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BAND 39 A. N:O 14.

STUDIES IN THE ECHINODERIDA

BY

KARL-GEORG NYHOLM

WITH 2 PLATES AND 22 FIGURES IN THE TEXT

COMMUNICATED MAY 14TH 1947 BY NILS VON HOFSTEN
AND SVEN HÖRSTADIUS

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Contents.

Previous knowledge of the Kinorhyncha or Echinoderida, as the group is called especially in literature written in English, is chiefly based on material from the Adriatic Sea and the Gulf of Naples, primarily through the works of ZELINKA (1913; 1928). More northerly occurrences of Echinoderids have been dealt with mainly by REMANE (1936) in studies of the microfauna in Kiel Bay. As the Echinoderida need special collecting methods, they have been neglected in faunistic investigations both in the littoral zone and in the deep sea. The finds made outside these research areas are mostly of accidental character, and least of all should zoogeographic and distributional-biologic argumentation be grounded on these sporadic finds.

A. Material and Methods.

The Echinoderida material discussed below has been taken exclusively off the West Coast of Sweden, primarily inside the Gullmar Fjord and along the littoral between Lysekil and Strömstad. By working on soft and semi-hard bottoms with light sledge-nets fitted with silk filtering-cloth (0—12), I have succeeded in obtaining a rich material of several blind Echinoderid forms belonging to the three separate main groups of Echinoderida, Cyclorhagae, Conchorhagae and Homalorhagae. Cf. Plate I, Figs. 6, 7, 1, 2 and 4.

As the majority of Echinoderids have a body length of less than 1 mm, they have to be mounted under a preparation microscope. As a representative material is desirable, the examination of mud or sand samples is an extremely time-consuming occupation. This work can, however, be rationalized by fairly simple means. The mud or the sandy clay taken from the stations is poured into tubs and air is blown through the contents of the tub: after a time one finds that a large number of tiny animals, including Echinoderids, by adhesion between the air and chitinous substances in the test, have risen to the surface, where the animals can be skimmed off. The algal zones were inventoried in the simplest way by rinsing and washing the algae. The yield of Echinoderids in the algal zone is extremely small on the West Coast of Sweden.

Studies in the Echinoderida offer difficulties not merely caused by the minute size of the animals but also by the sensitivity of the tissues to preserving fluids and, in adult forms, by the armour being with extreme difficulty permeable to most preserving fluids. ZELINKA (1928) holds that it is not technically possible to get good sections without cutting the animal so that the preserving fluid can work. In certain cases one has, therefore, to be content with an examination of living material, even if sectioning would have been desirable owing to the opacity of the material. This applies in the case of the younger larvae inter alia, where the size of cyclorhag larvae may be between 0.05—0.08 mm.

Sectioning proved most successful in my material when this was preserved with ZENKER's fixing fluid, where the solvent was sea water and embedding took place after methylbenzoate treatment. The best sectioning results with this difficultly permeable material were obtained with the following modified embedding process.

1) 80 % alcohol
2) a. a.
3) a. a. + methylbenzoate (equal parts, some hrs)
4) methylbenzoate (24 hrs)
5) methylbenzoate-celloidin (1 %), 48 hrs, changed twice
6) benzol 20—30 mins, twice
7) benzol-paraffin 12 hrs
8) 40° paraffin 1 hr
9) 40° + 52° paraffin (equal parts) 1 hr
10) 58° paraffin poured direct.

In other cases a celloidin-paraffin embedding was used. For total mounts several stains were tried. The results were good with Azure eosine dye; it should be pointed out that when using this, the object should not be arranged in celloidin. For special purposes (armour structure, etc.) picric acid treatment was tried with good effect, and in some cases this picric acid treatment was combined with Azure eosine staining.

B. Echinoderida in the Investigation Area.

Faunistically and zoogeographically the Echinoderida are so imperfectly known that an investigation with exclusively faunistic and zoogeographic ends in view would be well justified. And yet there are other questions in the biology of the Echinoderids that are not merely imperfectly known but entirely unsolved. One of these is the ontogeny (cf. ZELINKA, 1928, p. 208). As there is a possibility of phylogenetic connection or exclusive position becoming clearer when embryonic development and postembryonic development are completely known, it may at first appear more fruitful to attack these parts.

However, anyone tackling the postembryonic development in any Echinoderid species within a certain investigation area, will soon discover that he needs to be well acquainted with the Echinoderid fauna of that area, the reason for this being that the larval forms of the Echinoderida are abundant and manifold, whereas the number of adults is relatively small. In this troublesome connection a taxonomic-faunistic field study is necessary as a control of the cultivation experiments.

For reasons given above and as earlier data on the occurrence of the Echinoderida off the West Coast of Sweden are lacking, a survey is given below of some common Echinoderids from the West Coast of Sweden, chiefly in the Gullmar Fjord area close to the Kristineberg Zoological Station.

The three main groups of Echinoderids — Cyclorhagae, Conchorhagae and Homalorhagae — are all represented in the Swedish Echinoderid fauna. But it is manifest that the Cyclorhagae have considerably fewer representatives here than in the Mediterranean. The Homalorhagae, on the other hand, are very abundant, occurring in large numbers on the soft bottoms, to which these blind and dorso-ventrally flat forms belong. In the following survey ZELINKA's system has mainly been adopted.

I. *Sub-order Cyclorhagae.*

Zonite II forms by radial folding a closing device over the indrawn head. The ventral plates are narrower than the body width, so that parts of the dorsal plates are visible also ventrally.

Integument divided into 13 zonites Nomosomata.

Fam. Echinoderidae.

The family is characterized by the terminal zonite bearing two lateral spines and by the division into ventral plates beginning at the 4th zonite. ZELINKA distinguishes in the family two genera, *Echinoderes* and *Echinoderella*, of which *Echinoderes*, according to ZELINKA, has pigmented eyes, while *Echinoderella* lacks eyes. Cf. Text-figs. 1 and 12; Plate I, Fig. 6.

But this single generic character is not particularly well chosen, since, as ZELINKA has for the rest also stated himself, the pigmented eyes become lost in fixed material (cf. ZELINKA 1928 p. 102). This character is, however, usable for determining living material. Applying ZELINKA's system, the genus *Echinoderella* is the commonest of the cyclorhags on mud. Of this genus ZELINKA erects two species, *E. capitata* and *E. setigeva* (cf. ZELINKA 1928 p. 244), neither of which, however, coincides with the one that is commonest in the Gullmar Fjord area. It therefore seems necessary, unfortunately, — even if a revision in the genera of the fam. Echinoderidae should later prove needful — to erect a new species of the genus *Echinoderella*, at all events provisionally.

Genus *Echinoderella.*

Eyeless Echinoderids with two lateral terminal spines. (For further genus characters cf. ZELINKA 1928 p. 244.)

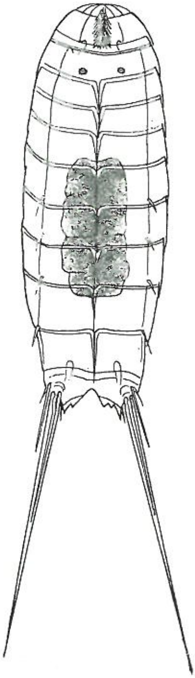
E. setigera with dorsal and lateral spines, long hairs in the cuticular pores. (Dorsal spines 4; straight dorsal spines.)

E. capitata without dorsal and lateral spines with short hairs without shining cuticular protuberances.

Echinoderella elongata n. sp. (Plate I, Fig. 6) with dorsal and lateral spines. Dorsal spines 5, on zonites VI to X inclusive. Dorsal spines (curved) fairly uniform in length, that on zonite X somewhat longer than those in front. Lateral terminal spines equal to not quite half the body length. Lateral spines shorter than the dorsal spines, present at least on zonites VIII—XI.

The species is particularly common on soft bottoms in the research area, especially down to a depth of c. 15 m. It appears to be strictly confined to soft bottoms and has never been met with at all in the algal zone.

In the algal zone there occurs, on the other hand, a representative of the genus *Echinoderes*, viz. *Echinoderes dujardinii* Clap. This form has never been secured in large numbers in the investigation area, a few specimens having been taken here and there among red algae. The form found seems to be identical with that known from the Mediterranean and the Adriatic. Length c. 0.25 mm.



Text-fig. 1. *Echinoderes dujardinii*. Ventral view. C. × 320. (From Remane.)

At certain times of the year there appear in the Gullmar Fjord area sexually immature Kinorhyncha of cyclorhag Echinoderid appearance. They have a soft cuticle and are not divided into plates.

Among these are some with 13 zonites and 2 lateral terminal spines, thus according with Zelinka's genera *Habroderes* and *Habroderella*. The difference between them, according to Zelinka (1928), is that *Habroderes* has eyes, while *Habroderella* lacks them. Representatives of the genus *Habroderes* have been secured in the Gullmar Fjord area among red algae, while *Habroderella* has been obtained from soft bottoms.

Neither the genus *Echinoderes* from the algal zone nor *Habroderes* from the same zone have hitherto been obtained in such quantities as to permit of cultivation experiments being set up.

Of the genus *Habroderella* Zelinka distinguishes four species, including *H. hyalina* (with 4 dorsal spines) and *H. ferox* (with 6 dorsal spines). *Habroderella* occurs on soft bottoms in the area investigated together with a form that, according to ZELINKA's key of classification, should be *Habroderella hyalina*. However, one discovers upon closer study of the text that comes after this author's diagnoses (1928, p. 259), that the forms cannot be identical. As sexual maturity has not been observed in *Habroderella*, not only is ZELINKA's basis of classification of the species in the genus not entirely unexceptionable, but it would also be unsuitable to increase the number of species in the sexually immature genus *Habroderella* by the addition of a new description. Consequently, the *Habroderella* form that has been found will in the following go under the designation of *Habroderella sp.* In the case of *Echinoderella elongata* n. sp. there were grounds for a specific epithet and diagnosis, since it is a sexually mature form, which does not seems to be so as regards *Habroderella sp.*

We will instead turn our attention to the second family in the Nomosomata, viz. the fam. Centroderidae, still according to ZELINKA.

Fam. Centroderidae.

This family is characterized in addition to the lateral spines on the XIII zonite by the median unpaired terminal spine. The family comprises, according to ZELINKA (1928, p. 261), two groups. One consists of sexually mature forms with cuticular armour of separate dorsal and ventral plates. In these the ventral plates begin at zonite IV. These forms are assigned to the genus *Centroderes*. The other group comprises forms with 11—13 zonites without division into plates, on the one hand the genus *Centropsis* (with eyes) and on the other the genus *Hapaloderes* (without eyes). The genus *Centroderes* is represented on the West Coast of Sweden. But there are reasons, the strongest of these being the still unknown postembryonic development, why this genus should not be treated in detail here.

With regard to the genera *Centropsis* and *Hapaloderes*, I have not yet met with *Centropsis*, although it ought in all probability to be found in the algal zone, at least during certain seasons of the year. A genus that from its abundance of forms on the West Coast of Sweden should here be more exhaustively dealt with than other Centroderidae, is *Hapaloderes* (cf. p. 12 and Text-fig. 4 a—b). Of the five species that ZELINKA (1928) assigned to *Hapaloderes*, three at least, principally during the early part of the year, seem to occur on soft mud bottoms in the Gullmar Fjord area. Cf. p. 23.

These are:

1) *Hapaloderes gracilis*
   (three dorsal spines, zonites VIII, IX and X)
2) *Hapaloderes minimus*
   (Two dorsal spines, zonites X and XI)
3) *Hapaloderes minutus*
   (Two dorsal spines, zonites IX and X).

The forms *Hapaloderes Kowalevskii*, described by REINHARD (1887), and *Hapaloderes armatus* have not yet been refound. The *Hapaloderes* forms dealt with by ZELINKA have 11—13 zonites and are without pigmented eyes.

The Fam. Mesitoderidae in the tribus Xenosomata (ZELINKA, 1928) has one representative of the genus *Campyloderes* in the investigation area. As it appears to be a new species of the genus and as new facts argue in favour of rejecting the tribus Xenosomata, the genus *Campyloderes* will be discussed in a special paper.

II. *Sub-order Conchorhagae.*

Zonites I and II retractile. Closing apparatus formed by zonite III and consisting of two cup-shaped parts, which at the free anterior end are pressed against each other like the halves of a mussel-shell.

Fam. Pentacontidae.

Zonite XIII with six spines.

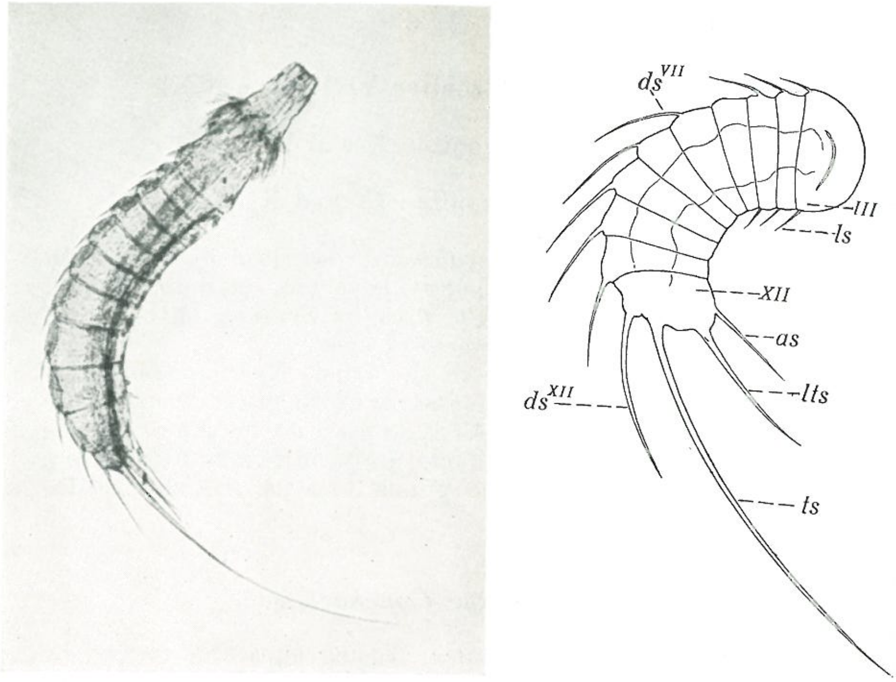
Genus *Semnoderes.*

Without eyes.

Semnoderes armiger.

Length: c. 0.3 mm. Five specimens of the species are previously known from the Adriatic (Trieste) (1 ♀, 4 ♂♂). ZELINKA has exhaustively described the species on these specimens (1928, pp. 289 sqq).

Semnoderes can be obtained with suitable catching methods in large numbers off Bohuslän on certain bottoms. The sandy mud bottoms are primarily good localities for this form. It is entirely absent on the shallower mud bottoms, rich in diatoms.



a) Side view of extended adult specimen. C. × 170.

b) Ventral view of a *Semnoderes* larva C. × 230.

Text-fig. 2. *Semnoderes armiger.*

Semnoderes off Bohuslän (Text-fig. 2 a—b) accords well with the *S. armiger* described by ZELINKA. The size of those described by ZELINKA and the adults taken off Bohuslän, is approximately 0.3 mm. ZELINKA's *Semnoderes* material was mainly sexually mature, this author not having been acquainted with younger stages in the life-cycle. Off the West Coast of Sweden occasional young *Semnoderes* forms can be secured with the closing apparatus typical of the Conchorhagae and the armature of spines characteristic of *Semnoderes armiger.* The number of zonites in these forms 0.17 mm long, is 12 (Text-fig. 2 b). Like the adult forms, they have soft zonite fields with stout lateral spines.

Homalorhagae.

Classification of the Echinoderida Homalorhagae (Plate I, Figs. 1 and 4) offers great difficulties. ZELINKA (1928) has dealt with the taxonomy of the homalorhag forms and has drawn up an identification key, whose practical use presents considerable difficulty. Several of ZELINKA's species have been erected on an extremely small material, some, for instance *Pycnophyes quadridentatus*, on only one specimen, this single specimen, in addition, not being alive. Some characters, especially the weak development of the sternal and episternal plates in zonite III, point to this being a juvenile form.

ZELINKA has included the structures of the armour among the fundamental distinguishing characters. This makes a reliable identification of young animals in general impossible. So much the stranger, then, is ZELINKA's establishment of the species *Pycnophyes echinoderoides*.

ZELINKA has given a faulty description of the species based on a specimen lying in the integument of a *Hyalophyes* (cf. ZELINKA, 1928, p. 313). The only fairly definite datum in the diagnosis is the length of the lateral terminal spines (=$^1/_3$ of the body length). It soon becomes evident, after working for some time with *Pycnophyes* material, that *P. echinoderoides* is much too weakly characterized to be retained. In the case of the remaining *Pycnophyes* species ZELINKA has associated the determinant characters with the armour. In *P. echinoderoides* the armoured form has not been observed! The structural details of the armour, not only the pachycycli and the so-called »Mittelwülste» but also the development of the cuticular fillets of the sternal plate, exhibit in one and the same species great variations during the laying out of the definitive armour in the imago.

Knowledge of the Echinoderida Homalorhagae is still so imperfect that it is probably impossible at present to give a taxonomical survey in monographic form of the homalorhag forms — a survey able to fulfil certain requirements in respect of permanency.

With reservation for the results of a possible future taxonomic study of the Homalorhagae, three types from the Homalorhagae material obtained from the West Coast of Sweden are below distinguished primarily by means of the structure of zonites III and XIII (ZELINKA, 1928, p. 309).

III. *Sub-order Homalorhagae.*

Zonite III has in the adults three ventral plates, which are pressed against the tergal plate of the zonite.

Fam. Pycnophyidae.

With mobile, paired lateral terminal spines.

Genus *Pycnophyes.*

With the family characters.

Pycnophyes communis.

Identification is possible with the aid of ZELINKA's drawings. Some of the characters set up are of little value for identification of *P. communis* and other *Pycnophyes* species. To these belong the so-called »Mittelwülste», ventral thickenings in the armour structure, to which ZELINKA attributes great importance for the separation of *Pycnophyes communis* and *P. calmani* (cf. ZELINKA, 1928, p. 309, classification key).

ZELINKA has probably not been quite unaware of the difficulties that might arise in distinguishing between *P. communis* and *P. calmani*, as in the same work that contains the classification key this author (ZELINKA, 1928, p. 327) states that in respect of the structure and appendages of zonite III the conditions are similar in *P. communis* and *P. calmani*, but that the body length is so much greater in *P. calmani* that confusion of the two is out of the question. In the Swedish *Pycnophyes* material several forms agree in many characters, except just the size, with the Mediterranean species. The body length is greater throughout in the Swedish material. Consequently, it seems impossible to keep ZELINKA's *P. communis* and *P. calmani* apart. (Cf. also LANG, 1936.)

P. communis is particularly common on soft bottoms in the area investigated. Cf. p. 11, diagram 1.

Pycnophyes flaveolatus.

In fairly good agreement with ZELINKA's description of the species (1928, p. 323) — but with the exception of the development of the so-called »Mittelwülste» — this form is found at many localities along the coast of Sweden. It seems to be especially abundant on the soft bottoms rich in diatoms (5—10 m).

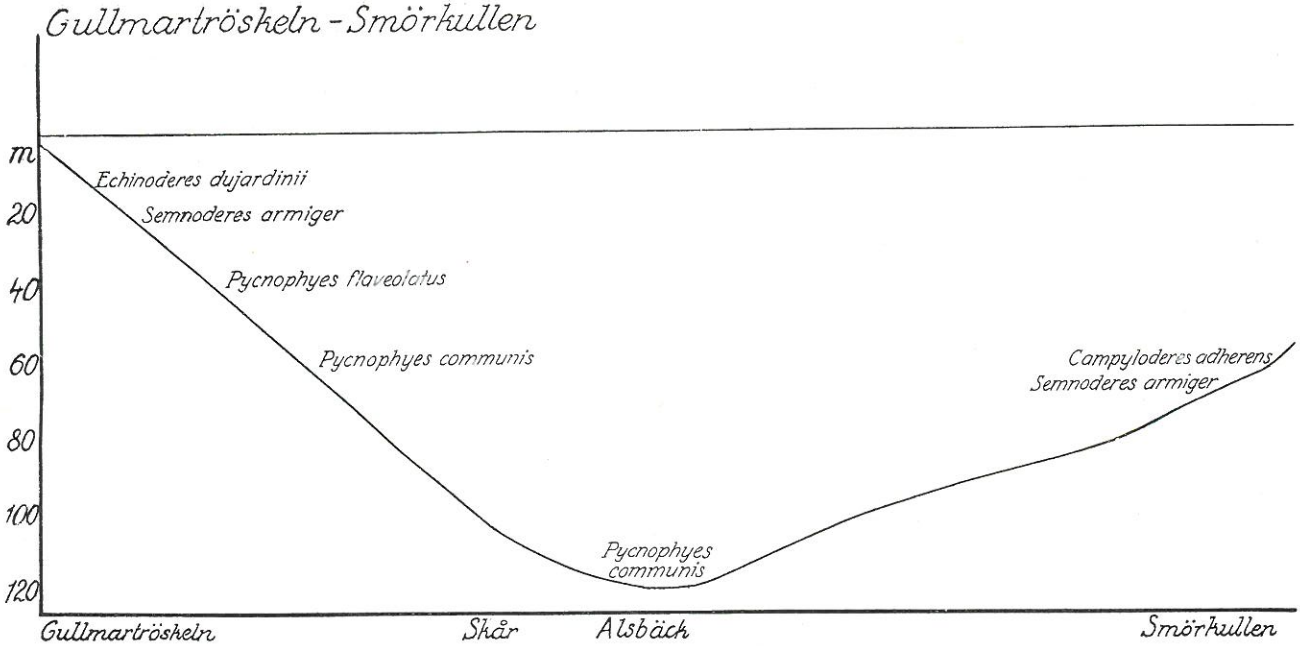


Diagram 1. Diagram giving an idea of the bathymetrical distribution of the Echinoderida in the Gullmar Fjord. The diagram is based on the sledge-net samples only.

The commonest *Pycnophyes* forms in the research area are undoubtedly *Pycnophyes communis* and *P. flaveolatus*. A form has been secured sporadically (i. a. outside the threshold of the Gullmar Fjord) that in habitus exhibits very good accord with the *Pycnophyes flagellatus* established by ZELINKA (ZELINKA, 1928, Taf. 14, Figs. 4—5).

A form showing good agreement with *P. quadridentatus* — although larger than ZELINKA's form measuring 0.37 mm — has a few times been taken in the inner part of the Gullmar Fjord. However, it is not entirely out of the question, as mentioned above, that this is a juvenile form, of which the incomplete plates division on the III zonite may, inter alia, be an indication.

C. Postembryonic Development in Echinoderida Cyclorhagae.

1. *Free-living Hapaloderes Forms.*

The youngest Echinoderida Cyclorhagae that have previously been described have a zonite number of 11 zonites.

Respecting *Hapaloderes Kowalewskii*, REINHARD (1887) does not definitely mention the number of zonites. REINHARD records 9 zonites, the ninth of which is twice as large as the others. ZELINKA (1928) in his diagnosis puts the zonite number at 11, because a lower number had not earlier been met with in his own material!

The *Hapaloderes* forms described by ZELINKA (1928) and PANCERI (1876) are the smallest Echinoderid types that had ever been the object of investigations before. The size of these, viz. *Hapaloderes minimus*, *H. minutus* and *H. gracilis*, varies between 0.116—0.098 mm.

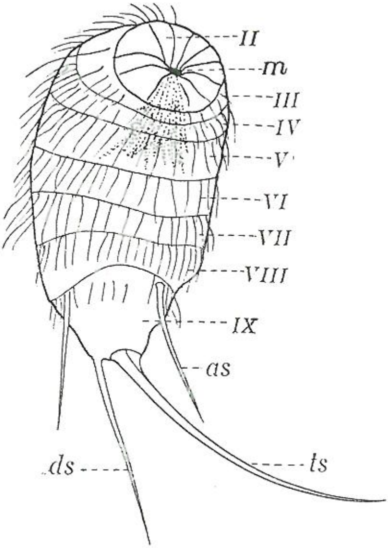
I will proceed from ZELINKA's data respecting *Hapaloderes minimus* (Text-fig. 4 b), which has 11 zonites and a maximum length of 0.098 mm. ZELINKA states (1928, p. 277) that »Das Tier dürfte eben der Eihaut entschlüpft sein». The almost oviform body has led ZELINKA to assume this.

However, the eggs of most of the known Echinoderids scarcely contain the large yolk-mass which would be needed for a development up to the fairly richly differentiated *Hapaloderes* type.

Earlier, it is true, *Hapaloderes* (cf. Text-fig. 4 b) was known only from the Adriatic Sea and the Gulf of Naples, but a systematic inspection of bottom samples taken at different seasons with a fine-meshed silk filtering-cloth showed that the

Hapaladeres type could be met with during certain periods of the year at several localities within the Gullmar Fjord area.

In these forms, which were in good accord with, on the one hand, *Hapaloderes gracilis* (Naples) and, on the other, *Hapaloderes minimus* (Trieste), there was a mesenteron not only developed but also filled with a yellowish green mass, in which round algae cells predominated. These animals with the fresh algal mass, could by no means have come directly out of the egg membrane! Certain possibilities should therefore exist of obtaining free-living, younger stages at the *Hapaloderes* localities. And this proved to be the case.



Text-fig. 3. A *Hapaloderes* form with 9 zonites (A_9).

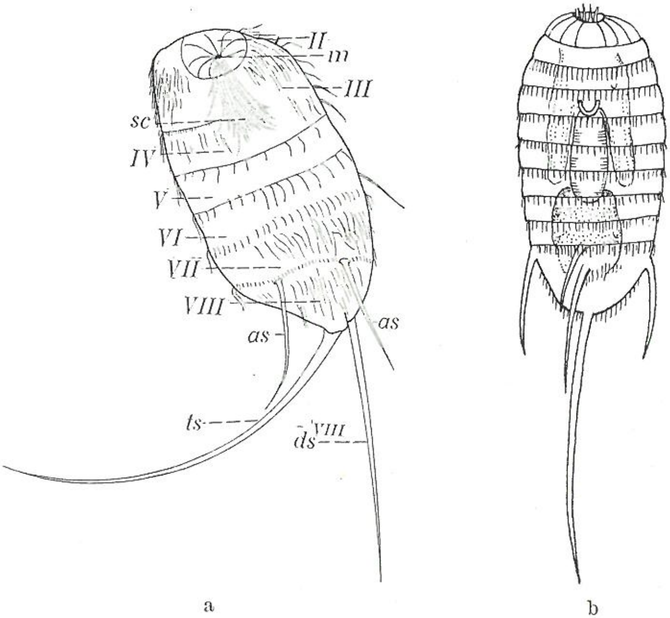
Text-fig. 3 (*A 9*) shows a form which has a certain connection with *Hapaloderes minimus*, although it is not identical with it. For several reasons (see below) this form is not established as a new species but is indicated by *A 9* in the following.

A 9. The form has 9 zonites. Length: 0.12 mm. The scalid equipment of the I zonite does not appear to be fully developed.

The structure of zonite II differs from that of the other zonites by forming the closing apparatus. Solid plates as in adult cyclorhags are lacking, but the cyclorhag character is revealed by the division of the zonite into radial fields, which converge at the centre.

Zonites III—VIII have, apart from their breadth, a fairly similar character superficially. Zonites V and VI have the largest circumference in these forms. All these zonites are fairly circular, lack plates but bear hairs proceeding from approximately the same level in the anterior part of the zonite.

The anal zonite is substantially higher than the other zonites. It is also furnished with hairs, although in less regular order than the preceding zonites.



Text-fig. 4. a) A *Hapalioderes* form with 8 zonites (A_8). b) *Hapaloderes minimus* (From Zelinka).

This zonite bears four spines, the longest of which is about as long as the animal's length without spines. This spine may be termed the median terminal spine (*ts*). Slightly in front of the attachment of this spine there proceeds another, somewhat shorter spine. The anal zonite, in contrast to the zonites in front of it, is weakly flattened on one side — corresponding to the ventral side in adult cyclorhags. The shorter spine in the posterior part of the anal zonite may therefore be said to correspond to a dorsal spine (*ds*). From the anterior part of the anal zonite, finally, there issue two lateral, ventrolateral spines (*as*).

Another *Hapaloderes* type that can be secured in the Gullmar Fjord area, is illustrated in Text-fig. 4 a. It will in future go under the designation of *A 8*. In this form the number of zonites is 8. Length: 0.09 mm. This form otherwise accords in essential respects with the preceding one. Zonites V and VI bear weak spines, corresponding to the dorsal spines in adult cyclorhags. The irregular border of hairs in the central part of zonite VIII indicates a new zonite formation within this area.

There can be no doubt that the previously unknown forms here discussed under the designations of *A 9* and *A 8* come closest to the *Hapaloderes* species described by ZELINKA. Even if forms *A 9* and *A 8* thus have the lowest number of zonites known from any forms of Echinoderids (cf. also ZELINKA, 1928, p. 277), they did not provide information about the organization of the young cyclorhag Echinoderid when it emerges from the egg. Cf. p. 25.

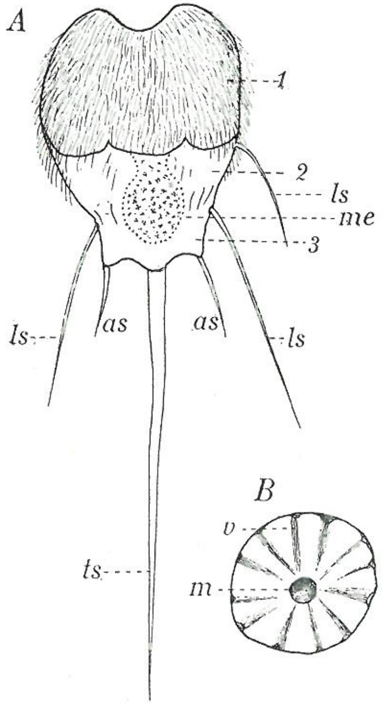
2. *Previously Unknown Free-living Cyclorhag Forms.*

By using a still finer filtering-cloth in the dredges and by sorting the bottom samples under a preparation microscope without previous sifting, which ruins small, brittle forms, it was possible to get, at *Hapaloderes* localities inter alia, bizarre forms of 0.05—0.07 mm in order of size. These forms (cf. for instance Text-fig. 5), owing to their slight differentiation, could not at first with certainty be ranged among the Echinoderids at all. Here it is a case of forms with few zonites (less than 8), and naturally for these forms to a still greater extent than for the above discussed A_8 and A_9 no possibility exists of connecting them with any Echinoderid form described in the literature. In order to get a taxonomic idea of these forms, I have, instead of choosing the easier way with new descriptions and a consequent increase in the number of genera and species, chosen the less easy one, which here goes via cultivation experiments and a reduced number of genera and species.

First the new forms:

The animal depicted in Text-fig. 5 (A_3) has in exterior very little in common with the characters otherwise associated with Echinoderids. The anterior, broader and rounder part of the body is opaque owing, inter alia, to a dense covering of small hairs directed backwards but without apparent division into rings of fields. The posterior, weakly conical part is produced to a terminal spine nearly twice the length of the body.

Lateral to this spine (median terminal spine, *ts*) there are two smaller lateral spines (*as*). The posterior, hairless, more transparent part is occupied by an at least functional counterpart to the mesenteron. This is filled with a yellowish green algal mass and tapers forwards (*me*, Text-fig. 5). The anus is lacking in this form. The pharynx with pharyngeal crown has not been established. The same applies to the proboscis and the row of scalids. The intestine debouches forwards into something that can best be described as a funnel. From the margin of the funnel there run folds converging towards the bottom and dividing the funnel into 12 sectors. These sectors lack plates. The position and number of these areas led to the assumption that the funnel with its division into sectors corresponded to the closing apparatus in the II zonite in Cyclorhagae Echinoderida.



Text-fig. 5. A young cyclorhag echinoderid (A_3). Cf. the text. *ts* Terminal spine; *as* lateral (anal) spine; *me* mesenteron.

How many zonites are there, then, in this form that through its »folded funnel» gave rise to the idea that it was a cyclorhag Echinoderid? In the densely hairy anterior part (*1*) no zonite boundaries can be detected. The posterior part has a weakly indicated division into an anterior part (*2*) and a posterior one (*3*). The posterior part (*3*) bears, in addition to the terminal spine (*ts*), two pairs of spines. Thus externally it would be possible to distinguish three zonites here, the first of which at least corresponds to the II zonite in adult Cyclorhagae Echinoderida.

The assumption propounded regarding the cyclorhag character of this form proved correct.

The above discussed form — here called A_3 — in fact changes, when cultivated, into a form according extremely well with A_8, individual specimens of which were at the same time obtainable from one of the Echinoderid localities (Kristineberg Bay, 8 m.) in the Gullmar Fjord area. A_3 is thus a younger developmental phase of A_8, which in its turn should be assigned to the genus *Hapaloderes*.

An intermediary type between the form whose external appearance has been described above (A_3) and the A_8 one regarded as a *Hapaloderes* form, is constituted by the specimen (A_4) shown in Text-fig. 6. The hairy covering on the anterior part is less dense especially in the posterior part, where new zonites are laid down and transferred backwards. Here are found the characteristic *Hapaloderes* rings of hair in the anterior part of the zonite, although they above all have not yet acquired the even course exhibited in *Hapaloderes* with its slower growth in length. It is evident from what has been stated above that *Hapaloderes* — quite contrary to what has been assumed hitherto (ZELINKA 1928 p. 277) — undergoes a relatively comprehensive postembryonic development, during which food is ingested and during which an increasing number of hairy zonites appear.

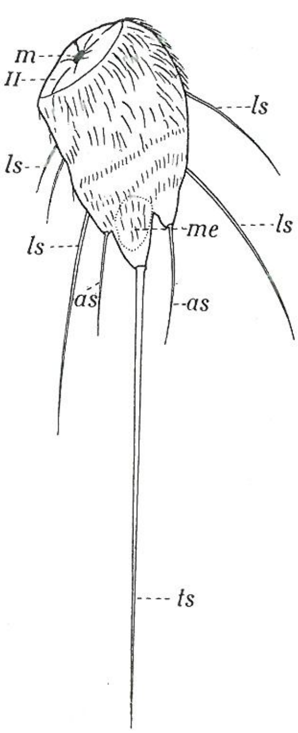
Instead of being named in accordance with distinctive methods — as has been done in the case of Echinoderids whenever new forms have been found, even if these were not adult, to such a great extent that the taxonomic classification has become confusing — the forms depicted in Text-figs. 3—4 and 5—6 should be referred to *Hapaloderes*.

A_3 and A_4 figured here just like A_8 and A_9 (*Hapaloderes*) lack a completely functional proboscis and are therefore very inactive. For development from the earliest stage, A_3, illustrated here, to A_8 and A_9 respectively, moulting does not seem to be absolutely necessary. Compare, however, Text-fig. 7. As plates are not found in *Hapaloderes* any more than in the younger forms, there is a lack of good possibilities for muscle attachments for the powerful proboscis musculature.

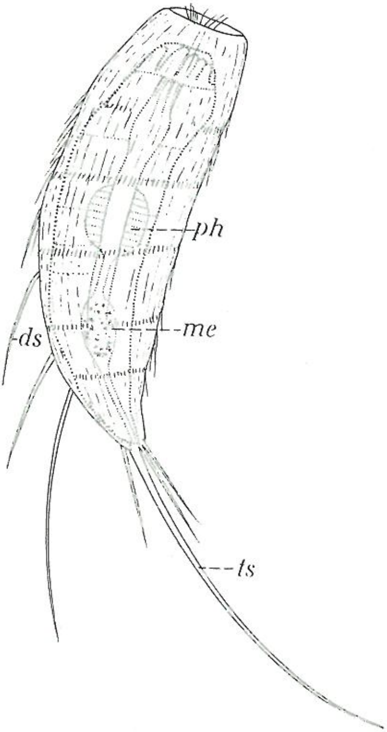
The *Hapaloderes* material obtained exhibits, like that described by ZELINKA, several larval characters, e. g. the lack of plakids in the closing apparatus, the absence of division into ventral plates, etc.

It should therefore be possible to proceed a step further in the connection between cultivation experiments and repeated control of the Echinoderid localities within the investigation area.

At the localities where the youngest forms in the *Hapaloderes* series were met with, the form (A_{11}) shown in Text-fig. 8 was also obtained. It has 11 zonites, not divided into plates. The I zonite is protrusible, but has a weak and incomplete scalid equipment. In zonite II the plakids of the closing apparatus have not yet developed. When zonite I is protruded, the »field» of zonite II forms a collar (II). All the following zonites (III—XI) bear hairs, although the rings of hairs on the anterior zonites are less regular than in younger forms. There can be no discussion about the existence of dorsal spines on zonites VIII, IX and X. These three dorsal spines issue from the central part of the zonites, well separated from the ring of hairs on the anterior margin of the zonites. Zonite VII has dorsally a process that is considerably weaker than the dorsal spines of the zonites situated behind, but which differs from the hairs in the ring of hairs, although it proceeds from the same level as the hairs in the row of hairs. This process very probably develops into a normal dorsal spine without moulting taking place.



Text-fig. 6.

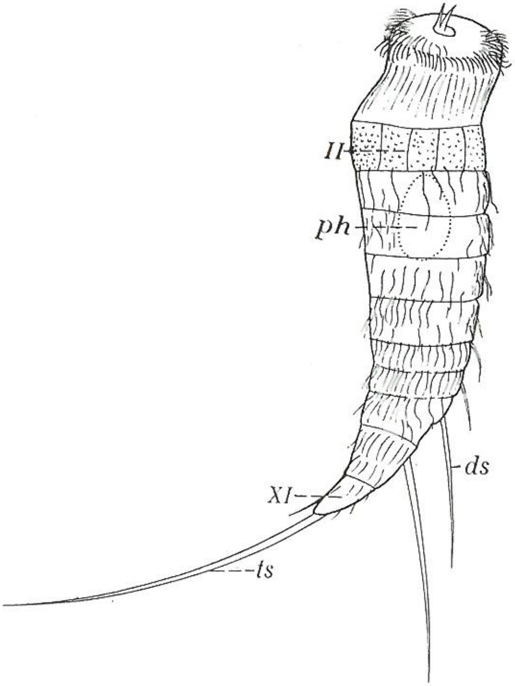


Text-fig. 7.

Text-fig. 6. A young echinoderid larva (A_4) giving the *Hapaloderes* series. Cf. the text. *m* Mouth: *II* zonite II; *ls* lateral spine; *me* mesenteron; *as* lateral (anal) spine; *ts* terminal spine.

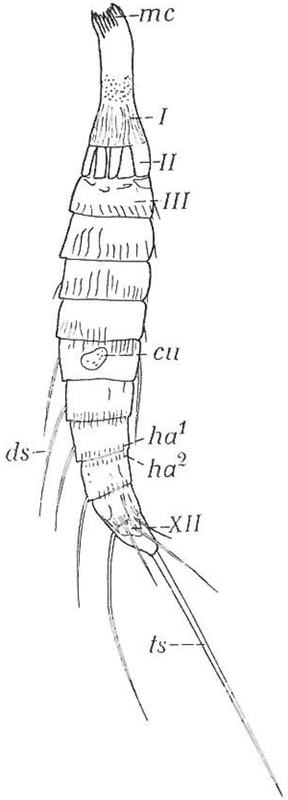
Text-fig. 7. Moulting in one of the *Hapaloderes* stages. *ph* Pharynx; *me* mesenteron; *ds* dorsal spine.

The median terminal spine is nearly as long as the length of the body (measured from the anterior margin of zonite III to the posterior margin of the last zonite). Body length 0.175 mm. This form is most abundant in May at depths ranging from 8—12 m in the Gullmar Fjord area. This form (A_{11}) belongs to the *Hapaloderes* series and comes close to the *Hapaloderes gracilis* erected by ZELINKA (1928). The *Hapaloderes gracilis* described by ZELINKA comes from the Gulf of Naples from the soft bottom immediately beneath the algae belt, and varied in size between 0.10866 and 0.1161 mm.

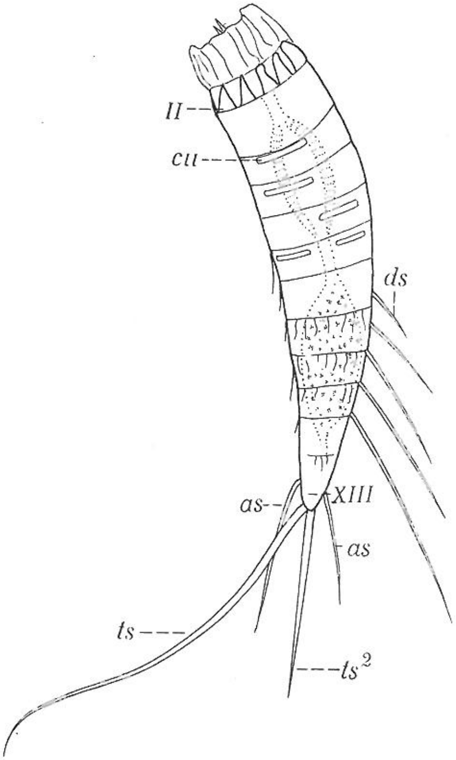


Text-fig. 8. A *Hapaloderes* form with 11 zonites (A_{11}). *ds* Dorsal spine; *ts* terminal spine; *ph* pharynx.

The next form has 12 zonites, the first of which lacks the structure characteristic of adult Echinoderida Cyclorhagae. The rows of scalids are, for instance, very poorly developed indeed. Zonite II has an incipient plakid formation in the areas belonging to the closing apparatus. The remaining zonites are without plates, but still retain their hairs. Only on zonite VII is there a cuticular formation (*cu*) — clearly a first beginning of plate formation on the zonites. There are five dorsal spines (on zonites VII—XI). The median terminal spine is c. $^{3}/_{4}$ of the body length. The size is 0.35 mm. On the borderline between zonites XI and XII there are three shorter spines. This form is designated A_{12}. Compare Text-fig. 9.



Text-fig. 9.



Text-fig. 10.

Text-fig. 9. A_{12}, a *Hapaloderes* stage with 12 zonites. *I*, *II*, etc., Zonites I, II; *cu* cuticular plate; *ha*^{1}, *ha*^{2} rings of hairs; *ds* dorsal spine; *ts* terminal spine; *mc* extended mouth cone.

Text-fig. 10. A_{13}, a *Hapaloderes* stage with XIII zonites. Cf. the text. *cu* Cuticular plate; *ds* dorsal spine; *as* lateral (anal) spine; *ts* terminal median spine; *ts*^{2} accessory terminal spine.

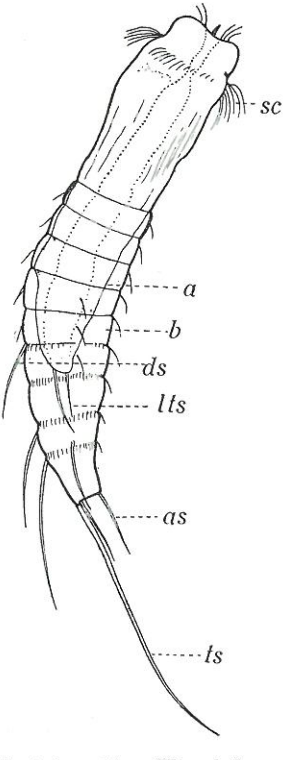
In the next form (A_{13}, Text-fig. 10) the number of zonites is 13 — that of the adult Echinoderida Cyclorhagae. In this form rings of hairs remain on at least some aboral zonites. The anterior zonites, on the other hand, lack hairs, and rudimentary plates can be detected on zonites IV—VII (Text-fig. 10, *cu*). A pharyngeal bulb is well developed here and is connected, as in adult forms, with a mesenteron filled with a yellowish green algal mass. Zonites VIII—XII bear dorsal spines and zonite XIII has four spines including a median terminal spine (*ts*), which is c. $^3/_4$ of the body length. Of the other three, the anterior two (*as*) are ventrolateral spines and the posterior straight one is an accessory median terminal spine (ts^2) replacing the soft, long, median terminal spine (*ts*). These last two spines both proceed from the apex of the anal zonite (cf. Text-fig. 10).

There is no doubt whatever that such a replacement of spines can take place in forms lacking a solid armour without a radical moult.

Moulting does not seem to be common among *Hapaloderes*-like forms, where, as we know, no homogeneous solid armour has yet been developed. A more or less complete moult can, however, clearly take place in these forms. Compare Text-fig. 7, which forms part of the *Hapaloderes* series. Undoubted proof of an imminent moult is found here, the fore-end being strongly contracted in old integuments. No plates are developed in these *Hapaloderes* forms and, consequently, no distinct plakids of the cyclorhag closing apparatus are observable in the old larval integument. A question — apparently unimportant — to which one would have liked to have an answer in this case, is whether the 11-zonite larva lying in the larger integument always has exactly the same equipment of spines when freed from the old integument. When the armour has really developed, that is the normal one. In the armoured animals the moults comprise the rows of scalids as well as the spines. In the case of these larvae without armour, it does not seem impossible that they emerge from the old integument with a somewhat defective spine equipment — to the confusion of the taxonomic classifications! To reach a complete explanation on this point in the latter part of the *Hapaloderes* series (larvae with 11 zonites), additional material of other *Hapaloderes* forms than those studied here would be needed. In Echinoderida Homalorhagae, where moulting is common and easily observed, moults occur also in forms that lack armour, e. g. young *Pycnophyes* species.

3. *The Connection between the New Forms A_3—A_8, Hapaloderes and Echinoderella.*

It has thus been established by cultivation experiments and by control of the natural localities that A_3, A_4, and A_9 are different developmental stages in one and the same species. The development from A_3 to A_9 can be effected within c. 2 months.



Text-fig. 11. *Hapaloderes-Echinoderella,* moulting. a) *Echinoderella;* b) *Hapaloderes* skin; *sc* scalids; *ds* dorsal spine; *lts* lateral terminal spine; *as* lateral (anal) spine; *ts* terminal spine.

New zonites are laid down in A_9, and after a few weeks it cannot be distinguished from *Hapaloderes minimus. Hapaloderes minimus* is, however, not an imago any more than any other of forms A_3—A_{13}, for, inter alia, it does not become sexually mature. None of the various forms touched upon above, are other than larvae in different degrees of development. In these larval forms sexual maturity, paedogenesis, does not occur, as may happen in the case of homalorhag Echinoderid larvae (cf. p. 33).

What does the adult form look like, then? A monocerk condition is common to the forms dealt with above. No monocerk cyclorhag form becomes sexually mature in Bohuslän — nor, probably, in the Mediterranean either. A more marked change in external appearance can, then, be expected to take place upon transition to the adult form. In other words, it should be extremely probable that the monocerk type A_{13} undergoes a moult in which the newly moulted animal exhibits greater changes in external appearance than at any of the few moults that can take place in the monocerk forms A_3—A_{13}.

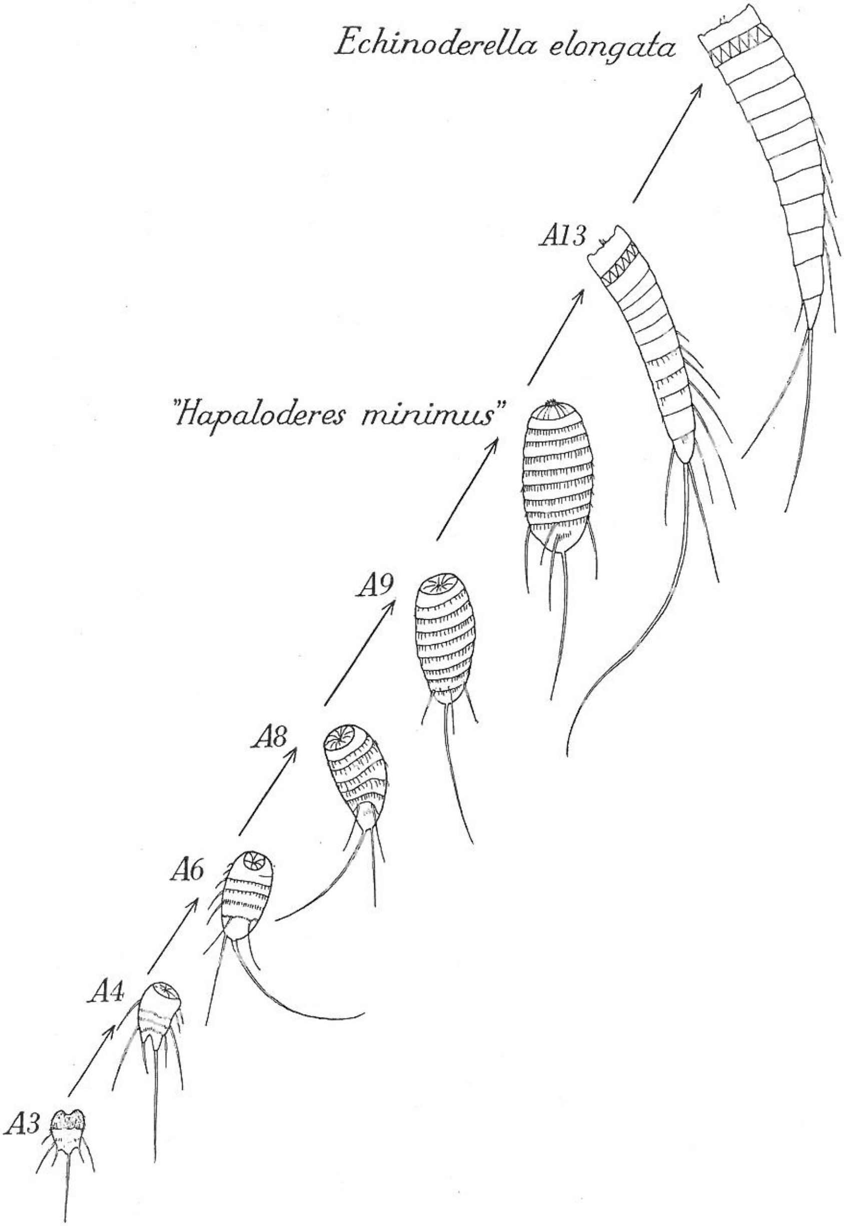
Text-fig. 11 shows a form corresponding to A_{13} that has lost the skin of the anterior zonites. Inside the old cuticle, where it still remains, lies the animal, which has an indistinct division into zonites but two terminal spines on the anal zonite — the future lateral terminal spines. Although the newly moulted animal lacks a full equipment of spines — it is a case of dorsal spines — the position of the two terminal spines on the anal zonite argues in favour of the view that the newly moulted animal is a bicerk form. This moult has been observed in June and must be regarded as strong evidence for the view that monocerk forms change to bicerk. Observations in the field at two of the most frequently examined, shallow localities (6—8 m) have shown that A_{12}—A_{13} decrease in numbers in the early summer, but that a characteristic bicerk form appears in greater abundance.

This bicerk form (cf. Pl. I, Fig. 6) becomes sexually mature. Already in the late summer oocytes are developed and in the autumn these are still growing. Egg maturity is probably reached in shallow localities during the winter. The form is a typical *Echinoderella*. The species is not identical with any of the *Echinoderella* forms established by ZELINKA. The *Echinoderella* species in question here varies slightly in the adult form and has been erected provisionally as *Echinoderella elongata* n. sp. Regarding the diagnosis of *Echinoderella elongata*, compare p. 5.

It seems to me necessary — in spite of my endeavours to reduce the number of species by elucidating the postembryonic development — to describe as new this imago under the name of *Echinoderella elongata*. In describing this imago as new, sufficiently weighty reasons do not, in my opinion, exist for using the specific names from the earlier (1928) described *Hapaloderes* forms, viz. *Hapaloderes gracilis* and *H. minimus*, as in the Mediterranean these can be juvenile forms of the *Echinoderella* forms known from the Mediterranean, viz. *Echinoderella setigera* and *E. capitata*. This course of action, which may at first appear as a breach of the Rules of Nomenclature, seems to me, on further consideration, to be the only one possible in view of a decrease in the taxonomical confusion resulting from a future increase in the knowledge of the postembryonic development of the *Echinoderella* species.

In my opinion, judging from ZELINKA (1928, pp. 277—279) and my own material, *Hapaloderes gracilis* should be interpreted as a somewhat older stage than *Hapaloderes minimus*. The fundamental difference between *Hapaloderes gracilis* and *Hapaloderes minimus* is, according to ZELINKA, the number of dorsal spines. As the dorsal spines in the »*Hapaloderes*» series are laid down successively backwards-forwards, *Hapaloderes gracilis* with its greater number of dorsal spines (cf. p. 7) ought to be somewhat older than *Hapaloderes minimus*. Both have eleven zonites.

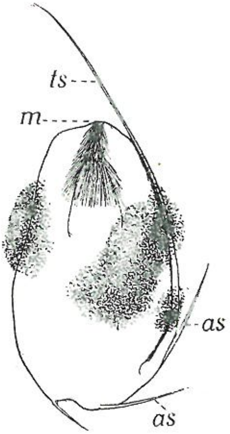
According to the above, *Echinoderella elongata* passes through a lengthy postembryonic development, in the course of which, inter alia, the number of zonites successively increases until it reaches the characteristic number for adult cyclorhags, namely 13. The vastly changed exterior as well as the formation of the rows of scalids should provide sufficient grounds for speaking here of a »successive metamorphosis». A cha-



Text-fig. 12. Diagram showing the postembryonic development in Echinoderida Cyclorhagae (*Echinoderella elongata* n. sp.). Cf. the text.

racter common to all these growth phases in the development of the larva to the imago is the median, so-called median terminal spine (monocerk forms). After a moult on the part of the 13-zonite larva there appears the imago equipped with two lateral terminal spines that reaches sexual maturity within 6 months. The transition from the monocerk to the bicerk form, which can attain sexual maturity, is called however metamorphosis in the following.

From this it is clear that the great wealth of species that has earlier been introduced in respect of monocerk cyclorhag Echinoderids is more likely to confuse than to stabilize our knowledge of the species. In an investigation of the postembryonic development, the wealth of species — even in the case of the Mediterranean Cyclorhagae — will probably be a wealth of »larval stages» terminating in the imago.



Text-fig. 13. A young cyclorhag larva. No division into zonites can be traced. *m* Mouth; *as* lateral (anal) spine; *ts* terminal spine.

The opinion has earlier (ZELINKA, 1928) been maintained that Echinoderida Cyclorhagae emerged from the egg with a relatively advanced organization corresponding to the large number of zonites (c. 11). The investigations made, however, plainly show that cyclorhag Echinoderids leave the envelope in which they develop very much earlier. Already when the larva is furnished with three zonites it lives independently, the intestine being sufficiently developed to ingest food.

This actualizes also the question of the larva's organization when it leaves the egg. Some few finds of larvae surrounded by a thin but homogeneous membrane show an extremely simple organization. Compare Text-fig. 13. No division into zonites can be traced. The entire larva apparently consists of a simple bladder with a differentiation at one end, the future closing apparatus. What is remarkable is the early development of spines. It is evident from the equipment of spines that it is a case of a cyclorhag Echinoderid larva. The long median terminal spine (*ts*) is here bent forwards along the side of the body and extends beyond the mouth opening.

D. On the Postembryonic Development in Echinoderida Homalorhagae.

When it is a case of trying to form an opinion of the postembryonic development in Echinodorida Homalorhagae, much help is provided by the frequent and fairly complete moults that are typical of homalorhag larvae. (Cf. Pl. I, Fig. 4.) By isolating young larvae in a suitable milieu, it is possible to obtain several consecutive »stages» of integuments and thus gain an idea of at least the external changes during the postembryonic development.

Several juvenile forms of Homalorhagae have been described. Several genera have been established: some of them have been assumed to be juvenile forms of fam. Pycnophyidae. Others have not given cause for attempts at connection. To the first group belongs the genus *Hyalophyes* (Pl. II, Fig. 7), to the second the genus *Centrophyes* (Pl. II, Figs. 4—5). Below the genus *Leptodemus* (Pl. II, Figs. 1—2), erected by ZELINKA in 1907, is also brought up for discussion.

ZELINKA's genus *Hyalophyes* has several distinct Pycnophyidae characters, e. g. 13 zonites and two mobile lateral terminal spines. In *Hyalophyes* the last two zonites are, however, joined to form a pygidium. The integument is soft, transparent, and without plates. If ZELINKA's classification key for *Hyalophyes* is followed, where the characters mainly comprise the length of the lateral terminal spines in relation to the length of the last zonites, several *Hyalophyes* species from the West Coast of Sweden could be accounted for. By observing the moults in *Hyalophyes*, new facts concerning the relationship between *Hyalophyes* and *Pycnophyes* have been obtained. Cf. Text-figs. 21—22 and Pl. I, Fig. 4.

There are no grounds for assuming that the genus *Hyalophyes*, whose forms have only a slightly shorter body length than those of *Pycnophyes*, is the earliest free-living stage of *Pycnophyes*. The internal organization recalling in its main features that of *Pycnophyes*, which in *Hyalophyes* (Cf. Text-fig. 21) also performs the functions expected of such an organization (e. g. the pharyngeal bulb, scalids, etc.), makes it a priori extremely likely — in view of the simple structure and small deutoplasm supply of the homalorhag Echinoderid egg — that there should also exist a much simpler organization than that exhibited by *Hyalophyes*.

Zonite III, forming the closing apparatus, has in Pycnophyidae characteristic features, including in the adults the appearance of the sternal and episternal plates. Although not equipped with the typical cuticular plates (plakids) in the closing apparatus, the triple division into sternal and episternal zones on the ventral side of zonite III can be traced also in *Hyalophyes*. This division of the ventral side in zonite III also occurs in forms taken at the same localities as *Pycnophyes* and *Hyalophyes*, but separated from these by a smaller number of zonites. Such forms are reproduced in Text-figs. 14—16.

The forms depicted share a common feature in the median terminal spine. Similar forms were placed by ZELINKA (1907, 1928) in the genus *Centrophyes*, comprising forms with homalorhag habitus, a median terminal spine and 11—13 zonites. According to the number of zonites, lateral spines and the more or less round or blunt form of the aboral end, ZELINKA (1928, p. 345) erects nine new species (*Centrophyes moderatus*, *C. curvatus*, *C. rectilineatus*, *C. longihastatus*, *C. denticulatus*, *C. biserratus*, *C. tenuis*, *C. validus*, *C. diffusus*), varying in size between 0.19 mm and 0.34 mm.

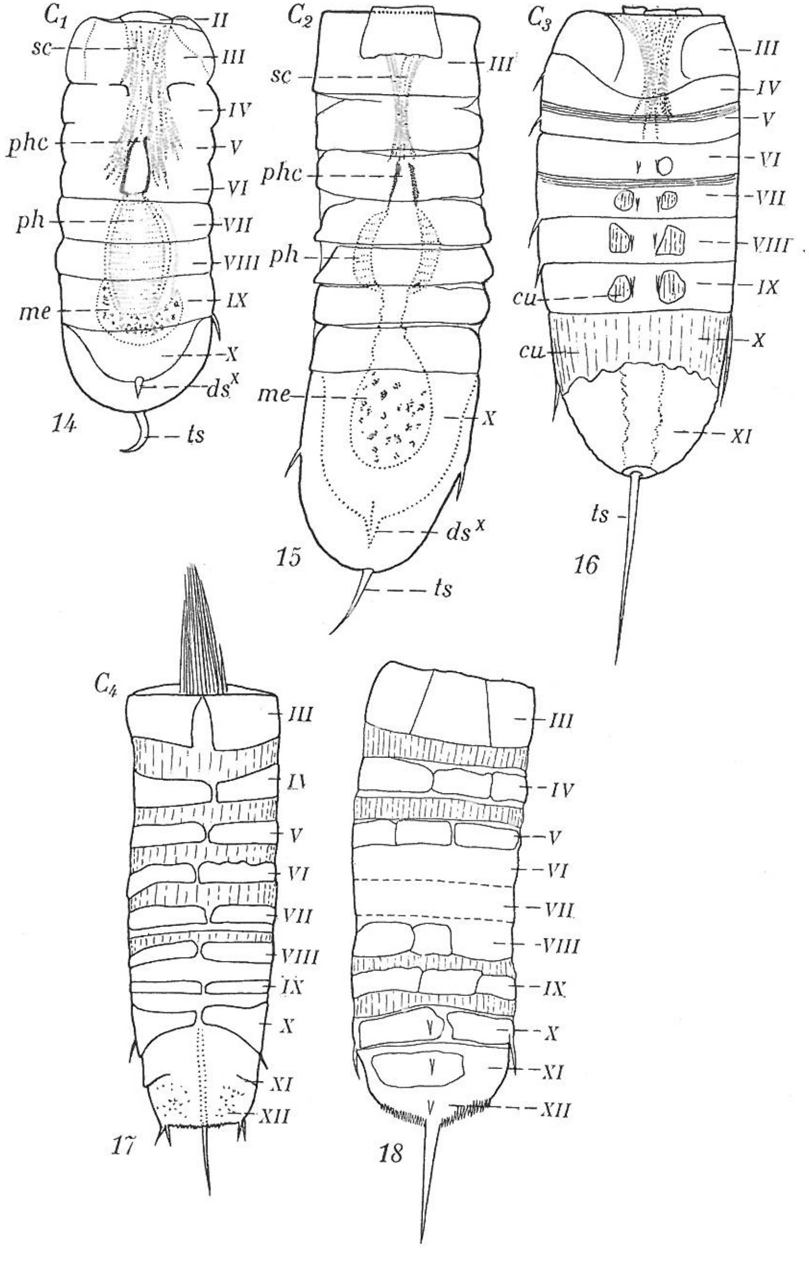
Among species with the 11 zonites — *Centrophyes moderatus*, *C. curvatus* and *C. rectilineatus* — forms are found in the Swedish West Coast material showing very great agreement with *Centrophyes curvatus* (Text-fig. 16) and also forms referable to *Centrophyes moderatus*.

ZELINKA has described some 12-zonite *Centrophyes* forms. Among these at least *Centrophyes biserratus* (Text-fig. 17) is represented off the West Coast of Sweden.

Besides these forms there occur in the catches during different seasons *Centrophyes* forms with 11 or 12 zonites, forms that cannot be determined with the aid of ZELINKA's descriptions of the species.

However, it is evident upon thorough examination of mud samples from localities at the West Coast of Sweden that the *Centrophyes* type is also represented by forms with a lower number of zonites than that given by ZELINKA. Thus there are *Centrophyes*-like forms with 7 zonites + pygidium without zonite boundaries and forms with 8 zonites + pygidium without a trace of zonite division. There can be no doubt about the *Centrophyes* character of these forms. Just as little as ZELINKA's fixing of the lower limit for the zonite number in Genus *Centrophyes* to 11 zonites can be considered defensible in view of the imperfect knowledge of the »genus'» multiformity, just as inappropriate would it be to erect a new genus for these forms with fever zonites but with typical *Centrophyes* appearance.

The *Centrophyes* types depicted in Pl. II, Fig. 5, and Text-figs. 17—18 are either opaque specimens or empty *Centrophyes* integuments. The former, even after sectioning, do not always



Text-figs. 14—18.

provide satisfactory data in respect of the internal organization. For this, newly moulted, transparent specimens are undoubtedly more suitable. Text-fig. 14 shows a »naked» *Centrophyes* form (C_1). This afterwards changes — when the cuticula has developed — into the type whose external appearance is represented by C_3 in Text-fig. 16.

It seems to be commonest for the *Centrophyes* characters to appear in the investigation area with a zonite number of ten. (Cf. however p. 30.) Zonite X (in C_1) bears a median, often somewhat mobile process, but not of spinal character. On the dorsal side of zonite X is laid down an equally soft process — the future dorsal spine on zonite X (ds^X). A lateral process on the borderline between zonites IX and X is also developed. Scalids, pharyngeal crown, pharyngeal bulb and mesenteron are well developed and able to function. The intestine contains a yellowish green algal mass. Zonite X forms a short pygidium. This pygidium increases in length especially in its anterior part and C_1 changes to C_2. Zonite X still constitutes in this *Centrophyes* form (C_2), which is portrayed in Text-fig. 15, the final zonite. This »pygidium» zonite here attains its greatest extent, its length corresponding to approximately five normal zonites in *Centrophyes*. Apart from this considerable enlargement of the »pygidium», no changes have occurred.

The C_2 shown in Text-fig. 15 is thus a *Centrophyes* form that is only slightly older than the C_1 in Text-fig. 14. In the C_2 forms cuticula is developed. The earliest discernible cuticular formation does not always arise at exactly the same place.

In many *Centrophyes* forms the cuticular formation nevertheless shows a tendency to be developed first in areas of rapid growth and stretching. This is so in C_3 (Text-fig. 16), where the development of cuticula has advanced so far that an almost continuous girdle has been formed in the anterior part of the former pygidium, thus delimiting this from the aboral

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Text-fig. 14. A nude *Centrophyes* form (C_1-type). *II, III,* etc., Zonites I, II, etc. *sc* Scalids; *phc* pharynx crown; *ph* pharynx; *me* mesenteron; ds^X dorsal soft process of future dorsal spine on zonite X; *ts* terminal soft and mobile process of future terminal spine.

Text-fig. 15. A nude *Centrophyes* form (C_2) older than C_1. Cf. the explanations of Text-fig. 14.

Text-fig. 16. A *Centrophyes* form with initial cuticular armour (*cu*). Cf. the explanations of Text-fig. 14.

Text-figs. 17—18. The skins of *Centrophyes* forms with twelve zonites.

end, which will later form zonite XI, bearing the characteristic median terminal spine.

The laying down of the cuticula proceeds backwards-forwards. Very often two narrow fillets first appear ventrally in each zonite. From these fillets, which should perhaps be interpreted as spines, the formation of more solid integumental parts progresses along the margins of the zonites. Cf. C_3, zonites VI—IX. When the »skin» is complete and envelops all the zonites except the two indrawn ones, a still weaker zone is noticeable median to the ventral side (cf. Text-fig. 17 and Pl. II, Fig. 5). This suture is put to no use, however, in a subsequent moult. This takes place as in *Hyalophyes* (cf. Fig. 4, Pl. I) by the protoplasmic parts being drawn out through the scalids, the animal then issuing forwards through the opening defined by zonite III.

The two types depicted (C_4 and C_5), of which C_4 comes closest to *Centrophyes biserratus* f. *secunda*, have lost the pygidium characteristic of younger forms. The zonite formation in the »pygidium» has resulted in an increase of the number of zonites to 12.

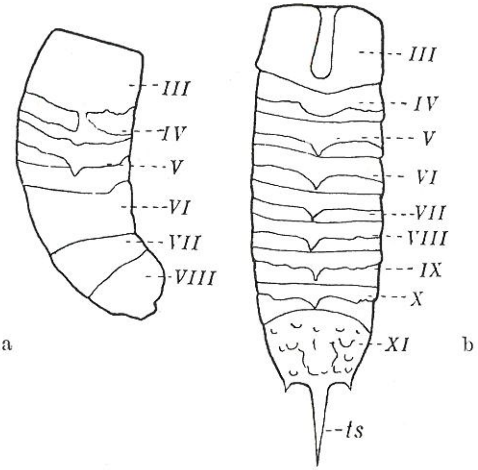
In the investigation area it will probably be commonest for the oldest *Centrophyes* types to have 12 zonites.

A form with 10 zonites, including 2 indrawn and the last of the 8 visible ones developed as a pygidium without a median terminal spine, is depicted in Fig. 2, Pl. II. This form has quite considerable mobility. Scalids, pharyngeal crown and bulb, and mesenteron are able to function. The form can change to one of the *Centrophyes* types with 10 zonites (C_1). It has not been described but, in reality, comes close to the larval genus *Leptodemus*, erected by ZELINKA in 1907.

Among the armoured, adult homalorhag forms from the Mediterranean, ZELINKA includes *Trachydemus giganteus* within fam. Trachydemidae, which in contrast to Pycnophyidae is stated to be acerk. Under the heading of »Larven vom Charakter der Trachydemidae» ZELINKA (1928, p. 297) gives the genus *Leptodemus*. The genus established is placed within the acerk family Trachydemidae. Acerky is indeed common to both *Leptodemus* and *Trachydemus*, but one should not, on that account, leap to the conclusion that *Leptodemus* comprises exclusively young forms of the homalorhag family Trachydemidae.

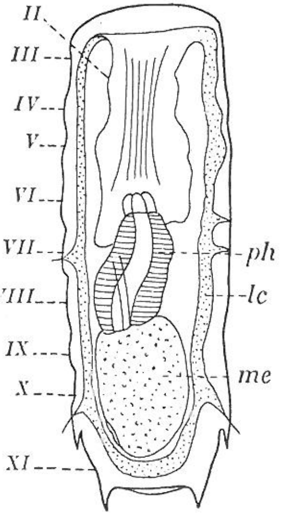
How firmly grounded the erection of the fam. Trachydemidae is, eludes my powers of appraisement, inter alia and primarily because I have not yet met with adult forms that, with the diagnoses given, can be assigned to fam. Trachydemidae. On the other hand, there is no longer any doubt that forms which Zelinka placed in the genus *Leptodemus*, occur in the Swedish investigation area.

Text-fig. 19 a and Pl. II, Fig. 1, show a *Leptodemus* form occurring at localities in the investigation area both at the threshold of the Gullmar Fjord and in the inner parts of the Fjord (the Saltkälle and Färle Fjords). Here the division into zonites is weakly indicated, above all aborally. In forms of this type the boundaries of 6—7 zonites can be traced in the integument. In reality, the broad, seemingly first zonite in *Leptodemus* corresponds to zonite III in adult homalorhags. The first two zonites in these *Leptodemus* forms are, when developed, indrawn.



Text-fig. 19. a) A *Leptodemus* form with eight zonites. This form develops into the *Centrophyes* form in Fig. 19 b.

Free-living *Leptodemus* forms would, according to the above, thus have 8—9 zonites. In the youngest Leptodemi with distinct zonite boundaries mainly in the anterior half of the body, the scalids are in process of development. Here the differentiation into zonite I and zonite II cannot be discerned. In older Leptodemi, scalids, pharyngeal bulb and mesenteron are found. The latter is filled with a yellowish green algal mass. Here, then, it is a case of forms of *Leptodemus* type that are able to ingest food. A prerequisite for this is that in these the pharyngeal bulb is distinct and the scalids laid down. In the material secured, forms of *Leptodemus* type built up of 8—9 zonites, can have a mesenteron filled with an algal mass. In the earlier literature, Leptodemi with 8—9 zonites are not described at all. In ZELINKA's »Monographie der Echinodera» (1928, p. 297) *Leptodemus* forms with the number of zonites varying between 11 and 13, are described. ZELINKA establishes 11 *Leptodemus* species separated into 3 groups, based on the number of zonites. 11 zonites: *L. metschnikoffii*, 1 dorsal spine, on the pygidium; *L. acercus*, 3 dorsal spines, on zonites VIII, X and XI; 12 zonites: *L. forceps* and *L. serratus*; 13 zonites: the remaining 7 species, *L. giganteus* owing to its length of 0.5 mm and the breadth of its anterior part being separated from the other forms with 13 zonites.

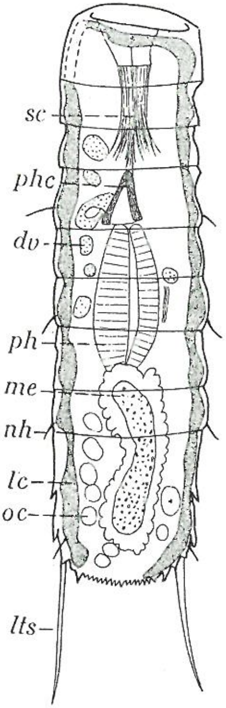


Text-fig. 20. *Leptodemus acercus.* (After Reinhard, 1887.) *Cf. Text-fig. 21.*

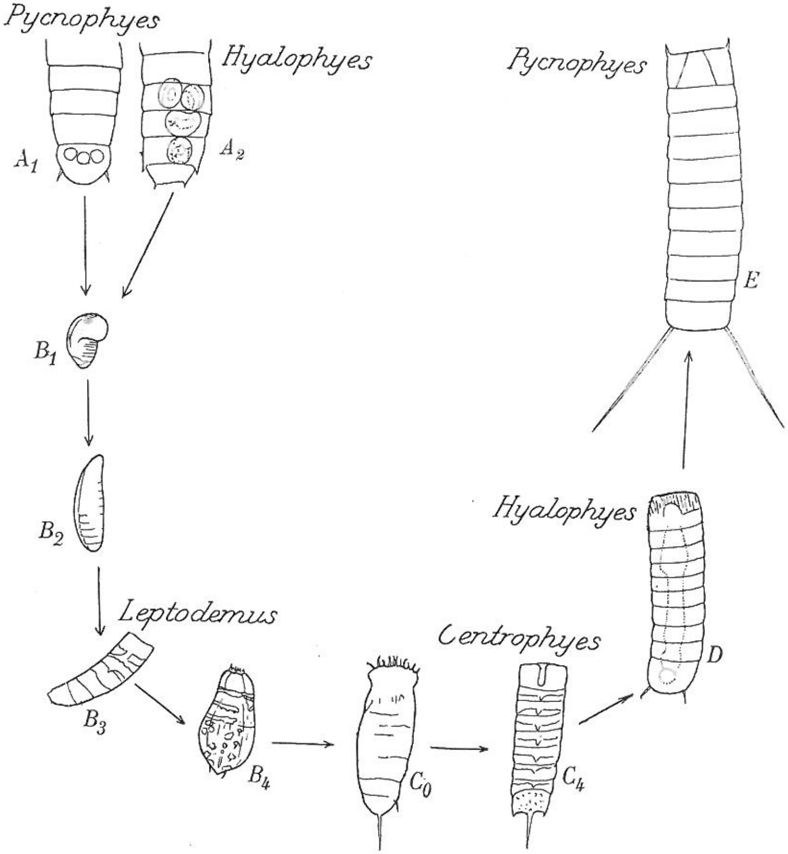
There are no grounds for erecting any new genus for the forms of *Leptodemus* type found that are furnished with 8—9 zonites. The conditions here are the same as in the case of *Hapaloderes* among the cyclorhag Echinoderids, namely that the forms found with the fewer number of zonites attain, after a time of growth and also a moult, the larger number of zonites considered to characterize the established genus *Leptodemus*. It is then perfectly obvious that the method of erecting different *Leptodemus* species according to the number of zonites is not a great success, as it here involves the risk of including two consecutive developmental phases in the *Leptodemus* framework as separate species. All the species (with 11—13 zonites) given by ZELINKA seem to have been free-living forms able to ingest food. Cf. Text-fig. 20 (also ZELINKA, 1928, p. 298).

The youngest forms from my own material assignable to the *Leptodemus* type (6—7 zonites and 8—9 zonites respectively) have not had the power of taking in nutriment themselves. They were discovered lying motionless or almost motionless in the bottom sediment often in pairs. These forms exhibit no differentiation into scalids — pharyngeal bulb — mesenteron. They ingest no food from outside until differentiation into pharynx and mesenteron can be proved when a higher number of zonites has been reached, which in these young forms is most suitably done by sectioning (cf. Pl. I, Fig. 3). The imperfect histological differentiation argues in favour of our here having to do with forms that have not yet embarked upon a burrowing, free mode of life in conjunction with independent food ingestion.

Their occurrence in twos or larger groups crowded together, motionless, and facing in different directions, points to the possibility of our having detected forms that have recently emerged from the egg and are thus on the point of beginning their postembryonic development. The eggs in the adult homalorhags are often laid in groups of a few eggs. In the paedogenetic forms of *Hyalophyes* (Cf. Text-figs. 21 and 22) special conditions can apparently prevail; I have, for instance, found that paedogenetic *Hyalophyes* forms, when moulting, discharge eggs in the old integument, from which they free themselves with great difficulty. In the empty integument embryonic development then takes place up to a stage corresponding to the organization exhibited by the *Leptodemus* forms. In adult *Pycnophyes* the eggs can be kept for a time in a ball of arenaceous character attached to zonite XIII (cf. Pl. II, Fig. 9). Eggs of adult *Pycnophyes* (cf. what has been said above about *Hyalophyes*) can also be obtained in the canals



Text-fig. 21. A nude *Hyalophyes* form. *sc* Scalids; *phc* pharynx crown; *ph* pharynx; *me* mesenteron; *nh* nerve hair; *lc* lateral nerve cord; *oc* oocytes; *do* dorsoventral musculature; *lts* lateral terminal spine.



Text-fig. 22. Diagram showing the postembryonic development in Echinoderida Homalorhagae. A_1. A *Pycnophyes* specimen with an aboral capsule enclosing eggs. A_2. A *Hyalophyes* skin with embryos. B_1—B_2. Young immobile larvae. B_3—B_4. *Leptodemus* stages. C_0—C_4. *Centrophyes* stages. *D*. *Hyalophyes* stage. *E*. *Pycnophyes* imago.

excavated by the animals in the uppermost detritus layer. As in the case of the cyclorhag genus *Echinoderella*, the homalorhag Pycnophyidae thus also lack pelagic larvae.

The general survey in Text-fig. 22 shows the developmental series obtained by cultures and field studies of *Pycnophyes communis* and *Pycnophyes flaveolatus*.

Summary.

Echinoderida Cyclorhagae.

1. Echinoderida Cyclorhagae are common all the year round on shallow soft bottoms in the investigation area. The cyclorhag Echinoderid material from the soft bottom is characterized in the area studied chiefly by three habitus groups: a) *Echinoderella*, b) *Hapaloderes*, c) cyclorhag forms with a small number of zonites (2—8 zonites).

2. A connection exists between these three groups. *Echinoderella* is the imago in a series of free-living, benthonic developmental phases, the youngest of which were not previously known. *Hapaloderes* constitutes the last link in the chain of development before the transition to *Echinoderella.*

3. Paedogenesis in *Hapaloderes* does not occur in the investigation area. *Echinoderella* alone reaches sexual maturity. In the area studied the life cycle of *Echinoderella elongata* n. sp. comprises c. 1 year.

Echinoderida Homalorhagae.

1. Echinoderida Homalorhagae of fam. Pycnophyidae (*Pycnophyes communis*, *P. flaveolatus*) lack pelagic larvae.

2. The youngest postembryonic stages are c. 0.15 mm long, motionless, with 6—7 faintly marked zonite boundaries. These larvae, which are already *Leptodemus*-like owing to acerky i. a., develop into forms that through their number of zonites, etc., should be connected with ZELINKA's youngest *Leptodemus* forms.

3. *Leptodemus* of 10—11-zonite type can change into a naked form with *Centrophyes* habitus (C_1). After the formation of zonites, stretching and cuticular development, this form best coincides with *Centrophyes moderatus* in the identification key given by ZELINKA for the genus *Centrophyes.*

4. Connection exists between *Centrophyes* forms and *Hyalophyes.*

5. The *Hyalophyes* forms within the investigation area moult several times. They can become sexually mature but they continue to grow and do not reach the imago until the change to *Pycnophyes* forms.

Literature: **Johnston, T. Harvey,** 1938. Report on the Echinoderida. Australasian Antarctic Expedition 1911—14. Scientific reports, series C vol. X part 7. Sydney 1938. — **Lang, K.,** 1936. Einige Kleintiere aus dem Öresund. Undersökningar över Öresund, Lunds univ. årsskrift N. F. avd. 2, bd. 31, nr. 10. — **Reinhard, W.,** 1887. Kinorhyncha (Echinoderes), ihr Anatomischer Bau und ihre Stellung im System. Zeitschrift f. wiss. Zool. Bd. 45. — **Remane, A.,** 1936. Gastrotricha und Kinorhyncha in Bronns Klassen u. Ordnungen. bd. 4. Leipzig 1936. — **Zelinka, C.,** 1907. Zur Kenntnis der Echinoderen. Zool. Anz. bd. XXXI. — **Zelinka, K.,** 1913. Die Echinoderen der deutschen Süd-polar Expedition, 14 (Zool. 6) 1913. — ——, 1928. Monographie der Echinodera. Leipzig 1928.

Explanation of Plates.

Plate I.

Fig. 1. *Pycnophyes flaveolatus.* Ventral view. *sc* Scalids; *ep* episternal plate; *ste* sternal plate. C. × 150.
Fig. 2. *Pycnophyes flaveolatus.* *t* Tergal plate; *v* ventral plates; *dv* dorsoventral musculature; *d* intestine; *te* testis. Transverse microtome section. C. × 400.
Fig. 3. *Leptodemus* stage. *sc* scalids; *ph* pharynx; *me* mesenteron. Longitudinal section. C. × 200.
Fig. 4. *Hyalophyes* moulting. C. × 50.
Fig. 5. *Hapaloderes* stage. Ventral view. C. × 170.
Fig. 6. *Echinoderella elongata* n. sp. Side view. C. × 130.
Fig. 7. *Semnoderes armiger.* C. × 110.

Plate II.

Fig. 1. *Leptodemus* stage, 8 zonites. Ventral view.
Figs. 2, 3. *Leptodemus* stages, 10—12 zonites.
Fig. 4. *Centrophyes* stage without armour.
Fig. 5. *Centrophyes* stage with armour. Ventral view.
Figs. 6, 7. *Hyalophyes* stage.
Fig. 8. *Pycnophyes flaveolatus.* Dorsal view. C. × 50.
Fig. 9. *Pycnophyes flaveolatus.* *ov* Eggs in arenaceous capsule. Dorsal view. C. × 50.

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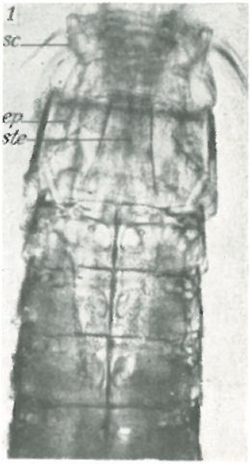

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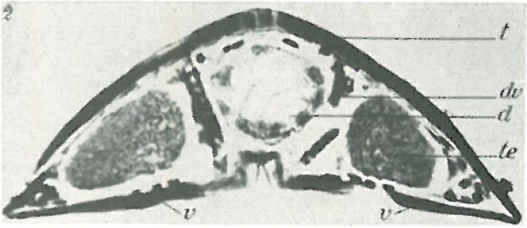

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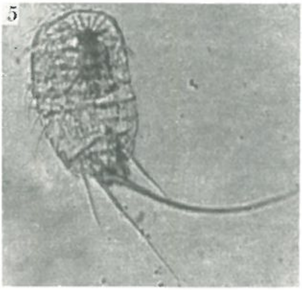

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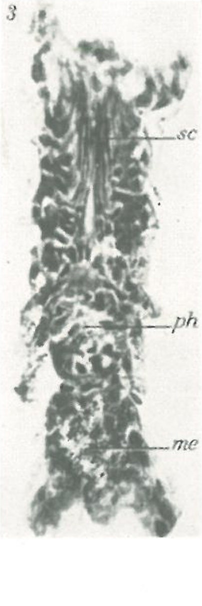

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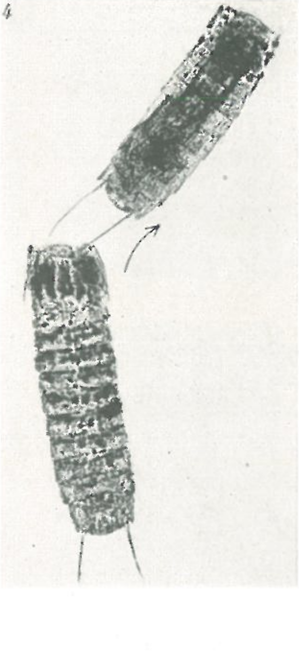

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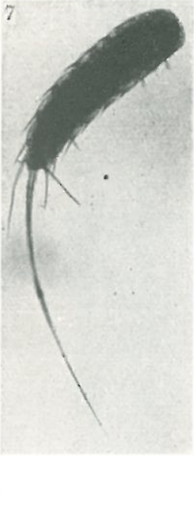

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