

CLASSIFICATION OF PALEOZOIC STRAIGHT-HINGED OSTRACODS

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A b s t r a c t. The straight-hinged Paleozoic ostracods are assigned to the new suborder Paleocopa (superfamilies Beyrichiacea and Leperditiacea) and the suborder Podocopa (family Quasillitidae). New taxonomic units are: family Sigmoopsiidae, subfamilies Sigmoopsiinae, Glossopsiinae, Beyrichiopsiinae, Conchoprimitiinae, Eridoconchinae, and the genera *Sigmoopsis*, *Sigmobolbina*, *Carinobolbina*, *Bolbina*, and *Hesslandella*. In the classification of the Beyrichiacea more attention is paid to type of dimorphism, submarginal structure (velate and carinal structures), and unusual features than to the degree of sulcation and lobation. Probable phylogenetic lines from trisulcate to unisulcate forms suggest that trisulcate forms need not be more advanced than unisulcate forms. Moults retention is described in the Conchoprimitiinae, and its bearing on the study of ontogeny and determination of orientation is discussed. The proposed classification of straight-backed Paleozoic ostracods is presented in a list (p. 266). A range chart (p. 276) shows the stratigraphical distribution of the families and subfamilies. The Healdiidae and Thlipsuridae are believed to be related to straight-hinged Podocopa (Quasillitidae). The relationships of the Paleocopa to other ostracod suborders are still uncertain.

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Suborder Paleocopa nov.

Diagnosis: — Shell without frontal opening. Hinge line straight and usually long. Apparently no calcareous inner lamella. There is a tendency to develop lobes and sulci, and submarginal ridges. Animal unknown.

Remarks: — It is regrettable that the animal is unknown, so that the diagnosis cannot be fully compared with those of recent suborders. Even in recent suborders, however, features of the shell are given considerable diagnostic importance. The new suborder Paleocopa constitutes such a large and well-defined group, that it may well be recognized even if it should prove to be close to one or another of recent suborders. The suborder Paleocopa embraces the two superfamilies Beyrichiacea and Leperditiacea.

SUPERFAMILY BEYRICHIACEA ULRICH & BASSLER, 1923.

Diagnosis: — See p. 262. *Included families:* — See list p. 266.

Terminology.

Beyrichiacean ostracods may be rather smoothly convex, but usually the surface of the valves consists of inflations and depressions. As pointed out by SCHMIDT (1941, p. 15), there are two types of terms for describing the features of the ostracod carapace, namely those which denote the type of structural elements (may be called general terms) and those which denote structural elements whose type may vary, but whose position in the carapace is determined (may be called special terms).

General terms are such as lobe, sulcus, ridge, frill, etc. The terminology used here follows that of KESLING (1951b), except for the introduction of the term *semisulcus*. The term is illustrated in text figure 1. Whereas a sulcus lies between two inflations, the semisulcus is only bordered on one side by an inflation. Usually a semisulcus is not considered as a sulcus. *Rigidella mitis* was described by ÖPIK (1935, p. 11) as being typically trilobate, and by HESSLAND (1949, p. 339) as being distinctly tetralobate. This species has four lobes, separated by two sulci and a semisulcus.



Fig. 1. The difference between sulcus (S) and semisulcus (Ss).

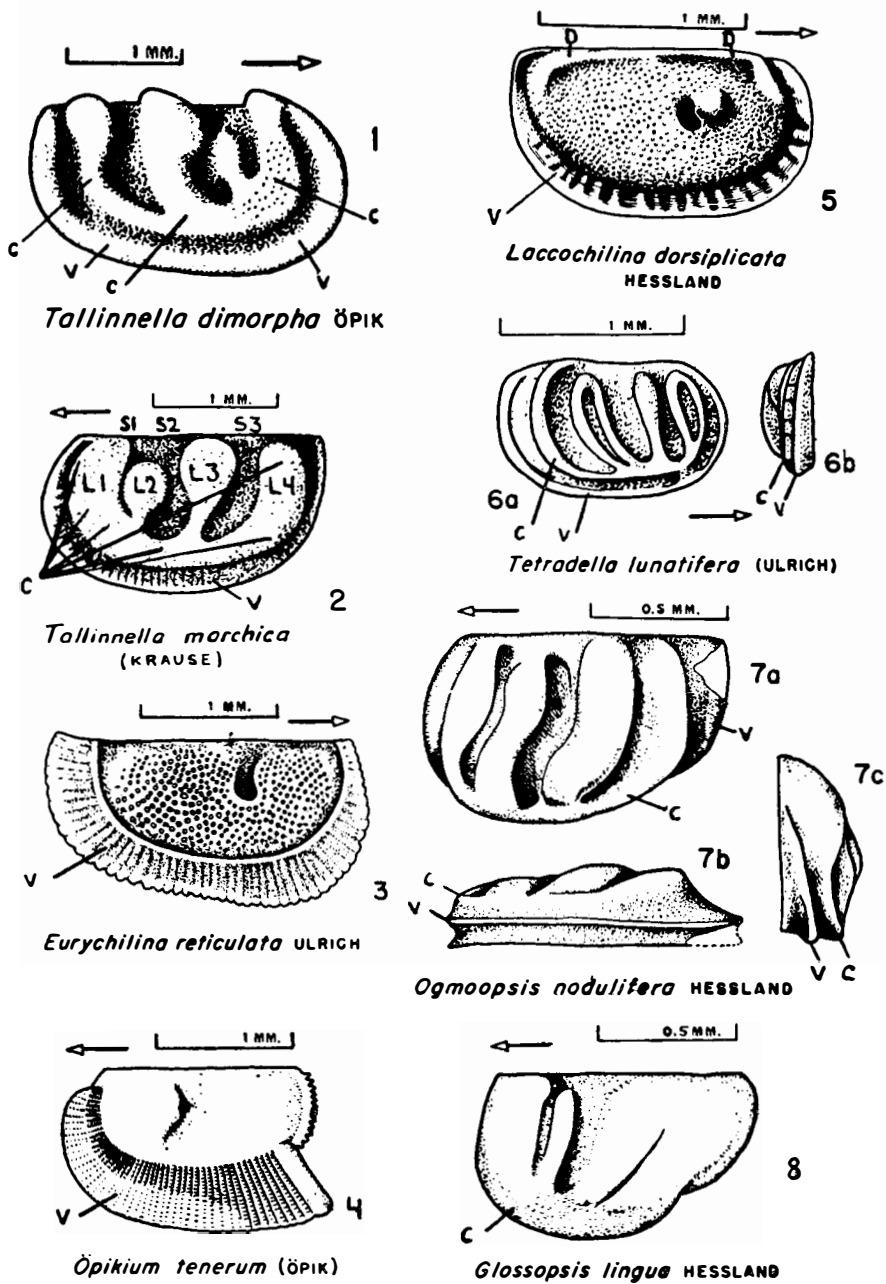


Fig. 2. Examples of velate structures (V), carinal structures (C), and dorsal ridge (D). (The figures, not the symbols, are reproduced from KESLING, 1951b).

Special terms are such as anterior lobe, median sulcus, velate frill, etc. The terminology here follows that of KESLING (1951b) except for the addition of the terms lobate area and extralobate area, and the definition of carina. The *lobate area* (HESSLAND, 1949: sulcate area) comprises the lobes and the intervening sulci. The *extralobate area* (introduced by HESSLAND, 1949) denotes the rest of the valve between the lobate area and the free border. KESLING (1951b, p. 118) defines *carina* as "A frill-like or ridgelike structure dorsal and parallel to the velate structure. A frill or velate ridge must also be present to have a structure designated as a carina". The writer strongly disagrees with this last statement. Velate and carinal structures are not homologous (cf. HESSLAND, 1949, p. 130), and a carinal structure can be distinguished even if no velate structure is developed (text fig. 2; 2). The *velate structure* may be developed as a velate frill, false border, row of spines, or a combination of these, and probably also as a velate bend. If the velate structure runs from the anterior to the posterior cardinal angle (or almost so) it may be called *entire* (text figs. 2; 1, 2, 3, 5, 6). If it is restricted to the anterior and ventral border areas, and is not developed in the posterior border area, it may be called *restricted* (text fig. 2; 4). The velate structure may be dimorphic.

Carinal structures. L1, L4 and the connecting ridge between these may be called a carinal ridge (text figs. 2; 1, 2). In tetralobate species the ventral ends of L2 and L3 may be united with this ridge (e.g. *Tallinnella*) or not (e.g. *Zygobolba*). Sometimes, at least a part of the carinal structure may form a protruding flange (HESSLAND, 1949, p. 130: ventral carina), as in *Glossopsis* (text fig. 2; 8). The carinal structure may also be developed as a carinal crest, carinal bend (Umbiegungskante), etc. It may be dimorphic.

HESSLAND (1949, p. 129) introduced the symbols L1, L2, L3, L4 for the lobes (and C1, C2, C3, C4 for the corresponding crests), and S1, S2, S3 for the sulci. L1 denotes the anterior lobe and S1 the anterior sulcus, etc. (text fig. 2; 2). These symbols were accepted by KESLING (1951b) and are also used here.















Degree of sulcation.

(Text figure 3).

The features mentioned above are liable to vary even in closely related species and need not be of greater taxonomic importance.

This does not exclude, however, that one or another feature (f. inst. development of certain crests or wide velate frills) may become fixed for a smaller or larger group. This appears to be generally accepted, but in the discussion of affinity too much stress seems to have been laid on as to whether the forms were non-, uni-, di-, or trisulcate. The writer quite agrees with SWARTZ (1936, p. 544) who points out that the degree of sulcation and lobation is of questionable genetic significance, and must be used cautiously. No doubt a unisulcate form may be closer to a trisulcate form than to other unisulcate forms, and vice versa. Compare (text fig. 3) f. inst. such pairs as *Glossopsis* — *Aulacopsis*, *Dizygopleura* — *Eukloedenella*, etc. The variation of the number of sulci is only an example of the common alternation between "smooth" forms (with "effaced relief") and forms with more or less well developed relief, also well-known in many other groups of shell-bearing animals. The pronunciation or obliteration of the sulci may be directly compared with that of the glabellar furrows in trilobites (cf. HENNINGSMOEN, 1951, p. 176). The sulci, at least S1 and S2 (cf. TRIEBEL, 1941, p. 310) may be assumed to represent points of muscle attachment. The same muscles may be assumed to be present also when no sulci are developed. The absence of sulci, or the presence of 1—3 sulci does not therefore indicate any important differences in the animal itself, but only modifications of the valve, which may be due to f. inst. mode of habitat. The smoothness of the valves is, to some degree, related to the convexity of the valves, length of the hinge, etc.; strongly convex forms with short hinge line are usually smooth (cf. TRIEBEL, 1941, p. 301).

In the discussion of the affinity of beyrichiacean ostracods, the forms with two or three sulci have generally been regarded as being more advanced than forms with no or one sulcus. From the above, it appears probable that forms with more sulci may have developed from forms with no or one sulcus. In fact, phylogenetic lines from tri- or disulcate forms to uni- and nonsulcate forms seem to have been established, whereas the opposite is not known with certainty. Phylogenetic lines of this type may, however, be expected to be found. As examples of the former type (reduction of the number of sulci) may be cited the probable development of *Steusloffia* (1 sulcus) from *Tallinnella* (3 sulci) via *Rigidella* (2 sulci and a semisulcus). The unisulcate *Plethobolbina* appears to have developed from earlier *ygobolbids*, which are di- or trisulcate (cf. range chart, p. 237). Furthermore the uni- to nonsulcate *Eukloedenella* seems to appear

3 SULCI (S1 + S2 + S3)	2 SULCI (S1+S2 OR S2+S3)	1 SULCUS (S2)	NO SULCUS
 1  2  3 <i>Glossopsis</i> <i>Aulacopsis</i>	 4 <i>Aulacopsis</i>	 5  9 <i>Sigmobolbina</i>	
 6 <i>Ogmoopsis</i>	 8 <i>Carinobolbina</i>	 10 <i>Bolbina</i>	
 7 <i>Sigmoopsis</i>	 12 <i>Ctenobolbina</i>		
 11 <i>Ctenobolbina</i>	 13 <i>Ceratopsis</i>		
	 14 <i>Ceratopsis</i>		

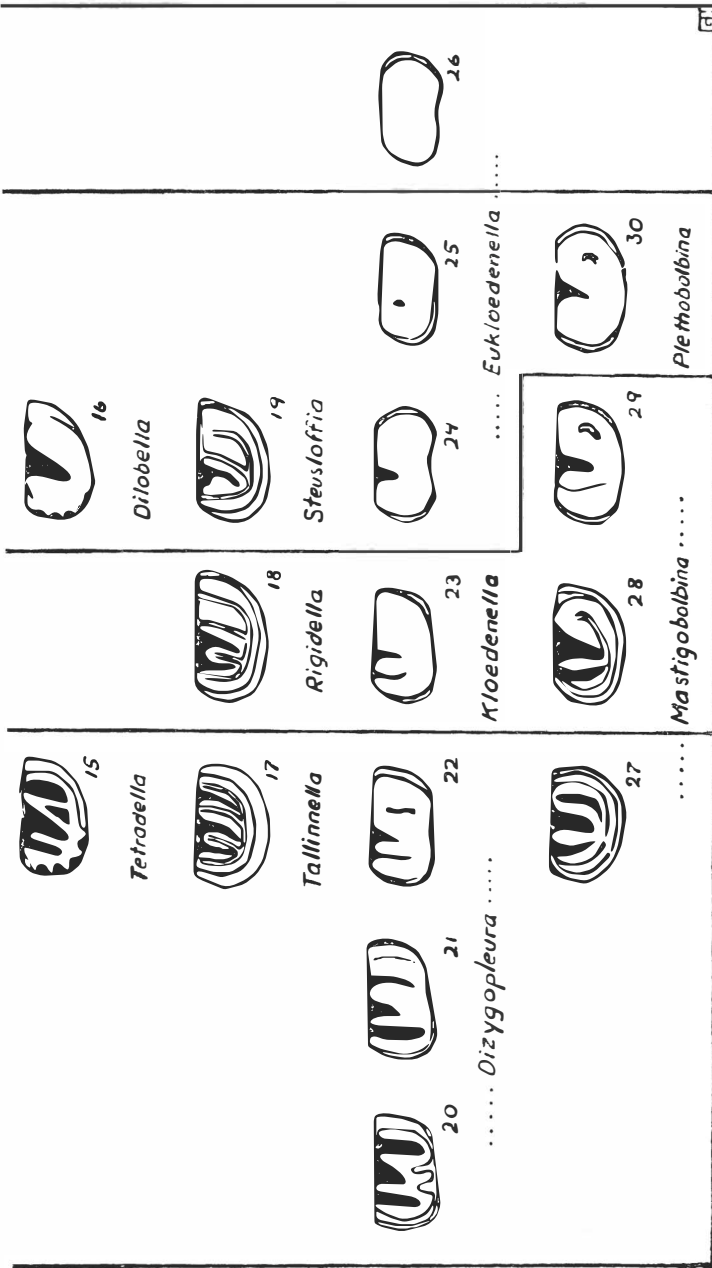


Fig. 3. Variation of sulcation in closely related forms. 1—5 Glossopsiinae (1 *Glossopsis acuta*, 2 *G. lingua*, 3 *Autiacopsis bifissurata*, 4 *A. monofissurata*, 5 *A. plana*), 6—12 Sigmooipsinae (6 *C. ...opsis nodulifera*, 7 *Sigmooopsis platyceras*, 8 *Carinobolbina estona*, 9 *Sigmobolbina kuckersiana*, 10 *Bolbina ornata*, 11 *Ctenobolbina citiata*, 12 *C. bispinosa*), 13—17 Tetradellinae (13 *Ceratopsis chambersi*, 14 *C. quadrifida*, 15 *Tetradella quadrifurcata*, 16 *Dilobella fulcrata*, 17 *Tallinnella grevingki*), 18—19 Bassleratiinae (18 *Rigidella cf. mitis*, 19 *Steusloffia polygularis*), 20—26 Kloedenellinae (20 *Dizygopleura costata*, 21 *D. stosi*, 22 *D. affinis*, 23 *Kloedenella rectanbifida*, 24 *Eukloedenella sinuata*, 25 *E. umbilicata*, 26 *E. punctata*), 27—30 Zygobolbinae (27 *Mastigobolbina bifida*, 28 *M. arguta*, 29 *M. punctata*, 30 *Plethobolbina typicalis*). (The sketches have been drawn after illustrations given by various authors.)

slightly later than the trisulcate *Dizygopleura*. It is possible that some of these uni- and nonsulcate genera are not strictly monophyletic, but include species which have developed from the allied tri- or disulcate forms at different times. When studying a form series from a trisulcate to uni- and nonsulcate forms, it is seen that a sulcus may become obliterated in two ways. In the one case the sulcus becomes shorter, to be replaced by a sulcal pit before it vanishes (text figs. 3; 20—26), or a sulcus may be substituted by a semisulcus and then disappear, as seems to be the case in the phylogenetic line *Tallinnella* — *Rigidella* — *Steusloffia*. The width of the sulci (and the lobes) also appears to vary rather much even in closely related forms. It is of interest to note that one of the very earliest beyrichiacean forms is the tetralobate *Tallinnella primaria* ÖRIK, 1935 or a closely related form (cf. p. 213).

Persistent features.

It is always S2 which is developed in unisulcate forms. S2 may be said to be more persistent than S1 and S3 (for this reason S1 and S3 have been called secondary sulci by SWARTZ, 1936, p. 551). In forms with two sulci, the second sulcus may be either S1 or S3; in some groups it appears that S1 is more persistent than S3, whereas the opposite is the case in other groups. Regarding a form series from sulcate to nonsulcate forms (text figs. 3; 20—26), it is seen that the sulcus diminishes and becomes a pit, corresponding in position to the middle and deepest part of the fully developed sulcus. This is the most resistant part of the sulcus. In the Glossopsiinae (text figs. 3; 1—5) the ventral end of the sulcus (at least in S1 and S3) is the most persistent part of the sulcus. The most persistent lobe is usually L2. The velate structure is very persistent in the beyrichiacean ostracods, but may be lacking, as in some Glossopsiinae. In more or less smooth ostracods, features which are well developed in closely related, more ornamented forms appear "effaced" or may be completely lacking. The persistent features may be both "efface-resistant" and persistent in phylogenetic lines.

Criteria of affinity in beyrichiacean ostracods.

The degree of sulcation, width and height of lobes, width and depth of sulci, width of velate structure, etc. may vary in closely

related forms. Nevertheless, some of these characters may become more or less fixed, and may then serve as criteria of affinity in some groups. The importance of such characters appears, however, to have often been overestimated.

The overestimation of the importance of the number of sulci is, to some degree, responsible for the inclusion in *Primitia* of a great number of unisulcate species with short sulcus, whereas those with a long sulcus have often been classed as unisulcate *Ctenobolbina* or *Ctenentoma* species. Similarly, disulcate forms with S2 and S3 are often assigned to *Ctenobolbina*, whereas forms with S1 and S2 have been placed in *Beyrichia*. Ordovician trisulcate species are usually included in *Tetradella*. In the writer's opinion this classification is too "mathematical" and does not pay proper attention to the affinity of the forms.

As in other groups of animals it is best to combine as many features as possible in tracing affinity. This does not exclude that a single, rare feature may be often very useful in establishing relationships.

The type of median sulcus (S2) (i.e. its shape, not its width or depth) has been found useful in some cases; also the types of lobes. Furthermore, the type of velate and carinal structures may be used as criteria of affinity, especially when they show dimorphism. When present, dimorphism may be of great help, as there are many different types of dimorphism, and these appear to be of supra-generic importance.

More or less smooth ostracods have caused much trouble in the taxonomy. It is often a good idea to compare these with contemporaneous ornamented forms and see if there is a form series from the one type to the other. The persistent features are often useful in tracing the affinity of smooth forms.

Dimorphism.

Several types of dimorphism have been described in the Beyrichiacea. Usually the one dimorph develops an extra swelling of the valve wall, or a more or less closed extraneous chamber or shelter. This dimorph is usually called the female. In *Beyrichia* the swelling (pouch) of the valve wall has been shown to be a brood pouch (HESSLAND, 1949, p. 124; SPJELDNÆS, 1951, p. 748), which supports the view that the pouch-bearing dimorph is the female.

It is possible that these forms are only fertilized females. Furthermore larval carapaces more or less agree with the so-called males. It may therefore be better to refer to these dimorphs as "female type" and "male type", the latter also probably including larval instars and possibly unfertilized females.

HESSLAND (1949, pp. 123—128) stresses the important difference between pouches formed by the carapace wall and the false pouches formed as extraneous chambers.

Orientation.

The Beyrichiacea are so oriented that the median sulcus (S2) generally is situated slightly in front of the middle in adult individuals. Non-sulcate beyrichiaceans are oriented in agreement with the nearest related sulcate forms. The orientation of Beyrichiacea has been thoroughly discussed by TRIEBEL (1941). Criteria for determining the orientation have been summarized by LEVINSON (1950, p. 65), and KESLING (1951, p. 94). As discussed below (p. 251) moult retention furnishes further support for this orientation. This orientation has sometimes been questioned for the brood pouch of *Beyrichia* would then have an anteroventral position, which would be an unusual feature. There seems, however, to be little doubt now that the dimorphic swellings of the Beyrichiidae and Kloedenellidae are developed in opposite ends of the carapace. If the orientation of the Beyrichiidae were reversed, this would imply that the orientation of the Kloedenellidae should also be reversed thus bringing *their* dimorphic swelling at the anterior end. The above-mentioned argument against the present orientation is thus considerably weakened.

Reversal of the valves.

COOPER (1941, p. 56) states that "The large number of reversed forms of *Sansabella* which have been discovered in the Chester series has shown the fallacy of trying to determine generic classification by overlap alone". And further (l.c., p. 59) "All other features being equal, the reversal of valves is not considered to be a generic or even specific character of the Kloedenellidae".

According to SOHN (1950, p. 35) *Aurikirkbya wordensis* (HAMILTON, 1942) has been proved to contain individuals that have a reversal of overlap and hingement. Similarly KELLETT (1936, p. 770)

believes, as suggested by JOHNSON (1936, p. 7), that *Paraparchites oviformis* CORYELL & ROGATZ, 1932 and *Antiparaparchites reversus* CORYELL & ROGATZ, 1932 are not only congeneric, but also conspecific.

It appears thus questionable to recognize genera or species which differ from others in the reversal of valves only.

Remarks on the classification of Beyrichiacea.

The classification of the Beyrichiacea has often been revised. Good progress was made by SWARTZ (1936) who stresses that the degree of sulcation and lobation is of questionable genetic significance. In addition to the families recognized by BASSLER & KELLET (1934) in the "Index" (Primitiidae, Beyrichiidae, Zygobolbidae, Kloedenellidae, Kirkbyidae, Glyptopleuridae, and Youngiellidae), SWARTZ erected the families Hollinidae, Tetradellidae, Drepanellidae, Aechminidae, Acronotellidae, and Primitiopsiidae. These families were split off from the families Primitiidae and Beyrichiidae, which had become too heterogeneous. SWARTZ removed the Eurychilininae from the Primitiidae to the Beyrichiidae, comparing the false pouch of the Eurychilininae with the pouch of the Beyrichiidae.

BOUČEK in a paper appearing slightly earlier (July 1936) than that of SWARTZ (October 1936) divides the Primitiidae into four subfamilies; besides Primitiinae and Eurychilininae the new subfamilies Bolliinae and Aechmininae.

ÖPIK (1937) adds the family Piretellidae.

KAY (1940) follows BOUČEK regarding the Primitiidae, but adds one more subfamily, the Dilobellinae. The Tetradellinae and Piretellinae are regarded as subfamilies of the Beyrichiidae. The writer agrees with SWARTZ (in SWARTZ & SWAIN, 1941, p. 416) that KAY's return to primary emphasis on the degree or strength of lobation is a backward step and leads to unnatural assemblages.

SCHMIDT (1941) follows SWARTZ to a certain extent, but seems to lay too much stress on the number of sulci. SCHMIDT includes the Tetradellinae as a subfamily of the Hollinidae, together with the two new subfamilies Ctenentominae and Ctenonotellinae. Furthermore the Aechmininae and the new subfamilies Ulrichiinae and Bassleratiinae are included in the Drepanellidae. The Primitiopsiinae are included in the Primitiinae, together with the Primitiinae and Eurychilininae.

HESSLAND (1949) agrees with SCHMIDT, except for the transference of the Eurychilininae from the Primitiidae to the Hollinidae, and also in including in this family the new subfamily Euprimitiinae. HESSLAND points out the important difference between the false pouch of f.inst. the Eurychilininae and the pouch of the Beyrichiidae.

The classification proposed here agrees best with that of SWARTZ (1936). When the present writer deviates from his classification in several points, this is mainly due to:

1) SWARTZ recognized *Primitia mundula* as type species of *Primitia*, as had become the custom. The recognition of *P. strangulata* as the type species (cf. p. 225) influences the classification considerably.

2) SWARTZ did not distinguish between the extraneous false pouch of the Eurychilinidae and the pouch of the Beyrichiidae, the latter pouch opening into the main cavity of the carapace. SWARTZ thus included the eurychilinids in the Beyrichiidae.

3) New material, especially of important early forms has been described since the appearance of his paper.

4) The writer has continued the "splitting up" of groups including forms with the same degree of sulcation and lobation, but probably not closely related.

Notes on affinities and trends of beyrichiacean families.

Some of the earliest known beyrichiacean ostracod faunas are those described by HESSLAND (1949) from the Lower Ordovician of the Siljan District in Sweden. They are also the largest early faunas described, and are of considerable interest in studying the affinities of beyrichiacean ostracod families.

A group of species with well defined velate or carinal structure was assigned to the genera *Euprimitia* (possibly not congeneric with the type species), *Euprimites*, *Eurychilina* (may be transferred to *Laccochilina*, cf. p. 228), *Laccochilina*, *Ctenentoma* (here transferred to *Aulacopsis* and *Hesslandella* gen. n.), *Aulacopsis*, *Glossopsis*, *Ogmoopsis*, *Ceratopsis* (Glossopsiinae, probably species of *Glossopsis*), *Tetradella* (here *Tallinnella*), and *Steusloffia*. In *Aulacopsis*, *Glossopsis*, and *Ogmoopsis* the carinal structure is the dominating submarginal structure, in the others it is the velate structure. When present, the velate structure is entire, and in the form of a wide frill, a narrow frill, or a ridge. The velate frill may show dimorphism, but of a simple

type, in being convex in some individuals. In the writer's opinion all these species are rather closely related, and could have been grouped in one family. As discussed above (p. 193), the degree of lobation is perhaps of no great importance. When the above genera are here assigned to different subfamilies and families, this is because these groups are clearly differentiated in later faunas. It is always difficult to know how far back such groups should be separated. These early faunas are probably near the bursting point of several groups.

Tallinnella, *Hesslandella* gen. n. and probably *Euprimites* may be assigned to the Tetradellinae (cf. p. 214). It is interesting to note that *Tallinnella* includes species with velate rim (as in *Hesslandella* gen. n. and *Euprimites*), forms with wide frill (as in *Laccochilina*), and forms with narrower frill (crest) and crests along the lobes (as in *Steusloffia*). *Steusloffia* is here assigned to the Bassleratiinae, although it is hardly to be doubted that the early *Steusloffia* and *Tallinnella* are very closely related. As discussed below (p. 223) it appears most reasonable to assume that *Steusloffia* developed from *Tallinnella*. *Laccochilina* shows the same type of frill as f.inst. *Tallinnella grewingki*, and might just as well have been included in the Tetradellinae as in the Eurychilinae.

Aulacopsis, *Glossopsis*, and *Ogmoopsis* are here included in the family Sigmoidopsiidae nov., characterized i.a. by the well developed carinal structure. There is, however, hardly any doubt that this group is closely related to early Tetradellinae, and that they had common origin, probably not far back in time.

It would, of course, be of interest to study still older faunas. The only likely older fauna related to those discussed above, is that of the Megalaspis Limestone described by ÖPIK (1935). It comprises i.a. *Ogmoopsis bocki*, *Tallinnella primaria*, *Rigidella mitis*, and *Laccochilina estonula*, all erected by ÖPIK, 1935. This fauna is probably slightly older than the one in the lower part of the succession described by HESSLAND.

Tallinnella primaria (or a very closely related form) has been observed by the writer in still older beds (Lower Didymograptus Shale) in Norway, and is probably the earliest known beyrichiacean species with velate structure.

One may possibly regard the Tetradellinae as a main stock. The Sigmoidopsiidae (Sigmoidopsiinae and Glossopsiinae) may have

branched off from this, or at least had a common origin. *Steusloffia* (and thus probably the whole subfamily Bassleratiinae) has most probably developed from the Tetradellinae, and this may be true of the Eurychilinae, too.

Proceeding now to later Ordovician beyrichiacean faunas, new groups appear, and the whole picture is more varied. The subfamily Sigmoidopsiinae develops a number of new forms (*Sigmoidopsis*, *Sigmobolbina*, etc.), and likewise the Tetradellinae. The velate structures and velate dimorphism become more differentiated, producing forms like *Tallinnella dimorpha*. In this species the dimorphic part of the frill is restricted to its anterior part; the frill, however, is still entire. The Piretellinae (including forms like *Piretella* and *Rakverella*) includes forms with restricted frill (not seen in early Ordovician genera). They have most probably developed from the Tetradellinae, where forms like *Tallinnella dimorpha* and *Tallinnella superciliata* point towards the Piretellinae regarding the structure of the frill and its dimorphism. The Primitiidae have appeared. They may have developed from the Tetradellinae such as (or *via*) forms like *Piretella*, or, possibly from the Eurychilinae, still represented here. *Steusloffia* is still present, as well as a number of other Bassleratiinae.

A difference between the early and later Ordovician faunas is that the velate and carinal structures are more varied in the later faunas, and there are more types of dimorphism.

The relationships of the Acronotellidae, Primitiopsiidae, and Aparchitidae to the above-mentioned families are still uncertain. The Aparchitidae comprises smooth forms which may have developed from one (or more) of these families.

The relationships of later families (appearing in Silurian and later systems) to the Ordovician families are still rather obscure. Such relationships can quite probably be traced when more forms have been studied, especially from near the Ordo-Silurian boundary.

It still seems uncertain whether the Beyrichiidae developed from the Eurychilinae (as is often suggested) or some other Ordovician family. It is also not quite certain that the Kirkbyidae developed from the Bassleratiinae *via* *Strepula*, which has sometimes been included in the Kirkbyidae. As discussed below (p. 239) the Hollinidae may not be closely related to *Ctenobolbina* as is generally believed. The relationships of the Kloedenellidae to the Ordovician or later families are also uncertain. As discussed below (p. 245) the glyptople-

urids are, however, closely related to the kloedenellids, and have for this reason been included in the Kloedenellidae. The position of the very little known families Youngiellidae and Miltonellidae is quite uncertain.

The Silurian beyrichiid faunas are especially characterized by the dimorphic swellings of the Beyrichiidae and Kloedenellidae. Furthermore wide velate frills are not so common as in Ordovician faunas.

Very few post-Silurian beyrichiaceans develop a well-marked dimorphic swelling. Instead overlap features become more prominent.

Early families.

These are the families which entirely or partly consist of Ordovician genera.

Family Sigmoidsiidae nov.

Diagnosis: — See p. 262. *Included genera:* — See list p. 266.

Remarks: — Characteristic for this family is especially the carinal structure which is often well developed, and often shows dimorphism, whereas a velate dimorphism is usual in other early families.

The family includes the two new subfamilies Sigmoidsiinae and Glossopsiinae. It appears probable that these two groups had common ancestors, which may have developed from early forms of *Tallinnella*, or at least from the same stock as *Tallinnella*. It is, however, also possible that the Sigmoidsiinae and Glossopsiinae represent two different off-shoots from the Tetradellinae. If so, they may be assumed to be rather "closely set" off-shoots, which may justify their grouping together.

Subfamily Glossopsiinae nov.

(Text fig. 3, 1—5).

Diagnosis: — See p. 262. *Included genera:* — See list p. 266.

Remarks: — This is a well defined subfamily, showing several unusual features. There are no or very faint velate structures. Instead the carinal structure is well developed as a flange (carina). The sulci are rather long; S3 is more persistent than S1. It is remarkable that the ventral part of S1 and S3 is the most persistent part of these

sulci. *Ctenentoma plana* HESSLAND, 1949 should be removed from *Ctenentoma* (cf. p. 224). HESSLAND (1949, p. 268) states that it will probably be referred to a new genus or subgenus, and that this species may be closely related to *Aulacopsis*. The difference between *C. plana* and *Aulacopsis monofissurata* HESSLAND, 1949 is very small; the latter differing in having a very faint impression corresponding to the ventral part of S3. In the writer's opinion *C. plana* should be transferred to *Aulacopsis*, which would then also include unisculate species. It appears unnecessary to erect a new genus for *Aulacopsis plana* alone. *Aulacopsis nodosa* HESSLAND, 1949 should on the other hand be removed from this genus. It does not have a carinal structure, but instead a well defined velate structure. As stated by HESSLAND (1949, p. 281) it is closest reminiscent of *Ctenentoma macroreticulata*, which is designated the type species of a new genus, *Hesslandella* (cf. p. 215). *Aulacopsis nodosa* should be included in this genus.

As demonstrated by HESSLAND, *Aulacopsis plana* shows a dimorphism in the carinal structure; the carina being better defined in some individuals (type *a*) than in others (type *b*). In the writer's opinion the same applies to *Glossopsis*, but its two types have been described as different species. *G. lingua* appears to be type *a* and *G. clavata* type *b* of the same species, which should then be called *G. lingua*. Similarly *G. acuta* may probably be type *a* and *G. tenuilimbata* type *b* of one species, which should be called *G. acuta*. The following comparison is rather interesting (based on data from HESSLAND, 1949):

<i>Aulacopsis plana</i>	type <i>a</i>	17 valves measured,	"mean size"	1.20 mm
—»—	type <i>b</i>	22	—»—	0.85 »
<i>Glossopsis acuta</i>	(type <i>a</i>)	369	—»—	0.97 »
(<i>G. tenuilimbata</i>)	(type <i>b</i>)	537	—»—	0.78 »
<i>Glossopsis lingua</i>	(type <i>a</i>)	131	—»—	1.04 »
(<i>G. clavata</i>)	(type <i>b</i>)	238	—»—	0.73 »

The table shows that type *b* of *Aulacopsis plana* is the more common one, but having the smaller "mean size" in the collected material. It is interesting to note that *G. clavata* which morphologically may represent type *b* of *G. lingua* is more common, and has a smaller "mean size" in the collected material than *G. clavata*. The same is the case with *G. tenuilimbata* vis-a-vis *G. lingua*. In *A. plana* the smallest carapace of type *a* which was measured, is slightly longer

than the largest carapace measured of type *b*. In *G. lingua* the smallest carapace measured has practically the same length as the largest carapace of *G. clavata*. This may favour the view held by HESSLAND (1949) that the types *a* and *b* represent adult and larval instars, respectively. Regarding *G. lingua* and *G. tenuilimbata* there is a certain overlap with regards to size, and it is possible that type *a* represents mature females, whereas type *b* represents mature males and larval instars.

HESSLAND (1949, p. 296) distinguishes between a *G. lingua* and a *G. tenuilimbata* group, assigning to the former *G. lingua* and *G. acuta*. As *G. tenuilimbata* may be a synonym of *G. acuta*, these groups may be united. The third group recognized by HESSLAND, the *G. perpunctata* group, is here assigned to the new genus *Sigmoopsis*.

Subfamily Sigmoopsiinae nov.

(Text fig. 3; 6—12).

Diagnosis: — See p. 262. *Included genera:* — See list p. 266.

Remarks: — Rather characteristic of this subfamily is the sigmoidal median sulcus (S2) and the corresponding shape of L3, which often appears slightly constricted ventrally. Furthermore these genera both have a velate and a carinal structure, the latter showing dimorphism (or may be missing in the one dimorph). This was already observed by BONNEMA (1909) in the species *Ctenobolbina carinata* KRAUSE sp. (here: *Carinobolbina estona* (ÖPIK, 1937)) and *Ctenobolbina Kuckersiana* BONNEMA, 1909 (= *Carinobolbina kuckersiana*). As pointed out by ÖPIK (1937, p. 26) and KESLING (1951, p. 108) "*Ceratopsis*" *obliquejugata* and allied (here assigned to *Sigmoopsis* gen. n.) show dimorphism in the carinal structure (referred to by these authors as "false border" and "velate structure" respectively).

Notes on the genera: —

Ogmoopsis HESSLAND, 1949.

(Text fig. 3; 6).

Ogmoopsis (type species *O. nodulifera* HESSLAND, 1949) is the earliest known genus of the Sigmoopsiinae. It is a typical member with sigmoidal median sulcus (S2), L3 somewhat restricted ventrally, and with a velate ridge as well as a carinal flange (carina). *O. paene-*

quisulcata HESSLAND, 1949 does not have the typical S2 and L3, and should probably rather be included in the Glossopsiinae (*Glossopsis*).

Sigmoopsis gen. n.

(Text fig. 4).

Derivation of name: — From “sigma“ and “opsis“ (appearance), alluding to the sigmoidal median sulcus.

Type species: — *Ceratopsis platyceras* ÖPIK, 1937. This species is chosen as type species as it is well described and illustrated by ÖPIK (1937, p. 26; pl. II, figs. 6—7; pl. X, figs. 12—14; pl. XIV, fig. 5) (Also refigured by KESLING, 1951, pl. VI, figs. 2—3). It is possible that *S. platyceras* may be shown later to be a synonym for one of the German drift boulder species, but the writer prefers not to select any of these as type species, as they are not very well known, and their stratigraphic horizon somewhat uncertain.

Diagnosis: — Carapace usually elongated, with forward swing. 2—3 sulci. S2 sigmoidal, with geniculum and backward curve of ventral end. S3 of about same length as S2, S1 much shorter or missing. L1 sometimes extended into a spine-like process dorsally. L2 short, not inclined to be bulbous. L3 bluntly constricted at its ventral end. Lobate area well separated from the extra-lobate area

by the carinal structure, except postero-dorsally, where the dorsal half of L4 may be confluent with the extralobate area. The carinal structure usually shows dimorphism, being developed as a ridge or a protruding flange (carina). An entire crest-like velate structure is present.

Remarks: — This is a very characteristic genus. Its species have earlier been assigned to *Beyrichia*, *Ctenobolbina*, and *Ceratopsis*. *Sigmoopsis* gen. n. is clearly different from *Beyrichia*, and differs from this genus and *Ceratopsis* in the sigmoidal S2, sausage-like L3, and the carinal structure (showing dimorphism). It may, however,

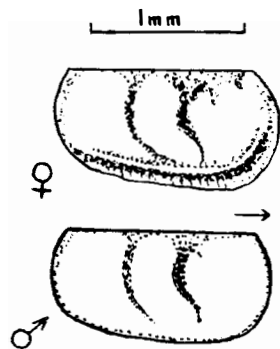


FIG. 4. *Sigmoopsis platycera* (ÖPIK, 1937). Reproduced from the drawings given by KESLING (1951, pl. VI, figs. 2—3) after photographs given by ÖPIK (1937, pl. II, figs. 6-7).

be related to *Ctenobolbina* (cf. p. 211) which has no carinal flange. The "Glossopsis *perpuncta* group" of HESSLAND (1949, p. 297) consists of typical *Sigmoopsis* species. *Sigmoopsis* differs from *Glossopsis* in the shape of the lobes and sulci, and in having a distinct velate ridge. It may be recalled that KESLING (1951, p. 108) states that *Ceratopsis* has some dimorphic species, and mentions *C. platyceras* and *C. obliquejugata*, both of which are here included in *Sigmoopsis*. The following forms may be assigned to *Sigmoopsis* gen. n.:

- Sigmoopsis obliquejugata* (SCHMIDT, 1858)
- » *perpuncta* (ÖPIK, 1937)
- » *perpuncta prominens* (ÖPIK, 1937)
- » *platyceras* (ÖPIK, 1937)
- » *rostrata* (KRAUSE, 1892)
- » *rostrata cornuta* (KRAUSE, 1896)
- » *schmidti* (BONNEMA, 1909)

A closer study of these forms may show that some are synonyms. ÖPIK (1937, p. 25) claims that *S. schmidti* appears to be identical with *S. obliquejugata*. If so it is quite probable that *S. platyceras* is also a synonym of *S. obliquejugata*. Furthermore some of the N. German drift boulder species may turn out to be conspecific with Baltic forms.

Carinobolbina gen. n.

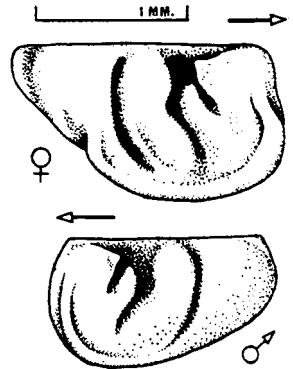
(Text fig. 5).

Type species: — *Ctenobolbina estona* ÖPIK, 1937 (= *Ctenobolbina carinata* KRAUSE in BONNEMA, 1909).

Remarks: — This genus is rather close to *Sigmoopsis* but differs in that the carinal structure is shorter, mainly being confined to the anteroventral and ventral areas. *Carinobolbina* is also probably close to *Ctenobolbina* but in the latter genus the carinal structure is still more reduced, forming a spine or alate extension only.

Species: — Besides *Ctenobolbina estona* ÖPIK, 1937, *Beyrichia* (*Tetradella*) *carinata* KRAUSE, 1892 and *Ctenobolbina kuckersiana* BONNEMA, 1909 are typical members. *Ctenobolbina aspera* ÖPIK, 1937 is not well enough known. If the submarginal crest seen in the specimen figured by ÖPIK (1937, pl. VIII, fig. 5) is a carinal structure, *C. aspera* is no doubt closely related to *C. kuckersiana* and should

Fig. 5. *Carinobolbina estona* (ÖPIK, 1937). Female type after ÖPIK (1937, pl. VIII, fig. 8), male type after BONNEMA (1909, pl. II, fig. 20).



be included in *Carinobolbina*. *Ctenobolbina polytropis* ÖPIK, 1937 and *Ctenobolbina ctenolopha* ÖPIK, 1937 have rather unusual types of carinal structures; parallel rows of pits with or without ridges between the rows. Apart from this, they agree very well with the Sigmopsiinae, especially *Carinobolbina* and should probably be included in this genus. The following species are thus assigned to *Carinobolbina*:

- Carinobolbina estona* (ÖPIK, 1937)
 » *carinata* (KRAUSE, 1892)
 » *kuckersiana* (BONNEMA, 1909)
 » ? *aspera* (ÖPIK, 1937)
 » ? *polytropis* (ÖPIK, 1937)
 » ? *ctenolopha* (ÖPIK, 1937)

Sigmobolbina gen. n.

(Text fig. 6).

Derivation of name: — The name alludes to the sigmoidal median sulcus, and the likeness to *Ctenobolbina*.

Type species: — *Entomis oblonga* STEUSLOFF var. *Kuckersiana* BONNEMA, 1909 = *Sigmobolbina kuckersiana* (BONNEMA, 1909), from Middle Ordovician Kukruse Beds, Esthonia.

Diagnosis: — Carapace elongate, with anterior swing. Unisulcate, although one may sometimes see traces of S1 and S3. Median

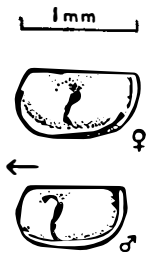


Fig. 6. *Sigmobolbina kuckersiana* (BONNEMA, 1909). Female type after BONNEMA (1909, pl. V, fig. 9), male type after BONNEMA (1909, pl. V, fig. 6).

sulcus (S2) sigmoidal, as in *Sigmoopsis* gen. n. Velate ridge narrow but distinct. Carinal structure shows dimorphism; may be developed as a flange (female type) or as a ridge (male type), often ending in a spur posteriorly.

Remarks: — Species here assigned to *Sigmobolbina* gen. n. were stated by KAY (1940, p. 254) to seem congeneric with *Winchellatia*. This is possible, but *Winchellatia*, as described by KAY, appears to differ in having a velate dimorphism (not carinal), and furthermore its sulcus is not distinctly sigmoidal. It is, however, quite possible that the spine of *Winchellatia* corresponds to the spur of *Sigmobolbina*. There is no doubt that *Sigmobolbina* is closely related to *Sigmoopsis*, and may be regarded as the unisulcate equivalent of this. For this reason *Sigmobolbina* may be regarded as a subgenus of *Sigmoopsis*.

The different forms assigned to *Sigmobolbina* vary especially in the development of the carinal structure. In some species it is rather flange-like (at least in the one dimorph), and posteriorly it may fade away or be extended into a spur. In some forms (cf. *S. obliqua* in THORSLUND, 1940) the area between this spur and the sulcus tends to be swollen, forming a kind of a ventral lobe.

Besides the type species, *Entomis variolaris* BONNEMA, 1909 and *Entomis obliqua kuckersiana* BONNEMA, 1909 belong no doubt to *Sigmobolbina*. *Entomis oblonga* STEUSLOFF, 1894 may belong here, if the specimens described under this name by KRAUSE (1896, p. 935) really are conspecific. These specimens should undoubtedly be assigned to *Sigmobolbina*. *Entomis obliqua* KRAUSE, 1892 is also congeneric; also the specimens described by THORSLUND (1940, p. 173). *Entomis sigma* KRAUSE, 1889 probably belongs to *Sigmobolbina*, although probably not the variety later called var. *antiquata* by KRAUSE (1891, p. 509). The latter form may be an *Öpikium* species. It is also uncertain whether *Entomis sigma ornata* KRAUSE, 1891 belongs here. *Ctenobolbina mammitata* THORSLUND, 1940 may belong here. Only one specimen is known, and it is therefore not ascertained if it is dimorphic and thus which type of dimorphism it displays. *Winchellatia gunnari* THORSLUND, 1948 should probably be assigned to *Sigmobolbina*, although in that case probably only the one dimorph (male type) has been described. *Ctenobolbina*? aff. *obliqua* KRAUSE described by ÖPIK (1937) is undoubtedly either a *Sigmobolbina* or *Bolbina* species. The following species may thus be included in *Sigmobolbina* gen. n.:

- Sigmobolbina kuckersiana* (BONNEMA, 1909)
 » *obliqua* (KRAUSE, 1892)
 » *obliqua kuckersiana* (BONNEMA, 1909)
 » *oblonga* (STEUSLOFF, 1894)
 » *sigma* (KRAUSE, 1889)
 » *variolaris* (BONNEMA, 1909)
 » ? *gunnari* (THORSLUND, 1948)
 » ? *mammilata* (THORSLUND, 1940)

It is possible that some of the above forms may later be shown to be synonyms. It may also be noted that *Sigmobolbina (oblonga) kuckersiana* and *Sigmobolbina obliqua kuckersiana* are homonyms, and cannot both be valid, whether they are considered subspecies or species. As a further study on these forms may prove that the one or the other may be a synonym for another species, none of them will be renamed here.

Bolbina gen. n.

(Text fig. 7).

Derivation of name: — The name indicates the likeness with *Sigmobolbina* and *Ctenobolbina*.

Type species: — *Bollia ornata* KRAUSE, 1896, from Ordovician drift boulder in N. Germany.

Diagnosis: — Elongated, ends subequal, sometimes with faint forward swing. Sulcus (S2) of median length. L2 forms a swollen

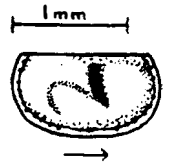


Fig. 7. *Bolbina ornata* (KRAUSE, 1896). After BONNEMA (1909, pl. IV, fig. 4).

lobe, connected ventrally to a postero-ventral lobe. The latter may end in a spur-like conical process, and appears to be dimorphic. These lobes form a more or less U-shaped area, and may be more or less well distinguished from the surrounding area. Velate structure short and ridge-like, sometimes wide (dimorphism?). In the latter case the velate structure (frill) is widest postero-ventrally.

Remarks: — *Bollia minor kuckersiana* BONNEMA, 1909, *B. minor robusta* BONNEMA, 1909, *B. ornata latimarginata* BONNEMA, 1909, and *B. ornata* KRAUSE, 1896 (as described and figured by BONNEMA, 1909) are no doubt congeneric. As suggested by BONNEMA (1909, p. 63) it is possible that *B. ornata latimarginata* (with wide velate frill) is only a dimorph of *B. ornata*. If this is so, this species appears to show dimorphism both in the carinal and velate structures. The postero-ventral lobe in *Bolbina* most probably corresponds to that sometimes seen in *Sigmobolbina* (especially in *S. obliqua*). It may therefore represent a carinal structure. It seems reasonable to assume that *Bolbina* has developed from *Sigmobolbina*. Because of the swollen U-shaped ridge, the sulcus in *Bolbina* is not as long as in *Sigmobolbina*, and cannot be sigmoidal. It agrees, however, very well with the corresponding part of the sulcus in *Sigmobolbina*. It is interesting to note that the velate structure, which has been developed as a velate ridge in earlier representatives of the Sigmoidopsinae (which may have developed from forms with wide frills), is again developed as a frill in *Bolbina ornata latimarginata*. Furthermore it is of interest to note that this frill is widest postero-ventrally, thus differing from the wide frills in other families.

Bollia minor ornata KRAUSE, 1896 is quite probably conspecific with the specimens assigned to this form by BONNEMA (1909). *Bollia minor* KRAUSE, 1892 and *Bollia major* KRAUSE, 1892 are no doubt congeneric, but the illustrations of these appear to be rather schematic. It is possible that some forms described by BONNEMA (1909) are conspecific. *Ctenobolbina? minor mitis* ÖPIK, 1937 appears to be congeneric. *Ctenobolbina* aff. *obliqua* KRAUSE described by ÖPIK (1937) is no doubt either a *Sigmobolbina* or *Bolbina* species. The following forms may thus be included in *Bolbina* gen. n.:

- Bolbina major* (KRAUSE, 1892)
- » *minor* (KRAUSE, 1892)
- » » *kuckersiana* (BONNEMA, 1909)
- » » *robusta* (BONNEMA, 1909)
- » » *mitis* (ÖPIK, 1937)
- » *ornata* (KRAUSE, 1896)
- » » *latimarginata* (BONNEMA, 1909)

Affinities: — Most of these forms have usually been assigned to *Bollia* JONES & HOLL. They are, however, probably not closely

related to this genus, from which they differ i.a. in having a velate structure. The U-shaped area of *Bolbina* does not seem to be quite homologous with the U-shaped ridge of *Bollia*. *Bolbina* is, however, no doubt close to *Sigmobolbina* and *Sigmoopsis*, and is confidently included in the Sigmoopsiinae.

Kiesowia ULRICH & BASSLER, 1908.

Type species: — *Beyrichia dissecta* KRAUSE, 1892.

Diagnosis: — Carapace elongate, with more or less pronounced forward swing. The lobes are developed as one or more nodes. The carinal structure thus also consists of a row of nodes (or bluntly pointed spines). It is not known if the carinal structure is subject to dimorphism. The velate structure is developed as a row of small tubercles (spine bases?). Median sulcus sigmoidal when well developed.

Remarks: — The type species was described from an Ordovician drift boulder in N. Germany. It is not very well known, only one drawing of it being given, and a none too detailed description. *K. pernodosa* and *K. margaritata*, both described by ÖPIK (1937), show so many features in common with *K. dissecta* that they may be regarded as congeneric and give us a more detailed picture of the genus. No doubt also *Beyrichia mammilosa* KRAUSE (1892) belongs here. The median sulcus (S2) of the Esthonian species is sigmoidal. *Beyrichia?* sp. described by ÖPIK (1937) is also a *Kiesowia*. It is characteristic of *Kiesowia* that its lobes (and carinal structure) are split up into nodes. In this respect *Ctenobolbina? octispina* ÖPIK, 1937 is rather similar. Here the carinal nodes are elongated into long and bluntly pointed spines. This species may perhaps belong to *Kiesowia*, in addition to the closely related *Entomis (Bursulella?) quadrispina* KRAUSE, 1892. *Beyrichia radians* KRAUSE, 1892, generally assigned to *Kiesowia*, has a wide frill. The following species may be included in *Kiesowia*:

- Kiesowia dissecta* (KRAUSE, 1892)
- » *mammilosa* (KRAUSE, 1892)
- » *margaritata* ÖPIK, 1937
- » *?octispina* (ÖPIK, 1937)
- » *pernodosa* ÖPIK, 1937
- » *?quadrispina* (KRAUSE, 1892)
- » *radians* (KRAUSE, 1892)

Affinities: — The general pattern of *Kiesowa*, well demonstrated in *K. margaritata* (ÖPIK, 1937, pl. XIV, figs. 7—8) reminds one of *Sigmoopsis*. The frill of *K. radians*, on the other hand, reminds one of the Tetradellinae, and *Kiesowia* is for the time being only tentatively included in the Sigmoopsiinae. *Kiesowia? octispina* appears to be a true sigmoopsiid.

Ctenobolbina ULRICH, 1890.

(Text fig. 3; 11—12).

This genus has long been a typical "sack" genus, into which a number of disulcate forms of the morphological type S2—S3 have been placed, as well as a number of unisulcate forms which did not fit into *Primitia* or *Eurychilina*. Some of the latter have later been removed to *Ctenentoma* (cf. p. 224) and *Parabolbina* (cf. p. 239). *Ctenobolbina* is here restricted to the type species, *Ctenobolbina ciliata* (EMMONS, 1855), and closely related forms.

Diagnosis: — Uni- to disulcate forms with entire velate structure, developed as a ridge or narrow frill. The sulci are long. Lobal area is continuous with the extralobal area. There are usually alate processes or a spur-like spine behind the ventral end of the median sulcus. Surface usually granulated.

Remarks: — As examples of this genus, besides the type species (*Ctenobolbina ciliata*), may be mentioned; *C. emaciata* ULRICH, 1890, *C. bispinosa*, and *C. alata* ULRICH, 1890. *C. jemtlandica* THORSLUND (1940) may also belong here.

The alate processes may possibly represent rudiments of the carinal structure, and may be compared with the carinal spur of *Sigmobolbina* gen. n., possibly also with the spine of *Winchellatia*. According to ULRICH (1890, p. 110) the alate processes in *C. alata* "seem to be rather variable features, since in some examples, apparently in a good state of preservation, they are considerably smaller, and more spine-like than in those figured". It is thus possible that these features show dimorphism.

Affinities: — *Ctenobolbina* may be close to *Carinobolbina* gen. n., especially if the alate processes can be shown to be dimorphic. For this reason *Ctenobolbina* may belong to the Sigmoopsiinae. *Cteno-*

bolbina may probably not be closely related to the Hollinidae, as is generally accepted (cf. p. 239).

Winchellatia KAY, 1940.

Remarks: — The type species, *Winchellatia longispina* KAY, 1940, has a spur-like spine, rather like that of *Sigmobolbina* gen. n. If it corresponds to the carinal spur in *Sigmobolbina* gen. n. (which seems quite possible), the frill of *Winchellatia* is a velate structure. As this frill is stated to be dimorphic (Kay, 1940, p. 253), it is the velate structure which is dimorphic in *Winchellatia*, and not the carinal structure as in *Sigmobolbina* gen. n. In addition *Winchellatia* does not have such a well-defined sigmoidal median sulcus as *Sigmobolbina* gen. n. Further study may show if these genera are related. For the present *Winchellatia* is tentatively included in the Sigmoidopsiinae.

Family Tetradellidae SWARTZ, 1936.

Diagnosis: — See p. 262. *Included genera:* — See list p. 266.

Remarks: — To the family Tetradellidae SWARTZ (1936, p. 551) originally attributed the following genera: *Tetradella*, *Dilobella*, *Ceratopsis*, *Kiesowia*, *Thomasatia*, *Bassleratia*, *Bellornatia*, and *Raymondatia*. The 4 last genera were transferred to the subfamily Bassleratiinae by SCHMIDT, 1941, who regarded the tetradellids as a subfamily of the Hollinidae. SCHMIDT included the following genera in the Tetradellinae: *Tetradella*, *Tallinnella*, *Ceratopsis*, *Kiesowia*, *Rigidella*, *Ctenobolbina*, and hesitatingly, *Dilobella*, *Pseudostrepula*, *Duhmbergia*, and *Polyceratella*. HESLAND (1949) followed SCHMIDT in regarding the Tetradellinae as a subfamily of the Hollinidae, and added the following genera to the Tetradellinae: *Glossopsis*, *Ogmoopsis*, and *Steusloffia*.

Glossopsis, *Ogmoopsis*, and *Kiesowia* have been transferred to the Sigmoidopsiidae. The other genera mentioned above are retained in the Tetradellidae.

As discussed below, the relationships between the Hollinidae and Tetradellidae are not clear, and the tetradellids are here regarded as constituting a separate family, divided into 3 subfamilies: Tetradellinae, Bassleratiinae, (probably including Ctenentominae), and Piretellinae (probably including Ctenonotellinae).

Subfamily Tetradellinae SWARTZ, 1936.

(Text fig. 3; 13—17).

Diagnosis: — See p. 263. *Included genera:* — See list p. 266.

Remarks: — This may be rather a central group, showing trends towards other groups. The oldest known beyrichiacean with a velate structure is *Tallinnella primaria* (ÖPIK, 1937) or a closely allied form from the Lower Didymograptus Shale in Norway. The subfamily Tetradellinae includes genera with entire velate structures (probably unspecialized conditions). Dimorphism may be present in that the frill (or part of it) may be convex in some individuals. *Tetradella* and *Dilobella* constitute a group of their own, characterized by the (dimorphic?) development of submarginal loculi between the velate and carinal structures in some individuals. It is hardly necessary, however, to restrict the subfamily Tetradellinae to these two genera alone.

Remarks on the genera *Tetradella* and *Tallinnella*.

(Text fig. 3; 15, 17 — fig. 9 e)

When establishing the genus *Tetradella*, ULRICH (1890) grouped its species into two "sections". The one section was later (1894) awarded generic rank (*Ceratopsis*). The remaining species assigned to *Tetradella* may, however, also be arranged in two groups, as pointed out by SCHMIDT (1941, p. 41); the *quadrilirata* group and the *subquadrans* group. *T. quadrilirata* was designated the type species by ULRICH (1894). This is most unfortunate, since the *quadrilirata* group is a small group of rather abberant forms, whereas the *subquadrans* group represents more that which has become the general concept of the genus, and includes the majority of species.

As will be discussed further below, it is not even certain that the *quadrilirata* group and *subquadrans* group are closely related. For this and other reasons the writer has found it safest and most correct to restrict *Tetradella* to the *quadrilirata* group, although it is regrettable that the *subquadrans* group will then have to be transferred to another genus.

In 1937 ÖPIK erected *Tallinnella* (type species *T. dimorpha* ÖPIK, 1937) and also assigned to it *Beyrichia marchica* KRAUSE, 1889. *Tallinnella* was stated to differ from *Tetradella* (s.l.) mainly in the development of a dimorphic pouch, formed by the frill. The

position of *Tallinnella* vis-a-vis *Tetradella* has been discussed in detail by SCHMIDT (1941, p. 38) and HESSLAND (1949, p. 338). SCHMIDT maintains that *T. dimorpha*, *T. marchica*, and probably also *T. grewingki* (BOCK, 1867) are congeneric, but, seeing their likeness to the *subquadrans* group, deems that *Tallinnella* should be regarded as a synonym or subgenus of *Tetradella*. HESSLAND, on the other hand, maintains *Tallinnella* to be a valid genus, and assigns *T. grewingki* to *Tetradella*, considering the sharply raised border of *Tallinnella* as an important distinguishing feature.

The anterior velate pouch of *Tallinnella dimorpha* is not sharply set off from the rest of the frill as is the velate pouch of the Primitiinae. In *T. grewingki* too, the anterior part of the frill may be more or less convex, although it has not been established if this is a dimorphic feature. *Öpikiium* and *Rakverella* (probable descendant of the Tetradellinae) show dimorphism in the frill, some individuals having a strongly convex frill. It is interesting to note that the same is true of *Laccochilina* which is an early genus closely related to the Tetradellinae. In the writer's opinion the whole of the *subquadrans* group should be assigned to *Tallinnella*, even if all species do not show such a marked dimorphism as *Tallinnella*. Such a dimorphism appears to be an early phylogenetic feature, and is not characteristic of *Tallinnella dimorpha* alone. The sharply raised border of *T. dimorpha* is in agreement with the accentuated relief as shown by the whole of this species. Furthermore a similar raised border occurs in the earliest known tetradellid species, *T. primaria* (ÖPIK, 1937).

Tallinnella, as defined here, includes forms showing different trends. Forms with crested lobes like *T. lanceolata* (HESSLAND, 1949) (text fig. 9e) point towards *Steusloffia*, whereas forms with swollen lobes and fainter sulci, as *T. teres* (HESSLAND, 1949) may be close to *Hesslandella* gen. n. In the Middle Ordovician there are forms like *T. superciliata* (REED, 1910) with the wide frill restricted to the anterior and ventral areas, thus pointing towards the genera here included in the Piretellinae. *T. scripta* (HARPER, 1947) and *T. bicuneiformis* (HARPER, 1947) are unusual in having L3 connected with the velate ridge by a short ridge. *T. duftonensis* (REED, 1910) may be close to *T. bohémica* (JONES, 1855 or BARRANDE, 1872). *T. subquadrans* may be a rather unspecialized form.

If the *quadrilirata* group has developed from the *subquadrans* group, *Tallinnella* may be regarded as a subgenus of *Tetradella*, but

this is, however, uncertain. In some respects the *subquadrans* group (*Tetradella* s.s.) agrees with *Pseudostrepula*. A specimen of *Pseudostrepula kuckersiana acuta* illustrated by BONNEMA (1909, pl. VI, fig. 26) shows an undulation of the area between the carinal and velate ridge which is reminiscent of the pitted area of *Tetradella*. In addition its ridges remind one of *Tetradella quadrilirata* and allied species.

As discussed by SWARTZ (1936, p. 551) *Tetradella* and *Dilobella* may be closely related. It is, however, not necessary to believe that *Tetradella* developed from *Dilobella*, the opposite being even more probable from analogy with *Tallinnella* — *Steusloffia*, where the unisulcate *Steusloffia* appears to have developed from the trisulcate *Tallinnella*. It may be said that *Dilobella* appears to be the unisulcate equivalent of *Tetradella*. As stated by SWARTZ (1936, p. 552) the peculiar terminal loculi seen in these two genera may be of sexual significance, although KAY (1940, p. 265) points out that there seems to be a gradation from forms lacking these pits to those having them well developed.

Tetradella (here restricted to the *quadrilirata* group) thus differs from *Tallinnella* (here including the *subquadrans* group) in having terminal loculi, at least in some individuals and also in having some of the lobes divided into two ridges.

Hesslandella gen. n.

(Pl. 1 fig. 1).

Derivation of name: — This genus is named after Ivar Hessland, who described the type species.

Type species: — *Ctenentoma macroreticulata* HESSLAND, 1949.

Diagnosis: — Unisulcate, straight-hinged ostracods with long sulcus, which may be geniculate. Presulcal node may be developed. Velate ridge entire. Carinal structure and dorsal ridge not developed. Dimorphism not observed.

Remarks: — As discussed below (p. 224) the type species of *Ctenentoma* is based on an internal mould, which probably belongs to *Steusloffia*. Apart from this, a number of different forms have been assigned to *Ctenentoma* because they are unisulcate and have a long sulcus. They are, however, not all closely related. *Hesslandella* is proposed as a new genus for *Ctenentoma macroreticulata* and allied

species. It appears to be rather an unspecialized genus. *C. falcatosulcata* HESSLAND, 1949 appears to be close to *H. macroreticulata* and should be included in the same genus. Despite having a more pronounced forward swing, *C. canaliculata* HESSLAND, 1949 may probably belong here too, and so may *Aulacopsis nodosa* HESSLAND, 1949, although the latter two species are not well known and may represent larval stages. *Ctenentoma rectangulocarinata* HESSLAND, 1949 (one valve known) is probably a young *Aulacopsis*.

Hesslandella macroreticulata (pl. 1, fig. 1) agrees rather well with *Tallinnella teres* (HESSLAND, 1949) regarding shape, velate ridge, and surface ornamentation, and may represent its unisulcate equivalent. The sulci in *T. teres* are rather faint, and it seems probable that these species are related. For this reason *Hesslandella* is included in the Tetradellinae.

Ceratopsis ULRICH, 1894.

(Text fig. 3; 13—14).

The type species, *C. chambersi* (MILLER, 1874), is close to *Tallinnella*, especially forms like *T. subquadrans*. Characteristic of *Ceratopsis* is the horn-like development of the dorsal end of L1. It seems that similar horns or spines may be developed in different groups, and that many species which have been assigned to *Ceratopsis* are not congeneric with *C. chambersi*. KESLING (1951, p. 108) states that *Ceratopsis* has some dimorphic species, mentioning *C. playtyceras* and *C. obliquejugate*. These species are here assigned to *Sigmoopsis* gen. n. (cf. p. 205) of the family Sigmoopsiidae. *C. chambersi* and allied forms have no carinal dimorphism as the Sigmoopsiinae and do not have the sigmoidal median sulcus of these forms. No dimorphism is known in *Ceratopsis*; if present, it may be expected in the velate structure. The following genera are now known to produce forms with L1 extending into a horn or spine dorsally; *Ceratopsis*, *Sigmoopsis*, *Dicranella*, *Rakverella*. In *Tallinnella dimorpha* too, L1 may be slightly protruding dorsally.

Polyceratella ÖRIK, 1937.

The position of this genus is uncertain. It has a velate structure, but the carinal ridge is dominant. It may have developed from *Tallinnella* and is tentatively included in the Tetradellinae.

Subfamily Piretellinae ÖPIK, 1937.

(including Ctenonotellinae SCHMIDT, 1941).

(Text fig. 11 a).

Diagnosis: — See p. 263. *Included genera:* — See list p. 267.

Remarks: — The development of the frill is especially characteristic of this group. The frill may be wide but may end more or less abruptly posteriorly and is confined to the anterior and ventral areas (restricted frill). It may show dimorphism, some individuals having a strongly incurved frill.

Most probably the genera included here developed from the Tetradellinae, probably from forms like *Tallinnella superciliata*. HARPER (1947, p. 351) writes that the rounded character of the lobes suggests that a new genus may have to be established for forms like *T. superciliata*. If this was done, this genus would probably be intermediate between the Tetradellinae and the Piretellinae, and may as well be assigned to the one as to the other. Although the Piretellinae have probably developed from the Tetradellinae, it is uncertain whether the Piretellinae represent a strictly monophyletic group, or rather embrace different but probably closely related phylogenetic lines. If this subfamily is split up again, Ctenonotellinae SCHMIDT is available as a subfamily name for *Ctenonotella* and allied.

The Primitiidae may be related to the Piretellinae (cf. p. 226).

Notes on the genera: — ÖPIK (1937, p. 46) erected a family Piretellidae and included in it *Piretella*, *Hesperidella*, *Steusloffia*, *Pseudostrepula*, *Strepula*, and *Rigidella*. THORSLUND (1940, p. 175) doubts the close relationship between *Piretella* and the other genera, stating that *Piretella* differs from these in the general outline of the carapace, in the structure of the false border, and in the presence of a dimorphic ventral pouch. SCHMIDT (1941) drops the family Piretellidae, and transfers its genera to different subfamilies.

The general outline of *Piretella* corresponds favourably well to that of *Steusloffia*, and the difference in structure of the frill in these two genera is not greater than f. inst. between *Chilobolbina dentifera* and *C. decumana*. Furthermore, HESSLAND (1949, p. 355) has later described a new species, *Steusloffia polynodulifera* with a U-shaped crest rather similar to that in *Piretella*. It is therefore mainly the development of a dimorphic ventral pouch which separates *Piretella* from the other genera assigned to the Piretellidae by ÖPIK. The

latter genera (here assigned to the Bassleratiinae, cf. p. 220) do not show any (at least not any conspicuous) dimorphism in the velate structures. This fact suggests that *Piretella* has not developed from early Bassleratiinae as *Steusloffia*.

In the writer's opinion *Piretella* may be closely related to forms like *Piretopsis* (HENNINGSMOEN, 1953) and *Rakverella*.

Piretopsis has a ridge similar to that in *Piretella*, but is (faintly) tetralobate, and has an additional ridge on L4. In the earliest known *Piretella* species, *P. margaritata* ÖPIK, 1937, a row of spines appear to occupy a similar position as this additional ridge (see ÖPIK, 1937, pl. XIV, fig. 10). Furthermore *Piretopsis* agrees with *Piretella* in not having an entire frill, and the frill may be convex. *Piretopsis* may be an intermediate stage between *Piretella* and Tetradellinae.

The ridge in *Piretella* is close to that in *Rakverella*, which differs mainly in being more lobe-like. *Rakverella*, too, has the frill confined to the anterior and ventral areas. The writer has in addition seen individuals of *Rakverella* with the frill incurved to form a false pouch very similar to that in *Piretella*.

ÖPIK (1937) describes as *Tetradella*? *pectinata* and *Tetradella*? sp. aff. *pectinata* some internal moulds, having the test only preserved in the marginal region. These are no doubt internal moulds of *Rakverella bonnemai* ÖPIK, 1937. The spines and ridges in the central area of *Rakverella* explain why this part of the test is often missing. A comparison of an internal mould of *Tetradella*? *pectinata* (ÖPIK, 1937, pl. XV, fig. 12) with a specimen of *Rakverella bonnemai* (l.c., pl. XV, fig. 10) shows that the internal lobation agrees well with the external pattern, although the tetralobation is better seen in the mould. Furthermore, in *Tetradella*? sp. aff. *pectinata* (l.c., pl. XV, fig. 15) the anterior spine of *Rakverella* is preserved. *Rakverella* displays an unusual feature: the ornamentation of the carapace wall extends well into the frill. The same is seen in *Tetradella*? *pectinata*. *Rakverella*, too, appears to have developed from the Tetradellinae, possibly from forms like *Tallinnella superciliata*.

Ctenobolbina duhmbergi, described by ÖPIK (1937, p. 32), most probably represents an early instar of the associated *Piretella margaritata*. The differences between these correspond to those of different instars of *Steusloffia costata*, as described by THORSLUND (1940, p. 176), where the crests first (ontogenetically) are missing to a large extent, then appear as rows of spines, to be developed as full crests

in adult stages. *Ctenobolbina duhmbergi* was made the type species of *Duhmbergia* by SCHMIDT (1941, p. 39). This genus is thus probably a synonym of *Piretella*.

Dicranella may be closely related to *Rakverella*, although they should probably not be regarded as synonyms as suggested by SCHMIDT (1941, p. 48).

SCHMIDT (1941) assigns *Dicranella* (including *Rakverella*) together with *Ctenonotella* to a subfamily, Ctenonotellinae, of the Hollinidae. In *Ctenonotella* L2 and L3 are developed as two ridge-like lobes, and the median sulcus is long. It agrees, however, with *Rakverella* in the general shape, and in having a shortened frill. For this reason *Ctenonotella* may be assigned to the Piretellinae, in which case Ctenonotellinae becomes a junior synonym of Piretellinae. *Ctenonotella* may be near to *Tallinnella dubitabilis* (ÖPIK, 1937), which may be related to *T. superciliata*. *T. dubitabilis* was suggested as a possible synonym of *T. turnbulli* (REED, 1910) by SCHMIDT (1941, p. 42). *T. turnbulli* was for good reasons regarded as a synonym of *T. superciliata* by HARPER (1947, p. 350).

Öpikium (= *Biflabellum* ÖPIK, 1937) appears to be related to *Ctenonotella*. L2 and L3 are not developed as nodes, but the sulcus is long, and the frill is of the abruptly ending type (restricted to the anterior and ventral areas), as in *Ctenonotella*. The frill shows dimorphism, being convex in some individuals.

Subfamily Bassleratiinae SCHMIDT, 1941.

(Text fig. 3; 18—19. figs. 8a—d, figs. 9a—d).

Diagnosis: — See p. ... *Included genera*: — See list p. ...

Remarks: — This subfamily was erected by SCHMIDT for the genera *Bassleratia*, *Thomasatia*, *Bellornatia*, and *Raymondatia*, all

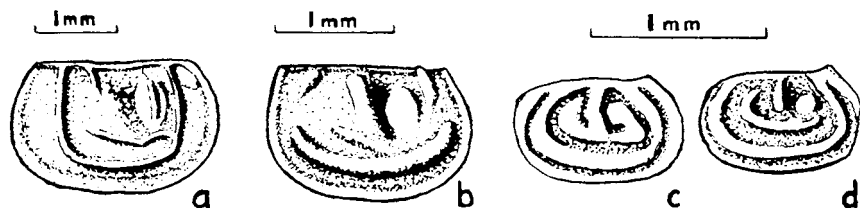
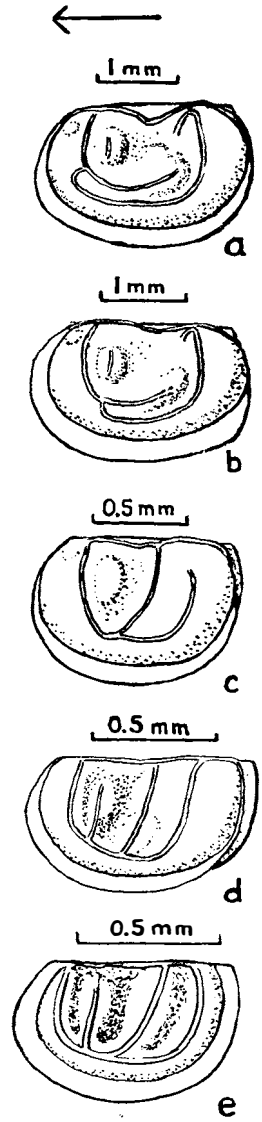


Fig. 8. a) *Steusloffia rigida* (after ÖPIK, 1937, pl. IV, fig. 1), b) *Steusloffia europaea* (after ÖPIK, 1937, pl. III, fig. 11a), c) *Bassleratia tyra* (after KAY, 1934, pl. 46, fig. 1), d) *Bassleratia tyra* (after KAY, 1934, pl. 46, fig. 12).

Fig. 9. Morphological series from *Tallinnella* via *Rigidella* to *Steusloffia*. a) *Steusloffia costata* (after THORSLUND, 1949, pl. XX, fig. 10) Middle Ordovician, b) *Steusloffia costata* (after THORSLUND, 1940, pl. 3, fig. 6) Middle Ordovician, c) *Steusloffia polynodulifera* (after HESSLAND, 1949, pl. X, fig. 2a) Lower Ordovician. d) *Rigidella* cf. *mitis* (cf. pl. 1 fig. 3) Lower Ordovician, e) *Tallinnella lanceolata* (after HESSLAND, 1949, figs. 10, 13). Lower Ordovician.



described by KAY (1934) from North America. Furthermore *Steusloffia* and *Polyzygia* were doubtfully included in this subfamily.

In 1937 ÖPIK described a new species as *Drepanella europaea* (text fig. 8b). As pointed out by SCHMIDT (1941, p. 51) this should not be assigned to that genus and was transferred by him to *Bassleratia*. In the writer's opinion it would be better to include it in *Steusloffia*, with which it agrees even more than with *Bassleratia*. *Steusloffia europaea* differs from the other known species of this genus in having somewhat coarser sculpture; some of the crests in other species are developed here rather as ridges, or (dorsal part of C3) even as a node. In the writer's opinion coarser or finer development of the sculpture often does vary in closely related species. *Steusloffia europaea* furthermore agrees very well with the other known *Steusloffia* species in the shape of the valve, the median lobe (L2) being developed as a large elliptical node, etc. It appears also very probable, however, that *Bassleratia typa* (text figs. 8c—d) is related to *S. europaea*. For this reason *Steusloffia* may be included in the Bassleratiinae.

The family Piretelliidae was erected by ÖPIK (1937) for the genera *Piretella*, *Steusloffia*, *Rigidella*, *Pseudostrepula*, *Hesperidella*, and *Strepula*. As discussed above (p. 217), all except *Piretella* have been excluded from the subfamily Piretelliinae, and are here included in the Bassleratiinae. *Rigidella*, *Hesperidella*, and *Strepula* appear to be

rather closely related to *Steusloffia*. The position of *Pseudostrepula* is perhaps slightly more uncertain.

Origin: — If *Bassleratia* really is related to *Steusloffia*, the origin of the Bassleratiinae is clear. Early forms like *Steusloffia polynodulifera* HESSLAND, 1949 (text fig. 9c) and *Rigidella* are so close to early Tetradellinae that the relationships can hardly be denied. *Tallinnella lanceolata* HESSLAND, 1949 (text fig. 9e) is so close to *Rigidella* that one may be in doubt as to whether it should be placed in the one genus or other. Somewhere, however, the boundary between the Tetradellinae and Bassleratiinae has to be drawn. *T. lanceolata* shows four lobes beneath the crests and three sulci. In *Rigidella* only a semisulcus separates L3 and L4, and in *Steusloffia* even this disappears. The disappearance of a true sulcus S3 is taken as the distinction between early Tetradellinae and early Bassleratiinae. This does not exclude the possibility of enclosing in Bassleratiinae later forms that may have developed a posterior sulcus (S3), and, on the other hand, including in the Tetradellinae species with no S3 but belonging to other trends.

Remarks on *Rigidella* ÖPIK, 1937.

(Text fig. 10, pl. 1 figs. 2—4).

The type species is *Beyrichia mitis* ÖPIK, 1935. According to ÖPIK's description and schematic drawing of the only known specimen, the area corresponding to L4 carries two ridges more or less parallel to the posterior border. The writer is inclined to believe that the posteriormost ridge is a velate structure, a continuation of the frill. The frill is not especially marked off on the schematic drawing, but is clearly visible on the photograph of the specimen (ÖPIK, 1935, pl. I, fig. 5) (here pl. 1, fig. 2). A close study of this photograph reveals that the test is partly missing in the specimen — it is mainly preserved anteriorly and along the frill. If the direction of the frill is continued posteriorly, it is seen that the posteriormost ridge lies in this direction. It would be rather odd if a lobal ridge should be developed so close to the frill or its extension. Furthermore, what at first glance appears to be the connecting ridge between the posteriormost ridge and the ridge behind L3 is most probably the edge of the test, which is preserved along the frill. It is seen that this line is *not* strictly confluent with the posteriormost ridge. A close

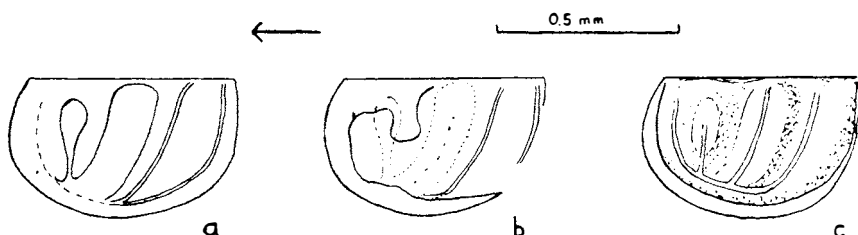


Fig. 10. *Rigidella mitis* (ÖRIK, 1935). Holotype. a) after sketch given by ÖRIK (1935, p. 11). b) The writer's interpretation of the photograph given by ÖRIK (1937, pl. 1, fig. 5). The test is preserved to the left and along the ventral border. c) Reconstruction suggested by the writer.

study further reveals that the ridge behind L3 (this ridge is here assumed to be C4) continues forwards ventrally, just above the line assumed here to be the edge of the test. The forward continuation of C4 joins a row of tubercles (corresponding to C3) on L3. C2 is not preserved. C1 is seen in the dorsal part of L1, where the test is preserved.

The writer believes that the crests (ridges) of *Rigidella mitis* form a normal tetradellid pattern, and that the posteriormost ridge is a continuation of the frill. This explanation is deemed likely by a find of an ostracod corresponding rather closely to *R. mitis* but having the crests as suggested here. If the writer's interpretation of the crests in *R. mitis* is correct, it should probably be assigned to this species. For the time being it may be safer to refer to it as *R. cf. mitis*. The material of *R. cf. mitis* (pl. 1, figs. 3—4) was collected in drift boulders at Humlenäs, Kristdala in Småland, Sweden by Prof. E. Stensiö of the State Museum of Natural History in Stockholm, who kindly drew the writer's attention to it. The figures of *R. cf. mitis* (text fig. 9d; pl. 1, figs. 3—4) may be compared with those of *R. mitis* (text figs. 10a—c). According to the associated fauna these boulders are probably of the same age as the *Megalaspis* Limestone from which *R. mitis* was described.

Whether the above explanation is correct, or *R. mitis* really has an additional ridge posteriorly, there can be little doubt that *Rigidella* is closely related both to such *Tallinnella* species as *T. lanceolata* (HESSLAND, 1949) and *Steusloffia*. The lobation of *Rigidella* shows an intermediate stage; whereas *Tallinnella* has 4 lobes and 3 sulci and *Steusloffia* has only one sulcus, *Rigidella* still has 4 lobes,

but L3 and L4 are separated by a semisulcus only, and there are thus only two real sulci in *Rigidella*. This is the reason why ÖPIK (1935, p. 11) states that *R. mitis* is trilobate, whereas HESSLAND (1949, p. 339) states that it is distinctly 4-lobate.

R. cf. mitis may possibly be conspecific with *Rigidella erratica* (KRAUSE, 1889), and it is not improbable that *R. mitis* may turn out to be a synonym of this species, if the writer's interpretation of the latter is correct. One of the valves figured by KRAUSE as belonging to *erratica* (KRAUSE, 1889, pl. II, fig. 8) was separated as a new species, *Rigidella krauseana* by SCHMIDT, 1941. The difference between *R. krauseana* and *R. erratica* is, however, not greater than that seen in the Småland material; the lobe L3 being more or less well developed in its ventral part. It is thus possible that *R. krauseana* is a junior synonym of *R. erratica*. The specimen figured by KRAUSE 1889 in pl. II, fig. 6 may not, however, belong to *R. erratica*. It was given the subspecific name *granulosa* by KRAUSE (1891), but, as suggested by ÖPIK (1935, pp. 10—11) (cf. HESSLAND, 1949, p. 344), may be identical with *Tallinnella grewingki*.

Remarks on *Steusloffia* ULRICH & BASSLER, 1908.

(Text figs. 8a—b, 9a—c).

This genus is of special interest, firstly because THORSLUND (1940) has studied its larval instars and has shown how the crests ontogenetically develop via rows of spines, and secondly because it appears to be an example of a unisulcate form having developed from trisulcate ancestors.

S. polynodulifera occurs in the Lower Ordovician, whereas *S. costata* (LINNARSSON, 1869) occurs in the Middle Ordovician. It is seen that one of the differences between these species is the position of the fusing point of C3 and C4, which phylogenetically moves forwards. This migration continues within the species *S. costata* (cf. THORSLUND, 1948, p. 369). If this trend is hypothetically extended backwards from *S. polynodulifera*, it would result in a form with "normal" tetradellid arrangement of the crests, as in *Rigidella cf. mitis* or *Tallinnella lanceolata* (cf. text fig. 9). It seems highly probable that *Steusloffia* has developed from forms like these, with which it agrees in general form, surface ornamentation, type of velate structure, and other details. It may be mentioned here that the area corre-

sponding to the ventral part of L3 may be swollen to form a lobe-like inflation in *Steusloffia*, thus agreeing with the swollen ventral part of L3 in *Rigidella* cf. *mitis*. As long as the lobes are developed, the crests follow their course. When the lobes become confluent, the crests more or less develop their own pattern.

As discussed above, *Drepanella europaea* ÖPIK, 1937 should perhaps be assigned rather to *Steusloffia* instead of *Bassleratia* as suggested by SCHMIDT (1941).

Remarks on *Ctenentoma umbonata* (STEUSLOFF, 1894).

This species is of special interest as it is the type species of *Ctenentoma* SCHMIDT (1941), which again is the type genus of the subfamily Ctenentominae SCHMIDT (1941).

The writer has not seen the holotype and only known specimen of this species. The description by STEUSLOFF is very brief. The specimen was, however, re-examined by KUMMEROW, who states (1924, p. 406) that it is an internal mould (Steinkerne). *Ctenentoma umbonata* is described from a glacial drift boulder and is stated to occur together with i. a. *Conchoprimitia erratica* (KRAUSE, 1891) and *Endoceras angelini* RÜD. As pointed out by STEUSLOFF (1894), this suggests Orthoceras Limestone age (Lower Ordovician).

It is often difficult to refer an internal mould of an ostracod to a certain genus. The only genus, however, with internal moulds exactly like that of *Ctenentoma* and occurring in Orthoceras Limestone appears to be *Steusloffia*. Internal moulds of *S. polynodulifera* HESSLAND, 1949 may be quite like that of *Ctenentoma*, showing the same long median sulcus and rather small but well defined elliptical median node (L2). The frill of *Ctenentoma umbonata* is stated by STEUSLOFF to be strongly convex. Even this has been observed in Norwegian material of internal moulds of *S. polynodulifera*. It is therefore most probable that *Ctenentoma umbonata* is the internal mould of a *Steusloffia* species, possibly *S. polynodulifera* or some closely related species, as f. inst. *S. lineata* KRAUSE (1889).

Many unisulcate beyrichiacean ostracods have been assigned to *Ctenentoma*. Some are here assigned to *Aulacopsis* and *Hesslandella* gen. n., others belong to *Sigmobolbina* gen. n. and related genera. None of these genera have, however, an internal mould like that

of *Ctenentoma umbonata*, but the internal mould of *Öpikium* may remind one of it to some extent. *Öpikium*, however, does not have such a well defined median node, and is a later genus (Middle Ordovician).

In the writer's opinion, *Ctenentoma* may be regarded as a younger synonym of *Steusloffia*. This means i. a. that the name Ctenentominae cannot be used for a subfamily. No new name is here proposed, as Ctenentominae becomes a younger synonym of Bassleratiinae, if *Ctenentoma* is a synonym of *Steusloffia*. SCHMIDT (1941, p. 34) included in the Ctenentominae a number of unisulcate genera; *Ctenentoma*, *Winchellatia*, *Parabolbina*, *Acronotella*, and, tentatively, *Hippa* and *Eoconchoecia*. In the writer's opinion the same degree of sulcation need not necessarily indicate relationships (cf. p. 191), and in this case the assemblage was most probably rather heterophyletic.

Family Primitiidae ULRICH & BASSLER, 1923.

(Text figs. 11b—c).

Diagnosis: — See p. 263. *Included genera:* — See list p. 267.

Remarks: — This family originally included the Primitiinae and the Eurychilininae. Later authors have sometimes added other subfamilies.

The recognition of *Beyrichia strangulata* MCCOY, 1851 as the type species of *Primitia* instead of *Beyrichia mundula* JONES, 1855 (cf. WARTHIN, 1948, p. 645) alters the concept, not only of *Primitia*, but also of the Primitiidae. The writer has had the opportunity of

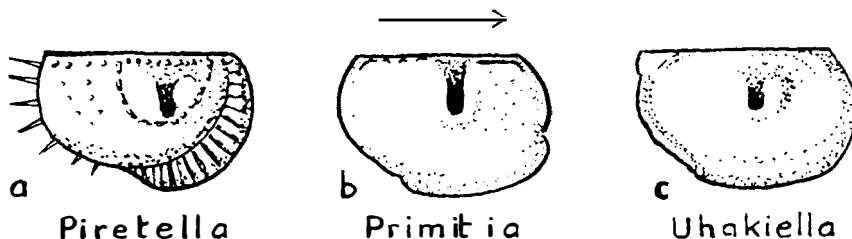


Fig. 11. a) *Piretella margaritata* ÖPIK, 1937 (based on illustrations given by ÖPIK, 1937), b) *Primitia strangulata* (MCCOY, 1851) (sketch based on type material), c) *Uhakiella kohltensis* ÖPIK, 1937 (after ÖPIK, 1937, pl. III, fig. 9).

studying the type material of *Primitia strangulata*. The results will be published in a special paper. It appears that *Uhakiella* is very close to, or more probably, a synonym of *Primitia* (cf. text figs. 11b—c). SCHMIDT (1941, p. 33) regarded *Uhakiella* as a synonym of *Bromidella*, and was followed in this i. a. by HENNINGSMOEN (1949, p. 416). *Bromidella*, too, may then be regarded as a synonym of *Primitia*. The strong dorsal ridge or rather swelling of *Bromidella* is, however, rather unique, and it may be better to retain *Bromidella* as a separate genus, undoubtedly closely related to *Primitia*. It appears that *Chilobolbina* is also related to *Primitia*. As discussed below, the family Primitiidae is here restricted to these genera with a dimorphic velate pouch (false pouch); *Primitia*, *Uhakiella*, *Bromidella*, and *Chilobolbina*.

Bromidella and *Chilobolbina* have hitherto been assigned to the Eurychilininae. If this group is monophyletic, this would involve all the eurychilinids being related to *Primitia*, and Eurychilininae could be regarded as a synonym of Primitiidae, or at least included as a subfamily in the Primitiidae. The eurychilinids do not produce such a well defined ventral pouch as the Primitiidae. It is, however, quite possible that the Primitiidae (earliest known occurrence: Middle Ordovician Kukruse formation) have developed from the eurychilinids (earliest known occurrence: Lower Ordovician), especially as the eurychilinids appear to tend towards forming a well-defined false pouch. There is, however, also the possibility that the Primitiidae developed from the Tetradellinae, possibly via *Piretella* or forms allied to *Piretella*. The Primitiidae agree with the Piretellinae in usually having the frill restricted to the anterior and ventral areas, and in forming a false pouch as a dimorphic feature (cf. text fig. 11). A form such as *Chilobolbina decumana* (BONNEMA, 1909) is rather similar to *Piretella*, save for the absence of the piretellid ridge. Furthermore the Primitiidae develop a dorsal ridge as in *Piretella*, whereas the eurychilinids do not develop such a ridge (excepting the early genus *Laccochilina*). The primitiids and eurychilinids may thus represent separate off-shoots (more or less along the same lines of development) from the Tetradellinae. For this reason it appears to be best to regard the Primitiidae and Eurychilinidae as separate families.

The Euprimitiinae have tentatively been assigned to the Eurychilinidae (cf. p. 228).

Family Eurychilinae ULRICH & BASSLER, 1923.

Diagnosis: — See p. 263. *Included genera:* — See list p. 267.

Remarks: — This family is here defined to include the subfamily Eurychilinae, and, tentatively, the subfamilies Euprimitiinae and Primitiopsiinae. The family Eurychilinae corresponds then to a certain extent to the family Primitiidae in its earlier sense.

Subfamily Eurychilinae ULRICH & BASSLER, 1923.

Diagnosis: — See p. 263. *Included genera:* — See list p. 267.

Remarks: — A number of genera have been included in the Eurychilinae, namely *Apatobolbina*, *Apatochilina*, *Bromidella*, *Chilobolbina*, *Craspedobolbina*, *Eurychilina*, *Laccochilina*, *Neochilina*, and *Platybolbina* (= *Platychilina*). As stated above, *Bromidella* and *Coelochilina* with a velate false pouch, may be close to *Primitia* and have been included in the Primitiidae. *Craspedobolbina*, too, develops a dimorphic pouch (egg-shaped). *Craspedobolbina* is described from a drift boulder in N. Germany. The associated fauna suggests that this form is of upper Ordovician age. It has many features in common with *Beyrichia*, and whether it should be assigned to the Primitiidae or Beyrichiidae depends on the pouch being a velate false pouch or a pouch opening into the main cavity of the carapace (as in the Beyrichiidae) or not. Much the same applies to the Silurian genus *Apatobolbina*. As remarked by ULRICH & BASSLER (1923, p. 522), its »pouch looks so much like that of *Beyrichia* and extends so far up on the slope of the ventral convexity of the valve as to suggest that in this type also it opens on the inner side of the contact margin«. It may be added that this applies to the Silurian species assigned by ULRICH & BASSLER (1923) to *Chilobolbina*. These species may be transferred to *Apatobolbina*, which will then include forms with or without sulcal pit. In these species it is even more clear that the frill continues between the pouch and the margin (cf. ULRICH & BASSLER, 1923, pl. XXXVII, figs. 7, 11). Until further investigations clarify the type of pouch in *Craspedobolbina* and *Apatobolbina*, the writer is inclined to believe, that they may be beyrichiids. It may be recalled that the rather similar Silurian genus *Dibolbina* was already claimed by ULRICH & BASSLER (1923, p. 658) to be a beyrichiid.

The position of the Devonian genus *Neochilina* is rather uncertain. As suggested by SWARTZ (1936, p. 551) it is removed from the Eurychilinidae.

This leaves *Eurychilina*, *Apatochilina*, *Coelochilina*, *Laccochilina*, and *Platybolbina* as probable members of the Eurychiliniinae.

The American species of *Eurychilina* have a peculiar frill with a small ridge subparallel to the edge along the greater part of the inner side of the frill. In the writer's opinion the genus should be restricted to this group. This feature has not been described from any of the other genera assigned to the Eurychiliniinae. It seems probable, nevertheless, that genera like *Laccochilina*, *Coelochilina*, and *Apatochilina* are closely related to *Eurychilina*, although there is always the danger that they may represent different trends developing in the same direction, especially with such rather smooth forms. Some species assigned by HESSLAND (1949) to *Eurychilina* may be transferred to *Laccochilina*, since they do not have the typical *Eurychilina*-frill. There seems to be an even transition of forms from these species to the type species of *Laccochilina*.

Platybolbina corresponds rather well with the other genera retained here in the Eurychiliniinae. *Öpikella* may probably be closely related to *Platybolbina*. The two species erected by THORSLUND (1940, pp. 181—182), *Ö. tvaerensis* without a frill and *Ö. asklundi* with a shortened, incurved frill represent most probably one dimorphic species. Apart from the loss of the frill in one dimorph, this genus agrees very well with *Platybolbina*. There is rather a short step from *Öpikella* to aparchitids, namely, the loss of the frill in the other dimorph as well and it is possible that at least some forms assigned to the Aparchitidae may have developed from Eurychiliniinae via forms like *Öpikella*.

? Subfamily Euprimitiinae HESSLAND, 1949.

Diagnosis: — See p. 263. *Included genera:* — See list p. 268.

Remarks: — The subfamily Euprimitiinae is not well known. It agrees apparently with the Eurychiliniinae in developing uni- or nonsulcate forms, in often having a pitted surface, and in (at least some forms) having a velate structure. The velate structure shows dimorphism as the Eurychiliniinae, but in the Euprimitiinae the dimorphism is usually confined to the antero-ventral part of the

velate structure. The Euprimitiinae do not, however, develop a false pouch as the Primitiidae. The Euprimitiinae are here tentatively included in the Eurychiliniidae.

The type species of *Euprimitia*, *E. sanctipauli* (ULRICH, 1894) has been described in detail by KAY (1940, p. 252), who points out that it is dimorphic. In some individuals the border is depressed, in others forming a flange obscuring a channelled area. *E. labiosa* (ULRICH, 1894) as described by KAY (1940, p. 252) is also dimorphic. Both dimorphs have a narrow frill, but in the one dimorph it is wider antero-ventrally, where it is also situated further from the margin. This part of the frill corresponds most probably to the flange in *E. sanctipauli*, this flange then being a velate structure.

As demonstrated by KAY (1940, p. 262), the type species of *Primitiella*, *P. constricta* ULRICH, 1894, also shows dimorphism. The anterior end is depressed in some individuals, whereas it is steeply raised in others. It may be compared with the dimorphism in *E. sanctipauli*. Whereas *E. labiosa* has a velate frill in both dimorphs, being wider and situated further from the margin antero-ventrally in the one dimorph, *E. sanctipauli* has no velate structure in the one dimorph, but an anteroventral flange in the other. In *Primitiella constricta* both dimorphs have no distinct velate structure, but in the one dimorph the anterior end is steeper and higher, as in *Euprimitia*. It is probable that *Primitiella* is related to *Euprimitia* and may have developed from *Euprimitia* through the loss of any distinct velate structures. If so, *E. sanctipauli* is intermediate between *E. labiosa* and *Primitiella constricta* regarding the velate structure.

Haploprimitia is not very well known, and its type species, *H. minutissima* ULRICH, 1894, has not been recognized in later collections (KAY, 1940, p. 248). It has no velate structure, and may possibly be related to *Primitiella*. The same is true of *Laccoprimitia*, at least if *L. fillmorensis* (ULRICH, 1894) (as described by KAY, 1940, p. 248) is congeneric with the type species. *Ectoprimitia* described by BOUČEK (1936) as a subgenus of *Haploprimitia* is probably not closely related to this, and its position is rather uncertain. *Halliella*, *Hallatia*, *Pyxiprimitia*, and *Punctoprimitia* are probably not related to the Euprimitiinae (cf. p. 248).

No dimorphism is described from the type species of *Euprimites*, *E. reticulogranulata* HESSLAND, 1949 (type material only two carapaces and two valves). *Ctenobolbina suecica* THORSLUND, 1940 may

be congeneric. This species shows a dimorphism very similar to that of *Euprimitia labiosa*. The main difference is that the widened part of the velate structure is situated more ventrally in *Euprimites suecica*. *Euprimitia minor* THORSLUND, 1940 (transferred to *Euprimites* by HESSLAND, 1949) may be conspecific with *E. suecica*, the latter representing adult individuals. It is thus possible that *Euprimites* is related to *Euprimitia*, as suggested by HESSLAND (1949, p. 242). No doubt the type species of *Euprimites* is closely related to early Tetradellinae and *Laccochilina*, and its narrow velate structure may be compared to that of *Hesslandella* and certain species of *Tallinnella*.

?Subfamily Primitiopsiinae SWARTZ, 1936.

Diagnosis: — See p. 263. *Included genera:* — See list p. 268.

Remarks: — *Primitiopsis* resembles *Euprimitia* in general outline, in lobation, in developing a dorsal ridge, and in having a velate false border. Whereas the dimorphic part of the velate structure is situated antero-centrally in *Euprimitia*, the velate false pouch of *Primitiopsis* is usually believed to be situated posteriorly. Good material of different growth stages of the type species, *P. planifrons* JONES, 1887 from Mulde, Gotland, Sweden shows that the sulcal pit migrates towards the end opposite to that bearing the false pouch in some adult individuals. It appears reasonable to assume that the pit migrates forwards during the ontogenetical development, just as the muscle scar migrates forwards in recent ostracods (cf. CLAUS, 1886). This supports the view that the false pouch of *Primitiopsis* is situated posteriorly.

Sulcicuneus was described by KESLING (1951a) as an additional primitiopsid genus. It agrees, however, very well with contemporaneous hollinids, and as its posterior false pouch may be a marginal rather than a velate structure, it is tentatively assigned to the Hollinidae.

Family Aparchitidae JONES, 1901.

Diagnosis: — See p. 263. *Included genera:* — See list p. 268.

Remarks: — A number of non-sulcate, more or less smooth genera have been included in this family. Some are transferred here to other genera.

It is possible that at least some of the forms assigned to this family developed from Eurychilinidae via forms like *Öpikella* (cf. p.228).

In any case, *Aparchites* shows traces of a velate structure and should be included in the Beyrichiacea and not in the Leperditiacea. In the type species, *Aparchites whiteavesi* JONES, 1889, there is a distinct velate ridge. In many other forms assigned to *Aparchites*, as *A. fimbriatus* ULRICH, 1892 and *A. granilabiatus* ULRICH, 1892 the velate structure is developed as a row of spines.

Leperditella (and thus the Leperditellinae) may, however, possibly belong to the Leperditiacea (cf. p. 250). The same may be true of *Eridoconcha*, *Schmidtella*, and *Paraschmidtella* of the new subfamily Eridoconchinae, and *Conchoprimitia* of the new subfamily Conchoprimitiinae (cf. p. 250).

Paraparchites, *Antiparaparchites*, *Proparaparchites*, *Microparaparchites*, and *Pseudoparaparchites* have usually been included in the Aparchitidae. As discussed below (p. 243) they are here transferred to the Kloedenellidae, where it has already become usual to place *Sansabella*.

This leaves but a few genera in the Aparchitidae; besides the type genus there are only *Neoaparchites*, *Punctaparchites*, and *Macronotella*. The writer agrees with SCHMIDT (1941) and HESSLAND (1949) who remove *Macronotella* from the Kirkbyidae. The relationships between *Aparchites* and *Macronotella* are, however, not fully known, and it appears best to assign *Macronotella* (and for the same reason *Punctaparchites* and *Neoaparchites*) only tentatively to the Aparchitidae. As ostracods of the rather simple *Aparchites* type may have developed in different groups, and no doubt have done so, it is not more than could be expected that several of the genera assigned to the Aparchitidae would not, on closer examination, turn out to be closely related to *Aparchites*.

Family Drepanellidae ULRICH & BASSLER, 1923.

Diagnosis: — See p. 263. *Included genera:* — See list p. 268.

Remarks: — The subfamily Drepanellinae ULRICH & BASSLER, 1923 was awarded family rank by SWARTZ (1936). SCHMIDT (1941) included four subfamilies in this family; Drepanellinae, Ulrichiinae (= Bolliinae), Aechmininae, and Bassleratiinae. The Bassleratiinae are here excluded from the Drepanellidae and transferred to the Tetradellidae. The Bassleratiinae differ from the Drepanellidae in a number of features, i. a. in having a velate structure, whereas the

submarginal ridge of the Drepanellidae appears to be a carinal structure, or at the best, a fused carinal and velate structure.

The Drepanellidae do not seem to develop either false pouches or pouches as swelling of the carapace wall. It is, however, possible that at least some of the forms of the Drepanellidae are dimorphic. SWARTZ & SWAIN (1941, p. 421) note that there is a considerable variation in the convexity of the postventral third of *Bollia diceratina* SWARTZ & SWAIN, 1941, and suggest that this may be due to sexual dimorphism.

Subfamily Drepanellinae ULRICH & BASSLER, 1923.

Diagnosis: — See p. 264. *Included genera*: — See list p. 268.

Remarks: — ULRICH & BASSLER (1923) established a subfamily Drepanellinae of the Zygobolbidae and included in it *Drepanella*, *Scofieldia*, *Mesomphalus*, and *Drepanellina*. The writer quite agrees with SWARTZ (1936) who transferred the latter two genera to the Kloedeninae (= Beyrichiinae) due to their subventral dimorphic pouches, and removed the drepanellids from the Zygobolbidae. It may be noted that *Mesomphalus* and *Drepanellina* differ from the Drepanellinae again in having a velate ridge. SWARTZ (1936) added *Jonesella* and *Bollia* to the Drepanellinae, and tentatively also *Ulrichia* and *Polyzygia*, whereas SCHMIDT (1941) included the following genera; *Drepanella*, *Scofieldia*, *Jonesella*, *Cornulina*, and *Lindsayella*.

If *Drepanella bigeneris* ULRICH, 1894 is a true member of *Drepanella* (and this seems probable), *Drepanella* appears to be close to *Bollia*. As pointed out by ULRICH & BASSLER (1908, p. 312) it is really difficult to give sufficient reasons for excluding *D. bigeneris* from *Bollia*. It may be remembered that the large size of *Drepanella* (about 2.5 mm long) is also attained by representatives of *Bollia*, as *B. americana zygocornis* SWARTZ, 1936.

Drepanella is, however, not sufficiently known. In a personal communication (2. Nov. 1950) Dr. B. KELLETT NADAU writes that "many figures of *Drepanella* are very misleading. They appear to be flat, with rather sharp, highly raised ridges rising abruptly as if stuck on to this flat surface. Instead, the surface is undulating and there is a deep, subcentrally located dorsal sulcus." It seems therefore best at present to restrict the subfamily Drepanellinae to *Drepanella* and *Scofieldia*, assigning *Bollia* to the Boliinae.

? Subfamily *Bollinae* BOUČEK, 1936.

(including subfamily *Ulrichiinae* SCHMIDT, 1941).

Diagnosis: — See p. 264. *Included genera*: — See list p. 268.

Remarks: — BOUČEK established this family in 1936 and referred it to the Primitiidae. He included in it *Bollia*, *Placentula*, *Jonesella*, and *Bolbibollia*, whereas *Ulrichia* was retained in the Primitiinae. SWARTZ (1936) included *Bollia*, and tentatively also *Ulrichia* in the Drepanellidae. SCHMIDT (1941) erected a new subfamily *Ulrichiinae*, and included in it *Ulrichia*, *Pseudulrichia*, *Pyxiprimitia*, *Bollia*, and tentatively *Jonesites* (= *Placentula*), *Halliella*, and *Hallatia*. If *Bollia* and *Ulrichia* are included in the same subfamily, the writer agrees with PŘIBYL (1951) who retains the name *Bolliinae*, regarding *Ulrichiinae* as a later synonym. There exists, however, the possibility that *Ulrichia* is not so closely related to *Bollia*, in which case *Ulrichiinae* may be revived for *Ulrichia* and allied genera.

Remarks on the genera: — *Bollia* has long been a collective name for forms with a U-shaped ridge (L2—L3). Several species earlier assigned to this genus have lately been transferred to new genera. The type species of *Bollia* is *B. uniflexa* JONES & HOLL, 1886 (not *B. bicollina* JONES & HOLL, 1886, cf. WARTHIN, 1948), and it is possible that the genus is still too heterogeneous. *Bollia*, especially early members like *B. subequata* ULRICH, 1894, agrees rather closely with *Ulrichia* in the general shape, the swollen submarginal ridge, and the two nodes, which may be only indistinctly joined by a ridge in some species of *Bollia*. It may be mentioned here that *Ulrichia* seems to develop some very persistent types. *U. paupera* SCHMIDT, 1941 from the Ordovician is remarkably like the Devonian form *U. pluripuncta* SWARTZ, 1936. Also other bolliid genera appear to develop rather stable forms.

Maratia may be close to *Bollia* and *Ulrichia*. *Parenthatia*, which has a similar submarginal ridge, but no nodes is probably related, too. In *Saccelatia* the submarginal ridge may be developed as in the above genera, or reduced to short alate processes, or may be even missing. *Warthinia*, although having additional nodes, may be near to *Ulrichia*, and was regarded as a synonym of *Ulrichia* by SCHMIDT (1941). *Pseudulrichia* was established by SCHMIDT (1941), who placed it close to *Ulrichia*. This is no doubt true of the species described by SCHMIDT. As type species he selected, however, *Leperditia bivertex*

ULRICH, 1879. It is unfortunately not well known, but appears to belong to the Bolliinae. *Pseudulrichia* has the two nodes of *Ulrichia*, but a submarginal ridge is not separated. *Parulrichia*, too, may be closer to *Ulrichia* and *Pseudulrichia*, than to *Aechmina* (as suggested by SCHMIDT, 1941). *Crescentilla* (cf. SCHMIDT's redescription in 1941) may be related to *Parulrichia*. *Richina* appears to be related to *Pseudulrichia*.

The following genera may be tentatively included in the Bolliinae; *Zygodolboides*, *Jonesella*, *Vogdesella* (= *Melanella*), *Kinnekullea*, *Jonesites* (= *Placentula*), and *Sacclatia*.

? Subfamily Aechmininae BOUČEK, 1936.

Diagnosis — See p. 264. *Included genera*: — See list p. 269.

Remarks: — In this subfamily BOUČEK included *Aechmina* and *Paraechmina*. A few months later SWARTZ (1936) independently erected a family Aechminidae for the same two genera. SCHMIDT (1941) added *Parulrichia* and *Crescentilla*, and, tentatively, *Aechminaria*. *Parulrichia* and *Crescentilla* are here assigned to the Bolliinae. *Aechminaria* appears, however, to be near to *Paraechmina*, having i. a. the same little pit in front of the base of the spine. This applies also to the related *Lindsayella* and the closely allied *Waldronites* (= *Cornulina*), probably a synonym of *Lindsayella*. *Ardmorea* is also possibly related to *Aechmina* (cf. COOPER, 1946, p. 40).

Aechmina bigeneris and *A. spinoterminatus* described from the Devonian by SWARTZ (1936) are interesting because they have the submarginal spine-row of *Aechmina* (no ridge), and the pit of *Paraechmina*.

? Family Acronotellidae SWARTZ, 1936.

Diagnosis: — See p. 264. *Included genera*: — See list p. 269.

Remarks: — The type genus, *Acronotella*, is insufficiently known, and its relationships are uncertain. SWARTZ (1936) established the "provisional" family Acronotellidae and included in it also *Monoceratina*, *Mooreina*, and *Eoconchoecia*, all having a pair of ventral spines. TEICHERT (1937a, p. 113) includes two more genera, *Tricornina* and *Monoceratella*, but believes that "the genera of this "family" are derived from different stocks and do not represent a natural assemblage of genetically related forms", and regards (1937b, p. 53)

the ventral spine as a recurrent homeomorphic feature. TRIEBEL (1941, p. 368) expresses much the same views, and maintains that this group of genera is, at the best, an ecological group. The writer agrees with TEICHERT and TRIEBEL, and removes *Monoceratina* (cf. p. 259), as well as *Mooreina*, and *Eoconchoecia* from the Acronotellidae. *Monoceratella* agrees with *Acronotella* in also having a produced anterior cardinal angle, and is tentatively retained in the Acronotellidae.

If *Acronotella* is related to *Tricornina*, here assigned to the Alanellidae, Acronotellidae may become a synonym of Alanellidae (cf. p. 248).

If *Acronotella* can be shown to be related to *Winchellatia*, as suggested by SCHMIDT (1941, p. 34), the Acronotellidae and Sigmoidoosidae nov. may be synonyms. This is, however, not very likely, and it is not even certain that the Acronotellidae belong to the Beyrichiacea.

Later families.

These are the post-Ordovician families. Besides the Paleozoic families discussed in this paper, the recent family Punciidae HORNIBROOK, 1949 may, as suggested by its author (1949, p. 471), possibly belong here. Unfortunately its two genera, *Puncia* and *Manawa*, both erected by HORNIBROOK (1949), are only known from separated valves without traces of appendages.

Family Beyrichiidae JONES, 1894.

Diagnosis: — See p. 264. *Included genera:* — See list p. 269.

Remarks: — Characteristic of this family is especially the subventral pouch (or swelling) which is not formed by the frill as in the Primitiidae, but by the carapace wall itself and opens into the main cavity. SWARTZ (1936) did not distinguish between a false, extraneous pouch and the pouch of the *Beyrichia* type and included the Eurychilinae in the Beyrichiidae. The Beyrichiidae are restricted here to those forms developing an antero-ventral dimorphic pouch as a swelling of the carapace wall. On the other hand, all forms with this type of dimorphism are included in the Beyrichiidae, thus also the zygodolbids. The family Zygodolbidae was established by ULRICH &

BASSLER (1923, p. 530) for the subfamilies Zygobolbinae, Kloedeninae, and Drepanellinae. The beyrichiid genera assigned to the Drepanellinae, namely *Drepanellina* and *Mesomphalus*, were transferred to the Beyrichiidae because of their beyrichiid pouch already by SWARTZ (1936, p. 553). *Kloedenia* is very close to *Beyrichia*, and in the writer's opinion the Kloedeninae may thus be regarded as a synonym of the Beyrichiinae. The Zygobolbinae are undoubtedly close to the Beyrichiinae, and are here regarded as constituting a subfamily of the Beyrichiidae, which will then be a well-defined, and, as it seems, natural unit. *Mastigobolbina* and *Plethobolbina* were included in the Kloedeninae (here = Beyrichiinae) by ULRICH & BASSLER (1923) but are here transferred to the Zygobolbinae.

The range chart shows the vertical distribution of the beyrichiid genera as recorded by ULRICH & BASSLER (1923) from the Silurian sequence in Maryland. ULRICH & BASSLER (1923, p. 651) described *Beyrichia emaciata* from the Lower Clinton. It is based on a single, imperfectly preserved specimen, which in the writer's opinion may not be a *Beyrichia* species but possibly a zygobolbid. This involves that whereas the Zygobolbinae range from the Lower to the Upper Clinton, the Beyrichiinae seem to appear later, ranging from the Upper Clinton and upwards. The vertical distribution of beyrichiids has not been comparatively so well studied in other areas, but it seems as if true *Beyrichia* species also occur in the lowermost Silurian beds. Anyhow, the early Beyrichiinae are very close to especially the the earliest Zygobolbinae. *Beyrichia* may be rather close to the very similar *Mastigobolbina incipiens* group. It is interesting that this group develops a velate frill, as do some *Beyrichia* species, not only a velate ridge as the other Zygobolbinae. *Zygobolba* is the earliest genus of the Zygobolbinae (and the Beyrichiidae) in the Maryland sequence. The remaining zygobolbid genera undoubtedly have developed directly or indirectly from *Zygobolba*. In the writer's opinion the origin of the Beyrichiidae is, however, still uncertain. When searching for the ancestors of the Beyrichiidae, it may be an idea to look for forms also resembling *Zygobolba*. Even if the pouch of the Beyrichiidae does not correspond to the dimorphic velate structures of the Primitiidae or Eurychilinidae, it is not of course improbable that the Beyrichiidae may have developed from one of these groups, or possibly from the Tetradellidae. The Beyrichiidae agree with these families in having a velate ridge or frill.

It may be recalled that the pouch of the Beyrichiidae most

Clinton			McKenzie	Wills Creek	Tonoloway	Sub-families			
Lower	Middle	Upper							
Zygo- bolba	Zygo- bolbina	Zygosella				Zygo- bolbinae			
		Bonnemaia							
		Mastigobolbina							
		Plethobolbina							
	Drepane- lina	Beyrichia							Bey- richiinae
		Kloedenia							
		Kyam- modes							
		Zygobey- richia							
Dizygo- pleura									
Eukloede- nella									
Kloedenella									

Range chart.

Stratigraphical range of Beyrichiidae (Zygo-
bolbinae and Beyrichiinae) and Kloedenellidae (Kloedenellinae) in the Silurian sequence in Maryland and Pennsylvania, based on data published by ULRICH & BASSLER (1923). The Lower Clinton *Beyrichia emaciata* has here been removed from *Beyrichia* (p. 236).

probably served as a brood pouch. HESSLAND (1949, p. 124) and SPJELDNÆS (1951, p. 748, pl. 103, figs. 1—2) have observed larval carapaces in the pouch. It may be noted that in the present terminology the carina of SPJELDNÆS is the velate ridge, whereas the velum of SPJELDNÆS is the marginal spine-row. The orientation of the carapace is here the reverse of that applied by SPJELDNÆS and in agreement with that applied i. a. by SWARTZ (1936) and KESLING (1951).

Subfamily *Beyrichiinae* JONES, 1894.

Diagnosis: — See p. 264. *Included genera:* — See list p. 269.

Remarks: — *Kloedenia* is so close to *Beyrichia* that the Kloedeninae are regarded here as a synonym of the Beyrichiinae. This subfamily will then include the genera *Beyrichia*, *Kloedenia*, *Welleria*, *Kyammodes*, *Zygobeyrichia*, *Treposella*, and *Dibolbina*. Furthermore SWARTZ (1936, p. 553) added *Drepanellina* and *Mesomphalus* because of their pouch, and *Bolbibollia* should be added for the same reason. As discussed above (p. 227), *Apatobolbina* may belong here, too.

A number of species not developing any dimorphic pouch of the beyrichiid type are no longer included in *Beyrichia*. *Beyrichia* has for a long time been a collective name for disulcate forms of the type S1—S2. No Ordovician species appear to belong to *Beyrichia*, nor many post-Silurian species such as *B. contracta*, *B. sagitta*, and *B. placida* described by COOPER (1941) from the Upper Mississippian of Illinois. No dimorphic pouch (or swelling) has been described in these species, which appear to be near to *Chesterella* and at least most probably belong to the Kloedenellidae. The latest known Beyrichiinae (and Beyrichiidae) appear to be Devonian species of *Beyrichia* (as *B. latispinosa* PŘIBYL, 1951) and the Devonian *Treposella* and *Mesomphalus*. It appears that the Beyrichiinae are restricted to the Silurian and Devonian.

Subfamily *Zygobolbinae* ULRICH & BASSLER, 1923.

Diagnosis: — See p. 264. *Included genera:* — See list p. 269.

Remarks: — This subfamily was originally established for the genera *Zygobolba*, *Zygobolbina*, *Zygosella*, and *Bonnemaia*. *Mastigobolbina* and the closely related *Plethobolbina* are removed here from the Kloedeninae (here = Beyrichiinae) to the Zygobolbinae. Thanks to

the paper on Silurian ostracods by ULRICH & BASSLER (1923), transitional forms are known between all these genera. Rather characteristic of the *Zygobolbinae* is the U-shaped ridge. In *Mastigobolbina* the posterior part of this ridge (the flagellum of ULRICH & BASSLER, 1923) is often whip-lash-like. There are, however, all transitions from this to the type found in other *zygobolbids*. As discussed above (p. 227), *Craspedobolbina* may belong to the *Beyrichiidae*. As it has a ridge resembling that of the *Zygobolbinae*, it is tentatively assigned to this subfamily. The *Beyrichiinae* may be rather close to the *Zygobolbinae* (cf. p. 236), and some of the early representatives, as *Beyrichia lakemontensis* ULRICH & BASSLER, 1923, show traces of a ridge similar to the U-shaped ridge of the *Zygobolbinae*. The *Kloedennellidae* may possibly be related to the *Zygobolbinae*.

Family Hollinidae SWARTZ, 1936.

Diagnosis: See p. 264. *Included genera:* See list p. 270.

Remarks: — SWARTZ (1936) included *Ctenobolbina* in the *Hollinidae*, and SCHMIDT (1941) and HESSLAND (1949) regarded the *Tetradellinae*, *Ctenentominae*, and *Ctenonotellinae* as subfamilies of the *Hollinidae*. In the writer's opinion the supposed close relationships between the *hollinids* on the one side and the *tetradellids* and *Ctenobolbina* on the other are based on false presumptions (not meaning, however, that such relationships may not yet be traced). The affinity between *hollinids* and *Ordovician ostracods* has been misunderstood partly because many *hollinids* have been assigned to *Ctenobolbina*, a typical "sack genus" in earlier days, whereas on the other hand *Ordovician forms* probably belonging to the *Eurychilinidae* have been assigned to the *hollinid* genus *Parabolbina*. The *Trenton species* assigned by KAY (1940) to *Parabolbina* are probably *eurychilinids*. They lack the *hollinid spur* and do not show any of the features peculiar to the *hollinids*, such as type of *frill* and specialized 3. lobe. The *Devonian species* assigned to *Ctenobolbina* by KESLING & McMILLAN (1951) are rather simple *hollinids* ("effaced lobation") but do show *hollinid features* as well developed spur and very marked dorsal swelling of the 3. lobe. These species should be regarded as true *hollinids* and may be transferred to the genus *Parabolbina*, or be allowed a new genus.

When *Ctenobolbina* is restricted to the type species and closely allied forms (cf. p. 211), it is seen that *Ctenobolbina* differs from the

hollinids in many respects, and the writer strongly doubts that there is any close relationship between them. *Ctenobolbina* (and the Sigmoopsiinae as a whole) has only a narrow and entire frill, shows no swelling of the dorsal end of the 3. lobe and does not develop a hollinid spur.

It would appear from the above that the Hollinidae are restricted to the Devonian and later systems. There is, however, at least one certain Silurian hollinid, namely *Parabolbina auricularis*, redescribed below.

The Devonian *Hanaites*, described as a subgenus of *Halliella* by POKORNÝ (1950) is a hollinid and appears to be very close to *Proplectrum*.

Sulcicuneus porrectinatum was described as a new primitiopsid ostracod from the Devonian of Michigan by KESLING (1951a). It has a posterior extraneous chamber, resembling that of *Primitiopsis*, but agrees otherwise remarkably well with contemporaneous hollinids. Its general outline and lobation may be compared f. inst. with those of *Subligaculum recurvisulcatum* KESLING & McMILLIAN (1951, pl. 2, figs. 5—12). Furthermore, the ridge-like frill of *Sulcicuneus* appears to be restricted to the anterior and ventral border areas, as in the hollinids. The extraneous chamber appears to be formed by the marginal structure, and not by the velate structure as in *Primitiopsis*. The dorsal ridge of *Primitiopsis* is missing in *Sulcicuneus*. It is thus possible that *Sulcicuneus* should be included rather in the Hollinidae than in the Primitiopsiinae.

Redescription of *Parabolbina auricularis* (JONES, 1887).

(Pl. 1, figs. 5—8)

Type data: — Holotype is the specimen described and figured by JONES (1887, p. 408, pl. XIII, figs. 10a—c) from the Wenlock at Ironbridge, Severn, England. It is apparently of the male type.

Material described here: — This consists of some 60 well preserved valves and carapaces (including larval forms) from the Wenlock at Mulde, Gotland, Sweden. The material belongs to the Paleozoological Department of the Swedish State Museum, Stockholm. *Parabolbina auricularis* was recorded from this locality already by CHAPMAN (1901, p. 150).

Description: — Carapace subrectangular, somewhat elongate,

with slight but conspicuous forward swing. Dorsal border straight, free border curved, both cardinal angles slightly obtuse. In the hinge a list in the left valve fits into a corresponding groove of the right valve. Median sulcus well developed, expanding ventrally, mostly in a forward direction. Both the pre-sulcal lobe (L1 + L2) and the post-sulcal lobe (L3 + L4) are inflated, the posterior mostly so. The frill is dimorphic. Female type: — The narrow frill extends from somewhat below the anterior cardinal angle to a point below and well behind the sulcus and therefore not along the posterior margin. The frill ends in a spine or spur pointing backwards. Male type: — The frill is discontinuous, and consists of a short anterior part along the lower half of the anterior border and a longer part along the ventral border. The latter part ends in a spine similar to that of the female type. In larval forms the type of frill mostly resembles the male type. It consists of two parts, but both are very short, almost spine-like. The marginal structure is tuberculate. The surface of the valves is granulose, except the sulcus and the frill. The adult specimens are about 0.9 mm long.

Remarks: — This species appears to be the earliest described undoubted hollinid. It was described as *Bollia auricularis* but has lately been usually assigned to *Ctenobolbina* or *Ctenentoma*. Its type of velate structures and dimorphism and the ventrally expanded sulcus are typically for hollinids, and it is here transferred to *Parabolbina*.

Family Kloedenellidae ULRICH & BASSLER, 1908.

Diagnosis: — See p. 264. *Included genera:* — See list p. 270.

Remarks: — This family is regarded here as including the sub-families Kloedenellinae, Beyrichiopsiinae nov., and Glyptopleurinae. No true kloedenellids appear to have been described from pre-Silurian formations. Ordovician ostracods which have been assigned to one or other of the kloedenellid genera do not appear on closer inspection to be kloedenellids. The origin of this family is still uncertain. The earliest true kloedenellids, especially species of *Dizygopleura* described from the Silurian sequence in Maryland by ULRICH & BASSLER (1923), show, however, some features in common with zygobolbids. The Zygobolbinae seem to appear somewhat earlier than the Kloedenellidae, at least in Maryland (cf. range chart p. 237). The U-shaped ridge of the zygobolbids resembles the lower half of the letter D.

The straight part of the ridge is L2, whereas the curved part belongs to L3. The same shape is formed by L2 and L3 in *Dizygopleura*. Furthermore S1 is usually longer than S2 both in zygotolbids and *Dizygopleura*, and S3 tends to become closed dorsally (in the zygotolbids this is seen in *Mastigobolbina bifida* ULRICH & BASSLER, 1923). These features are rather unusual but if they denote relationships is still uncertain. The main difference between the Beyrichiidae (including the Zygotolbinae) and Kloedenellidae, is, as stressed by SWARTZ (1936, pp. 556—557), their type of dimorphism. The Kloedenellidae do not develop an antero-ventral pouch or swelling as the Beyrichiidae, but, at least in the early genera, a posterior swelling of the carapace. This does not necessary exclude that the Kloedenellidae have developed from the Beyrichiidae.

Subfamily Kloedenellinae ULRICH & BASSLER, 1908.

Diagnosis: — See p. 264. *Included genera:* — See list p. 270.

Remarks: — The closely related *Kloedenella*, *Dizygopleura*, and *Eukloedenella* are typical members of this subfamily. *Poloniella* agrees so well *Dizygopleura*, even in the hinge structure, that it may be safely included in the Kloedenellinae. VAN VEEN (1921) first pointed out the resemblance between *Poloniella* and *Kloedenella*, and claimed that the latter (in its earlier, broad sense) was a synonym of *Poloniella*. It appears reasonable to regard *Poloniella* as a descendant of *Dizygopleura*, as suggested by WARTHIN (1934, p. 212).

Other Kloedenellinae are *Jonesina*, *Neokloedenella*, and *Lochriella*. *Ellipsella* is very near to *Lochriella* according to COOPER (1946, p. 109). *Lochriella* appears to be intermediate between *Neokloedenella* and *Sansabella* (COOPER, 1941, p. 57). Further Kloedenellinae are *Gillina*, *Kloedenellina*, and *Oliganisus*. *Oliganisus* may be closely related to *Jonesina*. Compare f. inst. *O. geisi* CRONEIS & GUTKE, 1939 (as figured by COOPER, 1941, pl. 12, figs. 2—5) with *Jonesina puncta* MOOREY, 1935 (as figured by COOPER, 1941, pl. 12, figs. 20—21).

Several Kloedenellinae develop a small tubercle or spine near the postero-dorsal angle, at least in some species, as f. inst. *Sansabella*, *Hastifaba*, *Geisina*, *Nuferella*, and *Perprimitia* (the latter being recognized as a kloedenellid by COOPER, 1941, p. 58). These genera appear to be rather closely related. They all have a typical sansa-

belloid hinge. Their sulcus may be more or less pronounced. Although apparently not developing any tubercle near the postero-dorsal corner, *Kirkbyina* may be near to *Geisina*, and *Knoxina* may be near to *Hastifaba*. *Sargentina*, transferred to the Kloedenellidae by COOPER (1946, p. 117), does not seem to develop any such tubercle but is nevertheless rather closely related to the above-mentioned genera. *Carboprimitia* has hitherto been assigned to the Primitiidae. It differs from this family (also in its old sense) in most features, except in being unisulcate. On the other hand it is very similar to the above-mentioned group in general outline, overlap features, and hingement (channelled between notches), and is here confidently regarded as a kloedenellid. It appears to be rather close to *Hastifaba*.

Microparaparchites and *Paraparchites* have until now been assigned to the Aparchitidae. In the writer's opinion they do not appear to be closely related to the Ordovician type species of *Aparchites*, which has a velate structure not known in *Microparaparchites* and *Paraparchites*. These two genera are most probably related to the contemporaneous *Sansabella* and allied genera, and may be regarded as unisulcate representatives of this group. Both *Microparaparchites* and *Paraparchites* have the characteristic little spine near the postero-dorsal corner often developed in this group. *Proaparchites* has no spine but is probably closely related to these genera. *Pseudoparaparchites*, with a postero-dorsal spine, probably belongs here, too.

Some kloedenellid genera have a more or less well developed ventral lobe; *Perprimitia*, *Chesterella*, *Geffenites*, *Geffenina*, and *Lokius*. *Kirkbyella* appears to be related to these, and is here transferred from the Kirkbyidae to the Kloedenellinae. *Beyrichiella* may be rather close to genera like *Lokius* and *Geffenina*. *Balantoides* may possibly also be related to this group with ventral lobe. *Cornigella* which was removed from the Drepanellidae and included in the Kirkbyidae by SWARTZ (1936, p. 549) may be related to *Balantoides*. *Cornigella tuberculospinosa* (JONES & KIRKBY, 1886), as figured by COOPER (1947, pl. 21, figs. 4—6), agrees rather well with *Balantoides reticulatus* CRONEIS & THURMAN, 1939, as figured by COOPER (1947, pl. 21, figs. 1—3), in general features, except in having more nodes. These extra nodes correspond, however, closely to lobes and ridges in *Balantoides*. *Aechminella*, too, was removed from the Drepanellidae by SWARTZ (1936, p. 549) and placed in the Kirkbyidae. This genus may perhaps also belong rather to the Kloedenellinae, as well as

the genus *Beyrichiana*. *Bicornella* resembles such genera as *Kirkbyella* and *Balantoides*. *Boursella* appears to be very close to *Balantoides*.

As discussed by SWARTZ (1933) at least the early genera of the Kloedenellidae show dimorphism. They develop terminal dimorphic swellings, as distinct from the pouches of the Beyrichiidae (SWARTZ, 1936, p. 556).

The hinge of the Kloedenellinae may have an overlap at its anterior end, or a tooth (Dizygopleurid hinge), or there may be a notch at each end of the channelled hinge (Sansabelloid type, cf. COOPER, 1941, p. 55). The hinge may be channelled or nonchannelled, sometimes partly or faintly channelled. The overlap or notches at the ends of the hinge may be more or less well developed, or even missing. Whereas the presence of a Dizygopleurid or Sansabelloid hinge may thus indicate relationships with the kloedenellids, the absence of these types of the hinge does not seem to exclude kloedenellid affinities. The hinge character appears also to vary much within one genus. According to COOPER (1941, p. 57) *Lochriella* may or may not possess the overlap at the anterior end of the hinge. The well developed tooth of *Dizygopleura* appears to be missing in the very closely related genera *Kloedenella* and *Eukloedenella*.

Subfamily Beyrichiopsiinae nov.

Diagnosis: — See p. 264. *Included genera:* — See list p. 269.

Remarks: — Some genera assigned to the Kloedenellidae differ from the other kloedenellid genera in having a conspicuous frill, and usually having transverse ridges and crests. They are here grouped in a new subfamily Beyrichiopsiinae. This subfamily may be allied both to the Kloedenellinae and the Glyptopleurinae. *Glyptopleurina* may develop a frill as the Beyrichiopsiinae. One of the crests in the Beyrichiopsiinae may extend across the sulcus, as is often the case in the Glyptopleurinae and in *Chesterella exuta* CRONEIS & GALE, 1938, as figured by COOPER, 1941, pl. 11, fig. 11. The Beyrichiopsiinae further remind one of *Hastifaba robusta* COOPER (1946), which has a rim and a dorsal crest. *Beyrichiopsis cornuta* JONES & KIRKBY (1886) has a small spine near the postero-dorsal corner. A similar spine or tubercle is common in many genera assigned to the Kloedenellinae.

Subfamily Glyptopleurinae GIRTY, 1910.

Diagnosis: See p. 264. *Included genera:* See list p. 272.

Remarks: — GIRTY (1910) erected a family Glyptopleuridae.

Later SWARTZ (1936, p. 557) suggests that the glyptopleurids may be related to the Kloedenellidae. In the writer's opinion this is most probable and the glyptopleurids are here considered as a subfamily of the Kloedenellidae.

The hinge of the Glyptopleurinae agrees very well with that of the Kloedenellinae (cf. f. inst. the hinge of *Glyptopleura circumcostata* COOPER, 1941, p. 40, pl. 7, figs. 1—3). Furthermore the general outline, overlap features, and lobation of the Glyptopleurinae is very similar to the Kloedenellinae. *Mesoglypha* appears to be intermediate between *Sargentina* of the Kloedenellinae and *Glyptopleura*.

Family Kirkbyidae ULRICH & BASSLER, 1923.

Diagnosis: — See p. 264. *Included genera:* — See list p. 272.

Remarks: — The Kirkbyidae are restricted to include only genera with a kirkbyan pit (if a sulcal depression is developed), often a kirkbyan node, and never a ventral lobe. This excludes some genera which have up to the present been included in the Kirkbyidae, such as *Kirkbyella* and *Balantoides*. These have no typical kirkbyan features and do not appear to be allied to any of the typical kirkbyids. They may be allied to such forms as *Chesterella*, and are transferred to the Kloedenellidae.

This leaves in the Kirkbyidae a group of closely related genera. They all have the typical kirkbyan pit, except for *Roundyella*, which only has a muscle scar. As noted by SOHN (1950, p. 35) the overlap and hingement may be reversed, even within one species. The hinge of the Kirkbyidae is very like that of Kloedenellidae. COOPER (1941, p. 47) erected the subfamily Amphissitinae for *Amphissites* and closely related genera. As the family Kirkbyidae has been restricted here, there does not seem to be any longer good enough reasons for retaining a subfamily Amphissitinae and it is considered a synonym of Kirkbyidae.

Strepula has sometimes been included in the Kirkbyidae. The type species of this genus does, however, not show the kirkbyan pit or node, and appears to be closer related to *Steusloffia*. *Strepula* is assigned here to the Bassleratiinae. The Kirkbyidae agree with

Strepula in having transverse crests or ridges, but it should probably still be regarded as an open question whether the Kirkbyidae developed from *Strepula* and allied genera or not.

? Family Youngiellidae KELLETT, 1933.

Diagnosis: — See p. 265. *Included genera:* — See list p. 273.

Remarks: — Since *Youngiella wapanuckensis* HARLTON, 1933 was transferred to *Moorites* by COOPER (1946, p. 123), the type genus of this family includes only one species, *Youngiella rectidorsalis* (JONES & KIRKBY, 1886). Its hinge is peculiar in having a crenulated ridge.

Moorea and *Moorites* have usually been referred to the Youngiellidae. As shown by COOPER (1941), *Moorites* does not have the crenulated hinge of *Youngiella*. Several species, however, agree with *Youngiella* in the general outline, being elongate and having a long, straight hinge.

If *Moorea? cincincta* COOPER, 1941 is a true member of *Moorea*, there can be little doubt that *Moorea* and *Moorites* are closely related. According to COOPER (1941, p. 64) this species has a sansabelloid hinge, which suggests affinities to the Kloedenellidae. Some species of *Moorites* have furthermore a concave ventral margin, as is also known in the Kloedenellidae.

The surface ornamentation of *Moorites* is rather faint, but sometimes peculiarly like that of the later genus *Cytherelloidea* ALEXANDER, 1929. Compare f. inst. *Moorites rhomboidalis* (CRONEIS & BRISTOL, 1939) (as figured by COOPER, 1941, pl. 14, fig. 30) with *Cytherelloidea* sp. SWAIN 1949 (as figured by SEXTON, 1951, pl. 116, fig. 20); and *M. brevis* COOPER (1941, pl. 14, fig. 43) with *C. navesinkensis* JENNINGS, 1936 (as figured by SEXTON, 1951, pl. 116, fig. 8). *Cytherelloidea*, too, tends to develop rather elongate forms, and has sometimes a concave ventral margin. This resemblance between *Moorites* and *Cytherelloidea* may be purely accidental. If not, *Moorites* may be related to the Platycopinae.

Hardinia was assigned to the Youngiellidae by CORYELL & ROZANSKI (1942). The relationships between *Youngiella* on the one hand and *Moorites*, *Moorea*, and *Hardinia* on the other are uncertain. For the time being the three latter genera may be retained in the Youngiellidae, but only tentatively. The relationships of *Youngiella*

(and thus the Youngiellidae) to other families are uncertain. The Youngiellidae are here only tentatively included in the Beyrichiacea.

? Family Miltonellidae SOHN, 1950.

Diagnosis: — See p. 265. *Included genus:* — *Miltonella*.

Remarks: — This family was erected by SOHN (1950) for the one genus *Miltonella*. Its relationships to other families are uncertain, but the family Miltonellidae is here tentatively assigned to the Beyrichiacea because of its straight hinge line, although this alone is no certain criterium for its inclusion in this superfamily.

? Family Alanellidae BOUČEK, 1936.

Diagnosis: — See p. 265. *Included genera:* — See list p. 273.

Remarks: — This family was established by BOUČEK for the one genus *Alanella* from the Ludlow in Bohemia. The valve has a very unusual shape; it is 3 to 4 times as long as high, has a long straight hinge line ending in a spine in each end, and has a well developed frill. Another genus, *Vltavina*, also described from the Bohemian Ludlow by BOUČEK, is, however, very similar to *Alanella* in its general shape; especially one specimen of *Vltavina bohémica* (BOUČEK, 1936, pl. IV, fig. 4). *Vltavina*, too, has the terminal spines. It differs from *Alanella* in not being smooth (it has some horizontal narrow ridges) and in having a sulcus. The sulcus is, however, rather faintly developed in *Vltavina perneri* BOUČEK, 1936, and there is a very faint sulcoid depression in *Alanella bohémica decurtata* BOUČEK, 1936. *Vltavina* does not have a frill. Nevertheless the rather unusual shape of *Alanella* and *Vltavina* and their terminal spines suggest that they are related. *Berounella*, a third genus described in the same paper, appears to be related. It has a frill, and shows a faint tetralobation. *Berounella* agrees with *Alanella* and *Vltavina* in having very long valves with terminal spines. The anterior spine is directed upwards and forwards, not straight forwards as in *Vltavina* and *Alanella*. In this feature *Berounella* is like *Tricornina*, a fourth genus described by BOUČEK from the Ludlow of Bohemia. It appears probable that these four genera are related and may be all included in the Alanellidae. BOUČEK (1936) classed *Tricornina* and *Vltavina* with the Primitiidae, and *Berounella* with the Beyrichiidae; the resemblance to these families is, however, rather superficial.

AGNEW (1942) doubts that *Alanella* is an ostracod. If its affinities to *Vltavina* and *Berounella* are accepted, it seems rather probable that *Alanella* is an ostracod, since *Vltavina* and *Berounella* show a faint lobation. It is possible that the Alanellidae are related to the Beyrichiacea, and they are tentatively assigned to this superfamily.

Both *Tricornina* and *Vltavina* were compared with *Acronotella* by BOUČEK (1936). If *Acronotella* should prove to be related to the Alanellidae, Acronotellidae (SWARTZ, October 1936) may become a synonym of Alanellidae BOUČEK (July 1936).

Boučekites and *Přibylites* were compared with *Tricornina* by PŘIBYL (1951). They differ from the Alanellidae in their general shape, and are only tentatively assigned to this family.

Genera of uncertain family reference.

Beside the many genera tentatively assigned to the different families, there are several others whose taxonomic positions are even more uncertain, often because they are not well enough known. These genera are listed in p. 273. A few remarks are presented below on some of these genera.

Halliella magnapunctata (KAY, 1934) and the type species of *Hallatia*, *H. particylindrica* (KAY, 1934) are no doubt closely related (see figures given by KAY, 1934 and 1940). KAY assumed that *Primitia? sculptilis* ULRICH, 1890 was the type species of *Halliella*. As pointed out by WARTHIN (1948), the type species is the Devonian *Halliella retifera* ULRICH, 1891. This species is not well known, but it may be rather doubtful if *H. magnapunctata* and *Primitia? sculptilis* are really congeneric with *Halliella retifera*. For this reason it seems better to include *H. magnapunctata* and *P.? sculptilis* in *Hallatia*, which will then also embrace forms with pitted surface. *Hallatia* has a very marked carinal bend, as well as a velate bend. No carinal structure seems to be developed in *Halliella magnapunctata*.

As defined here, *Halliella* and *Hallatia* do not appear to be closely related. *Halliella* may, however, be related to *Punctoprimitia* (cf. f. inst. *P. subaequalis* SWARTZ & ORIEL, 1948) and *Pyxiprimitia*. KESLING (1951, p. 157) has pointed out the close resemblance between *Amphissites lacrimosus* SWARTZ & ORIEL, 1948 and *Halliella retifera* as illustrated by ULRICH (1890, pl. XV, fig. 5). This may suggest that *Halliella* is related to the Kirkbyidae.

Mirochilina, *Novakina*, and *Hippa* are three probably related genera from the Ludlow of Bohemia (cf. BOUČEK, 1936), whose relationships to other beyrichiaceans are not known.

Neochilina has sometimes been assigned to the Eurychilinidae. SWARTZ (1936, p. 551) suggests that it should be included in the Hollinidae. It does not, however, show any typical hollinid features, and it appears to be best not to assign it to any of these families at present.

The writer has not seen any material or illustrations of the type species of *Binodella* BRADFIELD, 1935, *Kirkbyites* JOHNSON, 1936 (both originally assigned to the Kirkbyidae), and *Golcondella* CRONEIS & GALE, 1938 (originally assigned to the Drepanellidae) and therefore refrains from commenting their position in the present, revised classification. The same applies to *Kirkbyellina* and *Leioprimitia* (both KUMMEROW, 1939) and *Cornia*, *Sinusella*, and *Vertexia*, all three erected by LUTKEVITCH (cf. AGNEW, 1944) and *Tribolbina* LATHAM, 1932.

SUPERFAMILY LEPERDITIACEA BASSLER & KELLET, 1934.

Diagnosis: — See p. 265.

Remarks: — The superfamily Leperditiacea was erected for the two families Leperditiidae JONES, 1856 and Leperditellidae ULRICH & BASSLER, 1906. As *Aparchites* was assigned to the latter family, this has lately been referred to as Aparchitidae JONES, 1901. *Aparchites* appears, however, to be a beyrichiacean (cf. p. 231), and the family Aparchitidae is included here in the Beyrichiacea. *Leperditella* may be related to the Leperditiidae, and is tentatively retained in the Leperditiacea, in the family Leperditellidae.

Family Leperditiidae JONES, 1856.

Diagnosis: — See p. 265. *Included genera:* — See list p. 274.

Remarks: — The classification of this family has been discussed by SWARTZ (1949), who divides it into the two subfamilies Leperditiinae and Isochilinae.

HESSLAND (1949, p. 148) states that the shell of the Leperditiidae consists of extremely fine prisms, standing perpendicular to the surface, except for a thin layer, and that a prismatic structure is known in *Conchoprimitia* and many other genera. According to

LEVINSON (1951, p. 554) the Leperditiidae have two shell layers, whereas this has not been recognized in other ostracods. SCOTT (1951, p. 323) believes that the thin inner layer, and a corresponding thin layer on the outside of the shell may be interpreted as remnants of the inner and outer chitin layer. This would mean that the shell of the Leperditiidae need not be quite different from that of other ostracods.

? Family Leperditellidae ULRICH & BASSLER, 1906.

Diagnosis: — See p. 266. *Included genera:* — See list p. 274.

Remarks: — The position of the Leperditellidae is uncertain. They agree with the Leperditiidae in being rather smooth, and in the general outline; the anterior end being usually the lower, whereas the opposite is usual in the Beyrichiacea. They differ from most Beyrichiacea in having no frill (although the submarginal ridge in the Eridoconchinae may possibly be a velate structure). The Leperditellidae do not show the typical muscle scar or "eye spot" of the Leperditiidae. It is possible that the Leperditellidae are intermediate between the Leperditiidae and Beyrichiacea.

Besides Leperditellinae, two other subfamilies are, tentatively, included in the Leperditellidae, namely Conchoprimitiinae nov. and Eridoconchinae nov.

Subfamily Leperditellinae ULRICH & BASSLER, 1906.

Diagnosis: — See p. 266. *Included genus:* — *Leperditella*.

Remarks: — The type species of *Leperditella*, *L. rex* CORYELL & SCHENK, (1941, new name for *L. inflata* ULRICH, 1892) has been re-described by CORYELL & SCHENK (1941). *L. semen*, well figured by ÖPIK (1937, pl. I, figs. 11—14) appears to be closely related.

? Subfamily Conchoprimitiinae nov.

Pl. 2, fig. 7—9.

Diagnosis: — See p. 266. *Included genera:* — See list p. 275.

Remarks: — This subfamily differs from typical beyrichiaceans in not having any velate or carinal structures. It is as old as (if not older than) any certain beyrichiaceans. It differs from the Leper-

ditiidae in not having any muscle mark of the Leperditiid type, and no "eye tubercle", although the internal mould may show a corresponding node (cf. HESSLAND, 1949, p. 148). The Conchoprimitiinae resemble the Leperditiidae in the general outline (i.a. the anterior half being usually the lower), in attaining a large size (3—4 mm long), in being rather smooth, in the shell structure (cf. HESSLAND, 1949, p. 148), and in having no velate or carinal structures. The Conchoprimitiinae agree rather well with *Leperditella*, but the latter has a more leperditoid outline and is smaller and apparently more thick-shelled. Furthermore the unusual vascular (?) markings of the Conchoprimitiinae (cf. ÖPIK, 1937, p. 10) have not been described in *Leperditella*.

Moult retention in the Conchoprimitiinae.

Conchoprimitia gammae ÖPIK, 1935 as figured by ÖPIK (1935, pl. I, figs. 3a—c) has two concentric grooves, which, as remarked by ÖPIK (1935, p. 4) resemble the growth lines of lammellibranchs and brachiopods. The outer groove is no doubt the boundary between coherent valves of two moult stages (best seen in fig. 3b). This feature is even better demonstrated in a specimen of *Conchoprimites diminuta* figured by ÖPIK (1937, pl. XV, figs. 4—5 (here pl. 2, figs. 8—9). Here an older instar is retained on the right valve (fig. 5), but not on the left (fig. 4). The "primary" and "secondary" shell layers of ÖPIK (1937, p. 12) are thus nothing else than two coherent valves of two moult stages.

Moult retention has been described by LEVINSON (1951) in *Eridoconcha* and *Schmidtella*. The same has been shown by COOPER (1945) to occur in *Ectodemites*.

A faint concentric furrow in some conchoprimitiids may be taken as the impression of the free margin of a coherent moult, which was later shed. This impression was probably made when the new valve was still rather soft, and it is not surprising that this type of groove is rather variable in length and strength. The same feature is described in *Eridoconcha monopleuria* by SWAIN & PETERSON (1951, p. 799).

Moult retention, orientation, and ontogeny.

The moult retention is of interest for the orientation, not only of the Conchoprimitiinae, but also of the Beyrichiacea. Even if the

Conchoprimitiinae can be shown to be true members of the Leperditiaacea, the median sulcus of *Conchoprimites* may be assumed to be homologous with the median sulcus of the Beyrichiacea. In accordance with the orientation used in this paper, this sulcus is situated slightly in front of the middle.

In specimens with two coherent valves we have two moult stages which we know belong to the same individual (and species). In the holotype of *Conchoprimitia gammae* ÖPIK (1935, pl. I, figs. 3a—c) (here pl. 2, figs. 6—7) the inner groove (belonging to the attached moult) gives us further the outline of a third, earlier instar. When comparing the outlines of different instars from the same individual, we see that the supposed posterior end grows more than the anterior. This is in agreement with recent ostracods, and indicates that the accepted orientation of the Conchoprimitiinae is correct. As a result of the faster growth of the posterior part, the sulcus in *Conchoprimites* migrates forward during the ontogenetical development. This, too, is in agreement with recent ostracods, where the adductor muscle scar migrates forward (cf. f. inst. CLAUS, 1868).

The effects of the faster growth of the posterior end on the outline is best seen in the holotype of *Conchoprimitia gammae*. The outline of the smallest instar (indicated by the interior groove) has almost subequal ends, whereas the largest instar is pronounced leperditoid. This agrees well with the growth of *Eoleperditia fabulites*, as described by SCOTT (1951).

Remarks on the genera: —

Conchoprimitia ÖPIK, 1935.

Conchoprimitia was split into three genera by HESSLAND (1949, p. 142); *Conchoprimitia* with two concentric grooves and no sulcus, *Conchooides* with one concentric groove and no sulcus, and *Conchoprimites* with sulcus and with or without concentric grooves.

In the forms described with two grooves, the outer groove is the boundary between coherent valves of two moults. The inner groove is explained as the impression left by an earlier moult, which has later fallen off. One might expect also to find forms with three coherent valves, which would also produce two grooves. Such forms have, however, not been described. The retention of an earlier moult stage is more or less an accidental feature. *Conchoprimitia* (as defined

by HESSLAND) may be regarded as a *Conchooides* with an earlier moult attached, this moult showing the impression of a still earlier valve. *Conchooides* is here considered as a synonym of *Conchoprimitia*.

In forms with one groove, this may be either the boundary between valves of two moult stages, or the impression left by the preceding moult stage. Both types occur.

It may be added that many "*Conchooides*" specimens are practically devoid of any grooves, which means that the preceding moult did not leave any impression on the valve. It appears that some forms assigned to *Conchooides* are even conspecific with species of *Conchoprimitia*. It is f.inst. rather probable that *Conchoprimitia gammae* ÖPIK, 1935 (type species) is conspecific with the associated *Conchoprimitia* ("*Conchooides*") *glauconitica* KUMMEROW, 1924. A valve from the type material (illustrated by ÖPIK, 1935, pl. II, fig. 5) agrees exactly with *C. gammae* with regards to the length-height ratio. "*C. gammae*" may be regarded as specimens of *C. glauconitica* with a coherent instar, the latter showing impression of a still earlier instar.

Isochilina? *erratica* is no doubt a *Conchoprimitia* species. Other species are *Leperditia* (*Isochilina?*) *socialis* BRÖGGER, 1882 and *C. broeggeri* ÖPIK, 1939, as well as nine species assigned to *Conchooides* by HESSLAND (1949). *Eurychilina?* *symmetrica* ULRICH, 1894 was transferred to *Conchoprimitia* by KAY (1940, p. 249). This species is, however, not a conchoprimitiid, and its reference to *Conchoprimitia* was doubted already by HESSLAND (1949, p. 237). It shows a typical velate ridge, and probably belongs to the Eurychilinidae. It appears best to still refer to it as *Eurychilina?* *symmetrica*. The following species may thus be assigned to *Conchoprimitia*:

- Conchoprimitia socialis* (BRÖGGER, 1882)
- erratica* (KRAUSE, 1891)
- glauconitica* (KUMMEROW, 1924)
- gammae* ÖPIK, 1937 (prob. syn. of *C. glauconitica*)
- broeggeri* ÖPIK, 1939
- micropunctata* (HESSLAND, 1949)
- meganotifera* (HESSLAND, 1949)
- rugosa* (HESSLAND, 1949)
- ventropunctata* (HESSLAND, 1949)
- minuta* (HESSLAND, 1949)
- ventroincisurata* (HESSLAND, 1949)

Conchoprimitia dorsodepressula (HESSLAND, 1949)
circumstriata (HESSLAND, 1949)
levis (HESSLAND, 1949)

It is possible that some of these forms may later prove to be synonymous.

Conchoprimites HESSLAND, 1949.

Conchoprimites differs from *Conchoprimitia* in having a median sulcus. *Conchoprimites*, too, shows moult retention. A fine example is seen in *Conchoprimites tolli*. ÖPIK (1937, pl. IX) gives illustrations of three carapaces; in fig. 1 (*C. tolli integra*) the earlier moult has hardly left any impression, in fig. 2 (*C. tolli*) there is a marked groove, and in fig. 3 (*C. tallinnenses*) it is clearly seen that an earlier moult is still attached. These three forms are here considered to be conspecific (refigured here pl. 2, figs. 1—5). It is significant that ÖPIK (1937, p. 11) states that "The inner part of the exterior surface of the valve of *C. tallinnensis* inside the concentric groove corresponds completely to the valve of *C. tolli integra*".

According to ÖPIK (1937, p. 12) *C. deminuta* differs from *C. tallinnensis* (i. e. *C. tolli* with earlier moult attached) in having the sulcus placed more towards the middle of the valve, and having a more elliptical (less leperditoid) carapace. In the holotype of *Conchoprimitia gammae* it is demonstrated that the outline of Conchoprimitiidae may become more leperditoid in later stages (cf. p. 252). In *Conchoprimites* the faster growth of the posterior part results in a more anterior position of the sulcus in later stages (more toward the middle in early stages). If the distance from the sulcus to the posterior border is divided by the distance from the anterior border, this will give a ratio for comparison of the position of the sulcus. The ratio for *C. deminuta* is 1.4. In *C. tallinnensis* the corresponding proportion is 1.5 in the main valve (as measured on fig. 3c pl. IX), but is 1.4 in the attached earlier moult. (The corresponding proportion in the holotype of *C. tolli integra* is 1.5; in *C. tolli* (pl. IX, fig. 2) 1.6). *C. deminuta* corresponds closely with *C. tolli* regarding the height-length ratio.

C. ? inusitata may possibly be a still earlier instar, if it is really a conchoprimitiid.

Conchoprimitia leperditioides, *C. hallensis*, and *C. elongata* described by THORSLUND, (1940) should be included in *Conchoprimites*,

as pointed out by HESSLAND (1949, p. 236). *C. hallensis* differs from *C. leperditioides* in mainly lacking a concentric groove. As stressed above, such a groove appears to be an accidental feature, and *C. hallensis* is here regarded as a synonym of *C. leperditioides*. *C. elongata* appears to be very closely related to *C. leperditioides*. It differs mainly in being comparatively longer. It is not impossible that this is due to dimorphism, or tectonic influences.

Further species referable to *Conchoprimites* are: *Primitia sulcata* KRAUSE, 1889, *Primitia conchooides* HADDING, 1913, and the type species, *Conchoprimites reticulifera* HESSLAND, 1949.

List of species: —

- Conchoprimites sulcata* (KRAUSE, 1889)
conchooides (HADDING, 1913)
tolli (BONNEMA, 1909)
tolli integra (ÖPIK, 1937) (syn. of *C. tolli*)
tallinnensis (ÖPIK, 1937) (syn. of *C. tolli*)
deminuta (ÖPIK, 1937) (syn. of *C. tolli*)
leperditioides (THORSLUND, 1949)
hallensis (THORSLUND, 1949) (syn. of *C. leperditioides*)
elongata (THORSLUND, 1949)
reticulifera HESSLAND, 1949

Whereas *Conchoprimitia* and *Conchooides* were assigned to the Aparchitidae, *Conchoprimites* was included in the Primitiidae by HESSLAND (1949). *Conchoprimites* is, however, so close to *Conchoprimitia* that the writer confidently groups them together. The sulcus in *Conchoprimites* may be rather faint sometimes, thus approaching the non-sulcate *Conchoprimitia*.

Ceratocypris POULSEN, 1934 and *Pinnatulites* HESSLAND, 1945.

These genera were placed in the Aparchitidae together with *Conchoprimitia* and other genera by HESSLAND (1949). They are here tentatively assigned to the Conchoprimitiinae.

?Subfamily Eridoconchinae nov.

Diagnosis: — See p. 266. *Included genera*: — See list p. 275.

Remarks: — The position of this group is uncertain. Its genera have until now been assigned to the Primitiidae, Aparchitidae, and

Leperditellidae. The Eridoconchinae are like the Leperditiidae and Leperditellidae in being lowest in their anterior part. Furthermore the short, slit-like sulcus, tending to bifurcate ventrally reminds one more of the sulcus sometimes present in the Leperditiidae than the typical beyrichiacean sulcus. A somewhat similar sulcus is sometimes developed in the Conchoprimitiinae. The submarginal ridge of *Eridoconcha* resembles that of Bolliinae, but also that of the leperditiid *Saffordellina*. For the time being the Eridoconchinae are tentatively assigned to the Leperditellidae.

Remarks on the genera: — *Cryptophyllus* was split off from the closely related *Eridoconcha* by LEVINSON (1951). According to LEVINSON (1951, pp. 557, 558) *Milleratia* is near to both these genera. KEENAN (1951, p. 565) states that *Milleratia cincinnatiensis* (type species) appears to belong with the genus *Eridoconcha*. *Schmidtella* appears to be near to *Eridoconcha*, as discussed by LEVINSON (1951, p. 558) and KEENAN (1951, pp. 564, 565). The position of *Paraschmidtella* is less certain.

Suborder Podocopa G. O. Sars, 1866.

Many straight-hinged Paleozoic ostracods belong to groups which should be probably included in the suborder Podocopa. Some of these straight-hinged forms appear to be closely related to arcuate-hinged forms.

Family Quasillitidae CORYELL & MALKIN, 1936.

Included genera: — See list p. 275.

Remarks: — Many of the genera included in this family have an ornamental pattern consisting of an anterior curved ridge and two posterior nodes. The pattern resembles the anterior parenthesis sign and a colon, and may be called the *Bufina* pattern, as it is typically developed in *Bufina* (cf. text fig. 12). The pattern may be elaborated or reduced in different ways. As discussed below, it is also found in the Healdiidae.

The family Quasillitidae was established by CORYELL & MALKIN in November 1936 for the genera *Quasillites*, *Janetina*, *Jenningsina*, and *Graphiadactyllis*. In December 1936 KELLETT erected the family Graphiodactyllidae, which is here considered as synonym of Quasil-

litidae. In 1942 CORYELL & ROZANSKI added the genus *Paragraphylus*. As shown by SWARTZ & ORIEL (1948, p. 555), *Spinovina* may be a synonym of *Quasillites* and is here included in the family.

The family Ropolonellidae, erected by CORRELL & MALKIN in 1936, appears to be rather close to the Quasillitidae, and it is here proposed to regard the ropolonellids as constituting a subfamily of the Quasillitidae. The above-mentioned genera should then be placed in the subfamily Quasillitinae. It is difficult to separate these subfamilies. The Ropolonellinae have terminal flanges, but this is also true of *Paragraphylus*. *Bufina* was included in the Ropolonellidae by CORYELL & MALKIN (1936). It appears, however, to be closer to *Quasillites* than to *Ropolonellus*, and is transferred to the Quasillitinae. The remaining genera of the Ropolonellinae, namely *Ropolonellus*, *Euglyphella*, *Rudderina*, and *Plagionephrodes* have a rather *Cythereis*-like appearance, whereas the Quasillitinae on the whole resemble more the Healdiidae in general appearance.

Ropolonellus is, apart from its flanges, a smooth ostracod. There can, however, hardly be any doubt that it is closely related to *Euglyphella*. Although somewhat obscured by other ridges, *Euglyphella* has a *Bufina* pattern (see f. inst. *E. sigmoidalis*, *E. compressa*, and *E. jenningsi* as illustrated by CORYELL & MALKIN, 1936, figs. 17, 19, and 20). In *Quasillites* the anterior curved ridge is faintly developed (but clearly discernable, f. inst. in the type species, *Q. obliquus* CORYELL & MALKIN, 1936), and only the lower of the posterior nodes is developed. The same applies to *Spinovina*.

Relationships: — *Ponderodictya* has the *Bufina* pattern and also resembles *Quasillites* and *Bufina* in other features so much that relationships can hardly be denied. As *Ponderodictya* has an arcuate hinge line and is included in the Healdiidae, this means that the Quasillitidae and Healdiidae are rather closely related. Some of the quasillitid genera were earlier included in the Thlipsuridae. *Strepulites* appears to be intermediate between the thlipsurid *Octonaria* and *Euglyphella*. This suggests that the Quasillitidae are related to the Thlipsuridae. As discussed below (p. 261) the Thlipsuridae may be related to the Healdiidae.

KELLETT (1936, p. 774) points out the similarities between *Graphiadactyllis* and post-Paleozoic genera like *Cytheropteron*, and describes furthermore a calcareous inner lamella in *Graphiadactyllis arkansas*. The *Cythereis*-like appearance of the Ropolonellinae, which

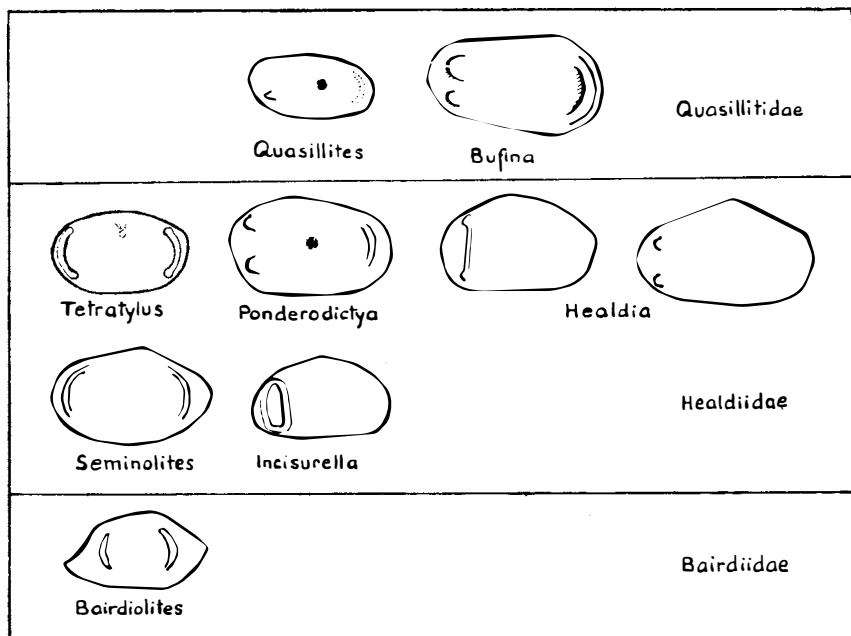


Fig. 12. Structural patterns in Quasillitidae, Healdiidae, and Bairdiidae (*Bufina* pattern and *Seminolites* pattern and varieties of these).

have marginal flanges and a caudal process, is also very suggestive. There seems to be good reasons for including the Quasillitidae in the suborder Podocopa, which is characterized i. a. by the calcareous inner lamella, marginal flanges, and caudal process. As the closely related Healdiidae are included in the suborder Platycopa, this would mean that the Quasillitidae and Healdiidae are near the branching point of these two suborders. (cf. p. 261). The Bairdiidae (arcuate-hinged family of Podocopa) may also develop an ornamental pattern related to the *Bufina* pattern (cf. text fig. 12), as f. inst. *Bairdiolites* which has a *Seminolites* pattern (cf. p. 260). This may indicate relationships between the Bairdiidae and Quasillitidae.

Remarks on *Monoceratina* ROTH, 1928.

Type species is the Pennsylvanian *Monoceratina ventrale* ROTH, 1928 (refigured by SWARTZ, 1936, pl. 83, fig. 3a—b). ALEXANDER (1934) describes some Cretaceous species which he assigns to *Mono-*

ceratina, and maintains that they belong to the Podocopa, i. a. because of their distinct caudal process (ALEXANDER, 1934, p. 58). He further suggests that they are related to *Orthonotacythere*. This relationship now appears to be doubted (cf. SYLVESTER-BRADLEY, 1948, p. 721).

SWARTZ (1936, p. 555) includes *Monoceratina* in the beyrichiacean family Acronotellidae because a caudal process is not developed in the type species. *Monoceratina* is, however, probably not closer related to *Acronotella*.

One may distinguish between species close to *Monoceratina ventrale* and species of the type described by ALEXANDER from the Cretaceous (*M. montuosa* group). *M. bradfieldi*, described by COOPER (1946, p. 39) may be assumed to be closely related to *M. ventrale*. The holotype of *M. bradfieldi* shows no caudal process (COOPER, 1936, pl. 1, figs. 3—6), whereas another specimen shows a small but distinct caudal process (COOPER, 1936, pl. 1, figs. 1—2). Such a caudal process is well developed in a third Pennsylvanian species, *M. macoupeni* SCOTT & BORGER, 1941 (see COOPER, 1946, pl. 1, fig. 13), also belonging to the *M. ventrale* group. Thus the *M. ventrale* group, too, may possibly belong to the Podocopa. Further research may show if the *M. ventrale* and *M. montuosa* group should rather be classed in two genera.

The simple hinge of *Monoceratina* (*montuosa* group); a narrow bar in the left valve, which fits into a shallow groove in the right valve, is similar to the hinge described in the Ropolonellinae by CORYELL & MALKIN (1936, p. 6).

Remarks on the family Healdiidae HARLTON, 1933 (? PLATYCOPA G. O. SARS, 1866).

SCOTT (1944, p. 169) drops this family and includes *Healdia* ROUNDY, 1926 in the Bairdiidae because of a similar muscle scar pattern. TRIEBEL (1950, p. 117), on the other hand, stresses that *Healdia* and *Ogmoconcha* TRIEBEL, 1941 differ from the Bairdiidae in having no true duplicature margin and classes the Healdiidae in the Platycopa, together with the Cytherellidae, which have a similar marginal structure. TRIEBEL (1950, p. 116) further removes *Cavellina* CORYELL, 1928 from the Cytherellidae and includes it in the Healdiidae, because the muscle scar pattern of *Cavellina* agrees with that of *Healdia*, but

differs from that of *Cytherella* JONES, 1849. *Ponderodictya* CORYELL & MALKIN, 1936, originally included in the Cytherellidae, has been shown by SCOTT (1944) to have a scar of the *Healdia* type and should also be included in the Healdiidae. Quite possibly also a number of other genera (such as *Cribroconcha* COOPER, 1941, *Incisurella* COOPER, 1941, *Paracavellina* COOPER, 1941, *Platychilella* COOPER, 1942, *Seminolites* CORYELL, 1928, *Sulcella* CORYELL & SAMPLE, 1942, and *Tetratylus* COOPER, 1941) should be included in the Healdiidae. To be sure of this, their muscle scar pattern, hinge, and marginal features should be examined. They agree with *Healdia* in having an ornamental pattern more or less of the *Bufina* type (cf. p. 256). In *Seminolites* and some other genera the pattern consists of an anterior and a posterior curved ridge, together resembling a parenthesis (*Seminolites* pattern). A similar pattern is found in the bairdiid *Bairdiolites* CRONEIS & GALE, 1938 (cf. text fig. 12).

Remarks on the family Thlipsuridae ULRICH, 1894¹.

This family with arcuate dorsal margin was revised by SWARTZ, 1932. It is mentioned in this paper because it may be related to the Quasillitidae, especially the Ropolonellinae.

The following genera assigned to the Thlipsuridae by BASSLER & KELLETT (1934, p. 36) are no longer included in this family: *Phreatura* JONES & KIRKBY, 1886 (here included in the Healdiidae), *Poloniella* (which is related to *Kloedenella* as suggested by VAN VEEN, 1921 and WARTHIN, 1934, p. 212), *Phanassymetria* ROTH, 1929 (probably a bairdiid, cf. MORRIS & HILL, 1952, p. 8, *Ropolonellus* and *Euglyphella* (the two latter were included in the Ropolonellidae by CORYELL & MALKIN, 1936)). The following genera may be retained in the Thlipsuridae: *Craterellina* ULRICH & BASSLER, 1913 (synonym of *Thlipsura* by SWARTZ, 1932), *Eucraterellina* WILSON, 1935, *Eustephanella* SWARTZ & SWAIN, 1942 (new name for *Eustephanus* SWARTZ & SWAIN, 1941 non REICHENBACH), ? *Favulella* SWARTZ & SWAIN, 1941, *Hyphasma* VAN PELT, 1933, *Octonaria* JONES, 1887, *Octonariella* BASSLER, 1941, ? *Ranapeltis* BASSLER, 1941, *Rothella* WILSON, 1935, ? *Stibus* SWARTZ & SWAIN, 1941, *Streputilites*

¹ Not JONES, 1887, cf. CORYELL & CUSKLEY, 1934, p. 8.

CORYELL & MALKIN, 1936, *Thlipsura* JONES & HOLL, 1869, *Thlipsurella* SWARTZ, 1932, *Thlipsurina* BASSLER, 1941, and *Thlipsuroides* MORRIS & HILL, 1952.

Relationships: — The Thlipsuridae may be related to the Ropolonellinae (especially *Euglyphella*) through forms like *Strepuvites*. *Favulella*, tentatively assigned to the Thlipsuridae by SWARTZ & SWAIN (1941, p. 439), resembles both *Octonaria* and the healdiid *Ponderodictya*. The healdiid *Healdioides* CORYELL & ROZANSKI, 1942 resembles much the thlipsurid genera *Eucraterellina* and *Rothella*. The Thlipsuridae thus appear to be related to the Healdiidae. It is of interest in this connection that KELLETT (1935, p. 142) in her discussion of *Healdia* states that there seems to be a weakening of the ornamentation with the passing of time in this genus. This may indicate that the Healdiidae developed from the usually more ornamented Thlipsuridae, a family which seems to appear earlier than the Healdiidae.

The Thlipsuridae do not seem to develop any calcareous inner lamella (although their marginal structure needs closer examination). If the Healdiidae belong to the Platycopa, it is thus possible that the apparently closely related Thlipsuridae should also be placed in this suborder.

Remarks on the relationships of the suborders Podocopa, Platycopa and Paleocopa.

The Quasillitidae, Healdiidae, Thlipsuridae, and possibly also the Bairdiidae appear to be more or less closely related, as discussed above. Both the Quasillitidae and Healdiidae appear later than the Thlipsuridae (cf. range chart p. 276) and may have developed from this family. Unfortunately the marginal structure of the Thlipsuridae is not well known. They seem, however, to lack an inner calcareous lamella and thus agree best with the Platycopa. This would be difficult to explain if the Quasillitidae belong to the Podocopa and the Healdiidae to the Platycopa, as the Bairdiidae (Podocopa) apparently appeared before the Thlipsuridae (cf. range chart, p. 276). It may mean that the earlier forms assigned to the Bairdiidae should not be included in this family (or even suborder), or it may mean that the marginal features are not so useful criteria of affinity. TRIEBEL (1950 p. 116) suggests that the margin of the Platycopa

type is primitive, but it is perhaps also possible that the *Platycopa* type is a reduced *Podocopa* type. This would seem more probable if the *Bairdiidae* (*Podocopa*), really appear earlier than the *Platycopa*. However, these questions lie beyond the scope of this paper and may probably only be solved when the marginal structures, muscle scar patterns, and hinge structures of the above-mentioned and related families are better known. If the Lower Ordovician species assigned to the *Bairdiidae* really belong to the *Podocopa*, this suborder may be at least as old as the *Paleocopa*, and their branching point be earlier than the known occurrences of ostracods. The relationships of the *Paleocopa* to other ostracod suborders are thus still uncertain.

Diagnoses of superfamilies, families and subfamilies of *Paleocopa*.

Superfamily *Beyrichiacea*: — Straight-hinged ostracods with subequal ends or forward swing. There is a tendency to develop lobes and sulci, carinal, velate, and marginal structures. Smooth forms may resemble smooth forms of other groups; they may differ from the *Leperditiacea* in the outline, and differ from the *Platycopa* in apparently not having any inner calcareous lamella. Dimorphism present in many families.

Family *Sigmoopsiidae*: — Carinal structure well developed. Carinal dimorphism, some individuals having the carinal structure better developed than others. Velate structure may be missing. No dorsal ridge. 1—3 sulci. Median sulcus (S2 usually very long, but may be short. S3 more persistent than S1.

Subfamily *Sigmoopsiinae*: — As family, but velate structure always present. When the median sulcus is long, it is characteristically sigmoidal.

Subfamily *Glossopsiinae*: — As family, but velate structure is missing or very faintly developed. Median sulcus always long, not sigmoidal. The ventral ends of S1 and S2 are their most persistent parts.

Family *Tetradellidae*: — Velate structure entire or restricted. Velate dimorphism (incurved frill or part of the frill in some individuals) or dimorphic pits between velate and carinal structure, or no dimorphism. Carinal structure may be developed as a ridge (L1 + connecting ridge + L4), or not separated from the extralobal area.

Dorsal ridge may be present. 1—3 long or short sulci. Lateral crests may be present.

Subfamily Tetradellinae: — As family, but velate structure always entire, although a frill may become narrower posteriorly.

Subfamily Piretellinae: — As family, but velate structure restricted (not developed posteriorly). May show dimorphism, some individuals having the frill incurved, sometimes to form a velate pouch (false pouch).

Subfamily Bassleratiinae: — As family, but velate structure always entire. No dimorphism. Always lateral crests or ridges. Only median sulcus well developed. L2 often rather large and node-like.

Family Primitiidae: — Velate structure entire or restricted. Velate dimorphism; some individuals developing a velate pouch (false pouch). One short sulcus. Dorsal ridge may be present, but no lateral ridges or crests. No distinct carinal structure.

Family Eurychilinidae: — Diagnosis depends on whether the Euprimitiinae and Primitiopsiinae are included or not. If they are included, their diagnoses are added to that of the Eurychilininae.

Subfamily Eurychilininae: — Velate structure well developed, entire. Velate dimorphism, some having the frill (or part of it) incurved, not developing, however, a real velate pouch. No or one short sulcus. Dorsal ridge usually not present. No carinal structure.

Subfamily Euprimitiinae: — Velate structure not very conspicuous or missing. Dimorphism in the anterior part of the velate structure, or only some individuals have a velate structure, or dimorphism only as an undefined velate swelling anteriorly in some individuals. One short sulcus, or no well-defined sulcus. Dorsal ridge present or not. No carinal structure.

Subfamily Primitiopsiinae: — Velate structure entire, not very conspicuous. Velate dimorphism, some individuals having a posterior extraneous velate chamber. One pit-like or no sulcus. Dorsal ridge present. No carinal structures.

Family Aparchitidae: — Smooth, nonsulcate, with velate structure. When the velate structure is developed as a frill, it may show dimorphism, some individuals having the frill incurved. No dorsal ridge or carinal structure.

Family Drepanellidae: — Diagnosis depends on whether the subfamilies Bolliinae and Aechmininae are included or not. If they are included, their diagnoses may be added to that of the Drepanellinae.

Subfamily Drepanellinae: — With submarginal ridge, probably a carinal ridge or a fused carinal and velate ridge. No dimorphism observed. No dorsal ridge. 1 sulcus. One or two lobes (L2, L3) may be developed as nodes. The two nodes may be united ventrally to form a U-shaped ridge.

Subfamily Bolliinae: — A submarginal ridge may be present or not, and so may one or two nodes (L2, L3). L2 and L3 may be united ventrally to form a U-shaped ridge. No typical sulcus. No dorsal ridge.

Subfamily Aechmininae: — A submarginal ridge may be present or not. L3(?) usually developed as a spine. A sulcal pit may be present or not. Otherwise no sulci. No dorsal ridge.

Family Acronotellidae: — Diagnosis is not given, as the only certain member, *Acronotella*, is not well enough known. It may be important that the anterior dorsal angle is protruded into a spine.

Family Beyrichiidae: — Velate structure entire. Dimorphism as (carinal?) swellings of the carapace wall, either as a not very well defined swelling, or as a more or less well defined pouch. 1—3 sulci, S1 more persistent than S2. L2 usually node-like.

Subfamily Beyrichiinae: — As family. Sulci short. Often well defined pouch. Velate structure developed as ridge or frill.

Subfamily Zygobolbinae: — As family. L2 and L3, or ridge on top of L3, joined ventrally to form a U-shaped ridge. Velate structure developed as ridge or narrow frill.

Family Hollinidae: — Velate structure well developed, restricted, often with a postero-ventral spine or spur. Different types of velate dimorphism. 1—3 sulci. Median sulcus long or short, in the latter case often widening ventrally. Dorsal part of L3 often bulb-like.

Family Kloedenellidae: — Velate structure present or missing, does not show dimorphism. 0—3 sulci. The early genera, at least, develop posterior dimorphic swelling. Often with conspicuous overlap of valves. Hinge with terminal notches (sansabelloid) or with tooth (dizygopleurid) or without notches or tooth.

Subfamily Kloedenellinae: — As family. Velate structure, when present, not developed as frill.

Subfamily Beyrichiopsiinae: — As family. Velate structure always present, developed as frill. Lateral crests usually present.

Subfamily Glyptopleurinae: — As family, but with ridges (carinae) across the lateral surface.

Family Kirkbyidae: — Velate and other ridges (crests) usually

present. When a sulcal depression is developed, this is in the form of a pit (kirkbyan pit). A more or less central, rather large node (kirkbyan node) often present. Surface reticulated. Dimorphism not known.

Family Youngiellidae: — Diagnosis is not given, as the only certain member, *Youngiella*, is not well enough known.

Family Miltonellidae: — Diagnosis, according to SOHN, 1950, p. 37: Straight backed, convex ostracods with a narrow, shallow groove that extends backward from the anterior cardinal angle and curves around and below center of the valve subconcentric with the free margins.

Family Alanellidae: — Typical forms very long, with anterior and caudal spine-like processes. Velate (?) structure present or not, may be developed as frill. 0—3 sulci, but the lobation is faint.

Superfamily Leperditiacea: — Outline leperditioid (backward swing) or with subequal ends. Usually smooth, but may have nodes and a submarginal ridge. Conspicuous dimorphism not observed. A more detailed diagnosis depends on which groups are included in this superfamily beside the Leperditiidae.

Family Leperditiidae: — (Diagnoses mainly after SWARTZ 1949, p. 311). Shells tend to be relatively thick-walled, and are comparatively large, ranging from about 5 to 20 mm in length, or rarely to 30 mm or more. Near the anterior cardinal angle is an inner pit and commonly a corresponding external tubercle, thought to have been the locus of the antero-lateral eye. An adductor scar lies in front of the middle, it is generally well-marked, large, suboval, and consists of numerous, closely spaced though discrete spots; venose lines radiate from the adductor scar. When a short sulcus is developed, it tends to bifurcate ventrally (as in *Isochilina ottawa* JONES, 1858, as illustrated by SWARTZ, 1949, pl. 67, figs. 6 and 9).

Subfamily Leperditiinae: — (Diagnosis after SWARTZ, 1949, p. 311) Inequivalved Leperditiidae, generally with right valve overlapping the left, especially in the ventral region. Flattened borders may be developed terminally, but do not continue along the ventral margin.

Subfamily Isochilinae: — (Diagnosis after SWARTZ, 1949, p. 321). Leperditiidae in which the valves developed flattened borders along the ventral as well as the terminal margins, and in which the closed shell appears essentially equivalved, though one valve may have a marginal flange overlapped by the other.

Family Leperditellidae: — Diagnosis depends on whether the Conchoprimitiinae and Eridoconchinae are included or not. If they are included, their diagnosis may be added to that of the Leperditellinae.

Subfamily Leperditellinae: — Outline leperditoid. Thick-shelled. No lobes or submarginal ridges. The left valve overlaps the right along the free margins. Comparatively small.

Subfamily Conchoprimitiinae: — Outline with subequal ends or slightly leperditoid. Thin-shelled. Left valve overlaps right. A short sulcus, faintly bifurcating ventrally, may be developed. Venose lines may be seen in internal moulds. Length ca. 1—4 mm.

Subfamily Eridoconchinae: — Outline with subequal ends or slightly leperditoid. Thick-shelled. Submarginal ridge may be present, as well as short sulcus, faintly bifurcating ventrally. Comparatively small.

Proposed classification of Paleozoic straight-hinged Ostracods.

Suborder PALEOCOPA nov.

Superfamily Beyrichiacea ULRICH & BASSLER, 1923

Family Sigmoidopsiidae nov.

Subfamily Glossopsiinae nov.

Glossopsis HESSLAND, 1949

Aulacopsis HESSLAND, 1949

Subfamily Sigmoidopsiinae nov.

Ogmoopsis HESSLAND, 1949

Sigmoidopsis gen. n.

Sigmobolbina gen. n.

Carinobolbina gen. n.

Bolbina gen. n.

?Kiesowia ULRICH & BASSLER, 1908

?Ctenobolbina ULRICH, 1890

?Winchellatia KAY, 1940

Family Tetradellidae SWARTZ, 1936

Subfamily Tetradellinae SWARTZ, 1936 (incl. Dilobellinae
KAY, 1940)

Tetradella ULRICH, 1890

Dilobella ULRICH, 1894

- Tallinnella ÖPIK, 1937
 Hesslandella gen. n.
 Ceratopsis ULRICH, 1894
 ?Polyceratella ÖPIK, 1937
 ?Subfamily Piretellinae ÖPIK, 1937
 Piretella ÖPIK, 1937
 Duhmbergia SCHMIDT, 1941 (prob. syn. of
 Piretella)
 Piretopsis HENNINGSMOEN 1953
 Rakverella ÖPIK, 1937
 Dicranella ULRICH, 1894
 Ctenonotella ÖPIK, 1937
 (Biflabellum ÖPIK, 1935 non DOEDERLEIN)
 Öpikum AGNEW, 1942 (new name for Biflabellum)
 Subfamily Bassleratiinae SCHMIDT, 1941 (incl. Ctenentominae
 SCHMIDT 1941)
 Bassleratia KAY, 1934
 Raymondatia KAY, 1934
 Thomasatia KAY, 1934
 Bellornatia KAY, 1934
 Steusloffia ULRICH & BASSLER, 1908
 Ctenentoma SCHMIDT, 1941 (prob. syn. of Steus-
 loffia)
 Hesperidella ÖPIK, 1937
 Pseudostrepula ÖPIK, 1937
 Rigidella ÖPIK, 1937
 Strepula JONES & HOLL, 1886
 Family Primitiidae ULRICH & BASSLER, 1923
 Primitia JONES & HOLL, 1865
 Uhakiella ÖPIK, 1937 (prob. syn. of Primitia)
 Bromidella HARRIS, 1931
 Chilobolbina ULRICH & BASSLER, 1923
 Family Eurychiliniidae ULRICH & BASSLER, 1923
 Subfamily Eurychililiniinae ULRICH & BASSLER, 1923
 Eurychilina ULRICH, 1889
 Laccochilina HESSLAND, 1949
 Coelochilina ULRICH & BASSLER, 1923
 Apatochilina ULRICH & BASSLER, 1923
 (Platyochilina THORSLUND, 1940, non KOKEN)

- Platybolbina HENNINGSMOEN, 1953 (new name
for Platybilina)
- Öpikella THORSLUND, 1940
- ?Subfamily Euprimitiinae HESSLAND, 1949
- Euprimitia ULRICH & BASSLER, 1923
- ?Primitiella ULRICH, 1894
- ?Euprimites HESSLAND, 1949
- ?Haploprimitia ULRICH & BASSLER, 1923
- ?Ectoprimitia BOUČEK, 1936
- ?Laccoprimitia ULRICH & BASSLER, 1949
- ?Subfamily Primitiopsiinae SWARTZ, 1936
- Primitiopsis JONES, 1887
- Family Aparchitidae JONES, 1901
- Aparchites JONES, 1889
- ?Neoparchites BOUČEK, 1936
- ?Punctaparchites KAY, 1934 (syn. of *Macronotella*
by KAY, 1940)
- ?*Macronotella* ULRICH, 1894
- ?*Sphenicibysis* KESLING 1952
- Family Drepanellidae ULRICH & Bassler, 1923
- Subfamily Drepanellinae ULRICH & Bassler, 1923
- Drepanella ULRICH, 1890
- Scofieldia ULRICH & BASSLER, 1908
- ?Subfamily Bolliinae BOUČEK, 1936 (incl. Ulrichinae SCHMIDT,
Bollia JONES & HOLL, 1886 1941)
- Maratia KAY, 1940
- Parenthatia KAY, 1940
- Ulrichia JONES, 1890
- Pseudulrichia SCHMIDT, 1941
- Parulrichia SCHMIDT, 1941
- Crescentilla BARRANDE, 1872
- Richina CORYELL & MALKIN, 1936
- Warthinia SPIVEY, 1939
- Zygobolboides SPIVEY, 1939
- Jonesella ULRICH, 1890
- ?(*Placentula* JONES & HOLL, 1886
- ?*Jonesites* CORYELL, 1930 (new name for *Placen-*
tula
- ?*Placentella* WILSON, 1935

- ?(*Melanella* WADE, 1911)
- ?*Vogdesella* BAKER, 1924 (new name for *Melanella*)
- ?*Kinnekullea* HENNINGSMOEN, 1948
- ?*Sacclatia* KAY, 1940
- ?Subfamily *Aechmininae* BOUČEK, 1936
 - Aechmina* JONES & HOLL, 1869
 - Paraechmina* ULRICH & BASSLER, 1923
 - Lindsayella* CORYELL & WILLIAMSON, 1936
(*Cornulina* CORYELL & WILLIAMSON, 1936 non
CONRAD)
 - Waldronites* CORYELL & WILLIAMSON, 1942 (new
name for *Cornulina*)
 - Aechminaria* CORYELL & WILLIAMSON, 1936
 - ?*Ardmorea* BRADFIELD, 1935
- ?Family *Acronotellidae* SWARTZ, 1936
 - Acronotella* ULRICH & BASSLER, 1923
 - ?*Monoceratella* TEICHERT, 1937a
- Family *Beyrichiidae* JONES, 1894
 - Subfamily *Beyrichiinae* JONES, 1894 (incl. *Kloedeninae* ULRICH
& BASSLER, 1923)
 - Beyrichia* MCCOY, 1844
 - Kloedenia* JONES & HOLL, 1886
 - Welleria* ULRICH & BASSLER, 1923
 - Kyammodes* JONES, 1888
 - Drepanellina* ULRICH & BASSLER, 1923
 - Zygobeyrichia* ULRICH, 1916
 - Treposella* ULRICH & BASSLER, 1908
 - Bolbibollia* ULRICH & BASSLER, 1923
 - Mesomphalus* ULRICH & BASSLER, 1913
 - Bolbiprimitia* KAY, 1940
 - Dibolbina* ULRICH & BASSLER, 1923
 - ?*Apatobolbina* ULRICH & BASSLER, 1923
 - Subfamily *Zygobolbinae* ULRICH & BASSLER, 1923
 - Zygobolba* ULRICH & BASSLER, 1923
 - Zygobolbina* ULRICH & BASSLER, 1923
 - Zygosella* ULRICH & BASSLER, 1923
 - Mastigobolbina* ULRICH & BASSLER, 1923
 - Plethobolbina* ULRICH & BASSLER, 1923
 - Bonnemaia* ULRICH & BASSLER, 1923

- ?Craspedobolbina KUMMEROW, 1924
- Family Hollinindae SWARTZ, 1936
- Hollina ULRICH & BASSLER, 1908
 - Hollinella CORYELL, 1928
 - Basslerina MOORE, 1929 (syn. of Hollinella by COOPER, 1946)
 - Hollites CORYELL & SAMPLE, 1932 (syn. of Hollinella by BASSLER & KELLETT, 1934)
 - Falsipolex KESLING & McMILLAN, 1951
 - Parabolbina SWARTZ, 1936
 - Proplectrum KESLING & McMILLAN, 1951
 - Hanaites POKORNY, 1950
 - Subligaculum KESLING & McMILLAN, 1951
 - Ctenoloculina BASSLER, 1941
 - Tetrasacculus STEWART, 1936
 - Workmanella CRONEIS & GALE, 1938 (syn. of Tetrasacculus by COOPER, 1941)
 - Pterocodella CRONEIS & GALE, 1938 (syn. of Tetrasacculus by COOPER, 1941)
 - Bisacculus STEWART & HENDRIX, 1945
 - Janischewskya BATALINA, 1924
- ?Sulcicuneus KESLING, 1951
- Family Kloedenellidae ULRICH & BASSLER, 1908
- Subfamily Kloedenellinae ULRICH & BASSLER, 1908
 - Kloedenella ULRICH & BASSLER, 1908
 - Eukoedenella ULRICH & BASSLER, 1923
 - Dizygopleura ULRICH & BASSLER, 1923
 - Poloniella GÜRICH, 1896
 - Jonesina ULRICH & BASSLER, 1908
 - Nuferella BRADFIELD, 1935 (syn. of Jonesina by COOPER, 1946)
 - Oliganisus GEIS, 1932
 - Gillina CORYELL & JOHNSON, 1939
 - Kloedenellina CORYELL & JOHNSON, 1939
 - Neokloedenellina CRONEIS & FUNKHOUSER, 1938
 - Lochriella SCOTT, 1942
 - Ellipsella CORYELL & ROGATZ, 1923
 - Sansabella ROUNDY, 1926
 - Lamarella CRONEIS & FUNKHOUSER, 1938 (syn.

- of *Sansabella* by COOPER, 1941)
Persansabella CORYELL & SOHN, 1938 (syn. of
Sansabella by COOPER, 1941)
Reversabella CORYELL & JOHNSON, 1939 (syn. of
Sansabella by COOPER, 1941)
Coelonella STEWART, 1936
Microcoelonella STEWART & SOHN, 1938
Hastifaba COOPER, 1946
Geisina JOHNSON, 1936
Knoxina CORYELL & ROGATZ, 1932
Sargentina CORYELL & JOHNSON, 1939
Perprimitia CRONEIS & GALE, 1938
Lokius CORYELL & JOHNSON, 1939 (syn. of *Per-*
primitia by COOPER, 1941)
Carboprimitia CRONEIS & FUNKHOUSER, 1938
Kirkbyina ULRICH & BASSLER, 1908
Microparaparchites CRONEIS & GALE, 1939
Paraparchites ULRICH & BASSLER, 1906
Antiparaparchites CORYELL & ROGATZ, 1932 (syn.
of *Paraparchites* by KELLETT, 1936)
Proparaparchites COOPER, 1941
Pseudoparaparchites KELLETT, 1933
Geffenina CORYELL & SOHN, 1938
Geffenites CORYELL & SOHN, 1938
Kellettella DELO, 1930
Chesterella CRONEIS & GUTKE, 1939
Beyrichiella JONES & KIRKBY, 1886
Kirkbyella CORYELL & BOOTH, 1933
Balantoides MOOREY, 1935
Verrucosella CRONEIS & GALE, 1938 (syn. of *Cor-*
nigella by COOPER, 1941)
Boursella TURNER, 1939
Cornigella WARTHIN, 1930
? *Bicornella* CORYELL & KUSKLEY, 1934
? *Beyrichiana* KELLETT, 1933
? *Aechminella* HARLTON, 1933
? *Mammoides* BRADFIELD, 1935 (syn. of *Aechmi-*
nella by KELLETT, 1936)
Subfamily *Beyrichiopsiinae* nov.

- Beyrichiopsis JONES & KIRKBY, 1886
 Deloia CRONEIS & THURMAN, 1938
 Leightonella CRONEIS & GALE, 1938 (syn. of
 Deloia by COOPER, 1941)
 (Denisonia CRONEIS & BRISTOL, 1939 non
 KREFFT)
 Denisonella CRONEIS & BRISTOL, 1942 (new name
 for Denisonia)
- Subfamily Glyptopleurinae GIRTY, 1910
 Glyptopleura GIRTY, 1910
 Ceratopleurina CORYELL & JOHNSON, 1939 (syn.
 of Glyptopleura by COOPER, 1941)
 Glyptopleurites CORYELL & JOHNSON, 1939 (syn.
 of Glyptopleura by COOPER, 1941)
 (Idiomorpha CRONEIS & GALE, 1939 non
 FÖRSTER)
 Idiomorphina CRONEIS & GALE, 1939 (in CRONEIS
 1939) (new name for Idiomorpha) (syn. of
 Glyptopleura by COOPER, 1941)
 Glyptopleurina CORYELL, 1928
 Glyptopleuroides CRONEIS & GALE, 1938
 Mesoglypha COOPER, 1941
 Venula COOPER, 1941
 Svantovites POKORNY, 1950
 ?Varix COOPER, 1947
- Family Kirkbyidae ULRICH & BASSLER, 1923 (incl. Amphissitinae
 COOPER, 1941)
 Kirkbya JONES, 1859
 Amphissites GIRTY, 1910
 Girtyites CORYELL & BOOTH, 1933 (syn. of
 Amphissites by JOHNSON, 1936, and KELLETT,
 1936)
 Kegelites CORYELL & BOOTH, 1933 (syn. of
 Amphissites by KELLETT, 1936)
 Albanella HARRIS & LALICKER, 1932
 Aurikirkbya SOHN, 1950
 Ectodemites COOPER, 1941
 Polytylites COOPER, 1941
 Knightina KELLETT, 1933
 Arcyzona KESLING, 1952

- Roundyella BRADFIELD, 1935
 Scaberina BRADFIELD, 1935 (syn. of Roundyella
 by COOPER, 1946)
 Kellettina SWARTZ, 1936
 Franklinella STEWART & HENDRIX, 1945
 Editia BRAYER, 1952
 Brillius BRAYER, 1952
 Savagella GEIS, 1932
- ?Family Youngiellidae KELLETT, 1933
 (Youngia JONES & KIRKBY, 1886)
 Youngiella JONES & KIRKBY, 1895 (new name)
 ?Moorea JONES & KIRKBY, 1867 for Youngia)
 ?Moorites CORYELL & BILLINGS, 1932
 ?Hardinia CORYELL & ROZANSKI, 1942
- ?Family Miltonellidae SOHN, 1950
 Miltonella SOHN, 1950
- ?Family Alanellidae BOUČEK, 1936
 Alanella BOUČEK, 1936
 Vltavina BOUČEK, 1936
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 ?Boučekites PŘIBYL, 1951
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- Genera of uncertain family reference.
 Allostraca ULRICH & BASSLER, 1932
 Balticella THORSLUND, 1940
 Bernix JONES, 1884
 Budnianella BOUČEK, 1936
 Cyathus ROTH & SKINNER, 1930
 Discoidella CRONEIS & GALE, 1938
 Entoprimitia KUMMEROW, 1939
 Eoconchoecia MOBERG, 1895
 Hallatia KAY, 1934
 Halliella ULRICH, 1891
 Hemiaechminoides MORRIS & HILL, 1952
 Hippa BARRANDE, 1872
 Hypotetragona MOOREY, 1935a
 Karlsteinella BOUČEK, 1936

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 Mirochilina BOUČEK, 1936
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 Punctoprimitia STEWART & HENDRIX, 1945
 Pyxion THORSLUND, 1948
 Pyxiprimitia SWARTZ, 1936
 Tetrasulcata MATERN, 1929
 (Ullia HENNINGSMOEN, 1949 non ROEWER)
 Ullerella HENNINGSMOEN, 1950 (new name for
 Ullia)
- Superfamily Leperditicaea BASSLER & KELLETT, 1934
 Family Leperditiidae JONES, 1865
 Subfamily Leperditiinae JONES, 1865
 Leperditia ROUAULT, 1851
 Eoleperditia SWARTZ, 1949
 Anisochilina TEICHERT, 1937
 Heterochilina POULSEN, 1937
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 Herrmannina KEGEL, 1933
 Briartina KEGEL, 1933
 Paenaequina SOLLE, 1935
 (Holtedahlina SOLLE, 1935 non FOERSTE)
 Holtedahlites SOLLE, 1936 (new name for Holte-
 dahlina)
- Subfamily Isochilininae SWARTZ, 1949
 Isochilina JONES, 1858
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 (Saffordella ULRICH & BASSLER, 1923 non
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Leperditella ULRICH, 1894

?Subfamily Conchoprimitiinae nov.

Conchoprimitia ÖPIK, 1937

Conchoides HESSLAND, 1949 (syn. of Conchoprimitia)

Conchoprimites HESSLAND, 1949

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?Subfamily Eridoconchinae nov.

Eridoconcha ULRICH & BASSLER, 1923

Cryptophyllus LEVINSON, 1951

Milleratia SWARTZ, 1936

Schmidtella ULRICH, 1892

?Paraschmidtella SWARTZ, 1936

Suborder PODOCOPA G. O. SARS, 1866

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Graphiadactyllis ROTH, 1929

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Paracythere ULRICH & BASSLER, 1932 (syn. of Graphiadactyllis by KELLETT, 1936)

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Quasillites CORYELL & MALKIN, 1936

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Janetina CORYELL & MALKIN, 1936

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Bufina CORYELL & MALKIN, 1936

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Euglyphella WARTHIN, 1934

Rudderina CORYELL & MALKIN, 1936

Plagionephrodes MOOREY, 1935b

STRATIGRAPHICAL DISTRIBUTION

of the subfamilies and undivided families of straight-hinged Paleozoic ostracods and of the families Thlipsuridae, Healdiidae, and Bairdiidae.

	Ordov.	Sil.	Devon.	Carb.		Pm.
				Mis.	Pen.	
Glossopsiinae	—					
Sigmoopsiinae	—					
Tetradellinae	—					
Piretellinae	—					
Bassleratiinae	—		—			
Primitiidae	—					
Eurychilininae	—					
Euprimitiinae	—					
Primitiopsiinae	—					
Aparchitidae	—					
Drepanellinae	—					
Bolliinae (+Ulrichiinae) ..	—					
Aechmininae	—					
Acronotellidae	—					
Beyrichiinae	—		—			
Zygobolbinae	—	—				
Hollinidae	—	—				
Kloedenellinae	—	—				
Beyrichiopsiinae	—		—	—		
Glyptopleurinae	—			—		—
Kirkbyidae	—					
Youngiellidae	—					
Miltonellidae	—					—
Alanellidae	—	—				
Leperdiinae	—	—				
Isochilininae	—	—	—			
Leperditellinae	—	—				
Conchoprimitiinae	—					
Eridoconchinae	—					
Quasillitinae	—			—		
Ropolonellinae	—		—	—		
Monoceratina (fam. incert.) .	—		—	—		
Thlipsuridae	—	—	—			
Healdiidae	—		—			
Bairdiidae	—					

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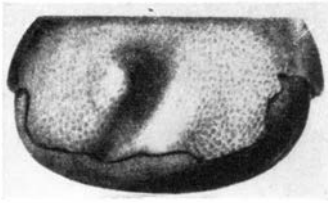
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PLATES 1-2

Plate 1.

- Fig. 1.* *Hesslandella macroreticulata* (HESSLAND, 1949) gen. n. 30 x. (From HESSLAND, 1949, pl. VI, fig. 15).
- Fig. 2.* *Rigidella mitis* (ÖPIK, 1935). 20 x. (From ÖPIK, 1935, pl. I, fig. 5).
- Figs. 3—4.* *Rigidella* cf. *mitis*. Swedish State Museum of Natural History, Paleozool. Dept., no. Ar. 18690. Collected in drift boulder at Humlenäs, Kristdala in Småland, Sweden by Prof. E. Stensiö. Fig. 3 magnified 37 x. Fig. 4 same specimen in different light, magnified 25 x.
- Figs. 5—8.* *Parabolbina auricularis* (JONES, 1887). 30 x. From Mulde, Gotland, Sweden. *Figs. 5—6:* Female type. *Figs. 7—8:* Male type.



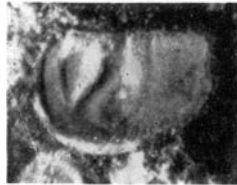
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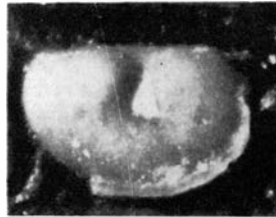
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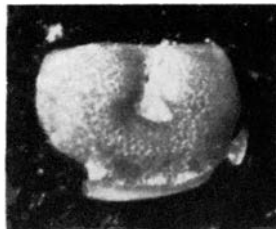
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Plate 2.

(All figures copied from ÖPIK, 1935 and 1937).

Figs. 1—5. Conchoprimites tolli (BONNEMA, 1909). 20 x.

Fig. 1. Figured by ÖPIK (1937, pl. IX, fig. 1) as *Conchoprimitia tolli integra*.

Fig. 2. Figured by ÖPIK (1937, pl. IX, fig. 2a) as *C. tolli*. This specimen shows a posterior groove left by the edge of an earlier moult.

Fig. 3. Figured by ÖPIK (1937, pl. IX, fig. 3a) as *C. tallinnensis*. This specimen has an attached earlier moult, which shows a faint impression posteriorly after a still earlier moult, which was later shed.

Figs. 4—5. Dorsal and ventral view of the same specimen as in fig. 3. The attached moult is clearly distinguished. (ÖPIK, 1937, pl. IX, figs. 3c and 3b).

Figs. 6—7. Conchoprimitia glauconitica (KUMMEROW, 1924). 20 x.

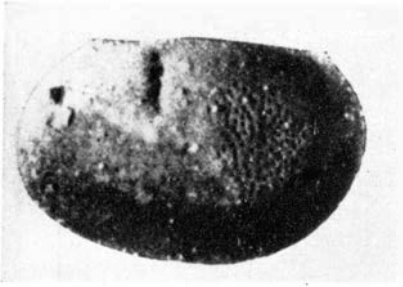
Fig. 6. Figured by ÖPIK (1935, pl. I, fig. 3a) as *C. gammae*. This specimen has an attached moult with a distinct impression left by the ventral edge of a still earlier moult.

Fig. 7. Same specimen in ventral view. (ÖPIK, 1935, pl. I, fig. 3b).

Figs. 8—9. Conchoprimites tolli (BONNEMA, 1909). 20 x.

Fig. 8. Figured by ÖPIK (1937, pl. XV, fig. 5) as *Conchoprimitia deminuta*. An earlier moult is attached.

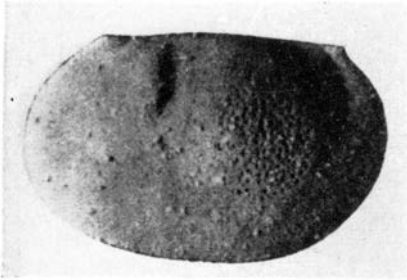
Fig. 9. Left view of the same specimen as in fig. 8. Here the earlier moult has been removed. Figured by ÖPIK (1937, pl. XV, fig. 4).



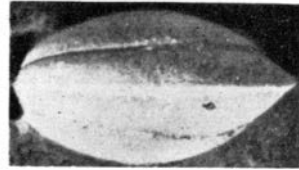
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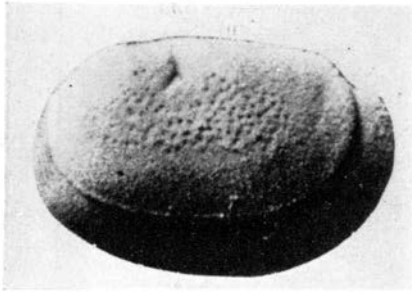
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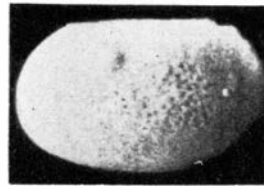
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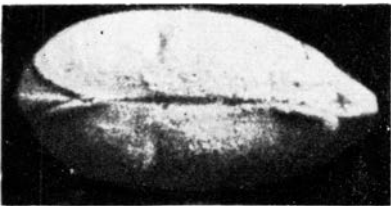
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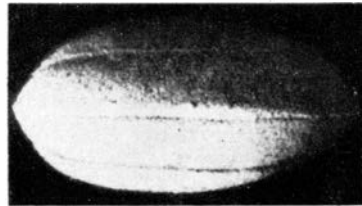
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