ONTOGENY OF TRILOBITA

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INTRODUCTION

For more than 100 years trilobite exoskeletons have been known, preserved as molds in shales, siltstones, and fine sandstones, and exhibiting a gradational size series. In these fine-grained sediments some of the exoskeletons, though flattened, are partly, or not at all, disarticulated. The smallest members of series that have been found are about 1 mm. in length or less, subcircular in outline, convex, and without articulation. The name **protaspis** (pl., protaspides) was coined for these minute shields by Beecher (3).

Somewhat larger exoskeletons exhibit an articulation between the part that is to become the cephalon, and that which is to become thorax and pygidium. In successively larger exoskeletons thoracic segments appear until the total number (characteristic of the particular species) is reached. Raw (16) proposed the terms **meraspid period** for the series beginning with subdivision of the protaspis, and **holaspid period** for the development that takes place after completion of the thorax. He also suggested a division of the meraspid period into "degrees" characterized and distinguished by the number of thoracic segments present. These terms are adopted here, and discussed below in the appropriate sections. The holaspid period may be attained at a length *(sag.)* of less than 1 cm. and this is followed by great increase in size during the period.

Growth stages of trilobites have also been found in calcareous rocks (15), particularly calcilutites, and in some of these rocks the exoskeletons are not flattened or distorted, though commonly they are disarticulated. Extraction of silicified specimens from such rocks, first by Beecher (2), has given much new information in recent years (19, 20, 21, 33, 37).

PROTASPID PERIOD

GENERAL CHARACTERS

The trilobite protaspis represents the earliest stage at which, presumably, the exoskeleton is mineralized and therefore may be preserved. A range in length *(sag.)* from about 0.25 to 1 mm. is known, rarely larger. Outline in dorsal aspect is usually subcircular, convexity moderate to strong, and a subspherical form may be attained. The axis

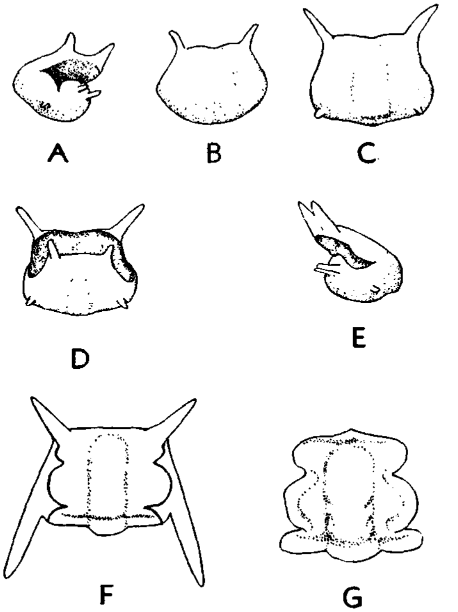


FIG. 86. Ontogenetic stages of *Menoparia genalunata* Ross, L.Ord., Utah; *A,B*, small protaspis, anteroventral and dorsal views; *C-E*, larger protaspis, dorsal, ventral, and lateral views; *F*, meraspid cephalon; *G*, late meraspid cranidium; all ×20 (19).

is at least partially defined in the smallest protaspides (Fig. 86*B*) and may be completely outlined by furrows. From a length of 0.4 mm. upwards it is in most specimens divided into rings, the anterior being longer (*sag.*) than those following it. The 5th (4th in *Shumardia*, Fig. 87*A*) ring is the occipital, and behind this is the short axial portion of the **protopygidium** (e.g., *Sao*, Fig. 88*A*). The pleural regions of the smallest known protaspides (Figs. 87*A*, 89*A*; Ross, 20, Pl. 32, figs. 2, 3) are either incompletely divided or not at all. At a length of 0.5 to 0.6 mm. the transverse ridge (posterior border of cephalon) and furrow have either appeared or been completed, thus dividing the protaspis into larger cephalic portion and smaller protopygidium (Figs. 88*B*, 89*B*, 90*A*, 91*A*). An exception is *Menoparia* (Fig. 86*C-E*), but the position of the occipital ring and presence of the doublure define the protopygidium.

BEECHER (3) suggested that the protaspid period might be divided into successive stages called **anaprotaspid, metaprotaspid,** and paraprotaspid but did not characterize these stages. STØRMER (24) defined the anaprotaspid stage as that in which the axis includes only 5 segments, and the metaprotaspid as including "secondary somites" forming the protopygidium. This interpretive definition is not satisfactory, and in practice STØRMER (24) and Ross (19) have recognized the metaprotaspid stage as beginning when the pleural region becomes divided by the posterior cephalic border and the protopygidium consequently is distinctly defined. This practice cannot be followed exactly in *Menoparia* (Fig. 86), for example. Accordingly, while early and late protaspides can be distinguished, no one morphological character can be used in all trilobites to subdivide the period (25, p. 350). BEECHER's term paraprotaspid stage has not been generally adopted. Substages of the metaprotaspid stage based on number of axial segments in the protopygidium (19, p. 584) have been proposed.

In the smallest protaspides of trilobites having compound eye lobes in the holaspid period, the eye lobe is recognizable by the relatively small, raised, palpebral lobe, connected by an eye ridge to the frontal axial lobe (Fig. 88*A-E*, 90). In protaspides like those of *Welleraspis* (Fig. 90) or *Sao* (Fig. 88*A-E*) the frontal axial lobe widens forward and is extended along the anterolateral margin of the shield by a sutural ridge. In protaspides such as belong to *Pseudocybele* (Fig. 89), *Acanthoparypha* (Figs. 91*A*), or *Flexicalymene* (Fig. 92) the palpebral lobe is connected to the anterior cephalic border by a sutural ridge, and in *Pseudocybele* the eye ridge appears later in ontogeny. In protaspides of *Paradoxides* (Fig. 93*A,B*) the eye lobe is exceptionally long and in those of *Menoparia* (Figs. 86*A,B*) the palpebral lobe is not raised. Probably in all protaspides there is a narrow doublure and a relatively large hypostoma (Fig. 88*E*, 92*B*). Wherever preservation is good enough (usually in late protaspid stages), it has been shown that facial sutures are present, as well as rostral, hypostomal, and probably connective sutures (Figs. 86*C-E*, 92, 94*B,C*, 95). Characteristically spines arise from the borders of protaspides: fixigenal, librigenal, and additional spines from the lateral and anterolateral cephalic borders; hypostomal from posterolateral borders of the hypostoma, and pygidial from the protopygidial borders. The external surface may be pitted, tuberculate, granulate, or spinose.

TYPES OF PROTASPIDES

Generalities just stated seem to apply to at least the later protaspid stages of all trilobites except agnostids and olenellids. The smallest known specimens of the latter group are about 1 mm. in length (STØRMER, 24, figs. 4, 5*a-e*), and silicified material described by PALMER (12) includes speci-

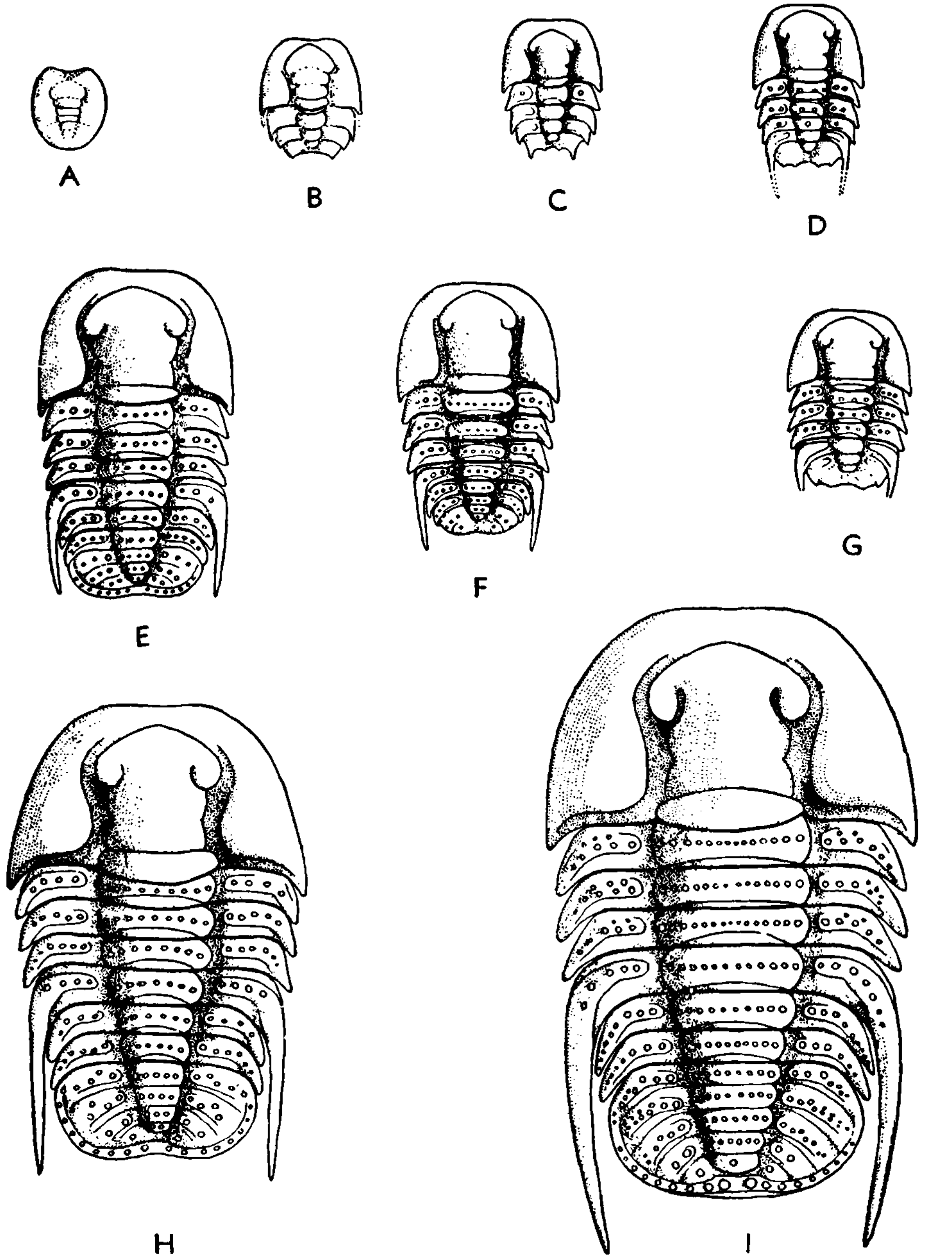


FIG. 87. Ontogenetic stages of *Shumardia pusilla* (SARS), L.Ord.(Tremadoc.), Eng.; *A*, protaspis, ×40; *B*, meraspis, "degree" 0, ×40; *C-G*, meraspis, "degrees" 1-5, ×30; *H*, holaspis, ×30; *I*, larger holaspis with additional segment in pygidium,. ×20 (25*).

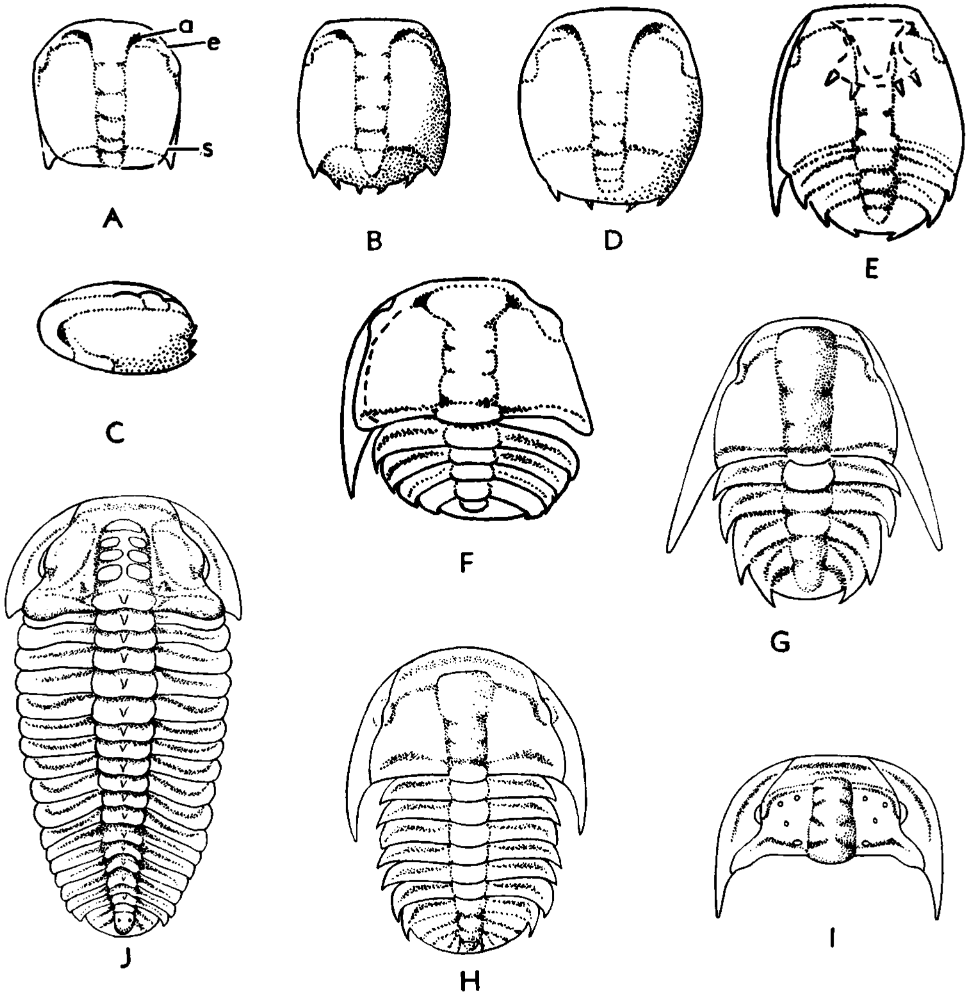


FIG. 88. Ontogenetic stages of *Sao hirsuta* BARRANDE, M.Cam., Bohemia; *A*, protaspis with librigena (*a*, anterior pit; *e*, eye ridge; *s*, suture), ×30; *B,C*, protaspis lacking librigenae, dorsal and anterolateral views, ×30; *D*, protaspis, ×30; *E*, protaspis with left librigena and hypostoma shown by dashed outline, ×30; *F*, "degree" 0 with left librigena, dashed line showing inner edge of doublure, ×30; *G*, "degree" 1, ×30; *H*, "degree" 6, ×15; *I*, "degree" 12 cephalon, ×7; *J*, holaspid exoskeleton, ×2 (41n).

mens (cephala of early meraspid "degrees") of this size and considerably smaller. STØRMER (24, p. 61) considered that the original of his figures 4 and 5e was probably an early meraspid cephalon. My reinvestigation of FORD's (6) original material of *Elliptocephala asaphoides* shows no trace of the "rudimentary thorax and pygidium" (6, p. 268, Pl. 4, fig. 2; cf. 46, fig. 3), the smallest specimens being meraspid cephala. This evidence combines to cast grave doubts on the view that any of the early olenellid stages so far described include the protopygidium within the unjointed shield, allowing them to be regarded as protaspides.

It seems possible that the exoskeleton of the protaspis is either so tiny that it has not yet been found, or was not mineralized and hence not preserved. Figure 96, emended from WALCOTT's drawings (28), shows present knowledge of early "degrees" in the ontogeny of *Paedeumias yorkense*. In the smallest specimen (Fig. 96*A*) tiny spines are present on the anterolateral cephalic border; long metagenal ("intergenal") spines, and 5 axial rings are preserved in the thorax.

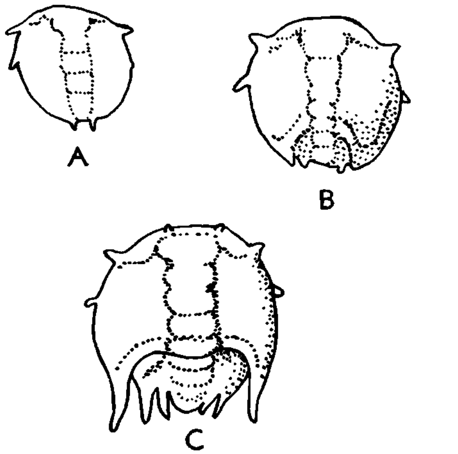


FIG. 89. Protaspides of *Pseudocybele nasuta* Ross, L.Ord.(U.Canad.), W.USA(Utah); *A-C*, growth series, ×30 (19).

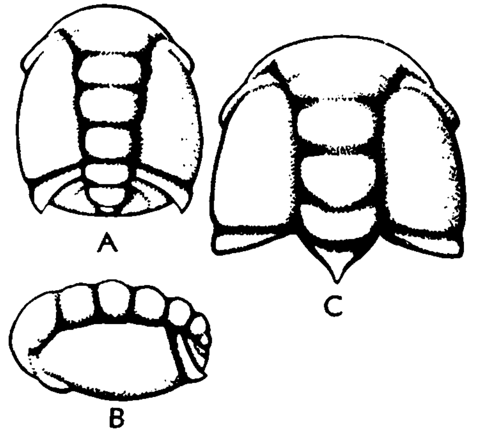


FIG. 90. Ontogenetic stages of *Welleraspis swartzi* (TASCH), U.Cam.(Dresbach.), E.USA(Pennsylvania); *A,B*, protaspis lacking librigenae, dorsal, lateral, ×60; *C*, meraspid cranidium, ×60 (39*).

The original of Figure 96*B* has short genal spines present outside the metagenal, and one can see 9 thoracic segments, including the 3rd with its long pleural spine. In the largest specimen (Fig. 96*C*) the anterior cephalic spines are lost, and while 12 thoracic segments can be counted, the pygidium is not preserved. The earliest known developmental "degrees" of this and possibly other olenellids, then, seem to be meraspides, and their peculiar features include the long eye lobes, lack of facial sutures (but rostral plate, relatively large hypostoma, and rostral suture present in stages corresponding to those shown in Figure 96), broad *(tr.)* genal region outside of the eye lobes, and long frontal area. The short genal and long metagenal spines have been observed frequently, but PALMER's investigations are the first to reveal the stage (Fig. 96*B*) in which anterior border spines also are present.

In meraspides of *Paedeumias yorkense* there is seemingly no trace of preocular ridges, and the postocular ridges (connecting the posterior end of the eye lobes to the base of the metagenal spine) are only faintly developed. In *Elliptocephala asaphoides* the postocular ridge is prominently displayed in the smallest stages known, and retained in the holaspis. It has been claimed by HUPÉ (8) and earlier authors that the postocular ridges follow the course of the fused, posterior section of the facial sutures. Recently HUPÉ (8) has also claimed that the preocular ridges, which in some genera run to points on the posterior border just inside the base of the genal spines, follow the course of the fused anterior section. Known olenellid ontogenies offer no support for these views, nor for the suggestion of STØRMER (24, p. 138) that the postocular ridges follow intersegmental boundaries. STUBBLEFIELD (26, p. 421) considered that the postocular ridges may be vestiges of a larval structure, and such they seem to be in *E. asaphoides*, but their significance is not known.

Knowledge of the ontogeny of *Paradoxides pinus?* begins with late protaspid stages (Fig. 93*A,B*). Smaller specimens have been described (30, p. 46, Pl. 4, figs. 1, 2; 24, p. 73, text-fig. 7a), but I think it likely that the lateral and posterior portions of these strongly convex shields are concealed in matrix and that there are spine-bearing librigenae, fixigenal spines, and perhaps pleural spines on margins of a tiny protopygidium. In other words, I consider that they are essentially like Figure 93*A,B*, but smaller and with fewer segments in the protopygidium, and not "anaprotaspides" as STØRMER claimed. Early meraspid "degrees" of paradoxidids show considerable similarity to corresponding olenellid "degrees," particularly in the length of the eye lobes and presence of fixigenal and metagenal spines, respectively. Especially distinctive of paradoxidids are the dorsal facial sutures.

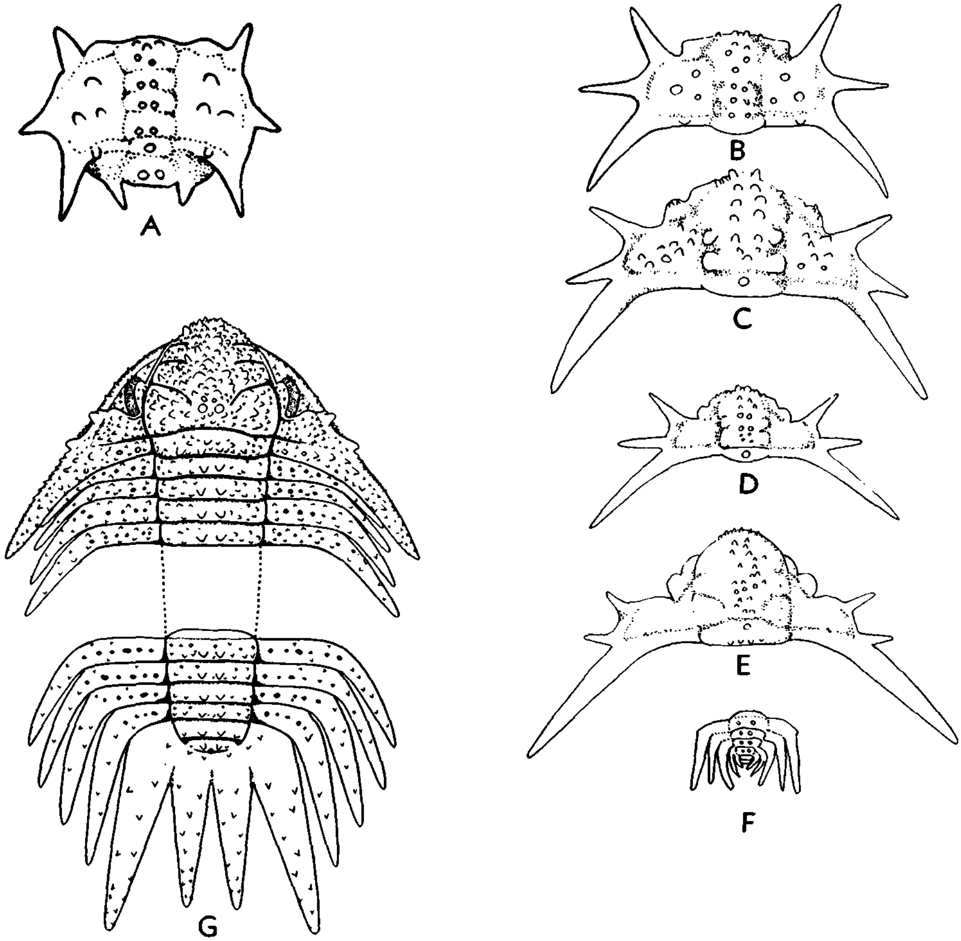


FIG. 91. Ontogenetic stages of *Acanthoparypha perforata* WHITTINGTON & EVITT, M.Ord., E.USA(Virginia); *A*, protaspis, ×30; *B-E*, series of cranidia showing development, ×20, ×20, ×10, ×12; *F*, transitory pygidium, ×10; *G*, incomplete exoskeleton, ×5 (*A-F*, 41n; G, 37*).

Figure 88 shows ontogeny of *Sao*, based on previous work (1, 22) and my own studies (36). The earliest stage (Fig. 88*A*) shows a length *(sag.)* of 0.6 mm., with the cephalic axis divided into 5 rings decreasing in length posteriorly, and the protopygidial axis short and low. Pleural regions are faintly divided at the posterior margin of the cephalon. Eye lobes are close to the margin of cephalon, eye ridges curve in to the axial furrow just behind anterior pits, and a sutural ridge is adjacent to the extremity of the frontal glabellar lobe. Librigenae are narrow, posteriorly extended into short librigenal spines and defined by sutures running a short distance inside anterior and lateral cephalic margins. The dorsal part of the librigenae is steeply inclined, so that in Figure 88*A* only the posterolateral portion is visible. The protaspis increases to a length *(sag.)* of about 1 mm. (Figs. 88*B-E*) and is strongly convex. The posterior cephalic border becomes distinct, the number of axial rings in the protopygidium increases to 4, and faint interpleural grooves appear. The relatively large, spinose hypostoma is known in specimens having a length *(sag.)* of 0.85 to 1 mm. At a length *(sag.)* of 1 mm., and slightly larger (Fig. 88*F*) the transverse joint between the cephalon and transitory pygidium becomes clear.

Protaspides of *Olenus* (24; 36, p. 467-468) range in size from a length of *(sag.)* 0.33 to 0.52 mm. They are like those of *Sao* ex-

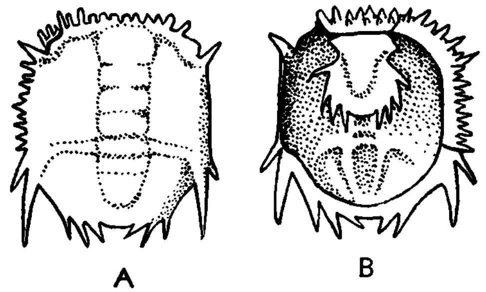


FIG. 92. Protaspis of *Flexicalymene senaria* (CONRAD), M.Ord., E.USA(Virginia); *A,B,* dorsal and ventral views, left librigena, rostral plate, and hypostoma present, ×30 (41n).

cept that fixigenal spines occur. These fixigenal spines are reduced and lost in early meraspid "degrees," as they are in *Leptoplastoides* (Fig. 97).

The protaspis of *Welleraspis* (Fig. 90), 0.40 mm. in length *(sag.),* is of a similar type, subhemispherical in form, and lacking librigenae. The latter must be narrow *(tr.),* the dorsal portion lying in the vertical plane. How readily they would be concealed in such specimens when flattened in shale is evident.

Protaspides of post-Cambrian trilobites exhibit a variety of types. That of *Menoparia* (Fig. 86*A-E,* lacking librigenae and hypostoma) is unusual in its subspherical form. In the smaller figured example only the anterior portion of the axis is outlined by furrows, but the suture is present, as well as anterolateral, mediolateral, and posterior pairs of spines. The larger specimen has the axis completely outlined, and the occipital

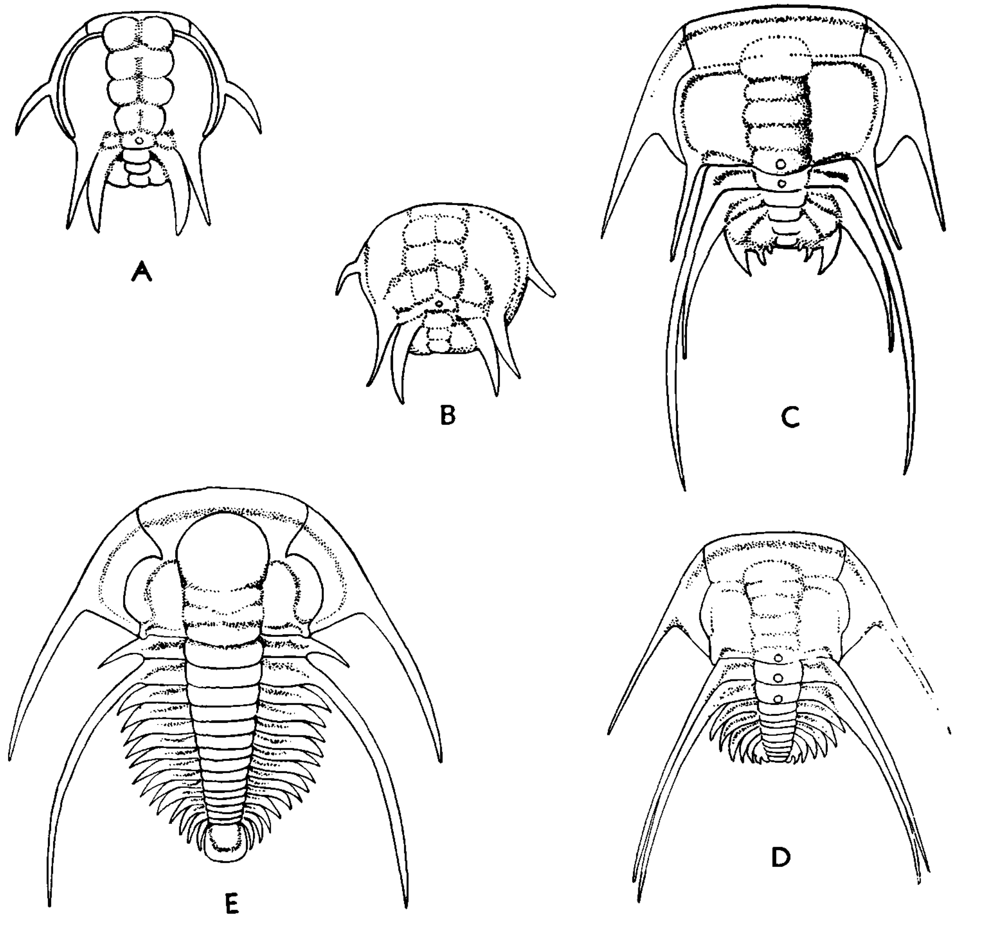


FIG. 93. Ontogenetic stages of *?Paradoxides pinus* HOLM, M.Cam., Swed.; *A,B,* protaspides (*A,* reconstr.), ×20; *C-E,* meraspid "degree" 1, ×20; "degree" 4, ×10, "degree" 15, ×5.4 (30).

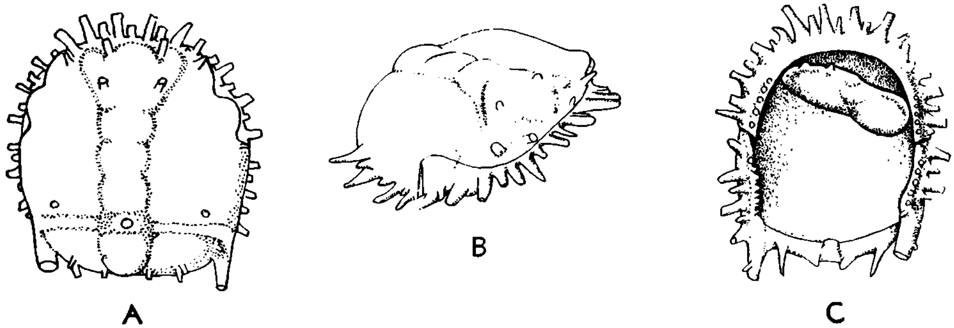


FIG. 94. Phacopid protaspis, L.Dev., E.USA(N.Y.); *A-C*, dorsal, anterolateral, ventral views (*C* with immature ostracode carapace adhering to specimen), ×30 (41n; 34*).

ring and 2 protopygidial rings are defined (Fig. 86*D*). The posterior pair of spines is on the posterior border of the protopygidium. Librigenae, bearing a librigenal spine, are known in early meraspid cephala (Fig. 86*F*).

The protaspis of the bathyurid *Licnocephala* (Fig. 98), recently described by Ross (21), is approximately 0.8 mm. in length *(sag.)*, and lacks librigenae. The axial region is divided into occipital ring, glabella with 3 rings of similar length and a longer anterior ring that narrows forward. There is a broad *(sag.)* preglabellar area, showing a striking difference from such Cambrian protaspides as those of *Sao* (Fig. 88*A-E*) and *Welleraspis* (Fig. 90).

The only known lichid protaspis (35; Fig. 95, length, *sag.*, 0.94 mm.) represents a late stage in the protaspid period. The 4 paired spines and median occipital spine suggest the typical 5 rings of the well-defined, parallel-sided glabella and occipital ring. The prominent eye lobes are well inside the borders of the genal regions, and facial sutures are present. There is a prominent librigenal spine and 4 pairs of spines on the protopygidium.

The protaspis of *Shumardia* (Fig. 87*A*) is extremely small (length, *sag.*, 0.24 mm.; length at "degree" 0, 0.31 mm.), strongly convex, and unusual in that the glabella is divided into only 4 segments.

Protaspides of post-Cambrian proparian trilobites show considerable resemblance to each other (Figs. 89, 91*A*, 92, 94, 99*A*). Their length *(sag.)* ranges from about 0.25 to 0.95 mm., only those of *Rossaspis* (20) and *Pseudocybele* (Figs. 89*A*) including examples less than 0.5 mm. long. These latter tiny shields are subcircular in outline, strongly convex, with the axis in larger specimens divided into 5 rings (of which the anterior is longest). The eye lobes are close to the anterolateral margins, dorsal sutures are present, and their form and the presence of shallow anterior pits suggests that librigenae, rostral plate, and hypostoma may have been present. There are 3 pairs of border spines, the posterior pair being fixigenals. The tiny region between these latter, which includes the tip of the axis, is the protopygidium, which may bear a pair of border spines *(Rossaspis)*.

The larger protaspides of these and other genera have the pleural regions subdivided so that cephalon and protopygidium are distinct. The well-defined glabella and occipital ring comprise 5 segments, the anterior markedly longer and wider, the occipital shorter *(sag.)* and, in some genera, narrower *(tr.)*, than the remainder. The posterior cephalic border runs out into the base of the fixigenal spine, and there may be spines of similar size on the lateral and anterolateral borders (Fig. 91*A*).

The protaspides of *Flexicalymene* (Fig. 92) and phacopids (Figs. 94, 99*A*) have a row of small spines around the anterior and lateral cephalic margins. The eye lobes are situated on the anterolateral part of the genal regions, close to the border, and the sutures are fully developed. A few tiny facets are probably present on the visual surface of the eyes. If present, the eye ridges run into the most anterior part of the glabella. The hypostoma in *Flexicalymene* (Fig. 92*B*) is relatively large and spinose. The small, down-bent protopygidium has a clearly defined axis and border bearing pairs of spines. Doublures of the cephalon and protopygidium are narrow and curled under posteriorly. Paired spines on the axis and symmetrically arranged spines on the genal regions commonly occur, and there may also be granulation or pitting of the external surface.

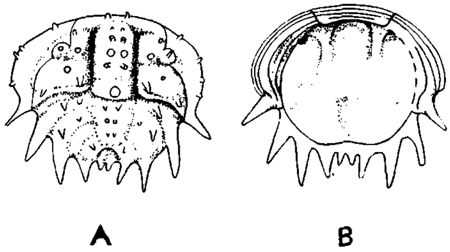


FIG. 95. Lichid protaspis, L.Dev., E.USA(N.Y.); *A,B*, dorsal, ventral, ×20 (35*).

MERASPID PERIOD

This period of trilobite larval development begins at "degree" 0 with appearance of the first transverse joint in the exoskeleton, separating the cephalon from what is now termed the **transitory pygidium.** As thoracic segments become fully formed in the anterior part of the transitory pygidium new joints appear between them. Successive "degrees" of the meraspid period are numbered to correspond with the number of segments released to form the thorax. For each species there is a constant number of these segments, and after this is reached no more are freed from the pygidium. The final "degree" of the meraspid period is here considered to be that in which there is one less than the complete number of freely articulating thoracic segments.

For the study of the meraspid period a series of complete specimens is necessary, such material being found in some shales, siltstones and fine-grained sandstones (1, 16, 25, 30). These fossils are disadvantageous for study in being compressed and some of them otherwise distorted, but they may show a progressively increased number of segments up to the holaspid number. The much-better-preserved silicified exoskeletons obtained by etching some limestones with acid almost invariably consist of dissociated parts, and consequently "degrees" of the meraspid period for all parts of the exoskeleton cannot be ascertained.

MANNER AND AMOUNT OF GROWTH

During the meraspid period the length *(sag.)* of the trilobite is augmented to some 6 to 12 times that of the largest protaspis. This increase is achieved by a series of larval molts (instars), but how many is a matter of debate. In *Leptoplastoides* (Fig. 97; 16, Table I; 31) and *Onnia* (Fig. 100; 32, Table I) the average size increases at each "degree," and more rapidly in *Onnia* than in *Leptoplastoides*. Size of individuals belonging in any one "degree" varies, suggesting that more than a single molt may occur within each "degree." In *Leptoplastoides* no example of "degree" 8 has been found, and "degrees" 7 and 9 are almost the same in length. This similarity in length of successive "degrees" may signify that more than one segment was added to the thorax during certain molts. In this connection, the "degree" 0 exoskeleton of *Ceraurinella typa* (Fig. 101) is instructive, for the transitory pygidium is found to have its maximum length (*ca.* 2 mm.) and to contain in a single unit the 11 segments destined to form the thorax, these lying in front of the part that is to become the true pygidium. The other transitory pygidia observed (37) have only 4, 3, and 1 segments, respectively, in front of the true pygidium and are 1.05 to 0.77 mm. in length. It seems possible that in this species perhaps 7 segments were released simultaneously into the thorax. These observations indicate that the count of free thoracic segments may not necessarily correspond with growth as measured by increase of length.

TRANSITORY PYGIDIUM

As pointed out by various authors, the transitory pygidium comprises a relatively longer part of the early meraspid exoskeleton than the pygidium in the holaspid exoskeleton. Examples of these proportions, contrasting early meraspides with late holaspides, are: *Leptoplastoides,* 33 per cent to 7 per cent (16); *Shumardia,* 44 per cent to 23 per cent (25, p. 268); *Onnia,* 48 per cent to 23 per cent (32); *Ceraurinella,* 63 per cent to 14 per cent (37). In *Dalmanitina* (1, Pl. 26) there is scarcely any change, the pro-

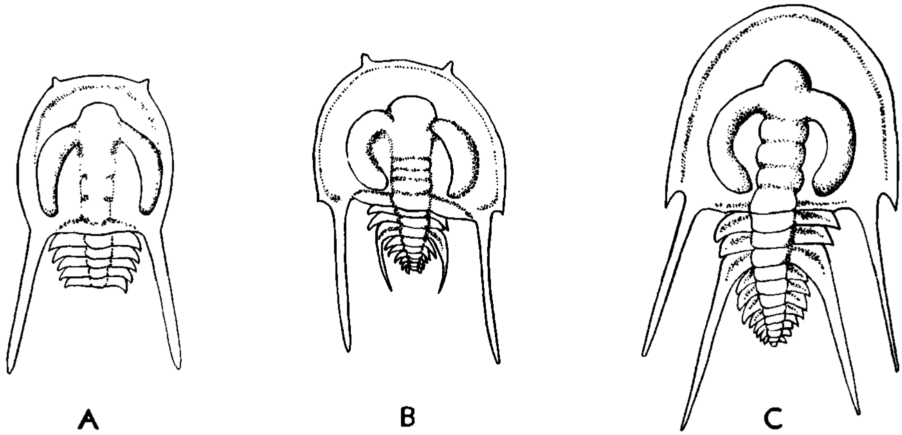


FIG. 96. Meraspid "degrees" of *Paedeumias yorkense* RESSER & HOWELL, L.Cam., E.USA(Pennsylvania); *A*, specimen with incomplete thorax showing 5 segments, ×20; *B*, specimen with 9 thoracic segments; pygidium not preserved, ×10; *C*, specimen with 12 thoracic segments, pygidium lacking, ×6.6 (WALCOTT, ref. 28, pl. 32, fig. 2, 5, 6, emended in accordance with advice of A. R. PALMER).

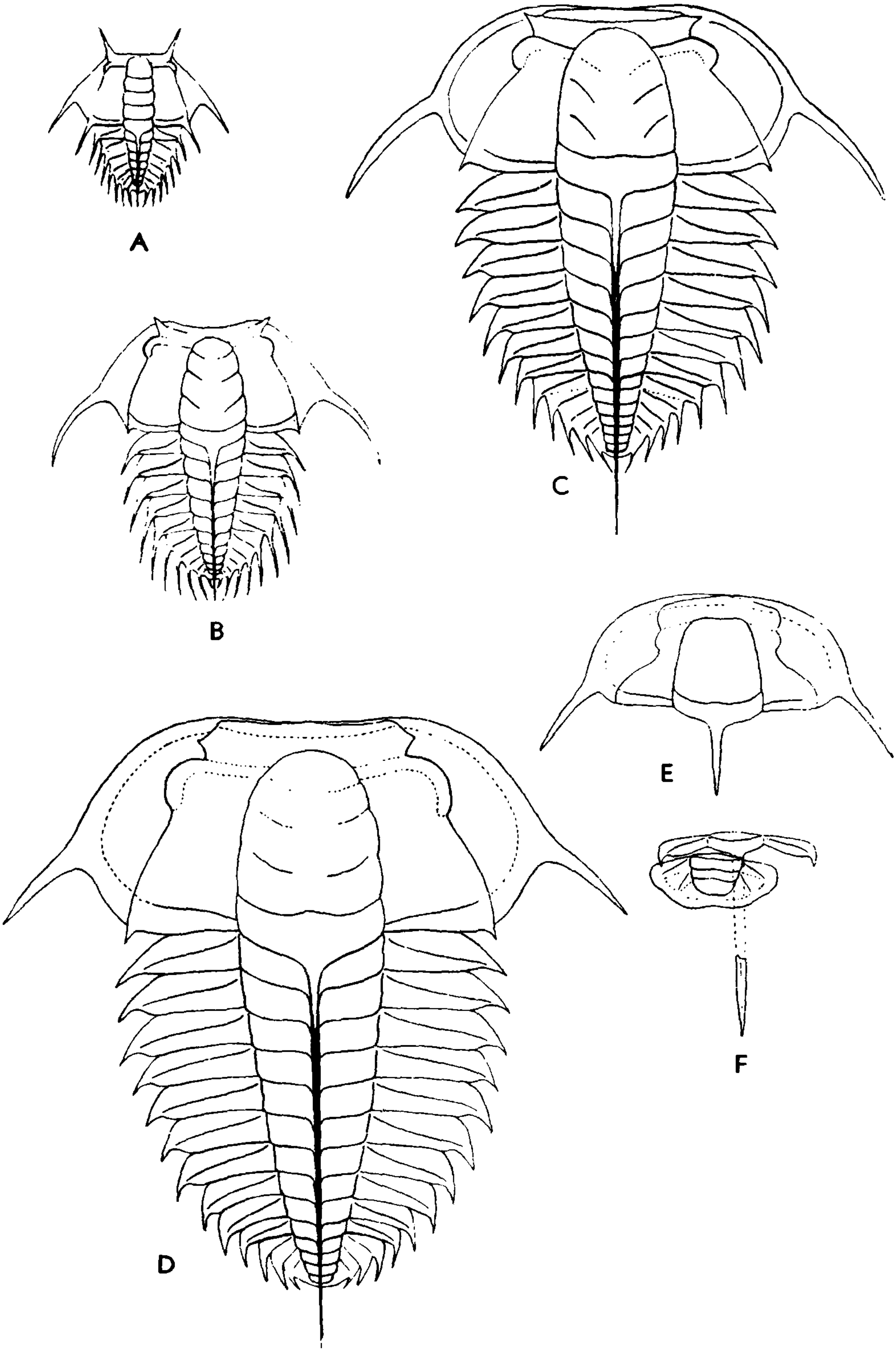
portion being about 22 per cent at "degree" 0 and in a large holaspis. As might be anticipated, the length *(sag.)* of the transitory pygidium usually increases in successive "degrees" (e.g., in *Leptoplastoides,* 16, and *Ceraurus,* 5). An exception is the transitory pygidium of *Ceraurinella,* which decreases in size (37).

Evidence of segmentation in the transitory pygidium may be found in the form of axial rings, median or paired spines on the axis, pleural furrows, pleural bands and spines on these bands, pleural spines at the margins, or interpleural grooves. Indications of new segments may appear first in the axial region or in the pleural region, or simultaneously in both regions (5, p. 44). The work of BARRANDE on *Sao* (1) and STUBBLEFIELD on *Shumardia* (25) shows that segments may be added to the transitory pygidium during individual "degrees." These observations may be taken as indicating growth, and the occurrence of more than one molt within each "degree." The anterior segments of the transitory pygidium are the most fully formed, that is, are most like the thoracic segments. This is true of both dorsal and ventral surfaces of the exoskeleton. The ventral surface of *Ceraurus* (Fig. 102), for example, shows the articulating half-ring, and doublure of the axial ring in front of it, growing as a single fold, and both this fold and the apodemes are progressively more complete anteriorly. The suture that develops to release new segments into the thorax divides the fold into its component parts and distally follows the interpleural grooves.

In the transitory pygidium axial and pleural spines show an increase in size from the most posterior to the anterior segments, and this size gradation is continued in the thorax. Exceptionally long median axial or pleural spines appear abruptly in a posterior position and after moving forward are released into the thorax (Fig. 87; also *Dimeropyge* and *Mesotaphraspis,* 37; *Menoparia,* 21). The change in position of these spines during growth, as well as the development of articulating structures, pleural subdivisions, and spines, are all consistent with the view that new somites are added by growth to the anterior border of the hindmost somite (25), and do not suggest that postcephalic segments were formed at the anterior margin of the "pygidium" and propagated anteriorly and posteriorly, as some have believed. In most species the large

(See facing page)

FIG. 97. Ontogenetic stages of *Leptoplastoides salteri* (CALLAWAY), L.Ord.(Tremadoc.), Eng.; *A-D,* meraspid "degrees" 1, 5, 7, 10, ×20; *E,F,* holaspid cephalon, last thoracic segment, and pygidium, ×1.3 (40*).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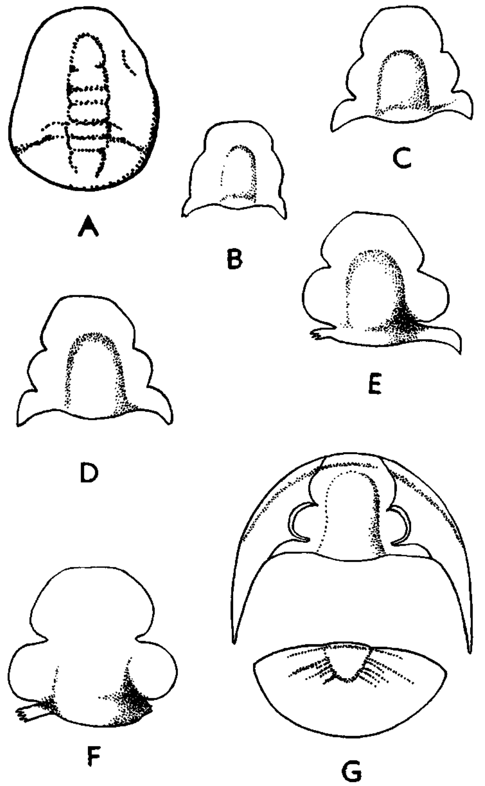

FIG. 98. Ontogentic stages of *Licnocephala cavigladius* (HINTZE), L.Ord., W.USA(Utah); *A*, protaspis lacking librigenae, ×30 (21); *B-F*, series of cranidia, ×20, ×14, ×14, ×7, ×7 (21); *G*, holaspid cephalon and pygidium, ×2 (38).

pleural spines that appear during the meraspid period are retained in the holaspis, but in *Paradoxides pinus?* (Fig. 93*C-E*) that on the 1st thoracic segment is reduced early in the meraspid period and that on the 2nd is also reduced by the end of this period (30, Pl. 5, fig. 10).

CEPHALON

During the meraspid period changes take place in the cephalon, both in the form and relative proportions of individual parts. The changes may be summarized as follows.

The glabella in many genera is widest and most convex anteriorly at "degree" 0. In *Onnia* (Fig. 100), *Dalmanitina* (Fig. 99), and, to a less extent, *Paradoxides* (Fig. 93), the initial anterior expansion is progressively augmented; TEMPLE (27) has shown that the frontal lobe in *Dalmanitina* grows at a rate 4 times that of any of the lobes behind it. On the other hand, in late meraspid "degrees" of such genera as *Sao* (Fig. 88), *Leptoplastoides* (Fig. 97), *Welleraspis* (15), *Acanthoparypha* (Fig. 91), and *Flexicalymene* (33), the widest and most convex part of the glabella has become the posterior part.

Licnocephala (Fig. 98) illustrates the development of a different type of glabella which is not expanded anteriorly at any time, and remains low and poorly defined (21).

Along with changes in outline and convexity of the glabella, the glabellar furrows change. In most protaspides the glabella is divided into 5 rings (4 in *Shumardia*, Fig. 87*A*, none in *Menoparia*, Fig. 86*A,B*) and there is a median longitudinal furrow in *Paradoxides* (Fig. 93*A,B*). This median furrow, and the median part of the anterior 3 (i.e., not the occipital) ring furrows, usually disappear in the early meraspid "degrees," while the lateral parts of the ring furrows deepen. This deepening may be accompanied by the development of lateral glabellar lobes. Development of these lobes is shown by *Sao* (Fig. 88) and is striking, for example, in odontopleurids (Fig. 103). In remopleuridids lateral glabellar furrows are not developed until the meraspid "degrees," whereas in *Isotelus* (33) and *Licnocephala* (Fig. 98) lateral furrows present in early meraspid "degrees" and ring furrows of the metaprotaspis, respectively, are later lost. Of the 4 ring furrows of the protaspid

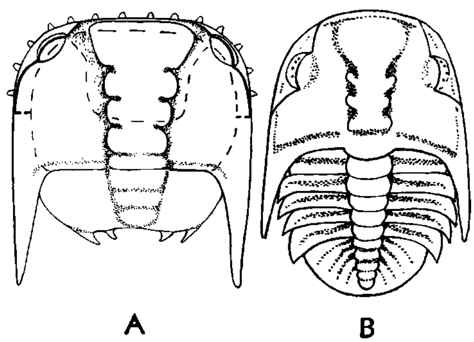

FIG. 99. Ontogenetic stages of *Dalmanitina socialis* (BARRANDE), M.Ord.-U.Ord., Bohemia; *A*, protaspis with librigenae (reconstr.), dashed lines showing inner margin of doublure, outline of hypostoma, and posterior sections of sutures crossing doublure, ×30 (34*); *B*, meraspid "degree" 5, ×15 (41n).

glabella, the posterior (occipital) is most persistent (though even the occipital furrow is lost in *Licnocephala*), and those adjacent to it develop into the deepest lateral furrows. *Paradoxides* (Fig. 93) is exceptional in retaining 2 complete ring furrows in front of the occipital in the holaspis. The deep lateral parts of these occipital and lateral glabellar furrows form ventral projections, the apodemes, to which it is believed the appendages are linked by muscles. In trilobites in which lateral glabellar furrows are lost, paired muscle scars, seemingly in the position of these furrows, are developed, e.g., in asaphids.

Genal regions and the frontal area also show some increase in convexity during the meraspid period, associated with an increase in convexity of the cephalon as a whole. The genal region, and particularly the inner, posterior portion, may show particularly marked inflation (Fig. 103). The frontal area, at first short *(sag., exsag.)* and steeply sloping, may become relatively longer, the glabella becoming relatively shorter, and the anterior border defined. This change is well shown by *Sao* (Fig. 88), *Leptoplastoides* (Fig. 97), *Paradoxides* (Fig. 93), and *Welleraspis* (15). In other trilobites the frontal area shows little change in relative size, for example, *Shumardia* (Fig. 87), *Acanthoparypha* (Fig. 91), *Dalmanitina* (Fig. 99; 34). In trinucleids (Fig. 100) rapid increase in width of the fringe occurs in early meraspid "degrees."

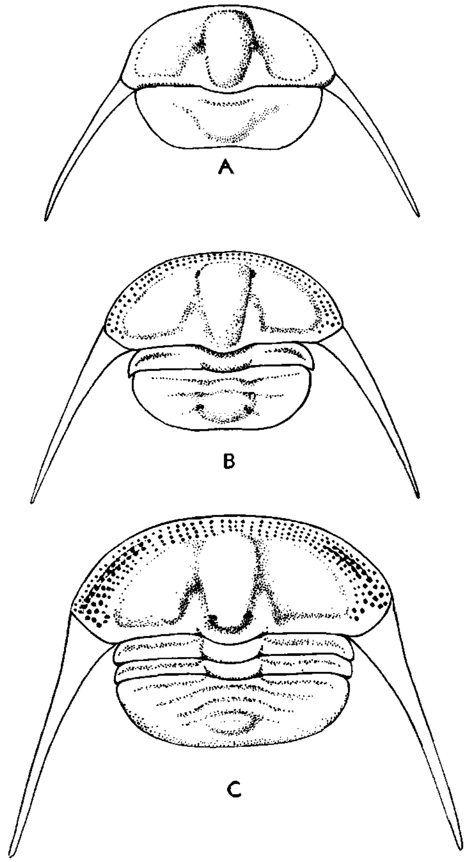

FIG. 100. Meraspid "degrees" of *Onnia ornata* (STERNBERG), M.Ord.-U.Ord., Bohemia; *A-C*, "degrees" 0 (×22), 1 (×10), 2 (×12.5) (41n).

EYE LOBES AND FACIAL SUTURES

In trilobites with compound eyes in the holaspid period the eye lobes are present on the dorsal surface of the protaspis near the anterolateral margin. During the meraspid period the lobes move inward and backward, number of facets on the eye surfaces increases, and the palpebral furrows and rims develop. The eye ridges, which run from eye lobe to axial furrow opposite the anterior glabellar lobe, pivot with movement of the eye lobes and may be reduced in prominence or lost.

During the meraspid period changes that take place in the course of the dorsal sections of the facial sutures are associated in part with change in position of the eye lobes. In *Leptoplastoides* (Fig. 97), *Sao* (Fig. 88), and *Welleraspis* (Fig. 90; 15), these changes do not affect the points where posterior sections of the sutures cross the cephalic margin and doublure. In *Acanthoparypha* (Fig. 91), *Sphaerexochus* (37), and *Rossaspis* (20), these points migrate backward considerably. Claim has been made that during the meraspid period of *Peltura scarabaeoides* (14) and other olenids (24, p. 88) the posterior sections of the dorsal sutures at first cut the lateral cephalic margins and later the posterior margins, so that the trilobite changes from proparian to opisthoparian during ontogeny. STØRMER (24, p. 88) has pointed out, however, that the development of facial sutures in the olenids he studied was not clear. In *Sao* and *Welleraspis,* the protaspides and meraspides are opisthoparian, the posterior segments of the sutures in the protaspis running back close

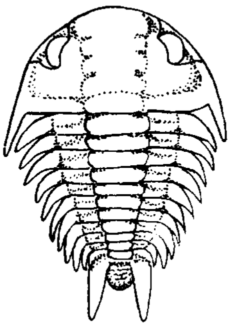

FIG. 101. Meraspid stage of *Ceraurinella typa* B.N. COOPER, M.Ord., E.USA(Virginia); "degree" 0, ×20 (37).

to the lateral margins before curving inward across the base of the librigenal spines. In this position, on the almost vertically sloping flank of the genae, the sutures readily may be concealed. Possibly they have the same course in late protaspides and early meraspides of olenids, but only a reinvestigation will confirm or deny this suggestion. In view of the theoretical importance that has been attributed to the supposed change from a proparian to opisthoparian condition in olenids (8, 26), such an investigation would be of great interest.

HYPOSTOMA

The development of the hypostoma is not known in relation to "degrees" of the meraspid period (37). Small cheirurid hypostomata have a prominent, crescentic, posterior lobe of the middle body. As growth proceeds, the posterior lobe decreases in size at expense of the anterior. Also, the shoulder becomes more prominent and relatively more anterior in position. To judge by known examples of the protaspid hypostoma (Figs. 88*E*, 92*B*) a reduction in relative size may be inferred to occur during the meraspid period.

GENAL AND OTHER LATERAL CEPHALIC SPINES

Characteristic of known protaspides are the stout spines at or near the genal angle, and spines of almost the same size may be present on the lateral and anterolateral cephalic borders. In *Flexicalymene* (Fig. 92) and phacopid protaspides (Fig. 94), many additional smaller spines are observed on the cephalic border. During the meraspid period the spine at or near the genal angles (genal spines) is retained and may be enlarged. It may be librigenal (*Sao,* Fig. 88; *Leptoplastoides,* Fig. 97; lichid, Fig. 95) or fixigenal (*Acanthoparypha,* Figs. 91, 106; *Dalmanitina,* Fig. 99). In genera such as *Flexicalymene* (33) and *Sphaerexochus* (37), the stout fixigenal spines are reduced during the meraspid period. The same is true of *Leptoplastoides* (Fig. 97) and *Paradoxides* (Fig. 93), in which reduction is rapid. In *Paradoxides,* as in some other genera, the librigenal spines are retained, increasing in size. In early meraspid "degrees" of olenellids (Fig. 96), a pair of stout metagenal ("intergenal") spines occurs and in some genera small spines are seen also on the anterior cephalic borders. At slightly larger size, before the anterior spines are lost, small spines (genal) begin to grow at the genal angles, just outside the metagenal spines. In considerably later "degrees" the metagenals are rapidly reduced, while the genals increase in size to become the main cephalic spines. This increase of genal spines and diminution of metagenal spines are not unlike the increase of librigenals and reduction of fixigenals in *Paradoxides, Leptoplastoides,* and other genera. Because of lack of facial sutures in olenellids, however, it cannot be shown that these differently designated spines are homologous.

OCCIPITAL SPINES

A median occipital tubercle is commonly present in protaspides and this is retained

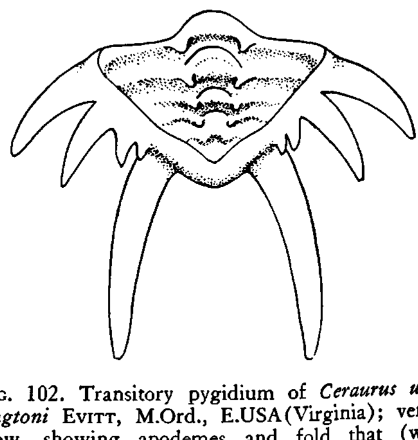

FIG. 102. Transitory pygidium of *Ceraurus whittingtoni* EVITT, M.Ord., E.USA(Virginia); ventral view, showing apodemes and fold that (when divided) forms articulating half-ring and doublure of axial ring, ×30 (41n).

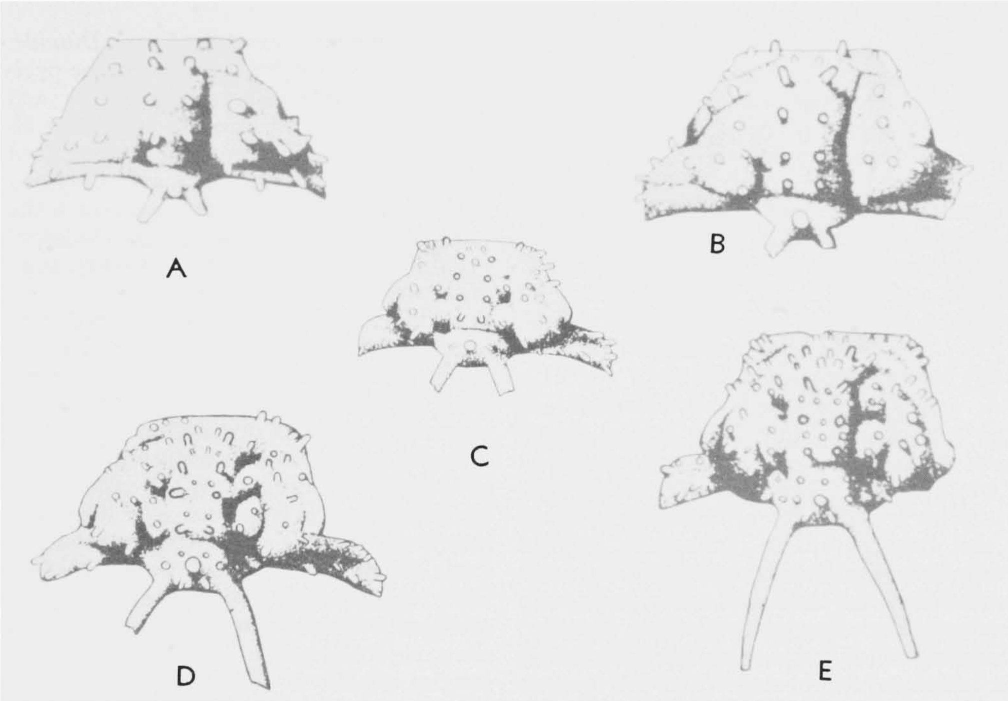

FIG. 103. Cranidia of *Diacanthaspis cooperi* WHITTINGTON, M.Ord., E.USA(Virginia); *A-E,* series showing growth stages, *A,B,* ×50, C-E, ×25 (33*).

through the meraspid period and into the holaspid. The tubercle may be relatively reduced in size or lengthen rapidly into a median occipital spine, e.g., in *Welleraspis* (15) and *Holia* (37). Similarly, paired occipital tubercles or short spines may increase in size and length into the holaspid period, e.g., in *Diacanthaspis* (Fig. 103).

EXTERNAL SURFACE

Short spines, tubercles, granules, and pits occur on the external surface of protaspides, including the hypostomal borders. A paired arrangement is common, especially on the axis. The spines and tubercles generally are reduced in relative size as the meraspid period progresses, and may disappear altogether. Among holaspides provided with spines, tubercles, or granules on the outer surface, growth during the meraspid period is characterized by an increase in number of these elements and loss or masking of their paired arrangement.

AGNOSTID TRILOBITES

The ontogeny of agnostid trilobites commonly is neglected in discussions of trilobite larval development, and this is true despite early observations by BARRANDE (1; Figs. 104, 105). The smallest known agnostid specimens seem to be meraspides representing "degree" 0; their length *(sag.)* ranges from 1 mm. to a little more than 2 mm. Ring furrows and interpleural grooves appear in the transitory pygidium, and 2 segments are released successively into the thorax. The tendency seems to be for furrows on the cephalon and glabella to deepen as size increases. STUBBLEFIELD (25, p. 366) refers to a similar suite of specimens of Early Ordovician (Tremadocian) age, and points out that "unless the process for the development of new segments in the Agnostidae is entirely different from that of all other Arthropoda," orientation of the agnostid pygidium must be as depicted by BARRANDE and others, and not as advocated by WAHLENBERG, DALMAN, and RAYMOND.

HOLASPID PERIOD

The view of RAW (16, p. 226) that cessation in the addition of segments to the thorax forms a convenient break in the de-

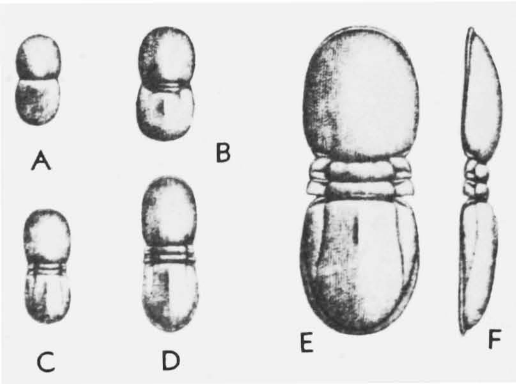

FIG. 104. Ontogenetic stages of *Phalacroma bibullatum* (BARRANDE), Cam., Bohemia; *A-C*, meraspid "degrees" 0 (×4), 0 (×3), 1 (×4); *D*, holaspis, ×3; *E,F*, holaspis, dorsal, lateral, ×6 (all 1*).

velopment of trilobites is accepted here, and, accordingly, the holaspid period is regarded as beginning when the last-formed segment (making a full complement for the species) is added to the thorax. When this period begins, the term "pygidium" is applied to the posterior shield of fused segments. The holaspid period extends to death of the individual.

No evidence is found to support RAW's suggestion (16, p. 226) that segments are added to the thorax of some trilobites throughout life; on the contrary, each species has its characteristic complement of thoracic segments. Most holaspides have fewer than 20 thoracic segments, but some have 25, the Devonian *Harpes* has 29, and one Upper Cambrian species of *Menomonia* is reported to have 42.

STUBBLEFIELD (25) has suggested that in view of the literal meaning of "holaspis" (complete shield), this term should be applied only to trilobite individuals in which complete postcephalic segmentation has been attained. Since in *Shumardia* (Fig. 87*H,I*) a 5th segment is added to the pygidium after the complete number of thoracic segments has been developed, STUBBLEFIELD called only the original of Figure 87*I* an holaspis, and not that of Figure 87*H*. Similar addition of segments to the pygidium has long been known to take place in *Dalmanitina* (1, Pl. 26). Probably it occurs also in other genera having many segments in the pygidium or with a larger number of axial rings than indicated segments in the pleural regions; examples are *Dionide*, which has 20 or more segments in the pygidium, Carboniferous proetids (29), and encrinurids. That such additions do not always take place, however, is demonstrated by *Ceraurinella* (Fig. 101) and *Ceraurus* (5). In species of both of these genera the complement of segments of the holaspid pygidium is present in the transitory pygidium and no later additions occur.

Addition of segments to the pygidium must be the result of continued activity of the zone of growth after the thorax is complete. Evidently one could select either completion of the thorax or cessation of budding of new segments as important points in development. Seemingly, in *Ceraurus* and *Ceraurinella* new segments cease to appear before the thorax is complete, whereas in many other trilobites the reverse is true. Future studies may call for recognition of ontogenetic stages that subdivide development at both points, but here prevailing practice is followed in making a subdivision only at completion of the thorax.

Records of minimum length *(sag.)* of holaspides include those of *Shumardia pusilla*, 1.8 mm. (25); *Leptoplastoides salteri*, 5.73 mm. (16); *Sao hirsuta*, 7.0 mm. (1); and *Paradoxides*, 13.5 mm. (30). Commonly, holaspides attain a length of several cm. but records (18) of much greater length are found, for example, holaspides of *Isotelus*

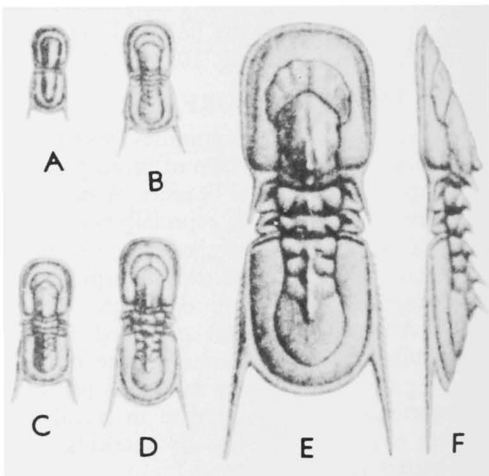

FIG. 105. Ontogenetic stages of *Pleuroctenium granulatum* (BARRANDE), Cam., Bohemia; *A-C*, meraspid "degrees" 0 (×6), 0 (×5), 1 (×4); *D*, holaspis, ×4; *E,F*, holaspis, dorsal, lateral, ×6 (all 1*).

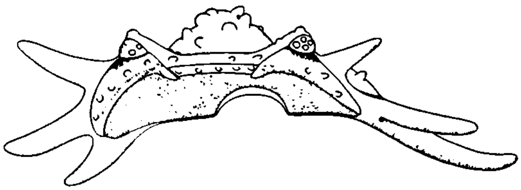

FIG. 106. Cranidium of *Acanthoparypha chiropyga* WHITTINGTON & EVITT, M.Ord., E.USA(Virginia); specimen showing librigenae and rostral plate, ×65 (37*).

gigas showing a range from 8 to 440 mm., and holaspides of species of *Paradoxides* attaining a length *(sag.)* of 300 to 400 mm. While at least a 5-fold increase in length may occur during this period, increase may be 30- or 40-fold. Augmentation of length during complete ontogeny of a trilobite is of the order of at least 50-fold (e.g., *Sao,* 0.6 mm. to about 30 mm.) and it may reach 400-fold (e.g., *Isotelus, Paradoxides*). *Uralichas ribeiroi,* from Lower Ordovician rocks of Portugal, is stated (18) to be the largest known trilobite, 70 cm. in length; no complete specimen is known, about a fifth of the reported length being that of the posterior pygidial spine.

Comparison of holaspides of different length *(sag.)* shows that changes occur during this period of growth. These include outline, relative proportions, convexity of parts of the exoskeleton, depth of furrows, and the nature of various other features. Adequate suites of complete exoskeletons are not many, so that it is rarely possible to go beyond generalities. One example is RAYMOND's (17) study of *Isotelus gigas*. The smallest known holaspis is 9.4 mm. in length (36). As size increases, both cephalon and pygidium becoming longer than the cephalon, the axial lobe widens, librigenal spines, after being reduced, disappear, and the genal angles become rounded. In what is probably the late meraspid period of *Isotelus* the glabella is convex, with lateral furrows and lobes and a median tubercle, and the transitory pygidium has a well-defined axis showing many axial rings, pleural furrows, and interpleural grooves (33, Pl. 75, figs. 27-29, 34-36). In small holaspides these convexities and furrows are smoothed out.

In the Devonian *Dipleura* COOPER (4) has described how holaspides ranging in length from 8 to 40 mm. undergo a series of changes that include loss of 3 pairs of lateral glabellar furrows (at 11 to 14 mm. length), gradual loss of ring and pleural furrows, smoothing of the pygidial axis, and widening of the thoracic axis. Some of these changes are like those observed in the ontogeny of *Isotelus,* a genus belonging to a very different family, although the changes occur at different stages in development.

In *Acanthoparypha* (Figs. 91, 106), *Holia* (37), and *Flexicalymene* (33), deep lateral glabellar furrows, occipital furrows, and axial ring furrows are retained in the holaspid period. Convexity of the axial regions may increase with size, and genal or occipital spines become longer and stouter. If the external surface is spinose or tuberculate, the symmetrical paired arrangement of larger spines or tubercles seen in the meraspid period is less conspicuous. While these changes in convexity, outline, and size of particular parts do occur, measurements made on Cambrian trilobites (7, 11, 23) suggest a general rectilinear relationship between dimensions at different sizes.

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(40) **Raw, Frank**
(41) **Whittington, H. B.**

CLASSIFICATION

By H. J. Harrington

CONTENTS

A wholly satisfactory, natural classification of trilobites is beyond possibility at the present moment. The truth of this assertion becomes immediately apparent by simply calling attention to the fact that among genera recognized in this volume 121 are regarded as *"incertae sedis,"* without familial allocation. It is true that some of these genera are imperfectly known, but many are as well known as most trilobites that can be readily classified into families. The fault is not with the fossils but with our understanding of the truly relevant and diagnostic characters to be used for establishment of familial and suprafamilial taxa.

Difficulties in the way of a natural classification are (1) entire lack of information concerning the internal anatomy of trilobites, particularly that referring to the nervous system, (2) inadequate knowledge of larval development, complete ontogenies being known only for a few species, (3) insufficiency of data on the nature of ventral appendages, (4) unsatisfactory knowledge of the ventral cephalic sutures in many genera, (5) inadequate understanding of the original cephalic segmentation, (6) homeomorphy of some trilobites, especially the so-called "smooth" forms, and (7) likely possibility that some trilobite lineages may have developed a mineralized carapace late in their phylogenetic evolution.

DEVELOPMENT OF CLASSIFICATION

EARLY WORK

As the number of described genera of trilobites steadily increased during the course of the last century, several paleontologists attempted at various times to classify them into families and taxa of suprafamilial rank. Most of these classifications laid undue stress on morphological characters that now are regarded as having less than secondary value. Some, however, contained the germs of ideas that when fully developed by different paleontologists during the present century led to proposal of more satisfactory groupings.

The first classification of trilobites, by BRONGNIART (1822), amounted only to division into 5 genera of species that previously had been referred to *Entomolithus paradoxus*. In 1827, DALMAN arranged the trilobites in 2 groups, according to whether they possessed eyes or lacked them. QUENSTEDT (1837) based his classification on structure of the eyes and number of thoracic segments. EMMRICH (1839) made use of ocular characters for his first classification, taking account also of shape of the pleurae. MILNE EDWARDS (1840) regarded the enrollment ability of trilobites as of primary importance. GOLDFUSS (1843), entertaining ideas similar to those of DALMAN, divided the trilobites into 3 groups based on the presence or absence of eyes, and on their structure. BURMEISTER (1843) accepted MILNE EDWARDS' ideas and stressed the importance of size of the pygidium and characters of the pleurae. EMMRICH's second classification (1845) took into account thoracic features, structure of the eyes and facial sutures. HAWLE & CORDA (1847) divided trilobites into 2 groups, one characterized by an entire pygidium and the other by a lobate or serrated pygidium. M'COY (1849) regarded the presence or absence of articulating facets on the pleurae as a character of prime importance. BARRANDE (1852) based his classification on the structure of the pleurae.

SALTER (1864) used a combination of different features, particularly number of the thoracic segments, size of the pygidium, presence and course of the facial sutures, and ocular characters. On these features, he divided the trilobites into 4 groups termed Agnostini, Ampycini, Asaphini, and Phacopini. The first 2 groups included genera with reduced number of thoracic segments and pygidium proportionally enlarged. The Agnostini lacked eyes and facial sutures, whereas the Ampycini had "eyes often absent" and "facial suture obscure, or submarginal, or none." The last 2 groups included genera with a "considerable number" of thoracic segments and reduced pygidium. The Asaphini had smooth eyes usually moderately developed and facial sutures "ending on the posterior margin," whereas the Phacopini had well-developed eyes (usually faceted) and facial sutures "ending on the external (=lateral) margin." SALTER's scheme was a great improvement over all previous attempts to classify the trilobites and, in truth, it contains the germs of both BEECHER's and GÜRICH's later classifications. CHAPMAN's (1889) and HAECKEL's (1896) groupings were certainly very inferior to SALTER's and are now forgotten. CHAPMAN recognized 4 primary groups of trilobites based on quite arbitrary morphological features, whereas HAECKEL proposed 2 orders (Protrilobita or Archiaspides, and Eutrilobita or Pygidata) based on the absence or presence of "true pygidium" and on characters of the thoracic segments.

BEECHER'S CLASSIFICATION

Near the close of the last century, C. E. BEECHER (1897) attempted to establish a "natural" classification of trilobites based on biological considerations. As his ideas have deeply influenced the thoughts of later paleontologists, it seems desirable to give a summary of his classification and of the underlying principles. BEECHER's conception, in its turn deeply influenced by HAECKEL's famous "law of morphogenesis" or "recapitulation theory," which asserts that the ontogenetic development of the individual recapitulates the phylogenetic development of the species, was based on the assumption that the trilobite protaspis was a phylembryo in JACKSON's (1890) sense. The protaspides, therefore, shared certain features regarded as characterizing the whole class. Using the recapitulation theory as a guiding principle, BEECHER analyzed the ontogenetic development of trilobites out of the so-called phylembryonic stage, and believed that he could unravel the natural sequence of evolutionary events. He regarded the eye-bearing librigenae as the most significant feature of trilobites and assumed that in the earliest larval stages of all but the highest trilobites they were ventral in position. During ontogeny the librigenae migrated from the ventral to the dorsal side of the cephalon together with the marginal suture, which thus gave origin to the facial sutures. This was accompanied by migration of the eyes from the ventral side, "first forward to the margin and then backward over the cephalon to their adult position." He concluded, therefore, that eyeless adult trilobites with ventral librigenae were primitive, whereas those possessing eyes and facial sutures were progressive, higher forms. To circumvent the difficulty raised by the presence of dorsal eyes in *Trinucleus* and *Harpes*, BEECHER assumed that these structures were "fixigenal ocelli," not homologous with the "librigenal eyes" of other trilobites.

These considerations led BEECHER to classify trilobites in 3 orders, which he named Hypoparia (Gr., *hypo,* below; *paria,* cheek piece), Opisthoparia (*opisthe,* behind), and Proparia (*pro,* in front of). The Hypoparia were characterized as having ventral librigenae, and ventral, marginal, or submarginal sutures, and lacking compound eyes. The Opisthoparia were defined to include trilobites with librigenae extending on to the dorsal side, bounded by facial sutures that cut the posterior margins of the cephalon so as to leave the genal angles with the librigenae. Librigenal holochroal eyes are well developed in all but the most primitive genera. Lastly, the Proparia were interpreted to comprise trilobites with librigenae extending on to the dorsal side but bounded by facial futures that cut the lateral margins of the cephalon, so as to leave the genal angles with the fixigenae. Librigenal eyes are scarcely developed or absent in the most primitive genera, but well developed and schizochroal in progressive genera.

At the time when Beecher's paper was published, only 14 trilobite families were recognized; they were distributed among the 3 orders of his classification as follows.

Summary of Trilobite Classification by Beecher (1897)

Order HYPOPARIA—Agnostidae, Harpedidae [=Harpidae], Trinucleidae

Order OPISTHOPARIA — Conocoryphidae, Olenidae (Paradoxinae, Oryctocephalinae, Oleninae, Dikelocephalinae), Asaphidae [incl. Illaenidae *(sic)*], Proetidae, Bronteidae [=Thysanopeltidae], Lichadidae [=Lichidae], Acidaspidae [=Odontopleuridae]

Order PROPARIA—Encrinuridae, Calymenidae, Cheiruridae, Phacopidae

BEECHER's classification, adopted readily and unqualifiedly by his former student, P. E. RAYMOND, gained widespread recognition through the latter's contribution (1913) to the ZITTEL-EASTMAN *Textbook of Palaeontology*. By the time of this publication, the number of recognized families had increased to 28, but RAYMOND's distribution of them among the Hypoparia, Opisthoparia, and Proparia was essentially the same as BEECHER's, particularly as regards the strange and unnatural grouping of agnostids, harpids, and trinucleids in the same order. Such grouping from the outset called forth objections to BEECHER's classification, opposing particularly his order Hypoparia.

The first to voice disagreement was POMPECKJ (1898). Subsequently, BEECHER's classification has been severely criticized by GÜRICH (1907), LAKE (1907, in LAKE, 1906-46), JAEKEL (1909), WOODS (1909), POMPECKJ (1912), SWINNERTON (1915, 1919), POULSEN (1927, 1934), RICHTER (1933), STUBBLEFIELD (1936), STØRMER (1942, 1944), HENNINGSMOEN (1951), and HUPÉ (1953). So many arguments have been accumulated against the classification that it is now completely untenable, even under the modified forms proposed by SWINNERTON (1915), RICHTER (1933), and STØRMER (1942). Most of the objections are based on discoveries made subsequent to the date of BEECHER's publication. Some of these may be summarized as follows. (1) It is now known that the agnostids have no cephalic sutures and therefore no reason exists for interpretation of the cephalic doublure as "ventral librigenae." (2) No trilobites are known, either in adult or larval stages, bearing ventral eyes on the librigenae. (3) The eodiscid genera *Pagetia* and *Opsidiscus* suggest that the agnostids are derived from eye-bearing ancestors; *Pagetia,* described by WALCOTT in 1916, has well-developed eyes and proparian sutures; *Opsidiscus,* described by WESTERGÅRD in 1950 (=*Aulacodiscus* WESTERGÅRD, 1936), has ocular tubercles and eye ridges but no facial sutures. (4) The lateral eyes of the harpids now are regarded, following RICHTER's investigations, as simplified or "degenerate" eyes derived from normal schizochroal eyes formed by numerous lenses; far from being "fixigenal ocelli," they are homologous with the "librigenal eyes" of other trilobites. (5) Proparian genera are now known in the midst of otherwise opisthoparian families, and conversely, opisthoparian genera are known in proparian families; these include the proparian *Saltaspis* and *Nericiaspis,* among the opisthoparian Olenidae, and the opisthoparian *Placoparia* and *Bouleia,* among the proparian Pliomeridae and Phacopidae, respectively.

BEECHER's classification, for all its defects, had the virtue of simplicity. Actually, it was a modification of SALTER's (1864) scheme, and the terms Opisthoparia and Proparia paid homage to SALTER's perspicacity in distinguishing the 2 types of facial sutures characterizing his Asaphini and Phacopini.

Though BEECHER's order Hypoparia has been rejected by most paleontologists, his orders Opisthoparia and Proparia have been accepted in many subsequent classifications, though more or less modified in content. This is readily understandable, because distinctions based on characters of the facial sutures provided a very objective and easy means of dividing trilobites into at least 2 main groups. Even at present, when the orders Opisthoparia and Proparia are discarded, the words are widely used (in adjectival form) to denote different conditions of the facial sutures.

GÜRICH'S CLASSIFICATION

BEECHER's classification was never well received by European paleontologists, particularly those of the German school. In 1907, GÜRICH proposed a very different arrangement of trilobites, which, though accepting some of BEECHER's ideas in a modified form, was based mainly on the number of thoracic segments and relative size of the pygidium. GÜRICH's classification, therefore, combined the ideas of QUENSTEDT, EMMRICH, BURMEISTER, SALTER, and BEECHER. His subdivisions were as follows.

Summary of Trilobite Classification by Gürich (1907)

Order OLIGOMERIA (Trilobites with few thoracic segments)
- Suborder ISOPYGIA (Pygidium about equal in size to cephalon) — Agnostidae, Microdiscidae [=Eodiscidae]
- Suborder HETEROPYGIA (Pygidium distinctly smaller than cephalon)—Trinucleidae [=Trinucleinae], Ampycinae [=Raphiophoridae], Dionideae [=Dionidinae], Aeglininae [=Cyclopyginae]

Order PLIOMERIA (Trilobites with many thoracic segments)
- Suborder MICROPYGIA (Pygidium minute, thoracic segments numerous)—Olenellidae, Remopleurideae [=Remopleuridinae], Ellipsocephalidae, (Triarthreae [=Triarthrinae]), Paradoxididae (Paradoxideae [=Paradoxidinae]), Harpedidae [=Harpidae], Olenidae, Cyphaspidae [=Otarionidae], Arethusinidae [=Aulacopleuridae]
- Suborder MACROPYGIA (Pygidium longer than half of cephalic length, thoracic segments fewer than half number of pygidial axial rings)
  - Group OPISTHOPARIA (Facial sutures crossing posterior edge of cephalon)—Proetidae, Dicellocephalidae [=Dikelocephalidae], Lichidae, Acidaspidae [=Odontopleuridae], Bronteidae [=Thysanopeltidae], Asaphidae (Asaphinae, Nileinae, Illaeninae)
  - Group GONATOPARIA (Facial sutures intersecting genal angles)—Homalonotidae, Calymenidae
  - Group PROPARIA (Facial sutures intersecting edges of cephalon in front of genal angles)——Phacopidae, Cheiruridae, Encrinuridae

As pointed out by SWINNERTON (1915), the main weakness of GÜRICH's system lies in its ignoring of the fact that progressive caudalization of thoracic segments is a tendency found in different, quite independent trilobite lineages, the micropygous, isopygous, and macropygous conditions being "evolutionary stages" in various trilobite stocks. Less open to criticism is GÜRICH's subdivision based on number of thoracic segments, but as JAEKEL (1909) remarked, the natural dividing line lies between trilobites having 2 or 3 segments and those having more than 5. JAEKEL (1909) proposed the order Miomera for the first group (including agnostids and eodiscids) and the order Polymera for the second (including all other trilobites). JAEKEL's divisions have been adopted by such modern authors as WHITEHOUSE (1936) and HUPÉ (1953).

SWINNERTON'S CLASSIFICATION

SWINNERTON (1915), like most paleontologists who have dealt with classification of the trilobites, disagreed with BEECHER mainly on the order Hypoparia. He regarded the agnostid trilobites as "secondarily sutureless," agreeing with JAEKEL (1909) that they "are forms in which the eyes have degenerated and the free cheeks have fused with the fixed cheeks." Accordingly, he placed the agnostids in the order Proparia. On the other hand, he regarded the Olenellidae as being "primarily sutureless," and as exhibiting "the trilobite organization just when these [suture] lines are coming into being." The Olenellidae, however, he placed in the order Opisthoparia. For the genera *Marrella* and *Nathorstia,* he proposed the order Protoparia designed for "the reception of Trilobites and Trilobite-like organisms in which the absence of facial sutures is primary." *Marrella,* however, is not a trilobite, whereas *Nathorstia* is now regarded as a "butter-crab" of *Olenoides serratus.* Accordingly these 2 genera should be removed from Protoparia, which thus fails as an ordinal unit.

SWINNERTON's classification had the merit of not only doing away with the Hypoparia (as GÜRICH had done) but of attempting for the first time to subdivide the Opisthoparia. The guiding principles were: (1) appearance of the facial sutures out of the protoparian stock at various times; (2) progressive caudalization of thoracic segments according to GÜRICH's ideas, but recognizing that this tendency appeared in different trilobite stocks; and (3) increasing importance of the pleurae. His classification is as follows.

Summary of Trilobite Classification by Swinnerton (1915)

Order PROTOPARIA—Marrellidae [=non-Trilobita], *Nathorstia* [=*Olenoides*]
Order OPISTHOPARIA
Suborder MESONACIDA—Mesonacidae [=Olenellidae], Remopleuridae [=Remopleurididae], Paradoxidae [=Paradoxididae], Zacanthoidae [=Zacanthoididae]
Suborder CONOCORYPHIDA
Section OLENINA—Olenidae, Proetidae, Oryctocephalidae
Section CONOCORYPHINA—Conocoryphidae
Section PTYCHOPARINA — Ptychoparidae [=Ptychopariidae], Solenopleuridae, Dicellocephalidae [=Dikelocephalidae], Bathyuridae, Asaphidae, Illaenidae
Section CALYMENINA—Calymenidae, Homalonotidae
Suborder TRINUCLEIDA—Trinucleidae, Harpedidae [=Harpidae], Raphiophoridae, Aeglinidae [=Cyclopygidae], ?Ellipsocephalidae, ?Shumardiidae
Suborder ODONTOPLEURIDA — Odontopleuridae, Lichadidae [=Lichidae], Bronteidae [=Thysanopeltidae]
Order PROPARIA—Encrinuridae, Cheiruridae, Phacopidae, Burlingidae [=Burlingiidae], ?Agnostidae

POULSEN'S CLASSIFICATION

Based on facial sutures, C. POULSEN's (1927) classification was somewhat different from those of BEECHER and SWINNERTON. He regarded the Olenellidae as having functional marginal (perrostral) and facial sutures *"in statu nascendi."* He also regarded the marginal suture of BEECHER's Hypoparia (trinucleids, harpids) as homologous with the perrostral suture of the Olenellidae and believed that the Conocoryphidae also have similar marginal sutures. He concluded that "all trilobites with real facial sutures are descendants from the Olenellidae."

POULSEN's conception was based on (1) objection to BEECHER's classification "because in several cases he has used sutures which are not homologous with the facial suture"; (2) belief that the Olenellidae "undoubtedly represent the most primitive type," since they have a marginal (perrostral) suture and incipient facial sutures with well-developed posterior sections but "not yet developed" anterior sections; (3) belief that the marginal suture of BEECHER's Hypoparia, as well as the marginal suture of the Conocoryphidae, is homologous with the perrostral suture of the Olenellidae; (4) belief that the hypoparian type of trilobite was "probably formed before the frontal branches (anterior sections) of the facial sutures came into being in the Opisthoparia"; and (5) belief that all trilobites with "real facial sutures" have descended from the Olenellidae.

POULSEN, therefore, raised SWINNERTON's suborder Mesonacida to the rank of order, and proposed 2 new orders for the remainder of the trilobites: Integricephalida, for those without facial sutures, and Suturicephalida, for those with facial sutures. The Integricephalida (equivalent to BEECHER's Hypoparia with addition of the Conocoryphidae), were divided into the suborders Opisthoparia and Proparia. In 1932, POULSEN replaced the etymologically hybrid term Suturicephalida with Epiparia, and, in 1934, he revived the name Hypoparia for Integricephalida. POULSEN's classification was as follows.

Summary of Trilobite Classification by Poulsen (1927-1934)

Order HYPOPARIA (=Integricephalida, 1927)—Conocoryphidae, Eodiscidae, Agnostidae, Trinucleidae, Harpidae, ?Shumardidae [=Shumardiidae]

Order MESONACIDA—Olenellidae

Order EPIPARIA (=Suturicephalida, 1927)

Suborder OPISTHOPARIA—Redlichidae [=Redlichiidae], Zacanthoidae [=Zacanthoididae], Ptychoparidae [=Ptychopariidae], Paradoxidae [=Paradoxididae], Corynexochidae, Oryctocephalidae, Illaenidae, Bronteidae [=Thysanopeltidae], Symphysuridae [=Nileidae], Dikelocephalidae, Asaphidae, Bathyuridae, Proetidae, Remopleuridae [=Remopleurididae], Raphiophoridae, Aeglinidae [=Cyclopygidae], Ellipsocephalidae, Anomocaridae, Solenopleuridae, Olenidae, Cyphaspidae [=Otarionidae], Calymenidae, Homalonotidae, Odontopleuridae, Lichadidae [=Lichidae]

Suborder PROPARIA—Burlingidae [=Burlingiidae], Norwoodiidae, Cheiruridae, Encrinuridae, Phacopidae, ?Menomoniidae

RUDOLF RICHTER'S CLASSIFICATION

RUDOLF RICHTER (1933) accepted BEECHER's orders Opisthoparia and Proparia but, like most authors, rejected the Hypoparia. He considered that the marginal sutures of the Harpidae are not facial sutures but a "new development" consequent on the loss of facial sutures and development of the cephalic fringe. The orders Opisthoparia and Proparia were divided into suborders and superfamilies that generally follow the arrangement of SWINNERTON. In essentials, therefore, RICHTER's classification amounts to a grouping of families in superfamilies according to their presumed affinities and assignment of these superfamilies to suborders. His classification is as follows.

Summary of Trilobite Classification by Rudolf Richter (1933)

Order OPISTHOPARIA

Suborder REDLICHIINA

Superfamily REDLICHIIDEA—Paradoxididae, Mesonacidae [=Olenellidae], Redlichiidae

Superfamily ZACANTHOIDIDEA—Lichidae, Odontopleuridae, Remopleurididae, Zacanthoididae, Ceratopygidae, Oryctocephalidae

Superfamily BATHYURISCIDEA — Corynexochidae, Bathyuriscidae, Scutellidae [=Thysanopeltidae], Illaenidae

Superfamily DIKELOCEPHALIDEA—Dikelocephalidae, Asaphidae, Symphysuridae [=Nileidae], Cyclopygidae

Suborder PTYCHOPARIINA

Superfamily ELLIPSOCEPHALIDEA—Olenidae, Otarionidae, Proetidae, Ellipsocephalidae

Superfamily CRYPTOLITHIDEA — Raphiophoridae, Cryptolithidae [=Trinucleidae], Shumardiidae

Superfamily PTYCHOPARIIDEA — Conocoryphidae, Harpidae, Ptychopariidae, Solenopleuridae

Superfamily CALYMENIDEA—Menomoniidae, Calymenidae, Homalonotidae

Order PROPARIA

Superfamily EODISCIDEA—Agnostidae, Eodiscidae

Superfamily NORWOODIDEA—Norwoodiidae

Superfamily BURLINGIIDEA—Burlingiidae

Superfamily PHACOPIDEA—Phacopidae, Cheiruridae, Encrinuridae

STØRMER'S CLASSIFICATION

LEIF STØRMER's (1942) classification, "based chiefly on the ontogenetic development" of trilobites, is actually a modification of BEECHER's scheme with addition of some of SWINNERTON's ideas. STØRMER is the only modern paleontologist who recognizes BEECHER's order Hypoparia. He places the Olenellidae, however, in what he considers to be SWINNERTON's Protoparia but he uses this term invalidly since SWINNERTON's original definition of the group did not include the Olenellidae. His classification is as follows.

Summary of Trilobite Classification by Størmer (1942)

Order PROTOPARIA (Primitive trilobites with ventromarginal or marginal cephalic suture; lateral eyes well developed; preantennal segment well developed on dorsal side of protaspis; intergenal [metagenal] spines present in anaprotaspid, metaprotaspid, meraspid, and partly in holaspid periods)—Olenellidae

Order HYPOPARIA (Trilobites with marginal, supramarginal or ?ventromarginal sutures; lateral eyes absent or little developed; protaspis broad with preantennal segment probably well developed on dorsal side; metagenal spines absent in meraspid and later periods)—Cryptolithidae [=Trinucleidae], Harpidae, ?Raphiophoridae, ?Agnostidae, ?Shumardidae [=Shumardiidae]

Order OPISTHOPARIA (Trilobites with facial sutures crossing margin behind genal angles, at corners, of which genal spines may occur; protaspis with preantennal segment slightly or not at all developed on dorsal side; metagenal spines present in the metaprotaspid and meraspid periods)—All remaining trilobite families exclusive of Proparia.

Order PROPARIA (Trilobites with facial sutures crossing margin in front of genal angles, at corner of which intergenal [metagenal] spines may occur; protaspis wtih preantennal segment not developed on dorsal side; metagenal spines present in metaprotaspid and later periods)—Eodiscidae Norwoodidae [=Norwoodiidae], Burlingiidae, Phacopidae

CLASSIFICATIONS OF HENNINGSMOEN AND HUPÉ

The most modern classifications, by GUNNAR HENNINGSMOEN (1951) and PIERRE HUPÉ (1953, 1953-55), are alike in doing away finally with all traces of BEECHER's scheme. Both agree with KOBAYASHI (1935), STUBBLEFIELD (1936), and RASETTI (1948) that no classification of trilobites can be based on a single feature and both pay special attention to STUBBLEFIELD's prediction that "it will probably be found that the safest criteria of affinity are collective characters developed in the axial region of the shield" and especially of the cephalon. HENNINGSMOEN in particular has stressed the importance of development of the glabella and its furrows, especially the "form, direction, and relative position of the glabellar furrows," accepting STØRMER's (1942) views that the glabellar furrows appear to be boundaries between primary cephalic somites.

HENNINGSMOEN's classification is actually an attempt to group trilobite families into superfamilies without further grouping into orders or suborders. HUPÉ's classification, on the other hand, recognizes JAEKEL's orders Miomera and Polymera, these being subdivided into various superfamilies. With this exception, and with some differences of opinion as to grouping of families into superfamilies, the 2 classifications are basically similar.

Summary of Trilobite Classification by Hupé (1953-1955)

Order MIOMERA (Diminutive trilobites with subequal cephalon and pygidium and with 2 or 3 thoracic segments)

Superfamily EODISCOIDAE — Hebediscidae, Weymouthiidae, Pagetiidae, Eodiscidae (Eodiscinae, Calodiscinae, Spinodiscinae, Brevidiscinae), Dawsoniidae, Aulacodiscidae

Superfamily AGNOSTOIDAE—Platagnostidae, Lejopygidae, Phalacromidae, Leiagnostidae, Sphaeragnostidae, Condylopygidae, Diplagnostidae, Agnostidae, Hastagnostidae, Micragnostidae, Spinagnostidae, Clavagnostidae, Geragnostidae, Cyclagnostidae, Trinodidae

Order POLYMERA (Trilobites having more than 3 thoracic segments, minimum 5)

Superfamily OLENELLOIDAE—Olenellidae (Fallotaspidinae, Nevadiinae, Olenellinae, Elliptocephalinae, Wanneriinae, Neltneriinae, Holmiinae, Olenelloidinae), Daguinaspidae [=Daguinaspididae], Lancastriidae

Superfamily REDLICHIOIDAE [=Paradoxidoidae] Redlichiidae (Redlichiinae, Pararedlichiinae), Neoredlichiidae, ?Yinitidae, Latiredlichiidae, Saukiandidae, Dolerolenidae, Abadiellidae, Bathynotidae, Metadoxididae, Protolenidae (Protoleninae, Termierellinae, Bigotininae, Myopsoleninae, Strenuellinae), Antatlasiidae, Ellipsocephalidae (Ellipsocephalinae, Aldoniinae), Palaeolenidae (Palaeoleninae, Kingaspidinae, Hartshilliinae), Paradoxididae (Paradoxidinae, Centropleurinae, Xystridurinae), Hicksiidae

Superfamily CORYNEXOCHOIDAE — ?Proerbiidae, ?Edelsteinaspidae [=Edelsteinaspididae], Dinesidae, Zacanthoididae, Albertellidae, Dolichometopidae (Bathyuriscinae [=Dolichometopinae], Mexicaspinae [=Mexicaspidinae], Orriinae, Glossopleurinae, Hanburiinae, Vanuxemellinae), Corynexochidae (Corynexochinae, Acontheinae), Ogygopsidae, Protypidae, Dorypygidae (Dorypyginae, Holteriinae), Oryctocephalidae (Oryctocephalinae, Oryctocarinae, Tonkinellidae [=Tonkinellinae])

Superfamily AGRAULOIDAE—Agraulidae, Micragraulidae, Pelthopeltidae

Superfamily PARASOLENOPLEUROIDAE [=Yokuseni-oidae] —— Yokuseniidae, Yunnanocephalidae, Parasolenopleuridae, Anomocarellidae

Superfamily PTYCHOPARIOIDAE [=Conocoryphoidae]——Alokistocaridae (Alokistocarinae, Amecephalinae), Nepeidae, ?Antagmidae, Elrathinidae (Elrathininae, Plagiurinae, Solenopleurellinae), Ptychopariidae (Ptychopariinae, Howellaspinae [=Howellaspidinae], Elrathiellinae, Clappaspinae [=Clappaspidinae], Iraniinae), Saoidae, Conocoryphidae (Conocoryphinae, Bailiellinae, Ctenocephalinae, Holocephalinae, Meneviellinae), Atopsidae

Superfamily SOLENOPLEUROIDAE — Solenopariidae, Solenopleuridae (Solenopleurinae, Menocephalinae, Heterocaryoninae), Acrocephalitidae, Lonchocephalidae, Talbotinidae, Burnetiidae [=Dokimocephalidae], Glyptometopidae, Hystricuridae, Toernquistiidae, Dimeropygidae, Bathyuridae (Bathyurinae, Bathyurellinae), Otarionidae (Otarioninae, Cyphaspididinae), Punctulariidae, Raymondinidae, Isocolidae

Superfamily UTIOIDAE [=Shumardioidae]——?Emmrichellidae, Utiadae [=Utiidae], Liostracinidae, Paracedariidae, Cedariidae, Norwoodiidae (Norwoodiinae, Levisaspidae [=Levisaspidinae]), Shumardiidae, Myindidae, Toxotididae

Superfamily ASAPHISCOIDAE [=Ceratopygoidae]——Asaphiscidae (Asaphiscinae, Lecanopleurinae), Blountiidae, Crepicephalidae (Crepicephalinae, Kopturinae), Tsinaniidae, Marjumiidae, Housiidae, Ceratopygidae (Ceratopyginae, Mansuyellinae, Hysteroleninae)

Superfamily OLENOIDAE—Damesellidae (Dameselllinae, Dorypygellinae, Drepanurinae), Missisquoiidae, Elviniidae (Elviniinae, Maladiinae [=Maladaiinae]), Richardsonellidae, Sarkiaidae [=Sarkiidae], Olenidae (Oleninae, Papyriaspinae [=Papyriaspidinae], Leptoplastinae, Triarthrinae, Jujuyaspinae [=Jujuyaspidinae], Aulacopleurinae), Lloydiidae, Eurekiidae, Illaenuridae, Leiostegiidae (Leiostegiinae, Mansuyinae [=Mansuyiinae], Eochuanginae [=Eochuangiinae]) Genevievellidae, Menomoniidae, Remopleurididae

Superfamily DIKELOCEPHALOIDAE—Anomocaridae, Changshaniidae, Dikelocephalidae (Dikelocephalinae, Osceolinae), Hungaidae [=Hungaiidae] (Hungainae [=Hungaiinae], Dikelokephalininae, Tingocephalinae)

Superfamily PTYCHASPIDOIDAE [=Conokephalinoidae]—Conokephalinidae, Saukiidae (Saukiinae, Prosaukiinae), ?Shirakiellidae, Euptychaspidae [=Euptychaspididae], Ptychaspidae [=Ptychaspididae]

Superfamily BURLINGIOIDAE—Burlingiidae

Superfamily PROETOIDAE—Holotrachelidae, Proetidae, (Proetinae, Proetidellinae, Prionopeltinae, ?Permoproetinae), Tropidocoryphidae (Tropidocoryphinae, Astycoryphinae, Denemarkiinae), Cyrtosymbolidae (Cyrtosymbolinae, Eodrevermanniinae, Pteropariinae), Dechenellidae, Phillipsiidae (Phillipsiinae, Griffithidinae, Ditomopyginae, Anisopyginae), Brachymetopidae

Superfamily ASAPHOIDAE—Nileidae (Nileinae, Parabarrandiinae), Asaphidae (Asaphinae, Taihungshaninae [=Taihungshaniinae], Ogygiocarinae [=Ogygiocaridinae], Macropyginae), Cyclopygidae

Superfamily SCUTELLOIDAE [=Illaenoidae]—Styginidae, Theamataspidae [=Theamataspididae], Phillipsinellidae, Scutellidae [=Thysanopeltidae], Illaenidae (Illaeninae, Bumastinae)

Superfamily LICHADOIDAE—Lichadidae [=Lichidae] (Lichadinae [=Lichinae] Homolichadinae, Tetralichadinae, Echinolichadinae), Trochuridae (Trochurinae, Dicranopeltinae, Platylichadinae, Euarginae)

Superfamily ODONTOPLEUROIDAE—Odontopleuridae (Odontopleurinae, Acantholominae [=Leonaspidinae]), Selenopeltidae, Ceratocephalidae (Ceratocephalinae, Dicranurinae, Miraspinae [=Miraspidinae])

Superfamily TELEPHOIDAE—Komaspidae [=Komaspididae], Ellipsocephaloidae [=Ellipsocephaloididae] Telephidae [=Telephinidae], Glaphuridae

Superfamily CALYMENOIDAE — Pharostomidae [=Pharostomatidae], Calymenidae (Calymeninae, Colpocoryphinae, Reedocalymeninae), Homalonotidae (Homalonotinae, Eohomalonotinae, Trimerinae)

Superfamily PHACOPOIDAE—Dalmanitidae (Dalmantinae, Zeliszkellinae, Pterygometopinae, Asteropyginae, Neosynphoriinae), Phacopidae (Phacopinae, Bouleinae [=Bouleiinae], Phacopidellinae, Acastinae, Calmoniinae)

Superfamily CHEIRUROIDAE — Pliomeridae (Pliomerinae, Protopliomeropsinae, Placopariinae, Pliomerillinae), Cheiruridae (Cheirurinae, Cyrtometopinae, ?Crotalurinae, Sphaerexochinae, Deiphoninae, Areiinae, Staurocephalinae, Heliomerinae), Encrinuridae (Encrinurinae, Cybelinae)

Superfamily HARPOIDAE—?Hypotheticidae, Loganopeltidae, Harpididae, Harpidae, Entomaspidae [=Entomaspididae]

Superfamily TRINUCLEOIDAE—Ithyophoridae, Trigryposidae [=Trigrypidae], Orometopidae, Raphiophoridae (Raphiophorinae, Ampyxininae), Selenecemidae, Endymioniidae, Dionididae, Trinucleidae (Trinucleinae, Tretaspinae [=Tretaspidinae], Cryptolithinae, Novaspinae [=Novaspidinae]

SUTURES AS CRITERIA FOR DEFINITION OF MAJOR TRILOBITE DIVISIONS

Since the early times of EMMRICH and SALTER, cephalic sutures have been granted a very prominent position in trilobite classification, and since publication of BEECHER'S (1897) classical paper, it has been almost mandatory to take them into serious consideration. It seems, therefore, worth while to discuss at some length the significance of cephalic sutures as bearing on taxonomic problems.

ORIGIN OF SUTURES

Most modern authors agree that cephalic sutures first developed in trilobites as an answer to the need of facilitating ecdysis. This applies particularly to the facial sutures, which played an important role during molting of the delicate ocular integument. But authors do not agree regarding the relationship of the sutures to the original cephalic segmentation. Do the purely exoskeletal sutures coincide with lines of fusion between cephalic somites, or do they cut across the original cephalic segmentation? Much depends on the answer to these questions. If sutures are purely mechanical devices of secondary origin, cutting across the original cephalic segmentation, as RAW (1953) believes, their taxonomic value is greatly impaired. If, on the other hand, they follow lines of fusion between somites, being, so to speak, a surface expression of deep-seated original segmentation, their taxonomic value is less open to challenge.

Theoretically, at least, it seems logical to accept the premise that lines of weakness represented by the exoskeletal sutures had better chances to develop along lines of fusion between somites than across them. If we but knew the number, position, and boundaries of the fused cephalic segments, it would be easy to settle the issue one way or another. As it is, the problem cannot be solved objectively. The fused cephalic segments have undergone such radical changes that it is impossible to ascertain, beyond dispute, their true number, distribution, and boundaries. This uncertainty is clearly reflected in the 10 different opinions on the subject expressed by 12 different paleontologists: M'COY (1849), BEECHER (1897), JAEKEL (1901, 1909), RAYMOND (1920), HOLMGREN (1916), WALCOTT (1918), WARBURG (1925), HENRIKSEN (1926), RICHTER (1933), STØRMER (1942), RAW (1953), and HUPÉ (1953). The crucial, most difficult, and most debatable point is the interpretation of anterior parts of the cephalon and the preoral ventral plates (hypostoma, rostral plate) in terms of original cephalic segmentation. Of all hypotheses proffered, I favor that of HUPÉ (1953). According to him, the rostral plate, hypostoma, and librigenae are different parts of a single cephalic (ocular) segment. The rostral plate presumably represents the mesotergite, the hypostoma (or at least its median body) the mesosternite, and the librigenae (probably together with the hypostomal borders and wings) pleural extensions of the segment. If this hypothesis is accepted, the hypostomal and connective sutures are intrasegmental, but corresponding to tergosternal (hypostomal suture) and tergopleural (connective sutures) boundaries. The rostral suture, on the other hand, is part of BARRANDE's "*grande suture*," and together with the facial sutures it bounds the ocular segment adaxially. The *grande suture* (rostral plus facial sutures) is thus truly intersegmentary, separating the ocular segment from the mesotergites and pleural extension of the fused postocular somites.

PRIMARY SUTURE PATTERN

With this hypothesis in mind we may now take up the problem of the primary sutural pattern of trilobites. Again, opinions differ greatly in this regard. Published discussions have centered mainly on the origin and interrelations of marginal, opisthoparian, and proparian sutures. BEECHER (1897), for instance, regarded the marginal suture of harpids and trinucleids as primary. SWINNERTON (1915) believed that the perrostral ("marginal") suture of the olenellids, as well as the opisthoparian and proparian sutures, arose independently at different times from sutureless ancestors. POULSEN (1927), and apparently also KIAER (1917) and WARBURG (1925), believed the perrostral suture of olenellids to be primary. RAW (1925) and RICHTER (1933), on the other hand, were inclined to regard the proparian sutures as the most primitive but STUBBLEFIELD (1936) and HUPÉ (1953), on the contrary, regard all proparian trilobites as "permanently neotenous opisthoparians."

If we adhere to the hypothesis mentioned above regarding relationship of sutures to original cephalic segmentation, it seems inevitable to conclude that the primary sutural pattern of trilobites was of ptychopariid type, characterized by functional facial, rostral, connective, and hypostomal sutures. Moreover, this is the only type of suture pattern that persisted uninterruptedly throughout the entire life span of the class, from earliest Cambrian times (redlichiids) to the late Permian (phillipsiids). All other sutural patterns were of transient appearance, and I believe that all of them were derived, at various times and in different ways, from the primary ptychopariid type.

OPISTHOPARIAN AND PROPARIAN SUTURES

Since BEECHER's time, facial sutures have been classed as opithoparian and proparian, without reference to whether they belong to a ptychopariid type of sutural pattern or some other. The distinction between these 2 types of facial sutures is based on relative position of the rear extremity of the posterior section of the sutures with regard to the genal angle of the cephalon. If the posterior section cuts the posterior cephalic margin "behind" (actually adaxially from) the genal angle, the suture is classed as opisthoparian. If it cuts the lateral margin "in front" of the genal angle, the suture is termed proparian. It should be evident that this purely morphological distinction is based on the conscious or unwitting assumption that the genal angle is a sort of "topographic fixed point" which can be recognized easily in all trilobites. By definition, the genal angle is the posterolateral extremity or "corner" of the cephalon, which is usually marked off bv a more or less clear angulation of the margin. Genal angles, however, are far from being "topographic fixed points." In the first place, no genal angles can be recognized objectively in many species belonging to such genera as *Telephina, Holotrachelus, Acerocare, Boeckaspis, Peltocare,* and *Peltura*—to mention a few. In these forms, the genal "angles" are perfectly rounded, and there is no way to ascertain the location of the "fixed points" along the cephalic margin. We assume that in these species the genal angles must lie somewhere in front of the rear extremities of the facial sutures, simply because we assume that the facial sutures are opisthoparian. This, however, involves a *"petitio principii,"* because we are now defining the genal angle in terms of the facial sutures.

In the second place, it is evident that in many trilobite families the genal angles show a marked tendency to "migrate" forward. This is manifest in such families as the Olenellidae, Zacanthoididae, Remopleurididae, and Olenidae, to mention a few. If the genal angles are produced into spines, and if within a family intermediate forms exist between those with "normal" and "advanced" genal angles, we can recognize that the advanced spines (which may spring from the anterolateral corners of the cephalon) are homologous with those borne by the "normal" genal angles of other species. This is the case in *Bristolia bristolensis* and *Laudonia bispinata* among the Olenellidae, and in several species of *Ctenopyge* among the Olenidae. It is evident that in these forms, the "genal angles" have shifted forward until they come to occupy an anterolateral position. However, in many of these forms, the posterolateral "corners" of the cephalon are sharply marked off by angulations of the margin. In *L. bispinata* the posterolateral angle even bears a stout spine. What has happened to our "fixed point"? Where now is the "true" genal angle? Our "fixed point" has changed position; whereas by definition the "true" genal angle is the posterolateral corner of the cephalon, by homology it is the anterolateral corner.

Consider now the case of such species as *Ctenopyge flagellifera* and *C. spectabilis.* If these forms lacked anterolateral ("advanced genal") spines, nobody would hesitate to classify the posterolateral angles as "true" genal spines. Moreover, since in both these species the rear extremities of the posterior sections of the facial sutures cut the lateral margins immediately *in front* of these angles, both species would be properly regarded as proparian. Indeed, these species, described respectively by ANGELIN in 1854 and BRØGGER in 1882, as well as several others belonging to the genus *Ctenopyge,* are actually proparian. If they have rarely been recognized as such, it has been due simply to the mesmeric effect of the "advanced genal spines." If these species were to be regarded as opisthoparian on the grounds that the posterolateral corners of the cephalon are not homologous with the "true" (advanced) genal angles, then *Saltaspis* and *Nericiaspis* should also be regarded as opisthoparian, and, for that matter, all classical proparian phacopid and cheirurid genera as well. Probably nobody will deny that the genal angles of *Phacops* and *Cheirurus* are not homologous with the "true" (advanced) genal angles of *Ctenopyge spectabilis.*

What, then, is the distinction between opisthoparian and proparian sutures? Accepting the conclusion that posterior sections of the sutures invariably bound the rear (adaxial) part of the ocular segment, the suture is opisthoparian if the posterolateral corners of the cephalon belong to this segment. On the other hand, if the posterolateral angles belong to one of the rear postocular segments, the suture is proparian. The olenellid trilobites differ from others in that the posterolateral angles of the cephalon belong to one of the anterior postocular segments ("frontal region" of HUPÉ), both sections of the facial sutures cutting the posterior cephalic margin. This suture is metaparian. It should be apparent that, in all 3 types, the relation between the posterior sections of the facial sutures and the ocular segment is the same, and that in all 3 the posterior sections of the sutures are homologous, even though they have different "topographic" positions. On the other hand, the relation between posterolateral cephalic angles and cephalic segmentation is different in the 3 cases, the "angles" being heterologous even if they have the same topographic position. Obviously, then, the distinction between opisthoparian and proparian sutures is one of degree, and accordingly it is not apparent why we grant it fundamental importance and stand in its awe. Whether the rear extremities of the sutures will cut the posterior or the lateral cephalic margins is an incidental feature depending on the differential growth of the fused cephalic segments during ontogeny. It is seemingly clear that reduction of the ocular segment leading to a proparian condition is a persistent feature characterizing whole trilobite lineages, but it is also evident that such a tendency appeared independently in many trilobite stocks characterized by opisthoparian sutures. Several olenids are now known to be proparian. These include not only the genera *Saltaspis* and *Nericiaspis*, but also several species of *Ctenopyge*, and possibly also of *Peltura*. *Illaenurus quadratus*, among the Illaenuridae, is another example of a proparian form in the midst of an otherwise opisthoparian family. Conversely, opisthoparian genera are known in the midst of otherwise proparian families. These include *Bouleia* among the Phacopidae, and *Placoparia* among the Pliomeridae. The genus *Pliomera* itself is not proparian, but gonatoparian.

In my opinion, the proparian condition is a progressive "evolutionary novelty" which appeared independently in several unrelated trilobite lineages after early Cambrian times. POULSEN's (1923) observations on the ontogeny of *Peltura scarabaeoides*, however, often have been quoted as proof to the contrary. *P. scarabaeoides*, a reputedly opisthoparian olenid, would pass, according to POULSEN, through a meraspid stage showing proparian conditions. If we take POULSEN's observations at their face value, this probably means that *P. scarabaeoides* (in the holaspid stage) is simply another proparian olenid. It should be recalled that this is one of the olenid species having smoothly rounded genal "angles"—so much so, in fact, that the genal angles simply cannot be recognized as such. The opisthoparian condition of *P. scarabaeoides* results from comparisons with closely related species, such as *P. paradoxa*, which bear small librigenal spines close to and in front of the posterior extremities of the facial sutures. From what is known about "migration" of genal angles, this is certainly not a sure way to locate the critical "fixed point" when no spine or angulation of the margin is present. The fact that at least 2 pelturid genera (*Saltaspis, Nericiaspis*) are decidedly proparian would make a similar condition in the adult *P. scarabaeoides* not at all strange. It should be recalled, moreover, that the alleged proparian condition in the ontogeny of *P. scarabaeoides* is of comparatively late (meraspid) appearance, a fact that seems accordant with the view that the proparian condition is derived from a primary opisthoparian suture. The early larval (protaspid) sutural condition of *P. scarabaeoides* is unknown, but POULSEN (1927) tried to show that it was also proparian by making comparison with conditions in the protaspides of *Sao hirsuta*, originally regarded as opisthoparian by BARRANDE (1852) but reinterpreted as proparian by POULSEN.

STRAND's (1927) description and illustrations of 2 protaspides of *Olenus gibbosus*, showing what he regarded as proparian sutures, seemed to lend support to POULSEN's contention. In 1942, STØRMER redescribed and illustrated STRAND's specimens, together with 3 other protaspides of *O. gibbosus*, and (though stating that "the development of the facial suture is not clear") he was prone to believe in a probable proparian condition. The force of these arguments in favor of an early protaspid proparian suture has been recently weakened by WHITTINGTON's re-examination of the ontogeny of *Sao hirsuta,* in which he has claimed the presence of opisthoparian sutures from early larval stages, and discrediting the proparian-sutured small forms figured by RŮŽIČKA.

In other Upper Cambrian trilobites, such as *Welleraspis,* both the protaspides and meraspides also have opisthoparian sutures. This renders likely a similar condition for the protaspides of *Olenus gibbosus.* Actually, no facial sutures can be observed in the protaspides illustrated by STØRMER, and it is conceivable that the sutures are concealed by the nearly vertical margins of the minute cephala. It seems, therefore, that no grounds exist for thinking that the early larval (protaspid) stage of *Peltura scarabaeoides* was characterized by a proparian suture. If we should accept the conclusion that in this species both the protaspid and the holaspid stages show opisthoparian sutures, we would be forced to admit that during ontogeny of this trilobite an early (protaspid) opisthoparian condition was succeeded by a proparian (meraspid) stage, lastly to be substituted by a permanent (holaspid) opisthoparian suture. The likelihood of such an ontogeny is more than doubtful. On the other hand, if an early opisthoparian condition were to be succeeded by a proparian condition during the meraspid stage, we would have discovered the first actual proof of the evolutionary origin of the proparian type of suture out of the opisthoparian. However, no matter how tempting this line of thought may be, the problem is plagued with so many uncertainties that it seems best to end this discussion with a *"non sequitur."* It may well be that *P. scarabaeoides* is an opisthoparian species after all, and that the proparian condition of the meraspid stage is nothing more than an appearance due to chances of preservation of the tiny specimens.

MARGINAL SUTURES

The name "marginal sutures" has been used to designate the sutures running directly along the margin, or close to the margin on either the dorsal or ventral sides of the cephalon of a number of trilobites. In the minds of many paleontologists, these sutures are structures independent of the dorsal facial sutures, and some authors believe that they were the first to appear in trilobites. Sutures classed as marginal, however, include such different structures as the perrostral sutures of olenellids, rostral sutures of some ptychopariids, dorsal intramarginal sutures of raphiophorids, dorsal submarginal sutures of some phacopids *(Ductina),* dorsal submarginal sutures of conocoryphids, submarginal sutures of trinucleids and dionidids, and wholly marginal sutures of harpids. It should be immediately apparent that the only thing held in common by most of these sutures is the name. Their origin is as different as that of the different trilobite groups just mentioned. None of these "marginal" sutures is primary. Their secondary derivation from primary facial sutures is evident in some forms and very plausible in others.

The so-called "marginal" sutures of the raphiophorids actually are dorsal opisthoparian sutures, which in some genera tend to be intramarginal in position. In all, the posterior extremities of the sutures are decidedly dorsal, cutting across the base of the genal spine, which is borne by the librigenae. It is evident that the dorsal intramarginal sutures of these blind trilobites are derived from normal opisthoparian sutures that have migrated outward (abaxially), probably accompanying migration, reduction, and final disappearance of the eyes. The same type of dorsal intramarginal sutures characterizes the blind Alsataspididae. In these we can be practically certain that the sutures were derived from normal opisthoparian structures. This is more than suggested by the close affinities between the eye-bearing Hapalopleuridae with normal opisthoparian sutures and the eyeless, sutureless Alsataspididae. Even more evident is the origin of the dorsal intramarginal proparian sutures of *Ductina.* RICHTER's detailed studies of Upper Devonian phacopids of central Europe have shown conclusively that the submarginal sutures of the eyeless *D. ductifrons* are "end products" in an evolutionary suite characterized by progressive outward migration, reduction, and final disappearance of the eyes. Here, however, the sutures are proparian, and as in most phacopids, they are ankylosed and nonfunctional.

The marginal sutures of blind conocoryphids also clearly are derived from normal opisthoparian facial sutures. The close similarities between such genera as *Ptychoparia* and *Conocoryphe* seem to dispel all possible doubts in this regard, making it evident that the conocoryphids are derived from the main ptychopariid stock characterized by well-developed eyes and normal opisthoparian sutures. Two types of "marginal" sutures, however, seem to be present among the Conocoryphidae. In such genera as *Conocoryphe, Bailiaspis,* and *Bailiella,* characterized by lack of eyes, ocular protuberances, or eye ridges, the sutures are marginal anteriorly, submarginal laterally, and dorsal intramarginally across the base of the genal spines, which are borne by the librigenae. In such genera as *Couloumania, Dasometopus,* and *Elyx,* which retain either ocular protuberances or eye ridges, the sutures seem to be wholly marginal. The "marginal" sutures of the first group seem to have originated by outward migration of normal opisthoparian sutures, accompanying outward migration, reduction, and disappearance of the eyes, much as in the Raphiophoridae and Alsataspididae. The wholly marginal sutures of the second group, however, seem to have originated in a manner similar to that of the marginal sutures of harpidids. This seems strongly suggested not only by the vestigial eyes of *Couloumania,* but especially by the notable homeomorphy between such genera as *Dasometopus* and *Loganopeltis.* If this is actually true, the Conocoryphyidae are to be regarded as a polyphyletic family, the members of which were derived along different lines from the main ptychopariid stock.

The marginal sutures of harpidids, though truly marginal almost all around the cephalon, become dorsal across the base of the genal spines (when present). These are borne by the librigenae, which are almost exclusively ventral and coincide with the cephalic doublure. RASETTI's studies on *Loganopeltoides* and *Loganopeltis* have proved beyond dispute that the marginal sutures originated, in this case, by forward migration of the posterior sections of normal facial sutures and backward migration on the anterior sections, until the 2 sections met, became fused, ankylosed, and finally were obliterated. The anterior parts of the marginal sutures therefore, are derived from the anterior sections of the ancestral facial sutures, while the posterior parts arose from the posterior sections. It should be noted, incidentally, that such forms as *Loganopeltoides zenkeri* are apparently opisthoparians, since the genal angles belong to the ocular segment. In these forms, the posterior sections of the facial sutures have migrated forward, their adaxial extremities pivoting on the eyes, but the genal angles seem to have remained in their original location at the posterolateral corners of the cephalon.

The submarginal sutures of trinucleids and dionidids and the wholly marginal sutures of harpids seem to have developed in a somewhat different way. The sutures of trinucleids and dionidids are actually dorsal-submarginal in position, though they run very close to the cephalic margin. Their rear extremities, however, are decidedly dorsal, cutting across the genal spines borne by the ventral librigenae or "lower lamellae." The sutures of harpids, on the other hand, are exactly marginal, running all along the margins of the cephalon, including its prolongations. Consider first *Entomaspis* and its relation with the harpids. In this genus the 2 sections of the facial sutures run outward-backward from the eyes to the vicinity of the genal angles. The posterior sections cut the posterior margin just a little adaxially from the base of the genal spines, whereas the anterior sections swing outward-forward and reach the lateral margins just in front of the genal spines. The entire marginal suture is, therefore, formed by the anterior section of the facial sutures. This condition resembles that of the metaparian sutures of olenellids, but in *Entomaspis* the posterolateral (genal) spines belong to the ocular segments, the condition being, therefore, opisthoparian. If the 2 sections of the facial sutures were to fuse, become ankylosed, and finally disappear (as in the *Loganopeltoides-Loganopeltis* suite), the harpid condition would be achieved. It seems, therefore, that in harpids, the marginal suture running along the cephalic rim and the outer rim of the prolongations is derived from the anterior sections of opisthoparian sutures of entomaspidiform type, while the marginal suture running along the inner rim of the prolongations is derived from the posterior sections of such sutures.

Attention next may be directed to the eye-bearing, suture-bearing *Orometopus* in relation to the trinucleids and dionidids. As LAKE suggested in 1909, the similarities between *Orometopus* and some Trinucleidae are so close that little doubt can remain that the latter were derived from the former. The relationship is strictly comparable to that between the Hapalopleuridae and the Alsataspididae. *Orometopus* has opisthoparian sutures of almost cedariiform type. Backward migration of the anterior sections by pivoting their adaxial extremities on the eyes, would bring a condition quite similar to that of *Entomaspis*. Fusion, ankylosis, and disappearance of the sutures will conduce to the trinucleid condition. Here, however, the submarginal suture becomes decidedly dorsal across the base of the genal spines, which are borne by the librigenae (lower lamellae). The double metagenal ridges observed in some species of *Dionide* (as *D. formosa*), springing from the axial furrows and running outward-backward toward the genal angles, actually suggest ankylosed facial sutures of entomaspidiform type. If this is truly so, the submarginal suture of trinucleids and dionidids is derived from the anterior sections of entomaspidiform sutures.

From what has been said, it should be clear that "marginal" sutures are heterologous and secondarily derived from metaparian, opisthoparian, or proparian sutures.

SECONDARILY DERIVED SUTURAL PATTERNS

From the above discussion it seems evident that if proparian, metaparian, and "marginal" sutures are secondary in origin, the opisthoparian sutures must be primary. "When you have discarded the impossible, whatever remains, no matter how improbable, must be the truth." As already mentioned, I believe that the primary sutural pattern of trilobites was of ptychopariid type with opisthoparian conditions, meaning that this was the first type to appear in adult trilobites. Clearly, however, trilobites descend from some sutureless, wormlike, metameric ancestor, and if the "law of morphogenesis" has any significance, we may accept the view that this ancestor had eyes located in anterolateral position. This ancestor, however, was not a trilobite. As the eyes began to migrate "backward-inward" on the dorsal side, and as facial sutures appeared, the earliest true trilobites came into being. They were probably late Precambrian creatures provided with a soft, nonmineralized, chitinous dorsal exoskeleton. The integument of the cephalic region must have been transected by a set of sutures of ptychopariid type, though it seems logical to admit that, in these primitive forms, the facial sutures ran on the dorsal side close to the lateral margins.

Trilobites characterized by an opisthoparian ptychopariid sutural pattern are plentiful among the earliest known Cambrian forms. These are the redlichiids, which seem to be the nearest known approach to the theoretical primitive Precambrian trilobites and descendants of the primitive stock along the main evolutionary line of the class. Since early Cambrian to late Permian times, trilobites characterized by a ptychopariid sutural pattern were always in existence and from this main stock, numerous lateral branches sprang at various times.

TRILOBITE TYPES DEFINED BY SUTURE PATTERNS

Evolution of the ptychopariid type was along different lines. Some of the evolutionary trends reappeared independently in several offshoots at different times, the end products showing a considerable degree of homeomorphy due to convergent or parallel evolution. The main progressive changes distinguished in ptychopariid trilobites include types indicated as follows.

Corynexochid type, characterized by ankylosis of the hypostomal suture leading to its final disappearance, represented by some Redlichiidae, some Paradoxididae, Gigantopygidae, Corynexochidae, Dolichometopidae, Dorypygidae, Zacanthoididae, and seemingly also by *Hemirhodon* (Dolichometopidae) and *Hysterolenus* (Ceratopygidae).

Oryctocephalid type, characterized by ankylosis of the hypostomal and connective sutures, represented by the Oryctocephalidae.

Asaphid type, characterized by reduction of the rostral plate until the connective sutures fused into a single median suture, represented by the Asaphidae, some species of *Theodenisia* (Catillicephalidae), *Stenopilus* (Plethopeltidae), some species of *Leiocoryphe* (Plethopeltidae), *Dikelocephalus* (Dikelocephalidae), *Housia* (Housiidae) and possibly also *Proceratopyge* (Ceratopygidae).

Nileid type, characterized by complete disappearance of connective or median sutures, represented by the Nileidae, Raphiophoridae, most Conocoryphidae, some species of *Dikelocephalus* (Dikelocephalidae), *Levisella* (Loganellidae), *Hungaia* (Hungaiidae), *Lauzonella* (Loganellidae), *Loganellus* (Loganellidae), some species of *Deiocoryphe* (Plethopeltidae), and *Rasettia* (Lecanopygidae).

Olenid type, characterized by complete disappearance of connective and hypostomal sutures, the hypostoma being separated from the anterior cephalic doublure and supported by the ventral membrane, represented by the Olenidae.

Dimeropygid type, characterized by disappearance of the hypostomal suture, the hypostoma becoming "free" and supported by the ventral membrane, with other features as in the primitive ptychopariid type, represented by the Dimeropygidae and apparently also by some Ptychopariidae, including various species of the genus *Ptychoparia* itself.

Bathynotid type, characterized by complete fusion of the hypostomal suture and reduction of the rostral suture to a point from which the connective sutures diverge backward, represented by the Bathynotidae.

Calymenid type, characterized by appearance of a gonatoparian and lastly of a proparian condition, owing to reduction of the posterior part of the ocular segment, represented by the Calymenidae, Pagetiidae, Cheiruridae, most Pliomeridae and Encrinuridae, and probably also Menomoniidae, Burlingiidae, and Norwoodiidae.

Homalonotid type, characterized by the forementioned evolutionary trends combined with others consisting of backward migration of the rostral suture to a dorsal position and backward convergence of the connective sutures, represented by the Homalonotidae.

Phacopid type, characterized by fusion and disappearance of the connective sutures, backward migration of the rostral suture to a dorsal intramarginal position, and ankylosis of the facial sutures, represented by the Dalmanitidae and most Phacopidae.

Proparian olenid type, characterized by development of proparian sutures in olenid stocks, represented by *Saltaspis, Nericiaspis,* some species of *Ctenopyge,* and probably also species of *Peltura* and *?Peltocare.*

Raphiophorid type, characterized by appearance of submarginal sutures by outward migration of the facial sutures in a nileid or phacopid type, represented by some Conocoryphidae, Raphiophoridae, and some Phacopidae like *Ductina.*

Trinucleid type, characterized by development of submarginal sutures by ankylosis and fusion of entomaspidiform sutures, represented by the Trinucleidae.

Harpid type, characterized by appearance of marginal sutures in the same manner as that just specified, represented by the Harpidae.

Harpidid type, characterized by appearance of submarginal sutures by forward migration of posterior sections of normal opisthoparian sutures and fusion with anterior sections, represented by Harpididae such as *Loganopeltoides* and *Loganopeltis.*

AGNOSTID TRILOBITES

No mention has been made, so far, of the agnostids. These sutureless, eyeless trilobites, regarded as primitive by Beecher (1887) and his school, are considered by Stubblefield (1936) and Hupé (1953) as probably "partly neotenic" forms. This partial neoteny could apply to the thoracic features, but certainly not to the cephalic characters. We now know that blindness is a secondary character developed in various trilobites, an "evolutionary novelty" that can hardly be accepted as a neotenic feature. Moreover, *Pagetia* and *Opsidiscus* indicate that in all likelihood the agnostids are descendants from eye-bearing trilobites. *Pagetia* shows that the sutureless agnostids probably descended from trilobites characterized by a ptychopariid sutural pattern with proparian conditions.

The total loss of eyes and sutures in the agnostids, far from indicating partial neoteny, seems to indicate that they are a progressive, specialized offshoot from stock characterized by a ptychopariid sutural pattern. *Pagetia bootes* has a well-developed hypostoma which, according to ÖPIK (1952), probably was attached to a wide rostral plate. Though RASETTI (1952) suggested that *Pagetia* has no rostral suture, there is nothing to substantiate this opinion. If *Pagetia* lacked this suture, it would be the only trilobite in which the 2 symmetrical facial sutures do not unite anteriorly but continue directly (and separately) to the inner margin of the doublure. Probably *Pagetia* has rostral and connective sutures, the sutural pattern being, therefore, of ptychopariid type (with proparian condition). The reduction of the ocular segment in a *Pagetia*-like trilobite would lead to gradual approach of the 2 sections of the facial sutures toward each other, then to their fusion, and finally to their disappearance in a manner illustrated by evolution of the sutures in the *Loganopeltoides-Loganopeltis* stock of the Harpididae. *P. bootes* is similar in this respect to *Loganopeltoides zenkeri,* while *Opsidiscus* practically duplicates the sutural conditions of *Loganopeltis*. This, of course, does not mean that *P. bootes* and *Opsidiscus* belong to the same evolutionary suite. They simply symbolize stages in the possible evolution of the agnostids. The marginal suture developed from the anterior and posterior sections of the facial sutures would finally disappear by ankylosis *"in situ."*

The foregoing discussion indicates that cephalic sutures cannot be used by themselves as criteria for major subdivisions in trilobite classification. They are useful in tracing lineages and establishing familial relationships, but their "evolutionary plasticity" and the obvious polygenetic origin of some recognized types, render them useless above superfamilial rank, or even above the familial category.

TRILOBITE CLASSIFICATION ADOPTED IN TREATISE

It is now abundantly clear that no single feature can be used to classify trilobites. Agreement is expressed with both STUBBLEFIELD and HENNINGSMOEN that in the present state of our knowledge the sum of the cephalic axial characters is the best guide for the establishment of major divisions. However, trilobites were "plastic" and "dynamic" in an evolutionary sense, and the end products of any given lineage may show marked deviations from the primitive or fundamental cephalic axial characters of the stock. This makes it exceedingly difficult to define taxa of more than superfamilial rank without giving extremely detailed descriptions. Moreover, exoskeletal homeomorphy resulting from parallel or convergent evolution is common among trilobites.

The classification adopted in this volume is based mainly on (1) cephalic axial characters, (2) pattern of sutures, and (3) caudalization of postcephalic segments. It may be stated that a majority of the contributors to this volume are in more or less close agreement with the arrangement but some hold very different opinions. Like all other trilobite classifications, it is provisional, for we must admit frankly that 60 years after BEECHER's announcement of what he believed to be a "natural" classification, we are still far from the goal.

In the tabular outline of classification that follows, the numbers of recognized genera and subgenera in each family-group and higher-rank taxa are recorded; where only a single number is given, this refers to genera, but if 2 numbers are given, the first indicates genera and the second, subgenera (for example, "4; 6" signifies 4 genera and 6 subgenera). The outline affords a useful means of explicit statement of the authorship of systematic descriptions in following pages of this volume; the authors are indicated by code letters as here listed.

Authorship of Systematic Descriptions

HARRINGTON, H. J.	HA
HENNINGSMOEN, GUNNAR	HE
HOWELL, B. F.	HO
JAANUSSON, VALDAR	JA
LOCHMAN-BALK, CHRISTINA	LB
MOORE, R. C.	MO
POULSEN, CHRISTIAN	PO
RASETTI, FRANCO	RA
RICHTER, RUDOLF, & RICHTER, EMMA	RR
SCHMIDT, HERTA	SC
SDZUY, KLAUS	SD
STRUVE, WOLFGANG	ST
TRIPP, RONALD	TR
WELLER, J. M.	WE
WHITTINGTON, H. B.	WH

OUTLINE OF CLASSIFICATION

Trilobita *(class)* (1,401; 128). *L.Cam.-M.Perm.* (MO)
  Agnostida *(order)* (79). *L.Cam.-U.Ord.* (MO)
    Agnostina *(suborder)* (66). *L.Cam.-U.Ord.* (MO)

Agnostidae (6). *M.Cam.-L.Ord.* (HO)
Clavagnostidae (1). *M.Cam.-U.Cam.* (HO)
Condylopygidae (3). *L.Cam.-M.Cam.* (HO)
Cyclopagnostidae (1). *M.Cam.* (HO)
Diplagnostidae (4). *M.Cam.* (HO)
Geragnostidae (6). *L.Ord.-U.Ord.* (HO)
Hastagnostidae (10). *M.Cam.-U.Cam.* (HO)
Micragnostidae (5). *U.Cam.-L.Ord.* (HO)
Phalacromidae (8). *M.Cam.-L.Ord.* (HO)
Pseudagnostidae (4). *U.Cam.-L.Ord.* (HO)
Sphaeragnostidae (1). *Ord.* (HO)
Spinagnostidae (17). *L.Cam.-U.Cam.* (HO)
Eodiscina *(suborder)* (13). *L.Cam.-M.Cam.* (MO)
Eodiscidae (6). *L.Cam.-M.Cam.* (HO)
Pagetiidae (7). *L.Cam.-M.Cam.* (HO)
Redlichiida *(order)* (107; 22). *L.Cam.-M.Cam.* (MO)
Olenellina *(suborder)* (22; 3). *L.Cam.* (MO)
Olenellidae (20). *L.Cam.* (PO)
Olenellinae (7). *L.Cam.* (PO)
Callaviinae (3). *L.Cam.* (PO)
Elliptocephalinae (1). *L.Cam.* (PO)
Fallotaspidinae (1). *L.Cam.* (PO)
Holmiinae (3). *L.Cam.* (PO)
Neltneriinae (1). *L.Cam.* (PO)
Nevadiinae (2). *L.Cam.* (PO)
Olenelloidinae (1). *L.Cam.* (PO)
Wanneriinae (1). *L.Cam.* (PO)
Daguinaspididae (2; 3). *L.Cam.* (PO)
Redlichiina *(suborder)* (83; 19). *L.Cam.-M.Cam.* (MO)
Redlichiacea *(superfamily)* (25; 2). *L.Cam.-M. Cam.* (MO)
Redlichiidae (10). *L.Cam.* (PO)
Redlichiinae (5). *L.Cam.* (PO)
Pararedlichiinae (5). *L.Cam.* (PO)
Neoredlichiidae (4; 2). *L.Cam.* (HA)
Saukiandidae (2). *L.Cam.* (HA)
Gigantopygidae (1). *L.Cam.* (HA)
Despujolsiidae (1). *L.Cam.* (HA)
Yinitidae (1). *M.Cam.* (HA)
Abadiellidae (3). *L.Cam.-M.Cam.* (HA)
Dolerolenidae (1). *Up.L.Cam.* (HA)
Family Uncertain (2). *L.Cam.* (HA)
Ellipsocephalacea *(superfamily)* (42; 17). *L. Cam.-M.Cam.* (HE)
Ellipsocephalidae (18; 9). *L.Cam.-M.Cam.* (HE)
Ellipsocephalinae (8). *L.Cam.-M.Cam.* (HE)
Strenuellinae (4; 7). *L.Cam.-M.Cam.* (HE)
Kingaspidinae (2; 2). *L.Cam.* (HE)
Palaeoleninae (3). *L.Cam.* (HE)
Antatlasiinae (1). *L.Cam.* (HE)
Protolenidae (21; 8). *L.Cam.* (HE)
Termierellinae (6; 3). *L.Cam.* (HE)
Myopsoleninae (3). *L.Cam.* (HE)
Protoleninae (8; 5). *L.Cam.* (HE)
Bigotininae (1). *L.Cam.* (HE)
?Aldonaiinae (1). *L.Cam.* (HE)
Subfamily Uncertain (2). *L.Cam.* (HE)
?Yunnanocephalidae (1). *L.Cam.* (HE)
Family Uncertain (2). *L.Cam.* (HE)
Paradoxidacea *(superfamily)* (16). *Up.L.Cam.-M.Cam.* (MO)
Paradoxididae (15). *Up.L.Cam.-M.Cam.* (PO)
Paradoxidinae (5). *M.Cam.* (PO)
Centropleurinae (3). *M.Cam.* (PO)
Metadoxidinae (3). *Up.L.Cam.* (PO)
Xystridurinae (2). *Up.L.Cam.-M.Cam.* (PO)
Subfamily Uncertain (2). *M.Cam.* (MO)
Hicksiidae (1). *L.Cam.* (HA)
Bathynotina *(suborder)* (2). *Up.L.Cam.-Low.M. Cam.* (LB)
Bathynotidae (2). *Up.L.Cam.-Low.M.Cam.* (LB)
Corynexochida *(order)* (73; 4). *L.Cam.-U.Cam.* (MO)
Dorypygidae (20). *L.Cam.-U.Cam.* (PO)
Ogygopsidae (1). *M.Cam.* (RA)
Oryctocephalidae (7). *L.Cam.-M.Cam.* (RA)
Dolichometopidae (29; 4). *L.Cam.-U.Cam.* (PO)
Corynexochidae (4). *M.Cam.* (PO)
Corynexochinae (3). *M.Cam.* (PO)
Acontheinae (1). *M.Cam.* (PO)
Zacanthoididae (8). *L.Cam.-M.Cam.* (RA)
Dinesidae (4). *Up.L.Cam.-Low.M.Cam.* (LB)
Ptychopariida *(order)* (798; 61). *L.Cam.-M.Perm.* (HE)
Ptychopariina *(suborder)* (474; 11). *L.Cam.-U. Ord.* (HE)
Ptychopariacea *(superfamily)* (63). *L.Cam.-L. Ord.* (MO)
Ptychopariidae (32). *L.Cam.-L.Ord.* (MO)
Ptychopariinae (10). *M.Cam.-U.Cam.* (HO)
Periommelinae (1). *L.Cam.* (RA)
Eulominae (2). *L.Ord.* (RA)
Nassoviinae (4). *M.Cam.* (HO)
Antagminae (13). *L.Cam.-Low.M.Cam.* (RA)
Conokephalininae (3). *M.Cam.-U.Cam.* (LB)
Alokistocaridae (30). *L.Cam.-U.Cam.* (HO)
Conocoryphacea *(superfamily)* (23). *L.Cam.-U. Ord.* (MO)
Conocoryphidae (16). *L.Cam.-L.Ord.* (PO)
?Shumardiidae (7). *?M.Cam., U.Cam.-U.Ord.* (PO)
Emmrichellacea *(superfamily)* (15). *M.Cam.-L. Ord.* (MO)
Emmrichellidae (13). *M.Cam.-L.Ord.* (MO)
Emmrichellinae (9). *M.Cam.-L.Ord.* (HO, MO)
Changshaniinae (4). *M.Cam.* (HO-MO)
Liostracinidae (2). *M.Cam.-U.Cam.* (HO)
Crepicephalacea *(superfamily)* (7). *M.Cam.-U. Cam.* (LB)
Crepicephalidae (5). *M.Cam.-U.Cam.* (LB)
Tricrepicephalidae (2). *U.Cam.* (LB)
Nepeacea *(superfamily)* (1). *M.Cam.* (LB)
Nepeidae (1). *M.Cam.* (LB)
Dikelocephalacea *(superfamily)* (34). *L.Cam.-U.Cam.* (LB)

Idahoiidae (7). *U.Cam.* (LB)
Dikelocephalidae (5). *U.Cam.* (LB)
Pterocephalidae (16). *U.Cam.* (LB)
Housiidae (1). *U.Cam.* (LB)
Andrarinidae (5). *L.Cam.-M.Cam.* (HO)
Olenacea *(superfamily)* (45; 5). *M.Cam.-U.Ord.* (HE)
Olenidae (37; 5). *U.Cam.-U.Ord.* (PO)
Oleninae (6). *U.Cam.-L.Ord.* (PO)
Leptoplastinae (6; 3). *U.Cam.-L.Ord.* (PO)
Pelturinae (16). *U.Cam.-L.Ord.* (PO)
Triarthrinae (9; 2). *U.Cam.-U.Ord.* (PO)
Papyriaspididae (6). *M.Cam.-U.Cam.* (PO)
Hypermecaspididae (2). *L.Ord.-M.Ord.* (HA)
Illaenuracea *(superfamily)* (13). *U.Cam.* (LB)
Illaenuridae (2). *U.Cam.* (LB)
Shirakiellidae (1). *U.Cam.* (LB)
Parabolinoididae (10). *U.Cam.* (LB)
Solenopleuracea *(superfamily)* (73). *M.Cam.-L. Ord.* (HE)
Solenopleuridae (33). *M.Cam.-L.Ord.* (PO)
Solenopleurinae (13). *M.Cam.-U.Cam.* (PO)
Acrocephalitinae (7). *M.Cam.-U.Cam.* (PO)
Saoinae (4). *M.Cam.* (PO)
Hystricurinae (9). *U.Cam.-L.Ord.* (PO)
Agraulidae (2). *M.Cam.* (HE)
Lonchocephalidae (11). *U.Cam.* (RA)
Dokimocephalidae (10). *U.Cam.* (LB)
Avoninidae (3). *Up.M.Cam.-U.Cam.* (LB)
Catillicephalidae (8). *U.Cam.* (RA)
Kingstoniidae (6). *M.Cam.-U.Cam.* (LB)
Anomocaracea *(superfamily)* (26; 2). *M.Cam.-U.Cam.* (HO)
Anomocaridae (26; 2). *M.Cam.-U.Cam.* (HO)
Asaphiscacea *(superfamily)* (19; 2). *M.Cam.-U. Cam.* (HO)
Asaphiscidae (19; 2). *M.Cam.-U.Cam.* (HO).
Asaphiscinae (16). *M.Cam.-U.Cam.* (HO)
Blountiinae (3; 2). *U.Cam.* (HO)
Burlingiacea *(superfamily)* (2). *M.Cam.-U.Cam.* (PO)
Burlingiidae (2). *M.Cam.-U.Cam.* (PO)
Komaspidacea *(superfamily)* (16). *M.Cam.-U. Ord.* (LB)
Komaspididae (8). *Up.M.Cam.-L.Ord.* (LB)
Elviniidae (5). *U.Cam.* (LB)
Telephinidae (1). *M.Ord.-U.Ord.* (WH)
Glaphuridae (2). *M.Ord.* (WH)
Raymondinacea *(superfamily)* (11). *U.Cam.* (LB)
Raymondinidae (11). *U.Cam.* (LB)
Raymondininae (5). *U.Cam.* (LB)
Cedariinae (2). *U.Cam.* (LB)
Llanoaspidinae (4). *U.Cam.* (LB)
Norwoodiacea *(superfamily)* (15). *M.Cam.-L. Ord.* (LB)
Norwoodiidae (5). *U.Cam.-L.Ord.* (LB)
Menomoniidae (6). *M.Cam.-U.Cam.* (LB)
Bolaspididae (4). *M.Cam.* (HO)
Marjumiacea *(superfamily)* (35). *M.Cam.-L. Ord.* (LB)
Marjumiidae (20). *M.Cam.-U.Cam.* (LB)
Coosellidae (4). *U.Cam.* (LB)
Pagodiidae (10). *M.Cam.-L.Ord.* (LB)
Cheilocephalidae (1). *U.Cam.* (LB)
Leiostegiacea *(superfamily)* (16; 2). *M.Cam.-L. Ord.* (LB)
Leiostegiidae (16; 2). *M.Cam.-L.Ord.* (LB)
Leiostegiinae (12; 2). *U.Cam.-L.Ord.* (LB)
Eochuangiinae (2). *M.Cam.-U.Cam.* (LB)
Iranaspidinae (2). *U.Cam.-L.Ord.* (LB)
Damesellacea *(superfamily)* (10). *M.Cam.-U. Cam.* (LB)
Damesellidae (6). *M.Cam. U.Cam.* (LB)
Damesellinae (4). *M.Cam.* (LB)
Drepanurinae (2). *M.Cam.-U.Cam.* (LB)
Kaolishaniidae (4). *U.Cam.* (LB)
Ptychaspidacea *(superfamily)* (24). *U.Cam.* (LB)
Ptychaspididae (13). *U.Cam.* (LB)
Saukiidae (6). *U.Cam.* (LB)
Eurekiidae (5). *Up.U.Cam.* (LB)
Remopleuridacea *(superfamily)* (25). *U.Cam.-U.Ord.* (WH)
Remopleurididae (21). *U.Cam.-U.Ord.* (WH)
Remopleuridinae (6). *L.Ord.-U.Ord.* (WH)
Richardsonellinae (12). *U.Cam. - M.Ord.* (WH)
Subfamily Uncertain (3). *U.Cam.* (WH)
Loganellidae (3). *U.Cam.* (RA)
Hungaiidae (1). *U.Cam.* (LB)
Superfamily Uncertain (1). *U.Cam.* (HE)
Diceratocephalidae (1). *U.Cam.* (HE)
Asaphina *(suborder)* (112; 20). *Up.M.Cam.-U. Ord.* (JA)
Asaphacea *(superfamily)* (94; 20). *U.Cam.-U. Ord.* (JA)
Asaphidae (68; 16). *U.Cam.-U.Ord.* (JA)
Asaphinae (11; 7). *L.Ord.-U.Ord.* (JA)
Isotelinae (27; 7). *L.Ord.-U.Ord.* (JA)
Niobinae (7). *U.Cam.-L.Ord.* (JA)
Ogygiocaridinae (5). *L.Ord.-M.Ord.* (JA)
Promegalaspidinae (2). *U.Cam.-L.Ord.* (JA)
Symphysurininae (5; 2). *L.Ord.* (JA)
Thysanopyginae (3). *L.Ord.* (JA)
Subfamily Uncertain (3). *U.Cam.-M.Ord.* (JA)
Unrecognizable asaphid genera (5). *Ord.* (JA)
Taihungshaniidae (4). *L.Ord.* (JA)
Tsinaniidae (2). *U.Cam.* (LB)
Nileidae (11; 4). *L.Ord.-U.Ord.* (PO)
Dikelokephalinidae (9). *L.Ord.* (LB)
Cyclopygacea *(superfamily)* (7). *Ord.* (RR)
Cyclopygidae (7). *Ord.* (RR)
Ceratopygacea *(superfamily)* (11). *M.Cam.-L. Ord.* (PO)
Ceratopygidae (11). *M.Cam.-L.Ord.* (PO)
Illaenina *(suborder)* (144; 33). *Ord.-M.Perm.* (JA)
Illaenacea *(superfamily)* (25; 10). *Ord.-Sil.*

(JA)
Styginidae (4). *L.Ord.-U.Ord.* (WH)
Thysanopeltidae (4; 6). *M.Ord.-Low.U.Dev.* (RR)
Illaenidae (17; 14). *L.Ord.-Sil.* (JA)
Illaeninae (7). *L.Ord.-Sil.* (JA)
Bumastinae (5; 4). *M.Ord.-Sil.* (JA)
Ectillaeninae (3). *L.Ord.-U.Ord.* (JA)
?Theamataspidinae (1). *M.Ord.-U.Ord.* (JA)
Subfamily Uncertain (1). *Ord.* (JA)
Bathyuracea *(superfamily)* (22). *U.Cam.-M.Ord.* (WH)
Bathyuridae (17). *L.Ord.-M.Ord.* (WH)
Lecanopygidae (5). *U.Cam.-L.Ord.* (LB)
Holotrachelacea *(superfamily)* (1). *U.Ord.* (JA)
Holotrachelidae (1). *U.Ord.* (JA)
Proetacea *(superfamily)* (96; 23). *L.Ord.-M.Perm.* (RR-ST)
Proetidae (41; 19). *M.Ord. - L.Carb.(Miss.)* (RR-ST)
Proetinae (4; 2). *M.Ord.-M.Dev.* (RR-ST)
Cornuproetinae (6; 3). *Ord.-U.Dev.* (RR-ST)
Dechenellinae (3; 4). *Up.L.Dev.-U.Dev.* (RR-ST)
Cyrtosymbolinae (13, 10). *L.Dev.-L.Carb.* (RR-ST)
Proetidellinae (9). *M.Ord.-M.Dev.* (RR-ST)
Tropidocoryphinae (6). *Sil.-Low.U.Dev.* (RR-ST)
Phillipsiidae (24). *L.Carb.(Miss.) - M.Perm.* (WE)
Otarionidae (4). *M.Ord.-U.Carb.* (RR-SC)
Otarioninae (3). *M.Ord.-U.Carb.* (RR-SC)
Cyphaspidinae (1). *L.Dev.-M.Dev.* (RR-SC)
Aulacopleuridae (2; 2). *M.Ord.-M.Dev.* (RR-SC)
Brachymetopidae (5; 2). *L.Dev.-U.Carb.* (SC)
Phillipsinellidae (1). *U.Ord.* (WH)
Celmidae (1). *L.Ord.* (JA)
Plethopeltidae (7). *U.Cam.-L.Ord.* (LB)
Dimeropygidae (5). *L.Ord.-U.Ord.* (WH)
Family Uncertain (6). *Sil.-Miss.* (RR-ST-WE)
Harpina *(suborder)* (18). *U.Cam.-U.Dev.* (WH)
Harpidae (12). *L.Ord.-U.Dev.* (WH)
Harpididae (4). *U.Cam.-L.Ord.* (WH)
Entomaspididae (2). *U.Cam.-L.Ord.* (RA)
Trinucleina *(suborder)* (50). *L.Ord.-M.Sil.* (WH)
Trinucleidae (27). *L.Ord.-U.Ord.* (WH)
Trinucleinae (2). *L.Ord.-M.Ord.* (WH)
Tretaspidinae (3). *M.Ord.-U.Ord.* (WH)
Cryptolithinae (21). *L.Ord.-U.Ord.* (WH)
Novaspidinae (1). *U.Ord.* (WH)
Orometopidae (1). *L.Ord.* (WH)
Dionididae (4). *M.Ord.-U.Ord.* (WH)
Raphiophoridae (9). *L.Ord.-M.Sil.* (WH)
Endymioniidae (2). *L.Ord.-M.Ord.* (WH)
Alsataspididae (2). *L.Ord.* (WH)
Hapalopleuridae (4). *L.Ord.* (HA)
Ityophoridae (1). *U.Ord.* (WH)
Phacopida *(order)* (173; 37). *L.Ord.-U.Dev.* (HE)
Cheirurina *(suborder)* (73; 9). *L.Ord.-M.Dev.* (HE)
Cheiruridae (32; 7). *L.Ord.(Tremadoc.)-M.Dev.* (HE)
Cheirurinae (11; 2). *L.Ord.-M.Dev.* (HE)
Cyrtometopinae (7; 5). *L.Ord.-Sil.* (HE)
Acanthoparyphinae (4). *L.Ord.-U.Ord.* (HE)
Sphaerexochinae (2). *M.Ord.-Sil., ?Dev.* (HE)
Deiphoninae (4). *M.Ord.-Sil.* (HE)
Areiinae (1). *M.Ord.-U.Ord.* (HE)
?Heliomerinae (2). *M.Ord.-U.Ord.* (HE)
Subfamily Uncertain (1). *Sil.-L.Dev.* (HE)
Pliomeridae (25). *L.Ord.-U.Ord.* (HA)
Pliomerinae (5). *L.Ord.-U.Ord.* (HA)
Pilekiinae (8). *L.Ord.* (HA)
Protopliomeropinae (9). *L.Ord.* (HA)
Pliomerellinae (1). *M.Ord.-U.Ord.* (HA)
Placopariinae (1). *M.Ord.* (HA)
Diaphanometopinae (1). *L.Ord.* (JA)
Encrinuridae (14; 2). *L.Ord.-Sil.* (HE)
Encrinurinae (4; 2). *M.Ord.-Sil.* (HE)
Cybelinae (5). *L.Ord.-U.Ord.* (HE)
Dindymeninae (3). *M.Ord.-U.Ord.* (HE)
Staurocephalinae (2). *M.Ord.-Sil.* (HE)
Family Uncertain (2). *L.Ord.-M.Ord.* (HE)
Calymenina *(suborder)* (27; 8). *LowL.Ord.-M.Dev.* (SD)
Calymenidae (15; 2). *L.Ord.(Arenig.)-M.Dev.* (WH)
Calymeninae (14; 2). *L.Ord.-M.Dev.* (WH)
Pharostomatinae (1). *M.Ord.-U.Ord.* (WH)
Homalonotidae (12; 6). *L.Ord.-M.Dev.* (SD)
Bavarillinae (1). *L.Ord.* (SD)
Eohomalonotinae (2; 2). *L.Ord.-U.Ord.* (SD)
Colpocoryphinae (3). *L.Ord.-M.Ord.(Llandeil.)* (SD)
Homalonotinae (5; 4). *M.Sil.-M.Dev.* (SD)
Phacopina *(suborder)* (73; 20). *L.Ord.-Up.U.Dev.* (RR-ST)
Phacopacea *(superfamily)* (18). *Sil.-U.Dev.* (RR-ST)
Phacopidae (18). *Sil.-U.Dev.* (RR-ST)
Phacopinae (10). *Sil.-U.Dev.* (RR-ST)
Bouleiinae (1). *Dev.* (ST)
Phacopidellinae (6). *Sil.-U.Dev.* (ST)
Subfamily Uncertain (1). *Sil.* (ST)
Dalmanitacea *(superfamily)* (55; 20). *L.Ord.-U.Dev.* (RR-ST)
Dalmanitidae (31; 9). *Low.M.Ord. - U.Dev.* (RR-ST)
Dalmanitinae (13). *Sil.-M.Dev.* (RR-ST)
Zeliszkellinae (4; 4). *Low.M.Ord. - U.Ord., ?M.Sil.* (ST)
Acastavinae (3). *U.Sil.-L.Dev.* (ST)
Asteropyginae (11; 5). *L.Dev.-U.Dev.* (ST)
Calmoniidae (15; 2). *Ord.-M.Dev.* (ST)
Calmoniinae (11). *Ord.-M.Dev.* (ST)
Acastinae (4; 2). *Ord.-L.Dev.* (ST)
Pterygometopidae (5; 6). *M.Ord.-U.Ord.* (ST)

(Continued on page O167)

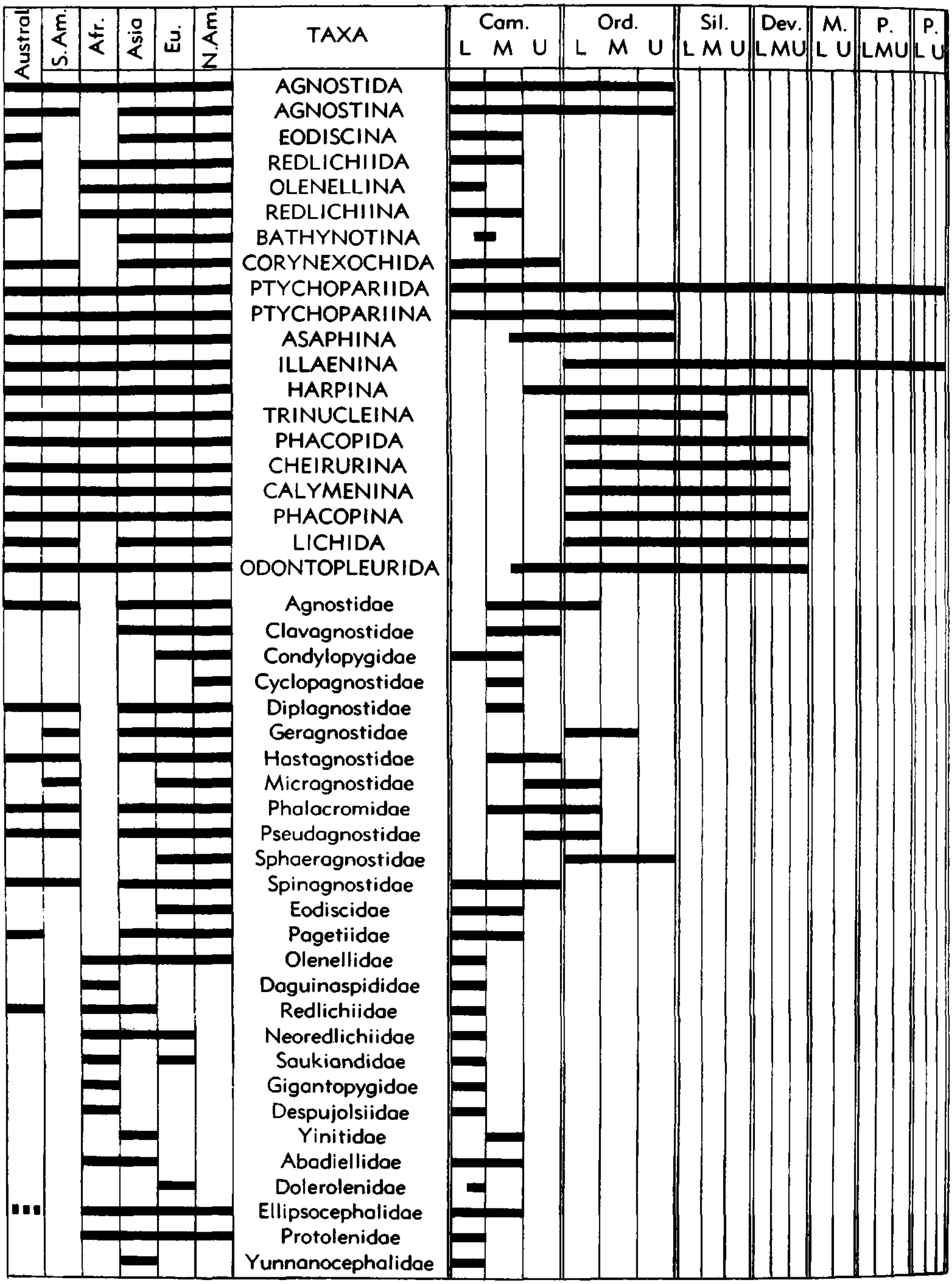

FIG. 107a. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 1 (MOORE, n). [Range of Geragnostidae revised; see p. O161.]

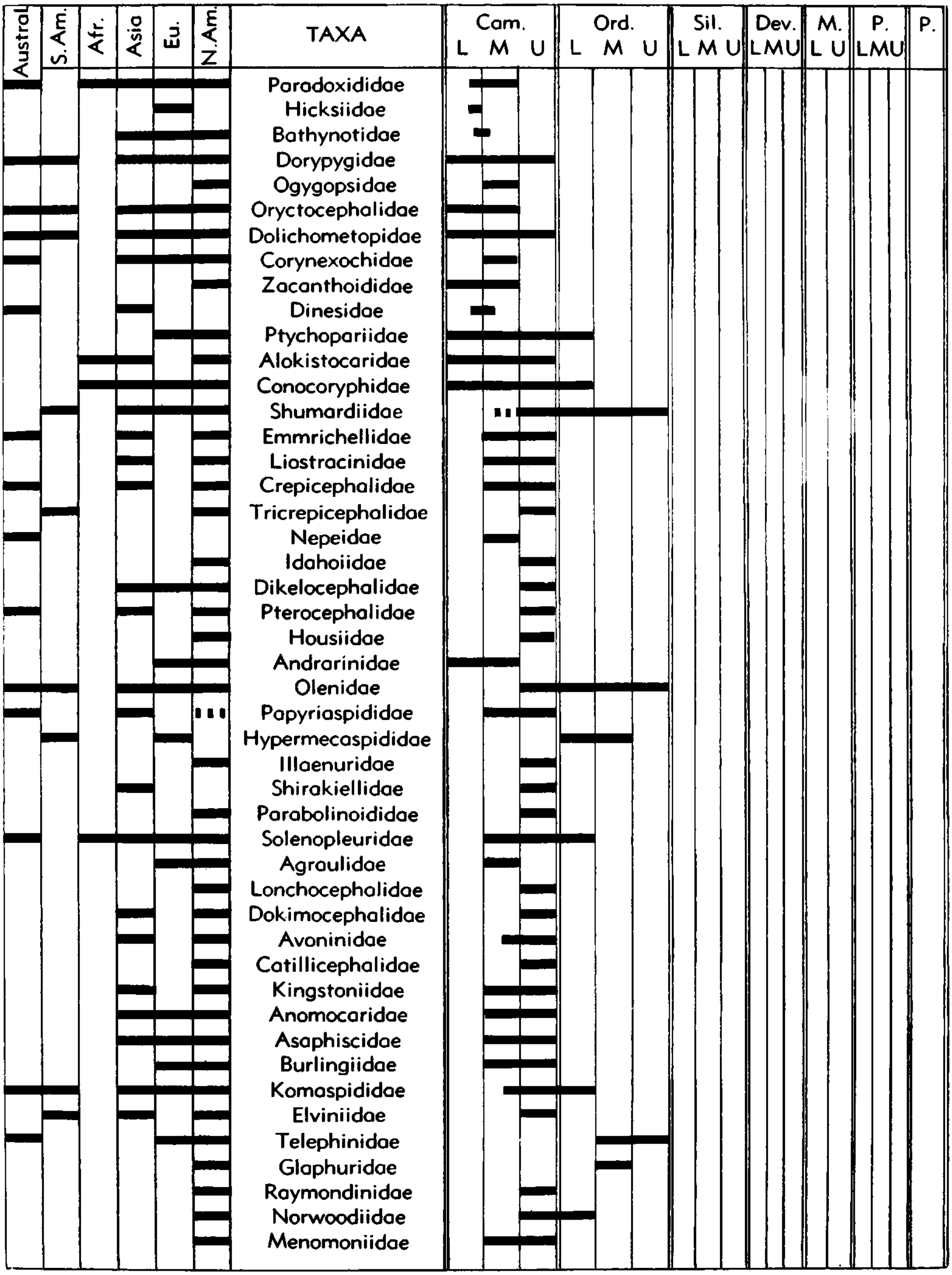

FIG. 107b. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 2 (MOORE, n). [Range of Emmrichellidae revised, see p. O161.]

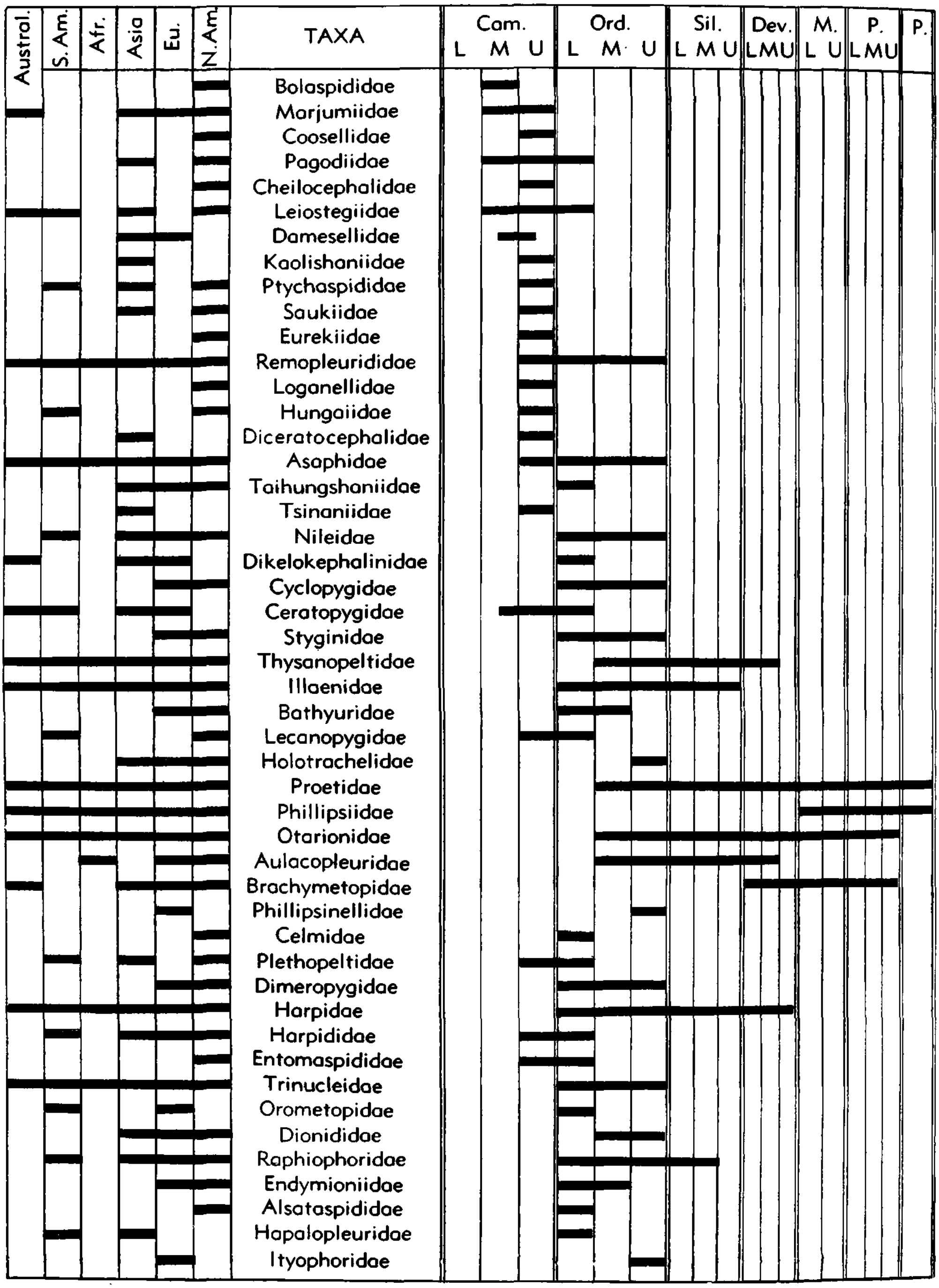

FIG. 107c. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 3 (MOORE, n).

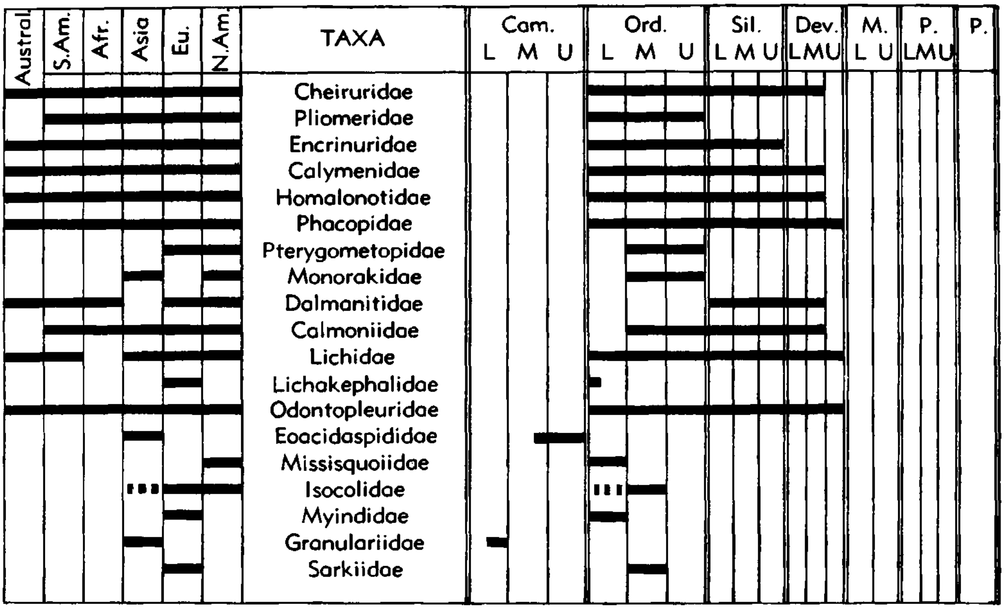

FIG. 107d. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 4 (MOORE, n). [Range of Phacopidae and Dalmanitidae revised; see p. O163.]

(Continued from page O163)

Pterygometopinae (4; 6). *M.Ord.-U.Ord.* (ST)
Chasmopinae (1). *Ord.* (ST)
Monorakidae (4; 3). *M.Ord.-U.Ord.* (ST)
Lichida *(order)* (25). *L.Ord.-U.Dev.* (MO)
Lichidae (24). *L.Ord.-U.Dev.* (TR)
Lichinae (10). *L.Ord.-M.Dev.* (TR)
Homolichinae (3). *L.Ord.-M.Sil.* (TR)
Tetralichinae (2). *M.Ord.-U.Ord.* (TR)
Ceratarginae (9). *M.Ord.-U.Dev.* (TR)
Lichakephalidae (1). *L.Ord.* (TR)
Odontopleurida *(order)* (25; 4). *Up.M.Cam.U.Dev.* (WH)
Odontopleuridae (22; 4). *L.Ord.-U.Dev.* (WH)
Odontopleurinae (7; 2). *M.Ord.-U.Dev.* (WH)
Miraspidinae (9; 2). *M.Ord.-M.Dev.* (WH)
Selenopeltinae (1). *M.Ord.-U.Ord.* (WH)
Apianurinae (2). *M.Ord.-U.Ord.* (WH)
Subfamily Uncertain (3). *L.Sil.-M.Dev.* (WH)
Eoacidaspididae (3). *Up.M.Cam.-U.Cam.* (JA)
Order Uncertain (8).
Missisquoiidae (1). *L.Ord.* (LB)
Isocolidae (4). *?L.Ord., M.Ord.-U.Ord.* (WH)
Myindidae (1). *L.Ord.* (WH)
Granulariidae (1). *Up.L.Cam.* (HE)
Sarkiidae (1). *M.Ord.* (HE)
Order and Family Uncertain (121)
Lower Cambrian genera (14). *L.Cam.*
Middle Cambrian genera (26). *M.Cam.*
Upper Cambrian genera (41). *U.Cam.*
Ordovician genera (38). *Ord.-U.Ord.*
Devonian genera (2). *Dev.*
Unrecognizable genera (60)
Nomina nuda (3)
Supposed Trilobita here rejected from class (2)

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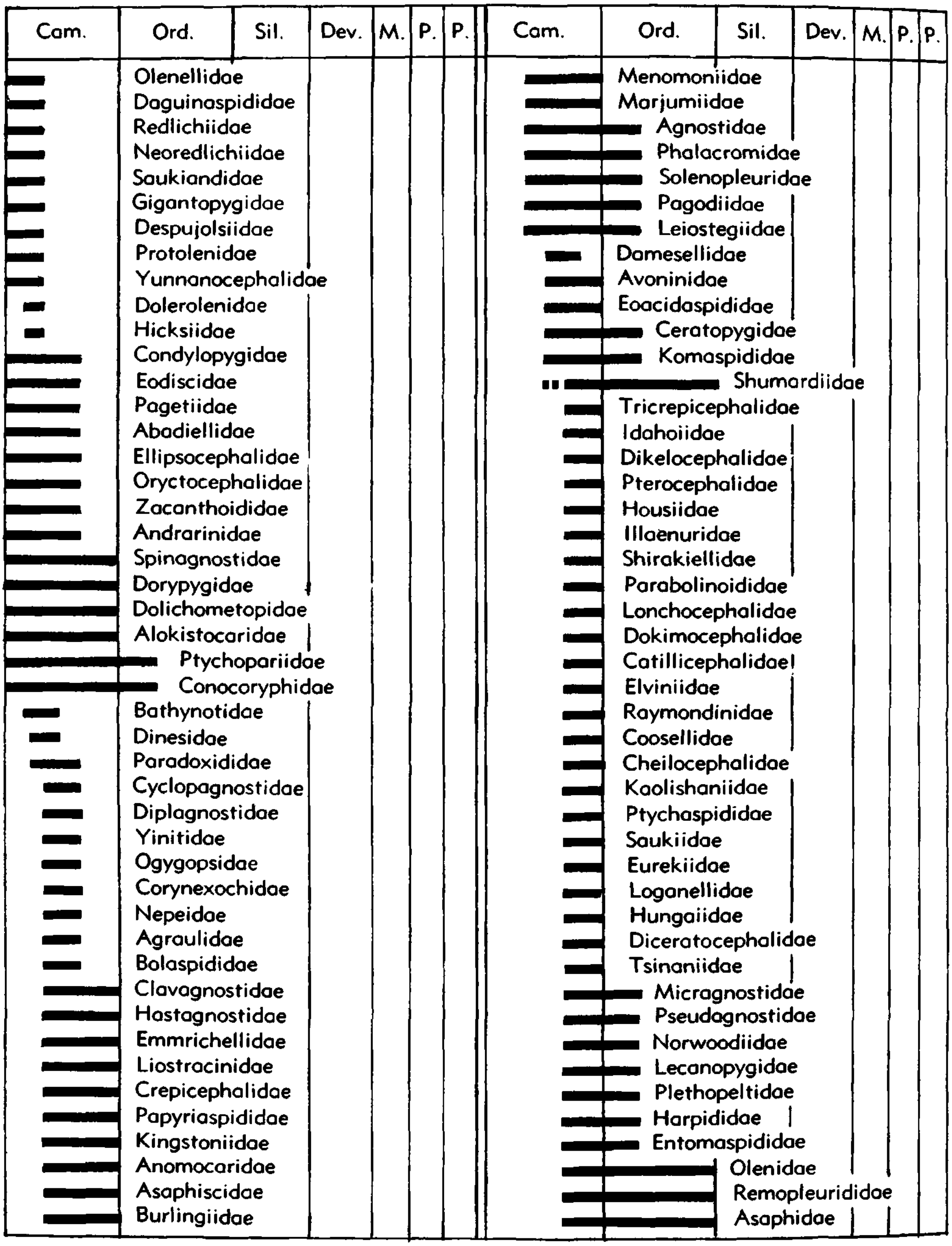

FIG. 107e. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 5. In this diagram only families present in Cambrian rocks are shown, stratigraphically arranged; of the group, which comprises two thirds of all currently recognized trilobite families, only 4 families persist through the Ordovician and none are post-Ordovician (MOORE, n). [Range of Emmrichellidae revised; see p. O161.]

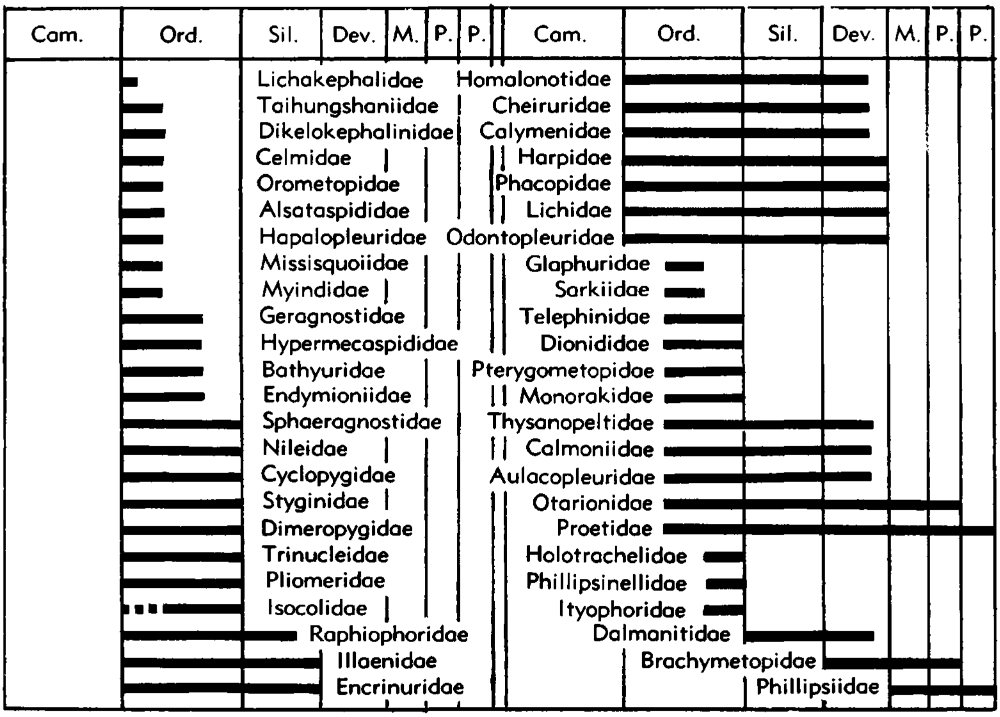

FIG. 107f. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 6. This diagram shows post-Cambrian families stratigraphically arranged, all except 3 families occurring in Ordovician rocks and two thirds of these being confined to the Ordovician (MOORE, n). [Ranges of Geragnostidae, Phacopidae, and Dalmanitidae revised; see p. O161, O163.]

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SYSTEMATIC DESCRIPTIONS

By H. J. Harrington, Gunnar Henningsmoen, B. F. Howell, Valdar Jaanusson, Christina Lochman-Balk, R. C. Moore, Christian Poulsen, Franco Rasetti, Emma Richter,[1] Rudolf Richter,[2] Herta Schmidt, Klaus Sdzuy, Wolfgang Struve, Ronald Tripp, J. M. Weller, and H. B. Whittington

CONTENTS

[1] Deceased 15 November 1956. [2] Deceased 5 January 1957.

As explained in the introduction to this volume, the authorship of sections concerned with the Trilobita is divided in a manner that makes explicit indication of parts contributed by different individuals difficult. This pertains especially to the systematic descriptions. By use of index letters associated with the names of taxa given in the tabular outline of divisions of the Trilobita (p. *O*160), the authors of diagnoses and discussions relating to each taxon are specified. It is needed to add the statement that just before submittal of the assembled typescript to the press, the Editor has inserted approximately 75 genera introduced in recent Russian publications on Trilobita, distributing these among families according to judgment of the respective Russian authors; the *Treatise* authors concerned with these families could not be asked to study the new genera unless a prospective considerable delay in publication was thought to be warranted. Such delay is considered undesirable, and therefore, the inclusion of various nominal genera in different families is by action of MOORE or HENNINGSMOEN (indicated by Mo or HE).

Class TRILOBITA Walch, 1771

[as Trilobitae WALCH, 1771] [Type—*Dalmanites* BARRANDE, 1852, designated by HARRINGTON, HENNINGSMOEN, and MOORE, herein]

Marine arthropods characterized by a generally subelliptical, arched or flat dorsal exoskeleton of mineralized chitinous composition, divided longitudinally into 3 distinct parts (lobes) and with a distinct, relatively large head shield (cephalon), which articulates axially with the thorax composed of articulated transverse segments, the hindmost almost invariably articulating with a tail shield (pygidium) formed by fusion of segments like those of the thorax. Margins of exoskeleton may bend inward ventrally to form a doublure. Length of average adults commonly 2 to 10 cm. but extreme range extending from approximately 2 mm. to a known maximum of 70 cm. Cephalon typically marked by a somewhat raised axial portion (glabella) that is bounded by a narrow furrow and surficially indented by transverse depressions (glabellar furrows); compound eyes present in most forms, located along lines (facial sutures) of ecdysial cleavage that divide the cephalon into a central portion (cranidium, comprising glabella and fixigenae) and lateral portions (librigenae), which tend to become dissociated. Cephalic doublure may include separate median plates such as hypostoma and also a rostral plate that exceptionally may encroach upon dorsal side. Thoracic segments 2 to 40 or more, each commonly with strongly defined axial portion and somewhat flattened and grooved lateral portions (pleurae). Pygidium highly variable in shape and size. Lateral and dorsal hollow spines may be present on cephalon, thorax, or pygidium. Ventral appendages (rarely preserved) include an anterior pair of uniramous antennae followed by a series of pairs of similarly constructed biramous limbs decreasing in size toward posterior end and distributed with one pair to each segment; in one genus *(Olenoides)* the posterior segment possesses a pair of antenniform cerci. Trilobite remains usually are found dissociated into their component skeletal elements. *L.Cam.-M.Perm.*

Order AGNOSTIDA Kobayashi, 1935

[=suborder Isopygia GÜRICH, 1907; order Miomera JAEKEL, 1909] [Type—*Agnostus* BRONGNIART, 1822]

Diminutive trilobites with subequal cephalon and pygidium and possessing only 2 or 3 thoracic segments. *L.Cam.-U.Ord.*

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* HARRINGTON & LEANZA, 1957 (*pro* Agnostini SALTER, 1864)] [=superfamily Eodiscidea RICHTER, 1933 *(partim)*; suborder Agnostida WHITEHOUSE, 1939; superfamily Agnostidea WESTERGÅRD, 1946; order Agnostida RASETTI, 1948; superfamily Agnostacea HENNINGSMOEN, 1951 *(partim)*; superfamily Agnostoidae HUPÉ, 1953] [Type—*Agnostus* BRONGNIART, 1822]

Cephalon without eyes or facial sutures; hypostoma unknown. Thorax with 2 segments. Pygidium with 3 or fewer rings on axis, border evenly rounded or bearing a pair of spines. *L.Cam.-U.Ord.*

Family AGNOSTIDAE M'Coy, 1849

[=Battoides HAWLE & CORDA, 1847]

Longitudinal furrow in front of glabella, which has 2 main lobes; axis of pygidium with 2 main lobes rounded at rear end. *M.Cam.-L.Ord.*

Agnostus BRONGNIART, 1822 [**Entomostracites. pisiformis* WAHLENBERG, 1821] [=*Battus* DALMAN, 1827]. Axis of pygidium with 3 lobes, posterior one only a little expanded at rear and not approaching border of shield; surface of genae

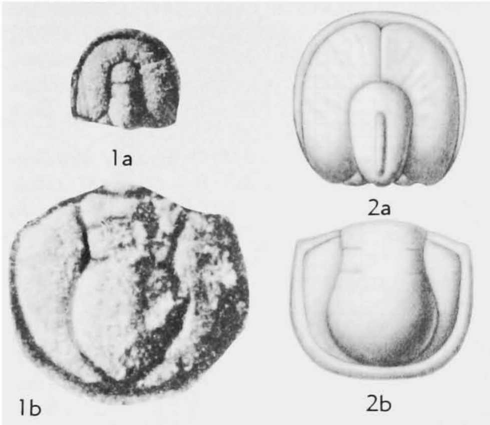


FIG. 108. Agnostidae (p. O173).

smooth or corrugated. *U.Cam.*, Eu.-China.——FIG. 109,*1*. **A. pisiformis* (WAHL.), Agnostus pisiformis Z., Swed.; *1a,b*, ceph., pyg., ×4.7 (331*).

Acmarhachis RESSER, 1938 [**A. typicalis*]. Longitudinal furrow in front of glabella poorly developed; rear lobe of pygidial axis expanded but bluntly pointed at posterior extremity, which reaches the border. *U.Cam.*——FIG. 108,*1*. **A. typicalis*, Nolichucky F., Ala.; *1a*, ceph., ×8.5; *1b*, pyg., ×14.5 (457*).

Aspidagnostus WHITEHOUSE, 1936 [**A. parmatus*]. Glabella with longitudinal furrow in front of single lobe that is half as long as cephalon; axis of pygidium expanded at rear, reaching back to border, and bearing 2 faint transverse furrows. *U.Cam.*, Queensl.——FIG. 108,*2*. **A. parmatus*, Elrathiella Z.; *2a,b*, ceph., pyg., ×6 (339*).

Fallagnostus HOWELL, 1935 [**F. blayaci*]. Cephalon like that of *Agnostus;* axis of pygidium distinctly lobed, with parallel sides, not reaching rear border. *M.Cam.*, Fr.——FIG. 109,*2*. **F. blayaci*, Paradoxides beds; *2a*, ceph., ×8; *2b*, pyg., ×8.85 (410*).

Homagnostus HOWELL, 1935 [**Agnostus pisiformis obesus* BELT, 1867] [=*Proagnostus* BUTTS, 1926; *Oncagnostus* WHITEHOUSE, 1936]. Longitudinal furrow in front of glabella poorly developed; axis of pygidium expanded and evenly rounded at rear, reaching almost to posterior end of shield; surface of shields smooth or corrugated. *U.Cam.*, Eu.-Newf.-Que.-Vt.-Tex.-B.C.-Sib.-China-Queensl.——FIG. 109,*3*. **H. obesus* (BELT), Olenus Z., Kiu-lung F., Rhodonaspis Stage, Queensl.; ×10.3 (331*).

Neoagnostus KOBAYASHI, 1955 [**N. aspidoides*]. Glabella narrow, with longitudinal furrow in front of anterior main lobe, which is divided into 3 subglobular parts of equal size; axis of pygidium rather small, trilobed, not reaching backward to border. *L.Ord.*, B.C.-Arg.——FIG. 110,*1*. **N. aspidoides*, McKay F., B.C.; *1a,b*, ceph., ×11; pyg., ×10.5 (108*).

Family CLAVAGNOSTIDAE Howell, 1937

Glabella with single main lobe, longitudinal furrow in front of it present or absent; axis of pygidium long and narrow, with pointed rear end dividing shield into 2 side lobes; dorsal exoskeleton smooth.

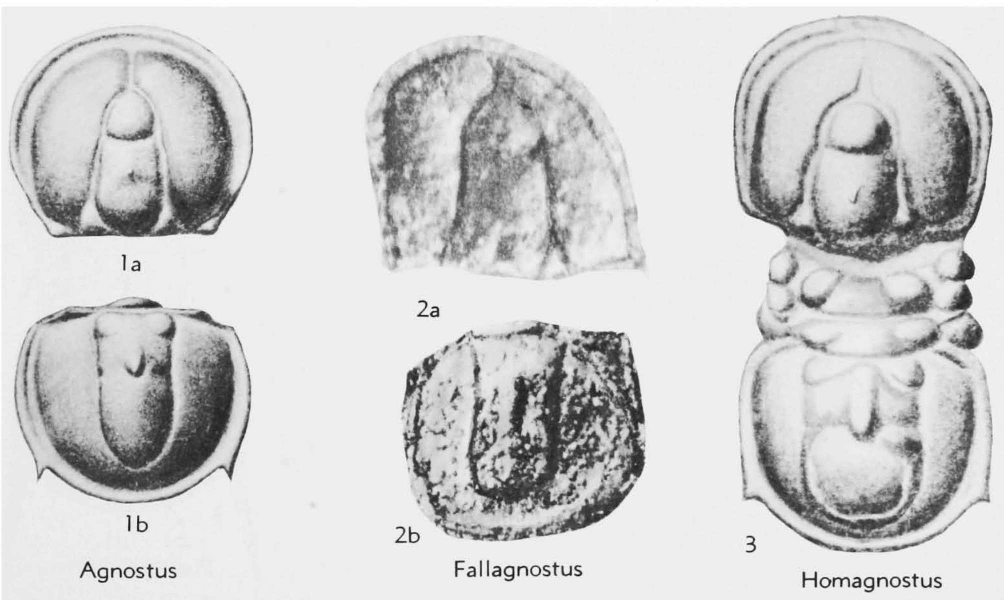


FIG. 109. Agnostidae (p. O172-O173).

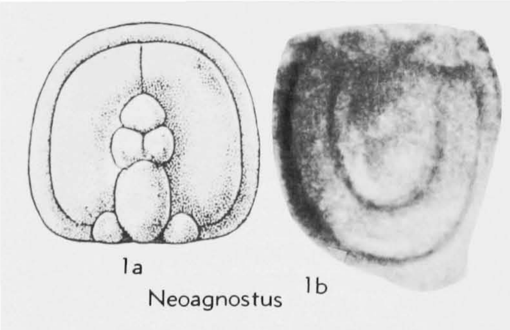


FIG. 110. Agnostidae (p. O173).

M.Cam.-U.Cam.

Clavagnostus HOWELL, 1937 [**Agnostus repandus* WESTERGÅRD, 1930] [=*Tomorhachis* RESSER, 1938]. *M.Cam.-U.Cam.*, Swed.-Sib.-Vt.-Ala.——FIG. 111,*1*. **C. repandus* (WESTERGÅRD), Paradoxides forchhammeri Z., Swed.; *1a,b*, ceph., ×12; *1c,d*, pyg., ×12 (334*).

Family CONDYLOPYGIDAE Raymond, 1913

[*nom. transl.* HOWELL, 1935 (*ex* Condylopygenae RAYMOND, 1913)] [=Mallagnostidae HOWELL, 1935]

Anterior lobe of glabella wider than main lobe; rear part of pygidial axis usually somewhat expanded and evenly rounded at posterior extremity. *L.Cam.-M.Cam.*

Condylopyge HAWLE & CORDA, 1847 [**Battus rex* BARRANDE, 1846] [=*Paragnostus* JAEKEL, 1909]. Front lobe of glabella semicircular in outline; surface smooth. *M.Cam.*, Boh.-Swed.-Wales-Eng.-Newf.——FIG. 112,*1*. **C. rex* (BARRANDE), Jince F., Boh.; ×4.8 (3*).

Mallagnostus HOWELL, 1935 [**Agnostus desideratus* WALCOTT, 1890]. Axis of pygidium rather short, not expanded at rear; surface smooth. *L. Cam.*, N.Y.——FIG. 112,*2*. **M. desideratus* (WALCOTT), Schodack F., N.Y.; pyg., ×6.7 (309*).

Pleuroctenium HAWLE & CORDA, 1847 [**Battus granulatus* BARRANDE, 1846; SD VOGDES, 1925] [=*Dichagnostus* JAEKEL, 1909 (obj.)]. Front lobe of glabella curved ovoid; surface granulose. *M. Cam.*, Boh.-Fr.-Scand.-Eng.-Wales-Newf. —— FIG. 112,*3*. **P. granulatum* (BARRANDE), Jince F., Boh.; ×4.5 (3*).

Family CYCLOPAGNOSTIDAE Howell, 1937

No frontal lobe on glabella, remaining lobe being evenly rounded in front; axis of pygidium short and ovally rounded at rear, with its transverse furrows faint or obsolete;

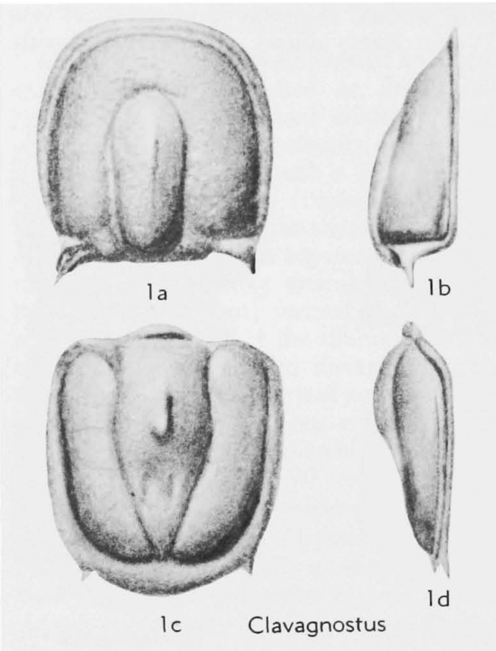


FIG. 111. Clavagnostidae (p. O174).

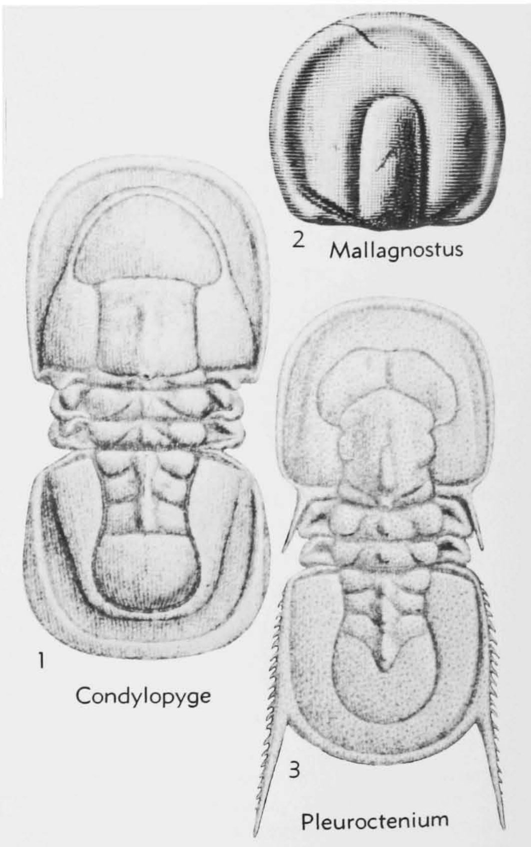


FIG. 112. Condylopygidae (p. O174).

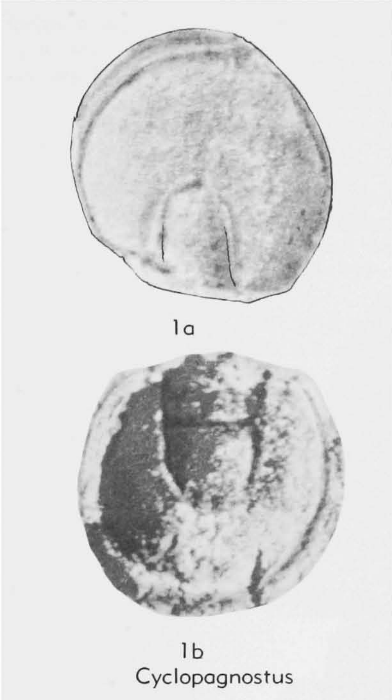


FIG. 113. Cyclopagnostidae (p. O175).

border moderate in width on both shields; dorsal exoskeleton smooth. *M.Cam.*

Cyclopagnostus HOWELL, 1937 [**C. hesperius*]. *M. Cam.*, Vt.——FIG. 113,*1*. **C. hesperius*, St. Albans F., Vt.; *1a*, ceph., ×13.5; *1b*, pyg., ×9.6 (72*).

Family DIPLAGNOSTIDAE Whitehouse, 1936

Glabella with 2 main lobes, anterior ones medially indented by longitudinal furrow; pygidial axis with 3 lobes and an elongate tubercle on its anterior portion; surface of cephalon smooth or corrugated, that of pygidium smooth. *M.Cam.*

Diplagnostus JAEKEL, 1909 [**Agnostus planicauda* TULLBERG, 1880 (*non* ANGELIN, 1851)] [=*Enetagnostus* WHITEHOUSE, 1936]. Axis of pygidium subtriangular in outline, reaching almost to border; genae smooth or rugose. *M.Cam.*, Eu.-Newf.-Arg.-Sib.-Queensl.——FIG. 114,*1*. **D. planicauda* (TULLBERG), Andrarum F., Swed.; *1a*, ceph., ×9.25; *1b*, pyg., ×8.85 (334*).

Linguagnostus KOBAYASHI, 1939 [**Agnostus kjerulfi* BRØGGER, 1878]. Axis of pygidium short and bluntly pointed at rear. *M.Cam.*, Eu.-Sib.-Newf.-Arg.——FIG. 114,*2*. **L. kjerulfi* (BRØGGER), Andrarum F., Swed.; *2a,b*, ceph., pyg., ×4.5 (334*).

Oidalagnostus WESTERGÅRD, 1946 [**O. trispinifer*]. Rear half of pygidial axis swollen and reaching back to border, which bears 3 spines. *M.Cam.*, Swed.——FIG. 114,*3*. **O. trispinifer*, Lejopyge laevigata Z., Swed.; *3a*, ceph., ×4.4; *3b*, pyg., ×6.85 (334*).

Tomagnostus HOWELL, 1935 [**Agnostus fissus* LUNDGREN in LINNARSSON, 1879]. Rear half of pygidial axis narrower and shorter than in *Diplagnostus* and not reaching so near to border; genae of cephalon rugose. *M.Cam.*, Eu.-Newf.-N.B.——FIG. 114,*4*. **T. fissus* (LUNDGREN), Ctenocephalus exsulans Z.-Tomagnostus fissus Z., Swed.; ×7.7 (334*).

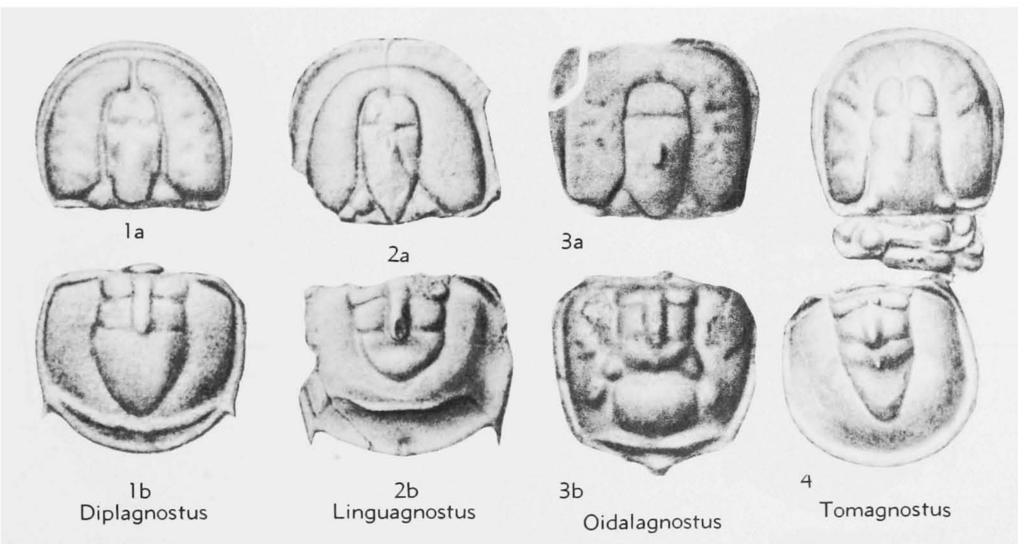


FIG. 114. Diplagnostidae (p. O175).

Family GERAGNOSTIDAE Howell, 1935

[=Arthrorhachinae RAYMOND, 1913; Trinodidae HOWELL, 1935]

Glabella having essentially only a single long main lobe that is evenly rounded in front, well-developed transverse furrow lacking; pygidial axis short in most genera but divided into 3 lobes. *L.Ord.-U.Ord.*

Geragnostus HOWELL, 1935 [**Agnostus sidenbladhi* LINNARSSON, 1869]. Glabella showing only faint trace of transverse furrow; pygidial axis parallel-sided, slightly more than half as long as whole shield; surface of both shields smooth. *L.Ord.*, Eu. - USA (Tex.)-Can. (B.C.)-Arg.-Colom.-China. ——FIG. 115,*3*. **G. sidenbladhi* (LINNARSSON), Tremadoc., Wales; ×11.5 (114*).

Corrugatagnostus KOBAYASHI, 1939 [**Agnostus perrugatus* BARRANDE, 1872]. Glabella wide at rear;

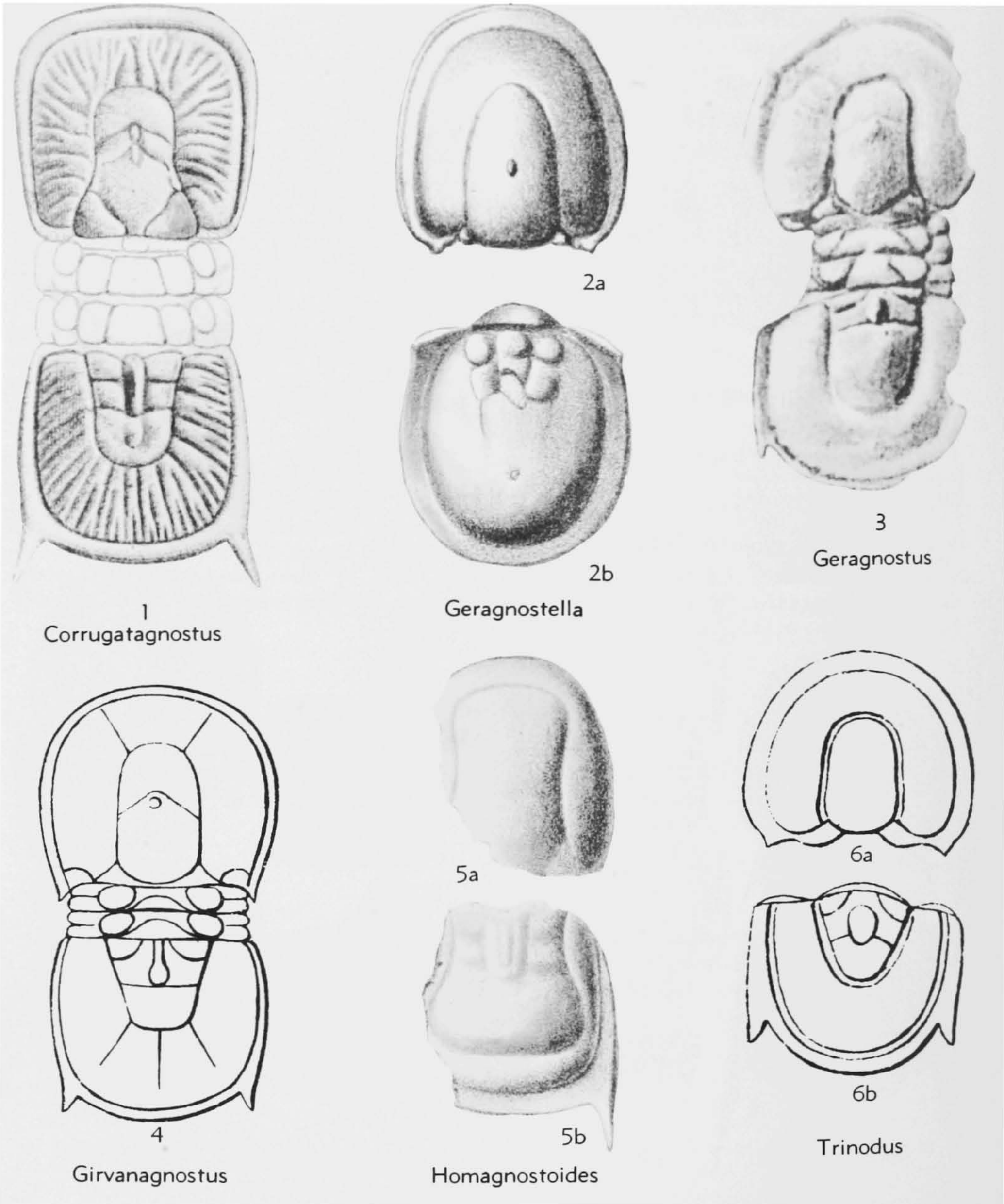


FIG. 115. Geragnostidae (p. O176-O178).

pygidial axis only half as long as pygidium; genal regions and pygidial pleural regions corrugated. *L.Ord.-M.Ord.*, Eu.-?Korea.——FIG. 115,*1*. **C. perrugatus* (BARRANDE), L.Ord., Boh.; ×4.6 (4*).

Geragnostella KOBAYASHI, 1939 [**Agnostus tullbergi* NOVÁK, 1883]. Glabella ovate in outline, with no trace of transverse furrow; pygidial axis trilobed but rear end not defined by axial furrow; surface smooth. *L.Ord.*, Boh.-Swed.——FIG. 115,*2*. **G. tullbergi* (NOVÁK), Boh.; *2a,b*, ceph., pyg., ×5.4 (159*).

Girvanagnostus KOBAYASHI, 1939 [**Agnostus girvanensis* REED, 1903]. Glabella 0.7 of length of cephalon, with faint curved transverse furrow; pygidial axis half as long as pygidium, subtriangular, roundly truncated at rear, trilobed; dorsal exoskeleton smooth. *M.Ord.*, Scot.——FIG. 115,*4*. **G. girvanensis* (REED), Balclatchie F.; ×4.8 (217*).

Homagnostoides KOBAYASHI, 1939 [**Agnostus ferralsensis* MUNIER-CHALMAS & BERGERON, 1889]. Glabella very large, subquadrate, lacking transverse furrows; pygidial axis very large, much expanded at rear but not reaching posterior border; surface smooth. *L.Ord.*, Fr.——FIG. 115,*5*. **H. ferralsensis* (MUNIER-CHALMAS & BERGERON), L. Tremadoc.; *5a,b*, ceph., pyg., ×7.2 (377*).

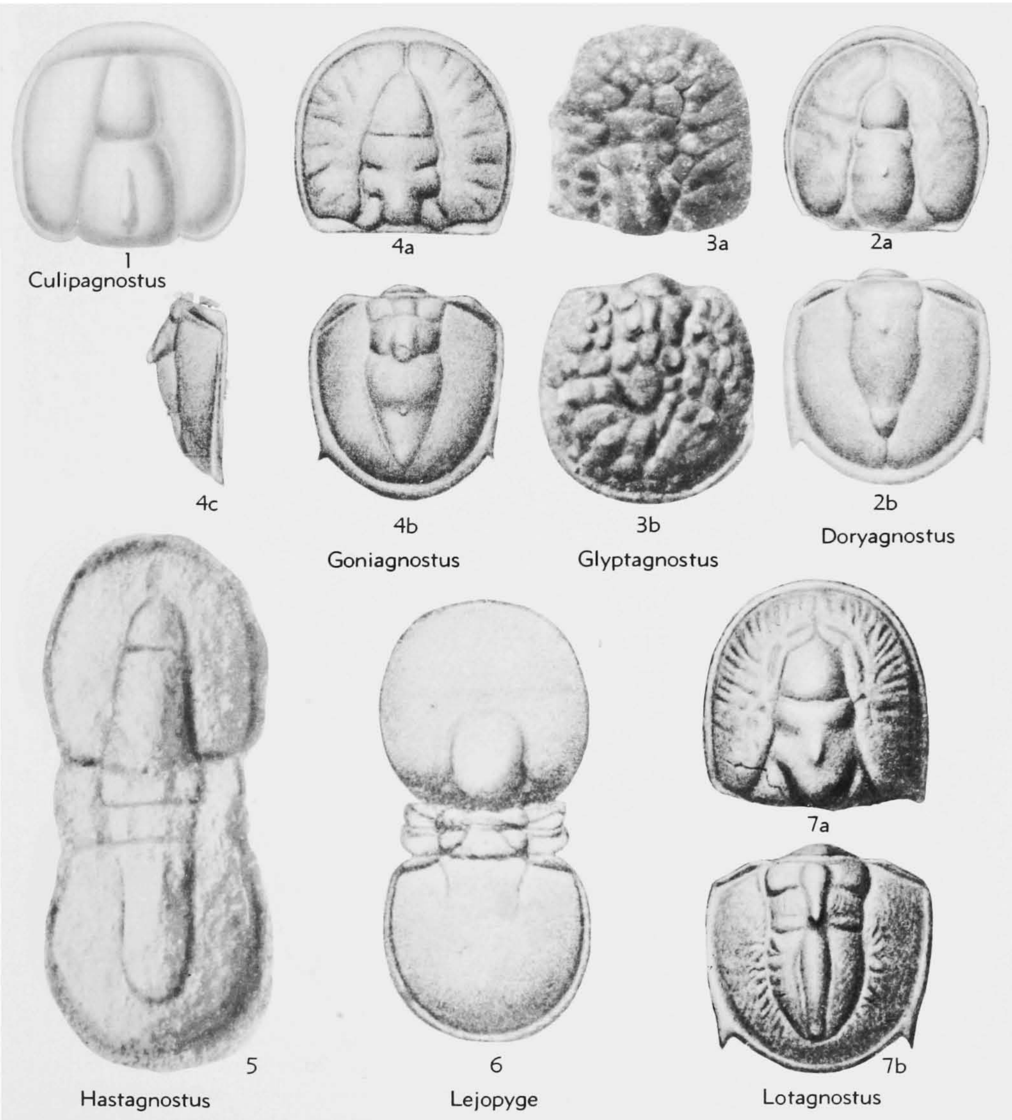


FIG. 116. Hastagnostidae (p. O178-O179).

Trinodus M'Coy, 1846 [**T. agnostiformis*] [=*Arthrorhachis* Hawle & Corda, 1847; *Metagnostus* Jaekel, 1909]. Glabella 0.5 to 0.7 of length of cephalon, without transverse furrow; pygidial axis ovoid, trilobed, only half as long as pygidium; dorsal exoskeleton smooth. *Ord.*, Eu.-Newf.-Que.-Va.-Tenn.-B.C.-Arg.-China-Burma.——Fig. 115,*6*. **T. agnostiformis*, Drummuck Group, Scot.; *6a,b*, ceph., pyg., ×4.9 (217*).

Family HASTAGNOSTIDAE Howell, 1937

Longitudinal furrow in front of glabella, which has 2 main lobes, front one triangular or subtriangular in outline; pygidial axis with 3 lobes, rear one reaching or not reaching to border, which is of moderate width or narrow; axial furrows mostly obsolete in *Lejopyge*. *M.Cam.-U.Cam.*

Hastagnostus Howell, 1937 [**H. angustus*]. Front of anterior glabellar lobe rounded; pygidial axis narrow, bluntly rounded at rear, not reaching backward to border, with longitudinal furrow behind axis of pygidium dividing pleural fields at rear; surface of both shields smooth. *M.Cam.*, USA.——Fig. 116,*5*. **H. angustus*, St. Albans F., Vt.; ×6 (72*).

Culipagnostus Rusconi, 1952 [**C. chipiquensis*]. Front lobe of glabella very long, reaching border of shield; pygidium as in *Hastagnostus* but longer, reaching border; surface of both shields smooth. *M.Cam.*, Arg.——Fig. 116,*1*. **C. chipiquensis*, Villavicencio F., Arg.; ceph., ×16.5 (259*).

Doryagnostus Kobayashi, 1939 [**Agnostus incertus* Brøgger, 1878] [=*Ceratagnostus* Whitehouse, 1939]. Front lobe of glabella bluntly subtriangular; pygidial axis sharply pointed at rear, bearing small tubercle on its middle lobe, not reaching border; pleural fields divided at rear by longitudinal furrow; surface of both shields smooth. *M.Cam.*, Eu.-Newf.-Queensl.——Fig. 116,*2*. **D. incertus* (Brøgger), Ptychagnostus punctuosus Z., Swed.; *2a*, ceph., ×4.75; *2b*, pyg., ×5.3 (334*).

Glyptagnostus Whitehouse, 1936 [**G. toreuma*]. Genae and pleural fields covered with reticulate pattern of furrows. *U.Cam.*, Eu.-Ala.-Queensl.——Fig. 116,*3*. **G. toreuma*, Glyptagnostus Stage, Queensl.; *3a*, ceph., ×4; *3b*, pyg., ×4.8 (339*).

Goniagnostus Howell, 1935 [**Agnostus nathorsti* Brøgger, 1878] [=*Huarpagnostus* Rusconi, 1950]. Front lobe of glabella triangular, genae crossed by radiating furrows; pygidial axis tapering to rounded rear end, not reaching border; surface of pleural fields granular. *M.Cam.*, Eu.-N.B.-Queensl.——Fig. 116,*4*. **G. nathorsti* (Brøgger), Goniagnostus nathorsti Z., Swed.; *4a*, ceph., ×6.5; *4b,c*, pyg., ×6.5 (334*).

Lejopyge Hawle & Corda, 1847 [**Battus laevigatus* Dalman, 1828] [=*Miagnostus* Jaekel, 1909 (obj.)]. Axial furrows of both shields obsolete except near base of glabella and at upper end of pygidial axis; genae smooth or rugose; surface of pygidium smooth. *M.Cam.-U.Cam.*——Swed.-Norway.——Fig. 116,*6*. **Lejopyge laevigata* (Dalman), Lejopyge laevigata Z., Swed.; ×7.7 (334*).

Lotagnostus Whitehouse, 1936 [**Agnostus trisectus* Salter, 1864]. Genae and pleural fields of

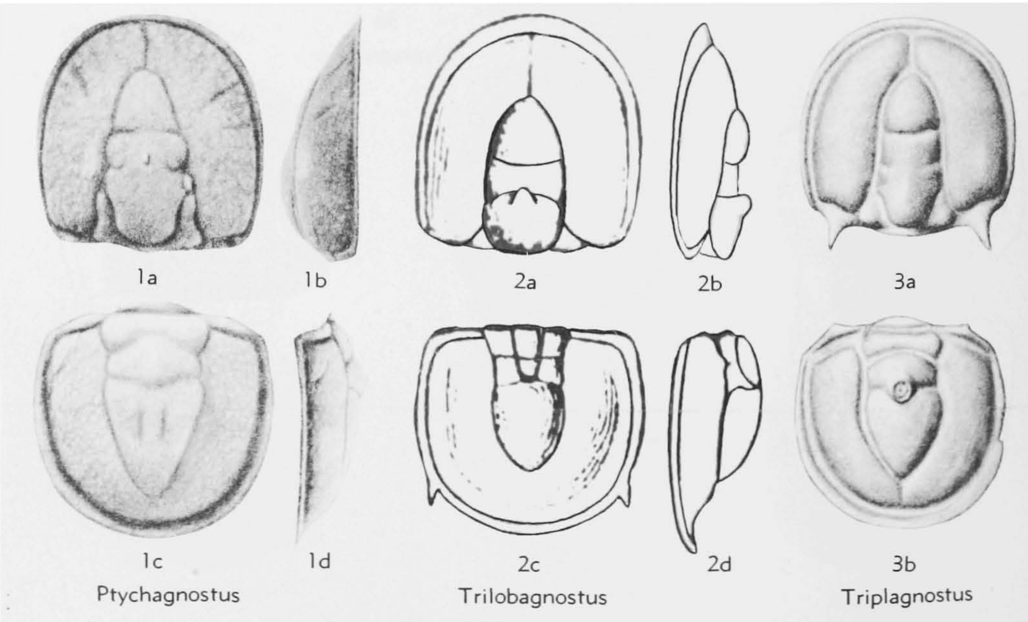


Fig. 117. Hastagnostidae (p. O179).

pygidium with radiating furrows, rear lobe of pygidial axis divided longitudinally into 3 lobes. *U. Cam.*, Eu.-N. Scot.-Que.-Vt.-Arg.-China. —— Fig. 116,*7*. **L. trisectus* (Salter), Peltura minor Z., Swed.; *7a,b*, ceph., pyg., ×6 (331*).

Ptychagnostus Jaekel, 1909 [**Agnostus punctuosus* Angelin, 1851; SD Vogdes, 1925] [=*Canotagnostus* Rusconi, 1951]. Front lobe of glabella subtriangular; pygidial axis subtriangular, not reaching posterior border, middle lobe of axis bearing a large tubercle that may extend backward over front part of rear lobe; surface of genae and pleural fields granular, genae crossed by radiating furrows. *M.Cam.*, Eu.-Newf.-N.B.-Arg.——Fig. 117,*1*. **P. punctuosus* (Angelin) Ptychagnostus punctuosus Z., Swed.; *1a,b*, ceph., ×5.4; *1c,d*, pyg., ×5.4 (334*).

Trilobagnostus Harrington, 1938 [**Agnostus innocens* Clark, 1924]. Main lobe of glabella with transverse furrow across middle; pygidial axis short, with elongate tubercle that extends across first 2 lobes; surface of both shields smooth. *U. Cam.*, Que.——Fig. 117,*2*. *T. innocens* (Clark); *2a,b*, ceph., ×7.1; *2c,d*, pyg., ×8 (385*).

Triplagnostus Howell, 1935 [**Agnostus gibbus* Linnarsson, 1869] [=*Solenagnostus* Whitehouse, 1936]. Front lobe of glabella subtriangular; pygidial axis wide, with bluntly triangular rear lobe not reaching backward to border but with longitudinal furrow behind it that does extend to border; dorsal exoskeleton smooth. *M.Cam.*, Eu.-Newf.-N.B.-Sib.-Queensl.——Fig. 117,*3*. **T. gibbus* (Linnarsson), Triplagnostus gibbus Z., Swed.; *3a*, ceph., ×5.1; *3b*, pyg., ×4.75 (334*).

Family MICRAGNOSTIDAE Howell, 1935

Glabella with 2 main lobes, anterior one evenly rounded at front; pygidial axis short, more or less segmented; surface of both shields smooth. *U.Cam.-L.Ord.*

Micragnostus Howell, 1935 [**Agnostus calvus* Lake, 1906]. Glabella with 2 well-defined main lobes, pygidial axis distinctly trilobed but rather short and not expanded toward rear, not reaching border. *U.Cam.-L.Ord.*, Eu.-Can.-Vt.——Fig. 118, *3*. **M. calvus* (Lake), Tremadoc., Wales; ×10 (114*).

Anglagnostus Howell, 1935 [**Agnostus dux* Callaway, 1877]. Glabella rather short; pygidial axis very short, with only 2 segments. *U.Cam.-L.Ord.*, Eng.-Fr.-Vt.-Arg.——Fig. 118,*1*. **A. dux* (Callaway), Tremadoc., Eng.; ×8 (114*).

Hyperagnostus Kobayashi, 1955 [**H. binodosus*]. Glabella with double triangular lobe between 2 main lobes; pygidial axis trilobed, bluntly rounded at rear, not reaching backward to border. *L.Ord.*, B.C.——Fig. 118,*2*. **H. binodosus*, McKay F.; *2a*, ceph., ×7; *2b*, pyg., ×7 (108*).

?**Rudagnostus** Lermontova, 1951 [**Agnostus princeps* var. *rudis* Salter, 1864 (=*Agnostus rudis* Salter, 1864, Lake, 1907)]. *U.Cam.*, Kazakstan, Eu.

?**Eurudagnostus** Lermontova, 1951 [**E. grandis*]. Cephalon with prominent rim and well-developed posterolateral short spines, glabella with fairly distinct rounded lobe in front; pygidium with

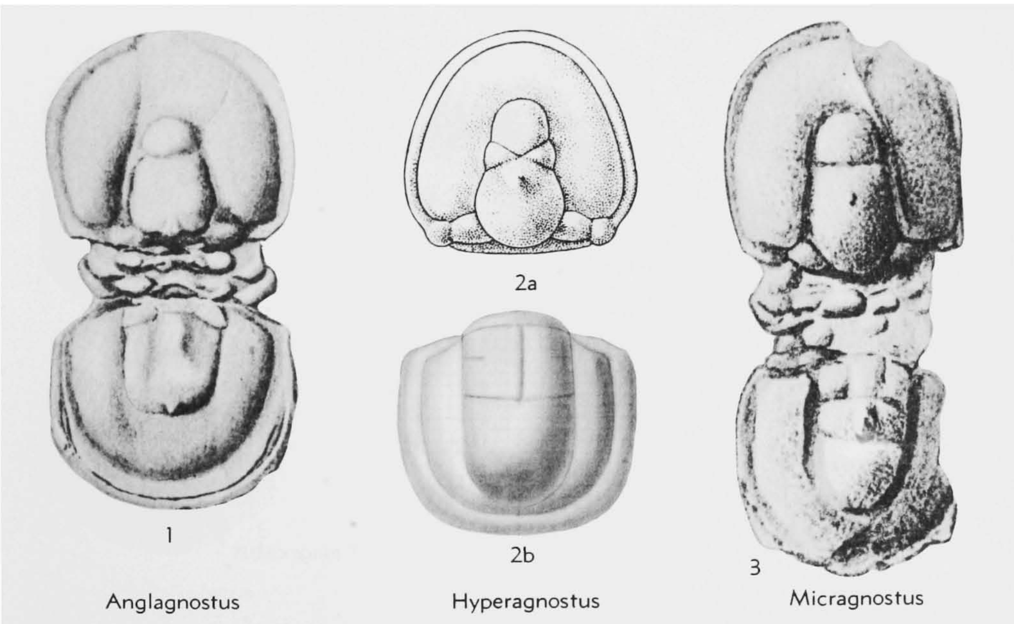


Fig. 118. Micragnostidae (p. *O*179).

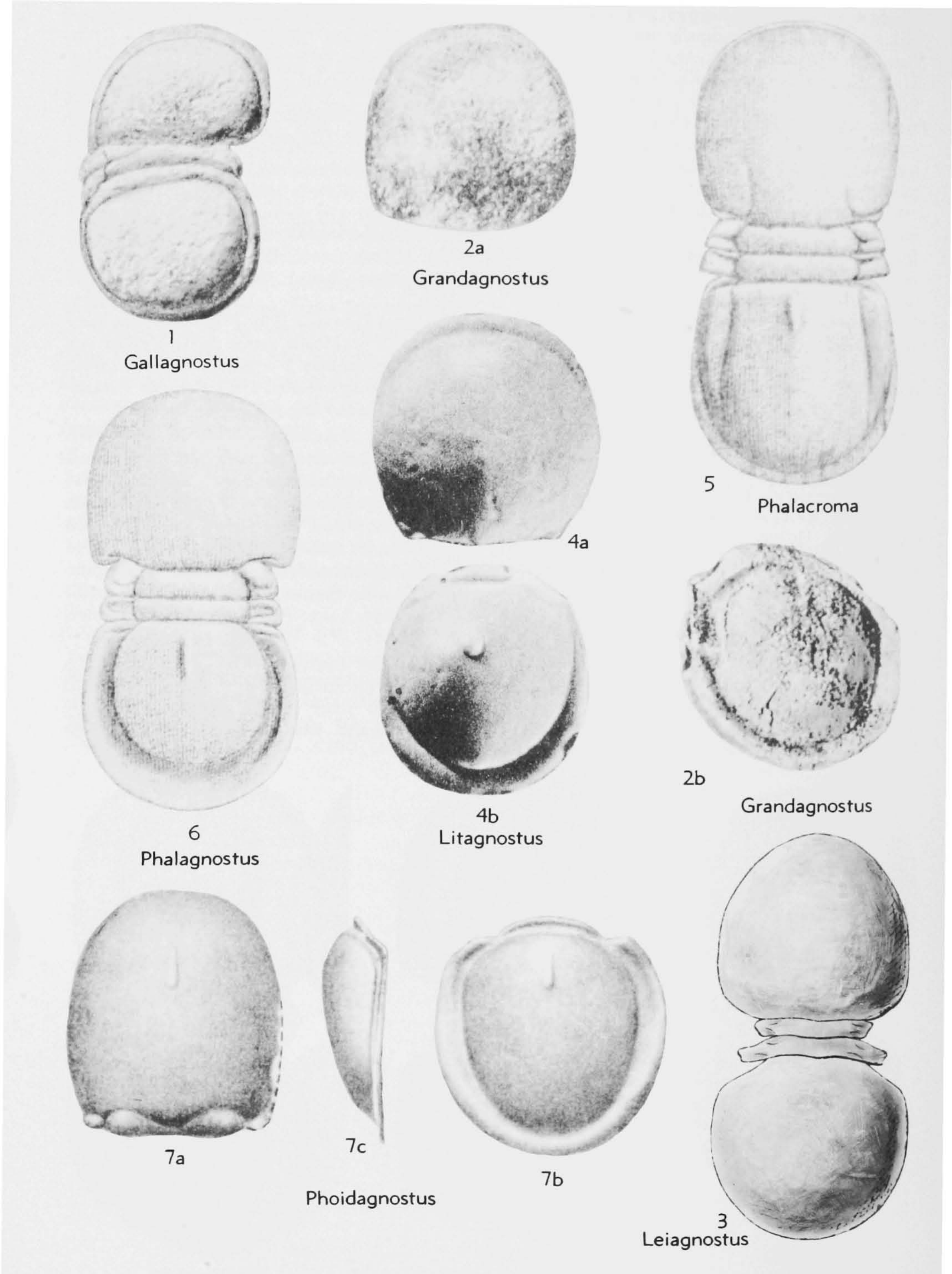


FIG. 119. Phalacromidae (p. O181).

broad, well-defined axis that bears strong tubercle, margin with pair of slender, long, slightly incurved spines. *U.Cam.*, Kazakstan.——FIG. 128,*1*. **E. grandis; 1a,b,* ceph., pyg., ×6 (423) (M).

Family PHALACROMIDAE Hawle & Corda, 1847

[*nom. correct.* HOWELL, 1935 (*pro* Phalacromides HAWLE & CORDA, 1847)] [=Leiagnostidae JAEKEL, 1909; Platagnostidae HOWELL, 1935]

Cephalon smooth, with little or no trace of axial furrow; pygidium smooth, dorsal furrow lacking or barely visible; surface smooth. *M.Cam.-L.Ord.*

Phalacroma HAWLE & CORDA, 1847 [**Battus bibullatus* BARRANDE, 1846; SD RAYMOND, 1913] [=*Platagnostus* HOWELL, 1935 (obj.)]. Cephalon smooth, with only faint traces of rear ends of dorsal furrow, border narrow; pygidium smooth, with faintly impressed axial furrow, axis only slightly expanded at rear, reaching backward to narrow border. *M.Cam.*, Boh.-Eng.-Newf.——FIG. 119,*5*. **P. bibullatum* (BARRANDE), Paradoxides beds, Boh.; ×11.5 (3*).

Gallagnostus HOWELL, 1935 [**G. geminus*]. Cephalon smooth, without trace of axial furrow but with border of moderate width; pygidium lacking axial furrow but with border of moderate width. *M. Cam.-L.Ord.*, Fr.-Arg.——FIG. 119,*1*. **G. geminus*, Paradoxides beds, Fr.; ×7.7 (71*).

Gallagnostoides KOBAYASHI, 1939 [**Aeglina boia* HICKS, 1875]. Like *Gallagnostus*, but with a narrower thoracic axis. *L.Ord.*, Wales.

Grandagnostus HOWELL, 1935 [**G. vermontensis*]. Cephalon smooth, with only faint trace of rear ends of axial furrow, and little or no indication of border; pygidium smooth, lacking axial furrow but with wide border; doublure present on both shields. *M.Cam.*, Vt.-Eu.-Sib.——FIG. 119,*2*. **G. vermontensis*, Centropleura vermontensis Z., Vt.; *2a*, ceph., ×4.5; *2b*, pyg., ×3.4 (71*).

Leiagnostus JAEKEL, 1909 [**L. erraticus*]. Cephalon smooth, lacking axial furrow but with moderately wide border. *L.Ord.*, Eu.——FIG. 119,*3*. **L. erraticus*, Echinosphaerites Z. (glacial erratic), N. Ger.; ×4.8 (83*).

Litagnostus RASETTI, 1944 [**L. levisensis*]. Cephalon smooth, lacking axial furrow but with narrow border; pygidium smooth, without trace of axial furrow, border moderately wide. *U.Cam.*, Que.-Vt.-Wis.——FIG. 119,*4*. **L. levisensis*, Que.; *4a,b*, ceph., pyg., ×10 (188*).

Phalagnostus HOWELL, 1955 [**Battus nudus* BEYRICH, 1845]. Cephalon smooth, lacking axial furrow and border or with very narrow border and no basal lobes; pygidium smooth, without axial furrow but with side border. *M.Cam.*, Eu.-Newf.-Queensl.——FIG. 119,*6*. **P. nudus* (BEYRICH), Paradoxides beds, Boh.; ×7.6 (3*).

Phoidagnostus WHITEHOUSE, 1936 [**P. limbatus*]. Cephalon smooth, lacking axial furrow but with narrow border and basal lobes; pygidium smooth, without axial furrow but with wide border. *M. Cam.*, Eu.-Sib.-Queensl.——FIG. 119,*7*. *P. bituberculatus* (ANGELIN), Solenopleura brachymetopa Z., Swed.; *7a*, ceph., ×8; *7b,c*, pyg., ×8.3 (334*).

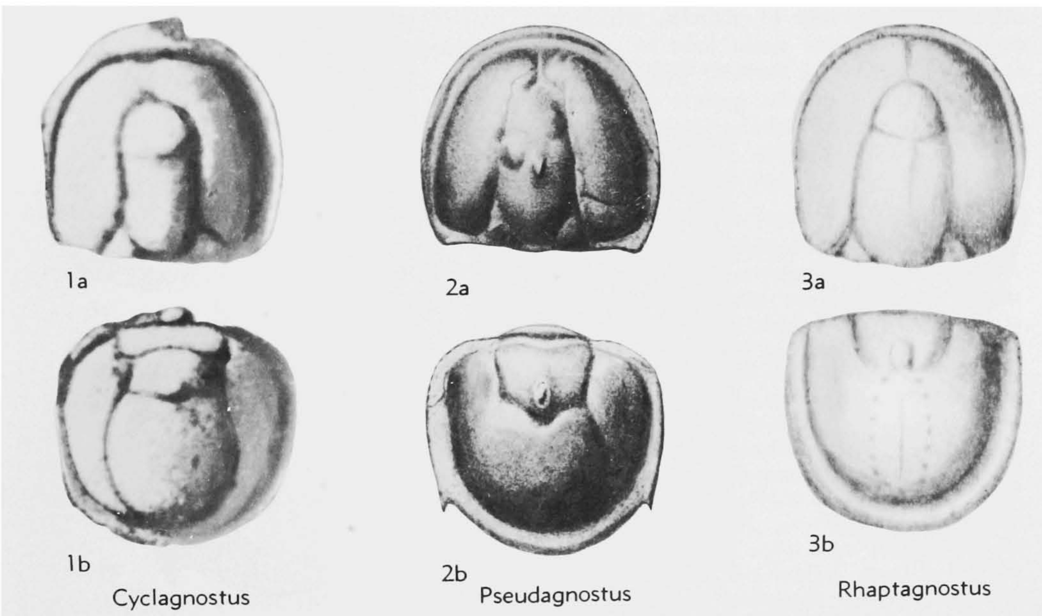


FIG. 120. Pseudagnostidae (p. O182-O183).

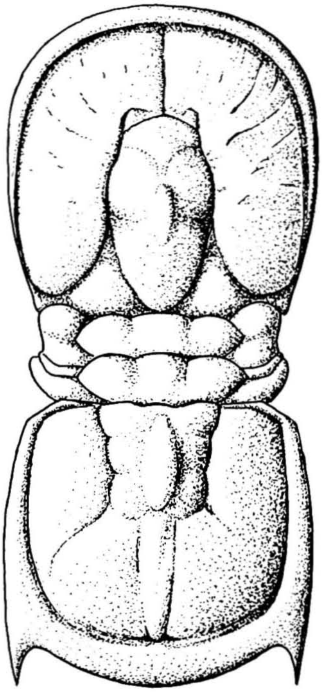


FIG. 121. *Machairagnostus tmetus HARRINGTON & LEANZA (Pseudagnostidae), L.Ord., Arg., ×18.5 (59*, 1957).

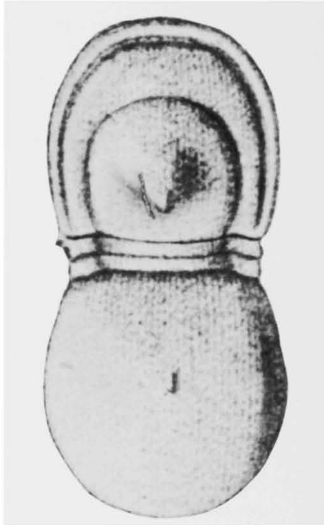


FIG. 122. *Sphaeragnostus similis (BARRANDE) (Sphaeragnostidae), Ord., Eu., ×15.5 (4*, 1872).

Family PSEUDAGNOSTIDAE Whitehouse, 1936

Longitudinal furrow in front of subtriangular anterior lobe of glabella, which is separated from rear main lobe by poorly developed transverse furrow; pygidial axis trilobed, with rear lobe greatly expanded, reaching border and reducing size of pleural fields; surface of cephalon smooth or rugose, that of pygidium smooth. *U.Cam.-L.Ord.*

Pseudagnostus JAEKEL, 1909 [**Agnostus cyclopyge* TULLBERG, 1880] [=*Plethagnostus* CLARK, 1924; *Euplethagnostus* LERMONTOVA, 1940]. Front lobe of glabella subtriangular in outline; surface of cephalon smooth or rugose; pygidial axis with front portion well defined by axial furrow but with greatly expanded rear lobe more or less indistinctly outlined; surface of pygidium smooth. *U.Cam.*, Swed.-Wales-Sib.-China-Korea-Queensl.-Que.-Vt.-Wis.-Nev.-Tex.-Alaska-Arg.——FIG. 120, 2. **P. cyclopyge* (TULLBERG), Francon., Swed.; *2a,b*, ceph., pyg., ×6.4 (334*).

Cyclagnostus LERMONTOVA, 1940 [**C. elegans*]. Glabella with 2 main lobes, anterior one evenly rounded at front; pygidial axis distinctly trilobed and clearly defined throughout by axial furrow. *U.Cam.*, Sib.-Que.-Vt.——FIG. 120,*1*. **C. elegans*, Sib.; *1a*, ceph., ×11; *1b*, pyg., ×11.7 (117*).

Machairagnostus HARRINGTON & LEANZA, 1957 [**M. tmetus*]. Glabella faintly trisegmented, blunt at front end; genae rugose; anterior half of pygidial axis trisegmented, rear half very much expanded, with narrow central elevated portion set off by 2 parallel-sided longitudinal furrows that reach backward to border; surface smooth. *L.Ord.*, Arg.

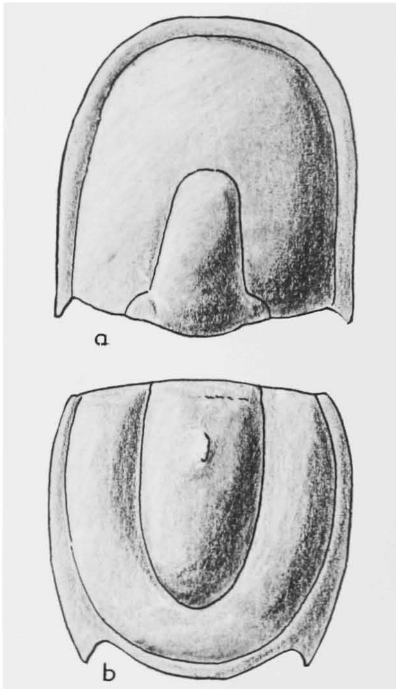


FIG. 123. *Spinagnostus franklinensis HOWELL (Spinagnostidae), M.Cam., Vt., ×13 (71, 1935).

——FIG. 121. **M. tmetus,* Tremadoc., Arg., ×18.5 (59*).

Rhaptagnostus WHITEHOUSE, 1936 [**Agnostus cyclopygeformis* SUN, 1924] [=*Pseudorhaptagnostus* LERMONTOVA, 1940]. Glabella faintly trisegmented, anterior main lobe rounded at front; pygidial axis trisegmented, with first 2 segments very short, 3rd greatly expanded, faintly outlined by axial furrow and marked along its medial axis by elongate elliptical ring of pits; surface smooth. *U.Cam.-L.Ord.,* China-Sib.-Arg.——FIG. 120,*3*. **R. cyclopygeformis* (SUN), China; *3a,* ceph., ×5.5; *3b,* pyg., ×6.3 (478*).

Family SPHAERAGNOSTIDAE Kobayashi, 1939

Cephalon smooth, without trace of axial furrow or border; pygidium smooth, with subcircular axis that is only a little more than half of shield length, border narrow. *Ord.*

Sphaeragnostus HOWELL & RESSER in COOPER & KINDLE, 1936 [**Agnostus similaris* BARRANDE, 1872]. Characters of family. *Ord.,* Eu.-Que.——FIG. 122. **S. similaris* (BARRANDE), Boh.; ×15.5 (4*).

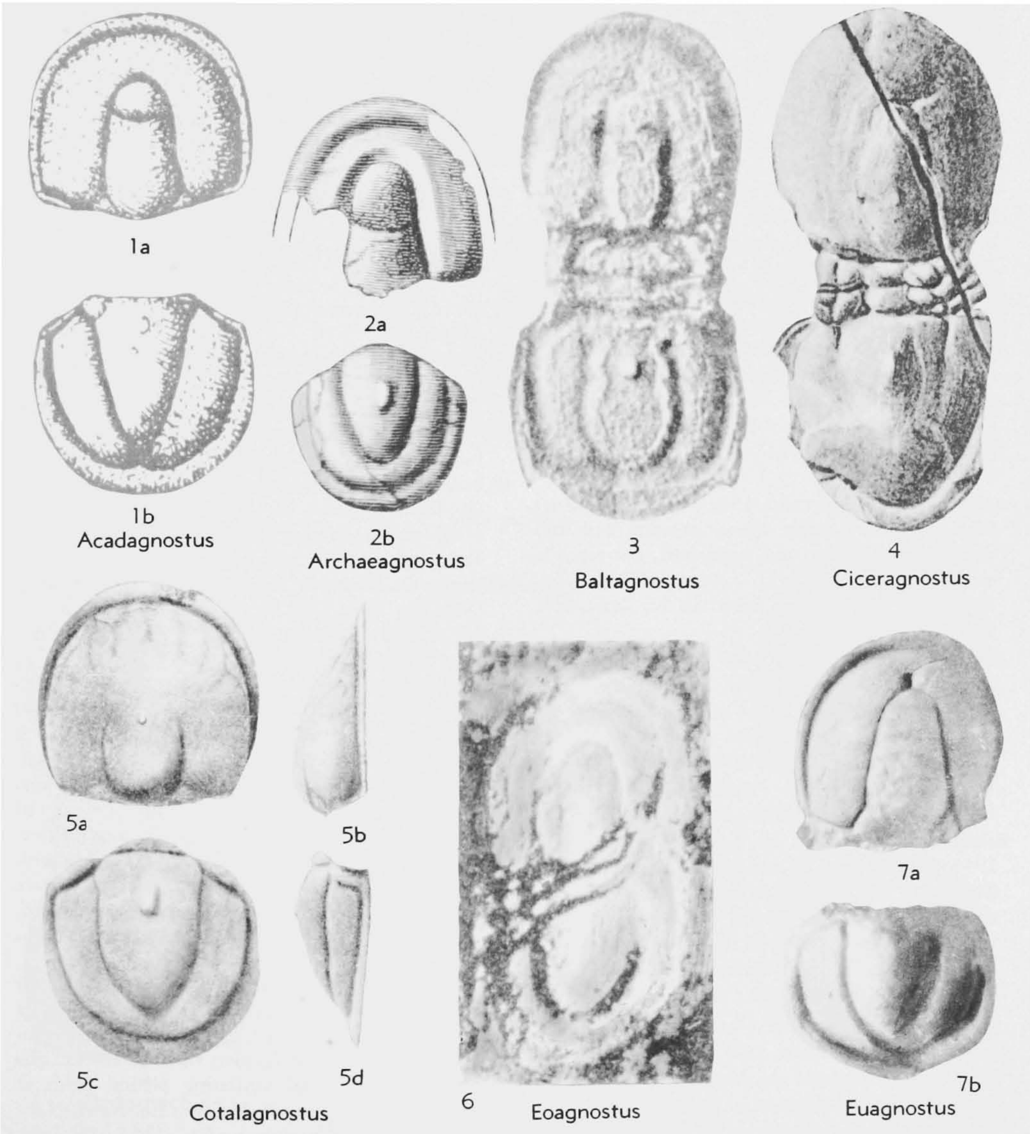


FIG. 124. Spinagnostidae (p. *O*184).

Family SPINAGNOSTIDAE Howell, 1935

[Incl. Quadragnostinae Howell, 1935; Hypagnostinae Ivshin, 1953] [=Peronopsidae Westergård, 1946; Rudagnostidae Lermontova, 1951]

Glabella with 2 main lobes, anterior one rounded in front or with this lobe partly or entirely obsolete, longitudinal furrow in front of glabella lacking or barely visible; pygidial axis varying from long narrow and pointed at rear (where it may or may not reach border) to long wide and more or less bluntly pointed (in some expanded and rounded at rear where it may reach border) or rather short and evenly rounded at rear, not approaching border. *L.Cam.-U.Cam.*

Spinagnostus Howell, 1935 [**S. franklinensis*]. Glabella lacking frontal lobe, small spines at posterolateral corners of cephalon; pygidium with wide flange bearing moderately large, backward-directed spines, axis bluntly rounded at rear, with submedian, inconspicuous tubercle; surface smooth. *M.Cam.*, NE.USA——Fig. 123,*1*. **S. franklinensis*, Up.M.Cam., Centropleura vermontensis Z., St. Albans Sh., NW.Vt.; *1a,b*, ceph., pyg., ×13 (71).

Acadagnostus Kobayashi, 1939 [**Agnostus acadicus* Dawson, 1868]. Front lobe of glabella small but present; pygidial axis long, not segmented, subtriangular in outline, separating pleural fields at rear; surface smooth. *M.Cam.*, Eu.-Newf.-N.B.-Mont.——Fig. 124,*1*. **A. acadicus* (Dawson), Fossil Brook F., N.B.; *1a,b*, ceph., pyg., ×7 (429*).

Archaeagnostus Kobayashi, 1939 [**A. primigeneus*]. Glabella with 2 main lobes; pygidial axis subtriangular in outline, not segmented, not reaching border; surface smooth. *L.Cam.*, N.Y.——Fig. 124,*2*. **A. primigeneus*, Schodack F.; *2a,b*, ceph., pyg., ×10 (309*).

Armagnostus Howell, 1937 [**A. megalaxis*]. Glabella with 2 main lobes; pygidial axis wide, somewhat expanded toward rear, with very poorly developed transverse furrows, posterior end evenly rounded, touching border; surface smooth. *M.Cam.*, Vt.——Fig. 125,*1*. **A. megalaxis*, St. Albans F.; *1a*, ceph., ×11.5; *1b*, pyg., ×12.3 (72*).

Baltagnostus Lochman in Lochman & Duncan, 1944 [**Proagnostus? centerensis* Resser, 1938]. Glabella with 2 main lobes; pygidial axis with slightly expanded rear lobe, bearing little or no trace of transverse furrows, reaching border; surface smooth. *M.Cam.-U.Cam.*, Ala. - Tenn. - Tex.-Mont.——Fig. 124,*3*. **B. centerensis* (Resser), Conasauga F., Ala.; ×14.25 (235*).

Ciceragnostus Kobayashi, 1937 [**Agnostus barlowi* Belt, 1868]. Glabella obsolete except for rear end; pygidial axis faint except at anterior end; shields thus like those of *Cotalagnostus* except for loss of most of axial furrow. *M.Cam.*, Eu.-Sib.——Fig.

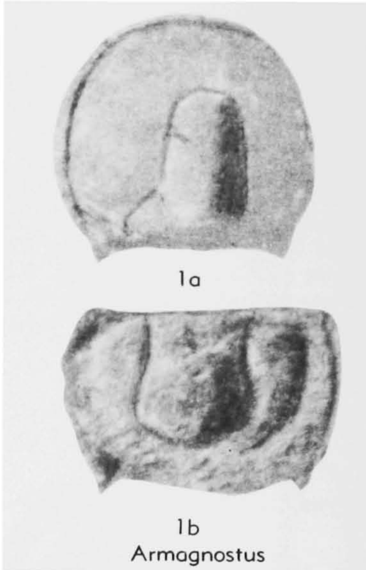


Fig. 125. **Armagnostus megalaxis* Howell (Spinagnostidae), M.Cam., Vt.; ceph., ×11.5; pyg., ×12.3 (72*, 1937).

124,*4*. **C. barlowi* (Belt), Menevian, Wales; ×8 (114*).

Cotalagnostus Whitehouse, 1936 [**Agnostus lens* Grönwall, 1902]. Glabella with only rear main lobe present and that only partly outlined; pygidial axis subtriangular in outline, with transverse furrows nearly or quite obsolete, not reaching border at rear; surface smooth. *M.Cam.*, Eu.-Newf.-Sib.-China-Queensl. —— Fig. 124,*5*. **C. lens* (Grönwall), Ptychagnostus punctuosus Z., Swed.; *5a,b*, ceph., ×8.3; *5c,d*, pyg., ×8.85 (334*).

Eoagnostus Resser & Howell, 1938 [**E. roddyi*]. Only rear main lobe of glabella outlined but that one defined by axial furrow and straight transverse furrow; pygidial axis rounded triangular in outline, evenly rounded at rear, not reaching backward to border; surface smooth. *L.Cam.*, Pa.——Fig. 124,*6*. **E. roddyi*, Kinzers F.; ×17 (241*).

Euagnostus Whitehouse, 1936 [**E. opimus*]. Anterior lobe of glabella subtriangular in outline, with faint longitudinal furrow in front of it; pygidial axis large, subtriangular in outline, extending almost, but not quite, back to border, with little or no trace of transverse furrows; surface smooth. *M.Cam.*, Queensl.——Fig. 124,*7*. **E. opimus*, Anomocare Stage, Queensl.; *7a,b*, ceph., pyg., ×4.6 (339*).

Hypagnostus Jaekel, 1909 [**Agnostus parvifrons* Linnarsson, 1869]. Single main lobe in glabella bluntly rounded in front; pygidial axis long, subtriangular, transverse furrows faint or absent, axis reaching border and separating pleural fields at the rear; surface smooth. *M.Cam.*, Eu.-Newf.-N.B.-Sib.-Arg.-China-Queensl.——Fig. 126,*1*. **H. parvifrons* (Linnarsson), Hypagnostus parvifrons Z., Swed.; *1a,b,* ceph., with thoracic segments, pyg., ×8.2 (334*).

Kormagnostus RESSER, 1938 [**K. simplex*]. No front lobe on glabella, rear main lobe truncated anteriorly by straight transverse furrow; pygidial axis large, slightly expanded backward, dividing narrow pleural fields widely at rear; surface smooth. *U.Cam.*, Tenn.-Que.-Mont.——FIG. 126,*2*. **K. simplex*, Nolichucky F., Tenn.; *2a,b,* ceph., pyg., ×7.6 (235*).

Oedorhachis RESSER, 1938 [**O. typicalis*]. Front main lobe of glabella subquadrate in outline; rear lobe of pygidial axis subcircular in outline, much wider than anterior part of axis; surface smooth. *U.Cam.*, Ala.——FIG. 126,*4*. **O. typicalis*, Nolichucky F.; ×8.5 (235*).

Pentagnostus LERMONTOVA, 1940 [**P. anabarensis*]. Anterior lobe of glabella evenly rounded in front, with slight trace of longitudinal furrow in front of it; pygidial axis trilobed, with rear lobe sub-

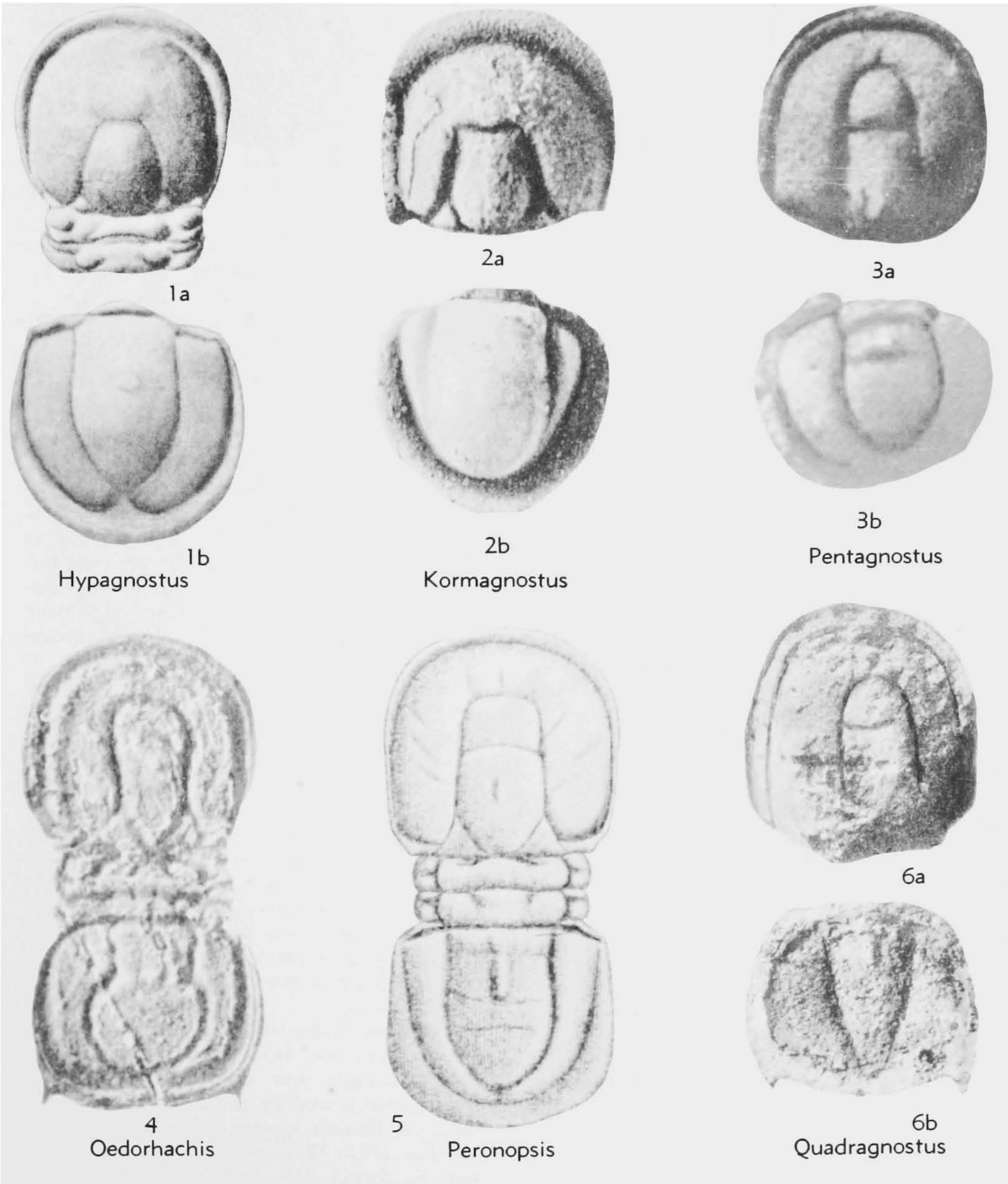


FIG. 126. Spinagnostidae (p. O184-O186).

triangular in outline and not reaching backward to border; surface smooth. *M.Cam.*, Sib.——FIG. 126,*3*. **P. anabarensis; 3a*, ceph., ×8.2; *3b*, pyg., ×7.6 (117*).

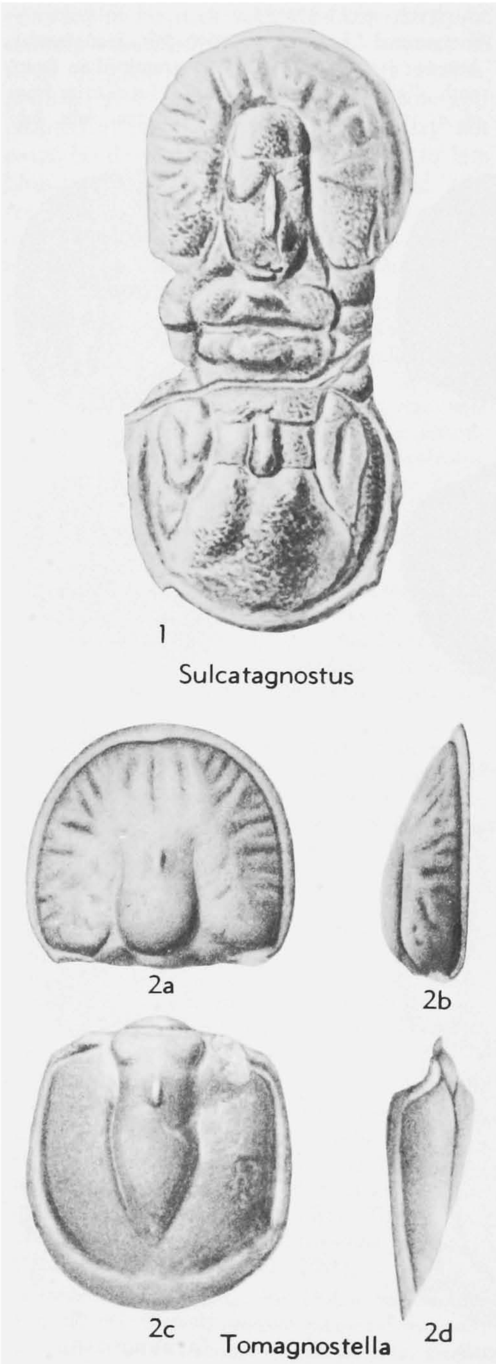


FIG. 127. Spinagnostidae (p. *O*186).

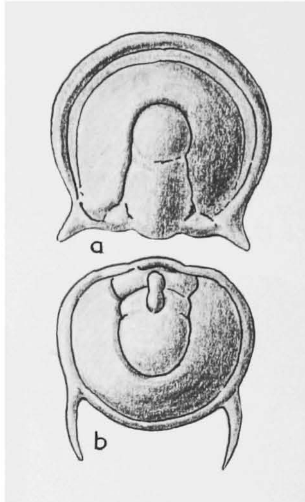


FIG. 128. **Eurudagnostus grandis* LERMONTOVA (?Micragnostidae), U.Cam., Kazakhstan; ceph., pyg., ×6 (423, 1951) (p. *O*179).

Peronopsis HAWLE & CORDA, 1847 [**Battus integer* BEYRICH, 1845] [=*Diplorrhina* HAWLE & CORDA, 1847; *Mesospheniscus* HAWLE & CORDA, 1847; *Mesagnostus* JAEKEL, 1909 (obj.); *Pseudoperonopsis* HARRINGTON, 1938]. Front lobe of glabella subquadrate; pygidial axis widely subtriangular in outline, with little or no trace of transverse furrows, reaching backward to border or not; surface smooth. *M.Cam.*, Eu.-Sib.-Manch.-N.B.-Mont. ——FIG. 126,*5*. **P. integra* (BEYRICH), Paradoxides beds, Boh., ×12 (3*).

Quadragnostus HOWELL, 1935 [**Q. solus*]. Cephalon like that of *Peronopsis;* pygidial axis narrowly triangular in outline, reaching back almost or quite to border; surface smooth. *M.Cam.*, Vt.-Swed.-Denm.——FIG. 126,*6*. **Q. solus*, St. Albans F., Vt.; *6a*, ceph., ×6.4; *6b*, pyg., ×5.3 (71*).

Sulcatagnostus KOBAYASHI, 1937 [**Agnostus securiger* LAKE, 1906]. Cephalon like that of *Peronopsis* but with furrows radiating across genae; rear lobe of pygidial axis broadaxe-shaped, greatly expanded at rear, where it reaches border, pleural fields narrow and widely separated by axis. *U.Cam.*, Eng. ——FIG. 127,*1*. **S. securiger* (LAKE); ×6 (114*). ×6 (114*).

Tomagnostella KOBAYASHI, 1939 [**Agnostus exsculptus* ANGELIN, 1851]. Front main lobe of glabella obsolete, rear main lobe truncated in front; genae crossed by radiating furrows; pygidium not definitely known. *M.Cam.*, Swed.-Denm. ——FIG. 127,*2*. **T. exsculpta* (ANGELIN), Andrarum F., Swed.; *2a,b*, ceph., ×5.5; *2c,d*, pyg., ×7.5 (334*).

Suborder EODISCINA Kobayashi, 1939

[*nom. correct.* MOORE, herein (*pro* Eodiscini KOBAYASHI, 1939)] [=superfamily Eodiscidea RICHTER, 1932 (*partim*); Dawsoniidea KOBAYASHI, 1943; order Dawsonida LERMONTOVA, 1951; superfamily Agnostacea HENNINGSMOEN, 1951 (*partim*); superfamily Eodiscoidae HUPÉ, 1953] [Type—*Eodiscus* HARTT in WALCOTT, 1884]

Small isopygous trilobites with 2 or 3 thoracic segments. Glabella usually well defined, subcylindrical or tapered; occipital ring rounded or spinose. Genae elevated laterally, depressed in front of glabella. Cephalic border may have tubercles or radial markings. Facial sutures either of proparian type, with small, lateral librigenae (Pagetiidae) or entirely lacking (Eodiscidae); eyes usually absent in latter case. Hypostoma present (*Pagetia*). Pygidial axis with normal segmentation, of 4 to 12 rings, usually long and prominent; pleural regions furrowed or not, with distinct, narrow border; margin smooth, rarely denticulate. Axial or terminal spine present in some genera. Cephalic and pygidial doublures invariably narrow. Animal possessing faculty of enrollment. *L.Cam.-M.Cam.* (46, 117, 339).

Family EODISCIDAE Raymond, 1913

[Incl. Calodiscinae, Spinodiscinae, Brevidiscinae KOBAYASHI, 1943] [=Dawsoniidae RESSER, 1937; Weymouthiidae KOBAYASHI, 1943]

Both eyes and facial sutures usually lacking; exceptionally (*Opsidiscus*) vestigial eyes may be retained but sutures are fused. Thorax with 2 or 3 segments. *L.Cam.-M. Cam.* (46, 117).

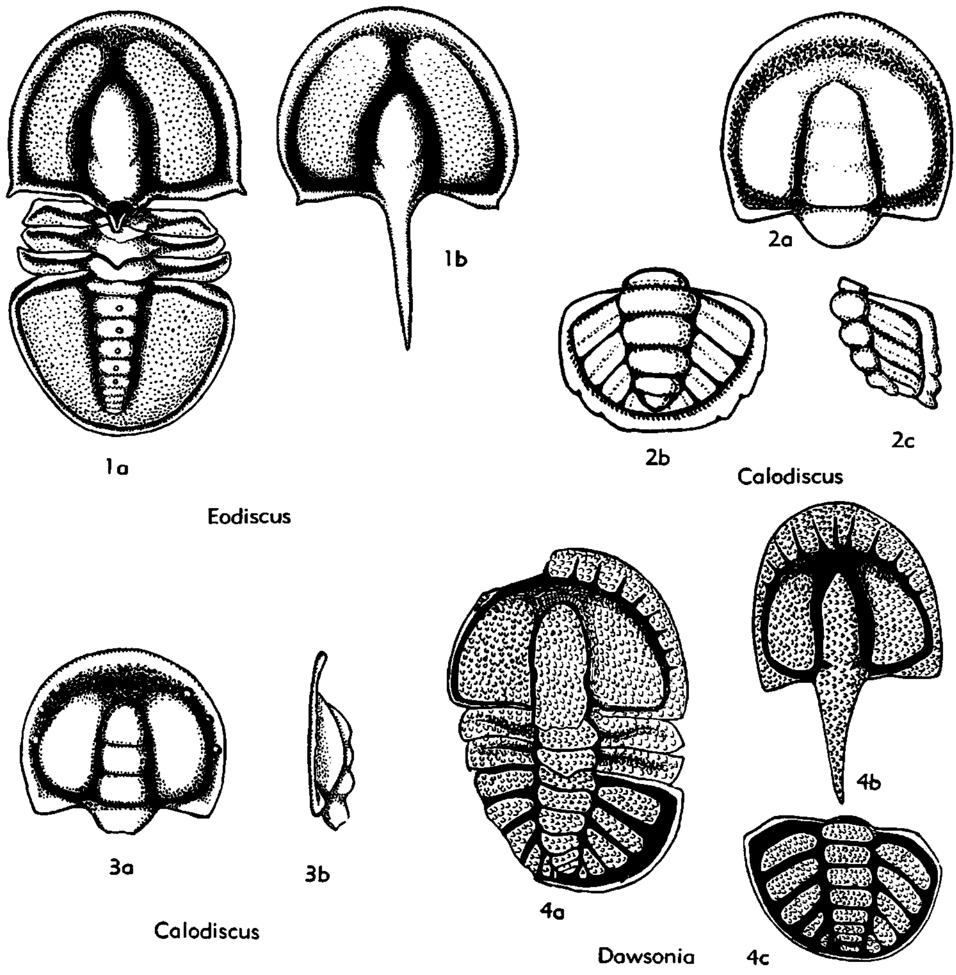


FIG. 129. Eodiscidae (p. O188).

Eodiscus HARTT in WALCOTT, 1884 [**E. pulchellus* (=*Microdiscus scanicus* LINNARSSON, 1883)] [=*Microdiscus* SALTER, 1864 (*non* EMMONS, 1855); *Spinodiscus, Deltadiscus* KOBAYASHI, 1943]. Glabella short, extended into strong spine; preglabellar depression in shape of longitudinal furrow; cephalic border narrow, finely crenulated or smooth. Thorax with 3 segments. Pygidium with long axis divided into numerous rings; pleural fields usually unfurrowed. Surface punctate or tuberculate. *M.Cam.*, E.N.Am.-NW.Eu.(Acad.-Balt. prov.)——FIG. 129,*1*. *E. punctatus* (SALTER), Newf.; *1a,b,* whole exoskel., ceph., ×7.5 (448n).

Calodiscus HOWELL, 1935 [*pro Goniodiscus* RAYMOND, 1913 (*non* MÜLLER & TROSCHEL, 1842)] [**Agnostus lobatus* HALL, 1847] [=*Brevidiscus* KOBAYASHI, 1943]. Cephalon semicircular; glabella parallel-sided to tapering, in some species with shallow transglabellar furrows; occipital furrow impressed, occipital ring rounded or with short spine; border of medium width, smooth or tuberculate. Pygidial axis prominent, segments few; pleural fields furrowed or smooth; margin entire or faintly serrate. Size small. *L.Cam.*, Eu.-N.Am. ——FIG. 129,*2*. **C. lobatus* (HALL), N.Y.; *2a,* ceph., ×12; *2b,c,* pyg., ×12 (448n).——FIG. 129,*3*. *C. meeki* (FORD), N.Y.; *3a,b,* ceph., ×7.5 (448n).

Dawsonia HARTT in DAWSON, 1868 [**Microdiscus dawsoni* HARTT in DAWSON, 1868] [=*Aculeodiscus* SNAJDR, 1951; *?Metadiscus* KOBAYASHI, 1943]. Glabella tapered; occipital ring extended into long spine; genae elevated, preglabellar depression deep; border wide, elevated, with coarse crenulations. Thorax with 2 segments. Pygidium with long, furrowed axis; pleural fields furrowed. Surface granulose. Size small. *M.Cam.*, E.N.Am.-NW.Eu. (Acad.-Balt. prov.)——FIG. 129,*4*. **D. dawsoni* (HARTT), N.B.; *4a-c,* whole exoskel., ceph., pyg., ×7.5 (448n).

Opsidiscus WESTERGÅRD, 1950 [*pro Aulacodiscus* WESTERGÅRD, 1946 (*non* DOUVILLÉ, 1921)] [**Aulacodiscus bilobatus* WESTERGÅRD, 1946]. Glabella divided by anterior transglabellar furrow; occipital furrow and spine developed; eyes marked as tubercles, but facial sutures fused. Pygidium with furrowed axis, smooth pleural fields. Size small. *M.Cam.*, Eu.——FIG. 130,*2*. **O. bilobatus* (WESTERGÅRD), Swed.; *5a,b,* ceph., pyg., ×12 (334).

Serrodiscus RICHTER & RICHTER, 1941 [**S. serratus*] [=*Paradiscus* KOBAYASHI, 1943]. Cephalon semielliptical; glabella tapered; occipital ring simple; border narrow, tuberculate; preglabellar depression shallow. Thorax with 3 segments. Pygidial axis long, with numerous rings; pleural fields unfurrowed; border narrow, with small marginal spines. Size large (15 to 40 mm.) for eodiscids.

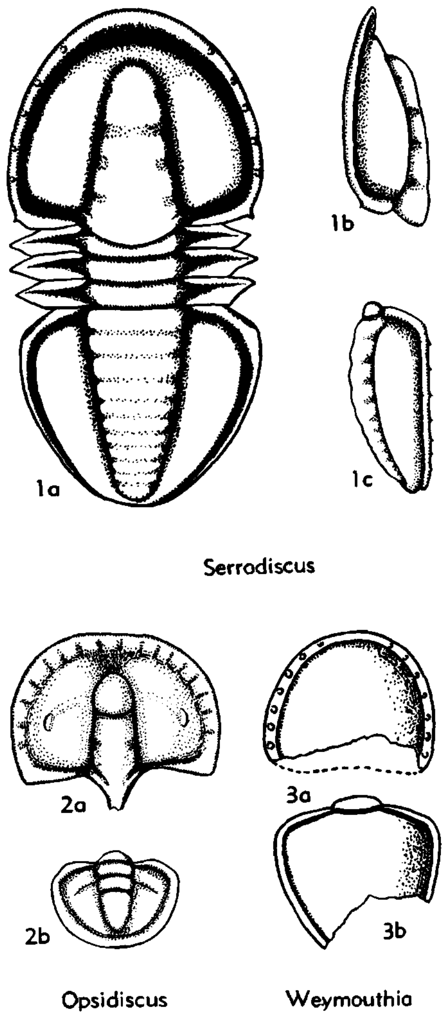


FIG. 130. Eodiscidae (p. *O*188).

L.Cam., Eu.-N.Am.——FIG. 130,*1*. *S. speciosus* (FORD), N.Y.; 1a-c, exoskel., ceph., pyg., ×4.5 (448n).

Weymouthia RAYMOND, 1913 [**Agnostus? nobilis* FORD, 1872]. Cephalon and pygidium subequal, with all furrows except border one obsolete, at least on outer surface. Thorax with 3 segments. Size small. *L.Cam.*, Eu.-N.Am.——FIG. 130,*3*. **W. nobilis* (FORD), N.Y.; *3a,b,* holotype, thorax lacking, ×9 (46).

Family PAGETIIDAE Kobayashi, 1935

[*nom. correct.* WESTERGÅRD, 1946 (*pro* Pagetidae KOBAYASHI, 1935)] [Incl. Delgadoiinae KOBAYASHI, 1943]

Eyes and facial sutures well developed; course of sutures proparian, librigenae small.

Thorax with 2 or 3 segments. *L.Cam.-M. Cam.* (46, 117, 339).

Pagetia WALCOTT, 1916 [**P. bootes*] [=*Eopagetia*, *Mesopagetia* KOBAYASHI, 1943; ?*Pagetina* LERMONTOVA, 1940 (*non* BARNARD, 1931)]. Glabella well defined, tapered; occipital ring extended into long spine; fixigenae elevated posteriorly, preglabellar depression well marked; border rather narrow, with radial markings; palpebral lobes short and narrow, eye ridges distinct in some species; librigenae lateral, small; facial sutures directed transversely to margin both in front and behind eyes. Thorax with 2 segments. Pygidium with long, well-seg-

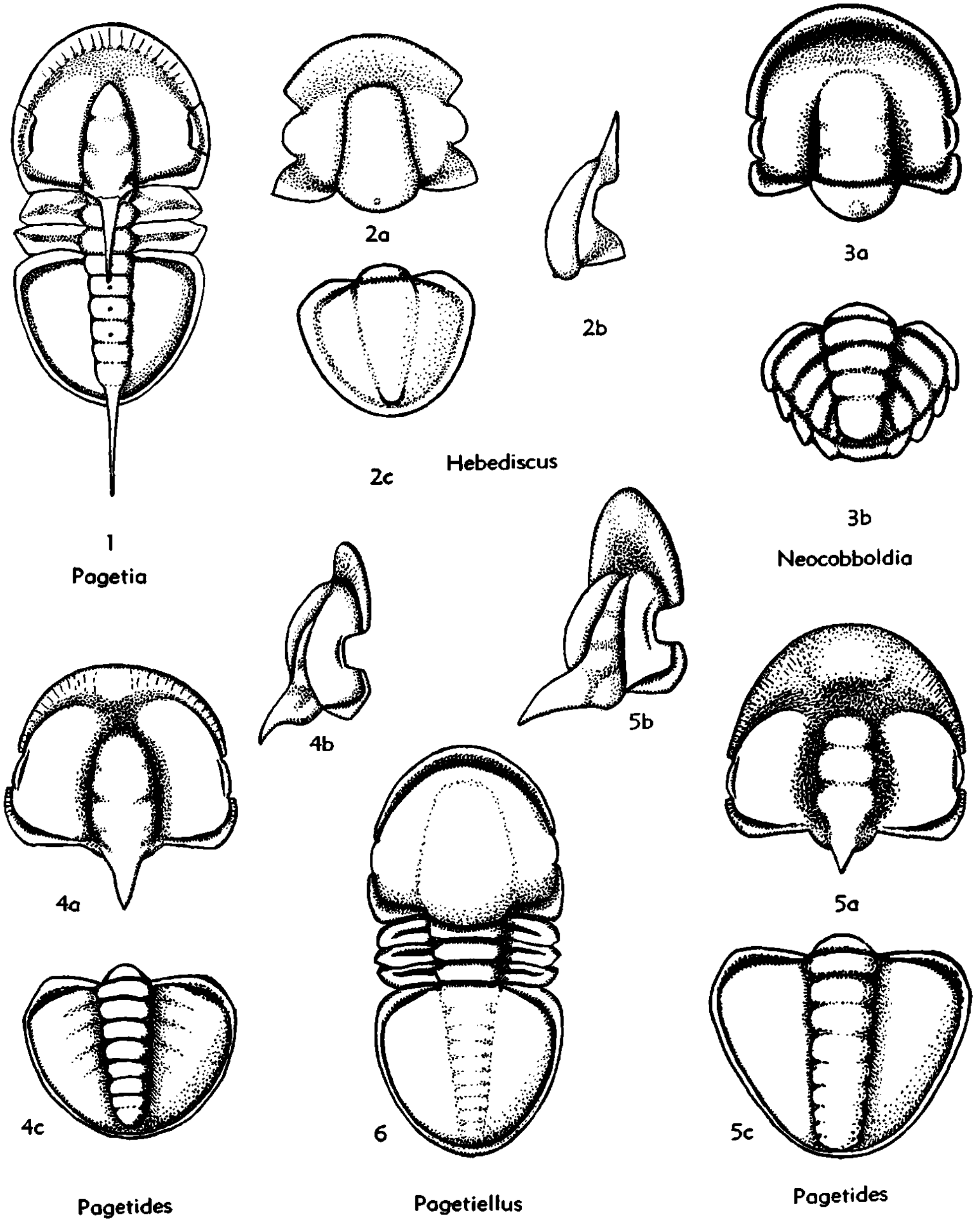


FIG. 131. Pagetiidae (p. *O*189-*O*190).

mented axis extended into spine; pleural regions furrowed or not, with narrow border; margin smooth. *L.Cam.-M.Cam.*, N.Am.-Asia-Austral.——FIG. 131,*1*. **P. bootes*, M.Cam., B.C.; whole exoskel., ×7.5 (448n).

Delgadella WALCOTT, 1912 [**Lingulepis lusitanica* DELGADO, 1904 (=*Microdiscus souzai, M. woodwardi* DELGADO, 1904)] [=*Delgadoia* VOGDES, 1917; *Delgadodiscus* KOBAYASHI, 1935; *Alemtejoia* KOBAYASHI, 1943]. Cephalon with undefined glabella, distinct border furrow, and narrow, smooth border; librigenae as in *Pagetia*. Thorax with 3 segments. Pygidium subtriangular, trilobed; border distinct, in some species extended into terminal spine (292). *L.Cam.*, Eu.(Port.).

Hebediscus WHITEHOUSE, 1936 [**Ptychoparia? attleborensis* SHALER & FOERSTE, 1888]. Glabella straight-sided, tapered, unfurrowed; occipital ring simple; border furrow shallow, border flat; palpebral lobes relatively long, palpebral furrows indistinct; librigenae larger than in other genera of family, sutures doubtfully proparian. Thorax with 3 segments. Pygidium of typical eodiscid shape; axial furrows shallow; pleural fields smooth; margin rounded. *L.Cam.*, Eu.-N.Am.(Acad.-Balt. prov.).——FIG. 131,*2*. **H. attleborensis* (SHALER & FOERSTE), Newf.; *2a,b*, cran., ×6; *2c*, pyg., ×6 (448n).

Neocobboldia RASETTI, 1952 [*pro Cobboldia* LERMONTOVA, 1940 (*non* BRAUER, 1887; *nec* LEIPER, 1910)] [**Cobboldia dentata* LERMONTOVA, 1940]. Glabella prominent, sides subparallel; occipital ring rounded; cephalic border rather narrow; palpebral lobes and furrows well developed. Thorax with 3 segments. Pygidial axis elevated, with few rings; pleural fields furrowed; margin denticulate. *L. Cam.*, Sib.——FIG. 131,*3*. **N. dentata* (LERMONTOVA), Lena Valley; *3a,b*, cran., pyg., ×12 (117).

Pagetides RASETTI, 1945 [**P. elegans*]. Similar to *Pagetia* but palpebral lobes and furrows more distinct; cephalic border expanded mesially, border and axial furrows meeting in preglabellar depression. Thorax with 3 segments. Pygidium with long, multisegmented axis lacking terminal spine; pleural fields usually smooth. *L.Cam.*, N.Am. (Appal.)——FIG. 131,*4*. **P. elegans*, Que.; *4a,b*, cran., ×7.5; *4c*, pyg., ×7.5 (448n).——FIG. 131,*5*. *P. rupestris* RASETTI, Que.; *5a,b*, cran., ×7.5; *5c*, pyg., ×7.5 (448n).

Pagetiellus LERMONTOVA, 1940 [**Microdiscus lenaicus* TOLL, 1899]. Cephalon highly convex; axial furrows almost obsolete, glabellar and occipital furrows lacking; border furrow and narrow border distinct; palpebral lobes poorly defined. Thorax with 3 segments, markedly trilobed. Pygidium strongly convex, with long, poorly defined axis; border furrow and narrow border present. *L.Cam.*, Sib.——FIG. 131,*6*. **P. lenaicus* (TOLL), Lena Valley; specimen lacking only librigenae, ×7.5 (117).

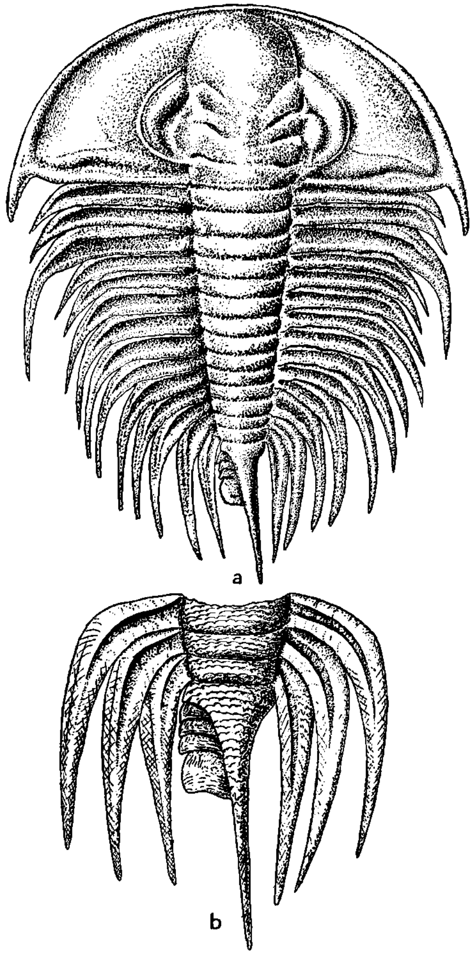


FIG. 132. **Olenellus thompsoni* (HALL), L.Cam., Vt.; *a*, dorsal exoskel., ×0.6; *b*, posterior extremity, ×1.7 (312).

?**Triangulaspis** LERMONTOVA, 1940 [**Ptychoparia meglitzkii* TOLL, 1899]. Glabella prominent, tapering, extended posteriorly into large spine; fixigenae wide, rising toward eyes; anterior border furrow straight, transverse, merging with axial furrows on mid-line; border wide *(sag.)*, swollen, subtriangular. [May be an eodiscid or multisegmented trilobite related to *Strenuaeva*.] *L.Cam.*, Sib.

Order REDLICHIIDA Richter, 1933

[*nom. correct.* MOORE, herein (*pro* Redlichiina RICHTER, 1933] [=suborder Micropygia GÜRICH, 1907 *(partim)*; suborder Mesonacida SWINNERTON, 1915 *(partim)*; order Mesonacida POULSEN, 1927; suborder Redlichiina RICHTER, 1933 *(partim)*] [Type—*Redlichia* COSSMANN, 1902]

Trilobites with relatively large semicircular cephalon, commonly with well-developed genal spines, numerous thoracic segments, and diminutive or rudimentary pygidium;

facial sutures of opisthoparian type or ankylosed, glabella typically well segmented, eyes tending to be elongate crescentic. *L. Cam.-M.Cam.*

Suborder OLENELLINA Resser, 1938

[*nom. correct.* Moore, herein (*pro* order Olenellida Resser, 1938)] [=suborder Mesonacida Swinnerton, 1915; order Mesonacida Poulsen, 1927; superfamily Olenellidea Richter, 1941; order Protoparia Størmer, 1942 (*non* Swinnerton, 1915); superfamily Olenellacea Henningsmoen, 1951; superfamily Olenelloidae Hupé, 1953] [Type—*Olenellus* Hall, 1881]

Exoskeleton elongate, nearly flat or with low convexity. Cephalon relatively large, subsemicircular, commonly with well-marked border and prominent genal spines; glabella elongate, generally with distinct furrows; eyes typically large, crescentic; facial sutures ankylosed. Rostral plate sickle-shaped, reaching to genal angles. Thorax composed of numerous segments that bear strong furrows and commonly terminate in spines. Pygidium diminutive to rudimenary. *L.Cam.*

Family OLENELLIDAE Vogdes, 1893

[=emend. Mesonacidiae Walcott, 1891] [Mesonacidae Walcott, 1910] [*nom. conserv.* proposed Moore, 1958, ICZN pend.]

Exoskeleton subovate to elongate, almost flat to moderately convex, micropygous. Cephalon subsemicircular to semielliptical, devoid of dorsal sutures, with well-defined border, 3 to 5 pairs of lateral glabellar furrows, eyes mostly large, genal spines usually present. Thorax generally composed of numerous segments with well-defined pleural furrows and well-developed pleural spines or acutely terminating, falcate distal portions. Pygidium of a single segment or with a couple of segments indicated. Outer

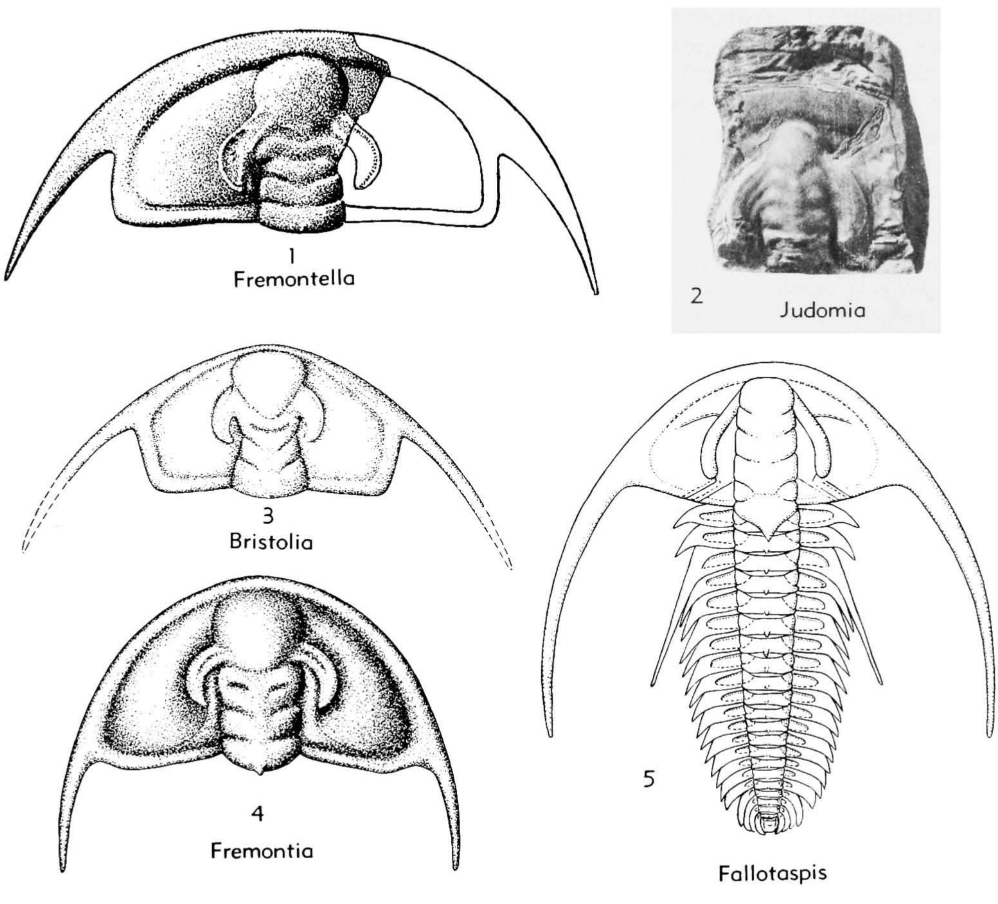


Fig. 133. Olenellidae (Olenellinae, Callaviinae, Fallotaspidinae) (p. O192-O194).

surface usually covered with granules or delicate network of raised lines or both. *L.Cam.*

Subfamily OLENELLINAE Vogdes, 1893

[*nom. transl.* Hupé, 1953 (*ex* Olenellidae Vogdes, 1893)]

Exoskeleton subovate or (rarely) elongate. Glabella usually subcylindrical, with 3 pairs of lateral furrows, 2nd pair separated from axial furrows by confluent lateral glabellar lobes (in mature specimens); metagenal spines may be present in adult specimens. Hypostoma with multidentate or (rarely) entire posterior margin. Thorax of 14 prothoracic segments with well-developed pleurae terminating in long, obliquely backward- to strictly backward-directed pleural spines, followed by a variable number (to 30 or more) of poorly developed opisthothoracic segments with more or less rudimentary pleura; 3rd prothoracic segment strongly macropleural; 1st opisthothoracic segment with long axial spine. Pygidium a minute, undivided plate. Outer surface irregularly line or finely reticulate or smooth. *L.Cam.*

Olenellus Billings, 1861 [*pro Barrandia* Hall, 1860 (*non* M'Coy, 1849)] [**Olenus thompsoni* Hall, 1859; SD Walcott, 1896] [=*Mesonacis* Walcott, 1885]. Glabella long, with rounded frontal lobe, usually reaching anterior border furrow; palpebral lobes mostly long, terminating, opposite occipital furrow or farther back. Hypostoma without stalk (241, 282, 312). *L.Cam.*, N. Am.-Greenl.-Scot.——Fig. 132. **O. thompsoni* (Hall), Vt.; *a,* dorsal exoskel., ×0.7; *b,* posterior part of same, ×1.7 (312).

Bristolia Harrington, 1956 [**Mesonacis bristolensis* Resser, 1928]. Differs from *Olenellus* in having hourglass-shaped glabella with pyriform frontal lobe, much shorter, slightly anterior palpebral lobes, narrowly obtuse to acute metagenal angles, well-advanced genal spines, and anteriorly narrowing cephalic border (56). *L.Cam.*, N.Am. ——Fig. 133,*3*. **B. bristolensis* (Resser), Calif.; ceph., ×1 (231).

Fremontella Harrington, 1956 [**Wanneria halli* Walcott, 1910]. Differs from *Bristolia* in having parallel-sided glabella with evenly rounded frontal lobe slightly encroaching on anterior border, slightly posterior palpebral lobes, and almost flat, much wider anterior border (56). *L.Cam.*, N. Am.——Fig. 133,*1*. **F. halli* (Walcott), Ala.; ceph., ×1 (56).

Fremontia Raw, 1939 [**Olenellus fremonti* Walcott, 1910]. Differs from *Olenellus* in having much shorter palpebral lobes, broadly obtuse metagenal angles, and somewhat advanced genal spines (56). *L.Cam.*, N.Am.——Fig. 133,*4*. **F. fremonti* (Walcott), Calif.; ceph., ×1.5 (231).

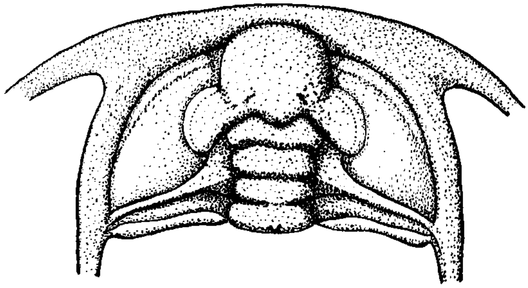


Fig. 134. **Laudonia bispinata* Harrington (Olenellinae), L.Cam., W.Can.(B.C.); ceph., ×3 (56).

Laudonia Harrington, 1956 [**L. bispinata*]. Differs from *Fremontella* in having conspicuous metagenal spines in direct continuation of lateral border, simulating true genal spines (56). *L.Cam.*, N.Am.——Fig. 134. **L. bispinata,* B.C.; ceph., ×4.5 (56).

Paedeumias Walcott, 1910 [**P. transitans*]. Differs from *Olenellus* in having median ridge extending from frontal glabellar lobe to anterior border, and stalk connecting hypostoma with rostral plate (312, 241). *L.Cam.*, N.Am.-Greenl.-Scot.-Sib.——Fig. 135,*5*. **P. transitans,* Vt.; dorsal exoskel., ×1.8.——Fig. 138,*2*. *P. yorkense* Resser & Howell, Pa.; median part of rostral plate with hypostoma, ×2 (312).

Peachella Walcott, 1910 [**Olenellus iddingsi* Walcott, 1884]. Differs from *Olenellus* in having tumid, bluntly terminating genal spines (312). *L.Cam.*, N.Am.——Fig. 135,*6*. **P. iddingsi* (Walcott), Nev.; *6a,* cephalon, ×2; *6b,* genal angle and genal spine, ×3 (312).

Subfamily CALLAVIINAE Poulsen, nov.

Exoskeleton subovate. Glabella subcylindrical to slightly clavate, with 3 to 5 pairs of glabellar furrows; occipital spine usually present; anterior and lateral cephalic border wide, slightly convex; palpebral lobes long, evenly curved. Posterior margin of hypostoma entire. Thorax (as far as known) consisting of 16 or 17 prothoracic and 1 or 2 slightly reduced opisthothoracic segments; a median axial spine usually present on each axial ring; pleurae straight to gently curved, sword-shaped, passing gradually into strong, falcate extremities; 3rd thoracic segment normal; articulation apparatus consisting of a row of articular cones and sockets in axial furrows. Pygidium a minute, apparently undivided plate. Outer surface finely reticulate. *L.Cam.*

Callavia Matthew, 1897 [**Olenellus (Mesonacis) bröggeri* Walcott, 1890; SD Walcott, 1910] [=*Cobboldus* Raw, 1936]. Glabella usually subcylindrical, fairly narrow, with 4 or 5 pairs of lateral furrows and frontal lobe tapering to a more or less narrowly rounded front; strong occipital spine usually present; posterior cephalic border generally with well-developed metagenal spines situated very close to genal angles. Hypostoma connected with rostral plate by median part of its anterior margin (204, 312). *L.Cam.*, E.N. Am.-Eng.-?Sp.-N.Afr.——Fig. 136. **C. broeggeri* (Walcott), Newf.; *a*, restored dorsal exoskel., ×0.5; *b*, median part of rostral plate wtih hypostoma, ×1.3 (312).

Judomia Lermontova, 1951 [**J. dzevanovskii*]. Differs from *Callavia* and *Kjerulfia* in having palpebral genal region occupied by obliquely backward-directed extensions of anterior and next following lateral glabellar lobe (118). *L.Cam.*, Sib.——Fig. 133,2. **J. dzevanovskii;* fragmentary ceph., ×1 (118*).

Kjerulfia Kiar, 1917 [**K. lata*]. Differs from *Callavia* in having frontal glabellar lobe expanded laterally beyond lateral glabellar lobes, 3 pairs of lateral glabellar furrows only, minute occipital

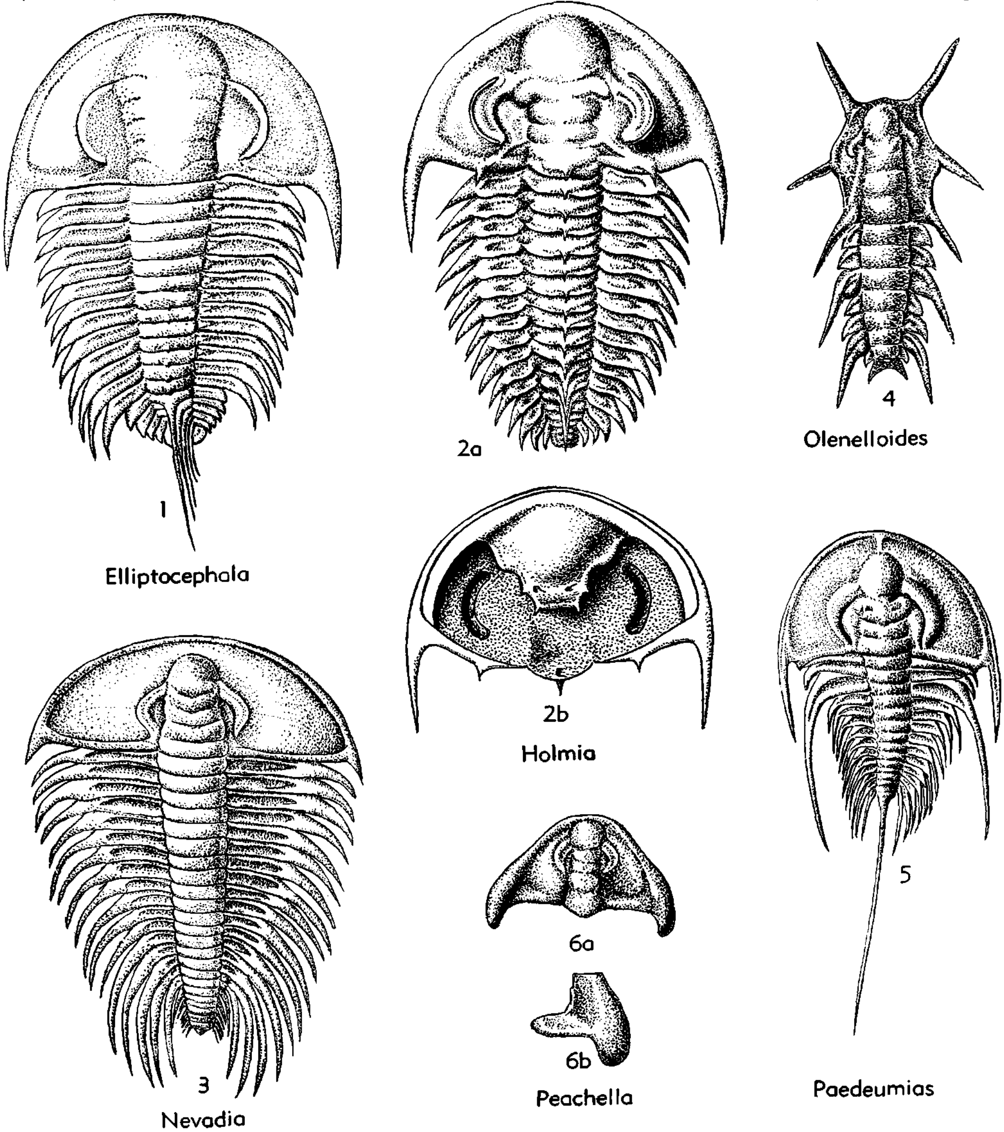


Fig. 135. Olenellidae (Olenellinae, Elliptocephalinae, Holmiinae, Nevadiinae, Olenelloidinae) (p. O192-O195).

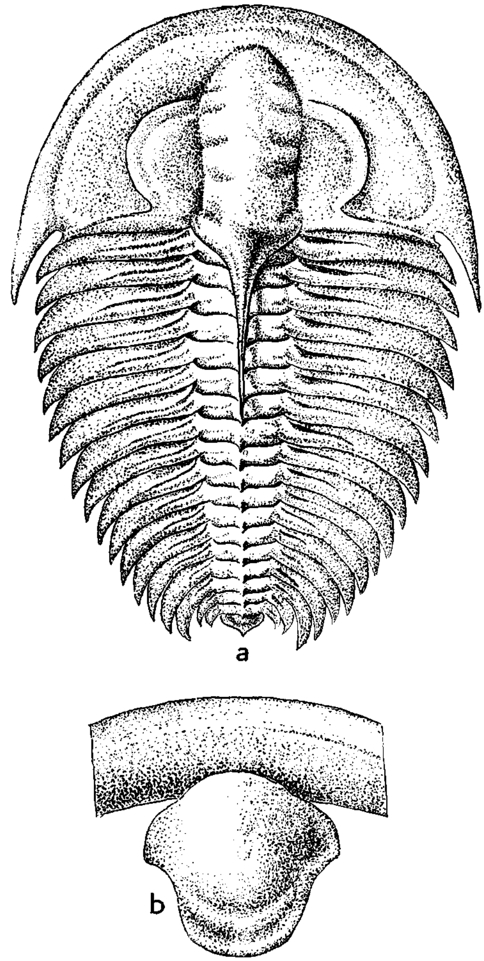


FIG. 136. **Callavia broeggeri* (WALCOTT) (Olenellidae, Callaviinae), L.Cam., Newf.; *a*, dorsal exoskel., ×0.4; *b*, hypostoma and part of rostral plate, ×1.8 (312).

spine, posterior cephalic border without metagenal spines, metagenal angles situated remote from genal angles and total anterior margin of much wider hypostoma connected with rostral plate (90). *L.Cam.*, Norway-?Swed.-?Eng.——FIG. 137, *1*. **K. lata*, Norway; *1a*, restored dorsal exoskel., ×0.57; *1b*, ventral side of ceph., showing rostral plate and hypostoma, ×0.57 (90).

Subfamily ELLIPTOCEPHALINAE Hupé, 1953

Exoskeleton subovate. Glabella very wide, somewhat clavate, with broadly rounded front and 4 pairs of lateral furrows; preglabellar field short in mature specimens; palpebral lobes long, semicircular, surrounding relatively large intra-ocular genal regions; cephalic border fairly narrow, moderately convex. Hypostoma not known with certainty. Thorax of 13 prothoracic segments with fairly wide axis, median axial nodes, and straight to gently curved pleurae passing gradually into strong, falcate extremities, and 5 considerably reduced opisthothoracic segments, typically with long, backward-directed axial spines. Pygidium minute, transverse, with only a trace of an anterior segment. Outer surface finely granulate and reticulate. Character of ventral parts unknown. *L.Cam.*

Elliptocephala EMMONS, 1884 [**E. asaphoides*] [=*Ebenezeria* MARCOU, 1888 (obj.); *Georgiellus* MOBERG, 1899 (obj.)] (303). *L.Cam.*, E.N.Am. ——FIG. 135,*1*. **E. asaphoides*, N.Y.; dorsal exoskel., ×0.45 (312).

Subfamily FALLOTASPIDINAE Hupé, 1953

Exoskeleton elongate. Cephalon much wider than thorax, with subconical glabella commonly separated from anterior border by short preglabellar field, 5 pairs of lateral furrows (anterior 2 pairs indistinctly defined in some), trilobate occipital ring, wide anterior and lateral border furrow, moderately wide, slightly convex anterior and lateral border, long, prominent, slightly curved palpebral lobes terminating opposite to occipital furrow or farther back, and very long genal spines. Hypostoma unknown. Thorax of 17 prothoracic and some opisthothoracic segments, with trilobate axial rings and broad, very short pleural furrows; prothoracic pleurae straight to slightly curved, with spined to obliquely truncated, pointed extremities; 3rd segment strongly macropleural; opisthothoracic pleurae strongly curved. Pygidium minute, of 1 or ?2 segments with very narrow pleural fields. Outer surface (as far as known) granulate. *L.Cam.*

Fallotaspis HUPÉ, 1953 [*pro Fallotia* HUPÉ, 1953 (*non* DOUVILLÉ, 1902)] [**F. typica*] (77). *L. Cam.*, N.Afr.-?Eng.——FIG. 133,*5*. **F. typica*, Morocco; restored dorsal exoskel., ×1 (77).

Subfamily HOLMIINAE Hupé, 1953

Exoskeleton subovate to elongate. Cephalon considerably wider than anterior part of thorax. Glabella subcylindrical to more or less clavate, with 3 pairs of lateral furrows. Metagenal angles situated fairly close to occipital ring. Thorax (as far as known) of 16 to 17 normally developed segments with wide axis and relatively narrow pleu-

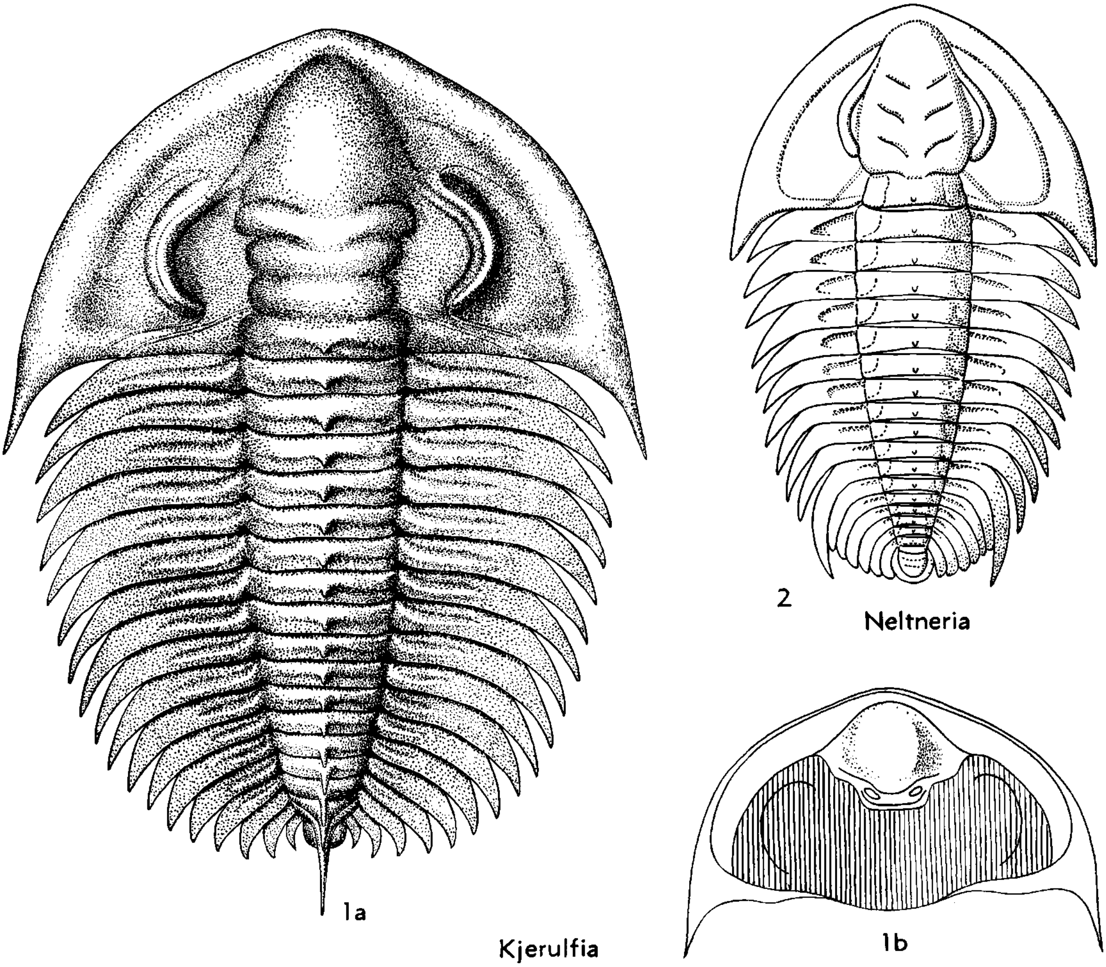


FIG. 137. Olenellidae (Callaviinae, Neltneriinae) (p. O193-O196).

ral regions. Pygidium minute, with 1 to ?3 segments. *L.Cam.*

Holmia MATTHEW, 1890 [**Paradoxides kjerulfi* LINNARSSON, 1871] [=*Esmeraldina* RESSER & HOWELL, 1938]. Cephalon considerably wider than thorax; glabella clavate, broadly rounded in front, with laterally expanded frontal lobe; small occipital spine present; palpebral lobes strongly and evenly curved; posterior cephalic border with well-developed metagenal spines in type species. Thorax of 16 segments with axial spines especially well developed near pygidium, and pleurae terminating in obliquely backward-directed spines, posterior ones being approximately falcate and almost enveloping pygidium. Pygidium with 2 axial rings in addition to rounded terminal portion, extremely narrow pleural fields gently curved lateral margins, and almost rectilinear posterior margin. Outer surface finely reticulate (90). *L.Cam.*, Eu.-N.Am.——FIG. 135,2. **H. kjerulfi* (LINNARSSON), Norway; *2a,* restored dorsal exoskel., ×0.7; *2b,* ventral view of ceph., showing rostral plate and hypostoma, ×0.7 (90).

Bondonella HUPÉ, 1953 [**B. typica*]. Differs from *Holmia* in having cephalon of about same width as middle portion of thorax, subcylindrical glabella, longer, moderately curved palpebral lobes, anteriorly contracted thorax of 17 segments without axial spines, and pygidium with 1 or 2 axial segments and probably dentate posterior margin. Surface markings unknown (77). *L.Cam.*, N.Afr.——FIG. 138,3. **B. typica,* Morocco; restored dorsal exoskel., ×1 (77).

?**Schmidtiellus** MOBERG in MOBERG & SEGERBERG, 1906 [*pro Schmidtia* MARCOU, 1890 (*non* VOLBORTH, 1869)] [**Olenellus mickwitzi* SCHMIDT, 1888]. Differs from *Holmia* in much-reduced frontal glabellar lobe, unevenly curved palpebral lobes with long, almost straight proximal

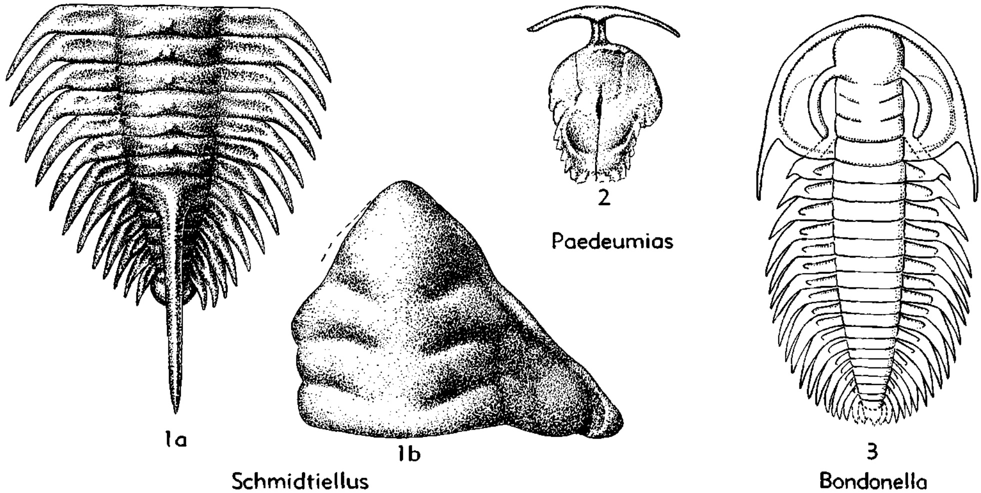


FIG. 138. Olenellidae (Olenellinae, Holmiinae) (p. O192-O195).

portion and short, more or less abruptly curved distal portion, thorax (number of segments unknown) with long axial spine on 6th segment from pygidium, which has narrower axis and wider pleural fields, and outer exoskeletal surface with finely granulate areas in addition to fine reticulation (270). *L.Cam.*, Balt.-?Swed.——FIG. 138,*1*. **S. mickwitzi* (SCHMIDT), Est.; *1a*, fragmentary glabella with palpebral lobe, ×2; *1b*, posterior part of dorsal exoskel., ×1 (270).

Subfamily NELTNERIINAE Hupé, 1953

Exoskeleton ovate. Glabella inverted ovate, encroaching on anterior cephalic border, with 3 pairs of oblique lateral furrows separated from axial furrows by confluent lateral glabellar lobes; occipital ring trilobate, narrower than glabella and 1st thoracic axial ring; anterior and lateral cephalic border very wide, slightly convex; palpebral lobes long, slightly curved, delimiting extremely narrow intra-ocular genal portion, their distal ends touching posterior lateral glabellar lobe; genal spines short, stout, rapidly tapering. Hypostoma unknown. Thorax of 11 prothoracic segments with trilobate axial rings, very short pleural furrows, and strong falcate extremities; 11th segment macropleural, followed by 5 or 6 opisthothoracic segments with more strongly curved, bluntly terminating pleurae. Pygidium minute, number of segments unknown, with evenly curved posterolateral margin. Surface markings unknown. *L. Cam.*

Neltneria HUPÉ, 1953 [**Wanneria jaqueti* NELTNER & POCTEY, 1950] (77). *L.Cam.*, N.Afr.——FIG. 137,*2*. **N. jaqueti* (NELTNER & POCTEY), Morocco; restored dorsal exoskel., ×0.7 (77).

Subfamily NEVADIINAE Hupé, 1953

Exoskeleton subovate. Cephalon very wide, with narrow, conical glabella, 3 transglabellar furrows, short to long, moderately to strongly curved palpebral lobes, very wide extra-ocular genal regions, and short, rapidly tapering genal spines. Hypostoma unknown. Thorax (as far as known) of 17 to 28 segments with gradually tapering axis, prothoracic ones having short-furrowed pleurae with long, acutely terminating, falcate distal portion; 3rd segment normal. Pygidium a minute, undivided plate. Outer surface minutely granulate and irregularly reticulate. *L.Cam.*

Nevadia WALCOTT, 1910 [**N. weeksi*]. Cephalon about 3 times as wide as long, with well-developed preglabellar field and narrow border. Thorax (as far as known) of 17 prothoracic segments, followed by 11 post-thoracic ones with rudimentary spinelike pleurae (312, 204). *L.Cam.*, W.N.Am.-?Eng.——FIG. 135,*3*. **N. weeksi*, Nev.; dorsal exoskel. without pygidium and posterior part of opisthothorax, ×0.45 (312).

Nevadella RAW, 1936 [**Callavia eucharis* WALCOTT, 1913; SD WHITEHOUSE, 1939]. Differs from *Nevadia* in having longer cephalon with longer glabella, short preglabellar field or lacking it, border wide. Thorax of 17 to 23 segments; character of posterior part of thorax incompletely known (204). *L.Cam.*, N.Am.

Subfamily OLENELLOIDINAE Hupé, 1953

Minute (?neotenic) forms. Exoskeleton narrow, elongate. Cephalon more or less distinctly hexagonal, with well-developed pergenal, genal, and metagenal spines, subtapering glabella extended to narrow anterior border, 3 pairs of lateral furrows (generally transglabellar), genae narrower than glabella, palpebral lobes very short. Hypostoma unknown. Thorax of 8 segments with axis about twice as wide as pleural regions, and macropleural development of 3rd and 6th segments. Pygidium unknown. Outer surface finely reticulate. *L. Cam.*

Olenelloides PEACH, 1894 [**O. armatus*] (114, 312, 164). *L.Cam.*, Scot.——FIG. 135,*4*. **O. armatus;* ceph. and thorax, ×3 (164).

Subfamily WANNERIINAE Hupé, 1953

Exoskeleton subovate. Cephalon inconsiderably wider than anterior part of thorax, with fairly wide anterior and lateral border. Glabella clavate, with strongly expanded frontal lobe and 3 pairs of lateral glabellar furrows. Metagenal angles remote from occipital ring. Thorax (as far as known) of 15 prothoracic and a few opisthothoracic segments; 3rd thoracic segment normal, and 15th furnished with long, very strong axial spine; pleural regions fairly wide. Outer surface finely granulate and more or less coarsely reticulate. *L.Cam.*

Wanneria WALCOTT, 1910 [**Olenellus (Holmia) walcottanus* WANNER, 1901]. Cephalon of adult specimens without metagenal spines. Prothoracic segments with axial nodes or spines, broad pleural furrows, and long, acutely terminating, falcate extremities; 16th and 17th (opisthothoracic) segments without axial spines and with somewhat reduced pleurae. Pygidium bilobate, apparently consisting of an axial ring and a pair of backwardly directed, incompletely fused pleurae (173, 241, 312). *L.Cam.*, N.Am.-Greenl.-?Eng.-Silesia.——FIG. 139. **W. walcottana* (WANNER), Pa.; *a,* dorsal exoskel., ×0.7; *b,* pygidium and posterior part of thorax, showing base of strong axial spine on 15th segment, ×2; *c,* posterolateral portion of hypostoma, showing reticulate surface and marginal spines, ×6 (312).

Family DAGUINASPIDIDAE Hupé, 1953

[*nom. correct.* POULSEN, herein (*ex* Daguinaspidae HUPÉ, 1953)]

Exoskeleton elongate, moderately convex, micropygous. Cephalon heart-shaped to subelliptical, devoid of dorsal sutures; taper-

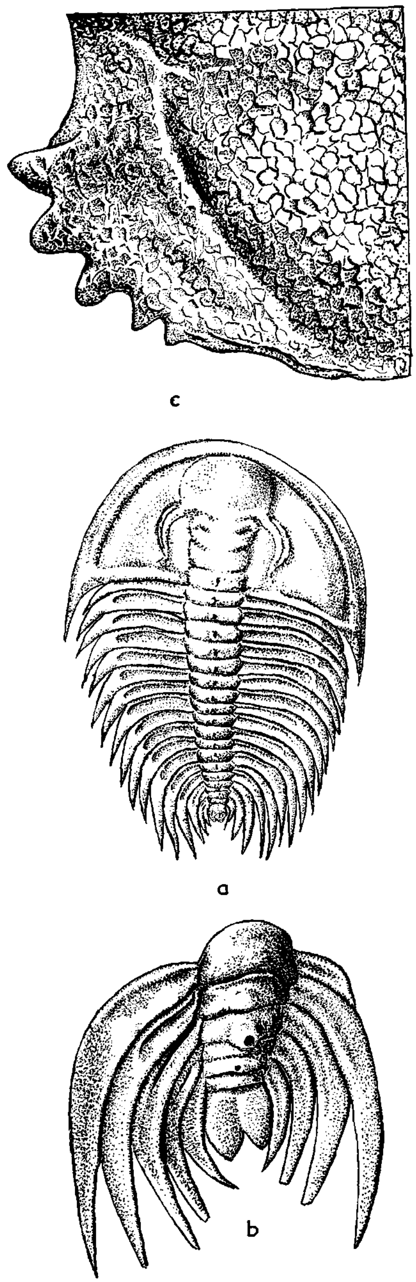
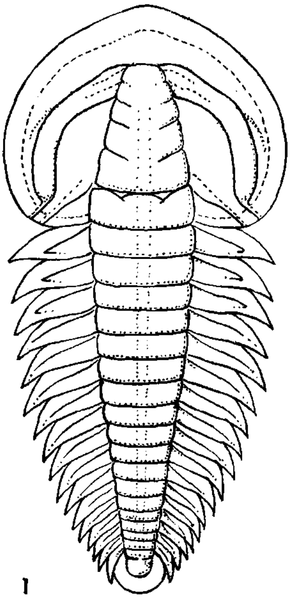


FIG. 139. **Wanneria walcottana* (WANNER) (Olenellidae, Wanneriinae), L.Cam., E.USA(Pa.); *a,* dorsal exoskel., ×0.7; *b,* pyg. and part of thorax, ×2; *c,* posterolateral part of hypostoma, ×6 (312).



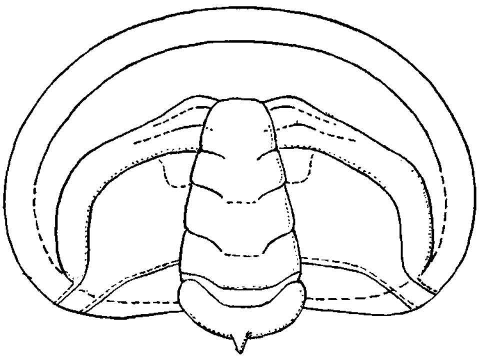


FIG. 140. Daguinaspididae (p. O198).

ing anteriorly truncated glabella with 3 to 5 pairs of lateral furrows; preglabellar field well developed; with very long, more or less distinctly trifid palpebral lobes; genal angles rounded, spineless; lateral portion of extra-ocular gena narrow, with broad border furrow and narrow border; hypostoma unknown. Thorax of 17 (?16) segments in the type genus, with gradually tapering axis and short, furrowed, acutely terminating pleurae. Pygidium very small. *L.Cam.*

Daguinaspis HUPÉ & ABADIE, 1950 [**D. ambroggii*]. Cephalon heart-shaped, more or less acuminate in front, almost as long as wide (in most subgenera), with intrapalpebral portion of genae considerably narrower than occipital ring. Pygidium subcircular, with single axial ring and rounded axial termination (77). *L.Cam.*, N.Afr.

D. (Daguinaspis). Length of cephalon generally exceeding 0.75 of width. Intrapalpebral genal region wider than posterior extra-ocular part of cephalon (77). *L.Cam.*, Morocco.——FIG. 140,*1*. **D. (D.) ambroggii;* restored dorsal exoskeleton, ×1.5 (445).

D. (Eodaguinaspis) HUPÉ, 1953 [**D. (E.) abadiei*]. Length of cephalon about 0.75 of width. Intrapalpebral genal region practically equal in width to posterior extra-ocular part of cephalon (77). *L.Cam.*, Morocco.

D. (Epidaguinaspis) HUPÉ, 1953 [**D. (E.) angusta*]. Cephalon almost as long as wide. Width of intrapalpebral genal region practically equal to that of posterior extra-ocular part of cephalon (77). *L.Cam.*, Morocco.

Choubertella HUPÉ, 1953 [**C. spinosa*]. Differs from *Daguinaspis* in having much wider, transversely subelliptical cephalon with broadly rounded anterior margin and wider intrapalpebral genal region (77). *L.Cam.*, N.Afr.——FIG. 140,*2*. **C. spinosa,* Morocco; restored ceph., ×3 (77).

Suborder REDLICHIINA Harrington, nov.

[=superfamily Redlichiidea RICHTER, 1933; Redlichiacea HENNINGSMOEN, 1951; Redlichioidae HUPÉ, 1953] [Type—*Redlichia* COSSMANN, 1902]

Dorsal exoskeleton elongate, subelleptical in outline. Cephalon semicircular to semielliptical, mostly with prominent genal spines; glabella with subparallel sides, narrowing forward, or expanding forward, generally well segmented; facial sutures opisthoparian; eyes mostly large, tending to be crescentic. Thorax with numerous segments. Pygidium small. *L.Cam.-M.Cam.*

Superfamily REDLICHIACEA Poulsen, 1927

[*nom. correct.* HENNINGSMOEN, 1951 (*pro* superfamily Redlichiidea RICHTER, 1933, *nom. transl., ex* Redlichidae POULSEN, 1927)]

Characters of the suborder, but distinguished by lack of expanded anterior part of glabella and very elongate, crescentiform nature of eyes; preglabellar field very narrow or lacking. *L.Cam.-M.Cam.*

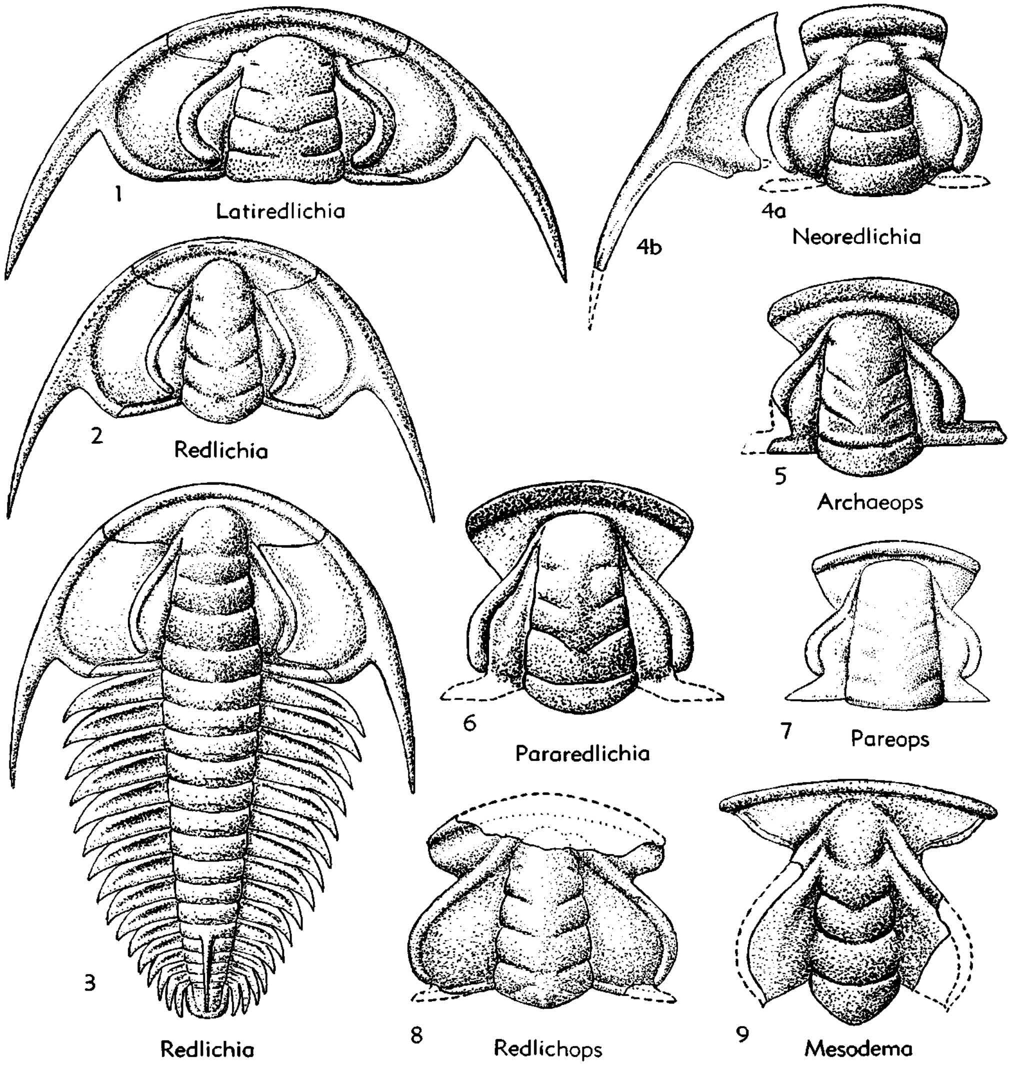


FIG. 141. Redlichiidae (Redlichiinae, Pararedlichiinae), Neoredlichiidae (p. *O*200, *O*201).

Family REDLICHIIDAE Poulsen, 1927

[*nom. correct.* RICHTER, 1933 (*pro* Redlichidae POULSEN, 1927)] [=Latiredlichiidae HUPÉ, 1953 (*partim*)]

Dorsal exoskeleton opisthoparian, ovate, very gently convex, micropygous. Cephalon semielliptical; glabella long, tapering forward, rounded in front, with 3 pairs of evenly spaced lateral glabellar furrows, anterior pair *(3p)* faint, short, slightly oblique forward-backward, remainder oblique backward-inward, subparallel to occipital furrow; preglabellar field narrow; anterior border wider, raised; eye lobes arcuate, long, arising from frontal glabellar lobe, extending to level of occipital furrow or farther back; facial sutures kainelliform, anterior sections very divergent (90° to 45°); posterior area of fixigenae narrow *(exsag.)*, librigenae wide, with advanced genal spines. Thorax of 11 to 17 segments; pleurae ending in spines, fulcrum distal. Pygidium small, 1 or 2 segments. Surface of exoskeleton smooth or very finely granulose. *L.Cam.*

Subfamily REDLICHIINAE Poulsen, 1927

[*nom. transl.* HARRINGTON, herein (*ex* Redlichiidae POULSEN, 1927)]

Proximal extremities of anterior sections of facial sutures close to axial furrow, meet-

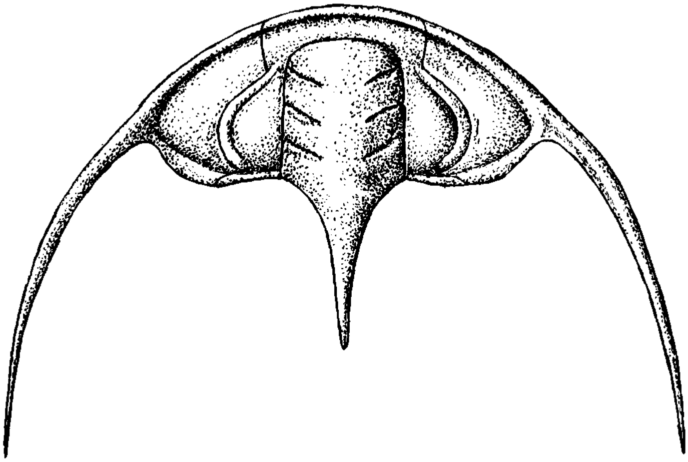


FIG. 142. **Redlichaspis finalis* (WALCOTT) KOBAYASHI (Redlichiidae, Redlichiinae), *L.Cam.*, China, ×2 (405).

ing eye lobe at level of mid-length of frontal glabellar lobe; posterior extremity of eye lobe close to axial furrow. *L.Cam.*

Redlichia COSSMANN, 1902 [*pro Hoeferia* REDLICH, 1899 (*non* BITTNER, 1895)] [**Hoeferia noetlingi* REDLICH, 1899]. Anterior lateral glabellar furrows almost normal to axis, remainder oblique, preoccipital and occipital furrows transglabellar in internal molds; anterior border furrow pits may be present in large individuals, anterior border striated; eye lobes reaching level of occipital ring. Thorax with 11 to 17 segments, 11th bearing long axial spine; mesial spine also may be developed on 4th or 5th ring. Pygidium small, 1 or 2 segments. Rostral plate long; hypostoma fused to rostral plate, with globose anterior body and 2 pairs of short posterolateral spines. *L.Cam.*, Korea-China-W. Pak.-Iran-Austral.-?Sib.——FIG. 141,*2*. **R. noetlingi* (REDLICH) COSSMANN, W.Pak.; ceph., restored (paratype librigenae attached to holotype cran.); ×1.35 (418).——FIG. 141,*3*. *R. chinensis* WALCOTT, China; restored, ×1.8 (488).

Latiredlichia HUPÉ, 1953 [**L. saitoi* (=*Redlichia* cf. *walcotti* SAITO, 1934; *non* MANSUY, 1912)]. Differs from *Redlichia* in having shorter, wider, and finely granulose glabella. Thorax and pygidium unknown. *L.Cam.*, China.——FIG. 141,*1*. **L. saitoi;* ceph., restored (paratype librigenae attached to holotype cran.); ×1 (465).

Redlichaspis KOBAYASHI, 1935 [**Redlichia? finalis* WALCOTT, 1913]. Like *Redlichia* but differs in nature of glabellar furrows, course of facial suture, and prominent occipital spine. *L.Cam.*, China.——FIG. 142. **R. finalis* (WALCOTT); *ceph.*, ×2 (405).

?**Bulaiaspis** REPINA, 1956 [**B. vologdini*]. *L.Cam.*, E.Sib. [Published as attributed to LERMONTOVA *"in coll."* but L. N. REPINA indicated as actual author; referred by author to Redlichiidae (RCM).]

Saukiandiops HUPÉ, 1953 [**Redlichia walcotti* MANSUY, 1912]. Differs from *Pseudosaukianda* in having chevron-shaped preoccipital furrow, straight occipital furrow, occipital ring wider at middle, no occipital node, transversely elongated anterior pits, anterior branches of facial suture diverging at 45° and longer eye lobes reaching level of occipital furrow. Thorax and pygidium unknown. *L.Cam.*, China.——FIG. 145,*3*. **S. walcotti* (MANSUY), cran., ×2.5 (411).

Subfamily PARAREDLICHIINAE Hupé, 1953

Proximal ends of anterior sections of facial sutures distant from axial furrows, meeting eye lobes at level of 1st lateral glabellar lobes *(3p)*; posterior extremities of eye lobes distant from axial furrows. *L.Cam.*

Pararedlichia HUPÉ, 1953 [**P. pulchella*]. Glabella rounded-subtruncate in front, occipital furrow transglabellar; eye lobes widening posteriorly, reaching level of occipital furrow. Thorax and pygidium unknown. *L.Cam.*, China-Morocco.——FIG. 141,*6*. **P. pulchella,* Morocco; cran. (holotype), ×3 (411).

Archaeops HUPÉ, 1953 [**A. lui* (=*Redlichia walcotti* LU, 1941; *non* MANSUY, 1912)]. Differs from *Pararedlichia* in having shorter frontal glabellar lobe. *L.Cam.*, China.——FIG. 141,*5*. **A. lui;* cran. (holotype), ×2 (426).

Mesodema WHITEHOUSE, 1939 [**M. venulosa*]. Differs from *Pararedlichia* in having narrower glabella, ill-defined axial furrow at level of 1st *(3p)* and preoccipital glabellar lobes, narrower anterior border, mesially subpointed occipital ring, more divergent anterior sections of facial suture,

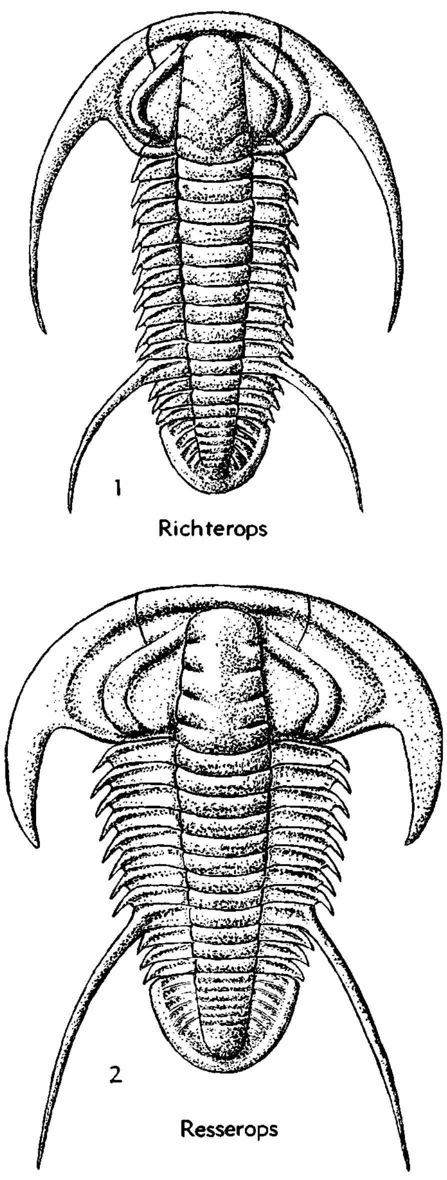


FIG. 143. Neoredlichiidae (p. *O202*).

more arcuate and longer eye lobes extending almost to level of posterior edge of occipital ring, and swollen areas of fixigenae directly behind eye lobes. *L.Cam.*, NE.Austral.——FIG. 141,*9*. **M. venulosa;* cran. (holotype), ×1.35 (493).

Pareops HUPÉ, 1953 [**P. transitans*]. Differs from *Pararedlichia* in having more arcuate eye lobes, disconnected occipital furrow and straight occipital ring. *L.Cam.*, Morocco.——FIG. 141,*7*. **P. transitans;* cran. (holotype), ×1 (411).

Redlichops RICHTER & RICHTER, 1941 [**Redlichia (Redlichops) blanckenhorni*]. Differs from *Pararedlichia* in having anterior lateral glabellar furrows *(3p)* directed obliquely forward, disconnected occipital furrow, small occipital node, shorter anterior sections of facial suture, longer and more arcuate eye lobes, widening anteriorly and extending back to level of mid-length of occipital ring, much wider fixigenae, and finely granulose surface. *L.Cam.*, Jordan.——FIG. 141,*8*. **R. blanckenhorni;* cran. (holotype), ×2.35 (461).

Family NEOREDLICHIIDAE Hupé, 1953

Dorsal exoskeleton opisthoparian, ovate, slightly convex, isopygous. Cephalon semielliptical; glabella conical, with 3 pairs of evenly spaced lateral glabellar furrows, anterior pair *(3p)* slightly oblique forward or backward, remainder oblique backward; preglabellar field narrow or absent; anterior border wide, flat; anterior pits generally present, transversely elongated; anterior sections of facial suture moderately divergent (less than 45°) to border furrow, slightly curved outward across border; eye lobes long, decurrent along frontal glabellar lobe, strongly arcuate posteriorly, reaching level of occipital furrow or farther back, posterior extremities distant from axial furrows, pseudopalpebral furrows usually present; proximal portion of posterior area of fixigenae swollen in front of posterior border furrow; librigenae wide, with advanced genal spine. Thorax of 12 to 14 segments; pleural regions narrower than axis; pleurae ending in spines, 9th or 11th macrospinose, fulcrum proximal. Pygidium parabolical; axis large, conical, with 5 to 10 rings; pleural regions with 5 to 8 pleurae; border smooth, not delimited by border furrow. *L.Cam.*

Neoredlichia SAITO, 1936 [**Redlichia nakamurai* SAITO, 1934]. Frontal glabellar lobe short, anterior lateral glabellar furrows *(3p)* normal to axis, remainder well marked, transglabellar, slightly bent backward; occipital furrow subparallel to preoccipital; occipital ring of uniform width; preglabellar field absent; pseudopalpebral furrow present; eye lobes reaching level of mid-length of occipital ring; genal spine stout, slightly advanced. Thorax and pygidium unknown. *L.Cam.*, China-Morocco.——FIG. 141,*4*. **N. nakamurai* (SAITO), China; *4a*, cran. (holotype), ×6; *4b*, librigena (paratype), ×2.65 (465).

Clariondia HUPÉ, 1953 [**C. chazani*]. Differs from *Neoredlichia* in having longer and narrower glabella, lateral glabellar and occipital furrows

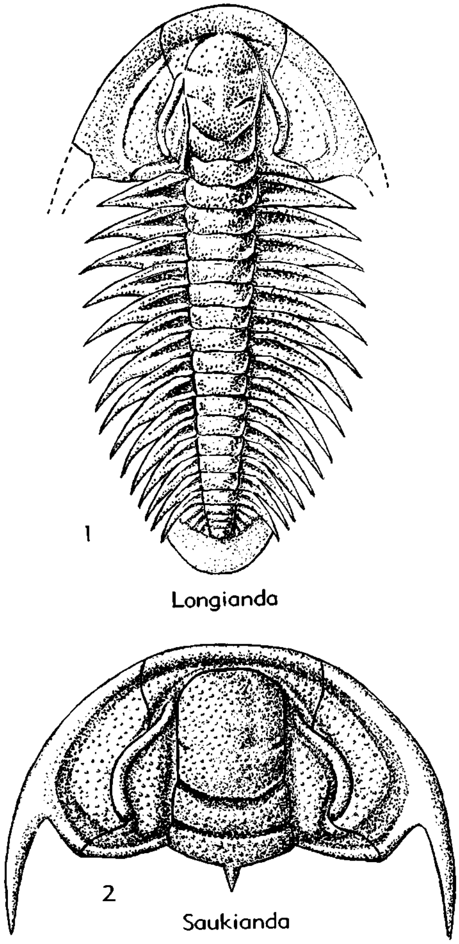


FIG. 144. Saukiandidae (p. O202, O203).

very oblique backward, discontinuous at middle, posterior edge of occipital ring semicircular, moderately wide preglabellar field and shorter eye lobes reaching level of occipital furrow. Thorax unknown. Assigned pygidium with 5 axial rings, short terminal axial piece and 5 pleurae. *L.Cam.*, Morocco.——FIG. 146,*1*. **C. chazani; 1a,* cran. (holotype), ×2; *1b,* assigned pyg.; ×3 (411).

Resserops RICHTER & RICHTER, 1940 [**R. resserianus*] [(=*Perrector* RICHTER & RICHTER, 1940) (=*R. (Rawops)* HUPÉ, 1953)]. Differs from *Neoredlichia* in having discontinuous lateral glabellar and occipital furrows and well-advanced genal spines. *L.Cam.*, Sp.-Morocco.

R. (Resserops). Lateral glabellar and occipital furrows slightly oblique backward, eye lobe reaching level of mid-length of occipital ring. Thorax of ?12 segments, ?9th macrospinose, pleurae slightly narrower than axis. Pygidium with 6 or 7 rings, large terminal axial piece and 6 to 8 pleurae. *L.Cam.*, Sp.-Morocco.——FIG. 143,*2*. **R. (R.) resserianus,* Sp.; exoskel. (reconstr.), ×3 (461).

R. (Richterops) HUPÉ, 1953 [**R. (R.) falloti*] [=*Marsaisia* HUPÉ, 1953]. Glabella narrower, frontal glabellar lobe longer, lateral glabellar and occipital furrows very oblique backward, eye lobe shorter, reaching level of occipital furrow; thorax of 14 segments, 11th macrospinose, pleurae much narrower than axis; pygidium with 7 axial rings, short terminal axial piece and 4 pleurae. *L.Cam.*, Morocco.——FIG. 143,*1*. **R. (R.) falloti;* holotype exoskel. (reconstr.), ×1 (411).

?**Eops** RICHTER & RICHTER, 1940 [**E. eo*]. Differs from *Saukianda* in having shorter glabella, longer frontal glabellar lobe, chevron-shaped preoccipital furrow, straight occipital furrow and ring, no occipital node, wider preglabellar field, anterior sections of facial suture diverging at 45°, longer eye lobes reaching level of midlength of occipital ring. *L.Cam.*, Sp.——FIG. 145,*4*. **E. eo;* cran. (holotype), ×2 (461).

Family SAUKIANDIDAE Hupé, 1953

Dorsal exoskeleton opisthoparian, ovate, gently convex, micropygous. Cephalon semielliptical; glabella long, cylindrical or constricted posteriorly, with 3 pairs of lateral glabellar furrows, 1st *(3p)* commonly obsolete, when present short, oblique backward, 2nd *(2p)* similar to 1st, preoccipital furrow transglabellar, deep, oblique backward abaxially and normal to axis at middle; occipital furrow deep; preglabellar field very narrow or absent; anterior border wide; facial sutures kainelliform, anterior sections moderately divergent to border furrow, gently curved outward across border; eye lobes arcuate, long, reaching level of occipital furrow; fixigenae swollen posteriorly; librigenae wide, genal spines present. Thorax of 15 segments; axis narrower than pleural regions; pleurae ending in spines, fulcrum proximal. Pygidium small, semielliptical, paucisegmented; axis short, tapering backward; pleural regions subtriangular, small; border very wide, flat. Surface of dorsal exoskeleton finely granulose. *L.Cam.*

Saukianda RICHTER & RICHTER, 1940 [**S. andalusiae*] [=*Pseudosaukianda* HUPÉ, 1953]. Glabella dikelocephaliform, cylindrical, subtruncate in front, anterior lateral glabellar furrows *(3p)* obsolete, middle furrows *(2p)* very short, occipital furrow slightly curved backwards; occipital ring of uniform width with short mesial spine; preglabellar field very narrow; genal spines advanced. Thoracic

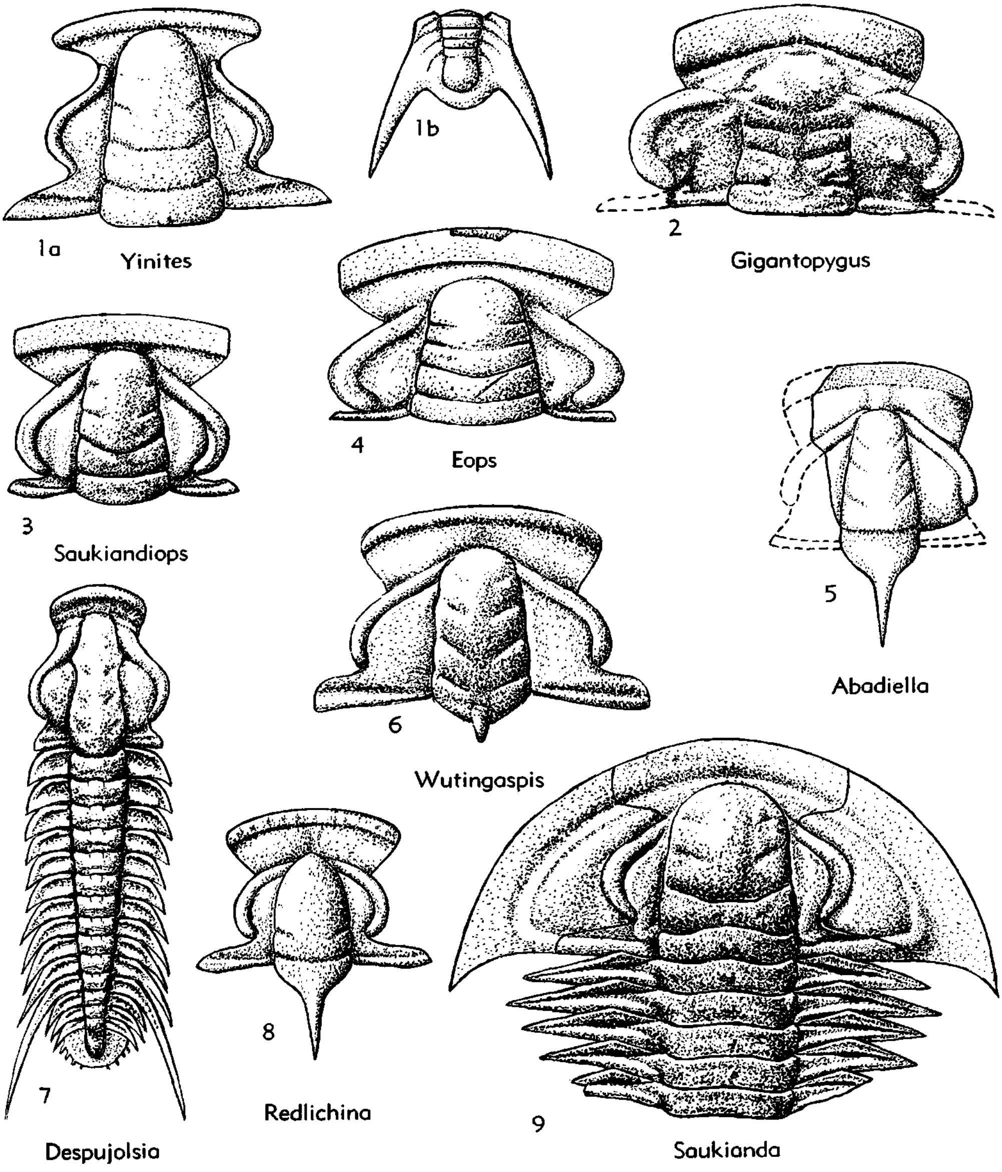


Fig. 145. Redlichiidae, Neoredlichiidae, Saukiandidae, Gigantopygidae, Despujolsiidae, Yinitidae, Abadiellidae (p. O200-O205).

segments 15. Pygidium unknown. *L.Cam.*, Sp.——Fig. 144,*2*. **S. andalusiae;* ceph., restored (based on holotype cran. and paratype librigenae), ×1 (461).——Fig. 145,*9*. *S. lata* (Hupé) (type species of *Pseudosaukianda*), Morocco; holotype, ×1.65 (411).

Longianda Hupé, 1953 [**L. termieri*]. Differs from *Saukianda* in having longer and narrower glabella constricted at level of preoccipital furrows, rounded in front, 3 pairs of lateral glabellar furrows, occipital furrow bent forward at middle, no occipital spine, no preglabellar field, anterior pits and normal genal spines. Thorax of 15 segments; backward curvature of pleural spines progressively increasing posteriorly. Pygidium with 3 axial rings, short terminal axial piece and 4 ?ribs. *L.Cam.*, Morocco.——Fig. 144,*1*. **L. termieri;* restored dorsal exoskel. (based on holotype and paratype specimens), ×1.2 (411).

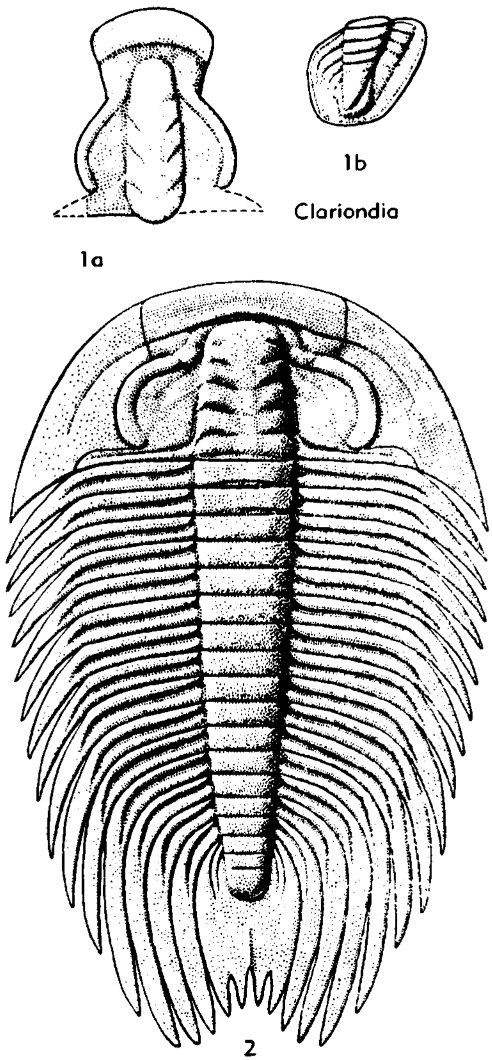


Fig. 146. Neoredlichiidae, Gigantopygidae (p. O201, O204).

Family GIGANTOPYGIDAE Harrington, nov.

Dorsal exoskeleton opisthoparian, ovate, gently convex, isopygous. Cephalon semielliptical; glabella conical, subtruncated in front, with 4 pairs of lateral glabellar furrows; occipital ring straight; preglabellar field absent; anterior border wide, flat; anterior pits present, transversely elongated; eye lobes long, decurrent along frontal and anterior glabellar lobes, strongly arcuate posteriorly, extending to level of occipital furrow; pseudopalpebral furrow present; anterior sections of facial sutures moderately divergent to border furrow, subparallel across border; librigenae wide, genal angle produced into broad spine. Thorax of 14 (or ?15) segments, wide; pleural region twice as wide as axis; pleurae ending in spines, fulcrum distal. Pygidium long, narrow; axis short with 3 rings; border very wide, flat, produced into 2 pairs of marginal spines directed backward. *L.Cam.*

Gigantopygus Hupé, 1953 [**G. papillatus*]. Anterior *(4p)* lateral glabellar furrows faint; posterior *(2p)* and preoccipital almost transglabellar; occipital furrow disconnected at the middle; eye lobes decurrent along frontal and anterior glabellar lobes, then semicircular to level of occipital furrow; fixigenae wide, posterior area narrow *(exsag.)* and long *(tr.)*. *L.Cam.*, Morocco.——Fig. 145,2. **G. papillatus;* cran. (holotype), ×1.1 (411).——Fig. 146,2. *G. bondoni* Hupé; exoskel. (reconstr.), ×0.7 (411).

Family DESPUJOLSIIDAE Harrington, nov.

Dorsal exoskeleton opisthoparian, ovate, very gently convex, micropygous. Cranidium long; glabella long, constricted at middle, with 3 pairs of faint, short, lateral glabellar furrows separated from axial furrows; occipital furrow faint, short; occipital ring wide *(sag.);* preglabellar field as wide as anterior border; eye lobes arcuate, expanded in front, tapering backward, extending from anterolateral corners of glabella to level of occipital furrow; anterior sections of facial sutures moderately divergent. Thorax narrow, long, with 14 segments; pleurae narrower than axis, spinose, 11th segment macrospinose, fulcrum distal. Pygidium small; axis narrow, unsegmented; pleural regions smooth, wide; 4 pairs of tiny marginal spines. *L. Cam.*

Despujolsia Neltner & Poctey, 1949 [**D. rochi*]. Glabella contracted at level of 2nd *(2p)* lateral lobe; pseudopalpebral furrow present; posterior area of fixigenae triangular; first 6 pleurae ending in short subequal spines, spines increasing rapidly in size between 7th and 11th pleurae, last 3 pleurae with short spines. *L.Cam.*, Morocco.——Fig. 145,7. **D. rochi;* incompl. exoskel. (holotype), ×1.75 (411).

Family YINITIDAE Hupé, 1953

Opisthoparian. Glabella long, conical, with 3 pairs of evenly spaced lateral glabellar furrows, anterior *(3p)* almost obsolete, middle *(2p)* furrows short, faint, oblique backward, preoccipital furrow transglabellar; occipital ring of uniform width; preglabellar field absent; anterior border narrow, raised; facial sutures kainelliform, anterior sections divergent (45°), palpebral lobe arcuate, long, touching axial furrows at level of anterior lateral glabellar lobe and extending back to level of mid-length of preoccipital lobe. Thorax unknown. Pygidium paucisegmented, axis tapering backward, pleural regions narrow, one pair of long lateral spines. *M.Cam.*

Yinites Lu, 1946 [**Y. typicalis*]. Glabella rounded in front, preoccipital and occipital furrows gently curved backward; small mesial occipital node; proximal end of anterior sections of facial suture near axial furrows; posterior area of fixigenae triangular. Pygidium with 4 axial rings, large terminal axial piece, 4 pleurae and pair of long backwardly directed lateral spines. *M.Cam.*, China.——Fig. 145,*1*. **Y. typicalis; 1a*, cran. (holotype), ×2.7; *1b*, pyg. (paratype), ×2.5 (426).

Family ABADIELLIDAE Hupé, 1953

Opisthoparian. Glabella conical to subovate, with 3 pairs of evenly spaced, faint lateral glabellar furrows oblique backward, anterior *(3p)* and middle *(2p)* furrows may be obsolete; occipital furrow slightly curved backward; occipital ring produced into stout mesial spine; preglabellar field wide; anterior border raised; anterior sections of facial sutures moderately divergent (less than 45°), proximal extremities distant from axial furrows; eye lobes arcuate, extending from anterolateral corners of glabella to level of anterior 3rd of preoccipital lobe. Thorax and pygidium unknown. *L.Cam.-M.Cam.*

Abadiella Hupé, 1953 [**A. bourgini*]. Glabella conical, rounded in front, with 3 pairs of lateral furrows; preglabellar field with low mesial ridge, anterior border as wide as preglabellar field, anterior sections of facial suture moderately divergent, posterior extremity of eye lobes distant from axial furrows. *L.Cam.*, Morocco.——Fig. 145,*5*. **A. bourgini;* cran. (holotype), ×1.75 (411).

Redlichina Lermontova, 1940 [**R. vologdini*]. Differs from *Abadiella* in having subovate glabella, rounded-subpointed in front, obsolete anterior *(3p)* and middle *(2p)* lateral glabellar furrows, wider preglabellar field with mesial depression, narrower anterior border with faint knobs, more divergent anterior sections of facial suture and posterior extremity of eye lobes nearer to axial furrows. *M.Cam.*, Sib.——Fig. 145,*8*. **R. vologdini;* cran., restored (holotype), ×1 (423).

Wutingaspis Kobayashi, 1944 [**W. tingi*]. Differs from *Abadiella* in having wider preglabellar field with shallow mesial depression, anterior sections of facial sutures slightly more diverging forward, occipital furrow disconnected at middle, and short mesial occipital spine. *L.Cam.*, China.——Fig. 145,*6*. **W. tingi;* cranidium (holotype), ×2.45 (419).

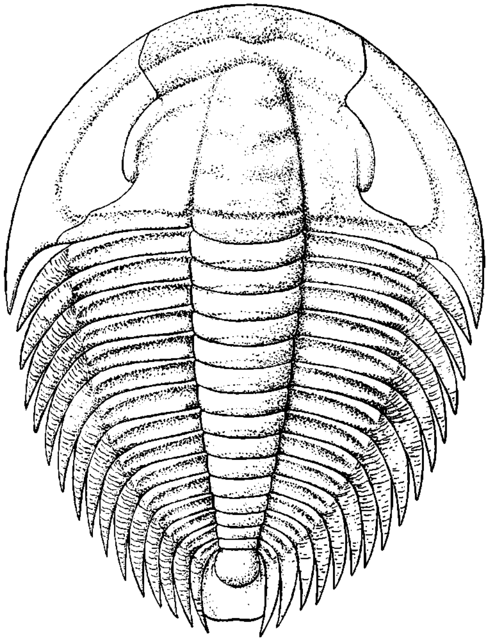


Fig. 147. *Dolerolenus zoppii* (Meneghini) Leanza (Dolerolenidae), M.Cam., Sardinia, ×3 (380, 488).

Family DOLEROLENIDAE Kobayashi, 1951

[*nom. subst.* Kobayashi, 1951 (*pro* Olenopsidae Kobayashi, 1935, invalid name based on junior homonym)]

Dorsal exoskeleton opisthoparian, ovate, gently convex, micropygous. Cephalon semielliptical to semicircular. Glabella long, tapering forward, with 3 pairs of very faint, evenly spaced, lateral glabellar furrows normal to axis; occipital furrow straight; preglabellar field wide; anterior border wide, flat; facial sutures ptychopariiform, anterior sections moderately divergent (less than 45°) to border furrow, curved outwards

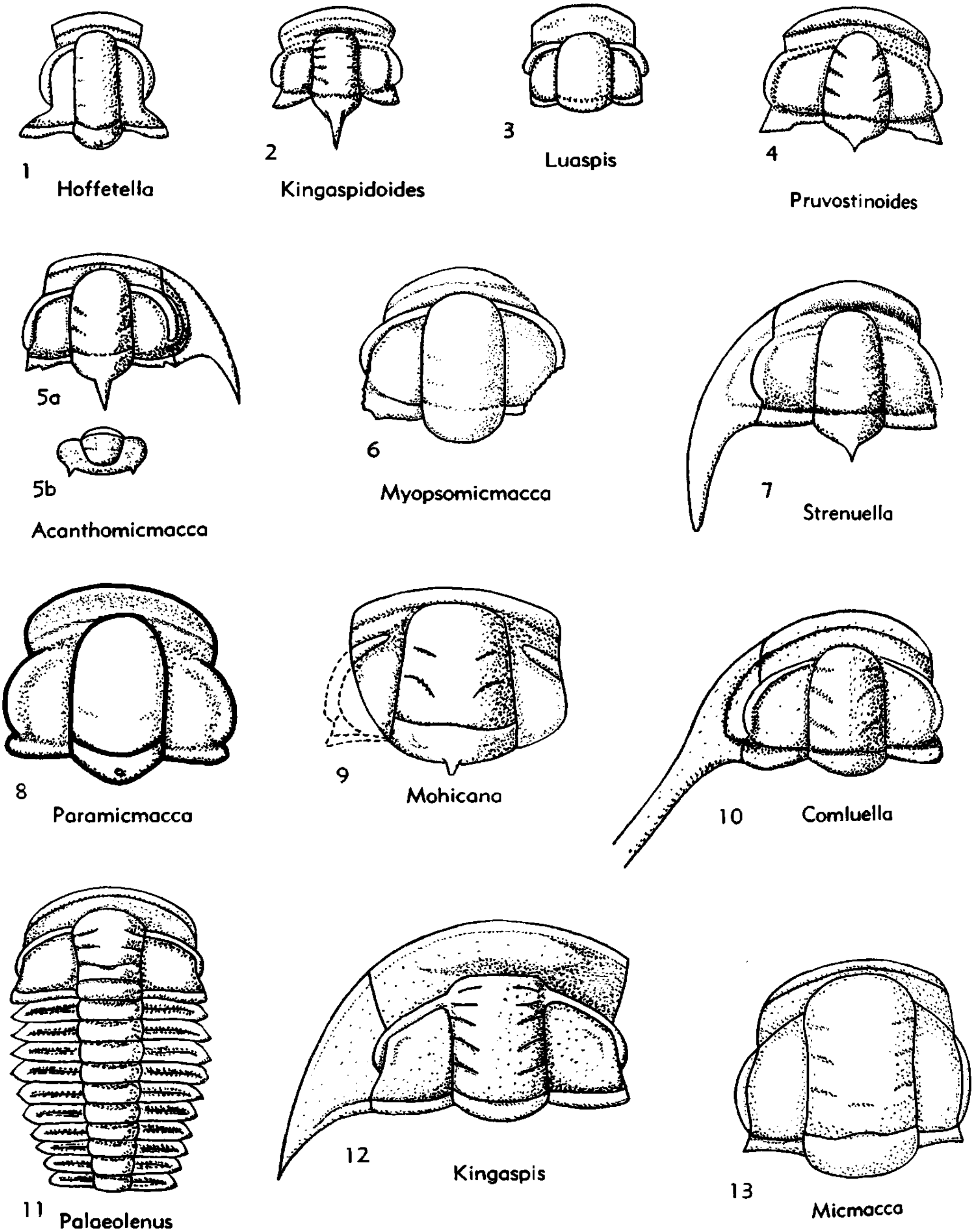


FIG. 148. Ellipsocephalidae (Strenuellinae, Kingaspidinae, Palaeoleninae) (p. O207-O209).

across border; palpebral lobe arcuate, long, subposterior; eye ridge wide, faint; fixigenae wide, posterior areas large, triangular; librigenae wide, genal angles produced into stout spines. Thorax with 14 to 15 segments; axis narrower than pleural regions; pleurae ending in spines progressively curved backward, fulcrum proximal. Pygidium small, axis short with 1 or 2 rings, posterior border wide, flat. *Up.L.Cam.*

Dolerolenus LEANZA, 1949 [*pro Olenopsis* BORNEMANN, 1891 (*non* AMEGHINO, 1889)] [**Olenus zoppii* MENEGHINI, 1882; SD WALCOTT, 1912]. Glabella rounded in front, posterior extremities of anterior sections of facial suture distant from axial furrows, palpebral lobe extending between level of mid-length of anterior *(3p)* lateral glabellar lobe and mid-length of preoccipital lobe. *Up.L.Cam.*, Italy(Sardinia).——FIG. 147. **D. zoppii* (MENEGHINI) LEANZA; restored dorsal exoskel., ×3 (488, pygidium from 380).

Family UNCERTAIN

Bathyuriscellus LERMONTOVA, 1951 [**B. robustus*]. *Up.L.Cam.*, E.Siberia.

Micmaccopsis LERMONTOVA, 1940 [**M. redlichoides*]. *L.Cam.*, Sib.

Superfamily ELLIPSOCEPHALACEA Matthew, 1887

[*nom. transl.* HENNINGSMOEN, herein (*ex* Ellipsocephalidae MATTHEW, 1887] [=Ellipsocephalidea RICHTER, 1933 *(partim)*; Ellipsocephaloidae HUPÉ, 1953; order Protolenida LERMONTOVA, 1951]

Like Redlichiacea, from which this superfamily probably developed, but generally with longer eye ridges, and with greater variety of forms. Many features used in distinguishing genera are easily affected by deformations subsequent to entombment (88). *L.Cam.-M.Cam.*

Family ELLIPSOCEPHALIDAE Matthew, 1887

Cephalic axis tapering forward or with subparallel or slightly concave sides; glabella with as many as 5 pairs of lateral furrows; preglabellar field present or not; thin eye ridges present except in very smooth forms, palpebral lobes not distinctly separated from eye ridges; librigenae with or without genal spine. Thoracic segments generally 12 to 14. Pygidium small. *L.Cam.-M.Cam.*

Subfamily ELLIPSOCEPHALINAE Matthew, 1887

[*nom. transl.* KOBAYASHI, 1935 (*ex* Ellipsocephalidae MATTHEW, 1887)]

With distinct preglabellar field or with more or less inflated frontal area; glabella with as many as 3 pairs of lateral furrows. *L.Cam.-M.Cam.*

Ellipsocephalus ZENKER, 1833 [**E. ambiguus* (=*Trilobites hoffi* SCHLOTHEIM, 1823) [=*Elleipsocephalus* ZENKER, 1833 (emend. to *Ellipsocephalus*, ICZN pend.)]. Cephalic axis widening slightly at anterior corners; librigenae with long rudimentary genal spine or none. Thoracic segments 12. Pygidium small but relatively wide. *L.Cam.-M.Cam.*, Eu.-Morocco-N.B.-?Austral.——FIG. 150, *3*. **E. hoffi* (SCHLOTHEIM), Eu.; exoskel. ×2 (406n).

Alanisia HUPÉ, 1953 [**Camaraspis guillermoi* RICHTER & RICHTER, 1940]. With well-developed preglabellar field, occipital spine, and long palpebral lobes reaching posterior border furrow. *L. Cam.*, Sp.——FIG. 149,*2*. **A. guilerrmoi* (RICHTER & RICHTER); cran., ×3.3 (461).

?Angusteva HUPÉ, 1953 [**Ptychoparia? annio* COBBOLD, 1910]. Like *Strenuaeva* but with shorter palpebral lobes. *L.Cam.*, Eng.-Sp.-Morocco.——FIG. 149,*1*. **A. annio* (COBBOLD), Eng.; cran., ×6.8 (387).

Ellipsostrenua KAUTSKY, 1945 [**Strenuella (Ellipsostrenua) gripi*]. Like *Ellipsocephalus* but cephalic axis not expanded at anterior corners. *L.Cam.*, Eu. ——FIG. 150,*7*. **E. gripi;* exoskel., ×2 (88).

Hindermeyeria HUPÉ, 1953 [**Strenuella (Strenuaeva) insecta* RICHTER & RICHTER, 1940]. Like *Alanisia* but preglabellar field inflated. *L.Cam.*, Sp.——FIG. 149,*8*. **H. insecta;* exoskel., ×5 (461).

Inoyellaspis IVSHIN, 1953 [**I. expectans*]. Resembles *Strenuaeva. M.Cam.*, Kazakstan.

Strenuaeva RICHTER & RICHTER, 1940 [**Arionellus primaevus* BRØGGER, 1879]. Like *Strenuella* but with inflated frontal area. *L.Cam.*, Eu.——FIG. 149,*3*. **S. primaeva* (BRØGGER); cran., ×2.2 (417).

?**Protagraulos** MATTHEW, 1895 [**P. priscus*]. Like *Strenuaeva* but with narrower *(tr.)* frontal area and facial sutures slightly converging in front of eyes; palpebral lobes long and thin. *L.Cam.*, N.B. ——FIG. 149,*7*. **P. priscus;* cran., ×2.5 (429).

Subfamily STRENUELLINAE Hupé, 1953

With short *(sag.)* preglabellar field or none, glabella with as many as 3 pairs of lateral furrows. *L.Cam.-M.Cam.*

Strenuella MATTHEW, 1887 [**Agraulos strenuus* BILLINGS, 1874; SD KIAER, 1916]. Cephalic axis tapering slightly forward or almost parallel-sided; palpebral lobes long, reaching posterior border; genal spines present. *L.Cam.*, NE.N.Am.-Eu.-Morocco.

- **S. (Strenuella).** With occipital spine. *L.Cam.*, NE. N.Am.-Eu.-Morocco.——FIG. 148,*7*. **S. (S.) strenua* (BILLINGS), N.Am.; incompl. ceph., ×2 (77, 471).
- **S. (Comluella)** HUPÉ, 1953 [**Anomocare platycephalum* COBBOLD, 1910]. Without occipital spine. *L.Cam.*, NE.N.Am.-Eu.-Morocco.——FIG. 148,*10*. **S. (C.) platycephala* (COBBOLD), Eu.; incompl. ceph., ×3 (387).

?Luaspis HUPÉ, 1953 [**Pseudoptychoparia reedi* LU, 1941]. Like *Micmacca (Myopsomicmacca)* but apparently with even shorter palpebral lobes. *L.Cam.*, Yunnan.——FIG. 148,*3*. **L. reedi* (LU); cran., ×2 (426).

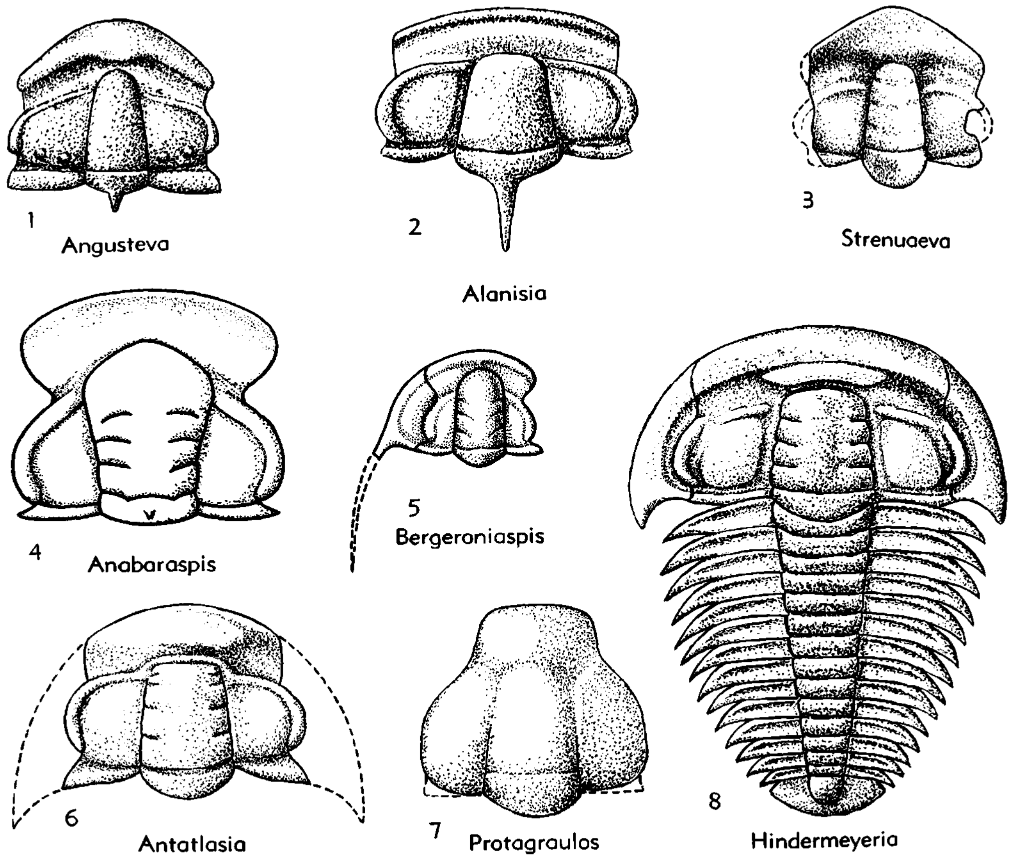


FIG. 149. Ellipsocephalidae (Antatlasiinae, Ellipsocephalinae), Protolenidae (Protoleninae) (p. O207-O212).

Micmacca MATTHEW, 1895 [**M. matthevi;* SD MILLER, 1897]. Cephalic axis generally wider than in *Strenuella. L.Cam.,* N.B.-Eu.-Morocco-Asia.

M. (Micmacca). Cephalic axis with slightly concave or subparallel sides; librigenae without genal spine. *L.Cam.,* N.B.-Eu.-Morocco-Asia.——FIG. 148,*13*. **M. (M.) matthevi,* N.B.; cran., ×1.5 (77, 429).

M. (Acanthomicmacca) HUPÉ, 1953 [**M. walcotti* MATTHEW, 1899]. Cephalic axis relatively slender, sides subparallel, with occipital and genal spines. *L.Cam.,* N.B.-?Morocco.——FIG. 148,*5*. **M. (A.) walcotti; 5a,b,* ceph., pyg., ×1 (77, 429).

M. (Myopsomicmacca) HUPÉ, 1953 [**M. protolenoides* COBBOLD, 1910]. With short palpebral lobes. *L.Cam.,* Eng.-N.B.-Asia.——FIG. 148,*6*. **M. (M.) protolenoides,* Eng.; cran., ×2.7 (77).

M. (Mohicana) COBBOLD, 1910 [**Micmacca? plana* MATTHEW, 1895; SD VOGDES, 1925] [=*Conomicmacca* HUPÉ, 1953 (obj.)]. Cephalic axis tapering forward or with subparallel sides. *L.Cam.,* N.B.-Eu.——FIG. 148,*9*. **M. (M.) plana* (MATTHEW), N.B.; cran., ×1.4 (77).

M. (Paramicmacca) LERMONTOVA, 1951 [**P. siberica*]. Cephalic axis with subparallel sides, large frontal area; close to *Strenuella. L.Cam.,* Sib.——FIG. 148,*8*. **M. (P.) siberica* (LERMONTOVA); cran., ×1.5 (423).

?**Pruvostinoides** HUPÉ, 1953 [**P. angustilineatus*]. Like *Strenuella* but with shorter and more strongly tapering cephalic axis. *L.Cam.-M.Cam.,* Morocco.——FIG. 148,*4*. **P. angustilineatus;* cran., ×1.5 (77).

Subfamily KINGASPIDINAE Hupé, 1953

Like Strenuellinae but cephalic axis with slightly concave sides and as many as 5 pairs of lateral glabellar furrows. *L.Cam.*

Kingaspis KOBAYASHI, 1935 [**Anomocare campbelli* KING, 1923]. Characters of subfamily. *L.Cam.,* Morocco-M.East.

K. (Kingaspis). Without occipital spine. *L.Cam.,* Morocco-M.East.——FIG. 148,*12*. **K. (K.) campbelli* (KING); incompl. ceph., ×2.2 (77, 461).

K. (Kingaspidoides) HUPÉ, 1953 [**K. (K.) armatus*]. With occipital spine. *L.Cam.,* Morocco.——

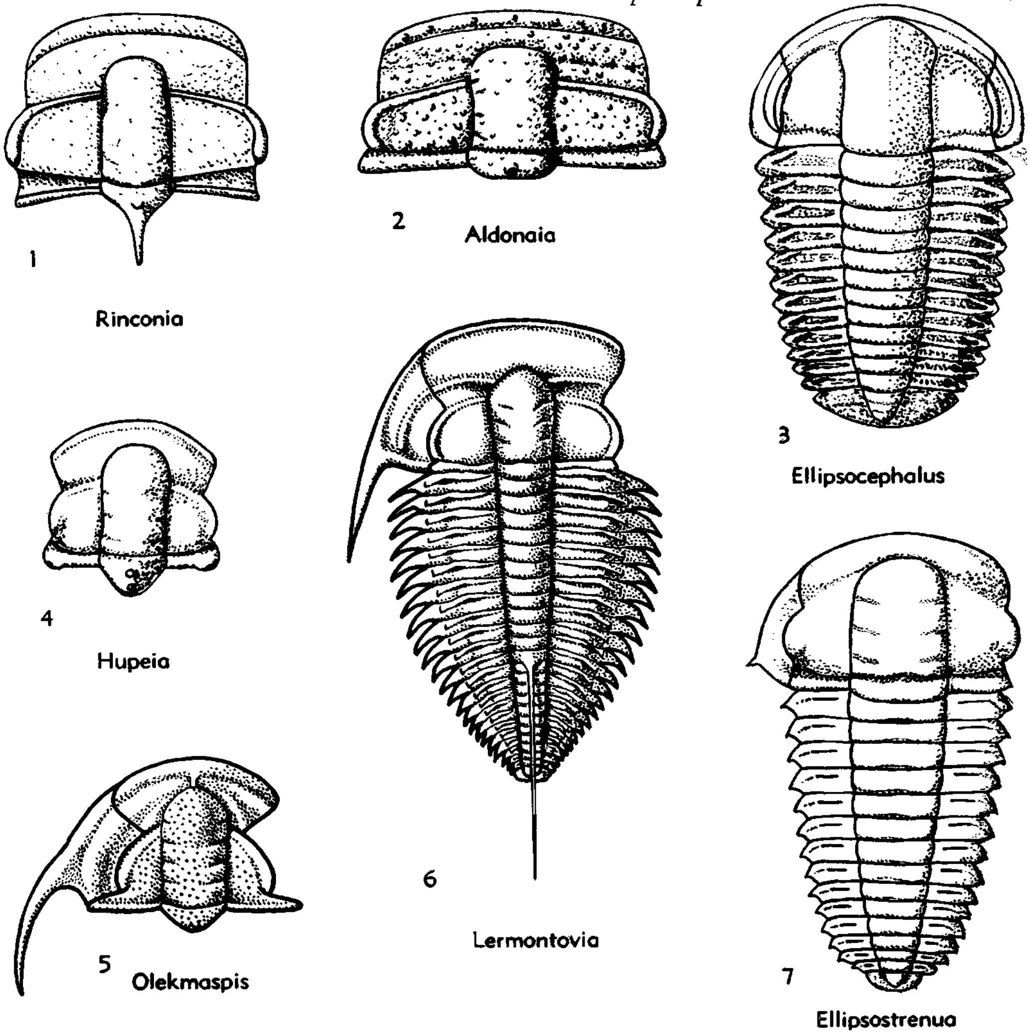


FIG. 150. Ellipsocephalidae (Ellipsocephalinae), Protolenidae (Protoleninae, Aldonaiinae), Family uncertain (p. O207-O212).

FIG. 148,*2*. **K. (K.) armatus;* cran., ×1.4 (77).

Mesetaia HUPÉ, 1953 [**Hartshillia marocana* GIGOUT, 1951]. Like *Kingaspis* but cephalic axial furrow effaced. *L.Cam.*, Morocco.

Subfamily PALAEOLENINAE Hupé, 1953

Cephalic axis expanding forward or with subparallel sides, glabella bearing 3-4 pairs of lateral lobes, posterior pair being connected across glabella in some genera; palpebral lobes small. *L.Cam.*

Palaeolenus MANSUY, 1912 [**P. douvillei;* SD VOGDES, 1925]. Characters of subfamily. *L.Cam.*, China.——FIG. 148,*11*. **P. douvillei;* incompl. exoskel., ×4 (428).

?**Hoffetella** HUPÉ, 1953 [**Micmacca elongata* LU, 1941]. Like *Palaeolenus* but without preglabellar field and with palpebral lobes closer to glabella. *L.Cam.*, China.——FIG. 148,*1*. **H. elongata* (LU), cran., ×2 (426).

?**Manchurocephalus** ENDO, 1944 [**Palaeolenus deprati* MANSUY, 1912]. *Low. U. Cam.*, S.Manch.

Subfamily ANTATLASIINAE Hupé, 1953

[*nom. transl.* HENNINGSMOEN, herein (*ex* Antatlasiidae HUPÉ, 1953)]

Cephalic axis slightly tapering forward, with 4 pairs of lateral glabellar furrows; parafrontal band present; palpebral lobes long, reaching posterior border furrow. *L. Cam.*

Antatlasia HUPÉ, 1953 [**A. hollardi*]. Characters of subfamily. *L.Cam.*, Morocco.——FIG. 149,*6*. **A. hollardi;* cran., ×2.75 (77).

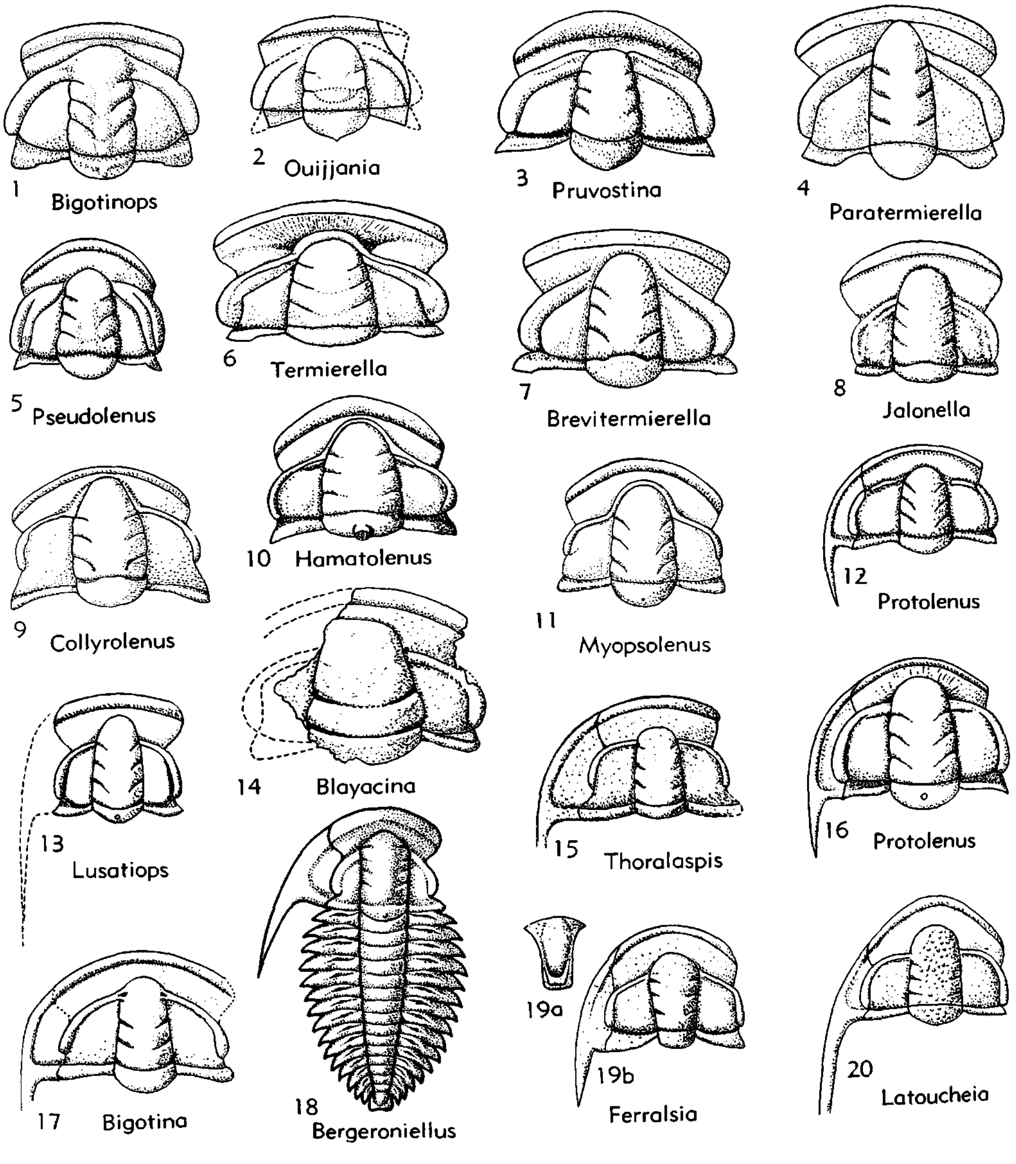


FIG. 151. Protolenidae (Termierellinae, Myopsoleninae, Protoleninae, Bigotininae) (p. *O211*, *O212*).

Family PROTOLENIDAE Richter & Richter, 1948

Cephalic axis tapering forward, or with subparallel sides, or widening slightly forward, rather narrow and with up to 4 pairs of lateral glabellar furrows. Preglabellar field present or not. Palpebral lobes more or less confluent with eye ridges. Librigenae with genal spine. Up to 25 thoracic segments. Pygidium very small. *L.Cam.*

Subfamily TERMIERELLINAE Hupé, 1953

With thick palpebro-ocular ridges, in part commonly bisegmented longitudinally. *L. Cam.*

Termierella HUPÉ, 1953 [**T. latifrons*]. Facial sutures diverging markedly in front of eyes; preglabellar field present; with 3 pairs of lateral glabellar furrows. *L.Cam.*, Morocco-Sp.

T. (Termierella). Palpebral lobes markedly broader than eye ridges, which are longitudinally bisegmented; with parafrontal band. *L.Cam.*, Morocco. ——FIG. 151,*6*. **T. (T.) latifrons;* cran., ×1 (77).

T. (Brevitermierella) HUPÉ, 1953 [**T. (B.) brevifrons*]. Like *T. (Termierella)* but palpebro-ocular ridges increasing evenly in width distally. *L.Cam.*, Morocco.——FIG. 151,*7*. **T. (B.) brevifrons;* cran., ×1 (77).

T. (Jalonella) HUPÉ, 1953 [**T. (J.) celtiberica* HUPÉ, 1953 (=**Lusatiops ribotanus* RICHTER & RICHTER, 1948)]. Like *T. (Brevitermierella)* but with narrower *(tr.)* fixigenae. *L.Cam.*, Sp.——FIG. 151,*8*. **T. (J.) ribotana* (RICHTER & RICHTER); cran., ×1 (252).

Bigotinops HUPÉ, 1953 [**B. dangeardi*]. Like *Termierella* but anterior sections of facial sutures less divergent and lateral glabellar furrows faintly connected across glabella. *L.Cam.*, Morocco.——FIG. 151,*1*. **B. dangeardi;* cran., ×3.35 (77).

Ouijjania HUPÉ, 1953 [**O. meridionalis*]. Like *Termierella* but anterior sections of facial sutures less divergent and only 2 pairs of lateral glabellar furrows, preoccipital pair bifurcating, both branches faintly connected across glabella. *L.Cam.*, Morocco. ——FIG. 151,*2*. **O. meridionalis;* cran., ×1.5 (77).

Paratermierella HUPÉ, 1953 [**P. elegans*]. Like *Termierella* but without preglabellar field. *L.Cam.*, Morocco.——FIG. 151,*4*. **P. elegans;* cran., ×1.5 (77).

Pruvostina HUPÉ, 1953 [**P. nicklesi*]. Like *Termierella* but anterior sections of facial sutures less divergent; proximal part of palpebro-ocular ridge longitudinally bisegmented. *L.Cam.*, Morocco.——FIG. 151,*3*. **P. nicklesi;* cran., ×1.3 (77).

Pseudolenus HUPÉ, 1953 [**P. ourikaensis*]. Like *Termierella* but anterior sections of facial sutures less divergent, and palpebro-ocular ridge longitudinally bisegmented even in distal end. *L.Cam.*, Morocco.——FIG. 151,*5*. **P. ourikaensis;* cran., ×2 (77).

Subfamily MYOPSOLENINAE Hupé, 1953

[Emend. HENNINGSMOEN, herein]

With more or less distinct parafrontal band. *L.Cam.*

Myopsolenus HUPÉ, 1953 [**M. magnus*]. Long palpebral lobes reaching posterior border furrow, parafrontal band distinct; with short auxiliary eye ridge close to each eye ridge and close to glabella. *L.Cam.*, Morocco.——FIG. 151,*11*. **M. magnus;* cran., ×0.6 (77).

Collyrolenus HUPÉ, 1953 [**C. staminops*]. Frontal lobe long and tapering markedly forward, rest of cephalic axis with slightly convex sides; palpebral lobes short, not reaching posterior border furrow; parafrontal band indistinct and disconnected. *L.Cam.*, Morocco.——FIG. 151,*9*. **C. staminops;* cran., ×0.6 (77).

Hamatolenus HUPÉ, 1953 [**H. continuus*]. Short palpebral lobes not reaching posterior border furrow; parafrontal band well developed. *L.Cam.*, Morocco.——FIG. 151,*10*. **H. continuus;* cran., ×0.9 (77).

Subfamily PROTOLENINAE Richter & Richter, 1948

[*nom. transl.* HUPÉ, 1953 (*ex* Protolenidae RICHTER & RICHTER, 1948] [*incl. Lermontoviinae* SUVOROVA, 1956]

With thin palpebro-ocular ridges and no parafrontal band. *L.Cam.*

Protolenus MATTHEW, 1892 [**P. elegans;* SD VOGDES, 1893] [=*Bergeronia* MATTHEW, 1895 (obj.); *Matthewlenus* HUPÉ, 1953 (**Protolenus articephalus* MATTHEW, 1895)]. Cephalic axis tapering slightly forward, with 3 pairs of lateral glabellar furrows; palpebral lobes long, reaching posterior border furrow; anterior border narrow; librigenae with stout genal spine. Thorax with many segments and bearing pleural spines. Pygidium very small. *L.Cam.*, N.B.-Eu.-Morocco.

P. (Protolenus). Test smooth. *L.Cam.*, N.B.-Eu.-Morocco.——FIG. 151,*12*. **P. (P.) elegans*, N.B.; incompl. ceph., ×1 (77).——FIG. 151,*16*. *P. paradoxoides* (MATTHEW), Eu.; incompl. ceph., ×0.8 (77, 387).

P. (Latoucheia) HUPÉ, 1953 [**P. latouchei* COBBOLD, 1910]. Surface tuberculate. *L.Cam.*, Eu.-Morocco.——FIG. 151,*20*. **P. (L.) latouchei* (COBBOLD), Morocco; incompl. ceph., ×0.9 (77, 387).

Anabaraspis LERMONTOVA, 1951 [**A. splendens*]. Palpebro-ocular ridges rather thick. Expanded frontal area. Cephalic axis expanding forward, widest at anterior corners. *L.Cam.*, Sib.——FIG. 149,*4*. **A. splendens;* cran., ×1.25 (423).

Bergeroniellus LERMONTOVA, 1940 [**B. asiaticus*]. Like *Protolenus*, but generally with more diverging facial sutures and wider anterior border; thoracic segments 15 to 17. Close to *Lusatiops*. *L.Cam.*, Sib.

B. (Bergeroniellus). Broad-based genal spine. *L. Cam.*, Sib.——FIG. 151,*18*. **B. asiaticus;* incompl. exoskel., ×1.5 (290).

B. (Bergeroniaspis) LERMONTOVA, 1951 [**B. kutorginorum*]. Genal spine with narrow base. *L.Cam.*, Sib.——FIG. 149,*5*. **B. kutorginorum;* incompl. ceph., ×1.3 (290).

B. (Olekmaspis) SUVOROVA, 1956 [**O. bobrovi*]. Like *B. (Bergeroniaspis)*, but with more diverging facial sutures. *L.Cam.*, Sib.——FIG. 150,*5*. **O. bobrovi;* incompl. ceph., ×1.5 (290).

Blayacina COBBOLD, 1931 [**B. miqueli*]. Glabella wide, tapering markedly forward, with transglabellar preoccipital furrow. *L.Cam.*, Fr.——FIG. 151, *14*. **B. miqueli;* cran., ×1 (387).

?**Ferralsia** COBBOLD, 1935 [**F. blayaci*]. Like *Protolenus* but with cephalic axis widening forward.

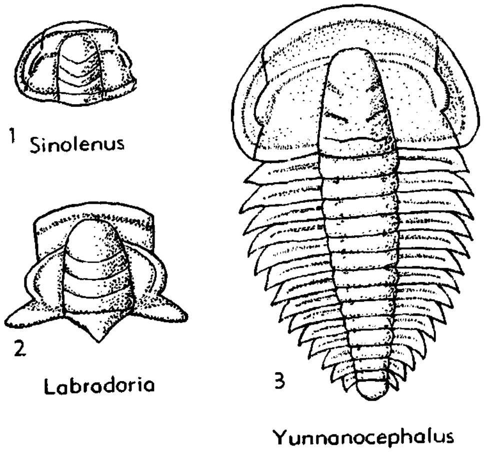


FIG. 152. Yunnanocephalidae, Ellipsocephalacea (Family uncertain) (p. O212).

L.Cam., Fr.——FIG. 151,*19*. **F. blayaci; 19a,b,* hypostoma, incompl. ceph., ×1 (387).

Lermontovia SUVOROVA, 1956 [**L. dzevanowskii*]. Like *Anabaraspis,* but with thin palpebro-ocular ridges, 20-25 thoracic segments. *L.Cam.*, Sib.——FIG. 150,*6*. **L. dzevanowskii;* incompl. exoskel., ×1 (290).

Lusatiops RICHTER & RICHTER, 1941 [**Protolenus lusaticus* SCHWARZBACH, 1934] [=*Coreolenus* HUPÉ, 1953 (**Protolenus coreanicus* SAITO, 1933)]. Like *Protolenus* but anterior sections of facial sutures more divergent. *L.Cam.*, Eu.-Korea.——FIG. 151,*13*. **L. lusaticus* (SCHWARZBACH), Eu.; cran., outline of librigena, ×0.7 (461).

Thoralaspis HUPÉ, 1953 [**Olenopsis thorali* COBBOLD, 1935]. Like *Protolenus,* but apparently with shorter palpebral lobes not reaching posterior border furrow. *L.Cam.*, Fr.——FIG. 151,*15*. **T. thorali;* incompl. ceph., ×1 (387).

Subfamily BIGOTININAE Hupé, 1953

Proximal end of thin eye ridges longitudinally bisegmented. *L.Cam.*

Bigotina COBBOLD, 1935 [**B. bivallata*]. Characters of subfamily. *L.Cam.*, Fr.——FIG. 151,*17*. **B. bivallata;* incompl. ceph., ×2 (387).

?Subfamily ALDONAIINAE Hupé, 1953

Cephalic axis with slightly concave sides; preglabellar field present, fixigenae markedly wider than cephalic axis. Surface tuberculate. *L.Cam.*

Aldonaia LERMONTOVA, 1940 [**A. ornata*]. Characters of subfamily. *L.Cam.*, Sib.——FIG. 150,*2*. **A. ornata;* cran., ×3.5 (423).

Subfamily UNCERTAIN

Hupeia KOBAYASHI, 1944 [**H. pulchra*]. Cephalic axis with slightly concave sides; fixigenae about as wide as cephalic axis, preglabellar field present, palpebral lobes reaching posterior border furrow. Surface smooth. *L.Cam.*, China.——FIG. 150,*4*. **H. pulchra;* cran., ×2.5 (419).

Rinconia HUPÉ, 1953 [**Protolenus schneideri* RICHTER & RICHTER, 1941]. Cephalic axis narrow, with subparallel sides and bearing occipital spine, facial sutures subparallel in front of eyes. *L.Cam.*, Sp.——FIG. 150,*1*. **R. schneideri;* cran., ×1.5 (461).

?Family YUNNANOCEPHALIDAE Hupé, 1953

Cephalic axis tapering markedly forward, with 2 pairs of lateral glabellar furrows; preglabellar field distinct; palpebral lobes small, not reaching posterior border furrow, confluent with eye ridges; librigenae without genal spine. Thoracic segments 14. Pygidium minute. *L.Cam.*

Yunnanocephalus KOBAYASHI, 1936 [**Ptychoparia yunnanensis* MANSUY, 1912] [=*Pseudoptychoparia* TING, 1940 (obj.)]. Characters of family. *L.Cam.*, China.——FIG. 152,*3*. **Y. yunnanensis;* exoskel., ×1.65 (411, 428).

Family UNCERTAIN

Labradoria RESSER, 1936 [**Conocephalites miser* BILLINGS, 1861]. Preglabellar field lacking; with 3 pairs of transglabellar furrows; palpebral lobes reaching posterior border furrow. *L.Cam.*, Labrador.——FIG. 152,*2*. **L. miser;* cran., ×2.25 (488).

Sinolenus KOBAYASHI, 1944 [**S. trapezoidalis*]. Like *Labradoria* but palpebral lobes short. *L.Cam.*, China.——FIG. 152,*1*. **S. trapezoidalis;* incompl. ceph., ×2.7 (419).

Superfamily PARADOXIDACEA Hawle & Corda, 1847

[*nom. transl.* POULSEN, herein (*ex* Paradoxides HAWLE & CORDA, 1847)] [=order Paradoxida Lermontova, 1951 (*partim*)]

Dorsal exoskeleton elongate, elliptical to pyriform in outline, medium to large in size. Cephalon semicircular, with rather prominent glabella that expands forward and generally reaches anterior border; facial sutures opisthoparian; eyes medium to large; librigenae with genal spines. Thorax with numerous segments (13 to 22); axis prominent, tapering backward; pleurae nearly flat, with well-defined furrows, terminating in spines. Pygidium usually small. *Up.L.Cam.-M.Cam.*

Family PARADOXIDIDAE Hawle & Corda, 1847

[*nom. correct.* RICHTER, 1932 (*pro* Paradoxides HAWLE & CORDA, 1847, ICZN opinion 496)]

Dorsal exoskeleton opisthoparian, ovate to elongate, usually large, micropygous to heteropygous, almost flat. Cephalon semicircular; glabella broadly clavate, with 2 to 4 pairs of lateral glabellar furrows; cephalic border well developed; palpebral lobes generally prominent, anterior sections of facial suture commonly diverging from eyes to front margin; eyes usually large to medium in size; librigenae medium in width, with genal spines. Thorax (as far as known) with 13 to 22 segments, axis evenly tapering, moderately convex, pleurae deeply furrowed, bearing spines. Pygidium with few segments. Hypostoma relatively large, subquadrate, with anterior corners somewhat extended at each side and in some fused with rostral plate. *Up.L.Cam.-M.Cam.*

Subfamily PARADOXIDINAE Hawle & Corda, 1847

[*nom. transl.* HOWELL, 1933, as Paradoxinae (*ex* Paradoxides HAWLE & CORDA, 1847), *nom correct.* POULSEN, herein]

Micropygous. Glabella extended to anterior border furrow; front end of palpebral lobes placed opposite or behind widest portion of glabella and separated from it, fixigenae narrow. Thorax with 16 to 21 segments. Pygidium usually elongate, with very narrow pleural fields and entire margin or with 1 to 3 pairs of small spines on posterior margin. Hypostoma with a small spine at posterior corners, and in some fused with reduced rostral plate. *M.Cam.*

Paradoxides BRONGNIART, 1822 [**Entomostracites paradoxissimus* WAHLENBERG, 1821; SD BARRANDE, 1852] [=*Hydrocephalus* BARRANDE, 1846; *Phanoptes, Phlysacium* HAWLE & CORDA, 1847; *Plutonia* HICKS, 1869; *Plutonides* HICKS, 1895] (3, 144, 114, 1, 143, 146, 322, 71). *M.Cam.*, Eu.-E.N.Am. (Atl.prov.)-N.Afr.-N.Zem.-?NE.Austral. —— FIG. 153,*2*. **P. paradoxissimus* (WAHLENBERG), Swed.; exoskel., ×0.75 (1).——FIG. 153,*1*. *P. minor* (BOECK), Boh.; rostral plate with hypostoma, ×3 (3).

Eccaparadoxides SNAJDR, 1957 [**Paradoxides pusillus* BARRANDE, 1846] (260). *M.Cam.*, Bohemia.

Acadoparadoxides SNAJDR, 1957 [**Paradoxides sacheri* BARRANDE, 1852] (260). *M.Cam.*, Bohemia.

Luhops SNAJDR, 1957 [**Paradoxides expectans* BARRANDE, 1852] (260). *M.Cam.*, Bohemia.

?**Vinicella** SNAJDR, 1957 [**Paradoxides desideratus* BARRANDE, 1846] (260). *M.Cam.*, Bohemia.

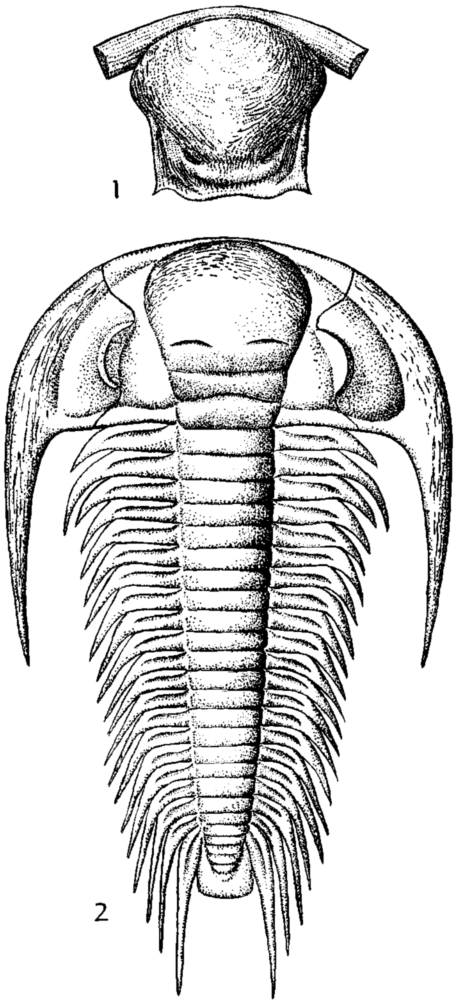


FIG. 153. *Paradoxides* (Paradoxididae, Paradoxidinae), M.Cam.——*1. P. minor* (BOECK), Bohemia; rostral plate with hypostoma, ×3 (3).——*2.* **P. paradoxissimus* (WAHLENBERG), Swed.; exoskel., ×0.5 (1).

Subfamily CENTROPLEURINAE Angelin, 1854

[*nom. transl.* HOWELL, 1933 (*ex* Centropleuridae ANGELIN, 1854)]

Heteropygous. Anterior pair of lateral glabellar furrows directed diagonally backward; anterior end of palpebral lobes in front of widest part of glabella; anterior sections of facial sutures at right angles to glabella or running obliquely backward paralleling anterior part of palpebral lobes and lateral portions of anterior border. Thorax with 14 or more segments. Pygidium wide, with well-developed pleural fields

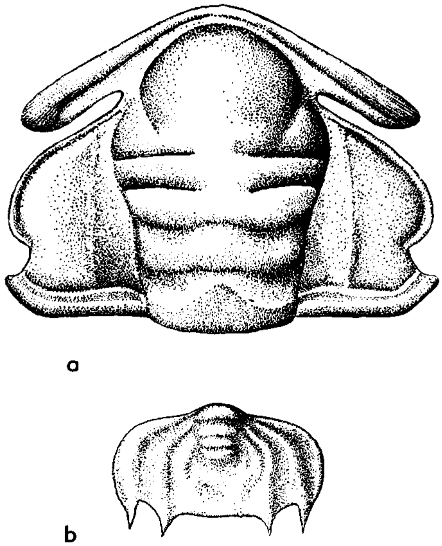


FIG. 154. *Centropleura loveni* (ANGELIN) (Paradoxidae, Centropleurinae), M.Cam., Swed.; *a,b,* cran., associated pyg., ×1 (337).

and small spines on posterior margin. *M. Cam.*

Centropleura ANGELIN, 1854 [**Paradoxides lovéni* ANGELIN, 1851]. Palpebral lobes curving in an uneven arc; anterior sections of facial suture paralleling anterior border and anterior part of palpebral lobes for a considerable length; metafixigenal spines present in some. Pygidium without border. Hypostoma without spines (337, 70). *M.Cam.,* Eu.-E. N. Am.-Sib.-SE.Austral. —— FIG. 154. **C. loveni* (ANGELIN), Swed.; *a,b,* cran., associated pyg., ×1, ×0.75 (337).

Anopolenus SALTER, 1864 [**A. henrici*]. Differs from *Centropleura* in having evenly curved palpebral lobes and distinctly defined pygidial border (337, 70). *M.Cam.,* Eu.-E.N.Am.(Atl.prov.)-E.Sib.

Clarella HOWELL, 1933 [**Anopolenus venustus* BILLINGS, 1874]. Differs from *Centropleura* and *Anopolenus* in having almost straight to slightly sigmoidal palpebral lobes (70, 337). *M.Cam.,* Eu.-Newf.

Subfamily METADOXIDINAE Whitehouse, 1939

Micropygous. Glabella strongly tapering forward; anterior and palpebral areas of fixigenae wide, with well-defined eye ridges and relatively small palpebral lobes. Thoracic segments up to 22, with broadly furrowed, more or less pointed pleura. *Up.L. Cam.*

Metadoxides BORNEMANN, 1891 [**Paradoxides torosus* MENEGHINI, 1881; SD VOGDES, 1925]. Cephalic border narrow, anterior sections of facial suture subparallel or slightly converging from eyes to anterior border, posterior sections long, directed obliquely backward. Pygidium elongated ovate, apparently unsegmented (14). *Up.L.Cam.,* Sard. ——FIG. 155. **M. torosus* (MENEGHINI); *a,b,* cran., fragment of thorax with pyg., ×0.7 (14).

Anadoxides MATTHEW, 1899 [**Paradoxides armatus* MENEGHINI, 1881; SD VOGDES, 1925]. Differs from *Metadoxides* in having wider, triangular pygidium with distinctly segmented axis and pleural fields (14). *Up.L.Cam.,* Sard.

Catadoxides MATTHEW, 1899 [**Metadoxides magnificus* MATTHEW, 1899]. Differs from *Metadoxides* and *Anadoxides* in having wide cephalic border, anteriorly expanded cranidium, short, backward-directed posterior sections of facial suture; and fairly wide, subreniform pygidium with indistinctly segmented axis and unfurrowed pleural fields. *Up.L.Cam.,* Newf.——FIG. 156,2. **C. magnificus* (MATTHEW); ceph., ×0.3 (429).

Subfamily XYSTRIDURINAE Whitehouse, 1939

Heteropygous, with dorsal side of cephalon similar to that of Paradoxidinae but without transglabellar furrows; rostral plate unreduced, crescentic, reaching to genal angles. Thorax with 13 segments and pygidium quadrispinose, of the same type as that of Centropleurinae. *Up.L.Cam.-M.Cam.*

Xystridura WHITEHOUSE, 1936 [**Olenellus browni* ETHERIDGE, 1897] [=*Milesia* CHAPMAN, 1929 (*non* LATREILLE, 1804)] (340). *M.Cam.* Austral.

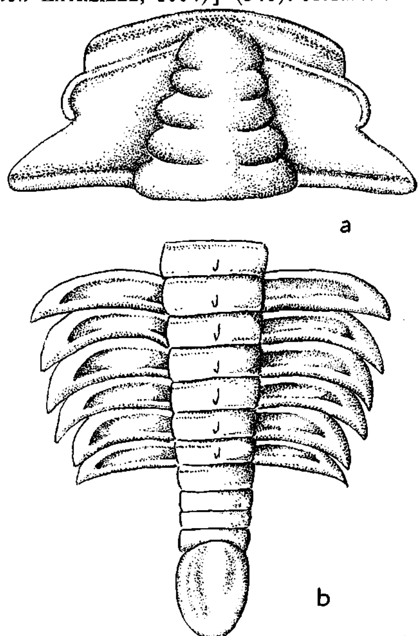


FIG. 155. **Metadoxides torosus* (MENEGHINI), M. Cam., Sardinia; *a,b,* cran., part of thorax with pyg., ×0.5 (14).

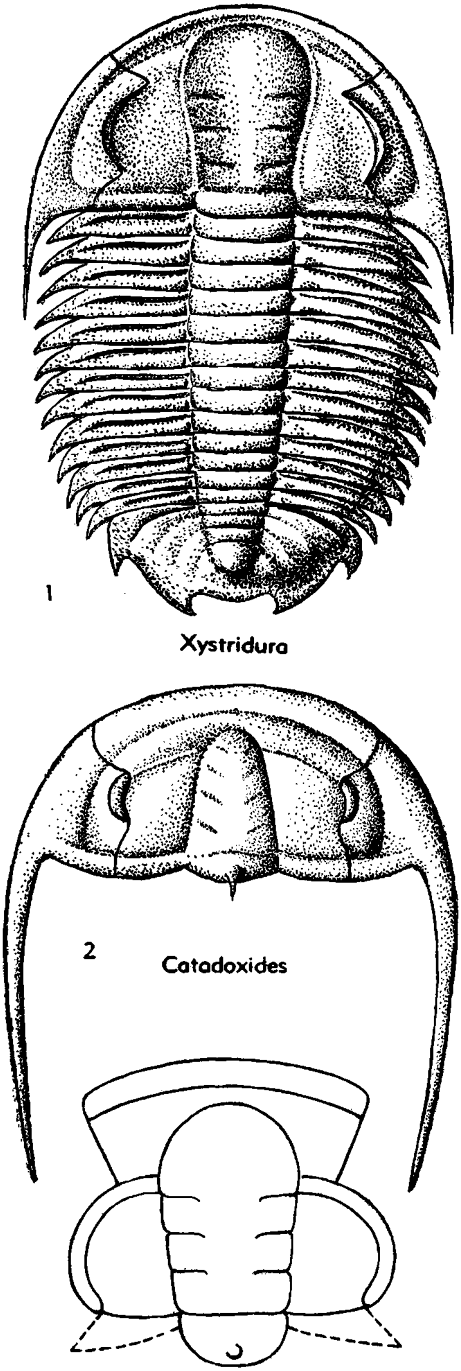


Fig. 156. Paradoxididae (Metadoxidinae, Xystridurinae) (p. O214, O215).

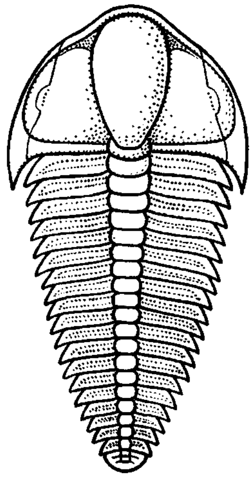


Fig. 157. **Hicksia elvensis* Delgado (Hicksiidae), L.Cam., Portugal; exoskel. (reconstr.), ×2 (31, 405).

——Fig. 156,*1*. *X. saintsmithi* (Chapman); ×1.5 (340).

?**Gigoutella** Hupé, 1953 [**G. atlasensis*]. Differs from *Xystridura* in having preglabellar field and less diverging anterior sections of facial suture (77). *Up.L.Cam.*, Morocco.——Fig. 156,*3*. **G. atlasensis;* cran., ×2.25 (77).

Subfamily UNCERTAIN

Schagonaria Poletaeva, 1956 [**S. tannuola*]. *M. Cam.* W.Sib. (RM).

Schistocephalus Chernysheva, 1956 [**S. enigmaticus*]. *M.Cam.*, C.Sib. [Although attributed to Lermontova *"in coll.,"* the description of the new genus and its type species is recorded as prepared by N. E. Chernysheva.] (RM).

Family HICKSIIDAE Hupé, 1953

Opisthoparian, micropygous, with ovoid outline. Cephalon semielliptical, strongly convex; glabella pyriform, strongly convex, smooth, reaching anterior border; fixigenae convex, wide, subtriangular in outline, palpebral lobes small, submedian, located far from glabella, without eye ridges; facial sutures slightly convergent forward from eyes and divergent backward, cutting posterior margin close to genal angles; librigenae small, narrow, with short genal spines. Thorax with 19 segments; axis much narrower than pleural regions, tapering backward; pleurae with wide oblique furrow, distal fulcrum and spinose extremities. Pygidium very small, semielliptical in outline, with 2 or ?3 axial rings and faint indi-

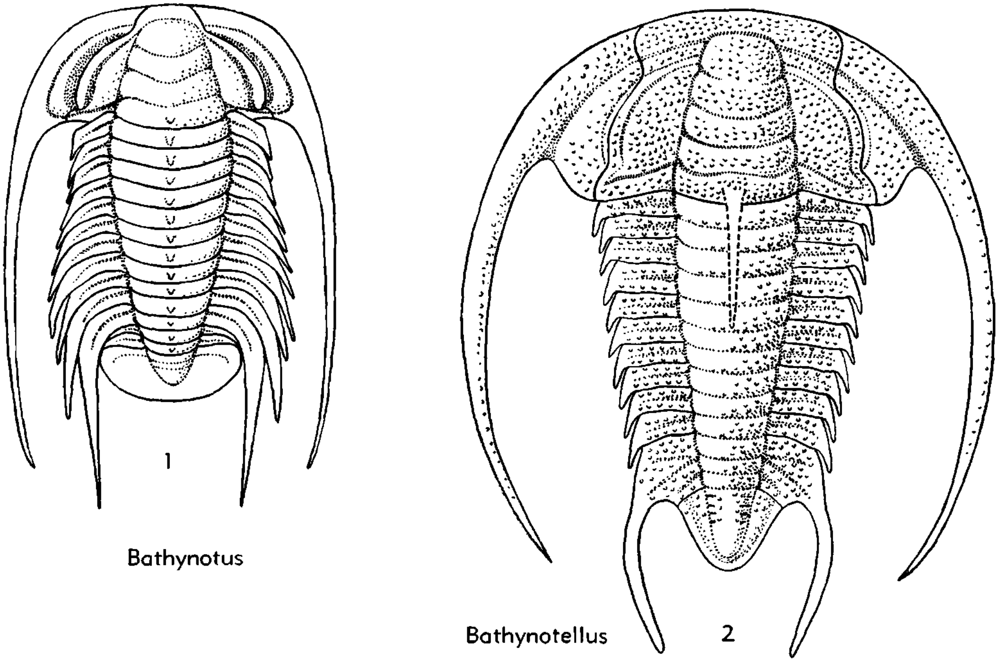


Fig. 158. Bathynotidae (p. O216, O217).

cations of ?2 pleural furrows; border absent; margin entire. *L.Cam.*

Hicksia Delgado, 1904 [**H. elvensis;* SD Vogdes, 1925 (=*H. sphaerica, H. transtaganensis, H. walcotti, H. castroi, H. hughesi, H. barroisi, H. dewalquei, H. minuta,* all Delgado, 1904]. Characters of family. [The 9 "species" described by Delgado from a single locality in Monte de Valbom, Alto Alemtejo, Portugal, are based on differently distorted specimens belonging to a single species.] *L.Cam.,* Portugal.——Fig. 157. **H. elvensis,* exoskel. (reconstr.), ×2, (405, based on 31).

Suborder BATHYNOTINA Lochman-Balk, nov.

[Type—*Bathynotus* Hall, 1860]

Exoskeleton opisthoparian, elliptical, micropygous. Glabella large, strongly convex, tapering to rounded front, with 2 to 3 pairs of glabellar furrows, posterior pairs complete; facial suture marginal anteriorly, on ventral side diverging from mid-point along sides of hypostoma; preglabellar area very small or lacking, all furrows well defined; eyes large, 0.75 of length of glabella, eye ridges wide; occipital spine or node present; fixigenae downsloping, palpebral area a little less than glabellar width, posterior area only slightly wider; librigenae with very narrow eye platform and long stout recurved genal spine. Thorax of 13 segments; axis wide, convex, may have axial spine or node; pleurae narrow, furrowed, ending in rigid spines, 11th segment macropleural, 12th and 13th reduced. Pygidium semicircular or subtriangular; axis wide, nearly full length, up to 5 faint axial rings; pleural regions very narrow, up to 4 faint pleurae, all furrows faint to obsolete. Outer surface granulose. *Up.L.Cam.-Low.M.Cam.*

Family BATHYNOTIDAE Hupé, 1953

Characters of the suborder. *Up.L.Cam.-Low.M.Cam.*

Bathynotus Hall, 1860 [**Peltura (Olenus) holopyga* Hall, 1859] [=*Pagura* Emmons, 1860; *Bathyonotus* Bigsby, 1868]. Glabella broad, front nearly straight. Thoracic axis with median node, size of pleural spines increasing regularly from 4th to 11th segment. Pygidium semicircular; axial furrow shallow but complete, axial rings 1 or 2; pleural furrows obsolete (307). *Up.L.Cam.-Low.M.Cam.,* E.N.Am.-Arct.Eurasia.——Fig. 158,*1*. **B. holopyga* (Hall), *Up.L.Cam.,* Vt.; exoskel., ×1 (307).

Bathynotellus Lermontova, 1940 [**B. yermolaevi*]. Glabella convex, with occipital spine. Thorax with pleural spines on 1st to 10th segments, all of medium size, only 11th segment macropleural. Pygidium triangular, with 5 faint axial rings (including terminal) and 3 to 4 faint pleurae; border furrow faint, narrow, border narrow (117). *Low.M.Cam.*, Arct. Eurasia.——FIG. 158,*2*. **B. yermolaevi*, N.Zem.; exoskel., ×0.75 (117).

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, herein (*ex* Suborder Corynexochida KOBAYASHI, 1935)] [=Superfamilies Bathyuriscidea RICHTER, 1933 (*partim*) + Zacanthoididea RICHTER, 1933 (*partim*); Corynexochidea RICHTER & RICHTER, 1941; Bathyuriscidea RASETTI, 1948 (attributed to RICHTER, 1933); Zacanthoidacea HENNINGSMOEN, 1951 (attributed to RICHTER, 1932); Corynexochoidae HUPÉ, 1953 (attributed to RICHTER & RICHTER, 1941)] [Type—*Corynexochus* ANGELIN, 1854]

Exoskeleton elongate subelliptical, mostly macropygous. Cephalon semicircular, mostly with well-developed genal spines; glabella long, with subparallel sides but in some genera expanding anteriorly, reaching anterior border, lateral furrows generally distinct; eyes elongate and narrow, commonly associated with eye ridges; facial sutures opisthoparian, with sections in front of eyes generally subparallel. Rostral plate fused with hypostoma or rudimentary. Thorax composed of 5 to 11 segments, pleurae with well-marked furrows, terminations spinose. Pygidium medium in size to large, commonly with marginal spines, but some genera with smooth border. *L.Cam.-U.Cam.*

Family DORYPYGIDAE Kobayashi, 1935

[*nom. transl.* RASETTI, 1948 (*ex* Dorypyginae KOBAYASHI, 1935)] [=Kooteniidae RESSER, 1939 (*nom. correct.* RASETTI, 1948, *pro* Kootenidae RESSER, 1939); Holteriinae HUPÉ, 1953]

Dorsal exoskeleton opisthoparian, ovate, almost isopygous to macropygous. Glabella strongly convex, reaching anterior border or (rarely) anterior margin, axial furrows deepening into a pair of pits near anterior corners of glabella; fixigenae of moderate width, palpebral lobes small to medium in size. Thorax (as far as known) commonly of 7 or 8 segments. Pygidium usually with border, 3 to 12 axial rings, and marginal spines. Hypostoma fused with rostral plate, the latter forming strong "anterior wings" and separating doublures of librigenae. *L. Cam.-U.Cam.*

Dorypyge DAMES, 1883 [**D. richthofeni*]. Glabella wide, more or less contracted at both ends; cephalic border moderately convex, genal spines of moderate length. Pygidium with 3 to 7 axial rings, strongly impressed pleural furrows, and 6 (rarely 5) pairs of well-developed marginal spines, 1 or 2 posterior pairs differing in size from the others; outer surface generally coarsely granulate (238). *M.Cam.* E.N.Am.-Br.I.-Denm.-Swed.-Arg.-Asia-N. E.Austral.——FIG. 159,*1*. *D. aenigma* (LINNARSSON), Swed.; *1a,b*, cran., dors. and lat. views, ×3; *1c*, librigena, ×3; *1d*, associated hypostoma, ×4; *1e*, incomplete thoracic seg., ×2 (336).——FIG. 159,*2*. *D. chihliensis* RESSER, China; pyg., ×3 (478).

Basocephalus IVSHIN, 1953 [**B. nominalis*]. *M.Cam.*, W.Sib.

Bonnaria LOCHMAN, 1956 [**Bonnia salemensis* RESSER, 1936]. Differs from *Bonnia* and *Bonniella* in shape of glabella, posterior half being narrow, with nearly parallel sides, anterior half markedly swollen, with strongly diverging sides (131). *L.Cam.*, N.Am.

Bonnia WALCOTT, 1916 [**Bathyurus parvulus* BILLINGS, 1861]. Small, strongly arched, with subcylindrical or clavate to ovate glabella, deeply impressed anterior border furrow, prominent anterior border. Thoracic segments 8. Pygidium almost semicircular, with 4 or 5 axial rings; narrow, well-impressed border furrow, narrow border, and 1 to 3 pairs of minute lateral marginal spines. Surface smooth or granulate, with granules commonly arranged in irregular concentric lines on glabella (194, 317). *L.Cam.*, N.Am.-Greenl.-E. Asia.——FIG. 159,*3*. *B. brennus* (WALCOTT), Que.; *3a,b*, cran., dors. and lat. views, ×4; *3c*, pyg., ×3 (194).

Bonniella RESSER, 1937 [**Olenoides (Dorypyge) desiderata* WALCOTT, 1890]. Differs from *Bonnia* in having pygidium with flattened marginal extension on each side behind 2nd segment, making a median marginal indentation (234). *L.Cam.*, E.N.Am.-?Sp.

Bonniopsis POULSEN, 1946 [**B. nasuta*]. Differs from *Bonnia* in having anteriorly tapering, bluntly acuminate glabella and pygidium without border (175). *L.Cam.*, Ellesm.

Dorypygina LERMONTOVA, 1940 [**D. delicatula*]. Differs from *Dorypyge* in having pygidium with strongly impressed interpleural grooves and no definite pygidial border (117). *M.Cam.*, USSR.

?**Erbiopsis** LERMONTOVA, 1940 [**E. grandis*]. Differs from *Dorypyge* in having strongly clavate glabella extending to anterior margin, 2 pairs of strongly impressed lateral furrows; thorax of 11 or more segments with narrower axis and wider pleural regions; and subtriangular, considerably convex pygidium of about 10 segments apparently without border and marginal spines (117). *M.Cam.*, Sib.——FIG. 160,*2*. **E. grandis*; incompl. exoskel., ×3 (423).

Fordaspis LOCHMAN, 1956 [**Solenopleura nana* FORD, 1878]. Differs from *Bonnia* in having glabella perfectly rounded at both ends, more for-

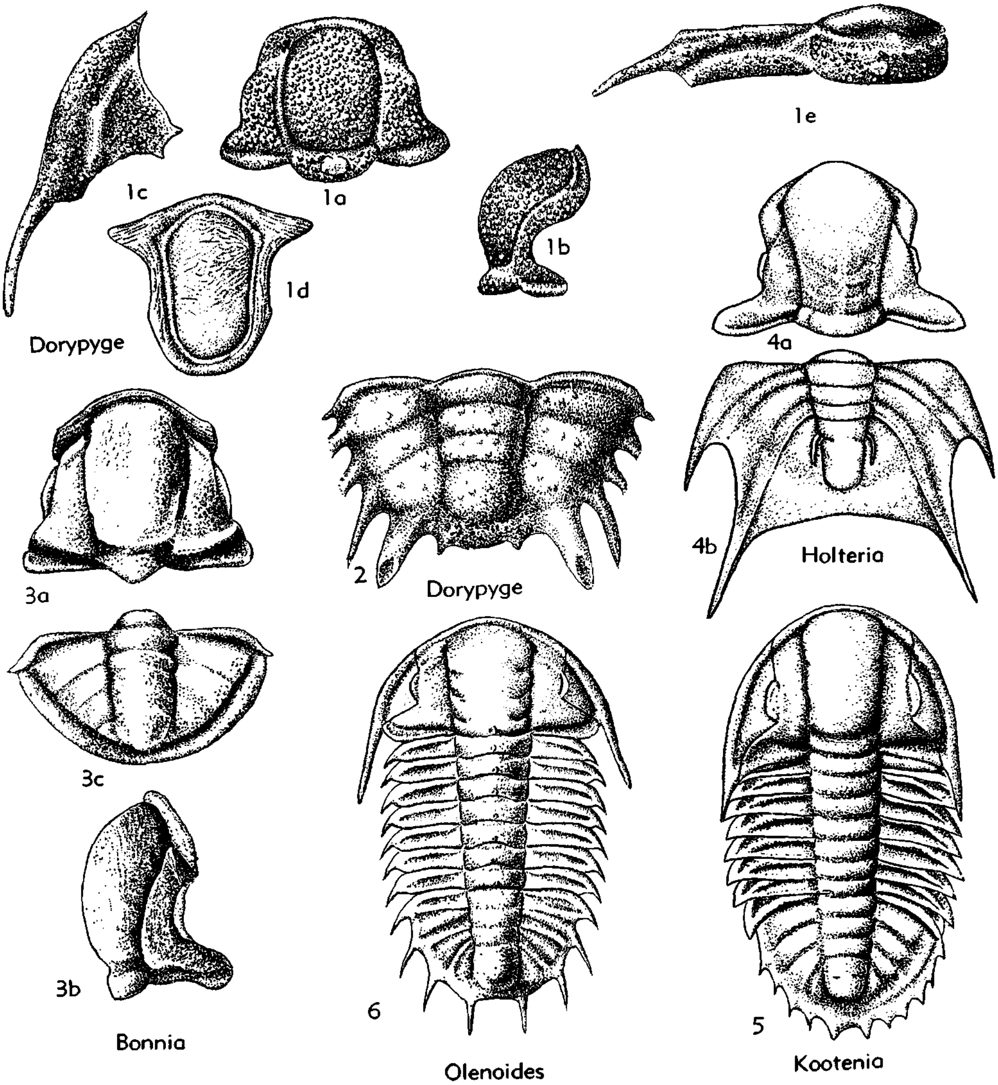


FIG. 159. Dorypygidae (p. O217-O219).

ward position of eyes, and greater number of pygidial segments (131). *L.Cam.*, N.Am.

Holteria WALCOTT, 1924 [**Ogygia? problematica* WALCOTT, 1884]. Differs from other Dorypygidae in lack of anterior border and in having subtrapezoidal pygidium with wider border and 2 pairs of well-developed pleural spines (321, 316). *U.Cam.*, N.Am.——FIG. 159,*4*. **H. problematica* (WALCOTT), Nev.; *4a,b,* cran., pyg., ×1 (488).

Kootenia WALCOTT, 1888 [**Bathyuriscus (Kootenia) dawsoni*] [?=*Kooteniella* LERMONTOVA, 1940]. Differs from *Dorypyge* in having narrower glabella, deeply impressed anterior border furrow and prominent anterior border; pygidium with better defined border, 4 to 7 (generally 6) pairs of marginal spines varying from mere scallops to long heavy spines of subequal size in the same species; and smooth or finely granulate surface of exoskeleton (196). *L.Cam.-U.Cam.*, N.Am.-S.Am.-Greenl.-N.Eu.-Asia-NE.Austral. —— FIG. 159,*5*. *K. burgessensis* RESSER, M.Cam., B.C.; exoskel., ×0.7 (488).

Notasaphus GREGORY, 1903 [**N. fergusoni*]. *M. Cam.*, E.Austral.

?**Paraolenoides** IVSHIN, 1953 [**P. medoevi*]. *M. Cam.*, W.Sib.

Olenoides MEEK, 1877 [**Paradoxides? nevadensis* MEEK, 1877] [=*Neolenus* MATTHEW, 1899]. Differs from *Dorypyge* in having parallel-sided to slightly clavate glabella; pygidium with 5 to 11 axial rings, distinctly marked interpleural grooves in addition to pleural furrows, and 4 to 8 pairs of marginal spines, generally of equal length; and surface covered with smaller granules (196, 311). *M.Cam., ?U.Cam.,* N.Am.-S.Am.(Arg.)-Asia.——Fig. 159,*6. O. curticei* Walcott, *M.Cam.,* Ala.; exoskel. (reconstr.), ×0.7 (488).

?**Strettonia** Cobbold, 1931 [**S. comleyensis*]. *L. Cam.,* Eng.

?**Tolanaspis** Ivshin, 1953 [**T. almaematris*]. *M. Cam.,* W.Sib.

Prokootenia Lermontova, 1940 [**P. rara*]. Differs from *Kootenia* in having much wider palpebral area of fixigenae, longer palpebral lobes, and pygidium with more strongly impressed pleural furrows and indistinctly defined border (117). *L.Cam.,* USSR.

?**Tabatopygellina** Sivov, 1955 [**T. babakoviensis*]. *Up.L.Cam.,* Sib. (MO)

?**Kooteniellina** Sivov, 1955 [**K. tubaenia*]. *Low. M.Cam.,* Sib. (MO)

?**Babakovia** Sivov, 1955 [**B. dorypygaeformis*]. *Up. L.Cam.-Low.M.Cam.,* Sib. (MO)

Family OGYGOPSIDAE Rasetti, 1951

[Generic names ending in *-opsis* have the stem ending in *-ops* (neo-Latin genitive, *-opsis*), according to Prof. Grensted, ICZN Classical Adviser.—Ed.]

Dorsal exoskeleton large, isopygous. Glabella approximately parallel-sided, reaching anterior border; eyes of medium size, at level of glabellar mid-point; anterior facial sutures moderately divergent; rostral plate present, not fused with hypostoma. Thorax with 8 segments. Pygidium rounded, with many axial and pleural segments (197). *M.Cam.*

Ogygopsis Walcott, 1889 [**Ogygia klotzi* Rominger, 1887] [=*Taxioura* Resser, 1939]. Glabella prominent, reaching anterior border, unfurrowed; occipital ring simple; palpebral areas about 0.3 of glabellar width; eye ridges present; palpebral lobes 0.25 of glabellar length; anterior border furrow merging with axial furrows; border present; anterior section of facial sutures directed slightly outward, curving inward across border, posterior section defining subtriangular posterior area; librigenae with moderately long genal spines. Hypostoma subrectangular, commonly attached to rostrum, suggesting incipient fusion; indistinct maculae present. Thorax with 8 segments; pleural furrows parallel to edges of pleurae, pleurae not extended into long spines. Pygidium with long, multisegmented axis almost reaching posterior border; pleural fields convex, with numerous pairs of furrows and shallow or indistinct interpleural grooves; border furrow and border poorly defined; margin usually entire. *M.Cam.,* N.Am.——Fig. 160,*1.* **O. klotzi* (Rominger), B.C.; *1a,* exoskel., ×0.7; *1b,* rostral plate and hypostoma, ×3 (448n).

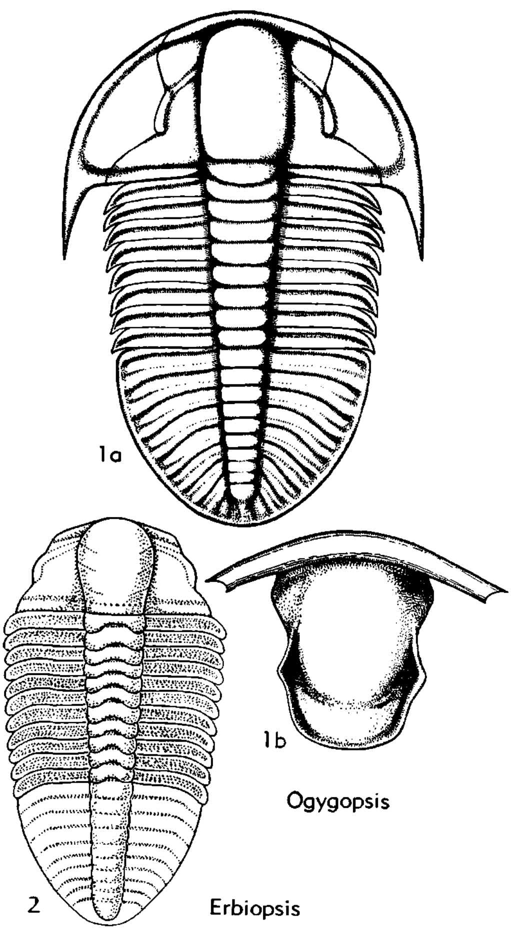


Fig. 160. Dorypygidae, Ogygopsidae (p. O217-O219).

Family ORYCTOCEPHALIDAE Beecher, 1897

[*nom. transl.* Rasetti, herein (*ex* Oryctocephalinae Beecher, 1897)] [=Tonkinellidae Reed, 1934; Lancastriidae Kobayashi, 1935 (*nom. correct.* Henningsmoen, 1951, *pro* Lancastridae Kobayashi, 1935); Oryctocephalinae Hupé, 1953]

Dorsal exoskeleton with low convexity, small or at most medium-sized. Glabella parallel-sided or expanded forward, reaching frontal border; glabellar and occipital furrows typically composed of pairs of pits not reaching axial furrow but commonly connected across glabella; occipital ring short, simple; fixigenae usually wide; palpebral lobes usually of medium length and distant from glabella; eye ridges developed; librigenae generally narrow, bearing long genal spines; hypostoma fused with rostrum

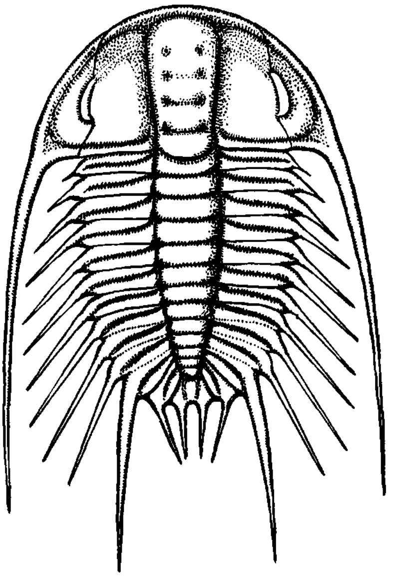


FIG. 161. *Oryctocephalus burgessensis* RESSER, M. Cam., W.Can.(B.C.); exoskel., ×2 (448n).

(Oryctocephalus). Thorax with 5 to 18 segments; pleurae typically extended into long spines, more rarely truncated. Pygidium small, and simple in earliest forms *(Lancastria)*, increasing in size at expense of thorax up to later, isopygous genera where pygidium comprises 6 to 7 segments; axis usually short; pleural regions generally with distinct, radially arranged pleural furrows and grooves; border undefined, margin generally extended into several pairs of spines, in a few genera rounded (97, 109, 117, 197, 198, 236, 237, 259, 265, 340). *L.Cam.-M. Cam.*

Oryctocephalus WALCOTT, 1886 [**O. primus*]. Glabella parallel-sided or slightly expanded forward; glabellar furrows well impressed as pits; palpebral lobes 0.3 of glabellar length, distant from glabella, posterior to glabellar mid-point; posterior areas of fixigenae not extending much beyond palpebral lobes, genal spines long. Thorax with 7 segments; pleurae extended into spines. Pygidium almost as large as cephalon; axis tapered, with 5 to 7 segments; pleural furrows and grooves impressed, not parallel to each other; 5 or 6 pairs of marginal spines, 4th pair strongest in most species. *M.Cam.*, Eu.-Asia-N.Am.-S.Am.——FIG. 162,*1*. **O. primus*, Nev.; *1a,b*, cran., pyg., ×2 (448n).——FIG. 161. *O. burgessensis* RESSER, W. Can.(B.C.); exoskel., ×2 (448n).——FIG. 162,*2*. *O. walcotti* RESSER, W.USA(Idaho); hypostoma and doublure of librigenae, ×2 (448n). [Genera considered synonymous with *Oryctocephalus* include *Oryctocephalina* LERMONTOVA, 1940, and *Viñakainella* RUSCONI, 1952.]

?**Cheiruroides** KOBAYASHI, 1935 [**Atops orientalis* RESSER & ENDO in KOBAYASHI, 1935 (=*Arthricocephalus? primigenius* SAITO, 1934)]. Glabella broad, parallel-sided with 3 pairs of lateral furrows, of which 2 connect across glabella; occipital ring short; fixigenae triangular; palpebral lobes small, at level of glabellar mid-point. Thorax of ?14 segments; pleurae rounded. Pygidium small, transverse, with rounded margin. *L.Cam.*, Manch.-Korea (97).

Lancastria KOBAYASHI, 1935 [**Olenopsis roddyi* WALCOTT, 1912]. Cephalon as in *Oryctocephalus.* Thorax long, with 18 segments; pleurae extended into spines. Pygidium small, elongated, with 2 segments. *L.Cam.*, N.Am.——FIG. 162,*4*. **L. roddyi* (WALCOTT), Pa.; complete, somewhat distorted holotype, ×2 (448n).

Oryctocara WALCOTT, 1908 [**O. geikiei*]. Very small. Cranidium differs from *Oryctocephalus* in narrower fixigenae, longer palpebral lobes, and much wider *(tr.)* posterior areas of fixigenae. Thorax with 11 segments; pleurae bluntly terminated. Pygidium rounded, with short, segmented axis and numerous pairs of pleural furrows and grooves, no marginal furrow or border. *M.Cam.*, N.Am.——FIG. 162,*5*. **O. geikiei*, Idaho; specimen lacking librigenae, ×5 (448n).

Oryctocephalites RESSER, 1939 [**O. typicalis*]. Similar to *Oryctocephalus* but anterior outline of cranidium less straight and glabella more definitely expanded forward. Pygidium with obsolete interpleural grooves and 5 pairs of marginal spines. *M.Cam.*, N.Am.——FIG. 162,*3*. **O. typicalis*, Idaho; *3a,b*, cran., pyg., ×2 (448n).

Oryctocephalops LERMONTOVA, 1940 [**O. frischenfeldi*]. Cephalon as in *Oryctocephalus.* Thorax with 12 segments. Pygidium small; pleurae with 2 pairs of spines. *M.Cam.*, Sib. (117).

Tonkinella MANSUY, 1916 [**T. flabelliformis*]. Cephalic proportions as in *Oryctocephalus* but glabellar furrows less distinctly pit-shaped. Thorax with 5 segments *(T. stephensis)*; pleurae bluntly terminated. Pygidium semicircular, as large as cephalon; margin rounded; axis tapered, segmented; pleural regions convex, with equally spaced, radially arranged furrows, lacking interpleural grooves; no marginal furrow or border. *M.Cam.*, E.Asia-N.Am.——FIG. 162,*6*. *T. stephensis* KOBAYASHI, B.C.; exoskel., ×1.5 (448n).

Family DOLICHOMETOPIDAE Walcott, 1916

[*nom. transl.* HUPÉ, 1953 (*ex* Dolichometopinae WALCOTT, 1916).] [=Bathyuriscidae RICHTER, 1933; Ptarmiganiidae RESSER, 1935 (*nom. correct.* RASETTI, 1948, *pro* Ptarmiganidae RESSER, 1935); Orriinae, Glossopleurinae HUPÉ, 1953]

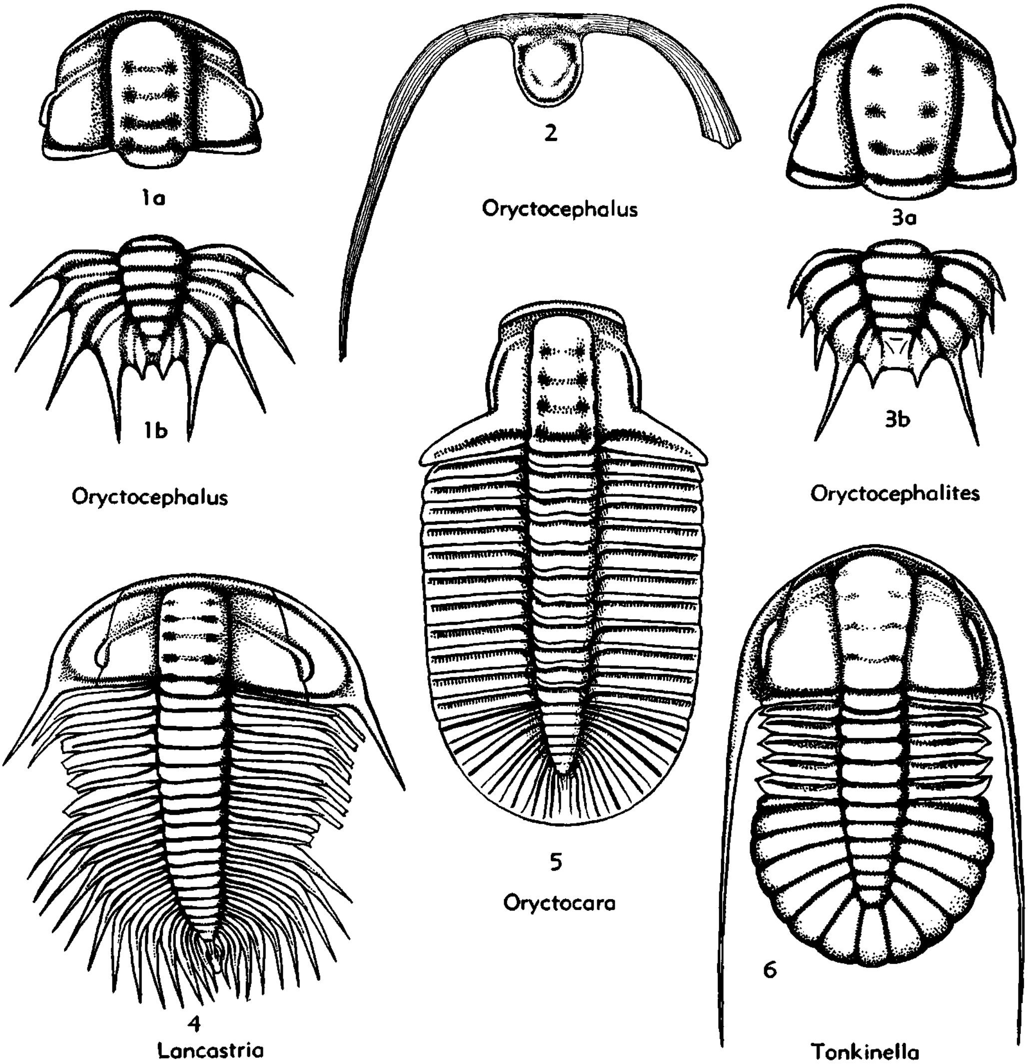


FIG. 162. Oryctocephalidae (p. O220).

Dorsal exoskeleton opisthoparian, ovate to elongate, heteropygous to macropygous. Cephalon semicircular, with parallel-sided to clavate glabella reaching anterior border or margin; anterior areas narrow; palpebral areas of fixigenae narrow to moderately wide; palpebral lobes usually very long, close to glabella, their front ends generally almost touching it; genal angles very commonly produced into spines. Thorax (as far as known) with 6 to 12 segments. Pygidium greatly varying in size, shape, and number of segments. Hypostoma fused with rostral plate, the latter forming strong "anterior wings." *L.Cam.-U.Cam.*

Dolichometopus ANGELIN, 1854 [**D. svecicus*]. Cephalon strongly arched transversely and longitudinally; glabella moderately convex, subcylindrical to slightly clavate, devoid of glabellar furrows in full-grown specimens, defined by shallow axial furrow, encroaching upon moderately wide, flat, or slightly convex anterior border; occipital ring widened medially, lenticular in outline; fixigenae posteriorly of about same width as glabella; eye ridges oblique; posterior areas of fixigenae with rounded, strongly sloping extremities terminating at genal angles; palpebral lobes half as long as glabella; genal angles bluntly pointed or with short, strong genal spines. Pygidium large, approximately semicircular, moderately convex, indistinctly segmented, with narrow, poorly defined axis extended into wide border; surface minutely punctate or granulate (101, 317, 336). *M.Cam.*, Eu.-E.N.Am.(Atl.prov.)-?Asia.——FIG. 163,*1*. **D. svecicus*, Swed.; *1a*, cran., ×2 (101); *1b*, pyg., ×1 (336).

Amphoton LORENZ, 1906 [**Dolichometopus deois* WALCOTT, 1905; SD KOBAYASHI, 1935]. Heteropygous. Glabella subcylindrical, extended to anterior border, occipital ring well defined; palpebral areas of fixigenae narrow, palpebral lobes slightly curved, upturned cephalic border narrow. Thorax with 7 segments bearing pointed pleurae. Pygidium with well-defined border and smooth outer surface (101). *M.Cam.*, E.Asia-E.Austral.

A. (Amphoton). Glabella with slightly concave sides, lacking lateral furrows; occipital ring very short, without median spine; palpebral lobes fairly long, situated opposite central portion of glabella; genal angles rounded, without genal spine. Pygidium almost semicircular, with 3 or 4 axial rings; pleural fields distinctly segmented, border wide, depressed; with shallow indentation behind moderately tapering axis (101). *M.Cam.*, E.Asia.——FIG. 163,*5*. **A. (A.) deois* (WALCOTT), ?Shantung; exoskel., ×2 (101).

A. (Amphotonella) KOBAYASHI, 1942 [**Dolichometopus alceste* WALCOTT, 1905]. Differs from *A. (Amphoton)* in having tapered glabella with straight sides and 4 pairs of deeply impressed lateral furrows, longer occipital ring, genal angles with short, rapidly tapering genal spine, narrower pygidium with narrow border, rapidly tapering axis, median axial nodes, and posterior margin without indentation (101). *M.Cam.*, E.Asia-SE. Austral.——FIG. 163,*2*. **A. (A.) alceste* (WALCOTT), Shantung; *2a,b*, ceph., pyg., ×1 (101).

A. (Fuchouia) RESSER & ENDO in KOBAYASHI, 1935 [**Bathyuriscus manchuriensis* WALCOTT, 1911]. Differs from *A. (Amphoton)* in having parallel-sided glabella with 3 pairs of lateral furrows, occipital node or short spine, palpebral lobes of medium length, long straight, slender genal spines, and pygidium with rapidly tapering axis of 5 or 6 rings, extremely narrow border, and posterior margin without indentation (101). *M.Cam.*, E.Asia.——FIG. 163,*10*. **A. (F.) manchuriensis* (WALCOTT), Manch.; *10a,b*, ceph., pyg., ×2 (101).

A. (Sunia) KOBAYASHI, 1942 [**A. (S.) typica*]. Differs from *A. (Amphoton)* in having long, stout occipital spine; long, stout, curved genal spines; and narrower pygidium, with narrow border and posterior margin without indentation (101). *M.Cam.*, E.Asia-NE.Austral.——FIG. 163,*4*. **A. (S.) typica*, Shantung; *4a-c*, ceph., thoracic seg., pyg., ×1 (101).

Anoria WALCOTT, 1924 [**Dolichometopus tontoensis* WALCOTT, 1916]. Cranidium without anterior border; glabella more or less clavate, smooth or indistinctly furrowed; axial furrow effaced between anterior corners of glabella; posterior areas of fixigenae rapidly tapering; palpebral lobes relatively short, slightly curved, situated opposite glabellar center; anterior sections of facial suture strongly converging toward frontal margin; librigenae with wide lateral border; genal angles produced into fairly strong, backward-directed genal spines. Thorax with 7 segments, wide axis, and pointed extremities, 5th segment commonly having long, backward-directed pleural spines. Pygidium slightly smaller than cephalon, relatively long, with evenly curved posterolateral margin, moderately tapering axis of 4 or 5 or more rings, indistinctly segmented pleural fields, and well-defined, wide, concave border (101, 316, 321). *M.Cam.*, N.Am.——FIG. 163,*7*. **A. tontoensis* (WALCOTT), Ariz.; exoskel. (reconstr.), ×0.5 (488).

Asperocare V. POULSEN, 1958 [**A. argentinum*]. *M.Cam.*, S.Am.(Arg.).

Athabaskia RAYMOND, 1928 [**A. ostheimeri*]. Glabella extending to frontal margin, its anterior half strongly expanding, with 3 or 4 pairs of lateral furrows; palpebral lobes of medium size, close to posterior part of glabella; posterior areas of fixigenae slightly tapering, divided into subequal parts by deep posterior border furrow; librigenae with moderately convex border and stout, flat, rapidly tapering, backward-directed genal spines. Thorax with 7 or 8 segments bearing pointed extremities. Pygidium with fairly short, moderately tapering axis of 6 or 7 axial rings, distinctly marked pleural furrows becoming increasingly deep and wide on wide, concave, indistinctly defined border, and in some faintly marked interpleural grooves. *?L.Cam.*, *M.Cam.*, N.Am.——FIG. 163,*8*. **A. ostheimeri*, Alba.; exoskel., ×0.5 (101).

Athabaskiella KOBAYASHI, 1942 [**Bathyuriscus (Poliella) probus* WALCOTT, 1916]. Differs from *Bathyuriscidella* in having narrow anterior border in front of glabella (101, 317). *M.Cam.*, N.Am. ——FIG. 163,*9*. **A. proba* (WALCOTT), Utah; *9a*, cran., ×4; *9b*, pyg., ×5 (317).

Bathyuriscidella RASETTI, 1948 [**B. socialis*]. Exoskeleton tapering from large cephalon to small pygidium. Glabella narrow, somewhat expanded anteriorly, reaching front margin, with 1 to 3 pairs of shallow anterior lateral furrows and a well-impressed oblique posterior pair; occipital ring very long; anterolateral border fairly narrow, upturned; eye ridges present; palpebral lobes relatively short, situated opposite or anterior to glabellar center; anterior sections of facial sutures straight between eyes and anterior border, parallel to axial furrows; posterior sections defining wide, triangular posterior areas of fixigenae; librigenae wide, with short, stout, somewhat outward-directed genal spine. Thorax with 9 segments, having narrow convex axis and flat, broadly furrowed pleurae that terminate in sharp, obliquely backward-directed spines, those of 5th and 8th segments longer than others (in type species). Pygidium with few segments, approximately semicircular, with very prominent axis, postaxial ridge, flat pleural regions, shallow pleural furrows and interpleural grooves, and poorly defined border, which may bear marginal spines (196). *M.Cam.*, E.N.Am.——FIG. 163,*6*. **B. socialis*, Que.; *6a,b*, cran., librigena, ×3; *6c*, hypostoma, ×4; *6d*, 2nd-

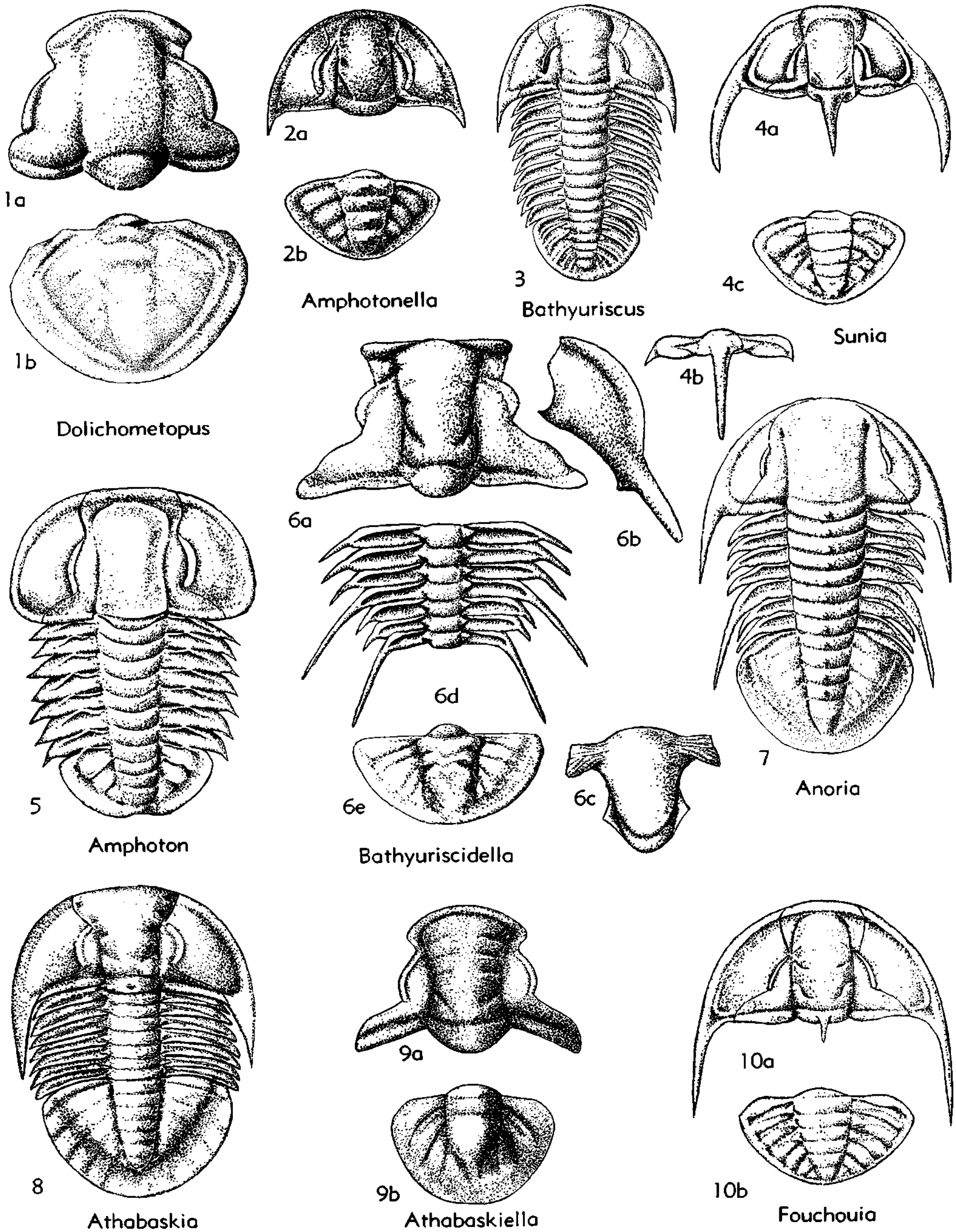


FIG. 163. Dolichometopidae (p. O222-O224).

8th thoracic segments, ×6; *6e*, pyg., ×3 (196).

Bathyuriscus Meek, 1873 [**Bathyurus? haydeni*]. Differs from *Bathyuriscidella* in having narrow anterior border in front of glabella; short occipital ring; narrower fixigenae with more slowly tapering posterior areas; longer, more posteriorly placed palpebral lobes; pointed pleurae or very short pleural spines; and larger pygidium with about 7 axial rings, deeper pleural furrows and interpleural grooves, narrower, well-defined border, and in some a pair of lateral spines (101, 197, 317). *M.Cam.*, N.Am.-?Eng.——Fig. 163,*3*. *B. rotundatus* (Rominger), W.Can.(B.C.); exoskel., ×1 (317).

Chilometopus Rusconi, 1952 [**C. asperoensis*]. Differs from *Bathyuriscus* in having narrower anterior area of fixigenae, longer, more prominent palpebral lobes, and smaller, very short (associated) pygidium of few segments with much more prominent, indistinctly segmented axis (259). *M.Cam.*, Arg.

Chilonorria Rusconi, 1952 [**C. perlotii*]. Differs from *Orria* in having semicircular pygidium with longer axis. Cephalon and thorax unknown (259). *M.Cam.-U.Cam.*, Arg.

Clavaspidella Poulsen, 1927 [**C. sinupyga*]. Differs from *Athabaskia* in having much wider palpebral and narrower posterior areas of fixigenae; relatively long, well-defined eye ridges; and pygidium with narrower axis, distinct border furrow, and broad, shallow marginal indentation behind axis (101, 172). *M.Cam.*, NW.Greenl.-?Arg.——Fig. 164,*1*. **C. sinupyga; 1a,b*, ceph., pyg., ×1 (101).

Corynexochides Rasetti, 1948 [**C. gregarius*]. Differs from *Bathyuriscidella* in having longer palpebral lobes, narrower posterior area of fixigenae, thorax of ?7 segments with bluntly terminating pleurae, and only 1st pygidial segment well differentiated (196). *M.Cam.*, E.N.Am.

Dolichometopsis Poulsen, 1927 [**D. resseri*]. Glabella parallel-sided to slightly clavate, reaching narrow, slightly convex anterior border, with 3 or 4 pairs of lateral furrows; occipital furrow deeply impressed; palpebral lobes moderately curved, about half as long as glabella, terminating opposite occipital furrow and anteriorly almost touching axial furrows, fixigenae here being almost completely reduced; posterior areas of fixigenae slightly wider than glabella; anterior sections of facial sutures diverging between eyes and anterior border; librigenae with almost flat lateral border, well-marked border furrow, and long flat slightly curved genal spine projecting from more or less rounded genal angle. Associated pygidium small, transverse, with short axis, 4 or 5 axial rings; wide, shallow pleural furrows, interpleural grooves between raised pleural edges; poorly defined border; and entire margin with shallow indentation behind axis (101, 172). *Up. L.Cam.*, NW.Greenl.-?N.Am.——Fig. 164,*3*. **D. resseri*, NW.Greenl.; *3a,b*, ceph., pyg., ×2 (101, slightly modified).

Glossopleura Poulsen, 1927 [**Dolichometopus boccar* Walcott, 1916] [*?=Sonoraspis* Stoyanow, 1952]. Differs from *Anoria* in its much longer palpebral lobes and wider, slightly tapering posterior areas of fixigenae (101, 172, 317). *M.Cam.*, N.Am.-NW.Greenl.-S.Am.(Arg.).——Fig. 164,*2*. **G. boccar* (Walcott), Mont.; exoskel. (reconstr.), ×1 (317).

Hemirhodon Raymond, 1937 [**H. schucherti*]. Glabella moderately convex, expanding from poorly defined occipital ring, reaching anterior margin; lateral furrows indistinct or effaced; anterior and palpebral areas of fixigenae very narrow, and posterior areas moderately wide, with rapidly tapering lateral extremities; palpebral lobes extremely short, moderately curved. Thoracic axis less than 0.3 of width of thorax; pleurae flat, with shallow furrows, terminating in falcate points. Pygidium about same in size as cephalon, almost flat, with little relief, nearly semicircular, with narrow, rapidly tapering axis of about 6 rings extending to wide, slightly concave border which may have a median marginal notch (101, 193, 213). *U.M.Cam.-U.Cam.*, N.Am.——Fig. 164,*9a*. **H. schucherti*, U.Cam., Vt.; cran. and thoracic segs., ×2 (213).——Fig. 164,*9b*, *H. simplex* Rasetti, U.Cam., Que.; pyg., ×3 (193).

Klotziella Raymond, 1928 [**Bathyuriscus ornatus* Walcott, 1908]. Differs from *Bathyuriscidella* in having narrow anterior border in front of glabella, more rapidly tapering posterior areas of fixigenae, extremely short palpebral lobes, narrower librigenae without genal spine; thoracic segments (except 1st) with rounded extremities; and larger pygidium with very narrow border (101, 197, 317). *M.Cam.*, N.Am.

Mendospidella Rusconi, 1952 [**M. asperoensis*]. Differs from *Athabaskia* in having shorter pygidium with more tapering axis and strongly marked interpleural grooves (259). *M.Cam.*, Arg.

Neochilonorria Rusconi, 1953 [**N. coronillensis*]. Differs from *Chilonorria* in having pygidial pleural furrows and interpleural grooves defined by very sharp ridges. Cephalon and thorax unknown (260). *U.Cam.*, Arg.

Orria Walcott, 1916 [**O. elegans*]. Glabella narrow, parallel-sided, reaching narrow anterior border, with 4 pairs of indistinctly defined lateral furrows; anterior and palpebral areas of fixigenae very narrow, and posterior areas very wide, extending obliquely backward to genal angles, divided into subequal parts by wide and deep posterior border furrow; palpebral lobes of medium size, slightly behind glabellar center; anterior sections of facial suture parallel between eyes and anterior border; librigenae wide, with irregular network of raised lines, and short backward-directed genal spine. Thorax with 9 segments, axis narrow, pleurae horizontal, broadly furrowed, and obliquely truncated. Pygidium semielliptical, longer than cephalon, with short axis of 8 or 9 rings, strongly marked pleural furrows and interpleural grooves, and very narrow, raised border (101, 317). *M.Cam.*, N.Am.——FIG. 164,*4*. **O. elegans,* Utah; exoskel., ×0.5 (317).

Orriella RASETTI, 1948 [**O. gaspensis*]. Intermediate between *Bathyuriscus* and *Orria,* differing from

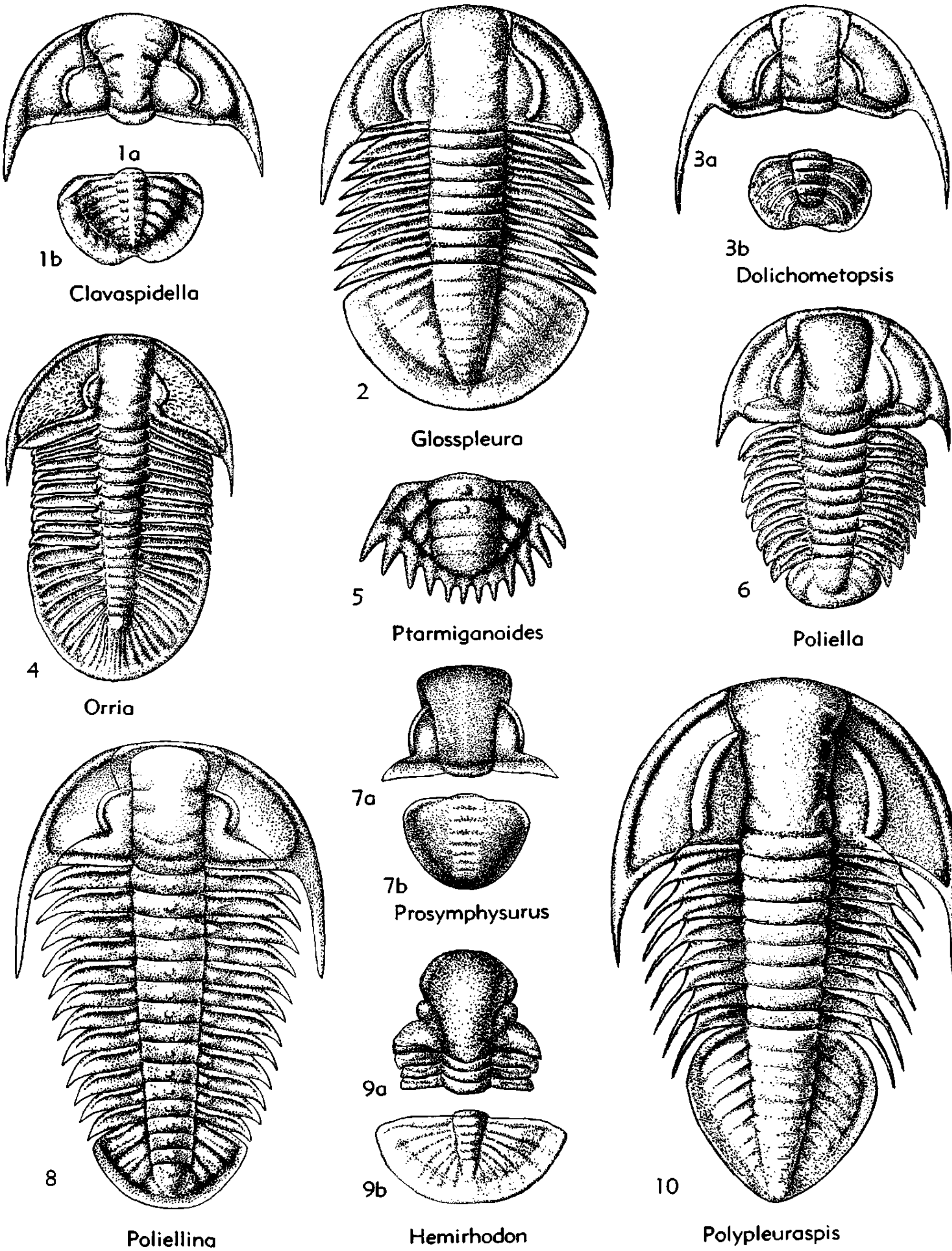


FIG. 164. Dolichometopidae (p. O224-O226).

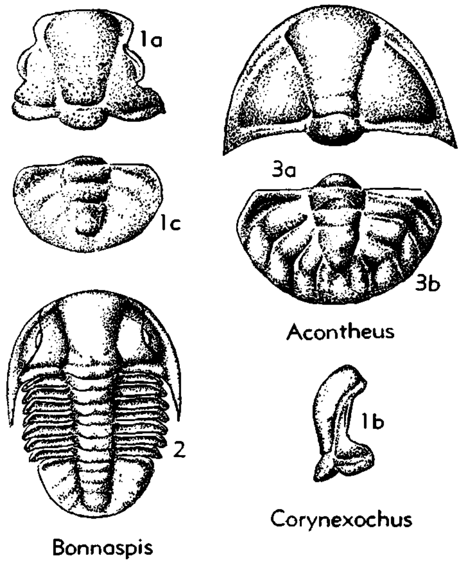


FIG. 165. Corynexochidae (p. O227).

the former in having much longer palpebral lobes, no anterior border in front of glabella, presence of occipital spine, and short pygidial axis; differing from the latter in having deeper axial furrow, more prominent glabella, wider anterior and narrower posterior areas of fixigenae, and fewer pygidial segments (196). *M.Cam.*, E.N.Am.

Parapoliella CHERNYSHEVA, 1956 [**Olenoides obrutchevi* LERMONTOVA, 1925]. *Up.L.Cam.*, USSR.

Parkaspis RASETTI, 1951 [**P. endecamera*]. Differs from *Bathyuriscus* in having 10 or 11 thoracic segments (*B.* has 9), smaller pygidium without border and with fewer segments, indistinctly marked interpleural grooves, and denticulated margin (197). *M.Cam.*, N.Am.

Poliella WALCOTT, 1916 [**Bathyuriscus (P.) anteros*] [=*Bornemannia* VOGDES, 1925]. Differs from *Bathyuriscus* in having only one pair of distinctly marked glabellar furrows, 7 to 11 thoracic segments, shorter pygidium with 2 or 3 axial rings, faintly marked or effaced interpleural grooves, indistinct border, with denticulate margin or median marginal notch in some (101, 317). *L.Cam.-M.Cam.*, N.Am.——FIG. 164,6. **P. anteros,* M.Cam., Idaho; exoskel., ×2 (317).

Poliellaspis LERMONTOVA, 1940 [**Poliellina sayanica* POLETAYEVA, 1936]. *M.Cam.*, Asia.

Poliellina POLETAEVA, 1936 [**P. lermontovae*]. Differs from *Poliella* in having up to 4 pairs of distinct lateral glabellar furrows, relatively short, strongly curved palpebral lobes, thorax of 10 to 12 segments with axial nodes and better-developed pleural spines, and pygidium with axial nodes and distinctly defined border (101, 117). *M. Cam.*, Asia-N.Am.——FIG. 164,8. **P. lermontovae,* Sib.; exoskel. (reconstr.), ×2 (101).

Polypleuraspis POULSEN, 1927 [**P. solitaria*]. Differs from *Glossopleura* in having more prominent axis; narrower thorax with long, obliquely backward-directed pleural spines; and much longer, more convex pygidium with about 10 fairly well-marked segments and narrower border (197). *M.Cam.*, NW.Greenl.-N.Am.——FIG. 164,*10*. *P. insignis* RASETTI, W.N.Am.; exoskel., ×2.5 (197).

Prosymphysurus POULSEN, 1927 [**P. kochi*]. Differs from *Glossopleura* in having evenly arched cranidium and almost evenly arched pygidium with flat, indistinctly defined axis, unfurrowed pleural field, and narrower, slightly convex border (101, 172). *M.Cam.*, NW.Greenl.——FIG. 164,7. **P. kochi; 7a,* cran., ×2; *7b,* pyg., ×1 (172).

Ptarmigania RAYMOND, 1928 [**Bathyuriscus rossensis* WALCOTT, 1917]. Differs from *Dolichometopsis* in having appreciably wide fixigenae at anterior end of palpebral lobes, well-defined eye ridges, and pygidium with flat marginal spines or scallops and pleural furrows extending across wide border almost to margin (101, 197). *M.Cam.*, N. Am.

Ptarmiganoides RASETTI, 1951 [**P. bowensis*]. Differs from *Dolichometopsis* in having longer pygidial axis and margin of pygidium extended into at least 4 pairs of strong, cylindrical spines (197). *M.Cam.*, N.Am.——FIG. 164,5. **P. bowensis,* W.Can.; pyg., ×3 (197).

Wenkchemnia RASETTI, 1951 [**W. walcotti*]. Differs from *Poliella* in having shorter palpebral lobes, rapidly tapering posterior areas of fixigenae, and last thoracic segment less curved, not enveloping pygidium (197). *M.Cam.*, N.Am.

Family CORYNEXOCHIDAE Angelin, 1854

Dorsal exoskeleton small, opisthoparian, subovate to subelliptical, moderately convex, heteropygous to almost isopygous. Glabella clavate, extended to anterior margin, lateral furrows more or less effaced; fixigenae moderately wide, librigenae narrow; palpebral lobes of small to medium size, placed opposite or a little posterior to glabellar center. Thorax (as far as known) with 7 segments. Pygidium, semicircular with 2 to 5 indistinctly defined axial rings, border slightly convex and margin entire. Hypostoma fused with rostral plate, the latter forming strong "anterior wings." *M.Cam.*

Subfamily CORYNEXOCHINAE Angelin, 1854

[*nom. transl.* RAYMOND, 1928 (*ex* Corynexochidae ANGELIN, 1854)]

Corynexochidae with eyes and facial sutures. *M.Cam.*

Corynexochus ANGELIN, 1854 [**C. spinulosus*] [=*Karlia* WALCOTT, 1889]. Exoskeleton elongate oval. Glabella strongly expanding from base to front; occipital ring long; anterior area of fixigenae extremely narrow; eyes of medium size. Thoracic pleurae deeply furrowed, pointed (233, 336). *M. Cam.*, Eu.-E.N.Am.(Atl.prov.)-N.E. Austral.-Asia.——FIG. 165,*1*. **C. spinulosus*, Swed.; *1a,b*, cran., dorsal, lateral, ×4; *1c*, pyg., ×4 (336).

Bonnaspis RESSER, 1936 [**Karlia stephenensis* WALCOTT, 1889]. Differs from *Corynexochus* in its nearly even elliptical outline, short occipital ring, wider anterior area of fixigenae, small eyes, bluntly terminating thoracic pleurae, and larger pygidium (233). *M.Cam.*, N.Am.——FIG. 165,*2*. **B. stephenensis* (WALCOTT), B.C.; exoskel. (reconstr.), ×2 (317).

Corynexochina LERMONTOVA, 1940 [**C. weberi*]. *M.Cam.*, USSR.

Subfamily ACONTHEINAE Westergård, 1950

Small forms lacking eyes and facial sutures; otherwise resembling Corynexochinae but somewhat doubtfully classed in the same family. *M.Cam.*

Acontheus ANGELIN, 1851 [**A. acutangulus*] [=*Aneucanthus* ANGELIN, 1854 (obj.); *Aneuacanthus* BARRANDE, 1856 (obj.)] (337). *M.Cam.*, Swed.-Br.I.——FIG. 165,*3*. **A. acutangulus*, Swed.; *3a,b*, ceph., pyg., ×4 (337).

Family ZACANTHOIDIDAE Swinnerton, 1915

[*nom. correct.* RICHTER, 1933 (*pro* Zacanthoidae SWINNERTON, 1915)] [=Albertellidae, Mexicaspinae, Vanuxemellinae HUPÉ, 1953]

Exoskeleton slender, of low convexity. Glabella long, parallel-sided or expanded forward, generally with 4 pairs of lateral furrows. Palpebral lobes long, semicircular, close to glabella; frontal area usually reduced to anterior border, rarely obsolete; posterior areas slender, in some genera bearing metafixigenal spines; genal spines present. Hypostoma fused with rostral plate. Thorax of 4 to 9 segments; axial rings usually spinose; pleurae generally bearing elongate, triangular ridges at proximal end, extended into long spines; macropleural segments may be present. Pygidium smaller than cephalon; axis of 4 to 8 segments; pleural fields with marginal spines. Closely allied to and not sharply separated from Corynexochidae. *L. Cam.-M.Cam.* (236, 197, 130).

Zacanthoides WALCOTT, 1888 [*pro Embolimus* ROMINGER, 1887 (*non* AGASSIZ, 1846; *nec* MARSHALL, 1868; *nec* WEISE, 1902)] [**Z. romingeri* RESSER, 1942 (*pro Embolimus spinosa* ROMINGER, 1887, *non Ogygia? spinosa* WALCOTT, 1884); SD RESSER, 1942]. Glabella parallel-sided; metafixigenal spines present. Thorax of 9 segments; pleurae obliquely furrowed; no macropleural segments. Pygidium with elevated, abruptly terminated axis; general outline subtriangular; pleural fields flat; marginal furrow and border indistinct; pleurae directed backward, extended into several pairs of marginal spines. *M.Cam.*, N.Am.——FIG. 166. **Z. romingeri*, W.Can.(B.C.); exoskel., ×0.6 (448n).

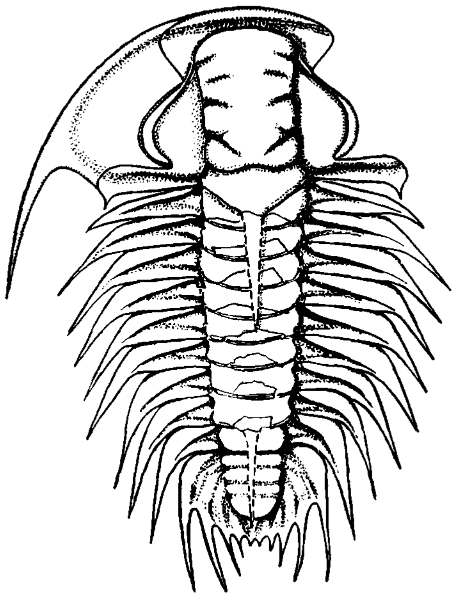


FIG. 166. **Zacanthoides romingeri* WALCOTT (Zacanthoididae), M.Cam., W.Can.(B.C.); exoskel., ×0.6 (448n).

Albertella WALCOTT, 1908 [**A. helena*]. Glabella parallel-sided; eyes of variable length; no metafixigenal spines. Thorax of 7 segments; third or fourth segment macropleural. Pygidium with one pair of marginal spines. *M.Cam.*, N.Am.——FIG. 167,*3a,b*. *A. limbata* RASETTI, W.Can.(B.C.); *3a,b*, cran., pyg., ×3 (448n).——FIG. 167,*3c*. *A. bosworthi* WALCOTT, W.Can.(B.C.); exoskel., ×1 (448n).——FIG. 167,*3d*. **A. helena*, Mont.; exoskel., ×1 (448n).

Fieldaspis RASETTI, 1951 [**F. furcata*]. Glabella expanded forward; eyes long; palpebral lobes close to axial furrow at both ends; no metafixigenal spines. Thorax of 9 segments, none macropleural; pygidial margin extended into pair of spines or rounded lobes. *M.Cam.*, N.Am.——FIG. 168,*1a-e*. **F. furcata*, W.Can.(B.C.); *1a*, cran., ×1.5; *1b*, librigena, ×1.5; *1c,d*, hypostoma, ventral, lateral, ×4; *1e*, pyg., ×1.5 (448n).——FIG. 168,*1f,g*. *F. superba* RASETTI, W.Can.(B.C.); *1f,g*, cran., pyg., ×1 (448n).

Mexicaspis LOCHMAN, 1948 [**M. stenopyge*]. Glabella expanded forward; axial furrow shallow; eyes short; no metafixigenal spines. Pygidium elongated, with 2 pairs of large, backward-directed spines. *M.Cam.*, N.Am.——Fig. 168,*4*. **M. stenopyge*, Mex.(Sonora); *4a*, cran., ×1.4; *4b*, pyg., ×2 (130).

Prozacanthoides Resser, 1937 [**Olenoides stissingensis* Dwight, 1889]. Cephalon as in *Zacanthoides*. Pygidial pleurae not directed sharply backward. *L.Cam.*, N.Am.——Fig. 168,*2*. *P. virginicus* Resser, Va.; *2a,b*, cran., pyg., ×2 (448n).

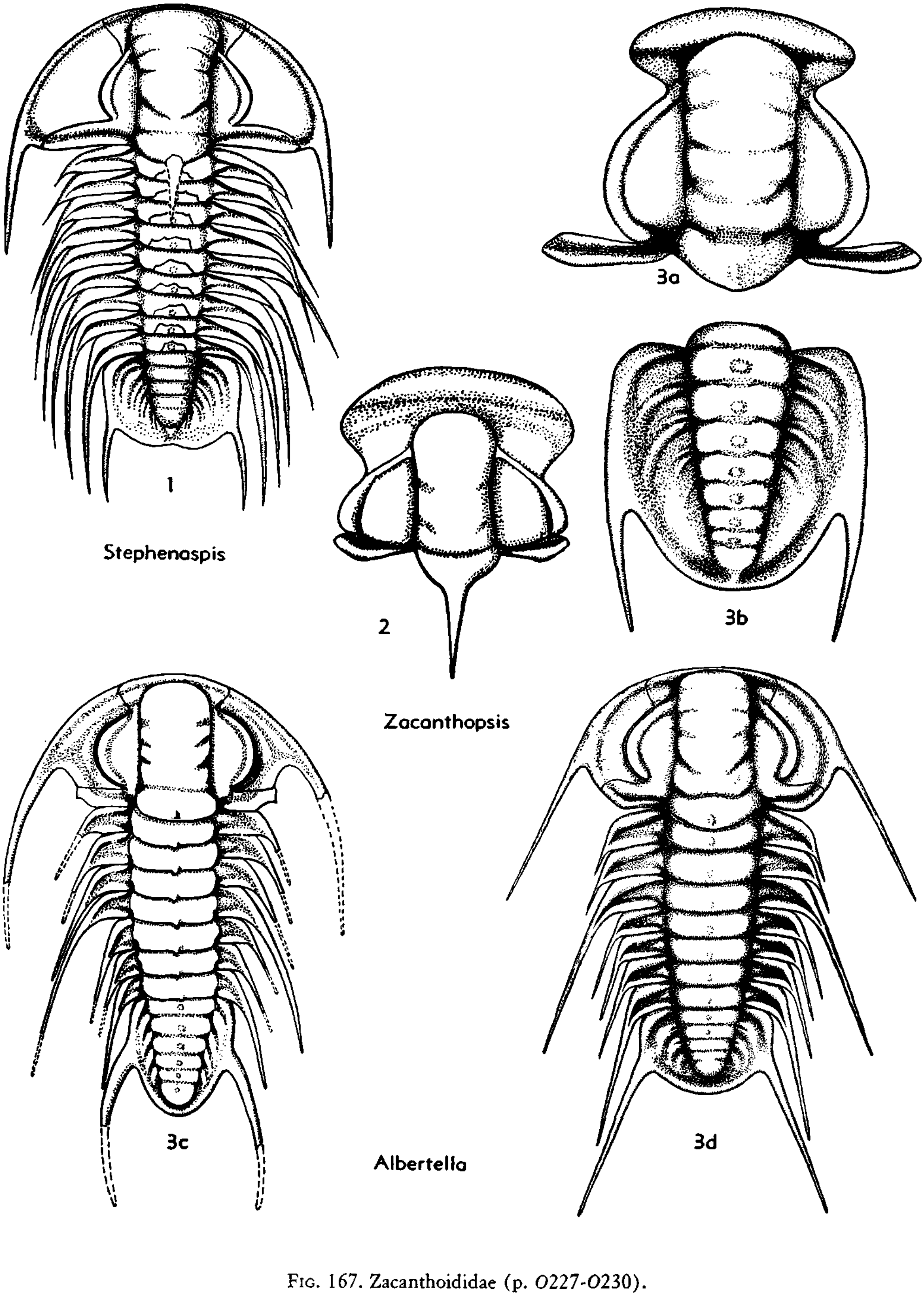


Fig. 167. Zacanthoididae (p. O227-O230).

Stephenaspis RASETTI, 1951 [**S. bispinosa*]. Cephalon as in *Fieldaspis*. Thorax of 9 segments, with axial spines. Pygidium subrectangular, with median notch and pair of marginal spines. *M.Cam.*, N.Am.——FIG. 167,*1*. **S. bispinosa*, W.Can.(B.C.); exoskel., ×1 (448n).

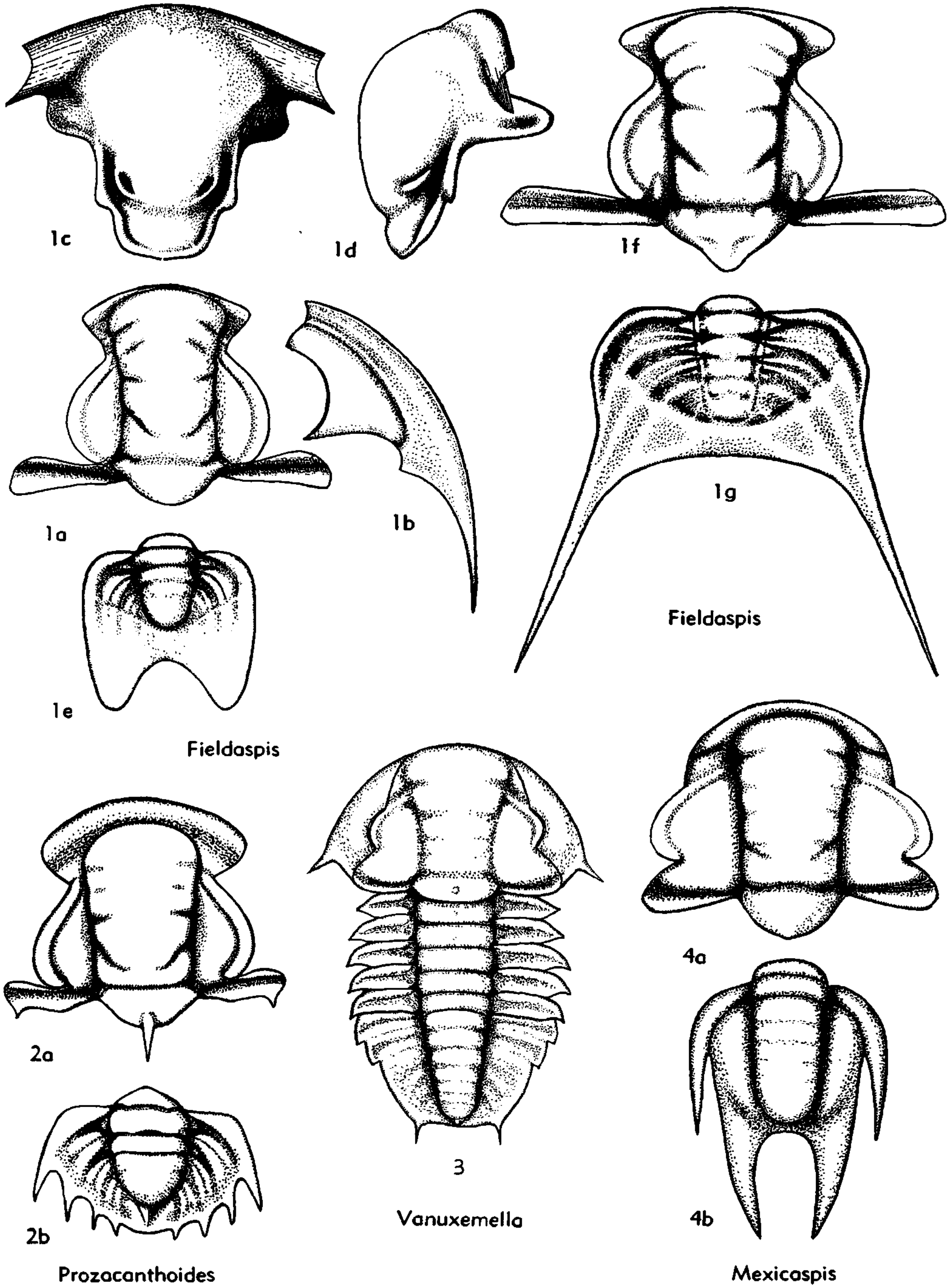


FIG. 168. Zacanthoididae (p. O227-O230).

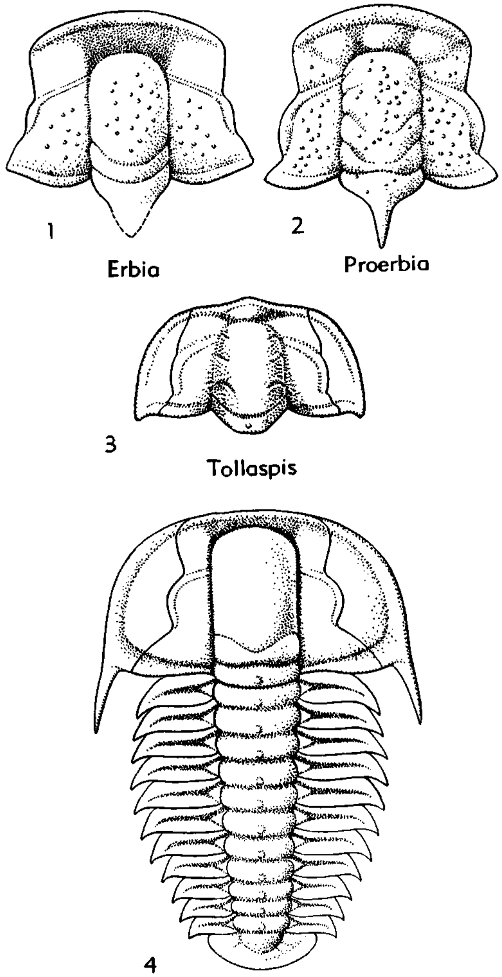


FIG. 169. Dinesidae (p. O230-O231).

Vanuxemella WALCOTT, 1916 [**V. contracta*] [=*Vistoia* WALCOTT, 1925]. Glabella expanded forward; axial and glabellar furrows shallow; palpebral lobes short; genal spines small; anterior border obsolete; librigenae narrow. Thorax of 4 or 5 segments; pleurae bluntly terminated. Pygidium trapezoidal; axis long, prominent; first 2 or 3 pleural segments less fused and extended into lateral spines; a pair of posterior marginal spines; size small. *M.Cam.*, N.Am.——FIG. 168,*3*. *V. nortia* WALCOTT, W.Can.(B.C.); exoskel., ×2 (448n).

Zacanthopsis RESSER, 1938 [**Olenoides levis* WALCOTT, 1886]. Differs from *Prozacanthoides* in shorter palpebral lobes, greater development of fixigenae in front of eyes, and posterior areas not extending much beyond palpebral lobes; frontal area concave. *L.Cam.*, N.Am.——FIG. 167,*2*. *Z. virginica* RESSER, Va.; cran., ×2 (448n).

Family DINESIDAE Lermontova, 1940

[=Tollaspidae KOBAYASHI, 1943; Proerbiidae HUPÉ, 1953; also Dinesidae HUPÉ, 1953, introduced as new family, evidently without knowledge of LERMONTOVA's prior publication]

Exoskeleton opisthoparian, elliptical, micropygous. Glabella hemicylindrical, front rounded, with 4 or fewer pairs of lateral furrows; eye ridges narrow but distinct, palpebral rim and furrow present, occipital spine present or absent; preglabellar field crossed by pair of furrows running diagonally outward from anterior corners of glabella, anterior border furrow narrow and curved, anterior border narrow; eyes of medium size, position variable; fixigenae very convex, horizontal, palpebral areas, about 0.75 of glabellar width, posterior area triangular, as long *(tr.)* or longer than occipital ring; librigenae quadrangular, with rounded genal angle or rather short genal spine. Thorax with 11 to 13 segments; axis wide, convex, with lateral nodes; pleurae about same in width *(tr.)*, flat, with short curved spine at end and broad deep pleural furrow. Pygidium very small, transverse; axis wide, convex broadly rounded, 0.5 of length, may have 1 axial ring and terminal; pleural fields low, narrower, 1 or 2 pleurae may show faintly, without border furrow, border ill defined, narrow. Outer surface granular. *Up.L.Cam.-Low.M.Cam.*

Dinesus ETHERIDGE, JR., 1896 [**D. ida*]. Glabella with single pair of posterior lateral furrows curved back to occipital furrow to produce basal lobes, with occipital node or small spine; preglabellar field very narrow; eyes of medium size, opposite center of glabella; fixigenae with palpebral areas more than 0.5 of glabellar width, posterior areas same length *(tr.)* as occipital ring. Thorax of 11 segments with short median axial spines or nodes. Pygidium narrowly transverse; axis semicircular, with poorly defined axial furrow; all pleural furrows obsolete (97, 340). *Low.M.Cam.*, Austral.——FIG. 169,*4*. **D. ida*, NW. Queensl.; exoskel., ×1 (411).

Erbia LERMONTOVA, 1940 [**Cyphaspis sibirica* SCHMIDT, 1886] [=*Paratollaspis* KOBAYASHI, 1943 (obj.)]. Glabella convex to globose, with single pair of deep posterior lateral furrows curved posteriorly, may touch occipital furrow to form basal lobes, with stout broad-based occipital spine; preglabellar field of variable width, depressed; eyes below medium size, near center of glabella; fixigenae with palpebral areas 0.75 of glabellar width, posterior areas longer *(tr.)* than occipital ring; librigenae with short genal spine. Thorax with 11 to 13 segments. Pygidium narrow-transverse; axis short and wide, with 1 or 2 poorly defined axial rings; pleurae 1 or 2, poorly defined (117). *Low. M.Cam.*, Sib.——Fig. 169,*1*. **E. sibirica* (Schmidt), near Krasnoyarsk; cran., ×2 (411).

Proerbia Lermontova, 1940 [**P. prisca*]. Glabella strongly convex, with 4 pairs of lateral furrows, anterior 2 pairs short, faint, diagonal forward, posterior 2 pairs strong, curved backward, last pair may touch occipital furrow, with occipital spine; preglabellar field of medium width, divided longitudinally by 2 additional furrows into 3 oval convex areas; eyes slightly above medium size, located a little behind center of glabella; fixigenae with palpebral areas slightly less than glabellar width, posterior areas same length *(tr.)* as occipital ring. Librigenae, thorax, and pygidium unknown. Surface coarsely granular (117). *Up. L.Cam.*, Sib.——Fig. 169,*2*. **P. prisca*, Lower course of River Lena; cran., ×3 (411).

Tollaspis Kobayashi, 1943 [**Anomocare pawlowskii* Schmidt, 1886]. Glabella strongly convex, subparallel-sided, with 3 pairs of lateral furrows, anterior 2 pairs very faint and short, posterior pair deeper, curved back to occipital furrow, occipital node present; preglabellar field of medium width, anterior margin broadly pointed; eyes of medium size, posterior to center of glabella; fixigenae with palpebral areas about 0.7 of glabellar width, posterior areas 0.7 of length *(tr.)* of occipital ring; librigenae with rounded genal angle. Thorax and pygidium unknown (102). *Low.M.Cam.*, Sib.——Fig. 169,*3*. **T. pawlowskii* (Schmidt), mouth of Little Batobiji on Wiliu River; ceph., ?×1 (419).

Order PTYCHOPARIIDA Swinnerton, 1915

[*nom. correct.* Henningsmoen, herein (*ex* Ptychoparina Swinnerton, 1915] [=Opisthoparia Beecher, 1897 *(partim)* + Hypoparia Beecher, 1897 *(partim)*; Conocoryphida Swinnerton, 1915 + Trinucleida Swinnerton, 1915] [Type—*Ptychoparia* Hawle & Corda, 1847]

A large order of trilobites having more than 3 thoracic segments. A few are proparian (some Ptychopariina) and some modified forms have marginal or submarginal sutures (some Ptychopariina, most Harpina and Trinucleina), but a large majority are opisthoparian. The glabella is primarily of simple, generalized type, tapering forward, and glabellar furrows, if present (many Ptychopariina) are commonly simple, subparallel linear depressions. In some modified forms, the glabella deviates in shape (Illaenina, Harpina, Trinucleina, most Asaphina, some Ptychopariina), and the different pairs of lateral glabellar furrows, if present, are more or less dissimilar. A preglabellar field commonly is present but may be secondarily reduced. A rostral plate and connective sutures are present or absent; if a rostral plate is lacking (modified forms), the librigenae are either separated by a median suture or fused together (Asaphina, Harpina, Trinucleina, some Ptychopariina). The hypostoma is separated from the cephalon by a hypostomal suture or uncalcified membrane. Most early forms have a relatively large thorax and small pygidium (e.g., *Alokistocare*), whereas later forms especially have fewer thoracic segments and a large pygidium (e.g., *Asaphus*).

Early representatives of the Ptychopariida resemble Redlichiina, but many of these latter have eye lobes that are longer or less separated from the eye ridges, or they are characterized by a glabella that expands forward. The Corynexochida differ from the Ptychopariida in having the hypostoma fused with the rostral plate; also, many of the Corynexochida differ from contemporaneous Cambrian Ptychopariida in having more divergent lateral glabellar furrows, and in having a glabella that expands forward. The Lichida and Odontopleurida differ from the Ptychopariida, among various features, in their peculiar types of glabella and glabellar furrows. Among the Phacopida, early forms, especially of Calymenina, resemble the Ptychopariida, but most differ in the pattern of the glabellar furrows and are predominantly proparian or gonatoparian.

The Ptychopariida seem to be closely related to the Redlichiina, and probably gave rise to most or all post-Cambrian trilobite groups (except, of course, post-Cambrian agnostids). *L.Cam.-M.Perm.*

Suborder PTYCHOPARIINA Richter, 1933

[Includes Olenina Swinnerton, 1915 *(partim)*; Conocoryphina Swinnerton, 1915; Ptychoparina Swinnerton, 1915 *(partim)*] [Type—*Ptychoparia* Hawle & Corda, 1847]

Exoskeleton typically with the following combination of characters; (1) simple, generalized glabella tapering forward; (2) simple, commonly subparallel lateral glabellar furrows (if present); (3) opisthoparian facial sutures; (4) preglabellar field; (5) relatively large thorax; and (6) small pygidium.

In some more or less specialized, derived, or advanced forms, one or more of these characters may differ from the norm. For example, shape of glabella is subrectangular in some Saukiidae; one or more lateral glabellar furrows are sigmoidal or bifurcate in Hypermecaspididae and some Olenidae; only longitudinal glabellar furrows are present in the Telephinidae; some Ptychopariina have proparian sutures (Norwoodiidae, Burlingiidae, some olenids and others), and some blind forms have marginal facial sutures or none at all (some Conocoryphidae); the preglabellar field is missing within various groups; and several genera included in the suborder have a relatively short thorax and large pygidium (e.g., Dikelocephalidae, Anomocaridae, Asaphiscidae).

No members of the Ptychopariina are known to have; (1) a glabella with concave sides, narrowest toward the rear; (2) a mesial glabellar node well in front of occipital furrow; or (3) a cephalic fringe (as in harpids and trinucleids). *L.Cam.-U.Ord.*

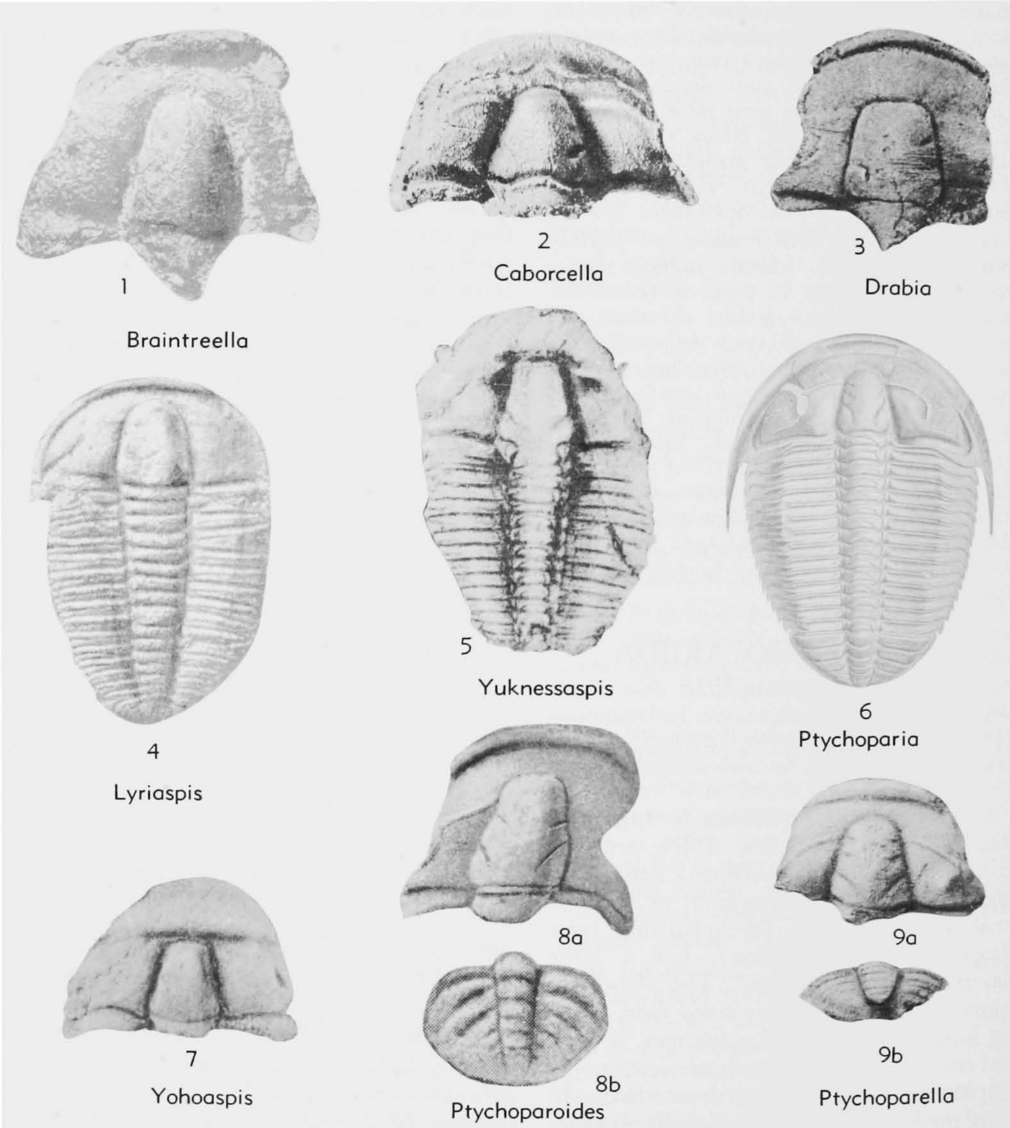


FIG. 170. Ptychopariidae (Ptychopariinae) (p. O233, O234).

Superfamily PTYCHOPARIACEA Matthew, 1887

[*nom. transl. et correct.* RASETTI, 1954 (*ex* Ptychoparidae MATTHEW, 1887)] [=Ptychopariidea RICHTER, 1933 (*partim*); Ptychoparioidae RASETTI, 1951 (*partim*); Ptychoparioidae HUPÉ, 1953 (attributed to RICHTER, 1933)]

Exoskeleton elongate oval, opisthoparian, with relatively large thorax and small pygidium. Cephalon semicircular, with well-defined border, glabella tapering forward, generally with 3 or 4 pairs of more or less distinct lateral glabellar furrows, with rounded or truncate front separated from border by a short to relatively long *(sag.)*, moderately convex to flat (or rarely concave) preglabellar field; facial sutures converging or diverging in front of eyes, eye ridges commonly present; librigenae commonly with genal spines of short to medium length. Thorax composed of 12 to 17 segments; axis moderately convex, sharply defined; pleurae nearly flat, with distinct grooves. Pygidium with few segments, lacking border. Surface generally smooth. *L.Cam.-L.Ord.*

Family PTYCHOPARIIDAE Matthew, 1887

[*nom. correct.* RICHTER, 1933 (*pro* Ptychoparidae MATTHEW, 1887)]

Dorsal exoskeleton elongate oval, opisthoparian, with relatively large thorax and small pygidium. Cephalon semicircular, with well-defined convex border; glabella tapering forward, generally with 3 or 4 pairs of distinct lateral furrows, with rounded or truncate front separated from border by a short, moderately convex to flat (or rarely concave) preglabellar field; facial sutures diverging in front of eyes; eye ridges commonly present; librigenae commonly with genal spines of short to medium length. Thorax composed of 12 to 17 segments; axis moderately convex, sharply defined; pleurae nearly flat, with distinct grooves. Pygidium with few segments, lacking border. Surface generally smooth. *L. Cam.-L.Ord.*

Subfamily PTYCHOPARIINAE Matthew, 1887

[*nom. correct.* WESTERGÅRD, 1950 (*ex* Ptychoparinae MATTHEW, 1887)]

Preglabellar area rather flat or somewhat concave, medium in length and width; glabella usually somewhat tapering, with or without glabellar furrows. Pygidium small. *M.Cam.-U.Cam.*

Ptychoparia HAWLE & CORDA, 1847 [**Conocephalus striatus* EMMRICH, 1839; SD WALCOTT, 1884]. Preglabellar area with radiating striae; 4 glabellar furrows. Pygidium half as long and half as wide as cranidium, with 5 segments. *M.Cam.*, Boh.——FIG. 170,*6*. **P. striata* (EMMRICH), Jince F.; exoskel., ×0.6 (3*).

Braintreella WHEELER, 1942 [**Ptychoparia rogersi* WALCOTT, 1884]. Cranidium subquadrate, with straight front margin and well-developed anterior border; glabellar furrows faint; short occipital spine. *M.Cam.*, Mass.——FIG. 170,*1*. **B. rogersi* (WALCOTT), Braintree F.; cran., ×2.7 (492*).

Caborcella LOCHMAN, 1948 [**C. arrojosensis*]. Cranidium short, wider than long; glabella broadly tapering, with rounded front and 3 pairs of furrows; anterior border furrow broad, with a low median rise; border upturned; curved eye ridges prominent; palpebral lobes small. *M.Cam.*, Sonora.——FIG. 170,*2*. **C. arrojosensis*, Los Arrojos F.; cran., ×3 (128*).

Drabia WILSON, 1951 [**D. acroccipita*]. Cranidium small; fixigenae wide; border narrow. *U.Cam.*, Pa.——FIG. 170,*3*. **D. acroccipita*, Ore Hill F.; cran., ×6.5 (363*).

Lyriaspis WHITEHOUSE, 1939 [**L. sigillum*]. Glabella bearing 2 pairs of short furrows; fixigenae wide; palpebral lobes small; eye ridges narrow; preglabellar area convex; anterior border narrow and convex. Thorax with 13 or 14 segments. Pygidium small, with prominent axis, 3 pleural furrows, border narrow or lacking. *M.Cam.*, Queensl.——FIG. 170,*4*. **L. sigillum*, Dinesus Stage; exoskel., ×2.5 (340*).

Ptychoparella POULSEN, 1927 [**P. brevicauda*]. Cranidium like that of *Ptychoparia* but pygidium very short, with well-developed border and very short axis containing only 4 segments. *M.Cam.*, Greenl.——FIG. 170,*9*. **P. brevicauda*, Cape Frederick VII F.; *9a*, cran., ×2; *9b*, pyg., ×3.5 (172*).

Ptychoparoides RŮŽIČKA, 1939 [**P. nobilis*]. Cranidium like that of *Ptychoparia* but more elongate and lacking striae on preglabellar area. *M.Cam.*, Boh.——FIG. 170,*8*. **P. nobilis*, Orthis Ss.; *8a,b*, cran., pyg., ×1.5 (264*).

Yohoaspis RASETTI, 1951 [**Y. pachycephala*]. Glabella strongly convex, with indistinct furrows; frontal area consisting of border only, border furrow running into axial furrows in front of glabella; palpebral lobes narrow, moderately long, set off by palpebral furrows; eye ridges poorly developed; fixigenae very convex. *M.Cam.*, B.C.——FIG. 170,*7*. **Y. pachycephala*, Cathedral F.; cran., ×1 (197*).

Yuknessaspis RASETTI, 1951 [**Y. paradoxa*]. Glabella moderately convex, sharply truncate in front; axial furrows very deep at sides; preglabellar area as wide *(sag.)* as glabella, with narrow anterior border and covered with longitudinal striae; palpe-

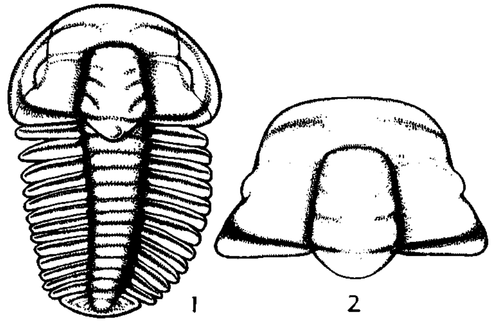


FIG. 171. Ptychopariidae (Antagminae). *1, Syspacephalus gregarius* RASETTI, M.Cam., W.Can.(B.C.); exoskel., ×5 (448n). *2. *S. charops* (WALCOTT), L.Cam., W.Can.(B.C.); cran., ×6 (448n).

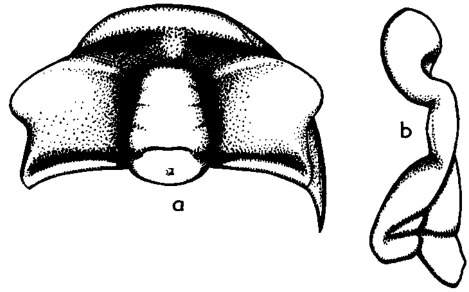


FIG. 172. **Periommella yorkensis* RESSER (Ptychopariidae, Periommellinae), L.Cam., Que.; *a,b,* ceph., ×6 (448n).

bral lobes short and narrow; eye ridges prominent. Thorax with at least 14 segments. *M.Cam.,* B.C. ——FIG. 170,*5*. **Y. paradoxa,* Stephen F.; exoskel., ×1.5 (197*).

?**Agraulopsis** RŮŽIČKA, 1940 [**A. resseri*]. Cephalon moderately convex with weak anterior border furrow; glabella elongate, tapering, truncate at front; eyes small, submedian; anterior and posterior sections of facial sutures divergent. *M.Cam.,* Boh.——FIG. 406,*5*. **A. resseri;* cran., ×2 (293) (HE).

Subfamily PERIOMMELLINAE Rasetti, 1955

Ptychopariidae with very wide palpebral area; margin of fixigenae downturned, placing small palpebral lobes in subventral position; posterior area of fixigenae deeply furrowed, not extending laterally beyond palpebral lobes. *L.Cam.*

Periommella RESSER, 1938 [**P. yorkensis*]. Glabella tapered, truncate in front, faintly furrowed; preglabellar field may have median boss; border convex; eye ridges directed forward from glabella; palpebral area twice as wide as glabella; border furrow on posterior areas not reaching cranidial margin; librigenae narrow, with genal spines. *L. Cam.,* N.Am.——FIG. 172. **P. yorkensis,* Que.; *a,b,* ceph., ×6, ×9 (448n).

Subfamily EULOMINAE Kobayashi, 1955

Late Ptychopariidae mainly characterized by deep glabellar furrows merging with the axial furrows, curving backward, posterior pair almost isolating basal lobes; eyes large to small; anterior border present; border furrow in most species with series of pits. Thorax of 13 segments, where known. Pygidium small, transverse, of generalized ptychopariid type. *L.Ord.*

Euloma ANGELIN, 1854 [**E. laeve* ANGELIN; SD VOGDES, 1925] [=*Calymenopsis* BERGERON, 1895]. Glabella about 0.7 of cranidial length, defined by deep axial furrows, with at least 2 pairs of deep lateral glabellar furrows; occipital furrow deep, occipital ring simple; eye ridges broad, poorly defined; palpebral lobes large (in type species) to medium *(E. monile),* semicircular; palpebral furrows deep; anterior sections of facial sutures slightly divergent; anterior border furrow with row of pits; posterior area slender, extending laterally well beyond palpebral lobes. Thorax of 13 segments *(E. monile). L.Ord.,* Eu.——FIG. 173,*1*. **E. laeve,* Swed.; *1a,* cran., ×2.5; *1b,* pyg., ×2.5 (299).

Pareuloma RASETTI, 1954 [**P. brachymetopa*]. Glabella narrow, almost parallel-sided, only half of cranidial length; axial furrows very deep laterally, shallow anteriorly; preglabellar field with median boss; eyes small, opposite anterior end of glabella; posterior areas of fixigenae large, broadly triangular, deeply furrowed. *L.Ord.,* N.Am.——FIG. 173,2. **P. brachymetopa,* Que.; cran., ×5 (448n).

Subfamily NASSOVIINAE Howell, 1937

[*nom. correct.* HOWELL, herein (*ex* Nassovinae HOWELL, 1937)]

Glabella with faint furrows or none at all, palpebral lobes small, frontal area rather narrow, more or less convex, fixigenae narrow or moderate in width. *M.Cam.*

Nassovia HOWELL, 1937 [**Liostracus globiceps* GRÖNWALL, 1902]. Preglabellar area rather large, border almost flat; eye ridges strongly developed. *M.Cam.,* Denm.——FIG. 174,*3*. **N. globiceps* (GRÖNWALL), Paradoxides davidis Z.; cran., ×2 (402*).

Brunswickia HOWELL, 1937 [**Conocephalites robbi* HARTT in DAWSON, 1868]. Preglabellar area of moderate size, border of cranidium low; fixigenae of moderate width; eye ridges not strongly developed; glabella subquadrate. *M.Cam.,* E.Can.(N.B.). ——FIG. 174,*1*. **B. robbi* (HARTT), Fossil Brook F.; exoskel., ×1.8 (429*).

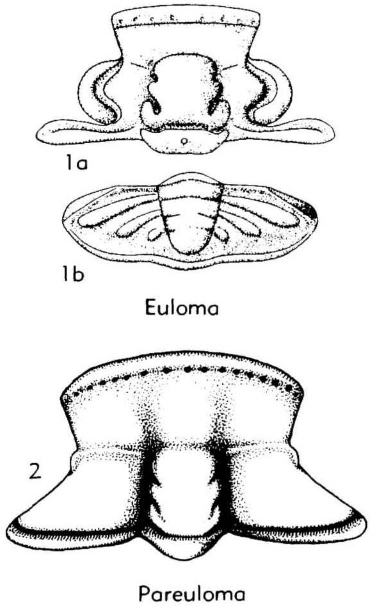


FIG. 173. Ptychopariidae (Eulominae) (p. O234).

Champlainia HOWELL, 1937 [**C. rectimargo*]. Glabella extending almost to convex border, front of which is straight, eye ridges poorly developed. *M.Cam.*, Vt.——FIG. 174,*4*. **C. rectimargo*, St. Albans F.; cran., ×6.7 (410*).

Vermontella HOWELL, 1937 [**V. clarae*]. Cranidium and glabella tapering forward; eye ridges poorly developed, border slightly convex and tilted upward. *M.Cam.*, Vt.——FIG. 174,*2*. **V. clarae*, St. Albans F.; *2a,b*, cran., librigena, ×3.8 (410*).

Subfamily ANTAGMINAE Hupé, 1953

[*nom. transl.* RASETTI, 1955 (*ex* Antagmidae HUPÉ, 1953)]

Generalized ptychopariids, usually of small size. Cephalon with all parts clearly defined; glabella tapering forward, rounded or truncate in front, with up to 4 pairs of furrows; occipital ring usually with node, never extended into spine; fixigenae from half to fully as wide as glabella, eye ridges distinct, palpebral lobes small or medium-sized, nearly opposite glabellar midpoint; frontal area usually divided into preglabellar field and border; border furrow with tendency to develop a median inbend; posterior border furrow invariably deep. Thorax of about 15 segments; pleurae rounded distally. Pygidium small, transverse. Surface generally granulated. [Includes earliest members of the superfamily. The genera intergrade and are difficult to characterize.] *L.Cam.-Low.M.Cam.*

Antagmus RESSER, 1936 [**A. typicalis* (=*Ptychoparia teucer* WALCOTT, 1887, *non* BILLINGS, 1861)]. Glabella convex; palpebral areas convex, on average horizontal, 0.5 to 0.7 times as wide as glabella at mid-length; palpebral lobes 0.25 to 0.3 as long as glabella, slightly behind glabellar mid-length; anterior border furrow with median inbend; anterior sections of facial sutures slightly divergent; posterior areas of fixigenae relatively slender, as wide *(tr.)* as occipital ring. *L.Cam.*, N. Am.——FIG. 175,*1*. *A. gigas* RASETTI, Que.; cran., ×1.5 (448n).

Austinvillia RESSER, 1938 [**A. virginica*]. Differs from *Antagmus* in shallower glabellar and axial furrows and almost obsolete, regularly curved border furrow delimiting long *(sag.)*, flat border from short *(sag.)* preglabellar field. *L.Cam.*, N. Am.——FIG. 175,*2*. **A. virginica*, Que.; cran., ×2 (448n).

Bicella RASETTI, 1955 [**Austinvillia bicensis* RESSER, 1938]. Glabella truncate in front; axial furrows deep; eye ridges wide; palpebral lobes convex, prominent; palpebral areas less than half as wide as glabella; anterior areas of fixigenae convex, divided by border furrow; border long *(sag.)*; anterior sections of facial sutures slightly convergent; posterior areas of fixigenae with deep

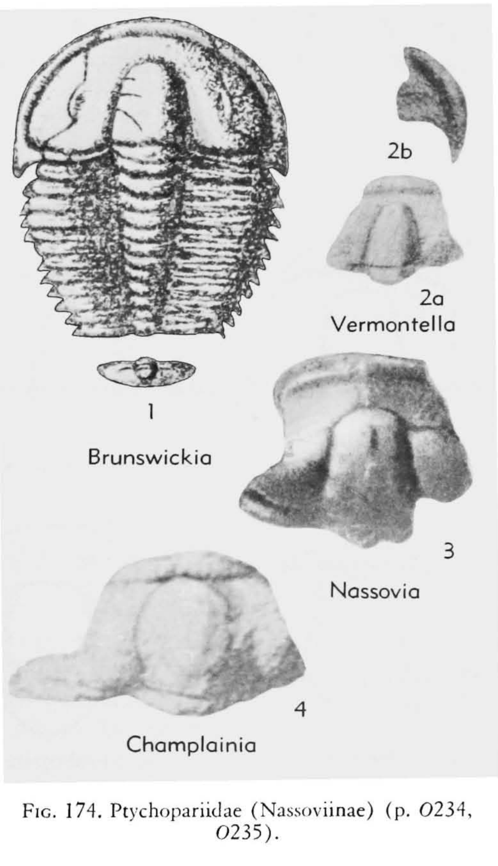


FIG. 174. Ptychopariidae (Nassoviinae) (p. O234, O235).

border furrows not reaching cranidial margin. *L.Cam.*, N.Am.——FIG. 175,*3*. **B. bicensis* (RESSER), Que.; cran., ×2.5 (448n).

Crassifimbra LOCHMAN, 1947 [**Onchocephalus walcotti* RESSER, 1937]. Glabella low, delimited by shallow axial furrows; palpebral areas narrow; eyes opposite glabellar mid-length; border furrow with median inbend; posterior areas of fixigenae narrower *(tr.)* than occipital ring. *L.Cam.*, N.Am. ——FIG. 175,*4*. **C. walcotti* (RESSER), Nev.; cran., ×8 (448n).

Eoptychoparia RASETTI, 1955 [**E. normalis*]. Similar to *Antagmus*, with anterior border furrow regularly curved. *L.Cam.*, N.Am.——FIG. 175,*5*. **E. normalis*, Que.; cran., ×3 (448n).

Luxella RASETTI, 1955 [**Ptychoparia lux* WALCOTT, 1917]. Glabella low, almost merging with preglabellar field, occupying about half of crani-

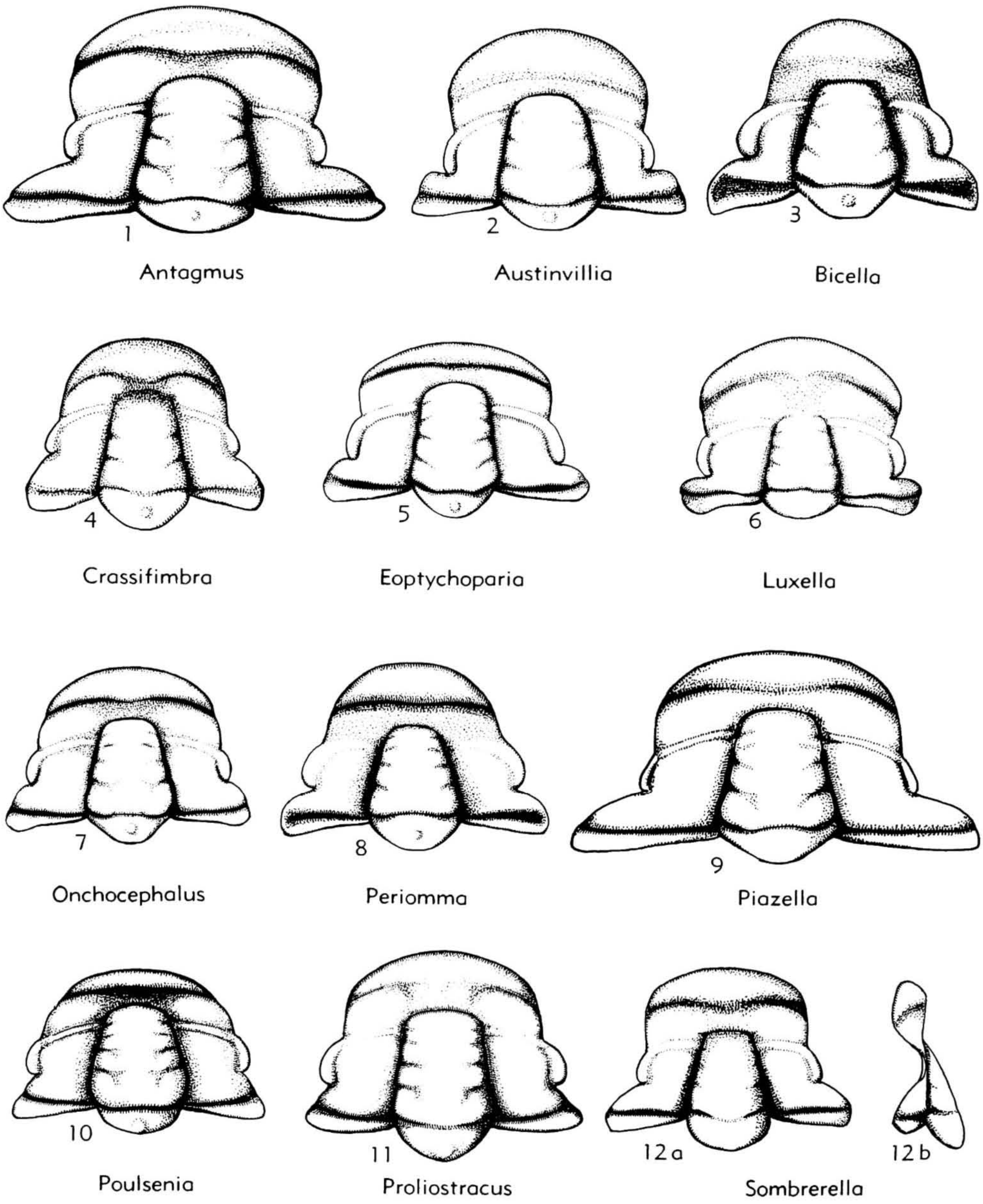


FIG. 175. Ptychopariidae (Antagminae) (p. O235-O237).

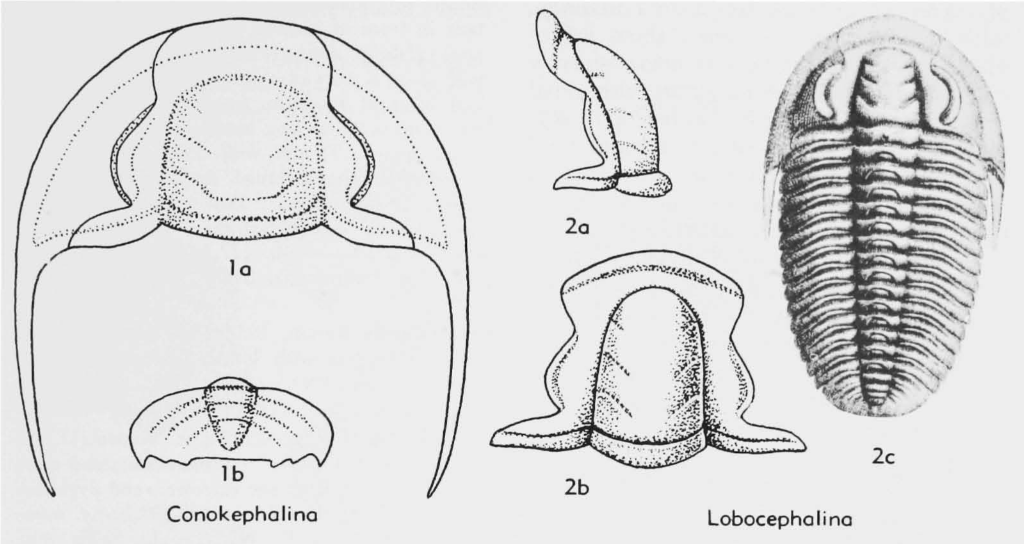


FIG. 176. Ptychopariidae (Conokephalininae) (p. O238).

dial length; palpebral areas wide; palpebral lobes relatively long; posterior areas of fixigenae short *(exsag.)*; anterior sections of facial sutures divergent. *L.Cam.*, N.Am.——FIG. 175,6. **L. lux* (WALCOTT), W.Can.(B.C.); cran., ×4 (448n).

Onchocephalus RESSER, 1937 [**Ptychoparia thia* WALCOTT, 1917]. Glabella low; eyes opposite glabellar mid-length, anterior sections of facial sutures parallel or slightly convergent; posterior areas of fixigenae as wide *(tr.)* as occipital ring. Intergrades with *Antagmus, Crassifimbra, Eoptychoparia* and *Proliostracus*. *L. Cam.-Low.M.Cam.*, N.Am.——FIG. 175,7. *O. sulcatus* RASETTI, L. Cam., Que.; cran., ×4 (448n).

Periomma RESSER, 1937 [**P. typicalis*]. Glabella strongly tapered; axial furrows deep; anterior border thick; preglabellar field commonly with median boss; palpebral areas wide, upsloping; palpebral lobes prominent; border furrow not reaching end of posterior areas of fixigenae. *L.Cam.*, N. Am.——FIG. 175,8. *P. walcotti* RESSER, Que.; cran., ×6 (448n).

Piaziella LOCHMAN, 1947 [**Ptychoparia pia* WALCOTT, 1917] Like *Antagmus*, with which it intergrades; glabella proportionately small, fixigenae wider. *L.Cam.*, N.Am.——FIG. 175,9. **P. pia* (WALCOTT), W.Can.(B.C.); cran., ×2 (448n).

Poulsenia RESSER, 1936 [**Solenopleura grönwalli* POULSEN, 1927]. Glabella convex; axial furrows deep; front border arched transversely; anterior sections of facial sutures slightly convergent. *L.Cam.*, Greenl.——FIG. 175,10. **P. groenwalli* (POULSEN). NW.Greenl.; cran., ×2.5 (172).

Proliostracus POULSEN, 1932 [**P. strenuelliformis*]. Glabella truncate in front; preglabellar field with faint median boss; palpebral lobes relatively long, opposite glabellar mid-length; anterior sections of facial sutures slightly convergent. *L.Cam.*, Greenl. ——FIG. 175,11. **P. strenuelliformis*, E.Greenl.; cran., ×6 (173).

Sombrerella LOCHMAN, 1948 [**S. mexicana*]. Glabella elevated posteriorly, low anteriorly, truncate in front; anterior border furrow with median inbend; palpebral lobes slightly in front of glabellar midlength. *L.Cam.*, N.Am.——FIG. 175,12. **S. mexicana*, Sonora; *12a,b*, cran., ×5 (128).

Syspacephalus RESSER, 1936 [**Agraulos charops* WALCOTT, 1917]. Glabella low, sloping down anteriorly; anterior border furrow more or less obsolete medially; palpebral lobes anterior to glabellar mid-point; anterior facial sutures convergent; genal angle rounded. Thorax of 13 to 15 segments. *L.Cam.-Low.M.Cam.*, N.Am.——FIG. 171,1. *S. gregarius* RASETTI, M.Cam. (Mt. Whyte F.), W.Can.(B.C.); exoskeleton slightly flattened, ×5 (448n).——FIG. 171,2. **S. charops* (WALCOTT), L.Cam., W.Can.(B.C.); cran., ×6 (448n).

Subfamily CONOKEPHALININAE Hupé, 1953

[*nom. transl.* LOCHMAN-BALK herein (*ex* Conokephalinidae HUPÉ, 1953) (not attributable to WALCOTT, 1913, on basis of "Conokephalinae," as published by him as a group designation without diagnosis or any indication of intent to introduce a family-group name)]

Exoskeleton opisthoparian, micropygous. Glabella tapering forward, truncate-rounded in front, with 2 or 3 pairs of well-defined, arcuate lateral furrows; faint eye ridges may be present; palpebral rims prominent, palpebral furrows deep, arcuate; preglabellar field of variable width, anterior border furrow well defined; eyes large, behind level of center of glabella, fixigenae horizontal, with arcuate palpebral areas, about 0.5 of glabellar width, posterior areas narrow *(exsag.)*; librigenae rectangular, with genal spine of medium length. Thorax of 14 segments; axis convex, about 0.5 of width *(tr.)* of pleurae; pleural furrows distinct, on front part of segments, ends rounded. Pygidium transverse; axis convex, tapering nearly full length, with 2 or 3 axial rings; 3 pleurae, interpleural grooves and border furrow very faint or obsolete, border narrow. Surface granulose. *M.Cam.-U.Cam.*

Conokephalina Brøgger, 1886 [**Conocephalites ornatus* Brøgger, 1878; SD Bassler, 1915]. Glabella low, front rounded or straight, with 3 pairs of lateral furrows; eyes behind glabellar midlength; fixigenae narrow anteriorly, posterior area narrow *(exsag.)*, 0.7 of length *(tr.)* of occipital ring. Pygidium narrow transverse; axis convex, equal to pleural field in width; interpleural grooves faint or obsolete, border furrow faint, posterior margin nearly straight; some bearing up to 3 pairs of very small spines. *M.Cam.-U.Cam.*, W.Eu.——Fig. 176,*1*. **C. ornatus* (Brøgger), *M.Cam.*, Norway; *1a,b*, ceph., pyg., ×1.3 (382).

Lobocephalina Růžička, 1940 [**Lobocephalus carinatus* Růžička, 1939] [=*Ružičkaia* Přibyl, 1950 (*pro Lobocephalus* Růžička, 1940, *non* Diesing, 1838, *nec* Kramer, 1898)]. Glabella moderately convex, tapering forward, front rounded, with 2 or 3 pairs of lateral furrows; eyes almost opposite posterior 0.3 of glabella; fixigenae of medium width anteriorly, posterior area narrow *(exsag.)*, equal in length *(tr.)* to occipital ring. Pygidium transverse; axis convex, as wide as pleural field; interpleural grooves obsolete, border furrow very faint or obsolete, posterior margin curved, without spines. *M.Cam.*, W.Eu.——Fig. 176,*2a,b*. **L. carinata* (Růžička), Czech.; cran., ×1.3 (464). ——Fig. 176,*2c*. *L. emmrichi* (Barrande), Czech.; exoskel., ×1.3 (370*).

Schoriella Sivov, 1955 [**S. schorica*]. *U.Cam.*, W. Sib. (276).

Family ALOKISTOCARIDAE Resser, 1939

Preglabellar area wide, glabella somewhat tapering, facial sutures rather deeply concave opposite glabella, eye ridges well developed, palpebral lobes small, genal spines of moderate length. Pygidium small. *L.Cam.-U.Cam.*

Alokistocare Lorenz, 1906 [**Ptychoparia subcoronatus* Hall & Whitfield, 1877] [=*Amecephalus* Walcott, 1924; *Strotocephalus* Resser, 1935]. Border of cranidium wide and flat except for low boss in front of glabella and shallow border furrow; glabella defined by strong axial furrows, with 2 or 3 pairs of short lateral furrows; palpebral lobes of moderate size, eye ridges crossing fixigenae; occipital ring bearing small node; librigenae spined. Thorax with 17 to 19 segments; axis narrow; pleurae broad, with well-defined furrows. Pygidium small; axis prominent, with 3 rings; pleural regions bearing 1 to 3 furrows. *M. Cam.*, W.USA.——Fig. 177,*1*. **A. subcoronatum* (Hall & Whitfield), Ute F., Utah.; cran., ×5 (488*).

Alokistocarella Resser, 1938 [**A. typicalis*]. Like *Alokistocare* but with border concave and narrower. *M.Cam.*, USA.——Fig. 178,*1*. *A. brighamensis* Resser, Utah; ×1.5 (457*).

Amecephalina Poulsen, 1927 [**A. mirabilis*]. Like *Alokistocare* but border concave, wider, and more bowed forward, fixigenae narrower, and pygidium larger. *M.Cam.*, Greenl.——Fig. 177,*2*. **A. mirabilis*, Cape Wood F., NW.Greenl.; *2a,b*, cran., pyg., ×3 (172*).

Annamitia Mansuy, 1916 [**Ptychoparia (Annamitia) spinifera*]. Like *Alokistocare*, but with narrower border, larger palpebral lobes, and occipital spine. *M.Cam.*, SE.Asia.——Fig. 177,*3*. **A. spinifera* (Mansuy), Indochina; exoskel., ×1.75 (142*).

Arellanella Lochman, 1948 [**A. caborcana*]. Three pairs of glabellar furrows, palpebral lobes small, axis of pygidium wide. *M.Cam.*, NW.Mex.——Fig. 177,*5*. **A. caborcana*, Los Arrojos F., Sonora; cran., ×2.6 (128*).

Bythicheilus Resser, 1939 [**B. typicum*]. Preglabellar area short, with medial depression; 14 thoracic segments; pygidium small. *M.Cam.*, NW.USA.——Fig. 177,*4*. **B. typicum*, Spence Sh., Idaho; exoskel., ×2.6 (457*).

Chancia Walcott, 1924 [**C. ebdome*]. Frontal area shorter and less bowed forward than in *Alokistocare*, palpebral lobes smaller; frontal area and pygidium wider than in *Alokistocare*. *M.Cam.*, NW.USA.——Fig. 179,*4*. **C. ebdome*, Spence Sh., Idaho; ×1 (320).

Chelidonocephalus King, 1937 [**C. alifrons*]. Anterior border of cephalon convex, glabella truncate, with very faint furrows, palpebral lobes large. *M.Cam.*, or *U.Cam.*, SW.Asia.——Fig. 179,*3*. **C. alifrons*, Iran; cran., ×3 (418).

Dunderbergia Walcott, 1924 [**Crepicephalus (Loganellus) nitidus* Hall & Whitfield, 1877]. Resembles *Alokistocare* but frontal area and glabella wider, fixigenae narrower; pygidium longer and rounder than in *Chancia*. *U.Cam.*, W.USA.-E.Sib. ——Fig. 179,*2*. **D. nitida* (Hall & Whitfield), Secret Canyon F., Nev.; *2a,b*, ×1 (320).

Ehmania Resser, 1935 [**E. weedi*]. Like *Ehmaniella* but with glabellar furrows shallower and surface smooth. *M.Cam.*, NW.USA.——Fig. 177,*6*.

**E. weedi*, Meagher Ls., Wyo.; exoskel., ×2.2 (488*).

Ehmaniella RESSER, 1937 [**Crepicephalus? (Loganella) quadrans* HALL & WHITFIELD, 1877] [=*Anomalocephalus, Clappaspis* DEISS, 1939]. Like *Ehmania* but with wider cranidium, heavier eye ridges, longitudinal striae on wider preglabellar area, commonly wtih tubercles on cranidium, and fewer segments in pygidium. *M.Cam.*, W.USA. ——FIG. 177,7. **E. quadrans* (HALL & WHIT-

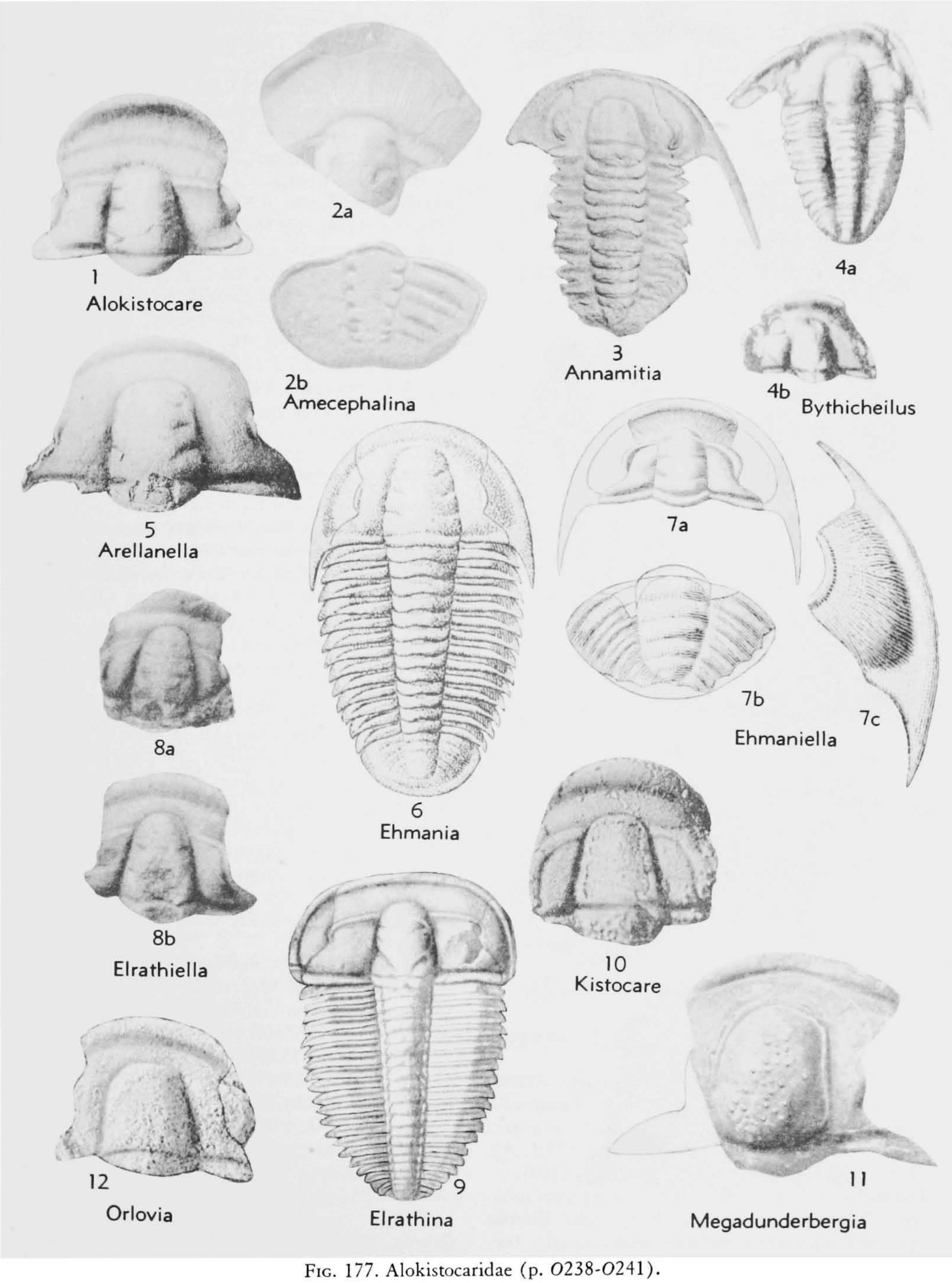


FIG. 177. Alokistocaridae (p. O238-O241).

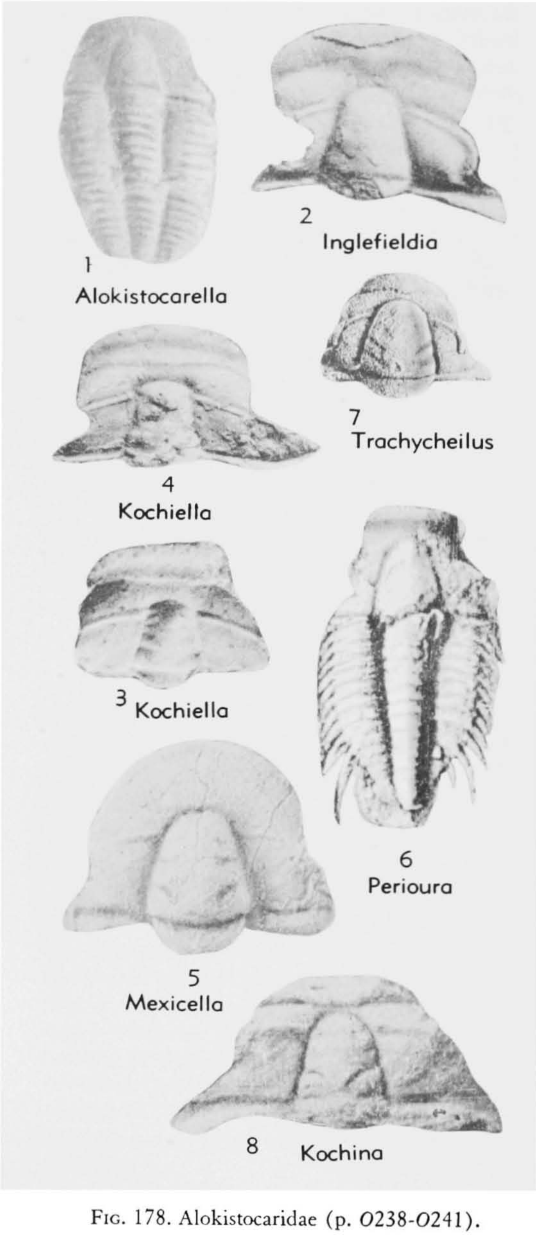


FIG. 178. Alokistocaridae (p. O238-O241).

FIELD), Ophir F., Utah; *7a-c,* ceph., librigena, pyg., enlarged (488*).

Elrathia WALCOTT, 1924 [**Conocoryphe (Conocephalites) kingii* MEEK, 1870]. Like *Ehmaniella,* but pygidium larger, with segmentation less well developed. *M.Cam.,* W.USA.——FIG. 179,*1.* **E. kingii* (MEEK), Wheeler F., Utah; ×1 (320).

Elrathiella POULSEN, 1927 [**E. obscura*] [=*Coelaspis, Glassocoryphus* DEISS, 1939]. Like *Elrathia* but with narrower cranidium, wider anterior border, longer and narrower glabella, and longer palpebral lobes. *M.Cam.,* Greenl.——FIG. 177,*8.* **E. obscura,* Pemmican River F.; *8a,b,* cranidia, ×2 (172*).

Elrathina RESSER, 1937 [**Conocephalites cordillerae* ROMINGER, 1887]. Like *Elrathia,* but with narrower border, more numerous thoracic segments, and smaller pygidium. *M.Cam.,* W.Can.——FIG. 177, *9.* **E. cordillerae* (ROMINGER), Stephen F., B.C.; exoskel., ×2.2 (319*).

Inglefieldia POULSEN, 1927 [**I. porosa*]. Like *Amecephalus* but with preglabellar area consisting of flat tract in front of glabella and with anterior border convex. *L.Cam.,* Greenl.——FIG. 178,*2.* **I. porosa,* Cape Kent F.; ×1.8 (172*).

Ithyektyphus SHAW, 1956 [**Marjumia? tetonensis* MILLER, 1936]. *Up.M.Cam.,* Wyo.

Kistocare LOCHMAN, 1948 [**K. corbini*]. Palpebral lobes beside posterior third of glabella, fixigenae nearly 0.7 of width of glabella, no trace of bulge or anterior border furrow on border. *M.Cam.,* NW. Mex.——FIG. 177,*10.* **K. corbini,* Los Arrojos F., Sonora; cran., ×7.2 (128*).

Kochiella POULSEN, 1927 [**K. tuberculata*]. Like *Chancia,* but with border concave and less flaring; scattered tubercles on cranidium. *L.Cam.-M.Cam.,* Greenl.——FIG. 178,*3.* **K. tuberculata,* Cape Kent F.; ×1.2 (172*).——FIG. 178,*4. K. propinqua* POULSEN, Cape Kent F.; ×1.2 (172*).

Kochina RESSER, 1935 [**Olenopsis americanus* WALCOTT, 1912]. Border narrower and palpebral lobes more anterior than in *Kochiella. M.Cam.,* NW. USA.——FIG. 178,*8.* **K. americana* (WALCOTT), Gordon F., Mont.; ×1 (488*).

?**Kounamkites** POLETAEVA & CHERNYSHEVA, 1956 [**K. virgatus* CHERNYSHEVA, 1956]. *Low.M.Cam.,* USSR. (MO).

Kujandaspis IVSHIN, 1956 [**K. kujandensis*]. Glabella short, tapered, truncate, 3 pairs of faint lateral furrows, anterior border and preglabellar field separated by a broad, deep, curved anterior border furrow, elliptical boss filling all of preglabellar field in front of glabella; eye ridges present, eyes of medium size, opposite center of glabella; fixigenae upsloping; palpebral area 0.5 of glabellar width, posterior area narrow, straplike. Fixigenae and pygidium unknown. Outer surface granulose. *U.Cam.,* SW.Sib.

Megadunderbergia KOBAYASHI, 1938 [**Ptychaspis pustulosa* HALL & WHITFIELD, 1877]. Like *Dunderbergia* but with cranidium more convex, palpebral lobes longer, and surface pustulose. *U.Cam.,* W.Can.——FIG. 177,*11. M. convexa* (KOBAYASHI), B.C.; cran., ×0.65 (419*).

Mexicella LOCHMAN, 1948 [**M. mexicana*]. Like *Alokistocare* but with smaller palpebral lobes, in front of mid-line of glabella, and with wider fixigenae. *M.Cam.,* NW.Mex.——FIG. 178,*5.* **M. mexicana,* Los Arroyos F., Sonora; cran., ×5 (128*).

Orlovia WALCOTT & RESSER, 1925 [**O. arctica*]. Without glabellar furrows, anterior border wide

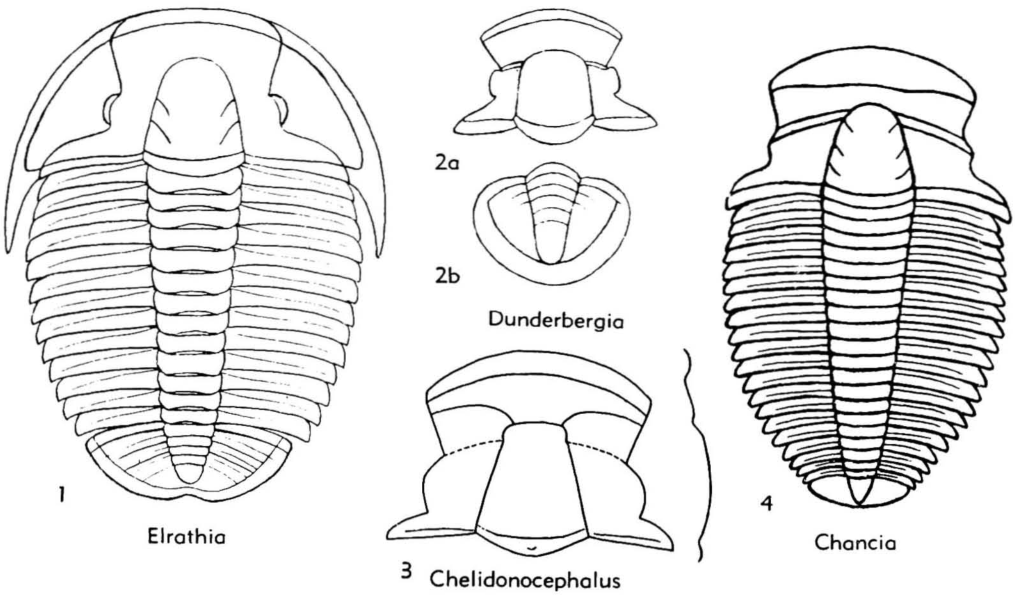


FIG. 179. Alokistocaridae (p. O238-O240).

and thickened, pygidium with a narrow, flattened border. *U.Cam.,* N.Russia.——FIG. 177,*12*. **O. arctica,* N.Zem.; cran., ×2.75 (322*).

Pachyaspis RESSER, 1939 [**P. typicalis*]. With 4 faint glabellar furrows, palpebral lobes small. *M.Cam.,* NW.USA.——FIG. 180,*2*. **P. typicalis,* Langston F., Idaho; cran., ×5 (457*).

Parehmania DEISS, 1939 [**P. princeps*] [=*Mcnairia, Rowia, Thompsonaspis* DEISS, 1939]. Like *Ehmania,* but with concave and wider border, upturned frontal area, more convex fixigenae, and stronger eye ridges, directed more nearly perpendicular to the axial furrow. *M.Cam.,* NW. USA.——FIG. 180,*1*. **P. princeps,* Pentagon F., Mont.; exoskel., ×3.8 (30*).

Perioura RESSER, 1938 [**P. typicalis*]. Differs from *Ehmania* in having ends of its 14 thoracic segments produced into spines and in having a longer and wider axis in pygidium. *M.Cam.,* SE.USA. ——FIG. 178,*6*. **P. typicalis,* Conasauga Sh., Ala.; exoskel., ×2.6 (457*).

Proveedoria LOCHMAN, 1948 [**P. starquistae*]. Like *Kochiella* but eyes relatively larger and glabella less broadly tapering. *M.Cam.,* NW.Mex.——FIG. 180,*4*. **P. starquistae,* Los Arroyos F., Sonora; cran., ×6.3 (128*).

Ptychoparopsis HUPÉ, 1953 [**P. issafenensis*]. Like *Alokistocare* but with front of cranidium more quadrate. *L.Cam.,* N.Afr.——FIG. 180,*3*. **P. issafenensis,* Morocco; ×1 (411*).

Trachycheilus RESSER, 1945 [**T. typicale*]. Like *Kochina* but with a much narrower preglabellar field. *M.Cam.,* SW.USA.——FIG. 178,*7*. **T. typicale,* Bright Angel or Muav beds, Ariz.; ×1 (457*).

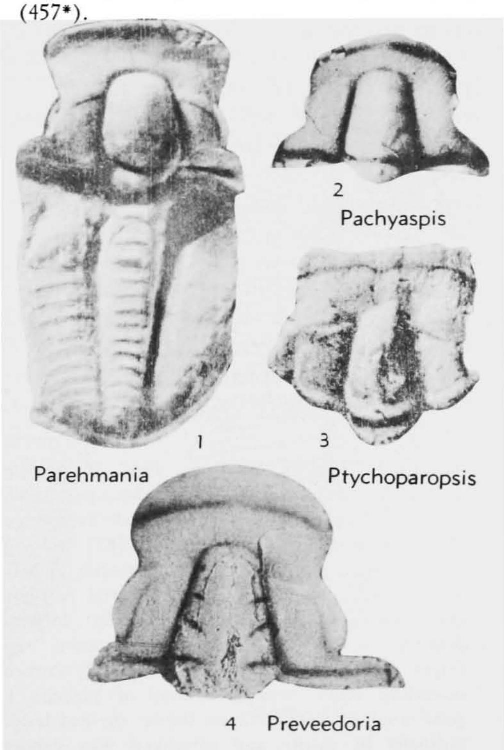


FIG. 180. Alokistocaridae (p. O241).

Superfamily CONOCORYPHACEA Angelin, 1854

[*nom. transl.* HENNINGSMOEN, 1951 (*ex* Conocoryphidae ANGELIN, 1854)] [HENNINGSMOEN's attribution of this superfamily name to SWINNERTON, 1915, is erroneous, inasmuch as neither SWINNERTON's "Suborder Conocoryphida" nor his "Section Conocoryphina" are definable as family-group taxa; rather, they are classifiable as belonging to the class/order category of taxa, which is entirely distinct nomenclaturally from the family-group (Copenhagen Decisions on Zoological Nomenclature, London, 1953). RCM.]

Dorsal exoskeleton very diminutive to medium in size, elongate oval in outline, mostly micropygous. Cephalon semicircular, to subtrapezoidal, with prominent glabella (except *Hartshillia*) defined by deep axial furrows, separated from anterior margin by narrow to wide preglabellar field, occipital ring generally distinct; eyes lacking; cephalic sutures at or near margins or lacking. Thorax with 6 to 25 or more segments. Pygidium with 1 to 8 axial rings. Postcephalic characters rather widely variable in different genera. *L.Cam.-U.Ord.*

Family CONOCORYPHIDAE Angelin, 1854

[=Campylopleuri BURMEISTER, 1843; Conocephalidae SALTER, 1864; Ptychopariidae MATTHEW, 1887 *(partim)*]

Ovate to elongate exoskeleton, micropygous to heteropygous. Cephalon, semicircular to trapezoidal, without eyes; glabella typically tapering forward, well defined; preglabellar field usually well developed, cephalic border narrow or lacking; ?facial sutures marginal or dividing lateral cephalic border longitudinally or trespassing on lateral border furrow. Thorax of 7 to 25 or more segments. Pygidium with 1 to 8 axial rings, posterolateral margin evenly curved, outer surface granulated, lined, or both. Hypostoma free in type genus and probably so in others of family; cephalic doublure and ventral sutures imperfectly known. *L.Cam.-L. Ord.(Tremadoc.).*

Conocoryphe HAWLE & CORDA, 1847 [**Trilobites sulzeri* SCHLOTHEIM, 1823; SD MILLER, 1889] [=*Conocephalus* ZENKER, 1833 (*non* THUNBERG, 1833); *Conocephalites* BARRANDE, 1852 (obj.)]. Exoskeleton ovate. Cephalon semicircular; glabella with 3 pairs of strongly oblique lateral furrows; axial furrows continued divergently forward defining low preglabellar lobate tract; eye ridges (when present) threadlike, evenly curved, extending from anterior corners of glabella to genal angles; lateral cephalic border divided longitudinally by suture and continued into slender, backward-directed genal spines. Thorax of 14 segments, with deeply furrowed pleurae and truncate extremities. Pygidium of about 6 to 8 segments, semicircular, with narrow, well-defined border (3, 233). *M.Cam.*, N.Am.(Atl.prov.), Eu.-Asia.——FIG. 181,*1*. **C. sulzeri* (SCHLOTHEIM), Czech.; *1a,b*, exoskel., hypostoma, ×1 (3).

Atops EMMONS, 1844 [**A. trilineatus*]. Differs from *Conocorpyhe* in having glabella extended to anterior border furrow, less oblique lateral furrows, shorter, less oblique eye ridges, suture trespassing on lateral border furrow. Thorax with 17 segments. Pygidium indistinctly segmented, with wide, rapidly tapering axis (75). *L.Cam.*, E.N.Am.-?Sp.——FIG. 181,*2*. **A. trilineatus*, N.Y.; exoskel., ×1 (488).

Bailiaspis RESSER, 1936 [**Conocephalites elegans* HARTT in DAWSON, 1868]. Differs from *Conocoryphe* in thickened anterior border in front of glabella, depressed preglabellar field without lobate tract; sutures cutting across lateral border at least to border furrow. Pygidium without border and with only 2 or 3 defined segments (337). *M.Cam.*, N.Am.(Atl.prov.)-Eu.——FIG. 181,*6*. *B. dalmani* (ANGELIN), Swed.; cran., ×1.5 (337).

Bailiella MATTHEW, 1885 [**Conocephalites baileyi* HARTT, 1868; SD RESSER, 1936] [=*Liocephalus* GRÖNWALL, 1902; ?*Tangshiella* HUPÉ, 1953]. Differs from *Bailiaspis* in having anterior border without median backward projection and pygidium with well-defined border (337). *M.Cam.*, N.Am. (Atl.prov.)-Eu.-N.Afr.-Asia.——FIG. 182. *B. emarginata* (LINNARSSON), Swed.; exoskel., partly restored, ×2 (337).

Cainatops MATTHEW, 1899 [**Conocoryphe pustulosa* MATTHEW, 1897]. Small forms with large glabella and wide cephalic border with median, forward-projecting spine (147). *M.Cam.*, N.Am.(Atl.prov.).

Couloumania THORAL, 1946 [**Conocoryphe heberti* MUNIER-CHALMAS & BERGERON, 1889]. Differs from *Bailiella* in having suture on lateral cephalic border like that of *Conocoryphe* (295). *M.Cam.*, Eu.-N. Afr.

Ctenocephalus HAWLE & CORDA, 1847 [**C. barrandei* (=*Conocephalus coronatus* BARRANDE, 1846)] [=*Harttella* MATTHEW, 1884]. Differs from *Conocoryphe* in semiglobular shape of preglabellar lobate tract reaching level of genae. Thorax of 15 segments. Pygidium very small, with extremely wide pleural fields, axis consisting of 1 or 2 rings and short terminal portion (3, 233, 337). *M.Cam.*, Eu.-N.Am.(Atl.prov.)-N.Afr.-E.Sib.——FIG. 181,*3*. **C. coronatus* (BARRANDE), Czech., exoskel., ×1 (3).

Dasometopus RESSER, 1936 [**Harpides breviceps* ANGELIN, 1854]. Cephalon approximately semicircular; glabella about half length of cephalon, with 2 or 3 pairs of lateral furrows, posterior pair recurved; genae moderately convex, separated from each other by considerable preglabellar depression; border and border furrow lacking, cephalic margin merely being upturned, forming wide, concave marginal zone; sutures apparently marginal or nearly so (233, 337). *M.Cam.*, Denm.-Swed.-E.Sib.——FIG. 181,*4*. **D. breviceps* (ANGELIN), Swed.; ceph. (?cran.), ×4 (337).

Elyx ANGELIN, 1854 [*pro Eryx* ANGELIN, 1851 (*non* DAUDIN, 1803; *nec* STEPHENS, 1832; *nec* SWAINSON, 1840)] [**Eryx laticeps* ANGELIN, 1851]. Differs from *Ctenocephalus* in trapezoidal cephalic outline, preglabellar lobate tract joining anterior border, and thoracic segments terminating

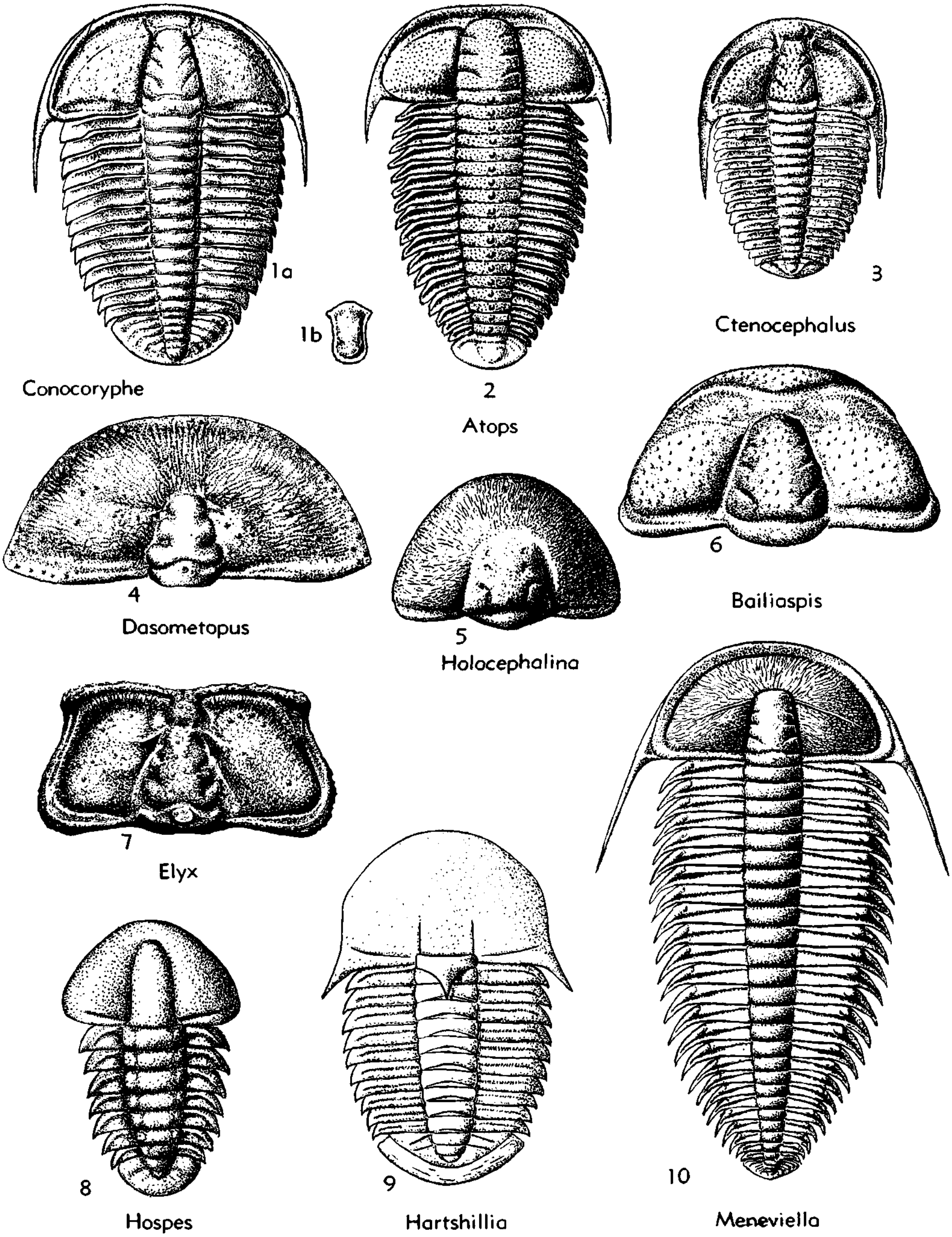


FIG. 181. Conocoryphidae (p. O242-O244).

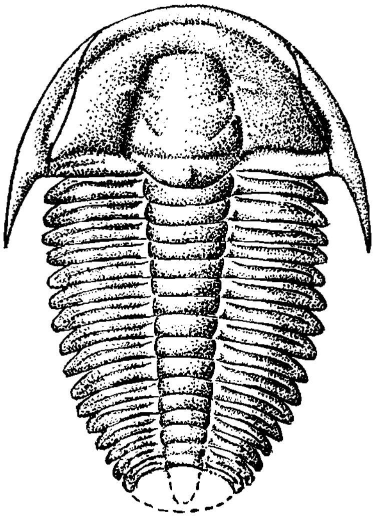


FIG. 182. *Bailiella emarginata* (LINNARSSON) (Conocoryphidae), M.Cam., Swed.; exoskel., ×2 (337).

in recurved pleural spines (337). *M.Cam.*, Scand.-E.N.Am.——FIG. 181,7. **E. laticeps* (ANGELIN), Swed.; ceph. (?cran.), ×2 (337).

Hartshillia ILLING, 1916 [**Holocephalina inflata* HICKS, 1872; SD VOGDES, 1925]. Broadly ovate, cephalon and thorax subequal in length, pygidium short. Cephalon evenly convex, almost semicircular, without border; glabella very little raised above genae, indistinctly defined in front, lateral furrows effaced and occipital ring with short, strong spine; preglabellar furrow and anterior portion of axial furrows obliterated; sutures apparently marginal; genal spines short, strong, somewhat outwardly directed. Thorax of 8 or more segments; axis a little narrower than pleural regions, fairly prominent; pleurae horizontal nearly to extremities, terminating in short backward-directed points. Pygidium very wide, with strongly tapering axis of 2 to 5 rings, and well-defined, wide, strongly sloping border (114). *M.Cam.*, Br.I.-E.N.Am.(Atl. prov.)-?N.Afr.——FIG. 181,9. **H. inflata* (HICKS), Br.I.; exoskel. (reconstr.), ×3 (446).

?**Hartshillina** LAKE, 1940 [**Hartshillia spinata* ILLING, 1916]. Differs from *Hartshillia* in lack of occipital and genal spines, and in having wider thoracic axis with median spines on axial rings, pleural regions of thorax and pygidium much narrower than axis, and pygidial segments probably terminating in spines (114). *M.Cam.*, Eng.

Holocephalina SALTER, 1864 [**H. primordialis*] [=*Carausia* HICKS, 1872]. General form ovate, thorax longer than cephalon, narrowing posteriorly to very small pygidium. Cephalon semielliptical, length exceeding half total width, evenly convex, with almost imperceptible anterior and lateral border furrows; glabella very little raised above genae, about half as long as cephalon and one-third as wide, rounded in front, with 3 pairs of usually obscure lateral furrows; preglabellar furrow and anterior part of axial furrows shallow; occipital furrow wide, well impressed; sutures practically marginal; genal spines strong, straight, extending backward to about 5th thoracic segment. Thorax of about 15 to 17 segments with prominent axis and obliquely truncated pleurae (114). *M.Cam.*, Br.I.-Denm.-E.N.Am.(Atl.prov.).——FIG. 181,5. *H. teres* (GRÖNWALL), Denm.; ceph. (?cran.), ×4 (51).

?**Hospes** STUBBLEFIELD, in STUBBLEFIELD & BULMAN, 1927 [**H. clonograpti*]. Ovate, very small. Cephalon relatively large, rounded triangular, without anterior and lateral borders; glabella convex, slender, narrowing anteriorly to a blunt termination, without lateral furrows, separated from anterior margin by short preglabellar field. Thorax of 7 segments with wide, convex axis, very narrow pleural regions, and strongly ridged pleurae terminating in backward-directed, falcate points. Pygidium small, convex, semielliptical, segments few (287). *L.Ord.(Tremadoc.)*, Eng.-Ger. ——FIG. 181,8. **H. clonograpti*, Eng.; exoskel., ×15 (287).

Meneviella STUBBLEFIELD, 1951 [*pro Erinnys* SALTER, 1865 (*non* AGASSIZ, 1846); *Salteria* WALCOTT, 1884 (*non* W.THOMSON, 1864); *Menevia* LAKE, 1938 (*non* SCHAUS, 1928)] [**Erinnys venulosa* SALTER, 1872]. General form elongate, tapering from wide cephalon to very small pygidium. Cephalon occupying less than 0.25 of total length, differing from that of *Bailiella* in having sutures on lateral borders; genal spines slender, extending obliquely backward to about 6th thoracic segment. Thorax of 25 or more segments with narrow axis and wide pleural regions; pleurae terminating in strong, backward-curving spines. Pygidium small, with flat border, narrow, rapidly tapering axis of about 3 rings and terminal portion, and distinctly segmented pleural fields (51, 114). *M.Cam.*, Br.I.-Denm.-E. N.Am.(Atl.prov.)-Asia. —— FIG. 181,*10*. **M. venulosa* (SALTER), Br.I.; exoskel., ×2 (114, somewhat modified).

Parabailiella THORAL, 1946 [**P. languedocensis*]. Differs from *Conocoryphe* in having sutures cutting across lateral borders at least to border furrows (295). *M.Cam.*, S.Fr.

Pseudatops LAKE, 1940 [**Conocoryphe reticulata* WALCOTT, 1890]. Differs from *Atops* in having glabella encroaching on anterior border, no indication of sutures on dorsal side of cephalon; surface covered with network of raised lines (75, 114). *L.Cam.*, E.N.Am.-Br.I.

?Family SHUMARDIIDAE Lake, 1907[1]

[1] Assignment of this family to superfamily Conocoryphacea is doubtful; alternatively it should be classified in Families Incertae Sedis.—Ed.

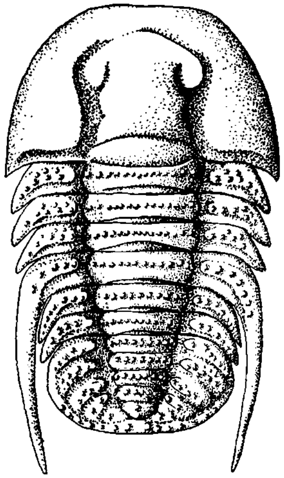


FIG. 183. *Shumardia pusilla* (SARS) (Shumardiidae), ?L.Ord.(Tremadoc.), Eng.; exoskel (reconstr.), ×22.5 (475).

Minute, ovate, convex, heteropygous. Cephalon semicircular, without eyes, and apparently without facial sutures; glabella delimited at sides by unusually deep and wide axial furrows and in front by their narrower and shallower, (in some) almost effaced continuation; occipital ring well defined; convex preglabellar field usually well developed; almost evenly convex genae with acute genal angles or with genal spines; posterior border furrows strongly impressed, posterior border narrow. Thorax (as far as known) with 6 or 7 segments. Pygidium greatly varying in shape, with 4 to 7 axial rings. Cephalic doublure, ventral sutures, and hypostoma unknown. *?M.Cam., U. Cam.-U.Ord.*

Shumardia BILLINGS, 1862 [**S. granulosa*] [=*Conophrys* CALLAWAY, 1877]. Glabella wide, slightly clavate, strongly inflated, with pair of eyelike lobes at anterior corners delimited by forward-curved anterior pair of lateral furrows, a pair of notches in glabellar margin representing a posterior pair of glabellar furrows; genal angles pointed. Thorax slightly narrower than cephalon; axis wide, strongly tapering, with wide, deeply impressed axial furrows; narrow pleural regions with obliquely backward-curved, pointed pleural extremities, and macropleural 4th thoracic segment terminating in long, backward-directed spines. Pygidium subquadrate to semicircular or (rarely) subtriangular in outline, with strongly tapering axis. Surface of thorax and pygidium bearing transverse rows of tubercles, a row on each axial ring and 1 or 2 rows on each pleura; pygidium with tuberculated border in some species (114, 153). *?M.Cam., U.Cam.-U.Ord.,* Eu.-N.Am.-S. Am.-Asia.——FIG. 183. *S. pusilla* (Sars), L.Ord. (Tremadoc.), Eng.; exoskel. (reconstr.), ×22.5 (475).

Acanthopleurella GROOM, 1902 [**A. grindrodi*]. Differs from *Shumardia* in having strongly impressed preglabellar furrow and long, slender, backward-directed genal spines; 4 pairs of long pleural spines (114). *L.Ord.(Tremadoc.),* Eng.

Eoshumardia HUPÉ, 1953 [**Shumardia orientalis* MANSUY, 1916]. Differs from *Shumardia* in having rounded genal angles and tapering, very wide glabella with broadly rounded front (78). *U.Cam.,* E.Asia.

Idiomesus RAYMOND, 1924 [**I. tantillus*] [=*Stigmametopus* RASETTI, 1944]. Differs from *Shumardia* in having narrower glabella that tapers forward-backward, front indistinctly delimited, eyelike lobes at anterior corners lacking, posterior pair of lateral furrows deeply impressed across glabella, and occipital furrow wider and deeper (192). *U.Cam.,* N.Am.——FIG. 184,2. **I. tantillus,* Vt.; ceph., ×9 (192).

?Lunacrania KOBAYASHI, 1955 [**L. trisecta*]. Differs from *Idiomesus* in having well-defined anterior and lateral cephalic borders, wide occipital ring, and

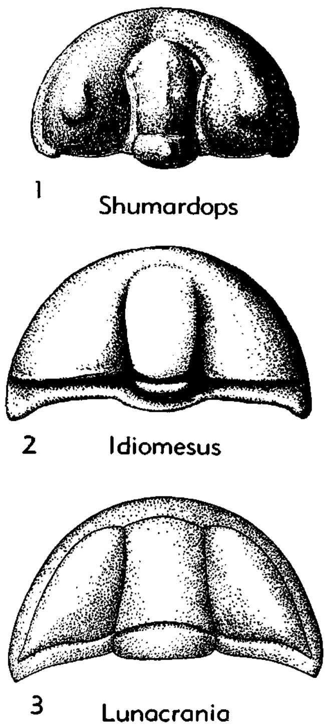


FIG. 184. Shumardiidae (p. O245, O246).

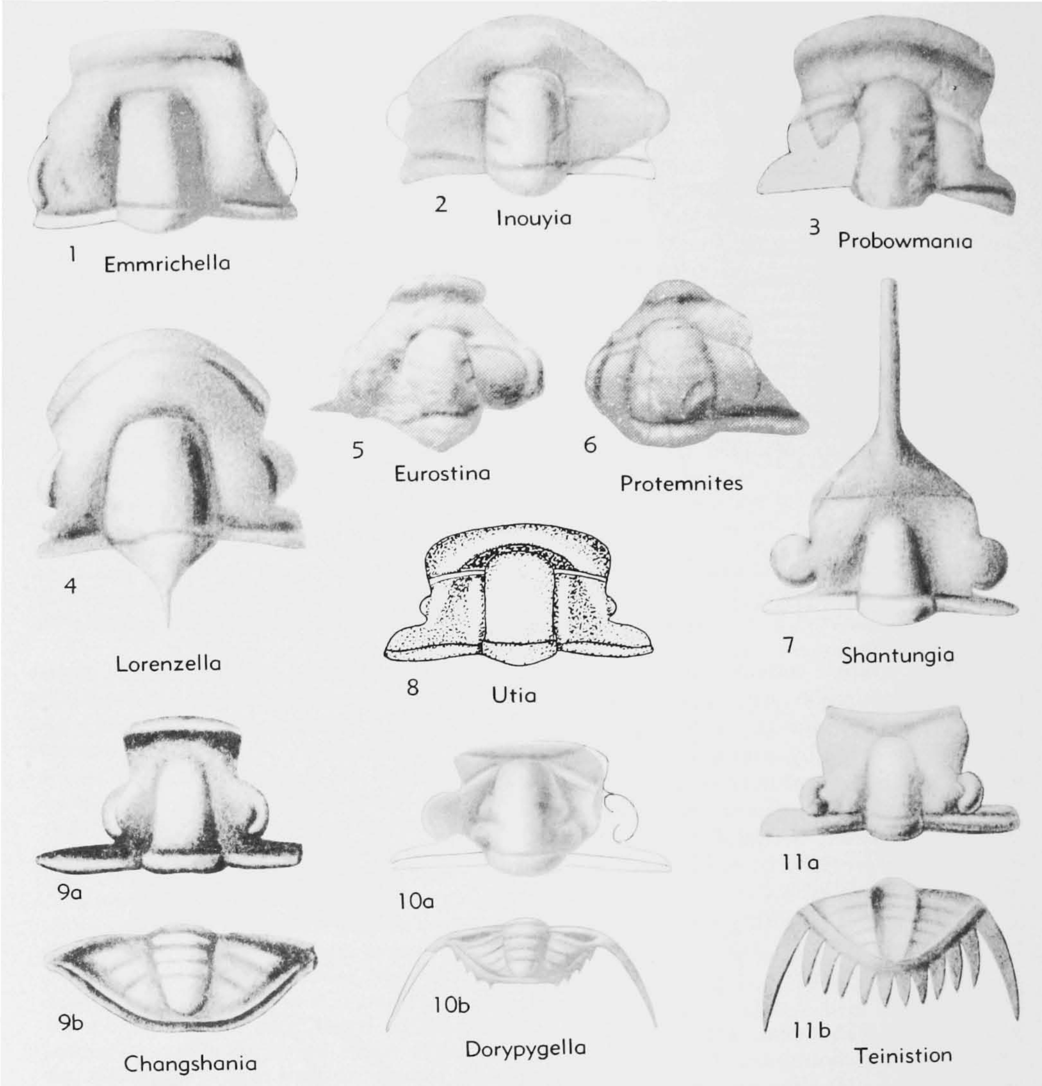


FIG. 185. Emmrichellidae (p. O247, O248).

tapering glabella devoid of transglabellar furrow and defined in front by anterior border furrow (108). *L.Ord.*, N.Am.——FIG. 184,*3*. **L. trisecta*, W.Can.(B.C.); ceph., ×20 (108).

Koldinioidia KOBAYASHI, 1930 [**K. typicalis*]. Differs from *Idiomesus* in having parallel-sided to tapering glabella, narrower and shallower occipital and posterior border furrows, and in lacking transglabellar extension of posterior pair of lateral furrows (37, 95). *U.Cam.-L.Ord.*, E.Asia.

Shumardops HUPÉ, 1953 [**Shumardia longifrons* TROEDSSON, 1937]. Differs from *Shumardia* in having wider cephalon, longer occipital ring, narrower glabella with median ridge, wider genae with rounded genal angles, a pair of eyelike swellings, and distinct lateral cephalic border (78). *L.Ord.* *(Tremadoc.)*, C.Asia.——FIG. 184,*1*. **S. longifrons* (TROEDSSON), Tien-shan; ceph., ×11 (301).

Superfamily EMMRICHELLACEA Kobayashi, 1935

[*nom. transl.* HOWELL, herein (*ex* Emmrichellidae KOBAYASHI, 1935)] [=Utioidae HUPÉ, 1953]

Cephalon relatively wide, semielliptical, cranidium quadrate to subtrapezoidal; glabella mostly with subparallel sides well impressed by axial furrows; fixigenae variable in width, gently to rather strongly convex; eyes generally small and palpebral lobes narrow. Pygidium small, transverse, with border. *M.Cam.-L.Ord.*

Family EMMRICHELLIDAE Kobayashi, 1935

[=Utiidae KOBAYASHI, 1935 (*nom. correct.* MOORE, herein, *pro* Utiadae KOBAYASHI, 1935, *nom. transl.* HUPÉ, 1953, *ex* Utianae KOBAYASHI, 1935)]

Cranidium subtrapezoidal to subtriangular *(Shangtungia),* with parallel-sided or forward-tapering glabella that is mostly separated from anterior border by distinct preglabellar area; fixigenae variable in width, bearing prominent posterior border. Pygidium much wider than long *(sag.),* with distinct axis tapering backward, border entire, smooth or with marginal spines. *M. Cam.-L.Ord.*

Subfamily EMMRICHELLINAE Kobayashi, 1935

[=Utiinae KOBAYASHI, 1935, *nom. correct.* RUD. RICHTER, 1943 (*pro* Utianae KOBAYASHI, 1935)]

Cranidium subtrapezoidal to semielliptical, with anterior margin nearly straight or strongly curved forward; glabella parallel-sided or tapering forward, with or without distinct lateral furrows; preglabellar field narrow to wide *(sag.),* convex; eyes mostly small, posterior to mid-length of cranidium, eye ridges present or absent. Pygidium with raised border, margin smooth. *M.Cam.-L. Ord.*

Emmrichella WALCOTT, 1911 [**Ptychoparia theano* WALCOTT, 1905]. Cranidium narrow *(tr.),* glabella narrow and lacking furrows. *M.Cam.,* E.Asia.——FIG. 185,*1*. **E. theano* (WALCOTT), Ch'anghia F., China; cran., ×6.6 (488*).

Eurostina WHITEHOUSE, 1939 [**E. trigona*]. Cranidium subtrigonal to subquadrate, anterior border prominent; glabella tapering forward, with 3 pairs of discontinuous furrows; librigenae and preglabellar field inflated, with pair of faint anterolateral depressions; palpebral lobes small but prominent. *M.Cam.,* Austral.——FIG. 185,*5*. **E. trigona,* Eurostina Stage, Queensl.; cran., ×3.9 (493*).

Inouyia WALCOTT, 1911 [**Agraulos? capax* WALCOTT, 1906]. Glabella subquadrate, with 3 pairs of discontinuous furrows; preglabellar area with boss in front of glabella; palpebral lobes small, not prominent. *M.Cam.,* E.Asia.——FIG. 185,*2*. **I. capax* (WALCOTT), Ki-chou F., China; cran., ×4 (488*).

Lorenzella KOBAYASHI, 1935 [**Agraulos abaris* WALCOTT, 1905]. Like *Inouyia* but without boss on convex preglabellar area, and with occipital spine. *M.Cam.,* E.Asia.——FIG. 185,*4*. **L. abaris* (WALCOTT), Kiu-lung F., China; cran., ×5 (488*).

Metabowmania KOBAYASHI, 1955 [**M. latilimba*]. *L.Ord.,* W.Can.(B.C.) [Author's assignment.]

Probowmania KOBAYASHI, 1935 [**Ptychoparia ligea* WALCOTT, 1905]. Cranidium and glabella medium in width, glabella bearing short furrows. *M.Cam.,* E.Asia.——FIG. 185,*3*. **P. ligea* (WALCOTT), Ch'anghia F., China; cran., ×4 (419*).

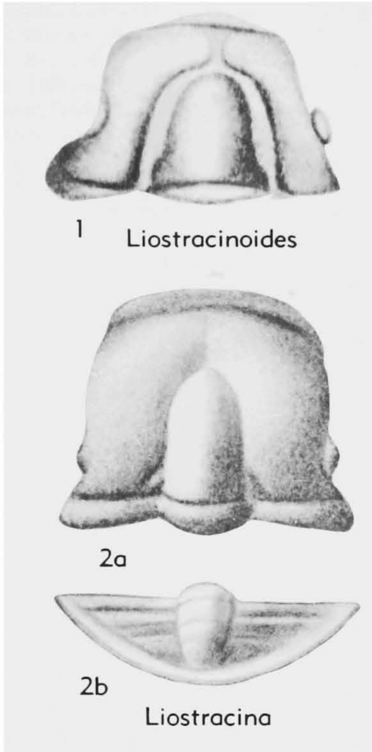


FIG. 186. Liostracinidae (p. O248).

Protemnites WHITEHOUSE, 1939 [**P. elegans*]. Cranidium like that of *Eurostina* but glabella with only 2 pairs of furrows, narrower fixigenae, and less prominent palpebral lobes and anterior border. *U.Cam.,* Austral.——FIG. 185,*6*. **P. elegans,* Elrathiella Stage, Queensl.; cran., ×3.3 (493*).

Utia WALCOTT, 1924 [**U. curio*]. Cranidium and glabella broad, glabella without furrows. *M.Cam.,* W.USA.——FIG. 185,*8*. **U. curio,* Spence Sh., Idaho; cran., ×1.8 (488*).

?**Inouyops** RESSER, 1942 [**Ptychoparia titiana* WALCOTT, 1905]. *M.Cam.,* China.

Subfamily CHANGSHANIINAE Kobayashi, 1935

[*nom. correct.* MOORE, herein (*pro* Changshaninae KOBAYASHI, 1935)] [=Changshaniidae HUPÉ, 1953]

Cranidium with parallel-sided to tapering truncate glabella that lacks furrows; palpebral lobes large, behind mid-length of cranidium; fixigenae narrow, with broad transverse posterior areas and raised borders. Pygidium short, wide. *M.Cam.*

Changshania SUN, 1923 [**C. conica*; SD SUN, 1924]. Preglabellar area subquadrate. Pygidium subtriangular, without spines. *M.Cam.*, E.Asia.——Fig. 185,*9*. **C. conica*, Kushan F., China; *9a,b*, cran., pyg., ×3 (478*).

Dorypygella Walcott, 1905 [**D. typicalis*]. Glabella tapering, truncate in front, with 2 pairs of faint lateral furrows; eye ridges strong; anterior border narrow; palpebral lobes rather large; librigenae elongate rectangular, with short genal spines. Pygidium with axis of 4 segments and pair of long recurved spines at anterolateral extremities, border with 4 pairs of short spines. *M.Cam.*, E. Asia.——Fig. 185,*10*. **D. typicalis*, Kushan F., China; *10a*, cran., ×5; *10b*, pyg., ×6.5 (488*).

Shangtungia Walcott, 1905 [**S. spinifera*] [=*Shantungia* Walcott, 1913]. Cranidium like that of *Changshania* but middle of preglabellar area extended forward as spine. *M.Cam.*, E.Asia.——Fig. 185,*7*. **S. spinifera*, Kushan F., China; cran., ×2.9 (488*).

Teinistion Monke, 1903 [**T. lansi;* SD Vogdes, 1925]. Cranidium short, wide and subquadrate; palpebral lobes small. Pygidium with numerous spines. *M.Cam.*, E.Asia.——Fig. 185,*11*. **T. lansi*, China; *11a*, cran., ×6.7; *11b*, pyg., ×6.3 (433*).

Family LIOSTRACINIDAE Raymond, 1937

Glabella ovate, palpebral lobes very small, fixigenae strongly convex, preglabellar area bearing median longitudinal furrow. *M. Cam.-U.Cam.*

Liostracina Monke, 1903 [**L. krausei*]. Glabella narrow, preglabellar area longer and fixigenae wider than in *Liostracinoides*. Pygidium short, wide. *M.Cam.*, E.Asia.——Fig. 186,*2*. **L. krausei*, China; *2a*, cran., ×5.5; *2b*, pyg., ×7 (433*).

Liostracinoides Raymond, 1937 [**L. vermontanus*]. Glabella wider and more tapering than that of *Liostracina*, and preglabellar area shorter, fixigenae narrower, and palpebral lobes not so far back. *U.Cam.*, E.USA.——Fig. 186,*1*. **L. vermontanus*, Gorge F., Vt.; cran., ×10 (449*).

Superfamily CREPICEPHALACEA Kobayashi, 1935

[*nom. transl.* Lochman-Balk, herein (*ex* Crepicephalidae Kobayashi, 1935]

Exoskeleton opisthoparian, elliptical, isopygous or heteropygous. Glabella convex, tapering, front rounded or straight, with 2 or 3 pairs of short diagonal lateral furrows (may be faint or obsolete); eye ridges present or absent, occipital spine or node common; eyes medium-sized, opposite or posterior to center of glabella; fixigenae variable in width and slope; librigenae with medium or long genal spine. Thorax of 13 or fewer segments; axis convex, less than 0.5 of width *(tr.)* of pleurae; pleural furrows well defined, pleural ends falcate. Pygidium compact, subquadrate to subpentagonal, axis and pleural regions about same in width, with 3 to 6 axial rings and pleurae, border narrow, bearing a pair of posterolateral spines derived from pleurae or border, variable in length and divergence. Surface finely to coarsely granulose, rarely smooth. Polyphyletic derivation. *M.Cam.-U.Cam.*

Family CREPICEPHALIDAE Kobayashi, 1935

[=Crepicephalidae Lochman, 1936]

Exoskeleton isopygous. Glabella convex, tapering, front rounded or straight, with 2 or 3 pairs of short diagonal lateral furrows; internal venation on preglabellar field and eye platforms usually prominent, eye ridges present or absent, occipital spine may be present; eyes of medium size, position variable; fixigenae horizontal; librigenae with medium to long, flat genal spine. Thorax of 12 segments, axis convex, less than 0.5 of width *(tr.)* of pleurae, pleural furrows distinct, pleural ends falcate. Pygidium subrectangular to subpentagonal, axis convex, tapered, about same width as triangular pleural platforms, with 3 to 6 axial rings and pleurae, border narrow anteriorly, and at posterior median line, expanding into broad bases of a pair of very short to medium-length flat spines at posterolateral corners. Outer surface smooth or very finely granulose. Derived from a ptychopariid stock. *M.Cam.-U.Cam.*

Crepicephalus Owen, 1852 [**Dikelocephalus? iowensis* Owen, 1852; SD Walcott, 1886] [=*Crepicocephalus* Bigsby, 1868; *Crepicepalus* Vogdes, 1890; *Sneedvillia* Resser, 1938; *Crepiceaphlus* Kobayashi, 1944]. Eyes opposite center of glabella; eye ridges and palpebral furrows prominent; fixigenae horizontal, with palpebral area about 0.3 of glabellar width, posterior area long *(tr.)*. Thorax of 12 segments. Pygidium subrectangular, axis 0.7 to 0.75 of its length, with 4 or 5 axial rings and pleurae, interpleural grooves ending at border, without border furrow, border flat or slightly concave, widest at base of spines, length and divergence highly variable (316). *Low. U.Cam.(Dresbach.)*, N.Am.-Sib.——Fig. 187,*3*. **C. iowensis* (Owen), Wis.; *3a,b*, cran., ×1; *3c*, librigena, ×1; *3d*, pyg., ×1 (316).

Bonneterrina Lochman, 1936 [**B. prima*] [=*Holstonia, Piedmontia* Resser, 1938]. Glabella broadly rounded in front, with 2 pairs of faint glabellar furrows; eyes opposite posterior 0.3 of glabella; eye ridges and palpebral furrows prominent; occipital furrow shallow, occipital spine prominent; fixigenae horizontal, with palpebral areas less than 0.5 of glabellar width, posterior area short *(tr.)*; librigenae with strong genal spine. Pygidium unknown (123). *Low.U.Cam.(Dresbach.),* N.Am.——FIG. 187,6. **B. prima;* cran. and librigena, ×1 (123, 126).

Crepicephalina RESSER & ENDO, in KOBAYASHI, 1935

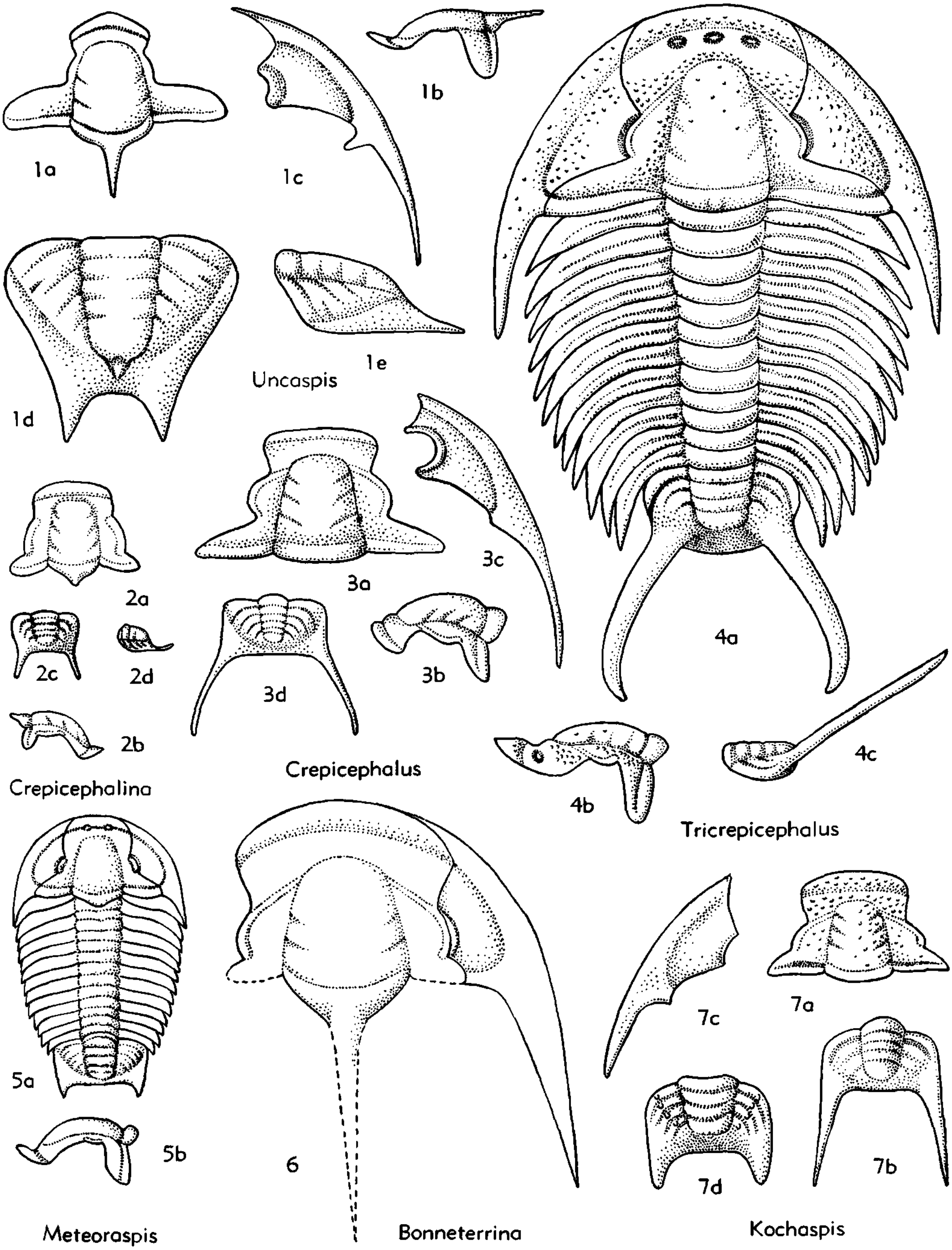


FIG. 187. Crepicephalidae (p. O248-O250).

KOBAYASHI (*non* RESSER & ENDO), 1935 [**Crepicephalus convexus* WALCOTT, 1913] [=*Mesocrepicephalus* KOBAYASHI, 1935]. Eyes slightly behind center of glabella; palpebral furrows deep but eye ridges faint; preglabellar area narrow to absent; with occipital node or short spine; fixigenae horizontal, with palpebral area less than 0.5 of glabellar width, posterior area of medium length *(tr.)*. Pygidium subquadrate; axis convex, wider than pleural regions, 0.8 of pygidial length, with 2 to 4 axial rings; 3 low, broad pleurae curve sharply back into base of spines, border along posterior only (37). *M.Cam.*, E.Asia.-Austral.——FIG. 187,*2*. **C. convexa* (WALCOTT), Liau-tung, Manch.; *2a,b,* cran.; *2c,d,* pyg., both ×2 (37).

Kochaspis RESSER, 1935 [**Crepicephalus liliana* WALCOTT, 1886] [=*Palaeocrepicephalus* KOBAYASHI, 1935 (obj.)]. Eyes opposite center of glabella, palpebral furrows and eye ridges present; fixigenae horizontal or upsloping, with palpebral areas almost 0.7 of glabellar width, posterior area long *(tr.)*. Pygidium subquadrate, axis wide, convex, 0.75 of length, with 3 or 4 axial rings; 3 or 4 low, broad pleurae curve abruptly back near margin into base of spines which are variable in length and divergence, border along posterior only (197, 307). *M.Cam.*, N.Am.——FIG. 187,*7a-c*. **K. liliana* (WALCOTT), Low.M.Cam., Nev.; *7a-c,* cran, pyg., librigena, ×1.——FIG. 187,*7d*. *K. cecinna* (WALCOTT), Low.M.Cam., Alba.; pyg., ×2 (307).

Uncaspis KOBAYASHI, 1935 (*emend.* RAASCH & LOCHMAN, 1943) [**Crepicephalus unca* WALCOTT, 1916]. Eyes slightly in front of center of glabella, glabellar furrows faint; palpebral furrows and eye ridges lacking; occipital spine may be present; fixigenae with palpebral areas consisting only of palpebral lobes, posterior area rectangular, wide *(sag.)* and long *(tr.)*. Thoracic segment may have axial spine. Pygidium subpentagonal; axis tapered through 0.75 of length, with a short postaxial ridge, with 4 or 5 axial rings; pleural regions narrow, triangular, 3 broad pleurae; border furrow faint, border narrow anteriorly, widening posteriorly with a median inward bend or short spine on each side (186). *Low.U.Cam.(Dresbach.),* N.Am.——FIG. 187,*1*. **U. unca* (WALCOTT), Wis.; *1a,b,* cran.; *1c,* librigena; *1d,e,* pyg.; all ×2 (186).

Family TRICREPICEPHALIDAE Palmer, 1954

Exoskeleton heteropygous. Glabella convex, elongate tapering, front rounded, glabellar furrows faint or obsolete, 2 or 3 pits on anterior border furrow; eye ridges present or absent; occipital spine or node common; eyes of medium size, opposite or posterior to center of glabella; fixigenae variable in width and slope; librigenae with medium or long genal spines. Thorax with 13 or fewer segments; axis convex, less than 0.5 of width *(tr.)* of pleurae, pleural furrows well defined, pleural ends falcate. Pygidium compact, subquadrate; axis wide, subparallel-sided, extending nearly full length, 3 or 4 axial rings; pleural regions narrow, with 3 or 4 pleurae; no border furrow, narrow border, pair of round, medium to long spines at posterolateral corners. Surface granulose. Derivation — ptychopariid stock. *U.Cam. (Dresbach.)*.

Tricrepicephalus KOBAYASHI, 1935 [**Arionellus (Bathyurus) texanus* SHUMARD, 1861] [=*Paracrepicephalus* LOCHMAN, 1936]. Eyes behind mid-level of glabella, lateral furrows shallow, with 3 evenly spaced, round or elliptical pits in anterior border furrow; palpebral furrows shallow, eye ridges narrow, with occipital spine or node; fixigenae horizontal, with palpebral area more than 0.5 of glabellar width, posterior area long *(tr.)*. Thorax of 12 segments. Pygidium quadrate; axis convex, wider than pleural regions, more than 0.7 of length, with 3 axial rings; 3 broad, low pleurae forming into a long hollow, rounded spine at posterolateral corners, narrow border along posterior continues under spines along sides (235, 316). *Low.U.Cam.(Dresbach.),* N.Am.-S.Am.——FIG. 187,*4*. **T. texanus* (SHUMARD), Tex.; *4a,* exoskel., ×0.9; *4b,* cran. profile, ×1; *4c,* pyg. profile, ×1 (123, 316).

Meteoraspis RESSER, 1935 [**Ptychoparia? metra* WALCOTT, 1890] [=*Meteraspis* KOBAYASHI, 1936; *Greylockia, Coleopachys* RAYMOND, 1937]. Eyes slightly behind mid-glabellar level, without glabellar furrows; 2 pits in anterior border furrow with rarely a faint 3rd median pit; palpebral furrows deep, without eye ridges; occipital node may be present; fixigenae upsloping, with palpebral area 0.2 to 0.3 or less of glabellar width, posterior area of medium length *(tr.)*. Thorax of 13 segments. Pygidium subquadrate; axis wide, 0.8 to 0.83 of length, with 3 or 4 axial rings; pleurae 3, broad, convex, interpleural grooves and pleural furrows ending at border which widens into base of posterior spines, border furrow lacking (125, 132). *Low.U.Cam.(Dresbach.),* N.Am.(E.Can.-Mont.-Tex.)-S.Am.——FIG. 187,*5*. *M. borealis* LOCHMAN, Mont.-Tex.; *5a,* exoskel.; *5b,* cran. profile; both ×3 (125).

Superfamily NEPEACEA Whitehouse, 1939

[*nom. transl.* LOCHMAN-BALK, herein (*ex* Nepeidae WHITEHOUSE, 1939)]

Exoskeleton apparently proparian, micropygous. Glabella short, tapering to subquadrate, with straight front, glabellar fur-

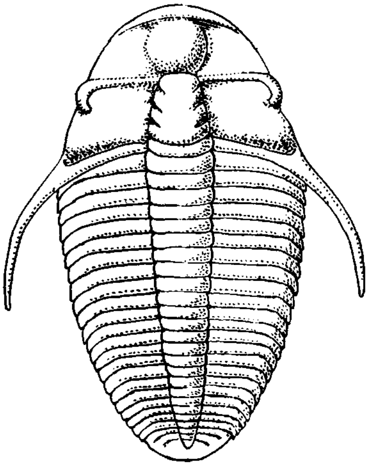


FIG. 188. **Nepea narinosa* WHITEHOUSE (Nepeidae), M.Cam., Queensl.; exoskel. lacking librigenae (reconstr.), ×2 (493).

rows present, with prominent median boss on preglabellar field; with anterior border and marginal furrow; occipital spine may be present; eye ridges present, may be double, eyes small, opposite anterior third of glabella; fixigenae upsloping, with palpebral areas as wide or wider than glabella, posterior area narrow, much wider *(tr.)* than occipital ring, posterior marginal furrow curving forward, genal spines present; librigenae forming small convex triangles. Thorax of 22 or fewer narrow segments, axis much narrower than pleurae, pleural furrows narrow, distinct, on anterior third of pleurae. Pygidium transverse; axis broad, tapered to rounded end, about same in width as pleural regions, border narrow. Surface unknown. *M.Cam.*

Family NEPEIDAE Whitehouse, 1939

Characters of superfamily. *M.Cam.*

Nepea WHITEHOUSE, 1939 [**N. narinosa*]. Glabella tapering forward, truncate at front, with 3 pairs of lateral furrows; swollen median boss occurs on preglabellar field, bounded laterally by furrows continuous from axial furrows, boss may impinge forward onto marginal furrow; anterior border very narrow; occipital spine present; fixigenae steeply upsloping, with palpebral areas 1.5 times width of glabella, posterior area elongate, about 3 times width *(tr.)* of occipital ring, with long or short slender genal spines. Thorax of no fewer than 22 segments. Pygidium very small, axis convex, with 2 or 3 axial rings; pleural regions low, with 2 or 3 pleurae (340). *Up.M.Cam.* (Amphoton Stage), NW.Queensl.——FIG. 188. **N. narinosa;* exoskel. lacking librigenae (reconstr.), ×2 (493, modified).

Superfamily DIKELOCEPHALACEA Miller, 1889

[*nom. transl.* HENNINGSMOEN, 1951, but attributed by him to RICHTER, 1933 (*ex* Dikelocephalidae MILLER, 1889)] [=Dikelocephalidea RICHTER, 1933 *(partim)*; Dikelocephaloidae HUPÉ, 1953 (attributed to RICHTER, 1933)]

Exoskeleton opisthoparian, medium-sized to large, ellipsoidal in outline, heteropygous to subisopygous. Cephalon mostly semicircular, with more or less broadly tapering glabella that bears 2 or 3 pairs of lateral glabellar furrows, posterior pairs commonly complete; frontal area broad *(sag.* and *tr.)*, anterior border furrow shallow to obsolete; palpebral lobes prominent, eyes usually medium-sized; librigenae bearing medium to long genal spine. Thorax with 13 or fewer segments. Pygidium broadly ovate to transverse, with interpleural and pleural furrows tending to curve conspicuously backward across broad border, some forms with pair of short posterolateral spines. Surface smooth to finely granulose. *L.Cam.-U.Cam.*

Family IDAHOIIDAE Lochman, 1956

Exoskeleton opisthoparian, heteropygous. Glabella tapering, truncate-tapering or subrectangular, with 3 pairs of arcuate lateral furrows distinct to very faint; eye ridges narrow; with broad palpebral furrows and wide palpebral rims; eyes medium-size to large, opposite or somewhat behind midlength of glabella; ratio of preglabellar field to anterior border highly variable; anterior border furrow narrow; fixigenae variable in position and width, with palpebral area arcuate, 0.3 to 0.5 of glabellar width, posterior area narrow *(exsag.)*, straplike, of medium length *(tr.)*; librigenae quadrate, with obsolete marginal furrows at genal angles, genal spines rounded. Pygidium with convex axis, tapered to broadly rounded end with usual median indentation and short postaxial ridge, with 3 or 4 axial rings and terminal ring; pleural field low, pleurae 3, with broad shallow furrows and narrower interpleural grooves that are distinct to very faint, without border furrow; border of variable width. Surface granulose. Derived from Ptychopariidae. *U.Cam.*