ONTOCIENCY 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
these stages. STJRMR (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 STJRMR (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 metaprotaspide 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 holaspis period, the eye lobe is recognizable by the relatively small, raised, palpebral lobe, connected by an eye ridge to the frontal axial lobe (Fig. 88A-E). In protaspides like those of Welleraspis (Fig. 90) or Sao (Fig. 88A-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. 91A), 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 Paradoxodes (Fig. 93A,B) the eye lobe is exceptionally long and in those of Menoparia (Figs. 86A,B) the palpebral lobe is not raised. Probably in all protaspides there is a narrow doublure and a relatively large hypostoma (Fig. 88E, 92B). Wherever preservation is good enough (usually in late protaspide stages), it has been shown that facial sutures are present, as well as rostral, hypostomal, and probably connective sutures (Figs. 86C-E, 92, 94B, 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, 5a-e), and silicified material described by Palmer (12) includes speci-
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 cephalas. 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. 96A) tiny spines are present on the anterolateral cephalic border; long metagenal (“intergenal”) spines, and 5 axial rings are preserved in the thorax.
Ontogeny

The original of Figure 96B 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. 96C) 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. 96B) in which anterior border spines also are present.

In meraspides of Paedeumias yorkense there is seemingly no trace of precocular 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 Huré (8) and earlier authors that the postocular ridges follow the course of the fused, posterior section of the facial sutures. Recently Huré (8) has also claimed that the precocular 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 Störmer (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 protaspis stages (Fig. 93A,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 93A,B, but smaller and with fewer segments in the protopygidium, and not “anaprotaspides” as Störmer 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.
Figure 88 shows ontogeny of Sao, based on previous work (1, 22) and my own studies (36). The earliest stage (Fig. 88A) 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 88A only the posterolateral portion is visible. The protaspis increases to a length (sag.) of about 1 mm. (Figs. 88B-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. 88F) 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-
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. 86A-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

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*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).*

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

The protaspis of the bathyurid Licnococephala (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. 88A-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 protaspid of Shumardia (Fig. 87A) 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, 91A, 92, 94, 99A). Their length (sag.) ranges from about 0.25 to 0.95 mm., only those of Rossaspis (20) and Pseudocybele (Figs. 89A) 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. 91A).

The protaspides of Flexicalymene (Fig. 92) and phacopids (Figs. 94, 99A) 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. 92B) 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.

**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 holaspide 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 *Leptagnostoides* (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 *Leptagnostoides*. Size of individuals belonging in any one “degree” varies, suggesting that more than a single molt may occur within each “degree.” In *Leptagnostoides* 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 holaspide exoskeleton. Examples of these proportions, contrasting early meraspides with late holaspides, are: *Leptagnostoides*, 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-
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 Dimeroptyge 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, meraspis "degrees" 1, 5, 7, 10, ×20; E,F, holaspis cephalon, last thoracic segment, and pygidium, ×1.3 (40*).
Trilobitomorpha—Trilobita

FIG. 98. Ontogenetic stages of Licnocephala cavigladius (HINTZE), L.Ord., W.USA(Utah); A, protaspis lacking librigenae, X30 (21); B-F, series of cranidia, X20, X14, X14, X7, X7 (21); G, holaspis cephalon and pygidium, X2 (38).

pleural spines that appear during the meraspid period are retained in the holaspis, but in Paradoxides pinus? (Fig. 93C-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), Leptoplaostoides (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. 87A, none in Menoparia, Fig. 86A,B) and there is a median longitudinal furrow in Paradoxides (Fig. 93A,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 remopleurids 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, X30 (34*); B, meraspid “degree” 5, X15 (41n).
Ontogeny

The 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."

EYE LOBES AND FACIAL SUTURES

In trilobites with compound eyes in the holaspis 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. Stromer (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. 100. Meraspid "degrees" of Onnia ornata (Sternberg), M.Ord.-U.Ord., Bohemia; A-C, "degrees" 0 (X22), 1 (X10), 2 (X12.5) (41n).
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 opisthparian 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. 88E, 92B) 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; *Leptoplaxoides*, 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 *Leptoplaxoides* (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*, *Leptoplaxoides*, 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...
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-
development of trilobites is accepted here, and, accordingly, the holaspis 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 holaspis 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. 87H, J) 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 87I an holaspis, and not that of Figure 87H. 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 Isotetes.
ontogeny

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 ribeiroy, 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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CLASSIFICATION

By H. J. Harrington

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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) homoeomorphy 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 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 sutures 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, Harpeditidae [=Harpidae], Trinucleidae

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

**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-
Trilobitomorpha—Trilobita

bearing ancestors; *Pagezia*, 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, Bur-
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 Protomachina, 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 [=Remopleuridae], Paradoxidae [=Paradoxidae], Zacanthidae [=Zacanthidae]

Suborder Conocoryphida

Section Olenina—Olenidae, Proetidae, Oryctoccephalidae

Section Conocoryphina—Conocoryphidae

Section Ptychoparia — Ptychopariidae [=Ptychopariidae], Solenopleuridae, Dicelloccephalidae [=Dikelloccephalidae], Bathuridae, Asaphidae, Illexiidae

Section Calymenina—Calymenidae, Homalono- tidae

Suborder Trinucleida—Trinucleidae, Harpedidae [=Harpidae], Raphiophoriidae, Aeglinidae [=Cyclopygidae], ?Ellipsocephalidae, ?Shumardiidae

Suborder Odontopleurida—Odontopleuridae, Lichadidae [=Lichidae], Bronsteidae [=Thysanopeltidae]

Order Proparia—Encrinuridae, Cheiruridae, Phacopidae, Burlingidae [=Burlingiidae], ?Agnosti- dae

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 Suturi-
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ccephalida, for those with facial sutures. The Integricephalida (equivalent to Becher’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 Mesonacidae — Olenellidae

Order Epiparia (=Suturicephalida, 1927)

Suborder Opisthoparia — Redlichidae (=Redlichidae), Zacanthoidae (=Zacanthoidae), Ptychopariae (=Ptychopariidae), Paradoxidae (=Paradoxiidae), Corynexochidae, Oryctocephalidae, Illaenidae, Bronteidae (=Thysanopeltidae), Symphysuridae (=Nileidae), Dikelocephalidae, Asaphidae, Bathyuridae, Proctidae, Remopleuridae (=Remopleuriidae), Raphiophoridae, Aeagnidae (=Cryptopygidae), Ellipsocephalidae, Anomocaridae, Solenopleuridae, Olenidae, Cyphaspidae (=Otarionidae), Calymenidae, Homalonotidae, Odontopleuridae, Lichadidae (=Lichidae)

Suborder Proparia — Burlingidae (=Burlingiidae), Norwoodiidae, Cheiruridae, Encrinuridae, Phacomidae, ?Menonomidae

RUDOLF RICHTER’S CLASSIFICATION

Rudolf Richter (1933) accepted Becher’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 Redlichina

Superfamily Redlitchidae — Paradoxidae, Mesonacidae (=Olenellidae), Redlichidae

Superfamily Zacanthoididae — Lichidae, Odontopleuridae, Remopleuridae, Zacanthoididae, Ceratopygidae, Oryctocephalidae

Superfamily Bathyuriscidae — Corynexochidae, Bathyuridae, Scutellicidae (=Thysanopeltidae), Illaenidae

Superfamily Dikelocephalidae — Dikelocephalidae, Asaphidae, Symphysuridae (=Nileidae), Cyclopygidae

Suborder Ptychoparia

Superfamily Ellipsocephalidae — Olenidae, Otarionidae, Proctidae, Ellipsocephalidae

Superfamily Cryptolithidae — Raphiophoridae, Cryptolithidae (=Trinucleidae), Shumardidae

Superfamily Ptychoparia — Conocoryphidae, Harpidae, Ptychopariidae, Solenopleuridae

Superfamily Calymenidae — Menonomidae, Calymenidae, Homalonotidae

Order Proparia

Superfamily Eodicidae — Agnostidae, Eodiscidae

Superfamily Norwoodiidae — Norwoodiidae

Superfamily Burlingiidae — Burlingiidae

Superfamily Phacopidae — Phacopidae, Cheiruridae, Encrinuridae

STORMER’S CLASSIFICATION

Leif Stormer’s (1942) classification, “based chiefly on the ontogenetic development” of trilobites, is actually a modification of Becher’s scheme with addition of some of Swinnerton’s ideas. Stormer is the only modern paleontologist who recognizes Becher’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 Stormer (1942)

Order Protoparia (Primitive trilobites with ventromarginal or marginal cephalic suture; lateral eyes well developed; preantennal segment well developed on dorsal side of protaspid; intergenal [metagenal] spines present in anaprotaspid, meta-protaspid, meraspid, and partly in holaspis periods)—Olenellidae
Order HYPOPARIA (Trilobites with marginal, supra-marginal or ?ventromarginal sutures; lateral eyes absent or little developed; protaspid 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 ORISTOPARIA (Trilobites with facial sutures crossing margin behind genal angles, at corners, of which genal spines may occur; protaspid with preantennal segment slightly or not at all developed on dorsal side; metagenal spines present in the metaprotaspis 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; protaspid with preantennal segment not developed on dorsal side; metagenal spines present in metaprotaspis and later periods)—Eodiscidae Norwoodiidae [=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 STÓRNER'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, Pagetidae, Eodiscidae (Eodiscinae, Calodiscinae, Spinodiscinae, Brevidiscinae), Dawsoniidae, Aulacodiscidae

Superfamily AGNOSTOIDAE—Platagnostidae, Lejop­gidae, Phalacromidae, Leagnostidae, Sphaeragnostidae, Condylopygidae, Diplagnostidae, Ag­nostidae, Hagnostidae, Micagnostidae, Spinagnostidae, Clavagnostidae, Geragnostidae, Cyclagnostidae, Trinodidae

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

Superfamily OLENELOIDAE—Olenellidae (Fallotaspidae, Nevadinae, Olenellinae, EIlitopecephalinae, Wannerinae, Neltnerinae, Holminiae, Olenelloidinae), Daguinaspidae [=Daguinsapidinae], Lancasteridae

Superfamily REDLICHIIDAE [=Paradoxoididae]

Redlichidae (Redlichinae, Pararedlichinae), Neoredlichidae, ?Yunitedinae, Laiuredlichidae, Saukiandidae, Doloresolenidae, Abadiellidae, Bathyn­notidae, Metadoxididae, Protolenidae (Protoleni­nae, Termierellinae, Bigotininae, Myopsoleninae, Surenellinae), Antatlasidae, Ellipsocephalidae (Ellipsocephalinae, Aldoninae), Palaeolenidae (Palaeoleninae, Kingaspidinae, Harthillinae), Paradoxididae (Paradoxidinae, Centroleuria, Xystriuridae), Hicksiidae

Superfamily CORYNECHOIDAE — ?Proebeiidae, ?Edesteinaspidae [=Edesteinaspidae], Dinesi­idae, Zacanthoididae, Albertellidae, Dolichometopidae (Bathyuriscinae [=Dolichometo­pinae], Mexicaspinae [=Mexicaspidae], Orri­inae, Glossopleurinae, Hanburinae, Vanumellinae), Corynexeochidae (Corynexeochinae, Acon­theinae), Ogygopsidae, Protypidae, Dorypygididae (Dorypyginae, Holteriinae), Oryctocephalidae (Oryctocephalinae, Oryctocarinae, Tonkineellinae [=Tonkineellinae])

Superfamily AGRAULIDAE—Agraulidae, Micrag­raulidae, Pelthopebellidae

Superfamily PARASOLENOPELUREIDAE [=Yokusen­ioidae]—Yokusenidae, Yunnanocephalidae, Parasolenopleuridae, Anomocarellidae

Superfamily PYCHOPAROIDAE [=Conocoryphoi­dae]—Alokistocaridae (Alokistocarinae, Ame­cecephalinae), Nepeidae, ?Antagmidae, Elrathii­idae (Elrathininae, Plagiurinae, Solenopleur­lineae), Pychoparidae (Pychoparininae, Howell­aspinae [=Howellaspidae], Elrathielinae,
Clappaspinae [=Clappaspidinae], Iraniinae), Saisidae, Conocoryphidae (Conocoryphinae, Baillellinae, Ctenocephalinae, Holoccephalinae, Meneviellinae), Atopsidae

Superfamily Solenopleuroidea — Solenopariidae, Solenopleuridae (Solenopleurinae, Menoccephalinae, Heterocoryphinae), Acrocephalidae, Longchocephalidae, Talbotinidae, Burnetidiae [=Dokimocephalidae], Glyptometopidae, Hysterocoryphidae, Toenquistidiae, Dimeropygidae, Bathyuridiae (Bathyurinae, Bathyurellinae), Otarionidiae (Otarioninae, Cyphaspidae), Punctulariidae, Raymondiidae, Isocolidae

Superfamily Utridae — ?Emmrichellidae, Utiidae [=Utidae], Liostraciidae, Paracedaridae, Cederidae, Norwoodidiae (Norwoodiinae, Levisaspidae [=Levisaspidinae]), Shumardiidae, Myidiae, Toxotidiae

Superfamily Asaphiscidae — Ceratopygidae, Asaphiscidae (Asaphiscinae, Lecanopleuridae, Otarionidae, Toernquistiidae, Dimeropygidae, Bathyuridae (Norwoodiinae, Levisaspidae [=Levisaspidinae]), Glauchanidae, Menomoniidae, Remoellidae

Superfamily Lichadoidea — Lichadidae [=Lichinae] Homolichadiinae, Menevillinae, Ogygiocarinae, Ogygiocaridinae, Macropyginae, Cyclopygidae

Superfamily Dikelocephalidae — Anomocaridae, Changshaniidae, Dike1okephalidiae (Dike1okephalinae, Osceoliniae), Hungaidiae [=Hungaiinae], Dike1okephalinae, Tingoocephalinae

Superfamily Psychaspidae — Conokephaloinae, Saukiidae (Saukiinae, Prosaukiinae), ?Shirakiellidae, Euptychaspidae, Euphytaspidae, Psychaspidae, Psychaspidae

Superfamily Burlingiidae — Burlingiidae

Superfamily Proetidae — Holotrachelidae, Proetidae, Proetellinae, Proetopelmatinae, ?Pemropoetinae), Tropidocoryphidae (Tropidocoryphinae, Astycoryphinae, Denemarkinae), Cyrtosymbolidae (Cyrtosymbolinae, Eodrevermanniinae, Pteropariinae), Dechenellidae, Phillipidiae (Phillipiiinae, Griffithiniinae, Ditomopyginae, Anisopyginae), Brachytoptidiae

Superfamily Asaphidae — Nileidae (Nileinae, Parabarrandinae), Asaphidae (Asaphinae, Taingushshinae, Canberra Nileiinae, Ogygiocarinae, ?Ogygiocaridinae), Macrotypinae, Cyclopygidae

Superfamily Cucullidae — Styginidae, Theamataspidae, Phillipisselidiae, Cucullidiae, ?Thysanopelmatinae, Illeinae, Iliinae, Illeinae, Bursatinae

Superfamily Lichidae — Lichadinae (=Lichinae), Homolichadinae, Tetralichadinae, Echinolichadinae, Trochuridiae (Trochurinae, Dicanopelmatinae, Platylichadinae, Eurylichadinae, Euraginae)

Superfamily Odontopleuroidea — Odontopleuridae, Acantholichadinae (Acantholichadinae, Damesellidae, Damesellinae, Damesellidae, Damesellinae, Damesellidae, Damesellinae)

Superfamily Telyphoidae — Komaspidae, Ellipsocephaloidae, ?Ellipsocephaloidae, Telyphidae [=Telyphinae], Glaphuridae

Superfamily Calymenidae — Phasmostomatidae, Calymenidae (Calymeninae, Colpocoryphinae, Redlocalymeninae), Homalonoitinae (Homalonoitinae, Eohomalonoitinae, Trimerinae)

Superfamily Phacopidae — Dalmanitidae (Dalmanitinae, Zeliszkellinae, Pterygometopinae, Astrophylinae, Neosynphorinae), Phacoidea (Phacoidea, Boulineae [=Boulineinae], Phacoidea, Acastinae, Calmaninae)

Superfamily Cheiruridae — Pliomeridae (Pliomerinae, Prototasteropiniae, Placoparinae, Pliomerillinae), Cheiruridae (Cheirurinae, Cyrtometopinae, ?Crotalurinae, Sphaerexochinae, Deiphoninae, Areininae, Staurocephalinae, Heliomerinae), Encrinuridae (Encrinurinae, Cybelinae)

Superfamily Harpidae — ?Hypotheticidae, Loganoptidae, Harpidae, Harpidae, Entomaspidae, Entomaspidae

Superfamily Trinucleidae — Ithyophoridiae, Trigryposidae (=Trigrypinae), Orometopidae, Raphiophoridiae (Raphiophorinae, Ampxininae), Seleucemidae, Endymionidae, Diodidae, Tranucleidae (Tranucleinae, Tretaspinae [=Tetraspidinae]), Cryptolithinae, Novaspinae (=Novaspinae)

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), Holmren (1916), Walcott (1918), Wurburg (1925), Hnriksen (1926), Richter (1933), Sturmer (1942), Raw (1953), and Hupe (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 Hupe (1953). According to him, the rostral plate, hypostoma, and librigenae are different parts of a single cephalic (ocular) segment. The rostral plate necessarily 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 Hupe (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 opisthoparian 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 by 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 Tetracoma, Acerocare, Bokeraspis, 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, Remopleuriridae, 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 L. 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 Brogger 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 quadra-tus, among the Ilaenuridae, 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. Poul sen’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 Poul sen, through a meraspid stage showing proparian conditions. If we take Poul sen’s observations at their face value, this probably means that P. scarabaeoides (in the holaspis 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 Poul sen (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 Bardande (1852) but reinterpreted as proparian by Poul sen.

Strand’s (1927) description and illustrations of 2 protaspides of Olenus gibbosus, showing what he regarded as proparian sutures, seemed to lend support to Poul sen’s contention. In 1942, Stö rmer 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 protaspis 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 Stöhrner, and it is conceivable that the sutures are concealed by the nearly vertical margins of the minute cephalon. It seems, therefore, that no grounds exist for thinking that the early larval (protaspis) stage of *Peltura scarabaeoides* was characterized by a proparian suture. If we should accept the conclusion that in this species both the protaspis and the holaspis stages show opisthoparian sutures, we would be forced to admit that during ontogeny of this trilobite an early (protaspis) opisthoparian condition was succeeded by a proparian (meraspis) stage, lastly to be substituted by a permanent (holaspis) 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 meraspis 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 meraspis 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 onocoryphids, submarginal sutures of trinucleids and dionids, 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 Hapalocheleidae 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. ducifrons* are "end products" in an evolutionary suite characterized by progressive outward migration, reduction, and final disappearance of the eyes. Here, however, the sutures are pro-
parian, 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 Raphiodoridae and Alsataspidae. The wholly marginal sutures of the second group, however, seem to have originated in a manner similar to that of the marginal sutures of harpids. This seems strongly suggested not only by the vestigial eyes of Couloumania, but especially by the notable homoeomorphy between such genera as Dasometopus and Loganopelis. If this is actually true, the Conocoryphidae 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 harpids, 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 Loganepeltoides and Loganopelis 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 Loganepeltoides 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 Loganepeltoides-Loganopelis suite), the harpoid 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

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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 Alsatacididae. *Orometopus* has opisthoparian sutures of almost cedariaiform 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 conduct 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, opisthonian, 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 opisthonian 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 sutureal pattern of trilobites was of ptychopariid type with opisthonian 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 transacted 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 opisthonian ptychopariid suture 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 Permain times, trilobites characterized by a ptychopariid suture 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, Zacanthoidea, and seemingly also by *Hemirhodon* (Dolichometopidae) and *Hysterozus* (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, re-
presented by the Asaphidae, some species of *Theodenisia* (Catilicephalidae), *Stenoplites* (Plethopeltidae), some species of *Leiocoryphe* (Plethopeltidae), *Dikeloecephalus* (Dikeloecephalidae), *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 *Dikeloecephalus* (Dikeloecephalidae), *Levisella* (Loganellidae), *Hungaia* (Hungaiidae), *Lauzonella* (Loganellidae), *Loganelius* (Loganellidae), some species of *Deiocoryphe* (Plethopeltidae), and *Rasettia* (Loganopygidae).

**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 aforementioned 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 *Loganopelitis*.

**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 Hopé (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
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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-Loganopelis stock of the Harpидidae. P. bootes is similar in this respect to Loganopeltoides zenkeri, while Opsidiscus practically duplicates the sutural conditions of Loganopelis. 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 Stubbsfield 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 ................................ HD
Howell, B. F. .................................................... HO
Jaunusson, 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)
Classification

Olenida (order) (20).
Eodiscidae (6).
Daguinaspididae (2; 3).
Spinagnostidae (17).
Sphaeragnostidae (1).
Clavagnostidae (1).
Ellipsocephalidae (18; 9).
Abadiellidae (3).
Dolerolenidae (1).
Family Uncertain (2).

Olenelloidinae (1).
Olenellinae (7).
Elliptocephalinae (1).
Holmiinae (3).
Fallotaspidinae (1).
Nevadiinae (1).
Pararedlichiinae (5).
StrenueIlinae (4; 7).
Kingaspidinae (2; 2).
Palaeoleninae (3).
Antatlasiinae (1).
Protolenidae (21; 8).
Termierellinae (6; 3).
Myopoleninae (3).
Protoleninae (8; 5).
Bigotininae (1).
?Aldonainae (1).
Subfamily Uncertain (2).

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)

Calliavinae (3).
L.Cam. (PO)

Elliptocephalinae (1).
L.Cam. (PO)

Fallotaspidinae (1).
L.Cam. (PO)

Holmiinae (3).
L.Cam. (PO)

Nevadiinae (2).
L.Cam. (PO)

Olenelloidinae (1).
L.Cam. (PO)

Wannerinae (1).
L.Cam. (PO)

Daguinaspididae (2; 3).
L.Cam. (PO)

Redlichina (suborder) (83; 19).
L.Cam.-M.Cam. (MO)

Redlichiacae (superfamily) (25; 2).
L.Cam.-M. Cam. (MO)

Redlichidae (10).
L.Cam. (PO)

Redlichidae (5).
L.Cam. (PO)

Pararedlichiinae (5).
L.Cam. (PO)

Neoredlichidae (4; 2).
L.Cam. (HA)

Saukiandidae (2).
L.Cam. (HA)

Gigantopygidae (1).
L.Cam. (HA)

Despoulosidae (1).
L.Cam. (HA)

Yinitidae (1).
M.Cam. (HA)

Abadilleidae (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)

Kingsapidinae (2; 2).
L.Cam. (HE)

Palaeoleninae (3).
L.Cam. (HE)

Antatlasinae (1).
L.Cam. (HE)

Protolenidae (21; 8).
L.Cam. (HE)

Termierellinae (6; 3).
L.Cam. (HE)

Myopoleninae (3).
L.Cam. (HE)

Protoleninae (8; 5).
L.Cam. (HE)

Bigotininae (1).
L.Cam. (HE)

?Aldonainae (1).
L.Cam. (HE)

Subfamily Uncertain (2).
L.Cam. (HE)

Yunnanoccephalidae (1).
L.Cam. (HE)

Family Uncertain (2).
L.Cam. (HE)

Paradoxidae (superfamily) (16).
Up.’L.Cam.-M. Cam. (MO)

Paradoxidae (15).
Up.’L.Cam.-M. Cam. (PO)

Paradoxidae (5).
M.Cam. (PO)

Centroleurinidae (3).
M.Cam. (PO)

Metadoxinidae (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 (7).
L.Cam.-M. Cam. (RA)

Dolichometopidae (29; 4).
L.Cam.-U.Cam. (PO)

Corynexochidae (4).
L.Cam. (PO)

Corynexochinae (3).
L.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)

Ptychoparicea (superfamily) (63).
L.Cam.-L. Ord. (MO)

Ptychoparidae (32).
L.Cam.-L.Ord. (MO)

Ptychopariinae (10).
M.Cam.-U.Cam. (HO)

Periommeleane (1).
L.Cam. (RA)

Eulominae (2).
L.Ord. (RA)

Nassovinae (4).
M.Cam. (HO)

Antigninae (13).
L.Cam.-Low.M. Cam. (RA)

Gonokenealeaninae (3).
M.Cam.-U. Cam. (LB)

Alokistocaridae (30).
L.Cam.-U.Cam. (HO)

Conocoryphaceae (superfamily) (23).
L.Cam.-U. Ord. (MO)

Conocoryphidae (16).
L.Cam.-L.Ord. (PO)

Pshumardilidae (7).
?M.Cam., U.Cam.-U.Ord. (PO)

Emmrichellaceae (superfamily) (15).
M.Cam.-L. Ord. (MO)

Emmrichellidae (13).
M.Cam.-L.Ord. (MO)

Emmrichellinae (9).
M.Cam.-L.Ord. (HO, MO)

Changshaniae (4).
M.Cam. (HO-MO)

Liostracinae (2).
M.Cam.-U.Cam. (HO)

Creipecephalacea (superfamily) (7).
M.Cam.-U. Cam. (LB)

Creipecephalidae (5).
M.Cam.-U. Cam. (LB)

Tricreipecephalidae (2).
U. Cam. (LB)

Nepeaceae (superfamily) (1).
M.Cam. (LB)

Nepeidae (1).
M.Cam. (LB)

Dikelocelaphaceae (superfamily) (34).
L.Cam.-U. Cam. (LB)
Trilobitomorpha—Trilobita

Idahoiiidae (7). U.Cam. (LB)
Dikelecocephalidae (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)
Leptoplacinae (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)
Dokimocephalidae (10). M.Cam.-U. Ord. (PO)
Piftyriaspididae (2). L.Ord.-M.Ord. (HA)
Iliaenuracea (superfamily) (13). U.Cam. (LB)
Iliaenuridae (2). U.Cam. (LB)
Shirakiellidae (1). U.Cam. (LB)
Parabolinoicoidea (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)
Saonae (4). M.Cam. (PO)
Hystricurinae (9). U.Cam.-L.Ord. (PO)
Agraulidae (2). M.Cam. (HE)
Lonchocephalidae (11). U.Cam. (RA)
Dokimoccephalidae (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)
Blountiidae (3; 2). U.Cam. (HO)
Burlingiacea (superfamily) (2). M.Cam.-U. Cam. (PO)
Burlingidae (2). M.Cam.-U. Cam. (PO)
Komaspidae (superfamily) (16). M.Cam.-U. Ord. (LB)
Elviniiidae (5). U.Cam. (LB)
Telephiniidae (1). M.Ord.-U.Ord. (WH)
Glaphuridae (2). M.Ord. (WH)
Raymondiacacea (superfamily) (11). U.Cam. (LB)
Raymondiidae (11). U.Cam. (LB)
Raymondininae (5). U.Cam. (LB)
Cedarinae (2). U.Cam. (LB)
Llanaspidae (4). U.Cam. (LB)
Norwoodiaceae (superfamily) (15). M.Cam.-L. Ord. (LB)
Norwoodiidae (5). U.Cam.-L.Ord. (LB)
Menonomiidae (6). M.Cam.-U. Cam. (LB)
Bolaspididae (4). M.Cam. (HO)
Marjumiaceae (superfamily) (35). M.Cam.-L. Ord. (LB)
Marjumiidae (20). M.Cam.-U. Cam. (LB)
Coosellidae (4). U.Cam. (LB)
Pagodidae (10). M.Cam.-L.Ord. (LB)
Cheliocephalidae (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)
Iranspididae (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)
Kaalishanidae (4). U.Cam. (LB)
Ptychaspidae (superfamily) (24). U.Cam. (LB)
Ptychaspidae (13). U.Cam. (LB)
Saukiidae (6). U.Cam. (LB)
Eurekiidae (5). Up.U.Cam. (LB)
Remopleuridae (21). M.Cam.-U.Ord. (WH)
Remopleurinae (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)
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). M.Cam.-L.Ord. (JA)
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Calmoniinae (11). Ord.-M. Dev. (ST)

Acasinae (4; 2). Ord.-L. Dev. (ST)

Pterygometopidae (5; 6). M. Ord.-U. Ord. (ST)

(Continued on page 0167)
### Fig. 107a. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 1
(Moore, n). [Range of Geragnostidae revised; see p. 0161.]
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**Fig. 107b.** Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 2 (Moore, n). [Range of Embrichellidae revised, see p. 0161.]
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Fig. 107c. Stratigraphic and geographic distribution of trilobite orders, suborders, and families—Part 3 (Moore, n).
### REFERENCES

**Barrande, Joachim**


**Beecher, C. E.**


**Gürich, G.**


**Henningsmoen, Gunnar**


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**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)

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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 Emmrichelliidae revised; see p. 0161.]

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**Fig. 1076. 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.]

**Hupé, Pierre**


**Jaekel, O.**


**Kobayashi, Teichi**


**Lake, Philip**


**Poulsen, Christian**


**Rasetti, Franco**


**Raw, Frank**

Raymond, P. E.

Richter, Rudolf

Salter, J. W.

Størmer, Leif
(20) 1942, Studies in trilobite morphology, II. The larval development, the segmentation and the sutures, and their bearing on trilobite classification: Norsk. geol. tidsskr., v. 21, p. 49-164, pl. 1-2, fig. 1-19.


Stubblefield, C. J.

Swinnerton, H. H.

Warburg, Elsa

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1 Deceased 15 November 1956.  2 Deceased 5 January 1957.
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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 edcsial cleavage that divide the cephalon into a central portion (cranidium, comprising glabella and fixigenae) and lateral portions (librigena), 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 some 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.Per.

Order AGNOSTIDA Kobayashi, 1935

==suborder Isopygia Gürich, 1907; order Miomera Jäger, 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 & Lanner, 1957) (pro Agnostina Salter, 1864) [==superfamily Eodiscidea Richter, 1933 (partim); suborder Agnostida WHITMORE, 1939; superfamily Agnostidea WESTFALL, 1946; order Agnostida RASSELL, 1948; superfamy Agnostidae HENNINGSMOEN, 1951 (partim); superfamy Agnostidae 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 McCoy, 1849

[==Battoides HAWLE & CORBA, 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 [Entomosktacites, pisiformis WALHAGEN, 1821] [==Battus DAL-MAN, 1827]. Axis of pygidium with 3 lobes, posterior one only a little expanded at rear and not approaching border of shield; surface of genae
smooth or corrugated. *U. Cam.*, Eu.-China.—Fig. 108.1. *A. pisiformis* (*Wahl.*), Agnostus **pisiformis** Z., Swed.; 1a, ceph., pyg., ×6 (331*).

**Acrarhachis** **Resser**, 1935 [*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. parrnatus*]. 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. parnatus*, Elrathia 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 subgloabal 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.
Clavagnostus HOWELL, 1937 [*Agnostus repandus WESTERGÅRD, 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 Condylopugidae 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 WALTGOTT, 1890]. Axis of pygidium rather short, not expanded at rear; surface smooth. L.Cam., N.Y.—Fig. 112.2. *M. desideratus (WALTGOTT), 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 ovaly rounded at rear, with its transverse furrows faint or obsolete;
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, cepha., ×9.25; 1b, pyg., ×8.85 (334*).

*Linguagnostus* KOBAYASHI, 1939 [*Agnostus kjerulfii* BRØGGER, 1878]. Axis of pygidium short and bluntly pointed at rear. *M.Cam.*, Eu.-Sib.-Newf.-Arg.—Fig. 114,2. *L. kjerulfii* (BRØGGER), Andrarum F., Swed.; 2a,b, cepha., 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, cepha., ×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*).
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 LÎNNARSSON, 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 (LÎNNARSSON), Tremadoc., Wales; X11.5 (114*).

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

Fig. 115. Geragnostidae (p. O176-O178).
Agnostida—Agnostina

Pygidial axis only half as long as pygidium; genal regions and pygidial pleural regions corrugated. *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*).

**Homagnostoids** Kobayashi, 1939 [*Agnostus ferralensis* 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. ferralensis* (Munier-Chalmas & Bergeron), L. Tremadoc.; 5a,b, ceph., pyg., ×7.2 (377*).

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**Fig. 116. Hastagnostidae** (p. O178-O179).
Trilobitomorpha—Trilobita

Trinodus M'Coy, 1846 [*T. aglostiformis*] [=Arthrorhachis HOWLE & 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.-B.C.-Arg.-China-Burma.—Fig. 115,6. *T. aglostiformis*, 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* BRUGGER, 1878] [=Ceragnostus 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* (BRUGGER), 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* BRUGGER, 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* (BRUGGER), 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

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**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. tricectus (SALTER), Peltura minor Z., Swed.; 7a,b, ceph., pyg., X6 (331*).

**Psychagnostus** Jaekel, 1909 [*Agnostus punctuosus Angelin, 1851; SD Vogdes, 1925] [=Caran­tagnostus 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 (Angelín) Psychagnostus punctu­osus Z., Swed.; 1a,b, ceph., X5.4; 1c,d, pyg., X5.4 (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., X7.1; 2c,d, pyg., X8 (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., X5.1; 3b, pyg., X4.75 (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.

**Micagnostus** 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; X10 (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. 118,7. *A. dux (Call­away), Tremadoc, Eng.; X8 (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., X7; 2b, pyg., X7 (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

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**Fig. 118. Micragnostidae (p. O179).**
Fig. 119. Phalacromidae (p. O181).
broad, well-defined axis that bears strong tubercle, margin with pair of slender, long, slightly incurved spines. U.Cam., Kazakhstan.—Fig. 128, 1. *E. grandis* 1a, b, ceph., pyg., ×6 (423) (M).

**Family PHALACROMIDAE Hawle & Corda, 1847**

[konc. correc. Howell, 1935 (pro Phalacromides Hawle & Corda, 1847)] (=Leiagnostidae JAEKEL, 1909; Phalagnostidae 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] (=Plagnostus 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*, Centroleura 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*, Echinophaeites 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. limbatis*]. 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* (ANGEVIN), Solenoploea brachymetopa Z., Swed.; 7a, ceph., ×8; 7b, c, pyg., ×8.3 (334°).

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Fig. 120. Pseudagnostidae (p. O182-O183).
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 Jaeckel, 1909 [*Agnostus cyclopyge Tullberg, 1880] [=Pleagnostus Clark, 1924; Eupleagnostus 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.-Alaska-Arg. — Fig. 120, 2. *P. cyclopyge (Tullberg), Francon., Swed.; 2ab, ceph., pyg., X6.4 (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., X11; 1b, pyg., X11.7 (117*).

Machairagnostus Harrington & Leanza, 1957 [*M. tmeius]. 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.

Spinagnostus franklinensis Howell (Spinagnostidae), M.Cam., Vt., X13 (71, 1935).
**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*).
Family SPINAGNOSTIDAE Howell, 1935

[Incl. Quadragnostinae Howell, 1935; Hypagnostinae Lychn., 1935] [=Peronopsidae Westerg., 1946; Rudagnostidae Lermanova, 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 tuberule; surface smooth. M.Cam., NE.USA—Fig. 123, 1. *S. franklinensis*, Up.M.Cam., Centopleura vermontensis Z., St. Albans Sh., NW.Vt.; 1a,b, ceph., pyg., x13 (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., x7 (429*).

Archaeagnostus Kobayashi, 1939 [*A. primigenius*]. 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. primigenius*, Schodack F.; 2a,b, ceph., pyg., x10 (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., x11.5; 1b, pyg., x12.3 (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.; x14.25 (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. 124, 4. *C. barlowii* (BELT), Meneuvian, Wales; x8 (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. 125, 5. *C. lens* (GRÖNWALL), Ptychagnostus punctuosus Z., Swed.; 5a,b, ceph., x8.3; 5c,d, pyg., x8.85 (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 back border; surface smooth. L.Cam., Pa.—Fig. 124, 6. *E. roddyi*, Kinzers F.; x17 (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., x4.6 (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.,...
Agnostida—Agnostina

Swed.; la, b, ceph., with thoracic segments, pyg., X8.2 (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., X7.6 (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.; X8.5 (235*).

Pentagnostus Lermontova, 1940 [*P. anaharenis]. 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. *P. anabarensis; 3a, ceph., ×8.2; 3b, pyg., ×7.6 (117*).

**Peronopsis Hawle & Corda, 1847** [*Battus integer Beyrich, 1845*] (=Diplorhina Hawle & Corda, 1847; Mesosphenicus Hawle & Corda, 1847; Mesoagnostus Jaekel, 1909 (obj.); Pseudoperonopsis Harrington, 1938). Front lobe of glabella sub-quadrate; 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.-Denn.*——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*).

**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.-Denn.*——Fig. 127,2. *T. exsculpta (Angelín), 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 Eodiscidae Richter, 1932 (partim); Dawsoniidae Kobayashi, 1943; order Dawsoniida Lermontova, 1951; superfamily Agnostacea Henningmoen, 1951 (partim); superfamily Eodiscoidae Hupe, 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 Reeser, 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).

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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), N.Y.; 1a,b, whole exoskel., ceph., ×7.5 (448n).

Calodiscus Howell, 1935 [pro Goniodiscus Raymond, 1913 [non Müller & Troeschel, 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., E.N.Am.—Fig. 129,2. *C. lobatus* (Hall), N.Y.; 2a, ceph., ×12; 2b–e, pyg., ×12 (488n).—Fig. 129.3. *C. meeki* (Ford), N.Y.; 3a,b, ceph., ×7.5 (488n).


Opsidiscus Westergård, 1950 [pro Aulacodiscus Westergård, 1946 [non Douville, 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., E.N.Am.—Fig. 130.1. *O. bilobatus* (Westergård), Swed.; 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., E.N.Am.—Fig. 130.3. *W. nobilis* (Ford), N.Y.; 3a,b, holotype, thorax lacking, ×9 (46).


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

*Pagetia* WALCOTT, 1916 [*P. bootes*] [=Epagetia, *Mesopagetia* KOBAYASHI, 1943; ?*Pagetina* LEMONTOVA, 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-
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).


Hebediscus WHITEHOUSE, 1936 [*Psycophoria? attlborensis SHALER & FOERSTE, 1888]. Glabella straight-sided, tapered, unfurrowed; occipital ring simple; border furrow shallow, border flat; palpebral lobes relatively long, palpebral furrows indistinct; librigena 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. attlborensis* (SHALER & FOERSTE), Newf.; 2a,b, cran., X6; 2c, pyg., ×6 (448n).

Hebediscus WHITEHOUSE, 1936 [*Psycophoria? attlborensis SHALER & FOERSTE, 1888]. Glabella straight-sided, tapered, unfurrowed; occipital ring simple; border furrow shallow, border flat; palpebral lobes relatively long, palpebral furrows indistinct; librigena 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. attlborensis* (SHALER & FOERSTE), Newf.; 2a,b, cran., X6; 2c, pyg., ×6 (448n).

Neocobboldia RASSETI, 1936 [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 RASSETI, 1945 [*P. elegans*]. Similar to Pagetta 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 RASSETI, Que.; 5a,b, cran., ×7.5; 5c, pyg., ×7.5 (448n).

Pagetides RASSETI, 1945 [*P. elegans*]. Similar to Pagetta 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 RASSETI, Que.; 5a,b, cran., ×7.5; 5c, pyg., ×7.5 (448n).

Pageticus 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 libriigenae, ×7.5 (117).

Pageticus 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 libriigenae, ×7.5 (117).

Order REDLICHIIDA Richter, 1933 [nom. correct. MOORE, herein (pro Redlichina RICHTER, 1933)]; suborder Micropygia GURICH, 1907 (parum); suborder Mesonacida SWINNE'TON, 1915 (partim); order Mesodiscida POULSEN, 1927; suborder Redlichina RICHTER, 1933 (partim) [Type—Redlichia COSMANN, 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 OLENNELINA Resser,** 1938

([nom. corrig. Moore, herein (pro ord. Olenellida RESSER, 1938)] [=suborder Mesonacida SWINNERTON, 1915; order Mesonacida POULSEN, 1927; superfamily Olenellidae RICHTER, 1941; order Protoparia STÖMER, 1942 (non SWINNERTON, 1915); superfamily Olenellacea HENNINGSMOEN, 1951; superfamily Olenelloidae Hopé, 1953] [Type—*Olenella 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 rudimentary. *L.Cam.*

**Family OLENNELLIDAE Vogdes, 1893**

([emend. Mesonacidae WALCOTT, 1891] [Mesonacidae WALCOTT, 1910] [nom. consav. 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

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![Fig. 133. Olenellidae (Olenellinae, Callaviinae, Fallotaspidinae) (p. O192-O194).](© 2009 University of Kansas Paleontological Institute)
surface usually covered with granules or delicate network of raised lines or both. *L.Carn.*

**Subfamily OLENELLINAE Voges, 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 pleuræ 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, 1885; SD Walcott, 1896] [=Mesonacis Walcott, 1885]. Glabella long, with rounded frontal lobe, usually reaching anterior border furrow; palebral 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 palebral 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 palebral lobes, and almost flat, much wider anterior border (56). *L.Cam.*, N.Am.—Fig. 133.1. *F. halli* (Walcott), Ala.; ceph., ×1 (56).

*Fremonitia* raw, 1939 [*Olenellus fremonti* walcott, 1910]. Differs from *Olenellus* in having much shorter palebral 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).

*Laudonia* howell, 1939 [*Olenellus iddingsi* walcott, 1884]. Differs from *Olenellus* in having conspicuous metagenal spines in direct continuation of lateral border, simulating true genal spines (56). *L.Cam.*, N.Am.—Fig. 134. *L. iddingsi*, B.C.; ceph., ×4.5 (56).

*Paedeumias* Walcott, 1910 [*P. transitans* (Walcott), 1910]. 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.—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 yorkensis* Walcott, 1884]. Differs from *Olenellus* in having tumid, bluntly terminating genal spines (312). *L.Cam.*, N.Am.—Fig. 135.6. *P. yorkensis* (Walcott), Nev.; 6a, cephalon, ×2; 6b, genal angle and genal spine, ×3 (312).

**Subfamily CALLAVINAE** 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; palebral 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; pleuræ 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) broggeri 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.Carn., E.N. Am.-Eng.-?Sp.-N.Afr.—Fig. 136. *C. broggeri (WALCOTT), Newf.; a, restored dorsal exoskel., ×0.5; b, median part of rostral plate with 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 KLAR, 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. 0192-0195).
Trilobitomorpha—Trilobita

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 cepha., showing rostral plate and hypostoma, ×0.57 (90).

Subfamily ELLIPTOCEPHALINAE Hupe, 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 Marcor, 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 Hupe, 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 spinous 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 Hupe, 1953 [pro Fallotia Hupe, 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 Hupe, 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-
eral 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 Schmidtiia 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

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**Fig. 137. Olenellidae (Callaviinae, Neltneriinae) (p. O193-O196).**
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. mickwitzii (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 (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.

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 NEVADINAE Hupé, 1953

Exoskeleton subovate. Cephalon very wide, with narrow, conical glabella, 3 translabellar 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; char-

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acter 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, sub-tapering 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*; cephal. and thorax, X3 (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

[non. correct. Poulsen, herein (ex Daguinaspidae Hupé, 1953)]

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

Daguinaspis Hupé & Abadie, 1950 [*D. ambroggi*]. 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.) ambroggi*; restored dorsal exoskeleton, x1.5 (445).

D. (Eodaguinaspis) Hupé, 1953 [*D. (E.) abadieri*]. 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 cephal., X3 (77).

Suborder REDLICHIINA

Harrington, nov.

[=superfamily Redlichioidea Richter, 1933; Redlichioidea Henningsmoen, 1951; Redlichioidei Hupé, 1953] [Type—Redlichia Coudmann, 1902]

Dorsal exoskeleton elongate, subelliptical in outline. Cephalon semicircular to semieliptical, 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 Redlichioidea Richter, 1933, nom. transl., ex Redlichioidea 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.
Family REDLICHIIDAE Poulsen, 1927
[nom. correct. Hitomi, 1933 (pro Redlichidae Poulsen, 1927)] (=Latiredlichiidae Hupe, 1953 [parsim.])

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; pleuræ 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 Redlichidae Poulsen, 1927)]

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

**Redlichia** Cossmann, 1902 [pro *Hoeferia* Redlich, 1899 (non Bittner, 1895)] [*Hoeferia noetlingi* Redlich, 1899]. Anterior lateral glabellar furrows almost normal to axis, remainder oblique, pre-occipital 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 postero-lateral spines. **L.Cam.**, Korea-China-W. Pak.-Iran-AustraI.-?Sib.--*FIG. 141,2.*

**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).

**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. luis (=Redlichia walcotti Lu, 1941; non Mansuy, 1912)]. Differs from *Pararedlichia* in having shorter frontal glabella. **L.Cam.**, China.—*FIG. 141,5.* *A. luis*; 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.
Redlichiida—Redlichina—Redlichiacae

(Redlichops) blanckenhorni. Differs from Para- 
redlichia in having anterior lateral labellar 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 
and extending back to level of mid-length of occip­
tal ring, much wider fixigenae, and finely granulous 
surface. L.Cam., Jordan.—Fig. 141.8. *R. 
blanckenhorni; cran. (holotype), X2.35 (461).

Family NEOREDLICHIIDAE Hupé, 1953

Dorsal exoskeleton opistharian, ovate, 
slightly convex, isopygous. Cephalon semi­
elliptical; glabella conical, with 3 pairs of 
evenly spaced lateral labellar furrows, an­
terior 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 sec­
tions of facial suture moderately divergent 
(less than 45°) to border furrow, slightly 
curved outward across border; eye lobes 
long, decurrent along frontal labellar 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 fixi­
genae 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; pleu­
ral regions with 5 to 8 pleurae; border 
smooth, not delimited by border furrow. 
L.Cam.

Neoredlichia Sargo, 1936 [*Redlichia nakamura­ 
Sargo, 1934]. Frontal labellar lobe short, an­
terior lateral labellar furrows (3p) normal to 
axis, remainder well marked, transglabellar, 
slightly bent backward; occipital furrow subparal­
lel 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. nakamura (Sargo), 
China; 4a, cran. (holotype), X6; 4b, librigena 
(paratype), X2.65 (465).

Clariondia Hupé, 1953 [*C. chazani]. Differs from 
Neoredlichia in having longer and narrower 
labella, lateral labellar and occipital furrows
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., Sp.-Morocco.—Fig. 143,1. *R. (R.) resserianus; exoskel. (reconstr.), X3 (461).

R. (Resserops) Richter & Richter, 1940 [*R. (R.) resserianus*] (=Perrector Richter & Richter, 1940) (=R. (Rawops) Hupé, 1953). Differs from Saukianda in having shorter glabella, longer frontal glabellar lobe, chevron-shaped pre-occipital 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 mid-length of occipital ring. L.Cam., Sp.—Fig. 145,4. *E. eo*; cran. (holotype), X2 (461).

Family SAUKIANDIDAE Hupé, 1953

Dorsal exoskeleton opisthoparian, ovate, gently convex, micropygous. Cephalon semi-elliptical; 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; libriegenae wide, genal spines present. Thorax of 15 segments; axis narrower than pleural regions; pleurae ending in spines, fulcrum proximal. Pygidium small, semi-elliptical, paucisegmented; axis short, tapering backward; pleural regions subtriangular, small; border very wide, flat. Surface of dorsal exoskeleton finely granulose. L.Cam.
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).
Family GIGANTOPYGIDAE 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 ending in spines, 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).

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, 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.

Family DESPUJOLSIIDAE Harrington, nov.

Dorsal exoskeleton opisthoparian, ovate, gently convex, isopygous. Cephalon semiepiprephal; 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.
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., China.

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; la, cran. (holotype), X2.7; 1b, pyg. (paratype), X2.5 (426).

Family ABADIELLIDAE Hupé, 1953

Opisthoparian. Glabella conical to sub-ovate, 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 sutures moderately divergent, posterior extremity of eye lobes distant from anterior borders. L.Cam., Morocco.—Fig. 145,5. *A. bourgini; cran. (holotype), X1.75 (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), X1 (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), X2.45 (419).

Family DOLEROLENIDAE Kobayashi, 1951

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

Dorsal exoskeleton opisthoparian, ovate, gently convex, micropygous. Cephalon semi-elliptical 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. 147. Dolerolenus zoppii (MENEGHINI) Leanza (Dolerolenidae), M.Cam., Sardinia, X3 (380, 488).
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. *Upl.L.Cam.*
**Dolerolenus** **LEANZA, 1949** [pro **Olenopsis** BORNEMANN, 1891 (non AEMEGHINO, 1889)] [**Olenus zoppii** MENEGHINO, 1882; SD WALCOTT, 1912]. Glabella rounded in front, posterior extremities of anterior sections of facial suture distant from axial furrows; palpbral 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* (MENEGHINO) LEANZA; restored dorsal exoskel., ×3 (488, pygidium from 380).

**Family UNCERTAIN**


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

**Superfamily ELLIPSOCEPHALACEA** **MATTHEW, 1887** [*nom. transl.* HENNINGMOEN, herein (ex Ellipsocephalidae MATTHEW, 1887) = Ellipsocephalidae RICHTER, 1933 (part.;) Ellipsocephaloidea MATTHEW, 1933; order Prololenidae HUPPI, 1953].

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; palpbral field present or not; thin eye ridges present except in very smooth forms, palpbral 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, 1895** [nom. transl. KOBAYASHI, 1935 (ex Ellipsocephalidae MATTHEW, 1887)].

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

**Ellipsiocephalus** **ZENKER, 1833** [**E. ambiguus* (=**Trilobites hoffi** SCHLOTHEIM, 1823) (=**Eelleipsocephalus** ZENKER, 1833 (emend. to **Ellipsiocephalus**, 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).

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

**Angusteva** **HUPÉ, 1953** [*Psychoparia? annio COBBOLD, 1910*]. Like *Strenuava* but with shorter palpbral 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 (Strenu­eva) insecta RICHTER & RICHTER, 1940*]. Like *Alania* but palpbral field inflated. *L.Cam.*, Sp.—Fig. 149,8. *H. insecta*; exoskel., ×5 (461).

**Inoyellaspis** **IVSHIN, 1953** [*I. expectans*]. Resembles *Strenuava* *M.Cam.*, Kazakhstan.

**Strenuava** **RICHTER & RICHTER, 1940** [*Arionellus primaeveus BRøGGER, 1879*]. Like *Strenuella* but with inflated frontal area. *L.Cam.*, Eu.—Fig. 149,3. *S. primaeveus* (BRøGGER); cran., ×2.2 (417).

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

**Subfamily STRENUELLINAE** **Hupé, 1953**

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

**Strenuella** **MATTHEW, 1887** [*Agraulos strenua BILLINGS, 1874; SD KIAER, 1916*]. Cephalic axis tapering slightly forward or almost parallel-sided; palpbral 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 platye­cephalum COBBOLD, 1910*]. Without occipital spine. *L.Cam.*, NE.N.Am.-Eu.-Morocco.—Fig. 148,10. *S. (C.) platyecephala* (COBBOLD), Eu.; incompl. ceph., ×3 (387).

**Luaspis** **Hupé, 1953** [*Pseudoptychoparia reedi LU, 1941*]. Like *Micmacca* (Myopimmacca) but apparently with even shorter palpbral lobes. *L.Cam.*, Yunnan.—Fig. 148,3. *L. reedi* (LU); cran., ×2 (426).

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 Voorges, 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. iberica]. Cephalic axis with subparallel sides, large frontal area; close to Strenuella. L.Cam., Sib.—Fig. 148,8. *M. (P.) iberica (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.


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

Subfamily PALAEOLENIINAE 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).


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).
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 biseg-
Redlichida—Redlichia—Ellipsoccephalacea

mented; with parafrenal band. L.Cam., Morocco.
——Fig. 151.6. *T. (T.) laitrons; cran., X1 (77).

T. (Brevitermierella) Hufé, 1953 [*T. (B.) brevi­
frons]. Like T. (Termierella) but palpebro-ocular
ridges increasing in width distally. L.Cam., Morocco.——Fig. 151.7. *T. (B.) brevi­
frons; cran., X1 (77).

T. (Jalonella) Hufé, 1953 [*T. (J. celiibera
Hufé, 1953 (=Lasioptis ribotatus Richter & Rich­
ter, 1948)]. Like T. (Brevitermierella) but
with narrower (tr.) fixigenae. L.Cam., Sp.—
Fig. 151.8. *T. (J. ribotana (Richter & Rich­
ter); cran., X1 (252).

Bigotinops Hufé, 1953 [*B. dangeardi]. Like Ter­
mierella but anterior sections of facetal sutures
less divergent and lateral glabellar furrows finely
connected across glabella. L.Cam., Morocco.——
Fig. 151.1. *B. dangeardi; cran., X3.35 (77).

Oujiania Hufé, 1953 [*O. meridionalis]. Like Ter­
mierella but anterior sections of facetal sutures
less divergent and only 2 pairs of lateral glabellar
furrows, preoccipital pair bifurcating, both branches
faindy connected across glabella. L.Cam., Morocco.——
——Fig. 151.2. *O. meridionalis; cran., X1.5
(77).

Paratermierella Hufé, 1953 [*P. elegans]. Like Ter­
mierella but without preglabellar field. L.Cam.,
Morocco.—Fig. 151.4. *P. elegans; cran., X1.5
(77).

Pruvostina Hufé, 1953 [*P. nicklesi]. Like Ter­
mierella but anterior sections of facetal sutures less
divergent; proximal part of palpebro-ocular ridge
longitudinally bisegmented. L.Cam., Morocco.——
Fig. 151.3. *P. nicklesi; cran., X1.3 (77).

Pseudolenus Hufé, 1953 [*P. ourikâensis]. Like Ter­
mierella but anterior sections of facetal sutures less
divergent, and palpebro-ocular ridge longi­
dinally bisegmented even in distal end. L.Cam.,
Morocco.—Fig. 151.5. *P. ourikâensis; cran.,
X2 (77).

Subfamily MYOPSOLENINAE Hufé, 1953
[Emend. Henningsen, herein]

With more or less distinct parafrenal
band. L.Cam.

Myopsolenus Hufé, 1953 [*M. magnus]. Long
palpebral lobes reaching posterior border furrow,
parafrenal 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., X0.6 (77).

Collyrodenus Hufé, 1953 [*C. staminops]. Frontal
lobe long and tapering markedly forward, rest
of cephalic axis with slightly convex sides; palpe­
bral lobes short, not reaching posterior border
furrow; parafrenal band indistinct and disconnect­
ed. L.Cam., Morocco.—Fig. 151.9. *C. staminops;
cran., X0.6 (77).

Hamatolenus Hufé, 1953 [*H. continus]. Short
palpebral lobes not reaching posterior border fur­
row; parafrenal band well developed. L.Cam.,
Morocco.—Fig. 151.10. *H. continus; cran.,
X0.9 (77).

Subfamily PROTOLENIINAE Richter & Richter,
1948

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

Protenus Matthew, 1892 [*P. elegans; SD
Vogdes, 1893] (=Bergeronia Matthew, 1895
(obi.); Matthewlenus Hufé, 1953 (*Protenus
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. Pygi­
dium very small. L.Cam., N.B.-Eu.-Morocco.
P. (Protenus). Test smooth. L.Cam., N.B.-Eu.-
Morocco.—Fig. 151.12. *P. (P.) elegans; N.B.-
 incompl. ceph., X1 (77).—Fig. 151.16. P.
paradoxoides (Matthew), Eu.; incompl. ceph.,
X0.8 (77, 387).

P. (Latouchia) Hufé, 1953 [*P. latouchia Co­
bold, 1910]. Surface tuberculate. L.Cam., Eu.-
Morocco.—Fig. 151.20. *P. (L.) latouchia
(Cobbold), Morocco; incompl. ceph., X0.9
(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., X1.25 (423).

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

B. (Bergeroniellus). Broad-based genal spine. L.
Cam., Sib.—Fig. 151.18. *B. asiaticus; incompl.
exoskel., X1.5 (290).

B. (Bergeroniopsis) Lermontova, 1951 [*B.
kutorginorum]. Genal spine with narrow base.
L.Cam., Sib.—Fig. 149.5. *B. kutorginorum;
incompl. ceph., X1.3 (290).

B. (Olekmaspis) Suvorova, 1956 [*O. bobrovi].
Like B. (Bergeroniopsis), but with more diverging
facial sutures. L.Cam., Sib.—Fig. 150.5.
*O. bobrovi; incompl. ceph., X1.5 (290).

Blayacina Cobbold, 1931 [*B. miqueli]. Glabellae
tapering markedly forward, with transglabellar
preoccipital furrow. L.Cam., Fr.—Fig. 151.

?Ferralisia Cobbold, 1935 [*F. blayaci]. Like Pro­
tolenus but with cephalic axis widening forward.
Trilobitomorpha—Trilobita

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; libriгенae without genal spine. Thoracic segments 14. Pygidium minute. L.Cam.

Yunnanocephalus KOBAYASHI, 1936 [*Psychoparia 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 [*Conoeephalites 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 Paradoxa Lermontova, 1951 (parum)]

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; libriгенae 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. 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; Phanopter, Physiaccum Hawle & Corda, 1847; Plutonia Hicks, 1869; Plutonides Hicks, 1895] (3, 144, 114, 1, 143, 146, 322, 71). M.Cam., Eu.-E.N.Am. (AtI.prov.)-N.Afr.-N.Zem.-?NE.Austral. — Fig. 153.1. *P. minor (Boeck), Boh.; rostral plate with hypostoma, X3 (3).—2. *P. paradoxissimus (Wahlenberg), Swed.; exoskel., X0.75 (1).—Fig. 153.7. P. minor (Boeck), Boh.; rostral plate with hypostoma, X3 (3).


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

**Centroleura** Angelin, 1854 [*Paradoxides loveni* 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; metapleural 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* (Angelín), Swed.; a, b, cran., associated pyg., ×1 (337).

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

**Clarella** Howell, 1933 [*Anopolenus venustus* Billings, 1874]. Differs from *Centroleura* 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. *C. magnificus* (Matthew); ceph., ×0.3 (429).

Subfamily XYSTRIDURINAE Whitehouse, 1939

Heteropogous, 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 *Centroleurinae*. *Up.L.Cam.-M.Cam.*

Redlichiida—Redlichiina—Paradoxidacea

FIG. 156. Paradoxididae (Metadoxidinae, Xystridurinae) (p. 0214, 0215).

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

— Fig. 156.1. *X. saintsmithi* (Chapman); ×1.5 (340).

†Gigoutella Hupé, 1953 [*G. atlensis*]. Differs from *Xystridura* in having preglabellar field and less diverging anterior sections of facial suture (77). Up.L.Cam., Morocco.— Fig. 156.3. *G. atlensis*; cran., ×2.25 (77).

Subfamily UNCERTAIN


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-
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 Hupe, 1953


Bathynotus Hall, 1860 [*Peltura (Olenus) holopyga Hall, 1859] [=Pagura Emmons, 1860; Bathynotus 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, 6. *B. holopyga (Hall), Up.L.Cam., Vt.; exoskel., X1 (307).

Bathynotellus Lemmonova, 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)] [cf Superfamilies Bathyruricaidea Richter, 1933 (parim) + Zacanthoidea Richter, 1933 (parim); Corynexochida Richter & Richter, 1941; Bathyruricaidea Rasetti, 1948 (attributed to Richter, 1933); Zacanthoidea Henningssen, 1951 (attributed to Richter, 1932); Corynexochida Hufn., 1953 (attributed to Richter & Richter, 1941)] [Type Corynexochida 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 Dorypygidae Kobayashi, 1935)] [=Kooteniidae Resser, 1939 (nom. correct); Rasetti, 1946, pro Kooteniidae Resser, 1939; Mellertinae Hufn., 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 subparallel. Rostral plate fused with hypostoma and rudimentary. Thorax composed 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; ephialtic 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* (Linnaeus), Swed.; 1a,b, cr. and dor. and lat. views, ×3; 1c, librigena, ×3; 1d, associated hypostoma, ×4; 1e, incomplete thoracic seg., ×2 (336).—Fig. 159,2. *D. ehihliensis* Resser, China; pyg., ×3 (478).

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

Bonaria Lochman, 1956 [*Bonnia salemensis* Resser, 1936]. Differs from *Bonnia* and Bonnella 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 clave 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, cr., dor. and lat. views, ×4; 3c, pyg., ×3 (194).

Bonnella 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.

Bonnopis 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.

?Eriopis 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). L.Cam., Sib.—Fig. 160,2. *E. grandis*; incompl. exoskel., ×3 (423).

Fordaspis Lochman, 1956 [*Solenepleura nana* Ford, 1878]. Differs from *Bonnia* in having glabella perfectly rounded at both ends, more for-
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 sub-trapezoidal pygidium with wider border and 2 pairs of well-developed pleural spines (321, 316). U.Cam., N.Am.— Fig. 159, 6. *H. problematica (WALCOTT), Nev.; 4a,b, cran., pyg., X1 (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., X0.7 (488).

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


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

Fig. 159. Dorypygidae (p. 0217-0219).
of marginal spines, generally of equal length; and surface covered with smaller granules (196, 311). M.Cam., ?U.Cam., N.Am.-S.Am.-Asia.—Fig. 159. O. curiticei WALCOTT, M.Cam., Ala.; exoskel. (reconstr.), ×0.7 (488).


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.


Family OGYGOPSIDAE Rasetti, 1951

[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 RESEER, 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).

Family ORYCTOCEPHALIDAE Beecher, 1897

[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]
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. 162J. *O. primus*, Nev.; 1a, b, cran., Pyg., X2 (448n).—Fig. 161. O. burgegensis Resser, W. Can.(B.C.); exoskel., X2 (448n).—Fig. 162, O. burgegensis Resser, M. Cam., W. Can.(B.C.); exoskel., X2 (448n).—Fig. 162, O. walcotti Resser, W. USA(Idaho); hypostoma and doublure of librigenae, X2 (448n). [Genera considered synonymous with Oryctocephalus include Oryctocephalina Lermontova, 1940, and Vitaliakia Resconi, 1952.]


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. 162A. *L. roddyi* (WALcott), Pa.; complete, somewhat distorted holotype, X2 (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, X5 (448n).

Oryctocephalites Resser, 1939 [*O. typicus*]. 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. typicus*, Idaho; 3a, b, cran., Pyg., X2 (448n).


Tonkinella MANSUY, 1916 [*T. flabelliformis*]. Cephalic proportions as in Oryctocephalus but glabellar furrows less distinctly pit-shaped. Thorax with 5 segments (*T. stephensii*); 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. 162,8. T. stephensii KOBAYASHI, B.C.; exoskel., X1.5 (448n).

Family DOLICHOMETOPIDAE

Walcott, 1916

[nom. transl. HUPE, 1953] [ex Dolicometopinae Walcott, 1916] [=Bathyuriscidae Richter, 1933; Parmignaniidae Resser, 1935 (nom. correct. RASERTI, 1948, pro Parmignaniidae Resser, 1935); Ortiinae, Glossopleurinae HUPE, 1953]
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
Trilobitomorpha—Trilobita

axis extended into wide border; surface minutely punctate or granulate (101, 317, 336). M.Cam., Eu.-E.N.Am.(Adl.prov.)-?Asia.—Fig. 163.1. *D. svecicus*, Swed.; 1a, cran., x2 (101); 1b, pyg., x1 (336).


A. (Amphoton). Glabella with slightly concave sides, lacking lateral furrows; occipital ring very short, without median spine; palpbral 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. (reconst.), x0.5 (488).

A. (Amphotonella) 1942 [*Dolichometopus alcestis* 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.-Austral.—Fig. 163.2. *A. (A.) alcestis* (WALCOTT), Shantung; 2a, b, ceph., pyg., x1 (101).

A. (Puchouia) 1935 [*Bathyuriscus manchurienensis* WALCOTT, 1911]. Differs from *A. (Amphoton) in having parallel-sided glabella with 3 pairs of lateral furrows, occipital node or short spine, palpbral 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. (P.) manchurienensis* (WALCOTT), Manch.; 10a, b, ceph., pyg., x2 (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., x1 (101).

Anoria WALCOTT, 1924 [*Dolichometopus tontoensis* WALCOTT, 1916]. Cranidium without anterior border; glabella more or less clavate, smooth or indistinctly furrowed; axial furrow efiaced between anterior corners of glabella; posterior areas of fixigenae rapidly tapering; palpbral 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 posteralateral 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. (reconst.), x0.5 (488).

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

Athanaskia RAYMOND, 1928 [*A. ostheimeri*], Glabella extending to frontal margin, its anterior half strongly expanding, with 3 or 4 pairs of lateral furrows; palpbral 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., x0.5 (101).

Athanaskiella KOBAYASHI, 1942 [*Bathyuriscoides (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., x4; 9b, pyg., x5 (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; palpbral 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. *B. socialis, Que.; 6a,b, cran., librigena, X3; 6c, hypostoma, X4; 6d, 2nd-

Dolichometopus

Amphotonella

Bathyuriscus

Sunia

Amphoton

Bathyuriscidella

Anoria

Athabaskia

Athabaskiella

Fouchouia

Fig. 163. Dolichometopidae (p. 0222-0224).
8th thoracic segments, \( X_6 \); 6 \( e \), pyg., \( X_3 \) (196).

**Bathyuriscus** MEER, 1873 [*Bathyuris? 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 pleure 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.*

**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).

**Chilonorria** RUSCONI, 1952 [*C. perlotti*].

Differs from *Orria* in having semicircular pygidium with longer axis. Cephalon and thorax unknown (259).

**Clavaspiddella** POULSEN, 1927 [*C. sinypya*].

Differs from *Athanaskia* 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., N.W.Greene.—Fig. 164,1.*

**Corynexochides** RASSETTI, 1948 [*C. gregarius*].

Differs from *Bathyuriscidella* in having longer palpebral lobes, narrower posterior area of fixigenae, thorax of 77 segments with bluntly terminating pleurea, and only 1st pygidial segment well differentiated (196). *M.Cam.—U.Cam.*

**Dolichometopsis** POULSEN, 1927 [*D. reserti*].

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; libri-genae 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). *U.p.

**Glossopleura** POULSEN, 1927 [*Dolichometopsis boccur 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.-N.W.Greene.—Fig. 164,2.*

**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; pleurea 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.*

**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 *Athanaskia* 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 back-
ward-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 RASSETTI, 1948 [*O. gaspensis]. Intermediate between Bathyuriscus and Orria, differing from

Fig. 164. Dolichometopidae (p. 0224-0226).
Trilobitomorpha—Trilobita

0226

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., X2.5 (197).

Prosymphysurus Poulsen, 1927 [*P. kochi]. Differs from Glossopleura in having evenly arched cranium 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., X2; 7b, pyg., X1 (172).

Ptarmigania Raymond, 1928 [*Bathyuriscus rosensis 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., X3 (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, heteropogous 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.
Corynexochida 0227

Corynexochus 1854 [*C. spinulosus*]


---Fig. 165, 1. *C. spinulosus*, Swed.; 1a,b, cran., dorsal, lateral, X4; 1c, pgp., X4 (336).

Bonnessaspis 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.), X2 (317).

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

Subfamily ACONTHEINAE Westergard, 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*]

= Anuecanthus Angelin, 1854 (obj.); Aneucanthus BARRANDE, 1856 (obj.) (337). M.Cam., Swed.-Br.I.—Fig. 165, 3. *A. acutangulus*, Swed.; 3a,b, ceph., pgp., X4 (337).

Family ZACANTHOIDIDAE

Swinnerton, 1915

[nom. correct. Richter, 1933 (pro Zacanthoidea SWINNERTON, 1915)] [=Albertellidae, Mexicaspinae, Vanuxemellinae Hurf, 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; pleurae obliquely furrowed; no macropleural segments. Pygidium with elevated, abruptly terminated axis; general outline subtriarangular; 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., X0.6 (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 RASSETI, W.Can.(B.C.); 3a,b, cran., pgp., X3 (448n).—Fig. 167, 3c. A. bosworthi Walcott, W.Can.(B.C.); exoskel., X1 (448n).—Fig. 167, 3d. *A. helena*, Mont.; exoskel., X1 (448n).

Fieldaspis RASSETI, 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., X1.5; 1b, librigena, X1.5; 1c,d, hypostoma, ventral, lateral, X4; 1e, pgp., X1.5 (448n).—Fig. 168, 1f-g. F. superba RASSETI, W.Can.(B.C.); 1f,g, cran., pgp., X1 (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).

Prozanthoides Resser, 1937 [*Olenoides stissin-gensis 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).

Stephenaspis

3a

3b

3c

Albertella

3d

Zacanthopsis

FIG. 167. Zacanthoididae (p. 0227-0230).
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).
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. noria* WALCOTT, W.Can.(B.C.); exoskel., X2 (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., X2 (448n).

Family DINESIDAE Lermontova, 1940

[=Tollaspidae KOBAYASHI, 1943; Proerbidae HÜPE, 1953; also Dinesidae HÜPE, 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. *Upl.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. Queens.; exoskel., X1 (411).

Erbia LERMONTOVA, 1940 [*Cyphaspis sibrica 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,
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 opistharian. 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 Redlichina, 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 Calymenia, resemble the Ptychopariida, but most differ in the pattern of the glabellar furrows and are predominantly proparian or gonotoparian. The Ptychopariida seem to be closely related to the Redlichina, and probably gave rise to most or all post-Cambrian trilobite groups (except, of course, post-Cambrian agnostids). L.Cam.-M.Perm.
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. 0233, 0234).
Superfamily PTYCHOPARIACEA
Matthew, 1887
[nom. transl. et correct. Rasetti, 1954 (ex Ptychopariidae Matthew, 1887)]

Exoskeleton elongate oval, opisthopharian, 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 convoluted to flat (or rarely concave) preglabellar field; facial sutures diverging or converging 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.

Family PTYCHOPARIIDAE Matthew, 1887
[nom. correct. Richter, 1933 (pro Ptychopariidae Matthew, 1887)]

Dorsal exoskeleton elongate oval, opisthopharian, 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.

Subfamily PTYCHOPARIINAE Matthew, 1887
[nom. correct. Westergård, 1950 (ex Ptychopariidae 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.

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 cranium, 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 Arroyos F.; cran., ×3 (128*).

Drabia Wilson, 1951 [*D. acrociptila]. Cranidium small; fixigenae wide; border narrow. U.Cam., Pa.—Fig. 170.3. *D. acrociptila, 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., Queens.—Fig. 170.4. *L. sigillum, Dineus 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, *Syspcephalus gregarius* Rasetti, M.Cam., W.Can.(B.C.); exoskel., X5 (448n). 2. *S. charops* (Walcott), L.Cam., W.Can.(B.C.); cran., X6 (448n).

Glabellar 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., X1.5 (197).

* Agraulopsis Röčka, 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 slightly divergent. M.Cam., Boh.—Fig. 406,5. *A. resseri*; cran., X2 (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; librigena narrow, with genal spines. L.Cam., N.Am.—Fig. 172. *P. yorkensis*, Que.; a,b, ceph., X6, X9 (448n).

Subfamily EUOLUMINAE 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 ptychoparid type. L.Ord.

* Euloma Angelin, 1854 [*E. laeve Angelin; SD Vogdes, 1925] [=Calymenopsis Bergeron, 1895].

Glabella about 0.7 of cranial 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., X2.5; 1b, pyg., X2.5 (299).

*Pareuloma* Rasetti, 1954 [*P. brachymetopa*]. Glabella narrow, almost parallel-sided, only half of cranial 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., X5 (448n).

Subfamily NASSOVINAE Howell, 1937

(*nom. correct. Howell, herein (ex Nassoviae 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., Den.—Fig. 174,3. *N. globiceps* (Grönwall), Paradoxides davidii Z.; cran., X2 (402).

*Brunswickia* Howell, 1937 [*Conoccephalites robbi Hartt in Dawson, 1868*]. Preglabellar area of moderate size, border of cranidium low; fixigenae of moderate width; eye ridges not strongly developed; glabella subquadrat. M.Cam., E.Can.(N.B.). —Fig. 174,1. *B. robbi* (Hartt), Fossil Brook F.; exoskel., X1.8 (429).
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. clareae*]. Cranidium and glabella tapering forward; eye ridges poorly developed, border slightly convex and tilted upward. 
M.Cam., Vt.—Fig. 174,2. *V. clareae*, St. Albans F.; 2a, b, cran., librigena, × 3.8 (410†).

Subfamily ANTAGMINAE  
Hupe, 1953
[nom. transl. Rasetti, 1955 (ex Antagminae Hupe, 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. typialis* (=*Ptychoparia tenuer* 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
border furrows not reaching cranial margin. L.Cam., N.Am.—Fig. 175.3. *B. bicennis (Resser), Que.; cran., X2.5 (448n).

**Crassifimbra** Logman, 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. 175.3.

**Eoptychoparia** Rasetti, 1955 [*E. normalis*]. Similar to *Antagmus*, with anterior border furrow regularly curved. L.Cam., N.Am.—Fig. 175.4. *E. normalis*, Que.; cran., X3 (448n).

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

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Fig. 175. Ptychopariidae (Antagminae) (p. 0235-0237).
dipl 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 (488n).

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 (tv.) as occipital ring. Intergrades with Antagmus, Crassifimbria, Eoptychoparia and Prolostracus. L.Cam.—Low.M.Cam., N.Am.—Fig. 175,7. O. sidcatus RASSETTI, L.Cam., Que.; cran., ×4 (488n).

Periomma Resser, 1937 [*P. typicdlis]. 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 (488n).

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 (488n).

Poulsenia Resser, 1936 [*Solenopleura gronwalli 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).

Prolostracus POULSEN, 1932 [*P. strinelliformis]. 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. strinelliformis, E.Greenl.; cran., ×6 (173).

Somberella 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 mid-length. 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 mediially; 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. J. gregarius RASSETTI, 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 (488n).

Subfamily CONOKEPHALININAE HuPe, 1953 [nom. transl. LOCHMAN-BALK herein (ex Conokephalinidae HuPe, 1953) (not attributable to WALCOTT, 1913, on basis of ‘Conokephalinidae’, as published by him as a group designation without designation of any indication of intent to introduce a family-group name)]

Exoskeleton opisthopian, 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 pleural, interpleural grooves and border furrow very faint or obsolete, border narrow. Surface granulose. M.Cam.-U.Cam.

**Conopephala** BRGrger, 1886 [*Conopephalites ornat us BrGger, 1878; SD BASSLER, 1915*]. Gla bella low, front rounded or straight, with 3 pairs of lateral furrows; eyes behind glabellar mid-length; 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. ornat us (BrGger), M.Cam., Norway; 1a,b, cephal., pyg., x1.3 (382).

**Lobocephalina** Ržžička, 1940 [*Lobocephalus carinatus Ržžička, 1939*] (=Ržžičkaia Přšyl, 1950 (pro Loboccephalus Ržžička, 1940, non DIESING, 1838, nec KRAMER, 1898)). Gla bella 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 (Ržžička), Czech.; cran., x1.3 (464).—Fig. 176,2c. L. emmrichi (BARRANDE), Czech.; exoskel., x1.3 (370).*


**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. M.Cam.-U.Cam.

**Alokistocare** LORENZ, 1906 [*Psychoparia 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., x5 (488)*.

**Alokistocarella** Resser, 1938 [*A. typicalis]. Like Alokistocare but with border concave and narrower. M.Cam., USA.—Fig. 178.1. *A. brighamensis Resser, Utah; x1.5 (457)*.

**Amecephalina** POULESEN, 1927 [*A. mirabilis]. Like Alokistocare but border concave, wider, and more bowed forward, fixigenae narrower, and pygidium larger. M.Cam., Greendl.—Fig. 177.2. *A. mirabilis, Cape Wood F., NW.Greenl.; 2a,b, cran., pyg., x3 (172)*.

**Annamitia** MANSUY, 1916 [*Psychoparia (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., x1.75 (142)*.

**Arellanella** LOCMAN, 1948 [*A. caborcana]. Three pairs of glabellar furrows, palpebral lobes small, axis of pygidium wide. M.Cam., NW.Mex.—Fig. 177,4. *A. caborcana, Los Arrojos F., Sonora.; cran., x2.6 (128)*.

**Bythichellellus** 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., x2.6 (457)*.

**Chancia** WALCOTT, 1924 [*C. ebdo me]. 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. ebdo me, Spence Sh., Idaho; x1 (320)*.

**Chelidonoccephalus** 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., x3 (418).

**Dunderbergia** WALCOTT, 1924 [*Crepicephalus (Loganella) 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, x1 (320).

**Ehmania** Resser, 1935 [*E. weedii]. Like Ehmania but with glabellar furrows shallower and surface smooth. M.Cam., NW.USA.—Fig. 177,6.
*E. weedii*, Meagher Ls., Wyo.; exoskel., X2.2 (488*).

**Ehmaniella** Resser, 1937 (*Crepicephalus? (Loganella) quadrans* Hall & Whitfield, 1877) [=Anomaloecephalus, Clappaspis Deiss, 1939]. Like *Ehmania* but with wider cranidium, heavier eye ridges, longitudinal striae on wider preglabellar area, commonly with tubercles on cranidium, and fewer segments in pygidium. M.Cam., W.USA.

---Fig. 177. *E. quadrans* (Hall & Whit-
Fig. 178. Alokistocaridae (p. 0238-0241).

**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).

**Elrathia** PoulSEN, 1927 [*E. obtusa* [=Coelaspis, Gleasocoryphus DESS, 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. obtusa*, Pemmican River F.; Tab, 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 narrower border, more numerous thoracic segments, and smaller pygidium. *M.Cam.*, W.Can.—Fig. 177, 9. *I. porosa*, Cape Kent F.; ×1.8 (172*).


**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 Arroyos 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. propinquia* PoulSEN, Cape Kent F.; ×1.2 (172*).

**Kochina** RESSER, 1935 [*Olenopsis americana* 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*).


**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 [*Psychaspis putulosa* HALL & WHITFIELD, 1877]. Like *Dunderbergia* but with cranidium more convex, palpebral lobes longer, and surface putulose. *M.Cam.*, W.Can.—Fig. 177, 11. *M. convexa* (KOBYASHI), 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.

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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*).

**Pachyaspis** Resser, 1939 [*P. princeps*] [=Mcnauria, Rowia, Thompsonaspid 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** Hupe, 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*).
Superfamily CONOCORYPHACEA

Angelin, 1854

[nom. transl. HENNINGSMOEN, 1951 (as 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

[=Campylopeltur BURMEISTER, 1843; Conocoryphidae Salter, 1864; Psychopariidae 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. Postcephalic characters rather widely variable in different genera. 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.), Eur.-Asia.—Fig. 181,1. *C. sulzeri (SCHLOTHEIM), Czech.; 1a,b, exoskel., hypostoma, X1 (3).

Atops EMMONS, 1844 [*A. trilineatus]. Differs from Conocoryphe 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., X1 (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.).—Fig. 181,6. B. dalmani (ANGELIN), Swed.; cran., X1.5 (337).

Bailiella MATTHEW, 1885 [*Conocephalites baileyi HARTT, 1868; SD RESSER, 1936] [=Liocephalus GRÖNWALL, 1902; ?Tangshielia 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.Af.-Asia.—Fig. 182. B. emarginata (LINNARSSON), Swed.; exoskel., partly restored, X2 (337).

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


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.).—Fig. 181,3. *C. coronatus (BARRANDE), Czech., exoskel., X1 (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 de-
pression; 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.), X4 (337).

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

Fig. 181. Conocoryphidae (p. 0242-0244).
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 [*Holocelaphina 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).

Hartshillia 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.

Holocelaphina Salter, 1864 [*H. primordialis] [=Carassia Hicks, 1872]. General form ovate, thorax longer than cephalon, narrowing posteriorly to very small pygidium. Cephalon semilopipidal, 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.-Denn.-E.N.Am.(Atl. prov.). — Fig. 181.5. *H. teres (Grönwall), Denn.; ceph. (?cran.), ×4 (51).


Meneviella Stubblefield, 1951 [pro Erinnyss Salt­er, 1865 (non Agassiz, 1846); Salteria Walcott, 1884 (non W.Thomson, 1864); Menevia Lake, 1938 (non Schaus, 1928)]. [*Erinnyss 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.-Denn.-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, 1907a

* Assignment of this family to superfamal Cono­coryphacea is doubtful; alternatively it should be classified in Families Incertae Sedis.—Ed.
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., Eu.-N.Am.-S.Am.-Asia.—Fig. 183. S. pusilla (Sars), L.Ord. (Tremadoc.), Eng.; exokel. (reconstr.), \( \times 22.5 \) (475).

**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 subcubulated 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.; exokel. (reconstr.), \( \times 22.5 \) (475).

**Acanthopleurella** Groom, 1902 [*A. grindrodii*]. 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** Hope, 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., \( \times 9 \) (192).

**?Lunacrania** Kobayashi, 1955 [*L. trisecta*]. Differs from *Idiomesus* in having well-defined anterior and lateral cephalic borders, wide occipital ring, and

![Fig. 183. Shumardia pusilla (Sars) (Shumardiidae), L.Ord. (Tremadoc.), Eng.; exokel (reconstr.), \( \times 22.5 \) (475).](image)

![Shumardopsis](image)

![Idiomesus](image)

![Lunacrania](image)
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).


**Shumardops** Hupe, 1953 [*Shumardia longifrons* Troedsson, 1937]. Differ 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.

**Superfamily EMMRICHELLACEA** Kobayashi, 1935

[nom. transl. Howell, herein (ex Emmrichellidae Kobayashi, 1935)] [=Utioidea Hupe, 1933]

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


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


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 subquadrato, anterior border prominent; glabella tapering forward, with 3 pairs of discontinuous furrows; hibrigenae 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 subquadrato, 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, with occipital spine. M. Cam., E.Asia.—Fig. 185,4. *L. abaris (WALCOTT), Kiu-lung F., China; cran., ×5 (488*).


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*).

Protemnites WHITEHOUSE, 1939 [*P. elegans]. Cranidium like that of Eurostina but glabella with only 2 pairs of furrows, narrower hibrigenae, and less prominent palpebral lobes and anterior border. U. Cam., Austral.—Fig. 185,6. *P. elegans, Elrathia 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*).


Subfamily CHANGSHANIINAE Kobayashi, 1935


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 subquadrato. Pygidium
subtriangular, without spines. M.Cam., E.Asia.—Fig. 185.9. *C. conica*, Kushan F., China; 9a,b, cran., pyg., X3 (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., X5; 10b, pyg., X6.5 (488*).

Shangtungia WALCOTT, 1905 [*S. spinifera*, Kushan F., China]; cran., X2.9 (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., X6.7; 11b, pyg., X6.3 (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 Liostracinaoides. Pygidium short, wide. M.Cam., E. Asia.—Fig. 186.2. *L. krausei*, China; 2a, cran., X5.5; 2b, pyg., X7 (433*).

Liostracinaoides 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., X10 (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

[=Crepicephaliidae 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 psychoparid stock. M.Cam.-U.Cam.

Crepiccephalus Owen, 1852 [*Dikelocephalus? iouisensis Owen, 1852*; SD Walcott, 1886] [=Crepicephalus Bigby, 1868; Crepicephalus Vogdes, 1890; Sneedvillia Resser, 1938; Crepicephalus 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. iouisensis* (Owen), Wis.; 3a,b, cran., X1; 3c, librigena, X1; 3d, pyg., X1 (316).

Bonneterrina Lochman, 1936 [*B. prima*] [=Hollstonia, 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, X1 (123, 126).

Crepicephalina Resser & Endo, in Kobayashi, 1935

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Trilobitomorpha—Trilobita

KOBAYASHI (non Resser & Endo), 1935 [*Crepeiphus convexus WALCOTT, 1913] [=Metrocrepeiphus KOBAYASHI, 1935]. Eyes slightly behind center of glabella; pleuropleural furrows deep but eye ridges faint; preglabellar area narrow to absent; with occipital node or short spine; fixigenae horizontal, with pleural 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 pleural curve sharply back into base of spines, border along posterior only (235, 132). M.Cam., E.Asia.-Austral.—Fig. 187,2. *C. convexa (WALCOTT), Liau-tung, Manch.; 2a,b, cran.; 2c,d, pyg., both X2 (307).

Kochaspis RESSER, 1935 [*Crepeiphus liliana WALCOTT, 1886] [=Palaeoercrepeiphus KOBAYASHI, 1935 (obj.)]. Eyes opposite center of glabella; pleuropleural furrows and eye ridges present; fixigenae horizontal or upsloping, with pleural 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 pleural 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, X1.—Fig. 187,7d. *K. cecina (WALCOTT), Low.M.Cam., Alba.; pyg., X2 (307).

Uncaspis KOBAYASHI, 1935 (emend. RAASCH & LOCHMAN, 1943) [*Crepeiphus unca WALCOTT, 1916]. Eyes slightly in front of center of glabella, glabellar furrows faint; pleuropleural furrows and eye ridges lacking; occipital spine may be present; fixigenae with pleural areas consisting only of pleural lobes, posterior area rectangular, wide (sag.) and long (tr.). Thoracic segment may have axial spine. Pygidium subpentagonal; axis tapered posteriorly with a median inward bend or short spine on each side (186). Low.U.Cam. (Dresbach.), N.Am.—Fig. 187,4. *U. unca (WALCOTT), Wis.; 1a,b, cran.; 1c, librigena; 1d,e, pyg.; all X2 (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—pycnopariid stock. U.Cam. (Dresbach.).

Tricrepicephalus KOBAYASHI, 1935 [*Arionellus (Bathyurus) texanus SHUMARD, 1861] [=Para­crepeiphus LOCHMAN, 1936]. Eyes behind middle of glabella, lateral furrows shallow, with 3 evenly spaced, round or elliptical pits in anterior border furrow; pleuropleural furrows shallow, eye ridges narrow, with occipital spine or node; fixigenae horizontal, with pleural 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, spine at posterolateral corners, narrow border along posterior continues under spines along sides (235, 316). Low.U.Cam. (Dresbach.), N.Am.—Fig. 187,4. *T. texanus (SHUMARD), Tex.; 4a, exoskel., X0.9; 4b, cran. profile, X1; 4c, pyg. profile, X1 (123, 316).

Meteoraspis RESSER, 1935 [*Pychopeia? metra WALCOTT, 1890] [=Metroaspis 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; pleuropleural furrows deep, without eye ridges; occipital node may be present; fixigenae upsloping, with pleural 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.)—Fig. 187,5. M. borealis LOCHMAN, Mon.-Tex.; 5a, exoskel.; 5b, cran. profile; both X3 (125).

Superfamily NEPEACEA

Whitehouse, 1939

[nom. transl. LOCHMAN-BALK, herein (ex Nepeidace White­house, 1939)]

Exoskeleton apparently proparian, micro­pygous. Glabella short, tapering to sub­quadrate, with straight front, glabellar fur­
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 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.

Superfamily DIKELOCEPHALA-CEA Miller, 1889
[nom. transl. HENNINGSWEN, 1951, but attributed by him to RICHTER, 1933 (ex Dikeolopephalidae MILLER, 1889)] [=Dikeolopephalidae RICHTER, 1933 (parim); Dikeolopephalidae HOWÉ, 1935 (attributed to RICHTER, 1933)]

Exoskeleton opisthoparian, medium-sized to large, ellipsoidal in outline, heteropygous to subsipopygous. Cephalon mostly semi-circular, 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 sub-rectangular, 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 mid-length 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 quadrata, 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.

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