Ordovician Ostracodes with Supravelar Antra

By

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ABSTRACT.—Heteromorphs of ostracodes with an extradomiciliar dimorphism are usually provided with concave channel-like areas, the antra of HENNINGSMOEN (1965). The antrum can be situated between the marginal ridge and the velar structure (infravelar antrum) or between the velar and histial structures (supravelar antrum). In a small group of Ordovician palaeocopes both the infravelar and supravelar antra occur on the same valve (biantral dimorphism). The present paper treats the Ordovician ostracodes which either possess a supravelar antrum alone or have a biantral dimorphism. Eight genera are described in some detail, among them the new genera *Ceratobolbina* (type: *Sigmobolbina monoceratina* JAANUSSON, 1957) and *Pelecybolbina* (type: *P. pelecyoides* n.sp.). The taxonomic treatment also includes the description of six species from the Upper Viruan of Scandinavia. The types of KRAUSE's (1892) species *Sigmoopsis rostrata* and *Carinobolbina carinata* are figured, and four new species are described.

Contents

Introduction

The study of the Ordovician ostracodes with a broad histial flange in heteromorphs has been hindered because of insufficient knowledge concerning structural details of the area between the flange and the free margin of the valve. The previously available material of such ostracodes consisted, with few exceptions, of valves or carapaces still embedded in hard rock, and with such specimens it has been very difficult to expose the area of the valve hidden below the histial flange. The structure of this area is, on the other hand, clearly shown

in loose valves or carapaces of ostracodes obtained either from washing soft marls or by etching out silicified specimens. When such material became available, it revealed that there is still much to be learnt about details of the heteromorphic subhistial structures.

The present study was initiated as a part of the description of the Swedish Upper Viruan ostracodes. However, the complexity of the subhistial structures as revealed in suitably preserved material made it necessary to extend the study so as to include a general revision of the Ordovician ostracode genera with a histial dolon. Only a part of the material studied is from Sweden because of the scarcity in the Swedish Ordovician of silicified ostracodes or of rocks from which ostracodes can be washed out. Much of the described material is from Estonia and was generously made available by Dr. LEMBIT SARV. Some additional material was collected by the writer in 1964. The material of *Dilobella* was collected from the Decorah Shale of Minnesota by the present writer in 1959. The taxonomic treatment also includes the description of six species with a histial dolon from the Upper Viruan of Scandinavia. In this connection two type specimens are figured of species which were described by KRAUSE (1892) from erratic boulders of Northern Germany.

The writer is very much indebted to Dr. LEMBIT SARV, Tallinn, for the ostracode material from different levels of the Ordovician of Estonia; to Dr. CURT DIEBEL, Humboldt University, Berlin, for loan of KRAUSE's types; to Dr. GUNNAR HENNINGSMOEN, Paleontologisk Museum, Oslo, for loan of material from the Oslo area and for stimulating discussions; to Dr. ROGER SCHALLREUTER, Greifswald, for a photograph of STEUSLOFF's type of *Strepula elliptica*; and to Dr. JEAN BERDAN, U.S. Geological Survey, Washington D.C., for information about the type of *Ctenobolbina fulcrata* ULRICH. The English manuscript has been revised by Dr. D. L. BRUTON, Leicester.

The following abbreviations are used: BM, Palaeontological Museum of the Humboldt University, Berlin; OM, Palaeontological Museum, Oslo; RM, Palaeozoological Department, Swedish Museum of Natural History, Stockholm; UM, Museum of the Palaeontological Institute of the Uppsala University.

Remarks on Taxonomy and Morphology

When studying palaeocope ostracodes either in thin sections or as valves embedded in the rock and prepared with a fine needle, attention has been focused on the development of various dimorphic ridges, flanges, and frills. Clean, free valves and carapaces, on the other hand, reveal that the primary importance in this type of shell dimorphism does not lie in the ornamental extensions themselves but in the areas between and below these structures. The purpose of the extradomiciliar dimorphism, either velar or histial, was obviously to form certain smooth, concave channel-like areas upon the shell and along a portion of the free margin. In thick-shelled ostracodes these areas, the *antra* of HENNINGSMOEN (1965), can simply be impressions on the surface of

the shell, but in this case they remain necessarily shallow and exposed. An increase of the depth of the antra can be attained by bordering the antrum with a flange or by moving a part or the whole of the antral concavity from the external surface of the domicilium to the inner side of a flange or frill (HENNINGSMOEN 1965). Thus the dolonal portions of the adventral ridges, flanges, and frills serve primarily to enlarge or house the antra. This mode of approach to extradomiciliar dimorphic structures in palaeocopes is especially fruitful when dealing with genera in which, as is the case with the Ordovician ostracodes possessing a histial dolon, the main part of the antrum is upon the external surface of the domicilium.

The ostracodes treated in this paper were included by JAANUSSON (1957) in the families *Tetradellidae* and *Sigmoopsidae*. Tecnomorphs of these ostracodes exhibit one or two adventral (excluding marginal) ridges or, in rare cases, lack distinct adventral structures. The lower (i.e. more peripheral) of these ridges has been referred to as the velar ridge since it has the same position in relation to the free margin as the frill in the eurychilinids. The upper ridge is termed the histial ridge (JAANUSSON 1957; carinal ridge of HESSLAND 1949). For the sake of clarity it is important to establish types for these structures which could serve as reference when comparing the adventral extensions of different ostracodes. For the velar structure the frill of an eurychilinid is a satisfactory type, e.g. that of a tecnomorphic *Eurychilina*. For the histial structure the best type seems to be the upper adventral ridge in *Sigmoopsis*, in particular the upper dolonal flange of heteromorphs.

In tecnomorphs of *Pentagona* and *Sigmobolbina* the relative distance of the lower ridge from the free margin is similar to that between the velum and free margin of tecnomorphs of the eurychilinid genus *Platybolbina*. The latter genus is used here for comparison because it includes species with a wide frill as well as others with only a velar ridge (e.g. *P. inflata* JAANUSSON and *P. temperata* SARV). Tecnomorphs of *Severella* resemble so closely those of certain *Euprimites* species that a clear distinction is occasionally difficult; both genera possess an adventral ridge or bend in the same position. The tecnomorphic velar flange in *Tetradella* has its counterpart in many piretellid genera. All this indicates that in the Ordovician ostracodes with a histial dolon the lower adventral ridge is comparable with the velum in the eurychilinids and can thus be termed a velar structure (HESSLAND 1949; HENNINGSMOEN 1953; JAANUSSON 1957).

Examination of several species of *Sigmobolbina* shows that in heteromorphs of this genus the main antral channel lies above the velar ridge, and that the velar ridge and the subvelar area have the same appearance in both tecnomorphs and heteromorphs (Text-fig. 6). This implies that in this genus the antrum is supravelar and not infravelar as it is in the eurychilinids and piretellids. In these latter two the antrum lies either between the velar ridge and the free margin or on the inner side of the velum. The same relationship between the

antrum and the velar ridge of *Sigmobolbina* is shown also in several other genera and in all the lateral (outer) fence of the antrum is formed by a dolonal list or flange comparable with the histial flange in *Sigmoopsis*.

Among other genera with a histial dolon the heteromorphic subhistial features are more complicated than previously thought. New material studied shows that the heteromorphs of *Sigmoopsis* and certain other genera possess two deep adventral channel-like structures (Text-fig. 3). The lower (more peripheral) of these channels is infravelar because it is developed between the velar structure and the free margin. The upper channel lies between the velum and histium and is thus supravelar and comparable with the antrum in *Sigmobolbina* and related genera. There does not seem to exist reason to doubt that both infra- and supravelar channel-like structures represent antra. They have the same appearance, height, and depth (Text-fig. 3), and occur only in heteromorphs. This type of antral dimorphism is here termed *biantral*. Some of those forms which exhibit this type of dimorphism (e.g. *Severella*) possess what appears to be one of the most spectacular cases of sexual shell dimorphism in ostracodes.

In the heteromorphs of the genera with biantral dimorphism, not only the histial structure is widened and forms a dolonal flange, but the velar structure too increases considerably in width between the antra. Thus, these heteromorphs possess a histial as well as a velar dolon, and it could be said that they exhibit a histio-velar dimorphism. However, the writer now prefers to discard the terms histial and velar when referring to types of dimorphism. Different types of the extradomiciliar dimorphism can be defined with more clarity and precision with reference to the antra. As pointed out above, antral dimorphism can be infravelar, supravelar, or both, biantral. It can be locular, when the whole antral area is partitioned by transverse septa into loculi (as in *Tetradella* which has a locular supravelar dimorphism), or semilocular, when only a part of the antral area is transformed into loculi (as in *Dilobella* which has a semilocular or bilocular supravelar dimorphism). It can be termed simply antral, when it is difficult to homologize the dolonal structures.

With respect to the development of subhistial heteromorphic structures three main morphological groups can be distinguished among the Ordovician ostracodes with a histial dolon.

(1) Only one antrum is developed on either valve, and this antrum is supravelar in position. In *Tetradella* the whole antral surface is transformed into loculi. *Foramenella* may be a related genus in which the histial and velar structures have become reduced so that the loculi appear to be impressed into the surface of the valve. In the other genera the anterior part of the antrum of either valve bears one (*Sigmobolbina*, *Pelecybolbina*) or two (*Dilobella*, *Perspicillum*) loculi, and the remaining part of the antrum is developed as a long, channel-like structure between the histial and velar flanges.

(2) Each valve of heteromorphs possesses two antra, one antral channel

being infravelar, the other supravelar (*Sigmoopsis*, *Carinobolbina*, *Pseudotallinnella*, *Severella*, *Pentagona*, *Lomatobolbina*, and *Ceratobolbina*). With the exception of *Ceratobolbina*, which possesses one loculus on either valve in front of the main supravelar antrum, no loculus is developed. Both the histial and velar structures are conspicuously broader in heteromorphs than in tecnomorphs. Thus these genera possess a histial as well as a velar dolon, whereas those of group (1) only have a histial dolon.

(3) Although both dimorphs have a ridge or flange in exactly the same position as the histial structure in groups (1) and (2), the antrum is exclusively infravelar and extends to the marginal ridge (*Glossomorphites*, *Polyceratella*). In the genera *Aulacopsis*, *Ogmoopsis*, *Reigiopsis*, and *Oecematobolbina* a shell dimorphism has so far not been demonstrated, but they may nevertheless belong to this group.

The present paper deals only with the groups (1) and (2), since the available material belonging to the genera of group (3) is still insufficient. Dr. A. L. GUBER is presently studying the shell morphology of *Tetradella* and thus only brief remarks on this genus are included here. No material for study has been available of the genera *Foramenella* and *Perspicillum*.

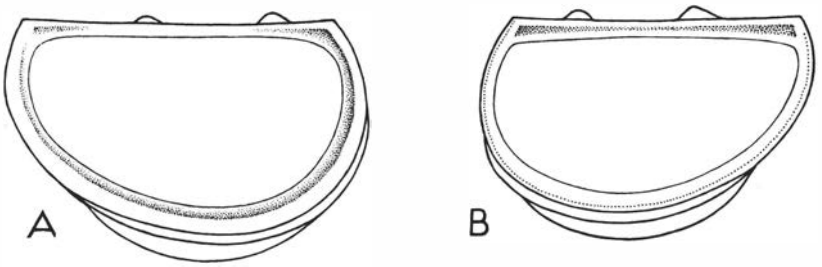
The suggested interpretation regarding the position of the antral structures in *Tetradella* calls for further comments because it is somewhat different from that given by HENNINGSMOEN (1965). In this genus the loculi are considered to be supravelar for the following reasons. (1) The surface of the subvelar area below the loculi is a direct continuation of that of the subvelar area in front of and behind the area with loculi. (2) Dr. GUBER has demonstrated to the present writer that occasional preadult valves of *Tetradella* show shallow, incipient loculi. In these juvenile heteromorphs the whole velar ridge is developed exactly as in adult tecnomorphs, and the incipient loculi are situated entirely between the velar ridge and the connecting ridge of the lobes, i.e. in a supravelar position like the loculi in *Dilobella*. (3) The relation of a loculus to the velar ridge is the same in *Tetradella* and *Sigmobolbina*. In the latter genus too the lateral margin of the velar ridge is arched towards the free margin below each loculus. (4) The roof of the loculi in *Tetradella* is, in part, formed by a histial component, but in an unusual manner. Although the ventral lobal crests appear to be similarly developed in tecnomorphs and heteromorphs, a close examination reveals that, along the ventral margin of the lateral surface of the valve, the position of the lobal crests relative to the free margin and the velar ridge is different in tecnomorphs and heteromorphs. In heteromorphs the most ventral part of the lobate area protrudes far more in a ventral direction than in tecnomorphs and, as visible in heteromorphic valves immersed in some fluid, forms part of the roof of the loculi. If the connecting crest had retained its tecnomorphic position in heteromorphs, the latter would have possessed a flange ventral to the connecting crest. This flange would have been quite similar, in position as well as appearance, to the histial dolon of the other

ostracodes treated in this paper. Thus *Tetradella* can be said to possess a kind of dolon which is of a histial nature (JAANUSSON 1957). The ring-shaped brim around the entrance of each loculus and the transverse walls between the loculi are probably neither velar nor histial but simply structures of the loculi.

The taxonomic value of the subhistial dimorphic structures depends upon, whether a certain position of the antrum has originated only once during the evolution or it has arisen repeatedly in different phylogenetic lineages.

The relative complexity of these structures, especially if they have had a definite and important function, favours the first of these alternatives. The possible function of antrum and dolon has lately been discussed by JAANUSSON (1957) and HENNINGSMOEN (1965). Both concluded that these structures may have been used for extradomiciliar egg-care. If these dimorphic structures had any function at all, it is difficult to find any other plausible explanation for the concave, channel-like areas which characterize the heteromorphs of a large group of palaeocope ostracodes. The transport of eggs by appendages to the surface of an infravelar antrum situated close to the free margin seems to be feasible even if the antrum has an anteroventral position (JAANUSSON 1957). More difficult to explain however, is how the eggs could be placed into a supravelar antrum especially when both supra- and infravelar antra are present and the supravelar antrum is bordered ventrally by a velar dolonal flange. Such intricate biological problems are frequently encountered by the palaeontologist, and they are difficult to solve by studying material which consists merely of fossil shells. Because of the total lack of knowledge about the construction of appendages or the behaviour of adult males and females in these fossil ostracodes, discussions concerning the function of the antra easily enter the realm of speculation. However, the wide-spread and constant occurrence of these dimorphic structures strongly suggests that they had a functional significance, and it seems reasonable to suppose that, in some way or other, they were connected with reproduction (JAANUSSON 1957). If this functional significance was connected with a certain degree of specialization of some of the soft parts of the animal, then the development of antra must reflect some of this specialization. Thus it is possible that the position of antra has a definite taxonomic importance above the genus level.

On the other hand, many genera look alike but can be distinguished according to the development of heteromorphic structures. Tecnomorphs of *Sigmobolbina* and *Pentagona* are almost indistinguishable and so are their heteromorphs when seen in lateral view. The antrum in *Sigmobolbina* is supravelar while *Pentagona* is biantral. Some species combine a *Sigmobolbina*-like lateral view with an infravelar antrum (e.g. *Henningsmoenia gunnari* (THORSL.) with an infravelar antrum is very similar to *Sigmobolbina prochowiensis* (NECKAJA) which has a typical supravelar antrum with a loculus). *Tetradella* has a supravelar locular antrum, but a species like "*Tetradella*" *litwiensis* NECKAJA, which possesses typical characters of a *Tetradella* in lateral view, has a distinct infravelar antrum



Text-fig. 1. *Dilobella typa* ULRICH. Diagrammatic drawing to show the main features of the contact area of the left (*A*) and right (*B*) valve. Drawn from specimens UM Nos. NA 146 and 147. × 40.

without loculi. Dr. G. HENNINGSMOEN has demonstrated other similar examples to the present writer. This suggests that the dimorphic structures may be phylogenetically less stable than might be believed. It could be that the change from an infravelar to a supravelar position of the antrum or to a biantral dimorphism may have repeatedly taken place in different phylogenetic lineages. If this is correct, the classification of these ostracodes becomes an extremely intricate problem since the remaining features of the carapace are known to be subject to a considerable degree of homoeomorphism. On the other hand, the similarity between valves with a different kind of antral dimorphism may be due to a striking homoeomorphism in the shape and sulcation of the valves. In this case the dimorphic characters may be the best clue to distinguishing between genera which look very similar but are remotely related. It is difficult to prove which of these alternatives is correct without a detailed examination of considerably more material and studies of additional structures like the hinge.

The hinge of the group of ostracodes treated in the present paper is rarely preserved in the available material. It could best be examined in *Dilobella* (Text-fig. 1). In this genus the left valve is provided with a well-defined contact furrow which is absent on the right valve therefore indicating that the left valve overlaps the right valve when the carapace is closed. All along the hinge-margin, the right valve possesses a longitudinal hinge-groove which is bordered by the inner and outer hinge-ridges. In the left valve the longitudinal hinge-groove is developed only terminally, and the terminal inner and outer hinge-ridges coalesce medially so as to form one hinge-ridge. Of interest is the fact that, in the left valve, the hinge-groove is continuous anteriorly with the contact furrow. In many respects the hinge of *Tetradella* is very similar to that of *Dilobella*. There is a contact furrow all along the free margin of the left valve and a longitudinal hinge-groove along the hinge-margin of the right valve. In most specimens the left valve seems to lack a hinge-groove, but anteriorly in some well preserved valves there is a very short terminal hinge-groove which is continuous with the contact furrow (specimen UM No. NA 153). In a form which SARV (1959) tentatively identified as *Sigmobolbina illativis* (NECKAJA)

(Estonia, Lehtmetsa, D_{II}), the hinge and contact furrow are very similar to those of *Tetradella* except that there is a short terminal hinge-groove also at the posterior end of the hinge of the left valve (specimen UM No. E 24). The above information about the hinge in these ostracodes is obviously insufficient to allow generalizations to be made.

The classification of Ordovician palaeocopes is still unsatisfactory, chiefly because the available characters of too few genera have been properly described and analyzed. In the following classification the dimorphic characters in heteromorphs are provisionally deemed to be more stable features than the shape and sulcation of the valves. Based on this assumption the writer has arrived at the following grouping of the genera treated in this paper.

Family *Tetradellidae* SWARTZ, 1936

Subfamily *Tetradellinae* SWARTZ, 1936

Tetradellids with a supravelar antrum and with a tecnomorphic shape of the subvelar area also present in heteromorphs.

Genera: *Tetradella* ULRICH, 1890; *Dilobella* ULRICH, 1897; *Sigmobolbina* HENNINGSMOEN, 1953; *Perspicillum* SCHALLREUTER, 1964; *Pelecybolbina* n.gen.; and possibly *Foramenella* STUMBUR, 1956.

Subfamily *Sigmoopsinae* HENNINGSMOEN, 1953

Tetradellids with a biantral dimorphism; either valve possesses an infravelar as well as a supravelar antrum.

Genera: *Sigmoopsis* HENNINGSMOEN, 1953; *Carinobolbina* HENNINGSMOEN, 1953; *Lomatobolbina* JAANUSSON, 1957; *Pseudotallinnella* SARV, 1959; *Severella* SCHALLREUTER, 1964; *Pentagona* SCHALLREUTER, 1964; *Ceratobolbina* n.gen.

Subfamily *Glossomorphitinae* HESSLAND, 1953

Tetradellids with a histial structure, at least in the heteromorphs, but with the antrum (if present) exclusively in an infravelar position.

Genera: *Glossomorphites* HESSLAND 1953; *Polyceratella* ÖPIK, 1937. Further genera which may belong to this subfamily, but which are insufficiently known are *Aulacopsis* HESSLAND, 1949; *Ogmoopsis* HESSLAND, 1949; *Oecematobolbina* JAANUSSON 1957; *Reigiopsis* SARV, 1959.

Provided the antra had served for egg-care, it would be possible to derive ostracodes with a supravelar antrum from forms with only an infravelar antrum, because the latter antrum is closest to the free margin and thus most easily accessible for fastening the eggs. Ostracodes like *Glossomorphites* satisfy many of the requirements as an ancestor for ostracodes with a supravelar antrum: in spite of having only an infravelar antrum, they resemble very closely certain sigmoopsines and are among the earliest palaeocopes so far known. From ostracodes with only an infravelar antrum the development could lead to those with a biantral dimorphism in which also the space between the velar and the

preexisting histial structures was modified into an antrum. Under these conditions a reduction of the infravelar antrum of ostracodes with a biantral dimorphism would readily explain the origin of those with only a supravelar antrum. A possible morphological intermediate stage is shown in the genus *Ceratobolbina* in which an anterior reduction of the infravelar antrum can be suggested, whereas posteriorly the biantral arrangement of antra is retained (Text-fig. 4).

During future studies of the palaeocopes the possibility ought to be kept in mind that there might occur antra which occupy the whole subhistial area, i.e. antra extending from the histial flange to the marginal ridge. Such "amphivelar" antra might have developed through reduction of the velar structure and the subvelar area or through suppression of the velar structure and the incorporation into the antrum of the area corresponding to the velar structure and the subvelar area.

Genus *Sigmoopsis* Henningsmoen, 1953

Type species.—*Ceratopsis platyceras* Öpik, 1937.

Diagnosis.—Quadrilobate; ventral part of L1, when developed, as a rule narrow, dorsal part bulbous or produced into a speral spine. Dorsal part of S1, when developed, narrow, constricted between the bulbous dorsal part of L1 and the ventral termination of L2. Tecnomorphs with a narrow histial ridge and an equally narrow velar ridge which runs in a broad arch upon the ventral surface of the valve and fairly close to the histial ridge. Heteromorphs biantral, with flange-like histial and velar dolons which either join (subgenus *Sigmoopsis* (*Sigmoopsoides*) Schallreuter, 1964) or do not join (subgenus *Sigmoopsis* (*Sigmoopsis*)) anteriorly.

Discussion.—In tecnomorphs of *Sigmoopsis* the velar ridge describes a broad curve in ventral view, the subvelar area being broadest somewhat in front of the mid-length of the valve and narrowing conspicuously in an anterior as well as in a posterior direction. The subvelar area is faintly concave, but no distinct canaliculus is formed. The histial structure forms a ridge at the ventral edge of the connecting lobe, and in ventral view its course is almost parallel to the velar ridge, being separated from the latter by a narrow, faintly concave channel. It is interesting to note that in *Sigmoopsis* the development of the tecnomorphic velar and histial ridges is similar to that in tecnomorphs of *Glossomorphites*.

In heteromorphs the velar dolon runs ventrally parallel to the free margin. The subvelar area is slightly narrower than in tecnomorphs along the middle part of the ventral free margin, i.e. during the formation of the velar dolon the velar structure assumes a somewhat lower position than in tecnomorphs.

In heteromorphs the histial structure expands to form a ventrally directed flange-like dolon which, in lateral view, conceals the underlying structures. *S. granulata*, one of the very latest species of the genus is an exception. Here, the histial flange is narrower and is situated much higher dorsally concealing

only a part of the supravelar antrum (Pl. II, figs. 9–10). In this respect this species resembles a *Carinobolbina*.

OCCURRENCE.—*Sigmoopsis* has been reported in situ from the East Baltic states and Sweden. It ranges from the Viruan Lasnamägi Stage (C_1b) to the lowermost Harjuan Rakvere Stage (E).

Sigmoopsis (*Sigmoopsis*) *rostrata* (KRAUSE, 1892)

Pl. II, figs. 2–6; Text-fig. 3 I–M

1892 *Beyrichia* (*Ctenobolbina*) *rostrata* n.sp. — KRAUSE, pp. 395–396, Pl. XXI, fig. 2.
1893 *Tetradella carinata* KR. — ANDERSSON, p. 127.
1893 *Tetradella rostrata* KR. — ANDERSSON, p. 127.
1937 *Ceratopsis obliquejugata* (SCHMIDT) — ÖPIK, p. 25 (partim), Pl. XIV, fig. 6.
1940 *Ceratopsis obliquejugata* (FR. SCHMIDT) — THORSLUND, pp. 170–171, Pl. 3, fig. 13.
1953 *Ceratopsis obliquejugata* (SCHMIDT) — NECKAJA, p. 334, Pl. V, figs. 3–6.
1953 *Sigmoopsis rostrata* (KRAUSE) — HENNINGSMOEN, p. 205.
1957 *Sigmoopsis* sp. A — JAANUSSON, pp. 383–384, Pl. XI, fig. 9.
1959 *Sigmoopsis lamina* n.sp. — SARV, pp. 117–118, Pl. XX, figs. 6–9, text-fig. 12 G.
1962 *Sigmoopsis rostrata* (KRAUSE) — JAANUSSON, p. 413.

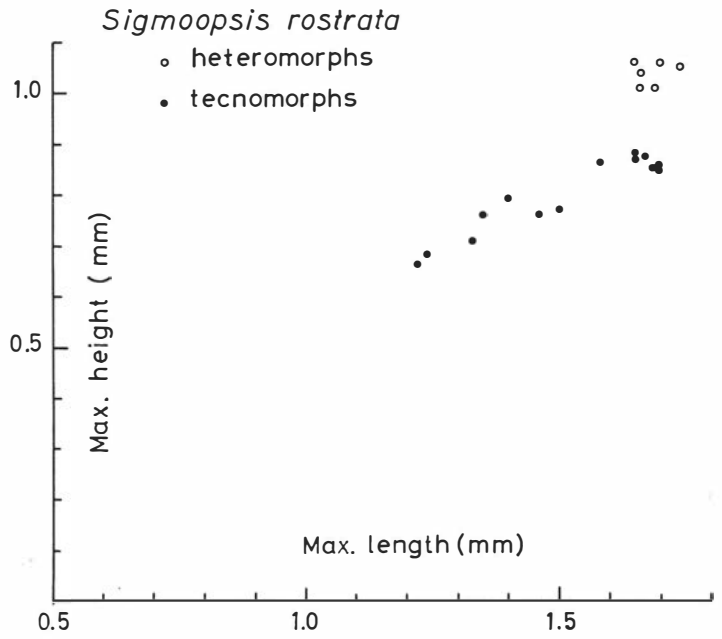
LECTOTYPE (designated by JAANUSSON 1962, p. 413).—Right heteromorphic valve, deposited in the BM, figured by KRAUSE (1892) as Pl. XXI, fig. 2, and refigured herein as Pl. II, fig. 6. KRAUSE's boulder No. 587.

DIAGNOSIS.—A species of *Sigmoopsis* (*Sigmoopsis*) with a low, rounded speral process, separated from L2 by a faint furrow, or merging into the dorsal part of that lobe without a distinct boundary. S2 distinctly wider than S3. In adult valves the dorsal end of L3 reaches the dorsal margin of the valve and is often poorly defined. Length of the heteromorphs 1.50 to 1.75 mm. Well-preserved specimens with a minute reticulated ornament.

DISCUSSION.—SARV (1959) fully described the species under the name *S. lamina*. It is characterized by a low, rounded, and sometimes somewhat poorly defined speral process of L1. The shape of the process is variable. Ventrally the process may be separated from the dorsal part of L2 by a shallow furrow or may merge into L2 without any distinct boundary (cf. also SARV 1959, p. 117).

All examined specimens, including some from Estonia, with a well-preserved surface of the valve exhibit a minute reticulation. This ornamentation is so faint that it is easily obliterated by weathering or abrasion and thus this may account for SARV's statement that the valves of this species are smooth. On the other hand, the possibility is not excluded that the variation within the species ranges from minutely-reticulated to smooth valves.

Dimensions of the specimens from the boulders of Öland are given in Text-fig. 2. The length of the heteromorphs ranges there from 1.65 to 1.74 mm. Some other populations have somewhat smaller adult valves. The lectotype is 1.54 mm long and 0.84 mm high, and the length of two heteromorphs from Estonia given by SARV (1959) is 1.53 mm.



Text-fig. 2. *Sigmoopsis rostrata* (KRAUSE). Size dispersion of valves collected from boulders of the *Macrourus* calcareous siltstone of Öland.

The drawing of the lectotype of *S.* (*S.*) *rostrata* given by KRAUSE (1892, Pl. XXI, fig. 2) is so schematic that the species could not be recognized from his description and figure alone. ANDERSSON (1893) identified it correctly, probably because the associated species are largely identical. He suggested erroneously that KRAUSE's *Beyrichia* (*Tetradella*) *carinata* and *B.* (*Ctenobolbina*) *rostrata* may be conspecific, and in his collection from Öland he designated tecnomorphs of *Sigmoopsis rostrata* as *Tetradella carinata.* HENNINGSMOEN (1953) recognized that KRAUSE's *Beyrichia* (*Ctenobolbina*) *rostrata* is a species of *Sigmoopsis.* A comparison of the lectotype and associated specimens of *S. rostrata* with the topotype material of *S. lamina* SARV revealed that these forms are conspecific (JAANUSSON 1962). JAANUSSON's (1957) *Sigmoopsis* sp. *A* is a tecnomorph of the same species and not a member of the subgenus *Sigmoopsis* (*Sigmoopsoides*) as SCHALLREUTER (1964, p. 88) suggested.

OCCURRENCE.—*Sigmoopsis* (*Sigmoopsis*) *rostrata* is a common species and has a considerable vertical range. In Estonia SARV (1959) reported the range of the species as being from the Kukruse (C_{II}) to the Keila (D_{II}) Stage. In Sweden the range is closely comparable.

For the occurrence in Estonia, see SARV (1959, p. 118). Sweden: *Gotska Sandön* boring at the levels of 128.46 and 131.80 m. *Tvären area*, in a boulder from the *Ludibundus* beds (THORSLUND 1940, Pl. 3, fig. 13; JAANUSSON 1957,

Pl. XI, fig. 9). *Siljan district*, Fjäcka, locality No. 9, *Macrourus* Limestone, 6.0–6.3 m from the upper boundary. *Öland*, boulders of the *Macrourus* calcareous siltstone.

Genus *Carinobolbina* Henningsmoen, 1953

Type Species.—*Ctenobolbina carinata estona* Öpik, 1937.

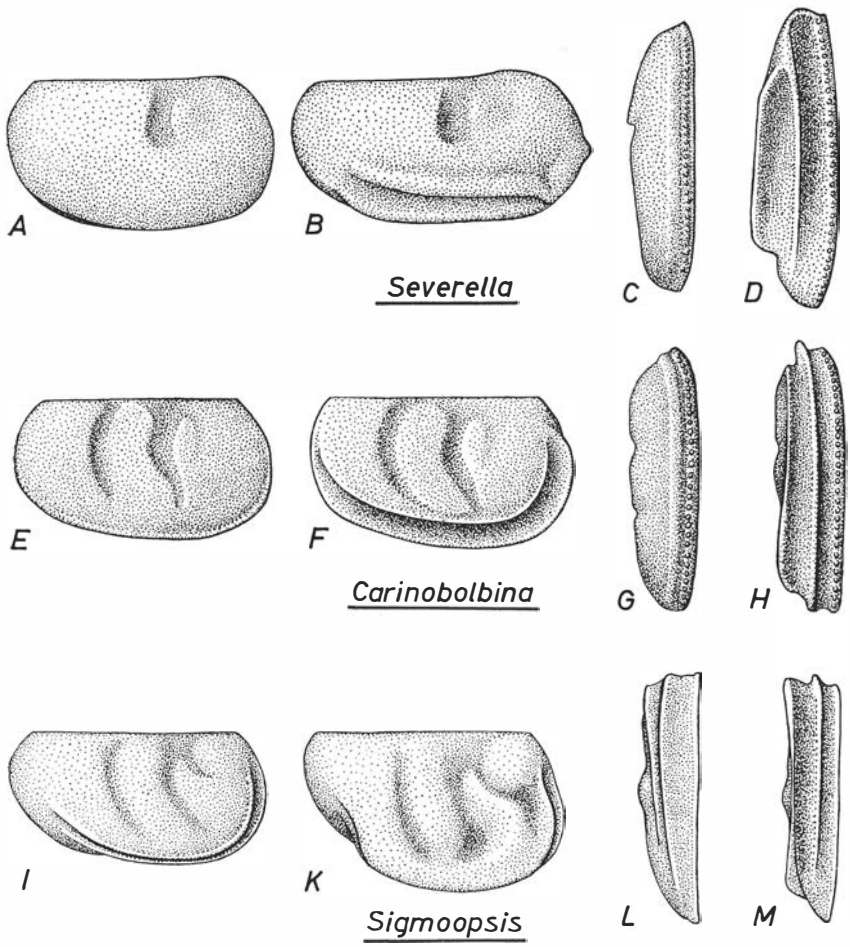
Diagnosis.—Valves almost amplete, bi- to trisulcate; S2 long and sigmoidal, lobes flattened. Tecnomorphs with a well-defined, broadly rounded velar ridge and a narrow canaliculus between the velar and marginal ridges. Heteromorphs with histial and velar dolons in the form of moderately broad flanges of about equal length. The histial flange is situated high on the surface of the valve and is almost laterally directed, concealing, in lateral view, only part of the supravelar antrum. The anterodorsal end of the histial flange does not curve towards the free margin.

Species.—*Beyrichia* (*Tetradella*) *carinata* Krause, 1892
Ctenobolbina carinata estona Öpik, 1937

Discussion.—In certain respects the type species of *Pseudotallinnella* Sarv, 1959 (*P. scopulosa* Sarv), closely resembles *Carinobolbina carinata*. Both species may be considered as quadrilobate, if the fairly large preadductorial node is interpreted as representing L2. *Pseudotallinnella scopulosa* differs mainly in that the position of the histial dolon is closer to the free margin and so, in lateral view, the histial flange completely conceals the supravelar antrum. If this feature is considered as being of generic importance, these genera are clearly distinct. In the other details of the heteromorphic structures, such as the approximately equal length of the histial and velar dolons and the lack of a distinct anterior curvature of the velar dolon towards the marginal ridge, *Pseudotallinnella* resembles *Carinobolbina*. In *Pseudotallinnella* the lobes are faintly convex, and the valves can be considered as lobate but in *Carinobolbina* the lobes are flattened and the valves can be described as sulcate. However, this difference is scarcely of importance at the genus level.

In *Carinobolbina* the tecnomorphic velar ridge is poorly defined in lateral view. It is separated from the lateral surface of the valve by a faint furrow which is scarcely noticeable in *C. estona*. In ventral view the tecnomorphic velar structure is a distinct broadly rounded ridge which is parallel to the free margin and is separated from the marginal ridge by a narrow, but fairly deep canaliculus. The position of the velar dolon upon the surface of the valve is much higher than that of the tecnomorphic velar ridge. Anteriorly the velar and histial dolons extend at least to the mid-height of the valve where they end at the rounded anterior termination of the supravelar antrum.

Occurrence.—The genus has been found in situ in Estonia and in erratic boulders of Sweden (Öland) and North Germany. Its known vertical range is from the Kukruse Stage to the Keila Stage.



Text-fig. 3. Drawings illustrating the characters of three genera which exhibit biantral dimorphism. Based on *Severella severa* (SARV), *Carinobolbina carinata* (KRAUSE), and *Sigmoopsis rostrata* (KRAUSE). *A*, *E*, *I* and *C*, *G*, *L:* lateral and ventral view of right tecnomorphic valves. *B*, *F*, *K* and *D*, *H*, *M:* lateral and ventral view of right heteromorphic valves. Not to scale.

Carinobolbina carinata (KRAUSE, 1892)

Pl. I, figs. 8–12, Pl. II, fig. 1; Text-fig. 3 E–H

1892 *Beyrichia* (*Tetradella*) *carinata* n.sp. — KRAUSE, pp. 394–395, Pl. XXI, fig. 9.
1953 *Carinobolbina carinata* (KRAUSE) — HENNINGSMOEN, pp. 205–206.
1959 *Carinobolbina estona magnifera* subsp. n. — SARV, pp. 136–137, Pl. XXIV, figs. 6, 7.
1962 *Carinobolbina carinata* (KRAUSE) — JAANUSSON, p. 413.
Non 1893 *Tetradella carinata* KR. — ANDERSSON, p. 127 [= *Sigmoopsis rostrata* (KRAUSE, 1892)].

LECTOTYPE (designated by JAANUSSON 1962, p. 413).—Right heteromorphic valve deposited in the BM, figured by KRAUSE (1892) as Pl. XXI, fig. 9, and refigured herein as Pl. I, figs. 10–11. KRAUSE's boulder No. 670.

DISCUSSION.—The differences between *C. estona* (ÖPIK) and *C. carinata* (*C. estona magnifera*) are listed by SARV (1959, pp. 136–137). In the present writer's opinion these differences are so distinct that it is preferable to treat the two forms as different species.

The lectotype is somewhat smaller (length of the valve 1.55 mm) than the other examined heteromorphs of this species (length of the valve commonly between 1.65 and 1.70 mm). The heteromorphic valve figured as Pl. II, fig. 1, is exceptionally large (length 1.83 mm). An adult tecnomorphic valve (Pl. I, figs. 11–12) in KRAUSE's collection from the same boulder as the lectotype has a size (length 1.69 mm) closely comparable to that of the tecnomorph measured by SARV (1959, p. 137; length 1.65 mm).

The posterior extension of the histial flange varies between fairly wide limits. In the specimen figured as Pl. II, fig. 1 the flange is also developed along the posterior margin of the valve and extends somewhat dorsally of the mid-height of the valve. In most specimens the flange ends considerably farther anteriorly, at about the mid-length of L4 (lectotype, Pl. I, figs. 10–11; SARV 1959, Pl. XXIV, fig. 6). This intraspecific variation of the length of the histial dolon is comparable to that described in *Severella kuckersiana* (cf. p. 15).

OCCURRENCE.—The species has been found in the upper Viruan Jõhvi (D_I) and Keila (D_{II}) Stages. For occurrence in Estonia, see SARV (1959, p. 137). *Sweden:* Öland, in a boulder of the *Macrourus* calcareous siltstone (Pl. I, figs. 8–9). *North German* erratic boulder No. 670.

Genus *Severella* SCHALLREUTER, 1964

Pl. I, figs. 1–5; Text-fig. 3

TYPE SPECIES.—*Strepula elliptica* STEUSLOFF, 1894.

DIAGNOSIS.—Valves almost amplete, without a distinctly inflated ventral part of the postadductorial area. Unisulcate; S2 curved, but without a distinct sigmoidal shape. Adult tecnomorphs with a faint velar bend and with a faintly concave subvelar canaliculus. Heteromorphs biantral, with broad histial and velar dolonal flanges; the histial flange joins the velar flange anteriorly. The velar flange extends considerably in anterodorsal direction beyond the histial flange, curves abruptly towards the free margin at about the mid-height of the valve, and joins the marginal ridge.

SPECIES.—*Strepula elliptica* STEUSLOFF, 1894
Ctenobolbina kuckersiana BONNEMA, 1909
Carinobolbina severa SARV, 1959

It is unfortunate that SCHALLREUTER (1964*a*) designated as the type species of this genus the poorly known species *Strepula elliptica* STEUSLOFF from an erratic boulder of Northern Germany. He suggested that this species should be a senior subjective synonym of *Carinobolbina severa* SARV, but overlooked the fact that, according to the Article 23*b* of the new International Code of Zoological Nomenclature (1961), a name that has remained unused as a senior

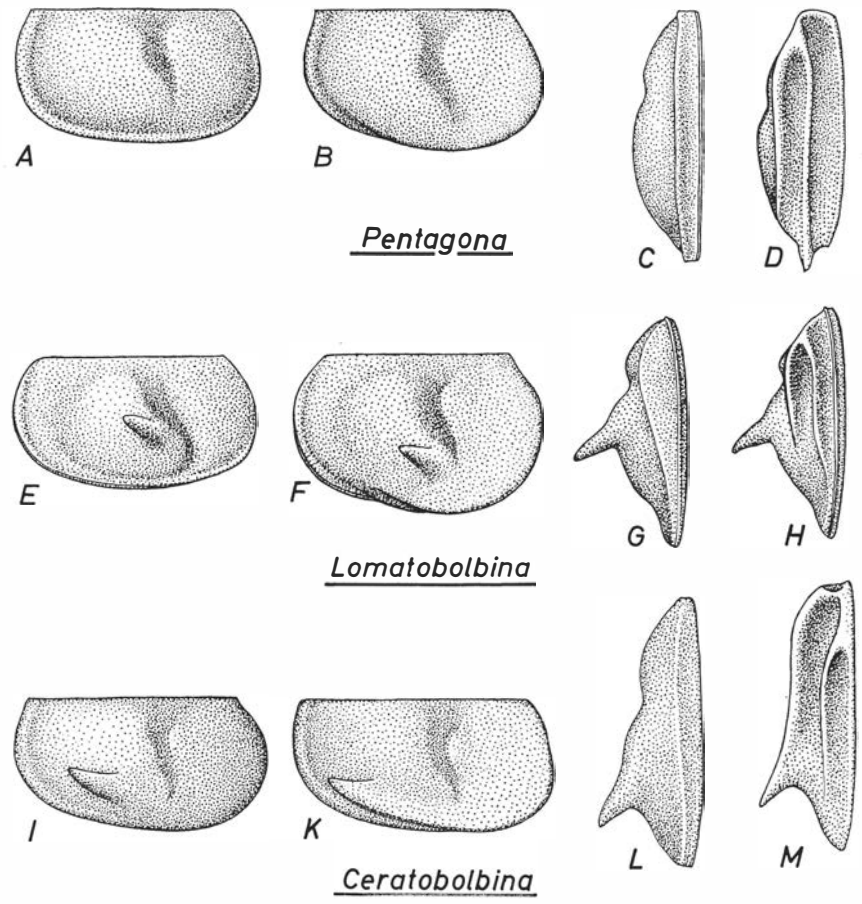
synonym in the primary zoological literature for more than fifty years is to be considered a forgotten name. Since its inception, the name *Strepula elliptica* has only been used in papers of a bibliographic character, and even if it is proved to be synonymous with SARV's *Carinobolbina severa*, the latter name would still be valid. However, the synonymy of these two species has not been proved beyond doubt. The specimen (holotype by monotypy) figured by STEUSLOFF (1894, Pl. 58, fig. 21) is a right heteromorphic valve which is evidently considerably weathered. The poor state of preservation of this specimen led KUMMEROW (1924, p. 407) to consider it to be an unidentifiable internal mould. Nevertheless, the generic characters are visible, and there is little doubt that it is congeneric with SARV's *C. severa*. However, the specific characters are poorly visible. The specimen is considerably smaller (length of the valve 1.78 mm according to Dr. R. SCHALLREUTER, personal communication) than any heteromorph of *Severella severa* examined by the present writer but it is similar in size to *Severella kuckersiana*. S2 seems to be relatively longer than in *S. severa*. As in *S. kuckersiana* the histial flange terminates at about the mid-length of the postadductorial area. Without additional material it is impossible to confirm if *S. elliptica* is conspecific with *S. kuckersiana*, whether it represents an aberrant specimen of *S. severa*, or belongs to a third species. The holotype has been found in an erratic boulder derived from the bedrock of an unknown area, and thus there is no type locality. For all practical purposes the name *S. elliptica* ought to be restricted to the holotype.

DISCUSSION.—The species referred to *Severella* have previously been included in *Carinobolbina* (HENNINGSMOEN 1953; SARV 1959). They are now excluded from the latter genus because of their unisulcate condition (*Carinobolbina* as typified by the type species is bi- to trisulcate) and because of differences in the development of the dimorphic structures. In *Carinobolbina* the velar and histial dolons have the same length, and the anterodorsal end of the velar dolon does not curve abruptly towards the free margin of the valve.

In the tecnomorphic valves of *Severella* the velar structure varies from a faint bend to a broadly rounded ridge which lies more or less parallel to the ventral free margin. The lateral surface of the velar structure merges into that of the domicilium without any boundary. In ventral view the velar structure is separated from the marginal ridge by a faintly concave canaliculus. These valves closely resemble tecnomorphs of some species of *Euprimites*.

The heteromorphic valves are provided with histial as well as velar dolonal flanges. As noted by BONNEMA (1909, p. 47) the length of the histial dolon varies. An extreme case is represented by a valve of *S. kuckersiana* (Pl. I, figs. 6–7) in which the histial dolon is developed as a short flap at about the mid-length of the valve.

OCCURRENCE.—*Severella* is known in situ from Estonia and Sweden (Gotska Sandö boring). It has been found in beds of Viruan age (Uhaku Stage to Jõhvi Stage).



Text-fig. 4. Drawings illustrating the characters of three genera which exhibit biantral dimorphism. Based on *Pentagona pentagona* (JAANUSSON), *Lomatobolbina mammillata* (THORSLUND), and *Ceratobolbina monoceratina* (JAANUSSON). *A, E, I* and *C, G, L:* lateral and ventral view of right tecnomorphic valves. *B, F, K* and *D, H, M:* lateral and ventral view of right heteromorphic valves. Not to scale.

Genus *Pentagona* SCHALLREUTER, 1964

Pl. III, figs. 1–4; Text-fig. 4 A–D

TYPE SPECIES.—*Sigmobolbina pentagona* JAANUSSON, 1957.

DIAGNOSIS.—Unisulcate, S2 long (tr.), broadest dorsally, tapering ventrally, sigmoidal. Tecnomorphs with a velar ridge roughly parallel to the ventral free margin and without histial structures; subvelar area flattened or faintly concave; ventral part of the preadductorial area inflated. Heteromorphs biantral, with histial as well as velar dolonal flanges; the velar and histial dolons join anteriorly, and the infravelar antrum continues anteriorly beyond the supravelar antrum; anteriorly the velar dolonal flange joins the marginal ridge. Loculi absent.

SPECIES.—*Sigmobolbina pentagona* JAANUSSON, 1957
Sigmobolbina prominesca SARV, 1959
Sigmobolbina prominesca var. *joehviensis* SARV, 1959

DISCUSSION.—The heteromorphic subhistial structures of *Pentagona* closely resemble those of *Lomatobolbina mammillata*. The main difference between these genera is in the development of tecnomorphic adventral structures: in *Pentagona* the velar ridge is roughly parallel to the ventral free margin, whereas in *Lomatobolbina* the adventral ridge runs in a broad arch. The taxonomic value of the presence or absence of a postadductorial spine is uncertain. The heteromorphic structures in *Severella* are constructed like those of *Pentagona*, but *Severella* differs clearly in the shape of the valves, the lack of a postadductorial inflation, the shape of the sulcus, and by a higher position of the histial dolon upon the valve.

Tecnomorphs of *Pentagona prominesca* and *P. joehviensis* have so far not been found. In all essential features the heteromorphs resemble *P. pentagona*.

OCCURRENCE.—Species of *Pentagona* have been found in Estonia and Sweden and range from the Kukruse Stage to the Keila Stage.

Genus *Ceratobolbina* n.gen.

Text-fig. 4 I–M

TYPE SPECIES.—*Sigmobolbina monoceratina* JAANUSSON, 1959.

DIAGNOSIS.—Unisulcate, S2 long (tr.), broadest dorsally, tapering ventrally, sigmoidal. Tecnomorphs with a velar ridge which is faint in most species and roughly parallel to the ventral free margin or running in a very low arch; ventral part of the postadductorial area inflated and with a prominent spine behind the ventral end of S2. Heteromorphs biantral; the supravelar antrum continues anteriorly beyond the infravelar antrum, curves towards the free margin, and is provided with a loculus in front of the main antrum; the histial flange joins the postadductorial spine posteriorly.

SPECIES.—*Entomis obliqua* KRAUSE, 1892
Sigmobolbina monoceratina JAANUSSON, 1957
Sigmobolbina monoceratina allikuensis SARV, 1959

DISCUSSION.—The above diagnosis is based on numerous specimens of *Ceratobolbina monoceratina* and *C. allikuensis*, but none of the specimens are well preserved or sufficiently clean to provide good photographs. In this genus the construction of the subhistial dimorphic structures is somewhat unusual. Posteriorly these structures are developed in a normal biantral fashion, i.e. one antrum is situated between the velar flange and the marginal ridge (infravelar antrum), and the other antrum between the velar and histial flanges (supravelar antrum). Anteriorly the supravelar antrum continues beyond the infravelar antrum, curves towards the free margin, and the foremost part is separated by a partition from the main antrum forming a loculus on either valve. The subvelar

area retains its tecnomorphic shape below (peripheral to) the anterior part of the main antrum. Thus anteriorly the heteromorphs of *Ceratobolbina* are like *Sigmobolbina* but posteriorly they are biantral like *Pentagona* or *Lomatobolbina.*

The peculiar development of antra readily distinguishes *Ceratobolbina* from all other tetradellids. The tecnomorphs closely resemble those of *Lomatobolbina,* but differ in that the tecnomorphic velar ridge is almost parallel to the ventral free margin.

OCCURRENCE.—Representatives of the genus *Ceratobolbina* have been found in situ from Estonia and Sweden. They range from the Uhaku Stage to beds corresponding to the Keila Stage.

Genus *Sigmobolbina* HENNINGSMOEN, 1953

TYPE SPECIES.—*Entomis oblonga* var. *kuckersiana* BONNEMA, 1909 [=*Entomis variolaris* BONNEMA, 1909, according to SARV 1959].

DIAGNOSIS.—Unisulcate, S2 long (*tr.*), broadest dorsally, tapering ventrally, sigmoidal. Tecnomorphs with a velar ridge roughly parallel to the ventral free margin; a histial structure absent except of a faint keel-like bend in some species; subvelar area flattened, without a canaliculus; ventral part of the postadductorial area inflated. Heteromorphs with a broad, flange-like histial dolon, a deep antrum between the histial flange and the velar ridge, and a loculus in front of the main antrum. The velar ridge retains its tecnomorphic shape in heteromorphs or becomes only slightly wider; the subvelar area is not affected by the dimorphic change.

SPECIES.—*Entomis variolaris* BONNEMA, 1909
Dilobella longocarinata NECKAJA, 1953
Ordovicia porchowiensis NECKAJA, 1958
Sigmobolbina cyclopa SCHALLREUTER, 1964
Sigmobolbina camarota n.sp.
Sigmobolbina tuberculata n.sp.
Sigmobolbina tropeota n.sp.

The generic reference of *Sigmobolbina sigmoidea* JAANUSSON, 1957 is uncertain because the writer has failed to develop the subhistial heteromorphic structures in any of the available specimens. Examination of the holotype of *Entomis sigma* KRAUSE, 1889 (KRAUSE 1889, Pl. I, fig. 12; right, probably tecnomorphic valve) has shown that it does not belong to *Sigmobolbina.* Its correct generic reference is not possible without a detailed knowledge of the adventral heteromorphic structures. An examination of the holotype of *Sigmobolbina unica* SARV, 1959, suggests that this species is related to *Aulacopsis* if not a member of this genus. The heteromorphs of *Ordovicia porchowiensis* have a supravelar antrum with a loculus (SARV, personal communication) and thus this species cannot possibly be congeneric with *Henningsmoenia gunnari* (THORSLUND) as SCHALLREUTER (1964*b*, p. 92) suggested.

DISCUSSION.—Tecnomorphs of some species of *Sigmobolbina* possess a faint, keel-like bend above the velar ridge. The area between this bend and the velar structure is somewhat concave and lacks ornamentation. The keel-like bend is probably an incipient histial structure, since its level roughly corresponds to that of the histial dolon. *Sigmobolbina tropeota* n.sp. is provided with an additional keel-like structure above the possible histial bend, and a somewhat similar keel is well developed on the postadductorial area of both dimorphs of *S. porchowiensis*. In the latter species this keel can be proved to lie above the histial structure because, in heteromorphs, it occurs above the histial flange.

Tecnomorphs of *Sigmobolbina* and *Pentagona* are indistinguishable as are their heteromorphs in lateral view. These genera seem to differ only in the subhistial heteromorphic structures, *Sigmobolbina* having a supravelar antrum and a loculus in front of the main antrum and *Pentagona* being biantral and without loculi. The type species of *Perspicillum*, *P. perspicillum*, differs from *Sigmobolbina* by the presence of two loculi and by the weak development of the histial flange in heteromorphs. Tecnomorphs of this species have not been figured but are, according to SCHALLREUTER's (1964*a*) description, probably similar to those of *Sigmobolbina*.

OCCURRENCE.—Undoubted representatives of *Sigmobolbina* have been found *in situ* only in the East Baltic states and Scandinavia. The earliest specimens are from the Uhaku Stage and the latest are from beds corresponding to the uppermost Viruan Oandu Stage (D_{III}).

Sigmobolbina camarota n.sp.

Pl. III, figs. 5–8; Text-fig. 5

1953*b* *Bolbina variolaris* (BONNEMA, 1909) — HENNINGSMOEN, p. 49, Pl. I, fig. 13.
1963 *Sigmobolbina* n.sp. — SKOGLUND, pp. 9, 12.

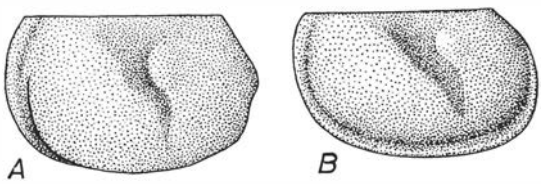
HOLOTYPE.—Left heteromorphic valve, OM No. 73666, Pl. III, fig. 5.

TYPE STRATUM AND LOCALITY.—Upper *Chasmops* Limestone (4 bδ). Oslo-Asker, Terneholmen.

DERIVATION OF THE NAME.—From Greek καμαρωτός, inflated.

DIAGNOSIS.—Carapace large for the genus (length of the heteromorphs 1.3–1.5 mm). Tecnomorphs without a distinct supravelar keel on the ventral surface of the valve. In heteromorphs the lateral surface of the histial flange merges without a distinct boundary into the lateral surface of the valve and follows the curvature of the latter. Postadductorial area strongly inflated, its ventral part in heteromorphs situated conspicuously above the level of the histial flange. Surface of the valves smooth or covered with scattered, low, rounded tubercles.

DESCRIPTION.—Tecnomorphs with a faintly convex preadductorial area, the anterior part of which slopes evenly towards the velar flange. Ventral part of the postadductorial area strongly convex, its ventral side sloping almost per-



Text-fig. 5. *Sigmobolbina camarota* n.sp. Diagrammatic drawings illustrating two left valves in lateral view. *A*, heteromorphic valve; *B*, tecnomorphic valve. × 22.

pendicular to the velar flange, somewhat concave peripherally, and overhanging the inner part of the velum. Highest point of the valve in ventral view at about the mid-length of the postadductorial area. In posterior view the highest point is fairly close to the ventral margin of the area.

Dimorphic structures in heteromorphs as characteristic for the genus. The posterior wall of the loculus is situated somewhat dorsal to the level of the ventral end of S2. The shape of the subvelar field is roughly the same as in tecnomorphs. Posteriorly the dolon is situated conspicuously below the main surface of the postadductorial area and its dorsal boundary is defined by a faint bend. In heteromorphs the preadductorial area of the lateral surface of the valve is moderately convex and rises above the level of the histial flange; the lateral surface of the histial flange merges into that of the preadductorial area without any distinct boundary.

The surface of the valve appears to be smooth in some specimens, but is usually ornamented with low, rounded, scattered, fairly large tubercles.

DIMENSIONS.—Heteromorph OM No. 73666 (holotype) length 1.44 mm, height 0.91 mm; tecnomorph OM No. 73667 (Pl. III, fig. 6) length 1.19 mm, height 0.69 mm; tecnomorph OM No. 73668 (Pl. III, fig. 7) length 0.94 mm, height 0.58 mm. Some incomplete heteromorphic valves have the restored length between 1.3 and 1.4 mm.

DISCUSSION.—The tecnomorphs of *S. camarota* differ from those of the contemporaneous species by the lack of a distinct keel on the ventral side of the postadductorial area and by ornamentation. The heteromorphs of *S. camarota* resemble those of *S. tropeota*, and poorly preserved specimens are difficult to distinguish. The preadductorial area of *S. camarota* is somewhat more convex than in *S. tropeota* in which the lateral surface of the histial flange lies at about the level of the preadductorial area. The ornamentation is different. *Sigmobolbina* ? *sigmoidea* is a much smaller species, and the postadductorial area in heteromorphs is flatter; moreover, the preadductorial node is smaller and consequently, the anterior margin of S2 is much straighter than in *S. camarota*. *Sigmobolbina cyclopa* SCHALLREUTER is smaller and clearly differs by having a considerably shallower and straighter S2 and a much less convex postadductorial area. In *S. cyclopa* the lateral surface of the conspicuously convex histial flange merges without any boundary into that of the valve and is situated only slightly below the general level of the postadductorial area.

OCCURRENCE.—*Oslo-Asker*, Terneholmen; Upper *Chasmops* Limestone (4 bδ). *Västergötland*, Kinnekulle, Mossen section; uppermost beds of the Mossen Formation (*Sigmobolbina* n.sp. in SKOGLUND 1963, p. 12). *Siljan district* (Dalarna), Fjäcka section; *Macrourus* Limestone (15–55 cm below the upper boundary). *Östergötland*, Smedsby Gård boring; *Macrourus* Limestone, at the levels of 74.25, 75.78, and 75.84 m.

Sigmobolbina tropeota n.sp.

Pl. III, figs. 9–11

HOLOTYPE.—Right heteromorphic valve, UM No. D 1168, Pl. III, fig. 11.

TYPE STRATUM AND LOCALITY.—Siljan district, Fjäcka section, locality No. 9. *Macrourus* Limestone, 2.20 m below the upper boundary.

DERIVATION OF THE NAME.—From Greek τρόπις, keel of a ship, alluding to the distinct keel on tecnomorphs.

DIAGNOSIS.—Carapace fairly large for the genus (length of heteromorphs 1.3 to 1.4 mm). Lateral surface of tecnomorphs bordered ventrally by a distinct keel which describes a broad arch the summit of which is considerably higher in ventral view than the level of the ventral end of S2. Lateral surface of the histial flange merges into that of the valve without a distinct boundary and is situated anteriorly at about the level of the preadductorial area. Surface of the valves covered with a distinct, dense tuberculation.

DESCRIPTION.—Tecnomorphs elongate. Lateral surface of the valve defined ventrally by a distinct keel which begins anteriorly and ends posteriorly at about the longitudinal level of the beginning of the transversely directed portion of S2. In ventral view the keel describes a broad arch the summit of which is at about the mid-length of the postadductorial area. An additional faint keel is developed on the ventral side of the valve between the distinct keel and the velar flange; the distance of this keel from the velar flange is about equal to or slightly less than the width of the flange; the keel is roughly parallel to the velar flange and is situated conspicuously below the level of the ventral end of S2. The surface of the valve between the keels is flattened and slopes almost perpendicular to the surface of the velar flange; its ornamentation is similar to that of the lateral surface of the valve. The surface of the valve between the ventral keel and the velar flange is slightly concave and without a distinct ornamentation.

Heteromorphs with a broad histial flange, the lateral surface of which merges into that of the valve without any distinct boundary. Anteroventrally the lateral surface of the flange is situated at the general level of the flattened pradductorial area; posteroventrally the lateral surface of the flange follows the curvature of the postadductorial area and forms the ventral margin of the downward slope of the moderately convex postadductorial area. Development of the dimorphic structures as characteristic for *Sigmobolbina*. The posterior wall of the loculus is situated considerably higher dorsally than the ventral end of S2.

Surface of the valves ornamented with a distinct, dense tuberculation.

DIMENSIONS.—Heteromorph UM No. D 1168 (holotype) length 1.31 mm, height 0.78 mm; heteromorph UM No. D 1170 (Fjäcka, loc. 9, 34–45 cm below the upper boundary of the *Macrourus* Limestone) length 1.39 mm, height 0.80 mm; tecnomorph UM No. D 1169 (Pl. III, figs. 9–10) length 1.35 mm, height 0.74 mm.

DISCUSSION.—*Sigmobolbina tropeota* differs from all known species of *Sigmobolbina* by the presence of a distinct keel high upon the ventral surface of the tecnomorphic valve.

OCCURRENCE.—*Siljan district*, Fjäcka, locality No. 9. *Macrourus* Limestone, 0.35–2.25 m from the upper boundary.

Sigmobolbina tuberculata n.sp.

Pl. III, figs. 12–31

HOLOTYPE.—Left heteromorphic valve, UM No. D 1171, Pl. III, figs. 13.

TYPE STRATUM AND LOCALITY.—Macrourus Limestone, 5.20 m below the upper boundary. Siljan district, Fjäcka section, locality No. 9.

DIAGNOSIS.—Carapace of medium size for the genus (length of the heteromorphs 1.05–1.25 mm), elongate. Lateral surface of the valve in tecnomorphs bordered ventrally by a faint keel which is roughly parallel to the velar flange. The histial flange in heteromorphs separated by a furrow from the lateral surface of the valve. Lateral surface of the valve ornamented with closely-spaced coarse tubercles.

DESCRIPTION.—Tecnomorphs with a strongly convex ventral portion of the postadductorial area the surface of which slopes evenly towards the velar flange until it reaches the level of the dorsal end of S2. At this level the lateral surface is bordered by a faint keel which is roughly parallel to the velar flange. The part of the surface of the valve between the keel and the lateral surface of the velar flange is faintly concave, slopes almost perpendicular to the lateral surface of the velar flange, and lacks tubercles.

Heteromorphs with a moderately wide histial flange which is separated from the lateral surface of the valve by a furrow. The furrow is faint anteriorly and well defined posterior to the sulcus. Subhistial area of the general *Sigmobolbina* type. Posterior wall of the loculus begins at about the longitudinal level of the posterior end of S2 or only slightly dorsally from that level.

The ornamentation consists of coarse, densely spaced, rounded tubercles which occur all over the lateral surface of the valve and on the lateral surface of the histial flange. The tubercles are coarser than in any other known species of *Sigmobolbina*.

DIMENSIONS.—See Table 1.

DISCUSSION.—*Sigmobolbina tuberculata* resembles *S. variolaris*, but has a larger adult carapace, a much coarser ornamentation, and a more ventral posi-

Table 1. Dimensions (in mm) of *Sigmobolbina tuberculata* n.sp.

All specimens are from the *Macrourus* Limestone of Fjäcka, locality No. 9. The horizon gives the distance from the upper boundary of the *Macrourus* Limestone. In heteromorphs the height of the valve is given as being the distance between the dorsal valve margin and the ventral margin of the histial dolon. In tecnomorphs the height is defined as the distance between the dorsal valve margin and the ventral margin of the velar ridge. These same definitions of the height of the valve have been used when treating other species of *Sigmobolbina*.

No.	Length	Height	Horizon	Remarks
UM D 1171	1.23	0.66	5.20 m	Holotype, hetero m
UM D 1172	1.13	0.66	2.1–2.2 m	Tecnom.
UM D 1173	1.07	0.59	3.5–3.6 m	Tecnom.
Pal. Inst. Lund	1.12	0.62	5.15–5.25 m	Heterom.
Pal. Inst. Lund	1.06	0.66	2.70–2.80 m	Heterom.

tion of the posterior wall of the loculus. The lateral surface of the histial flange is covered with tubercles and not by fine striae as in *S. variolaris*.

OCCURRENCE.—*Siljan district*, Fjäcka, locality No. 9. *Macrourus* limestone, 2.1–5.3 m from the upper boundary.

Genus *Pelecybolbina* n.gen.

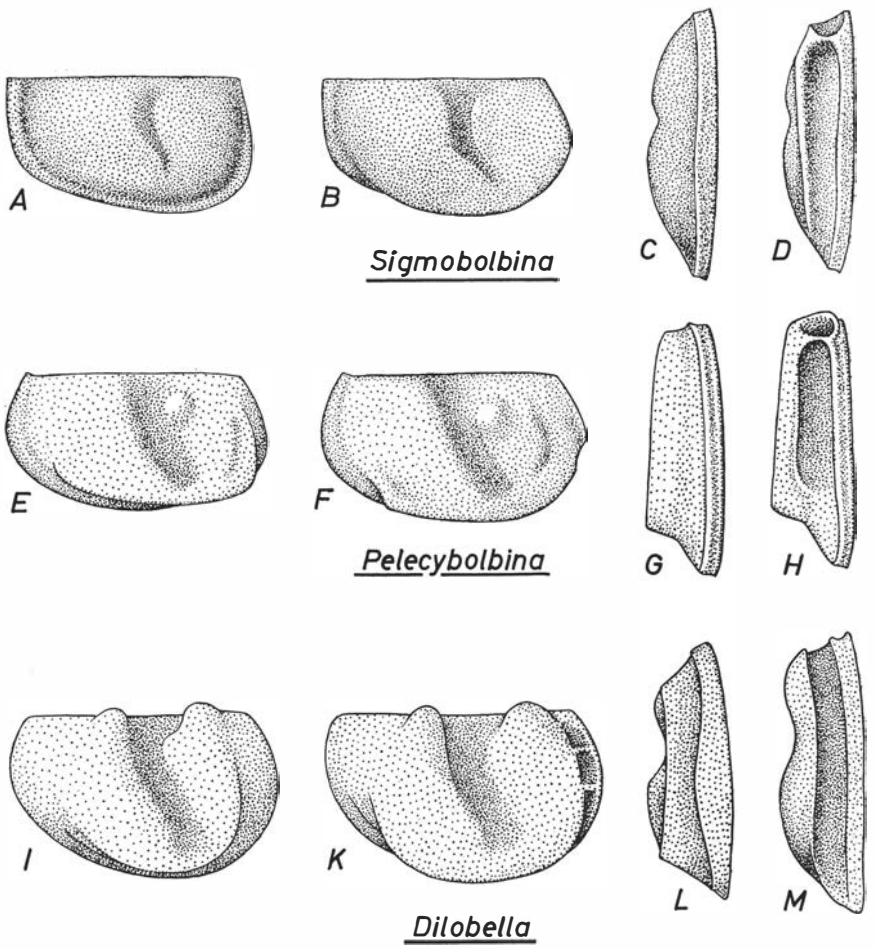
TYPE SPECIES.—*Pelecybolbina pelecyoides* n.sp.

DERIVATION OF THE NAME.—From Greek πέλεκνς, ax + *bolbina*, alluding to the shape of the carapace.

DIAGNOSIS.—Unisulcate; S2 long, sigmoidal, of uniform width throughout its whole length or slightly expanding ventrally. Adult tecnomorphs with a thick histial flange which borders the lateral surface of the valve anteriorly and ventrally, and terminates abruptly posteriorly. Velar ridge narrow, and roughly parallel to the ventral free margin. Heteromorphs and tecnomorphs distinguished with difficulty in lateral view, but in ventral view the differences are distinct. In heteromorphs the area between the histial and velar structures is conspicuously concave and forms a main supravelar antrum with a large loculus in front of it; velar ridge and subvelar field the same in heteromorphs and tecnomorphs.

SPECIES.—In addition to the type species, *Dilobella illativis* NECKAJA, 1952 and *Dilobella illativis* var. *bisulcata* NECKAJA, 1952 may also belong to this genus. However, the published information concerning these species is so brief that it is impossible to decide to which genus they belong.

DISCUSSION.—The general characters of *Pelecybolbina* are similar to those of *Dilobella*. In the latter genus, S2 is of a uniform width throughout its whole length, tecnomorphs possess a histial ridge, and heteromorphs have a supravelar antrum which is similar in appearance to that of *Pelecybolbina*. These two genera are probably closely related, *Pelecybolbina* representing the North European



Text-fig. 6. Drawings illustrating the characters of three genera in which only a supravelar antrum is developed. Based on *Sigmobolbina variolaris* (BONNEMA), *Pelecybolbina pelecyoides* n.sp., and *Dilobella typa* ULRICH. *A, E, J* and *C, G, L:* Lateral and ventral view of right tecnomorphic valves, *B, F, K* and *D, H, M:* lateral and ventral view of right heteromorphic valves. Not to scale.

counterpart of the North American *Dilobella*. *Pelecybolbina* differs from *Dilobella* in (1) the abrupt posterior termination of the histial flange in both dimorphs. (2) a sigmoidal curvature of S2 (in *Dilobella* S2 shows a simple curvature), (3) the development of the velar ridge roughly parallel to the ventral free margin (in *Dilobella* the tecnomorphic velar ridge runs ventrally in a broad arch as in *Sigmoopsis*), and (4) the presence of only one loculus (*Dilobella* has two in both species for which the heteromorphs are known).

Sigmobolbina has a similar dimorphism with a main supravelar antrum and a loculus in front of it, but it differs distinctly in the absence of a histial flange

in tecnomorphs, ventrally tapering S2, and the absence of an abrupt posterior termination of the histial dolon.

OCCURRENCE.—Uppermost Viruan (Middle Ordovician) of Estonia and Sweden. The species described by NECKAJA (1952), which possibly belong to this genus, are from Lithuania and, according to NECKAJA, from the lowermost Harjuan Rakvere Stage.

Pelecybolbina pelecyoides n.sp.

Pl. III, figs. 14–18; Text-fig. 6 E–H

HOLOTYPE.—Left heteromorphic valve, UM No. D 1164, Pl. III, figs. 16–18.

TYPE STRATUM AND LOCALITY.—*Macrourus* Limestone, 1.15–1.25 m from the upper boundary. Siljan district, Fjäcka, locality No. 9.

DIAGNOSIS.—A species of *Pelecybolbina* with a fairly large preadductorial node, well defined anteriorly by a distinct furrow. No dorsal plica.

DESCRIPTION.—Lateral surface of the valve faintly to moderately convex. S2 wide, fairly deep, of about uniform width along its whole length or slightly expanding ventrally. Preadductorial node rounded to somewhat ovate, well defined anteriorly by a crescent-shaped furrow. The lateral surface of the valve is bordered anteriorly and ventrally by a thick histial flange the posterior end of which is fairly abrupt. The posterior half of the postadductorial portion of the flange is curved laterally and in ventral view its posterior termination forms the highest point of the valve. The anterior half of the postadductorial portion of the flange and a narrow portion of the flange just in front of the sulcus merge into the surface of the valve without any distinct boundary. Farther forwards the boundary between the lateral surface of the histial flange and that of the preadductorial area is defined by a distinct crescentic furrow the dorsal end of which reaches almost to the longitudinal level of the dorsal end of the preadductorial node.

In technomorphs the histial flange seems to be somewhat narrower than in heteromorphs. However, the difference is small and, when only the lateral surface of the valves is visible, it is difficult to distinguish between tecnomorphs and heteromorphs. The subhistial field is high (Pl. III, fig. 14) and flattened. The narrow velar ridge is situated close to the free margin and is roughly parallel to it ventrally.

In heteromorphs the main part of the subhistial area is developed as a concave, channel-like antrum whereas the lateral third of the area retains its tecnomorphic appearance. The lateral boundary of the antrum is formed by a distinct keel which is roughly parallel to the velar ridge and diverges from the margin of the histial flange in a posterior direction (Pl. III, fig. 16). No such keel is developed upon the subhistial field of the tecnomorphs (Pl. III, fig. 14). The loculus is large, rounded, and separated from the main antrum by a thin partition (Pl. III, fig. 17). In heteromorphs the development of the velar ridge and the subvelar area is the same as in tecnomorphs except that below the loculus, where the

velar ridge is slightly arched towards the free margin, the subvelar area is narrower.

In many specimens the surface of the valve appears to be smooth, but some have low, rounded, scattered tubercles of a medium size.

DIMENSIONS.—Heteromorph UM No. D 1164 (holotype) length 1.27 mm, height 0.69 mm; heteromorph UM No. D 1165 (Fjäcka, *Macrourus* Limestone, 2.10–2.20 m from the upper boundary) length 1.34 mm, height 0.76 mm; tecnomorph UM No. 1166 (Pl. III, figs. 14–15) length 1.34 mm, height 0.69 mm; tecnomorph UM No. D 1167 (Fjäcka, *Macrourus* Limestone, 2.45–2.55 m from the upper boundary) length 1.10 mm, height 0.66 mm.

DISCUSSION.—*Pelecybolbina pelecyoides* differs from *P. ? illativis* NECKAJA in a number of characters (SARV, personal communication). A close comparison between *P. pelecyoides* and *P. ? bisulcata* NECKAJA is not possible until the characters of the latter species are adequately described. However, the figure of *P. ? bisulcata* given by NECKAJA (1952, Pl. I, fig. 2) shows that this species cannot possibly be conspecific with *P. pelecyoides*.

OCCURRENCE.—*Siljan district*, Fjäcka, locality No. 9; *Macrourus* Limestone, 1.15–4.75 m from the upper boundary. *Gotska Sandön boring*; at the levels of 125.90 and 126.70 m. *Estonia*, Oandu; Oandu Stage (D_{III}).

Genus *Dilobella* ULRICH, 1897

Pl. II, figs. 11–15; Text-fig. 6 I–M

TYPE SPECIES.—*Dilobella typa* ULRICH, 1897.

DIAGNOSIS.—Unisulcate, S2 long, of about uniform width, curved but not sigmoidal. Adult tecnomorphs with a histial ridge formed by the thickened ventral and anteroventral edge of the lateral surface of the valve, and with a narrow velar ridge which runs ventrally in a broad arch, the subvelar area being widest at about the mid-length of the valve. Heteromorphs with a thick, broad histial flange the lateral surface of which merges into that of the valve without any boundary; antrum supravelar, deep, provided anterodorsally with two loculi, the most dorsal loculus being situated close to the anterior cardinal corner; subvelar area narrower than in tecnomorphs along the middle part of the ventral margin, but otherwise of tecnomorphic appearance. In either dimorph the histial structure merges posteriorly into the general surface of the valve without an abrupt termination.

SPECIES.—*Dilobella typa* ULRICH, 1897
Ctenobolbina fulcrata ULRICH, 1897

KAY (1940, p. 256) pointed out that the specimens figured as *Dilobella typa* by ULRICH (1897, Pl. 46, figs. 30–34) are poorly preserved specimens of *Ctenobolbina crassa* ULRICH described in the same paper. The latter specimens are tecnomorphs and are, according to KAY, conspecific with ULRICH's (1897) *Ctenobolbina fulcrata* which is based on heteromorphs. The writer agrees with

KAY that the left valve (right valve according to the orientation used by ULRICH) figured by ULRICH (1897, Pl. XLIV, figs. 10–11) as *Ctenobolbina fulcrata* is a heteromorph of *Dilobella typa*. However, the right valve of *Ctenobolbina fulcrata* figured by ULRICH (1897, Pl. XLIV, figs. 8–9) quite evidently belongs to a different species of *Dilobella*, and several specimens of this have been found in the material collected by the writer. Dr. JEAN BERDAN has informed the present writer (*in litt.*) that the catalogue number of the lectotype of *Ctenobolbina fulcrata* (41322 US.) given by KAY (1940, p. 257) refers to the syntype lot and not to a particular specimen. Thus no formal designation of the lectotype of this species has been made. The specimen figured by ULRICH (1897, Pl. XLIV, figs. 8–9) is here selected as the lectotype of *Ctenobolbina fulcrata*. There seems little doubt that the lectotype is that which has since been identified among the syntypes as the specimen which now bears the catalogue number 142847 of U.S. National Museum collections. Under these conditions, *Dilobella fulcrata* is not conspecific with *D. typa*.

Dilobella simplex KAY, 1940 is probably based on a juvenile tecnomorphic carapace of a species of *Dilobella*.

DISCUSSION.—In the material examined by the present writer the number of loculi of *Dilobella* is invariably two.

The adventral structures of the tecnomorphs of *Dilobella* recall, to some extent, those of *Sigmoopsis*. In both genera the tecnomorphic histial structure is formed by the thickened ventral and anteroventral edge of the lateral surface of the valve, and the velar ridge runs ventrally in a broad arch. The heteromorphs of *Dilobella* however, resemble those of *Sigmobolbina* and *Pelecybolbina*. The differences between *Dilobella* and *Pelecybolbina* are given in the discussion of the latter genus.

OCCURRENCE.—As far as known to the present writer, *Dilobella* has been found only in the middle and upper part of the Decorah Formation and beds of corresponding age. It has been reported from Minnesota, Wisconsin, and Iowa.

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Explanation of plates

Plate I

Severella severa (SARV, 1959)

The figured specimens come from Estonia, Aluvere, Jõhvi Stage (D_I) and were collected by L. SARV.

Figs. 1–2. Right tecnomorphic valve in lateral and ventral view. UM No. E 19. × 30.

Figs. 3–5. Right heteromorphic valve in lateral and ventral view. UM No. E 18. × 30.

Severella kuckersiana (BONNEMA, 1909)

Figs. 6–7. Left heteromorphic valve in ventral and lateral view. Estonia, Kukruse, Kukruse Stage ($C_{II}\alpha$). UM No. E 23. × 30.

Carinobolbina carinata (KRAUSE, 1892)

Figs. 8–9. Left tecnomorphic valve in lateral and ventral view. Öland, Eriksöre, erratic boulder of the *Macrourus* calcareous siltstone. RM No. Ar. 19817. Collected by J. G. ANDERSSON in 1892. × 30.

Figs. 10–11. Lectotype. Left heteromorphic valve in lateral and lateroventral view. Figured by KRAUSE 1892, Pl. XXI, fig. 9. North Germany, Müggelsheim, erratic boulder No. 670. Deposited in BM. × 30.

Figs. 11–12. Right tecnomorphic valve in lateral and lateroventral view. From the same erratic boulder as the lectotype. Deposited in BM. × 30.

Plate II

Carinobolbina carinata (KRAUSE, 1892)

Fig. 1. Right heteromorphic valve in ventral view. Estonia, Alliku, Jõhvi Stage (D_I), collected by L. SARV. UM No. E 22. × 30.

Sigmoopsis rostrata (KRAUSE, 1892)

Figs. 2–3. Right heteromorphic valve in ventral and anterior view. Estonia, Peetri, Jõhvi Stage (D_I), collected by V. JAANUSSON in 1964. UM No. E 30. × 30.

Figs. 4–5. Right tecnomorphic valve in lateral view and the tecnomorphic carapace in ventral view. Öland, Eriksöre, erratic boulder of the *Macrourus* calcareous siltstone. RM No. Ar. 19804. Collected by J. G. ANDERSSON in 1892. × 30.

Fig. 6. Lectotype. Right heteromorphic valve in lateral view. Figured by KRAUSE 1892, Pl. XXI fig. 2. Erratics of North Germany, KRAUSE's boulder No. 587. Deposited in BM. × 30.

Sigmoopsis granulata (SARV, 1956)

The figured specimens come from Estonia, Rakvere, Oandu Stage (D_{III}) and were collected by A. ÖPIK. Magnification × 30.

Figs. 7–8. Left tecnomorphic valve in lateral view and the tecnomorphic carapace in ventral view. UM No. E 21.

Figs. 9–10. Left heteromorphic valve in lateral view and the heteromorphic carapace in ventral view. UM No. E 20.

Dilobella typa ULRICH, 1897

The figured specimens come from the Twin City Brickyard, Minneapolis. Decorah Shale (15–16 m above the base of the formation). Collected by V. JAANUSSON in 1959. Magnification × 30.

Figs. 11–13. Left heteromorphic valve in ventral, lateral, and anterior view. UM No. NA 146.

Figs. 14–15. Tecnomorphic carapace in ventral view and its left valve in lateral view. UM No. NA 145.

Plate III

Pentagona pentagona (JAANUSSON, 1957)

The figured specimens are from boulders of the *Ludibundus* Limestone of Ringsö, Tvären and were collected by JAANUSSON in 1954. Magnification × 40.

Figs. 1–2. Left tecnomorphic valve in lateral view and the tecnomorphic carapace in ventral view. UM No. T 311.

Figs. 3–4. Left heteromorphic valve in lateral and ventral view. Peripheral parts of the histial and velar dolons are broken off. Figured by JAANUSSON 1957, Pl. XII, figs. 4–5. UM No. T 144.

Sigmobolbina camarota n.sp.

All figured specimens are from Norway, Oslo-Asker district, Terneholmen; Upper *Chasmops* Limestone (4 bδ). Magnification × 30.

Fig. 5. Holotype. Left heteromorphic valve in lateral view. OM No. 73666.

Fig. 6. Right tecnomorphic valve in lateral view. OM No. 73668.

Figs. 7–8. Left tecnomorphic valve in lateral and ventral view. OM No. 73667.

Sigmobolbina tropeota n.sp.

The figured specimens come from Siljan district, Fjäcka, locality No. 9; *Macrourus* Limestone, 2.10–2.20 m below the upper boundary. Magnification × 30.

Figs. 9–10. Right tecnomorphic valve in lateral and ventral view. UM No. D 1169.

Fig. 11. Right heteromorphic valve in lateral view. Holotype. UM No. D 1168.

Sigmobolbina tuberculata n.sp.

The figured specimens come from the *Macrourus* Limestone, Siljan district, Fjäcka, locality No. 9. Magnification × 30.

Fig. 12. Left tecnomorphic valve in lateral view. 2.10–2.20 m from the upper boundary of the *Macrourus* Limestone. UM No. D 1172.

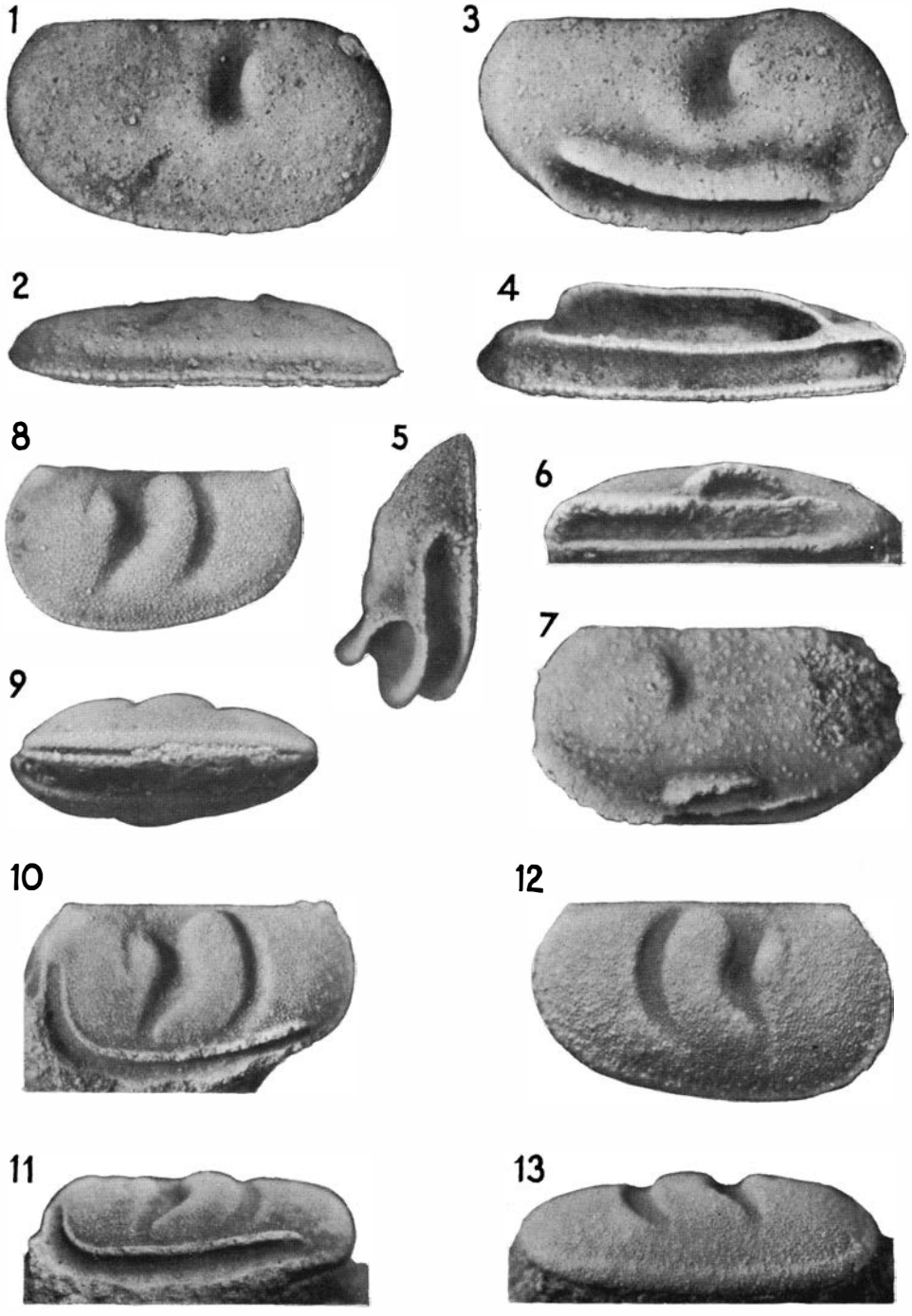
Fig. 13. Holotype. Left heteromorphic valve in lateral view. 5.20 m from the upper boundary of the *Macrourus* Limestone. UM No. D 1171.

Pelecybolbina pelecyoides n.sp.

The figured specimens come from the *Macrourus* Limestone, Siljan district, Fjäcka, locality No. 9. Magnification × 30.

Figs. 14–15. Tecnomorphic carapace in ventral view and its right valve in lateral view. 1.90–2.00 m from the upper boundary of the *Macrourus* Limestone. UM No. D 1166.

Figs. 16–18. Holotype. Left heteromorphic valve in ventral, anterior, and lateral view. 1.15–1.25 m from the upper boundary of the *Macrourus* Limestone. UM No. D 1164.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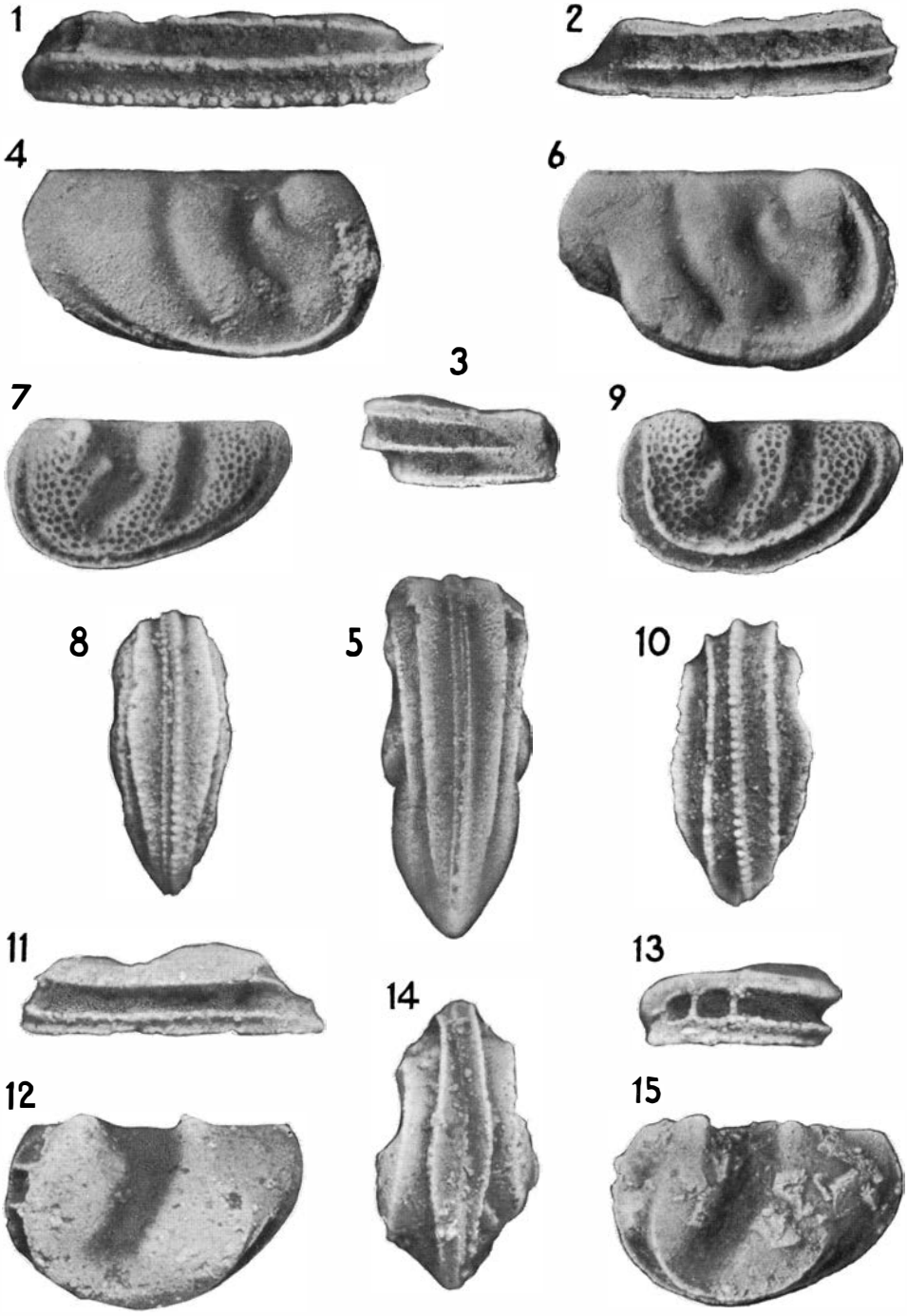
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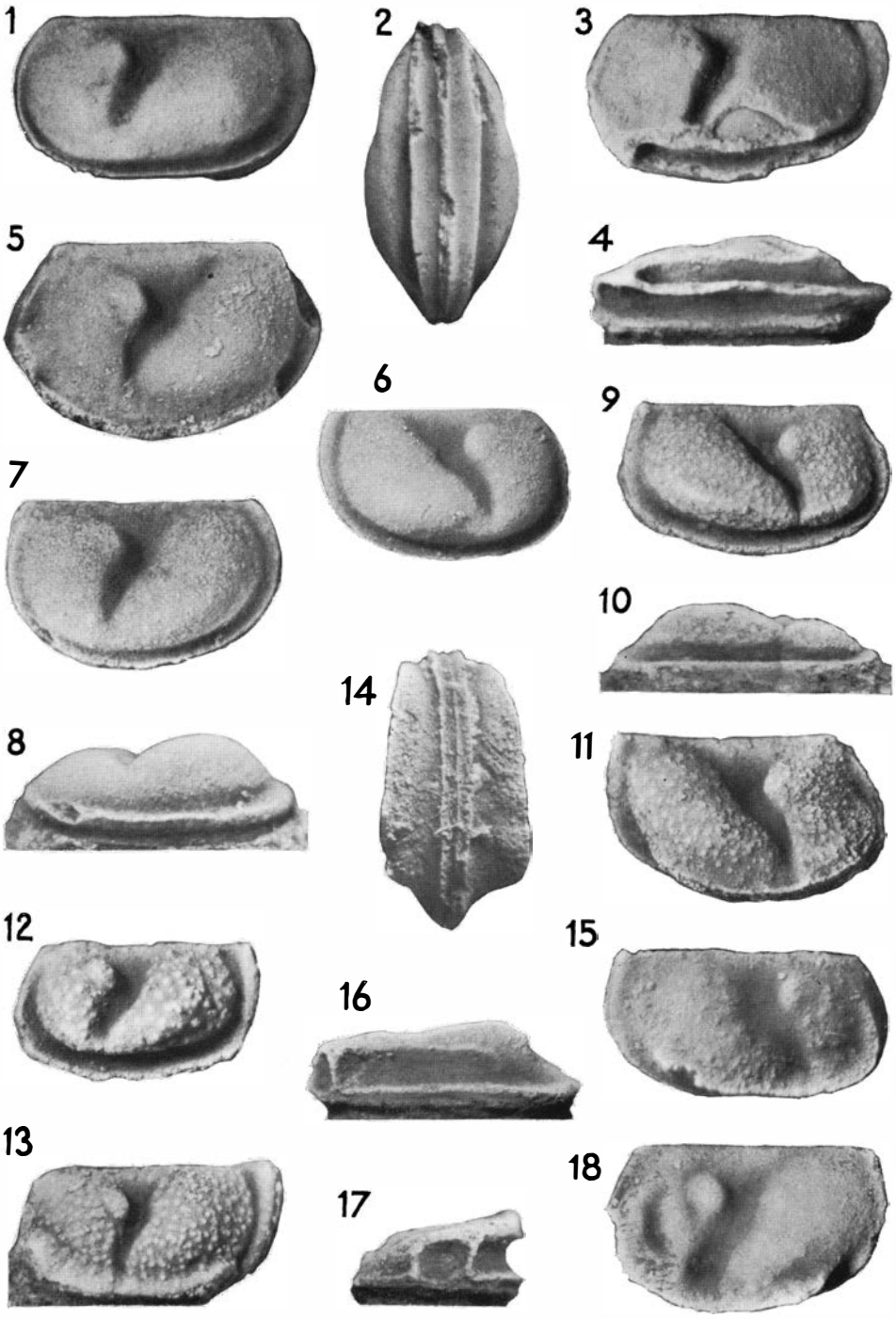
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