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ECHINODERMS (HYDROPHORIDEA, OPHIOCISTIA) FROM THE ORDOVICIAN (UPPER SKIDDAVIAN, 3 c β) OF THE OSLO REGION

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With 2 plates and 6 figures in the text.

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Introduction.

In the Upper Skiddavian (Upper Arenigian) strata of the Oslo region echinoderm remains are met with very rarely. Through the courtesy of Professor Leif Størmer the present writer has had the welcome opportunity of studying the small collection of such fossils kept in the Paleontological Museum in Oslo (PMO). This collection comprises a very restricted number of specimens, but is nevertheless of considerable importance and interest for the knowledge of the Old Paleozoic echinoderm faunas in the Scandinavian-Baltic area, and also sheds some fresh light upon certain features of general interest.

Four species of Hydrophoridae are represented, each of them belonging to a separate genus. There is, besides, a member of the Ophiocistia which has been designated as a new species of the genus *Volchovia*. The relationships of the different species are discussed in the descriptions below. As a result of this study it can be said that there is a clear affinity between the composition of this early Ordovician echinoderm fauna and that of the East Baltic area.

Information on the geological conditions at the localities from which the material treated in the present paper was derived, is found in Brøgger (1882), on the pages here indicated for the different localities: Gjeitungholmen (pp. 22, 28, 201, 229—230) Huk (p. 192 seq.), Tøyen (p. 197 seq.), Vaekkerø (pp. 22, 28, 184 seq.).

Subphylum **PELMATOZOA** Leuckart 1848.

Class **Cystoidea** Buch 1846, emend. Jaekel 1918.

Subclass **Hydrophoridea** Zittel 1903.

Order RHOMBIFERA Zittel 1879, emend. Bather 1899.

Superfamily GLYPTOCYSTITIDA (Bather 1913) Regnéll 1945.

Family Cheirocrinidae Jaekel 1899, emend. Bather 1913.

Genus *Cheirocrinus* Eichwald 1856.

Cheirocrinus hyperboreus n. sp.

Pl. 1, fig. 1. Pl. 2, figs. 1—3. Text-figs. 1—2.

Derivation of name: — The specific name is given with regard to the northern situation of the country from where the species was obtained.

Holotype: — PMO 2271 a.

Type locality: — Gjeitungholmen, Slemmestad, Asker.

Type stratum: — Bluish grey limestone with yellow weathering, of the stage 3 c β (Expansus shale), Upper Skiddavian.

Material: — In a rather large piece of rock, numbered 2271, there are a lot of fragments of different parts of the skeleton, such as isolated plates and a few plates still connected, detached brachioles, stem fragments (e. g. that figured in Pl. 2, fig. 2), and what are presumably stem bases. From the large slab were split two minor pieces, one of them, numbered 2271 a, containing the holotype and some other remains. The other, 2271 b, shows a crowd of isolated plates and stem fragments. A further hand specimen, 2272, also contains some fragments of this species. The material available was collected in 1909 by J. Kiær.

Diagnosis: — A species of *Cheirocrinus* with large theca, sub-ovate in anterior and posterior faces; base almost flat, only slightly invaginate; all pectinirhombs visible disjunct; pectinirhombs present i. a. in plates *IL* 1—*L* 2; test smooth, the ornament of plates made

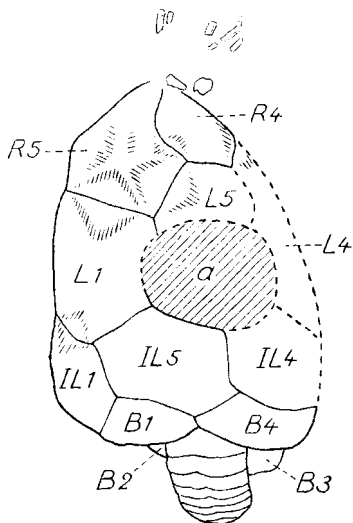


Fig. 1. *Cheirocrinus hyperboreus* n. sp., restoration of posterior face, based on the holotype; the pectinirhomb *L1* — *IL1* not safely established; above the theca there are some fragments of brachioles; *a*, anus. Nat. size.

up of rather faint axial ridges only; opening for the stem occupying a little less than a third of the base diameter; stem tapering gradually in its proximal region, of about uniform width in its median region, tapering slowly towards the distal region.

Description:—The general shape of the theca. As already mentioned, the only specimen preserved well enough to give an idea of the general shape of the theca is the holotype. This, too, is rather crushed, however, but it may be inferred that in anterior and posterior faces the theca has been sub-ovate. The appearance of the lateral face cannot be decided safely. In its present state of preservation the theca is strongly asymmetric. It is mainly concavo-convex, the anterior side being the concave one; but it is possible that this is a secondary feature caused by deformation.

Measurements of the theca. Height 47 mm; width at base about 36 mm.

Thecal skeleton. On account of the incompleteness of the holotype the orientation of the theca offers some difficulties, and it is necessary to deduce the composition of the skeleton from comparison with the conditions in other species of *Cheirocrinus*. In this way the author arrived at the restoration shown in text-fig. 1. An analysis of the thecal skeletal elements more or less preserved is given in the slightly diagrammatic text-fig. 2. In those figures the determinations of the plates are based upon the distribution of the pore-rhombs in the Glyptocystitida according to the diagram published by Bather (1913, text-fig. 45, p. 439). In examining Bather's figure and beginning with the basal series of plates we note that the only plate bearing any more than half of a demirhomb — and thus the only plate which has demirhombs — is the plate designated by Bather as 1, which corresponds to *B2* according to the symbols adopted by the

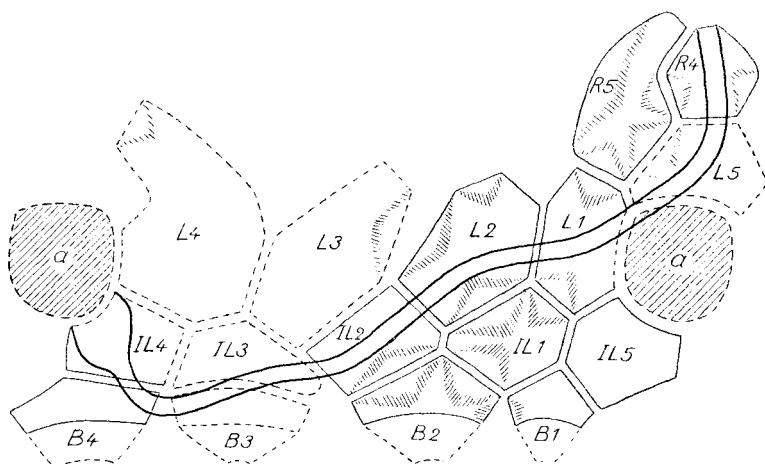


Fig. 2. *Cheirocrinus hyperboreus* n. sp., analysis of the theca in the holotype; certain skeletal elements completed (indicated by broken lines); the pectinirhomb $L1-IL1$ not safely established; the demirhombos on $L3, L4, L5$, and the lower one on $B2$ not actually stated but concluded to be present on theoretical grounds (the number of pore-slits in each rhomb is conditional); the heavy lines indicate the approximate course of the gut along the inner side of the test; a , anus. Slightly diagrammatic.

present writer.¹ Three BB only are preserved in the actual specimen. One of these has two demirhombos easily visible. Hence the plate in question has to be designated as $B2$. As a corollary the identification of the remaining plates follows. In the different circlets several plates are wanting (the greater part of $B3; IL3, IL4; L3, L4, L5; R1, R2, R3$; all 00). Several of those present are badly preserved, because of which their exact outline often cannot be determined. On the whole, the plates of the basal circlet are more or less pentagonal, those of the other circlets more or less hexagonal. Several plates are rather strongly umbonated.

Surface structures of stereom. The test is nearly smooth. The plate ornament is made up exclusively of rather faint axial ridges which originate from the umbo and proceed — without dilating to any great extent — to the edge of the plate. Here, perpendicularly

¹ The terminology in the present paper is the same as that used by Regnéll 1945. Bather's symbols are thus replaced by those used in the paper just referred to. The equivalence of the symbols in the two systems appears from text-fig. 5, p. 62, in Regnéll 1945.

to the suture and bisecting it, the ridge fuses with a corresponding ridge of a neighbouring plate. The *BB* have no radiating ridges.

Pores of the thecal plates. Since *B 1* shows a demirhomb, the base line of which is the suture between that plate and *B 2*, the plate last mentioned must necessarily have had a third demirhomb in addition to those developed towards *IL 1* and *IL 2*. The demirhomb towards *B 1* cannot be detected in the holotype, however, probably because the edge of *B 1* seems to have been thrust over the adjacent margin of *B 2*. *B 4*, as in all known Glyptocystitida, has no pore-rhombs. The rhombs *IL 1* — *B 2* and *B 2* — *IL 2* were just referred to. Furthermore, the following rhombs are present: *IL 1* — *L 2*, *L 2* (— *R 2*), *L 2* (— *L 3*), (*L 5* —) *R 5*, (*L 4* —) *R 4*, *R 4* — *R 5*, *R 5* — *L 1*, *R 5* (— *R 1*). The symbols within brackets denote that demirhombs must have been developed in these plates. This cannot be observed directly in the actual specimen (the holotype), however, since the plates concerned are destroyed. In *L 1* — *IL 1* a pectinirhomb is possibly present, but the state of preservation does not admit of a definite statement.

Except in the case of two rhombs, the distribution of the pores agrees perfectly with Bather's scheme. The two rhombs that are not represented there are *IL 1* — *L 2* and the somewhat doubtful *L 1* — *IL 1* (6 — 11 and 12 — 6 acc. to Bather's designations). It need hardly be said that the above list of pore-rhombs does not correspond to the total number in a complete specimen. — All exposed pectinirhombs are disjunct. In 5 mm there are about 15 pore-slits.

Ambulacral system. The very apex of the theca is not preserved sufficiently well in the material available to show the structure of the ambulacral area. But a number of brachioles are present. Some fragments seem to lie more or less in situ above the apex of the theca in the holotype (Pl. 1, fig. 1; Pl. 2, fig. 1). Their proximal parts are not preserved, and owing to this they have lost their connexion with the theca. Detached and fragmentary brachioles are also found in the hand specimen 2271. On account of the fragmentary state of the brachioles their number and length cannot be settled. The brachioles are of the usual type found in cystoids, biserial, the ossicles of the two rows alternating, and with small ventral cover-plates which are more or less finger-shaped (Pl. 2, fig. 1). The individual ossicles have an average width in lateral view of 0.7 mm in their proximal region and a height of 0.5 mm. They taper, however, in a distal direction. The presence of brachioles in this species

is remarkable, since, as far as the writer knows, this is the first instance in which such structures have been observed in Scandinavian material.

The hydropore cannot be recognized in consequence of the non-exposed thecal apex.

Alimentary canal. For the same reason as in the case of the hydropore the mouth is not visible. The periproct with the anal opening, according to the interpretation of the thecal skeleton here advanced, answers to the demand in the diagnosis of *Cheirocrinus*. Thus it is relatively large, being enclosed by the plates *IL* 4, *IL* 5, *L* 1, and *L* 4. Covering plates of the periproct are not preserved.

Bather (1900, p. 58; 1913, p. 439) has demonstrated how in the Glyptocystitida the distribution of pore-rhombs is governed by the course of the gut in as far as no pores could develop in those places of the theca where the gut was supposed to press against the inner wall. The track left free between the pore-rhombs, therefore, gives an idea of the probable course of the gut. In *Cheirocrinus hyperboreus*, as mentioned above, there is one or, possibly, two pore-rhombs which were not recorded in the material upon which Bather founded his diagrams. These additional pores, however, do not block the given course of the gut, but only indicate a slightly higher position of part of the gut, caused by the pore-rhomb *IL* 1 — *L* 2, and made possible by absence of the pore-rhomb *L* 1 — *L* 2, which is developed in certain forms (cf. our text-fig. 2 with text-fig. 45 in Bather 1913, p. 439).

The gonopore cannot be observed.

Several fragments of the stem are present in our material. The completest one is that figured in Pl. 2, fig. 2, which consists of 36 columnals and has a length of 43 mm. The proximal region — here arbitrarily thought to comprise the 26 most proximal of the columnals preserved — tapers from 8 mm to 2.8 mm. The median region, made up of 7 columnals, has an approximately uniform width of about 2.8 mm. It merges imperceptibly into the distal region, represented in the stem fragment under consideration by 3 columnals only, the most distal of which is 2 mm wide. Further distally, the diameter decreases still more, so that the stem becomes almost pointed at its lower end, as is apparent from other fragments. The morphological differentiation of the stem elements is very much the same as described by Jaekel (1899, p. 215) and Bather (1913, pp. 446—447).

In the proximal region the columnals are low in relation to their width, varying in height between 1.5 and 1 mm. The walls are thin and the lumen, in consequence, wide. The columnals have a conspicuous flange and might have been constructed as represented in Bather's text-figs. 57 and 58 (1913, p. 447). As far as can be recognized there has actually not been a system of independent outer and inner rings in this species. The columnals in the median region are about 2 mm high, which is also true of those in the distal region. In both regions the walls of the columnals are very thick, enclosing a narrow lumen, circular in transverse section. There is no ornamentation on the stem.

Jaekel (1899, p. 215, text-fig. 41; see also p. 183, text fig. 35) called attention to certain discoid and irregular bodies occurring at certain localities along with thecae of *Cheirocrinus* and interpreted by him as roots of *Cheirocrinus*. Bather (1913, pp. 440, 447) declined this interpretation. Indeed it is impossible that the wide-lumened bodies described by Jaekel can have been roots of a *Cheirocrinus*, the stem of which has been constructed in the same way as that of the present species. As a matter of fact Jaekel (1899, p. 215) pointed out himself that the lumen of the distal columnals is quite inconsiderable, attaining a third only of the stem diameter. Ehrenberg (1929, p. 57) related Jaekel's view of the structures concerned but did not give a definite personal opinion of their nature. Bather (1913, p. 440) was inclined to assume that the stem in *Cheirocrinus* tapered continuously to the distal extremity and that a root organ was entirely absent. Furthermore, he suggested "that the animal no longer retained the normally erect pelmatozoic position, at least in adult life, and that, in harmony with this change, it also relinquished its primitive attachment". This, though not substantially declared, was also the opinion of Kirk (1911, pp. 5, 13), who placed *Cheirocrinus* in the type of cystoids which were "provided with a prehensile column which attached themselves at will, probably not by cementation, but rather by looping the distal portion of the stem about some fixed object" (op. cit., p. 5). The Norwegian material, however, corroborates an interpretation of the organization similar to that presented by Jaekel. In the large slab (PMO 2271) and in PMO 2271a which was split from the former there are some ten peculiar conical bodies lying among the scattered skeletal elements of *Cheirocrinus hyperboreus* (Pl. 2, fig. 3). At the base they have a diameter of about

20 mm. The height is 12—15 mm. In some cases one or two concentric hollows are seen to run some millimetres above the base. In the figured specimen some distal columnals of the stem lie close beneath the cone. In the author's opinion, these have been attached to the apex of the cone by the interposition of a few more columnals now not preserved. Then it is difficult to imagine what function may be ascribed to the conical bodies, were they not acting as a sort of root organ. Thus, if we have a look at the animal as a whole, we get the following picture: the theca was raised over the sea-ground by means of a stem having at least the same length as the height of the theca and being anchored in the mud by a conical organ. The latter might also have served as a sucking disk, but this seems unlikely. The distal and median regions of the stem might have been rather rigid, whereas the proximal portion was strongly flexible in all directions and capable of a certain concertina-like contraction effected by strong muscles.

Cheirocrinus hyperboreus is a relatively early representative of the genus. Therefore the mode of life here outlined does not, of course, exclude the possibility that the later members were characterized by different habits. In consequence, the above version does not affect the probability of Bather's suggestion (1913, p. 509) that *Cheirocrinus* was influenced by eleutherozoic tendencies which became predominant due to some environmental changes, and gave rise to the new line that ended in *Pleurocystites*, which lay flat on the sea-floor and was potentially free-moving.

Discussion: — A survey of the species of *Cheirocrinus* was published by Jaekel (1899, pp. 219—221). His list was emended and completed by Bather (1913, p. 441),¹ and further commented upon by the present writer (Regnéll 1945, pp. 71, 74). *Cheirocrinus hyperboreus* belongs to the group of forms with pectinirhombs all disjunct, and only with axial ridges between the umbones. From all other members in this group it differs in the presence of the pectinirhomb *IL* 1 — *L* 2 (and possibly *L* 1 — *IL* 1). Nor is there any species which agrees with *Cheirocrinus hyperboreus* with regard to the distribution of the other pore-rhombs. Furthermore, most species of

¹ The few species discovered since that date [*Ch.* (?) *langedocianus* Thoral 1935, *Ch. ardmoresis* Bassler 1943, *Ch.* ? *loeblichii* Bassler 1943, *Ch. holmi* Regnéll 1945] have no bearing on the discussion, showing no very close affinities with the Norwegian form now considered.

this group are of a smaller size. The only one which is comparable with the Norwegian species in this respect is *Cheirocrinus granulatus* Jaekel 1899, which, apart from other differences, has granulated thecal plates and occurs in considerably younger strata, viz. the Kukruse ($C_{2\beta-8\alpha}$) of Estonia. Of species probably approximately synchronous with our form, *Cheirocrinus interruptus* Jaekel 1899 has multidisjunct pectinirrhombs and *Cheirocrinus volborthi* (F. Schmidt 1874) evidently more prominent axial ridges. In *Cheirocrinus penniger* (Eichwald 1842) the plate $R2$ is depressed into the lower circlet so as to separate $L2$ and $L3$. Whether it differs from *Cheirocrinus hyperboreus* in this respect too cannot be ascertained, since this part of the theca is not preserved in the material available. The older East Baltic species *Cheirocrinus ornatus* Eichwald 1860 (probably $B_{2\alpha}$; cf. Regnéll 1945, p. 70, foot-note 4) and *Cheirocrinus radiatus* Jaekel 1899 ($B_{2\beta}$) differ further from the present species, the former by its axial ridges dilating in a centrifugal direction, the latter by its lack of the demirhomb $B1-B2$. There are two more species belonging to the group under consideration, both of them younger, viz. the Scandinavian *Cheirocrinus nodosus* Jaekel 1899 (Ogygiocaris shale, Lower Llandeilian; a closely related form is known from somewhat older strata in Sweden) with protuberances on the axial ridges, and the North American *Cheirocrinus logani* (Billings 1857) (Trenton) with conical base. *Cheirocrinus leuchtenbergi* (Angelin 1878) from the Expansus limestone of Sweden is homotactic with the Norwegian species. In general appearance the two species come rather close but differ e. g. in the distribution and character of certain pore-rhombs. Thus in *Cheirocrinus leuchtenbergi* the pore $L2-L3$ is conjunct.

Regional distribution: — Norway, Asker: Gjeitungholmen off Slemmestad.

Stratigraphic range: — Expansus shale ($3c\beta$), Upper Skiddavian.

Family Echinoencrinitidae (Bather 1913) Bassler 1938.

Genus *Echinoencrinites* Meyer 1826.

Echinoencrinites senckenbergii acutangulus n. subsp.

Pl. 1, fig. 2. Text-fig. 3.

Derivation of name: — The name of this subspecies was chosen so that attention might be called to the acute angle formed by the extraordinarily high reaching upper sutures of the plate $B2$.

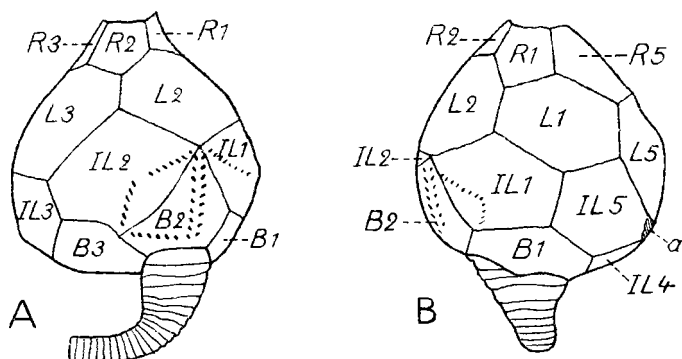


Fig. 3. *Echinoencrinites senckenbergii acutangulus* n. subsp., holotype. A, anterior view. B, left lateral view. a, anus. $\times 1.5$.

Holotype: — PMO 65571.

Type locality: — Gjeitungholmen, Slemmestad, Asker.

Type stratum: — Grey calciferous shale, of the stage 3c β (Expansus shale), Upper Skiddavian.

Material: — One single specimen is available, collected in 1917 by B. Parmann. The anterior side, which has been exposed to weathering, shows several details pretty well. In the rest of the theca, which was free-prepared from the shale, observations are more difficult on account of the intimate connexion between the test and particles of the rock. For the examination of this specimen, as well as for the other material here dealt with, the use of refracting liquids (alcohol, aniseed oil) was a great aid, and in certain cases quite indispensable.

Diagnosis: — A subspecies of *Echinoencrinites senckenbergii* Meyer 1826 in which B2 is produced into a long apex reaching as high as to touch the lower suture of L2, and separating IL1 and IL2 so that these plates meet at one point only.

Description: — In general shape the theca is pyriform, tapering in oral direction. The transverse section is subcircular. The base is somewhat flattened with a square opening (length of sides about 6.5 mm) for the stem.

Measurements. Height of the theca (apex not preserved) 23 mm. Greatest diameter 22.5 mm.

Thecal skeleton. Apart from the peculiar development of B2 mentioned in the diagnosis, the construction of the theca agrees fully with that of the nominate form.

Surface structures of stereom. The surface of the theca is cancellated all over by a frame of low and relatively broad ridges. The number of axial ridges occurring in a single plate cannot be determined owing to the poor state of preservation. At the periphery of the plates, however, there are 4 in 2 mm. In the few specimens available for comparison the corresponding number is also (3—) 4. Between two radial elements there are 4—5 transverse ridges in 2 mm. The special structure on the plates bordering the anal opening in *Echinoencrinites senckenbergii* as is well known (see e. g. Regnéll 1945, p. 82), is so poorly preserved that it can only be traced in the present specimen. The plates are rather flat and slightly umbonate.

Pores of the thecal plates. In *IL 1—B 2* and *B 2—IL 2* the pore-rhombs stand out very clearly, but these are the only pores which can be recognized. As is always the case in *Echinoencrinites*, the pore-rhombs are strictly disjunct, leaving only a small oval opening at the distal ends of the pore-slits. In each half-rhomb there are 16—17 pores.

Since the very apex of the specimen is wanting, the ambulacral area, the hydropore, the gonopore, and the mouth cannot be studied. The anus is enclosed by the plates *IL 4—L 5—IL 5*. It is oval, having a long diameter (in transverse direction) of 4 mm, and a short one of 3.5 mm. The periproct hardly protrudes at all.

Part of the stem is preserved. In anterior view it emerges from the basal invagination of the theca almost in the vertical plane of the animal, but curves rapidly to the right (to the left of the observer), nearly perpendicularly to its proximal course. When examined in lateral view, the stem is seen to be inserted obliquely to the vertical plane, being inclined in an anal direction. In the vertical portion of the stem the columnal diameter decreases from 6.5 mm proximally to 4 mm. Then it tapers more slowly, so that in the most distal of the 22 columnals still attached to the theca it is 3 mm. The exposed columnals are typical "Kragenglieder". They are circular in transverse section, thick-walled at least in the distal region, where the circular lumen occupies slightly more than a third of the entire diameter. The columnals are ornamented by minute denticles, visible especially at the distal edge of the ossicles. In the transverse section of the lowermost columnal about 20 such denticles are recognizable along the circumference.

Discussion: — The form now considered is well characterized by the special shape of the plate *B* 2. Irrespective of this feature, however, it agrees in different points so closely with *Echinoencrinites senckenbergii* that its legitimate category might be that of a subspecies, as suggested here. In a previous paper (Regnéll 1945, pp. 83—84), the author has had reason to point out that *Echinoencrinites senckenbergii* is liable to vary a good deal with regard to the general shape of the theca and certain details of ornamentation, differences which might be constitutive of a number of subspecies. They may also be based on variations in the development of elements in the thecal armour, as exemplified by the present form. It would have been desirable to investigate to what extent disturbances occur in the regular connexion between the plates of the several circlets, but the material needed for this purpose is unfortunately not at the writer's disposal. For direct comparison with the Norwegian form two specimens only are available, viz. the unique theca of *Echinoencrinites senckenbergii* obtained from Swedish deposits (RM Ec 3370, described by Regnéll 1945, p. 81 seq.), and a Russian specimen from Isvos (RM Ec 5523; RM=State Mus. Nat. Hist., Stockholm).

From the thecal analysis communicated by Meyer (1826, Pl. 2, fig. 1), it is evident that in the type specimen of *Echinoencrinites senckenbergii* all circlets were closed,¹ *B* 2 thus not interfering with the *ILL*, which appears also from the description of the skeleton (Meyer 1826, p. 183). Nor is there anything to indicate that Jaekel (1899) should have observed any anomaly in this respect. It is true that in Jaekel's summary description of *Echinoencrinites senckenbergii* (1899, pp. 248—249), nothing is said about the arrangement of the thecal plates, and that his figures (1899, Pl. 13, figs. 1—3) do not give any information about the condition of *B* 2, since the plate in question is not visible otherwise than in basal view (Jaekel's fig. 3 in Pl. 13).² But in the diagnosis of *Echinoencrinites* (Jaekel 1899,

¹ As noted by Regnéll (1945, p. 82) in accordance with Buch, the holotype has been lost.

² In Jaekel's Pl. 13, figs. 1—3, a number of plate symbols have been inserted erroneously. The *BB* have got their proper designations. But in fig. 1 read *l*₄ for *l*₅, *l*₁ for *l*₂, *l*'₄ for *l*'₅, *l*'₅ for *l*'₁, *l*'₁ for *l*'₂; in fig. 2 read *l*₅ for *l*₁; in fig. 3 read *l*₅ for *l*₁, *l*₁ for *l*₂, *l*₂ for *l*₃, *l*₃ for *l*₄, *l*₄ for *l*₅ (in the symbol system adopted by the present writer *IL* corresponds to *l* of Jaekel, *L* to *l*', and *R* to *l*'; cf. Regnéll 1945, p. 61). It is obvious that the designations here

p. 242) it was stated that the plates of each circlet come into lateral contact with each other and thus form closed circlets. In the Swedish specimen referred to above, the *IL*-circlet is also closed, but the apex of *B* 2 is sufficiently high to reduce the length of the suture between *IL* 1 and *IL* 2 to 2 mm.¹ And in the Russian specimen (RM Ec 5523) *IL* 1 and *IL* 2 are entirely separated from each other by the apex of *B* 2, which reaches as far as to the lower suture of *L* 2. This specimen must accordingly be referred to the subspecies *acutangulus* hereby erected. It should be noted that Lamansky (1905, p. 178) announced the presence of two forms in the East Baltic area which were said to be closely allied to *Echinoencrinites senckenbergii*. One of these (the two forms were not described and not named) is perhaps identical with our new subspecies.

In recognition of this gradual transition between the nominate form of *Echinoencrinites senckenbergii* and the form now discussed, it is, in the author's opinion, convenient to regard the latter as a subspecies, and not as a well-defined species or, still less, as a representative of a separate genus. This view is further corroborated by the general agreement in the shape and ornamentation of the theca, as emphasized above, and also by the similarity in the ornamentation of the columnals, as appears from a comparison between the Swedish specimen of *Echinoencrinites senckenbergii* at the author's disposal, and the Norwegian form. It is clear that the acceptance of this new subspecies has some bearing upon the diagnosis of *Echinoencrinites* as presented by Jaekel (1899, p. 242). The claim that all plate circlets are closed must thus be modified as far as

altered were put in by accident, for they do not fit with the diagrammatic analysis of the theca in *Echinoencrinites* published by Jaekel (1899, text-fig. 36 F, p. 196; the same diagram repeated in text-fig. 47, p. 243). Furthermore, Jaekel mentioned expressly (1899, p. 249) that, in *Echinoencrinites senckenbergii*, the anus was enclosed by the plates *IL* 4, *IL* 5, and *L* 5 (in all Glyptocystitida the anus is surrounded by these plates to which *L* 4 is added in several instances). This, however, would not be the case, if Jaekel's designations were correct.

¹ The lengths of the sutures between the other plates in the *IL*-circlet are as follows: *IL* 2 — *IL* 3: 3 mm; *IL* 3 — *IL* 4: 9 mm; *IL* 4 — *IL* 5: 9 mm; *IL* 5 — *IL* 1: 3.5 mm. In the Russian specimen RM Ec 5523 all corresponding measurements cannot be obtained, since the basal portion of the theca is not perfectly preserved. In the Norwegian specimen the suture *IL* 2 — *IL* 3 is 3 mm, and *IL* 5 — *IL* 1 5 mm.

the *ILL* are concerned. The writer has found this emendation of the diagnosis of *Echinoencrinites* much preferable to the alternative formation of a new species, for reasons which he hopes that he has explained in the above lines.

Our insufficient knowledge of the relative stratigraphic appearance of the several forms of *Echinoencrinites senckenbergii* does not allow us to form a clear idea of any tendency predominant in the species; is there a trend towards greater symmetry in the thecal skeleton, by gradual suppression of the differences in development of the skeletal elements in the basal series; or is the asymmetry a feature acquired during evolution? From a theoretical point of view the latter alternative seems the most probable one. It is a well-known fact that the radial symmetry in echinoderms is affected in various ways when a pelmatozoic type is transformed into a more or less free living form. This might have happened in *Echinoencrinites*. The reasons for this assumption were set forth by Jaekel (1918, p. 95), who suggested that the constant proximal curvature in the stem, and the character of the base of the theca, indicate that the Echinoencrinitidae were resting freely on the substratum with recumbent stem. Possibly they were even capable of a certain degree of locomotion by wriggling the contractile and muscular stem. But it cannot be doubted, with regard to the perfectly developed stem, that these free forms were derived from statozoic ancestors.¹ The eleutherozoic tendency is likely to have become more and more defined in the course of time, and the asymmetry of the theca simultaneously increased. But for what reason does the asymmetry manifest itself in a prolongation in oral direction of the plate *B2*? The answer to this question seems to be the following: In resting on the sea-floor the animal evidently ran the risk of getting the lower part of its theca buried in the ooze. In *Echinoencrinites senckenbergii* the thecal pores, excepting the pore-rhomb *R3 — L4*, are concentrated in the lowermost circlets of plates, and mainly in *B2*. If the base of the theca sunk into the soft bottom-layer, a good deal of the pore-slits very likely became clogged with mud. In this way the respiratory

¹ In this instance the liberation from the substratum is a secondary feature, and because of this the line of reasoning is in no way involved in the question concerning the statozoic or eleutherozoic nature of the organisms which gave rise to the different lines of echinoderms.

function must have been disturbed and considerably reduced.¹ In order to counteract this trouble, the pore-bearing plate *B 2* tended to be prolonged in an apical direction. As a consequence, part of the pores were elevated above the actual „risk-zone“.² The same result was acquired more safely in other Echinoencrinitidae by locating the main part of the pore-rhombs in the upper portion of the theca.

Regional distribution: — Norway, Asker: Gjeitungholmen off Slemmestad. — The USSR: Iswos.

Stratigraphic range: — The Norwegian specimen is from the Expansus shale (3 c β), and the East Baltic specimen probably from the Vaginatum limestone (B_{III}), both of which are of Upper Skiddavian age.

Genus *Erinocystis* Jaekel 1899.

Erinocystis brøggeri n. sp.

Pl. 1, figs. 3—4. Text-fig. 4.

? 1882 *Cryptocrinus laevis*, Pander [non Pander 1830]. — Brøgger, p. 41 (cf. pp. 23, 174).
1882 *Echinoencrinus senckenbergii*, H. v. Meyer [non Meyer 1826]. — Brøgger, p. 42 (cf. pp. 23, 174).

Derivation of name: — The species is named after W. C. Brøgger, who gave the first information on the occurrence of Echinoencrinitidae in the Ordovician series of strata in Norway.

¹ The writer is not inclined to deprive the pore-rhombs of any respiratory function. The suggestion of Delpy (1941) that they should be interpreted as balancing organs does not seem to be sufficiently corroborated.

² By the stretching of *B 2*, the long axis of the pore-rhombs *IL 1* — *B 2* and *B 2* — *IL 2* was extended. In connexion with this, the number of pore-canals in the pectinirhombs ought to have increased. The information which can be extracted from literature and from the sparse material at hand is of course far too scanty to be really significant. The number of pore-canals in the pectinirhomb *B 2* — *IL 2* is as follows in some different specimens: —

Nominate form: holotype figured by Meyer (1826, Pl. 2, fig. 1), about 15 the Swedish specimen RM Ec 3370 (the same as figured by Jaekel 1899 Pl. 13, fig. 3), 14 (in Jaekel's fig. no more than 12—13 are represented).

Subsp. *acutangulus*: PMO 65571 (holotype), 17; RM Ec 5523 (Russian specimen), 19.

The Norwegian specimen is smaller than the three other ones. Had it been of a size comparable with theirs, the increase of the number of pore-canals in the subsp. *acutangulus* would probably have been still more pronounced, for the absolute size of the theca (and the stage of development of the specimen) might have had some importance too in this respect.

Holotype: — PMO 20148.

Type locality: — Tøyen, Oslo.

Type stratum: — 3 c β (Expansus shale), Upper Skiddavian. Inconsiderable rock fragments only are attached to the holotype.

Material: — The holotype is a rather worn specimen, unfortunately devoid of the apical part of the theca. Another specimen [PMO 20149], which is considered conspecific, is somewhat more complete but in a rather poor state of preservation. These specimens were collected in 1876 by N. Wille and Th. Münster and are those referred to by Brøgger 1882 as "*Echinoencrinus senckenbergii*". As appears from the list of synonyms above, the very imperfect specimen [PMO 20157, coll. Th. Kjerulf] determined by Brøgger as "*Cryptocrinus laevis*" possibly belongs here. Part only of the test is preserved. About this specimen, cf. the discussion below.

Diagnosis: — A species of *Erinocystis* with medium-sized theca; *BB* tolerably equally developed; thecal ornamentation restricted to certain areas in the adult; periproct protruding moderately.

Description: — General shape of the theca. According to the diagnosis of the genus *Erinocystis* (Jaekel 1899, p. 249), the theca has to be "umgekehrt feigenförmig" with strongly tapering upper part. Whether this is also true of the species added here must be left undecided, because of the imperfection of the material at hand. The preserved portion of the holotype, as well as of the so-called "*Cryptocrinus*", is largely globular, whereas in PMO 20149 it is compressed from the sides, either primary or secondarily.

Measurements (it is emphasized again that the upper part of the theca is wanting in all specimens).

(Measurements in mm)	PMO 20148 (holotype)	PMO 20149	PMO 20157
Height	15	12	12
Greatest diameter in sagittal direction	17	11.5	12.7
" " " transverse "	16.7	10.3	12

Thecal skeleton. The most significant feature in the construction of the thecal armour is the depression of *L* 3 into the *IL* circlet so as to border on *B* 3 by a long suture. This can be

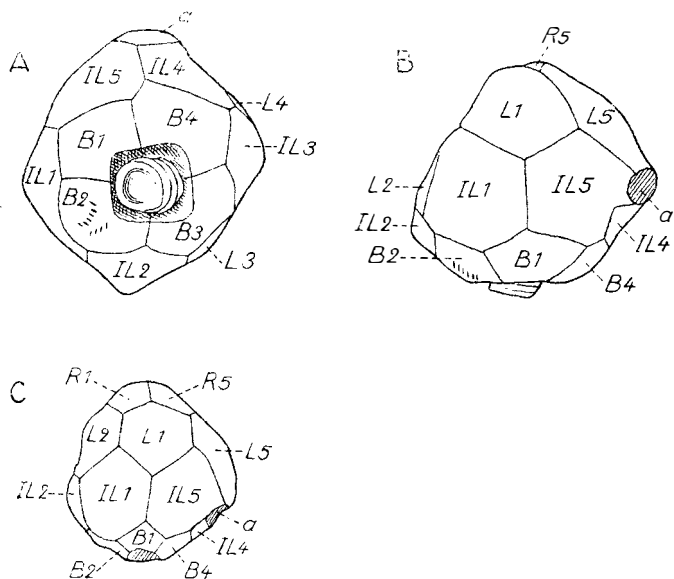


Fig. 4. *Erinocystis broggeri* n. sp. A, holotype in basal view. B, the same in left lateral view. C, PMO 20149, left lateral view. $\times 2$.

ascertained readily in the holotype only (cf. text-fig. 4 A), but can be traced in the other specimens too. Of the plates in the *R*-circlet almost nothing is preserved in the holotype, and the basal parts only in PMO 20149. The number can be settled as 5. Typically these are long and narrow in *Erinocystis*, which, of course, cannot be controlled in our material.

Surface structures of stereom. In the holotype radiating ridges running from umbo to umbo are found in the plates *B* 1, *IL* 5, *IL* 1, *L* 5, and *L* 1. At the periphery of the plates there are 4—5 such ridges in 2 mm. Between the radiating stereom folds there are transverse elements, 6—8 in 2 mm. All other plates preserved are smooth, or show faint growth-lines only, which is also true of PMO 20157 ("*Cryptocrinus*"), where, as mentioned, a minor part only of the test is present. The specimen PMO 20149 has been covered all over with the cancellated ornamentation, which has been abraded, however, in certain parts of the theca. There are, on an average, 5 radiating ridges in 2 mm at the periphery of the plates, and 9—10 transverse elements i 2 mm. The smaller dimensions

indicate that this specimen is no adult one. The differences in the character of the plate ornamentation might be due to this fact. — The plates are well umbonated.

Pores of the thecal plates. The pectinirhombs are partially clearly visible in the holotype. The following ones are present: *IL 1—B 2* (6 pore-canals; rather long pore-slits in *B 2*, those in *IL 1* just traceable), *B 2—IL 2* (4 pore-canals only visible; 4 rather long pore-slits in *B 2*, those in *IL 2* not recognizable), and *R 3—L 4* (the total number of pore-canals might have been 11; in *R 3* a few pore-slits only are traceable; in *L 4* there are 8, somewhat shorter than in *B 2*). No thecal pores are recognizable in PMO 20149. After moistening the specimen, two basal pore-rhombs stand out very clearly as internal casts in the so-called "*Cryptocrinus*". In the pore-rhomb *IL 1—B 2* there are 6, and in *B 2—IL 2* 5 pore-canals,

The ambulacral area with its apertures is not preserved in any specimen, as already mentioned.

The anus is rather small (diameter in the holotype 2.5 mm), subcircular in outline. It is located in a periproct, in the shape of a triangular pyramid well elevated over the general surface of the theca, but not protruding nearly as much as in certain other Echinoencrinitidae. The plates forming the periproct, and thus bordering the anal opening, are *IL 4*, *L 5*, and *IL 5*.

The stem is of the type regularly met with in the Echinoencrinitidae, as appears from 3 or 4 proximal columnals still attached to the theca in the holotype. The diameter is 3.5 mm. The stem is inserted obliquely to the vertical axis of the theca. The columnals have an exceedingly faint spinose ornamentation similar to that described above for the preceding form.

Discussion: — There has been some difficulty in settling the generic affinity of the present species, mainly because the character of the *RR* and the number of brachioles (2 in *Erinocystis*) cannot be established. Yet the writer did not think it necessary to add a mark of interrogation to the generic name. For in its main features the species conforms well to the diagnosis of *Erinocystis*, though in general shape the theca is not so outrageous as in the three species described by Jaekel (1899, pp. 252—253). The remarkable depression of *L 3* into the *IL*-circlet so as to rest directly upon *B 3* is found, as well as in *Erinocystis*, in *Glaphyrocystis compressa* Jaekel (1899, pp. 253, 257) and in *Proctocystis* Regnéll (1945, p. 85). The former,

which is an Upper Ordovician or Lower Silurian species¹ from the East Baltic area, is rather different from our form, e. g. with regard to the number and character of the pore-rhombs and the location of the anus which lies between the plates $L\ 4-IL\ 4-L\ 5$. In *Proctocystis* the periproct is much more protruding, and the number of RR is reduced to 4.

The species of *Erinocystis* previously known were probably about synchronous with the new one. In the general shape of the theca this seems to be most closely allied to *Erinocystis sculpta* Jaekel 1899 (no fig. was given of the outline of the theca), in which the periproct is considerably less protruding than in the two other species, where it is extraordinarily conspicuous. In *Erinocystis volborthi* Jaekel 1899 the BB , besides, are very asymmetric. *Erinocystis sculpta* is ornamented all over the theca. In this it differs from the adult of *Erinocystis brøggeri*.

The restricted number of pore-canals, especially in the basal rhombs, makes the pectinirhombs seem somewhat abortive, a feature which is demonstrated in *Erinocystis angulata* Jaekel 1899 also. The tendency towards restriction of the ornamentation to limited areas of the theca prevails in *Erinocystis angulata* and *Erinocystis volborthi* as well.

Taking it all in all, it seems that the species now under discussion should be referred to *Erinocystis*. The holotype and the specimen PMO 20149 were determined by Brøgger (1882, p. 42) as *Echinoencrinites senckenbergii*, as mentioned above. Brøgger expressed doubt regarding the specific rank of such forms of *Echinoencrinites* as were described as species distinct from *Echinoencrinites senckenbergii*, and listed their names as synonyms. If, however, they were to be looked upon as valid species, Brøgger would be inclined to identify the Norwegian material with *Echinoencrinites angulosus* (Pander). As should have appeared from the above description, *Echinoencrinites* as defined nowadays, cannot be considered at all in this instance; and especially not *Echinoencrinites angulosus*, where the anal opening is bordered invariably by 4 plates.

It cannot be proved definitely that it is correct to refer the specimen from Huk in Bygdøy, which Brøgger called *Cryptocrinus laevis*, to *Erinocystis brøggeri*. But what can be proved is that the

¹ The horizon was not specified by Jaekel (1899, p. 257) but designated as "F" only.

specimen, by the presence of thecal pores, is no member of the Eocrinoidea, but, owing to the presence of pore-rhombs, belongs to the cystoid order Rhombifera. The construction of the thecal skeleton and the location and development of the pore-rhombs bring it into line with the Echinoencrinitidae. As far as can be recognized in the poorly preserved theca, it agrees fairly well with the holotype of the species hereby established and may, therefore, be conveniently included under this category.

Regional distribution: — Norway, Oslo: Tøyen. —? Bygdøy: Huk.

Stratigraphic range: — Expansus shale (3 c β), Upper Skiddavian. In the case of the specimen from Bygdøy (the so-called "*Cryptocrinus*"), the horizon is not settled quite safely (cf. Brøgger 1882, p. 42).

Superfamily HEMICOSMITIDA (Jaekel 1918) Regnéll 1945.

? Family Hemicosmitidae Jaekel 1918.

? Genus *Hemicosmites* Buch 1840.

Hemicosmites? sp.

Text-fig. 5.

1865 (?) *Hemicosmites pyriformis* v. Buch. — Kjerulf. p. 4.

1882 *Hemicosmites* sp. — Brøgger, p. 42 (cf. pp. 23, 174).

Material: — The material at the writer's disposal consists of an isolated thecal plate lying in a piece of grey limestone with rust-coloured weathered surface. The specimen [PMO 20147] is that mentioned by Kjerulf (1865) and Brøgger (1882) (cf. also Regnéll 1945, p. 100), and represents a unique discovery of its kind in Norway.

Description: — The plate, which is most probably an *IL*, has a height of 12 mm and a greatest width of 9 mm. It is about 1.5 mm thick and is heptagonal in outline. The upper surface is uneven and corroded and is not likely to give an idea of the original structure of the plate surface. There are 14 radiating rows of circular pore-openings showing the presence of 7 half-rhombs, one at each side of the plate. The pore-canals are thus entirely overbridged by stereom except at their very distal ends.

Remarks: — It is hardly possible to make an unassailable generic determination of the present plate, for the structure of the

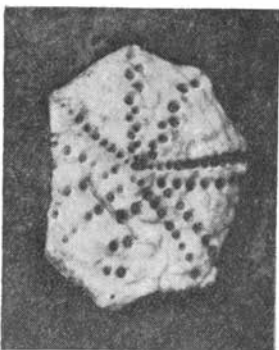


Fig. 5. *Hemicosmites* ? sp. [PMO 20147]. $\times 3$. — Vaekkerø. (Photo. in alcohol; green filter; retouched.)

individual skeletal elements, and especially of the *ILL*, is as a principle so uniform in the several genera of Hemicosmitida that the characterization of the genera is based mainly on the number of plates in the circlets, on the structure of the apical area, and on the location of the anus (cf. the diagrams communicated by Dreyfuss 1939, p. 126).

The genera which would then be taken into consideration are *Hemicosmites* and *Caryocrinites*. That the latter should be included is doubtful, however. The partial alternating of pores in adjacent rows shown in a few instances (the rows of pores turned upwards in text-fig. 5) indicates that the pores have hardly been arranged along each side of radiating ridges, as in the "normal series" in *Caryocrinites*. On the other hand, the plate is not very likely to have belonged to a member of the "*Stribalocystites* series", where ridges are not developed, or merged into the plate, but where the pores are often obscure (cf. the short survey of the genus *Caryocrinites* in Regnéll 1945, p. 103).

Turning to *Hemicosmites*, we have to state that a closer comparison with previously known species of this genus cannot be made since the original surface structure of PMO 20147 is not preserved. Unfortunately the knowledge of the stratigraphic distribution of the East Baltic species is very meagre. According to Jaekel (1899, p. 308) *Hemicosmites malum* (Pander 1830) is the first one to appear, viz. in the so-called Echinospaerites limestone ($C_{1\beta}$) which is somewhat younger than the stratum from which the Norwegian specimen was derived. The horizon of *Hemicosmites pyriformis* Buch 1840, to which the present plate was tentatively referred by Kjerulf (1865), is not known in detail. In Sweden, as far as our knowledge goes, no species occurs in strata lower than the Lower Chasmops limestone (Upper Llandeilian). For reasons here explained it seems wisest, therefore, to designate the fragment in question as *Hemicosmites* ? sp. Provided that this species really belongs to *Hemicosmites*, a special interest is attached to it in being one of the oldest known representatives of the genus.

Regional distribution: — Norway, Lysaker: Vaekkerø. In a label (written by Kjerulf?) accompanying the specimen, the locality is given as "Vaekkerø 3".

Stratigraphic range: — The horizon of this species is not established quite safely. According to Brøgger (1882, p. 42) the specimen originates either from the Expansus shale (3 c β , Upper Skiddavian) or from the Orthoceratite limestone s. str. (3 c γ , Lowermost Llandeilian).

Subphylum **ELEUTHEROZOA** Bell 1891, emend. Bather 1900.

Class **Ophiocistia** (Sollas 1899, order) Sollas & Sollas 1912,
emend. Hecker 1938.

Family Volchoviidae Hecker 1940.

Genus *Volchovia* Hecker 1938.

Volchovia norvegica n. sp.

Pl. 2, fig. 4. Text-fig. 6 A.

Holotype: — PMO 2229 and 2230, the two specimens being counterparts. The first mentioned one represents the positive portion of the fossil. The remains contained in specimen nr. 2230 are not an impression, however, but display (as well as nr. 2229) an inner layer of the test, since the plates have broken along tangential cleavages when the piece of rock was split.

Type locality: Gjeitunholmen, Slemmestad, Asker.

Type stratum: — Bluish grey, dense limestone, with yellow weathering, of the stage 3 c β .

Material: — Besides the holotype, the material available demonstrates displaced but mutually coherent plates of other individuals. Thus in 2229, on the "reverse side" of the handspecimen, there are some few fragmentary plates showing the internal side of the test. Likewise on the "reverse side" of handspecimen 2230 there is a larger fragment of the armour composed of some ten more or less incomplete plates forming a bond of skeletal elements that reaches probably from the area round the anal opening to the margin. These plates show the upper surface of the test. The material was collected by a member of a field excursion in 1913.

Diagnosis: — A species of *Volchovia* with slightly vaulted dorsal shield, the greatest diameter of which amounts to about 70 mm;

grèatest diameter of the shield plates (exclusive of the marginal plates) not, or only slightly exceeding 20 mm; submarginal plates, with the exception of the hindmost ones, extended rather much in a radial direction; plates smooth, with no axial ridges; anus separated from the marginal zone by a single row of plates.

Description: — General shape of the body. In *Volchovia* as far as is known, only the dorsal shield has been skeletized strongly and, therefore, is the only part that is likely to become preserved. The weak skeletization of the ventral shield might be considered a primitive feature, to be compared with the observation by Spencer (1914, p. 34) that the most primitive Asterozoa had a leathery skin in which small irregular plates were embedded.

Like other species of this genus, *Volchovia norvegica* is ovate, with a long transverse axis and a shorter longitudinal one. The former measures about 70 mm, and the latter probably about 50 mm (exact measurements cannot be secured because of the incompleteness of the specimen). If the ring of marginal plates is left out of account, the lengths of the long and the short axes are 57 mm and 37 mm respectively. The central part of the firm armour is in the holotype slightly kidney-shaped in outline, the posterior margin being somewhat curved in a centripetal direction. This portion of the test forms a low dome, the highest point of which is elevated about 10 mm above the flattened marginal zone.

Arrangement, shape, and size of plates. Characteristic of *Volchovia* is a marginal zone of "10 pentagonal plates with rounded exterior apexes forming an undulating margin, and a protruding central part formed by plates reaching up to 30 in number" (Hecker 1938, p. 425; cf. also Hecker 1940, p. 75). In the holotype of the present species larger or smaller fragments of 9 marginal plates are preserved.¹ It is evident that the total number has been 10 originally. The outline of a perfect marginal plate does not appear from the material available, all the plates of the marginal zone being more or less incomplete distally. So it cannot be decided whether they ended in a rounded apex, in agreement with previously known species of *Volchovia*, or in an angular apex. The proximal side of these plates is slightly arched, or almost straight, so that the central part of the dorsal shield is somewhat

¹ The posterior area of the marginal zone is rather incomplete, but the position of the two most posterior plate fragments, in relation to the marginal plate to the left of them, indicates that they form part of the marginal zone.

polygonal in outline. This, moreover, is also true of the Russian representatives of the genus. In the holotype of *Volchovia norvegica* the length of the proximal side of the marginal plates varies between 11.5 mm and 20 mm. The narrowest marginal plates are those situated behind the anal opening. The radial sides of the marginal plates have an average length of 3.5 mm, whereas the distance from the middle of the proximal side to the apex can be estimated at 13 mm. But, as just mentioned, the several plates of the marginal zone vary in size and probably also in shape. They may reach a thickness of about 1 mm.

In the holotype of *Volchovia norvegica* the central disk is made up of rather polymorphous plates, which, so far as can be ascertained, are 21 in number.¹ They are disposed in an external, submarginal circlet of 15 plates, and 6 more plates irregularly arranged, as it would seem, inside the submarginal zone. Those inner plates are pentagonal to octogonal, the two largest ones having a long diameter of about 17 mm, whereas in the fragmentary specimen (on the "reverse side" of the handspecimen 2230), certain plates attain a length of 20 mm or still more. On the whole, the position and relative size of the inner plates in the holotype is very much the same as in *Volchovia mobilis* (cf. our figs. and Hecker 1940, text-fig. 35). There are considerable variations in the shape and size, but this is still more true of the submarginal plates. These are quadrangular, pentagonal, or hexagonal. The two plates behind the anus are the smallest by far of all plates present in the shield armour (here no attention is paid to any existing covering plates to the anal opening). They measure about 3 mm only in radial direction, whereas other plates in the same circlet reach a radial extension of 12 mm or even 15 mm.

Surface structures of stereom. As mentioned above, the upper surface of the test is not visible in the holotype, but is shown

¹ According to the diagnosis of the genus *Volchovia* quoted above, the central part is "formed by plates reaching up to 30 in number". It has obviously not been possible to settle the "normal" number for this kind of plate on the basis of the fossil material hitherto available. In the only specimen (a *Volchovia mobilis* Hecker) figured by Hecker (1940, text-fig. 35, p. 45) in which the number of central plates can be calculated tolerably safely there are about 20 of them. In the plastical restoration of *Volchovia mobilis* figured by Hecker (1940, Pl. 10, fig. 1) the number seems to be 23, which thus agrees well with the conditions stated as prevailing in the new species.

in the largest of the skeleton fragments mentioned above. Here the test is largely smooth, with no axial ridges, pits, or tubercles. Nor are the plates pierced by pores.

The ambulacral system is rather curiously developed in the Ophiocistia. The arms are actually very short and are incorporated in the disk, but support a restricted number of extraordinarily large ambulacral podia, serving as walking feet at least in certain genera. In the known post-Ordovician representatives of Ophiocistia, the ambulacral podia have been well skeletized externally by small scales. In the single Ordovician genus, *Volchovia*, the conditions must have been different, as emphasized by Hecker (1938, p. 426; 1940, p. 74). With regard to the fact that no traces of ambulacral podia could be detected in the East Baltic material, Hecker concluded that these organs, though probably otherwise well developed, were very weakly, if at all, skeletized. The Norwegian material causes no modification of this interpretation, for neither in this case are there any structures referable to the ambulacral podia.

In *Volchovia mobilis*, Hecker found indications of a small aperture behind the anus and bisected by the suture between the two most posterior marginal plates. Hecker did not give any positive opinion on its nature, but obviously did not expect it to be a hydropore, since in the diagnosis of the class Ophiocistia he stated that the madreporite is "large, actinal, in most forms not observed" (Hecker 1938, p. 427; 1940, p. 75). Undoubtedly this "second opening" represents either the gonopore or the hydropore, yet it might be impossible to decide which of them, since both openings are liable to vary a good deal, with regard to position and development, within the different groups of echinoderms.¹ As suggested originally by MacBride (1906, p. 487), and repeated by Spencer (1914, p. 35), there should exist a certain correlation between the size of the madreporite and the greater or lesser activity of the ambulacral podia, these

¹ In the other genera of Ophiocistia the conditions in this respect are as follows: — *Euthemon* Sollas (Wenlock): both pores lacking on the ventral surface (dorsal shield not known). *Sollasina* Fedotov (Lower Ludlow): pores absent. *Eucladia* Woodward (Lower Ludlow): a large madreporite of the same structure as in recent starfish located on the ventral surface, in a plate next to the adoral plate of an interradius; in the third plate of the same interradius there are 4 papillae which probably represent the gonopores; the gonad is supposed to have been unpaired (Fedotov 1926, p. 1149). *Rhenosquama* Richter (systematic position not quite safely established; Middle Devonian): not known,

factors being directly proportional to one another. The reasoning is based on the assumption that the loss of fluid by diffusion is greater in vigorously moving appendages, and the demand for replacing fluid from the water vascular system greater in consequence. On this assumption, *Eucladia*, which is the only known ophiocistid with a large composed madreporite, is believed to have moved by using the ambulacral podia as walking feet, while the locomotion in the other genera would have been accomplished by wriggling (Fedotov 1926, p. 1153; Delpy 1944, p. 271). In the case of *Volchovia*, walking feet seem to have been developed (Hecker 1940, p. 74), but the animal might not have been very active (cf. "Mode of life" below). The madreporite, therefore, ought not to have been especially large, and because of this we cannot exclude the possibility that the "second opening" in *Volchovia* represents the madreporite. It is also possible that the pore has been a common opening for the stone canal and the gonad. In the material available to the writer the pore mentioned cannot be studied because of the lack of the hindmost part of the disk in the holotype.

no part of the body but ambulacral feet having been discovered as yet (Richter 1930, p. 287).

In recent Ophiuroidea (Myophiuroidea of Matsumoto 1915, p. 45; 1917, p. 6) the madreporite is usually a single pore which, during ontogeny, migrates from a dorsal position to the ventral surface (see e. g. Bury 1895, p. 85; Dawydoff 1928, p. 761), whereas in the mainly Paleozoic Oegophiuroidea (Matsumoto 1915, p. 45; 1917, p. 5) it is either dorsal or ventral. Thus, e. g. in *Protaster*, which ranges from the Ordovician into the Ludlow, the madreporite is probably dorsal (Schuchert 1915, p. 226), and in *Bohemura primaeva* Fedotov, one of the oldest known representatives, from the Middle Ordovician, it is probably ventral (Fedotov 1936, p. 20; it should be remarked that in these old forms, owing to the state of preservation, the position of the madreporite is often hard to determine conclusively). From an embryological point of view, one is inclined to consider the dorsal position of the madreporite as the primary one. From a functional point of view, however, the reverse seems more probable, as is actually the case in the starfish (cf. below). For in "most cases the water vascular system got its protection [from being clogged by whirling mud] by the madreporic plate wandering towards the aboral side of the animal which was turned away from the bottom" (Gislén 1934, p. 7; cf. also Spencer 1914, p. 38). The position of the madreporite in Asterozoa was discussed at some length by Sollas & Sollas (1912, p. 214 seq.) and, following them, by Spencer (1914, p. 36 seq.). According to these authors, the dorsal position has been assumed secondarily; yet in the case of Ophiuroidea the question does not seem to be definitely solved. [To be continued on p. 40.]

Alimentary canal. A rather large sub-circular opening near the posterior margin of the test cannot be interpreted otherwise than as the anus. In the holotype of *Volchovia norvegica* it measures 9 mm along its long diameter (parallel to the transversal plane of the body), and 7 mm along the short one. The anal opening is enclosed by 5 plates of very different size, as pointed out above. An anal pyramid of numerous wedge-shaped plates observed by Hecker in his material is not preserved, nor are there any traces of a ring of minute plates between the shield plates and the anal pyramid as described by Hecker (1940, p. 73, text-fig. 36).

Considering the fact that the remains of *Volchovia* are found in limestones rich in organogenous detritus, Hecker (1938, p. 426; 1940, p. 74) concluded that the animal has been no mud eater but "possessed a powerful biting and masticating apparatus, which probably resembled the Aristotel's lantern of sea-urchins" (Hecker 1938, l. c.). Such a structure, to which Hecker called attention, has actually been cited as occurring in the later members of Ophiocistia. Being located on the lower surface of the shield, which was probably not, or only

In Ophiuroidea the sexual products are let out into the bursae, which open ventrally by a slit at each side of the arm bases.

In Asteroidea the madreporites vary considerably in number as well as in position. *Asterina* and *Palasteriscus* have a ventral madreporite, but in the recent adult starfish the madreporic aperture is generally abactinal after having been actinal in the early stages (see e. g. Bather 1915 b, p. 400). The orifices of the gonads are marginal. The Echinoidea have one madreporite and (generally) 5 gonopores in the apical system of the periproct. In the Holothuria the single madreporite lies generally in the body cavity, and the genital duct opens by a single median dorsal pore near the anterior extremity of the body.

Finally, we will have a look at the Pelmatozoa. In Edrioasteroidea the madreporite, when present, is situated on the actinal surface; apertures of gonads uncertain. In Blastoidea and in Carpoidea Marginata (Gislén 1930, p. 215), the hydropore and the gonopore had probably merged into the anal opening so as to form a cloaca. In Carpoidea Soluta they open on the thecal surface, to the left of the mouth. In Hydrophoridae a gonopore is sometimes present on the ventral region of the theca. It is often reduced, however. This being the case, the stone canal and the gonad might have had a common aperture. When a hydropore is present, the gonopore is situated below that organ. Certain Paleozoic Crinoidea have a madreporite between mouth and anus. In later crinoids the stone canal is differentiated into several weak tubes hanging down from the water-ring into the coelom. Here, of course, there is no madreporite in the body wall. The gonads are located in the arms.

weakly, skeletized in *Volchovia*, the mouth is not exposed in our material. The presumable jaws of the dental apparatus have not been detected either.

Mode of life: — In consequence of the proposal that *Volchovia norvegica*, as well as other Ophiocistia, was in possession of strong jaws and hypertrophied ambulacral podia which had taken over the function of arms in the ophiuroids, it follows that the animal was vagile and carnivorous. With regard to the outline of the shield possessing slight marginal projections, represented by the apices of the pieces in the marginal zone, *Volchovia* is not likely to have been very active. Bather (1915 a, p. 317) has pointed out that in the Asteroidea the active forms have as a rule longer arms (corresponding morphologically to the marginal plates in *Volchovia*) than the more sluggish types, and that the sedentary Edrioasteroidea are more rounded (forms with non-discoïd theca are of course left out of account) and less stellate than the starfish. Furthermore, when we consider the disk-like shape of the body and the large tubefeet, we may suggest that at rest *Volchovia* was attached by the ventral surface to hard objects on the sea-bottom, the whole of the body acting as a sucking disk. This is the habit of the ophiuroids *Astrophiura* (Matsumoto 1917, p. 245) and *Ophiophycis* (Mortensen 1933 a, p. 396), the general shape of which is much the same as in *Volchovia*. The genera just mentioned have been dredged from depths of about 300 m, or even more (*Astrophiura kawamurai* 300 fathoms, about 600 m, Matsumoto 1917, p. 240). Otherwise organisms acting as sucking disks, such as chitons and limpets, with which *Astrophiura* has been compared in mode of life (Matsumoto 1917, p. 245; Mortensen 1933 a, p. 396; Ziesenhenné 1942, p. 117), are characteristic of — though not exclusively confined to — the intertidal zone, as is well known (see e. g. Walther 1893, p. 71; Ziesenhenné, l. c.). *Volchovia*, however, must have lived in deeper regions where the formation of the enclosing limestone could take place.

Discussion: — There can be no doubt as to the generic affinity of the fossil now dealt with, for it fits perfectly in every detail into the plan of organization demanded for *Volchovia*. This genus was established in 1938 by Hecker for certain fossils from the Leningrad province, which had previously been considered by Jaekel (1900, p. 672; 1918, p. 124) and Bather (1913, p. 369) to be part of the theca of the fantastically interpreted carpoid genus

Rhipidocystis Jaekel. Hitherto two species only, described by Hecker, have been known. To these we have to add the new Norwegian species. In *Volchovia mobilis* Hecker 1938 the diameter of the test does not exceed 60—70 mm. The plates reach dimensions of up to 15—20 mm. They are comparatively thin, and with a smooth surface. The species occurs in the Megalaspis limestone (zones B_{IIβ} and B_{IIγ}), and rarely in the Vaginatum limestone (B_{III}).¹ *Volchovia volborthi* Hecker 1938 is confined to the Vaginatum limestone. It differs in its greater dimensions (diameter of test up to 80—90 mm, plates attaining 30 mm and being slightly thicker than in *V. mobilis*), and in having the plates covered with densely set fine tubercles (specific characters according to Hecker 1938, p. 426, and 1940, p. 75). It differs in the features mentioned from the Norwegian species as well.

Volchovia norvegica seems to come close to *V. mobilis* in dimensions and general appearance, yet it presents a sufficient number of characters to justify its specific rank. These are as follows: The dorsal shield is evidently considerably less vaulted in its central part (cf. Hecker 1940, text-fig. 36, p. 46, and Pl. 9, fig. 3 a), and the relative length of the transverse axis seems to be greater; the plates of the submarginal zone are more extended in a radial direction, with the exception of the hindmost ones (cf. Hecker 1940, text-figs. 34 and 35, p. 45); between the anal opening and the marginal zone there is one row of shield plates only, whereas in *V. mobilis* there are two (cf. Hecker 1940, text-figs. 35, p. 45, and 36, p. 46; see also text-fig. 42, p. 53, Pl. 9, fig. 3 a, and Pl. 10, fig. 1); the plates are devoid of any axial ridges (cf. Hecker 1940, text-figs. 35, p. 45, and 36, p. 46).

Regional distribution: — Norway, Asker: Gjeitungholmen off Slemmestad.

Stratigraphic range: — Expansus shale (stage 3 c β), Upper Skiddavian. In comparison with the series of strata in the Leningrad district, this stage is younger than the Megalaspis limestone which, as mentioned, is the main horizon of *Volchovia mobilis*. The Expansus shale is equivalent to at least the lower part of the Vaginatum limestone.

¹ For the section B_{II} of the East Baltic series of strata, Hecker used the term "Glauconite limestone" in accordance with F. Schmidt (the upper portion, B_{2b}, of Schmidt's B₂ is now referred to the stage B_{III}; cf. Öpik 1930, table facing p. 48). The section B_{III} was called by Hecker "Orthoceratite limestone". The terms in current use in recent Estonian literature are "Megalaspis limestone" (B_{II}) and "Vaginatum limestone" (B_{III} + C_{1a}) respectively.

An attempt at an analysis of the dorsal shield in *Volchovia*: — In the above description of the arrangement of the plates in the holotype of *Volchovia norvegica* the writer made no distinction between radial and interrarial skeletal elements. The reason for this was that there is no pronounced radial pentamerous symmetry except in the marginal zone. On that account an attempt at an analysis of the dorsal shield would seem liable to be affected by certain sources of error. The ventral shield in *Ophiocistia*, on the other hand, has not proved so hard to interpret in such genera where the material has admitted of a closer investigation (cf. Fedotov 1926).

The only post-Ordovician species of *Ophiocistia* in which the dorsal surface has been known is *Sollasina woodwardi* (Sollas). According to Sollas (1899, p. 695), the plates of this surface "are not arranged according to any discoverable law, though there may be a tendency to run parallel with the ambitus" (cf. Sollas 1899, fig. 1, p. 694, and Fedotov 1926, Pl. 2, fig. 1). Fedotov (1926, p. 1152) pointed out that the dorsal shield of *Sollasina* differs from that of *Ophiuroidea*¹ by the irregular arrangement of the disk plates and by the absence of primary plates. In *Volchovia* the plan of organization does not seem to be so completely obscured as in the more recent *Sollasina*. A tentative analysis of the dorsal shield in *Volchovia*, as conceived from a study of the two species *norvegica* and *mobilis*, is shown in text-fig. 6 A—B. Starting from the supposition that the aperture bisected by the suture of the two most posterior marginal plates is either a hydropore or a gonopore, or a common opening for both of them, we arrive at the conclusion that the pore in question is situated in interradius I—V (symbols for the radii according to the system developed by Jaekel 1918, p. 6 seq.). The hydropore as well as the gonopore of echinoderms is actually located in the dorsal vertical mesentery, or closely connected with it (see Jaekel 1899, p. 139). In this way we have determined the orientation of the skeleton and will try to trace the character of its elements. Since the two posterior marginal plates are interrarial in position, the same ought to be true of the remaining plates in this zone, each two being situated in one interradius. The plating of the central part of the dorsal shield seems at first sight to be quite irregular. Yet according to the tentative interpretation illustrated in text-fig. 6, the organization is as follows:

¹ For the relations between *Ophiocistia* and *Ophiuroidea*, cf. below.

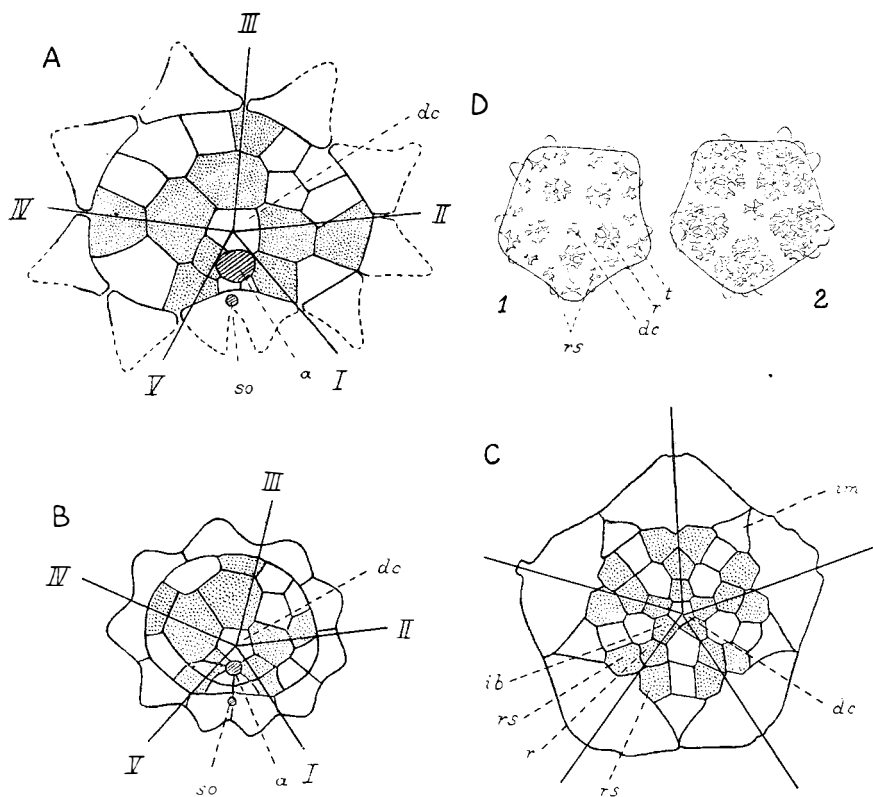


Fig. 6. A, *Volchovia norvegica* n. sp., holotype, dorsal shield, slightly restored in the marginal zone. B, *Volchovia mobilis* Hecker, dorsal shield, restoration (after Hecker 1940, Pl. 10. fig. 1). C, *Astrophiura permira* Sladen, dorsal shield, details of plating omitted in the distal radial parts (drawn after Koehler 1915, text-fig. 2). D 1—2, *Ophiophycis gracilis* Mortensen, embryos, dorsal shield in two consecutive stages of development (from Mortensen 1933 b, text-fig. 23, lettering by the present writer). Radial elements dotted in figs. A—C; I—V, radii I—V; a, anal opening; dc, dorsocentral; ib, infrabasal; im, interradian median plate; r, radial; rs, radial shield; so, "second opening"; t, terminal plate.

The plate lying above the anal opening should be considered as a dorsocentral.¹ It is surrounded by 5 radial plates (in *Volchovia mobilis* the plate in radius V is divided into two by a suture in the tangential direction). These, along with the dorsocentral, occupy the summit of the shield and may be looked upon as primary plates forming a sort of an apical system with an excentrally situated anus.

¹ The proper designation for this plate should possibly be "sur-anal".

Outside the primary radials¹ there is one more radial plate in each ray (in *Volchovia norvegica* the outer radial has coalesced with the primary one in radius I). The spaces between the radial elements are filled up with interrarial plates, one or more in each interradius. The interpretation here advanced seems to be fairly reasonable in spite of the fact that the elements of the different rays are not very regularly arranged. It may be observed that the test shows a tendency towards bilateral symmetry.

Sollas (1899, p. 699, foot-note 2) called attention to certain analogies in the organization of Ophiocistia and that of the recent ophiuroid *Astrophiura* Sladen.² Some further comments were made by Fedotov (1926, p. 1152 seq.), after the structural relations between Ophiocistia and Ophiuroidea had been elucidated by Bather (1907, p. 70; 1910, p. 880). According to Fedotov (l. c.) it "can be accepted that the radial parts of the oral surface of the disc of Ophiocistia are homologous with the basal segments of radii of recent Ophiuroidea". This statement was based upon an analysis of the ventral face in *Eucladia johnsoni* Woodward. As mentioned already, the plates of the dorsal surface were known then in *Sollasina woodwardi* (Sollas) only where no primary plates can be recognized and where the plates are quite irregular in arrangement. According to Fedotov (1926, p. 1152), there "is no analogy between the dorsal surface of the disc of Ophiocistia and *Astrophiura*, because the large pentagonal body of *Astrophiura* consists of the disc proper and of dorsal and very strongly expanded lateral plates of arms (Sladen 1879, pl. XX, figs. 3, 7; Koehler 1915, p. 3, fig. 1; Matsumoto 1917, p. 241, fig. 68 a)

¹ The term "radial" in this connexion does of course not imply that the plates concerned are homologous with the radialia of certain Pelmatozoa.

² Sladen (1879) was of the opinion that *Astrophiura* goes a long way towards bridging the gap between ophiuroids and asteroids. Koehler (1915, p. 311), on the contrary, looked upon *Astrophiura* as a true ophiuroid, not archaic in its structure, but highly specialized. Its proper classification was determined by Matsumoto (1915, p. 76; 1917, p. 234) and further emphasized by Hertz (1927, p. 83). Mortensen (1933 a, p. 394—395), in accordance with some previous authors, found that *Astrophiura cavellae* Koehler 1915 is identical with *A. permira* Sladen 1879, the genotype, and that the specific rank of *A. kawamurai* Matsumoto 1913 is questionable. The few specimens of *Astrophiura* hitherto obtained were derived from the South African Seas, the Sagami Sea of Japan, and, as reported lately by Ziesenhenné (1942, p. 117), from the waters of Southern California.

so that a large size of the body is a secondary feature. In Ophiocistia only the disc is present but no arms, and the large size of the disc is a primary feature". Now it is interesting to note that it seems possible to trace points of comparison between the organization of the dorsal shield in Ophiuroidea and in the primitive ophiocistid *Volchovia* as interpreted here (see text-fig. 6). It is true that the presence of the anal opening and the "second opening" on the dorsal surface marks a considerable difference from *Astrophiura* and the other ophiuroids. In these, as is well known, no gut and anus are developed, and a dorsal hydropore is present in early larval stages only (cf. above, p. 39, footnote 1). Neither is it possible to compare in detail the skeletal elements in *Volchovia* with those of *Astrophiura*, but it can be claimed that an analogy exists in the general plan of arrangement. In both there is an "apical system" made up of a dorsocentral and radial plates surrounding it, and in both the radial elements predominate in the central region of the dorsal shield. In this connexion it should be mentioned that, according to observations by Mortensen (1933 b, p. 459; cf. our text-fig. 6 D) on embryos of *Ophiophycis gracilis* Mortensen, which is closely related to *Astrophiura*, it "appears that the first formed skeletal elements are the five radial plates and the terminal plates; next follow the radial shields and the central plate". This, moreover, is the general order in which the skeletal elements appear in immature ophiuroids (cf. Sladen 1884, p. 41; see also Chadwick 1914, pp. 11—12, Pl. 4), and, furthermore, with certain variations, is characteristic of the pentactula-stage in the ontogeny of existing echinoderms except the Holothuria. *Astrophiura* is peculiar in having a secondary marginal zone of the disk formed by the specially developed proximal parts of the arms. Each of these is separated from the neighbouring one by a triangular interrarial median plate (text-fig. 6 C, *im*).¹ The interrarial median plates correspond in position to the roughly triangular marginal plates in *Volchovia*. Notwithstanding the fact that in *Volchovia* there are two marginal plates in each interradius, there is very probably no reason to conclude that the marginal plates have played a similar role to that of the interrarial median plates of *Astrophiura*. The material available of *Volchovia norvegica* gives no positive evidence in this

¹ This plate was termed "plaque interrarial médiane" by Koehler (1915), "second interrarial" by Matsumoto (1913, 1917), and "dreieckige Schaltplatte" by Hertz (1927).

question, but Hecker (1940, p. 74) emphasized, as regards the East Baltic species, that the rounded apices of the marginal plates do not suggest the presence of further distal plates firmly connected with the plates in the actual marginal zone.

On the systematic position of Ophiocistia and their relations to other echinoderm groups: — The Ophiocistia have generally been looked upon as Asterozoa, and in the text-books they have been placed along with the Ophiuroidea (e. g. Delage & Hérouard 1903, p. 147; Sedgwick 1909, p. 206; Zittel — Broili 1924, p. 240; Moret 1940, p. 220) or as a distinct group in the neighbourhood of these (e. g. Lameere 1931, p. 415). A short review of different opinions regarding the systematic status of the Ophiocistia was given by the present writer in a former paper (Regnéll 1945, p. 49). The tentative analysis of the dorsal shield in *Volchovia* set forth now may offer some further clues to the relations between the Ophiocistia and the other eleutherozoic echinoderms.

The most penetrating discussion of the systematic position of the Ophiocistia we owe to Fedotov (1926, 1928). He arrived at the conclusion that the Ophiocistia combine features from the Asterozoa, Echinoidea, Holothuria, and Hydrophoridae, and that they became extinct without leaving any descendants (Fedotov 1928, p. 69). These suggestions do not seem to be contradicted by information gathered after Fedotov's studies were published.

Fedotov laid special stress upon the remarkable fact that "on the whole Ophiocistia had a general resemblance to the very young of Ophiuroidea, Asteroidea, and Echinoidea" (Fedotov 1926, p. 1153; cf. also 1928, p. 68). Now this resemblance is not restricted only to the general shape of the body but, as demonstrated above, can be traced also in the arrangement of the skeletal elements in the dorsal shield of *Volchovia*. In the later (Lower Ludlovian) *Sollasina*, where the dorsal surface is covered with "numerous, imbricated, irregularly polygonal plates" (Fedotov 1926, p. 1155), this feature is quite obliterated. Extensive analogies, if not homologies, have been shown to exist between the ventral surface of the Silurian Ophiocistia and that of adult Ophiuroidea. In the case of *Volchovia* these analogies pertain also in some degree to the dorsal face, if the line of reasoning which we have followed on the preceding pages can be trusted.

The organization of the alimentary system in *Volchovia* differs from that in the ophiuroids by having an anal opening. This outlet,

as is well known, is not present in the Ophiuroidea, and is also lacking in the later members of Ophiocistia as far as our knowledge goes. The development within the Ophiocistia possibly offers a parallel in this respect to the phylogenetic development within the Ophiuroidea. An anal opening may actually have been present in *Stenaster* (cf. Fedotov 1936, p. 14), though this is not definitely established. There is a possibility that the parallel just referred to should be extended to the Asterozoa as a whole. For it has been proposed by several authors that the Ophiuroidea were derived from the Asteroidea, and the latter, with few exceptions, are in possession of an abactinal anal opening. There are, however, still many obscure points in the theories of the affinities within the Asterozoa, and it is equally, or even more probable, that the asterozoic and the ophiuroid branches developed independently from a common stem (cf. Fedotov 1936, p. 16). And it may be noticed that the members of the Astropectinidae, which are the only Asteroidea devoid of an anus,¹ according to Bather (1900, p. 248) "are more primitive than *Asterias* in many respects", an opinion which was not shared, however, by Lameere (1931, p. 406), who remarked about the Astropectinidae that they have lost the anus ("ont perdu l'anus"). What the real facts of this case are, may be left undecided. Anyhow, the disappearance of the anus during the phylogenetic development of Ophiocistia cannot have very important bearing on the solution of the question of phylogenetic development within the Asterozoa in general.

It was mentioned above (p. 38) that the real character of the "second opening" in *Volchovia* cannot be determined conclusively. Provided that it is a hydropore, it corresponds approximately in position to that in most Asteroidea, in the ophiuroid larva, and in the Echinoidea. This interpretation being accepted, we are forced to state that the organ has been subject to considerable changes during the development of the Ophiocistia, so that in some it has migrated to the ventral surface (*Eucladia*), and in others it has disappeared altogether (*Sollasina*). If present in the somewhat older (Wenlockian) *Euthemon*, the madreporite was dorsal (cf. p. 38, foot-note 1). Similar changes have affected the gonopore in Ophiocistia, supposing that the "second opening" represents that aperture, or is a combined

¹ This may also be true of the Porcellanasteridae. Délage & Herouard (1903, p. 89) stated it as definite, but Sedgwick (1909, p. 189) was more cautious ("Anus said to be absent").

hydropore and gonopore, as presumably in certain Hydrophoridae. Where other echinoderms are concerned, the gonopores open dorsally in most Asteroidea and in the Echinoidea.

Thus the "second opening" in *Volchovia*, and the behaviour of the anal opening in Ophiocistia, do not contribute very much to the elucidation of the relations of the group. But the construction of the skeleton, both as regards the dorsal shield in *Volchovia* and the ventral shield in the Silurian forms, enables us to conclude, in agreement with earlier suggestions, that the Ophiocistia were decidedly asterozoan in nature and had their closest affinities with ophiuroid forms.

As mentioned above (p. 39), the ambulacral podia very likely acted as walking feet in certain Ophiocistia, viz. in *Eucladia* and *Volchovia* and possibly in other genera too. For this purpose they may have been capable of quite considerable changes in extension. These, as is well known, are due to variations in the hydrostatic pressure of the fluid in the tube-feet. Smith (1946, p. 290) has proved that in a medium-sized starfish the volume of fluid in the stone canal, circumoral and radial water vessels does not exceed 1—2% of the total capacity of all the tube foot-ampulla systems. Therefore he found it most likely that the fluid which may be drawn from the radial vessel serves merely to replace fluid lost by diffusion, and that the tube foot and ampulla function as a closed mechanical system, for the regulation of which the size of the ampulla is decisive in so far as a relatively larger ampulla affords greater capacity for extension of the tube feet than does a relatively smaller ampulla. The tube feet of Ophiuroidea, which are totally devoid of ampullae, are capable of only very restricted extension. If it is true that the ambulacral podia in *Eucladia* and *Volchovia* were at least moderately extensible, we have to imagine that these forms were in possession of a tube foot-ampulla system. In this respect the Ophiocistia — at least as far as the genera mentioned are concerned — differ from the Ophiuroidea, but rather recall the conditions in the Asteroidea and Echinoidea.

It remains to say a few words about the affinities with the Eleutherozoa, other than asterozoans, and with the Hydrophoridae.

In the case of the Echinoidea, the similarities manifest themselves in the structure of the biting and masticating apparatus, which in the Ophiocistia was also developed as Aristotle's lantern. As a result of the recent investigations by MacBride & Spencer (1938) it has transpired that the early (Ashgillian) echinoids *Aulechinus* and *Ectinechinus* had

an isolated anal pyramid, very much the same as in *Volchovia* and in the Hydrophoridae.

The same feature is also found in *Eothuria* (Ashgillian), which the authors just quoted regard as a primitive holothurian (see MacBride & Spencer 1938, pp. 104, 106). Thus the anus covered by valves forming a pyramid is a primitive character present in several early members of the Eleutherozoa, as well as of the Pelmatozoa. It does not, of course, necessarily indicate that the forms concerned have stood in closer genetic relationship to each other, for it may have been acquired independently in different lines. There are, however, some more points on which the Ophiocistia and the Holothuria are brought into relationship. MacBride & Spencer (1938, p. 129) called attention to the similarity in ornamentation of the interambulacra of *Eothuria* on the one hand, and of the Silurian Ophiocistia on the other. They also showed (op. cit., pp. 131—132) that *Eothuria* and the Ophiocistia are the only echinoderms which have a mouth covered by ten plates, which were supposed on certain grounds to be homologous with the teeth of the Echinodea, and their distal processes homologues of jaws. They found no evidence of any functional lantern apparatus in *Eothuria*, however. Finally, it may be observed that the Ophiocistia, along with the holothurians and the cystoids (at least the bulk of them) had a single gonad, i. e. they were anactinogonid (Bell 1891) or monorchid (Sollas 1899). MacBride & Spencer (1938, p. 131) hold out the prospect of a closer discussion of the relationship between *Eothuria* and the Ophiocistia.

The main features by which the Ophiocistia approach the Hydrophoridae have been partly touched upon already. These are the character of the anal pyramid (*Volchovia*), as pointed out by Hecker (1938, p. 427; 1940, p. 75), and, eventually, the combined opening for the hydropore and the gonopore. As for *Eucladia*, Fedotov (1926, p. 1154) observed that "in the form of the external skeleton, with madreporite and genital pores near the mouth, it has general resemblance to the Cystoidea".

Summing up what has been said now, the present writer wants to emphasize once more that Fedotov's view of the Ophiocistia as a collective type, lying in the direct lineage of none of the later echinoderm groups, but presenting features from several of them, seems to be well corroborated as far as the Ophiocistia are known at present.

Accepting the isolated position of the Ophiocistia, we can hardly say that the group has any very important bearing upon the question of the relations between the Pelmatozoa and the Eleutherozoa and the phylogeny of the echinodermal stock as a whole. This problem, moreover, has recently got into the field of vision again after the remarkable early Middle Cambrian echinoderms *Peridionites* Whitehouse (of the new class Cyamoidea Whitehouse) and *Cymbionites* Whitehouse (of the new class Cycloidea Whitehouse), discovered in the north-west of Queensland, were brought into the discussion (Whitehouse 1941).

On the contrary, the main interest of the Ophiocistia lies in their being an example of an early offshoot from the eleutherozoic echinoderms which did not meet with any noteworthy success, and became extinct within a relatively short time. Yet the known range of the Ophiocistia was extended a long way back in time by the detection of *Volchovia*.

On the derivation of Ophiocistia: — It has been almost axiomatic among echinodermologists that the ancestors of the eleutherozoic echinoderm groups were pelmatozoic types. This view was expressed very clearly e. g. by Gislén (1934), as appears from the following quotation: — “Long ago in the dawn of time the predecessors of the echinoderms gave up their free-living existence [as represented by the hypothetical, bilateral, unattached dipleurula; remark by the present writer] and (in this all who have worked with these problems agree) fixed themselves to the sea bottom. In the beginning there was only a cementation to the substratum, later on, within several of these fixed form-series there evolved a stalk raising the animal from the bottom. Contemporaneously with acquiring a fixed existence the echinoderms more and more were transformed from sac-shaped beings (Cystideans) to forms with a radial symmetry” (op. cit., p. 3).¹ And further: “Rather early and relatively easily three of the echinoderm groups seem to have reattained the free moving

¹ To visualize those stages, Gislén communicated figures of *Caryocystites angelini* (Haeckel) (in the explanation of Gislén's text-fig. 1 referred to as *Amorphocystis* — by misprint *Amphorocystis* — *buchi*) as a representative of the sac-shaped form, and of *Asteroblastus foveolatus* Eichwald, *A. volborthi* F. Schmidt, and *Cyathocystis plautinae* F. Schmidt as representatives of the consecutive forms with a radial symmetry. Indeed the species chosen are not very illustrative of the proposition which they are intended to explain. For according to Jaekel (1899, p. 389) the two species of *Asteroblastus* originate from “Unteres Untersilur” of the Leningrad district — in the case of *A. foveo-*

existence — echinoids, asterids and ophiurans. Probably they are all to be derived from the Edrioasteroids (a less plausible hypothesis traces them from the Cystideans)" (op. cit., p. 4). These radical changes involved "Liberation from the substratum, a functional reversal of the ventral and dorsal side, the creation of a new organ for locomotion (the feet), an elimination of the old food supplying organ and the forming of a new apparatus for catching nourishment" (op. cit., p. 5).

Now the foundations upon which the line of reasoning thus unfolded rests, have been attacked by evidence from the previously mentioned Middle Cambrian echinoderms made known by Whitehouse (1941). According to the stimulating interpretation of that author,¹ the radially symmetrical Cycloidea (with the genus *Cymbionites*) represent the ancestral free pentactula, from which arose the Eleutherozoa, whereas the bilaterally symmetric Cyamoidea (with the genus *Peridionites*) represent the early hypothetical dipleurula, from which the Pelmatozoa were derived.² The Cycloidea were thought to have

latus the horizon is given more precisely as "Vaginatenkalk" (Upper Skiddavian) — and *Cyathocystis plautinae* from the "Echinosphäritenkalk, C₁" (Jaekel 1899, p. 43) of Tallinn. *Caryocystites angelini*, on the other hand, is from the Lower Chasmops limestone (Upper Llandeilian) of Öland, the equivalent of which in the East Baltic area is the Kukruse, C_{2β}—C_{3α} (the correlation according to V. Jaanusson, Zur Fauna und zur Korrelation der Kalksteine mit *Illaeus crassicauda*, Geol. Fören. Förh. 69, 1947, p. 49). Thus the type which was supposed to be the primitive one is in reality found in strata which are younger than those containing the forms which were supposed to represent consecutive stages in the evolutionary series. The examples, therefore, do not demonstrate an evolutionary series, but are more or less synchronous representatives of different lines, the course of which, however, may be that indicated by Gislén.

¹ It should be remembered, however, that pelmatozoic types (Eocrinoidea, Edrioasteroidea) are already known from Lower Cambrian deposits.

² Whitehouse (1941, p. 22) suggested a separate group, Homalozoa, to receive the Carpoidea and the Machaeridia which were found not to fit into the pelmatozoic scheme. As the Pelmatozoa, the Homalozoa were thought to be derived from early Cyamoidea, or from an even more primitive group. The Carpoidea differ undoubtedly in several respects from typical pelmatozoans, and so do the Machaeridia. But in the case of the latter there are strong doubts as to their echinodermic nature at all (cf. Regnéll 1945, p. 47 seq.) Very likely, therefore, the Machaeridia have to be excluded from the Homalozoa. The establishing of a new group for the carpoids, however, might not be uncalled for (it may be noted that the present writer in preparing his memoir printed in 1945 had no knowledge of Whitehouse's paper, which had then not been forwarded to Sweden and, therefore, could not pay due attention to the views set forth there).

branched off from the Cyamoidea at about the same stage of evolution as the rise of the Pelmatozoa. As one result of his investigations Whitehouse (1941, p. 24) made the following declaration: "An attached stage in the phylogeny of the Eleutherozoa generally has been postulated although without confirmation in ontogeny. The existence of these two early forms and their correspondence, morphologically, with the two chief larval stages, makes it unnecessary to require an attached stage in the ancestry of the Eleutherozoa". And "since in ontogeny the free pentactula is the starting point in the development of asteroids, ophiuroids and echinoids, so in phylogeny the Cycloidea may be regarded, I would suggest, as the immediate common ancestor of these three classes" (Whitehouse 1941, p. 19). This theory, interesting as it is, yet seems to require further consideration before it can be accepted throughout.

There are not many observations on the origin of the Ophiocistia to be found in literature. In fact, the present writer has noticed one instance only in which a direct suggestion is made on the subject, viz. by Delpy (1944, p. 274): "Cependant, plus directement, il n'y a pas d'objection pour passer de *Stromatocystis* aux Ophiocysties, aux Astérides et aux Ophiurides les plus anciens". On the other hand, several authors have written about the ancestry of the Asterozoa; and to this group the Ophiocistia belong, as we have cause to believe. It is a fairly commonly accepted view, the reasons for which were stated mainly in the careful studies of Bather 1901, p. 31; 1915 a; 1915 b), and corroborated e. g. by Schuchert (1919, p. 6), that the Asterozoa arose from an early edrioasteroid like the Cambrian *Stromatocystites*,¹ the process being initiated by turning over of the theca and performed by considerable changes in the organization of the intestine and skeleton (cf. above p. 52, quotation from Gislén 1934).² This elaborately founded theory cannot be upheld any longer, however, if we approve the results arrived at by Whitehouse referred to above.

¹ It has been proposed, moreover, that not only the Asteroids but the other groups of Eleutherozoa also arose from the Edrioasteroidea (cf. e. g. the table in Bather 1900, p. 35). As to the Echinoidea, their linking together with the Edrioasteroidea has been discussed more recently by Mortensen (1928, 1930) in objection to the *Bothriocidaris* theory.

² For different opinions on the relations of the Edrioasteroidea, see the brief account in Regnéll 1945, p. 43 (the concluding parenthesis in foot-note 2, p. 52 above, is applicable here too).

According to him, the Eleutherozoa, as just pointed out, cannot be derived from any pelmatozoic type. In consequence, in our present state of knowledge, we must realize that the predecessors of the Ophiocistia, and the Asterozoa in general, were possibly free living forms as represented by the Cambrian Cycloidea. At the same time we have to state that organisms actually linking together the Upper Skiddavian Asterozoa with the Middle Cambrian Cycloidea still remain to be discovered.

Addendum.

After the present paper was already sent to the press, the author got knowledge of T. Gislén's remarks "On the Haplozoa and the Interpretation of *Peridionites*" (Zool. Bidr. Uppsala. 25 = Festskr. tillägnad Nils von Hofsten. Uppsala and Stockholm 1947. Pp. 402—408). Here the interpretation of *Cymbionites* and *Peridionites*, and their significance, advanced by Whitehouse, is rejected throughout. Gislén is of opinion that *Cymbionites* may be regarded provisionally "as a cystid with a calcified aboral pole, the animal for the rest being devoid of larger calcareous plates and sticking in the calcified cup" (p. 403). Whitehouse's comparison between *Peridionites* and the hypothetical dipleurula is shown to be untenable. Gislén not even agrees in referring *Peridionites* to the echinoderms. Rather is he inclined to look upon this fossil as a ctenophoran. By this, Whitehouse's interesting attempt at revising the older views of the early history of echinoderms seems to have been deprived of its postulate.

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Plate 1.

- Fig. 1. *Cheirocrinus hyperboreus* n. sp., holotype [PMO 2271 a]. Posterior view (cf. text-fig. 1). N. B. Fragments of brachioles above the apex of the theca. $\times 1.5$. — Gjeitungholmen, Slemmestad, Asker. (P. 15).
- Fig. 2. *Echinoencrinites senckenbergii acutangulus* n. subsp., holotype [PMO 65571]. $\times 2$. — Gjeitungholmen, Slemmestad, Asker. (P. 22).
- 2 a. Anterior view (cf. text-fig. 3 A).
- 2 b. Left lateral view (cf. text-fig. 3 B).
- Figs. 3—4. *Erinocystis brøggeri* n. sp. $\times 3$. — Oslo, Tøyen. (P. 28).
3. Theca in left lateral view [PMO 20149] (cf. text-fig. 4 C).
4. a. Theca in left lateral view, holotype [PMO 20148] (cf. text-fig. 4 B).
- 4 b. The same in basal view (cf. text-fig. 4 A).
- (All specimens photographed in alcohol and with the use of a green filter).
- Phot. G. Ahl. Ret. S. Ekblom.

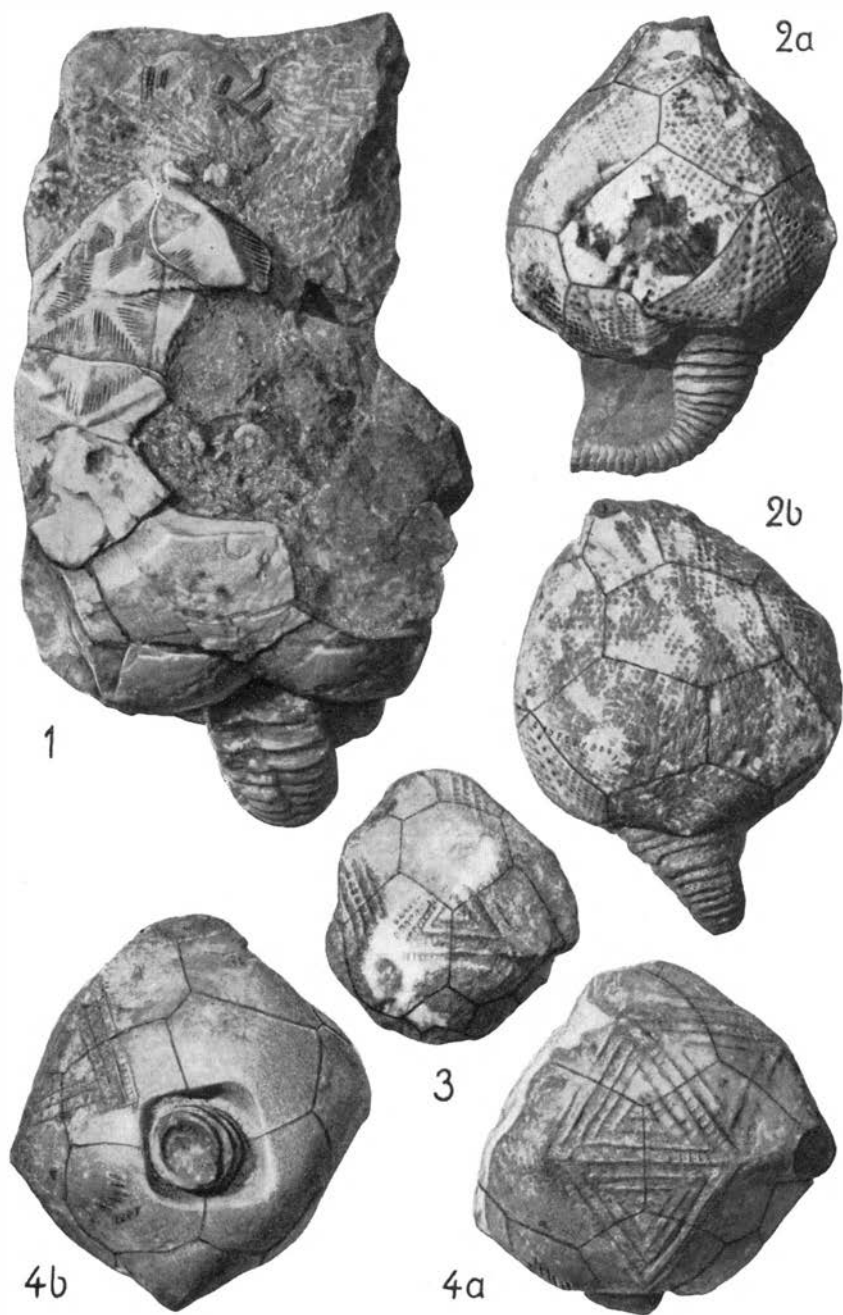


Plate 2.

Figs. 1—3. *Cheirocrinus hyperboreus* n. sp. — Gjeitungholmen, Slemmestad, Asker. (P. 15).

1. Fragments of brachioles (cf. Pl. I, fig. 1). Holotype [PMO 2271 a]. $\times 6$.
2. Part of the stem [PMO 2271]. $\times 2$.
3. Supposed root organ and, to the left of it, part of the distal region of the stem [PMO 2271 a]. $\times 2$.

Fig. 4. *Volchovia norvegica* n. sp., holotype. Dorsal shield. Nat. size. — Gjeitungholmen, Slemmestad, Asker. (P. 35).

4 a. Positive of the holotype [PMO 2229].

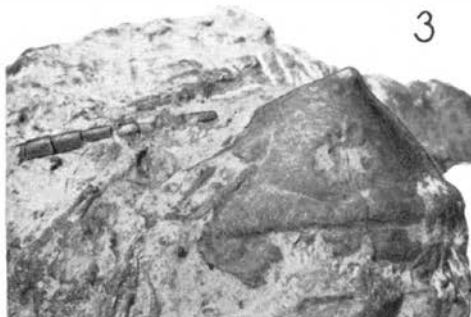
4 b. Counterpiece of the holotype [PMO 2230].

(All specimens, except that figured in fig. 3, photographed in alcohol and with the use of a green filter).

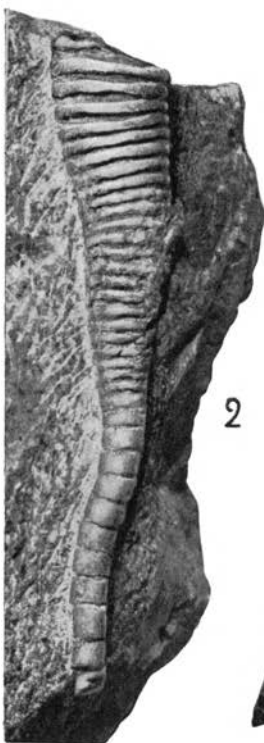
Phot. G. Ahl. Ret. S. Ekblom.



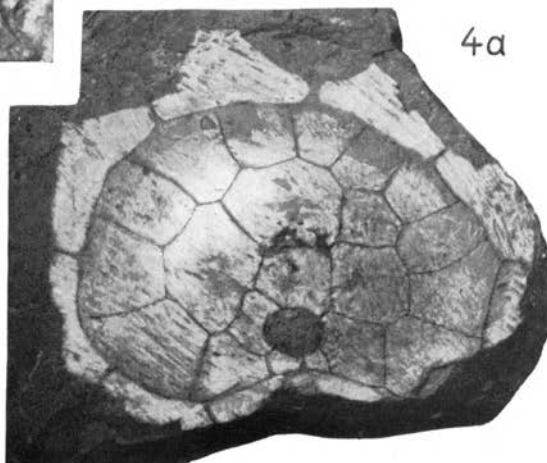
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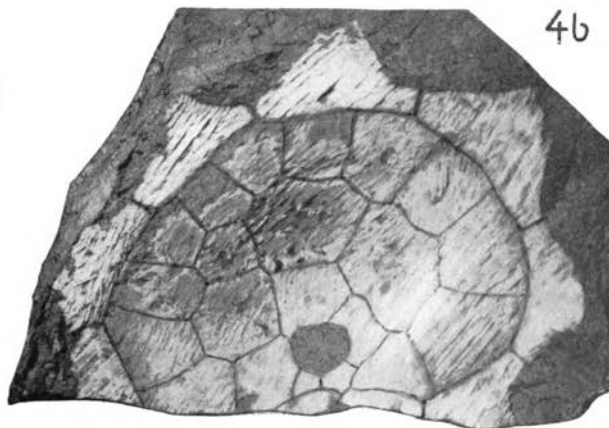
3



2



4a



4b