2. On the genus *Dartmuthia* Patten, with special reference to the minute structure of the exoskeleton.

By

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(With 5 text-figures and 3 plates.)

The present investigation of the exoskeleton of *Dartmuthia* is based on certain limited material collected by the writer on the Isle of Saaremaa (Oesel), Esthonia, in the summer of 1938. The locality lies in the vicinity of Kuigu in the district of Lümanda. The fossil horizon is in the upper part of the Silurian of Saaremaa (K_1, Lower Ludlow, cf. SÄVE-SÖDERBERGH 1941, p. 235—238). The material, which belongs to the Paleontological Institute of Uppsala, includes two comparatively complete cephalic shields and several fragments of cephalic shields. It is chiefly the latter remains that have been subject to investigation and used for the preparation of sections. Since the rock was rather loose, the sections were difficult to make and do not show all the details desirable. For comparison, I had access to rather extensive material of *Tremataspis* deriving from the same locality, together with various preparations and thin sections of *Tremataspis* and Cephalaspids, partly used by STENSIÖ for his work on Cephalaspids from Spitsbergen (1927) and kindly placed at my disposal.

According to the opinions maintained by previous authors, *Dartmuthia* is a form to some extent intermediate between *Tremataspis* and the Cephalaspids proper. This opinion, however, is based chiefly on the general external characteristics of the genus and needs to be corroborated by more detailed investigations, particularly on the endoskeleton. Unfortunately however, the endoskeleton is so poorly preserved that it exhibits little or nothing of the internal characteristics of the genus. In these circumstances, I have undertaken a detailed examination of the exoskeleton to find out whether its minute structure throws any light on the relationship of the genus. The exoskeleton hat not earlier been subject to a closer examination. Only ROBERTSON (1935 a) gives a brief account of the internal structure (p. 333), but any clear conception of most of the peculiarities of the exoskeleton cannot be gained from his description.

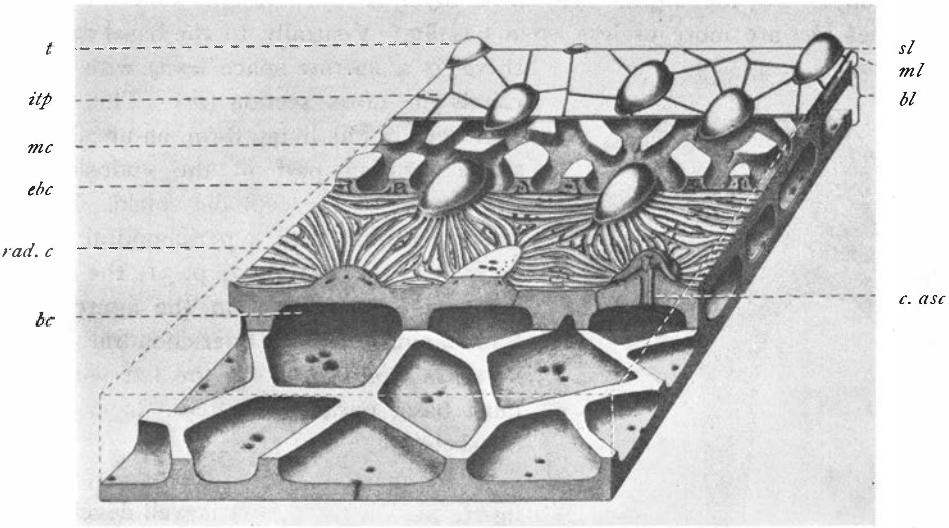
Description.

The aspect of the external face of the exoskeleton has been described at length by ROBERTSON (1935 a, p. 326). This face is very characteristic. It is ornamented with numerous small glossy black or brown-black, rounded (or, towards the posterior part of the cephalic shield, rather lengthened), more or less raised, tubercles, between which there are small bright-coloured, shiny, polygonal plates, the intertubercular plates (text-figs. 1, *itp*, 3; pl. V, fig. 2, *sl*). Along the rostral and lateral margins, around the naso-hypophysial opening and also along the dorsal ridge, the tubercles are large and coarse, sometimes flattened, and the intertubercular plates are inconsiderable. Along the rostral and lateral margins, the tubercles join together to form more or less continuous longitudinal ridges. On the posterior part of the dorsal shield and on both sides of the dorsal ridge there are often, as in *Thyestes*, two more or less distinct and regular rows of large tubercles. On both sides of the naso-hypophysial aperture, the tubercles lie in two not particularly conspicuous rows along the infra-orbital sensory canal grooves on each side.

The basal face of the exoskeleton has a different appearance in those parts of the exoskeleton which are not underlain by endoskeleton from that obtaining in the parts which cover the endoskeleton. In the former regions, its basal face is plane and smooth, without any impressions of canals, and presents scattered fairly narrow pores of the vascular canal system. On the other hand, where it rests on endoskeleton (hence in the rostral, median and lateral parts of the dorsal shield, see text-fig. 2) the exoskeleton is devoid of the most basal parts of the basal layer and the basal face in such places is divided by anastomosing ridges into polygonal areas (see below the account of the basal layer).

As in the Cephalaspids in general and as in *Tremataspis* (STENSIÖ 1927, p. 34—40; 1932, p. 13—27; GROSS 1935, p. 4—9), the exoskeleton in *Dartmuthia* consists of three different layers, viz. a superficial layer, a middle layer, and a basal layer (text-fig. 1; pl. VI, fig. 3). The tubercles lie with their bases in the middle layer, whence they extend outwards through the superficial layer; they thus belong both to the middle and superficial layers.

The basal layer (text-fig. 1; pl. V, fig. 1; pl. VI, figs. 2, 3, *bl*) is completely developed in the posterior part of the cephalic shield, where the exoskeleton does not overlie the endoskeleton; it is there considerably thicker than the two other layers together. It consists of horizontal fibrous lamellae (pl. VI, fig. 2) with numerous flattened cell-spaces between them. The fibres of each such lamella lie at right angles to those in the lamellae next above and below (as in other Cephalaspids, STENSIÖ 1927, p. 35, and in *Tremataspis,* PATTEN 1912, p. 291). The basal layer encloses large cavities, the basal cavities (text-fig. 1; pl. VI, figs. 2, 3, *bc*; cf. *Tremataspis,* PATTEN 1912, fig. 193, *c*; STENSIÖ 1927, pl. 72, fig. 1, *ms*), which in horizontal section are polygonal, often 6-sided in outline (pl. V, fig. 1). The partitions between the basal cavities are often comparatively thin and in some places perforated, so that the cavities are in open com-



Text-fig. 1. *Dartmuthia gemmifera* PATTEN. Schematic sketch in the form of a block-diagram, showing the structure of the exoskeleton.

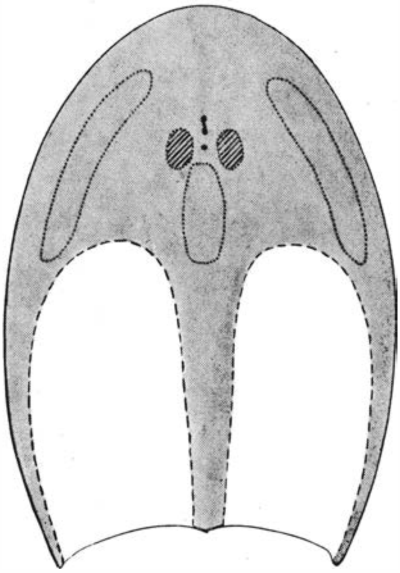
Different layers successively removed. The remotest zone shows the development of the superficial layer in and between the tubercles. In the next zone the intertubercular plates are removed in order to show the mucous canals in the middle layer. In the front wall of this zone the subepidermal vascular canal plexus is exposed in transverse section. In the third zone the upper division of the middle layer is removed, exposing the basal parts of the radiating vascular canals. In the transverse sectioned wall in front of this, three tubercles are cut in different ways, to the right with ascending and radiating vascular canals and also subepidermal vascular canal plexus; close at hand there is a descending vascular canal. The anterior zone is cut through the basal cavities and shows the bottom of the exoskeleton, pierced by vascular canals.

bc, basal cavity; *bl,* basal layer; *c. asc,* ascending vascular canal; *ebc,* external branches of the radiating canals (subepidermal vascular canal plexus); *itp,* intertubercular plate; *mc,* mucous canal; *ml,* middle layer; *rad. c,* radiating vascular canals; *sl,* superficial layer.

munication with each other (pl. VI, fig. 2, bc_1). The parts of the basal layer situated above and below each basal cavity are pierced by a group of vertical canals belonging to the vascular canal system. Along the lateral rim of the cephalic shield, the basal layer is particularly thick and contains irregular cavities and large branching vascular canals (pl. VI, fig. 1).

As mentioned above, the basal layer is not so completely developed in those places where the exoskeleton rests on the endoskeleton (text-fig. 2). It is here often thin and lacking the most basal parts, so that the basal cavities are more ot less open ventrally. The persisting parts of the partitions between the basal cavitîes form the anastomosing ridges referred to above.

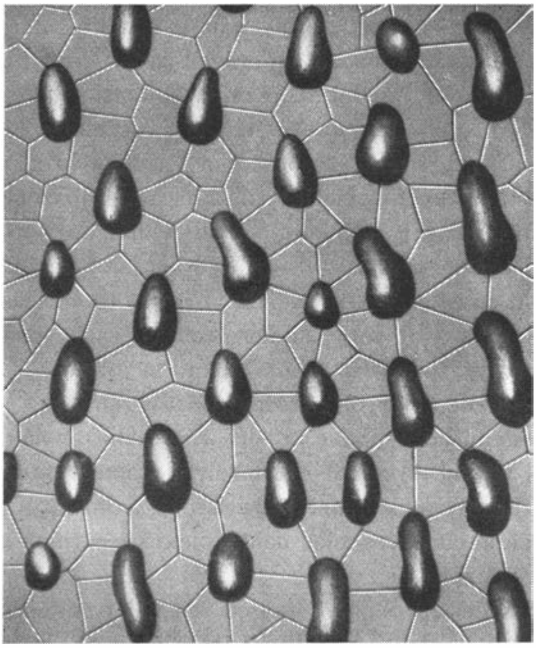
In pl. VI, fig. 2 a transverse section through the lateral portion of the posterior part of the cephalic shield is exposed, thus revealing the different development of the basal layer. We see here, to the left, the basal layer with the basal parts completely developed, the basal cavities (bc_1) closed ventrally. To the right, the basal layer is much thinner and the basal cavities (*bc*) are more or less open basally. Ventrally to the basal cavities there is a narrow space (*end*) with small canals in cross section (*vc*). This space enclosed, in the living form, an uncalcified tissue forming part of the endoskeletal component of the cephalic shield. It was lined ventrally with a perichondral bone-layer (cf. STENSIÖ 1927, p. 31, the external layer), appearing in the figure as a thin lamina (*l*). The perichondral bone-layer is continuous on the left with the most basal parts of the basal layer of the exoskeleton.



Text-fig. 2. *Dartmuthia gemmifera* PATTEN. Attempted restoration of the cephalic shield, showing also the approximate extent of the endoskeletal component (shaded). Dorsal view. × 1½ diam.

The middle layer (text-fig. 1; pl. V, fig. 1; pl. VI, fig. 3, *ml*) is well developed, but is usually considerably thinner than the basal layer. Basally it passes over into the basal layer without any distinct boundary. Cell-spaces are observed in the basal parts of the middle layer. As in other Cephalaspids and *Tremataspis*, so, in *Dartmuthia*, it is traversed by numerous canals belonging to the vascular canal system and to the mucous canal system. In the areas between the tubercles, two divisions are distinguishable in this layer; an upper one with the mucous canals, and a lower one with the radiating canals (text-fig. 1). Both these divisions are pierced by so great a number of canals that they consist only of thin trabecles. The tubercles are largely thickenings in the middle layer. Topographically they have such a position that each of them lies above a basal cavity. Each tubercle constitutes the centre of a special area. Each such area is bordered in the basal layer by the walls around the underlying basal cavity, whereas its extent in the middle layer is defined through the extent of the radiating vascular canals issuing from the group of vascular canals ascending from the basal cavity. (For the canals of the middle layer, see the account below of the mucous and the vascular canal systems.)

The superficial layer (text-figs. 1, 3; pl. V, figs. 1, 2; pl. VI, figs. 1, 3, *sl*) forms a continuous covering of the middle layer, being present both on, and between, the tubercles. However, it is differently developed in the tubercles and in the spaces between them (the intertubercular spaces). In the tubercles it constitutes the uppermost part that lies above the external branches of the ascending vascular canals (the subepidermal



Text-fig. 3. *Dartmuthia gemmifera* PATTEN. Part of the exoskeleton from the posterior portion of the cephalic shield, external view, showing the superficial layer as a covering on the tubercles, and also as a continuous field between those, divided by shallow grooves into polygonal plates (the intertubercular plates). Approx. × 17 diam.

vascular canal plexus). The superficial layer in the tubercles to a large extent consists of dentine. In some of the largest tubercles (e. g. in those along the lateral margins, pl. VI, fig. 1) the dentine is well developed (*sl.t*) with distinct dentine-canals; and outside the dentine, we find a bright, strongly refractive zone which is probably made up of enamel (cf. *Tremataspis,* GROSS 1935, p. 5; pl. I, fig. 3). It could not be ascertained whether the dentine-canals reach the actual external face. The superficial layer in the tubercles is separated from that of the intertubercular spaces by open mucous grooves around the tubercles.

Between the tubercles, the superficial layer is represented by the thin, bright, smooth, glossy, polygonal plates (ROBERTSON 1935 a, p. 326), the intertubercular plates referred to above. These plates are separated from one another by shallow grooves, pierced by the narrow pores of the underlying mucous canals; often the pores are confluent, thus forming openings of greater or lesser length. The intertubercular plates rest on, and are continuous with, the trabecles of the middle layer which separate the mucous canals (pl. VI, figs. 1, 3) and accordingly are not independent elements. No dentine-canals have been observed in them; possibly they consist entirely of an enamel-like tissue.

In places there are intertubercular plates which cover a dark thickening in the middle layer (pl. V, fig. 2, t_1). These can be interpreted as imperfectly developed tubercles, whose superficial layer does not however differ in structure from that of the intertubercular plates.

The vascular canal system in the exoskeleton of *Dartmuthia* is, as in Cephalaspids in general, disposed in vascular areas. We shall now give a description of the disposition of the canals in such an area.

In those parts of the cephalic shield which do not cover the endoskeleton, canals travel upwards from the basal face of the exoskeleton through the most basal parts of the basal layer to the basal cavities. In general a group of two or three canals lead to each basal cavity; one of the canals is usually somewhat wider than the others. They open more or less centrally in the floor of the cavity (text-fig. 1).

In those parts of the cephalic shield where the exoskeleton covers the endoskeleton (pl. VI, fig. 2) small endoskeletal canals enter the basal cavity from beneath; these canals must have issued from larger vascular canals or from the subcutaneous vascular canal plexus — which are not preserved in the material available.

The basal cavities probably lodged vascular sinuses and they correspond to the similar cavities in the exoskeleton of *Tremataspis* (PATTEN 1912, fig. 193, *c*; STENSIÖ 1927, pl. 72, figs. 1, 2, *ms*).

From the central part of the roof in each basal cavity a group of fairly wide canals issue in a superficial direction, perforating the upper parts of the basal layer and passing up to the upper parts of the middle layer in each tubercle (text-fig. 1; pl. V, fig. 1, *c. asc*). In this part of their course, the canals in this group do not generally branch. These canals correspond to the ascending vascular canals in the Cephalaspids proper (see e. g. STENSIÖ 1927, pl. 65, fig. 2; pl. 67, fig. 1; 1932, pl. 66, fig. 1, *c. asc*) and in *Tremataspis* (STENSIÖ 1927, pl. 72, fig. 1, *sc*).

In the outer part of the middle layer in the tubercle, the ascending vascular canals break up into numerous anastomosing canals which, peripherally in the tubercle, gradually pass over into the typical radiating canals. These radiating canals continue from the tubercle in a slightly basal direction, spreading into the surrounding basal parts of the middle layer, where they pass below the mucous canals (text-fig. 1; pl. V, fig. 1; pl. VI, fig. 3, *rad. c*; cf. the radiating vascular canals in Cephalaspids, e. g. STENSIÖ 1927, pl. 67; 1932, pl. 41; pl. 44, figs. 2, 3, *rad. c*). The radiating canals sometimes branch in the peripheral part of their course. They unite with those of the neighbouring areas straight above the partitions between the basal cavities.

In the tubercle, we find small, frequently branching canals issuing in a superficial direction from the upper parts of the ascending vascular canals, or from the anastomosing canals; these form a vascular canal plexus in the outer part of the tubercle (text.-fig. 1). This plexus corresponds to the subepidermal vascular canal plexus in Cephalaspids proper and in *Tremataspis* (STENSIÖ 1927, p. 34—35 and e.g. pl. 72; GROSS 1935, text-fig. 3 A, *splx*). From this plexus issue the dentine-canals of the superficial layer (see pl. VI, fig. 1, *sl.t*).

In the intertubercular spaces likewise, the radiating canals send out numerous canals of various calibres in a superficial direction into the upper division of the middle layer. These canals anastomose frequently, forming a plexus which occupies the upper division of the middle layer between the mucous canals (pl. VI, fig. 3, *ebc*). They extend to just underneath the superficial layer. The plexus formed by them is also an equivalent to the subepidermal vascular canal plexus in the Cephalaspids (cf. STENSIÖ 1932, pl. 29, fig. 1; pl. 44, fig. 1; pl. 59, fig. 3; pl. 60, figs. 2, 3, *ebc*) and in *Tremataspis* (pl. VII, fig. 2; text-fig. 5, *ebc*; cf. STENSIÖ 1927, pl. 72, figs. 1, 2, *rad.c*; GROSS 1935, pl. I, figs. 1, 6; text-figs. 1, 2, 4, *ohsplx*).

Here and there, narrow canals are to be seen which connect the radiating canals and the subepidermal vascular canal plexus with the mucous canals (see pl. VI, figs. 1, 3).

The radiating canals are also connected with the underlying basal cavity by a few narrow canals, the descending vascular canals (STENSIÖ 1932, p. 25); they usually open in the roof of the cavity near the lateral walls (text-fig. 1; pl. VI, fig. 3, *c.des*).

Along the anterior and lateral margins of the dorsal shield the radiating canals are replaced by more irregular vascular canals (pl. VI, fig. 1).

The mucous canal system (text-fig. 1; pl. V, fig. 1; pl. VI, figs. 1, 3, *mc*, mc_1, mc_2) lies in the upper division of the middle layer immediately beneath the superficial layer and consists of well-defined wide canals, the circumtubercular canals (pl. V, fig. 1, *mc*), around each tubercle, and short cross commissural canals (mc_1) which connect the circumtubercular canals. Between tubercles which lie comparatively far apart, interstitial canals (mc_2) of varying length are inserted, which are in communication with the cross commissural canals. Along the rostral and lateral margins of the cephalic shield, in the grooves between the longitudinal ridges produced by the fusion of tubercles, the circumtubercular canals are replaced by narrow longitudinal canals; in the bottom of each groove they lie in two parallel rows (pl. VI, fig. 1, *mc*), connected with each other by very short cross canals. The circumtubercular canals abuts upon the basal parts of the tubercles and here produce a slight concavity on the sides of the tubercles under a distinct shelf (see pl. V, fig. 1; pl. VI, fig. 3, *t*). All the mucous canals are approximately of the same calibre, we cannot therefore distinguish between wide circum-areal canals (GROSS, »inter-areal canals» STENSIÖ) and narrower intra-areal canals as in Cephalaspids proper.

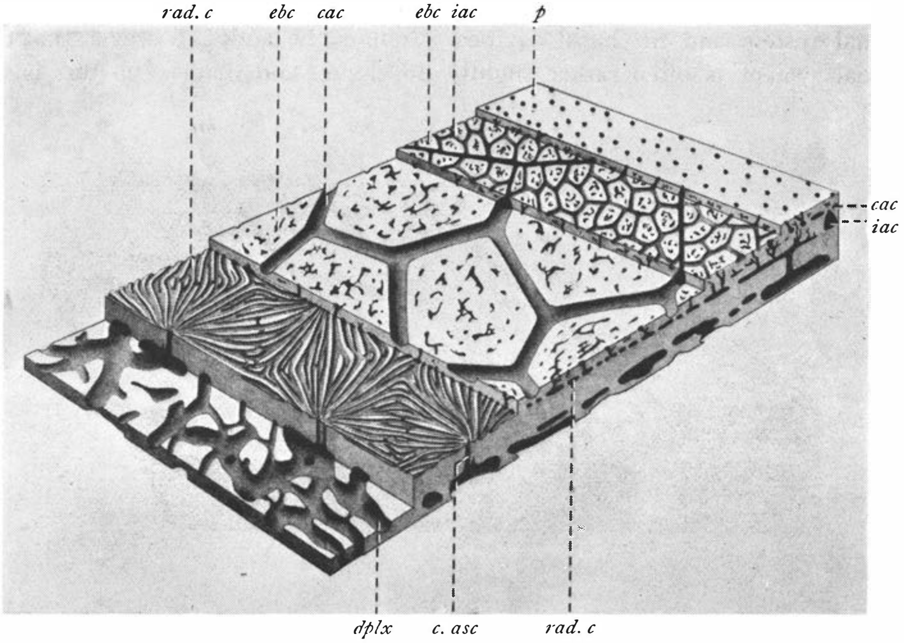
The circumtubercular canals are open outwards along the bases of the tubercles, as the intertubercular plates of the superficial layer are not continuous with the tubercles. The cross commissural and the interstitial canals open outwards in the grooves between the intertubercular plates by means of fine pores or shorter or longer openings (cf. similar conditions in *Hemicyclaspis murchisoni*, STENSIÖ 1932, pl. 9, p_1 and *iac*). The mucous canals in *Dartmuthia* may otherwise be described as grooves which are considerably widened basally and more or less closed to the exterior. In transverse section these grooves sometimes show a certain resemblance to the mucous grooves in Pteraspids (pl. VI, fig. 1; cf. STENSIÖ 1932, pl. 65, fig. 4; p. 191—192).

Comparison with other types of *Osteostraci.*

As regards the structure of the exoskeleton of the *Osteostraci* so far known in detail, we can in the main distinguish three different types, viz. (I) the cephalaspid type, which is found in most of the family *Cephalaspidae* (e. g. in the best known genera *Cephalaspis* and *Hemicyclaspis*), (II) the sclerodus type, found only in the genus *Sclerodus*, and (III) the tremataspid type, characterizing the genus *Tremataspis*.

In the cephalaspid type (text-fig. 4; STENSIÖ 1927, p. 32—37; 1932, p. 13—27), the three different layers are as a rule well developed; the outer layers may, however, be more or less reduced (e. g. several species of *Cephalaspis, Thyestes*, *Didymaspis*). The exoskeleton is divided into polygonal areas; in many species the mucous canals or grooves form the boundary between these polygonal areas. In the middle layer, the vascular canal system situated basally to the mucous system is, in the main, developed as radiating canals, which have an intra-areal position. In several Cephalaspids there are regular vascular canals descending from the radiating canals, which lie beneath the mucous canals or grooves and which thus have a strictly circum-areal position; in several species, they open in ring-sinuses in the basal layer, also with a circum-areal position. By means of all these vascular canals, the areal division is realized through all the three layers of the exoskeleton.

In the sclerodus type (STENSIÖ 1932, p. 15, 22, 176, 179), only the middle and basal layers of the exoskeleton are developed. No polygonal areas are formed, and the vascular canals are not developed as radiating canals; nor are they disposed in vascular areas but form an irregular vascular canal plexus. No traces of any mucous canals are preserved. The irregular disposition of the vascular canals in the middle layer does not, however, exclude the possibility that a mucous canal system may have been present in the soft tissue outside the exoskeleton (cf. STENSIÖ 1932, p. 179).

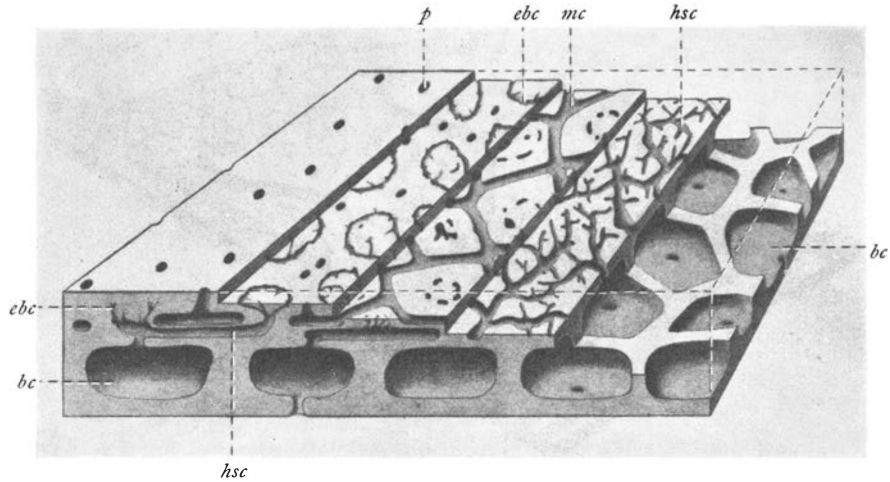


Text-fig. 4. Block-diagram, showing the structure of the exoskeleton in the cephalaspid type. The figure represents a generalized form with the three layers well developed, with a continuous smooth superficial layer and with the mucous canals divided into wide circum-areal and narrower intra-areal canals; the basal layer is simple and encloses canals belonging to the sub-cutaneous vascular plexus.

cac, circum-areal mucous canals; *c. asc*, ascending vascular canal; *dplx*, sub-cutaneous vascular canal plexus; *ebc*, external branches of the radiating vascular canals; *iac*, intra-areal mucous canals; *p*, pore of mucous canal; *rad. c*, radiating vascular canals.

The tremataspid type (text-fig. 5; PATTEN 1912, p. 290—292; STENSIÖ 1927, p. 38—40; GROSS 1935, p. 6—9) has the three layers in the exoskeleton well developed. Thanks to the disposition of the mucous canals, polygonal areas are developed in the middle layer. These areas are represented (in the basal layer) by basal cavities, the partitions of which have a circum-areal position directly beneath the mucous canals. On the other hand, the vascular canals in the middle layer are not disposed into regular vascular areas, nor are they developed as radiating canals. In *Tremataspis*, however, in the basal parts of the middle layer, there is sometimes a very well developed horizontal submucous vascular canal system.

This system has not been described by previous authors but it is partly shown in STENSIÖ 1927, pl. 72, fig. 1 and also clearly shown in GROSS 1935, text-figs. 1, 2, 4 (in the explanation to the figures called »lower horizontal net of the subepidermal vascular plexus» [translated]). This system is figured in superficial view in pl. VII, fig. 2, *hsc*, (see also text-fig. 5, *hsc*). It consists of horizontal, irregularly branching anastomosing canals which are not disposed in groups according to the areas formed by the mucous canal system and the basal cavities. It must be added, however, that this canal system is often rather slightly developed and that, when this is the



Text-fig. 5. *Trematapsis mammillata* PATTEN. Block-diagram, showing the structure of the exoskeleton.

bc, basal cavities; *ebc,* external branches of the horizontal submucous vascular canals (subepidermal vascular canal plexus); *hsc,* horizontal submucous vascular canals; *mc,* mucous canal; *p,* pore of mucous canal.

case, each group of canals is confined to a single area and has no connection with other groups. The canals of this system ramify from the ascending vascular canals and lie immediately ventrally to the mucous canals From the horizontal canals there ascend to the outermost parts of the middle layer small external branches, forming a subepidermal plexus (text-fig. 5; pl. VII, fig. 2, *ebc*); this plexus is differently developed in various species of *Trematapsis* (cf. STENSIÖ 1927, pl. 72, fig. 2, *rad. c*; GROSS 1935, text-figs. 2 A, 4, *ohsplx*). It is clear that the system of horizontal submucous canals in question corresponds to the radiating vascular canal system in the Cephalaspids proper and in *Dartmuthia*. On closer examination therefore, the difference between the trematapsid and the cephalaspid types proves to be not so marked as might appear from previous descriptions.

Unfortunately, the interesting genera *Oeselaspis*, *Rotsiküllaspis*, *Saaremaspis* and *Witaaspis* from Saaremaa are so imperfectly known, as regards the structure of their exoskeleton, that for the present it is impossible to make sure to which types they belong.

A comparison of the exoskeletal structure in *Dartmuthia* and the above-mentioned types reveals that, in the main, *Dartmuthia* most closely corresponds to the cephalaspid type. It agrees with this type in that the three layers are well developed; in that the polygonal areas distinguishable in the exoskeleton of *Dartmuthia* correspond to the polygonal areas in the Cephalaspids; and, above all, in that the vascular canal system is disposed in regular areas, while the horizontal canals in the middle layer, developed basally to the mucous canals, appear as typical radiating canals. *Dartmuthia* differs from the cephalaspid type in the minute development of the polygonal areas. These areas are, in *Dartmuthia*, not clearly separated in the superficial layer, being indicated only by the tubercles which form their centres. The mucous canals do not, as generally in the Cephalaspids, form the boundary between the areas. In *Dartmuthia* there are no regular circum-areal descending canals opening into basal ring-sinuses. We see instead that in the basal layer the partitions between the cavities have a strictly circum-areal position. There are thus marked differences in the structure of the basal layer between *Dartmuthia* and the cephalaspid type. In this connection it must be emphasized that the basal layer in different Cephalaspids may also present considerable differences.

There is in fact a remarkable agreement between *Dartmuthia* and the tremataspid type in the structure of the basal layer. This layer is, in the latter type, almost exactly like that of *Dartmuthia*; here, too, we have large cavities, the floors of which are pierced by canals and from the roofs of which issue ascending canals. *Dartmuthia* differs from the tremataspid type in the development of regular vascular areas with horizontal radiating canals.

The tubercles are much more strongly developed in *Dartmuthia* than in other forms with a continuous superficial layer. In *Dartmuthia* the tubercles have also a much more constant position in relation to the mucous and the vascular canal system than in other *Osteostraci*, with the possible exception of *Thyestes* and *Didymaspis*.

As regards its exoskeleton, *Sclerodus* represents a line of its own, very different from other Cephalaspids, even though the genus has been included in this family thanks to other characteristics. Its exoskeleton shows no very close resemblance to that of *Dartmuthia*.

As is obvious from the above, *Dartmuthia*, as far as its exoskeleton is concerned, on the whole agrees more closely with the Cephalaspids proper than with other *Osteostraci*. It is evident, however, that with regard to the basal layer it reminds us more of *Tremataspis*.

Judging from the structure of the exoskeleton, *Dartmuthia* is thus most akin to the family *Cephalaspidae*. We shall now see to what extent other known features support or contradict this opinion.

ROBERTSON (1935 b, p. 282—283) considers *Dartmuthia* as most closely related to *Tremataspis* because of the absence of the pectoral sinuses, a characteristic which he thus gives a decisive significance. Cornua and pectoral sinuses may, however, be more or less reduced in several Cephalaspid genera. This may be the manifestation of a general tendency towards the reduction of these formations, and the ultimate stage in such an evolutional series is then the total absence of cornua and pectoral sinuses. Such an absence in a form may thus only signify a difference in degree and not mark a divergent development between this form and other forms provided with cornua and pectoral sinuses. There is every reason to assume that *Dartmuthia* in this respect represents the ultimate stage in a lineage among the Cephalaspids and this appears clearer still from comparison between *Dartmuthia* and the Cephalaspid genus *Didymaspis*. There is thus no reason why, on account of the absence of these features, it should be placed apart from the Cephalaspids proper.

BERG (1940, p. 102, 357) classifies *Dartmuthia* in his order *Cephalaspidiformes*, which is distinguished from the order *Tremataspidiformes* by the presence of a single lateral electric field on each side of the cephalic shield. But even this peculiarity is not decisive. As an example, an as yet undescribed form from Spitsbergen may be mentioned. It shows a still more advanced subdivision of the lateral electric fields into separate portions than we find in *Tremataspis* and *Oeselaspis*, but its internal anatomical structures show that it must be regarded as a typical Cephalaspid.

In a specimen of *Dartmuthia* at my disposal, there are in the lateral electric fields fragments of the terminal branches of the canals for the electric nerves, which seem to show that the number of the lateral electric nerve canals was five (pl. VII, fig. 1, sel_{1-6}), and that, just as in e. g. *Thyestes* and *Didymaspis*, the foremost canal was the common canal for the two first electric nerves. The foremost canal ($sel_{1,2}$) was in all probability located at some distance behind the orbit, in a manner corresponding to that found in *Didymaspis*, *Thyestes*, *Witaaspis* and *Sclerodus*. In *Tremataspis* there are only three canals for the lateral electric nerves on each side, two entering the anterior, one the posterior, field. In this respect, *Dartmuthia* evidently differs from *Tremataspis* and decidedly approaches the Cephalaspids proper. In establishing the systematic position of *Dartmuthia*, I believe we must lay much stress upon this characteristic; and on account of this we must also regard *Dartmuthia* as closely related to, if not an actual member of, the family *Cephalaspidae*.

Dartmuthia approaches *Tremataspis* in the important respect that the large exoskeletal plates in the oralo-branchial fenestra — the ventral visceral exoskeleton — to a certain extent show a similar development and disposition (cf. ROBERTSON 1935 a, p. 329—330; 1938, p. 275—279). The actual systematic significance of this is difficult to ascertain, since the corresponding plates are unknown in the vast majority of Cephalaspids.

Conclusions.

Previous authors have advanced different opinions concerning the systematic position of *Dartmuthia*. It was regarded by PATTEN (1931, p. 671—673) as a representative of a family »in some respects intermediate between the *Cephalaspidae* and *Trematapidae*». ROBERTSON (1935 b, p. 282—283) regarded it as closely allied to *Trematapis*. HEINTZ (1939, p. 107) maintained that it is probably closely related to *Didymaspis*, a genus which he seems to classify with the Tremataspids. Finally, BERG (1940, p. 102, 357) placed *Dartmuthia* among the cephalaspid-like *Osteostraci*.

In the present state of our knowledge, it is most appropriate to regard *Dartmuthia* as a Cephalaspid, nearest related to *Didymaspis*. *Dartmuthia* seems to belong to the same branch of the Cephalaspids as *Didymaspis*; it is probably more primitive in the development of the exoskeleton, but is more advanced in the reduction of the cornua and the pectoral sinuses. *Dartmuthia* is also presumably related to the imperfectly known genus *Rotsiküllaspis*.

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Explanation of the plates.

Plate V.

Fig. 1. — *Dartmuthia gemmifera* PATTEN. Part of the dorsal exoskeleton of the cephalic shield between the dorsal and the lateral electric fields, external view. (Same specimen as in pl. VII, fig. 1). Approx. × 16 diam.

The superficial layer is made transparent by means of xylol in order to show the disposition of the mucous canals in the upper part of the figure. The superficial and middle layers partly removed.

bc, basal cavity; *bl,* basal layer; *c. asc,* ascending vascular canal; *mc,* circumtubercular mucous canal; mc_1, cross commissural mucous canal; mc_2, interstitial mucous canal; *ml,* middle layer; *rad. c,* radiating vascular canals; *sl,* superficial layer; *t,* tubercle.

Fig. 2. — *Dartmuthia gemmifera* PATTEN. Part of the exoskeleton from the posterior part of the cephalic shield, superficial layer, external view. Approx. × 35 diam.

f, grooves dividing the superficial layer into the intertubercular plates; *mc,* mucous grooves (or openings to the mucous canals); *sl,* intertubercular plate of the superficial layer; *t*, t_1, tubercles.

Plate VI.

Fig. 1. — *Dartmuthia gemmifera* PATTEN. Transverse section through the exoskeleton from the lateral rim of the cephalic shield, showing i. a. the dentine and enamel structure in the upper parts of the tubercles. Approx. × 36 diam.

bc, basal cavity; *c. asc,* ascending vascular canal; *mc,* mucous canal; *sl,* superficial layer (intertubercular plate); *sl. t.* superficial layer in the tubercle.

Fig. 2. — *Dartmuthia gemmifera* PATTEN. Transverse section through the lateral and posterior part of the cephalic shield, medial parts to the left, lateral to the right. Approx. × 30 diam.

bc, bc_1, basal cavities; *bl,* basal layer; *end,* space, lodging the endoskeleton, in the living form consisting of cartilage or another uncalcified tissue; *l,* perichondral bone lamella; *vc,* vascular and/or nerve canal.

Fig. 3. — *Dartmuthia gemmifera* PATTEN. Transverse section through the exoskeleton from the posterior part of the cephalic shield. Approx. × 40 diam.

bc, basal cavity; *bl,* basal layer; *c. des,* descending vascular canal; *ebc,* external branches from the radiating canals; *mc,* mucous canals; *ml,* middle layer; *rad. c,* radiating vascular canals; *sl,* superficial layer; *t,* tubercle.

Plate VII.

Fig. 1. — *Dartmuthia gemmifera* PATTEN. Part of the cephalic shield, dorsal view. The dorsal exoskeleton is imperfectly preserved. In the lateral electric field several canal fragments are preserved. (Same specimen as in pl. V, fig. 1). Approx. × $3^1/_3$ diam.

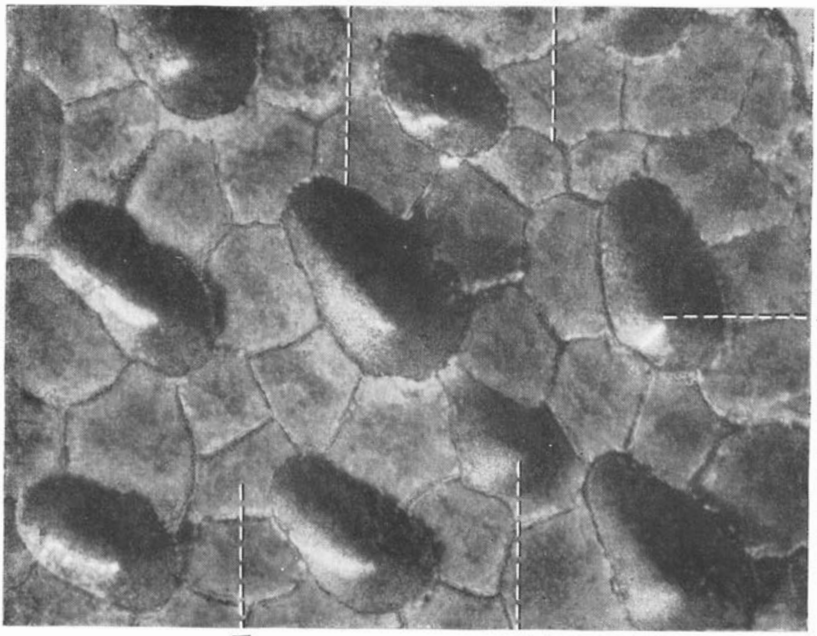
dsf, dorsal electric field; *lsf,* lateral electric field; n_2, posterior division of naso-hypophysial aperture; *orb,* orbital opening; *pin,* pineal opening; $sel_{1,2}$, common canal for the two most anterior nerves to the lateral electric field; sel_{3-6}, canals of nerves 3—6 of the lateral electric field.

Fig. 2. — *Tremataspis mammillata* PATTEN. Part of the exoskeleton of the cephalic shield, external view. Approx. × 30 diam.

The superficial layer is made transparent by means of xylol in order to show the disposition of the mucous and vascular canals in the middle layer.

ebc, external branches of the horizontal submucous vascular canals (subepidermal vascular canal plexus); *hsc,* horizontal submucous vascular canals (equivalent to the radiating vascular canals in Cephalaspids); *mc,* mucous canal; *p,* pore of mucous canal.

2



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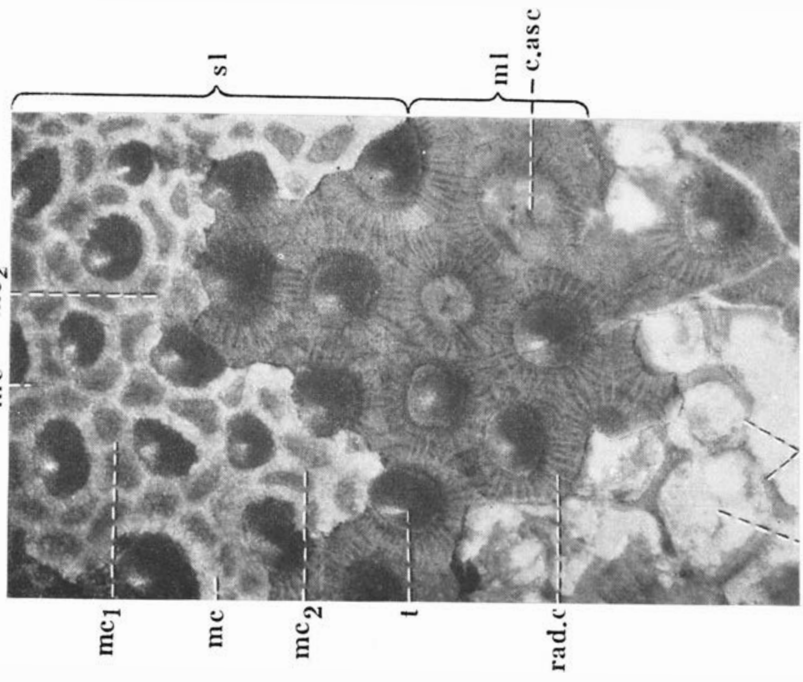

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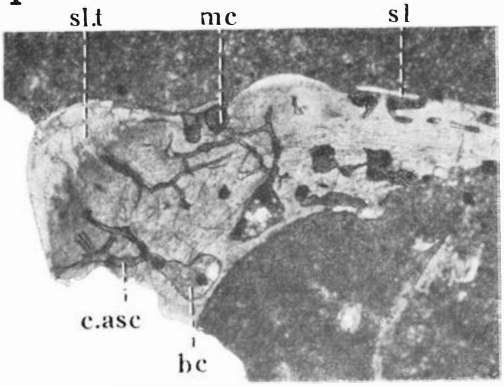
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sl
c.asc
bc

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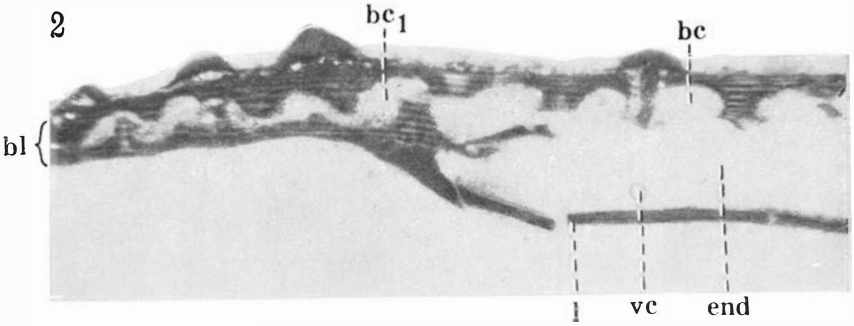
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bc
bl
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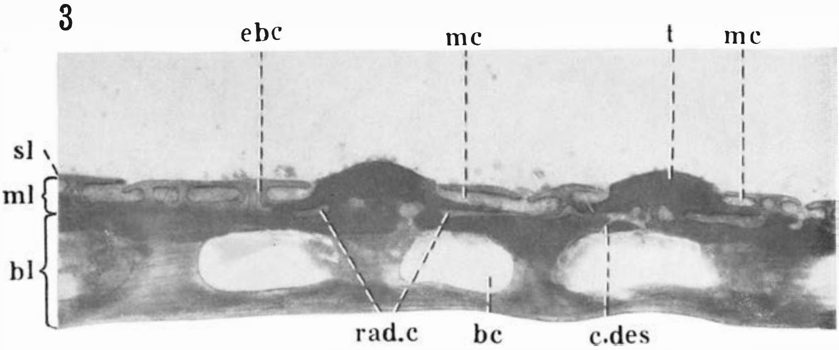
vc
end

3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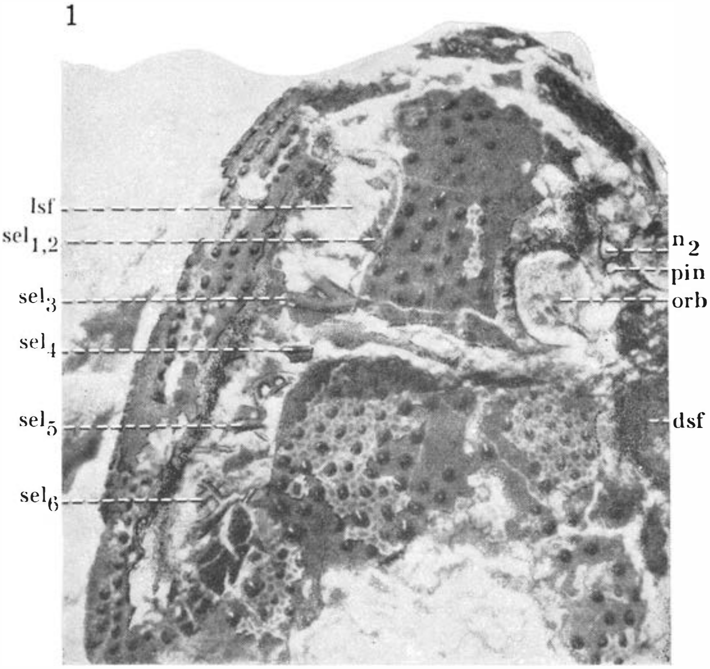

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