastic substances is approximately horizontal until the point of disintegration. In highly elastic substances as, for example, rubber we find—just as in a muscle fibre—a linear increase in stiffness at increasing load; this effect first appears, however, after the substance has

[1] In a plane system containing an elastic angle, we have an angular force ($K\varphi$) which may be expressed as

$$K\varphi = (\varphi - \varphi_0)(S\varphi) \tag{1}$$

if the sides of the angle are = 1. In this equation

φ = the deformed angle
φ_0 = the angle of the system in an unloaded state
$S\varphi$ = the angle stiffness
$\varphi - \varphi_0$ = the deformation present.

Hence,

$$K_L = \frac{K\varphi}{\cos\frac{\varphi}{2}} \tag{2}$$

where K_L is the force in the longitudinal direction of the system.

$$L = 2\sin\frac{\varphi}{2} \tag{3}$$

where L is the length of the system in the direction of loading.

By differentiation of K_L and L with respect to φ we get

$$K'_L = \frac{K'\varphi}{\cos\frac{\varphi}{2}} + \left(\frac{1}{\cos\frac{\varphi}{2}}\right)' K\varphi \tag{4}$$

$$L' = \cos\frac{\varphi}{2}. \tag{5}$$

The required stiffness (S_L) in the longitudinal direction of the system becomes

$$S_L = \frac{\frac{dK_L}{d\varphi}}{\frac{dL}{d\varphi}} = \frac{K'_L}{L'} = S\varphi\left(\frac{1}{\cos^2\frac{\varphi}{2}} + \frac{\sin\frac{\varphi}{2}\times(\varphi-\varphi_0)}{2\cos^3\frac{\varphi}{2}}\right). \tag{6}$$

From the equations (2), (3), and (6) we find corresponding values of force, length, and stiffness, respectively; at natural angles from 30° to 90°, the length-tension and the stiffness-load dependence are of the same type as found in the resting muscle fibre.

been sufficiently orientated by elongation (Fig. 63). In the case of a muscle, we find the linear part of the curve already at slight stretch, thus indicating (in agreement with birefringence, diffraction pattern, etc.) that the substance is orientated in the state of equilibrium. In a series of experiments carried out with slightly vulcanized caoutchouc threads, using the same arrangement as employed for the investigations of the muscle fibre, a length-tension diagram was found (Fig. 62) corresponding to that known from the literature. The stiffness-loading diagram of rubber threads shows an approximately linear course after an elongation of about 400 per cent. The length-tension diagram is S-shaped and corresponds after a stretch of 400 per cent to the diagram of the resting muscle fibre.

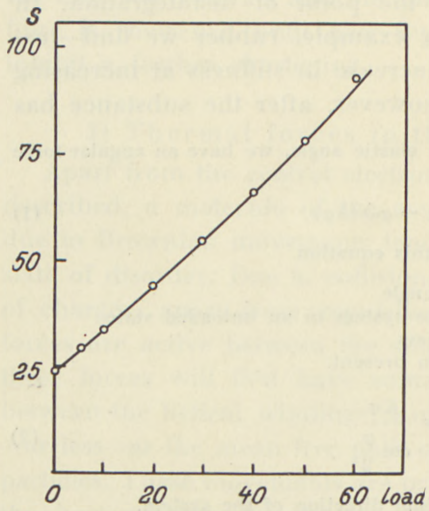


Fig. 61. Stiffness-load diagram of the length-tension diagram Fig. 59, curve 3. abscissa = load in relative units; ordinate = stiffness in relative units.

Assuming the described molecule equivalents (Fig. 58) which do not take into account the mutual effect of different molecules, the contraction might occur in the following way. By means of an external influence, the distance between a_1 and a_2 is reduced and, hence, the potential difference between a_1 and a_2 decreases, as their charges are constant; the capacity however, increases due to the changed distance. a_1 receives an increase of negative potential and a_2 an increase of positive potential. Part of this charge alteration is transferred to b_1 and b_2, respectively; the potential difference between these two points is therefore increased. Consequently, the attractive forces are augmented so much that also these two points approach each other. This process is followed by a similar one in the charge series c_1 and c_2, and the process is continued through the helix until the distance between the not yet contracted parts of the chain is so great that the forces arising are unable to continue the process. The chain will

then consist of contracted and non-contracted elements. If contraction is introduced at small length (tensionless), the whole chain will enter into contraction; if, however, contraction is introduced at greater length (under load), only part of the chain will participate in the contraction until the tension inhibits a further propagation of the process. Contractions from the greatest

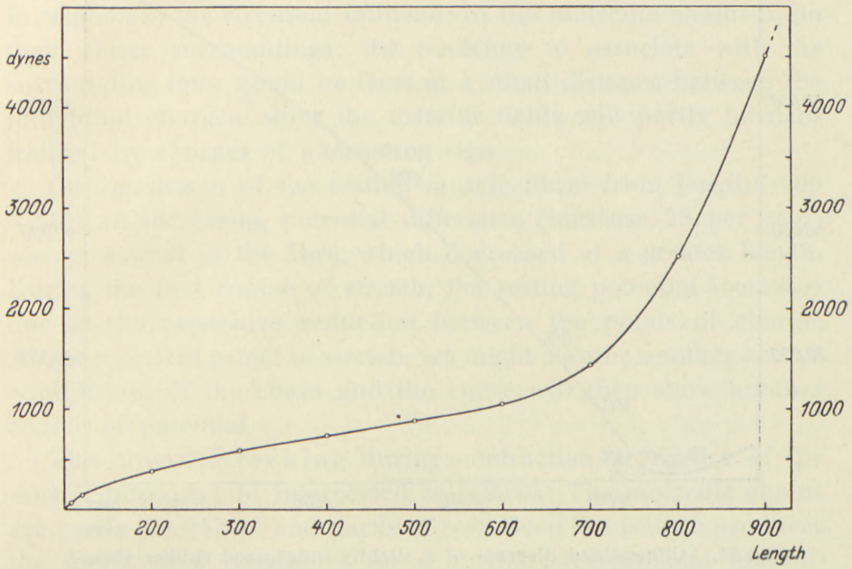


Fig. 62. Length-tension diagram of a slightly vulcanized rubber thread. abscissa = length (equilibrium length = 100); ordinate = load in dynes.

possible length cannot be brought about because the process cannot start. This picture corresponds to the length-tension diagram of the muscle fibre where the extra-tension decreases continuously with increasing stretch after the coarse micellar adjustment of the first part of the curve is finished. Maximum stretch of the contracted fibre produces generally somewhat higher tension than a stretch at rest followed by isometric contraction. In an already contracted molecule, the attractive forces play a greater part—due to smaller distances—than in the case of stimulation of a highly stretched molecule.

In the proposed system, a reduction of the distance between only two neighbouring particles of a chain suffices to produce

contraction. This reduced distance may be obtained in different ways: by addition or neutralization of a charge on one link of the chain by a mechanical, local deformation, or by a violent compression of the whole fibre (pressure contraction, Brown 1933 and 1936, Ebbecke and Hasenbring 1935). Furthermore,

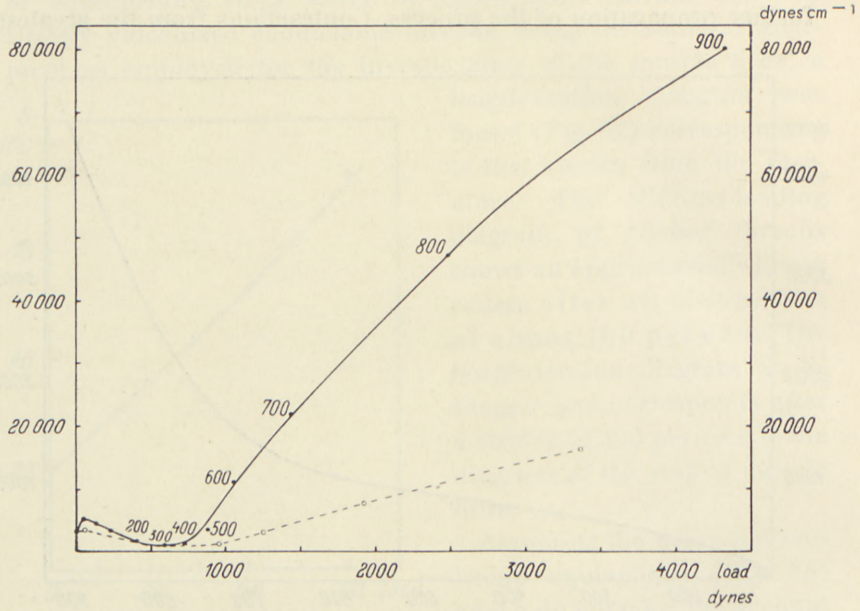


Fig. 63. Stiffness-load diagram of a slightly vulcanized rubber thread.
——●——● = dynamic stiffness;
———o———o = static stiffness.
The figures on the curve denote the length of the thread at the respective load.
abscissa = loading in dynes;
ordinate = stiffness in dynes cm^{-1}.

observations on thermo-elastic properties, where heating causes a shortening due to the increased thermal attractive forces, are in agreement with the given picture.

Yielding, as it appears after stretch of the contracted fibre, might be explained in the following way. We suppose the fibre to be stretched so much that, for example, half of the single molecule chain is contracted while the rest of the molecule chain is passively extended. If the tension of the molecule chain is increased by exterior forces beyond a given point, the forces in the contracted part of the chain are no longer able to maintain equilibrium with the exterior forces and, thus, the links of the

molecules will become straightened successively until the exterior forces are equal to the attracting forces of the contracted links.

When the stimulation ceases, we must necessarily assume the occurrence of neutralization or reduction of charges contracting the chain. These charges must be rebuilt in the period of rest. The increased conductivity during contraction might stand in relation to the electrical influence of the molecule chains upon their closer surroundings: the tendency to associate with the surrounding ions would be least at a small distance between the individual charges, since the exterior fields will partly be neutralized by charges of alternating sign.

During stretch of the resting muscle fibre[1] from lengths 100—140, an increasing potential difference (increase 28 per cent) was measured in the fibre, which decreased at a greater length. During the first course of stretch, the resting potential increases due to the capacitive reduction between the points of charge. Above a certain extent of stretch, we might assume another charge equilibrium of the chain and the curve will then show another course of potential.

The observed locking during contraction at release of the muscle fibre may be interpreted as follows: The molecule chains are partly contracted and partly at rest. Even if a release produces the mechanical possibility for a further development of contraction of the molecule chain, the locking indicates that this does not occur. We might assume that this effect originates in the charge distribution on the boundary between the contracted and the non-contracted parts of the molecule. Before propagation of the contraction wave over the molecule chain, an electric potential increase runs along the points of the charge series which causes the transition from rest to contraction; when the mechanical conditions for the further development of contraction are no longer present, the increase in potential will stop at the first, non-contracted link of the molecule chain. This link will presumably exchange one charge with its surroundings and thus obtain a decreased electric activity. If the mechanical tension of the molecule is reduced, the contraction wave will not continue due to lack of the electrostatic prerequisites,—the fibre is locked.

[1] Unpublished experiments.

Therefore, the fibre must be brought into a new state before the contraction wave is propagated along the fibre.

The properties of the molecule model mainly represent those of the anisotropic substance (increase in tension and stiffness due to contraction, and diminution of the equilibrium length). The resulting properties of the isotropic substance, which does not exhibit a noticeable change in equilibrium length under contraction, are not directly represented by the model. However, there is reason to suppose that the molecules in the I-substance are only slightly orientated compared with those of the A-substance (cf. the difference in birefringence). A parallel orientation of the molecules is the prerequisite for a deformation, i. e. a contraction of the micellae. An increase in tension in the individual molecules will therefore not lead to a noticeable deformation, but only to an increase in stiffness. The difference between the A and the I substance may thus be due to a difference in orientation of the same molecular structure.

The very simple form of the model, as described above, does not include elastic after-effects present in the muscle fibre at rest and during contraction. H. H. Weber (1934, 1941) explained the elastic after-effects in the myosin thread by assuming that the single link of the molecule chain can only exist either in a contracted or in a stretched state. A certain tension must be exceeded in order that a link is brought from a contracted into a straightened state, and this tension which must be available within a very short time, only, might originate from thermal collisions. If the chain is exposed to a tension just high enough to insure that the molecule can be in equilibrium in a partly unfolded state, but not so high that the molecule can be brought from a folded to a straightened state, Weber assumed that thermal collisions may produce the resulting tension necessary for the straightening out of the folded elements. If the probability of collision of one single folded element per time unit is the same for all elements, the number of straightened elements per time unit is porportional to the total number of folded elements which can be kept in an unfolded state by the exterior tension available. Hence, $\Delta L = l \times k$, where L is the length of the molecule, l is the length of the folded elements of the molecule, k is a proportionality factor determined

by the collision probability per time unit. $\frac{\Delta L}{\Delta t}$ must be an exponential function of time.

As previously mentioned, WEBER's molecule model cannot satisfy the requirements as revealed by the experimental results. In accordance with WEBER, we assume in the present model that the elastic after-effects must be ascribed to intramolecular linkages which are dependent on the extent of load ("crystallization", WÖHLISCH 1941, H. H. WEBER 1941). The transition from one type of linkage to another (it may be possible that there are two types of linkages, only) lasts some time, and this transition may depend upon ion reactions or purely mechanical, thermal collisions. The velocity with which the substance is transformed from one modification to another must be assumed to be determined by the three time constants previously discussed (cf. p. 103). If the mechanical changes occur very rapidly, the modification of the substance cannot follow, and we must measure a great (dynamic) stiffness with a relatively low damping. At moderate velocities, the stiffness will be reduced relative to that at rapid changes and the damping will play a larger part. In static experiments, the change of linkages is adjusted according to load, and here we find the lowest stiffness.

In this connection, it might be of interest to recall some experiments which indicate an increased chemical activity during stretch (EDDY and DOWNS 1921. In these experiments, care was taken to avoid stimulations during the experiment).

Rubber shows viscous properties similar to those of a muscle fibre, and it is not improbable that the assumption of loaddependent modifications of the linkages may be valid also for this substance. In a range of length, 200—300 (Fig. 63), the static and the dynamic stiffnesses of rubber are equal, showing a minimum value. At greater length, dynamic stiffness increases more markedly than static stiffness, the ratio being finally 4 : 1. In a range of length 200—300, no change of the linkages occurs—according to our assumption. In the following range of length, viz. 300—900, alterations of the linkages appear which are dependent upon stretch. X-ray diagrams[1] of the rubber thread, the length-tension diagram of which is exhibited in Fig. 62, show rather

[1] The X-ray diagrams were taken by Dr. R. W. ASMUSSEN, Chemical Department A, Royal Technical Institute, Copenhagen.

sudden modifications at length 500 and at length 700—800, respectively, thus indicating a change of orientation in this range.

The author wishes to express his gratitude to Mr. E. KAISER, Engineer, for valuable advice as regards the mathematical treatment and the interpretation of the material, and to Mr. G. G. KNAPPEIS for assistance in numerous experiments and the measurements of microphotographs. Furthermore, my thanks are due to Professor EM. HANSEN and Professor J. LINDHARD for stimulating suggestions concerning the elaboration of the manuscript and to Professor A. LANGSETH for the helpful discussion for the problem of molecular structure.

The present work has been supported by grants from the Michaelsen Fond, the Rask-Ørsted Fond, and the Insulin Fond.

List of definitions and abbreviations.

A substance	anisotropic substance of the cross-striated muscle fibre.
I substance	isotropic substance of the cross-striated muscle fibre.
Equilibrium length	the length at which the fibre just begins to develop tension when it is stretched. In all experiments, the length is given in relative units and the equilibrium length of the resting fibre is put = 100.
Indifference point	denotes an extension, at which the tension developed during isometric contraction just becomes zero and corresponds in the majority of the experiments to twice the equilibrium length = length 200.
Load (= total tension)	in the individual experiments measured in dynes. For comparative purposes, the load at the indifference point is put = 100.
Cross section load	load in relation to a unit cross section, $\frac{\text{load}}{\text{cross section}}$; at length 100 the cross section is put = 1.
Extra-tension	tension increase due to contraction (total tension of the contracted fibre minus tension of the resting fibre at the same length).
Isometric maximum	resting tension + extra tension (= total tension) during isometric tetanic contraction under maximal stimulation.
Static length-tension diagram	tension as a function of elongation (stretch). The tension values are measured after complete consolidation, i. e. the elastic after-effects have ceased.

Consolidation	transition to static tension after a variation in length or tension of the fibre.
Semi-dynamic length-tension diagram	simultaneous registration of tension with the variations of length. Duration of stretch 10—1 sec.
Release contraction	the isometrically contracted fibre is allowed to shorten during continuous stimulation, and the new length and tension are registered after consolidation. In a number of experiments, the fibre was released to the same tension as when at rest before stimulation. In semi-dynamic length-tension experiments, relaxation, in contrast to release denotes the decrease in length resp. tension of the resting fibre.
Partial length-tension diagram	corresponding values of length and consolidated tension, when the fibre is released from the isometric maximum.
Elastic "locking"	a conception introduced to explain the fact that the partial length-tension diagrams of the contracted fibre do not coincide with the curve of isometric maxima, but represent a system of parallel curves running downwards from all points of the curve of isometric maxima. The fibre must be regarded as "locked" to one of these partial diagrams as long as the stimulation continues and the fibre is not stretched above the resp. length in isometric contractions.
Yielding	characterized by a reduction of steepness in the curve of the isometric maxima, and by the critical decrease in stiffness when the yielding tension is reached. By definition yielding is an increase in equilibrium length of the contracted fibre, which is irreversible during contraction, and due to the fibre tension.
Early yielding fibres	fibres with the critical point of yielding at tensions below the equilibrium length at rest.
Late yielding fibres	fibres with the critical point of yielding at tensions above the equilibrium length.
Stiffness (S)	ratio between corresponding increases in tension and length. $\frac{\Delta \text{ tension}}{\Delta \text{ length}}$ is measured in dynes cm^{-1}, and is always expressed in arbitrary units. When characterizing the elastic pro-

perties of orientated anisotropic substances which display considerable changes in cross section during length alterations, stiffness is preferred to the elasticity modulus.

Static stiffness — consolidated values of $\frac{\Delta \text{ tension}}{\Delta \text{ length}}$ derived from static length-tension diagrams.

Dynamic stiffness — $\frac{\Delta \text{ tension}}{\Delta \text{ length}}$ as a rule determined by periodic length alterations of the fibre.

Softness — $\frac{1}{\text{stiffness in dynes cm}^{-1}}$; when two or more elastic bodies are connected in series, the total softness = the sum of the individual softnesses; when two or more elastic bodies are connected in parallel, the total stiffness = the sum of the individual stiffnesses.

Elasticity modulus — the force necessary to increase the length of a wire with a cross section of 1 cm^2 to twice its length.

elasticity modulus

$$= \frac{\text{stiffness}}{\text{cross section}} \text{ length}$$

$$= \text{stiffness of a 1 cm cube in dynes cm}^{-2}.$$

Viscosity — internal friction in the fibre measured as the decrease in vibration energy:

$$\frac{\text{friction force}}{\text{velocity of length alteration}}.$$

Damping constant (p) — expression for the non-elastic resistance in dynes which retards an oscillating system when the velocity of motion = 1 cm per sec; dimension: dyne cm^{-1} sec.

Elastic after-effect — ratio between the decrease in tension during consolidation and the increase in tension due to instantaneous stretch.

Bouckaert et al. (1930) express the elastic after-effects as $\frac{\text{viscous extension}}{\text{total extension}}$, Weber (1941) as $\frac{\text{instantaneous length increase}}{\text{viscous length increase}}$ due to a sudden loading; in Weber's definition,

	the coefficient becomes ∞ when the elastic after-effect = 0.
Time constant (τ)	the time necessary to diminish the difference between the instantaneous value (the tension after stretch) and the consolidated value to $\frac{1}{e}$ (e = base of the nat. log.) of the initial difference. The time constant is inversely proportional to the consolidation velocity.

Summary.

(Cf. list of definitions p. 125.)

A new type of myograph is described for the recording of tension developed by a single muscle fibre. The tension arising by stretch or contraction displaces one movable plate of a condenser. The change in capacity is registered by means of a high frequency circuit, an amplifier, and an oscillograph. The same arrangement is employed for measurements of the dynamic stiffness in vibration experiments.

Length-tension diagrams of the single muscle fibre are registered under different conditions.

The tension developed by the resting fibre increases slowly with increasing stretch and then rapidly after an increase in length of 20—30 per cent. The smaller initial gradient of the length-tension diagram is due to a length orientation of micellar elements.

The tension of the isometric maxima (tetanic contraction) increases with increasing length, and the extra-tension (difference between contraction-tension and rest-tension) is constant up to 40 per cent of stretch. With further stretch, the extra-tension developed during contraction decreases, so that the rest curve and the contraction curve overlap at 60—100 per cent of stretch. The decrease in extra-tension originates from a reduced contractility, partly due to the decreasing stiffness of the I-substance during contraction at a higher stretch.

During extension of the isometrically contracted fibre —in contrast to observations on total muscle—we cannot find any deviations from the curve of the isometric maxima up to elongations of 50—60 per cent. At higher extent of stretch, the extra-tension developed during contraction does not decrease to zero. A structural interpretation of the difference in the behaviour of

the extra-tension during stretch of the isometrically contracted fibre, and during isometric contraction of a fibre stretched at rest, is suggested in connection with the description of a molecule model.

Special regard is paid to length-tension diagrams in which fibres at rest and during contraction are compared under the same exterior mechanical conditions (tension). Release of the isometrically contracted fibre to the same tension as when at rest leads to considerably lower values of length and tension than indicated by the corresponding points on the curve of isometric maxima—in spite of a complete consolidation after release. This difference may be explained by an "elastic locking" of the fibre at the maximum of the isometric contraction. Hence, the curve of isometric maxima is irreversible, and every point of the isometric length-tension diagram represents the starting point of a partial diagram which connects the respective isometric point with the corresponding point of the release diagram.

The length - mean tension diagram of single contractions indicates the main increase in tension at a frequency between 10 and 20 stimulations per sec. At 8 stimulations per sec, the mean extra-tension is about $^1/_5$ of the tension during complete tetanic contraction (frequency 30 stimulations/sec; temperature 18° C). Even in long-lasting experiments, a contraction remainder does not appear as long as the stimulation frequency is below 5 per sec.

The duration of the development of tension in single contractions is only slightly influenced by stretching as long as the fibre is not fatigued.

In semi-dynamic length-tension diagrams, where the time of stretching varies between 10 and 1 sec, length and tension are registered simultaneously. The difference between the static and the semi-dynamic length-tension diagram of the resting fibre is exclusively due to the viscosity of the fibre. During contraction, the difference—apart from viscosity—is due to yielding (irreversible length alteration) and to elastic locking. Increasing stretch causes in the contracted fibre a steeper ascent in the beginning of the curve. At further stretch, the gradient decreases due to the yielding which is irreversible during contraction. Increasing release during contraction of the stretched

fibre leads to considerably lower tensions than stretching of the contracted fibre (elastic locking). As long as the initial extent of stretch is not exceeded, stretch and release during contraction produce the same tension at the same respective lengths and, hence,—apart from viscosity—the curve is reversible.

Work diagrams are recorded with a technique similar to that applied to the registration of semi-dynamic length-tension diagrams. The fibre is extended at rest about 50 per cent, then stimulated tetanically, and released during contraction. The net work obtained is equal to the area of the length-tension diagram during release contraction minus the area of the length-tension diagram of the resting fibre. The mean total net work performed during tetanic contraction is 10,000 erg/gm of the fibre. The net work of a fibre during release contraction is considerably higher (45 per cent) if the stimulation is interrupted for a short time. Control experiments proved that this increase in work is not due to a restitution of the fibre during this short period of rest. After the recommencement of the briefly interrupted stimulation, the fibre starts with an isometric maximum which corresponds to the respective length, the tension being markedly higher than that developed during release contraction.

Work diagrams from single contractions at a stimulation frequency of 6 per sec provide a net work of 3000 erg/gm, increasing with increasing frequency to 9000 erg/gm at a frequency of 16 stimulations per sec.

Length-tension diagrams of the anisotropic (A) and isotropic (I) substance of the single fibre can be determined from the length-tension diagram of the total fibre (A + I) and from the ratio $\frac{\text{length of A}}{\text{length of I}}$ as a function of A + I. The ratio $\frac{\text{length of A}}{\text{length of I}}$ is evaluated from microphotograms of the fibre at various states of extension at rest and during contraction.

The gradients in the length-tension diagram of the I curve of the resting fibre are steeper than those of the A curve. During isometric contraction of the fibre, the length-tension diagrams of the A and the I substance show at first a markedly steeper slope than when at rest; the steepness decreases with increasing load. The length-tension diagram of the I substance cannot be regarded

as a diagram obtained under isometric conditions, since I is not only stimulated but also extended due to the shortening of A. We can to some extent correct for this increase in length on the basis of the length-tension diagram of I during release contraction. The corrected "isometric" length-tension diagram of the I substance does not reveal any increase in tension during contraction at equilibrium length. Above the equilibrium length (up to a stretch of the fibre of 30 per cent), however, an extra-tension appears which considerably exceeds the extra-tension produced by a corresponding stretch at rest. The development of tension during contraction of the I substance is caused by an increase in stiffness; in the A substance it is, furthermore, due to a reduction of the equilibrium length.

The length-tension diagram of A and I during stretch- and release contractions deviates essentially from the curve of the isometric maxima. This irreversibility is caused by an "elastic locking" of both substances. The previously mentioned "yielding" obtained during contraction above a certain tension is mainly located in the A substance.

Static and dynamic elasticity are investigated on single fibres. In an ideal elastic body, these magnitudes are identical; the muscle fibre, however, contains viscous elements causing a difference between dynamic and static elasticity. Static measurements give an expression for the total stiffness, while dynamic measurements with short-lasting length alterations (vibrations) represent the elastic properties of those fibre elements the length alterations of which are not markedly retarded by viscosity.

The length-tension diagram serves as a basis for the static determination of elasticity, while the dynamic measurements are performed as vibration experiments. The frequency of the vibrating system applied is 5 vibrations per sec.

In isotropic bodies, the elasticity modulus is generally used as a comparative measure of the elastic properties; in anisotropic, i. e. highly elastic bodies, however, the elasticity modulus is less suited to characterize the structural properties of the substance than the stiffness $\left(\frac{\Delta \text{length}}{\Delta \text{force}}\right)$ measured directly in dynes cm^{-1}.

The stiffness and the elasticity modulus of the single fibre are measured at rest, during isometric contraction, and during

release contraction. The various magnitudes are studied as a function of the extent of stretch and of load.

In the resting fibre, the stiffness increases linearly with increasing load, after the coarse micellar adjustment is accomplished. This behaviour allows us to draw conclusions concerning the structural properties of the fibre.

During isometric contraction, the stiffness is considerably higher than the stiffness of the resting fibre (referring to the same length at rest and during contraction). At equilibrium length, the stiffness during contraction is about 5 times the stiffness at rest. This difference decreases with increasing extent of stretch. However, this increase in stiffness is only partly caused by the contraction itself but by the mechanical tension developed during contraction. The amount of tension developed during isometric contraction at equilibrium length and up to 40 per cent of stretch is predominantly due to the increase in stiffness, while the decrease in equilibrium length is quantitatively of minor importance.

The curve expressing the comparison of stiffness at rest and during contraction at the same load reveals a very typical and elucidative course. At first, the stiffness during contraction is somewhat higher than the stiffness of the resting fibre, increasing rapidly with increasing load until a maximum is reached (point of yielding). After this maximum, the stiffness decreases rapidly with increasing load and may even reach a value below the rest curve. The position of the yielding point varies from fibre to fibre lying sometimes above and sometimes below the equilibrium length. The present material is classified according to the position of the yielding point: one group of fibres yielding at loads above the equilibrium length, and another group yielding below the equilibrium length. Each of these two groups shows a characteristic course of the respective length-tension diagram, and it may be assumed that the extra-tension developed during contraction determines the classification of the fibre with respect to the position of the yielding point.

A comparison at the same load (but different lengths) during release contraction indicates that the stiffness during contraction up to loads of 30 units (length 130) lies above the stiffness of the resting fibre.

In dynamic measurements, the elasticity modulus of the

resting fibre is on the average $(0.81 \pm 0.11) \times 10^6$ dynes cm^{-2}, increasing during contraction, unless we compare rest with contraction at the same tension, i. e. an essential part of the increase is due to the influence of tension. A comparison of the moduli of fibres at rest and during contraction at the same tension makes it clear that in release contractions, the modulus during contraction is up to 30 per cent above the modulus of the resting fibre. During isometric contraction, the difference between rest and contraction depends on whether the comparison is made below or above the point of yielding.

The ratio $\frac{\text{modulus (contraction)}}{\text{modulus (rest)}}$ of the non-fatigued fibre during release contraction is 1.97 ± 0.13. In a fatigued fibre, this ratio is considerably less (1.13 ± 0.06). Fibres poisoned with monoiodoacetic acid show the same behaviour, and the lactic acid formed during fatigue cannot be the cause of the change in the elastic properties.

The statically measured modulus of the single fibre is 0.5×10^6 dynes cm^{-2}. During contraction, the ratio $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$ decreases with increasing stretch from 0.8 to 0.2. In the range about equilibrium length, the total elastic mass participates uniformly in the elastic deformation; at a stretch of 80 per cent, the dynamic measurements comprise only $^1/_5$ of the total elasticity of the fibre.

The static softness $\left(\frac{1}{\text{stiffness}} = \frac{1}{S}\right)$ of the A and the I substance is determined from the curve of the total softness of the fibre $\left(\frac{1}{S} = \frac{1}{S}\text{A} + \frac{1}{S}\text{I}\right)$ and from the ratio $\frac{\Delta\text{A}}{\Delta\text{I}}$. The softness of both substances decreases with increasing length. In the resting fibre, the A substance shows the greater softness—mainly due to its greater length—(i. e. A = twice the softness of the I substance). During contraction, the softness of both substances decreases markedly if the same lengths at rest and during contraction are compared. A becomes 7 times and I 4 times stiffer than at rest. At lengths below equilibrium length, the increase in stiffness must be mainly ascribed to a change in the I substance.

The load-stiffness diagrams of the A and the I substance of the resting fibre are linear.

A comparison of the static elasticity modulus of A and I in the resting fibre as a function of fibre length reveals only slight differences between the two substances (not more than 20 per cent). The moduli increase with increasing extension. Also during contraction at equilibrium length, the moduli of both substances increase, modulus A being about 50 per cent higher than modulus I. With increasing stretch, modulus A decreases while modulus I increases during contraction.

In the resting fibre, the elasticity moduli as a function of cross section load reveal the modulus of I to be about 30 per cent higher than the modulus of A. During contraction, the modulus of A increases to 5 times the value of I and up to 10 times the corresponding modulus of the resting fibre. The increases become smaller with increasing load.

The damping constant (viscosity) of the fibre at rest and during contraction may be determined from vibration experiments employed for the measurement of the dynamic stiffness. At rest and at equilibrium length, the damping constant is 3 dynes cm^{-1} sec (fibre stiffness = 200 dynes cm^{-1}), increasing to 6 dynes cm^{-1} sec (fibre stiffness = 1200 dynes cm^{-1}) at 80 per cent of stretch. During isometric contraction, the damping is about 4 times its value at rest. The determination of damping during release contraction proves that the increase in viscosity during contraction is mainly conditioned by the contraction as such and only to a minor extent by the tension developed.

Apart from damping, also elastic after-effects are an expression of the viscosity of the fibre. These elastic after-effects are investigated after sudden small stretchings (10 per cent) at rest and during contraction. Compared with those found on the total muscle, the after-effects in the single fibre are small relative to the increase in tension in the range of moderate elongations. The determinations of elastic after-effects are in good agreement with the variations of the ratio $\frac{\text{static elasticity}}{\text{dynamic elasticity}}$.

The consolidation after sudden stretch follows a curve which represents the sum of at least three vastly different exponential curves. In agreement with Levin and Wyman (1927), the course of

consolidation must be considered an expression of the viscosity which is not distributed uniformly over the fibre (like a shunt) but over part of the fibre, only, in series with an elasticity. Determinations of the damping at vibrations of different frequencies, where a lower damping is found at higher frequency, can be interpreted in the same way.

On the basis of the three time constants of the consolidation curve, an equivalent system is calculated which represents the viscous and elastic properties of the fibre. The transport of fluid—by GASSER and HILL regarded as the essential cause of the increasing damping—is quantitatively of minor importance.

On the basis of the experimental results described, an attempt is made to derive the most simple molecular structure which might be regarded as an equivalent of the mechanical-elastic and the electrostatic properties of the muscle fibre. The length-tension and stiffness-load diagrams originating from resulting central forces and angular forces present in such a model are calculated and compared with the mechanical properties of the muscle fibre at rest and during contraction. For the molecule model as well as for the resting muscle fibre, a linear interdependence of stiffness and load is found. The dependence of stiffness on loading indicates the existence of angular movements during the adjustment of minute structure elements. The simplest molecule equivalent is represented by a spiral structure with three series of charges, as a plane system with two series of charges will be unstable. Contraction is interpreted as the propagation of a change in electrostatic charge initiated at one point of the molecule chain. The model may further account for elastic "locking" and yielding. The properties of the model correspond to those of the anisotropic substance, while the properties of the isotropic substance cannot yet be interpreted in a simple way. The difference between the A and I substance may, however, be due mainly to a difference in orientation of the same molecular structure.

(From the Laboratory for the Theory of Gymnastics, University of Copenhagen).

Working with a fellowship from the MICHAELSEN FOND.

References.

Asmussen, E., Skand. Arch. Physiol. 1934. **70.** 233.
— Skand. Arch. Physiol. 1936. **74.** 129.
Astbury, W. T., Nature 1936. **137.** 803.
Beck, O., Pflügers Arch. Physiol. 1922. **193.** 495.
— Pflügers Arch. Physiol. 1923. **199.** 63.
Bethe, A., Pflügers Arch. Physiol. 1924. **205.** 63.
Blix, M., Skand. Arch. Physiol. 1892. **4.** 399.
— Skand. Arch. Physiol. 1895. **5.** 150.
— Skand. Arch. Physiol. 1895. **5.** 173.
Bouckaert, I. P., Capellen, L. and de Blende, I., J. Physiol. 1930. **69.** 473.
Bozler, E., Protoplasma 1933. **19.** 293.
Briscoe, Grace, J. Physiol. 1923—24. **58.** 30.
Brown, D. E. S., J. cell. and comp. Physiol. 1933—34. **4.** 257.
— and Sichel, F. J. M., J. cell. and comp. Physiol. 1936. **8.** 315.
— J. cell. and comp. Physiol. 1936. **8.** 141.
Buchthal, F. and Nielsen, J. O., Skand. Arch. Physiol. 1936. **74.** 202.
— and Knappeis, G., Skand. Arch. Physiol. 1938. **78.** 97.
— and Lindhard, J., D. Kgl. Danske Vidensk. Selskab, Biol. Medd. XIV 6. 1939.
— and Knappeis, G., Skand. Arch. Physiol. 1940. **83.** 281.
— Acta psychiatr. et neurolog. 1940. **15.** 43.
Doi, Yasukazu, J. Physiol. 1920. **54.** 218.
Ebbecke, U. and Hassenbring, O., Pflügers Arch. Physiol. 1935. **236.** 405.
— Pflügers Arch. Physiol. 1935. **236.** 662.
Eddy, N. B. and Downs, A. W., Amer. J. Physiol. 1921. **56.** 182 and 188.
Engelmann, Th. W., Arch. für die ges. Physiol. 1875. **11.** 432.
Enko, P., Arch. f. Anat. & Physiol., Physiol. Abt. 1880. 95.
Ernst, P., Pflügers Arch. Physiol. 1925. **209.** 613.
Ewans, L. and Hill, A. V., J. Physiol. 1914. **49.** 10.
Fick, A., Mechanische Arbeit und Wärmeentwicklung bei der Muskeltätigkeit. Leipzig 1882.
— Pflügers Arch. Physiol. 1892. **51.** 541.
Gasser, H. S. and Hill, A. V., Proc. Roy. Soc. B. 1924. **96.** 398.
Hermann, L., Hdb. d. Physiol. Leipzig 1879. **1.** 3.
Hill, A. V., J. Physiol. 1913. **46.** 435.
— J. Physiol. 1926. **61.** 494.
Hogben, L. T. and Pinkey, K. F., Brit. J. of exp. Biol. 1926, **4.** 196. (cit. from Ber. Physiol. 1927. **39.** 790).

Kaiser, K., Z. Biol. 1899. **38.** 1.
v. Kries, J., Arch. f. Anat. & Physiol., Physiol. Abt. 1880. 348.
— Arch. f. Anat. & Physiol., Physiol. Abt. 1892. 1.
— Pflügers Arch. Physiol. 1921. **190.** 66.
Levin, A. and Wyman, J., Proc. Roy. Soc. 1927. **101.** 218.
Lindhard, J., Collect. Pap. dedic. to A. Krogh. 1926. p. 188.
— and Møller, J. P., J. Physiol. 1926. **61.** 73.
— — Skand. Arch. Physiol. 1928. **54.** 41.
— Ergebn. Physiol. 1931. **33.** 337.
Ludwig, C., Lehrbuch der Physiologie des Menschen. 1858. **1.** 457.
Meyer, K. H., Biochem. Z. 1929. **208.** 1.
— Die hochpolymeren Verbindungen. Leipzig 1940.
— and Picken, L. E. R., Proc. Roy. Soc. B. 1937. **124.** 29.
Meyerhof, O. and Möhlen, W., Biochem. Z. 1933. **260.** 454.
Nakamura, T., Pflügers Arch. Physiol. 1924. **205.** 92.
Ramsey, R. W. and Street, Sybil, F., J. cell. and comp. Physiol. 1940. **15.** 11.
Reichel, H., Z. Biol. 1936. **97.** 429.
— Z. Biol. 1938. **98.** 510.
Richter, F., Pflügers Arch. Physiol. 1928. **218.** 1.
Schenck, F., Beiträge zur Physiologie, Festschrift für A. Fick, 1899. p. 15.
— Pflügers Arch. Physiol. 1900. **81.** 595.
Seeman, J., Pflügers Arch. Physiol. 1905. **103.** 446.
— Pflügers Arch. Physiol. 1905. **106.** 420.
Sichel, F. J. M., J. cell. and comp. Physiol. 1934. 1935. **5.** 21.
— and Prosser, C. L., Amer. J. Physiol. 1940. **128.** 203.
Steinhausen, W., Pflügers Arch. Physiol. 1924. **205.** 76.
— Pflügers Arch. Physiol. 1926. **212.** 31.
— Abderhaldens Hdb. d. biol. Arbeitsmeth. Abt. V. Teil. 5 A. Hälfte 1. 1936.
Sulzer, R., Z. Biol. 1930. **90.** 13.
— Z. Biol. 1930. **90.** 29.
Sichel, F. I. M., Amer. J. Physiol. 1941. **133.** 446.
Triepel, H., Einführung in die physikalische Anatomie. Wiesbaden 1902. **1.** 102.
Voigt, W., Lehrbuch der Kristallphysik. Leipzig, Berlin 1910.
Weber, E., Wagners Handwörterbuch der Naturwissensch. 1846. **3.** 1—122.
Weber, H. H., Pflügers Arch. Physiol. 1934. **235.** 205.
— Ergebn. Physiol. 1934. **36.** 109.
— Kolloid. Zs. 1941. **96.** 269.
Wöhlisch, E., du Mesnil de Rochemont, R. and Gerschler, H., Z. Biol. 1927. **85.** 325.
— Z. Biol. 1931. **91.** 137.
— Die Naturwissensch. 1940. **28.** 305.
— Kolloid. Zs. 1941. **96.** 261.
Wundt, W., Die Lehre von der Muskelbewegung. Braunschweig 1858.
Zakariás, I., Tungsram Technische Mitteilungen. 1938. August. p. 103.

CONTENTS

Indleveret til Selskabet den 13. Marts 1942.
Færdig fra Trykkeriet den 19. August 1942.

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 3

STUDIEN ÜBER DIE FLÜGELZEICHNUNGEN DER INSEKTEN

II. BLATTOIDEA

VON

HENNING LEMCHE

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

INHALT

Printed in Denmark
Bianco Lunos Bogtrykkeri A/S

1. Einleitung.

In einer früheren Arbeit (LEMCHE 1935) wurde das Bindenmuster (eine aus breiten Querbinden in Beziehung zum Adernetz stehende Zeichnung) »Ur-Zeichnung« genannt, d. h. eine Zeichnung, die auf den Flügeln aller pterygoten Insekten prinzipiell vertreten sein soll. Später (LEMCHE 1937)[1] wurde versucht, eine genauere Analyse der Variationen dieser Zeichnung bei verschiedenen primitiven Schmetterlingen durchzuführen, wobei sie gleichzeitig in Beziehung zu anderen Zeichnungen der Flügel (Kleinzeichnung, Randzeichnung, Sektorzeichnung, Eckstrich) gestellt wurde, soweit diese sich mindestens teilweise als phylogenetisch der Bindenzeichnung gleichwertig erwiesen. Leider benutzte ich in dieser Arbeit die Termini »Zeichnung« und »Muster« in verkehrter Bedeutung; da ich darauf aufmerksam gemacht worden bin, habe ich im folgenden meine Nomenklatur in Anpassung an die allgemein übliche Fachsprache geändert.

Durch eine sehr umfassende und tiefgehende Analyse der Zeichnungsmuster der Saturniiden stellte HENKE (1936) für diese Lepidopterengruppe einen Grundplan auf, der eine Bindenzeichnung des gleichen Typus enthielt wie die von mir ein Jahr später bei primitiven Schmetterlingen gefundene. Vor kurzem ist es HENKE & KRUSE (1941) gelungen, entsprechende Verhältnisse bei nahezu sämtlichen übrigen Schmetterlingsgruppen nachzuweisen. Schon früher schien es jedoch wünschenswert, Insektengruppen mit primitiveren Mustertypen zu studieren, noch bevor man zu weit in die Analyse der hochspezialisierten Schmetterlinge vordrang.

Nach einer neueren Arbeit (LEMCHE 1940) betrachte ich die Blattoideen als die nächsten Verwandten der Stammgruppe der meisten rezenten Pterygota, und eine Analyse der Flügelzeich-

[1] Hier ist auch ein historischer Überblick zu finden, weshalb ich in der vorliegenden Arbeit auf einen solchen verzichte.

nungen dieser Gruppe schien daher am besten geeignet, Einblicke in die grundlegenden Prinzipien der Zeichnungsmuster der Insekten zu schaffen. Ich habe mich daher im zweiten Teil meiner Zeichnungsstudien mit dieser Gruppe beschäftigt.

Eine wichtige Frage bei der Flügelmusteranalyse ist folgende: Wie viele Zeichnungen stehen in unmittelbarem Zusammenhang mit den für die Flügel speziellen Strukturen, und wie viele sind nur ein Ausdruck dafür, dass die Flügel ein Teil des Körpers und daher auch denselben Gesetzen wie dieser unterworfen sind? Oder in phylogenetischer Fragestellung: Welche Zeichnungen fanden sich bereits (potentiell oder reell) bei den Vorfahren der geflügelten Insekten auf den Seitenteilen des Meso- und Metathorax, und welche sind gleichzeitig mit oder als Folge der Umbildung dieser Anhänge zu Flügeln erschienen? Aber selbst abgesehen vom morphologischen und phylogenetischen Interesse dieser Frage bildet eine derartige Untersuchung die notwendige Grundlage für jede zweckmässige entwicklungsphysiologische Wertung der Prinzipien der musterschaffenden Prozesse im Insektenflügel; werden doch dadurch die Phänomene in zwei Gruppen geteilt: solche, deren Ursachen im Verhalten des ganzen Körpers zu finden sind, und andere, die durch die besondere Struktur der Flügel verursacht sind.

Die oben erwähnte Frage hat sich, wenigstens teilweise, durch das Studium des Farbmusters der Schaben lösen lassen; die vorliegende Untersuchung wurde daher in der Weise durchgeführt, dass zuerst die ungeflügelten, und dann die geflügelten Segmente behandelt werden, worauf schliesslich eine eingehende Diskussion der allgemeinen Ergebnisse folgt.

Die Untersuchung wurde nahezu ausschliesslich an der ziemlich grossen Blattoideen-Sammlung des Zoologischen Museums der Universität Kopenhagen durchgeführt. Dem vor kurzem leider verstorbenen Leiter der Arthropod-Abteilung dieses Museums, Dr. K. L. Henriksen, sei an dieser Stelle für sein stetiges Interesse und viele wertvolle Ratschläge herzlich gedankt. Sowohl ihm als dem Assistenten, mag. scient. S. L. Tuxen, bin ich zu grossem Dank dafür verpflichtet, dass sie mir die Möglichkeit gaben, meine Untersuchungen leicht durchführen zu können.

In der Systematik bin ich im grossen und ganzen Handlirsch (1930) gefolgt.

2. Analyse der Zeichnungsmuster der einzelnen Arten.

Soweit mir bekannt, wurde bisher niemals versucht, eine vergleichend-morphologische Analyse der Zeichnungen der Schaben vorzunehmen, und es ist daher notwendig, die zu benutzenden Termini neu zu bilden. Vorweg sei betont, dass im allgemeinen in der vorliegenden Arbeit die weissen Pigmente — welche übrigens ähnlichen Gesetzen gehorchen wie die dunklen — ausser Acht gelassen wurden. Dunkle Areale werden je nach ihrer Form als »Flecken« oder »Striche« bezeichnet, während helle Partien »Räume« genannt werden. Dadurch wird das Wort »Binde« bewusst vermieden, da diesem schon ein ganz bestimmter Begriff im Flügelmuster zugewiesen ist, der offensichtlich nicht mit irgendeinem Element am ungeflügelten Schabensegment identifizierbar ist. Inwieweit einige Blattoideen auf ihren Flügeln Binden zeigen, wird noch näher zu erörtern sein.

Das Notum des Prothorax ist allseitig in eine flache Falte ausgezogen; sämtliche anderen Segmente tragen dieselbe Falte mehr oder weniger deutlich an beiden Seiten und hinten, nicht aber am Vorderrand. Die seitlichen Falten werden gewöhnlich Paranota genannt; es wäre daher naheliegend, die entsprechende, vordere Falte als Antenotum und die hintere Falte als Postnotum zu bezeichnen. Leider ist jedoch das letztgenannte Wort schon für ein besonderes Sklerit hinter dem eigentlichen Notum vergeben, weshalb die erwähnte Falte einfach als »hintere Notalfalte« bezeichnet wird. Ebenso wie das Antenotum geht die hintere Notalfalte ohne Grenze seitlich in die Paranota über. Wie im folgenden nachgewiesen werden soll, entspricht die normale, hintere Ecke des Paranotums der Flügelspitze (siehe auch Lemche 1940), weshalb sie ohne weiteres Apex (*a*) genannt wird.

Das Muster des typischen Blattoideensegmentes wird danach folgendermassen eingeteilt (Abb. 1): Eine Schwärzung längs des Randes der ganzen notalen Falte, sowohl an Ante- und Paranota wie an der hinteren Notalfalte: der Marginalstrich (*am, pm, om*). Innerhalb dieses findet sich der Marginalraum (*ar, pr, or*). Der ganze mittlere Teil des Segmentes ist oft gleichmässig geschwärzt; dieser grosse Flecken ist der Dorsalflecken (*d*). Dieser ist aber im mittleren Teil oft heller, und er besteht dann

im wesentlichen aus einem dunklen Ring längs der Basis der notalen Falte. Dieser Ring wird als Dorsalstrich (*ad, pd, od*) bezeichnet. Wenn es zweckmässig erscheint, entweder nur den vorderen, oder nur den hinteren, oder die beiden seitlichen Teile dieser Zeichnungen zu erwähnen, werden die Vorsilben Ante-, Post-, oder Para- (z. B. Antemarginalraum, Postmarginalstrich, Paradorsalstrich usw.) benutzt. Der helle Raum innerhalb des Dorsalstriches wird Dorsalraum (*dr*) genannt; dieser Raum ist jedoch oft durch einen medianen Längsstrich, den Medianstrich (*m*), geteilt, der manchmal bis zum Hinterrand reicht.

Weiter finden sich einige dunkle Striche, die den Dorsalstrich mit dem Marginalstrich verbinden können; diese laufen somit radiär über die notale Falte. Selten liegt ein solcher Strich vorn zu beiden Seiten der Mittellinie: der Frontalstrich (*f*). Etwas häufiger sieht man einen schräg nach aussen-vorwärts laufenden Strich, den Parafrontalstrich (*pf*). Der am weitesten seitlich liegende Teil des Dorsalfleckens trägt oft kurz vor der Mitte einen kleinen Vorsprung, der etwas in das Paranotum hinausreicht, oder aber der Dorsalfleck selbst kann an dieser Stelle etwas über die Grenze des Paranotums hinaus erweitert sein. Von dieser Stelle aus läuft zuweilen ein mehr oder weniger breiter Strich, der Aderstrich (*v*), auf den Apex zu. Endlich entsteht häufig zwischen dem Postdorsalstrich und dem Postmarginalstrich eine Schwärzung, die möglicherweise als Erweiterung des Dorsalfleckens anzusehen ist und sich etwas ins Paranotum hinaus erstrecken kann; dieses Zeichnungselement wird die Analschwärzung (*s*) genannt.

Im Dorsalraum findet sich oft ein Muster aus dunklen Punkten oder Strichen; in günstigen Fällen lässt sich an getrockneten Individuen beobachten, dass die Lage dieser Elemente durch Muskelansätze bestimmt wird. Eine zwischen verschiedenen Arten durchgeführte, genaue Homologisierung dieser Elemente erfordert entweder ein sehr sorgfältiges Studium der Muskulatur oder zum mindesten ein grosses Material geeigneter Arten. Eine solche Untersuchung würde aber den Rahmen der vorliegenden Arbeit vollkommen sprengen; an ihrer wichtigsten Aufgabe — dem Studium der Flügelzeichnungen in ihrem Verhältnis zu den Zeichnungen des Rumpfes — könnte dann nicht mehr festgehalten werden.

Obwohl die genannte Homologisierung wahrscheinlich durchführbar ist, habe ich aus diesem Grunde von ihr abgesehen und nur dort, wo besondere Gründe dafür sprechen, diese Frage angeschnitten.

Als wesentlich für die hier durchgeführte Untersuchung hat sich indessen ein schräg vom mittleren Teil des Medianstriches zum äussersten Teil des Postdorsalstriches laufender Strich, der Submedianstrich (*ms*), erwiesen. Dieser Strich ist oft durchbrochen. Der Raum zwischen diesem und dem Medianstrich wird als Submedianraum (*mr*) bezeichnet. Weiter ist im Postdorsalstrich gerade ausserhalb der Einmündung des Submedianstriches ein dunkler Muskelansatz, der Subanalflecken (*sa*), von welchem ein durch den Dorsalraum laufender Längsstrich entspringen kann: der Subanalstrich (*ss*).

An der Unterseite des Paranotums finden sich zuweilen ähnliche Zeichnungselemente, die mit den gleichen Bezeichnungen wie auf der Oberseite belegt werden; nur werden dann stets Anführungszeichen gesetzt, um anzudeuten, dass die genannten Bildungen eigentlich nicht als vollkommen homolog betrachtet werden können. Auf der Unterseite des Paranotums können demnach »Marginalstrich«, »Marginalraum«, »Aderstrich« und »Analschwärzung« vorkommen.

Die Unterseite des Paranotums darf nicht mit jener des Seitenteiles der Sternite verwechselt werden. Die Sternite sind nämlich bei gewissen Blattoideen (*Cutilia* spp. *Polyzosteria* spp. u. a.) an den Abdominalsegmenten in ganz ähnliche, flache Bildungen ausgezogen wie die Paranota und tragen auch ähnliche Zeichnungsmuster. Solche »Parasternite« können aber am Thorax darum nicht entwickelt werden, weil die Sternite selbst hier rückgebildet sind. Hier handelt es sich also wirklich um die Unterseite der dorsalen Paranota.

2a. Das Muster des Prothorax.

Blattidae.

Polyzosteriinae. Bei *Cosmozosteria polyzona* Walk. findet sich ein einfaches Muster, nämlich ein von einem Marginalraum ohne Marginalstrich ganz umgebener Dorsalflecken. *C. multifasciata* Stål. (Abb. 2) zeigt dasselbe Muster mit der Abweichung,

dass hier der Dorsalflecken etwas innerhalb des Apex in einer Spitze nach dem Hinterrand verläuft. Diese Anastomose deute ich als Aderstrich. Bei *Polyzosteria limbata* Burm. ist der Postmarginalraum immer, der Antemarginalraum oft verschwunden; nur der Paramarginalraum ist fast immer vorhanden. Zuweilen hat sich jedoch der Dorsalflecken ins Paranotum hinein erweitert; bei einigen Exemplaren verbreitet sich der Dorsalflecken sogar über den ganzen Paramarginalraum und bedeckt dann die ganze Oberseite des Segmentes.

Bei einer *Platyzosteria* sp. (Abb. 3a) aus Australien findet sich ein Muster desselben Typus, aus Dorsalflecken, Paramarginalraum und Paramarginalstrich bestehend. Aber interessanterweise hat sich hier der Paramarginalstrich bis nahezu über den ganzen Paramarginalraum erweitert, während der Dorsalflecken unbeeinflusst blieb. Dieser Gegensatz zur vorigen Spezies kommt vielleicht noch deutlicher bei der Untersuchung der Unterseiten der Paranota zum Ausdruck. Die mit breitem Paramarginalraum versehenen Individuen von *Polyzosteria limbata* weisen auch einen breiten »Paramarginalraum« auf, obwohl dieser von einem deutlichen »Aderstrich« durchsetzt ist, der an jener Stelle liegt, wo an der Oberseite von *Cosmozosteria* die Grenze zwischen Dorsalflecken und Paramarginalraum verläuft. Exemplare mit schmalem Paramarginalraum an der Oberseite zeigen ganz denselben »Aderstrich«; dieser ist aber dann so stark erweitert, dass fast die ganze Unterseite von ihm ausgefüllt erscheint. Während also hier sowohl an der Ober- wie an der Unterseite der Dorsalflecken und der Aderstrich die Ausfüllung bewirken, ist an der Unterseite von *Platyzosteria* (Abb. 3b) eine Schwärzung zu sehen, die sich vom Rande her ausbreitet, also ein »Marginalstrich«, während sich der »Dorsalflecken« innerhalb des schmalen »Paramarginalraumes« in seiner gewöhnlichen Lage befindet.

Nocticolinae konnte ich nicht zur Untersuchung verwenden.

Blattinae. *Methana marginalis* Sauss. besitzt ein Vorderbrustmuster ähnlich wie *Polyzosteria*, d. h. nur die Ante- und Paramarginalräume sind hell; doch ziehen sich hier ausserdem noch deutliche Ante- und Paramarginalstriche längs der Kante hin. Bei *Methana soror* Sauss. (Abb. 4) ist der Paramarginalraum breiter, und hierzu kommen noch ein paar helle Räume

im hinteren Teil des Dorsalflecken. Der Postmarginalraum fehlt; der Postmarginalstrich ist mit dem Postdorsalstrich durch eine Analschwärzung verbunden, die allerdings weniger dunkel als die Striche ist, so dass bei Betrachtung von oben die Grenze zwischen Notum und notaler Falte leicht erkennbar ist. Die besprochenen beiden Räume im Dorsalflecken sind durch einen Medianstrich getrennt, der im hinteren Teil zwei deutliche Submedianstriche abgibt. Dass die dunkle Anastomose zwischen dem lateralen Teil des Dorsalflecken und dem Postmarginalstrich wirklich dem hinteren Teil des Paradorsalstriches entspricht, wird auch durch eine Untersuchung der Unterseite bestätigt; denn hier sehen wir nur eine Erweiterung des »Dorsalflecken«.

Ein ähnliches Muster weist die Vorderbrust eines *Methana* sp. aus Java auf, die ich im Zoologiska Institutionen in Lund gesehen habe (Abb. 5). Wohl fehlt hier der Antemarginalraum, aber der Paramarginalraum ist deutlich, und der Dorsalflecken besitzt helle Räume. Diese sind aber nicht auf den hinteren Teil des Dorsalflecken beschränkt; sie erstrecken sich vielmehr auch in den vorderen Teil hinein. Der hintere Abschnitt des Paradorsalstriches läuft wie bei der vorigen Art direkt nach hinten, und die sehr schmale hintere Notalfalte wird von einer Analschwärzung ausgefüllt.

Von hier aus ist nur ein kleiner Sprung zu dem stark differenzierten Muster von *Dorylaea rhombifolia* Stoll. mit Ante- und Paramarginalräumen und deutlichem Marginalstrich. Stark gezeichnete Individuen (Abb. 6) besitzen, ähnlich wie *Methana soror*, einen grossen Dorsalflecken mit zwei Räumen im hinteren Teil, welche durch einen Medianstrich getrennt sind, der seinerseits zwei nicht ganz vollständige Submedianstriche abgibt. Dazu kommen aber noch zwei Räume im vorderen Abschnitt des Dorsalflecken, die diesen Flecken vollständig in gewundene Streifen auflösen. Der hintere Teil des Paradorsalstriches verläuft schräger nach innen gerichtet als bei der vorigen Art. Er ist ganz hinten beinahe abgebrochen und dann nur noch durch eine kurze Analschwärzung mit dem Postmarginalstrich verbunden. Es entsteht dadurch auf dem Paradorsalstrich ein eigentümlicher Knick. Weiter lateral verläuft ein deutlicher Aderstrich vom Dorsalflecken gegen den Apex hin. Ein ähnlicher, noch deutlicherer »Aderstrich« findet sich an der Unterseite.

Bei anderen Individuen (Abb. 8) fehlt der Aderstrich, oder sie besitzen nur schwache Andeutungen eines solchen; oft ist auch das Muster dadurch reduziert, dass der hintere Teil des Paradorsalstriches ganz abgebrochen ist. Die ganze hintere Notalfalte ist immer geschwärzt, so dass auch diese Spezies keinen Postmarginalraum aufweist. Im Gegenteil wird durch die Reduktion des hinteren Teiles des Paradorsalstriches an schwach gezeichneten Individuen eine Verbindung zwischen dem Paramarginalraum und dem hinteren Raum des Dorsalfleckens geschaffen.

Bei einer *Dorylaea* sp. aus Australien (Abb. 10) ist das Muster viel einfacher. Wie bei der vorigen Art ist die hintere Notalfalte geschwärzt, und auch das Antenotum ist wie bei *D. rhombifolia* gezeichnet. Der Dorsalflecken aber ist als Dreieck entwickelt, dessen hintere Grenze auffallend weit medial liegt, wodurch die beiden Paradorsalstriche hinten nahezu aneinander stossen. Weiter anastomoziert der Paradorsalstrich vorne über eine kurze Strecke mit dem Marginalstrich, was als kurzer Parafrontalstrich angesehen werden kann. Der Aderstrich fehlt, und alle vier Dorsalräume sind miteinander verbunden. Das Muster der Unterseite des Paranotums entspricht ganz dem der Oberseite.

Die Analyse der schwach gezeichneten Individuen von *Dorylaea rhombifolia* ermöglicht nun das Verständnis des Musters der *Periplaneta*-Arten (*P. americana* L. und *P. australasiae* F. — Abb. 11). Auch hier ist die hintere Notalfalte schmal und geschwärzt, die verschiedenen Marginalräume sind miteinander verbunden, und der Marginalstrich ist am Paranotum schwach, am Antenotum stark entwickelt. Weiter erscheint hier wieder die Verbindung zwischen den hinteren Teilen des Paramarginalraumes und des Dorsalraumes, wodurch ein heller Ring um den vorderen Teil des Dorsalfleckens herum entsteht. Dagegen fehlt der helle Raum im vorderen Teil des Dorsalfleckens, und seine beiden symmetrischen Hälften sind oft teilweise vorne und hinten durch helle Einschnitte getrennt. Mitunter ist der Medianstrich angedeutet, und bei *P. americana* ist der Submedianstrich oft vorhanden. Die Grösse des Dorsalfleckens variiert bedeutend; bei einigen Individuen verschmilzt dieser Flecken mit dem Paramarginalstrich, während andere Andeutungen eines Aderstriches aufweisen. Auch bei abweichend gezeichneten Individuen tragen die Unterseiten das normale Muster, d. h. ein deut-

licher »Marginalraum« trennt den »Dorsalflecken« und den »Marginalstrich«, während der »Aderstrich« fehlt.

Bei diesen Arten variiert der Hinterrand in der Weise, dass er bald gerade, bald gebogen verläuft. Im letzteren Falle ist es ziemlich schwierig, die Lage des Apex genau festzustellen; ein Vergleich mit anderen Individuen ergibt aber, dass er dann dem vorderen der beiden Höcker entspricht. Möglicherweise gilt dies auch für *Homalosilpha ustulata* Burm. (Abb. 12). Das reduzierte Muster besteht hier nur aus Teilen des Dorsalfleckens und der durch eine Analschwärzung vollständig geschwärzten hinteren Notalfalte samt einem schmalen Marginalstrich.

Bei *Syntomaptera heydeniana* Sauss. (Abb. 13) ist der Marginalstrich nur schwach angedeutet; die ganze Oberseite des Pronotums ist hell bis auf einen schwarzen, etwas geschwungenen Paradorsalstrich, der hinten in eine nur angedeutete Analschwärzung übergeht. Die hintere Notalfalte ist, wie gewöhnlich bei dieser Familie, schmal und nur wenig verdunkelt.

Blattellidae.

Blattellinae. Ein ganz ähnliches Muster weist *Ceratinoptera diaphana* F. (Abb. 14) auf. Die wohlentwickelten Paradorsalstriche sind hier jedoch durch einige Querstriche verbunden: den Antedorsalstrich vorne, dann einen Strich mitten durch den Dorsalraum, und hinten die Analschwärzung, die die ganze hintere Notalfalte ausfüllt. Einige Unebenheiten an der Innenseite des Paradorsalstriches deuten den Platz einiger hier nur wenig entwickelter Elemente an, die bei *Temnopteryx* sp. (Abb. 15) deutlich sind. Hier ist der ganze Umkreis des vorderen Dorsalraumes geschwärzt, auch die Analschwärzung ist deutlich; der hintere Teil des Paradorsalstriches fehlt jedoch. Hierdurch nähert sich dieses Muster dem der schwach geschwärzten Exemplare von *Dorylaea rhombifolia* (vgl. Abb. 7).

Ein »*Platyzosteria*-Muster« (vgl. Abb. 3 a) ist unter den Blattellinen weit verbreitet; es findet sich bei einigen *Loboptera*-Arten wie z. B. *L. decipiens* Germ., *Pseudischnoptera lineata* Oliv. (Abb. 51), *Blattella dido* und einigen Exemplaren von *Bl. supellectilium* Serv. (Abb. 52), während andere Arten ausserdem noch einen hellen Postmarginalraum besitzen, z. B. *Loboptera* sp.,

Pseudothyrsocera sp., *Hemithyrsocera soror* Brunn., *Pseudomops cincta* Burm., *Ps. crinicornis* Burm. und *Ps. neglecta* Shelf. *Ps. crinicornis* hat im hinteren Teil der Seitengrenze des Dorsalfleckens eine Einbuchtung, die der Unterbrechung des Paradorsalstriches von *Temnopteryx* sp. (vgl. Abb. 15) entspricht. Bei *Ps. intercepta* Burm. (Abb. 16) ist diese Einbuchtung so stark entwickelt, dass der Postdorsalstrich nahezu isoliert liegt. Den am deutlichsten ausgeprägten Postdorsalstrich habe ich jedoch bei einer unbestimmten Blattelline aus Mejico gefunden, an der dieser Strich das einzige stark geschwärzte Element und ganz vom vorderen, hellbraunen Rest des Dorsalfleckens getrennt ist. Die übrigen Zeichnungselemente fehlen hier völlig.

In den meisten Fällen verläuft die Bildung des Musters bei dieser Familie in anderer Richtung, indem nämlich das »*Cosmozosteria*-Muster« (Marginalraum ringsum entwickelt) durch einen hellen Längsstreifen mitten durch den Dorsalfleck umgebildet wird. Bisweilen ist dieser Streifen schmal und erreicht nicht den Hinterrand (*Thyrsocera histrio* Burm. — Abb. 50), bisweilen geht er bis zum Rande durch (*Blattella* sp. aus Amoy — Abb. 17). Auf diese Weise entsteht zu beiden Seiten der Mitte ein länglicher Flecken. Bei *Blattella germanica* L. finden sich ähnliche Bildungen, die aber viel schmäler sind und daher den eben erwähnten kaum ganz entsprechen, was sich auch aus einem Vergleich mit dem detailreichen Muster von *Pseudophyllodromia alternans* Serv. ergibt. Hier besitzen einige Individuen ein Muster (Abb. 18), das sehr an jenes von *Dorylaea rhombifolia* erinnert (vgl. Abb. 6). Am weitesten lateral liegt der Paradorsalstrich, der nach hinten in den Aderstrich übergeht. Der Paradorsalstrich verläuft aber hinten etwas nach innen und geht dann in den Postdorsalstrich über, der in der Mittellinie abgebrochen ist. Bei einem anderen Exemplar (Abb. 19) ist dieses Muster etwas vereinfacht; hier zieht sich die breiteste Schwärzung der Länge nach durch den Dorsalflecken. Dies gilt noch klarer ausgeprägt für ein weiteres Individuum (Abb. 20), welchem der Aderstrich fehlt. Auch an der Unterseite ist hier kein »Aderstrich«, während ein solcher bei den obengenannten Exemplaren zu finden ist. In Abb. 20 läuft folglich ein dominierender, breiter Strich zu beiden Seiten der Mittellinie hin. Durch Reduktion des vorderen Teiles des Paradorsalstriches und des Postdorsalstriches

ist dann das Muster von *Blattella germanica* L. (Abb. 21) entstanden, das also nicht aus dem Paradorsalstrich, sondern aus dem mehr medial liegenden Subanalstrich gebildet wird, was auch daraus erhellt, dass diese Schwärzung nicht über der Grenze des Paranotums, sondern weiter medial liegt.

Das Muster von *Pseudophyllodromia alternans* kann sich übrigens auch so verändern, dass nur der vordere Teil des Dorsalfleckens zurückbleibt (Abb. 22). Dies zeigt, dass die Schwärzung des Notums nicht einfach ein mehr oder weniger ausgedehntes Areal trifft, sondern durch die Wirkung mehrerer verschiedener Prinzipien entsteht.

Bei den Ectobiinae liegen die Verhältnisse ganz ähnlich wie bei den Blattellinen. Einige Formen zeigen »*Cosmozosteria*-Muster« mit schmalen Marginalräumen um den Dorsalflecken herum (*Ectobia sylvestris* Scop., *Hololampra maculata* Schreb. und *H. brevipennis* Fisch.), bei anderen ist der Postmarginalraum ganz verschwunden (*Theganopteryx aethiopica* Sauss. und *Hololampra marginata* Schreb.), oder nur die Paramarginalräume sind hell (*Anaplecta* sp. aus Südamerika).

[Chorisoneuridae wird aus Gründen, welche vermutlich nichts mit dem Flügelbau zu tun haben, als eine selbständige Familie von den Ectobiinen getrennt. Das Farbmuster des Prothorax ähnelt dem der Ectobiinen. *Areolaria* sp. aus Java hat ein »*Cosmozosteria*-Muster«, während *Plectoptera* sp. aus Costa Rica einen eingeschnitteneren Dorsalflecken besitzt, in welchem dieselben Elemente wie bei *Pseudophyllodromia* angedeutet sind. Einige Exemplare von *Chorisoneura* sp. zeigen deutliche Spuren eines Dorsalstriches, die bei einem einzigen Individuum der Sammlung sogar einen vollständigen, ringförmigen Dorsalstrich bilden.]

Nyctiborinae. Hier liegt ebenfalls ein starker und vollständig ausgebildeter Dorsalflecken vor. Einige Arten haben sogar einen ganz dunklen Prothorax (*Megaloblatta blaberoides* Walk., *Nyctibora tomentosa* Serv.), während bei anderen zusammenhängende Para- und Antemarginalräume entwickelt sind, die den Dorsalflecken vom Marginalstrich trennen. *Nyctibora crassicornis* Burm. (Abb. 23) hat einen vollständigen Marginalraum längs des ganzen Randes, aber nur hinten einen Marginalstrich. Bei dieser Art kann beobachtet werden, dass der

Hinterrand stark gebogen ist, wodurch der Apex seitlich etwas nach vorne geschoben wird (Abb. 23a). Diese Auffassung wird auch dadurch gestützt, dass der Postmarginalstrich in seinem lateralen Teil etwas breiter ist, so wie dies — wie oben besprochen — bei den *Periplaneta*-Arten der Fall sein kann. Diese Verhältnisse sind für die Deutung des Musters der Phoraspinen von Wichtigkeit und werden deshalb hier erwähnt.

Epilamprinae. Die beiden Untergruppen weichen in der Form der Vorderbrust voneinander ab und werden aus diesem Grunde hier getrennt behandelt.

Die Epilamprini haben gewöhnlich einen Prothorax mit normalem Umriss, der Apex ist jedoch vielleicht etwas nach aussen gezogen und der Hinterrand dadurch erweitert. Das Muster wird durch zwei verschieden grosse Sorten kleiner, dunkler Punkte kompliziert. Jeder kleinere Punkt bedeckt eine Punktgrube (falls solche Strukturen überhaupt sichtbar sind; sonst liegen die Punkte über die ebene Oberfläche verstreut). Die grösseren Punkte erinnern in ihrer Form an teilweise kontrahierte Chromatophoren. Beide Sorten sind mehr oder weniger gleichmässig über die hellen Teile des Musters verteilt und können, wenn sie dicht beieinander liegen, die Zeichnungsanalyse erschweren.

Sowohl *Phoetalia pallida* Burm. (Abb. 24) als auch *Molytria inquinata* Stål. (Abb. 25) besitzen einen vollständigen Dorsalflecken. Die Paramarginalräume sind breit, und der Antemarginalraum ist deutlich, während der Postmarginalraum entweder fehlt (*Phoetalia*) oder undeutlich ist (*Molytria*). Bei diesen wie bei vielen anderen Arten dieser Gruppe zeigt die laterale Grenze des Dorsalfleckens einen charakteristischen Vorsprung kurz vor der Mitte des Segmentes. Bei dem abgebildeten Exemplar von *Phoetalia* entspringt ein »Aderstrich« auf der Unterseite genau aus dem entsprechenden Vorsprung des »Dorsalfleckens«, was ich nur dahin deuten kann, dass ein Aderstrich der Oberseite fehlt, und der ganze breite hintere Seitenteil des Dorsalfleckens eine Analschwärzung darstellt. Sowohl bei einem anderen Exemplar derselben Spezies als auch bei allen vorhandenen *Molytria* fehlt der »Aderstrich« auf der Unterseite. Bei *Heterolampra erubescens* Gerst. finden wir ein ähnliches, aber viel undeutlicheres Muster, doch zeigen einige Individuen eine gewisse Zusammenziehung der kleinen Punkte zu einem Strich vom oben besprochenen Vor-

sprung bis zum Apex, wodurch die Andeutung eines Aderstriches entsteht. Es sieht daher so aus, als ob der Aderstrich bei diesen Formen gewöhnlich »an der Stelle« verschwindet und nicht mit dem Dorsalflecken verschmilzt.

Einige Epilamprinen haben einen weit differenzierteren Dorsalflecken, so z. B. eine leider ganz unbestimmte Spezies (vielleicht eine *Calolampra* — Abb. 26) aus Kenya, deren Prothorax hinten in der Mitte so ausgezogen ist, dass die hintere Notalfalte eine stumpfe Spitze zwischen den Vorderflügelwurzeln bildet. Hier ist der Marginalstrich hinten als eine ganz schmale Randlinie angedeutet, vorne fehlt er aber völlig. Nur am Apex, der hier sehr weit vorn liegt, bildet er einen kleinen, deutlichen Flecken dort, wo ein eventuell vorhandener Aderstrich anstossen könnte; dieser Strich fehlt aber hier fast ganz. Der Dorsalflecken ist wohlentwickelt und besitzt nur die gewöhnlichen vorderen und hinteren — hier nur kleinen — Räume. Die Submedianstriche sind offensichtlich nicht vom Medianstrich getrennt, und die hintere Erweiterung des Dorsalfleckens scheint wenigstens teilweise eine Analschwärzung zu sein.

Ähnlich wie bei der letztgenannten Art ist der Prothorax der meisten Phoraspini abgeändert, nur ist der Hinterrand etwas gleichmässiger gebogen. Der Apex liegt daher an oder vor der Mitte des Segmentes, was eine entsprechende Verschiebung des Musters mit sich bringt. Dies ist bei *Phoraspis picta* Drury (Abb. 27) deutlich zu sehen, wo nur Ante- und Paramarginalraum hell sind. Doch wird der Antemarginalraum, durch die schmale Verlängerung eines Medianstriches, die vom wohlentwickelten Dorsalfleck zum Vorderrand verläuft, in zwei Teile geteilt. Bei anderen Arten (*Ph. atomaria* Blanch., *Ph. fastuosa* Blanch., *Ph. leucogramma* Perty u. a.) ist nur dieser schmale Medianstrich geschwärzt, während das übrige Notum hell ist. Eine Zwischenstellung nimmt in dieser Hinsicht *Cyrtilia convexa* Thunb. ein, bei welcher der hintere Teil des Dorsalfleckens geschwärzt ist. Diese Schwärzung läuft dann in der Mittellinie in eine nach vorn gerichtete Spitze aus.

Ähnlich wie *Phoraspis picta* sind auch die *Paratropes*-Arten gezeichnet, nur ist hier der Paramarginalraum breiter; er wird nach hinten zu immer breiter, um kurz vor dem Apex abgerundet zu enden. Bei einer dieser Arten, *Paratropes bilunata*

Sauss & Z., ist der Antemarginalraum verschwunden; bei *P. phalerata* Erich. (Abb. 28) und *P. subsericeus* Sauss. bildet er dagegen eine helle Verbindung zwischen den beiden Paramarginalräumen. Bei dem abgebildeten Exemplar ist noch dazu ein Rest eines Postmarginalraumes zu sehen, der von seinem Gegenstück durch einen breiten Medianstrich getrennt ist. Inwieweit ein Aderstrich in das vorhandene Muster einbezogen ist, lässt sich auf Grund des vorliegenden Materials nicht entscheiden.

Blaberidae.

Panchlorinae. Innerhalb der Blaberiden besitzt diese Gruppe die am wenigsten spezialisierte Vorderbrust, ihre Zeichnungsmuster erinnern daher auch am meisten an die bisher besprochenen. *Nauphoeta occidentalis* F. hat nur einen Marginalraum — ohne Marginalstrich — rings um ein sonst dunkles Notum. *Gyna capucina* Gerst. verhält sich ähnlich, nur ist hier der Hinterrand in eine mediane, breite Spitze ausgezogen, was dem Postmarginalraum in der Mitte eine grosse Breite verleiht, während die übrigen Marginalräume schmal sind. Umgekehrt ist der Postmarginalraum von *Leucophaea surinamensis* L. verschwunden; die Paramarginalräume sind verkümmert, der Antemarginalraum aber ist wohlentwickelt. Bei allen diesen Arten ist der Dorsalflecken vollständig (bis auf zwei rudimentäre Submedianräume bei *Nauphoeta occidentalis*).

Zetebora spp., *Oniscosoma granicollis* Sauss., und *Tribonidium signaticollis* Burm. (Abb. 29) besitzen eine ähnlich wie bei den Phoraspini quer ausgezogene Vorderbrust und ein entsprechend verändertes Zeichnungsmuster. Wie bei *Paratropes* (vgl. Abb. 28) sind die Ante- und Paramarginalräume verschmolzen und der Dorsalflecken vollständig. Der hintere Teil des Paramarginalraumes aber kann entweder bräunlich (*Zetebora*) oder sogar vollkommen schwarz sein (*Tribonidium*); die Grenze zwischen Paramarginalraum und Dorsalflecken verläuft so, dass der Aderstrich in den Dorsalflecken einbezogen zu sein scheint. Die Unterseiten von *Oniscosoma* und *Zetebora* bestätigen diese Auffassung, denn hier findet sich wirklich ein deutlicher »Aderstrich« an der entsprechenden Stelle. Bei *Tribonidium* ist dagegen das Muster der Unterseite genau wie das der Oberseite gebaut.

Ferner ist hervorzuheben, dass der genannte »Aderstrich« nicht genau nach der am stärksten gebogenen Stelle des Seitenrandes, vielmehr etwas mehr nach hinten zu verläuft, nach einer Stelle, wo bei vielen Exemplaren von *Tribonidium* (siehe Abb. 29) ein zahnartiger Vorsprung des Randes zu sehen ist. Diese Stelle fasse ich daher als den eigentlichen Apex auf, was durch einen Vergleich mit den Blaberinen (siehe unten) bestätigt wird.

Viel reicher differenziert ist das Muster von *Tribonium spectrum* Esch. (Abb. 30), in dem der Dorsalflecken stark zerteilt ist. Der Antedorsalstrich ist in der Mitte durchbrochen, und der Paradorsalstrich fehlt ganz, wodurch das Areal des Dorsalfleckens stark eingeschränkt wird. Die beiden Längsstreifen, die bei *Blattella germanica* (vgl. Abb. 21) das ganze Muster ausmachen — nämlich die Subanalstriche — sind dagegen wohlentwickelt und setzen sich bis zum Hinterrand fort. Dies ist jedoch so zu verstehen, dass sie eigentlich nur den Postdorsalstrich erreichen, dieser aber infolge der sehr schmalen hinteren Notalfalte recht nahe am Postmarginalstrich liegt und mit diesem verschmolzen ist. Mediad zum Subanalstrich liegt dicht zu beiden Seiten der Mittellinie ein gewöhnlicher Submedianstrich, wie zu erwarten, wenn das eigentliche Notum — wie hier — schmal ist. Dagegen ist jedes Paranotum ungeheuer breit; Zeichnungselemente fehlen aber mit Ausnahme des Post- und des in geringerem Ausmass vorhandenen Paramarginalstriches.

Bei *Nauphoeta cinerea* Oliv. (Abb. 31) besteht das Muster aus vielen, grösstenteils bräunlichen Elementen, die den bereits bei *Tribonium* besprochenen entsprechen. Von beiden Seiten des vorderen Seitenrandes des Dorsalfleckens geht ein stark geschwärzter Längsstrich aus, der sich gegen den Apex zieht. Der hintere Teil dieses Längsstriches dürfte der Aderstrich sein, während der vordere Teil zum Paradorsalstrich gehört, dessen vorderster Abschnitt etwas nach aussen in die Andeutung eines Parafrontalstriches verlängert erscheint.

Ähnlich gemustert ist auch *Nauphoeta* sp. aus Afrika (Abb. 32), nur sind die dunklen Teile ihres Dorsalfleckens stark geschwärzt. Die Grenze zwischen Aderstrich und Dorsalflecken ist hier undeutlich (oder vielleicht fehlt der Aderstrich, und was wie ein solcher aussieht, könnte der Paradorsalstrich sein). Wie bei *Tribonium* ist der Subanalflecken deutlich und gibt den

wirklichen Platz des Postdorsalstriches an, d. h. die hintere Notalfalte ist relativ breit.

Bei *Rhyparobia maderae* F. (Abb. 33) ist das Muster nur wenig geschwärzt, den Einzelheiten nach aber ungefähr wie bei der vorigen Art. Der Paradorsalstrich ist nur vorne deutlich verdunkelt, nämlich an jener Stelle, von der der Aderstrich ausgehen sollte. Bei einigen Exemplaren dieser Art verläuft auch wirklich von hier aus nach hinten, dem Seitenrand parallel, ein schwacher Schatten; in vielen Fällen ist jedoch hier die Anhäufung weissen Pigmentes charakteristischer als die des schwarzen.

Bei den *Panchlora*-Arten fehlt das schwarze Pigment vollkommen; die Zeichnung besteht nur aus einem durch weisses Pigment angedeuteten Aderstrich.

Die Panesthiinae der Sammlung haben alle einen einfarbigen Prothorax, der jedoch oft mit Buckeln und Unebenheiten versehen ist, deren Plätze offensichtlich denen gewisser Zeichnungselemente entsprechen. Solche Phänomene sind aber noch deutlicher bei den

Perisphaeriinae, wo Buckel in einer ganzen Reihe von Gattungen vorkommen (*Hormetica*, *Brachycola* etc.). Hier sind die am weitesten vorspringenden Teile stark gefärbt, während tiefliegende Areale durchweg hell sind. Es dürften die Muskelansätze sein, die sowohl die Verteilung der Buckel als der betreffenden Zeichnungselemente bedingen. Bei *Hormetica verrucosa* Brunn. (Abb. 34) besitzt der Dorsalflecken einen deutlichen, vorderen Raum und einen Einschnitt in der Mitte hinten. Vom starken Marginalstrich ist der Dorsalflecken durch einen schmalen Marginalraum getrennt, der hinten an zwei Stellen durchbrochen oder zumindest verschmälert ist, nämlich nahe der Mitte und dort, wo sonst die äussere Grenze der Analschwärzung liegt. Der Platz des Aderstriches ist dagegen nur durch einen kleinen Vorsprung des Dorsalfleckens angedeutet, sonst ist er vermutlich mit dem Dorsalflecken verschmolzen. *Hormetica laevigata* Burm. hat oft gar kein eigentliches Muster, in einigen Fällen jedoch einen deutlichen, nahezu ringförmigen Dorsalstrich, der nur in der Mittellinie vorn und hinten abgebrochen ist. Hierzu kommen noch einige Andeutungen ähnlicher innerer Dorsalfleckenelemente, wie sie auch bei der oben besprochenen *Nauphoeta* spp. vorkommen. *Parahormetica bilobata* Sauss.

(Abb. 35) hat einen vollständigen, ringförmigen Dorsalstrich; im Gegensatz zu *Hormetica verrucosa* erstreckt sich aber der Dorsalraum auch noch in den hinteren Teil des Dorsalfleckens hinein.

Bei *Brachycola tuberculata* Dalm. (Abb. 36) ist der Dorsalflecken vorn und hinten in der Mitte eingeschnitten, und diese beiden Einschnitte können sogar durch einen schmalen, hellen, medianen Streifen verbunden sein. Vom vorderen Rand des Dorsalfleckens führt zu beiden Seiten der Mitte ein dunkler Frontalstrich zum Vorderrand; ein Marginalstrich ist nur am Vorderrand zu sehen.

Unter den Arten mit glattem Prothorax besitzt der männliche *Aptera fusca* Thunb. einen etwas unscharf abgegrenzten Dorsalflecken, während das Weibchen nur wenig hellere Para- und Postmarginalräume aufweist, sodass seine Vorderbrust nahezu einfarbig ist. Das scharf gezeichnete Muster von *Proscratea complanata* Perty (Abb. 37) besteht aus einem schmalen Marginalstrich und einem vollständigen Dorsalflecken, der mit dem Postmarginalstrich durch eine breite Analschwärzung und einen relativ breiten Aderstrich verbunden ist. Bei *Paranauphoeta* sp. (Abb. 38) läuft ein breiter Raum der Länge nach zu beiden Seiten der Mitte durch den Dorsalfleck hin und teilt diesen gänzlich in laterale, ungefähr wie bei *Nauphoeta cinerea* (vgl. Abb. 31) gelagerte, aber etwas breitere Paradorsal-Aderstriche und eine mediane, das ganze Segment durchziehende Schwärzung auf.

Blaberinae. *Blaptica dubia* Serv. (Abb. 39) besitzt eine halbmondförmige Vorderbrust der typischen Form. Die hintere Notalfalte ist schmal, und der Dorsalflecken hat sich mit dem Postmarginalstrich verbunden. Ein gesonderter Aderstrich ist nicht zu finden; wahrscheinlich ist er in den grossen Dorsalfleck einbezogen worden, denn dieser bedeckt einen grossen Teil des Paranotums.

Monastria biguttata Thunb. (Abb. 40) ist ähnlich gemustert, nur ist ihr Dorsalraum gross. Da ihre hintere Notalfalte noch schmäler ist als die der vorigen Art, wird aus den vereinigten Postdorsal- und Postmarginalstrichen nur ein ziemlich schmaler Streifen, während das wohlentwickelte Paranotum einer breiten Schwärzung Platz macht, die aus dem Paradorsal- und dem Aderstrich besteht. Ähnlich kommen ein »Aderstrich« und eine

mit diesem zusammenhängende »Analschwärzung« an der Unterseite vor, und ganz wie an der Oberseite kann dieser Teil des Musters von dem »Paramarginalstrich« durch einen schmalen »Paramarginalraum« getrennt, oder der letztgenannte verwischt sein. Wo die Grenze zwischen Paramarginalraum und Dorsalflecken usw. an den Rand stösst, findet sich ein kleiner, aber deutlicher Dorn, den ich für den eigentlichen Apex halte. Beim ausgewachsenen Männchen wird der Hinterrand gebogen, statt wie bei den Larven und Weibchen nahezu gerade zu verlaufen; dann liegt die abgerundete Ecke ungefähr in der Höhe der Segmentmitte, während der Dorn etwas weiter hinten liegt und wie zuvor der Grenze zwischen Paramarginalraum und Dorsalstrich usw. folgt. Bei *Petasodes reflexa* Thunb. und *P. dominicana* Burm. ist diese Umbildung des Prothorax auf die Spitze getrieben; Vorder- und Seitenkante sind aufwärts gebogen, und die bei *Monastria* gefundene Ecke ist spitzer geworden. Der Apex ist hinter dieser Ecke als Dorn markiert, wodurch der Seitenrand zwischen Ecke und Apex konkav wird. Ein Muster findet sich bei diesen *Petasodes*-Arten nicht.

Bei den Gattungen *Monachoda* und *Blabera* (Abb. 41) tritt dasselbe Muster wie bei *Blaptica* auf; das Paranotum ist aber viel breiter, und der Dorsalflecken erscheint deshalb im Verhältnis zum breiten Paramarginalraum relativ klein. Der Postmarginalraum und der Marginalstrich sind gewöhnlich verschwunden, doch ist der letztere bei *Monachoda grossa* Thunb. und *M. latissima* Brunn. hinten entwickelt. Ein dunkler Schatten kann bei diesen Arten einen Aderstrich vom vorderen Teil des Dorsalfleckens in Richtung nach dem Apex zu andeuten.

Diplopteridae hat kein deutliches Zeichnungsmuster.

Corydiidae. Leider ist diese Familie — von einer Anzahl *Corydia petiveriana* L. abgesehen — in der bearbeiteten Sammlung nur sehr spärlich vertreten, und die genannte Spezies besitzt kein Vorderbrustmuster. Ein Exemplar von *Corydia plagiata* Walk. hat einen hellen Paramarginalraum; sonst ist der Prothorax auch bei diesem ganz dunkel. Dasselbe gilt für *Euthyrrhapha pacifica* Coq., während das undeutliche Muster von *Holocompsa nitidula* F. an einem Exemplar eine Schwärzung längs des Hinterrandes des Paranotums aufweist, die etwas an die Verhältnisse bei *Periplaneta* usw. (vgl. Abb. 11) erinnert. Die

Männchen von *Polyphaga aegyptiaca* L. und einer unbestimmten Art derselben Gattung haben helle Ante- und Paramarginalräume am sonst schwarzen Prothorax.

2 b. Das Muster des Meso- und Metathorax ungeflügelter Individuen.

Die Analyse des Musters dieser Segmente muss zuerst an ungeflügelten Altersstufen oder Spezies vorgenommen werden; denn erst danach ist es möglich, an den geflügelten Individuen genau zu bestimmen, welcher Teil der Segmente an der Flügelbildung teilnimmt. Nur ein geringer Teil des gesamten Materials kann daher in diesem Abschnitt verwertet werden, da geflügelte Imagines den grössten Teil der Sammlung ausmachen. Die Familien und Unterfamilien werden in der gleichen Reihenfolge wie im vorigen Abschnitt behandelt.

Blattidae.

Polyzosterinae. *Cosmozosteria polyzona* Walk. trägt an den sichtbaren Teilen von Meso- und Metathorax ganz dasselbe Muster wie am Prothorax, nämlich einen von einem Marginalraum umgebenen, wohlentwickelten Dorsalflecken. Die hintere Notalfalte des Prothorax verbirgt jedoch den Vorderrand des Mesothorax und die Notalfalte dieser letzteren den Vorderrand des Mesothorax, weshalb nicht untersucht werden konnte, inwieweit ein Antemarginalraum entwickelt ist. Es dürfte doch jedenfalls kein Antenotum entwickelt sein und daher vermutlich auch kein Antemarginalraum. Wo nichts anderes vermerkt ist, gilt derselbe Vorbehalt auch mit Rücksicht auf die vordersten Teile des Musters der im folgenden besprochenen Arten.

Cosmozosteria multifasciata Stål. (Abb. 2), *Polyzosteria limbata* Burm. und mehrere *Cutilia*-Arten haben an den hinteren Thoraxsegmenten ein ganz ähnliches Muster wie am Prothorax.

Blattinae. Hier sind die Verhältnisse bei der Gattung *Periplaneta* am leichtesten übersehbar. Man bemerkt sofort, z. B. an der abgebildeten Larve von *P. australasiae* F. (Abb. 11), dass hier — im Gegensatz zur vorigen Unterfamilie — der Hinterrand der Mittel- und Hinterbrust zwar im mittleren Teil wie gewöhn-

lich verläuft, gegen die Seiten hin aber ein wenig nach hinten umbiegt, um für die Flügelanlagen Platz zu machen. Dadurch wird das Zeichnungsmuster etwas verschoben und abgeändert. Ganz wie am Prothorax nur der vordere Teil des Dorsalfleckens entwickelt ist, hat sich an den übrigen Thorakalsegmenten nur eine Dorsalschwärzung der vordersten Bereiche ihres sichtbaren Teiles entwickelt. Trotzdem findet sich wieder die kleine Spitze hinten am Dorsalflecken, die am Prothorax die Fortsetzung des Paradorsalstriches andeutet. Die hintere Notalfalte ist an allen drei Segmenten vollständig verdunkelt, aber am Prothorax ist der laterale (paranotale) Teil des Postmarginalstriches breiter als der mediane Teil, und dies ist an den beiden anderen Brustsegmenten noch ausgeprägter, obgleich der laterale Teil infolge der veränderten Richtung des Hinterrandes schräg nach aussen hinten verläuft. Hierzu kommt eine Ausbuchtung der inneren Enden der verbreiterten Zonen in Richtung nach vorne, wodurch sich die Schwärzung am Mesothorax der genannten Spitze nähert und sich am Metathorax mit ihr vereinigt. Die dadurch entstandene dreieckige Schwärzung ist als ein Teil des Paradorsalstriches in Verbindung mit dem Postmarginalstrich aufzufassen. Endlich findet sich eine kleine Spitze am äusserten Teil des Postmarginalstriches, die ich für die Andeutung eines Aderstriches ansehe.

Am Prothorax ist ein medianer, hellbrauner Schatten zwischen dem Dorsalflecken und dem Postmarginalstrich. Ein entsprechender, viel breiterer Schatten liegt am Mesothorax, und auch hier füllt er nicht den ganzen Dorsalraum aus. Dies ist dagegen an der Hinterbrust der Fall, wo nur noch ein ganz kleiner Raum innen am Paradorsalstrich hell ist. Der Unterschied zwischen Meso- und Metathorax ist vermutlich teilweise durch die verschiedene Breite dieser Segmente verursacht.

Bei der früher (unter Prothorax) besprochenen *Methana* sp. aus Java (Abb. 5) herrschen ähnliche Verhältnisse trotz des etwas anderen Aussehens des Prothorax. Der breite, hintere Teil des Paradorsalstriches entspricht dem oben genannten dreieckigen Flecken. Dieser ist aber am Mesothorax schmaler, und am Metathorax ebenfalls schmaler und mit einem hellen Einschnitt von vorne versehen. Bei beiden Segmenten sitzt an

der Aussenseite des Fleckens eine kleine Spitze, die einen Teil des Aderstriches darstellt. Der Subanalfleck ist an der Vorderbrust ein kleines Element nahe der Aussenseite des Submedianstriches; am Mesothorax ist er etwas mehr laterad gerückt, während er am Metathorax nahe der Innenseite des hinteren Teiles des Paradorsalstriches gelagert ist.

Auch bei *Dorylaea rhombifolia* Stoll. ist der hintere Teil des Paradorsalstriches aller Thoraxsegmente mehr oder weniger deutlich markiert. Bei der abgebildeten Larve (Abb. 9) ist er an allen drei Segmenten abgebrochen, und auch der Aderstrich ist unvollständig. Beim Imago (Abb. 6) ist der Aderstrich am Pro- und Metathorax vollständig, während dies nur am Prothorax für den Paradorsalstrich zutrifft. Im medianen Teil, in den ja die Flügel nicht hineinreichen, lassen sich alle drei Segmente vergleichen. Hier ist am Pro- und Mesothorax ein deutlicher Submedianstrich zu sehen. Weiter laterad liegt der Subanalfleck (der am Prothorax im Postdorsalstrich eingeschlossen ist). Am Metathorax ist der Subanalflecken so weit nach hinten gerückt, dass er mit dem Postdorsalstrich verbunden ist; der Submedianstrich ist nur vorne angedeutet. Das von beiden Submedianstrichen eingefasste Areal ist aber noch breiter als an der Mittelbrust. Der Dorsalflecken bildet nur vorn eine zusammenhängende Schwärzung, denn der vordere Dorsalraum fehlt. Umgekehrt ist der hintere Dorsalraum gross und durch den Bruch im Paradorsalstrich (ganz wie am Prothorax in Abb. 9) mit dem Paramarginalraum offen verbunden. Zusammenfassend lässt sich daher sagen, dass die hinteren Brustsegmente dem Prothorax in allen jenen Verhältnissen weitgehend ähneln, die nicht von der durch die Entwicklung eines Antenotums bedingten Sonderstellung dieses Segmentes beeinflusst werden.

Auch bei *Dorylaea* sp. (Abb. 10) fehlt in der Hinterbrust die Verbindung zwischen dem vorderen Teil des Dorsalfleckens und eine Schwärzung an der hinteren Notalfalte, die wie bei *Periplaneta, Methana* und *Dorylaea rhombifolia* von dem Marginalstrich — im mittleren Abschnitt mit dem Postdorsalstrich zusammen — gebildet wird.

Am Metathorax von *Syntomaptera heydeniana* Sauss (Abb. 13) entspricht das Muster ganz dem des Prothorax, nur ist hier wie

bei *Periplaneta* der hintere Teil des Paradorsalstriches zu einem Dreieck entwickelt, das nach der Mitte hin in eine schmale, schwache Analschwärzung übergeht. Die übrigen Teile der Segmente sind hell.

Blattellidae.

Blattellinae. Einige *Loboptera*-Spezies, die am Prothorax nur einen hellen Paramarginalraum besitzen, weisen ähnliche Verhältnisse auch an den übrigen Thoraxsegmenten auf. Ist jedoch auch ein heller Postmarginalraum vorhanden, so gilt dies nicht für die übrigen Brustsegmente. Von den anderen Blattellinen stehen — mit Ausnahme einiger Larven von *Blattella germanica* L. — nur geflügelte Individuen zur Untersuchung zur Verfügung. Bei dieser Art finden wir am Meso- und Metathorax dieselben Längsstreifen wie am Prothorax. Bei ganz jungen Tieren sind jedoch die dadurch eingeschlossenen, hellen Räume breiter als bei älteren.

Ectobiinae. *Hololampra maculata* Schreb. besitzt am ungeflügelten Metathorax wie am Prothorax einen hellen Post- und Paramarginalraum (im Gegensatz zu der obengenannten *Loboptera*-Art).

Nyctiborinae. Die Sammlung enthält nur eine einzige Larve eines *Heminyctibora* sp., die am Prothorax einen hellen Paramarginalraum aufweist. An den übrigen Thoraxsegmenten ist auch dieser nahezu verwischt.

Auch die Epilamprinae sind nicht durch artbestimmte Larven mit deutlich gezeichnetem Meso- und Metathorax vertreten. Dagegen findet sich reichliches Material einer *Epilamprinae* sp. mit kurzen, mesothorakalen Flügeln und ungeflügeltem Metathorax, sowie einige Larven derselben Spezies. Das Vorderbrustmuster dieser Art (Abb. 42) besteht im wesentlichen aus einem ähnlichen Muster wie bei *Nauphoeta* (vgl. Abb. 32), nämlich einem in Einzelelemente aufgelösten Dorsalflecken und hellen Marginalräumen. Die letzteren sind jedoch mit den für die Epilamprini charakteristischen kleinen Punkten überstreut, welche im Postmarginalraum zu kurzen Längsstreifen verschmelzen. Diese Streifen laufen vom Postdorsalstrich zum Hinterrand des Pronotums. Mittel- und Hinterbrust sind ganz ähnlich

gemustert; auch hier ist der Paramarginalraum heller und der Postmarginalraum von kleinen Längsstreifen durchsetzt. Die Stärke des Dorsalfleckens variiert unabhängig von der Intensität dieser Längsstreifen; es gibt sowohl Exemplare mit stark verdunkelten Dorsalflecken als solche (Abb. 42) mit einer so geringen Schwärzung dieses Fleckens, dass er nahezu hell erscheint, obwohl die kleinen Längsstreifen stark pigmentiert sind. Diese sind dann mit dem Paradorsalstrich zusammen die schwärzesten Elemente des Musters und machen charakteristischerweise an der Grenze der hinteren Notalfalte halt. Ein Aderstrich ist zuweilen an der Mittel- und (seltener) der Hinterbrust, nicht aber am Prothorax entwickelt.

Die Larve einer verwandten Art (Abb. 43) zeigt ähnliche Verhältnisse, nur ist der Dorsalfleck der Vorderbrust beinahe ganz schwarz. Jedes der beiden anderen Segmente hat einen Dorsalflecken, der besonders im hinteren Teil reduziert ist. Der Teil des Paradorsalstriches, der der inneren Grenze der Flügelanlage folgt, ist jedoch breit und stark geschwärzt und erinnert an die früher besprochenen, dreieckigen Schwärzungen bei *Periplaneta* usw. (vgl. Abb. 11). Auch Meso- und Metathorax zeigen Andeutungen eines Aderstriches.

Blaberidae.

Panchlorinae. Bei den Larven von *Nauphoeta* sp. aus Afrika (Abb. 32) fällt, wie bereits oben erwähnt, ein ähnliches Muster auf, das jedoch einen wohlentwickelten, bis zum Hinterrand reichenden Paradorsalstrich enthält; die hintere Notalfalte ist sehr schmal. Die für die Epilamprinen charakteristischen Längsstriche fehlen somit. Ein Exemplar hat einen deutlichen Aderstrich im Paramarginalraum und im hinteren Teil des Dorsalfleckens einen Subanalflecken, der in allen drei Brustsegmenten dieselbe Lage einnimmt.

Panesthiinae. Im Gegensatz zum Prothorax sind bei *Panesthia javanica* Serv. Meso- und Metathorax mit einem hellen Raum zu beiden Seiten der Mittellinie versehen, der offenbar als äusserer Teil des hinteren Dorsalraumes ausserhalb des Subanalstriches zu deuten ist, während der mittlere Teil des Dorsalfleckens sowie das Paranotum dunkel sind.

Die von mir untersuchten ungeflügelten Exemplare der Perisphaeriinae sind nur schwach gezeichnet. Das Weibchen von *Aptera fusca* Thunb. trägt oft am Prothorax die Andeutung eines Postmarginalraumes, der an den anderen Brustsegmenten etwas deutlicher wiederzufinden ist. Ein Individuum hat ausserdem einen etwas aufgehellten Paramarginalraum an allen drei Segmenten. Gleichlaufend variieren auch die drei Thoraxsegmente bei den sechs untersuchten Exemplaren von *Dasyposoma bicolor* Brunn., deren Muster oft von einem mit einem mehr oder weniger hellen oder bräunlichen Marginalraum umgebenen Dorsalflecken gebildet wird. Bei einigen Individuen erscheinen mehrere kleine, dunklere Flecken im Dorsalflecken, welche den Einzelelementen z. B. bei *Nauphoeta cinerea* (Abb. 31) entsprechen. Das am kontrastreichsten gemusterte Individuum (Abb. 45) besitzt am Dorsalflecken der Vorderbrust einen kleinen Vorsprung gegen den Apex hin, der an den übrigen Thoraxsegmenten noch deutlicher ist und einen Aderstrich oder vielleicht einen Teil einer Analschwärzung darstellt. Auch die schwache Verdunkelung des Paranotums kommt an allen drei Segmenten vor.

Blaberinae. Die Larven von *Blabera atropos* Brunn. (Abb. 46) besitzen am Prothorax einen rechtwinkligen Dorsalflecken mit vorderen und hinteren, von denen der anderen Seite durch einen breiten Medianstrich getrennten Dorsalräumen. Am Meso- und Metathorax ist dieser Medianstrich vorne schmal, hinten aber so breit wie am Prothorax. Der Subanalflecken ist noch dunkler als die übrigen geschwärzten Teile und hebt sich auch durch seine völlig glatte Oberfläche ab, ist aber in den Postdorsalstrich eingelagert. Am Prothorax finden wir eine ganz kleine Spitze unmittelbar vor diesem Flecken; diese Spitze ist an den beiden anderen Segmenten zu einem vorwärts gerichteten Strich durch den hinteren Dorsalraum entwickelt. Die hintere Notalfalte ist stärker geschwärzt als an der Vorderbrust, und die Paranota verhalten sich etwas abweichend: am Prothorax sind nur die Spitze und andeutungsweise der Hinterrand verdunkelt, während das ganze Paranotum der anderen Segmente vollkommen pigmentiert ist. Die Larve von *Blaptica dubia* Serv. ist mit einem sehr undeutlichen Muster versehen, doch sind auch hier fast dieselben Elemente wie bei der vorigen Art zu spüren.

Die Larve einer *Monachoda* sp. aus Brasilien (Abb. 47) trägt am Prothorax ein sehr verwischtes Muster, dessen Elemente schwer identifizierbar sind. Der am stärksten geschwärzte Flecken im vorderen Teil des Musters dürfte jedoch dem vorderen Teil des Paradorsalstriches entsprechen, der hier auffallend weit hinten am Segment liegt. Dies ist dadurch bedingt, dass das Antenotum ungemein breit und, umgekehrt, die hintere Hälfte des Dorsalfleckens stark eingeschränkt ist. Der deutliche, quer durch die Mitte des Dorsalfleckens laufende Strich liegt daher sehr weit nach hinten. Dagegen ist der Postdorsalstrich sehr schmal und schwach. Dies ist an den anderen Thoraxsegmenten weniger grell, weshalb ihre Muster mehr an jene der früher besprochenen Arten erinnern. An diesen Segmenten ist der Medianstrich wenigstens hinten breit, und der querliegende Strich durch den Dorsalflecken ist zu einem Flecken reduziert; der Postdorsalstrich fehlt. Dagegen ist der Paradorsalstrich besser entwickelt als am Prothorax. Die Wurzel des Aderstriches ist zu einem dunklen Flecken ausgebildet; ihr mittlerer Teil ist aber undeutlich und fehlt oft ganz, während die apikale Spitze des Striches wieder kräftiger geschwärzt ist.

Zusammenfassend lässt sich daher feststellen, dass alle drei Brustsegmente — wenn sie nicht eigentliche Flügel tragen — grundsätzlich übereinstimmend gemustert sind, obwohl die Unterschiede zwischen den verschiedenen Arten bedeutend sein können, ebenso wie die einzelnen Segmente eines Tieres nicht notwendig einander ganz ähnlich zu sein brauchen, obwohl sie meist ziemlich gleichlaufend variieren. Dies stellt eine Bestätigung der früher geäusserten Auffassung (Lemche 1940) dar, dass die Flügelanlagen der Schaben ihre ursprüngliche Stellung einnehmen. Es ist daher mit Hilfe des Zeichnungsmusters möglich, genauer zu erfassen, welcher Teil des Paranotums zum endgültigen Flügel wird. Bevor eine Lösung dieser Frage durch Untersuchung der geflügelten Segmente versucht wird, soll hier der Vollständigkeit halber eine Analyse der Muster der Abdominalsegmente im Vergleich zu denen des Thorax folgen.

2c. Das Muster des Abdomens.

Blattidae.

Polyzosteriinae. Bei den untersuchten Arten ist am Abdomen das gleiche Muster wie am Thorax, nur ist der Paramarginalraum — wenn überhaupt vorhanden — viel schmäler als an den Brustsegmenten. Bei den *Cosmozosteria*-Arten (vgl. Abb. 2) ist das Homologon des Dorsalfleckens am Abdomen eine dunkle Zone, die vom vordersten sichtbaren Teil des Segmentes bis zur hinteren Notalfalte reicht. Hinter diesem Bereich finden wir dann denselben Postmarginalraum wie am Thorax.

Blattinae. Einige Larven von *Cutilia* sp. haben am Thorax und am Abdomen einen hellen Paramarginalraum. Bei einem Imago der kurzflügeligen *Cutilia soror* Brunn. (Abb. 48) sind aber solche Paramarginalräume nur an den Abdominalsegmenten 2, 3 und 4 entwickelt; an drei weiteren Exemplaren sind sie verkümmert oder gar ganz verschwunden, während sie am Thorax erhalten sind. Bei *Syntomaptera heydeniana* Sauss. (Abb. 13) ist der gleichartige Aufbau des Musters aller Segmente deutlich zu sehen. Der Paradorsalstrich, der ja annähernd die Lage der Grenze zwischen Körper und Paranotum angibt, ist am Abdomen relativ weit nach aussen geschoben, was mit der geringen Grösse der abdominalen Paranota gut übereinstimmt. Dem entspricht auch der kleine Knick des Hinterrandes, dort, wo dieser Strich zum Rande stösst.

Methana sp. (Abb. 5) hat am Abdomen den gleichen Marginalstrich wie am Thorax, und innerhalb dieses liegt der Paramarginalraum; der Postmarginalstrich ist in seinem lateralen Teil breit und verhindert die Annäherung dieses Raumes an den Hinterrand. Der kleine Vorsprung an der Stelle des Aderstriches ist jedoch auch an den Abdominalsegmenten erhalten, wodurch der Paramarginalraum gewissermassen zweiteilig wird. Im Gegensatz zum Mesothorax ist der seitlicher liegende dieser Räume kürzer und reicht nicht so weit nach hinten als der mediale. (In dieser Hinsicht verhält sich der Metathorax intermediär.) Der Paradorsalstrich ist zwar unterbrochen, aber durch eine kleine Spitze am Postdorsalstrich markiert.

Dorylaea rhombifolia Stoll. bietet in der Deutung gewisse Schwierigkeiten. Bei einem schwach gezeichneten Individuum (Abb. 8) tragen die Abdominalsegmente deutliche Analschwär-

zungen, d. h. die ganze hintere Notalfalte zwischen Postdorsal- und Postmarginalstrich ist dunkel. Am ungeflügelten Mesothorax ist der paranotale Teil des Postmarginalstriches breiter als die Analschwärzung; dies gilt auch für das Abdomen, wo die seitlichen Teile der hinteren Schwärzung deutlich breiter sind als die grössere, mittlere Partie. Die Dicke der Segmente weist auch darauf hin, dass die abdominalen Paranota schmal sind, und dass daher der am Metathorax schmale Paradorsalstrich am Abdomen vollkommen reduziert ist. Etwas weiter mediad findet sich aber an den hintersten Segmenten ein dunkler Streifen, den man nach oberflächlicher Betrachtung mit einem Paradorsalstrich identifizieren könnte. Dies dürfte jedoch falsch sein, denn das Paranotum müsste dann sehr breit und teilweise mit Eingeweiden gefüllt sein; die obengenannte grössere Breite des äussersten Teils des Postmarginalstriches stimmt übrigens auch nicht mit einer solchen Auffassung überein. Dazu kommt, dass der dunkle Flecken der Abdominalsegmente, der dem Subanalflecken der Thoraxsegmente zu entsprechen scheint, offenbar einen Teil des genannten Striches ausmacht, der deshalb eher als Subanalstrich zu deuten ist. Dieses Abdominalmuster möchte ich daher folgendermassen beschreiben: ein Medianstrich ist vorhanden, der Submedianstrich fehlt, der Subanalstrich ist hinten vorhanden, an den vordersten Segmenten unterbrochen. Ein Paradorsalstrich fehlt (mit Ausnahme des 6. Segmentes), und die ganze hintere Notalfalte ist geschwärzt.

Bei anderen Individuen ist das Areal mediad zum Subanalstrich nahezu oder ganz geschwärzt (Abb. 6); schwache Andeutungen eines Paradorsalstriches können vorkommen.

Bei *Dorylaea* sp. (Abb. 10) ähnelt das abdominale Muster dem des Metathorax. Eine Analschwärzung bedeckt die hintere Notalfalte, und die Schwärzung am vorderen Teil der Segmente entspricht der vorderen Hälfte des Dorsalfleckens. Hieran schliessen sich ein Medianstrich und ein schmaler Paramarginalstrich.

Das Muster von *Periplaneta australasiae* F. (Abb. 11) (und undeutlicher von *P. americana* L.) lässt sich durch das von *Dorylaea rhombifolia* erklären. Wie dort fällt auch hier eine breite, dunkle Zone (vgl. Abb. 6) auf, die zu beiden Seiten durch einen dunkleren Längsstreifen begrenzt wird, der daher als

Subanalstrich anzusehen ist. Der Raum ausserhalb dieses Striches ist also nicht nur, wie man beim ersten Anblick leicht vermuten könnte, der Paramarginalraum, sondern schliesst auch den äussersten Teil des hinteren Dorsalraumes ein. Am Metathorax ist dies nicht der Fall, denn hier breitet sich die Flügelanlage infolge der Vergrösserung der Analpartie so stark aus, dass der Paradorsalstrich dicht an den Subanalflecken heranrückt, wodurch der Paramarginalraum allein so breit wie die kombinierten äussersten Teile der hinteren Dorsalräume und die Paramarginalräume der Abdominalsegmente wird.

Die Imagines der *Periplaneta*-Arten haben viel weniger dunkle Zeichnungen an den durch die Flügel bedeckten Teilen des Abdomens als an den freien larvalen Hinterleibssegmenten. Die gewöhnlichen zeichnungschaffenden Prinzipien scheinen jedoch hierdurch unverändert zu sein. Die Frage der weniger intensiven Schwärzung der bedeckten Teile soll später behandelt werden.

Blattellidae.

Blattellinae. *Temnopteryx capensis* Br. hat helle Para- und Postmarginalräume; der Dorsalflecken ist an jedem Segment nur vorn als schmaler, dunkler Streifen vorhanden. Der Hinterleib erscheint daher deutlich quergestrichelt. Bei einer *Temnopteryx* sp. sind umgekehrt die hintere Notalfalte, der Subanalstrich und das ganze Paranotum verdunkelt. Der Raum zwischen Subanalstrich und paranotale Schwärzung dürfte daher der laterale Teil des hinteren Dorsalraumes sein.

Einige *Loboptera*-Arten (*L. decipiens* Germ. u. a.) haben helle Paramarginalräume wie am Thorax. Eine *Loboptera* sp. hat sowohl am Thorax wie an den Abdominalsegmenten einen hellen Postmarginalstrich, der an den einzelnen Segmenten sehr verschieden breit ist.

Die meisten übrigen Blattelinen haben einfarbige Abdominalsegmente; *Thyrsocera histrio* Burm. und *Blattella germanica* L. besitzen jedoch helle Paramarginalräume, und *Th. histrio* hat einen schmalen Postmarginalraum, welcher dem am Prothorax entspricht.

Ectobiinae. *Hololampra maculata* Schreb., *Ectobia lappo-*

nica L. und *E. sylvestris* Scop. verhalten sich wie die letztgenannte Art.

[Chorisoneuridae. Die untersuchten Arten haben undeutliche Abdominalmuster.]

Nyctiborinae. Zwei Weibchen der untersuchten *Nyctibora* sp. haben am Abdomen einen hellen Dorsalraum, aber dunkle Paranota und eine dunkle hintere Notalfalte. Etwas innerhalb des Paranotums liegt der dunkle Subanalflecken im Dorsalraum. Bei *Opisthoplatea orientalis* Burm. gibt es laterale Räume, während die Mittelpartie dunkel ist. Die Grenze zwischen hell und dunkel verläuft bei einem der Individuen an der Stelle, wo an den eben genannten *Nyctibora*-Weibchen der Subanalflecken liegt, weshalb ich die Verhältnisse so deute, dass der helle laterale Bereich dem Paramarginalraum samt dem äusseren Teil des hinteren Dorsalraumes entspricht (vgl. *Periplaneta*, Abb. 11, und *Dorylaea*, Abb. 6). Bei anderen Individuen sind die hellen Räume des Abdomens schmäler.

Epilamprinae. *Paratropes phalerata* Erich. und *Phlebonotus pallens* Serv. haben breitere oder schmälere, helle Seitenpartien ähnlicher Art wie *Opisthoplatea*; bei *Phlebonotus* ist auch ein ganz schmaler Postmarginalraum angedeutet.

Phaetalia pallida Burm. und *Calolampra irrorata* F. tragen ähnliche Abdominalmuster, aber die hellen Areale sind so schmal, dass sie nur als Paramarginalräume gedeutet werden können. Diese Auffassung wird noch dadurch gestützt, dass an der weniger stark geschwärzten *Calolampra* der sehr dunkle Subanalflecken etwas innerhalb des dunklen Mittelbereiches liegt. Auch hier finden wir die übliche Parallelität zwischen dem Muster des Thorax und dem des Abdomens: bei *Phaetalia* ist der Dorsalflecken sowohl am Prothorax als an den Abdominalsegmenten sehr dunkel, während bei *Calolampra* alle Dorsalflecken weniger geschwärzt (an der Vorderbrust in kleinere Elemente aufgelöst) sind.

Andere Epilamprinen haben viel detailreichere Muster, so z. B. das Weibchen von *Molytria inquinata* Stål. (Abb. 25) und einige *Epilamprinae* spp. (Abb. 42—44). Am Prothorax der letzteren ziehen sich — wie bereits früher erwähnt — kleine Längsstreifen durch den Postmarginalraum, und solche Streifen werden auch am Abdomen wiedergefunden. Dies gilt auch für

Molytria, wo die Längsstreifen mit gleichmässigen Zwischenräumen zum Hinterrand laufen, von einem schwach verdunkelten, über die Mitte des Segmentes führenden Querstrich, dem Postdorsalstrich, ausgehend. Der Raum vor diesem Strich wird von einigen wenigen, breiteren Längsstrichen durchzogen, welche als Medianstrich, Submedianstrich und Subanalstrich gedeutet werden. Etwas seitlich vom Subanalstrich neigt der Postmarginalstrich nach vorne und zieht sich dann als Paradorsalstrich gegen die vordere Ecke des Segmentes hin. Es macht durchaus den Eindruck, als ob das Paranotum schmal sei, was dadurch bestätigt wird, dass ein kleiner Fleck nahe der vorderen Ecke dem kleinen Vorsprung an der Seite des prothorakalen Dorsalfleckens zu entsprechen scheint. Eine der genannten *Epilamprinae* sp. (Abb. 44) weist ein jenem nahezu in allen Einzelheiten identisches Muster auf, während eine andere (Abb. 42) einen rudimentären Dorsalflecken, aber besonders deutliche kleine Längsstreifen besitzt. Die Lage der Grenze zwischen Paranotum und Körper ist bei allen diesen Epilamprinen undeutlich, was vermutlich auf die sehr geringe Breite der Paranota zurückzuführen ist.

Blaberidae.

Viele Panchlorinae haben ein einfarbiges Abdomen; ist dieses dunkel, so findet sich zuweilen ein ganz schwach angedeuteter, schmaler Paramarginalraum (*Leucophaea surinamensis* L. und *Tribonidium signaticollis* Burm.). Bei *Nauphoeta occidentalis* F. haben sowohl der Prothorax wie die Abdominalsegmente einen deutlichen Postmarginalraum, wogegen der Paramarginalraum am Prothorax sehr schmal ist und am Abdomen ganz fehlt.

Sowohl Larven als Imagines einer *Nauphoeta* sp. (Abb. 32) haben eine grosse, dunkle Mittelzone an jedem Segment. Von hier aus breitet sich eine aus Postdorsal- und Postmarginalstrich bestehende Schwärzung den Hinterrand entlang bis zum Subanalstrich aus. Der Paradorsalstrich scheint ganz nahe am Seitenrand zu liegen, was mit der geringen Breite des Paranotums übereinstimmt. Der äussere Teil des Postmarginalstriches fehlt. Bei anderen Exemplaren ist der ganze Bereich innerhalb der Subanalstriche geschwärzt. Ganz wie bei *Periplaneta* (vgl. Abb. 11) setzt sich der Paradorsalstrich der Thorakalsegmente anscheinend

in den Subanalstrich des Abdomens fort. Dies dürfte jedoch für die Homologisierung ohne Bedeutung sein, denn der Subanalflecken liegt am Abdomen weiter laterad als am Thorax (vgl. auch unten die Blaberinae, wo eine entsprechende Deutung sicher erscheint). Es bleibt noch die Frage ungelöst, weshalb am Abdomen nicht der ganze Dorsalraum verdunkelt ist, wenn dies doch am Thorax der Fall ist.

Rhyparobia maderae F. (Abb. 33) hat ein nahezu ganz helles Abdomen; einige Muskelansätze am Thorax sind jedoch dunkel, namentlich der deutliche, breit ovale Subanalflecken. Vor diesem liegt am Thorax in einigem Abstand ein anderer Flecken, der offenbar einen Teil des Subanalstriches darstellt (ss). Beide Flecken sind auch am Abdomen ungefähr in gleicher Form wie am Thorax zu finden, und sie liegen genau dort, wo sie nach der oben stehenden Deutung des Musters von *Nauphoeta* sp. zu erwarten sind.

Panesthiinae. Das Abdomen aller untersuchten Arten ist wie der Thorax einfarbig dunkel.

Perisphaeriinae. Das Männchen von *Aptera fusca* Thunb. besitzt am Abdomen wie am Thorax wohlentwickelte Postmarginalräume, die gegen die Seiten hin allmählich in die Paramarginalräume übergehen. Sonst füllen die Dorsalflecken die Segmente aus. Auch eine *Paranauphoeta* sp. weist sehr deutlich die Übereinstimmung zwischen Thorax und Abdomen auf: an beiden ist der mittlere Teil des Postmarginalraumes schmal, der laterale Teil dagegen (ausserhalb des Subanalfleckens) breiter. Eine andere *Paranauphoeta*-Art trägt nur Reste des Postmarginalraumes an den seitlichen Teilen; hier ist aber das Muster des Prothorax stark verändert (vgl. Abb. 38), ohne dass dies Veränderungen im Abdominalmuster bewirkt hätte.

Das abdominale Muster von *Proscratea complanata* Perty ist durch ein Netzwerk dunkler Linien undeutlich gemacht und lässt sich nicht durch eine Untersuchung des einzigen in der Sammlung vorhandenen Individuums mit dem deutlichen und leicht analysierbaren Vorderbrustmuster vergleichen.

Dem hellen Prothorax von *Hormetica laevigata* Burm. entsprechend ist auch das Abdomen dieser Art hell, während *H. verrucosa* Brunn. (Abb. 34) und *Brachycola tuberculata* Dalm. helle Paramarginalräume am sonst geschwärzten Abdomen auf-

weisen, was gut mit dem Muster des Prothorax übereinstimmt, besonders da beide Arten breite Verbindungen zwischen dem prothorakalen Dorsalflecken und dem Hinterrand dieses Segmentes besitzen, was sozusagen eine Verschmelzung des Dorsalflecken mit dem Postmarginalstrich andeutet.

Bei (?)*Dasyposoma bicolor* Brunn. (Abb. 45) sind die Postmarginalräume des Thorax wie des Abdomens so wohlentwickelt, dass der ganze Körper quergestrichelt erscheint. Ähnliches gilt auch für *Parahormetica bilobata* Sauss. (Abb. 35), wo der Dorsalflecken an den Brustsegmenten als ein ringförmiger Dorsalstrich ausgebildet ist. Hier trägt jedes Abdominalsegment einen schmalen Strich an der Grenze zwischen Körper und hinterer Notalfalte, welcher daher einen — wenn auch nur angedeuteten — Postdorsalstrich darstellt.

Blaberinae. Diese Unterfamilie ist durch breite Paranota charakterisiert. Das gewöhnlich sehr deutliche abdominale Muster ist bei der Larve von *Blabera atropos* Stoll. (Abb. 46) typisch entwickelt; ganz wie am Thorax ist hier die hintere Notalfalte geschwärzt. Am zweiten Abdominalsegment ist auch das Paranotum verdunkelt, und das Muster entspricht somit in dieser Hinsicht ganz dem des Thorax, was auch für verschiedene andere Zeichnungselemente zutrifft. So liegt der Subanalflecken am Thorax genau hinter einem buchtigen Subanalstrich und nur wenig mediad zur Wurzel der Flügelanlage. Auch am zweiten Abdominalsegment liegt er fast an der entsprechenden Stelle nur ein wenig nach vorn geschoben. Auch der Subanalstrich wird hier — durch den äusseren Teil des Dorsalraumes ziehend — wieder gefunden. Der breite, etwas mehr medial liegende Längsstrich dürfte danach der Submedianstrich sein, welcher am Abdomen ein viel grösseres Areal als am Thorax umschliesst. Der mittlere Strich ist daher der Medianstrich. Die anderen Abdominalsegmente verhalten sich genau ebenso, mit der einzigen Ausnahme, dass ein heller Raum, der Postmarginalraum, an der Wurzel des Paranotums (wie auch am Mesothorax angedeutet) den Paradorsalstrich nach aussen hin begrenzt. Dieser Strich ist in einigen Fällen unterbrochen, in anderen dagegen nicht.

Bei *Blaptica dubia* Serv. (Abb. 39) fehlt der Medianstrich, sie besitzt aber sonst ein ganz ähnliches abdominales Muster. Der

Submedianstrich ist sehr breit, der Subanalstrich etwas schmäler, und der Paradorsalstrich schmal aber deutlich, und er liegt sehr weit laterad. Bei einigen anderen Weibchen derselben Art ist der Paradorsalstrich weniger deutlich oder garnicht vorhanden. Bei den Larven ist das Muster ähnlich, aber sehr verwischt; nur die subanalen Muskelansätze sind deutlich und liegen am Abdomen genau in demselben Verhältnis zum Paranotum wie am Thorax. Der Subanalstrich ist bei dieser Art immer wohlentwickelt, dagegen variiert der Submedianstrich, der bei den Weibchen oft in seinem vorderen Teil reduziert ist und nur als eine schwache Ausbuchtung der Analschwärzung hervortritt.

Monastria biguttata Thunb. besitzt am Prothorax einen deutlichen Paramarginalraum und am Abdomen deutliche Paranota, hat aber trotzdem ein ganz schwarzes Abdomen.

Die Larve von *Monachoda sp.* (Abb. 47) ist mit einem abdominalen Muster versehen, das durch einen Vergleich mit dem Muster von *Blabera* (vgl. Abb. 46) teilweise gedeutet werden kann. Ihre sehr breiten Paranota bewirken, dass der Paradorsalstrich sehr weit mediad liegt. Der Zwischenraum zwischen Paradorsalstrich und Subanalstrich ist äusserst schmal und vorne verwischt; anscheinend ist der Submedianstrich etwas nach der Seite hin verschoben. Infolge der Undeutlichkeit des mittleren Teiles des Musters ist es aber unmöglich, die Grenzen des Submedianstriches genau festzustellen. Es sei hier nur noch auf die Lage des Paradorsalstriches hingewiesen, der vor der dunkelsten Partie am Thorax den schwachen Aderstrich abgibt. Dieser Strich scheint am Abdomen zu fehlen, während sich hier der Paradorsalstrich hinten längs des Paranotum-Randes in einen Postmarginalstrich verlängert.

Diplopteridae

besitzen am Abdomen auch kein Zeichnungsmuster.

Corydiidae.

Die Paranota sind bei *Corydia petiveriana* L. schmal, und die seitlichen Räume dieser Art dürften daher (wie bei *Periplaneta* etc., siehe Abb. 11) aus dem Paramarginalraum und dem äusseren Teil des hinteren Dorsalraumes zusammengesetzt sein. Die übrigen Teile der Segmente sind schwarz.

Der Vollständigkeit halber sei hier noch kurz erwähnt, dass die Unterseiten der Abdominalsegmente ein Muster tragen, das genau wie das der Oberseiten aufgebaut (*Cosmozosteria polyzona*, *Cutilia* sp., *Dorylaea rhombifolia*, *Blabera atropos*) oder verwischter und gleichmässig gefärbt ist (*Blaptica dubia*, *Paranauphoeta* sp., *Aptera fusca* etc.). Mitunter ist die Unterseite hell (*Cosmozosteria multifasciata*).

Das Muster des Abdomens ähnelt daher prinzipiell dem des Thorax, obwohl das thorakale Muster oft infolge grösserer Spezialisierung dieser Segmente besonders reich gegliedert ist.

2 d. Das Muster der geflügelten Segmente.

Hier sind besonders folgende Fragen zu beantworten: Welcher Teil des Paranotums wird zum Flügel? Können die einzelnen Felder der Flügel genauer am ungeflügelten Segment lokalisiert werden? Und welche Zeichnungsprinzipien machen sich auf den Flügeln geltend?

Blattidae.

Polyzosteriinae. Alle untersuchten Arten dieser Gruppe sind ungeflügelt mit Ausnahme von *Melanozosteria nitida* Brunn., deren kurze Flügel und deren ganzer Körper einfarbig schwarz sind.

Blattinae. Wie früher erwähnt, ist der Paramarginalraum bei der Gattung *Methana* (und *Cutilia*) oft — im Gegensatz zum übrigen Körper — hell, und bei *M. marginalis* Sauss. (Abb. 49) und *M. soror* Sauss. ist entsprechend der subcostale Teil des Flügels hell (bei *M. soror* läuft der helle Teil durch das ganze Radiusareal). In der Ruhestellung des Flügels liegt der helle Bereich genau so wie der Paramarginalraum am ungeflügelten Segment; es soll daher untersucht werden, ob diese beiden Bildungen wirklich zu homologisieren sind.

Bei *Cutilia soror* Brunn. (Abb. 48) sind die Muster der vorderen Segmente einander ähnlich; nur der Paramarginalraum ist hell. Bei flüchtiger Betrachtung fällt es überhaupt nicht auf, dass am Mesothorax ein kleiner Flügel freigelegt ist. Das Muster ist davon ganz unabhängig, und der helle Teil längs des »Vorderrandes« des Flügels, wie wir ihn bei *M. marginalis* finden, dürfte

dem Paramarginalraum entsprechen. Nur ist bei *Cutilia soror* der »hintere«, vom Rand des Dorsalfleckens geschwärzte Flügelteil sehr klein, während er am wohlentwickelten Flügel viel grösser als der Paramarginalraum ist. Weiter geht hieraus vor, dass der Dorsalflecken schon determiniert ist, wenn der Einschnitt den Flügel freilegt, denn dadurch wird ja ein Teil des Dorsalfleckens vollständig vom übrigen abgetrennt.

Hieraus können wir erstens schliessen, dass dieser Flügel in seiner ursprünglichen, nach hinten gerichteten Stellung liegt (vgl. Lemche 1940), und zweitens, dass der Apex mit der hinteren Ecke des Paranotums homolog ist.

Dasselbe Flügelmuster findet sich auch bei *Periplaneta australasiae* F. (und mitunter, wenn auch sehr undeutlich, bei *P. americana* L.); hier stimmt das Muster aber nicht so gut mit dem des Prothorax überein; dort ist der Paramarginalraum weniger breit, dafür aber teilweise mit dem hinteren, äusseren Dorsalraum verschmolzen. Bei den Larven lässt sich durch einen Vergleich mit dem Verlauf der Tracheen nachweisen, dass der helle Paramarginalraum bedeutend mehr als den subcostalen Teil des fertigen Flügels umfasst. Hier setzt daher eine Reduktion des Areals der hellen Zeichnung während der Entwicklung ein.

Bei *Methana* und *Periplaneta* ist der Körper der flügeltragenden Segmente immer hell, mit Ausnahme eines dunkleren Areals am Mesothorax von *P. australasiae*, das sicher dem vorderen Teil des Dorsalfleckens entspricht. Da die hintere Notalfalte schmal und das Paranotum zum Flügel geworden ist, bleibt im wesentlichen nur der Dorsalflecken am Rest des Segmentes zurück, und der hintere Teil dieses Fleckens erscheint am Prothorax hell (Abb. 11). Die Helligkeit des hinteren Teiles des Segmentes entspricht daher vollkommen der am Prothorax.

Die kurzflügelige *Syntomaptera heydeniana* Sauss. (Abb. 13) weist ganz ähnliche Verhältnisse wie *Cutilia soror* (vgl. Abb. 48) auf, jedoch mit dem Unterschied, dass an allen Segmenten der ganze Dorsalraum hell ist. Ein kleiner Teil des Dorsalfleckens ist dem Flügel mitgegeben.

Dorylaea rhombifolia Stoll. (Abb. 7) erlaubt durch ihr an Einzelheiten reicheres Muster einen viel genaueren Vergleich der ungeflügelten und geflügelten Segmente. Nach Entfernung eines Flügels finden wir am Mesothorax nur noch die dem Dorsal-

flecken angehörenden Zeichnungselemente. In genau derselben Weise wie der Paradorsalstrich am ungeflügelten Metathorax erstreckt sich längs des sekundären Seitenrandes eine dunkle Zunge von vorne nach hinten, und auch der hinterste Teil dieses Striches ist zum Teil vorhanden. Am Flügel finden wir eine mediale Schwärzung, die offenbar auch als ein Teil des Paradorsalstriches aufzufassen ist. Es dürfte also auch hier wie bei *Syntomaptera* so sein, dass der den Flügel freilegende Einschnitt ungefähr der Mitte dieses Striches entlang verläuft. Der Flügel trägt weiter einen deutlichen Aderstrich und an seiner Aussenseite einen durch einen Paramarginalstrich begrenzten Paramarginalraum. Hier ist daher ohne Zweifel das Paranotum zum Flügel geworden, hat aber seine ursprüngliche Grösse und Stellung beibehalten. Es geht hieraus hervor, dass der sekundäre Seitenrand des Segmentes einen ganz anderen Charakter hat und andere Zeichnungselemente trägt als der primäre Seitenrand des Paranotums.

Blattellidae.

Blattellinae. *Ceratinoptera diaphana* F. (Abb. 14) ist *Syntomaptera* (vgl. Abb. 13) sehr ähnlich. Der Paradorsalstrich der Vorderbrust ist etwas S-förmig geschwungen, was auch am Flügel erkennbar ist, und der Paramarginalraum bedeckt beinahe den ganzen Radiusteil. Etwas fraglicher erscheint es, inwieweit die helle Analpartie des Flügels als ein Teil des hellen Dorsalraumes des Prothorax anzusehen ist. Der Aderstrich ist weder am Prothorax noch am Flügel allein zu sehen.

Loboptera indica Brunn. besitzt wie *Methana marginalis* (vgl. Abb. 49) einen hellen Paramarginalraum am Prothorax und am Flügel. Dagegen trägt die übrige Mittelbrust vorne zu beiden Seiten der Mitte einen grossen Raum, der einem Teil des Dorsalraumes entspricht, am Prothorax aber nicht entwickelt ist. Geflügelte Individuen anderer *Loboptera*-Spezies wurden nicht untersucht.

In ähnlicher Weise hat *Pseudomops neglecta* Shelf. ziemlich breite Marginalräume am Prothorax und — jedenfalls bei einigen Exemplaren — auch einen relativ breiten Raum am costalen Flügelrand. *Pseudomops cincta* Burm. und viele *Ps. crinicornis* Burm. tragen am Prothorax viel schmalere Paramarginalräume

und entsprechend verschmälerte Räume am costalen Flügelrand, oder diese sind verkürzt, so dass sie nur das subcostale Areal bedecken. *Thyrsocera histrio* Burm. (Abb. 50) und gewissermassen auch *Hemithyrsocera soror* Burm. verhalten sich ähnlich, nur ist die Grenze zwischen Paramarginalraum und Dorsalflecken am Flügel etwas stärker gefärbt, wodurch ein Übergang zum Muster von *Pseudischnoptera lineata* Oliv. (Abb. 51) gebildet wird. Die prothorakalen Ante- und Paramarginalräume sind hier deutlich gegen das sonst schwarze Notum abgesetzt, und sowohl am Vorder- wie am Hinterflügel ist daher der Paramarginalraum wohlentwickelt. Um ganz dem Vorderbrustmuster zu entsprechen, müsste dann der übrige Flügel dunkel sein, dies ist aber nur am Hinterflügel der Fall, und auch dort nur annäherungsweise. Am inneren Teil des Vorderflügels sind jedoch nur die Adern geschwärzt. Dagegen sind die Stämme der grossen Adern so stark verdunkelt, dass ein sehr augenfälliger schwarzer Streifen über die Flügelwurzel hinaus noch zwei Drittel der Flügellänge durchzieht.

Blattella germanica L. hat ganz helle Paranota am Prothorax und dementsprechend ganz helle Flügel. *Bl. supellectilium* Serv. (Abb. 52) hat aber sowohl am Prothorax wie am Flügel einen hellen Paramarginalraum, der sich über die Subcostalpartie ausbreitet. Die übrige Flügelfläche ist im grossen Ganzen dunkel, die Verdunklung bildet aber zwei sehr breite Bänder quer über den Flügel, das innere läuft durch die Analpartie, während das äussere am Weibchen bis nahe an die Spitze des etwas verkürzten Flügels reicht. Beim längeren Flügel des Männchens ist die ganze Flügelspitze hell. Am Weibchen stossen die beiden Bänder am medialen Rand des Flügels zusammen, und der Zwischenraum ist daher auf den lateralen Flügelteil begrenzt, wo er als eine Ausbuchtung des Paramarginalraumes erscheint, die einer kleinen Ausbuchtung am Paramarginalraum des Prothorax entspricht.

Pseudophyllodromia alternans Serv. (Abb. 19) und *Ps. histrio* Sauss. haben einen hellen prothorakalen Paramarginalraum und dementsprechend auch einen deutlich hellen subcostalen Flügelteil; aber ebenso wie der Dorsalflecken des Prothorax vielfach unterteilt ist, ist auch die Zeichnung des übrigen Teiles des Flügels zersplittert, und zwar als Aderzeichnung. Nur liegt ein schwacher

Schatten schräg über der Flügelfläche längs der Grenze des durch den anderen Flügel verdeckten (oder dieses verdeckenden) Areals. Von dort an nimmt die Stärke der Färbung gegen den Apex und den Hinterrand des Flügels allmählich ab. Am Hinterflügel rückt der entsprechende Streifen etwas mehr gegen den (lateralen) Flügelvorderrand und erreicht deutlicher die Flügelspitze. Das Analfeld ist, wie gewöhnlich, hell.

Ectobiinae. Bei zwei kurzflügeligen Individuen von *Hololampra maculata* Schreb. sind am Prothorax alle Marginalräume entwickelt. Das eine Exemplar besitzt fast ganz helle Vorderflügel, aber bei dem anderen, dessen Flügel noch kleiner sind, liegt das Muster am Flügel ebenso wie am Prothorax, d. h. der subcostale Flügelteil und die Flügelspitze sind hell, während der Analteil und sein angrenzender Bereich wie der Dorsalflecken des Prothorax verdunkelt sind. Das metathorakale Paranotum ist entsprechend gefärbt. Der etwas grössere Flügel von *Hololampra brevipennis* Fisch. verhält sich ähnlich, dagegen ist bei *H. marginata* Schreb. ein grösserer Teil des Flügels geschwärzt; hier sind nur der Paramarginalraum und ein Streifen längs des Randes der Analpartie hell.

Ectobia lapponica L. und *E. sylvestris* Scop. tragen Schwärzungen fast nur an den grossen Aderstämmen, d. h. an der Grenze zwischen Paramarginalraum und Dorsalfleck, ähnlich wie die oben besprochene *Pseudischnoptera lineata* (vgl. Abb. 51). Auch bei diesen Arten ist der Paramarginalraum des Flügels wohlentwickelt. Der übrige Teil der Flügelfläche ist aber nur wenig verdunkelt (auch am Prothorax von *E. lapponica* sind die Schwärzungen schwach), und die Zeichnung liegt nicht an den Adern selbst, sondern in den Zwischenräumen (was übrigens auch bei *Hololampra brevipennis* angedeutet ist). *Theganopteryx aethiopica* Sauss. dagegen hat am Prothorax und längs des »Vorderrandes« des Flügels denselben hellen Paramarginalraum wie *Methana marginalis* (vgl. Abb. 49). Der Hinterflügel dieser Art ist praktisch ohne Schwärzungen.

[Chorisoneuridae zeigen auch im Zeichnungsmuster des Flügels Anknüpfungen an die oben besprochenen Unterfamilien; so hat *Chorisoneura* sp. sowohl am Vorder- wie am Hinterflügel dasselbe Muster wie *Pseudischnoptera*. Auch liegt die Schwärzung vorzugsweise in den Zwischenräumen. *Areolaria* sp. zeigt ein

ähnliches Muster sowohl am Prothorax wie am Flügel, nur ist der Paramarginalraum immer schmal.]

Nyctiborinae. *Nyctibora crassicornis* Burm. (Abb. 23) trägt am Prothorax sowohl einen Para- als einen Postmarginalraum, und dementsprechend sind auch beide Flügelpaare grösstenteils hell, obwohl im Gegensatz zum Prothorax ein Aderstrich über den grossen Aderstämmen liegt. Weiter ist der »Hinterrand« des Flügels mit einer Verdunkelung versehen, die am Vorderflügel besonders von der Spitze des Analfeldes bis zum Apex ausgeprägt ist, während am Hinterflügel die Schwärzung des Analfeldes breiter ist. Am Prothorax findet sich als Homologon zur letztgenannten Bildung nur ein etwas verbreiteter Marginalstrich am Hinterrand des Paranotums. Bei den übrigen Nyctiborinen sind die Flügel einfarbig dunkel; ebenso bei der am Prothorax mit einem Paramarginalraum versehenen *Heminyctibora* sp.

Epilamprinae. Bei den Phoraspinen liegen die gleichen Verhältnisse vor wie bei den übrigen Unterfamilien. Die *Paratropes*-Arten haben am Prothorax einen wohlentwickelten Paramarginalraum und am Vorderflügel einen hellen Raum über das subcostale Feld und dessen Fortsetzung gegen den Apex zu, oft mit einem mehr oder weniger breiten Marginalstrich längs der Kante (wozu kein entsprechender an der Vorderbrust entwickelt ist). Bei einem Exemplar von *Paratropes phalerata* Erich. (Abb. 28) ist ein Teil des prothorakalen Postmarginalraumes entwickelt. Dies deutet eine gewisse Neigung zur Bildung heller Areale am Hinterrand an, wie sie auch bei dem oben besprochenen *Nyctibora crassicornis* verwirklicht sind, und es ist daher auch an beiden Flügelpaaren ein der letztgenannten Art entsprechendes Muster entwickelt, nur mit einer einzigen Hinzufügung. Die Schwärzung am ganzen Hinterrand von *Nyctibora* wird unverändert an beiden Flügelpaaren von *Paratropes* wiedergefunden, und selbst der Unterschied zwischen den beiden Flügeln tritt in der Färbung des Analfeldrandes unverändert auf. Am Vorderflügel von *Paratropes* reicht der Aderstrich etwas näher an den Apex heran als bei *Nyctibora*, so dass er sich mit der Hinterrandschwärzung nahe der Flügelspitze vereinigt. Hierzu kommt aber als neues Element noch ein Strich mitten zwischen den bereits genannten Strichen, wodurch der ganze Flügel aller

drei untersuchten *Paratropes*-Arten drei längslaufende Räume trägt, die durch schmale Striche von einander getrennt werden: Der »vordere« Raum ist der Paramarginalraum, der mittlere reicht von der Wurzel des Analfeldes bis zum Apex, und der »hintere« Raum bedeckt den letzten Teil des Flügels.

Unter den Zeichnungselementen der besprochenen Arten fällt im besonderen der Marginalstrich auf, der an den Flügeln der früher erwähnten Familien und Unterfamilien beinahe immer fehlt. Bei den *Phoraspis*-Arten ist dieser Strich am Vorderflügel noch kräftiger, obwohl er nicht am Prothorax vorkommt. Er ist am Flügel von *Ph. picta* Drury (Abb. 27), *Ph. leucogramma* Perty und *Ph. fastuosa* Blanch. deutlich gegen den hellen Paramarginalraum abgesetzt. Aber nur *Ph. picta* trägt am Prothorax einen entsprechenden Paramarginalraum; bei den anderen ist die ganze Vorderbrust hell, was auch auf einige Individuen einer Varietät von *Ph. picta* zutrifft. Bei der letztgenannten Art ist übrigens der Dorsalflecken des Vorderflügels so wenig verdunkelt, dass die Färbung bräunlich erscheint; nur der Marginalstrich ist schwarz. Dieser dürfte daher nicht auf dasselbe Prinzip wie der Dorsalflecken zurückzuführen sein.

Die Epilamprini sind auch im Flügelmuster durch das Vorkommen der bei der Besprechung der ungeflügelten Segmente erwähnten kleinen Punkte charakterisiert; diese sind hier so angebracht, dass die Verschiedenheit der beiden Sorten deutlich hervortritt. So finden wir z. B. bei *Calolampra irrorata* F. (Abb. 53) und einer unbestimmten, verwandten Spezies, dass die grösseren Punkte an den Flügeladern liegen, während sie an den Aderzwischenräumen ganz fehlen. Der erstgenannten Art fehlt die kleine Punktsorte am Flügel völlig; bei einer *Homalopteryx* sp. aus den Nicobaren stehen jedoch umgekehrt viele kleine Punkte dicht nebeneinander, und zwar jeder in eine Punktgrube zwischen den Adern versenkt, und bilden regelmässige Punktreihen, während die grösseren Punkte nur über den Adern als vereinzelte, schwache Schatten erkennbar sind. Die scharfe Unterscheidung zwischen den beiden Punktsorten tritt aber bei den meisten Epilamprinen nur undeutlich zutage, da die grösseren Punkte zu weiter ausgebreiteten Flecken über den Flügeln geworden sind, in welche die kleineren als Bausteine eingehen, so wie die Punkte eines Rasters in der Autotypie.

Calolampra irrorata (Abb. 53) besitzt ausserdem am Prothorax wie am Vorderflügel einen deutlichen Paramarginalraum, der nach innen durch einen aufgelösten Dorsalflecken begrenzt ist. Die Grenze zwischen beiden Arealen ist am Flügel durch einen kräftigen Aderstrich hervorgehoben, welchem an der Vorderbrust nur eine schwache Verdunkelung der Elemente entspricht. Bei *Phaetalia pallida* Burm. fehlen die Punkte beider Sorten sowohl am Prothorax wie am Flügel; dieser besitzt jedoch einen Aderstrich, und die Grenze zwischen dem Paramarginalraum und dem Dorsalflecken am Prothorax ist schwärzer als der übrige Teil des Fleckens. Umgekehrt sind bei einer unbestimmten Epilamprine die kleinen Punkte sowohl über die Vorderbrust als den Flügel verstreut, aber der Aderstrich fehlt.

Das halbgross-geflügelte Weibchen von *Molytria inquinata* Stål. weicht vom vollgeflügelten Männchen ab. Das Weibchen (Abb. 25) besitzt wie die genannte *Calolampra* einen Paramarginalraum sowohl am Prothorax als am Vorderflügel, während der Dorsalflecken bei beiden dunkel ist. Die Schwärzung ist jedoch nicht gleichmässig, da sie und die Räume mit beiden oben erwähnten Punktsorten versehen sind; die grösseren Punkte sind ziemlich häufig. In den Räumen liegen sie noch deutlich getrennt, aber im Dorsalflecken der Vorderbrust — und ähnlich am grössten Teil des Flügels — sind sie zu einem Netzwerk grösserer Figuren verschmolzen, das am Prothorax einen beinahe zusammenhängenden Dorsalflecken bildet, am Flügel aber den Charakter eines Netzwerkes mit eingesprengten, kleinen, hellen Partien beibehalten hat. Das Männchen zeigt wohl prinzipiell die gleiche Zeichnung, aber die weit grössere Streckung des Flügels zieht das Netzwerk stärker auseinander, und in den hellen Bereichen tritt eine Tendenz zur Bildung von Querlinien hervor, an deren inneren Grenzen die schwärzesten Teilen des Netzwerkes liegen. Dies ist bei einem Exemplar von *Molytria plana* (Abb. 54) noch augenfälliger: hier erscheinen die dunkelsten Zonen als grosse Flecken innerhalb der Räume. Anderen Exemplaren (falls die vorhandene Artbestimmung richtig ist) fehlt diese Zeichnung nahezu oder völlig. Ähnlich verhält sich *Heterolampra lurida* Burm. und in gewissem Grade auch *Pseudophoraspis nebulosa* Burm. Bei letztgenannter Art besteht nahezu das ganze Flügel-

muster aus den beschriebenen Räumen und Flecken, wodurch die Ähnlichkeit mit typischen, früher an verschiedenen Insekten nachgewiesenen Querbinden (v. Linden 1901, Lemche 1935) noch deutlicher wird. Ob wir es hier wirklich mit einem diesen Querbinden homologen Zeichnungstypus zu tun haben, dürfte allerdings etwas unsicher sein. Die vielen Aderverzweigungen an den Blattoideenflügeln machen es nahezu unmöglich, eine etwaige Abhängigkeit zwischen Muster und Adern sicher nachzuweisen, denn viele Verzweigungen werden immer mit irgendeiner Deutung übereinstimmen, selbst wenn ihnen überhaupt keine gemeinsamen Prinzipien zu Grunde liegen. Eine gemeinsame Rhythmik zwischen Adern und Muster ist nur am Subcostalfeld deutlich.

Eine kleinflügelige *Epilamprinae* sp. (Abb. 44) hat am Prothorax einen kräftigen, jedoch nicht ganz ausgefüllten Dorsalflecken mit einem lateralen, kleinen Vorsprung (der die Wurzel des Aderstriches darstellt). Ähnlich ist es auch am Mesothorax, nur liegt der genannte Vorsprung weiter vorn und setzt sich unmittelbar im Aderstrich des Flügels fort. Der Flügel ist aber sehr unvollständig; jede Spur eines Flügelgelenkes fehlt vollkommen, und die Oberfläche des Flügels stellt eine unmittelbare Fortsetzung der Oberfläche des übrigen Segmentes dar. Weiter wird seitlich des Aderstriches ein normaler Paramarginalraum sichtbar, der das Subcostalfeld und den »vorderen« (eigentlich lateralen) Teil des Radiusfeldes deckt. Die früher erwähnten dunklen Punkte sind nicht im Paramarginalraum, wohl aber am inneren Teil des Flügels erkennbar, wo sie sich an der Stelle eines Teiles des Dorsalfleckens befinden. Der nicht zum Flügel gewordene Bereich der Mittelbrust ist grösstenteils vom Dorsalflecken bedeckt, doch gibt es auch eine kräftige, hintere Notalfalte, die wie am Prothorax mit kleinen Längsstrichen versehen ist. Der mittlere Teil des Dorsalfleckens ist vom hinteren Dorsalraum ausgefüllt, und der ganze — am unveränderten Segment verbliebene — Flecken hat daher die Form eines quer ausgezogenen Ringes oder Viereckes. Es ist somit möglich bei dieser Art mit grosser Sicherheit die verschiedenen Elemente am Pro- und Mesothorax zu homologisieren und dadurch nachzuweisen, welcher Teil des Prothorax als Homologon des Flügels anzusehen ist. Der kräftigere Aderstrich am Mesothorax ist viel-

leicht in der Weise zu erklären, dass er hier über die stark konzentrierten Aderstämme verläuft, die wahrscheinlich am Prothorax etwas weiter voneinander entfernt liegen und daher von geringerem Einfluss auf das Muster sind.

Blaberidae.

Panchlorinae. *Nauphoeta cinerea* Oliv. und *Nauphoeta* sp. (Abb. 32) tragen am Prothorax einen sehr kräftigen Paradorsalstrich, der sich nach hinten in eine als Aderstrich gedeutete Bildung fortsetzt. Am Flügel läuft ein etwas schwächerer Strich den grossen Adern entlang. Bei *N. testacea* Brunn. ist der Aderstrich am Flügel deutlicher, dafür aber an dem sehr schwach gezeichneten Prothorax verschwunden. Noch deutlicher ausgeprägt ist er bei den *Panchlora*-Arten, und infolge des hier vorherrschenden, weissen Pigmentes wird die Übereinstimmung zwischen Vorderbrust und Flügel noch mehr unterstrichen. Der Paradorsalstrich liegt an Prothorax und Flügel genau in einer Linie, was aber in diesem Fall einfach dadurch bewirkt sein dürfte, dass der Flügel — wenn zurückgeschlagen — in seiner ursprünglichen Stellung liegt, und dass der genannte Streifen als ein längslaufendes Element der Zeichnung aufzufassen ist, ganz wie die Grenze zwischen Paramarginalraum und Dorsalflecken bei *Cutilia soror* (vgl. Abb. 48).

Das einzig helle Element im Muster des Prothorax von *Leucophaea surinamensis* L. ist der schmale Marginalraum; an den Flügeln ist ein kleines Subcostalfeld gleichfalls hell, während der übrige Flügel schwach verdunkelt ist. Die Schwärzung ist aber nicht gleichmässig; sie liegt am äusseren Teil des Flügels über den Adern, am ganzen inneren Flügelteil dagegen in den Punktgruben, die wie bei den Coleopteren die Zwischenräume des Archedictyon darstellen und reihenweise angeordnet sind. Dieser Widerspruch wird durch eine Untersuchung des Übergangsgebietes zwischen den beiden Teilen aufgeklärt. Es zeigt sich nämlich, dass auch aussen am Flügel das Pigment eigentlich an die Seiten der Adern und nur wenig an deren mittleren Kiel gebunden ist. Auch die dünne Membran der Aderzwischenräume ist ungefärbt. Nun finden wir die Punktreihen genau an jenen Stellen, wo die Adern so dicht aneinanderliegen, dass die Zwischenräume äusserst klein werden. Dann bildet sich

die dunkle Einfassung der Adern zu kleinen Kreisen um jeden Zwischenraum herum aus, und wenn diese genügend klein — d. h. in Punktgruben verwandelt — werden, schliesst sich jeder kleine Kreis zu einem Punkt; gleichzeitig erweitern sich die Adern so, dass ihre hellen Mittelstreifen besonders breit werden. Es liegt also der Schwärzung der Punktgruben der inneren Flügelteile das gleiche Zeichnungsprinzip zu Grunde wie der Aderzeichnung der äusseren Flügelteile.

Der dem Flügel entsprechende Teil der Vorderbrust von *Zetebora* sp. und *Tribonidium signaticollis* Burm. ist ebenso wie der ganze Vorderflügel geschwärzt. *Tribonium spectrum* Eschr. (Abb. 30) dagegen trägt — dem grossen Paramarginalraum des Prothorax parallel — am Vorderflügel ein grosses, helles Subcostalfeld, während der übrige Teil des Flügels mit unregelmässigen Flecken überstreut ist, ohne dass hier eine Ordnung dieser Flecken wie bei den Epilamprinen zu entdecken wäre.

Trotzdem die Vorderbrust nur schwach gezeichnet ist, trägt der Vorderflügel von *Rhyparobia maderae* F. einen starken Aderstrich und einen etwas schwächeren Strich an der Grenze zwischen Costal- und Analteil. Hierzu kommen dann aussen am Flügel eine Menge Queraderschwärzungen, welche auch am Hinterflügel vorkommen und beiden Flügelpaaren ein nahezu gerieseltes Aussehen verleihen.

Gyna capucina Gerst. besitzt einen dunklen Flügel ähnlich dem von *Leucophaea*, aber bei einem der beiden untersuchten Exemplare ist die Schwärzung des Dorsalfleckens nur an zwei Stellen intensiv, nämlich nahe dem äusseren Teil des Vorderrandes und im besonderen mitten auf dem Flügel unmittelbar vor der Spitze des Analfeldes, ohne dieses jedoch zu berühren. Der letztgenannte Flecken erinnert in seiner Lage sehr an den unten zu erwähnenden, querbindenähnlichen Flecken von *Blabera* etc.

Die Panesthiinae besitzen in der Regel ganz dunkle Flügel; das innere Drittel des Vorderflügels von *Panesthia regalis* Walk. ist jedoch hell bis zum schwarzen Hinterrand, und die distale Grenze des hellen Bereiches liegt ungefähr in der Höhe der Spitze des Analfeldes. Diese Grenze stimmt daher mit der Innengrenze des eben genannten Fleckens von *Gyna capucina* überein. *Panesthia transversa* Burm. besitzt einen viel kleineren, hellen Raum mit derselben Aussengrenze wie die vorige Art;

die innere Grenze liegt dagegen viel weiter aussen als dort. Die Vorderbrust beider Arten ist dunkel.

Perisphaeriinae. Der besprochene äussere Flecken von *Gyna capucina* lässt sich bei Exemplaren von *Hormetica laevigata* Burm. als ein quer über einen Teil der Flügelmitte laufender Strich wiederfinden. Bei dieser Art tritt jedoch ein kräftigerer Flecken im äusseren Teil des Analfeldes regelmässiger auf. Dazu kommt noch eine ganz kleine Schwärzung an der Wurzel der Aderstämme, die wohl dem kleinen Vorsprung des vorderen Teiles des prothorakalen Dorsalfleckens einiger Individuen entspricht und an der Stelle des grossen Knotens liegt. Dieser basale Flecken ist — der kräftigeren Prothorax-Zeichnung entsprechend — bei *Hormetica verrucosa* Brunn. (Abb. 34) deutlicher entwickelt. Auch bei dieser Art ist die basale Schwärzung nur angedeutet. Der übrige Teil der Mittelbrust zeigt dasselbe Muster wie die Vorderbrust — wenigstens soweit ich ohne Beschädigung des Flügels des einzigen zur Verfügung stehenden Exemplares sehen kann.

Brachycola tuberculata Dalm. (Abb. 36) weist dieselbe basale Schwärzung wie die obengenannten Arten auf, dazu aber noch drei weitere Flecken. Der eine liegt im Analfeld und berührt den inneren Teil des Aderstriches, lässt aber nur einen kleinen Teil der Spitze des Analfeldes frei. Der äussere Teil dieses Fleckens scheint dem oben erwähnten Fleck im Analfeld von *Hormetica laevigata* zu entsprechen. Die anderen Flecken liegen mehr distal, und wenigstens der eine darf wohl als Homologon zum querlaufenden Flecken von *Hormetica* angesehen werden; möglicherweise ist auch der andere, etwas grössere Flecken ein abgesprengter Teil desselben. Die laterale Ausbuchtung des Dorsalfleckens am Prothorax entspricht dem basalen Teil eines Aderstriches am Flügel, aber die übrigen Flügelzeichnungselemente dieser Art finden kein Gegenstück am Prothorax.

Paranauphoeta sp. (Abb. 56) besitzt am Flügel ein Muster, das etwas an das von *Blattella supellectilium* (vgl. Abb. 52) erinnert. Ein heller Raum geht vom Vorderrand des Flügels auf die Spitze des Analfeldes zu, und der ausserhalb dieses Raumes liegende Teil dürfte daher dem querlaufenden Flecken von *Hormetica* entsprechen. Hier wie bei *Blattella* nimmt die Färbung gegen die Spitze hin nach und nach ab. Die andere untersuchte *Paranauphoeta*-Art besitzt ein ähnliches Flügelmuster, nur

sind die hellen Zonen sehr klein. Die Schwärzung des Prothorax verhält sich am Paranotum beider Arten nahezu identisch, am inneren Teil des Dorsalfleckens aber sehr verschieden (vgl. Abb. 38 und 56). Der Flügel von *Proscratea complanata* Perty (Abb. 37) trägt ein der erstgenannten *Paranauphoeta*-Art sehr ähnliches Muster, nur fehlt der helle Raum an der Spitze des Analfeldes fast vollständig.

Blaberinae. Das Weibchen von *Blaptica dubia* Serv. (Abb. 39) ist kurzflügelig und trägt ein einfaches Flügelmuster, das aus einem, einen hellen Paramarginalraum und ein helles Analfeld trennenden, kräftigen Aderstrich besteht. Das helle Analfeld hat kein entsprechendes Muster am Prothorax, wo nahezu der ganze Dorsalflecken schwarz ist. Gegen die Flügelspitze breitet sich der Analstrich stark aus und bedeckt den grössten Teil der äusseren Flügelhälfte. Am vollgeflügelten Männchen ist dieses Muster undeutlich, der Aderstrich aber unscharf angedeutet.

Monastria biguttata Thunb. (Abb. 40) weicht eigentlich nur wenig von *Blaptica dubia* ab. Ein schmaler Paramarginalraum ist am Prothorax vorhanden und zuweilen durch einen Marginalstrich seitlich begrenzt. Dasselbe gilt auch für den Flügel einiger weniger Weibchen; in den meisten Fällen fehlt ihnen jedoch der Marginalstrich und oft auch der Paramarginalraum. Sehr häufig finden wir eine kleine, helle Partie an der Wurzel des Analfeldes. Man ist geneigt, sie als einen Rest des Dorsalraumes anzusehen, was dann auch für den basalen Raum von *Paranauphoeta* und *Blattella* zutreffen dürfte; diese Deutung ist jedoch nicht sicher genug begründet. Der Flügel des Männchens ist in gleicher Weise gemustert.

Ein *Blaptica*-ähnliches Muster findet sich noch deutlicher bei den *Blabera*-Arten, z. B. *Bl. trapezoidea* Burm. (Abb. 41). Hier verläuft ein kräftiger Aderstrich bis an die Höhe der Analfeldspitze und stösst dann an ein querlaufendes Band etwas geringeren Schwärzungsgrades. Dieses Band entspricht somit dem oben erwähnten querlaufenden Flecken von *Hormetica laevigata*, *Gyna capucina* etc. Bei einer einzigen *Blabera* sp. hat sich indessen eine Schwärzung vom Aderstrich über den basalen Teil des Analfeldes hinaus ausgebreitet. Beim selben Exemplar ist auch die distale Grenze des Bandes undeutlich, und die äussere Flügel-

hälfte etwas verdunkelt (verschieden stark an beiden Flügeln, von welchen der rechte der hellere ist). *Monachoda grossa* Thunb. und *M. latissima* Brunn. weisen nur einen Aderstrich auf, während die übrige Flügelfläche hell ist.

Diplopteridae.

Diploptera dytiscoides Serv. hat kein Flügelmuster.

Corydiidae.

Polyphaga aegyptiaca L. besitzt trotz des hellen Paramarginalraumes am Prothorax einfarbig dunkle Flügel.

Corydia petiveriana L. (Abb. 57) trägt dagegen ein deutliches Vorderflügelmuster, während der Hinterflügel klein ist und nur einen dunklen Streifen am Aussenrande zwischen Apex und Tornus aufweist. Am Vorderflügel liegen einige weissgelbe Räume auf samtschwarzem Grund. Drei dieser Räume liegen am sogenannten Vorderrand des Flügels, nur durch einen sehr schmalen Marginalstrich von diesem getrennt; ein vierter Raum ist am Hinterrand. Möglicherweise lassen sich die drei vorderen Räume als Reste eines zusammenhängenden Paramarginalraumes auffassen; diese Deutung ist jedoch wegen des Mangels an Vergleichsmaterial ganz willkürlich. Besonderes Interesse kommt dem hinteren Raum zu. Dieser ist nämlich am linken Flügel so gross wie jeder der drei vorderen Räume und vom Flügelrand durch einen schmalen Marginalstrich getrennt. Da der linke Flügel in der Ruhe über dem rechten liegt (umgekehrt wie in der Abbildung), wird am Tier mit zurückgelegten Flügeln die gesamte sichtbare Zeichnung von sieben hellen Räumen gebildet, die wie ein H geordnet sind. Zwei der untersuchten Individuen tragen am rechten Flügel einen ovalen Hinterrandraum, der ähnlich wie der des linken Flügels aussieht und in Ruhestellung verdeckt ist. Zwei weitere Individuen (Abb. 57) tragen auch eine Andeutung desselben Raumes, der aber schwer sichtbar ist, weil der ganze überdeckte Bereich (von einer schmalen Randzone an der Kante nahe des Apex abgesehen) hellbraun ist. Bei anderen Exemplaren ist diese Partie so vollständig aufgehellt, dass der weissliche Raum überhaupt nicht aufzudecken ist. Es dürfte daher ausser Zweifel sein, dass die beiden übereinandergelagerten hellen Partien ganz verschiedenen Ursprungs sind.

Von *Corydia plagiata* Walk. und *Corydia* sp. ist nur je ein einziges Exemplar in der Sammlung vorhanden. Beide zeigen dunkle Flecken auf hellem Grund, die so liegen, dass sie Teilen der schwarzen Zeichnung von *C. petiveriana* zu entsprechen scheinen. Das dürftige Material reicht aber zu einer genaueren Analyse und einem sonst vielversprechenden Vergleich mit den Blaberiden nicht aus.

3. Formvariation der Segmente.

Aus dem bisher Gesagten ergibt sich die Möglichkeit, homologe Zeichnungselemente auf verschiedenen Segmenten nachzuweisen. Die Form der Segmente ist jedoch so verschieden und ihre einzelnen Teile sind von so schwankender Grösse, dass es zweckmässig erscheint, eine zusammenfassende Übersicht über die Formvariation der Segmente zu geben. Ziel dieser Untersuchungen ist, das Verhalten der Flügel zu den übrigen Teilen der Segmente aufzuklären, und es wird daher — wie in den vorigen Abschnitten — in der Regel von einer Beschreibung der Unterseiten abgesehen. Besonders am Thorax liegen ja die Verhältnisse schon allein wegen der Beine ganz anders. Es sei nur kurz erwähnt, dass die Bauchseite der Abdominalsegmente ungefähr dasselbe Aussehen und dieselben Proportionen wie die Rückenseite aufweist, ja, dass selbst einige, der Paranota entsprechende, laterale Erweiterungen der Sternite auftreten, die ganz wie die dorsalen Paranota gezeichnet sein können (*Cutilia* sp.). In einigen Fällen sind diese sternalen Erweiterungen des Abdomens genau so gross wie die tergalen (*Cutilia, Dorylaea*), meist sind sie aber reduziert, und die tergalen allein bilden die dünnen Erweiterungen der Körperseiten.

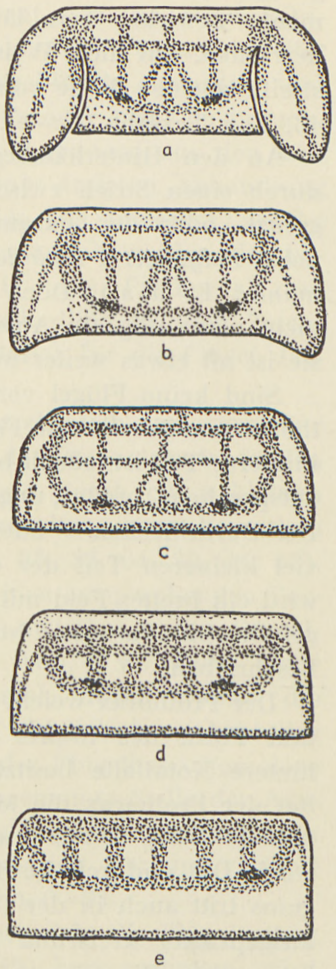
Nach dem bisher Gefundenen hat sich das Zeichnungsmuster als an bestimmte Strukturen oder Areale des Körpers geknüpft erwiesen, weshalb es im folgenden als Indikator für die Formvariation benutzt wird.

3 a. Die Formvariation der ungeflügelten Segmente.

Stellen wir uns ein »Idealsegment« vor (womit eine rein formale Abstraktion gemeint ist, ohne Rücksicht darauf, ob ihr irgendeine phylogenetische Bedeutung zukommt), so

müssen wir es uns mitten in einer ganzen Reihe von Segmenten denken; denn das vorderste und hinterste Segment können auf Grund ihrer besonderen Lage nicht als »ideal« betrachtet werden. Ein solches, verallgemeinertes Blattoideen-Segment (Textabb. 1) besteht aus einem grösseren, mittleren Teil, in welchen die inneren Organe eingelagert sind, und einem flachen, lateralen Auswuchs am Tergum oder Notum, der notalen Falte, die sich nach den Seiten und nach hinten erstreckt. (Hieran reiht sich eigentlich, wie oben erwähnt, eine entsprechende sternale Falte, die aber meist verschwunden ist). Nach vorne kann sich die Falte wegen der hinteren Notalfalte des voranliegenden Segmentes nicht entwickeln. Wie in den vorigen Abschnitten gezeigt wurde, ist der grössere, mittlere Teil des Segmentes normalerweise vom Dorsalflecken bedeckt, dessen Grenze jedoch sehr oft etwas in die notale Falte hinein verlagert ist. Die Falte ist typisch hell (Marginalraum) und nur mit einem schwarzen Rand versehen (Marginalstrich).

Die Abdominalsegmente haben einen breiten, mittleren Teil und entsprechend schmale Paranota. Oft ist aber die hintere Notalfalte breit, was in dem häufigen Vorkommen eines hellen Postmarginalraumes zum Ausdruck kommt, der eine Querstreifung des Abdomens bewirkt (Abb. 2 und 45 nebst *Temnopteryx capensis* Br., *Aptera fusca* Thunb. u. a.). In anderen Fällen ist diese Falte einfarbig und weniger kräftig; dann be-



Textabb. 1. Schemata zur Erläuterung der Formvariation der Segmente. a) Geflügeltes Segment. e) Abdominalsegment. b—d) Hypothetische Zwischenstadien, von denen b) ungefähr den Verhältnissen an Meso- und Metathorax entspricht, während c) gleich Abb. 1 ist.

stimmen Grösse und Gestalt des Dorsalfleckens das Muster. Infolge der Breite der Segmente ist der Dorsalflecken quer ausgezogen, und eine Auflösung dieses Fleckens in kleinere Elemente bewirkt, dass längslaufende Zeichnungselemente vorherrschen. Auf diese Weise entsteht die charakteristische Längsstreifung einer Reihe von Arten (Abb. 6, 8, 25, 32, 39, 43, 44, 46, und Textabb. 1 c—e).

An den Hinterleibssegmenten ist das Paranotum zuweilen durch einen Strich zwischen Para- und Postmarginalraum begrenzt, oder der Paramarginalraum allein ist hell (Abb. 48 nebst *Polyzosteria limbata* Burm., *Loboptera* spp., *Blattella germanica* L. u. a.). Doch braucht die Grenze des Paranotums nicht notwendig am Aussenrande des Dorsalfleckens zu liegen; sie ist oft etwas weiter innen zu finden.

Sind keine Flügel vorhanden, so nehmen Meso- und Metathorax annähernd die Form eines Abdominalsegmentes an. Ihr mittlerer Teil ist jedoch bedeutend schmäler und das Paranotum entsprechend breiter, ungefähr so wie in Texttabb. 1 b angegeben. Der Dorsalflecken — oder seine Überreste — nimmt dann einen viel kleineren Teil der Oberfläche ein, und zu beiden Seiten wird ein breites Feld mit paranotalen Zeichnungselementen ausgefüllt. Die Variation ist dieselbe wie oben für das Abdomen beschrieben.

Der Prothorax weicht hiervon erheblich ab, was mit Stellung und Form des Kopfes zusammenhängt. Da der Kopf keine hintere Notalfalte besitzt und etwas nach unten gerichtet ist, hat der Prothorax die Möglichkeit zur Entwicklung einer antenotalen Falte benützt, wodurch der Kopf von oben verborgen wird. Die dadurch bewirkte Veränderung der Form des Tergums tritt auch in der Gestalt des Dorsalfleckens zutage; er ist ausgeprägter kreisrund oder quadratisch als an den übrigen Segmenten. Die grössere Variationsmöglichkeit des Vorderrandes zeigt sich auch darin, dass viele Arten an diesem Segmente einen nach aussen statt nach hinten gerichteten Apex haben, wodurch der Prothorax breit spindelförmig wird (Abb. 23, 26, 27, 28, 47, und teilweise 53). In solchen Fällen liegen homologe Teile am Prothorax etwas anders als an den übrigen Thoraxsegmenten; der Winkel zur Längsachse ist daher nicht für alle Paranota der gleiche.

3b. Die Formvariation der geflügelten Segmente.

Meso- und Metathorax sind bei vielen Formen — sowohl Larven als Imagines — ähnlich gebaut wie die Hinterleibssegmente, nur mit dem Unterschied, dass die Paranota breiter sind. Bei anderen Formen sind diese zu Flügeln geworden, und zwar entweder zu kleinen oder grösseren oder sogar zu brauchbaren Flügeln. Die phylogenetischen Folgerungen aus den hier gemachten Beobachtungen sollen in einer anderen Abhandlung gezogen werden; hier ist nur die Frage von Interesse, welche Teile der Segmente in den Flügeln verwandelt werden. Im besonderen wird es dadurch notwendig, den Prothorax zum Vergleich heranzuziehen, da seine stark differenzierten Zeichnungselemente das beste Vergleichsmaterial für die Flügel darstellen.

Jedes der drei Brustsegmente besitzt ziemlich weit vorn eine Art Zentrum für die Ausbreitung der in das Paranotum laufenden Tracheen. Diese Stelle ist am Prothorax durch einen kleinen Vorsprung des Dorsalfleckens hervorgehoben, ganz besonders wenn dieser viereckig ist (Abb. 17, 24, 26, 32, 34, 39, 44, 53). Larven geflügelter Imagines zeigen oft einen entsprechenden Vorsprung an der Seite des meso- und metathorakalen Dorsalfleckens (*Periplaneta australasiae*, und Abb. 47 v). Diese Stelle wird bei der Imago zur Flügelwurzel, durch welche die grossen Tracheenstämme laufen, und folglich bezeichnet der genannte Vorsprung am Prothorax die der Flügelbasis homologe Stelle. Damit stimmt überein, dass die genannte Stelle der Ausgangspunkt des Aderstriches ist, wenn ein solcher am Prothorax seiner ganzen Länge nach vom Dorsalstrich getrennt verläuft (Abb. 31, 47 und, weniger deutlich, Abb. 6—9).

Der hinteren Ecke des Prothorax entspricht die Flügelspitze; dies wurde schon früher (Lemche 1940) hervorgehoben, wird aber nun vielfach bestätigt. So lässt sich z. B. der Verlauf der ähnlich wie bei *Blatta orientalis* L. (Textabb. 2, S. 63) gelagerten Tracheen des Prothorax an mehreren getrockneten Exemplaren einiger Blattoideen verfolgen (*Petasodes reflexa* Thunb. und *Homalopteryx* sp.). Auch der Verlauf der Adern des Prothorax, wenn solche entwickelt sind, stimmt damit gut überein. Der dem Flügel homologe Teil des Prothorax wird daher durch eine

schräg nach vorn verlaufende Linie in der Nähe des genannten Vorsprungs an der Seite des Dorsalfleckens begrenzt. Am schrägsten verläuft diese Linie bei solchen Formen, deren Apex nach aussen gedreht ist. Das Antenotum entspricht somit nicht einem Teil des Flügels (siehe auch Textabb. 1 c-b-a).

Der dem subcostalen Feld homologe Teil des Prothorax ist schlechthin das von der entsprechenden Trachee versorgte Areal. Diese Trachee ist durch viele, laterale Seitenäste gekennzeichnet und reicht am Prothorax bis zum Apex. Die subcostale Partie des Prothorax ist daher das vom normalgrossen Paramarginalraum bedeckte Bereich. Der radio-cubitale Teil ist am Prothorax nur wenig entwickelt und wird nur von einem schmalen Sektor — von der der Basis entsprechenden Stelle bis zum Apex — repräsentiert; hier breitet sich dieses Areal ein wenig aus und erreicht so den Rand.

Viel schwieriger ist die Entscheidung, wie das dem Analteil homologe Bereich des Prothorax abzugrenzen ist. Es dürfte jedoch sicher sein, dass hierin nicht viel vom Hinterrande einbezogen ist; denn der grösste Teil des Hinterrandes ist ja auch an den flügeltragenden Segmenten beibehalten, und der äusserste Teil des Randes gehört — wie eben erwähnt — der radiocubitalen Partie an. Rein typisch dürfte das anale Feld den Hinterrand nur mit der Spitze erreichen (siehe auch Lemche 1940), und nach der Lage des Musters zu urteilen, entspricht dem Analteil nur eine Partie im lateralen Teil des Dorsalfleckens hinter der »Basis«. Die ganze Zone erscheint am Prothorax auffallend klein, ganz besonders im Vergleich mit dem grossen Analfeld des Hinterflügels; aber die ausgesprochene Regelmässigkeit im Aderverlauf dieses Feldes weist darauf hin, dass gerade hier eine lokale »Vervielfältigung« der Adern durch starken Wuchs eines kleinen Areales stattgefunden hat. Dass trotzdem nicht die ganze Partie als neuentstanden zu betrachten ist, ist z. B. durch das deutliche Netzwerk primitiver Strukturelemente am Analteil des männlichen Vorderflügels von *Aptera fusca* Thunb. erwiesen (Einzelheiten siehe Lemche 1942).

Weiter ist hervorzuheben, dass die Proportionen zwischen den einzelnen Flügelteilen in charakteristischer Weise bei klein- und vollflügeligen Arten variieren. Dies ist z. B. bei *Monastria biguttata* Thunb. deutlich, wo das Weibchen beinahe kurz-

flügelig, das Männchen aber vollflügelig ist. Wie früher erwähnt, ist das Muster des Vorderflügels des Weibchens (Abb. 40) dem des Prothorax sehr ähnlich. Am letztgenannten Segment erstreckt sich nun der Paramarginalraum nicht weiter zurück als die Subcostaltrachee, d. h. bis nahe an die scharfe Spitze, die meiner Meinung nach den Apex darstellt. Dagegen reicht er gerade an der abgerundeten Erweiterung vor dem Apex vorbei. Am Vorderflügel geht der Paramarginalraum bis zur Hinterecke und biegt längs des Hinterrandes ein wenig um; die subcostale Trachee versorgt dasselbe Areal. Der Apex liegt somit vermutlich weiter innen am Hinterrand und ist nur sehr wenig vorspringend. Besonders interessant ist es, dass der Flügel derart abgestumpft ist, dass sowohl das Subcostalfeld als das Analfeld mit ihren Spitzen den Hinterrand gerade berühren, und dass die radio-cubitale Partie des Flügels sehr wenig entwickelt ist. Dasselbe gilt auch für *Temnopteryx capensis* Br. Dadurch bekommt der Flügel dieselbe Form wie bei den Dermapteren, Staphylinen etc. Am Männchen reichen dagegen sowohl Subcosta als Analfeld kaum den halben Flügel hindurch, was für die Opisthoptera (d. h. die Pterygota mit Ausnahme der Odonaten und Ephemeriden) typisch ist (vgl. auch Abb. 19, 23, 28, 30, 41). Letztere Auffassung wird dadurch bestätigt, dass eben diese Adern an nahezu allen Neuropteroidea u. a. bis an denselben Binden-Zwischenraum heranreichen (zwischen den Binden III und IV — siehe Lemche 1935, 1937). Die beim Männchen stattfindende Vergrösserung der Flügelfläche, die den Unterschied zwischen klein- und vollflügeligen Individuen verursacht, ist somit wesentlich durch die Vergrösserung der ursprünglich sehr kleinen radio-cubitalen Partie bewirkt. Hiermit stimmt überein, dass die Zellen des Archedictyon in der distalen Flügelhälfte viel grösser als in der proximalen sind, was auf eine Streckung der erstgenannten schliessen lässt. Sehr oft haben sogar Subcostal- und Analfeld eine stark an die der übrigen Körperfläche erinnernde Struktur.

Die meisten anderen, kleinflügeligen Blattoideen haben eine etwas andere Flügelform, bei welcher das Analfeld nicht so weit distal reicht wie das Subcostalfeld. Dadurch wird die Flügelform eher dreieckig mit einem bis nahe an den Apex reichenden, subcostalen Rand, einem schräg an der Analfeldspitze vorbei

verlaufenden Hinterrand und einem letzten, kürzeren Innenrand von hier bis zur Flügelwurzel (Abb. 39, nebst *Blaptica obscura* S. & Z., *Nyctibora* sp., *Hemiblabera brunneri* Sauss.). Der Unterschied zwischen dieser und der erstgenannten Flügelform liegt daher eigentlich nur in der Länge des Analfeldes.

Es ist ferner bemerkenswert, dass Formen mit halbgrossen Flügeln, d. h. solche, die in der Ruhestellung nicht das ganze Abdomen, sondern nur einen wesentlichen Teil desselben bedecken, einen verhältnismässig kleinen, distalen Flügelteil besitzen. Hier sind die Subcostal- und Analfelder etwa halb so lang wie der ganze Flügel (Abb. 34, 37, 52, nebst *Heminyctibora* spp., *Blatta orientalis* L. ♀, u. a.).

Die Erweiterung des Hinterflügels ist etwas anders vor sich gegangen: hier ist der Hinterrand am stärksten gestreckt, während die Ausbreitung des Spitzenteiles im Anschluss an die des Vorderrandes erfolgt ist. Dementsprechend gehört ein grosser Teil des Hinterrandes dem Analfeld an, während die Subcostalpartie nicht viel länger als im Vorderflügel ist.

Die vorstehenden Beobachtungen sind von Wichtigkeit für das Verständnis der Flügelmorphologie und besonders des Auftretens des Bindenmusters in verschiedenen Insektengruppen. Früher wurde nachgewiesen (Lemche 1937), dass bei den Panorpaten und Schmetterlingen Subcosta und erste Analader nahe der Ausmündung der Binde IV zum Vorder- bzw. Hinterrand stossen. Auf die Blattoideen übertragen, bedeutet dies einerseits, dass Subcostal- und Analfeld ungefähr gleich weit in die Flügel hinaus reichen, was — wie oben erwähnt — normalerweise zutrifft; anderseits, dass die Binde IV an einem Platz im Flügel sehr nahe am ursprünglichen Hinterrand des Paranotums liegt. Diese Annahme dürfte aber bedeuten, dass man an Flügeln mit unvergrösserter Spitze (wie die kleinen Flügel vieler Blattoideen und die Vorderflügel der Coleopteren) nur das Vorhandensein von 3—4 Binden erwarten dürfte, und dies hat sich auch tatsächlich durch Untersuchung zahlreicher Coleopteren bestätigt (obwohl eine erschöpfende Untersuchung dieser umfangreichen Gruppe durchaus noch nicht vorliegt). Die eigentümlichen Verhältnisse an den Hinterflügeln der Coleopteren und einiger Blattoideen wie z. B. *Diploptera dytiscoides* Serv., u. a., wo der äussere Teil gefaltet ist, lässt sich vielleicht unter ähnlichen Gesichts-

punkten betrachten, denn es ist ja auch hier nur der ausserhalb der Verbindungslinie zwischen Anal- und Subcostalfeldspitze liegende Teil des Flügels, der dieser besonderen Faltung unterworfen ist.

Es dürfte hier am Platze sein, ein paar frühere Versuche, die Flügel in Bezirke verschiedenen Ursprungs einzuteilen, zu erwähnen. Martynov (1925) teilt den Flügel in Palaeala und Neala, und betrachtet dabei als Neala nur den kleinen, an der Wurzel des Analfeldes umgebogen liegenden Flügelteil, der das Analfeld mit dem Körper verbindet. Dieser Einteilung kommt meiner Meinung nach insofern eine reale Bedeutung zu, als die Palaeala wirklich als ein Teil des verbreiterten Notums älter sein mögen als die durch Neubildung entstandenen, kleinen Neala zwischen der Flügelwurzel und dem hinten nach innen davor liegenden Teil des Dorsums. Die praktische Bedeutung dieser Einteilung dürfte jedoch fraglich sein.

Unbegründet erscheint dagegen der Versuch von Berlese (1909), die Flügel in vier hintereinander liegende Abschnitte einzuteilen, die den von ihm postulierten, hintereinander liegenden Regionen jedes Segmentes entsprechen sollten. Berlese geht dabei von der Voraussetzung aus, dass die Flügel seitlich verbreiterte Paranota sind, d. h. also eine Entwicklung, die ich nur als für die Plagioptera (Palaeodictyoptera und Odonata), nicht aber für die Opisthoptera zutreffend auffasse. Es wurde ja eben gezeigt, dass der Blattoideen-Flügel durch die Bildung einer Spalte entsteht, die hinten innen um das Paranotum läuft, und dass die Flügelwurzel daher nur einem Bereich begrenzten Umfanges vorne am Segment entspricht. Folglich haben der Analteil, und im besonderen der letzte der Berleseschen Abschnitte, Postala (der Martynovs Neala entspricht) mit dem hintersten Teil des Segmentes nichts zu tun. Die einzige rezente Gruppe, für die die Berlesesche Einteilung möglicherweise richtig sein könnte, ist die Odonata; aber Berlese benutzt gerade die Verhältnisse in der Flügelanlage von *Periplaneta* als Ausgangspunkt für seine Darstellungen.

4. Zerlegung des Musters in verschiedene Zeichnungen.

Im vorstehenden wurde gezeigt, dass sich ein Grundschema des Musters aller Segmente einschliesslich der Flügel konstruieren lässt. Im folgenden soll versucht werden, durch Auf-

teilung des Musters in verschiedene Zeichnungen die einzelnen bei der Musterbildung wirksamen Faktoren genauer zu erfassen.

4 a. Die Randzeichnung.

Am Prothorax zieht sich zuweilen ein Marginalstrich den ganzen Rand entlang (Abb. 37); oft ist er jedoch mit benachbarten Elementen verschmolzen, so z. B. hinten mit dem Dorsalflecken (Abb. 24, 25, 27, 39, 41, 48, 49, 51, 52) oder mit dem Postdorsalstrich (Abb. 14, 40). In solchen Fällen kann der hinterste Teil des Dorsalfleckens von der grösseren, vorderen Partie getrennt und nur als eine Verbreiterung des Postmarginalstriches zu erkennen sein (Abb. 6, 12, 15). Der Marginalstrich kann sich jedoch auch — wie bei *Platyzosteria* sp. (Abb. 3) — nach innen ausbreiten.

Alle übrigen Segmente verhalten sich in bezug auf Para- und Postmarginalstrich wie der Prothorax. Dagegen konnte durch Freilegung der Vorderkante von Meso- und Metathorax bei *Dorylaea rhombifolia* Stoll. (Abb. 7) und *Periplaneta australasiae* F. nachgewiesen werden, dass der Antemarginalstrich fehlt. Vermutlich ist dies die Regel für alle Segmente mit Ausnahme des Prothorax, denn es scheint, als ob dieser Wegfall durch den Mangel eines Antenotums verursacht sei. Der Marginalstrich tritt nur im Anschluss an eine Kante auf, ist dann aber häufig.

Falls dies auf alle Körperteile zutrifft, muss die gleiche Zeichnung am Flügel erwartet werden; und sie lässt sich auch in der Tat sowohl an kleinen (Abb. 7, 8, 10) als an vollentwickelten Flügeln (Abb. 27, 28, nebst *Periplaneta australasiae* F.) nachweisen. Bei *Phoraspis picta* Drury (Abb. 27) zeigt sie sogar dieselbe Tendenz zur Ausbreitung in den Marginalraum hinein wie am Prothorax von *Platyzosteria* (Abb. 3 a).

Bei *Dorylaea* sp. (Abb. 10) liegt die Randzeichnung nicht nur an der Flügelvorderkante, die der Aussenkante des Segmentes entspricht, sondern auch am sogenannten Hinterrand (eigentlich dem Innenrand) des Flügels. Hier, an der Grenze zwischen Paranotum und Körper, ist ja eigentlich kein Marginalstrich zu erwarten, und ein Vergleich mit *Cutilia soror* Brunn. (Abb. 48) und *Syntomaptera heydeniana* Sauss. (Abb. 13) deutet darauf hin, dass diese Schwärzung vielmehr als ein abgeschnittener

Teil des Dorsalflecken aufzufassen ist. Wenn — wie bei dieser *Dorylaea* — kein deutlicher Dorsalflecken am restlichen Segment sichtbar ist, gibt es zwei mögliche Erklärungen für eine solche Schwärzung: nämlich einmal, dass sie eine durch den neuentstandenen »Innenrand« verursachte Randbildung, oder zweitens, dass sie ein Teil des Dorsalflecken ist. Vielleicht ist sie Ausdruck eines Zusammentreffens beider Ursachen in der Weise, dass sich eine subminimale Dorsalflecken-Induktion und eine gewisse, durch den neuen Rand verursachte Randzeichnungs-Induktion gegenseitig so verstärken, dass die Schwärzung entsteht. Dagegen sollte meiner Meinung nach die Möglichkeit ausgeschlossen werden, dass sie ein vorwärts gezogener Teil des Postmarginalstriches sein könnte, denn die Spalte zwischen Flügel und Körper ist nicht durch Einbuchtung des Hinterrandes, sondern durch Bersten des Gewebes entstanden (Lemche 1942).

Ein Vergleich mit den in den letzten Jahren wiederholt analysierten Flügelzeichnungen der Schmetterlinge zeigt, dass auch dort die Randzeichnung häufig ist (»Randbinden« Süffert (1929), »Externa« Schwanwitsch (siehe z. B. 1929), »Randflecksystem« Kühn & Henke (1929), »Randmuster« Lemche (1937) u. a.). Es liegt jedoch nach dem obenstehenden kaum mehr ein Grund dafür, die Randzeichnung als spezifischen Flügelcharakter zu betrachten; sie dürfte vielmehr ein allgemeines Zeichnungsprinzip des Insektenkörpers sein.

4b. Die Dorsalfleckenzeichnung.

Der Dorsalflecken bedeckt das ganze Dorsum mit Ausnahme der Notalfalte. Er ist daher am Prothorax allseitig vom Rande getrennt, an den übrigen Segmenten reicht er bis an die antecostale Sutur (mindestens bei den untersuchten *Periplaneta australasiae* F. und *Dorylaea rhombifolia* Stoll.).

Die Form des Dorsalfleckens hängt von der Form des Körperteiles des Segmentes ab. Am Prothorax ist er oft annähernd kreisrund (Abb. 23) oder quadratisch (Abb. 41), an den anderen, viel kürzeren Segmenten rechteckig (Abb. 35). Sein Inneres ist zuweilen ganz oder teilweise hell. Manchmal verschwindet der hintere Teil des Fleckens, wodurch der hintere Teil des Seg-

mentes von einem hellen Querstreifen durchzogen wird (Abb. 10). Wenn aber in einem solchen Fall einige Längsstriche im Inneren des Fleckens erhalten bleiben, wird der Gesamteindruck des Tieres von diesen Längsstrichen beherrscht (Abb. 25, 39, 46). Das Muster der Unterseite des Abdomens scheint einen dem Dorsalflecken der Oberseite entsprechenden »Ventralflecken« zu besitzen (*Dorylaea rhombifolia* Stoll., *Blabera* spp., *Blaptica dubia* Serv.).

Bei den kleinflügeligen Formen mit deutlichem Paramarginalraum am Prothorax und entsprechenden, hellen Zonen an den Vorderflügeln (Abb. 6, 39, 48) ist zu sehen, dass die Verbreitung des Paramarginalraumes der Flügel im Verhältnis zur ganzen Flügelfläche variiert, dass aber die innere Grenze des Raumes den grossen Aderstämmen entlang verläuft. Dies kommt auch bei einigen vollgeflügelten Arten vor (Abb. 37, 49, 50, nebst *Periplaneta australasiae* F., *Nyctibora sericea* Burm. u. a.). Der Zusammenhang ist jedoch nicht immer vollkommen, denn die Grenze liegt zuweilen etwas mehr lateral als die Adern, d. h. näher an der sogenannten Vorderkante des Flügels (*Theganopteryx aethiopica* Sauss., *Blattella fasciata* Brunn., *Chorisoneura* sp. u. a.).

Obwohl der übrige Teil des Flügels der obengenannten Formen einfarbig dunkel ist, ist dies doch keine feste Regel. Ebenso wie wir am Prothorax helle Partien längs der postnotalen Falte finden, kommen solche auch an den Flügeln vor. So besitzt *Blattella fasciata* Brunn. nur eine dunklere Grenzlinie gegen den Paramarginalraum, während der Teil des Flügels innerhalb (»hinter«) dieser Grenze hell ist. *Paratropes* spp. tragen sogar zwei längliche Räume in der Dorsalfleckenzeichnung des Flügels, wodurch der Flügel vier dunkle Längsstreifen bekommt: einen Paramarginalstrich, einen Grenzstrich zwischen Dorsalflecken und Paramarginalraum, einen Strich von der Mitte des Analfeldes bis zum Apex, und einen Strich des »Hinterrandes« (eigentlich Innenrandes) den Flügel entlang (Abb. 28). Auch das Muster von *Nyctibora crassicornis* Burm. (Abb. 23) und *Pseudischnoptera lineata* Oliv. (Abb. 51) ist vermutlich ähnlich aufzufassen, obwohl der Aderstrich — siehe unten — hier mitzuwirken scheint. Trotz des abweichenden Aussehens des Flügels gilt dasselbe auch von *Pseudophyllodromia alternans* Serv.

(Abb. 19), denn die Tendenz zur Dorsalfleckenzeichnung scheint die Grundlage des Musters auszumachen, dessen Einzelheiten durch andere zeichnungschaffende Prinzipien bestimmt sind.

Im vorigen Abschnitt wurde bereits ein solches Prinzip — die Randzeichnung — eingehender besprochen. Im folgenden seien noch fünf weitere Zeichnungen erwähnt, die von der Randzeichnung dadurch abweichen, dass sie sich in Arealen auswirken, die mindestens zum überwiegenden Teil innerhalb der Grenze des Dorsalflecken liegen, und daher unmittelbarer als Modifikatoren der Dorsalfleckenzeichnung erscheinen.

4c. Die Muskelansatzzeichnung.

Wird der Dorsalflecken des Prothorax reduziert, so bleiben oft kleine, scharf umrissene, dunkle Bereiche zurück (Abb. 12, 30—34, 42, 47, 53). Dies hat sich als Ausdruck einer Neigung der Muskelansatzstellen erwiesen, sich dunkel zu färben, was auch an anderen Segmenten vorkommt (Abb. 8, 33, u. a.). Es muss daher zwei verschiedene Prinzipien geben, deren eines den ganzen Dorsalflecken, das andere nur die Ansatzstellen schwärzt. Wie einleitend erwähnt, wurde das Studium der Muskulatur, das allein zur sicheren Homologisierung dieser einzelnen Flecken führen kann, unterlassen, um vom eigentlichen Thema der Abhandlung nicht zu weit abzukommen. Es sei daher nur angedeutet, dass ein solches Studium geeigneten Materials sicher einige, im speziellen Teil versuchte Deutungen zu verifizieren vermag.

Ein einziges solches Problem soll hier noch etwas eingehender besprochen werden. Eine Muskelansatzzeichnung tritt nämlich auch sowohl an den tergalen als an den sternalen Ansätzen der tergo-sternalen Abdominalmuskeln auf, und sie liegt am Tergum als kleiner, runder Flecken ein wenig innerhalb des Paradorsalstriches. Ein Vergleich mit den Thoraxsegmenten vermittelt den bestimmten Eindruck, dass dieser Flecken dem Subanalflecken homolog ist. Auch dieser liegt über einem Muskelansatz, und falls dieser Muskel mit dem tergo-sternalen Abdominalmuskel homolog ist, so wird er sich mediad zu den Beinen dem reduzierten Sternum anheften. Dass er wirklich im dorsalen Teil des Thorax nach der Mitte zu verläuft, lässt sich z. B. unmittelbar bei Betrachtung von unbeschädigten *Dorylaea rhombifolia* Stoll. nachweisen, denn seine Fasern können durch das Chitin wahrgenommen werden; es ist mir aber nicht gelungen, in der Literatur irgendeine Angabe über

den übrigen Teil des Verlaufes zu finden, und nach der Meinung früherer Autoren (Miall & Denny 1886, u. a.) sollen tergo-sternale Thorax-Muskeln nicht vorkommen. Ich kann mich aber von dem Gedanken nicht ganz freimachen, dass ein Zusammenhang zwischen den erwähnten Muskeln doch vielleicht besteht.

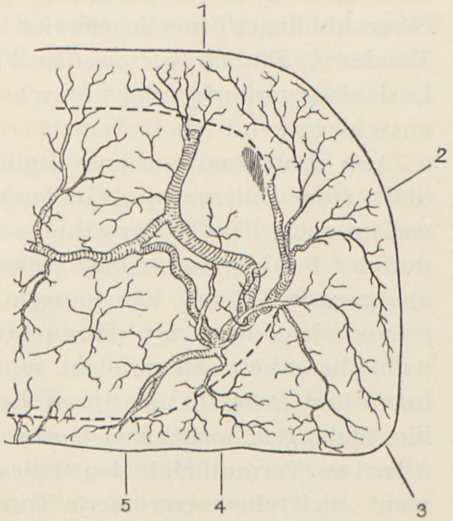
Jedenfalls dürfte feststehen, dass das Muster — mit genügender Vorsicht benutzt — in schwierigen Fällen zur Homologisierung von Muskeln beitragen kann, und umgekehrt, dass besonders im Dorsalflecken eine genaue Kenntnis des Muskelverlaufs und der Muskelansatzstellen für eine sichere Analyse der Einzelheiten des Musters unbedingt nötig ist.

Da im Flügel infolge seiner Struktur keine grösseren Muskelansätze vorkommen, kann die besprochene Zeichnung nicht einen Teil des Flügelmusters ausmachen. Dies dürfte jedoch kaum jede Möglichkeit ausschliessen, eine Abhängigkeit zwischen dieser Zeichnung und Teilen des Flügelmusters zu finden. Denn es könnte ja sein, dass die Muskelansatzzeichnung z. B. durch die Tracheen oder die Bluträume bedingt ist, welche auch im Flügel vorhanden sind; dann könnte vielleicht doch eine Art Abhängigkeit bestehen, obwohl bisher keine unmittelbar mit der Muskelansatzzeichnung des Rumpfes parallel variierende Schwärzung am Flügel nachgewiesen werden konnte.

4 d. Die Aderzeichnung.

An den Flügeln vieler Blattoideen laufen die grossen Aderstämme entlang eines dunklen Streifens, den ich den Aderstrich nennen möchte. Wie bekannt, verlaufen aber in den Adern sowohl Tracheen als Bluträume, und da schon früher (Lemche 1940) der Tracheenverlauf im Paranotum von *Blatta orientalis* L. studiert wurde, lag es nahe zu untersuchen, ob irgendein Zusammenhang zwischen den Tracheenstämmen und den Strichen zu finden ist. In der notalen Falte der genannten Art finden sich — ausser einigen kleinen Tracheen mitten im Antenotum — folgende Tracheenbündel, die sich in der Falte stark verzweigen (Textabb. 2): (die hier benutzten Nummern beziehen sich auf die Nummern der Abbildung) 1) Eine kleine Gruppe geht nach vorne und biegt in die notale Falte dort ein, wo zuweilen ein Frontalstrich auftritt (Abb. 36, 37, 50). 2) Eine grössere Gruppe entspringt etwas vor der Mitte des Paranotums, wo gewisse

Arten einen Parafrontalstrich tragen (Abb. 10). 3) Die nächste Gruppe liegt weiter hinten und ist gegen den Apex gerichtet, was an die Lage des Aderstriches bei der mit *Blatta* nahe verwandten *Dorylaea rhombifolia* Stoll. (Abb. 5) erinnert; anscheinend entsprechen diesem Verhalten auch die Verhältnisse anderer, mit einem Aderstrich versehener Formen (Abb. 18, 19, 40; bei der letztgenannten jedoch mit dem Parafrontalstrich verschmolzen). 4) Eine weitere Tracheengruppe läuft gegen den Hinterrand etwas innerhalb des Apex, dort wo oft die seitliche Grenze der Analschwärzung vorkommt (Abb. 6, 7, 14, 24, 32). 5) Etwas weiter medial liegt eine letzte Tracheengruppe, während die mediane Partie der postnotalen Falte durch einige kleine, weiter auseinander liegende Tracheen versorgt wird. Alle die erwähnten Tracheen liegen innerhalb des Bereiches der Analschwärzung.



Textabb. 2. Tracheenverlauf in der notalen Falte des Prothorax von *Blatta orientalis* L. Nur die rechte Hälfte des Segmentes dargestellt. — — — — innere Grenze der notalen Falte. Die grossen Tracheenstämme sind eingezeichnet, insofern sie von oben sichtbar waren. Von den kleineren sind nur die oberflächlichen (dorsalen) und die in die notale Falte laufenden eingezeichnet. Die Bedeutung der Nummern ist im Text erläutert. × 11.

Es darf natürlich nicht vergessen werden, dass ein solcher Vergleich nur orientierend sein kann, solange nicht mehrere Arten zu diesem Zweck sorgfältig untersucht werden; dazu reicht das vorliegende Material leider nicht aus. Ein ähnlicher Verlauf der Adern am Prothorax gewisser Blaberiden (*Monastria biguttata* Thunb. und *Petasodes reflexa* Thunb.), dessen Zusammenhang mit dem Verlauf der Tracheenstämme in einigen Fällen konstatiert wurde (Lemche 1942), legt aber die Vermutung nahe, dass der Tracheenverlauf von *Blatta orientalis* typisch ist, obwohl die Einzelheiten gewiss sehr variabel sind.

Die genannten, radiär verlaufenden Striche sind daher wahrscheinlich teilweise durch die Lage der Tracheenstämme der notalen Falte bedingt. Dies bedeutet aber nicht notwendig, dass diese Zeichnungselemente primär vom Verlauf der Tracheen abhängen; möglicherweise laufen die Bluträume längs der Tracheen, ähnlich wie in den Flügeln vieler Insekten, und es lässt sich vorläufig nicht entscheiden, welches dieser Systeme ausschlaggebend ist.

Am Prothorax gewisser Epilamprinen (*Molytria inquinata* Stål., *Homalopteryx* sp., *Calolampra irrorata* F.) finden sich — wie im speziellen Teil erwähnt — zwischen einer Menge kleiner, dunkler Punkte auch einige grössere, die an mehr oder weniger abgegrenzte, kleine Erhebungen geknüpft sind. Bei *Homalopteryx* sieht man am Paranotum schwache Aderspuren, obwohl diese bei weitem nicht so ausgeprägt sind wie bei *Monastria* und *Petasodes*. Dort, wo diese Adern sich nach dem Apex hin schlängeln, ordnen sich nun die grösseren Punkte auf den Adern an. Vermutlich bedeutet dies, dass mit dem erhöhten Integument auch eine vergrösserte Tendenz zur Schwärzung auftritt. *Calolampra irrorata* F. (Abb. 53) zeigt ähnliche Punkte sowohl am Prothorax, wo die übrigen Zeichnungen aber die Verhältnisse verschleiern, als an den Vorderflügeln, wo die Punkte auffallend genau auf den Adern angebracht sind, obwohl sie sich etwas über beide Seiten der einzelnen Adern hinaus ausbreiten. Bei dieser Art wechselt das dunkle Pigment mit weissem ab, während die Aderzwischenräume farblos sind, und beide Pigmentsorten zeigen eine Tendenz zur Verbreiterung längs der Queradern. Es scheint daher, als ob in dieser Hinsicht kein prinzipieller Unterschied zwischen Längs- und Queradern existiert; alle Adern sind eben einfach Stellen, wo sich das Pigment vorzugsweise konzentriert.

Von den oben genannten, radiär verlaufenden Zeichnungselementen, die ich zur Aderzeichnung rechne, kommt für die Flügelfärbung nur ein einziges in Betracht, der Aderstrich, der aber ein häufiges und kräftig entwickeltes Element im Flügelmuster ist (Abb. 7, 8, 28, 39, 41, 44). Im vorigen Abschnitt wurde erwähnt, dass die Dorsalfleckenzeichnung ihre laterale Grenze an den grossen Aderstämmen hat. Diese Grenze wird durch einen Aderstrich hervorgehoben, und wenn am Flügel

der innere Teil des Dorsalfleckens hell ist, wird es schwer, einen Aderstrich von einem einfachen Paradorsalstrich zu unterscheiden. Es ist auch möglich, dass eine scharfe Trennung dieser beiden Elemente (und eventuell auch der Analschwärzung) nicht durchführbar ist, doch halte ich es für notwendig, einen begrifflichen Unterschied zwischen dem allgemeiner schwärzenden, Dorsalflecken-erzeugenden Prinzip und der Schwärzungstendenz der Tracheenstämme usw. aufrechtzuerhalten.

Die im Verhältnis zur Flügelmembran besonders an den Hinterflügeln oft vorkommende Verdunkelung des Adernetzes kann kaum als Aderschwärzung betrachtet werden, da schon eine Verdickung der Cuticula der Adern eine gewisse Verdunkelung hervorrufen dürfte. Dagegen ist die bei einigen Individuen von *Monastria biguttata* Thunb. vorkommende Schwärzung des proximalen Teiles der im Antenotum auslaufenden Adern als eine typische Aderzeichnung aufzufassen. Hier wird die allgemeine Schwärzungstendenz des Dorsalfleckens durch die Adern verstärkt, und sie erstreckt sich an diesen mehr distal als in den Zwischenräumen. Bemerkenswert ist, dass diese Adern gar nicht in einem den Flügeln homologen Teil der notalen Falte liegen, was beweist, dass die Aderzeichnung nicht an spezielle Flügelstrukturen gebunden sein kann, sondern ein dem Integument als solches charakteristisches Zeichnungsprinzip ist.

Wie die Randzeichnung ist auch die Aderzeichnung mehrerer Insektengruppen bereits bekannt (»Querzeichnung« v. Linden 1901); besonders bei den Schmetterlingen macht sie einen sehr verbreiteten und augenfälligen Bestandteil des Musters aus (»Les colorations des nervures« Botke 1916; »venosae« Schwanwitsch 1929 usw.; »Aderzeichnung« Süffert 1929 u. a.).

Die Besprechung eines merkwürdigen Zeichnungselementes soll hier noch angefügt werden. An der vorderen (eigentlich äusseren) Grenze des basalen Teiles des Analfeldes findet sich bei den Blattoideen ein eigentümlicher Lappen, der auf einer kurzen Strecke die benachbarten Aderstämme überdeckt. Genau dort, wo dieser Lappen distal in die normale Flügelfläche übergeht, findet sich bei *Blabera atropos* Stoll. und *Bl. stollii* Brunn. eine mehr oder minder deutliche Schwärzung, die als vom Aderstrich ins Analfeld diffundiert erscheint.

Es entsteht hierdurch ein rundlicher Flecken, der merkwürdigerweise überhaupt keine Tendenz zur Verbreitung längs der Adern aufweist. Da die Analadern nicht von dieser aus dem Aderstrich kommenden Schwärzung gefärbt werden, bin ich ganz im Unklaren darüber, wie diese zu deuten ist.

4 e. Die Kleinzeichnung.

Viele Epilamprinae besitzen am Prothorax eine ausgesprochene, punktierte Skulptur, die aus einer grösseren oder geringeren Menge kleiner, rundlicher Punktgruben in einer sonst glatten Oberfläche besteht. Wenn diese Gruben deutlich sind, werden sie meist durch dunkles Pigment betont (*Heterolampra lurida* Burm., *Molytria plana* Burm. u. a.). Oft sind aber die Gruben undeutlich oder sie fehlen ganz, obwohl die kleinen Pigmentflecken in derselben Weise vorhanden sind (*Molytria inquinata* Stål., *Heterolampra erubescens* Gerst., *Pseudophoraspis nebulosa* Burm.). Diese Zeichnung kommt oft auch an den Flügeln vor, besonders am Subcostalfeld der Vorderflügel; doch liegen die Gruben hier etwas mehr in Reihen geordnet und entgehen die Adern oder — anders ausgedrückt — sie lassen schmale Streifen zwischen sich offen: die Adern. Die etwas grösseren Flecken, die häufig bei denselben Arten vorkommen, wurden schon bei der Aderzeichnung besprochen.

Wie in einer anderen Arbeit (Lemche 1942) gezeigt wird, entsprechen die Punktgruben den Zwischenräumen des Archedictyon, d. h. die Kleinzeichnung füllt die Zwischenräume aus. Obwohl sich zuweilen eine einzelne Grube in einen Zwischenraum verwandelt, vereinigen sich meistens mehrere Gruben (in der Regel 6—8 in zwei Reihen) zu einem einzigen Aderzwischenraum. Dann zeigt es sich, dass sich die Schwärzung der Gruben an den Grenzen zwischen Adern und Zwischenräumen am längsten erhält, und folglich bildet sich dann eine Art sekundärer Aderzeichnung, die die Mitte der Adern ungeschwärzt zwischen zwei Reihen dunkler Punkte belässt. Zeichnungen dieser Art finden sich bei *Leucophaea surinamensis* L., *Gyna capucina* Gerst., *Molytria plana* Brunn. und an kleineren Flügelteilen von *Pseudischnoptera lineata* Oliv. (Abb. 51) und (weniger deutlich) *Nyctibora crassicornis* Burm. Bei *Pseudischnoptera* erscheint der

Aderstrich auf den ersten Blick nach aussen verästelt; aber eine genauere Untersuchung zeigt, dass die Adern selbst hell, jedoch beiderseits von Reihen dunkler Punkte begleitet sind. Bei *Nyctibora* sind die Verhältnisse zwar undeutlicher; jedenfalls handelt es sich aber auch hier um eine Zwischenaderschwärzung, und keiner der beiden Fälle kann als Beispiel für eine Aderzeichnung gedeutet werden.

Ferner ist zu erwähnen, dass *Rhyparobia maderae* F. eine ausgesprochene Queraderzeichnung besitzt, die ich nach den eben besprochenen Erfahrungen über die Entstehung der Zwischenaderzeichnung — trotz der hier viel schärfer hervorgehobenen Queraderbildung — als eine solche auffasse. Es dürfte jedoch unsicher sein, ob die Zeichnung von *Rhyparobia* nicht ebenso gut als Aderzeichnung gedeutet werden kann.

Verschiedene Formen der Kleinzeichnung wurden schon von früheren Autoren bei den Insekten gefunden (»Längsstreifung« v. Linden 1901; eine ganze Reihe verschiedener Zeichnungen von Botke 1916; »Rieselung« Henke 1928; »Die rhythmische Flächenmusterung« (einschliesslich Rieselung) Süffert 1929). Die Rieselung ist in ihrer typischen Form sehr charakteristisch, aber die Abgrenzung des Begriffes scheint nicht ganz klar, und die von mir als Kleinzeichnung aufgefassten Zeichnungen sind nicht unbedingt damit identisch. Jedenfalls dürfte es feststehen, dass die bei den Blattoideen gefundene Kleinzeichnung keine spezielle Flügelstruktur, sondern ganz allgemein ein Charakteristikum des Integumentes ist.

4 f. Die Bindenzeichnung (?).

Bindenzeichnung wurde früher bei Neuropteren u. a. (»Längsbinden« v. Linden 1901), Panorpaten, Saltatorien u. a. (Lemche 1935), und Schmetterlingen (»Media 1—2« Schwanwitsch 1929 usw.; »Zentrales Symmetriesystem« Süffert 1929, Henke 1933; »Kerne« Henke 1929) nachgewiesen, ist aber bei den Blattoideen nie typisch entwickelt. Es sei daher vorausgeschickt, dass die unten zu besprechenden Zeichnungen nicht mit voller Sicherheit als wirkliche Bindenzeichnung betrachtet werden dürfen, obwohl mehrere Umstände auf eine Übereinstimmung mit dieser hindeuten.

Bindenähnliche Zeichnungen wurden unter den Corydiidae, Blaberidae, Epilamprinae und bei *Blattella supellectilium* Serv. gefunden, aber immer nur an den Vorderflügeln (nur *Panesthia transversa* Burm. besitzt am vordersten Teil des Hinterflügels eine innere, helle und eine äussere, dunkle Partie, die vielleicht mit Bindenelementen am Vorderflügel homologisiert werden können. Die Unterschiede zwischen den beiden Flügelpaaren sind aber zu gross, als dass man mit nur einem einzigen zur Verfügung stehenden Individuum sichere Ergebnisse erreichen könnte.)

Der Aderstrich am Flügel von *Blabera* spp. (Abb. 41) breitet sich über die ganze äussere Flügelhälfte aus und bildet eine zusammenhängende Schwärzung, die ich für einen Teil des Dorsalflecken halte. Diese Schwärzung ist jedoch nicht einfarbig dunkel, nimmt vielmehr nach aussen hin an Intensität schnell ab, wodurch sie den Eindruck einer breiten Querbinde erweckt. Diese Binde findet sich als »querlaufender Flecken« bei vielen Blaberiden wieder. Die Dorsalfleckenzeichnung des Flügels wird daher durch unbekannte Ursachen in eine Querbinde verwandelt, und dieses modifizierende Prinzip kann möglicherweise dem der Bindenzeichnung anderer Insekten homolog sein. Weiter besitzen einige Blaberiden eine basale Schwärzung und — zwischen dieser und dem »querlaufenden Flecken« — seltener noch einen Flecken; bei einer leider unbestimmten *Paranauphoeta* sp. (Abb. 56) sind diese Zeichnungselemente teilweise so miteinander verschmolzen, dass der Eindruck einer Querbindenzeichnung entsteht.

Bei *Corydia petiveriana* L. (Abb. 57) und (nach einer Abbildung in Handlirsch (1930) p. 832 zu urteilen) noch deutlicher bei *C. nuptialis* Gerst. finden sich Querbinden in ähnlicher Lage, so dass eine Identifizierung mit denen der Blaberiden nicht unmöglich erscheint. Bei dieser Gattung trifft ein Zwischenraum die Spitze des Analfeldes, und da dieser sehr verkürzt ist, dürfte die distal hierzu liegende Binde mit dem querlaufenden Flecken der Blaberiden identisch sein. Dann entsprechen aber auch die inneren Schwärzungen von *Corydia* denen von *Blabera*, und nur die äusserste Schwärzung von *Corydia* findet bei *Blabera* kein Homologon.

Blattella supellectilium Serv. (Abb. 52) hat ganz ähnliche

Binden. Die äusserste liegt gerade ausserhalb der Spitze des Analfeldes und dürfte somit dem querlaufenden Flecken der Blaberiden entsprechen, während die innere Binde quer über die Subcostal- und Analfelder zieht, was gleicherweise an Blaberiden und Corydiiden erinnert.

Etwas anders verhalten sich die Epilamprinae, deren Binden viel undeutlicher sind. Die dunklen Punkte bilden hier bei vielen Formen die Grundlage der Färbung, gerade wie die Punkte eines Rasters in der Autotypie. An einigen Stellen sind die Punkte klein und die Färbung daher hell, an anderen sind sie grösser und die Zeichnung dunkler, oder die Punkte verschmelzen zu grösseren Flächen, ohne dass sich die Abstände zwischen den einzelnen Punktzentren verändern. Es muss daher ausser dem punktgrubenschwärzenden Prinzip, welches die Gruben als Schwärzungszentren bestimmt, noch ein anderes Prinzip vorliegen, das die Verbreitung und Verschmelzung an einigen Stellen bewirkt. Da die Adergabeln eine gewisse Tendenz zur Orientierung an den Grenzen zwischen hell und dunkel zeigen, und da sich die grösseren, dunklen Flecken in undeutliche Querbinden ordnen, erinnert das ganze Muster etwas an Querbinden. Die undeutliche Abgrenzung und der unregelmässige Verlauf der Zeichnung verhindern aber eine sichere Entscheidung darüber, ob diese Bildungen wirklich als Querbindenzeichnung aufzufassen sind.

Zusammenfassend lässt sich nur sagen, dass bei den Blattoideen keine sichere Homologien zur Bindenzeichnung anderer Insekten gefunden wurden, obwohl einige Formen querbindenähnliche Zeichnung aufweisen. Das wichtigste Resultat ist indessen wohl dies, dass am übrigen Körper keine einzige Spur von Querbinden gefunden wurde. Binden dürften daher für den Flügel spezifisch sein; da sie auch nicht bei kleinflügeligen Formen auftreten, lässt sich vermuten, dass sie an vollentwickelte Flügel (oder sekundär reduzierte) gebunden sind. Da die Blattoideen die primitivsten Pterygoten darstellen (siehe Lemche 1940 und 1942), liegt die Erklärung nahe, dass die querbindenerzeugenden Strukturen im Flügel dieser Gruppe mangelhaft oder gar nicht entwickelt sind.

Henke (1933) hat den übereinstimmenden Aufbau der Körperzeichnung und der Querbindenzeichnung der Flügel bei

den Saturniiden (Lepidopteren) nachgewiesen. Dies bedeutet jedoch nicht, dass die von mir dargelegte Auffassung hinfällig ist, denn der HENKEsche Vergleich beider Zeichnungen ist nur formal und zeigt, dass — wenn Flecken oder Binden überhaupt auftreten — diese immer den gleichen inneren Aufbau haben. Darum brauchen sie nicht auf dieselbe Ursache zurückzugehen. Auch am Körper vieler Blattoideen finden sich Längsbinden (Abb. 6, 13, 25, 32, 39, u. a.), die natürlich nicht ohne weiteres mit den bindenähnlichen Bildungen der Flügeln verglichen werden können. Es muss also doch irgendein Prinzip geben, das Querbinden an den Flügeln vieler Insekten hervorruft.

4g. Die Überdeckungsbleichung.

Mit diesem Wort bezeichne ich die Erscheinung, dass die Färbung an den überdeckten Teilen des Körpers oder Flügels heller ist als an entsprechenden, unbedeckten Teilen. Dieses Phänomen ist von der Oberseite des Abdomens der Coleopteren wohlbekannt, aber auch bei Blattoideen ist es ziemlich häufig. So ist der von den kleinen Flügeln bedeckte, vordere Teil des Abdomens von *Nyctibora* sp. oben wesentlich heller als der übrige Hinterkörper. Bei *Periplaneta australasiae* F. u. a. besitzen die Larven ein deutliches Zeichnungsmuster an den freien Teilen des Thorax, während bei den Imagines dieselben Teile von den Flügeln überdeckt werden und hell sind.

Noch auffallender wird dasselbe Phänomen, wenn es auf den vom anderen Flügel bedeckten Flügelteilen auftritt. *Corydia petiveriana* L. (Abb. 57) besitzt z. B. am rechten Vorderflügel auf dunklem Grund einen hellbraunen Raum längs des ganzen Hinterrandes, genau über demselben Areal, welches in der Ruhestellung vom linken Vorderflügel überdeckt wird (von einer kleinen Partie an der Flügelspitze abgesehen, die trotz der Überdeckung schwarz ist). Trotzdem lässt sich bei einigen Exemplaren der kleinere und noch hellere Hinterrandflecken nachweisen (Abb. 57). Die Überdeckungsbleichung ist daher von den anderen Zeichnungen prinzipiell verschieden. Das hier wirksame Prinzip beeinflusst aber nicht nur die Schwärzung, sondern verursacht auch die Bildung einer erhabenen Leiste längs der Grenze zwischen normalem und überdecktem Flügel-

teil. Ähnliche Verhältnisse finden sich auch bei *Diploptera dytiscoides* Serv., wo die schmale, überdeckte Partie des rechten Flügels heller als der übrige Flügel und von diesem durch eine deutliche Leiste getrennt ist. Bei *Leucophaea surinamensis* L. sind aber sowohl der rechte wie der linke Vorderflügel am überdeckten bzw. überdeckenden Teil mit normalen, ziemlich spärlichen Queradern versehen, während die übrigen Flügelteile eine typische Punktstruktur aufweisen. Daraus erhellt, dass eine durch die Überdeckung bedingte Entwicklungshemmung nicht für Erklärung der veränderten Oberflächenstruktur ausreicht, sondern dass das Problem tiefer liegt. Viel häufiger sind jedoch Flügel, die nur Unterschiede im Schwärzungsgrad der bedeckten und unbedeckten Teile aufweisen (Abb. 30, 41, und viele andere Arten).

Über die Ursachen dieses Phänomens habe ich keine begründete Meinung. Die Möglichkeit liegt nahe, dass es phänotypisch bedingt ist (z. B. durch Einwirkung von Sauerstoff, Eintrocknen, usw. an den blossgelegten Teilen), viel wahrscheinlicher aber ist es erblich fixiert. Es bietet eine interessante Parallele zur Ausbildung der Flügeldecken der Heteropteren, die ja auch eine spezielle Struktur im überdeckten bzw. überdeckenden Teil besitzen.

5. Schlussbemerkungen.

Im Körper der Blattoideen gehen ein oder mehrere Prozesse vor sich, die zur Schwärzung des Integumentes führen. Mehrere Faktoren wirken jedoch modifizierend ein, wodurch die verschiedene Zeichnungen entstehen. Die Schwärzungen werden vermutlich zur Erscheinung gebracht durch scharfe Ränder (Randzeichnung), Tracheen oder Bluträume (Aderzeichnung), Muskelansatzstellen (Muskelansatzzeichnung), Gruben (Kleinzeichnung), und noch ein weiteres, unbekanntes Prinzip (Bindenzeichnung(?)). Den Dorsalflecken betrachte ich dagegen als Ausdruck des unmodifizierten Schwärzungsprinzips, und es wäre vielleicht richtiger von einer negativen Schwärzungstendenz der umliegenden Marginalräume zu sprechen. Eine Diskussion darüber, ob eine Schwärzung oder der Mangel einer solchen das primäre ist, dürfte jedoch unfruchtbar sein.

Alle Zeichnungen der Blattoideen, mit Ausnahme der etwas

fraglichen Bindenzeichnung, können sowohl am Flügel als am Körper selbst gefunden werden. Binden erscheinen aber jedenfalls bei dieser Gruppe sehr undeutlich, wenn sie überhaupt vorhanden sind.

Viele Blattoideen tragen ganz dasselbe Muster an der Ober- und Unterseite des Paranotums des Prothorax (*Dorylaea rhombifolia* Stoll., *Nyctibora sericea* Burm., *Paratropes* spp., *Pseudophyllodromia alternans* Serv. u. a.), während bei anderen Formen die Muster der beiden Seiten trotz gewisser Übereinstimmung in Einzelheiten voneinander abweichen. Dies erinnert auffallend an die Verhältnisse bei den Schmetterlingen, deren Muster an den Ober- und Unterseiten wohl aus denselben Zeichnungen aufgebaut, nur selten aber völlig identisch sind (wie bei *Ceromitia wahlbergi* Zell. — siehe Lemche 1935 p. 209). Hieraus lässt sich der Schluss ziehen, dass beide Muster von denselben Prinzipien verursacht werden, die endgültige Determination aber verschieden verläuft.

6. Zusammenfassung.

1. Das Zeichnungsmuster der Dorsalseite aller Segmente der Blattoideen lässt sich von einem einzigen Schema ableiten (Abb. 1). Eine Analyse des zentralen Teiles der Segmente ist jedoch in der vorliegenden Arbeit nicht restlos durchgeführt.

2. Die Unterseite der tergalen Paranota ist nach denselben Prinzipien wie die Oberseite gezeichnet; Einzelheiten weichen aber oft voneinander ab.

3. Die Bauchseite des Abdomens ist ähnlich wie die Rückenseite gezeichnet. »Sternale« Paranota desselben Charakters wie die tergalen kommen bei gewissen primitiven Blattoideen vor.

4. Die Vorderbrust besitzt im Gegensatz zu den übrigen Segmenten eine starke, antenotale Falte. Dadurch und durch die relativ beträchtliche Länge des Prothorax werden die vorderen Zeichnungselemente oft an Einzelheiten reich.

5. Die ungeflügelten Meso- und Metathoraces verhalten sich typisch.

6. Die Abdominalsegmente weichen im Zeichnungsmuster durch die starke Reduktion der ganzen vorderen Hälfte der Segmente ab.

7. Der Flügel ist durch die Entstehung einer vom Hinterrand des Segmentes etwas innerhalb der Hinterecke (Apex) bis nahe an den Vorderrand laufenden Spalte entstanden. Die Flügelwurzel gehört somit dem vordersten Teil des Segmentes an.

8. In vielen Fällen wird das Muster unverändert an den Flügeln beibehalten, und es entspricht dann dem der normalen Paranota.

9. Wenn der Flügel zu voller Grösse anwächst, bewirkt seine Streckung oft Veränderungen im Flügelmuster.

10. Folgende Zeichnungen können unterschieden werden: a) Randzeichnung, b) Dorsalfleckenzeichnung, c) Muskelansatzzeichnung, d) Aderzeichnung, e) Kleinzeichnung, f) Bindenzeichnung (möglicherweise der Bindenzeichnung der übrigen Insekten homolog), g) Überdeckungsbleichung.

(Aus dem Zoologischen Laboratorium der Königl. Tierärztlichen und Landwirtschaftlichen Hochschule und dem Zoologischen Museum der Universität, Kopenhagen).

Literatur.

Berlese, A. (1909): Gli insetti I. Milano.

Botke, J. (1916): Les motifs primitifs du dessin des ailes des Lepidoptères et leur origine phylétique. Onderz. Zool. Lab. Rijksuniv. Groningen. Leyden 1916.

Handlirsch, A. (1930): Blattariae oder Schaben; in Kükenthal: Handbuch der Zoologie IV. 1.

Henke, K. (1928): Über die Variabilität des Flügelmusters bei Larentia sordidata F. und einigen anderen Schmetterlingen. Z. Morph. Ökol. Tiere 12.

— (1933): Zur vergleichenden Morphologie des zentralen Symmetriesystems auf dem Schmetterlingsflügel. Biol. Zbl. 53.

— (1936): Versuch einer vergleichenden Morphologie des Flügelmusters der Saturniiden auf entwicklungsphysiologischer Grundlage. N. Acta Leopold. N. F. 4.

— & G. Kruse (1941): Über Feldgliederungsmuster bei Geometriden und Noctuiden und den Musterbauplan der Schmetterlinge im allgemeinen. Nachr. Ak. Wiss. Göttingen. Math. phys. Klasse Heft 3.

Kühn, A. & K. Henke (1929): Genetische und entwicklungsphysiologische Untersuchungen an der Mehlmotte Ephestia kühniella Zeller. Abh. Ges. Wiss. Göttingen Math. phys. Klasse N. F. 15.

Köhler, W. (1932): Die Entwicklung der Flügel bei der Mehlmotte Ephestia kühniella Zeller mit besonderer Berücksichtigung des Zeichnungsmusters. Z. Morph. Ökol. Tiere 24.

Lemche, H. (1935): The primitive Colour-Pattern on the Wings of Insects and its Relation to the Venation. Vid. Medd. Dansk naturh. Foren. 99.

— (1937): Studien über die Flügelzeichnung der Insekten I. Hepialina, Micropterygina, Tineoidea, Castnoidea und Zygaenina. Zool. Jahrb. Anat. 63.

— (1940): The Origin of Winged Insects. Vid. Medd. Dansk naturh. Foren. 104.

— (1942): The Wings of Cockroaches and the Phylogeny of Insects. Vid. Medd. Dansk naturh. Foren. 106.

Linden, M. v. (1901): Die Flügelzeichnung der Insekten II. Die Zeichnung der Neuropteren, Orthopteren, Homopteren und Dipteren und ihre Beziehungen zur Zeichnung der Schmetterlinge. Biol. Zbl. 21.

Miall, L. C. & A. Denny (1886): The Structure and Life History of the Cockroach. London.

Schwanwitsch, B. N. (1929): Two Schemes of the Wing Pattern of Butterflies. Z. Morph. Ökol. Tiere 14.

Süffert, F. (1929): Morphologische Erscheinungsgruppen in der Flügelzeichnung der Schmetterlinge, insbesondere die Querbindenzeichnung. Roux' Arch. Entw. mech. 120.

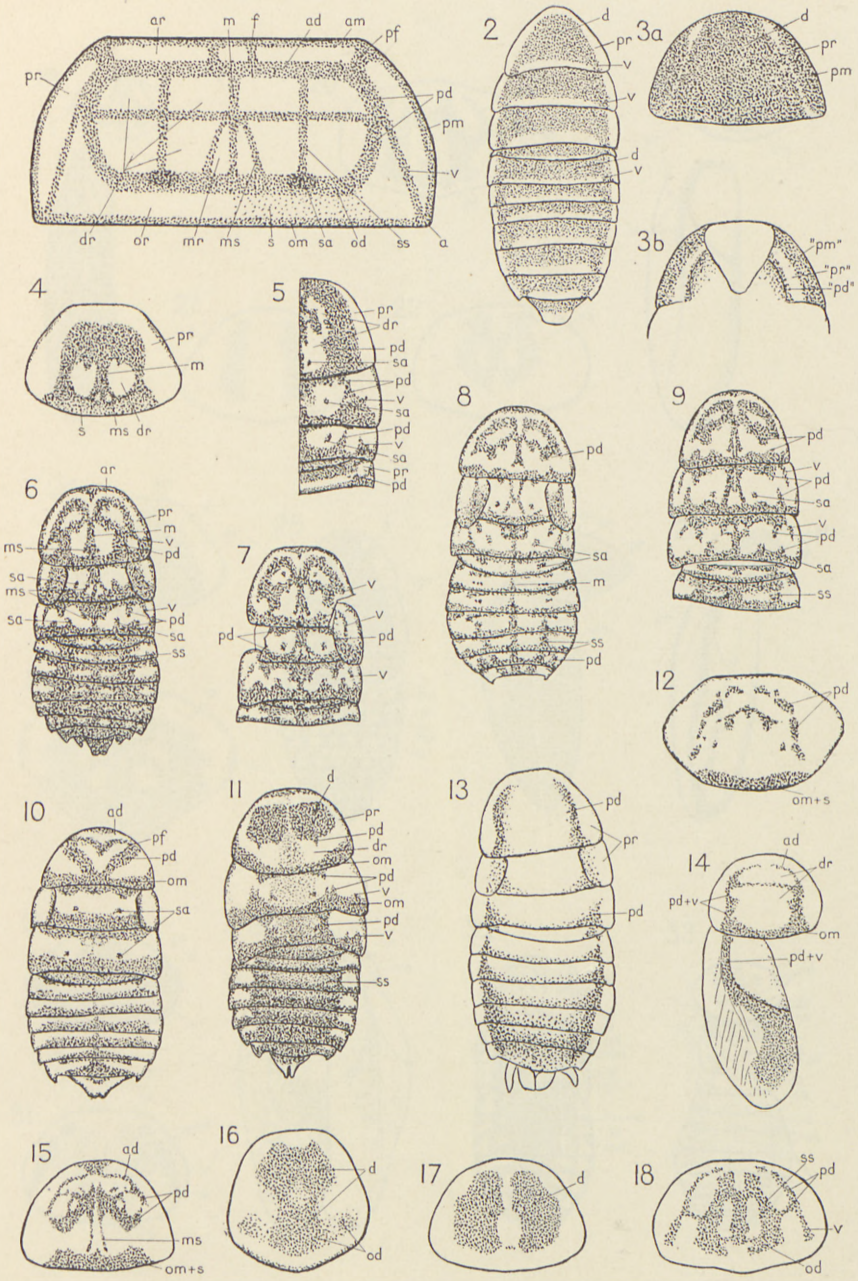
Indleveret til Selskabet den 25. Septbr. 1941.
Færdig fra Trykkeriet den 26. August 1942.

Erklärung der Tafeln.

Alle Abbildungen zeigen das Muster der Dorsalseite (Abb. 3 *b* ausgenommen). *a* Apex. *ad* Antedorsalstrich. *am* Antemarginalstrich. *ar* Antemarginalraum. *d* Dorsalflecken. *dr* Dorsalraum. *f* Frontalstrich. *m* Medianstrich. *mr* Submedianraum. *ms* Submedianstrich. *od* Postdorsalstrich. *om* Postmarginalstrich. *or* Postmarginalraum. *pd* Paradorsalstrich. *pf* Parafrontalstrich. *pm* Paramarginalstrich. *pr* Paramarginalraum. *q* Querlaufender Flecken. *s* Analschwärzung. *sa* Subanalflecken. *ss* Subanalstrich. *v* Aderstrich.

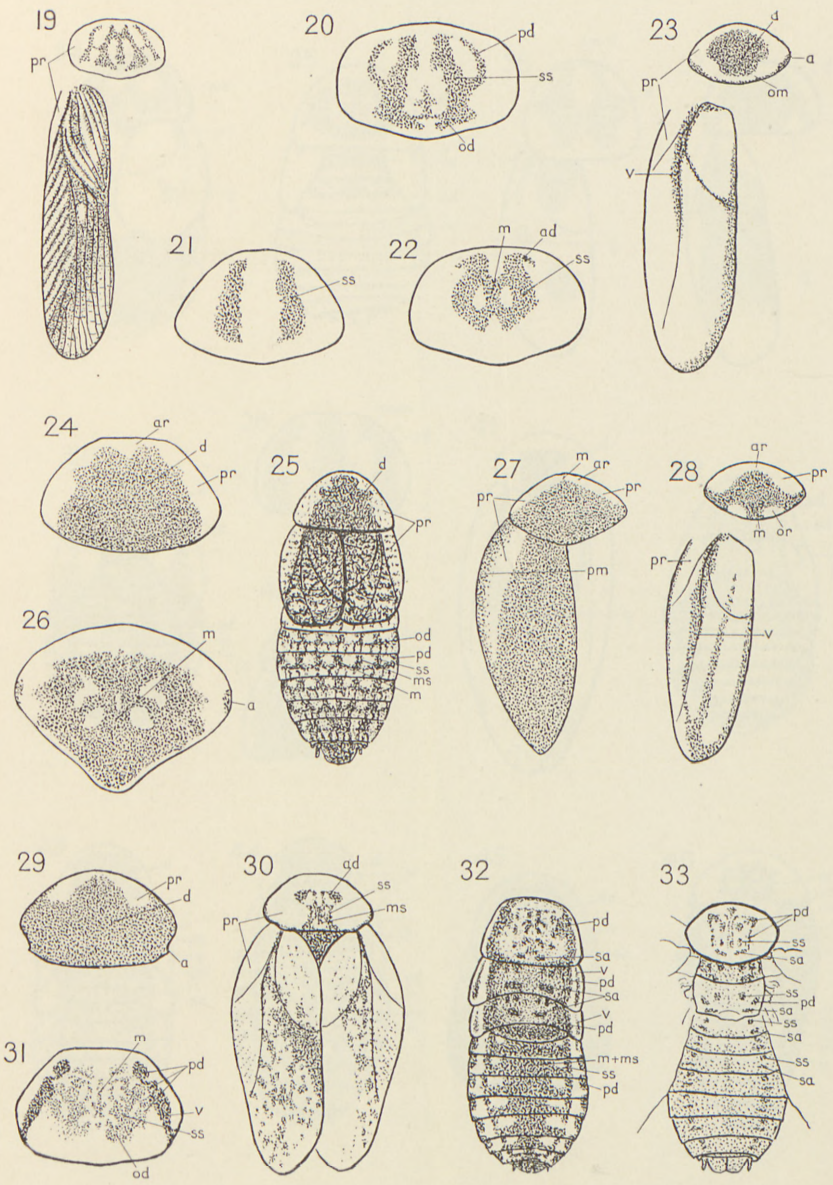
TAFEL I.

Abb. 1. Schema des Musters eines generalisierten Segmentes.
— 2. *Cosmozosteria multifasciata* Stål. × 3/2.
— 3. *Platyzosteria* sp. *a* Oberseite, *b* Unterseite des Prothorax. × 2.
— 4. *Methana soror* Sauss. ad. Prothorax. × 5/2.
— 5. *Methana* sp. (aus Java), Larve. Rechte Hälfte des Thorax und der beiden ersten Abdominalsegmente. × 5/2.
— 6. *Dorylaea rhombifolia* Stoll. ad. × 5/4.
— 7. Dieselbe. ad. Der Thorax und die beiden ersten Abdominalsegmente. Die Wurzel des rechten Vorderflügels blossgelegt; linker Vorderflügel entfernt. × 3/2.
— 8. Dieselbe. ad. × 3/2.
— 9. Dieselbe. Larve. Der Thorax und die drei ersten Abdominalsegmente. × 2.
— 10. *Dorylaea* sp. ad. × 3/2.
— 11. *Periplaneta australasiae* F. Larve. × 3/2.
— 12. *Homalosilpha ustulata* Burm. ad. Prothorax. × 5/2.
— 13. *Syntomaptera heydeniana* Sauss. ad. × 5/2.
— 14. *Ceratinoptera diaphana* F. ad. Prothorax und Flügel. × 7/2.
— 15. *Temnopteryx* sp. ad. Prothorax. × 7/2.
— 16. *Pseudomops intercepta* Burm. ad. Prothorax. × 6.
— 17. *Blattella* sp. ad. Prothorax. × 7.
— 18. *Pseudophyllodromia alternans* Serv. ad. Prothorax. × 6.



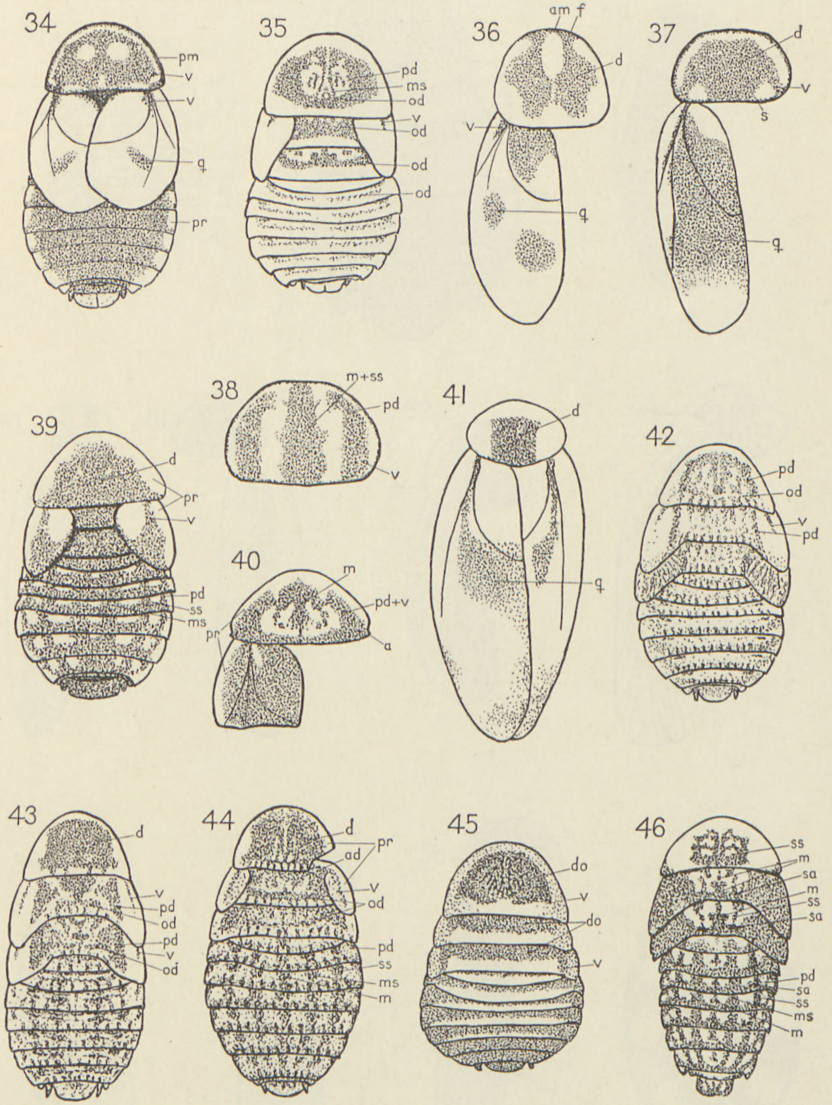
TAFEL II.

Abb. 19. *Pseudophyllodromia alternans* Serv. ad. Prothorax und Vorderflügel. × 7/2.
— 20. Dieselbe. ad. Prothorax. × 6.
— 21. *Blattella germanica* L. Prothorax. × 5.
— 22. *Pseudophyllodromia alternans* Serv. ad. Prothorax. × 7.
— 23. *Nyctibora crassicornis* Burm. ad. Prothorax und Flügel. × 3/2.
— 24. *Phaetalia pallida* Burm. ad. Prothorax. × 7/2.
— 25. *Molytria inquinata* Stål. ♀. × 1.
— 26. *Calolampra* (?) sp. Prothorax. × 7/2.
— 27. *Phoraspis picta* Drury ad. Prothorax und Vorderflügel. × 2.
— 28. *Paratropes phalerata* Erich. ad. Prothorax und Vorderflügel. × 3/2.
— 29. *Tribonidium signaticollis* Burm. ad. Prothorax. × 3.
— 30. *Tribonium spectrum* Esch. ad. × 5/4.
— 31. *Nauphoeta cinerea* Oliv. ad. Prothorax. × 5/2.
— 32. *Nauphoeta* sp. Larve. × 2.
— 33. *Rhyparobia maderae* F. ad. Körper. × 1.



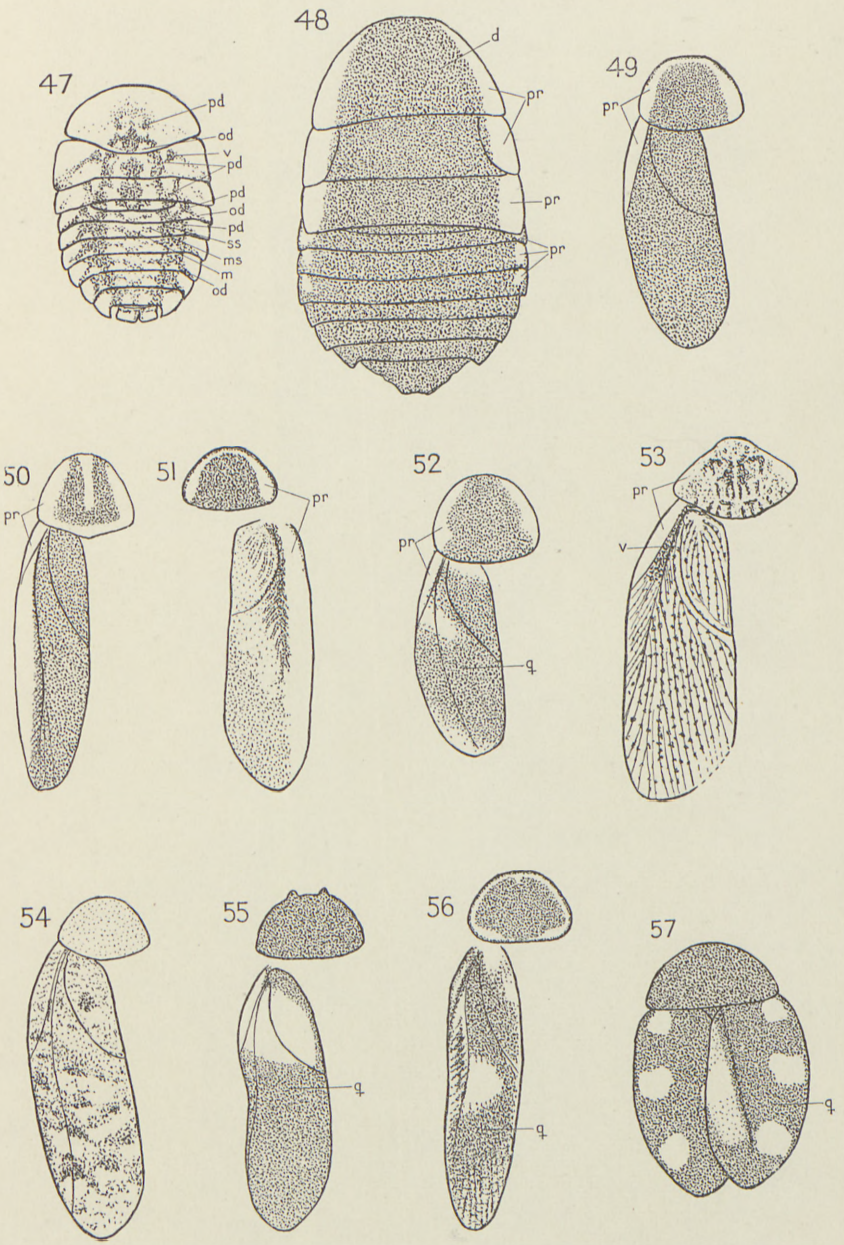
TAFEL III.

Abb. 34. *Hormetica verrucosa* Brunn. ad. × 1.
— 35. *Parahormetica bilobata* Sauss. ad. × 5/4.
— 36. *Brachycola tuberculata* Dalm. ad. Prothorax und Vorderflügel. × 7/4.
— 37. *Proscratea complanata* Perty. ad. Prothorax und Vorderflügel. × 2.
— 38. *Paranauphoeta* sp. ad Prothorax. × 7/2.
— 39. *Blaptica dubia* Serv. ♀. × 5/4.
— 40. *Monastria biguttata* Thunb. ♀. Prothorax und Vorderflügel. × 5/4.
— 41. *Blabera trapezoidea* Burm. ad. × 2/3.
— 42. *Epilamprinae* sp. Larve. × 5/2.
— 43. *Epilamprinae* sp. Larve. × 9/4.
— 44. *Epilamprinae* sp. ad. (Ein kleiner Teil des Prothorax rechts entfernt). × 7/4.
— 45. (?) *Dasyposoma bicolor* Brunn. × 3/2.
— 46. *Blabera atropos* Stoll. Larve. × 2/3.



TAFEL IV.

Abb. 47. *Monachoda* sp. Larve. × 1.
— 48. *Cutilia soror* Brunn. ad. × 7/2.
— 49. *Methana marginalis* Sauss. ad. Prothorax und Vorderflügel. × 3/2.
— 50. *Thyrsocera histrio* Burm. ad. Prothorax und Vorderflügel. × 7/2.
— 51. *Pseudischnoptera lineata* Oliv. ad. Prothorax und Vorderflügel. × 2.
— 52. *Blattella supellectilium* Serv. ♀. Prothorax und Vorderflügel. × 7/2.
— 53. *Calolampra irrorata* F. ad. Prothorax und Vorderflügel. × 5/2.
— 54. *Molytria plana* Brunn. ad. Prothorax und Vorderflügel. × 5/4.
— 55. *Panesthia regalis* Walk. ad. Prothorax und Vorderflügel. × 5/4.
— 56. *Paranauphoeta* sp. ad. Prothorax und Vorderflügel. × 7/4.
— 57. *Corydia petiveriana* L. ad. Der rechte Vorderflügel, der in der Ruhe vom linken überdeckt wird, ist hier nach oben gelegt, um den Unterschied zwischen Überdeckungsbleichung und den übrigen Zeichnungen zu zeigen. × 3/2.



DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 4

TWO NEW WEST GREENLAND LOCALITIES FOR DEPOSITS FROM THE ICE AGE AND THE POST-GLACIAL WARM PERIOD

BY

AD. S. JENSEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

CONTENTS

Printed in Denmark.
Bianco Lunos Bogtrykkeri A/S

Introduction.

On a journey which the then Royal Inspector of South Greenland, O. BENDIXEN, made some years ago with the purpose of preparing a topographic-statistical description of the Holsteinsborg District in West Greenland, he collected a number of shells of marine animals from raised deposits. Mr. BENDIXEN himself realized that they were remains of marine animals from the Quaternary period thus testifying that formerly this district was considerably below the present level of the sea.

These shells Mr. BENDIXEN has been kind enough to hand over to me for identification, and I now give an account of this collection which is of no small quaternary-geological interest.

The shells derive from two localities, one situated at North Strømfjord (Nagssugtôk of the Greenlanders), the other at South Strømfjord (Kangerdlugssuak of the Greenlanders). These fjords cut deep into the country, and form administratively the northern and southern limits of the Holsteinsborg district.

The collection contains parts of three faunas: a high-arctic, an arctic, and a boreal. We shall begin with the locality at North Strømfjord, whence there are representatives only of the high-arctic element.

The clay plain at North Strømfjord.

Mr. BENDIXEN has given me the following information concerning this locality which gives a good idea of the local conditions and will make it easy to find the place again in a later investigation.

On the northern side of North Strømfjord 18 miles inside the entrance of the fjord there is a bay by BENDIXEN called Depot

Bay, and on the western side of this there is a point with a deposit of fine clay; this point is bounded by low mountain ridges towards the fjord which have prevented its being washed away by the fjord water; on the southern side alone the clay plain is connected with the fjord by two creeks, one on either side of a low ridge which cuts through the plain dividing it for a stretch into two parts. A river has forced its way through the clay plain to the eastern creek, and on the slopes of this river-course the fossil

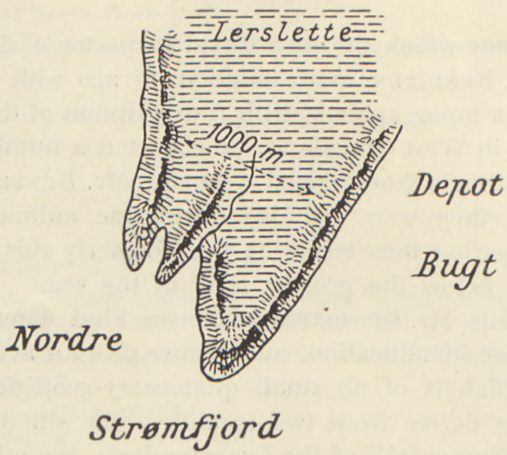


Chart 1. The clay plain (Lersletten) in North Strømfjord and surroundings.

shells were found in the uppermost part of the layer to a height of about 70 m above the sea. Reference is made to the attached sketch (chart 1) of the clay plain with its surroundings prepared after Mr. BENDIXEN's draft in his diary.

The fossils collected in this place (fig. 1) belong to two species of bivalves, viz.

Portlandia (*Yoldia*) *arctica* (Gray), 6 specimens, length up to 20 mm.

Pecten groenlandicus Sow., 4 specimens, length up to about 20 mm.

Both these bivalves have the shells connected and the cavity between them filled with a stony nucleus of clay. That they have been deposited in fine clayey mud in calm water can be concluded from the fact that *Pecten groenlandicus*, the shells of which are very fragile, have been preserved, and that the pe-

riostracum has been partly preserved in *Portlandia* (*Yoldia*) *arctica*.

The predominant representative of the high-arctic element is *Portlandia* (*Yoldia*) *arctica*. In order to make this clear we shall thoroughly discuss below the distribution at the present time of this bivalve which is of the greatest importance as a

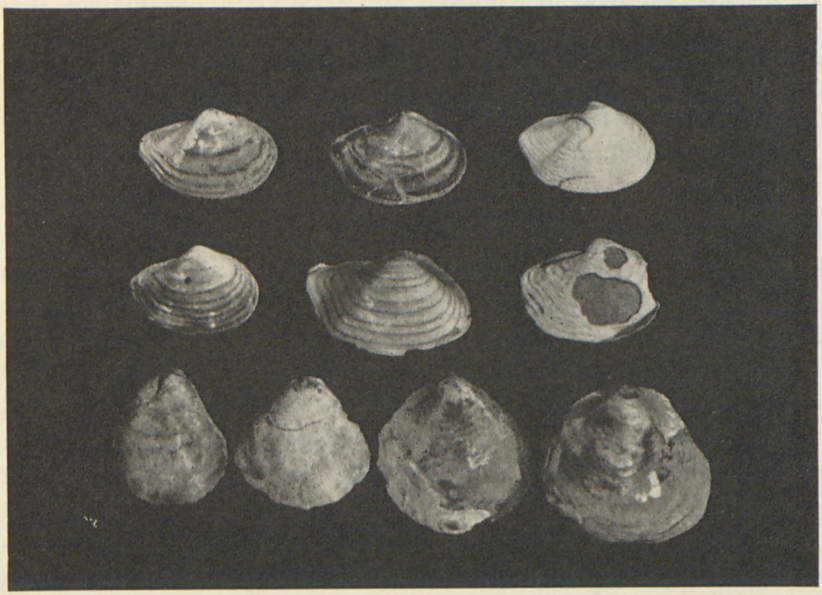


Fig. 1. *Portlandia* (*Yoldia*) *arctica* and *Pecten groenlandicus*. (× 1 1/8). The clay plain in North Strømfjord, from the uppermost part of the deposit, about 70 m above the level of the sea.

leading fossil, going like a red thread through the history of the investigation of the Ice Age[1]. In elucidation hereof the present author has already given in Danish a contribution, but

[1] In the literature on the Ice Age the designations "*Yoldia*-sea", "*Yoldia*-clay" and "*Yoldia*-time" have been adopted long ago. This is in so far unfortunate as the mollusc after which they were named is not a *Yoldia*. The genus *Yoldia* was established by H. P. C. Møller (Index Molluscorum Groenlandiæ p. 91. Naturhist. Tidsskrift, vol. 4, 1842—43), for a bivalve which he erroneously believed to be identical with the Polar Sea bivalve *Nucula arctica* Gray; it appears from Møller's detailed description that his *Yoldia arctica* is an entirely different mollusc, *Yoldia hyperborea* (Lovén) Torell. *Nucula arctica* Gray was later referred to Hancock's genus *Portlandia* and in the zoological literature it is generally called *Portlandia arctica* (Gray) (cf. G. O. Sars: Mollusca Regionis Arcticæ Norvegiæ, 1878, p. 37), while geologists often retain the designation *Yoldia arctica*. For the guidance of the reader it is called *Portlandia* (*Yoldia*) *arctica* in this paper.

this account came in an appendix to the paper by another author[1]. Besides, in the 38 years which have passed since then so many new contributions have appeared, especially from Russian, Swedish, Danish, Norwegian, and Canadian sources (Siberian Ice Sea, Barents Sea, Spitzbergen, Greenland, the Archipelago north of Canada, and Arctic Alaska) in elucidation of the geographical distribution and ecology of this bivalve that an up-to-date account is desirable.

On the distribution of *Portlandia* (*Yoldia*) *arctica* (cf. chart 2, p. 11) and its ecology.

We shall begin with Canada. *Portlandia* (*Yoldia*) *arctica* is known from the western side of the narrow channel which separates Northwest Greenland from Arctic America, viz. from Discovery Bay on Grinnell Land (81°41′ N), 5 fms.[2]. In the Stockholm Riks-Museum I have seen numerous specimens dredged by the Swede E. Nilson (1894) near Baffin Land (72°38′ N 77°10′ W and 72°27′ N 74°52′W) at depths of $10^1/_2$ and 13—19 fms. The southernmost place near eastern Canada in which the species was found alive lies on the east side of Hudson Bay, where it was dredged in Richmond Gulf (about 56° N), on a muddy bottom, in 15—25 fms.[3]. From the high-arctic archipelago north of America it is mentioned also from the following localities: Assistance Bay (74°40′ N 94°16′ W) and the coast of Barrow Strait, 7—20 fms.[4]; Port Kennedy (72° N 94° W), 15 fms.[5]; north of Beechey Island, 74 fms.[6]. The Sverdrup expedition found it to be common in Gaasefjord on the southern side of King Oscar's Land (about $76^1/_2$° N 89° W); at

[1] Helgi Pjetursson: Om Forekomsten af skalførende Skurstensler i Búlandshófði, Snæfellsnes, Island. Med Bemærkninger om Molluskfaunaen af Ad. S. Jensen. D. Kgl. Danske Vidensk. Selskab, Overs. 1904, No. 6, pp. 386—392.

[2] E. A. Smith: On the Mollusca collected during the Arctic Expedition of 1875—76. ("Alert" & "Discovery"). Ann. Mag. Nat. Hist., Ser. 4, vol. XX, p. 142. 1877. ("*Leda glacialis* Leach").

[3] Whiteaves: Catalogue of the Marine Invertebrata of Eastern Canada, p. 127. Geolog. Survey of Canada. 1901.

[4] Sutherland, Journal of a voyage in Baffin's Bay and Barrow Straits, vol. II, App. p. 202. 1852. ("*Nucula* (*Yoldia*) *arctica*").

[5] Walker: Notes on the Zoology of the last Arctic Expedition etc. Journ. Roy. Dublin Society, vol. III, p. 72). 1860. ("*Nucula truncata* Brown").

[6] Reeve in Belcher, The last of the Arctic Voyages, vol. II, p. 396. 1855. ("*Nucula portlandica* Hitsch." & "*Nucula siliqua* Reeve").

a depth of about 14 m nearly 600 specimens were taken in one haul[1]. Farther west near arctic Canada it was taken by the Canadian arctic expedition in Dolphin and Union Strait (about 70° N 115° W), off Stapylton Bay, in about 30 fms., mud[2].

On the arctic coast of Alaska it was taken off Collinson Point, 3 fms., mud and gravel, and off Sea Horse Islands (70°24′ N 161°25′ W), 9—10 fms., mud[2]. DALL records *Portlandia* (*Yoldia*) *arctica* from the eastern side of Bering Strait, in Norton Sound on Alaska[3]. But he does not mention it in his (later) lists of the molluscs of the Bering Sea, and it has not been collected in this sea either by the Vega expedition or by ARTH. KRAUSE, so it goes hardly south of the entrance proper to the sea between America and Asia.

Portlandia (*Yoldia*) *arctica* is extremely common along the north coast of Asia, as it has been taken in many places from Cape Wankarema (176°6′ E) to the western side of the Kara sea, according to LECHE[4]; it occurs in large numbers at depths of 5—15 fms., but has also been met with so deep as 85 fms. Of special localities MOSSEVITCH further mentions the western side of the northern Novaya Zemlya island, the mouths of the rivers Ob, Jenissei, and Lena, and the Lapteff sea and the area at the island of Kotelnyi and the New Siberian islands[5].

Off European Russia *Portlandia* (*Yoldia*) *arctica* was unknown until the end of the last century, when Prof. KNIPOWITSCH, to whom we are indebted for important hydrological and biological

[1] J. A. GRIEG: Brachiopods and Molluscs, p. 6. Rep. of the Second Norwegian Arctic Exped. in the "Fram" 1898—1902, No. 20. 1909.

[2] W. H. DALL: The Mollusca of the Arctic Coast of America collected by the Canadian Arctic Expedition. Rep. of the Canadian Arctic Expedition 1913—18, Vol. III, Part A, pp. 8, 10 and 16. Ottawa 1919. — DALL entered the species partly under the name of *Leda* (*Portlandia*) *arctica* Gray, partly as *Leda* (*Portlandia*) *collinsoni* n. sp. It appears both from the description (p. 19) and the figures (pl. II, figs. 3, 4) of the latter that it is only one of the numerous varieties of *Yoldia arctica*; among other things it is said about it: "The curious vermiculation of the surface is probably in great part if not entirely a function of the periostracum"; it is just one of the characteristics of *Yoldia arctica* that fine and dense, undulating concentric stripes can be seen under a lens.

[3] W. H. DALL: Catalogue of Shells from Bering Strait; Proc. California Acad. of Sciences, Vol. V, p. 250. 1873—74.

[4] Kgl. Sv. Vetensk.-Akad. Handl. Bd. 16, Nr. 2, 1878, p. 23 & Vega-Expeditionens Vetensk. Iakttag., Bd. III, p. 444, 1883.

[5] N. MOSSEVITCH: Contributions à la Systématique, l'Écologie et la Distribution de *Yoldia arctica* Gray récente et fossile. Matériaux de la Commission pour l'Étude de la République Autonome Soviétique Socialiste Iakoute, Livr. 19. Leningrad, 1928.

investigations in the waters north of Russia, in a series of papers has given us the following information:

On the south coast of Novaya Zemlya, i. e. in the eastern part of the Barents Sea *Portlandia* (*Yoldia*) *arctica* is abundant, attaining a very considerable size; but here it lives, it is true, at the great depth of 93 fms. and in a cold current, the deeper layers of which in summer show so low temperatures as —1.6° and —1.8° C.[1].

Along the west coast of Novaya Zemlya (the northern island) the Norwegian zoologist ØKLAND took it in the following places: Mashigin fjord, 7—8 m, clay from the glaciers, rather common; Litchutin Island, 5 m, clay, common[2]. It has also been taken at the mouth of the Petschora river[3].

Finally, it lives in the White Sea in which very peculiar hydrographical conditions prevail. The deeper water layers (below about 15 fms.) of this cauldron-shaped basin are secluded from free interchange with the water masses of the ocean by a narrow and rather shallow inlet, retaining, therefore, constantly a very low temperature which is nearly the same as the absolute minimum of the surface water (—1.4° to —1.6° C.). The conditions in the shallower parts of the White Sea are entirely different (especially in Onega Bay), since a strong heating of the water takes place here in summer. It now appears that *Yoldia arctica* generally occurs only in the deeper parts of the White Sea (below about 20 fms.), where the yearly amplitude is small (at a depth of 40—50 fms. it is not greater than about 2° C., as the temperature fluctuates between +0.5° and —1.4° C.), and which Prof. KNIPOWITSCH, therefore, called the "cold area"[4]. There is an exception, however, as KNIPOWITSCH also found large numbers of living *Yoldia arctica* in the bay near Kandalakscha (in the northwestern corner of the White Sea) at small depths

[1] N. KNIPOWITSCH: Zur Kenntniss der geologischen Klimate, p. 284. Verhandl. d. Kais. Russ. Mineralog. Gesellsch., Bd. XL, 2. 1903.

[2] JAMES A. GRIEG: Molluscs, Brachiopods and Echinoderms from Novaya Zemlya. Rep. of the scient. results of the Norwegian Expedition to Novaya Zemlya 1921, No. 26, p. 7, 1924.

[3] N. KNIPOWITSCH, ibid.

[4] N. KNIPOWITSCH: Eine zoologische Excursion im nordwestlichen Theile des Weissen Meeres im Sommer 1895. (Ann. du Musée zool. de l'Acad. Imp. des sci. St.-Pétersbourg. 1896, p. 304). Idem: Zur Kenntniss der geologischen Geschichte der Fauna des Weissen und des Murman-Meeres (Verhandl. Kais. Russ. Mineralog. Gesellsch. St. Petersburg. Bd. XXXVIII, Nr. 1, 1900).

(up to a depth of 14 fms.) and at a temperature which in the first half of July rises to 3.6° C.—"eine sehr merkwürdige Thatsache, die für mich jetzt vollständig unbegreiflich ist", writes KNIPOWITSCH (l. c. 1896, p. 307 and 1900, p. 20)—cf. with this p. 10 and pp. 13—14.

According to O. TORELL's classical investigations[1] *Portlandia* (*Yoldia*) *arctica* lives at Spitzbergen on clay bottoms from 5 to 30 feet; he found it especially in the clay carried down from the glaciers at 8 to 15 feet depth. According to the same author it is very rare on the west coast of Spitzbergen, where the bottom temperature is +1° C., whereas it is abundant in the ice-filled Hinlopen Strait on the east coast[2].

In the Stockholm Riks-Museum I have seen *Portlandia* (*Yoldia*) *arctica* from the following Spitzbergen localities: Storfjord, 4—7 and 5—10 fms.; Bellsund 15 fms.; Isfjord, 10—20 and 20—40 fms.; Hinlopen Strait, 55 fms. Russian expeditions also have taken it in large numbers near Spitzbergen, at only small depths, mainly $3^1/_2$—10 fms. The majority of the stations at which living specimens were secured were lying near glaciers; the bottom temperatures in summer ruled between —1.2° and +2.5° C.[3].

Finally, ODHNER, who has worked up the collection of molluscs from the Swedish expedition to Spitzbergen in 1908 under the leadership of Prof. G. DE GEER, records *Portlandia* (*Yoldia*) *arctica* from 20 stations in Isfjord[4]. Its vertical distribution lies between 6—8 and 100 m. It is most abundant in the inner parts of the fjord and in shallow water; at depths of 6—8 and 19—27 m, 161 and 111 living individuals respectively were taken in a single haul, and it was so dominant here that the number of individuals represented 53.2 and 67 per cent. of the total number of molluscs. The places of capture are situated most densely in the immediate vicinity of the glaciers, and it occurs close to the edge of the glaciers; but it was also found in places where no glacier debouches, i. e. although it often occurs in the out-

[1] O. TORELL: Bidrag till Spitsbergens Molluskfauna, p. 148. 1859.

[2] O. TORELL: Undersökningar öfver istiden. III. Öfvers. K. Sv. Vetensk.-Akad. Handl. 1887, Nr. 6, p. 434.

[3] N. KNIPOWITSCH: Zool. Ergebn. d. Russ. Exped. nach Spitzbergen. Mollusca und Brachiopoda. I, II und III. Ann. du Musée Zool. de l'Acad. Imp. des sci. St.-Pétersbourg, T. VI, 1901 (p. 502) & T. VII, 1902 (p. 395).

[4] NILS HJ. ODHNER: Die Molluskenfauna des Eisfjordes, p. 58—60. Kungl. Svenska Vetenskapsakad. Handl., Bd. 54, No. 1. 1915.

flowing glacier water it is not strictly bound up with such localities. The temperature limits lie between —0.59° and +3.7° or +4°, which is a little more than hitherto indicated. The highest temperatures apply to the localities where the water is most shallow, i. e. where the insolation has a direct heating influence, but—ODHNER adds—as the bottom in all the localities consists of more or less soft mud, it is probable that the temperature of the bottom is somewhat lower than that of the water. The salinity of the water lies between 33.40 and 34.18 $^0/_{00}$. The species attains its maximal size in the outer and deeper parts of the fjord[1]. ODHNER was the first—and presumably hitherto the only one—to examine the diet of this mollusc; its food consists of different micro-organisms of plankton and benthos which are devoured together with the mud.

Turning to East Greenland we find that *Portlandia* (*Yoldia*) *arctica* is absent in the southern part. Thus, it has not been found alive in the Angmagssalik District; it is true that a specimen has been taken in Sermilikfjord in the Angmagssalik District, but its shells were empty[2]. The southernmost place on the east coast at which it has been taken alive, is in a river mouth in Mikis fjord in Kangerdlugssuak (68°10′ N); here the 7th Thule Expedition 1933 took 3 specimens in two dredge hauls at a depth of 3.5—4 m, sandy clay, and 18 specimens at 7—8 m on clay bottom[3]. A little farther north 15 living specimens were taken in Turner Sound (69°44′ N) at about 6 m[4].

Farther to the north, from about 70° up to about 73$^1/_2$° N *Portlandia* (*Yoldia*) *arctica* is among the most common of the molluscs; this was shown first by investigations made by Swedish expeditions (NATHORST 1899, KOLTHOFF 1900[5]) and Danish

[1] In NATHORST's book: Två Somrar i Norra Ishavet, 1. D., 1900 it is recorded (p. 297) that the expedition in 1898 took *P. arctica* alive at the limit of the pack-ice north of Spitzbergen (81°14′ N 22°50′ E), where the depth was 80 fms. and the bottom temperature 2° C.; but NILS ODHNER records that this mollusc is *Portlandia intermedia*.

[2] E. BERTELSEN: Contributions to the animal ecology of the Fjords of Angmagssalik and Kangerdlugssuak in East Greenland. Medd. om Grønl., Bd. 108, No. 3, 1937, p. 25.

[3] E. BERTELSEN, l. c. p. 25.

[4] AD. S. JENSEN: On the Mollusca of East Greenland, I, Lamellibranchiata. Medd. om Grønl., Vol. XXIX, 1905, p. 317.

[5] R. HÄGG: Mollusca und Brachiopoda gesammelt von der Schwedischen zoologischen Expedition im J. 1900. Arkiv för Zoologi, Bd. 2, No. 2, 1904, p. 14. — AD. S. JENSEN, l. c., p. 318.

(RYDER 1891—92, AMDRUP 1900[1]). Later numerous bottom samples were taken with the PETERSEN grab during the three years expedition to Christian X's Land in 1931—1933 under the leadership of LAUGE KOCH, and numerous dredge hauls were also made

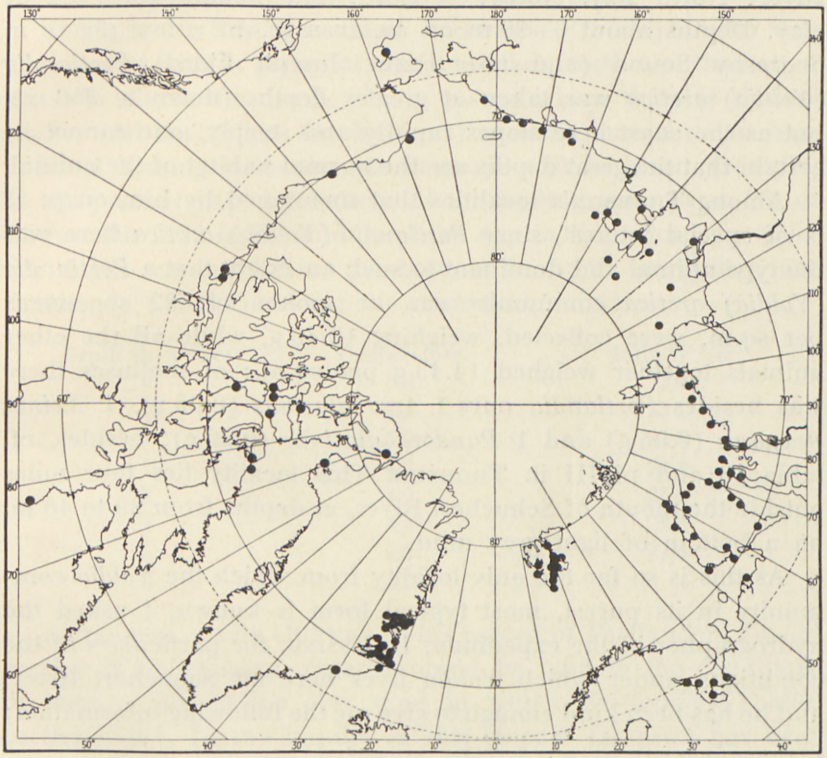


Chart 2. The present distribution of *Portlandia* (*Yoldia*) *arctica* worked out on the basis of the treatises quoted on pp. 6—14, with additions after EKMAN[2].

in Scoresby Sound and the Franz Joseph Fjord complex; these investigations also showed that *Portlandia* (*Yoldia*) *arctica* is extremely common in these areas.

In the Scoresby Sound area *Portlandia* (*Yoldia*) *arctica* was taken in the following places[3]: Off Cape Tobin; off the mouth

[1] AD. S. JENSEN, l. c., p. 317.

[2] SVEN EKMAN: Tiergeographie des Meeres, 1925, p. 250, Abb. 140.

[3] G. THORSON: Contributions to the animal ecology of the Scoresby Sound fjord complex. Medd. om Grønl., Bd. 100, No. 3, 1934. This paper also contains an excellent map showing the situation of the localities.

of Hurry Inlet; Hurry Inlet, off Konstabel Point; east side of Hurry Inlet; Hurry Inlet by the Fame Islands; west coast of Jameson Land off the Bjørn Islands; off Cape Hooker; Hekla harbour; off Cape Leslie; Northeast fjord off the delta of Schuchert River; North Bay, Northwest fjord. The bottom consisted of clay. Depths about 6—90 m on an average. In a few places in Scoresby Sound (and also Franz Joseph Fjord) *Portlandia* (*Yoldia*) *arctica* was taken at greater depths (down to 350 m), but as the coast here slopes rapidly and steeply, one cannot be certain that the great depths are the normal habitat of the animal.

Among THORSON's localities that mentioned by him on p. 43 is of special interest, since *Portlandia* (*Yoldia*) *arctica* here was the type animal and dominant to such an extent that a *Portlandia* (*Yoldia*) *arctica* community can be spoken of; 82 specimens per sq.m. were collected, weighing 19.40 g, while all the other animals together weighed 14.43 g per sq.m.; of molluscs there was besides *Portlandia* only 1 *Arca glacialis* (0.05 g), 1 *Axinus flexuosus* (0.05 g) and 1 *Pandora glacialis* (0.20 g); besides, cf. table 13 and pl. III in THORSON. This locality lies four miles outside the mouth of Schuchert River, at depths from 29 to 46 m, on a bottom of light grey mud.

As this is so far the only locality from which the *Yoldia* community in its purest, most typical form is known, I asked the hydrographer of the expedition, H. USSING, for particulars of the conditions under which *Yoldia* lives here off Schuchert River, and he has been kind enough to give me the following information:

St. VII. Depth: 25 m. $^{23}/_{7}$ 1933[1].

Depth in metres	Temperature	Salinity ‰
2	+ 7.97	17.94
10	— 0.95	28.64
20	— 1.12	32.21

Also other localities in Scoresby Sound, and by the way in Franz Joseph Fjord too, showed a distinct *Yoldia* community, with a great dominance of *Portlandia* (*Yoldia*) *arctica*. THORSON writes that this community was especially associated with the brackish water off river mouths, where large glaciers near the

[1] July is the warmest month in the water.

heads of the fjords descended, carrying a material which gives to the water a milky appearance and covers the bottom with a layer of loose, light-grey clay or mud. In deeper water, or at greater distances from the river mouths, the *Yoldia* community passes evenly into the surrounding communities.

In northern East Greenland *Portlandia* (*Yoldia*) *arctica* may also be met with in places at which the temperature of the bottom water is above the usual, viz. in places where there is shallow water, and the bright sunshine of the arctic summer can have a direct heating influence. An example will be given according to the journal kept by SPÄRCK of the hydrography at st. 28, on August 4th 1932 in the middle of the day in Northfjord, in which the depth was only 8 m, the bottom fine, soft, grey clay, and *Portlandia* (*Yoldia*) *arctica* the dominant animal:

Depth in metres	Temperature	Salinity ‰
0	6.6	13.5
1/2	5.3	23.1
1	5.0	24.5
1 1/2	4.9	24.8
2	4.9	25.0
3	4.4	26.6
5	4.3	27.6
8	4.1	

As pointed out by ODHNER in his record of *Portlandia* (*Yoldia*) *arctica* at Spitzbergen, regard should be paid to the conditions of temperature in the clay mud in which *Portlandia* (*Yoldia*) *arctica* lives[1]. To my inquiry in this respect THORSON has been

[1] The foot in *Portlandia* (*Yoldia*) *arctica* is a very large muscular organ having, as in other nuculids, a deep furrow along the middle which indicates that the lateral parts can be spread out, so that the foot becomes disc-shaped, and the mollusc can, as some authors believe, hereby creep like a gasteropod. But according to DREW the foot is wedge-shaped in closed condition in the nuculids and can be pushed far down into the bottom, whereupon the lateral parts are spread out to the sides and their borders are bent backwards; the foot buried in the bottom thus acts as an anchor by means of which the mollusc can sink into the mud, when the restractor muscles of the foot contract. DREW has watched living nuculids (*Yoldia limatula, Nucula delphinodonta* and *N. proxima*) for hours "in dishes containing the soft mud in which the animals normally live; they all burrow with rapidity and in the same manner, but in no case was a specimen observed to creep, even for the shortest distance". GILMAN A. DREW: Some Observations on the Habits, Anatomy and Embryology of the Protobranchia. Anat. Anz., 15. Bd., 1899, p. 496. — Idem: *Yoldia limatula*, p. 9, Note *. Memoirs from the Biological Laboratory of the Johns Hopkins University, IV, 3, 1899. — Idem: Locomotion in *Solenomya* and its Relatives. Anat. Anz., 17. Bd., 1900, p. 258.

kind enough to give me the following information: "Through many examples from the east Greenland fiords I can confirm that the mud layer on the bottom where the depth is 5 to 15 m has a considerably lower temperature in summer than the bottom water just over the mud. While the bottom water at these depths may even reach a temperature of about 4° C., mud samples from the same depths were much colder; they were icy to the touch and their temperature was hardly more than $^1/_2$° C.".

In the fjord area north of Scoresby Sound *Portlandia* (*Yoldia*) *arctica* has been taken in several localities, distributed as follows:

Fleming Inlet; Forsblad Fjord; Solitær Bay, Ella Island; Dusén Fjord; Isfjord, Franz Joseph Fjord; Eleonore Bay, Franz Joseph Fjord; North Fjord, Franz Joseph Fjord; Moskusoksefjord; Cape Bennet; Mackenzie Bay. The bottom consisted of clay, the depths were generally from about 8 to 90 m[1].

As far as I know there is no record to the effect that *Portlandia* (*Yoldia*) *arctica* has been taken in the sea farther north in East Greenland, but there can be no doubt that it occurs there. It is true that the Danmark Expedition 1906—1908, which explored this area, did not bring home a single specimen, but this negative result should not be misinterpreted. THORSON who did me the favour to go through the molluscs collected by this expedition informed me that the whole collection bears the aspect of having been collected in quite shallow water on the vegetation, and here *Yoldia arctica* never lives.

As fossil in raised strata, in heights of about 5—120 m above sea level, *Portlandia* (*Yoldia*) *arctica* was, on the other hand, taken in the following localities in northeastern Greenland from 76°10′—82°46′ N by the geologists of the Danmark Expedition: Great Koldewey Island; an island due north of Edwards Island in Dove Bay; north of Sne Ness; Hval Plain; Île de France; east coast of Peary Land[2]; (cf. chart 3, p. 19).

In older records of the molluscs of West Greenland *Portlandia* (*Yoldia*) *arctica* is stated to occur in different places,

[1] R. SPÄRCK: Contributions to the animal ecology of the Franz Joseph Fjord and adjacent East Greenland waters. Medd. om Grønl., Bd. 100, Nr. 1, 1933, p. 28 and table 3. — G. THORSON: Investigations on shallow water animal communities in the Franz Joseph Fjord and adjacent waters. Medd. om Grønl., Bd. 100, Nr. 2, 1932.

[2] AD. S. JENSEN: Quaternary Fossils collected by the Danmark Expedition. Medd. om Grønl., XLIII, 1917, pp. 621—632.

especially in the area round Disko Bay. In a previous paper the present author, however, showed that these records in all cases referred to "dead" shells, which had either been taken up from the sea bottom or belonged to specimens of a very old, fossil appearance and consequently could not be taken as a proof of the present occurrence of the species there[1].

Although energetic collecting has been done off West Greenland both in the last and present centuries by Swedish and especially by numerous Danish expeditions and private persons, no living specimen of *Portlandia* (*Yoldia*) *arctica* has hitherto been found from the southernmost parts up to Upernavik district. So late as the summer of 1936 23 samples were taken with the grab and 3 with the dredge near Upernavik, where the depths varied from 8 to 64 m, and the bottom consisted of clay and sandy clay, but *Portlandia* (*Yoldia*) *arctica* was not to be found. In the same district 6 samples were taken at Prøven with the grab and one with the dredge, depths 8—19 m, the bottom consisting of sand and sandy clay, but no *Yoldia* was to be found[2].

From northern West Greenland WALKER mentions it from Melville Bay, 80 fms., but without stating whether they were living specimens or "dead" shells[3]. On August 17th 1936 VIBE took 6 samples with the grab and one with the dredge in Melville Bay (Savigsivik), where the depth was 23 m and the bottom consisted of sandy clay, but he did not get any specimen of *Portlandia* (*Yoldia*) *arctica*[4]. This negative result indicates that *Yoldia* does not live in Melville Bay, and the dubious record in WALKER has therefore been omitted on chart 2 and chart 3.

Still farther north, in North-Star Bay, VIBE took 10 samples with the grab and one with the dredge; the bottom consisted of clay, the depth was 14 m, but he got no *Portlandia* (*Yoldia*) *arctica*[5].

We thus come to the surprising result that not a single living

[1] AD. S. JENSEN: On the fossil quaternary Mollusc-Fauna of Greenland. Medd. om Grønl., XXIX, 1905 (1909), pp. 289—290.

[2] CHR. VIBE: Preliminary investigations on shallow water animal communities in the Upernavik- and Thule districts. Medd. om Grønl., Bd. 124, Nr. 2, 1939, tables 1, 2, and 3.

[3] D. WALKER: Notes on the Zoology of the last Arctic Expedition under Captain Sir F. L. M'Clintock, R. N. The Journ. Roy. Dublin Society, Vol. III, 1860, p. 72 ("*Nucula Portlandica*").

[4] CHR. VIBE l. c. table 5.

[5] CHR. VIBE l. c. table 4.

Portlandia (*Yoldia*) *arctica* has been found on the west coast of Greenland, from the southernmost parts right up to Thule ($76^1/_2°$ N). Not until Murchison Sound, in about $77^1/_2°$ N does it occur; I have myself seen recent specimens from this place, collected by the Swedish zoologist A. Ohlin at a depth of 40 m; the specimens are kept in the zoological museum in Lund.

Conclusion.

On the basis of the examination of the localities at which *Portlandia* (*Yoldia*) *arctica* lives, and on the information available of the conditions prevailing there, we can form an idea of the life habits of this mollusc:

Portlandia (*Yoldia*) *arctica* is very sensitive to changes of temperature, being a "stenotherm" animal form, since it can bear only a slight variation in the temperature of the sea water, viz. from its absolute minimum (i. e. freezing point, which varies somewhat according to the salinity, and which may sink to about —2° C.) to about +2.5°. In shallow water, which is strongly heated in summer, it has apparently accustomed itself to bear higher temperatures, as the temperature of the bottom water may rise as high as 4° C.; but the clay mud in which the mollusc lives (i. e. its "bio-climate") is considerably colder than the bottom water and is hardly much over 0° C. Therefore *Portlandia* (*Yoldia*) *arctica* is a circumpolar animal form widely distributed in high-arctic seas; outside this area it is met with only in places where an icy current flows in (the south side of Novaya Zemlya), or where a cauldron-shaped deep is secluded from interchange with the ocean and so has icy water at the bottom (the White Sea), in other words under conditions as in high-arctic seas[1].

Portlandia (*Yoldia*) *arctica* is not very sensitive to changes in the salinity, being an "euryhaline" animal form. The salinity in the places where it lives, near glaciers or at the mouths of large rivers, is often low, in east Greenland it has been found to be so low as 27.6 $^0/_{00}$; but it can also thrive in very salt water, e. g. over 35 $^0/_{00}$ on the south side of Novaya Zemlya.

[1] In the White Sea *Portlandia* (*Yoldia*) *arctica* should, according to Knipowitsch, be regarded as a survivor from the glacial period.

In high-arctic areas it occurs often in very large numbers.

The bathymetric distribution of *Portlandia* (*Yoldia*) *arctica* generally falls between about 6 and 100 m.

Its food consists of different micro-organisms from plankton and benthos, which it devours together with the mud in which it lives.

The ability of *Portlandia* (*Yoldia*) *arctica* to subsist in such places as where glacier rivers discharge their masses of clay which colour the outflowing water milky white, covering the bottom with a layer of light grey mud, is remarkable.

Owing to the adaptability mentioned here *Portlandia* (*Yoldia*) *arctica* is presumably the most typical high arctic of all the shell-bearing animal forms; it thrives well in the icy mud discharged by the glacier rivers on the bottom of the icy seas, and can only subsist under the very hard conditions which the Polar Sea offers living organisms.

On the distribution of *Pecten groenlandicus.*

Together with *Portlandia* (*Yoldia*) *arctica* another mollusc, *Pecten groenlandicus*, was taken on the clay plain at North Strømfjord.

The four specimens present should — on account of their considerable size, length up to 20 mm—be referred to the arctic form, since the Atlantic form, var. *minor* Locard, is a dwarf form which only attains a length of up to about 11 mm, while the species in arctic seas may attain a size of 32 mm and by Collin was called var. *major*[1].

From West Greenland it is not known farther south than Umanak Fjord; still farther north it is known from Baffin Bay, Melville Bay, and Cape York, as also from Sherard Osborn Fjord on the north coast of Greenland (Thorild Wulff coll.). In high-northern seas it is one of the most common molluscs, and it is frequently taken together with *Portlandia* (*Yoldia*) *arctica*, e. g. in Scoresby Sound; by way of an example it can be mentioned that a dredge-haul from the North Bay taken at

[1] Ad. S. Jensen: The Danish Ingolf Expedition, Vol. II, 5, Lamellibranchiata, p. 32.

a depth of 10 to 18 m, on light grey clay contained 22 *Pecten groenlandicus* together with 108 *Portlandia* (*Yoldia*) *arctica*; another dredge-haul from the same locality, from the same kind of bottom, and made on the same day, yielded 69 *Pecten groenlandicus* besides 280 *Portlandia* (*Yoldia*) *arctica*[1].

Pecten groenlandicus may thus live under the same conditions as *Portlandia* (*Yoldia*) *arctica*. It may be added, that *Pecten groenlandicus* probably is the only lamellibranch which, in Northeast Greenland fjords, constantly occurs at temperatures below 0° C.[2].

Why is *Portlandia* (*Yoldia*) *arctica* extinct along the greater part of West Greenland? And why has it not immigrated again?

While *Portlandia* (*Yoldia*) *arctica*, according to the above, goes down to 68°10′ N on the east coast of Greenland, it stops on the west coast as far north as about $77^1/_2$° N.

The latter is the more strange as formerly it extended much farther to the south on the West Greenland coast, as is shown by its occurrence in the raised strata. The last locality recorded from North Strømfjord lies in about $67^3/_4$° N. That it was formerly common appears from the fact that it has often been found in raised strata on that part of the west coast of Greenland which has been specially explored, viz. the Disko Bay area (about $68^1/_2$°—$69^1/_2$° N). Thus I have been able to examine *Portlandia* (*Yoldia*) *arctica* collected in the past from the following localities: clay-terraces at the inner end of Southeast Bay; Orpigsôk south of Christianshaab; Kiakusuk north of Christianshaab; the Clay Bay at Claushavn; Niakornak at Jakobshavn. It appeared from a special investigation made in the summer of 1906 by Jensen and Harder that *Portlandia* (*Yoldia*) *arctica* is very common in the raised strata on the south and southeast coasts of Disko Bay: On the north side of the large clay-plains between Tasiursarssuak and Southeast Bay (e. g. Padusarniarfik and Sarpiussak), at

[1] G. Thorson l. c. 1934, pp. 43—44.
[2] Cf. G. Thorson, Medd. om Grønland, Bd. 100, Nr. 6, p. 112. 1936.

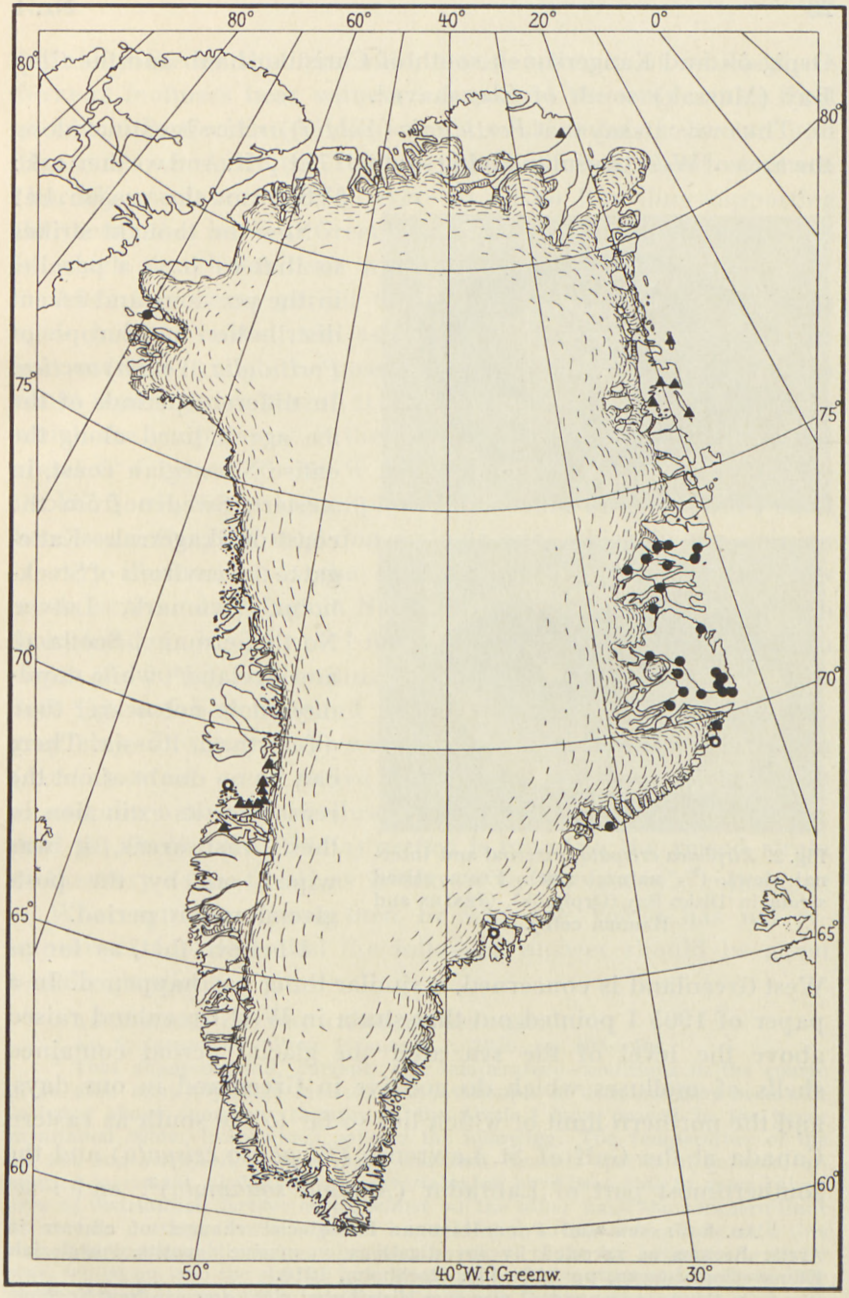


Chart 3. Sketch map of Greenland showing distribution of *Portlandia* (*Yoldia*) *arctica*.

- ● Occurrence of Recent specimens.
- ○ Occurrence of dead shells on the bottom of the sea.
- ▲ Occurrence of fossil shells in raised inland strata.

Orpigsôk and Kangersunek south of Christianshaab and the Clay Bay (Marrak) south of Claushavn[1].

Thus we can say that *Portlandia* (*Yoldia*) *arctica* is extinct along the area of West Greenland lying south of 77 $^1/_2$° N. And we then ask: What can the reason be?

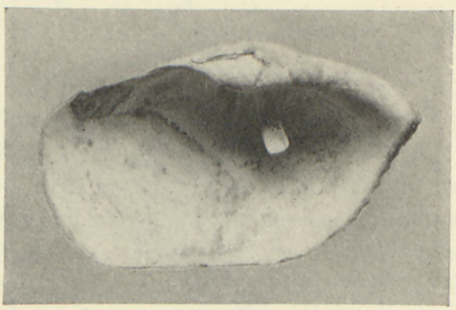


Fig. 2. *Zirphaea crispata*, external and internal views. ($^3/_4$ natural size). From raised strata in Disko Bay (Orpigsôk). (Jensen and Harder coll.).

Now the thought strikes us that we have a parallel in the previous and recent distribution in Europe of *Portlandia* (*Yoldia*) *arctica*. In different periods of the ice age it lived along the entire Norwegian coast, in western Sweden from the coast of Skagerrak—Kattegat to the environs of Stockholm, Denmark, Latvia, North Germany, Scotland, and Iceland[2], while nowadays it is not nearer than off northern Russia. There can be no doubt about the reason for its extinction in these vast areas, it was wiped out by the post-glacial warm period.

I believe that, as far as West Greenland is concerned, a similar thing has happened. In a paper of 1905 I pointed out that strata in West Greenland raised above the level of the sea after the glacial period contained shells of molluscs which do not live in Greenland in our days, and the northern limit of which lies so far to the south as eastern Canada at the Gulf of St. Lawrence (*Zirphaea crispata*) and the southernmost part of Labrador (*Anomia squamula*)[3], and I set

[1] Ad. S. Jensen and Poul Harder: Post-glacial changes of climate in Arctic Regions as revealed by investigations on marine deposits. Postglaziale Klimaveränderungen, pp. 402—406. Stockholm, 1910.

[2] On the American side it was once distributed right down to New England, while its southern limit is now in Richmond Gulf on the eastern side of Hudson Bay.

[3] On the European side of the Atlantic they have their northern boundary in West Finmark, and in the "warm area" of the White Sea and Murman coast respectively; westward they reach Iceland.

forth the theory that the mild marine climate of which these boreal molluscs bear witness has passed the temperature limit at which *Portlandia* (*Yoldia*) *arctica* could subsist[1]. JENSEN and HARDER[2] succeeded in 1906 in again finding these southern (boreal) species in raised layers at Disko Bay thus supporting the theory that in West Greenland there was a post-glacial period in which the climate was warmer than it is now[3].

After this warm period the climate of West Greenland has again become colder; and as far as the temperature in its fjords is concerned it might be possible that *Portlandia* (*Yoldia*) *arctica* could again thrive there, at any rate in some of the fjords in which the temperature at the depth suitable for this mollusc lies about 0° C. But hitherto it has not been found in any of the "cold" fjords. Several examples of this could be given, but I shall here restrict myself to giving a single one, which in my opinion is very illustrative. In the summer of 1911 Dr. V. NORDMANN made several dredgings in North Strømfjord from near its mouth to its head. In his journal I find no less than 14 stations at which depth (6—60 m), temperature (—1.2°—+1.5° C.), salinity (3.09—3.45 ‰) and bottom (sand mixed with clay, grey clay, greasy grey clay, fine grey clay) were of such a nature that *Portlandia* (*Yoldia*) *arctica* could thrive there; but it was completely absent among the numerous molluscs which came up with the dredge. And yet *Portlandia* (*Yoldia*) *arctica* is found in the raised strata at the very same fjord, as is shown by BENDIXEN's collection!

What can the reason then be why the *Yoldia* has not re-appeared? I believe that the following answer should be given to this question:

[1] AD. S. JENSEN l. c. 1905 (1909), pp. 292—297.

[2] AD. S. JENSEN and POUL HARDER l. c. 1910, pp. 403—404.

[3] That changed wind, current, and temperature conditions in the course of an even relatively short interval (the last couple of decades) have been able to bring about enormous changes in the Arctic I have proved in the paper mentioned below, from which appears the following: The temperature of the air and sea has risen, so that many southern (boreal) species of animals, including mammals, birds, fish and invertebrates, have been able to extend their area of distribution farther north, whilst on the other hand the southern limit for certain northern (arctic) species has retreated northwards. Along with this rise of temperature there has also been a retreat of the ice boundary in arctic seas, whilst on land the glaciers have been in a recessive stage and the boundary of the ground-ice is moving northwards. (AD. S. JENSEN: Concerning a change of climate during recent decades in the arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. D. Kgl. Danske Vidensk. Selskab, Biol. Medd. XIV, 8, 1939).

After the *Yoldia* had been pushed back far northwards during the post-glacial warm period its larvae would have to go south if the species was to regain its old places of occurrence. But as is well known the currents of the sea along the west coast of Greenland go northwards, thus preventing the spreading of the larvae in a southerly direction[1].

The only possibility of finding *Yoldia* in the southern part of West Greenland would be if it had subsisted as a survivor (relict) from the glacial period in some "cold" fjord; I dare not deny the possibility of its surviving as such, but hitherto it has not been found.

On remains previously found of an arctic fauna in raised deposits far within North Strømfjord.

In the year 1879 the geologist KORNERUP travelled by woman's boat (Umiak) in North Strømfjord and its southern principal branch and a river debouching there (Nagssugtôk river) which springs from the inland ice[2]. More than 150 km from the mouth of the fjord KORNERUP found the following bivalves, determined by TRAUSTEDT, in a low clay terrace along the sides of the river: *Mya arenaria* L., *Mya truncata* L., *Saxicava rugosa* L., (= *S. arctica* L.), *Astarte striata* Leach (= *A. Montagui* Dillw. var. *striata* Leach), *Cardium ciliatum* Fabr., *Pecten islandicus* Ch. and *Tellina calcarea* Ch.[3].

This fauna resembles that which now lives in West Green-

[1] There can be no doubt that *Portlandia* (*Yoldia*) *arctica* has pelagic larvae. THORSON kindly informed me that in August 1932 he watched larvae taken by plankton hauls in Northfjord, in the Franz Joseph Fjord area, of a very characteristic, barrel-shaped appearance which he had no doubt were the larvae of a taxodont mollusc. In Northfjord *Portlandia* (*Yoldia*) *arctica* was the dominant species, and as other taxodont molluscs can be left out of consideration, THORSON considers it very likely that the pelagic larvae observed were *Portlandia* (*Yoldia*) *arctica*. The peculiar thing in this type of larva—in contrast to other molluscan larvae—is, according to THORSON, that in its free-swimming stage it develops exclusively on its own yolk mass, and does not absorb nourishment from the outside which is made impossible because its shells are completely surrounded by surface cells (test cells). It is thus possible for it to spread through the sea without running the usual risk of pelagic larvae of perishing through the absence of nourishment.

[2] Reference is made to an excellent chart by the leader of the expedition I. A. D. JENSEN in Medd. om Grønland, 2. Hefte, 1881, plate V.

[3] A. KORNERUP: Geologiske Iagttagelser fra Vestkysten af Grønland, p. 187; Medd. om Grønland, 2. Hefte, 1881.

land. Thus we find remains both of a high-arctic and of an arctic fauna in the raised strata in North Strømfjord; this

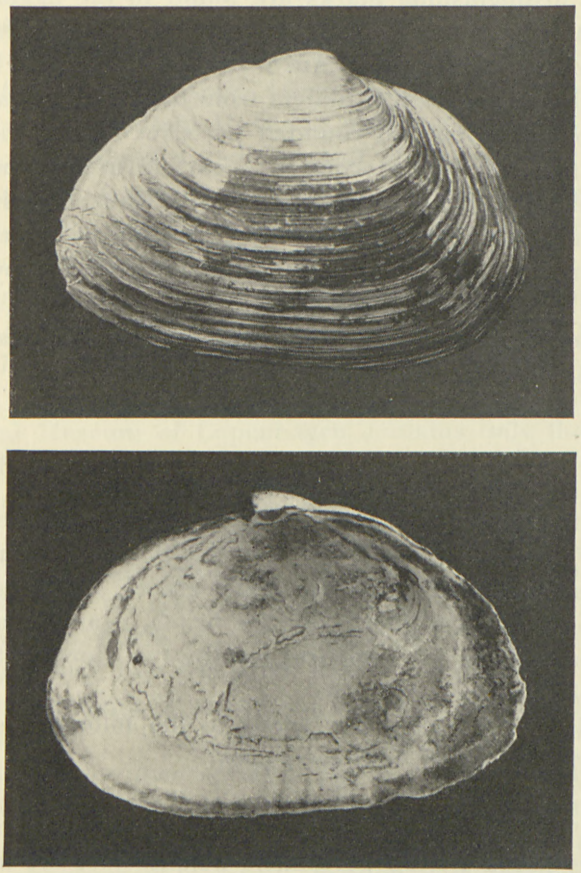


Fig. 3. *Mya truncata f. ovata*, external and internal views. ($^9/_{11}$ natural size). From raised deposits far within North Strømfjord (collected by KORNERUP).

arctic fauna probably corresponds to that found in South Strømfjord and discussed in the next chapter.

The recorded occurrence of *Mya arenaria* which—as I showed on a previous occasion[1]—is not an arctic species, seems to be against this supposition. An examination of the shells kept in the Zoological Museum of Copenhagen, six in all, shows, however,

[1] AD. S. JENSEN: Studier over nordiske Mollusker, I, *Mya*. Vidensk. Medd. Naturhist. Foren. 1900, p. 133.

that they resemble, truly enough, *Mya arenaria* in their contours, but that they agree with *Mya truncata* in the decisive characters: the safest distinguishing marks are found in the ligament plate in the left valve and the ligament pit in the right valve and in the beak of the left valve (cf. Ad. S. Jensen l. c. fig. 1 a, b and fig. 2 a, b). This variety, which differs from the typical *Mya truncata* by the oblong shape and rounded posterior end of the shell, I called *A. truncata* forma *ovata*. It occurs in arctic seas, also in West Greenland. Thus, it was taken by V. Nordmann in 1911 in North Strømfjord, at depths from 6 to 18 and 80 metres, where the bottom consisted of clay, the temperature being by the end of July about 0° C.

The fauna found by Kornerup in the raised strata at the Nagssugtôk river is thus as a whole arctic.

The locality at South Strømfjord.

According to Mr. Bendixen there are, inside the head of the Itivdlek-Fjord, in the region between this fjord and South Strømfjord, deposits of clay, and especially gravel, with huge masses of shells, especially a little inside the beach, near the lake which fills up part of the interval between the two fjords[1]; the height is about 35 m above the sea.

The shells collected here belong to the following species of molluscs, gasteropods, and barnacles:

Pecten islandicus Müll. 1 shell of an adult specimen (alt. 104 mm, lat. 97 mm). A fragment, also of an adult specimen, with holes bored by the polychaete *Polydora* on the inner side.

Cardium ciliatum Fabr. Fragments of 6 shells of large and medium-sized specimens.

Astarte borealis Ch. 1 shell of an adult specimen.

Cyprina islandica L. 1 left valve of an adult specimen (alt. 77 mm, lat. 81 mm). A fragment of a shell, also of an adult specimen, with holes bored by *Polydora* both on the outer and inner sides.

Panopaea norvegica Spengl. One right valve, rather thick, of

[1] This plain is known under the name Itivnek and formerly was the place where the Greenlanders carried their woman's boats from one fjord to the other.

an adult specimen (alt. 49 mm, lat. 82 mm). 1 left valve of a somewhat smaller specimen (alt. 45 mm, lat. 68 mm).

Saxicava arctica L. 2 right valves, rather thick, 30 and 31 mm long; one with two holes bored by *Natica*, of which, however, only one penetrated the valve.

Mya truncata L. 1 shell, 50 mm long.

Buccinum undulatum Møller. 2 specimens.

Balanus Hammeri Ascan[1]. 8 shell plates, alt. max. 75 mm.

Among the fossils from this locality one notices *Cyprina islandica* in the first place, as it can be taken for granted that it no longer lives in Greenland.

Cyprina islandica, has, it is true, previously been included in the lists of the molluscan fauna of Greenland by Mørch (1857 and 1877), and Posselt (1898), but in my opinion on doubtful grounds. The Greenland collection of molluscs kept in the Zoological Museum of Copenhagen contains only the following (dating from the first half of the last century):

a. A right valve, according to the label taken in Davis Strait. It is of a very old appearance, and may derive from a submarine layer or may have been carried passively out into the strait from a deposit on land.

b. The two valves of a shell, 43 mm long, according to the label originating from Rudolph, who was a physician in Jakobshavn. Periostracum is preserved, but there are no traces of the soft parts.

The latter specimen seems to me to be dubious; it may also be that a change of labels has taken place in the course of time, since it is unthinkable to me that such a mollusc as *Cyprina islandica* should have escaped attention if it did live at Greenland nowadays. Its size is in itself remarkable, so it cannot have been overlooked, as the west coast of Greenland is well explored as far as the coastal belt is concerned. It should also be borne in mind that *Cyprina islandica* is often washed ashore on the beach off which it lives; but it is not found among the large

[1] Everywhere in the literature the name is written erroneously *Hameri*, because Ascanius used this spelling by a mistake; he says himself that he named the species after the county sheriff in Finmarken G. Hammer who was the first to find and give him this barnacle. The specific name should, therefore, be written *Hammeri*, according to Hj. Broch: *Cirripedia Thoracica* von Norwegen und dem Norwegischen Nordmeere, p. 90. Vidensk. Selsk. Skrifter, I, Mat.-Naturv. Klasse, 1924, No. 17. Kristiania 1924.

number of shells washed ashore and brought home from Greenland. I have myself looked for it during my Greenland expeditions

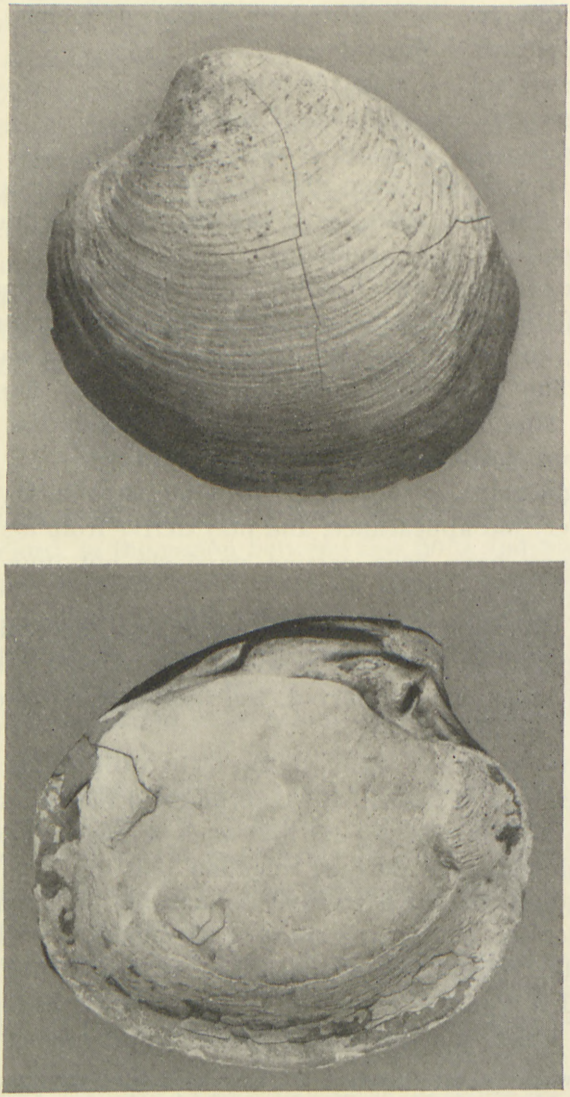


Fig. 4. *Cyprina islandica*, external and internal views. ($^3/_4$ natural size). From raised deposits in South Strømfjord.

by dredging or among the shells washed ashore, e. g. in Disko Bay, where Jakobshavn is situated, but in vain.

The literature also contains records to the effect that *Cyprina islandica* occurs in other arctic seas. On a previous occasion I have gone critically through these records also, and I succeeded in showing that they are erroneous[1].

After deleting the arctic localities for *Cyprina islandica* its present range of distribution should be limited as follows:

In North America *C. islandica* occurs from Cape Hatteras to New Foundland Bank and the southern part of the Gulf of St. Lawrence. In Europe it is distributed from southwestern France to the Murman coast and the "warm area" of the White Sea, and westwards it extends over the Faroes to Iceland; from the Kattegat it enters the Sound and through the Belts it penetrates into the southwestern Baltic.

Cyprina islandica has not, as previously presumed, a boreal and arctic distribution, but is a distinctly boreal form.

On account of this knowledge of the present distribution of *Cyprina islandica* this mollusc can be reckoned to be a leading fossil *par excellence*: Its presence in deposits on land gives evidence that they were formed under boreal climatic conditions.

Among the rest of the shells two belong to a mollusc which possibly lives no longer in Greenland, viz. *Panopaea norvegica*. The literature contains numerous records of this mollusc in different sea areas, and it is described as having a circumpolar distribution. But if the original records be examined it is found that they nearly always refer to "dead" shells. As regards Greenland, we have from here only empty shells[2] dredged in the following place:

North Strømfjord, 375—380 m, bottom temperature 0.2 C. V. Nordmann legit 1911. Two valves with periostracum partly intact and connected by the ligament, but empty; length 66.5 mm, altitude 45 mm. Also a right valve, length 61.5 mm, altitude 39 mm; a left valve, length 61 mm, altitude 38 mm.

In addition some ten fossil specimens have been collected in the raised strata at Pagtorfik in Umanak district, up to 110 mm long, with shells connected.

[1] Ad. S. Jensen: Studier over nordiske Mollusker. II. *Cyprina islandica*. Vidensk. Medd. naturhist. Foren., 1902, pp. 33—42.

[2] Posselt writes (Grønlands Brachiopoder og Bløddyr, 1898, p. 94), that *P. norvegica*, according to Woodward's Manual, was taken alive in Baffin Bay. I have not been able to find anything to this effect in Woodward.

In European waters *Panopaea norvegica* occurs alive, at any rate in the North Sea, especially on the Dogger Bank, according to JEFFREYS. G. O. SARS has taken a young specimen near Lofoten, and AURIVILLIUS two specimens (long. max. 65 mm) in Kvænangen Fjord, in the northernmost part of Tromsø county,

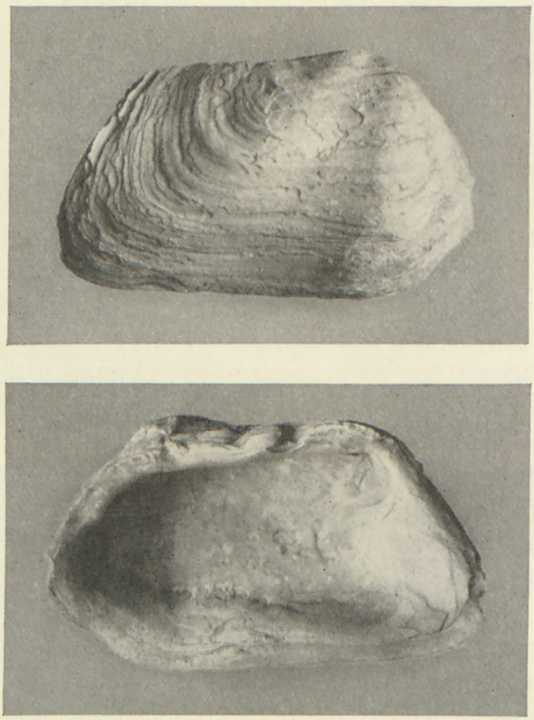


Fig. 5. *Panopaea norvegica*, external and internal views. ($^{7}/_{10}$ natural size). From raised deposits in South Strømfjord.

on the boundary towards West-Finmarken. Further, the Icelandic zoologist, BJARNI SÆMUNDSSON long ago sent me a specimen taken on line near South Iceland (Vestmannø) in 65 fms.; it was 100 mm long, 58 mm high and contained the soft parts; finally, SÆMUNDSSON informed me that he had still another specimen from the same place, also alive, about 70 mm long. It has also been taken alive near the Skaw, in a few places in the eastern Kattegat, and off Landskrona.

If conclusions should be drawn only from the places in which *P. norvegica* has been found to occur alive—from northern

Norway and southern Iceland to the North Sea and the Sound—it should be regarded as a boreal form, and its occurrence in Greenland then derives from a warmer period than the present. But as *P. norvegica* lives buried in the bottom and therefore is difficult to take with the dredge the possibility exists that it may be found alive in arctic seas, from which only its empty shells are now known.

A different form of *P. norvegica* was described by DONS as var. *triangula*: shell thick, shape triangular, length: altitude = about 4:3; greatest length 70 mm. In *P. norvegica f. typica* the shells are of medium thickness or thin, trapeziform, length: altitude = 5:3; greatest length 102 mm. DONS regards the variety *triangula* as a high-arctic form like the variety *uddevallensis* of *Mya truncata*, and the typical form as boreal[1]. All the shells found in Greenland belong to *f. typica* and should thus be referred to the boreal climatic period.

It can be said about the remaining molluscs from this locality, viz. *Pecten islandicus*, *Cardium ciliatum*, *Astarte borealis*, *Saxicava arctica*, *Mya truncata* and *Buccinum undulatum*, that they live in West Greenland waters and are common there nowadays and thus belong to an arctic fauna. On the other hand, it is probable that some of the species recorded have lived together with *Cyprina islandica*, since they have a wide distribution and occur both in boreal and arctic seas. This is the case of *Mya truncata*; the only valve available is rather elongate and may occur both in arctic and boreal seas[2]. On the other hand, *Pecten islandicus*, *Cardium ciliatum*, the thick-shelled *Saxicava arctica* and *Buccinum undulatum* may be regarded as belonging to the arctic faunistic element.

As regards the distribution of *Balanus Hammeri* the following can be said: This barnacle, remarkable from its size, which, as a fossil, was first known from Scandinavia under the name *Balanus Uddevallensis*, is given the following distribution by CHARLES DARWIN in his famous work on the *Cirripedia*: The British islands, Finmarken, the Faroes, Iceland and Mas-

[1] CARL DONS: Zoologiske Notiser X. *Panopæa norvegica* var. *triangula* nov. var. Det Kgl. Norske Vidensk. Selskabs Forhandl. Bd. IV, Nr. 2, 1931, p. 5, Fig. 1—4.

[2] AD. S. JENSEN: Studier over nordiske Mollusker, I, *Mya*, pp. 153—156, Fig. 8 a, b and c. Vidensk. Medd. Naturhist. Foren., 62. Aarg., 1900 (1901).

sachusetts[1]. Since then its northern limit has been extended to the White Sea[2] and Nova Scotia[3]. BROCH also records *B. Hammeri* from a series of localities along the Norwegian coast at depths from about 40 to 120 metres[4]. In the Zoological Museum of Copenhagen are specimens from the North Sea and the Skagerrak (NE of the Skaw, 70 fms. and 33 miles SE of Oksø,

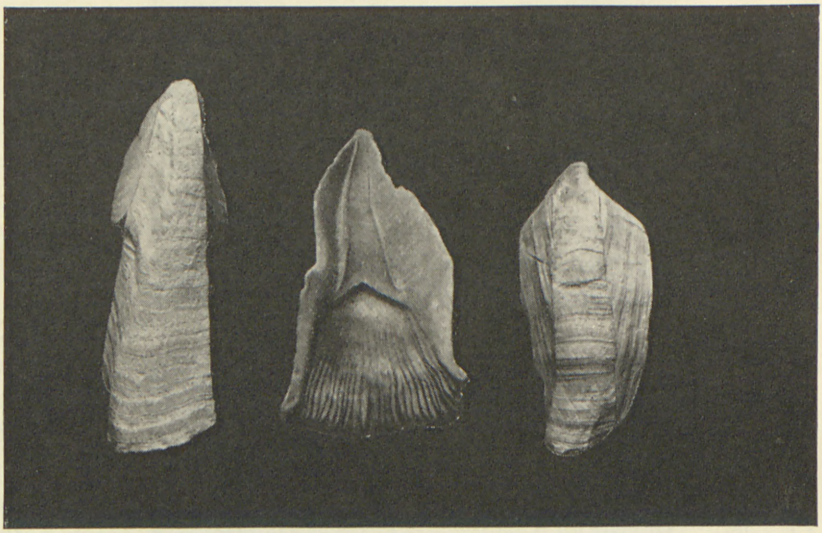


Fig. 6. *Balanus Hammeri*, 3 shell plates, that in the middle seen from the inside, the two others from the outside. ($^2/_3$ natural size). From raised deposits in South Strømfjord.

259 metres). From Greenland it was known only as a fossil, but in 1911 V. NORDMANN got a living specimen up with the dredge in North Strømfjord from a depth of 14—38 m and at a bottom temperature (end of June) of 0.3°—0.2° C. According to the distribution hitherto known *B. Hammeri* would be characterized as a purely boreal species[5]; but it actually appears that it can also live under arctic conditions at a temperature which, in the middle of the summer, is very near 0° C. *Balanus Hammeri* should consequently be designated both as a boreal and arctic

[1] DARWIN: A monograph on the sub-class *Cirripedia*, vol. II, p. 277. The Ray Society, 1854.
[2] WELTNER: Die Cirripedien der Arktis. Fauna Arctica, I, p. 298. 1900.
[3] DAWSON: The Canadian Ice Age, 1894, p. 262.
[4] HJ. BROCH l. c. 1924, pp. 89—90.
[5] Cf. HJ. BROCH l. c. 1924, pp. 114—115.

species. It is also in good agreement with this that in the series of strata in Disko Bay (Orpigsôk and South East Bay) *B. Hammeri* is frequently met with in the layers the fauna of which resembles that living at present in West Greenland[1].

Conclusion.

From the locality at South Strømfjord we have, according to the above, two fauna-elements represented, viz. a boreal and an arctic. The certain representative of the boreal element is *Cyprina islandica*, which no longer lives in Greenland, but belongs to warmer seas. The other species are good arctic species, at present occurring in Greenland. Most likely *Pecten islandicus* and *Cardium ciliatum* together with *Buccinum undulatum* and the thick-valved *Saxicava arctica* represent an arctic level; the two last mentioned forms are found exclusively in arctic waters, and *Pecten islandicus* and *Cardium ciliatum* have such narrow distributions that they occur only now and then together with *Cyprina islandica*, whereas the latter, in many places, lives together with *Astarte borealis*, *Mya truncata*, and *Balanus Hammeri*. To which group *Panopaea norvegica* should be reckoned is doubtful; in Greenland it has hitherto been taken only as a fossil, living specimens are only known from more southern seas; but, being a species which lives buried in the sea bottom, it may have escaped capture in Greenland.

Summary.

We see thus that remains of animal species of high-arctic origin have been found in the raised shell deposits at North

[1] For completeness' sake it should be mentioned that Inspector Bendixen found still another deposit from the Quaternary period in Holsteinsborg District with remains of marine animals. The fjord Ikertôk is situated south of the Holsteinsborg settlement and has three branches, of which Avatdlek runs to the southeast. At the head of Avatdlek fjord Mr. Bendixen found marine shells in a deposit 70—80 metres above the present level of the sea, i. e. on the same level as in Depot Bay. Three shells were brought home of *Mya truncata*, very thick ones, the posterior end short, obliquely cut off and sloping forewards to the ventral side, and thus having a high-northern appearance. There is also a valve of *Tellina calcaria* Chemn. (with a hole bored by *Natica*).

Strømfjord; at South Strømfjord they are of an arctic and boreal character. The question then arises in what sequence these faunas have followed each other.

The detailed stratigraphy of these deposits being unknown, reference must be made to a paper by the geologist Poul Harder, whose early death we regret, and the present author, in which, on the basis of investigations which we made in 1906 into the raised marine deposits in the southeastern part of Disko Bay, we have been able to form the following review of the quaternary-geological history of this region[1].

The oldest layers (horizon A) were deposited in a sea on the bottom of which lived high-arctic forms such as *Portlandia (Yoldia) arctica*.

Then follow layers (horizon B) with a fauna indicating a climate which was not high-arctic but rather like that of the present time, i. e. arctic.

In the next layers (horizons C and D) the gradual change of the fauna indicates that the climate has gradually become colder until it became high-arctic characterized by *Portlandia (Yoldia) arctica*; at the same time a considerable sinking occurred, so that the sea-level stood about 100 m higher than at present.

The fauna in the following layers (horizon E) shows that these were deposited under conditions similar to those which now prevail in the sublittoral region; these layers have been formed at a time when the land had again been raised to a height of about 50 m below the present level and the climate had become almost as at present.

In the most recent link in the series (horizon F) the southern (boreal) forms *Anomia squamula* and *Zirphaea crispata* are found which were hitherto unknown in Greenland, the latter in such large numbers that it was found to be common throughout the whole deposit of strand gravel up to 7 m in thickness. The occurrence of these boreal forms shows that the temperature rose during the further raising of the land, so that there has been a temperature maximum at a time when the sea stood only about 10 m higher than at present, but single specimens of them were also taken up to a height of about 30 m.

[1] Ad. S. Jensen and Poul Harder, l. c. 1910, pp. 402—406 and the scheme with the horizons (p. 405).

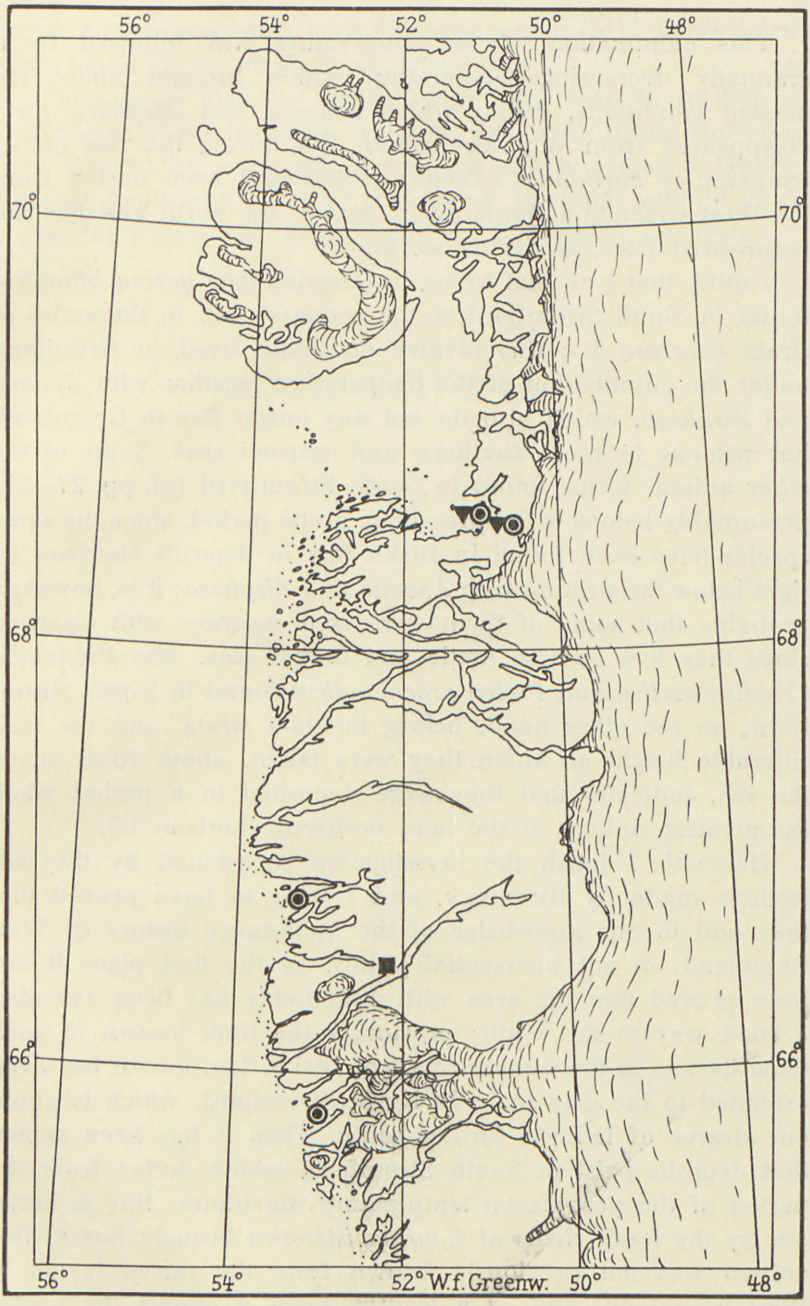


Chart 4. Localities for fossil shells of thermophile molluscs in raised strata on the west coast of Greenland from the post-glacial warm period.

◉ *Anomia squamula.*
▼ *Zirphaea crispata.*
■ *Cyprina islandica.*

This culmination of the temperature was followed by a gradually decreasing temperature which brought about the present conditions, during which *Anomia* and *Zirphaea* have disappeared from West Greenland. But during the rise of the temperature *Portlandia* (*Yoldia*) *arctica* had been ousted from the West Greenland fjords and coasts to the north and has not reappeared later, as far as we know.

I think that I am not wrong in referring the *Cyprina islandica*, found in South Strømfjord, to the youngest link in the series of strata (horizon F); this bivalve no doubt lived in Greenland under the culmination of the temperature together with *Anomia* and *Zirphaea*, which also do not any longer live in Greenland, but belongs to more southern and warmer seas. Some of the other animal forms found in South Strømfjord (cf. pp. 27—31) presumably belong to the preceding, arctic period, since the same species have been found in Disko Bay in deposits (horizon E) right below the stratum with *Anomia* and *Zirphaea*; it is, however, probable that some of them were contemporary with *Cyprina*, since they live both in arctic and boreal seas. The *Portlandia* (*Yoldia*) *arctica* and *Pecten groenlandicus* found in North Strømfjord, on the other hand, belong to older strata, and the considerable height at which they were taken, about 70 m above the sea, indicates that they were deposited in a period when the greatest sinking of the land occurred (horizon D).

Herewith I finish the investigation occasioned by the collections made by BENDIXEN, and I hope to have proved that they add to our knowledge of the quaternary history of West Greenland on not unessential points. In the first place it has been proved that the area with *Yoldia*-clay has been extended a good way to the south; previously the limit known of such deposits was at the southern part of Disko Bay, now it has been extended to the clay plain in North Strømfjord, which is about one degree of latitude further south. Then it has been shown that deposits exist in South Strømfjord which derive from the period of the post-glacial temperature maximum; this is borne out by the fossil shells of *Cyprina islandica* brought home; this animal was not previously known from the raised layers in West Greenland, and as a leading fossil it equals the boreal

forms *Anomia squamula* and *Zirphaea crispata* which previously were found in the deposits in Disko Bay.

I also hope that the present paper will lead to further investigations of the localities found by BENDIXEN in the Holsteinsborg District by a qualified geologist and a zoologist familiar with the molluscan fauna of Greenland. Here lies without doubt a grateful future task to be taken up by Danish scientists.

Indleveret til Selskabet den 13. April 1942.
Færdig fra Trykkeriet den 13. Juli 1942.

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 5

SOME MARINE ALGAE FROM MAURITIUS

III. RHODOPHYCEAE

PART 1

PORPHYRIDIALES, BANGIALES, NEMALIONALES

BY

F. BØRGESEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

Printed in Denmark.
Bianco Lunos Bogtrykkeri A/S

In the introduction to Part I of this publication, The *Chlorophyceae*, it was mentioned that copious collections of algae from the Mascarene Islands are found in the Muséum National d'Histoire Naturelle, Paris, and that Dr. FELDMANN had begun taking out a collection of Dr. JADIN's duplicates to be sent to me for examination, when the war broke out and made all postal communication impossible.

Meanwhile when the postal communication with Paris was reestablished last summer I wrote to Professor P. ALLORGE, Director of the Laboratoire de Cryptogamie, Paris, asking if it would be possible for him to send me the collection mentioned above. Professor ALLORGE was good enough soon to let me know that the collection would be sent to me through the intermediation of L'institut Allemand de Paris. Doctor G. HAMEL was so very kind as to take out the collection of algae and at the end of last year it arrived here safely.

The collection seems to be rather copious and is of much interest because Dr. JADIN has based his list of algae from the Mascarene Islands upon it. But several of the species are present only in a single small specimen, are often sterile, and some of them being collected by a native by name Daruty bear witness to be cast ashore specimens.

I am also much indebted to Professor R. PILGER, Botanisches Museum, Berlin-Dahlem who has most kindly sent me some very good material of *Dermonema amoena* Pilger.

From Naturhistoriska Riksmuseet, Botaniska Avdelningen, Stockholm, through the kind help of Dr. TH. ARVIDSSON, a collection of algæ from Mauritius has been lent me for examination.

Finally I owe thanks to Professor OTTO CHR. SCHMIDT, Botanisches Museum, Berlin-Dahlem for the loan of a collection of *Liagora*.

While the former two parts: I. *Chlorophyceae* and II. *Phaeophyceae* are for the most part based upon the collection of Dr. TH. MORTENSEN and Dr. R. E. VAUGHAN, this third part containing the beginning of the *Rhodophyceae* is not only due to the above-mentioned collections, but also to the rich collection of Dr. JADIN, quite recently received from Paris.

I should like here to acknowledge my indebtedness to Dr. O. HAGERUP of The Botanical Museum, Copenhagen who has not only been so kind as to make a series of microscopical sections of some algae for me but who has also drawn some of the figures in Chinese ink for reproduction.

RHODOPHYCEAE

A. BANGIOIDEAE

I. Porphyridiales.

Fam. 1. Porphyridiaceae.

Asterocytis Gobi.

1. Asterocytis ornata (Ag.) Hamel.

Hamel, Bangiales, p. 40 where literature is mentioned. — *Conferva ornata* C. Ag., Systema Alg., 1824, p. 104. *Asterocytis ramosa* Gobi in Arbeiten St. Petersb. Naturf. Gesellsch. X., p. 85, 1878.

Ramified specimens very like Hamel's fig. VII B drawn from an original specimen of C. Agardh were found upon *Chnoospora implexa*. The filaments had a breadth of about 12 μ and the cells were about 6—7 μ broad and had a well developed pyrenoid.

Mauritius: Tamarin Bay, "in pools behind reef", R. E. V. no. 293.
Geogr. Distr.: Atlantic coast of Europe and America, West Indies, Mediterranean Sea, Canary Islands, etc.

Goniotrichum Kütz.

1. Goniotrichum elegans (Chauv.) Le Jolis.

Le Jolis, A., Alg. mar. Cherb., p. 103. Berthold, Bangiaceen, p. 26. Rosenvinge, Mar. Alg. Denm., p. 75. Børgesen, Mar. Alg. D. W. I., vol. II, p. 4, fig. 2. Hamel, Bangiales, p. 37.

The plant from Mauritius is rather slender, having a breadth of about 25 μ. The cells are about 9—11 μ broad and as is gener-

ally the case in this species have a rather variable shape, being often only half as long as broad. In a very few cases only have I found two cells side by side in the filament. The plant was found as an epiphyte upon *Sphacelaria tribuloides*.

Mauritius: Lagoon at Flic-en-Flacq, R. E. V. no. 250.
Geogr. Distr.: Seems to occur in most temperate and warm seas.

II. Bangiales.

Fam. 1. Bangiaceae.

Erythrotrichia Aresch.

1. Erythrotrichia carnea (Dillw.) J. Ag.

J. Agardh, Till Alg. Syst., III, 1883, p. 15. Rosenvinge, Mar. Alg. Denmark, 1909, p. 67, fig. 8. — *Conferva carnea* Dillw., Brit. Conf., 1809, pl. 84. *Conferva ceramicola* Lyngb., Hydrophyt. Dan., 1819, p. 144, tab. 48 D. For more synonyms comp. Rosenvinge, l. c.

The plant is found as an epiphyte upon various algæ. The filaments had a breadth of about 15 μ. Spore-formation was observed in several of the specimens.

Mauritius: Barachois, Ilôt Brocus, R. E. V. no. 204. Tamarin Bay, "in pools behind reef", R. E. V. no. 293.
Geogr. Distr.: Widely distributed in temperate and warm seas.

Porphyra C. Ag.

1. Porphyra tenera Kjellm.(?)

Kjellman, F. R., Japanska Arter af Slägtet Porphyra, 1897, p. 20, pl. 1, fig. 6; pl. 4, figs. 2—5; pl. 5, figs. 22—26. Yendo, Notes on Algæ new to Japan IV, p. 52—54. Okamura, Onda and Higashi, Preliminary notes on the development of the carpospores of Porphyra tenera Kjellm. Tseng, C. K., Economic seaweeds of Kvantung Province, S. China, 1935, p. 99, pl. fig. 2; Notes on some Chinese marine algae, 1938, p. 594.

The reason why I have put a ? after the specific name is that the question as to the real value of KJELLMAN's species seems not to have been at all satisfactorily settled yet in Japan. YENDO (l. c.) sharply critisized KJELLMAN's definition of this and other of his species, and is very much inclined to consider *P. tenera* as a mere form of *Porphyra leucosticta* Thur. TSENG, in his paper 1935, p. 99 called it *Porphyra tenera*; in a later paper (1938, p. 594) basing his examination upon Chinese material and referring to several publications in Japanese and especially to a paper by ONDA, Studies in the Japanese species of Porphyra (Journ. Fish. Expt. Sta., vol. 28, 1931) (in Japanese) he pointed out that *Porphyra tenera* in reality does not seem to be separable from *P. leucosticta*. But since ONDA, on the basis of some minor characters, prefers to keep up KJELLMAN's name for the Japanese species, he thinks it better to await further examination.

From Mauritius I have seen only a quite small specimen collected by JADIN who in his list mentions this species as *Porphyra umbilicalis* J. Ag. f. *purpurea*. The specimen agrees quite well with some specimens from Japan which YAMADA has sent me. The thallus is thin, a transverse section about 22 μ thick. Seen from the surface the cells are irregularly polygonal of shape and arranged without any order. KJELLMAN described this species as dioecious but, as pointed out by YENDO, it is monoecious. The thallus becomes fertile along the margin; the cystocarps contain 8 carpospores.

JADIN collected the plant in a very exposed locality.

Mauritius: Mahébourg, Septembre 1890, F. JADIN, no. 475.
Geogr. Distr.: Japan, China, India, most probably wide-spread.

B. FLORIDEAE

I. Nemalionales.

Fam. 1. Chantransiaceae.

Acrochaetium Nägl.

1. Acrochaetium crassipes Børgs.

Børgesen, Mar. Alg. D. W. I., vol. II, 1915, p. 20, fig. 11. Some Indian Rhodophyceae, 1931, p. 2, fig. 1. — *Chantransia crassipes* Børgs., Some new or little known W. I. Florideae, 1909, p. 1, fig. 1.

var. *typica* Børgs., l. c. p. 20.

This variety is found in several of the collections of Dr. Vaughan. The basal cells had a breadth of about 8—10 μ. The hostplants were *Murrayella, Polysiphonia* and *Griffithsia Weber-van-Bosseae* Børgs.

var. *longiseta* Børgs., l. c. p. 2, figs. 12—13.

Specimens agreeing very well with my above-quoted figures were found fixed to an old specimen of *Acanthophora*. The basal cells had a breadth of 10 μ.

Mauritius: Ilôt Brocus, Aug. 1938, R. E. V. no. 191. Barkley Island, Aug. 1939, R. E. V. no. 338 (var. *longiseta*). Black River Bay, 9. Aug. 39, R. E. V. no. 282.

Geogr. Distr.: West Indies, India etc.

2. Acrochaetium candelabrum nov. spec.

Thallus usque ad 400—500 μ altus. Spora germinans, ca. 13—14 μ longa et 8—9 μ lata, in texturam hospitis paululum penetrans, a superiore parte non immersa, filum erectum ramosum emittens.

Supra sporam ex cellulis basalibus filamenta duo opposita arcuatim suberecta oriuntur.

Filamenta, in inferiore parte ca. 7—8 μ lata, ad apicem versus gradatim attenuata ca. 2—3 μ lata, simplicia, aut ramis paucis instructa. Cellulae ca. 20—25 μ longae.

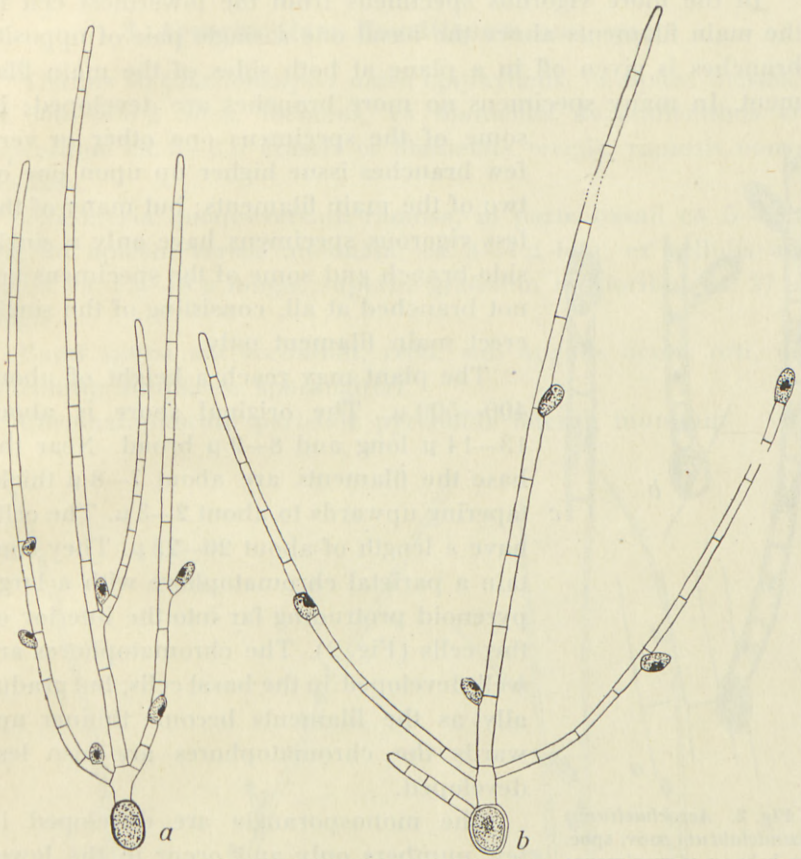


Fig. 1. *Acrochaetium candelabrum* nov. spec. Two specimens. (× 340).

Monosporangia sessilia, pauca et sparsa, interdum in summis filamentorum terminalia, ovato-ovalia, 10—11 μ longa et 7—8 μ lata.

Chromatophorum parietale, pyrenoide laterali instructum.

Mauritius: Tamarin Bay in *Sphacelaria furcigera* socialiter nidulans, R. E. V. no. 316.

This fine little species (Fig. 1) grows gregariously upon *Sphacelaria furcigera* in the epidermal wall of which the oblong somewhat oblique original spore is a little immersed (Fig. 2). When the spore germinates an erect filament is given out, sometimes a less vigorous adventitious filament also issues below it.

In the more vigorous specimens from the lowermost cell in the main filaments above the basal one a single pair of opposite branches is given off in a plane at both sides of the main filament. In many specimens no more branches are developed; in some of the specimens one other or very few branches issue higher up upon one or two of the main filaments; but many of the less vigorous specimens have only a single side-branch and some of the specimens are not branched at all, consisting of the single erect main filament only.

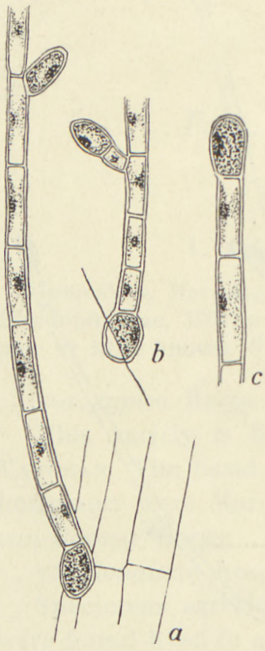


Fig. 2. *Acrochaetium candelabrum* nov. spec. *a*, *b*, bases of specimens; *c*, a terminally placed sporangium. (× 500).

The plant may reach a height of about 400—500 μ. The original spore is about 13—14 μ long and 8—9 μ broad. Near the base the filaments are about 7—8 μ thick, tapering upwards to about 2—3 μ. The cells have a length of about 20—25 μ. They contain a parietal chromatophore with a large pyrenoid protruding far into the interior of the cells (Fig. 2). The chromatophores are well developed in the basal cells, but gradually as the filaments become thinner upwards the chromatophores are also less developed.

The monosporangia are developed in few numbers only and occur in the lower part of the plant with the exception that now and then it happens that a sporangium terminates one of the erect filaments. The sporangia are obovate-oval, broadly rounded above or with a small apiculum; they are sessile, rarely pedicellate. Their length is about 10—11 μ and their breadth about 7—8 μ.

Because of its resemblance to a trifurcate candelabrum this species may show some likeness to the *Acrochaetium trifilum* (Buff.) Batters, 1902, p. 58; compare Hamel, Recherches 1927, p. 12, fig. 14a—d. But this species is a very small one, only 27—30 μ high, and consists only of very few cells.

3. Acrochaetium Mauritianum nov. spec.

Thallus in *Chaetomorpha aerea* epiphyticus, caespites densos, ca. 500—800 μ altos, formans, ex filamentis decumbentibus et repentibus ca. 5—6 μ crassis et filamentis erectis, ramosis compositus.

Fila erecta quoqueversum ramosa, in parte basali ca. 5—7 μ lata ad apicem versus attenuata, ca. 3—4 μ lata, ex cellulis ad basim ca. 15—18 μ longis, superne gradatim longioribus ca. 27 μ longis.

Rami sparsi aut secundati, recti, sub angulis acutis orti, ut plurimum simplices, sporangiferi.

Chromatophorum parietale pyrenoide laterali munitum.

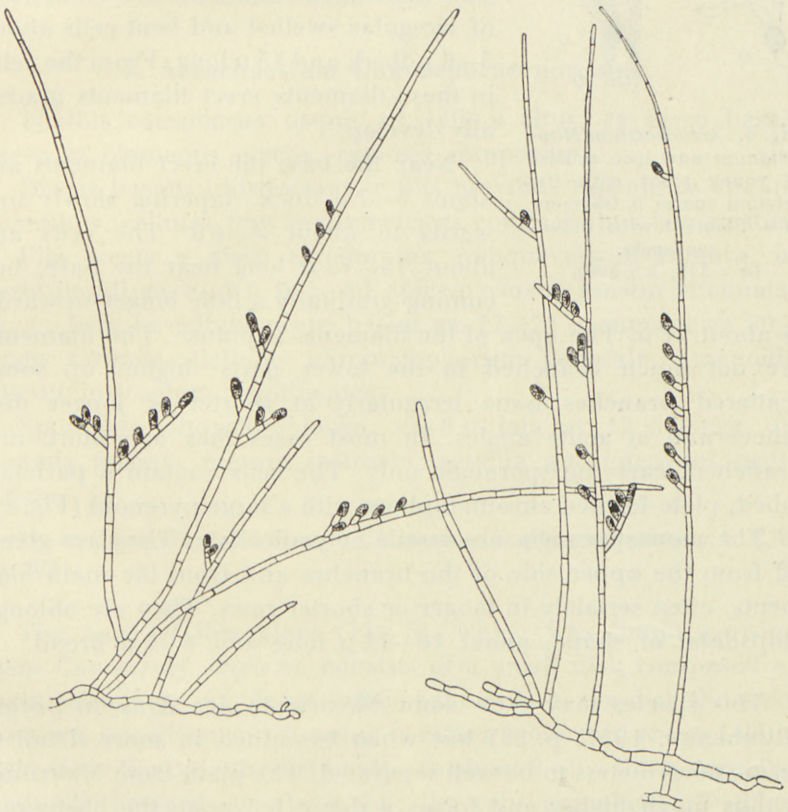


Fig. 3. *Acrochaetium Mauritianum* nov. spec. Parts of the thallus. (× 265).

Sporangia sessilia aut pedicellata, oblongo-ellipsoidea, ca. 10—12 µ longa et 6—7 µ lata.

Mauritius: Barachois, Ilôt Brocus, R. E. V. no. 204.

The plant (Fig. 3) grows gregariously upon *Chaetomorpha aerea*, forming a dense felt round the thallus of the host. It is composed of decumbent creeping filaments and straight erect branched filaments about 500—800 µ high.

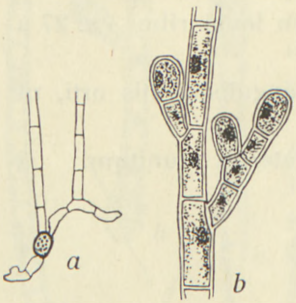


Fig. 4. *Acrochaetium Mauritianum* nov. spec. *a*, base of young plant with the original spore; *b*, fragment of a filament with monosporangia. (*a* × 340, *b* × 500).

From the upward-turned side of the germinating spore (Fig. 4 *a*) an erect filament is given out; and at the same time decumbent filaments begin to grow out, creeping along the surface of the host. The decumbent filaments are composed of irregular swelled and bent cells about 5—6 µ thick and 15 µ long. From the cells in these filaments erect filaments gradually develop.

Near the base the erect filaments are about 5—7 µ thick, tapering slowly upwards to about 3—4 µ. The cells are about 15—18 µ long near the base, becoming gradually a little longer upwards to about 27 µ. The apex of the filaments is obtuse. The filaments are not much branched in the lower parts; higher up some scattered branches issue irregularly at shorter or longer distances and at acute angles. In most cases they are short, unbranched, carrying sporangia only. The cells contain a parietal, lobed, plate-formed chromatophore with a large pyrenoid (Fig. 4).

The monosporangia are sessile or pedicellate. They are given off from the upper side of the branches and from the main filaments, often seriately in longer or shorter rows. They are oblong-ellipsoidal of shape, about 10—12 µ long and 6—7 µ broad.

This species may show some likeness to *Acr. Krusadii* Børgs. (Børgesen, 1937, p. 33) but when examined in more detail it seems nevertheless to be well separated. The plant from Mauritius is thus much higher and forms a dense felt upon the hostplant, while the Indian plant growing upon *Dictyota* only forms small

cushions. The cells in the creeping filaments of the Indian plant are much shorter. The filaments in the plant from Mauritius are slender and more erect, while these in the Indian plant are often curved. In the erect filaments of the Indian plant the cells are somewhat shorter than in the plant from Mauritius.

Also, the monosporangia are somewhat slender in the plant from Mauritius.

The plant from Mauritius may also be compared to the West Indian *Acr. caespitiforme* Børgs. (Børgesen 1920, p. 446, fig. 416), forming tufts upon *Padina Vickerssiae* Hoyt (= *P. Howeana* Børgs.) but in this plant the cells in the basal filaments are shorter, the ramification is more developed, and the sporangia are as a rule placed upon short branchlets, which is not the case in the plant from Mauritius.

4. Acrochaetium Chnoosporae nov. spec.

Thallus caespitosus usque ad 1400 μ altus, ex disco basali parvo et filamentis erectis, ramosis compositus.

Discus basalis unistratosus, e filis brevibus repentibus et confluentibus, cellulas fere isodiametricas continentibus compositus.

Fila erecta a disco egrediuntur, quoqueversum ramosa, in parte basali ca. 8—9 μ lata, ad apicem versus sensim attenuata, ca. 4 μ lata, ex cellulis prope basim ca. 17—25 μ, superne ca. 30 μ longis formata. Cellulae chromatophorum parietale, pyrenoide laterali instructum, continentes.

Sporangia obovato-oblonga, ca. 8 μ lata et 12 μ longa, in summis apiculo minore instructa, sessilia aut interdum pedicellata.

Mauritius: Tamarin Bay, in *Chnoospora implexa* epiphytica, R.E.V. no. 293.

The base of this plant (Fig. 5), which was found growing upon *Chnoospora implexa*, consists of a small disk composed of short cells (Fig. 5*b*). From some of the cells in the disk the erect filaments are given off, forming a rather loose tuft about 1400 μ high. Near the base the filaments are about 8—9 μ thick, tapering gradually upwards to about 4 μ; the cells are about 17—25 μ, the uppermost up to 30 μ long.

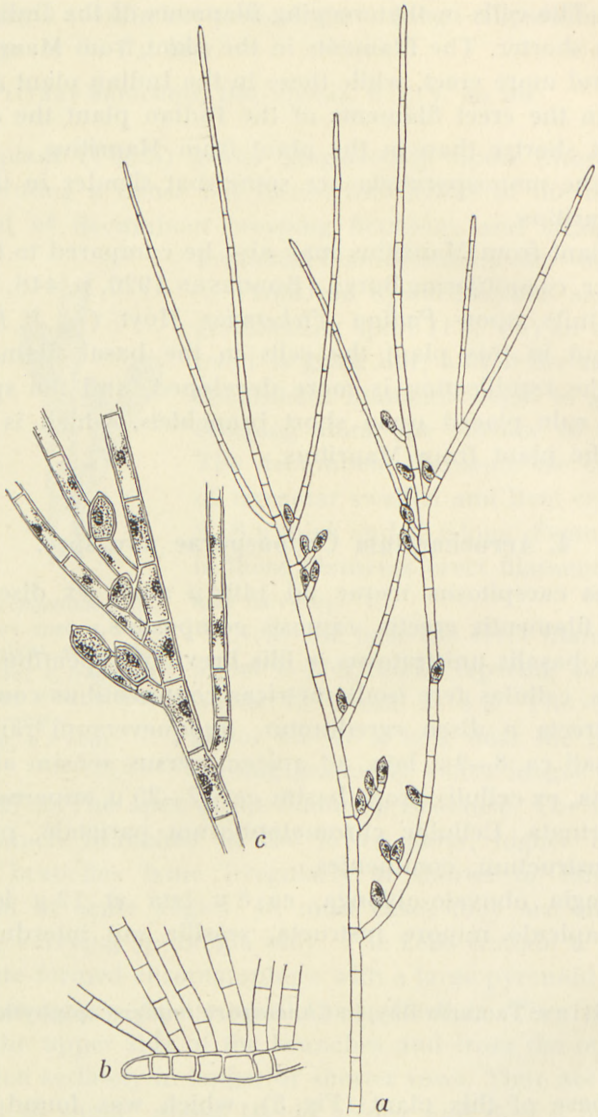


Fig. 5. *Acrochaetium Chnoosporae* nov. spec. *a*, part of the thallus; *b*, part of the base in transverse section; *c*, fragment of filaments with monosporangia. (*a* × 225, *b* and *c* × 500).

The lower parts of the filaments are unbranched; higher up branches are given out irregularly at shorter or longer intervals on all sides. The branches are of unequal strength; some are

quite short, some few nearly as vigorous as the mother filament and branch again. The upper, often rather long and thin, parts of the filaments are unbranched; their summits are obtuse. The branches issue at acute angles and carry monosporangia near their bases.

The monosporangia are obovate-oblong of shape, about 8 μ broad and 12 μ long; at their upper ends they have in most cases a well-marked apiculum (Fig. 5*c*). They are mostly sessile but sometimes also pedicellate.

The chromatophore is a lobed disk with a large pyrenoid (Fig. 5*c*).

The plant is surely nearly allied to *Acr. robustum* Børgs. (Børgesen 1915, p. 40) from the West Indies, but it is smaller in all respects, the cells being proportionally shorter; and I have not been able to ascertain the presence of the characteristic downward-directed process developed from the basal disk in *Acr. robustum*. In this species the sporangia are broadly rounded above, lacking the small apiculum found in *Acr. Chnoosporae*.

5. Acrochaetium subseriatum Børgs.

Børgesen, Some Indian Rhodophyceae, II, 1932, p. 118, figs. 6—7.

Upon *Griffithsia Weber-van-Bosseae* there occurred an *Acrochaetium* (Fig. 6) which I do not hesitate to refer to *Acr. subseriatum* described upon material from South-India. I have compared it with some preparations of the specimens from Tuticorin and found that the Indian specimens are perhaps a trifle larger than those from Mauritius, but so little that it is quite unessential. Nevertheless I give here a short description and a figure of the plant.

From the germinating spore short decumbent branchlets issue on all sides, which fix the plant to the host. In one specimen a rhizoid issued from the second basal cell in the erect main stem and when it came in contact with the surface of the *Griffithsia* it became attached to it (Fig. 6*a*).

In the very few specimens found, only a single erect shoot issued from the base; at a short distance from the base branches are given off irregularly on all sides.

The plant reaches a height of about 1 mm. Near the base the

Fig. 6. *Acrochaetium subseriatum* Børgs. *a*, a specimen with monosporangia. *b*, base of a young plant. (*a* × 200, *b* × 500).

main stem is about 8 μ thick; upwards the thallus decreases slowly, the uppermost ends being about 6 μ thick. The cells have a length of about 28 μ near the base, nearly keeping this length

upwards, the cells in the uppermost tips having a length of about 35 μ.

The branches are given out at acute angles and are directed upwards. The distance between the branches is rather irregular, and they issue sometimes unilaterally, sometimes on all sides, with various numbers of joints between them. They are unilaterally or more irregularly ramified.

Only monosporangia occurred. In most cases these are sessile, but now and then also pedicellate. They issue unilaterally one from each joint from the lower parts of the branches, more rarely higher up upon the filaments and on the upward-turned side of the branches. They are oblong-ovate of shape, about 12 μ long and 8 μ broad, with broadly rounded upper ends.

The chromatophore is a parietal lobed plate with a large greatly protruding pyrenoid.

Mauritius: Black River Bay, "in quiet lagoons", R. E. V. $^{9}/_{7}$ 39, no. 282.

Geogr. Distr.: India at Tuticorin.

Fam. 2. Helminthocladiaceae.

a. Nemalieae.

Trichogloea Kütz.

1. Trichogloea Requienii (Mont.) Kütz.

Kützing, Spec. Alg., p. 544. Zanardini, Pl. mar. rubr., p. 67, tab. V, fig. 1. J. Agardh, Epicrisis, p. 514. Schmitz und Hauptfleisch in Engl. u. Prantl, Natürl. Planzenfam. I, 2, 1897, p. 333, fig. 203 A—C. — *Batrachospermum Requienii* Mont. Quatrième Cent. de pl. cell. exot., 1843, no. 72, p. 355.

Of this species I have seen only a single specimen collected by Jadin. The specimen is about 16—17 cm high with several main branches forming a broad much ramified tuft; all the branches are nearly cylindrical, keeping the same breadth to near the top.

Jadin in his list calls it *Trichogloea lubrica* (Harv.) J. Ag. = *Liagora lubrica* Harv., Friendl. Isl. Alg. no. 46, being the other

of the two species known of this genus. I refer the plant from Mauritius to *Tr. Requienii* known from the Red Sea, but I must point out that I have had no material at all of this species to compare it with. But it seems to me that it agrees rather well with the description and figures of ZANARDINI, l. c. On the other hand, it deviates a good deal from HARVEY's above-mentioned species, of which we have a specimen in the Botanical Museum, and likewise from a specimen of *Helminthocladia Cassei* Crn. in MAZÉ et SCHRAMM's, Algues de la Guadeloupe, no. 728, which is considered to be the same as HARVEY's plant. In this species the branches taper much from base to top. And since, furthermore, several species known from the Red Sea have gradually been found to occur southwards also, down to the Mascarene Islands, this too speaks in favour of the occurrence of the species here.

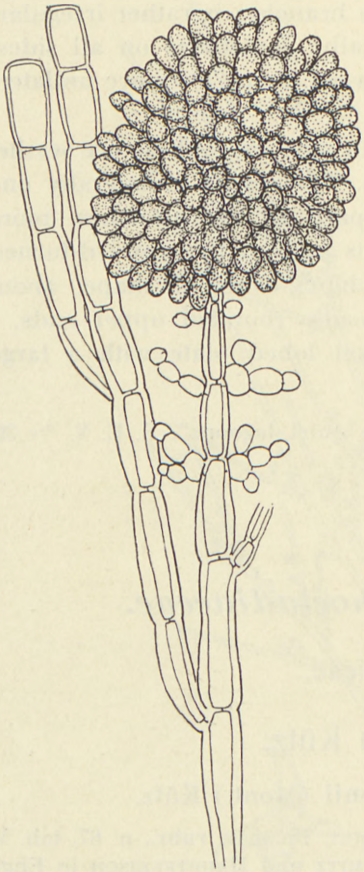


Fig. 7. *Trichogloea Requienii* (Mont.) Kütz. A gonimoblast and assimilating filaments. (× 220).

Its anatomical structure seems to be about the same as that of *Trichogloea lubrica* of which BUTTERS (1903, p. 11) has given a detailed description, pointing out that the structure of the gonimoblasts comes near to that of *Nemalion*, while its vegetative structure is nearest to that of *Liagora*.

The specimen showed abundantly fructification but was not so well suited for anatomical examination. The gonimoblasts (Fig. 7) are terminally placed upon the peripheric filaments. The cells in the stalk of the gonimoblasts become shorter upwards and short vertically placed branchlets issue from their upper

ends. The cells in the assimilating filaments are long, subcylindrical below, becoming shorter upwards, uppermost about double as long as broad, having a breadth of about 8—9 μ. No antheridia were present.

About its occurrence at the island JADIN writes: "Sur les récifs, balayés par le courant violent des lames, mais du côté intérieur regardant la lagune".

Mauritius: Flacq, Sept. 1890, JADIN, no. 458.
Geogr. Distr.: Red Sea, Malayan Archipelago.

Nemalion Targ. Tozzetti.

1. Nemalion perpusillum nov. spec.

Frons cylindrica, teres, solida, gelatinoso-cartilaginea, nana, ca. $^1/_2$ cm alta et $^1/_2$ mm crassa, ad apices versus paululum attenuata, apicibus late obtusis, iterum fastigiata-subdichotoma, axillis suberectis, disco subplano basali ad saxa adfixa et ramis inter se saepe per discos adnatis, in saxis caespites densos formans.

Punctum vegetationis paululum immersum.

Frons ex duobus stratis composita. Medulla ex filamentis crassioribus, subdichotomis in directione longitudinali thalli percurrentibus ad peripheriam vertens filamenta sparsa emittentibus ex quibus stratum corticale oritur.

Stratum corticale ex filamentis assimilantibus iterum subditrichotome divisis, horizontaliter positis formatum. Filamenta assimilantia ex cellulis oblongis in parte basali majoribus, sursum gradatim minoribus, superne cellulis pyriformibus et majoribus stratum peripheriicum formantibus composita.

Ex filamentis assimilantibus fila tenuiora formata sunt inter filamenta assimilationis et eorum medullam in varias directiones percurrentia.

Antheridia in cellulis subsuperioribus filamentorum assimilantium evoluta caespites parvos subdensos formantia.

Mauritius: Savinia, Aug. 1939, R. E. V. no. 303, "in rock crevices, thallus deep brown".

The description of this small alga (Fig. 8) is based upon some very diminutive material preserved in formol in Dr. VAUGHAN's collection.

The plant is about a $^1/_2$ cm high. The thallus is terete, about $^1/_2$ mm thick, and keeps this size up to the broadly rounded

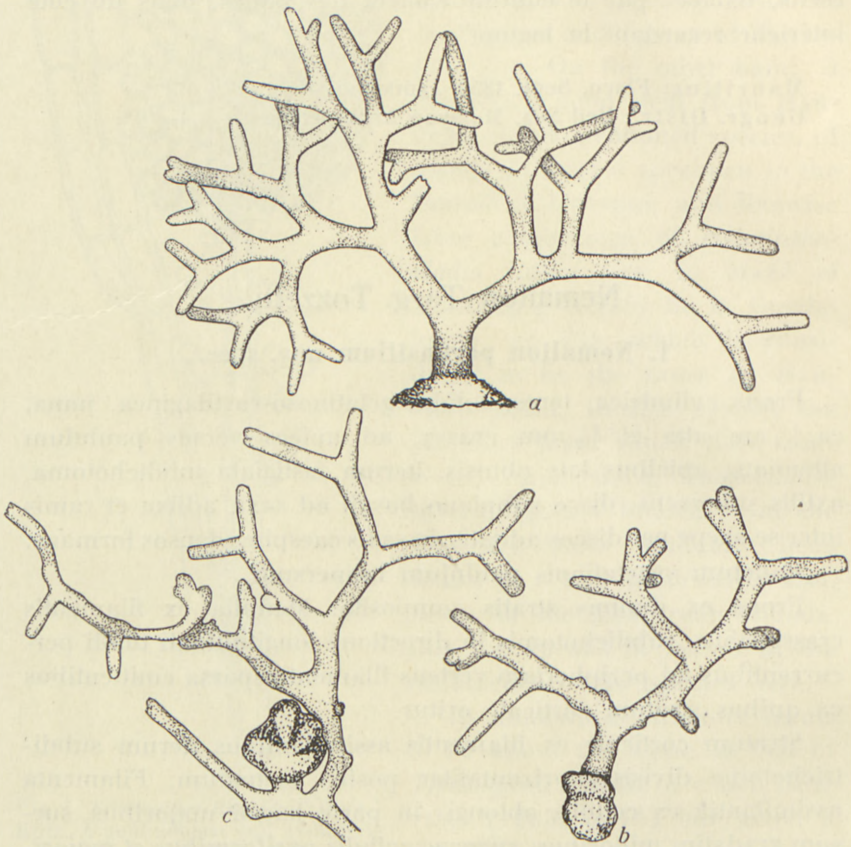


Fig. 8. *Nemalion perpusillum* nov. spec. *a*, *b*, two specimens; *c*, part of a specimen with an adhering part of another one. (× 9).

apical ends. The consistency of the thallus is slippery and tough, and it makes great resistance against pressure.

The thallus is furcated several times, the intervals between the furcations being about 2—4 mm. It is fixed to pieces of rocks by means of a flat disk composed of numerous coherent rhizoids, and as the thallus is capable of forming groups of rhizoids when-

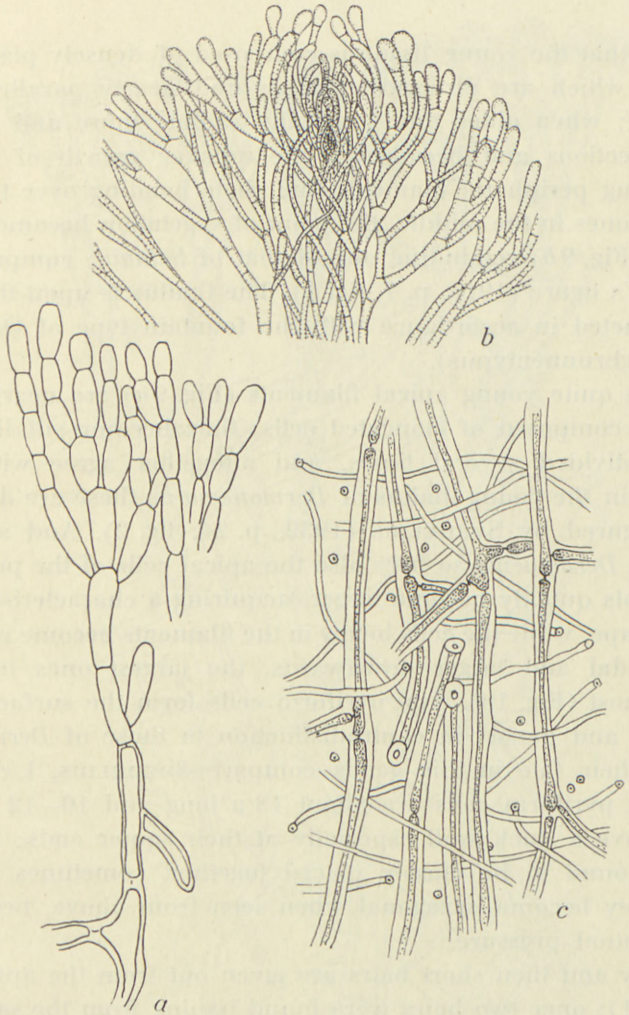


Fig. 9. *Nemalion perpusillum* nov. spec. *a*, longitudinal section of the apex; *b*, young filaments from the apex; *c*, filaments of the medulla. (*a*, *b* × 600; *c* × 350).

ever it comes in contact with the substratum the result is that the plant forms low cushions upon the rocks; also the tips of the thallus are often fused, compare Fig. 8*c*.

Upon superficial examination the structure of this small plant in several respects shows much likeness to *Dermonema*, but a more careful study recalls essential differences. This will be seen from the following description of its anatomical structure.

A longitudinal section of the apical tips of the thallus (Fig. 9*a*)

shows that the young tissue is composed of densely placed filaments which are directed upwards and nearly parallel in the middle; when older they gradually radiate more and more in all directions and because of the quicker growth of the surrounding peripheric filaments and their bending over the quite young ones in the middle, the point of vegetation becomes a little sunk (Fig. 9*b*) reminding one of that of *Scinaia*; compare SVEDELIUS's figure (1915, p. 7, fig. 1). The thallus is upon the whole constructed in accordance with the fountain type of OLTMANNS (Springbrunnentypus).

The quite young apical filaments (Fig. 9*a*) are nearly cylindrical, composed of elongated cells; they become subdichotomously divided several times, and altogether agree with those found in the young thallus of *Dermonema* as these are described and figured by SVEDELIUS (1939, p. 24, fig. 2). And as is the case in *Dermonema* so here also the apical cells of the peripheric filaments quickly become larger, acquiring a characteristic pear-like shape, while the cells below in the filaments become elongated ellipsoidal and larger downwards, the largest ones being the lowermost (Fig. 10). The pyriform cells form the surface of the thallus and persist in contradistinction to those of *Dermonema*; as to their fate in this genus compare SVEDELIUS, l. c., p. 25.

The pyriform cells are about 18 μ long and 10—12 μ broad and have a thick wall especially at their upper ends; they are often found to be closely placed together, sometimes so close that they become hexagonal when seen from above, because of the mutual pressure.

Now and then short hairs are given out from the apical cells (Fig. 11); once two hairs were found issuing from the same cell. They consist of a few, 2—3 cells and seem to be very like those SVEDELIUS has found in *Dermonema*, l. c. p. 26, fig. 6.

All round among the interstices between the assimilating filaments numerous thin rhizoid-like filaments run in all directions (Fig. 10). These filaments are given out from the cells of the assimilating filaments; compare Fig. 9*a* and Fig. 10 above. They are about 3 μ thick and now and then subdichotomously divided. They not only run all round among the assimilating filaments, but traverse the medullary tissue (Fig. 9*c*) and serve to keep the thallus together.

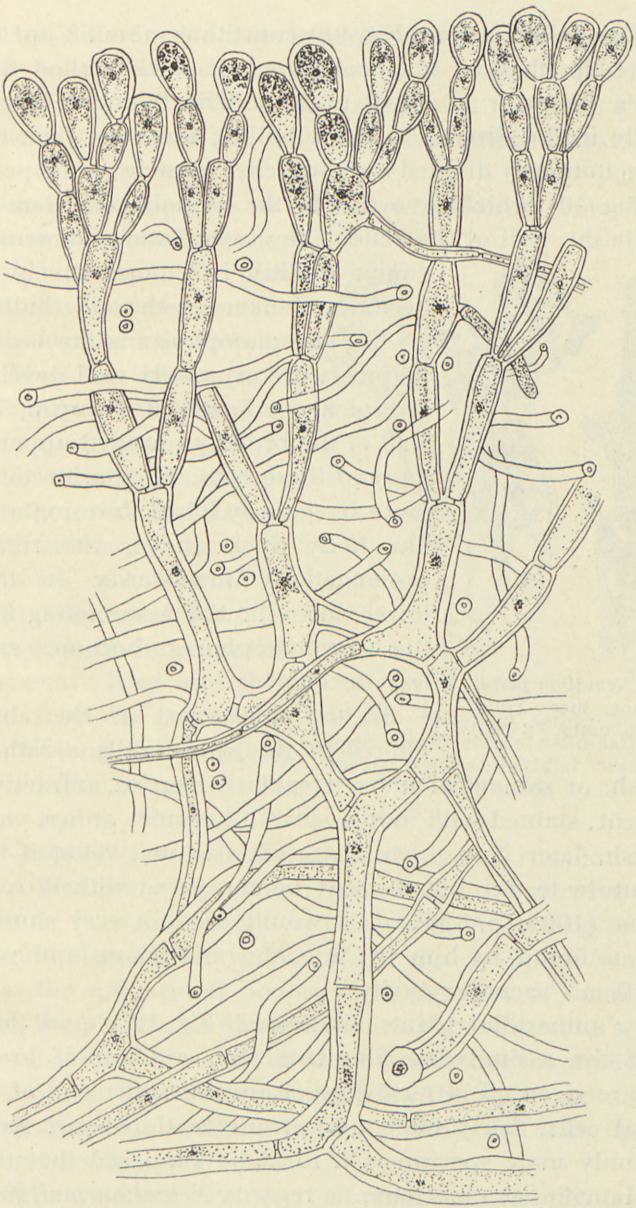


Fig. 10. *Nemalion perpusillum* nov. spec. Transverse section of the thallus showing the assimilating filaments issuing from the filaments of the medullæ. Among the assimilating filaments numerous thin rhizoid-like filaments are running. (× 600).

The medullary layer (Fig. 9*c*) constitutes about $^1/_3$ of the diameter of the thallus; it is composed of thick walled filaments having a diameter of about 8—12 μ. The filaments run nearly vertically in the direction of the thallus; now and then they are subdichotomously divided and branches issue from the peripheric ones (Fig. 10) which give rise to the assimilating filaments.

While the wall of the cells of the assimilating filaments in the young thallus is comparatively thin it becomes thicker in the old thallus.

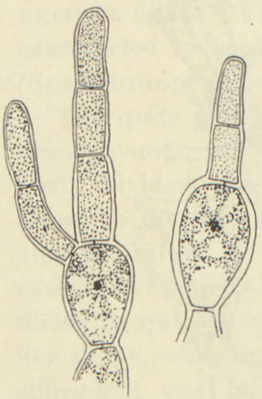


Fig. 11. *Nemalion perpusillum* nov. spec. Apical cells with hairs. (× 700).

The chromatophores in the assimilating filaments are especially well developed in the apical pyriform cells covering the inner wall of the broadly rounded upper half or more of these cells. They are reticulate or more irregularly lobed, forming a cupola-like body thick above, with ribbon-like prolongations downwards. In the cells lower down in the assimilating filaments the chromatophores become gradually less developed.

In the thick part of the chromatophores in the apical cells a rather large roundish, or somewhat more irregularly shaped, refractive body is present; stained with iodine-spirit it becomes at first yellowish-brownish, later it assumes a greenish colour. What it is I will not venture to say but it must be compared with Wolfe's description (1904, p. 610) of, it would seem, a very similar phenomenon found by him in *Nemalion multifidum* and which he thinks is a "vacuolar cavity".

Only antheridial plants are found. Fig. 12 shows the upper part of the assimilating filaments with antheridial branchlets. These are given off in most cases from the upper end of the subterminal cells, fairly often also from the third one. As I have found only male specimens it must be supposed that the plant from Mauritius is dioecious; as regards *Nemalion multifidum* this species, according to Rosenvinge (1909, p. 146), is mostly dioecious in Danish waters.

When compared with *Nemalion multifidum* (comp. Chester, Bot. Gaz., vol. 21, 1896, p. 340) *Nemalion perpusillum* must be

said to show differences in several respects and this applies not only to its much furcated thallus but also to the much firmer, tough consistency of its thallus originating from the many rhizoid-like filaments traversing not only the assimilating filaments but also the medullary layer.

But some other species of *Nemalion*, referred, correctly or not, to the genus *Nemalion*, show very much likeness to the plant from Mauritius for instance the small *N. pulvinatum* Grunow (in Holmes, Mar. Alg. Japan, 1896, p. 259). Not only is it about the same in appearance being repeatedly forked and forming low tufts upon the rocks, but its anatomical structure also agrees in many features with that of the plant from Mauritius. Thus the uppermost cells in the assimilating filaments are large and pyriform, and from the lower part of the assimilating filaments long, thin rhizoid-like filaments are given out which traverse the interstices between the assimilating filaments and run downward among the medullary filaments. And finally the growing point also seems to be a little sunk in this plant. According to Okamura's description (1909, p. 39, pl. IX, figs. 2—9) of *Nemalion pulvinatum* the antheridial bodies form "groups of small cells terminating the peripheral filaments", but when Okamura's figure is closely considered it seems to me to show that the antheridial bodies are lateral branchlets issuing from the upper cells in the assimilating filaments and thus agreeing fairly well with those of *Nemalion perpusillum*.

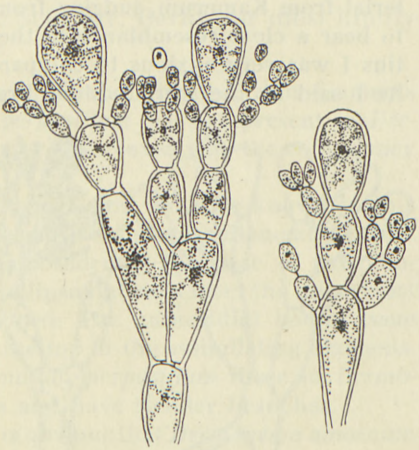


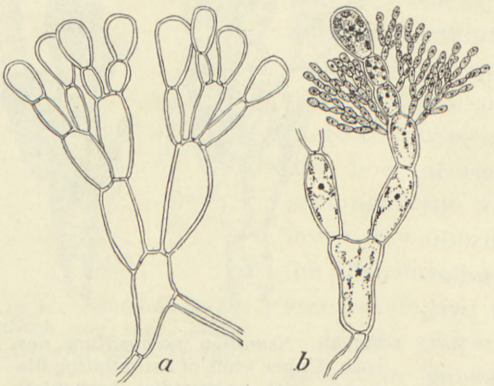
Fig. 12. *Nemalion perpusillum* nov. spec. Upper ends of assimilating filaments with antheridial branchlets. (× 700).

As it appears from this short comparison the plants show great agreement and for the present therefore it seems most natural to place the plant from Mauritius in the genus *Nemalion*, even if the female organs are as yet unknown.

This does not mean that these small forms, very different in

several respects from typical *Nemalion* forms not only by their much ramified thallus but also by their cartilaginous consistency originating from the much firmer structure, when they become better known may not very probably be separated generically from the genus *Nemalion*[1].

[1] As the *Dermonema amoenum* Pilger (1912, p. 299) described upon material from Kamerum, judging from the description and figures seemed to bear a close resemblance to the above-mentioned plant from Mauritius I was very auxious to compare some material of it with my plant. As I said in the introduction, Professor PILGER was kind enough at my request to send me some very good material so that I could make a comparison of the structure of both plants.



Nemalion amoenum (Pilger) Børgs. *a*, assimilating filament. *b*, assimilating with antheridial bodies. (× 300).

Already PILGER, when describing the plant, pointed out that in several respects it differed from *Dermonema* and as the female plant was unknown its reference to *Dermonema* was "immerhin etwas unsicher".

In this statement PILGER is surely quite right. But if PILGER nevertheless referred it to *Dermonema*, it must be taken into consideration that at that time we did not know the anatomical structure of *Dermonema*, and especially the peculiar development of the cortical layer, so well as we now know it from SVEDELIUS's detailed description (1939). As we now know *Dermonema* it must be admitted that it is entirely out of the question to refer PILGER's plant to that genus, even if its as yet unknown female organs should show some likeness to those of *Dermonema*.

When compared with the plant from Mauritius, it will be found that these two plants agree better, even if some differences are also present, the Kamerun plant being bigger and its consistency softer.

As to the anatomical structure of both plants, the apical tips in *Dermonema amoenum* are obtuse and no trace of a sunk growing point has been found but it must be pointed out that I have not been able to examine any really young tips, all of them being seemingly quite mature, having well developed antheridial bodies in the uppermost tips also.

The assimilating filaments are very much alike in both plants, and they have both large and pyriform peripheral calls (Fig. *a*).

Liagora Lamouroux.

In Dr. JADIN's material I came across some apparently new species of *Liagora* which made a comparison with some species described by W. ZEH (1913, p. 268) upon material from Madagascar and Dar-es-Salaam very desirable. ZEH's material is kept in the Botanisches Museum, Berlin-Dahlem and I am much indebted to Professor OTTO CHR. SCHMIDT, Berlin for most kindly

But the numerous periclinal, or otherwise directed, thin filaments found so abundantly in *Nemalion perpusillum* are not present in *Dermonema amoenum* and this is of course the reason why the consistency of its tissue is so loose and soft.

As stated by PILGER antheridial specimens only are known in this plant; the antheridial bodies (Fig. *b*) consist of slender filaments divided several times di-trichotomously, composed near the base of subcylindrical, higher up somewhat shorter ellipsoidal cells from the uppermost of which the spermatia are developed. The antheridial bodies issue from the second or third cell from the top in the assimilating filaments. When compared with those of *Nemalion perpusillum* those in *Dermonema amoenum* form larger bushes and have slender branches.

As a result of this comparison it is obvious that *Dermonema amoenum* as regards its anatomical structure differs in some respects from *Nemalion perpusillum* and in a way agrees better than this with *Nemalion*. The final decision as to its real place can of course not be taken before its female organs are found; nevertheless I think that at present its right place is in the genus *Nemalion*, its name being thus ***Nemalion amoenum*** (Pilger) Børgs.

In this connection it seems to be of some interest that judging from a small dried specimen of *Nemalion amoenum* in my herbarium its outer habit is very like the original specimen of *Nemalion virens* J. Ag. (1847, p. 8) from St. Augustine, Mexico kept in the Botanical Museum, Copenhagen; it has also the same yellow or brownish-green colour as the Mexican species, but *Nemalion amoenum* is smaller and more gracile. And after an indeed rather superficial examination of the specimen of *Nemalion virens* the anatomical structure also seems to be very much the same in both plants. Thus in the Mexican plant the uppermost peripheral cells in the assimilating filaments are likewise pyriform; but the cells below these in the assimilating filaments are, however, much bigger than those in *Nemalion amoenum*, reaching a breadth of about 40—50 μ or more. No longitudinal periclinal filaments emerging from the cells of the assimilating filaments are found in the Mexican plant, either, and the consistency of its thallus is also very soft. I have not succeeded in finding fructiferous organs in the specimen of *Nemalion virens* found here.

sending me these species on loan on my request. ZEH's descriptions of the species are short but good enough; but they are without figures, and the want of these, especially of drawings of the shape of the assimilating filaments, makes it rather difficult to arrive at any safe result.

In his list of algae of Mauritius DICKIE (1875, p. 195) has described 4 new species of *Liagora* from the island. Two of these *Liagora lurida* and *L. crassa* are referred to *L. farinosa* Lamx. by HOWE (1920, p. 554). Regarding the first-mentioned species, of which I have seen a specimen, I cannot agree with HOWE and in the following list it is therefore considered as a separate species. Concerning the two remaining species: *Liagora galaxauroides* and *L. obtusa*, it is quite impossible to tell from the very poor descriptions what they are, and because of the war it is out of the question to see the specimens (they are in the Kew Herbarium, London). They must therefore be left out of consideration.

1. Liagora ceranoides Lamx.

LAMOUROUX, J., Hist. Polyp. corallig. flexib., 1816, p. 239. HOWE, Algae in BRITTON & MILLSPAUGH, The Bahama-Flora, 1920, p. 555. BØRGESEN, Mar. Alg. Can., 1927, p. 58. YAMADA, Spec. of Liagora from Japan, 1938, p. 20, pl. VI. — *Liagora pulverulenta* Ag., Sp. Alg., 1821, p. 396. BØRGESEN, Mar. Alg. D. W. I., vol. II, p. 80, figs. 87—92. — *Liagora leprosa* J. Ag., Alg. Liebm., 1847, p. 8.

Several specimens in JADIN's collection are referable to this species. If, as proposed by YAMADA l. c., one would distinguish as separate forms a var. *pulverulenta* and a var. *leprosa* both forms are present in the collection. JADIN classes both forms as separate species, and in addition *Liagora distenta* Lamx. is mentioned in his list, but according to a specimen from his collection which I have seen, this specimen is a female plant of *Liagora ceranoides*.

Mauritius: Baie de la Grande Rivière, Sept. 1890, JADIN no. 414. Port Louis, Sept. 1890, JADIN no. 414 bis. Flacq, July 1890, JADIN no. 250 and no. 304.

Geogr. Distr.: West Indies, Red Sea, India, Malayan Archipelago, Japan etc.

2. Liagora Jadinii nov. spec.

Frons caespitosa, 8 cm alta et ultra(?), teres, e basi sensim attenuata, in parte basali ca. $1^1/_2$, superne $^3/_4$ mm lata, plus minus irregulariter furcata, internodiis 4—5 mm longis.

Crusta calcarea satis continua, superficie in specimine exsiccata farinosa-subscabrida, superne longitudinaliter canaliculata.

Color thalli albidus, in apicibus ramorum rubicundus.

Stratum peripheric um ex filamentis assimilantibus dichotomis, cellulas oblongo-subcylindricas, in parte inferiore ca. 50 μ longas et 15—20 μ latas, ad apicem vertens gradatim minores, superiores pyriformes ca. 15 μ longas et 7 μ latas continentibus, formatum est.

Cellulae superiores pyriformes satis aggregatae supra superficiem crustae calcareae paululum conspicuae.

Rami carpogonici 15 μ lati ex 4 cellulis compositi. Gonimoblastae ex filamentis carposporiferis dense aggregatis formatae et filamentis sterilibus involucrum formantibus circumcinctae.

Mauritius: Without locality, F. Jadin 1892.

The only specimen I have seen of this species (Pl. I, fig. 2) form a dense tuft about 8 cm high. In the dried condition the branches are much intermingled and adhere to each other, indicating that the thallus has had a soft and mucilaginous consistency. Nevertheless the chalky incrustation is much developed close up to the summits of the filaments. The surface is rather uneven, longitudinally shrivelled, and of a farinose appearance. The colour of the dried specimen is whitish with the exception of the reddish tips. The thallus is rather irregularly furcated, the length of the joints is about 4—5 mm. The thallus is terete but in the dried condition a good deal compressed; above, the filaments are about $^3/_4$ mm thick; below, the thick stems have a breadth of about $1^1/_2$ mm.

The assimilating filaments (Fig. 13) are repeatedly divided several times and composed of oblong-subcylindrical cells, in the lower part about 50 μ long and 15—20 μ broad. Upwards the cells become gradually smaller. The uppermost have a characteristic pyriform shape, about 15 μ long and 7 μ broad. They are rather densely placed, forming the peripheric layer of the

thallus and just at the level of or a little above the surface of the chalky incrustation.

The medullary layer is composed of thick-walled filaments now and then divided and having a diameter of about 20—25 μ or more.

The carpogonial branches (Fig. 13 *a*) are formed laterally upon a cell in the middle of the assimilating filaments. It consists of

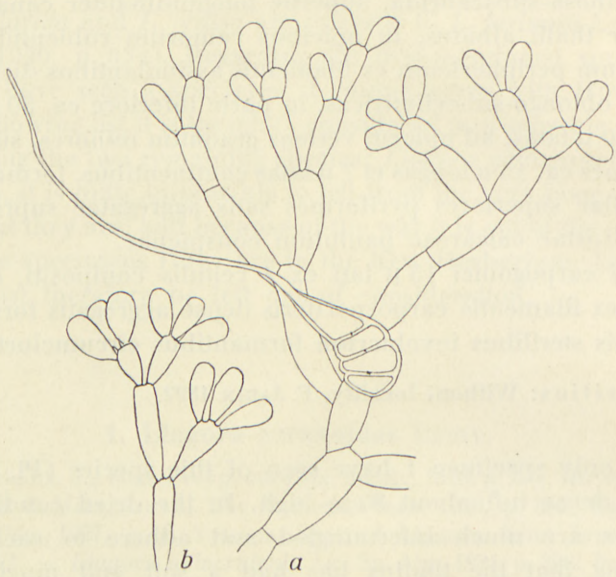


Fig. 13. *Liagora Jadinii* nov. spec. *a*, *b*, parts of assimilating filaments; *a*, with a carpogonial branch. (× 300).

4 cells and is somewhat curved. It is about 15 μ thick and about 40 μ long without the trichogyne, which is long, reaching up above the assimilating filaments.

The gonimoblasts, of which I have seen only very few, consist of a dense bundle of carposporic filaments surrounded by an involucrum of sterile filaments.

3. **Liagora rugosa** Zanardini.

Zanardini, J., Algae Novae, 1851, p. 36; Plant. Mar. Rubr., 1858, p. 65, tab. IV, fig. 2.

This species is mentioned in Jadin's list of algæ from Mauritius. I have been able to examine some quite small specimens from his collection.

They agree well with ZANARDINI's description and figures. They have a dense calcareous layer, whitish in the older parts of the thallus, brownish red in the younger parts and the surface is clearly annulated. But I have not seen any original specimen of ZANARDINI.

The assimilating filaments (Fig. 14*a*) are rather vigorously built, composed in their basal parts of elongated oblong cells,

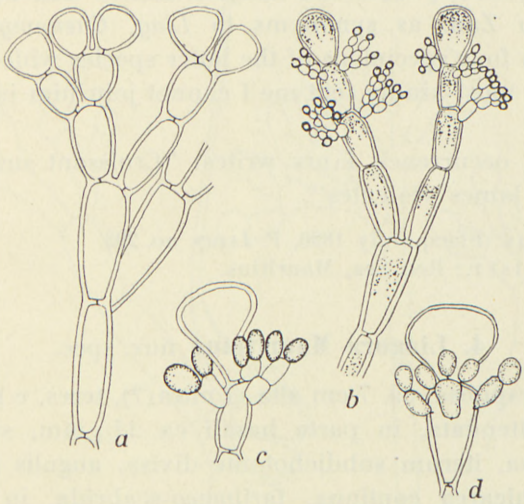


Fig. 14. *Liagora rugosa* Zanard. Parts of assimilating filaments. *b*, with antheridial bodies; *c*, *d*, tips of assimilating filaments with young antheridial bodies. (*a*, *b* × 300; *c*, *d* × 700).

the largest of these being about 12—13 μ broad; above these the following cells become smaller up to the uppermost broadly-pyriform ones which are about 13—15 μ thick. The last-mentioned cells protrude a little above the calcareous incrustation, adhere more or less to each other and form the surface of the thallus.

Antheridia only were found in these specimens. The antheridial bodies (Fig. 14*b*, *c*, *d*) form small clusters given out oppositely or verticillately from the uppermost cells in the assimilating filaments below the peripheric ones. They consist of branchsystems several times unilaterally divided, the uppermost of these being the mother cells of the spermatia.

No traces of female organs were met with in the specimens.

Liagora Holstii Zeh (1913, p. 272) of which I have seen an original specimen from Dar-es-Salaam, leg. HOLST no. 1276

belonging to the Botanisches Museum, Berlin, has assimilating filaments very like those of *Liagora rugosa*. But the thallus of *Liagora Holstii* is much more densely ramified; the filaments are very crooked and felted together; and its colour is greyish-green. The shape of the filaments and the structure as a whole of the thallus of *Liagora rugosa* comes near to *Liag. Caenomyce* Decsne, as pointed out by Mme Weber (1921, p. 202).

Yamada (1938, p. 6) refers *Liagora Holstii* Zeh and with a? *Liag. rugosa* Zan. as synonyms to *Liag. Caenomyce* Decsne. According to four specimens of the latter species which Professor Yamada has most kindly sent me I cannot join him in this interpretention.

About its occurrence Jadin writes: "Croissant sur les récifs, exposé aux lames violentes".

Mauritius: Flacq, July 1890, F. Jadin no. 293.
Geogr. Distr.: Red Sea, Mauritius.

4. Liagora Mauritiana nov. spec.

Frons caespitosa, ca. 7 cm alta et ultra(?), teres, e basi sensim paululum attenuata, in parte basali ca. $1^1/_2$ mm, superne ca. $^1/_2$ mm crassa, iterum subdichotome divisa, angulis acutis.

Crusta calcarea continua, farinaceo-scabrida, in specimine exsiccata superne plus minus evidenter canaliculata.

Color frondis canescente-rubescens. Stratum periphericum ex filamentis in parte basali paululum divisis cellulas subcylindricas continentibus constructum, superne irregulariter divisis cellulas breves oblique pyriformes aut rotunde-polygonatas et inter se implicatas continentibus formatum est.

Species monoica. Antheridia ad apices filamentorum assimilantium evoluta.

Rami carpogonii plus minus incurvi, ex 4 cellulis compositi, ca. 18 μ lati.

Gonimoblastae subsphaericae ex filis carposporiferis et involucro dilatato constructae.

Mauritius: Without locality, 1892, Herb. F. Jadin.

A single specimen only is found of this species (Pl. II, fig. 3); it forms a dense roundish tuft about 7 cm high. The filaments

are terete, below about $1^1/_2$ mm thick tapering slowly upwards to $^1/_2$ mm or less. They are irregularly divided, the length of the internodes between the furcations being rather variable, now less now more than 1 cm. In the dried specimen the filaments are often nearly parallel and stick together, indicating that in the

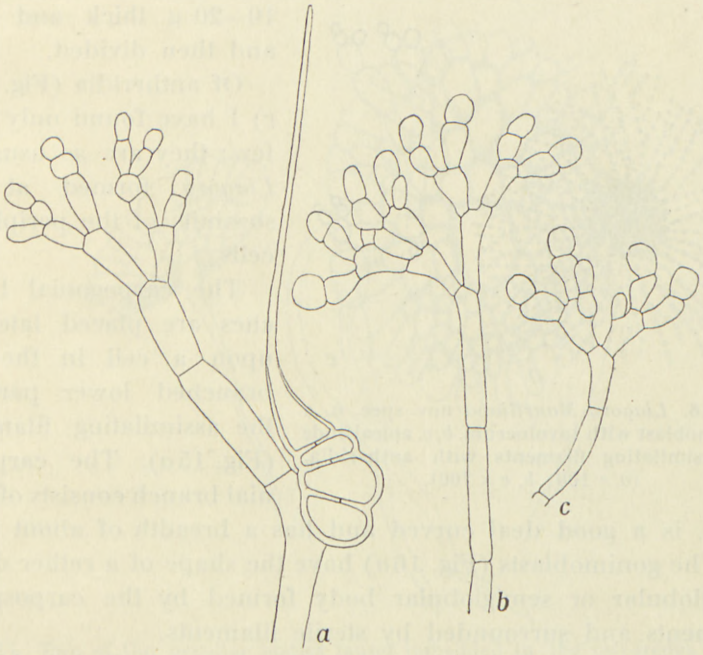


Fig. 15. *Liagora Mauritiana* nov. spec. *a*, *b*, *c*, parts of assimilating filaments, *a* with a carpogonial branch. (× 400).

living condition the thallus has probably had a soft and mucilaginous consistency.

The calcareous incrustation is rather strongly developed, forming a dense coating with a somewhat uneven farinose surface. The colour is greyish-red or dirty-red, more greyish in the upper parts. The red colour is due to the fact that the assimilating filaments protrude somewhat above the chalky incrustation.

In their lower part the assimilating filaments (Fig. 15) consist of thin, unbranched or very little branched filaments about 7—8 μ thick and composed of cells about 30—40 μ long. At their upper ends they are branched several times and broaden; the

cells here are short, irregularly-pearshaped; the uppermost peripheral ones are irregularly shaped, roundish or edged; they become mingled with the cells of the neighbouring filaments, thus forming a rather dense layer. The surface cells have a breadth of 6—7 μ.

The medullary layer consists of thick-walled filaments about 10—20 μ thick and now and then divided.

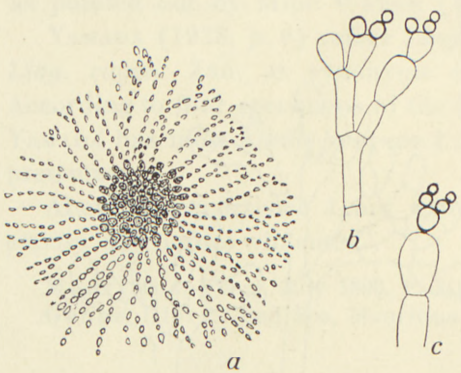


Fig. 16. *Liagora Mauritiana* nov. spec. *a*, a gonimoblast with involucrum. *b*, *c*, apical ends of assimilating filaments with antheridia. (*a* × 100; *b*, *c* × 700).

Of antheridia (Fig. 16*b*, *c*) I have found only very few; they are as usual in *Liagora* formed at the summits of the peripheric cells.

The carpogonial branches are placed laterally upon a cell in the unbranched lower part of the assimilating filaments (Fig. 15*a*). The carpogonial branch consists of four cells, is a good deal curved and has a breadth of about 18 μ.

The gonimoblasts (Fig. 16*a*) have the shape of a rather dense subglobular or semiglobular body formed by the carposporic filaments and surrounded by sterile filaments.

Dickie (1875, p. 195) mentions *Liag. coarctata* Zan. in his list of algae from Mauritius. This species has been described by Zanardini in Flora 1851, p. 36; and in Tab. Phycol., vol. 8, p. 43, pl. 90 II Kützing gives some figures of it. According to these figures Zanardini's species might bear some likeness to the above-described plant, but to clear up their possible identity an examination of Zanardini's plant would be necessary.

In this species some endophytic bodies were present similar to those Howe (1920, p. 1, pl. 1) and I (1920, p. 455, fig. 421) have found in several species of *Liagora* from the West Indies. While I considered these bodies as endophytes living in the slime and chalky incrustation of these algæ without any direct organic connection with *Liagora*, Howe regards them as organs belonging

to the *Liagora*, supposing "that these discs arise from gonidia, gemmae or aplanospores, derived from the terminal or subterminal cells of the assimilating filaments of the *Liagora*". In this interpretation HOWE accepts that of KÜTZING (1858, p. 43, tab. 90), who was the first to mention these bodies, which he supposed were developed from the assimilating filaments.

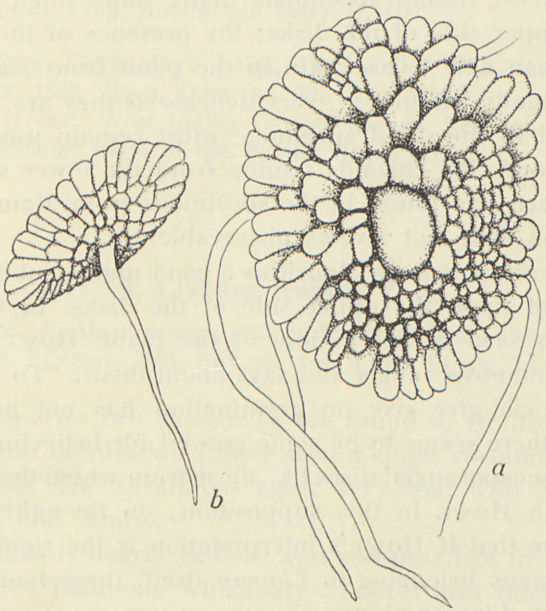


Fig. 17. Two of the peculiar bodies found imbedded in the calcareous incrustation among the assimilating filaments of *Liagora Mauritiana*. *a*, seen from above, *b*, from the side below; compare the text. (× 300).

Besides from the West Indies, the Red Sea, according to KÜTZING (l. c.), and now from Mauritius, these peculiar bodies are mentioned from the Malayan Archipelago by Mme WEBER (1921, p. 201). They do not seem to have by far the wide distribution that *Liagora* has; thus I did not find them at the Canary Islands (1927, p. 38), and YAMADA does not mention them in his monographic treatment of the genus *Liagora* in Japan (1938, p. 1). This seems to speak in favour of my view that they are a kind of facultative endophytes, having no organic connection with the host plant.

As to the plant from Mauritius (Fig. 17), the youngest specimens

I have found are very like those HOWE has shown in Figs. 11 and 12. The largest discs I have seen had a diameter of about 200—300 μ. Like those from the West Indies the specimens have a very dark red colour, which was well preserved even in the dried condition, and which forms a great contrast to the much paler colour of the surrounding assimilating filaments of *Liagora*.

In the West Indian specimens many hairs often protruded from the upper side of the disks; the presence of these hairs I have not been able to ascertain in the plant from Mauritius; if they are actually wanting or, very delicate as they are, may have disappeared in the dried specimen, must remain unsettled. On the other hand, the rhizoids issuing from the lower side of the specimens are also found in the specimens from Mauritius even though these were not always observable.

In the specimens from Mauritius a good many globular bodies were present upon the upper side of the disks. In Fig. 17*a* a large one is seen in the middle of the plant. HOWE considers these to be monosporangia and says about them: "To what these monosporangia give rise on germination has not been determined but there seems to be some ground for believing that they produce monosporangial discs like those from which they sprang". I agree with HOWE in this supposition; on the other hand; it seems to me that if HOWE's interpretation is the right one, and they are organs belonging to *Liagora* itself, these bodies should develop new *Liagora*-plants.

But to be able to clear up the real nature of these little bodies it seems necessary to examinate living material.

5. Liagora farinosa Lamx.

LAMOUROUX, J., Hist. Polyp. corallig. flex., 1816, p. 240. HOWE, Algae in Britten and Millspaugh, The Bahama Flora, 1920, p. 554. BØRGESEN, Mar. Alg. Canar. Isl., 1927, p. 59, figs. 32—33. YAMADA, Species of Liagora from Japan, 1938, p. 23, figs. 15—16. — *Liagora elongata* Zanard., Alg. novae etc. 1851, p. 35. BØRGESEN, Mar. Alg. D. W. I., vol. II, p. 67.

Several specimens of this species are found in the collections. Some fine well-prepared male and female specimens have been collected by Dr. MORTENSEN. In JADIN's list the plant is called *Liagora elongata* Zanard. In the collection of Naturhistoriska

Riksmuseet, Stockholm, a large female rather badly prepared specimen is found; it is determined as *Liagora pulverulenta* and has been collected by Colonel PIKE.

Two of DICKIE's new species, namely *Liag. crassa* and *Liag. lurida*, described upon material from Mauritius (DICKIE, 1875, p. 195) are, according to HOWE, (1920, p. 554) referable to this species; about *Liag. lurida* see later p. 40.

Mauritius: Cannonier's Point, Th. M., Oct. 1929. Barkley Island, Colonel PIKE, 1868. Flacq, JADIN no. 305, July 1890.

Geogr. Distr.: West Indies, Canary Islands, Red Sea, Malayan Archipelago, warmer parts of the Pacific Ocean etc.

6. Liagora fragilis Zan.

ZANARDINI, J., Algae novae, 1851, p. 36. Plant. Mar. Rubr., 1858, p. 64, tab. V, fig. 2. KÜTZING, Tab. Phycol., vol. 8, tab. 94, fig. 1.

Of this species two specimens are found in Dr. MORTENSEN's collection and in addition I have seen a single specimen collected by Dr. JADIN. The specimens agree very well with ZANARDINI's description and figures.

The thallus is nearly globose and composed of the dichotomously divided filaments which are about 1 mm thick near the base tapering gradually upwards to the very thin upper ends. From its base the much incrusted thallus has a continuous calcareous coating becoming gradually thinner upwards, the uppermost summits being free of chalk. The assimilating filaments are composed of long subcylindrical cells in the basal part and are not much divided; higher up they are several times divided and composed of somewhat broader, but shorter oval cells, about 7—8 μ broad.

In the apical ends of the filaments a few antheridial bodies were found; otherwise no fructiferous organs were met with.

Regarding its occurrence JADIN writes: "Très abondant sur les récifs, croissant en touffes roses d'un très joli effet".

Mauritius: Flat Island, Th. M., $^{17}/_{10}$ 29. Flacq, Sept. 1890, JADIN no. 474.

Geogr. Distr.: Red Sea, Mauritius, Malayan Archipelago.

7. Liagora cladonioides nov. spec.

Frons caespitosa, ca. 9 cm et ultra(?) alta, filiformis, teres, fere aequicrassa, ca. $^3/_4$—1 mm lata, laevis sed ubique transversim annulata, iterum di-trichotoma divisa, axillis acutis, articulis $^1/_2$—1 cm longis.

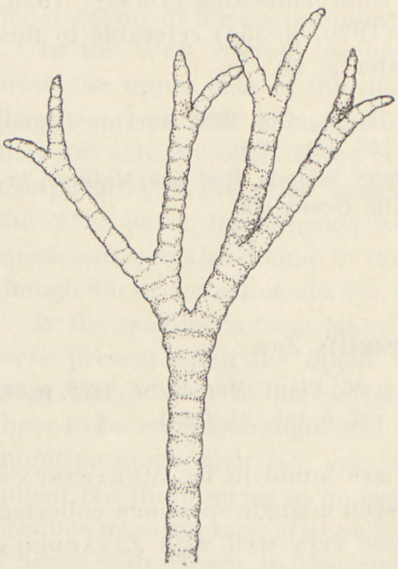


Fig. 18. *Liagora cladonioides* nov. spec. Fragment of the thallus showing the annulated surface. (× 8).

Crusta calcarea in specimine exsiccata plus minus longitudinaliter collabens, continua, apicibus ramorum breviter subacutis excepta.

Color frondis flavo-albidus, apicibus purpureis.

Axis centralis ex filamentis subcylindricis, ramosis, ca. 15 μ latis formatus est.

Stratum periphericum ex filamentis assimilantibus, iterum divisis, corymbiformibus compositum est.

Filamenta assimilantia ex cellulis in parte basali oblongo-subcylindricis, in media parte crassioribus, oblongo-pyriformibus, ca 50 μ latis, ad apicem versus gradatim minoribus, superioribus oblongis, ca. 15—18 μ longis et 7—10 μ latis constructa.

Species monoica. Rami carpogonii ex 3 cellulis compositi; cellula carpogonica conica in trichogynum longum producta.

Antheridia ad apices filorum assimilantium evoluta.

Mauritius: Without locality, Herb. Jadin.

The single specimen I have seen of this species (Plate II, fig. 4) characteristic by its annulated thallus (Fig. 18) forms an intricate tuft 9 cm high. It is rather regularly di- sometimes trichotomously furcated; the length of the joints between the divisions varies from $^1/_2$—1 cm.

The thallus is terete, $^3/_4$—1 mm thick, rarely more, tapering at the upper ends of the filaments to $^1/_2$ mm and less. The

plant has a vigorous continuous calcareous layer, above which the uppermost small peripheral cells of the assimilating filaments protrude. A transverse section of the thallus shows that the cal-

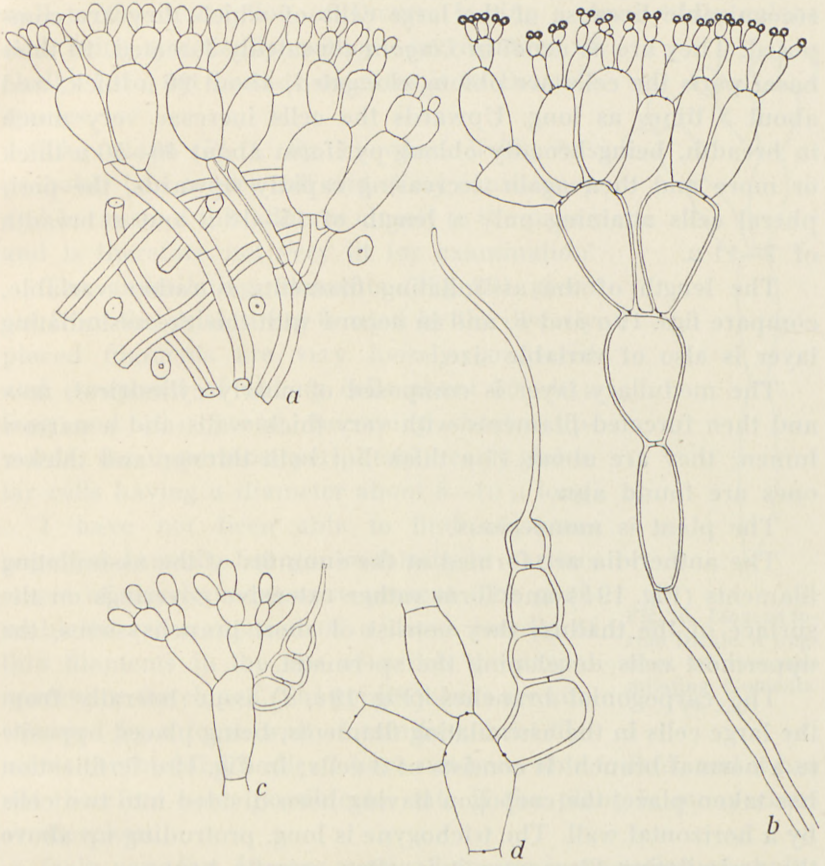


Fig. 19. *Liagora cladonioides* nov. spec. Parts of assimilating filaments. *a*, fragment of the thallus with short assimilating filaments; *b*, long assimilating filament with antheridial bodies; *c*, assimilating filament with young carpogonial branch; *d*, a fertilized carpogonial branch, the carpogonium is divided into two cells. (*a* × 250; *b*, *d* × 600; *c* × 300).

careous layer fills up the part of the assimilating filaments composed of the large cells. At the articulation the chalky incrustation is broken, and longitudinally it is also much shrivelled in the dried condition. The colour of the dried specimen is light yellow greyish with a rosy tinge.

The plant does not adhere to the paper, the thallus is rather stiff, and the dried specimen has much the same appearance as a *Cladonia*.

The assimilating filaments (Fig. 19) make the plant easily recognizable because of the large cells of which they are composed. They are as usual in *Liagora* repeatedly furcated. In their basal parts the cells are oblong-elongated, about 20 μ thick, and about 5 times as long. Upwards the cells increase very much in breadth, being broadly oblong-pyriform about 40—50 μ thick or more and then again decreasing rapidly upwards, the peripheral cells attaining only a length of 15—18 μ and a breadth of 7—11 μ.

The length of the assimilating filaments is rather variable, compare figs. 19*a* and *b*, and in accord with this the assimilating layer is also of variable size.

The medullary layer is composed of nearly cylindrical, now and then furcated filaments with very thick walls and a narrow lumen; they are about 15 μ thick but both thinner and thicker ones are found also.

The plant is monoecious.

The antheridia are formed at the summits of the assimilating filaments (Fig. 19*b*) and form rather extensive coverings on the surface of the thallus; they consist of short branchsystems, the uppermost cells developing the spermatia.

The carpogonial branches (Fig. 19*c*, *d*) issue laterally from the large cells in the assimilating filaments, being placed opposite to a normal branch. It consists of 3 cells; in Fig. 19*d* fertilization has taken place, the carpogon having been divided into two cells by a horizontal wall. The trichogyne is long, protruding up above the assimilating filaments; it is often spirally bent.

I have not seen any ripe gonimoblast.

8. **Liagora lurida** Dickie.

Dickie, G., Algae of Mauritius, 1875, p. 190.

Among the *Liagora* described in Dickie's list this species is also included. The very short description of it runs: "Fronde lurida, parce ramosa, ramis longe attenuatis, crusta calcarea fere nulla". That is all, but to this must be added that Dickie's list

is based upon a collection of algæ from Mauritius gathered by Colonel PIKE, and among the algæ which Dr. VAUGHAN has sent to me for determination is a specimen of *Liagora* collected by Col. PIKE. And as this specimen must be said to answer very well to the description of DICKIE, having a dead white colour and being practically without incrustation of chalk, I do not hesitate to refer it to DICKIE's species.

The plant (Pl. I, fig. 1) when living has probably had a very soft and slimy consistency and because of this adheres closely to the paper and is therefore not very fit for examination.

The assimilating filaments (Fig. 20) given out from the axial string formed by the densely placed filaments are very loosely connected and composed of oblong cells about 30—40 μ long and 12 μ broad, becoming shorter upwards, the uppermost peripheral nearly globular cells having a diameter about 8—10 μ long.

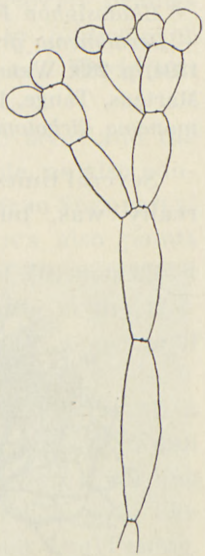


Fig. 20. *Liagora lurida* Dickie. A fragment of the assimilating filaments. (× 350).

I have not been able to find any carpogonial branch, but gonimoblasts in various stages of development were present. The gonimoblasts are composed of a dense bundle of thin filaments in the tips of which the carpospores are developed. The gonimoblasts are surrounded by a loose wall of ramified, bent filaments. Antheridial bodies I have not been able to find, and it has not therefore been possible to state if the plant is monoecious or dioecious.

Only very few *Liagora*-species have no incrustation of chalk; besides this species DE-TONI in Syll. Alg., vol. IV, p. 92 mentions *Liagora pectinata* Coll. and Herv. and *L. dubia* (Bory) Born.

Dr. HAMEL, Paris, has been kind enough to compare the plant with the collection of *Liagora* found in the Museum National but has not found any like it.

Mauritius: Colonel PIKE.
Geogr. Distr.: Endemic.

b. Dermonemeae.

Dermonema (Grev.) Harv.

1. Dermonema Frappieri (Mont. et Millard.) comb. nov.

Cladosiphon Frappieri Mont. et Millard., 1862, p. 20, pl. XXVI, fig. 1. — *Dermonema gracile* Schmitz in Heydrich, Beiträge Algenfl. Ost-Asien, 1894, p. 289. Weber-van Bosse, Alg. Siboga, p. 204. *Gymnophloea gracilis* Martens, Tange, 1866, p. 146. Kützing, Tab. Phycol., vol. 17, tab. 1. *Dermonema dichotomum* Harv., Alg. Ceyl. no. 93 (nomen nudum).

Several times I have wondered what the *Cladosiphon Frappieri* really was, but when I became better acquainted with the anatomical structure of *Dermonema gracile*, it became clear to me that the plant of Montagne and Millardet is in reality *Dermonema*.

Fig. 21. *Dermonema Frappieri* (Mont. et Millard.) Børgs. The original specimen. Natural size.

When the description and figures of these authors are considered, not only their description but especially their figures give quite a good picture of the plant. This applies not merely to the habit figure of the plant in natural size, but also the figures of the structure of the thallus really illustrate this quite well.

But even if I was left in no doubt as to the correctness of this observation, an examination of the authentic specimen was of course the best way to make sure, and so I asked Professor P. Allorge, Director of the Laboratoire de Cryptogamie, Paris, if it was possible to lend me a piece of the plant. On my request Dr. G. Hamel most kindly sent me the authentic specimen. A study of the plant convinced me that it was *Dermonema*. Fig. 21 shows a photo of the plant. This is quite like some specimens in Dr. Vaughan's collection.

That Montagne and Millardet's species has been unobserved

for so many years is perhaps to be wondered at, but partly the paper of MONTAGNE and MILLARDET is certainly very little known, partly it must be said to have been buried pretty well, having been referred to KÜTZING's rather unfortunate Phaeophycé-genus *Cladosiphon*. In DE-TONI, Sylloge Alg., it is also found in vol. III, *Phaeophyceae*, p. 417. DE-TONI says here that it scarcely belongs to *Cladosiphon* but should rather be referred to *Eudesme* or *Castagnea*; but he adds: "Ex icone depicta quasi Florideam partim decoloratam et virescentem crederes".

As to the peculiar development of the cortical layer and the anatomical structure of *Dermonema* upon the whole, as also concerning the development of the gonimoblasts I refer to SVEDELIUS' instructive paper (1939). In this paper SVEDELIUS also points out that in reference to the systematic position of *Dermonema* it may perhaps be doubtful whether it really belongs to the *Helminthocladiaceæ*, and he thinks that together with *Cumogloia* it should perhaps form a new separate family.

The few specimens from Mauritius I have seen have all a small, slender thallus only 3—4 cm high, thus attaining about half the size only of what the plant attains at Ceylon according to SVEDELIUS. Most probably the plant from Mauritius is like the delicate form which Mme WEBER mentions from Atja Tuning, New Guinea.

One of the specimens of Dr. VAUGHAN is female.

JADIN who in his list calls it *Dermonema dichotomum* Harv. writes about its occurrence: "Sur les récifs, ou sur des pointes rocheuses. Exposé aux lames violentes, croissant en touffes compactes".

Mauritius: Pointe aux Roches, R. E. V. no. 284 (no date). Flacq, June 1890, JADIN no. 212. Mahébourg, Sept. 1890, JADIN no. 451.

Geogr. Distr.: Ceylon, Formosa, New Guinea etc.

Fam. 3. Chaetangiaceae.

Actinotrichia Decsne.

1. Actinotrichia fragilis (Forssk.) Børgs.

Børgesen, A revision of Forsskål's Algae, 1932, p. 6, pl. 1, fig. 4. — *Fucus fragilis* Forssk., Flora Ægypt.-Arab., 1775, p. 190. *Actinotrichia rigida* (Lamour.) Decsne, Sur les Corallines, 1842, p. 118.

Dr. Vaughan's collection contains a single specimen of this species.

For many years *Actinotrichia* has been known only in the sterile condition and because of the great resemblance of the anatomical structure of *Actinotrichia* to that of *Galaxaura* this genus was referred to *Galaxaura* for instance by Askenasy (1888, p. 32). But in the collections of the Siboga expedition Mme Weber succeeded (1921, p. 207) in finding fertile material, not only specimens with tetrasporangia but also sexual specimens, and by means of these she has published a very good figure of a transverse section of a cystocarp. As pointed out by Mme Weber, this shows that the construction of the cystocarp in *Actinotrichia* is quite different from that of *Galaxaura* and very much resembles that of *Scinaia* as we know the development of the cystocarps in this genus from Svedelius' minute description (1915, p. 23).

Quite recently Svedelius has made thorough cytological studies of the development of the cystocarps etc. in some species of *Galaxaura*. According to a preliminary report in Svensk Bot. Tidsskr., 1941, vol. 35, p. 100 Svedelius sums up his results as follows: the whole carpogonial branch system is used as the starting-point in the formation of the gonimoblasts and no special wall is developed round the gonimoblasts. *Galaxaura* is thus in conformity with another genus of the *Chaetangiaceæ*, namely *Chaetangium* (compare Margaret T. Martin, 1939, p. 115) in which the gonimoblasts have no wall, either, and these two genera should thus have no real cystocarps in contradiction to the other genera of the *Chaetangiaceae*: *Scinaia*, *Gloiophloea* and *Actinotrichia* in which a wall of sterile filaments surrounds the gonimoblasts.

Actinotrichia is mentioned in Dickie's list p. 196.

Mauritius: Black River Bay, "forms low cushions pink in colour", R. E. V. no. 288.

Geogr. Distr.: Red Sea, Indian and Pacific Oceans.

Galaxaura Lamouroux.

Since Howe's important discovery (1917, p. 621 and 1918, p. 191) of the noteworthy dimorphism not only in the habit but also in the anatomical structure of the asexual and sexual phases of the same species which prevails in the genus *Galaxaura*, the determination of the species of this genus not only requires a large material but in fact makes a study of living plants in situ necessary to be able to make out the two connected forms of each species and thus arrive at a real knowledge of the species.

When Kjellman (1900) worked out his large detailed monograph of the genus *Galaxaura* the correlation of the sexual and asexual forms was unknown and the result therefore has been that in cases where he had the opportunity of examining both forms of the same species these have in his monograph been referred to two separate species. And to this must be added that Kjellman because of the scarce material he had access to in many cases has surely described as distinct species several forms which when more material is available will prove to belong together.

It must be a problem of the future to try to trace the two phases of each species and altogether the real limitation of the species; and in my later papers (see for instance 1927, p. 64 and 1939, p. 104) I have indeed made some attempts in this direction.

It seems regrettable therefore that Tanaka in his monographic paper on the genus *Galaxaura* in Japan (1936) has not tried to clear up as far as possible the correlation of the two phases of each species although he considers Howe's discovery very convincing, and he himself has also pointed out the dimorphism in some of the species.

In the very scarce material from Mauritius, a single or a couple of specimens of each form only, I have had for examination, 9 species in sensu Kjellman are found; 5 of these belong to groups comprising sexual forms and 4 to groups of asexual forms.

It is of course out of the question to clear up, by means of so little material, how these 9 species actually belong together; I shall merely make some suggestions on the subject at the end of the list of species.

Sectio I. ***Rhodura*** Kjellm.

1. Galaxaura lapidescens (Sol.) Lamx.

Lamouroux, J. V., Hist. Polyp. corall. flexibl., 1816, p. 264. Kjellman, Galaxaura, p. 39—43. Børgesen, Mar. Alg. D. W. I., II, p. 95, figs. 102—104. — *Corallina lapidescens* Solander in Ellis and Solander, Nat. History etc. 1786, p. 112, pl. 21, fig. *g*.

In the material from Mauritius only one sample is found which comprises two specimens of a tetrasporic form belonging to this species. Regarding their appearance the specimens show a great likeness to the plant from the West Indies for which I (1916, p. 95, fig. 102) kept Solander's specific name *Galaxaura lapidescens* (Sol.) Lamx. When the specimens from Mauritius are compared with the form which Solander mentions (1786, p. 113) and has pictured in pl. 21, fig. *g* the resemblance to the Mauritius plant is indeed very striking.

The specimens are densely covered by the assimilating filaments, the thallus including the hairs being about 2 mm broad. One of the specimens is about 6 cm high, the other one about 5 cm. They are repeatedly irregularly furcated. The colour of the small specimen is a fine dark-red, while the larger one is more dirty reddish and this specimen is also rather overgrown with small *Corallinaceae* etc. Most probably the small specimen has grown in a more shaded place than the bigger one, and this is perhaps also the reason why the anatomical structure is a little different in the two specimens.

Fig. 22*a* shows a small part of a transverse section of the bigger specimen. The supporting cells from which the erect filaments originate are small, triangular-quadrangular in shape. From these one or two erect assimilating filaments are given off. The basal cell in these is oblong-ovoid, up to 80 μ long and

32—42 μ broad; the following cell is much smaller but still somewhat inflated in the middle, then the cells become cylindrical, keeping about the same breadth higher up in the filaments. These are about 20 μ thick and composed of about 20 cells; their length is about 33 μ and the cells have thick walls. In the smaller

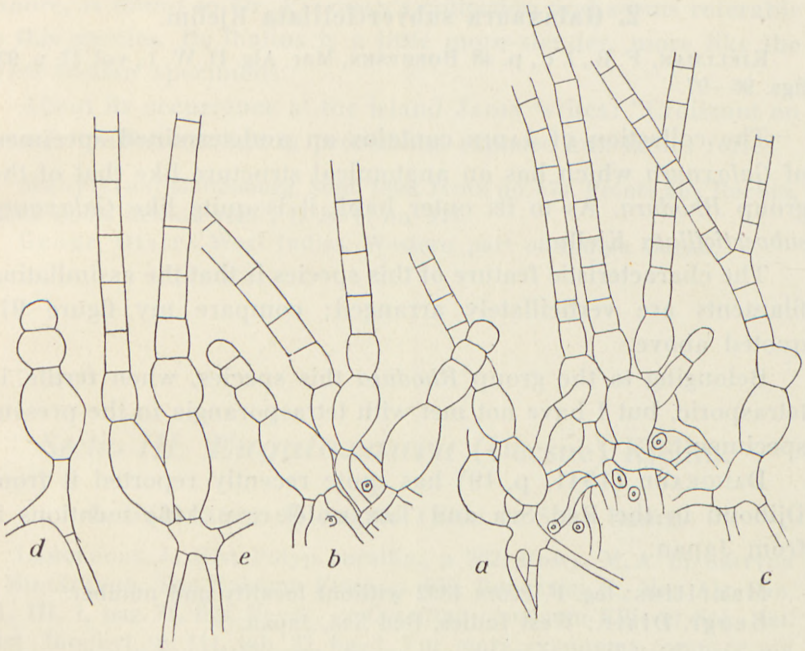


Fig. 22. *Galaxaura lapidescens* (Sol.) Lamx. *a*, *b*, *c*, parts of peripheral tissue with assimilating filaments of the large specimen. *d*, *e*, the same of the small specimen. (*a*, *c* × 220; *b*, *d*, *e*, × 300).

specimen (Fig. 22 *d*, *e*) the filaments were a little thinner, about 18 μ, and the cells a little longer, about 38 μ; the wall was thinner and they were composed of about 30 cells.

Besides the long assimilating filaments short ones are also present. In the bigger specimen the short filaments (Fig. 22 *b*) above the large basal cell have 2—3 cells becoming successively smaller upwards, while in the small specimen in most cases only two cells were present (Fig. 22 *d*). In the large specimen I only once found a ramified filament.

The medullary tissue is composed of thick-walled filaments about 8—10 μ thick, densely intermingled.

Mauritius: Pointe aux Sables, R. E. V., no. 354, Aug. 1939. Dr. VAUGHAN writes about its appearance: "Thallus usually deep purple or red". JADIN in his list mentions this species from Mauritius but I have not seen any of his specimens.

Geogr. Distr.: West Indies, Mauritius, etc.

2. Galaxaura subverticillata Kjellm.

KJELLMAN, F. R., l. c., p. 48. BØRGESEN, Mar. Alg. D. W. I., vol. II, p. 92, figs. 96—97.

The collection of JADIN contains an undetermined specimen of *Galaxaura* which has an anatomical structure like that of the group *Rhodura*. As to its outer habit it is quite like *Galaxaura subverticillata* Kjellm.

The characteristic feature of this species is that the assimilating filaments are verticillately arranged; compare my figure 97, quoted above.

Belonging to the group *Rhodura* this species, when fertile, is tetrasporic, but I have not met with tetrasporangia in the present specimen.

DANGEARD (1941, p. 49) has quite recently reported it from Djibouti in the Red Sea and TANAKA (l. c. p. 146) mentions it from Japan.

Mauritius: leg. F. JADIN 1892 without locality and number.

Geogr. Distr.: West Indies, Red Sea, Japan.

Sectio II. ***Microthoë*** J. Ag.

3. Galaxaura rugosa (Soland.) Lamx.

LAMOUROUX, J. V., Hist. Polyp. corallig. flexib., 1816, p. 263. KÜTZING, Tab. Phycol., vol. 8, tab. 33, 1. AGARDH, J., Epicrisis, p. 528. KJELLMAN, Galaxaura, p. 55. BØRGESEN, F., Mar. Alg. D. W. I., vol. II, p. 100, figs. 105—107. — *Corallina rugosa* Solander in ELLIS and SOLANDER, The Natural History etc. 1786, p. 115, tab. 22, fig. 3.

This species is mentioned in JADIN's list and a specimen of his collection agrees perfectly well with a specimen in my her-

barium collected by HILDEBRANDT at Lasgori, Somali and determined by HAUCK (1886, p. 220). Compared with West Indian specimens the thallus of those from the Indian ocean is a little broader up to about $1^1/_2$ mm.

A piece of a less well prepared specimen most probably cast ashore, is found in Dr. VAUGHAN's collection and seems referable to this species. Its thallus is a little more slender, more like the West Indian specimens.

About its occurrence at the island JADIN writes: "Croissant en grosses touffes, comme la précédente exposée aux lames fortes".

Mauritius: Mahébourg, Sept. 1890, JADIN no. 474. Pointe aux Roches, "deep pools behind reef", R. E. V. no. 171.

Geogr. Distr.: West Indies, Western part of Indian Ocean.

Sectio III. ***Eugalaxaura*** (Decsne) Kjellm.

4. Galaxaura oblongata (Ellis et Sol.) Lamx.

LAMOUROUX, J., Hist. Polyp. corallig., p. 262. HOWE, M. A. in BRITTON & MILLSPAUGH, The Bahama Flora, p. 559. BØRGESEN, F., Mar. Alg. Can. Isl., III, 1, pag. 71, figs. 39—41. — *Corallina oblongata* Ellis et Sol., Nat. Hist. Zoophyt., p. 114, tab. 22, fig. 1. For more synonyms compare my above-quoted paper.

Some few specimens in Dr. JADIN's collection, called in his list *G. dichotoma*, and some collected by Dr. VAUGHAN agree very well with specimens I have collected at the Canary Islands and referred to this species; compare the description and figures in my above-quoted paper.

The thallus of the plant from Mauritius had a breadth of up to about $1—1^1/_4$ mm, rarely $1^1/_2$ mm, and the length of the joints is as a rule about 7—8 mm. The thallus is clearly annulated. The specimens were female.

The peripheric cells are hexagonal-polygonal, having a diameter of about 12—15, rarely 18 μ, and the lowermost cells in the peripheric wall are subglobular to oval with a diameter of about 25 μ.

As already pointed out by me in 1931, p. 3, I find it impossible to separate *Galax. Schimperi* Decsne from the Red Sea from this species, as the dimensions and appearance of the thallus and the anatomical structure according to KJELLMAN's description and figures agree quite with the Canarian plant as well as with Indian specimens and those from Mauritius. The only difference I can find as to the latter is that this seems to be a little more calcified, and so more brittle than Indian (Dwarka) and Canarian specimens.

About its occurrence at the island JADIN writes: "Très abondant; croissant en grosses touffes roses sur des coraux ou sur le grosses coquilles, dans les lagunes. Recouvertes a marée basse".

Mauritius: Tamarin Bay, "on or near reef", R. E. V. no. 295. Flacq, Juin 1890, JADIN no. 407.

Geogr. Distr.: Mediterranean Sea, Canary Islands, Red Sea, West Indies, India etc.

5. Galaxaura cylindrica (Solander) Kjellm.

KJELLMAN, F. R., l. c., p. 64, pl. 8, figs. 34—42; pl. 20, fig. 53. — *Corallina cylindrica* Solander in ELLIS and SOLANDER, 1786, p. 114.

Some few specimens in Dr. JADIN's collection from Réunion (I have not seen any from Mauritius) called by him *Galaxaura dichotoma* Lamour. seem to me to agree so well with West Indian specimens that I have no hesitation in referring them to this species.

Galaxaura cylindrica is nearly related to *Galax. oblongata* but its joints are slender and more cylindrical, in the case of the specimens from Réunion about $^1/_2$ mm near their base, up to about $^3/_4$ mm or a little more at their upper end; and their length is about 6 mm. Also the colour of the plant from Réunion was the same characteristic greyish green as was found in the West Indian specimens.

Belonging to the group *Eugalaxaura* of KJELLMAN, the anatomical structure of this species is the same as in this group, which comprises sexual plants only.

Réunion: Saint-Gilles, Avril 1890, F. JADIN no. 115.

Geogr. Distr.: West Indies, Atlantic coast of South America, Canary Islands, Red Sea.

6. Galaxaura pilifera Kjellm.

KJELLMAN, Floridé-Slägtet Galaxaura, p. 65, tab. 9, figs. 4—12; tab. 20, fig. 8.

This species is described by KJELLMAN upon a female specimen gathered by Colonel PIKE at Mauritius. I am much indebted

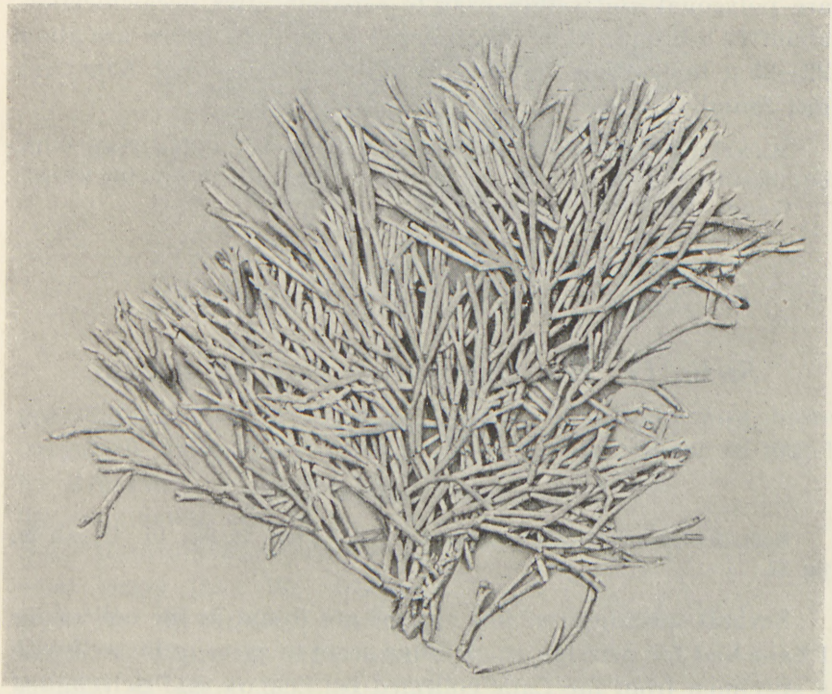


Fig. 23. *Galaxaura pilifera* Kjellm. 4/5 natural size.

to Dr. TH. ARWIDSSON, Riksmuseet, Stockholm, for having been allowed to see this specimen and having thus been able to compare a specimen in Dr. VAUGHAN's collection with the original specimen.

The specimen of Dr. VAUGHAN is a completely bleached plant, most probably cast ashore. It seems to agree fairly well with KJELLMAN's original specimens and his figures and description, with the exception that hairs are not present; most probably the hairs have dropped off or been torn away, at any rate annular

scars evidently originating from the hairs are found in the walls of many of the peripheral cells.

Fig. 23 shows a photo of the plant. It forms a roundish tuft about 9 cm high. The thallus is nearly cylindrical and annulated about 1 mm thick or a little more. It is repeatedly furcated and the joints reach a length from about $^1/_2$ cm in the lower part to about $1^1/_2$ cm in the upper parts of the frond. The surface cells are polygonal and rather easy to separate after decalcification, about 12 μ broad, while the rounded larger cells below are about 22—25 μ thick, thus in good accordance with what KJELLMAN has found.

Mauritius: Barkley Island, month of December, Colon. PIKE. Without locality, R. E. V. no. 14 in "pools near reef usually in running water".

Geogr. Distr.: Endemic.

*Sectio IV. **Brachycladia*** Sonder, Kjellm.

*Dissiminatae.

7. Galaxaura tenera Kjellm.

KJELLMAN, Floridé-Slägtet Galaxaura, p. 77, tab. 14, figs. 10—19, tab. 20, fig. 32.

Several specimens of this species are found in the collections I have had for determination. They seem to agree quite well with a specimen from the Cape collected by ECKLON and determined by KJELLMAN; the specimen belongs to the Naturhistoriska Riksmuseet, Stockholm. The description of this species is based upon a specimen from Mombassa-Sansibar but KJELLMAN points out that the specimen from Cape only deviates slightly from that.

Fig. 24 shows the habit of the plant from Mauritius. The thallus is about $5^1/_2$ cm high and has a reddish-grey to olive-green colour with a dull or only very slightly shining surface. The lobes of the thallus are about $1^1/_2$—2 mm broad, irregularly subfurcated near the base with more acute angles, higher up with more open ones the internodes being about 5 mm long.

A transverse section of the thallus (Fig. 25) shows that the peripheric assimilating cells are of rather variable shape, often

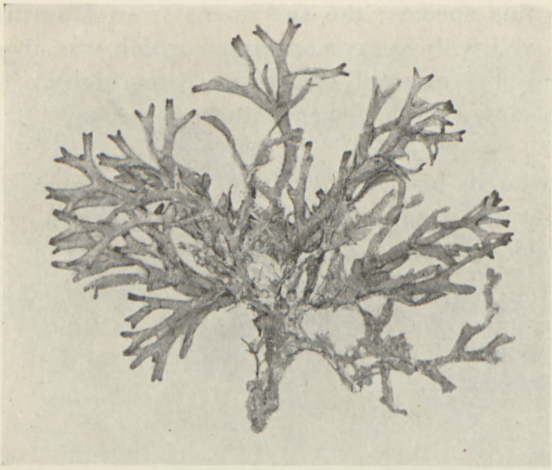


Fig. 24. *Galaxaura tenera* Kjellm. Natural size.

pearshaped, obovate or more oblong, sometimes also more irregularly oblique, having thus about the same shape as found by KJELLMAN; as to the size of the assimilating cells of the plant from Mauritius these were somewhat larger than the measures given by KJELLMAN, having a length of about 38—42 μ and a breadth of about 27—30 μ; but in the above-mentioned specimen from Cape in the Riksmuseum some assimilating filaments I have measured had a length of 38 μ and a breadth of 31 μ, being thus very like those in the specimens from Mauritius.

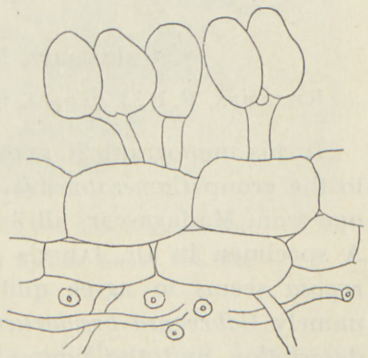


Fig. 25. *Galaxaura tenera* Kjellm. Transverse section of the peripheric tissue. (× 250).

The specimens from Mauritius were sterile but according to their anatomical structure they belong to the group *Brachycladia*, comprising tetrasporic plants;

most probably *Galax. veprecula* known from Madagascar is the sexual form of this species.

Kylin, 1938, p. 5, fig. 1 and pl. 1, fig. 2 refers a plant from Durban to this species; the specimens from Mauritius seem to agree very well with Kylin's specimen which was also somewhat smaller than the original specimen (8 cm high) of Kjellman. Kylin's specimen which was gathered in June had tetrasporangia.

Jadin, who in his list calls it *Galaxaura marginata* Schmitz, writes about its occurrence: "Abondant, croissant en touffes; souvent mêlées à *Liagora elongata*".

Mauritius: Isle Marianne, Oct. 1929, Th. M. Without locality, R. E. V. no. 35. Flacq, June 1890, Jadin no. 209. Baie de la Grande Rivière, July 1890, Jadin no. 239. Mahébourg, Sept. 1890, Jadin no. 473.

Geogr. Distr.: East Africa, Cape.

Sectio V. ***Dichotomaria*** Decsne.

*Cameratae.

8. Galaxaura breviarticulata Kjellm.

Kjellman, F. R., l. c. p. 84, pl. 18, figs. 1—13; pl. 20, fig. 51.

In his monograph Kjellman mentions 3 species as belonging to the group *Cameratae* two of which are from Port Natal and one from Madagascar, all 3 species based upon scarce material. A specimen in Dr. Jadin's collection determined as *Galaxaura rugosa* seems to agree quite well with one of these species, namely *Galaxaura breviarticulata* Kjellm. according to the short description and the figures especially the habit figure, pl. 20, fig. 51.

Fig. 26 shows a habit figure of the plant from Mauritius. The oval-elongated joints are 5—6 mm up to 8 mm and $1^1/_4$—$1^1/_2$ mm broad; when strongly compressed about 2 mm broad. The surface is smooth and dull. It is rather incrusted with chalk but

nevertheless not especially breakable. Its colour is greyish- to whitish-red. The plant forms a roundish much ramified tuft up to 9 cm high.

Fig. 26. *Galaxaura breviarticulata* Kjellm. About nat. size.

Its anatomy is that characteristic of the group *Cameratae*. Fig. 27 shows a piece of a transverse section of the epidermal layer; further I refer the reader to KJELLMAN's figures.

The specimens belonging to this group are all tetrasporic but the present specimen was sterile.

In his list JADIN calls it *G. rugosa* and writes about its occur-

rence: "Croissant en grosses touffes, comme la précédente exposée aux lames fortes".

Mauritius: Mahébourg, Sept. 1890, JADIN no. 474.
Geogr. Distr.: Port Natal.

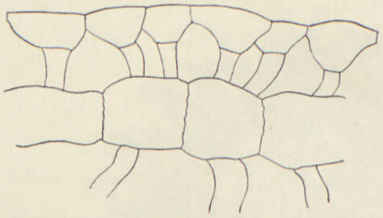


Fig. 27. *Galaxaura breviarticulata* Kjellm. Transverse section of the peripheric tissue. (× 250).

**Spissæ.

9. Galaxaura corymbifera Kjellm.

KJELLMAN, Galaxaura, p. 87, tab. 19, figs. 21—27, tab. 20, fig. 50.

The reason why I refer a specimen collected by Dr. MORTENSEN and preserved in spirit to this species is not only that KJELLMAN's rather short description (the plant is described upon a "specimen unicum et mancum") seems to agree fairly well with the specimen from Mauritius but it is also because KÜTZING's figure of *Galaxaura oblongata*, to which KJELLMAN refers, shows great likeness to the plant from Mauritius. KÜTZING's figure in Tab. Phycol., vol. 8, pl. 35 is drawn from a plant from Port Natal.

The plant is much incrusted with chalk and very breakable; it collapses entirely after decalcification.

The size and shape of the joints is very variable. Near the base they are cylindrical-clavate, tapering somewhat towards the base, ca. $1^1/_4$—$1^1/_2$ cm long and ca. 2 mm broad. The following joints are cylindrical, about $2^1/_2$ mm broad and 1—2 cm or even more long; they are broadly rounded above and below at the articulations. Higher up in the thallus the joints get shorter, ellipsoidal-cylindrical, often with a somewhat waved surface; their length varies from about $^1/_2$—1 mm and likewise the breadth

from $1^1/_2$—$2^1/_2$ mm. The lower part of the thallus is furcated, higher up it is sometimes trifurcated, KJELLMAN says "umbellatim ramosa" but I have not seen more than 3 branches issuing from a single joint.

The surface cells are polygonal, ca. 20—25 μ broad and are easily separated after decalcification. The cells under the surface cells are roundish, c. 40 μ broad and likewise easy to separate.

Besides this species KJELLMAN has, in the group *Spissae*, *Galaxaura insignis* Kjellm. from Madagascar, but according to KJELLMAN's description this plant has a somewhat broader thallus.

Also rather near as to shape and the size of the joints is *Galaxaura obtusata* (Soland.) Lamx. (comp. TANAKA, 1936, p. 171, fig. 40) belonging likewise to the group *Spissae* and, first known from the West Indies, according to TANAKA distributed in the Pacific Ocean, Malay Archipelago, Polynesia and Australia. But the plant from Mauritius is much more incrusted with chalk and accordingly a much more breakable plant, and furthermore the peripheral cells are coherent in *Galaxaura obtusata*, whereas they are easy to separate after decalcification in the plant from Mauritius.

KYLIN (1938, p. 6, fig. 1F and Pl. 2, fig. 5) refers some specimens from Durban to this species; the plant from Mauritius seems to agree fairly well with KYLIN's figures.

Mauritius: Tombeau Bay, dredged at a depth of about 40 fathoms on sandy bottom with corals, 8th Oct. 29, TH. M.

Geogr. Distr.: Port Natal.

Suggestions as to the supposed mutual connection of the species named in the list and based upon KJELLMAN'S monograph.

The first species mentioned in the list: *Galaxaura lapidescens* most probably, in conformity with HOWE's supposition concerning the West Indian species, has its sexual phase in *Galaxaura cylindrica* belonging to the group *Eugalaxaura* of KJELLMAN which is very different in habit. And as regards *Galaxaura oblongata*, a

species nearly related to *G. cylindrica* and to which species I have referred some specimens from Mauritius, HOWE supposes that it has its tetrasporic phase in *Galaxaura comans* Kjellm., a form very closely related to *G. lapidescens*. As to this supposition HOWE makes the following remarks, 1918, p. 197: "And just as the line of demarkation between *Galaxaura oblongata* and *G. cylindrica* seems a little uncertain and arbitrary, so also is the line of separation between *G. comans* and *G. lapidescens*". In this I quite agree with HOWE and would like to point out in this connection also that *Galaxaura pilifera* shows a great likeness to both *G. cylindrica* and *G. oblongata* so that its tetrasporic phase must most probably be looked for in a form coming near to *Galax. lapidescens* or *G. comans*.

The following species, *G. subverticillata*, likewise belonging to the tetrasporic group *Rhodura*, has surely, as in the West Indies, its sexual phase in *G. rugosa* with which species HOWE often found it growing in the West Indies. In their outer habit, for instance their size and the annular constrictions of the thallus these forms are very much alike, too.

The next species mentioned in the list is *Galaxaura tenera* which belongs to the group *Brachycladia* comprising asexual forms, the sexual forms of which according to HOWE are to be found in the group *Veprecula*. The characteristic species of the latter group is *G. veprecula*, and having been found at Madagascar, it must be presumed to occur also at Mauritius.

As to the two last-mentioned species in the list, namely *G. breviarticulata* and *G. corymbifera* belonging respectively to the tetrasporic group *Cameratae* and the sexual group *Spissae*, it was precisely upon members of these groups that HOWE (1916, p. 622) first arrived at the conclusion that the species of these groups actually represented the tetrasporic and the sexual forms respectively of each species. He came to this conclusion not only because the forms belonging to the same species are so very like in habit that they cannot be separated without microscopical examination, but also because both forms nearly always grow intermingled with each other.

Fam. IV. ***Bonnemaisoniaceae.***

Asparagopsis Mont.

1. Asparagopsis taxiformis (Delile) Collins and Hervey.

Collins and Hervey, Alg. Bermuda, 1917, p. 117. Børgesen, Mar. Alg. D. W. I., vol. II, 1918, p. 352, figs. 347—51. — *Fucus taxiformis* Delile, Flore d'Égypte, 1813, p. 151, pl. 57, fig. 2. C. Agardh, Spec. p. 368. *Asparagopsis Delilei* Mont., in Webb et Berthelot, Îles Canaries, vol. II, part 2, sectio 4, 1840; Addenda, p. XIV.

For more literature compare De-Toni, Syll. Alg., vol. IV, p. 771 and vol. VI, p. 367.

Dr. Vaughan's collection contains a small specimen preserved in formol. It is a female plant with young cystocarps.

I agree with Grunow who says in Alg. Fidschi, p. 46 about *Asparagopsis Sandfordiana* Harv.: "Scheint mir nicht genügend von *Asp. Delilei* verschieden zu sein".

Mauritius: Îlot Brocus, "washed into lagoon", R. E. V. no 218, 31. Dec. 38. It is mentioned from Mauritius in the lists of Dickie.

Geogr.: Distr.: Widely distributed in warm seas.

List of Literature.

AGARDH, C., Systema Algarum. Lundae 1824.

— Species Algarum rite cognitae. Vol. I, 1821. Vol. II, 1828. Gryphiswaldiae.

AGARDH, J., Nya alger från Mexico. Öfversigt af Kungl. Vetenskaps-Akademiens Förhandlingar för den 13 Januari 1847.

— Species, genera et ordines algarum. Vol. II, 1851—63. Vol. III, Part 1. Epicrisis, 1876. Lund.

— Till Algernes Systematik. Sjette afdelningen. Lund 1890.

— Analecta Algologica. Continuatio III. Lundae 1896.

ARESCHOUG, J. E., Phyceae Capensis. Upsaliae 1851.

BATTERS, E. A. L., Catalogue of the British Marine Algae. Supplem. to the Journ. of Botany. London 1902.

BERTHOLD, G., Die Bangiaceen des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Eine Monographie. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Herausg. v. d. Zoolog. Station von Neapel. VIII Monographie. Leipz. 1882.

BRITTON, N. L. and C. F. MILLSPAUGH, The Bahama Flora. New York 1920.

BUTTERS, FR. K., Observations on Trichogloea lubrica. Minnesota bot. Studies, Series 3. Minneapolis 1903.

BØRGESEN, F., Some new or little known West Indian Florideae. I, 1909. II, 1910. Botanisk Tidsskrift, vol. 30. København.

— The marine Algae of the Danish West Indies. Vol. II. Rhodophyceae. 1915—20. Copenhagen.

— Marine Algae from the Canary Islands, especially from Teneriffe and Gran Canaria. III. Rhodophyceae, Part 1. D. Kgl. Danske Vidensk. Selskab, Biol. Medd. VI, 6. København 1927.

— Some Indian Rhodophyceae, especially from the shores of the Presidency of Bombay, I—IV. Bulletin of Miscellaneous Information. Royal Botanic Gardens. Kew 1931—1934.

— A Revision of Forsskåls Algae mentioned in Flora Ægyptiaco-arabica and found in his Herbarium in the Botanical Museum of the University of Copenhagen. Dansk Bot. Arkiv, Vol. 8, Nr. 2, 1932.

— Contributions to a South Indian Marine Algal Flora, I—III. Journ. of the Indian Bot. Soc. Madras 1937—8.

COLLINS, FR. S. and A. B. HERVEY, The Algae of Bermuda. Proc. of the Amer. Academy of Arts and Sciences. Vol. 53. Boston 1917.

Dangeard, P., Algues de la Mer Rouge et de la Côte de Djibouti. Mémoires de la Soc. Linnéenne de Normandie. Nouv. Série. Sujets divers. 1. Vol. 1941.

Decaisne, J., Mémoire sur les Corallines ou Polypiers calcifères. Annales des Sciences Naturelles. II. Sér. Botanique. T. 18. Paris 1842.

De-Toni, J. B., Sylloge Algarum, Vol. IV. Florideae. 1897—1905. Patavii. Vol. VI. Florideae. 1924.

Dickie, G., On the Algae of Mauritius. Journal of the Linnean Society. Botany. Vol. XIV. London 1875.

Dillwyn, L. W., British Confervae or colored Figures and Descriptions of the British Plants referred by Botanists to the Genus Conferva. London 1809.

Ellis, J., and D. Solander, The Natural History of many curious and uncommon Zoophytes collected from various parts of the globe. London 1786.

Gardner, N. L., New Pacific Coast Marine Algae. I. University of California Publications in Botany. Vol. 6, Nr. 14. 1917. Berkeley.

Grunow, A., Algen der Fidschi-, Tonga- und Samoa-Inseln. Journ. de Mus. Godeffroy, Bd. 3. 1873—4.

Hamel, G., Bangiales. Floridées de France. Revue Algologique. Tome I. Paris 1924—5.

— Recherches sur les genres Acrochaetium Naeg. et Rhodochorton Naeg. Saint-Lo 1927.

Hauck, F., Die Meeresalgen Deutschlands und Oesterreichs. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Zweiter Bd. Leipz. 1885.

— Über einige von I. M. Hildebrandt im Rothen Meere und Indischen Ocean gesammelte Algen. Hedwigia 1886, 1887, 1888, 1889. Dresden.

Hering in Krauss, F., Pflanzen des Cap- und Natal-Landes, gesammelt und zusammengestellt von F. Krauss. Flora. 1846.

Heydrich, F., Beiträge zur Kenntniss der Algenflora von Ost-Asien. Hedwigia. Bd. 33. 1894. Dresden.

Holmes, E. M., New marine Algae from Japan. The Journal of the Linnean Society. Botany. Vol. 31. London 1895—7.

Howe, M. A., A note on the structural dimorphism of sexual and tetrasporic plants of Galaxaura obtusata. Bulletin of the Torrey Botanical Club. Vol. 43. New York 1916.

— Further notes on the structural dimorphism of sexual and tetrasporic plants in the genus Galaxaura. Brooklyn Botanic Garden. Memoirs. Vol. I. 1918. Brooklyn.

— Observations on monosporangial discs in the genus Liagora. Bull. Torrey Bot. Club. Vol. 47. 1920.

— Algae in Britton and Millspaugh, The Bahama Flora. New York 1920.

Jadin, F., Algues des Îles de la Réunion et de Maurice. Annales de Cryptogamie exotique. Tome VII. Paris 1934.

KJELLMAN, F. R., Japanska Arter af Slägtet Porphyra. Bihang till K. Svenska Vet.-Akad. Handlingar. Bd. 23, Afd. III, no. 4. Stockholm 1897.
— Om Floridé-Slägtet Galaxaura, dess Organografi och Systematik. Kungl. Svenska Vetenskaps-Akademiens Handlingar. Bd. 33. No. 1. Stockholm 1900.
KÜTZING, F. T., Tabulae Phycologicae. Bd. 1—19. Nordhausen 1845—69.
— Diagnosen und Bemerkungen zu neuen oder kritischen Algen. Bot. Zeit. 1847.
— Species Algarum. Lipsiae 1849.
KYLIN, H., Anatomie der Rhodophyceen. Handb. der Pflanzenanatomie, II. Abt., Bd. VI, 2. Teilband, Algen. Berlin 1937.
— Über eine marine Porphyridium-Art. Kungl. Fysiogr. Sällsk. i Lund Förhandlingar. Bd. 7. No. 10. 1937.
— Verzeichnis einiger Rhodophyceen von Südafrika. Lunds Univ. Årsskr. N. F. Avd. 2. Bd. 34. Nr. 8. 1938.
LAMOUROUX, J. V. F., Histoire des Polypiers coralligènes flexibles, vulgairement nommés Zoophytes. Caen 1816.
LE JOLIS, AUG., Liste des Algues Marines de Cherbourg. Paris—Cherbourg 1863.
LYNGBYE, H. L., Tentamen Hydrophytologiae Danicae. Hafniae 1819.
MAILLARD, L., Notes sur l'île de la Réunion. Botanique, Cryptogamie, Algues par C. MONTAGNE et M. MILLARDET. Paris 1862.
MARTENS, G., Die Tange. Die preussische Expedition nach Ost-Asien. Botanischer Theil. Berlin 1866.
MARTIN, MARGARET T., The structure and reproduction of Chaetangium saccatum (Lamour.) J. Ag. II. Female plants. The Journ. of the Linnean Soc. of London. Botany. Vol. LII. 1939. London.
MONTAGNE, C., Quatrième centurie de plantes cellulaires exotiques nouvelles. Ann. Sc. Naturelles. II. Sér. t. 20. Bot. Paris 1843.
OKAMURA, K., Icones of Japanese Algae. Vol. I—II, 1909—1912. Tokyo.
OKAMURA, ONDA and HIGASHI, Preliminary notes on the development of the carpospores of Porphyra tenera Kjellm. Botanical Magazine. Vol. 34. Tokyo 1920.
PAPENFUSS, G. F., Notes on South African Marine Algae 1. Botaniska Notiser 1940. Lund.
PILGER, R., Die Meeresalgen von Kamerun. Engler, Bot. Jahrb. Bd. 46. Leipzig 1911—12.
ROSENVINGE, L. KOLDERUP, The Marine Algae of Denmark. Part I. Rhodophyceae. D. Kgl. Danske Vidensk. Selskab, Skrifter, Naturv. og mathem. Afd. 7, VII, 1. København 1909.
SCHMITZ, FR., Marine Florideen von Deutsch-Ostafrika. Engler, Bot. Jahrb. Bd. 21. Leipz. 1896.
SUHR, I. N., Beiträge zur Algenkunde. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher. Bd. 18. 1stes Supplement. Breslau und Bonn 1841.
SVEDELIUS, N., Zytologisch-Entwicklungsgeschichtliche Studien über Scinaia Furcellata. Ein Beitrag zur Frage der Reduktionsteilung der

nicht tetrasporenbildenden Florideen. Nova Acta Regiae Soc. Scient. Upsaliensis. Ser. IV. Vol. 4, no. 4. 1915. Upsala.

Svedelius, N., Über den Bau und die Entwicklung der Spermatangiengruben bei der Florideengattung Galaxaura. Botaniska Notiser. Lund 1939.

— Anatomisch-entwicklungsgeschichtliche Studien über die Florideengattung Dermonema (Grev.) Harv. Botaniska Notiser 1939. Lund.

— Cystokarpieutvecklingen hos Galaxaura Diesingiana Zanard., en ny utvecklingstyp bland floridéerna. Svensk Botanisk Tidskrift. Bd. 35. 1941. Uppsala.

Tseng, C. K., Economic Seaweeds of Kwangtung Province, S. China. Lingnan Science Journal, Vol. 14, 1935. Canton, China.

— Notes on some Chinese Marine Algae, Lingnan Science Journal, Vol. 17. 1938.

Weber-van Bosse, A., Liste des Algues du Siboga. Siboga-Expeditie, LIX a, b, c, d. Leide 1913—28.

Wolfe, J. J., Cytological Studies on Nemalion. Annals of Botany. Vol. XVIII. London 1904.

Yamada, Y., The species of Liagora from Japan, Scientific Papers of the Institute of Algological Research. Vol. II, No. 1. Sapporo, Japan 1938.

Yendo, K., Notes on Algae new to Japan. I—VIII. The Botanical Magazine. Tokyo 1909—18.

Zanardini, J., Algae novae vel minus cognitae in mari rubro a Portiero collectae. Flora. Regensburg. 1851.

Zeh, W., Neue Arten der Gattung Liagora. Notizblatt des Königl. bot. Gartens und Museums zu Berlin. Bd. V (1908—12) p. 268. Leipz. 1913.

INDEX OF SPECIES

together with some more important synonyms, the latter printed in italics.

Indleveret til Selskabet den 26. Februar 1942
Færdig fra Trykkeriet den 13. Juli 1942.

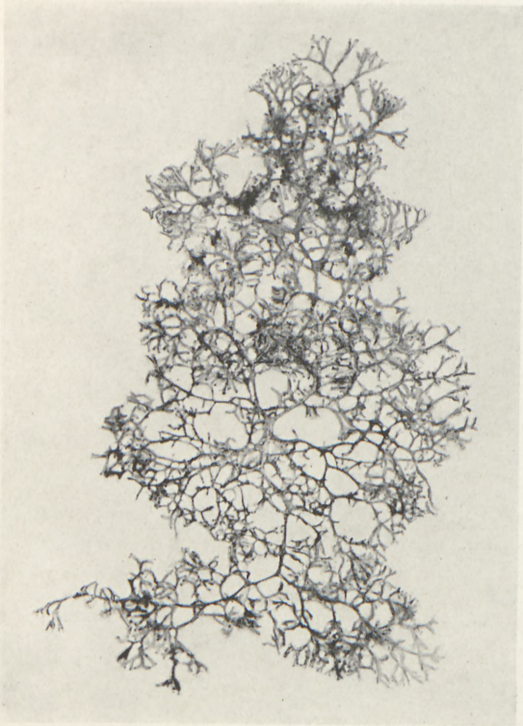


Fig. 1. *Liagora lurida* Dickie. ($^{9}/_{10}$ natural size).

Fig. 2. *Liagora Jadinii* Børgs. ($^{9}/_{10}$ natural size).

Fig. 3. *Liagora Mauritiana* Børgs. ($^9/_{10}$ natural size).

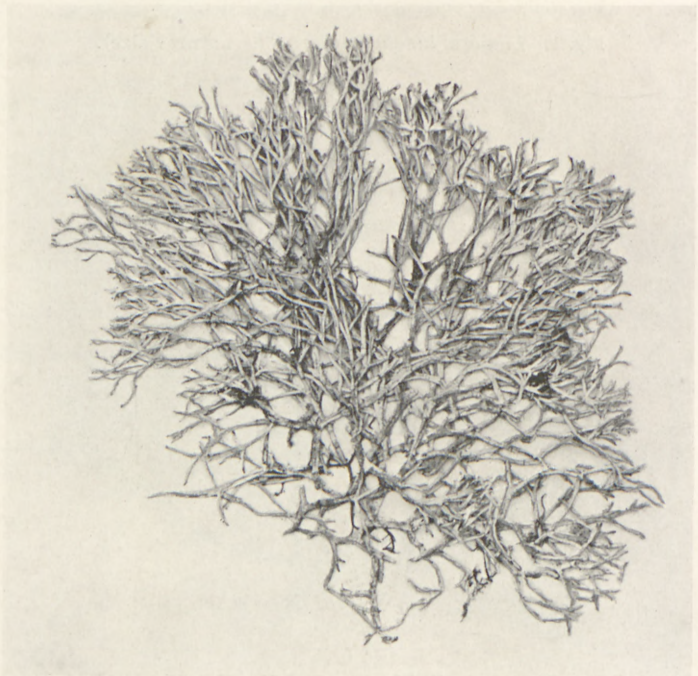


Fig. 4. *Liagora cladonioides* Børgs. ($^9/_{10}$ natural size).

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 6

THE MORPHOLOGY AND BIOLOGY OF THE *CORYLUS*-FRUIT

BY

O. HAGERUP

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

CONTENTS

Printed in Denmark
Bianco Lunos Bogtrykkeri A/S.

Preface.

My manuscript has been read through by Professors K. JESSEN and O. PAULSEN of Copenhagen, and I owe a debt of gratitude to these gentlemen for valuable critical hints.

To the trustees of the CARLSBERG Foundation, who have rendered possible my studies for a number of years, I tender respectful thanks.

The translation from the Danish has been done by Miss Annie I. FAUSBØLL M. A.

1. Introduction. The Problems.

An attempt to make clear the structure of the fruit of *Corylus* by means of the available literature will soon show that—on close consideration—surprisingly little is known about this common object, though in most lessons in botany it is used to exemplify the structure of a nut, or serves to illustrate the definition of this conception itself. It was in order to remove this uncertainty that I first began to study the organogeny of the fruit.

One of the most admirable investigations of the flower of *Corylus* has already been made by BAILLON. In 1875 he followed the organogenesis from its first stages, but owing to the primitive technical aids of his time there were several of the finer details which he was unable to examine.

Later morphological contributions to the understanding of the structure of the catkin and flower were made by EICHLER (1878), TROTTER (1929), and ABBE (1935), and a comprehensive list of the literature before 1913 has been given by BÜSGEN. It appears from this, however, that the few available observations are often contradictory, while several are incorrect. It was for these reasons that I started the investigations here presented. They are based on fresh material, gathered near Lyngby, north of Copenhagen.

The specimens were collected at intervals of a few days and at all seasons of the year. For the investigation of histological problems the objects were fixed and afterwards cut into series of thin sections with a microtome.

For the present study *Corylus avellana* was almost the only species used, and only on rare occasions *C. maxima* for comparison, these two species being almost similar in the features dealt with below. The fruit of *C. maxima*, however, differs in its involucre which remains, enveloping the nut, because the two leaves of which it is formed are concrescent and, in addition, have only very small swelling bodies at their base.

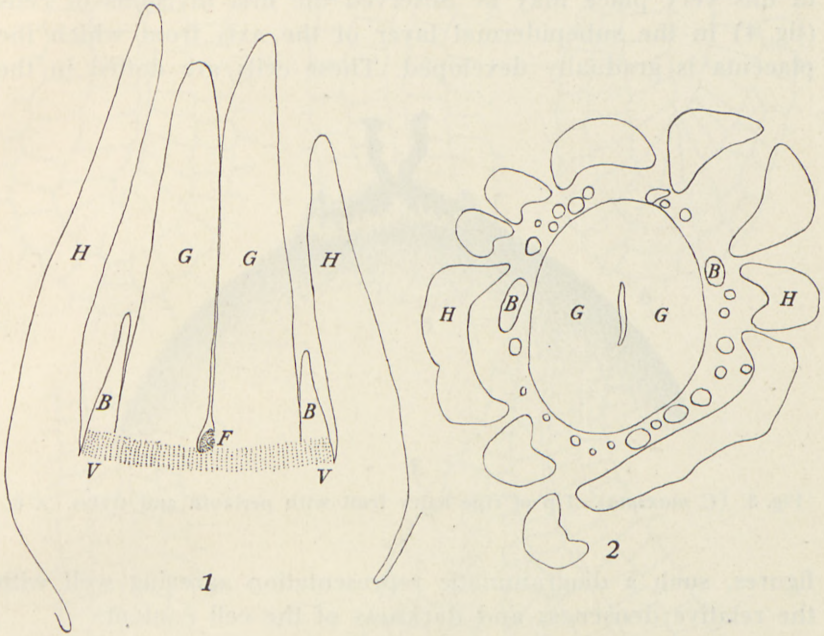
2. Organogeny.

Baillon found the first delicate primordium of the female flower already on June 15th the year before the flowering. About a month later the styles begin to form and already in August the female flower terminates its development for the year. Growth is not resumed until the next spring (March) when the well-known red styles are found exserted from the catkin and soon able to receive pollen.

On a closer inspection of the female flower in the pollination stage it is difficult to see anything resembling the full-grown fruit that develops later on. Thus during the flowering (March) no ovary has as yet been evolved; the gynaecium merely consists of the two long styles which are so close together that there is only a quite narrow space between them. The ovules, too, do not appear till a couple of months later (May). The subjoined figures show a longitudinal section (fig. 1) and a transverse section (fig. 2) of female flowers gathered on the 5th May. The two styles (*G*) enclose a narrow fissure, at the bottom of which there is a quite young ovule (*F*) on its placenta. Outside the styles there is a circle of small scales (*B*) which constitute the perianth; how many leaves these represent altogether is unknown; but this may perhaps be decided by examining the first developmental stages of the perianth which are found in July (the year before the flowering).

The above-described remarkable recently pollinated flower which, as already stated, lacks an ovary with ovules, remains in

its undeveloped state for a couple of months. Not until about the close of April and the beginning of May is growth resumed; and this then happens in a characteristic way. A narrow intercalary growing zone (*V—V* in fig. 1) arises which extends right across the apex of the floral axis near the place where the styles are attached.



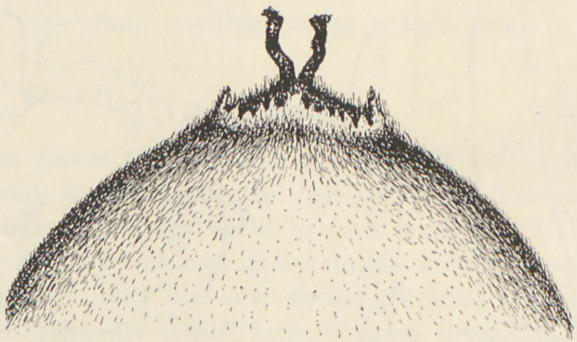
Figs. 1 and 2. Longitudinal (Fig. 1) and transverse (Fig. 2) sections of a flower. *H*, involucre; *B*, perianth; *G*, style; *F*, young placenta and ovule; *V—V*, intercalary growing zone (dotted). 5. May, × 50.

By the action of this intercalary growing zone the perianth and the styles are then gradually raised to the apex of the emerging ovary, whereas the bracteoles (*H*) remain below the fruit because the zone of growth is situated above the point where they are attached but below the perianth.

Special interest attaches to the development of the placenta, which is also one of the results of the activity of the aforementioned growing zone. And since the literature has no description of this remarkable process, it is illustrated by the appended figures (4—8), which show part of the region around the bottom

of the cavity between the styles; it is seen as a vertical fissure—clothed with epidermis—through the central part of all the sections shown.

To understand the morphology of the placenta it is important to keep in mind that the tissue under the bottom of the stylar fissure belongs to the floral axis which carries the styles; and in this very place may be observed the first divisions of cells (fig. 4) in the subepidermal layer of the axis from which the placenta is gradually developed. These cells are dotted in the



3

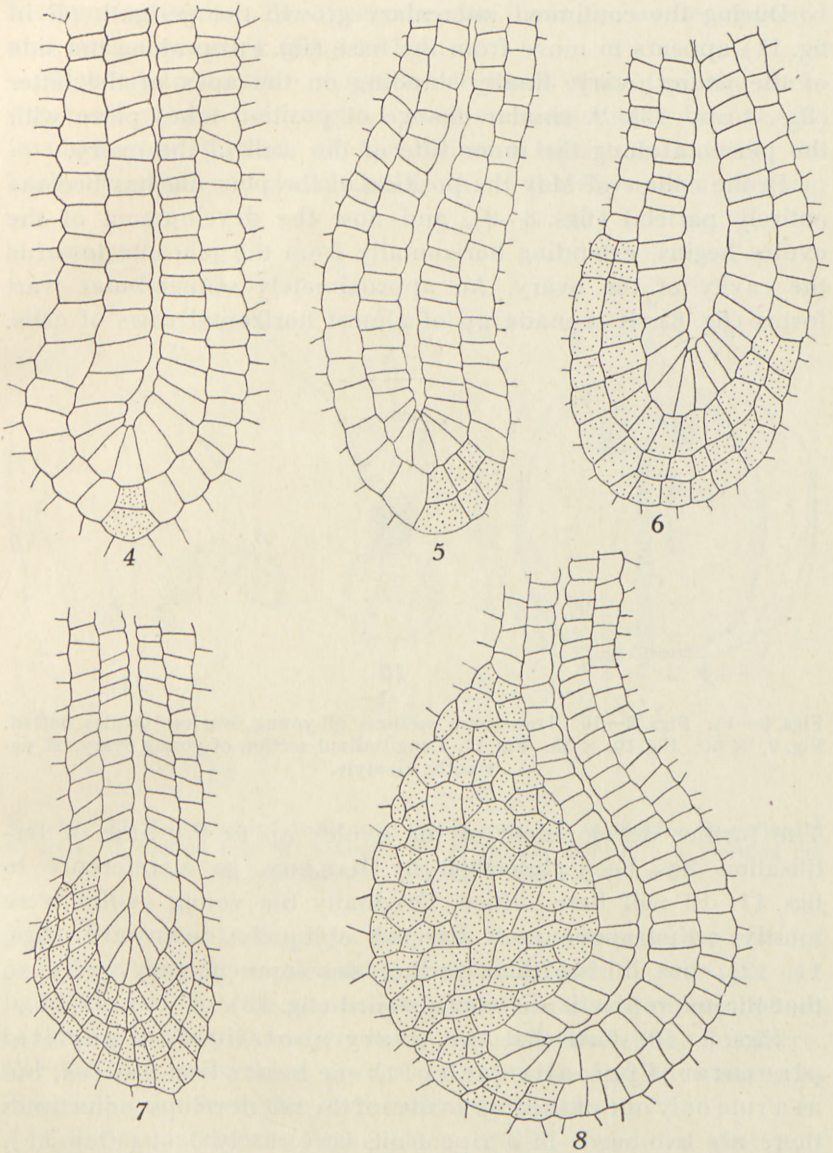
Fig. 3. (*C. maxima*). Tip of ripe hairy fruit with perianth and styles. × 6.

figures, such a diagrammatic representation agreeing well with the relative denseness and darkness of the cell content.

Fig. 4 shows the very first inception of the placenta in the tip of the axis below the cavity between the styles. Here a subepidermal cell has divided by means of a horizontal wall, and the two daughter cells continue their development, two subepidermal layers of cells arising from them (fig. 5). By similar continual horizontal division more and more layers gradually arise (figs. 6 and 7) from the original single subepidermal layer. In addition numerous vertical walls appear and by the continued activity of the intercalary zone of growth the young placental tissue soon extends upward too, along the inner side of the cavity of the young ovary (figs. 6—7).

Thus the originally basal young placenta, which belonged to the axis, gradually becomes parietal.

During the continued growth the cells below the subepidermal

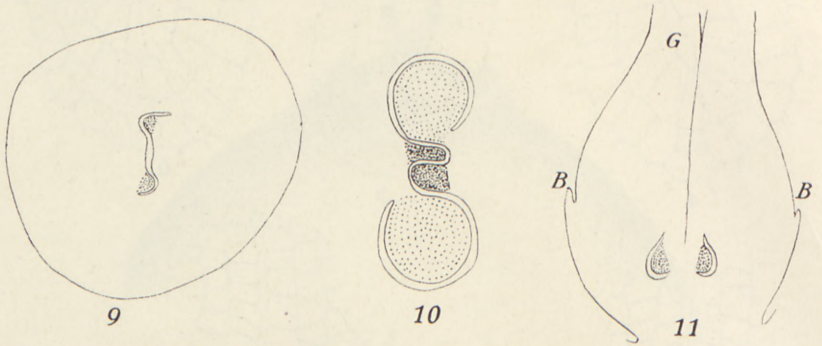


Figs. 4—8. The placenta (dotted) beginning to develop at the tip of the stem below the bottom of the ovarial cavity (in the middle of the figures). × 500. 5. May. See also text.

layer also divide—the greater part vertically—so that the originally fairly regular arrangement of the cells is obliterated.

During the continued intercalary growth the perianth (*B* in fig. 11) appears to move from the base (fig. 1) up along the side of the young ovary, finally standing on the apex of the latter (figs. 3 and 13). A similar change of position takes place with the placenta along the inner side of the wall of the ovary.

In the course of May the position of the placenta has become entirely parietal (figs. 8—9), and now the development of the ovules begins, extending horizontally from the placenta towards the cavity of the ovary. An approximately semiglobular wart forms (fig. 8). It is made up of almost horizontal rows of cells.



Figs. 9—11. Figs. 9—10. Transverse sections of young ovaries. Ovules dotted. Fig. 9, × 60. Fig. 10, × 35. Fig. 11. Longitudinal section of young ovary. *B*, perianth; *G*, style.

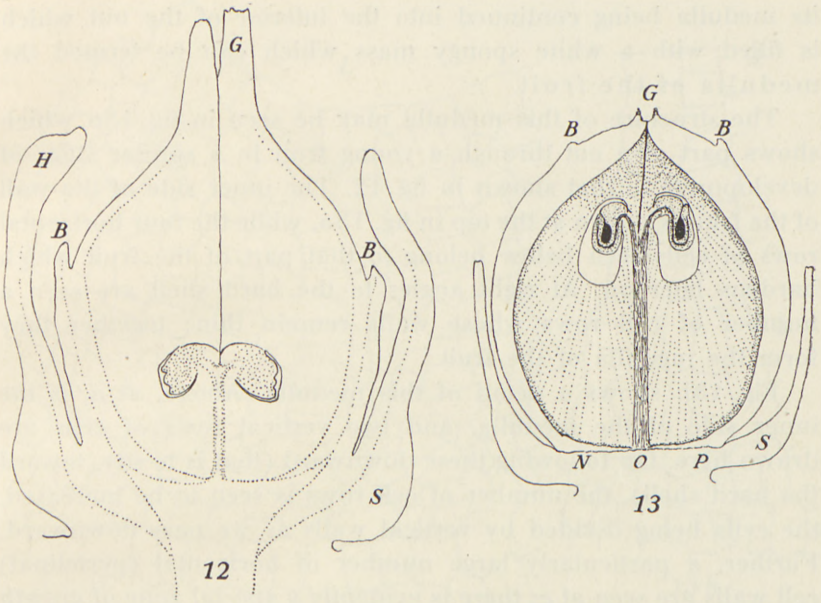
The further development of the ovules up to the time of fertilisation has been described by Baillon, so a reference to figs. 11—13 will here suffice. Originally the young ovules were mostly orthotropous and directed obliquely downward (figs. 11—12); but during their further development they curve so that the micropyle is directed upward (fig. 13).

Figs. 9—10 show that the ovary contains two parietal placentae. Typically each of these bears two ovules, but as a rule only one of the four ovules of the nut develops; sometimes there are two seeds in a ripe fruit, very rarely 3—4 (Eichler).

Owing to incorrect statements in the literature it should here be emphasised that the ovary has only one locule: but later the placentae are pressed so close together that only a very narrow and sinuous cavity remains between them (fig. 10); and this may make the ovary look as if it contained a septum and

a central placenta. This pressure also turns the ovules outward and later downward (fig. 10—13).

Right up to the time of full development of the fruit the growing zone retains its original position immediately above the involucre and through all the different layers of the axis, the bark, the wood and the medulla, which, therefore, come to form



Figs. 12—13. Longitudinal sections of young nuts. *H*, involucre; *B*, perianth; *G*, style; *O*, central hole of "hilum"; *N*—*P*, "hilum of fruit"; *S*, swelling bodies. See also the text. Fig. 12, × 20; Fig. 13, × 6.

part of the nut. In the ripe nut, too, the position of the zone of growth is readily ascertained, for its individual cells are not lignified, and they lie immediately on the outside of the bottom of the nut in the place where it has been attached to the involucre. For the soft cells there are easily ruptured and thus serve to detach the nut from the surrounding involucre.

Fertilisation does not take place until 2—3 months after pollination (in July); and only then does the fruit begin to increase appreciably in size. But in spite of this another month or two will pass before the seeds commence to grow in earnest. This does not happen until the nut is fully developed and begins to lignify at the apex (at the close of July).

During the activity of the growing zone the ovules also seem to change their place in the ovary. Originally their position was basal (fig. 11) but they are soon lifted upward (fig. 12), and finally stand near the apex of the fully developed fruit (fig. 13).

The hard outer layer of the fruit forms a direct continuation of the bark and wood of the axis beneath the growing zone, its medulla being continued into the interior of the nut which is filled with a white spongy mass which can be termed the medulla of the fruit.

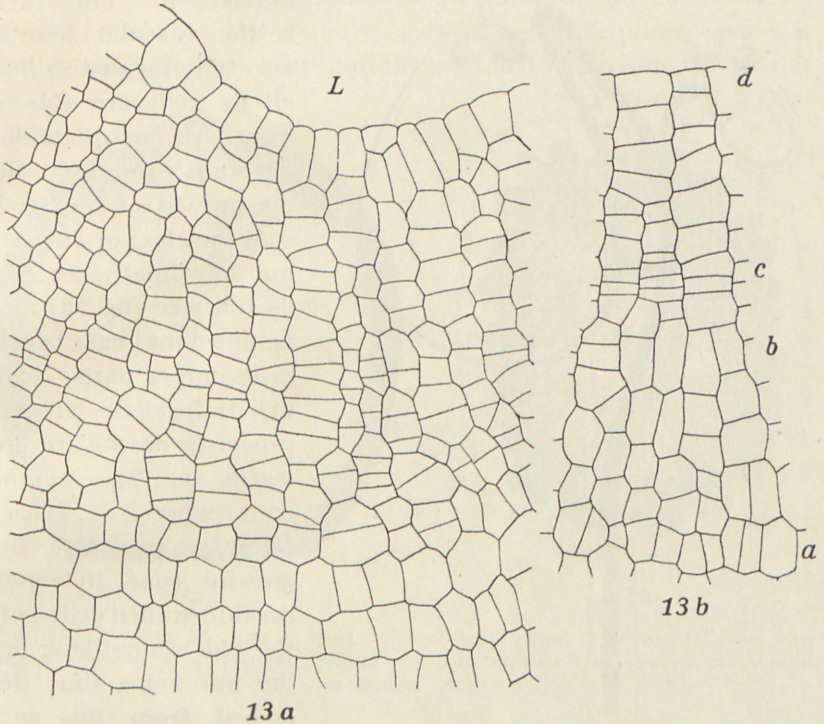
The structure of this medulla may be seen in fig. 13a which shows part of a cut through a young fruit in a similar stage of development to that shown in fig. 12. The inner side of the wall of the fruit is shown at the top in fig. 13a, while the four horizontal rows of cells seen below belong to that part of the fruit which hardens later on. At right angles to the hard shell are seen a number of cell rows whose walls remain thin; together they form the medulla of the fruit.

Fig. 13b shows a detail of this medulla. Above, at *d*, is the inner side of the medulla, and two vertical rows of cells are drawn here. On following these downward (that is to say, toward the hard shell), the number of cell rows is seen to be increased, the cells being divided by vertical walls as we pass downward. Further, a particularly large number of horizontal (periclinal) cell walls are seen at *c*; there is evidently a special zone of growth (a cambium) here, where the medullary layer increases in thickness. On the stretch *b*—*a* below this part, the medullary cells are more irregularly placed, until at *a*, and below, they are arranged in rows at right angles to the vertical columns of the medulla. These horizontal rows of cells (fig. 13a) lignify later and become part of the hard outer portion of the nut shell.

Finally fig. 13 shows in detail how the cell-rows of the medulla, which are indicated by dotted lines, exhibit a fan-like or almost radial arrangement with the cavity of the ovary in the centre.

On the stretch *N*—*P* in fig. 13 lies one of the intercalary growing zones. Here the nut grows fast in thickness (breadth), the cell-rows of the medulla being at the same time pressed sideways. But in addition the longitudinal growth of the fruit likewise takes place near its base, some few layers of cells above the zone *N*—*P* (at *c* in fig. 13b).

In accordance with its original position at the tip of the floral axis the placenta receives a vascular bundle from this stalk which, in spite of subsequent changes of position retains its original central position, as seen in the sections shown in figs. 12—13 and 25.



Figs. 13 a and 13 b. Part of transverse sections through "hilum" of young ovary. *L*, cavity of ovary. Innermost (above in figures) vertical columns of medullary cells; outermost (below in figures) horizontal rows of young sclerenchyma cells. × 500. See also text.

The young nut has thus an axillary medullary vascular bundle. This phenomenon is rare; it is found now and then in the axis of other plants (e. g. in the *Burseraceae*), but it does not occur in the vegetative branches of *Corylus*.

Fig. 13 shows that the axillary vascular bundle of the nut runs through the centre (*O*) of the intercalary growing zone (*N—P*). From this it again follows that the vascular bundle must take a share in the longitudinal growth of the nut and that right

through the base of the bundle there is a zone of embryonal cells which can only in very slight degree function as the cells in a fully developed vascular bundle. This is perhaps one of the reasons why the seed does not begin to grow till the whole fruit is fully developed in size. For only then is the vascular bundle also fully formed so that all its cells are able to transport the quantities of stuffs necessary for the growth of the seed.

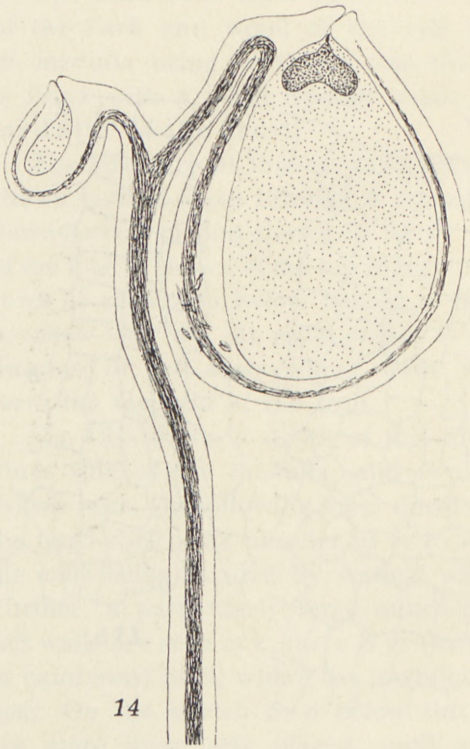


Fig. 14. The central vascular bundle carries one abortive (left) and one fertile ovule at its tip. × 18.

At the close of July the nut has finally reached its full size (fig. 13) and lignification has begun in its upper parts. Soon the induration process proceeds downward towards the base of the fruit where it ceases immediately above the growing zone, in which the thin-walled cells persist which burst later on, the nut being thus detached from the surrounding involucre.

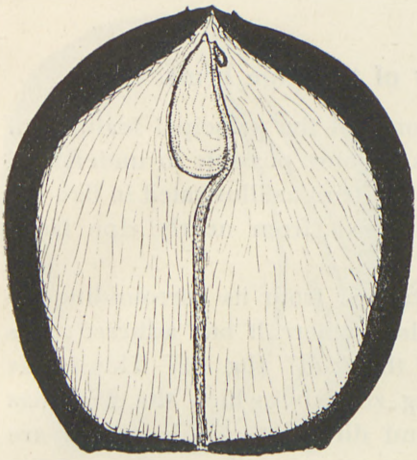
Thus the apex of the nut with the perianth and styles is a little more than a year older than its base.

When the fruit has attained its full size at the close of July a new phase in its development begins. Now at last the seed also grows with astonishing rapidity, and in the course of about one month only it can fill up nearly the whole cavity in its hard shell. But, as will appear from the subjoined figures, this growth of the seed takes place in a very peculiar way.

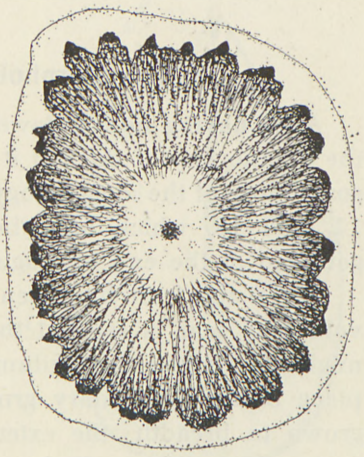
Of the 2—4 young ovules there is generally only one which continues its growth; the rest are suppressed, and one of these

is nearly always found as a desiccated remnant at the upper end of the fully developed seed (fig. 15).

Fig. 14 shows that the central vascular bundle in a fruit (collected August 1st) gives off two branches at the top which are connected by a short funicle each with its ovule, of which only one (on the right) contains an embryo and continues its development. As the rapidly growing seed requires space it has pushed the vascular bundle a little to one side so that it



15



16

Figs. 15—16. Fig. 15. Young fruit opened lengthwise. The fertile seed has begun to grow. × 5. Fig. 16. "Hilum" of fruit viewed from below, with hole in centre. × 4.

forms a curve. During the continued growth of the seed the vascular bundle is pushed more and more sideways (fig. 15). In the ripe nut it has been forced away from its original axillary position, right over towards the inner side of the hard shell.

An inspection of figs. 12 and 13 will show that the cavity of the young fruit is remarkably small and at any rate not big enough by far to hold the rapidly growing seed, subsequently so voluminous, which fills up the entire interior of the hard shell. But the space is enlarged in a peculiar way. During its continued growth the one seed which develops presses together the medullary cells below, so that they are killed. Further and

further the seed pushes its way down in the axis, and finally there is nothing left of the medulla but the dried up cell walls which, like a whole layer of brown fibres, lie squeezed in between the seed and the hard shell. So, morphologically, this medullary layer belongs to the inner part of the wall of the ovary (not to the testa).

If the nut is split some of the dead medulla-fibres will often remain on the outside of the seed, whereas the rest will adhere to the inside of the hard shell.

3. The Morphology of the Ripe Fruit.

After having now followed some of the principal features of the organogeny of the nut it has become possible to understand some more of the morphology of this fruit as illustrated in figs. 16, 17, and 18, which have been drawn from nearly ripe fruits gathered at the end of August.

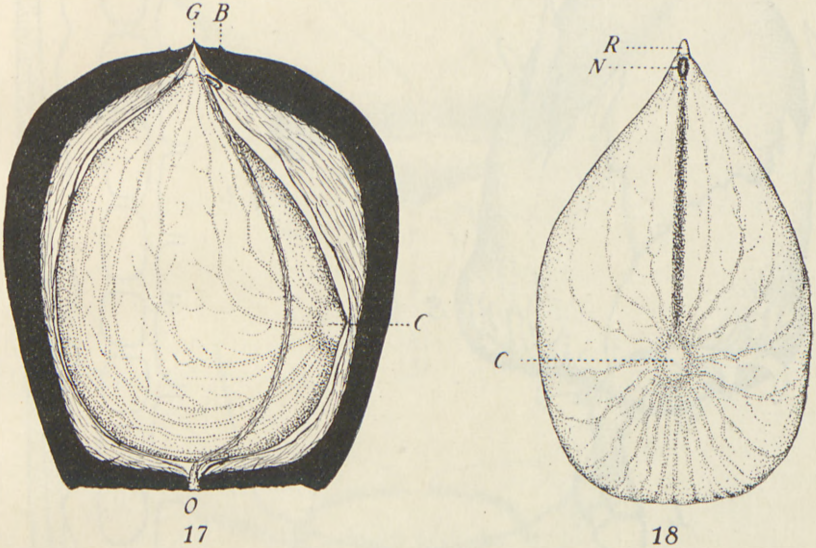
When the fruit has been detached from its surrounding involucre a scar is seen at the place where it has adhered; this might be termed the "hilum of the fruit" (fig. 16). This is the place of the intercalary growing zone by which the fruit has grown in breadth: the extent and direction of this growth are expressed by the radiating stripes covering the surface of the scar which are the remains of disrupted vascular bundles and parenchyma.

In the centre of the "hilum" (fig. 16) is seen a more or less distinct, small, dark mark; it is most easily distinguished if the surface of the hilum is smoothed with a file or a sharp knife. And if you insert a fine needle into the above-mentioned mark it turns out that in this place there is a very fine hole right through the hard nut-shell. If the nut is split into its two halves, the crack will as a rule run through this very hole, and it is then easily observed (fig. 17) that the vascular bundle of the seed passes through the hard shell and enters the soft interior of the fruit through this little hole.

From the centre of the "hilum" (*O* in fig. 17) the long vascular bundle passes up along the seed, generally following the raphe. The vascular bundle is not, as sometimes stated, the remnant of a septum, for the fruit of *Corylus* has no septum but is uni-

locular (figs. 9—10). The seed is attached at the upper end of the vascular bundle, and there is a fairly distinct real hilum (*N* in fig. 18) and next to it a sterile ovule. Just above the hilum there is an indistinct micropyle with the embryonal root hidden under it (*R* in fig. 18).

A distinct raphe issues from the hilum, running only about halfway down one side of the seed to the chalaza (*C* in fig. 18).



17 18

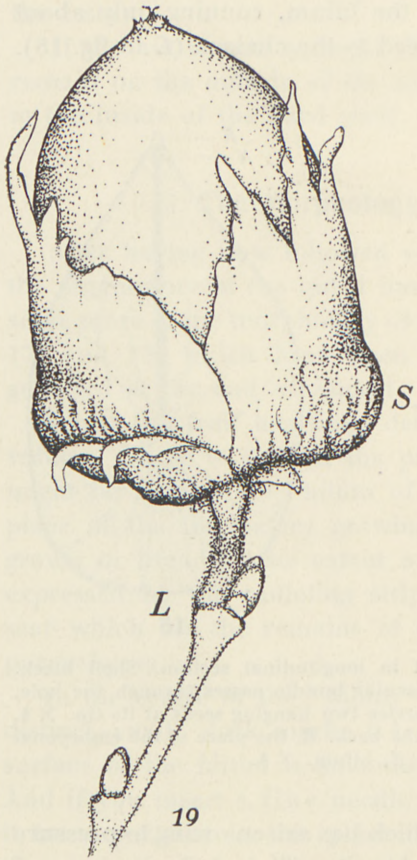
Figs. 17—18. Fig. 17. Nearly ripe fruit in longitudinal section. Shell black. *G*, style; *B*, perianth; *C*, chalaza; the vascular bundle passes through the hole, *O*, in the centre of the "hilum", and carries two hanging seeds at its tip. × 4. Fig. 18. Scarcely ripe seed viewed from the back. *R*, the place of the embryonal root; *C*, chalaza; *N*, hilum. × 4.

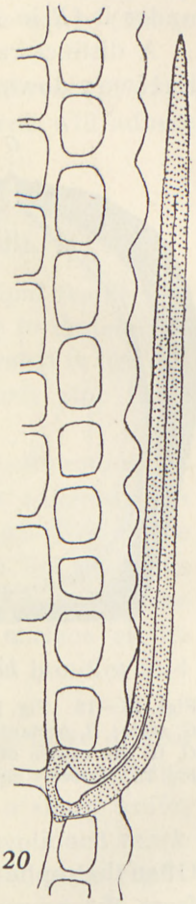
Often the raphe lies in a groove which has arisen owing to pressure from the squeezed in vascular bundle. The chalaza gives off numerous vigorous branched vascular bundles which are distributed over the whole of the testa like the nerves in a leaf (figs. 17, 18).

Hence the seed is plainly campylotropous but it is not so curved as for instance the seed of *Phaseolus*. In addition the embryo is straight as in anatropous ovules. Thus the seed in *Corylus* is intermediate between a campylotropous and an anatropous seed.

4. Dispersion of the Fruits.

When finally, at the close of August, the embryo is fully developed the fruit will normally remain on the tree for yet





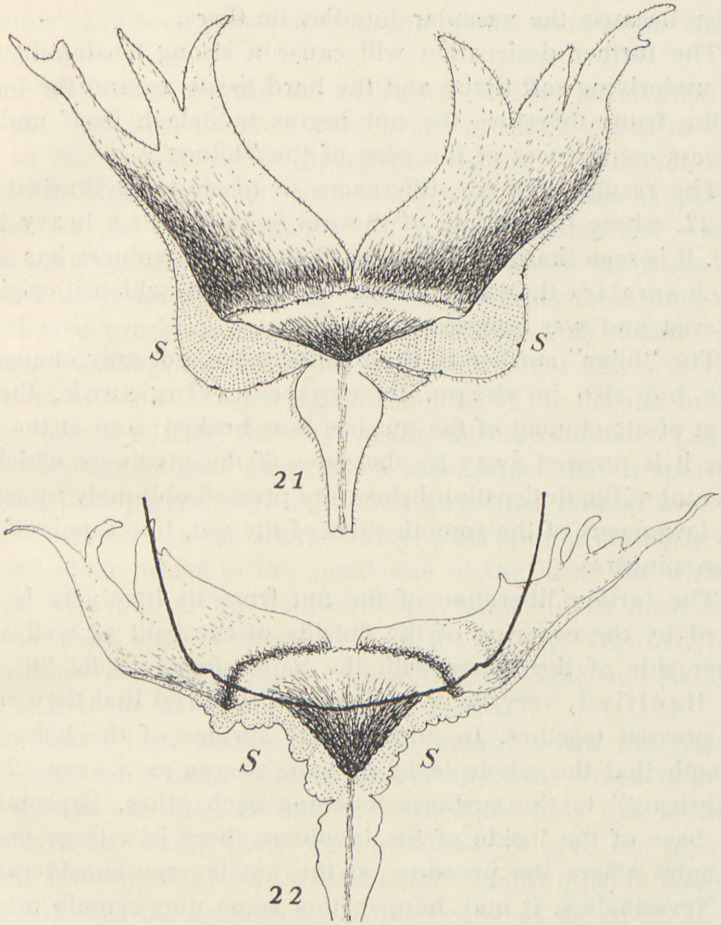
Figs. 19—20. Fig. 19. Ripe fruit with involucre. *S*, water tissue; *L*, joint where the stem breaks. × 2. Fig. 20. Hair from surface of fruit. × 600.

another month and no great external changes can be seen in it. But in the course of September the nut will gradually detach itself and it can then without difficulty be picked out of its involucre.

In October most of the nuts come loose without any external action. Several biological peculiarities are associated with this

liberation process, among which especially the structure and function of the involucre will be discussed below.

As long as the fruit is not yet ripe the involucre is pressed



Figs. 21—22. Involucre. *S*, swelling bodies. The outline of the fruit drawn in a heavy black line. × 3. See also text.

close up against it. But in October when the nut detaches itself the tip of the involucre begins to bend outward (fig. 21). This movement is due to the fact that nearly all the tissue surrounding the place at which the nut adheres (*S*, i figs. 19—21) is built up of large thin-walled cells filled with liquid. At the time of the leaf-fall the water supply stops and the water tissue (*S*) slowly

begins to dry, and at the same time it will also shrink considerably. This reduction of volume is greatest on the outside of the involucre where the desiccation is greatest, while the inside is stiffer because the vascular bundles lie there.

The further desiccation will cause a strong tension between the underlying soft tissue and the hard tissue around the bottom of the fruit; therefore the nut begins to detach itself and this process commences at the edge of the "hilum".

The results of these differences in tension are illustrated in fig. 22, where the outline of the nut is shown in a heavy black line. It is seen that the "hilar" surface of the involucre has grown much smaller than the "hilum" of the fruit, which it originally covered and was concrescent with.

The "hilar" surface of the involucre has not only changed in size but also in shape. Its centre having sunk, the last point of attachment of the nut has thus broken; and at the same time it is pressed away by the sides of the involucre which, on account of the desiccation below, are pressed obliquely up against the lower part of the smooth sides of the nut, like a pair of wide open pincers.

The further liberation of the nut from its involucre is facilitated by the covering of the outside of the fruit as well as the inner side of the leaves with the hairs shown in fig. 20; these are lignified, very thick-walled, and so hard that they cannot be pressed together. In addition the surface of the hairs is so smooth that the whole layer of hairs serves as a very effective "lubricant" to the surfaces touching each other. Especially at the base of the inside of the involucre there is a large number of hairs where the pressure on the nut is very considerable.

Nevertheless, it may happen that some nuts remain attached to the involucre; this may occur for instance in a very wet autumn, when desiccation is slight. Fruits whose seeds have been killed, for instance by the attacks of insects, also often remain on the bushes because no detachment layer has been formed.

But when the autumn storms lash the trees nearly all the fruits come off because their stalks break, a special detachment layer having formed (*L* in fig. 19) right through the thin branch.

Thus the autumn storms fling the heavy fruit down among the surrounding branches and thence to the ground where a

nut not free from its involucre is now rarely seen. Then the hunt for the nuts has long been in full swing, and so eagerly are they sought by many mammals and birds that nearly all the fruits have been removed from the mother trees in the course of October.

The dispersion by the aid of various birds (*Sitta, Picus*) is very effective, because their hard beaks are little suited to keep hold of the smooth fruits during the vigorous motion of their flight. The birds, however, wish to carry off the fruits as quickly as possible out of the reach of all rivals, to some tree with a rough bark or branches at suitable angles, where the fruits can be fixed while they split them open. But during these long and complicated processes many fruits are dropped all around and often the seedlings are found far from the mother tree next year.

To understand the sociological relations of the *Corylus* bushes it is of interest to study the ways of the northern nuthatch (*Sitta*). For wherever this little bird, which is no larger than a sparrow, is found it disperses more nuts than any other animal over the greatest distances in the shortest time. This special ability is due amongst other things to the small size of the bird; for when it flies off with one of the comparatively large nuts it must keep its beak wide open, biting hard on the plump, smooth fruit which may very easily slip from it during its flight, and likewise when it is to be fixed and pecked to pieces.

The small bird must exert all its energy when the fruit is to be split. So it often perches above the fruit which it keeps hold of with one foot. During its work it not only lifts its head but moves its whole body up and down to give the greatest possible force to its blows. A good result is most quickly attained if the bird hits the nut exactly in the centre of the apex. If, on the other hand, it hits the nut a little beside the apex its beak will glance off the oblique smooth sides of the nut and the fruit will easily slip and fall to the ground. Even if the bird tries to find the fruits that have been dropped many will be lost; and so the seeds for a hazel copse will be sown.

It is necessary, therefore, for the bird to find a particularly favourable tree in which to lodge the fruit. And if such a tree is not present near by it will fly a good distance with the fruit in its open beak. It has found itself a workshop beforehand,

the good quality of which is somewhat of a life condition for it. Young trees are as a rule useless because their bark is too smooth. For the same reason it also avoids *Fagus* and our other smooth-barked trees. Sometimes it will use *Ulmus* and *Fraxinus*, especially when these trees grow in avenues or gardens where they are allowed to grow old and form a thick bark with crevices.

Among our native trees there is none, however, which is so well suited for the purpose of the nuthatch as *Quercus*. Notably where there are old and solitary specimens one is generally sure to find traces of the activity of the nuthatch. For here there are as a rule both good places for nests in holes, for instance in old gnarls. And outside the breeding period the bird may pass the night there or use the nest as a storing place for the greater or smaller number of nuts collected. Further *Sitta* is also satisfied with the fruits of *Quercus*, just as it will feed on the fruits of *Fagus*, *Cerasus*, *Acer*, *Coniferae* and others.

The fruits of *Quercus*, too, are most effectively dispersed by the nuthatch (*Sitta*); and in Sweden, for instance, the northern limit of the oak and *Sitta* almost coincide. It may also be noted that *Corylus* and *Quercus* came into Denmark at about the same time (IVERSEN).

But in the cold season its favourite food is above all the fruit of *Corylus*, of which it consumes as much as it can on the spot, while, as already stated, any surplus is stored, the nuts being either buried singly in the ground, or several are collected in crevices under bark, under roofs, in the cracks of walls, between stones etc. The whole store is not collected in the same place, however, as the animal might then risk being robbed of its whole supply at once, for instance by a squirrel or other larger animal attacking it.

The nuthatch (*Sitta*) may stay hour by hour and day after day near the same old oak trunk to which it returns again and again after its forays in the neighbourhood. From this starting point it gradually strays in all directions and often it is from comparatively long distances that it returns with nuts. Some of them are dropped and disappear under withered leaves or in the grass where they will perhaps be buried by other animals so that they can germinate next spring.

In close growths of *Fagus*, *Corylus* does not occur; it will

not tolerate the deep shade, and the smooth stems offer little opportunity for dispersion by *Sitta*. More frequently hazel is found under old specimens of *Fraxinus* and *Ulmus* with cracked bark.

The mixed forest of big oaks with a luxuriant undergrowth of hazel known in so many countries has no doubt in great part grown up and obtained its characteristic composition as a result of the activities of the nuthatch and other nut-feeders as dispersers of seeds. The term symbiosis might perhaps with some justice be employed about the interrelationship between the oak and hazel community and the nuthatch, the constant companion and disperser of the nut.

Mice, too, disperse a great many nuts. Not only do they thoroughly search the ground under the trees, but in the night they climb the trees and search the branches. I have often found the stomach of *Hypudaeus glareola* filled with gnawed male catkins which chiefly in the winter constitute a very important food stuff for a particularly numerous stock of mice living under *Corylus*, especially where this shrub grows in abundance. The fruits, too, are well suited for being stored as winter food, and they are gathered together in the well-known underground burrows where they are kept under suitable conditions of moisture (and are exceedingly tasty). In the evening all through the autumn you may hear the rustling of the mice among the fallen leaves under the hazel-bushes. And even if snow falls the work with the nuts is still continued with great energy below the sheltering cover, where the mice now move about more hidden, and so in less danger of being attacked. The underground stores may also harbour male catkins which give evidence of the nocturnal activity of the animals in the treetops.

Many nuts are consumed at the place where they are found. Here the empty shells may then be seen with holes gnawed in them which are different for the different species of mammals. This has been more closely investigated by Degerbøl who has kept the animals in captivity to study their different working methods when nuts are fed to them.

The rivalry of the pugnacious mice during the gathering and transport of the comparatively large smooth fruits will hardly

proceed without fighting and the consequent loss of nuts on the way. At any rate nearly all the fruits are quickly removed from their original position under the trees and are soon dispersed far and wide.

As many mice are consumed by other animals in the course of the winter not a few subterranean stores will be left without owners. And then with the advent of spring the many nuts gathered together will germinate in the same spot, and a dense growth of seedlings will emerge from the ground. The finding of such abandoned stores has provided a rich material of the remarkable seedlings which will be dealt with in more detail below.

In the course of the summer all the weaker seedlings that have come up from the subterranean stores of mice die off, and one or two vigorous plants remain which—thanks to the mice—have been sown under favourable conditions in the ground.

To ensure successful germination it is probably necessary for the fruits to be buried in the soil. At any rate, I have never found germinating nuts above ground, but always under ground. How the fruits are sown remains an enigma.

It has been shown above, however, that mice can bury them effectively, and something similar can be done by squirrels (*Sciurus*) and *Sitta*.

When the nuts ripen this means that a great amount of food has suddenly become available; and this also happens at a time of year when it is very important both for many birds and for mammals to have a store to draw upon in the coming unfavourable season. However, the season for gathering them in is very short, and perhaps the animals know that the chances of finding nuts in larger quantities will only last a few weeks.

So rival collectors flock to the place from all directions, each of them merely trying to carry off as many fruits as possible in the shortest possible time. But since the nuts can be kept concealed, it is not necessary that this spoil—as so many other kinds—should be eaten at once.

Therefore the lucky finders hurry off as quickly as possible in all directions to hide their spoil from their rivals, afterwards hastening back as fast as they can, hardly allowing themselves

time to eat. According to oral information, M. DEGERBØL has seen squirrels work in this way; one by one the fruits were carried off, buried not very deeply, and covered with mould. Some of them were indeed later found by woodpeckers (*Picus*) and devoured; but a number of the nuts buried singly will easily be forgotten, even though the competitors prey very much on the stores so hurriedly laid down by the others.

While mice laboriously gnaw a hole at the top of the nuts, the squirrel can quickly open them by splitting them lengthwise into two halves. It bites off the tip and bores down its teeth where the nut anatomically has its weakest point (DEGERBØL).

The strong beak of the woodpeckers (*Picus*), too, is remarkably well suited for opening the hard fruits. On the other hand, the beak of the titmouse (*Parus*) is usually too weak to bring about any very successful results; these birds, however, also try their luck.

Among our common indigenous birds it is, however, the Northern Nuthatch (*Sitta*) which helps most to spread the nuts; often it is seen flying off with one in its beak and it will also bury the fruits one at a time, if it cannot consume the whole harvest at the same time.

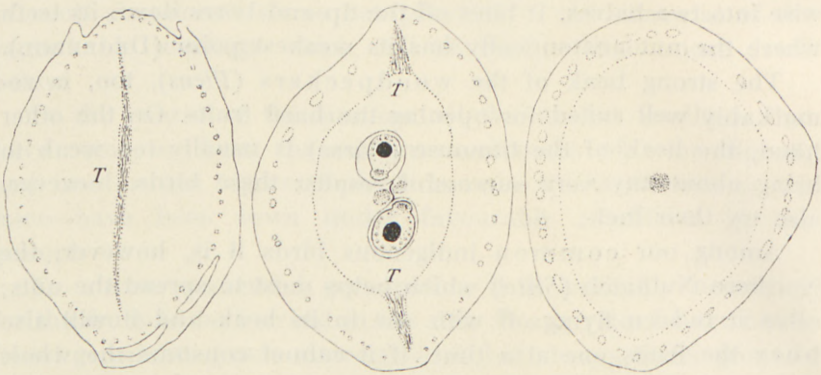
The dispersion and burying of the *Corylus* fruit is thus very effective; it takes place both by day and by night and especially in one short period of the year (October). It is true that the great majority of the fruits are consumed by animals, but the growth of seedlings in their natural habitats shows that several of the hard smooth fruits either slip from the animals or are forgotten where they were buried, under good conditions for germination, at a shorter or longer distance from the mother plant.

5. Germination.

At germination the embryo must first overcome the difficulties due to the fact that its tenderest parts are imprisoned in a very hard shell. And as a matter of fact it turns out that some remarkable features in the structure are designed for this purpose and serve to break the shell so that the embryonal root can emerge.

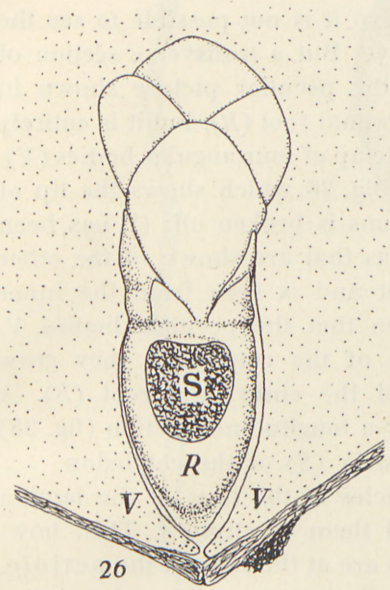
If the tip of the fruit is removed by a transverse cut near the place where the perianth is attached, a cutting surface is

obtained similar to that shown in fig. 23. In the lengthwise direction of the section the dark line (*T*) is plainly seen which is well known to any one who tries to open a nut by sticking the point of a knife into this very line. As already mentioned, it is here that the squirrel bores its teeth into the nut with a successful result (DEGERBØL), and *Sitta*, too, can break open the nut by a vigorous vertical thrust into the apex of the nut. More rarely the little bird splits open the hard fruit by pecking at the side.

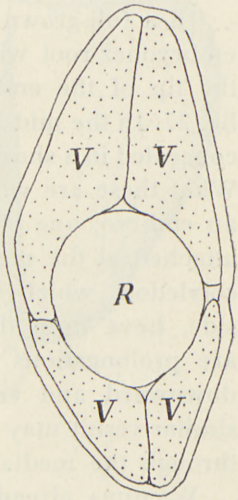


Figs. 23—25. Fig. 23. Transverse section through apex of fruit. *T*, soft tissue in a fissure in the hard surrounding shell. × 50. Fig. 24. Transverse section striking the ovules. *T*, groove in shell. × 15. Fig. 25. Transverse section through middle of nut; in the centre the vascular bundle. × 10. See also text.

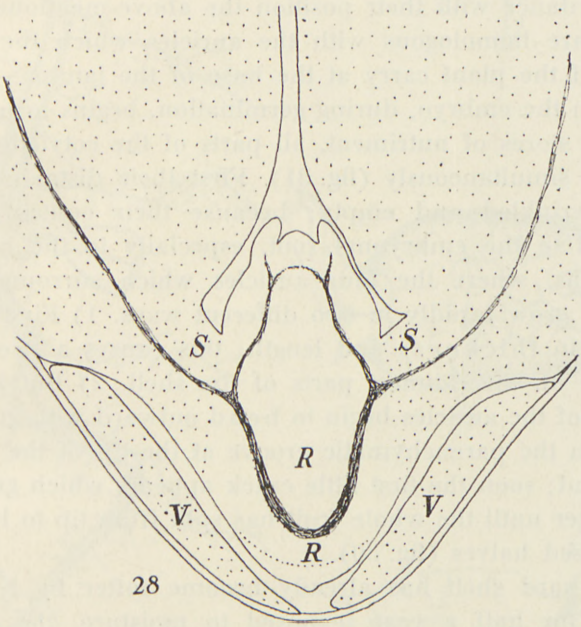
Just inside the above-mentioned black line (*T* in fig. 23) the embryonal root lies concealed; this is the thinnest part of the shell, so this offers the best opportunity for the embryo to disengage itself from the shell. Microscopical examination shows that at the mark (*T*) there is a complete layer of soft thin-walled tissue in the middle of the hard shell. In transverse sections it can be observed that the parenchyma in question is continued in a groove downward along the inner side of the shell (fig. 24), which is thinnest at and along the two lines where the edges of the cotyledons lie. At the natural bursting of the shell—as at germination—the split runs through this parenchyma down to the "hilum" of the fruit, which often cracks through the above-mentioned central hole (*O* in fig. 13) through which the vascular bundle of the seed runs.



26



27



28

Figs. 26—28. Sections of ripe embryo showing appendages (*V*) of cotyledons pointing downward. *R*, embryonal root; *S*, stalk of cotyledon. Cotyledon dotted. × 25. Fig. 26. One cotyledon is broken off at *S*, the other is seen from the inner side. Fig. 27. Transverse section through apex of embryo. Fig. 28. Longitudinal section striking both cotyledons medianly.

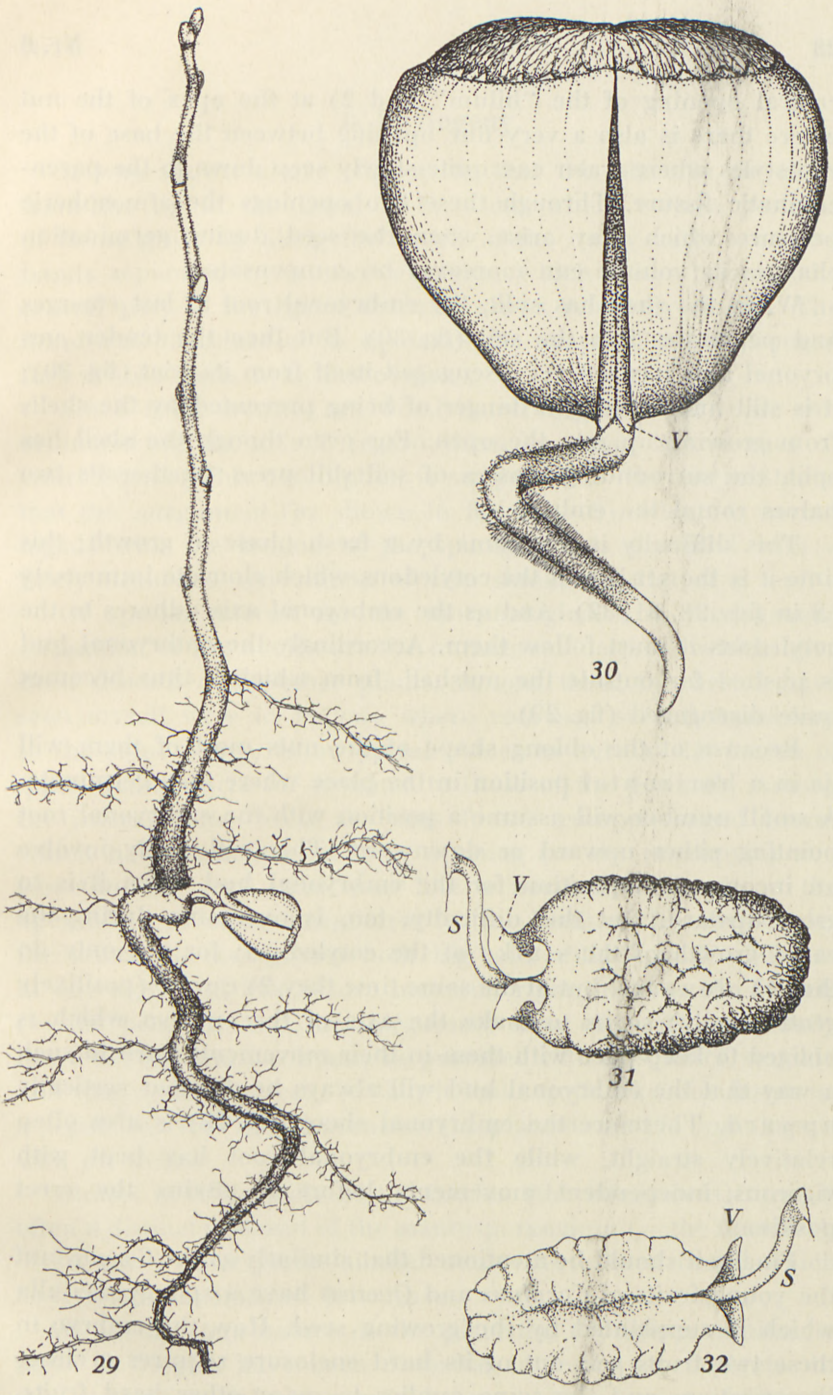
In a full-grown prepared embryo it is not possible to see the embryonal root with the naked eye. But a transverse section of the tip of the embryo provides the peculiar picture shown in fig. 27. In the middle lies the embryonal root (*R*), but it is entirely concealed in a sheath which is made up of four angular bodies (*V*). What these are will appear from fig. 26 which shows the tip of an embryo, one of whose cotyledons is broken off; (it has been attached at the mark *S*). The parts that are shown of the other cotyledon, which is still adherent and is seen from the inner side, have been dotted. It is seen that the peculiar bodies, *V*, are prolongations from the base of the cotyledon; they grow downward and entirely surround the embryonal root (*R*). A similar result may be obtained by a longitudinal section (fig. 28) through the median part of the stalk (*S*) of the cotyledon.

WICHURA already saw the auricles at the base of the lamina of the cotyledons and interpreted them as stipules. This, however, cannot be correct, as stipules are at the base of the petiole. In accordance with their position the above-mentioned peculiar organs are homologous with the auricles which the vegetative leaves of the plant carry at the base of the lamina.

When the embryo, during germination, begins to use some of its large stores of nutriment, all parts of the cotyledons are not emptied simultaneously (fig. 31). First their distal points begin to be wrinkled and empty; because their content has been removed to the embryonal root, especially to the base of the cotyledons, where the four auricles which surround the root begin to grow rapidly in two different ways. 1) First they grow quickly in thickness and length; this causes a strong inward pressure on the thinnest parts of the shell. 2) But in addition the tips of the auricles begin to bend outward with great vigour, and then the parenchymatic groove at the tip of the nut begins to expand; soon the first little crack appears which grows larger and larger until the whole fruit has split from tip to base in two equal-sized halves (fig. 30).

The hard shell has already become softer by lying in the ground for half a year, exposed to moisture, the inroads of fungi, and great variations in the climatic conditions.

Further, the water in the surrounding soil can penetrate directly through the shell in two places, namely through 1) the



Figs. 29—32. Fig. 29. Seedling from October. × 2/3. Fig. 30. Incipient germination. × 3. Fig. 31. Cotyledon viewed from the back, desiccated at tip but still alive at base. October. × 3. Fig. 32. Cotyledon viewed from the inner side. October. × 3. The cotyledons in all the figures with long stalks (*S*) and auricles (*V*) at base of lamina. See also text.

central opening of the "hilum" and 2) at the apex of the nut where there is also a very fine opening between the base of the two styles where water can quite slowly seep down to the parenchymatic fissure. Through these two openings the atmospheric pressure which may arise when the seed during germination changes its volume can moreover be compensated.

When the shell has split, the embryonal root at last emerges and penetrates into the soil (fig. 30). But then the tender embryonal axis has not yet disengaged itself from its coat (fig. 30); it is still imprisoned, in danger of being prevented by the shells from growing up into the open. For even though the shell has split, the surrounding masses of soil still press together its two halves round the embryo.

This difficulty is overcome by a fresh phase of growth; this time it is the stalks of the cotyledons which elongate immensely (*S* in figs. 28, 31, 32). And as the embryonal axis adheres to the cotyledons it must follow them. Accordingly the embryonal bud is pushed far outside the nutshell, from which it thus becomes quite disengaged (fig. 29).

Because of the oblong shape of the nuts most of them will lie in a horizontal position in the place where they germinate. A small number will assume a position with the embryonal root pointing either upward or downward. This will easily involve an inconvenient position for the embryonal bud when it is to grow upward. But this difficulty, too, is overcome during the rapid growth of the stalks of the cotyledons; for not only do they 1) elongate, but at the same time they 2) curve (positively geotropically) so as to make the axis of the embryo which is obliged to keep pace with them in their movements, turn in such a way that the embryonal bud will always be directed vertically upward. Therefore the embryonal shoot (fig. 29) is also often relatively straight, while the embryonal root has bent with vigorous independent movements before it attains the erect position.

Finally it should be mentioned that similarly as the *Corylus* nut the young fruits of *Carpinus* and *Quercus* have a spongy medulla which is supplanted by the growing seed. How the embryo in these two fruits gets out of its hard enclosure requires a closer investigation, and the same applies to many other hard fruits.

6. Phylogeny.

It was shown above (figs. 4—8) that the placenta develops from the tip of the floral axis, from which certain portions of tissue grow up along the inside of the ovary as two narrow bands separated by a narrow cavity, which arises because the central part of the tip of the axis grows relatively slowly. The floral axis therefore at its tip takes the shape of a two-pronged fork whose parts bear the ovules.

Since these ovules are dorsiventral organs which are co-ordinated on an axis I regard them as being homologues of entire leaves. This assumption is supported by the circumstance that the integument (as shown in figs. 17—18), which is homologous with the lamina of the sporophyll, is provided with a finely branched reticulation of ribs similar to that of a leaf.

Of special interest for the morphological and phylogenetic estimation of the ovules are the numerous "oolyses" which have been described for other plants. Among these the best I have seen myself were in *Petunia* where you may see all transitions in the same ovary, from typical ovules to normal flat leaves of quite similar form for instance to those of the perianth. Among the intermediate forms are thus found trumpet-shaped leaves which have sometimes a large opening (= the micropyle) and sometimes a very small one like a normal micropyle at the apex of an urceolate integument (= the lamina). In other ovules the micropyle has grown both big and oblique with a fissure at one side, and this fissure may run right down to the funicle (= the petiole). And the integument then often expands flatly like a normal lamina: it may be provided with ribs, hairs, stomata and may even be green, so that it looks quite like, for instance, a sepal. But this leaf is borne on the placenta and is homologous with an ovule.

Almost in the middle of the lamina (the integument) there is often a distinct remnant of the macrosporangium (= the nucellus).

In many other plants similar ovules have been found which have been transformed into leaves.

As to the stem-nature of the placenta, conditions similar to those in *Corylus* have been observed in many other plants. In this connection reference may be made to a series of investi-

gations by J. M. THOMPSON who even thinks that the revision of the classic conception of the gynaecium should be extended to the *Leguminosae*. I myself have found an organogenesis of the parietal placenta similar to that of *Corylus* in *Mesembryanthemum*, *Cactaceae*, *Gesneriaceae*, *Orobanchaceae*, and *Salix*. Within the most nearly related species of several of the above-mentioned groups of plants there are other plants (e. g. within the *Personatae*) with a central placenta which is a direct prolongation of the floral axis and not formed of the "concrescent edges of the carpels".

Further information and references to the literature concerning the phylogenetic problems are found in THOMPSON'S and HAGERUP'S works. Here it should merely be noted that my view—as indicated above—is that an ovule is a monosporangiate macrosporophyll of a similar type to those occurring in the *Lycopodiales*.

This view opens up new perspectives for an elucidation of the phylogeny of the angiosperms. And there seems to be a phylogenetic line running down from certain angiosperms over *Gnetales* and *Coniferae* (especially *Juniperus* and *Lebachia*) to the *Lycopodiales*.

7. Summary.

1. The various phases of the development of the female flower occur approximately at the times given in the following example:

a. Styles and perianth begin to form: June-August 1941.
b. Resting period: August 1941—February 1942.
c. Pollination: March—April 1942.
d. Placenta and ovules begin to form: May 1942.
e. The fruit grows: May—July 1942.
f. Fertilisation: July 1942.
g. Seed begins to grow: The beginning of August 1942.
h. Termination of the growth of the seed: Close of August 1942.
i. Ripening of the fruit: September 1942.
j. Dispersion of fruit: October 1942.
k. Resting period for the fruit in the soil: October 1942—spring 1943.
l. Germination: Spring 1943.

2. The organogeny and final aspect of the nut is characterised by the fact that soon after the flowering an intercalary growing zone develops right across the tip of the floral axis in the internode between the perianth and the involucre (fig. 1).

3. During the intercalary growth the hard shell of the nut develops as a direct continuation of the cortex and xylem of the floral axis; and the medulla of the latter is continued as a soft white tissue, filling the interior of the young nut.

4. During the growth of the seed the medulla of the fruit is compressed to such an extent that it is killed; and in the ripe fruit it lies as a brown scaly layer between the shell and the seed.

5. Through the centre (*O*) of the "hilum" of the fruit there is a hole (figs. 13, 16, 17) through which runs a vascular bundle carrying at its tip 2—4 hanging epitropic seeds. These are somewhat campylotropous, still with rather a long raphe (fig. 18). The funicle is very short. The central vascular bundle has erroneously been interpreted as a funicle or as "the remains of a septum". Originally, however, the fruit was unilocular with 2 parietal placentae.

6. The fruit is disengaged from its involucre as a consequence of desiccation and shrivelling of the water tissue in this sheath (figs. 21—22).

7. The fruits are especially dispersed and sown by birds (*Sitta, Picus*), but also by mice and squirrels.

8. As birds try to split open the fruits in crevices of the bark of trees, particularly *Quercus*, this tree will often be seen to have a vegetation of *Corylus* growing under it.

9. From the base of the lamina of the cotyledons issue four elongations (auricles) which entirely surround the embryonal root like a sheath (figs. 26—28). At germination these split the hard fruit, growing rapidly in length and thickness and also bending outward. The stalk of the cotyledons grows considerably in length (figs. 29, 31, 32) and thus pushes the embryonal bud right out of the shell.

10. The organogenesis shows that the two parietal placentae begin to form at the tip of the floral axis which soon assumes the form of a two-pronged fork (figs. 4—7).

11. As the ovules begin to form at the tip of a stem I consider them homologous with entire independent leaves. This view is explained in more detail on pp. 29—30 and in my earlier works.

12. Since the ovules are monosporangiate macrosporophylls I assume a phylogenetic connection with the *Lycopodiales*.

8. Bibliography.

ABBE, E. C. (1935): Studies in the Phylogeny of the *Betulaceae* I. Floral and Inflorescence Anatomy and Morphology. Bot. Gaz., Vol. XCVII.

BAILLON, H. (1875): Traité du développement de la fleur et du fruit. Adansonia, Bd. 11, p. 163.

BENSON, M. (1894): Contributions to the Embryology of the *Amentiferae*. Transact. Linn. Soc., London. 2nd Ser. Bot. Vol. 3, p. 409.

BÜSGEN, M. (1913): *Cupuliferae* in KIRCHNER, O., LOEW, E. und SCHRÖTER, C.: Lebensgeschichte der Blütenpflanzen Mitteleuropas.

DEGERBØL, M. (1935): Danmarks Pattedyr. København.

EICHLER, A. W. (1878): Blüthendiagramme. II. S. 16.

HAGERUP, O. (1939): On the Origin of some Angiosperms through the *Gnetales* and the *Coniferae*. IV. The Gynaecium of *Personatae*. D. Kgl. Danske Vidensk. Selskab, Biol. Medd. XV, 2.

IVERSEN, J. (1941): Land Occupation in Denmark's Stone Age. Danmarks Geologiske Undersøgelse. II. Række, No. 66.

THOMPSON, J. M. (1937): On the Place of Ontogeny in Floral Enquiry. Publ. Hartley Bot. Lab., No. 17.

TROTTER, A. (1929): Osservazioni morfologiche e genetiche sui "*Corylus*". Ann. R. Istituto Sup. Agr. Portici. Ser. III. Vol. III, p. 209—234.

WICHURA (1857): Über das Blühen, Keimen und Fruchttragen der einheimischen Bäume und Sträucher. Flora Bd. 15, S. 573.

Indleveret til Selskabet den 16. Januar 1942.
Færdig fra Trykkeriet den 29. Juni 1942.

Bark of *Quercus* in which *Sitta* has lodged two nuts. The lower nut is hacked at the tip and has begun to split lengthwise.

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 7

FURTHER EXPERIMENTS ON REGENERATION-PROBLEMS IN PLANARIANS

BY

H. V. BRØNDSTED

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

Printed in Denmark
Bianco Lunos Bogtrykkeri A/S

The scope of the experiments described in this paper is to investigate some basic problems in regeneration, especially the problems of regulation and inhibition in adult tissue and that of "organisatorstoffe" in regeneration.

The problems had to be attacked by a much varied set of cuts and transplantations, which may perhaps at first seem not to have much in common.

To understand fully the bearing of the experiments it is perhaps necessary to recall the phenomenon called by CHILD the head-frequency of planarians: when a planarian has had its head with a shorter or longer part of the body cut away transversely then it may regenerate a head from the wounded surface. The ability to do so may be different at various levels of the body, and so a "head frequency curve" may be plotted.

The head-frequency of e. g. Bdellocephala starts with 100 per cent anteriorly, decreasing a little caudad, then suddenly dropping to zero just before the pharynx.

I.

In a previous paper (1939) I have shown that when a transverse cut is made on a planarian, then the regeneration from the wounded surface may be stopped by the grafting upon this surface of a piece of adult tissue with reversed polarity.

This was observed in several cases under different conditions. In one instance, however, there was some doubt: when a head was grafted upon the anterior surface of a transversely cut body-segment of *Planaria lugubris*, but in such a way that the ventral side of the head pointed upward, that is with reversed dorso-ventral axis against the body, then it happened in two

instances out of 15 experiments that the body regenerated a head beneath the grafted head. It was natural to suspect that in that case the cut surface of the grafted head did not completely cover the cut surface of the body, so that this latter had some small free surface, from which the regeneration of a head had started.

In order to test a certain question to be mentioned later it was necessary to clear up this problem.

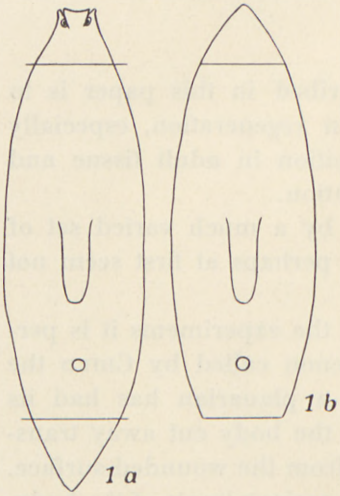


Fig. 1. *Bdellocephala*. *a*, the animal with transverse lines indicating cuts. *b*, tail transplanted to the anterior part of the body from which the head has been removed.

The animal used was *Bdellocephala punctata* (Pall.), the body of which is 2—3 cm in length. The head-frequency curve of this animal is described in my paper from 1939. Partly on account of the peculiar form of this curve and partly also on account of the hardiness of this species, I have made extensive use of this animal which may be taken from late autumn to the spring in quantity and in sufficiently large specimens.

The experiment was done as indicated in fig. 1. The head with some of the forepart was removed by a transverse cut. The tail was likewise removed by a transverse cut and grafted upon the anterior cut surface. Care was taken that the two cuts were as nearly as possible of the same size, so that no considerable part of the wounds remained uncovered when grafting had taken place. The technique employed was that described in my paper from 1939.

After 8 days only 4 specimens were in a proper state, the others were either dead or the tails separated from the main pieces. 38 days later there appeared some unpigmented tissue between tail and main piece in all four specimens, but no trace of head or eyes could be detected. 48 days after the starting of the experiment the situation was the same.

From this experiment it can be concluded that the forepart of Bdellocephala is not able to regenerate a head when the cut surface is completely blocked by adult tissue.

The controls, decapitated animals without grafted tails, regenerated heads 6—8 days after the operation.

After the settling of this question another problem could be attacked. The problem is this: will a head, grafted upon the side of Bdellocephala, reorganize itself and the body unto which it has been grafted, in such a way that it will become the "working" head of the animal?

The question is of considerable interest in so far as it may be able to throw light upon the problem of regulative powers in the adult planarian body.

From the foregoing experiment we know that a tail grafted upon an anterior cut surface inhibits the regeneration of a new head from this surface. Therefore I made the experiment as indicated in fig. 2.

The graftings were all autoplastic. Transverse cuts were made just as in the foregoing experiments, but in addition an oblique cut on the right side of the body was made to receive the head. The cut surfaces were as nearly as possible of the same size.

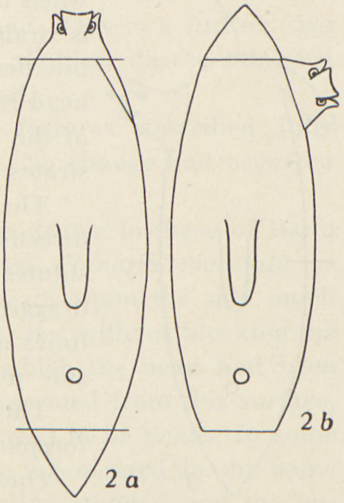


Fig. 2. *Bdellocephala*. *a*, the animal with lines indicating cuts. *b*, grafting of the tail upon the anterior surface, head upon the side surface.

The idea is that the tail blocks the regeneration of a head in the main axis of the body, and so the opportunity should be given to the sideward grafted head to take the leading so to speak and regulate itself and the body into a new functional entity.

The experiment is a rather difficult one, it could be foreseen that only very few specimens would succeed. 40 animals were operated on, but only two survived in the proper state. But some others showed interesting features in the course of the experimental period.

The two complete chimeras (fig. 3) show the same phenomenon. Tail and head have grown smoothly together with the animal; some unpigmented blasteme tissue has appeared between animal-tail and animal-head. It is plain that the head

has not taken up a position as head for the animal. This fact can be seen both from the oblique position which it still holds and from the movements of the chimeras. When the worm itself is lying still, it may be seen that the head tries some forward movements of its own, it stretches forward and becomes alternately long and thin and short and thick. But when the whole chimera moves, then the path is straight forward when the head is inactive, but bending somewhat to the right when the head is also moving forward. The movements of the chimera in this case strikingly demonstrates the parallelogram of forces.

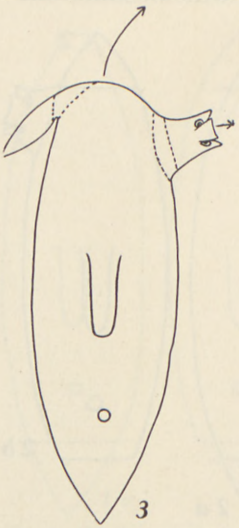


Fig. 3. *Bdellocephala.* The chimera from fig. 2 *b* after 20 days. The short arrow indicates the movement of the head, the longer arrow that of the entire worm. The dotted lines mark the boundary of the unpigmented tissues.

The tail has no active influence upon the direction of the worm's movements; it constitutes only an inconvenient burden to be dragged along. The position of the tail is sometimes along the side, sometimes at the ventral side under the worm.

There is no trace of head or eyes in the forepart of the worm itself.

One of the other chimeras has lost its grafted tail. It has regenerated a head of its own which is well developed in spite of the grafted head. The forward movement of this chimera is not straight but bending in a curve somewhat in the direction of the grafted head. It is an interesting feature that this curve has a bigger radius than that of the just described chimera without its own head. This proves that the moving energy of the chimera with its own regenerated head is stronger than that of the chimera without its own head.

Three chimeras have lost the grafted head but retained the grafted tail. These are therefore in the same state as those issuing from the experiment indicated in fig. 1. Here the movement is straight forward along the main axis of the worm itself.

From these experiments may be deduced 1. that a tail grafted upon an anterior cut surface inhibits the formation of a head and 2. that a head grafted anteriorly upon the side of the worm

remains a foreign element to the worm, and 3. that a grafted head does not inhibit the formation of a new head upon the free anterior cut surface.

Several animals have lost both the grafted tail and the head. They served as controls. They of course regenerated new heads. But it should be noted that these heads are not better developed than the heads regenerated upon the worm which has lost its grafted tail but retained its grafted head. This is a further sign that the grafted head has not in the slightest degree inhibited the regeneration of a new proper head.

All the experiments showed the features described fully developed 20 days after the operation. No change had occurred after 41 days.

These experiments contrast in some degree to those of RAND & BROWN (1926). These authors used *Planaria maculata* as experimental animals. They grafted heads upon the side much as in the above described experiments, but without blocking the anterior surface of the animal from which the head had been cut away. Accordingly new heads regenerated from this surface, but were cut away as soon as they proved to be heads. In some instances new heads were continually regenerated in the same place, but in other cases the regeneration stopped and the implanted head swung into the main axis of the animal and seems to be the working head of the animal. It is not stated whether this phenomenon is an outward, apparent one, or whether it comprises a remoulding of the inner organs. The figures given are not decisive.

II.

A question of some theoretical interest is this: does the head of planarians exercize a reorganizing, morphallactic influence upon already existing structures in the body? To test this question two sets of experiments were made.

The material was again Bdellocephala. The animals were taken ultimo August, so the animals were not fully mature. Bdellocephala usually lays its cocoons in February—April.

In the first set of experiments the following procedure was employed: by transverse cuts a shorter or longer forepart of the body was separated from the rest of the animal. 20 animals

were operated on as indicated in fig. 4 *bI*, 20 as in *bII*, 20 as in *bIII* and 20 as in *bIV*.

It was tried to make exact measurements of the distance between cut and pharynx. This could not be done, however, neither with nor without anesthesia. In the first case the animals

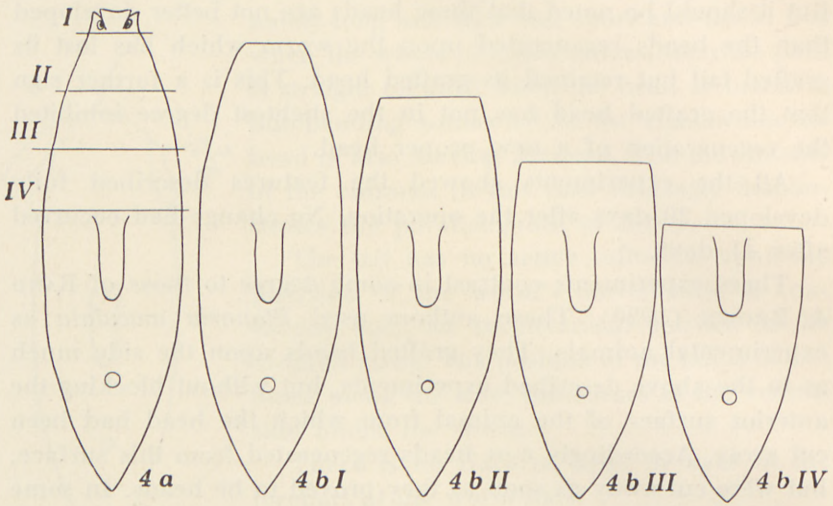


Fig. 4. *Bdellocephala*. *a*, diagram showing the four sets of cuts producing the four groups of experiments shown in *b*.

would contract somewhat irregularly so that the exact place of the cut in relation to the pharynx could not be determined, and in the second case the worms would move in being operated on. The cuts were therefore made by eye measure. The rather large number of experiments, 80 in all, should in some degree serve to eliminate the deviations.

The head-frequency curve of Bdellocephala terminates just before the pharynx. It could therefore be expected that group IV would not regenerate heads, and so was the case.

After 9 days 19 specimens of both group *I* and *II* had regenerated heads but only three of group *III*.

Now it may be asked: 1. does the regenerated head exercise some morphallactic influence upon the rest of the body in so far that this is remoulded in relation to the head, or 2. must the regenerated tissues adapt themselves to the old tissues? If the latter be the case then the distance between the regenerated

head and the borderline of the old tissue, which is easily recognizable by its pigmentation, must be maximal in group *III*, minimal in group *I* when the regeneration processes have been completed.

The experiment proves that the question must be answered as foreseen under 2. 35 days after the beginning of the experiment the regeneration has been brought to a standstill. It is now seen, as shown in fig. 5, that the head in group *I* is separated from the old pigmented tissues by an unpigmented part of about the same length as the head. In group *II* this unpigmented part is about double the length of the head, and in group *III* it is about three times the length of the head. One feature was especially studied: the distance between the pharynx and the head. This distance is of course shortest in group *III* during the first part of the experimental period, but at the end of the experiments the distance has been regulated up, so that it is the same in all groups, comparatively of course, because the absolute distance in group *III* is smaller on account of the smaller size of these animals, which have lost more material by the operation than the other groups, and therefore have to bring up more material from the body to establish regeneration of new tissues.

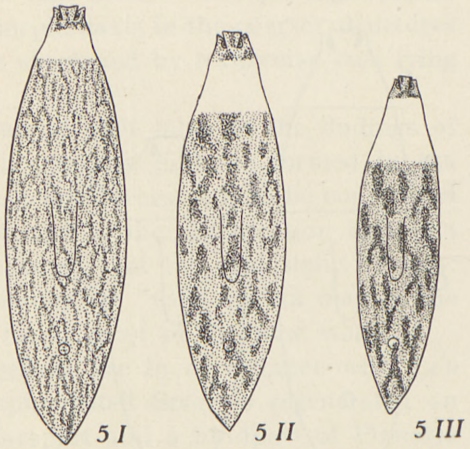


Fig. 5. *Bdellocephala*. Result of the experiment outlined in fig. 4 after 40 days. The unpigmented areas are the regeneration tissues intercalated between the now pigmented heads and the body.

From these experiments may be concluded that the regenerated tissues must adapt themselves to the already existing old tissues so that a harmoniously built animal comes forth not by morphallaxis in the old tissues but by a suitable moulding of the regenerated tissues, the cells of which must of course be derived from the old body. So in Bdellocephala a head in regeneration does not exert a reorganizing influence upon the old parts of the body.

A second set of experiments were made to test the question if an already adult head may possible reorganize the old body.

In order to secure conditions as close as possible to those of the first set of experiments the following procedure was employed.

20 Bdellocephala were cut as indicated in fig. 6*a*. Then the

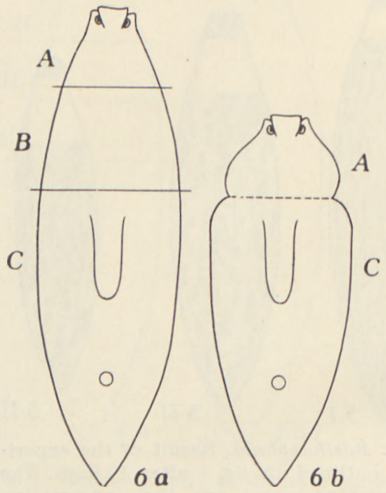


Fig. 6. *Bdellocephala.* In *a* the transverse lines indicate the operation. *A* the head to be grafted. *B* the body-segment to be removed. *C* the body to receive the grafted head. *b* the completed grafting.

Fig. 7. *Bdellocephala.* The result after 44 days of the experiment outlined in fig. 6. Unpigmented regeneration tissue is intercalated between head and body.

head *A* was grafted to the anterior surface of *C* as indicated in fig. 6b. The piece *B* was not used in this experiment. By this procedure the animal was artificially shortened.

We may now ask: 1. will the head reorganize the whole body so that the organs are remoulded in accordance with the now shortened body length, or 2. will regenerated tissue be intercalated between the body and head to restore the normal animal without any remoulding of the coarser structure of the old tissues?

The result of the experiment shows that 2. must be answered in the affirmative. 6 days after the operation 9 successfully carried out chimeras were living. 14 days after only 5, two having been fixed in Zenker's fluid. Of these five one separated

its head. The remaining four showed varied constructions in the now intercalated unpigmented regeneration tissue as shown in fig. 7. 44 days after the four animals were still living and they all show that the head distance had been regulated in accordance with the unmolested animal.

So these experiments show that neither heads in regeneration nor normal heads produce morphallaxis in the coarser structures of the old body when this is shortened by transverse cuts lying before the pharynx.

These results seem to contrast with some of the findings of T. H. Morgan 1898, where a pharynx may be formed in the old tissues, e. g. in regenerating side-pieces. It is to be considered if such morphallaxis is not due to the regeneration blastema penetrating into the old tissues so that the real status is this: most of the cells of the old tissues are "used up" in making the blastema which in its turn forms most of the new worm.

On the other hand my results are in accordance with Li's findings (1928) that new unpigmented tissue is regenerated on the grafting place where a forepart and a hindpart of Planaria lugubris are grafted together after the middle portion with the pharynx had been removed.

III.

A question of considerable theoretical importance is this: if two median halves from two separate animals are grafted together, and then the heads cut away, how will it be with the regeneration from the cut surface? 1. Will each half animal regenerate its own head, or 2. will both together form one single common head?

If the first should prove to be the case then it would be as if each of the two animals said to its own blastema: make a head for me. And so it is, when only half an animal regenerates singlehanded. Therefore one should expect to see two heads regenerated from the chimera.

It is of course known that when half an animal regenerates, then a new complete head will be formed. It is now also known from the foregoing experiments that a transplanted head or tail or whatsoever other part of the body will behave as a foreign

part of the animal upon which the graft is implanted. It is therefore understandable if ones first thought is that the suggested experiment should result in two heads being regenerated, one for each half animal.

The experiment was carried out in two ways. In each set of experiments light and dark coloured animals were used, so that

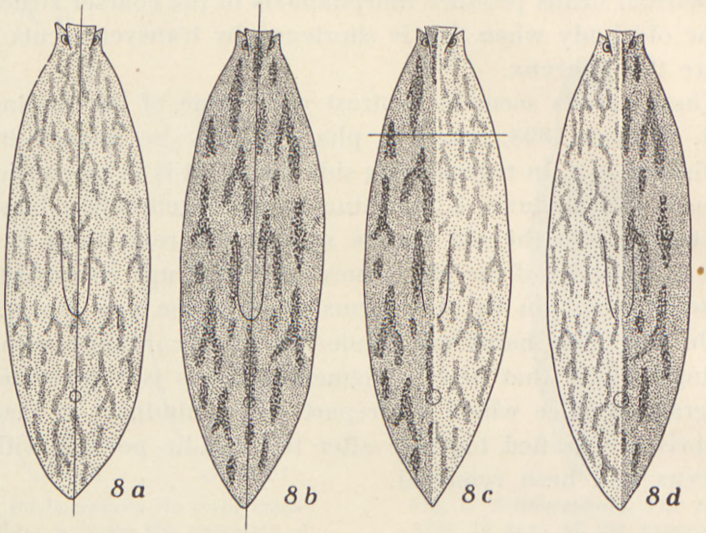


Fig. 8. *Bdellocephala*. A light coloured animal, *a*, and a dark coloured, *b*, cut in longitudinal halves as indicated by the lines. *c* and *d* after the completed grafting.

when grafted together the two halves could at every stage be distinguished from one another. In the first set of experiments 10 worms, 5 dark and 5 light ones, were cut in two by a longitudinal median cut. The light halves were grafted together with dark ones, fig. 8.

The experiment is exceedingly difficult, because the animals, although in deep narcosis, are bending semilunarly or circularly towards the wounded side. Several readjustments during the next 36 hours were needed. Only two well-shaped chimeras survived.

The next step in the operation is to cut away the heads by a transverse cut.

Ten days after the chimeras have regenerated a single head, fig. 9.

The other set of experiments were made in this way: 10

animals, 5 light- and 5 dark-coloured, were operated upon and grafted together as shown in fig. 10*a*. Here also the mortality was considerable, so that only two chimeras survived.

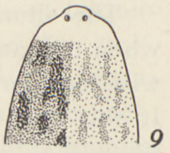


Fig. 9. *Bdellocephala.* The chimera 8c has had its heads cut away by a transverse cut. From the surface a common head is regenerated.

After secure coalescence had taken place the animals were operated on as shown in fig. 10*a*.

This experiment was made in order to see if the amount of tissue, which is very different in the dark and light part of the chimera, should make any difference in the result. Fig. 10*b* shows that the result was the same as in the foregoing experiment: one single common head was regenerated covering the cut surface without the slightest tendency for assymmetry towards the bigger part of the chimera.

These results are rather startling. They prove that both parts of the chimera take part in the formation of the single common head. They further prove that the two parts, the dark and the light coloured animal, are not able to direct their regeneration blastema as after their own ways. They show that such coworking blastemas have had the order from each worm: form a head. But they disobey an order formulated thus: form a head for me alone. It seems that the blastemas have the general order to form head, but they now, in fusing, collaborate and form one head.

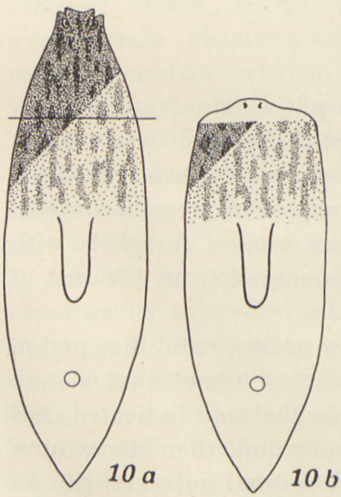


Fig. 10. *Bdellocephala.* A chimera was produced as indicated in *a*. The transverse line indicates the cut made. *b*, a common median and symmetrical head is regenerated.

What is going on? I think the most likely answer is this: the cells in the blastema are so to speak embryonic in their behaviour, they are loosened from the rigid order of the adult body, they have lost their original individuality although they have been born from two separate animals. They have been stamped only to form a head, and they do it regardless of the two separate sources from which they come.

The situation is, it seems, the same, mutatis mutandis, as when two amphibian eggs in the two-cell stage are placed crosswise together, so that the grey crescent regions touch one another. In this case the two embryonic groups collaborate and form one single giant embryo (MANGOLD and SEIDEL 1927).

I therefore think that these experiments are very strongly in favor of the view that the regeneration blastema is of embryonic character.

A further significant parallel may be drawn between this behaviour of the blastema and that of the developing egg. We know from the works of several investigators that each of the two first blastomeres of the amphibian egg has the power to develop into a whole animal, when separated, provided that the first cleavage furrow coincides tolerably with the future median plane of the animal. When these two cells collaborate in the normal egg to form only one animal, it must depend upon the ability of each blastomere to inhibit the total development of the other. So also in the blastemas of the just described chimeras. Each of them may, when separated, form a head, but brought together, they inhibit the tendency for totality in each other.

IV.

A well known feature in regeneration-phenomena in planarians is the fact that by splitting the foreend of the animal by a median cut the two halves may regenerate a new complete head provided that the split parts are prevented from growing together again. LUS (1924) has succeeded in producing several foreparts with heads stretching forward much as a boucquet from the rest of the body.

We here have to grapple with that most vague and dim notion in regeneration called inhibition. The fact about that notion remains that when the animal is split in the way indicated, but the two halves not prevented from coalescing, then the wound is simply closed and heals up, and the animal goes on with its ordinary single head. But when the two parts regenerate separately two normal heads are formed. This proves that every half and fourth and so on has the power to build head. Why do they not do so when separated by a cut but again allowed to coalesce?

We here use the word inhibition, we say that each half inhibits the other from exercising its power to make a head for itself. This phenomenon has of course the same underlying cause as when the two first blastomeres only form half an embryo each, when they are working together, although each of them has the power to form a whole embryo.

In both cases, that of the egg and that of the planarian, it is obvious that contact between the cells releases the mechanism of inhibition, whereas when they are separated in space this mechanism cannot unfold itself. It is therefore probable that the mechanism must work by contact from cell to cell and not by substances liberated and circulating in the body.

Meanwhile several facts both in embryonic development and in regeneration suggest that somehow inhibitory forces reveal themselves over certain distances without immediate contact between the areas which seem to inhibit one another.

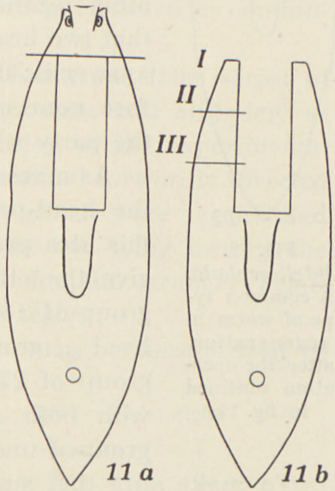


Fig. 11. *Bdellocephala.* After the operation indicated in *a*, *b* was produced. 3 groups were cut as indicated by the roman figures.

In planarians for instance Rand & Ellis (1926) in a very suggestive study claim that the length relation of the two parts originated by splitting the animal decides whether the shorter part is able to regenerate a head or not.

In order to penetrate a little into this mystery some series of experiments were devised. The idea in the first series was this (fig. 11): Bdellocephala was operated on so that first the head was cut away and thereafter a median section of the body reaching nearly to the pharynx. So we get decapitated animals with two "arms". Bdellocephala is known not to regenerate head from a body-level just before the pharynx, the two "arms" may therefore be regarded as independent head-forming areas.

If hypothetical inhibiting substances should exist circulating independent of cells throughout the body, then it should be expected that substances from one arm should inhibit regener-

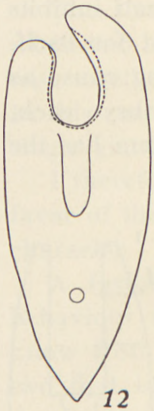


Fig. 12. *Bdellocephala.* A common type of worm in regeneration after the operation outlined in fig. 11.

ation processes of the same sort in the other. So far, we have the same situation as in the before mentioned splitting experiment where two heads were formed.

If we uphold the hypothesis of freely circulating inhibitory forces then how can we explain that two heads are regenerated? I think the proper answer is: the two halves are equally strong, therefore none can conquer the other, and therefore the party will be even, both will regenerate heads.

As a result of this conception and the fact that the head-producing capacity is greatest anteriorly this idea presents itself: by shortening one arm to give the other some predominance. Therefore a group of 18 animals had their left arm shortened by $^1/_3$, group *II* as shown in fig. 11. Another group of 22 had it shortened by $^2/_3$ (*III*). Those with both arms unshortened, 18 animals, were grouped under *I*.

To make sure that such lateral tissue which constitutes the arms is able to regenerate head, devoid as it is of median tissue in which the regeneration of heads normally starts, preliminary experiments were made without shortening the arms. The result showed that both arms were able to regenerate heads. But it is to be emphasized that they do so only after a length of time double that of a normal regeneration from an entire transversely cut surface.

Clear-cut as the idea in the experiment seems to be, it proved to be a complicated thing to carry through the experiment and many unforeseen situations occurred.

In the first place, in most animals the arms would coalesce soon after the operation. Repeated separating was necessary. Then the arms shortened and curved inward in such varied manners that the original scheme of the experiment was obscured. From these now distorted wounds blastemas often issued

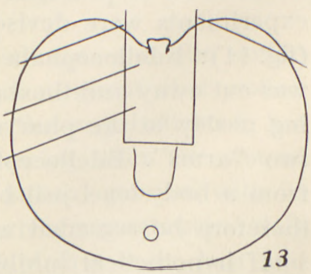


Fig. 13. *Bdellocephala.* Outline of the operations on the animal when in narcosis.

which differed much in size and position. Some of the animals lost their arms by basic constriction or they cytolized.

Notwithstanding these irregularities the main part of the experiments throw light upon our problem. The most common form of the course of the regeneration is that of fig. 12. It is here seen that the terminal wound is brought inward in continuation of the median wound.

In order to secure more terminal blastemas later series of experiments were made, where the cuts were laid obliquely as shown in fig. 13. In spite of this variation of the experimental procedure it was rather rare to see a terminal forwardly directed blastema. Therefore most of the heads which were regenerated had one eye made first, and always the eye lying nearest the front of the arm: a striking evidence for the stronger head-forming capacity of the anterior body region.

The result of the useful experiments may be summarized in this way:

		left	right
Group *I*	no head	8	7
	head	7	9
Group *II*	no head	11	5
	head	4	10
Group *III*	no head	14	6
	head	2	10

Before discussing these figures it must be born in mind that the right arms all are of the original length, they have not been shortened. They are therefore a sort of control for the power to regenerate heads at this rather anterior level of the body. After the previously found head-frequency curve of Bdellocephala the head-formation should in this place be somewhere in the neighbourhood of 95 %. But here only 62 % are arrived at. I think that this result must be taken as a token of a feature which I have elsewhere (Brøndsted 1942) given account of: the eye-building force is at a maximum in the field, wherein the eyes themselves are lying in the animal and from here tapering towards all sides. It is therefore safe, I think, to conclude that the

sides of the body in each transverse level have smaller eye-building capacity than the middle part in which the normal eyes are placed closely together.

But now as to our main problem: does the regeneration of eyes (heads) in the right arms inhibit the formation of eyes in the other arm, where on account of the forces underlying the head-frequency curve the eyes will normally be formed later?

A glance at the summary of the experimental results proves that this is not the case. Eyes are built also on the very short arms in group *III*. It may be asked if the two cases are samples in which no eyes have been formed in the right arm. But this is not so. In both cases beautiful heads have already been regenerated in the right arm.

If we now take the percentage of eye-formation in group *II* left arm, we find 27 %. Put into relation to the head-frequency curve there should have been something like 80 %. In group *III* left arm we find 13 % corresponding to about 50 % in the normal head-frequency curve at the corresponding level of the body.

The figures are admittedly too small to form any basis for elucidating the real power of forming heads in the sides of the body at this level. But a control experiment on 5 animals which had both right and left arm cut down to this level gave the result that no eyes were formed. Here no inhibition can be at work. I therefore think it safe to conclude that the lower figures of regenerated heads in group *II* and *III* are not due to any inhibiting force from the right arms but to a low ability in these parts of the body to regenerate heads at all.

Some of the unsuccessful experiments proved a very interesting fact: the shorter and longer arm of some of the operated animals succeeded in coalescing during the later part of the experimental period, and I let them have their way. Here the blastema of the shorter arm was built into the blastema of the longer, and a fine median head was the result of the cooperation. I think that we here once more have evidence of the strong regulating power and embryonic character of the blastema contrasting to the more rigid frame of the adult tissues. And here, in the blastema, it is therefore manifest that inhibitory processes are and must be at work.

Quite another question is this: when more points of the worm

are damaged it is of course plain that the regenerative power of the entire worm is more stressed than when only one point is damaged. It therefore seems natural that the regeneration will proceed somewhat slower in a worm which has been severely operated on (as those described in these experiments) than in a worm which has not lost so much material, and which has not so big a wounded surface. This latter circumstance I lay some stress upon, and the fact has been dealt with in another paper (1942). The regeneration of any part of the body will to some extent retard the regeneration of any other body part. But this coarser physiological problem has of course nothing to do with the more subtile one here dealt with: a supposed inhibitance of the regeneration of structures of the same kind because they are of the same kind.

V.

The problem of the existence of inhibition in regeneration in planarians working through the adult tissues I have approached in quite another set of experiments, which were planned also to give answer to another question of some importance.

As far as I know all regeneration-experiments on planarians have dealt with wounds made so that a free outwardly directed surface of the body has been exposed, apart from such grafting experiments as those e. g. by SANTOS (1929) where holes were made to receive grafts.

I now put the question: if we take out some tissue in the centre of the body, if we so to speak make a window in the body, will the wound then be closed by a blastema regenerating the lost parts, or will, say, a head be regenerated in the window.

The result was rather a startling one: a head was in fact regenerated in several instances.

Big individuals of Bdellocephala were operated on and the experiment was carried out in this way: the animals were anaesthetized in nicotine. When they had duly contracted and were immobile a triangular or quadrangular hole was made with a fine knife given the form of a mortise-chisel. As in all my other experiments of this kind the operation was carried out on wax with sterilised instruments. The procedure is illustrated on fig. 14.

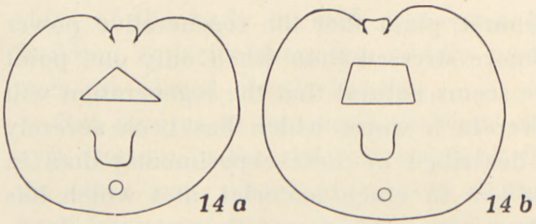


Fig. 14. *Bdellocephala.* Outlines of the anaesthetized animals with *a* triangular and *b* quadrangular window.

The operation was always made so that the caudal border of the window was lying well in the region of the animal which is able to regenerate a head when the animal is cut transversely at this level. The animals were placed in tap-water immediately after the operation.

In the following 3—4 days the wound must be continually cut open again because the animals will contract so that edges of the wound will glue together.

In the course of the experiment most of the animals were damaged in a rather discomforting way: when a Bdellocephala moves forward it will stretch its body, glue to the support with the underside of its head and then drag the body forward. This is sometimes a rather laborious task because the body itself may be pasted to the support by its own jelly. The head of the operated animal is connected with the body only by two comparatively thin bands of tissue on either side of the window, and these bands will therefore very often break, and so the animal is useless for the experiment. In order to avoid this calamity as much as possible there was nothing to be done except to keep the animals as long as possible in complete darkness, where their movements are nearly stopped. But the regular daily examination had to be done in light and then the mishaps took place. Therefore a large number of experiments had to be done in order to secure some results. 104 animals were operated on, but only 19 saw the whole game through, 4 of these had in the course of 22—31 days regenerated heads in the window, fig. 15.

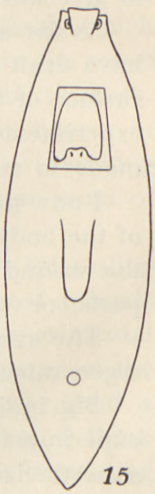


Fig. 15. *Bdellocephala.* Regeneration of a head in the window made as indicated in fig. 14 *b*.

This head is formed by the blastema which had been built from the posterior border of the window. The other borders have their own blastemas without traces of eye-formation.

This experiment, I think, makes it difficult to uphold the rather cherished notion of a "Ganzheitsfaktor" working in the bodies of multicellular animals. It also makes it difficult to uphold the more comprehensible conception of the existence of an inhibiting

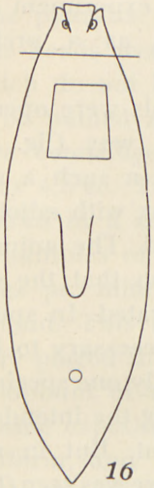


Fig. 16. *Bdellocephala.* Besides the making of a window a transverse cut separated the head from the body.

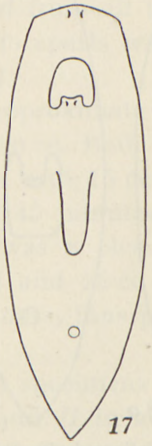


Fig. 17. *Bdellocephala.* Regeneration of a head in the window in spite of the regeneration of a head from the transverse cut anteriorly as indicated in fig. 16.

factor emanating from the already existing head and working freely in the tissues.

Now the possibility remains that a head in process of formation from a more anteriorly laid cut may inhibit the formation of a head in the window. It is possible that inhibiting forces are regenerated in a blastema in which head-formation is going on in the form of substances circulating freely in the body.

To test this possibility several of the animals with windows were cut transversely as indicated in fig. 16. Only a few specimens came through safely, but two of these had formed heads in the window besides a big head regenerated from the anterior cut surface, fig. 17. This experiment also rejects the assumption that inhibiting forces or inhibiting substances generated in a head-forming blastema were able to inhibit the formation of heads elsewhere in the body.

VI.

The experiments just related were made with a new technique which seems to open new possibilities in studying the formbuilding potencies of the planarian tissues.

The following experiment deserves a short account as a preliminary statement.

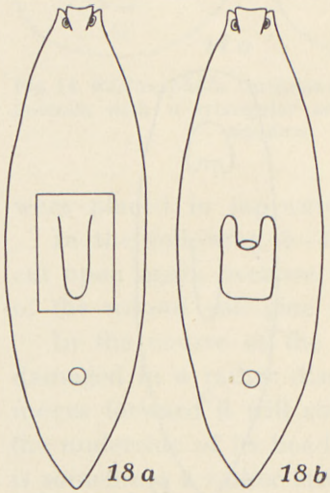


Fig. 18. *Bdellocephala*. *a* the operation: the pharynx with the adjoining tissues is cut away so producing a window. *b* the result: a new pharynx stretching freely into the window is regenerated.

Several animals were operated on in the following way (fig. 18 *a*): a window was cut in such a way that the whole pharynx with adjoining tissues was removed. The animals contracted strongly so that the windows were quite obliterated. In spite of repeated cutting—necessary to hold the window open—only one specimen succeeded in fulfilling the intended scope of the experiment. But in return a very striking feature was seen (fig. 18 *b*): a new pharynx had been regenerated, and this pharynx was nakedly protruding into the empty window. So this experiment gives evidence that an organ may be formed isolated without the co-regeneration of the usual adjoining tissues. This experiment is now to be repeated on a bigger scale and a microscopical investigation made. This is worth while because it seems to point in the direction of a certain and very curious self-differentiation of the planarian pharynx.

VII.

I should like here to take the opportunity to relate a few experiments concerning the question about the possible existence of organizing substances in the planarian body.

It has been stated (Brøndsted 1939) that only the part of Bdellocephala lying anteriorly to the pharynx is able to regenerate a head. Although the experiments in the paper cited and those related in the paper in hand strongly point in the direction,

that the organizing powers are bound up with the living cells, the possibility is still open that organizing substances may exist independently in the body fluids.

To try this possibility the following experiments were made.

190 specimens of Bdellocephala were transversely cut just before the pharynx. All the fore-parts possessing the ability to regenerate heads were treated together apart from all the hind-parts which do not have this ability. The foreparts will hence-forward be named *I* and the hind-parts *II*.

I were centrifuged to determine the approximate volume, which was 4,5 cc. The volume of *II* was 7,0 cc. Both *I* and *II* were ground in a mortar with glasspowder and 15 cc alcohol. The two samples of gruel were centrifuged 45 minutes at 2500 revolutions pr. minute. Over the residue was a clear yellow-reddish fluid. This fluid was 10 cc from *I* and 15 cc from *II*. They were placed in an exsiccator for 24 hours, thus producing a small amount of a yellow-reddish paste.

The same experiment was done with 100 specimens *I* and *II* in chloroform, and with 100 specimens *I* and *II* in acetone.

Now the hind-parts of several Bdellocephala were cut from the bodies just behind the genital pore. Several others were cut between the genital pore and the pharynx. The anterior cut surfaces of some of each series were smeared with paste *I* and some with paste *II* of each of the three solutions. In the same way some were smeared with the residue of *I* and *II* from each series. All the specimens were laid on silk-gauze suspended on Schotté-tables (Brøndsted 1939). Here they remained for 48 hours, then they were placed in water. Several died, but in all others, where regeneration took place, no head-formation occurred.

The only thing these crude experiments tell is that they do not sustain the hypothesis about head-organizing substances circulating freely in the planarian body.

VIII. Conclusions.

From the foregoing and from my papers 1939 and 1942 may be seen that two cardinal problems in regeneration have been the main topic of my investigations: organizing forces and inhibiting forces.

In surveying the vast literature upon Planarian regeneration it is a striking fact that so many contradictory statements have been made. It is not the aim of this paper to reconcile these statements. Many more experiments are needed to do that. But I venture to think that now a certain general scheme in these obscure matters is beginning to reveal itself. The scheme may briefly be formulated thus:

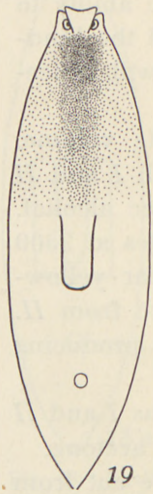


Fig. 19. *Bdellocephala.* The headproducing field. The capacity for regenerating head is strongest where the dots are lying most densely, from here tapering both towards the sides and towards the pharynx.

1. The regeneration (organizing) powers for building up the various organs are unevenly distributed throughout the planarian body. The evidence for this is plainly exhibited in the head-frequency curve. This distribution is fixed for every species.

2. The conception of "fields" so brilliantly set forth by Huxley & de Beer in their book "The Elements of Experimental Embryology", 1934, has a very definite meaning in the planarian body. There exists f. i. a distinct head-forming field of larger or smaller extension in the various species. The field has a center of maximum activity, from here tapering unevenly towards all sides (fig. 19, and Brøndsted 1942).

3. The field is already determined in the embryonic state of the animal: the head-frequency curve of the newly hatched Bdellocephala is the same as that in the adult.

4. The organizing powers of the field is associated with cells lying in the field and therefore manifests itself in the regeneration blastema.

5. The development of the blastema is at the beginning seemingly broadly determined by the body. But looking more closely into the matter it is seen that this "determination" is not to be understood as an undefinable power emanating from the body but as a more definite matter: the cut has set free to work the already determined cells lying in the tissue on the place, where the cut has hit the cells. Here we meet the conception of Goetsch 1932, who claims that there are head- and tailbuilding cells in the planarian body. Here also the idea of Child about a physiological dominant region comes in.

When a cut is made and, say, head forming cells among others are set to work, these cells take the lead and by and by organize the other cells in the blastema. There are potencies for more than one head in the very young blastema (by separating the blastema in two or more distinct areas as in Lus's experiments, many heads may be formed), but in the undivided blastema inhibiting as well as organizing forces are transmitted from cell to cell just as in the young embryo, and so a harmonious result of the regeneration processes is arrived at. That this is so depends on one thing, namely that a formbuilding gradient is set up at once after the wound is made. Let us consider Bdellocephala. The head-building potencies, the head-building field as we may call it, has a form and an extension probably as that depicted in fig. 19. Cells responding to a call for regeneration of a head are lying most densely in the anterior middle portion of the animal, from here tapering towards all sides. It will be hard to make a wound in the forepart of the animal where a gradient for head-building forces will not at once display itself. As soon as the gradient goes to work, the result must be harmonious. If the gradient is not set up at once two or more head-building centres may start simultaneously and as many heads or at least rudiments of heads will be formed.

I think that this working hypothesis will solve many of the difficulties associated with regeneration problems in planarians and perhaps elsewhere. But many more experiments are necessary to establish the idea on firm ground.

Summary.

1. The head of Bdellocephala was removed with a transverse cut. A tail was transplanted to the wound. No head is regenerated. Fig. 1.

2. The same experiment was done but besides a cut was made on the side of the body just caudad to the transplanted tail. The removed head was transplanted to this wound. Fig. 2. The head will not develop into the "working" head of the animal. Fig. 3. If the tail is removed a new head will regenerate anteriorly despite of the old head.

3. A large number of Bdellocephala were transversely cut at various distance between head and pharynx. Fig. 4. In all cases new regeneration tissue was intercalated between the new head and the old tissues, so that no morphallaxis took place in this latter. Fig. 5.

4. A section of the forepart of Bdellocephala was cut away by a transverse cut and the head grafted upon the thus shortened body. Fig. 6. New regeneration tissue was intercalated between head and body, so restoring the normal relative length of the animal. Fig. 7.

5. Light and dark coloured animals were divided in halves by longitudinal median cuts. Fig. 8*a*, *b*. A light and a dark half were grafted together so forming a chimera the two halves of which were easily recognizable. Fig. 8*c*, *d*. The heads were removed by a transverse cut. A new head was regenerated, common for both halves. Fig. 9.

6. The same experiment was done so that the amount of tissue of the two partners of the chimera were differing much in volume. Fig. 10*a*. The result was however the same: a new median common head was regenerated showing no asymmetry. Fig. 10*b*.

7. The median portion with head of Bdellocephala was removed so that two "arms" remained. Fig. 11. Heads may be regenerated upon both arms regardless of different length of the arms. So no force will travel from one arm to another to inhibit head-building there.

8. A window was made in the fore-part of Bdellocephala. Fig. 14. A head may be regenerated from the caudal border of this window as well in the presence of the old head, fig. 15, as during regeneration of a new head instead of the old one removed. Fig. 17.

9. A preliminary statement of another experiment with this new technique is given: the pharynx with surrounding tissues is removed leaving a window open. Fig. 18*a*. Into this window a pharynx without surrounding tissues is regenerating. Fig. 18*b*.

10. Extracts from foreparts of Bdellocephala (which alone are able to regenerate heads) in chloroform, alcohol and acetone are not able to induce head-regeneration in hind-parts of the worm, neither are the residues.

11. From all the experiments the conclusion is drawn that during regeneration organizing power is transmitted from cell to cell and is not due to freely circulating "organisatorstoffe". So also with the conception of inhibiting forces or substances during formbuilding processes. The experiments sustain the hypothesis that inhibiting forces are also transmitted from cell to cell in the regeneration blastema.

12. A preliminary working hypothesis for a comprehensive understanding of regeneration—especially in planarians—is set forth.

Laboratory for experimental morphology and cytology. Birkerød. Denmark.

Literature cited.

BRØNDSTED, H. V.: Regeneration in Planarians investigated with a new Transplantation Technique. D. Kgl. Danske Vidensk. Selskab, Biol. Medd. XV, 1. 1939.

— A study in quantitative Regeneration: the Regeneration of Eyes in Polycelis nigra. Vid. Medd. D. Naturh. Foren. 1942.

GOETSCH, W.: Die Regeneration der Landplanarien und die Theorie der "Relativen Determination". Die Naturwiss. 20. 1932.

LI, Y.: Regulative Erscheinungen bei der Planarienregeneration unter anomalen Bedingungen. Arch. Entw. mech. 114. 1928.

LUS, J.: Studies on Regeneration and Transplantation in Turbellaria. Bull. Soc. Nat. Moskau. Sect. Biol. Exper. 1. 1924.

MANGOLD & SEIDEL: Arch. Entw. mech. 111. 1927.

MORGAN, T. H.: Experimental Studies of the Regeneration of Planaria maculata. Arch. Entw. mech. 7. 1898.

RAND & BROWNE: Inhibition of Regeneration in Planarians by Grafting: Technique of Grafting. Proc. Nat. Acad. Sc. 12. 1926.

RAND & ELLIS: Inhibition of Regeneration in two-headed or two-tailed Planarians. Proc. Nat. Acad. Sc. 12. 1926.

SANTOS, F. W.: Studies on Transplantation in Planaria. Biol. Bull. 57. 1929.

Indleveret til Selskabet den 6. Maj 1942.
Færdig fra Trykkeriet den 27. August 1942.

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 8

WIRKUNG DER RÖNTGENSTRAHLEN AUF DEN UMSATZ DER NUKLEINSÄURE IM JENSEN-SARKOM

VON

H. v. EULER UND G. v. HEVESY

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1942

Printed in Denmark.
Bianco Lunos Bogtrykkeri A/S

Der Nachweis der Wirkung der Röntgenstrahlen auf Sarkome wird in der Regel auf folgende Weise erbracht: Bruchstücke der bestrahlten Sarkome werden durch Impfung auf normale Tiere übertragen und es wird untersucht, ob die Sarkome nach Verlauf von einigen Tagen angehen oder nicht. Wir waren bestrebt, dieses Verfahren durch einen chemischen Nachweis zu ersetzen. Nun sprechen zahlreiche Erfahrungen dafür, dass Dosen, welche den Sarkomen gegenüber wirksam sind, die in den Gewebezellen vor sich gehenden Stoffwechselvorgänge nicht wesentlich beeinflussen und es die im Zellkern verlaufenden Vorgänge sind, welche in erster Linie der Einwirkung der Strahlen unterliegen. Bei der Suche nach einem chemischen Nachweis der Wirkung der Röntgenstrahlen auf das Sarkom lag es deshalb nahe, die im Zellkern sich abspielenden Prozesse eingehender zu betrachten. Unter den Bestandteilen des Zellkerns gehören die Nukleinsäuren zu den wichtigsten.

Der Nukleinsäure fällt eine wesentliche Rolle bei der Zellteilung zu. So zeigte z. B. KOSSEL, dass die im Laufe der Spermiogenese auftretenden Veränderungen in einem Ab- und Umbau der Eiweisstoffe sowie in der Synthese des verhältnismässig sehr eiweissarmen Histon- oder Protaminnukleats bestehen, und CASPERSSONS[1] Untersuchungen der Absorption der ultravioletten Strahlen durch die Bestandteile der ruhenden sowie der sich teilenden Zellkerne haben es sehr wahrscheinlich gemacht, dass das KOSSELsche Eiweissumbauschema auch für die gewöhnliche mitotische Zellteilung gilt.

Die mitotische Zellteilung wird durch verhältnismässig kleine Dosen von Röntgenstrahlen gehemmt, und man sollte auf Grund der obigen Betrachtungen erwarten, dass die Bestrahlung des Gewebes mit Röntgenstrahlen eine Verminderung des Nuklein-

[1] T. CASPERSSON, Chromosoma 1, 562, 1940.

säureumsatzes im Zellkern bewirkt. Diese Überlegung hat uns dazu veranlasst, die Bildung von Nukleinsäure[1] im Jensen-Sarkom der Ratte vor und nach der Bestrahlung mit Röntgenstrahlen zu untersuchen.

Die Untersuchung wurde unter Anwendung der Methode der radioaktiven Indikatoren ausgeführt. Diese Methode ermöglicht die Unterscheidung von Nukleinsäuremolekülen, die vor bzw. nach Beginn des Versuches gebildet worden sind. Die letzteren, die in einem aktiven Milieu, nämlich in aktives Phosphat enthaltenden Zellen entstanden sind, werden aktiv sein (d. h. radioaktiven Phosphor enthalten) im Gegensatz zu den bereits vor Beginn des Versuches vorhandenen inaktiven Molekülen.

Beschreibung der Methode.

Führt man dem Versuchstier, z. B. durch subkutane Injektion, eine ganz geringe Menge Natriumphosphats zu, das durch Beimischung von radioaktivem Phosphor ($^{32}_{15}P$) gekennzeichnet ist, so treten die gekennzeichneten Phosphationen bald in die Sarkomzellen ein und nehmen an den in den Zellen vor sich gehenden Aufbauprozessen mit derselben Wahrscheinlichkeit teil wie die übrigen in den Sarkomzellen vorhandenen Phosphationen. Werden in der Sarkomzelle Nukleinsäuremoleküle aufgebaut, so werden sie radioaktiv gekennzeichnet sein. Wenn alle am Ende des Versuches im Sarkom vorhandenen Nukleinsäuremoleküle im Laufe des Versuches gebildet worden sind, so wird 1 mg Nukleinsäure-P denselben Gehalt an ^{32}P, dieselbe Radioaktivität, aufweisen wie 1 mg Phosphat-P. Zeigt dagegen nach Abschluss des Versuches 1 mg Nukleinsäure-P eine Aktivität, die z. B. nur 1 % der Aktivität von 1 mg Phosphat-P ausmacht, so beträgt die während des Versuches gebildete Nukleinsäuremenge 1% der gesamten, im Sarkom vorhandenen Nukleinsäuremenge. Dabei wird vorausgesetzt, dass die nach Beendigung des Versuches gemessene Aktivität von 1 mg Phosphat gleich der zu jedem anderen Zeitpunkt im Laufe des Versuches vorhandenen Aktivität ist (vgl. hierzu die Ausführungen auf S. 7).

[1] Die im Tumor vorhandene Nukleinsäure ist nach Vowles (Sv. Vet. Akad. Arkiv f. Kemi 14 B, Nr 10, 1940) identisch mit der Thymusnukleinsäure.

Darstellung und Messung der Aktivität des radioaktiven Phosphors.

Der in den im folgenden zu beschreibenden Versuchen angewandte radioaktive Phosphor war in den meisten Fällen durch die Einwirkung von Neutronen auf Schwefelkohlenstoff gewonnen worden[1]. Als Neutronenquelle diente eine Radium-Beryllium-Mischung, die 600 mg Radium-Element enthielt. Für die Überlassung dieser Quelle sowie vieler anderer Hilfsmittel sind wir Herrn Professor Niels Bohr zu grösstem Dank verpflichtet. Ausserdem stand uns radioaktiver Phosphor zur Verfügung, der gleichfalls durch die Einwirkung schneller Neutronen auf Schwefelkohlenstoff gewonnen wurde, wobei jedoch die Neutronen mit Hilfe einer Hochspannungsanlage erzeugt worden sind, und zwar in den meisten Fällen im Institut für theoretische Physik der Universität Kopenhagen, in einzelnen Fällen dagegen im Forschungslaboratorium der Glühlampenfabrik Philips in Eindhoven. Wir sind Herrn Dr. O. Bøggild bzw. den Herren Dr. Heyn und Dr. A. H. W. Aten für die Herstellung dieser Präparate zu besonderem Dank verpflichtet.

Die mit Hilfe der Radiumquellen erzeugten Präparate enthielten keine chemisch nachweisbaren Phosphormengen. Sie wurden durch Schütteln der verwendeten 10 l Schwefelkohlenstoff mit verdünnter Salpetersäure gewonnen. Nach dem Eindampfen der salpetersauren Lösung blieb das aktive Phosphat im Rückstand zurück; es wurde mit Wasser aufgenommen, und die Lösung wurde durch einen Glasfilter filtriert. Dieser Prozess wurde einigemal wiederholt. Zuletzt wurde die Aktivität in physiologischer Kochsalzlösung gelöst und danach den Versuchstieren injiziert. Jeder Ratte wurde 0.1—1 ccm injiziert. Die Aktivität der injizierten Lösung betrug etwa $^1/_{10}$ μCurie.

Messung der Radioaktivität des Nukleinsäure-Phosphors.

2 Stunden nach Injektion wurde die Ratte getötet und die Nukleinsäure des Sarkoms isoliert. Dabei kam die Isolierungsmethode von Klein und Beck[2] zur Anwendung. Im Laufe des

[1] O. Chievitz und G. Hevesy, D. Kgl. Danske Vidensk. Selskab, Biol. Medd. XIII, 9, 1937.

[2] O. Klein und Beck, Z. f. Krebsforschung 42, 172, 1935.

Versuches bilden sich in den Sarkomen neben schwach aktiver Nukleinsäure sehr stark aktive, säurelösliche Verbindungen sowie stark aktive Phosphatide; eine Verunreinigung der Nukleinsäure mit den geringsten Mengen säurelöslichen Phosphors oder mit Phosphatidphosphor kann daher die Resultate der Messung der Aktivität der Nukleinsäure störend beeinflussen. Die Nukleinsäurepräparate wurden aus diesem Grund noch weitergehend gereinigt als dies in der oben genannten Untersuchung von KLEIN und BECK beschrieben wird (siehe S. 9). Die gereinigte Nukleinsäure wurde nass mit Schwefelsäure und 30 %igem H_2O_2 verascht. $^1/_5$ der gewonnenen Lösung wurde zur kolorimetrischen Phosphorbestimmung verwendet; $^4/_5$ der Lösung wurden 80 mg Natriumphosphat zugesetzt und der Phosphorgehalt als Ammoniummagnesiumphosphat isoliert. Dadurch wurde erreicht, dass der aktive Phosphorgehalt der Probe mit etwa 70 mg inaktivem Ammoniummagnesiumphosphat vermengt vorlag. Alle unsere Präparate wurden in dieser Weise behandelt, und es gelang uns dadurch, bei der Aktivitätsbestimmung stets Präparate von nahezu gleichem Gewicht und gleichem Volumen zu vergleichen. Es erübrigt sich dadurch eine etwaige Korrektion für die verschiedene Absorption der β-Strahlen in den zu vergleichenden Präparaten.

Die Aktivität des Ammoniummagnesiumphosphats oder eines bekannten Bruchteils der Probe wurde mit dem GEIGER-MÜLLER Zählrohr gemessen. Aus der gemessenen Aktivität, dem Gewicht der Ammoniummagnesiumphosphatprobe und dem auf chemischem Wege bestimmten Phosphorgehalt der Nukleinsäure berechneten wir die Aktivität von 1 mg P wie aus folgendem Beispiel hervorgeht:

$$\text{Aktivität von 1 mg Nukleinsäure-P} = \frac{8.60}{2.44}\,\frac{80}{71}\,\frac{5}{4} = 4.98$$ Zählrohrstösse per Minute. 8.60 bedeutet hier die Aktivität des den Nukleinsäure-P enthaltenden Ammoniummagnesiumphosphats, 2.44 den P-Gehalt der gesamten Nukleinsäure des Sarkoms in mg; 80 ist das Gewicht der gesamten gefällten Ammoniummagnesiumphosphatprobe in mg, und 71 das Gewicht der unter dem Zählrohr angebrachten Probe. $\frac{5}{4}$ ist die Korrektion, die vorzunehmen ist, da wir nur $\frac{4}{5}$ der durch die Veraschung der Nuklein-

säure erhaltenen Lösung zur radioaktiven Untersuchung verwendet haben.

Hiernach haben wir die Radioaktivität von 1 mg Nukleinsäure-P mit der Radioaktivität von 1 mg freiem Phosphat-P des Sarkoms zu vergleichen. Die auf S. 4 erwähnte Voraussetzung — dass der aus dem Sarkom isolierte Phosphat-P dieselbe Aktivität hat, die wir zu einem beliebigen Zeitpunkt während des Versuches gefunden hätten — ist jedoch nicht gegeben. Die Absorption des injizierten Phosphats beansprucht mehrere Minuten und — obgleich die Membran der Sarkomzellen, wie an anderer Stelle besprochen[1], für den Durchtritt des Phosphats sehr permeabel ist — nimmt das Eindringen des Phosphats aus dem Plasma (bzw. der extrazellularen Flüssigkeit) in die Sarkomzellen gleichfalls Zeit in Anspruch. Ferner ändert sich die Aktivität des Plasma-Phosphats während des Versuches. Sie steigt zunächst und sinkt dann infolge des Einströmens des gekennzeichneten Phosphats in die Organzellen und dgl. wieder ab. Korrekterweise müssten wir daher die Aktivität von 1 mg Sarkom-Phosphat zu verschiedenen Zeitpunkten messen und auf diese Weise den Mittelwert der Phosphataktivität während des Versuches berechnen. Diese mittlere Aktivität von 1 mg Phosphat sollte dann mit der Aktivität von 1 mg Nukleinsäure-P, die nach Beendigung des Versuches gefunden wurde, verglichen werden. Wir sind jedoch nicht sosehr an den genauen Werten des Nukleinsäureumsatzes der Nukleinsäure im Sarkom interessiert wie an der Wirkung der Röntgenstrahlen auf den Nukleinsäureumsatz. Wir haben deshalb das obige, etwas langwierige Verfahren durch das folgende ersetzt.

Wir verglichen die Aktivität von 1 mg Nukleinsäure-P mit der Aktivität von 1 mg freiem Plasma-P, die am Ende des Versuches festgestellt wurde. Die Aktivität des Plasma-P steigt zunächst während des Versuches und sinkt später wieder ab; der 2 Stunden nach erfolgter Injektion gemessene Wert der Aktivität ist nicht sehr verschieden von dem Mittelwert der Aktivität, der im Laufe des Versuches vorlag. Wir haben ferner einen Vergleich der Aktivität von 1 mg Nukleinsäure des Sarkoms mit der Aktivität von 1 mg freiem P der Leber vorgenommen, wodurch wir in den Besitz

[1] G. v. Hevesy und H. v. Euler, Sv. Vet. Akad. Arkiv f. Kemi 15 A, Nr 15, 1940.

einer zweiten Vergleichsskala gelangten. In unseren späteren Versuchen haben wir auch einen Vergleich der Aktivität des Nukleinsäure-P mit der Aktivität des freien P des Sarkoms vorgenommen. Bei letzterem Verfahren muss ein Bruchteil des Sarkoms zur Isolierung des freien Phosphats geopfert werden; trotzdem ist dieses Verfahren dem zuerst geschilderten und von uns auch zuerst angewandten Verfahren entschieden vorzuziehen (vgl. S. 19).

Plasma- bzw. Leberproben wurden mit 10 bzw. 25 %iger Trichloressigsäure behandelt; zu $^4/_5$ der Lösung wurden 80 mg Natriumphosphat zugesetzt, das freie Phosphat der Lösung wurde als Ammoniummagnesiumphosphat gefällt und die Radioaktivität der Probe, wie oben geschildert, unter dem GEIGER-MÜLLER Zählrohr gemessen. $^1/_5$ der Lösung wurde zur kolorimetrischen Bestimmung des freien P verwendet. Die Ammoniummagnesiumproben wurden vor der Messung ihrer Aktivität in Aluminiumschälchen von 1.2 cm Durchmesser und 2 mm Höhe angebracht; die Schälchen wurden unter das Fenster des Zählrohrs geschoben[1]. Während die zu messenden Leberfraktionen über 1000 Stösse per Minute im Zählrohr auslösten, betrug die Aktivität der Sarkom-Nukleinsäure meist nur einige Stösse per Minute; in einzelnen Fällen mussten wir sogar Aktivitäten messen, die nur wenige Zehntel Stösse per Minute betrugen. Solche Messungen wurden in der Weise durchgeführt, dass wir abwechselnd 24 Stunden lang die Aktivität des Präparates und 24 Stunden lang die Aktivität von inaktivem Ammoniummagnesiumphosphat gemessen haben. Die letztere, die sogenannte »natürliche Stosszahl«, betrug etwa 4 per Minute und konnte oft mit einer Genauigkeit von 2 % reproduziert werden. Um eine solche Genauigkeit zu erreichen sind etwa 1° übersteigende Temperaturschwankungen der Zählanordnung zu vermeiden.

Ermittlung des Prozentsatzes des injizierten ^{32}P, der in der Nukleinsäure des Sarkoms vorgefunden wird.

Bei der Bestimmung des Prozentsatzes des injizierten, radioaktiv gekennzeichneten Phosphors, der in die Nukleinsäure des

[1] Eine genaue Beschreibung des verwendeten Zählrohrs findet sich bei H. LEVI, Acta Physiol. Scand. **2**, 311, 1941.

Sarkoms eingebaut wird, verfährt man folgendermassen: Zu einem bekannten, kleinen Bruchteil, z. B. $^1/_{300}$, der zur Injektion verwendeten Lösung werden 80 mg Natriumphosphat zugesetzt; der P-Gehalt der Lösung wird danach als Ammoniummagnesiumphosphat gefällt. Die Aktivität dieser Probe wird mit der Aktivität des aus dem Sarkom isolierten Nukleinsäure-P verglichen, der ebenfalls als Ammoniummagnesiumphosphat des gleichen Gewichtes wie die erstgenannte Probe vorliegt. Ist die Aktivität von $^1/_{300}$ Teil der injizierten Lösung = 100 Stösse per Minute, so wurden der Ratte 30 000 Stösse injiziert. Wird die Aktivität von 1 mg Nukleinsäure-P gleich 10 gefunden, so enthält 1 mg Nukleinsäure-P 0,033 % des injizierten ^{32}P. Durch Division mit dem kolorimetrisch ermittelten Gewicht des Nukleinsäure-P ergeben sich die in den Tabellen 1—6 aufgeführten Zahlen.

Die verwendeten Sarkome.

Zu allen bisher angestellten Versuchen haben wir Jensen-Sarkome der Ratten verwendet, welche durch Transplantation eines von der Abteilung für experimentelle Pathologie der I. G. Farbenindustrie-A. G., Elberfeld, Professor D. Domagk, erhaltenen Sarkoms weiter gezüchtet worden waren.

Die Transplantation erfolgte stets subkutan durch Anbringung eines etwa 1 mm tiefen Gewebeschnitts. Die Sarkome entwickelten sich in unserem Rattenstamm in etwa 3 Wochen bis zur Grösse von etwa 20 g. Zu den Bestrahlungsversuchen wurden meistens Ratten mit einem Sarkomgewicht von etwa 20 bis 30 g verwendet.

Die Isolierung der Nukleinsäure.

Das Sarkomgewebe wurde fein zerschnitten und nach der von Klein und Beck[1] angegebenen Methode auf Nukleinsäure verarbeitet. Die Rohfällung wurde in 1 n Natronlauge gelöst, mit etwa 80 mg sek. Natriumphosphat versetzt und mit 5 %iger Eisenhydroxydlösung gefällt. Um etwa vorhandene radioaktive Phosphate zu entfernen, wurde diese Reinigung der Nukleinsäure noch zweimal wiederholt. Das so erhaltene Produkt wurde dann zweimal mit methylalkoholischer Salzsäure nach Klein

[1] O. Klein und Beck, Z. f. Krebsforschung **42**, 163, 1935.

und Beck umgefällt. Da das säurelösliche Phosphat viel aktiver ist als das Phosphat der Nukleinsäure, ist die weitgehendste Reinigung der Nukleinsäure von fremden Phosphaten von grösster Bedeutung.

In der endgültig gereinigten Fällung wurde das Phosphat kolorimetrisch nach Fiske und Subbarow[1] (Modifikation von Teorell[2]) bestimmt. Ein anderer Teil wurde als Ammoniummagnesiumphosphat gefällt und dann zur Aktivitätsbestimmung verwendet.

Bezüglich der bei diesem Verfahren zur Anwendung gelangten Mengen verweisen wir auf ein als Beispiel mitgeteiltes Protokoll (S. 6) und weiter auf die Tabellen 1—6 (S. 12—16).

Die Blut- und Leberproben wurden folgendermassen aufgearbeitet:

Das Blut, das in einem Gefäss mit einigen mg Na-Citrat aufgefangen worden war, wurde zentrifugiert; das Plasma (in der Regel 2—3 ccm) wurde mit 3 ccm 10 %iger Trichloressigsäure versetzt, die Lösung zentrifugiert und filtriert, und der abzentrifugierte Rückstand noch einmal mit 2 ccm Trichloressigsäure extrahiert und filtriert. Das gesamte Filtrat wurde mit Wasser auf 25 ccm verdünnt; davon wurden 2 ccm zur kolorimetrischen P-Bestimmung nach Fiske-Subbarow-Teorell verwendet. 20 ccm Filtrat wurden mit 80 mg sek. Natriumphosphat versetzt, und das gesamte Phosphat wurde als Magnesiumammoniumphosphat gefällt. Diese Fällung wurde nach dem Trocknen bei 110° für die Aktivitätsbestimmung verwendet.

Die Leber (in der Regel 5—8 g) wurde zunächst 15 Min. mit 20 ccm 25 %iger Trichloressigsäure und dann nochmals 10 Min. lang verrieben. Der Trichloressigsäureextrakt wurde filtriert und das Filtrat mit Wasser auf 100 ccm verdünnt. In 1 ccm wurde P kolorimetrisch bestimmt. 80 ccm der Lösung wurden nach Zusatz von 80 mg Natriumphosphat zur Fällung des für die Aktivitätsbestimmung erforderlichen Magnesiumammoniumphosphat verwendet.

Sämtliche chemisch-analytischen Arbeiten sind von Dr. phil. L. Ahlström und Assistent Ing. B. Högberg ausgeführt worden, denen wir auch an dieser Stelle für ihre Mitarbeit bestens danken.

[1] Fiske und Subbarow J. Biol. Chem. **66**, 375, 1925.
[2] Teorell, Biochem. Z. **230**, 1, 1931.

Die Bestrahlung des Sarkoms.

Die Sarkome wurden 26 bis 67 Minuten lang mit Röntgenstrahlen bestrahlt, die eine mit 165 KV und 7 mA betriebene Röhre aussandte. Als Strahlungsfilter kamen eine Kupferfolie von 0.5 mm und eine Aluminiumfolie von 1 mm in Anwendung. Die Bestrahlung erfolgte aus einer Entfernung von 25—42 cm. Bestrahlt wurde allein das Sarkom; die übrigen Körperteile der Ratte wurden gegen die Einwirkung der Bestrahlung durch Bedecken mit Bleiplatten geschützt. 20 Minuten nach Beendigung der Bestrahlung erfolgte die Injektion der NaCl-Lösung, die radioaktiv gekennzeichnetes Natriumphosphat enthielt.

Die Ausführung von so kurzdauernden Versuchen hat u. a. den Vorteil, dass die Wirkung der Röntgenstrahlen kurz nach Beendigung der Bestrahlung untersucht werden kann. Im Laufe der Zeit gehen bekanntlich weitgehende Veränderungen im bestrahlten Gewebe vor sich, und die Wirkung dieser Veränderungen auf den Nukleinsäureumsatz lässt sich auf die Weise studieren, dass man die Injektion der radioaktiven Lösung nicht sofort nach Unterbrechung der Bestrahlung, sondern einen oder mehrere Tage später vornimmt. Über das Ergebnis solcher Versuche soll demnächst berichtet werden.

Die Bestrahlungen wurden im Radiopathologischen Institut des Karolinischen Krankenhauses, Stockholm, ausgeführt. Den Herren Prof. Dr. Elis Berven und Prof. Dr. Olle Reuterwall, welche uns die Bestrahlungseinrichtungen freundlichst zur Verfügung stellten, sind wir zu besonderem Dank verpflichtet. Auch Herrn Laborator A. Forsberg und Frau Björkgren möchten wir für ihre freundliche Hilfe bei der Bestrahlung bestens danken.

Messresultate.

Das Ergebnis der ausgeführten Versuche ist aus den Tabellen 1—6 zu ersehen. Tabellen 1—3 enthalten Angaben über den Nukleinsäureumsatz in nicht bestrahlten und schwach bzw. stärker bestrahlten Sarkomen. Tabellen 4—6 enthalten Angaben über den Bruchteil der injizierten ^{32}P-Menge, die in 1 mg freiem Plasma-Phosphat-P bzw. 1 mg freiem Leber-Phosphat-P nach Verlauf von 2 Stunden zu finden ist.

Tabelle 1.

Nukleinsäureumsatz im nicht-bestrahlten Jensen-Sarkom. Versuchsdauer 2 Stunden.

Nr. der Ratte	Gewicht des gereinigten Sarkoms in g	Nukleinsäure-P-Gehalt von 1 g Sarkom in mg	^{32}P-Gehalt von 1 mg Nukleinsäure-P in % des ^{32}P-Gehaltes von		% der injizierten ^{32}P-Menge vorhanden in 1 mg Nukleinsäure-P
			1 mg Leber anorgan. P	1 mg Plasma anorgan. P	
I + II	36.2	3.8	2.60	..	0.013
III + IV	34.5	12.3	2.23	..	0.010
V + VI	19.3	7.5	3.10	..	0.015
VII + VIII	31.9	6.6	1.76	2.98	0.015
IX + X	23.2	8.3	1.30	2.15	0.012
XI + XII	2.9	0.9	1.35	..	0.019
XIII	16.7	1.3	2.33	1.76	0.032
XIV	22.5	6.3	1.14	1.06	0.017
XV	17.9	2.4	1.13	1.21	0.021
XVI	17.7	5.7	1.25	1.52	0.020
Mittelwert	22.3	5.5	**1.82**	**1.78**	**0.017**

Tabelle 2.

Nukleinsäureumsatz im schwach bestrahlten Jensen-Sarkom. Dosis 77 bis 310 r (internat. Röntgen-Einheiten). Versuchsdauer 2 Stunden.

Bezeichnung der Ratte	Dosis in r	Gewicht des gereinigten Sarkoms in g	Nukleinsäure-P-Gehalt des Sarkoms in mg	^{32}P-Gehalt von 1 mg Nukleinsäure-P in % des ^{32}P-Gehaltes von		% der injizierten ^{32}P-Menge vorhanden in 1 mg Nukleinsäure-P
				1 mg Leber anorgan P	1 mg Plasma anorgan. P	
A	77	6.2	10.1	1.74	1.53	0.040
B	77	11.2	16.0	0.26	0.22	0.006
C	77	5.7	11.0	1.33	1.74	0.038
D	155	13.0	6.4	1.39	1.03	0.031
E	155	9.4	13.7	1.80	3.71	0.037
F	155	15.0	35.0	1.92	2.54	0.042
G	310	13.8	1.3	1.20	1.47	0.018
H	92	12.3	2.3	0.95	0.80	0.0139
J	92	10.0	1.0	1.04	1.53	0.0173
K	92	3.1	2.5	1.65	1.51	0.0306
L	186	6.3	5.0	2.14	3.32	0.0381
M	186	6.8	1.2	1.93	3.71	0.0374
N	186	3.8	0.47	0.54	0.50	0.0086
Mittelwert	..	9.0	8.1	**1.38**	**1.82**	**0.028**

Tabelle 3.

Nukleinsäureumsatz im bestrahlten Jensen-Sarkom. Dosis 460 bis 7000 r (internat. Röntgen-Einheiten). Versuchsdauer 2 Stunden.

Nr. der Ratte	Dosis in r	Gewicht des gereinigten Sarkoms in g	Nukleinsäure-P-Gehalt des Sarkoms in mg	^{32}P-Gehalt von 1 mg Nukleinsäure-P in % des ^{32}P-Gehaltes von		% der injizierten ^{32}P-Menge vorhanden in 1 mg Nukleinsäure-P
				1 mg Leber anorgan. P	1 mg Plasma anorgan. P	
1	2080	11.1	1.33	0.20	..	0.0016
2	2080	18.2	2.33	0.41	..	0.0032
3	2080	18.5	8.30	0.37	..	0.0029
4	2080	5.3	1.36	0.17	0.32	0.0023
5	2080	5.5	2.30	0.20	0.27	0.0025
6	2080	6.0	1.86	0.21	0.44	0.0066
7	1000	14.9	4.05	0.22	..	0.0015
8	1000	13.0	2.05	0.35	..	0.0011
9	1000	6.8	1.70	0.39	..	0.0014
10	2080	18.0	0.36	0.10	0.19	0.0044
11	1240	13.4	1.33	0.25	0.48	0.0011
12	620	17.0	2.11	0.13	0.24	0.0053
13	1025	13.9	6.20	0.36	0.21	0.0063
14	460	12.0	5.30	0.02	0.01	0.0003
15	460	8.6	5.31	0.56	0.29	0.0095
16	1025	5.9	21.0	0.28	0.35	..
17	1025	2.2	6.71	1.04	1.50	..
18	1025	11.8	52.0	0.31	0.54	..
19	1025	3.4	6.70	0.51	0,66	..
20	465	9.7	16.2	0.84	1.04	..
21	465	10.0	27.2	2.12	1.29	..
22	620	6.3	8.80	1.31	3.41	..
23	900	7.7	25.0	0.78	0.99	0.0123
24	1180	4.8	2.31	0.60	0.82	0.0137
25	1395	4.6	2.00	0.42	0.56	0.0096
26	1025	7.3	7.12	0.80	0.91	0.0087
27	1025	17.5	10.9	0.076	0.18	0.0017
28	1025	6.7	11.0	0.65	0.70	0.0099
29	1180	12.3	4.72	0.34	0.34	0.0051
30	1400	6.0	3.70	0.47	0.64	0.0090
31	1730	9.3	2.27	1.40	1.51	0.0130
32	2550	8.2	1.80	0.75	0.95	0.0100
33	7000	9.1	0.28	0.40	0.50	0.0071
34	7000	14.2	0.65	0.11	0.080	0.0017
Mittelwert	..	9.9	7.5	**0.50**	**0.65**	**0.0056**

Tabelle 4.

^{32}P-Gehalt des freien Phosphats des Blutplasmas und der Leber. Nicht bestrahlt.

Nr. der Ratte	Gewicht der Leber in g	P-Gehalt des Leber-Phosphats in mg %	P-Gehalt des Plasma-Phosphats in mg %	% des injizierten ^{32}P vorhanden in	
				1 mg Leber-P	1 mg Plasma-P
I + II	16.9	39	..	0.48	..
III + IV	17.0	50	..	0.44	..
V + VI	15.2	52	..	0.48	..
VII + VIII	13.6	57	5.7	0.85	0.59
IX + X	14.5	58	6.4	0.89	0.61
XI + XII	12.2	45	..	1.37	..
XIII	6.0	53	8.2	1.35	1.79
XIV	5.0	58	8.5	1.52	1.61
XV	6.3	47	7.7	1.42	1.32
XVI	6.4	46	9.6	1.63	1.33
Mittelwert	7.1	51	7.7	**1.04**	**1.21**

Tabelle 5.

^{32}P-Gehalt des freien Phosphats des Blutplasmas und der Leber. Schwach bestrahlt. (77 bis 310 r).

Bezeichnung der Ratte	Gewicht der Leber in g	P-Gehalt des Leber-Phosphats in mg %	P-Gehalt des Plasma-Phosphats in mg %	% des injizierten ^{32}P vorhanden in	
				1 mg Leber-P	1 mg Plasma-P
A	6.6	49	4.0	2.27	2.60
B	6.8	57	4.3	2.31	2.74
C	6.5	53	4.4	2.84	2.15
D	6.2	54	4.0	2.19	2.97
E	7.0	41	7.8	2.31	1.08
F	5.9	54	5.6	2.23	1.64
G	6.6	46	9.2	1.47	1.21
H	8.3	50	6.4	1.55	1.84
J	6.6	48	6.5	2.23	1.52
K	5.9	42	5.6	1.88	2.05
L	5.7	43	7.4	1.89	1.22
M	6.0	40	7.9	1.92	1.00
N	5.2	53	6.0	1.59	1.81
Mittelwert	6.3	47	6.1	**2.05**	**1.83**

Tabelle 6.

^{32}P-Gehalt des freien Phosphats des Blutplasmas und der Leber. Bestrahlt.
(Dosis 460—7000 r).

Nr. der Ratte	Gewicht der Leber in g	P-Gehalt des Leber-Phosphats in mg %	P-Gehalt des Plasma-Phosphats in mg %	% des injizierten ^{32}P vorhanden in	
				1 mg Leber-P	1 mg Plasma-P
1	4.8	79	..	0.81	..
2	5.2	69	..	0.88	..
3	8.0	52	..	0.79	..
4	5.9	50	7.4	1.76	0.94
5	7.1	55	6.8	1.25	0.91
6	4.0	48	6.8	3.15	1.51
7	7.0	47	..	0.67	..
8	6.6	36	..	0.43	..
9	5.2	41	..	0.37	..
10	4.4	48	10.0	4.55	2.31
11	5.0	45	6.9	4.45	2.33
12	4.6	48	8.3	3.90	2.24
13	5.5	79	5.7	1.94	3.50
14	5.1	89	4.5	1.70	3.21
15	4.1	98	6.0	1.77	3.23
16	5.9	49	9.2	3.0	2.5
17	7.2	45	5.6	2.5	2.1
18	4.0	53	4.4	4.7	2.7
19	5.8	52	4.9	3.6	2.7
20	6.2	60	7.9	1.5	1.0
21	6.1	64	7.7	1·1	1.8
22	6.6	46	9.2	1.7	0.6
23	4.8	69	7.6	1.8	1.3
24	5.5	60	5.9	1.7	1.1
25	4.9	67	4.0	1.7	1.7
26	7.3	50	6.6	1.2	1.1
27	7.5	59	6.7	1.8	0.9
28	6.7	57	5.0	1.3	0.7
29	5.1	27	5.4	3.6	1.5
30	5.4	46	5.0	1.9	1.4
31	6.5	54	4.5	0.9	0.9
32	6.2	52	5.8	1.3	1.0
33	5.3	58	5.8	1.7	1.4
34	5.5	62	9.6	1.5	2.1
Mittelwert	5.7	59	6.0	**2.0**	**1.7**

Besprechung der Ergebnisse.

Wie aus den Zahlen der Tabellen 1—3 und der zusammenfassenden Darstellung in Tabelle 7 zu ersehen ist, wird durch die Einwirkung einer Röntgendosis von über 450 r die Bildung neuer (radioaktiver) Nukleinsäuremoleküle in den meisten Fällen stark herabgesetzt. In den mit weniger als 450 r bestrahlten Sarkomen erfolgte die Bildung der radioaktiv gekennzeichneten Nukleinsäure nahezu im selben Ausmasse wie in den unbestrahlten Sarkomen.

Tabelle 7.

Nukleinsäureumsatz im unbestrahlten, schwach bestrahlten (mit weniger als 450 r) und stärker bestrahlten (oberhalb 450 r) Jensen-Sarkom.

Sarkom	^{32}P-Gehalt von 1 mg Nukleinsäure-P in Prozenten des ^{32}P-Gehaltes von	
	1 mg Leber anorgan. P	1 mg Plasma anorgan. P
	Mittelwert	
Unbestrahlt	1.82	1.78
Schwach bestrahlt	1.38	1.81
Bestrahlt	0.50	0.65
	Höchstwert	
Unbestrahlt	3.10	2.98
Schwach bestrahlt	2.14	3.71
Bestrahlt	2.12	3.41
	Tiefstwert	
Unbestrahlt	1.13	1.06
Schwach bestrahlt	0.26	0.22
Bestrahlt	0.076	0.080

In 5 von den 34 Sarkomen, die wir mit über 450 r bestrahlt haben, konnten wir keine Wirkung der Bestrahlung auf die Bildung der Nukleinsäure nachweisen. Eines dieser Sarkome wurde mit 1730 r bestrahlt, ein anderes mit 1025 r, ein weiteres mit 620 r, und zwei weitere mit 465 r. Es lagen hier vermutlich der Strahlenwirkung gegenüber mehr resistente Sarkome vor. Bei der Untersuchung des Angehens von bestrahlten Sarkomen nach erfolgter Transplantation fand man, dass die einzelnen Sar-

kome der Wirkung der Strahlung gegenüber verschieden empfindlich sind. Russ und Scott[1] geben z. B. an, dass sich von 100 mit 1000 r bestrahlten Jensen-Rattensarkomen 75 zurückgebildet haben, und bezüglich der Empfindlichkeit des nahe verwandten »Sarkom 180« gibt Suguria[2] an, dass nach der Bestrahlung mit 1000 r die Hälfte der Sarkome abstarb. Alle, im Verlauf weiterer Versuche (siehe S. 22) untersuchten 7, mit 2000 r bestrahlten Rattensarkome zeigten eine verminderte Nukleinsäurebildung während der der Bestrahlung folgenden 2 Stunden; solche Sarkome werden gelegentlich angetroffen.

In den meisten Fällen ist der Unterschied in der Bildung von radioaktiv gekennzeichneten (also neugebildeten) Nukleinsäuremolekülen im unbestrahlten und im bestrahlten Sarkom so ausgeprägt, dass man unmittelbar nach Anbringung der Probe unter dem Zählrohr qualitativ entscheiden kann, ob ein unbestrahltes Sarkom vorliegt. Eine vollständige Unterdrückung der Bildung aktiver Nukleinsäuremoleküle lässt sich allerdings auch durch Anwendung starker Dosen nicht erreichen. So wurde nach der erfolgreichsten Bestrahlung mit 7000 r die Aktivität von 1 mg Nukleinsäure-P gleich 0.1 % der Aktivität von 1 mg freiem Leber-P und gleich 0.08 % der Aktivität von 1 mg freiem Plasma-P gefunden. Die mit Ehrlich-Carcinomen an Mäusen bisher ausgeführten Versuche haben teilweise andere Ergebnisse erbracht als die mit Jensen-Sarkomen gewonnenen, wie demnächst mitgeteilt werden soll.

Durch die Möglichkeit, die Wirkung, welche die Röntgenstrahlen auf die Bildung von Nukleinsäuremolekülen im Sarkom ausüben, mit Hilfe von radioaktiven Indikatoren zu messen, kann die Wirkung der Röntgenstrahlen auf die Sarkome auf chemischem Wege verfolgt werden. Hierzu sei bemerkt, dass die beschriebenen Versuche leicht auszuführen sind — am besten in der Weise, dass man die Aktivität des Nukleinsäure-P des Sarkoms mit der Aktivität des freien P des Sarkoms vergleicht — und ferner, dass es von Bedeutung sein könnte, die wirksame Röntgendosis festzustellen, die eine nachweisbare Reduktion der Bildung von radioaktiv gekennzeichneter Nukleinsäure bewirkt.

In den beschriebenen Versuchen wurde die Bildung von radio-

[1] S. Russ and G. M. Scott, Brit. J. Radiol. **13**, 267, 1940.

[2] K. Suguria, Radiology **29**, 352, 1937.

aktiv gekennzeichneter Nukleinsäure im Laufe der auf die Bestrahlung folgenden 2 Stunden ermittelt (die Bestrahlung selbst dauerte höchstens 42 Minuten). Es steht dem nichts im Wege, die Bildung von radioaktiv gekennzeichneter Nukleinsäure z. B. in der ersten Stunde, der ersten halben Stunde, oder noch kürzere Zeit nach erfolgter Bestrahlung zu bestimmen. Wir sind somit in der Lage, die chemische Wirkung der Röntgenstrahlen auf das Sarkom unmittelbar nach erfolgter Bestrahlung zu ermitteln.

Phosphorgehalt von Leber und Plasma.

Wie aus den Zahlen der Tabellen 4—6 hervorgeht, ist kein wesentlicher Unterschied zwischen dem freien Phosphorgehalt des Plasmas und der Leber der bestrahlten, schwach bestrahlten und stärker bestrahlten Tiere zu finden. (Bestrahlt wurden stets nur die Sarkome.) Der durchschnittliche freie P-Gehalt der Leber beträgt 51, 47 bzw. 59 mg %; für den freien P-Gehalt des Plasmas sind die entsprechenden Zahlen 7.7, 6.1 bzw. 6.0 mg %.

In 1 mg freiem Leber-P der unbestrahlten, schwach bestrahlten, bzw. stärker bestrahlten Ratten finden sich 2 Stunden nach erfolgter Injektion 1.04[1], 2.05 bzw. 2.00 % des injizierten ^{32}P. Die Leber enthält demnach zu diesem Zeitpunkt (Durchschnittswert des Lebergewichtes = 7.1, 6.3 bzw. 5.7 g) etwa 7 % des injizierten ^{32}P als freien P.

In 1 mg freiem Plasma-P finden sich 2 Stunden nach erfolgter Injektion 1.21, 1.83 bzw. 1.72 % des injizierten ^{32}P. Demnach enthält 1 mg freier Leber-P 2 Stunden nach erfolgter Injektion nahezu dieselbe Menge ^{32}P wie 1 mg Plasma-P.

Vergleich der Aktivität des Nukleinsäure-P mit der Aktivität des freien P des Sarkoms.

Aus dem letzten Abschnitt geht hervor, dass sich im bestrahlten Sarkom weniger aktive Nukleinsäure bildet als im unbestrahlten. Aus dieser Feststellung darf jedoch nicht unbedingt gefolgert werden, dass die Bestrahlung den Nukleinsäureumsatz

[1] In späteren Versuchen (siehe S. 23) wurde in 1 mg freiem Leber-P unbestrahlter Ratten 2.13 % und in den mit 2000 r bestrahlten Tieren 2.16 % des injizierten ^{32}P gefunden. Für das Plasma-P waren die entsprechenden Zahlen 1.21 bzw. 1.15.

im Sarkom herabsetzt. Es wäre auch denkbar, dass die Bestrahlung das Eindringen des Indikators in die Sarkomzellen erschwert, und dass der beobachtete Effekt von einer Herabsetzung der Permeabilität der Zellwand für Phosphat unter der Wirkung der Bestrahlung herrührt. Erfahrungen, die an verschiedenen biologischen Systemen über die Wirkung der Bestrahlung auf die Permeabilität gesammelt worden sind und die demnächst mitgeteilt werden sollen, sprechen zwar gegen die letztgenannte Deutung der beobachteten Verminderung der Bildung von aktiver Nukleinsäure im bestrahlten Sarkom; wir haben jedoch — um die Erklärungsmöglichkeit, dass wir eine Beeinflussung der Phosphatpermeabilität durch die Bestrahlung beobachten, zu eliminieren — Versuche angestellt, in denen die Aktivität des Nukleinsäure-P mit der Aktivität des freien P des Sarkoms verglichen wurde. Der grösste Teil des freien P des Sarkoms besteht aus innerhalb der Zellen befindlichem P; falls ein Vergleich der genannten Aktivitäten eine wesentlich kleinere Zahl im Falle des bestrahlten Sarkoms liefert, so beweist diese Feststellung eindeutig, dass die Bestrahlung den Nukleinsäureumsatz hemmt und nicht etwa nur das Eindringen des Indikators in die Zellen erschwert.[1]

Die Ergebnisse dieser Versuche sind aus den Tabellen 8 und 9 ersichtlich. Wie aus diesen Tabellen zu ersehen ist, beträgt die radioaktiv gekennzeichnete, demnach während der 2-stündigen Versuchsdauer gebildete Nukleinsäure nach vorangehender Bestrahlung mit 2000 r etwa $^1/_3$ der Menge, die sich im unbestrahlten Sarkom bildet. Dieses Ergebnis stützt sich auf Zahlen, die durch einen Vergleich der Aktivität des Nukleinsäure-P mit der Aktivität des freien Sarkom-P an frischem Gewebematerial gewonnen worden sind. (Das Verhalten des nekrotischen Gewebes wird im nächsten Abschnitt besprochen.)

Wie bereits erwähnt, besteht der freie P des Sarkoms teilweise aus P, der aus der extrazellularen Flüssigkeit des Gewebes herrührt, und dieser P hat eine andere spezifische Aktivität (Aktivität per mg P) als der intrazellulare P. Die spezifische Akti-

[1] In unseren früheren Versuchen haben wir auf die Untersuchung der Aktivität des freien Sarkom-P verzichtet, um das gesamte Sarkomgewebe zur Gewinnung der Nukleinsäure verwenden zu können; später fanden wir es jedoch entschieden ratsam, auch die spezifische Aktivität des freien P jedes untersuchten Sarkoms zu bestimmen.

vität des extrazellulären P entspricht nahezu der Aktivität des freien Plasma-P. Der extrazellulare Anteil am freien Sarkom-P ist jedoch gering und, da die Aktivität des Sarkom-P sich von der des Plasma-P nicht wesentlich unterscheidet, ist der Fehler, den wir begehen, wenn wir von der komplexen Natur des freien Sarkom-P absehen, nicht erheblich. Die Ratte 47 : 1 enthält z. B. 1.45 mg % extrazellularen P und 44.8 mg % intrazellularen P. Wir gewinnen diese Zahlen auf Grund der Annahme, dass $^1/_4$ des Sarkoms aus extrazellularer Flüssigkeit besteht, ferner aus dem P-Gehalt des Plasmas (5.8 mg %) und des Sarkoms (46.3 mg %). Die 1.45 mg % extrazellularer P haben nicht dieselbe spezifische Aktivität wie die 44.8 mg % intrazellularer P, sondern eine 5 % höhere (siehe Tabelle 8); somit überschätzen wir bei Vernachlässigung des extrazellularen Anteils die spezifische Aktivität des intrazellularen P mit $\frac{0.07}{44.8} = 0.14\,\%$.

Was die Wirkung der Bestrahlung auf die Sarkomzellenpermeabilität betrifft, so ist womöglich eine beschränkte Wirkung der Bestrahlung auf die Permeabilität vorhanden. Während das Verhältnis der Aktivität von 1 mg Sarkom-P zu der Aktivität von 1 mg Plasma-P in unbestrahlten Sarkomen im Durchschnitt (siehe Tabellen 8 und 9) 1.07 beträgt, ist das entsprechende Verhältnis im Falle der bestrahlten Sarkomen 0.94; diese Differenz vermag jedoch den grössten Teil des beobachteten Effektes nicht zu erklären.

Nukleinsäureumsatz und Phosphatpermeabilität des nekrotischen Sarkomgewebes.

Wie aus Tabelle 8 hervorgeht, ist der Nukleinsäureumsatz im nekrotischen Sarkomgewebe zwar wesentlich kleiner als im frischen Gewebe, doch ist der Umsatz im nekrotischen Gewebe durchaus nicht vernachlässigbar. Dasselbe gilt für die Ersetzungsgeschwindigkeit des intrazellularen Phosphates durch Plasma- (Lymphe-) Phosphat. Der Austauschausgleich ist im nekrotischen Gewebe nicht so weit fortgeschritten wie im frischen Gewebe; im Laufe von 2 Stunden wird jedoch ein wesentlicher Teil des freien Sarkomphosphats durch Plasmaphosphat ersetzt. Daraus folgt, dass im nekrotischen Gewebe eine recht gute Blut- (Lym-

Tabelle 8.

Nukleinsäureumsatz in unbestrahlten Sarkomen.

Ratte	Sarkomvolumen in ccm		Aktivität von 1 mg Nukleinsäure-P in Prozenten der Aktivität von 1 mg		
			Leber-P	Plasma-P	Sarkom-P
47 : 1 (200 g)	38	frisch	0.77	1.13	1.18
		nekrotisch	0.41	0.55	1.08
47 : 2 (145 g)	13	frisch	1.58	3.31	2.12
		nekrotisch	—	—	—
47 : 3 (158 g)	14	frisch	1.15	1.67	1.23
		nekrotisch	0.71	1.03	1.20
47 : 4 (168 g)	18	frisch	0.81	2.77	1.93
		nekrotisch	0.29	0.97	1.15
51 : 1 (160 g) + 51 : 2 (132 g)	19+15	frisch	0.97	1.23	4.64
		nekrotisch	0.78	0.96	1.06
48 : 4b (188 g)	23	frisch	1.13	1.47	1.20
Mittelwert		frisch	1.07	1.93	**2.05**
		nekrotisch	0.55	0.88	**1.12**

Prozent des injizierten ^{32}P vorhanden in 1 mg.

	Leber-P	Plasma-P	Sarkom-P		Nukleinsäure-P	
			(frisch)	(nekrot.)	(frisch)	(nekrot.)
47 : 1	1.73	1.18	1.12	0.635	0.0133	0.0065
47 : 2	1.99	0.95	1.49	1.29	0.0313	—
47 : 3	1.83	1.26	1.72	1.08	0.0212	0.0130
47 : 4	3.73	1.12	1.61	0.95	0.0311	0.0109
51 : 1 + 2	1.98	1.56	0.46	1.45	0.019	0.015
48 : 4b	1.51	1.21	1.43	—	0.017	—
Mittelwert	2.13	1.21	1.30	1.08	0.022	0.011

Tabelle 9.

Nukleinsäureumsatz in mit 80 Röntgen per Minute (25 Minuten lang) bestrahlten Sarkomen.

Ratte	Sarkomvolumen in ccm		Aktivität von 1 mg Nukleinsäure-P in Prozenten der Aktivität von 1 mg		
			Leber-P	Plasma-P	Sarkom-P
49 : 1	18	frisch	0.68	0.90	0.72
		nekrotisch	0.40	0.60	0.88
49 : 2	23	frisch	1.00	0.85	0.79
		nekrotisch	0.42	0.33	0.46
49 : 3	13	frisch	0.70	1.01	1.00
		nekrotisch	0.025	0.036	0.036
49 : 4	19	frisch	0.12	0.50	0.54
		nekrotisch	—	—	—
50 : 1	7	frisch	0.45	1.14	0.80
		nekrotisch	—	—	—
50 : 2	8	frisch	0.21	0.37	0.31
		nekrotisch	—	—	—
50 : 3	33	frisch	0.14	0.13	0.33
		nekrotisch	0.073	0.063	0.23
Mittelwerte		frisch	0.47	0.63	**0.65**
		nekrotisch	0.23	0.26	**0.16**

Prozent des injizierten ^{32}P vorhanden in 1 mg.

	Leber-P	Plasma-P	Sarkom-P		Nukleinsäure-P	
			(frisch)	(nekrot.)	(frisch)	(nekrot.)
49 : 1	1.53	0.92	1.15	0.67	0.0083	0.0059
49 : 2	0.64	1.00	0.82	0.58	0.012	0.0026
49 : 3	1.71	1.18	1.19	1.17	0.012	0.00043
49 : 4	6.23 (?)	1.60	1.48	1.27	0.0077	—
50 : 1	1.69	0.74	1.05	0.25	0.0084	—
50 : 2	2.04	1.15	1.38	—	0.0043	—
50 : 3	1.29	1.50	0.55	0.42	0.0018	0.00095
Mittelwert	2.16	1.16	1.09	0.73	0.0078	0.0025

phe-) Zirkulation vorhanden sein muss. Der an sich reduzierte Nukleinsäureumsatz im nekrotischen Gewebe ist durch die Wirkung der Röntgenstrahlen weiter herabgesetzt.

Tabelle 10.

Vergleich des Durchschnittswertes des Nukleinsäureumsatzes und der Phosphatpermeabilität im frischen und im nekrotischen Gewebe.

		Frisches Gewebe	Nekrotisches Gewebe
Aktivität von 1 mg Nukleinsäure-P in Prozenten der Aktivität des freien Sarkom-P	Unbestrahlt.....	2.05	1.12
	Bestrahlt mit 2000 r	0.65	0.16
Verhältnis der Aktivität von 1 mg freiem P des nekrotischen und des frischen Sarkomgewebes	Unbestrahlt.....	0.66	
	Bestrahlt.....	0.76	

Menge der im Laufe von 2 Stunden im Sarkomgewebe neu gebildeten Nukleinsäure.

Wir fanden (Tab. 8), dass 2 Stunden nach erfolgter subkutaner Injektion des radioaktiven Phosphats die Aktivität des Nukleinsäure-P 2 % der Aktivität des freien Sarkom-P beträgt. Wäre im Laufe der Versuchszeit die Aktivität des freien Sarkom-P dieselbe, die wir am Ende des Versuches feststellen, so könnten wir aus den obigen Zahlen schliessen, dass während der 2-stündigen Versuchszeit Nukleinsäuremoleküle aufgebaut worden sind, die 2 % der gesamten im Sarkom vorhandenen Nukleinsäure ausmachen, also durchschnittlich — bei Sarkomen, die weniger als 40 g wiegen — 0.18 mg per g Gewebe (vgl. Tab. 12). Die Aktivität des Sarkom-P ändert sich jedoch im Laufe des Versuches. Wenn wir z. B. annehmen, dass sie mit der Zeit linear zunimmt, so beträgt der Prozentsatz der neu gebildeten Nukleinsäuremoleküle nicht 2 %, sondern 4 %. Die Änderung der spezifischen Aktivität des freien P der Sarkomzellen mit der Zeit erfolgt jedoch nicht nach einer einfachen Gesetzmässigkeit: an-

fangs ist sie einige Minuten lang praktisch gleich 0, da die Absorption des injizierten P und dessen Eindringen in den extrazellularen und weiter in den intrazellularen Raum Zeit braucht. Anderseits steigt die spezifische Aktivität mit der Zeit in der letzten Phase des Versuches nur wenig; wenn ein Ausgleich zwischen der Aktivität des Plasma- (extrazellularen) P und des zelullaren P nahezu erreicht ist, ändert sich nämlich die spezifische Aktivität des Sarkom-P nur wenig mit der Zeit. In einer Reihe von Fällen ist nach 2 Stunden nicht nur ein Ausgleich zwischen der spezifischen Aktivität des Sarkom-P und des Leber-P erreicht, sondern die erstere überflügelt sogar die letztere. Dieser Vorgang ist der Ursache zuzuschreiben, dass die Aktivität des Plasma-P innerhalb der ersten halben Stunde ein Maximum erreicht und dann allmählich abnimmt. Aus dem sehr aktiven Plasma dringt sehr aktiver P in die Zellen: dieser P wird zwar wieder durch neu ankommenden, weniger aktiven Plasma-P abgelöst, der Aktivitätsausgleich zwischen Sarkom-P und Plasma-P erfolgt jedoch langsamer als die Änderungen der Plasma-Aktivität, und so erklärt es sich, dass wir nach 2 Stunden den Sarkom-P aktiver antreffen können als den Plasma-P. Bei den obigen Überlegungen müssen wir berücksichtigen, dass der freie P der Sarkomzellen nicht nur Ein- und Austrittsmöglichkeiten durch die Zellwand hat, sondern auch verschiedene Einbaumöglichkeiten in die organischen, P-haltigen Moleküle der Sarkomzellen. Nach dem Eintritt des sehr aktiven Plasma-P tritt entsprechender P rasch in Adenosintriphosphat-, Hexosemonophosphat- und ähnliche Moleküle ein, die dann als Aufspeicherungsraum für den stark aktiven P dienen. Strömt der letztere wieder in das — inzwischen verarmte — Plasma zurück, so wird der Aktivitätsverlust des freien Sarkom-P durch Abgabe von stark aktivem P aus dem Aufspeicherungsraum kompensiert, und dieser Vorgang trägt dazu bei, das höhere Aktivitätsniveau des freien Sarkom-P aufrechtzuerhalten. Nicht nur nimmt die Aktivität des Sarkom-P in den späteren Phasen des Versuches nicht linear mit der Zeit zu, unter Umständen kann sie sogar eine Abnahme erleiden. Wenn wir den Endwert der spezifischen Aktivität des Sarkom-P mit etwa $1^1/_2$ multiplizieren, so dürften wir den Wert erhalten, den der freie Sarkom-P durchschnittlich im Laufe des Versuches hatte und der als Ausgangsmaterial zur Bildung der aktiven Nukleinsäure diente. Wir haben

den erhaltenen Wert dann für das Verhältnis der Aktivität von 1 mg Nukleinsäure-P und 1 mg Sarkom-P mit $1^1/_2$ zu multiplizieren, um zu dem Wert der prozentualen Nukleinsäurezunahme des Sarkoms im Laufe von 2 Stunden zu gelangen. Dieser Wert beträgt demnach etwa 3 % der gesamten Nukleinsäuremenge oder im Durchschnitt 0.26 mg per g Sarkom.

Zuwachs und Erneuerung.

Die im Laufe des Versuches gebildete und deshalb radioaktiv gekennzeichnete (^{32}P-haltige) Nukleinsäure ist entweder in dem neu entstandenen Gewebe zu finden, oder aber ist sie der Erneuerung bereits vorhandener Nukleinsäure zuzuschreiben. Im Falle der Adenosintriphosphorsäure und auch einiger anderer, säurelöslicher Phosphorverbindungen erfolgt eine Erneuerung der Moleküle im Sarkom und in anderen Organen mit sehr grosser Geschwindigkeit. In Gegenwart von radioaktiv gekennzeichnetem Phosphat zeigen sich die genannten Verbindungen nach Ablauf ganz kurzer Zeit radioaktiv. Die Nukleinsäuremoleküle werden dagegen in den normalen Organen sehr langsam erneuert. Angaben über die Erneuerungsgeschwindigkeit der Nukleinsäure in den Organen erwachsener Ratten werden demnächst mitgeteilt.

Wir nehmen an, dass der Nukleinsäuregehalt der Sarkome seinem Gewicht bzw. Volumen proportional ist. Diese Annahme wird durch Feststellungen gestützt, die weiter unten mitgeteilt werden. Der prozentuale Zuwachs des Nukleinsäuregehaltes ist dann gleich dem prozentualen Volumenzuwachs des Sarkoms. Mit Hilfe unserer radioaktiven Versuche bestimmen wir den Prozentsatz der Nukleinsäuremoleküle, die im Laufe der 2 letzten Stunden vor dem Töten der Ratte gebildet worden sind, und durch Untersuchung der Volumenzunahme des Sarkoms stellen wir den in den letzten 2 Stunden erfolgten Zuwachs fest. Doch ist diese Grösse zu klein, um durch Ausmessung der Dimensionen des Sarkoms festgestellt werden zu können. Der Zuwachs, der im Laufe der letzten 24 Stunden erfolgt ist, kann dagegen gemessen und daraus der Zuwachs, der im Laufe von 2 Stunden erfolgt ist, berechnet werden. Es scheint uns jedoch richtiger zu sein, die Berechnung des im Laufe von 2 Stunden erfolgten Volumen-

Tabelle 11.

Volumenzunahme der Sarkome.

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen[1] des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
48 : 1a	15 g; (2.5) 3.6 mg	16/5	2.77	—	25.0[2]
		18/5	4.88	38.1	
		19/5	5.63	15.3	
		20/5	6.10	8.4	
48 : 2a	8 g; (2.3) —	18/5	0.80	—	34.4
		19/5	1.13	41.2	
		20/5	1.62	43.2	
		21/5	2.16	33.4	
		22/5	2.49	15.3	
		23/5	3.46	38.8	
48 : 3a	8 g; (2.4) 4.9 mg	18/5	1.09	—	27.9[3]
		19/5	1.59	46.0	
		20/5	2.64	66.6	
		21/5	2.64	0	
		22/5	3.35	26.8	
		23/5	3.35	0	
48 : 1b	19 g; (2.5) 9.5 mg	26/5	1.42	—	30.5
		27/5	2.01	41.5	
		29/5	3.81	44.8	
		30/5	4.23	11.0	
		1/6	6.03	21.5	
		2/6	7.75	28.5	
48 : 2b	28 g; (2.0) 7.1 mg	26/5	3.23	—	20.3
		27/5	5.24	62.3	
		29/5	7.37	20.4	
		30/5	8.77	19.0	
		1/6	14.25	31.1	
		2/6	14.25	0	
48 : 5b	11 g; (1.8) 12.6 mg	29/5	0.84	—	28.0
		30/5	1.42	69	
		1/6	1.80	13.4	
		2/6	2.47	37	
		3/6	3.52	42.6	
		4/6	4.53	28.7	
		5/6	6.03	33.1	

[1] Das Volumen des Sarkoms wurde aus der Länge, Breite und Tiefe berechnet, wobei eine elliptische Gestalt des Sarkoms angenommen wurde.
[2] Zuwachs nur 4 Tage lang beobachtet.
[3] Zuwachs nur 5 Tage lang beobachtet.

Tabelle 11 (fortgesetzt).

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
48 : 6 b	15 g; (1.7) 12.3 mg	26/5	0.34	—	22.7
		27/5	1.01	197	
		29/5	1.17	7.9	
		30/5	1.34	14.5	
		1/6	1.34	0	
		2/6	1.84	37.3	
		3/6	2.89	57	
		4/6	2.80	0	
		5/6	3.81	36.1	
		6/6	4.53	18.7	
		8/6	6.54	22.2	
		9/6	8.97	37.2	
48 : 12 b	26 g; (1.9) —	9/6	1.8	—	36.3
		13/6	6.12	60	
		15/6	11.28	42	
		16/6	14.08	25	
48 : 13 b	20 g; (1.9) —	9/6	1.93	—	24.0
		13/6	5.7	49	
		15/6	7.84	18.8	
		16/6	10.56	34.5	
49 : 1	36 g; (2.0) 9.1 mg	18/5	1.93	—	23.6
		19/5	2.81	45.7	
		20/5	3.69	31.4	
		21/5	5.36	45.3	
		22/5	6.37	18.8	
		23/5	8.13	27.6	
		26/5	13.49	22.0	
		27/5	13.49	0	
		28/5	18.44	36.9	
49 : 3	20 g; (2.1) 9.3 mg	18/5	1.47	—	25.0
		19/5	1.84	25.0	
		20/5	2.60	52.2	
		21/5	3.18	22.5	
		22/5	3.77	18.5	
		23/5	5.24	38.8	
		26/5	7.04	11.4	
		27/5	11.0	56.4	
		28/5	13.28	20.7	

Tabelle 11 (fortgesetzt).

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
49 : 4	30 g; (1.6) 13.7 mg	18/5	1.51	—	21.5
		19/5	2.43	61.0	
		20/5	3.27	34.5	
		21/5	4.69	43.4	
		22/5	6.37	35.9	
		23/5	9.05	42.0	
		26/5	11.56	9.2	
		27/5	16.13	39.9	
		28/5	19.32	19.6	
50 : 1	18 g; (2.5) 9.9 mg	4/6	2.6	—	35.6
		9/3	7.25	35.6	
50 : 2	18 g; (2.1) 4.6 mg	4/6	3.35	—	30.2
		9/6	8.40	30.2	
48 : 3b	51 g; (1.7) 13.0 mg	26/5	2.93	—	21.3
		27/5	4.32	47.8	
		29/5	8.46	47.7	
		30/5	12.57	21.7	
		1/6	14.54	7.8	
		2/6	15.50	6.6	
		3/6	18.81	18.2	
		4/6	20.53	9.1	
		5/6	29.30	42.7	
48 : 4b	42 g; (1.9) 14.5 mg	26/5	2.43	—	19.4
		27/5	4.48	84.4	
		29/5	5.49	11.3	
		30/5	8,46	53.3	
		1/6	11.10	15.0	
		2/6	13.20	18.9	
		3/6	15.50	17.4	
		4/6	21.37	37.9	
		5/6	22.63	5.9	
48 : 7b	75 g; (1.9) 14.5 mg	26/5	2.51	—	16.0
		27/5	4.06	61.6	
		29/5	8.42	53.5	
		30/5	9.23	9.6	
		1/6	14.71	30	
		2/6	16.97	15.4	
		3/6	17.18	1.2	

Tabelle 11 (fortgesetzt).

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
48 : 7 b (fortgesetzt)	75 g; (1.9) 14.5 mg	4/6	22.46	—	12.8
		5/6	26.4	17.5	
		6/6	29.87	13.1	
		8/6	36.87	11.6	
		9/6	40.56	10.0	
48 : 8 b	81 g; (1.6) 10.8 mg	26/5	4.69	—	7.1
		27/5	6.37	35.9	
		29/5	7.75	10.2	
		30/5	10.89	40.5	
		1/6	15.71	31.5	
		2/6	20.66	15.2	
		3/6	21.37	3.4	
		4/6	27.15	27.0	
		5/6	35.95	32.0	
		6/6	34.32	0	
		8/6	38.17	5.6	
		9/6	42.57	11.5	
		10/6	49.15	15.4	
		11/6	51.29	4.3	
		12/6	51.29	0	
48 : 9 b	79 g; (1.5) —	26/5	3.52	—	11.9
		27/5	4.99	42	
		29/5	7.0	21	
		30/5	10.39	49	
		1/6	13.62	15.5	
		2/6	19.19	41.1	
		3/6	23.51	22.5	
		4/6	29.41	25.3	
		5/6	29.86	1.5	
		6/6	31.68	6.0	
		8/6	41.36	15.1	
		9/6	37.75	0	
		10/6	47.85	29 2	
		11/6	45.77	0	
		12/6	51.33	12.1	
48 : 10 b	83 g; (1.7) —	26/5	2.35	—	35.7
		27/5	3.69	57.2	
		29/5	5.53	25	

Tabelle 11 (fortgesetzt).

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
48 : 10 b (fortgesetzt)	83 g; (1.7) —	30/5	6.83	23.5	8.7
		1/6	8.84	14.7	
		2/6	9.51	7.6	
		3/6	12.07	26.8	
		4/6	16.89	40.0	
		5/6	19.90	17.7	
		6/6	20.82	4.6	
		8/6	26.15	12.8	
		9/6	26.15	0	
		10/6	29.87	2.8	
		11/6	34.91	16.8	
		12/6	39.13	12.1	
		13/6	39.13	0	
		15/6	41.94	3.6	
		16/6	48.27	14.8	
48 : 11 b	78 g; (1.8) —	26/5	1.13	—	8.4
		27/5	1.76	56.0	
		29/5	2.81	30.0	
		30/5	7.04	93.0	
		1/6	9.22	15.5	
		2/6	11.31	22.6	
		3/6	15.25	34.7	
		4/6	16.89	11.4	
		5/6	18.77	11.1	
		6/6	23.59	25.6	
		8/6	31.68	17.1	
		9/6	34.32	8.2	
		10/6	35.2	2.6	
		11/6	36.29	3.1	
		12/6	41.4	14.4	
		13/6	43.45	5.0	
49 : 2	44 g; (1.9) 10.1 mg	16/5	3.02	—	12.7
		18/5	4.99	33	
		19/5	6.29	26.1	
		20/5	7.25	15.3	
		21/5	9.30	27.7	
		22/5	11.44	24.1	
		23/5	11.44	0	

Tabelle 11 (fortgesetzt).

Ratte	Gewicht und spez. Gewicht des Sarkoms samt Nukleinsäuregehalt per g	Datum	Volumen des Sarkoms in ccm	Täglicher prozentualer Volumenzuwachs	Durchschnitt des täglichen prozentualen Volumenzuwachses im Laufe der 6 letzten Tage
49 : 2 (fortgesetzt)	64 g; (1.9) 10.1 mg	$^{26}/_{5}$	17.30	17	13.7
		$^{27}/_{5}$	20.91	20.8	
		$^{28}/_{5}$	23.09	10.2	
50 : 3	64 g; (1.9) 10.2 mg	$^{26}/_{5}$	3.77	—	12.2
		$^{27}/_{5}$	6.75	79	
		$^{29}/_{5}$	7.42	15.0	
		$^{30}/_{5}$	9.13	23.9	
		$^{1}/_{6}$	12.19	16.8	
		$^{2}/_{6}$	15.08	24.0	
		$^{3}/_{6}$	17.56	14.5	
		$^{4}/_{6}$	20.11	16.4	
		$^{5}/_{6}$	21.24	5.6	
		$^{6}/_{6}$	27.36	28.8	
		$^{8}/_{6}$	33.44	11.1	
		$^{9}/_{6}$	33.44	0	

Die Trockensubstanz der untersuchten Sarkome variierte zwischen 18.5 und 20.7 % (Mittelwert 19.2 %) des Sarkomgewichtes.

zuwachses nicht auf eine einzige, mit Unsicherheiten behaftete Messung (vgl. Tab. 11) zu gründen, sondern auf eine Reihe von Messungen aufzubauen, die im Laufe der letzten 6 Versuchstage ausgeführt worden sind. Die Ergebnisse solcher sowie anderer Messungen sind aus den Tabellen 11 und 12 zu ersehen[1]. Die letztgenannte Tabelle enthält eine Zusammenstellung der gewonnenen Ergebnisse getrennt für Sarkome, die weniger bzw. mehr als 40 g wiegen. Die mit Hilfe der radioaktiven Methode untersuchten Sarkome waren in den allermeisten Fällen leichter als 40 g, und wir sind deshalb in besonderem Mass an dem Volumenzuwachs der erstgenannten Sarkomgruppe interessiert.

Es ist leicht verständlich, dass bei Sarkomen, die in die Nähe der Grenze ihrer Wachstumsmöglichkeit gelangt sind, der tägliche

[1] Berechnet man den prozentischen Volumzuwachs der Sarkome auf Grund von Messungen, die zu Beginn und am Ende des letzten Tages vorgenommen worden sind, so erhält man die Zahlen 26.5 bzw. 14.3.

Tabelle 12.

Durchschnittlicher Volumenzuwachs von 14 bzw. 10 Sarkomen innerhalb eines Tages	Durchschnittlicher Nukleinsäuregehalt per g Sarkom
Sarkome, die weniger als 40 g wiegen	
27.4 %	8.8 mg
Sarkome, die mehr als 40 g wiegen	
12.8 %	12.0 mg

prozentuale Volumenzuwachs wesentlich kleiner ist als im Falle von Sarkomen, die über eine nahezu unbegrenzte Wachstumsmöglichkeit verfügen. Der durchschnittliche Nukleinsäuregehalt per g Sarkom wird jedoch in beiden Fällen nicht wesentlich verschieden gefunden; er beträgt 8.8 bzw. 12.0 mg per g Sarkom. Diese Feststellung, die sich auf zwei Sarkomgruppen sehr verschiedener Grösse bezieht, stützt die Richtigkeit unserer Annahme, dass der prozentuale Zuwachs an Nukleinsäure dem prozentualen Volumen-(Gewichts-)zuwachs ungefähr parallel läuft.

Das durchschnittliche spezifische Gewicht der schweren Sarkome schwankt zwischen 1.5 und 1.9 g bei einem Durchschnittswert von 1.8; für die weniger als 40 g wiegenden Sarkome sind die entsprechenden Grenzen 1.6 und 2.5; der Durchschnittswert beträgt hier 2.1.

Bei den uns interessierenden Sarkomen beträgt der Volumen- und dementsprechend der Nukleinsäurezuwachs 27 % täglich, oder rund 2 % im Laufe von 2 Stunden[1]. Der neugebildete Anteil an Nukleinsäure (Zuwachs + Erneuerung) ergab sich aus den radioaktiven Messungen zu etwa 3 %. Ein wesentlicher Bruchteil der radioaktiv gekennzeichneten Nukleinsäure ist demnach dem Wachstumsprozess zuzuschreiben. Eine genaue Festlegung des Anteils der neu gebildeten, nicht dem Wachstumsprozess zuzuschreibenden Nukleinsäure ist durch einen Vergleich der durch radioaktive Messungen erzielten Resultate mit den Ergebnissen von Volumzuwachsmessungen kaum durchführbar. Die Untersuchung von in ihrem Wachstum vollständig gehemmten Sarkomen mit Hilfe der radioaktiven Methode sollte jedoch zum Ziele führen, da ja in solchen Sarkomen kein Nukleinsäurezuwachs stattfindet.

[1] Da der Volumzuwachs des Sarkoms im Laufe des Tages womöglich rythmisch erfolgt, ist das obige Ergebnis mit Vorsicht zu deuten.

Solche Versuche sind in Vorbereitung. Aus den obigen Erörterungen kann jedoch geschlossen werden, dass die Röntgenstrahlen eine Verminderung des gesamten Umsatzes der Nukleinsäure im Jensen-Sarkom bewirken (innerhalb 2 Stunden nach der Bestrahlung festgestellt).

Wirkung der Röntgenstrahlen auf die Bildung von säurelöslichen Phosphorverbindungen im Sarkom.

Im Gegensatz zu dem Aufbau der Nukleinsäuremoleküle wird die Bildung von säurelöslichen Phosphorverbindungen im Sarkom durch die Wirkung einer einige 1000 r betragenden Dosis nicht nachweisbar beeinflusst, wie dies aus Tabelle 13 hervorgeht.

Tabelle 13.

Bildung von radioaktiv gekennzeichneten, säurelöslichen Phosphorverbindungen im bestrahlten Sarkom.

Ratte	Dosis	Fraktion gekennzeichnet durch die Hydrolysenzeit	Prozent des injizierten ^{32}P per mg P
I	1395 r	0 Min.	100
		7 »	95
		180 »	85
II	1670 r	0 Min.	100
		7 »	88
		180 »	84
III	2040 r	0 Min.	100
		7 »	100
		180 »	84
IV	2000 r	0 Min.	100
		7 »	100
		100 »	98
		180 »	93
V	2000 r	0 Min.	100
		7 »	85
		100 »	85
		180 »	100
VI	2100 r	0 Min.	100
		7 »	92
		100 »	98
		180 »	98

Wie aus Tabelle 13 ersichtlich, hat die 7 Min.-Fraktion nahezu dieselbe spezifische Aktivität wie die 0 Min.-Fraktion, und der grösste Teil der übrigen Fraktionen ist gleichfalls radioaktiv gekennzeichnet, d. h. im Laufe des Versuches neu gebildet. Röntgendosen von 2000 r Einheiten verhindern demnach nicht die nahezu vollständige Erneuerung der Moleküle der hydrolysierbaren, säurelöslichen Phosphorverbindungen im Sarkom. Der Umsatz der säurelöslichen P-Verbindungen steht in naher Beziehung zu den in den Zellen vor sich gehenden Oxydations- und Reduktionsprozessen, und es ist bekannt, dass diese letzteren Prozesse der Wirkung von Röntgenstrahlen gegenüber recht unempfindlich sind[1].

Enzymaktivität in bestrahlten Jensen-Sarkomen.

In Anbetracht der im letzten Abschnitt erwähnten Unempfindlichkeit des Ab- und Aufbaus der säurelöslichen P-Verbindungen der Wirkung von Röntgenstrahlen gegenüber war eine Wirkung der Röntgenstrahlen auf die an diesen Prozessen beteiligten Enzyme nicht zu erwarten.

Versuche, in denen die Wirksamkeit der aus dem Sarkom isolierten Katalase 1 Stunde nach erfolgter Bestrahlung mit 3000 r untersucht wurde, ergaben, dass die Wirksamkeit der Katalase durch die Bestrahlung des Sarkoms nicht gelitten hatte. Während die Katalaseaktivität des Muskels der normalen Ratten = 0.0252 gefunden worden ist, zeigte die Muskel-Katalase der bestrahlten Ratten einen Wert von 0.0385[2].

Die Untersuchung der Wirkung der Strahlung auf die Aktivität der Nuklease gab gleichfalls ein negatives Resultat. Die Einwirkung der aus dem mit 3000 r bestrahlten Sarkom gewonnenen Nuklease auf als Substrat verwendete Thymusnukleinsäure blieb keinesweges hinter der Wirksamkeit der aus dem unbestrahlten Sarkom gewonnenen Nuklease zurück. Während die erstere im Laufe von 4 Stunden 66 % der Thymusnukleinsäure spaltete, betrug die entsprechende Zahl für das unbestrahlte Sarkom 46 %.

[1] Während $^4/_5$ der Sarkome durch die Bestrahlung mit 1800 r am Angehen nach erfolgter Transplantation verhindert worden ist, war der Sauerstoffverbrauch dieser Sarkome von dem der Kontrollen nicht verschieden. (W. Keil, Arch. exp. Pathol. **167**, 338, 1932).

[2] Diese Versuche werden an anderer Stelle näher beschrieben.

Die Frage, ob die beim Aufbau der Nukleinsäure sich betätigenden Enzyme strahlungsempfindlich sind oder nicht, kann zur Zeit nicht beanwortet werden.

Aus den in dieser Abhandlung mitgeteilten Versuchen geht hervor, dass die Bestrahlung die Nukleinsäurebildung hemmt. Die Hemmung kann dadurch zustande kommen, dass die Bestrahlung solche Bestandteile, deren Gegenwart der Aufbau der Nukleinsäure und somit der Vorgang der Zellteilung erfordert, unmittelbar zerstört. Doch braucht dies nicht unbedingt der Fall zu sein.

Vom chemischen Standpunkt aus betrachtet ist die Zellteilung eine Folgeerscheinung des sehr intensiven synthetischen Prozesses, der in den Zellkernen vor sich geht. Ein Eingreifen in diesen synthetischen Prozess kann die Zellteilung unterbinden. Ein Eingreifen durch die Wirkung der Bestrahlung kann entweder dadurch erfolgen, dass für die Synthese unumgänglich notwendige Moleküle rascher zerstört als aufgebaut werden, oder aber dadurch, dass infolge der Einwirkung der Strahlung Fremdprodukte entstehen, die sich in die in den Zellkernen, oder in bestimmten Teilen der Zellkerne, vor sich gehenden chemischen Prozesse einschalten und dadurch den normalen Ablauf dieser Prozesse — und ihre Folgeerscheinung, die Zellteilung — hemmen. Unter der Einwirkung der Röntgenstrahlen erfolgt z. B. — wie wir aus den Versuchen von Svedberg und Broholt[1] wissen — eine Zerlegung von hochpolymeren Molekülen, z. B. Plasmaproteinen, in niedriger molekulare Teilchen. Während das Ansammeln solcher Bruchstücke im Cytoplasma — wenn dies nicht in hoher Konzentration, also unter der Einwirkung von sehr grossen Dosen erfolgt — keine wesentlichen Änderungen verursacht, könnten dieselben Bruchstücke, wenn sie im Zellkern erzeugt werden oder wenn sie dorthin gelangt sind, durch Eintreten in die im sich teilenden Kern stattfindenden synthetischen Prozesse eine sehr weitgehende Wirkung ausüben. Dass unter der Einwirkung der Röntgenstrahlen auf das Gewebe degenerierte Zellen auftreten, kann im Sinne der obigen Auffassung gedeutet werden.

Neben Spaltstücken von hochpolymeren Produkten treten eine Reihe anderer Fremdprodukte im bestrahlten Gewebe auf,

[1] Th. Svedberg und S. Broholt, Nature **143**, 938, 1938.

wie z. B. naszierender Sauerstoff, der die Bildung von Wasserstoffsuperoxyd und anderen Oxydationsprodukten veranlasst.

Die Röntgenstrahlen haben keine selektive Affinität für die eine oder andere Molekülart des Gewebes; ein beliebiges Atom des bestrahlten Gewebes hat ungefähr die gleiche Wahrscheinlichkeit ionisiert zu werden wie ein anderes beliebiges Atom; sie kann auf 4×10—11 bei einer Bestrahlung mit einer Dosis von 1 r geschätzt werden[1]. Es ist möglich, dass die Röntgenstrahlen bzw. die durch die Strahlen ausgelösten Ionen unmittelbar auf einen zur Synthese der Nukleinsäure erforderlichen Bestandteil einwirken, z. B. durch Spaltung eines solchen Moleküls, es ist aber nicht weniger wahrscheinlich, dass die Einschaltung von Fremdprodukten in die die Zellteilung einleitende synthetische Phase das entscheidende Moment ist.

Zusammenfassung.

Ratten mit Jensen-Sarkom wird eine radioaktiv gekennzeichnete Phosphatlösung subkutan injiziert; nach Verlauf von 2 Stunden wird die Nukleinsäure des Sarkoms isoliert.

Wenn die Nukleinsäure radioaktiv gefunden wird, so folgt hieraus, dass im Laufe des Versuches Nukleinsäuremoleküle im Sarkom aufgebaut worden sind.

Ein Vergleich der Aktivität von 1 mg Nukleinsäure-P mit der Aktivität von 1 mg freiem Sarkom-P ermöglicht eine Bestimmung der Menge der neu gebildeten Nukleinsäure.

Die im Laufe von 2 Stunden gebildeten Nukleinsäuremoleküle betragen 2—3 % des gesamten Nukleinsäuregehaltes, der per g Sarkom durchschnittlich 9 mg ausmacht.

Die Bestrahlung des Sarkoms mit 1000 internationalen Röntgeneinheiten und zum Teil bereits mit einer Dosis von über 450 r bewirkt in den allermeisten Fällen einen Rückgang der Nukleinsäurebildung auf durchschnittlich $^1/_2$—$^1/_3$ des beim unbestrahlten Sarkom gefundenen Wertes. Einzelne (5 von 45), vermutlich besonders strahlungsresistente Sarkome zeigen auch nach erfolgter Bestrahlung eine normale Nukleinsäurebildung.

Die beschriebene Methode ermöglicht den Nachweis der Wir-

[1] P. Jordan, Radiologica 2, 25, 1938.

kung der Strahlen auf das Sarkom unmittelbar nach erfolgter Bestrahlung auf chemischem Wege.

Im nekrotischen Sarkomgewebe beträgt der Nukleinsäureumsatz etwa die Hälfte bis ein Viertel des im frischen Gewebe festgestellten. Das freie Phosphat der Sarkomzellen wird durch Plasmaphosphat im nekrotischen Gewebe langsamer ersetzt als im frischen Gewebe, doch wird auch im nekrotischen Gewebe der grössere Teil des in den Sarkomzellen ursprünglich vorhandenen freien Phosphats im Laufe von 2 Stunden ersetzt.

Der säurelösliche, organische P des Sarkoms zeigt 2 Stunden nach erfolgter Injektion nahezu denselben Gehalt an radioaktiv gekennzeichnetem Phosphor wie 1 mg freier P des Sarkoms. Fast alle Moleküle der säurelöslichen Phosphorverbindungen des Sarkoms werden demnach im Laufe von 2 Stunden erneuert. Eine Bestrahlung mit 2000 r ruft keine nachweisliche Beeinflussung der Geschwindigkeit der Erneuerung der säurelöslichen P-Verbindungen im Sarkom hervor.

Stockholms Högskolas Vitamininstitut und Københavns Universitets Institut for teoretisk Fysik, Juni 1942.

Indleveret til Selskabet den 22. Juni 1942.
Færdig fra Trykkeriet den 9. November 1942

DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVII, NR. 9

SOME HALOBION SPECTRA
(DIATOMS)

BY

JOHS. BOYE PETERSEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1943

Printed in Denmark
Bianco Lunos Bogtrykkeri A/S

Of recent years not a little has been done to clear up the ecology of the Diatoms. The work carried out in this field has been reviewed by KOLBE (1932). The durability of the valves of Diatoms, which renders it easy to make lasting preparations of them, offers a strong inducement to statistical treatment of the composition of the individual communities; in this way more distinct results can no doubt be obtained than by the methods so far adopted.

Within the ecology of the Diatoms the best known field at present is their relation to the salinity of the water (more especially to its content of Cl ions), thanks to KOLBE's fundamental researches (1927, 1932) as well as the efforts of several other authors. These latter have partly tried to develop KOLBE's Halobion system by extending our knowledge as to how the individual species should be placed in the system (SCHULZ 1928; BUDDE 1930, 1931, 1932, 1933; BOYE PETERSEN 1930, 1932; KRASSKE 1932, 1933, 1939; HUSTEDT 1938, 1939), partly passed some criticism on it (LEGLER und KRASSKE 1940), and partly tried to apply it in ecological investigations.

KOLBE (1927, p. 129) already pointed out that in order to characterise the diatomaceous vegetation of a body of water with respect to its Halobia it is not enough to enumerate the species and mention their place in the system, account must also be taken of the proportional numbers of the individual species; and he adopted a method of estimation by which the species were given points from 1—100 according to their frequency. In this way a spectrum may be set up which will show, much better than a mere list of species, the dominance of the individual species in the vegetation and therefore give a truer picture of its Halobion character. Further, the percentage representation

of the individual categories is calcutated, comparable spectra from the various bodies of water being thus obtained. This method was used by BOYE PETERSEN (1930) and in a modified (but not improved) form by SPRENGER (1930).

It depends on estimate, however, and the reliability of the figures is thus considerably diminished. Several authors have made counts of Diatoms, for instance BUDDE (1931), but he did not use the counts to set up Halobion spectra. A mode of investigating the microphytes in the limnetic littoral and profundal zones has been devised by THOMASSON (1925). His model must have been the method for pollen analysis adopted in the investigation of bogs, and it has the advantage of attempting a determination of the absolute amount of organisms found in a definite volume of a bottom sample or a definite area of the stem of a reed at the shore of a lake. The result is set out in a diagram which is reminiscent of a pollen diagram. This method was later adopted by CHOLNOKY (1929) for epiphyte investigations in the Balaton Lake. Its prerequisite is that the material should be collected in a certain way, but this cannot always be done, for instance in the case of expedition material from remote regions. The method has not been applied especially to the examination of Halobia.

For geological purposes J. IVERSEN (1937)[1] has mentioned, in a temporary communication, the results of counts of Diatoms in gytje deposits in various localities in northern Sealand. The percentage results are set down on the same principle as pollen diagrams and afford excellent support for the supposition that salt water periods have alternated with inland lake periods. The procedure adopted is not described in detail; but it would seem that a consistent systematic count of the Diatoms from certain layers of soil will afford reliable information as to the salinity of the water bodies of the past.

Presentation of the Problem.

The object of the present investigation is

1. To try to set up Halobion spectra from waters with a known chloride content on the basis of the generally accepted

[1] The method from B. HALDEN: Geologiska Föreningens i Stockholm Förhandlingar 1929, 311—366.

view as to the place of the species in the Halobion system; it will then appear whether or not these spectra change in proportion to the amount of chloride in the water. If they do, it will be an indication that the view as to the place of the species is correct; if they do not, it will show that the view is incorrect. By examining the Halobion spectra and chloride content of numerous water bodies, it will perhaps be possible to correct, in a rational manner, our conception of the position of the species in the system. This, however, has not been attempted in the present work.

2. By setting up Halobion spectra from water bodies with an unknown chloride content to try to draw conclusions as to their chloride content. Such conclusions can hardly be very far-reaching in the first instance; but it is probable that in the future, when more experience has been gained, it will be possible to draw fairly accurate conclusions from the Halobion spectrum as to the chloride content of the water.

Author's own Method.

Of the available material I made an ordinary styrax preparation either 1) by mixing a little of the material with a drop of distilled water on a cover glass, heating it on an iron plate, and then mounting it in styrax; or 2) by first treating the sample with sulphuric acid and sodium nitrate and then making the preparation of the cleansed material.

In each preparation a count was now made of how many cells of each species there occurred in 25 random fields of vision. For this purpose I used a Zeiss apochromatic 60 ×, ap. 1.40 and c. oc. 15 ×, allowing a field of vision with a diameter of 180 μ. Whether the field of vision be a little larger or a little smaller will hardly affect the final result, since this is ultimately calculated in percentages, which are tabulated. For each species is given the number of individuals found in the 25 fields of vision, how many per cent of the total this number constitutes, and the place of each species in the Halobion system (euhalobous, mesohalobous, halophilous, indifferent, halophobous). Finally the whole is summed up in a spectrum where it can be seen how many per cent of each category were found in the sample.

The absolute figures for each species should be included in

the table, but they cannot be regarded as an expression of the absolute amount of the species in the samples, for the preparation may be made with more or less close-lying frustules of the same sample. On the other hand, these figures will tend to indicate how reliable the count is, for the more individuals you have counted the more it gains in this respect. The percentages show the relative proportions of the species occurring in the preparation and render possible a comparison with similar figures from other localities.

For the counts to be made in a satisfactory manner it is very important that the frustules should be evenly distributed throughout the preparation and should not lie too close together. If larger clumps of frustules are present it will be impossible to count the diatoms. Another difficulty will be that you may sometimes find entire frustules and sometimes loose valves. In preparations made by simple heating on cover-glasses by far the greater part of the frustules will be whole and this is indeed the most convenient; but in such preparations it is often difficult to get the cells evenly distributed on the cover-glass. This is more easily attained with material purified with acid, which, however, has the defect that many of the frustules have fallen apart. If it be assumed that the valves of all species are separated with equal ease this fact will not affect the final result, but there is some probability that the larger species are more fragile than the smaller ones.

Erroneous determinations may occur during the count, amongst other things because not all individuals are seen in valve view. Thus *Fragilaria* and *Eunotia* species are very difficult to identify in girdle view.

The spectra must be supposed to yield the best picture when many species are present. If, on the other hand, but few species are represented, you run the risk of obtaining a very one-sided spectrum, which perhaps on comparison with others may prove exaggerated. In the sequel I shall be able to show examples of how several spectra from the same locality proved surprisingly uniform despite the fact that they contained a different number of species, just as these were only partly the same in the different samples.

In the tables and spectra appearing in the sequel the species

have as far as possible been referred to the categories in KOLBE'S Halobion system by means of the information drawn from the works of a number of authors (KOLBE, KRASSKE, HUSTEDT, SCHULZ, BUDDE and others). These do not always agree in their view of the place of the species; but for most of the species there is general agreement. In cases where the authors have proved at variance I have placed the species according to the best of my judgment without considering my immediate experience. As to this question I refer the reader to my comments under the various species. The ecology of some species is still so little known that it has been impossible to place them in the system. This applies for instance to a number of species which will possibly prove to be more or less markedly halophobous. Altogether, their place in the system is the least known because the authors who have studied Halobia have principally concerned themselves with waters of such high chloride content that halophobous species have scarcely been present. Possibly some of the species now regarded as halophobous are more probably calciphobous.

It will often be difficult to decide whether a species is halophilous or mesohalobous, and as a matter of fact there is considerable vacillation among authors in their opinion of many species belonging to these groups.

We have seen examples of species being regarded by some as mesohalobous by others as indifferent. In such cases the species are markedly euryhaline. Such species I have classed as indifferent.

HUSTEDT (1935) and KRASSKE (1938) have maintained that some species which are usually considered halophilous are actually aerophilous species growing principally among mosses and in cushions of algae above the surface of the water. In the present work I have disregarded this view since these species, when growing in water, turn out to be halophilous.

Localities investigated.

The localities investigated fall into three groups:

1. Lakes and similar localities with alkaline-slightly acid water and a larger or smaller content of chloride.

2. Bogs. The water contains humus, is sometimes acid, sometimes alkaline, with a varying content of lime and chloride.

3. Heterogeneous localities, the chloride content of which is quite unknown or at least uncertain.

In each group the localities poorest in chloride are mentioned first.

Magle Lake.

The lake is situated in Asmindrup parish in Sealand near Tølløse and is surrounded by high hills (Grøntved Overdrev). Mentioned by WIINSTEDT (Bot. Tidsskr. 42: 298) in a report of an excursion. It does not appear from this that there is anything especially noteworthy about the vegetation.

Analyses of the water made by SIG. OLSEN on the $^{20}/_{7}$ 41 yielded the following data:

Cl′	16 mg/l.
Hardness (D. H.)	8.5
pH actual	7.5
Min.	6.4
Max.	7.5[1]

The water must therefore be characterised as soft freshwater of about neutral reaction with a low chloride content.

The spectrum shows that the sample contains almost exclusively indifferent forms.

Gurre Lake.

Situated in the parish of Tikjøb in northern Sealand. Size 243 ha. Mentioned by IVERSEN (1929, p. 316).

On the $^{27}/_{7}$ 41 SIG. OLSEN examined the water with the following result:

Cl′	19 mg/l.
Hardness (D. H.)	5.2
pH actual	7.4
Min.	6.2
Max.	8.8

Isoëtes echinospora and *Lobelia Dortmanna* as well as *Littorella uniflora* are known to occur in the lake.

[1] These pH values were found by the method of IVERSEN (1929).

Table 1.

Magle Lake near Grøntved Overdrev (near Tølløse).
$^{20}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes Clevei	+	—	indifferent
— minutissima v. crypt.	71	24.0	indiff.
— Østrupii	7	2.4	?
Amphora ovalis v. Pediculus	28	9.4	indiff.
Cocconeis placentula	17	5.8	indiff.
— — v. euglypta	+	—	indiff.
Cyclotella comta	6	2.0	indiff.
— Kützingiana?	1	0.3	indiff.
Cymbella affinis	19	6.4	indiff.
— lanceolata	+	—	indiff.
— microcephala	52	17.6	indiff.
— prostrata	5	1.7	indiff.
— ventricosa	2	0.7	indiff.
Epithemia sorex	+	—	indiff.
— zebra v. saxonica	12	4.1	indiff.
Fragilaria brevistriata	2	0.7	indiff.
— construens	+	—	indiff.
— — v. binodis	25	8.4	indiff.
— — v. venter	2	0.7	indiff.
— pinnata	9	3.0	indiff.
— sp. (in girdle view)	6	2.0	?
Gomphonema intricatum v. pumila	5	1.7	indiff.
— olivaceum	1	0.3	indiff.
Melosira arenaria	+	—	indiff.
— italica	2	0.7	indiff.
Navicula cocconeiformis	1	0.3	halophobous
— cryptocephala v. intermedia	5	1.7	indiff.
— — f. minuta	9	3.0	?
— radiosa	2	0.7	indiff.
— rotaeana	+	—	indiff.
— scutelloides	+	—	indiff.
Nitzschia sp.	5	1.7	?
Synedra rumpens?	+	—	indiff.
Tabellaria flocculosa	2	0.7	halophobous
	296	100.0	

Table 2.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	2	1.0
	indifferent	28	89.9
	halophilous	0	0.0
Mesohalobous		0	0.0
Euhalobous		0	0.0
?		4	9.1
	Total	34	100.0

The sample is from a crust of algae on sand by the shore. The preparation was made of material purified with acid.

Among the Diatoms the indifferent forms show marked dominance. It is true that as many as 6 species of halophobes were found, but in a very small number of individuals only. A remarkable feature is the occurrence of one mesohalobous species, viz. *Amphora coffæiformis*, which constituted 1.3% of the individuals counted. Perhaps the determination of this species is not quite reliable. The individuals were small and all seen in girdle view.

Table 3.
Gurre Lake. On sand; purified. $^{27}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes lanceolata	1	0.7	indifferent
— linearis	32	21.4	indiff.
— minutissima v. cryptoc.	16	10.7	indiff.
Amphora coffæiformis	2	1.3	mesohalobous
— ovalis	1	0.7	indiff.
Cocconeis placentula	16	10.7	indiff.
Cyclotella comta	8	5.3	indiff.
— sp.	3	2.0	?
Cymbella cistula v. maculata	1	0.6	indiff.
— microcephala	36	24.0	indiff.
— prostrata	1	0.7	indiff.
— sinuata	+	—	indiff.
Eucocconeis flexella v. alpestris	1	0.7	indiff.
Eunotia gracilis?	1	0.7	halophobous

(continued)

Table 3 (continued).

	Number of individuals	%	
Fragilaria construens	8	5.3	indiff.
— — v. binodis	+	—	indiff.
— pinnata	7	4.7	indiff.
— sp.	3	2.0	?
Gomphonema acuminatum	+	—	indiff.
Navicula cryptocephala v. exilis	1	0.6	indiff.
— — v. intermedia	2	1.3	indiff.
— — — f. minuta	3	2.0	?
— pseudoscutiformis	+	—	?
— pupula	1	0.7	indiff.
— radiosa	1	0.6	indiff.
Neidium affine v. amphirhynchus	+	—	halophobous
— — f. hercynica	+	—	halophobous
Nitzschia sp.	3	2.0	?
Pinnularia mesolepta	+	—	halophobous
Tabellaria flocculosa	2	1.3	halophobous
	150	100.0	

Table 4.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	6	2.7
	indifferent	18	88.0
	halophilous	0	0.0
Mesohalobous		1	1.3
?		5	8.0
	Total	30	100.0

Fure Lake.

Situated in northern Sealand. Its vegetation and other physical features have been described by Wesenberg-Lund in Furesøstudier (1917), and its plankton in Wesenberg-Lund, De danske Søers Plankton (1904).

The material for the spectrum was collected by Sig. Olsen on the $^{23}/_{11}$ 41 on the south-shore of the lake and consisted in scrapings off stones by the shore. Numerous *Cyanophyceae*

(*Rivularia, Nostoc* and others) as well as Diatoms occurred in the sample. The preparation was made of material purified with acid.

As to the character of the water the following data were found:

Cl′	20 mg/l.
Hardness (D. H.)	7.0
pH actual	8.2
Min.	6.8
Max.	8.6

In the above-mentioned works WESENBERG-LUND speaks of an abundant development of *Tabellaria fenestrata*, partly in the plankton, partly attached in the winter time; he also mentions *Tabellaria flocculosa* as very commonly attached to stones. I have observed none of these species in my material.

The spectrum shows marked dominance of indifferent forms, while no halophilous and no halophobous forms have been observed with certainty.

Of forms whose place in the Halobion system is not mentioned in the literature 11.2 % were found, *Navicula cryptocephala* f. *minuta* alone constituting 9.9 %.

Table 5.

Fure Lake; scrapings off stones. $^{23}/_{11}$ 41. Leg. SIG. OLSEN.

	Number of individuals	%	
Achnanthes Clevei	2	1.0	indifferent
— — v. rostrata	+	—	indiff.
— exigua	1	0.5	indiff.
— minutissima v. cryptoc.	8	3.9	indiff.
— lanceolata	1	0.4	indiff.
Amphora ovalis	+	—	indiff.
— — v. pediculus	18	8.9	indiff.
Asterionella formosa	+	—	indiff.
Cocconeis Pediculus	1	0.5	indiff.
— Placentula	+	—	indiff.
Cymatopleura solea	+	—	indiff.
Cymbella cuspidata	1	0.5	indiff.
— helvetica	9	4.4	indiff.
— microcephala	10	4.9	indiff.

(continued)

Table 5 (continued).

	Number of individuals	%	
Cymbella prostrata	+	—	indiff.
— ventricosa	+	—	indiff.
Diatoma vulgare	50	24.8	indiff.
Epithemia intermedia	+	—	?
— sorex	16	7.9	indiff.
— zebra v. porcellus	5	2.4	indiff.
Fragilaria construens	+	—	indiff.
— — varr.	15	7.4	indiff.
— crotonensis	2	0.9	indiff.
— pinnata	+	—	indiff.
— Vaucheriae	4	1.9	indiff.
— — v. capitellata	2	0.9	indiff.
Melosira islandica	+	—	indiff.
Navicula cryptocephala v. intermedia	2	0.9	indiff.
— — f. minuta	20	9.9	?
— scutelloides	+	—	indiff.
— tuscula	2	0.9	indiff.
— vulpina	1	0.9	?
Nitzschia dissipata	3	1.4	indiff.
— fonticola	12	5.9	indiff.
— gracilis	8	3.9	indiff.
— palea	+	—	indiff.
— sigmoidea	+	—	indiff.
Pinnularia sp.	1	0.4	?
Rhoicosphenia curvata	+	—	indiff.
Rhopalodia ventricosa	3	1.4	indiff.
Stephanodiscus Astræa	+	—	indiff.
— — v. minutula	3	1.4	indiff.
Synedra Acus	2	0.9	indiff.
— Ulna	2	0.9	indiff.
	204	100.0	

Table 6.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	39	88.8
	halophilous	1	0.0
Mesohalobous		0	0.0
?		4	11.2
	Total	44	100.0

Bure Lake.

Situated in the parish of Uggeløse in northern Sealand, it is an elongate lake with an outlet into Roskilde Fjord. The sample was of algae from sand by the shore; collected on the $^{3}/_{7}$ 41 by Sig. Olsen, who found the following data for the character of the water:

Cl′	22 mg/l.
Hardness (D. H.)	7.0
pH actual	8.2
Min.	7.2
Max.	8.2

The water must therefore be characterised as alkaline and poor in lime and chloride. The spectrum shows pronounced dominance of indifferent forms with a small number of halophobous and halophilous species.

Table 7.
Bure Lake; on sand. $^{3}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes conspicua	1	0.3	indifferent
— exigua	3	0.9	indiff.
— lanceolata	1	0.3	indiff.
— minutissima v. cryptoceph.	39	11.6	indiff.
Amphora ovalis v. pediculus	69	20.6	indiff.
Asterionella formosa	2	0.6	indiff.
Cocconeis placentula	2	0,6	indiff.
— — v. euglypta	+	—	indiff.
Cyclotella comta	+	—	indiff.
— Kützingiana?	8	2.4	indiff.
Cymbella affinis	37	11.0	indiff.
— lacustris	+	—	indiff.
— microcephala	44	13.2	indiff.
— obtusiuscula	+	—	?
— parva	+	—	indiff.
— prostrata	19	5.7	indiff.

(continued)

Table 7 (continued).

	Number of individuals	%	
Cymbella ventricosa	2	0.6	indiff.
— sp. (in girdle view)	2	0.6	?
Diploneis ovalis	1	0.3	indiff.
Epithemia Argus	1	0.3	indiff.
— intermedia	1	0.3	?
— sorex	10	3.0	indiff.
— zebra	1	0.3	indiff.
— — v. saxonica	3	0.9	indiff.
Eunotia arcus v. fallax	+	—	halophobous
Fragilaria brevistriata	21	6.2	indiff.
— construens	+	—	indiff.
— — v. venter	9	2.7	indiff.
— — v. binodis	6	1.8	indiff.
— pinnata	1	0.3	indiff.
— Vaucheriae	8	2.4	indiff.
— sp.	11	3.3	?
Gomphonema acuminatum v. coronatum	1	0.3	indiff.
— intricatum v. pumilum	3	0.8	indiff.
— olivaceum	2	0.6	indiff.
— parvulum	1	0.3	indiff.
— ventricosum	+	—	?
— sp. (in girdle view)	2	0.6	?
Mastogloia Smithii v. amphicephala	1	0.3	indiff.
— — v. lacustris	+	—	indiff.
Navicula cryptocephala v. intermedia	6	1.8	indiff.
— — f. minuta	3	0.9	?
— hungarica var.?	1	0.3	halophilous
— radiosa	+	—	indiff.
— scutelloides	+	—	indiff.
— subtilissima	2	0.6	?
— tuscula f. minor	1	0.3	halophilous
Nitzschia amphibia	1	0.3	indiff.
— sp.	3	0.9	?
Rhoicosphenia curvata	+	—	indiff.
Rhopalodia gibba	2	0.6	indiff.
Stephanodiscus Astræa	+	—	indiff.
Synedra amphicephala	1	0.3	?
— ulna	1	0.3	indiff.
Tabellaria flocculosa	2	0.6	halophobous
	335	100.0	

Table 8.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	2	0.6
	indifferent	40	91.0
	halophilous	2	0.6
Mesohalobous		0	0.0
?		11	7.8
	Total	55	100.0

Sct. Jørgens Lake.

The lake is an artificial one, a remnant of a former fortification, situated within the bounds of Copenhagen. It is about 5 m. deep, rectangular in shape, its greatest length extending in a N. N. E.—S. S. W. direction. It now belongs to the Copenhagen Water Works, and is used as a reservoir. In a dam laid across the middle of the lake runs a concrete aqueduct which leads the groundwater from borings at Sønder Lake to Copenhagen. When this aqueduct sometimes carries more water than necessary, the superfluous water is allowed to run into the lake. According to Mr. PAPE'S analyses the water in the lake contains 35 mg. Cl′ per l. Its lime content is high, measuring 16 German degrees of hardness.

I have examined two preparations from Sct. Jørgens Lake, viz.

a. From parts of plants; depth $5^1/_2$ m., north end of lake $^{31}/_7$ 1916. Material not purified. The spectrum is typical of pure freshwater whose species are all indifferent, while the halophobous species only constitute 1.6 %.
b. Bottom mud from a depth of 5 m., south end of lake $^{11}/_9$ 1912. Material purified with acid. This contained almost twice the amount of species found in the north end. Nevertheless the spectrum has almost the same appearance with a preponderance of indifferent species. Only there is a suggestion here that the halophilous species are somewhat more numerous. The difference between the two spectra is so insignificant, however, that it may easily be accidental.

Table 9.

Sct. Jørgens Lake, north end, on parts of plants $5^1/_2$ m. depth. $^{31}/_7$ 1916. Non-purified material.

	Number of individuals	%	
Achnanthes minutissima v. cryptoc...	42	22.1	indifferent
Amphipleura pellucida	+	—	indiff.
Cocconeis placentula	7	3.7	indiff.
Cyclotella comta	91	47.9	indiff.
Cymbella affinis	3	1.5	indiff.
— cymbiformis	3	1.5	indiff.
— lanceolata	+	—	indiff.
Epithemia Zebra v. saxonica	2	1.1	indiff.
Eunotia pectinalis	3	1.6	halophobous
Gomphonema acuminatum v. Brebissonii	2	1.1	indiff.
— — v. coronata	2	1.1	indiff.
— constrictum	2	1.1	indiff.
— intricatum v. pumilum	18	9.4	indiff.
— longiceps f. gracilis	4	2.1	?
Navicula vulpina	+	—	?
— sp.	4	2.1	?
— sp.	3	1.6	?
Nitzschia sp.	3	1.6	?
Rhoicosphenia curvata	1	0.5	indiff.
Rhopalodia gibba	+	—	indiff.
Synedra Ulna v. biceps	+	—	indiff.
	190	100.0	

Table 10.

Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	1	1.6
	indifferent	15	91.0
	halophilous	0	0.0
Mesohalobous		0	0.0
?		5	7.4
	Total	21	100.0

Table 11.

Sct. Jørgens Lake, bottom mud, 5 m. depth $^{11}/_{9}$ 1912.
South end; purified material.

	Number of individuals	%	
Achnanthes Clevei	+	—	indifferent
— lanceolata	1	1.6	indiff.
— minutissima v. cryptoceph.	1	1.6	indiff.
Amphora ovalis	1	1.5	indiff.
— — v. pediculus	9	14.0	indiff.
Caloneis sp.	+	—	?
Campylodiscus noricus v. hibernicus	2	3.1	indiff.
Cocconeis placentula	3	4.7	indiff.
Cyclotella comta	3	4.7	indiff.
— stelligera	+	—	indiff.
Diploneis ovalis	+	—	indiff.
Epithemia zebra v. porcellus	1	1.6	indiff.
Eunotia arcus	+	—	halophobous
— sp.	+	—	?
Fragilaria brevistriata	1	1.5	indiff.
— capucina	+	—	halophobous
— construens-forms	6	9.4	indiff.
— leptostauron	1	1.5	halophobous
— pinnata	2	3.1	indiff.
Gomphonema acuminatum	1	1.6	indiff.
— constrictum	+	—	indiff.
— intricatum	+	—	indiff.
— — v. pumilum	4	6.3	indiff.
Gyrosigma acuminatum	1	1.6	indiff.
— attenuatum	5	7.8	indiff.
Melosira arenaria	+	—	indiff.
— varians	+	—	indiff.
Navicula gregaria	1	1.6	halophilous
— oblonga	+	—	indiff.
Nitzschia acuta	1	1.6	indiff.
— dissipata	2	3.1	indiff.
— sp.	1	1.6	?
Pinnularia sp.	1	1.5	?
Stauroneis acuta	+	—	indiff.
Stephanodiscus astraea	4	6.3	indiff.
Surirella Capronii	+	—	indiff.
— elegans	3	4.7	indiff.
— robusta	+	—	halophobous
Synedra acus	+	—	indiff.
— parasitica	1	1.6	indiff.
— Ulna v. danica	2	3.1	indiff.
— — v. amphirhynchus	1	1.5	indiff.
	64	100.0	

Table 12.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	4	1.5
	indifferent	31	93.8
	halophilous	2	1.6
Mesohalobous		0	0.0
?		5	3.1
	Total	42	100.0

Dybe Lake.

Small lake near Rørvig. According to WIINSTEDT (1940, 327) it is a lagune only separated from the Kattegat by the low dunes and with the raised sea floor as a substratum.

SIG. OLSEN has found the following data for the water:

Cl′	35 mg/l.
Hardness (D. H.)	9.5
pH actual	8.0
Min.	6.6
Max.	8.4

From this lake there are two spectra, one of a sample of material scraped off stones by the shore, and another from sand with a coating of algae in shallow water. Both spectra show predominance of indifferent forms, with a small number of halophobous and halophilous species. In each of them there was also a small number of mesohalobous forms. In both samples it was a small *Amphora* determined as *A. coffaeiformis*, but the determination is hardly quite conclusive. The sample from sand further contained *Mastogloia elliptica* v. *Dansei*, which is not regarded as mesohalobous by all authors.

Nors Lake

is situated in Thy about 10 km. west of Thisted. Its size is about 350 ha. The lake has been described by SIG. OLSEN (1941) and only a few of its physical features will here be pointed out. The substratum is of chalk, sometimes cropping up freely and sometimes covered with sand or mud. The water might have been expected to be highly calciferous owing to the nature of the substratum but, as will appear from the analyses made by

Table 13.

Dybe Lake, scrapings off stones. 5/6 41. Leg. Sig. Olsen.
Purified material.

	Number of individuals	%	
Achnanthes lanceolata	1	0.3	indifferent
— linearis	1	0.3	indiff.
— minutissima v. cryptoc.	171	54.9	indiff.
Amphora coffæiformis	1	0.3	mesohalobous
— ovalis	+	—	indiff.
— — v. pediculus	2	0.6	indiff.
Cocconeis placentula	9	2.9	indiff.
Cyclotella comta	40	12.8	indiff.
Cymatopleura elliptica	+	—	indiff.
— solea	+	—	indiff.
Cymbella affinis	1	0.3	indiff.
— Ehrenbergii	+	—	indiff.
— microcephala	22	7.0	indiff.
— obtusiuscula	+	—	?
— parva	14	4.5	indiff.
— prostrata	6	1.9	indiff.
— sinuata	+	—	indiff.
— ventricosa	1	0.3	indiff.
Diatoma elongatum	1	0.3	halophilous
Epithemia sorex	1	0.3	indiff.
— zebra v. saxonica	3	1.0	indiff.
Eucocconeis flexella	+	—	halophobous
— lapponica	3	1.0	halophobous
Fragilaria brevistriata	2	0.6	indiff.
— construens	+	—	indiff.
— crotonensis	5	1.6	indiff.
— Vaucheriae	2	0.6	indiff.
Gomphonema olivaceum	1	0.3	indiff.
Gyrosigma attenuatum	+	—	indiff.
Mastogloia elliptica v. Dansei	2	0.6	mesohalobous
— Smithii v. amphicephala	8	2.5	indiff.
— — v. lacustris	3	1.0	indiff.
Navicula cryptocephala v. intermedia	+	—	indiff.
— — f. minuta	2	0.6	?
— — v. veneta	+	—	indiff.
— oblonga	+	—	indiff.
— pupula	+	—	indiff.
— radiosa	3	1.0	indiff.

Table 13 (continued).

	Number of individuals	%	
Navicula tuscula	+	—	indifferent
— — f. minor	+	—	halophilous
— sp.	3	1.0	?
Neidium Iridis	1	0.3	halophobous
Nitzschia angustata	1	0.3	indiff.
Rhopalodia gibba	2	0.6	indiff.
Tabellaria flocculosa	+	—	halophobous
Synedra Ulna	1	0.3	indiff.
	313	100.0	

Table 14.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	4	1.3
	indifferent	34	95.6
	halophilous	2	0.3
mesohalobous		2	0.9
?		4	1.9
	Total	46	100.0

Table 15.
Dybe Lake, on sand. 5/6 41. Leg. Sig. Olsen.
Purified material.

	Number of individuals	%	
Achnanthes lanceolata	1	0.2	indifferent
— minutissima v. cryptoc.	236	52.6	indiff.
Amphora coffæiformis	1	0.2	mesohalobous
— ovalis	+	—	indiff.
— — v. pediculus	+	—	indiff.
Caloneis Silicula v. truncatula	1	0.2	indiff.
Cocconeis placentula	20	4.5	indiff.
Cyclotella comta	29	6.5	indiff.

(continued)

Table 15 (continued).

	Number of individuals	%	
Cymatopleura elliptica	+	—	indiff.
— solea	1	0.2	indiff.
Cymbella affinis	1	0.2	indiff.
— Ehrenbergii	2	0.5	indiff.
— microcephala	31	6.8	indiff.
— parva	3	0.7	indiff.
— prostrata	5	1.1	indiff.
— sinuata	+	—	indiff.
Diatoma elongatum	1	0.2	halophilous
Epithemia sorex	5	1.1	indiff.
— zebra v. saxonica	1	0.2	indiff.
Eucocconeis flexella v. alpestris	13	2.9	halophobous
Fragilaria brevistriata	4	0.9	indiff.
— construens	1	0.2	indiff.
— pinnata	+	—	indiff.
— Vaucheriae	3	0.7	indiff.
Gyrosigma attenuatum	2	0.5	indiff.
Mastogloia Smithii v. amphicephala	44	9.8	indiff.
Navicula cryptocephala	10	2.2	indiff.
— — v. intermedia	3	0.7	indiff.
— — f. minuta	9	2.0	?
— cuspidata	+	—	indiff.
— gastrum	+	—	indiff.
— oblonga	+	—	indiff.
— pupula	1	0.2	indiff.
— radiosa	2	0.4	indiff.
— tuscula	+	—	indiff.
— — f. minor	1	0.2	halophilous
— sp.	2	0.5	?
Neidium Iridis	+	—	halophobous
Nitzschia angustata	9	2.0	indiff.
— dissipata	2	0.5	indiff.
— sp.	1	0.2	?
Rhopalodia gibba	3	0.7	indiff.
Stauroneis Phoenicenteron	+	—	indiff.
Surirella sp.	+	—	?
Synedra sp.	1	0 2	?
	449	100.0	

Table 16.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	2	2.9
	indifferent	34	93.6
	halophilous	3	0.4
Mesohalobous		1	0.2
?		5	2.9
	Total	45	100.0

Nygaard (1938), this is not the case. Nygaard found between 43.1 and 52 mg. CaO/l. Olsen (l. c.) determined the pH and found that it ranged from 6.8 to 8.7 (artificial minimum and maximum according to Iversen's method). In May 1942 I received a sample of the water which Mr. Pape kindly analysed for me. He found the following data:

pH	7.29
Cl′	42 mg/l.
Total hardness (D. H.)	6.6
Carbonate	5.6
permanent	1.0
SO_3	traces
HCO_3	122 mg/l.

The water must therefore be characterised as alkaline with a small content of lime, chloride, and sulphate.

Two samples from Nors Lake were examined, both of them scrapings from stones in shallow water, but one of them from a limestone, the other from granite.

Unfortunately one of the spectra is not very informative since 15.3 % of the Diatoms present could not be referred to any place in the Halobion system by the aid of the literature. The other spectrum (from the limestone) shows that the flora consists almost exclusively of indifferent forms with an admixture of some few halophilous species (0.9 %).

Table 17.

Nors Lake, scrapings off granite stones. $^{21}/_{8}$ 39 Leg. Sig Olsen. 1.50—1.75 m. depth.

	Number of individuals	%	
Achnanthes Clevei	4	2.9	indifferent
— linearis	6	4.5	indiff.
— minutissima v. cryptoc.	5	3.7	indiff.
Amphora ovalis	+	—	indiff.
— — v. pediculus	32	23.5	indiff.
Caloneis bacillum	+	—	indiff.
Cocconeis placentula	7	5.2	indiff.
Cyclotella comta	2	1.5	indiff.
Cymbella æqualis	+	—	indiff.
— helvetica	+	—	indiff.
— lacustris	2	1.5	indiff.
— leptoceros	1	0.7	indiff.
— microcephala	6	4.5	indiff.
— parva	+	—	indiff.
— prostrata	+	—	indiff.
— ventricosa	+	—	indiff.
Diploneis ovalis	2	1.5	indiff.
Epithemia Hyndmannii	+	—	indiff.
— sorex	6	4.4	indiff.
— zebra v. porcellus	1	0.7	indiff.
— — v. saxonica	12	8.8	indiff.
Fragilaria brevistriata	2	1.5	indiff.
— construens	10	7.4	indiff.
— pinnata	1	0.7	indiff.
— Vaucheriae (small form)	1	0.7	indiff.
Gomphonema acuminatum	1	0.7	indiff.
Mastogloia Smithii v. amphicephala	+	—	indiff.
— — v. lacustris	2	1.5	indiff.
Navicula cryptocephala v. intermedia	7	5.2	indiff.
— — f. minuta	6	4.4	?
— radiosa	+	—	indiff.
— rhynchocephala	+	—	indiff.
— scutelloides	4	2.9	indiff.
— subhamulata	1	0.7	?
— subtilissima	8	5.9	?
— sp.	1	0.7	?
— sp.	1	0.7	?
Nitzschia palea	1	0.7	indiff.
— sp.	4	2.9	?
	136	100.0	

Table 18.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	30	84.7
	halophilous	2	0.0
mesohalobous		0	0.0
?		7	15.3
	Total	39	100.0

Table 19.
Nors Lake, scrapings off limestones; 0.25 m. depth. 14/8 39.
Leg. Sig. Olsen

	Number of individuals	%	
Achnanthes linearis	2	0.9	indifferent
— minutissima v. cryptoc.	23	10.6	indiff.
Amphora ovalis	1	0.5	indiff.
— — v. pediculus	6	2.8	indiff.
Cocconeis placentula	2	0.9	indiff.
Cyclotella comta	+	—	indiff.
Cymbella affinis	5	2.4	indiff.
— helvetica	1	0.5	indiff.
— lacustris	6	2.8	indiff.
— microcephala	66	30.1	indiff.
— parva	6	2.8	indiff.
— prostrata	14	6.4	indiff.
— ventricosa	3	1.4	indiff.
Diatoma elongatum	2	0.9	halophilous
Epithemia sorex	5	2.4	indiff.
Eucocconeis lapponica	+	—	halophobous
Fragilaria brevistriata	1	0.5	indiff.
— construens v. binodis	3	1.4	indiff.
— — v. venter	9	4.1	indiff.
— crotonensis	10	4.6	indiff.
— pinnata	1	0.5	indiff.
— Vaucheriae	+	—	indiff.
Gomphonema olivaceum	4	1.8	indiff.
— — v. calcareum	4	1.8	indiff.

(continued)

Table 19 (continued).

	Number of individuals	%	
Mastogloia Smithii v. amphicephala ..	3	1.4	indiff.
— — v. lacustris.....	27	12.4	indiff.
Navicula cryptocephala v. intermedia.	1	0.5	indiff.
— radiosa.....	+	—	indiff.
— tuscula f. minor.....	+	—	halophilous
Nitzschia denticula	+	—	indiff.
— fonticola	8	3.7	indiff.
— sp.....	2	0.9	?
Rhopalodia gibba.....	1	0.5	indiff.
Stephanodiscus Astraea.....	1	0.5	indiff.
Surirella linearis v. helvetica	+	—	indiff.
	217	100.0	

Table 20.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	1	0.0
	indifferent.....	30	98.2
	halophilous	2	0.9
mesohalobous		0	0.0
?		2	0.9
Total.....		35	100.0

Amager Fælled, pool ($^{15}/_{7}$ 41).

The sample consists of *Characeae* with epiphytes. Purified Diatom material was made from it. On examination of the water Sig. Olsen found:

Cl′	97 mg/l.
Hardness (D. H.).....	17.8
pH actual	7.4
Min.	6.8
Max.	8.2

According to these data the water from this locality seems to be of much the same sort as that from the lakes, so I have

compared its spectrum with those from the lakes. The greater content of chloride is manifested in a vigorous development of *Navicula halophila* (34.7 %), which is regarded as a mesohalobe, whereas very few halophilous species occur (1.0 %).

Table 21.
Amager Fælled, pool. $^{15}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes lanceolata	+	—	indifferent
— minutissima v. cryptocephala	22	23.2	indiff.
Amphora ovalis	2	2.1	indiff.
Anomoeoneis sphærophora	1	1.0	halophilous
Gomphonema constrictum	1	1.0	indiff.
— intricatum	3	3.2	indiff.
— parvulum	3	3.2	indiff.
Navicula cryptocephala	4	4.2	indiff.
— halophila	33	34.7	mesohalobous
— hungarica	+	—	halophilous
— minima	2	2.1	indiff.
— pupula	3	3.2	indiff.
— rhynchocephala	+	—	indiff.
Nitzschia amphibia	2	2.1	indiff.
— frustulum	3	3.2	indiff.
— hungarica	+	—	mesohalobous
— sp.	4	4.2	?
Rhopalodia gibba	12	12.6	indiff.
	95	100.0	

Table 22.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	13	60.1
	halophilous	2	1.0
Mesohalobous		2	34.7
?		1	4.2
	Total	18	100.0

Compared with the succeeding sample it is an instance of the difficulty of drawing a line of distinction between halophilous and mesohalobous species.

It should be noted that in this sample *Navicula halophila* partly occurs in a small form approaching *N. Gregaria* and yet differing plainly from it by a more distinct striation and a somewhat dissimilar form.

Amager Fælled, ditch east of the shooting grounds.

The sample collected by Sig. Olsen on the $^{15}/_{7}$ 41 consisted of *Characeae* with epiphytes. Purified material was prepared of it.

The water was examined by Sig. Olsen with the following results:

Cl′	135 mg/l.
Hardness (D. H.)	19.5
pH actual	7.5
Min.	6.7
Max.	9.0

The spectrum shows a vigorous development of halophilous species (27.8%), especially *Navicula hungarica*, *N. Gregaria* and *Diatoma elongatum*. Of mesohalobes there are 7.9%, especially *Achnanthes Hauckiana* (7.4%).

Table 23.
Amager Fælled, ditch. $^{15}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes Hauckiana	13	7.4	mesohalobous
— lanceolata	22	12.4	indifferent
— minutissima v. cryptoc.	4	2.3	indiff.
Amphora ovalis	9	5.1	indiff.
Anomoeoneis sphærophora	7	4.0	halophilous
Caloneis silicula	+	—	indiff.
Cocconeis placentula	11	6.2	indiff.
Cyclotella Meneghiniana	1	0.6	halophilous
Diatoma elongatum	5	2.8	halophilous

(continued)

Table 23 (continued).

	Number of individuals	%	
Epithemia sorex	+	—	indiff.
— zebra	+	—	indiff.
Gomphonema sp.	2	1.2	?
Navicula cryptocephala	34	19.2	indiff.
— — v. intermedia	+	—	indiff.
— gregaria	7	4.0	halophilous
— halophila	+	—	mesohalobous
— hungarica	29	16.4	halophilous
— minima	8	4.5	indiff.
— pupula	+	—	indiff.
— pygmæa	1	0.5	mesohalobous
— rhynchocephala	3	1.7	indiff.
Nitzschia amphibia	+	—	indiff.
— apiculata	+	—	mesohalobous
— frustulum	19	10.7	indiff.
Pinnularia sp.	+	—	?
Rhoicosphenia curvata	1	0.5	indiff.
Synedra pulchella	+	—	mesohalobous
	177	100.0	

Table 24.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	15	62.6
	halophilous	5	27.8
Mesohalobous		5	7.9
?		2	1.7
	Total	27	100.0

Flynder Lake

is situated only ½ km. distant from Dybe Lake. SIG. OLSEN found the following data for the character of the water:

Cl′	590 mg/l.
Total hardness (D. H.)	9.0
transient	0.3
permanent	8.7
pH actual	7.6
Min.	7.2
Max.	8.6

Thus the water is very much like that of Dybe Lake but differs from it especially by its high chloride content.

The Halobion spectrum shows this very plainly: 26.1 % halophilous and 12.3 % mesohalobous forms.

Table 25.

Flynder Lake, scrapings off stones. 5/6 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes minutissima v. cryptoc.	129	30.7	indifferent
Amphora coffæiformis	24	5.7	indiff.
— commutata	+	—	mesohalobous
— ovalis	2	0.5	indiff.
Cocconeis placentula	2	0.4	indiff.
Cymbella æqualis	15	3.6	indiff.
— microcephala	5	1.2	indiff.
— parva	4	1.0	indiff.
— pusilla	46	11.0	halophilous
Diatoma elongatum	17	4.1	halophilous
Epithemia Argus	25	6.0	indiff.
Fragilaria brevistriata	4	1.0	indiff.
— lapponica	34	8.1	indiff.
Hantzschia amphioxys	1	0.2	indiff.
Mastogloia Braunii	1	0.2	mesohalobous
— elliptica v. Dansei	3	0.7	mesohalobous
— Smithii v. lacustris	10	2.4	indiff.
Navicula cincta	21	5.0	halophilous
— — v. Heufleri	+	—	halophilous
— cryptocephala v. veneta	7	1.7	indiff.
— elegans	+	—	euhalobous
— halophila	21	5.0	mesohalobous
— hungarica	+	—	halophilous

(continued)

Table 25 (continued).

	Number of individuals	%	
Navicula oblonga	+	—	indiff.
— protracta	+	—	mesohalobous
— pupula	1	0.2	indiff.
— radiosa	2	0.4	indiff.
Nitzschia capitellata	25	6.0	halophilous
— denticula	8	1.9	indiff.
— sp.	8	1.9	?
Pinnularia microstauron	1	0.2	indiff.
Rhopalodia gibba	1	0.2	indiff.
Synedra affinis	+	—	halophilous
— pulchella	3	0.7	mesohalobous
	420	100.0	

Table 26.
Spectrum.

	Number of forms	% of individuals
Oligohalobous — halophobous	0	0.0
Oligohalobous — indifferent	18	59.7
Oligohalobous — halophilous	7	26.1
Mesohalobous	7	12.3
Euhalobous	1	0.0
?	1	1.9
Total	34	100.0

Præstø Fjord.

The sample was taken in the narrow water inside the Mader at the mouth of the fjord and consists of filiform algae and Characeae with epiphytes. Collected by Sig. Olsen on the $^{18}/_{8}$ 41 (station 64). *Potamogeton pectinatus*, *Chara crinita* and *Zanichellia major* occurred here. The material was purified with acid.

About the water in the fjord Dr. Kaj Hansen says: The salinity shows some seasonal fluctuations, just as it varies somewhat in the different parts of the water. According to analyses made in the summer of 1941 the chloride content lies between

4000 and 6000 mg/l. The pH is likewise variable but always shows an alkaline reaction of the water; values ranging from 7.18 to 8.08 were found.

The water is sea-water diluted with freshwater, thus literally brackish water. According to its chloride content it corresponds to Redeke's mesohaline area.

The spectrum shows a predominance of indifferent forms (66.8%) while the halophilous forms are sparse (6%). In ad-

Table 27.

Præstø Fjord, on filiform algae and Characeae. Aug. 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes brevipes	+	—	euhalobous
— longipes	+	—	euhalobous
— Hauckiana	4	3.0	mesohalobous
Amphora coffæiformis	3	2.3	mesohalobous
Campylodiscus Echeneis	+	—	euhalobous
Cocconeis pediculus	1	0.7	indifferent
— placentula	27	20.5	indiff.
— scutellum	11	8.3	euhalobous
— — v. parva	+	—	mesohalobous
Cyclotella Meneghiniana	1	0.7	halophilous
Epithemia sorex	16	12.3	indiff.
— turgida	32	24.3	indiff.
— zebra	8	6.1	indiff.
Fragilaria pinnata	+	—	indiff.
Grammatophora marina	+	—	euhalobous
Hyalodiscus scoticus	+	—	euhalobous
Mastogloia elliptica	8	6.1	mesohalobous
— pumila	9	6.8	euhalobous
— Smithii v. amphicephala	2	1.5	indiff.
Navicula gregaria	+	—	halophilous
Rhopalodia musculus	+	—	mesohalobous
— ventricosa	1	0.7	indiff.
Rhoicosphenia curvata	1	0.7	indiff.
Surirella ovata	+	—	indiff.
Synedra pulchella	1	0.7	mesohalobous
— tabulata	7	5.3	halophilous
	132	100.0	

Table 28.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	10	66.8
	halophilous	3	6.0
Mesohalobous		6	12.1
Euhalobous		7	15.1
	Total	26	100.0

dition there are 12.1% of mesohalobous forms and 15.1% of euhalobous littoral forms. It would seem that there is a mixture of two groups of species, euryhaline freshwater forms and euryhaline mesohalobous and euhalobous forms.

Lyngby Mose.

Situated on the northern side of Lyngby Lake in N. Sealand.

Table 29.
Lyngby Mose, squeeze of Sphagnum. $^{31}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Eunotia exigua	27	34.6	halophobous
— — forma	30	38.5	halophobous
Hantzschia amphioxys	+	—	indiff.
Pinnularia borealis	+	—	indiff.
— söhrensis v. inflata	11	14.1	halophobous
— subcapitata v. Hilseana	10	12.8	halophobous
	78	100.0	

Table 30.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	4	100.0
	indifferent	2	0.0
	Total	6	100.0

The analysed sample is a squeeze of Sphagnum collected by Sig. Olsen on the $^{31}/_{7}$ 41. He found the following data for the water:

Cl′	6 mg/l.
Hardness (D. H.)	1.6
pH actual	3.6
Min.	3.6
Max.	6.0

Hence the water must be termed extremely acid with an unusually small content of chloride and other salts in solution.

Accordingly the Diatom flora comprises exclusively halophobous species, especially *Eunotiae*, as well as *Pinnularia söhrensis* v. *inflata* and *Pinnularia subcapitata* v. *Hilseana*.

Bøllemosen, near Skodsborg.

The sample was of bottom material collected by Sig. Olsen on the $^{31}/_{7}$ 41. It was purified with acid.

Sig. Olsen found the data of the water to be:

Cl′	22 mg/l.
Hardness (D. H.)	2.5
pH actual	3.7
Min.	3.7
Max.	3.8

Table 31.

Bøllemosen; Bottom material, purified. $^{31}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Cymbella sp.	1	0.3	?
Eunotia alpina	263	75.2	halophobous
— lunaris	45	12.9	halophobous
— tenella	6	1.7	halophobous
— veneris	1	0.3	halophobous
Gomphonema sp.	1	0.3	?
Pinnularia Hilseana	28	8.1	halophobous
— sp.	1	0.3	?
Tabellaria flocculosa	3	0.9	halophobous
	349	100.0	

Table 32.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	6	99.1
	indifferent	0	0.0
	halophilous	0	0.0
Mesohalobous		0	0.0
?		3	0.9
	Total	9	100.0

The water must therefore be characterised as highly acid with a strong buffer effect, a small content of lime, but with a normal content of chloride.

The Diatom flora turned out to consist almost entirely of halophobous species intermixed with a few whose place in the Halobion system could not be determined.

Peatbog I, Lille Lyngby south of Arre Lake.

The sample was collected in a place where peat had been cut. It consisted of filiform algae and bottom parts adhering to Characeae. Sample collected by Sig. Olsen on the $^{27}/_{7}$ 41. Material purified with acid was prepared.

Sig. Olsen found the following data for the water:

Cl′	114 mg/l.
Hardness (D. H.)	17.2
pH actual	8.6
Min.	6.6
Max.	9.0

The water must thus be said to be alkaline, of considerable hardness, and containing no small amount of chloride. Whence this originates cannot be said.

The spectrum shows a predominance of indifferent forms but has a distinct contingent of halophilous and mesohalobous

forms. A *Nitzschia* determined as *N. frustulum* constituted 24% of the total of individuals. This species has been regarded as halophilous, but I have considered it best to be cautious and tabulate it as indifferent.

Table 33.

Peatbog I, Lille Lyngby near Arre Lake. $^{27}/_{7}$ 41. Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes lanceolata	14	2.3	indifferent
— linearis	21	3.5	indiff.
— minutissima v. cryptoc.	84	13.9	indiff.
Amphora ovalis	2	0.3	indiff.
Cocconeis placentula	23	3.8	indiff.
Cyclotella Meneghiniana	+	—	halophilous
Cymbella helvetica	+	—	indiff.
Eunotia lunaris	6	1.0	halophobous
Fragilaria brevistriata	1	0.2	indiff.
Gomphonema acuminatum	19	3.1	indiff.
— lanceolatum	7	1.0	indiff.
— parvulum	30	5.0	indiff.
Hantzschia amphioxys	1	0.2	indiff.
Navicula cryptocephala	11	1.8	indiff.
— — v. exilis	24	4.0	indiff.
— — f. minuta	3	0.5	?
— gregaria	16	2.6	halophilous
— halophila	26	4.3	mesohalobous
— hungarica	11	1.8	halophilous
— minima	59	9.8	indiff.
— viridula	1	0.2	indiff.
— sp.	1	0.2	?
Nitzschia amphibia	40	6.6	indiff.
— dissipata	4	0.6	indiff.
— frustulum	145	24.0	indiff.
— gracilis forma?	1	0.2	indiff.
Nitzschia sp.	26	4 3	?
Rhoicosphenia curvata	8	1.3	indiff.
Stephanodiscus Astræa v. minuta	18	3.0	indiff.
Synedra affinis	2	0.3	halophilous
— ulna	+	—	indiff.
	604	100.0	

Table 34.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	1	1.0
	indifferent	21	85.0
	halophilous	4	4.7
Mesohalobous		1	4.3
?		4	5.0
	Total	31	100.0

Peatbog II, Lille Lyngby near Arre Lake.

Situated near the former. The material which was from Chara, that is to say, consisting largely of epiphytes, was purified with acid. The sample was collected by SIG. OLSEN on the $^{22}/_{5}$ 41. The following data were found:

Cl′	124 mg/l.
Hardness (D. H.)	16.5
pH actual	8.3
Min.	6.6
Max.	8.6

The water resembles that of peatbog I in character, but it contains a little more chloride. The spectrum shows the distinct occurrence of halophilous species, especially *Synedra tabulata* (= *affinis*), while the only mesohalobous form is *Navicula halophila* (0.6%).

Table 35.
Peatbog II, Lille Lyngby near Arre Lake $^{27}/_{7}$ 41. Leg. SIG. OLSEN.

	Number of individuals	%	
Achnanthes lanceolata	6	1.9	indifferent
— linearis	4	1.3	indiff.
— minutissima v. cryptoc.	73	23.4	indiff.
Amphora ovalis	1	0.3	indiff.
— — v. pediculus	2	0.6	indiff.
Cocconeis placentula	1	0.3	indiff.

(continued)

Table 35 (continued).

	Number of individuals	%	
Cyclotella Meneghiniana	1	0.3	halophilous
Diatoma elongatum	2	0.6	halophilous
Fragilaria capucina v. mesolepta	10	3.2	indiff.
— construens var.	1	0.3	indiff.
— Vaucheriae	2	0.6	indiff.
Gomphonema lanceolatum	3	1.0	indiff.
— parvulum	6	1.9	indiff.
Meridion circulare	+	—	halophobous
Navicula cryptocephala	2	0.7	indiff.
— — v. exilis	16	5.1	indiff.
— gregaria	8	2.6	halophilous
— halophila	2	0.6	mesohalobous
— hungarica	16	5.1	halophilous
— minima	45	14.4	indiff.
Nitzschia amphibia	10	3.2	indiff.
— frustulum	17	5.4	indiff.
— sp.	7	2.2	?
Stephanodiscus Astræa v. minutula	33	10.6	indiff.
Synedra tabulata	45	14.4	halophilous
— Ulna	+	—	indiff.
	313	100.0	

Table 36.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	1	0.0
	indifferent	18	74.2
	halophilous	5	23.0
Mesohalobous		1	0.6
?		1	2.2
	Total	26	100.0

Peatbog by Ullerup Forest near Hundested.

The sample consisted of Chara with parts of the soil attached. The material was purified with acid. The sample was collected by Sig. Olsen ($^{22}/_{6}$ 41), who found the following data for the character of the water:

Cl′	170 mg/l.
Hardness (D. H.)	32
pH actual	7.4
Min.	6.8
Max.	8.9

The water must be characterised as alkaline hard water with a comparatively high content of chloride.

The spectrum suffers from the defect that there appears a small form of *Navicula* (resembling *N. cryptocephala*) which does not seem to agree with any of the described forms of this species[1]. Consequently no information as to its place in the Halobion system can be gathered from the literature; but judging from its occurrence in my samples it seems probable that it is somewhat halophilous, though highly euryhaline. As in the samples from the peatbogs near Lille Lyngby the mesohalobous *N. halophila* occurs here too (4.6%).

Table 37.

Peatbog by Ullerup Forest near Hundested. $^{22}/_{5}$ 41.

Leg. Sig. Olsen.

	Number of individuals	%	
Achnanthes minutissima v. cryptoceph.	83	21.4	indifferent
Anomoeoneis exilis	9	2.3	indiff.
Cyclotella Meneghiniana	+	—	halophilous
Cymbella Cesatii?	3	0.8	?
— cymbiformis	5	1.2	indiff.
— microcephala	67	17.2	indiff.
— parva	2	0.5	indiff.
Diatoma elongatum	13	3.3	halophilous
Epithemia argus	20	5.6	indiff.
Gomphonema intricatum	37	9.5	indiff.
— — v. pumila	53	13.5	indiff.
Navicula cryptocephala f. minuta	69	17.7	?
— halophila	18	4.6	mesohalobous
— radiosa	4	1.0	indiff.
Rhopalodia gibba	1	0.2	indiff.
Synedra Acus	4	1.0	indiff.
— Ulna	1	0.2	indiff.
	389	100.0	

[1] Described as *N. cryptocephala* var. *intermedia* f. *minuta* n. f.

Table 38.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	12	73.6
	halophilous	2	3.3
Mesohalobous		1	4.6
?		2	18.5
	Total	17	100.0

Well No. 629 at Reinsbjerg near Lejre $^{21}/_{4}$ 41.

This is an artesian well sunk by the Copenhagen Water Works by boring on the $^{9}/_{9}$—$^{4}/_{10}$ 1933. Its situation is at the bottom of a valley 1.31 m. above the level of the sea. When it was sunk a layer of mud containing seashells was traversed to a depth of 6.8 m, then various ice age strata down to green sand at a depth of 37.2—51.5 m. Lime with flint was met with here down to a depth of 55.2 m. The superimposed layer must be supposed to be a strand formation from the stone age, that is to say, elevated sea bottom, and it might therefore be anticipated that marine Diatoms were to be found in the mud of the well. This was not the case to any great extent, however, but there occurred a number of more or less demolished frustules of *Campylodiscus echeneis;* no entire shells of this species seemed to be present, so it must be presumed that it does not at the present day live on the spot.

The well was examined in April 1941. The bottom of the valley had been under water in the winter of 1940—41, but at the time of examination the water had sunk and there was now a small basin into which the water from a tube ran. From the basin a rill (c. 2 dm. wide) ran for 3—4 m. to a hole where the water disappeared into a drain-pipe. The temperature of the water in the emerging jet was 9° C.; it was ascertained, by Mr. Pape after the boring that it contained 3000 mg/l. Cl′, and it has therefore a distinctly salt taste.

Four samples in all were taken from the basin of the well and the rill, and the Diatoms in these determined. The number of species proved to be rather small, whereas some species

were developed in very great number. Halobion spectra were made for all four samples. The dominant form in them all agrees closely with *Navicula cincta* f. *minuta* in Van Heurck Types Nr. 83. As to the place of this form in the Halobion system no information is available; I presume that it is halophilous just like the species (see p. 79). Subject to this supposition the halophilous species will show marked dominance (80.7—99.3%), the indifferent species being sparsely represented (0.7—19.3%). Only 2 mesohalobous species were present, viz. *Diploneis didyma* and *D. interrupta*. Only the latter was found in so great a number that it could be included in one of the spectra (sample 3) as 0.5% of the total number. No halophobous species were present in any of the samples.

According to the scale in BUDDE (1931) this water would be referable to the boundary between the Oligohalobia and the β-Mesohalobia, and this agrees well with the 3000 mg Cl′/l. which were found.

For comparison we may also quote KRASSKE (1933), who examined the Diatom vegetation in "Drei Quellen" in Erfurt containing 1604—2248 mg. NaCl per l. or about 972—1356 mg Cl′ per l. KRASSKE has given lists of species, stating the frequency of the individual species in the various samples. Converting the frequencies into figures according to KOLBE, I have tried to set up Halobion spectra for the individual samples. It turns out that the spectra are almost the same for all the samples, so I shall only give one, that for sample 6. The species in this were:

	Number of species	%
halophobous	0	0.0
indifferent	23	54.9
halophilous	15	24.3
mesohalobous	13	20.8
	51	100.0

This spectrum differs from that from Lejre by the great number of indifferent and mesohalobous individuals. Hence despite the lower chloride content, the springs at Erfurt have a higher percentage of Mesohalobes than the spring at Lejre, but on the other hand the number of indifferent species is also far higher. Apart from the fact that no conclusive comparison can

be drawn between the spectra since they are calculated in different ways, it is nevertheless probable that the results from the springs at Erfurt would have turned out to be much the same had my method of counting been adopted, and the question then arises what the cause of the disparity in the spectra may be. It is possible that the chemical composition of the water in other respects, which is unknown for both springs, may be the cause. But the disparity might also be due to the fact that, while the springs at Erfurt are ancient natural springs, the spring at Lejre has been produced artificially a few years ago. When the water began to flow, there were presumably in the place a number of Diatoms of the kind usually found in freshwater, the greater part indifferent and some halophilous. These were the species now present, which thrive best in very salt water, while many of the indifferent species died off. Even if mesohalobous species might grow excellently in the water, it may be conceived that they have not appeared yet. The circumstance that the well and its surroundings have been under water in the winter may also have contributed to destroy the mesohalobous species. It is only natural then that the halophilous forms which will tolerate the freshwater in the winter just as well as the salt water of the well, should have gained the ascendancy.

Table 39.
Well 629, sample 1. $^{24}/_{4}$ 41.

	Number of individuals	%	
Diploneis interrupta	+	—	meso-euhalob.
Hantzschia amphioxys	+	—	indiff.
Navicula cincta	+	—	halophilous
— — f. minuta	281	93.6	halophilous
— cryptocephala	1	0.4	indiff.
— Gregaria	13	4.3	halophilous
— viridula	1	0.4	indiff.
Nitzschia amphibia	+	—	indiff.
— commutata	3	1.0	halophilous
Pinnularia appendiculata v. budensis	+	—	mesohalobous
Surirella ovata	1	0.3	indiff.
	300	100.0	

Table 40.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	5	1.1
	halophilous	4	98.9
Mesohalobous		2	0.0
	Total	11	100.0

Table 41.
Well 629, sample 2. $^{21}/_{4}$ 41.

	Number of individuals	%	
Anomoeoneis sphærophora	+	—	halophilous
Diploneis didyma	+	—	mesohalobous
— interrupta	1	2.2	mesohalobous
Hantzschia amphioxys	2	4.5	indifferent
Navicula cincta f. minuta	36	80.0	halophilous
— Gregaria	4	8.9	halophilous
— rhynchocephala	+	—	indiff.
— viridula	1	2.2	indiff.
Nitzschia commutata	+	—	halophilous
Pinnularia microstauron	+	—	indiff.
Surirella ovata	+	—	indiff.
Synedra Ulna f.	1	2.2	?
	45	100.0	

Table 42.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	5	6.7
	halophilous	4	88.9
Mesohalobous		2	2.2
?		1	2.2
	Total	12	100.0

Table 43.
Well 629, sample 3 $^{21}/_{4}$ 41.

	Number of individuals	%	
Diploneis interrupta	1	0.5	mesohalobous
Hantzschia amphioxys	2	1.0	indifferent
Navicula cincta	1	0.5	halophilous
— — f. minuta	175	83.5	halophilous
— cryptocephala v. veneta	1	0.5	indiff.
— Gregaria	1	0.5	halophilous
— rhynchocephala	+	—	indiff.
— viridula	15	7.2	indiff.
Nitzschia commutata	10	4.8	halophilous
Pinnularia microstauron	2	1.0	indiff.
Surirella ovata	1	0.5	indiff.
	209	100.0	

Table 44.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	5	10.2
	halophilous	5	89.3
Mesohalobous		1	0.5
	Total	11	100.0

Table 45.
Well 629, sample 4. $^{21}/_{4}$ 41.

	Number of individuals	%	
Diploneis interrupta	+	—	mesohalobous
Navicula cincta f. minuta	147	76.5	halophilous
— Gregaria	2	1.0	halophilous
— integra	1	0.6	halophilous
— rhynchocephala	1	0.6	indifferent
— viridula	17	8.8	indiff.
Nitzschia commutata	5	2.6	halophilous
Pinnularia microstauron	6	3.1	indiff.
Surirella ovata	13	6.8	indiff.
	192	100.0	

Table 46.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	4	19.3
	halophilous	4	80.7
Mesohalobous		1	0.0
	Total	9	100.0

Spring moor in Hammer Bakker.

The algal vegetation in this little spring moor, situated at the upper end of the so-called long valley of the preserved area of Hammer Bakker, has been described by Boye Petersen (1932, p. 13), and already then I called attention to the remarkably large number of halophobous species of Diatoms as well as to the occurrence of 12 species of *Desmidiaceae*. From a Halobion spectrum erected on the basis of a preparation of Diatoms from withered leaves on the mud between the mounds in the spring moor (9/8 1928) it appears that the halophobous and the indifferent species constitute more than 90%, while there are only 2.0% of halophilous species. But notably it is remarkable that the Halophobes constituted 45.6%; it must be inferred, then, that the water is very poor in chlorides.

Table 47.
Hammer Bakker, spring moor; on withered leaves on mud between mounds. 9/8 1928.

	Number of individuals	%	
Cymbella gracilis	+	—	halophobous
— ventricosa	4	4.0	indifferent
Diploneis ovalis v. oblongella	+	—	indiff.
Eunotia gracilis	8	8.1	halophobous
— lunaris	1	1.0	halophobous
— pectinalis v. impressa	3	3.1	halophobous
— tenella	3	3.1	halophobous

(continued)

Table 47 (continued).

	Number of individuals	%	
Gomphonema gracile v. naviculaceum	15	15.2	indiff.
— parvulum	+	—	indiff.
— subclavatum	2	2.0	halophilous
Navicula cocconeiformis	7	7.1	halophobous
— cryptocephala v. veneta	4	4.0	indiff.
— Placenta	1	1.0	indiff.
— variostriata	2	2.0	halophobous
Neidium affine v. amphirhynchus	1	1.0	halophobous
Nitzschia communis	5	5.1	indiff.
— debilis	2	2.0	indiff.
— thermalis v. intermedia	7	7.1	indiff.
— vermicularis v. terrestris	2	2.0	?
Pinnularia acrosphæria	1	1.0	indiff.
— divergens v. elliptica	+	—	?
— nodosa v. formica	+	—	halophobous
— subcapitata	1	1.0	indiff.
— viridis	3	3.0	indiff.
— sp.	3	3.0	?
Rhopalodia gibberula v. producta	3	3.0	indiff.
Surirella constricta	+	—	indiff.
— linearis	1	1.0	indiff.
Tabellaria flocculosa	20	20.2	halophobous
	99	100.0	

Table 48.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	10	45.6
	indifferent	15	47.4
	halophilous	1	2.0
?		3	5.0
	Total	29	100.0

Langemose at Ullerslev (Fyen).

The vegetation and topographical conditions of the bog have been described by Svend Andersen (1930). It is a very long-drawn bog harbouring in certain areas various halophytes among

Table 49.

Langemose at Ullerslev. Bottom material. Aug. 1930.
Leg. GRAVERSEN.

	Number of individuals	%	
Achnanthes minutissima v. cryptoc. ..	72	17.0	indifferent
Amphipleura pellucida	+	—	indiff.
Amphiprora paludosa	+	—	mesohalobous
Amphora coffæiformis	2	0.5	mesohalobous
— — v. acutiuscula ..	2	0.5	mesohalobous
— commutata	1	0.2	mesohalobous
— Normannii	+	—	halophobous
— ovalis	14	3.3	indiff.
— veneta	+	—	indiff.
Anomoeoneis sphærophora	+	—	halophilous
— exilis	+	—	indiff.
Caloneis amphisbæna v. subsalina	+	—	mesohalobous
— bacillum	1	0.2	indiff.
— Silicula	1	0.2	indiff.
— — v. truncatula	1	0.2	indiff.
Cocconeis placentula	2	0.5	indiff.
Cyclotella Meneghiniana	1	0.2	halophilous
Cymatopleura solea	+	—	indiff.
Cymbella æqualis	2	0.5	indiff.
— Cistula	1	0.2	indiff.
— obtusiuscula	2	0.5	?
— lanceolata	+	—	indiff.
— microcephala	2	0.5	indiff.
— parva	+	—	indiff.
Denticula tenuis	1	0.2	?
Diatoma elongatum	8	1.9	halophilous
Diploneis elliptica	2	0.5	indiff.
— interrupta	3	0.7	mesohalobous
— oculata	1	0.2	indiff.
— ovalis	7	1.7	indiff.
— pseudovalis	1	0.2	mesohalobous
Epithemia Argus	1	0.2	indiff.
Fragilaria brevistriata	32	7.6	indiff.
— construens v. venter	156	36.5	indiff.
— pinnata	3	0.7	indiff.
Gomphonema bohemicum	1	0.2	?
— constrictum	1	0.2	indiff.
— intricatum	19	4.4	indiff.
— olivac. v. subramosum .	1	0.2	indiff.
Gyrosigma acuminatum	2	0.5	indiff.
Hantzschia elongata	+	—	indiff.
Mastogloia Smithii	+	—	indiff.
— — v. lacustris	3	0.7	indiff.

(continued)

Table 49 (continued).

	Number of individuals	%	
Navicula cincta	+	—	halophilous
— cryptocephala v. intermedia	3	0.7	indifferent
— — var?	1	0.2	indiff.?
— dicephala	+	—	indiff.
— elegans	+	—	euhalobous
— Falaisensis	10	2.3	?
— Gregaria	+	—	halophilous
— halophila	4	0.9	mesohalobous
— — v. subcapitata	3	0.9	mesohalobous
— hungarica	15	3.5	halophilous
— oblonga	1	0.2	indiff.
— pupula	1	0.2	indiff.
— pygmæa	1	0.2	mesohalobous
— peregrina	4	0.9	mesohalobous
— radiosa	1	0.2	indiff.
— rhynchocephala	10	2.3	indiff.
— salinarum	1	0.2	mesohalobous
— viridula	3	0.7	indiff.
Neidium affine v. amphirhynchus	+	—	halophobous
— Iridis v. ampliata	1	0.2	halophobous
Nitzschia amphibia	5	1.2	indiff.
— communis	2	0.5	indiff.
— debilis	1	0.2	indiff.
— Denticula	+	—	indiff.
— hungarica	1	0.2	mesohalobous
— palea	1	0.3	indiff.
— Sigma	5	1.2	mesohalobous
— sigmoidea	+	—	indiff.
— sinuata	+	—	indiff.
— vitrea	+	—	mesohalobous
Pinnularia viridis	+	—	indiff.
Rhoicosphenia curvata	+	—	indiff.
Rhopalodia gibba	+	—	indiff.
— musculus	+	—	mesohalobous
Stauroneis legumen	1	0.3	indiff.
— producta	1	0.3	halophilous
— Smithii	+	—	indiff.
Surirella Moelleriana	+	—	halophilous
— ovata	+	—	indiff.
Synedra acus	1	0.2	indiff.
— pulchella	1	0.3	mesohalobous
— tabulata	1	0.3	halophilous
— ulna	2	0.5	indiff.
— — v. biceps	+	—	indiff.

Table 50.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	3	0.2
	indifferent	53	83.7
	halophilous	9	6.2
Mesohalobous		17	6.7
Euhalobous		1	0.0
?		4	3.2
	Total	87	100.0

the phanerogams. Their occurrence is supposed to be due to the presence of saltish groundwater which wells forth in certain places. JOHS. ANDERSEN and ØDUM (1930) have mentioned the same locality (p. 74) and have had the water from the various parts of the bog analysed for *sodium chloride*. They found that the amount of this substance was rather variable, the values mentioned are from 0.26 to 0.77 ‰ NaCl (=160—470 mg. Cl′/l.), but it is intimated that the values are most probably too low, the samples having been collected after a heavy rain by which the water must be supposed to have received a rather large admixture of freshwater. Mr. GRAVERSEN collected Diatom material from the bog for me in August 1930. He took two samples, partly of mud from the bottom, partly of *Chara*, both samples being from SV. ANDERSEN's upper area of the bog, but from different places there. The *Chara* was identified by Dr. JOHS. IVERSEN as a typical *Chara hispida*. A single specimen was, however, somewhat different and corresponded most nearly to *Ch. hispida* f. *longifolia* A. Br. A lot of epiphytic Diatoms were found on the *Chara*.

Part of each of the two samples was purified with sulphuric acid and potassium bichromate and from this styrax preparations were made. In the bottom mud a total of 87 forms was found, and 28 forms on the *Chara*.

The spectra for the two samples differ somewhat, that for the *Chara* showing a higher percentage of halophilous forms, whereas the bottom mud has the higher percentage of Mesoha-

lobes; but both of them have thus a distinct contingent of brackish water forms.

If these spectra are compared with spectra from localities with a known chloride content, it turns out that they correspond most nearly to a salinity such as the lowest of the values found by ANDERSEN and ØDUM.

Table 51.

Langemose at Ullerslev, Aug. 1930. Leg. GRAVERSEN.
From Chara.

	Number of individuals	%	
Achnanthes minutissima v. cryptoc....	107	30.2	indifferent
Amphora coffæiformis	2	0.6	mesohalobous
— Normannii	1	0.2	halophobous
— ovalis	1	0.2	indiff.
Anomoeoneis exilis	39	11.0	indiff.
Cyclotella Meneghiniana	1	0.3	halophilous
Cymbella Cesatii	7	2.0	?
— cistula	+	—	indiff.
— cymbiformis	1	0.3	indiff.
— microcephala	38	10.7	indiff.
— parva	2	0.6	indiff.
Diatoma elongatum	39	11.0	halophilous
Eunotia Arcus	9	2.5	halophobous
Fragilaria brevistriata	+	—	indiff.
— capucina	2	0.6	halophobous
— crotonensis	1	0.3	indiff.
Gomphonema constrictum	+	—	indiff.
— intricatum	42	11.8	indiff.
— parvulum	1	0.3	indiff.
Navicula cincta	2	0.6	halophilous
— Gregaria	4	1.1	halophilous
— halophila	9	2.5	mesohalobous
— peregrina	1	0.3	mesohalobous
— viridula	+	—	indiff.
Nitzschia capitellata	7	2.0	halophilous
— palea	9	2.5	indiff.
Synedra Acus v. angust.	25	7.0	indiff.
— Ulna	5	1.4	indiff.
	355	100.0	

Table 52.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	3	3.3
	indifferent	16	76.3
	halophilous	5	15.0
Mesohalobous		3	3.4
?		1	2.0
	Total	28	100.0

Watering Trough for Camels, east gate of Kairouan.

The sample was collected in N. Africa by Professor C. RAUNKJÆR on the $^{22}/_{2}$ 1910. It consists of an *Oedogonium* sp. (sterile) with a number of Diatoms. The preparation is made of non-purified material and only contains 9 forms, one of which is very dominant, viz. *Synedra pulchella* (85%), which is generally classified as a Mesohalobe. KOLBE and TIEGS (1929) regard it as one of the most constant species in saliferous inland lakes. Indifferent species are very sparse and halophobous ones entirely absent. The obvious inference is that the water must have been of rather high salinity; but I shall refrain from any further comments hereon; these must be postponed till the future when it is better known what degree of salinity *Synedra pulchella* requires to develop vigorously. HUSTEDT (1939) regards it as fairly euryhaline.

Table 53.
Camels' watering trough, east gate, Kairouan. $^{22}/_{2}$ 1910.
Leg. C. RAUNKJÆR.

	Number of individuals	%	
Amphora coffæiformis	2	1.2	mesohalobous
— veneta	+	—	indifferent
Navicula cryptocephala v. veneta	3	1.8	indiff.
— hungarica	6	3.6	halophilous
Nitzschia fonticola	12	7.2	indiff.
— hungarica	2	1.2	mesohalobous
— palea	+	—	indiff.
Synedra tabulata	+	—	halophilous
— pulchella	140	85.0	mesohalobous
	165	100.0	

Table 54.
Spectrum.

		Number of forms	% of individuals
Oligohalobous	halophobous	0	0.0
	indifferent	4	9.0
	halophilous	2	3.6
Mesohalobous		3	87.4
	Total	9	100.0

General Remarks.

In some cases I have drawn up more than one spectrum for the water body in question, thus for Sct. Jørgens Lake, Dybe Lake, Nors Lake, Langemose, and Well No. 629. For each locality the spectra showed very good agreement despite the fact that the number of species in the samples often differed much, just as the composition of the flora frequently varied a good deal. This shows that the Halobion spectrum for a body of water is not something fortuitous but bears a relation to the character of the water.

As already mentioned at p. 7, the localities in which the chloride content of the water is known fall into two groups, 1) lakes and the like, and 2) bogs. These may again be divided into two subgroups a) bogs with acid water, poor in lime (Lyngby Mose, Bøllemose), and b) bogs with alkaline water more or less rich in lime. In Denmark we have, in addition, an important type of lake with acid water poor in lime; of such I have had no samples or analyses at my disposal.

The acid bogs occupy a special position by the fact that the spectra almost exclusively show halophobous forms (99—100 %), whereas the spectra of the alkaline bogs are more like those of the lakes. I have, however, preferred to tabulate separately the spectra from the lakes and the bogs since it turned out that the results in the two groups did not quite agree. The reason why this is so is presumably that, even though the chloride content, degree of acidity, and hardness of the water in the two kinds of localities are much the same, the water is nevertheless

very different, seeing that the lake water does not contain humous substances in any appreciable amount, while such are present in abundance in the water of the bogs.

In both groups (Tables 55 and 56) it is seen that when there is more than 100 mg. Cl′ per litre, this is distinctly visible in the Halobion spectrum. As far as the bogs are concerned this appears less distinctly, amongst other reasons on account of the insufficiency of the material. If the lakes are considered separately, (Table 55), it turns out that up to about 100 mg. Cl′ per litre the indifferent forms constitute 80—95 %, but above this limit their number drops to 56—70 %, while halophilous and mesohalobous species increase correspondingly in number.

This agrees closely with Redeke's (1922) division of waters according to their salinity, for he puts the lowest limit for oligohaline water at 100 mg. Cl′ per litre. He has arrived at this result by considering entirely different organisms from those treated here, namely plankton forms and animals, hence it is worth noting that in dealing with the Diatoms we arrive at almost the same limit, which may therefore be supposed to be a real biological limit.

This is somewhat in opposition to several other authors who hold that a far higher content of chloride is required for the water to be classed as brackish water. Thus Kolbe (1927), who has not investigated waters with less than 500 mg. Cl′/l., and the same applies to Budde (1930, 1931).

That the threshold for the effect of the chloride factor lies at approximately 100 mg. Cl′/l. seems to me to appear distinctly from the spectra.

If now we consider the spectra for waters below the limit indicated above, it will appear quite plainly that here other factors than the chloride content determine the character of the spectrum. On comparing the spectrum from Bøllemose (with 22 mg. Cl′/l.) with that from Bure Lake (with 22 mg. Cl′/l.), it will be seen that the halophobous species are absolutely dominant in Bøllemose, while only 6 % of the Diatoms in Bure Lake are halophobous. This disparity cannot be due to a difference in the chloride content of the water; more probably it is caused by the fact that the water in Bøllemose has pH 3.7—3.8, while that of Bure Lake has pH 7.2—8.2, or that the water in Bølle-

Table 55.

Lakes and similar localities	Cl′ mg/l.	Hardness (D.H.)	pH			Oligohalobous			Mesohalobous	Euhalobous	?	No. of species	Individuals counted
			Min.	actual	Max.	halophobous	indifferent	halophilous					
Magle Lake	16	8.5	6.4	7.5	7.5	1.0	89.9	0.0	0.0	0.0	9.1	34	296
Gurre Lake	19	5.2	6.2	7.4	8.8	2.7	88.0	0.0	1.3	0.0	8.0	30	150
Fure Lake	20	7.0	6.8	8.2	8.6	0.0	88.8	0.0	0.0	0.0	11.2	44	204
Bure Lake	22	7.0	7.2	8.2	8.2	0.6	91.0	0.6	0.0	0.0	7.8	55	335
Sct. Jørgens Lake, bottom mud	35	16.0	?	?	?	1.5	93.8	1.6	0.0	0.0	3.1	42	64
— — — epiphyte vegetation	—	—	—	—	—	1.6	91.0	0.0	0.0	0.0	7.4	21	190
Dybe Lake, scrapings off stones	35	9.5	6.6	8.0	8.4	1.3	95.6	0.3	0.9	0.0	1.9	46	313
— — on sand	—	—	—	—	—	2.9	93.6	0.4	0.2	0.0	2.9	46	449
Nors Lake, scrapings off lime	42	6.6	6.8	7.29	8.7	0.0	97.3	0.9	0.0	0.0	1.8	35	217
— — , scrapings off granite	—	—	—	—	—	0.0	84.7	0.0	0.0	0.0	15.3	39	136
Amager Fælled, pool	97	17.8	6.8	7.4	8.2	0.0	60.1	1.0	34.7	0.0	4.2	18	95
— — , ditch	130	19.5	6.7	7.5	9.0	0.0	62.6	27.8	7.9	0.0	1.7	27	177
Flynder Lake, scrapings	590	9.0	7.2	7.6	8.6	0.0	56.1	26.1	12.3	0.0	5.5	34	420
Præstø Fjord	4-6000	?	7.2	?	8.08	0.0	66.8	6.0	12.4	15.1	0.0	26	132

Table 56.

Bogs	Cl′ mg/l.	Hardness (D. H.)	pH			Oligohalobous			Mesohalobous	Euhalobous	?	No. of species	Individuals counted
			Min.	actual	Max.	halophobous	indifferent	halophilous					
Lyngby Mose	6	1.6	3.6	3.6	6.0	100.0	0.0	0.0	0.0	0.0	0.0	6	78
Bøllemosen	22	2.5	3.7	3.7	3.8	99.1	0.0	0.0	0.0	0.0	0.9	9	349
Peatbog I, Ll. Lyngby	114	17.2	6.6	8.6	9.0	1.0	81.5	4.7	4.3	0.0	8.5	31	604
— II, — —	124	16.5	6.6	8.3	8.6	0.0	72.9	23.0	0.6	0.0	3.5	26	313
— , Ullerup forest	170	32.0	6.8	7.4	8.9	0.0	73.6	3.3	4.6	0.0	18.5	17	389
Other localities													
Langemose at Ullerup	?	?	?	?	?	0.2	83.7	6.2	6.7	0.0	3.2	87	422
— - — (from *Chara*)	?	?	?	?	?	3.3	76.3	15.0	3.4	0.0	2.0	28	355
Well 629, sample 1	3000?	?	?	?	?	0.0	1.1	98.9	0.0	0.0	0.0	11	300
— —, — 2	—	?	?	?	?	0.0	6.7	88.9	2.2	0.0	2.2	12	45
— —, — 3	—	?	?	?	?	0.0	9.7	89.8	0.5	0.0	0.0	11	209
— —, — 4	—	?	?	?	?	0.0	19.3	80.7	0.0	0.0	0.0	9	192
Camels' watering trough, Kairouan	?	?	?	?	?	0.0	9.0	3.6	87.4	0.0	0.0	9	165
Hammer Bakker, spring moor	?	?	?	?	?	45.6	47.4	2.0	0.0	0.0	5.0	29	99

mose has a hardness of 2.5, but that of Bure Lake has 7.0. The lime content and the degree of acidity are to a certain extent interdependent quantities. Whether the species in Bøllemose should be called calciphobous or acidophilous in contrast with the normal freshwater species must be left open.

If, on the other hand, we compare the samples from Peatbogs I and II (Ll. Lyngby) and the peatbog at Ullerup Forest with the two almost similar ones, as far as the chloride content is concerned, derived from Amager Fælled, the spectra are in much better agreement. Here it is evident that the chloride factor has asserted itself.

The spectra for Magle Lake, Gurre Lake, Fure Lake, Bure Lake, Sct. Jørgens Lake, Dybe Lake, and Nors Lake resemble each other so much that no real difference can be held to exist between them, since the species whose place in the Halobion system is uncertain, could they be introduced into the spectrum, would do away with all differences. It is a natural inference, therefore, that in these lakes, where the chloride content ranges from 16 to 42 mg. Cl′ per litre, it is of no importance for the Diatom flora; other factors are of greater significance. In all these lakes the indifferent forms show great dominance, and in some of them there occurs a small percentage of halophobous and halophilous species, while Mesohalobes are practically absent.

If we pass from these to localities with a higher chloride content, such as Amager Fælled and Flynder Lake, with more than 100 mg. Cl′/l., it will be seen that halophobous forms do not occur at all. Halophilous forms are present in quantity, and Mesohalobes are represented by a distinct percentage. There is a difficulty here in keeping halophilous and mesohalobous species distinct. In one spectrum we find 34.7 % Mesohalobes but only 1 % halophilous species (pool, Am. Fælled); in another there are 27.8 % halophilous species and 7.8 % Mesohalobes (ditch, Am. Fælled), in spite of the fact that the two waters do not differ much in chloride content. The cause of these disparities is no doubt that several species are in reality on the border-line between halophilous and mesohalobous forms. Similar considerations apply to the samples from bogs.

Finally, euhalobous forms are represented in Præstø Fjord (15 %).

The material is not sufficient for an attempt to establish the limits of the chloride content in oligohalobous, mesohalobous, and euhalobous waters; but the method can presumably be used in future investigations with this object in view.

It is likewise probable that if several investigations of the same kind as this are made, it will be possible to introduce essential corrections in our conception of the place of the individual species in the Halobion system. In the present work I have almost entirely refrained from drawing such conclusions.

Summary.

1. It has proved possible, by using KOLBE's Halobion system in conjunction with the statistical method here described, to set up spectra that show fairly accurately the relation to the salinity of the water investigated.
2. From this it may be inferred that the generally accepted view of the place of the species in the Halobion system is on the whole correct, but with a reservation in the case of halophobous and halophilous-mesohalobous species.
3. The spectra set up would seem to show that the threshold for the influence of the chloride factor on the composition of the Diatom flora lies at about 100 mg. Cl′/l.
4. It will presumably be possible in future to draw fairly far-reaching conclusions as to the salinity of the water from a Halobion spectrum.

List of the Species Found.

With Remarks on the Place in the Halobion System.

Achnanthes brevipes Ag. Præstø Fjord (small number). KOLBE (1927) regards it as euhalobous, HUSTEDT (1939) as mesohalobous, euryhaline.

Euhalobous.

— *Clevei* Grun. Nors Lake (2.9 ‰), Fure Lake (1.0 ‰), and in Sct. Jørgens Lake and Magle Lake in small number, i. e. in lakes with at most 42 mg. Cl′/l. KOLBE (1927) and HUSTEDT (1938, 1939) regard the species as indifferent; SCHULZ (1928) takes it to be at least halophilous,

more probably mesohalobous. My observations do not indicate that it is halophilous; I must therefore at present regard it as: Indifferent.

Achnanthes Clevei Grun. v. *rostrata*. Only found in a few specimens in Fure Lake; not referred to the Halobion system in the literature. Indifferent?

— *conspicua* A. Mayer. Found in small number in Bure Lake. Not referred to the Halobion system in the literature. ?

— *exigua* Grun. In Fure Lake and Bure Lake in small number. All authors agree in classing it as: Indifferent.

— *Hauckiana* Grun. According to Schulz (1928) and Hustedt (1939) the species is mesohalobous; in my material it does not occur in water with less than 130 mg. Cl′/l.: Præstø Fjord (3.0‰), Am. Fælled, ditch (7.4‰). Mesohalobous.

— *lanceolata* (Bréb.) Grun. Occurred in lakes with between 19 and 130 mg. Cl′/l., but only numerous (12.4‰) at the latter value (Am. Fælled, ditch). Further in bogs with 114 to 124 mg. Cl′/l. Regarded by Kolbe (1927) and Hustedt (1938) as indifferent and euryhaline; Hustedt states that it is most frequent in running water. Hustedt (1929) mentions it as mesohalobous and euryhaline. According to my material the species might seem to be somewhat halophilous, but highly euryhaline. For the present I will, however, regard it as: Indifferent.

— *linearis* W. Sm. Of the place of this species in the Halobion system no definite opinion is expressed in the literature. I have found it in water containing from 19—124 mg. Cl′/l., both in lakes and bogs, but only in great quantity at the lowest chloride content (Gurre Lake 21.4‰). It must therefore be regarded as oligohalobous and presumably most nearly Indifferent?

Achnanthes longipes Ag. Only found in Præstø Fjord in small number. According to HUSTEDT (1939) it is euhalobous. Euhalobous.

— *minutissima* KÜTZ. var. *cryptocephala* Grun. Species very common in the lake samples, occurs in them all, and in Dybe Lake constitutes more than 50 % of the Diatoms present. Likewise common in the samples from bogs with slightly acid-alkaline water, whereas it has not been seen in the highly acid bog localities. Distinctly indifferent and euryhaline. KOLBE (1927), SCHULZ (1928), and HUSTEDT (1938) all regard this form as oligohalobous. Indifferent.

— *Østrupii* (A. Cl.) Hustedt. Only observed in Magle Lake (2.4 %). HUSTEDT (1939) oligohalobous, indifferent. Indifferent.

Amphipleura pellucida Kütz. According to KOLBE (1927) and HUSTEDT (1939) oligohalobous, indifferent. Only observed in few specimens in Sct. Jørgens Lake and Langemose. Indifferent.

Amphiprora paludosa W. Sm. Only found in few specimens in Langemose. According to KOLBE (1927) mesohalobous and according to HUSTEDT (1939) also euryhaline. Mesohalobous.

Amphora coffæiformis Ag. All authors agree in classing the species as mesohalobous; but HUSTEDT (1938, 1939) adds that it is euryhaline, while LEGLER and KRASSKE (1940) regard it as stenohaline. In my material, forms which I have referred to this species occurred in Gurre Lake, Dybe Lake, Flynder Lake and Præstø Fjord, i. e. in water with from 19—6000 mg. Cl′/l. However, it is evident that deviating forms occur, which may also differ ecologically from the typical form. This will perhaps explain the above-mentioned disagreement among the authors as to whether it is steno- or euryhaline. Mesohalobous.

Amphora coffæiformis v. *acutiuscula* (Kütz). Only observed in Langemose in small number. KOLBE (1927): Mesohalobous.

— *commutata* Grun. Observed in Flynder Lake and Langemose in small numbers. According to KOLBE (1927) and HUSTEDT (1939) mesohalobous. Mesohalobous.

— *Normannii* Rabh. Only observed in Langemose in small number. According to HUSTEDT (1938) halophobous and aërophilous. Halophobous.

— *ovalis* Kütz. According to KOLBE (1927), SCHULZ (1928), and HUSTEDT (1938, 1939) the species is oligohalobous, and SCHULZ also terms it indifferent. I have found it, though in small quantity, in all lakes with between 19 and 590 mg. Cl'/l., also in two of the non-acid bogs. Evidently rather euryhaline. Indifferent.

— — v. *pediculus* Kütz. KOLBE (1927) and HUSTEDT (1939) tabulate this variety as oligohalobous; SCHULZ (1928) is doubtful whether to regard it as indifferent or halophilous. In fairly large numbers I have it from Nors Lake (23.5 ‰), Sct. Jørgens Lake (14.0 ‰), and Bure Lake (20,6 ‰), also in smaller number from Magle Lake, Fure Lake and Dybe Lake, as well as from Peatbog II, Ll. Lyngby (0.6 ‰). This does not seem to indicate that it is halophilous, so I class it as Indifferent.

— *veneta* Kütz. Found in small number in Langemose and a watering trough for camels in Kairouan. KOLBE (1927) regards it as indifferent and euryhaline, while BUDDE (1932) classes it as a doubtful Mesohalobe and highly euryhaline. It will therefore be best for the present to regard it as Indifferent.

Anomoeoneis exilis (Kütz.) Cl. HUSTEDT (1938): oligohalobous, prefers alkaline water. Found in small number in a peatbog at Ullerup (2.3 ‰), but in greater number in one of the samples from Langemose (11 ‰). Presumably: Indifferent.

Anomoeoneis sphærophora (Kütz.) Pfitzer. All authors agree in regarding the species as halophilous. Found in rather a small number (4.0 and 1.0 %) in the samples from Amager Fælled (97—130 mg. Cl'/l.), as well as in Well No. 629 and in Langemose, that is to say, all in all in distinctly saliferous localities. Halophilous.

Asterionella formosa Hass. This pronounced plankton species was found in Bure Lake and Fure Lake in small quantity. HUSTEDT (1939): oligohalobous. Presumably: Indifferent.

Caloneis amphisbaena (Bory) Cl. v. *subsalina* (Donk.) Cl. Occurred in small numbers in Langemose. According to SCHULZ (1928) and HUSTEDT (1939) it must be classed as: Mesohalobous.

— *bacillum* (Grun.) Mereschk. Occurred in small number in Nors Lake and Langemose. Regarded by HUSTEDT (1939) as oligohalobous and is presumably: Indifferent.

— *silicula* (Ehrb.) Cl. Occurred in small number in a ditch on Amager Fælled and in Langemose. All authors consider the species oligohalobous; only KOLBE (1927) suggests that it may be slightly halophilous. For the present it is best to regard it as: Indifferent.

— — v. *truncatula* (Grun.) Cl. Occurred in small quantity in Dybe Lake and Langemose. Regarded by KOLBE (1927) and HUSTEDT (1939) as oligohalobous like the species and is then presumably: Indifferent.

Campylodiscus Echeneis Ehrb. Only occurred in Præstø Fjord. The species is a pure saltwater form and must therefore be regarded as Euhalobous.

— *noricus* Ehrb. v. *hibernicus* (Ehrb.) Grun. Found in the bottom mud of Sct. Jørgens Lake in appreciable numbers (3.1 %). Regarded by KOLBE (1927) and HUSTEDT (1939) as oligohalobous and is probably: Indifferent.

Cocconeis pediculus Ehrb. This species which I have found in the sample from Præstø Fjord and from Fure Lake is classed by Budde (1930) and Schulz (1928) as halophilous, while Kolbe (1927) only regards it as euryhaline. Hustedt (1939) also considers it euryhaline, perhaps somewhat halophilous. For the present I will regard it as: Indifferent.

— *placentula* Ehrb. Occurred in all the lakes but not in the acid bogs. The highest percentage was found in Præstø Fjord (20.5 ‰), and in Gurre Lake (10.7 ‰). All authors agree that the species is indifferent. Hustedt (1938) notes that it avoids waters with a low pH. This applies to my samples also, where it proves to be highly euryhaline. Indifferent.

— — v. *euglypta* (Ehrb.) Cleve. Occurred in small number in Bure Lake and Magle Lake. Kolbe (1927) regards it as ecologically identical with the species. Indifferent.

— *scutellum* Ehrb. Occurred in Præstø Fjord only (8.3 ‰). According to Hustedt (1939) meso-euhalobous, highly euryhaline. It is essentially a marine species and I will therefore for the present regard it as: Euhalobous.

— — v. *parva* Grun. Only observed in small number in Præstø Fjord. Both Kolbe (1927) and Hustedt (1938) regard v. *parva* as verging between euhalobous and mesohalobous. Schulz (1928) simply classes it as Mesohalobous.

Cyclotella comta (Ehrb.) Kütz. Plankton form from lakes and streams, of very common occurrence. In my samples it was found in all the lakes with at most 42 mg. Cl′/l., and in several of them in considerable numbers. (Sct. Jørgens Lake 47.9 ‰!). Regarded by Kolbe (1927) and Hustedt (1939) as oligohalobous, but there seems to be a low limit to how much Cl′ it will tolerate in order to thrive. For the present it must be tabulated as: Indifferent.

Cyclotella Kützingiana Thw. I have found no information in the literature about the place of the species in the Halobion system. According to HUSTEDT (1930) it especially develops in plenty in forest pools. The form which I have with some doubt referred to this species was found in small number in Bure Lake and Magle Lake (with less than 22 mg. Cl′/l.), which would seem to indicate that it is very sensitive to Cl′. Provisionally it may be regarded as Indifferent?

— *Meneghiniana* Kütz. Only occurred in small quantity in the samples with at least 97 mg. Cl′/l. (Præstø Fjord; Amager Fælled, ditch; peatbog at Ullerup and peatbogs I and II, as also in Langemose). Regarded by all authors as Halophilous.

— *stelligera* Cleve et Grun. Observed in small number in the bottom sample from Sct. Jørgens Lake. HUSTEDT (1939) says that it is an Oligohalobe, so for the present I class it as: Indifferent?

Cymatopleura elliptica (Bréb.) W. Sm. Occurred in small number in the samples from Dybe Lake. Regarded by KOLBE (1927) and HUSTEDT (1939) as oligohalobous, and I presume that it must be classed as: Indifferent.

— *solea* (Bréb.) W. Sm. Occurred in small numbers in Dybe Lake and Fure Lake as well as in Langemose. According to KOLBE (1927) the species is oligohalobous (euryhaline?) and according to HUSTEDT (1939) oligohalobous, indifferent. Hence I regard it as: Indifferent.

Cymbella æqualis Sm. Found only in Flynder Lake in any number worth mentioning (3.6 %). According to HUSTEDT (1929) oligohalobous, so for the present I class it as: Indifferent.

— *affinis* Kütz. Occurred in small number in the lakes containing at most 42 mg. Cl′/l., most frequently in Bure Lake (11.0 %) with 22 mg.

Cl'/l. HUSTEDT (1938) calls the species oligohalobous and points out that he has found it in quantity at pH 8.5. Most probably it is: Indifferent.

Cymbella Cesatii (Rabh.) Grun. In small amount (0.8 %) in the peatbog at Ullerup Forest. Place in the Halobion system ?

— *cistula* (Hempr.) Grun. This otherwise widespread species I have only found in Langemose. According to KOLBE (1927) and SCHULZ (1928) indifferent, while HUSTEDT (1938, 1939) calls it oligohalobous. Indifferent.

— — v. *maculata* (Kütz.) V. H. Found in small number in Gurre Lake and Langemose. The variety probably has the same ecological requirements as the species, so it is presumably: Indifferent.

— *cuspidata* Kütz. Only observed in Fure Lake in small number. According to all authors oligohalobous, and according to KOLBE (1927): Indifferent.

— *cymbiformis* (Ag.) V. H. Observed in rather small number in Sct. Jørgens Lake, the peatbog at Ullerup, and in Langemose. According to SCHULZ (1928) and HUSTEDT (1938, 1939) oligohalobous, so it is probably Indifferent.

— *Ehrenbergii* Kütz. Observed in small number only in Dybe Lake. According to KOLBE (1927) oligohalobous, in the table: Indifferent.

— *gracilis* Rabh. Only observed in the spring moor in Hammer Bakker, in small number. According to SCHULZ (1928) and HUSTEDT (1939): Halophobous.

— *helvetica* Kütz. Occurred in waters with from 42—114 mg. Cl'l., but everywhere in rather small number. Tabulated by HUSTEDT (1939) as oligohalobous; for the present, however, best regarded as Indifferent.

Cymbella lacustris (Ag.) Cleve. Only found in noteworthy quantity in Nors Lake (1.5—2.8 %). According to Cleve (Syn. I, p. 167) it has been found in freshwater as well as in slightly brackish water, which would seem to indicate that it is rather euryhaline. For the present I will class it as Indifferent.

— *lanceolata* (Ehrb.) V. H. Only seen in small number in the samples. Is probably: Indifferent.

— *leptoceros* (Ehrb.?) Grun. Only seen in Nors Lake in rather small quantity (1.7 %). According to Hustedt (1938) it is an oligohalobous littoral form, especially in stagnant waters with an alkaline reaction. Probably: Indifferent.

— *microcephala* Grun. It was one of the commonest species in my samples, and one of those that showed the highest percentage. Found in Magle Lake (17.6 %) as well as in Flynder Lake (1.2 %). It showed the highest percentage in one of the samples from Nors Lake (30.1 %). Also in a peatbog at Ullerup (17.2 %) and in Langemose. So it occurred in water with from 16—590 mg. Cl′/l. and thus proved highly euryhaline. According to Kolbe (1927) oligohalobous, in the table indifferent, and according to Hustedt (1938) oligohalobous, mainly occurring in alkaline waters. Indifferent.

— *obtusiuscula* (Kütz.) Grun. The place of the species in the Halobion system is only mentioned by Schulz (1928) as oligohalobous; in my material it is very scarce. ?

— *parva* (W. Sm.) Cl. According to Schulz (1928) and Hustedt (1939) oligohalobous. Found in Bure Lake, Dybe Lake, Nors Lake and Flynder Lake, that is to say, in water with 22—590 mg. Cl′/l. Also in the peatbog at Ullerup (170 mg. Cl′/l.). It should then no doubt be regarded as: Indifferent.

Cymbella prostrata (Berk.) Cl. According to KOLBE (1927) indifferent, SCHULZ (1928) oligohalobous, HUSTEDT (1939) oligohalobous, indifferent. In my material it only occurs in lakes but not in those with more than 42 mg. Cl′/l. Indifferent.

— *pusilla* Grun. According to HUSTEDT (1938) halophilous-mesohalobous and (1939) halophilous. I have only found it in Flynder Lake (11.0 ‰) with 540 mg. Cl′/l. Halophilous.

— *sinuata* Greg. The species, which is considered oligohalobous by all authors (KOLBE 1927: indifferent), has only been observed in few specimens from Dybe Lake and Gurre Lake. Indifferent.

— *ventricosa* Kütz. Regarded by all authors as oligohalobous; KOLBE (1927) put it down as indifferent and euryhaline. Only seen in Nors Lake, Dybe Lake, Bure Lake and Magle Lake in rather a small number, also in the spring moor in Hammer Bakker. Indifferent.

Denticula tenuis Kütz. Not referred to the Halobion system. Only observed in Langemose. ?

Diatoma elongatum Ag. KOLBE (1927), SCHULZ (1928), and BUDDE (1930) all agree in classing the species as halophilous, but HUSTEDT (1939) considers it oligohalobous, indifferent. In my samples it was not observed at less than 35 mg. Cl′/l. Most abundant in Flynder Lake (4.1 ‰) (590 mg. Cl′/l.). Further it was found in 11.0 ‰ in the sample from *Chara* in Langemose. Halophilous.

— *vulgare* Bory. Constituted a very essential part of the sample from Fure Lake (24.8 ‰). According to KOLBE (1927) halophobous—at most indifferent, while SCHULZ (1928) regards its position as doubtful. Provisionally I will class it as: Indifferent.

Diploneis didyma Ehrb. Only observed in small number in one of the samples from Well No. 629. Both

Schulz (1928) and Hustedt (1939) regard it as mesohalobous; the latter adds that it is euryhaline. Mesohalobous.

Diploneis elliptica (Kütz.) Cl. Only observed in Langemose (0.5 %). According to Kolbe (1927) and Schulz (1928) indifferent. Indifferent.

— *interrupta* (Kütz.) Cl. In small number in the samples from Well No. 629 and Langemose. According to Schulz (1928) and Hustedt (1939): Mesohalobous.

— *oculata* (Bréb.) Cleve. Only observed in Langemose (0.2 %). Regarded by Hustedt (1938) as oligohalobous. For the present I will class it as: Indifferent?

— *ovalis* (Hilse) Cleve. Schulz (1928) considers the species indifferent, Hustedt (1939) calls it oligohalobous. Only observed in small numbers in some of the lakes with less than 42 mg. Cl′/l., as also in Langemose. Indifferent.

— — v. *oblongella* Nägeli. Observed in small number in the spring moor in Hammer Bakker. Schulz (1928) regards it as indifferent, Hustedt (1939) as oligohalobous. Indifferent.

— *pseudovalis* Hustedt. The species only observed in Langemose (0.2 %). Also found by Hustedt in slightly saliferous inland waters. For the present I will put it as Mesohalobous?

Epithemia argus Kütz. Hustedt (1938) is not indisposed to regard the species as halophobous. My samples do not tend to show this, they seem to indicate that it is fairly euryhaline, as it was found in Flynder Lake (590 mg. Cl′/l. (6 %)) and in Bure Lake (22 mg. Cl′/l. (0.3 %)); also in the peatbog at Ullerup and in Langemose. Indifferent.

— *Hyndmannii* W. Sm. The species only observed in small number in Nors Lake. Classed by Kolbe (1927) as: Indifferent.

Epithemia intermedia Fricke. Scarce in the samples from Bure Lake (0.3 ‰). Its place in the Halobion system is not mentioned in the literature. Probably oligohalobous. ?

— *sorex* Kütz. KOLBE (1927) tabulates the species with doubt as halophilous; in which SCHULZ (1928) agrees with him. My material affords no support for this supposition, the species being common (12.3 ‰) in Præstø Fjord and found in small number in the lakes, except in Fure Lake where it was represented by 7.9 ‰. It must at any rate be highly euryhaline. This would also seem to be shown by MEISTER's statement (1912) that it is specially common in alpine lakes at a height of 1500—2200 m. I must conclude, therefore, that the species is: Indifferent.

— *turgida* (Ehrb.) Kütz. Both KOLBE (1927) and SCHULZ (1928) regard the species as indifferent, euryhaline. In my material I have only observed it from Præstø Fjord where it is represented by 24.3 ‰. Indifferent.

— *zebra* (Ehrb.) Kütz. Found in Præstø Fjord (6.1 ‰), on Amager Fælled in ditch, and in Bure Lake (0.3 ‰). The species is commonly regarded as indifferent. This is confirmed by my observations. According to HUSTEDT's observations (1938) it should be more sensitive to pH and prefer alkaline water. It is characteristic that neither the species nor any of the varieties has been found in any of the bog localities, in spite of the high pH values of some of these. Possibly, then, this is not the decisive factor, but perhaps the content of humous substances in the water. Indifferent.

— — v. *saxonica* (Kütz.) Grun. Usually regarded as indifferent (KOLBE 1927, HUSTEDT 1938, 1939). Found in nearly all the lakes with less than 42 mg. Cl′/l., but not in any of the bogs. Indifferent.

Epithemia zebra v. *porcellus* (Kütz.) Grun. KOLBE (1927) thinks that this variety is more halophilous than the other forms of the species. SCHULZ (1938) and HUSTEDT (1938), however, also regard this form as indifferent. Observed in Nors Lake (0.7 %), Sct. Jørgens Lake (1.6 %), and Fure Lake (2.4 %). Indifferent.

Eucocconeis flexella (Kütz.) Cl. Observed in very few specimens from Dybe Lake. Is the same as *E. minuta* Cl. which according to KOLBE (1927) is:
Halophobous.

— — v. *alpestris* Brun. Observed in Dybe Lake on sand (2.9 %) and Gurre Lake (0.7 %). According to KOLBE (1927): Halophobous.

— *lapponica* Hustedt. Observed in small number in Nors Lake and Dybe Lake. According to HUSTEDT's information in Rabh. Kryptogamenfl. Bd. VII, 2: 415 it is presumably:
Halophobous?

Eunotia alpina (Naeg.) Hustedt. Constituted 75.2 % of the Diatoms in the sample from Bøllemose. Occurs in swamps, springs and on wet rocks (HUSTEDT in Rabh. Kryptogamenfl. VII, 2). Is presumably, like most of the Eunotiaspecies,
Halophobous?

— *arcus* Ehrb. Found in small numbers in Sct. Jørgens Lake and in Langemose. According to HUSTEDT (Rabh. Kryptogamenfl. VII, 2) less sensitive to lime than the other species of the genus; therefore possibly not so markedly halophobous. SCHULZ (1928) tabulates it as:
Halophobous.

— — v. *fallax* Hustedt. Found in Bure Lake in small number. Presumably, like the species,
Halophobous?

— *exigua* (Bréb.) Rabh. Constituted 34.6 % of all Diatoms in the sample from Lyngby Mose. All authors refer to the species as markedly sphagnophilous (SCHULZ 1928, KRIEGER 1930, HUSTEDT

1938). It must therefore be regarded, as by HUSTEDT 1939, as Halophobous.

Eunotia exigua forma. In Lyngby Mose 38.5 %. This somewhat diverging form is remarkable by the valve being nearly straight; such forms HUSTEDT likewise refers to *E. exigua.* It is therefore presumably: Halophobous.

— *gracilis* (Ehrb.) Rabh. Occurred in small number in Gurre Lake, but constituted 8.1 % in the spring moor in Hammer Bakker. Regarded by KOLBE (1927) and SCHULZ (1928) as halophobous, whereas HUSTEDT intimates that it is more probably indifferent. For the present I will class it as: Halophobous.

— *lunaris* (Ehrb.) Grun. Found in Bøllemose (12.9 %) and in the spring moor in Hammer Bakker (1.2 %). KOLBE (1927) and SCHULZ (1928) both consider the species halophobous. HUSTEDT (1938) thinks that it is not a pronounced halophobe, and this agrees with the fact that it occurs in appreciable numbers (1.0 %) in Peatbog I, Lille Lyngby with 114 mg. Cl'/l. Nevertheless it is probably in the main Halophobous.

— *pectinalis* (Kütz.) Rabh. Found in Sct. Jørgens Lake (1.6 %). Classed by KOLBE (1927) and SCHULZ (1928) as halophobous, while HUSTEDT thinks (1939) that it is not so pronounced a halophobe as the other species. Halophobous.

— — v. *impressa* O. Müll. Found in the spring moor in Hammer Bakker (3.1 %); like the species it is presumably: Halophobous.

— *tenella* (Grun.) Hustedt. According to HUSTEDT (1939) halophobous. Occurred in the spring moor in Hammer Bakker (3.1 %) and in Bøllemosen (1.7 %). Halophobous.

— *veneris* Kütz. Occurred in small quantity in Bøllemosen (0.3 %). According to SCHULZ (1928) and HUSTEDT (1939): Halophobous.

Fragilaria brevistriata Grun. KOLBE (1927) thinks that the species may be halophilous; but this is denied by SCHULZ (1928) and HUSTEDT (1938). According to my observations it must be rather euryhaline, since it occurs in lakes with from 16—590 mg. Cl′/l., though in rather small number. Most frequent in Bure Lake (22 mg. Cl′/l.) where it constitutes 6.2 %. Also found in Peatbog I, Ll. Lyngby and in Langemose. Indifferent.

— *capucina* Desm. Occurred in Sct. Jørgens Lake and in Langemose in small number. KOLBE (1927) tabulates the species as possibly halophobous, HUSTEDT (1939) classes it only as oligohalobous. Halophobous?

— — v. *mesolepta* (Rabh.) Grun. KOLBE (1927) gives the variety as oligohalobous and possibly halophobous. Its occurrence in water with 124 mg. Cl′/l. (Peatbog I, Ll. Lyngby) in appreciable number (3.2 %) would rather seem to indicate that it is indifferent. Indifferent.

— *construens* (Ehrb.) Grun. Both KOLBE (1927) and SCHULZ (1928) regard both the species and the varieties as indifferent and euryhaline. In the material at hand they have only been found in lakes with less than 42 mg. Cl′/l. Indifferent.

— — v. *binodis* (Ehrb.) Grun. Occurred in some of the same lakes as the species. Particularly abundant in Magle Lake (8.4 %). Indifferent.

— — v. *venter* (Ehrb.) Grun. Occurred together with the species in some of the lakes. It is remarkable that it constituted 36.5 % of all Diatoms in one of the samples from Langemose. Indifferent.

— *crotonensis* Kitt. Occurred in Fure Lake, Dybe Lake, and Nors Lake, as well as in Langemose in

a rather small number. Regarded by KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) as: Indifferent.

Fragilaria leptostauron (Ehrb.) Hustedt (= *F. Harrisonii*). Occurred in rather a small quantity in the bottom sample from Sct. Jørgens Lake. KOLBE (1927) classes it with doubt as halophobous, while HUSTEDT (1939) merely calls it oligohalobous. Halophobous?

— *lapponica* Grun. SCHULZ (1928) terms the species indifferent. I have only found it in Flynder Lake (8.1 ‰). If it is indifferent it must also be euryhaline. Indifferent?

— *pinnata* Ehrb. Commonly recognised as an indifferent species. Only occurred in lakes with at most 42 mg. Cl′/l. and in negligible number in Præstø Fjord, possibly introduced accidentally. Indifferent.

— *Vaucheriae* (Kütz.) Boye P. (= *F. intermedia*). Occurred in rather a small amount in most of the lakes with under 42 mg. Cl′/l., as well as in Peatbog II, Ll. Lyngby (0.6 ‰). SCHULZ (1928) and KOLBE (1927) regard it as an oligohalobous, indifferent species. My observations indicate the same. Indifferent.

Gomphonema acuminatum Ehrb. Appeared in Gurre Lake, Sct. Jørgens Lake, and Nors Lake in small number. Also in Peatbog I, Ll. Lyngby (3.1 ‰). KOLBE (1927) and SCHULZ (1928) consider the species oligohalobous, indifferent. Indifferent.

— — v. *Brebissonii* (Kütz.) Cleve. Found in small quantity in Sct. Jørgens Lake. Supposed to bear the same relation as the species to the chloride content of the water. Indifferent.

— — v. *coronata* Ehrb. Noted from Sct. Jørgens Lake and Bure Lake in small number. KOLBE (1927) and SCHULZ (1928) both regard it as oligohalobous, Indifferent.

Gomphonema bohemicum Reichelt et Fricke. Identification uncertain. The species is very rare and so it has not been referred to the Halobion system in the literature. Noted in small number in the sample from Langemose. ?

— *constrictum* Ehrb. Occurred in Sct. Jørgens Lake, a pool on Amager Fælled, and Langemose in small number. Both Kolbe (1927), Schulz (1928) and Hustedt (1939) are agreed in regarding the species as indifferent, euryhaline. Indifferent.

— *gracile* Ebrb. v. *naviculacea* W. Sm. Occurred in the spring moor in Hammer Bakker (15.2 ‰). Regarded by Kolbe (1927) as indifferent, while Schulz (1928) and Hustedt (1938, 1939) class the species as a whole as oligohalobous. Indifferent.

— *intricatum* Kütz. All authors agree in regarding the species as oligohalobous, and Kolbe (1927) tabulates it as indifferent. In my material it occurred in waters with from 35—170 mg. Cl′/l., most frequently in the latter kind. Noted in Sct. Jørgens Lake, a pool on Amager Fælled (3.2 ‰), a peatbog at Ullerup (9.5 ‰), and in Langemose (4.4 and 11.8 ‰). Indifferent.

— — v. *pumila* Grun. Occurred in Magle Lake, Bure Lake, Sct. Jørgens Lake (6.3 and 9.4 ‰), in the peatbog at Ullerup (13.5 ‰), that is to say, in water with from 16—170 mg. Cl′/l. Probably stands in the same relation as the species to the chloride content of the water. Kolbe 1927: Indifferent.

— *lanceolatum* Ehrb. Occurred in Peatbogs I and II, Ll. Lyngby in rather a small quantity. Schulz (1928) and Hustedt (1938, 1939) tabulate the species as oligohalobous. It is presumably: Indifferent.

— *longiceps* Ehrb. f. *gracilis* Hustedt. Occurred in Sct. Jørgens Lake (2.1 ‰). This form does

not seem to have been placed in the Halobion system in the literature. By HUSTEDT (1939) v. *subclavata* is tabulated as oligohalobous, indifferent. ?

Gomphonema olivaceum (Lyngb.) Kütz. Classed by KOLBE (1927) as oligohalobous, indifferent. HUSTEDT (1930) mentions that it also occurs in brackish water. In my material it was only sparsely represented in lakes with less than 42 mg. Cl′/l. (Magle Lake, Bure Lake, Dybe Lake, Nors Lake). Indifferent.

— — v. *calcareum* Cleve. Only observed in Nors Lake (1.8 %). SCHULZ (1928) tabulates the variety as oligohalobous; it is presumably: Indifferent.

— — v. *subramosum* (Kütz). V. H. Occurred in Langemose in small number. The ecology of the variety does not seem to be mentioned. Presumably: Indifferent.

— *parvulum* (Kütz.) Grun. According to KOLBE (1927) and BUDDE (1930, 1932) the species is halophilous. This is doubted by SCHULZ (1928) and denied by HUSTEDT (1938, 1939). The occurrence of the species in my samples might very well indicate that it is somewhat halophilous; at any rate it is highly euryhaline. For the present, however, I will class it as indifferent. Occurred in Bure Lake (0.3 %), Amager Fælled, pool (3.2 %), Peatbog II, Ll. Lyngby (1.9 %), and Peatbog I, Ll. Lyngby (5.0 %), that is to say, in water with from 22—124 mg. Cl′/l. Also in the spring moor in Hammer Bakker and in Langemose. Indifferent.

— *subclavatum* Grun. This species, which is regarded as halophilous by KOLBE (1927) occurred in the spring moor in Hammer Bakker (2.0 %). Halophilous?

Gomphonema ventricosum Greg. Occurred in small number in Bure Lake. Place in the Halobion system unknown. ?

Grammatophora marina (Lyngb.) Kütz. Purely marine form, seen only in small number in Præstø Fjord. According to HUSTEDT (1939) euhalobous, euryhaline. Euhalobous.

Gyrosigma acuminatum (Kütz.) Rabh. Occurred in Sct. Jørgens Lake (9.4 ‰) and in Langemose. SCHULZ (1928) and HUSTEDT (1939) without further explanation class it as oligohalobous. Presumably it is: Indifferent.

— *attenuatum* Kütz. This species is often stated to occur chiefly in brackish water; KOLBE (1927) says that in his experience it is oligohalobous, indifferent; and SCHULZ (1928) and HUSTEDT (1939) are of the same opinion. Found in Sct. Jørgens Lake (7.8 ‰) and in Dybe Lake in small number. Indifferent.

Hantzschia amphioxys (Ehrb.) Grun. All authors agree in classing the species as oligohalobous; but HUSTEDT (1938, 1939) points out its great power of adaptation to different environments. In my samples it only occurred sparsely, but in waters poor in salts as well as in waters rich in salts: Lyngby Mose, Peatbog I, Ll. Lyngby, Flynder Lake, and Well No. 629. Indifferent.

— *elongata* (Hantzsch) Grun. Only occurred in small number in Langemose near Ullerslev. KOLBE (1927): Indifferent.

Hyalodicus scoticus (Kütz.) Grun. Seen in small number in the sample from Præstø Fjord. Marine species, but may also occur in brackish water. HUSTEDT (1939): euhalobous, euryhaline. Euhalobous.

Mastogloia Braunii Grun. Only observed in Flynder Lake (0.2 ‰). SCHULZ (1928): Mesohalobous.

— — v. *Dansei* (Thwaites) Cl. In small number in Flynder Lake and Dybe Lake. According to

Kolbe (1927) and Schulz (1928) this variety is mesohalobous, in fact Kolbe (1927) even thinks that it is stenohaline. In Hustedt's opinion it is halophilous-mesohalobous. My observations do not give any decisive evidence. Mesohalobous.

— *elliptica* Ag. Only observed in Præstø Fjord (6.1 ‰). Regarded by Schulz (1828) and Hustedt (1939) as mesohalobous; the last-named author adds that it is euryhaline. Mesohalobous.

— *pumila* (Grun.) Cleve. Only in Præstø Fjord (6.8 ‰). Marine form, more rarely occurring in brackish water. Hustedt (1939): euhalobous, euryhaline. Euhalobous.

— *Smithii* Thw. v. *amphicephala* Grun. Occurred in Dybe Lake (up to 9.8 ‰), Nors Lake (1.4 ‰), and Præstø Fjord (1.5 ‰); finally in Langemose in small number. Var. *amphicephala* is said to be especially common in brackish water, while var. *lacustris* is presumed to be a freshwater form. Schulz (1928) considers the species as a whole as mesohalobous; whereas Kolbe (1927) does not venture to express any decisive opinion on the question. My observations mainly seem to indicate that both varieties are highly euryhaline. For the present, therefore, it will be most correct to regard it as indifferent. Indifferent.

— — v. *lacustris* Grun. Found in the same waters as v. *amphicephala*, most numerously in Nors Lake (12.4 ‰). See further var. *amphicephala*. Indifferent.

Melosira arenaria Moore. Occurred in small number in Sct. Jørgens Lake and Magle Lake. Kolbe (1927) and Schulz (1928) both regard the species as Indifferent.

— *islandica* (Ehrb.) Kütz. Observed in Fure Lake in small quantity. Schulz (1928) regards subsp. *helve-*

tica as indifferent and limnophilous, and the same probably applies to the species.
Indifferent?

Melosira varians Ag. Only observed in Sct. Jørgens Lake in small number. According to KOLBE (1927) indifferent, and according to HUSTEDT (1939) oligohalobous. Indifferent.

Meridion circulare Ag. KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) regard the species as halophobous. Its occurrence in Peatbog II (Ll. Lyngby) may be accidental. Halophobous.

Navicula cincta (Ehrb.) Kütz. Many authors (KOLBE 1927, SCHULZ 1928, SPRENGER 1930, KRASSKE 1932, HUSTEDT 1938, 1939) simply regard the species as halophilous; BUDDE (1930) classes it as halophilous-mesohalobous, while later the same author (1932) calls it highly euryhaline and regards its position as obscure. Occurred in Flynder Lake (5.0‰), in Well No. 629 (small number), and in Langemose.
Halophilous.

— — v. *Heufleri* Grun. Only observed in Flynder Lake (small number). Not mentioned by any of the authors who have referred species of Diatoms to the Halobion system. Provisionally I will regard it as behaving like the species and class it as Halophilous?

— — f. *minuta* Grun. (V. H. Types 83). Was the dominant form in the samples from Well No. 629 and was found in as much as 76.5—93.6 ‰. This small form does not seem to be mentioned in the literature, but it is found in V. H. Types No. 83 in great quantity. It occurs here in company with several brackish water forms. For the present it must be presumed to be at least halophilous, possibly even mesohalobous. Halophilous?

— *cocconeiformis* Greg. According to HUSTEDT (1930) common in mountain streams; my own experience

from Jan Mayen and Iceland shows a similar occurrence; I will therefore, like HUSTEDT (1939), regard it as Halophobous.

Navicula cryptocephala Kütz. Not observed in the waters poorest in chlorides (not under 35 mg. Cl′/l.). Most abundantly in a ditch on Amager Fælled (19.2 %), less numerously in a pool in the same place (4.2 %), in Dybe Lake, Peatbogs I and II, Ll. Lyngby.

According to KOLBE (1927) probably halophilous; SCHULZ (1928), BUDDE (1930) and SPRENGER (1930) are of the same opinion. BUDDE (1932) says that the species is strongly euryhaline, and LEGLER und KRASSKE (1940) call it extremely euryhaline. HUSTEDT (1938) classes the species as indifferent, almost ubiquist, occurring in fresh water. Here regarded as: Indifferent.

— — v. *exilis* (Kütz.) Grun. KOLBE (1927) and SCHULZ (1928) regarded v. *exilis* as probably halophilous like the species. BUDDE (1932) takes the variety to be highly euryhaline, and it may then for the present be most correct to class it as indifferent. Occurred in Gurre Lake (0.6 %), Peatbogs I and II Ll. Lyngby (4.0 % and 5.1 %). Indifferent.

— — v. *intermedia* Grun. Found in most of the lakes, though in rather a small number: Magle Lake (1.7 %), Gurre Lake (1.3 %), Fure Lake (0.9 %), Bure Lake (1.8 %), Dybe Lake (0.7 %), Nors Lake (0.5 % and 5.2 %), also in small number in a ditch on Amager Fælled and in Langemose. This form, which was transferred by CLEVE (Syn. II, p. 19) to *N. salinarum*, has been restored by HUSTEDT (1930) to N. *cryptocephala*. There are no definite indications of its place in the Halobion system; but judging by the statements as to its occurrence it must be inferred that it is Indifferent.

Navicula cryptocephala f. *minuta* n. f.

Valva lineari-lanceolata, levissime rostrata, long. 23 µ, lat. 5 µ striis 18 in 10 µ, radiantibus, prope apices convergentibus, in medio valvæ sæpe alternatim longioribus et brevioribus, area apicali angusta, centrali rotundata (Fig. 1).

Fig. 1. × 1700.

This small form, which is most similar to *N. cryptocephala* v. *intermedia*, in company with which it often occurs, differs especially from the smaller forms of the species by the fact that the midmost striae often are alternately long and short. Here is a list of the localities in which it occurs, and its percentage frequency: Nors Lake (4.4%), Dybe Lake, sand (1.3 %), stones (0.6 %), Bure Lake (0.9 %), Fure Lake (9.9 %), Gurre Lake (2.0 %), Magle Lake (3.0 %), Peatbog Ullerup (17.7 %), Peatbog I, Ll. Lyngby (0.5 %).

It will be seen from this that it occurs in water with from 16—170 mg. Cl′/l. Most numerous in the peatbog at Ullerup and in Fure Lake. This would seem to indicate that it is highly euryhaline. For the present I shall refrain from placing it in the Halobion system. ?

— — v. *veneta* (Kütz.) Grun. Occurred in Dybe Lake and Flynder Lake (1.7 %), in the spring moor in Hammer Bakker (4.0 %), in a watering trough for camels in Kairouan (1.8 %), and in Well No. 629 (0.5 %). According to Kolbe (1927) and Schulz (1928) it is probably halophilous. Budde (1932) and Legler und Krasske (1940) point out that it is highly euryhaline. It will therefore be most cautious to class it as Indifferent.

— *cuspidata* Kütz. Only observed in small number in Dybe Lake. According to Kolbe (1927) and Hustedt (1939) oligohalobous, indifferent. Indifferent.

Navicula dicephala (Ehrb.) W. Sm. Only observed in small number in Langemose. According to Kolbe (1927) oligohalobous, indifferent. Indifferent.

— *elegans* W. Sm. Observed in Flynder Lake and Langemose in small number. Actually a salt water form which often occurs in brackish water. Presumably euhalobous, euryhaline. Euhalobous.

— *Falaisensis* Grun. Only observed in Langemose (2.3 ‰). Does not seem to have been placed in the Halobion system by any investigator. ?

— *gastrum* Ehrb. Only observed in Dybe Lake in small number. According to Kolbe (1927): Indifferent.

— *gregaria* Donk. Found chiefly in localities with more than 100 mg. Cl′/l., though in small number in Sct. Jørgens Lake (1.6 ‰). Other localities: Amager Fælled, ditch (4.0 ‰), Præstø Fjord (small number), Peatbogs I and II, Ll. Lyngby (2.6 ‰), as well as Well No. 629 and Langemose. According to Schulz (1928) and Budde (1930, 1932), halophilous. Hustedt (1938) says: halophilous or perhaps more probably indifferent. Hustedt (1939): mesohalobous, euryhaline. Halophilous.

— *halophila* (Grun.) Cleve. According to Kolbe (1927) mesohalobous and Hustedt (1938) halophilous-mesohalobous. Only occurred in waters with c. 100 mg. Cl′/l. or more, viz. Amager Fælled, pool (34.7 ‰), ditch (in small number), Flynder Lake (5.0 ‰), Peatbog, Ullerup (4.6 ‰), Peatbog I, Ll. Lyngby (4.5 ‰), II (0.6 ‰). Further in Langemose. Mesohalobous.

— — v. *subcapitata* Østr. Only observed in Langemose (0.7 ‰). Kolbe (1927): Mesohalobous.

— *hungarica* Grun. As to the position of this species in the Halobion system opinions have been somewhat divided. Kolbe (1927) regards v. *capi-*

tata as halophilous?; SCHULZ (1928) considers the species halophilous, but v. *capitata* as indifferent. BUDDE (1930): halophilous, and HUSTEDT (1938 and 1939): the species indifferent, in some forms halophilous. I have only found the species in any considerable quantity in a ditch on Amager Fælled (f. *typica*, 16.4 %) and in Peatbog II, Ll. Lyngby (f. *typica*, 5.1 %). Observed in small quantity in Bure Lake, a pool on Amager Fælled, Peatbog I, Ll. Lyngby, watering trough for camels at Kairouan, and in Langemose. Altogether it seems to me most probable that the species must be regarded as Halophilous.

Navicula integra (W. Sm.) Ralfs. Found in small quantity only (0.6 %) in one of the samples from Well No. 629. HUSTEDT (1939): Halophilous.

— *minima* Grun. Found in a pool and ditch on Amager Fælled (2.1 and 4.5 %), as well as in Peatbogs I and II, Ll. Lyngby (9.8 % and 14.4 %). According to HUSTEDT (1938) oligohalobous and eurytopic, so it is presumably: Indifferent.

— *oblonga* Kütz. Only occurred in small number in my samples: Sct. Jørgens Lake, Dybe Lake, Flynder Lake and Langemose. According to KOLBE (1927) indifferent, while SCHULZ (1928) and HUSTEDT (1938, 1939) class it as oligohalobous. Indifferent.

— *peregrina* (Ehrb.) Kütz. In rather a small amount (0.3, 0.9 %) in Langemose. According to KOLBE (1927), SCHULZ (1928) and HUSTEDT (1939): Mesohalobous.

— *placenta* Ehrb. Only observed in the spring moor in Hammer Bakker (1.0 %). According to HUSTEDT (1938) oligohalobous, aerophilous, atmophytic spring form. It is possible that the species is actually halophobous: but for the present I will regard it as: Indifferent.

Navicula protracta Grun. Only observed in small number in Flynder Lake. According to KOLBE (1927) and SCHULZ (1928) it is mesohalobous, while HUSTEDT (1939) classes it as halophilous.
Mesohalobous.

— *pseudoscutiformis* Hustedt. Observed in small quantity in Gurre Lake. HUSTEDT (1930) states that it occurs in bottom mud in lakes in Holstein as well as in Fichtelgebirge. Place in the Halobion system doubtful. ?

— *pupula* Kütz. Occurred in rather a small number in several of the lakes, indeed both in Gurre Lake and in Flynder Lake (0.7 ‰ and 0.2 ‰). Further in Dybe Lake, a pool and a ditch on Amager Fælled, and in Langemose. KOLBE (1927), SCHULZ (1928) and HUSTEDT (1938) regard the species as indifferent.
Indifferent.

— *pygmæa* Kütz. Only observed in small number in a ditch on Amager Fælled and in Langemose. Regarded by KOLBE (1927) and SCHULZ (1928), as well as HUSTEDT (1938, 1939) as
Mesohalobous.

— *radiosa* Kütz. KOLBE (1927) and SPRENGER (1930) think that this species is somewhat halophilous; but SCHULZ (1928) and HUSTEDT (1938) regard it as indifferent. This agrees well with my experience, for it is found in small number in all the samples from the lakes, regardless of their degree of salinity; whereas it has not been observed in any of the samples from bogs. Indifferent.

— *rhynchocephala* Kütz. Occurred in small number in Nors Lake, ditch and pool on Amager Fælled, Well No. 629, and Langemose; that is to say, not in waters with less than 42 mg. Cl′/l. KOLBE (1927) and HUSTEDT (1938, 1939) consider it indifferent. Only SCHULZ (1928) thinks that it is somewhat halophilous. Indifferent.

Navicula rotaeana (Rabh.) Grun. Only observed in small number in Magle Lake. According to SCHULZ (1928), HUSTEDT (1938, 1939): oligohalobous. For the present I will regard it as: Indifferent.

— *salinarum* Grun. Only observed in Langemose (0.2 %). Regarded by KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) as mesohalobous. Mesohalobous.

— *scutelloides* W. Sm. Found in small number in Magle Lake, Fure Lake, and Bure Lake, also in Nors Lake (2.9 %), that is to say, only in waters with less than 42 mg. Cl′/l. By KOLBE (1927) and HUSTEDT (1938) regarded as indifferent, while SCHULZ (1928) thinks that it has a somewhat halophilous character. Indifferent.

— *subhamulata* Grun. Only seen in Nors Lake (0.7 %). There seems to be no information about the place of this species in the Halobion system. ?

— *subtilissima* Cleve. According to SCHULZ (1928) it is halophobous. The occurrence of the species in Nors Lake (5.9 %) does not seem to indicate that it is markedly halophobous. ?

— *tuscula* (Ehrb.) Grun. Only seen in Fure Lake and Dybe Lake in small number. In KOLBE's opinion (1927) it is indifferent, while SCHULZ (1928) takes it to be slightly halophilous. For the present, however, it is no doubt best to regard it as: Indifferent.

— — f. *minor* HUSTEDT. Observed in small number in Bure Lake, Dybe Lake, and Nors Lake. According to HUSTEDT (1930, p. 309) it is this form which is mentioned by SCHULZ (1926) and KOLBE (1927) by the name *N. torneensis*, and is taken by KOLBE to be: Halophilous?

— *variostriata* Krasske. Only observed in the spring moor in Hammer Bakker (2.0 %). HUSTEDT (1930) says: In swamps, especially with *Sphagnum*. Hence it is presumably sphagnophilous and: Halophobous.

Navicula viridula Kütz. Met with in Peatbog I, Ll. Lyngby (0.2 %) as well as in Well No. 629 and in Langemose. Kolbe (1927), Schulz (1928), and Hustedt (1938, 1939) all state that the species is oligohalobous. Is probably Indifferent.

— *vulpina* Kütz. Does not seem to have been placed in the Halobion system by any author. Only observed in Fure Lake (0.9 %) and Sct. Jørgens Lake (in small number). ?

Neidium affine (Ehrb.) Cl. v. *amphirhyncus* (Ehrb.) Cl. Occurred in Gurre Lake and Langemose in small numbers, likewise in the spring moor in Hammer Bakker. Regarded by Kolbe (1927) as halophobous, while Schulz (1928) thinks it is indifferent. Hustedt (1939) classes it as oligohalobous. It is probably somewhat, though not markedly: Halophobous.

— — f. *hercynica* (A. Mayer) Hustedt. Only observed in Gurre Lake in small number. Its ecology is probably the same as for var. *amphirhyncus*. Halophobous?

— *iridis* (Ehrb.) Cl. Only occurred in small number in Dybe Lake. Both Kolbe (1927), Schulz (1928) and Hustedt (1938) agree that the species is somewhat halophobous. Hustedt in 1939 is more cautious and classes it as oligohalobous. Halophobous.

— — v. *ampliata* (Ehrb.) Cl. Only noticed in Langemose. Schulz (1928) says: presumably halophobous (because it lives in bog water). Halophobous?

Nitzschia acuta Hantzsch. Only in Sct. Jørgens Lake (1.6 %). According to Kolbe (1927), indifferent. Schulz (1928) regards it as var. of *N. dissipata*, but also considers it: Indifferent.

— *amphibia* Grun. Kolbe (1927), Schulz (1928) and Hustedt (1938) agree in regarding the species as oligohalobous, while Kolbe calls it indifferent and Hustedt eurytopic. Budde (1932) differs in

regarding it as β-mesohalobous. For the present I will regard it as indifferent. Occurred in Bure Lake (0.3 %), a pool on Amager Fælled (2.1 %), a ditch in the same locality (in small number), Peatbogs I and II, Ll. Lyngby (6.6 %, 3,2 %), and in Langemose (1.2 %), as also in Well No. 629 (in small number). These occurrences would seem to indicate that the species is somewhat halophilous.

Indifferent.

Nitzschia angustata (W. Sm.) Grun. It is with some doubt that I have referred a form in Dybe Lake to this species. It was represented by 2.0 % and 0.3% in the samples. According to Kolbe (1927) indifferent, while Hustedt (1939) merely calls it oligohalobous. Indifferent.

— *apiculata* (Greg.) Grun. Only observed in small number in a ditch on Amager Fælled. According to Kolbe (1927) and Schulz (1928).

Mesohalobous.

— *capitellata* Hustedt. Occurred in Flynder Lake (6.0 %) and Langemose. Hustedt (1930) says: in fresh and slightly saline water, scattered, perhaps halophilous. Halophilous?

— *communis* Rabh. Observed in the spring moor in Hammer Bakker (5.1 %) and in Langemose (0.5 %). Kolbe (1927) regards it as indifferent, while Schulz (1928) and Hustedt (1938) more cautiously class it as oligohalobous. Indifferent.

— *commutata* Grun. Occurred in the sample from Well No. 629 in varying number (1.0—4.8 %). According to Hustedt (1938) halophilous-mesohalobous and Hustedt (1939) halophilous.

Halophilous.

— *debilis* (Arnott) Grun. Found in the spring moor in Hammer Bakker (2.0 %) and in Langemose (0.2 %). Kolbe (1927) does not venture to place it in the Halobion system. Schulz (1928) thinks that it is probably mesohalobous, while Hu-

STEDT (1938, 1939) points out that it occurs in heterogeneous localities and regards it as: Indifferent.

Nitzschia denticula Grun. Occurred in Nors Lake and Langemose, in small numbers, also in Flynder Lake (1.9 %). According to KOLBE: Indifferent.

— *dissipata* (Kütz.) Grun. Occurred in Fure Lake (1.4 %), Sct. Jørgens Lake (3.1 %), Dybe Lake (0.5 %), and in Peatbog I, Ll. Lyngby (0.6 %). According to KOLBE (1927) it is indifferent, and according to SCHULZ (1928) and HUSTEDT (1938) it is oligohalobous. Indifferent.

— *fonticola* Grun. Occurred in Fure Lake (5.9 %), Nors Lake (3.7 %), and a watering trough for camels at Kairouan (7.2 %). According to SCHULZ (1928) it is oligohalobous, and HUSTEDT (1938 and 1939) is of the same opinion. LEGLER und KRASSKE (1940) characterise it as extremely euryhaline. It is therefore denoted as Indifferent.

— *frustulum* (Kütz.) Grun. Occurred in a pool and ditch on Amager Fælled (3.2 % and 10.7 %) as wel as in Peatbogs I and II, Ll. Lyngby (24.0 and 5.4 %). Highly different opinions have been expressed about the position in the Halobion system of this species; thus KOLBE (1927) indifferent and euryhaline; SCHULZ (1928) oligohalobous; BUDDE (1932) euhalobous!; HUSTEDT (1938) the larger forms halophilous, the small forms indifferent; LEGLER und KRASSKE (1940) extremely euryhaline. Disregarding BUDDE's view, the species must be supposed to be Indifferent.

— *gracilis* Hantzsch forma. In KOLBE's opinion (1927) the species is oligohalobous, indifferent, while SCHULZ (1928) and HUSTEDT (1938) call it oligohalobous. Occurred in Fure Lake (3.9 %) and in Peatbog I, Ll. Lyngby (0.2 %). Indifferent.

Nitzschia hungarica Grun. Occurred in a pool on Amager Fælled (small number), in a watering trough for camels at Kairouan (1.2 %), and in Langemose (0.2 %). KOLBE (1927) and SCHULZ (1928) regard the species as mesohalobous, while HUSTEDT (1938, 1939) thinks that it is more probably halophilous. Mesohalobous.

— *palea* (Kütz.) W. Sm. Occurred in Fure Lake (small number), Nors Lake (0.7 %), camels' watering trough at Kairouan and in Langemose (0.3 % and 2.5 %), KOLBE (1927) and HUSTEDT (1938) think that the species is: Indifferent.

— *sigma* W. Sm. Occurred in Langemose (1.2 %). According to SCHULZ (1928) mesohalobous and according to HUSTEDT (1938) also euryhaline. Mesohalobous.

— *sigmoidea* (Ehrb.) W Sm. Observed in small numbers in Fure Lake and Langemose. According to KOLBE (1927) and HUSTEDT (1939) indifferent. Indifferent.

— *sinuata* (W. Sm.) Grun. Only in Langemose (small number). According to SCHULZ (1928) oligohalobous. Indifferent?

— *thermalis* Kütz. v. *intermedia* Grun. Found in the spring moor in Hammer Bakker (7.1 %). According to KOLBE (1927): Indifferent.

— *vermicularis* (Kütz.) Grun. v. *terrestris* Boye P. Only observed in the spring moor in Hammer Bakker (2.0 %). Place in Halobion system uncertain. ?

— *vitrea* Norm. Only observed in Langemose, in small number. Accordingto KOLBE (1927) mesohalobous, and according to HUSTEDT (1939) also euryhaline. Mesohalobous.

Pinnularia acrosphœria Bréb. Found in the spring moor in Hammer Bakker (1.0 %). Taken by SCHULZ (1928) and HUSTEDT (1938, 1939) to be oligohalobous. For the present I will therefore regard it as: Indifferent?

Pinnularia appendiculata (Ag.) Cl. v. *budensis* Grun. Found in small number in one of the samples from Well No. 629. According to KOLBE (1927): Mesohalobous?

— *borealis* Ehrb. Found in small number in Lyngby Mose. Characterised thus by the various authors: KOLBE (1927) oligohalobous, indifferent; SCHULZ (1928) oligohalobous; HUSTEDT (1938) oligohalobous, eurytopic; HUSTEDT (1939) oligohalobous. Indifferent.

— *divergens* W. Sm. v. *elliptica* Grun. In small quantity in the spring moor in Hammer Bakker. SCHULZ (1928) the species oligohalobous. Should probably not for the present be placed in the system. ?

— *mesolepta* (Ehrb.) W. Sm. In small number in Gurre Lake. According to SCHULZ (1928) halophobous, while HUSTEDT (1938) calls it indifferent and HUSTEDT (1939) oligohalobous. Is no doubt somewhat: Halophobous.

— *microstauron* (Ehrb.) Cleve. Occurred in Flynder Lake (0.2 ‰) and Well No. 629. According to SCHULZ (1928), and HUSTEDT (1938, 1939) oligohalobous. I have previously supposed this species to be halophobous; but it would be more cautious to regard it as: Indifferent.

— *nodosa* Ehrb. v. *Formica* Ehrb. Occurred in small number in the spring moor in Hammer Bakker. I have previously (Boye Petersen 1932) taken it to be: Halophobous.

— *söhrensis* (Krasske) Boye P. v. *inflata* Krasske. Boye Petersen (1932, p. 21), mentions the occurrence of this form in Hammer Bakker and arrives at the result that it must be regarded as a halophobe. Found in Lyngby Mose with 6.2 mg. Cl′/l. (14.1 ‰). Halophobous.

— *subcapitata* Greg. Occurred in Hammer Bakker in the spring moor, in small number. Supposed by SCHULZ (1928) to be a halophobe, while Hu-

STEDT (1938, 1939) regards it as indifferent and oligohalobous. Indifferent.

Pinnularia subcapitata v. *Hilseana* (Janisch) O. Müll. Occurred in Lyngby Mose (12.8 %) and Bøllemosen (8.1 %). According to SCHULZ (1928) it is halophobous, while HUSTEDT (1938) thinks that, like the species, it is indifferent. Halophobous?

— *viridis* (Nitzsch) Ehrb. Found in the spring moor in Hammer Bakker (3.0 %) and in Langemose (small number). According to KOLBE (1927) and HUSTEDT (1939): Indifferent.

Rhoicosphenia curvata (Kütz.) Grun. Found in Fure Lake and Bure Lake (in small numbers), also in Sct. Jørgens Lake (0.5 %), a ditch on Amager Fælled (0.5 %), Præstø Fjord (0.7 %). Peatbog I, Ll. Lyngby (1.3 %), and Langemose. The following authors have classified this species: SCHULZ (1928) oligohalobous and euryhaline, BUDDE (1930) hardly halophilous, HUSTEDT (1939) euryhaline, halophilous. Should for the present be regarded as: Indifferent.

Rhopalodia gibba (Kütz.) O. Müll. Found in Bure Lake, Sct. Jørgens Lake, Dybe Lake, Nors Lake, Flynder Lake (everywhere less than 1 %); further in a pool on Amager Fælled (12.6 %), and in a peatbog at Ullerup (0.2 %). KOLBE (1927), SCHULZ (1928), HUSTEDT (1938, 1939) all agree in denoting the species as: Indifferent.

— *gibberula* (Ehrb.) O. Müll. v. *producta* (Grun.) O. M. Only in the spring moor in Hammer Bakker (3.0 %). KOLBE (1927) has the species as indifferent, while HUSTEDT (1939) says: An extremely eurytopic species, which may occur in freshwater as well as in the sea and in addition can do with very small amounts of moisture. Indifferent.

— *musculus* (Kütz.) O. Müll. Occurred in Præstø Fjord and Langemose, both places in small amounts.

According to KOLBE (1927), SCHULZ (1928), HUSTEDT (1938 and 1939), and KRASSKE (1932): mesohalobous, while LEGLER und KRASSKE (1940) say: mesohalobous, euryhaline.

Mesohalobous.

Rhopalodia ventricosa (Kütz.) O. Müll. Found in Fure Lake (1.4 %) and Præstø Fjord (0.7 %). According to KOLBE (1927) and HUSTEDT (1938, 1939):

Indifferent.

Stauroneis acuta W. Sm. Only observed in the bottom sample from Sct. Jørgens Lake (in small number). According to KOLBE (1927) indifferent, whereas SCHULZ (1928) and HUSTEDT (1939) merely call it oligohalobous. Indifferent.

— *legumen* (Ehrb.) Kütz. Only in Langemose at Ullerslev (0.3 %). According to KOLBE (1927) indifferent, while SCHULZ (1928) designates it as oligohalobous. Indifferent.

— *phoenicenteron* Ehrb. Seen only in Dybe Lake in small number. Both KOLBE (1927) and HUSTEDT (1938, 1939) class it as Indifferent.

— *producta* Grun. Only observed in Langemose (0.3 %). According to HUSTEDT (1939) halophilous, perhaps mesohalobous. Halophilous.

— *Smithii* Grun. Only in Langemose (small number). According to KOLBE (1927) indifferent, while SCHULZ (1928) and HUSTEDT (1939) designate it as oligohalobous. Indifferent.

Stephanodiscus astræa (Ehrb.) Grun. Found in small numbers in Fure and Bure Lakes, also in Sct. Jørgens Lake (6.3 %) and Nors Lake (0.5 %). According to KOLBE (1927) and SCHULZ (1928):

Indifferent.

— — v. *minutula* (Kütz.) Grun. Found in Fure Lake (1.4 %) and in Peatbogs I and II at Ll. Lyngby (3.0 % and 10.6 %). HUSTEDT (1939) states that its place in the system is the same as that of the species.

Indifferent.

Surirella Capronii Bréb. Only in Sct. Jørgens Lake in small number. According to KOLBE (1927) and HUSTEDT (1938): Indifferent.

— *constricta* Ehrb. Occurred in the spring moor in Hammer Bakker in small number. Regarded by SCHULZ (1928) and HUSTEDT (1938) as oligohalobous. For the present I will class it as Indifferent.

— *elegans* Ehrb. Occurred in the bottom material from Sct. Jørgens Lake (4.7 %). Classed by SCHULZ (1928) and HUSTEDT (1938, 1939) as oligohalobous, by KOLBE (1927) as: Indifferent.

— *linearis* W. Sm. Only in the spring moor in Hammer Bakker (1.0 %). Tabulated by SCHULZ (1928) and HUSTEDT (1938, 1939), as oligohalobous. Probably: Indifferent.

— — v. *helvetica* (Brun) Meister. In small number in Nors Lake. In the literature there is no definite statement about its place in the Halobion system. Probably, like the species, it is: Indifferent?

— *Moelleriana* Grun. Only seen in Langemose in small number. HUSTEDT (1930) classes it as probably halophilous. Halophilous?

— *ovata* Kütz. Found in Præstø Fjord and in Langemose in small numbers, in addition in all the samples from Well No. 629 (up to 6.8 %). Registered by KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) as indifferent. KRASSKE (1932) tabulates it as halophilous. Indifferent.

— *robusta* Ehrb. Only observed in small number in the bottom sample from Sct. Jørgens Lake. SCHULZ (1928) considers it oligohalobous, whereas HUSTEDT (1938) classes the species as halophobous, but v. *splendida* as indifferent. Halophobous.

Synedra acus Kütz. Found in Fure Lake (0.9 %), the peatbog at Ullerup (1.0 %) and Langemose (0.2 %), as well as in Sct. Jørgens Lake in small

amount. According to KOLBE (1927) it is oligohalobous, indifferent, while SCHULZ (1928) and HUSTEDT (1938) merely designate it as oligohalobous. Indifferent.

Synedra acus v. *angustissima* Grun. Only in Langemose from *Chara* (7.0 %). According to SCHULZ (1928) indifferent and limnophilous. Indifferent.

— *amphicephala* Kütz. Only found in Bure Lake (0.3 %). Does not seem to have been classified in the Halobion system in the literature. ?

— *capitata* Ehrb. Only in the peatbog at Ullerup (0.3 %). Designated by KOLBE (1927) as: Indifferent.

— *parasitica* (W. Sm.) Hustedt. Only in the bottom sample from Sct. Jørgens Lake (1.6 %). Classed by KOLBE (1927) as indifferent, by SCHULZ (1928) and HUSTEDT (1938, 1939) as oligohalobous. Indifferent.

— *pulchella* Kütz. Represented by less than 1 % in a ditch on Amager Fælled, Flynder Lake, Præstø Fjord, and Langemose. In a watering trough for camels at Kairouan the species was dominant (85.0 %). According to KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) it is mesohalobous; the latter adds: euryhaline. Mesohalobous.

— *rumpens* Kütz. Only in Magle Lake, in small number. KOLBE (1927) designates v. *familiaris* as indifferent, while HUSTEDT (1938) states that the species and varieties are oligohalobous. Indifferent?

— *tabulata* (Ag.) Kütz. (= *S. affinis*). Occurred in Præstø Fjord (5.3 %), Peatbogs I and II, Ll. Lyngby (0.3 % and 14.4 %), as also in Langemose (0.3 %). It was likewise found in small numbers in Flynder Lake and in a watering trough for camels at Kairouan. By KOLBE (1927), SCHULZ (1928), SPRENGER (1930) and HUSTEDT (1939) regarded as mesohalobous. BUDDE

(1932) and HUSTEDT (1938, 1939) strongly emphasise that it is euryhaline, so here I have merely classed it as: Halophilous.

Synedra ulna (Nitzsch) Ehrb. Found in Fure Lake (0.9 %), Bure Lake (0.9 %), Sct. Jørgens Lake (4.6 %), Dybe Lake (0.3 %), Peatbogs I and II, Ll. Lyngby (small number), Peatbog at Ullerup (0.2%), Well No. 629 (sample 2: 2.2 %), and Langemose (0.3 % and 1.4 %). By KOLBE (1927), SCHULZ (1928), and HUSTEDT (1938, 1939) stated to be indifferent and euryhaline. Indifferent.

— — v. *biceps* (Kütz.) v. Schönf. Only in Langemose, in small number. According to HUSTEDT (1939) oligohalobous and: Indifferent.

Tabellaria flocculosa (Roth) Kütz. Found in Magle Lake (0.7 %), Gurre Lake (1.3 %), Bure Lake (0.6 %), and Dybe Lake (in small number); likewise in Bøllemosen (0.9 %) and in the spring moor in Hammer Bakker (20.2 %). That is to say, that it has not been observed in water with more than 35 mg. Cl'/l. Stated by KOLBE (1927), SCHULZ (1928), and HUSTEDT (1939) to be: Halophobous.

I am greatly indebted to Mr. SIGURD OLSEN for letting me have a large number of samples with their physico-chemical data, and to Civil Engineer C. H. PAPE who has assisted me in various ways. Finally I offer thanks to the Trustees of the Carlsberg Foundation who granted financial aid for the execution of the work, and to the Rask-Ørsted Foundation for a grant to the translation.

The translation into English has been done by Miss ANNIE I. FAUSBØLL. M. A.

Literature cited.

ANDERSEN, JOHS. og ØDUM, H. 1930. Om Forekomsten af saltførende Aflejringer i Danmarks Undergrund. Danmarks geol. Unders. II. Række Nr. 52.

ANDERSEN, S. 1930. Nye Fund af Halophyter i Storebæltsomraadets Indland. Bot. Tidsskr. **41**: 100.

BUDDE, H. 1930. Die mesohaloben und halophilen Diatomeen der Lippe in Westfalen. Ber. d. d. bot. Ges. **48**: 415.

— 1931. Die Algenflora der Westfälischen Salinen und Salinengewässer (I Teil). Arch. f. Hydrobiologie **23**: 462.

— 1932. Versuche über die Anpassung einiger Algen an den wechselnden Salzgehalt. Ber. d. d. bot. Ges. **50**: 343.

— 1933. Die Algenflora der westfälischen Salinen und Salzgewässer II. Arch. f. Hydrobiologie **25**: 305.

CHOLNOKY, B. 1929. Epiphyten-Untersuchung im Balaton-See. Internat. Revue d. ges. Hydrobiol. u. Hydrogr. **22**: 313.

HUSTEDT, F. 1935. Die Diatomeenflora von Poggenpohls Moor. Abh. und Vorträgen der Bremer Wiss. Ges. **8/9**: 362.

— 1938. Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali und Sumatra. Systematischer Teil. Arch. f. Hydrobiologie Suppl. Bd. 15. (1937–1938).

— 1939. Die Diatomeenflora des Küstengebietes der Norden vom Dollart bis zur Elbemündung I. Abh. Nat. Ver. Bremen **31**: 572.

IVERSEN, J. 1929. Studien über die pH-Verhältnisse dänischer Gewässer und ihren Einfluss auf die Hydrophyten-Vegetation. Bot. Tidsskr. **40**: 277.

— 1937. Undersøgelser over Litorinatransgressioner i Danmark. Medd. fra Dansk Geol. Forening **9**: 223.

KOLBE, R. W. 1927. Zur Ökologie, Morphologie und Systematik der Brackwasserdiatomeen. Die Kieselalgen des Sperenberger Salzgebiets. Pflanzenforschung Heft 7.

— 1932. Grundlinien einer allgemeinen Ökologie der Diatomeen. Ergebnisse der Biologie, herausgegeben von K. v. Fritsch, R. Goldschmidt etc. **8**: 221.

KOLBE und TIEGS 1929. Zur mesohaloben Diatomeenflora des Werragebietes. Ber. d. d. bot. Ges. **47**: 408.

KRASSKE, G. 1932. Diatomeen deutscher Solquellen und Gradierwerke II. Hedwigia **72**: 135.

KRASSKE, G. 1933. Die Diatomeen-Vegetation der „Drei Quellen" in Erfurt. Hedwigia **73**: 243.

— 1938. Beiträge zur Kenntnis der Diatomeen-Vegetation von Island und Spitzbergen. Arch. f. Hydrobiologie **33**: 503.

— 1939. Diatomeen deutscher Solquellen und Gradierwerke III. Beih. Bot. Centralbl. **59**: Abt. A: 413.

LEGLER und KRASSKE. 1940. Diatomeen aus dem Vansee (Armenien). Beitr. z. Ökologie der Brackwasserdiatomeen I. B. B. C. **60 B**: 335.

OLSEN, SIGURD 1941. Om Vegetationen i Nors Sø. Naturens Verden.

PETERSEN, JOHS. Boye. 1930. Algae from O. Olufsen's second Danish Pamir Expedition 1898—1899. Dansk Bot. Arkiv **6**: Nr. 6.

— 1932. The Algal Vegetation of Hammer Bakker. Bot. Tidsskr. **42**: 1.

REDEKE, H. C. 1922. Zur Biologie der nederländischen Brackwassertypen. Bijdragen tot de Dierkunde; Feest-Nummer von Dr. Max Weber.

SCHULZ, P. 1926. Die Kieselalgen der Danziger Bucht.Bot. Archiv **13**: 149.

— 1928. Brackwasserdiatomeen a. d. Gebiete Danzig. 50. Bericht d. Westpreuss. Bot.-Zool. Vereins. Danzig.

SPRENGER, E. 1930. Bacillariales aus den Thermen der Umgebung von Karlsbad. Arch. f. Protistenkunde **71**: 502.

THOMASSON, H. 1925. Methoden zur Untersuchung der Mikrophyten der limnischen Litoral- und Profundalzone. Abderhalden's Handbuch d. biol. Arbeitsmeth. Abt. IX, Teil 2, I: 681.

WESENBERG-LUND, C. 1904. De danske Søers Plankton.

— 1917. Furesøstudier. D. Kgl. Danske Vidensk. Selskab, Skrifter, Naturv. og math. Afd. 8 Rk. III, 1.

Indleveret til Selskabet den 7. Maj 1942.
Færdig fra Trykkeriet den 19. April 1943.