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Section des Sciences, 9<sup>me</sup> série, t. VII, n° 1.

CONTRIBUTIONS  
TO  
THE STUDY OF THE DEVELOPMENT AND  
LARVAL FORMS OF ECHINODERMS  
III  
BY  
TH. MORTENSEN

WITH PLATES I—XV

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURV. OG MATH. AFD. 9. RÆKKE, VII. 1.

KØBENHAVN  
LEVIN & MUNKSGAARD  
EJNAR MUNKSGAARD  
1937

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The present third "Contribution to the study of the development and larval forms of Echinoderms"<sup>1</sup> comprises the results of studies carried out during a visit to the Marine Biological Station of the University of Egypt, at Ghardaqa on the Red Sea Coast, a little South of the Gulf of Suez, in the summer of 1936.

I beg here first of all to tender my sincere thanks to the authorities of the University of Egypt, Cairo, for the hospitality offered me in placing the facilities of this excellent laboratory at my disposal, as also for obtaining permission for me to use the Egyptian research steamer "Mabahiss" for trawling and dredging in the Gulf of Suez for some days. My no less sincere thanks are due to the director of the station, Dr. CYRIL CROSSLAND, for his untiring efforts to help me in every way, meeting my — rather insatiable — requirements for material, and helping me in all practical matters. Also the assistant of the station, H. A. F. GOHAR EFFENDI, M. Sc., was ever ready with his kind help, not the least important because of the difficulty in making the sailors of the station understand what one wanted — the Arab language being not easily mastered in the course of two or three months. Last, not least, my sincere homage to Mrs. CROSSLAND, who together with her husband, the director, made me feel at home and comfortable in their fine house, which fact, combined with the success of my scientific work at the laboratory, made my visit to this Red Sea Station an unforgettable experience.

I am very much indebted to the Carlsberg Foundation for the economical support without which it would have been impossible for me to undertake this visit.

The time spent at the station was from April 18th to June 27th. Originally I had planned to come about a month earlier, but for various reasons I had to postpone the voyage a little — which was by no means a disadvantage. The essential thing for me was to find the various Echinoderms in their breeding season. Hardly anything was known about this; but as the temperature of the sea water during the winter season is some 10° C. lower than during the summer season, it was to be expected that the breeding season of most of the Echinoderms would not begin so very early. As a matter of fact I found several species to become mature only much later, e. g. *Asthenosoma varium*, *Phyllacanthus imperialis*, which will probably not have their breeding season until July—August. Still a good many species had ripe sexual products at the time of my arrival, so that there was at once enough to do. Some species, e. g.

<sup>1</sup> "Contributions" I—II were published 1931 in 9. Ser. Vol. IV of these Memoirs.

*Tripneustes gratilla* and *Echinometra Mathæi* were nearly spent, so they must have had their (first?) breeding season at least as early as the middle of April.

A problem of great interest was, how the cultures of the larvæ would stand the high salinity prevailing in the Red Sea. In this sea, with no rivers and usually several years between the rains, the strong evaporation raises the salinity, so that in the part of the Red Sea to the North of 20° N. the salinity amounts to c. 40—44 ‰, against the usual oceanic salinity of c. 35 ‰.<sup>1</sup> It might well be expected that in general this high salinity would not be detrimental to the larvæ, and so I found it actually to be the case. I even had the impression that this high salinity was very favourable to the larvæ; probably even a higher salinity would not be detrimental. It happened sometimes that I put some larvæ into small dishes in which water had evaporated so that the bottom was covered with salt crystals, which dissolved when new water was added. The salinity in such dishes was accordingly considerably higher than normal — but it did not seem to affect the larvæ in the least; they were swimming as actively as in normal sea-water. (I did not measure the salinity in such dishes, or undertake experiments as to how high salinity the larvæ would bear; an investigation of this problem would be of no small interest).

On previous occasions I have found it an excellent method for rearing Echinoderm larvæ to give them fresh sea-water daily, transferring them by means of a pipette to the fresh water; in this way the larvæ get access to their natural food, and usually thrive very well. As it would evidently be much easier, if one could give the larval cultures artificial food and thus the changing of water be unnecessary, I tried bringing with me samples of cultures of various food organisms for raising fresh cultures on my arrival at the laboratory. I thus brought along with me culture samples of the usual *Nitzschia closterium*, var. *tenuissima* and of *Chlorella Spärcki*, given me from the Physiological Institute of the University of Copenhagen. Further my friend Professor BRINKMANN, Bergen, sent me samples of a *Chlamydomonas* sp. and a *Dunaliella* sp. Of all these four types I succeeded in raising very fine new cultures at the laboratory, in the usual way adding Miquel-solution to the filtered sea-water (cf.

<sup>1</sup> During the recent researches in the Red Sea of the Egyptian research vessel "Mabahiss" the hydrographer ABD EL FATAH MOHAMED, M. Sc., found the following salinity and P<sub>H</sub> values at a station between Sha'b Abu Qalawa and Sha'b Abu Fanadir (in the immediate neighbourhood of Ghardaqa) on Dec. 12th, 1935:

Depth (m.)	Temperature	Salinity ‰	P <sub>H</sub>
0.....	23.66	40.32	8.02
10.....	23.67	40.37	8.03
20.....	22.68	40.44	8.03
30.....	22.45	40.49	8.03
40.....	22.05	40.52	8.02
50.....	21.75	40.52	8.02

I am indebted to Dr. CROSSLAND for this information. A report on the Hydrography of the Northern Red Sea, in which the above observations will be found included, will be published later by ABD EL FATAH MOHAMED.

ALLEN & NELSON. On the artificial culture of marine Plankton Organisms. J. Mar. Biol. Assoc. VIII. 5. 1910). I did not, however, find any of these cultures wholly reliable as food for the larvæ, and gradually I gave up the use thereof and returned to my old method of giving the larvæ fresh sea-water every day, or at most every few days.

This method proved completely successful<sup>1</sup> — but, of course, it involves considerably more work, and as I had several cultures going at the same time, and always at least three or four dishes of each culture, (— there is always the risk that, if one has only one dish of a culture, it may fail for some reason or other and thus the whole culture be spoiled; as a matter of fact, it happened often that in one or other dish the larvæ would not go on developing, whereas in other dishes, under exactly the same treatment, the larvæ were growing excellently —) work gradually increased so as to be too much for one. It was therefore a great help to me, when Professor A. NAEF of the Egyptian University, Cairo, sent his Assistant, ZAKY EL DESSOUKI, down to the laboratory to assist me in my work, from June; I am deeply obliged to Prof. NAEF for rendering me this service. ZAKY EFFENDI proved to be very able, indeed, and helped me excellently; moreover, when I left the station, he took charge of those of my cultures not yet finished — particularly *Eucidaris metularia* and *Stichopus variegatus* — reared them to metamorphosis and sent me the various stages, excellently preserved so that I could study them at home. I beg here to tender my sincere thanks to ZAKY EFFENDI for his excellent and genial help.

As for the preservation of the larvæ I found 4 % formalin, neutralized with borax, to be most excellent; it preserved these delicate objects in the most perfect way, without any shrinkage, as also the skeleton was perfectly preserved. In several cases I had to kill the larvæ on the microscopical slide for drawing them, it being not desirable to press the cover so much as to keep them immovable for a camera lucida drawing. The method used was to put a drop of formalin on the slide, sucking it slowly into the water under the cover by means of a small piece of filter paper. Thus the larvæ were made immovable, in perfect shape, their colour usually remaining unchanged for some time; and then, of course, I could check all the details on the living specimens.

No special effort was made for keeping the cultures at a constant temperature; as a matter of fact the temperature of the water in the laboratory was usually somewhat lower than that of the surface water outside. But also outside the temperature varies very considerably, at least near the coast, so that also under natural conditions the larvæ are exposed to considerable changes of temperature, and it is therefore not surprising that they are not very sensible to such changes when raised in cultures in the laboratory. I kept the dishes covered with glass-plates, but so as to leave

<sup>1</sup> KATZUSO ONODA ("Notes on the development of some Japanese Echinoids with special reference to the structure of the larval body". Japanese Journ. of Zool. VI. 4. 1936) used with equal success a different method. To filtered sea-water was added every day a small quantity of food, collected by filtering water in which sea-weeds had been washed. The water of the cultures was not changed.

free access of air, in good light, but usually avoiding direct sun upon them; still even exposure for a couple of hours to the morning sun, involving some rise of the temperature, did not have any bad effect on them. On the whole I found the larvae rather surprisingly resistent. I ascribe this mainly to the unusually fine condition of the sea-water at the laboratory, it being, — except when strong winds to some degree stirred up the bottom — very pure, almost as pure as in mid ocean; and then the unusually high salinity, as mentioned above, is another most important factor. Another very important factor is the high  $P_H$  value, 8.02—8.03, as stated above, p. 4 Note.

Altogether, the physical conditions for such work as that undertaken by me during my stay at the Ghardaqa laboratory are the best possible. Unfortunately the Echinoderm fauna is not particularly rich, not nearly as rich as in corresponding localities in the Indian Ocean (e. g. Mauritius) — not to speak of the Malay region, the richest region in the whole world. Of course a good number of typical coral reef Echinoderms are found, e. g. *Diadema*, *Ophiocoma*, various Comatulids — but the absence of such forms as *Astropyga*, *Echinothrix*, *Stomopneustes*, *Echinoneus*, *Archaster*, and the scarcity of a number of other forms is a regrettable fact. Probably several of these forms may be found in other parts of the Red Sea — but distances are great, which makes it difficult to get such forms alive at the laboratory for biological work. This difficulty was felt the more strongly, because the motor launch of the station was out of working order during the time of my visit. It was thus only such forms as could be found on the coral reefs close to the station and in the littoral region, and such as could be dredged by means of a small sailing boat in the immediate neighbourhood of the station at depths not exceeding some 25 fathoms, that were available for my work. In spite of this drawback I had the opportunity of studying the development of no less than 30 different species of Echinoderms — a record which by far exceeds what has been achieved anywhere else in the world by the present author or by anybody else. This is in itself proof enough of the exceptionally favourable physical conditions found at this Red Sea laboratory. As a matter of fact not one of my cultures failed — a very fortunate circumstance, since in several cases I succeeded only once in getting a ripe male and female at the same time, so that it would have been impossible to start new cultures of such species.

The species the development of which was studied are the following:

#### Echinoidea:

1. *Eucidaris metularia* (Lamk.), reared to metamorphosis
2. *Diadema setosum* (Leske), reared through metamorphosis
3. *Temnotrema scillæ* (Mazetti), reared to metamorphosis
4. *Nudechinus Gravieri* (Koehler), reared through metamorphosis
5. *Tripneustes gratilla* (Linn.), reared to metamorphosis
6. *Echinometra Mathæi* (Blv.), reared to metamorphosis
7. *Heterocentrotus mammillatus* (Linn.), reared through metamorphosis
8. *Fibularia craniolaris* (Leske), reared through metamorphosis

9. *Clypeaster humilis* (Leske), reared through metamorphosis
10. *Echinodiscus auritus* Leske, reared to full larval shape
11. *Lovenia elongata* (Gray), reared to full larval shape

Asteroidea:

12. *Astropecten polyacanthus* Müll. & Troschel, reared through metamorphosis
13. *Astropecten velitaris* v. Martens, reared through metamorphosis
14. *Asterope carinifera* (Lamarck), reared to metamorphosis

Ophiuroidea:

15. *Ophiothrix triloba* v. Martens, reared to metamorphosis
16. *Ophiomaza cacaotica* Lyman, reared through metamorphosis
17. *Ophiocoma erinaceus* Müll. & Troschel, reared to full larval shape
18. *Ophiocoma scolopendrina* (Lamarck), reared through metamorphosis
19. *Ophiocoma lineolata* (Desjardins) Müll. & Troschel, reared through metamorphosis

Holothurioidea:<sup>1</sup>

20. *Synaptula reciprocans* (Forskål), reared to full (?) larval shape
21. *Synaptula vittata* (Forskål), reared to full (?) larval shape
22. *Stichopus variegatus* Semper, reared through metamorphosis
23. *Actinopyga serratidens* Pearson, reared through metamorphosis
24. *Actinopyga mauritiana* (Quoy & Gaimard) (var.), reared to full larval shape
25. *Holothuria (Bohadschia) marmorata* Jäger, reared to full larval shape
26. *Holothuria arenicola* Semper, var. *Boutani* Hérouard, reared through metamorphosis
27. *Holothuria scabra* Jäger, reared to full larval shape
28. *Holothuria spinifera* Théel, reared through metamorphosis

Crinoidea:<sup>2</sup>

29. *Tropiometra Audouini* A. H. Clark, reared to young Pentacrinoid
30. *Lamprometra Klunzingeri* (Hartlaub), reared to young Pentacrinoid

Foremost in importance of these stand *Eucidaris metularia*, the first Cidarid of which we know now the full developmental history until metamorphosis, and *Diadema setosum*, the postembryonal development of this very important type being herewith made known.

The other Echinoids, the development of which has been studied here, are important in giving further proof for the correctness of my assertion (cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 201—217) that the larvae offer a classification corresponding to the classification of the adult forms, the study of the larval forms thus affording an important test of the classification of the

<sup>1</sup> I am indebted to Mr. S. HEDING, Zoological Museum, Copenhagen, for the identification of the Holothurians.

<sup>2</sup> I am indebted to my friend Professor T. GISLÉN, Lund, for the identification of the Crinoids.

adult forms. — I may point out the strange character of the body rods in the *Nud-echinus* larva and the extraordinary beauty of the *Clypeaster humilis* larva.

It was a great disappointment to me that I did not find *Asthenosoma varium* ripe, and thus could not study the development of this important type. It will probably be ripe in July—August, since by the end of June the spermatozoa began to ripen. The fact that the spermatozoa have a very elongate head, quite unlike that of other Echinoid spermatozoa, is very interesting and indicates that the development may offer unusual features.

The Asteroids are rather poorly represented in these researches, the larvae of only three species having been studied. This is due to various circumstances. One, *Luidia Savignyi* (Audouin), resisted all my efforts. It is a curious fact that the eggs of several Asteroids do not lend themselves directly to fertilization, such as is the case with the Echinoid eggs. When taken out of the ovaries they have a large, distinct nucleus, and are not ripe for fertilization; but when left in the water for some hours some of them will ripen, the nucleus disappearing, and such eggs are then ready for fertilization — often it is only a few percent, but by the great number of eggs even a few percent of them may yield a sufficient number of larvae, the more so as the embryos are generally of a fair size and thus easily handled. Then comes another difficulty: that the spermatozoa are generally immovable when removed from the testes to a dish with sea-water. It is then necessary to raise the alcalinity of the water by adding NaOH; it is rather astonishing how much NaOH must be added, before the spermatozoa will move; but when this finally has been achieved, the eggs in which the nucleus has disappeared may be fertilized. (In nature such difficulties, of course, cannot exist; when the female sheds its eggs they will evidently all be ready for fertilization, and the alcalinity ( $P_H$ ) of the sea-water must be high enough for the spermatozoa to move). In this way I succeeded in getting cultures of the two *Astropecten* species and of the *Asterope*; but of the *Luidia* I could not, in spite of repeated efforts, get any fertilization, and though I kept a number of them in the tanks of the laboratory, they would not shed their sexual products. Of other species I could never get ripe males and females at the same time, even though they were kept in the tanks for a long while, and others again, like *Echinaster purpureus*, the large, yolky (nearly black) eggs of which do not lend themselves for artificial fertilization, would not shed their sexual products, though kept in good numbers in the tanks. The same was the case with *Fromia monilis*(?) which, by the way, I found to be a *proterandric hermaphrodite*, this species, together with *Asterina gibbosa* (cf. L. CUÉNOT. Notes sur les Echinodermes. III. L'hermaphroditisme protandrique d'*Asterina gibbosa* Penn. et ses variations suivant les localités. Zool. Anz. 1898, p. 273) representing the only cases of normal hermaphroditism known till now among Asteroids.<sup>1</sup>

<sup>1</sup> According to H. OHSHIMA (Hermafrodita marstelo, *Asterina Batheri* Goto. Ann. Zool. Japon. 12. 1929) hermaphrodite specimens are of fairly common occurrence in *Asterina Batheri*; but the majority of the specimens are unisexual.

In Ophiuroids it seems to be a nearly constant rule that eggs taken out of the ovaries, even if they look ever so ripe, cannot be fertilized; there is always a distinct nucleus, and even when left for hours in the water they will not ripen, such as is usually the case, to a more or less extent, with the Asteroids — whereas there is never any trouble with the moveability of the spermatozoa of Ophiuroids. The only way to get the embryos of Ophiuroids is to let them spawn in the aquaria, and this, fortunately, they are not unwilling to do, when a number of ripe males and females are put together — sometimes they may spawn even in quite small dishes. In this way I got the larvæ of the five above mentioned species — the only ones of which a fair material of ripe males and females was accessible to me. — Of particular interest are here *Ophiomaza cacaotica*, the larva being of the typical Ophiotrichoid type, as should be expected according to my theory of the larval classification, and *Ophiocoma lineolata* on account of the remarkable reduction of the larval skeleton.

The Holothurians proved the great surprise! Very little work has been done on the development of such Holothurians as have pelagic larvæ, viz. the Synaptids and the Aspidochirotes. The species, the development of which has been studied from the egg onwards are: *Leptosynapta inhærens* (O. Fr. Müller), *Holothuria tubulosa* Gmelin, *H. floridana* Pourtalès, *H. Poli* delle Chiaje, *H. nigra* Peach, *Holothuria* sp., *Stichopus californicus* (Stimpson), and *St. Kefersteini* Selenka. Of these *Leptosynapta inhærens* and *Holothuria floridana* have direct development, without a pelagic larva, and none of the others have been reared to full larval shape, still less through metamorphosis. (*Labidoplax digitata* (Montagu), the classical object for studying Holothurian development, has not been reared directly; the various developmental stages have been taken pelagically).

As pointed out already by SELENKA (Zur Entwicklung der Holothurien (*Holothuria tubulosa* und *Cucumaria dololum*). Zeitschr. wiss. Zool. XXVII. 1876, p. 157) artificial fertilization of Holothurians very rarely succeeds; the eggs when taken from the ovary always have a distinct nucleus, and even when left in the water for several hours very few eggs will become ripe for fertilization, so that it is very difficult to get larval cultures in this way. By means of keeping a number of specimens in a live-box SELENKA succeeded in getting good cultures of *Holothuria nigra*, and EDWARDS of *Holothuria floridana*, the specimens having spawned in the live-box. Only HÖRSTADIUS (Entwicklungsmechanische Studien an *Holothuria Poli* d. Ch. Arkiv för Zoologi. 17. B. 1925) has succeeded in getting a large number of eggs artificially fertilized, having raised the  $P_H$  of the water. Perhaps this method will prove successful also in other difficult cases.

At Ghardaqa Holothurians are plentiful, several species being quite common in shallow water at the station. On keeping a number of specimens (each species separate, of course) in the tanks of the laboratory, where they would live quite well for some days, though without food, I had the pleasure of seeing some of them spawn. Particularly *Holothuria marmorata* was very interesting to observe in the act of spawning. First a male would raise its foreend almost vertically, spreading it out

behind the tentacles and flattening it so as to recall, indeed, a cobra in attacking position; a distinct genital papilla would appear, from which the sperma would stream, forming a milky cloud in the water. Then a female would raise its foreend in the same way and shed its eggs. Several specimens might be seen spawning at the same time. Particularly the males would move the raised foreends to the sides, thus producing a better spreading of the sperma in the water. When the spawning had ended they assumed their normal horizontal position. The spawning usually took place in the evening or the night.

The eggs thus spawned naturally I always found immediately fertilized, and I could then remove the eggs from the bottom of the tank by means of a pipette and put them into dishes with pure water. In some cases, when I did not directly observe the spawning, and the eggs were not numerous enough to be sucked up from the bottom of the tank, I filtered all the water from the tank through a fine net of silk gauze and thus got the eggs removed to dishes with fresh sea-water.

In this way I got larval cultures of all the 9 species of Holothurians named in the above list. Some species would, however, not spawn, though they were apparently ripe. I tried then to fertilize the eggs artificially, but in spite of repeated efforts, always without success.

All the cultures obtained in the way described proved perfectly successful, the larvæ reaching their full shape, and four of the species, the *Stichopus*, *Actinopyga serratidens*, and two of the *Holothuria* species even metamorphosed. The larvæ were found to be extraordinarily uniform in shape and colour, so as to be distinguishable only by the calcareous bodies in their posterior end. But then I was surprised to find the larvæ, when about to begin metamorphosing, to develop in their lobes large, clear, elastic balls, these balls remaining distinct also in the young Holothurian after metamorphosis.

This recalls the observations of JOH. MÜLLER in his II., III., IV., and VI. "Abhandlungen über die Larven und die Metamorphose der Echinodermen" 1848—1853. He there describes and figures excellently some "Holothurienlarven mit Blasen", the metamorphosis of which into young Holothurians he has followed in details on material taken pelagically. Nobody has observed these peculiar larvæ since JOH. MÜLLER studied them nearly a hundred years ago, and it was quite problematic to which Holothurian they belonged, the suggestion of JOH. MÜLLER that they might be the larvæ of *Stichopus regalis* being quite uncertain (and, indeed, as it now appears, incorrect). In my "Echinodermenlarven d. Plankton-Expedition" (1899, p. 19) I named them *Auricularia sphærigera* and *A. stelligera* finding the figures given by JOH. MÜLLER to represent two distinct species of larvæ. It is now made certain that they belong to the genus *Holothuria*, and as the *Stichopus* larva has the same sort of elastic balls, it seems evident that we have here a larval type characteristic of the *Aspidochirotes*. That such balls were not found in the above mentioned *Holothuria* and *Stichopus* species, the development of which was hitherto studied, is due to the

fact that the balls do not appear until the larva is fully formed and ready to metamorphose, whereas only the young stages of the larvæ of the said species were reared.

The two Comatulids of which the development was studied, did not present any external features of special interest, the development agreeing in all essential features with that of *Tropiometra carinata*, as described in my "Studies on the development of Crinoids" (Papers from the department of Marine Biology, Carnegie Inst. XVI. 1920). But it is important that in both of them the eggs are free, not attached to the pinnules, this latter mode being apparently a secondary adaptation for protection of the brood, the principal and probably the commonest mode being that of the eggs being free. *Lamprometra* offers the very remarkable feature that no gastrula-invagination takes place, the stomach differentiating secondarily in the mass of cells filling up the blastula.

The main object of these researches was to make known the larval forms of the various species of Echinoderms available, with regard especially to their importance for classification. The same point of view has been the leading principle in my former investigations in Echinoderm development (cf. my "Studies of the development and larval forms of Echinoderms" 1921, and my "Contributions to the study of the development and larval forms of Echinoderms" I-II. 1931). Of course, I do not mean to say that with these researches we have gained sufficient information of the divers forms studied, even when the development is traced from the egg to full larval shape and through metamorphosis. The whole question of the organogeny is left nearly untouched — not because it does not interest me, but because it would involve much more work than one man could do. Each of the species dealt with might deserve a full monographic treatment, and most interesting results would be sure to be achieved thereby. But that was not my purpose, and will not be for my future researches either, if I may have the good fortune of continuing these studies. The study of the larval forms alone is a most important (and fascinating) work, and very much remains to be done in this field; we are only just so far that we can see a glimpse of what can be achieved.

In my "Studies" 1921 I gave a short summary of what had hitherto been achieved in the knowledge of the development and larval forms of Echinoderms up to 1921, and in the "Contributions" I-II. I did the same for the period 1921—1931. It may be practical here to summarize likewise what has been done in regard to this subject in the time from 1931 till now. Nearly all of it relates to the Echinoids.

MARTIN W. JOHNSON in his "Notes on the larval development of *Strongylocentrotus franciscanus*" (Publ. Puget Sound Biol. Station. VII. 1930) figures the various stages of this larva, which he has reared till beginning metamorphosis, thus ascertaining that the larva figured Pl. IX. Fig. 4 of my "Studies" and referred to *Strongylocentrotus franciscanus* really belongs to this species (The younger stages figured Pl. IX. 1—3, I had reared). We thus have now a fairly complete knowledge of the larval development of this species.

MARY M. MOORE in "Notes on the development of the sea-urchin *Temnopleurus hardwickii*" (Sci. Rep. Tôhoku Imp. Univ. 4. Ser. Biology. VIII. 1933) figures the larva of this species, evidently without knowledge of the literature on Echinoderm larvæ. The larvæ are figured upside down, and only outline figures, without the skeleton, are given of the larva about to metamorphose; but of the younger stages good figures are given, showing this larva to be of the usual Temnopleurid type.

AMADO T. FELICIANO ("Studies on the early development of *Arachnoides placenta* (Linn.). Natural & Applied Sci. Bulletin Univ. Philippines. III. 4. 1933) describes and figures, rather crudely, the larva of this species; from his Pl. II. Figs. 23, 24 it can be concluded that it must be very much like the larva of *Arachnoides zelandiae* Gray, described and figured in my "Studies" 1921, p. 96, Pl. X. 7 (under the name of *Arachnoides placenta*, as it was at that time generally assumed, on the authority of A. AGASSIZ, that the New Zealand form was identical with the Indo-Pacific *A. placenta*; in my paper on the Echinoderms of New Zealand and the Auckland—Campbell Isl. I. Echinoidea (Papers from Dr. Th. Mortensen's Pacific Expedition. 1914—16. VIII. Vid. Medd. Dansk Naturh. Foren. Bd. 73. 1922, p. 180) I showed it to be quite a distinct species, as had, indeed, already been pointed out by LOVÉN).

Much more important than the three above mentioned papers are those of KATSUZO ONODA. In his "Notes on the development of *Heliocidaris crassispina*, with special reference to the structure of the larval body" (Mem. Coll. of Sci. Kyoto Imp. University. Ser. B. VII. 1931) he gives a very elaborate description and figures of this larva in all its stages and of the metamorphosis and the young sea-urchin. (The larva of this species was, however, already described in my "Studies" 1921, p. 64, Pls. VI. 3; XI. 1—2, though under the erroneous name *Heliocidaris tuberculata* (Lamk.); cf. my paper quoted above on the Echinoidea of New Zealand and the Auckland—Campbell Isl., p. 174. Note). — Further in 1936, in his "Notes on the development of some Japanese Echinoids, with special reference to the structure of the larval body" (Japanese Journ. of Zoology. VI. 4) ONODA describes and figures excellently the larvæ of *Mespilia globulus*, *Echinometra Mathæi*, *Toxopneustes pileolus*, *Echinostrephus moralis* (sic! for *molaris*), *Temnopleurus teoreumaticus*, *Tripneustes gratilla*, *Diadema setosum*, *Strongylocentrotus pulcherrimus*, and *Pseudocentrotus depressus*, that of *Echinostrephus* being entirely unknown up till then, the others being more or less completely known (cf. my "Studies" 1921). The postembryonal development of *Mespilia globulus* is very carefully described. The larva of *Echinostrephus* is shown to be of the Echinometrid type, a fact of importance for judging of the classification of this aberrant type.

Finally R. GOPALA AIYAR has given a very fine and elaborate account of the "Early development and metamorphosis of the tropical Echinoid *Salmacis bicolor* Agassiz" (Proc. Indian Acad. Sci. I. 1935). He has not only reared the larvæ from the egg through metamorphosis, but also succeeded in keeping the young sea-urchins in the laboratory for a year, evidently showing normal growth.

Mention may also be made of a paper by M. KUME on the development of the Echinoids of Misaki, 1929, in the Japanese Journal of Zoology, No. 41. It is wholly

in Japanese, and thus wholly closed to me. But a couple of figures, one of *Strongylocentrotus pulcherrimus*, the other of *Pseudocentrotus depressus* are valuable, the latter having been reared a little further than it was reared by ONODA, though still not nearly to full larval shape.

Nothing has been done on the larval development of Asteroids or Crinoids, but on Ophiuroids important observations are made by GUNNAR THORSON and by NARASIMHAMURTI. In his paper "On the reproduction and larval stages of the brittle-stars *Ophiocten sericeum* (Forbes) and *Ophiura robusta* Ayres in East Greenland (Medd. om Grönland. Bd. 100. 4. 1934) THORSON describes the larvæ of these two Ophiuroids, which he has been able to identify from the plankton catches. Particularly the *Ophiocten* larva is interesting in having a recurrent rod, a fact not helping to solve the difficult problem of the Ophiolepidid larvæ.

NARASIMHAMURTI has published an important paper on "The development of *Ophiocoma nigra*" (Qu. Journ. Micr. Sci. 76. 1. 1933), in which the whole larval and postembryonal development is elaborately described. Evidently NARASIMHAMURTI did not know anything of what was previously known about the development of this Ophiuroid; that the larva was figured by GRAHAM KERR 1912 (The Glasgow Naturalist. IV); that fertilization was made by me at the Plymouth laboratory and the first development stages described in my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X, p. 12); that the nervous system of the larva was represented in my "Notes on the development and the larval forms of some Scandinavian Echinoderms" Vid. Medd. Dansk Naturh. Foren. 71. 1926); that the larva was figured and described in my "Handbook of the Echinoderms of the British Isles" 1927, p. 178; and in my "Contributions to the study of the development and larval forms of Echinoderms" I—II. (Mem. Acad. Copenhagen. 9. Ser. IV. 1931, p. 34. Pl. IV. 1), all these papers being represented in the library of the Plymouth station, where he reared the larvæ.

Finally may be mentioned the discovery of viviparity in a great number of mainly Antarctic Ophiuroids, as set forth in my Report on the Echinoidea and Ophiuroidea of the "Discovery" Expedition (Discovery Reports, Vol. XII. 1936). The whole subject of the viviparity, and the therewith connected hermaphroditism, is dealt with there, pp. 204—208. To enumerate here all the new cases of viviparous Ophiuroids I think superfluous; it may suffice to refer to the said work.

As for the Holothurians I may recall the fact (overlooked in my "Contributions" of 1931) that HÖRSTADIUS (Op. cit. 1925) has reared the larva of *Holothuria Poli* d. Ch.; he does, however, not describe or figure this larva, which is thus still unknown.

*Echinoidea.*1. *Eucidaris metularia* (Lamarck).

Pls. I—II.

Specimens of this species — which is not common at Ghardaqa, apparently occurring only on the outer reefs — were not found to be ripe until early in June. A number of specimens were kept in the tanks of the station, where they lived quite well for some time. On June 4th some specimens were found to have ripe sperma, but no specimens to have ripe eggs. Then the next day a number of females had the eggs perfectly ripe — as if on command! (I had formerly found this species ripe early in April at Hawaii; cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 24). Fertilization was thus undertaken on June 5th, and proved perfectly successful.

The eggs are small, c. 0.09 mm., quite clear. The fertilization membrane lies so close to the egg-surface as to be almost indiscernible; only at the first cleavage stages it becomes discernible across the notch between the cleavage cells. Already after 6 hours the embryos are beautiful blastospheeras, very clear, and about twice the size of the egg, the cells being very low (Pl. I. Fig. 4). The cells, the limits of which are very distinct, are rather unequal sized; I have, however, been unable to discern any distinct difference in the size of the cells in the first cleavage stages (Pl. I. Figs. 2—3); also I find the number and distribution of the larger cells rather variable, so it would seem that no great importance attaches to this difference in the size of the cells in the blastospheara.

At the age of about 24 hours the gastrula-stage has been reached. The archenteron is remarkably slender and elongate; a conspicuous proliferation of mesenchyme cells takes place at the upper end of the archenteron (Pl. I. Fig. 5). At this stage the limits of the ectoderm cells are still quite distinct; in the following stage of the development these cell limits are no longer discernible.

Whereas the young gastrula is still almost spherical, like the blastospheara, the shape changes very markedly in the course of the next 24 hours into an almost triangular, flattened form (Pl. I. Fig. 6). The proliferation of the mesenchyme cells gradually stops, and the upper end of the archenteron widens, evidently for the formation of the mesoderm pouches (which I have not directly observed, however). At the same time the archenteron curves dorso-ventrally, its upper end meeting an ectodermal invagination, the larval mouth, and the ventral surface of the embryo becomes somewhat sunken round the mouth.

At the age of four days the embryo begins to assume the larval shape, and the first rudiments of the skeleton appear (Pl. I. Fig. 7). The larva at this early stage closely resembles that of *Eucidaris tribuloides*, as figured by TENNENT in his "Studies of the hybridization of Echinoids, Cidaris tribuloides". (Publ. No. 312 of the Carnegie Inst. Washington, 1922, fig. 4, p. 10). Its nearly horizontally directed postoral processes suggest that it will develop into a form with long horizontal arms like the

*Diadema* larva, the *Echinoplateus transversus*, as, indeed, I formerly thought the conclusion inevitable that *Echinoplateus transversus* must be a Cidarid larva (cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 251). Even after I had proved the larva of *Diadema* to be the *Echinoplateus transversus*, I still thought the young larva of *Eucidaris tribuloides* figured by TENNENT (Op. cit.) to prove that the Cidarid larvæ must belong to the same larval type, although "it would

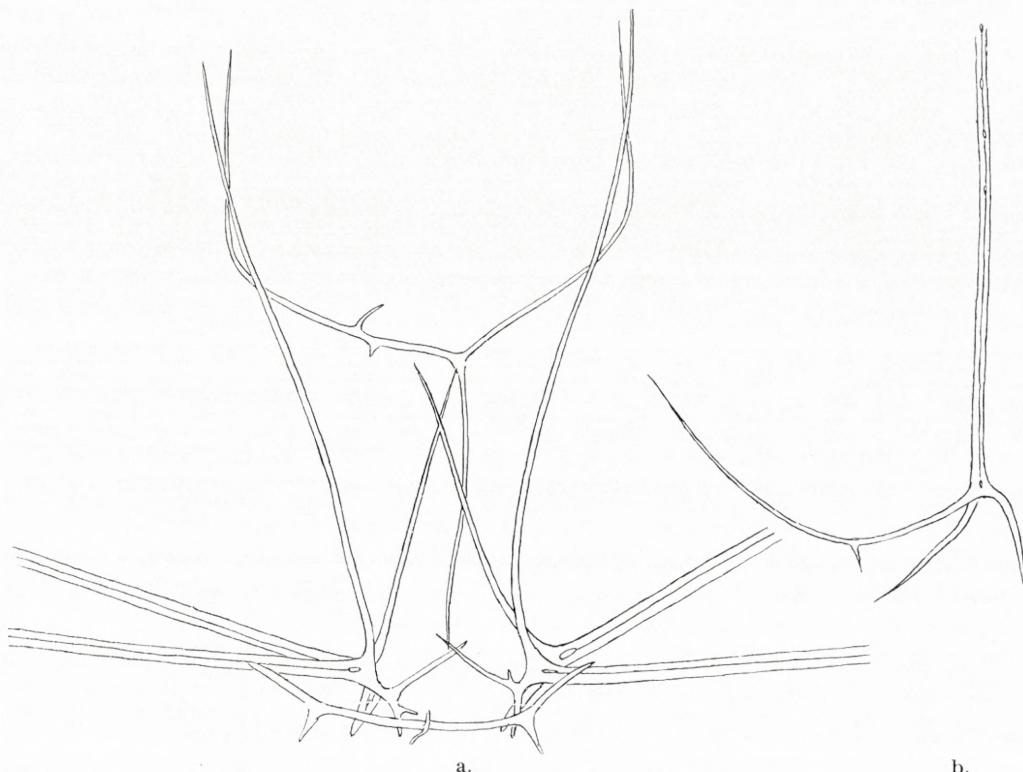
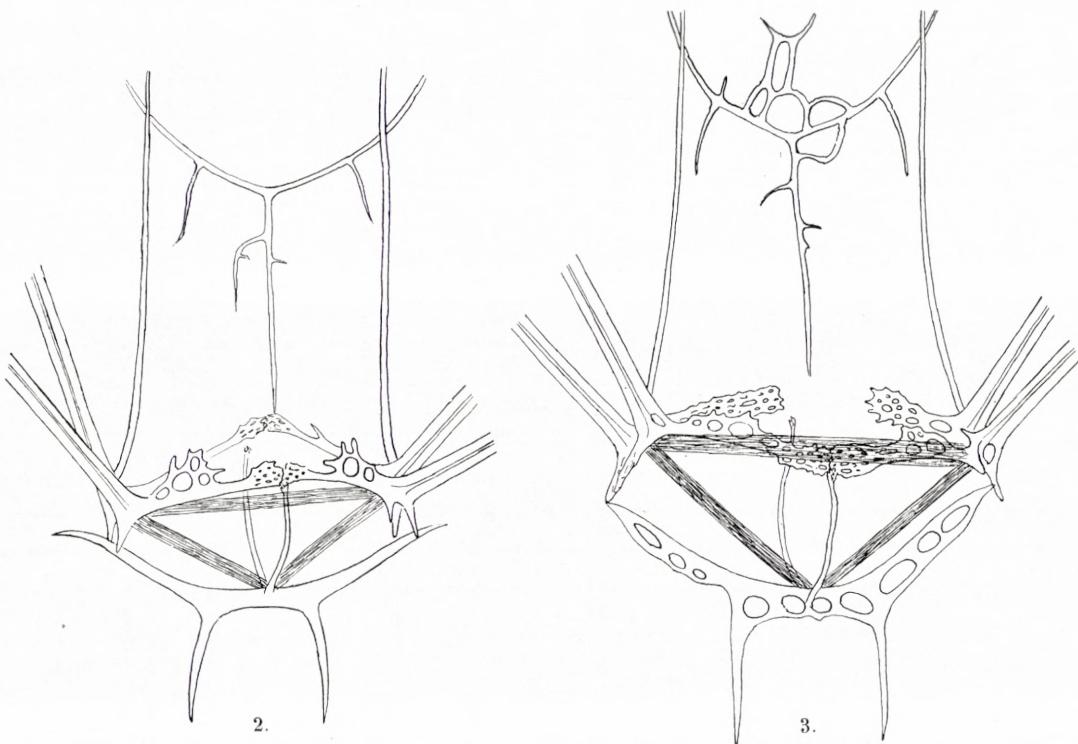


Fig. 1. Skeleton of the larva of *Eucidaris metularia* (Lamk.). a. From a larva three weeks old, with posterodorsal rods, dorsal arch, and posterior transverse rod. b. The postoral rod of a larva 9 days old, showing the very small and distant holes of the fenestrated rod; from the anterolateral rod proceeds a rudimentary recurrent rod; body rod short, rudimentary.  $\times 290$ .

be highly remarkable to find in two so widely different families as the Cidaridæ and the Diadematidæ the same highly specialized larval type" (cf. my "Contributions to the study of the development and larval forms of Echinoderms", I-II, p. 17). Also the young larva of *Eucidaris Thouarsii*, figured in my work quoted of 1921, Pl. V. 2, points in the same direction. It was therefore with great excitement that I watched the further development of the *Eucidaris metularia* larva, expecting now finally to get the solution of the perplexing problem offered by the Cidarid larval type. In the course of a few days it became clear that this larva would not develop

into a form like the *Echinoplateus transversus*. As seen in Pl. I. Fig. 8, representing a larva 9 days old, the postoral arms gradually become more upwards directed, the shape being now more of the usual type of young Echinoid larvae.

Characteristic of the young larva is the very slight development of the body skeleton. There is no basket structure, the body rods being quite short, and there is only the merest indication of a recurrent rod, this being even not of constant occur-



Figs. 2—3. Skeleton of fully formed larva of *Eucidaris metularia* (Lamk.), 3. slightly older than 2., as appears from the more complicate posterior transverse rod and dorsal arch. The dark bands in these figures, and in fig. 4, represent the larval muscular system.  $\times 215$ .

rence. The postoral rod is of the fenestrated type, but the holes are not distinct till a good distance out; they are at first very small and distant, farther out they are gradually larger and closer together. The rod is perfectly smooth (fig. 1, b; fig. 5, c, d). The anterolateral rod is simple, entirely smooth, as is the whole skeleton. Anterolateral arms are only indicated; the frontal lobe is high and arched, and the whole body unusually broad and swollen, but perfectly clear and transparent, apart from some few, scattered crimson pigment spots; also some peculiar clear balls are found in the end of the postoral arms. The suboral cavity is very conspicuous, as was also the case in the younger stages.

At the age of three weeks the larva had assumed the shape shown in Pl. I. Fig. 9. Posterodorsal arms have appeared, but they are still only short; the posterodorsal rod is fenestrated like the postoral rod. Posterolateral lobes have begun to form, and a pair of conspicuous postoral vibratile lobes have formed, whereas the corresponding dorsal lobes are still indistinct. The corners of the postoral lobe are markedly produced, whereas the anterolateral arms are still merely indicated. The dorsal arch

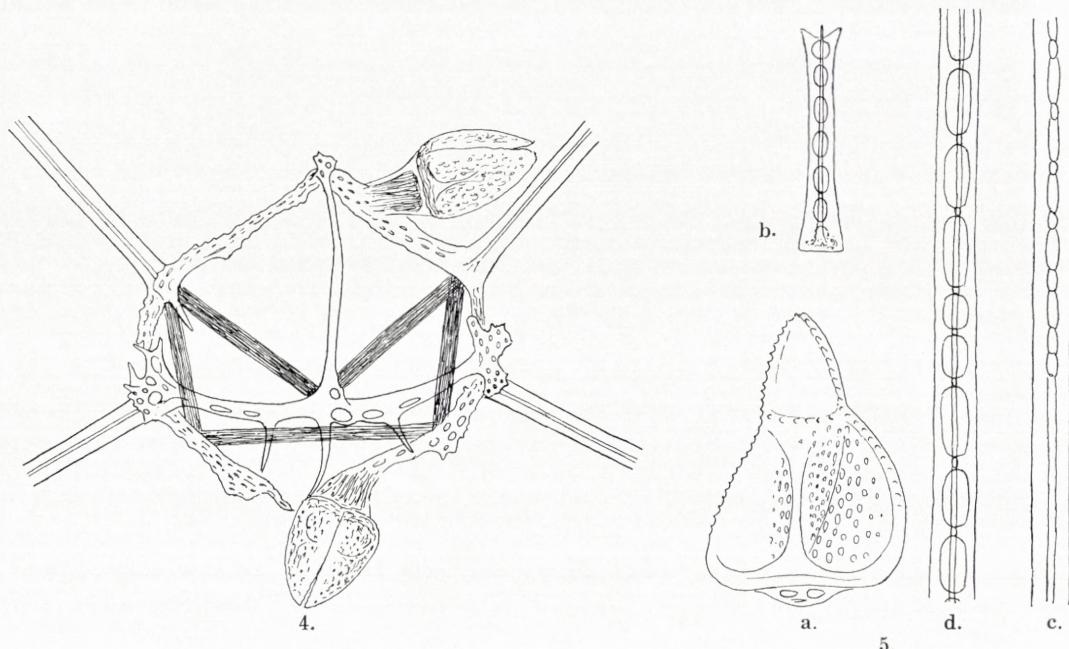


Fig. 4. Skeleton of a larva in beginning metamorphosis, seen half from behind. Two pedicellariae have appeared.  $\times 215$ .

Fig. 5. a. Valve of globiferous pedicellaria; b. embryonal spine; c—d. parts of the postoral (or posterodorsal) rod, c. from the basal, d. from the distal part, showing the characteristic difference in the size of the holes. a, c, d.  $\times 430$ ; b.  $\times 240$ .

has been formed, but has not yet developed far enough to provoke the formation of preoral arms. The first rudiment of a posterior transverse rod is seen (fig. 1, a). There is a conspicuous spot of crimson pigment at the point of the long arms, as also in the lobes, and scattered small crimson spots are found all over the body.

So far the *Eucidaris* larvae had reached in their development by the time I had to leave the station. Fortunately my assistant, ZAKY EFFENDI, could go on looking after the larvae, and in the samples later on received from him I found the fully formed larvae up till beginning metamorphosis, in perfect state of preservation. Only about the colour of the fully formed larvae there is no information, beyond the fact that these larvae, as preserved in Canada balsam, show the intestine strongly pigmented with light brownish spots.

The fully formed larva is particularly characteristic by its numerous large ciliated lobes. Not only has it the usual posterolateral, postoral and posterodorsal lobes, but there is also a pair of anterodorsal lobes, and the anterior corners of the postoral area have been produced into a pair of lobes corresponding to the anterodorsal ones (Pl. I. Fig. 10; Pl. II). Anterolateral and preoral arms are well developed, though not very long, particularly in comparison with the very long postoral and posterodorsal arms. These latter, which are slightly widened at the base, must be actively movable, as evinced by the well developed muscular system connecting their bases (figs. 2—4). The posterodorsal rod is exactly like the postoral one.

In the skeleton the most characteristic part is the posterior transverse rod. It is gracefully curved and has a pair of strong thorns, directed backwards; from the middle of it proceeds a long ventral and a dorsal median process, which reach up to the ventral and dorsal transverse rods (figs. 2—4). In the later stages some meshwork develops along the posterior edge of the posterior transverse rod, and its ends, as well as the ends of its median processes, develop into fenestrated plates. At the same time the ventral and dorsal transverse rods — which are originally simple, slender rods — develop into fenestrated plates, which form a conspicuous calcareous ring around the posterior end of the body (fig. 4). In this ring also takes part the body rod and an inconspicuous prolongation from the posterodorsal rod; but these parts are evidently of much less importance than the transverse rods. On these widened transverse rods the first pedicellariae and spines appear; further a pedicellaria develops on the dorsal arch, which likewise develops into an irregular, fenestrated plate (figs. 3—4). It may be added that at the stage, where the first pedicellariae and spines have appeared, also the first tubefeet have been formed; but the details, particularly the formation of the plates of the test could not be followed on the material available. It is clear, however, that the widened transverse rods and dorsal arch represent the five genital (basal) plates (cf. v. UBISCH. Anlage u. Ausbildung d. Skeletsystems einiger Echiniden. Zeitschr. f. wiss. Zool. CIV. 1913. Taf. VII; I. GORDON. Skeletal development in *Arbacia*, *Echinarachnius* and *Leptasterias*. Phil. Trans. B. 217. 1929; ONODA. Notes on the development of some Japanese Echini. Japanese Journ. of Zool. VI. 1936). The ocular plates have not yet been formed at this stage.

The pedicellariae are recognizable already as of typical Cidarid structure, of the small globiferous type (fig. 5, a).

Having thus traced a Cidarid larva to its final shape we see that there is no real resemblance between the Cidarid and the Diadematid larval type, the remarkable resemblance between the young Cidarid larva and the fully formed Diadematid larva, the *Echinoplateus transversus*, being merely a curious coincidence of no real morphological value — judging from the very few larvæ hitherto traced with full certainty, viz. the *Diadema* and the *Eucidaris* larvæ. But there are two other larvæ to take into consideration here, viz. the larva of *Dorocidaris papillata* (= *Cidaris cidaris* L.), and the larva figured by JOH. MÜLLER on Taf. V. 1—3 of his VII. Abhandlung über die Metamorphose der Echinodermen (Abh. d. Akad. Berlin, 1855).

The larva of *Cidaris cidaris* was studied very carefully by PROUHO in his "Recherches sur le Dorocidaris papillata" (Arch. Zool. Exp. et Gén. 2. Ser. V. 1888, Pls. XXIII—XXV). The youngest stages differ rather conspicuously in shape from those of *Eucidaris*, and also the last stage figured by PROUHO (Pl. XXV. 2) is conspicuously different from the final shape of the *Eucidaris* larva; but evidently PROUHO did not succeed in rearing his larvæ to the final stage, as may be concluded from the fact that the posterior transverse rod is represented as quite small. As a matter of fact this larva is only slightly older than the stage of the *Eucidaris* larva represented here in Pl. I. Fig. 9. This fact, combined with the very different mode of drawing (— artistically PROUHO's figure is far beyond my drawings —) makes out for the differences, and it seems certain enough that the *Cidaris (Dorocidaris)* larva belongs to the same type as the *Eucidaris* larva, characterised, besides by the strong development of the vibratile lobes, by the faint development of the body skeleton, which does not form a basket structure.

The larva of JOHS. MÜLLER, which I designated in my "Echinodermenlarven d. Plankton-Expedition" 1898, p. 79, by the name *Echinopluteus Mülleri*, was thought by JOHS. MÜLLER to belong either to *Cidaris* or *Diadema*. Finding it to differ too much from the *Cidaris* larva as figured by PROUHO, I concluded that it would belong to *Centrostephanus longispinus*, the only Diadematid found in the Mediterranean. At that time it was also generally accepted that there was only one Cidarid in the Mediterranean, *Stylocidaris affinis* being regarded as identical with *Cidaris cidaris (Dorocidaris papillata)*. The perfect resemblance between this larva of JOHS. MÜLLER and the fully formed *Eucidaris* larva makes it practically certain that the former is also a Cidarid larva, either of *Stylocidaris affinis* or of *Cidaris cidaris*, the two only species of Cidarids occurring in the Mediterranean — to which of the two species the larva belongs cannot be decided, because of the different character of JOHS. MÜLLER's and PROUHO's drawings, and of the different age of the larvæ represented by the two authors. Further it may now be concluded almost with certainty that the larva figured on Pl. V. 7 of my "Studies" (1921) which I referred (Op. cit., p. 29) with some little doubt to *Astropyga pulvinata* — "be it not *Eucidaris Thouarsi*, which I would not think very probable, judging from the shape of the young larva reared" (viz. on account of its horizontal arms), is in reality the larva of *Eucidaris Thouarsi*.

The rather certain demonstration of the said larva of JOHS. MÜLLER being a Cidarid larva, and that my quite similar larva from the Gulf of Panama is the *Eucidaris Thouarsi* larva, indicates that there is a larval type peculiar to the family of the Cidarids, characterised by the strong development of the vibratile lobes and by the rudimentary condition of the body skeleton. Of course this has to be corroborated by the study of the development of other Cidarids; but for the present evidences point in this direction.

The removal of JOHS. MÜLLER's larva from the Diadematids (*Centrostephanus longispinus*) does away with another difficulty, viz. the remarkable difference between the supposed *Centrostephanus* larva and the *Diadema* larva (*Echinopluteus transversus*).

It would, indeed, be just as remarkable to find within the same family larvæ so different as the *Echinoplateus transversus* and the *Echinoplateus Müller*, as it was to find the *Echinoplateus transversus* larval type within the two widely different families of the Cidaridæ and the Diadematidæ, both of these alternatives equally irreconcilable with the fact that otherwise we find the Echinoid larvæ grouping themselves into well marked "families" corresponding to the families of the adult Echinoids — the Temnopleuridæ, the Echinidæ, Clypeastridæ, Spatangidæ, etc. By the removal of the *Echinoplateus Müller* to the Cidarids the apparent non-conformity of the larvæ within the family of the Diadematidæ disappears, and we may reasonably expect that the divers genera of the Diadematids will prove all to have larvæ of the *Echinoplateus transversus*-type, as already indicated by the fact that we know quite a number of different "*Echinoplateus transversus*", as shown in my "Studies of the development and larval forms of Echinoderms", pp. 78—95. But that is for future researches; till now we know for certain only the larva of the genus *Diadema* itself.

## 2. *Diadema setosum* (Leske).

Pl. IX. Fig. 1.

A single ripe female and some ripe males were found on the 9th of May; but the great majority of the specimens were still unripe at that time, the 9th being two days after fullmoon. Also later on I found in general only very few specimens ripe at a time, and not specially at full moon, so that I could not confirm the observations of MUNRO FOX on a lunar periodicity in the reproduction of this species (Proc. R. Soc. B. Vol. 95, 1923, p. 525—530). However, this may be due to the breeding season of this species being mainly later on in the summer (MUNRO FOX found the largest percentage of mature specimens in July, the number being smaller in August and very small or nil in September), so that it would be exceptional to find mature specimens earlier in the summer.

Fertilization was thus undertaken on May 9th. The development proceeded as described in my "Contributions to the study of the development and larval forms of Echinoderms" I. 1931, p. 11—17, Pls. I, II. 1—3; there is no reason for giving here again a detailed description. It took a little longer for the larvæ to reach the second, the *Echinoplateus transversus*-stage, than I had found it to be the case at Onrust, viz. nearly three weeks against only two weeks at Onrust, in the Java Sea.

By my researches at Onrust I did not succeed in rearing the larvæ till beginning metamorphosis, and thus the skeleton of the second larval stage had not yet reached its full shape in my oldest larvæ; still, I thought it probable that this larva would be identical with the *Echinoplateus transversus*, *species f.* (from the Bay of Bengal and off the Maldives Islands) described in "Studies of the development and larval forms of Echinoderms", p. 91, Pl. XIII. 3—4. The larvæ in beginning metamorphosis from my Red Sea investigations in general bear out this suggestion. The skeleton is alike in both, as is also the general shape. It is, however, noteworthy that the length of

the arms appears to be smaller than in the *Echinopluteus transversus*, species f.; in none of the specimens reared at Ghardaqa did the arms reach a greater length than 5 mm., whereas in the said sp. f. the best of the incompletely preserved arms was 6 mm., so that the complete arm would be sure to be a good deal longer, even if perhaps not so long as in the West Indian species, 12 mm. This shorter arm length in the Red Sea larvæ may perhaps be due to the artificial rearing in small dishes; unfortunately I did not succeed in catching even a single one of the larvæ in pelagic hauls by day or night, so there were no means of comparing my artificially reared larvæ with such as were reared in nature. The possibility remains, therefore, that the said species f. from the Indian Ocean belongs to *Diadema Savignyi* (or perhaps to some other Diadematid). In the larvæ reared at Onrust the arms did not surpass 2 mm. in length, but they did not reach so far as the beginning of metamorphosis, so it is rather safe to say that the arms had not grown to their normal full length. ONODA, who has reared the larva of *Diadema setosum* (Op. cit. p. 648, Pl. XIII. Fig. 11) does not say anything about the length of the arms in his larvæ; judging from the figure quoted they were not longer than in my larvæ from Onrust, and like these latter his larvæ were not near metamorphosis, so, evidently, they had not reached the normal full arm length.

As regards the shape of the larval body it may be mentioned that the vibratile band on the dorsal side makes a conspicuous downward bend so as to form a pair of dorsal lobes. The complete resorption of the anterolateral arms, combined with the widening on the middle of the dorsal side, gives the larval body a very unusual shape, as shown in Pl. IX. Fig. 1.

With beginning metamorphosis the long arms become somewhat narrower and gradually shorter — evidently, they become completely resorbed, and the calcareous material in the long rods used in the formation of the body skeleton. I have, however, directly observed only the beginning resorption of the long arms; but it is clear that they cannot be thrown off (such as is the case with the long arms in the *Ophiothrix* larvæ), since their basal part enters into the composition of the skeleton of the sea-urchin.

In larvæ near metamorphosis, when swimming, the primary tubefeet are extended to a considerable length; it looks as if they were fumbling for something to attach themselves to — and this probably is actually the case. I did, unfortunately, not observe this until just before my departure, so there was no time for further observation or for making a drawing of the larva with its extended primary feet.

When I left Ghardaqa, the larvæ, which were now 6 weeks old, were near metamorphosis, and one of them had just metamorphosed. I took then a number of the best larvæ along with me, in a jar with sea-water and a few algæ, hoping that I might thus succeed in getting some more of them metamorphosed. Although I had no sort of laboratory facilities onboard the ship, and no microscope, but only a pocket lens, I actually succeeded in getting some few more young sea-urchins in more advanced stages, so that I can here give some information of the postembryonal development of this important Echinoid type.

The newly metamorphosed sea-urchin is represented in fig. 6, seen from the aboral side. Parts of the larval skeleton are seen to develop into the genital plates, much as we know it from other Echinoids. The posterior transverse rod can be recognised, carrying a pedicellaria; also the basal part of one of the long postoral rods is seen. A third large plate, also carrying a pedicellaria, is likewise developing from part of the larval skeleton, very probably the rudimentary dorsal arch. The two other genital plates are new formations. The basal part of the second postoral rod is seen lying above one of the oculars, possibly the ocular is developing in connection

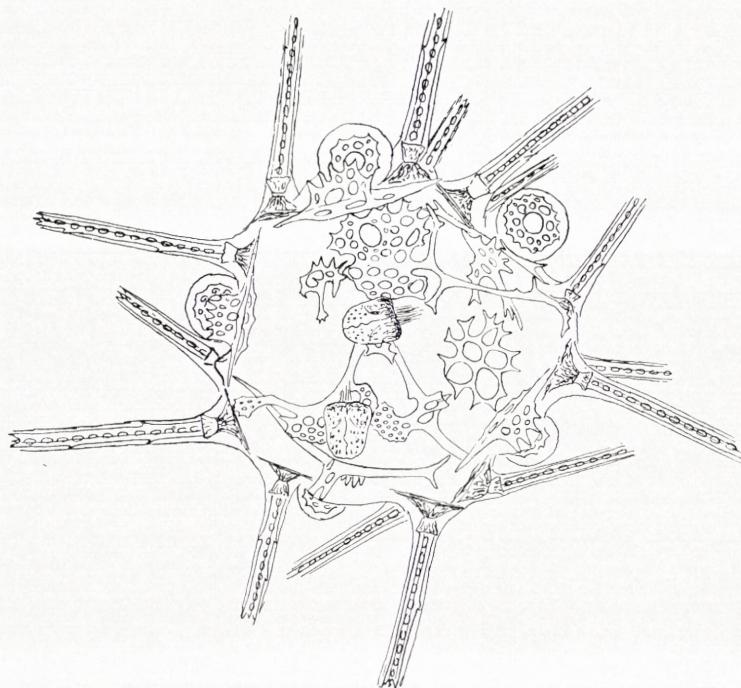


Fig. 6. Young *Diadema setosum*, newly metamorphosed. Aboral side.  $\times 100$ .

with it — this I have been unable to ascertain. The oculars are peculiar in having an erect superstructure, recalling the tables of the Holothurians; this serves to recognise the ocular plates also in the later stages.

On the oral side are seen the rudiments of the five pairs of buccal plates, all equally developed. No traces of the masticatory apparatus are seen as yet, and the mouth is still closed (fig. 8). In the interambulacra the first five plates have been formed (fig. 7); it is very important that there is no trace of the plate No. 4 having originally been situated in the midline of the interambulacrum, such as is figured by GORDON for *Psammechinus miliaris* (cf. I. GORDON. The development of the calcareous test of Echinus miliaris. Phil. Trans. B. 214. 1926, p. 282).

Rather plate 5 is nearer the median line, but I do not see in the following stages any sign of its being in a median position. It is noteworthy that the plate 1, the primordial plate, is remarkably small, and its spine less developed than those of the following plates, which might indicate that it is not the first to be laid down — but this cannot be ascertained from the single specimen available of this stage. — Only the first pair of ambulacrinal plates have appeared. The sucking disk of the primordial tubefoot

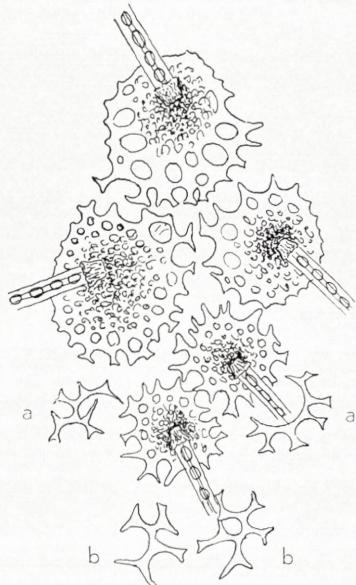


Fig. 7.

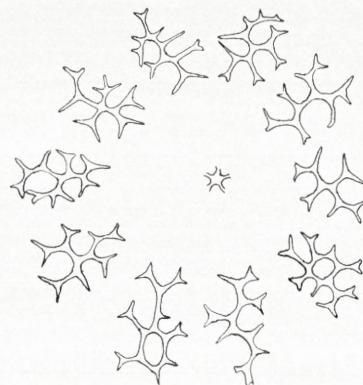


Fig. 8.

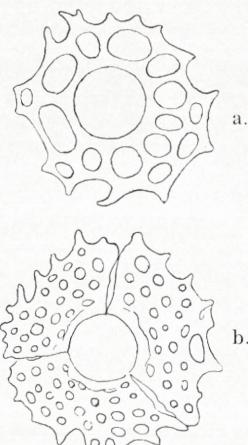


Fig. 9.

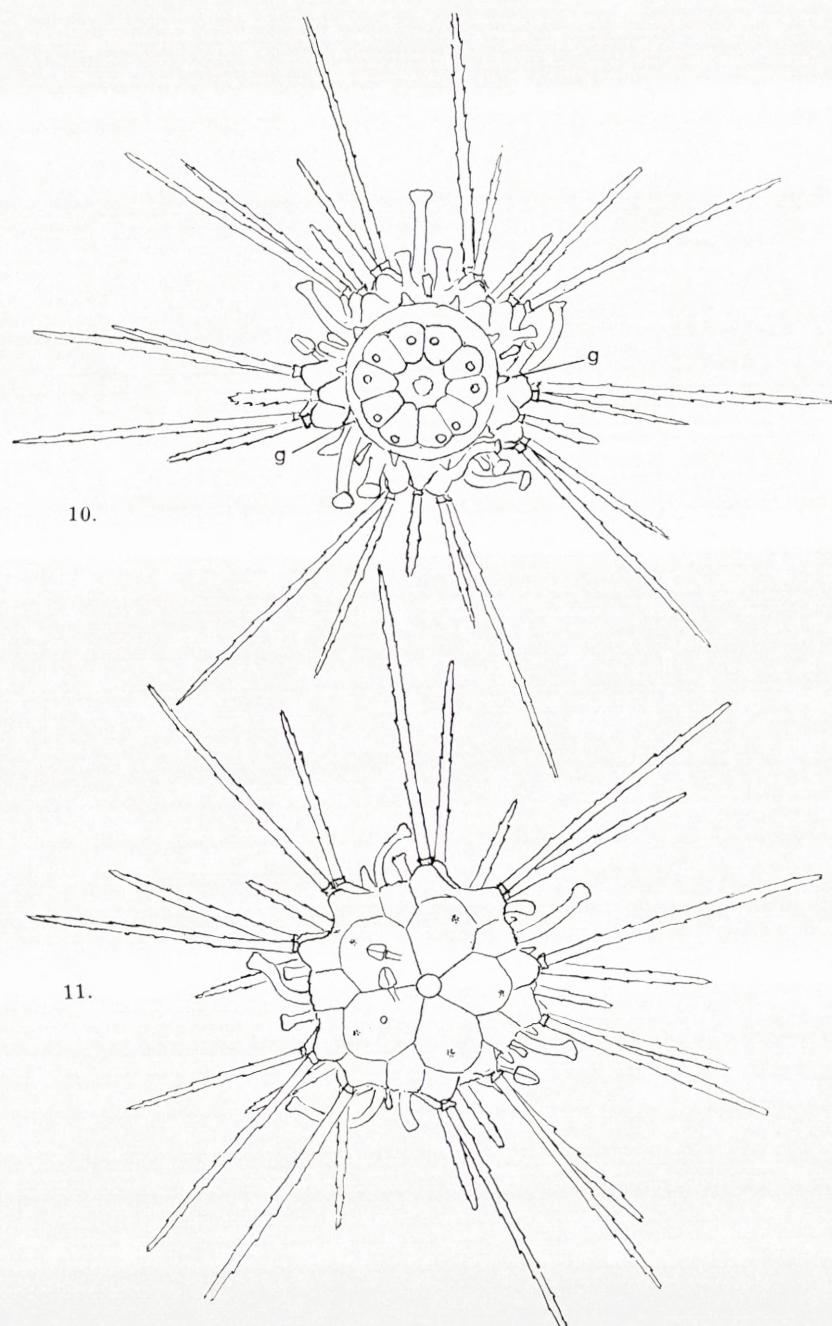
Fig. 7. Interambulacrinal plates of newly metamorphosed *Diadema setosum*; the lowermost plate is no. 1, the primordial plate, the uppermost plate no. 5. a. The first ambulacrinal plate of the two adjoining ambulacra. b. Buccal plates.  $\times 240$ .

Fig. 8. Buccal plates of newly metamorphosed *Diadema setosum*; in the centre is seen the first trace of the future mouth.  $\times 240$ .

Fig. 9. Sucking disk of primordial tubefoot (a) and of the second pair of tubefeet (b) of the young *Diadema setosum*.  $\times 400$ .

is a complete ring (fig. 9, a); in the following tubefeet to be developed the disk is composed of three separate pieces (fig. 9, b), corresponding to what was found by GORDON in *Psammechinus miliaris* (Op. cit. figs. 12—13).

In the following stage, 2 months of age, the genital plates are fully formed, though the plates 4 and 5 are not yet as large as the others. The original larval rods are still distinguishable. The ocular plates are widely excluded from the periproct, in which no anal plates have as yet been formed (fig. 13). The buccal plates are fully formed, all of equal size; but there are still no buccal tubefeet. The masticatory apparatus is nearly ready, but there is still no mouth or anal opening (fig. 15). In another specimen of the same age there are five anal plates of nearly equal size (fig. 14).



Figs. 10—11. Young *Diadema setosum*, 9 weeks old, oral (10) and aboral side (11). g. Gills.  $\times 40$ .

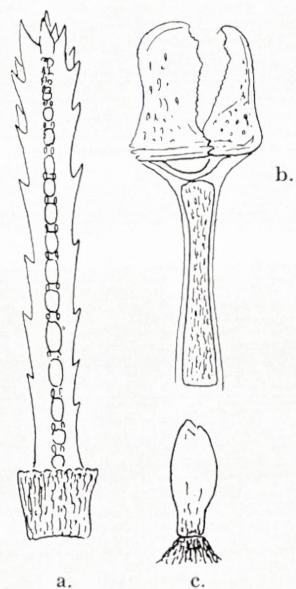


Fig. 12. Spine (a), ophi-cephalous pedicellaria (b), and sphæridium (c) of young *Diadema setosum*, 8 weeks old.  
 $\times 250$ .

In one of the oldest specimens, 9 weeks old (figs. 10—11), the buccal feet have been formed. The ocular plates are still widely exsert — a fact of importance, since later on three of them become very broadly insert. In this specimen there are only two anal plates, which shows that no morphological importance attaches to the fact that in the younger specimen there are five anal plates (figs. 14, a-b).

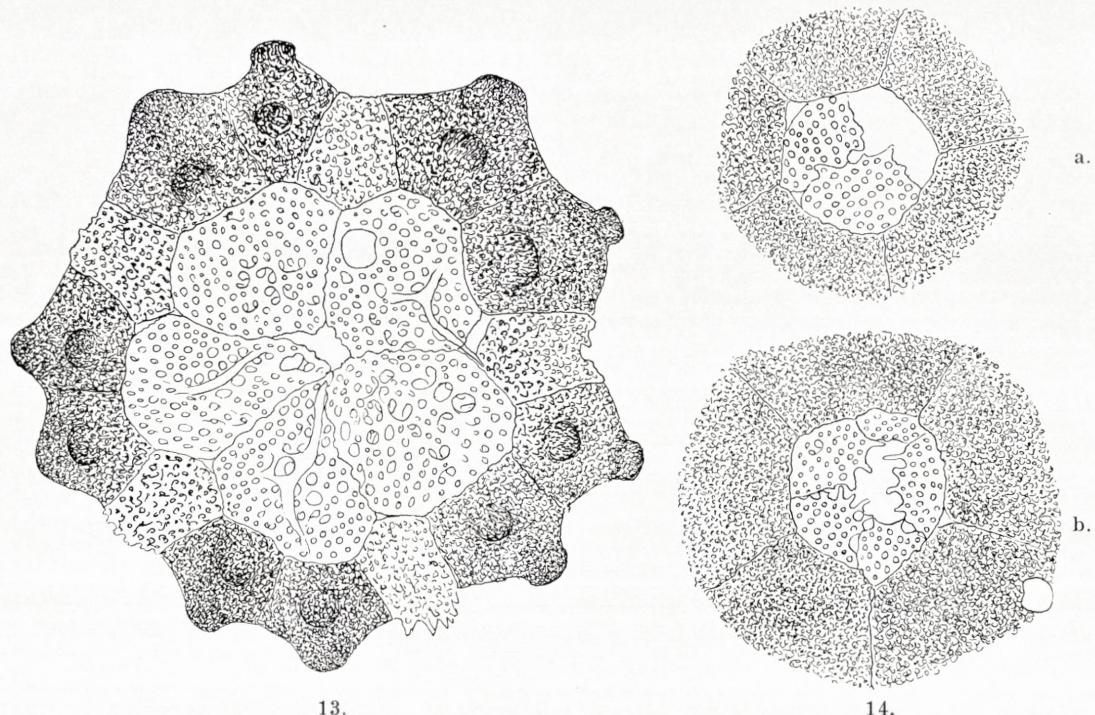


Fig. 13. Denuded test of young *Diadema setosum*, 2 months old.  $\times 150$ . In three of the genital plates remnants of the larval skeleton are still seen.

Fig. 14. Periproct, with anal plates, and the upper part of the genital plates of young *Diadema setosum*; a. from a specimen 9 weeks old, b. from a specimen 8 weeks old. The large hole in the right lower plate in fig. b. is the primary pore of the madreporite. The same is seen in the right upper genital plate in fig. 13.  $\times 150$ .

The spines of these young specimens are quite simple, thorny, fenestrated, not of a special embryonal type (fig. 12, a); there are no spines on the apical plates, and as the apical system is relatively large, this looks very naked (fig. 11). Sphaeridia have appeared in the specimens of 8 weeks (figs. 12, c; 15). The pedicellariæ are of the ophicephalous type, without neck (fig. 12, b). — The specimens of 8—9 weeks were already black coloured on the aboral side; the rather thick, black skin had to be removed, before the structure of the test could be seen.

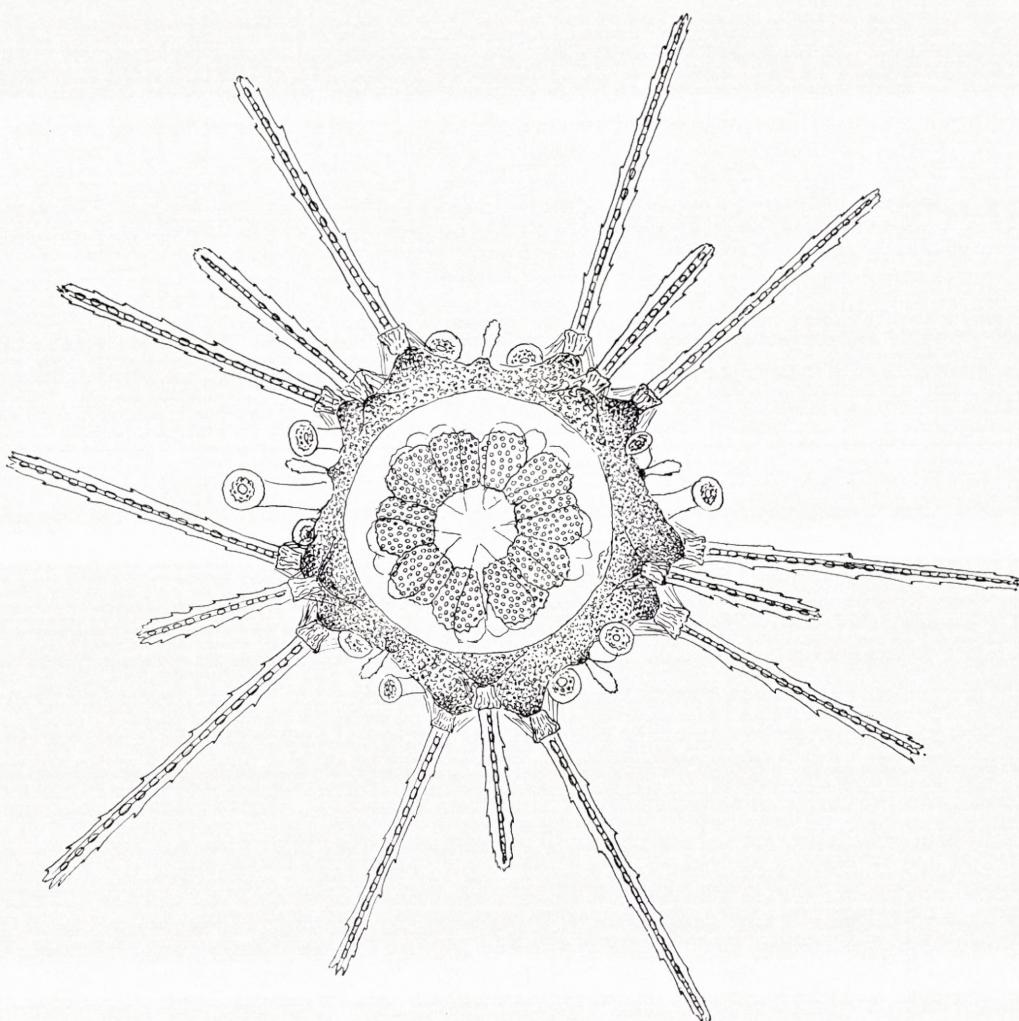


Fig. 15. Young *Diadema setosum*, two months old; oral side.  $\times 90$ . The masticatory apparatus nearly fully formed, but there is still no mouth-opening; buccal plates fully formed, but the buccal tube feet have not yet appeared. In the middle of each ambulacrum, between the tube feet, is seen the first sphæridium.

### 3. *Temnotrema scillæ* (Mazetti).

Pl. III. Figs. 1—2; Pl. X. Fig. 1.

On the dredging trip to the Gulf of Suez with the "Mabahiss" in the middle of May a good number of specimens of the small Echinoid *Temnotrema scillæ* (Mazetti) were dredged off Ashrafi Light, at a depth of c. 80 meters, on a muddy-sandy bottom. They were taken alive to the laboratory, where I found a few of them to contain some ripe eggs and a little sperma; it was apparently just in the beginning

of the breeding season. Fertilization was undertaken on May 15th. The eggs are very small, only c. 0.08 mm., very clear and transparent.

The cleavage passed very rapidly, the 32—64 cell stages being reached already in two hours. There seems to be some inequality in the size of the cleavage cells — but I did not follow the cleavage process in details, so I do not venture to say definitely that there is such inequality. After 22 hours the embryos were gastrulae, with beginning formation of the skeleton. At the upper end of the archenteron a pair of thin mesoderm-pouches, almost without lumen, proceed, reaching to and apparently attaching themselves to the ectoderm (Pl. X. Fig. 1).

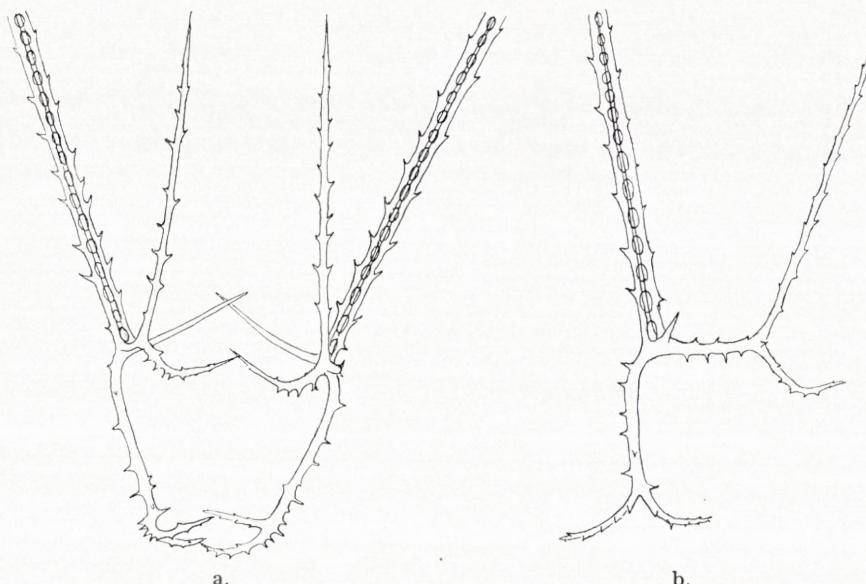


Fig. 16. Skeleton of the larva of *Temnotrema scillæ* (Maz.), I. stage. a. From the dorsal side, b. in side view.  $\times 240$ .

The young pluteus-stage is reached on the second day. It has a typical Temnopleurid skeleton (fig. 16, a-b), with the body rod ending in two diverging branches; there is no basket structure. The postoral rod is fenestrated. The whole skeleton is strongly thorny.

At the age of two weeks the larva had reached its full shape, the first rudiments of the amnion being discernible, and the first pedicellariæ having appeared. This larva (Pl. III. Figs. 1—2) is of great beauty. The four main arms are very broad in the proximal part, but the distal part, about a fourth of the length, is slender, the narrowing being quite abrupt. There is a vibratile epaulet at the base of each of these four arms, but no ventral or dorsal vibratile lobes, whereas the posterolateral lobes are well developed. The anterolateral and preoral arms are quite short and narrow. A number of small reddish pigment spots are scattered all over; they are

a little more numerous along the epaulets, but there are none in the end part of the arms. The stomach is a very faint yellowish.

The posterodorsal rod is fenestrated like the postoral ones; the posterior transverse rod is simple, bifurcating at the ends, the lower branch being simple, straight, without thorns (fig. 17). A muscular system makes the four main arms movable.

I did not succeed in rearing the larvæ through metamorphosis, the culture being quite small and only very few larvæ reaching the full shape.

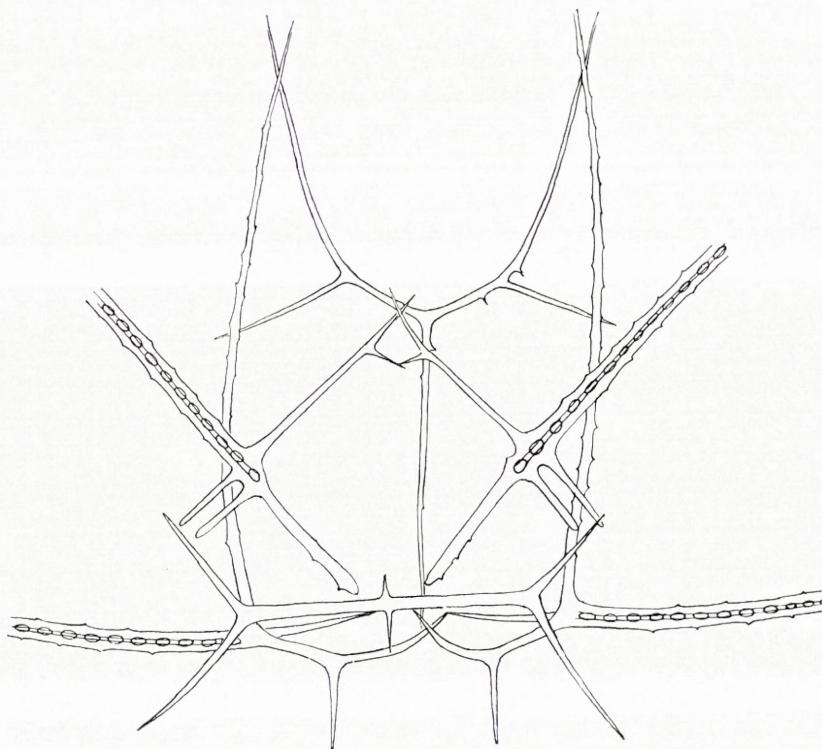


Fig. 17. Skeleton of the fully formed larva of *Temnotrema scillæ* (Maz.).  $\times 250$ .

The larva of another species of the genus *Temnotrema*, *T. sculptum* A. Agassiz, was described in my "Studies" of 1921, p. 54, Pl. VI. 4, having been reared during my stay at Misaki, Japan, in April—May 1914. It was, however, not reared till full larval shape, and is thus incompletely known; but so far as known, it agrees in the main features with the larva of *Temnotrema scillæ*.

#### 4. *Nudechinus Gravieri* (Koehler).

Pl. IV. Fig. 1.

This little Echinoid, which occurs fairly commonly under stones on the reef flat at the coast, as well as on sandy bottom at a depth of c. 5—10 m off the Abu Sadaf

reef at Ghardaqa, was found ripe early in May, and fertilization was undertaken on May 7th. The eggs are c. 0.09 mm., very clear and transparent. Development proceeds rapidly, the embryos having begun to assume the Pluteus-shape already after about 20 hours.

In the young larva, stage I, the body skeleton forms a typical basket structure, the posterior end of the body rods being rather broad and strongly thorny (fig. 18, a, b); the postoral rod is fenestrated. Very soon, by the time the posterodorsal rod appears, a remarkable thickening of the posterior part of the basket sets in (figs. 18, c; 19, a). By the time the dorsal arch appears, the recurrent rod begins to be resorbed (fig. 19, b), and when the posterior transverse rod appears, scarcely a trace of the recurrent rod

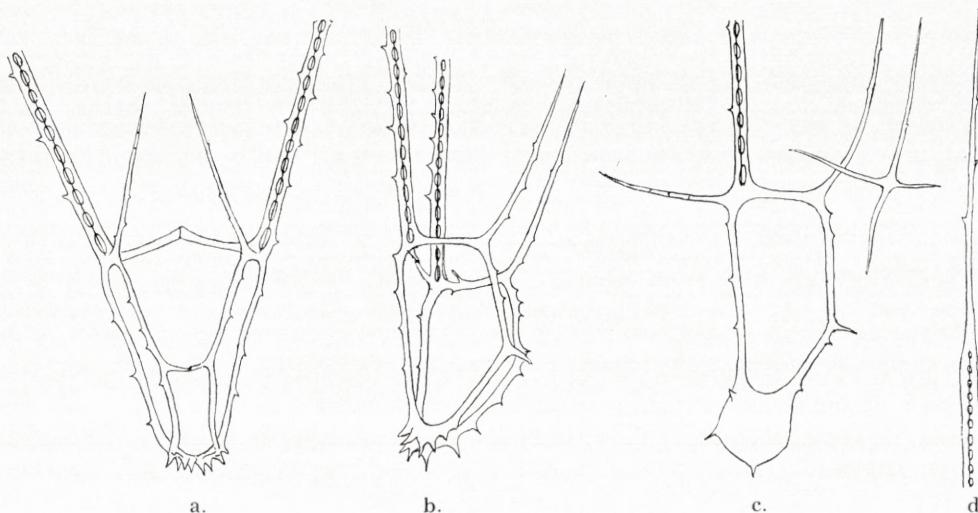


Fig. 18. Skeleton of the larva, I. stage, of *Nudechinus Gravieri* (Koehler); a. from the aboral side. b. in side view. c. Skeleton of a slightly older larva, side view, showing the thickening of the posterior end of the basket; the posterodorsal rod has appeared. d. Terminal part of postoral rod.  $\times 240$ .

is left, and the large terminal swelling is borne alone by the body rod, which now looks exactly like a golf club (figs. 19, b, c). With the growth of the transverse rod, the terminal swellings begin to dissolve; they no longer join in the midline, and then the body rod breaks, and the two balls remain lying in the posterior end of the body, one to each side of the first pedicellaria, gradually becoming smaller, evidently resorbed and their calcareous matter used in the formation of the skeleton of the young sea-urchin (fig. 19, d). The posterodorsal rods are simple, and the fenestrated postoral rods terminate as a simple rod (fig. 18, d). The ventral transverse rods are unusually long. The posterior transverse rod is of a quite unusual shape, like a bow, the upturned ends not bifurcating (fig. 19, d).

The fully formed larva (Pl. IV. Fig. 1) has rather short arms, the four main arms being wide in the basal part, slender in the distal part. There is a pair of large vibratile lobes on the ventral side, the corresponding dorsal lobes being smaller.

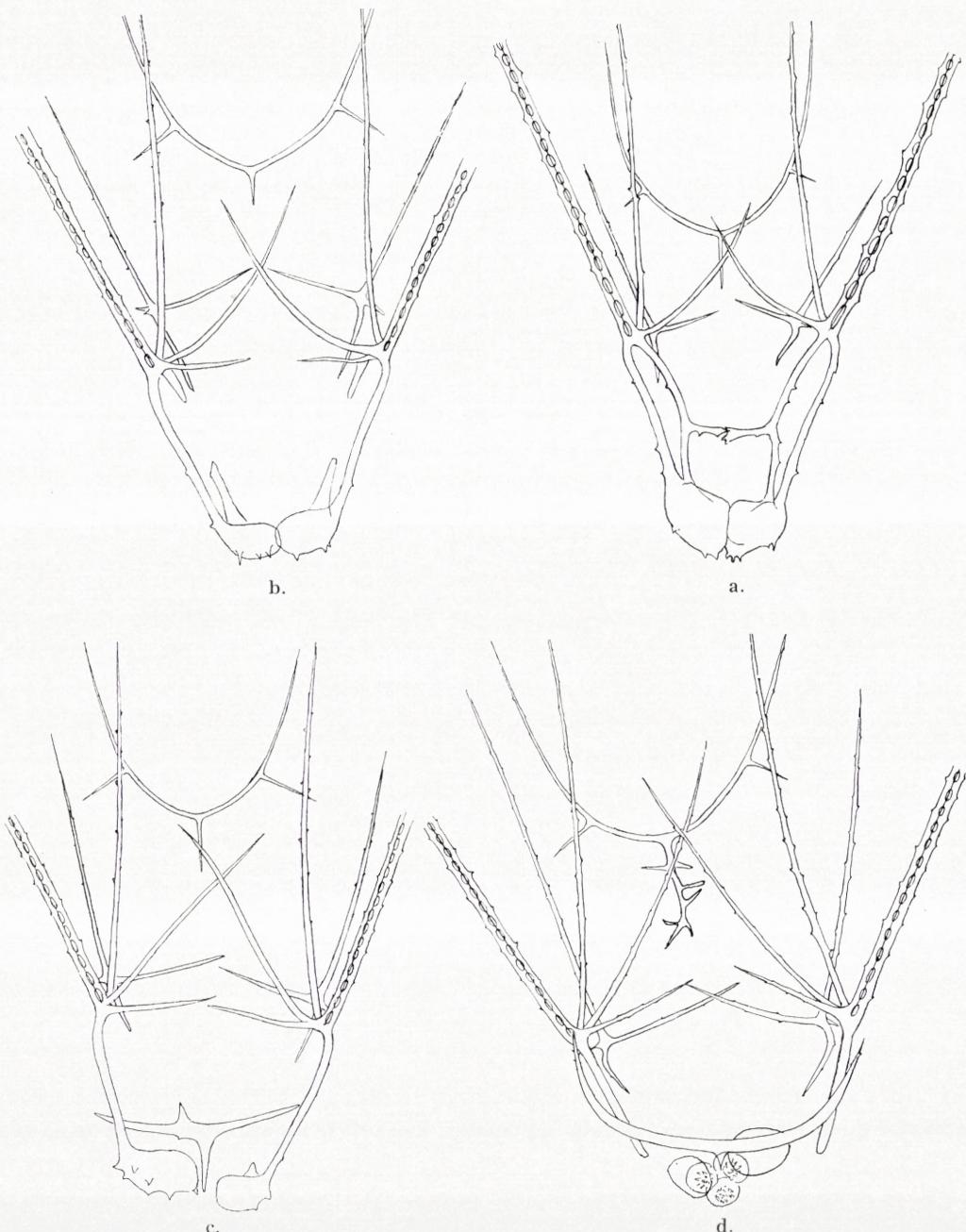


Fig. 19. Skeleton of larva of *Nudechinus Gravieri*, I-II. stage. In fig. a. the terminal thickening is seen fully developed; in fig. b. the recurrent rod has begun to be resorbed; in fig. c. only the last vestige of it is seen on the right side; the posterior transverse rod has appeared. In fig. d. the last rests of the thickening are seen in the middle of the posterior end, beside the incipient first pedicellaria. The posterior transverse rod is fully formed.  $\times 240$ .

Below the lobes are a pair of large epaulets, which originate from the outer corners of the vibratile lobes, gradually growing inwards and finally meeting in the midline so as to form a broad transverse band across the ventral and dorsal side of the body. The posterolateral lobes are small. The colour is very marked on account of a large dark brownish patch on the middle of each arm, in the large ventral lobes, and in the produced corners of the postoral area. Besides, there are some scattered small reddish spots, more numerous along the epaulets, which also have a light tinge of yellowish.

A couple of the larvae metamorphosed, but as, unfortunately, the skeleton of the preserved specimens had been completely dissolved (on account of acid from the cork?), I cannot give any information of the skeletal structure.

This very interesting larva agrees in the main with the Toxopneustid larval type, but shows such surprising special features as were hardly to be expected in a genus, the main distinctive character of which is the complete absence of deposits in the buccal membrane (excepting, of course, the buccal plates), a character that would not beforehand seem to be of great morphological importance. But evidently then it is a very important character.

It seems beyond doubt that the larva described in my "Studies" 1921, p. 60, Pl. XI. 3, as *Echinopluteus* of *Temnopleurid*(?) species c. must be very closely related to the *Nudechinus* larva, as it agrees with the latter in the main characters of the skeleton — the peculiar shape of the posterior transverse rod, the postoral rods terminating in a simple point, the posterodorsal rods simple. It is then certainly not a *Temnopleurid* larva. No *Nudechinus* species being known from off Jolo, where this larva was found, the suggestion lies at hand that it is the larva of a *Gymnechinus*, but this can be no more than a suggestion at present. The fact that there is no terminal swelling of the body rods (I have reexamined the specimens for ascertaining this point) does indicate that it belongs to another genus.

##### 5. *Tripneustes gratilla* (Linn.).

Pl. IV. Fig. 2.

The development of this species has been dealt with repeatedly. In my "Studies" 1921, p. 34, Pl. VIII. 5—6 I described the young larva, reared during a stay at Hilo, Hawaii, in March—April 1915. In my "Contributions" I—II, 1931, p. 24, Pl. III. 5, I gave a more detailed description of the first development stages, and a coloured figure of the larva by the end of the first stage, reared at Mauritius in September 1929; but although the larvae lived for more than five weeks they did not reach the final shape. — Further, ONODA, in his paper of 1936, p. 647, Pl. XIII. 8—9, again figures the larva in the I. stage (and an embryo showing the beginning formation of the skeleton). It may suffice then here to describe and figure the as yet unknown fully formed larva. Fertilization was undertaken at Ghardaqa the 29th of April, and at the age of about 18 days several of the larvae were in beginning metamorphosis.

This proves that the long time it took for the larvæ at Mauritius to begin only to pass into the second larval stage, c. 30 days, was due to unfavourable circumstances, as I suggested (Op. cit.).

The fully formed larva (Pl. IV. Fig. 2) is a very beautiful object, with large vibratile lobes on the ventral and dorsal sides and at the posterior corners. The corners of the postoral area are produced into narrow lobes.

The diagrammatic figure 20 shows the arrangement of the vibratile lobes. The postoral and posterodorsal arms are rather broad, not very long (— the posterodorsal arms gradually reach the same length as the postoral ones —); the anterolateral and preoral arms are quite short, but the frontal lobe is high. The colour consists of

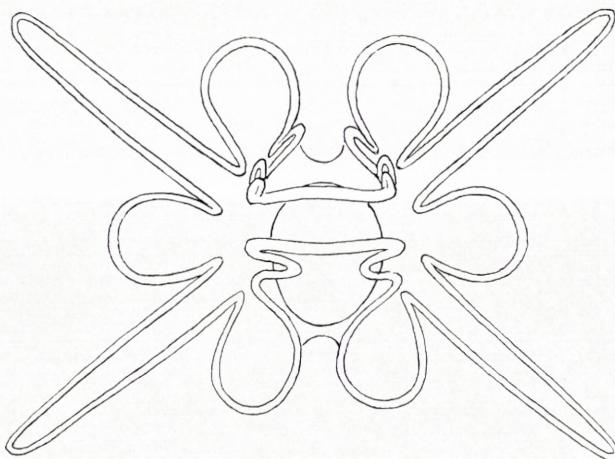


Fig. 29. Diagrammatic figure of the fully formed larva of *Tripneustes gratilla* (L.), showing the relation of the vibratile lobes to the four main arms.

scattered irregular carmine spots, somewhat more prominent along the vibratile band of the lobes. The postoral rod is fenestrated, but the terminal part is simple; the posterodorsal rods are simple, unfenestrated. The posterior transverse rod is simple, straight, with a bifurcation at the ends, the lower branch being simple, straight, a little longer than the upper one.

The young postembryonal stages were not observed.

As was to be expected the larva of *Tripneustes gratilla* is like that of *Tr. esculentus* (cf. "Studies", 1921, Pl. II) in all main features, so much so, indeed, that I doubt whether it would be possible to distinguish them with certainty from one another, if specimens of both were mixed together.

#### 6. Echinometra Mathæi (Blv.).

Pl. V. Fig. 1.

As was the case with *Tripneustes gratilla*, the development of this species has been the object of repeated studies. The first note on its development was given in

my "Studies" 1921, p. 75, from my stay at Hilo, Hawaii, in April 1915. Next TENNENT (Early development and larval forms of three Echinoids of the Torres Strait region. Publ. Carnegie Inst. No. 391, 1929, p. 118) gave a detailed description and figures of the earliest stages till the I. larval stage. Finally ONODA in his paper of 1936, p. 641, Pls. XI. 5—7; XII. 1—2, described and figured the larva from the young, beginning pluteus to the fully formed larva in beginning metamorphosis. I can thus confine myself here to giving a coloured figure of the fully formed larva (Pl. V. Fig. 1).

Comparison of this figure with ONODA's Pl. XII. Fig. 2 shows a rather conspicuous difference between them. As regards the postoral region and the ventral and dorsal vibratile lobes, the difference may be due to the different mode of drawing, and a different stage of contraction in these parts, when they were drawn (my figure represents them in a state of non-contraction); but as for the posterolateral lobes I have never seen the vibratile band to develop into such conspicuous epaulets as shown in ONODA's figure, even in stages as far advanced as that shown in ONODA's figure.

The colour of the larva consists of scattered small carmine spots, somewhat more numerous in the ends of the main arms and along the band of the vibratile lobes.

This larva was reared at Ghardaqa in April—May, the full larval form being reached in about 18 days, whereas ONODA found the metamorphosis to begin only after 40 days. This fact again shows the great variation in the time required for the development, depending, evidently, on the conditions of temperature, food, etc.

As was to be expected, this larva resembles that of *Echinometra lucunter* ("Studies" 1921, Pl. I) very closely, there being only very minor points of difference, if, indeed, any.

#### 7. *Heterocentrotus mammillatus* (Linn.).

Pl. V. Fig. 2.

Till now our knowledge of the development of *Heterocentrotus mammillatus* was confined to the observations recorded in my "Studies" 1921, p. 77, amounting to little more than that it has a pelagic larva, probably of the Echinometrid type. It was therefore a matter of satisfaction that this species, which is fairly common on the reefs of Ghardaqa, proved to be ripe already in April, so that fertilization could be undertaken one of the first days of my stay at the station, April 23rd. The culture was fairly good, the larvæ not very numerous, but I succeeded in rearing them to full larval shape, and a few of them even through metamorphosis.

The eggs are of the usual small size, c. 0.1 mm, not very clear. The early development processes did not offer anything of special interest. The skeleton begins to develop at the age of 24 hours, and at the age of two days the embryos have assumed the Pluteus-shape, beautifully coloured with scattered small red spots. The skeleton is that typical of the Echinometrid larvæ, the body skeleton forming a complicate basket structure, the recurrent rod being double (figs. 21, a, b); it is rather strongly thorny. The postoral rod is fenestrated.

The full larval shape was reached after about three weeks. The larva has rather unusually long and slender arms, not only the four main arms but also the anterolateral

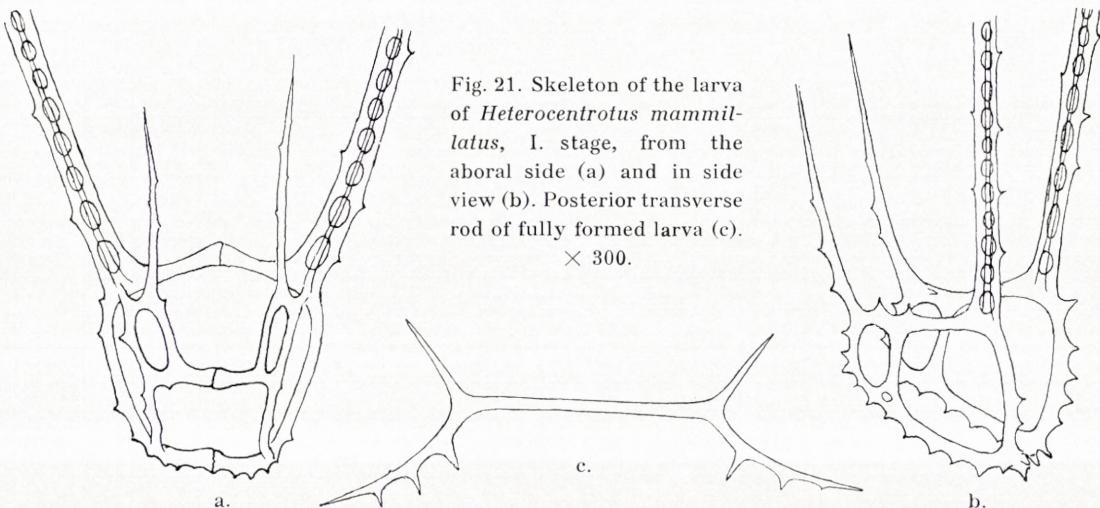


Fig. 21. Skeleton of the larva of *Heterocentrotus mammillatus*, I. stage, from the aboral side (a) and in side view (b). Posterior transverse rod of fully formed larva (c).  
× 300.

and preoral ones (Pl. V. Fig. 2). There are well developed ventral, dorsal<sup>1</sup>, and posterolateral lobes, and also the corners of the postoral area are produced so as

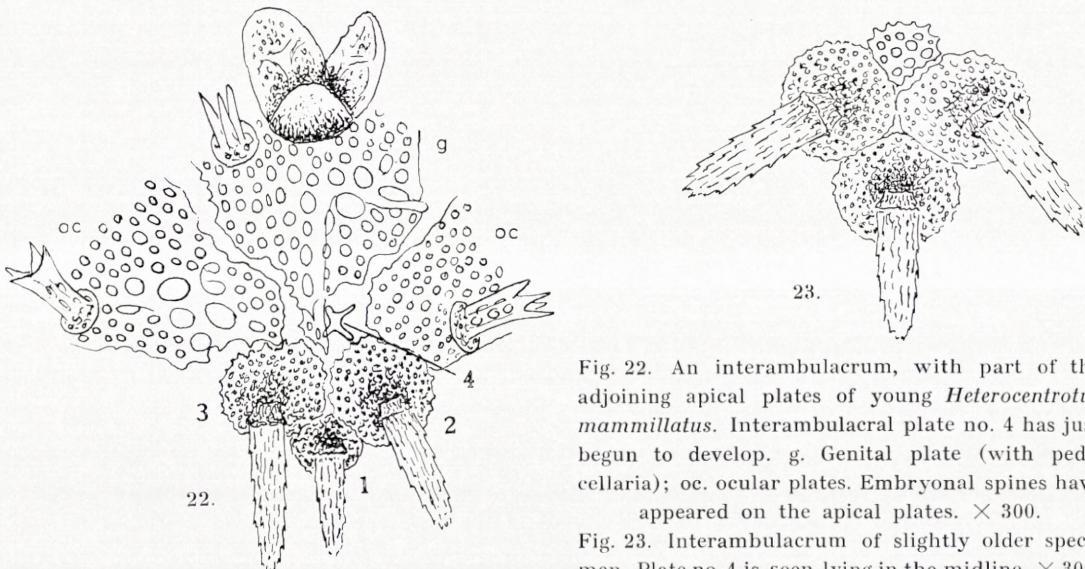


Fig. 22. An interambulacrum, with part of the adjoining apical plates of young *Heterocentrotus mammillatus*. Interambulacral plate no. 4 has just begun to develop. g. Genital plate (with pedicellaria); oc. ocular plates. Embryonal spines have

appeared on the apical plates. × 300.

Fig. 23. Interambulacrum of slightly older specimen. Plate no. 4 is seen lying in the midline. × 300.

to form narrow lobes. The colour consists of isolated red spots, more numerous along the band of the vibratile lobes, the postoral and preoral band, and in the point of the arms.

<sup>1</sup> The dorsal lobes are not shown in Pl. V. Fig. 2; but they are as well developed as the ventral ones.

The posterior transverse rod (fig. 21, c) is of the usual Echinometrid type, the lower branch of the terminal bifurcation with some thorns along its underside. Both postoral and posterodorsal rods fenestrated in their whole length; the anterolateral and preoral rods rather strongly thorny.

On the 3rd of June I found a couple of specimens metamorphosed. They show the genital plates developing around the basal parts of the larval skeleton, in the usual

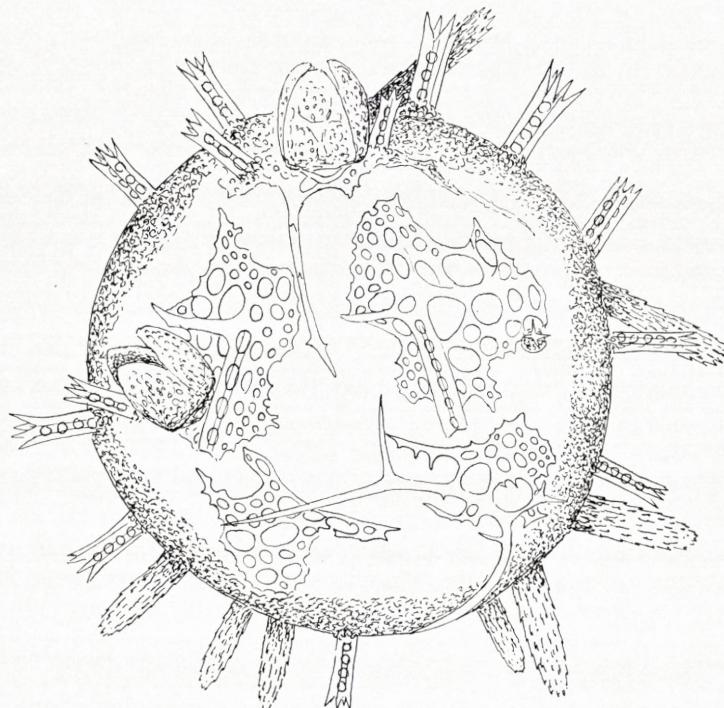


Fig. 24. Young *Heterocentrotus mammillatus*, just metamorphosed, 6 weeks old.  
From the aboral side  $\times 225$ .

way (fig. 24). The buccal plates are only partly developed (fig. 25), one preceding the other in each pair, in one radius only one of the buccal plates has appeared. The first rudiments of the masticatory apparatus are seen in three of the radii; the first pair of ambulacral plates have appeared in three of the radii, but not in the two others. The mouth opening not yet formed. Only the primary tubefoot has developed. In the interambulacra only the four first plates are formed (figs. 22—23), plate 4 lying in the midline as known from *Psammechinus miliaris* (cf. GORDON, Op. cit.). The spines of the apical plates end in four points, being of an embryonal type. The spines of the interambulacral plates are already rather thick, as might be expected in view of the character of the spines of the adult. — No specimen developed beyond this stage.

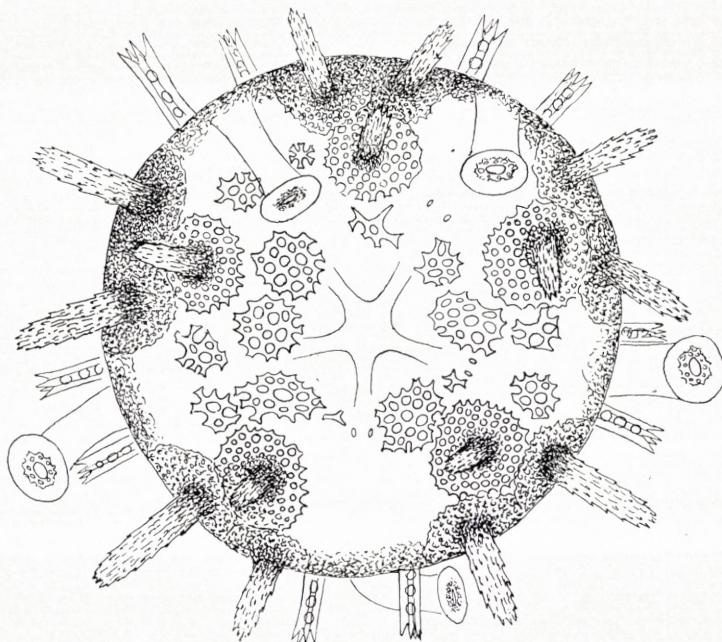


Fig. 25. Young *Heterocentrotus mammillatus*, just metamorphosed, 6 weeks old.  
From the oral side  $\times 225$ .

#### 8. *Fibularia craniolaris* (Leske).

Pl. VII. Fig. 1.

Fertilization of this species, which occurs in fair numbers on sandy bottom at a depth of c. 5—10 m. off Ghardaqa, was undertaken on May the 7th. The eggs are very small, c. 0.09 mm., very clear. The cleavage is of the usual regular type.

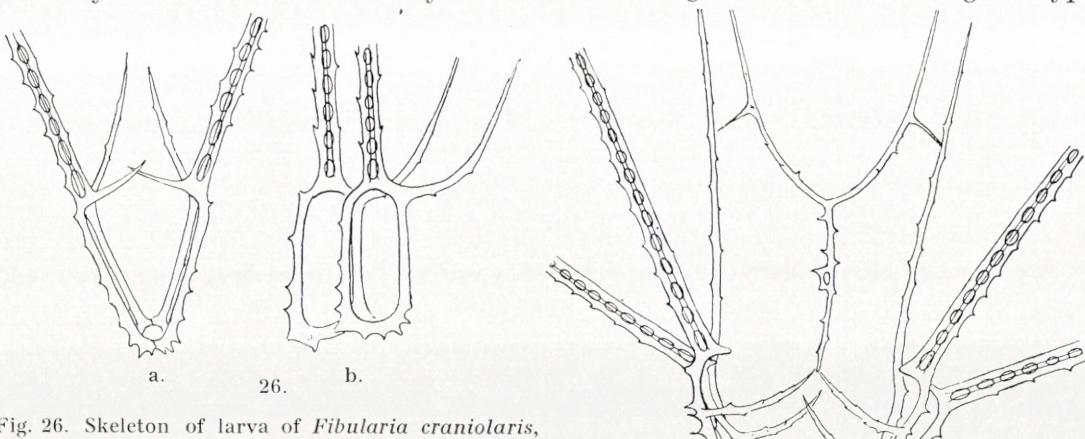


Fig. 26. Skeleton of larva of *Fibularia craniolaris*, I. stage, from the oral side (a) and in side view (b).  
In fig. b. the two halves of the skeleton have been  
slightly displaced.  $\times 250$ .

Fig. 27. Skeleton of fully formed larva of *Fibularia craniolaris*.  $\times 250$ .

On the second day the embryos were beautiful plutei of the I. stage. The body skeleton (figs. 26, a, b) forms a basket structure, rather thorny; the postoral rods are fenestrated.

The fully formed larva (Pl. VII. Fig. 1), two weeks old, is a very active swimmer, standing usually in a vertical position directly under the surface. It is of quite simple shape, without vibratile lobes; only between the two main arms there is a small prominence, outlined by the vibratile band. The colour is very feeble, only a faint yellowish-brown in the ends of the four main arms. In the skeleton the curious feature is observed that the original ventral transverse rod has almost disappeared and a new one developed some distance below on the body rod. The posterior part of the body skeleton has become a little more thorny and more complicate, forming an irregular, fenestrated plate of varying size. The posterodorsal rod is fenestrated like the postoral rod (fig. 27).

Some of the larvae metamorphosed; but I missed the metamorphosis-stages, the youngest stage preserved being already a fully formed sea-urchin, so I cannot give information about the postembryonal development of this species, which will, no doubt, be quite conform with that of *Echinocyamus*, so fully described by THÉEL in his excellent paper "On the development of *Echinocyamus pusillus*" (Nova Acta R. Soc. Sc. Upsala. III. 1892). Also the larva is very similar to that of *Echinocyamus pusillus* (cf. my "Contributions" 1931. Pl. IV. 2), as might be expected on account of the undoubtedly close relation between the genera *Fibularia* and *Echinocyamus*.

#### 9. *Clypeaster humilis* (Leske).

Pl. VI. Figs. 1—2.

Specimens of this species examined on April the 22nd were found to be in the end of spawning, but there was still enough of eggs and sperma for making a fertilization, which proved very successful. The eggs are of the usual small size, c. 0.1 mm., very clear and transparent. The fertilization membrane stands widely out from the surface of the egg; I did not notice any mucilaginous coat around the eggs, such as I found to exist in *Clypeaster japonicus* ("Studies" 1921, p. 95). The cleavage is regular. At the age of one day the gastrula is beginning to form, at the age of three days the first Pluteus-stage is reached. The postoral arms gradually become quite broad and flat and have a conspicuous carmine spot at the end; also a few small spots of the same colour are found scattered on the body. The body skeleton is a typical basket (fig. 28, a, b), very smooth, only the posterior connecting rod is a little thorny, may even be a little widened, fenestrated. The ventral transverse rods are finely thorny towards the end. The postoral rod is finely fenestrated, perfectly smooth.

The fully formed larva, about two weeks old, is a strikingly beautiful object (Pl. VI. Figs. 1—2). The arms are very broad, moderately long, the anterolateral and preoral arms quite short; there are large vibratile lobes, ventral, dorsal, and postero-lateral, and further the corners of the postoral area are produced so as to form small lobes, and on the middle of the dorsal side the vibratile band forms a large,

slightly raised fold. In the end of each arm (except the preoral ones) and likewise in all the lobes there is a conspicuous carmine spot; red spots are found sparsely all along the vibratile band, and some scattered small red spots in the posterior end of the body.

The skeleton of the fully formed larva affords unusually interesting features. The body skeleton gradually becomes completely resorbed, the four main rods terminating as quite simple rods in the body; also the ventral transverse rods disappear. But a more extraordinary fact is that the postoral rods, which originally are fenestrated

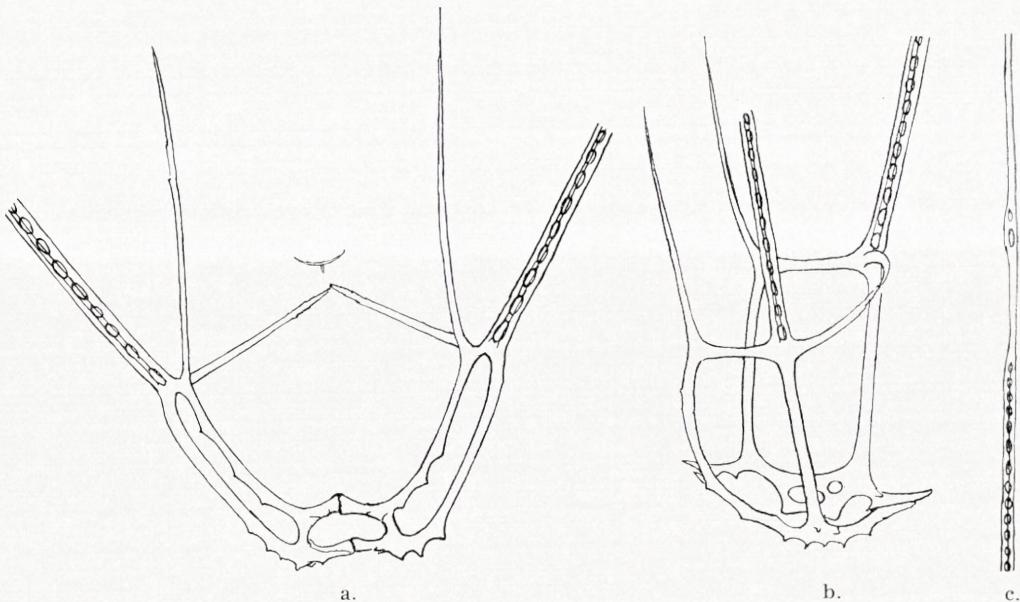


Fig. 28. Skeleton of larva of *Clypeaster humilis*, I. stage, seen from the dorsal side (a) and in side view (b). Part of postoral rod transforming from the original fenestrated condition into a simple rod (c).  $\times 300$ .

throughout, gradually transform into simple, exceedingly slender rods, the transformation beginning at the point of the rod about at the time when the posterodorsal rods and the dorsal arch appear. Not only the holes of the rod disappear, but the whole rod becomes thinner than in the I stage (fig. 28, c); thus a very remarkable resorption and reapposition of the calcareous matter must take place. The posterodorsal rod is simple from the beginning. On the whole the skeleton is very delicate.

Some of the larvae metamorphosed, but not having preserved any of the metamorphosis-stages, I cannot give any information about the development of the skeleton of the young sea-urchin.

The only other *Clypeaster*-species the development of which has been studied is *Clypeaster japonicus* Döderl.; only the first larval stage of this species is known (cf. my "Studies" 1921, p. 95, Pl. XIV. 3), but judging therefrom the fully formed larva may be expected to be similar to that of *Clypeaster humilis*. This seems to indicate

that there is a special type of larva in the family of the Clypeastridæ, differing from that of the other Clypeastroids in the large vibratile lobes, the resorption of the body skeleton, and the transformation of the postoral rods from originally fenestrated into simple rods.

#### 10. *Echinodiscus auritus* Leske.

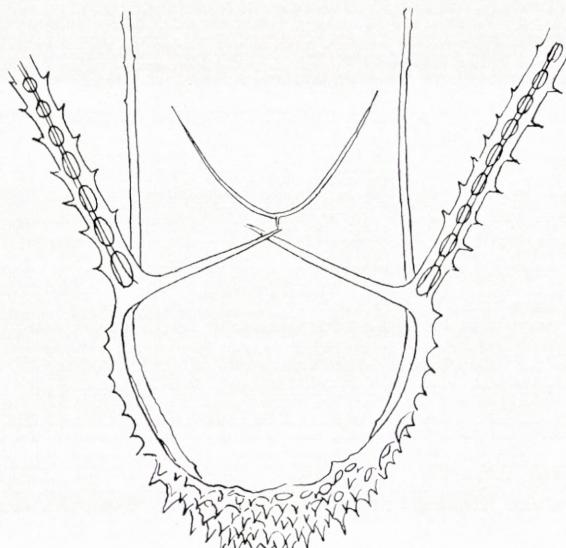
Pl. VII. Fig. 2.

In the immediate neighbourhood of Ghardaqa this species does not occur, so far as known; but the sailors brought home some specimens from Abu Mingar on June the 1st. They proved to contain ripe sexual products, and fertilization was undertaken. The eggs are surrounded by a thick mucilaginous coat with purple spots, such as I have found to exist in several other Clypeastrids (cf. "Studies" 1921, p. 107, fig. 43). The spermatozoa penetrate through this coat, as I was able to ascertain here. It is uncertain, whether the coat is found on the normally spawned eggs; at least it disappears almost immediately after the fertilization membrane has been formed (inside the coat). The eggs are not very clear, and the embryos correspondingly rather opaque. After 30 hours the embryos were small plutei, and in the two days old larvæ the posterodorsal rods and the dorsal arch have already begun to form. At the age of five days the larvæ had reached their full size (Pl. VII. Fig. 2); the four main arms could now be moved actively, the body skeleton having thus already been partly resorbed.

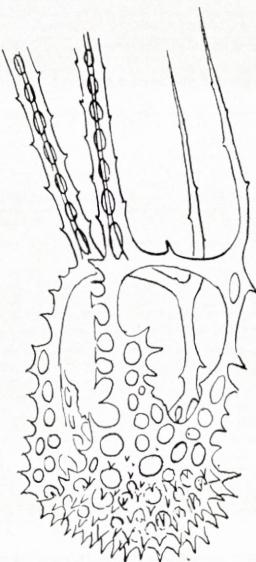
By this very fast development from the egg to full larval shape I very naturally expected to see them metamorphose very soon — but herein I was strongly disappointed. Although the cultures seemed to be in good condition, the larvæ living apparently quite well for a long time, only a couple of the larvæ showed the first sign of metamorphosis (the amnion), and by the end of June the larvae began to deteriorate.

The fully formed larva (Pl. VII. Fig. 2) is very much like the *Mellita* and *Astriclypeus* larvæ figured in my "Studies" 1921, Pl. IV, being without vibratile lobes, in striking contradistinction to the *Clypeaster* larva. It has a patch of red colour in the end of the postoral arms, and some scattered small red spots particularly in the quite intransparent hind end of the body. Along the vibratile band and over the stomach there are a number of small, oval, yellow spots. On the whole the colour is rather faint.

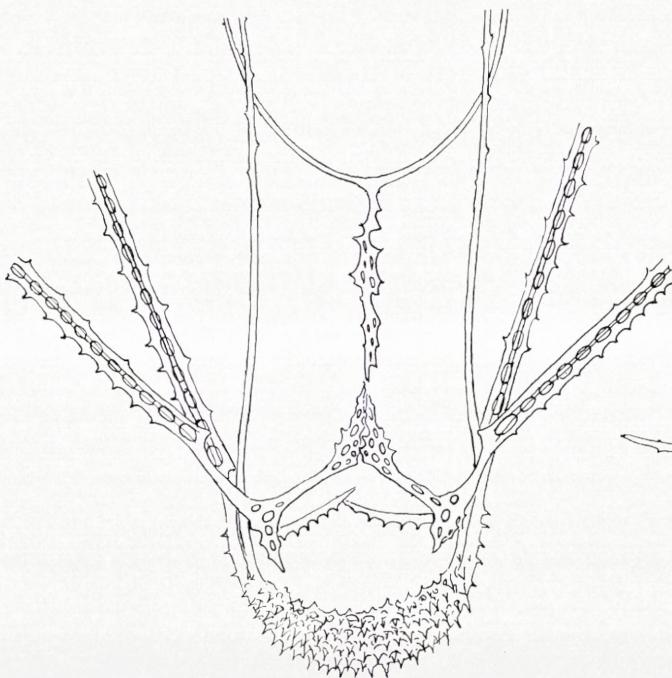
The skeleton of the young larva is very characteristic, the posterior part of the body skeleton forming a large, irregular, fenestrated, and strongly thorny plate (figs. 29—30). The postoral and posterodorsal rods are fenestrated, strongly thorny till the point. In the fully formed larva the body rod is partly dissolved, the fenestrated plate in the posterior end of the body remaining connected only with the recurrent and the anterolateral rod; also the connection between the postoral rod and the recurrent and anterolateral rods is severed; the postoral arms thus become movable like the posterodorsal arms, the skeletal rod of the latter having never been coalesced with



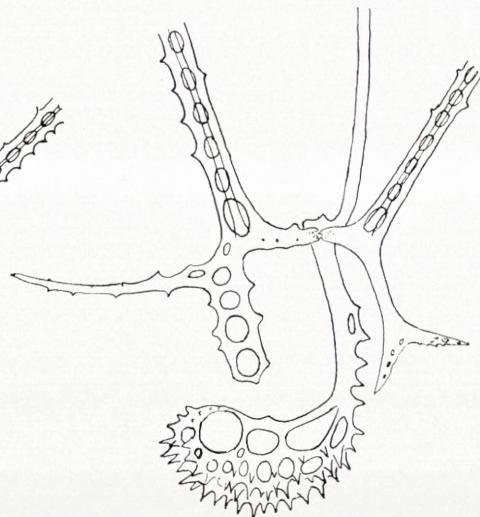
29.



30.



31.



32.

Figs. 29—32. Skeleton of the *Echinodiscus auritus* larva; 29—30. of the young larva, from the oral side (29) and in side view (30). Fig. 31. shows the skeleton of the fully formed larva, from the dorsal side; fig. 32. shows the beginning resorption of the body rod, side view.  $\times 300$ .

the body skeleton (figs. 31—32). Whether the large plate in the posterior end of the body is resorbed or enters into the final skeleton remains an unsolved question for the present.

### 11. *Lovenia elongata* (Gray).

Pl. VII. Fig. 3.

Some specimens of this fine species were dredged on sandy bottom at a depth of c. 10—20 meters off the Abu Sadaf reef, close to the station, as also some specimens were found living in the sand in quite shallow water close to the station (together with *Astropecten polyacanthus* and *Luidia Savignyi*).

Fertilization was undertaken on May the 4th. The eggs are of the usual small size, c. 0.09 mm., very clear and transparent. The cleavage passes very rapidly, the embryos being swimming blastulae already after 6—7 hours, "beautiful as a diagram" I have said in my notebook. At the age of 18 hours they were small plutei, strongly

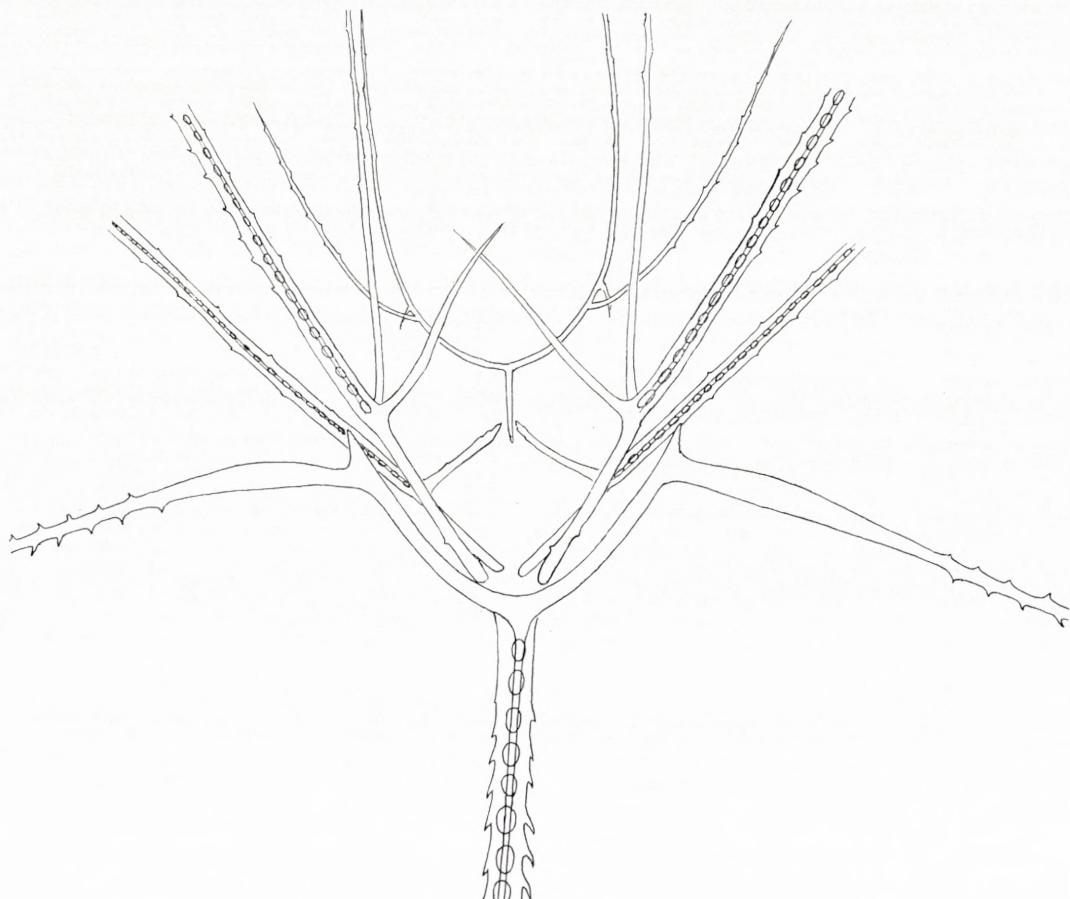


Fig. 33. Skeleton of the fully formed larva of *Lovenia elongata*.  $\times 240$ .

D. K. D. Vidensk. Selsk. Skrifter, naturv. og math. Afd., 9. Række, VII, 1.

pigmented, particularly a carmine patch in the end of the postoral arms and in the posterior end of the body; at the age of 25 hours the posterior rod had begun to form. At the age of 12 days the full larval shape (Pl. VII. Fig. 3) is reached, the posterolateral arms having developed, and the amnion appeared. It is a perfectly typical Spatangoid larva, with a very long posterior process, with a large carmine spot in the end. Also the postoral, posterodorsal, and posterolateral arms have a conspicuous carmine spot in the end; scattered small spots of the same colour are found in the body and arms, and a larger spot below the postoral and above the preoral band. The stomach is a light yellow.

The skeleton (fig. 33) is quite the usual type, the only special feature being a light swelling of the basal part of the posterolateral rods. Both postoral and posterodorsal rods are fenestrated and thorny throughout, the holes in the posterodorsal rod being distinctly smaller than those of the postoral rod.

The larva of this species — no *Lovenia* larva being known till now — serves to emphasise the uniformity of the larvae within the family of the Spatangidæ.

### *Astroidea.*

#### 12. *Astropecten polyacanthus* Müller & Troschel.

Pl. X. Figs. 2, 5.

This species, which lives in good numbers in the sand in shallow water at the station, was found to have ripe sexual products by the end of May. I was greatly surprised in finding this species to have serial gonads, other *Astropecten* species having only a single, large gonad on each side at the base of the arm. This raises the question, whether all the forms usually identified as *Astropecten polyacanthus* are really the same as the Red Sea form, which latter is the typical *polyacanthus*, MÜLLER & TROSCHEL having based their description of *A. polyacanthus* on specimens from the Red Sea. Particularly it seems that the Japanese form, originally described by MÜLLER & TROSCHEL as *Astropecten armatus*, cannot really be identical with the true *polyacanthus*, as is otherwise generally accepted. I have reared the larva of this Japanese form ("Studies" 1921, p. 186) after artificial fertilization. It is rather unthinkable that I should not have noticed it, if it had serial gonads; but I have said nothing about it. And on opening a specimen preserved in alcohol I also find it to have only one gonad on each side at the base of the arm (— so far as it is possible to make sure on an old specimen, in which the gonads are very hard and brittle —). But it is quite out of question that specimens of so different anatomical characters, some having serial gonads, others single gonads, could belong to one and the same species — it would rather seem questionable whether they can really be referred to the same genus. — It is not the place here to enter into details of this question; but after this discovery of the true *A. polyacanthus* having serial gonads it will be necessary to

investigate the anatomy of also the other *Astropecten* species and eventually subdivide the large genus *Astropecten* after the character of the gonads.

Fertilization of *A. polyacanthus* was undertaken on May the 26th; it proved successful, and I had a good number of gastrulae the next day. The fertilization being made late in the afternoon I had no opportunity of ascertaining whether the blastulae are folded within the egg-membrane as is so often the case in Asteroids. The development proceeds very rapidly, the larvae having reached their full shape and beginning to metamorphose already on the third day. The larva (Pl. X. Figs. 2, 5) is of the simple type, without Brachiolaria-stage; it is nearly colourless, only with the merest indication of a yellowish tinge on the vibratile bands and the stomach. Numerous small glandular cells are found along the vibratile band and also scattered over the body.

Several of the larvae metamorphosed; the young sea-stars do not offer any features of special interest, so I think it superfluous to figure them.

### 13. *Astropecten velitaris* v. Martens.

Pl. X. Fig. 3.

On muddy bottom outside the station, at a depth of c. 10—20 m., this beautiful little species is quite common. It was found to be ripe at the end of May, and fertilization was undertaken on May the 27th. This species has single gonads. It was very difficult to induce the spermatozoa to move, even by adding NaOH (— which had also to be used by *A. polyacanthus* —), and only very few eggs were fertilized. In all I got only c. 50 normal gastrulae, but as they were rather large it was easy enough to deal with them, and they developed quite normally, though not quite as fast as *A. polyacanthus*, the metamorphosis not beginning till the 5th day. The larvae of this species, as well as of *A. polyacanthus*, are very active swimmers, usually keeping close to the surface, swimming horizontally.

The fully formed larva (Pl. X. Fig. 3) is so closely alike that of *polyacanthus* that I do not think it possible to distinguish them with certainty; I have, however, not observed the glandular cells along the vibratile band in this species, so this may perhaps prove to be a specific difference.

The larvae metamorphosed, the young sea-star being indistinguishable from the young *polyacanthus*.

As we know now with certainty the larvae of five different species of *Astropecten*, *A. irregularis*, *aranciacus*, *scoparius*, *polyacanthus*, and *velitaris*, all these larvae being so closely alike as to be hardly distinguishable from one another, we can now say with certainty that there is a special type of Bipinnaria corresponding to the family Astropectinidae, characterized by its broad, round anterior lobes and by having no Brachiolaria stage. The larval body is completely absorbed during the metamorphosis.

14. *Asterope carinifera* (Lamarck).

Pl. X. Fig. 4.

Two specimens of this species — the only ones seen — were brought by the sailors on April the 24th from the outer reef. They proved to be a male and a female, both ripe, and fertilization was undertaken and proved to be successful. The eggs are rather large, c. 0.2 mm., reddish. The fertilization membrane is very clear, widely outstanding. The embryo is folded within the membrane. The gastrula stage was reached on the next day; the gastrulæ are rather elongate. At the age of three days the larval mouth had been formed, but as yet no vibratile band differentiated, the first indication of the preoral band appearing on the fourth day. At the age of six days the band is complete. The development on the whole proceeds slowly, particularly as compared with the *Astropecten* larvæ, the full larval shape and beginning metamorphosis not being reached until at the age of one month. The larvæ are strong swimmers, keeping close under the surface of the water, swimming horizontally.

The fully formed larva (Pl. X. Fig. 4) is a Brachiolaria, having a sucking disk and Brachiolaria-arms, without papillæ, however,—possibly such will appear later on, when the larva is about to metamorphose. The larva is characteristic by the dorsal median lobe being much shorter than the ventral, and by the dorsal side being conspicuously broader than the ventral side. The posterolateral arms are short, not contractile. The colour is a very faint yellowish, which is scarcely stronger on the vibratile band; only the stomach is more distinctly yellowish-grey. There are a number of gland-cells in the vibratile band, particularly that of the anterior lobe. The fact that the preoral band is strongly upwards bent in the young larva figured in my "Studies" Pl. XXXIII. 6 is evidently due to contraction on preservation.

None of the — very few — larvæ metamorphosed.

The young larva of this species I described in my "Studies" 1921, Pl. XXXIII. 6, having reared it at Hilo, Hawaii, in April 1915, when I likewise found its development to pass very slowly, the larvæ having not yet reached their full shape when 26 days old. It is very satisfactory now to have ascertained that this larva has a Brachiolaria stage, as was to be expected from the fact that the related *Porania* larva has such a stage (cf. GEMMILL. The larva of the starfish *Porania pulvillus* (O. F. M.). Qu. J. Micr. Sc. 61. 1915. Pl. 5). In general these two larvæ are much alike, apart from the existence of series of papillæ along the Brachiolaria-arms and the anterior lobe in the *Porania* larva.

*Ophiuroidea.*15. *Ophiothrix triloba* v. Martens.<sup>1</sup>

Pl. IX. Figs. 2—3.

Some specimens of this species, which is not rare in the coral blocks on the reefs at Ghardaqa, spawned during the night of May 21st, being kept in a rather small dish. The eggs are red, apparently rich in yolk, and I rather expected that they would not develop into a typical Ophioplateus, which they did, however. Two days old the embryos were already young plutei, distinctly of the *Ophiothrix* type.

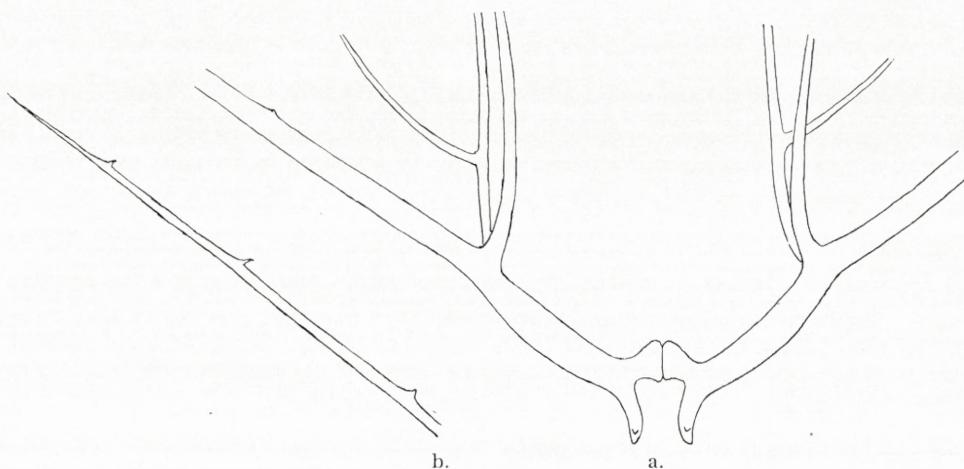


Fig. 34. a. Skeleton of the larva of *Ophiothrix triloba* v. Martens; b. end of the posterolateral rod.  $\times 250$ .

The young embryos, 12 hours old, did not show the "crest" of vacuolated cells described by MACBRIDE in his paper on "The development of *Ophiothrix fragilis*" (Qu. J. Micr. Sc. 51. 1907. Pl. 31. 3—5; 33. 25—28); they were simply round, red internally. This red colour is seen again in the stomach of the young larva (Pl. IX. Fig. 2), which evidently subsists on the red matter, not yet taking in food from the outside; as a matter of fact there seems to be no distinct rectum as yet. Gradually the red colour disappears completely from the stomach, which in the fully formed larva is only of a faint yellow tinge.

The fully formed larva (Pl. IX. Fig. 3) is a quite typical *Ophiothrix* larva, distinguishable only by its peculiar coloration: a more or less irregular brownish-black spot above the stomach and a similar smaller spot off each corner of the preoral area, these latter spots being usually connected with that above the stomach by a

<sup>1</sup> Very probably it is this species which KOEHLER (Echinides, Astéries et Ophiures recueillis par M. Gravier dans la Mer Rouge. Bull. Mus. d'Hist. nat. 1905. 3) mentions under the name *Ophiothrix propinqua* Linné (erroneously for Lyman). As a matter of fact I have grave doubts as to the possibility of distinguishing *triloba* and *propinqua* from one another. The type locality of *triloba* is the Red Sea.

less clearly defined strand to each side of the oesophagus. These colour spots, which are usually very conspicuous, though subject to much variation, lie on the dorsal side of the larva. A faint reddish tint is found along posterolateral rod in its lower part; the arms are otherwise uncoloured.

The skeleton (fig. 34) is quite like that of other *Ophiothrix* larvæ; the body rods are slightly swollen. Usually there is no median process from the transverse rods, but in some cases a simple, styliform process is found. The posterolateral rods are sparsely set with small thorns along the inside.

The larvæ did not metamorphose, though kept till the end of June.

#### 16. *Ophiomaza cacaotica* Lyman.

Pl. IX. Figs. 4—5.

A couple of specimens of this species were brought by the sailors on May the 30th, taken by dredging at a depth of about 20 m off Abu Sadaf, outside the station; no doubt they were attached to some Comatulids taken in the same place. Making a slit in an interradius of one of them I found it to be a ripe female, the eggs coming out isolated and apparently ready for fertilization. Finding another to be a ripe male, I tried to obtain artificial fertilization, but without success. Few minutes after, however, the female that had been slit open in one interradius shed by itself the rest of the eggs; I took then sperma from the other specimen and added to the eggs, and now fertilization followed immediately.

The eggs are of the usual small size, c. 0.1 mm., brownish, intransparent. By the cleavage a transparent layer is formed around the cleavage cells. The first divisions occurred after one hour, and the blastospheæra stage was reached after six hours in the evening, so that the further development could not be followed very closely. The

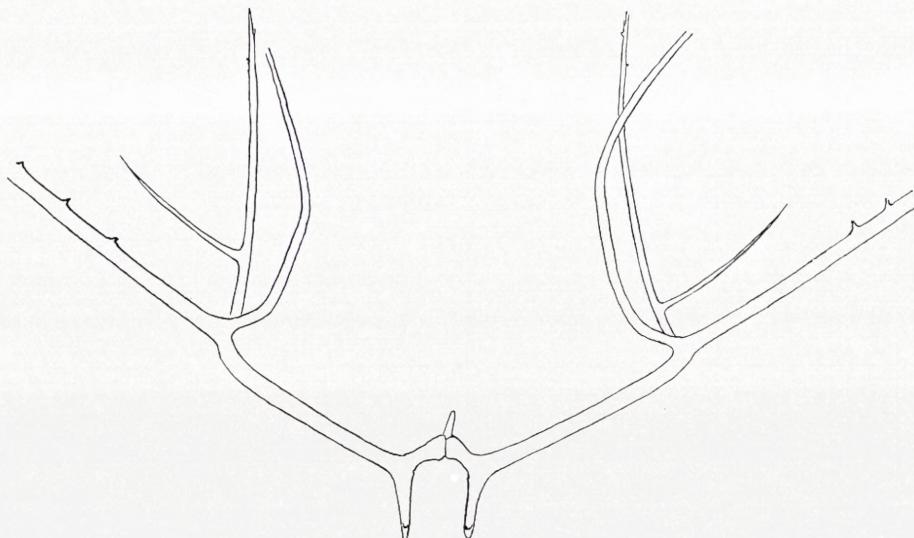


Fig. 35. Skeleton of the larva of *Ophiomaza cacaotica* Lym.  $\times 250$ .

gastrulae are rather elongate, pear-shaped, the anterior end being transparent, the broader posterior end dark, intransparent, evidently containing the yolk of the egg, whereas the clear cells of the anterior end, the "crest", are no doubt vacuolated, as described by MACBRIDE (Op. cit.) in *Ophiothrix fragilis* (no sections have been made of them).

The larva had reached nearly full shape at the age of 5—6 days; it is remarkable in the enterocoel vesicles lying unusually far out towards the side, away from the



Fig. 36. Metamorphosing young *Ophiomaza cacaotica*, using the long posterolateral arms as a floating apparatus. Fig. b. shows the young brittle star about to detach itself from the floating apparatus.  $\times 125$ .

stomach, and even in the later stages at the beginning metamorphosis (Pl. IX. Fig. 5) the enterocoel does not attach itself so closely to the stomach as is usually the case in Ophiurid larvae.

The shape of the larva is that of a typical *Ophiothrix* larva, with long, nearly horizontally directed posterolateral arms. The colour is very faint; there is a small red spot in the end of the posterolateral arms and a little black pigment in the vibratile band along these arms. Along the body rods and the posterolateral rods is a faint yellowish-red tint, and the stomach is faintly yellowish; otherwise the larva is colourless. — The skeleton (fig. 35) differs from that of the *Ophiothrix* larva only in the body rods being longer and more slender, and the postoral rod characteristically curved in the basal part. — It recalls that figured in my "Studies" 1921, p. 130, as *Ophiopluteus*

of *Ophiothrix* species d, and leads to the suggestion that this larva also belongs not to the genus *Ophiothrix* itself, but to one of the other genera within the family of the Ophiothrichids.

Several of the larvae metamorphosed, the metamorphosis beginning at the age of 12—14 days. I found the hydrocoel to grow round below the oesophagus, as it is figured for *Ophiothrix fragilis* by MACBRIDE (Op. cit. Pl. 32, fig. 13, b). The metamorphosis on the whole proceeds exactly as in *Ophiothrix*, the long posterolateral arms remaining intact and serving as floating apparatus for the young brittle-star (figs. 36, a, b), then to be thrown off by completed metamorphosis and perish after having continued pelagic life for a little while. The young brittle-star has its arm-spines developed into long, simple claws. A curious fact is that in some cases there is no central plate in the young brittle-star (fig. 36, a).

It is very satisfactory to have thus ascertained that the *Ophiomaza* larva is a typical Ophiothrichid larva, a rather certain proof that we have a very distinct larval type characteristic of the family of the Ophiothrichidæ.

#### 17. *Ophiocoma erinaceus* Müller & Troschel.

Pl. VIII. Fig. 4.

Ripe specimens of this species, which is fairly common on the reefs at the station, were found in the end of April, and spawned in the aquarium on April the 24th. The eggs are small, c. 0.1 mm., reddish, intransparent, and surrounded by a thorny fertilization membrane, which must undoubtedly be of some importance for keeping the eggs floating, as suggested in my "Studies" 1921, p. 131. That the eggs lie on the bottom in the dish, with no movement of the water, does not mean that the spiny egg-membrane cannot have such function in the free, where the water is in constant movement; it is also evident that they sink more slowly to the bottom

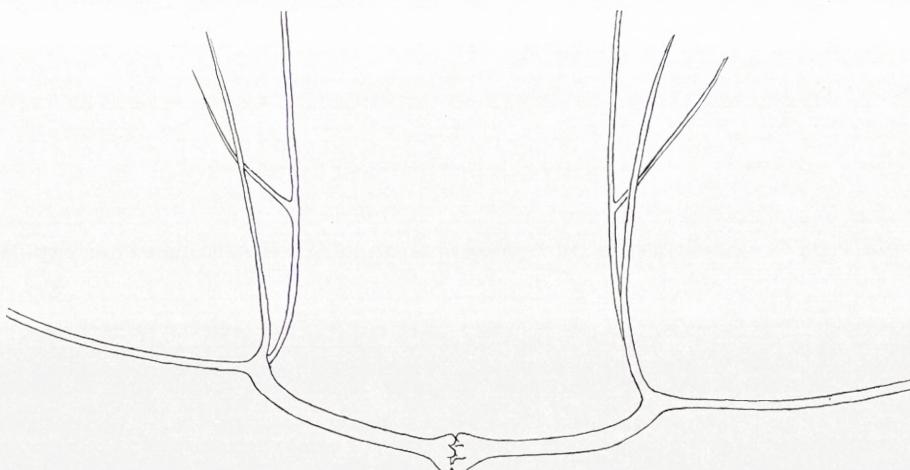


Fig. 37. Skeleton of the *Ophiocoma erinaceus* larva.  $\times 250$ .

than eggs without such thorny membrane. I have no detailed observations of the development of the younger stages. The gastrula stage is reached after one day, the skeleton beginning to appear on the third day. At the age of six days the larvæ were exactly like the young *Ophiocoma echinata* larva figured in my "Contributions" 1931, p. 27, fig. 11. a, this larva being only  $2\frac{1}{2}$  days old. Eleven days old the larvæ were exactly like the six days old *Ophiocoma echinata* larva figured in fig. 11. b of the "Contributions" 1931, p. 27. The development of this species thus takes about twice the time that does the development of *Ophiocoma echinata*. At the age of about a month the larvæ were nearly fully formed (Pl. VIII. Fig. 4), though not yet showing any sign of metamorphosis. They did not develop any farther.

The larva is colourless, only a dark-grey spot in the end of the posterolateral and anterolateral arms. Vibratile lobes are indicated; they will undoubtedly be more developed, when the larva is about to metamorphose. The strong upwards bend of the preoral band is not a reliable specific character, as it is subject to change in the live specimens. — The skeleton (fig. 37) is a quite typical *Ophiocoma* skeleton, the body rods lying horizontally, forming like a joint in the middle, where they meet. The skeleton is entirely smooth.

#### 18. *Ophiocoma scolopendrina* (Lamarck).

Pl. VIII. Fig. 5.

This species is very common on the littoral reef-flat at the laboratory, their arms protruding from every crevice; often they are also seen crawling free in the small pools left at low tide. They were found to be ripe in the beginning of May (probably their breeding season begins at least as early as April), and some specimens spawned in the aquarium on May the 8th. The egg-membrane is thorny (fig. 38), as in other *Ophiocoma* species (but apparently not in *Ophiocomina nigra*, since nothing is said about it neither by myself, Op. cit. 1913, nor by NARASIMHAMURTI, Op. cit.). It appeared that some of the embryos had difficulty in getting out of the egg-membrane (such as is so evidently often the case also in the Comatulids, cf. below, p. 61); this will most probably not occur in the free under natural conditions. The gastrulæ are elongate, intransparent. At the age of two days the first rudiments of the skeleton are seen.

The young larvæ are very much like the *Ophiocoma erinaceus* larva, only the anterolateral arms somewhat larger. The one figured Pl. VIII. Fig. 5 was eleven days old, that of *O. erinaceus* five weeks old. Thus the development of the young stages passes much quicker in *scolopendrina* than in *erinaceus*; but the later development is slow, the metamorphosis having not yet begun at the age of six weeks, although the larvæ were apparently quite healthy.

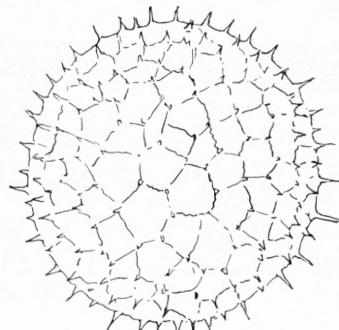


Fig. 38. Egg of *Ophiocoma scolopendrina*.  $\times 540$ .

The fully formed larva (fig. 39) has well developed vibratile lobes. The antero-lateral arms are rather long; the anterior part of the body is somewhat widened.

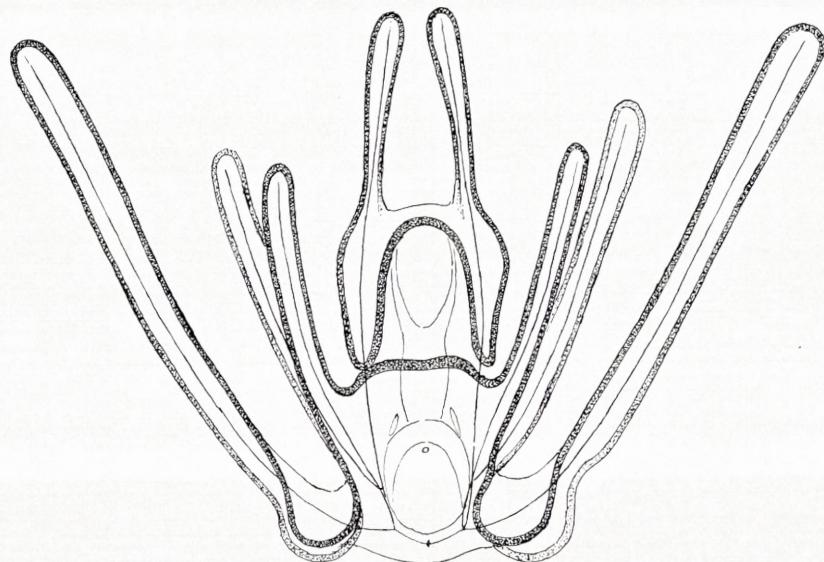


Fig. 39. Fully formed larva of *Ophiocoma scolopendrina*.  $\times 70$ .

The strong upwards bend of the preoral band is, as in *O. erinaceus*, no reliable specific character, but may change actively in the live larva. The colour is a faint yellow, due to numerous small spots all over the body; in the end of the posterolateral arms

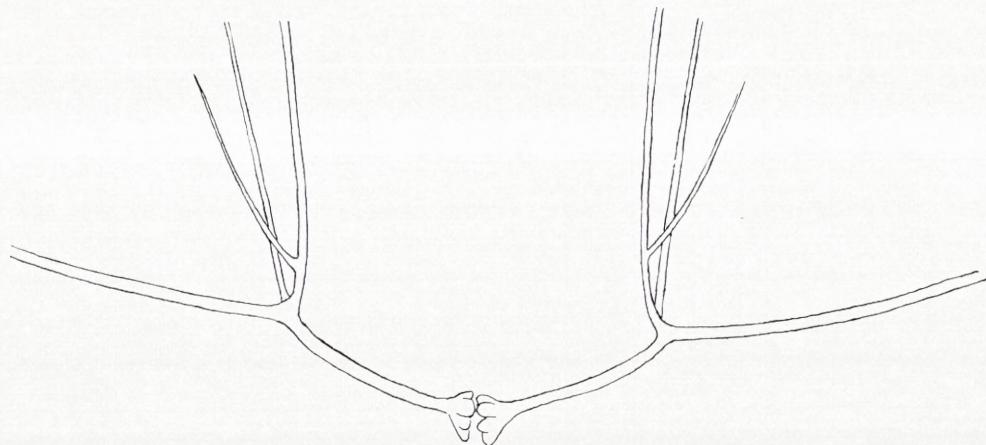


Fig. 40. Skeleton of the *Ophiocoma scolopendrina* larva.  $\times 250$ .

there is a more conspicuous yellowish spot. The stomach also is a faint yellowish. — The skeleton (fig. 40) is as typical in *Ophiocoma* larvae, hardly distinguishable from that of the *erinaceus* larva; only the body rods are slightly less horizontal.

19. **Ophiocoma lineolata** (Desjardins) Müller & Troschel.<sup>1</sup>Syn. **Ophiocoma pica** Müller & Troschel.

Pl. VIII. Figs. 1—3.

The present species occurs, though not very commonly, on the reefs at Ghardaqa. Some specimens were brought me on May the 20th; they were put into a rather small dish in which they spawned during the night. The egg-membrane is not thorny, such as is the case in the species *Ophiocoma echinata*, *erinaceus* and *scolopendrina*; still the eggs are almost floating, on account of the presence in the surface layer of numerous small yellowish-brown yolk-granules; in the cleavage stages these granules form a beautiful mosaic, lying in the surface layer of the cells, but not along the cell-limits, only in the middle of the cells. The cleavage proceeds rather slowly; it appears that no blastosphaera is the result of the cleavage, but a solid morula; but the early development could not be followed in details because of the night. The first rudiments of the skeleton appear in the two days old embryos; but not until the age of six days have they assumed distinctly the shape of a young Ophiopluteus, as represented in Pl. VIII. Fig. 1, peculiar especially by the large size of the preoral part of the body, by the presence of distinct nerve-bands, and by the apparent slow development of the skeleton, the body rods having not yet reached to the posterior end of the body. In the course of the further development, however, the surprising fact was revealed that the body skeleton remains in a rudimentary condition, the body rods being simple, short, not reaching down to join in the posterior end of the body, and transverse rods being absent (fig. 41). On the other hand the rods of the arms are normally developed. This is a quite unique condition among normal plutei; in the few cases known, where the larva is reduced to a rudimentary condition, the body skeleton remains, whereas the arm-rods have disappeared (cf. "Studies" 1921, p. 229).

The larva in its further development is peculiar by the rather enormous size of the preoral part of the body, the anterolateral arms not being set off distinctly, the vibratile band only outlining the side edges of the large preoral part of the body (Pl. VIII. Fig. 2). In the fully formed larva, about a month old, the anterolateral arms have become differentiated, but they remain short and broad. There are now also distinct vibratile lobes as in the other *Ophiocoma* larvæ; the arms are rather broad and flat as usual in *Ophiocoma*. Rather characteristic of the larva is the large suboral cavity, distinct already in the youngest pluteus. The nerve-strands remain distinct also in the fully formed larva, as I have ascertained on the preserved specimens; (evidently I overlooked them when drawing the larvæ from life, and I have thought

<sup>1</sup> There can be no doubt that *Ophiocoma pica* and *lineolata* are identical, and most authors adopt the name *pica*, because it is placed first in MÜLLER & TROSCHEL's "System der Asteriden". But the name *lineolata* is the older, since it was given by DESJARDINS, as a manuscript name, and taken over by MÜLLER & TROSCHEL. As this name *lineolata* also gives the peculiar character of the species in the best possible way, so that one can, so to say, recognize it by the name, whereas *pica* says nothing, I think *lineolata* is the name to be used.

it better not to introduce them into the figures afterwards, the exact location being difficult to ascertain). The colour of the young larvæ is rather conspicuous: a number of yellow or orange spots along the vibratile band, especially in the end of the postero-lateral and anterolateral arms, and in the posterior part of the body. In the fully formed larvæ the colour is much fainter, though of the same yellowish tint.

A few of the larvæ metamorphosed; but I have not followed the metamorphosis in details on the living specimens, and the preserved specimens are insufficient for giving valuable information. Thus e. g. I cannot say whether the hydrocoel grows round above or below the oesophagus.

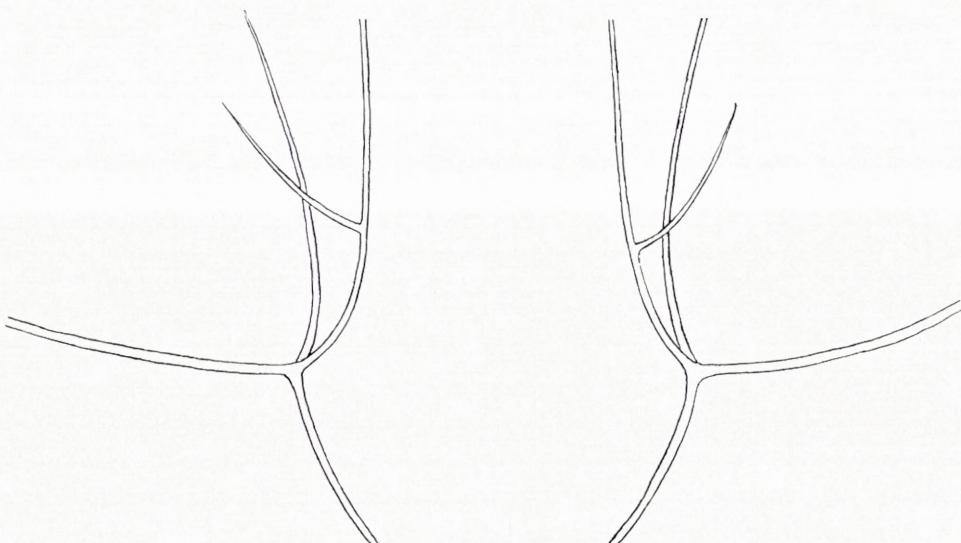


Fig. 41. Skeleton of the fully formed larva of *Ophiocoma lineolata*. No resorption has taken place, the body rods never joining in the posterior end of the body.  $\times 300$ .

Although *Ophiocoma lineolata* differs conspicuously from the other *Ophiocoma* species in its coloration, it is surprising to find its larva to differ so much from the larvæ of the other species. One might even be tempted to conclude from the character of the larva that the species *lineolata* should be removed from the genus *Ophiocoma*. However, I do not think it advisable to do so, so long as we do not know the larvæ of all the various *Ophiocoma* species, and of the other genera of the Ophiocomidæ. As a matter of fact the *O. lineolata* larva to some degree recalls the larva of *Ophiocomina nigra*, and thus lends support to the general acceptance of this North-Atlantic Ophiurid belonging to the Ophiocomidæ, against H. L. CLARK's idea that it belongs to the Ophiacanthidæ, even to the genus *Ophiacantha* itself, as set forth in his "Catalogue of the recent Ophiurans" where he even designates it by the quite unacceptable name *Ophiacantha sphærulata* (Pennant) (cf. my "Notes on some Scandinavian Echinoderms". Vid. Medd. Dansk Naturh. Foren. 72. 1920, p. 50—53).

### Holothurioidea.

#### 20. *Synaptula reciprocans* (Forskål).

Pl. X. Fig. 6.

This species occurs together with the following, *Synaptula vittata*, in great numbers on the shore flats at Ghardaqa. During day-time they usually hide themselves away under algæ and loose blocks of coral or stone in the small pools left by the tide, at sunset and early in the morning they come out and creep about like small snakes, the two species, one black, the other grey, striped, mixed together. It is surprising that they can stand the very high temperature that prevails in these localities at low tide under the glare of the sun.

A number of specimens were put together into a big dish on May the 19th and spawned during the night. The eggs are very small, only c. 0.05 mm. Early in the morning they were blastulæ, though not yet free-swimming; in the course of the day, scarcely more than some 18 hours old they were gastrulae, rather elongate, but otherwise quite typical. On the next day the mouth had been formed, but the Auricularia shape was still hardly indicated and only the first traces of the postoral and preoral vibratile bands were to be discerned. Three days old they were young Auricularias, exceedingly clear and transparent, and with 1—3 small spheres in one of the postero-lateral corners. At the age of about two weeks they were apparently fully formed larvae, with a number of small wheels scattered over the body. Beyond this stage they did not develop, though kept alive for another week.

The larva (Pl. X. Fig. 6) is of very simple shape, merely with a fold on the middle of the band along the dorsal side. Seen in side view it is very thick in the anterior part, with the postoral area somewhat projecting, as a lip, like the following species, cf. Pl. XI. Fig. 6. The larva is perfectly clear, without the slightest trace of colour. — The wheels are of a quite simple type, with 12—13 spokes (fig. 42).

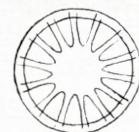


Fig. 42. Wheel of Auricularia of *Synaptula reciprocans*.  
× 240.

#### 21. *Synaptula vittata* (Forskål).

Pl. X. Fig. 7; Pl. XI. Fig. 6.

As stated above this species occurs in great numbers together with *S. reciprocans* on the shore flats at Ghardaqa, under the same life conditions. A good number of specimens were put into the tank of the laboratory with some of the algæ among which they usually occur, and here they lived very well for some days and spawned during the night of June the 6th.

The eggs are like those of *S. reciprocans*; the first development stages offer the unusual feature that gastrulation begins already before the embryos have left the egg-membrane. Otherwise there seems to be no difference from *S. reciprocans*. (I did not observe whether the gastrulation of *S. reciprocans* starts before the embryo leaves

the egg-membrane). The larva (Pl. X. Fig. 7; Pl. XI. Fig. 6) is very clear and transparent, without any trace of colour, very thick in the anterior part. As in *S. reciprocans* there are 1—3 spheres in the left posterolateral lobe, and in the later stages a number of Auricularia-wheels scattered irregularly over the body. The nerve strands are very distinct, as is also the oesophageal vibratile band, the adoral band, as it was termed by SEMON, who was the first to describe it (Die Entwicklung der Synapta digitata und ihre Bedeutung für die Phylogenie der Echinodermen. Jen. Zeitschr. XXII. 1888. p. 125).

The figure of this larva shows it to be more folded than that of *S. reciprocans*; this, however, is probably due to some difference in age, and it is to be expected that the latter larva will be just as much folded in the later stages as is the *S. vittata* larva — and very probably both of them will be still more complicitely folded by the time metamorphosis sets in. Among the larvæ of *S. vittata*, preserved the last day before my departure — thus three weeks old — I find one specimen very much more folded, and with a great number of wheels all over the body. Unfortunately the anterior end of it has been destroyed, so I cannot give a figure of it — the more so as the fact that there are no spheres in the posterolateral lobe makes me a little uncertain, whether it is really the same species, and not one which has happened to be in the water from the outside. But in any case it is a Synaptid larva.

This said larva approaches to some degree the famous *Auricularia nudibranchiata* of CHUN and makes it probable that this fine *Auricularia* does really belong to some Synaptid, as suggested by MACBRIDE and recently by Densaburo Inaba (On some Holothurian larvæ and young from New Guinea. Bull Jap. Soc. Scientif. Fisheries. II. 1934, p. 213). One might be tempted to suggest that it belongs to the large Synaptids of the genus *Synapta* or *Opheodesoma*; in any case it would be of the greatest interest to study the development of these gigantic Synaptids. Unfortunately my efforts to induce the *Synapta maculata* Ch. & Eysen. and *Opheodesoma serpentina* (Joh. Müller), found in fair numbers near Ghardaqa, to spawn were not crowned with success, although I had a good number of them living for some time in the tank. Artificial fertilization, which I also tried, did not succeed either. Possibly it was too early for their breeding, although the eggs seemed to be ready for spawning.

## 22. *Stichopus variegatus* Semper.

Pl. XI. Figs. 1—5.

Owing to the peculiar property of *Stichopus* (at least some species of the genus) that its skin dissolves when it is kept under unnatural circumstances, I had much trouble in getting the development of this species, which is rather common at the reefs near the station. But finally during the night of June the 20th some specimens spawned in the tank of the laboratory. By the time I left Ghardaqa, June the 27th, the embryos were only young Auriculariæ; but after my departure ZAKY EFFENDI looked after the culture in the most excellent way till the end of July, preserving

specimens in the various stages. On the material received from him I could then follow the development until the young Holothurian. As the larva is perfectly colourless, nothing was lost either in regard to colour by having only preserved material for study.

When observed in the morning of the 21st the embryos were already in the blastula stage; they were very clear, rather unusually large (I have forgotten to note anything about the size of the eggs). On the next day they were beginning to assume the Auricularia shape; on the third day the first rudiments of the spicules in the posterolateral corners were seen, but the Auricularia shape was not fully assumed till the fourth day.

The young Auricularia (Pl. XI. Fig. 1) is very simple; it differs from the *Holothuria* larva in having a spicule in each posterolateral corner, but no spicule or sphere in the middle of the hind end. The spicule is irregularly star-shaped. In the fully formed larva, before beginning metamorphosis (Pl. XI. Figs. 2, 4), the vibratile lobe forms a small postoral fold or lobe and a larger, more complicate dorsal fold resulting ultimately in the formation of a rather distinct antero- and posterodorsal lobe. The posterolateral corners are produced into more distinct lobes, in each of which a granular mass has appeared. The spicules may sometimes be entirely absent, sometimes only one of them is present, but normally there is one in each posterolateral lobe. The nerve strands are distinct. The enterocoel has begun to grow downwards. In one larva of this stage there is a double hydrocoel, with a common hydropore; here a small separate enterocoel vesicle lies below the stomach (Pl. XI. Fig. 3). A granular sphere is seen in the right anterodorsal lobe.

In the next stage (Pl. XI. Fig. 4) the hydrocoel has developed the primary lobes, and the madreporite, with its calcareous skeleton, is distinct, and the large, transparent, elastic balls have appeared in the posterolateral and the two dorsal lobes; in one of the anterolateral corners a similar ball is found, but not in the other. These anterolateral balls are not of constant occurrence; thus in the metamorphosed specimen, Pl. XI. Fig. 5, there are only three balls to each side, both the anterolateral ones lacking. Below the ball in the posterolateral corners is seen the granular mass.

The metamorphosed young (Pl. XI. Fig. 5) has the typical barrel-shape, with five vibratile bands. Beside the posterior balls are seen the larval spicules, and then under the granular masses are seen a number of small glassy disks. These are seen

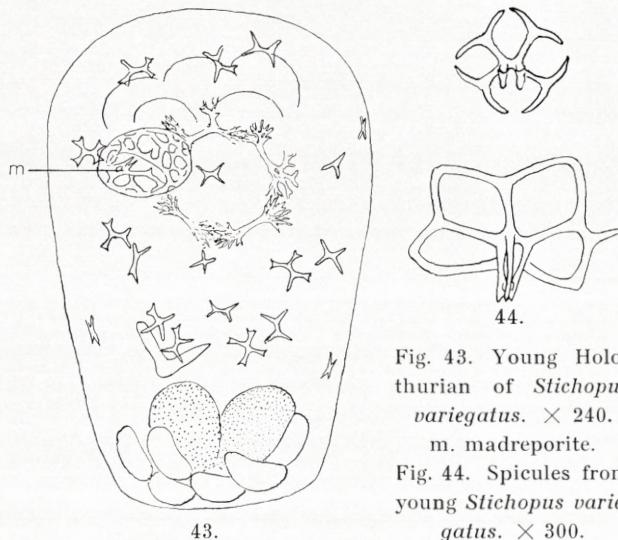


Fig. 43. Young Holothurian of *Stichopus variegatus*.  $\times 240$ .

m. madreporite.  
Fig. 44. Spicules from young *Stichopus variegatus*.  $\times 300$ .

more developed in the more advanced stage fig. 43. Here the balls have disappeared, but the granular bodies still remain distinct; it would appear that they have something to do with the formation of the glassy disks, which are here seen to have a lenticular shape, a little concave on the side turning inwards. There is still a trace of the larval spicule, but then the formation of the spicules of the body wall of the Holothurian has begun; the madreporic skeleton is finely developed, and the five radialia of the calcareous ring have appeared. In a slightly more advanced specimen the body spicules are beginning to assume the shape of tables (fig. 44). In this latter specimen only two of the glassy disks are left, one of them much reduced in size, and the granular masses are no longer distinct. It thus appears that both these bodies, the disks and the granular masses, have some kind of function only for the metamorphosing Holothurian, as must also be the case with the elastic balls, which likewise have disappeared by the time the calcareous ring and the spicules of the Holothurian have appeared.

The only other *Stichopus* larva known, that of *Stichopus californicus* (Stimpson) (cf. my "Studies" 1921, p. 196, Pl. XXXIII. 8—9) agrees with the present larva in having an irregular, star-shaped spicule in each posterolateral corner, but nothing in the middle of the hind end of the body. It would appear thus that this is a character distinguishing the *Stichopus* larva from the *Holothuria* larva. In the shape of the larval body there is no difference between the larvae of these two genera.

### 23. *Actinopyga serratidens* Pearson.

Pl. XIII. Figs. 1—3.

Some specimens of this species, which is common on grass bottom at a depth of c. 10 m. near the station, were put into a big dish at 7 o'clock in the evening of May the 19th. After an hour I found them in the act of spawning. They raise the anterior end when shedding the sexual products, but I did not observe this species to move the upraised part to the sides, such as was the case with *Holothuria (Bohadshia) marmorata* Jäger.

The development proceeds rather slowly. The gastrula stage is reached about 18 hours after fertilization; at the age of one and a half day the mouth is only just beginning to form, and not until the fourth day I found the embryos to be typical young Auricularias with beginning formation of a spicule in the posterior end of the body. In this stage they remained nearly unaltered for about two weeks (Pl. XIII. Fig. 1). The vibratile band is quite simple, forming only a small lobe on the middle of the dorsal side. A number of distinct yellow spots are found, almost symmetrically arranged, in the band all round. The nervous strands

are very distinct. The calcareous body in the posterior end is an irregular star (fig. 45, a).

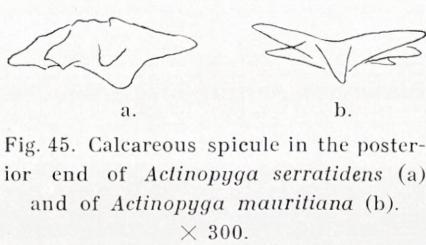


Fig. 45. Calcareous spicule in the posterior end of *Actinopyga serratidens* (a) and of *Actinopyga mauritiana* (b).

× 300.

In larvae about three weeks old (Pl. XIII. Fig. 2) the metamorphosis is beginning, the hydrocoel has begun to form lobes, and the enterocoel vesicles are prolonging backwards. The larva has now the usual folds very well developed, and elastic balls have been formed in all the lobes, besides one in the middle of the posterior end, above the calcareous body, which has developed into a finely spiny sphere. The yellow spots of the vibratile band are fairly distinct, and small yellow spots scattered on the body.

At the age of nearly four weeks several of the larvae had metamorphosed, the young Holothurians having the usual barrel-shape, with five vibratile bands and five pairs of elastic balls, besides the one in the posterior end (Pl. XIII. Fig. 3). The fifth pair of balls, which I did not observe in the larva, evidently develops in the slight dorsal fold below the anterior end.

In the oldest specimens obtained, four weeks old (fig. 46), the spicules of the body wall have begun to form, and the radials of the calcareous ring have appeared. The elastic balls are about to disappear, but the sphere in the posterior end is still in full shape.

#### 24. *Actinopyga mauritiana* (Quoy & Gaimard) (Var.).

Pl. XIII. Fig. 4.

On May the 22nd the sailors brought home a number of specimens of this species from the outer reef. They must have spawned at once on being put into the tank, numerous blastulae being found already at 9 o'clock in the evening. I have no detailed observations concerning the development processes.

Pl. XIII. Fig. 4 represents an 8 days old larva, evidently fully formed, but not yet in beginning metamorphosis. The larva has an irregular star-shaped spicule (fig. 45. b) in the middle of the posterior end, which is not produced — a character which distinguishes this larva from the *Holothuria* larvae, in which the middle of the posterior end, containing the spicule, is usually produced. Apart from this feature and the different shape of the spicule these larvae are otherwise closely alike.

As was to be expected, the larva of the present species agrees very closely with that of *Actinopyga serratidens* in the character of the spicule, in the young larval stage. Whether it will develop into a spiny ball in the later stages also of the present species remains to be seen; if so, we may have herein a character peculiar to the *Actinopyga* larva.

The larvae did, unfortunately, not develop beyond the stage figured; I have thus also been unable to ascertain whether elastic balls will be present in the metamorphosis stage; but there is, of course, no reason to doubt that they will be formed here as in other Aspidochirote larvae.

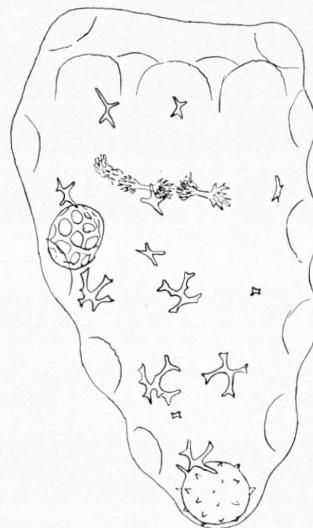


Fig. 46. Young Holothurian of *Actinopyga serratidens*.  
X 225.

25. **Holothuria (Bohadschia) marmorata** Jäger.

Pl. XII. Figs. 5—6.

This species is common on grass bottom at a depth of c. 10 m at the station. It is highly variable in colour, so that at first I took it for being two different species and therefore got two different cultures of the larvae, on May the 12th and May the 19th. The fact that the larvae in both cultures were exactly alike testifies the correctness of regarding all the colour variations as merely individual variations. The more general colour was a more or less dark brown on the dorsal side, the ventral side being somewhat lighter. The larger specimens, when caught in the trawl, usually assumed a shape almost exactly like a football; when put into the tank of the laboratory they again assumed the normal sausage-shape. As described above (p. 9—10) this species raised the foreend of the body when spawning, spreading it out and flattening it, the genital papilla coming out quite distinctly. It moved the foreend to the sides during the spawning.



a.

b.

Fig. 47. Spicules of the *Holothuria marmorata* larva, a. from the middle of the hind end, b. from the right posterolateral lobe.  $\times 300$ .

old they were beginning to assume the Auricularia shape. At the age of four days the formation of the spicules had begun. None of the larvae reached the metamorphosis stage.

The larva (Pl. XII. Figs. 5, 6) does not show any peculiar features in regard to shape, but in its spicules it differs very markedly from the other *Holothuria* larvae reared. The spicules are slightly irregular stars, generally with 5—6 rays (fig. 47). They are found both in the middle of the posterior end (which is not produced) and in all the lobes, varying in number from 1—3 in the posterior end and in the posterolateral lobes, usually only one in the other lobes (probably more in older larvae). The rays of the stars may be distinctly curved so as to resemble wheels in formation. The colour is a very faint yellowish on the body, more distinct yellowish spots on the vibratile band. — The nerve strands were rather indistinct.

None of the larvae reaching beyond the stage figured, I cannot say whether the elastic balls will be found in the metamorphosis stages; but it may well be expected that they will be found here as in the other larvae.

26. **Holothuria arenicola** Semper, var. **Boutani** Hérouard.

Pl. XII. Figs. 3—4.

The present species occurs very commonly in the sand on the flats near the station, buried rather deep down, not visible on the surface; also under the stones on the flat it is found quite commonly. Some specimens were put into a large dish,

without sand, on May the 21st, and spawned during the night. The embryos were in the gastrula stage already next morning. I have no detailed information of the development processes.

The young larva (10 days old), Pl. XII. Fig. 3, is of the usual shape. In the middle of the posterior end lies, in a distinct prominence, a rounded, lobed, calcareous



Fig. 48. Spicule from the posterior end of the larva of *Holothuria arenicola*.  
× 300.

spicule (fig. 48); sometimes, as in the specimen figured, it lies unsymmetrically. The larvae near metamorphosis (Pl. XII. Fig. 4), about four weeks old, have elastic balls present in all the lobes, also one in the posterior end, above the spicule; no balls were seen as yet in the anterolateral corners, but no doubt they will develop there before metamorphosis. — The larva is very transparent, with only some small yellow spots in the vibratile band and a very few similar spots scattered on the dorsal side (none on the ventral side).

A few of the larvae had transformed at the age of four weeks. The young Holothurians were opaque, yellowish-grey, the number of balls being not distinctly observable. On specimens cleared in Canada balsam (fig. 49) it seems that there are five pairs, but they are not very distinct. The madreporite skeleton is very well developed, the calcareous ring and the first spicules have appeared. The calcareous body in the posterior end is conspicuously larger than in the larvae, a rather curious fact indicating that this spicule may perhaps persist for some time in the young Holothurian; it would be interesting to follow its fate during the further growth of the young Holothurian.



Fig. 49. Young Holothurian of *Holothuria arenicola*.  
× 250.

### 27. *Holothuria scabra* Jäger (*H. tigris* Selenka).

Pl. XII. Figs. 1—2.

This species, usually very strikingly coloured, with narrow white transverse bands on the dorsal side, is common on grass bottom, at a depth of c. 10 m, near the laboratory. Specimens were repeatedly put into the tank in the hope that they would spawn, but without success. Once I tried to induce them to shed their sexual products by making a slit in the body wall — a proceeding which I have on some occasions found to lead to the desired result — but still nothing happened. Finally, on June the 8th, when I had again put several specimens into the tank, I had the pleasure of finding the next morning numerous gastrulae in the water, which gave a very good culture. On the next day they had assumed the shape of young Auriculariae, without special features. Five days old the larvae had the shape as represented in Pl. XII. Fig. 1, characteristic by a long median prominence of the posterior end, in which lies a calcareous sphere. This sphere is smooth in the present stage, but I found

its surface a little uneven in younger larvae. The prominence was generally somewhat unsymmetrically placed. The nerve strands were very conspicuous, and with a distinct nerve proceeding towards the dorsal vibratile band (this nerve appears to be a constant feature of the Auriculariæ). The oesophageal band is unusually broad and has the appearance of being also of nervous structure.

At the age of 18 days I found the larvæ near metamorphosis and with elastic balls beginning to appear (Pl. XII. Fig. 2). The shape of the fully formed larva is quite as usual. The colour is the usual, faint yellow spots along the vibratile band and a few along the posterior end. — The larva figured was abnormal in having a right, not a left hydrocoel.

None of the larvæ metamorphosed.

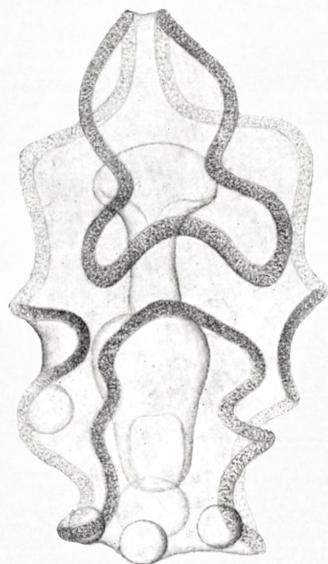
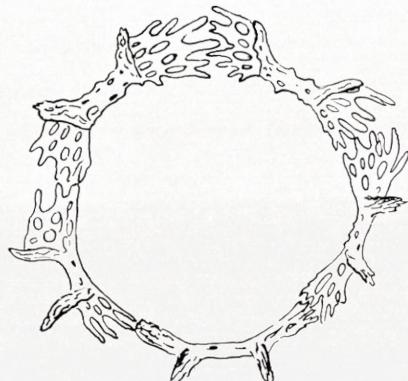


Fig. 50. Auricularia of *Holothuria spinifera*, showing beginning formation of the elastic balls.  $\times 200$ .

calcareous sphere in the middle of the posterior end in a small prominence. Sometimes there may be two or even three of these spheres. The colour is the usual: small faint yellow spots in the vibratile band and in the posterior end.



51.

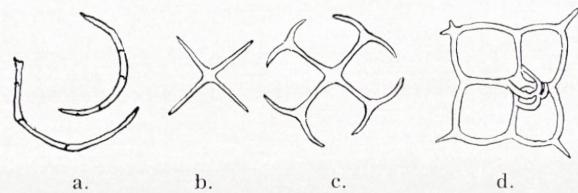


Fig. 51. Calcareous ring (radials) of young *Holothuria spinifera*.  
Fig. 52. Spicules from young *Holothuria spinifera*; a. from the tentacles; b—d. developmental stages of spicules (tables) from the skin. All  $\times 300$ .

After my departure from the laboratory ZAKY EFFENDI looked after the culture and sent me the preserved specimens of the metamorphosis stages. As seen from fig. 50, elastic balls are present (still only beginning to form in the specimen figured). A couple of specimens had metamorphosed; the calcareous ring (radials), and also the first spicules of the body wall and of the tentacles have been formed (figs. 51—52). The skeleton of the madreporite is of the usual type, an irregular network. The elastic balls are not visible.

### Crinoidea.

#### 29. *Tropiometra Audouini* A. H. Clark.

Pl. XIV. Figs. 1—2.

This Comatulid, which occurs in good numbers on the reefs close to the station, mainly on the underside of old, loose coralblocks, was found ripe by the end of April. Some specimens were put into a large dish on the 18th and the next morning a good number of eggs were found lying on the bottom of the dish. The egg-membrane is spiny as in *Tropiometra carinata* (cf. my "Studies on the development of Crinoids". Papers from the Department of Marine Biology, Carnegie Inst. Washington. XVI. 1920). About 24 hours old the embryos were partly free-swimming, and on the next day there were some hundreds normal larvæ, with ciliated bands and vestibular invagination. A number of embryos were still enclosed within the egg-membrane; it seemed clear that they had considerable difficulty in getting out of the shell in the still water in the dish, as I have formerly found it to be the case with *Antedon petasus* (cf. my "Notes on the development and the larval forms of some Scandinavian Echinoderms". Vid. Medd. Dansk Naturh. Foren. 71. 1920, p. 151). I then put these embryos into a plankton net in the tank, under the tap, so as to have them in constant movement in the water, and in this way I succeeded in getting another good lot of free-swimming embryos.

All the embryos were then put into some dishes with the bottom covered by small pieces of broken shells and corals, to which I hoped to see them attach themselves. Not till the 25th, thus after 5—6 days free-swimming, did I find a few of them attached and having assumed the Pentacrinoid shape; by May the 1st there were some 30 Pentacrinoids, all the rest of the larvæ still swimming, and no more of them did attach themselves. In the course of the following five days a few larvæ tried to attach themselves to the bottom of the dish, but without success, and in 2—3 days more all of them had disappeared. Evidently the difficulty with these Crinoid larvæ is to find suitable objects for them to attach themselves to, as I found it to be the case with *Tropiometra carinata* (cf. my "Studies in the development of Crinoids", p. 5).

Having already studied the embryological development of *Tropiometra carinata* in detail (Op. cit.), I did not preserve any of the larvæ for sectioning, wanting to have as much material as possible for eventually studying the further postembryonal development of the Pentacrinoids. I expected that by means of the various cultures

of food-organisms that I had at disposal it would be easy enough to keep the Pentacrinoids growing in the dishes. Unfortunately, this did not prove successful. Repeated attempts to get new cultures of the larvæ failed; evidently the breeding season had passed — at least no more eggs were got. Thus the information I can give of the development of this *Tropiometra* species is confined to the above statements, and to the figures of the young Pentacrinoid.

This Pentacrinoid (Pl. XIV. Figs. 1—2) has much resemblance with that of *Tropiometra carinata* (Op. cit. Pl. X. Figs. 6—8). The oralia have no outturned edge, such as is found in the Pentacrinoids of the Antedonids. There are three well developed infrabasalia. The anal plate has appeared (Pl. XIV. Fig. 2), but there is no trace of the radial and neither have I found the spicules of the tentacles or the first sacculus in any of the Pentacrinoids, though kept alive till the age of three weeks. It may, however, be mentioned that as in *Tropiometra carinata* (Op. cit. Pl. X. Fig. 6) I have found in one specimen a small, young plate lying some distance out in the primary tentacle. It may be suggested that it is the first axillary; but in the absence of further development stages this remains a little uncertain.

### 30. **Lamprometra Klunzingeri** (Hartlaub).

Pl. XIV. Figs. 3—8; Pl. XV. Figs. 1—10.

This very beautiful Crinoid is common on the reefs at Ghardaqa, but not found under the loose blocks like *Tropiometra*. As a matter of fact they are not easily discovered at day time; but at sunset they come out from their hiding places and crawl up on top of the corals and sit there fully expanded, as big flowers. In places they may be found in good numbers and then afford a most gorgeous sight.

On May the 1st a number of specimens were put into a big dish, under a moderately running tap, and the next morning I had the pleasure of finding a number of eggs lying on the bottom of the dish. As the specimens were evidently in very good condition I kept them in the dish for eventually getting some more eggs from them. During daytime nothing happened, but in the evening a new spawning took place. By careful observations the following days I could ascertain that spawning takes place almost exactly at 7 o'clock in the evening.

The eggs are small, c. 0.1 mm., and the egg-membrane spiny as in *Tropiometra*. 14 hours old some of the embryos were free-swimming, the others rotating within the egg-membrane. Also in this species the embryos had difficulties in rupturing the egg-membrane in the dishes with the still-standing water; when put into a plankton-net in the tank, and the water from the tap running through the net, a much larger percentage of the embryos became free-swimming.

The embryos, when leaving the egg-membrane, are uniformly ciliated all over, but almost immediately the arrangement in distinct bands begins. In embryos one and a half day old there were four distinct bands and an apical tuft of longer cilia. They have a well developed sucking disk and are apt to attach themselves to the

bottom of the dish; they are rather strong swimmers and show some positive phototropism. The skeleton of the Pentacrinoid has already begun to form (Pl. XIV. Figs. 3—4).

Like the *Tropiometra* larvæ the *Lampropmetra* larvæ were put into dishes with the bottom covered by fragments of shells and corals, and also some algæ (*Halimeda*, *Sargassum*, etc.). On the 5th I found some 50 specimens attached and about to assume the Pentacrinoid shape; on the following day some few more had attached themselves, but the great majority (several hundreds) were unattached. I tried then to put some small pieces of floating *Posidonia* leaves into the dishes, and to put gravel on the bottom of the dishes for making it appear more like the natural sea-bottom — but with negative result; a few larvæ attached themselves to the glass itself, more or less successfully — but the great majority of the larvæ remained free-swimming till 11—12 days old, some of them in the shape of "hump-backed" Pentacrinoids, as described for *Tropiometra carinata* (Op. cit. Pl. IX. 5—6). Then they died off, without attaching themselves.

This curious fact observed now in three different species of Comatulids that the larvæ will not attach themselves, but remain swimming for several days, must, evidently, be of importance as a means of dispersal (cf. Op. cit. p. 4); but one cannot help thinking whether perhaps also under natural conditions numbers of the larvæ do not succeed in finding a suitable place for attachment. If they did all succeed in attaching themselves, one would expect young specimens of the Comatulids to be very common, in accordance with the enormous number of eggs produced. But, as a matter of fact, young specimens are almost not to be found; of course, they are difficult to see — especially the Pentacrinoids, but will that difficulty alone account for their scarcity?

As was the case with *Tropiometra* the Pentacrinoids would not thrive in the dishes, in spite of the adding of *Nitzschia*, *Chlamydomonas*, and other food-organisms, or of giving them fresh sea-water daily. An attempt to keep them in the tank with running sea-water did not succeed either. Wishing then to try to rear the Pentacrinoids by putting them out on the reef in such a way that they could be found again, I wanted to start some new cultures of the larvæ; but now the breeding season evidently was over; repeated attempts with new specimens of the Comatulid put into dishes, like done at first, gave no results. Thus the postembryonal development, beyond the first Pentacrinoid stage, could not be studied of this species either. A method for rearing the Pentacrinoids till the Comatulid stage has still to be found.

A fair number of larvæ of various ages were preserved (formol-sublimate) in order to be sectioned, as it would be of considerable interest to see, whether this representative of the family Mariametridæ would differ from the other forms, the development of which has been studied in detail, viz. *Antedon*, *Isometra*, and *Compsometra* of the Antedonidæ, and *Tropiometra* of the Tropiometridæ. (*Notocrinus*, of the family Notocrinidæ, is so highly specialized, and moreover the first stages unknown, that a direct comparison with the present form is hardly possible; cf. for *Compsometra*,

*Isometra*, *Tropiometra*, and *Notocrinus* my "Studies in the development of Crinoids". 1920).

Unfortunately, the preservation of the embryos of *Lampronemata* is not all that could be desired, as a matter of fact not nearly as good as that of the above named forms, previously studied, preserved simply in alcohol. To this comes the difficulty caused by the very small size of the nuclei, particularly those of the ectoderm. I cannot, therefore, give a detailed description of the whole development, particularly as concerns the pore-canal and the enterocoel cavities. But so far as can be seen there is herein no essential difference from *Tropiometra*. In regard to the younger stages, however, there is a very remarkable difference between *Lampronemata* and the other forms, the corresponding stages of which are known, and these stages are, fortunately, sufficiently well preserved so that no doubt can obtain as to the correctness of the results.

The cleavage is perfectly regular, as seen from Pl. XV. Figs. 1—2; the 4-cell stage is reached already after two hours. Embryos four hours old have already reached the blastula stage, but the blastocoel cavity is completely filled by cells, which have wandered in, or budded off from the ectoderm (Pl. XV. Fig. 3). Sections of embryos 6—10 hours old show them still having the blastocoel cavity completely filled up by mesenchyme cells, lying close together, pressing each other into irregular polygonal shapes (Pl. XV. Fig. 4). There is no trace of a gastrula invagination and no gastrula mouth, and such is not seen either in the later stages; the gastrular cavity develops as a sort of schizocoel by some of the cells of the blastocoel cavity arranging themselves so as to form an epithelium, limiting a cavity (Pl. XV. Figs. 5—6).

It is very interesting to compare this peculiar origin of the entoderm in *Lampronemata* with the way it originates in *Tropiometra* (cf. my "Studies in the development of Crinoids" p. 8; Pl. II. Fig. 2). Here the blastocoel cavity is nearly filled up with mesenchyme cells, before the gastrula invagination takes place, and the mesenchyme cells then arrange themselves on the top of the archenteron and participate in the formation of the entoderm. *Tropiometra* thus represents an intermediate step in regard to the entoderm formation, from *Antedon*, with a typical gastrula invagination, to *Tropiometra*, with the entoderm formed partly by mesenchyme cells, partly by a regular gastrula invagination, to *Lampronemata*, without any gastrula invagination, the entoderm formed solely by mesenchyme cells. (It may be incorrect to designate these cells filling the blastocoel cavity as "mesenchyme" cells. I do not attach any special importance to the use of this designation for these cells; it is merely for giving them some designation, without entering on a discussion of what might be a more appropriate term).

In embryos 22 hours old (Pl. XV. Fig. 7) the gastrular cavity has divided into a lower and an upper part, the enterocoel and the hydrocoel vesicle; the vestibulum is beginning to form. In embryos  $1\frac{1}{2}$  days old (Pl. XV. Figs. 8—9) the vestibulum is formed; the enterocoel is dividing into a right and a left vesicle, and the stomach has begun to differentiate. Finally Pl. XV. Fig. 10 shows the beginning closure of

the vestibulum and the beginning formation of the chambered organ. The details about the pore canal could not be made out.

Attention may be called to the fact that the ciliated bands are not distinctly recognizable in the sections, such as I found them to be in *Tropiometra*; this may, partly at least, be due to the unusually small size of the nuclei.

The young Pentacrinoids are remarkable by the relatively large size of the anal plate (Pl. XIV. Figs. 5, 7). The oral plates are in the main as in *Tropiometra*, without outturned edges. There are no infrabasalia, as I have ascertained by very carefully dissolving some calyces under the microscope; neither is there any trace of infrabasalia observable in the embryos. This is then a conspicuous difference from *Tropiometra*; but, as I have pointed out in my "Studies in the development of Crinoids" pp. 75—76, the presence or absence of infrabasalia seems to be of no primary importance.

In the 6 days old Pentacrinoid Pl. XIV. 7 the mouth has just opened. Pl. XIV. 8 represents the farthest differentiation reached, in a Pentacrinoid 18 days old. There is still no trace of the radials, but the first sacculus and the spicules of the primary tentacle have appeared.

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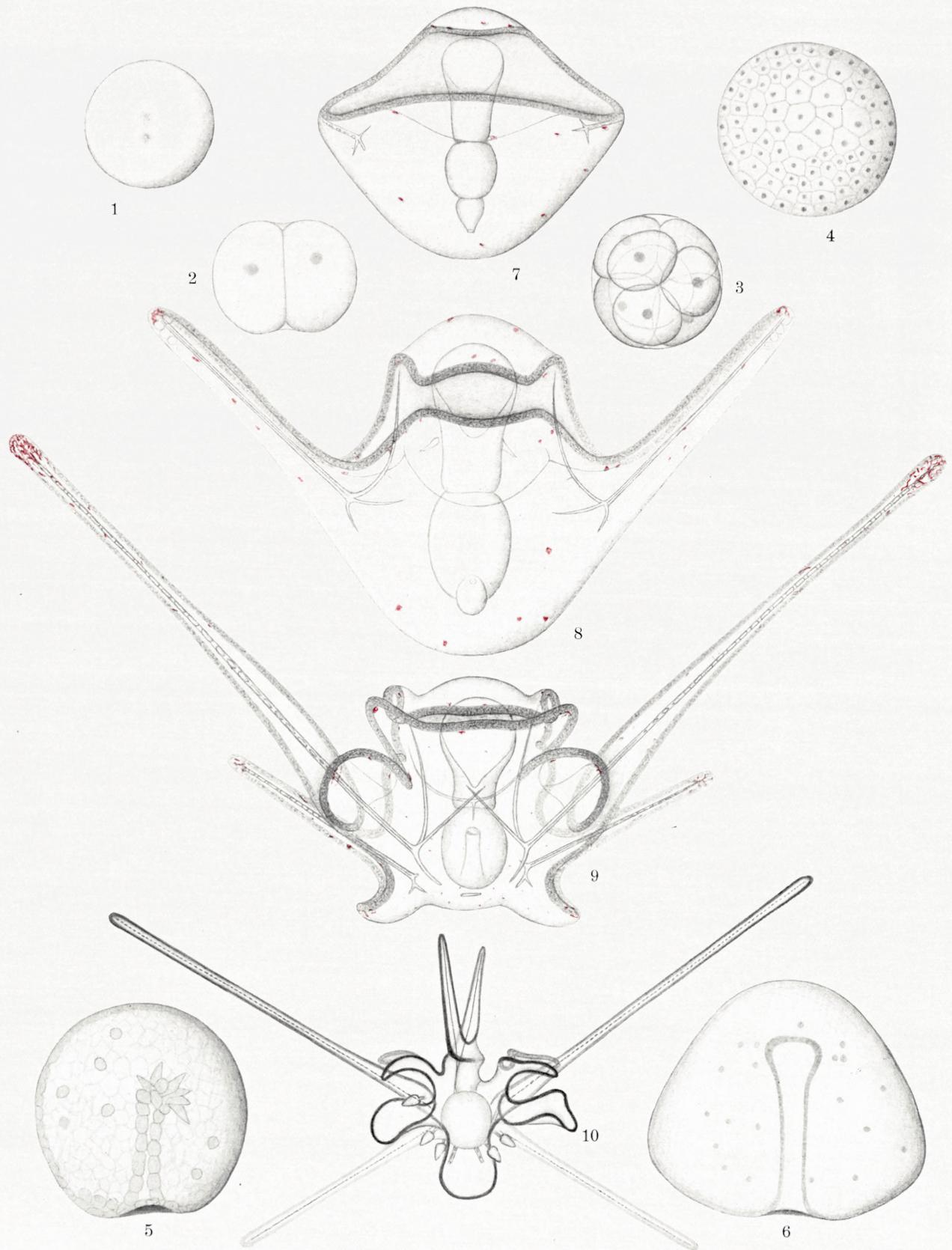
## Plate I.

All figures of *Eucidaris metularia* (Lamarck).

- Fig. 1. Egg, immediately after fertilization.  
- 2. First cleavage.  
- 3. Eight cell stage.  
- 4. Blastula stage; 6—8 hours after fertilization.  
- 5. Gastrula, 24 hours old. Mesenchyme cells proliferating from upper end of archenteron.  
- 6. Gastrula, 2 days old. Upper end of archenteron widening to form the mesoderm pouches.  
- 7. Embryo, 4 days old, beginning to assume the Pluteus shape; the postoral rods have just begun to form. The suboral cavity distinct. Pigment has begun to appear.  
- 8. Young larva, 9 days old.  
- 9. Larva, 22 days old. Posterodorsal arms are developing, and the posterior transverse rod has appeared, the small horizontal rod below the stomach.  
- 10. Fully formed larva, in side view. Pedicellariæ and spines have appeared. Drawn from a preserved specimen.

Figs. 1—6  $\times$  290; figs. 7—9  $\times$  125; fig. 10  $\times$  40.

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## Plate II.

All figures of *Eucidaris metularia* (Lamarek).

Fig. 1. Fully formed larva, seen from above.

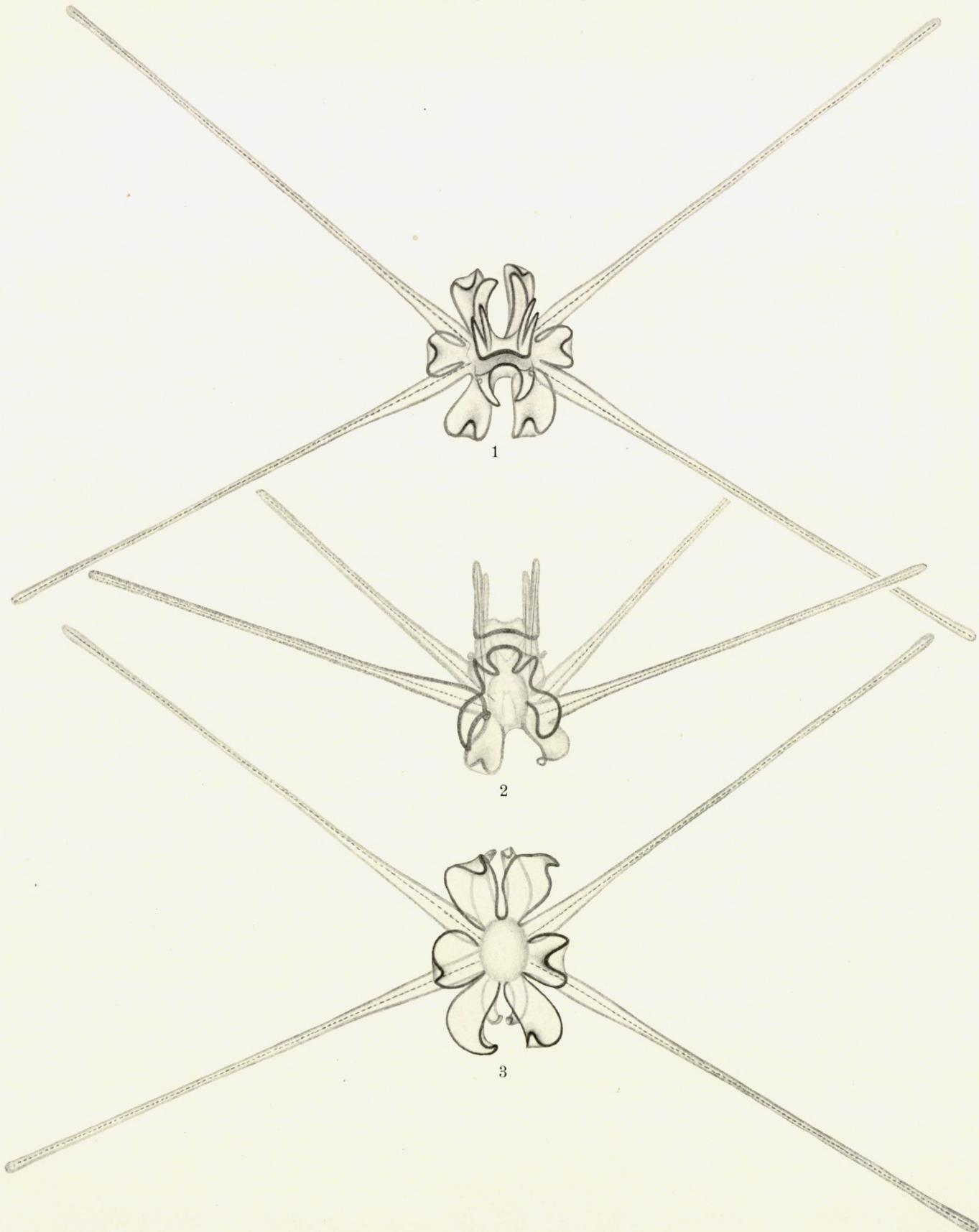
- 2. Same, seen from the oral side.
- 3. Same, seen from below.

Drawn from preserved specimens.

The exact age of these larvæ not stated, but they are about 7 weeks old.

All  $\times 40$ .

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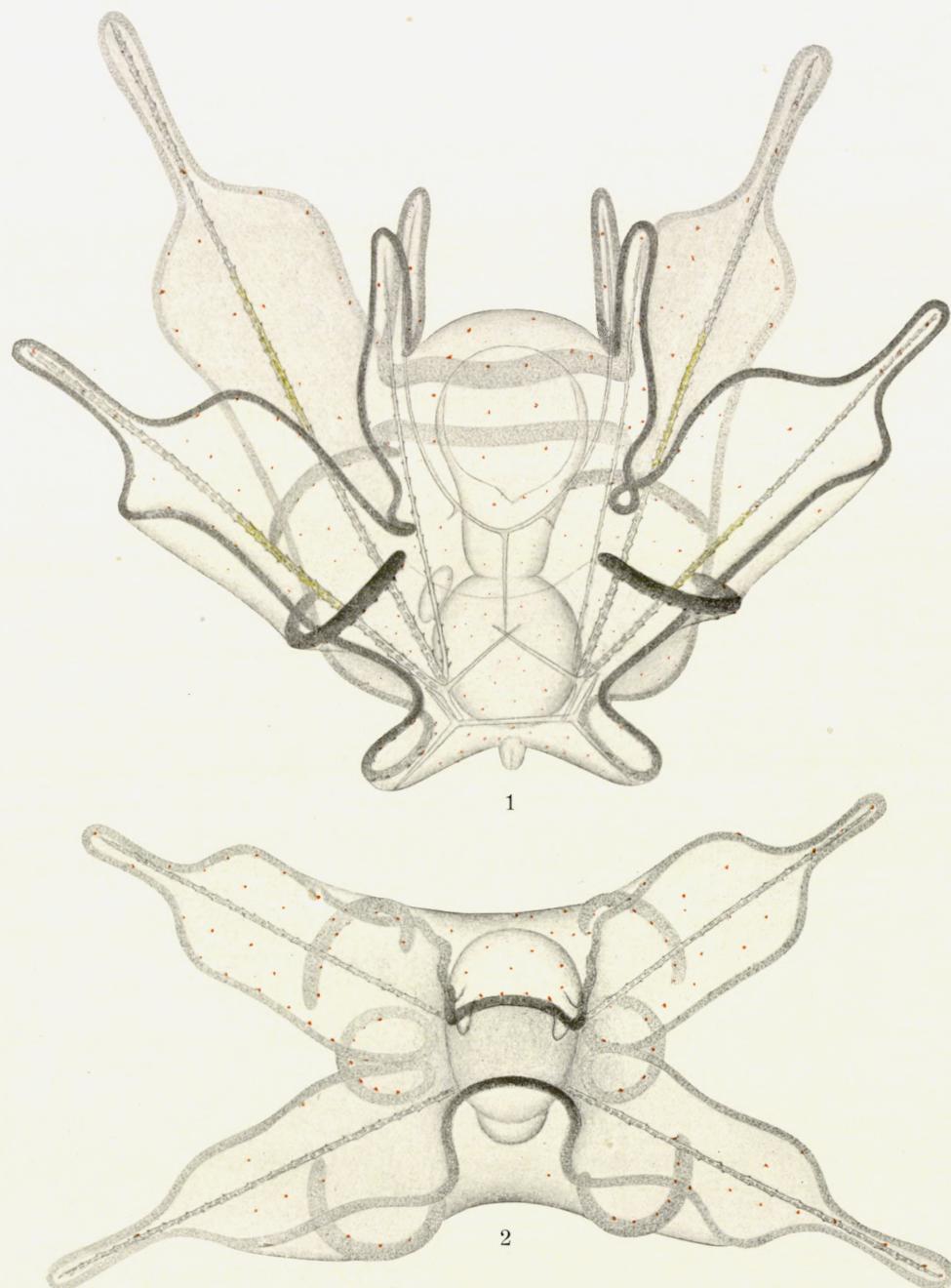


**Plate III.**

*Temnotrema scillæ* (Mazetti).

Fig. 1. Fully formed larva, 15 days old; from the dorsal side.  $\times 115$ .  
- 2. Same, from above.  $\times 100$ .

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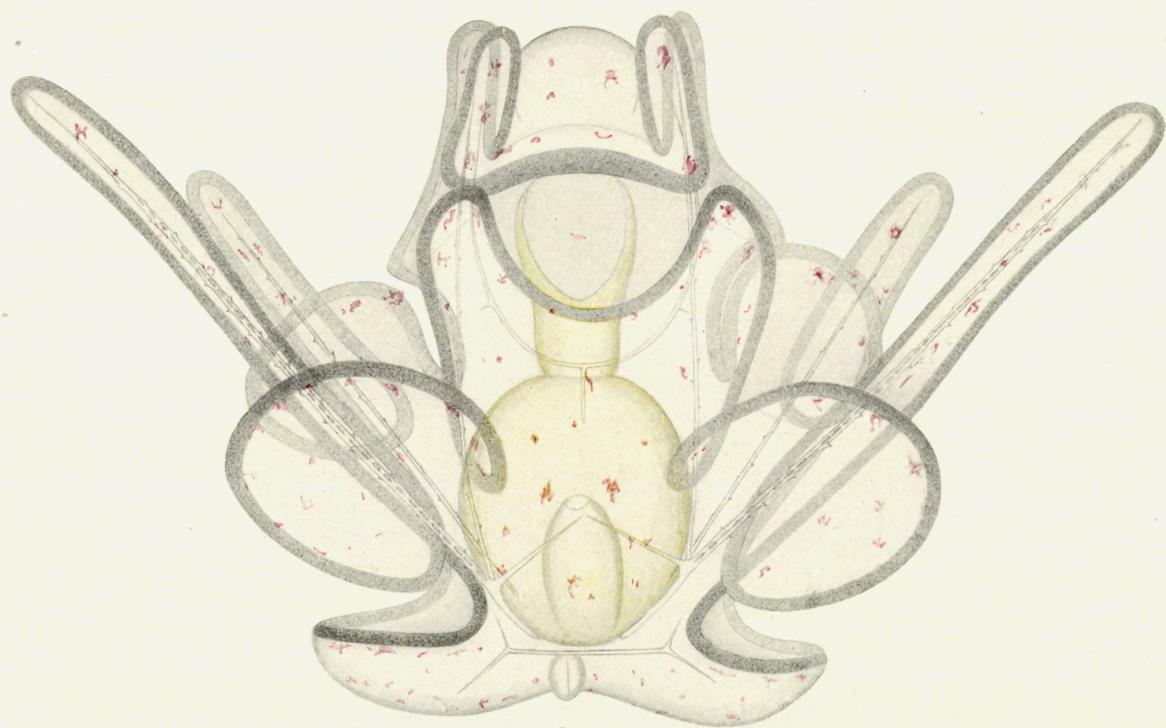


## Plate IV.

- Fig. 1. Larva, 15 days old, of *Nudechinus Gravieri* (Koehler), in beginning metamorphosis, from the oral side.  $\times 145$ .
- 2. Fully formed larva, 19 days old, of *Tripneustes gratilla* (Linn.) from the oral side. In the posterior end the first pedicellaria has appeared.  $\times 145$ .



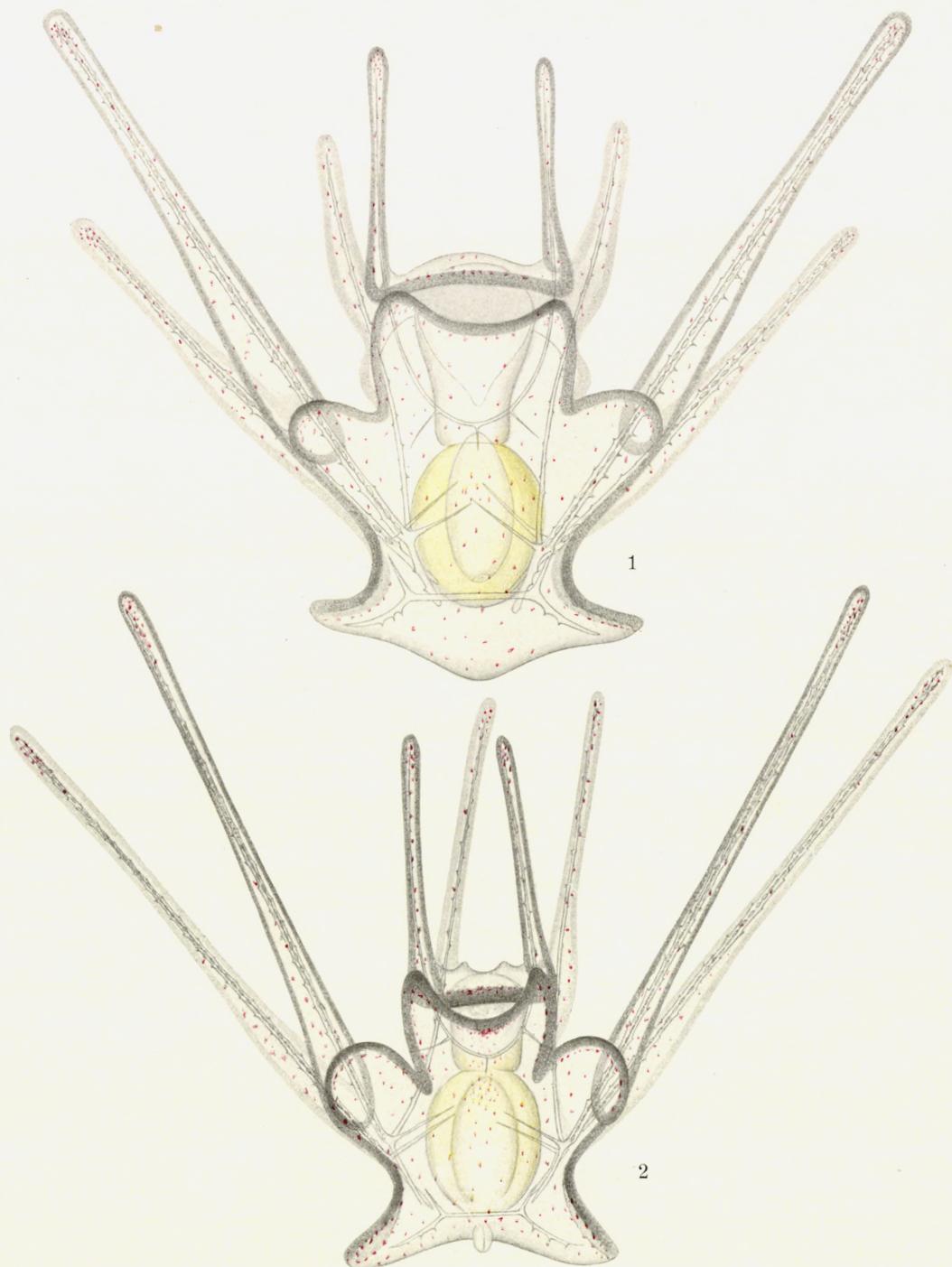
1



2

**Plate V.**

- Fig. 1. Fully formed larva of *Echinometra Mathæi* (Blainv.), from the oral side. 28 days old.  
× 120.
- 2. Fully formed larva of *Heterocentrotus mammillatus* (Linn.), from the oral side, 24 days old. In the posterior end the first pedicellaria has appeared. × 105.



**Plate VI.**

- Fig. 1. Nearly fully formed larva of *Clypeaster humilis* (Leske), from the dorsal side; 14 days old. The posterodorsal arms have not yet reached their full size. The amnion has just appeared.  $\times 110$ .
- 2. Same, seen from the oral side, a little from behind. The posterodorsal arms more developed, but not full size, which will be like the postoral arms.  $\times 110$ .
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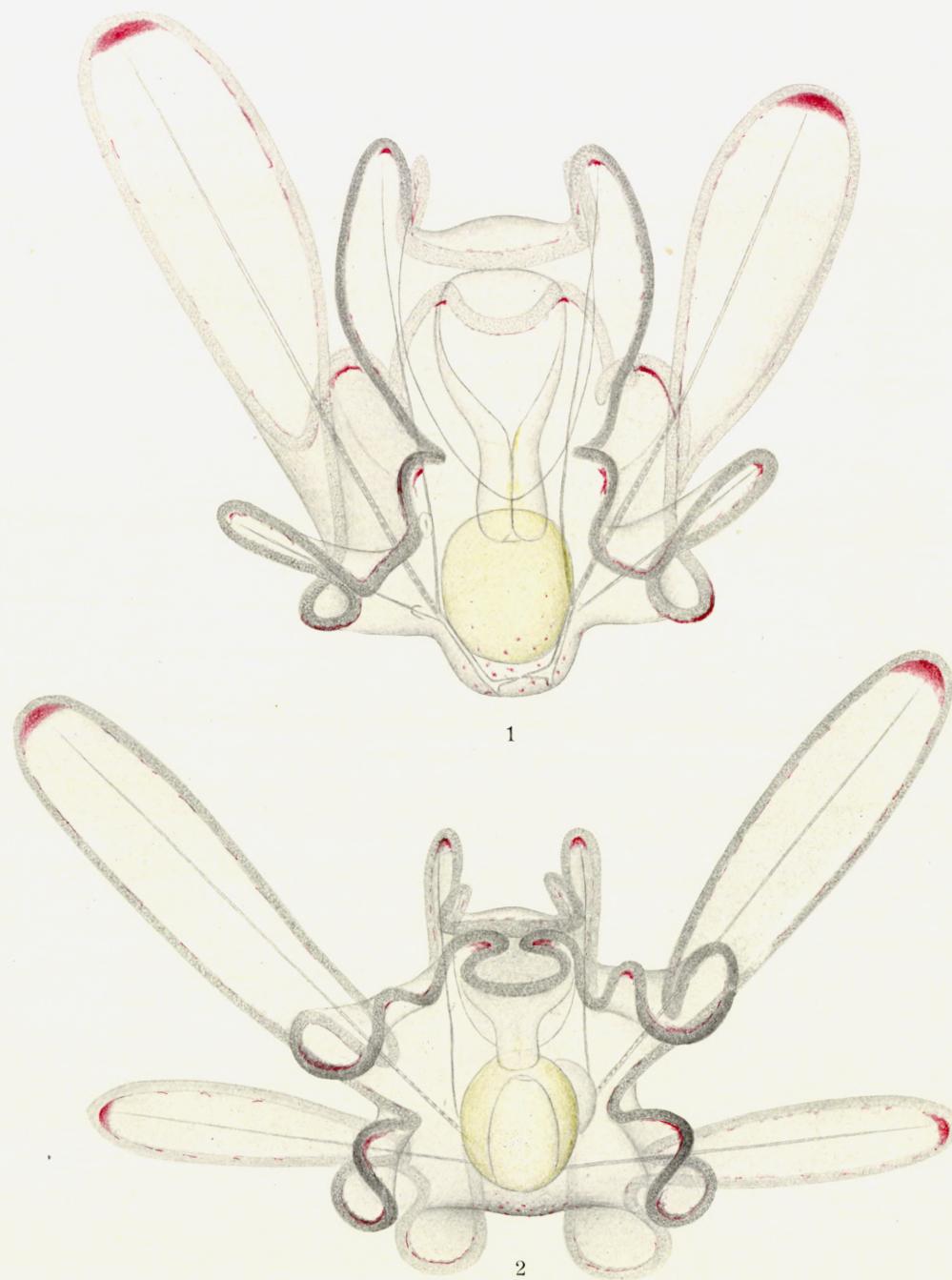
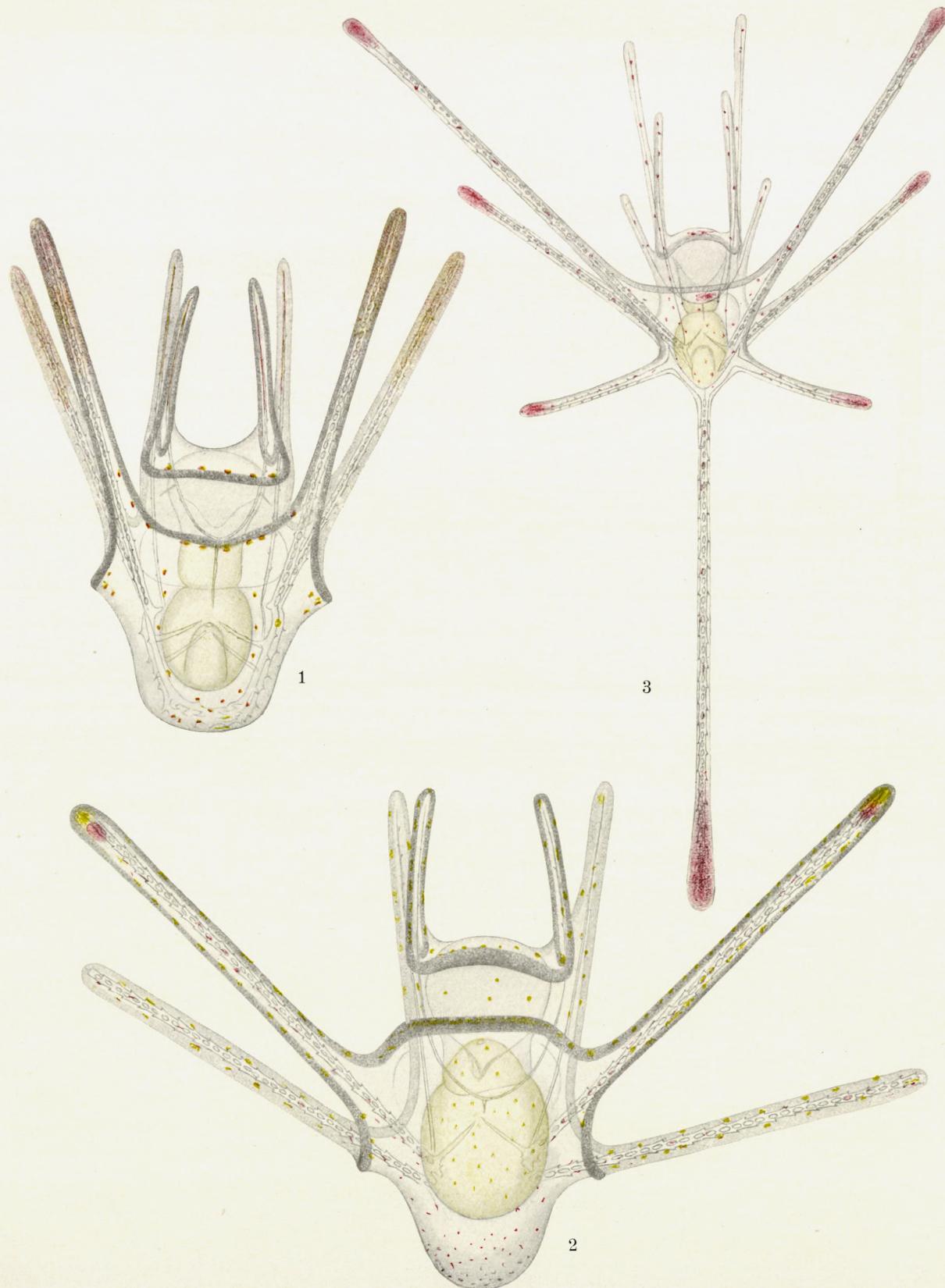


Plate VII.

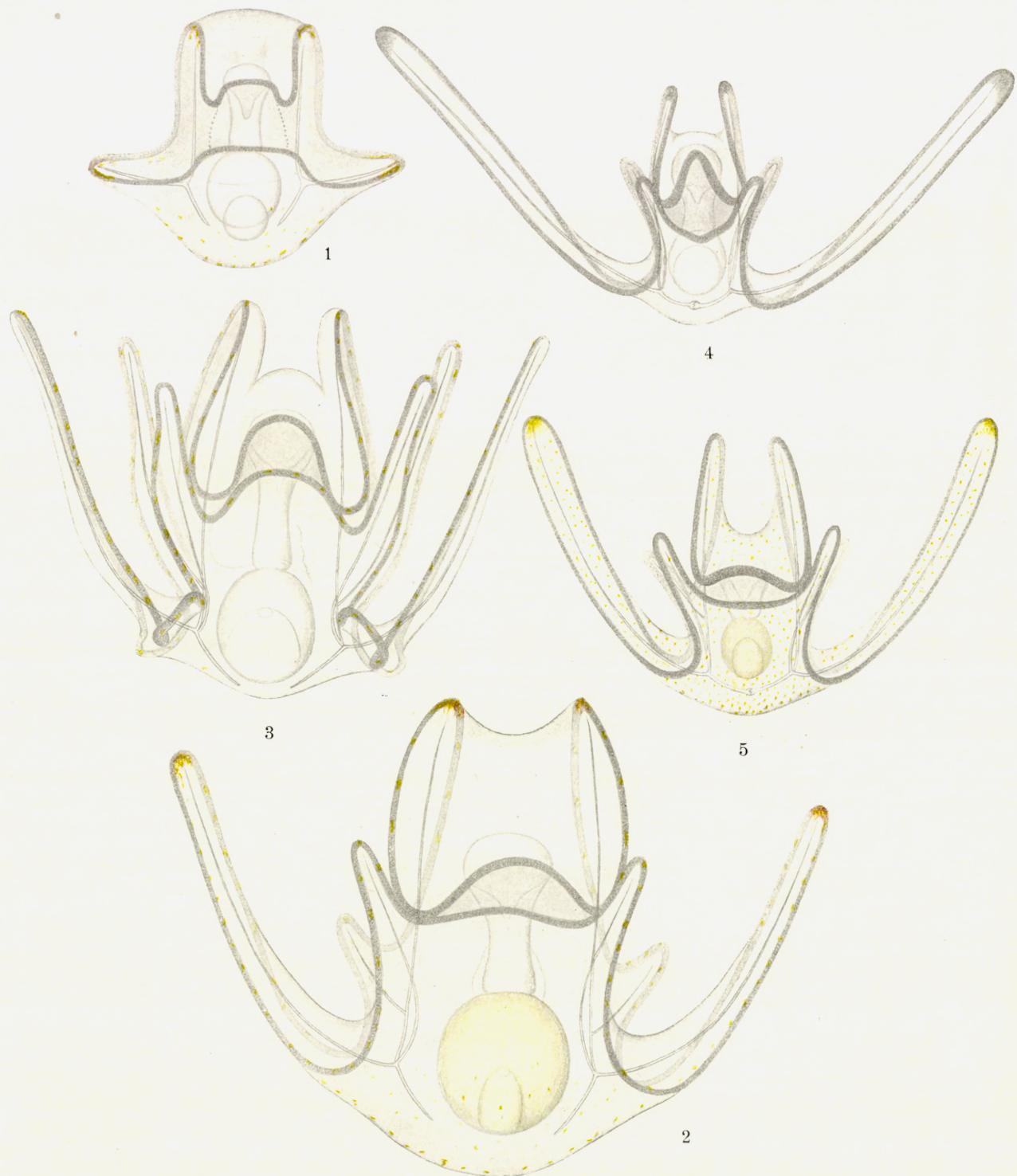
- Fig. 1. Fully formed larva of *Fibularia craniolaris* (Leske), from the oral side. 19 days old.  
× 100.
- 2. Fully formed larva of *Echinodiscus auritus* (Leske), from the oral side. 5 days old.  
× 130.
  - 3. Fully formed larva of *Lovenia elongata* (Gray), from the oral side. 14 days old. × 60.



## Plate VIII.

- Fig. 1. Young larva of *Ophiodoma lineolata* Desjardins (Müll. & Troschel) 6 days old.  $\times 110$ .  
- 2. Same, 18 days old.  $\times 110$ .  
- 3. Fully formed larva of *Ophiodoma lineolata* Desj. (Müll. & Troschel) 5 weeks old; near metamorphosis, the hydrocoel having begun to form lobes.  $\times 80$ .  
- 4. Larva of *Ophiodoma erinaceus* Müll. & Troschel. 5 weeks old.  $\times 80$ .  
- 5. Larva of *Ophiodoma scolopendrina* (Lamarck). 11 days old.  $\times 80$ .

All from the oral side.

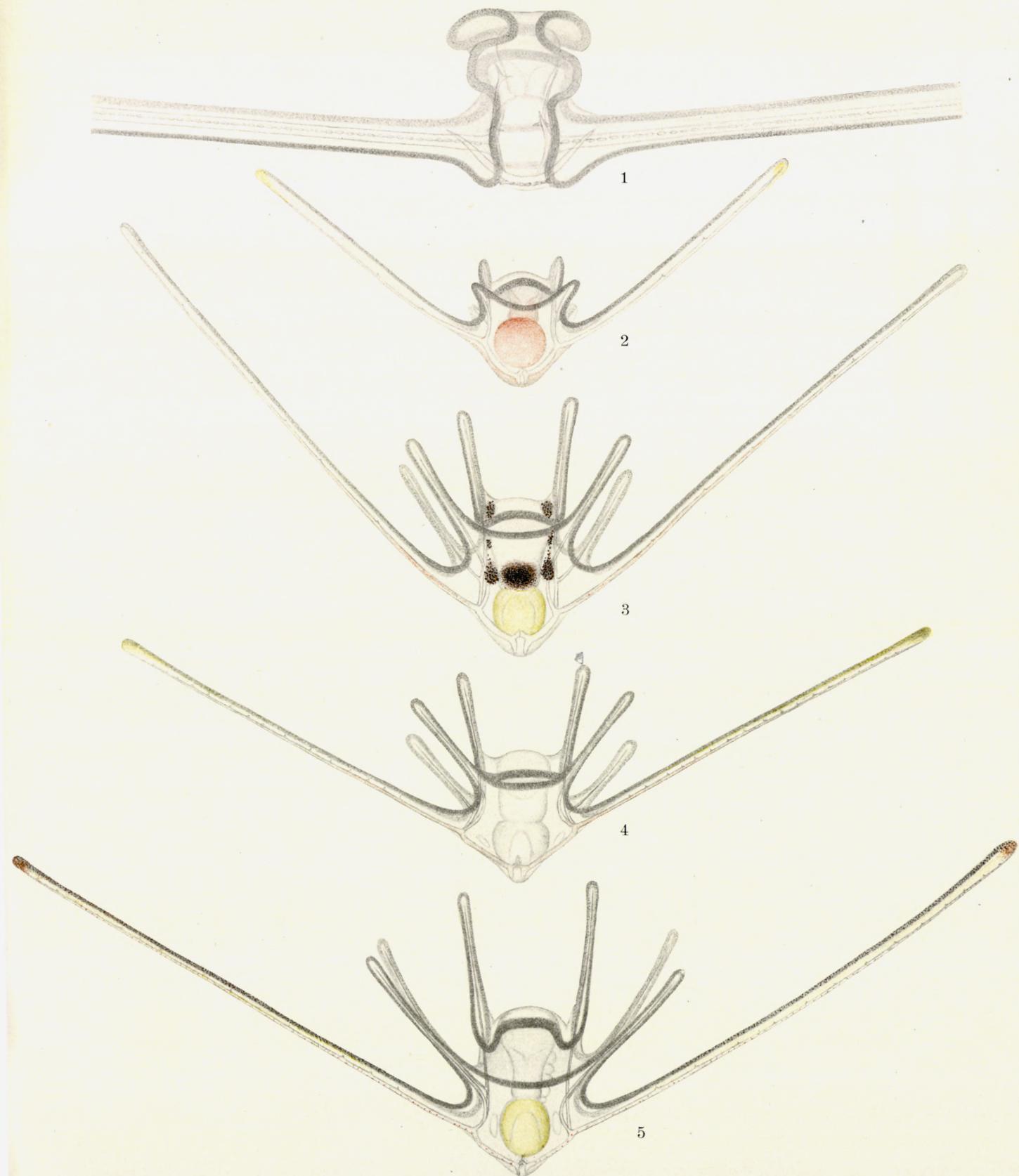


## Plate IX.

- Fig. 1. Fully formed larva of *Diadema setosum* (Leske), from the dorsal side. 30 days old.  
From a preserved specimen.  $\times 120$ .
- 2. Young larva of *Ophiothrix triloba* v. Martens, 4 days old.  $\times 90$ .
  - 3. Fully formed larva of *Ophiothrix triloba* v. Martens, 15 days old.  $\times 90$ .
  - 4. Young larva of *Ophiomaza cacaotica* Lyman, 5 days old.  $\times 90$ .
  - 5. Larva of *Ophiomaza cacaotica* Lyman, 17 days old; in beginning metamorphosis, the hydrocoel having begun to form lobes.  $\times 90$ .

Figs. 2—5 from the oral side.

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**Plate X.**

- Fig. 1. Gastrula of *Temnotrema scillæ* (Mazetti), 22 hours old. The mesoderm pouches beginning to form from the upper end of the archenteron.  $\times 260$ .
- 2. Larva of *Astropecten polyacanthus* Müll. & Troschel, 3 days old; from the oral side. In beginning metamorphosis.  $\times 80$ .
  - 3. Larva of *Astropecten velitaris* v. Martens, 4 days old; from the dorsal side. In beginning metamorphosis.  $\times 80$ .
  - 4. Larva of *Asterope carinifera* (Lamarck), 30 days old; from the oral side. In beginning metamorphosis.  $\times 80$ .
  - 5. Larva of *Astropecten polyacanthus* Müll. & Troschel, 5 days old; in side view. In beginning metamorphosis.  $\times 50$ .
  - 6. Young larva of *Synaptula reciprocans* (Forskål), 4 days old; from the oral side.  $\times 110$ .
  - 7. Larva of *Synaptula vittata* (Forskål), 4 days old; from the oral side.  $\times 110$ .
-

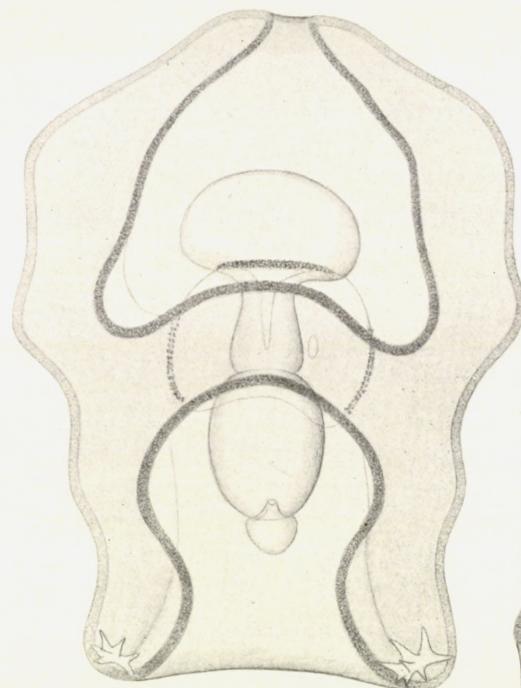


**Plate XI.**

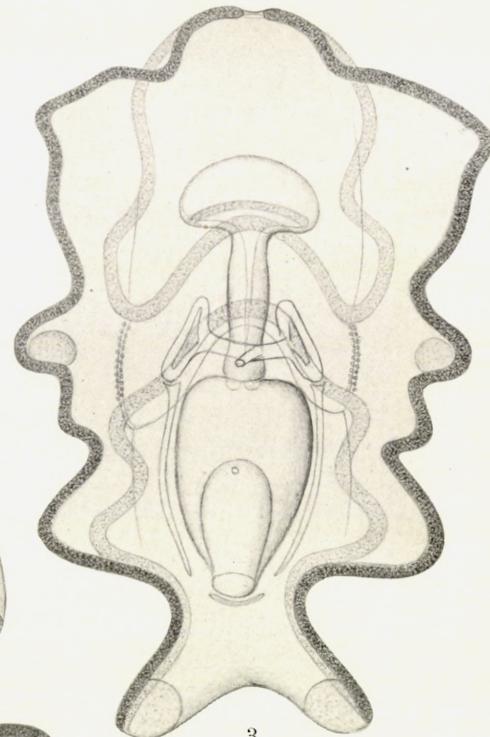
Fig. 1. Young larva of *Stichopus variegatus* Semper, 7 days old; from the oral side.  $\times 200$ .

- 2. Larva of same, nearly fully formed, from the oral side.  $\times 130$ .
- 3. Larva of same, from the dorsal side. Showing double hydrocoel.  $\times 130$ .
- 4. Larva of same, from the dorsal side; in beginning metamorphosis.  $\times 130$ .
- 5. Young Holothurian of *Stichopus variegatus* Semper, just metamorphosed.  $\times 130$ .
- 6. Young larva of *Synaptula vittata* (Forskål), in side view; 11 days old.  $\times 100$ .

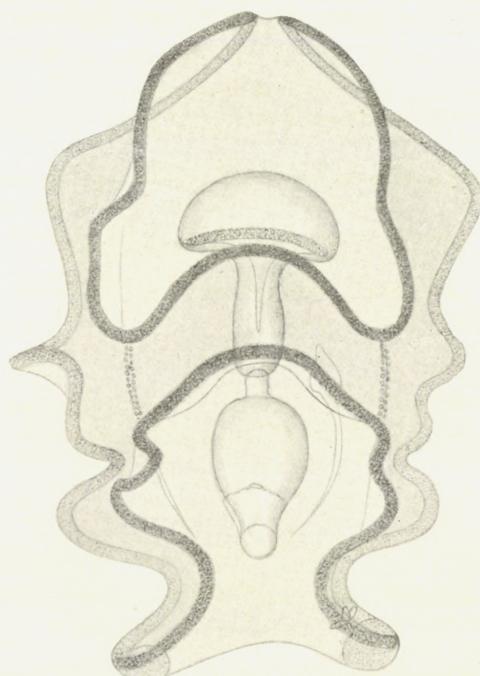
Figs. 2—5 drawn from preserved specimens; exact age unknown.



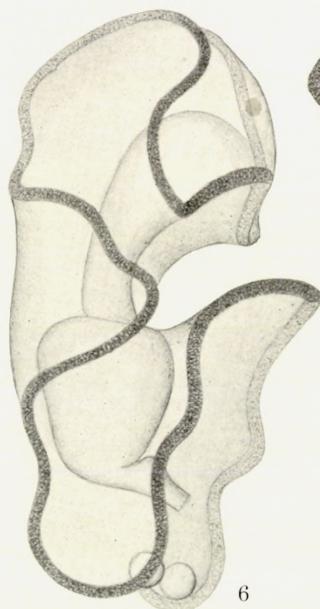
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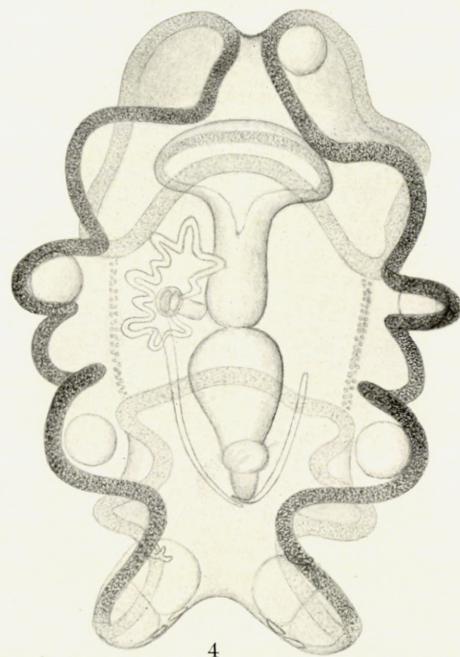
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## Plate XII.

Fig. 1. Larva of *Holothuria scabra* Jäger, 6 days old.  $\times 80$ .

- 2. Same, 18 days old; in beginning metamorphosis. Abnormally with a right hydrocoel.  $\times 80$ .
- 3. Larva of *Holothuria arenicola* Semper, var. *Boutani* Hérouard; 10 days old.  $\times 80$ .
- 4. Same in beginning metamorphosis; 26 days old.  $\times 80$ .
- 5. Larva of *Holothuria (Bohadschia) marmorata* Jäger. 11 days old.  $\times 110$ .
- 6. Same, 10 days old. (From another culture than the larva represented in fig. 5).  $\times 80$ .

All from the oral side.

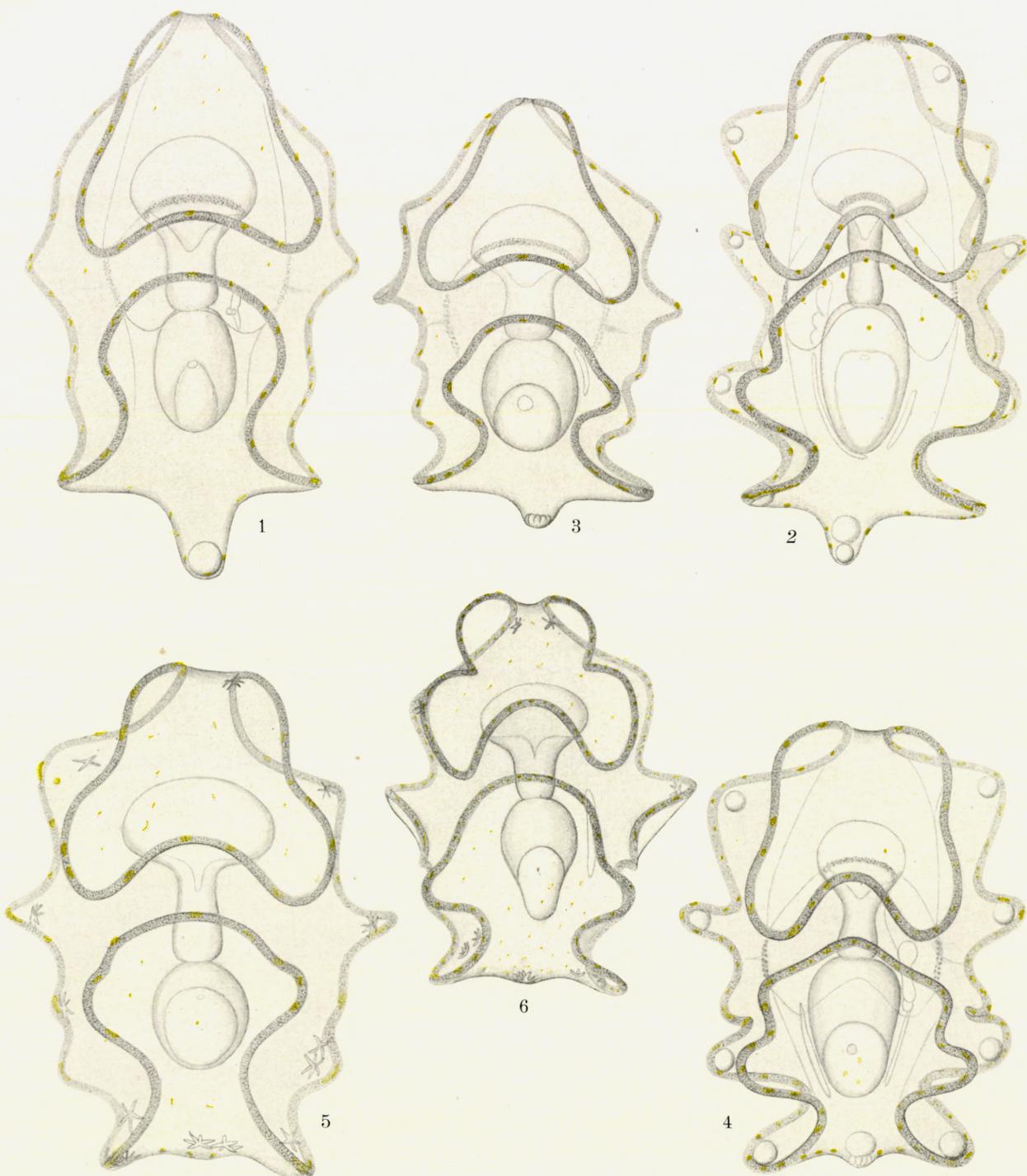
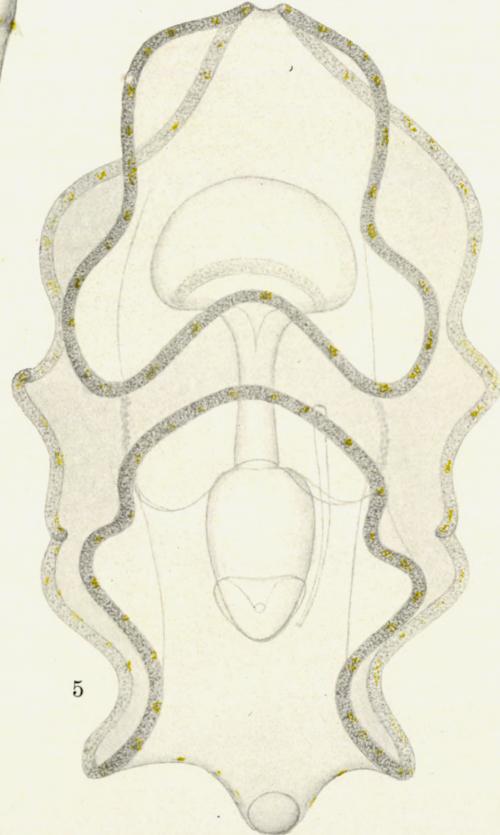
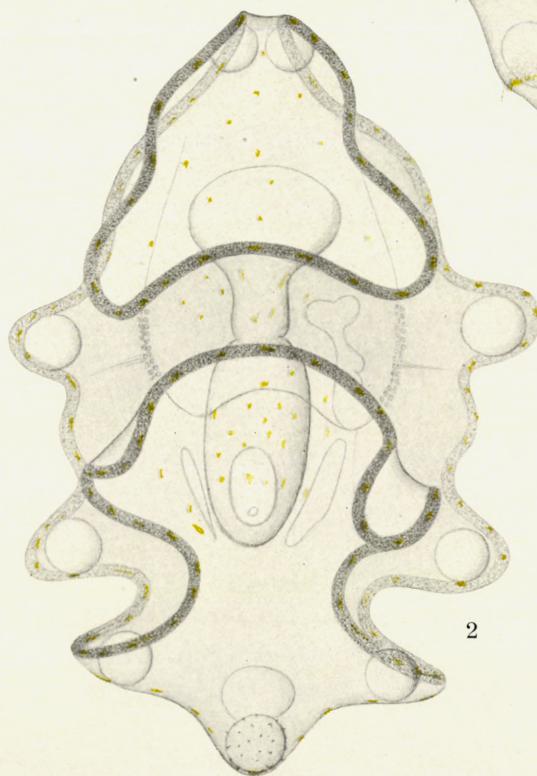
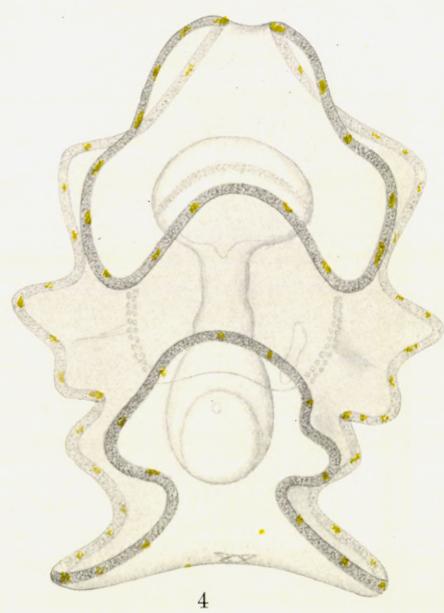
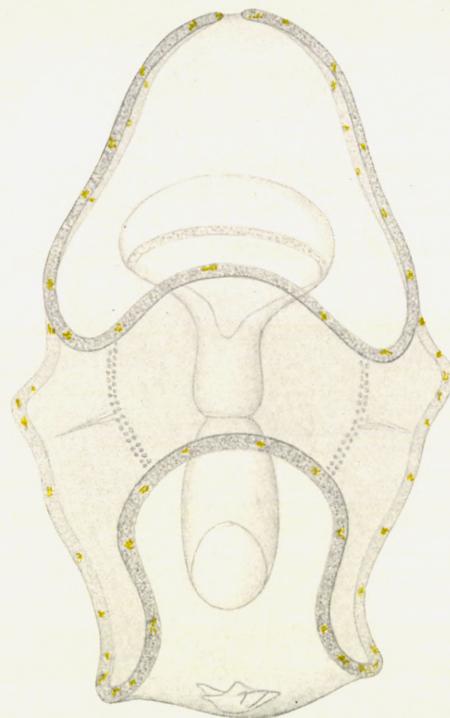


Plate XIII.

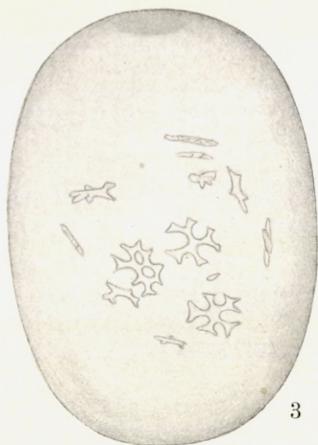
- Fig. 1. Young larva of *Actinopyga serratidens* Pearson, 10 days old; from the oral side.  $\times 125$ .
- 2. Larva of same, 3 weeks old; from the oral side. In beginning metamorphosis.  $\times 100$ .
  - 3. Young Holothurian of *Actinopyga serratidens* Pearson, newly metamorphosed. 26 days old.  $\times 125$ .
  - 4. Larva of *Holothuria mauritiana* Quoy & Gaimard, Var. 8 days old. From the oral side.  $\times 90$ .
  - 5. Larva of *Holothuria spinifera* Théel, 8 days old; from the oral side.  $\times 200$ .
-



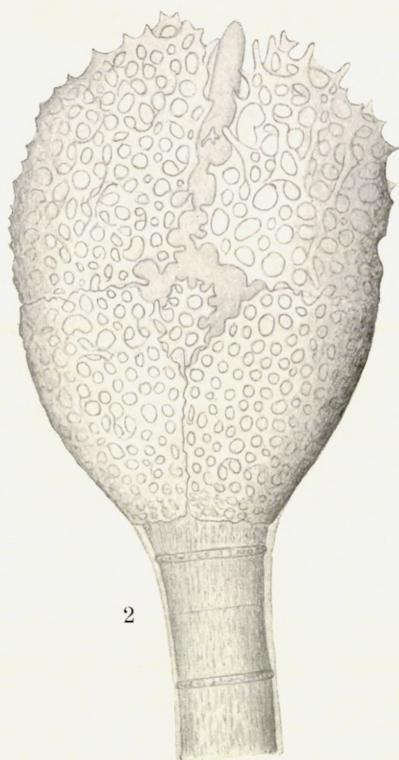
**Plate XIV.**

Fig. 1. Pentacrinoid, 3 weeks old, of *Tropiometra Audouini* A. H. Clark.  $\times 100$ .

- 2. Calyx of another Pentacrinoid of *Tropiometra Audouini*, same age; showing anal plate.  $\times 200$ .
  - 3—4. Embryos of *Lamprometra Klunzingeri* (Hartlaub), 36 hours old, showing development stages of calyx-plates and stalk.  $\times 300$ .
  - 5—7. Young Pentacrinoids of *Lamprometra Klunzingeri*, figs. 5—6 five days old, fig. 7 six days old.  $\times 125$ .
  - 8. Calyx of Pentacrinoid, 18 days old, of *Lamprometra Klunzingeri*, showing the first sacculus and spicules in the primary tentacle, but still no trace of the radial.  $\times 200$ .
-



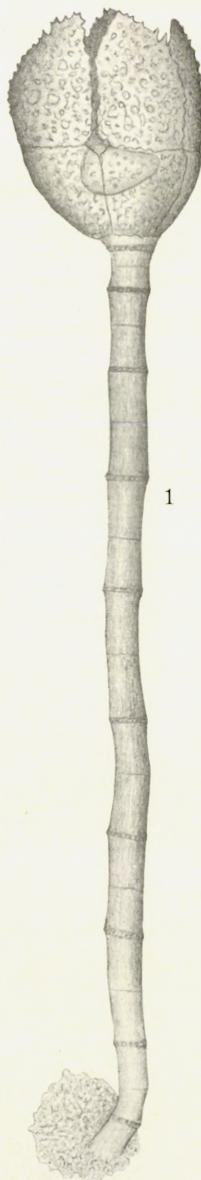
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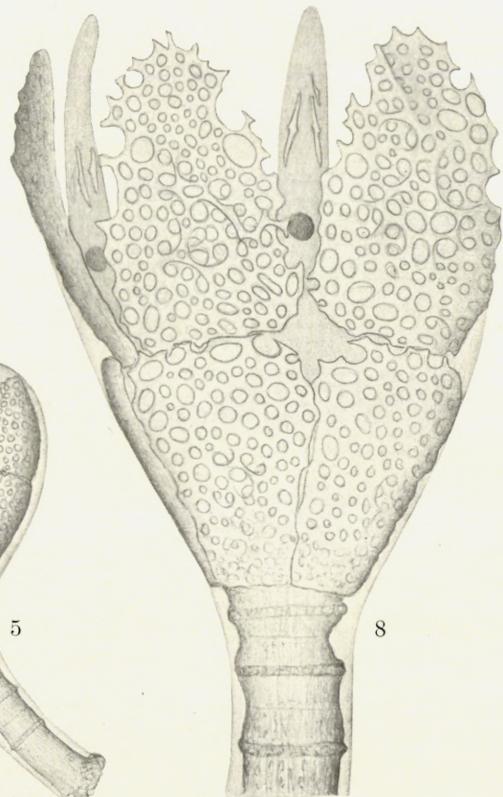
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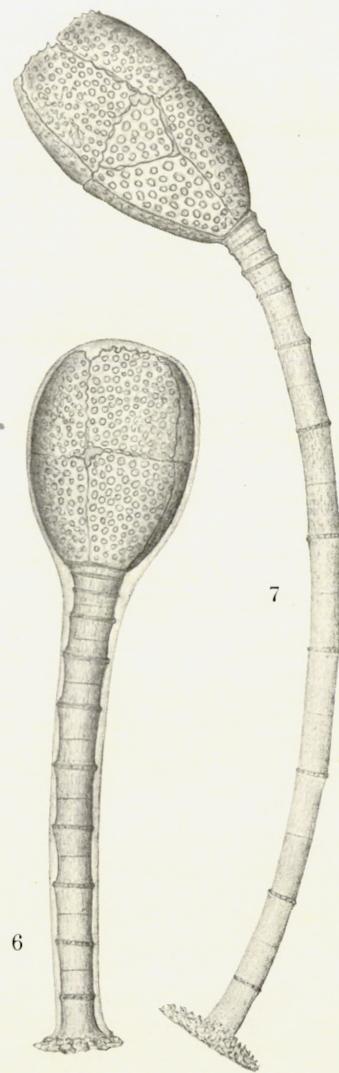
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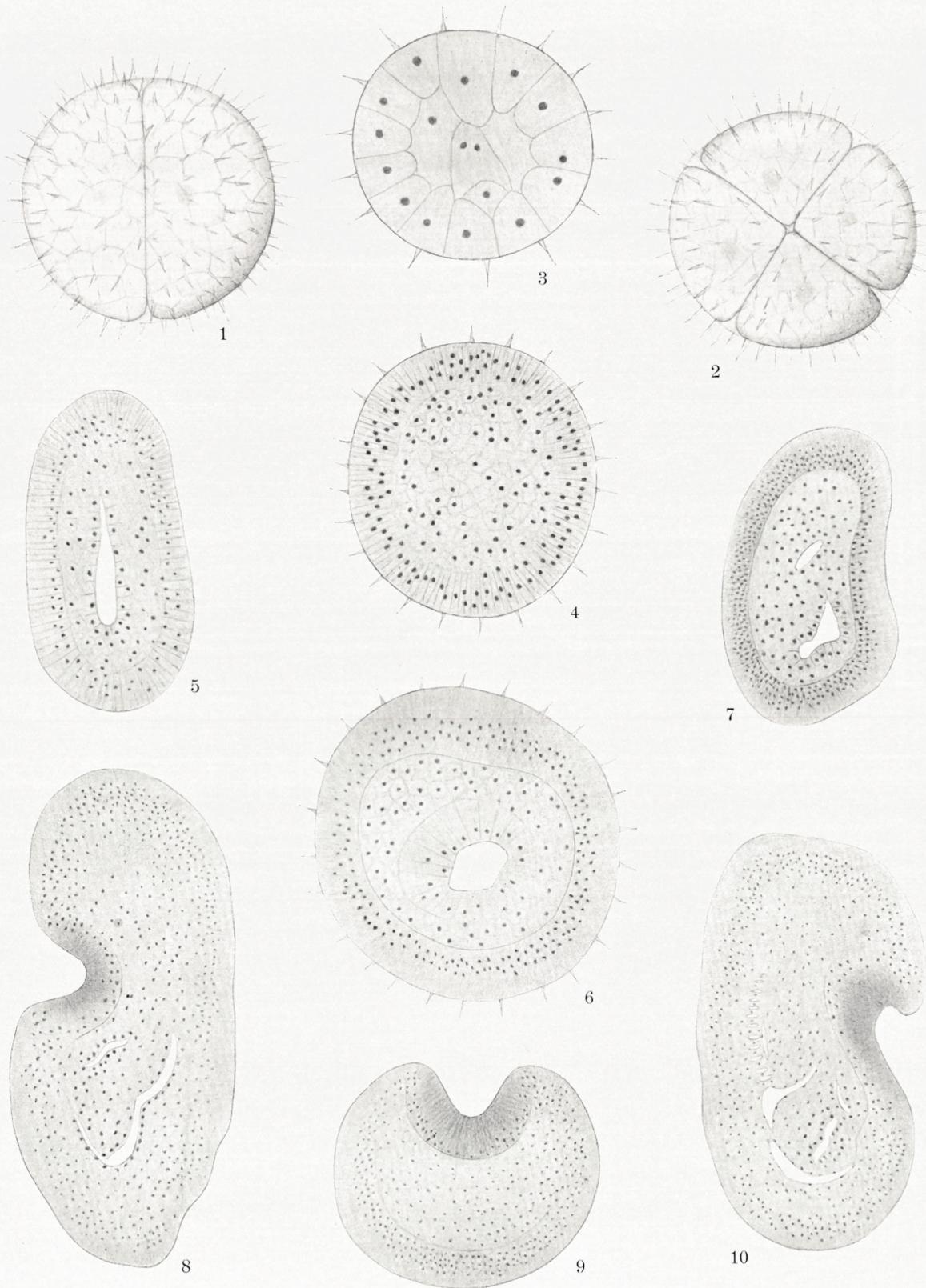
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**Plate XV.**

All figures of *Lamprometra Klunzingeri* A. H. Clark. All  $\times 300$ .

Fig. 1—2. The two first cleavage stages, lying within the thorny egg-membrane; 2 hours old. The nuclei very indistinct, the stain penetrating only with difficulty the egg-membrane.

- 3. Section through embryo 4 hours old, still within the egg-membrane. Shows the blastocoel cavity wholly occupied by cells derived from the ectoderm.
- 4. Section through embryo 10 hours old, still within the egg-membrane. The blastocoel cavity quite filled by numerous mesenchyme cells. No gastrula invagination. Ectoderm not distinctly limited from mesenchyme cells.
- 5. Longitudinal section through a free-swimming embryo, 15 hours old. The gastral cavity has been formed.
- 6. Transverse section of embryo, 15 hours old, still within the egg-membrane. Gastral cavity distinct. The thickening of the ectoderm is either the beginning formation of the vestibulum or of the sucking disk; the impossibility of orientation by sectioning prevents deciding which of the two alternatives is the correct.
- 7. Longitudinal section of an embryo 22 hours old, showing the division of the gastral cavity into an upper and lower part, the former the entero-hydrocoel, the latter the coelomic vesicle.
- 8. Longitudinal section through an embryo,  $1\frac{1}{2}$  days old, with the vestibulum formed. The small cavity below the vestibulum is the stomach, the other cavity the coelomic vesicle, dividing into a right and a left part.
- 9. Transverse section through embryo  $1\frac{1}{2}$  days old, showing vestibulum.
- 10. Longitudinal section through an embryo 3 days old. The vestibulum beginning to close. Beginning formation of the chambered organ.



# Det Kongelige Danske Videnskabernes Selskab.

Skrifter, naturvidenskabelig og mathematisk Afdeling.

## 9. Række.

	Kr. Øre
<b>I</b> , med 35 Tavler .....	30. 50.
1. <b>Ravn, J. P. J.</b> : De regulære Echinider i Danmarks Kridtaflejringer. Med 6 Tavler. 1928 .....	7. 00.
2. <b>Clausen, Hans</b> : On the Crystal Structure of Cryolithionite. With 4 Figures in the text. 1928 ..	2. 25.
3. <b>Boas, J. V. E.</b> : Biologisch-anatomische Studien über den Hals der Vögel. Mit 23 Tafeln und 20 Figuren im Text. 1929 .....	20. 00.
4. <b>Berg, Kaj</b> and <b>Gunnar Nygaard</b> : Studies on the Plankton in the Lake of Frederiksborg Castle. With 6 Plates and 27 Figures in the text. 1929 .....	11. 50.
<b>II</b> , med 30 Tavler og 8 Skemaer .....	23. 25.
1. <b>Wesenberg-Lund, C.</b> : Contributions to the Biology of the Rotifera. Part II. The Periodicity and Sexual Periods. With 15 Plates and 8 Schemata. 1930 .....	20. 00.
2. <b>Bøggild, O. B.</b> : The Shell Structure of the Mollusks. With 15 Plates and 10 Figures in the text. 1930 .....	11. 00.
<b>III</b> , med 1 Kort og 10 Tavler .....	23. 20.
1. <b>Ostenfeld, C. H.</b> : The Distribution within Denmark of the higher Plants. Results of the topographic-botanical Investigation. I. A brief Historical Survey of the Investigation. With one Plate. 1931 .....	1. 40.
2. <b>Jessen, Knud</b> : Samme. II. The Distribution of the Papilionaceæ within Denmark. With nine Plates. 1931 .....	7. 00.
3. <b>Mølholm Hansen, H.</b> : Nørholm Hede, en formationsstatistisk Vegetationsmonografi. Med 1 Kort. With English Summary. 1932 .....	10. 00.
4. <b>Sørensen, William</b> : Descriptiones Laniatorum (Arachnidorum Opilionum subordinis). Opus posthumum recognovit et edidit Kai L. Henriksen. With a Preface and Notes in English and 29 Text-figures. 1932 .....	12. 50.
<b>IV</b> , med 9 Kort og 70 Tavler .....	41. 75.
1. <b>Mortensen, Th.</b> : Contributions to the Study of the Development and Larval Forms of Echinoderms I—II. With Plates I—VII. 1931 .....	9. 80.
2. <b>Brøndsted, H. V.</b> : Bygningen af Snuden og Ansigtsmuskulaturen hos nogle Pinnipedier med særligt Hensyn til Oppustningssækken hos Klapmydsen. Med 12 Tavler. Mit einem deutschen Résumé. 1931 .....	5. 70.
3. <b>Wesenberg-Lund, C.</b> : Contributions to the Development of the Trematoda Digenea. Part I. The Biology of Leucochloridium Paradoxum. With 6 Plates and 7 Textfigures. 1931 .....	6. 25.
4. <b>Mortensen, Th.</b> : New Contributions to the Knowledge of the Cidarids. I—II. With 13 Plates. 1932 .....	10. 00.
5. <b>Nielsen, Niels</b> : Contributions to the Physiography of Iceland. With particular reference to the Highlands west of Vatnajökull. With 32 Plates and 9 Maps. 1933 .....	10. 00.
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BY

MOGENS KØIE

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WITH 9 FIGURES IN THE TEXT, 2 PLATES AND 23 TABLES

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D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURV. OG MATH. AFD. 9. RÆKKE, VII. 2.



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## INTRODUCTION

**T**hough Denmark lies outside the zone of forest-forming coniferous trees, there has, during the 150—200 years in which Denmark has harboured coniferous forests, developed a ground flora very similar to that which occurs where there is a spontaneous growth of conifers.

Though it cannot be said that generally speaking the planting or colonisation of an area with coniferous trees will involve a simplification of the original vegetation, coniferous forests throughout their geographical area of distribution have a ground flora consisting of few but widely dispersed plant communities. The geographical situation has of course some influence on the delimitation of the plant communities; the soil vegetation of the conifer plantations of Denmark shows affinities both with the plant communities which CAJANDER (1909) analysed and described for the south German highland and with the plant communities of the Swedish, Finnish, and Russian coniferous forests, on which an extensive literature has been published. In Denmark it is the edaphic factors which decide to which of the vegetations of these two areas the ground flora of the coniferous forests is most closely allied.

The presence in Denmark of a ground flora differing from that of spontaneous coniferous forests is due to the fact that the coniferous trees in Denmark are forced, so to speak, to grow where they are planted, and this may be on soil where a natural competition with foliiferous trees would lead to the destruction of the conifers. This applies to the good soil; the poorest soil on which forests are planted will not, even though the forest can only be maintained by forestal care, have an essentially different soil vegetation from that known from territories covered with natural forest.

By far the greater part of the Danish conifer plantations consists of *Picea exelsa*, *Pinus silvestris*, and *Pinus montana*, though *Abies pectinata* has also a fairly wide distribution. It is only of recent years that various other coniferous trees have begun to be planted on a larger scale, and these are not included in the present study. Nor has the ground flora of the larch forests been investigated here. Whenever coniferous forest is mentioned in the sequel, indeciduous forest is always implied.

The forestal treatment of woods causes greater changes in the life conditions of the soil vegetation than occur in natural forests. Hence the vegetation does not always achieve stability, but will contain elements which are either relicts from a previous plant community or new immigrants. What plant community will dominate with a certain constellation of environmental factors will in part depend on how

quickly the character plants are able to immigrate, and how long they take in attaining the development necessary for the characterisation of a plant community. This time differs widely; it is longest for the sub-shrubs and the lichens, brief for *Deschampsia flexuosa* and for mosses, which appear very quickly and form a population in places where they find favourable life conditions. Though I have as far as possible kept to the stable plant communities, there are, therefore, several cases where the phanerogamic vegetation, owing to its slow rejuvenation, has not yet attained the development which it will probably attain later under the conditions at hand.

In woods under forestal care the light conditions on uniform soil will differ, though they will be uniform over larger areas, so that better opportunities are afforded for the study of the influence of light on the ground vegetation than in natural forests, where the density of the crowns of the trees is often dependent on the condition of the soil.

None of the forests investigated stands on high moor soil, but otherwise I have sought as different soils as possible. A conspectus of the localities from which vegetation analyses are at hand appears at p. 55.

There exist but few works dealing with the vegetation of Danish coniferous forests. WARMING (1916—19) gives a number of species lists from more or less purely coniferous forests and mentions some of the most conspicuous plant communities; and BORNEBUSCH (1925) has attempted to apply CAJANDER's forest types mentioned below to Danish coniferous forests. Finally OLSEN (1921) has investigated the succession of the vegetation in cleared coniferous forests.

CAJANDER's works are of fundamental importance for the modern plant-sociological investigation of coniferous forests (the most important (1909) being those on the S. German highlands and on Finland (1921)). CAJANDER's researches have led to the erection of a series of forest types, the chief of which are the *Cladina*, *Calluna*, *Vaccinium*, and *Myrtillus* types. An *Oxalis* type has been set up, too, but it would seem to occur under *Abies pectinata* only, or where there is an admixture of foliiferous trees.

From Sweden there is a work by HESSELMAN (1926), which describes, in connection with investigations on nitrogen and acidity, a series of analyses of the soil vegetation of conifer forests, carried out by the same method as that adopted by me.

A survey of the forest types of the Soviet Union is found in SUKATSCHEW (1928, 1932).

The present treatise is based on a prize essay submitted to the University of Copenhagen and awarded the gold medal of the University in 1935.

I should like here to express my thanks to the Rask-Orsted Foundation for a grant which has rendered possible the translation into English of the present work, and to Botanisk Rejsefond and Japetus Steenstrup's Legat for financial aid towards the work in the field.

To Professors KNUD JESSEN and C. RAUNKIÆR I owe a debt of gratitude for much good advice during the final working up of the treatise.

### Analysis of the Plant Communities.

For the analysis of the vegetation RAUNKJÆR's circling method (1909) was adopted. After a floristically and physiognomically uniform test area had been selected, 20 circles of 0.1 sq. m each were marked off along a straight line at equal distances from one another, generally 1 m. If the stump of a tree was within a circle it was skipped. The occurrence of all vascular plants and mosses, and of the chief lichens was noted for each circle, and stated in percentage occurrence in all circles from the test area. To be regarded as occurring within the circle, the plant in question must have either a basal shoot, or a basal petiole, or a perennating shoot apex within the circle.

All the chief species except *Rubus idaeus* and *Pteridium aquilinum* have such a degree of density that, where they form typical plant communities, they occur in all the circles, i. e. their frequency percentage ( $fr\%$ ) is 100. A plant is said to be a frequency dominant when its  $fr\%$  exceeds 80. The limit has been made so low in order to secure a margin for irregularities in the structure of the plant community.

A concept analogous to frequency is constancy (DU RIETZ 1930, p. 433, BEGER 1932, 485). While the  $fr\%$  conveys an idea of the distribution of the species within a test area, the constancy percentage ( $k\%$ ) is a means of expressing the variation within a plant community, the  $k\%$  showing in how many of all the test areas, in which the same plant community occurs, the species are present in at least one of the circles. Since 20 circles of 0.1 sq.m. each were examined in each test area, the constancy shows in how many per cent a species occurs within an area of 2 sq.m. A species is said to be constant when its  $k\%$  exceeds 80. A survey of  $k\%$  for a number of species will be found at p. 29 (Table 1).

### Plant-sociological Terminology.

The nomenclature proposed by DU RIETZ (1930, p. 307 ff.) has been adopted for the designation of the plant communities. The smallest plant-sociological units into which it has proved convenient to divide the soil vegetation of conifer forests are termed sociations. A sociation is defined on p. 307 as a stable plant community of an essentially homogeneous composition of species, that is to say, at least with constant dominants in each layer; and a dominant is a species "which alone or in company with one or more almost as dominant species forms the bulk of the vegetation in its layer"<sup>1</sup>.

<sup>1</sup> In my opinion, a division into layers which does not refer absolutely to the relative height of the species entering into a plant community can only serve to create confusion. In DU RIETZ's remark (1930, p. 387) that in *Loiseleuria-Cetraria nivalis* sociation an upper layer (Feldschicht, *Loiseleuria*) may lie embedded in a lower layer (Bodenschicht, *Cetraria*) it is not the height which has been decisive. It is of course of interest that the *Cetraria* layer, which is most frequently the lower one, may also be the upper one, but this is not expressed by this use of the term "layer" instead of, for instance, population, and the division into layers becomes unjustified in plant-sociology. On this principle one might with equal propriety refer *Hedera helix* and *Lonicera periclymenum* to the shrub or forest layer when they creep among the herbs of the forest-soil.

By the character species of a sociation are meant species which have formed the basis for its erection, and which enter into the name of the sociation. Hence the character species are constant dominants, but most sociations possess other constant dominants which it would be inconvenient to include in the name of the sociation.

A species is said to form a population when it constitutes an essential part of the vegetation. The term says nothing as to the importance of the species for the systematics of the plant community.

When a plant community is designated in the sequel by two species, one of which is placed in parenthesis, the two sociations are meant of which one is designated by the two species, and the other by the species not placed in parenthesis; thus *Deschampsia-(Scleropodium) soc.* means the *Deschampsia* sociation + the *Deschampsia-Scleropodium* sociation.

For the vascular plants the same systematic names have been adopted as in RAUNKLÆR (1934). The nomenclature of the mosses accords with C. JENSEN (1915, 1923) and that of the *Cladonia* species with MØLHOLM HANSEN & LUND (1929).

### The Systematic Grouping of the Plant Communities.

In the systematic grouping the principle has been adopted of disregarding the taxonomic position of the dominant species. In practice several mosses must occupy a subordinate position as character plants compared with the phanerogams (except *Deschampsia flexuosa*) owing to their occurrence in the greater part of the soil vegetation of coniferous forests. Only where these widely dispersed species form independent populations have they been used as a basis for the erection of sociations. Even though environmental factors have not been directly employed as indicators in the division of the plant communities into sociations, by the above procedure species which are closely associated with certain constellations of environmental factors within coniferous forests will primarily be used as character plants.

The figures in the vegetation tables will not show in all cases to what plant community a sociation individual belongs. It applies to the mosses especially that the deviation is often too small for the quantitative composition to be read from the frequency percentages.

The tree population does not enter into the systematics of the plant communities, but is merely treated as the creator of the environmental conditions which the trees offer the soil vegetation by their species, density, etc.

For the sake of clearness I have chosen to divide the soil vegetation of conifer forests into as few sociations as possible, and in my opinion a further subdivision would in most cases serve no purpose. However, more extensive investigations may perhaps show the justification of distinguishing for instance a *Luzula pilosa* sociation, or of dividing the *Empetrum* sociation into an *Empetrum-Hylocomium parietinum* sociation and an *Empetrum-Scleropodium* sociation.

### The Nomenclature of the Soil.

For the characterisation of the upper layers of the soil which are mixed with humus I have adopted the nomenclature proposed by HESSELMAN (1926, p. 204 ff.). In many instances it is, however, impossible to distinguish between "råhumus" and "mår". Hence I have used the term "peat" for HESSELMAN'S "råhumus" + "mår", and have only employed "raw humus" where it is indubitable that the humus layer deserves this designation, that is to say, where the humus layer is interwoven with fungal hyphae and roots to a felty mass (fibrous peat).

The term "surface soil" denotes the upper layer of soil admixed with humus, washed-down humous particles being, however, left out of consideration. The subsoil is the unmixed mineral soil.

*Rubus idaeus* grows in soil which, compared with other soils under conifers, must be designated as good. This designation is unsatisfactory from a general ecological point of view, since it only tells us that the edaphic-ecological factors are at their optimum for the greatest number of species. The facts are too complicated to be expressed numerically, even though the pH value of the soil gives us some information of its quality. To obtain some holds for a characterisation of the soil beyond what can be directly observed, a characterisation which at the same time furnishes some information of the edaphic-ecological relationship of the species entering into the soil vegetation of conifer forests, I will call such soil suitable for a species on which the species may be supposed, with a probability bordering on certainty, to be willing to form populations in some state of the remaining ecological factors. The soil, for instance of a test area covered with *Thuidium tamariscifolium*, is thus said to be suitable for *Rubus* if a change in the tree population may lead to a forest climate which will permit *Rubus* to form a stable population.

### Light Measurement.

For the light measurements the method with WIESNER's hand insulator evolved and fully described by BOYSEN JENSEN (1932) was used.

The principle of the method is that sensitive paper in order to darken to a certain standard tone requires a time corresponding to the intensity of the light. The generally accepted law that the intensity of light required for the same darkening of the photometric paper is inversely proportional to the time of exposure does not apply to the paper used. The adjusting showed that to a fourfold increase in the light intensity corresponds a darkening period 3.522 times as short. Hence to estimate the relative light intensity, "*i*"<sup>1</sup>, in a forest it is necessary, instead of directly calculating the percentage of the time of exposure, to convert this into absolute light intensity (expressed in  $k \times \text{lux}$ , where  $k$  is a constant characteristic of the standard tone) by means of curves constructed on the basis of the factor found, and to calculate "*i*" from this.

<sup>1</sup> "*i*" is used by RÜBEL (1928) as a term for the light percentage.

In dark forests the difference is very considerable. If for instance the period of illumination in the open is 1 % of the period of illumination in the forest, the light percentage will in reality be 0.69. To 10 % in time corresponds an i-value of 8.15.

Since it must be taken for granted that the rays important for the CO<sub>2</sub> assimilation determine the light minimum of a plant community, that is to say, the red yellow rays in particular, the paper was made especially sensitive to these by treatment with Rhodamin-B. But since Rhodamin-B paper, too, is somewhat sensitive to blue rays a red yellow filter was further used (filter glass 1 mm thick from Schott & Gen., Jena, F 21707 EK 50).

So as not to cut off the light the isolator was held at arm's length. The time was measured by a stop watch. The measurement over the area tested was made during even movement — walking or running — and I endeavoured to expose the isolator to the light in the sunny spots during the length of time due to them according to the area they occupy. Each measurement was repeated once or several times, and the results generally agree very well, especially for the lower i-values, nor are the deviations in relation to the light percentages very large for the lighter areas. To determine the full daylight it was necessary to take the average of several measurements, because the darkening of the photometric paper to the light standard tone employed in order that the measurements in the dark forests should not be too time-consuming, was arrived at in a very short time, in extreme cases 10 seconds, hence it was difficult to measure. The measurements in and outside the forest were made directly after one another. In dark forests, where a single measurement may take more than an hour, the full daylight was measured before and after it, and the average value used in the calculation of "i".

The light percentage in forests depends in various ways on the light conditions in the open. The light percentage falls with the decreasing height of the sun as a result of the fact that at a low height of the sun the crowns of the trees allow a smaller percentage of the sunbeams to reach the forest soil, and the sunlight constitutes 60—70 % of the total amount of light at full daylight.

If the full daylight diminishes because the sun is covered by clouds, the light percentage is higher than when the sun is uncovered.

Information as to the light percentage gathered from the literature shows that other photometric methods than that employed by me give corresponding results. On measuring diffuse light SALISBURY (1916, p. 94) found an increasing light percentage in oak forests in the course of the spring until leafing occurred. FEHÉR (1929, p. 43) found a light percentage in a fir forest varying between 30 % and 55 % in the course of the year, with the minimum in January and the maximum in June. At p. 37 the same author has a curve of the light percentage in a pine forest where a distinct increase is seen on rainy days, that is to say, when the sun is covered with clouds.

The influence of the above-mentioned factors on the light percentage varies with the varying density and height of the trees. Hence it is understandable that no

table of corrections can be made. In order to make the light measurements comparable, the determinations, with a few exceptions, were made in sunlight between 9 and 3 o'clock, but around the solstice between 8 and 4 o'clock. This arrangement of course involved the giving up of a number of measurements, but because the sunlight was particularly abundant during the two summers the investigation was in progress, it was possible to adhere to it without any great loss of i-values.

Besides insisting on a relative stability I have also demanded a uniform development of the plant community over a fairly large area, rarely less than 400 sq.m. By choosing such a large test area I obtained the most satisfactory light measurements, the intensity of the light over a small test area being too largely dependent on the momentary position of the sun. Where the investigation of environmental factors other than light intensity was of importance it was in certain cases necessary to reduce the demands in respect of the size of the test area.

## Determination of the Hydrogen-Ion Concentration of the Soil.

### Sampling.

In the present investigation the actual acidity only has been determined, i. e. the concentration of free hydrogen ions present in the soil extract.

Most peat plants have the greater part of their roots in the lower stratum of the peat which rests with a sharply defined limit on the mineral soil. Since acidity as an ecological factor is of course most important for the roots I have chosen to take the samples in the lower part of the peat, though only where the thickness did not exceed 8—10 cm. In places where there is not an actual peat formation the consistent application of a definite principle is more difficult. In such places the roots often penetrate far down into the subsoil, and the humus layer is more or less mixed with the subsoil. In most instances, however, there will be a layer, a few centimetres thick, of almost pure humus, and it is from this that the samples of soil have been taken for the determination of the acidity. Such a procedure renders it possible to obtain some pH values from the rhizosphere of some of the phanerogams occurring in this soil (*Oxalis*, *Asperula*, *Milium*).

From each test area three measurements were as a rule made, each comprising 3—4 mixed samples of soil. A sample was thus taken for about every second circle. The pH values from the subsoil, however, are derived from a single sample taken in all instances at a depth of 15—20 cm.

By far the greatest number of samples were measured in the fresh state on the same day that they were taken, but in some cases the measurement could not be made till later on; the samples were then dried in the air and kept in paper bags. The change in the pH caused by drying and keeping is stated by most authors to be very slight for acid soil (ARRHENIUS 1926, HESSELMAN 1926, JENNY 1926, FRANK 1927, HOSS 1932).

### Method of Measuring the Acidity.

In measuring the acidity the electrometric method with kinhydron was used. The apparatus employed (Betriebs-Ionometer nach Trenel) was in the shape of a box and proved excellent for work in the field. The extraction was made in flasks of a capacity of 100 c.c. They were filled three parts with soil, and the smallest possible amount of distilled water was added, only so much as was necessary to decant the c. 10 c.c. used for the measurement.

The time of extraction for the fresh samples was at least one hour, extraction longer than this proved quite unnecessary. An extraction time of 24 hours in the few experiments I made with it showed no great difference and no particular tendency; nor was this to be expected, since the samples are mostly damp at the outset. The dried samples, on the other hand, need a longer time for extraction; I used at least three hours. On preservation for some length of time in an ordinary glass there is a risk of pH undergoing a change in a basic direction (ZOLLITSCH 1927, p. 138).

Corrections for temperature up to 18° were made according to a table fixed to the apparatus. This is of importance in measurements with kinhydron, especially for the study of the acidity requirements of the plants here considered, their deviations in pH being very small. A difference of for instance + and - 8° will cause a difference of + and - 0.13 for pH 4.00.

If the second decimal in the pH value exceeded 4 it was increased to the next tenth.

In the course of the investigations the accuracy of the "Ionometer" was tested several times, and it always showed a pH value agreeing very closely with that given for the standard fluid.

The pH values obtained by this method are somewhat lower than those obtained by the colorimetric method and by the electrometric determination of the acidity of a soil filtrate; for in the pH determination of a soil suspension the physiologically active hydrogen ions loosely connected with the soil particles are measured in addition to the free ions (PALLMANN & HAFFTER 1933).

### Abbreviations and Conspectus of the Plant Communities.

The following abbreviations have been used for some frequently mentioned species:

<i>Brach.</i>	= <i>Brachythecium curtum</i> .
<i>Clad.</i>	= <i>Cladonia impexa</i> .
<i>Desch.</i>	= <i>Deschampsia flexuosa</i> (= <i>Aira f.</i> ).
<i>Dicr. scop.</i>	= <i>Dicranum scoparium</i> .
<i>Eur. prael.</i>	= <i>Eurhynchium praelongum</i> .
<i>H. par.</i>	= <i>Hylocomium parietinum</i> (= <i>Pleurozium Schreberi</i> = <i>Hypnum S.</i> ).
<i>H. prol.</i>	= <i>Hylocomium proliferum</i> (= <i>H. splendens</i> ).
<i>Loph. het.</i>	= <i>Lophocolea heterophylla</i> .

<i>Plag. dent.</i>	= <i>Plagiothecium denticulatum</i> .
<i>Rubus</i>	= <i>Rubus idaeus</i> .
<i>Scl.</i>	= <i>Scleropodium purum</i> (= <i>Pseudoscleropodium p.</i> ).
<i>Ster.</i>	= <i>Stereodon cupressiformis</i> var. <i>ericetorum</i> (= <i>Hypnum c.</i> ).
<i>V. myrt.</i>	= <i>Vaccinium myrtillus</i> (= <i>Myrtillus nigra</i> ).
<i>V. vit.</i>	= <i>Vaccinium vitis-idaea</i> .

A survey of light percentages will be found at p. 41, of the thickness of the peat at p. 44 (Table 2), and of pH at p. 48 (Table 3 and 4).

Below we give a list of the plant communities investigated, with references to the vegetation tables and the page at which they are described.

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<i>Rubus</i> — <i>Brachythecium</i> — <i>Geranium Robert.</i> soc.	I, 12—15	13
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<i>Vaccinium myrtillus</i> — <i>V. vitis-idaea</i> soc.	V, 3	18
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<i>Calluna vulgaris</i> soc.	VII, 8—19	20
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	Table	Page
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Cladonia impexa soc. ....	XIII, 1—9	28

## Description of the Plant Communities.

### *Asperula odorata*—*Oxalis* soc.

Table I, 2.

This typical plant community of foliiferous forests only occurs very rarely under coniferous trees. It appears here on particularly damp soil under *Picea excelsa*, forming a zone round a ditch. The layer of moss does not cover the ground, the dominant species is *Eurhynchium striatum*. *Oxalis* here attains its most luxuriant development in the coniferous forest. The immediate vicinity bears an extremely luxuriant *Rubus*—*Brach.* soc. with *Stellaria glchidosperma*, *Milium effusum*, and some *Asperula* (Table I, 4—5).

Light intensity 9.17 %, pH 5.07. The humus layer is typical mould, the subsoil but slightly sandy.

### *Melica uniflora* soc.

Table I, 1.

The *Melica* soc., too, is ecologically closely allied to the *Rubus*—*Brach.* soc. Well-developed specimens were only found at Sonnerup under *Picea excelsa* where *Melica* forms very dense growths at a higher light percentage than the surrounding *Rubus* populations. *Eurhynchium striatum* forms a dense carpet.

The humus layer takes the shape of a sharply delimited layer with a granular structure. Here *Melica* has all its roots. pH is the highest measured in peat, on the average 5.07, and it is no doubt due to the high pH that *Brach.* which forms the moss layer in the *Rubus* populations is here replaced by *E. striatum* as in the *Asperula*—*Oxalis* soc. Close to this soc.-individual there occurred a feebly developed *Asperula* soc. on peat.

### *Urtica dioica* soc.

Table I, 3.

*Urtica* enters into several *Rubus* soc. individuals and is altogether ecologically closely allied to *Rubus*. The soc. individual here described is on a level with and close to the *Rubus*—*Brach.*—*Geranium Rob.* soc., but with more light. The roots of *Urtica* are found in the humus layer which is very loose and mouldlike. The average pH is 4.27.

### *Rubus idaeus*—*Brachythecium curtum* sociations.

Table I, 4—17.

These sociations were met with almost exclusively under *Picea excelsa*. The reason is that they only develop on soil of such a nature that *Picea excelsa* is con-

sidered the most profitable of the coniferous trees in a forestal respect. Table 1 gives the  $k\%$  of some species in the sociations. Compared with the other plant communities pH is high, viz. 4.40. From the table it will be seen that the light percentage may be as low as 4.28.

The sociations may be naturally divided into sociations with *Oxalis* and sociations with *Deschampsia*, but it will be necessary to set up a third sociation for the sociation individuals from Sonnerup, because *Oxalis* has not immigrated into this isolated wood, and because the composition of the vegetation is here otherwise somewhat different.

#### Rubus idaeus—Brachythecium—Oxalis soc.

Table I, 4—11.

*Oxalis* is vigorously developed, and *Brach.* forms a continuous carpet. *Eurhynchium praelongum*, which shows a very strong affinity to *Brach.* and is presumably never absent where *Brach.* forms a population, has a  $k\%$  of 88. *Mnium rostratum* here attains its most vigorous development within coniferous forests with a  $k\%$  of 100. *Scl.* too occurs constantly but always with a low frequency percentage.

The sociation individual richest in species is No. 4 which contains many mould plants, such as *Asperula odorata*, *Stellaria glochidisperma*, *Urtica*, *Brachypodium silvaticum*, and *Milium effusum*. In this pronouncedly hemicryptophytic community the hemicryptophyte moss *Mnium undulatum* occurs with a frequency percentage of 100. (All other mosses forming populations in coniferous forests are chamaephytes).

Where the light allows, *Milium* may form an essential part of the sociation. In No. 5, at a light percentage of 7.5, it showed distinct signs of the want of light and was almost sterile, in No. 6, at 18.3 % light, it was extremely well developed.

At 4.28, the lowest light percentage, *Rubus* is stunted for want of light and does not become the frequency dominant.

The humus layer is everywhere mould-like, under *Milium* it is typical mould. *Rubus* has the greater part of its roots in this, at any rate quantitatively; the roots of all the rest of the phanerogams only rarely penetrate to the sub-soil.

Sociations were only found in older growths on somewhat clayey moraine sand and in sheltered situations. All the analyses given are derived from North Sealand, but the sociation does not seem to have any geographical limits in Denmark; it has been found for instance in Bromme plantation at Sorø and at Aunsbjerg between Viborg and Silkeborg.

#### Rubus idaeus—Brachythecium—Geranium Robertianum soc.

Table I, 12—15.

This sociation was only met with in Sonnerup. It differs from the preceding sociation by the absence of *Oxalis* and by the presence of *Geranium Rob.* as a dominant, in addition to some other therophytes, especially *Galium aparine* and *Stellaria media*

pH is higher than in the *Rubus*—*Oxalis* sociation, and the light percentage is very low, ranging from 4.57 to 5.82.

The humus layer is of a peaty consistency. The subsoil consists of coarsely alluvial sand with a pronounced podsol profile.

### ***Rubus idaeus*—*Brachythecium*—*Deschampsia flexuosa* soc.**

Table I, 16—17.

*Deschampsia* enters into the sociation as a character plant. However, it differs from the rest of the *Rubus* sociations by being less rich in species and by the presence of several of the species which characterise soil of less dispersion than that on which *Rubus* is usually found. These species are *Lophocolea bidentata*, *Ster.*, *H. par.*, *Galium harcynicum*, and *V. myrt.* The soil is the same as that on which the *V. myrt.* sociation may be found, but somewhat moister, which is the reason why *Dryopteris* occurs. Though physiognomically rather prominent, *Dr. dilatata* has only a low frequency percentage.

The humus layer is peaty.

CAJANDER mentions a plant community showing great agreement with this one from *Picea excelsa* and *Abies pectinata* forests in the South German highlands. It is regarded as a subtype of the *Myrtillus* type, bordering on the *Oxalis* subtype, but it does not contain *Oxalis*. In northern forests in Sweden and Finland *Rubus* seems to occupy a subordinate place in the soil vegetation.

### ***Oxalis acetosella* soc.**

Table II, 2—11.

The *Oxalis* sociation is often developed on soil suitable for *Rubus* at a low intensity of light. It attains its best development under *Abies pectinata*, or where there is a growth of foliiferous trees, but *Oxalis* may form populations together with *Brach.* in pure *Picea excelsa* growths (6—8). In the rest of the sociation individuals under *Picea excelsa* leaf-bearing trees were present, in No. 10 in the form of a fairly luxuriant growth of *Sambucus nigra*; in Nos. 5 and 9 there were beeches so near by that the soil was manured by their leaves. It is hardly by chance that *Brach.* and other mosses are absent from these sociation individuals. Mosses cannot grow in situations where they are covered by broad leaves, though the leaves of *Rubus* seem to form an exception, probably because of their rapid decomposition.

In addition to *Brach.* the mosses especially represented are the three very shade-tolerant forms *Eur. prael.*, *Loph. het.*, and *Plag. dent.* *Thuidium* and *Dicranum majus* occur now and then.

The nearness of foliiferous trees diminishes the importance of the i-values as a basis for comparison with pure coniferous plant communities. The following values are from a pure population of coniferous trees; 1.73 (No. 7), 1.74 (No. 2), 4.15 (No. 3), 5.28 (No. 6), 8.20 (No. 11), 9.32 (No. 8).

The humus layer is mostly somewhat mixed with the mineral soil. Under *Abies pectinata*, however, it is always a typical mould layer, consisting of a layer of dark brown crumbling mould, a few centimetres thick, under a thin layer of needles. In this *Oxalis* has all its subterranean parts.

The acidity is subject to great fluctuations, varying between 3.5 and 5.6. Even within the same test area the deviation in a single instance amounts to 0.9 (No. 9), which is the greatest divergence in pH measured within a single sociation individual. *Oxalis* attains its best development at the highest pH values. A particularly high acidity is found in No. 6, where the subsoil down to at least 1 metre's depth was greasy bog soil with a pH of 3.5. The other sociations analysed were found on more or less clayey moraine deposits.

The Finnish *Oxalis*- and *Oxalis—Myrtillus* type contains leafbearing trees in greater or smaller numbers. From Germany the *Oxalis* sociation is mentioned as a subtype of the *Oxalis* type (CAJANDER 1909, p. 24). The tree population here consists mostly of *Abies pectinata*.

#### **Deschampsia flexuosa—Oxalis soc.**

Table II, 1.

In the *Oxalis* sociation *Desch.* is only rarely found and the specimens are feeble. On the other hand, *Oxalis* is occasionally found in *Desch.* sociations. In the sociation individual analysed *Desch.* was so weak compared with *Oxalis* and *Brach.* that it is most nearly allied to the *Oxalis* sociation. The sociation was somewhat exposed to wind and probably stable. The lower part of the peat layer was black and granular in structure, the upper part more like raw humus. Most of the roots of *Deschampsia* were in the upper part of the peat.

#### **Oxalis—Thuidium tamariscifolium soc.**

Table III, 7—8.

*Thuidium*, on account of its strong vegetative propagation, forms a dense carpet on the forest soil. *Brach.* and *Thuidium* are the only mosses forming populations with which *Oxalis* can successfully compete for room. In Table III, 7—8 the results of the analysis of the *Oxalis—Thuidium* sociation are given. The sociation links up with the *Oxalis* sociation individual in Table II, 3.

Apart from the fact that No. 7 was considerably richer in moss than No. 8 the sociation individuals showed great resemblances in spite of the considerable difference in the thickness and nature of the humus layer. In No. 7, under *Abies pectinata*, there occurred *Hylocomium lorenii* and *Plagiochila asplenoides*, the latter, however, only where the soil was almost devoid of humus. *Polytrichum attenuatum* has a frequency percentage of 70, but is very poorly developed. In No. 8 under *Picea excelsa* the humus layer consisted of peat of a thickness of 5—12 cm. *Mnium rostratum* was the frequency dominant here.

**Thuidium—Polytrichum attenuatum soc.**

Table III, 6.

Of mosses *Polytrichum* alone, on account of its deviating growth form, is able to become the frequency dominant as well as the physiognomical dominant in a *Thuidium* carpet. *Polytrichum* carries its underground parts right down into the mineral soil, and multiplies by means of rejuvenation shoots from there.

**Thuidium tamariscifolium soc.**

Table III, 1—5.

The sociation is very pure. *Thuidium* is only present on moraine suitable for *Rubus* and *V. myrt.* and requires rather a large amount of moisture, but the light intensity in the *Thuidium* sociation is too low for phanerogams to thrive; it ranges from 0.82 to 4.24 %.

In Nos. 1 and 4 *Mnium undulatum* occurred, but only where the humus layer was thin. Its stolons are always found in the mineral soil.

*Thuidium* is indifferent to the acidity and the nature of the humus, it may even grow directly on mineral soil. In No. 1 *Thuidium* formed a zone round places which were covered with water in the winter. *Senecio silvaticus* was the only plant occurring in the dry depressions.

**Brachythecium curtum soc.**

Table IV, 3—14.

*Brach.* is one of the most widely occurring mosses in coniferous forests. Where it forms an independent sociation it covers the forest soil with an even but not always quite continuous carpet.

Grass does not occur in the sociation, and other phanerogams are scarce. The most frequent species are *Oxalis* and *Lactuca muralis*. As everywhere where *Brach.* forms populations there is a constant occurrence of *Eurhynchium praelongum*. *Loph. heterophylla* and *Scl.* are of common occurrence in the sociation, though generally with a low frequency percentage. Of rare occurrence as essential elements are *Mnium rostratum*, *Plag. dent.*, and *P. undulatum*; *Ster.* may become the frequency dominant, but as a rule it is poorly developed. *Thuidium* occurs fairly often.

The light intensity is low, varying between 0.96 and 6.66. The lightest sociation individual, No. 7, forms a transition to the *Oxalis* sociation.

The humus layer is thin throughout. The variations in its thickness are given in Table 2. The humus is always peat and may be developed as a pronounced raw humus abundantly interwoven with the hyphae of fungi. The sociation is fairly independent of the subsoil and acidity, but it does not occur on the driest sandy soil. It may be found homogeneously developed in places where the subsoil passes from clayey moraine sand into turf in overgrown lakes, and it also occurs on blown sand where the moraine does not lie very deep down.

The *Brach.* sociation occurs almost exclusively in fir woods, but it may also be found under *Abies pectinata* (No. 5).

KUJALA (1926, p. 22) mentions *Brach.* as one of the most frequent and most abundant forest mosses in Finland on fresh soil in fir woods.

### Vaccinium myrtillus sociations.

Table V.

The forestal treatment of the wood rarely allows *V. myrt.* to form populations in coniferous forests. The species only grows on moraine deposits, where the soil is of such a kind that the trees often give too much shade. The lowest i-value measured was 20.9. At much lower i-values it does not form populations, but it may occur in small groups or in scattered specimens in areas with a light percentage of down to about 4.

*V. myrt.* has the lowest pH of the phanerogams, the average being 3.73, with a minimum and a maximum of 3.4 and 4.3. OLSEN (1921, p. 63) found it at pH 3.5 to 3.8.

The peat below *V. myrt.* is loose but interwoven with its numerous stolons and as a rule with the plant structure preserved. It is in great part formed by *V. myrt.* itself. *V. myrt.* has all its roots in the peat and it probably never occurs as a pioneer in mineral soil.

*V. myrt.* would seem to have a rather intensive generative propagation, rapidly colonising localities suitable for *V. myrt.* as soon as the light becomes favourable. In Denmark it seems to be an obligatory shade plant, but it is not dependent on the trees. Thus it will form small but stable populations in the shade of rocks and will successfully compete with *Calluna* on slopes with a northern exposure.

In other localities, for instance in the Alps, it will form dense growths above the tree line both on slopes with a northern and with a southern exposure, though the intensity of the light is there much greater than in Denmark; but in such localities *Calluna* is poorly developed and but little fit to compete with it. Hence it is most probable that it is the competition with *Calluna* which makes it appear as if *V. myrt.* cannot tolerate undiminished light in Denmark.

The *Myrtillus* type, which is a somewhat more comprehensive concept than *V. myrt.* sociations, is one of the most widely distributed of CAJANDER's forest types. It is particularly abundant on moraine in the southern half of Finland (CAJANDER 1921, p. 35) and over most of the Scandinavian peninsula.

### Vaccinium myrtillus soc.

Table V, 4—9.

*Desch.* is constant and well developed, wherever *V. myrt.* does not occur in such dense growths that it shuts out the light. Now and then *Luzula pilosa*, *Majanthemum* and *Trientalis* are met with. Other phanerogams are rare. *Scl.* and *H. par.* form a well-developed layer of moss, though usually only one of the species is well developed in the same sociation individual. *Dicr. rugosum*, *H. prol.* and *Ster.* occur constantly but with low frequency. *Dicr. scop.* often finds good growth conditions (low pH).

**Vaccinium myrtillus—Vaccinium vitis-idaea soc.**

Table V, 3.

The sociation was only met with on moraine gravel in the neighbourhood of Silkeborg, and must be supposed to be rare. It only differs from the *V. myrt.* sociation by the presence of *V. vit.* In more northerly regions, on the other hand, the two *Vaccinium* species often occur together.

**Pteridium aquilinum—V. myrtillus soc.**

Table V, 1—2.

Well-developed sociations were only met with on soil suitable for *V. myrt.*—*V. vit.* near Silkeborg. *Pteridium* requires much light, 28—30 % were measured, and below that i-value it occurs scattered but does not form populations.

The pH values tell us nothing about the acidity requirements of *Pteridium* since its rhizomes and roots are in the sub-soil. I have observed on several occasions that *Pteridium* develops its leaves earliest in the year in the most shady situations.

**Vaccinium vitis-idaea and Empetrum nigrum sociations.**

Table VI.

*V. vit.* and *Empetrum* are often closely allied in an ecological respect. They are both facultative shade plants which may form populations in full daylight under other edaphic conditions. In forests they only occur in part of the area where the environmental factors are favourable to them. This is connected with the great difficulty they experience in generative rejuvenation, a difficulty especially marked in places with a dense carpet of moss (KUJALA 1926, p. 15 and 33), the sole situations where the species find life conditions in coniferous forests. Once they have immigrated they form dense populations by vegetative propagation. The difficulties of immigration are plainly apparent to the observer who notices one of the fairly frequent instances where one of the species forms a single luxuriant clone in a large homogeneous area. The stolons of *V. vit.* grow about 10 cm. annually (KUJALA 1926, p. 14), those of *Empetrum* show a similar growth, so that a clone of, for instance, 10 m. in diameter must be at least 50 years old. Though it turns out that the plant has good growth conditions, no new individual has immigrated during this period, a long one, especially if we consider the frequent changes to which Danish forests are subject.

*Empetrum* requires more light than *V. vit.* and is more resistant to drought. The differences are not very great. The fact that *Empetrum* is most frequently found in forests in moister situations than *V. vit.* has nothing to do with their relative capacity to withstand moisture. For they are both found in bogs in far moister situations than in forests. The most considerable ecological difference lies in the acidity requirements of the species. As will be shown later, it is pH which determines at what degree of moisture the species occur in the forest. Expressed in pH the difference is small, *V. vit.* has an average pH of 3.83 (3.3—4.5) while that of *Empetrum* is 4.02 (3.7—4.4),

and the sociations in which they are character species have pH 3.80 and 4.03 respectively.

KOTILAINEN (1928, p. 65) found the same relation between the acidity of the two species in bogs.

#### Vaccinium vitis-idaea soc.

Table VI, 7–15.

Phanerogams other than the character species occur but sparsely. *Carex arenaria* may become the frequency dominant and *Desch.* often occurs, but in very feeble specimens. In one instance only (No. 14), where the soil came very near to being suitable for *V. myrt.*, was it found as a frequency dominant. On the other hand, the moss carpet is always exceedingly luxuriant. It often attains a thickness of 15 cm. *H. par.* constitutes the chief part; only in one of the sociation individuals analysed was *Scl.* the physiognomical dominant. *Dicr. rugosum*, *D. scop.*, *H. prol.* and *Ster.* are constant, and *Bleph.* often occurs; but all these mosses together occupy a modest place compared with *H. par.* Lichens rarely occur. Throughout, the sociation has a very homogeneous character.

The lowest i-value for the sociation is 7.5, but at so low a light percentage it is etiolated. Here the density of the shoots is so small that in spite of even spreading it only barely attains a frequency percentage of 100. Under more favourable environmental conditions the shoots may stand very close together; their density depends exclusively on the environmental conditions, for where two or several clones adjoin, the density of shoots will be the same in their common area as in the single clone.

The peat has often a magnitude of 6–8 cm. *V. vit.* is considered one of the most peat-producing plants. It seems strange that a plant with so slow a growth and such a small leaf-fall — its leaves are bi- or triennial — should have any essential influence on the production of peat. *Carex arenaria* could with equal justice be called peat-producing. It is beyond doubt that it is the mosses which produce the peat, and as a matter of fact, it has quite the same appearance as the *H. par.*-peat.

The roots of *V. vit.* are most commonly found at the lower edge of the peat, but where this is particularly thick (e. g. No. 11), they do not go so deep. They do not penetrate into the mineral soil. In several cases I have found a layer of black plastic peat, up to 12 cm. thick, without roots, under the moss peat in younger forests on the heath; the pH values were very low in this layer (3.5–3.6–3.6). It was quite evidently the heather peat which was here preserved, whereas this is rarely demonstrable in *H. par.* sociations in the same localities. It is presumably more probable that *V. vit.* finds the best life conditions in such places than that it should be able to conserve the heather peat. The heather peat is not included in the peat thicknesses given. A layer of hard pan up to 22 cm. was met with under the sociation.

The *V. vitis-idaea* soc. is found on very sandy subsoil only. In some few instances it forms colonies on moraine gravel, but its main area is the Jutland heaths. It also occurs on blown sand, principally where the moraine lies deep down (Svinklov, Blykobbe, Tisvilde, Hornbæk).

In more northerly regions *V. vit.* is far less exclusive in its requirements than in Denmark. It is of common occurrence in all the Finnish types of coniferous forests (ILVESSALO 1922, p. 22), whereas, according to ADAMSON, it has a smaller edaphic-ecological amplitude in the Pennine range than *V. myrt.*

### **Empetrum—Vaccinium vitis-idaea soc.**

Table VI, 5—6.

This sociation is most like the preceding one and forms a transition to the

### **Empetrum nigrum soc.**

Table VI, 1—4.

*Empetrum*, where it forms independent populations, is associated with fairly moist sandy soil. A fact connected with this is that *Scl.* is mostly the physiognomical dominant, completely taking over the part of *H. par.* in *V. vit.* sociations. *Calluna* occurred in all the sociation individuals analysed, but otherwise the floristic composition was the same as in *V. vit.* sociations. The separate sociation individuals will be discussed in more detail in a later section (p. 33).

### **Calluna—Empetrum soc.**

Table VII, 2—7.

Where *Empetrum* grows in company with *Calluna* its requirement of moisture is much less than where it forms independent sociations, it will even grow on the driest gravel in company with *Cladonia impexa* (No. 7).

The *Calluna—Empetrum—Clad.* sociation is highly reminiscent of the high northern "tall heath", but the latter is also found on much better soil than in Denmark (TAMM 1920, p. 169).

### **Calluna vulgaris soc.**

Table VII, 8—19.

In Denmark *Calluna* rarely forms stable sociations in forests; it requires too much light to do so (see p. 40). By far the greater number of analyses of *Calluna* populations have as a matter of fact been made to investigate the succession and ecological relationships of the plant communities.

Nos. 2—4 and 14 are probably stable. At the low light percentage in 3 and 14 (13—14 %) it suffers distinctly from want of light and has to share the space with *Carex arenaria*, and at 27 % also (No. 4) it does not attain as vigorous a development as in full light. It is difficult to decide which of the other sociation individuals would be preserved unchanged if the light conditions did not change.

*Desch.* occurs scattered, only forming populations where *Calluna* has recently immigrated after clearing (No. 18). *Dicr. scop.* and *H. par.* are constants, but the reason why *H. par.* often occurs in very small numbers is the ephemeral character of the plant community (see under Succession). *Ster.* occurs in all the sociation

individuals, and mostly in abundance. *H. prol.* often occurs, and here, as usual, it is closely associated with *Scl.*

*Calluna* has the same pH requirements as *Empetrum*, the mean value being 4.01 (3.5—4.7) for the sociations and 4.03 (3.7—4.4) for the species.

The heath peat differs from peat formed of moss by being black and structureless. The subsoil is always podsolated, but a formation of hard pan only takes place on particularly sandy soil.

#### **Deschampsia flexuosa sociations.**

Where *Desch.* forms stable populations it is nearly always sterile. At a light percentage exceeding c. 12—15 it may, however, flower, but never as luxuriantly as where it occurs as a "ruderal plant" after clearing. Stability and fertility are inversely proportional, the ratio being quite independent of the nature of the soil.

In coniferous forests *Desch.* has perennial above-ground stolons and might thus be classed among the chamaephytes; but the apices of the shoots are protected in the winter by a layer, often very thick, of its own leaves and of moss which, biologically, acts as a layer of soil. In several places I have seen that the shoots in the winter were not only covered by the green leaves from the same year, but the withered leaves from last year, too, lay as a continuous layer over the apices of the shoots.

*Desch.* is the most shade-tolerant grass. It forms populations at i-values ranging from c. 7 to 100. While it may thus occur at almost all light intensities, its moisture amplitude is rather narrow. The pH variation curve for the species is given in fig. 8. As will appear, *Desch.* is closely associated with peat with a pH around 4.0. Its pH border values are 3.5 and 4.9 (165 measurements), and its dispersal is very small — though not compared with that of other peat plants. OLSEN (1921, p. 79) found the same average value for the species.

*Desch.* always grows in a layer of peat. Only rarely do its roots penetrate to the subsoil. In thick layers of peat they do not reach the lower part of the layer. Where stable, it is a pronounced peat-producing plant.

CAJANDER (1909, p. 64 ff.) mentions plant communities with *Desch.* as the dominant as a sub-type of the *Myrtillus* type (Southern Germany). It contains much more *Polytrichum* than the Danish *Desch.* sociations (cp. BORNEBUSCH 1925, p. 210). In the north *Desch.* seems to be of less importance.

#### **Deschampsia—Scleropodium purum soc.**

Table VIII.

The sociation is one of the most widely distributed in Danish coniferous forests, and occurs on nearly all kinds of subsoils. *Scl.* may be very vigorously developed, particularly in moist depressions in dunes, and *Desch.* forms a dense carpet and is almost solely prevalent among the phanerogams. *Trientalis* may be the frequency dominant, and *Oxalis* too may become a frequency dominant without being a relict.

Of constant occurrence are *H. par.* and *H. prol.* but always of low or moderate frequency, while *Lophocolea bidentata*, *Dicr. scop.*, and *Ster.* are common. *Thuidium* only occurs in sociation individuals which also harbour *Oxalis*. Lichens never occur.

The thickness of the peat is seen to vary between 2.5 and 11 cm. The peat may vary a good deal in structure. In many cases there is a distinctly preserved plant structure, in other instances the structure is granular, and both may occur within the same test area.

#### **Deschampsia flexuosa soc.**

Table IX, 1—11.

The distinction between this sociation and the preceding one is in some instances somewhat casual. *Scl.* is a constant but with low frequency. Where *Desch.* is so luxuriant that *Scl.* does not form populations for want of space or light, we are in reality concerned with a sociation corresponding completely to the typical *Desch.—Scl.* sociation, but under conditions where *Desch.* has such growth facilities that it supplants *Scl.* which it otherwise protects.

The chief difference in the composition of the vegetation, besides that given in the designation of the sociations, is the constant presence of *Ster.*, often as the physiognomical dominant, among the mosses. In No. 1 *Lycopodium annotinum* forms a dense population.

The i-values are on the average somewhat higher than in the *Desch.—Scl.* sociation, and the thickness of the peat as a rule lies 2 cm. higher. For the *Desch.—(Scl.)* sociation the average pH is 4.02 (3.5 to 4.9).

The sociation occurs most commonly on moraine sand suitable for *Rubus* and *V. myrt.*

#### **Deschampsia—Galium hareynicum soc.**

Table IX, 12—13.

This sociations was met with on soil suitable for *V. vit.* No. 12 is closely allied to the *Desch.* sociation, No. 13 most closely resembles the succeeding sociation. *Galium* was well developed and fertile in both sociation individuals. A sociation corresponding entirely with No. 12, but containing several non-forest plants, occurs in summer-dry green bogs between *Calluna* heath and *Carex Goodenoughii* populations on open heath (MØLHOLM HANSEN 1932, p. 145).

#### **Deschampsia—Hylocomium parietinum soc.**

Table IX, 14—17.

*Desch.* is somewhat poorly developed, allowing a luxuriant growth of *H. par.*, *H. prol.*, *Dicr. rugosum*, *D. scop.* and *Ster.* No. 17 appeared two years after clearing in a forest with *H. par.* sociation and will gradually pass into *Calluna* heath, the rest of the sociation individuals are stable. The *Desch.—H. par.* sociation has an average pH of 3.86 (3.4—4.2). The subsoil always consists of sand.

**Carex arenaria soc.**

Table X, 1—11.

This sociation is very widely distributed in coastal dune plantations. In these forests *C. arenaria* attains a density rarely seen outside them, and has a diverging appearance. The leaves may attain a length exceeding 1 m., and are partly procumbent. It is mostly sterile but may flower at a light percentage of c. 12—15 and on the whole shows good agreement with *Desch.* in its relation to light. Its light minimum lies at 7—9 %, and it forms sociations in the open dunes and on the heath.

*Scl.* is constant in the sociation and is very luxuriant; and *H. prol.* often attains a considerable development. *Dicr. rugosum*, *D. scop.*, *H. par.* and *Ster.* are nearly always present, but as a rule with low frequency. In a single instance *Empetrum* was the frequency dominant (No. 1). The sociation individuals from Sonnerup are remarkable by their content of *Brach.* and *Mnium rostratum*.

There is no reason to regard *C. arenaria* as a relict from the dune. As already mentioned, it thrives remarkably well in the forest, even in situations where it must be supposed not to have formed sociations originally.

The magnitude of the peat varies between 5 and 11 cm. and it is noteworthy that *C. arenaria* always has its stolons as well as its roots in it. Though in forests *C. arenaria* is indissolubly associated with the peat, it only occurs where the subsoil is almost pure sand.

*C. arenaria* has the highest pH of the moor plants forming populations, pH being 4.15 (3.7—4.8) for the species, and 4.12 (3.7—4.6) for the sociation.

**Carex arenaria—*Oxalis* soc.**

Table X, 12—13.

This peculiar composition of the vegetation may be found in situations where water from moraine deposits penetrates into overlying sandy strata (here half a metre to one metre thick). The sociation is rare but interesting by the fact that it shows how *Oxalis* can thrive on blown sand when under the influence of moraine deposits, and that this does not unfavourably influence *C. arenaria* which, unlike *Oxalis*, does not thrive on moraine. The layer of peat is 6—7 cm. thick, and all the roots are in it. *Luzula pilosa* and *Hylocomium triquetrum*, both with similar pH requirements to *Carex arenaria*, are well developed.

***Scleropodium purum* soc.**

Table XI.

*Scl.* is an oceanic-boreal moss, having its south-eastern limit in the Caucasian beech region. Its oceanic character is so pronounced that even in Denmark distinct differences in its edaphic requirements may be observed. It is one of the most widely dispersed of the mosses of Danish coniferous forests, and occurs both on moraine sand and in dune forests.

The *Scl.* sociation only occurs on soil where *Desch.* or *C. arenaria* will also thrive, so that its upper light limit is dependent on the lower light limit of these species;

and since the latter is lower than that of most other phanerogams, the sociation is an almost pure moss sociation. The shade-tolerant *Luzula pilosa* is the frequency dominant in one instance. *Brach.* occurs in many of the sociation individuals, and limited to the same are *Mnium rostratum*, *Loph. heterophylla* and *Plag. dent.* The *Brach.* sociation and the *Scl.* sociation often merge, whereas the line between the *Scl.* sociation and the *H. par.* sociation is fairly distinct. *H. par.* is, however, found as a constant in the *Scl.* sociation, though mostly with low frequency. *Dicr. scop.* may become the frequency dominant, but it never becomes the physiognomical dominant. *H. prol.* and *Ster.* are constants of from low to moderate frequency.

Where *Scl.* attains its best development it forms a dense carpet with ascending or erect shoots, very similar to those of *H. par.* In other cases it creeps along the ground.

The *Scl.* sociation has nearly the same light requirements as the *Brach.* sociation.

The thickness of the peat shows that *Scl.* only occurs where the magnitude of the peat exceeds 6 cm. In accordance herewith it is only found in old forests, often in younger growths of the second generation, because dark forest soil is here combined with a thick layer of peat. Where *Scl.* is luxuriant and forms the chief part of the peat itself, the latter is loose and somewhat felt-like. In other instances it is like raw humus and often interwoven with the roots of trees.

pH for *Scl.* sociations is low. It averages 3.82 (3.4—4.4), whereas pH is considerably higher for the species, viz. 4.01 (3.4—4.8).

#### *Hylocomium parietinum* soc.

Table XII.

The *H. par.* sociation is beyond comparison that which occupies the largest area of all the plant communities of coniferous forests. There is no doubt, however, that it will become rarer when the large areas with *Pinus montana* of the first generation on the heath, which is its chief domain, are replaced by the more shelter- and shade-giving *Picea excelsa*.

*H. par.* occurs on all kinds of soil except that suited for *Rubus* (there only on the rotten stumps of trees), but it only forms populations on soil suitable for *V. vit.* or still drier soil.

Comparison with the k % for the *H. par.* and *V. vit.*—(*Empetrum*) sociation shows extremely good agreement. *Clad.*, however, forms an exception, being found in the *H. par.* sociation only. Actually the moss populations in the two plant communities are exactly similar, but the agreement in the k % is somewhat misleading, because *Scl.* may form a population in the *V. vit.* sociation without it being found necessary to divide it into two sociations on that account. In the *H. par.* sociation *Scl.* is rare and of low frequency. The composition of the species is extremely uniform, with *H. par.* as the absolute physiognomical dominant and *Dicr. rugosum*, *D. scop.*, *H. prol.* and *Ster.* as constants. *Dicr. rugosum* may be almost solely prevalent in small spots. The moss carpet is often 20 cm. thick. *Desch.* has a k % of 64, but is of low frequency and always very slender.

The uniform development of the *H. par.* sociation is due to its great influence

on the surface soil owing to its rapid growth and lively vegetative propagation. KUJALA (1926, p. 40) found an annual augmentation of 10—13 mm., but the rate of growth is doubtless very variable under different conditions (see also the discussion of the production of peat at p. 46).

The light percentage in the *H. par.* sociations is highly variable. On rare occasions it has been found to be 3.46, but at such low intensities of light it grows slowly and will only with difficulty be able to compete with the more shade-tolerant *Stereodon*. The *H. par.* sociation may be found in full light (plate II).

The peat under the *H. par.* sociation is loose and felt-like and is for the most part formed of the character species. The average thickness of the peat mostly lies between 4 and 7 cm. The pH of the peat ranges around 3.87 within such narrow limits that in 22 out of 100 sociation individuals it will lie within an interval of 0.1 around the mean value. The lower and upper limits of pH are 3.4 and 4.3. The pH amplitude for the species is, as was to be expected, somewhat wider than for the *H. par.* sociation with a regular distribution around pH 3.85 (fig. 8).

### *Hylocomium proliferum* soc.

Table XV, 7—9.

The *H. proliferum* sociation has exactly the same qualitative composition as the *Scl.* sociation, but differs from it in the fact that *H. prol.* with *H. par.* are physiognomical dominants.

*Scl.* and *H. prol.* show great biological similarities and seem to alternate in different climates. In coniferous forests the *H. prol.* population is much better developed in Finland and in the Scandinavian peninsula than in Denmark. As far south as Småland the luxuriance of *H. prol.* is striking. KUJALA (1926, p. 30) designates *H. prol.* as the most important forest moss next to *H. par.*, while the same author in his very comprehensive studies of Finland's forest moss vegetation does not find *Scleropodium* at all.

*H. prol.* is a pronounced acidiphile, the average for the species being 3.80, which is considerably below that of *Scleropodium*. But a comparison of the sociations of the two species shows no distinct difference in the acidity.

A comparison of the k % of the two species (Table 1) furnishes good information as to their relative relation to moisture. It is seen that *H. prol.* has the highest k % in the *Clad.*, *H. par.* and *V. vit.*—(*Empetrum*) sociations, whereas *Scl.* is most frequent in the *Desch.* populations. Thus *H. prol.* is more tolerant of drought than *Scl.* This was immediately seen in No. 8. The soil had here been ploughed, and there was a very regular distribution with pure *H. prol.*—*H. par.* on the ridges and a very great admixture of *Scleropodium* in the furrows. Strictly, this sociation individual is a mosaic of two sociations.

The *H. prol.* sociation has a somewhat higher light minimum than the *Scl.* sociation. It also occurs at a somewhat higher light percentage than the latter, in places where *Deschampsia* cannot immigrate owing to a lack of water — which is never the case in the *Scl.* sociation.

*H. prol.* mostly occurs on soil suitable for *V. myrt.* and *V. vit.* but may also be met with on sand where these species would hardly grow. It seems here to be dependent on the leaves falling from foliiferous trees, at any rate a very few birches scattered among the conifers will be able to change a pure *H. par.* sociation into a *H. prol.* sociation, which was the very thing that happened in No. 7. The phenomenon may be observed very frequently, for instance in Tisvilde.

#### **Hylocomium triquetrum soc.**

Table XV, 3—6.

This sociation only occurs under special conditions in coniferous forests, viz. in situations where the peat, owing to a calciferous subsoil or for other reasons, has a particularly high pH. Thus it is of common occurrence in Svinkløv, where the *H. parietinum* sociation was to be expected, and it forms a zone round limestone quarries. In Sonnerup, too, it dominates in several places over its most common accompanying mosses *H. par.*, *H. prol.*, and *Scl.* Scattered birches have a very favourable effect on *H. triquetrum* (the leaves of foliiferous trees increase the pH).

#### **Luzula pilosa—H. triquetrum soc.**

Table XV, 1—2.

The examples are derived from the vicinity of the *Carex arenaria—Oxalis* sociation and under similar conditions, but the sociation has probably appeared as a result of birches in the neighbourhood.

#### **Dieranum majus soc.**

Table XV, 10—12.

The sociation has been found on soil suitable for *V. vit.* and *V. myrt.* near Silkeborg, and in Grib Forest it occurs at the top of slopes bearing *Thuidium* sociation at a lower level.

The two other common *Dicranum* species do not form sociations. *Dicranum scoparium* occurs in most sociations and is as a rule equally distributed over the test area. It has not nearly the same power of vegetative reproduction as *D. majus*, but *D. scop.* is indifferent to light and very resistant to drought. Its pH is the lowest that has been measured, averaging 3.71.

*D. rugosum* resembles *Calluna* and *Empetrum* in its relation to absolute moisture. It is a constant in the dry *Cladonia* sociation and occurs among *Sphagnum* in bogs. Its light requirements are slightly in excess of those of the *H. par.* sociation.

#### **Stereodon cupressiformis soc.**

Table XIV.

The *Stereodon* sociation occurs on soil both slightly drier and slightly moister than that of the *H. par.* sociation. In many instances the composition of the species

differs only quantitatively in the two sociations, but the difference is so considerable that there can hardly ever be any doubt to which sOCIATION a plant community belongs. *Stereodon* forms a continuous carpet and where the sOCIATION is best developed has an ascending growth; at a lower intensity of light it creeps along the forest ground. It is always the variety *ericetorum*, by some authors regarded as a separate species, which forms sOCIATIONS.

The reason why *Stereodon* is able to resist the competition of *H. par.* is that it is more tolerant of shade and requires less moisture than the latter. The sOCIATION has been found at a light intensity of 1 %, but at such a low intensity of light it grows slowly and will, particularly in old growths, become covered with needles. At 2—3 % its growth is so vigorous that it may rise above the fallen needles. Where the soil is very dry, the *Stereodon* sOCIATIONS may be stable at high values of i, the highest measured being 20.7.

### Lophocolea heterophylla sOCIATIONS

Table XVI, and

### Eurhynchium striatum soc.

Table IV, 1—2.

Table XVI gives the results of the analyses of some sOCIATION individuals on very dark forest soil, which all contain *Loph. het.* *Plagiothecium denticulatum* var. *curvifolium* may form populations at as faint an illumination as somewhat below 2 %, at a lower light intensity all the mosses are attached to prominent objects, especially to roots and fallen branches.

The lowest of all i-values found was 0.37 (No. 4). At this low light intensity *Lophocolea heterophylla*, *Plagiothecium denticulatum*, and *Stereodon* still occur.

HABERLANDT (1886, p. 476) observed that the rhizoids of *Eur. praelongum* penetrate into fallen beech leaves and produce haustoria-like lobed formations. Hence he conjectures that it is a semi-saprophyte. Another of the species most tolerant of shade, *Loph. het.*, is invariably associated with fresh or decaying parts of plants. As far as I know, no investigations are available on its nutrition, but there can hardly be any doubt that it is a semi-saprophyte. In the course of a very few years it may in very dark forests form a pale green coating on the end surfaces of splinters from the felling of trees or on stumps of trees, a rate of growth which no other moss ever attains at a similar light intensity. *Loph. het.* most frequently occurs in dark forests. It can, however, thrive at more light, but is very susceptible to drought. Thus it has been found at 15 % on splinters soaked with water.

In very dark localities with a high pH *Eur. striatum* was in one or two instances found to be the dominant moss. One case was under young *Picea excelsa* of the first generation on marly sand in Nørlund plantation and the other was on moraine clay under old *Abies pectinata* in Rø plantation. In both places *Eur. striatum* was scattered and accompanied by *Eur. prael.* and *Plag. dent.*

**Cladonia impexa soc.**

Table XIII.

*Cladonia impexa* forms a continuous carpet, mostly with *Cladonia rangiferina* tufts interspersed. Physiognomically the mosses play an insignificant part, but the following mosses will nearly always be found:

*Bleph.*, *Dicranum rugosum* and *D. scop.*, *H. par.* and *Ster. Desch.* may occur. It is very slender, but often fertile.

*Cladonia* is found on the same kind of soil as *H. par.*, but its slow growth makes it incapable of competing with it, so it is confined to places too dry for *H. par.* Otherwise the species is quite independent of the absolute moisture. According to MØLHOLM HANSEN and M. LUND (1929, p. 27) it occurs wherever there is a possibility of lichen vegetation.

The *Cladonia* sociation has been found at i-values as low as c. 10, but the measurements are from the insolated slopes of dunes, so the values are somewhat too low. The sociation has no upper light limit.

pH is very low, the average value being 3.72 (3.4—4.3). The peat is as a rule thin. Such low pH values will not be found anywhere else in peat of so slight a thickness, whereas it may occasionally be found in the lower part of a thick layer of peat.

The list of lichens in the Table is not complete.

The plant communities described in Table XVII belong to the rarer kinds hence they will not be discussed in detail. They are of interest by the fact that they form members in ecological series, so they will be mentioned in subsequent sections.

### The Distribution of the Vegetation on different Soils.

In the following we shall give a series of typical examples of the ecological factors influencing the distribution of the vegetation in the separate instances. Localities have been chosen which, as far as can be judged, show agreement in respect of as many environmental factors as possible, while one factor or rather, since the environmental factors usually constitute a more or less indissoluble complex, a complex of factors, varies. Thus, for instance, an increase in the intensity of the light will involve greater desiccation, and the moisture conditions of the soil decisively affect its acidity, a state of dependence which cannot be explained exclusively by the effect of the species associated with certain degrees of moisture.

The figures merely give an outline of the variations in the environmental factors and the plant communities to which they give rise, some attention having, however, been paid to the relative extension within the area of the plant communities.

#### Dune and Level Heath.

The ground vegetation in coniferous forests on dunes and level heath has many points of resemblance, but the dunes bear a more variable vegetation, because moraine

Table 1. Constancy percentage of some species in some of the plant communities.

Number of sociation individuals . . . . .	Rubus—Brach. sociations		Oxalis acetosella sociation		Brach. curtum sociation		Vacc. myrt. sociations		Vacc. v.-l.—(Empetr). sociations		Calluna sociations		Desch.—Sel. sociation		Desch. sociation		Carex arenaria sociation		Scleropodium sociation		Hyl. parietinum sociation		Stereodon sociation		Cladonia imp. sociation			
	14	Tab. I	10	Tab. II	12	Tab. IV	9	Tab. V	11	Tab. VI	19	Tab. VII	22	Tab. VIII	11	Tab. IX	11	Tab. X	19	Tab. XI	33	Tab. XII	19	Tab. XIII	9	Tab. XIV		
Oxalis acetosella . . . . .	57	100	33	0	0	0	0	32	9	0	0	0	64	58	64	58	0	0	0	0	0	0	0	0	0	0	0	
Deschampsia flexuosa . . . . .	64	30	0	100	64	69	100	100	64	58	64	58	64	58	64	58	44	44	44	44	44	44	44	44	44	44	44	
Blepharozia ciliaris . . . . .	0	0	0	0	55	26	14	0	0	0	0	0	0	0	0	0	39	11	89	89	89	89	89	89	89	89	89	
Brachythecium curtum . . . . .	100	80	100	22	9	11	32	45	36	63	9	22	14	18	55	16	88	37	89	89	89	89	89	89	89	89	89	
Dicranum rugosum . . . . .	0	0	0	78	91	58	14	18	55	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
— scoparium . . . . .	14	40	67	78	100	95	77	45	45	100	91	100	91	100	91	100	100	100	100	100	100	100	100	100	100	100	100	
Eurhynchium paelongum . . . . .	79	70	83	11	0	0	0	5	0	18	16	0	11	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylocomium parietinum . . . . .	21	40	50	89	100	89	82	82	55	89	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
— proliferum . . . . .	29	10	75	78	91	53	86	64	73	95	94	74	74	74	74	74	74	74	74	74	74	74	74	74	74	74	74	
— triquetrum . . . . .	21	10	16	11	9	11	32	27	27	32	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27
Lophocolea heterophylla . . . . .	29	90	100	33	0	5	5	27	0	47	6	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mnium rostratum . . . . .	86	40	50	11	0	0	5	0	27	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiothecium denticulatum . . . . .	36	80	58	44	9	0	14	55	0	47	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scleropodium purum . . . . .	93	70	92	89	27	42	100	91	100	100	91	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
Stereodon cupressiformis . . . . .	21	60	42	100	91	100	50	100	55	89	94	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
Thuidium tamariscifolium . . . . .	21	50	42	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladonia impexa . . . . .	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	42	32	100	100	100	100	100	100	100	100	100	

GAMS (1932, p. 332) gives a list of affinities between mosses and vascular plants (the Alps, but partly also Danish species).

deposits often lie near the surface, and under such conditions that they may influence the moisture of the surface (Hornbæk, Tisvilde, Blykobbe, Svinklov). These are the woods that show the greatest floristic resemblance to the N. Scandinavian forests because of the presence of *Pirola* species, *Chimaphila* species, *Linnaea*, *Listera cordata*, *Goodyera repens*, and a luxuriant growth of *Ctenium crista-castrensis*. Common to dune and heath according to the increasing degree of moisture is the succession *Clad.* sociation, *Ster.* sociation, *H. par.* sociation, (or *V. vit.* sociation), *Desch.* sociations, (or *Carex arenaria* sociation on dunes). *Deschampsia*, however, is much better developed on dune than on heath; on the heath it usually occurs in company with *H. par.*, on dune with *Scl.* The *Scl.* sociation, which is very frequent in dune forests, only occurs on the heath in old fir woods with a well-developed layer of peat.

### Example 1.

Locality: Frederikshaab Plantation (level heath). The subsoil consists of coarse sand with stones, the finer heath sand being blown away. The tree population consists of 70 year old *Pinus montana* with open and low growth. At a light percentage of c. 30 there is *Clad.* sociation (Table XIII, 5), and if the light intensity increases essentially, the *Clad.* sociation cedes its place to a lichen plant community in which *Cladonia rangiformis* occupies a prominent place. Under the trees, where the largest amount of needles is found and where there is least desiccation by the sun, there occur small *H. par.* populations, now and again with *Empetrum*.

### Example 2.

Very close upon the preceding one, but the sand is but little blown away or not at all. Among 40 year old *Picea excelsa* of the first generation *Ster.* forms populations at 3.08 % of light (Table XIV, 18). In slightly lighter situations, at 3.46 %, *H. par.* is well developed (Table XII, 14). This is the lowest i-value found for the *H. par.* sociation. In a growth about 40 years old in the immediate vicinity, where the soil must be supposed to be the same, the *Desch.*—*H. par.* sociation occurs at 10.9 % of light (Table IX, 16). Below the light minimum of *Deschampsia* the *H. par.* sociation (XII, 15) appears, and at high i-values, as a result of the desiccation, the *H. par.* sociation recurs, followed by the *Ster.* sociation and the *Clad.* sociation.

Hence, with increasing intensity of light, we have: *Ster.* soc.—*H. par.* soc.—*Desch.*—*H. par.* soc.—*H. par.* soc.—*Ster.* soc.—*Clad.* soc.

### Example 3.

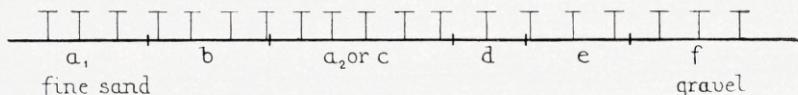


Fig. 1. a = *V. vit.* soc. (Table VI, 14 and 12). b = *Desch.*—*H. par.* soc. (Table IX, 14). c = *H. par.* soc. (Table XII, 4). d = *Ster.* soc. e = *Clad.* soc. (Table XIII, 1). f = *Calluna-Empetrum-Clad.* soc. (Table VII, 7).

The locality (Sandheden) is situated 4 km. to the east of Silkeborg immediately to the north of the high road to Aarhus. The soil is a gently sloping deposition cone with a gradual transition from gravel to fine sand, which is adjacent to moraine deposits. The *Pinus silvestris* population is 40—50 years old and of the first generation; over f, however, it is 20 years old. The light is everywhere the optimum for all the sociations concerned except f. f is in process of passing into a pure *Clad.* sociation, in the more open spots the dwarf shrubs have died. Under the older *Pinus silvestris*, at the top of the cone, a *Clad.* sociation is to be seen, abutting on the *Ster.* sociation, which forms transitions to the *H. par.* sociation. This contains *V. vit.* clones. *V. vit.* is associated with a greater thickness of the peat and a higher frequency of *H. prol.* Where the sand is finest, the *Desch.*—*H. par.* sociation makes its appearance likewise the *V. vit.* sociation, with an unusually large admixture of *Desch.* and a little *V. myrt.*

On the moraine slope this series is continued in the *V. myrt.* sociation.

This example comprises all the most important plant communities from the heath, and they will be found in the same succession whether the differences in dryness, as in this case, are due to the porosity of the soil or to the effects of the wind or the sun.

#### Example 4.

Locality: Bredlund Plantation (level heath). The growth consists of 30—40 year old *Pinus montana* of the first generation. The light intensity ranges from 15 to 20 % and is thus the optimum for all four sociations. Fig. 2 shows diagrammatically the distribution of the sociations according to the height above the ground-water level. The differences in height are very small, but distinctly demonstrable. At the lowest level, where also *Molinia coerulea* occurs, the *Desch.—G. harcynicum—H. par.* sociation is met with. Then follow the *Empetrum—V. vit.* sociation and the *V. vit.* sociation. Below the layer of peat in which the roots are found, and which has retained the plant structure, both these sociations have a 6—8 cm. thick layer of black, greasy peat, which, however, does not seem to limit the *V. vit.* sociation for the benefit of *H. par.* sociation, the highest lying sociation. A layer of hard pan, 4—7 cm. thick, is present everywhere.

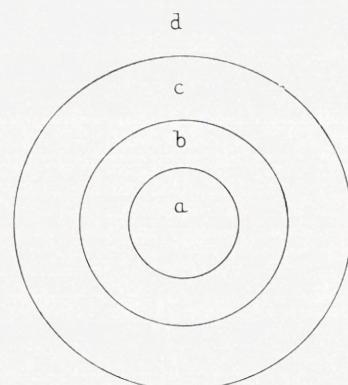


Fig. 2. a = *Desch.—G. harcynicum—H. par.* soc. (Table IX, 13) pH 4.13. b = *V. vit.—Empetrum* soc. (Table VI, 5) pH 4.07. c = *V. vit.* soc. (Table VI, 10) pH 3.90 (lower peat 3.6). d = *H. par.* soc. (Table XII, 7) pH 3.87.

#### Example 5.

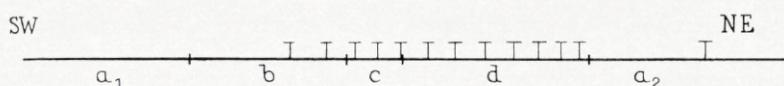


Fig. 3. a = *Calluna-Empetrum* soc. (Table VII, 5). b = *Clad.* soc. (Table XIII, 9). c = *Ster.* soc. d = *H. par.* soc. (Table XII, 1).

The tree population is c. 40 year old *Pinus silvestris* of the first generation on a level terrain of blown sand at Dueodde. The original vegetation is a *Calluna—Empetrum* sociation very poor in species, which does not differ much from the one here analysed (*a*<sub>2</sub>) in which there are scattered trees. To the south-west of the forest and some distance into it there is a zone with a *Clad.* sociation which is bounded on the south-west by the original vegetation, and in the interior of the forest, at 30—35 % light, there is a narrow zone with a *Ster.* sociation, which forms a transition to a *H. par.* sociation or an *Empetrum* sociation (Table VI, 4), harbouring some *Calluna* and a luxuriant moss population. Although the intensity of the illumination is far above the minimum for *Empetrum*, *Empetrum* will disappear gradually as *Calluna* dies, and it will hardly immigrate here again. To the north-east the *Calluna—Empetrum* sociation extends right up to the edge of the forest.

The reason why the *Clad.* sociation occurs in the south-western part of the forest is to be found in an interaction of two factors. The ground-water level has been lowered as a result of the afforestation, and the place is exposed to the wind. In sheltered situations farther inside the forest the *H. par.* sociation is found at a similar ground-water level and outside the north-eastern part, where there is shelter, the original vegetation can be maintained, in spite of the lowered ground-water level.

In other places at Dueodde as well as in other dune forests the *Carex arenaria* sociation (Table X, 4) will be found in depressions of the dunes, surrounded by the *H. par.* sociation. In the locality here analysed the percentage of illumination is 11.3 %, so that the *Empetrum* sociation will probably be excluded for want of light.

#### Example 6.

The test areas are on dunes in the Blaabjerg Plantation. The dune is steep and with about the same slope towards the north-east and the south-west. The tree population consists of open *Pinus montana*, and the light intensity is 20–30 % (measured horizontally).

On the side exposed to the sun and the wind there occurs a *Clad.* sociation which, as the dune becomes less sloping, passes into a *H. par.* sociation. On the upper part of the north-eastern slope there is a well-developed *Ster.* sociation with

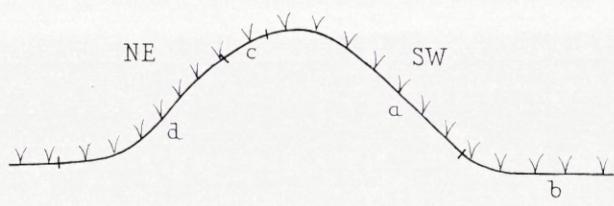


Fig. 4. a = *Clad.* soc. (Table XIII, 6). b = *H. par.* soc. (Table XII, 5). c = *Ster.* soc. (Table XIV, 12). d = *Desch.*—*Scl.* soc. (Table VIII, 1).

a thick layer of peat. This is an exception. *Desch.* is frequency dominant here, but it is very slender. A little lower, in more sheltered situations, *Desch.* becomes more vigorous and occurs in company with *Scl.* *Desch.*—*Scl.* here passes into a pure *Scl.* sociation when the light falls below the minimum for *Deschampsia*, but in some places the zonation *Desch.*—*Scl.* soc. *H. par.* soc. will be found, when *Deschampsia* is excluded owing to lack of light.

On less steep dunes the *Desch.*—*Scl.* sociation is replaced by a *H. par.* sociation, and this is a very common distribution of the vegetation on dunes. The following is an example from the inner sands of Frederikshaab Plantation; on the southern slope occurs a *Clad.* sociation (Table XIII, 3) and on the northern slope an *H. par.* sociation (Table XII, 11).

#### Example 7.

The example is derived from Hornbæk Plantation. The subsoil is blown sand deposited in a more or less deep layer over moraine deposits. The figure shows relief conditions and the relative thickness of the blown sand. At the top, in a fir wood with 3.18 % illumination occurs the *Scl.* sociation with *Luzula pilosa* as the frequency dominant. Here and there are found smaller *H. par.* sociation individuals. A little above the foot of the slope where there are scattered specimens of *Pinus silvestris*

the *Empetrum* sociation appears, with a very luxuriant population of *Scl.*, and at the lowest level occurs a *H. par.* sociation or a *V. vit.* sociation with *H. par.*, but no *Empetrum*. As will appear from several examples, *Scl.* and *H. par.* are sufficiently good indicators of moisture to show that the moisture is greatest in the *Empetrum* sociation. Here, then, we have *Empetrum* as a “well plant”, while *V. vit.* only occurs

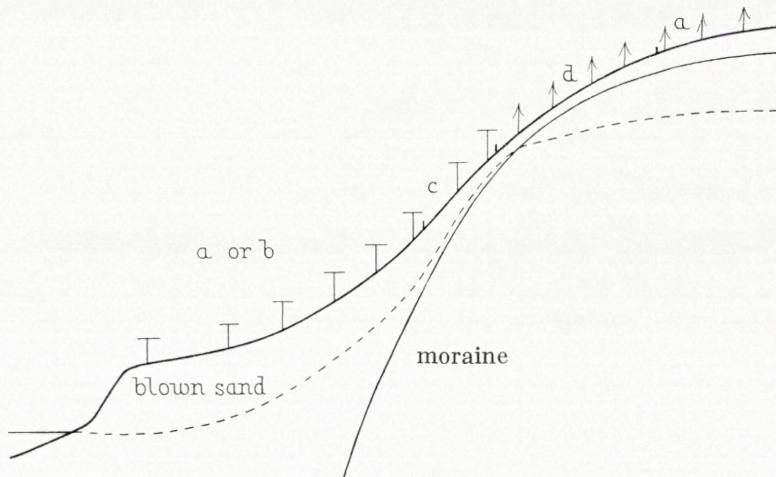


Fig. 5. Diagram showing the moisture conditions in Exemple 7. The moraine is overlain by a layer of blown sand. The stippled line denotes the probable position of the ground-water level (partly after SUKATSCHEW 1932, p. 202). *a* = *H. par.* soc. (Table XII, 22, the lowest lying *H. par.* sociation individual). *b* = *V. vit.* soc., *c* = *Empetrum* soc. (Table VI, 3), *d* = *Scl.* soc. (Table XI, 18).

in the driest area. Since *Empetrum* is more resistant to drought than *V. vit.*, the degree of moisture can only be regarded as a factor influencing the distribution of the vegetation as far as the mosses are concerned.

In Tisvilde Plantation, too, *Empetrum* sociation may be observed in several places in the eastern part at the foot of the slope facing the sea. Such a pronounced lime and well plant as *Equisetum hiemale* forms populations here in some few places and furnishes conclusive evidence of the influence of the ground-water. Below the *Equisetum hiemale* zone occurs the *Empetrum* sociation (Table VI, 2), which passes into the *Calluna* sociation (Table VII, 13). Still further removed from the moraine hill there are beginnings of a *Cladonia* sociation, which in more shaded situations passes into the *H. par.* sociation (Table XII, 16). On the moraine hill the aforementioned *Carex arenaria*—*Oxalis* sociation appears, besides the same plant communities as those mentioned for Hornbæk.

#### Example 8.

Locality: Rønne Plantation. Light % 10.5. The *H. par.* sociation (Table XII, 31, both *Scl.* and *Desch.* are frequency dominants, but very feeble), occurs at high levels somewhat lower down appears a very pure *Desch.*—*Scl.* sociation (Table VIII, 5).

## Example 9.

Locality: Tisvilde Plantation. The subsoil is blown sand over moraine deposits, and the light intensity is 5—6 %, i. e. below the minimum for *Desch.* At the lowest level there occurs a *Scl.* sociation rich in *Luzula pilosa* (Table XI, 19). A little higher up there is a *H. par.* sociation with an abundance of *H. prol.* (Table XII, 24). At a still higher level and at a higher light intensity a purer *H. par.* sociation (Table XII, 6) appears. Under scattered young firs there is a very luxuriant growth of *Scl.* and *H. prol.*, corresponding entirely to the occurrence of *H. par.* under pine in the *Clad.* sociation in Frederikshaab Plantation (Example 1).

## Moraine.

The three moraine areas most thoroughly investigated are the neighbourhood of Silkeborg, Almindingen, and Grib Forest. Round Silkeborg the moraine contains stones and gravel, in Almindingen it consists of nearly pure sand, and in Grib Forest it is more or less clayey. The moraine hills around Silkeborg are suitable for *V. vit.*—*V. myrt.*, *Rubus* only occurs below round the lakes, the *H. par.* sociation appears on isolated slopes of hills or such as are exposed to the wind. Almindingen, to which Gjøding Plantation may be added, is suitable for *V. myrt.*, and *Rubus* only forms populations in the *Rubus*—*Brach.*—*Desch.* sociation which characterise moist soil suitable for *V. myrt.* The *H. par.* sociation is not stable. The third area, Grib Forest with surrounding forests (Tokkekøb Hegn, Store Dyrehave, Rudeskov, to which may be added Rø Plantation), is suitable for *V. myrt.* and *Rubus*.

## Example 10.

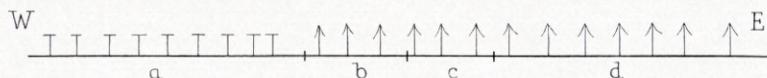


Fig. 6. a = *Calluna* soc. (Table VII, 12). b = *Ster.* soc. c = *Desch.*—*Scl.* soc. (Table VIII, 14). d = *Scl.* soc. (Table XI, 12).

Locality: Moraine hill near Silkeborg. To the west, on the original *Calluna* sociation, there is a 10 year old population of *Pinus silvestris*, two to three metres high, which only affords slight shelter to the forest ground vegetation in an adjacent growth of *Picea excelsa*, about 70 years old. On the outskirts of the *Picea excelsa* growth there occurs a *Ster.* sociation interrupted now and again by fragments of a *Desch.*—*H. par.* sociation. Further in, where there is more shelter in the forest, there occurs *Desch.*—*Scl.* sociation, but where the side light has no influence it is too dark for *Desch.* and we get a *Scl.* sociation (cp. Dueodde, Example 5).

## Example 11.

Table IX, 7 shows a *Desch.* sociation individual containing *Molinia caerulea* and *V. myrt.* The light % is 22 and thus the optimum for the three species. The surface of the soil is slightly broken and the vegetation is distributed according to increasing

height in *Molinia* sociation, *Desch.* sociation, and *V. myrt.* sociation. Only where the ground is so low (near Bastemose, where swamping of the coniferous forest has been found) that the ground-water is near the surface, can *Desch.* form a stable population where the light is strong enough for *V. myrt.* However, it may persist several years after clearing (Table VIII, 21).

Over fairly large stretches, in light pine forest, on the previous Højlyng, there occurs a *Desch. caespitosa* sociation with *Oxalis* (Table XVII, 6). The sociation is rather uniformly developed, but in moist situations it may pass into a very pure *Carex hirta* sociation (Table XVII, 7). At the same level as these two sociations *Thuidium* forms populations in dark growths of fir, often in the shape of belts round spots covered with water in the winter.

In Almindingen the distribution of the most common vegetation according to the illumination is as follows: In the darkest situations a moss sociation rich in *Ster.* or *Plag. dent.* (Tables XIV, 3 and XVI 5—7); then follow the *Desch.—(Scl.)* sociation (Table IX, 5) and the *V. myrt.* sociation (Table V).

#### Example 12.

Table IX, 3 represents a *Desch.* sociation individual situated in the windy outskirts of Tokkekøb Hegn. *Rubus* sociations rich in species (Table I, 4—5, 8) occur in sheltered situations within the forest. A quite similar relation prevails between Table IX, 2 and Table XVII, 1—2 from Rø. *Desch.* is exceedingly vigorous here. While *Desch.* will only thrive in sheltered situations on the heath (when the ground-water does not exert its influence), and is fairly indifferent to wind on soil suitable for *V. myrt.*, the influence of wind is an essential condition if *Desch.* is to be able to colonise soil with a marked disposition for *Rubus*.

If the intensity of the light falls below the minimum for *Rubus*, *Brach.* will be left as the only species forming populations (in some instances, however, *Thuidium* will form sociations). At the same time the formation of mould ceases. That this is the reason why *Oxalis* disappears together with *Rubus* is rendered probable by the following example: A *Brach.* sociation individual (Table IV, 8) is intersected by a ditch, and only around this does an *Oxalis* sociation occur (Table II, 7). A formation of mould takes place at the ditch, while peat is produced in the *Brach.* sociation. This zonation is very common, and in pure coniferous forests *Oxalis* almost only forms sociations under such extreme conditions (and in young growths, which have not yet had time to form peat). It never attains the luxuriance which it has under *Rubus*.

#### Example 13.

A similar zonation to that mentioned, for instance, in Example 5, may be found at full light in the granite terrain of Bornholm. The soil consists of humous substances and weathered granite. It is black and amorphous with few mineral particles interspersed. Where the layer of soil is thinnest there occurs a *Clad.* sociation with the same composition as that of the forest; thus both *Bleph.*, *Ster.*, *Cladonia* and *Dicr. scop.* will as a rule be found. If the layer of soil is a little thicker, a pure *H. par.*

sociation will appear, which passes into a *Desch.* or a *Calluna* sociation. With a still greater thickness of the soil, a waste land vegetation rich in species appears.

Small but typically developed sociations occur in the same succession as was mentioned above around isolated stones, even if the layer of soil has a uniform thickness. Plate II shows a case where *Cladonia impexa*, *H. par.* and *Deschampsia—Calluna* are seen to form fragments of zones round denuded crags.

### Succession of the Vegetation.

For a species to form a stable population it is not sufficient that the environment is favourable. Conditions must be such that the often considerable changes in the environmental factors (including the biotic factors) which accompany the immigration of the species, are no greater than that the environment is still within the ecological amplitude of the species. If, for instance, *Desch.* immigrates in large amounts into a *H. par.* sociation on dry soil, the result will be a deterioration of the environmental conditions for *H. par.*, *H. par.*, however, conditions the moisture which enabled *Desch.* to immigrate, and thus *Desch.* lays the foundation of its own destruction. Here and there conditions are such that a constant balance can be maintained (*Desch.—H. par. soc.*), but usually the two species will form separate populations.

When a species has carried the change too far, the result will be that its vitality is reduced, and thus the effect will be diminished. If this does not happen simultaneously with an improvement in the environmental conditions for a competing species, so that the latter will take its place (*Ster.—H. par.*), the species itself will be able to regulate the environmental conditions in such a way that it forms a stable population. As examples of this may be mentioned *H. par.* and probably *Calluna*, which both exercise a great influence on the soil.

In the soil vegetation of conifer forests the balance between the reversible factors (particularly the thickness of the peat and its acidity) and the vegetation will in most instances be quickly established, while an irreversible process such as the washing away of calcareous soil with the resulting increase in acidity and the size of the grains will take place too slowly for the course of the mutual interaction of the various soil vegetations and the degree of washing to be observable in our conifer plantations.

We shall here give some examples of the course of the succession upon afforestation of areas covered with *Calluna*, since it is most frequently on such that conifer forests are planted.

#### Example a.

In the sociation individual described in Table VII, 7 the original *Calluna—Emeptrum—Clad.* sociation is passing into a *Clad.* sociation, as is usually the case in the driest places where *Calluna* forms populations.

#### Example b.

The example is derived from Søgaard Plantation on the central heath of Jutland. The original vegetation is given in Table VII, 1 (10 circles). It is seen to be a *Calluna—*

*Empetrum* heath with a scattered occurrence of *Arctostaphylos uva-ursi*, *V. vit.* and *Molinia coerulea*; *H. par.* and *Ster.* are dominant mosses. Under a layer of black peat, 2–7 cm. thick, there are 20–25 cm. bleached sand and 5–15 cm. hard pan.

The first result of planting with *Pinus montana* is a more vigorous growth of *Calluna*, which thrives exceedingly well as long as the trees afford shelter without giving very much shade (e. g. Table VII, 8, where the trees are planted in close rows with wide interspaces between the rows). The rest of the phanerogams are not able to grow at the same rate, and gradually as the trees give more shade they will, therefore, die for want of light. *Empetrum*, however, forms an exception. Table VII, 6 shows the vegetation under 11 year old *Pinus montana*. The light intensity is 12.7 %, but the light is somewhat irregularly dispersed under the low trees. *Calluna* is rapidly declining, being now found almost only in the spots of light, and it is followed by *Empetrum*. Under the trees there is an even luxuriant carpet of *Ster.*, and the absence of *H. par.* is noted. In an adjacent growth, five years older, with the same light conditions, *Calluna* is half dead with long etiolated shoots. It cannot be decided with certainty whether *Empetrum* has also grown here originally, but at any rate it is the rule that *Empetrum* disappears at this stage. The vegetation approaches a pure *Ster.* sociation, nor is *H. par.* present in noticeable quantity. It might be thought that *H. par.*, in contrast with the more shade-tolerant *Ster.*, had been ousted by the shade and had not had time to immigrate after the dying down of *Calluna*, but the next example will show that this is not the case. The decisive factor here is the moisture associated with the thickness of the peat.

The heather peat decomposes rapidly, and simultaneously a fresh layer of peat is formed of needles and *Ster.*, but this formation takes place more slowly than the decomposition of the original peat. In the examples mentioned here the heather peat is hardly demonstrable any longer, and the new layer of peat has not yet attained a thickness of three cm.; and at such a slight thickness of the peat *H. par.* has never been found on the heath. The peat may long keep its slight thickness which on this soil is absolutely essential for *Ster.* to be able to compete with *H. par.* if there is the optimum illumination for both species. In some few instances, however, the *Ster.* soc. was found at a somewhat greater thickness of the peat (Table XIV, 7 and 16). In very dry places the thickness of peat essential to *H. par.* will never be attained, we have then a stable *Ster.* sociation (e. g. Table XIV, 11, which is adjacent to a *Clad.* sociation).

After its disappearance *V. vit.* will not immigrate again until the peat has reached the thickness typical of *H. par.*; and — as mentioned when we discussed the vegetation at Dueodde (p. 31) — *Empetrum* will only come back again together with *Calluna*.

The succession *Ster.*—*H. par.*—*V. vit.* will be found in all the moisture zones of the heath, from *Calluna*—*Arctostaphylos* and at any rate to *Carex Goodenoughii*. These zones depend on the height above ground-water level, which in the place here mentioned hardly has any influence on the distribution of the vegetation, since planting here has made the ground-water sink.

I do not know the details of the succession when coniferous forest is planted on cleared oak scrub with *V. myrt.*, but from the *H. par.* stage there is at any rate no difference to be seen in younger growths either in the vegetation or in its succession. This applies to oak scrub adjoining heath (Søgaard Plantation).

#### Example c.

The locality lies in the southern part of Almindingen. The original vegetation is a *Calluna* sociation, differing in the main from the one mentioned under b by the absence of lichens, *V. vit.*, and *Empetrum*. The sub-soil consists of fine moraine sand with the admixture of some clay, and the heather peat is 2—6 cm. thick. On the sociation individual represented in Table VII, 19 there is six-year-old *Pinus silvestris* but the ground vegetation does not differ from the vegetation in the open. *Molinia coerulea* does not enter into the circles, but it is present. The great resemblance to the heath in example b is due to *Calluna*, which acts very largely as an “edificator” by securing good conditions for several species. The resemblance may be more striking than the examples show, but the difference in the soil is manifested both in a deviating vegetation in spots where *Calluna* does not occur, and it is also particularly marked after planting. As on the heath, so here, there is in some parts a competition between *Calluna* and oak.

Table VII, 10 shows the vegetation of a fifteen-year-old growth at 18 % light. *Calluna* is still the frequency dominant but the growth is open. A considerable advance of *H. par.* at the expense of *Ster.* is already noticeable, a change, of which the frequency only gives a slight idea. The thickness of the peat given here is for heather peat; a new layer of peat has not been formed yet.

Table XII, 32—33 gives the vegetation in an adjoining 30—35 year old *Pinus silvestris* and *Picea excelsa* growth with a *H. par.* sociation. No light measurements are available, but the light % lies above the minimum for *Desch.* In No. 32 there is still a little heather, and the peat has the black colour of the heather peat. The thickness is only 2—3 cm., the lowest observed under the *H. par.* sociation., and this is not by chance. The greater capacity of the subsoil to retain the water here replaces the greater thickness of the peat which is essential on the heath for the colonisation of *H. par.*

That the pH of the subsoil should have any influence on the difference in the succession is excluded, for at Almindingen the pH is considerably above the upper limit of pH for *H. par.*, being near its optimum in Søgaard Plantation. A slighter thickness of the peat would, therefore, be more likely to favour *H. par.* on the heath than on moraine sand.

The *H. par.* sociation in Almindingen is even less stable than *Ster.* on the heath, and like the latter when ousted by *H. par.*, it does not reappear when it has been superseded by *Desch.* or *V. myrt.*

In some few places on comparatively dispersed soil *H. par.* is superseded by *Molinia coerulea*. The fact that *Molinia* can form a population in such localities, but not on the heath where it was found before afforestation, requires further explanation. On the heath the ground-water is of the greatest significance for the water supply of

plants which, like *Molinia*, cannot grow on the highly acid peat. The evaporation from the trees will, however, cause a lowering of the ground-water level (RAMANN, 1911, p. 454), so that the ground flora is limited to the buffer-free rainfall. On more dispersed soil the rain is retained by the mineral soil, and a lowering of the ground-water level will not, therefore, have such a revolutionary effect on the water supply of the surface, the effect being cancelled by the reduction in evaporation which the trees cause by affording shelter and shade.

#### Example d.

In Grib Forest, where the soil is more fine-grained than in the previous examples, it has been observed that, after planting, a *Calluna* sociation will pass directly into a *Desch.* sociation (Table VII, 18, which, however, still contains some *Calluna*). The material was here too small for the succession to be accounted for in detail.

The succession after clearing has not been investigated. We shall merely offer a few remarks on the behaviour of *Desch.* on different soils. After extensive clearing of forest with *H. par.* sociation in Søgaard Plantation, there will in the same year only be few *Desch.* individuals which are fertile, and they will probably be relicts. The next summer, one and half years after the clearing, *Desch.* forms a dense flowering carpet (Table IX, 17), even if it did not form a population in the forest before the clearing. *Calluna* will very quickly immigrate. On soil suitable for *V. myrt.* *Desch.* will appear after the same lapse of time, and may be preserved here for several years. Thus MÜLLER (1887, p. 49) mentions a ten-year-old *Desch.* population on soil cleared of beeches in Grib Forest. OLSEN (1921, p. 87) gives an example of how *Desch.* does not immigrate until 4—5 years after clearing, the soil being only then sufficiently acid for it. This is the case on soil suitable for *Rubus*.

### The Dependence of the Vegetation on the Intensity of the Light.

Numerous investigations are available on the depression of the various rays of light in the forest, but the results are so conflicting that it is difficult to say with certainty what rays reach the forest ground in the relatively largest amount. WIESNER (1907) could not demonstrate any difference in the spectral composition of the light by measurements with normal photographic paper and paper treated with Rhodamin-B at light intensities exceeding 0.12 %. LUNDEGÅRDH (1923, p. 419 and 1925, p. 75) finds the blue rays most reduced, and DAXER (1934) arrives at the opposite result. In dense fir growths, where the blue rays constitute 0.12 % of the blue rays in the open, KLUGH (1925) found the red rays reduced to 0.005 % of the red rays in the open, i. e. a very considerable reduction of the red rays.

By electrometric measurements in which they used filters of different colours ATKINS & POOLE (1931) arrived at the same result as LUNDEGÅRDH. The light in forests is said to be very poor in blue rays, equalling sunlight in orange red, and

much richer in deep red than the light of the sky and sunlight. This result is probably correct, for the filters used in most of the light determinations with photometric paper permitted the action of rays with a shorter wave breadth than that of orange red.

The great difficulties connected with giving equivalent expressions to the results obtained by the different methods render problematic the value of a comparison with the results of the various authors. Thus LINDQUIST gives i-values for *Vaccinium myrtillus* sociation as low as 2 in beech forest, while I have not found this deciduous species forming sociations at i-values below 20 in coniferous forest.

The upper light limit of a plant community is often determined by the lower light limit of another plant community. Hence it is in some degree dependent on the soil on which a plant community occurs what its light limits will be.

In open forests the desiccating effect of the sun will affect the distribution of the vegetation. This is plainly evident on sloping ground. If a terrain in the geographical latitude of Denmark inclines 34° towards the north, the rays of the sun will never reach it at all in the winter months, and at the summer solstice the highest angle of incidence will be 23° at noon. On a southern slope with the same inclination the angle of incidence of the sun's rays will be up to 68° at the equinox, and at the summer solstice the rays of the sun will even fall vertically on the surface of the soil. Though dunes have not so large an inclination, and trees somewhat counterbalance the desiccating action of the sun at different degrees of exposure, it is clear that the direction of the inclination must be of great importance as a plant-distributing factor. The i-values afford no information as to those effects of the sun which are dependent on the exposure, since they are measured horizontally.

In the eastern, dry regions of Europe *Calluna* occurs in denser forests than further west (RAMANN 1911, p. 472), and according to RUBNER (1921, p. 333) it has this in common with numerous other plants. RUBNER has observed that many plants only occurring outside forests in western Germany are forest plants in eastern Germany, and he thinks the reason is that the sky during the summer months is much oftener cloudless in the eastern than in the western part of Germany, so that the plants, in spite of the shade of the trees, receive an adequate amount of light. This explanation agrees with the results of WIESNER's enquiry into the light requirements of *Betula nana* and other species (1907, p. 155). He found that they required the highest relative light intensity in their most northerly situations. It is probably due to the above-mentioned facts that it has been possible to erect a *Calluna* type in Finland, whereas in Denmark it is difficult to distinguish it from the *Vac. vit.* type (BORNEBUSCH 1925, p. 209), and it is probably also the reason why *Arctostaphylos uva-ursi* does not appear at all as a forest plant in Denmark.

There are of course conifer growths still darker than those whose ground vegetation is described in Tables III, IV, and XVI (down to 0.37 % light) (mentioned at p. 27), though probably none are so dark that the want of light entirely prevents moss vegetation; but the plentiful supply of needles in connection with the slow growth of the mosses limits the latter to projecting points where the needles do not remain. Hence older growths, where the surface has become even and the supply of needles

is large, are often more sterile than younger growths at the same intensity of light, and *Abies pectinata* with its flatter needles will be more liable to check the growth of mosses than *Picea excelsa*.

Below we give a list of the lowest i-values found in a number of plant communities.

<i>Vaccinium myrtillus</i> soc.	21
<i>Empetrum nigrum</i> soc.	15
<i>Cladonia impexa</i> soc.	10
<i>Vaccinium vitis-idaea</i> soc.	7.5
<i>Deschampsia flexuosa</i> soc.	6.8
<i>Carex arenaria</i> soc.	6.2
<i>Rubus idaeus</i> soc.	4.3
<i>Hylocomium parietinum</i> soc.	3.5
<i>Oxalis acetosella</i> soc.	1.5
<i>Scleropodium purum</i> soc.	1.2
<i>Brachythecium curtum</i> soc.	1.0
<i>Stereodon cupressiformis</i> soc.	0.9
<i>Thuidium tamariscifolium</i> soc.	0.8

All moss sociations with the exception of the *H. par.* sociation which requires most light, have an upper light limit. The *Ster.* sociation may with increasing light % be superseded by the *Brach.* sociation, but usually the moss sociations are replaced by phanerogam sociations. The sociation most tolerant of shade, the *Oxalis* sociation, which can exist at a light percentage as low as 2, is of slight or no importance in that respect, for it only occurs on soil suitable for *Brach.*, and the light minimum of the *Brach.* sociation almost coincides with that of the *Oxalis* sociation. The two last-mentioned sociations will as a rule be superseded by a *Rubus—Brach.—Oxalis* sociation, which may occur at a light percentage as low as 5—6.

*Deschampsia* will often be replaced by *V. myrt.* at 20 % light or somewhat below, but under other circumstances it may form populations at 100 %. At about 10 % light *V. vit.* can colonise areas with a *H. par.* sociation. In contrast with the *V. myrt.* sociation, it has no upper light limit (see p. 17). Both species will most frequently be superseded by *Calluna* at a high light intensity. Fig. 7 gives a diagram of the zonation in a glade in a low growth of *Abies pectinata* (3—4 m.) of the first generation in a scattered birch growth with heather. In the middle we still find the *Calluna* sociation; in a zone surrounding it *V. myrt.*; and at the edge of the glade *Desch.* The only effect of the trees is from the shade they afford.

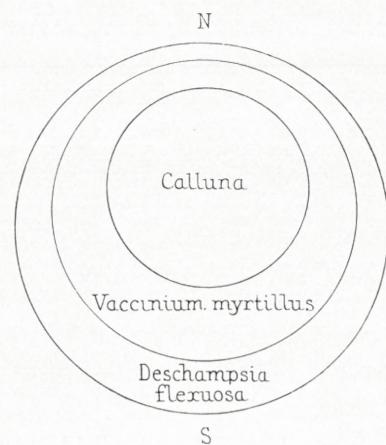


Fig. 7. Zonation of *Calluna*, *Vaccinium myrtillus*, and *Deschampsia flexuosa* according to decreasing light intensity in a glade.

When the light percentage exceeds 15—20 the desiccation caused by the sun will most affect the distribution of the vegetation on sandy soil; grasses with a predilection for light and other plants will immigrate onto clayey soil, especially *Anthoxanthum odoratum*, *Holcus lanatus*, *Agrostis stolonifera*, and *Desch. caespitosa* (see Table XVII).

### The Carbon Dioxide Concentration of the Forest Air.

In connection with the light we will discuss the CO<sub>2</sub> tension of the forest air. For there cannot be any doubt that the differing CO<sub>2</sub> conditions in forests are of great importance for the plants. They may be compared with that of light where light affects the distribution of plants because it is at the minimum of CO<sub>2</sub> assimilation.

In the open air EBERMAYER (1878) found 0.04 % CO<sub>2</sub>; in a closed fir and beech forest 0.08 % at a height of 2 m.; and 0.15 % in the humus cover; that is to say, an increasing CO<sub>2</sub> tension with decreasing height. RUSSEL and APPLEYARD (1915) always find a higher CO<sub>2</sub> concentration in soil air than in the atmosphere. LUNDEGÅRDH (1921, p. 86 and 1925, p. 363) measured 0.08 % in a *Oxalis* population in an alder and beech forest, and FEHÉR (1929, e. g. p. 37) measured a CO<sub>2</sub> amount of c. 1 mg per litre at a height of 0.30 m. in a pine forest, which corresponds to a volume percentage of c. 0.07.

LUNDEGÅRDH found that the CO<sub>2</sub> curve for *Oxalis* ascends with increasing CO<sub>2</sub> tension, and DAXER (1934), in assimilation experiments on *Oxalis* on forest soil, found that the assimilation varied with the CO<sub>2</sub> concentration of the forest air.

No investigations are available on the dependence of the assimilation on the CO<sub>2</sub> tension in mosses, but the high CO<sub>2</sub> tension in the moss carpet must be supposed to be of importance for its growth at low intensities of light. Under a dense *Rubus*—*Oxalis* population at, for instance, 8 % of light, "i" must be exceedingly low, lower than the i-value required for the *Brach.* sociation to attain a similar vigorous development as the *Brach.* population under *Rubus*—*Oxalis* (2—3 %). When the *Rubus* population is near the outskirts of a wood, where the wind may act as a ventilator, the soil will as a rule be found devoid of both *Oxalis* and *Brachythecium* (which can only be explained by desiccation in the case of *Oxalis*), even if these occur under the same edaphic conditions further in.

As LUNDEGÅRDH (1925) points out, the increase of the CO<sub>2</sub> tension with decreasing height to a certain degree compensates for the decrease in the same direction of the light intensity.

### The Influence of the Species of Tree on the Ground Vegetation.

According to CAJANDER (1909, p. 17), the similarity of the vegetation under different species of trees is fairly marked. ILVESSALO (1922, p. 34) finds greater similarity within pine and birch than within the latter and fir, and BORNEBUSCH (1925, pp. 211 and 214) arrives at a similar result. For the more luxuriant types of forest

he finds the greatest agreement in the vegetation under foliiferous trees and pine, less under pine and fir.

This does not agree with my experience in cases where the light conditions under pine and fir are uniform, or in cases where the tree population is so dense that the form and nature of the leaf, besides the differences in illumination, according as the trees are deciduous or evergreen, may affect the ground vegetation.

Under different foliiferous trees there may occur differences in the vegetation which are due to the nature of the leaves. In Grib Forest, in an *Oxalis* sociation under beech, I have observed a regular zonation of *Mercurialis perennis* around interspersed oaks. It is improbable that the differences in the light conditions which are due to the later leafing of the oak are of any importance, for the same zonation was found both in the interior of the forest and at much higher intensities of light on the outskirts. These conditions agree with the fact that beech is much more liable to form peat than oak (MÜLLER 1887).

The difference in the soil vegetation under *Picea excelsa*, *Pinus silvestris*, and *Pinus montana* may in all cases be traced to the differing influence of these trees on the forest climate, especially the light conditions, as well as to the circumstance that these trees are planted on different soils. Where the species form growths of the same density on similar soil, it has been impossible to show any difference in the soil vegetation (see e. g. Table I, 13—14, where the tree populations are so dense that their waste materials may possibly exercise a specific influence on the vegetation).

For *Abies pectinata* other conditions prevail, and the reason is that its fallen needles are changed into mould quicker than those of the other conifers on the same soil. In places where *Abies pectinata* forms peat, the ground vegetation will not be any different from that on peat under the other conifers. On more fine-grained soil, where *Abies pectinata* does not form peat, a ground flora will appear which deviates from that of the other conifers, for the latter nearly always form peat if their needles are not mixed with the leaves of foliiferous trees or of *Rubus*. In Almindingen, Rø, and Rude Forest the *Oxalis* sociation only occurs under *Abies pectinata*, often with a moss vegetation rich in species (Tables II, 11 and III, 7) which is absent in *Oxalis* sociations under foliiferous trees. On soil suitable for *V. myrt.* *Oxalis* will be found under closed beech growths just as well as under *Abies pectinata*, but perhaps with *Anemone nemorosa* and *Asperula odorata* interspersed (cp. BORNEBUSCH 1925, p. 211).

In a beech growth with a light percentage of 3.95, which was adjacent to a growth of firs with a *Rubus—Oxalis* sociation (Table I, 5, Tokkekøb) with 7.50 % light, *Anemone nemorosa* was found to be the physiognomical dominant. *Oxalis* was sparsely and evenly developed, and *Milium effusum*, *Stellaria glchidosperma*, and *Asperula* etc. were present, but not *Rubus* and *Brach.* Here the light conditions are of importance, for *Rubus* cannot grow in the shade of the beech, and *Anemone* will not thrive in the evergreen fir forest. But even where there is a slight admixture of foliiferous trees in a coniferous forest their effects will be felt, on dry soil especially by the much more luxuriant growth of *Hylocomium triquetrum* and *H. proliferum* to which they give rise.

### The Dependence of the Vegetation on the Moisture and the Thickness of the Peat.

Table 2 gives a general view of the thickness of the peat for some of the chief plant communities. The figures denote the number of occurrences within peat thickness classes of 1 cm. The values used are the mean values of the highest and lowest thicknesses of the peat found when the samples of soil were taken for the determination of acidity. Neither the green nor the dead layers of moss, which were fairly distinct from the peat proper, were included.

Table 2. The thickness of peat from a number of plant communities.

	Thickness of the peat (cm.)												Total
	1—1.5	2—2.5	3—3.5	4—4.5	5—5.5	6—6.5	7—7.5	8—8.5	9—9.5	10—10.5	11—11.5	12—12.5	13—13.5
Scleropodium purum soc. ....	...	...	...	...	2	6	4	2	1	1	..	1	17
Brachythecium curtum soc. ....	1	2	2	1	3	1	..	..	..	..	..	..	10
Carex arenaria soc. ....	...	...	..	4	3	3	..	..	..	1	..	..	11
Vaccinium myrtillus soc. ....	...	1	1	2	4	1	..	..	..	..	..	..	9
Vaccinium vitis-idaea (Empetrum) soc. ....	...	..	..	1	1	4	4	..	..	1	..	..	11
Deschampsia-Scleropodium soc. ....	..	1	4	3	2	4	1	1	1	1	1	..	19
Deschampsia flexuosa soc. ....	..	..	1	..	2	3	3	..	1	1	..	..	11
Hylocomium parietinum soc. ....	..	1	3	8	5	6	6	..	1	..	..	..	30
Stereodon cupressiformis soc. ....	..	..	4	6	3	4	1	..	..	..	..	..	18
Cladonia implexa soc. ....	1	1	1	2	1	3	..	..	..	..	..	..	9

Of the first members in the moisture series *Clad.* soc., *Ster.* soc., *H. par.* soc. (to which *V. vit.* belongs), the driest have the smallest peat thickness. The thickness of the peat under the *Desch.*—*Scl.* sociation and the *Carex arenaria* sociation varies very much. The magnitude of the peat becomes less in the *Desch.*—*Scl.* sociation and in the *Carex arenaria* sociation after these have invaded an area with a *Scl.* sociation. The peat under *V. myrt.* sociations is comparatively thin, its thickness varying from 4 to 7 cm.

The most striking example of how the thickness of the peat may influence the distribution of the vegetation, and not only be a consequence of the differing capacity of the species to produce peat, is afforded by the *Scl.* and the *Brach.* sociations. Both sociations are often found on the same kind of soil, and their light requirements are almost identical. The peat is derived from the waste products of the trees. As already mentioned, *Brach.* does not produce peat, and *Scl.*, which at a stronger light is just as productive of peat as *H. par.*, often, at the low light % of the *Scl.* sociation, has too slow a growth to have any influence of consequence on the formation of peat. The pH

of the sociations differs somewhat, but *Scl.* occurs in other sociations at the same pH as the *Brach.* sOCIATION, and *Brach.* is almost indifferent as regards pH. The average difference in the thickness of the peat is c. 4 cm. The reason why there is a very sharp limit at 6 cm. is that the character species do not form pure sociations where the thickness of the peat is about 6 cm., but a mosaic which is difficult to analyse.

The reason why the thickness of the peat is such an important factor in the distribution of the plants is in the first place that the peat, with its large capacity for retaining water, serves to regulate the moisture. But for some surface mosses, among these *Brach.*, the fir peat must be supposed to lack certain nutrient substances; it is of importance therefore, that, when the thickness of the peat is slight, the moss and the subsoil should be in close contact with each other. As far as can be judged, the moisture is greater in the *Brach.* sOCIATION individuals on turf than in the *Scl.* sOCIATION individuals with the highest degree of moisture.

While in other parts of the country the *Scl.* sOCIATION only occurs on blown sand when the sand forms a layer not excessively thick over moraine deposits, this sOCIATION is very widely distributed in Blaabjerg and Oxbol plantations. The growth of *Scl.* on dry soil must be explained by the climatic conditions, and probably especially by the comparatively cool and moist summer with frequent sea-fogs. The rainfall on the southwestern coast of Jutland is no greater than in central Jutland. The figures given for Houstrup and Aal are 675 and 745 mm. respectively; for Høllund Søgaard near Frederikshaab Plantation, where *Scl.* does not occur in the dune terrain, the figure is 758 mm.

The thickness of the peat in the *Desch.*—*Scl.* sOCIATION is less than that of the *Scl.* sOCIATION, half of the peat thickness of the sOCIATION individuals investigated lying below the minimum for the *Scl.* sOCIATION. The reason why *Scl.* can still grow here is that *Desch.* protects the moss layer from desiccation (RAUNKIÆR 1922, PALLMANN & HAFFTER 1933) and thus makes up for the effect of the slighter thickness of the peat. Where the *Desch.* population, as is often the case with the *Desch.* sOCIATION, is dependent on the desiccating action of the wind, *Scl.* has been replaced by *Ster.* which is more tolerant of drought; and it likewise depends on how much a *V. myrt.* sOCIATION individual is exposed to the wind whether the moss population is made up of *H. par.* or *Scl.*

Since it turns out that the thickness of the peat may be of importance for the distribution of the plants, the factors which affect the formation of peat are the actual plant-distributing factors. The climate is of some importance in Denmark, but it plays a subordinate part compared with that of the soil. A large amount of rain and a low temperature will favour the formation of peat. If we compare the humus layer under a growth of *Abies pectinata* of almost the same denseness and age in Sonnerup (Table XI, 8, light % 6.71) and Almindingen (Table III, 7, light % 8.26), we shall find that in Sonnerup it consists of a layer of peat 8—12 cm. deep, in Almindingen of a layer of mould a few centimetres deep. *Abies pectinata* does not form peat anywhere in Almindingen, and *Picea excelsa* only a thin layer (the *Scl.* sOCIATION does not occur in Almindingen), whereas everywhere in Sonnerup Plantation there is an

unusually vigorous formation of peat with a forest ground vegetation usually occurring on rather moist soil. Outside the plantation there is a dry vegetation typical of sandy fields. The difference in the climate in these two places is great compared with the climatic fluctuations within the area investigated, but the climate in Almindingen is best suited for the formation of peat. There is an average rainfall of 635 mm., and the average temperature is 7.1 (at the High School). In Sonnerup the corresponding figures are 509 and 7.9 (Odden). Hence the decisive difference is in the soil. In Almindingen this is fine moraine sand, at Sonnerup alluvial sand containing gravel, stones, and mollusk shells; but the ground-water level is high enough for the trees to benefit by it. Since draughtiness in forests with less porous soil may lead to the formation of peat (see p. 53), one might receive the impression that desiccation is a main condition for the formation of peat, whether or not this takes place by the water leaking away or evaporating. But since the possibilities of peat formation increase with increasing rainfall, one arrives at the conclusion that peat formation is in the first place dependent on the waste products of the plants being washed away. The reason why there is usually but a slight formation of peat on dry soil is that the vegetation is too sparse to supply the necessary waste material.

The capacity of the species for forming peat differs greatly. Where there is no soil vegetation there will always be peat under *Picea excelsa* and pine, and where there is a luxuriant growth of moss on dry soil, the production of peat is more rapid than where it is prevented by want of light, though in such places there is a more abundant supply of needles. In other words, in such cases the mosses supply the major part of the raw material for the formation of peat.

*Rubus* does not produce peat, on the contrary, it prevents the production of peat in fir woods. Species which will always form peat where they occur in stable plant communities are *Calluna*, *V. myrt.*, and *Desch.* For these species, which can grow on a subsoil whose pH is far beyond their pH amplitude, it is a life condition to be able to produce peat. *Carex arenaria* and *Brach.* do not produce peat, and *V. vit.* and *Empetrum* are probably only in slight degree productive of peat. The rather thick layer of peat in which one will always find these phanerogams, which mostly occur in open forests where the waste products of the trees are small, is chiefly derived from the moss vegetation.

Within a single *H. par.* sociation individual there will often occur a mosaic of moss cushions 20—25 cm. thick with a thin layer of peat underneath, and a moss layer a few centimetres thick underlain by a thicker layer of peat. The most natural explanation of this is that it is a consequence of an unstable equilibrium between the rate of growth of *H. par.* and the environmental factors produced by its growth. *H. par.* is one of the principal peat-producers of the conifer forests, and is thus able to augment the moisture in so far as this process is dependent on an increasing thickness of the peat. But *H. par.* has very specific moisture requirements, hence it will attain a very luxuriant growth under temporarily favourable conditions. Only after the lapse of some years will this cause so great an increase in the addition of humus

that the production of new peat exceeds the decomposition of the peat, the moisture increasing to such a degree that the growth will be checked.

*Scl.* probably behaves in the same way as *H. par.*, while *Ster.*, by adding to the thickness of its peat from another cause lowers its own life conditions, for by so doing it establishes good possibilities of existence for *H. par.* against which it cannot hold its own in the competition for space.

The dependence on the thickness of the peat seen in the *H. par.* sociation is an example of how the effect of a great porosity of the subsoil can be counterbalanced by a great thickness of the peat. On the coarse-grained soil in Sonnerup, *H. par.* (and other plants) are found at the greatest thickness of the peat, and conversely, the thickness of the peat is least on more dispersed soil (Almindingen, though here it is labile, see example c, p. 38).

The succession of the dwarf shrubs according to their ability to tolerate drought is as follows:

*Calluna*—*Empetrum*, *V. vit.*, *V. myrt.* These species are recorded from the high moor, hence they are fairly indifferent as regards the absolute moisture. From the order of the species we may already suspect a connection between the degree of xeromorphism and the ability to resist drought, the least xerophilous, *V. myrt.*, being the least xeromorphic. The facts become plainer if we consider other highmoor plants which are even less resistant to drought, for instance the *Drosera* species. These are invariably associated with a very moist substratum, and in accordance herewith their structure is hygromorphic.

*Clad.* and *Dicr. rugosum* behave exactly like the dwarf shrubs as regards moisture; most other species have a rather narrow moisture range, narrowest for *H. par.* and *Scl.*

None of the vascular plants which form extensive growths on the soil of coniferous forests are specific to these forests. On the other hand, the mosses *Brachythecium curtum* and *Ctenium crista-castrensis* only occur in coniferous forests. Both species are distributed throughout Denmark, but only *Brachythecium* forms populations over large areas. All the common species are circumpolar. Only *Scleropodium purum* and *Plagiothecium undulatum* are pronounced oceanic species.

### The Dependence of the Vegetation on the Acidity of the Soil.

After OLSEN (1921) has shown how largely acidity acts as a plant-distributing factor, and gradually as the technique has made acidity one of the most easily accessible of the chemical ecological factors, it has become the rule that an acidity investigation should form part of all more extensive ecological works. A survey of the results gained in this field in recent years will be found for instance in HOSS (1932, with a full list of the literature).

Nevertheless it is in many cases difficult to compare the results gained, partly because the samples have been taken with different objects in view, partly because

Table 3. Distribution of pH values from plant communities in which the species are frequency dominants (%).

Table 4. Distribution of pH values from the plant communities (%).

Table 5. Distribution of observed pH values in sociations with *Deschampsia flexuosa*, *Hylocomium parietinum*, and *Stereodon cupressiformis* respectively as frequency dominants, as compared with the calculated distribution.

pH .....	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9
<i>Deschampsia</i>																	
y observed (%) .	..	1.2	4.2	5.5	9.1	10.3	13.3	13.9	13.3	10.9	7.3	4.2	1.8	1.8	1.8	0.6	0.6
y calculated (%) .	..	1.7	3.2	5.4	8.1	10.8	13.0	<b>13.7</b>	13.0	10.8	8.1	5.4	3.2	1.7	0.8	0.3	0.1
Difference.....	..	+0.5	+1.0	+0.1	+1.0	-0.5	+0.3	+0.2	+0.3	+0.1	-0.8	-1.2	-1.4	+0.1	+1.0	+0.3	+0.5
<i>Hylocomium</i>																	
y observed (%) .	1.3	3.1	5.8	8.9	12.9	<b>19.1</b>	<b>16.4</b>	12.9	8.9	6.2	2.7	1.3	0.4	..	..	..	..
y calculated (%) .	1.0	2.5	5.4	9.6	14.1	<b>17.1</b>	<b>17.1</b>	14.1	9.6	5.4	2.5	1.0	0.3	..	..	..	..
Difference.....	+0.3	+0.6	+0.4	-0.7	-1.2	+2.0	-0.7	-1.2	-0.7	+0.8	+0.2	+0.3	+0.1	..	..	..	..
<i>Stereodon</i>																	
y observed (%) .	0.5	2.5	4.9	8.3	13.7	17.6	14.7	12.3	10.8	6.9	4.4	2.0	1.0	0	0.5	..	..
y calculated (%) .	0.8	2.0	4.2	7.6	11.6	14.9	<b>16.2</b>	14.9	11.6	7.6	4.2	2.0	0.8	0.3	0.1	..	..
Difference.....	-0.3	+0.5	+0.7	+0.7	+2.1	+2.7	-1.5	-2.6	-0.8	-0.7	+0.2	0	+0.2	-0.3	+0.4	..	..

Table 6. Constants of the pH variation curve for *Deschampsia flexuosa*, *Stereodon cupressiformis*, *Hylocomium parietinum*, and H. par. soc. at 18° C.

	Desch.	Ster.	H. par.	H. par. soc.
Number of determinations (n) ....	165	204	225	80
Mean value ( $M \pm m$ ).....	$4.01 \pm 0.02$	$3.89 \pm 0.02$	$3.85 \pm 0.02$	$3.87 \pm 0.02$
Standard deviation (s) 0.1 in pH as unit .....	2.92	2.46	2.30	1.80
Parameter (h).....	0.24	0.29	0.31	0.39
Most probable frequency in a pH interval of 0.1 about the mean value in % (x = 0) ..	13.7	16.2	17.5	22.0

the results will differ somewhat according as the colorimetric or the electrometric method is adopted. KOTILAINEN (1927), by adopting a special electrometric method, finds very low values. However, the relation between the pH of the species often shows good agreement.

OLSEN (1921) has first shown that pH values from the same species or plant community may range round a mean value in conformity to law, and JENNY (1926)

has shown that the pH values may be regarded as links in the statistic chain which is described by GALTON's equation of variation. As to the application of the latter to measurements of pH, see JENNY 1926, or FREY 1932.

Tables 3 and 4 show that equal intervals in the hydrogen ion concentration expressed in pH are of equal biological importance, that is to say, for the same species or plant community. Thus it is quite permissible to compute the average pH values according to the usual rules, i. e. by adding the pH values and dividing the sum by the number of determinations. This method is allowable neither for the frequency percentage nor for the light percentage.

A large number of pH measurements are necessary for these calculations, lest experimental errors, irregularities in the taking of the samples or the like should have a disturbing influence on the result.

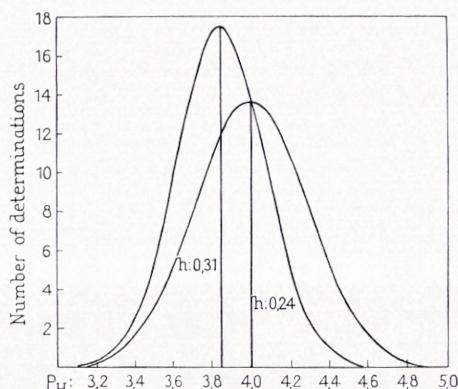
The curve of the variation of pH has been computed for *H. par.*, *Ster.*, and *Desch.* In calculating the theoretical pH curve for *H. par.*, x-values of + and - 0.5, + and - 1.5 etc., from the mean value (pH 3.85) have been used in order to render comparable the observed and calculated values of y.

Fig. 8. pH variation curve for *Hylocomium parietinum* ( $h = 0.31$ ) and *Deschampsia flexuosa* ( $h = 0.24$ ).

Table 5 will show the good agreement between the observed and the calculated values of y. The deviations are smallest for *H. par.* which always grows on a fairly thick and well delimited layer of peat, largest for *Ster.* which often grows on so thin a layer of peat that it is difficult to avoid taking up some of the subsoil, so that some of the values will be a little too high.

The pH curve for *H. par.* and *Desch.* is shown in fig. 8. The value of h is very high for all three species, that is to say, the species have a narrow range of pH. Table 6 gives some pH data for the two species, as also for *Ster.* and the *H. par.* sociation (the pH curve not calculated). The h value for *Desch.* is 0.24; somewhat higher for *Ster.* and *H. par.*, viz. 0.29 and 0.31 respectively; and highest for the *H. par.* sociation, 0.39. For comparison we may state that JENNY (1926) finds the following values of h: *Carex curvula* 0.20 (pH 4.98) and for the *C. curvula* sociation 0.28 (pH 4.82) (corresponding to *H. par.* and the *H. par.* sociation); for *Elyna myosuroides* 0.15; and for *Carex firma* 0.36 (pH 7.19). Not only peat plants but also a typical calciphilous plant such as *C. firma* show the same conformity to law in their distribution in regard to pH.

Table 3 gives the distribution of the most frequently occurring species in pH classes of 0.1 arranged according to decreasing mean value of pH. The figures give the percentage of all pH values from plant communities in which the frequency percentage of the species exceeds 80. Further the number of pH measurements (n) is given and the mean value (M) has been calculated.



In conifer forests pH is not sufficiently high to furnish any information as to the behaviour in regard to acidity of *Rubus* and *Oxalis*, which will both grow in mould. Hence I will especially deal with the acidity requirements of the peat plants. Several of the plants which are obligatory peat plants in conifer forests may, however, occur as pioneers on mineral soil without any layer of humus (*Carex arenaria*, *Calluna*, *Empetrum*, *Desch.*). *Luzula* shows the highest pH, averaging 4.21, and *Dicr. scop.* the lowest, averaging 3.71, the greatest difference in the average values thus being 0.50.

For most species of peat plants there is a great probability that the mean value will correspond closely to the pH value most characteristic of the species. There is often a distinct maximum with a gradual and fairly regular decrease to both sides. If the values were not characteristic of the species a more abrupt fall might be expected towards the low pH values, which on the whole are rarer, than towards the more frequent higher ones, at any rate for species with a particularly low pH. It is true that this is the case for some species, though not more so than would be explainable if some of the subsoil, which in this connection is of no importance for the plants, had been included in the sample of soil.

HESSELMAN (1926, p. 212) gives an average difference in the pH of the F layer and the H layer of minus 0.18—0.22 in conifer forests rich in mosses. In some cases, when the layers of peat have been especially thick, I have, besides determining pH as usual, measured the pH of the upper layer of peat and often found values exceeding by 0.1 the pH of the lower layer. The pH values for the mosses (with the exception of *Polytrichum*) will thus be a little too low.

The values found must likewise be supposed to represent approximately the whole pH amplitude of the species. A larger number of measurements will of course somewhat enlarge the amplitude and doubtless without essentially altering the mean value. pH values much lower than those found do not occur, and wherever pH is higher than that found to be characteristic of a species, that species will be replaced by others. *Brach.* for instance, will be superseded by *Eurhynchium striatum*, the pH of which rises to about 4.8, though there is no competition for room, and *Desch.* will, with a higher pH, be replaced by *Molinia*, *Desch. caespitosa*, *Holcus lanatus* or other species.

There can be no doubt, however, that competition with other species will in some cases determine the pH amplitude of a species. This is no doubt the case with *Cladonia impexa* which cannot hold its own in the competition for space with those species of the conifer forest with which it is most closely associated ecologically (*H. par.*, *Ster.*), if the external conditions are but tolerably favourable to the latter. The figures show that there is an increase in the pH % up to 3.8 followed by a great decrease at the pH maximum for *H. par.* (3.85). The mean value of pH presumably corresponds to its occurrence on mineral soil in coniferous forests, but where *H. par.* is excluded owing to other ecological conditions (great moisture), *Clad.* has a much larger ecological amplitude, which must be assumed to include the pH amplitude also.

The pH values from the rhizosphere of the peat plants where they appear as pioneers on sandy soil will as a rule prove to be higher than those found to be charac-

teristic here. As an example I may mention that under dense *Carex arenaria* populations on open dune I have found pH to be 4.5 (Sonnerup), 4.8, and 5.1 (Dueodde). Pure sand has a higher pH. It is very doubtful, however, whether these values are those found round the roots. Pure sand contains very little buffer, so that even a very slight influence from the roots ( $\text{CO}_2$ ) will be able to cause an alteration in their immediate vicinity (cp. OLSEN 1921, pp. 112 and 131). It will then generally be the pH of the sand rather than the pH of importance for the roots which the investigator measures. JENNY (1926) finds the same pH under *Carex curvula* on peat and where it is a pioneer on granite.

In peat, on the other hand, only strong influences will cause a change in the acidity, so that the pH values for peat, at any rate, represent those to be found around the roots where the plants grow in peat, but they must be supposed to be generally valid.

Table 4 gives a similar view of the pH of the plant communities. In most cases one or several character species will be frequency dominants, but to some of the species this does not always apply, as for instance *Rubus*, *Thuidium*, and *Calluna*.

The horizontal variation within the separate sociation individuals is often about 0.1—0.2. The difference is least in typical moor, somewhat greater in mould, but it is so great compared with the difference in the pH of the sociations, that the statistic treatment of the material is necessary to demonstrate a possible characteristic acidity for the sociations.

In most cases the pH values of the species and of the plant community of which it is the character plant coincide. The *Rubus*—*Brach.* sociation has, however, a higher mean value (4.40) than the two character species. The reason is that we have here included the values of some *Rubus* sociation individuals where *Rubus* is not the frequency dominant. The *Brach.* sociation has a pH 0.15 lower than the species, for where *Brach.* forms populations without *Rubus* in pure conifer woods the humus layer is always peat.

The slight difference in pH shown by the peat species as well as the peat plant communities does not mean that the acidity of the peat is an indifferent environmental factor. However, one would hardly venture to ascribe any great importance to the pH figures, if it did not turn out that the difference in the mean values entirely corresponds to the natural conditions. Thus we find *Hylocomium triquetrum* where there is an influx of ground water, where there is an admixture of foliiferous trees, or where there is a supply of lime — all factors which raise pH. Nor can it be by chance that *Dicr. scop.* which is often the frequency dominant in most of the plant communities of the coniferous forests, has the lowest average pH.

As already mentioned, the dying off of *Calluna* in *Calluna*—*Empetrum* sociations will invariably mean that *Empetrum*, too, disappears, if the ground water level is low. The reason must be that *Calluna* forms the main part of the peat in which the species grow, and the pH of the peat is c. 4.0, which is the optimum value not only for *Calluna* but also for *Empetrum*. *Empetrum* is not itself able to maintain its pH

level. Otherwise where the ground water comes to the rescue. In example 7 (p. 32) we have described the interrelation of *Empetrum* and *V. vit.* at the foot of moraine hills. *Empetrum* is only present where the ground water has any influence, *V. vit.* only where it has no influence. This quite agrees with the relation of the two species to pH. Where the ground water makes the peat less acid, *Empetrum* occurs, and on soil which only receives water in the form of rainfall *H. par.* and *V. vit.* are able to obtain the low pH which is necessary to their existence. It would seem natural to infer that *Calluna* can form a population below *Empetrum* because it has a greater influence on the soil in a way favourable to itself, but the zonation was only observed in the place mentioned.

Example 4 (p. 31) shows an analogous case which is perhaps better because the moss population is the same in all the sociations.

The *Calluna* may play the same part as the ground water as a factor in plant distribution.

It will be seen, then, that even among the extremely acidiphilous forest and bog plants there may be differences in the distribution which are exclusively due to the difference of acidity.

In the high moor, where other biotic factors than those active in forests on mineral ground make the stagnant surface water acid in the extreme, similar conditions prevail for the pH of the dwarf shrubs (KOTILAINEN 1927) and we arrive at the conclusion, therefore, that acidity is the most important edaphic plant distributing factor for these species, which are eurytrophic as regards moisture (see p. 47).

For most other peat plants it holds good that their requirements of acidity are just as specific while their moisture amplitude is considerably smaller, so that in most cases it will be difficult to decide whether the acidity or the moisture corresponding to a certain acidity is the most important environmental factor.

As a dune forest plant *Carex arenaria* has much in common with *Empetrum*, they may even form populations together (Table X, 1), and in accordance with its higher pH *Carex arenaria* is even more dependent on the ground water than *Empetrum*. Hence it always grows in company with *Scl.* It is improbable that moisture should be the decisive factor, for after planting *Carex arenaria* disappears from sandy soil where the ground water has no influence. Owing to the planting the sand receives materials (needles, moss) which make it highly acid. Only where this acidity is diminished by the ground water can *C. arenaria* grow. A (not excessive) influence of the ground water will secure a luxuriant growth of the peat-forming moss *Scl.*, which is the reason why *C. arenaria* in forests always grows in a thick layer of peat.

The most probable explanation of why *Desch.* requires exposure to the wind on soil suitable for *Rubus* seems to me to be as follows. When in a fir forest *Rubus* is ousted by shade, and the needles are no longer mixed with its leaves, the fir will always form peat. *Rubus* and the other mesophilous plants which accompany it will not, however, tolerate exposure to the wind, so that there will be a possibility that pH will come within the pH amplitude of *Desch.* Once *Desch.* has immigrated, it will continue the formation of peat up to a thickness rarely found under the *Brach.* sociation.

*Rubus* is almost indifferent to pH. The reason why it has the highest average value is that it most frequently grows on soil mixed with clay which is not as much washed out as the more porous soil. In Bromme Plantation where *Rubus* forms sociations of quite the same composition as for instance in Grib Forest, the soil is more sandy than otherwise found under *Rubus*, but the trees have been planted on arable land (cp. Table XVII, 8, where the tree population is *Pinus silvestris* of the first generation on arable).

The influence of the light on the pH of the surface soil depends on the vegetation it supports. This is most distinctly seen in forests suitable for *V. myrt.* In dark forests the ground is sterile or covered by a carpet of moss (*Ster.*, *Plag. dent.*), in both cases pH is about 3.8. If the light is strong enough for *Desch.* to immigrate, pH will rise to 4.0, only to fall again to 3.7—3.8 when the light allows *V. myrt.* to immigrate. In full light or slight shade there will again be a rise in pH about 4.0, when *Calluna* has superseded *V. myrt.* If *Calluna* does not immigrate, but for instance *Anthoxanthum*, there will be a further rise in pH because this species forms no peat.

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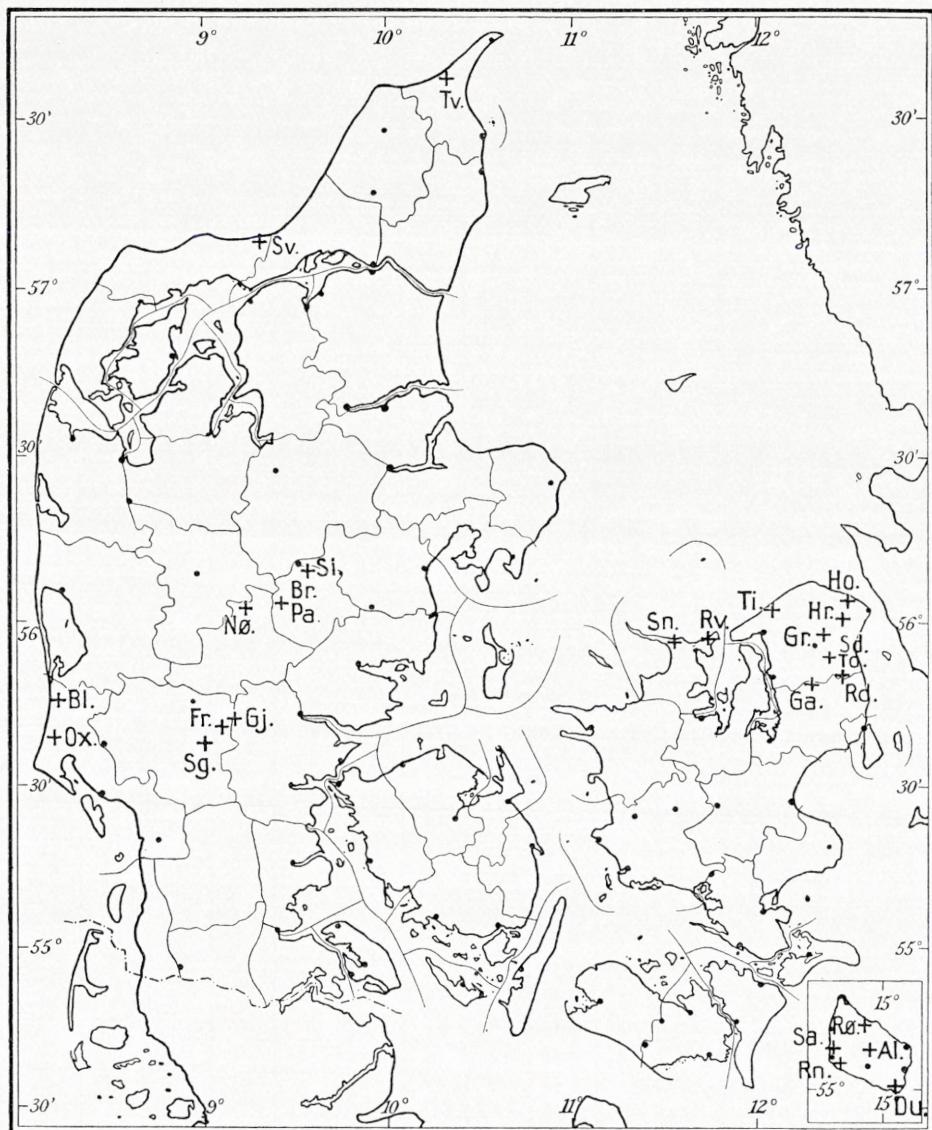


Fig. 9. Map of localities investigated.

## List of Abbreviations of the Names of Localities:

Al.: Almindingen. Bl.: Blaabjerg plantage. Br.: Bredlund plantage. Du.: Dueodde. Fr.: Frederikshaab plantage. Ga.: Ganløse Ore. Gj.: Gjøding plantage. Gr.: Grib skov. Ho.: Hornbæk plantage. Hr.: Horserød hagn. Nø.: Nørlund plantage. OX.: Oxbøl plantage. Pa.: Palsgaard plantage. Rd.: Rudeskov. Rn.: Rønne plantage. Rv.: Rorvig plantage. Rø.: Rø plantage. Sa.: Sandflugtskoven (Blykobbe plantage). Sd.: Store Dyrehave. Sg.: Søgaard plantage (Høllund). Si.: Silkeborg. Sn.: Sonnerup plantage. Sv.: Svinkløv plantage. Ti.: Tisvilde hagn. To.: Tokkekøb hagn. Tv.: Tversted plantage.

## The following Abbreviations for the Conifers have been used in the Tables:

P. exl.: *Picea exelsa* (= *P. abies*). P. can.: *Picea canadensis* (= *P. alba*). P. sit.: *Picea sitkaënsis*. P. sil.: *Pinus silvestris*. P. mon.: *Pinus montana*. P. aus.: *Pinus austriaca* (= *P. nigra*). A. pec.: *Abies pectinata* (= *A. alba*).

The fr<sup>o</sup>/ of the trees refer to cotyledonous plants.

1 as index to the age of the tree population means of the first generation.

2 means of the second or a later generation.

Table I. *Rubus idaeus* sociations.

	Melica uniflora soc.	Asperula odorata soc.	Urtica dioeca soc.	Rubus—Brachythecium—Oxalis sociation										Rubus—Brachythecium—Geranium Robertianum soc.				
No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Locality .....	Sn.	To.	Sn.	To.	To.	Gr.	Gr.	To.	Sd.	Rd.	Rd.	Sn.	Sn.	Sn.	Sn.	Gj.	Al.	
Picea abies .....	..	..	..	..	..	..	..	..	..	..	..	20	20	..	..	45	..	
Sambucus nigra .....	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	
Sorbus aucuparia .....	..	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	
Rubus fruticosus .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	
— idaeus .....	35	25	10	95	100	100	95	70	95	100	80	55	65	100	65	100	100	
Vaccinium myrtillus .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	30	..	
Anemone nemorosa .....	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	
Arenaria trinervia .....	5	..	10	5	30	10	5	..	5	5	5	65	30	..	25	..	..	
Asperula odorata .....	..	100	..	60	15	..	..	..	25	..	5	..	..	..	..	..	..	
Campanula rotundifolia ..	..	..	..	..	..	..	..	..	..	..	..	10	15	15	..	..	..	
Chamaenerium angustif...	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	50	..	
Dryopteris dilatata .....	..	5	..	..	5	..	..	..	..	..	..	..	..	..	..	35	15	
Epilobium montanum .....	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..	
Equisetum arvense .....	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	
— silvaticum .....	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Fragaria vesca .....	..	..	..	..	..	..	..	..	5	..	..	5	..	..	..	..	..	
Galeopsis tetrahit .....	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	
Galium aparine .....	..	5	5	20	10	..	..	..	..	..	..	90	35	50	15	..	..	
— hircinum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	40	..	
— uliginosum .....	..	..	..	..	..	..	5	10	..	..	..	..	..	..	..	..	..	
Geranium Robertianum ..	35	..	45	10	..	..	..	..	5	..	..	85	95	70	95	..	..	
Hypericum perforatum ..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	
Lactuca muralis .....	..	55	20	..	..	..	..	15	35	15	..	35	90	15	45	5	..	
Lampsana communis .....	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	
Majanthemum bifolium ..	..	..	..	..	..	..	..	15	..	15	..	..	..	..	..	..	..	
Oxalis acetosella .....	..	100	..	100	100	100	100	95	100	95	100	..	..	..	..	..	..	
Potentilla erecta .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	
Stellaria glochidiosperma ..	..	75	..	80	45	..	..	..	..	..	..	60	80	5	5	..	..	
— vulgaris .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Urtica dioeca .....	..	..	100	90	20	..	..	..	25	..	..	..	10	30	85	..	..	
Veronica chamaedrys .....	..	..	..	..	..	..	..	..	..	..	..	10	25	..	25	..	..	
— officinale .....	..	..	..	..	..	..	..	..	..	..	..	25	5	40	..	..	5	
Viola Riviniana .....	..	..	..	15	..	..	..	..	..	..	..	..	..	..	..	..	..	
— tricolor .....	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	
Anthoxanthum odoratum ..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	
Brachypodium sylvaticum ..	..	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	
Carex arenaria .....	..	..	..	..	..	..	..	..	..	..	..	..	..	35	5	..	..	
Dactylis glomerata .....	..	..	..	10	..	..	..	..	5	..	5	..	5	40	..	..	..	
Deschampsia caespitosa ..	..	..	..	..	5	..	..	..	5	..	..	..	..	..	..	..	..	
— flexuosa .....	..	..	..	..	..	..	..	10	..	5	5	55	15	30	40	100	100	

Table I (continued).

No. ....	Melica	Rubus—Brachythecium—Oxalis sociation											Rubus—Brachythecium—Geranium Robertianum soc.					
	uniflora soc.	Asperula																
	odorata soc.	dioeca soc.	4	5	6	7	8	9	10	11	12	13	14	15	16	17		
Locality .....	Sn.	To.	Sn.	To.	To.	Gr.	Gr.	To.	Sd.	Rd.	Rd.	Sn.	Sn.	Sn.	Gj.	Al.		
Holcus lanatus.....	..	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Juncus supinus.....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..
Luzula pilosa.....	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..
Melica uniflora.....	100	..	5	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Milium effusum.....	..	20	..	70	90	100	30	5	..	..	..	..	..	..	5	..	..	..
Poa nemoralis.....	..	5	..	25	5	..	..	..	..	..	..	25	..	..	..	..	..	..
Brachythecium curtum.....	..	5	55	100	100	100	100	90	95	100	100	75	100	85	100	100	100	100
Catharinaea undulata.....	..	..	..	..	..	..	10	..	5	..	..	..	..	..	..	..	..	..
Dicranum scoparium.....	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	10	..
Eurhynchium praelongum.....	5	..	..	95	..	25	35	25	45	15	10	..	35	5	35	10	..	..
— striatum.....	100	85	..	10	75	..	10	..	..	..	..	..	..	..	..	..	..	..
Hylocomium parietinum..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	15	20
— proliferum.....	..	..	..	..	..	..	..	..	..	..	..	35	10	..	5	..	..	10
— squarrosum.....	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..	20	..	5
— triquetrum.....	..	..	..	..	..	..	..	..	..	..	..	..	5	35	..	10	..	..
Lophocolea bidentata.....	5	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	5	100
— heterophylla.....	..	..	..	..	..	30	..	5	..	5	..	35	10	..	..	..	..	..
Mnium hornum.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— rostratum.....	25	..	..	35	90	30	55	70	65	75	40	35	25	15	90	..	..	..
— undulatum.....	..	55	..	100	65	..	..	25	50	..	..	..	..	..	..	..	..	..
Plagiothecium denticulatum.....	..	5	..	..	..	5	10	..	10	5	40	..	..	..	..	..	..	90
— repens.....	..	..	..	..	..	..	..	..	..	5	20	..	..	..	..	..	..	..
— silvaticum.....	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..
— undulatum.....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..
Polytrichum attenuatum.....	..	..	..	..	..	..	..	5	10	..	..	..	..	..	..	..	..	5
Rhodobryum roseum.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10	..
Scleropodium purum.....	60	..	..	30	15	40	15	20	25	..	10	55	65	5	70	40	..	5
Stereodon cypressiformis.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	55	20
Thuidium tamariscifolium.....	..	..	..	..	..	..	..	..	5	5	15	..	..	..	..	..	..	..
Light % (i).....	9.52	9.17	13.6	14.2	7.50	18.3	12.2	9.09	14.0	5.08	4.28	4.76	4.76	5.82	4.57	9.34	11.8	
pH of the surface soil .....	4.9	5.0	4.2	4.3	4.7	4.0	4.0	3.9	4.1	3.6	3.9	4.7	4.8	4.6	4.9	3.8	4.5	
- - - — - .....	5.0	5.0	4.3	4.3	4.8	4.3	4.1	4.0	4.2	3.8	4.0	5.0	5.0	4.7	4.9	4.0	4.5	
- - - — - .....	5.3	5.2	4.3	4.4	4.8	4.3	4.3	..	4.3	3.8	4.1	5.0	5.2	5.1	5.2	4.0	4.6	
pH of the subsoil .....	4.7*	..	4.3	..	..	..	..	3.7	..	3.8	3.9	..	..	..	..	..	..	
Thickn. of the surf. soil(cm.)	2-7	0-5	5-7	2-4	1-4	4-7	2-8	4-5	3-6	3-10	0-3	4-5	3-5	1-6	1-5	5-9	1-2	
Subsoil .....	gravel	sandy clay	gravel	sandy clay	sandy clay	sandy clay	sandy clay	clayey sand	sand	clayey sand	clayey sand	gravel	gravel	gravel	gravel	clayey sand	clayey sand	
Species of tree .....	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	A. pec.	P. exl.	P. exl.	P. sil.	P. exl.	P. exl.	P. sil.	
Age of tree.....	50	60	50	60	60	70	70	70	70	65	100	50	50	60	50	70	50	

\* In a depth of 30 cm. pH: 5.4.

Table II. *Oxalis acetosella* sociations.

Table II (continued).

	Desch.-Oxalis	Oxalis sociation									
		1	2	3	4	5	6	7	8	9	10
No. ....		Rd.	Rø	Al.	Ho.	To.	Ga.	Gr.	Si.	Rn.	Al.
Locality ....	Gr.										
Plagiochila asplenoides.....	..	..	..	..	..	..	..	..	..	..	15
Plagiothecium denticulatum.....	15	15	30	65	30	..	25	10	..	10	70
— undulatum .....	..	..	..	..	..	..	..	..	..	..	5
Polytrichum attenuatum.....	5	..	..	..	..	..	..	..	..	..	..
Scleropodium purum .....	15	..	5	5	25	5	15	70	..	5	..
Stereodon cypressiformis.....	5	..	5	25	5	..	..	5	5	..	60
Thuidium tamariscifolium.....	15	20	40	..	..	10	..	..	10	30	
Light % (i) .....	7.20	1.74	4.15	1.45	..	5.28	1.73	9.32	10.8	3.10	8.20
pH of the surface soil.....	3.9	3.7	4.9	4.6	4.1	3.5	3.9	4.0	4.2	5.3	4.3
- - - — - .....	4.0	3.9	5.0	4.8	4.1	3.6	4.1	4.0	5.1	5.6	4.8
- - - — - .....	4.1	4.0	..	..	4.3	3.6	4.5	4.2	..	..	..
pH of the subsoil.....	..	..	..	5.0	..	3.5	..	..	4.9	5.5	5.4
Thickness of the surface soil (cm)	4-7	1-4	0-2	2-3	5-7	..	2-6	4-7	2-4	2-4	1-4
Subsoil.....	clayey sand	sandy clay	clayey sand	sand	sand	turf	clayey sand	clayey sand	clayey sand	sandy clay	clayey sand
Species of tree.....	P. exl.	A. pec.	A. pec.	A. pec.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	A. pec.
Age of tree .....	55	80	50 <sup>2</sup>	40 <sup>2</sup>	65	70	80	70	60	80	60

Table III. Thuidium tamariscifolium sociations.

		Thuidium sociation					Th.-Polytr. attenuat. soc.	Oxalis— Thuidium soc.	
		1	2	3	4	5		7	8
No. ....		Al.	Rø	Hr.	Rø	Gr.	Gr.	Al.	Gr.
Locality .....									
Sorbus aucuparia.....	5	..	..	..	..	..	..	..	..
Picea abies .....	..	..	..	..	10	25	..	..	10
Rubus idaeus .....	..	..	..	..	..	..	5	..	..
Vaccinium myrtillus .....	5	..	..	..	..	..	..	10	..
Anemone nemorosa .....	..	..	..	40	..	..	..	..	..
Dryopteris dilatate .....	..	..	..	..	..	10	..	..	5
Oxalis acetosella.....	..	..	..	..	..	10	100	100	

Table III (continued).

	Thuidium sociation					Th.-Polytr. attenuat. soc.	Oxalis— Thuidium soc.	
	1	2	3	4	5		7	8
No. ....	Al.	Rø	Hr.	Rø	Gr.	Gr.	Al.	Gr.
Locality .....								
Agrostis stolonifera .....	..	..	..	..	..	..	5	..
Carex hirta .....	..	..	..	..	..	..	5	..
— pilulifera .....	..	..	..	..	30	20	5	15
Deschampsia flexuosa .....	..	..	..	..	..	..	5	10
Luzula pilosa .....	..	..	..	..	..	..	5	..
Brachythecium curtum .....	10	..	..	..	5	5	5	35
Dicranum majus .....	..	..	..	..	35	75	35	15
— scoparium .....	5	..	..	..	..	..	5	5
Eurhynchium praelongum .....	15	..	..	..	..	..	40	..
— striatum .....	10	..	..	..	..	..	50	15
Hylocomium loereum .....	..	..	..	..	..	10	40	..
— parietinum .....	10	..	..	..	25	10	..	20
— proliferum .....	10	..	..	..	10	5	..	25
— squarrosum .....	..	..	5	..	..	..	..	..
— triquetrum .....	10	..	..	65	10	..	..	..
Lophocolea heterophylla .....	45	5	20	..	..	10	55	..
Mnium hornum .....	..	..	5	..	..	..	5	5
— rostratum .....	..	..	..	..	..	..	..	90
— undulatum .....	25	..	..	50	..	..	5	..
Plagiochila asplenoides .....	..	..	..	..	..	..	55	..
Plagiothecium denticulatum .....	..	5	..	5	..	10	35	10
— undulatum .....	5	..	..	..	..	..	..	..
Polytrichum attenuatum .....	..	5	..	..	5	100	70	..
Scleropodium purum .....	50	25	..	..	25	..	30	40
Stereodon cupressiformis .....	45	..	..	..	..	..	10	..
Thuidium tamariscifolium .....	80	100	50	100	100	100	90	100
Light % (i) .....	2.50	0.82	1.39	0.91	4.24	4.78	8.26	7.73
pH of the humus layer .....	4.0	3.4	3.9	5.1	3.8	3.6	4.3	4.1
- - - — — .....	..	3.8	..	5.2	3.8	3.7	4.5	4.1
- - - — — .....	..	3.8	..	..	3.9	3.9	..	4.2
pH of the subsoil .....	4.7	..	..	5.4	..	..	..	..
Thickness of the humus layer (cm.) ....	0-8	4-8	7-8	0	5-10	4-7	0-2	5-12
Subsoil .....	sand	clayey sand	sand	sandy clay	clayey sand	clayey sand	clayey sand	clayey sand
Species of tree .....	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	A. pec.	P. excl.
Age of tree .....	50	70	35 <sup>1</sup>	60	60	55	70	80

Table IV. *Brachythecium curtum* sociation.

	Eurhynch. striatum soc.		Brachythecium curtum sociation												
	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Locality .....	No.	Rø	Gr.	Al.	Rø	To.	Sd.	Ga.	Sn.	Ti.	Ti.	Rø	Gr.	Si	
Abies alba .....	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..
Picea abies .....	..	..	..	..	..	5	..	..	5	90	..	40	..	..	..
Rubus idaeus .....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Vaccinium myrtillus .....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..
Arenaria trinervia .....	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..
Asperula odorata .....	..	..	..	..	..	..	..	..	15	..	..	..	..	..	..
Lactuca muralis .....	..	..	..	..	5	10	25	..	40	..	..	..	..	..	..
Oxalis acetosella .....	..	..	..	..	..	30	85	5	5	..	..	..	..	..	..
Stellaria media .....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Veronica officinalis .....	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..
Viola silvestris .....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Brachythecium curtum .....	..	..	100	80	95	100	90	100	100	100	80	95	100	45	
Dicranum scoparium .....	5	..	20	20	..	15	..	..	..	55	40	80	40	10	
Eurhynchium praelongum .....	15	20	60	5	40	35	..	35	30	15	5	..	20	50	
— striatum .....	70	20	..	..	..	..	..	..	..	..	..	..	..	10	
Hylocomium parietinum .....	5	..	5	15	..	5	..	..	..	15	..	20	..	10	
— proliferum .....	5	..	..	15	..	5	..	5	70	20	40	20	5	30	
— triquetrum .....	..	..	..	..	..	5	..	..	65	..	..	..	..	..	
Lophocolea heterophylla .....	..	75	25	20	100	30	10	15	25	45	55	70	35	25	
Mnium hornum .....	..	..	..	..	..	5	..	..	..	..	..	10	..	..	
— rostratum .....	..	..	..	..	..	..	95	20	65	75	50	..	..	35	
— undulatum .....	..	10	..	..	..	..	..	..	..	..	..	..	..	..	
Pylaisia polyantha .....	..	..	..	..	..	..	..	..	..	5	..	..	..	..	
Plagiothecium denticulatum .....	45	20	20	15	55	..	5	..	..	..	..	100	65	5	
— repens .....	..	25	..	..	..	5	..	..	..	..	..	..	..	..	
— silvatica .....	..	..	..	..	..	35	..	..	..	..	..	..	..	..	
— undulatum .....	..	..	..	5	..	..	..	..	..	..	5	..	100	..	
Scleropodium purum .....	..	..	70	20	..	5	65	20	55	35	60	20	10	35	
Stereodon cupressiformis .....	20	..	..	40	..	..	..	..	..	35	95	95	..	60	
Thuidium tamariscifolium .....	..	15	..	60	..	..	..	30	5	..	20	15	..	..	
Light % (i) .....	0.41	0.60	4.28	..	5.45	2.80	6.66	1.69	3.33	0.96	..	1.09	4.09	3.24	
pH of the peat .....	4.8	4.7	3.6	3.9	4.5	3.6	3.7	3.7	4.5	3.7	3.8	4.0	3.7	4.3	
- - - — .....	4.8	5.2	3.8	4.0	4.7	3.6	3.8	3.8	4.8	3.9	3.9	4.0	3.7	4.4	
- - - - .....	4.9	..	4.0	4.2	..	..	..	4.0	4.9	..	..	4.1	3.7	4.4	
pH of the subsoil .....	..	5.7	..	..	5.4	3.6	4.3	..	..	4.7	4.4	..	..	5.1	
Thickness of the peat (cm.)	1-3	0-4	4-8	1-4	0-2	..	4-7	1-4	3-5	4-6	2-5	3-7	..	2-4	
Subsoil .....	sand	sandy clay	turf		clayey sand	turf	clayey sand	sand	gravel	sand	sand	sandy clay	turf	stony sand	
Species of tree .....	P. excl.	A. pec.	P. excl.	P. excl.	A. pec.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	
Age of tree .....	20 <sup>1</sup>	80	40 <sup>2</sup>	40 <sup>1</sup>	60	70	70	..	50 <sup>1</sup>	40-70	20 <sup>2</sup>	70 <sup>2</sup>	40	40	40 <sup>1</sup>

Table V. *Vaccinium myrtillus* sociations.

	Pteridium— <i>V. myrt.</i> soc.			<i>V. myrt.</i> <i>V.v.-i.soc.</i>	Vaccinium myrtillus sociation					
	1	2	3		4	5	6	7	8	9
No. ....	Si.	Si.	Si.	Al.	Si.	Al.	Si.	Al.	Al.	Al.
Locality .....	Si.	Si.	Si.	Al.	Si.	Al.	Si.	Al.	Al.	Al.
Calluna vulgaris.....	...	...	20	10	..	..	..	10	..	..
Vaccinium myrtillus.....	100	100	100	100	100	100	100	100	100	100
— <i>vitis-idaea</i> .....	5	35	100	..	..	..	..	..	..	..
Galium harcynicum.....	..	5	..	..	..	..	..	..	..	..
Majanthemum bifolium.....	..	..	..	25	..	..	..	..	..	..
Potentilla erecta.....	..	..	..	15	..	..	..	..	..	..
Pteridium aquilinum.....	65	75	..	..	..	..	..	..	..	..
Trientalis europaea.....	..	90	80	..	..	..	..	..	..	..
Deschampsia flexuosa.....	5	100	100	100	65	80	60	95	50	..
Luzula pilosa.....	..	75	70	..	..	..	..	15	..	..
Molinia coerulea.....	5	..	..	5	..	..	..	..	..	..
Brachythecium curtum.....	..	..	..	..	..	..	..	15	20	..
Dicranum rugosum.....	5	10	15	5	10	20	5	..	..	..
— <i>scoparium</i> .....	..	20	25	45	..	90	80	95	10	..
Eurhynchium praelongum.....	..	..	..	..	..	..	..	..	..	5
Hylocomium loereum.....	..	..	..	..	..	..	5	..	..	..
— <i>parietinum</i> .....	..	10	80	35	100	85	100	95	5	..
— <i>proliferum</i> .....	15	..	30	30	90	55	10	45	..	..
— <i>squarrosum</i> .....	..	..	..	15	..	10	..	..	..	..
— <i>triquetrum</i> .....	..	..	..	..	5	..	..	..	..	..
Lophocolea bidentata.....	..	10	15	90	..	100	..	20	25	..
— <i>heterophylla</i> .....	..	..	5	..	..	15	..	..	25	..
Mnium rostratum.....	..	..	..	..	..	..	..	..	..	15
Plagiothecium denticulatum.....	..	..	..	5	..	25	..	55	80	..
— <i>undulatum</i> .....	..	..	5	5	..	..	5	..	..	..
Polytrichum attenuatum.....	5	..	..	..	..	..	..	10	..	..
Rhodobryum roseum.....	..	..	..	..	..	..	..	..	..	5
Scleropodium purum.....	40	100	100	100	25	30	..	45	20	..
Stereodon cupressiformis.....	95	10	5	5	5	95	100	10	80	..
Light % (i) .....	30.9	28.3	31.5	23.0	24.0	20.9	27.1	23.9	39.6	..
pH of the peat .....	3.4	3.8	3.9	3.4	3.7	3.5	3.5	3.8	4.1	..
- - - — .....	3.6	3.8	3.9	3.5	3.7	3.6	3.7	3.9	4.3	..
- - - — .....	3.6	3.9	4.0	3.5	3.7	3.6	3.8	..	..	..
pH of the subsoil .....	..	..	..	..	..	..	..	4.5	5.4	..
Thickness of the peat (cm.).....	6-8	4-7	5-7	4-8	5-8	4-8	4-7	2-6	2-5	..
Subsoil .....	stony sand	stony sand	sand	sand	sand	sand	stony sand	clayey sand	stony sand	..
Species of tree.....	P. sil.	P. sil.	P. sil.	P. exl.	P. sil.	P. exl.	P. sil.	A. pec.	P. sil.	..
Age of tree.....	65	75	75	70	40 <sup>2</sup>	70	45	18 <sup>1</sup>	70	..

Table VI. *Vaccinium vitis-idaea* and *Empetrum* sociations.

No. ....	Empetrum soc.				Emp.— V. vit. soc.		Vaccinium vitis-idaea sociation									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Locality .....	Sa.	Ti.	Ho.	Du.	Br.	Sg.	Sg.	Sg.	Br.	Si.	Si.	Sv.	Si.	Si.	Sa.	
Picea abies.....	..	..	..	..	..	..	..	..	..	..	45	..	..	..	..	..
Pinus silvestris .....	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..
Sorbus aucuparia .....	..	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..
Juniperus communis .....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..
Calluna vulgaris .....	5	35	15	45	..	5	..	5	..	..	..	..	..	..	..	..
Empetrum nigrum .....	100	100	100	100	100	90	25	5	5	..	..	5	20	..	..	..
Erica tetralix.....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..
Vaccinium myrtillus.....	..	..	..	..	..	..	..	..	..	..	..	..	15	10	..	..
— vitis-idaea.....	..	..	..	..	100	100	100	100	100	100	100	100	95	100	100	100
Galium harcynicum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	15	..	..
Goodyera repens.....	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Polypodium vulgare.....	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	15
Potentilla erecta .....	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..
Trientalis europaea.....	..	..	..	..	..	..	..	..	..	..	..	..	10	45	..	..
Carex arenaria.....	..	15	..	5	..	..	..	..	..	..	..	..	100	..	25	..
— pilulifera .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
Deschampsia flexuosa .....	100	..	85	..	..	15	20	30	50	..	..	35	..	100	20	..
Luzula pilosa .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
Blepharozia ciliaris .....	..	..	..	..	15	25	..	5	20	15	..	..	20	..	..	..
Brachythecium curtum .....	45	..	..	..	..	..	..	..	..	..	..	..	..	35	..	..
Ctenium crista-castreensis .....	..	..	..	5	5	..	10	..	..	..	..	..	..	..	..	..
Dicranum rugosum .....	10	20	10	35	15	70	20	15	25	15	15	10	..	5	20	..
— scoparium .....	5	20	15	45	75	55	35	35	55	50	90	45	10	25	30	..
Hylocomium loereum .....	..	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..
— parietinum .....	90	60	90	100	100	100	100	95	100	100	100	100	60	50	85	..
— proliferum .....	100	40	90	25	35	20	20	..	10	5	95	90	60	35	25	..
— squarrosum .....	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
— triquetrum .....	..	..	..	..	..	..	..	..	..	..	..	..	50	..	..	..
Lophocolea bidentata .....	..	..	..	..	..	..	..	5	..	..	..	..	30	35	..	..
Plagiothecium denticulatum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	25	..	..
Polytrichum attenuatum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	35	..	..
Scleropodium purum .....	100	100	95	..	..	..	..	..	..	..	..	..	..	45	10	95
Stereodon cupressiformis .....	5	10	25	95	90	25	60	100	45	45	100	80	85	85	..	..
Light % (i) .....	14.8	..	18.2	34.4	16.9	25.0	17.0	19.5	14.5	15.2	7.50	37.0	26.5	36.7	41.2	..
pH of the peat .....	4.1	4.0	3.7	3.7	4.0	3.7	3.6	3.5	3.8	3.8	3.3	3.3	4.0	3.7	4.3	..
- - - — .....	4.2	4.3	4.0	3.9	4.0	3.7	3.8	3.8	3.8	4.0	3.3	3.5	4.0	3.9	4.4	..
- - - — .....	4.4	..	4.1	3.9	4.2	..	3.9	3.9	..	..	3.5	3.6	4.5	4.0	..	..
pH of the subsoil (everywhere sand) .....	..	..	..	..	..	..	..	..	4.6	..	3.2	..	..	..	..	5.4
Thickness of the peat (cm.) .....	6-10	4-6	4-8	5-7	7-8	6-9	4-8	5-8	6-8	6-8	8-15	4-7	2-6	3-9	4-9	..
Species of tree .....	P. sil.	P. sil.	P. sil.	P. sil.	P. mon.	P. mon.	P. mon.	P. mon.	P. mon.	P. mon.	P. excl.	P. sil.	P. sil.	P. sil.	P. sil.	..
Age of tree .....	45 <sup>2</sup>	70	70	40 <sup>1</sup>	30 <sup>1</sup>	40 <sup>1</sup>	40 <sup>1</sup>	30 <sup>1</sup>	35 <sup>1</sup>	35 <sup>1</sup>	55	45 <sup>1</sup>	30 <sup>1</sup>	45 <sup>1</sup>	80	..

Table VII. *Calluna vulgaris* sociations.

	Heath	Calluna—Empetrum soc.						Calluna-Empetr.-Cladonia soc.	Calluna sociation												
		1	2	3	4	5	6		7	8	9	10	11	12	13	14	15	16	17	18	19
No. ....		Sg.	Sa.	Rv.	Ti.	Du.	Sg.	Si.	Sg.	Sn.	Al.	Si.	Si.	Ti.	Rv.	Si.	Sg.	Sn.	Gr.	Al.	
Locality .....																					
Rubus idaeus .....		..	..	..	..	..	..		..	..	..	..	..	5	..	..	..	..	20	..	
Arctostaphylos uva-ursi .	40	..	..	..	..	..	..		..	..	..	..	..	..	..	..	..	..	..	..	
Calluna vulgaris.....	100	95	100	100	95	55	80	100	100	100	100	100	100	100	55	60	90	65	100		
Empetrum nigrum.....	100	85	95	60	100	75	65	35	5	..	..	..	..	15	..	..	..	..	..		
Erica tetralix .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..		
Myrica gale.....	..	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		
Vaccinium vitis-idaea ..	70	..	..	..	..	..	15	..	..	..	..	..	..	..	..	..	..	..	..		
Galium harcynicum.....	..	..	..	..	..	..	..	..	..	..	..	..	15	..	..	5	..	..	5		
Polypodium vulgare .....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	10	
Potentilla erecta .....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..		
Trientalis europaea .....	..	..	..	..	..	..	..	..	..	..	..	..	15	5	..	15	..	..	..		
Carex arenaria .....	..	20	60	..	..	..	..	..	..	85	..	..	..	5	95	10	5	100	..	..	
— pilulifera .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	
Deschampsia flexuosa ..	10	10	..	10	..	..	..	..	70	20	20	90	10	..	30	5	100	100	15		
Luzula pilosa .....	..	..	..	15	..	..	..	..	..	..	..	..	15	..	..	..	..	..	5		
Molinia coerulea .....	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		
Scirpus caespitosus .....	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..		
Blepharozia ciliaris .....	..	..	..	..	..	..	..	15	..	20	75	5	..	..	..	..	..	..	..	90	
Brachythecium curtum ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	15	..	5	..	..		
Ctenium crista-castrensis ..	..	15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		
Dicranum rugosum .....	20	70	65	60	..	..	5	10	15	..	30	15	30	30	..	..	..	..	..		
— scoparium .....	20	35	15	10	10	15	5	10	75	30	25	40	..	20	10	10	40	50	90		
Hylocomium parietinum ..	100	95	100	100	90	..	5	15	80	95	100	100	95	85	55	10	..	65	80		
— proliferum .....	..	50	85	85	..	..	..	..	..	5	..	75	45	40	..	5	5	15	..		
— triquetrum .....	..	..	5	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..		
Leucobryum glaucum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..		
Lophocolea bidentata ..	..	..	..	30	..	..	..	..	..	..	..	..	..	..	..	5	5	..	..		
— heterophylla .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..	..		
Polytrichum attenuatum ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5		
— juniperinum .....	10	..	..	..	..	..	..	20	..	10	..	5	..	..	15	..	..	..	..		
— piliferum .....	..	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	..		
Scleropodium purum .....	..	85	45	35	..	..	..	..	..	..	..	..	5	20	25	10	..	..	5		
Stereodon cupressiformis ..	100	65	95	100	100	100	65	100	100	70	95	100	70	100	90	100	85	95	100		
Cladonia impexa .....	70	..	..	..	..	..	5	100	40	..	..	..	..	10	..	..	..	..	..		
— rangiferina .....	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		
— sp. ....	..	..	..	..	..	..	..	5	..	..	..	..	..	..	5	..	..	..	..		

Table VII (continued).

Heath	Calluna—Empetrum soc.							Calluna-Empetr.-Cladonia soc.							Calluna sociation						
	No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
Locality .....	Sg.	Sa.	Rv.	Ti.	Du.	Sg.	Si.	Sg.	Sn.	Al.	Si.	Si.	Ti.	Rv.	Si.	Sg.	Sn.	Gr.	Al.		
Light % (i).....	100	16.0	13.8	27.0	65.0	12.7	60	43.4	52.2	18.1	67.3	14.3	..	13.6	8.52	11.4	7.9	11.5	70		
pH of the peat .....	3.7	4.1	3.8	4.1	4.1	3.6	3.5	4.0	4.0	4.2	3.8	3.7	4.0	3.9	4.3	3.9	3.8	3.6	4.2		
- - - — .....	..	4.2	3.9	..	4.1	3.6	3.7	4.1	4.1	4.2	3.9	3.9	4.0	3.9	4.7	..	4.2	4.0	4.3		
- - - — .....	..	4.2	3.9	..	..	..	..	..	4.4	4.3	3.9	3.9	..	3.9	..	..	4.2	4.1	..		
pH of the subsoil .....	..	..	..	..	..	..	..	4.3	..	..	..	..	..	..	..	5.2	4.1	..	..	5.2	
Thickness of the peat (cm.)	2-7	3-5	4-6	5-8	2-4	1-2	0-3	1-5	..	2-5	2-6	4-8	5-6	4-6	1-3	2-3	8-10	..	2-6		
Subsoil .....	sand	sand	sand	sand	sand	sand	gravel	sand	sand	clayey sand	sand	gravel	sand	sand	stony sand	sand	gravel	clayey sand	clayey sand		
Species of tree .....	..	P. sil.	P. aus.	P. sil.	P. sil.	P. mon.	P. sil.	P. mon.	P. sil.	P. sil.	P. sil.	P. sil.	P. sil.	P. aus.	P. mon.	P. mon.	P. sil.	P. sil.	P. sil.		
Ages of tree .....	..	60	60	65	10-40	11 <sup>1</sup>	20 <sup>1</sup>	27 <sup>1</sup>	25 <sup>1</sup>	15 <sup>1</sup>	8 <sup>1</sup>	10 <sup>1</sup>	75	60	9 <sup>1</sup>	16 <sup>1</sup>	13 <sup>1</sup>	16 <sup>2</sup>	6 <sup>1</sup>		

Table VIII. *Deschampsia flexuosa*—

No. ....	1	2	3	4	5	6	7	8
Locality .....	Bl.	Ti.	Sa.	Ho.	Rn.	Rn.	Rn.	Sn.
<i>Sorbus aucuparia</i> .....	..	..	..	..	..	5	..	..
<i>Lonicera periclymenum</i> .....	..	..	65	..	..	20	..	..
<i>Rubus fruticosus</i> .....	..	..	15	..	..	10	..	..
— <i>idaeus</i> .....	..	..	..	..	..	..	..	10
<i>Calluna vulgaris</i> .....	..	..	..	..	..	..	20	5
<i>Vaccinium myrtillus</i> .....	..	..	..	..	..	..	..	..
— <i>vitis-idaea</i> .....	..	..	5	..	..	..	..	..
<i>Dryopteris dilatata</i> .....	..	..	..	..	..	..	..	..
<i>Campanula rotundifolia</i> .....	..	..	..	..	..	..	..	..
<i>Convallaria majalis</i> .....	..	..	25	..	..	..	..	..
<i>Galium harcynicum</i> .....	..	..	..	..	..	..	..	..
— <i>verum</i> .....	..	..	..	..	..	..	5	..
<i>Goodyera repens</i> .....	..	25	..	..	..	..	..	..
<i>Hieracium umbellatum</i> .....	..	..	..	..	5	..	..	..
<i>Lactuca muralis</i> .....	..	10	..	..	..	..	..	65
<i>Majanthemum bifolium</i> .....	..	..	..	..	..	..	..	..
<i>Melampyrum vulgarum</i> .....	..	..	..	20	..	..	..	..
<i>Oxalis acetosella</i> .....	..	..	20	..	..	..	..	..
<i>Polypodium vulgare</i> .....	..	..	5	..	..	..	..	..
<i>Potentilla erecta</i> .....	..	..	..	..	..	..	..	..
<i>Pteridium aquilinum</i> .....	..	..	..	..	..	..	..	..
<i>Senecio sylvaticus</i> .....	..	..	..	..	..	..	..	..
<i>Trifolium europaea</i> .....	65	15	..	..	..	..	..	..
<i>Agrostis stolonifera</i> .....	..	..	..	..	..	..	..	..
— <i>tenuis</i> .....	..	..	..	..	..	..	..	..
<i>Anthoxanthum odoratum</i> .....	..	..	..	..	..	..	20	..
<i>Avena elatior</i> .....	..	..	..	..	..	..	..	..
<i>Carex arenaria</i> .....	..	..	90	..	..	20	..	35
— <i>hirsuta</i> .....	..	..	..	..	..	..	..	..
— <i>panicea</i> .....	..	..	..	..	..	..	..	..
— <i>pilulifera</i> .....	..	..	..	..	..	..	..	..
<i>Dactylis glomerata</i> .....	..	..	..	..	..	..	..	..
<i>Deschampsia flexuosa</i> .....	100	95	95	100	100	100	100	100
<i>Holcus lanatus</i> .....	..	..	..	..	..	..	..	..
<i>Luzula congesta</i> .....	..	..	..	..	..	..	..	..
— <i>pilosa</i> .....	..	35	..	75	..	10	..	..
<i>Poa pratensis</i> .....	..	..	..	..	..	..	..	..
<i>Blepharozia ciliaris</i> .....	10	..	..	..	..	..	..	..
<i>Brachythecium curtum</i> .....	..	..	..	..	15	..	..	..
<i>Ctenium crista-castrensis</i> .....	..	..	5	5	..	..	..	..
<i>Dicranum majus</i> .....	..	..	..	..	..	..	..	..
— <i>rugosum</i> .....	..	..	5	..	..	5	..	5
— <i>scoparium</i> .....	10	5	5	5	5	15	5	45

### Scleropodium purum sociation.

9 \*

Table VIII

No. ....	1	2	3	4	5	6	7	8
Locality . . . . .	Bl.	Ti.	Sa.	Ho.	Rn.	Rn.	Rn.	Sn.
<i>Eurhynchium praelongum</i> . . . . .	..	..	..	..	..	..	..	..
<i>Hylocomium loereum</i> . . . . .	..	..	..	..	..	..	..	..
— <i>parietinum</i> . . . . .	15	..	60	5	5	35	..	10
— <i>proliferum</i> . . . . .	25	10	65	30	..	15	10	5
— <i>squarrosum</i> . . . . .	..	..	..	..	..	..	..	..
— <i>triquetrum</i> . . . . .	10	25	..	40	..	..	..	5
<i>Lophocolea bidentata</i> . . . . .	..	5	..	..	..	..	..	5
— <i>heterophylla</i> . . . . .	..	..	..	..	..	..	..	..
<i>Mnium rostratum</i> . . . . .	..	..	..	..	..	..	..	..
<i>Plagiothecium denticulatum</i> . . . . .	..	..	..	..	..	..	..	..
— <i>silvaticum</i> . . . . .	..	..	..	..	..	..	..	..
— <i>undulatum</i> . . . . .	..	..	..	..	..	..	..	..
<i>Polytrichum attenuatum</i> . . . . .	..	..	..	..	..	..	..	..
<i>Scleropodium purum</i> . . . . .	100	100	100	100	100	100	100	95
<i>Stereodon cupressiformis</i> . . . . .	100	..	..	..	5	..	..	45
<i>Thuidium tamariscifolium</i> . . . . .	..	..	..	..	..	..	..	..
Light % (i) . . . . .	..	..	..	6.82	7.16	16.7	21.8	24.4
pH of the peat . . . . .	3.5	3.9	4.3	3.8	4.2	4.1	4.7	3.8
- - - — . . . . .	3.6	4.0	4.3	3.8	4.2	4.3	4.9	3.8
- - - — . . . . .	3.7	..	4.4	3.8	4.3	4.3	..	3.9
pH of the subsoil . . . . .	..	4.6	..	..	5.2	..	..	..
Thickness of the peat (cm.) . . . . .	6-9	7-10	4-9	4-7	2-5	2-5	2-4	..
Subsoil . . . . .	sand	sand	sand	sand	sand	sand	gravel	gravel
Species of tree . . . . .	P. mon.	P. exl.	P. sil.	P. exl.	P. sil.	P. sil.	P. sil.	P. sil.
Age of tree . . . . .	45 <sup>1</sup>	50 <sup>2</sup>	80	70	70	70	80	75

(continued).

9	10	11	12	13	14	15	16	17	18	19	20	21	22
Tv.	Ox.	Bl.	Al.	Ho.	Si.	Fr.	Si.	Al.	To.	Gr.	Gr.	Al.	Sn.
..	..	..	..	..	..	..	..	..	..	..	15	..	..
..	..	..	..	..	..	..	..	..	..	..	10	..	..
50	10	70	5	5	40	5	60	30	..	20	5	5	..
75	30	35	65	..	10	10	40	5	15	45	60	..	15
..	..	..	15	..	..	..	..	5	..	..	..	25	35
10	..	5	..	..	..	..	..	..	..	..	25	..	..
55	45	80	45	10	..	..	85	5	20	5	50	20	..
..	..	..	10	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	45	..	..
..	..	..	10	..	5	5	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	5	10	..
70	100	85	95	95	95	100	85	100	90	100	100	90	100
15	25	95	..	30	90	..	60	15	..	40	..	..	..
..	..	..	..	..	..	..	..	5	..	10	5	5	..
17.7	9.32	21.4	..	..	6.75	10.4	8.30	12.3	..	9.17	12.7	28.2	41.1
4.3	3.5	3.7	4.4	3.9	4.1	4.0	3.6	4.1	3.8	3.7*	3.6	4.3	4.0
4.6	3.7	3.7	4.7	3.9	4.2	4.2	3.8	4.3	3.9	3.9	3.7	4.4	4.0
4.8	..	3.7	..	3.9	..	4.2	3.8	..	4.0	3.7	..	4.2	..
..	..	4.3	5.0	..	..	..	..	4.6	3.7	..	..	5.5	..
5-8	3-8	6-7	1-6	..	4-8	2-6	3-5	3-5	..	8-14	8-13	1-4	7-11
sand	sand	sand	sand	sand	gravel	stony sand	sand	clayey sand	clayey sand	clayey sand	clayey sand	stony sand	gravel
P. mon.	P. mon.	P. mon.	P. excl.	P. excl.	P. excl.	P. excl.	P. mon.	P. excl.	P. excl.	P. excl.	P. excl.	P. sil.	P. sil.
40 <sup>1</sup>	50 <sup>1</sup>	45	80	70	70	120	15 <sup>1</sup>	15 <sup>1</sup>	70	60	80	70	80

\* Upper peat pH 3.9.

Table IX. Deschampsia flexuosa sociations.

	Deschampsia flexuosa sociation											Desch.— Galium harcynicum soc.		Deschampsia—Hylocomium parietinum soc.			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. ....	Rø	Rø	To.	Gj.	Al.	Ti.	Al.	Ox.	Sn.	Sn.	Gr.	Si.	Br.	Si.	Si.	Fr.	Sg.
Locality ....	Rø	Rø	To.	Gj.	Al.	Ti.	Al.	Ox.	Sn.	Sn.	Gr.	Si.	Br.	Si.	Si.	Fr.	Sg.
Picea abies.....	...	...	...	...	...	...	...	...	...	...	...	...	...	5	...	...	...
Populus tremula.....	...	...	...	...	...	...	5	...	...	...	...	...	...	...	...	...	...
Sorbus aucuparia.....	...	...	...	...	...	...	...	5	...	...	...	20	...	...	35	...	...
Lonicera periclymenum	100	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Rubus fruticosus .....	...	5	...	...	...	...	...	...	...	...	...	20	...	...	...	...	...
— idaeus .....	25	..	..	10	..	..	..	..	..	..	55	..	..	..	..	..	..
Calluna vulgaris .....	5	..	..	..	..	5	..	20	..	10	10	..	5	..	5	10	..
Vaccinium myrtillus .....	..	..	..	..	5	..	25	..	..	..	..	5	..	15	..	..	..
— vitis-idaea .....	..	..	..	..	..	..	..	..	..	..	..	5	35	..	..	5	..
Arenaria trinervia .....	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Dryopteris dilatata .....	..	..	..	..	..	..	..	25	..	..	..	..	..	..	..	..	..
Galium harcynicum .....	..	..	..	..	..	..	..	..	..	..	..	100	100	..	10	5	..
Hieracium sp. .....	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..
Lactuca muralis .....	..	..	10	..	..	5	..	..	..	..	..	..	..	..	..	..	..
Lycopodium annotinum	100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Melampyrum vulgatum .....	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	..	..
Oxalis acetosella .....	..	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Polypodium vulgare .....	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	..
Potentilla erecta .....	..	..	..	..	..	..	..	30	..	..	..	..	..	..	..	..	..
Senecio silvaticus .....	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Trientalis europaea .....	..	..	..	..	..	..	..	..	30	..	..	5	..	..	..	..	25
Veronica officinalis .....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..
Agrostis tenuis .....	..	..	..	..	..	..	..	..	..	..	..	50	..	..	..	..	..
Anthoxanthum odorat. ....	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	..
Carex pilulifera .....	5	..	..	..	5	..	..	..	..	..	..	10	..	..	..	..	15
Dactylis glomerata .....	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Deschampsia caespitosa .....	..	..	5	..	..	..	5	..	..	..	..	5	..	..	..	..	..
— flexuosa .....	100	100	100	100	100	100	100	95	100	100	100	100	100	100	90	100	95
Festuca rubra .....	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Holcus lanatus .....	..	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..
Luzula congesta .....	15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pilosa.....	5	5	10	5	75	90	..	..	..	..	..	..	..	..	..	..	..
Melica uniflora .....	..	..	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Molinia coerulea .....	..	..	..	..	..	..	..	25	..	..	..	..	..	10	..	..	..
Sieglungia decumbens..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..
Blepharozia ciliaris .....	..	..	..	..	..	..	..	..	..	..	..	20	..	30	25	..	..
Brachythecium curtum .....	..	..	40	20	..	20	5	..	..	10	..	25	..	..	10	..	..
Ceratodon purpureus .....	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..

Table IX (continued).

No. ....	Deschampsia flexuosa sociation											Desch.— Gallium har- cynicum soc.		Deschampsia—Hyloco- mium parietinum soc.			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Locality .....	Rø	Rø	To.	Gj.	Al.	Ti.	Al.	Ox.	Sn.	Sn.	Gr.	Si.	Br.	Si.	Si.	Fr.	Sg.
Dicranella heteromalla .....	..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..
Dicranum rugosum .....	..	..	..	..	..	5	..	..	10	..	..	..	..	40	15	5	10
— scoparium .....	..	..	..	..	35	10	..	..	35	15	65	..	30	35	30	85	10
Hylocomium loereum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..
— parietinum .....	20	5	..	70	..	75	20	5	35	10	20	25	95	100	95	95	100
— proliferum .....	..	5	..	75	5	25	15	5	..	5	..	..	..	30	65	35	5
— squarrosum .....	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..
— triquetrum .....	..	..	..	..	..	10	5	..	..	20	..	..	..	..	..	..	..
Lophocolea bidentata .....	85	20	..	60	..	100	10	45	..	..	10	..	..	90	40	5	..
— heterophylla .....	..	..	25	25	5	..	..	..	..	..	..	..	..	..	..	..	..
Plagiothecium denticul.	5	5	5	15	25	..	5	..	..	..	..	..	5	..	..	..	..
— undulatum .....	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..
Polytrichum attenuatum .....	..	5	..	..	..	..	..	..	..	..	40	..	..	15	..	..	..
Scleropodium purum .....	45	50	45	35	50	20	20	50	5	..	25	20	..	20	10	..	..
Stereodon cupressif....	85	20	60	75	15	50	20	90	100	55	80	60	90	85	95	80	95
Light % (i) .....	26.9	32.7	12.9	8.77	11.4	..	22.3	..	15.6	18.2	..	17.6	21.1	20.0	7.83	10.9	70
pH of the peat .....	4.0	4.0	4.0	4.2	3.5	4.0	4.1*	3.7	3.7	4.0**	3.9	3.7	4.0	3.4	3.8	3.6	4.1
- - - — .....	4.1	4.1	4.0	4.3	3.7	4.1	4.4	3.8	3.9	4.2	3.9	3.8	4.2	3.5	3.9	3.7	4.1
- - - — .....	..	4.4	4.2	4.3	..	4.3	4.5	4.1	4.2	4.4	4.1	4.2	4.2	3.6	4.1	..	..
pH of the subsoil .....	4.4	4.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4.1
Thickness of the peat (cm.) .....	6-9	3-7	6-7	5-10	5-8	6-9	2-4	5-7	4-6	8-12	6-12	4-9	7-9	3-8	2-6	1-4	5-6
Subsoil .....	clayey sand	clayey sand	clayey sand	clayey sand	clayey sand	sand	clayey sand	sand	sand	sand	clayey sand	sand	sand	sand	sand	sand	sand
Species of tree .....	P. sil.	P. sil.	P. exl.	P. exl.	P. exl.	P. exl.	P. sil.	P. mon.	P. aus.	P. exl.	P. exl.	P. sil.	P. mon.	P. sil.	P. mon.	P. mon.	
Age of tree .....	80	80	50	70	40	60	90	50	45	..	6 <sup>2</sup>	45	35 <sup>1</sup>	40 <sup>1</sup>	30	40	50

\* under Molina pH 4.7. \*\* upper peat pH 4.3.

Table X. *Carex arenaria* sociations.

No. ....	Carex arenaria sociation											C. arenaria— Oxalis soc.	
	1	2	3	4	5	6	7	8	9	10	11	12	13
Locality .....	Sa.	Ti.	Sa.	Du.	Rv.	Ti.	Rv.	Sn.	Sn.	Sn.	Sn.	Ti.	Ti.
<i>Sorbus aucuparia</i> .....	..	5	..	..	..	..	..	..	..	..	..	..	5
<i>Rubus idaeus</i> .....	..	..	..	..	..	..	..	20	..	..	..	..	..
<i>Calluna vulgaris</i> .....	..	15	..	10	5	..	..	..	..	..	..	..	..
<i>Empetrum nigrum</i> .....	95	..	25	20	..	..	..	..	..	..	..	..	..
<i>Arenaria trinervia</i> .....	..	..	..	..	..	..	..	55	20	..	..	..	..
<i>Campanula rotundif.</i> .....	..	..	..	..	..	..	..	..	..	10	..	..	..
<i>Galium aparine</i> .....	..	..	..	..	..	..	..	..	40	..	..	..	..
<i>Geranium Robertianum</i> .....	..	..	..	..	..	..	..	..	40	70	..	..	..
<i>Lactuca muralis</i> .....	..	..	..	..	..	..	..	85	5	..	..	..	..
<i>Luzula pilosa</i> .....	..	..	..	..	..	..	..	..	..	..	..	85	70
<i>Oxalis acetosella</i> .....	..	..	..	..	..	..	..	..	..	..	..	100	100
<i>Polypodium vulgare</i> .....	..	..	..	..	..	..	..	..	10	..	..	..	..
<i>Anthoxanthum odoratum</i> ..	..	..	..	..	..	..	..	..	..	..	20	..	..
<i>Carex arenaria</i> .....	100	100	100	100	100	100	100	100	100	100	100	100	100
<i>Dactylis glomerata</i> .....	..	..	..	..	..	..	..	10	10	..	..	..	5
<i>Deschampsia flexuosa</i> .....	10	35	40	..	..	..	..	70	70	95	65	50	60
<i>Holcus lanatus</i> .....	..	..	..	..	..	..	..	..	..	35	5	..	..
<i>Poa pratensis</i> .....	..	..	..	..	..	..	..	..	..	..	25	..	..
<i>Brachythecium curtum</i> .....	..	15	..	..	..	..	..	40	65	10	..	20	15
<i>Ctenium crista-castrensis</i> ..	..	..	..	5	..	..	..	..	..	..	..	..	..
<i>Dicranum rugosum</i> .....	..	25	20	30	15	30	20	..	..	..	..	..	..
— <i>scoparium</i> .....	..	40	..	30	30	15	..	5	..	..	..	25	..
<i>Eurhynchium praelongum</i> ..	..	..	..	..	..	..	..	..	15	5	..	..	..
<i>Hylocomium parietinum</i> ..	..	40	70	85	65	10	90	..	..	..	..	95	..
— <i>proliferum</i> .....	20	15	70	85	45	90	95	..	..	5	..	80	5
— <i>squarrosum</i> .....	..	..	..	..	..	..	..	..	5	..	..	..	..
— <i>triquetrum</i> .....	..	..	..	..	..	..	20	..	15	20	..	95	85
<i>Lophocolea bidentata</i> .....	..	15	..	..	5	..	..	..	5	60	..	10	..
<i>Mnium rostratum</i> .....	..	..	..	..	..	..	..	20	35	20	..	..	..
<i>Rhodobryum roseum</i> .....	..	..	..	..	..	..	..	..	..	5	5	..	..
<i>Scleropodium purum</i> .....	100	100	100	95	90	100	45	30	95	95	25	75	95
<i>Stereodon cupressiformis</i> ..	..	35	..	10	100	..	25	85	..	10	85	45	..
Light % (i) .....	25.7	16.2	24.2	11.3	8.14	8.84	9.22	11.9	6.24	10.0	22.7	..	..
pH of the peat .....	4.0	3.7	3.7	3.9	4.1	3.7	4.2	4.0	4.1	4.0	4.4	4.1	4.2
- - - — .....	4.1	3.9	3.8	4.0	4.3	3.8	4.2	4.1	4.3	4.1	4.4	4.2	4.4
- - - — .....	4.2	..	3.9	4.0	4.3	..	4.2	4.2	4.4	4.2	4.4	4.5	4.6
Thickness of the peat (cm.)	10-12	6-8	6-8	4-6	4-7	6-8	4-7	5-7	4-7	6-7	4-8	6-8	5-7
Species of tree .....	P. sil.	P. sil.	P. sil.	P. sil.	P. aus.	P. excl.	P. aus.	P. aus.	P. sil.	P. excl.	P. excl.	P. sil.	P. sil.
Age of tree .....	60 <sup>2</sup>	13 <sup>2</sup>	60 <sup>2</sup>	40 <sup>1</sup>	60 <sup>1</sup>	100	60 <sup>1</sup>	50	65	45	65	50 <sup>2</sup>	50 <sup>2</sup>

The subsoil is in every place sand.

Table XI. *Scleropodium purum* sociation.

No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Locality .....	Sa.	Gr.	Sa.	Sa.	Sa.	Rv.	Rv.	Sn.	Si.	Si.	Pa.	Si.	Sa.	Sa.	Sg.	Si.	Bl.	Ho.	Ti.
Picea abies .....	..	..	..	..	..	..	5	80	..	..	..	..	..	..	..	..	..	20	25
Sorbus aucuparia .....	..	..	..	..	10	..	..	..	..	..	..	..	5	..	..	..	..	5	..
Calluna vulgaris .....	..	..	..	..	..	..	..	..	..	..	5	5	..	..	..	..	..	..	..
Vaccinium myrtillus ..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..
Galium harcynicum ..	..	..	..	..	..	..	..	..	..	..	15	5	..	..	..	..	..	..	..
Lactuca muralis .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	15
Melampyrum vulgaratum ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	30	..
Trientalis europaea ..	..	..	..	..	..	..	..	..	..	..	30	..	..	..	..	..	..	30	..
Carex arenaria .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	30	..
Deschampsia flexuosa ..	..	5	5	..	..	..	..	5	..	10	..	20	5	15	..	5	5	10	5
Luzula pilosa .....	..	..	..	5	..	..	..	..	..	..	35	..	5	..	..	..	..	95	45
Brachythecium curtum ..	90	80	65	45	65	50	25	30	5	..	..	..	5	10	..	..	..	..	15
Ctenium crista-castr. ..	30	..	5	..	..	..	5	..	5	..	..	..	..	..	..	..	..	30	..
Dicranum rugosum ..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	5	..
— scoparium .....	95	10	95	75	95	60	65	50	70	5	40	15	100	20	5	35	10	55	10
Eurhynchium prael. ..	..	5	..	5	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..
Hylocomium pariet. ..	60	5	60	15	90	45	40	20	50	95	75	15	100	..	..	25	10	30	15
— proliferum .....	25	35	35	5	10	20	10	60	45	90	90	25	5	5	10	5	..	30	30
— triquetrum .....	..	..	..	..	..	60	..	20	..	..	10	..	10	..	..	..	..	15	5
Lophocolea bidentata ..	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— heterophylla .....	5	50	..	50	20	65	..	90	..	..	..	..	10	85	..	15	..	..	..
Mnium rostratum .....	..	..	..	..	10	40	5	35	..	..	..	..	..	..	..	..	..	..	..
Plagiothecium dent. ..	75	35	50	75	35	15	..	..	..	..	..	..	45	10	..	15	..	..	..
Polytrichum attenuat. ..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhodobryum roseum ..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Scleropodium purum ..	100	100	100	90	95	100	100	100	95	90	100	95	90	100	100	100	100	100	100
Stereodon cupressif. ..	35	25	100	65	45	60	55	50	60	60	45	90	15	10	85	95	95	..	..
Light % (i) .....	5.85	7.39	1.19	..	2.16	4.25	6.48	6.71	5.08	10.0	4.15	5.72	..	2.24	4.24	7.31	..	3.18	5.19
pH of the peat .....	3.8	3.5	3.8	3.6	3.6	3.7	4.2	3.7	3.4	3.4	4.0	3.7	3.7	3.8	3.7	3.6	3.6	4.2	4.1
- - - — .....	3.8	3.7	4.0	3.8	3.9	3.8	4.2	3.8	3.5	3.6	4.1	3.9	3.8	3.9	3.7	3.6	3.7	4.2	..
- - - — .....	..	3.7	..	..	3.9	3.9	4.4	3.8	3.6	3.7	4.3	..	..	4.0	3.8	..	3.8	4.2	..
Thickness of the peat (cm.) .....	7-11	6-8	8-10	11-15	7-9	6-9	6-8	8-12	4-8	5-9	7-10	4-8	..	7-9	5-10	..	5-9	10-12	7-9
Subsoil .....	sand	sand	sand	sand	sand	sand	sand	gravel	sand	clayey sand	clayey sand	gravel	sand	sand	sand	clayey sand	sand	sand	sand
Species of tree .....	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	A. pec.	P. excl.	A. pec.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	
Age of tree .....	45 <sup>2</sup>	60	35 <sup>2</sup>	35 <sup>2</sup>	35 <sup>2</sup>	45 <sup>2</sup>	55 <sup>1</sup>	70	60	45 <sup>2</sup>	80	70	35 <sup>2</sup>	20 <sup>2</sup>	65 <sup>1</sup>	45 <sup>2</sup>	45 <sup>1</sup>	70	100

No. 2: upper peat pH 3.7.

Table XII. *Hylocomium*

No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13
Locality . . . . .	Du.	Ti.	Sv.	Si.	Bl.	Ti.	Br.	Nø.	Nø.	Fr.	Fr.	Fr.	Sg.
Picea abies . . . . .	...	...	...	...	...	...	...	...	...	...	...	...	...
Calluna vulgaris . . . . .	...	...	...	5	..	...	...	...	...	...	...	...	...
Empetrum nigrum . . . . .	...	...	...	..	10	..	..	..	..	..	..	..	5
Vaccinium myrtillus . . . . .	...	...	...	..	..	..	..	..	..	..	..	..	..
— vitis-idaea . . . . .	...	...	...	..	..	..	..	..	..	..	..	..	..
Potentilla erecta . . . . .	...	...	...	..	..	..	..	..	..	..	..	..	..
Scorzonera humilis . . . . .	...	...	...	..	..	..	..	..	..	..	..	..	..
Carex arenaria . . . . .	35	30	15	..	70	10	..	..	..	..	..	..	..
Deschampsia flexuosa . . . . .	..	10	..	30	5	10	..	..	..	15	55	45	..
Festuca ovina . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Luzula pilosa . . . . .	..	..	..	..	..	15	..	..	..	..	..	..	..
Molinia coerulea . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Sieglungia decumbens . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Blepharozia ciliaris . . . . .	..	..	..	..	10	..	20	70	15	..	80	5	5
Brachythecium curtum . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Cephaloziella sp. . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Ctenium crista-castrensis . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Dicranum majus . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
— rugosum . . . . .	10	50	5	20	5	65	25	30	40	20	20	10	15
— scoparium . . . . .	60	..	..	60	40	40	30	40	95	30	55	70	55
Hylocomium lorense . . . . .	..	..	..	..	..	..	..	..	..	..	..	10	..
— parietinum . . . . .	100	100	100	100	100	100	100	100	100	100	100	100	100
— proliferum . . . . .	20	40	20	10	5	15	15	10	45	30	20	25	5
— triquetrum . . . . .	..	10	20	..	..	..	..	..	15	..	..	..	..
Lophocolea bidentata . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
— heterophylla . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	5
Plagiothecium undulatum . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhodobryum roseum . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Scleropodium purum . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Stereodon cupressiformis . . . . .	55	60	15	60	80	50	40	20	30	65	65	95	100
Cladonia impexa . . . . .	..	..	..	15	5	..	10	5	10	30	15	..	35
— rangiferina . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Light % (i) . . . . .	32.6	23.0	15.2	25.9	21.6	25.4	15.6	9.00	7.20	6.50	11.4	7.88	8.59
pH of the peat . . . . .	3.6	3.7	3.9	3.4	3.5	4.0	3.8	3.9	3.7	3.6	3.9	3.7	4.0
- - - — . . . . .	3.7	..	4.0	3.5	3.6	..	3.9	4.0	3.9	3.7	3.9	3.8	4.2
- - - — . . . . .	4.0	..	4.0	3.6	3.7	..	3.9	4.1	3.9	..	..	3.8	..
pH of the subsoil . . . . .	..	..	..	..	..	..	..	..	..	..	..	..	..
Thickness of the peat (cm.) . . . . .	3-5	6-7	1-6	3-6	3-8	..	6-9	6-8	5-9	7-8	3-5	5-10	3-6
Subsoil . . . . .	sand	sand	sand	sand	sand	sand	sand	stony sand	stony sand	sand	sand	sand	sand
Species of tree . . . . .	P. sil.	P. sil.	P. sil.	P. sil.	P. mon.	P. sil.	P. mon.	P. mon.	P. exl.	P. mon.	P. exl.	P. mon.	P. mon.
Age of tree . . . . .	40	70	35 <sup>1</sup>	45 <sup>1</sup>	45 <sup>1</sup>	100	40 <sup>1</sup>	40 <sup>1</sup>	40 <sup>1</sup>	70	70	70	40

No. 18, 32 and 33 are labile.

## parietinum sociation.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Fr.	Fr.	Ti.	Ti.	Sg.	Sg.	Sg.	Fr.	Ho.	Sa.	Ti.	Sn.	Ho.	Rv.	Rv.	Sn.	Ti.	Rn.	Al.	Al.
..	5	..	..	..	..	..	..	..	..	80	..	..	..	..	15	100	..	..	..
..	10	5	..	40	..	..	..	40	..	..	..	5	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	10	..	..	..	45	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..
..	..	..	..	15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..
..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	25	..	..	..	..	..	..	..	5	10	..	..	..	..	..	..	..
40	65	..	25	45	35	70	20	35	5	..	70	55	..	..	35	..	90	15	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	..
..	..	..	10	..	..	..	..	..	..	55	..	..	..	..	..	..	..	..	20
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
10	5	..	..	5	30	..	..	..	..	..	..	..	..	..	..	..	..	10	30
..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	30	10	..	..	..
..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	10	..	..	15	..	..	..	..	..	20	..	25	..	5
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10
..	15	25	60	15	50	15	25	..	90	..	20	90	35	20	15	20	25	..	15
100	80	55	40	50	50	10	40	90	45	45	80	35	45	..	90	25	35	55	100
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..
100	100	100	100	100	100	100	100	100	100	100	100	100	95	100	95	100	100	100	100
..	5	5	35	15	5	75	75	75	35	100	20	90	30	80	60	20	30	..	60
..	..	30	..	..	..	..	..	..	5	15	..	..	..	10	35	..	..	5	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	40	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	15	..	..	..	..	..	..	70	10	..	10	20	40	20	85	..	..
95	70	90	55	85	25	65	95	..	..	20	100	50	80	20	80	40	20	55	95
20	5	10	..	..	10	5	..	..	..	..	..	..	..	..	..	..	..	..	10
5	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
3.46	4.55	..	..	..	21.1	10.5	13.8	35.1	17.4	5.45	12.3	15.4	10.4	8.89	5.20	4.41	10.5	..	..
3.6	3.6	3.8	3.9	3.7	3.8	4.0	3.7	3.9	3.8	4.0	3.8	3.7	3.9	4.1	3.8	3.8	4.1	4.2	3.8
3.8	4.0	3.8	3.9	3.8	3.8	4.0	3.7	..	3.8	4.1	3.9	4.0	3.9	4.1	3.8	3.9	4.1	4.3	3.8
..	..	..	..	..	..	4.1	3.8	..	3.8	..	4.0	4.1	4.0	4.3	3.8	..	4.1	..	..
..	..	4.5	..	3.9	..	..	..	..	..	..	..	..	..	..	..	..	..	5.0	..
3-6	2-6	..	3-7	2-5	4-8	3-8	7-8	4-8	4-6	..	2-5	4-8	5-7	4-6	8-12	5-8	2-6	2-3	3-6
gravel	gravel	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	gravel	sand	sand	clayey sand	clayey sand
P. excl.	P. can.	P. sil.	P. sil.	P. mon.	P. mon.	P. excl.	P. sil.	P. sil.	P. excl.	P. excl.	P. sil.	P. sil.	P. mon.	P. aus.	P. excl.	P. excl.	P. sil.	P. sil.	P. excl.
40	40	40	70	45 <sup>1</sup>	45 <sup>1</sup>	70	60	75	95	30 <sup>2</sup>	70	35	..	80	35 <sup>2</sup>	70	30 <sup>1</sup>	35 <sup>1</sup>	

Table XIII. *Cladonia impexa* sociation.

No. ....	1	2	3	4	5	6	7	8	9
Locality .....	Si.	Fr.	Fr.	Nø.	Fr.	Bl.	Fr.	Fr.	Du.
Empetrum nigrum .....	...	...	...	...	...	...	...	...	5
Deschampsia flexuosa.....	10	..	5	..	..	35	..	10	..
Festuca ovina.....	..	..	..	10	..	..	..	..	..
Blepharozia ciliaris .....	20	20	60	10	10	45	10	5	..
Dicranum rugosum .....	25	5	10	25	5	..	5	25	20
— scoparium .....	90	40	90	45	10	30	30	70	35
Hylocomium parietinum .....	65	45	90	60	35	..	85	100	35
— proliferum .....	10	..	5	..	..	..	..	10	..
Rhacomitrium hypnoides.....	..	..	..	20	40	..	..	..	..
Stereodon cupressiformis .....	100	90	95	90	35	55	100	50	70
Cetraria aculeata .....	..	..	..	..	5	5	..	..	20
— islandica.....	..	..	..	..	..	20	..	..	..
Cladonia impexa .....	90	100	95	95	100	100	100	85	90
— rangiferina.....	..	35	35	..	..	65	15	10	5
— rangiformis .....	..	..	..	..	10	..	..	..	..
— silvatica .....	15	..	..	..	..	..	..	..	..
— uncialis.....	..	..	..	..	..	..	..	..	15
Light % (i) .....	26.0	11.4	20.0	9.87	29.2	..	21.9	23.4	ca. 80
pH of the peat .....	3.4	3.8	3.5	4.1	3.6	3.5	3.7	3.4	3.5
- - - — .....	3.5	3.8	3.6	4.1	3.7	3.6	3.7	3.8	3.7
- - - — .....	..	3.8	3.8	4.3	3.7	3.6	3.8*	3.9	3.7
Thickness of the peat (cm.).....	1-4	4-9	3-6	3-6	1-2	0-6	5-8	4-8	3-7
Subsoil .....	gravel	sand	sand	sand	gravel	sand	sand	sand	sand
Species of tree.....	P. sil.	P. mon.	P. mon.	P. mon.	P. mon.	P. mon.	P. mon.	P. mon.	P. sil.
Age of tree.....	45 <sup>1</sup>	70	70	35 <sup>1</sup>	70	45 <sup>1</sup>	70	70	40

\* Besides pH: 3.8 and 3.8. The list of lichens is not complete.

Table XIV. *Stereodon cupressiformis* sociation.

No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Locality .....	Al.	Rv.	Al.	Fr.	Rn.	Si.	Sg.	Sg.	Sg.	Si.	Tv.	Bl.	Sv.	Sg.	Sg.	Sg.	Fr.	Ti.	
Picea abies .....	..	..	..	..	..	..	..	..	..	50	..	..	..	..	..	..	..	..	
Pinus sylvestris .....	..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	..	..	
Calluna vulgaris.....	..	..	..	..	5	..	..	..	..	..	..	..	..	5	20	5	..	..	
Empetrum nigrum.....	..	..	..	..	..	..	..	..	..	..	..	..	..	10	..	5	10	..	
Erica tetralix .....	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	

Table XIV (continued).

No. ....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Locality .....	Al.	Rv.	Al.	Fr.	Rn.	Si.	Sg.	Sg.	Sg.	Si.	Tv.	Bl.	Sv.	Sg.	Sg.	Sg.	Sg.	Fr.	Ti.
Vaccinium myrtillus .....	5	..	..	..	..	..	..	..	..	15	..	..	..	..	..	..	..	..	
— vitis-idaea .....	..	..	..	..	..	..	..	..	5	10	..	..	..	..	..	..	..	..	
Potentilla erecta .....	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Trientalis europaea .....	..	..	..	..	..	..	..	..	..	..	15	..	..	..	..	..	..	..	
Carex arenaria .....	..	35	..	..	..	..	..	..	..	..	..	20	..	..	..	..	..	..	
— pilulifera .....	55	..	..	..	..	..	20	..	..	..	..	..	10	20	..	..	..	..	
Deschampsia flexuosa .....	90	5	15	5	85	..	5	20	..	..	..	90	..	5	..	20	..	5	
Amblystegium Juratzkan.	..	..	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Blepharozia ciliaris .....	..	..	..	..	..	..	..	..	..	..	..	30	5	..	..	..	..	..	
Brachythecium curtum .....	..	..	..	..	5	..	10	..	10	..	..	..	..	..	..	..	..	5	
Ctenium crista-castrensis .....	..	..	..	..	..	..	..	..	5	..	..	..	..	5	..	5	5	10	
Dicranum rugosum .....	..	..	..	..	..	30	10	20	..	..	40	10	..	..	10	..	..	..	
— scoparium .....	35	40	90	20	60	85	80	60	30	35	55	50	10	15	20	55	25	20	
— spurium .....	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	
Eurhynchium praelongum .....	..	..	..	..	..	..	..	20	..	..	..	..	..	..	..	..	..	15	
Hylocomium loereum .....	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	
— parietinum .....	30	35	30	50	95	100	90	90	70	100	100	40	40	25	35	45	40	60	
— proliferum .....	..	15	15	25	..	65	10	10	30	100	40	5	..	5	..	20	5	5	
— triquetrum .....	..	60	..	..	..	5	..	..	..	..	5	40	5	..	..	..	..	..	
Gymnocybe palustris .....	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..	..	..	..	
Leucobryum glaucum .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	15	..	..	
Lophocolea bidentata .....	..	..	..	..	55	30	10	20	..	..	..	..	..	..	..	..	..	..	
— heterophylla .....	..	..	10	..	..	30	5	..	35	..	..	..	..	..	..	..	..	5	
Mnium hornum .....	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	5	35	
Plagiothecium denticulat..	..	..	15	..	..	5	..	15	5	..	..	..	..	..	..	..	..	..	
— undulatum .....	..	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	5	
Polytrichum attenuatum ..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— juniperinum .....	..	..	..	..	..	5	..	..	..	..	..	..	10	..	..	..	..	..	
Scleropodium purum .....	100	80	45	50	80	50	..	5	..	..	..	15	..	..	..	..	5	..	
Stereodon cupressiformis ..	100	90	80	75	100	100	95	100	95	100	100	100	100	100	95	100	100	90	
Cladonia impexa .....	..	..	..	..	..	..	10	..	..	..	20	15	10	..	30	10	..	..	
— rangiferina .....	..	..	..	..	..	..	..	..	..	..	10	..	..	..	5	..	..	..	
— surrecta .....	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	
Light % (i) .....	2.62	6.25	2.45	2.84	3.37	4.34	6.97	2.44	2.94	6.00	20.7	..	16.7	12.0	11.8	7.60	..	3.08	0.93
pH of the peat .....	4.1	4.2	3.4	3.6	4.0	3.4	3.8	3.7	3.9	3.4	4.0	3.5	3.7	4.2	4.0	4.1	3.7	3.8	3.9
- - - — .....	4.2	4.3	3.6	3.9	4.0	3.6	3.8	3.8	3.9	3.5	4.0	3.6	3.7	4.3	4.0	4.2	3.9	3.9	3.9
- - - — .....	..	4.3	..	..	4.1	3.7	3.9	3.9	..	3.6**	4.0	3.7	3.7	..	..	..	..	3.9	..
pH of the subsoil .....	4.4	..	..	..	..	..	..	..	..	3.3	..	..	..	..	..	..	..	..	
Thickness of the peat (cm.)	3-5	4-6	3-6	3-7	2-4	4-8	5-8	3-5	5-7	6-9	2-4	4-9	..	3-5	3-4	4-7	2-6	2-4	3-5
Subsoil .....	sand	sand	clayey sand	stony sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	sand	
Species of tree .....	P. sit.	P. aus.	P. exl.	P. pec.	P. exl.	P. exl.	P. exl.	P. exl.	P. exl.	P. mon.	P. mon.	P. sil.	P. mon.	P. mon.	P. exl.	P. exl.	P. exl.	P. exl.	
Age of tree .....	20 <sup>1</sup>	60 <sup>1</sup>	40	120	25 <sup>2</sup>	25 <sup>2</sup>	60	45 <sup>1</sup>	65	40-60	40 <sup>1</sup>	45 <sup>1</sup>	20 <sup>1</sup>	30 <sup>1</sup>	30 <sup>1</sup>	40	65	40	35 <sup>2</sup>

\* Besides: 4.3—4.4—4.4.    \*\* Upper peat: pH 3.6.

Table XV. *Luzula pilosa* and moss sociations.

	Luzula— H. triq. soc.		Hylocomium triquetrum soc.				Hylocomium proliferum soc.			Dicranum majus soc.			
	No. ....	1	2	3	4	5	6	7	8	9	10	11	12
Locality .....	Ti.	Ti.	Sn.	Sv.	Sn.	Sn.	Sa.	Si.	Si.	Gr.	Gr.	Gr.	
Ilex aquifolium .....	..	..	..	..	..	..	..	..	..	5	..	..	..
Picea abies .....	..	10	..	..	20	..	..	..	..	80	..	..	5
Pinus silvestris .....	..	..	45	..	..	..	..	..	..	..	..	..	..
Sorbus aucuparia .....	..	..	..	..	5	..	..	..	..	..	..	..	..
Calluna vulgaris .....	..	..	..	..	..	..	10	..	..	..	..	..	..
Empetrum nigrum .....	..	..	..	..	..	..	5	..	..	..	..	..	..
Vaccinium myrtillus .....	..	..	..	..	..	..	..	..	10	..	..	..	..
Arenaria trinervia .....	..	..	..	..	..	5	..	..	..	..	..	..	..
Lactuca muralis .....	..	..	10	..	10	15	..	..	..	..	..	..	..
Listera cordata .....	..	..	..	20	..	..	..	..	..	..	..	..	..
Oxalis acetosella .....	95	..	..	..	..	..	..	..	..	..	..	..	..
Polypodium vulgare .....	..	..	..	..	..	..	5	..	..	..	..	..	..
Trifolium europaea .....	..	..	..	20	..	..	..	..	..	..	..	..	..
Veronica officinalis .....	..	..	..	..	5	..	..	..	..	..	..	..	..
Carex arenaria .....	55	..	80	5	..	..	10	..	..	..	..	..	..
Deschampsia flexuosa .....	60	20	100	..	..	100	..	35	10	..	..	..	..
Luzula pilosa .....	90	95	..	5	..	..	..	..	..	..	..	..	..
— sp.....	..	..	..	5	..	..	..	..	..	..	..	..	..
Brachythecium curtum .....	10	15	..	..	55	10	..	..	..	15	20	40	
Ctenium crista-castrensis .....	..	..	..	..	..	..	20	5	..	10	..	..	
Dicranum majus .....	..	..	..	..	..	..	..	..	30	100	100	100	
— rugosum .....	5	..	..	..	..	..	45	10	..	..	..	..	
— scoparium .....	20	45	5	..	10	40	25	20	..	..	30	..	
Eurhynchium praelongum .....	..	..	..	..	25	5	..	..	..	..	..	..	
Hylocomium loereum .....	..	..	..	..	..	..	..	..	55	55	..	..	
— parietinum .....	95	30	..	75	40	45	100	90	100	95	100	20	
— proliferum .....	25	65	30	75	75	85	100	85	95	80	80	45	
— triquetrum .....	95	100	100	100	95	90	20	..	30	10	5	15	
Lophocolea bidentata .....	10	..	..	15	..	5	..	..	5	..	..	..	
— heterophylla .....	..	..	..	..	75	..	..	10	25	..	20	15	
Mnium rostratum .....	..	..	..	..	15	..	..	..	..	..	5	..	
Plagiochila asplenoides .....	..	..	..	..	..	..	..	..	..	25	..	5	
Plagiothecium denticulat. ....	..	..	..	..	..	..	..	..	..	..	..	5	
— undulatum .....	..	..	..	..	..	..	..	..	25	45	55	..	
Polytrichum attenuatum .....	..	..	..	..	..	..	..	..	..	5	5	..	
Rhodobryum roseum .....	..	..	..	..	5	..	..	..	..	..	..	..	
Scleropodium purum .....	50	30	100	85	60	20	70	50	25	50	..	..	
Stereodon cupressiformis .....	100	75	5	5	10	15	..	30	15	15	25	10	
Thuidium tamariscifolium .....	..	..	..	..	..	..	..	..	25	10	15	40	
Peltigera canina .....	..	..	..	10	..	..	..	..	..	..	..	..	
Light % (i) .....	..	..	3.38	..	7.73	10.0	..	6.30	5.91	9.13	3.50	3.13	
pH of the peat .....	3.8	4.2	4.1	4.0	4.3	3.8	4.0	3.7	3.4	3.6	3.5	3.5	
- - - — .....	3.9	4.2	4.1	4.1	4.6	3.9	4.2	3.8	3.5	3.7	3.6	3.8	
- - - - — .....	4.1	4.4	4.3	4.1	4.7	4.0	..	..	3.5	3.8	3.8	3.8	

Table XV (continued).

	Luzula— H. triq. soc.		Hylocomium triquetrum soc.				Hylocomium proliferum soc.			Dicranum majus soc.		
	No. ....	1	2	3	4	5	6	7	8	9	10	11
Locality .....	Ti.	Ti.	Sn.	Sv.	Sn.	Sn.	Sa.	Si.	Si.	Gr	Gr.	Gr.
pH of the subsoil .....	...	...	4.1	...	4.2	...	...	4.9	...	...	...	...
Thickness of the peat (cm.)	5-9	4-7	8-14	...	2-6	4-7	3-7	4-7	7-10	10-15	3-8	5-10
Subsoil .....	sand	sand	gravel	sand	gravel	gravel	sand	stony sand	sand	clayey sand	clayey sand	clayey sand
Species of tree .....	P. sil.	P. sil.	P. excl.	P. sil.	P. excl.	P. excl.	P. sil.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.
Age of tree.....	50	50	80	30 <sup>1</sup>	55	50	40 <sup>2</sup>	40 <sup>1</sup>	60	80	60	60

Table XVI. *Lophocolea heterophylla* sociations.

No. ....	1	2	3	4	5	6	7	8	9
Locality .....	Sn.	Gr.	Rø	Rø	Al.	Al.	Al.	Sn.	Sg.
Abies alba .....	...	...	...	...	...	...	...	10	..
Vaccinium myrtillus .....	...	...	...	...	...	...	5	..	..
Brachythecium curtum .....	15	5	15	..	..	20	..	..	5
Dicranum scoparium.....	...	20	..	..	5	25	..	..	..
Eurhynchium praelongum.....	...	..	..	..	..	..	..	5	10
Hylocomium parietinum .....	..	5	..	..	..	10	..	..	..
Lophocolea heterophylla .....	55	30	95	45	95	90	15	30	..
Plagiothecium denticulatum .....	10	45	55	30	85	100	20	..	..
Polytrichum attenuatum .....	..	..	..	..	..	5	..	..	..
Scleropodium purum.....	..	..	..	..	..	5	..	..	..
Stereodon cupressiformis .....	..	..	20	30	50	95	55	5	20
Thuidium tamariscifolium .....	..	..	..	..	..	..	10	..	..
Light % (i) .....	..	1.84	0.45	0.37	1.58	2.92	1.43	1.38	0.65
pH of the peat .....	3.8	3.8	3.7	3.6	3.7	3.7	3.4	3.8	4.0
- - - - - .....	3.9	3.8	3.7	..	3.7	3.7	3.5	4.0	4.0
- - - - - .....	..	3.8	3.9	..	..	3.7	..	4.1	..
pH of the subsoil .....	..	..	..	5.0*	..	..	3.9	..	..
Thickness of the peat (cm.).....	7-10	4-8	4-6	6-8	4-6	3-5	5-8	5-7	1-3
Subsoil .....	gravel	clayey sand	clayey sand	clayey sand	clayey sand	sand	sand	gravel	sand
Species of tree.....	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	P. excl.	A. pec.	P. excl.
Age of tree.....	35 <sup>2</sup>	40 <sup>2</sup>	70	80	65	50 <sup>2</sup>	50 <sup>2</sup>	20 <sup>2</sup>	35 <sup>1</sup>

\* In a depth of 10 cm.: pH. 4.3.

Table XVII.

	Rubus—Holcus lanatus soc.	Anthoxanthum odoratum soc.	Dryopteris dilatata soc.	Equisetum silv.—Holcus lanatus soc.	Molinia coerulea soc.	Deschampsia caespitosa soc.	Carex hirta soc.	Holcus mollis soc.
No. ....	1	2	3	4	5	6	7	8
Locality .....	Rø	Rø	Rø	Rø	Al.	Al.	Al.	Fr.
Lonicera periclymenum.....	95	100	..	100	..	..	..	..
Rubus fruticosus.....	..	..	5	..	..	..	..	..
— idaeus .....	95	30	40	35	..	20	..	..
Calluna vulgaris .....	..	..	..	..	10	..	..	..
Arenaria trinervia.....	..	..	5	..	..	..	..	..
Campanula rotundifolia.....	..	..	..	..	..	..	..	10
Dryopteris dilatata.....	10	..	60	35	..	30	..	..
— filix-mas .....	..	..	..	..	..	5	..	..
Equisetum arvense.....	..	..	..	..	..	5	..	..
— silvaticum .....	..	..	..	50	..	..	..	..
Galeopsis tetrahit.....	..	..	5	..	..	..	..	..
Galium boreale .....	..	..	..	..	5	..	..	..
— harcynicum.....	..	..	..	..	..	..	..	5
— uliginosum .....	..	..	..	..	..	5	..	..
Geranium Robertianum.....	..	..	10	..	..	..	..	..
Hypericum maculatum .....	..	..	..	..	5	..	..	..
— pulchrum.....	..	..	..	..	..	..	..	15
Lactuca muralis .....	..	..	..	15	..	..	5	..
Lathyrus montanus .....	..	..	..	..	15	..	..	..
— pratensis .....	..	..	..	..	..	10	..	..
Majanthemum bifolium.....	..	..	..	70	..	..	..	..
Oxalis acetosella .....	10	..	15	40	..	100	..	..
Pirola minor .....	..	..	..	..	10	..	..	..
Potentilla erecta .....	..	5	..	25	45	..	5	..
Stellaria graminea.....	..	..	..	..	..	10	..	..
— media .....	5	..	..	..	..	..	..	..
Urtica dioeca .....	10	..	..	..	..	..	..	..
Veronica officinalis .....	..	..	..	..	..	5	..	..
Viola canina.....	..	..	..	..	..	..	..	5
— silvestris .....	50	..	..	..	..	..	..	..
Agrostis stolonifera.....	..	..	..	5	40	100	10	85
— tenuis.....	..	..	..	..	..	..	..	5
Anthoxanthum odoratum .....	50	100	..	15	5	..	..	..
Carex arenaria.....	..	..	..	..	..	..	..	5
— hirta.....	..	..	..	..	..	55	100	..
— pallens .....	..	..	..	..	5	..	..	..
— panicea .....	..	..	..	5	..	15	..	..
— pilulifera .....	..	10	..	..	5	..	..	..
— sp. .....	..	..	..	..	..	5	..	..
Dactylis glomerata .....	..	..	..	..	5	..	5	..

Table XVII (continued).

	Rubus—Holcus lanatus soc.	Anthoxanthum odoratum soc.	Dryopteris dilatata soc.	Equisetum silv.—Holcus lanatus soc.	Molinia coerulea soc.	Deschampsia caespitosa soc.	Carex hirta soc.	Holcus mollis soc.
No. ....	1	2	3	4	5	6	7	8
Locality .....	Rø	Rø	Rø	Rø	Al.	Al.	Al.	Fr.
Deschampsia caespitosa.....	..	..	..	20	..	95	..	..
— flexuosa.....	25	100	5	40	55	15	70	20
Holcus lanatus .....	85	90	..	45	25	10	10	..
— mollis.....	..	20	..	..	..	..	..	95
Juncus conglomeratus .....	..	..	..	..	5	25	..	..
Luzula multiflora .....	..	..	..	..	..	..	..	10
— pilosa.....	..	..	10	..	..	..	..	..
Melica uniflora .....	..	..	25	..	..	..	..	..
Molinia coerulea .....	..	..	..	55	90	10	..	..
Nardus strictus .....	..	..	..	..	..	15	..	..
Poa pratensis .....	..	..	..	..	..	..	..	10
Blepharozia ciliaris .....	..	..	..	..	..	..	..	5
Brachythecium cursum .....	30	15	95	40	15	..	45	..
Catharinaea undulata.....	..	..	15	..	..	..	..	..
Dicranum scoparium .....	..	..	..	..	..	..	..	5
Eurhynchium praelongum.....	..	..	10	..	..	..	..	..
— striatum .....	..	..	..	..	..	..	..	10
Hylocomium parietinum .....	..	..	10	..	..	..	..	85
— proliferum.....	..	..	20	10	..	..	..	..
— squarrosum.....	..	..	5	..	..	30	..	..
— triquetrum .....	..	..	35	..	..	..	..	..
Lophocolea bidentata .....	90	30	20	40	15	..	60	..
Mnium rostratum .....	..	..	80	..	..	..	..	..
Plagiothecium denticulatum.....	..	5	25	5	..	..	..	..
— repens .....	..	..	15	..	..	..	..	..
— silvaticum.....	..	..	20	5	5	..	..	..
Polytrichum attenuatum .....	..	..	20	..	5	..	..	..
Scleropodium purum .....	90	95	75	60	95	65	70	..
Stereodon cupressiformis .....	..	..	10	5	5	..	..	55
Thuidium tamariscifolium .....	..	..	55	5	..	5	..	..
Light % (i) .....	15.4	34.6	9.00	13.9	..	42.3	14.8	20.2
pH of the surface soil.....	4.4	4.6	3.5	4.5	4.6	5.2	4.3	3.6
— — — — — .....	4.5	4.7	3.6	4.8	4.8	5.4	4.3	3.7
— — — — — .....	..	4.8	3.6	4.9	..	..	4.4	..
pH of the subsoil .....	..	..	..	5.8	5.5	5.8	..	..
Thickness of the peat (cm.) .....	..	..	..	..	..	..	2-6	2-4
Subsoil .....	clayey sand	clayey sand	clayey sand	clayey sand	clayey sand	clayey sand	sand	sand
Species of tree .....	P. sil.	P. sil.	A. pec.	P. sil.	P. sil.	P. sil.	P. sil.	P. sil.
Age of tree .....	80	80	100	80	30 <sup>1</sup>	60	60	40 <sup>1</sup>

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Fig. 1. *Rubus idaeus*—*Brachythecium curtum*—*Oxalis acetosella* sociation rich in *Milium effusum*.  
Table I, 6. Grib Forest.



Fig. 2. *Pteridium aquilinum*—*Vaccinium myrtillus* sociation. Table V, 1—2. Silkeborg.



Populations of *Cladonia impexa*, *Hylocomium parietinum*, and *Deschampsia flexuosa*—*Calluna* (Example 13, p. 35). At bottom, left, *Polyodium vulgare* and *Rumex acetosella*. South is to the left in the figure.

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TO  
THE STUDY OF THE DEVELOPMENT AND  
LARVAL FORMS OF ECHINODERMS  
IV

BY  
TH. MORTENSEN

WITH PLATES I—XII

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURV. OG MATH. AFD., 9. RÆKKE, VII. 3.

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Bianco Lunos Bogtrykkeri A/S.

The present fourth "Contribution to the study of the development and larval forms of Echinoderms"<sup>1</sup> comprises the results of studies carried out from July 1st to September 12th 1937 at the Marine Biological Station of the University of Egypt, at Ghardaqa on the Red Sea Coast, in continuation of the studies made there from April 28th to June 27th 1936.

It is a very agreeable duty to me to renew my sincere thanks to the authorities of the Egyptian University, Cairo, for the hospitality offered me in placing the facilities of this excellent laboratory at my disposal again this summer. In particular I beg to tender my thanks to the authorities of the University for allowing the demonstrator of Zoology of the University, KHALAF EL DEWEINI, B. Sc., to act as my assistant during the whole of my stay. This was of the greatest importance to me, since the cultivation of the many different larvæ requires a great amount of work, much more than is possible for one. KHALAF Eff. proved a very capable and very much interested assistant and companion, and I beg to extend my cordial thanks to him, expressing the hope that he also had some profit of his work with me, and that he may get some opportunity of continuing in the future these studies of the development of the Echinoderms of the Red Sea. Likewise I beg to tender my cordial thanks to the director of the Station, Dr. CYRIL CROSSLAND, who together with Mrs. CROSSLAND made all efforts to help me in every way, and to make my stay at Ghardaqa this year a no less delightful experience than was my stay there in the summer of 1936.

Last, not least, my sincerest thanks are due to the Carlsberg Foundation for the grant which enabled me to undertake this second voyage to the Red Sea.

The fact that last year I found a considerable number of species not to have ripe sexual products even up till the end of June made me expect that I would find these species to have their breeding season in high summer, viz. the months July and August, perhaps also September, so I had to arrange for staying at the station during these months. To a great extent my expectations came true — still, a good number of species were not yet ripe by the time I had to leave the station, September 12th. This holds good of such species as *Briopsis luzonica* (Gray), *Phyllacanthus imperialis* (Lamarck), *Ophiocoma valenciae* (Müller & Troschel), and *Ophiothrix hirsuta* Müller & Troschel — the development of all of which I was very anxious to study. They showed signs of becoming ripe by the end of September (probably by full moon), or perhaps not even till October. Other species did become ripe in July or

<sup>1</sup> "Contributions" I—II were published in 1931 in 9. Ser. Vol. IV. 1, „Contributions" III in 1937 in 9. Ser. VII. 1 of these Memoirs.

August, but resisted all my efforts to induce them to spawn or to make artificial fertilization of them — as e. g. *Holothuria atra* Jäger, one of the commonest of the Holothurians at Ghardaqa, these large, black sea-cucumbers which occur in great numbers all over the littoral reef-flat, lying almost dry at low tide. I kept them in great numbers in the tanks of the laboratory, also in the large outside-tank, but they would not spawn, although it was their breeding time, and repeated experiments in undertaking artificial fertilization of them all failed, the eggs never ripening in spite of being left at varying lengths of time in the water, with or without the adding of NaOH (or KOH) to the water. As mentioned in my "Contributions" III, p. 9, Hørstadius succeeded in getting a large number of eggs of *Holothuria Poli* D. Ch. fertilized by means of raising the pH of the water, so I was expecting to get similar good results with the Red Sea Holothurians. This was, however, by no means the case. I tried with a number of different species, also some Asteroids, but never found a larger percentage of eggs to have ripened in the dishes with raised pH than in the control dishes to which no NaOH had been added — whereas I found it constantly necessary to raise the pH of the water in order to induce the spermatozoa of Asteroids to move.

Special mention must be made of *Phyllacanthus imperialis* and *Asthenosoma varium*, two species the development of which I was particularly anxious to study. The fine, large Cidarid *Phyllacanthus imperialis* is quite common on the reefs at Ghardaqa, usually concealed in the crevices between the coral blocks. I have examined great numbers of them as to sexual maturity, last year in May—June, this year in July—September, and never found any of them fully ripe. On the 31st of July I found a single female with the ovaries full of apparently ripe eggs — large, c. 0.5 mm in diameter, yellowish-white, rich in yolk, floating at the surface. Only in one specimen did I find a trace of ripe spermatozoa, which I thought might suffice for fertilizing at least some of the eggs — but no fertilization occurred, very probably because the eggs were not yet fully ripe for fertilization; at least, I thought I could discern the nucleus in the opaque eggs. Later on I never found a single ripe female, and only some few males with some spermatozoa — whether spent or only in beginning maturity I could not make out definitely. In September some specimens had the appearance of being in incipient maturity, so it is likely that by the end of September (at full moon?) a number of specimens would be ripe; but more probably the real breeding season will be in October. Both large and smaller specimens were examined, with the same negative result. It was a great disappointment to me that I could not study the development of this Cidarid. That it will be possible to fertilize the eggs artificially may be concluded from the fact that this was achieved with the closely related Australian species *Phyllacanthus parvispinus* Tenison Woods, which has also large, yolk eggs, which float at the surface. The very remarkable young development stages of this latter species (cf. my "Studies of the Development and Larval forms of Echinoderms". 1921. p. 24, Pl. V. 3—4) indicate that the development of these *Phyllacanthus* species may probably be abbreviated.

*Asthenosoma varium* Grube, as one of the family of the Echinothurids, in my

opinion the direct descendants of the Palaeozoic Lepidocentrids, will no doubt show features of the greatest interest in its development, particularly postembryonally. I was therefore very anxious to study the development of this species — but here again all my efforts were in vain. The eggs are large, c. 0.8 mm, red, and quite transparent, on account of their rich content of yolk, for which reason they also float at the surface like the eggs of *Phyllacanthus*. Females with apparently ripe eggs were found repeatedly during the whole time of my stay this summer, as also specimens with quite young eggs, and such as were evidently spent, so that the species appears to have no definite breeding season. Specimens with ripe spermatozoa were also found most of the time, but only a small amount of sperma; not till the 10th of September did I find a single male with the testes full of ripe spermatozoa, which might indicate that *Asthenosoma* breeds mainly towards the end of the summer, September—October. Fertilization was tried many times, but always without success. The trouble is, with this species as with all those species with large, yolk, transparent eggs, that it is impossible to see whether the eggs are ripe for fertilization or not. Sections of supposed ripe eggs show the presence of a large distinct nucleus, which explains why no fertilization took place. I have also tried to keep the eggs for varying lengths of time, up to 24 hours, in the water before adding sperma, and in water with added KOH, but always without success. I think it will be found that for obtaining fertilization of this species it is necessary that the eggs are shed by the female itself, not taken out of the ovary. There is here again the difficulty that *Asthenosoma* is very hard to keep alive in the tanks; most specimens are found more or less injured in the trawl, and such will remain alive for only a few hours; but even specimens in fine condition I have been unable to keep alive in the tanks for more than one day. The only possibility for getting normally shed eggs of *Asthenosoma* would seem to be that intact specimens might spawn directly when put from the trawl into a container with water — as I have repeatedly found it to occur with various species of Holothurians.

It is of no small interest that the spermatozoa of *Asthenosoma varium* have a very long and slender head (fig. 1), thus differing considerably from the usual type of spermatozoa of Echinoderms. Also the spermatozoa of *Phyllacanthus imperialis* are somewhat elongate, but not nearly so much as those of *Asthenosoma*.

Besides *Phyllacanthus* and *Asthenosoma* there was quite a number of other species the development of which I failed to get; some of them for want of sufficient material, others because they would not spawn, artificial fertilization being impossible. The latter was the case with a small Comasterid, *Comissia Hartmeyeri* A. H. Clark<sup>1</sup>, common on *Lobophyllia*, on the reefs off the laboratory. The specimens were ripe, and lived perfectly well for more than a month in the tank under running



Fig. 1. Spermatozoa of *Asthenosoma varium* Grube.  $\times 850$ .

<sup>1</sup> Identification due to Professor GISLÉN, Lund, Sweden, for which I beg to thank.

water, even regenerating lost parts of arms; but they would not spawn — a very regrettable fact, since till now the embryonal development is not known of any Comasterid.

The small Ophiuran *Ophiura Kinbergi* Ljungman is quite common off Abu Sadaf on sandy bottom at a depth of c. 5—10 fathoms. I tried repeatedly to keep it alive in dishes with sand on the bottom and thus induce it to spawn, ripe specimens being found both in July and August; but whereas *Ophiolepis cincta* did spawn under similar conditions, *Ophiura Kinbergi* would not, to my great regret, both because it would be of the greatest interest to learn to know the larvæ of other species of the great genus *Ophiura* than the few species of the North Atlantic the larvæ of which are known till now, and also because the eggs of this species, unique (so far as known till now) by having a small red spot, almost like an oildrop, would seem to indicate its development to be of unusual interest. — Another Ophiurid, *Ophionereis dubia* (Müll. & Troschel) likewise would not spawn, though it lived quite well in the dishes for a long time.

The giant Synaptid *Synapta maculata* Chamisso & Eysenhardt, up to c. 5 metres long, I tried repeatedly to keep alive for spawning in the tanks. At first it did not live well in the tanks, because it does not tolerate it well to be hurt and lose a large part of its body, as does *Opheodesoma grisea*, — and because of its huge, disgustingly adhesive anchors it is quite difficult to extricate the specimens undamaged from one another when (— as is usually the case —) brought home by the sailors in an almost inextricable bunch. At length I succeeded in getting a small number of complete specimens, which then lived very well in the tank for some weeks, their long snake-like bodies creeping over one another without becoming entangled. They offered a glorious sight — but did not spawn, very naturally, since when I opened them in the beginning of September I found them to be quite unripe — probably spent long ago. Their breeding season must be either in June—July or late in September—October. Now that it is known how they can be kept alive in the tank, it will probably be possible to induce them to spawn. The study of the development of this species will be of great interest, especially in view of its possible relation to the remarkable *Auricularia nudibranchiata* (cf. "Contributions" III. p. 54). The species does not seem to be hermaphrodite as is *Opheodesoma grisea*.

*Holothuria curiosa* Ludwig is fairly common at Ghardaqa, particularly on grass-bottom at a depth of a few fathoms. Repeatedly I had a number of specimens standing in large dishes for eventual spawning. Twice they did spawn, but only the males, the females kept together with them happening to be either spent or unripe. Another time all the specimens happened to be females — there being no means of ascertaining the sex of the intact specimens. Artificial fertilization I could not try, never having a ripe female and a ripe male at the same time. — This species is remarkable for its Cuvierian organs; only a single thread is thrown out at a time, but it is very long, about one meter at least, and unusually thick, c. 1 mm in diameter. It is evidently a very effective means of defence.

Another Holothurian which I kept in vain in the tanks for spawning was *Holo-*

*thuria edulis* Lesson; as the specimens were all rather small, scarcely more than c. 15 cm long, they may have been too young (none of them were found to contain ripe sexual products). They, however, afforded an opportunity for an interesting observation. They would be seen rising perpendicularly from the bottom, standing on the posterior tip of the body, and then turning slowly round, quite gracefully, as if they were dancing. No doubt the meaning of this was to find some new place of support. They may even release their hold on the bottom and float freely at the surface of the water, moving quite slowly, not actively swimming. I am not aware that such a way of moving has till now been observed in this or any other Holothurian<sup>1</sup>.

A Holothurian the development of which it would have been of great interest to study is *Holothuria pleuripus* Haacke. This peculiar small, white Holothurian, which resembles, indeed, much more a naked land-snail, like *Vaginulus*, than a *Holothuria*, is rather commonly found attached to the underside of stones on the littoral reef-flat at Ghardaqa. I kept a considerable number of them in a dish under a water-tap, where they lived very well for quite a long time, but no spawning took place. In the several specimens which I opened I found no ripe sexual products, thus apparently August, at least, is not its breeding time.

Of *Labidodemas semperianum* Selenka only very few specimens were found, and only one at a time, so there was no possibility of studying the development of this very interesting Holothurian.

Once on the reef at the small islet Fanadir, a few miles from the station, I got two specimens of the beautiful seastar *Mithrodia clavigera* (Lamarck). They proved to be ripe, but both of them males. They were kept alive in the tank for more than a month, in the hope that a third, possibly female, specimen might be found. But no more specimens were found. — Another day a fine large specimen of *Leiaster Leachi* (Gray) was brought home by the sailors, likewise from Fanadir. It was a ripe female, and it was likewise kept quite a while in the tanks waiting for a hoped for male — but no more specimens of this species turned up.

From all the difficulties thus met with it was evident that the number of species, the development of which could be studied, could not possibly reach the record number of 30 species of last summer's researches. It is only surprising that it did amount to 18 species (two of them partly studied already last year). The total number of species of Echinoderms studied as regards their development during my two visits to Ghardaqa thus amounts to no less than 46. It may well be said that nowhere in the world has so large a percentage of the local Echinoderm fauna been made known in regard to the development as that of the Northern part of the Red Sea, a fact bearing radiant witness to the excellent conditions for such studies offered by the Ghardaqa laboratory.

The species, the development of which was studied this summer (1937) are the following:

<sup>1</sup> I am indebted to KHALAF Eff. for calling my attention to this curious habit of *Holothuria edulis*. The tank in which the specimens were kept was in another room than that in which I was working, so that if he had not seen it, I should probably have missed making this interesting observation.

1. *Prionocidaris baculosa* (Lamarck). Reared through metamorphosis.
2. *Laganum depressum* L. Agassiz. Reared through metamorphosis.
3. *Echinodiscus auritus* Leske. Reared through metamorphosis; larvæ reared till nearly full size last year.
4. *Luidia Savignyi* (Audouin). Reared through metamorphosis.
5. *Fromia ghardaqana* Mrtsn. (n. sp.) Reared through metamorphosis.
6. *Pentaceraster mammillatus* (Audouin) Reared through metamorphosis.
7. *Linckia multifora* (Lamarck). Reared to metamorphosis.
8. *Echinaster purpureus* (Gray). Reared to metamorphosis.
9. *Ophiothrix Savignyi* (Müll. & Troschel). Reared through metamorphosis.
10. *Ophiolepis cincta* (Müll. & Troschel). Reared through metamorphosis.
11. *Synaptula vittata* (Forskål). Reared through metamorphosis. Young larva reared last summer.
12. *Opheodesoma grisea* (Semper). Reared to near metamorphosis.
13. *Holothuria impatiens* (Forskål). Reared through metamorphosis.
14. *Holothuria pardalis* Selenka. Reared to full larval shape.
15. *Holothuria papillifera* Heding (n. sp.). Reared to full larval shape.
16. *Holothuria difficilis* Semper. Reared through metamorphosis.
17. *Holothuria (Microthelie) nobilis* (Selenka). Reared to young larva.
18. *Heterometra Savignyi* (Joh. Müller). Reared to young Pentacrinoid.

I am indebted to Mr. S. G. HEDING for the identification of the Holothurians.

Foremost among these species, in regard to the importance of the results achieved easily ranks *Prionocidaris baculosa*, the first Cidarid reared through metamorphosis. Especially the fact now disclosed that the young Cidarid actually passes through an *Archæocidaris* stage, having a pluricolumnar interambulacrum, is of the highest importance, raising beyond doubt the suggestion of *Archæocidaris* being the ancestor of the Cidarids s. str.; that it is in direct opposition to the theory of *Bothriocidaris* being the ancestor of the Echinoids need hardly be pointed out.

That the *Prionocidaris* larva closely resembles the other Cidarid larvæ known till now, thus corroborating the result reached through last year's researches ("Contributions" III) that the Cidarid family has a larval type of its own, is, of course, a fact of considerable importance. Of great interest is also the observation of the active movements of its long arms, and the complicate muscular system that makes these movements possible. Further the rather common normal occurrence of one-egged twins in this species is an embryological fact of quite unusual interest, being a rather unique case of nature itself making embryological experiments.

Among the Asteroids studied *Luidia Savignyi* and *Fromia ghardaqana* are of particular interest, the former in supporting the assumption that the family of the Luidiids has a larval type of its own, but at the same time showing that within this larval type there is a marked gradation from a primitive form of small size, the larval body of which is resorbed on metamorphosis, to the highest specialized form (the larva of *Luidia Sarsi*), which grows to a very large size, the larval body being thrown off, not resorbed, on metamorphosis.

*Fromia ghardaqa* is very interesting in being a protandric hermaphrodite, a rather rare case among Asteroids, and in having abbreviated development, the larva being a rudimentary Brachiolaria. Also in regard to the cleavage it is of unusual interest, belonging to the type in which the nuclei are at first scattered irregularly in the undivided yolk-mass. This type of cleavage, which was not hitherto known in Asteroids, has now been proved to exist in all Echinoderm classes: in the Holothurian *Cucumaria glacialis* Ljungman, in the Ophiuran *Amphiura vivipara* H. L. Clark (= *Amphiura Stimpsoni* Lütken), in the Echinoids *Hypsiechinus coronatus* Mrtsn., *Amphipneustes Koehleri* Mrtsn., and *Abatus cavernosus* (Philippi), and in the Crinoid *Isometra vivipara* Mrtsn.<sup>1</sup> All these forms have large eggs, rich in yolk — which fact does not, however, mean that all Echinoderms with large, yolky eggs have this type of cleavage. Thus e. g. *Echinaster purpureus* Gray, with large, yolky, black eggs, has total and regular cleavage.

Among the Holothurians the giant Synaptid *Opheodesoma grisea* (Semper) is particularly interesting in being a hermaphrodite and capable of self-fertilization. The various *Holothuria* larvae described here corroborate the result reached last summer ("Contributions" III) that the formation of elastic balls at metamorphosis is a feature common to all these larvæ, and that the general shape of the larvæ within the family of the Holothuriidae is so similar in all of them that specific characters hardly exist, except in the shape of the calcareous bodies in the posterior end of the larva. These latter, however, appear to afford important systematic characters, as evinced e. g. by the fact that the larva of *Microthele nobilis* differs conspicuously herein from that of *Holothuria difficilis*, likewise referred to the genus *Microthele* on account of the character of its spicules, but in spite of the fact that in general appearance it differs so strikingly from *M. nobilis* that anybody who has had an opportunity of seeing the two species alive together would protest against the idea that they could be congeneric — and the character of their larval spicules is in full agreement therewith.

The duration of the larval life, mind well within one and the same species, may be subject to great variation, as pointed out in my "Contributions" I. p. 23—24, and III. p. 32—33, with regard especially to *Tripneustes gratilla* and *Echinometra Mathæi*. It was found e. g. that at Mauritius the larva of *Tripneustes gratilla* was only about to begin to reach the second larval stage at the age of 30 days, whereas at Ghardaqa it was in beginning metamorphosis at the age of 18 days. Similarly the larva of *Echinometra Mathæi* was found by ONODA (1936) to take 40 days from fertilization to metamorphosis in Japan, whereas I found the same species at Ghardaqa to reach its full larval shape in about 18 days, thus in only about half the time

<sup>1</sup> Cf. the author's papers "Zur Anatomie und Entwicklung von *Cucumaria glacialis* (Ljungman)" (Zeitschr. f. wiss. Zool. LVII. 1894); "Studies in the development of Crinoids" (Papers from the Department of Marine Biology, Carnegie Inst. XVI. 1920. p. 32 and 34. Pl. XIV); "Studies of the development and larval forms of the Echinoderms". 1921. p. 177. Pl. XXXI. 7—8; and my Report on the Echinoidea of the Swedish S. Polar Expedition. 1910. p. 75.

it took in Japan. I suggested ("Contributions" III, loc. cit.) that temperature and the amount of food available to the larvae might account for this great difference in the duration of the larval life (cf. also my "Studies of the development and larval forms of the Echinoderms". 1921. p. 245).

The observations recorded in the present report, particularly on *Holothuria impatiens* and *difficilis*, (cf. pp. 53—54 and p. 56), prove that in these cases the reason for the prolonged duration of the larval life cannot possibly be sought in temperature, which remained the same all the time, it can only be due to lack of food, as also evidenced by the fact that, when the food supply (in the case of *Holothuria impatiens*) again became normal, metamorphosis promptly occurred. This does not imply that temperature may not play the same rôle, as would seem beyond doubt in the case of *Echinometra*.

But in other cases neither temperature nor scarcity of food can be the reason for the prolonged duration of the larval life. This applies to the *Prionocidaris* larvae, which were constantly carefully attended to, the water being shifted every day, and further to such cases where the larva does not feed, but subsists on the yolk-substance of the egg, e. g. *Fromia ghardaiana* and *Heterometra Savignyi* (and apparently all Comatulids with free-swimming larvae). As mentioned on p. 39, some of the *Fromia* larvae metamorphosed at the age of 16 days, while others went on swimming for 2—4 weeks more before attaching themselves and metamorphosing. In *Heterometra* a number of the larvae attached themselves and metamorphosed into Pentacrinoidea already at the age of 2 days, others not attaching themselves till about 1—2 weeks later. Even a good number of larvae of both these two species would not attach themselves at all for metamorphosing, but went on swimming, gradually deteriorating and perishing. In these cases the reason for the failing metamorphosis of the larvae can hardly be anything but that they did not find any place to their liking for attaching themselves to.

These observations have an important bearing on the very interesting problem: do these larvae all find a suitable place to attach themselves to for metamorphosis under natural conditions? Considering the immense number of eggs shed by a single female specimen, one would expect to find both adults and young specimens to be exceedingly common; but even though the said species are fairly common, particularly *Heterometra*, their number is nothing in comparison with the number of the eggs. That many of such conspicuous eggs and embryos as those of *Fromia* and *Heterometra* are eaten by young fishes and other organisms can scarcely be doubted; but it would seem equally probable that great numbers perish because they cannot find a suitable place to attach themselves to — especially, of course, if they are carried out with the currents to the open sea. — The latter case, of course, holds good of all larvae which are carried so far out to sea by the currents that when metamorphosing and sinking to the bottom they do not find suitable conditions (depth, kind of bottom etc.) for living in such places.

These observations together with those on the *Prionocidaris* larva mentioned below, p. 18, are in conformity with the highly interesting results reached by

DOUGL. P. WILSON & DAY in their studies on the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* and by DOUGL. P. WILSON in his researches on the influence of the substratum on the metamorphosis of the *Notomastus* larvæ (J. Mar. Biol. Assoc. XIX, 1934 and XXII, 1937).

The scarcity of the adults in comparison with the immense numbers of eggs produced cannot, however, in many cases at least, be explained either by the larvæ not finding a place to attach themselves, or not finding suitable conditions when sinking to the bottom after metamorphosing, or by great numbers of them being eaten by other organisms. With the millions of eggs produced e. g. by each specimen of *Diadema*, it is an extraordinary fact that young specimens are as a rule a great rarity (though the adult Diademas are common and conspicuous enough, usually living in large flocks). *Luidia ciliaris* (Philippi) especially affords a very striking case. In my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X. 1913) I have stated that the number of eggs produced by a single adult specimen amounts to c. 200 millions. When in spite of this the species is apparently nowhere very common, none of the above named causes will explain this scarcity in a satisfactory way. I think that in this and many other cases the main reason is that a very great percentage of the eggs fail to be fertilized. In cases where some species occurs in great numbers in a locality, there is of course no risk of the eggs failing to be fertilized, but in all such cases where specimens are scarce, and do not collect for breeding purpose (and, of course, where no copulation takes place), I think it beyond doubt that lack of fertilization of the eggs is a main reason for the number of specimens not increasing.

The faculty of the larvæ to continue life as larvæ for a long period beyond the normal duration of larval life, be it on account of insufficient food, or because they do not find a suitable place for attaching themselves, must be of material importance for the dispersal of such species; this means chances for the larvæ of being carried a long way from the place where they came into existence, and they may thus be able to colonize places where the species did not hitherto occur.

A few words may still be said about the lunar periodicity in reproduction, as discussed by H. MUNRO FOX (Proc. Royal Soc. B. Vol. 95. 1923). He finds a pronounced lunar periodicity in *Diadema setosum* at Suez, whereas no such periodicity exists in the Mediterranean Echinoid *Paracentrotus lividus*, against the common belief in the Mediterranean countries. (I might suggest that it would be worth while to examine in this regard a couple of other Echinoids much used for food in the Mediterranean countries, viz. *Sphærechinus granularis*, *Echinus acutus*, and *Ech. melo*, perhaps these might form the basis for the general belief in the lunar periodicity in these countries).

As regards *Diadema setosum* it seems that at Ghardaqa this species agrees in the main with the observations of Fox. But as for the other Echinoderms studied, there is not much support for a lunar periodicity. Of some species ripe specimens may be found during a longer, continuous period e. g. *Laganum depressum*; many species appear to have only one breeding season during the summer — which may

very well for many species coincide with a full moon (e.g. probably *Briissopsis luzonica*), but other species I have found ripe at new moon, or any time. I must emphasize, however, that I have not made special researches regarding this problem, but my general impression is that lunar periodicity in the reproduction of the Echinoderms at Ghardaqa is a rare exception.

Whether other marine forms of the Red Sea show any distinct lunar periodicity I am not aware; but since a distinct lunar periodicity, in reproduction or otherwise, occurs in various Molluses, Polychætes ( — "Palolo" —), and Crustaceans, (I must refrain from quoting the extensive literature relating to this subject — I will mention only the names of AMIRTHALINGHAM, BATTLE, ORTON, and WHEELER), it is probable that similar observations could be made also at Ghardaqa. And whatever the result would be, proving or disproving the existence of lunar periodicity, regularly continued observations would be sure to be of great value.

My observations on the breeding seasons of the Echinoderms at Ghardaqa also have an important bearing on the question whether the tropical marine animals breed continuously throughout the year, as has been maintained by SEMPER and ORTON (cf. my "Studies of the development and larval forms of Echinoderms", 1921, pp. 245—246). As pointed out already, pp. 3—4, several species did not become ripe at all till July or August, or even September. Such species evidently breed only once or twice, possibly three times a year. It is probable that such species as were found ripe already in April—May, e. g. *Echinometra Mathæi* and *Tripneustes gratilla*, will breed continuously (every full moon?) throughout the summer — but I did not pay attention to this problem. It should be pointed out, however, that, although the northern part of the Red Sea must be regarded as tropical in spite of its higher latitude (Ghardaqa lies at 27° 13' N.), it has a distinct winter-season, during which the temperature of the sea water may fall as much as 10° C. This, of course, must have some influence on the breeding of the marine animals. It is quite probable that species which breed here only once or twice a year may breed more often, perhaps continuously, in the properly tropical seas, where no distinct winter season lowers the temperature. It may be recalled here that Gopala Aiyar (Early development and metamorphosis of *Salmacis bicolor*. Proc. Ind. Acad. Sc. I. 1935, p. 726) found *Salmacis bicolor* ripe at all times of the year. Direct researches into this problem are much required.

I may take the opportunity here of correcting an erroneous statement in my "Contributions" III, p. 9. It is said there that "by means of keeping a number of specimens in a live-box SELENKA succeeded in getting good cultures of *Holothuria nigra*". This is a rather curious slip of the pen. The species thus reared by SELENKA was *Holothuria tubulosa* — as evident already from the title of his paper quoted four lines above! And *Holothuria nigra* was reared not by SELENKA, but by myself, as described in my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X. 1913. p. 17).

*Echinoidea.*1. *Prionocidaris baculosa* (Lamarck).

Pls. I—III.

This species does not actually occur in the neighbourhood of Ghardaqa. During the dredging trip in the Egyptian research steamer "Mabahiss" to the Gulf of Suez in May 1936 (mentioned on p. 3 of my "Contributions" III) I got a great number of specimens — about 250 specimens in a single haul! — off Ashrafi Light, at a depth of 40 fathoms, on hard bottom with a rich growth of algae. These I carried alive to the station, hoping to be able to study their development. As they were, however, far from being mature, part of them were kept alive in the tanks of the station (where they lived excellently, feeding on algae that were put with them into the tank), others were set out at the pier and on the reef-flat near the station, where they could easily be found again. But even by the end of June, when I had to leave the station, they did not show any sign of becoming ripe in a very near future.

It was one of my ardent hopes this year to find again some of these specimens of *Prionocidaris baculosa* liberated near the station last year, and thus to be able to study the development of this species — a hope which was to be fulfilled. On July 28th Dr. CROSSLAND brought home some specimens found at the pier in the very place where they were liberated last year. They proved to have ripe sexual products, and artificial fertilization was undertaken. The first experiment, however, gave no result. Although the fertilization membrane had been formed, no cleavage followed, and the following morning the eggs were found lying dead on the bottom of the dishes. A new fertilization was then undertaken, and most of the fertilized eggs put into a fine plankton-net suspended in the tank so as to hang in running sea-water, a smaller part of them only being left in the usual dishes. This time it was a perfect success, cleavage going on normally, not only of the eggs in the plankton-net, but also of those lying on the bottom of the dishes. The reason for the failure of the first fertilization, where the eggs were lying on the bottom of the dishes, remains unknown, all the usual precautions having, of course, been taken.

The eggs are of the usual small size, c. 0.15 mm in diameter, perfectly clear and transparent; the fertilization membrane stands widely off from the egg. The cleavage is total and perfectly regular, the two first cells lying perfectly isolated from one another (Pl. I, Fig. 2), so that I could not help wondering, how they would be able to join into a normal single blastula on further development. The 4- and 8-cells stages seemed more of the usual form, but in the 16—32-cells stages the cells were arranged in a rather unusual way, forming a two-layer plate, leaving a rather large empty space on both sides of it within the membrane (Pl. I, Fig. 4). Ultimately the cells, on further development, arranged themselves so as to form a normal blastula of perfectly spherical shape (Pl. I, Fig. 5) — i. e. in the majority of the eggs. But a large percentage of the embryos were of a more or less irregular shape (Pl. I, Fig. 6), evidently due to the original isolation of the two first blastomeres, showing that actu-

ally the cells originating from the two first halves of the egg had difficulty in uniting into a single embryo, as it was my first impression that they would perhaps have. Moreover, quite a number of the embryos proved to be double, there being two separate blastulae within the membrane, sometimes, indeed, even three of them (Pl. I. Figs. 7—8), proof that in these cases the cells originating from the first two blastomeres had actually been unable to join together to form a single, normal embryo. We have thus here the very unusual, but highly interesting case of normal one-egged twins, and even one-egged triplets. (I did not observe any case of quadruplets, but that such may occur also there is hardly reason to doubt). Nature itself thus makes here the experiment of isolating the first blastomeres, as has so often been done artificially by experimental biologists. And as has been found experimentally, the isolated blastomeres develop into normal larvæ, only of half size. Although I did not isolate the twins, the much smaller size of some of the larvæ was proof enough that the twins develop into normal larvæ; these small larvæ reached full shape, identical in all their characters with the normal, full-sized larvæ, differing from them only in their much smaller size. That they would also metamorphose I cannot have the slightest doubt, though I have not definitely ascertained it. Of course, I quite realized that it would have been of the greatest interest to have the twin-larvæ isolated and observed throughout their development and through metamorphosis, but there was simply no time to do so, the work with the divers other cultures of Echinoderm larvæ occupying all my time. But it is clear that this Cidarid would be a marvellous object for experimental researches on its development.

So far as known to me the only other case known of one-egged twins (viz. quadruplets) occurring normally is that of the armadillo, *Tatusia*. That exceptionally one-egged twins may occur in several animal forms, man included, is a different matter. The polyembryony of some parasitic Hymenoptera may be recalled, but this is scarcely comparable to the case of *Prionocidaris baculosa*. Likewise the twin-embryos of the earth-worm *Lumbricus trapezoides* (cf. KLEINENBERG. Development of the Earthworm *Lumbricus trapezoides*. Quart. Journ. Mier. Sc. 19. 1879. p. 206. Pls. IX—XI) are something different, being a secondary division of the embryo in a later stage of development. It should further be emphasized that the *Prionocidaris*-twins are something quite different from the so-called twin larvæ of Echinoderms, with double hydrocoel or double alimentary canal, artificially produced or occurring casually in normal cultures of Echinoderm larvæ (cf. e. g. NEWTH. The early development of *Astropecten irregularis*, with remarks on duplicity in Echinoderm larvæ. Qu. Journ. Mier. Sc. 69. 1925). Such larvæ are monsters, whereas the twins of *Prionocidaris* are perfectly normal larvæ. More similar to the case of the *Prionocidaris* twins is that of one-egged twins in *Arbacia lixula* ("pustulosa") quite recently described by P. E. LINDAHL ("Über eineiige Zwillinge aus Doppeliefern". Biol. Zentralblatt. 57. 1937. p. 389). But here it is an abnormal formation of the polar bodies, resulting in the polar body sometimes being as big as the egg itself. Each of the two are ferti-

lized and apparently develop normally, so that twin blastulæ within the same membrane become the result. Still, this is principally different from the case of *Prionocidaris*, it being here a parallel development of twin eggs, not twins developing from one and the same egg.

The first development stages take a very short time, the blastulæ beginning to rotate within the egg-membrane only 6 hours after fertilization (Pl. I. Fig. 5); immediately afterwards the egg-membrane dissolves and the embryos become free-swimming. They are rather thick-walled, the cells not being large and flat as is the case in *Eucidaris metularia*, and the cell-mosaic not nearly as large and conspicuous as in the latter (cf. "Contributions" III. Pl. I. 4). 9 hours old the embryos had assumed the shape of elongate gastrulæ, without apical thickening of the ectoderm (Pl. I. Figs. 9—10). — The gastrulæ developing from such "half-twins" as Pl. I. Fig. 6 were observed to be more or less irregular, according to the degree of irregularity of the blastulæ. Whether they would ultimately develop into normally shaped embryos, I do not know, as I had no time to isolate such irregular gastrulæ and follow their further fate.

In embryos 26 hours old the first traces of the skeleton were already found, viz. the future postoral rods, situated in the lower corners of the embryo, the shape of which is, on the whole, much more slender than that of *Eucidaris metularia*, in which latter the young gastrula is almost spherical, at the beginning differentiation of the archenteron almost triangular (Pl. I. Figs. 9—10 to compare with Pl. I. Figs. 5—6 of "Contributions" III, which represent the corresponding stages of *Eucidaris metularia*). Also in regard to the first appearance of the skeleton the *Prionocidaris* embryo differs markedly from that of *Eucidaris*, the first rudiments of the skeleton appearing only at the age of four days in the latter, against scarcely more than one day in *Prionocidaris*. The formation of the enterocoel-pouches was not followed in details.

As is apparently the rule in Cidarid embryos the postoral rods are from the first directed outwards, or, indeed, a little backwards (Pl. I. Fig. 10), but very soon they are turned obliquely upwards, the young larva having a fairly normal Echinopluteus shape (Pl. I. Fig. 11). In this stage — the figure represents a larva  $2\frac{1}{4}$  days old — the larva differs from the *Eucidaris* larva of the corresponding stage in the oral lobe being much broader and the posterior part of the body much smaller (comp. Pl. I. 8. of "Contributions" III). The *Eucidaris* larva of the corresponding stage is 9 days old, against the  $2\frac{1}{4}$  days of *Prionocidaris* — an enormous difference in the rate of the developmental processes of these two species, the more remarkable as the two larvæ in their full shape are so very closely alike; apparently the difference is due to the somewhat smaller size of the eggs in *Eucidaris* and therewith probably a smaller amount of nutrient material in these latter.

The skeleton of the young larva is, on the whole, very much like that of the *Eucidaris*-larva, only the body rods are somewhat more developed, almost joining in the posterior end of the body, and the postoral rods are fenestrated throughout (Fig. 2), whereas there are no holes in the basal part of this rod in *Eucidaris*.

The larva in this stage has already the pigment well developed (— the very first traces of pigment are observable already in the gastrula with the first rudiments of the skeleton —), a good number of carmine spots along the vibratile band, more densely accumulated at the ends of the postoral arms, and a few scattered spots in the posterior end of the body.

In larvæ four days old the posterodorsal rods have appeared. At the age of 10 days the larva is nearly fully formed (Pl. I. Fig. 12), the posterior transverse rod and the dorsal arch and the divers lobes developed, the larva being at this age a good deal more advanced than the 22 days old *Eucidaris* larva ("Contributions"

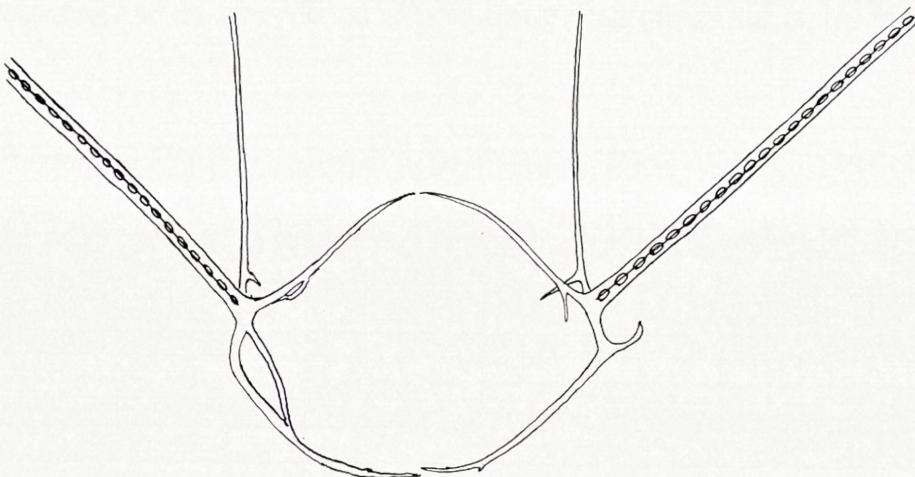


Fig. 2. Skeleton of young larva,  $2\frac{1}{4}$  days old, of *Prionocidaris baculosa* (Lamk.).  $\times 300$ .

III. Pl. I. 9). The full larval shape was reached in the course of another week, the posterodorsal arms being now as long as the postoral ones, the anterolateral and preoral arms being more slender and elongate, and all the divers lobes fully developed (Pls. II—III). The larva now so closely resembles the *Eucidaris* larva ("Contributions" III. Pl. II) that they are hardly to be distinguished from one another. It is an exceedingly beautiful microscopical object, with its long, slender arms and its five pairs of large vibratile lobes, bordered by the vibratile band, decorated with delicate carmine spots.

A very interesting fact is that the larva is able to move its four long arms very actively, not only from a normally forward directed to a horizontal position, but even to a straight backward position (Pl. II. Figs. 1—2). The movement of the arms from the forward to the backward position is very quick; usually the movement is repeated two to three times in quickly succeeding strokes, after which the arms are held quiet in a horizontal position. It is evidently not a normal swimming movement, but an averting movement, occurring only when something touches the larva (— thus always when I sucked them up with a pipette). Of course, there must be quite a powerful and complicate muscular system for making such

active movements possible. Such a one also exists, as shown in figs. 3—4; it consists of two pairs of straight horizontal muscles connecting the bases of the postoral and posterodorsal rods of both sides with one another, one straight dorsoventral muscle on each side, connecting the bases of the postoral and the posterodorsal rods of the same side, and four muscles going obliquely from the bases of the four main rods to the middle of the posterior transverse rod.

There can be no doubt that the *Eucidaris* larva moves its four main arms in the same way as does the *Prionocidaris* larva. In figures 2—4, p. 16—17 of "Contributions" III, representing the basal part of the skeleton of the fully formed *Euci-*

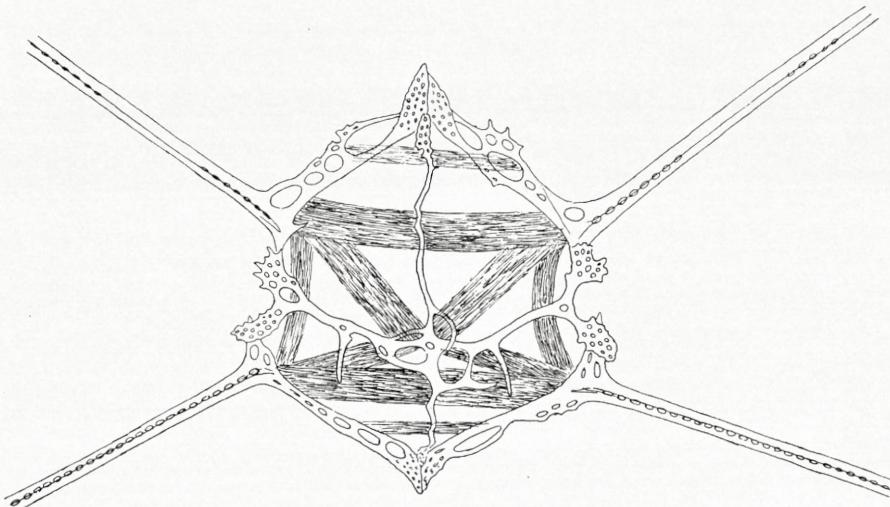


Fig. 3. Skeleton and muscular system of the fully formed larva of *Prionocidaris baculosa* (Lamk.). Seen obliquely from behind. The oral side is turning upwards.  $\times 200$ .

*daris* larva, both straight and oblique muscles are shown — but not the complete muscular system, the small outer horizontal muscles having been overlooked; not at that time knowing anything of the peculiar movements of the arms, I was, of course, not intent on seeking the complete muscular system on which such movements depend. On a re-examination of the *Eucidaris* larva I find, however, the muscular system to be in full accordance with that of the *Prionocidaris* larva.

The skeleton of the fully formed larva (figs. 3—4) very closely resembles that of the *Eucidaris* larva, particularly in the highly characteristic shape of the posterior transverse rod, with its long dorsal and ventral median processes, which reach up to the transverse rods from the postoral and posterodorsal rods. These latter are quite smooth, fenestrated rods, as in the *Eucidaris* larva, the only difference being that here they are fenestrated from the base, whereas in the *Eucidaris* larva the fenestration only begins a good distance out. It is, however, an interesting fact that in the larva about to metamorphose the posterodorsal rods usually show stretches near

the base where the fenestration has disappeared (fig. 3); but this is no constant feature, both being sometimes fenestrated throughout (fig. 4), while sometimes only one of the rods is partly unfenestrated. This may have something to do with the preparation for metamorphosis.

The beginning metamorphosis, indicated by the presence of pedicellariæ and embryonal spines, was not observed till the age of 25 days, and the first metamorphosed young sea-urchins were found exactly a month after fertilization. So far as I have been able to ascertain the four long rods of the larva are not wholly resorbed

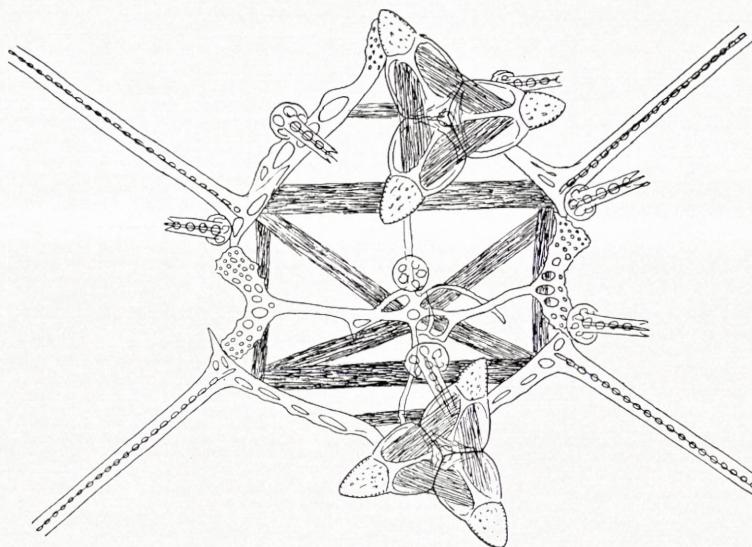


Fig. 4. Skeleton of larva of *Prionocidaris baculosa* (Lamk.) in beginning metamorphosis. Two pedicellariæ and some spines have appeared. Seen from behind, so as to show also the muscular system. The oral side turning upwards.  $\times 200$ .

on metamorphosis, but only their proximal part, the distal part being dropped after the skin has retracted therefrom. The vibratile lobes were observed to be gradually resorbed.

Whereas the first metamorphosed sea-urchins were found by the end of August, many of the larvae kept on swimming for another two weeks, till I left Ghardaqa, and would quite evidently have remained unmetamorphosed for a still longer time. When the first larvae showed distinct signs of metamorphosis, they were put into a separate dish containing some algae to which the young sea-urchins might attach themselves. Though I did not find any of these directly on the algae, it seemed evident that the presence of the algae in the dish accelerated the metamorphosis (— probably by the larvae on swimming coming into touch with the algae —); at least all the larvae transferred to this dish metamorphosed in the course of one or two days, whereas the larvae not transferred, though apparently in the same advanced stage, did not metamorphose until much later.

The larvæ are good swimmers, and do not lie on the bottom of the dishes, as so many other Echinoid larvæ do when near metamorphosis; on the contrary, they were often swimming close under the surface, which caused a good number of them to be caught in the surface film and thus killed. A more remarkable fact was that not a few of the larvae metamorphosed at the surface, the young sea-urchins being found floating directly under the surface film. A good number of the young, newly metamorphosed Cidarids were found attached to the sides of the dish, others on the bottom.

In the dish with the algæ the young Cidarids lived very well, the algæ affording

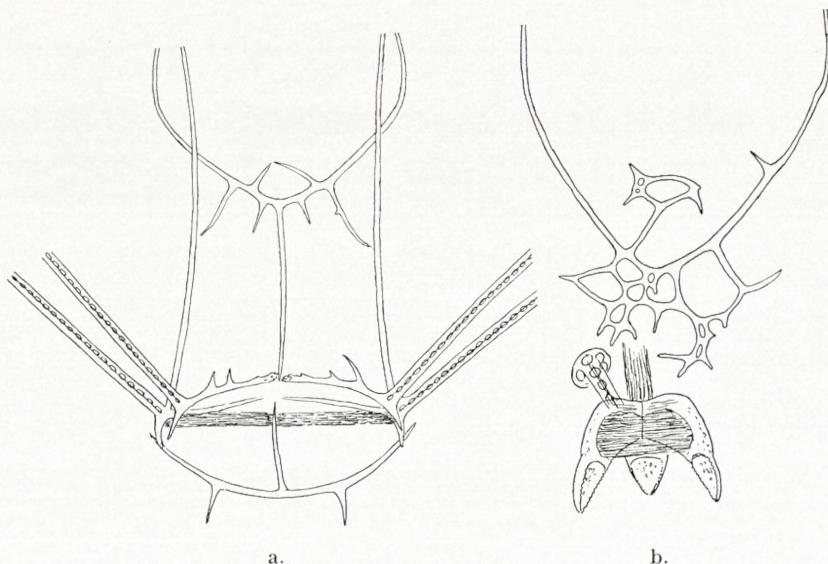


Fig. 5. a. Skeleton of a 10 days old larva of *Prionocidaris baculosa* (Lamk.); b. dorsal arch of a larva of same in beginning metamorphosis. A pedicellaria and an embryonal spine have developed on the dorsal arch.  $\times 200$ .

both the necessary oxygen and food, mainly by the numerous diatoms and other microscopical organisms living on them and propagating actively — a whole microcosmus gradually developing in the dish, in which the young Cidarids were living and growing very well. When I had to leave, most of the young Cidarids were preserved; the rest of them Dr. CROSSLAND very kindly looked after till the beginning of October, when they were preserved and sent me. They had, however, not grown noteworthy beyond the size of the most advanced of the specimens preserved on September the 10th. They had then been kept in a small dish, without change of water, for more than a month! In larger dishes, and with some changing of water and algæ, it would evidently be quite easy to rear the young Cidarids to a much larger size — but that is for those, who have access to undertake such experiments.

The first sign of metamorphosis is the appearance of pedicellariæ, three of them appearing almost simultaneously, viz. on the left ventral and dorsal transverse

rods, and on the dorsal arch, one on each of these parts of the larval skeleton (figs. 4 and 5 b); on the young sea-urchin these three pedicellariae are found again, attached to three of the ocular plates, the origin of which from the said parts of the larval

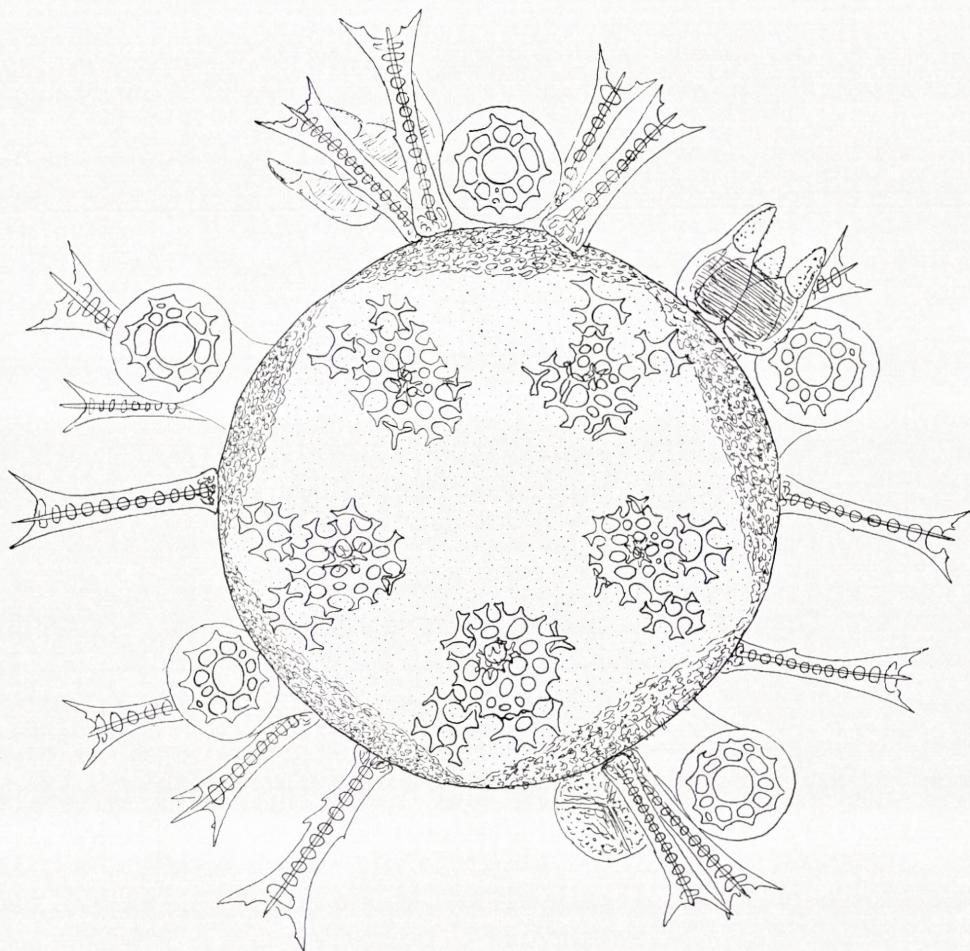


Fig. 6. Newly metamorphosed *Prionocidaris baculosa* (Lamk.), from the oral side. Showing the interambulacral plates 1—3, and under the adoral edge of I. A. 1 (the primary interambulacral plate) the first rudiments of the buccal plates; corresponding to the ocular plates (the five dense marginal plates) are seen the embryonal spines, the primary tube feet and the three pedicellariae, the one on the lower right hand side seen from its base.  $\times 200$ .

skeleton being thereby ascertained. (The exact parts of the larval skeleton from which the two other ocular plates originate, or whether they represent new, independent formations, I have been unable to ascertain).

Figs. 6—7 represent the newly metamorphosed sea-urchin, from the oral and the aboral side. On the buccal membrane, which is continuous, without mouth-opening, are seen the five primary interambulacral plates, the first pair of inter-

ambulacral plates, near the edge, and the buccal plates, still quite small and partly concealed under the primary interambulacral plates. On the aboral side (fig. 7) are seen the five genital plates, one of them developed from the posterior transverse rod, another from the right (dorsal?) transverse rod; a third one shows an indication of being developed from the dorsal arch, which latter would then form the origin

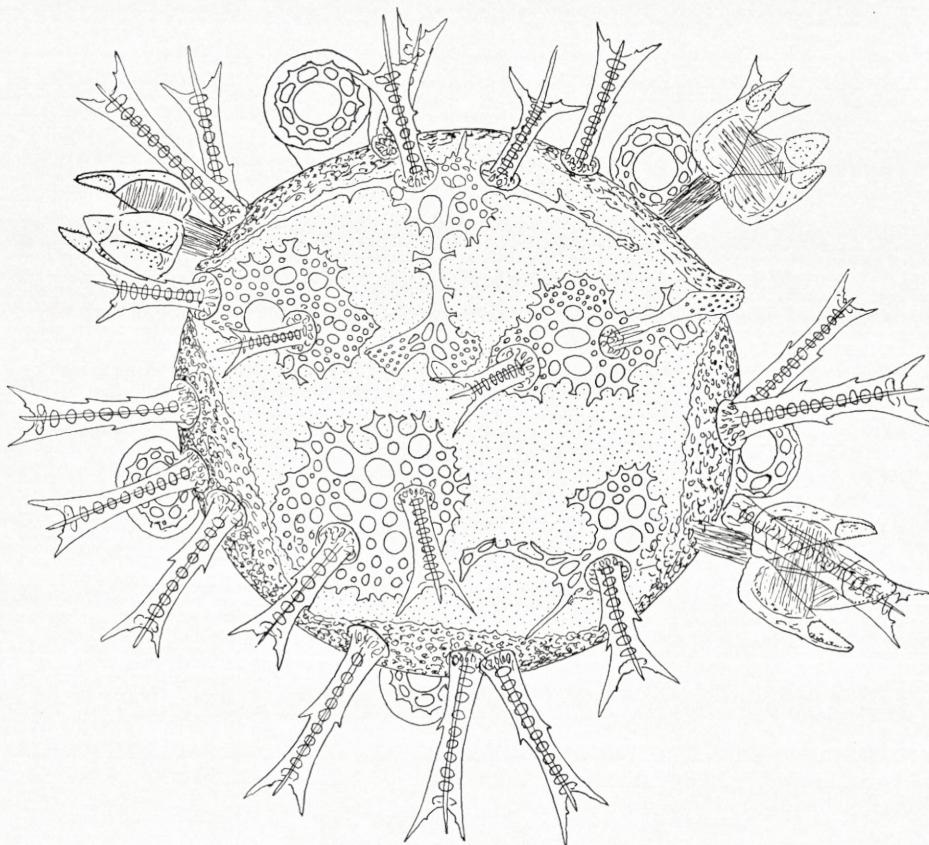


Fig. 7. Same as fig. 6, seen from the aboral side. Showing the young genital plates, the one on the upper side of the figure developing from the posterior transverse rod, the one on the right side from one of the transverse rods, the one on the lower right hand side apparently developing from the dorsal arch.  $\times 200$ .

partly of an ocular plate, partly of a genital plate — but I have been unable to ascertain this definitely.

In this young stage all the spines are of the embryonal type, terminating in three diverging points; there are three to four to each ocular plate, one or two on each genital plate. The primary tubefoot is large and has a fine ring-shaped plate in the sucking disk.

Fig. 8 represents the oral side of a more advanced stage. The buccal plates have grown considerably, forming a nearly closed ring, in the center of which is

an indication of the future mouth. The buccal tubefeet are about to appear, all at about the same time, as evident from the size of the holes for them in the buccal plates. Below the adoral end of the buccal plates are seen the first rudiments of the

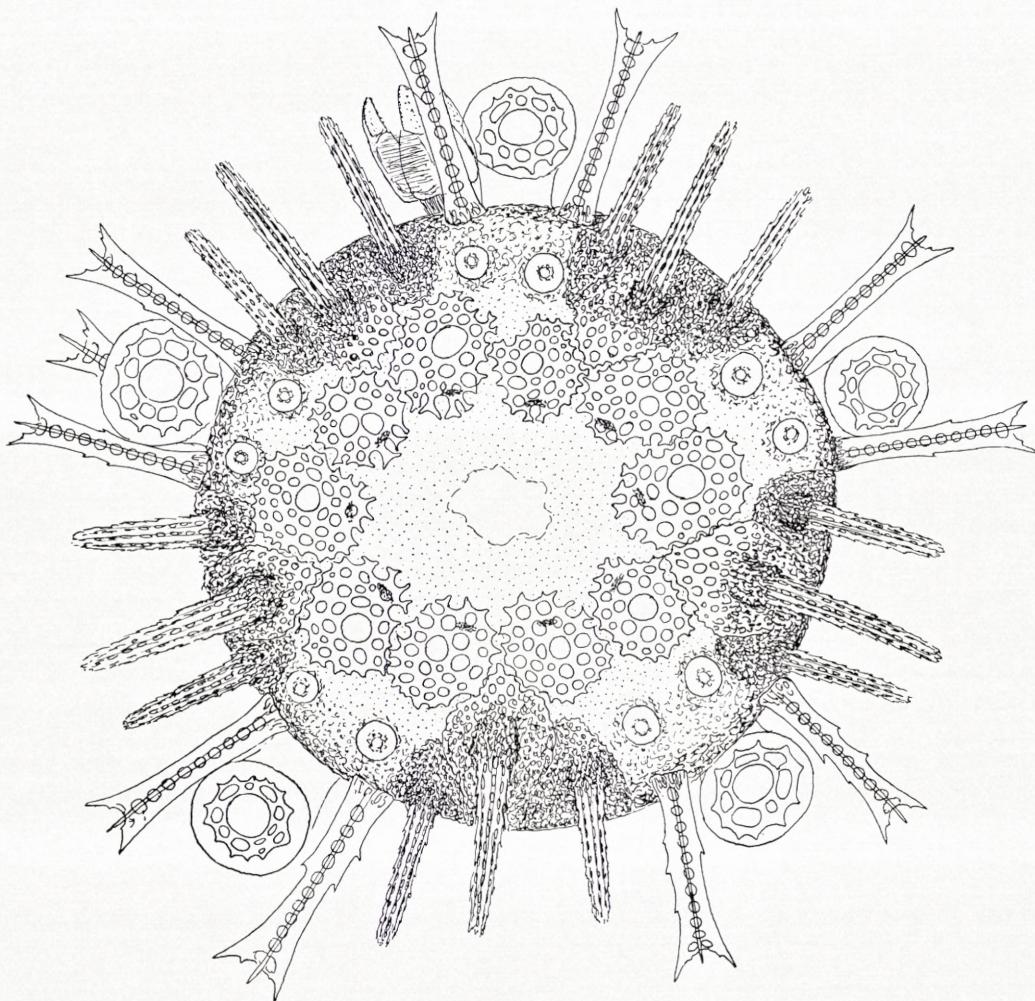


Fig. 8. More advanced stage of *Prionocidaris baculosa* (Lamk.), from the oral side. The plates arranged in a ring in the middle are the buccal plates, under the adoral edge of which are seen the first rudiments of the dental apparatus. The three first interambulacral plates carry young spines, not yet fully formed. The first pair of tubefeet have appeared.  $\times 200$ .

dental apparatus. The primary and the first pair of interambulacral plates have grown very considerably and the primary spine of each of them is already fairly developed, though not yet fully formed; they are quite different in shape from the three-pointed embryonal spines found on the ocular plates. The first pair of tube-feet have appeared; they are much smaller than the primary tubefoot, and their

sucking disk very small and indistinct. The corresponding ambulacrinal plates could not be made out distinctly.

In fig. 9 is shown the aboral side of the most advanced stage reached. Here

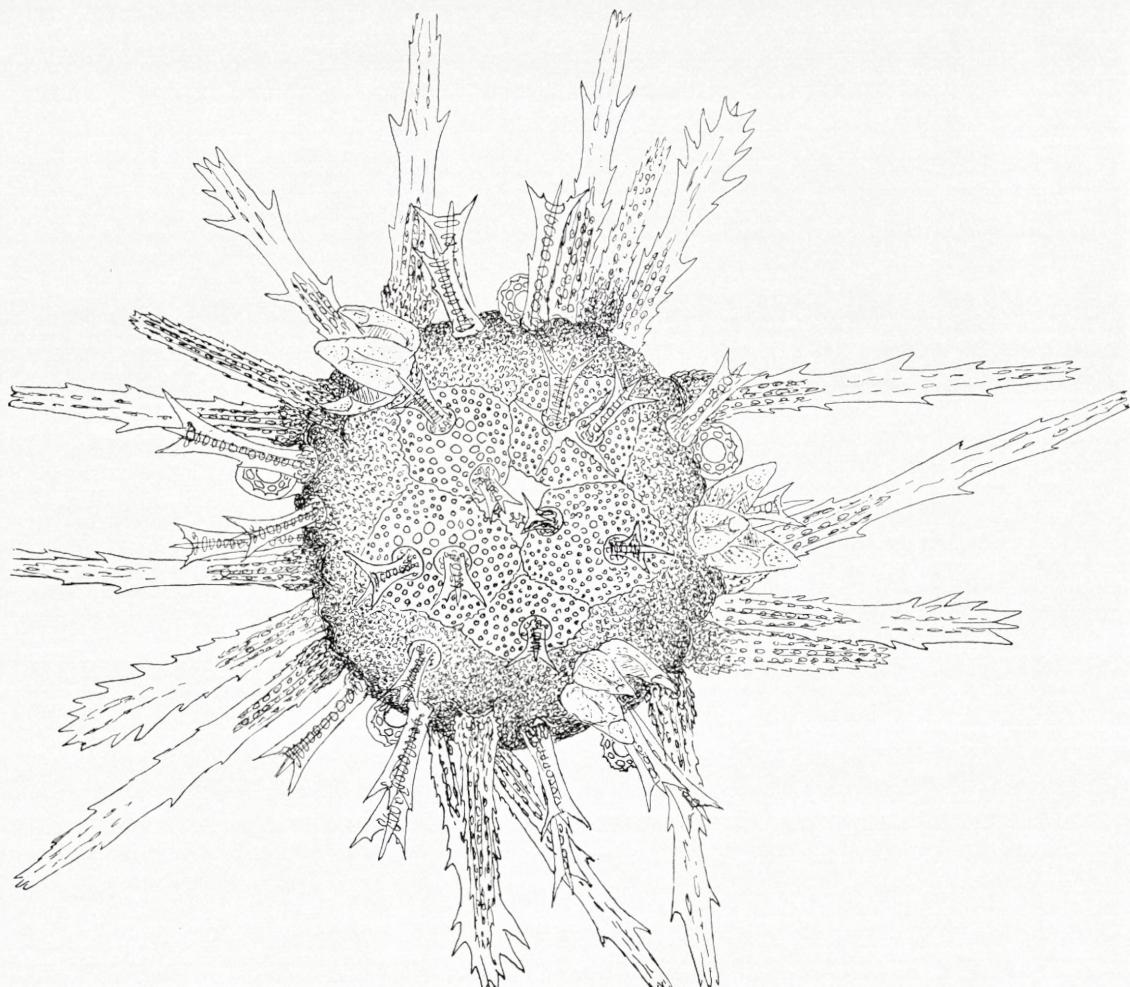


Fig. 9. Aboral side of more advanced stage of *Prionocidaris baculosa* (Lamk.). The genital plates form a closed ring, leaving a central space, in which are seen the first rudiments of two anal plates. The interambulacrinal spines partly fully formed.  $\times 105$ .

the genital plates have joined so as to form a rosette enclosing a small central membranous area, the future periproct. Two small plates have just appeared therein, the first of the future anal plates, which are thus seen to develop separately and gradually, the five plates in the radial corners of the periproct of adult specimens having no separate preponderance or morphological value, and there is, of course, no sign of a central plate originally covering the periproct. One of the genital plates

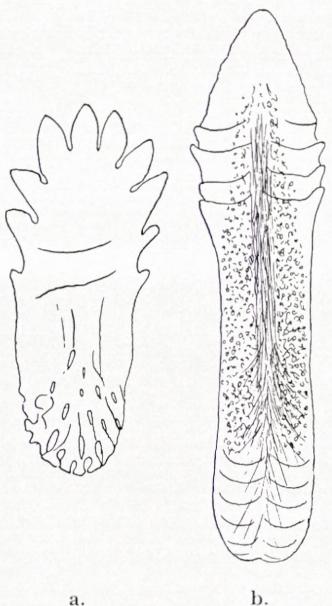
lags a little behind, not reaching the edge of the periproct; another of them still shows traces of the part of the larval skeleton (evidently the posterior transverse rod) from which it originated. The primary spines of the first two or three interambulacral plates are fully developed and with colour bands already indicated. These spines are very characteristic by their strong thorns, especially the one on the primary interambulacral plate, which makes it easy to recognize them with certainty in the following growth-stages (cf. my description of the young *Eucidaris metularia* in my paper "On the postlarval development of some Cidarids". Mem. Acad. Copenhague. 8. Sér. XI. 1927).

In this stage the buccal tube-feet have appeared, and a spine has appeared on the adoral edge of each buccal plate. The mouth has opened and the teeth have been formed. These latter are, however, still in an embryonal stage, of a very curious shape, with the point coarsely serrate and the aboral end in the shape of an irregular fenestrated plate (fig. 10 a). How this is transformed into the definite form, with the new lamellæ constantly forming at the aboral end, would seem rather difficult to understand. I have, however, succeeded in finding in a very young specimen of *Eucidaris metularia* from Banda a slightly more advanced stage in the development of the teeth, which seems to show that the lamellæ begin to appear outside the fenestrated part of the young tooth, this fenestrated part not being directly transformed into lamellæ (fig. 10 b). But it seems that the fenestrated part of the young *Eucidaris* tooth is rather different from that of *Prionocidaris* and occupies a much larger part of the tooth than in the latter, a difference which makes the conclusion as to the transformation of the young tooth into that of the adult form a little uncertain.

Fig. 10. Tooth of young *Prionocidaris baculosa* (Lamk.) (a.), and of *Eucidaris metularia* (Lamk.) (b.). a.  $\times 410$ ; b.  $\times 150$ .

These peculiar serrate young teeth recall the remarkable serrate teeth of *Meek-echinus*, figured on Pl. 76, fig. 7 of JACKSON's "Phylogeny of the Echini". In my Monograph of the Echinoidea, II. p. 79 I suggested that the serration of the teeth of *Meek-echinus* may perhaps rather be due to fracture. The character of the teeth of *Prionocidaris* (and evidently also of *Eucidaris*) does not lend support to this suggestion.

A point of the greatest morphological importance is the appearance of the interambulacral plates 4—6. As shown in fig. 11, plate No 4 lies nearly in the midline of the interradius, plate 5 and the — still quite young — plate 6 lying to the sides of plate 4, so that we have here a transverse series of three plates. This means that we have in this young stage a pluriserial interambulaerum, exactly like what is found in palaeozoic Echinoids. In *Archæocidaris* the basal part of the corona is resorbed during growth (just as it is in recent Cidarids), so we do



not actually find these first interambulacral plates; but there cannot be the slightest doubt that they must have been there, arranged as shown by JACKSON in the theoretical restoration Pl. 9 fig. 8 of his "Phylogeny of the Echini". A comparison of fig. 11 with the said figure in JACKSON's work, as well as with the quite similar figure of an interambulacrum of the Lepidocentrid *Hyattechinus elegans* Jackson

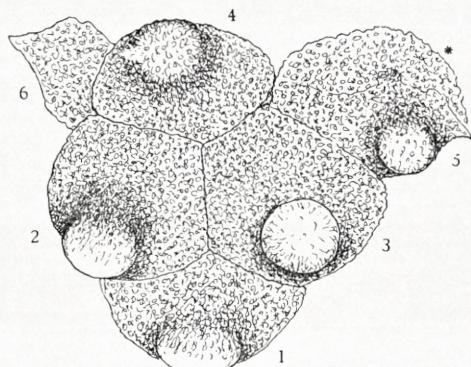
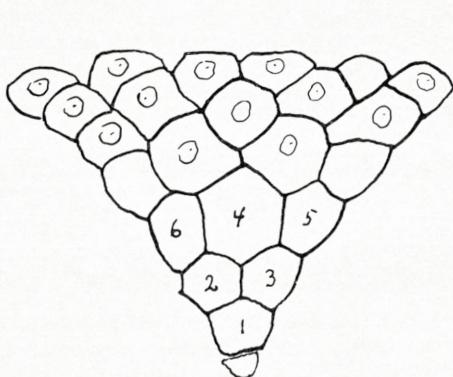


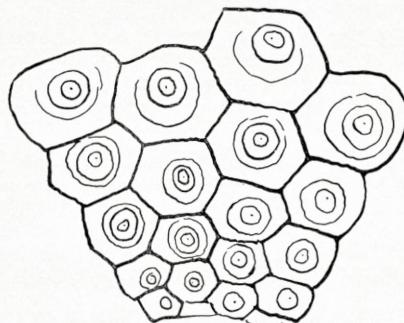
Fig. 11.

Fig. 11. Interambulacrum of young *Prionocidaris baculosa* (Lamk.). At the asterisc on the upper right side the limit between the interambulacral plate 5 and the adjoining ocular plate could not be made out distinctly.  $\times 225$ .

Fig. 12. Interambulacrum of *Hyattechinus elegans* (Jackson) (a.) and of *Archaeocidaris worteni* (Hall) (b.). Adapted from JACKSON's »Palaeozoic Echini of Belgium», fig. 5, p. 25 (a.), and from the same author's "Phylogeny of the Echini" Pl. 9. 6 (b.).



a.



b.

(fig. 12 a) shows the arrangement of the first 6 interambulacral plates to be exactly the same (that JACKSON's numeration of the plates differs from mine does not alter this fact). We may thus say that the young *Prionocidaris* (and probably all recent Cidarids) passes through an *Archaeocidaris* stage, a fact decidedly indicating the correctness of seeing in *Archaeocidaris* the ancestor of the Cidarids. — That not the slightest support of the *Bothriocidaris* theory is to be found in the Cidarid development need hardly be mentioned.

The knowledge of the *Prionocidaris* larva now obtained shows it to be in complete accordance with the other Cidarid larvae thus far known (cf. "Contributions" III. p. 18—20) and makes it practically certain that there is a special larval type peculiar to the Cidarid family, characterised by the very long, smooth, fenestrated

postoral and posterodorsal rods, by the posterior transverse rod being provided with a very long and slender ventral and dorsal median process, and by the very strong development of the ciliated lobes. No doubt also the strongly developed larval muscular system, enabling the two pairs of long arms to be moved straight backwards, is a common character of the Cidarid larval type.

## 2. *Laganum depressum* (L. Agassiz).

Pl. IV. Fig. 1.

This species, which is very common at depths of c. 5—25 fathoms on a sandy or muddy bottom off Abu Sadaf, a little outside the laboratory, was found partly ripe in the beginning of July (most of the specimens were still unripe at that time);

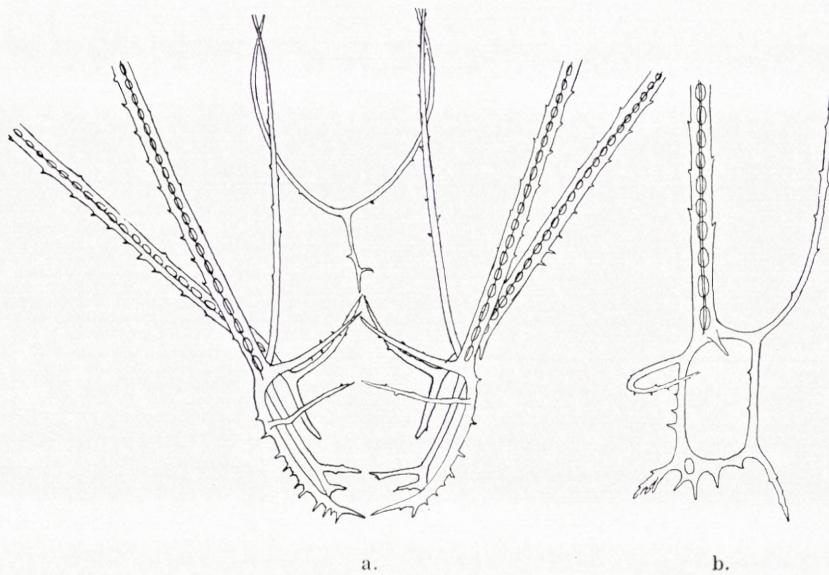


Fig. 13. a. Skeleton of fully formed larva of *Laganum depressum* (L. Agassiz). a. Front view, from the oral side. b. Half of skeleton of a younger larva, seen from the inside.  $\times 200$ .

fertilization was undertaken on July the 2nd and proved successful. The larvae of this culture having died before metamorphosis, a new culture was started on June the 24th, the larvae of this latter culture being carried successfully through metamorphosis.

The eggs are small, c. 0.1 mm in diameter, perfectly transparent, without any pigmented mucilaginous coat, such as occurs e. g. in *Echinodiscus auritus*. The cleavage is perfectly regular and does not offer any specially noteworthy features. 18 hours after fertilization the embryos were beautiful, a little elongate, transparent blastulae, containing a varying number of free mesenchyme cells; some of the blastulae showed a beginning of the gastrula invagination. Two days old the embryos had assumed

the shape of young plutei, with a rather strongly thorny skeleton, and without pigment. At the age of 6 days they showed the first rudiments of the posterodorsal rods, which are fenestrated like the postoral rods; still no pigment. At the age of 10 days the larvae showed the first signs of metamorphosis, viz. the formation of the amnion;

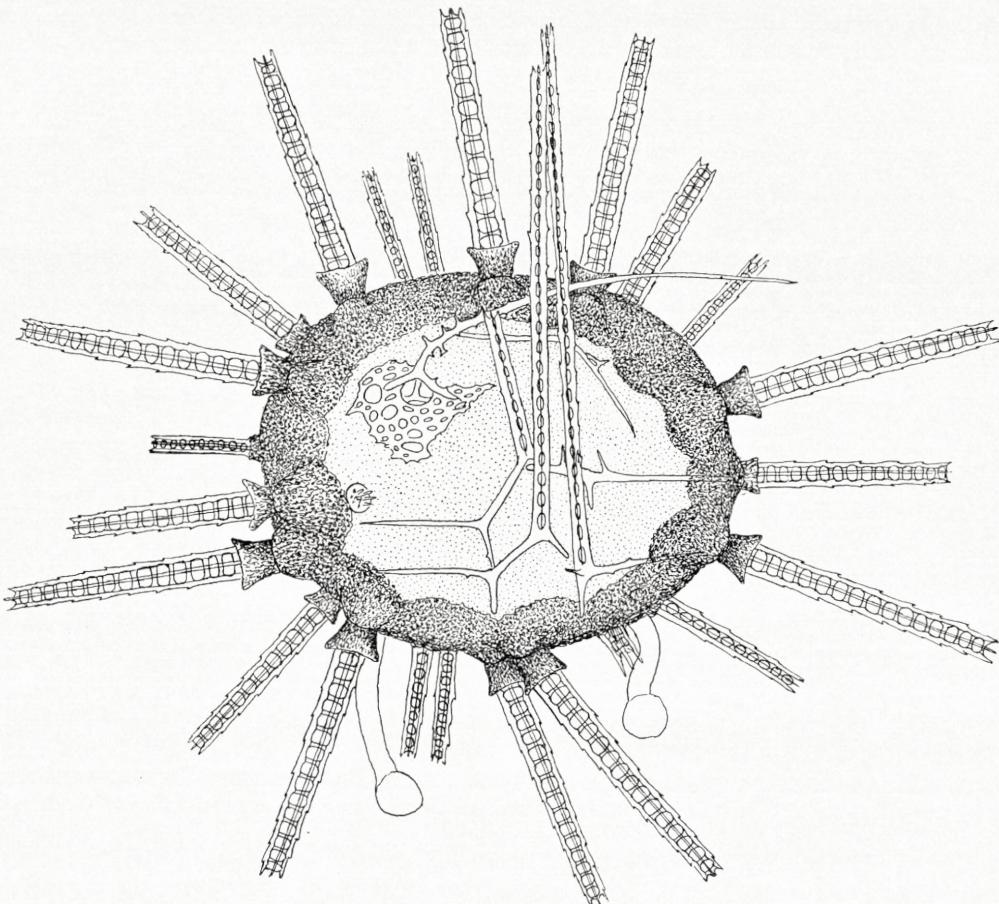


Fig. 14. Newly metamorphosed *Laganum depressum* (L. Agassiz). Aboral side; showing the main parts of the larval skeleton beginning to transform into the apical skeleton of the sea-urchin.  $\times 200$ .

and now also some scattered yellowish pigment spots had appeared. Beyond this stage the larvae of the first culture did not develop.

In the second culture the development proceeded at about the same rate, the larvae having metamorphosed at the age of about two weeks.

The fully formed larva (Pl. IV. Fig. 1) has rather long, slender arms, with only a very slight terminal widening. The lateral lobes are small and inconspicuous; the postoral band forms a small lobe on the transition to the postoral arms. The pigmentation is very inconspicuous, consisting only in a few small yellowish spots

scattered in the vibratile band and over the body. There is no distinct accumulation of these spots at the end of the arms, only an exceedingly faint yellowish tinge.

The skeleton of the larva (fig. 13) is of the usual Clypeastroid type, the body skeleton forming the typical basket structure; but it does not develop into a large fenestrated plate in the posterior end, as is the case in *Echinodiscus*. At metamorphosis the basket is partly resorbed, and the remaining part of the body rod, as well as the posterior prolongation of the posterodorsal rods are connected by horizontal muscles enabling an active movement of the four arms.

The young, newly metamorphosed sea-urchin shows the transformation of the basal part of the four main rods and of the dorsal arch into the apical system of the sea-urchin (fig. 14). There is herein such complete accordance with what obtains in *Echinocyamus pusillus*, so admirably described by THÉEL in his paper of 1892, that I find it superfluous to give a detailed description and figures of the postembryonal metamorphosis of the present species.

### 3. *Echinodiscus auritus* (Leske).

Pl. IV. Fig. 2.

As I did not succeed last year in rearing the larva of this species through metamorphosis, I made an attempt to do so again this year and succeeded. Artificial fertilization was undertaken on July the 7th and on the 21st some specimens had metamorphosed.

The larva figured on Pl. VII. Fig. 2 of "Contributions" III has not quite reached the full larval shape, the arms being not yet of full length. I therefore give a new figure of the larva, in beginning metamorphosis (the amnion formed), from which it will appear that the arms are a good deal longer than shown in the figure from last year; they are slightly curved towards the point, which may be a little widened.

The ciliated band forms a somewhat more prominent lateral lobe than in the figure quoted and the postoral band also forms a fairly conspicuous lobe at the base of the postoral arms, and there is a corresponding lobe on the dorsal side. The colour consists of isolated spots of a faint reddish-carmine tint; only at the point of the postoral (not the posterodorsal) arms is there a slightly more conspicuous reddish spot.

In its general features the young sea-urchin agrees so closely with the young *Laganum* that I think it superfluous to figure it. Also the larval skeleton forms the base of the apical skeleton of the sea-urchin in the same way as in the young *Laganum*, cf. fig. 14. I may only mention specially that the complicate fenestrated plate occupying the posterior end of the larva is actually dissolved before metamorphosis, not incorporated into the final skeleton — a fact which I was unable to ascertain from the non-metamorphosing larvæ from last year's culture.

It would have been of very great interest to have reared the young sea-urchins till the beginning formation of the slits in the test. In order to try to rear them so far I put them into a dish with some coarse sand at the bottom; but they did not develop

any further. And as only very few adult specimens were found on the only locality in the neighbourhood of the station (Abu Mingar), where the species occurs (on the very beach, lying dry at low tide), it was hopeless to try to find the quite young stages in the sand there.

### Astroidea.

#### 4. *Luidia Savignyi* (Audouin).

Pl. V. Figs 2—5.

As mentioned on p. 8 of "Contributions" III, I did not succeed last year in getting any fertilization of this *Luidia* species, artificial or natural, in spite of repeated attempts. This year I made a fresh attempt, thinking it of great interest eventually to compare the larva of this species with that of the two other species, the larvae of which are known so far, viz. the two European species, the 5-armed *Luidia Sarsi* and the 7-armed *Luidia ciliaris*. The species *L. Savignyi* not being of common occurrence at Ghardaqa I had some trouble in getting the necessary material, the single specimens brought home now and then by the sailors all being males; finally on August the 3rd they brought home 6 specimens, among which one ripe female, the rest of them males. I then tried to make artificial fertilization. Although some of the eggs showed no nucleus, fertilization seemed as unsuccessful as in last year's attempts. Still, after 6 hours I found a very few apparently normal cleavage stages, from which I got the next morning about 20 normal gastrulae. Another attempt was then made (the female specimen having been kept alive in the tank; only two of its arms were used at the first attempt, and the loss of a couple of arms does not, of course, matter to a *Luidia*, which practises autotomy on the least bit of rough treatment, and regenerates the lost parts with great ease). The eggs were left in the sea-water about 3 hours, before the sperma (activated by adding a drop of KOH to the water) was added. This attempt gave a somewhat better result — some 200 blastulae. So far as I could ascertain (by the evening light) the wall of the blastulae was folded, as usual in Asteroids. From the two attempts together I got in all c. 45 young larvae, which had at the age of two days assumed the shape of young Bipinnariae.

Pl. V. Fig. 2 represents the young larva, 5 days old. It is rather remarkably short, the anterior part not at all elongate, as was to be expected from our knowledge of the young *Luidia ciliaris* larva (cf. fig. 9, p. 7 of my paper "On the development of some British Echinoderms" J. Mar. Biol. Ass. X. 1913). At the age of about a week the larvae began, however, to become more elongate in the anterior part of the body, viz. the median lobes, as seen best in Pl. V. Fig. 4 representing a fully formed larva in side view. The two median lobes are movable, but only slowly, and they are by no means used actively in swimming, as is the case in *L. Sarsi* and *ciliaris*. This accords with the fact that there is no trace of the strongly developed muscular system found in the anterior lobe of the two latter species, as described and figured by TATTERSALL & SHEPPARD, in their paper "Observations on the Bipinnaria of the

Asteroid genus *Luidia*" (James Johnstone memorial volume. Liverpool 1934. p. 44—48).

The larvæ represented in Pl. V. Figs. 3—4 are only 12 days old, but already in beginning metamorphosis and have thus reached their full shape. They are entirely transparent, without any trace of colour, whereas the young, newly metamorphosed sea-star is faintly yellowish, with the stomach orange-coloured.

The larva of this *Luidia* species accordingly differs very conspicuously from the two European *Luidia* larvæ, remains so to say in a much more embryonal stage. The elongation of the anterior part of the body, though distinct, is very much smaller than in the latter; also the paired arms are much shorter and not transformed into ciliated, food-collecting channels, as so excellently described particularly by TATTERSALL & SHEPPARD. Another, very noteworthy, difference is that the anterodorsal arms remain simple, not becoming double (or even triple), as they are in the fully developed larvæ of *L. Sarsi* and *ciliaris* — whereas in the younger stages of the said larvæ the anterodorsal arms are still simple as in the *L. Savignyi* larva.

From the relatively small size of the *L. Savignyi* larva it was to be expected that the larval body would be resorbed on metamorphosis, not thrown off, as is the case in the *L. Sarsi* larva. It took me some time to ascertain this. Repeatedly, in the evening, I put some larvæ near metamorphosis, but with the larval body still in perfect form, into a separate dish, expecting then early next morning to find either the resorption stages or the thrown off larval bodies; but I found only the completely metamorphosed young sea-stars, without any trace of the larval body attached, and no free, thrown off larval bodies. Finally, observing some metamorphosing larvæ from hour to hour under the microscope, I succeeded in following the resorption of the larval body (Pl. V. Fig. 5). The whole process takes only a couple of hours, and it thus became clear why I could not see anything of the process in metamorphosing larvæ, which had been kept the night over.

It is in accordance with the small size of the larva, only c. 1.5 mm full length, that the development takes so much shorter a time — only c. 12—15 days — than in the much larger European larvæ, *L. ciliaris* c. 7 mm, *L. Sarsi* c. 30 mm (according to TATTERSALL & SHEPPARD only 15—18 mm). It is true, we do not know exactly the time the development of the two latter larvæ requires; but the young larva of *L. ciliaris* figured on p. 8 of my paper of 1913 quoted above, with the arms still quite short and simple, and evidently far from metamorphosis, is 5 weeks old<sup>1</sup> — proof enough that this larva will require at least a couple of months for completing its development, and the much larger *L. Sarsi* larva probably a much longer time.

Knowing now the larva of *L. Savignyi*, we are able to form a better judgment

<sup>1</sup> TATTERSALL & SHEPPARD, Op. cit. p. 44, say that I described the early stages of the *L. ciliaris* larva "from material collected at Plymouth". This seems to indicate that they overlooked the fact that I reared the young larvæ from artificially fertilized eggs. I did not "collect" these young larvæ; if collected from pelagic material it would have been impossible to identify them with certainty as the *L. ciliaris* larva.

of the real characteristics of the *Luidia* larva in general, than was possible from the knowledge of the two European species alone. These latter are now seen to be a highly specialized form of the *Luidia* larva. The general characters of the *Luidia* larva are: the more or less pronounced elongation of the anterior part, viz. the median lobes; further the total absence of Brachiolaria arms and sucking disk. In the latter character they agree with the larvæ of Astropectinids, from which they differ only in the more developed arms and the elongation of the median lobes. The larvæ of the two families of the Astropectinidae and the Luidiidæ would seem, according to our present stage of knowledge of the Asterid larvæ, to stand apart from all the other Asterid larvæ, these latter having all, so far as is known, a Brachiolaria-stage (much reduced, but still recognizable, in those which have direct development). It would be of very great interest to learn whether the third family of the Paxillosa, the Porcellanasterids, agree with the Astropectinids and Luidiids in having no Brachiolaria-stage. Judging from the embryo of *Ctenodiscus australis* figured by LIEBERKIND ("Ctenodiscus australis Ltk., a brood-protecting Asteroid". Vid. Medd. Dansk Naturhist. Foren. 82. 1926, p. 193, fig. 6) there seems to be no trace of a Brachiolaria stage in this species.

Of the three *Luidia* larvæ known till now the *L. Savignyi* larva is much the simplest; the *L. ciliaris* and *Sarsi* larvæ, with the much more elongate median lobes, forming even active swimming organs, with the paired arms developed into ciliated channels, and the anterodorsal arms divided from the base into two (or three) equally developed branches, are much more specialized, particularly the *L. Sarsi* larva, which grows to such an excessive size that, as pointed out by TATTERSALL & SHEPPARD, the larval body has become too big for being resorbed on metamorphosis, and is simply thrown off, remaining free-swimming for some time, even for months! It is in accordance herewith that the young sea-star of the *L. Sarsi* larva grows to a much larger size, before the larval body is thrown off, than that of *L. ciliaris*, the larva of which reaches only a smaller size and is resorbed, not thrown off at metamorphosis (cf. TATTERSALL & SHEPPARD, Op. cit.).

The newly metamorphosed sea-star of *L. Savignyi* is at first rather amoeboid, changing its shape, being usually somewhat elongate (fig. 15), and only gradually assuming the final circular shape (fig. 16). At metamorphosis it has only the two first pairs of tube-feet developed<sup>1</sup>—whereas the newly metamorphosed *L. ciliaris* has 5 pairs<sup>2</sup>, the newly liberated *L. Sarsi* no less than 10 pairs; the relative size of the young sea-stars of the three species is in accordance therewith.

<sup>1</sup> In fig. 15 a. only one pair of tube-feet is shown, the second pair not being discernible in the unstained specimens (which show the skeleton distinctly, and therefore were used for drawing), but in stained specimens the second pair of tube-feet also is seen to be present.

<sup>2</sup> According to TATTERSALL & SHEPPARD (Op. cit. p. 57, fig. 7c.) the young sea-star of *L. ciliaris* has only 5 pairs of tube-feet at metamorphosis. GEMMILL (On a new brachiate Asteroid larva and on the advanced Bipinnaria of *Luidia ciliaris* (Philippi) Gray. Proc. R. Phys. Soc. Edinburgh. XIX. 1915, p. 197), however, states that the young sea-star has 12 pairs of tube-feet in each arm. I am unable to account for this discrepancy; but it would seem probable that the statement of TATTERSALL & SHEPPARD is the correct one.

The young sea-stars were put into a dish with some sand from the locality where the adults were found; they lived very well in it, and after about four weeks had reached the stage shown in fig. 16, with two pairs of tube-feet distinct. I shall not enter on a detailed description of the development of the skeleton — it appears plainly enough from a comparison of the figures — I would only point out the peculiar shape of the terminal plates, each carrying two bundles of two-pointed spines; fur-

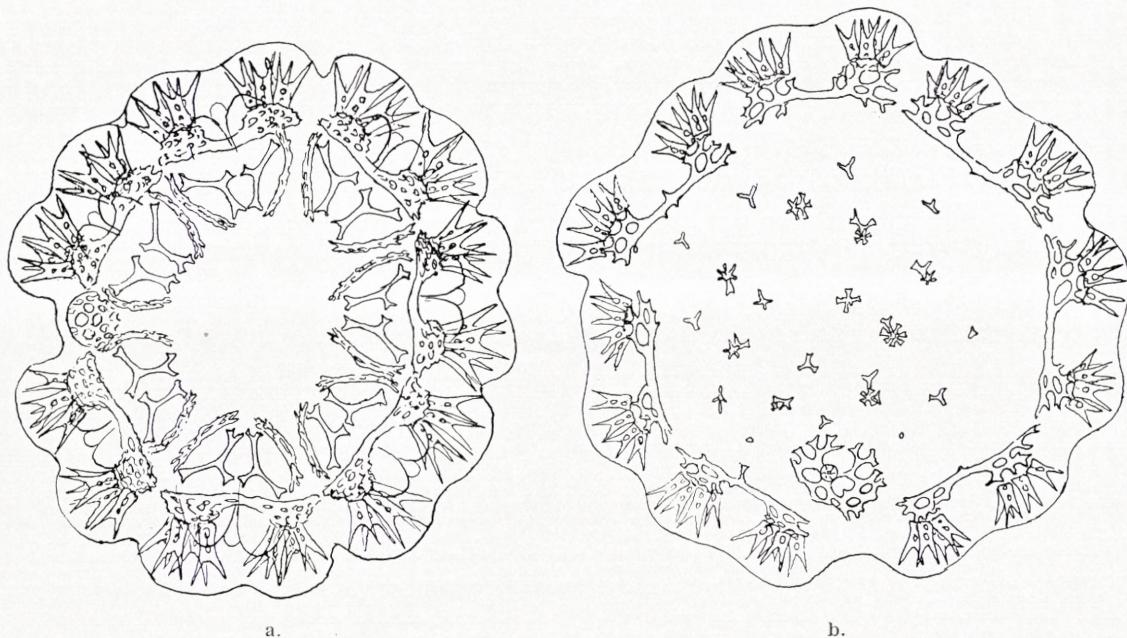


Fig. 15. Newly metamorphosed *Luidia Savignyi* (Audouin). a. Oral side, showing the first pair of ambulacral and adambulacral plates; b. aboral side, showing the beginning formation of the dorsal skeletal plates. The larger plate at the lower edge is the madreporite.  $\times 135$ .

ther the fact should be noted that the dorsal skeleton shows no regular arrangement, and especially that there is no central plate (figs. 15, b; 16).

According to Hörstadius (Embryologische Beobachtungen über *Luidia ciliaris* Phil., L. Sarsi Düb. & Kor. und *Phyllophorus urna* Grube. Arkiv för Zoologi, Bd. 18. B. 1926) the hydrocoel of *L. ciliaris* at first only develops 5 radial pouches, the 6th and 7th appearing later, after the hydrocoel has closed into a ring. I regret very much not to have followed the formation of the radial pouches in the live larvae; in the preserved larvae all the 7 radial pouches are formed, and in an equally advanced stage. But it is an important fact that the young ambulacral and adambulacral plates of the 7 radii are all of exactly the same size and equally advanced in their development — which, however, says nothing about the time of the appearance of the 6th and 7th radial pouch, the ambulacral skeleton not appearing till after the hydrocoel has formed the 7 radial pouches.

The fact that the *L. Savignyi* larva differs so strikingly from the larvae of *L. ciliaris* and *Sarsi*, being so much more primitive than these latter, makes it rather urgent to study the development of other *Luidia* species also. DÖDERLEIN, in his excellent Monograph of the great genus *Luidia* ("Siboga" Exped. Monogr. XLVI. b. 1920) came to the result that the *ciliaris*-group, to which the species *Sarsi* and *ciliaris* belong

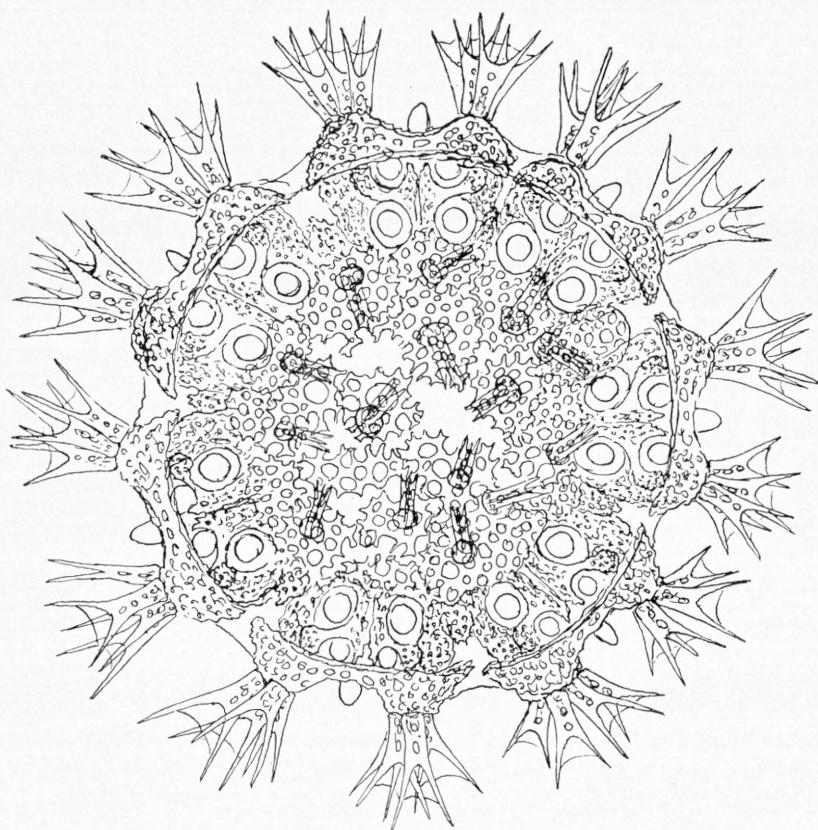


Fig. 16. Young *Luidia Savignyi* (Audouin), 5 weeks old. Aboral side. Two pairs of tube feet developed.  $\times 135$ .

(subgenus *Hemicnemis* Müll. & Troschel) is the most specialised of all the Luidiids, whereas the group to which *L. Savignyi* belongs, the *alternata*-group (subgenus *Maculaster* Döderlein) represents a less specialised type (although not the most primitive of all). The shape of the larvae of the three said species is in full accordance with the results reached by DÖDERLEIN from a comparative study of the characters of the adult; even the fact that the *Sarsi* larva is more highly specialised than the *ciliaris* larva is in accordance with the result of DÖDERLEIN that within the genus *Luidia* the many-armed forms are the more primitive, the 5-armed the more specialised. It would now be of the greatest interest to learn whether the other species of the *ciliaris*-group have the same highly specialised larval type as *ciliaris* and *Sarsi*

(— it is of interest in this connection that a “*Bipinnaria asterigera*” is recorded from off Celebes in the “Summary of the Scientific Results of the “Challenger” p. 836; as I pointed out in my “Echinodermenlarven d. Plankton-Expedition” (1898), p. 39, this cannot, of course, be identical with the “*Bipinnaria asterigera*” of SARS, which is the *Luidia Sarsi* larva, but must belong to another *Luidia* species —). It will be equally interesting to learn whether the other species of the *alternata*-group, or even those of the *clathrata*-group, the most primitive of all the Luidias, have a similar primitive larva to that of *L. Savignyi*.

##### 5. *Pentaceraster mammillatus* (Audouin).

Pl. V. Figs. 6—7.

On the 15th of July the sailors brought home from Abu Mingar, a few miles South of the station (in the immediate neighbourhood of which this species does not occur), 10 specimens of *Pentaceraster mammillatus*, 8 of which proved to be ripe males, 2 females, one of which had ripe eggs, the other being unripe. Artificial fertilization was undertaken (late afternoon) and proved in some degree successful, although the sperma was very little movable (not treated with KOH).

The eggs are small, c. 0.1 mm, quite transparent. The cleavage was regular and very beautiful; the 32-cell stage was reached after three hours. The next morning I could isolate c. 200 fine gastrulae, which after 2 days had developed into normal young Bipinnariæ. 12 days old the larvæ had the shape shown in Pl. V. Fig. 6; the enterocoel pouches have grown forwards and have joined in the preoral lobe. At the age of 16 days the larvæ showed the first indication of Brachiolaria arms and sucking disk, and three weeks old they had developed into typical Brachiolarias and showed the first signs of metamorphosis. On the 7th of August, thus after 24 days, I found the first larvæ about to metamorphose.

The larvæ are, as usual among Asteroids, very active swimmers; but they did not keep near the surface, and did not swim horizontally, as I found it to be the case last year with the *Astropecten* larvæ, and especially the larvæ of *Asterope carinifera*. Whereas up till the beginning metamorphosis the larvæ had been very healthy, scarcely a single one having been lost, now suddenly a strong mortality set in — probably because of some sort of infection. But a few metamorphosed successfully and, having been transferred to a dish with some small pebbles and shells on the bottom, grew a good deal in size, as appears from figs. 17, a, b, representing a newly metamorphosed and an 8 weeks old specimen.

Concerning the larva, represented in its young and its final shape in Pl. V. Figs. 6—7 it is to be mentioned that the arms, particularly in the fully formed larva, are rather strongly movable, but not contractile. The ventral median lobe varies considerably in length, especially in the fully formed larva, may even be conspicuously longer than the dorsal median lobe. The Brachiolaria is of the type with a series of papillæ along each side of the ventral lobe and a short series of papillæ along the

Brachiolaria arms, much as in the *Porania* larva, not with a terminal crown of papillæ as in the *Asterias* larva. The colour is very faint; only the oesophagus is fairly distinctly yellowish, and, mainly in the fully formed larva, there is the merest indication of yellowish colour on the preoral and postoral transverse band; otherwise it is colourless.

The young sea-star does not call for a more detailed description, the figures giving the necessary information. In comparison with the young *Luidia* it is re-

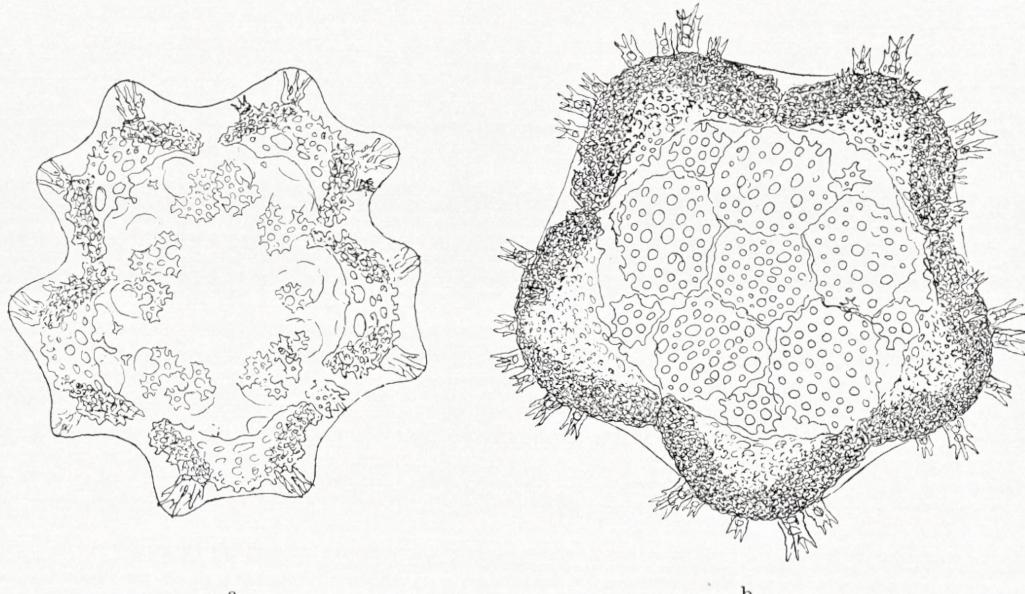


Fig. 17. *Pentaceraster mammillatus* (Audouin). a. Newly metamorphosed, from the oral side: b. 8 weeks old specimen, from the dorsal side.  $\times 105$ .

markably strongly built, the plates being rather heavy, in conformity with the strong build of the adult *Pentaceraster*. The perfectly regular dorsal skeleton is in strong contrast to that of the young *Luidia*.

#### 6. *Linckia multifora* (Lamarck).

Pl. IV. Figs. 3—4.

This species, the "kaf Mirjam" (hand of the Virgin Mary) of the natives, has specialised to such a high degree in the propagation by autotomy that one could scarcely help being a little surprised to find it to propagate in the normal way also, by means of eggs and pelagic larvae. And it was the more surprising to find the small, dividing specimens to contain ripe sexual products, as it appears that it is mainly in young age it propagates by autotomy; larger specimens — and it grows to a large size, I have specimens of all intermediate sizes up to 170 mm arm-length — do not appear to practise autotomy, and it might therefore be expected that young specimens propagated by autotomy alone, adult specimens by eggs and pela-

gic larvæ alone. But such then is not the case. However, it is evident that the propagation by autotomy is by far the dominant in the young specimens. The gonads — which are serial — were found developed only in the larger arms, usually very irregularly, only in one or two arms, and usually only few of the gonads, now one at the base on one side of the arm, now a few farther out on the other side of the arm. In the smaller regenerating arms I never found gonads developed — but in such arms that had thrown off the distal part of the arm and were about to regenerate it. Specimens with ripe sexual products could be found most of the time from about the middle of May (last year) to September. I did not succeed in getting ripe specimens of both sexes at the same time last year, although they may be kept alive very easily for quite a long time in the tanks of the station. But this year I got some ripe specimens of both sexes on July the 23rd and then tried to undertake artificial fertilization. Only rather few eggs were obtained, the gonads being small and few, and as moreover only a very small percentage of the eggs would ripen for fertilization, even after being kept some hours in the water before the sperma was added, it is no wonder that the result of the fertilization was very poor. After two days I had in all 9 gastrulæ, most of them apparently not quite normal. After five days I had 5 young Bipinnariæ left. After two weeks I had only two larvæ left, one of them not even quite normal, its left anterodorsal lobe being undeveloped.

These two larvæ, however, went on developing normally, the incomplete one even ultimately developing a quite normal anterodorsal arm. On the 9th of August, at the age of 17 days, the enterocoel pouches had united above the oesophagus, not prolonged into a long point but simply rounded above the oesophagus. Three weeks old the larvæ showed the first indication of Brachiolaria arms, and 27 days old they were near metamorphosis and had assumed full Brachiolaria shape. As, in order to have them figured correctly, it was necessary to narcotise them (— which proved to be very difficult; both sulphate of magnesia and alcohol, added dropwise, had to be used —) they were now preserved. Thus I did not get the young, metamorphosed sea-star, but the full larval stage was obtained in spite of the very scarce material.

The fully formed larva, not the young one, proved to be exceedingly sensible; at the slightest touch — thus when sucked up in a pipette for being transferred to fresh sea-water — it would fold all its arms tightly up around the body and remain so for quite a long while before unfolding its arms again to begin swimming.

In the young stage the larva so closely resembles the young *Luidia* larva, as represented in Pl. V. Fig. 2, that I did not think it advisable (or necessary) to sacrifice one of my few larvæ for making a camera drawing of it. The only difference from the young *Luidia* larva, I could find, was that the dorsal median lobe of the *Linckia* larva is narrower than the ventral one, and with perfectly straight sides. The fully formed larva (Pl. IV. Figs. 3—4) has moderately long arms, very movable, as explained above, though not used actively for swimming; they are not distinctly contractile. The posterolateral arms are usually bent forwards. The Brachiolaria arms are as in the *Pentaceraster* larva, the median lobe with a series of papillæ along each

side, and the paired arms with a short series of papillæ at the tip. The ventral median lobe usually bends down towards the paired Brachioralia arms; the dorsal median lobe, which is somewhat longer than the ventral one, is usually bent dorsalwards, as shown in Pl. IV. Fig. 4.

The colour of the fully formed larva is a very faint, diffuse yellowish, the stomach dark, almost black, in young larvæ more reddish-violet.

The skeletal plates of the beginning sea-star do not present any specially characteristic features, as is the case with the young *Fromia*.

### 7. *Fromia ghardaqana* Mrtsn. (n. sp.)<sup>1</sup>.

Pls. VI. 1—4; VII.

In the report on my researches of last year ("Contributions" III, p. 8) it was mentioned, under the name of *Fromia monilis*(?), that I had found it to be a protandric hermaphrodite, but that I did not succeed in studying its development; artificial fertilization was impossible because of the eggs being large and full of yolk, and although I kept a number of specimens alive in the tank for a long time no spawning took place. This year (1937) I was more successful, getting its complete development. Also the statement of its being a protandric hermaphrodite was verified.

Having put a good number of specimens together into a dish, I had the pleasure of seeing them spawning on July the 8th, in the afternoon at about 3 o'clock. On the following days again some specimens were spawning, always at about 3 o'clock in the afternoon. On the 14th of July the last spawning took place (fresh material having repeatedly been brought in from the reef). Later on no spawning occurred, though I repeatedly had fresh material brought in.

The spawning specimens always came up along the sides of the dish to the surface of the water, sometimes with an arm stretched out horizontally under the surface film. Always some males would start, the sperma coming out in a white stream from each of the genital pores, which lie on the dorsal side, two in each interradius, a little distant from the edge. Soon the water became quite milky, and then the spawning of the females would begin. The female genital pores are likewise situated on the dorsal side, two in each interradius. The pores being quite small,

<sup>1</sup> This new species of the genus *Fromia* belongs to the group with relatively long and slender arms (cf. H. L. CLARK. Echinoderms of the Torres Strait. 1921. p. 39) and appears to be the nearest related to *Fr. pacifica* H. L. Clark, from which it differs, however, especially in having a series of enlarged plates (blue in life) along the dorsal midline of the arms; further the granular covering is different, not nearly so close in *pacifica*, in which also the granules are pointed, so that the surface feels rough, whereas in the present species the granules are not pointed and the surface is smooth, according to kind information from H. L. CLARK, who has compared a specimen of the Red Sea species with the type of *Fr. pacifica*.

It is this species which was mentioned under the name of *Fromia monilis*(?) on p. 8 of "Contributions" III, and apparently it is also the same species which TORTONESE (Echinodermi del Mar Rosso. Ann. Mus. Civico Storia Nat. Genova. LIX. p. 213) mentions as *Fromia monilis* Perrier. I have had an opportunity of comparing the Red Sea species with the type of *Fr. monilis* in the Paris Museum and found them to be quite different.

and the eggs large, c. 1 mm in diameter, this necessitates the eggs coming out slowly, one by one, and pressed into the shape of long, thin sausages. After being liberated they gradually assume, more or less completely, the normal spherical shape, but they often remain elongate, elliptical. On account of the rich content of yolk they do not sink to the bottom, but float freely in the water or, more generally, directly under the surface of the water. Gradually there would be at the surface of such dishes with spawning Fromias a dense layer of these large, intensely high-red eggs. Apparently they were fertilized immediately after liberation, which, however, was not easy to ascertain, owing to the fact that the fertilization membrane lies close to the egg-surface.

The first lot of eggs, simply removed to a dish with fresh sea-water, did not seem to develop normally; those spawned the following day were then put into a plankton-net in the tank, under a very faint stream from a tap. The following day only a very few of them were left, the rest of them dissolved, evidently smashed by that gentle stream of water; the eggs are, indeed, exceedingly brittle, on account of the great amount of yolk contained in them. The eggs spawned the following days were then put partly into the tank itself, with only a very faint stream through, and the outlet so secured that the floating eggs could not pass through, partly into a plankton-net suspended in the tank, with the stream from the tap outside the net, so that the eggs could not be hurt by it. With these precautions I succeeded in getting the normal development of the eggs.

What makes it especially difficult to see whether the eggs are developing normally is the fact that the cleavage is not externally observable. Only when the cilia have developed, and the embryo is beginning to rotate within the egg-membrane, which stage is reached after about 18 hours, does it become clear that the development has proceeded normally. At the age of c.  $1\frac{3}{4}$  days the embryo leaves the egg-membrane,

The young free-swimming embryo is a simple, thick, oval, perfectly intransparent, red lump (Pl. VI. Fig. 1). At the age of three days they are assuming their full larval shape — a uniformly ciliated round or oval body, with a pair of short, thick lobes and an unpaired, somewhat longer one, usually bending a little downwards towards the two shorter lobes. It is beautifully high-red, perfectly intransparent (Pl. VI. Figs. 1—4). Later on a thickening becomes apparent at the base of the unpaired process; this, of course, corresponds to the sucking disk of a Brachiolaria, and the three processes accordingly represent the Brachiolaria arms. It is thus proved that *Fromia* has a rudimentary Brachiolaria-stage, corresponding to what is found in other Asteroids with direct development, e. g. *Asterina*, *Solaster*, *Asterias Müller*. Pl. VI. Fig. 3 represents a larva with a pair of smaller inner lobes, evidently an anomaly.

The larva swims with the round end forwards, the lobes directed posteriorly; it seems never to use the sucking disk for attaching itself, before it metamorphoses.

At the age of 6—7 days the larvae began to become flattened, or rather compressed, in the broad main part of the body, and indistinctly pentagonal, indication of the approaching metamorphosis, but not till the age of 16 days did any of the larvae complete metamorphosis. In the course of the following 2—4 weeks several

more larvæ metamorphosed; but a great percentage of them went on swimming, without showing signs of completing metamorphosis. And still at the end of my stay at the laboratory I found a pair of apparently normal, free-swimming larvæ, while a good number of other, not metamorphosed, larvæ were more or less reduced in size, having of course subsisted that long time upon the rich yolk content of the egg.

Owing to intransparency of the eggs the cleavage and the developmental processes could only be studied by means of sections, a number of which, representing divers developmental stages, are represented on Pl. VII.

No direct cleavage of the egg takes place. The nuclei alone divide and are scattered irregularly in the yolk-mass, as shown in Pl. VII. Fig. 1, which is a section of an embryo 3 hours old. The yolk is very distinctly vesicular, more finely in the central, more coarsely in the peripheral part. At the age of 5—6 hours the nuclei are beginning to wander out towards the surface of the egg (Pl. VII. Fig. 2), where gradually they arrange themselves in a single layer. But the nuclei gradually become much too numerous for forming a regular single layer, so that a most peculiar folding must take place. The nuclear layer, in order to find room, is pressed inwards as irregular strands (Pl. VII. Fig. 3), the embryo in this stage (c. 15 hours old) rather recalling a miniature walnut. The yolk vesicles arrange themselves in such a way that the larger of them in the main follow the strands of nuclei. While still enclosed in the egg-membrane the nuclei gradually again wander out towards the surface, but now in a thick layer, as necessary on account of their great number, and form now a definitely limited, thick ectoderm (Pl. VII. Fig. 4, from an embryo 28 hours old). At the same time the gastrula invagination takes place; the space between the ectoderm and the archenteron is filled out by a rather coarsely vesicular yolk with scattered nuclei, the mesenchyme. One cannot help wondering how the nuclei can know where they have got to go — and as a matter of fact the process sometimes does not happen in quite the typical way — as in the embryo represented in Pl. VII. Fig. 5. Here the nuclei have not got to the surface of the egg, but have collected to form the ectoderm layer some way inside the yolk, leaving a large portion of the yolk outside, so as not to participate in the embryo-formation. Such embryos, of course, become a good deal smaller than normal; I have observed some such smaller embryos among the larger normal ones, but I regret not having isolated them for following their further fate, so I cannot say definitely whether they can develop through metamorphosis like the normal embryos; my impression is, however, that none of these smaller embryos reached metamorphosis.

It may not be superfluous to point out that the fact of the gastrula invagination being in the embryo represented in Pl. VII. Fig. 4 on the broader side, in that shown in Pl. VII. Fig. 8 at the posterior end, has no morphological significance. The apparent difference is due to the simple fact that the eggs do not all assume the normal spherical shape after having been pressed out through the small genital pores — and there is, of course, no guarantee that the long axis of the elongate eggs corresponds with the future longitudinal axis of the embryo.

The further development of the embryo, from the gastrula stage through metamorphosis, is exceedingly difficult to follow. Whereas the ectoderm remains a very distinctly limited epithelial structure, this is not the case with the entoderm and its derivates, the enterocoel and the hydrocoel. They are very distinctly limited against the mesenchyme, but they show no epithelial structure, and they have no distinctly limited cavities, these being more or less completely filled by yolk-substance, which leaves, at most, only irregular free cavities. It is merely the arrangement of the nuclei which makes it possible to distinguish the archenteron and the enterocoel and hydrocoel derived from it. To work out the whole process of transformation from the gastrula to the young sea-star would require an enormous amount of work — reconstructions from the divers series of sections — and a great number of figures. I have not thought this worth while, as also I could not very well spare the time for such work, so I have had to content myself with giving figures 6—12, Pl. VII, to illustrate these later stages of the embryonal development, from which it appears that in the main features there is a general agreement with what is known from MASTERMAN's report on the development of *Cribrella oculata* (= *Henricia sanguinolenta* (O. Fr. Müller)), the eggs of which latter are large and full of yolk like those of *Fromia ghardaqana*.

In Pl. VII. Fig. 8 is seen the beginning separation of the entero-hydrocoel from the archenteron; the latter still remains in connection with the ectoderm through the gastrula invagination which is, evidently, about to undergo resorption. (The cavity seen at the upper side of this figure is an artefact, due to preservation. Normally the whole space between ectoderm and entoderm is completely filled with mesenchyme, of the usual vesicular structure). This embryo is  $2\frac{1}{4}$  days old. In Pl. VII. Fig. 7, from an embryo  $1\frac{3}{4}$  days old, the division of the archenteron is only beginning. The section is not median, therefore does not show the gastrula invagination; on the other hand the pouch to the left at the upper end of the archenteron may probably represent the incipient formation of the hydropore. Pl. VII. Fig. 9, which is a medial sagittal section of an embryo  $3\frac{3}{4}$  days old, shows the very well developed sucking disk of the Brachiolaria. In Pl. VII. Fig. 10, which is from the same series of sections, but more laterally, the hydropore is seen distinctly; the large cavity from which it proceeds can only be the combined hydro-enterocoel vesicle. That the latter is not yet entirely separated from the entoderm vesicle appears from Pl. VII. Fig. 12, which is a frontal longitudinal section of an embryo 4 days old. Pl. VII. Fig. 11, which represents a transverse section through another embryo 4 days old, shows the hydropore distinctly; in the following sections of the same series the hydropore is seen to connect with the lobed vesicle seen below it in the figure. This accordingly is the hydrocoel; the central vesicle is the entoderm, that to the left in the figure the enterocoel. But, as said above I cannot go into further details of the transformation of the Brachiolaria into the young sea-star.

It should be pointed out that a similar walnut-like folding of the young embryo as shown in Pl. VII. Fig. 3, was found by MASTERMAN to occur also in *Henricia sang-*

*uinolenta* (cf. MASTERTON. "The early development of *Cribrella oculata* (Forbes)." Trans. R. Soc. Edinb. XL. 1902, Pl. I. Figs. 5, 16—17). But it is evidently only an exaggeration of a feature commonly found in embryos of Asteroids, also such as have small eggs and normal, total cleavage, the blastula having the wall irregularly folded, and only assuming the normal regular shape when the embryo leaves the egg-membrane. It seems beyond doubt that it is lack of space within the egg-mem-

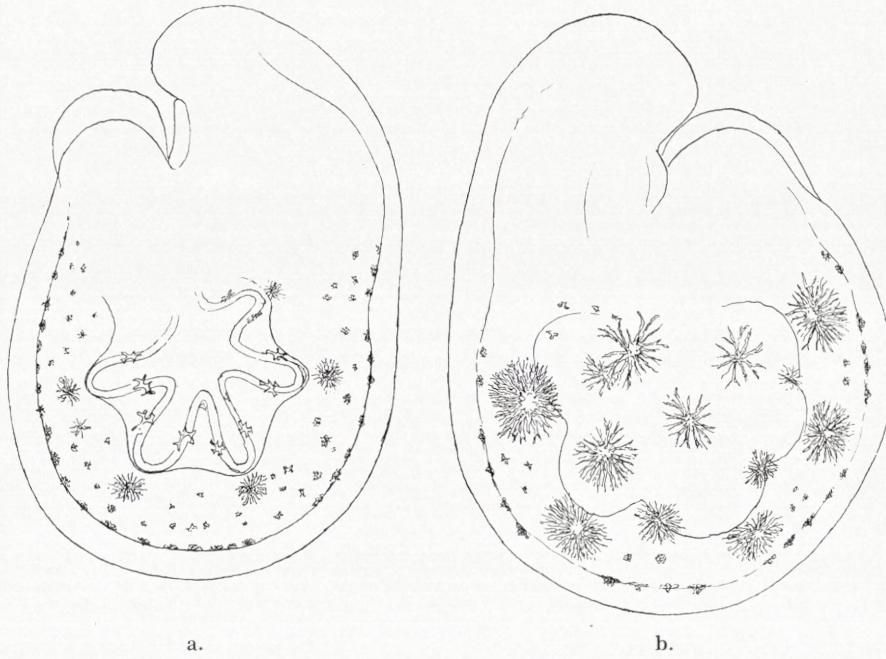


Fig. 18. Embryos of *Fromia ghardagana* Mrtsn. a.  $6\frac{1}{4}$  days old; oral side; showing the first rudiments of the ambulacral skeleton. b. 12 days old; dorsal side; showing the 5 terminal plates, and the primary dorsal plates.  $\times 72$ .

brane which necessitates this folding of the skin, and the embryo, when it has straightened its skin after leaving the egg-membrane, is at once much larger, in contradistinction to other Echinoderms, in which no such folding of the skin of the blastula occurs.

The development of the skeleton may be studied on larvae made transparent in Canada balsam. The first rudiments of skeletal plates are found in larvae about  $3\frac{3}{4}$  days old, having just assumed the Brachiolaria shape (Pl. VI. Fig. 2). A great number of small crystals are seen there, strewn without any apparent order over the posterior end of the body, both on the dorsal and the ventral side. Any direct interpretation of these young plates is impossible, but evidently they all represent plates of the dermal skeleton, especially the small plates occurring in varying numbers in the later stages between the primary skeletal plates (fig. 18).

The first ambulacral plates are seen in fig. 18, a, from a larva  $6\frac{1}{4}$  days old;

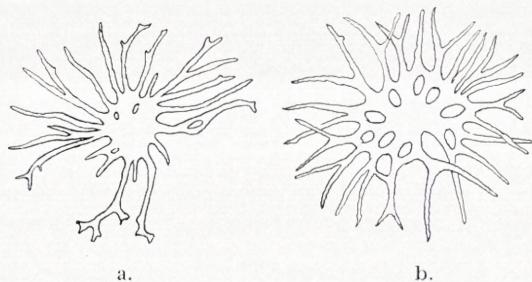


Fig. 19. Radial (a.) and terminal plate (b.) of embryo of *Fromia ghardaqana* Mrtsn. 8 days old.  
× 225.

seen a number of quite small plates, each carrying a spine. It is noteworthy that the first circle of dorsal plates are placed interradially, though very early some irregul-

also the terminal plates and the first plates of the dorsal skeleton are laid down here, but are shown somewhat more developed in fig. 18 b, from a larva 12 days old. They are of a very unusual, highly characteristic structure, irregularly star-shaped (fig. 19), and only gradually do they assume the usual shape of fenestrated plates, as seen in fig. 20, representing the dorsal side of a newly metamorphosed sea-star, 16 days old. Between the main plates are

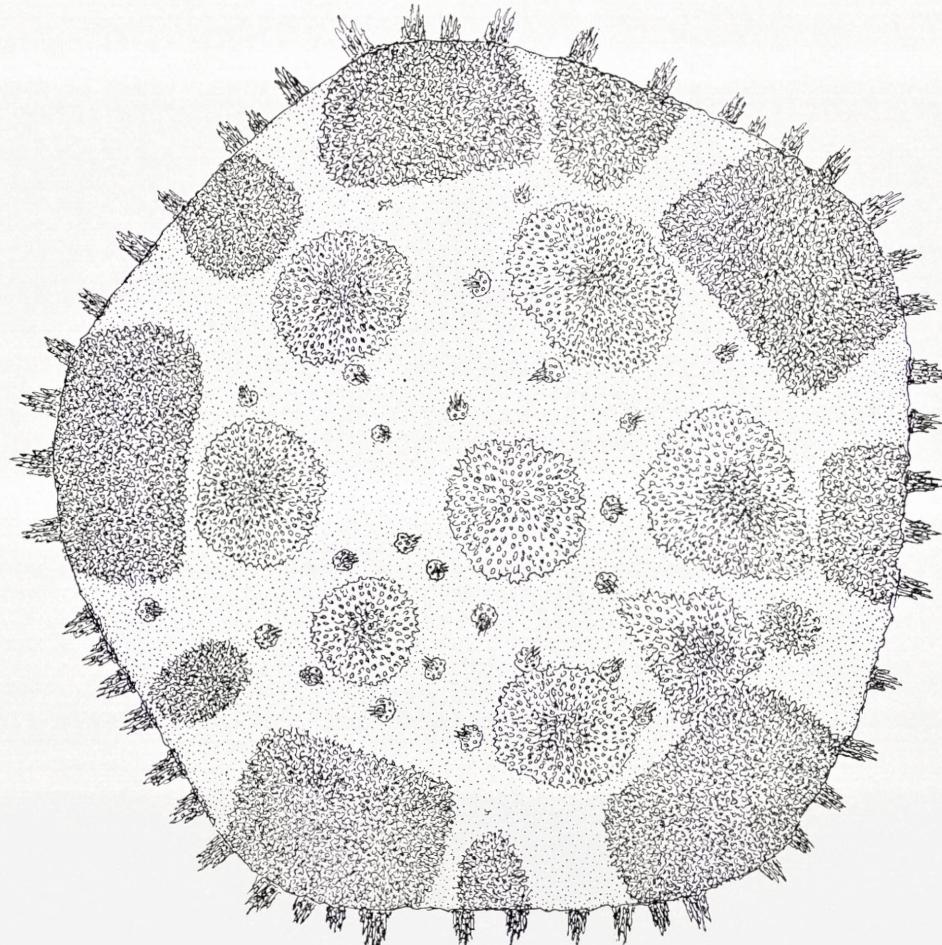


Fig. 20. Young sea-star of *Fromia ghardaqana* Mrtsn. 16 days old. Dorsal side. × 100.

arity appears in their arrangement (figs. 18 b and 20). The most advanced stage obtained, two months old, is represented in fig. 21, in which two pairs of tube-feet have developed. Very noteworthy is the large size of the terminal plates (with their ventral furrow for the terminal tentacle), which join in the interradial midline, no trace of marginal plates having appeared as yet. The ambulacral armature has begun to form, as well as the mouth-spines. Very noteworthy is also the fringe of marginal spines, such not being found in the adult sea-star. The dorsal side is wholly covered by skeletal plates, among which the central plate is the most conspicuous; the other plates are so closely packed that their identification is scarcely possible.

A few words may still be added concerning the hermaphroditism of *Fromia ghardaiana*. On gonads of the live specimens the hermaphrodite character is very easily ascertained directly under the microscope, the red eggs showing very distinctly in the whitish testicular tissue, and especially against the white mass of sperma-

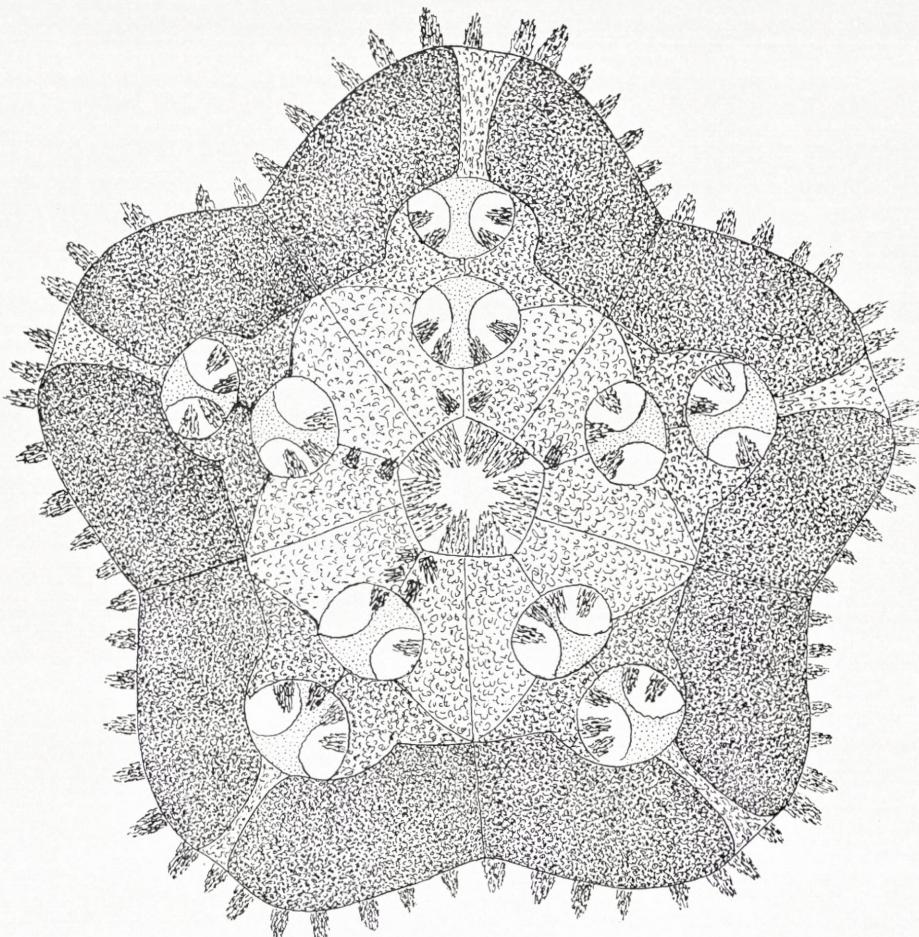


Fig. 21. Young sea-star of *Fromia ghardaiana* Mrtsn. Two months old. Oral side.  $\times 65$ .

tozoa. Fig. 22 shows part of a section of a gonad from a specimen of only 10 mm arm-length (R). The young specimens I have constantly found to be almost pure males, but with a few, scattered eggs in the gonad walls. With age more eggs develop, and large specimens usually are almost pure females, with only rather insignificant traces

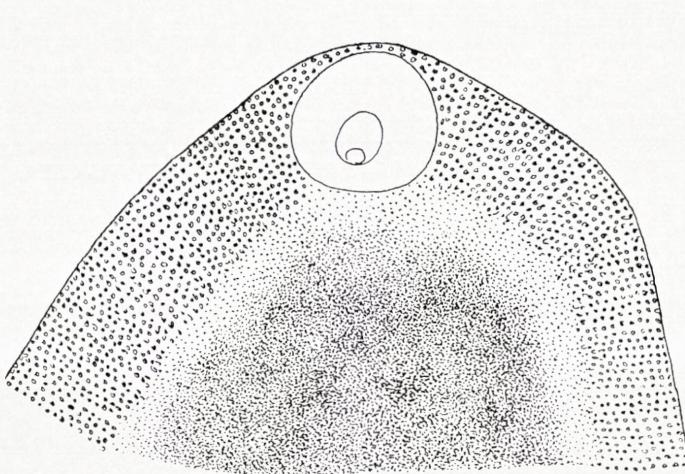


Fig. 22.

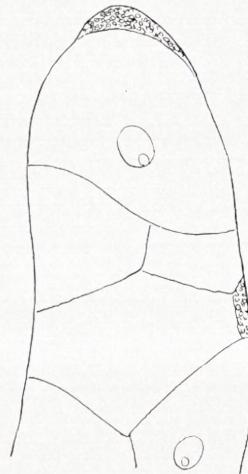


Fig. 23.

Fig. 22. Part of transverse section of gonad of *Fromia ghardaqana* Mrtsn., from a specimen of 10 mm. R. In the testicular mass is seen a single young egg. Fig. 23. Longitudinal section through the end of a gonad branch of an adult female *Fromia ghardaqana*. Indistinct remnants of testicular tissue are seen.

$22 \times 300$ ;  $23 \times 40$ .

of sperma or testicular structure (Fig. 23). Still, also some adult specimens are functional males, but then always with a fair number of eggs in the gonads.

As pointed out in my "Contributions" III, p. 8, the only other Asteroid known to be a normal protandric hermaphrodite is *Asterina gibbosa* (Penn.), so the demonstration of *Fromia ghardaqana* being a protandric hermaphrodite is of considerable interest.

#### 8. *Echinaster purpureus* (Gray).

Pl. VI. Fig. 5.

During my stay at Ghardaqa in 1936 I tried repeatedly, but in vain, to get material for studying the development of this sea-star, by artificial fertilization or through voluntary spawning of specimens kept in the tank. The large, almost black eggs, like other eggs full of yolk, resist artificial fertilization, and no spawning took place, though a great number of specimens were kept alive in the tank for a long time.

This year I again kept a good number of specimens in the tank of the laboratory, and on the morning of July the 11th I had the pleasure of finding that some spawning had taken place during the night. Unfortunately no precaution had been taken to prevent the eggs, which float at the surface like those of *Fromia*, from being carried

away with the water flowing out through the outlet of the tank; the result was that I could secure only 10 eggs in all from this spawning. They were put into the plankton-net in the tank, together with the red *Fromia* eggs, the two species being, of course, very easily distinguished by their colour.

For the following nights all precautions were made to prevent eventual new eggs from being carried away with the water — but no new spawning took place, now or later, although a considerable number of specimens were kept the whole time till my departure in September.

The very scant material obtained was, of course, quite insufficient for a detailed study of the development of this species — the more so as after a couple of days only two embryos were left. But these two were taken great care of, and they developed normally till near metamorphosis, when they were preserved.

It was observed that the cleavage, in spite of the great yolk-content of the eggs, is total and regular; but only the 2- and 4-cell-stages were observed, and no drawings were made, as I was expecting to get new material the following days and therefore would not risk losing the few eggs I had. The young larvæ were very like the *Fromia* larvæ, differing from the latter only in their dark, blackish colour; but in contradistinction to the *Fromia* larvæ they attached themselves to the bottom of the dish by means of their sucking disk. At the age of four days they showed signs of metamorphosis, the young sea-star being indicated.

A characteristic feature of the *Echinaster* larva is the large size of the anterior Brachiolaria-arm, the paired Brachiolaria-arms remaining quite small (Pl. VI. Fig. 5). There is a rather large sucking disk at the base of the large Brachiolaria-arm (not very distinct in the figure, which represents the larva in half side view). — The skeleton of the young sea-star at this stage is represented only by a number of quite small crystals, which cannot be identified with certainty, so I refrain from giving a figure thereof.

The development of *Echinaster purpureus*, as far as known, agrees very closely with that of the Mediterranean *Echinaster sepositus*, as described by NACHTSHEIM (*Über die Entwicklung von Echinaster sepositus* (Gray). Zool. Anzeiger. XLIV. 1914). Here, too, the larva is a reduced (red) Brachiolaria with a very large anterior arm. In the preserved *Ech. purpureus* larva the shape of this lobe is, in its somewhat contracted shape, even rather exactly as shown in NACHTSHEIM's fig. 6, p. 604 (Op. cit.). — I shall not enter on a criticism of NACHTSHEIM's paper, but confine myself to pointing out that what he regards as the mouth of the larva is the sucking disk of the Brachiolaria.

*Ophiuroidea.*

9. *Ophiothrix Savignyi* (Müller & Troschel).

Pl. V. Fig. 1.

On the very first day of my stay at Ghardaqa this summer, July the 1st, I got some specimens of this species, from a large sponge taken by dredging. They proved to be ripe, and on being put into a dish with water taken from off the pier, which was a good deal warmer than that in which they had at first been kept, they immediately spawned. During spawning they moved one or two arms at a time with rapid, snake-like movements (—much as a swimming *Nereis*—), at the same time raising

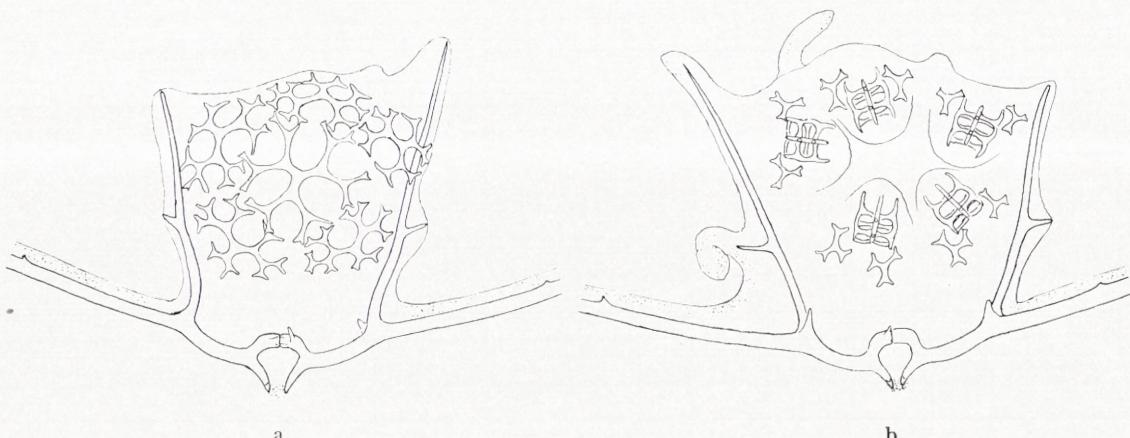


Fig. 24. Skeleton of larva of *Ophiothrix Savignyi* (Müll. & Troschel), in beginning metamorphosis. a. Dorsal side, showing the central and radial plates; b. oral side, showing the terminals and the first pair of lateral plates.  $\times 105$ .

the corresponding part of the disk, shedding the genital products. (I have not observed such spawning movements in any other Ophiuroid).

The eggs are whitish, intransparent, c. 0.1 mm in diameter. The fertilization membrane lies close to the surface of the egg. The cleavage (the 2-cell stage reached one hour after fertilization) is regular, the cleavage-cells with a very distinct, transparent outer layer. The next morning, 14 hours after fertilization, the embryos were dense, transverse-oval gastrulæ, without apical crest, and with the first rudiments of the skeleton already formed. At the age of 22 hours they had the shape of young plutei.

The fully formed larva, two weeks old, is of the typical *Ophiothrix*-shape, distinguishable from the *Ophiothrix triloba* larva ("Contributions" III. Pl. IX. 2–3) only by its colour: 3–4 yellowish gray bands on the posterolateral arms; no black spots on the body. The stomach is a very faint yellowish-gray (Pl. V. Fig. 1).

At the age of three weeks the larvae were in metamorphosis. I have been unable to ascertain definitely whether the hydrocoel grows round above the oesophagus; evidently the hydrocoel-development proceeds at great speed, which may account

for the lack of the intermediate stages. Otherwise, the metamorphosis is as typical of *Ophiothrix*, the long arms remaining unresorbed as floating organs of the young brittle-star, to be thrown off when the metamorphosis is completed.

Figs. 24, a—b show a developmental stage, where the main parts of the skeleton have been laid down, figs. 25, a—b the young brittle-star, with the first arm-spines of the characteristic hook-shape. Very characteristic is the central plate, with its unusually large holes. A conspicuous feature is also the large size of the first ventral plate.

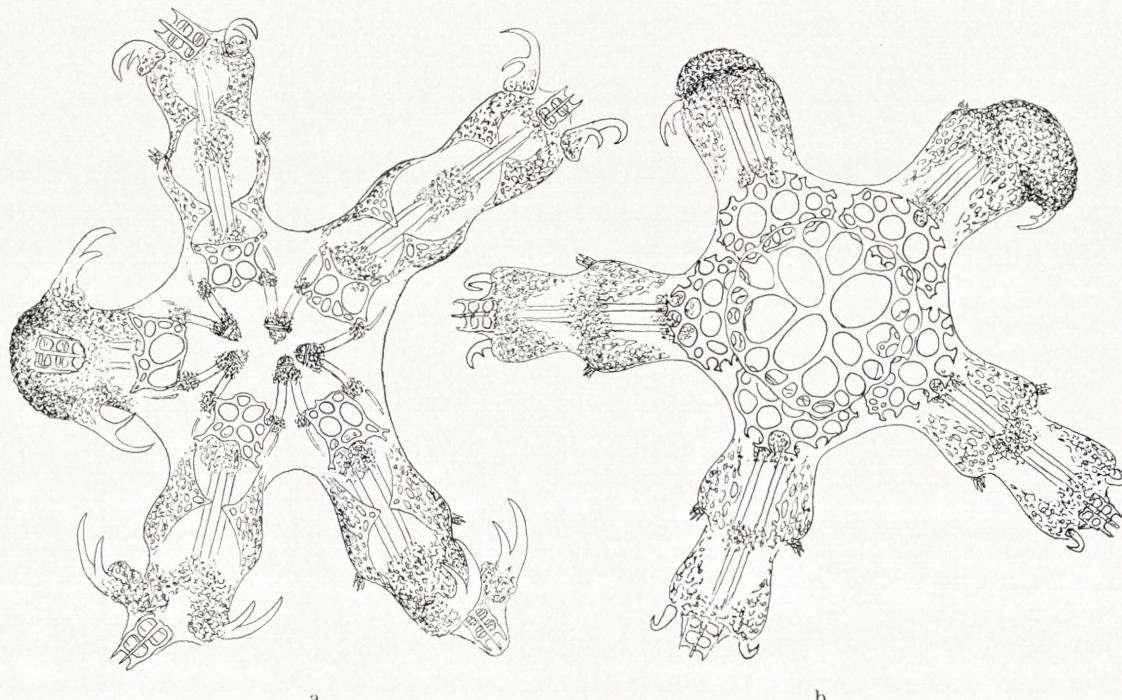


Fig. 25. Newly metamorphosed brittle-star of *Ophiothrix Savignyi* (Müll. & Troschel). a. Oral side, showing the mouth-skeleton, the first ventral plate, and the first two pairs of ambulacral plates (vertebrae); b. dorsal side, showing the remarkably developed central plate and the radial plates.  $\times 105$ .

It may be mentioned that I found fully ripe specimens of this species again in September, so that it must have at least two spawning seasons; but as I did not continually pay attention to the state of maturity of this species, I cannot say anything more definite about its spawning, but the facts available rather tend to indicate a monthly breeding during the summer time.

#### 10. *Ophiolepis cineta* Müller & Troschel.

Pl. VI. Figs. 6—9.

A number of specimens of this species (which is rather common under coral blocks on the reefs and on the shore-flat at Ghardaqa) were put together into a dish

on July 23rd, and were found the next morning to have spawned during the night. The eggs were reddish-brown, intransparent, 0.3 mm in diameter. They were found, as it were, attached to the arm-spines nearly to the tip of the arms.

Nothing of the cleavage process could be observed, partly because of the intransparency of the eggs, partly because the cleavage had taken place in the course of the night. In the morning, when c. 12 hours old, the embryos, still enclosed in the egg-membrane, were blastulae, showing the beginning gastrula formation (Pl. VI. Fig. 7). In the afternoon the embryos were free-swimming elongate, flattened gastrulae,

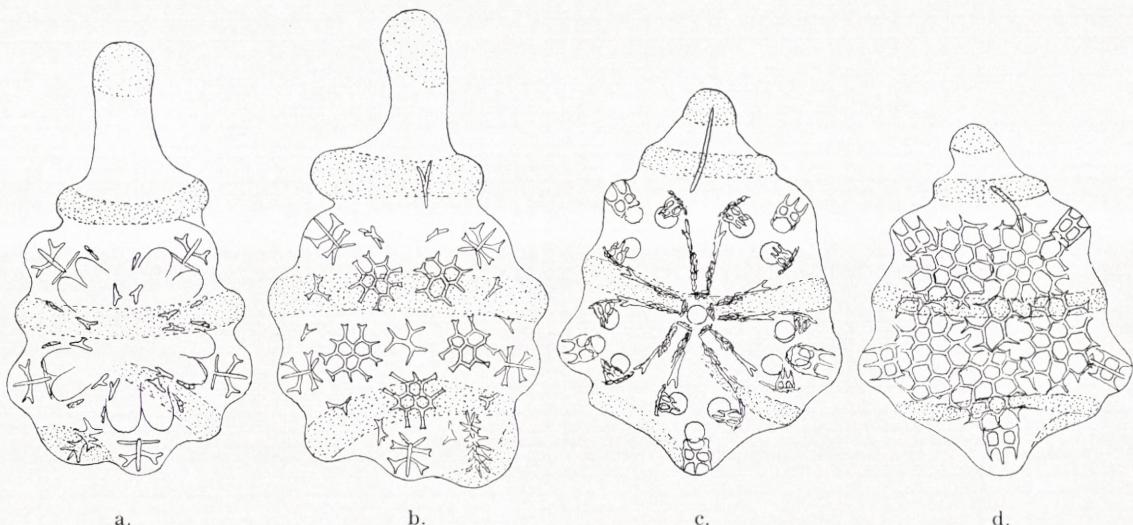


Fig. 26. Two stages in the development of *Ophiolepis cineta* Müll. & Troschel. a. and c. from the oral side, b. and d. from the aboral side. In figs. b.—d. is seen the rudimentary larval skeleton in the anterior end, in figs. a. and b. the complicate skeletal rod in the posterior end.  $\times 135$ .

which collected at the surface, close to the edge of the dish, forming, as it were, a string of beads. In Pl. VI. Fig. 8 is represented a section of the gastrula stage, c. 18 hours, showing no distinct archenteron or blastocoel cavities. Pl. VI. Fig. 9 is a sagittal section of an embryo c.  $1\frac{1}{2}$  days old. The notch on the left side probably represents an incipient larval mouth, which however, does not develop any farther.

About  $2\frac{1}{2}$  days old the embryos were already in beginning metamorphosis, the development being direct, without an Ophiopluteus stage. The shape of the larva (Pl. VI. Fig. 6) is triangular, with a narrow anterior lobe, surrounded at its base with a ciliated band, and with an apical ciliated tuft; the main part of the body is pentagonal, on account of the developing young brittle-star. There is a median ciliated band, nearly complete, and two incomplete bands in the lower part. The colour of the larva is uniformly reddish (in transmitted light; in reflected light it is more redbrown). The edges of the ciliated bands are dark.

A very interesting fact is that there is a rudimentary larval skeleton in

this larva: usually, but not constantly, a slender rod, simple or branched, in the anterior lobe and an unsymmetrically placed, irregular, very complicate, branched rod in the posterior end (figs. 26, a—b). In figs. 26, a—d are represented two stages in the development of the skeleton of the brittle-star; a detailed description seems to me superfluous, the figures giving directly all the information available. Note-worthy is the small size of the central plate, which lags far behind the radials in its development. The details of the ambulacral (oral) skeleton in the more advanced stage are rather difficult to make out, the divers plates mainly standing on edge. The presence of the first arm-spine makes the interpretation of the plate to which it is attached as the first lateral (adambulacral) plate certain.

The young brittle-stars, after the complete resorption of the larval body, were put into a dish with sand on the bottom, in the hope that they would go on growing; but evidently they did not find conditions suitable, and I did not succeed in getting them any farther in their development.

The development of *Ophiolepis cincta* agrees very closely with that of the West Indian *Ophionereis squamulosa* Koehler, as described and figured in my "Studies of the development and larval forms of Echinoderms" (1921), p. 171—177, Pl. XXXI. 1—6. I gave there a detailed discussion of the literature relating to Ophiuroids with direct development, without an Ophiopluteus larva, to which it may suffice to refer.

### *Holothurioidea.*

#### 11. *Synaptula vittata* (Forskål).

Pl. IX. Figs. 1—3.

In my researches of last year (1936) I did not succeed in rearing to metamorphosis the larva of this species, so very common on the littoral reef-flat at Ghardaqa. The larva was figured on Pl. X. 7 and XI. 6 of my "Contributions" III, but I stated (Op. cit. p. 54) my expectation that the larva in its later stages would prove to be a good deal more complicate. I was therefore anxious to try again this summer (1937) to rear this larva through metamorphosis — in which I succeeded. Some specimens put into the tank of the laboratory on July the 10th spawned during the night. The embryos were distributed in three dishes, all dealt with in the same way, being put into fresh sea-water every day. After 12 days the larvae in one of the dishes were near metamorphosis, those of the two other dishes being in poor condition or having died already, as it happened last year. But the one dish with the larvae in good condition was enough to secure success, the larvae herein not only reaching their full shape and size, but also metamorphosing.

The fully formed larva, c. 12 days old, is rather complicitely lobed, and full of wheels all over (Pl. IX. Fig. 1). It is perfectly transparent, without any pigment. When two weeks old, some of the larvae were metamorphosing, having assumed the typical barrel-shape (Pl. IX. Fig. 2), so well known especially from SEMON's beautiful

figures (Die Entwicklung der *Synapta digitata*. Jenaische Zeitschr. XXII. 1888, Taf. VI—VII), with the ciliated band transformed into closed rings. Whereas the larva swims quietly along, it begins, when about to transform into the barrel-shaped "pupa" (or *Doliolaria*), to whirl round, and when it has assumed the barrel-shape it whirls round and round, always to the right, in a quite frantic hurry, standing, generally, upright in the water.

The young, fully metamorphosed *Synaptula* is, as usual, much reduced in size, much smaller than the larva and the pupa. I tried to keep them for further growth, putting them into a dish with a few small stones and algæ from the localities where the adults were common, and succeeded to some extent. The most advanced specimen, 5 weeks old, represented in Pl. IX. Fig. 3, has still only 5 simple tentacles; but both the radial and interradial pieces of the calcareous ring have been laid down. The body wall is full of wheels, the shape of which is given

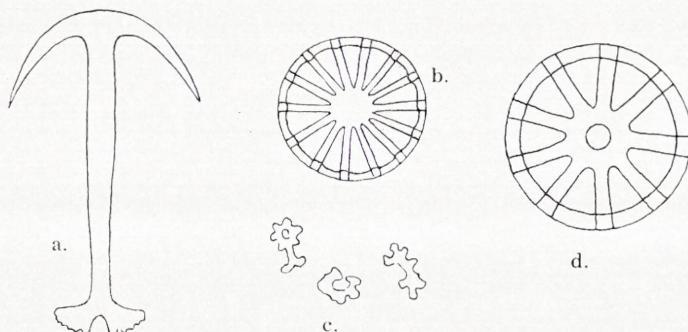


Fig. 27. Anchor (a.), wheel (b.), and rosettes (c.) of the young *Synaptula vittata* (Forskål). Wheel of *Opheodesoma grisea* (Semper) (d.). a.—c.  $\times 540$ ; d.  $\times 850$ .

more enlarged in fig. 27 b; they are very small, only c. 0.005 mm. Anchors have begun to appear, lying transversally; they are simple, without knobs on the vertex; the anchor-plates are still of quite irregular shape. In the tentacles rosettes have begun to appear — and in the posterior end the balls of the larva are still lying undissolved. The young *Synaptula* is able to crawl along on the bottom by means of its tentacles, on which some small papillæ are found; it is also able to attach itself quite firmly to the bottom, so that it requires quite a strong jet from a pipette to remove it.

I regret very much having omitted to look for the statocysts in the live specimens; in the preserved ones I cannot find them.

Some of the larvæ did not metamorphose till 4—5 weeks old.

## 12. *Opheodesoma grisea* (Semper).

Pls. VIII. Figs. 1—18; IX. Fig. 4.

This large, fine, reddish-mottled Synaptid (up to 2—3 metres long), which occurs in good numbers near the station, especially at Abu Sadaf, — together with the still larger, up to 5 metres long, grey *Synapta maculata* (Chamisso & Eysenhardt) — was found (like the latter) to live very well in the tanks of the laboratory; even if quite a large part of the body had been lost, the anterior part would live quite well

(— and, no doubt, under natural conditions, would regenerate the lost part —). Although kept for nearly a month, a good number of specimens together, they did not, however, spawn, so I thought it advisable to try artificial fertilization, even though I hardly expected any success.

When opening some specimens, on August the 28th, I was very much surprised on finding this species to be a hermaphrodite. It was clear that the specimens were in the main either males or females, but in the male gonads always a varying number of eggs were found, and in the female gonads always some sperma. Sections of the gonads fully verified the observations made on the living material (fig. 28). Still more surprising was the fact that within the gonads a small number of embryos in the gastrula-stage were present, which means that self-fertilization may take place. (Also I found that when I kept pieces of gonads of a "female" separately, a good number of the outstreaming eggs would become fertilized and start normal cleavage. On isolating some of the gastrulae from within the gonads I saw them develop into young Auriculariae, and there is no reason to doubt that they would be able to go on developing and metamorphosing. Still, it is clear that this species does not normally propagate by self-fertilization, but by cross-fertilization in the usual way.

The eggs of the opened "females" were found to be, for the greater part, ripe for fertilization, no nucleus being visible, and fertilization, with sperma from a "male" specimen, succeeded completely. The eggs are c. 0.1 mm in diameter, quite clear and transparent. The young cleavage-stages, exceedingly beautiful ('like a diagram' I have said in my notebook), up to the 32-cell stage, were observable after two hours. Four hours old the embryos were in the blastula-stage, eight hours old the gastrula invagination was beginning to form, the embryo still lying within the fertilization membrane; but immediately after the formation of the gastrula invagination the membrane dissolves, and the embryo becomes free-swimming. (Pl. VIII. Figs. 1—10). The gastrula now becomes more and more elongate, and at the age of 15 hours it is very elongate and slender (Pl. VIII. Figs. 11—13), the remarkably long and slender gastrula invagination beginning to curve towards the future ventral side (for the formation of the larval mouth); a number of mesenchyme cells have wandered into the blastocoel cavity from the upper end of the invaginated part. The formation of the enterocoel pouches I have not followed in details; Pl. VIII. Fig. 13 apparently represents a stage in their formation; they seem to be attached to the ectoderm wall,

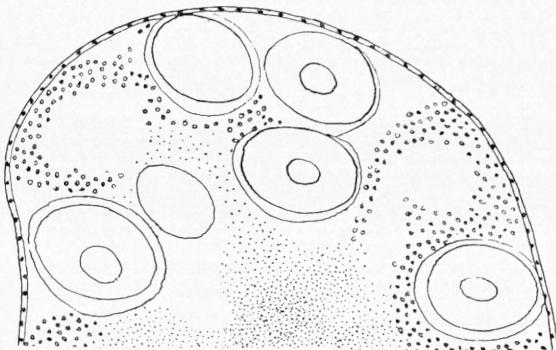


Fig. 28. Part of section of hermaphrodite gonad of *Opheodesoma grisea* (Semper).  $\times 165$ .

much as I found it to be the case in the gastrula of *Temnotrema scillæ* (Mazetti) ("Contributions" III, Pl. X. 1).

At the age of c.  $1\frac{3}{4}$  days the embryos had assumed the shape of young *Auriculariæ*, perfectly transparent, still without indication of wheels (Pl. VIII. Figs. 14—15). Three days old they showed the beginning formation of calcareous balls in the left, sometimes also in the right, posterolateral lobe (Pl. VIII. Figs. 16—17), and in larvae 7 days old the first formation of wheels was observed (Pl. VIII. Fig. 18), sometimes in the left, sometimes in the right posterolateral lobe.

At the age of 11 days (September the 9th) the most advanced larvae (Pl. IX. Fig. 4) were, evidently, near metamorphosis, as indicated by the fact that the left enterocoel had grown so much as to reach the end of the stomach, the right enterocoel also beginning to grow (in the previous stages both enterocoel and hydrocoel vesicles were so small as to be exceedingly difficult to distinguish). The hydrocoel also had grown somewhat, but was still unlobed. There was still only one wheel in each posterolateral lobe, but some small cell-groups here, and also in the anterior end of the larva, seemed to indicate that a few more wheels would be present in the metamorphosing larva.

The larva at this age (Pl. IX. Fig. 4) — which is perfectly clear, without any trace of colour — must be very nearly fully formed, which means that the *Opheodesoma* larva is scarcely more complicate than the *Synaptula* larva, both of them being very far from reaching the exceedingly complicate shape and large size of the famous *Auricularia nudibranchiata*. The rather more complicate Synaptid larva mentioned on p. 54 of "Contributions" III can, according to the observations here recorded, hardly have been an *Opheodesoma* larva; it may have been the *Synapta maculata* larva, which is still unknown.

When I left Ghardaqa, September the 12th, only a very few larvae of *Opheodesoma* were still alive; as there was evidently no hope of keeping them till metamorphosis, they were then preserved.

It may be added that the *Opheodesoma serpentina* mentioned on p. 54 of "Contributions" III should be *Opheodesoma grisea*, which is the common *Opheodesoma* species found at Ghardaqa. *O. serpentina* is much more rare, usually found only in single specimens on the outer reefs, and I never had specimens enough of this species for keeping them in the tanks for eventual spawning.

### 13. *Holothuria impatiens* (Forskål).

Pl. X. Figs. 1—6.

During my stay at Ghardaqa last summer (1936) I had kept a good number of this species, so common under stones on the reef-flat close to the station, in a big dish with stones on the bottom for nearly two months, May—June, in the hope that they would spawn. Although apparently ripe they did not, however, spawn. On my arrival at the station this summer, July 1st, 1937, I at once again put a number of

specimens into a big dish with stones, and now I had the pleasure of finding them to have spawned during the night of the 2nd—3rd July, the dish containing on the morning of the third numerous, not yet swimming, blastulæ. Towards the evening, thus about 18 hours old, they were fine gastrulæ. Two days old the embryos had assumed Auricularia-shape, with a rather distinct yellowish pigment, but still without any skeletal elements. At the age of 5 days the larvæ had formed a calcareous ball in the posterior end of the body, often lying asymmetrically; more rarely there were two balls (Pl. X. Figs. 1—2). Usually the posterior end of the body is simply drawn out, the ball not lying in a slender prominence, as is often the case in Auriculariæ, e. g. in that of *Holothuria scabra* ("Contributions" III. Pl. XII. 1); in the more advanced larva there is, however, a fairly distinct prominence from the posterior end, in which the ball is situated. The ball is covered with low, spiny prominences or warts (fig. 29, b).

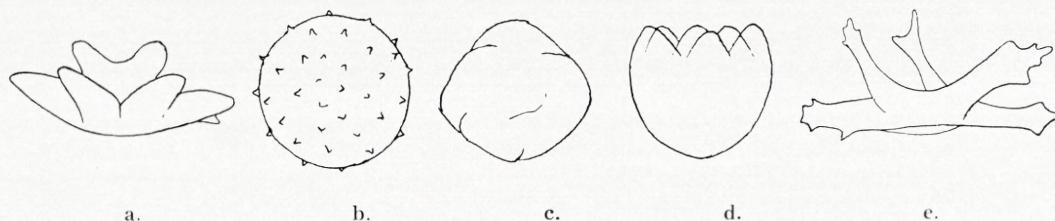


Fig. 29. Spicules from the posterior end of divers Auriculariæ, a. *Holothuria papillifera* Heding; b. *H. impatiens* (Forskål); c. *H. pardalis* Selenka; d. *H. difficilis* Semper; e. *H. (Microthelae) nobilis* (Selenka).  
a. and e.  $\times 700$ ; b.—d.  $\times 450$ .

At the age of about two weeks some of the larvæ were in beginning metamorphosis, the hydrocoel having formed lobes, the enterocoel being prolonged backwards, and the elastic balls having appeared (Pl. X. Fig. 3). It is a very interesting fact that the madreporite-skeleton has formed already at this stage. The larva is of the common type, not distinguishable by its shape from the other *Holothuria* larvæ known till now. It has a number of rather regularly distributed yellow pigment spots in the ciliated band, none in the body, except along the posterior end.

The various stages of metamorphosis were easily observable (Pl. X. Figs. 4—5), showing the breaking up of the ciliated band of the larva, the pieces uniting so as to form the rings of the pupa or "Doliolaria", as was described and figured in details by SEMON for *Synapta* (i. e. *Labidoplax*) *digitata* (Op. cit. 1888, Taf. I—II). I was able to ascertain definitely on these pupæ that the elastic balls are not always present in their full numbers, 5 pairs; not only those in the upper corners are often wanting, but some of the others may be present only on one side (Pl. X. Figs. 4—5).

Whereas a number of the larvæ metamorphosed when three weeks old, many of them continued life as fully formed, normal larvæ, not metamorphosing. Having already got a number of them metamorphosed, I did not take special care of these larvæ, and they were not transferred to fresh sea-water for a quite a long while. After three weeks more, still finding about 30 of them apparently quite normal and healthy

looking, I thought that perhaps lack of sufficient food might be the reason for their not having metamorphosed, and so I started again transferring them to fresh seawater every day to see, whether they would now perhaps metamorphose — and so they did. After 6—7 days most of them had metamorphosed. This rather casual experiment throws important light on the ability of the larvae to survive for a considerable time beyond their normal life-time and thus postpone metamorphosis when under unfavorable conditions (cf. above, pp. 9—10).

The young, newly metamorphosed Holothurians were put into a separate dish with small stones with algae and a little sand on the bottom, thus under about normal conditions, in the hope that they would develop a little farther; and so they did, at least a few of them. At the age of 5—6 weeks some of them had the first tube-foot

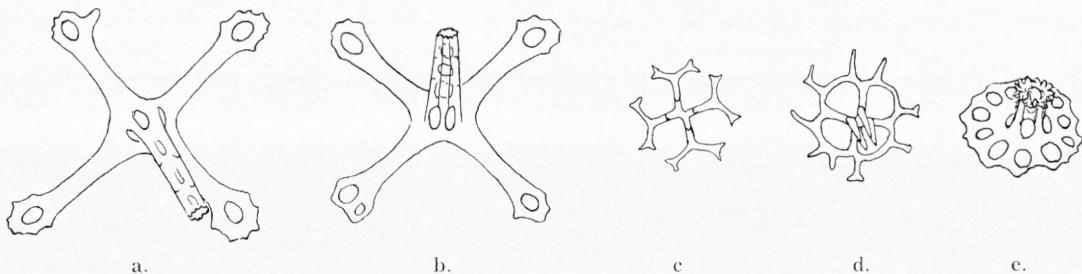


Fig. 30. Calcareous deposits from the skin of the young *Holothuria impatiens* (Forskal). a.—b. Slender form of tables; c.—d. development stages of the second type of tables (e.), from the posterior end of the body.  $\times 300$ .

developed, and the tentacles were distinctly knob-shaped (Pl. X, Fig. 6). Calcareous bodies, young tables, had begun to appear in the body wall and at the base of the tentacles, forming small prominences, like small feet; the larval calcareous ball from the posterior end of the larva remains undissolved in the posterior end of the body. The calcareous ring has been formed, but apparently as yet only the radials (their shape not to be made out distinctly). The elastic balls have disappeared.

When about to leave the station I searched the dish for eventually surviving specimens and succeeded in finding two, which were now 10 weeks old. They had grown quite considerably, the best one being about 2 mm long. There are still only 5 tentacles, but three tube-feet, close together, on the ventral side. The body wall is studded with spicules, viz. tables with a long, slender spire rising from a base with four long, slender arms, each with a small terminal widening with a single hole (abnormally sometimes two holes). In the posterior end of the body, where the larval ball is still distinct, are found a few tables of quite a different shape (fig. 30 e), in the main like those of the adult. No buttons formed as yet. The calcareous ring and the internal anatomy not to be observed through the dense coat of spicules.

The fact that the tables of the young *Holothuria impatiens* are so very different from those of the adult is, of course, of phylogenetic importance. The conclusion seems unavoidable that the ancestor of *H. impatiens* had tables of this primitive

type — but I think it preferable to put off a detailed discussion of this problem till the postembryonal development of more species of *Holothuria* (sensu lat.) has been studied.

#### 14. *Holothuria pardalis* Selenka.

Pl. IX. Figs. 5—6.

A number of specimens of this beautiful species, which occurs — rather sparingly — on the reefs at Ghardaqa, particularly Abu Sadaf, were kept in the tanks of the station for quite a long time for eventual spawning. But no spawning took place, and the only hope of studying its development was then to try artificial fertilization, which was done on August the 26th — rather late in the afternoon. Although a good number of the eggs were ready for fertilization, showing no nucleus, it seemed at first that no fertilization had taken place. However, after about 20 hours there were a fair number of free-swimming gastrulæ, so that a small percentage of the eggs had actually been fertilized, the reason why it could not be ascertained at once being that the fertilization membrane lies very close to the egg-surface; and on account of the late hour when the fertilization was undertaken the cleavage did not begin till it was dark. But here, anyhow, was a case, where artificial fertilization of a Holothurian had succeeded.

At the age of two days the embryos were beginning to assume the Auricularia-shape, and on the third day a small ball had appeared in the posterior end of the body (Pl. IX. Fig. 5). At the age of two weeks the larva had reached its full shape, showing the signs of beginning metamorphosis, viz. the elongation of the enterocoel and hydrocoel vesicles, and the formation of the elastic balls. No lobes were visible as yet on the hydrocoel, but the madreporite spicule had already begun to form. The shape of the larva is quite as usual, as is also the colour (Pl. IX. Fig. 6), the only character by which this larva can be distinguished being the calcareous ball in the posterior end of the body, which is spherical, or somewhat angular, quite smooth, only with a couple of more or less irregular furrows (fig. 29, c).

As the larva only reached its full shape at the time when I had to leave the station, there was no possibility of having it reared through metamorphosis, the more so as only very few of the larvae were then still in good condition.

#### 15. *Holothuria papillifera* Heding (n. sp.)<sup>1</sup>.

Pl. XI. Figs. 1—3.

Of this new species, so highly characteristic by its numerous long, soft, backward directed papillæ, only a few specimens were found on Abu Sadaf and Abu

<sup>1</sup> According to information from Mr. S. G. HEDING, who has kindly undertaken to identify my Ghardaqa-Holothurians, this new species recalls by its calcareous deposits *H. vagabunda* Selenka, but differs strikingly from that species by its peculiar long, soft dorsal papillæ, and by lacking the Cuvierian organs. The colour is a uniform grayish-brown. The tables are c. 45  $\mu$ , with one cross-bar and c. 8 spines in the crown, disk usually well developed, with 10 large holes. Buttons very regular, 50  $\mu$  long, with 6 angular holes. In the longitudinal muscles 30—40  $\mu$  large oblong rings.

Fanadir. On the 19th of August two specimens, which I had in the tank, spawned — but both were males. On the 21st I got two more specimens, which spawned when put into the tank, and this time, fortunately, one of them was a female.

The eggs are 0.1 mm in diameter, of a very faint reddish colour. The fertilization membrane lies quite close to the egg-surface. About 12 hours old the embryos were in the blastula stage, but still lying within the membrane; also the gastrula stage begins within the membrane. At the age of about 22 hours the gastrulae were free-swimming. Four days old the young *Auriculariae*, which are unusually broad at the anterior end (Pl. XI. Fig. 1), have formed the spicule in the posterior end. At the age of two weeks the larvae showed the first sign of the formation of the elastic balls, and at the time when I had to leave the station, the now nearly three weeks old larvae were in beginning metamorphosis, the elastic balls having formed, and the enterocoel and hydrocoel vesicles being elongated, though lobes had not yet begun to appear on the hydrocoel.

The fully formed larva (Pl. XI. Fig. 3) is scarcely to be distinguished with certainty from the other *Holothuria* larvae by its shape alone. Also its colour is as usual. But the larval spicule is highly characteristic (fig. 29 a; p. 53), a rather thick-lobed star, and distinguishes it at once from the other larvae thus far known.

These larvae were rather unusual in swimming so close to the surface that many of them were caught by the surface-film and thus killed. This was probably the main reason, why the few larvae still alive when I left the station, disappeared without metamorphosing.

#### 16. *Holothuria (Microthele) difficilis* Semper.

Pl. XI. Figs. 4—5.

Most of the specimens of this species, which is rather common on the reefs at Ghardaqa, were small and showed more or less evident signs of regeneration after autotomy. But in the beginning of August the sailors brought home a number of specimens, which were evidently adult (some 10 centimetres long, when fully extended). They were put into a separate dish under a faint current from the tap, and on the 10th of August I had the great pleasure of finding that they had spawned during the night. The embryos were free-swimming gastrulae in the morning, so I have no observations on the earliest stages. Judging from the size of the gastrulae the eggs must be of the usual size, c. 0.1 mm in diameter. Next day the embryos were young *Auriculariae*, and two days old they had formed the calcareous spicule in the posterior end of the body.

At the age of 10 days the larvae showed the first signs of metamorphosis, viz. the presence of elastic balls and the elongation of the enterocoel and hydrocoel vesicles. Two weeks old several of the larvae had metamorphosed. After another two weeks the young Holothurians had developed the first tubefoot — while several of the larvae still remained unmetamorphosed, but evidently normal. No doubt it would have been possible to induce these belated larvae to metamorphose, as was

the case with the *Holothuria impatiens* larvæ; but there was no time to try this experiment.

The fully formed larva (Pl. XI. Fig. 5) is of the usual shape, not to be distinguished from the other larvæ except by its larval spicule, which shows a number of tight lobes (fig. 29, d; see p. 53). The madreporite spicule is beginning to appear in the fully formed larva.

In the most advanced of the young Holothurians tables were not yet fully formed, but still so far in their development as to show that they are not going to assume the same characteristic shape as that of the tables of the young *H. impatiens*.

As this species is referred to the subgenus (or genus) *Microthele* Brandt, I expected that it would differ to a fair extent from the larvæ of the *Holothuria* s. str. This, however, proved not to be the case.

### 17. *Holothuria (Microthele) nobilis* (Selenka).

Pl. XI. Fig. 6.

This large and very fine Holothurian is not rare on Abu Sadaf, where it is found lying on the sand, having covered itself with sand and algæ so that it is not very easily distinguished. A number of them were kept in the tank, where they spawned on July the 25th. The result of this spawning was, however, very poor, only few of the embryos reaching the gastrula-stage, and none of them beyond that stage.

Some other specimens were soon put into the tank, where they appeared to live quite well, though without food; they would usually come up to the edge of the water and stretch the fore-end out under the surface of the water, with the mouth turned upwards and the tentacles widely extended, affording quite a fine show. On the 15th of August, after they had been kept in the tank for more than two weeks, I found that they had spawned during the night, a great number of swimming gastrulæ being found in the tank. This time the embryos appeared normal and healthy. One day old they were beginning to assume the Auricularia shape, three days old they were young, fine Auriculariæ, but still without calcareous spicules. Not till the fourth day did the spicules appear — and proved to differ very conspicuously from those of *H. (Microthele) difficilis*, there being not a single spicule in the middle of the posterior end of the body, but one in each posterolateral corner (Pl. XI. Fig. 6). The spicules have the shape of irregular stars (fig. 29, e; see p. 53). The larva is a little broader than usual, but otherwise not peculiar.

In the course of the next few days the larvæ rapidly decreased in numbers and soon disappeared altogether, without having developed any further. They were on the whole very weak swimmers and evidently unusually delicate, so it will probably be a very difficult task to rear them beyond the first larval stage.

The fact that the larva of *H. nobilis* differs so very conspicuously from the larva of *H. difficilis* in the important character of the larval spicules, seems to indicate that

it is not justifiable to refer both these species to the same (sub)genus *Microthele*, a suggestion supported also by the fact that the two species differ so very considerably in their size and general appearance.

### *Crinoidea.*

#### 18. **Heterometra Savignyi** (Joh. Müller).

Pl. XII. Figs. 1—12.

During my stay at Ghardaqa in April—June last summer (1936) this very fine, large Comatulid, which is particularly common on grass bottom, at depths of 1—2 fathoms, never showed the slightest sign of ripeness. This summer (1937) I again found the same to be the case during July. But finally in the last week of August, at full moon, I found it to contain ripe sexual products. A good number of specimens were put together into a large dish, under a fairly strong jet of water from the tap, and on the 23rd I had the pleasure of seeing them spawning. The males first emitted the sperm, so that the water became quite milky, and immediately after the females spawned, the eggs, which were at once fertilized, sinking to the bottom. The following four days renewed spawning took place, always at about 3 o'clock in the afternoon. Later on no spawning took place, although I had a number of fresh specimens put into the dish. It would have been of considerable interest to see, whether they would spawn again at the next full moon, in September, but this could not be done, because I had to leave the station before then. But, at least, it is certain that this Crinoid is not ripe till August.

The eggs are small, 0.15 mm in diameter, rather intransparent. The egg-membrane is spiny, as usual. The cleavage is perfectly regular (Pl. XII. Figs. 1—2); the gastrula invagination is distinct already about 6 hours after fertilization, while the embryo is still lying within the egg-membrane. At the age of c. 15 hours they are leaving the egg-membrane. It appears that the embryos have not so much difficulty in leaving the egg-membrane, as I found it to be the case in the other Crinoids, the development of which I have studied formerly.

Already at the age of  $1\frac{3}{4}$  days many of the larvae were attaching themselves, at the uppermost edge of the water in the light side of the dish, they showing a very pronounced positive phototropism. Here they formed a dense line, like a string of beads. The next morning, thus about  $2\frac{3}{4}$  days old, they were young Pentacrinoids. Some few specimens had attached themselves to the underside of the surface-film, hanging head downwards; a few other specimens had attached themselves to the bottom of the dish, or the pieces of shells that I had put on the bottom of the dish.

This habit of the larvae of attaching themselves mainly at the upper edge of the water was very advantageous for the further rearing of the Pentacrinoids. I could then place the dishes with the Pentacrinoids *in situ* directly in the tank under a faint jet of water from the tap; they were thus under constant renewal of the water, with the normal source of food, and not in danger of being killed by the unavoidable residue

from the tap-water. Even in their position high up on the sides of the dish such residue would attach itself to their stalks, which could, however, easily be removed by a gentle jet of water from a pipette. The Pentacrinoids thus lived very well, and after my departure Dr. CROSSLAND very kindly undertook the care of them.

My hope that the Pentacrinoids would under these fairly natural conditions grow normally was, however, not fully realised. They did grow somewhat, but rather slowly, probably much more slowly than they would have grown under normal conditions. The most advanced stage reached (specimens sent me by Dr. CROSSLAND by the end of September and thus one month old) was the formation of the radial plates (Pl. XII. Fig. 12); but there is still here no beginning of the formation of free arms.

It is a rather curious fact that the Pentacrinoids attached to the sides of the dish were not nearly as long-stalked as those which had attached themselves to the bottom of the dish. The number of joints in the stalk is a little larger (24) in the more long-stalked specimens than in the more short-stalked ones (c. 20), but the joints themselves are also slightly longer in the former (Pl. XII. Figs. 9—10). This may perhaps indicate that the normal attachment of the larvæ is on the bottom, so that they must stand in an upright position.

Whereas, as said above, many of the larvæ attached themselves already about two days old, a great number continued swimming for a longer period, a few of them attaching themselves by and by. These older larvæ had evidently lost their phototropism; they were no longer collecting at the upper edge in the light side, but swimming freely in the water, mainly near the bottom. Even after two weeks I found numerous larvæ, now swimming close to or lying on the bottom, only quite few of them having just attached themselves and formed Pentacrinoids. No doubt most of these larvæ would have perished without metamorphosing. But it is clear that this Crinoid larva, like the other three Comatulids (with free swimming larvæ), the development of which I have studied till now, has the property of putting off the metamorphosis for quite a while and continuing the free-swimming life, if it does not find conditions for attaching itself suitable, a fact of importance as a means of dispersal (cf. "Contributions" III. p. 63).

In regard to the skeleton the important fact is to be noticed that there are no Infrabasalia. The shape of the oral plates recalls that of the Antedonids, they being somewhat excavated in the anterior part, with outturned edges (Pl. XII. Figs. 11—12).

The cleavage is total and perfectly regular, and the further embryonal development is exactly as in *Tropiometra carinata*, as I have described it in my "Studies on the development of Crinoids" (1920), pp. 6—13, Pls. I—IV; I do not see any reason to go into details here, but may confine myself to giving a few figures, Pl. XII. 1—5, from which the perfect agreement with the development of *Tropiometra carinata* appears clearly.



**Plate I.**

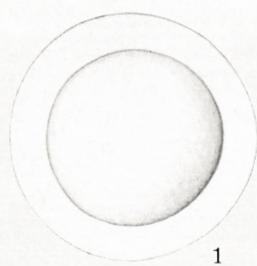
All figures of *Prionocidaris baculosa* (Lamarck).

Fig. 1. Egg with fertilization membrane.

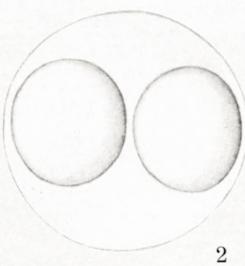
- 2—3. First cleavage-stages, 2- and 4-cells stage.
- 4. 16-cells stage.
- 5. Blastula, typical form.
- 6. Abnormal blastula, "half-twin".
- 7—8. One egged twin and triplet; blastula stages.
- 9. Young gastrula, 19 hours old.
- 10. Gastrula, 26 hours old, showing incipient formation of the enterocoel pouches and the first rudiments of the skeleton.
- 11. Young Echinopluteus,  $2\frac{1}{4}$  days old.
- 12. Nearly fully formed Echinopluteus, 10 days old.

Figs. 1—11  $\times$  150; fig. 12  $\times$  112.

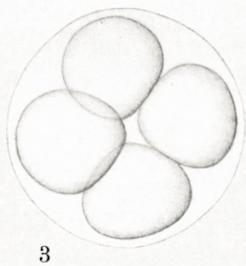
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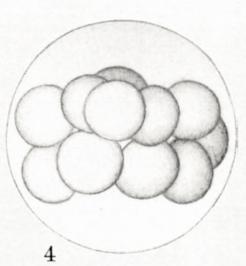
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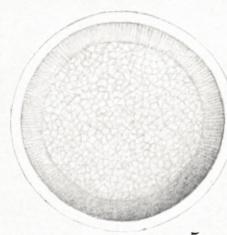
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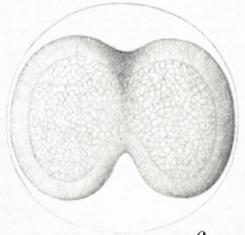
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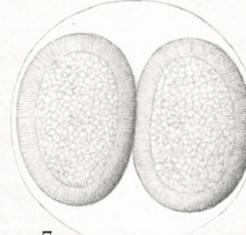
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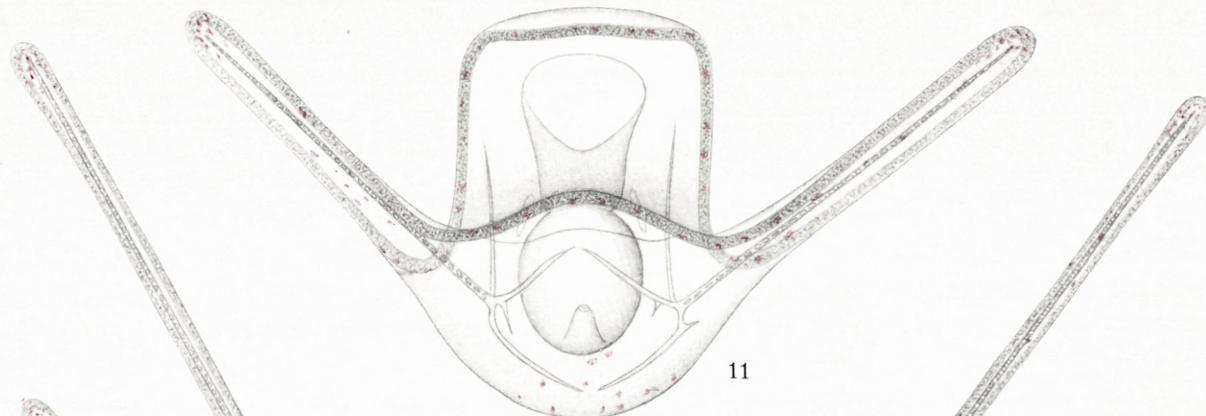
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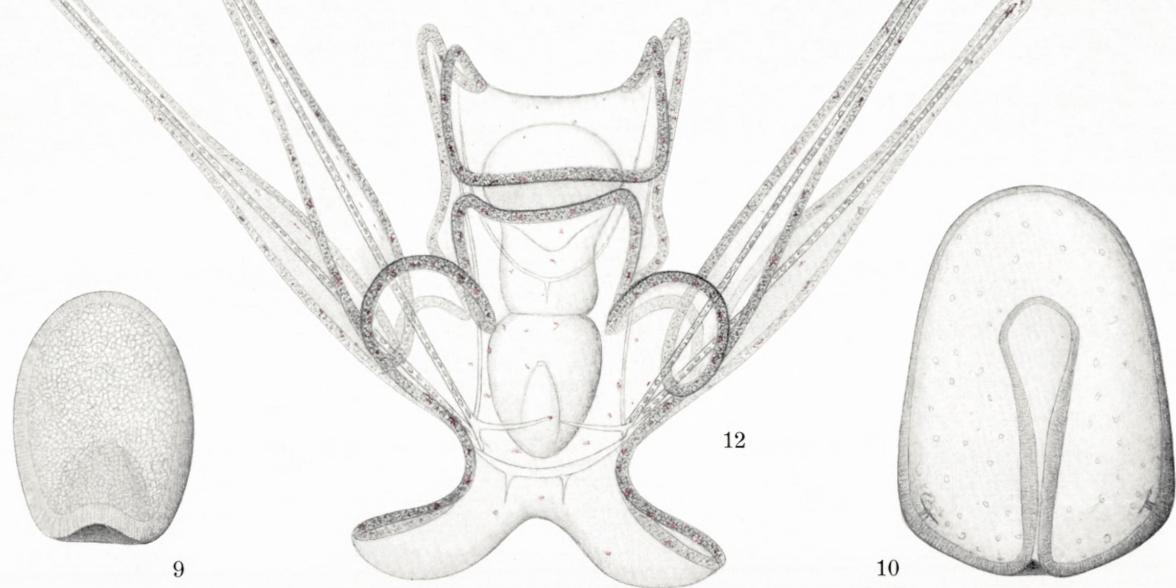
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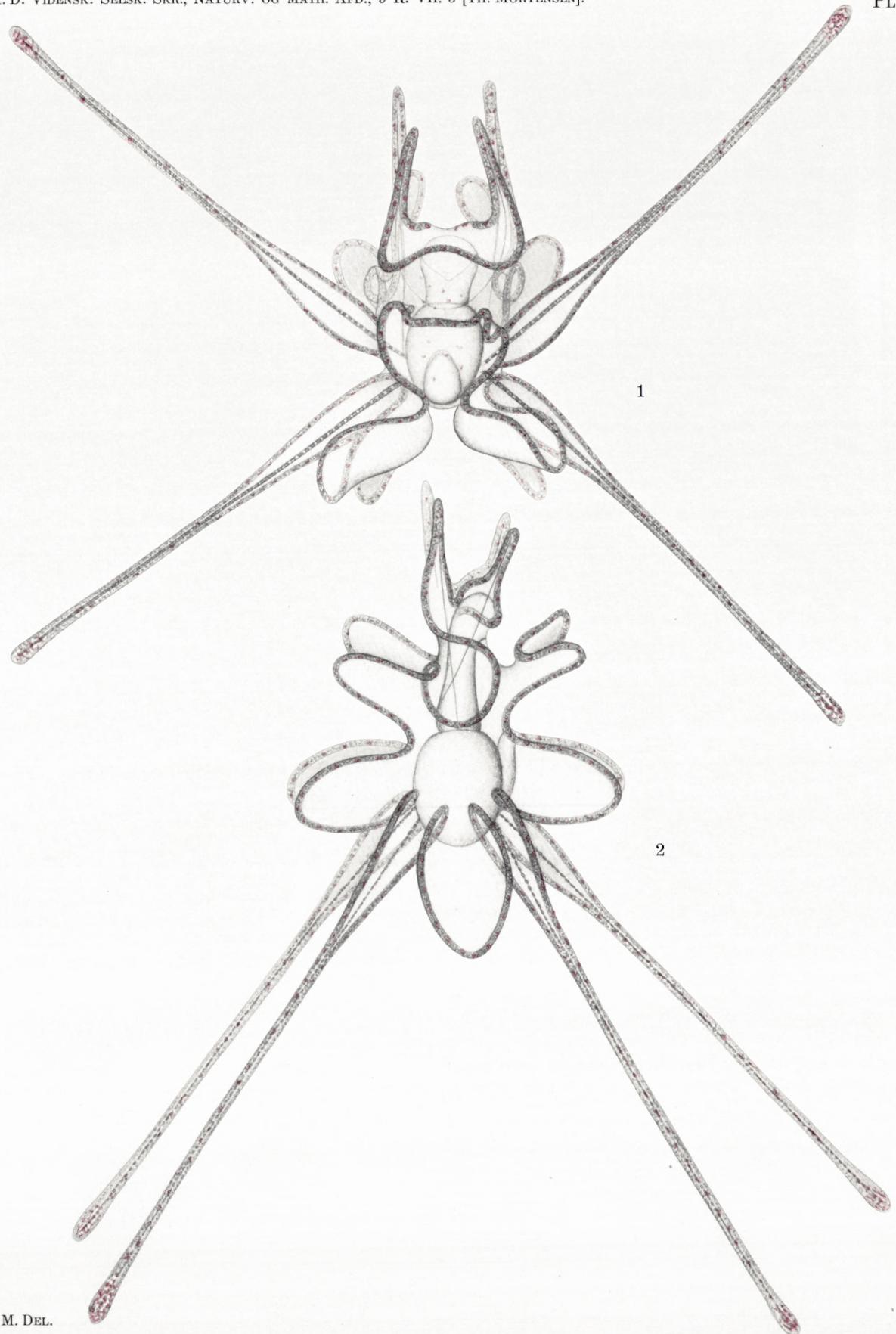


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## **Plate II.**

*Prionocidaris baculosa* (Lamarck).

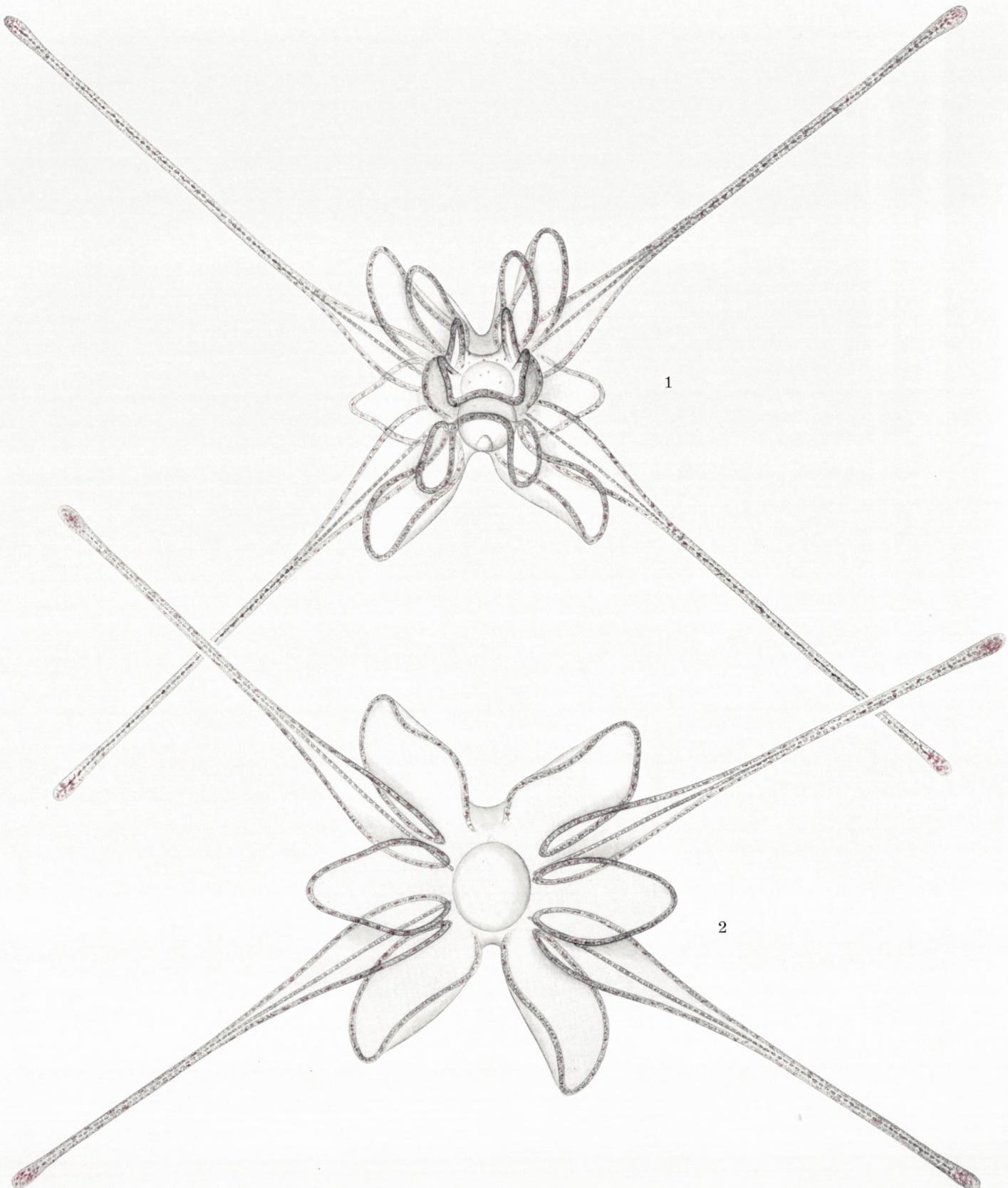
- Fig. 1. Fully formed Echinopluteus, from the oral side.  $\times 60$ .  
- 2. Fully formed Echinopluteus in side view, with the postoral and posterodorsal arms thrown backwards.  $\times 60$ .
-



## Plate III.

*Prionocidaris baculosa* (Lamarck).

- Fig. 1. Fully formed Echinopluteus, seen from above.  $\times 60$ .
- 2. Fully formed Echinopluteus, seen from below. The four long arms drawn a little too short (because they would too much exceed the frame of the plate), they should be as long as in fig. 1.  $\times 60$ .
-



## Plate IV.

- Fig. 1. Fully formed Echinopluteus of *Laganum depressum* L. Agassiz, 15 days old. Oral side.  $\times 115$ .
- 2. Fully formed Echinopluteus of *Echinodiscus auritus* Leske. Oral side.  $\times 115$ .
  - 3—4. Larva of *Lineckia multifora* (Lamarck) in the Brachiolaria stage. 24 days old. 3. Oral side, 4. side view.  $\times 65$ .

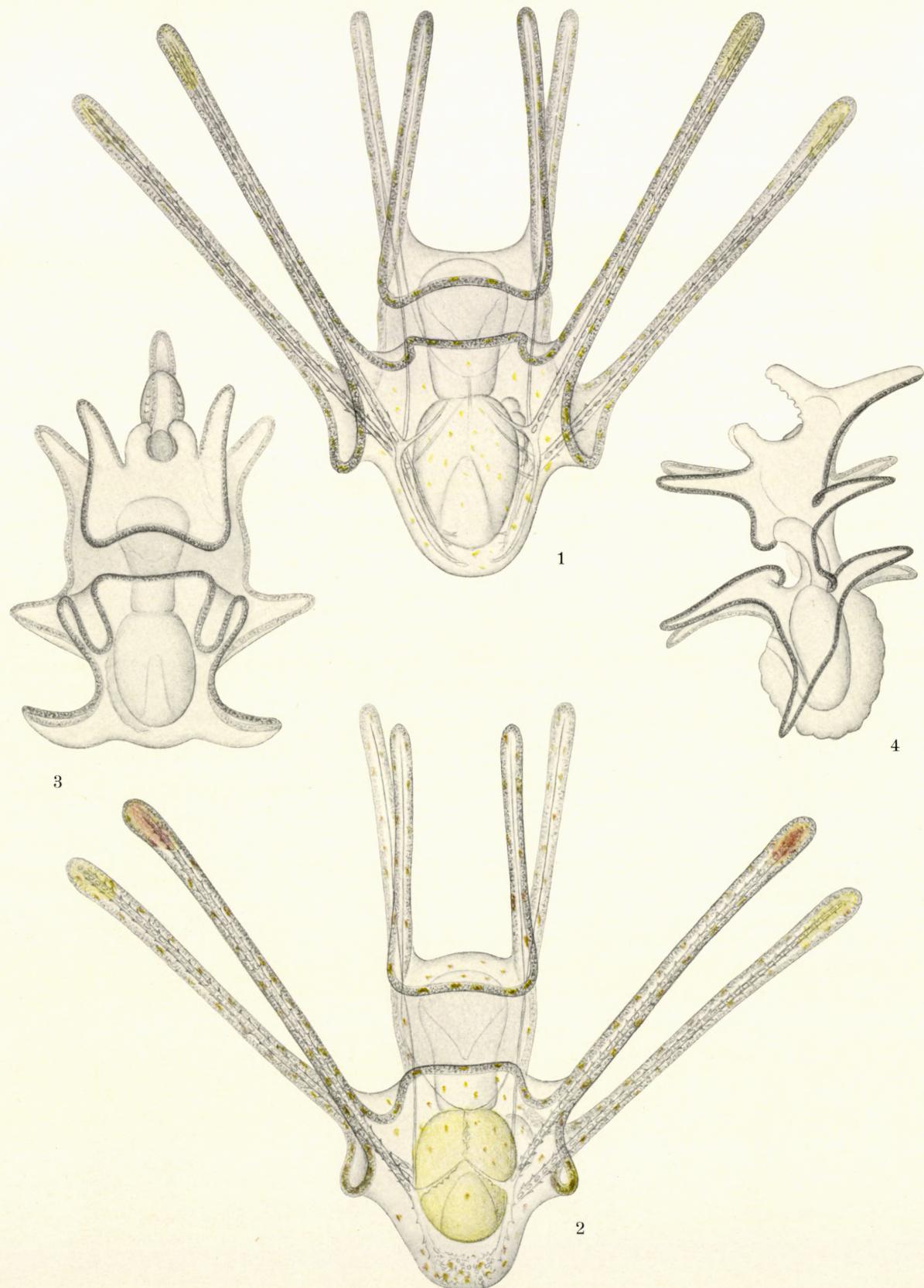


Plate V.

- Fig. 1. Ophiopluteus of *Ophiothrix Savignyi* (Müll. & Troschel). 2 weeks old.  $\times 115$ .
- 2. Young Bipinnaria of *Luidia Savignyi* (Audouin). Oral side. 5 days old.  $\times 150$ .
  - 3—4. Fully formed Bipinnaria of *Luidia Savignyi* (Audouin). Beginning metamorphosis. Oral side (3) and side view (4). 12 days old.  $\times 60$ .
  - 5. Metamorphosis stage of *Luidia Savignyi*. The larval body nearly resorbed.  $\times 80$ .
  - 6. Young Bipinnaria of *Pentaceraster mammillatus* (Audouin). 12 days old. Oral side.  $\times 60$ .
  - 7. Fully formed Bipinnaria of *Pentaceraster mammillatus* (Audouin). 3 weeks old. Oral side.  $\times 50$ .

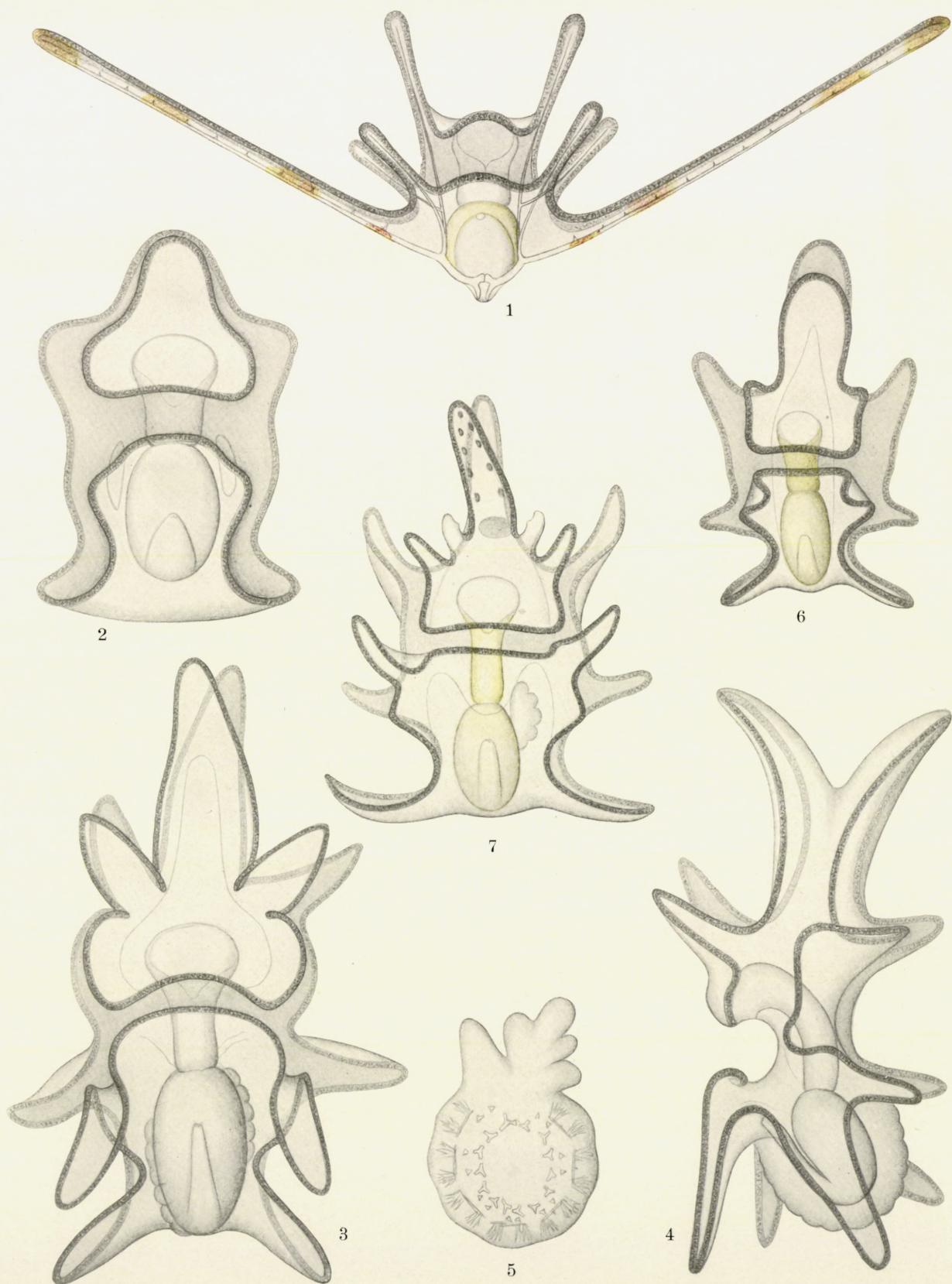
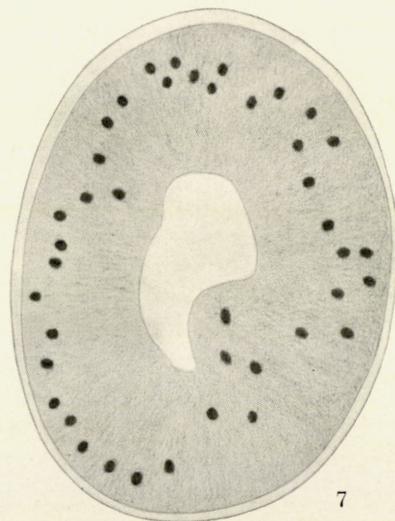
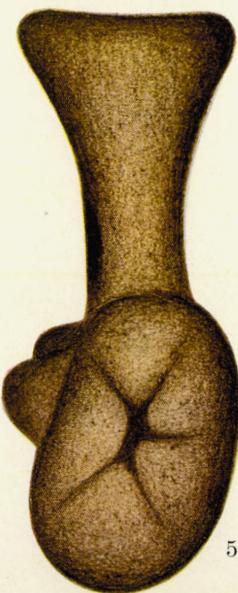
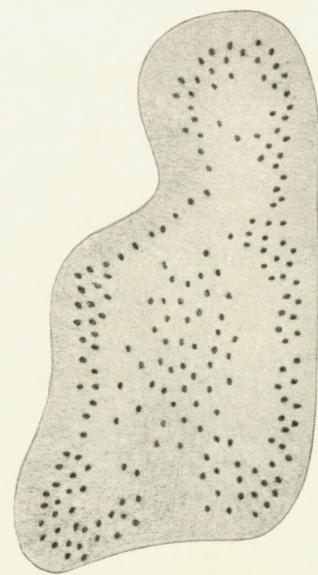
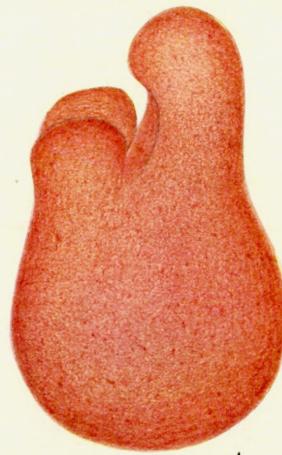
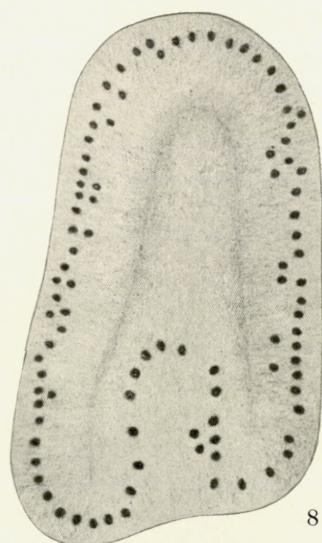
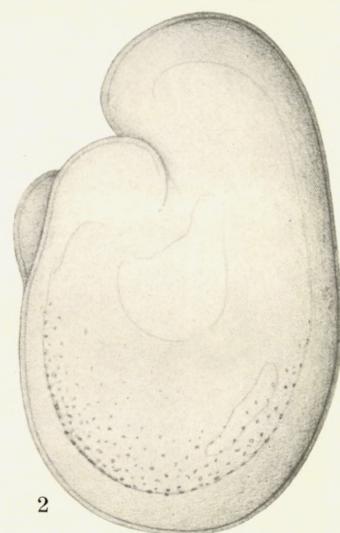
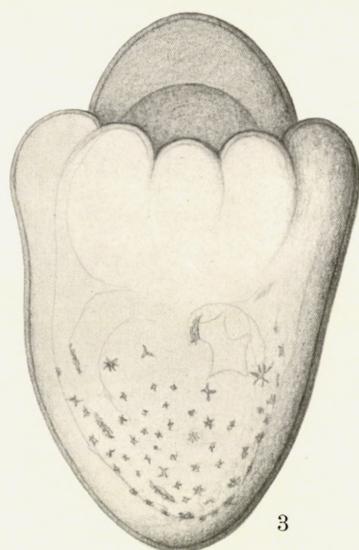
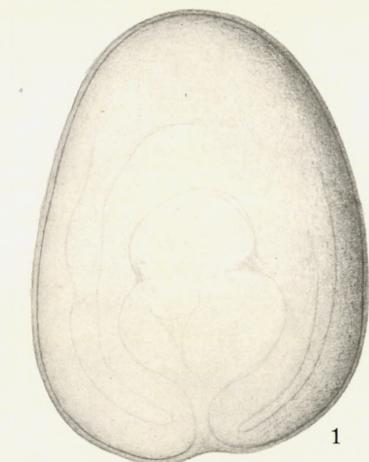


Plate VI.

- Figs. 1—3. Embryos of *Fromia ghardaqana* Mrtsn. 1. Advanced Gastrula stage,  $2\frac{1}{4}$  days old.  
2. Young Brachiolaria stage,  $3\frac{3}{4}$  days old, side view; beginning formation of dermal skeleton.  
3. Brachiolaria stage, 8 days old; from the oral side. Secondary lobes on the paired Brachiolaria arms; behind these the large sucking disk on the anterior, unpaired Brachiolaria arm. The dermal skeleton somewhat more developed. All drawn from preserved specimens, cleared in Canada Balsam.  $\times 65$ .
- 4. Embryo of *Fromia ghardaqana* Mrtsn., side view, drawn from life; natural colour.  $\times 50$ .
  - 5. Embryo of *Echinaster purpureus* (Gray), 6 days old; half side view. Natural colour.  $\times 50$ .
  - 6. Embryo of *Ophiolepis cincta* Müll. & Troschel. 4 days old. Natural colour.  $\times 150$ .
  - 7—9. Sections of embryos of *Ophiolepis cincta* Müll. & Troschel. 7. Incipient Gastrula stage, still within the egg-membrane, c. 12 hours old. 8. Gastrula stage, c. 18 hours old. 9. Sagittal section through an embryo  $1\frac{1}{2}$  days old.  $\times 300$ .



## Plate VII.

All figures of *Fromia ghardaqana* Mrtsn.

- Fig. 1. Section of embryo, 3 hours old. The nuclei scattered irregularly in the yolk.  
- 2. Section of embryo, 5—6 hours old. The nuclei beginning to arrange themselves along the surface.  
- 3. Section of embryo, 14—15 hours old. The nuclei are arranged in a single layer along the surface, and in irregular folds penetrating into the yolk.  
- 4. Section of embryo, 28 hours old. Gastrula stage.  
- 5. Section of embryo, 28 hours old. The embryo is abnormal, the nuclei having not reached the surface, a large proportion of the yolk thus being left outside the embryo.  
- 6. Transverse section of embryo,  $1\frac{3}{4}$  days old.  
- 7. Longitudinal section of embryo,  $1\frac{3}{4}$  days old.  
- 8. Longitudinal section of embryo,  $2\frac{1}{4}$  days old. The apical space is an artefact, due to preservation; naturally, the mesenchyme fills out completely the space between ectoderm and endoderm.  
- 9. Median sagittal section of embryo,  $3\frac{3}{4}$  days old. The invagination is the sucking disk.  
- 10. Lateral sagittal section of embryo,  $3\frac{3}{4}$  days old. Showing the hydropore.  
- 11. Transverse section of embryo, 4 days old. Showing the hydropore.  
- 12. Frontal longitudinal section of embryo, 4 days old.

All figures  $\times 65$ .



## Plate VIII.

All figures of *Opheodesoma grisea* (Semper).

Fig. 1. Ripe egg.

- 2—6. Young cleavage stages; 2—16 cells-stages; 2 hours old.
- 7—8. Blastula stages, 4 hours old.
- 9—13. Gastrula stages at various ages: fig. 9, 8 hours old, fig. 10, 12 hours old, figs. 11—13, 15 hours old.
- 14—15. Embryos beginning to assume the Auricularia shape. Oral side (14) and side view (15).
- 16—18. Young Auricularias, from the oral side (16 and 18) and in side view (17). In fig. 18 the first wheel has appeared, and the larval nervous system is distinct.

Figures 1—15  $\times$  150. figs. 16—18  $\times$  125.

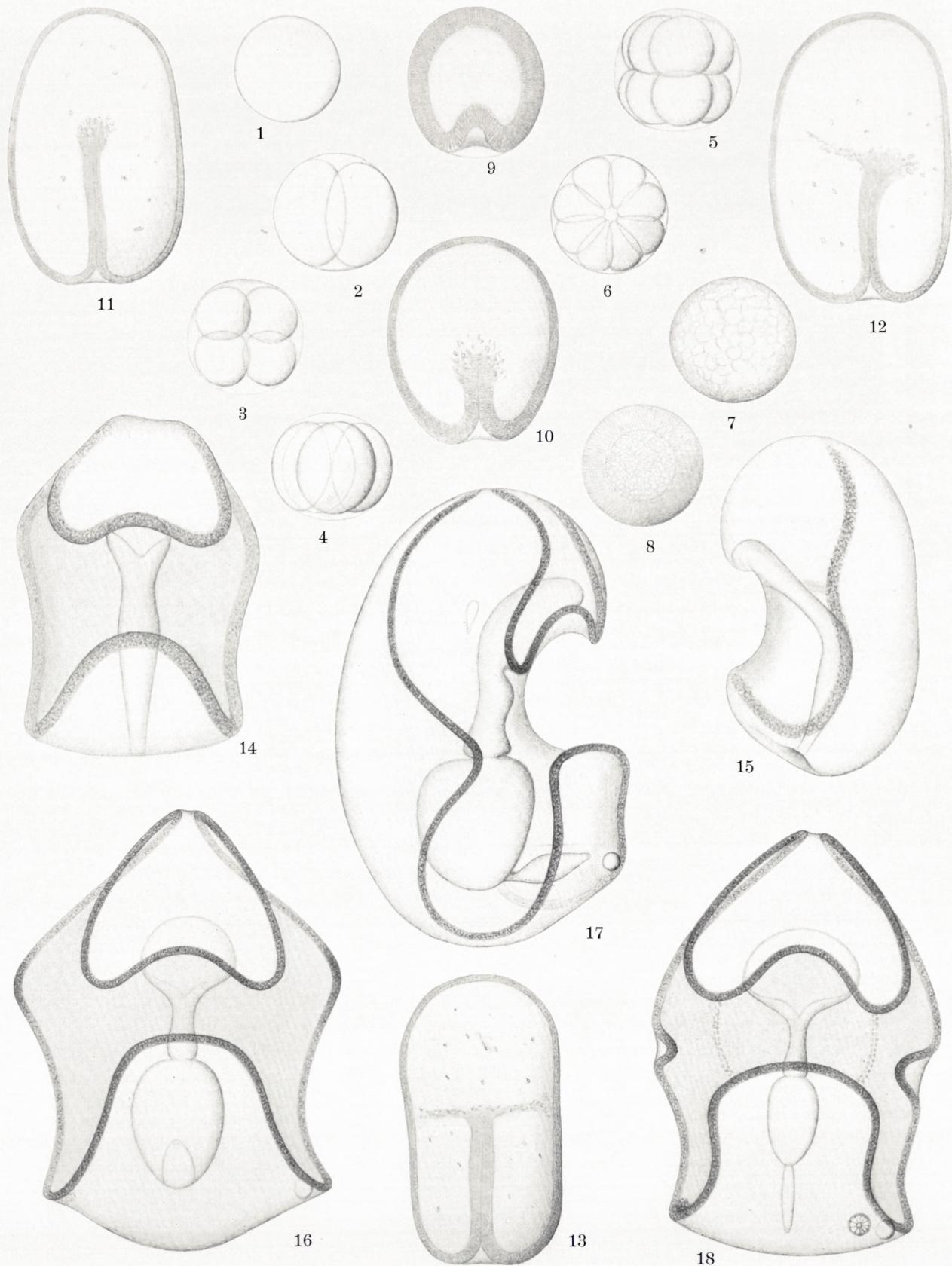


Plate IX.

- Fig. 1. Fully formed Auricularia of *Synaptula vittata* (Forskål), oral side. 13 days old.  $\times 85$ .
- 2. Metamorphosis stage (Doliolaria) of *Synaptula vittata* (Forskål). 17 days old.  $\times 130$ .
  - 3. Young *Synaptula vittata* (Forskål). 5 weeks old.  $\times 160$ .
  - 4. Fully formed Auricularia of *Opheodesoma grisea* (Semper), oral side. 11 days old.  $\times 100$ .
  - 5. Young Auricularia of *Holothuria pardalis* Selenka, oral side. 3 days old.  $\times 100$ .
  - 6. Fully formed Auricularia of *Holothuria pardalis* Selenka, dorsal side. 2 weeks old.  $\times 100$ .

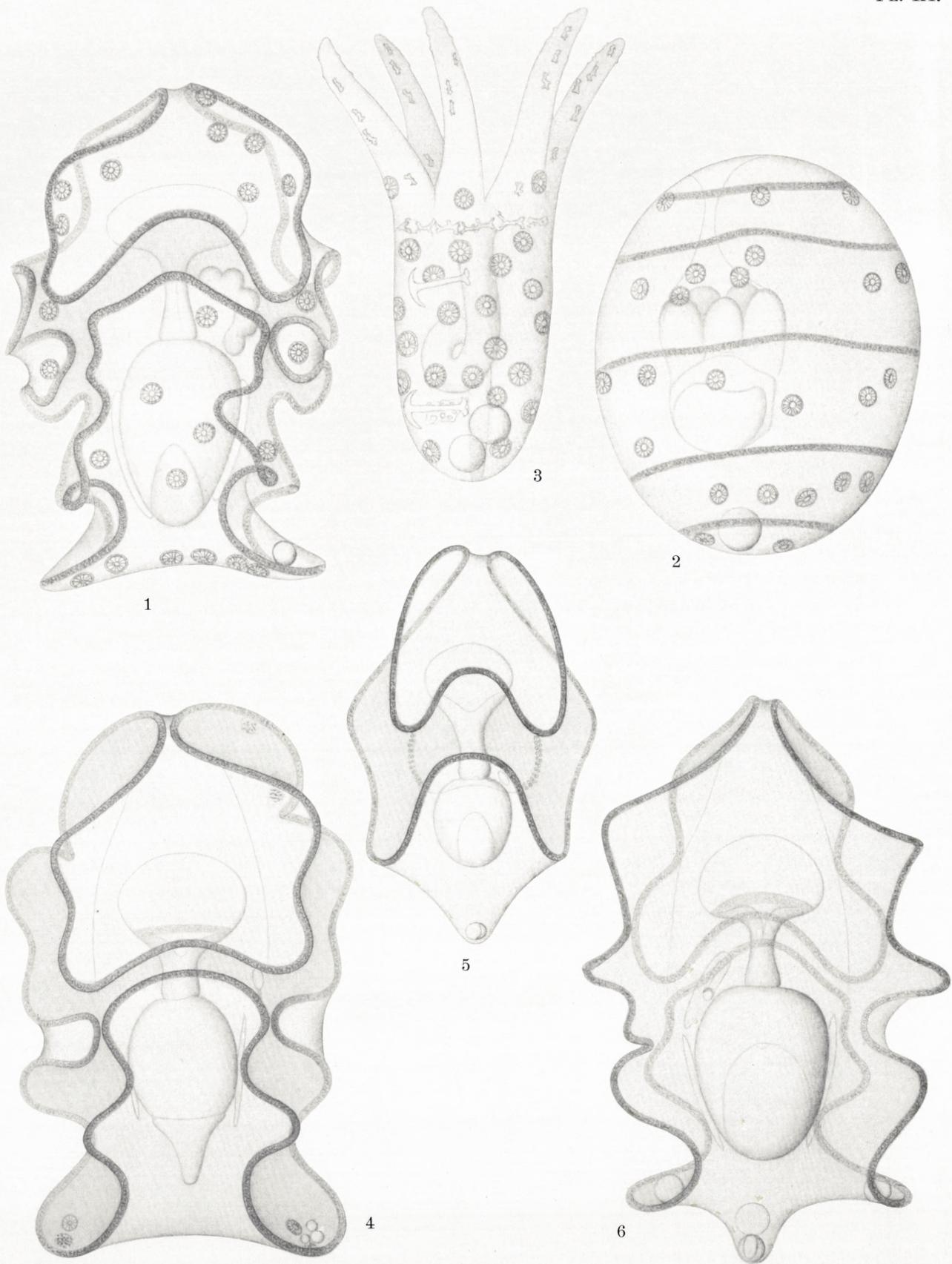


Plate X.

All figures of *Holothuria impatiens* (Forskål).

- Fig. 1. Young Auricularia, oral side. 8 days old.  $\times 125$ .  
- 2. Young Auricularia, oral side. 9 days old, showing the unusual feature of having two calcareous bodies in the posterior end.  $\times 125$ .  
- 3. Fully formed Auricularia, oral side. 14 days old.  $\times 100$ .  
- 4—5. Metamorphosis stages (Doliolaria). 16 days old.  $\times 100$ .  
- 6. Young Holothurian, 6 weeks old. (Drawn on free hand.)  $\times c. 80$ .
-

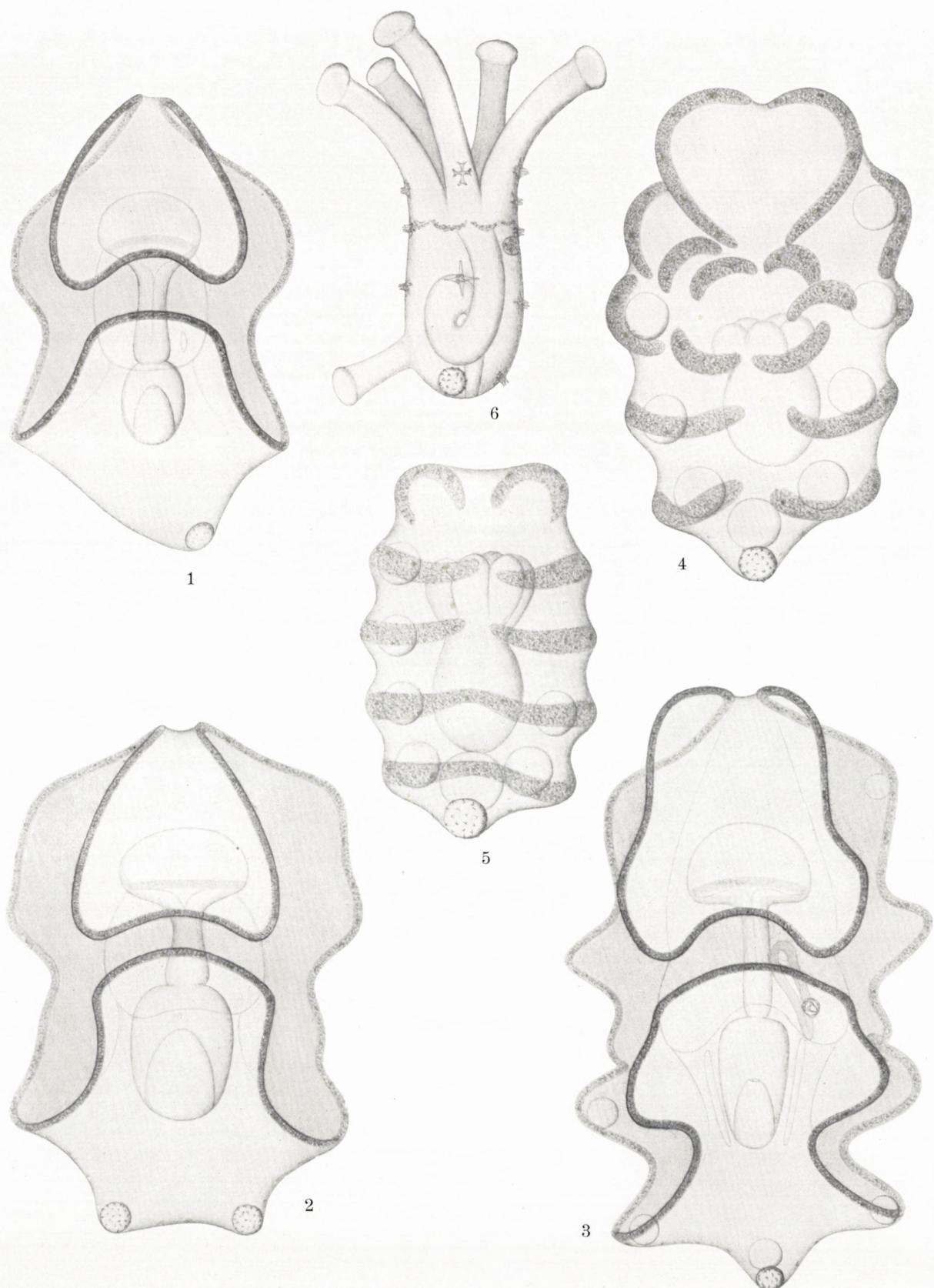


Plate XI.

- Fig. 1. Young Auricularia of *Holothuria papillifera* Heding. 4 days old.  $\times 150$ .  
- 2. Nearly fully formed Auricularia of *Holothuria papillifera* Heding. 2 weeks old.  $\times 115$ .  
- 3. Fully formed Auricularia of *Holothuria papillifera* Heding. 18 days old.  $\times 100$ .  
- 4. Young Auricularia of *Holothuria diffcilis* Semper. 5 days old.  $\times 125$ .  
- 5. Fully formed Auricularia of *Holothuria diffcilis* Semper. 16 days old.  $\times 100$ .  
- 6. Young Auricularia of *Holothuria (Microthele) nobilis* Selenka. 7 days old.  $\times 150$ .

All from the oral side.

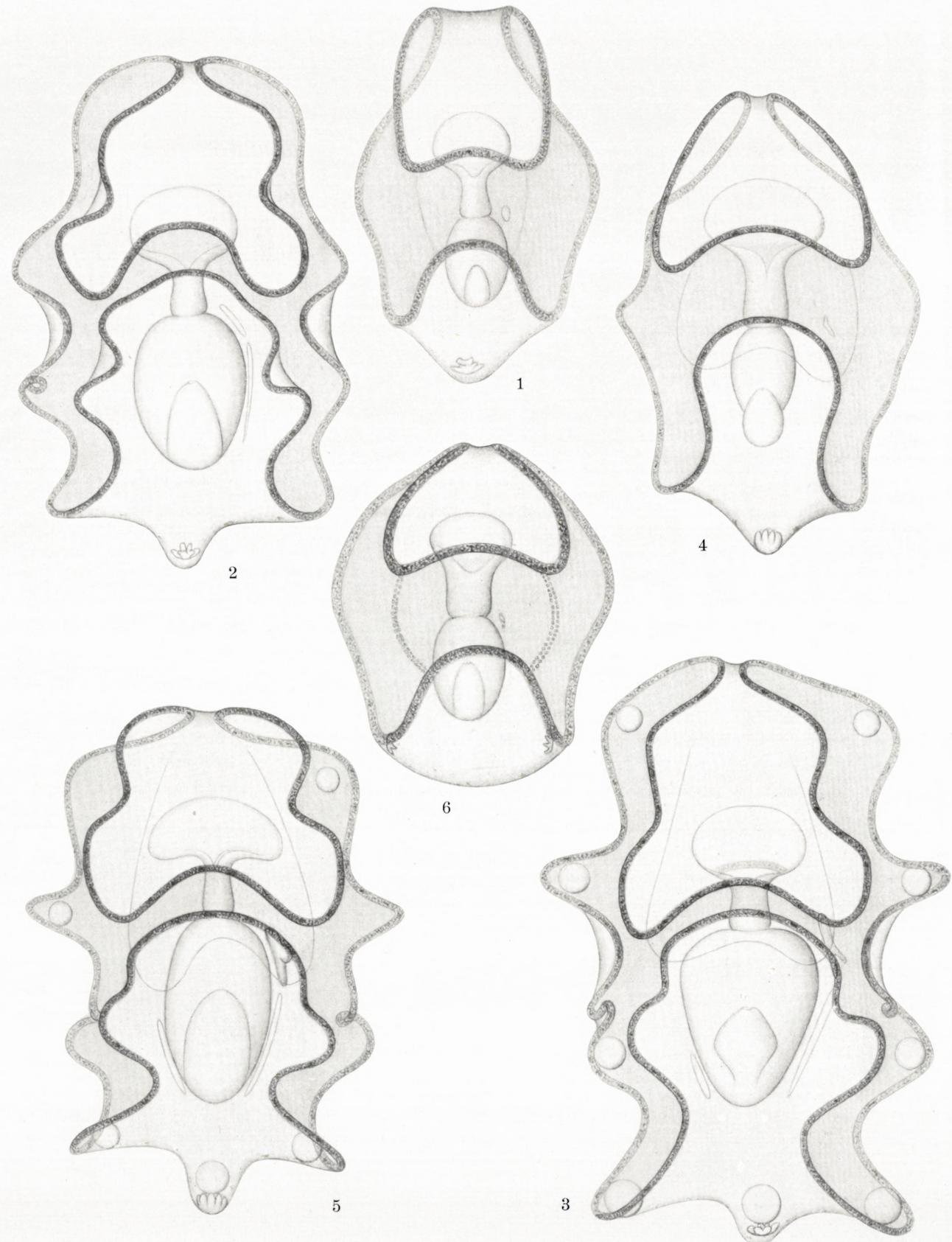
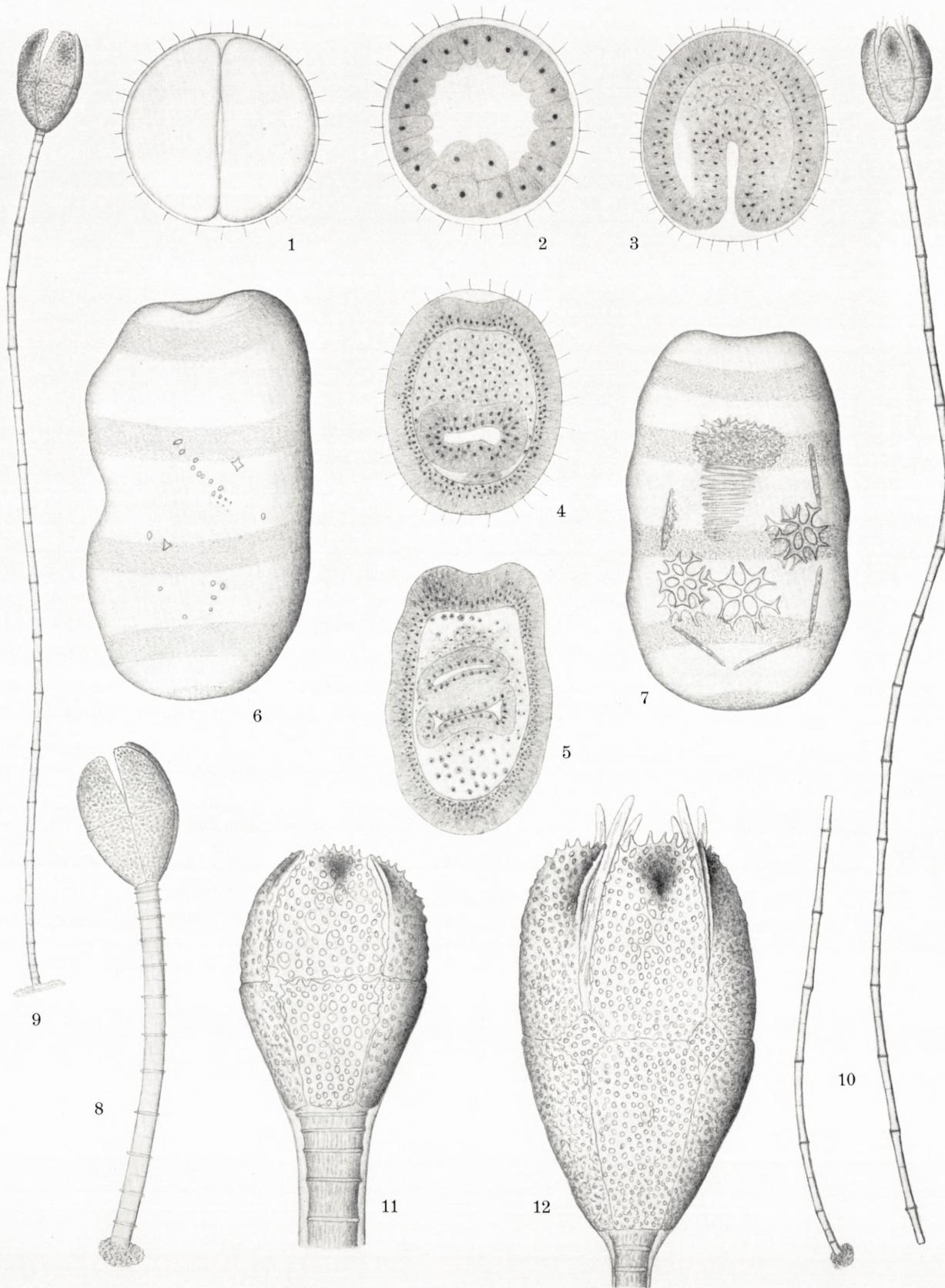


Plate XII.

All figures of *Heterometra Savignyi* (Joh. Müller).

- Fig. 1. First cleavage stage, 2 hours old.  $\times 200$ .  
- 2. Section of embryo, 5 hours old. Blastula with incipient formation of mesenchyme.  $\times 200$ .  
- 3. Section of embryo, 6 hours old. Gastrula.  $\times 200$ .  
- 4. Section of embryo, 9 hours old. The archenteron separated from the ectoderm. The apical sucking disk beginning to form. The embryo still enclosed by the egg-membrane.  $\times 200$ .  
- 5. Section of embryo 20 hours old. The archenteron has divided into two parts, the upper representing the entero-hydrocoel, the lower the entoderm. The embryo, which is now free-swimming, has begun to form the vibratile bands. The depression at the upper end is the sucking disk.  $\times 200$ .  
- 6. Embryo, 25 hours old, showing the first rudiments of the skeleton. The notch on the left side is the incipient formation of the vestibulum.  $\times 300$ .  
- 7. Embryo, 30 hours old. The skeleton in an advanced stage of development.  $\times 300$ .  
- 8. Young Pentacrinoid.  $\times 85$ .  
- 9. Pentacrinoid, later stage; from side of the dish.  $\times 35$ .  
- 10. Pentacrinoid, later stage; from bottom of the dish. The stalk being too long for the plate, the basal part has been placed separately alongside the main part.  $\times 35$ .  
- 11. Head of young Pentacrinoid.  $\times 160$ .  
- 12. Head of more advanced Pentacrinoid. The radials have appeared.  $\times 120$ .
-



Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark, Copenhague,  
Section des Sciences, 9<sup>me</sup> série, t. VII, n° 4.

# TIMMESÖBJERG EN BIOLOGISK STUDIE I BOKSKOGEN PÅ MÖENS KLINT

AV

B. LINDQUIST

MED 19 TAVLER

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURV. OG MATH. AFD., 9. RÆKKE, VII. 4.

KØBENHAVN  
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Oversigt over Det Kgl. Danske Videnskabernes  
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# TIMMESÖBJERG

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## Indledning.

Under arbeten i bokskogarna på Möens klint sommaren 1929 påträffade jag på Timmesöbjerg i Klinteskoven inom ett mindre område några humusbildningar, som väckte mitt intresse. På den kritbemängda mulljorden hade fläckvis en typisk råhumus utbildats. Denna råhumus bar emellertid en flora av lundväxter och den visade vid närmare undersökning en svagt sur till alkalisk reaktion. De intressanta pedologiska och biologiska förhållandena på lokalen ledde till ett första ganska kort omnämnde därav i min utredning av den skandinaviska bokskogens biologi. Då emellertid skogsbeståndet — gammal naturskog av bok — på denna lokal visade flera mycket ursprungliga drag och i mera än ett hänseende biologiskt anknöt till skogsförhållanden typiska för norra Sverige ansåg jag en mera allsidig utredning av skogsvegetationen härstädes vara av intresse. De år 1929 påbörjade undersökningarna över vegetationen på Timmesöbjerg kom därigenom att fortsättas under åren 1931, 1932 och 1934—37. Då det år 1936 visade sig, att undersökningsområdet inneslöt en dittills okänd fornborg, utvidgades undersökningen att omfatta även enklare arkeologiska data och deras förhållande till de biologiska företeelserna.

Då arbetet nu framlägges för dansk publik vill jag betona, att de intressanta vegetationsproblem, som möter på Timmesöbjerg, kanske icke utretts så grundligt som de förtjänat, och att en fördjupad undersökning kommer att ge en rikare bakgrund åt de frågor, som här beröras. Samma sak gäller i än högre grad den kulturgeografiska delen av undersökningen, eftersom bl. a. inga undersökningar i fältet med enbart arkeologiskt syfte företagits.

Väsentligt är emellertid, att de danska vetenskapsmännens uppmärksamhet genom denna uppsats riktas på detta ur biologisk och kulturgeografisk synpunkt intressanta område, där de skilda disciplinernas forskningsobjekt så intimt gripa in i varandra, att man vid kommande undersökningar måste gå fram med största försiktighet för bevarande av såväl biologiskt som arkeologiskt forskningsmaterial.

Under hela den tid undersökningen pågått har Kammarherre S. SCAVENIUS, Klintholm, med stort intresse följt arbetet och välvilligt lämnat mig all erforderlig hjälp, för vilket jag ber att få framföra mitt hjärtliga tack. För undersökningens utförande har jag ytterligare erhållit värdefull hjälp av Dr. OLOF ARRHENIUS, vilken på sitt laboratorium vid Kagghamra utanför Stockholm låtit verkställa större delen av

de kemiska analyser, som här publiceras. Några av de tidigaste analyserna ha likvälförts under min vistelse på Carlsbergslaboratoriet i Köpenhamn åren 1929 och 1930. För det bistånd, som jag erhållit av Dr. ARRHENIUS och för den beredvillighet varmed Prof. S. P. L. SØRENSEN ordnat arbetsplats för mig på Carlsbergslaboratoriet, är jag synnerligen tacksam. Slutligen önskar jag rikta ett tack till Dr. H. BERLIN, Lund, som för denna uppsats företagit bestämning och bestämningskontroll av insamlad daggmask samt till Dr. HERMAN PERSSON, som bestämt mossorna.

## Kapitel I. Borgvallarna på Timmesöbjerg.

(Härtill fig. 1—5, tavl. II—IV).

**Borgen.** Timmesöbjerg är ett av de fyra skogklädda kritberg, som relativt brant resa sig inom södra delen av Möens Klinteskov på omkring en knapp kilometers avstånd från de tvärbranta stupen på Möens östkust. Timmesöbjerg bildar en kupol med en höjd av omkring 30 meter över den omgivande terrängen och intar en areal av c:a 4 hektar; det når en total höjd över havet av 113 meter. I öster, söder och väster reser sig berget brant över omgivningen med en maximal sluttning av 7 meter på 10 eller c:a 35 graders lutning, på norra sidan sluttar terrängen mindre starkt och i nordväst tillstöter en av ett tjockare moräntäcke uppbyggd ås. Utsikten är mot norr, nordväst och nordost skymd av närliggande höjder, men från ostsydost till västsydväst är horisonten fri med utsikt över Västmöen, Falster och Östersjön ända bort mot Rügen.

Kalotten består helt av krita och saknar lösa mineraljordsavlagringar. Sluttningarna omgivs emellertid av sandlager och lerig morän. Mot norr, nordväst och nordost avskäres själva kalotten av trenne med konst uppförda vallar och två mellan dessa vallar löpande gravar, vilket vallsystem är av samma typ som tidigare beskrivits från engelska kritterränger av ALLCROFT (1908). Det har kraftigt tilltagna dimensioner, medelsiffran 7 meter mellan gravarnas bottnar anger deras ungefärliga bredder. Ett tvärsnitt av vallsystemet återfinnes å fig. 2, och vallarnas läge i terrängen framgår av fig. 1. Det av vallar och tvärstup (mellan 25 och 35 graders lutning) omgivna området bildar en oval med diometrarna 100 m × 80 m. Till arealen är området innanför vallarna omkring  $\frac{1}{2}$  hektar.

Dessa vallar äro praktiskt taget stenfria, såväl i ytan som på djupet, vilket ju är att vänta, då den naturliga stenen på berget, flinta, är mycket sparsam. I vallen har en del tydligt bearbetad flinta påträffats, och i vallens västligaste partier ha ställvis djupt liggande kolskikt uppdagats, upp till 5 cm:s mächtighet. I nordväst finnes ett avbrott i vallarna, vilket sannolikt är borgens huvudingång. — Innanför vallarna på den i övrigt stenfria kritkalotten (se PUGGARD 1851, sid 182) har påträffats ansamlingar av sten — flinta, gneiss, granit och sandsten — i storlek från 5 till 40 cm:s diam. inom begränsade fläckar i oregelbundna förband. Att dessa stensamlingar stå i förbindelse med mänsklig verksamhet på berget är ställt utom allt tvivel. Ty dels

har det kunnat konstateras, att stenarna på vissa ställen äro lagrade kant i kant, dels äro här typisk rullsten och typisk moränsten blandade om varandra i mulljorden utan någon inblandning av annat moränmaterial, eller svallat eller rullat material, dels har slutligen bland dessa stenar funnits klart bearbetad flinta och en typisk knacksten. Stensamlingarna äro koncentrerade till de lägre delarna av området; på kalottens krön ha inga dylika påträffats och ej heller några sådana oregelbundenheter i terrängen, som tyda på mänsklig verksamhet. Däremot har här påträffats kol i mindre utsträckning och invid en rotvälta nära krönet har på ett djup av c:a 30 cm ned i mullen funnits underkäksdelar med tänder av ungt nötkreatur, avbrutna revbensfragment (de båda främsta revbenen) jämte fragment av femur och (troligen) humerus av nötboskap samt slutligen nedre delen av en tibia av hund av en småväxt ras. Flera av benen voro krossade i färskt tillstånd<sup>1</sup>. Inom detta område fanns även de högsta fosfatvärdena, upp till 215 fosfatgrader, då samtidigt inom området i övrigt fosfatvärdena i mulljorden lågo mellan 0 och 24.

Ett trettiotal meter öster om kalottens topp ligger en fyrkant av svaga vallar med ungefärliga dimensionerna  $7 \times 9.5$  m, i stort sett orienterad i de fyra väderstrecken. Den ligger i sluttning mot öster (se fig. 1) och är inuti rikt bemängd med sten. Min biologiska undersökning har icke givit anledning till några grävningar inom detta område.

**De vendiska borgarna.** Otvivelaktigt står vi på Timmesöbjerg inför en anläggning, som till typ och storlek erbjuder stora likheter med svenska, tyska och engelska fornborgar, kanske i första hand med de vendiska borgarna i norra Tyskland.. En jämförelse med dessa kan möjligen ge vissa uppslag i en diskussion över Timmesöborgens forna betydelse. Jag tänker därvid i första hand på Arkona, Rethre och Garz. Av dessa känna vi väl förhållandena i Arkona genom SAXOS utomordentliga skildring av borgen och dess tempel.

Arkona hade ett dominerande läge vid branten av kritklipporna på Wittow på norra delen av Rügen. Enligt SAXO var Arkona under 1100-talet ett av de västliga vendarnas sista fästen inom Östersjöområdet, med ett tempel helget åt Svantevit. — Borgen begränsades på tre sidor av stup och var på den fjärde sidan befäst med en 50 alnar hög vall, vars övre delar uppbyggts av timmer och grästorp (SAXO; OLRIK 1909, sid. 122 ff.). Vid ingången, som liksom vid Timmesöbjergborgen och Rethre låg i nordväst, fanns ett torn av trä, innanför vallarna funnos talrika byggnader och mitt i borgområdet låg templet. Av SAXOS skildring att döma voro kultplats och försvarsanläggning kombinerade i Arkona och samma synes ha varit förhållandet i många andra vendiska borgar t. ex. i Garz och Rethre. Om borgen i Garz säger SAXO: »i övrigt var det her som hist (i Arkona): i Fredstid stod Byen öde, men nu var den fuld af Folk» (OLRIK l. c. sid. 142—143), vilket synes mig vara av intresse för tolkningen av liknande anläggningar.

Enligt SCHUCHARDT (1926, sid. 61—62) var det regel, att de vendiska borgarna av detta slag lågo högt, med fortifikatorisk placering. Han påpekar i ett senare arbete

<sup>1</sup> Bestämningarna välvilligt meddelade av fiskeriintendenten, fil. dr. ELIAS DAHR.

(SCHUCHARDT *et cons.* 1928, sid. 468), hurusom de högt liggande vendiska huvudborgarna på Rügen synas ha varit förbundna genom ett signalsystem från borg till borg. Mot bakgrunden härav kan man se Timmesöbjergs orientering med fri utsikt över södra Östersjön och Rügen; i klart väder kan man från Timmesöbjerg se över till kritklipporna strax norr om Arkona. Ett signalsystem, som innefattade de vendiska fästena på Rügen, har mycket väl även kunnat nå fästet på Timmesöbjerg. Detta fäste torde f. ö. ha legat ganska avskilt från västra och mellersta Möens tätt befolkade områden. Höje Möen och dess närmaste förland skildes nämligen tidigare från sagda västligare områden genom de djupt in i landet gående vikarna och träskmarkerna vid Borre (se HINTZE 1937, sid. 8 f.) Om dess avskildhet vittnar f. ö. även den första beskrivningen vi äga över Höje Möen, nämligen AGRICOLAS omnämndande av densamma av år 1546. Han beskriver Möen som en öde ö med kritklinter — »deserta maris Balthici insula . . .»

Enligt SAXO voro de vendiska borgarna även kultplatser med tempel placerade inom borgområdena. Han omnämner sålunda ingående templet i Arkona och i Garz med beskrivning av templens inre och av deras gudabilder, men han har ingenstädes lämnat några uppgifter till belysning av dessa tempels storlek eller grundplan. Ej heller ha de utgrävningar, som under SCHUCHARDTS ledning (se SCHUCHARDT 1926 och SCHUCHARDT, STIEHL o. PETSCH 1928) företagits i Arkona, Rethre och Garz i detta avseende lämnat tillförlitliga resultat. Sålunda har KNUTSSON (manuskr.<sup>1</sup>) uppvisat, att den kvadratiska grundplan med 20 m:s sida, som SCHUCHARDT rekonsruerat och utpekat som tempelplats i Arkona, med största sannolikhet icke är platsen för Svantevits tempel; och de fakta på vilka SCHUCHARDT baserat sina uppgifter om storleken och formen hos templet i Garz äro alltför vaga. De enda resterna som funnits av dessa »tempel« utgöras av smärre stensättningar, vilka lett SCHUCHARDT till en ganska godtycklig rekonstruktion av kvadratiska tempelgrunder på  $6 \times 6$ , resp.  $7\frac{1}{2} \times 7\frac{1}{2}$  meter.

De enda hållpunkterna för det vendiska templets grundplan, som för närvarande stå till buds — för en jämförelse med den vallomgärdade, stensatta kvadraten på Timmesöbjerg — är KNUTSSONS på en analys av SAXOS skildring av förstörelsen av Svantevittemplet i Arkona 1168/69 grundade förmodan, att det varit mindre än de av SCHUCHARDT uppgivna männen  $20 \times 20$  meter. Vi få tills vidare nöja oss med ett konstaterande av, att den stensatta vallanläggningen på Timmesöbjerg är av samma storleksordning, som templet i Arkona kan förmodas hava varit och av samma storleksordning som de fyrkantiga rekonstruktioner, som SCHUCHARDT uppgiver vara tempelplatserna i Garz.

Likheterna mellan Timmesöborgen och de vendiska borgarna framträder alltså ifråga om dess läge och befästning samt i förekomsten av tydligt stensatta områden inom borgen.

**Ortnamnen.** Ytterligare omständigheter kring borgen på Timmesöbjerg tala

<sup>1</sup> Docenten K. KNUTSSON har välvilligt ställt ett manuskript om templet i Arkona till mitt förfogande, från vilket följande refereras.

för dess nära relation till de vendiska fästena: Genom SAXO känna vi åtskilligt om vendiska kolonisationsförsök på de syddanska öarna. Att denna kolonisation stundom blivit framgångsrik synes framgå av förekomsten av ortnamn av tydlig slavisk karatär t. ex. Tillidse på Lolland, Corselitzé på Falster. Måhända skall det visa sig, att även en del svårtolkade ortnamn från Möens Klint-området, såsom Rud, Risk, Budsemarke och Busene kunna räknas till denna grupp.

**Svantevit och Jöden Opsal.** Ett indirekt stöd för en teori om Svantevitskult på Möen ge de gamla östmöenska sagnerna, sådana de till nyare tid bevarats och nu senast relaterats av ELLEKILDE (1928), vilkens undersökningar omfattar ett synnerligen rikt material och går tillbaka till uppteckningar från 1600-talets mitt, nämligen HANS JENSEN VIBORG'S *Descriptio insula Monae* av 1681. Östmöens sagofigur är Klintekongen eller Jetten af Upsal — på folkspråket Jöden Opsal — vilken av sagnerna lokaliseras till Möens klint, där han uppgives bo på varierande platser utemot Klinten, vid Stottet, vid Dronningstolen, vid Hvidskud och framför allt vid Kongsbjerg och i områdena mellan Kongsbjerg och Klintens östra branter.

Klintekongens namn förbindes i många sagn med Rügen, han far till Rügen, han råder över Rügen och kämpar mot sjörövare från Rügen. Klintekongen, Jöden Opsal, rider en vit häst liksom goden i Svantevits tempel på Arkona och han är, liksom Svantevit, en fruktbarhetssymbol, till vilken man offerar höstoffer (se OLRIK 1908, sid. 124). Han är enl. ELLEKILDE (l. c. sid. 115) det enda sydöstdanska sagoväsende av denna typ, till vilken man offerar höstoffer; åt de övriga frambäras offer vid midvintertid.

Den folkliga benämningen Jöden Opsal har tolkats på skilda sätt. VIBORG (l. c.) och flera senare danska forskare ha velat härleda namnet direkt från det svenska Uppsala och om denna tolkning är riktig skulle namnet närmast utläsas som Goden eller Oden från Uppsala. ELLEKILDE (l. c. sid. 113) godtager emellertid icke denna förklaring, utan anser, att Opsal eller Upsal i detta sammanhang betyder »Höje Möen» och att namnet skulle bli Oden från Möens Klint. Han tolkar därvid Upsal som »Höjsalen» och anser att med höjsalen just skulle betecknats höjderna vid Klinten. — Utan att taga ställning till vad som i denna sak är riktigt eller oriktigt önskar jag påpeka möjligheten av att Jöden icke nödvändigtvis behöver betyda Oden utan att det rätt och slätt kan vara Goden, d. v. s. hednaprästen och att Höjsalen likaväl som att helt allmänt beteckna Möens Klint kan avse en bestämd lokal därstädes. — Timmesöbjerg har även kallats Timmersöbjerg. Förleden torde närmast kunna härledas ur det urnordiska timbr, som betyder byggnad eller sal, tolkningen av den senare leden är dock vanskligare. Ty bredvid berget ligger ett litet kärr, som av PUGGARD (1851, sid. 21) beskrivs som en igenvuxen sjö och kallades Timmesö med efterleden -sö. Troligt är emellertid, att detta namn ursprungligen överflyttats från berget till sjön i analogi med Aborrebjerg och Aborresö, ty det synes föga troligt, att det dominerande, i förhistorisk tid betydelsefulla kritberget skulle ha uppkallats efter det lilla kärrret vid dess fot, Timmesöen. Därav anser jag mig kunna sluta, att efterleden i namnet Timmesöbjerg icke är sö utan hö d. v. s. höj. Namnet skulle då på modern danska just bli Höj-salen.

**Svanesesten.** Inne i Klinteskoven på vägen mellan Sandskredsfald och Aborrebjerg ligger ett flyttblock av stora dimensioner, som i gångna tider har gått under namnet Svantesesten eller Svanesesten. I sen tid har den även kallats Svantvitsten (se namnformerna hos SCHMIDT 1932, sid. 164 f; av vilka dock inga äro äldre än 200 år). Omkretsen är ungefär 10 meter och höjden 2,5 meter. Blocket avslutas med en markerad rygg och har en åt sydost vänd flat sida. Omkring detta block ligger fyra mindre och dessutom finnes ett hål efter ytterligare ett. Stenen har väckt forskarnas uppmärksamhet redan under 1700-talet och förorsakat åtskillig gissning och legendbildning. Sålunda säger PALUDAN (1822) »muligen ock at der i Hedningetiden har vaeret et Tempel, en offerplads för en Gudinde Svanese». Sagorna kring stenen förtälja bl. a., att stenen slingats mot Magleby kyrka av en häxa, som ömsom upp-gives vara svensk och rygisk. Det vill sålunda synas, som om Svantevits namn skulle ha knutits till denna sten på blott något över en kilometers avstånd från Timmesöbjerg. Möjligen kan dock en annan tolkning av namnet erhållas med utgångspunkt från HAAS' uppgifter om de rygiska svanestenarna (HAAS 1891, sid. 143 f).

## Kapitel II. Bokskogen.

(Härtill fig. 6—14, tavl. I, V—IX).

**Klinteskoven.** Bokskogen har tidigare haft en vida större utbredning på Möens Klint än i våra dagar. Skogarna ha under gångna århundraden skövlats och i viss utsträckning övergått i vidsträckta enefälader. Möens Östland d. v. s. Höje Møen öster om den gamla Borreviken kallades förr Enebaerland (se HINTZE 1937, sid. 12 etc.). Genom infredning och skogsplantering har emellertid skogen i sen tid ånyo utbrett sig över de kala markerna; sålunda ha Plantehaverne, där rudera och talrika gravhögar vittna om tidigare mänsklig odling, ånyo klätts med bokskog och Bjergene, vilka sannolikt under hela nyare tiden varit trädlösa, ha planterats med övervägande barrskog. Klinteskoven av idag är således i ganska stor utsträckning en kulturprodukt, men den rymmer likväl inom sina gränser bestånd, vilka bibehållit väsentliga drag av ursprunglighet.

Sådana finns inom det egentliga Storeklintområdet, en triangel med hörnen vid Hylledalsklint i norr, Busene i väster och Graaryg i söder, vilket område alltid har varit skogklätt. Mera ursprungliga skogsbestånd finns här framför allt på kritgrundens, där topografien ofta försvårat eller omöjliggjort en forstlig behandling av skogen. Till bevarandet av dessa bestånd har ägarens rent estetiska hänsyn och naturvårds hänsyn spelat in. — Ett av de intressantaste och bäst bevarade natur-skogsområdena är Timmesöbjerg, det forntida borgområdet, där utdrivningssvårigheterna varit så stora och virket så mindervärdigt, att beståndet icke ens medtagits i skogsdistrikts nuvarande hushållningsplan. Skogen på detta berg är starkt olikåldrig och dess äldsta partier leda sitt ursprung från slutet av 1500-talet.

**Beståndet.** Över trädbeståndet på detta berg har en detaljerad karta upp-

rättats under åren 1936 och 1937 (Tavla I), varvid hjälp med kartläggningsarbetena under 1936 erhållits av forstkandidaten H. KELP. På denna karta ha levande och döda träd inlagts jämte stubbar och vindfällen, varvid dimensionerna ha angivits medelst olika beteckningar. Dessutom har topografien markerats genom nivåkurvor med en meters ekvidistans, och planen för den gamla fornborgen har inlagts. — Analysen av detta trädbestånd, dess uppkomst, ålder och utvecklingshistoria, har väsentligen skett genom en åldersbestämning av träden. Åldersbestämningen har gjorts genom borring med ett Beus & Mattsons tillväxtborr med 45 cm:s borrlängd. Trots de mycket starka påfrestningarna har borret visat sig vara effektivt under förutsättning av riklig inoljning före varje borring. I ett trettiofall har jag lyckats erhålla borrspår genom märgen c:a 3 dm ovan markytan. Åldersbestämningarna på klendimensionerna ha likväl överrepresenterats på grund av svårigheterna att borra de grova bokstammarna i märgen. För åldersbestämningen har dessutom sex träd avsågats så nära markytan som möjligt och åldersräknats på stubbsnittet.

Åldersbestämningen av denna som regel mycket senvuxna bok är svår. Borrspånen ha snittats med rakblad och därefter behandlats med järnalun, varvid årsringsgränserna ofta klart framträda. Sedan åldersbestämningen vid stubbhöjd verkläts återstod att med någorlunda tillförlitlighet beräkna åldern mellan markytan och stubbhöjd för bestämning av trädets verkliga ålder. Denna beräkning har utförts på basis av en undersökning över småplantornas ålder i förhållande till deras höjd. Som regel ha bokplantorna på denna lokal under sina första år visat extremt svag tillväxt, i viss mån påminnande om den svaga tillväxten hos tallplantorna på de norrländska tallhedarna. Tilläggsåldern vid 3 dm:s höjd sattes för träd med de innersta 10 årsringarna mindre än 0.75 mm pr. årsring till 25 år, mellan 0.75 mm och 1 mm till 15 år och över 1 mm till 5 år. För andra avstånd mellan borrspåns- resp. stubbhöjd och marken ha värdena beräknats i relation härtill.

En exakt åldersbestämning av detta material kan icke genomföras. Trots noggrannast möjliga tillvägagångssätt torde avvikeler från de riktiga åldersvärdena av upp till tiotalet år förekomma, dels beroende på svårigheterna att räkna mycket smala årsringar hos bok, dels beroende på att markytans läge vid tiden för plantans uppkomst icke kan exakt bestämmas, ej heller en noggrannare rekonstruktion företagas av plantans utveckling mellan markytan och stubbhöjd. Så som åldersbestämningen utförts här ger den likväl möjligheter att i grova drag skissera beståndets utvecklingshistoria.

Den äldsta bokgenerationen på Timmesöbjerg utgöres av ett mindre antal stammar — efter den gjorda åldersbestämningen som grundval för en uppskattning med ledning av trädens habitus summa 23 st. — av nu mera än 300-åriga träd, resterna av ett till synes olikåldrigt bestånd, som grundats under 1500-talet och förra hälften av 1600-talet. Trots sin höga ålder torde dessa träd dock i genomsnitt tillhöra en något yngre åldersgrupp än den generation urgamla, merendels döda och döende bokar, som förekomma här och där ytterst på Klinten, t. ex. vid Dronningstolen, vid Röde Udfald (se fig. 17) och nära Maglevands pynt. För dessa gamla bokar går trädåldern

enligt utförda borrhningar upp till 400—450 år — de tillhör en bokgeneration, som i Danmark i övrigt är utdöd på få undantag närr. — De undersökta träden tillhörande den äldsta bokgenerationen på Timmesöbjerg visa en sen ungdomsutveckling, vilket

**Åldersbestämning å bokar från Timmesöbjerg år 1936.**  
Altersbestimmung der Buchen auf dem Timmesöbjerg im Jahre 1936.

Nr.	Diam. brh. cm.	Avläst ålder i stubbhöjd	Medelbredd av de 10 in- nersta årsrin- garna i mm	Beräknad trädålder	Födelse- år
1.....	40	324	0.4	349	1587
2.....	53	268 (vid 1.7 m)	0.4	338	1598
3.....	29	273	0.7	298	1638
4.....	53	265	0.8	280	1656
5.....	36	246	0.5	271	1665
6.....	40	247	2.0	252	1685
7.....	40	236	1.0	251	1686
8.....	8	222	0.5	247	1691
9.....	38	208	0.6	233	1703
10.....	45	211	0.75	226	1710
11.....	14	199	0.4	224	1712
12.....	35	215	1.5	220	1716
13.....	46	194	1.0	209	1727
14.....	23	185	1.0	200	1736
15.....	18	179	1.0	194	1742
16.....	40	178	0.75	193	1743
17.....	17	177	0.75	192	1744
18.....	38	187	1.5	192	1744
19.....	11	185	1.5	190	1746
20.....	33	183	1.5	188	1748
21.....	35	170	1.0	185	1751
22.....	32	174	1.5	179	1757
23.....	30	163	1.0	178	1758
24.....	14	132	0.75	147	1789
25.....	42	118	2.5	123	1813
26.....	33	92	0.75	107	1829
27.....	8	85 (vid stambasen)		85	1851
28.....	4	85 - —		85	1851
29.....	4	74 - —		74	1862
30.....	16	53	1.0	68	1868

tyder på att de uppkommit under skärm eller i luckor i ett äldre bestånd. Dessa träd ha i många fall en ganska grov grenbildning och äro stundom spärrvuxna. På grund av den starka reduktionen av stamantalet i denna generation äro luckorna och luckföryngringen numera svåra att iakttaga.

Rikligare förekomma bokar i åldrar mellan 220 och 300 år, vilka i regel även visa långsam ungdomsutveckling och f. n. äro mellan 30 och 40 cm i brh. I ett par fall kan det fortfarande konstateras, att dessa träd uppkommit i luckor i det äldre beståndet, i det att fortfarande de äldre rändträden kunna skönjas och gammalt, multnat virke från lågor kan iakttagas och med ganska stor säkerhet åldersbestämmas (till ett sådant fall återkommer jag nedan). — Huvudmassan av träden i den nuvarande skogen härstamma från 1700-talets förra hälft. Dessa träd ha genomgående en snabbare ungdomsutveckling och ha i större utsträckning uppkommit som stubb-skott eller rotskott. I några fall har direkt kunnat konstateras, att denna skogsgenerations uppkomst influerats av en äldre avverkning. Slutligen kan omnämñas förekomsten av en ungskogsgeneration uppkommen vid mitten av förra århundradet (se fig. 7), vilken utfyllt några smärre luckor. Dessa luckor ge knappast intryck av att vara stormluckor, utan torde ha uppstått efter någon mindre avverkning vid sagda tid eller möjligen genom ett naturligt avdöende av skärmträd. I dessa luckor har bokföryngring ganska rikligt infunnit sig, varjämte de stundom ha ett inslag av enbuskar. Denna 100-åriga ungskog är synnerligen senvuxen och mäter mellan 2 och 5 meter i höjd — en senvuxenhet som påminner om den norrländska stavagranskogens.

**Torrträd och lågor.** Endast ett mindre antal lågor och stående, döda träd förekomma på berget, vilket sett mot bakgrunden av det betydliga antalet äldre stubbar måste tydas så, att man under de senaste århundradena hämtat virke här. Den äldsta av de till ett tiotal uppgående lågorna ligger på toppen av berget nära rotvältan till en år 1934 fallen bok och framträder i markytan endast som ett grönt mossbelupet band i den ganska rika ört- och gräsvegetationen (se fig. 8). Under mosstäcket består humusen här till ett djup av 15 cm av stora mängder oförmultnat virke. En ungefärlig beräkning av den tidpunkt, då lågan uppkom, kan göras på basis av den nu stormfällda bokens ålder och utveckling. Denna stormfällda bok har uppkommit strax intill lågan, men utan något samband med denna. På grund av föryngringsvårigheterna kring bokstammarna — beroende på uttorkningen runt stambaserna — kunna dessa tvenne träd knappast samtidigt ha vuxit på platsen. Möjligen kan dock det 1934 stormfällda trädet kommit upp som en marbuske under den gamla boken. I första fallet, vilket synes mig vara mest antagligt, skulle lågans ålder bli minst 350 år, i senare fallet däremot 245 år beräknat på grund av en kraftig tillväxtreaktion hos det yngre trädet vid c:a 105 års ålder. Ett par andra bestämningar av åldern hos lågor i ungefär samma nekrotiseringensgrad ge liknande höga värden och illustrera tydligt förmultningens långsamma förlopp. — I västra delen av berget har längs utmed kanterna av en gammal låga föryngring uppkommit, nu representerad av fem stycken utefter lågan stående stammar bildande en lågföryngring av samma typ som den, vi finna på de norrländska hedmarkerna. Stamrnarnas ställning utefter lågan omöjliggör en teori att det döda trädet vid en relativt sen tidpunkt skulle kunnat falla in mellan dessa fem stammar och stammarnas jämna årsringsutveckling tyder icke på, att förhållandena under deras uppväxt väsentligen

<sup>1</sup> Svensk term för dött, på marken liggande träd.

ändrats. Lågan torde — i analogi med lågföryngringen på tallhedarna — vara direkta orsaken till utvecklingen av dessa fem stammar. Den torde ha gynnat deras utveckling från dvärgplantor till normala plantor — man behöver däremot icke nødvändigtvis antaga, att lågan orsakat plantornas uppkomst. Vid en beräkning av lågans ålder måste man således gå ut ifrån, att lågan och plantorna äro ungefär jämngamla. Åldern på en av dessa till synes jämnåriga stammar har bestämts till 216 år, vilket skulle bli lågans ungefärliga ålder (Fig. 13).

Icke långt från denna låga ligger en annan med ungefär samma nekrotiseringssgrad (fig. 25; se SERNANDER 1936, sid. 164 ff). Dess ålder kan beräknas genom åldersbestämning av en gren från en bredvidstående c:a 340-årig bok (nr 2), vilken gren skjutit ut i det hål, som uppstått då trädet dog och lågan uppkom. Denna gren visar en kraftig reaktion för c:a 180 år sedan, vilket sálunda får antagas vara lågans minimialder, eftersom reaktionerna på denna torra mark ofta låta vänta länge på sig.

Med ovanstående ha påvisats de möjligheter, som finns för en bedömning i stort av lågornas ålder och de approximationer, som därvid alltid måste ske. En reaktion hos kringstående träd, uppkomsten av en luckföryngrings eller en föryngrings kraftiga och genombärende reaktion ge hållpunkter för bedömningen. — Av de framlagda exemplen framgår tydligt, att förmultningen på Timmesöbjerg är anmärkningsvärt svag och att en fullständig förmultning av lågorna får beräknas draga en tid av flera århundraden. Just därför synes det mig märktigt, att icke lågor eller spår av lågor rikligare uppträda här och detta måste leda till slutsatsen, att de under tidernas lopp avlägsnats.

**Stubbar.** Inom det karterade området har antalet stubbar taxerats till 153 st. med en diameterfördeling, som framgår av nedanstående allmäna översikt över trädbeståndet:

#### Tabell

över förekomst och fördelning av levande och döda bokar samt över stubbar och lågor inom det karterade området på Timmesöbjerg: Tabelle über das Vorkommen und die Verteilung von frischen und dürren Buchen auf dem Timmesöbjerg.

Diam. i cm.....	10—	20—	30—	40—	50—	Summa	Totalsumma
Levande träd. Frische Bäume .....	134	151	90	83	17	475	
Döda stående stammar. Dürre Bäume .....	3	3	1	2	1	10	
Stubbar. Stubben .....	67	37	24	13	12	153	
Lågor. Fallstämmen .....	4	1	2	2	1	10	648

Förutom de färskha stubbar, som föreliggande undersökning förorsakat och av vilka endast en fällts inom borgområdet<sup>1</sup>, torde inga stubbar finnas under 100 år; flertalet äro sannolikt närmare 200 år gamla. Ett studium av stubbarna ge vissa möjligheter att bedöma, huruvida de uppkommit genom regelrätt avverkning eller på

<sup>1</sup> Denna hade året efter fällningen kraftiga stubbskott.

naturlig väg genom att de torra träden avbrutits vid rothalsen. Ett mindre antal stubbar visa tydligt övervallning i kanterna och en liknande övervallning kan iakttagas på stubbar i organiskt sammanhang med ännu levande träd. Detta måste tydas som tecken på avverkning, vilken i de fall den genom närliggande träds reaktioner kunnat till tiden bestämmas, härrör från tiden mellan 1720 och 1820. Att en radikal åtgärd påverkat skogsutvecklingen under denna tidsperiod framgår f. ö. tydligt av den stora procent stammar i det nuvarande beståndet, som härleda sitt ursprung från ett mycket begränsat tidsavsnitt, åren 1736—1758. De större och äldre stubbarna visa icke denna bild av övervallning och äga genomgående en ojämnn övre yta, tydande på att de tillhört träd, som torkat på rot och därefter så småningom fallit och borttagits. De äldre stubbarna äro liksom lågorna mycket svåra att åldersbestämma. I de fall en sannolik åldersbestämning kunnat göras varierar åldern mellan 150 och 300 år.

**Spår efter stormfällningar.** Marken på Timmesöbjerg representerar en ur stormfällningssynpunkt i hög grad instabil jordmån och kan karakteriseras som grund märgeljord. De grunda märgeljordarnas relationer till stormskador har SERNANDER närmare utvecklat (SERNANDER 1936, sid. 36). Skogen på bergets topp och dess södra och västra sluttningar ligger i stark exposition mot södra Östersjöbäckenet. — Inom området finnas några under det senaste årtiondets starka stormar vindfällda träd, som fallit mot nordost. Dessa stormar ha i första hand berört krönet och sydvästslutningen. Av gamla vindfällen finnas däremot inga spår, ty de lågor, som ovan omtalats, härröra från torrskogsfäll, ej från vindfällen. Likaledes saknas här tydliga rotvältor med lågförmultnat virke, men däremot finner man flerstädes åtskilliga oregelbundenheter i markytan, som visat sig vara märken efter rotvältor, ehuru nu oförmultnat trä där icke längre kan påvisas. Dessa forna rotvältor, vilkas antal uppgår till över 20-talet, ge sig tillkänna som svaga upphöjningar av kritblandad mulljord och därvid en grop, vars mäktighet kan variera mellan 50 och 80 cm:s djup och vars bredd i genomsnitt uppgår till mellan 0.5 och 1.0 meter. Denna fördjupning är fyllt med en från omgivande mulljord starkt avvikande humus, vanligen råhumus, av en konsistens och färgton, som tyder på att trä-virke varit ett väsentligt utgångsmaterial för bildningen. Fördjupningen har här icke uppstått efter det av rotvältesulan borttransporterade materialet, utan därigenom, att rotssystemet i fallrikningen grävt sig ned i marken och skjutit den humusblandade mineraljorden bakåt. KIAER, som ingående studerat rotvältekullarnas struktur på de jylländska hedarna (KIAER 1907, sid. 157 ff) behandlar endast mineraljordskoncentrationen och den svaga fördjupningen efter den mineraljord, som rotvälten lyft upp, men nämner intet om någon dylik djupare grop. Den intilliggande svaga upphöjningen med kritblandad mulljord har bildats av den jord, som följt med rotvälten upp och som vid stubbens och rötternas förmultning koncentrerats på markytan. — På den inbördes orienteringen av mullhögen och råhumusbildningen kan således det gamla trädetts fallrikning rekonstrueras. En sådan rekonstruktion ger vid handen, att träden övervägande fallit för sydliga och sydvästliga stormar. Bildningarna äro analoga med de av DALGAS (1884, sid. 6—10), KIAER (1907, sid. 151 ff), OPPERMANN (1924, sid. 346)

och senast av HATT (1931, sid. 134) beskrivna rotvältorna från de jylländska hedarna. — Deras ålder kan icke ens tillnärmelsevis bestämmas, såsom fallet är med vissa jylländska rotvältehogars (se HATT I. s.), men eftersom de icke innehålla spår av oförmultnat virke, torde åldern få räknas i åtskilliga århundraden.

**Föryngringen.** Bokskogens reproduktion sker som en typisk luckföryngring, en föryngring i stormluckor, torrskogsluckor och hyggesluckor under biologiskt sett ganska varierande förhållanden. Samma generella och i naturskogen vanliga föryngringstyp har nyligen av SERNANDER (I. c., sid. 58 ff) uppskisserats från granskogen i Granskär och Fiby urskog i Uppland. På den torra mullmarken på Timmesöbjerg synas olika lucktyper ge olika föryngringsresultat. Den rikaste föryngringen uppkommer i torrskogsluckorna, där uttorkningen till en början icke blir så extrem och där till en tid ingen generande ansamling av förnamaterial äger rum. — Karakteristiskt för denna lågföryngring är även, att plantmaterialet i stor utsträckning är äldre än resp. luckor och att sedan luckan uppstått endast få plantor tillkomma.

Föryngringen på Timmesöbjerg är ur skoglig synpunkt icke tillfredsställande, ty ehuru åtskilliga plantor förekomma såväl i luckorna som inne i den slutna bokskogen, visa de genomgående en markant oväxtlighet, närmast påminnande om tallplantornas på de norrländska hedmarkerna (Fig. 9). Detta trots att marktillståndet ur kemisk och fysikalisk synpunkt synes vara mycket fördelaktigt och under de mångestadies goda ljusförhållandena borde lämna en förstklassig föryngring. Den bästa föryngringen finna vi på bergets östra sida, under det att däremot de starkt exponerade luckorna i söder och väster även som den rika mulljorden inne i skogen har en synnerligen otillfredsställande återväxt. Ur föryngringssynpunkt särskilt otjänliga områden äro de mot söder exponerade, förbrända luckorna samt områdena runt trädstammarna — trädbaseafiderna —, där torrheten är den helt dominerande föryngringsfaktorn. Koncentrationer av unghplanter förekomma f. n. endast ytterligt begränsat, varemot man kan konstatera föryngringsvillighet i de c:a 100-åriga luckorna och utefter ett par äldre lågor (se ovan). Att denna lågföryngring icke är ett tillfälligt fenomen framgår av de tydliga rader av medelålders bokar, som finns särskilt i områdets västra delar (se kartan Tavla I).

Ett närmare studium av föryngringsförhållandena på Timmesöbjerg har lämnat som resultat, att trenne faktorskomplex kunna sägas bestämma föryngringsresultatet här. Det goda mulitillståndet, kalkhalten och det höga  $p_H$ -värdet är ett faktorskomplex, som gynnar föryngringen under givna och gynnsamma ljusförhållanden. Där emot försvåras föryngringens uppkomst och vidare utveckling väsentligt genom den svåra vår- och sommartorkan samt genom förekomsten av en rik svampflora av aggressiva parasitsvampar.

I ett tidigare arbete (LINDQUIST 1931) har jag påpekat, huru kalkhalten synes i mycket bestämd riktning påverka föryngringsresultatet på bokskogens naturliga ståndorter: på kalkfattiga och kalkfria marker blir bokens självföryngring utan speciella markberedningsåtgärder svag, men ju mera  $p_H$ -värdet stegras desto större plantantal erhåller man per arealenhet, desto mera lättföryngrad blir marken. Enligt dessa mina tidigare undersökningar skulle per hektar på de neutrala bokskogs-

markerna i Skåne och Danmark i normalt gallrad, mogen bokskog utan särskild markberedning finns c:a 28.000 plantor. Även om denna siffra endast får anses vara ett uttryck för medeltalet hos det material, som den gången förelåg, och man därför har all anledning att här vänta en vid variation, så har denna regel vid senare undersökningar i saken visat sig gälla för alla mera normala fall d. v. s. då ingen annan faktor på mullmarkerna blir minimifaktor.

Föryngringen på Timmesöbjerg lyder alls icke denna allmänna regel. Den är icke särskilt riklig; enligt taxering förekommer på mullmarken 11.500 plantor pr har, på den förbrända mullmarken 3.700 plantor, och på råhumusen endast 450 plantor pr har, allt räknat inom områden, där garantier finns för att ljusfaktorn icke är i minimum. Plantantalet är alltså betydligt ringare än vad som tidigare kunnat konstateras som medeltal och därtill är plantornas tillväxt abnormt låg. Föryngringstypen stämmer emellertid icke heller med den, som domineras de verkligt sura mullmarkerna, ty där är plantantalet pr hektar under samma förhållanden mycket starkare nedpressat, under det att däremot de mera enstaka plantor, som väl stabiliseras på denna mark, icke visa någon tillväxtstagnation, utan gå upp vid passande ljustillträde. — Talrika iakttagelser över huru ungplantorna på Timmesöbjerg under stark solexposition på våren vissna och dö synes ge ett tydligt belägg för att föryngringen där hålls tillbaka av i första hand den starka vår- och försommartorkan. Nederbördens på Möens klint är för danska förhållanden relativt låg, och verkan av den nederbörd, som faller på Timmesöbjerg försvagas ytterligare genom den starka expositionen och bergets utomordentligt effektiva dränering. Den härigenom skapade starka uttorkningen sätter sin prägel på humustäcket, på fältskiktsvegetationen och därvid även på föryngringen. Enbuskarnas förekomst till och med i den slutna, örtrika bokskogen på typisk mullmark och deras utveckling i örtvegetationen även i obetydliga luckor är ett klart uttryck för denna uttorkning. Härigenom erhålls ytterligare kraftigt stöd för teorien, att vår- och sommartorkan är huvudorsaken till föryngringssvårigheterna. Detta stämmer väl överens med den förklaring på det analoga norrländska tallhedproblemet, som för icke länge sedan lämnats av HOLMBÄCK (1932, sid. 174 ff), vilken framhåller att sommartorkan på hedarna är den primära orsaken till tallplantornas tillväxtstagnation och hedarnas föryngringsvillighet. Samme författare påpekar vidare, att lågornas betydelse för föryngringen väsentligen ligger i en genom lågorna förbättrad vattenhushållning i marken. — Skillnader mellan den starkt uttorkade marken under bokarna på Timmesöbjerg och den något fuktigare marken invid lågorna och i enbuskagerna har jag kunnat konstatera varje vår under åren 1935—37. — Däremot torde kväveomsättningen för föryngringsgången på mullmarken på Timmesöbjerg icke spela någon avgörande roll, vilket tydligt framgår av de kväveanalyser, som företagits på dessa mullmarker, vilka i regel visa tillfredsställande till god nitrifikation. — De faktiska iakttagelserna över föryngringen på Timmesöbjerg och de helt analoga förhållandena på tallhedarna synes mig styrka HOLMBÄCKS forskningsresultat beträffande orsakerna till tallhedsföryngringens utveckling. Markens extrema torrhet torde vara den enda gemensamma faktorn i dessa biologiskt vitt skilda naturtyper.

En ytterligare faktor, som ogynnsamt påverkar bokens normala föryngring på Timmesöbjerg utgör den synnerligen rika flora av parasitsvampar, vilken i utförda kulturförsök visat sig snabbt döda granplantor eller nedsätta deras tillväxt. Vi har skäl att antaga, att dessa svampar uppträda på samma sätt gentemot bokplantor, eftersom det kunnat konstateras en rik intracellulär infektion av de undersökta bokrötterna. Bland de på Timmesöbjerg vanligaste parasitsvamparna märkas *Mycelium radicum atrovirens* Melin, *M. r. nigrostrigosum* Hatsch (massuppräddande), *Mycelium* 17 a och 19 f (LINDQUIST 1937, sid. 30 ff) samt *Mucor Ramannianus* Möller och ett mycelium snarlikt det, som förekommer i de nedre delarna av den norrländska stavagranråhumusen, möjligt en *Cortinarius*-art (se härom vidare LINDQUIST l. c., sid. 308). Dessa svampar och deras betydelse behandlas ytterligare å sid. 22.

Ännu en föryngringsform förekommer på Timmesöbjerg, vilken tidigare i förbigående omnämnts, nämligen bokens föryngring genom rotskott<sup>1</sup> och stubbskott. Denna föryngringstyp hos boken har tidigare omnämpts från de engelska bokskogarna på kritgrund av A. S. WATT (1925, sid. 48). En regional översikt av denna föryngringsforms uppträdande i den skandinaviska bokskogen oberoende av kreatursbetet ger vid handen, att den är en ganska sällsynt företeelse i den normalt behandlade skogen, där den i huvudsak förekommer på bokens subneutrala<sup>2</sup> ständer. Bokens förmåga att från stambasen eller rothalsen utveckla skott synesstå i intimaste samband med markens kalkhalt och allmänna näringstillgång. I hårt betad skog bli förhållandena andra; där kan en utbildning av sådana rotskott ofta komma till stånd oberoende av marktypen.

Rotskott på boken förekomma rikligt på berget, i alla åldrar och utvecklingsstadier som en normal företeelse, trots att betningen varit avlyst ur skogen i mera än ett århundrade. Ett 80-tal av de äldre stammarna kunna med säkerhet konstateras ha uppkommit som rotskott eller stubbskott. Denna föryngringsform ger boken på dessa marker en ytterligare möjlighet i konkurrensen med andra trädslag och torde möjlichen vara en av huvudorsakerna till att detta trädslag tidigt blivit allenarådande i Möens klinteskov (se VAUPELL 1863, sid. 268). Ett extremt fall av denna förmåga av reproduktion på vegetativ väg visar bild 11.

### Kapitel III. Humusformer och markprofiler.

(Härtill fig. 15—21, tavl. X—XIII).

**Humusformerna.** För beskrivningen av de synnerligen komplicerade pedologiska förhållandena på Timmesöbjerg har jag begagnat en terminologi, som i väsent-

<sup>1</sup> Med rotskott betecknar jag här de skott, som utgå från trädbasen, från övergångsområdet mellan rot och stam.

<sup>2</sup> En gemensam beteckning för svagt sura-alkaliska jordar och ständer (se DU RIETZ 1930, LINDQUIST 1931).

liga stycken avviker från den i den skandinaviska skogliga litteraturen allmänt nyttjade, sådan denna föreligger, t. ex. hos HESSELMAN (1926) och i Beretning fra Nordisk Jordbrugsforskeres Kongres i Helsingfors (1929). En ingående motivering av de orsaker, som tvingat mig till ett försök att länka in humusterminologien på nya linjer, kan här av utrymmesskäl icke lämnas, utan får anstå till ett senare specialarbete. Nedan måste jag inskränka mig till att genom definitioner klarrätta min ställning till termer och begrepp inom den moderna skogliga markläran — till förståelse av här lämnade beskrivningar av markprofilerna.

I överensstämmelse med Kongressens kommitébetänkande av år 1929 upptagas här de trenne terrestra humusformerna, förnan, mullen och råhumusen, medan ärenot måren slopas som särskild humusform. Förna användes i den mening, som HESSELMAN (1912, sid. 38) och SERNANDER (1918, sid. 646) givit denna term, nämligen som en sammanfattning av de döda växt- och djurresterna, som avlagrats på markytan. Ovannämnda kommittés definition liksom en av HESSELMAN senare (HESSELMAN 1926, sid. 205) lämnad definition, enligt vilken förnan skall bestå av de »oförändrade<sup>1</sup> döda resterna eller avfallsprodukterna ur växt- och djurriket», synes mig icke vara hållbar, emedan snart sagt allt det växtmaterial, som årligen tillföres marken, är förändrat. Förneskiktet kallas i det följande i överensstämmelse med vedertaget bruk beträffande mull och råhumus för förna (se t. ex. HESSELMAN 1926, sid. 207), varmed betecknas det skikt, vars huvudmassa utgöres av fornematerial. — Förnan indelas här ytterligare efter graden av sammanhållning mellan dess beståndsdelar i lösförna och filtförna. Med lösförna vill jag därvid beteckna det lösa skiktet av i huvudsak bladmateriel, som SERNANDER kallat fallförna, jämte de löst sammanfogade, av svamphyfer icke sammanfiltade mossbaserna (SERNANDERS bottensorna) samt med filtförna den del av förnan, fallförnan och bottensornan, som sammanfiltats genom svamphyfer till en sammanhängande humusbildning. En ytterligare indelning av förnan, som här användes parallellt med ovannämnda, ger den Sernanderska tredelningen i fallförna, bottensorna och markförna (SERNANDER 1918, sid. 650 ff). — HESSELMANS förmultningsskikt (HESSELMAN 1926, sid. 207) räknar jag till förnan och icke såsom HESSELMAN till råhumusen eller mullen.

Råhumus har i detta liksom i ett tidigare arbete (LINDQUIST 1931, sid. 218) använts som en beteckning för det amorfa, icke mineralinblandade, ofta strukturlösa humusskiktet i P. E. MÜLLERS »mor».

Mull har använts i den inskränkta bemärkelse, som P. E. MÜLLER gav den (MÜLLER 1878, sid. 10). För mellanformen mellan mull och råhumus, den svagt mineralinblandade, grynpig till korniga humusen, har icke SERNANDERS term »mår» kunnat användas (se härom bl. a. ROMELL 1934), emedan den alltför ofta givit anledning till förväxling med P. E. MÜLLERS »mor», som är råhumus. Denna intermediära bildning har här förts in under mullbildningarna på grund av sin struktur och relativt höga halt av mineraljord och har för undvikande av framtida missförstånd belagts med en ny term, råmull, vilken alltså avser att omfatta de korniga

<sup>1</sup> kursiverat här.

till grynpjölen, svagt mineralinblandade mulljordarna. — De mera humusfattiga mullformerna betecknas här i analogi med den HEIBERG-ROMELLSKA terminologien (HEIBERG och ROMELL 1931) efter skillnaderna i struktur och benämns grovmull och finmull.

Olika varianter av dessa tre terrestra humusformer, förnans, mullen och råhumusen, konstituera i skilda kombinationer humustäcket i de skandinaviska skogarna. I vissa fall bildas hela humustäcket av en enda av dessa humusformer (t. ex. mullmarken i vissa ängar, förnarker i vissa myrtillusskogar i Norrland, amorf råhumus i klippspringor), i andra fall konstitueras humustäcket av två eller tre av dessa humusformer jämte deras varianter i bestämd lagerföljd (t. ex. förna på råhumus i råhumusmarkerna, förna och råhumus på mull på Timmesöbjerg etc.).

Humustäcket i de skandinaviska skogarna har emellertid hittills betecknats antingen som mull eller som råhumus(mor) och förnans närvaro eller frånvaro eller dess utbildning har därvid icke beaktats, ehuru den av ovannämnda jordbruksforskningskommitté anförlts som en humusform. Ett mera allmänt hänsynstagande till förnans såsom humusform synes mig desto mera berättigat, som stundom hela humustäcket kan utgöras av enbart förna. En genomförd samordning av förnans med mull och råhumus ger även en bättre översikt över mullens och råhumusens morfologi och en lösning synes möjlig ur det konfliktläge, som uppstått kring klassifikationen av de sammanfiltade förnebildningarna, vilka för närvarande uppfattas som en del av råhumusen.

**Metodik.** Den metodik enl. vilken den kemiska analysen av ifrågavarande jordar skett är för  $p_H$ -bestämningarna en kolorimetrisk metod enl. GILLESPIE (1916). Bestämningarna äro i övrigt gjorda för Ca som med NaCl utbytbart kalcium (ARRHENIUS, opublicerad metod), K enligt RIEHM (1935),  $NO_3$  enligt RIEHM (1930) och  $P_2O_5$  enligt ARRHENIUS (1929). Detta gäller för de analyser, som utförts på d:r OLOF ARRHENIUS laboratorium på Kagghamra. Analyserna från tidigare år ha samtliga utförts på Carlsbergslaboratoriet i Köpenhamn, varvid den hos mig (LINDQUIST 1931, sid. 214 f) tidigare anförda metodiken kommit till användning. Metoderna ha sålunda varierat för bestämningen av ett och samma kemiska komplex och värdena bli alltså teoretiskt sett icke fullt jämförbara. De torde likväld vara tillräckligt användbara för de jämförelser, vartill materialet här använts.

**Förnan. Omvandlingen** Förförnan täcker stora delar av Timmesöbjerg, den saknas eller är svagt utbildad endast på de starkare exponerade partierna av berget eller i dess alltför branta sluttningar. Den består till huvudsaklig del av bokblad, kvistar, knoppfjäll och fruktskålar av bok i alla stadier av förmultning samt därjämte av fältskiktets sedentära fallförna. Dessutom förekommer, där marken är täckt av mossor, en bottenförna av mossrester och en markförna av döda rötter och svamphyfer. Fallförnan är dominerande och egentligen ensamt skiktbildande, under det att ändemot bottenförnan och markförnan aldrig dominera något humusskikt och därfor icke bli av väsentlig betydelse för skiktens eller profilens karaktäristik.

På de normala mullmarkerna i icke exponerade lägen förekommer förförnan

huvudsakligen som ett löst och luckert lager på mullen, ett lager som icke har fast sammanhang med underliggande delar av humustäcket och som under vissa omständigheter lätt kan avlägsnas från underlaget. Den utbildas som lösförna. Dess tjocklek varierar mellan 3 och 20 cm och den innehåller stora mängder kalk, kali och fosforsyra (se tab. s. 26). Omvandlingen av detta lösförneskikt sker olika allteftersom förnan är avlagrad på normal mullmark eller på filtförna, eventuellt med råhumus. På den normala mullmarken omvandlas förnan förutom av bakterier och daggmask även av insekter, sniglar och snäckor. De tre sistnämnda kategorierna av förnanedbrytare spela likväld ringa roll i förhållande till de båda förstnämnda.

Daggmaskfrekvensen på de normala mullmarkerna på Timmesöbjerg är av samma storleksordning som man i allmänhet funnit på de sydsvenska och danska mullmarkerna (se BORNEBUSCH 1931, tab. II—XIII och JULIN 1937, sid. 68). Nedanstående tabell ger en översikt över frekvensen och artsammansättningen hos daggmaskfaunan pr kvadratmeter på skilda humustyper på Timmesöbjerg.

Daggmaskfaunan är icke artrik, men maskarna förekomma i tillräckligt hög frekvens för att under någorlunda normala fuktighetsförhållanden omvandla förnan till amorft material. *Lumbricus*-arterna uppträda sällsynt. De ersättas av *Allolobophora caliginosa*, som enligt BORNEBUSCH är de danska mullmarkernas vanligaste daggmask och *A. longa*, båda två ganska effektiva mullbildare. Dessutom förekomma rikligt *Eisenia rosea* och *Dendrobaena octaedra*. — *Lumbricus*-arterna och *Allolobophora*-arterna äro de förnämsta mullbildarna, *Eisenia* förekommer visserligen ganska rikligt, men är en liten art, som för mullbildningen är av mindre betydelse, och *Dendrobaena* får i detta avseende anses mycket ineffektiv (se BORNEBUSCH l. c.). — Vid starkare uttorkning av mulljorden minskar maskfrekvensen och de maskar, som erhållits från sådana partier, ha ofta en starkt nedsatt vitalitet. Sålunda kunna även smärre, ogynnsamma förändringar i markens fuktighetstillstånd hämma förnaomvandlingen genom att omöjliggöra maskarnas verksamhet. Under de kraftiga torrperioderna på våren och sommaren går masken djupare ned mot kritgrundens och synes ligga i fullständig vila. Däremot har jag i mars, april och augusti under fuktiga perioder funnit den i full verksamhet i övre delarna av mullen.

Förutom daggmaskarna deltaga, som ovan nämnts, insekter, snäckor och sniglar i omvandlingen av förnan. Insekternas roll för omvandlingen har jag icke studerat och här kan endast lämnas en allmän uppgift om ett rikt insektsliv i förnan och rikligt med insektsexkrementer framför allt i de mäktiga filtförnelagren. Insekternas betydelse för förnaomvandlingen är sannolikt mycket stor, framför allt för omvandlingen av de här abnorma förneskikten.

Sniglarna äro ganska sällsynta i förnan och på mulljorden och spela ganska ringa roll för förnaomvandlingen. Sällsynt förekommer *Arion circumscriptus* och *A. reticulatus*. Markens torrhets gynnar icke uppträdet av någon rikare snigelfauna.

Snäckornas betydelse för omvandlingen har jag däremot närmare studerat. Snäckfaunan på berget är mycket artfattig men individfrekvensen är hög (se tabellen, sid. 21). Allmänt förekomma *Cepaea hortensis*, *Helicigona lapicida* och *Cochladinia*

## Tabell

över förekomsten av daggmask på skilda humustyper på Timmesöbjerg. Antal pr. m<sup>2</sup>.  
(beträffande de undersökta skiktens mächtigkeit se tab. sid. 39—51).

Tabelle über das Vorkommen von Regenwürmern auf verschiedenen Humusböden auf dem Timmesöbjerg. Anzahl pr. m<sup>2</sup>. Mächtigkeit der untersuchten Schichten siehe Tabelle S. 39—51.

Humusform	Pro- vyta nr.	Lum- briucus sp.	Allolobophora		Eisenia rosea	Dendro- baena	Smärre obe- stämbbara former Kleinere unbe- stimmbarer Formen	S : a	Medel- tal Mittel
			longa	cali- ginosa					
Grovmull . . . . .	7	4	—	17	26	—	—	47	
	8	—	48	21	—	—	80	149	
	9	1	12	153	5	—	48	219	
	10	—	—	31	10	107	25	173	147
Forbränd grovmull . .	6	—	—	119	—	—	—	119	
	7	—	—	—	—	—	—	0	
	8	—	—	21	—	—	11	32	50
Lösförna-filtförna- grovmull . . . . .	4	—	—	11	2	—	7	20	
	5	—	—	76	8	13	15	112	
	6	—	—	22	43	—	20	85	72
Lösförna-filtförna- rähumus . . . . .	3	—	—	3	—	—	—	3	
	4	—	—	—	—	—	—	0	
	5	—	—	—	—	—	11	11	5
Rähumus . . . . .	3	—	—	—	—	—	—	0 <sup>1</sup>	
	4	—	—	—	—	—	—	0	
	5	—	—	—	—	—	—	0	
	6	—	—	—	—	—	—	0	
	7	—	—	—	—	4	—	4 <sup>2</sup>	
	8	—	—	38	—	1	18	57	10
Rämull . . . . .	8	—	—	—	—	—	—	0	
	9	—	4	25	4	—	—	33	
	10	—	—	20	—	35	25	80	
	11	—	—	—	—	—	—	0	28

<sup>1</sup> I underlagranda rämmullen 12 st. Allolobophora caliginosa.

<sup>2</sup> I underlagranda mullen 22 st. Allolobophora caliginosa.

*laminata*, mindre allmänt *Helix arbostorum*, *Ena obscura* och *Trichia hispida*. Under fuktiga perioder angripa dessa förnematerialet, framför allt fältskiktsvegetationens sedentära förna och bidraga till dess nedbrytning och angripa dessutom enstaka förekommande hattsvampar. Under torrperioder och under soliga dagar vandra snäckorna dock främst från marken allmänt upp i bokarna, så att förnan och mullen då synas vara helt fria från dessa djur. Orsakerna till deras vandringar har icke

kunnat utrönas. — För erhållande av en allmän uppfattning av snäckornas frekvens ha samtliga snäckor på de nedre delarna av ett antal bokstämmar på berget räknats, upp till en stamhöjd av 3 meter. Resultatet av denna inventering föreligger nedan. Det skall emellertid framhållas, att det därigenom erhållna värdet pr stam icke representerar totalantalet snäckor, eftersom frekvensen icke nämnvärt synes avtaga uppåt stammen.

### Tabell

över förekomsten av levande snäckor på bokstammarna på Timmesöbjerg. Uppgifterna gälla antalet snäckor på stammen upp till 3 meters höjd.

Tabelle über das Vorkommen von lebenden Schnecken auf Timmesöbjergs Buchenstämmen.  
Die Daten geben die Anzahl der Schnecken bis zu 3 Meter Stammhöhe.

Nr.	Stam-diam. i brh.	Cepaea hortensis		Heli-eigona lapicida	Cochla-dinia laminata	Ena obsecura	Summa	
		fullvuxna	ungar				Stora former	Total
1.....	13 cm	2	6	4	2	1	6	15
2.....	13 cm	—	8	2	—	—	2	10
3.....	17 cm	2	12	4	4	—	6	22
4.....	20 cm	—	8	6	2	0	6	16
5.....	21 cm	—	22	14	—	6	14	42
6.....	22 cm	2	66	24	—	—	26	92
7.....	28 cm	10	120	48	16	—	58	194
8.....	37 cm	26	42	52	10	—	78	130
9.....	37 cm	—	71	46	2	3	46	122
10.....	43 cm	2	72	70	2	—	72	146
11.....	53 cm	5	17	22	1	—	27	45
12.....	61 cm	40	210	128	20	—	168	398

En grov beräkning över totalantalet snäckor inom det karterade området, med hänsyn tagen till dimensionsfördelningen, ger omkring 50.000 st.

Lösförnan har en såväl morfologiskt som mikrobiologiskt annan karaktär än filtförnan. Den förra utgör ett löst och luckert lager, utan fastare sammanhang med humusprofilens undre delar; dess mikrobiologiska omsättningstyp är övervägande bakteriell. Filtförnan är däremot alltid mer eller mindre sammanvävd genom svamphyfer, den har ett fastare samband med underlagrande humusskikt och dess mikrobiologiska omsättningstyp är fungid. Lösförnan utgöres på Timmesöbjerg av bokblad, knoppfjäll, fruktskålar och kvistar av bok och dessutom av den s. k. *megaxyla* förnan d. v. s. av döda, stormslagna träd och fallna torrträd, vilka såsom lågor tillhörta marken och äro under nedbrytning. Härtill kommer som ett viktigt moment fältskiktsvegetationens sedentära förna. Lösförnan förekommer genomgående som ytlager på humusbildningarna på Timmesöbjerg, men saknas på sådana lokaler, där dess kvarliggande omöjliggöres av en för stark exposition. Normalt bildar den således ett lager på mullen i den normala mullprofilen och på filtförnan i råhumusprofilen.

*Filtförfan*, som i stort sett motsvarar HESSELMANS F-skikt (HESSELMAN 1926, sid. 207), har till sin typ ovan karakteriseras. Dess beståndsdelar äro desamma som lösförnans, men i regel i starkare sönderdelning och med fastare samband inbördes och med underlaget. Dess förekomst och utbildning är beroende på förlängsammad omvandling av fornematerialet till amorf humus, vilket här orsakas antingen av extrem uttorkning eller extrem anhopning av fornmaterial eller bådadera. Om-sättningen, sådan den fått sitt uttryck i nitrifikationen, är starkt hämmad i den mulljord, på vilken filtförfan är under utbildning; men den kan bli livlig om filtförneskiktet av en eller annan anledning håller på att avvecklas.  $p_{\text{H}}$ -värdet är genomgående något högre i filtförfan än i lösförnan. Nedan, sid. 29 ff skall närmare redogöras för de omständigheter under vilka filtförfan här utbildas och dess roll för utbildningen av råhumustyperna. — Den för filtförfan karakteristiska svampfloran domineras av *M. r. nigrostrigosum*, *M. r. atrovirens*, *Corticium croceum*, jämte de av mig tidigare beskrivna *M. 19 f* och *M. 17 a* (se ovan sid. 16), vilka synas vara ogynnsamma för bokrötterna. Mykorrhiza utbildas stundom — genom bl. a. *M. r. nigrostrigosum* och *M. 19 f* — men blir merendels förkrympt, varjämte *M. r. nigrostrigosum* synes angripa rötterna intracellulärt. Svampfloran är i många fall av samma typ som den svampflora, man finner i förneskiktet hos starkt degenererade norrländska råhumusformer och når kvantitativt samma rika utbildning som denna. Särskilt anmärkningsvärd är massförekomsten av *M. r. nigrostrigosum*, som starkt gynnas av extrem uttorkning (HATSCH 1937).

**Humusbildning ur färskt växtmaterial.** Skildringen av förnan och dess omvandling skall avslutas med påpekandet, att icke all amorf humusbildning nödvändigtvis måste utgå från ett fornmaterial. Stundom kan nämligen en ansamling av amorf humus ske på markytan med utgångspunkt direkt ur färskt växtmaterial. Detta är ett allmänt förhållande, som icke på något sätt är karakteristiskt för Timmesöbjerg, men det har även iakttagits där och omnämnes av den anledningen. — Omedelbart efter bokens lövsprickning angripes så t. ex. de nyutsprungna bokbladen av en *Cheimatobia*-art, vilken särskilt våren 1935 härjade där, varvid ansenliga kvantiteter färskt boklöv direkt omsättes till humus. Detta angrepp upphör visserligen vad boken beträffar redan då bokbladen mista sin första ljusa grönska och bli hårdta och mindre smakliga för larverna, snäckorna, insekter m. fl. Men i fältskiktsvegetationens gröna delar finnes för larver, insekter och snäckor ett gott näringssubstrat i form av *Primula*-blad, *Primula*-stjälkar, *Mercurialis*-blad, *Actaea*-blad, blad av unga bokplantor samt hattsvampar. På hösten vittnar den starkt avbetade fältskiktsvegetationen om dessa djurs verksamhet.

**Råhumusen.** Råhumus har på åtskilliga ställen på Timmesöbjerg kommit till utbildning under filtförfan. Redan filtförnans förekomst tyder på en stagnation i fornematerialets omvandling till amorf humus och på maskfaunans ineffektivitet inom sagda områden. Nedgången i maskarnas frekvens och effektivitet synes på dessa lokaler väsentligen bero på markens torrhets. På den normala mullmarken är maskstammen tillräcklig för fornematerialets omvandling, men den uttorkning, som in-

träder genom markens direkta eller indirekta exponering för sol och vind genom att krontaket på ett eller annat sätt brytes, åstadkommer en stark reduktion av maskarnas antal och vitalitet (se tab. s. 20). På en sådan otjänlig mark ansamlas genom döda trädgrenar eller genom en vegetation av enbuskar högar av förna, vilka väsentligen hindra den normala nederbördens tillträde till mullen. Denna bibehåller därigenom sin stora torrhet. I och med att maskarnas frekvens hålls nere vid ett minimum och en abnorm förneanrikning inträder, skapas betingelser för utbildning icke blott av en typisk filtförna utan även för dennas överförande i en råhumus. På normalt fuktiga, subneutrala mullmarker behöver man emellertid icke riskera denna råhumusbildning även vid en kraftig filtförnebildning, emedan den normala fuktigheten skapar utmärkta betingelser för ett rikt daggmaskliv. Sådana förhållanden kunna observeras i många av de sydsvenska och danska kulturgranskogar, där mull underlagrar en tjock filtförna och typiska exempel härpå finna vi i Timmesöbjergs närhet i de för Möens klint så typiska »jordfallshullerne», på vilkas botten ofta en mäktig förneansamling skett, kanske i många fall dubbelt tjockare än den tjockaste fornana på Timmesöbjerg, men där likväl ingen råhumus utbildas.

Råhumusen är i sina övre delar fibrös, d. v. s. i den amorfa grundsubstansen finns fortfarande ganska stora mängder fibröst material. I sina nedre delar har den ärenemot som regel övergått till en helt amorf bildning. Dess uppkomst beror till övervägande grad på de insekter, som i största mängd förekomma såväl i fornana som i humusen. Den vanligast förekommande råhumusen är en gryning, amorf råhumus, i sina övre delar mera lucker, i de nedre ofta fast.

Råhumusen innehåller rikliga mängder mineralsalter och fosforsyra. Nitritifikationen är ärenemot i regel svag framför allt i den helt amorf typen utan överlagrande filtförna. Surhetsgraden ligger i denna råhumustyp vid neutralpunkten med funna värden mellan 5.7 och 7.4 (se tab. sid. 45, 47).  $p_H$ -värdet synes vara något lägre i ytskikten, i filtförnan och i den mera fibrösa råhumusen, ärenemot högre och stundom överskridande neutralpunkten i råhumusens djupare, starkt amorf skikt. En bestämning av humushalten i denna råhumus har gjorts med värden varierande mellan 89 och 96 % humus mot 8–23 % för mullen. Den direkta orsaken till att denna råhumusbildning har subneutral reaktion torde vara förnamaterialets höga  $p_H$  och den stora impregneringen av kalkstoft, som följer av exponeringen (se HINTZE 1937, sid. 299 f).

Råhumusen innehåller stora mängder svamphyfer av delvis samma slag, som förut beskrivits för filtförnan. Dominerande uppträder *Mycelium r. nigrostrigosum*, som här har en abnormt rik förekomst, och den basidiomyiset, som jag tidigare omnämnt från norrländsk stavagranskog och förmodat vara en *Cortinarius*-art. Denna har ställvis angripit råhumusen och förtärt den, kvarlämnande endast ett gulvitt mjöl (se fig. 19). Även levande rötter, mull och stora stenar få genom denna svamps angrepp en grågul till gulvit färg. Svampen synes vara en vitrötesvamp med kraftigt destruerande inverkan på humus. En analys av den humus, som angripits av svampen i jämförelse med bredvidliggande oangripen humus visade följande:

	Nitrat	strax	30 dagar	P <sub>2</sub> O <sub>5</sub>	pH
Angripen humus . . . . .	...	0	70	2	5.2
Oangripen humus . . . . .	...	9	645	24	7.7

Den subneutrala råhumusen på Timmesöbjerg har sålunda utbildats under förhållanden, som till synes skulle indicera mullbildung. De faktorer som bestämt dess utbildning äro den extrema torrheten och den abnorma förneansamlingen. Den förekommer fläckvis på kalotten på Timmesöbjerg och synes vara inskränkt till äldre luckor i beståndet (se fig. 16). Det är en för denna mark fullt naturlig företeelse.

**Mullen.** Mullen på Timmesöbjerg innehåller flera undertyper. Den vanligaste typen, som omfattar större delen av området, benämnes här grovmull tack vare sin utpräglade klumpstruktur med grova klumpar. Den mera finfördelade mullen kallar jag finmull. Skild från dessa förekommer en humusrik mullform, råmullen, karakteriserad av hög humushalt och grynstruktur. Den motsvarar närmast SERNANDERS mår.

Råmullen är en mullform, som uppkommer såsom ett direkt stadium i utvecklingen av råhumusen mot vanlig mull. Den kommer till utbildning i första hand på sådana råhumusmarker, som genom förbättrade läförhållanden, belysningsförhållanden och bevattningsförhållanden kraftigt omsatts och luckrats, under medverkan av daggmask. De daggmaskar, som därvid äro verksamma, äro i första hand *Allolobophora caliginosa* och *Dendrobaena octaedra*, vilka båda gynna en utbildning av råmull ur råhumusen.

Råmullen har, som ovan nämnts, korn- eller grynstruktur, är tydligt men svagt mineraljordsblandad och har här en humushalt mellan 55 och 85 %. Den äger en svampflora av liknande sammansättning som i föregående fall. Kalk-, kali- och fosfathalten är i råmullen av samma storleksordning som i råhumusen (se tab. s. 26), medan däremot en mycket kraftig nitrifikation tyder på starkt ökad omsättning i råmullen. pH-värdet har stigit i förhållande till råhumusens pH-värde och har i medeltal passerat neutralpunkten. — Bildningen motsvarar direkt de mellanformer mellan råhumus och mull, som tidigare beskrivits som mårformer på sura, humusrika marker i mellersta och norra Sverige (se t. ex. SERNANDER I. c., HESSELMAN 1926). Typen har i nästan lika hög grad som råhumusen ansetts karakterisera ett surt substrat. Här förekommer den emellertid på ett alkaliskt underlag och har själv oftast alkalisk reaktion.

Grovallen på Timmesöbjerg visar kemiskt och biologiskt en ganska stark variation. Den förekommer dels med ytlig lagring således utan överlagrande förna inom områden, där stark exposition eller terrängens stora lutning undanskaffat förnan, dels under ett lösförneskikt — den normala situationen för mullen i de skandinaviska bokskogarna — dels under lösförna med filtförna och slutligen under råhumus eller råmull.

Den ytligt exponerade mullen blir ofta uttorkad, framför allt om den är direkt exponerad för solljuset. Klumpstrukturen kan vid exposition för nederbödsvattnet förstöras i ytan — ehuru icke på långt när lika effektivt som hos vanliga sandiga till svagt leriga mulljordar — och den biologiskt betingade aktiviteten sjunker därmed. Samtidigt sker på de exponerade markerna en snabb urtvättning av mineral-salterna i övre delen av mullen, halten av fosfat, kalium och kalcium visa nedgång i förhållande till värdena i den normalt förnetäckta och beskuggade mullen. Däremot sker ingen nedgång i denna solexponerade och urtvättade mullmarks  $p_H$ -värde i förhållande till den normala mullmarkens.

Den normala grovmulljorden, överlagrad av en ganska tunn lösförna, har på hela berget en mycket lucker struktur, samtidigt som de enstaka klumparna besitta en avsevärd hårdhet. Den är en typisk grovmull, är genomgående starkt uttorkad och av ovanlig mäktighet. I sina nedre delar är den kritbemängd och vilar direkt på kritgrunden. En slamning av mulljorden, vilken välvilligt utförts vid Sveriges Geologiska Undersökning i Stockholm har givit till resultat, att denna mulljord har hög lerhalt, vilket delvis förklrar den utpräglade klumpstrukturen. Tvenne analyser av mullen i lösförna-mull-profilen gav följande värden:

	Prov. I	Prov. II
Finjord (under 2 mm) . . . . .	100 %	100 %
Grovsand (2—0.6 mm) . . . . .	3.0 -	3.5 -
Mellansand (0.6—0.2 mm) . . . . .	24.0 -	25.8 -
Grovmo (0.2—0.06 mm) . . . . .	15.9 -	16.7 -
Finmo (0.06—0.02 mm) . . . . .	5.5 -	4.9 -
Grovmjäla (0.02—0.006 mm) . . . . .	6.9 -	6.9 -
Finmjälja (0.006—0.002 mm) . . . . .	15.9 -	18.7 -
Ler (< 0.002 mm) . . . . .	28.8 -	23.5 -

Samtidigt var humushalten bestämd genom glödförlusten för det första provet 22.9 % och för det senare 19.6 %, vilket i båda fallen representerar högre värden än övriga av mig funna (se ovan). Nitrifikationen är den för mulljordar i allmänhet i de torrare mullbokskogarna i Danmark normala, liksom halten av kalk, kali och fosforsyra.  $p_H$ -värdet varierar snävt omkring 7.5.

Den bakteriella omsättningen är av nitrifikationen att döma relativt god. Mullen är emellertid dessutom anmärkningsvärt rik på svampmycelier, vilka stundom om-spinna mullklumparna och utfylla hålrummen mellan dessa. Vanligast av dessa mulljordens mycelier äro *M. r. nigrostrigosum*, *M. 19 f*, *M. 17 a* (se sid. 16), samt dessutom *Trichoderma Koenigii*, *Mucor Ramannianus* och vissa *M. r. atrovirens*-liko mycel. Flera av dessa ha visat sig vara effektiva parasiter på granplantor och kunna på grund av intracellulära angrepp på bokrötterna förmadas vara detsamma på bokplantorna.

Genom ansamling av ris och grenar eller genom uppväxande av enbuskar på denna mullmark uppkommer ofta ett tjockt förnalager på den tidigare genom ex-

position blottlagda mullmarken och en sådan abnorm förneanhopning återställer så småningom till en viss grad den biologiska aktiviteten i humusprofilen. Nitrifikationen ökar, och antalet daggmaskar pr ytenhet, som på de exponerade mullmarkerna är låg, ökar likaledes något. Emellertid blir mullmarkens aktivitet under ett sådant filtförnelager på grund av den fortsatta, kraftiga uttorkningen aldrig så stor, att en mera väsentlig omsättning av den starkt anhopade förnan kan ske.

*Finmull.* När råmullen genom maskars och bakteriers verksamhet ombildas uppstår merendels först en ganska starkt nitrifierande mullform med korn- eller grynsstruktur, en finmull. Den skiljer sig ganska väl från den på berget vanliga grovmullen.

### Tabell

över några medeltal för kemiska karaktäristika i de skilda humustyperna på Timmesöbjerg. (Siffrorna inom parentes ange antalet prov pr. grupp).

Tabelle einiger Mittelwerte der chemischen Charakteristikum in der verschiedenen Humustypen.

	Grovmull under lösförna	Förbränd grovmull	Filtförna i grovmull- profilen	Filtförna i rähumus- profilen	Rähumusens tidigare stadium	Rähumusens senare stadium	Råmull
P <sub>2</sub> O <sub>5</sub> i fosfatgrader...	11 (4)	4 (4)	32 (4)	29 (3)	19 (3)	25 (4)	21 (7)
pH.....	7.5 (7)	7.5 (6)	6.5 (5)	6.5 (4)	7.0 (4)	6.8 (5)	7.2 (9)
Ca-utb. i mg/kg....	600 (1)	400 (1)	290 (2)	720 (1)	800 (1)	850 (1)	700 (3)
K i mg/kg .....	23 (1)	12 (1)	29 (2)	31 (1)	19 (1)	31 (1)	13 (3)
NO <sub>3</sub> i mg/kg (vid 30 dagars lagring)...	37 (6)	45 (6)	96 (3)	200 (2)	45 (3)	2 (5)	111 (9)

### Tabell

över några medeltal för kemiska karaktäristika i grovmullen i skilda markprofiler på Timmesöbjerg. Grovmullen i tabellen i relation till överlagrande skikt. (Siffrorna inom parentes ange antalet prov pr. grupp).

Tabelle einiger Mittelwerte der chemischen Charakteristikum im Grobmull in verschiedenen Bodenprofilen. Die Tabelle zeigt die verschiedenen chemischen Verte des Grobmulls im Verhältnis zu den überlagernden Schichten.

	Icke överlagrad	Överlagrad av				
		Förbränd Grovmull	Lösförna	Filtförna	Rähumus; tidigare stadium	Rähumus; senare stadium
P <sub>2</sub> O <sub>5</sub> .....	4 (4)	11 (4)	4 (3)	7 (2)	8 (4)	9 (6)
pH.....	7.5 (6)	7.5 (7)	7.5 (5)	7.2 (3)	7.5 (4)	7.5 (8)
Ca.....	400 (1)	600 (1)	370 (1)	—	450 (1)	460 (2)
K .....	12 (1)	23 (1)	5 (1)	—	—	7 (2)
NO <sub>3</sub> .....	45 (6)	37 (6)	41 (4)	23 (2)	70 (4)	69 (7)

mullen med dess klumpstruktur och torde här utgöra ett stadium i utvecklingen mot denna. På den blottlagda mulljorden, som icke är under exposition, synes den likvälv vara en mera konstant typ.

**Markprofilerna.** Dessa humusformer på Timmesöbjerg samlas till givna humusprofiler, där dels bokskogens normala mullprofil, förna-mull-profilen, återfinnes och dessutom profiltyper, vilka troligen äro unika och vilka jag icke funnit beskrivna i litteraturen.

Förna-mull-profilen är som lösförna-mull-profil den normalt utbildade humusprofilen i bokskogen. Den består här av en lösförna av 2—10 cm:s tjocklek och därunder av en abnormalt tjock mull — omkring 40 cm — vilken i sina nedre delar är starkt kritinblandad. Den har avlagrats direkt på kritan. Denna profil kan under för omsättningen ogynnsamma markförhållanden övergå i en lösförna-filtförna-mull med abnormalt tjocka förnaskikt.

Ur denna typ kan därefter utbildas en förna-råhumus-mullprofil, till en början med såväl lösförna som filtförna, med ett karakteristiskt amorft råhumusskikt och med en därunder liggande mull. Denna underlagrande mull är lucker och av utpräglad klumpstruktur; den visar en måttlig nitrifikation och innehåller daggmaskar. Denna kombination av råhumus och mull har mig veterligen tidigare icke beskrivits. När en råhumus utbildas på en tidigare mullmark, sker detta vanligen sedan mullen destruerats, och icke längre kan betraktas som mull i MÜLLERS mening. På Timmesöbjerg har emellertid mullen bibehållits till strukturen nära nog oförändrad under råhumusen, varvid ovannämnda profiltyp uppstått. Orsaken till att mullen bibehållits under råhumusbildningen torde i första hand få sökas i substratets låga surhetsgrad, vilken väsentligen torde inverka på klumpstrukturen och omsättningen. Möjligens bidrager denna även att vidmakthålla maskfaunan.

Lösförnan försvinner ganska snart ur sagda profil och så småningom omvandlas filtförnan till amorf råhumus; därmed uppstår en råhumus-mull-profil av samma typ som i föregående fall. Så småningom destrueras råhumusen både från sin övre och sin undre yta, övergår på ytan till råmull och i sina undre delar vidare till finmull. I ett skede av denna utveckling kan profilen bli mycket komplicerad, den blir en råmull-råhumus-råmull-finmull-grovsmull-profil.

## Kapitel IV

### Råhumusbildningen och dess orsaker.

(Härtill fig. 22—29, tavl. XIV—XVIII).

**Mull och råhumus.** Mullbildningens och råhumusbildningens natur ha varit under diskussion alltsedan dessa humustyper är 1878 för första gången klart definierades av P. E. MÜLLER. Principkonflikten MÜLLER—RAMANN blev till att börja med en seger för RAMANN och för uppfattningen av råhumusbildningen som en övervägande kemiskt betingad process. I Skandinavien och framför allt i Danmark har

emellertid MÜLLERS klara framställning av humusformernas biologiska grundvalar skapat en säker basis för den biologiskt orienterade markläran. MÜLLERS verk har i Danmark fullföljts av WARMING (1916—19), BORNEBUSCH (1923, 1930 etc.) och WEIS (1924) och i Sverige har framför andra ROMELL (1934) framfört de biologiska synpunkterna på humusbildningen.

Enligt MÜLLER, WARMING och BORNEBUSCH spela daggmaskarna en väsentlig roll för humusbildningen och även ROMELL framhåller deras stora betydelse, ehuru han synes vara böjd att tillskriva mikrosamhällets typ den avgörande betydelsen för utbildningen av humustypen (l. c. sid. 8). — Omfattande, ännu icke publicerade undersökningar över daggmaskarnas roll för fornans nedbrytning i skogsmarken, vilka jag utfört under åren 1935 till 1937, bestyrka MÜLLERS åsikter i dessa frågor.

**Daggmaskarnas roll för utbildningen av humustypen.** Råhumusbildningen i Skandinavien betingas av frånvaron i humusen av sådana djur, som äga förmåga att effektivt och intimt blanda humus med den underliggande mineraljorden. I våra trakter torde endast daggmaskarna äga en sådan förmåga, under det att i t. ex. Nordamerika även bland insekterna typiska mullbildare uppträda (ROMELL 1935, sid. 67 ff). Alla de faktorer, som begränsa de stora och medelstora daggmaskarnas förekomst kunna i Skandinavien anses bestämma humusbildningens karaktär av mullbildning eller råhumusbildning. Sådana faktorer äro dels klimatiska och dels edafiska. Den allmänna klimattypen, närmare bestämt en sjunkande årsmedeltemperatur, en minskning i den frostfria periodens längd samt en avtagande markfuktighet, torde direkt eller indirekt påverka daggmaskarnas vitalitet och frekvens. Substratets och fornämaterialets kemiska tillstånd, framför allt dess surhet, och fornans biologiska typ torde bestämma den glupskhet med vilken den angripes av daggmaskarna under varierande klimatiska förhållanden. Inom sådana områden, där ett eller flera av dessa faktorskomplex närmar sig och överskrider de normala gränsvärdena för en effektiv daggmaskfaunas existensmöjligheter, kan ett av ett annat faktorskomplex förorsakat särskilt gynnsamt tillstånd ge maskfaunan nya möjligheter att fortleva och mullbildningen att fortsätta. Exempel härpå möta vi snart sagt överallt i Skandinavien. Så kan t. ex. i det mera ogynnsamma nordsvenska klimatet maskarna i huvudsak fortleva på ett kalkrikt eller fuktigt, syrerikt substrat med god tillgång på smakligt fornämateriel, under det att de på samma breddgrader på ett mera kalkfattigt substrat med enbart tillgång på mossförna och barrträdsförna duka under. Likaså kan denna fauna på kalkhaltiga marker utstå vida kraftigare uttorkning än på kalkfattigare marker. År marken moig till lerig och kalkhalten så hög, att  $p_H$  stiger över ett värde av omkring 5.5 torde möjligheterna för råhumusbildning i sydskandinaviska skogsmarker överhuvudtaget vara mycket små även under för mullbildningen i övrigt ogynnsamma omständigheter, eftersom vi på de svagt sura substraten synas ha  $p_H$ -optimum för daggmaskarnas verksamhet. Om däremot  $p_H$ -värdet sjunker under 5.5, kommer inom samma klimatområde en råhumusbildning lätt till stånd, då en dylik markreaktion är ogynnsam för maskfaunan. Vi känner väl, huru vissa sandiga mulljordar genom en oförsiktig exposition och därmed följande uttorkning av markytan

eller genom alltför stark beskuggning kunna övergå till råhumusjordar (MÜLLER 1878, WARMING 1916—1919, LINDQUIST 1931).

Möjligheterna att kompensera en ogynnsam klimatfaktor med en hög markreaktion och därigenom bibehålla existensmöjligheter för en effektiv maskfauna och således även för en mullbildning äro så stora, att så vitt jag vet, hittills intet fall av råhumusbildning på subneutral skogsmark i Sydkandinavien eller Västeuropa är närmare beskrivet. Den subneutrala råhumus, som inledningsvis omtalats från Timmesöbjerg, är tills vidare unik<sup>1</sup>.

#### **Den subneutrala råhumusens uppkomst och utbildning.**

1) *Ojämnheter i topografien.* De vallgravar, som i väster och norr omger Timmesöbjerg-borgen, ha under århundradens lopp fyllts med fallförna av boklöv, som diförts med vinden från bergets starkt exponerade partier. Även andra topografiska ojämnheter t. ex. fördjupningarna efter de urgamliga rotvälvorna (se sid. 13) ha abnormt anrikats med förna. På grund av humustäckets ovan omtalade extrema torrhet, som än mer markeras genom det tjocka förneskiktet, reduceras maskfaunan starkt och förnan kommer att nedbrytas i huvudsak genom insekter och svampar, varvid så småningom en typisk råhumus med en subneutral reaktion kommit till utbildning. Råhumusbildningen är här upp till 70 cm djup. Inom dessa områden har råhumusbildningen i stort sett nått ett slutstadium i och med förnämaterialets fullständiga omvandling till amorf humus. I dessa fall har således den forntida odlingen direkt orsakat utbildningen av den subneutrala råhumusen.

2) *Lågor och ris.* Denna råhumusbildning kan även orsakas av stormfällning eller avverkning i beståndet. Marken, som även i full beskuggning lider av vår- och sommartorkan, blir extremt torr, när mullen vid stormfällning eller vid avverkning direkt exponeras för solljuset. Mullen blir därvid ofta förbränd, varvid bakterielivet starkt försvagas och daggmaskarna reduceras i antal. I det fallna trädets grenverk ansamlas ganska snart fallförna i stora kvantiteter. Maskfaunan har förlorat sin effektivitet och nedbrytningen omhändertages av insekter och svampar. Ovanpå mullen utbildas liksom i föregående fall först en filtförna, vilken så småningom ger upphov till en typisk amorf råhumusbildning. Sedan den fallna bokens finare grenverk bortmultnat, upphör förneansamlingen och kvarliggande lösförna blåser bort. Filtförnan blir humuslagrets ytskikt, och underlagras av en amorf råhumus. Hela denna bildning ligger ovanpå den gamla mullen, vilken fortfarande bibehåller en utpräglad klumpstruktur (se fig. 23).

3) *Juniperussnår.* Utvecklingen blir en helt annan i de fall, då torrskogsluckor och torrträdluckor utbildas. Torrträden mista nämligen sitt finare grenverk långt innan de falla till marken och övergå till lågor. Härigenom förlänges den tid väsentligt, under vilken mullen i den solexponerade luckan utsättes för extrem uttorkning, då någon förneansamling till att börja med icke kan äga rum på mullens yta. Uppkomsten av torrskogsluckor får emellertid oftast till följd en utbildning av ett *Juniperus*-

<sup>1</sup> Möjligens skulle LINSTOWS »süßen Humus« (LINSTOW 1929, sid. 121 f.) vara en dylik alkalisk råhumustyp. Så länge en beskrivning saknas, kan emellertid detta icke avgöras.

samhälle på den starkt uttorkade marken, och när detta samhälle nått full utveckling kommer enen att spela samma roll som förneansamlare som i förra fallet vindfällets grenverk. Daggmaskfaunan har ofta helt försvunnit från denna starkt förbrända mullmark och fornans rikliga anhopning följes därför av materialets nedbrytning till råhumus genom insekter och svampar. Fornans nedre partier bindas så småningom till filtförna, överlagrad av lösförna och underlagrad av en råhumus. Då så småningom kronskiktet ånyo slutes, avdö enarna, vilka icke väl synas tåla beskuggningen och anrikningen av fornamsmaterial. De stå dock åtskilliga tiotal år såsom döda skelett och orsaka ytterligare förneansamling. Slutligen multna de likväl, förneansamlingen avbrytes och lösförnan föres oftast bort med vinden. Samma humustyp som i förra fallet har kommit till utbildning (se fig. 25—28).

Råhumusbildningen blir sålunda på denna egendomliga lokal i huvudsak en följd av skogens naturliga avdöende och föryngring; den följer i stormluckornas, hyggesluckornas och torrskogsluckornas spår. Den har dessutom utbildats under inflytande av den forntida bebyggelsen inom området. Råhumusen överlagrar här mullen, vilken likväl icke mist sin karaktär av mull: den vanligaste profilen blir där en forna-råhumus-mull-profil. Råhumusen är mångenstädes stadd i snabb omvandling mot råmull, en humusbildning, som uppträder inom en större areal än råhumusen och denna råmull visar på några punkter tendenser att övergå i grovmull. Därmed är ringen slutet och utvecklingen fullbordad från grovmull över råhumus och råmull tillbaka till grovmull. Råhumusens och råmullens utbredning på Timmesöbjerg framgår av kartan, fig. 16.

**Surhetsgraden och råhumusbildningen.** Ovan lämnade rekonstruktion över råhumusens utbildning och slutliga omvandling till råmull ger vid handen, att råhumus kan utbildas inom sydskandinaviska skogssamhällen även på ett med hänsyn till surhetsgraden för mullbildningen optimalt substrat, där intet synes kunna väsentligt påverka den en gång bildade mullens struktur. Exemplet har ganska stort värde i en diskussion med de kemiskt orienterade pedologer, vilka icke synas räkna med möjligheterna av råhumusbildning å basiska substrat i Sydskandinavien och Mellaneuropa. Hur allmän en sådan uppfattning om råhumusens beroende av substratets surhetsgrad är, framgår bl. a. av WAKSMANS (1936, sid. 8) senaste framställning av humusspörsmålet, där han skiljer mellan fornannedbrytning under stark surhet eller under låg temperatur, råhumus, och fornannedbrytning under mindre sura, neutrala eller alkaliska förhållanden, dit han hänför mullen. I samma anda ha KIRCHNER, LOEW och SCHRÖTER (1911, sid. 22), HESSELMAN (1912, sid. 47), WARMING (1919, sid. 401) och LUNDEGÅRD (1931, sid. 358) yttrat sig, och i en modern engelsk framställning om skogsmarksproblemen (CLARKE 1936), en handbok för pedologiska fältstudier, indelas humusformerna i bl. a. råhumus eller sur humus samt mild eller neutral humus eller mull. Sådana framställningar äro i den moderna markläran vanliga och torde ytterst bottna i en utpräglat kemisk syn på markproblemen.

## Kapitel V

### Om växtsamhällena på de skilda marktyperna på Timmesöbjerg.

(Härtill fig. 30, tavl. XIX).

**Allmänna synpunkter.** Den sociologiska analysen av vegetationen på Timmesöbjergs olika marktyper belyser några extrema drag av humusformens betydelse för fältskiksvegetationen. Av särskilt intresse är därvid analysen av den vegetation, som koloniserar de kraftiga, starkt försvampade, amorfa råhumustäckena.

För vegetationsanalysen på Timmesöbjerg har jag använt samma metodik, som beskrivits i min avhandling om den skandinaviska bokskogen, nämligen punktmetoden (LINDQUIST 1931, sid. 204 ff). Om denna metod och betydelsen av frekvens-talen i analyserna hänvisas till tidigare beskrivning. — För de enkla, i regel enskiktade bokskogssamhällen, som nedan beskrivas, har icke den av mig tidigare brukade nomenklaturen använts (efter DU RIETZ 1930), av den anledningen, att jag här vänder mig till en läsekrets, för vilken denna terminologi torde vara främmande. De enskiktade sociologiska enheterna ha genomgående benämnts växtsamhällen, vilket i stort sett motsvarar WARMINGS samlag (WARMING 1916—19), RAUNKIAERS formation (RAUNKIAER 1909), min socion (LINDQUIST 1931) och DU RIETZ' och GAMS societet (DU RIETZ 1936, GAMS 1936). För nomenklaturen hänvisas till LINDMANS flora (1926), vilken med vissa undantag följts samt för mossor och lavar till Lunds Botaniska förenings förteckning (1937).

De skilda marktyperna ha i föregående kapitel behandlats och närmare karakteriseras kemiskt och morfologiskt. Vid den beskrivning av vegetationen, som nedan lämnas, skall en uppdelning av växtsamhällena på skilda humustyper göras, eftersom humusbildningarna ju anses i stora drag påverka vegetationsfördelningen. De humusprofiler, som skola behandlas ur vegetationssynpunkt, äro följande: 1. Grovmull (förbränd eller vindexponerad mulljord). 2. Lösförna-grovmull (den normala mulljorden). 3. Lösförna-filtförna-grovmull. 4. Lösförna-filtförna-råhumus. 5. Filtförna-råhumus. 6. Råhumus och 7. Råmull. De fyra senare typerna underlägras av grovmull.

**Anemone hepatica-Carex digitata-samhället** är det växtsamhälle av högre sociologisk rang, som domineras vegetationen på Timmesöbjerg. Det är typiskt för torra skogar på något degenererad mull, på råmull eller på godartad råhumus. Dess subordinerade enheter präglas alla av torka och kalkrikedom. — De i den följande framställningen omtalade växtsamhällena kunna samtliga inordnas härunder. Ju mera marktillståndet närmar sig den normala, genomfuktade mullmarkens, ju mindre utpräglat blir detta växtsamhälle. Det visar därvid en jämn övergång i ett annat växtsamhälle, *Anemone nemorosa*—*Oxalis acetosella*-samhället. Växtsamhällen snarlika eller identiska med ovannämnda *Anemone hepatica*—*Carex digitata*-samhälle ha tidigare beskrivits av WARMING (1919, sid. 545), DU RIETZ (1925, sid. 19 f) och av LINKOLA (1929, sid. 32 ff).

1. *Grovmullmarker utan förna*. Denna fornablottade mulljord kommer till utbildning i exponerade lägen genom borttransporterande av lösförnan; den blir som mest accentuerad, där själva topografiens icke tillåter förneanhopning t. ex. på branta sluttningar. Mullen blir genom blottläggningen starkt uttorkad vare sig denna bildning är normalt beskuggad eller direkt exponerad för soljuset. Ett *Anemone hepatica*—*Carex digitata*-samhälle av lägre sociologisk rang uppträder på de normalt till starkt beskuggade, fornablottade mullmarkerna, framför allt i de starka sluttningarna, där mulljorden ofta utbildas som rasjord. *Carex digitata* och *Anemone hepatica* uppträda vanligen med normaldispersion i låg till medelmåttig frekvens. Dessutom förekomma spridda exemplar av *Anemone nemorosa*, *Asperula odorata*, *Brachypodium silvaticum*, *Carlina vulgaris*, *Hedera helix*, *Mercurialis perennis*, *Melampyrum pratense* och *Viola silvestris* jämte ungplantor av *Juniperus communis* samt enstaka mossor. — Detta samhälle förekommer dessutom i kombination med ett mossrikt bottenskikt, i vilket *Porella platyphylla*, *Camptothecium lutescens*, *Rhytidadelphus triquetrus*, *Eurhynchium Swartzii* och *Isothecium viviparum* dominera. Detta samhälle kan ytterligare övergå i fragment av ett mossrikt *Festuca ovina*-samhälle med samma dominerande mossor — en för den subneutrala bokskogen i sanning ovanlig kombination.

Övriga samhällen, typiska för den normalt beskuggade, förnefria mullmarken, äro framför andra de, som domineras av *Brachypodium silvaticum*, *Dactylis Aschersoniana*, *D. glomerata*, *Festuca rubra* och *Poa nemoralis*, vilka dominanter ge namn åt respektive samhällen. Dominanterna förekomma här endast i medelmåttig till låg frekvens, men ha en jämn spridning. En högre frekvens hos de fanerogama elementen omöjliggöres såväl genom det uttorkade, något degenererade substratet, som genom konkurrensen med bottenskiktets mossor.

På den extremt torra, förnefria grovmullen i beståndsluckorna, där mullen har en förbränd karaktär och omsättningen i stort sett avstannat, utbildas genomgående inga stabila växtsamhällen. Man finner däremot fragment av dylika med arter tillhörande dels förna-mull-bokskogens normala flora och dels de torra ängsbackarnas vegetation. Bland de första märkas t. ex. *Actaea spicata*, *Mercurialis perennis*, *Vicia silvatica*, *Viola silvestris* jämte flertalet ängsbokskogsgräs, bland de senare *Arabis arenosa*, *Avena pratensis*, *Carlina vulgaris*, *Clinopodium vulgare*, *Fragaria vesca*, *Gnaphalium dioicum*, *Pimpinella saxifraga*, *Poa compressa*, *Polygala vulgaris*, *Prunus spinosa*, *Sanguisorba minor* och *Solidago virgaurea* samt därjämte *Juniperus communis*. Av dessa träffas f. ö. flera sparsamt även inne i den normalt slutna bokskogens örutmatta. Denna de förbrända luckornas vegetation synes närmast sträva till utbildning av artrika samhällen med *Dactylis glomerata*, *Dactylis Aschersoniana* eller *Festuca rubra* som dominanter.

2. *Lösförna-grovmullmarker*. Så betecknas den i sydkandinaviska mullbokskogar vanligt uppträdande marktyp, vilken under ett skikt av lösförna mellan 2 och 10 cm:s mäktighet har en omkring 30—60 cm mäktig mull med grov klumpstruktur.

Även på denna mark kommer stundom ett rent *Anemone hepatica*—*Carex digitata*-samhälle till utbildning, likväл med ett rikare inslag av örter och lundgräs såsom t. ex. *Mercurialis perennis*, *Brachypodium silvaticum* etc. Förna-mull-bokskogens vanligaste samhälle är emellertid ett *Mercurialis perennis*-samhälle, vilket jag tidigare beskrivit från sagda lokalitet (LINDQUIST 1931, sid. 287 f). *Mercurialis*-samhället och dessas varianter har genomgående *Anemone hepatica* och *Carex digitata* som konstanter, oftast i låg frekvens. Att döma av de utförda analyserna skulle här även *Anemone nemorosa* och *Viola silvestris* vara konstanta. *Asperula odorata* uppträder rikligt, men dock icke konstant. Av samhällets många varianter äro de gräsrika vanligast, gynnade av de torra markerna. Allmänt uppträder sálunda en *Poa nemoralis*-rik variant och en *Brachypodium silvaticum*-rik variant. Dessa båda övergå på torrare och mera solöppna lokaler i skogen till *Mercurialis perennis*—*Poa nemoralis*-samhälle och *Mercurialis perennis*—*Brachypodium*-samhälle, vilka kunna utvecklas vidare till rena grässamhällen.

Grässamhällena äro rikt företrädda på denna mullmarkstyp; de gynnas starkt av marktorkan. Här förekomma ett *Dactylis*-samhälle, där båda *Dactylis*-arterna växa i blandning, ett *Poa angustifolia*-samhälle och ett *Festuca rubra*-samhälle, samtliga förekommande i den normalt beskuggade bokskogen på typisk förna-mull-jord och samtliga med konstant förekommande *Anemone hepatica*, *Carex digitata* och *Mercurialis perennis*.

3. *Grovsmullmarker med filtförneanhopning*. Som tidigare omtalats utbildas här och var på mullen i detta bestånd tjocka filtförneskikt, ofta utgörande initialstadier till en råhumusbildning. Genom den rikliga tillförseln av förna sprängas de ovan omtalade mullbokskogssamhällena och den abnorma humusbildningen leder till utbildning av samhällen eller fragment av samhällen, där sådana arter dominera, vilka genom sina stoloner äga förmåga att klara sig undan företäckningen. *Asperula*-samhället har härvid största möjligheterna att bibehållas och utbildas antingen som ett rent *Asperula*-samhälle eller som ett *Asperula odorata*—*Mercurialis perennis*-samhälle med tillfälligt uppträdande *Carex digitata*, *Vicia silvatica*, *Actaea spicata* o. a. (se analyserna). Allteftersom denna förneanhopning fortsätter, blir samhället artfattigare, då i huvudsak arter med effektiv stolonbildung i längden kunna hålla sig kvar. Vid alltför stark förneanhopning spränges växtsamhällena i fragmentariska rester.

4. *Råhumus med lösförna och filtförna*. Denna humusbildning, som underlagras av grovmull, utgör en direkt fortsättning av den föregående och de växtsamhällen och växtsamhällesfragment, som anträffas på de förneanrikade mullmarkerna, finna vi även här. *Asperula*-samhället är som regel sprängt och vegetationen utgöres av spridda exemplar av *Actaea spicata*, *Convallaria majalis*, *Hedera helix*, *Mercurialis perennis*, *Orobus vernus*, *Pteridium aquilinum* och *Vicia silvatica* m. fl. samt av enstaka enbuskar. Här finna vi områdets pr arealenhet artfattigaste vegetation.

Då omsättningen av förnan forskridit så långt, att ett stabilt filtförnelager utbildats, händer det ofta, att lösförnan blåser bort t. ex. genom de lövsamlande enbuskarnas död och försvinnande. Därigenom konstitueras en markprofil av filt-

förna-råhumus överlagrande mull. Denna humusbildning är till en början som regel säte för ett *Asperula*-samhälle, vilket emellertid under de förbättrade markförhållanden snabbt förändras. Det innehåller spridda *Mercurialis perennis*, *Melampyrum pratense* och *Pteridium aquilinum*, någon gång även *Vicia silvatica*. Den utgör ett initialstadium till en rikare vegetationsutveckling på råhumusen.

Filtförmans ytlager koloniseras nu av ett *Asperula*-samhälle, vilket blir alltmera artrikt, ju starkare filtförmans nedbrytning är. I första hand återföres vegetationen till *Anemone hepatica*—*Carex digitata*-samhälle och här invandra bl. a. *Actaea spicata*, *Hedera helix*, *Melampyrum pratense* och *Pyrola secunda*. Vegetationens slutstadium blir mossrikt *Asperula*-samh., där mossorna — *Isothecium viviparum*, *Eurhynchium praelongum*, *E. Swartzii* m. fl. — icke förekomma i högre frekvens.

6. *Råhumus*. Efter filtförmans nedbrytning till amorf humus kommer råhumusen att bilda humustäckets ytlager direkt på grovmullen. Vegetationen på denna råhumus går i regel mot utbildning av samhällen, där kalkmossorna dominera. Stundom kunna mossamhällena spränga *Asperula odorata*-samhället, stundom kommer *Anemone hepatica*-samh. till utbildning med en rik mossvegetation i bottenskiktet. Artrillan på denna råhumus synes mig vara värd en alldelers särskild uppmärksamhet (se sid. 46—47). Den upptager ett antal växter, vilka allmänt ansetts vara ängsskogselement och vilka är intimit knutna till de rika mullmarkerna. Däremot innehåller den knappast någon av de växter, som vi vant oss att anse som karakteristiska för råhumusmarkerna. Här märkas sålunda *Actaea spicata*, vilken rikligt självår sig på råhumusen även vid svagt ljustillträde, *Mercurialis perennis*, som allmänt ansetts vara indikator för ett gott mulltillstånd, *Cephalanthera alba*, *Neottia nidus avis*, *Viola silvestris*, *Vicia sepium*, *Orobus vernus*, *Hedera helix* och *Anemone nemorosa* samt bland lundgräsen *Brachypodium silvaticum*, *Bromus Benekenii*, *Dactylis Aschersoniana* och *Melica uniflora*, alla karakteriserande våra bästa mullmarker. Av verkligt karakteristiska råhumusväxter visar däremot som ovan nämnts denna artlista ej ett spår. Närvaron av *Pteridium aquilinum*, vilken i Klinteskoven h. o. d. uppträder även på god mullmark, samt av *Pyrola secunda*, *Corallorrhiza trifida*, *Melampyrum pratense* och *Monotropa hypopitys* synas möjligen ge vid handen, att substratet icke är i god omsättning, ty dessa arter förekomma ju ofta på sura råhumusmarker.

Den rika floran av ängsväxter på råhumusen karakteriseras genom sina talrika hungerformer, vilket visar att ehuru dessa växter rikligt kunna gro och kvarleva på råhumusen de likväl icke där erhålla någon luxurierande utveckling.

7. *Råmullen*. Genom att maskarna så småningom genomarbeta råhumusen övergår den successivt såväl från ytan som från gränsen till den underlagrande grovmullen i en svagt mineralblandad råmull. Vegetationen har icke i större utsträckning stabilisering sig. Moss-samhällena dominera vissa av dessa råmullmarker med talrika kalkbetonade mossor och med spridda dvärgexemplar av *Anemone nemorosa*, *A. hepatica*, *Asperula odorata*, *Mercurialis perennis*, *Orobus vernus*, *Carex digitata* m. fl. Artrikedomen kan vara mycket stor, men exemplaren äro små och frekvensen av varje art är ringa till medelmåttig. De vanligaste fanerogama växtsamhällena på

denna marktyp äro *Anemone hepatica*—*Carex digitata*-samhället, *Convallaria majalis*-samhället och *Festuca ovina*-samhället (se fig. 30).

**Arternas fördelning.** För en allmän översikt över arternas frekvens och fördelning på de skilda marktyperna på Timmesöbjerg har följande sammanställning gjorts på basis av vegetationsanalyserna. Den avser att illustrera fördelningen av ängsbokskogsväxter, hedbokskogsväxter och torrängsväxter. Tabellen upptager dessa arters fördelning på humustyper och därjämte fördelningen av sådana arter, som tillhöra tvenne av ovanstående grupper. Härutöver erhålls en obetydlig rest av arter,

### Tabell

över fördelningen av skilda ekologiska typer av fanerogama växter på de skilda humustäckena samt översikt över totala artantalet på dessa. Tabellen baserad på provytematerialet. (a = ängsskogselement, b = hedskogselement, c = torrängselement, ab, ac etc. angiva, att resp. arter kunna uppträda som både denna och denna, d betecknar sådana arter, som icke kunna inräknas i detta schema.

Tabelle über die Verteilung verschiedener ökologischer Typen phanerogamer Pflanzen auf verschiedenen Humusdecken sowie eine Übersicht über die totale Artanzahl auf den letzteren. Die Tabelle gründet sich auf das Probenflächenmaterial. (a = Laubwiesenpflanzen; b = Pflanzen des sauren Rohhumusbodens; c = Trockenwiesenpflanzen; ab, ac etc. bezeichnen das Vorkommen der Arten in beiden Gruppen; d bezeichnet Pflanzen, die in das Schema nicht eingereiht werden können.

	a		b		c		ab		ac		bc		d		Summa	
	st.	%	st.	%	st.	%	st.	%	st.	%	st.	%	st.	%	Fane- rog. st.	Total st.
1. Lösförna-grovmall .....	18	64	—	—	4	14	3	11	3	11	—	—	—	—	28	33
2. Förbränd grovmall .....	19	38	1	2	17	34	5	10	7	14	—	—	1	2	50	60
3. Lösförna-filtförna-grovmall..	8	57	—	—	1	7	3	22	2	14	—	—	—	—	14	14
4. Lösförna-filtförna råhumus..	8	73	—	—	1	9	2	18	—	—	—	—	—	—	11	11
5. Råhumus .....	19	56	—	—	4	12	4	12	4	12	1	2	2	6	34	48
6. Råmall .....	18	50	2	6	6	17	4	11	5	13	—	—	1	3	36	63

vilka icke närmare kunna klassificeras med hjälp av detta enkla schema. — Av tabellen framgår, hurusom inom alla dessa humustyper lundväxter dominera t. o. m. på råhumusbildningarna och huru växter tillhörande torrängarna rikligt förekomma. De arter, som kunna uppträda på sura råhumusmarker, spela däremot här en mycket underordnad roll och utgöra i genomsnitt omkring 15 % av hela artantalet. De mera typiska råhumusväxterna saknas alldelens. — Tabellen visar det totala artantalets fördelning på olika humustyper. Av intresse i denna tabell är den klart framträdande reduktionen i artantalet på de humustyper, där stark förneansamling är förhanden och dessutom — och mot all förmodan — det stora antalet arter på den subneutrala råhumusen — summa 35 stycken.

**Mullflora och råhumusflora.** Alltsedan mull och råhumus uppställdes som

skilda humustyper ha de stora skillnaderna i deras flora framhållits. Sålunda redogjorde redan P. E. MÜLLER (1878) för dessa olikheter och där efter har skillnaderna mellan dessa floror alltmera specificerats (KIRCHNER, LOEW & SCHRÖTER 1911, HESSELMAN 1912, WARMING 1916—19, LUNDEGÅRDH 1931 o. a.). — I stora drag gäller otvivelaktigt denna uppdelning av skogsfloran i mullflora och råhumusflora; men vi måste dock hålla i minne att undantag finns och att ett studium av dessa kunna bli av stort värde för en rätt tolkning av vegetationsfördelningen.

I min utredning av den skandinaviska bokskogen (LINDQUIST l. c.) påvisade jag med stöd av bl. a. ett par vegetationsanalyser från Timmesöbjerg, hurusom ett stort antal växter, vilka vanligen betraktas som typiska för mullmarkerna i våra skogar, rikligt förekomma på den subneutrala råhumusen på Timmesöbjerg, och därav drog jag den slutsatsen, att varken det allmänna marktillståndet eller nitrifikationen i dessa fall var avgörande för denna fördelning mellan ängsbokskogs hällena och hedbokskogssamhällena, utan att därstädes surhetsgraden som sådan bestämde vegetationsutvecklingen ganska oberoende av marktillstånd och omsättning. — De 48 analyser av vegetationen på detta berg, som här framläggas och som sammanfattats nedan, äro ägnade att styrka detta mitt forskningsresultat. De visa tydligt, huru ett stort antal växter av de typiska ängsskogselementen uppträda på en ofta svagt eller icke nitrificerande råhumus, delvis av mycket dålig typ med extrem anhopning av parasitiska råhumussvampar. På ett råhumuslager av c:a 30 cm:s mächtigkeit, helt genomvävt och destruerat av svamphyfer (se fig. 19) har t. ex. anteknats strödd till riklig förekomst av *Actaea spicata*, *Anemone nemorosa*, *Orobus vernus* och *Viburnum Opulus*.

Efter vad som här anförts ha vi således anledning att i viss mån revidera vår uppfattning om begreppet råhumusflora och uppfattningen av de faktorer, som bestämmer ängsbokskogsflorans fördelning. De verkliga råhumusväxterna (se ovan citerad litteratur) synas i vissa fall vara mera beroende av humusens surhetsgrad och den biologiska omsättningstypen än av den form i vilken humusen uppträder. De för ängsskogarna typiska arterna äro å sin sida på basiska substrat icke med nödvändighet bundna till mullmarken.

**Ekskogsväxter i bokskogen.** Även förekomsten av buskar tillhörande ängs-ekskogssamhällena är av intresse. Den normala förra-mull-marken i bokskogen i Danmark och Sydsverige har ju ingen underskog av vare sig *Corylus*, *Crataegus*, *Viburnum opulus*, *Prunus spinosa*, *Lonicera xylosteum* eller andra buskar ej heller av *Juniperus* (WARMING 1919, LINDQUIST 1931). Detta kan icke bero på att detta buskskikt genom kulturinflytanden försvunnit, utan måste närmast orsakas av en olämplig kombination av näringsfaktorer och belysningsfaktorer. — Timmesöbjerg-skogen släpper i genomsnitt ned ganska små ljusmängder till marken, men trots detta förekomma här och där buskar och plantor av *Crataegus*, *Prunus spinosa*, *Lonicera xylosteum* och *Viburnum opulus* och inom liknande områden närmare klinten t. ex. i bokskogen vid Sommerspiret och Dronningstolen finner man en rik vegetation av samma slag under ogynnsamma belysningsförhållanden (se WARMING 1919, sid.

545 f). Ljusförhållanden synas således här icke avgöra, om detta buskskikt når utbildning eller ej, ej heller synes buskskiktet väsentligen bero av humusformen, ty ungplantor av dessa buskar ha anträffats t. o. m. på den subneutrala råmullen. Man vill söka en förklaring till deras förekomst helt enkelt däri, att bokskogen på subneutrala substrat mycket väl kan uppträda med samma arter i buskskiktet som ekskogen och askskogen på de surare mulljordarna, dock i betydligt mindre frekvens. Den höga kalkhalten uppväger här bokskogens med avseende på ljus och näringssförhållanden ofta ogynnsammare miljö.

Samma synes vara förhållandet med örтvegetationen och med lundgräsen. Vi ha vant oss vid att betrakta sådana arter som *Actaea spicata*, *Orobus vernus*, *Agropyrum caninum*, *Brachypodium silvaticum* m. fl. såsom typiska ekskogselement och anse dem behöva ekskogens nitrifikation och dess goda ljusförhållanden för sin trivsel. I skogen på Timmesöbjerg växa emellertid dessa arter i stark beskuggning i bokskogen. Även härväldag torde bokskogens sämre ljusförhållanden och i stort sett sämre ekologiska betingelser kompenseras av det gynnsamma subneutrala substratet, vilket jag f. ö. tidigare framhållit med en rikare exemplifiering i översikten över de skandinaviska bokskogssamhällena (LINDQUIST 1931, sid. 306 ff). Denna teori står i god samklang med de åsikter om samspelet mellan ljusfaktorer och markfaktorer, som antyts redan av RAMANN (1893, sid. 299 f). Analoga förhållanden ha för övrigt experimentellt utretts av GAST (1936), som för utvecklingen av granplantor på skilda substrat visat, att försämrade ljusförhållanden kunna kompenseras av god kvävetillgång,. ÅSLANDER har påvisat en liknande kompensation av surhetsgraden med en större näringshalt (ÅSLANDER 1929).

### Vegetationsanalyser och markprofiler.

Nedan publiceras de vegetationsanalyser, som gjorts på Timmesöbjerg under åren 1929 till 1936. Analyser ha icke kunnat göras i den utsträckning, som varit önskvärd, och de här publicerade  $1 \times 1\text{m}^2$ :s rutanalyserna äro i många fall icke fullt representativa för de växtsamhällen inom vilka analyserna utförts. De ha utlagts i första hand för att erhålla korrelation mellan markprofiler och vegetation och därför ha regelrätta förband om ett större antal rutor ej kunnat utläggas (se LINDQUIST 1931). För utredning av bergets växtsamhällen har det därför varit nödvändigt, att ett 100-tal analysrutor enl. Hult—Sernander utlagts i förband i de viktigaste vegetationstyperna. Dessa ha emellertid av utrymmesskäl måst uteslutas från publicering.

Som förut omtalats ha de analyserade rutorna behandlats med punktmetoden sådan jag beskrivit den 1931.

Markprofilerna ange humusformernas mäktighet i cm som ett medeltal av fyra mätningar i varje profilgrop och dessutom med angivande av täckningsgraden för den tunna, icke täckande lösförnan.

Fosfathalten har angivits i fosfatgrader enl. Arrhenius ( $1\text{ fosfatgrad} = 1/1000\text{ mg P}_2\text{O}_5$  lösligt i  $2\%$ -ig citronsyra). Kalkhalten har angivits som i NaCl utbytbart kalcium

i mg pr kg lufttorr jord, kalium som mg pr kg lufttorr jord enl. Riehm och NO<sub>3</sub> och NH<sub>3</sub> ävenledes som mg N pr kg lufttorr jord. Littera a och b angiver här värdena strax efter provtagningen och efter en månads lagring.

De skilda profiltyperna och deras vegetation följa här enl. den utvecklingscykel, som på Timmesöbjerg har konstaterats leda från mullbildning över råhumusbildning och ånyo till mullbildning.

### I. Lösförna-mull (Normal mullmark).

	1	2	3	4	5	6	7	8	9	10	Ekologisk typ
A <sub>2</sub> Olikåldrig bokskog. Medelhöjd 11 m.											
C Fagus sylvatica .....	1	—	4	1	1	+	3	1	1	+	ab
Actaea spicata .....	—	—	—	—	—	7	3	—	—	—	a
Anemone hepatica .....	7	6	+	5	3	6	7	2	2	3	a
Anemone nemorosa .....	4	15	+	11	22	+	—	8	+	17	a
Asperula odorata .....	+	5	7	4	7	5	—	+	+	+	a
Fragaria vesca .....	—	—	—	—	—	—	4	—	+	—	c
Hedera helix .....	—	—	—	—	3	—	2	—	+	—	ac
Lathyrus pratensis .....	+	—	—	—	—	—	—	—	—	—	c
Lonicera xylosteum .....	—	—	—	—	—	2	—	—	—	—	a
Melampyrum pratense .....	+	—	—	+	—	5	—	—	—	—	ab
Mercurialis perennis .....	13	7	18	7	—	38	57	1	5	9	a
Orobus vernus .....	—	—	—	1	—	—	—	+	—	—	a
Oxalis acetosella .....	—	—	—	—	8	—	—	1	+	—	a
Pimpinella saxifraga .....	—	—	—	—	1	—	2	—	—	—	c
Polygonatum multiflorum .....	—	—	—	—	—	4	—	—	—	—	a
Primula elatior .....	—	—	—	6	+	—	—	—	—	—	a
Pyrola secunda .....	—	—	—	—	—	+	+	—	—	—	ab
Vicia sepium .....	—	—	—	+	—	—	—	2	—	—	a
Vicia sylvatica .....	—	+	10	—	3	3	—	—	—	—	a
Viola canina × silvestris .....	—	—	—	2	—	—	—	—	—	2	a
Viola silvestris .....	+	15	2	1	+	+	4	5	2	6	a
Brachypodium sylvaticum .....	3	2	3	3	8	14	—	—	8	5	a
Carex digitata .....	3	6	2	3	1	2	—	—	5	1	ac
Dactylis Aschersoniana .....	—	—	—	5	1	—	2	2	—	—	a
Dactylis sp. (steril) .....	—	—	—	—	—	—	—	—	1	—	—
Festuca rubra .....	—	+	+	—	—	+	7	—	+	1	c
Melica nutans .....	—	—	—	—	1	—	—	—	—	—	a
Poa angustifolia .....	—	—	—	—	—	—	—	2	2	—	ac
Poa nemoralis .....	—	—	—	—	—	—	—	—	18	—	4
D Brachytegium rutabulum .....	—	—	—	—	—	—	—	7	—	—	—
Brachytegium velutinum .....	—	—	—	—	—	—	+	—	—	—	—
Mnium sylvaticum .....	—	—	—	—	—	—	2	—	—	—	—
Tortella tortuosa .....	—	—	—	—	—	—	+	—	—	—	—
Tortula mutica .....	—	—	—	—	—	—	+	—	—	—	—

*Markprofiler.*

	1	2	3	4	5	6	7	8	9	10
Lösförna (mäktighet, cm) .....	6	6	7	6	6	6	2	6	3	10
Grovmull (mäktighet, cm) .....	24	28	18	21	20	15	18	23	18	30
P <sub>2</sub> O <sub>5</sub> .....	..	..	22	..	..	..	..	8	4	10
p <sub>H</sub> .....	7.4	..	7.4	..	..	7.6	7.6	7.5	7.4	7.5
Ca .....	..	..	600	..	..	..	..	..	..	..
K .....	..	..	23	..	..	..	..	..	..	..
NH <sub>3</sub> b .....	..	..	..	..	..	120	27	..	..	..
NO <sub>3</sub> a .....	..	..	20	..	..	..	..	0	0	0
NO <sub>3</sub> b .....	..	..	80	..	..	20	61	19	21	21
Grovmull med kritinblandning (mäktighet i cm) .....	20	24	21	18	14	15	23	9	25	30
Krita .....	..	..	..	..	..	..	..	..	..	..
Daggmask i grovmullen, antal pr. kvm .....	..	..	..	..	..	..	47	149	219	173

*Markprofilens allmänna utseende.*

*Lösförnan* består av boklöv och är alltigenom lucker, icke sammanfiltad av svamphyfer, nedåt fuktig och stadd i livlig sönderdelning.

*Grovmullen* med utpräglad klumpstruktur av maskexkrementer i mera är ärtstora, hårda klumper. Massförekomst av vita, grå och svarta svamphyfer, tillhörande *Mycelium radicis nigrostrigatum*, *M. 19 f* och *M. 17 a* samt *Trichoderna Koenigii*. Grovmullen genomgående innehållande skal av döda snäckor (markförna!) och nedåt starkt blandad med ärtstora till hönsäggstora kritstycken. I båda dessa lager förekommer rikligt med daggmask, framför andra *Allolobophora caliginosa*. Mulllagret vilar direkt på kritan. Det mera kompakta humusblandade lager, som i modern svensk markterminologi kallas »brunjordslagret», saknas här alldeles.

*Markprofilens kemiska karaktäristik.*

Grovmullen är synnerligen kalkrik, karaktäriseras av högt p<sub>H</sub>-värde och stor halt av assimilerbar kalk. Däremot är halten av fosforsyra och kali låg. Såväl ammonifikationen som nitrifikationen visa anmärkningsvärt låga värden.

*Vegetationsanalyserna* utförda: nr 1—5 i maj 1935, 6 i juni 1929, 7 i maj 1931 samt 8—10 i maj 1936.

## II. Förbränd mull (utan förneskikt).

	1	2	3	4	5	6	7	8	Ekologisk typ
A <sub>2</sub> Olikåldrig bokskog med smärre luckor. Medelhöjd 11 m. Analyserna utförda i luckorna utan vertikaltäckning av <i>Fagus</i> .									
B <sub>2</sub> <i>Juniperus communis</i> .....	—	—	—	—	20	—	—	—	
C <i>Fagus sylvatica</i> .....	1	—	+	1	—	+	—	1	ab
<i>Actaea spicata</i> .....	—	—	—	—	—	+	—	—	a
<i>Anemone hepatica</i> .....	2	1	+	2	10	2	2	3	a
<i>Anemone nemorosa</i> .....	5	4	1	2	9	+	—	+	a
<i>Arabis arenosa</i> .....	—	—	—	—	—	+	4	—	ac
<i>Arabis hirsuta</i> .....	—	+	+	1	—	—	—	—	ac
<i>Asperula odorata</i> .....	—	—	—	—	5	—	1	—	a
<i>Carlina vulgaris</i> .....	—	—	—	+	—	—	—	—	c
<i>Chrysanthemum leucanthemum</i> .....	—	—	—	—	—	—	1	—	c
<i>Circium arvense</i> .....	—	—	—	—	—	+	—	—	c
<i>Fragaria vesca</i> .....	—	+	1	1	—	1	—	—	c
<i>Galium mollugo</i> .....	—	+	—	—	—	—	—	—	ac
<i>Galium saxatile</i> .....	+	1	—	—	—	—	—	—	c
<i>Geranium, groddpl.</i> .....	—	—	—	—	—	—	—	+	a
<i>Gnaphalium dioicum</i> .....	—	—	—	—	—	—	—	2	c
<i>Hedera helix</i> .....	2	2	1	+	1	+	—	1	ac
<i>Hieracium</i> sp. ....	—	+	—	—	—	—	—	—	d
<i>Hypericum montanum</i> .....	—	1	—	—	+	—	—	—	c
<i>Lactuca muralis</i> .....	—	—	—	—	—	—	2	—	ab
<i>Lonicera xylosteum</i> .....	+	—	—	—	—	—	—	—	a
<i>Melampyrum pratense</i> .....	+	+	+	+	4	+	—	1	ab
<i>Mercurialis perennis</i> .....	7	2	1	4	16	4	3	3	a
<i>Orobus vernus</i> .....	+	+	1	4	—	+	—	—	a
<i>Pimpinella saxifraga</i> .....	+	—	+	+	—	—	—	—	c
<i>Polygala vulgaris</i> .....	—	1	—	—	—	—	—	—	c
<i>Polygonatum multiflorum</i> .....	+	1	+	—	—	—	+	+	a
<i>Prunus spinosa</i> .....	1	—	—	—	—	—	—	—	c
<i>Pyrola secunda</i> .....	—	—	—	—	—	+	1	—	ab
<i>Sanguisorba minor</i> .....	—	—	—	—	2	1	—	—	c
<i>Sanicula europaea</i> .....	1	1	—	—	—	+	—	—	a
<i>Satureja vulgaris</i> .....	+	—	—	—	—	—	—	—	c
<i>Solidago virgaurea</i> .....	—	—	—	+	—	—	—	—	c
<i>Trifolium medium</i> .....	—	—	—	—	—	—	—	2	c
<i>Viburnum opulus</i> .....	+	—	—	—	—	—	—	+	a
<i>Vicia sepium</i> .....	—	—	—	—	—	—	1	—	a
<i>Vicia silvatica</i> .....	+	—	—	—	—	—	—	1	—
<i>Viola hirta</i> .....	—	—	—	+	—	—	—	—	ac
<i>Viola silvestris</i> .....	2	+	+	+	—	+	—	+	a
<i>Brachypodium sylvaticum</i> .....	+	1	1	5	—	1	—	—	a
<i>Carex digitata</i> .....	4	1	8	5	9	2	10	9	ac

	1	2	3	4	5	6	7	8	Ekologisk typ
Carex diversicolor . . . . .	3	5	—	—	10	14	—	—	c
Dactylis Aschersoniana . . . . .	—	—	—	6	1	—	—	3	a
Dactylis glomerata . . . . .	—	1	1	—	—	—	—	—	a
Festuca ovina . . . . .	—	2	8	+	—	9	—	—	c
Festuca rubra . . . . .	3	4	2	—	—	3	8	12	c
Luzula pilosa . . . . .	—	—	—	—	—	+	—	—	b
Melica nutans . . . . .	—	+	—	2	—	—	—	—	a
Poa angustifolia . . . . .	—	+	2	—	5	—	—	—	ac
Poa nemoralis . . . . .	6	4	+	—	—	1	1	—	a
Pteridium aquilinum . . . . .	+	—	—	—	—	—	—	+	ab
D Brachythecium velutinum . . . . .	—	3	—	—	+	+	—	—	
Camptothecium lutescens . . . . .	—	—	—	—	—	+	15	—	
Encalypta contorta . . . . .	—	+	+	—	—	—	9	—	
Homalothecium sericeum . . . . .	—	—	—	—	—	1	1	—	
Hypnum cupressiforme . . . . .	—	+	—	—	+	—	—	—	
Isothecium viviparum . . . . .	—	—	4	—	—	—	12	7	
Neckera complanata . . . . .	—	—	—	+	—	—	—	—	
Porella platyphylla . . . . .	—	—	+	—	—	—	18	—	
Rhytidadelphus triquetrus . . . . .	—	—	—	—	—	—	1	—	
Tortella tortuosa . . . . .	+	+	+	+	—	—	—	+	

*Markprofiler.*

	1	2	3	4	5	6	7	8
Lösförna (täckningsgrad) . . . . .	2	3	4	3	5	4	1	4
Grov mull (mäktighet cm) . . . . .	17	18	7	14	10	40	5	12
P <sub>2</sub> O <sub>5</sub> . . . . .	..	4	..	..	..	2	6	4
pH . . . . .	7.4	7.4	..	..	7.8	7.5	7.5	7.5
Ca . . . . .	..	400	..	..	..	..	..	..
K . . . . .	..	12	..	..	..	..	..	..
NO <sub>3</sub> a . . . . .	..	10	..	0	0	18	0	0
NO <sub>3</sub> b . . . . .	..	0	..	0	0	36	190	42
NH <sub>3</sub> b . . . . .	..	..	..	..	248	..	..	..
Grov mull med kritinblandning (mäktighet cm.) . . . . .	18	15	16	11	12	10	20	32
P <sub>2</sub> O <sub>5</sub> . . . . .	..	..	..	..	..	..	2	..
pH . . . . .	..	..	..	..	..	..	7.5	..
NO <sub>3</sub> b . . . . .	..	..	..	..	..	..	58	..
Krita								
Daggmaskar i grovmullen, antal pr. m <sup>2</sup> . . . . .	..	..	..	..	..	119 <sup>1</sup>	0	32

<sup>1</sup> Siffran är ej representativ för detta samhälle.

*Markprofilens allmänna utseende.*

*Lösförna* av boklöv, kvistar och knoppfjäll av bok i ett tunt lager, icke fullständigt täckande grovmullen.

Grovmullen starkt uttorkad, av maskexkrementer med utpräglad klumpstruktur i ärtstora, hårda klumper. Dess färgton ljust grå. Huvudsakligen mycelier av *Mycelium radicum nigrostrigatum* och *Mycelium radicum atrovirens*, varemot vita mycelier synas spela en mera underordnad roll. Mullen nedåt inmängd med ärtstora till hönsägg-stora kritstycken. Daggmask förekommer, men icke så talrikt som i de normala mulljordarna (se sid. 20). Mullen har avlagrats direkt på *kritan*.

*Markprofilens kemiska karaktäristik.*

I förhållande till den normala mulljorden kan en betydlig urtvätning av mineral salter,  $P_2O_5$ , K och Ca, konstateras, vilket dock icke förorsakat någon stegring av surhetsgraden. Nitrifikationen har i flera fall helt avstannat och ej ens vid lagring bildas några större mängder nitrat i grovmullen.

*Vegetationsanalyserna* nr 1—4 ha utförts i maj 1935, nr 5 i maj 1931 och 6—8 i maj 1936.

**III. Lösförna-filtförna-mull.**

	1	2	3	4	5	6	Ekologisk typ
A <sub>2</sub> Olikåldrig bokskog, 11 m:s medelhöjd							
B <sub>2</sub> Juniperus communis . . . . .	1	—	—	3	4	—	
Fagus sylvatica . . . . .	—	—	1	—	—	+	
C Anemone hepatica . . . . .	—	1	1	—	—	—	a
Anemone nemorosa . . . . .	—	7	2	—	—	+	a
Asperula odorata . . . . .	1	4	3	1	2	1	a
Melampyrum pratense . . . . .	—	—	—	—	—	+	ab
Mercurialis perennis . . . . .	3	7	4	4	6	+	a
Pyrola secunda . . . . .	—	—	—	+	—	—	ab
Vicia sylvatica . . . . .	—	5	—	—	—	—	a
Viola silvestris . . . . .	—	2	1	—	—	—	a
Carex digitata . . . . .	—	+	3	—	—	—	ac
Dactylis Aschersoniana . . . . .	—	—	1	—	—	—	a
Dactylis glomerata . . . . .	—	1	—	—	—	—	a
Festuca rubra . . . . .	—	1	—	—	—	—	c
Poa angustifolia . . . . .	—	1	2	—	—	—	ac
Pteridium aquilinum . . . . .	—	—	—	—	12	—	ab

## Markprofiler.

	1	2	3	4	5	6
Lösförna (mäktighet cm.) . . . . .	7	18	25	20	16	12
Filtförna (mäktighet cm.) . . . . .	16	4	2	12	8	1
P <sub>2</sub> O <sub>5</sub> . . . . .	18	..	16	..	42	52
p <sub>H</sub> . . . . .	6.9	..	6.7	6.9	5.9	6.3
Ca . . . . .	300	..	..	..	280	..
K . . . . .	25	..	..	..	32	..
NO <sub>3</sub> a . . . . .	20	..	..	0	6	..
NO <sub>3</sub> b . . . . .	240	..	..	46	1	..
NH <sub>3</sub> b . . . . .	..	..	..	178	..	..
Grovmull (mäktighet cm.) . . . . .	30	32	32	6	18	15
P <sub>2</sub> O <sub>5</sub> . . . . .	0	..	0	..	..	12
p <sub>H</sub> . . . . .	7.5	..	7.5	7.5	7.5	7.3
Ca . . . . .	370	..	..	..	..	..
K . . . . .	5	..	..	..	..	..
NO <sub>3</sub> a . . . . .	10	..	..	..	..	0
NO <sub>3</sub> b . . . . .	60	..	..	54	40	10
NH <sub>3</sub> b . . . . .	61	..	..	61	144	..
Grovmull med kritinblandning . . . . .	10	16	16	16	20	18
Krita						
Daggmaskar, antal pr. m <sup>2</sup> . . . . .	..	..	..	20	112	85

## Markprofilens allmänna utseende.

Lösförnan består av boklöv, är lucker, i ytan torr, nedåt fuktig. Den har i sina undre delar talrika gula och vita mycelier. Filtförnan är fuktig, starkt sammanfiltad genom vita, gula och svarta hyfer, bland vilka märkas *Mycelium radicis atrovirens*, *Mycelium radicis nigrostrigosum* och *M. 19 f*, *M. 17 a*, *Corticium croceum* m. fl. I detta skikt även enstaka bokrötter, vilka stundom ha typiskt utbildade ektotrofa mykorrhizor. Skiktet visar en skarp övergång till grovmullen. Denna är i regel torr, har utpräglad klumpstruktur med stundom mera än ärtstora klumper. Mullen är starkt bemängd med svamphyfer, med i stort sett samma svampformer som i föregående skikt.

Nedåt blir denna grovmull uppbländad med ärt- till hönsäggstora kritstycken. Även denna nedre del av mullen är rik på svamphyfer. Daggmaskar äro icke sällsynta (se sid. 20).

## Markprofilens kemiska karaktäristik.

Filtförnan har ganska hög kalkhalt, och dess p<sub>H</sub> ligger vid och strax under neutralpunkten. På grund av den stagnerade omsättningen håller detta skikt ganska stora mängder fosforsyra och kali. Den underliggande grovmullen visar sig däremot innehålla mycket små kvantiteter av dessa ämnen, en sak som torde få tillskrivas

den omständigheten, att den under ett tidigare skede varit urtvättad och där efter icke erhållit erforderligt tillskott av förna.

En svag omsättning av kvävet till nitrat synes vara regel såväl i filtförnan som i grovmullen.

*Provytorna utlagda dels i lövanhopning, som uppkommit genom närvoro av enbuskar (1, 4 och 5), dels i lövanhopningar, som orsakats av på marken liggande döda grenar (2 och 6), och dels i lövanhopning, som orsakats av topografien (3).*

*Vegetationsanalyserna utförda: nr 1—3 i maj 1935, nr 4 i juni 1929 och 5—6 i maj 1936.*

#### IV. Lösförna-filtförna-råhumus.

	1	2	3	4	5	Ekologisk typ
A <sub>2</sub> Olikåldrig bokskog, 11 m:s medelhöjd						
B <sub>2</sub> <i>Fagus silvatica</i> . . . . .	—	+	—	+	—	
<i>Juniperus communis</i> . . . . .	—	1	—	1	2	
C <i>Anemone hepatica</i> . . . . .	—	—	+	1	1	a
<i>Anemone nemorosa</i> . . . . .	—	—	2	+	—	a
<i>Asperula odorata</i> . . . . .	+	—	1	+	—	a
<i>Melampyrum pratense</i> . . . . .	—	+	+	—	—	ab
<i>Mercurialis perennis</i> . . . . .	—	+	2	4	+	a
<i>Orobus vernus</i> . . . . .	—	—	+	1	+	a
<i>Stellaria holostea</i> . . . . .	—	—	—	+	—	a
<i>Vicia silvatica</i> . . . . .	+	1	1	+	—	a
<i>Festuca rubra</i> . . . . .	—	—	1	—	—	c
<i>Poa nemoralis</i> . . . . .	—	—	—	1	—	a
<i>Pteridium aquilinum</i> . . . . .	—	+	—	4	+	ab
	maj 1935		juni 1931		maj 1936	

#### Markprofiler.

	1	2	3	4	5
Lösförna (mäktighet, cm) . . . . .	6	16	5	8	16
P <sub>2</sub> O <sub>5</sub> . . . . .	34	..	76	..	36
pH . . . . .	6.3	..	6.3	4.5	6.9
Ca . . . . .	460	..	..	..	530
K . . . . .	31	..	..	..	..
NO <sub>3</sub> a . . . . .	8	..	..	5	0

	1	2	3	4	5
NO <sub>3</sub> b . . . . .	0	..	..	0	0
NH <sub>3</sub> b . . . . .	..	..	..	326.0	..
Filtförna (mäktighet, cm) . . . . .	5	12	3	10	4
P <sub>2</sub> O <sub>5</sub> . . . . .	18	..	34	..	36
p <sub>H</sub> . . . . .	6.0	..	6.7	6.5	6.9
Ca . . . . .	720	..	..	..	..
K . . . . .	31	..	..	..	..
NO <sub>3</sub> a . . . . .	12	..	..	0	..
NO <sub>3</sub> b . . . . .	0	..	..	..	400
NH <sub>3</sub> b . . . . .	..	..	..	163	..
Råhumus (mäktighet, cm) . . . . .	16	9	5	5	7
P <sub>2</sub> O <sub>5</sub> . . . . .	14	..	24	..	20
p <sub>H</sub> . . . . .	6.4	..	6.3	6.6	7.4
Ca . . . . .	800	..	..	..	..
K . . . . .	19	..	..	..	..
NO <sub>3</sub> a . . . . .	10	..	..	0	20
NO <sub>3</sub> b . . . . .	0	..	..	0	135
NH <sub>3</sub> b . . . . .	..	..	..	52	..
Grovsmull (mäktighet, cm.) . . . . .	27	19	18	10	20
P <sub>2</sub> O <sub>5</sub> . . . . .	..	..	12	..	2
p <sub>H</sub> . . . . .	..	..	6.9	7.2	7.4
NO <sub>3</sub> a . . . . .	..	..	..	..	0
NO <sub>3</sub> b . . . . .	..	..	..	0	45
NH <sub>3</sub> b . . . . .	..	..	..	0	..
Grovsmull med kritinblandning(mäktighet,cm)	4	3	10	8	10
Krita					
Daggmaskar i råhumusen, antal pr. kvm . . . . .	..	..	3	0	11

*Markprofilens allmänna utseende.*

Lösförnan av boklöv, lucker, i ytan torr, nedåt mera fuktig. Övergår utan tydlig gräns i *filtförnan*, som är fuktig, utpräglat lagdelad av sammanfiltade, förmultnande, gula löv. I nedre delen av detta skikt är lövens färg brun — mörkbrun, och här och där förekommer en maceration genom insekter och — i ringa utsträckning — daggmask. Hela skiktet är sammanvävt av svamphyfer och bokrötter. I övre delarna dominera gula mycel (*Corticium croceum*) och vita mycel och här ha bokrötterna utbildats med typisk ektotrof mykorrhiza. I nedre delen dominera *Mycelium radicum nigrostrigosum* och *Mycelium radicum atrovirens* jämte vita mycel (bl. a. *M. 17 a* och *M. 19 f*). Mykorrhizabildningen synes här hämmad, och talrika abnorma mykorrhizor anträffas på bokrötterna. Dessa äro långa och tunna och bära relativt få sidorötter. Råhumusen består av starkt packad, amorf humus, här och där med rester av blad och knoppfjäll. Strukturen ger tydligt vid handen, att nedbrytningen försiggått väsent-

ligen genom insekter och mikroorganismer. Enstaka maskexkrementer finns dock inlagrade i denna råhumus. Ingen mykorrhiza på bokrötterna, svarta svamphyfer dominera (*Mr. nigrostrigosum* m. fl.). Här och där kraftig infektion av *Mucor Ramanianus*. Grovmullen i regel torr, med finare fördelning än i den normala mulljorden. Mullen är starkt bemängd av svamphyfer, såväl *M. r. atrovirens*, *M. r. nigrostrigosum* som *M. 17 a* och *M. 19 f*. Nedåt blir mullen kritblandad med kritkorn från ärtstorlek till hönsäggstorlek. Mullagret med talrika snäckskal (framför allt av *Helicigona lapicida* och *Cepaea hortensis*).

#### *Markprofilens kemiska karaktäristik.*

Förnan har mycket hög halt av mineralsalter, fosforsyra, kalk och kali. Den visar från fall till fall en anmärkningsvärd variation i pH. Nedåt sjunker koncentrationen av kali och fosforsyra successivt och visar de lägsta värdena i mullen. Samtidigt stiger emellertid kalkhalten och pH-värdet. Nitrifikationen har i ett par fall helt avstannat och visar i andra fall låga till medelmåttiga värden. Ammonifikationen har endast undersökts i ett fall och visar där ett regelbundet avtagande mot djupet.

*Vegetationsanalyserna utförda: nr 1—3 i maj 1935, nr 4 i juni 1931 och nr 5 i maj 1936.*

#### V. Råhumus (utan egentligt fornaskikt).

	1	2	3	4	5	6	7	8	Ekologisk typ
A <sub>2</sub> Sluten, olikåldrig bokskog, medelhöjd 11 m.									
C <i>Actaea spicata</i> .....	—	—	—	+	—	—	1	—	a
Anemone Hepatica.....	+	+	+	2	+	—	+	—	a
Anemone nemorosa.....	1	2	2	2	1	—	+	—	a
Asperula odorata .....	+	+	1	—	+	—	+	2	a
Cephalanthera alba.....	—	—	—	—	+	—	—	—	a
Coralliorhiza trifida .....	—	—	—	—	+	—	+	—	ab
Hedera helix .....	—	—	+	—	1	—	+	—	ac
Juniperus communis .....	—	—	—	—	—	—	+	—	c
Lathyrus pratensis.....	—	—	—	—	1	—	—	—	c
Melampyrum pratense .....	2	1	+	1	1	—	+	—	ab
Mercurialis perennis.....	1	5	+	4	2	6	1	+	a
Neottia nidus avis .....	—	—	+	—	—	—	—	—	a
Orobus vernus.....	—	—	+	—	—	—	—	—	a
Pimpinella saxifraga .....	—	—	—	+	—	—	—	—	c
Polygonatum multiflorum .....	..	1	—	—	—	—	—	—	a
Pyrola secunda .....	2	—	—	+	1	—	—	—	ab
Sanicula europaea .....	—	—	—	+	1	—	—	—	a

	1	2	3	4	5	6	7	8	Ekologisk typ
Senecio sylvaticus.....	—	—	—	+	—	—	—	—	bc
Taraxacum sp.....	+	—	—	—	—	—	—	—	d
Vicia sepium .....	—	—	—	—	+	—	—	—	a
Vicia sylvatica .....	—	—	—	—	+	2	1	1	a
Viola hirta .....	—	—	—	—	1	—	—	—	ac
Viola silvestris.....	+	+	+	2	2	—	+	—	a
Brachypodium sylvaticum .....	+	+	+	3	—	—	+	—	a
Bromus Benekenii .....	—	—	—	—	1	—	—	—	a
Carex digitata .....	3	—	—	2	5	—	1	—	ac
Carex diversicolor .....	—	—	+	—	—	—	—	—	d
Dactylis Aschersoniana .....	..	—	—	—	+	—	—	—	a
Dactylis glomerata.....	—	+	—	—	—	—	—	—	a
Festuca rubra .....	—	—	—	2	—	—	—	—	c
Melica uniflora .....	—	—	—	—	+	—	—	—	a
Poa angustifolia .....	—	—	—	—	+	—	—	—	ac
Poa nemoralis .....	1	—	—	—	—	8	—	—	a
Pteridium aquilinum .....	—	+	—	—	—	—	—	+	ab
D Anomodon viticulosus .....	—	—	—	—	—	2	—	—	
Brachythecium velutinum .....	—	—	—	—	—	31	—	—	
Bryum capillare .....	—	—	—	—	—	1	—	—	
Camptothecium lutescens.....	—	—	—	—	—	3	—	—	
Dicranum scoparium .....	—	—	—	—	—	2	—	—	
Encalypta contorta .....	+	—	—	—	—	2	8	—	
Hypnum cupressiforme .....	4	—	—	—	—	5	+	—	
Isothecium viviparum .....	—	—	—	—	—	20	—	—	
Mnium hornum .....	—	—	—	—	—	2	—	—	
Mnium sylvaticum .....	+	—	—	—	—	—	—	—	
Rhytidadelphus triquetrus .....	1	—	—	—	—	+	—	—	
Tortella tortuosa .....	2	—	—	—	—	+	—	—	
Cladonia sp.....	+	—	—	—	—	4	+	—	
Peltigera canina .....	4	—	—	—	—	—	+	—	

## Markprofiler.

	1	2	3	4	5	6	7	8
Lösförna (täckningsgrad).....	2	2	2	3	3	..	3	5
Råhumus (mäktighet, cm) .....	6	9	14	5	19	6	10	6
P <sub>2</sub> O <sub>5</sub> .....	..	..	36	..	..	20	28	16
pH .....	..	..	7,5	..	7,1	7,3	6,5	5,7
Ca .....	..	..	850	..	..	..	..	..
K .....	..	..	31	..	..	..	..	..

	1	2	3	4	5	6	7	8
NO <sub>3</sub> a .....	..	..	15	..	0	0	0	0
NO <sub>3</sub> b .....	..	..	8	..	0	0	0	0
NH <sub>3</sub> b .....	..	..	..	..	40	..	40	42
Grovmull (rämull = r, finmull = f) (mäktighet, cm) .....	15 f	21	22	25	25	15	20	4 r + 15
P <sub>2</sub> O <sub>5</sub> .....	..	..	2	..	..	4	4	30 + 20
p <sub>H</sub> .....	..	..	7.5	..	..	7.4	7.4	6.7 + 7.5
Ca .....	..	..	450	..	..	..	..	..
K .....	..	..	..	..	..	..	..	..
NO <sub>3</sub> a .....	..	..	0	..	..	0	10	0 + 0
NO <sub>3</sub> b .....	..	..	55	..	..	35	90	30 + 100
NH <sub>3</sub> b .....	..	..	..	..	..	..	..	..
Grovmull med kritinblandning (mäktighet, cm) .....	15	10	8	15	10	30	20	15
Krita .....	..	..	..	..	..	..	..	..
Daggmaskar i råhumusen, antal pr. m <sup>2</sup> ....	..	..	0	0	0	0	4	57

#### Markprofilens allmänna utseende.

Lösförna tunn, ofta icke täckande råhumusen. Filtförna kan förekomma, men är då endast ett par centimeter mäktig. Råhumusskiktet är amorft, men innehåller dock alltid en hel del bladmateriel med bibehållen struktur. Det är hårt sammanfiltat av bokrötter och svamphyfer, varvid tidigare omnämnda bruna och svarta mycel dominera. *Mucor Ramannianus* har inom dessa råhumusfläckar en vidsträckt utbredning. Ett hittills obestämt basidiomycet-mycel, troligen en *Cortinarius*-art, uppträder här och där dominerande såväl i råhumus, rämull och mull, varvid humustäcket så gott som fullständigt nedbrytes och får en ljus gulgrå ton. Se härom vidare fig. 19. Skikten innehåller mycket insektskrement och döda insekter. Det övergår antingen i ett tunt rämullskikt eller med skarp gräns i grovmullen. Denna är grovkornig, torr och rikt försedd med mycel. Den blir i sina nedre partier starkt kritinblandad. Daggmask förekommer sparsamt framför allt går *Allolobophora caliginosa* från den underliggande mullen upp i råhumusen och bidrager till dess omvandling. *Dendrobaena octaedra*, som är en typisk råhumusmask, förekommer här och där i råhumusen.

#### Markprofilens kemiska karaktäristik.

Råhumusen har en mycket hög halt av mineralsalter, framför allt kalk och fosforsyra. Dess reaktion är svagt sur till alkalisk. Den nitrificerar svagt eller icke alls, däremot har ammoniakomsättning påvisats. Askhalten är låg, 5–11 %.

Vegetationsanalyserna utförda: nr 1–4 i maj 1935, nr 5 i juni 1931, nr 6–8 i maj 1936.

## VI. Råmull (utan egentligt fornaskikt).

	1	2	3	4	5	6	7	8	9	10	11	Ekologisk typ
A <sub>2</sub> Sluten, olikåldrig bokskog. Medelhöjd 11 m												
B <sub>2</sub> <i>Fagus silvatica</i> .....	—	—	—	—	—	+	—	—	1	—	+	
<i>Juniperus communis</i> .....	—	—	—	—	—	—	—	+	—	+	—	
C <i>Actaea spicata</i> .....	+	5	—	+	3	+	—	—	—	—	—	a
<i>Anemone hepatica</i> .....	2	+	—	1	2	+	1	+	3	+	—	a
<i>Anemone nemorosa</i> .....	4	2	+	4	+	+	+	1	—	4	4	a
<i>Arabis hirsuta</i> .....	—	—	—	—	—	—	—	—	+	—	—	ac
<i>Asperula odorata</i> .....	1	+	3	+	2	+	2	—	1	—	—	a
<i>Cephalanthera alba</i> .....	—	—	—	—	—	—	—	+	—	—	—	a
<i>Convallaria majalis</i> .....	—	—	—	+	1	+	+	—	—	—	—	ab
<i>Coralliorrhiza trifida</i> .....	—	—	—	—	—	—	—	—	1	—	—	ab
<i>Dentaria bulbifera</i> .....	—	—	—	1	—	2	—	—	—	—	—	a
<i>Galium boreale</i> .....	—	—	—	—	1	—	+	—	—	—	—	c
<i>Hedera helix</i> .....	—	—	+	—	+	—	+	1	—	—	—	ac
<i>Hieracium</i> sp. .....	—	—	—	—	—	—	+	—	—	—	—	d
<i>Lathyrus pratensis</i> .....	—	—	—	—	1	—	—	1	—	—	—	c
<i>Majanthemum bifolium</i> .....	—	—	—	—	—	+	—	—	—	3	—	b
<i>Melampyrum pratense</i> .....	+	1	—	+	1	3	—	1	+	+	—	ab
<i>Mercurialis perennis</i> .....	3	3	+	+	+	2	+	2	—	—	—	a
<i>Orobus vernus</i> .....	+	—	+	—	+	+	+	1	2	+	+	a
<i>Oxalis acetosella</i> .....	—	—	—	—	—	—	—	—	—	+	—	a
<i>Pimpinella saxifraga</i> .....	—	—	—	—	—	—	—	—	1	—	—	c
<i>Pyrola secunda</i> .....	—	—	—	—	—	—	—	—	—	—	+	ab
<i>Sanicula europaea</i> .....	+	—	+	—	—	—	—	+	—	—	—	a
<i>Vicia sepium</i> .....	—	—	—	—	—	—	—	—	1	—	—	a
<i>Vicia sylvatica</i> .....	—	—	+	—	—	—	—	—	—	—	—	a
<i>Viola hirta</i> .....	—	—	—	—	—	—	—	—	1	—	—	ac
<i>Viola silvestris</i> .....	+	+	+	+	+	1	+	2	—	1	—	a
<i>Brachypodium sylvaticum</i> .....	—	3	—	—	—	1	1	—	—	—	—	a
<i>Bromus Benekenii</i> .....	—	—	—	—	—	—	—	—	1	—	—	a
<i>Carex digitata</i> .....	+	1	—	+	2	3	4	5	8	—	4	ac
<i>Carex diversicolor</i> .....	—	+	—	—	—	—	—	—	—	—	—	c
<i>Dactylis Aschersoniana</i> .....	—	—	—	—	—	—	—	—	1	4	—	a
<i>Festuca ovina</i> .....	—	—	—	—	—	—	—	—	—	1	—	c
<i>Festuca rubra</i> .....	—	—	—	—	—	—	—	—	—	6	1	c
<i>Luzula pilosa</i> .....	—	—	—	—	+	—	+	—	1	1	—	b
<i>Melica nutans</i> .....	—	—	—	—	1	—	+	1	—	—	—	a
<i>Poa angustifolia</i> .....	—	—	—	—	+	—	1	2	7	—	—	ac
<i>Poa nemoralis</i> .....	+	—	—	4	1	1	3	—	+	—	—	a
D <i>Amblystegium serpens</i> .....	—	1	—	—	—	+	—	+	—	—	—	
<i>Barbula rubella</i> .....	—	—	—	—	3	—	—	—	—	—	—	
<i>Brachythecium rutabulum</i> .....	+	+	—	4	—	—	5	—	—	—	—	
<i>Brachythecium velutinum</i> .....	1	1	—	6	3	2	3	3	11	—	18	

	1	2	3	4	5	6	7	8	9	10	11	Ekologisk typ
Bryum capillare.....	—	—	—	—	+	—	—	—	—	—	—	—
Bryum sp. ....	—	—	—	—	—	—	+	—	—	—	—	—
Campylium chrysophyllum....	—	—	—	—	—	—	—	—	—	1	—	—
Campylium hispidulum v. Sommerfeltii.....	—	—	—	1	—	—	—	+	—	—	—	—
Dicranum scoparium.....	—	—	—	—	—	—	—	+	—	+	4	—
Encalypta contorta .....	+	—	—	4	—	—	4	—	—	—	—	+
Eurhynchium Swartzii .....	—	—	—	—	—	—	+	1	+	—	—	—
Homalothecium sericeum .....	—	1	—	—	—	+	—	+	—	—	—	—
Hypnum cupressiforme .....	4	—	+	+	+	+	2	—	—	+	3	—
Isothecium viviparum .....	3	—	—	—	9	+	9	7	+	1	18	—
Metzgeria furcata.....	+	—	—	—	1	—	—	—	—	+	1	—
Mnium hornum .....	—	—	—	—	—	—	—	—	—	1	—	—
Mnium marginatum .....	—	—	—	—	+	—	1	—	—	—	—	—
Mnium silvaticum .....	—	—	—	+	+	—	—	8	—	+	4	—
Neckera complanata .....	—	—	—	—	1	—	—	—	—	—	—	—
Neckera crispa .....	—	—	—	—	—	—	—	—	—	—	—	—
Porella platypylla .....	1	—	—	—	5	—	—	—	—	—	—	—
Rhytidadelphus triquetrus....	—	—	—	—	—	—	—	1	—	—	—	—
Tortula subulata .....	2	—	—	2	6	—	—	—	—	—	—	—
Tortella tortuosa .....	—	+	+	2	14	+	—	+	—	+	6	—
Peltigera canina .....	3	—	—	—	4	1	+	—	—	—	3	—

## Markprofiler.

	1	2	3	4	5	6	7	8	9	10	11
Lösförna (täckningsgrad) .....	0	4	3	2	1	2	1	1	0	3	3
Råmull (mäktighet, cm) .....	4	10	5	7	3	5	3	11	9	4	9
P <sub>2</sub> O <sub>5</sub> .....	24	12	..	8	28	12	..	..	..	30	30
p <sub>H</sub> .....	6.9	7.4	..	7.4	6.9	7.0	..	7.1	7.4	7.3	7.4
Ca.....	600	700	..	800	..	..	..	..	..	..	..
K .....	20	11	..	9	..	..	..	..	..	..	..
NO <sub>3</sub> a .....	10	15	..	12	5	50	..	..	0	0	22
NO <sub>3</sub> b .....	200	110	..	10	400	170	..	0	85	30	90
NH <sub>3</sub> b .....	..	..	..	..	..	..	..	0	848	..	..
Finnmull (mäktighet, cm) .....	0	0	0	5	6	6	6	0	2	0	0
Grov mull (mäktighet, cm) .....	12	22	20	5	14	12	14	10	12	21	20
P <sub>2</sub> O <sub>5</sub> .....	2	2	..	..	10	8	..	..	..	22	10
p <sub>H</sub> .....	7.4	7.5	..	..	7.5	7.5	..	7.6	7.3	7.5	7.5
Ca.....	500	420	..	..	..	..	..	..	..	..	..
K .....	7	7	..	..	..	..	..	..	..	..	..
NO <sub>3</sub> a .....	12	15	..	..	18	15	..	..	0	24	14
NO <sub>3</sub> b .....	130	140	..	..	52	63	..	..	63	9	9

	1	2	3	4	5	6	7	8	9	10	11
Grovmull med kritinblandning (mäktighet, cm) .....	14	15	15	22	16	15	20	5	28	45	25
P <sub>2</sub> O <sub>5</sub> .....	2	..	..	..	..	..	..	..	..	..	..
pH .....	7.5	..	..	..	..	..	..	..	..	..	..
Ca .....	540	..	..	..	..	..	..	..	..	..	..
K .....	3	..	..	..	..	..	..	..	..	..	..
NO <sub>3</sub> a .....	20	..	..	..	..	..	..	..	..	..	..
NO <sub>3</sub> b .....	270	..	..	..	..	..	..	..	..	..	..
Krita .....											
Daggmaskar i råmullen, antal pr. m <sup>2</sup> .....	..	..	..	..	..	..	0	33	80	0	

*Markprofilens allmänna utseende.*

Förna saknas så gott som fullständigt. Den täcker icke råmullen. Den utgöres av knoppfjäll, ollonskålar och kvistar av bok samt av snäckskal, men däremot icke i någon större utsträckning av blad.

Råmullen bildar ett övre 5—10 cm mäktig lager, ganska starkt hopfiltat av bokrötter och med bruna och svarta mycelier genomvävande hela skiktet. Den håller en icke oväsentlig halt av mineralbeståndsdelar, som genom daggmaskarna transporterats upp från underlagrande skikt. Råmullen övergår ofta utan gräns i ett tunt skikt av *finmull*, vilket utgör rester av ett äldre råhumuslager, vilket genom maskarnas arbete nu omvandlats till mull. Detta överlagrar *grovmullen*, vilken visar typisk klumpstruktur och är hård och torr. Den innehåller mycket rikligt svarta och vita mycel. De mörka mycelierna utgörs huvudsakligen av *Mycelium radicis atrovirens* och *M. radicis nigrostrigosum*. Ovannämnda basidiomycet är vanlig. Nedåt är grovmullen starkt kritblandad. *Dendrobaena octaedra* förekommer sporadiskt tillsammans med *Allolobophora caliginosa*.

*Markprofilens kemiska karaktäristik.*

Råmullen befinner sig i stark omsättning. Den nitrificerar i regel väl och har en hög halt av fosforsyra, kalk och kali. Surhetsgraden är låg. Askhalten i detta skikt är betydligt högre än i råhumusen. Den underliggande grovmullen visar låg halt av fosforsyra och kali, men ger en kraftig nitratreaktion även i skiktets nedre delar.

*Vegetationsanalyserna utförda: nr 1—7 i maj 1935, nr 8 i juni 1931, nr 9 i juni 1929, nr 10—11 i maj 1936.*

## Zusammenfassung.

### Biologische Untersuchungen im Buchenwald auf Möens Klint.

*Die Burgwälle auf dem Timmesöbjerg.* Meine Untersuchungen der Wald- und Bodenverhältnisse auf dem Timmesöbjerg führten zur Entdeckung einer bisher unbekannten, vom Wällen umgebenen Burg auf der Bergspitze. Diese Anlage hat gewissermassen zur Entwicklung des eigenartigen Humustyps beigetragen, was näher in den Kapiteln 3 und 4 berührt wird. Innerhalb des Burgplatzes sind Pflasterungen sowie eine kleine, quadratische, schwach markierte Anlage vorgefunden worden. Ausserdem sind bei den pedologischen Untersuchungen ziemlich bedeutende Kohenschichten im westlichen Teil der Anlage zutage gekommen, sowie verarbeitete Knochen von Rindern und einem Hund. Die Burg liegt 113 m ü. d. M. mit freier Aussicht über die südliche Ostsee nahe Möens Ostküste und ragt 30 bis 40 m über das umgebende Terrain. Eine grössere Ähnlichkeit besteht zwischen dieser Buraganlage und den norddeutschen Wendenburgen, vor allem denen auf Rügen. Uebereinstimmungen sind ebenfalls festgestellt worden zwischen Saxos Schilderung des Wendengottes Svantevit in Arkona und den Volkstraditionen über »Jöden Opsal« von Möens Klint. Überdies ist das Vorkommen eines Wanderblocks behandelt worden, der vom Volk Svantesestein oder Svantevitstein genannt wird. Dieses nebst anderem, bekräftigt eine Theorie über einen nahen Zusammenhang der Kultur der Wenden mit der von Ostmöen aus fröhistorischer Zeit. Eine archeologische Untersuchung der Timmesöbjerg Burg, wo man ein unberührtes archeologisches Material finden würde, könnte dieses Problem sicher weiter beleuchten. Hierzu Fig. 1—5,

*Der Buchenwald.* Der Buchenwald im Timmesöbjergs alten Burggelände ist ein ungleichaltriger Naturwald, der keine Spuren eines älteren Kulturzustands trägt. Er dürfte einer der sehr wenigen Naturwälder Dänemarks sein. Die ältesten Bäume stammen aus dem 16. Jahrhundert, der Hauptteil des Bestandes aber aus der ersten Hälfte des 18 Jahrhunderts. Der Wald weist durchgehend eine Lückenstruktur von der Art auf, die neulich von SERNANDER in seinem Aufsatz über »Granskär und Fiby Urskog« beschrieben wurde. Im Verlauf meiner Untersuchung ergab es sich jedoch, dass in diesem Naturwald vor 100—200 Jahren eine Abholzung obgleich von geringerem Umfange stattgefunden hat. Sowohl friche als alte Sturmschläge kommen hier vor. Interessant sind in diesem Zusammenhang die Windwurfhügel — diejenigen der jülländischen Heiden sind vorher eingehend behandelt worden — welche von früher auf dem Berge verbreiteten Sturmschlägen zeugen.

Zahlreiche ältere Stubben kommen im Bestande vor, doch erwies sich dass der grösste Teil dieser nicht die Spuren einer Abholzung, sondern von Dürrbäumen herrüren. Das im Verhältnis zur Anzahl der Stubben sparsame Auftreten von Fallstämmen zeigt, dass der Dürrwald des Berges früher genutzt wurde. Eine Untersuchung des Alters der Fallstämme zeigt, dass diese sehr alt sind; in einigen näher untersuchten Fällen konnte man feststellen, dass sie von Bäumen herstammen, die

vor ein Paar hundert Jahren eingegangen sind. Die Vermorderung des Holzes erfolgt sehr langsam.

Der Kalkreichtum, die extreme Bodentrockenheit und die starke Infektion des Bodens durch Schmarotzerpilze bestimmt der Verjüngungsgang. So wird die Verjüngung durch das kalkreiche Substrat beschleunigt, was wie früher bewiesen für die Buchenverjüngung in den skandinavischen Buchenwäldern die Regel ist (LINDQUIST 1931). Im Laufe des letzten Jahrhunderts erfolgte die Verjüngung sowohl in den Lücken als auch unter Schirm, die Pflanzenentwicklung zeigte aber durchweg eine Tendenz zur Stagnation. Der Zuwachs der Pflanzen ist oft ebenso schwach wie der der norrländischen Kiefernheidepflanzen. In einigen Fällen ist eine veritable Fallstamverjüngung (»Kadaververjüngung«) gleicher Art, wie auf norrländischen Kiefernheideböden beobachtet worden. Neben der Samenverjüngung kommt eine effektive Verjüngung auf vegetativem Wege durch Wurzelhals- und Stockausschlag vor. Diese Verjüngungsform — charakteristisch für einige Buchenwälder Skandinaviens — ist unabhängig von der Viehweide. Die Fallstamverjüngung, die Zuwachsstagnation der Buchenpflanzen und die langsame Vermorderung auf diesem subneutralen Buchenwaldboden haben bemerkenswerte Analogien mit den norrländischen Kiefernheideböden. Hierzu Fig. 6—14.

*Humusformen und Bodenprofile.* Die terrestrischen Humusformen, die die Humusdecke der Skandinavischen Wälder bilden, sind die »Förna«, der Rohhumus und der Mull. Für eine annehmbare Beschreibung und Benennung der Humusprofile ist es von grosser Bedeutung, dass Rücksicht auf die Entwicklung sowohl der »Förna« als auch des Rohhumus und des Mulls genommen wird. Als »Förna«-schicht, hier »Förna« genannt, bezeichne ich die Schicht des Humusprofils, deren Hauptmasse aus makroskopischen Tier- und Pflanzenresten besteht. Die Rohhumusschicht, oder der Rohhumus, ist die amorphe, wenig mineralische Beimenungen enthaltende, oft ganz strukturierte Schicht und die Mullschicht oder der Mull ist eine an mineralischen Beimengungen reiche Humusschicht, die auf Timmesöbjerg eine mehr oder weniger ausgeprägt körnige Struktur hat. Was die Charakteristik des Rohhumus betrifft, so gibt es einen prinzipiellen Unterschied zwischen der oben gegebenen Definition und der in Schweden üblichen Auffassung (siehe z. B. HESSELMAN 1926) dahingehend, dass hier die Vermorderungsschicht nicht zum Rohhumus, sondern zu der »Förna« gerechnet wird.

Timmesöbjergs »Förna« entwickelt sich teils als eine lose »Förna« und teils als eine filzige »Förna«. Die lose »Förna« (schwedisch Lösförna) die der Streuschicht entspricht ist locker und nicht zusammenhängend, die filzige »Förna« (schwedisch Filtförna) bildet dagegen eine vor allem durch Pilzhypfen verflochtene, zähe, filzartige Masse mit überwiegend grober Struktur von makroskopisch erkennbaren Pflanzenresten. Die mikrobiologische Abbauform ist für die Lösförna hauptsächlich durch Bakterien die Filzförna vorwiegend durch Pilze bedingt. Die Regenwürmern sind für den Abbau der Lösförna von wesentlicher Bedeutung, dagegen beteiligen sie sich nur in einem geringen Grad an dem Abbau der Filzförna. Die lose »Förna«

bildet beinahe im ganzen Gelände dieses Waldes eine dünne Schicht an der Oberfläche der Humusdecke und wird nur an den dem Winde ausgesetzten Stellen vermisst. Wo die Zersetzung aus irgendwelcher Ursache gehemmt wird, wird die lose »förla» von einer filzigen »Förna» unterlagert. Chemisch ist der Unterschied zwischen diesen »Förna»-typen nicht besonders gross. Der Gehalt an Phosphat, Ca und K ist in beiden Förnaschichten ungefähr derselbe; er ist hier aber bedeutend höher als in den unterliegenden Schichten. Der  $p_H$ -Wert der »Lösförna» ist ein wenig niedriger als der der »Filtförna».

Timmesöbjergs Rohhumus ist subneutral ( $p_H$  5.7—7.4), amorph und nicht nennenswert mineralisch (89—96 % organische Stoffe). Bei Zersetzung ist gehemmt, die Nitrifikation in der Regel schwach oder bleibt ganz aus. Diese Rohhumusform enthält ziemlich grosse Mengen Phosphate, Ca und K und ist von Pilzmycelen durchwoben, welch letztere zuweilen den wesentlichen Teil der Schichtmasse bilden. Den Rohhumus findet man auf dem Berge innerhalb kleiner begrenzter Flächen (siehe Fig. 16), bald von Filzförna überlagert, bald als Oberflächenschicht der Humusdecke. Der Abbau im Rohhumus geschieht zum grössten Teil durch Pilze und Insekten.

Der Mull ist entweder ein Grobmull, mit grober Krümmelstruktur, oder ein Feinmull mit feiner Krümmelstruktur, oder ein Rohmull mit feiner Krümmelstruktur und ausserdem mit erheblicher Beimengung von organischem Material. Der Grob- und Feinmull enthält im Durchschnitt 5—25 % organisch Substanz, der Rohmull dagegen bis zu 60 %. Der Grobmull ist die hier am meisten vorkommende Mullform. Derselbe überlagert direkt den Kreidegrund und bedeckt beinahe die ganze Bergfläche. Diesen Entwicklung dürfte wohl meistens von dem reichen Gehalt an Feinerde im Mineralboden abhängig sein. Der Feinmull entsteht entweder als eine Degenerationsform des Grobmulls in den Lücken des Bestandes, wo die Mullerde der Sonne und den Niederschlägen ausgesetzt wird, oder als eine Übergangsform zwischen Rohmull und Grobmull. Der Grobmull und der Feinmull haben einen  $p_H$ -Wert von c:a 7.5 mit geringen Variationen. Der  $p_H$ -Wert des Rohmulls liegt durchschnittlich etwas tiefer (bei 7.2). Der Rohmull ist reicher an Phosphaten, Ca und K als die übrigen Mullarten und hat hier eine stärkere Nitrifikation. Die Zersetzung im Mull ist überwiegend bakteriell, doch kommen Pilzmyzele in dieser Mullerde reichlicher vor als ich sie in irgendeiner anderen Mullerde der skandinavischen Wälder finden konnte. Vielleicht trägt hierzu der hohe Kalkgehalt und die starke Vertrocknung bei.

Die Untersuchung ergab, dass Timmesöbjergs morphologisch sehr gut charakterisierte Rohhumus in wesentlichen chemischen Eigenschaften mit den sauren Rohhumusbildungen der skandinavischen Wälder übereinstimmt. Der Humusgehalt ist hoch und die Nitratbildung schwach oder ganz gehemmt. Auch mikrobiologisch sind Uebereinstimmungen mit den sauren Rohhumusbildungen vorhanden, und zwar das zahlreiche Vorkommen von typischen Pilzmyzelen. Der subneutrale Rohhumus besitzt jedoch einen hohen Kalkgehalt und reagiert schwach sauer bis alkalisch.

Timmesöbjergs Bodenprofile sind aufgebaut von Kombinationen einer oder

mehrerer Arten dieser Humustypen sowie von deren Varianten. Das vorherrschende Bodenprofil ist das »Förna«-Grobmull-Profil, welches grösstenteils das Gelände bedeckt. Aus diesem Profiltyp entwickelt sich ein »Förna«-Rohhumus-Profil, das auf dem Grobmull lagert. Diese Kombination von Rohhumus und Grobmull ist in den skandinavischen Wäldern ebenso wenig bekannt wie der subneutrale Rohhumus. Eine weitere Entwicklung dieses Profils kann zu einem Grobmullprofil leiten mit einem sukzessiven Uebergang in einem Rohhumus-Grobmull-Profil. Dieser Entwicklungszyklus dürfte sich jedoch über einen langen Zeitraum spannen. Dieses wird im nächsten Kapitel näher besprochen. Hierzu Fig. 15—21.

*Die Rohhumusbildung und deren Ursachen.* In den skandinavischen Wäldern spielen die Regenwürmer bei der Humusbildung eine grosse Rolle. Die Faktoren, die das reiche Vorkommen dieser Tiere begrenzen, grenzen auch im allgemeinen die Mullbildung von der Rohhumusbildung ab. Diese Hauptfaktoren sind die Azidität des Bodens, die Art des »Förna«-Materials, die Bodenfeuchtigkeit und gewisse thermische Verhältnisse. Die Azidität ist für das Gedeihen der Regenwürmer von grosser Bedeutung und auf subneutralen Substraten der südkandinavischen Wälder ( $p_H$  5.5—) findet man durchweg eine effektive Regenwurmfauna. Da meines Wissens eine Rohhumusbildung auf subneutralen Substraten der südkandinavischen Wälder nicht bekannt ist, hielt ich es für zweckmässig die Verhältnisse zu untersuchen, unter welchen sich Timmesöbjergs Rohhumus sich entwickelt hat. Die Entwicklung begann mit einer abnormen »Förna«-Ansammlung auf einem vertrocknetem Substrat. Die »Förna«-Anhäufung fand in Mulden und Senken im Riesig und Zweigen von gefallenen Buchen, sowie in der Wacholdervegetation statt. Diese »Förna«-Ansammlung war aber zu reichlich, um eine Zersetzung durch den vorhandenen Regenwürmerbestand zu erlauben, welch letzterer zufolge der starken Vertrocknung sehr reduziert war. Das »Förna«-Material wird langsam im amorphen Rohhumus abgebaut hauptsächlich von Insekten und Schnecken und durch die zahlreich vorkommenden Myzele der Humuspilze zusammengefilitzt. Die zuweilen extrem niedrige Azidität dieses Rohhumus ( $p_H$  bis zu 7.4) wird teilweise durch die reichliche Kalkverwehung im Klintgebiete verursacht. Hierzu Fig. 22—29.

*Ueber die Pflanzengesellschaften auf den verschiedenen Bodenarten des Timmesöbjergs.* Die dominierende Pflanzengesellschaft auf dem Timmesöbjerg ist eine *Anemone hepatica*—*Carex digitata*-Gesellschaft. Im Rahmen dieser Pflanzengesellschaft kann eine Anzahl von Gesellschaften niedrigeren soziologischen Ranges beobachtet werden (meine früheren Soziationen entsprechend). Nur der »Lösförna«-Grobmull kann eine grössere Anzahl solcher Gesellschaften mit einer reichlicheren Variation innerhalb derselben aufweisen. Hier kommen ausser einer *Anemone hepatica*—*Carex digitata*-Ges., eine *Mercurialis perennis*-Ges., eine *Actaea spicata*-Ges. sowie zahlreiche Gräser-Gesellschaften vor. Das Verschwinden der »Förna« unter gegebenen Verhältnissen und das Aussetzen der Mullerde der Sonne und dem Winde führt zu einer starken Reduktion der Anzahl und der Verbreitung dieser Gesellschaften. Für gewöhnlich entstehen Fragmente von Pflanzengesellschaften mit Arten aus dem Buchenwald

und den trockenen Hügeln in einer ziemlich regelloser Vermischung. Einige Gräsergesellschaften entwickeln sich hier, vor allem die *Dactylis*- und die *Festuca rubra*-Ges. Da auf die Vertrocknung des Mulls eine »Förna»-Ansammlung folgt (verursacht durch das Heranwachsen von Wacholder oder durch die Reisigdecke) werden die obenerwähnten Gesellschaften in der Regel vollständig zersprengt. Dies ist vor allem auf dem »Filtförna»-Boden der Fall wo selten oder ausnahmsweise eine *Mercurialis perennis*- oder eine *Asperula odorata*-Ges. gebildet werden. Auch auf dem Rohhumus und auf dem Rohmull kann man nicht von der Entwicklung wirklicher Feldschichtgesellschaften sprechen. Hier kommt dagegen eine Anzahl Bodenschichtgesellschaften von Kalkmoosen vor. Auf diesen entsteht eine ziemlich reiche Kraut- und Grasvegetation, artenreich aber aus Hungerformen bestehend. Bei dem Uebergang des Rohhumus und des Rohmulls in Mull gelangen *Anemone hepatica*—*Carex digitata*-Ges. aufs neue zur Entwicklung.

Das Studium der Vegetationsverteilung auf den verschiedenen Humustypen des Timmesöbjergs zeigt, wie ein typischer Rohhumus, obgleich mit subneutraler Reaktion, der in vielen Fällen nicht nitrifiziert und von typischen Rohhumuspilzen stark durchsetzt ist, eine reiche Krautflora von der Art trägt, die wir sonst in unseren besten Eichen- und Buchenwäldern auf Mullboden finden. Unter der Kraut- und Grasflora auf diesem Rohhumus findet man *Mercurialis perennis*, allgemein als Merkmal eines guten Mullzustandes angesehen, *Cephalanthera alba*, *Neottia nidus avis*, *Anemone nemorosa*, *Hedera helix*, *Orobus vernus*, *Vicia sepium*, *Viola silvestris*, sowie unter den Haingräsern *Brachypodium silvaticum*, *Bromus Benekenii*, *Dactylis Aschersoniana* und *Melica uniflora*, die alle unsere besten Mullböden charakterisieren. Von wirklich charakteristischen Rohhumuspflanzen weist dagegen diese Artenliste keine Spur auf. Die Anwesenheit von *Pteridium aquilinum*, das im Klinteskoven hier und da auch auf gutem Mullboden auftritt, sowie von *Pyrola secunda*, *Corallorrhiza trifida*, *Melampyrum pratense* und *Monotropa hypopitys* kann vielleicht damit erklärt werden, dass das Substrat sich nicht in einer guten Zersetzung befindet, da diese Arten ebenfalls auf saurem Rohhumusboden vorkommen. — Das angeführte Beispiel ergibt, dass in diesem Falle nicht die Humusform als solche, sondern deren Azidität, die Vegetationsverteilung bestimmt. Es liegt für uns somit eine Veranlassung vor, unsere Auffassung von der Rohhumusflora zu revidieren.

Es muss auch bemerkt werden, dass in diesem Gelände sowohl Büsche als Kräuter und Haingräser vorkommen, die für gewöhnlich nicht zu der Buchenwaldflora gerechnet werden können, sondern typische Eichenwaldelemente sind, und muss das Vorkommen dieser Arten von dem alkalischen Substrat bedingt sein.

#### *Vegetationsanalysen und Bodenprofile.*

Seite 38 bis 51 werden Vegetationsanalysen angeführt, die während 1929—1936 auf dem Timmesöbjerg gemacht worden sind. Die Analysen konnten nicht in der gewünschten Ausstreckung gemacht werden, und die hier gegebenen  $1 \times 1$  m Analysen

nach der Punktmethode sind oft für die Pflanzengesellschaften, welche sie absehen, nicht ganz representativ. Die Analysen sind in erster Linie gemacht worden, um eine Korrelation zwischen den Bodenprofilen und den Bodenanalysen zu erhalten. Zwecks Klarstellung der Pflanzengesellschaften des Timmesöbjergs sind außer dem hier genannten Material noch hunderte von quadratmetergrossen Analysen in Verband angelegt und nach der Methode Hult—Sernander geschätzt.

Wie vorerwähnt, sind die analysierten Quadranten nach der von mir im Jahre 1931 beschriebenen Punktmetode behandelt worden. Die Bodenprofile geben die Mächtigkeit der Humusformen in cm als Durchschnittszahl von 4 Messungen in jeder Profil an, und außerdem für die nicht deckende »Lösforna« den Deckungsgrad laut der Hult—Sernander-Skala.

Der Phosphatgehalt wird in Phosphatgraden nach Arrhenius angegeben (1 Phosphatgrad = 1/1000 mg  $P_2O_5$  löslich in 2 %-iger Zitronensäure), Ca als in NaCl austauschbares Kalzium in mg pro kg lufttrockenen Erde, K in mg Kalium pro kg lufttrockener Erde, sowie  $NO_3$  und  $NH_3$  ebenfalls in mg N pro kg lufttrockener Erde. Lit. a und b bei  $NO_3$  geben die Werte gleich nach der Probenahme und nach 1-Monatlicher Lagerung an.

Die verschiedenen Profiltypen und deren Vegetation folgen hier dem Entwicklungszyklus, der auf dem Timmesöbjerg, wie konstatiert, von der Mullbildung über die Rohhumusbildung wieder zur Mullbildung leitet.

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## LITTERATUR

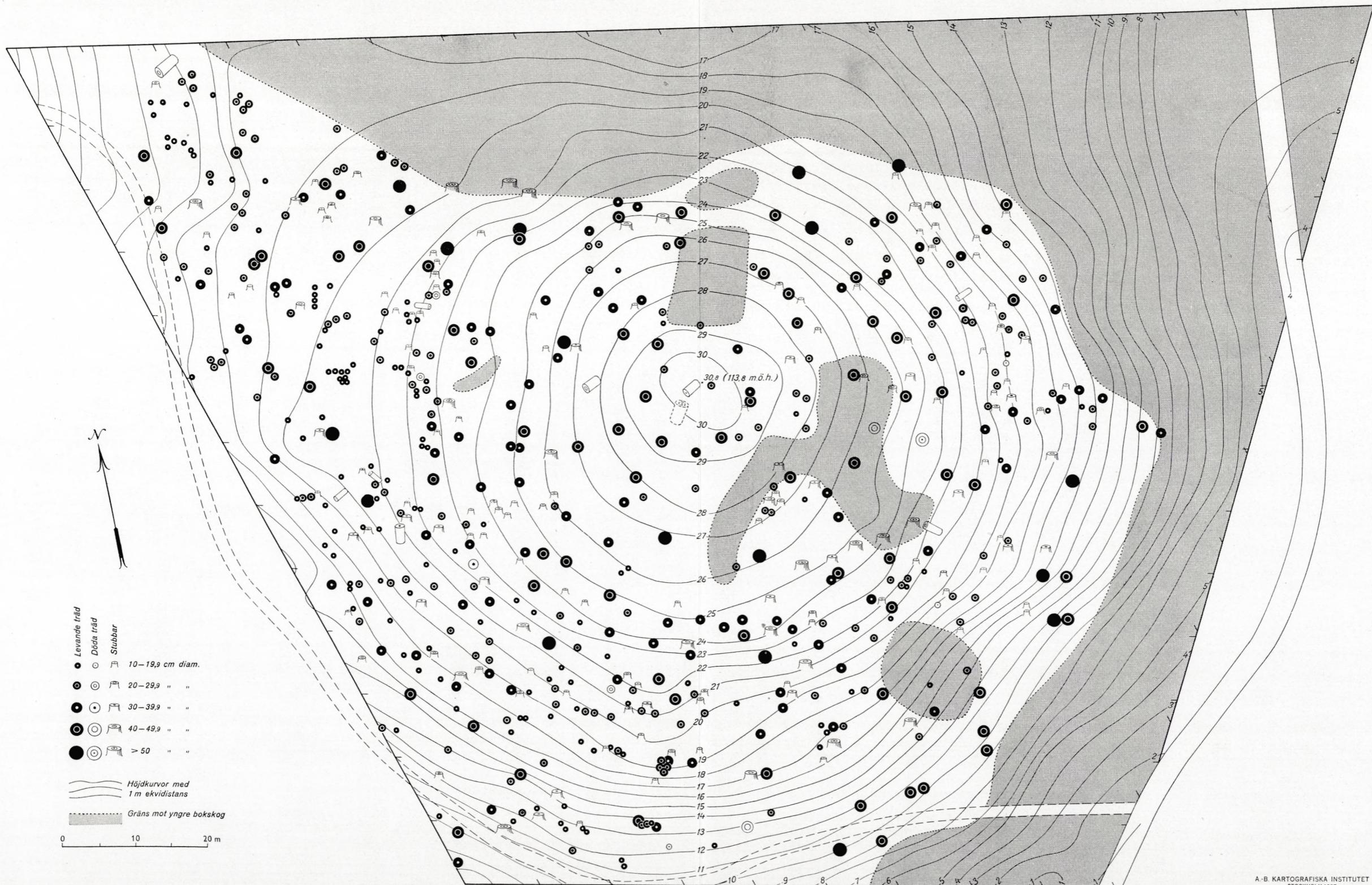
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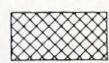
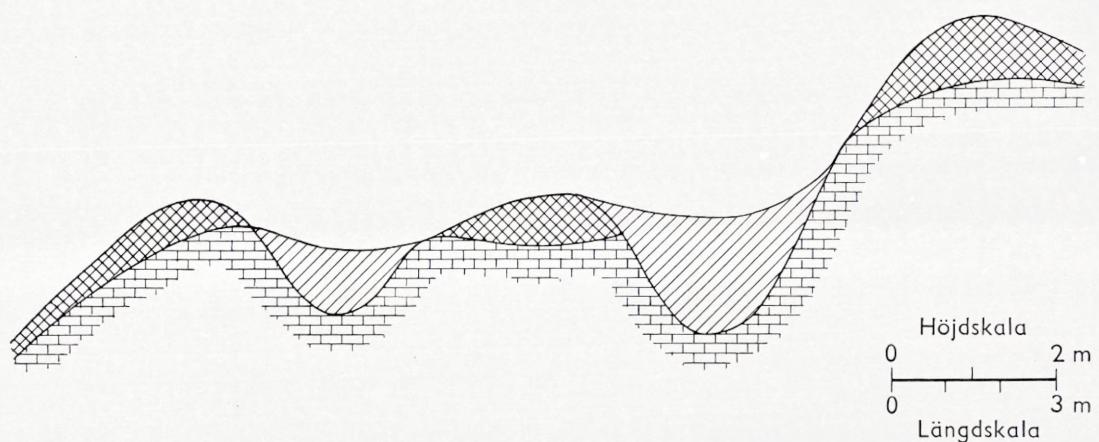


Taylor.

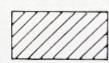




1



Kritblandad mull



I vall/graven  
ansamlad humus



Krita

2

Fig. 1. Vallarnas läge på Timmesöbjerg jämt läget av den inre fyrkanten. Höjdkurvorna visa borgens naturliga begränsning i sydväst till sydost.

Abb. 1. Die Lage der Wälle auf dem Timmesöbjerg sowie die Lage des inneren Vierecks. Die Höhenkurven zeigen die natürliche Begrenzung der Burg im Südwesten bis Südosten.

Fig. 2. Profil genom vallgravarna i västra delen av Timmesöbjerg med nuvarande och ursprungligt djup inlagt.

Abb. 2. Profil durch die Wallgräben im westlichen Teil des Timmesöbjergs, die gegenwärtige und ursprüngliche Tiefe zeigend.

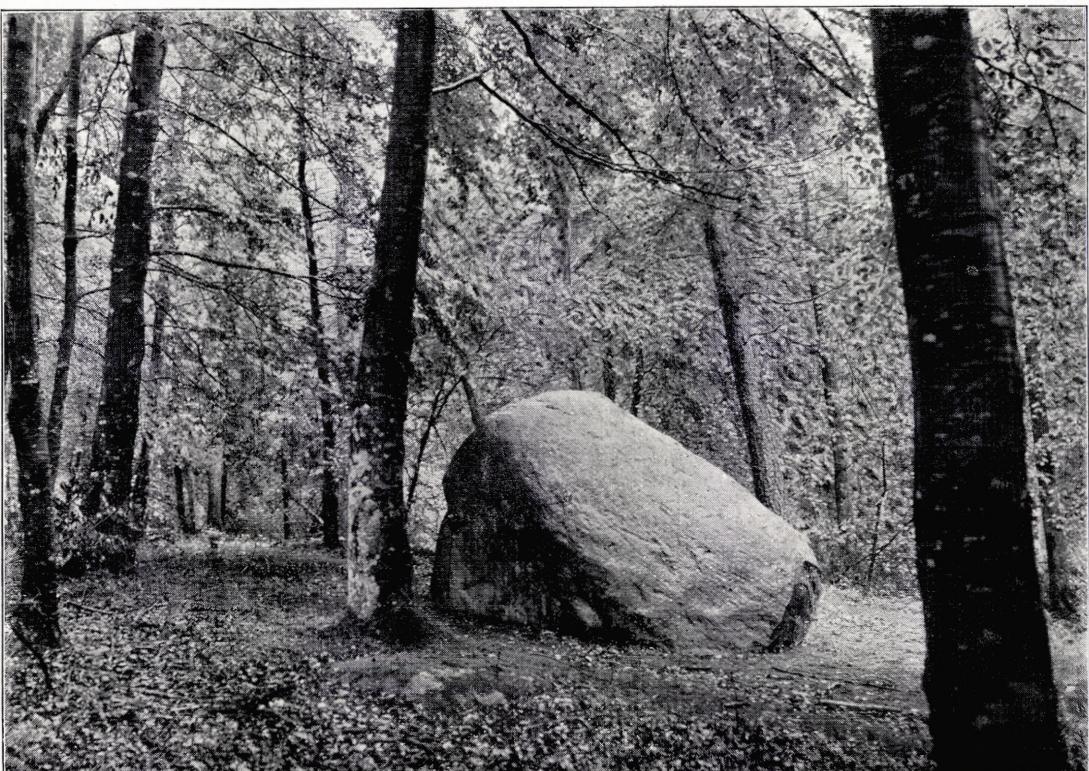
Fig. 3. Innanför borgvallarna förekommer i östra delarna av kalotten ett inre system av svaga vallar bildande en fyrkant av c:a  $7 \text{ m} \times 9.5 \text{ m}$ . Den innehåller rikligt med sten, otvivelaktigt ditförd av människohand. Den stenbelagda fyrkanten företer viss likhet med de svaga stensättningar man funnit vid utgrävningarna vid Garz på Rügen och vid den plats vid Feldberg i Preussen, som man antagit vara Rethre. Dessa stensättningar ha där — ehuru på mycket vaga grunder — tolkats som borgarnas tempelplatser.

Abb. 3. Innerhalb der Burgwälle findet man im östlichen Teil der Kalotte ein Innensystem von schwachen Wällen, ein Viereck von ca.  $7 \text{ m} \times 9.5 \text{ m}$ , das reichlich Steine enthält, die zweifellos von Menschenhänden hingebracht worden sind. Das gepflasterte Viereck weist eine gewisse Ähnlichkeit mit der schwachen Pflasterung auf, die man bei den Ausgrabungen bei Garz auf Rügen vorfand, sowie an dem Ort bei Feldberg in Preussen, der als Rethre angesehen wird. Diese Pflasterungen werden dort, obgleich auf sehr vagen Gründen, für Tempelplätze dieser Burgen gehalten.





4



5

Fig. 4. En bild av vallsystemet visande övre och mellersta vallarna i sydvästra delen. I övre vallen har här ett omkring 5 cm mäktigt kollager påträffats. I gravarnas bottnar har h. o. d. utbildats råhumus och råmull och såväl lösförneskiktet som filtförneskiktet är mäktiga. Forntidsmänniskan har därigenom indirekt blivit en orsak till utbildning av den unika råhumusformen.

Abb. 4. Die oberen und mittleren Wälle im südwestlichen Teil. In den oberen Wällen ist hier eine Kohlenschicht von ca. 5 cm Stärke angetroffen worden. In der Sohle der Gräben hat sich stellenweise Rohumus und Rohmull gebildet; sowohl die lose Streuschicht als auch die flichtige Streuschicht sind sehr stark. Der Vorzeitmensch ist dadurch zur indirekten Ursache dieser uniken Bildung von subneutraler Rohhumusform geworden.

Fig. 5. När Aborrebjerg ligger den s. k. Svantesestenen eller Svantevitstenen, ett stort flyttblock till vilket åtskilliga sägner äro knutna. Stenen har antagits vara en hednisk offersten och omnämnes här, då namnet möjligen kan tyda på tidiga förbindelser mellan Møen och vendarna söder om Östersjön.

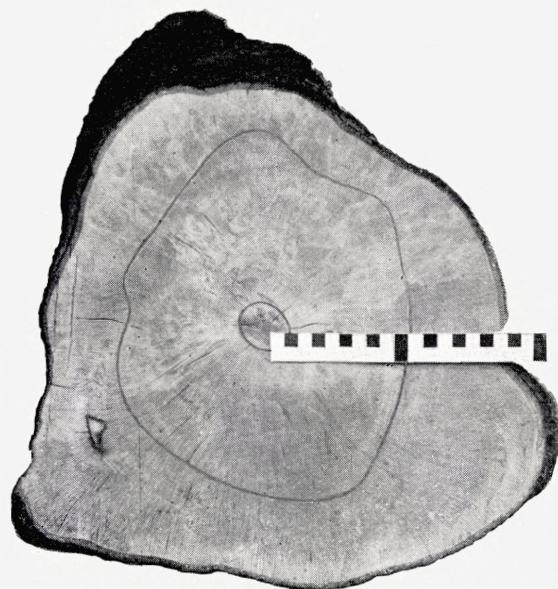
Abb. 5. Nahe dem Aborrebjerg liegt der sog. Svantesstein oder Svantevitstein, ein grosser Wanderblock, an den sich mehrere Sagen knüpfen. Dieser Block, der ein heidnischer Opferstein gewesen sein soll, wird hier deshalb erwähnt, weil der Nahme möglicherweise auf frühe Verbindungen zwischen Møen und den Wenden südlich der Ostsee hindeutet.

Fig. 6. Stubbensnitt av det stormfällda trädet å fig. 8. De markerade ringarna ange trädets dimension vid 100 år och vid 200 år. På stubbensnittet har räknats 324 årsringar.

Abb. 6. Stubbenschnitt des auf Fig. 8 abgebildeten Fallstammes. Die markierten Ringe geben die Dimensionen des Baumes bei einem Alter von 100 und 200 Jahren an. Der Querschnitt weist 324 Jahrringe auf.

Fig. 7. Den yngsta skogsgenerationen på Timmesöbjerg är 80—100-årig och av klena dimensioner. Den har kommit upp i torrskogsluckor och stormluckor vid början av 1800-talet.

Abb. 7. Die jüngste Waldgeneration von Timmesöbjerg ist 80 bis 100 jährig und von schwachen Dimensionen, sie ist in Dürrwald- und Sturmlücken zu Beginn des 19 Jahrhunderts entstanden.



6



7

8



6



Fig. 8. På grund av den långsamma förmultningen på Timmesöbjerg kunna lågorna ännu iakttagas efter århundraden. Den mossklädda strimman i ängsvegetationen å bilden härrör från en gammal låga, vars stubbe skyntar svagt invid den färska rotvältan ovanför. Ett studium av tillväxten hos det nyligen fallna, c:a 350-åriga trädet, som på bilden representeras av rotvältesulan, kan ge en möjlighet till bestämning av lågans ålder. Den torde vara minst 245 år, möjligens 350 år gammal (se texten sid. 11).

Abb. 8. Zufolge der langsamen Vermorderung auf Timmesöbjerg sind Fallstämme Jahrhunderte nach dem Umstürzen noch zu erkennen. Der bemoste Streifen inmitten von Wiesenvegetation röhrt von einem alten Fallstamm her., dessen Stubben neben dem frischen Windwurfballen schwach zu sehen ist. Ein Studium des Zuwachses des kürzlich umgestürzten, ca. 350-jährigen Baumes, dessen Wurzelballensohle auf dem Bilde zu sehen ist, gibt eine Möglichkeit das Alter des ersterwähnten Fallstamms zu bestimmen. Dieser dürfte wenigstens 245, möglicherweise 350 Jahre alt sein (siehe Text S. 11).

Fig. 9. Bokskogens föryngring sker här dels genom plantuppslag i luckorna och under skärm, dels genom stubbskott och rotorskott. Föryngringen med fröplantor sker långsamt och är ganska otillfredsställande ur förstlig synpunkt. Tillyväxten hos ungplantorna är dessutom mycket svag; den oväxtliga föryngringen påminner starkt om den oväxtliga tallhedsföryngring, som ofta uppträder i norra Sverige. Plantan å bilden har vid c:a 40 års ålder uppnått en höjd av endast 22 cm, trots att ljustillträdet icke varit särskilt svagt.

Abb. 9. Die Verjüngung des Buchenwaldes erfolgt teils durch Aufschlag in den Lücken und unter Schirm, teils durch Stubben- und Wurzelausschlag. Die Verjüngung mittelst Keimpflanzen erfolgt langsam und ist wirtschaftlich ziemlich ungenügend. Außerdem ist der Zuwachs junger Pflanzen sehr schwach: die langsam wachsende Verjüngung erinnert sehr an die kümmerliche Kieferverjüngung auf nordschwedische Kiefernheiden. Die Pflanze auf dem Bilde hat bei einem Alter von ca. 40 Jahren eine Höhe von nur 22 cm erreicht, obgleich der Lichtzutritt nicht besonders schwach war.

Fig. 10. Rotskottsföryngring är vanlig på kalkmarkerna på Timmesöbjerg. Bilden visar en c:a 200-årig stam, som sannolikt uppkommit som rotskott på den äldre boken.

Abb. 10. Die Wurzelstockverjüngung ist eine gewöhnliche Erscheinung auf Kalkböden von Timmesöbjerg. Die Abbildung veranschaulicht einen ca. 200-jährigen Stamm, der wahrscheinlich als Wurzeltrieb der älteren Buche zu betrachten ist.

Fig. 11. Här och var i Klinteskovens kritterräng möter man extrema utslag av denna förmåga till rotskottsbildning. Bilden, från i ett bestånd vid Röde Udfald i norra delen av Klintområdet, visar den vegetativa reproduktionen hos en gammal bok, vars ålder beräknats till minst 400 år.

Abb. 11. Hier und dort im Klinteskovens Kreideterrain trifft man extreme Fälle dieser Fähigkeit des Wurzelstockausschlags. Die Aufnahme ist in einem Bestand bei Röde Udfald im nördlichen Teil des Klintgebietes gemacht worden und veranschaulicht die vegetative Reproduktion einer alten Buche, deren Alter auf wenigstens 400 Jahre berechnet wird.



11



10

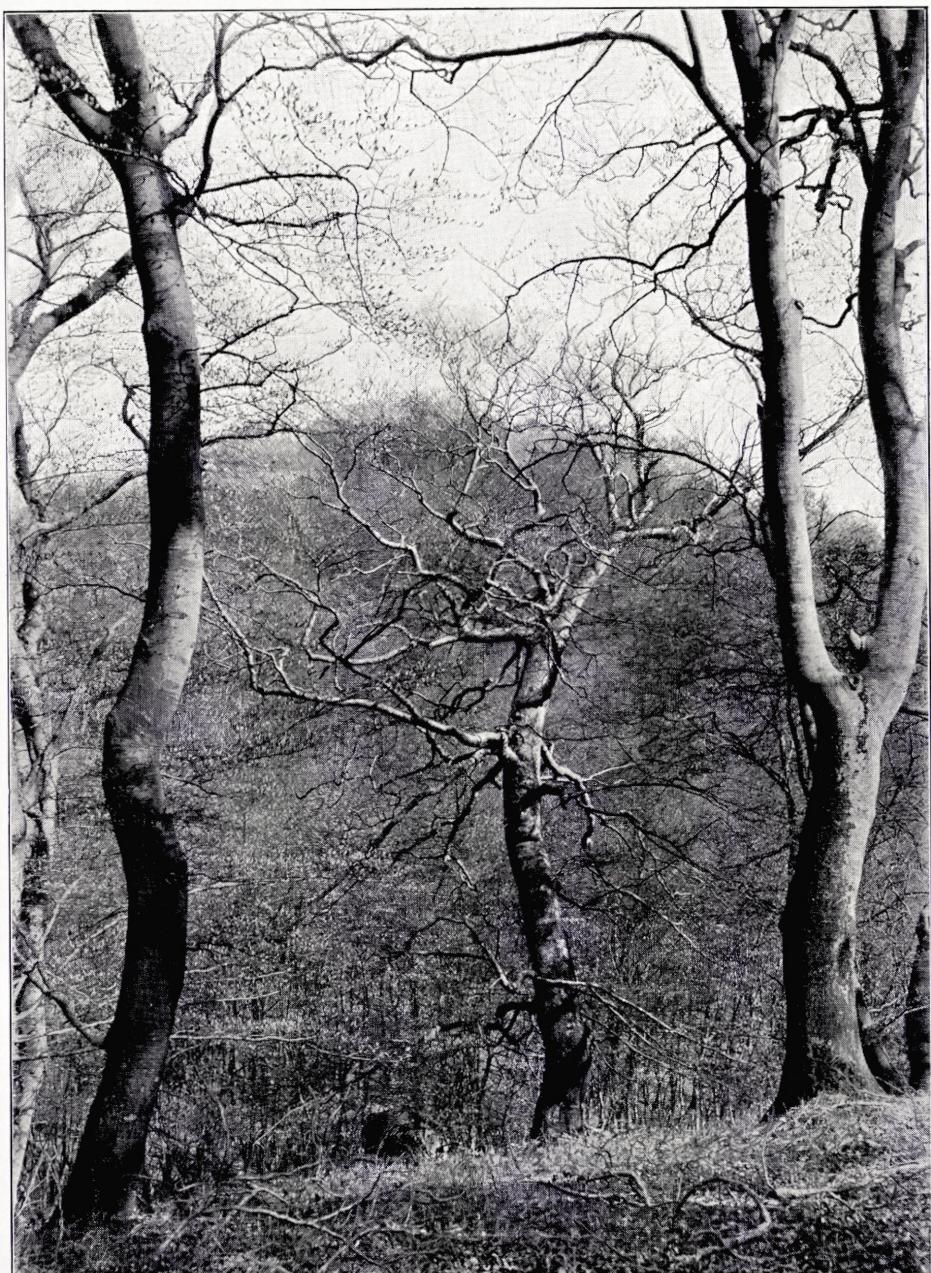


Fig. 12. Utsikten från den omtalade inre vallanläggningen mot Siesöbjerg, vars topp når 111 meter ö. h. Rakt i öster stänges utsikten av Siesöbjergs bokskogsklädda kalott, men i söder och sydost är utsikten fri över södra Östersjöbäckenet. — Vegetationen utgöres av *Dactylis*- och *Poa nemoralis*-samhällen. Trädet å bildens mitt tillhör den äldsta, c:a 300-åriga bokskogsgenerationen.

Abb. 12. Siesjöbjerg von der erwähnten Wallanlage von Timmesöbjerg gesehen. In östlicher Richtung wird die Aussicht durch die buchenbewachsene Kalotte von Siesöbjerg gesperrt. Im Süden und Südosten hat man dagegen einen freien Blick auf die südliche Ostsee. — Pflanzengesellschaften von *Poa nemoralis*, *Dactylis glomerata* und *D. Aschersoniana* etc. Der Baum in der Mitte gehört zu der ältesten ca. 300 jährigen Buchengeneration.

Fig. 13. En ur föryngringssynpunkt ytterst intressant företeelse på Timmesöbjerg är här avbildade fall av veritabel lågföryngring av samma typ som lågföryngringen på de norrländska tallhedsmarkerna. Lågan på bilden föll någon gång under 1700-talets första år och måste efter all rimlighet ha givit upphov till de fem trädens anordning. Denna slutsats görs i direkt analogi med lågföryngringen på tallhedarna. — Bokarna på bilden omkring 220 år gamla. Förmultningen på denna mullmark är kraftigt hämmad.

Abb. 13. Eine äusserst interessante Erscheinung auf dem Timmesöbjerg bietet der hier abgebildete Fall einer veritablen Fallstammverjüngung (»Kadaververjüngung«) von dem Typ wie in norrländischen Kieferheiden. Der fragliche Stamm stürzte in den ersten Jahren der 18. Jahrhunderts und dürfte allem Anschein nach der Urheber der fünf abgebildeten Bäume sein. Dieser Schluss wird in direkter Analogie mit der Fallstammverjüngung in Kiefernheiden gezogen. Die Vermorderung auf diesem Mullboden ist stark gehemmt.



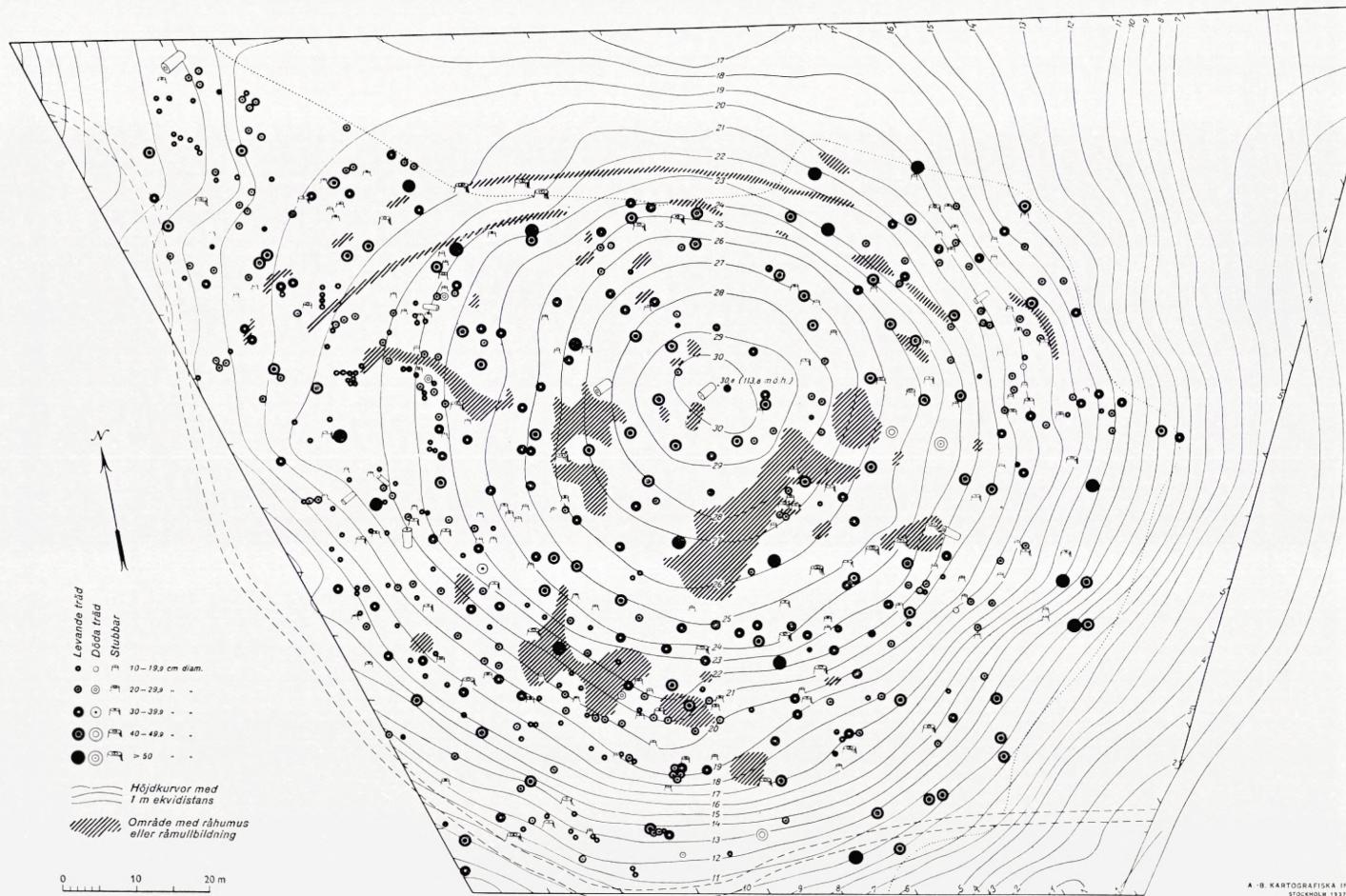
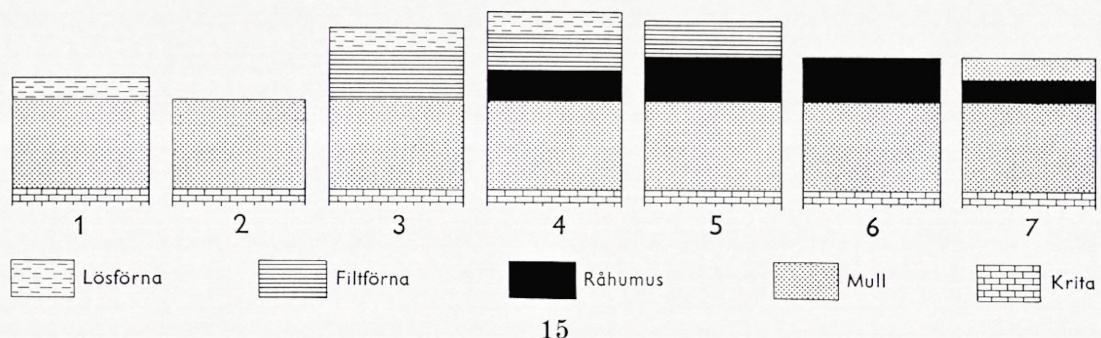


Fig. 15. En schematisk framställning av humusprofilerna på Timmesöbjerg. Utgångsläget, en lösförna-mull-profil, genomloper en utveckling motsvarande n:r 2—7, om vilket närmare kan läsas i texten. Profilbenämningarna sker med angivande av i profilen ingående humusformer och deras varianter t. ex. för n:r 4: lösförna-filtförna-råhumus-grovmull-profil. — Mulljorden har förutsatts äga en konstant tjocklek och kritgrundens har i samtliga fall lagts på samma nivå. Skiktens olika tjocklek i en profil skall illustrera den relativa skillnaden dememellan. Råhumusens olika tjocklek i 4—7 avser att illustrera utvecklingen från dess begynnande daning i n:r 4 till dess övergång i råmull i n:r 7.

Abb. 15. Eine schematische Darstellung der Humusprofile des Timmesöbjergs. Die Ausgangslage, ein »Lösförna-Grobmull-Profil«, durchläuft eine Entwicklung entsprechend Nr. 2—7 oben, worüber näheres im deutschen Resumé. Die Benennung der Profile erfolgt unter Angabe der in den Profilen vorkommenden Humusformen und deren Varianten, z. B. No. 4: »Lösförna-Filtförna-Rohhumus-Grobmull«-Profil. Man setzt voraus, dass die Mullschicht eine konstante Tiefe besitzt und dass der Kreideboden in sämtlichen Fällen auf denselben Niveau liegt. Die verschiedenen Tiefen der Schichten eines Profils sollen die relative Mächtigkeit zwischen denselben darstellen. Die Variation des Rohhumus in No. 4—7 illustriert die Entwicklung desselben von Anfang an (No. 4) bis zu seinem Übergang in Rohmull (No. 7).

Fig. 16. Översikt över förekomsten av råhumus och råmull på Timmesöbjerg. De smärre ovala partierna härröra i flertalet fall från gamla rotvältor; de långsträckta områdena i norr ha bildats i gravarnas bottnar.

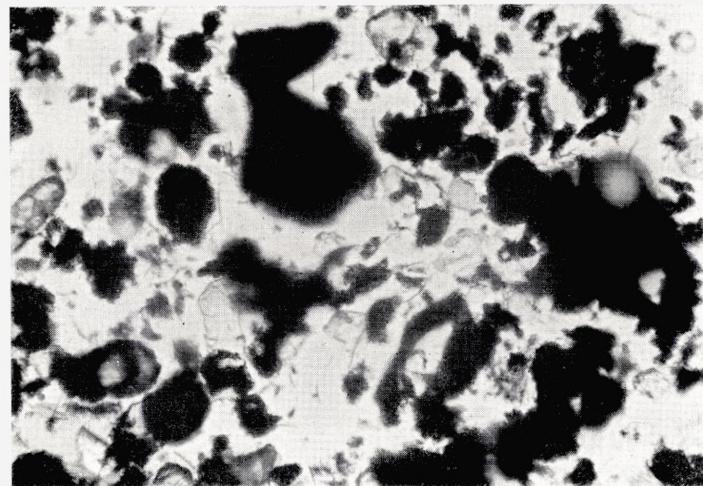
Abb. 16. Übersicht über das Vorkommen von Rohhumus und Rohmull auf dem Timmesöbjerg (schräffierte Flächen). Die kleineren, ovalen Flächen stammen in mehreren Fällen von alten Fallstämmen; die langen Flächen im Norden haben sich auf den Sohlen der Wallgräben gebildet.

Fig. 17. Prov av grovmullen på Timmesöbjerg, 300 × förstoring. Mineraljordskornen framträda tydligt bland de mörka konkretionerna av finfördelat vegetativt material och bakteriekolonier. Även korta trådar av *M. r. nigrostrigosum* framträda tydligt.

Abb. 17. Grobmullprobe vom Timmesöbjerg, 300 fach vergrössert. Mineralerdteile fallen deutlich zwischen den dunklen Konkretionen von feinverteiltem, vegetativem Material und Bakterieansiedlungen ins Auge. Auch kurze Fasern der *M. r. nigrostrigosum* Hatsch treten deutlich hervor.

Fig. 18. Prov på råhumusen på Timmesöbjerg, 300 × förstoring. Skiktet består genomgående av sönderdelat växtmaterial med ännu bibehållen struktur.

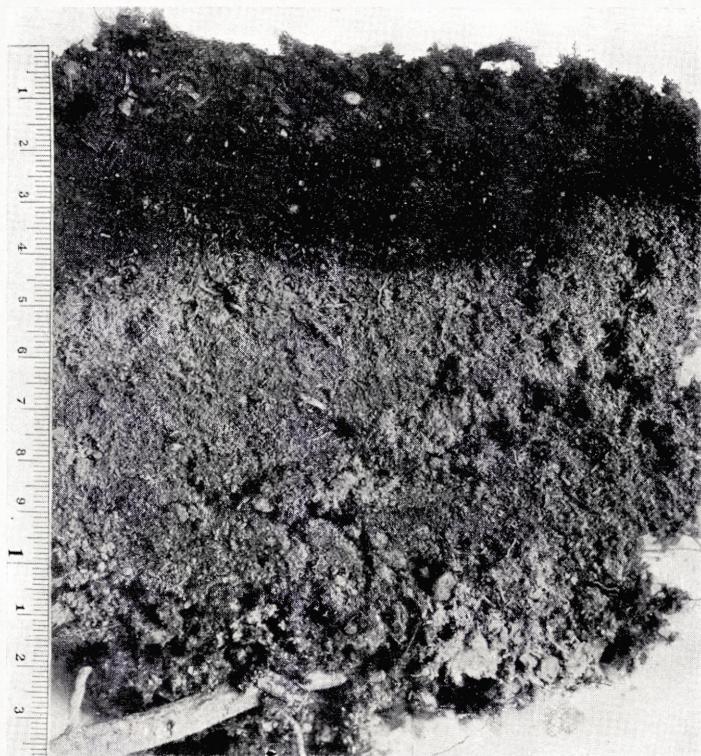
Abb. 18. Rohhumusprobe von Timmesöbjerg, 300 fache Vergrösserung. Die Schicht besteht durchgehend aus zersetzem Pflanzenstoff mit noch beibehaltener Struktur.



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Fig. 19. Inom vissa partier av Timmesöbjerg förekommer en infektion av såväl råhumusen som mullen förorsakad av svampar bland vilka ett gråvitt vitrötemycelium, troligen en *Cortinarius*-art syner spela huvudrollen. Svampen avfärgar humusen och ger åt levande bokrötter, som kommer i dess väg, en gulvit färgton. Samma degenerationsfenomen återfinnes i större utsträckning i de norrländska stavagranskogarna och i de gamla *Myrtillus*-granskogarna.

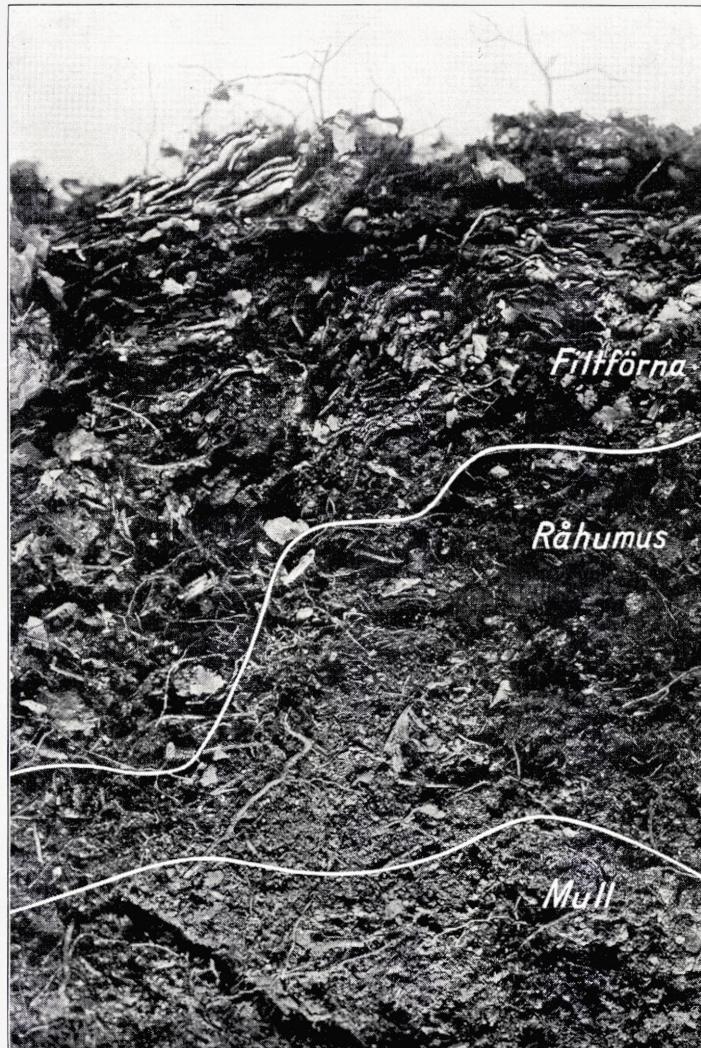
Abb. 19. Stellenweise ist auf dem Timmesöbjerg sowohl der Rohhumus, als auch der Mull infiziert. Diese Infektion ist durch Pilze verursacht, unter welchen ein grauweisses ligninabbauendes Mycel, vermutlich eine *Cortinarius*-art, die Hauptrolle spielen dürfte. Der Pilz entfärbt den Humus und verleiht den in seinen Weg gelangenden Buchenwurzeln einen gelbweissen Farbton. Das gleiche Degenerationsphänomen findet man auch, obgleich in grösserem Umfang, in den norrländischen Stavakiefern- und in den alten *Myrtillus*-kiefernwäldern.

Fig. 20. Den subneutrala mullen på Timmesöbjerg har ett  $p_H$  av c:a 7.5. Den är en typisk grovmull, men skiljer sig från de normala grovmulljordarna genom en mycket rik svampflora av sådana arter som *M. r. nigrostrigosum*, *M. r. atrovirens*, *M. 17 a* och andra. Mulljorden är trots svamfloran och den starka uttorkningen djup och lucker och underlagras direkt av kritan.

Abb. 20. Der subneutrale Mull von Timmesöbjerg hat einen  $p_H$ -Wert von ca. 7.5. Er ist ein typischer Grobmull; doch unterscheidet er sich von den normalen Grobmull-Arten durch eine sehr reiche Pilzflora solcher Art wie: *M. r. nigrostrigosum*, *M. r. atrovirens*, *M. 17 a* (siehe LINDQUIST 1937). Die Mullerde ist trotz der Pilzflora und der starken Vertrocknung tief und locker und wird direkt von Kreide unterlagert.

Fig. 21. En filtförna-råhumus-mull-profil från Timmesöbjerg.

Abb. 21. Ein »Filzförna«-Rohhumus-Mull-Profil vom Timmesöbjerg.



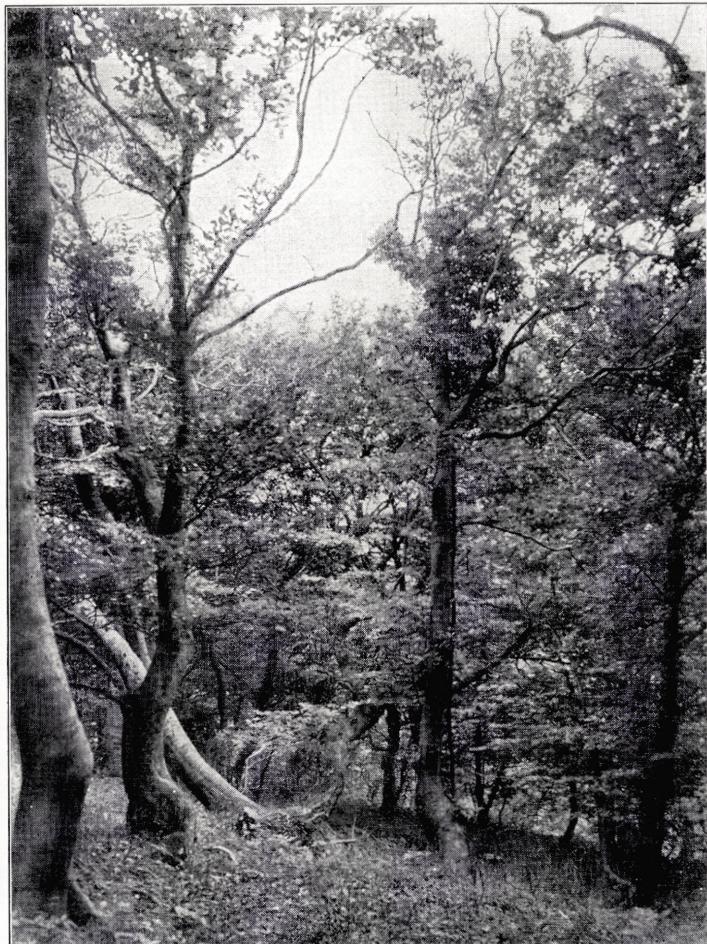


Fig. 22. Timmesöbjerg-skogen visar, trots att den står på uråldrig kulturmark, många typiska urskogsdrag och torde vara en av de verkligt få och sällsynta skogsrester i Danmark, som kan förtjäna namn av naturskog. Stormluckor och torrskogsluckor förekomma och urgamla lågor ligga fortfarande orörda och svagt förmulnade på marken. Bilden visar en nyslagen stormlucka, efter vinterstormen 1934, där den starkt dränerade marken förbränts av solen och enbuskarna börjat invandra. En äldre, döende enbuskvegetation på denna plats röjer tidigare förekomst av en liknande lucka. Till höger å bilden en murgrönestam, som går upp i bokens krona. Bredvid det stormslagna trädet ett stånd av *Lonicera Xylosteum*.

Abb. 22. Timmesöbjerger Wald hat viele typische Urwaldzüge, obgleich er auf einem uralten Kulturboden stockt, und dürfte einer der wenigen und seltenen Waldreste Dänemarks sein, die den Namen Naturwald verdienen. Sturm- und Dürrwaldlücken kommen vor und uralte Fallstämme liegen immer noch ungerührt und schwach vermodert auf dem Boden. Das Bild zeigt eine Stormlücke nach dem Wintersturm 1934, der stark dränierte Boden ist von der Sonne verbrannt worden und die Einwanderung von Wacholderbüschchen hat begonnen. Eine ältere Wacholdervegetation auf diesem Platze deutet darauf hin, dass hier auch früher eine ähnliche Lücke vorhanden war. Rechts ein Efeu, der sich am Stamm in die Buchenkrone emporrankt. Neben dem sturmgeschlagenen Baume sieht man *Lonicera Xylosteum*.

Fig. 23. På Timmesöbjerg upptäcktes sommaren 1929 en hittills opåaktad, subneutral råhumusbildning med ett  $p_H$ -värde av upp till 7.4. I föreliggande uppsats har utbildningen av denna råhumusbildning gjorts till föremål för en undersökning. Råhumusbildningen har visat sig bero bl. a. av en abnormt stark förneansamling kring fallna grenar och stammar samt kring enbuskar, en föreansamling, som accentueras genom markens starka exposition för sydliga vindar. Utvecklingen från mull till råhumus illustreras här med bilderna 22 till 29. Vidstående bild visar, huru förneansamlingen blir effektiv kring lågor med ett rikt grenverk och kring fallna relativt färska grenar. Kring grenarna på bilden har förna ansamlats till ett djup av 40 c:m och nedbrytningen har i detta material förlängsammats. Förneanhopningen utgör ett initialstadium till råhumusbildningen.

Abb. 23. In Sommer 1929 ist auf Timmesöbjerg eine bisher unbeachtete, subneutrale Rohhumusbildung mit einem  $p_H$ -Wert bis zu 7.4 entdeckt worden. Die Entstehung einer solchen Rohhumusbildung ist in diesem Aufsatz zum Gegenstand einer Untersuchung gemacht worden. Die Entwicklung ist u. a. von der abnorm starken Streuansammlung um die gefallenen Äste und Stämme, sowie um die Wacholderbuche abhängig. Diese Streuansammlung wird durch die starke Exposition gegen Süden weiter akzentuiert. Die Entwicklung von Mull zum Rohhumus wird durch die Abbildungen 22 bis 29 illustriert. Die beistehende Abbildung zeigt, wie eine Streuansammlung um Fallstämme mit reichem Zweigwerk, sowie um relativ frisch gefallene Äste effektiv wird. Um die abgebildeten Äste hat sich die Streu bis zu einer Tiefe von 40 cm angesammelt, wodurch der Abbau in diesem Material verzögert wurde.

Fig. 24. Torrträden äga icke denna förmåga att ansamla förna, eftersom det finare grenverket i regel förstörts innan träden övergå till lågor. Marken blir på detta sätt mera effektivt förbränd och i luckorna efter torrträden får man senare en rik ansamling av *Juniperus*.

Abb. 24. Die Dürrbäume besitzen nicht die Fähigkeit zur Streuansammlung, da das feinere Zweigwerk in der Regel schon vor dem Falle des Baumes zerstört wird. Der Boden wird dadurch effektiver ausgetrocknet und in den Dürrbaumlücken erhält man danach reichliche Entwicklung von *Juniperus*.



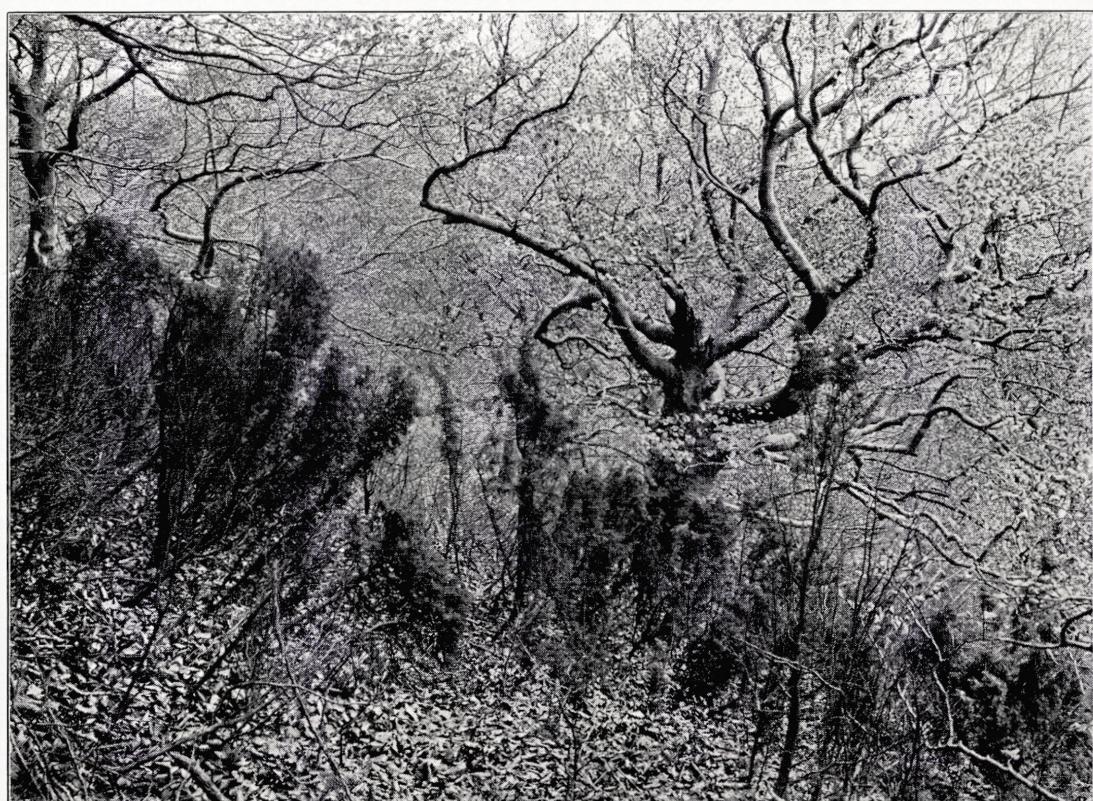
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Fig. 25. Förnaansamlingen accentueras ytterligare genom uppkomsten av enbuskar på den förbrända mulljorden i luckorna. Detta är särskilt fallet i torrträdluckorna, där oftast enbuskarna övertaga det finare grenverkets förnesamlande roll. Den kraftigare utvecklade enbuskvegetationen är begränsad till luckorna, men på grund av den starka torkan på detta berg förekommer smärre enbuskar även inne i det örtrika bokbeståndet.

Abb. 25. Die Streuschichtansammlung wird noch mehr durch das Vorkommen von Wacholder auf der verbrannten Mullerde der Lücken akzentuiert. Dieses ist besonders in den Dürrholzlücken der Fall, wo der Wacholder oft die Aufgabe des feineren Zweigwerks, die Streuschicht anzusammeln, übernimmt. Die stärker entwickelte Wacholdergeneration ist in den Lücken zu Hause, doch können zufolge der starken Trockenheit auf diesem Berge, kleine Wacholderbüsche auch innen im krautreichen Buchenbestand vorkommen.

Fig. 26. Bilden visar en lucka i bokskogen, där enbuskarna på grund av den kraftiga expositionen och starka uttorkningen snabbt invandrat. Ånnu omkring 100 år efter det att denna lucka uppkommit har icke krontaket kunnat sluta sig och den nu mellan 50- och 90-åriga vegetationen av enbuskar florarar och ansamlar rikligt med förne-material. Denna förna har givit upphov till en typisk råhumus ovanpå den gamla mullen.

Abb. 26. Eine Lücke im Buchenwalde, wo die Wacholdereinwanderung wegen starke Exposition und Dürre rach vor sich ging. Noch nach ca. 100 Jahren seit der Entstehung der Lücke hat sich das Kronendach nicht schliessen können. Die heute 50—90-jährige Wacholder florieren und sammeln reichliches Streumaterial an. Die »Förna« ist die Urheberin eines typischen Rohhumus oberhalb des alten Mulls.

Fig. 27. När emellertid krontaket ånyo sluter sig över en gammal lucka med enbuskar, är dessa dödsdömda. Ty de äldre enarna synas icke tåla den starkare beskuggningen samtidigt med stark humusanhopning. Enarna kvarstår emellertid under årtionden som skelett i lövhögarna, och därigenom kan förneanhopningen ytterligare någon tid fortsättas.

Abb. 27. Wenn sich aber das Kronendach wieder über eine halte Lücke mit Wachholdervegetation schliesst, so ist der Untergang der letzteren besiegt. Der ältere Wachholder scheint nähmlich hier eine stärkere Beschattung mit einer gleichzeitigen starken Humusanhäufung nicht zu vertragen. Die Wachholder bleiben aber als Gerippe mitten in Laubhaufen stehen wodurch die Streuschichtansammlung noch einige Zeit fortsetzen kann.

Fig. 28. Till slut kommer i denna utvecklingscykel det moment, då de döda enbuskarna i halvmultnat tillstånd falla omkull och icke längre kunna befordra förneansamlingen. Lösförnan bläser då bort med vinden och filtförneskiktet blottas och kommer att bilda humustäckets ytlager. På denna filtförna invandrar nu en ganska artrik flora av ängsskogselement. Filtförnan övergår under gynnsamma omsättningförhållanden i en amorf råhumus, varur så småningom en råmull erhålls. Bilden visar den typtiska, fläckvis förekommande råhumus-råmull-terrängen med stubben av det träd, som varit yttersta orsaken till den abnormala utvecklingen av markprofilen.

Abb. 28. Zum Schluss zeigt dieses Entwicklungscyklus das Stadium, wo die toten Wachholder im halbvermorderten Zustande zu Boden fallen und somit die Streuansammlung nicht mehr fördern können. Die lose Schicht trägt dann der Wind fort, wonach die entblösste filzige Streuschicht zur Oberflächenschicht der Humusdecke wird. In diese filzige Humusschicht wandert eine artenreiche Flora von Wiesenpflanzen ein. Die Streuschicht geht bei günstigen Verhältnissen in einen amorphen Rohhumus über, aus welchem allmählich ein amorpher Rohmull entsteht. Die Abbildung zeigt dieses typische Rohhumus-Rohmull-Terrain mit dem Stubben des Baumes, der die letzte Ursache dieser abnormen Bodenentwicklung war.



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Fig. 29. Äldre luckor där en gång en tidigare, kraftig förneansamling ägt rum röja sig under århundraden därigenom, att de stammar, vilka berörts av förneansamlingarna ofta vid stambasen beklädas av en tunn, seg, svart, amorf råhumus, vilken stundom kan nå flera decimeter uppåt stammen.

Abb. 29. Ältere Lücken, wo einmal eine stärkere Streuansammlung vorkam, verraten sich dadurch, dass die Stämme, die von der Ansammlung berührt wurden, an der Basis oft mit dünnem, zähem, schwarzem, amorphem Rohhumus bekleidet sind, welche Bekleidung bisweilen eine Höhe von mehreren Dezimetern erreicht.

Fig. 30. Råhumusen på Timmesöbjerg äger icke den vanliga vegetationen av ris och råhumusgräs, utan en örtflora med *Mercurialis perennis*, *Asperula odorata*, *Anemone hepatica*, *Carex digitata*, *Brachypodium silvaticum* o. a.

Abb. 30. Der Rohhumus auf dem Timmesöbjerg besitzt nicht die gewöhnliche Vegetation von Zwerpsträuchern und Rohhumusgräsern, sondern eine Krautflora, bestehend aus *Mercurialis perennis*, *Asperula odorata*, *Anemone hepatica*, *Carex digitata*, *Brachypodium silvaticum* u. a.



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