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COPULATORY ADAPTATIONS IN OSTRACODS

PART III. ADAPTATIONS IN SOME EXTINCT OSTRACODS

BY

ROBERT V. KESLING



MUSEUM OF PALEONTOLOGY  
THE UNIVERSITY OF MICHIGAN  
ANN ARBOR

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*Director:* ROBERT V. KESLING

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# COPULATORY ADAPTATIONS IN OSTRACODS

## PART III. ADAPTATIONS IN SOME EXTINCT OSTRACODS

ROBERT V. KESLING

**ABSTRACT**—Extinct ostracods with strong dimorphism of their carapaces seem adapted to favor some mating positions and to exclude others. Copulatory habits of fossil species cannot, of course, be precisely determined; yet the shapes of male and female carapaces within a taxonomic group strongly suggest that certain positions were feasible, others highly improbable, and some seemingly impossible. There is little reason to doubt that the configuration of the carapace was functional in copulation as well as locomotion. Its detailed study, therefore, may improve taxonomy and illuminate evolutionary trends.

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### INTRODUCTION

EVOLUTION OF THE OSTRACOD has involved the total animal. Nowadays most micropaleontologists will agree that changes in function have been integrated with changes in morphology. Carapace, appendages, and organs have not evolved independently. In any particular ostracod, the characters are attuned to successfully perform the necessary functions, such as food gathering, respiration, locomotion, and reproduction.

Evolution is thus an interlocking succession of physical forms, within each of which there is (or was) a multitude of morphological parts. During the life of each animal, these parts have interrelationships and interdependencies in carrying out vital functions. The zoologist and paleontologist cannot hope to learn all of these factors immediately. They are too complex and too many. It is difficult to isolate even a few characters which seem to have clear functional linkage.

Nevertheless, I wish to focus attention on possible copulatory adaptations in extinct ostracods. Presumably, dimorphic features of the carapace in fossil species are convincing evidence of syngamic reproduction, requiring mating of the two sexes. Living ostracods, insofar as they have been investigated, display different adaptations in different taxa. If function and morphology evolve together, then particular mating procedures would have characterized each lineage, and carapace modifications for copulation would be useful in taxonomy.

The role of carapace dimorphism in taxonomy is currently a field of deep concern in micropaleontology. Some carapaces show strong dimorphism, some weak dimorphism, and others none at all. Furthermore, carapaces exhibit a variety of shapes. The same general shape may occur in both dimorphic and non-dimorphic species. In recent years, classification systems for Ostracoda by competent workers have differed most on the significance of dimorphism.

This is amply demonstrated by comparisons of the comprehensive works by Porkorný (1958), Zanina & Polenova in the Russian *Treatise* (1960), and various authors in the *Treatise on Invertebrate Paleontology* Ostracoda volume (1961), as well as by suggested revisions by Martinsson (1962) and Henningsmoen (1965).

The question remains: Are genetic relationships more clearly revealed by shape of carapace or by presence or absence of dimorphism? In probing for a meaningful answer, micropaleontologists are re-examining ostracod carapaces in all taxa, looking for some conservative character which will define lineages. So it is that some investigators study muscle scars, for example, hoping to establish kinship of species through the preserved marks left by the closing muscles. Notwithstanding the rapid advances in our knowledge of fossil ostracods, the search for a satisfactory taxonomy goes on. Additional means of assessing morphology are seriously needed.

The copulation trouble occasioned by a bivalved carapace is not new for the ostracod. Obviously, the problem existed from the time the bivalved carapace developed. We must assume that, by necessity, the solution for the problem evolved at the same time. The first ostracod must have had special adaptation for the male to copulate with the female. We would like to learn whether these adaptations have left discernible evidence in the preserved carapaces.

Caution is required in applying generalizations from living to extinct ostracods. Not all dimorphic features of the carapace are related to mating. The female carapace may also be modified for egg storage and brood care. Especially, this applies to the beyrichiids, which had a conspicuous pouch or crumina in each valve of one dimorph. Most students of these prominent Paleozoic forms now agree that the crumina was borne by the female and used to hold eggs and to house the young brood.

Even so, non-copulatory dimorphic characters of the carapace cannot be ignored in this study. For instance, the voluminous cruminae in the beyrichiids eliminate the possibility of male overlap in the region where they are situated. The whole carapace must come under scrutiny.

In my opinion, generalizations from living ostracods can lead to new assessments and understanding of dimorphic carapaces in extinct ostracods. As examples I offer these notes on some strongly dimorphic Paleozoic ostracods of the suborder Beyrichicopina, including examples of the families Eurychiliniidae, Piretelliidae,

Beyrichiidae, Tetradellidae, Oepikiumidae, Holiniidae, Primitiopsidae, and Oepikellidae.

I am particularly indebted to Professor Anders Martinsson for his generous permission to reproduce illustrations modified from those published in the *Bulletin of the Geological Institutions of the University of Uppsala* and in the *Publications from the Palaeontological Institution of the University of Uppsala*. Many of these illustrations are reversed, so that they now appear to represent lateral views of right valves instead of left. They are combined with my illustrations, some new, so that all ostracods are oriented the same; because the differences between left and right valves in the Beyrichicopina are very minor, the reversal does not affect the pertinent details of lobation and ornamentation.

#### PREVIOUS WORK

Ostracod literature abounds with speculations on the function of such dimorphic structures as cruminae in the Beyrichiidae and dolons in the Eurychiliniidae and Piretelliidae. A complete bibliography would include nearly all the authors on Paleozoic ostracods. Strangely, very few statements concerned copulation.

One author who expressed definite ideas on copulation was Ivar Hessland. Of *Eurychilina* he stated (1949, p. 127):

The difference in appearance of the velum may have developed for facilitating the copulation: the distance between the free margin is shorter in this case than if the vela of both sexes had been convex.

And of *Beyrichia* he said (1949, p. 125-126):

Would it not have been better if the brood pouches [cruminae] had been situated posteroventrally? The fertilized eggs would then have dropped direct from the genital opening into the brood pouch. The brood pouch could not be situated there for the reason that it would have been a serious hindrance during copulation or it might have made this process impossible. . . . If the protruding brood pouches of for instance *Beyrichia kloedeni* had been situated posteroventrally they would have caused a rather large distance between the posteroventral free margins of two copulating animals.

In summarizing his discussion of dimorphism, Hessland stated (1949, p. 128):

The sexual dimorphism as regards the velum may have been an arrangement for facilitating copulation.

Recently, Becker (1968b, p. 131) suggested that hamal structures, curious hook-shaped processes on the anterior margins of assumed male valves in *Nodella hamata* Becker, might be clamping devices used by the male in copulation.

## Order PALAEOCOPIA Henningsmoen 1953

Of all ostracods known, the order Palaeocopa contains those with the most kinds and the strongest development of dimorphism. Becker (1968a, p. 55) recognized two types of dimorphism in carapaces: "Domicildimorphismus," which affects the available space for the organs and appendages, and "Ornamentaler Dimorphismus," which involves only structures in the shell material.

Later (1968b, p. 119–122), Becker made three divisions of domiciliar dimorphism:

- (1) "Unterschiedliche Grössenverhältnisse" — in which small differences exist in the sizes of the male and female valves.
- (2) "Unterschiede im Gehäuseumriss" — in which males and females differ primarily in outline and the height/length ratio of the carapace.
- (3) "Gehäuseauftreibungen" — in which the valves of one sex have additional inside space because of "swellings" or localized convexities not present in valves of the other sex. In Recent cytherellids the additional space is an accommodation in the female for the brood; hence, in the extinct palaeocopes the valves with the extra domiciliar space are considered to be those of the female. Becker distinguished two kinds:
  - (a) "Kloedenellider Dimorphismus" — in which the rear part of the female carapace is much enlarged. This was called *kloedenellid* or *domiciliar* dimorphism by Scott & Wainwright in the *Treatise* (1961, p. 37).
  - (b) "Cruminaldimorphismus" — in which an anteroventral to ventral brood pouch is formed in each valve of the female. This is discussed below in the family Beyrichiidae, of which it is the chief characteristic. In Scott & Wainwright's classification, this includes both their *lobate* (as in *Zygobolbina*) and their *beyrichiid* (as in *Beyrichia*) types of dimorphism.

Becker also (1968b, p. 123–131) divided ornamental dimorphism into:

- (1) "Antraldimorphismus" — in which velar and histial structures (adventral structures) form different areas between their edges and the margin of the valve in the two sexes. Henningsmoen (1965, p. 341) introduced the term *antrum* for the area associated with the inward-facing surface of adventral structures and the adjacent

concave part of the ventral surface of the valve.

- (2) "Marginaldimorphismus" — in which one dimorph has a structure along the margin that is absent in the other. This rare kind of dimorphism is known only in *Nodella*, particularly in *N. hamata* Becker, in which the assumed male has an anterior hook-shaped process directed downward and apparently bordering a narrow incisure. Becker (1968b, p. 129) called the process a "Hamalstruktur" and the dimorphism "Hamaldimorphismus." He suggested that the dimorphism might be related to different swimming capabilities in male and female, or (as stated above) that the process might be a clamping device used by the male in copulation.

The antral dimorphism of Becker includes many different kinds of dimorphism in the Beyrichiopinina. Henningsmoen (1953) distinguished between "velate" and "carinal" dimorphism in Paleozoic straight-backed ostracods. These terms were changed by Jaanusson (1957, p. 199) to "velar" and "histial" dimorphism. Both authors were drawing a fine line of separation between the structures which lie ventral to a connecting lobe or in the corresponding position if a connecting lobe is absent (velar), and those which form a continuation of the ventral end of a connecting lobe or lie in the corresponding position if no connecting lobe is present (histial). In ostracods lacking a connecting lobe, the interpretation of the structure may be debated; hence, authors still disagree on the velar or histial nature of the dimorphic structures in the prominent family Hollinidae.

Scott & Wainwright (1961, p. 37) divided the antral type of dimorphism into *velate* and *histial* dimorphism. Martinsson (1962, p. 87–88) referred to *velar* and *histial* dimorphism. Henningsmoen (1965, p. 344–345) stated:

... the term antral dimorphism, like locular dimorphism, does not commit one in stating whether the dimorphic structure is of velar or histial origin.

In discussing the dimorphism in various palaeocopes, however, Henningsmoen identified the associated structure wherever possible. Thus, he referred to "histial dimorphism" in the Sigmoopsinae (1965, p. 347), "velar dimorphism" in certain hollinids with narrow venter (1965, p. 352), and "histiovelar dimorphism" in hollinids having both velar and lobal structures involved (p. 352).

Henningsmoen (1965, p. 349) and others have used the term "locular dimorphism" to refer to any kind of dimorphism involving loculi in the female. As Scott & Wainwright (1961,

p. 42) pointed out, the loculi of *Tetradella* and *Ctenoloculina* seem to have different origins.

Recently, in discussing the Ordovician Tetradellidae, Jaanusson (1966, p. 4) altered his position of 1957, stating, ". . . the writer now prefers to discard the terms histial and velar when referring to types of dimorphism." For all kinds of dimorphism involving vela and histia, Jaanusson used the term "extradomiciliar dimorphism." This term is certainly preferable to "ornamental dimorphism." In the tetradellids, Jaanusson found three kinds of antral dimorphism (1966, p. 8):

(1) Supravelar—dimorphic antrum above the velum, as in *Tetradella*. (2) Biantral—dimorphic antra above and below velum, as in *Sigmoopsis*. (3) Infravelar—dimorphic antrum below velum, as in *Glossomorphites*. In this treatment of antra, Jaanusson made clear distinctions between vela and histia, and substantiated the position of various antra with excellent photographs.

Inasmuch as authors do not yet agree upon one set of terms for dimorphic types, it seems advisable here to describe the dimorphism involved in each genus rather than to rely upon a particular term. In view of the close phylogenetic relationships between the Eurychilinae and the Beyrichiidae suggested by Kesling (1957) and Martinsson (1962), the major divisions into domiciliar and extradomiciliar dimorphism seem to be the most satisfactory. Nevertheless, problems persist. The antral (velar) dimorphism in eurychilinae (see text-fig. 1) differs drastically from that in primitiopsids (see text-fig. 21), and no series is known leading from one to the other.

Classification is likewise beset with lack of general agreement. In creating the Palaeocopa, Henningsmoen (1953, p. 188) included two superfamilies, the Beyrichiacea and the Leperditiaea. Later in the same year, Pokorný (1953, p. 213–231) placed these superfamilies in his orders Beyrichiida and Leperditida respectively. In his book (1958) Pokorný filled out the content of each of these orders, dividing the Beyrichiida into 17 families.

In the *Treatise* (1961) the order Palaeocopa was proposed and divided into two suborders, Beyrichicopina and Kloedenellocopina. The leperditids were placed in the order Leperditicopida. The Palaeocopida of the *Treatise*, therefore, approximately equals the Beyrichiacea of Henningsmoen's original Palaeocopa.

Martinsson (1962, p. 127) further restricted the Palaeocopa, which he ranked as a suborder, by removing the kloedenellids to the suborder Kloedenellocopa. His Palaeocopa corresponds to the Beyrichicopina of the *Treatise*.

Recently, Henningsmoen (1965, p. 384–390) proposed the following classification of certain ostracods in his order Palaeocopa:

Group BEYRICHIIDA Pokorný—all forms with antral or cruminal dimorphism, "and possibly also non-dimorphic off-shoots." No ventricular concavity. Suborder BEYRICHIOMORPHA Henningsmoen — all palaeocopes with cruminal dimorphism.

Superfamily Beyrichiacea Matthew.

Suborder HOLLINOMORPHA Henningsmoen — all palaeocopes with antral dimorphism.

Superfamily Eurychilinaea Ulrich & Bassler—hollinomorpha with anteroventral to ventral antra. Includes hollinids, eurychilines, chilobolbinines, oepikellines, piretellines, tvaerenellines, glossomorphitines, sigmoopsines, oepikiines, tetradellines, ceratopsines, and possibly others.

Superfamily Primitiopsacea Swartz — hollinomorpha with posterior antra.

Suborder(s) ?

Superfamily Drepanellacea.

Superfamily Leperditellacea.

?Group KLOEDENELLIDA Henningsmoen — forms with kloedenellid dimorphism, "and possibly non-dimorphic off-shoots." Ventricular concavity present in many.

Suborder KLOEDENELLOCOPINA Scott

Superfamily Kloedenellacea

Superfamily Paraparchitacea

Suborder ? (Kloedenellocopina?)

Superfamily Kirkbyacea

?Group LEPERDITIIDA Pokorný—dimorphism unknown. No ventricular concavity.

Suborder LEPERDITIOCOPINA Scott

This brief review demonstrates some of the problem areas and uncertainty in classification, particularly as regards the importance of dimorphism in higher taxa. Here, I follow mostly the suprafamilial classification of the *Treatise* (1961), the beyrichiid classification of Martinsson (1962), the eurychilinean classification of Jaanusson (1957), and the tetradellid classification of Jaanusson (1966).

#### Suborder Beyrichicopina Scott 1961 Superfamily EURYCHILINACEA

Velar structures are well developed in typical eurychilineans. Many genera possess a wide frill extending from end to end and projecting in front, below, and behind the free edge of the valve. Others, however, have a velar structure reduced to a ridge, either in its entirety or in the posterior region, or modified as spines.

Development of velar structures seems to be in direct proportion to the degree of dimorphism. In fact, if the Bassleratiidae and Quadrijugatoridae are included in the superfamily, most ostracods in those families have only velar ridges and no dimorphism at all. On the other hand, such genera as *Laccochilina* and *Chilobolbina* have wide frills and pronounced velar dimorphism, in which the female is pro-

vided with a convex to globose section of frill called the dolon.

The frill in eurychilinids differs from that in many beyrichiids by the angle which it forms with the valve. For example, well-developed frills are present in both *Eurychilina* and *Apatobolbina*; but in the former the frill extends primarily downward with a little outward flare because of its concave surface (Kesling, 1960, pls. 3, 4), whereas in the latter the frill is directed primarily outward so that it forms nearly a horizontal surface in opened valves (text-fig. 7a-d).

This orientation of the frill presented a critical factor in copulation of the eurychilinaeans. The ventral position was practically impossible because of a four-way dilemma. If the frills of the male were inserted between those of the female, the gape of the male valves was too narrow for extrusion of the hemipenes; if the frills of the male were placed around those of the female, her valves may have been held too close together for access; if the frills of the male were interleaved with those of the female, his body was laterally offset from that of his prospective mate; and if the frills of the male were not between nor around nor interleaved with the female frills, then the domicilia of the two partners were held apart by the combined widths of their frills, which touched edge-to-edge. As will be discussed below, the laterally directed frills of some beyrichiaceans would not constitute such an obstacle.

Family EURYCHILINIDAE  
Subfamily CHILOBOLBININAE  
Text-fig. 1

Although dimorphism to some degree is present in several ostracods of the subfamily Eurychilinae, it is strongly represented in the other subfamily, the Chilobolbininae. Genera in the latter subfamily show similarities to the family Piretelliidae, as pointed out by Jaanusson (1957, p. 231). The Chilobolbininae were selected here to show also the strong similarities between their dimorphic dolon and the dimorphic crumina of the Beyrichiidae.

In contrast to the subfamily Eurychilinae, the subfamily Chilobolbininae has the female dolon extended the entire width of the frill. In some genera, the dolon protrudes dorsally, so that the line of frill-domicilium contact is locally higher in the female than in the male (Jaanusson, 1957, fig. 13). Within the genera assigned to the subfamily, the dolon may be delimited only by general curvature, as in *Cystomatochilina* (text-fig. 1b); it may be strongly

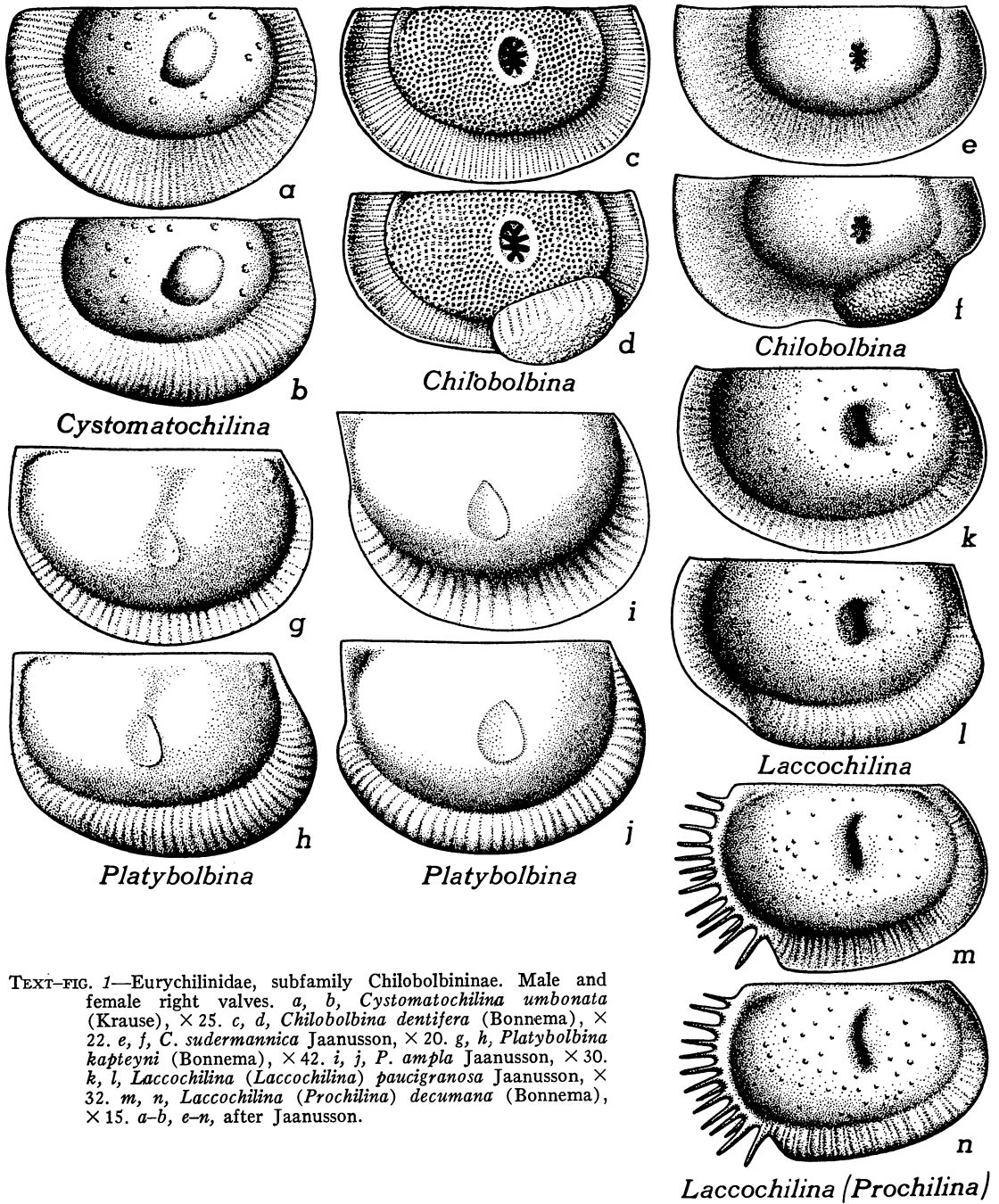
emphasized by convexity, as in *Platybolbina* (text-fig. 1h, j); it may be elongate with well-defined ends, as in *Laccochilina* (text-fig. 1l, n); or it may be extremely convex and localized, as in *Chilobolbina* (text-fig. 1d, f). In any case, the convexity of the dolon makes it recurve toward the plane of closure, and the edges of the egg-shaped dolons in *Chilobolbina* "seem to lie together when the carapace is closed" (Hessland, 1949, p. 126).

The frill in the male not only lacks a dolon but it is concave. Nevertheless, it is directed at least as much downward as outward, and the edges of the two frills in a closed carapace do not leave a great distance between them—especially when compared to those of certain beyrichiids. The frill in both dimorphs may continue to the posterior corner without much change in width, as in *Cystomatochilina* (text-fig. 1a, b) or *Laccochilina* (*Laccochilina*) (text-fig. 1k, l); it may even expand somewhat in the posterior section, as in *Chilobolbina sudermanica* (text-fig. 1e, f); it may be replaced posteriorly by velar spines, as in *Laccochilina* (*Prochilina*) (text-fig. 1m, n); or it may decrease considerably toward the posterior corner or even fail to reach it, as in *Actinochilina* and *Platybolbina* (text-fig. 1g-j).

Any expression of lobation is confined to the central area of the valve. In cross section, the carapace of all eurychilid ostracods is acuminate dorsally, with the upper area of each valve relatively smooth, gently convex, and void of any sort of projection near the hinge line.

Hence, the eurychilid female valve is exemplified by a dolon that is wide and ventrally convex and by a domicilium that is smooth and gently curved dorsally. Whereas some genera (such as *Platybolbina*) have the female frill obsolete or absent along the posterior border, others (such as *Chilobolbina*) have a very wide frill there.

It would seem that all the Eurychilinae are particularly well suited for the dorsal mating position, similar to that illustrated in part 2 of this series for *Entocythere*. In utilizing the dorsal position, the smooth upper area of the female valves in *Chilobolbina* would offer no hindrance to overlap by the male, and the female frills would separate enough posteriorly to allow access of the male organs into the female domicilium. Other genera of the family could have mated in this position with even greater ease. In *Actinochilina* and *Platybolbina*, a posterodorsal position would also have been possible. In all genera, the ventral position would have proved extremely disadvantageous.



TEXT-FIG. 1—Eurychiliniidae, subfamily Chilobolbinae. Male and female right valves. a, b, *Cystomatochilina umbonata* (Krause),  $\times 25$ . c, d, *Chilobolbina dentiifera* (Bonnema),  $\times 22$ . e, f, *C. sudermannica* Jaanusson,  $\times 20$ . g, h, *Platybolbina kapteyni* (Bonnema),  $\times 42$ . i, j, *P. ampla* Jaanusson,  $\times 30$ . k, l, *Laccochilina (Laccochilina) paucigranosa* Jaanusson,  $\times 32$ . m, n, *Laccochilina (Prochilina) decumana* (Bonnema),  $\times 15$ . a-b, e-n, after Jaanusson.

Family PIRETELLIDAE

Text-figs. 2, 3

Jaanusson (1957) separated the Piretelliidae from the Eurychiliniidae by the supposed development of the velar structure (if present) as a solid extension of the shell rather than a series of fused tubules. Subsequently, Schallreuter (1964, p. 385) discovered that *Piretella* has a

frill composed of hollow tubules, like that of the Eurychiliniidae. He proposed his new subfamily Hithinae to replace the Piretelliinae of Jaanusson. This did not, however, totally resolve either the synonymy or the classification problems. By Schallreuter's analysis, *Piretella* belongs in the Eurychiliniidae, the name Chilobolbinae is a junior synonym of Piretelliinae,



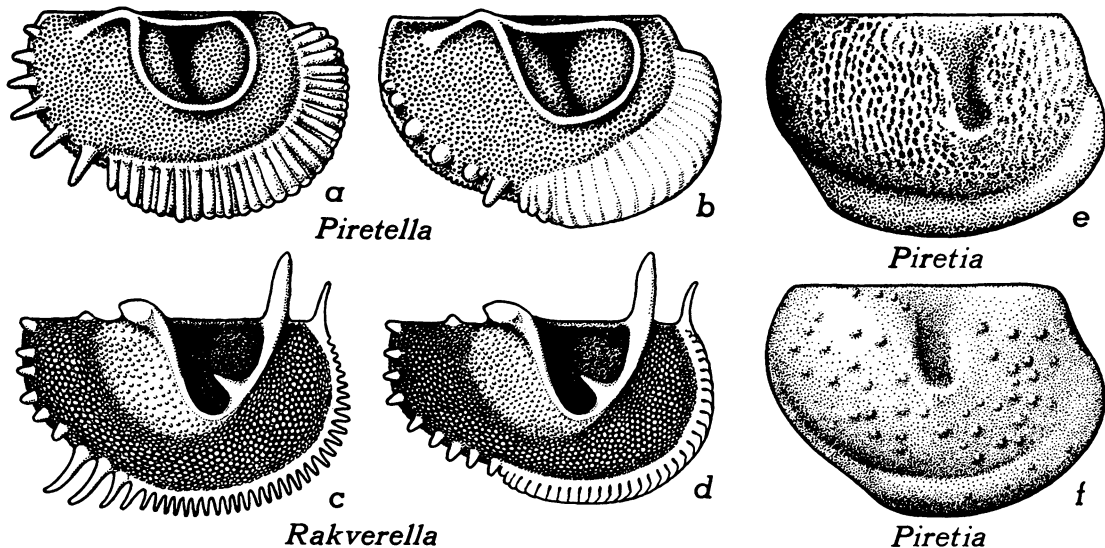
and the name Piretelliidae is a junior synonym of Eurychilinidae. Accordingly, he put *Piretella* and *Chilobolbina* in the subfamily Piretelliinae; *Bromidella*, *Uhakiella*, *Piretia*, *Brevibolbina*, and *Hithis* in the subfamily Hithinae; and both subfamilies in the family Eurychilinidae.

Inasmuch as the velar structure of all Eurychilinaea has not been thoroughly substantiated by thin sections or polished surfaces, the taxonomic distinctions still seem to be anticipatory. Herein, the Piretelliidae are retained as a unit, but with the recognition that velar structure in at least some genera is not a solid extension of the shell.

As constituted, the piretelliids all show velar dimorphism. The male has either a slightly concave velar structure, a ridge, or none at all. The female always has a velar structure, set

higher on the domicilium than the corresponding structure in the male. Three subfamilies have been erected on the different widths and curvatures of the female velar structure: Euprimitiinae, with only a velar ridge, like that of the male but set higher and at a different angle on the domicilium; Tvaerenellinae, with a broad, convex, flange-like dolon, not extending very far back toward the plane of closure; and Piretelliinae, with a well-developed pouchlike dolon, large enough to fill most if not all of the major velar structure and so strongly convex that its edge closely approaches or meets that of the opposite valve in a closed carapace. The family presents, therefore, a rather broad spectrum of dimorphism.

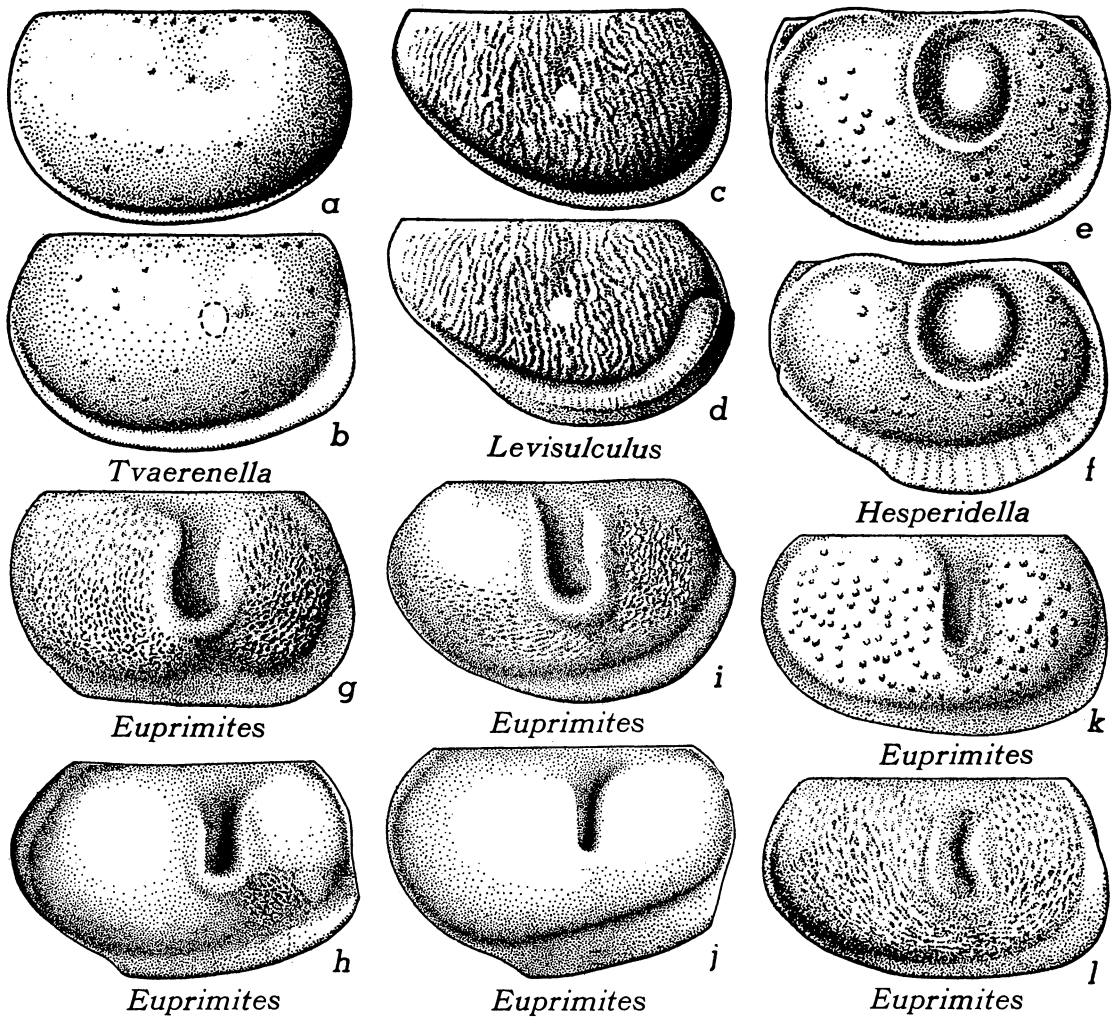
Lobation tends to be basically simple. It does not display tendencies to follow sub-



TEXT-FIG. 2—Piretelliidae, subfamily Piretelliinae. Male and female right valves. *a, b*, *Piretella acmaea* Öpik,  $\times 18$ . *c, d*, *Rakverella bonnemai* Öpik,  $\times 25$ . *e*, female *Piretia geniculata* Jaanusson,  $\times 42$ . *f*, female *P. clypeolaria* Jaanusson,  $\times 33$ . *e-f*, after Jaanusson.

familial lines. In *Tvaerenella* (text-fig. 3a, b), and *Levisulculus* (text-fig. 3c, d) of the Tvaerenellinae the only expression of lobation is at most a faint depression from the hinge line trending down toward the adductor muscle scar. In *Euprimitia* of the Euprimitiinae, *Euprimites* (text-fig. 3g-l) of the Tvaerenellinae, and *Piretia* (text-fig. 2e, f) of the Piretelliinae, the median sulcus is deep and sharply defined, in some species further emphasized by a U-shaped ridge bordering its sides and ventral end. *Uhakiella* of the Piretelliinae has a similar sulcus, but not as deep. Both *Dicranella* of the Tvaerenellinae and *Rakverella* (text-fig. 2c, d) of the Piretelliinae have a broad central sulcus with

large spinose projections in front and behind; the anterior projection (probably representing L1) extends upward, whereas the posterior one (probably representing L3) extends upward and backward in *Dicranella* and backward and laterally in *Rakverella*; both genera show some suggestion of an L2 or presulcal structure, a small node in *Dicranella* and a sharp spine in *Rakverella*. *Hesperidella* (text-fig. 3e, f) of the Tvaerenellinae and *Piretella* (text-fig. 2a, b) of the Piretelliinae are primarily unisulcate, but both have a complex of conspicuous crests and dorsal plicae that widen the dorsal area of the carapace. A dorsal plica in *Bromidella* of the Piretelliinae also forms a high and extended dor-



TEXT-FIG. 3.—Piretelliidae, subfamily Tvaerenellinae. Male and female right valves. *a, b, Tvaerenella carinata* (Thorslund),  $\times 38$ . *c, d, Levisulculus lineatus* Jaanusson,  $\times 40$ . *e, f, Hesperidella esthonica* (Bonnema),  $\times 40$ . *g, female Euprimites locknensis* (Thorslund),  $\times 34$ . *h, female E. effusus* Jaanusson,  $\times 30$ . *i, female E. anisus* Jaanusson,  $\times 30$ . *j, female E. suecicus* (Thorslund),  $\times 26$ . *k, female E. eutropis* (Öpik),  $\times 32$ . *l, female E. bursellus* Jaanusson,  $\times 40$ . All figures after Jaanusson.

sum. Quite obviously, lobation has no correlation with the degree or kind of dimorphism.

Both *Piretella* and *Rakverella* are based on specimens from the Middle Ordovician Kukuruse Shale or kuckersite in Estonia. Solution of the calcareous carapaces makes them very fragile, and tends to etch away fine details. Nevertheless, fairly well-preserved female carapaces have been described that seem to have short blunt nodes in the posteroventral region, whereas male carapaces have fairly well-developed spines there. It would appear that dimorphism may extend behind the dolonate section of the frill and affect the velar spines as well.

The piretelliids are so diverse in lobation that

it is difficult to characterize them as a group. All have one feature in common: the female valve has no frill or prominent projections at the posterior end. The mating position best suited to this arrangement seems to be the posterodorsal. Even in *Dicranella* and *Rakverella*, with their spinose projections of L3, there was ample room for overlap by the male. It cannot be ruled out that these ostracods mated in a modified ventral position, more of a posteroventral-to-posteroventral; but the male would have encountered considerable difficulty in clasping the female carapace. Clasping devices would seem to have been even more important for the piretelliid male in positioning on the

complex female carapace than for the living cypridid males on the simple and unornamented female carapaces; in living ostracods, clasping devices do not extend in use very far laterally from the gape of the valves, and one may suppose that the same restrictions applied to the piretellids. It is clear that the dorsal position would have been impossible in *Rakverella* (text-fig. 2d) because of the spines, and it would have been very difficult in *Piretella* (text-fig. 2b) and *Hesperidella* (text-fig. 3f) because of the wide dorsal plica and crests.

#### Superfamily BEYRICHIACEA

##### Family BEYRICHIIDAE

Text-figs. 4-14

The beyrichiids have long been recognized as a group of extinct ostracods with a "brood pouch" or crumina in one dimorph. In fact, Ulrich & Bassler (1923, p. 310-312) employed the term *brood pouch* as if no question existed as to its actual function. German authors termed it Brutkammern, Brutraum, Bruttasche, and Bruthöcker, still without any evidence that it was connected with the brood. As later shown, they made a fortunate guess. As investigation of ostracods continued, however, doubts were raised.

At one time (Schmidt, 1941, p. 11), the suggestion was made that the globose pouches, which open internally, might have been gas-filled chambers for buoyancy. It was also thought that the pouches belonged to the males, used to house spermatozoa (Schmidt, 1941, p. 12) or to carry sperm vesicles (Triebl, 1941, p. 365).

The first concrete evidence was presented by Hessland (1949, p. 125; pl. 14, fig. 9), who described and illustrated a cross section of a pouch-bearing specimen of *Beyrichia kloedeni* in which the adult carapace enclosed carapaces of very young instars, apparently of the same species. Spjeldnaes (1951, pl. 103, fig. 1) demonstrated the same situation in "*Beyrichia jonesii*" (now recognized as *Craspedobolbina clavata*). Martinsson (1956) checked sections of numerous dimorphs of *C. clavata*, discovering immature instars inside half of the pouched carapaces and none inside the non-pouched carapaces. Others have supplemented the evidence that the cruminae were used to house the young; and practically all current workers accept the conclusion that the dimorph carrying the brood is the female.

In recent years, Kesling (1957) and Martinsson (1960, 1962) have discussed the probable evolution of crumina, adding to the suggestions by Hessland (1949), Henningsmoen

(1954), and Jaanusson (1957). All agree generally that the crumina developed in stages from a strongly convex dolon, and that the beyrichiid ancestors were eurychilinaceans.

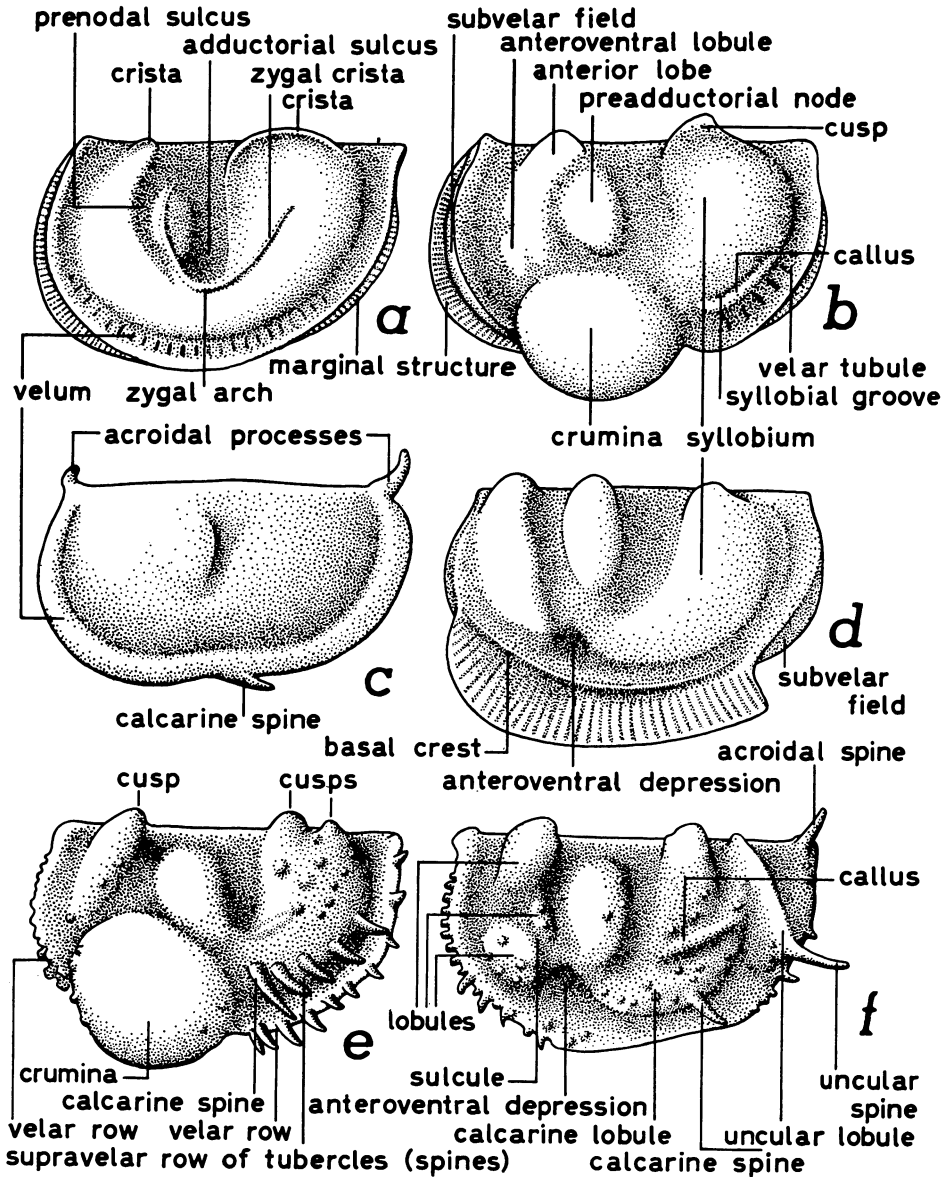
There is less unanimity on taxonomic treatment of cruminate ostracods. Henningsmoen (1953, p. 264) recognized the family Beyrichiidae with subfamilies Beyrichiinae and Zygobolbinae. Later (1954, p. 20) he gave a more precise definition of the family and divided it into four subfamilies, adding Kloedeniinae and Treposellinae. In 1962 Martinsson placed all cruminate ostracods into one family, which he divided (p. 131) into Craspedobolbinae, Treposellinae, Amphitoxotidinae, Zygobolbinae, Beyrichiinae, Kloedeniinae, and Hexophthalmoidinae. The following year, he proposed (1963, p. 54) to split them into two families, Craspedobolbinidae and Beyrichiidae, with subfamilies Craspedobolbininae, Treposellinae, and Amphitoxotidinae, in the former and Beyrichiinae, Zygobolbinae, Kloedeniinae and Hexophthalmoidinae in the latter. His division was based on the tubular structure of the frill present in Craspedobolbinidae and absent in Beyrichiidae (as restricted).

Henningsmoen (1965, p. 387-388) stated that splitting of the superfamily Beyrichiacea into two families "presupposes that a tubulous velar structure could not reappear in a phyletic lineage, after not having been developed in intervening forms." He favored the theory that the amphitoxotidine ostracods developed from certain of the beyrichiines and were more closely related than indicated by Martinsson's revised system. He combined all cruminate ostracods again into one family.

Disputes over classification arise from the taxonomic weight placed on velar construction, lobation, cruminal formation, and surface ornamentation. Herein, the classification proposed by Martinsson in 1962 is adopted, in which crumina-bearing ostracods are united in one family and their supposed differences are relegated to the subfamily level.

Even though beyrichiid ostracods have been studied for over a century, their diversity is still being explored. Of the 60 genera now recognized, 43 were established since 1953. In one monograph, Martinsson (1962) named 30 new genera, of which 18 were based on only the type species. At the present trend, one can expect a more sophisticated picture of the Beyrichiidae in the next decade.

Because of their specialization, the beyrichiids possess unusual structures which require some unique terms. The terminology is well discussed and illustrated by Martinsson (1962, p. 63-79, fig. 15), whose sketches are



TEXT-FIG. 4.—Terminology of beyrichiid ostracods. Left valves. *a*, male *Craspedobolbina* (*Craspedobolbina*). *b*, female *Craspedobolbina* (*Mitrobeyrichia*). *c*, male *Hamulinavis*. *d*, male *Amphitoxotis*. *e*, female *Beyrichia* (*Beyrichia*). *f*, male *Calcaribeyrichia*. All figures from Martinsson.

reproduced here as text-figure 4. Note that syllobial cusps and cristae extend above the hinge line and add to the width of the posterodorsal region, acroidal processes or spines project from the posterior corner, and uncular and supravellar spines jut out from the posteroventral area.

At this point, a few comments on ostracod molting are in order, since molting in the beyrichiids determined the final form of the carapace in both male and female. Even after watch-

ing the molting of freshwater ostracods, I must concede that very little is known about the methods of casting off the old covering, growing, and secreting new chitin and carbonate, and that almost nothing is known of the physiological chemistry involved. Nevertheless, some observations on the sequence of molting seem pertinent. In those species whose molting I have seen, the process proceeds from anterior to posterior. Even before the old valves are cast off, a new layer lies wrinkled under them. As

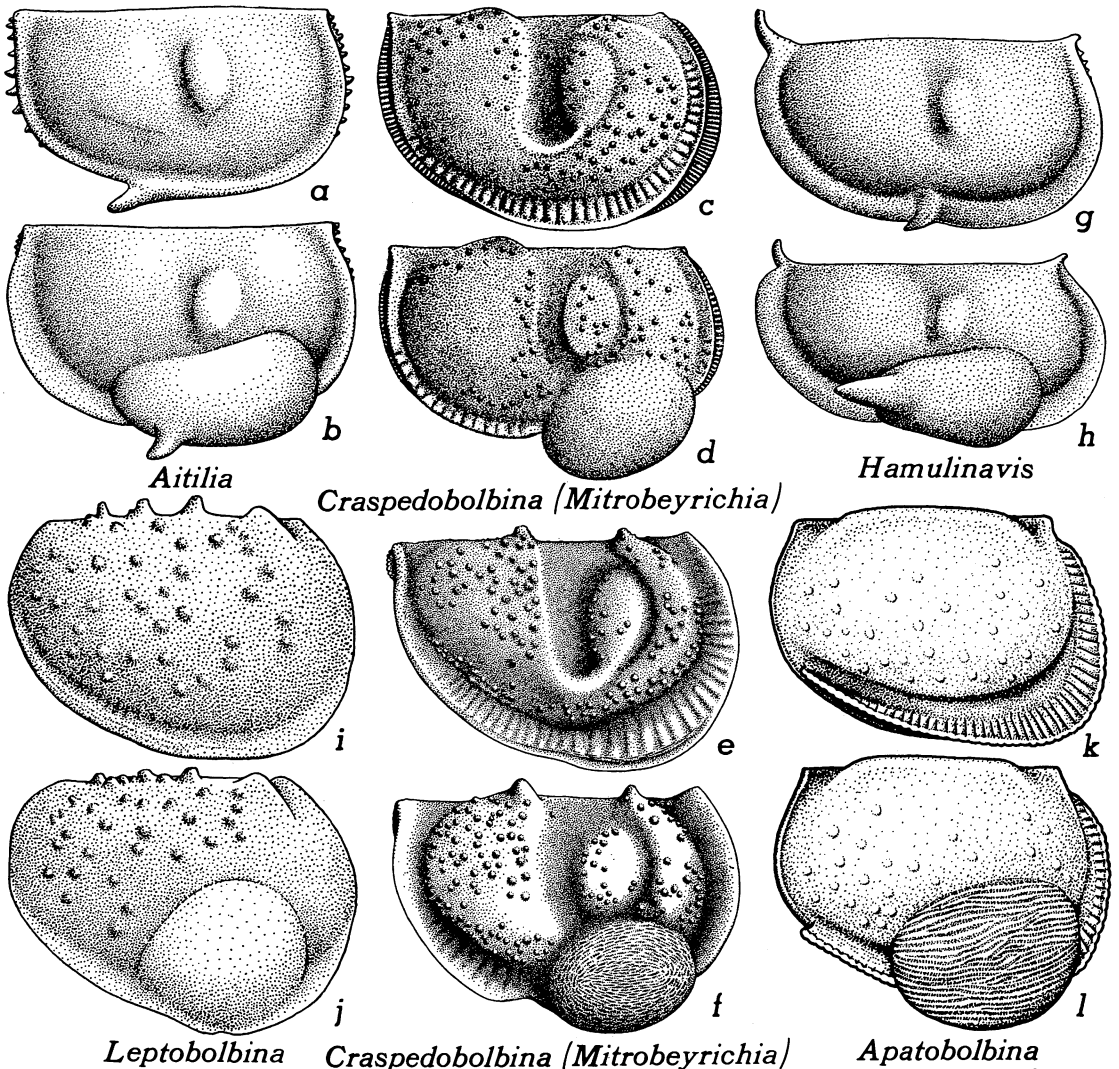
soon as part of the animal is free from the old carapace, a section of the wrinkled layer snaps into the form of the new carapace. From its elasticity, I believe the layer is the chitin coating of the new shell, or at least the initial film of it. The whole of the new carapace seems to derive its final form as increments produced continuously in a narrow zone of activity which progresses backward from the front end. Within this narrow zone, new chitin forms under the old carapace, temporarily wrinkled by its confinement, and springs into definitive form as soon as free. I cannot be certain how the surface film, wrinkled at its inception, can spring out into the smooth shape of the new shell; probably it is the result of almost simultaneous tissue growth and expansion which "stretches" the chitinous skin into the final shape, much as baking "stretches" the crustal layer and tends to eliminate wrinkles in the dough of rolls and other pastry. In any case, such smooth ostracods as *Cypridopsis* and *Candona* never have even a moment when the old carapace has been completely shed and the new carapace is yet to form. Both shedding and secreting take place at about the same time in a narrow migrating zone.

The procedure was probably similar in beyrichiid ostracods. If so, it helps to explain the formation of such fragile structures as tubulous frills and such complex structures as cruminae. Clearly, the whole adult velum must have assumed its definitive form during the final brief and critical interval of ecdysis. The tissue secreting a tubulous frill must have consisted of numerous tiny rods of hypodermal cells set side-by-side in a curved row, with scarcely more rigidity than so many pieces of cooked spaghetti. Yet the final frill has remarkable coherence of all tubulous elements and curves about the same in all individuals of the same species and sex. The junction of each tubule to its neighbors, it would appear, came about from the following sequence: (1) freeing of the hypodermis from the old shell at the site of the anterior end of the frill, (2) sudden growth of a rod of cells, (3) secretion of a thin film of chitin around the rod, (4) growth of a second rod of cells and a covering film along the edge of the first, and (5) further casting of the old shell to permit freedom of frill expansion. The final form of the frill seems to have come about from (1) differential growth pressures within the hypodermal cells of the rods, by their expansion forcing the covering films into the final shape, and (2) calcification in the outer layer of each rod. From the presence of concentric ridges on the frill, I am led to believe that before the growth of one rod of hypodermal cells

had reached its limit, other rods behind it were already starting to form. I cannot conceive of a freshly molted beyrichiid with no part of the new carapace covering the soft sides of the animal or the soft rods of the velum.

The formation of a crumina was at least as complex. Somehow, an anteroventral layer of hypodermal tissue assumed the more or less globular shape of the crumina, and assumed it very precisely, during the final ecdysis. The shape of the crumina must have been determined before calcification; on the other hand, some initial rigidity must have been present for otherwise the weight of the ostracod body would have seriously deformed the structure. In accord with ecdysis of living ostracods, I consider that the crumina may logically have resulted from the following sequence of events: (1) freeing of the hypodermal layer from the old valve in the anteroventral region, (2) local proliferation of cells to cover an area equal to that of the crumina, but with a wrinkled surface because of the old valve lying just outside, (3) secretion of a somewhat pliable elastic film of chitin, (4) further (posterior) freeing of the hypodermal layer of the valve, (5) further growth and expansion of hypodermal cells to force the film to spring into the final form, and (6) calcification of the outermost layer of the dermis. I do not believe the crumina took its final shape by pressure generated within the carapace and directed against the inner surface of the dermal layer of tissue, for from whence could such localized pressure originate? The "inflation" was not comparable to the puffing out of one's cheeks or the blowing up of a balloon; instead, it came from growth pressure *within* the relatively thin layer of hypodermal tissue that finally came to line the crumina, springing the previously secreted film of chitin into the globular shape. The several specimens discovered by Martinsson (1962, p. 92-113, figs. 27-36) having abnormal cruminae seem thus to be individuals in which the normal sequence of events did not occur; in some, the proliferation of cells was insufficient to produce a large crumina; in others, the expansion of hypodermal cells seems to have taken place before the anteroventral region was fully clear, thus forcing the chitin film against the inside of the old valve and producing an abnormal lateral indentation of the crumina; and in all, calcification was completed regardless of preceding irregularities.

Many published statements about beyrichiids and other extinct ostracods treat carapace structures as though they were formed from without rather than within. They promote misunderstanding of the nature and evolution of specialized features in the Ostracoda.



TEXT-FIG. 5—Beyrichiidae, subfamily Craspedobolbininae. Male and female right valves. *a, b*, *Aitilia calcarata* Martinsson,  $\times 30$ . *c, d*, *Craspedobolbina (Mitrobeyrichia) jonesi* (Boll),  $\times 23$ . *e, f*, *C. (M.) variolata* Martinsson,  $\times 23$ . *g, h*, *Hamulinavis pirulifera* Martinsson,  $\times 28$ . *i, j*, *Leptobolbina quadricuspida* Martinsson,  $\times 50$ . *k, l*, *Apatobolbina michiganensis* Martinsson,  $\times 28$ . *a-j*, after Martinsson.

Subfamily CRASPEDOBOLBININAE  
Text-figs. 5-7

Genera are grouped in the subfamily Craspedobolbininae as ostracods "with cruminal metamorphosis passing a complete dolonoid stage, implying a completed closing off of the dolonoid space by a flap" (Martinsson, 1962, p. 131). According to the hypothesis advocated by Martinsson (1962, p. 102-109), the subfamilies differ in the degree to which the frill or velum enters into the formation of the crumina during the final ecdysis, which he terms the "metamorphosis." In *Chilobolbina*, the dolon is ovate but its distal edge does not contact the margin of

the valve; in *Craspedobolbina*, a "closing flap" of calcium carbonate extends as a thin layer to complete the enclosure of the pouch. Supposedly, "inflation" of the space between the two walls of the crumina took place before calcification was complete, thus affording access into the interior of the domicilium. The junction along which the flap contacts the margin appears as a scar in the craspedobolbines, interpreted to mean that they are primitive members of the Beyrichiidae. The "ontogenetic evidence" presented by Martinsson (1962, p. 90-102, 116-118) is based on valves of female ostracods that presumably died before completion of the final "metamorphosis." These cases of "inter-

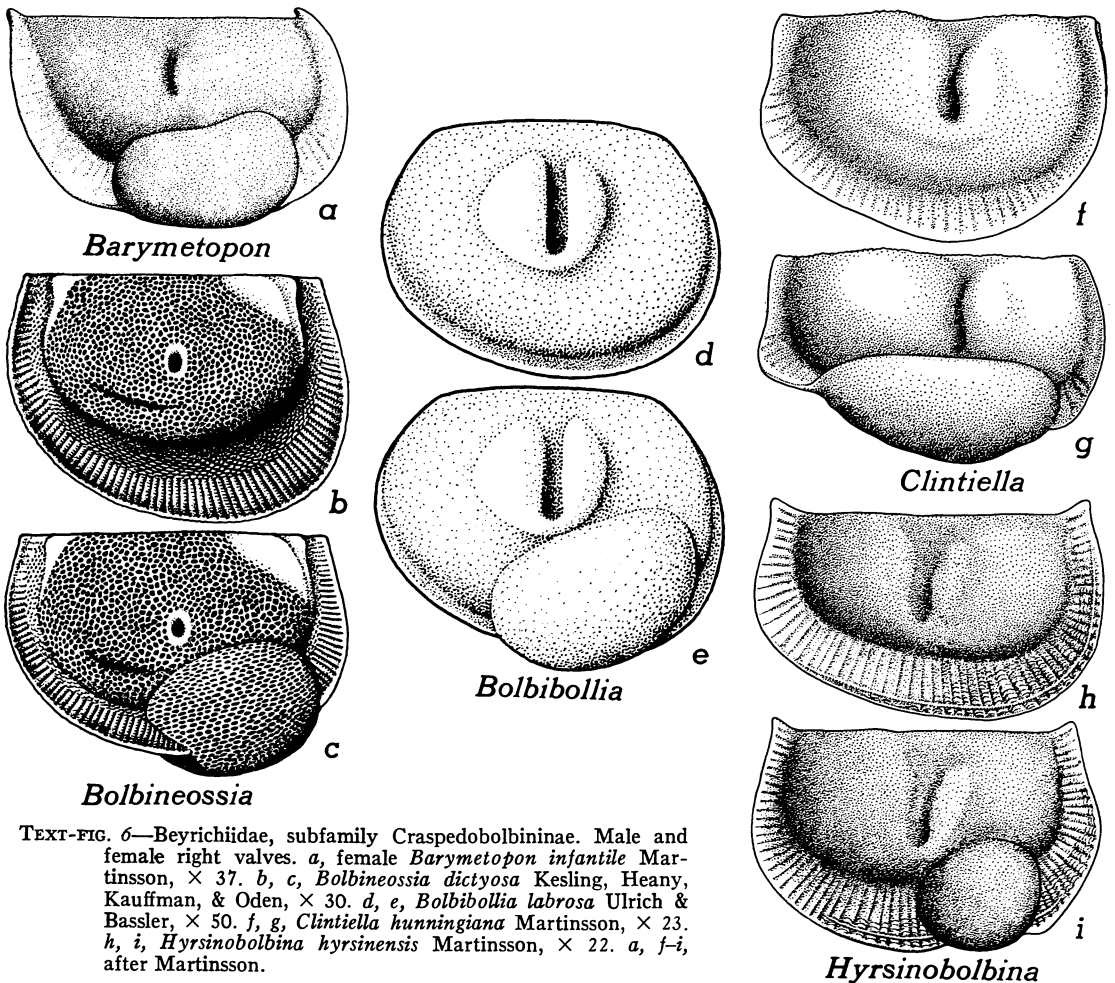
rupted cruminal metamorphosis" may indeed have been normal individuals which (fortunately for our science) died at critical stages of molting; yet the question arises as to why they died in the condition in which they are found. As suggested above, more logically, such specimens can be looked upon as suffering from some accident or pathological deficiency that affected the molting sequence and prevented their normal development into the adult stage.

As currently constituted, the Craspedobolbininae exhibit a wide range in the form of the velum, the lobation, and the ornamentation. *Apatobolbina* (text-figs. 5k, l, 7a-d) and *Bolbineossia* (text-fig. 6b, c) have broad tubulous frills or vela; the former has the frill directed more laterally than ventrally, whereas the latter has the frill directed more ventrally. *Hyrsinobolbina* (text-fig. 6h, i) also has a wide tubulous frill from corner to corner. *Hamulinavis* (text-fig. 5g, h) has a wide but non-tubulous velum.

*Aitilia* (text-fig. 5a, b) has a reduced velum that is said to be indistinctly tubulous, and *Mesomphalus* (see Kesling & Rogers, 1957, pl. 130, figs. 11-15) has a still narrower velar structure, a ridge showing no signs of tubulosity. Other genera have intermediate expressions of velar construction.

The subfamily shows other differences, as in the extent of the velar structure. In *Hamulinavis* (text-fig. 5g, h), *Hyrsinobolbina* (text-fig. 6h, i), and probably in *Bolbineossia* (text-fig. 6b, c) the frill is entire, from one corner to the other, with a wide posterior section. In *Craspedobolbina* (text-fig. 5c-f) the frill tapers to the posterior corner. In *Apatobolbina* (text-fig. 5k, l) the frill is definitely restricted, with no posterior extent.

Lobation is just as variable as the velum. *Apatobolbina* (text-figs. 5k, l, 7a-d) and *Lep-tobolbina* (text-fig. 5i, j) are non-sulcate. *Bol-bineossia* (text-fig. 6b, c) has only a small, dis-



TEXT-FIG. 6—Beyrichiidae, subfamily Craspedobolbininae. Male and female right valves. a, female *Barymetopon infantile* Martinsson,  $\times 37$ . b, c, *Bolbineossia dictyosa* Kesling, Heany, Kauffman, & Oden,  $\times 30$ . d, e, *Bolbibollia labrosa* Ulrich & Bassler,  $\times 50$ . f, g, *Clintiella hunningiana* Martinsson,  $\times 23$ . h, i, *Hyrsinobolbina hyrsinensis* Martinsson,  $\times 22$ . a, f-i, after Martinsson.

tinctly outlined, central adductorial pit (S2) and a shallow posteroventral groove that lies in the position of the syllobial groove in *Beyrichia*. An adductorial sulcus (S2) is present in other Craspedobolbininae, and some expression of a preadductorial node (L2). In *Aitilia* (text-fig. 5a, b), *Hamulinavis* (text-fig. 5g, h), *Barymetopon* (text-fig. 6a), *Clintiella* (text-fig. 6f, g), and *Hyrsinobolbina* (text-fig. 6h, i), the L2 is indistinct anteriorly, partly merged with L1, the anterior lobe. The peculiar U-shaped elevation around S2 in *Bolbibollia* (text-fig. 6d, e) could be interpreted as a preadductorial node (L2) joined by a zygial arch to a reduced syllobium (L3). *Craspedobolbina* (text-fig. 4a) and *Mitrobeyrichia* (text-figs. 4b, 5c-f), the two subgenera of *Craspedobolbina*, stand apart from other ostracods of the subfamily in their lobation: their syllobium is strongly developed and extends above the hinge line as a cusp or crista, and their L2 is clearly defined and set off from L1. A zygum, weakly developed as a low zygial ridge in *Hyrsinobolbina* (text-fig. 6h, i), attains full expression as a zygial arch in *Craspedobolbina* (text-fig. 5c-f). Of all the craspedobolbinines, only *Craspedobolbina* exhibits definite resemblance to the beyrichiines in lobation.

The crumina in *Hyrsinobolbina* and *Craspedobolbina* is subspherical; in *Apatobolbina*, *Leptobolbina*, *Bolbibollia*, and *Bolbineossia* ovoid; in *Aitilia* and *Barymetopon* elongate; in *Hamulinavis* and *Clintiella* still longer; and in *Mesomphalus* (see Kesling & Rogers, 1957, pl. 130, figs. 13-15) and *Dolichoscapha* (see Kesling & Ehlers, 1958, pl. 24, figs. 18-20) long and sausage-shaped. Surface of the valve is smooth in *Hamulinavis*, *Bolbibollia*, *Hyrsinobolbina*, and *Barymetopon*, granulose in *Apatobolbina* and *Clintiella* (not shown in text-fig. 6f, g), granulose and spinulose in *Leptobolbina*, verrucose in *Craspedobolbina*, granulose and punctate in *Mesomphalus*, punctate in *Aitilia*, and reticulate in *Bolbineossia* and *Dolichoscapha*.

Dorsal, posterior, and ventral structures likewise show few tendencies to conform to a standard pattern. The only genus with major projections above the hingeline is *Craspedobolbina*, although the shoulder-like dorsum of *Apatobolbina* may form a low ridge-shaped hump and the dorsal spinules of *Leptobolbina* make an irregular dorsal border. At the rear corner, *Hamulinavis* has an upturned acroidal spine, *Hyrsinobolbina* has an acuminate posterodorsally directed end of the frill, and *Craspedobolbina* tends to develop a posteriorly directed tip. Along the posterior end of the valve, *Hyrsinobolbina* and *Hamulinavis* have exten-

sions of the frill. Calcarine spines in *Aitilia* and *Hamulinavis* only affect the ventral border in that they increase the effective width of the velar structure in the male. The ventral sections of the frills have considerable vertical extent only in *Bolbineossia* and *Hyrsinobolbina*.

With ostracods of such diverse morphology, no copulatory adaptation is obvious for the subfamily as a whole. For all genera except *Craspedobolbina*, the dorsal position is the most feasible. In this mating position, the posterior frills of *Hyrsinobolbina* and the acroidal spines of *Hamulinavis* present no barrier for the introduction of the hemipenes. For *Craspedobolbina* the most logical position would be the posterodorsal. From the configuration of the ventral border and crumina, the ventral position would at first seem possible in most genera; there are reasons to doubt that it was used.

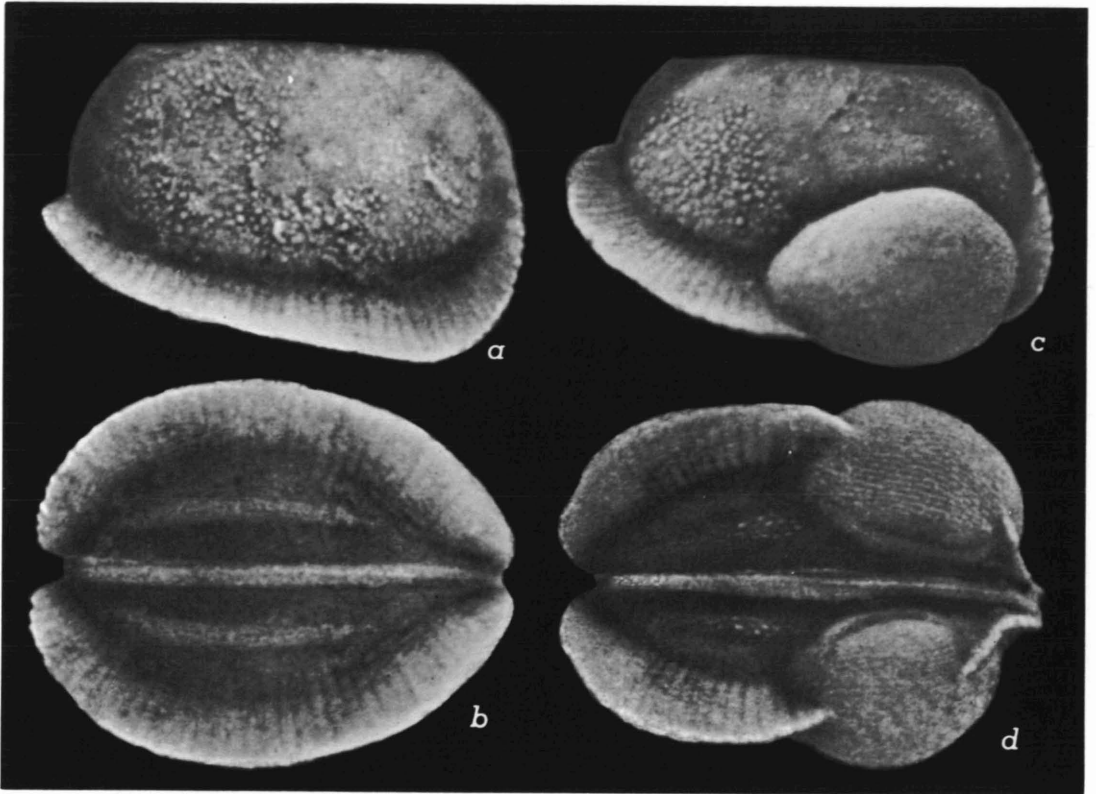
The carapace of these ostracods is heavy, particularly that of the female. Henningsmoen has already pointed out (1965, p. 358-362) that the velar ridges and frills tend to have a rather straight section on the ventral border, so that complete carapaces stand upright on a horizontal surface. He states (p. 359):

The longer and wider apart the straight parts of the borders are, the steadier does the carapace stand on the substratum, but even forms with a somewhat convex ventral outline will stand upright on a horizontal surface, although they are then easily rocked like a rocking-chair. The parts of the shell which, in life, could be adpressed to the substratum, may be termed the *sole areas*. . . . In some forms the sole areas are formed by a pair of ridges or frills.

He further discussed the detailed modifications of the cruminae and frills in *Craspedobolbina* (1965, p. 360) and *Apatobolbina* (1965, p. 361). Particularly, the section of the frill directed laterally in *Apatobolbina* (text-fig. 7) seems adapted to give the maximum stability to each dimorph; when the valves were slightly agape, the carapace rested partly on the frill surface and partly on a toric ridge on the marginal surface.

For *Apatobolbina* to have copulated in the ventral position, it would have been necessary for both male and female to have lain on their sides. Yet even if these heavy-shelled ostracods did assume such positions, their ventral borders would not come in contact on a flat substrate. Because of the large crumina in the lower valve of the female, the ventral surface of her upper valve would slope away from the male; and because of the frill in the lower valve of the male, his upper valve would similarly cant away from the female. Any contact between the dimorphs ventrally would have to be brought about and maintained by strong clasp-





TEXT-FIG. 7.—Beyrichiidae, subfamily Craspedobolbininae. *Apatobolbina gutnica* Martinsson. *a-d*, right lateral and ventral views, male and female,  $\times 40$ . Restored after Martinsson, 1962, fig. 46.

ing organs, holding the entire weight of the male in precise adjustment on the steeply inclined ventral surface of the female. This would not seem to have been possible. The same situation would have existed to some degree in all other Craspedobolbininae, so that the dorsal and posterodorsal positions are the only ones reasonable. It may be pointed out that in most of the genera of this subfamily, the sole areas of the female are such that the anterior corner was normally higher than the posterior, with the hinge line inclined toward the rear. Thus, the mounting by the male, similarly oriented, was facilitated.

Subfamily AMPHITOXOTIDINAE  
Text-figs. 8, 9

Martinsson (1962, p. 214) created this subfamily for beyrichiids in which the crumina displays no evidence of a closing dolonoid flap in its ancestry or development, being produced by direct inflation of tubules in the frill. He stated (1962, p. 214):

The derivation of this crumina from the craspedobolbinine type is evident. The crumina in the am-

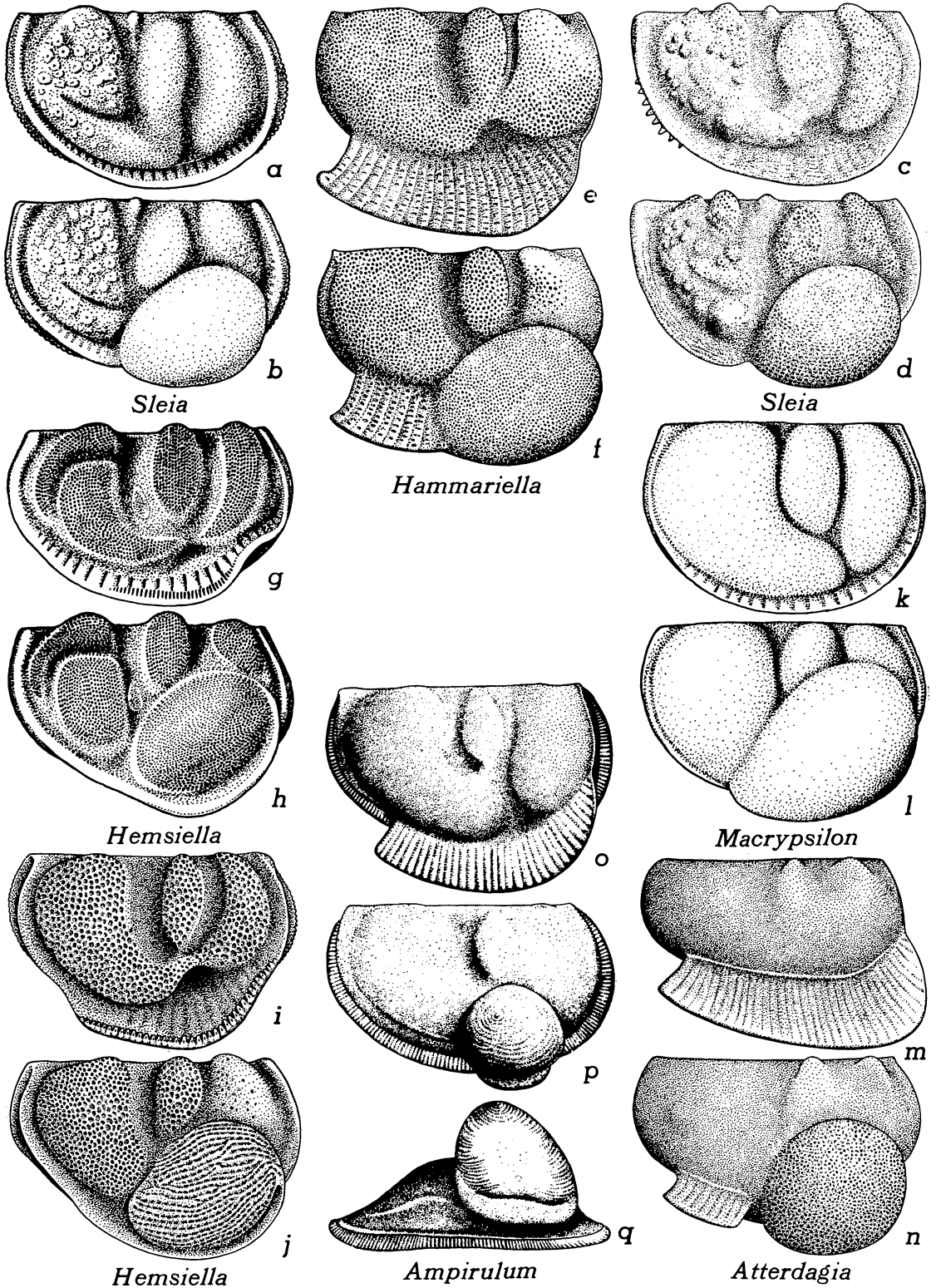
phitoxotidine ancestors has passed through a phylogenetic development like that in *Leptobolbina*, and the traces of the dolonoid closing mechanism are reduced to a low tubercle or pit in or near the velar edge . . .

He also said that in the Amphitoxotidinae (1962, p. 105):

. . . the insertion of the flap has been entirely abandoned, but in more or less primitive forms the point of the velum situated on the most distal part of the crumina is more or less drawn up towards the ventral margin of the crumina.

The following year (1963), Martinsson divided the superfamily Beyrichiacea into two families, Craspedobolbinidae and Beyrichiidae, with the former including the subfamilies Craspedobolbininae, Treposellinae, and Amphitoxotidinae. The family Craspedobolbinidae was defined as (1963, p. 54):

*Beyrichiacea* primarily with tubular structures in the velum which may occasionally be reduced. Crumina originating by invasion of the velar fold along tubules in the anteroventral region; an earlier phylogenetic stage with a dolonoid pouch, tending to be closed by a flap, may be traced in all subfamilies by a dolonoid scar or a deflection of the velar edge on the crumina.



TEXT-FIG. 8—Beyrichiidae, subfamily Amphitoxotidinae. Male and female right valves. *a, b*, *Sleia kochii* (Boll),  $\times 30$ . *c, d*, *S. equestris* Martinsson,  $\times 30$ . *e, f*, *Hammariella pulchrivelata* Martinsson,  $\times 33$ . *g, h*, *Hemiella maccoyiana* (Jones),  $\times 18$ . *i, j*, *H. loensis* Martinsson,  $\times 37$ . *k, l*, *Macrypsilon salteriana* (Jones),  $\times 33$ . *m, n*, *Atterdagia paucilobata* Martinsson,  $\times 30$ . *o-q*, *Ampirulum reuteri* (Krause),  $\times 24$ . *c-f, i-j, m-q*, after Martinsson.

Ostracoda of the Amphitoxotidinae have no zygial ridge and they are typically reticulate, in contrast to the Beyrichiinae. In dividing the beyrichiaceans into two families, Martinsson (1963) was convinced that tubulosity of the frill was irrevocably lost in the Beyrichiidae.

Henningsmoen (1965) raised doubts, as already pointed out. He interpreted the lack of tubules in the Beyrichiinae and others to be "due to a non-realization of a capability, rather than to the loss of this ability" and proposed that "the amphitoxitidines [*sic*] with a tubulous frill may then have developed from forms without tubulous frill such as *Beyrichia* (*Alti-beyrichia*) or *Neobeyrichia* . . ." (1965, p. 388). He further suggested that reticulation may have appeared and stabilized at the same time that the tubulous frill redeveloped in the beyrichiid evolution, thus establishing the Amphitoxotidinae.

The course of beyrichiid lineages will not be fully treated here. Henningsmoen (1965, p. 388–389) has focused attention on several resemblances in lobation of amphitoxotidines (particularly the early genus *Sleia*) and beyrichiines, such as isolation of the anterior lobe (L1), union of the preadductorial node (L2) with the ventral part of the syllobium (L3), dissection of the syllobium by grooves, and the anteroventral depression in male valves (text-fig. 4f). Diversity of lobation and cruminae in the Amphitoxotidinae suggests that, despite the carefully documented observations and the prolific spawning of generic names in recent years, we still have no clear-cut, convincing, and universally accepted suprageneric classification.

*Sleia*, as the oldest known genus of the subfamily, receives special attention. It tends to combine reticulation characteristic of the Amphitoxotidinae with tuberculation characteristic of the Beyrichiinae. It is the only genus of the subfamily to have a syllobial groove like the Beyrichiinae (text-fig. 8a–d), but L2 tends to be joined by a ridge to the ventral (calcarine) section of the syllobium (L3) rather than by a true zygial ridge to the dorsal part of the syllobium. The velar structure of the male is developed as a frill anteroventrally, but tapers posteriorly into a velar ridge; that of the female is constricted on each side of the crumina.

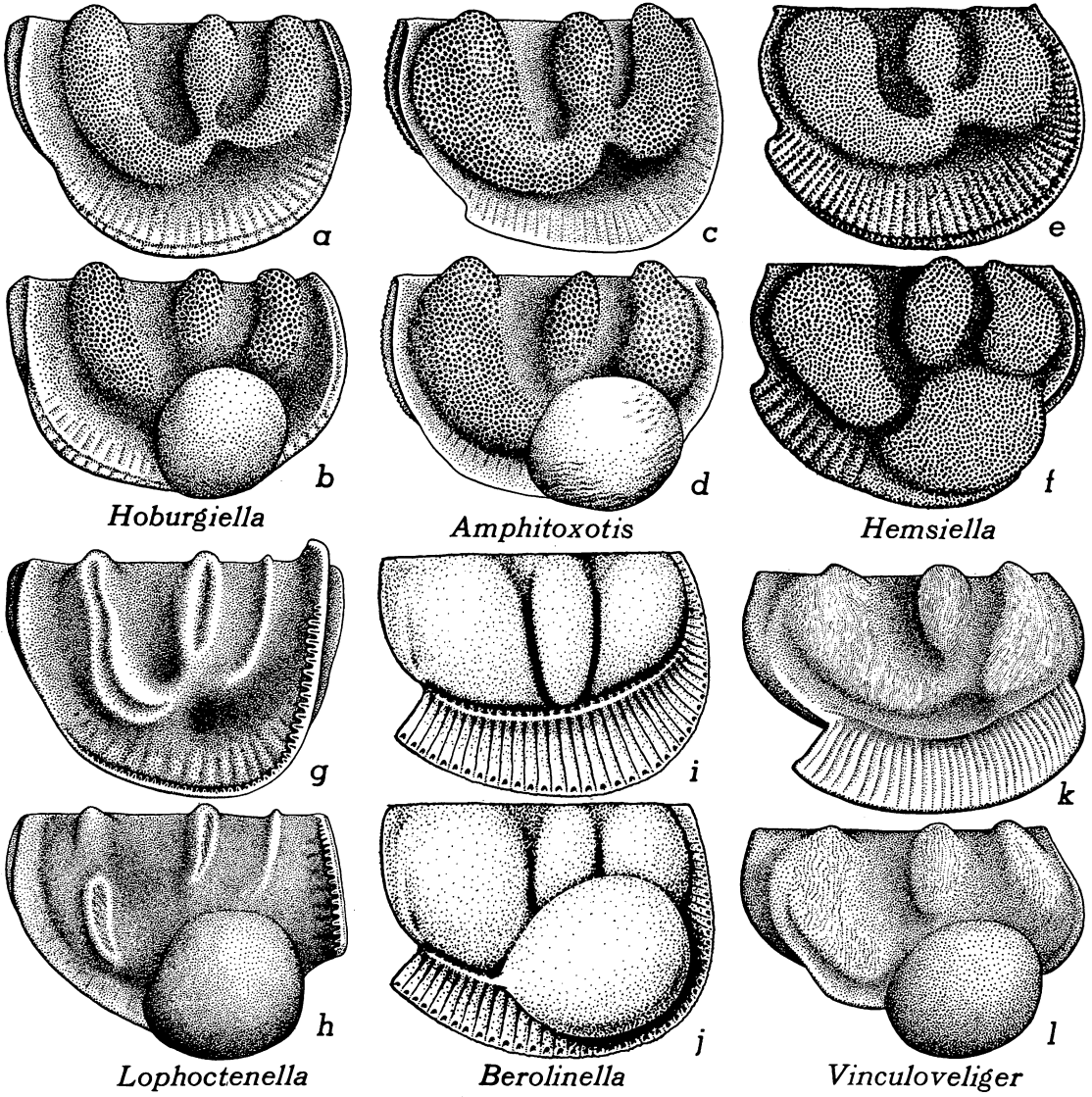
Considerable variation exists in the velar development in the female. One group has no velum in front of the crumina, including *Hemsiella* (text-fig. 8h, j), *Hammariella* (text-fig. 8f), *Juviella*, *Loella*, *Atterdagia* (text-fig. 8n), and *Ampirulum* (text-fig. 8p, q). Another group has some kind of precruminal velum, including *Amphitoxotis* (text-fig. 9d), *Velibeyrichia*, *Hoburgiella* (text-fig. 9b), *Grogarina*, *Berolinella*

(text-fig. 9j), *Dibolbina*, and *Macrypsilon* (text-fig. 8l); *Lophoctenella* (text-fig. 9h) has an anterior section, complete with denticulate border crest, which is widely separated from the crumina.

Velar expression in the male also varies. The frill is entire, from corner to corner, in *Velibeyrichia* and *Dibolbina*; the narrow frill of *Macrypsilon* (text-fig. 8k) has the same extent, but it tapers into velar ridges toward the corners. Other genera have the well-defined tubulous section somewhat tapered and constricted posteriorly, such as *Hemsiella* (text-fig. 8g, i; text-fig. 9e) and *Lophoctenella* (text-fig. 9g) with denticulate border crests and anteroventral deflection or undulation, *Hoburgiella* (text-fig. 9a) *Amphitoxotis* (text-fig. 9c), and *Cryptolophobus*. Many have the frill terminated quite abruptly in the posteroventral region, including *Hammariella* (text-fig. 8e), *Ampirulum* (text-fig. 8o), *Atterdagia* (text-fig. 8m), and *Berolinella* (text-fig. 9i).

Dimorphism of velar structures may be insignificant or drastic. In *Berolinella* (text-fig. 9i, j) the frill of male and female are quite similar, and the section crossing the crumina still preserves its tubulosity. The same continuation of the frill across the crumina is met with in *Amphitoxotis* (text-fig. 9c, d), although the cruminal section does not show tubules. The other extreme occurs in *Vinculoveliger* (text-fig. 9k, l) and *Ampirulum* (text-fig. 8o–q), in which the ventral frill in the male has only a velar ridge as its counterpart in the female, or in *Atterdagia* (text-fig. 8m, n), in which the female has only a posteroventral remnant of frill.

Lobation also shows a wide range in genera assigned to the Amphitoxotidinae. The most unusual form is that in *Atterdagia* (text-fig. 8m, n), in which the sulci are nearly obsolete, with slight dorsal projections to indicate the locations of L1 and L2. On the other hand, the broad lobes of *Berolinella* (text-fig. 9i, j) and *Macrypsilon* (text-fig. 8k, l) are clearly defined and separated by narrow sulci; the preadductorial lobe (L2) of the former extends to the frill, whereas that of the latter terminates well above the frill. Of the remaining genera, one group has the anterior lobe (L1) isolated, including *Sleia* (text-fig. 8a), *Loella*, *Grogarina*, and *Ampirulum* (text-fig. 8o). The other group has a ventral connection between L1 and L2, clearly shown in *Hoburgiella* (text-fig. 9a), *Amphitoxotis* (text-fig. 9c), *Hemsiella* (text-fig. 9e), and *Hammariella* (text-fig. 8e). Somewhat intermediate between the two groups are such genera as *Lophoctenella* (text-fig. 9g) and *Vinculoveliger* (text-fig. 9k), in which the prenodal



TEXT-FIG. 9.—Beyrichiidae, subfamily Amphotoxotidinae. Male and female right valves. *a, b, Hoburgiella tenerima* Martinsson, × 36. *c, d, Amphitoxotis curvata* Martinsson, × 40. *e, f, Hemiella andincola* Martinsson, × 28. *g, h, Lophoctenella angustilaequeata* Martinsson, × 27. *i, j, Berolinella steusloffii* (Krause), × 36. *k, l, Vinculoveliger catenulatus* Martinsson, × 22. *a-h, k-l*, after Martinsson.

sulcus (S1) is cut off from the anteroventral depression (text-fig. 4d) by a low rise or col. Lobes may be broad, as in *Amphotoxotis*, *Hemiella*, *Berolinella*, *Hamuariella*, *Macrypsilon*, and *Ampirulum*; they may be narrow, as in *Hoburgiella* and *Juviella*; or they may be reduced to cristal ridges and loops, as in *Lophoctenella* and *Cryptolophobus*. In *Velibeyrichia*, an exclusively American genus, the large lobes extend to the frill, with only a small indentation for the anteroventral depression. In *Juviella*, known only from Europe, the lobes are narrower and withdrawn from the frill and the ventral connections of the lobes are more weakly

developed than in *Velibeyrichia*. In *Dibolbina*, the L2 is partly fused with L1 and both are isolated from L3 by a sulcus, shallow ventrally; a cristal ridge is developed on the calcarine area of the syllobium, a feature somewhat atypical of the subfamily. No standard pattern of lobal width, extent, linkage, or arrangement can be said to characterize these genera.

Cruminae are subspherical or globular, as in *Hoburgiella* (text-fig. 9b) and *Vinculoveliger* (text-fig. 9l), to ovoid, as in *Sleia* (text-fig. 8b), *Hemiella* (text-fig. 8h, j), and *Amphotoxotis* (text-fig. 9d); none are elongate, as in *Hamulinavis* (text-fig. 5h) and *Clintiella*

(text-fig. 6g) of the Craspedobolbininae. They may be so large that they extend high up on L1 and L2, as in *Macrypilson* (text-fig. 8l) or small and set low on the valve, as in *Vinculoveliger* (text-fig. 9l). The crumina of *Lophocotenella* (text-fig. 9h) protrudes, but that of *Ampirulum* (text-fig. 8p, q) extends even farther, nearly paraboloid in shape.

Most amphitoxotidines are reticulate to some degree, but *Atterdagia* (text-fig. 8m, n) and *Berolinella* (text-fig. 9i, j) are essentially smooth. Reticulation is combined with tuberculation in *Sleia* (text-fig. 8a-d) and with striation in *Vinculoveliger* (text-fig. 9k, l).

Dorsal structures are inconspicuous in most genera. No cusps or other lobal projections above the hinge line are developed in the syllobium of *Velibeyrichia*, *Hammariella* (text-fig. 8e, f), *Macrypilson* (text-fig. 8k, l), *Atterdagia* (text-fig. 8m, n), *Ampirulum* (text-fig. 8o, p), or *Berolinella* (text-fig. 9i, j); nor are there significant projections for the anterior lobe in these genera. The syllobium does not project in *Dibolbina*. In *Hemsiella* (text-figs. 8g-j, 9e, f), the dorsal borders of the lobes are smoothly formed and only slightly above the hinge. *Amphitoxotis* (text-fig. 9c, d) and *Hoburgiella* (text-fig. 9a, b) have lobes definitely extending above the hinge but without sharp cusps. *Lophocotenella* (text-fig. 9g, h) has cusplike terminations of the narrow lobes, and *Sleia* (text-fig. 8a-d) and *Vinculoveliger* (text-fig. 9k, l) possess syllobial cusps. The posterior borders of all amphitoxotidines are conspicuously devoid of protuberances or projections.

Ventrally, male frills and female cruminae project in most genera to form potential hindrances to mating in the ventral position. Strong projections occur in *Hammariella* (text-fig. 8e, f), *Atterdagia* (text-fig. 8m, n), *Hoburgiella* (text-fig. 9a, b), and *Berolinella* (text-fig. 9i, j), intermediate ones in *Sleia* (text-fig. 8a-d), and weak ones in *Macrypilson* (text-fig. 8k, l).

The one mating position to which all amphitoxotidines were adapted is the postero-dorsal. Because of the low dorsal structures in several, the dorsal position would have been equally feasible, as in *Macrypilson* (text-fig. 8k, l) or *Berolinella* (text-fig. 9i, j); but this would have been disadvantageous in such genera as *Hoburgiella* (text-fig. 9a, b) or *Sleia* (text-fig. 8c, d).

#### Subfamily BEYRICHIINAE

##### Text-fig. 10

As restricted by Martinsson (1962, p. 266), the subfamily includes

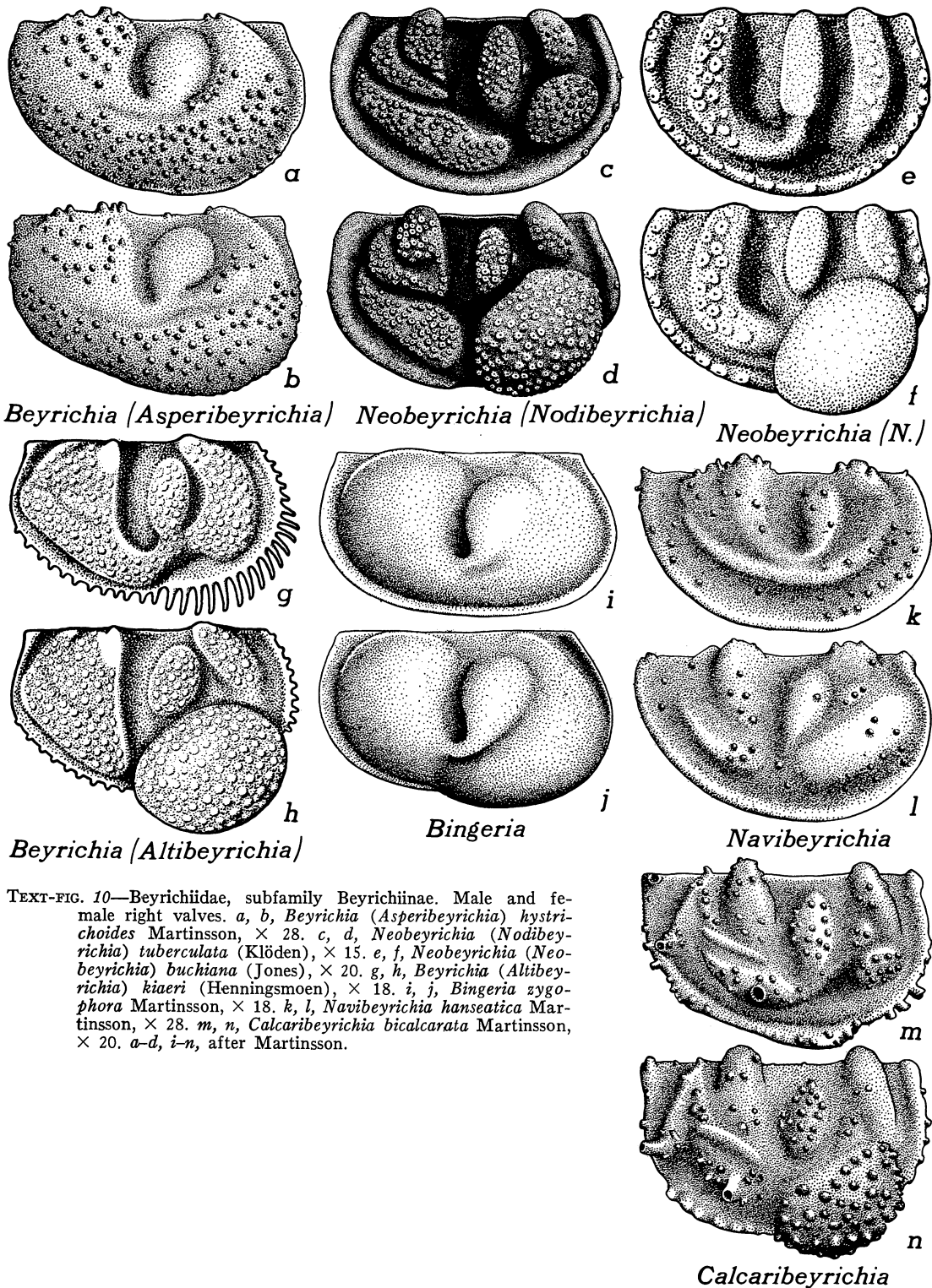
*Beyrichiidae* forming the crumina by direct occupation of the anteroventral part of the shallow

velar fold and adjoining parts of the carapace wall, without a dolonoid scar but often with a striate area on the ventral part of the crumina. Remains of the zygial ridge, if present at all, obviously influenced but sometimes only slightly displaced by the inflation of the crumina.

The wording of this diagnosis would be improved by recognition that hard parts are invariably secreted by soft hypodermal tissue. The "velar fold" referred to is a calcareous feature of the carapace, both in the last immature instar and in the adult female. Hence, it cannot be converted into a crumina or any other structure by "occupation." Martinsson quite properly draws attention to the site where the crumina is formed, to the lack of a secreted flap, and to the extent of the crumina in the adult valve.

The velum is basically a broad ridge in the beyrichiines, apparently secreted by dermal cells arranged in a narrow band along the velar site rather than in a series of tiny rods, as in the tubulous-frilled amphitoxotidines. Nevertheless, the hypodermal cells did have a tendency to extend into rods which were clearly separated and not adjoining, particularly in the anteroventral region. The subgenus *Altibeyrichia* (text-fig. 10g, h) has a velar fringe of spaced spines anteroventrally and tubercles toward the rear. *Calcaribeyrichia* (text-fig. 10m, n) shows irregular spines or tubercles along the velar ridge. Other beyrichiines have velar tubercles developed to some degree, including *Eobeyrichia*, *Beyrichia* (*Scabribeyrichia*), *B.* (*Asperibeyrichia*) (text-fig. 10a, b), *B.* (*Simplicibeyrichia*), *B.* (*Lunulibeyrichia*), *Neobeyrichia* (text-fig. 10e, f), and *N.* (*Nodibeyrichia*) (text-fig. 10c, d). *Plicibeyrichia* resembles *Craspedobolbina* of the craspedobolbines in having an ornamental ridge on the velar ridge. *Gannibeyrichia* and *Navibeyrichia* (text-fig. 10k, l) have thick velar ridges without tuberculation. A thin flangelike velum characterizes the European *Bingeria* (text-fig. 10i, j) and the American *Lophokloedemia*, *Welleriopsis*, and *Zygebeyrichia*; these genera differ in other respects from the typical beyrichiines and, as Martinsson suggested (1962, p. 347), with redescription and revision could be separated as a new subfamily.

Lobation is expressed in various combinations of lobal and zygial development. Two groups can be distinguished on the nature of the anterior lobe (L1): one in which the lobe is isolated by a long S1, and the other in which it is joined ventrally to the lower (calcarine) part of the syllobium (L3). The first includes *Neobeyrichia* (text-fig. 10e, f), in which L1 is entire, and *N.* (*Nodibeyrichia*) (text-fig. 10c, d), in which L1 is divided into dorsal and



TEXT-FIG. 10.—Beyrichiidae, subfamily Beyrichiinae. Male and female right valves. *a, b*, *Beyrichia (Asperibeyrichia) hystrichoides* Martinsson,  $\times 28$ . *c, d*, *Neobeyrichia (Nodibeyrichia) tuberculata* (Klöden),  $\times 15$ . *e, f*, *Neobeyrichia (Neobeyrichia) buchiana* (Jones),  $\times 20$ . *g, h*, *Beyrichia (Altibeyrichia) kiaeri* (Henningsmoen),  $\times 18$ . *i, j*, *Bingeria zygo-phora* Martinsson,  $\times 18$ . *k, l*, *Navibeyrichia hanseatica* Martinsson,  $\times 28$ . *m, n*, *Calcaribeyrichia bicalcarata* Martinsson,  $\times 20$ . *a-d, i-n*, after Martinsson.

ventral lobules. The second group includes *Eobeyrichia*, *Beyrichia* (*Asperibeyrichia*) (text-fig. 10a, b), and *Bingeria* (text-fig. 10i, j) and its allies, in which the connection is broad; *Plicibeyrichia*, *Gannibeyrichia*, and *Navibeyrichia* (text-fig. 10k, l), in which the connection is elevated, sharply defined, narrow lateroventral lobe; and *Beyrichia* (*Altibeyrichia*) (text-fig. 10g, h), *B.* (*Lunulibeyrichia*), and *Calcaribeyrichia* (text-fig. 10m, n), in which S1 is separated from an anteroventral depression only by a col. The syllobium may be undivided, as in *Bingeria* (text-fig. 10i, j); with a faint, high syllobial groove, as in *Eobeyrichia* and *Beyrichia* (*Altibeyrichia*) (text-fig. 10g, h); or trisected by sulcules into calcarine, callic, and cuspidal lobules, as in *Neobeyrichia* (*Nodibeyrichia*) (text-fig. 10c, d), *Calcaribeyrichia* (text-fig. 10m, n), *Plicibeyrichia*, and *Gannibeyrichia*. A zygum is strong in *Eobeyrichia*, weak in *Navibeyrichia* (text-fig. 10k, l), and indistinguishable in such genera as *Plicibeyrichia* and *Gannibeyrichia*; within sub-genera of *Beyrichia*, a zygum arch is present in *Scabribeyrichia*, weak in *Asperibeyrichia* (text-fig. 10a, b), and absent in *Simplicibeyrichia*.

Two kinds of cruminae are represented in the beyrichiines. The kind most characteristic of the subfamily is ovoid and clearly defined along all boundaries; its junction with the side of the valve is more or less angular; it occurs in *Neobeyrichia* (text-fig. 10e, f), *N.* (*Nodibeyrichia*) (text-fig. 10c, d), *Beyrichia* (*Altibeyrichia*) (text-fig. 10g, h), *Calcaribeyrichia* (text-fig. 10m, n), and others. The other kind is expressed as a swelling, tending to blend into the lobation, with poor delimitation; it includes *Beyrichia* (*Asperibeyrichia*) (text-fig. 10a, b), *Navibeyrichia* (text-fig. 10k, l), *Bingeria* (text-fig. 10i, j), and the American genera. In *Navibeyrichia*, the velar edge crosses the crumina without interruption.

In ornamentation, *Bingeria* and its allies have irregular reticulation and punctation. In contrast, the typical beyrichiines are tuberculate, verrucose, and spinose. Some species exhibit tubercles or verrucae on a granulose background. *Beyrichia* (text-fig. 4e) and *B.* (*Scabribeyrichia*) tend to develop a supravelar row of spines on the calcarine region of the syllobium. The acme of irregular ornament and spinosity is *Calcaribeyrichia* (text-figs. 4f, 10m, n).

*Bingeria* and the American genera *Lophokloedenia*, *Welleriopsis*, and *Zygobeyrichia* have at most a smooth crista or plica atop the syllobium and no projections on the other lobes. Typical beyrichiines develop some sort of cusp or cusps. Cusps are especially prominent in

*Calcaribeyrichia* (text-fig. 4f), both on L3 and L1, and acroidal and unocular spines project posteriorly. Other beyrichiines have no sharp processes beyond the posterior edge of the domicilium. Most genera have no prominent projections along the ventral border, but velar spines are well developed in certain species of *Beyrichia* (text-fig. 4e), *B.* (*Altibeyrichia*) (text-fig. 10g, h), *Neobeyrichia*, and *Calcaribeyrichia*.

From a consideration of lobation and ornamentation, the one mating position feasible for all beyrichiines is the posterodorsal. For the rough-carapaced *Calcaribeyrichia*, all positions appear to be beset with some disadvantages, but the posterodorsal less than others. The large syllobium, dorsally cusped, would seem to negate the dorsal position; and the extensive cruminae, as already pointed out for the craspedobolbines, are deterrents for the ventral position.

#### Subfamily ZYGOBOLBINAЕ

##### Text-fig. 11

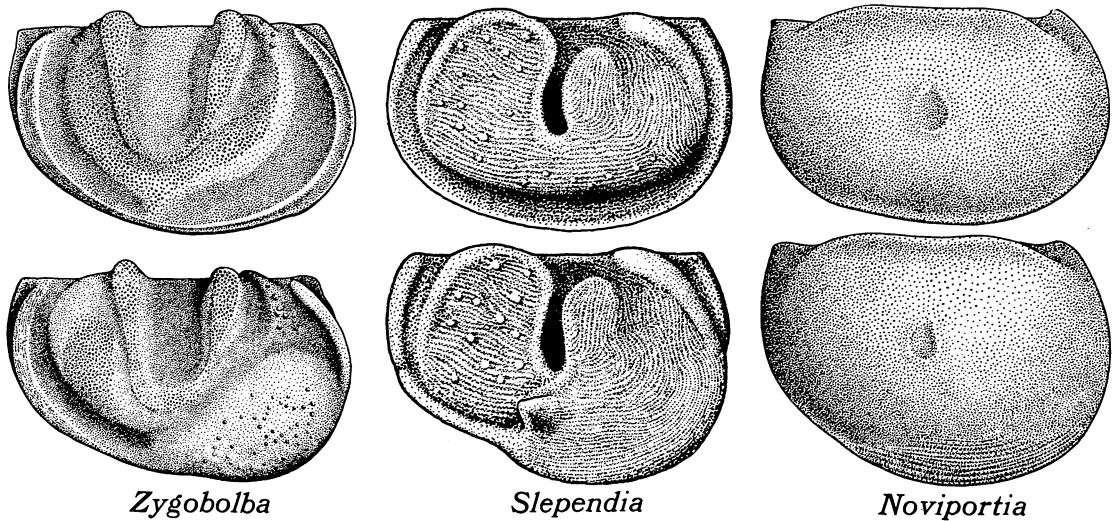
Martinsson (1962, p. 258) restricted the subfamily to:

*Beyrichiidae* with a flange- or ridge-like velum. Anteroventral crumina; the dolonoid scar consists of a fissure or fold breaking through the margin.

As with other subfamilies, lobation does not enter into his classification. Inclusion of the zygobolbines in the family Beyrichiidae is a step forward from the *Treatise* (1961) classification, in which they were separated as a family.

Velar structures are not wide in any genera of the subfamily. *Zygobolba* (text-fig. 11a, b) has a velar ridge flattened in lateral view, much like that of *Plethobolbina*. *Zygobolbina* and *Zygosella*, American genera, have rather thick velar ridges. *Mastigobolbina* and *Bonnemaia*, also American genera, have low velar ridges. *Slependia* (text-fig. 11c, d) has a velar ridge or flange, and *Noviportia* (text-fig. 11e, f) has a very narrow velum, scarcely defined in lateral view. *Drepanellina* has only a plicate part of the crumina that can qualify as a velum.

Lobation varies from non-sulcate in *Noviportia* (text-fig. 11e, f) to quadrilobate in *Drepanellina*. There is a tendency for a U-shaped lobe to ventrally connect L2 and L3; this is clear in both dimorphs of *Zygobolba* (text-fig. 11a, b), and in *Zygobolbina*, *Plethobolbina*, and *Bonnemaia*; the ridge in *Zygosella* is more nearly V-shaped, and a peculiar zygum extension in *Mastigobolbina* is recurved onto the syllobium. There is also a tendency for L1 and L2 to fuse; in *Zygobolba* S1 is a short depression



TEXT-FIG. 11—Beyrichiidae, subfamily Zygobolbinae. Male and female right valves. *a, b*, *Zygobolba decora* (Billings),  $\times 16$ . *c, d*, *Slepandia armata* (Henningsmoen),  $\times 27$ . *e, f*, *Noviportia simpliciuscula* Martinsson,  $\times 30$ . *a-b*, *e-f*, after Martinsson.

behind the crescentic anterior lobe; in *Zygosella* and *Mastigobolbina* the anterior lobe is expressed as a narrow ridge, much lower than L2; in *Zygobolbina* the anterior region is distinct because of the elevation of L2 behind it, but it has no elevation; and in *Plethobolbina* the valves are broadly bilobed, with the anterior and posterior lobes connected ventrally. *Slepandia* (text-fig. 11c, d) differs from the North American zygobolbines in lacking vertical development of its lobes. Some of the lobate genera have dorsal plicas on the anterior lobes and the syllobia; *Noviportia* has a dorsal plica along most of the dorsal border. This genus (text-fig. 11e, f) also has an adductor spot or shallow pit.

The crumina does not extend laterally like that of typical beyrichiines, for which reason some authors have placed these genera in a separate family. *Zygobolba* (text-fig. 11a, b) has a large crumina, interrupting the connection of L1 and the ventral lobe. *Mastigobolbina* has a crumina spread over most of the anterior part of the valve. The structure in *Bonnemaia* is anteroventral and ovate, poorly defined dorsally; in *Plethobolbina*, an inconspicuous anteroventral swelling; in *Zygosella*, a narrow ridge-like anterior lobe; in *Zygobolbina*, it has been described as bilobed with anterior and anteroventral parts; and in *Noviportia*, it is a simple ventral swelling confluent dorsally with the valve surface. In *Drepanellina* the crumina features a distinct, striated flap, limited by plications fore and aft. Only *Slepandia* (text-fig.

11c, d) has a calcarine spur associated with the crumina.

Ornamentation is weak in all zygobolbines. *Drepanellina* and *Bonnemaia* are smooth. *Noviportia* is granulose, and *Slepandia* is reticulostriate. Other genera are smooth to finely punctate or reticulate. *Mastigobolbina* is the only genus to develop pustules.

Dorsally, L2 and L3 terminate in cusps in *Zygobolba* (text-fig. 11a, b), *Zygobolbina*, *Zygosella*, *Bonnemaia*, and *Drepanellina*. L2 projects above the hinge line in *Mastigobolbina*, and L3 has a crista-like rim in *Slepandia* (text-fig. 11c, d). *Noviportia* (text-fig. 11e, f) has a long dorsal plica. *Plethobolbina* is the only genus of the subfamily with no dorsal projections. Posteriorly and ventrally all genera are free of protuberances.

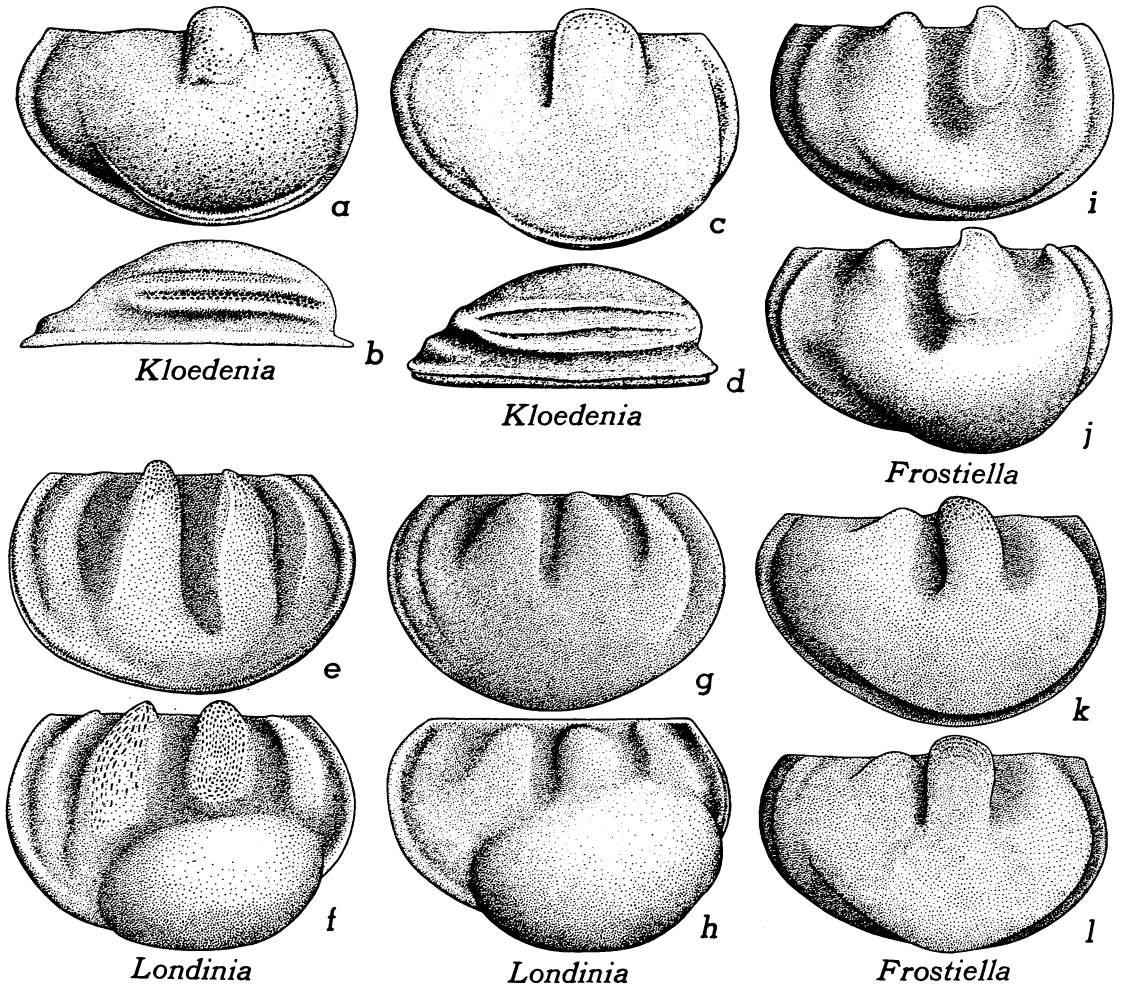
The mating position which seems most feasible for all zygobolbines is the posterodorsal, or perhaps more nearly posterior as reported in part II of this series for the living freshwater *Cypria turneri* Hoff and *Physocypria pustulosa* (Sharpe).

#### Subfamily KLOEDENIINAE Text-fig. 12

Martinsson gave a brief diagnosis and discussion of the Kloedeniinae in 1962 (p. 351), but examined the subfamily in greater depth in 1963 (p. 19):

*Beyrichiidae* with a longish, more or less distinctly anteroventral crumina, extending from the an-





TEXT-FIG. 12—Beyrichiidae, subfamily Kloedeniinae. Male and female right valves, except as noted. *a, b, Kloedenia wilckensiana* (Jones), female, lateral and ventral views,  $\times 18$ . *c, d, K. leptosoma* Martinsson, female, lateral and ventral views,  $\times 18$ . *e, f, Londinia reticulifera* Martinsson,  $\times 22$ . *g, h, L. kiesowi* (Krause),  $\times 16$ . *i, j, Frostiella groenvalliana* Martinsson,  $\times 18$ . *k, l, F. pliculata* (Jones),  $\times 16$ . All figures after Martinsson.

terior lobe to the mid-length of the syllobium, set off from the domiciliar part of the carapace—without any marked proximal constriction—as an ellipsoidal structure, or strongly assimilated with the domicilium. The formation of the crumina does not influence the free margin or marginal structures. The lobes tend to protrude considerably over the hingeline and to develop lateral facets or cristal loops.

In the subfamily, Martinsson (1963) included *Kloedenia*, *Frostiella*, and *Londinia*. He noted again that the North American species called *Kloedenia* do not agree morphologically with the type species, and again placed them with *Bingeria* in the Beyrichiinae.

The velar structure is at most a ridge, and tends to become a bend-like swelling in some species. Martinsson noted in *Frostiella plicatula* (Jones) that (1963, p. 37), "The posterior, lunular lobule of the syllobium, known from all kloedeniines, lies very close to the posterior margin of the valve and bends down below the level of the structure identified as the velum." This relationship is particularly clear in *Kloedenia* (text-fig. 12a-d).

Lobation varies in development vertically as well as horizontally. In *Kloedenia* (text-fig. 12a-d), the essential elements are restricted to the dorsal half of the valve, where an exceptionally large L2 forms a linguiform preadductor lobe extending above the hinge line. The sulci along the front and back borders of this lobe are short, and the scar of the closing muscles lies rather high on the valve. *Londinia* (text-fig. 12e-h) is the opposite, with four clearly defined lobes and sulci extending far down on the valve, separated from the ventral border by a narrow connecting lobe. *Frostiella* (text-fig. 12i-l) is intermediate, essentially trilobate.

The crumina of the type genus develops in stages during ontogeny and only adult females have been discovered. For this reason, Martinsson (1963, p. 19) considered that *Kloedenia* might be parthenogenetic. The crumina merges dorsally with the domicilium, without any line of separation (text-fig. 12a, c), and develops striate ridges between the velar ridge and the marginal ridge (text-fig. 12b, d). *Frostiella* (text-fig. 12i-l) has intermediate differentiation of the crumina, which is better defined in *F. groenvalliana* (text-fig. 12j) than in *F. plicatula* (text-fig. 12l). In *Londinia* (text-fig. 12f, h) the crumina is large and ovate, with a clear sulcule or semisulcus between the crumina and L2.

Ornamentation consists of sparse punctation in most species. *Londinia groenvalliana* has some reticulation on the lobes. Most kloedeniines have some kind of cristal loop associated with the preadductor lobe, forming a

wrinkle or ridge along the top surface of the lobe.

Cusps of L2 and/or L3 project dorsally, in most species above the hinge line. The posterior region has low topography, even in the quadri-lobate *Londinia*.

From the configuration of the carapaces, either the posterodorsal or ventral mating positions would have been possible. The massive construction of the valves and the lateral extent of the cruminae in *Londinia* make the former position the more advantageous.

#### Subfamily TREPOSELLINAE

##### Text-fig. 13

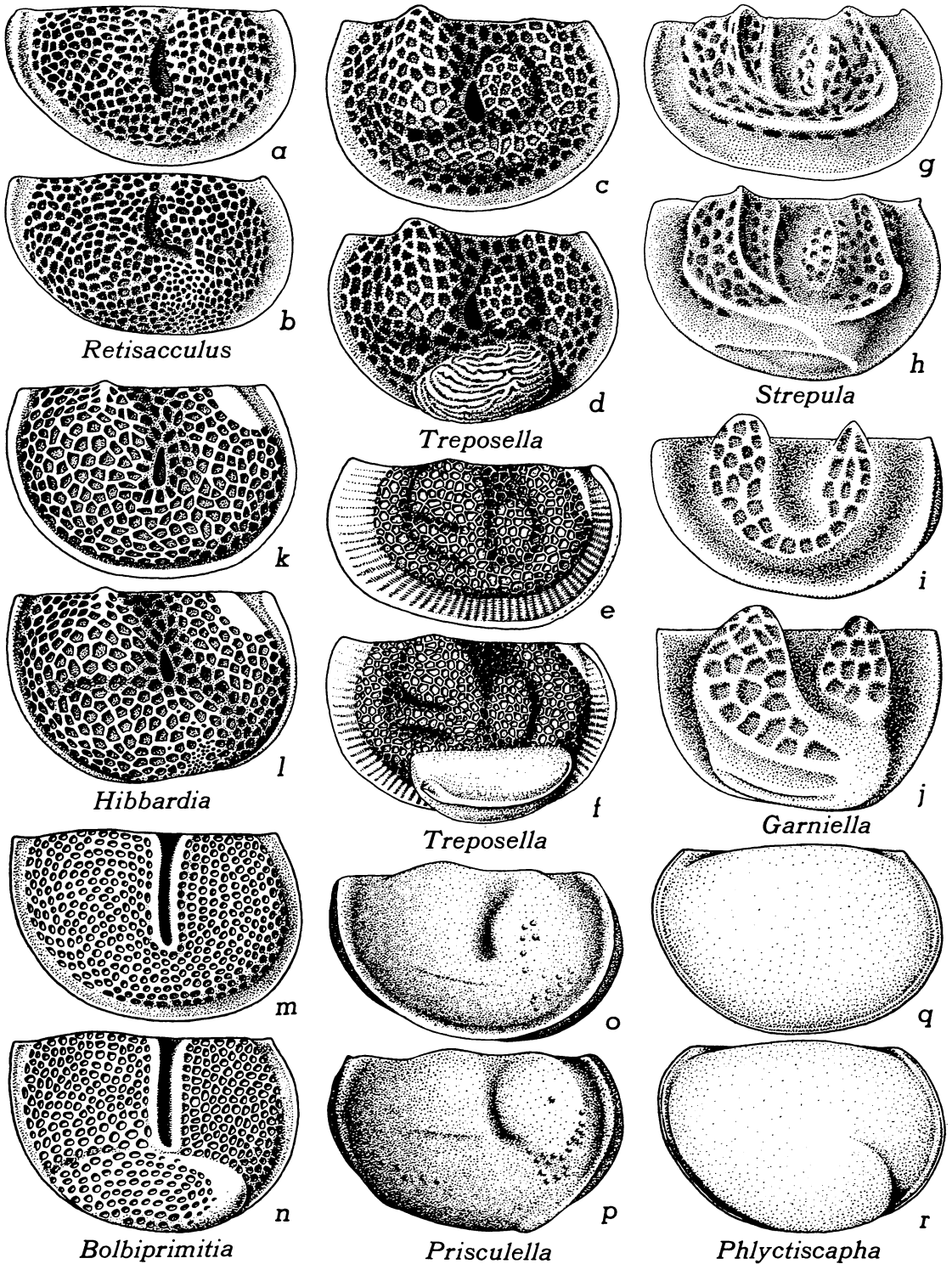
The Treposellinae terminate the great family of beyrichiids. These last survivors are no more diverse in lobation, no more variable in ornamentation, and no more divergent in form of crumina than some of their ancestral subfamilies, such as the Craspedobolbininae. They were diagnosed by Martinsson (1962, p. 196) as:

*Beyrichiidae* tending to incorporate, or incorporating, a large part of the syllobium with an originally anteroventral crumina, the dolonoid mechanism of which has largely become obsolete.

Actually, the crumina is more nearly ventral, with its greatest convexity along the front edge and its posterodorsal surface merging into the syllobium. The typical treposelline crumina is as well developed in the Silurian *Strepula*, *Garniella*, and *Retisacculus* as in the Devonian *Hibbardia* and *Phlyctiscapha*. In this respect, the treposellines are more closely knit and conservative than the craspedobolbinines, amphitoxitidines, beyrichiines, or kloedeniines.

The velum may be expressed as a narrow, low ridge, as in *Hibbardia* (text-fig. 13k, l), *Kozlowskiella*, and *Phlyctiscapha* (text-fig. 13q, r); or it may be a frill with tubulous radial structure, as in *Strepula* (text-fig. 13g, h) and *Treposella stellata* (text-fig. 13e, f); or it may be an intermediate narrow flange, as in *Garniella* (text-fig. 13i, j), *Bolbiprimitia* (text-fig. 13m, n), *Retisacculus* (text-fig. 13a, b), *Treposella lyoni* (text-fig. 13c, d), and *Prisculella* (text-fig. 13o, p).

Apart from the nonlobate, nonsulcate *Phlyctiscapha* (text-fig. 13q, r), the treposellines vary in the degree to which L2 (the preadductor node) is fused with L1 (the anterior lobe). *Strepula* (text-fig. 13g, h) has full expression of three lobes: L1 is elongate with a median crista continuing ventrally and posteriorly to the posteroventral section of the valve; L2 is a large node with a median zygale crista that forms a U and ends at the cusp on L3; and the



TEXT-FIG. 13.—Beyrichiidae, subfamily Treposellinae. Male and female right valves. *a, b*, *Retisacculus commatus* Martinsson,  $\times 33$ . *c, d*, *Treposella lyoni* (Ulrich),  $\times 28$ . *e, f*, *T. stellata* Kesling,  $\times 22$ . *g, h*, *Strepula concentrica* Jones & Hall,  $\times 33$ . *i, j*, *Garniella lineolata* Martinsson,  $\times 66$ . *k, l*, *Hibbardia lacrimosa* (Swartz & Oriol),  $\times 25$ . *m, n*, *Bolbiprimitia fissurella* (Ulrich & Bassler),  $\times 40$ . *o, p*, *Prisculella garnieloides* Martinsson,  $\times 42$ . *q, r*, *Phlyctiscapha apleta* Kesling,  $\times 26$ . *a-b*, *g-j*, *o-p*, after Martinsson.

syllobium is large and cusped, not clearly divided into lobes but with the zygial crista indicating L3 and the lunular posterior area (above the crista from L1) perhaps corresponding to L4 in quadrilobate ostracods. In *Treposeella* (text-fig. 13c-f) and in *Garniella jugata* Martinsson, L2 is a clearly defined preadductorial node; because S1 is shallow as compared with S2, the node appears to have close association with L1. In *Bolbiprimitia* (text-fig. 13m, n), L2 is expressed only as a bulge into the major sulcus. In *Retisacculus* (text-fig. 13a, b), *Hibbardia* (text-fig. 13k, l), and *Kozlowskiella*, L2 is poorly expressed if at all. In *Garniella lineolata* (text-fig. 13i, j), the fused L2 and L1 form a lanceolate lobe connected zygally with the posterior lobe. All lobate genera have a ventral connecting lobe below S2, which is expressed as a short sulcus or an adductorial pit.

Except for *Treposeella* (text-figs. 13d, f), in which the crumina has distinct boundaries all around, the treposellines have a distinctive crumina that varies little in shape from the Silurian *Garniella* (text-fig. 13j) to the Middle Devonian *Phlyctiscapha* (text-fig. 13r). The ornamentation, however, varies considerably. *Retisacculus* (text-fig. 13b) and *Hibbardia* (text-fig. 13l) have the same reticulation on the cruminae as on the rest of the valve, except that the anteroventral end of the cruminae has an area with finer meshes. *Bolbiprimitia* (text-fig. 13n) is similar except that the anterior end of the crumina is smooth. *Strepula* (text-fig. 13h) and *Garniella* (text-fig. 13j) have cristate cruminae, and *Treposeella* (text-fig. 13d, f) has entirely different ornamentation on crumina and valve surface.

The subfamily contains genera with reticulate to coarsely reticulate valves. The only exception is the smooth *Phlyctiscapha* (text-fig. 13q, r).

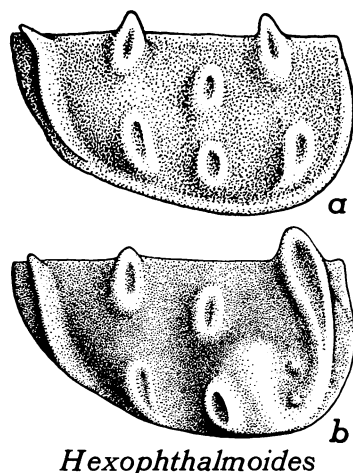
In the dorsal region, the syllobial region tends to be full and slightly protruding. *Strepula* (text-fig. 13g, h) has a cuspidal plica on L3, *Garniella* (text-fig. 13i, j) has a large cusp or a dorsal ridge, *Bolbiprimitia* (text-fig. 13m, n) a slight arching of L3 above the hingeline, and *Treposeella* (text-fig. 13c-f) and *Hibbardia* (text-fig. 13k, l) have low acuminate cusps on L3. *Retisacculus* (text-fig. 13a, b) has very little dorsal projection, and *Phlyctiscapha* (text-fig. 13q, r) has only a slight hump.

Posteriorly and ventrally, some treposellines have projecting flangelike vela, such as *Strepula* (text-fig. 13g, h) and *Treposeella stellata* (text-fig. 13e, f), but others have only a low velar ridge, such as *Hibbardia*, *Kozlowskiella*, *Phlyctiscapha*, and *Prisculella*.

As in many other beyrichiids, the mating position to which the carapace configuration seems well adapted is dorsal to posterodorsal.

Subfamily HEXOPHTHALMOIDINAE  
Text-fig. 14

This subfamily contains only *Hexophthalmoides craterilobatus* Martinsson. The cruminal swelling is anteroventral and poorly defined except for its effect on lobation. The velum is limited to the posterior region and terminates in a caudal spine. The lobes are dissected into lobules or nodes with cristal loops. There are two nodes for each L1, L2, and L3 in the male



TEXT-FIG. 14—Beyrichiidae, subfamily Hexophthalmoidinae. Male and female right valves. a, b, *Hexophthalmoides craterilobatus* Martinsson,  $\times 30$ . After Martinsson.

(text-fig. 14a). The crumina develops between the two anteroventral nodes (text-fig. 14b).

It is difficult to suggest a probable copulatory position for this unique little ostracod. A dorsal position seems impossible because of the prominent cusps on L1 and L3. A posterodorsal position would have been difficult because of the caudal spines. By elimination, a posterior (modified posterodorsal) or ventral position is left.

Superfamily HOLLINACEA  
Family TETRADELLIDAE

In his classic little paper on supravelar antra, Jaanusson (1966, p. 8) divided the tetradellids into subfamilies Tetradellinae, Sigmoidinae, and Glossomorphitinae. His divisions are clear cut, and no reason exists at this time to make the sigmoidines a separate family, as was

done by Henningsmoen (1953), Jaanusson (1957), and Kesling (1961, *in* T. I. P.). The subfamilies were diagnosed as:

Tetradellinae—supravelar antrum; male shape of subvelar area also present in females.

Sigmoopsinae—biantral dimorphism; male and female possess infravelar as well as supravelar antra.

Glossomorphitinae—antrum infravelar if present, histial structure at least in females.

The infravelar antra are defined as channels between the velum and the marginal structure, and supravelar antra as channels between the velum and the histium.

#### Subfamily TETRADELLINAE

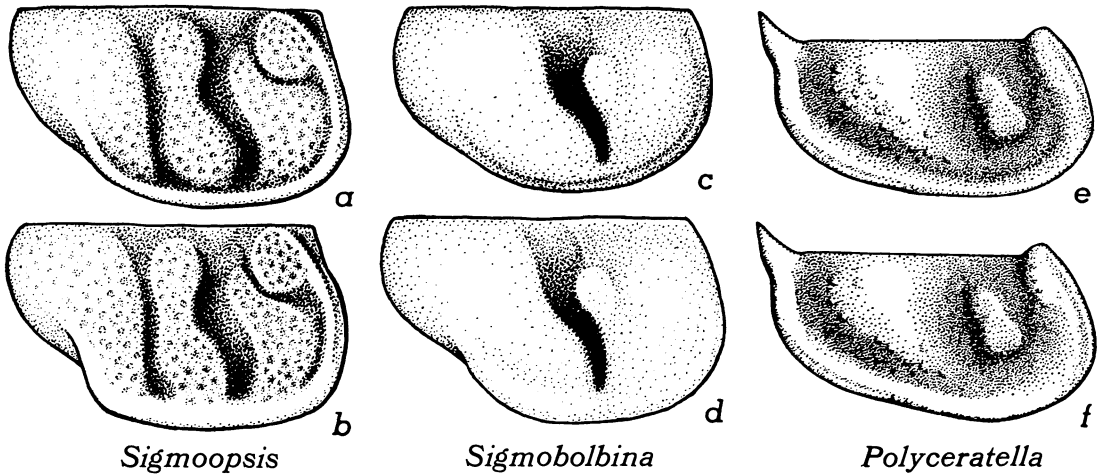
Text-figs. 15c, d, 16

Of the genera definitely assigned by Jaanusson (1966, p. 8), only *Tetradella* is strongly lobate. Despite the attention focused on the adventral structures, it is still indefinite as to whether the ridge around the lobate area of the male (text-fig. 16a) is a ventral ridge connecting L1 and L4 or a histial ridge. Of course, it may be a combination, as I am inclined to believe. In the female (text-fig. 16b), the upper

rims around the loculi seem to be partly set off from this ridge; these rims may be simply locular structures, as Jaanusson suggested, rather than the true histium. Considering the origin of the rims during the final ecdysis, they were formed from bands of hypodermis tangent to the band which secreted the ridge around the lobate area (the "technomorphic" ridge).

The other genera are separated by minor differences in the major sulcus, the development of adventral structures, and the number of loculi separated from the rest of the antrum. *Sigmobolbina* (text-figs. 15c, d; 16g-j) has a ventrally tapering sigmoidal S2 much like that in *Perspicillum*, differing in having one loculus instead of two and a stronger histial flange in the female. *Pelecymbolbina* (text-fig. 16c-f) has a uniformly wide S2, narrow velar ridge, and histial flange like those in *Dilobella* (text-fig. 16k-n), differing in the sigmoidal curvature of S2, velar ridge parallel to the free edge, abrupt termination of the histium posteriorly, and one loculus instead of two in the supravelar antrum. *Foramenella* is similar to *Dilobella*, but has five loculi.

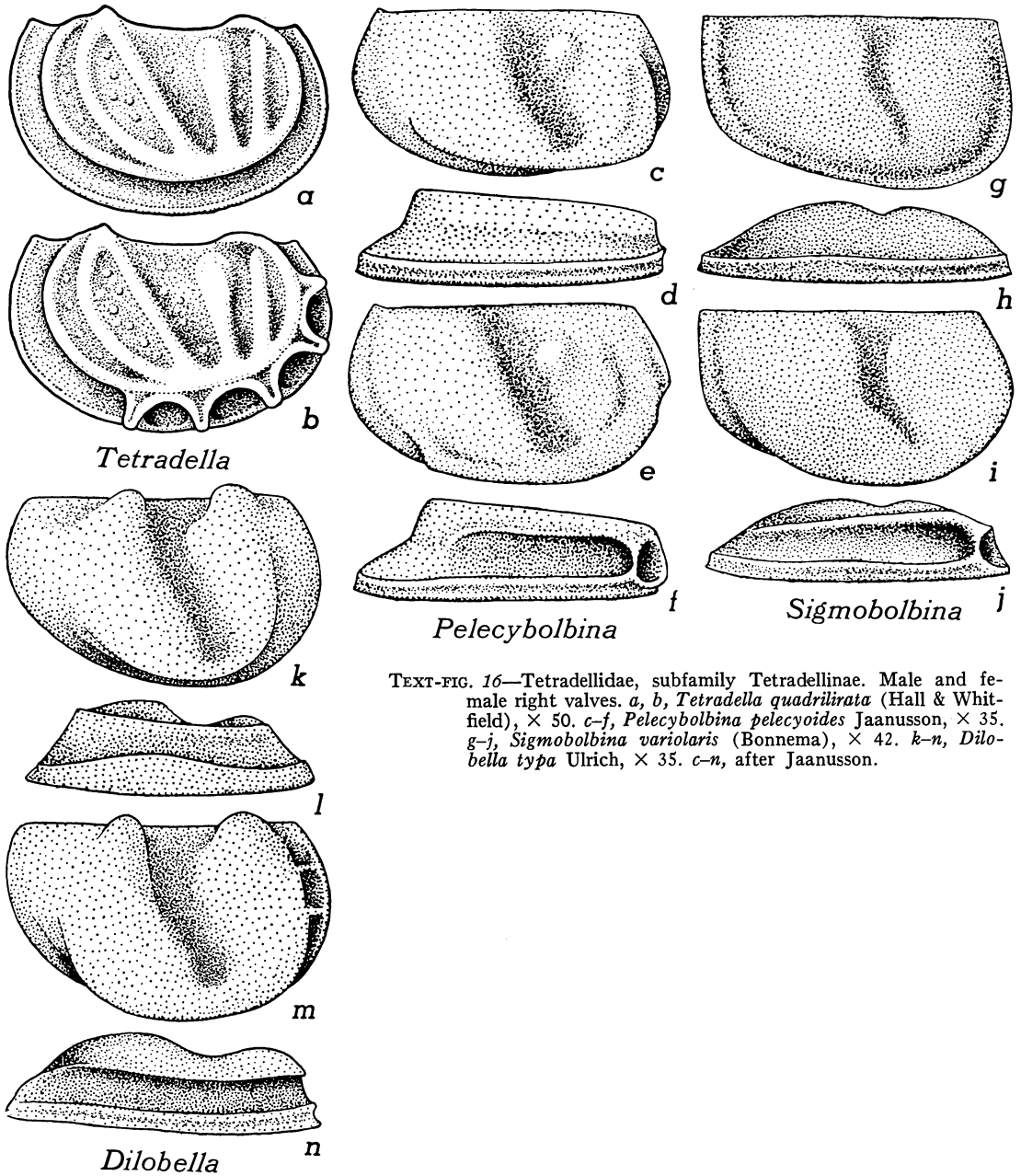
Even in the lobate *Tetradella*, the dorsal and posterior areas are free of major protuber-



TEXT-FIG. 15—Tetradellidae. Male and female right valves. a, b, *Sigmoopsis bergsbrunnae* Jaanusson,  $\times 40$ ; subfamily Sigmoopsinae (cf. text-fig. 17a-d). c, d, *Sigmobolbina sigmoidea* Jaanusson,  $\times 40$ ; subfamily Tetradellinae (cf. text-fig. 16g-j). e, f, *Polyceratella kuckersiana* (Bonnema),  $\times 33$ ; subfamily Glossomorphitinae. f, after Jaanusson.

ances. The upper ends of the cristae on L3 conform with the general outline in end view. Either the dorsal or the posterodorsal mating position would have been convenient in the tetradellines. Through the region within the supravelar antra, the carapaces of male and female are exception-

ally thin, particularly in *Tetradella*, suggesting that the genitalia were carried in the more spacious lobate part of the domicilium. Whatever the function of the adventral structures and their associated dimorphic antra, they did not facilitate mating.



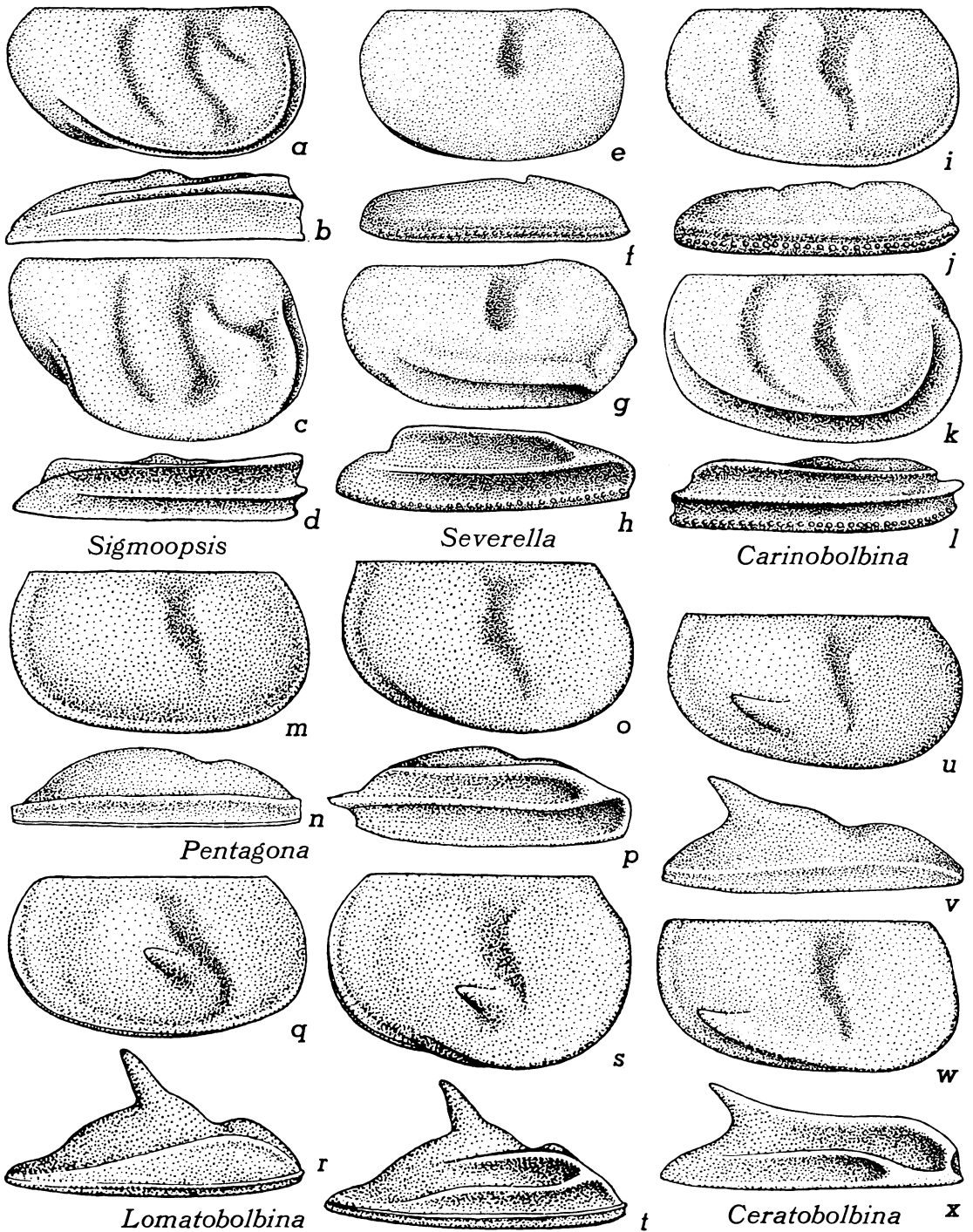
TEXT-FIG. 16—Tetradellidae, subfamily Tetradellinae. Male and female right valves. a, b, *Tetradella quadrilirata* (Hall & Whitfield),  $\times 50$ . c-f, *Pelecybolbina pelecyoides* Jaanusson,  $\times 35$ . g-j, *Sigmobolbina variolaris* (Bonnema),  $\times 42$ . k-n, *Dilobella typa* Ulrich,  $\times 35$ . c-n, after Jaanusson.

Subfamily SIGMOOPSINAE  
Text-figs. 15a, b, 17

The sigmoopsines, as Jaanusson suggested (1966, p. 8, 9), probably developed two antra from glossomorphitine ancestors with only an infravelar antrum and gave rise to the tetradellines with only a supravellar antrum. *Ceratobolbina* (text-fig. 17u-x) is intermediate in development between sigmoopsines and tetradellines,

with the infravelar antrum only in the ventral region and the supravellar antrum continuing beyond it anteriorly.

The genera differ in details of lobation and in the form and extent of the two antra. *Sigmoopsis* (text-figs. 15a, b, 17a, c) is quadrilobate, with L1 dorsally bulbous or produced into a hollow spine. S1 is short and curved around the expansion of L1; S2 and S3 are long. L2 is somewhat sigmoid, tapering dorsally, and not



TEXT-FIG. 17—Tetradellidae, subfamily Sismoopsinae. Male and female right valves, lateral and ventral views. a-d, *Sismoopsis rostrata* (Krause),  $\times 30$ . e-h, *Severella severa* (Sarv),  $\times 23$ . i-l, *Carinobolbina carinata* (Krause),  $\times 30$ . m-p, *Pentagona pentagona* (Jaanusson),  $\times 45$ . q-t, *Lomatobolbina mammillata* (Thorslund),  $\times 33$ . u-x, *Ceratobolbina monoceratina* (Jaanusson),  $\times 45$ . After Jaanusson.

attaining the dorsal border. *Carinobolbina* (text-fig. 17i, k) is tri- to quadrilobate, depending on the degree to which L2 is distinguishable from L1. Its lobes are flattened, somewhat like those of *Sigmoopsis*, and its S2 is long and sigmoid, resembling those in the unisulcate *Pentagona*, *Lomatobolbina*, and *Ceratobolbina*. *Pseudotallinella* has similar lobation, but may have some of the lobes dissected. *Severella* (text-fig. 17e, g) has S2 curved but not sigmoid. *Pentagona* (text-fig. 17m, o), *Lomatobolbina* (text-fig. 17q, s), and *Ceratobolbina* (text-fig. 17u, w) have long, ventrally tapering, sigmoid S2's.

The sigmoopsines may be divided into two groups on the position of the histium. In the first, including *Severella* (text-fig. 17e-h) and *Carinobolbina* (text-fig. 17i-l), the histium is set rather high on the valve, exposing most of the supravelar antrum in lateral view. In the second group, including *Sigmoopsis* (text-fig. 17a-d), *Pentagona* (text-fig. 17m-p), *Lomatobolbina* (text-fig. 17q-t), *Ceratobolbina* (text-fig. 17u-x), and *Pseudotallinella*, the histium extends ventrally to conceal most of the supravelar antrum. In *Severella* (text-fig. 17f) and *Carinobolbina* (text-fig. 17j), the male has a low velar ridge or bend separated from the marginal ridge by a shallowly concave infravelar canaliculus. The females have somewhat different arrangements of the two antra: in *Severella* (text-fig. 17h) the histial and velar dolonal flanges coalesce anteroventrally and the infravelar antrum continues forward and upward until the velum joins the marginal ridge; in *Carinobolbina* (text-fig. 17l) the histium does not curve toward the velum at its anterior end and remains free throughout its length.

*Sigmoopsis* (text-fig. 17b) and *Lomatobolbina* (text-fig. 17r) have the velar ridge arched away from the free edge in the male; *Sigmoopsis* also has a histial ridge in the male which seems to have no counterpart in *Lomatobolbina*. In the female, the histium and velum join anteroventrally in all species of *Lomatobolbina* (text-fig. 17t); they join in some species of *Sigmoopsis* but not in others (text-fig. 17d).

In the males of *Pentagona* (text-fig. 17n) and *Ceratobolbina* (text-fig. 17v), the velar ridge is nearly parallel to the free edge of the valve. In the females, the two antra are of different lengths; however, in *Pentagona* (text-fig. 17p) it is the infravelar antrum which continues anteriorly and no loculus is developed, whereas in *Ceratobolbina* (text-fig. 17x) it is the supravelar antrum which continues anteriorly and a loculus is present; the striking difference between the two may also be stated that anteroventrally the velum joins the histium in

*Pentagona* but joins the marginal ridge in *Ceratobolbina*. Throughout the family, loculi develop within the supravelar antrum (*Sigmoobolbina*, *Pelecycobolbina*, *Dilobella*, *Tetradella*, and *Ceratobolbina*) but never within the infravelar antrum.

In all sigmoopsines, the dorsal and posterior areas of male and female carapaces are remarkably free of protuberances, the smooth general surface interrupted only by sulci. They appear to be ideally adapted for dorsal or posterodorsal mating positions.

#### Subfamily GLOSSOMORPHITINAE Text-fig. 15e, f

The glossomorphitines show strong similarities to the sigmoopsines in the kinds of lobation. Thus, *Glossomorphites* is very much like *Sigmoopsis*, *Oecematobolbina* is like the unisulcate *Pentagona*, and *Ogmoopsis* like *Carinobolbina*. *Polyceratella* (text-fig. 15e, f) seems to have no counterpart; and *Aulacopsis* (if it is actually dimorphic) is considerably modified, more triangular than oblong in lateral view.

The histial structure appears to play a minor role in formation of the dimorphic antrum. The velum, closely associated with the histium in this subfamily, forms the outer antral fence. *Oecematobolbina* seems to have modified loculi, different from those in *Tetradella*, *Dibolbina*, and *Ceratobolbina*, and possibly nonfunctional in known species. Possibly, they are relict structures.

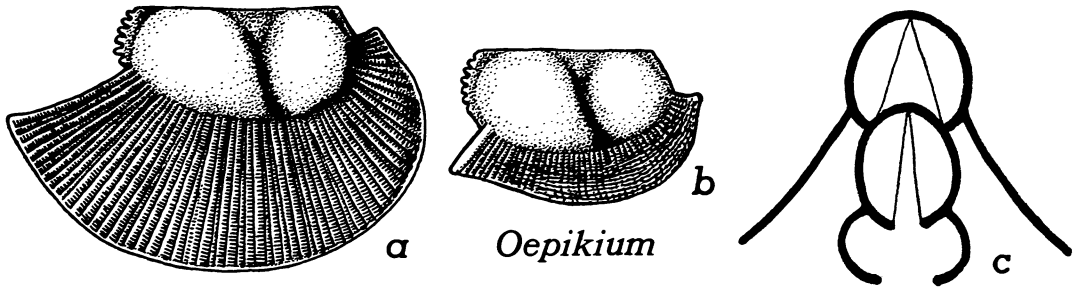
Feasible copulatory positions are like those for the sigmoopsines. Only the ventral position seems unlikely.

#### Family OEPIKIUMIDAE Text-fig. 18

As I understand the genus *Oepikium*, it could be regarded as an Ordovician evolutionary attempt to produce a hollinid ostracod. The tubulous adventral structure I classify as velar rather than histial, a point on which Jaanusson (1957, p. 406) disagrees. It forms an especially wide frill in the male (text-fig. 18a) and a considerably narrower convex dolon-like velum in the female. In this respect, it has much in common with the eurychilinids (especially the chilobolbinines) and the piretellids.

The long tapering S2 is very much like that in many Sigmoopsinae, such as *Sigmobolbina* (cf. text-fig. 16g, i), but it is not very different from that in *Grammolomatella* (cf. text-fig. 19e, f). Hence, lobation seems to be duplicated in tetraddellids, oepikiumids, and hollinids, just as





TEXT-FIG. 18—Oepikiumidae. a-c, *Oepikium tenerum* (Öpik), male and female right valves and very generalized cross section through male and female carapaces,  $\times 16$ .

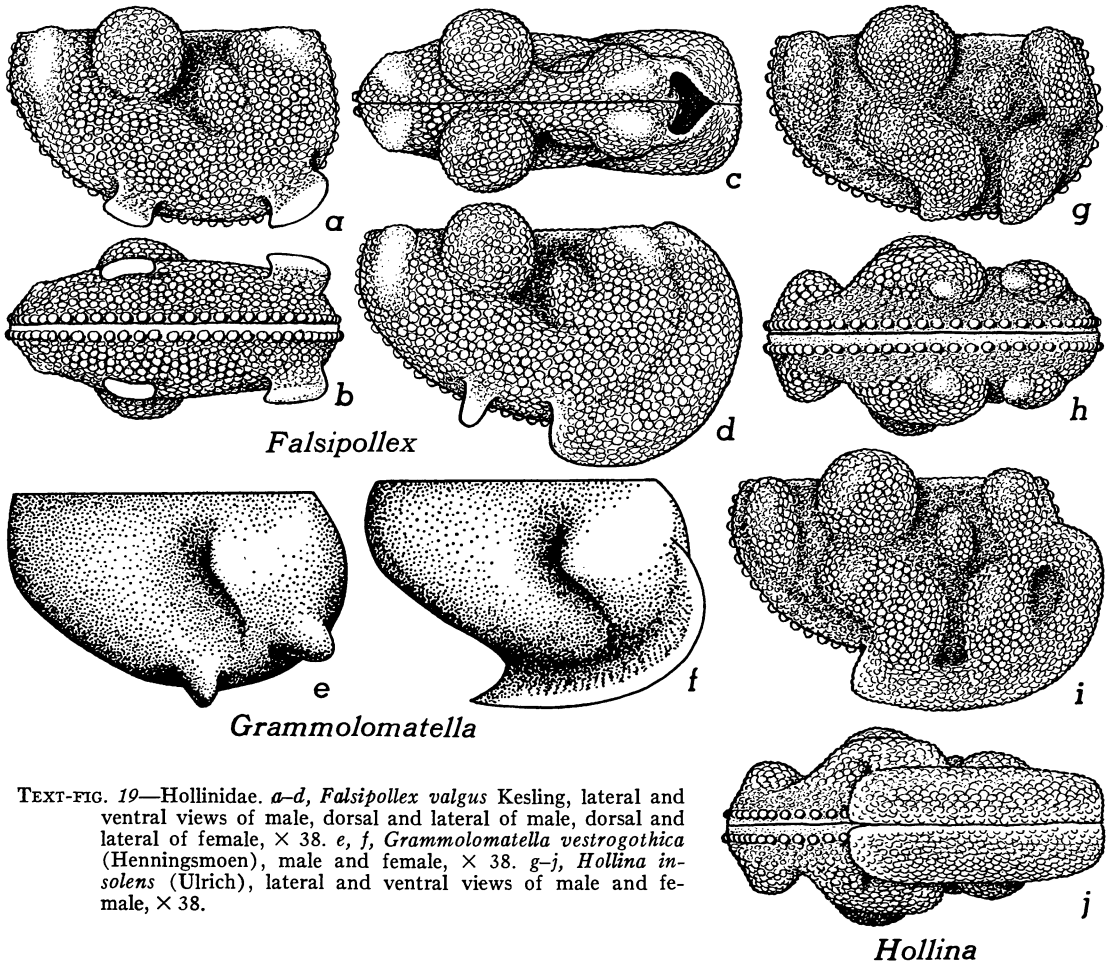
velar structure is duplicated in eurychilines, chilobolbinines, oepikiumids, and hollinids.

The great frill of the male, elevating the domicile high above the substrate, must have had a strong limiting influence on the copulatory position. It is difficult to conceive of any but the dorsal mating position in the oepikiumids, as suggested in text-figure 18c.

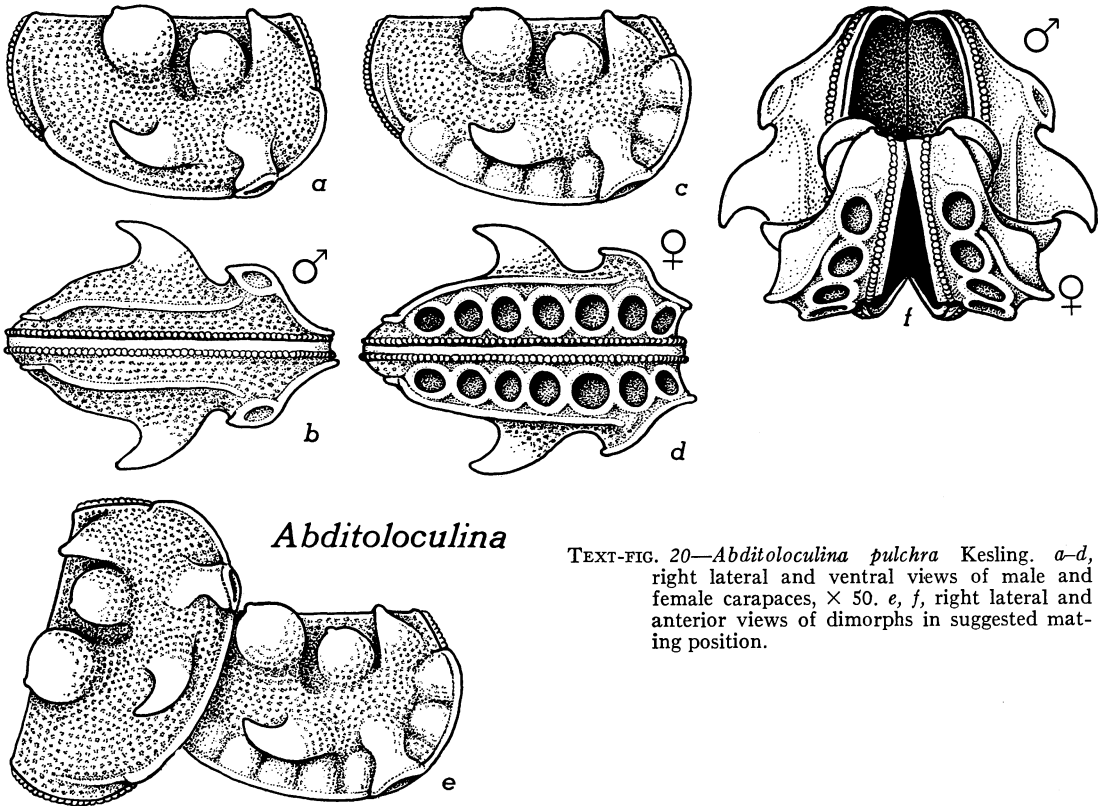
#### Family HOLLINIDAE

Text-figs. 19–20

The hollinids are noted for their dimorphic carapaces, particularly in Devonian and later species. Kesling (1952, p. 764) reviewed the history of recognition of dimorphism in the family and established the strongly dimorphic



TEXT-FIG. 19—Hollinidae. a-d, *Falsipollex valgus* Kesling, lateral and ventral views of male, dorsal and lateral of female,  $\times 38$ . e, f, *Grammolomatella vestrogothica* (Henningsmoen), male and female,  $\times 38$ . g-j, *Hollina insolens* (Ulrich), lateral and ventral views of male and female,  $\times 38$ .



### *Abditoloculina*

TEXT-FIG. 20—*Abditoloculina pulchra* Kesling. *a-d*, right lateral and ventral views of male and female carapaces,  $\times 50$ . *e, f*, right lateral and anterior views of dimorphs in suggested mating position.

genus *Abditoloculina*. In the *Treatise* (1961, p. 133–140), he brought the content of the family up-to-date.

The structures most involved in the dimorphism have been called by various authors frills, vela, velate or velar structures, adventral structures, and histial structures. The finer points of terminology were recently discussed by Henningsmoen (1965, p. 339–341). Here they are called velar structures, which may be broad (frills), narrow (ridges), or localized (spurs). By whatever name they are known, those of all hollinids seem to correspond.

In general, three kinds of dimorphism can be recognized in the females: (1) velar structure developed as an incurved frill [*Hollina* (text-fig. 19g–j), *Hollinella*, *Adelphobolbina*, *Falsipollex* (text-fig. 19a–d), *Flaccivelum*, and *Ruptivelum*]; (2) “scalloped” frill, with opposing frills of closed valves forming a series of cuplike enclosures [*Parabolbina* and *Subligaculum*]; and (3) loculi [*Ctenoloculina*, *Abditoloculina* (text-fig. 20c–d), *Tetrasacculus*, and *Bisacculus*]. The female of *Triemilomatella* appears to possess incipient loculi, developed as shallow pits between the frill and margin of the valve.

In the males, the velar structure in each

valve may be (1) a flared frill [*Hollinella* and *Adelphobolbina*], (2) a ridge [*Flaccivelum*], (3) interrupted frill [*Ruptivelum*, *Abditoloculina* (text-fig. 20a–b), and *Triemilomatella*], (4) spur and short frill [*Subligaculum*], (5) a pair of spurs [*Grammolomatella* (text-fig. 19e), *Falsipollex* (text-fig. 19a–b), *Parabolbina*, and *Ctenoloculina*], or (6) slightly emphasized ventral ends of L1 and L3 lobation [*Hollina* (text-fig. 19g–h), *Tetrasacculus*, and *Bisacculus*].

Lobation of most hollinids (*Hollina*, *Hollinella*, *Abditoloculina*, *Falsipollex*, et al.) contains a bulbous L3 in each valve, by far the widest part of the carapace. In *Ctenoloculina*, the dorsal part of the vertically elongate L3 is likewise the position of the widest part of the carapace, but not strongly inflated. The L3 is the widest part of the carapace in some other hollinids, such as *Parabolbina*, *Triemilomatella*, *Bisacculus*, and *Tetrasacculus*, although it is a poorly delineated part of the lobation. Only in the early *Grammolomatella* (text-fig. 19e–f; M. Ord. -Sil.) and *Ctenobolbina* (M. Ord.-U. Ord.) is L3 indistinct and not especially wider than adjacent parts of the valve; these genera may be ancestral to other hollinids, and their taxonomic position deserves closer inspection.

Hence, the typical carapaces in Hollinidae

are widest through the very large L3's and have the dimorphic velar structures in the female restricted to the anterior and ventral margins. As shown for *Abditoloculina pulchra* Kesling (text-fig. 20), *Hollina insolens* (Ulrich) (text-fig. 19g-j), and *Falsipollex valgus* Kesling (text-fig. 19a-d), the width of L3's in the female restrict forward encroachment by the male in mating.

Absence of velar structures on the posterior margin and the gently convex L4's of the female would have permitted convenient overlap of this region by the male. Ventral velar structures in both sexes would have made the ventral mating position difficult. Lobation and dimorphic features of the carapace seem to have been adapted for a posterodorsal to posterior mating position in the Hollinidae.

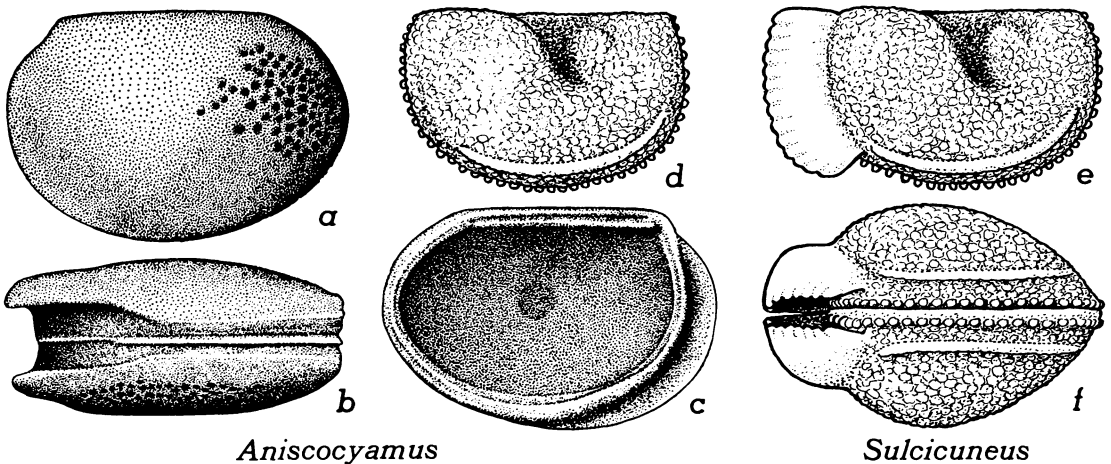
Superfamily PRIMITIOPSACEA  
Family PRIMITIOPSIDAE  
Text-fig. 21

In his treatment of the family, Martinsson (1960a, p. 148-149) divided the genera into five subfamilies. The dimorphism is practically the same in all primitiopsids, however, and only *Aniscocyamus* (subfamily Aniscocyaminae) and *Sulcicuneus* (subfamily Sulcicuneinae) are illustrated and discussed.

The dimorphic structure is the velum, which in the female forms posteriorly a flange (text-fig. 21a-c) or dolon (text-fig. 21e, f). Antral dimorphism was suggested by Henningsmoen (1965, p. 353-357) to be a means for egg care by the female. If so, the transfer and attachment of eggs in primitiopsids was probably accomplished by different appendages from those used for the purpose in eurychilids, piretellids, and hollinids.

Most subfamilies are smooth or reticulate and nonsulcate, like *Aniscocyamus* (text-fig. 21a-c). The Ordovician and Silurian forms have at most a pit to mark the position of the adductor muscle attachment. The Devonian *Sulcicuneus* (text-fig. 21d-f), however, has a well-developed sulcus for S2 and coarsely granulate ornamentation. In contrast to other primitiopsids, it also has a tubulous structure of the velum, featuring terminal tubercles along the edge.

The posterior dolon of such genera as *Sulcicuneus* effectively negates the posterodorsal mating position. The most logical position in the family was dorsal, with the hemipenes of the male lowered through the gape in the dolon of the female and extended forward into her opened carapace.



TEXT-FIG. 21—Primitiopsidae, subfamily Aniscocyaminae. a-c, *Aniscocyamus elegans* (Harris), right lateral and ventral views of female carapace, inside view of right valve,  $\times 40$ . Primitiopsidae, subfamily Sulcicuneinae. d-f, *Sulcicuneus porrectinatum* Kesling, male and female carapaces,  $\times 50$ . a-c, after Martinsson.

Superfamily OEPIKELLACEA  
Family OEPIKELLIDAE  
Text-fig. 22

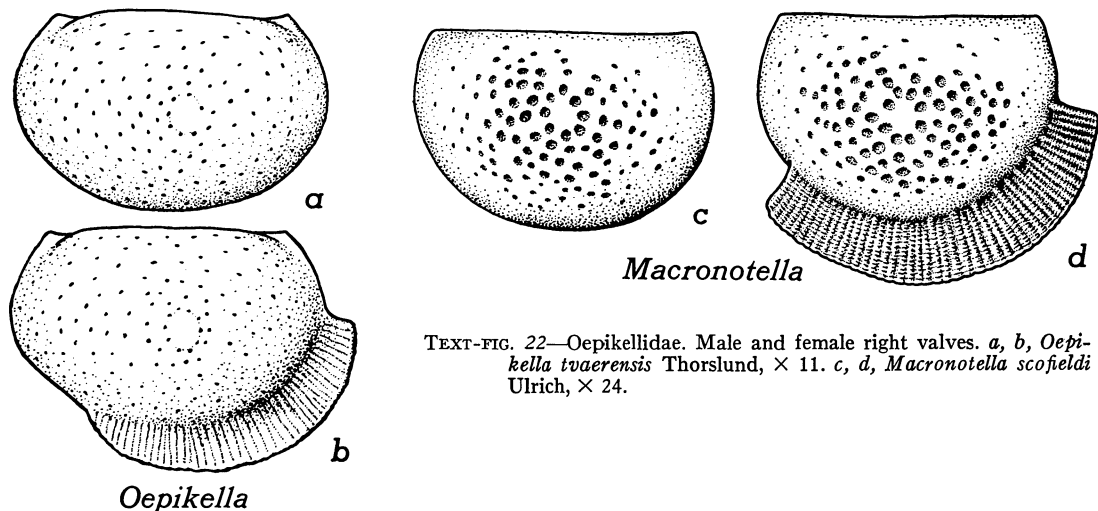
The heteromorphic adults, those with ventral velar dolons or frills, may have been fe-

males; certainly, such an interpretation would agree with that used in other Beyrichicopina, in which the heteromorph is invariably called the female. The derivation from the eurychilids by reduction of the technomorphic velum in ostracods like *Platybolbina*, as suggested by

Henningsmoen (1953, p. 228), seems reasonable. As compared with such genera as *Chilobolbina* (text-fig. 1d, f) and *Cystomatochilina* (text-fig. 1b), however, the greater development of the velum in the female of *Oepikella* (text-fig. 22b) is strange and presents an entirely different kind of dimorphism. It is almost the direct opposite of the dimorphism in *Oepi-*

*kium* (text-fig. 18a, b), in which the frill of the male far exceeds the rather narrow velar dolon of the female. Nevertheless, I must conclude that the heteromorph in oepikellids is the female—to propose that it is the male would make the ontogeny of this family unique among Paleozoic Ostracoda.

It is interesting that *Oepikella* was assigned



TEXT-FIG. 22—Oepikellidae. Male and female right valves. *a, b, Oepikella tvaerensis* Thorslund,  $\times 11$ . *c, d, Macronotella scofieldi* Ulrich,  $\times 24$ .

to the Eurychiliniidae (subfamily Eurychiliniinae) by Henningsmoen in 1953 (p. 268), to the Eurychiliniidae (subfamily Oepikellinae) by Jaanusson in 1957 (p. 269), and to the Oepikellidae of the superfamily Oepikellacea in the *Treatise* in 1961 (p. 93, 169, 170).

At this time, only two genera can be definitely assigned to the family: *Oepikella* and *Macronotella*. No sulcus of any kind is known. The position of the adductor muscle attachment is marked externally by an oval area void of pits.

The velum of the female is definitely tubulous in the type species of *Oepikella* (text-fig. 22b) and *Macronotella* (text-fig. 22d).

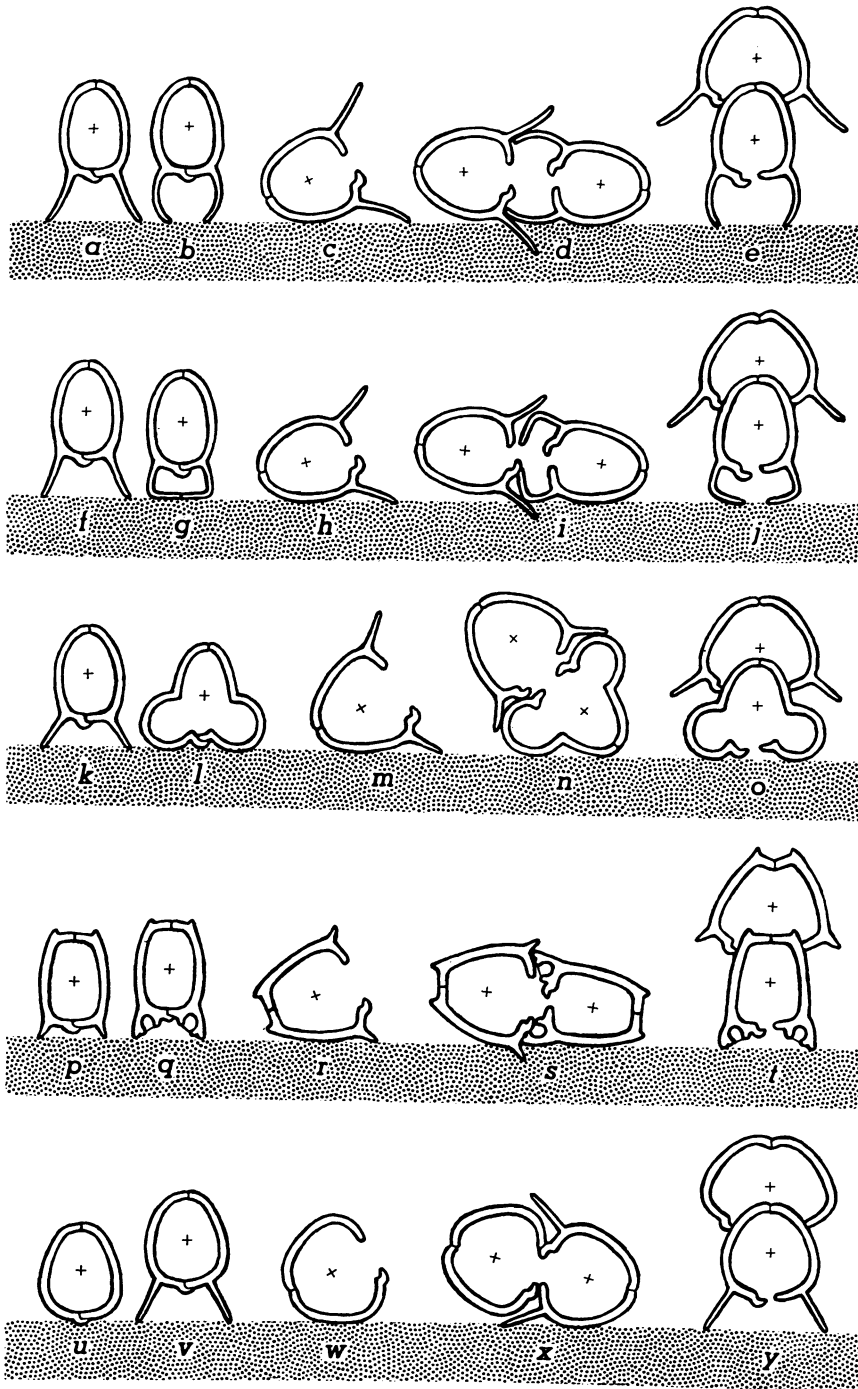
Whatever the function of the female velum, it does not seem to have assisted in copulation. On the contrary, the elevation of the female domicilium would have hindered the approach of the male. In a ventral position, the male would have to place the ventral edges of his valves between the frills of the female. For copulation to occur in this position, the female must have actively participated in the procedure. This would differ from the habits in living ostracods, in which the female appears to take no initiative in the mating; in fact, the male mates at considerable risk, for the female will clamp her valves shut if disturbed in any way.

The advantageous position on the smoothly shaped female carapace of oepikellids was dorsal to posterodorsal.

#### CONCLUSIONS

Aside from the primitiopsids, with posterior antral dimorphism, there are five basic types of dimorphism displayed in the ostracods discussed above. These may be termed for convenience the eurychilid (text-fig. 23a–e), the piretelliid (text-fig. 23f–j), the beyrichiid (text-fig. 23k–o), the locular (text-fig. 23p–t), and the oepikellid (text-fig. 23u–y). Each type has certain characteristics which bear on the problem of copulation. Although the cross sections in text-figure 23 are somewhat idealized, they represent the essential forms through the anterior regions of male and female.

One might suppose that the ventral mating position was ideal for the heavy-shelled Beyrichiopinina, but it was made difficult by the hinged valves and the weight of the carapace. The male valve on its side lay with the free edges of the valves practically parallel to the substrate only as long as the carapace remained closed. When the carapace opened, the upper valve lifted like the lid of a chest (text-fig. 23c, h, m, r, w). For male valves with strongly con-



TEXT-FIG. 23—Cross sections through anterior regions of idealized dimorphic ostracods, showing male and female in upright position, male lying on side, possible ventral copulatory position, and possible dorsal copulatory position. Center of carapace marked by + sign. *a-e*, representing eurychiliniids, oepikiumiids, and certain hollinids, with a convex dolon in each female valve. *f-j*, representing piretelliids, with strongly convex dolon in each female valve. *k-o*, representing beyrichiids, with a crumina in each female valve. *p-t*, representing certain hollinids, with loculi in each female valve. *u-y*, representing oepikelliids, with frill in each female valve.

vex sides, the orientation of both valves changed with the opening of the carapace in response to the shift in the center of gravity. The same factors applied to the female carapace lying on its side. Hence, the two partners in a venter-to-venter position had the edges of their upper valves far apart when their carapaces were open.

Even if the male could lift his carapace and adjust his orientation to the female by powerful clasping appendages (text-fig. 23d, i, n, s, x), the ventral mating position was beset with difficulties. At best, the ventral edges of the male valves were separated from those of the female by the full width of the female dolon in the eurychilinid (text-fig. 23d) and the piretellid (text-fig. 23i) types; they were separated by the greatest width of the velum in the locular (text-fig. 23s) type; and they were held somewhat apart by the cruminal extent in the beyrichiid (text-fig. 23n) type. Another difficulty originates with the frill of the male. To be functional, the frills must slope or curve away from the plane of commissure; yet in the horizontal mating position, such an outward slant necessitates the insertion of the frill of the lower valve into the substrate (text-fig. 23d, i). Undoubtedly, this digging of the frill into the sediment would tend to shove foreign particles into the ventral regions of the mating animals.

From observations of living ostracods, one must question whether the female of most Beyrichicopina would assume a horizontal position for mating. In all living species that have been observed, the female does not actively seek a role in mating; indeed, she seems to react only to threats to her safety, clamping the valves together even while copulation is in progress. This behavior pattern may have evolved differently from that in Paleozoic Ostracoda, it is true. The highly stable, base-heavy carapace of the beyrichiid female (text-fig. 23n), nevertheless, does not seem to have been designed for turning onto its side without some assistance from the male. I conclude that the ventral position was scarcely feasible in the eurychilinids, oepikiumids, hollinids, piretellids, or beyrichiids.

Ventral copulation in oepikellids (text-fig. 23x) by necessity would have been entirely under control of the frilled heteromorph, which I assume to be the female. The male valves could have approached the female domicilium only between the frills of the latter. Such initiative and cooperation on the part of the female seems very improbable.

The dorsal and posterodorsal mating positions seem better suited to all strongly dimorphic Paleozoic ostracods. The dorsal position (text-fig. 23e, j, o, t, y) brings the centers of

the male and female bodies rather close together. In benthonic ostracods with anteroventral vela in the female, the sole area may have been posteroventral, tilting the hinge line toward the rear and thus facilitating mounting by the male. This may have been particularly important in the oepikellids (text-fig. 22b, d), although it was undoubtedly a significant factor in other families.

The posterodorsal position may be regarded as a modification of the dorsal. It results in lowering of the male body with respect to that of the female and in narrowing the distance between the posteroventral edges of their carapaces. Both effects would assist copulation in animals having posteroventral or posterocentral genitalia. Such location of genitalia seems plausible, at least in the strongly lobate species.

Characters which seem to be copulatory adaptations are:

(1) *dorsum smooth or free of projections or protuberances*. This occurs in the eurychilinids, many of the beyrichiids, tetradellids, oepikiumids, and oepikellids. It seems to be an adaptation for the dorsal mating position.

(2) *posterior end of carapace smooth and evenly tapered*. This applies to several families, but especially to the hollinids. In typical genera, such as *Hollina*, *Hollinella*, *Abditoloculina*, and *Adelphobolbina*, the L3's are so bulbous or inflated that they form the widest part of the carapace. In contrast, the L4 part of the carapace is gently convex and tapers to the rear border. Thus, in the region where the encasing armor of the ostracod might be expected to bear spines for added protection, the carapace of hollinids is markedly free of protuberances. This I interpret as an adaptation for the posterodorsal mating position.

(3) *restriction of velum to anterior and anteroventral margins*. In the female, this leaves the posterior region free of projections. It may also produce a cant to the upright female carapace, so that the female hinge line slopes back. This feature is typical of tetradellids, hollinids, oepikiumids, and oepikellids. It appears to be an adaptation for the posterodorsal mating position, for such restriction seems to serve no other useful purpose.

(4) *anteroventral location of cruminae in beyrichiids*. This has the same effects as the restriction of the frill in other families, and may be presumed to be the same kind of adaptation.

(5) *outward slant or flare of the male velum*. This is notable in eurychilinids, piretellids, hollinids, and oepikiumids. Whereas it effectively increases stability of the animal on the substrate, it also facilitates mating.

(6) *long straight hinge line*. The exceptional

length of the hinge in Palaeocopa, as compared with the short hinges of many living ostracods, can scarcely be considered a necessity for hinging. Furthermore, the shape of the palaeocope carapace, dominated by the long hinge, does not yield the maximum internal volume for the area of secreted shell material. It may be suggested, therefore, that the universal straight hinge in all ostracods in this order is an adaptation for the dorsal and posterodorsal mating positions.

From this review of family characteristics, some generalizations may be made that are not directly concerned in copulation:

(1) *lobation is secondary to dimorphism*. In the beyrichiids, which assuredly constitute a well-defined taxon, all kinds of lobation occur (text-figs. 4-14). To a lesser degree, this is also true of eurychilinids, piretellids, tetradellids, hollinids, and primitiopsids.

(2) *ornamentation is secondary to dimorphism*. In the beyrichiids, carapaces are tuberculate, reticulate, smooth, granulose, spinulose, verrucose, and punctate. Tetradellids, and hollinids also show some variation in ornamentation, yet they are clear taxa on the basis of their dimorphism.

(3) *the heavy-shelled Beyrichicopina appear adapted to benthonic life*. The stability imparted by vela and histia, developed as frills, flanges, and dolons in the Beyrichicopina, appears to match that by fundia in recent benthonic ostracods.

(4) *strongly dimorphic Paleozoic ostracods must have had long retractable appendages*. Elevation of the domicilium above the substrate by velar structures undoubtedly made long appendages necessary for feeding and locomotion. The well-developed closing structures along the edges further indicates that the appendages could be withdrawn into the domicilium and the valves closed for safety. One must also assume that the palaeocope ostracod after the final molting was able to right itself from the horizontal position, as do living ostracods. It would be logical to further assume that this ability was retained in the adult, and could

prove useful when the carapace was accidentally tipped over. The leverage required to attain the upright position in the male *Oepikium* (text-fig. 18a), for example, must have been derived from unusually long and powerful appendages.

In summary, some carapace features impose limitations on mating methods, some facilitate a particular method, and others so compound the difficulties that they practically preclude the utilization of certain mating positions. To establish the relationship of carapace to copulation more observations of living ostracods will be necessary, together with new examination of fossil representatives. For extinct taxa, the configuration of the carapace must be considered from a functional viewpoint in the light of generalizations based on living species. Potentially, such considerations could produce a more satisfactory system of classification.

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Amphitoxotidinae	Martinsson 1962
Aniscocyaminae	Martinsson 1960
Bassleratiidae	Schmidt 1941
Beyrichiidae	Matthew 1886
Chilobolbininae	Jaanusson 1957
Craspedobolbininae	Martinsson 1962
Eurychilinidae	Ulrich & Bassler 1923
Glossomorphitinae	Hessland 1953
Hexophthalmoidinae	Martinsson 1962
Hollinidae	Swartz 1936
Kloedeniinae	Ulrich & Bassler 1923
Oepikellidae	Jaanusson 1957
Oepikiumidae	Jaanusson 1957
Piretellidae	Öpik 1937
Primitiopsidae	Swartz 1936
Quadrijugatoridae	Kesling & Hussey 1953
Sigmoopsinae	Henningsmoen 1953
Sulcicuneinae	Martinsson 1960
Tetradellidae	Swartz 1936
Treposellinae	Henningsmoen 1954
Tvaerenellinae	Jaanusson 1957
Zygobolbininae	Ulrich & Bassler 1923

#### AUTHORS, DATES, AND ASSIGNMENT OF GENERA AND SUBGENERA MENTIONED

<i>Abditoloculina</i>	Kesling 1952	Hollinidae
<i>Actinochilina</i>	Jaanusson 1957	Eurychilinidae, Chilobolbininae
<i>Adelphobolbina</i>	Stover 1956	Hollinidae
<i>Aitilia</i>	Martinsson 1962	Beyrichiidae, Craspedobolbininae
<i>Altibeyrichia</i>	Martinsson 1962	Beyrichiidae, Beyrichiinae
<i>Amphitoxotis</i>	Martinsson 1962	Beyrichiidae, Amphitoxotidinae
<i>Ampirulum</i>	Martinsson 1966	Beyrichiidae, Amphitoxotidinae
<i>Aniscocyamus</i>	Martinsson 1960	Primitiopsidae, Aniscocyaminae
<i>Apatobolbina</i>	Ulrich & Bassler 1923	Beyrichiidae, Craspedobolbininae
<i>Asperibeyrichia</i>	Martinsson 1962	Beyrichiidae, Beyrichiinae

<i>Atterdagia</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Aulacopsis</i> Hessland 1949 .....	Tetradellidae, Glossomorphitinae
<i>Barymetopon</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Berolinella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Beyrichia</i> M'Coy 1846 .....	Beyrichiidae, Beyrichiinae
<i>Bingeria</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Bisacculus</i> Stewart & Hendrix 1945 .....	Hollinidae
<i>Bolbibollia</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Craspedobolbininae
<i>Bolbineossia</i> Kesling, Heany, Kauffman, & Oden 1958 .....	Beyrichiidae, Craspedobolbininae
<i>Bolbiprimitia</i> Kay 1940 .....	Beyrichiidae, Treposellinae
<i>Bonnemaia</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbiniae
<i>Bromidella</i> Harris 1931 .....	Piretellidae, Piretellinae
<i>Calcaribeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Carinobolbina</i> Henningsmoen 1953 .....	Tetradellidae, Sigmoidinae
<i>Ceratobolbina</i> Jaanusson 1966 .....	Tetradellidae, Sigmoidinae
<i>Chilobolbina</i> Ulrich & Bassler 1923 .....	Eurychilinae, Chilobolbininae
<i>Clavobolbina</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Clantiella</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Craspedobolbina</i> Kummerow 1924 .....	Beyrichiidae, Craspedobolbininae
<i>Cryptolophobus</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Ctenobolbina</i> Ulrich 1890 .....	Hollinidae
<i>Ctenoloculina</i> Bassler 1941 .....	Hollinidae
<i>Cystomatochilina</i> Jaanusson 1957 .....	Eurychilinae, Chilobolbininae
<i>Dibolbina</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Amphitoxotidinae
<i>Dicranella</i> Ulrich 1894 .....	Piretellidae, Tvaerenellinae
<i>Dolichoscapha</i> Kesling & Ehlers 1958 .....	Beyrichiidae, Craspedobolbininae
<i>Drepanellina</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbiniae
<i>Eobeyrichia</i> Henningsmoen 1954 .....	Beyrichiidae, Beyrichiinae
<i>Euprimites</i> Hessland 1949 .....	Piretellidae, Tvaerenellinae
<i>Eurychilina</i> Ulrich 1889 .....	Eurychilinae, Eurychilinae
<i>Falsipollex</i> Kesling & McMillan 1951 .....	Hollinidae
<i>Flaccivelum</i> Kesling & Peterson 1958 .....	Hollinidae
<i>Foramenella</i> Stumbur 1956 .....	Tetradellidae, Tetradellinae
<i>Frostiella</i> Martinsson 1963 .....	Beyrichiidae, Kloedeniinae
<i>Gannibeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Garniella</i> Martinsson 1962 .....	Beyrichiidae, Treposellinae
<i>Glossomorphites</i> Hessland 1953 .....	Tetradellidae, Glossomorphitinae
<i>Grammolomatella</i> Jaanusson 1957 .....	Hollinidae
<i>Grogarina</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Hammariella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Hamulinavis</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Hemsiella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Hesperidella</i> Öpik 1937 .....	Piretellidae, Tvaerenellinae
<i>Hexophthalmoides</i> Martinsson 1962 .....	Beyrichiidae, Hexophthalmoidinae
<i>Hibbardia</i> Kesling 1953 .....	Beyrichiidae, Treposellinae
<i>Hoburgiella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Hollina</i> Ulrich & Bassler 1908 .....	Hollinidae
<i>Hollinella</i> Coryell 1928 .....	Hollinidae
<i>Hyrinobolbina</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Juviella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Kloedenia</i> Jones & Holl 1886 .....	Beyrichiidae, Kloedeniinae
<i>Kozlowskiella</i> Příbyl 1953 .....	Beyrichiidae, Treposellinae
<i>Laccochilina</i> Hessland 1949 .....	Eurychilinae, Chilobolbininae
<i>Leptobolbina</i> Martinsson 1962 .....	Beyrichiidae, Craspedobolbininae
<i>Levisulculus</i> Jaanusson 1957 .....	Piretellidae, Tvaerenellinae
<i>Loella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Lomatobolbina</i> Jaanusson 1957 .....	Tetradellidae, Sigmoidinae
<i>Londinia</i> Martinsson 1963 .....	Beyrichiidae, Kloedeniinae
<i>Lophoctenella</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae



<i>Lophokloedenia</i> Swartz & Whitmore 1956 .....	Beyrichiidae, Beyrichiinae
<i>Lunulibeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Macronotella</i> Ulrich 1894 .....	Oepikellidae
<i>Macrypsilon</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Mastigobolbina</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbinae
<i>Mesomphalus</i> Ulrich & Bassler 1913 .....	Beyrichiidae, Crapedobolbinae
<i>Mitrobeyrichia</i> Henningsmoen 1954 .....	Beyrichiidae, Crapedobolbinae
<i>Navibeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Neobeyrichia</i> Henningsmoen 1954 .....	Beyrichiidae, Beyrichiinae
<i>Nodibeyrichia</i> Henningsmoen 1954 .....	Beyrichiidae, Beyrichiinae
<i>Noviportia</i> Martinsson 1962 .....	Beyrichiidae, Zygobolbinae
<i>Oecematobolbina</i> Jaanusson 1957 .....	Tetradellidae, Glossomorphitinae
<i>Oepikella</i> Thorslund 1940 .....	Oepikellidae
<i>Oepikium</i> Agnew 1942 .....	Oepikiumidae
<i>Ogmoopsis</i> Hessland 1949 .....	Tetradellidae, Glossomorphitinae
<i>Parabolbina</i> Swartz 1936 .....	Hollinidae
<i>Pelecypolbina</i> Jaanusson 1966 .....	Tetradellidae, Tetradellinae
<i>Pentagona</i> Schallreuter 1964 .....	Tetradellidae, Sigmoidopsinae
<i>Perspicillum</i> Schallreuter 1964 .....	Tetradellidae, Tetradellinae
<i>Phlyctiscapha</i> Kesling 1953 .....	Beyrichiidae, Treposellinae
<i>Piretella</i> Öpik 1937 .....	Piretellidae, Piretellinae
<i>Piretia</i> Jaanusson 1957 .....	Piretellidae, Piretellinae
<i>Platybolbina</i> Henningsmoen 1953 .....	Eurychilinidae, Chilobolbinae
<i>Plethobolbina</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbinae
<i>Plicibeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Polyceratella</i> Öpik 1937 .....	Tetradellidae, Glossomorphitinae
<i>Prisculella</i> Martinsson 1966 .....	Beyrichiidae, Treposellinae
<i>Prochilina</i> Jaanusson 1957 .....	Eurychilinidae, Chilobolbinae
<i>Pseudotallinella</i> Sarv 1959 .....	Tetradellidae, Sigmoidopsinae
<i>Rakverella</i> Öpik 1937 .....	Piretellidae, Piretellinae
<i>Retisacculus</i> Martinsson 1962 .....	Beyrichiidae, Treposellinae
<i>Ruptivelum</i> Kesling & Weiss 1953 .....	Hollinidae
<i>Scabribeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Severella</i> Schallreuter 1964 .....	Tetradellidae, Sigmoidopsinae
<i>Sigmobolbina</i> Henningsmoen 1953 .....	Tetradellidae, Tetradellinae
<i>Sigmoidopsis</i> Henningsmoen 1953 .....	Tetradellidae, Sigmoidopsinae
<i>Simplicibeyrichia</i> Martinsson 1962 .....	Beyrichiidae, Beyrichiinae
<i>Sleia</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Slependia</i> Martinsson 1962 .....	Beyrichiidae, Zygobolbinae
<i>Strepula</i> Jones & Holl 1886 .....	Beyrichiidae, Treposellinae
<i>Sulcicuneus</i> Kesling 1951 .....	Primitiopsidae, Sulcicuneinae
<i>Triemilomatella</i> Jaanusson & Martinsson 1956 .....	Hollinidae
<i>Tvaerenella</i> Jaanusson 1957 .....	Piretellidae, Tvaerenellinae
<i>Uhakiella</i> Öpik 1937 .....	Piretellidae, Piretellinae
<i>Velibeyrichia</i> Henningsmoen 1954 .....	Beyrichiidae, Amphitoxotidinae
<i>Vinculoveliger</i> Martinsson 1962 .....	Beyrichiidae, Amphitoxotidinae
<i>Welleriopsis</i> Swartz & Whitmore 1956 .....	Beyrichiidae, Beyrichiinae
<i>Zygobeyrichia</i> Ulrich 1916 .....	Beyrichiidae, Beyrichiinae
<i>Zygobolba</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbinae
<i>Zygobolbina</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbinae
<i>Zygosella</i> Ulrich & Bassler 1923 .....	Beyrichiidae, Zygobolbinae

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