A REVIEW OF THE TRILOBITE FAMILY AULACOPLEURIDAE

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ABSTRACT. The Aulacopleuridae and Otarionidae are considered to be synonymous. The composition and phylogeny of the family are discussed, and new family, subfamily, and generic diagnoses given.

OPINIONS concerning the classification of the trilobite families Aulacopleuridae and Otarionidae have varied; the former was commonly classified with the olenids because of the olenid-like gross morphology of *Aulacopleura*, but both are now universally assigned to the Proetacea. Some authors (e.g. Přibyl 1947, p. 537; Prantl and Přibyl 1951, p. 441) considered the two groups to be subfamilies of the Otarionidae, while Richter, Richter, and Struve (*in* Moore 1959, pp. O382, O403, and O406) regarded them as independent proetacean families. Most subsequent authors have followed the latter classification, though Bergström (1973, p. 42) and Fortey and Owens (1975, p. 230) reverted to that of Prantl and Přibyl, but used Angelin's (1854) name Aulacopleuridae since this has precedence over Otarionidae Richter and Richter, 1926.

The most recent review of the family was that of Prantl and Přibyl (1951). Much information has become available since that date and this paper summarizes our current knowledge of the family.

SYSTEMATIC PALAEONTOLOGY

Order PROETIDA Fortey and Owens, 1975

Family AULACOPLEURIDAE Angelin, 1854

(= Otarionidae Richter and Richter, 1926; Pseudotrinodidae Kobayashi and Hamada, 1972)

Diagnosis. Glabella tapering forwards or subparallel sided, commonly inflated; up to three pairs of glabellar furrows, S1 typically deep and partially defining isolated L1; S2 and S3 weak, shallow, or absent; occipital ring without lateral lobes; preglabellar field usually developed, typically convex; no panderian notch on doublure of free cheek; connective sutures converging backwards, rostral plate usually small and triangular, but may occupy most of doublure or be shaped like an inverted T; thorax of 6–22 segments, no preannulus; pygidium with 2–13 axial rings; pleural areas with 1–7 pairs of ribs with scalloped profile or with posterior pleural band elevated above anterior; cephalic doublure narrow and convex, forming with border a tube; dorsal exoskeleton smooth or granulose.

Stratigraphical range. Ordovician (Tremadoc) to Carboniferous (Dinantian).

Remarks. Most aulacopleurines, and all scharyiines in which the ventral morphology is known, have a small, triangular rostral plate (e.g. Whittington and Campbell 1967,

[Palaeontology, Vol. 21, Part 1, 1978, pp. 65–81, pl. 7.]

pl. 7, fig. 6). In *Harpidella* (*Rhinotarion*) the rostral plate extends forwards beneath the anterior cephalic spine and consequently is shaped like an inverted T (Whittington and Campbell 1967, pl. 4, figs. 10–12). There are no published illustrations of the *Namuropyge* rostral plate, but unpublished work by R.M.O. shows it to be greatly expanded like that of *Brachymetopus* (Owens and Thomas 1975, p. 818) and to occupy almost the whole cephalic doublure. In aulacopleurids and some other Proetacea the cephalic border and doublure form a 'tube' (Fortey and Owens 1975, p. 236; Owens and Thomas 1975, p. 819, text-fig. 2), where the inner margin of the doublure coincides with the border furrow. This doublure structure and type of rostral plate, together with the type of pygidial pleural rib structure, are important in distinguishing aulacopleurids from the superficially similar brachymetopids.

Following Whittington (1960, p. 407) and Owens and Thomas (1975, p. 812) we consider *Tschernyshewiella* Toll, 1899 to be a brachymetopid rather than an otarionid (i.e. aulacopleurid) as believed by Richter, Richter, and Schmidt (*in* Moore 1959, p. O406). The latter authors (p. O407) questionably assigned *Aulacopleurina* Přibyl, 1949 to the family. This genus displays no features by which it could be unequivocally assigned to the Aulacopleuridae, and the deep S2 and S3 furrows and large, well-segmented pygidium (see Schmidt 1958, pl. 1) suggest that it might be more closely related to *Eodrevermannia* (see Moore 1959, fig. 298.8, p. O391). Both genera, however, possibly have origins in the Scharyiinae.

Herein we recognize two aulacopleurid subfamilies—Aulacopleurinae and Scharyiinae. Richter, Richter, and Schmidt (*in* Moore 1959, p. O406) followed Přibyl (1947, p. 538) and Prantl and Přibyl (1951, pp. 441, 475) in assigning *Cyphaspides* to the monotypic subfamily Cyphaspidinae. Although *Cyphaspides* displays some unusual features it is not dissimilar from *Namuropyge* (see discussion p. 78). Because of this, and until the relationships of *Cyphaspides* are clarified, we assign it to the Aulacopleurinae along with *Namuropyge*. We consider the Aulacopleurinae and Otarioninae to be synonymous, and reasons for this are given below.

Subfamily AULACOPLEURINAE Angelin, 1854
(= Otarioninae Richter and Richter, 1926; Cyphaspidinae Přibyl, 1947)

Diagnosis. Glabella commonly strongly inflated; rostral plate small and triangular, or shaped like an inverted T, or occupying most of cephalic doublure; median thoracic axial spine present in several genera, arising from fifth, sixth, or seventh segments; pygidial pleural ribs of scalloped profile, or with posterior pleural band elevated above anterior. Cephalic and pygidial margins entire or spinose.

Genera and subgenera. Otarion (*Otarion*) Zenker, 1833; *O.* (*Aulacopleura*) Hawle and Corda, 1847; *Cyphaspides* Novák, 1890; *Cyphaspis* Burmeister, 1843; *Harpidella* (*Harpidella*) M'Coy, 1849; *H.* (*Rhinotarion*) Whittington and Campbell, 1967; *Namuropyge* Richter and Richter, 1939; *Otarionella* Weyer, 1965; *Otarionides* Alberti, 1969; *Pseudotrinodus* Kobayashi and Hamada, 1971*a*.

Genus OTARION Zenker, 1833

Type species. Otarion diffractum Zenker, 1833; from Silurian (Ludlow Series), Dlouhá hora, near Beroun, Prague district, Czechoslovakia; by monotypy.

Diagnosis. Aulacopleurine with deep S1 defining isolated, elongate L1; eye small, placed anterior of outer end of S1; preglabellar field convex; rostral plate small and triangular; thorax of 13–22 segments, inner edge of articulating facet about two-thirds of way out from axial furrow; pygidium with 5–8 axial rings and pleural areas much broader anteriorly than axis, with 3–7 pairs of pleural ribs with scalloped profile.

Remarks. The type species of *Aulacopleura* (*A. koninckii*) and *O. diffractum* have many common features. They differ principally in that *A. koninckii* has a more depressed exoskeleton, more thoracic segments with wider pleural areas and no thoracic axial spine, and a proportionately shorter, wider, pygidium (compare Pl. 7, figs. 10 and 3, 5, 6). The two species are evidently closely related and we see no reason to separate them above the subgeneric level.

Subgenus OTARION (OTARION) Zenker, 1833

Type species. As for genus.

Diagnosis. Otarion with faint eye ridge; 13–15 (?17) thoracic segments, axial spine on the sixth.

Stratigraphical range. Silurian (Ludlow Series).

Remarks. The name *Otarion* has been indiscriminately applied to a large number of proetaceans, ranging in age from lower Ordovician to Devonian, because they share a broadly similar morphology. By analysis of character combinations it is possible to restrict *Otarion* as suggested below, and to place many other species in *Cyphaspis* and *Harpidella*. New taxa will eventually be required for other species which cannot at present be placed in any of the above. A full revision of these species is needed since existing descriptions and illustrations are mostly inadequate, cranidia often being the only parts illustrated. As Schrank (1972, p. 25) has indicated, thoracic features are likely to prove useful in defining aulacopleurid genera. The thoracic segments of *Otarion* (*Otarion*) and *O.* (*Aulacopleura*), for example, differ from those of *Cyphaspis* and *Harpidella*; in the former the inner edge of the articulating facet is about two-thirds of the pleural width out from the axial furrow, while in the latter it is about half-way out (Pl. 7, figs. 4*a*, 6, 9, 10). There is also a marked boss on the anterior pleural band at the inner end of the articulating facet in *Cyphaspis* (Pl. 7, fig. 4*b*) and in many *Harpidella* species. Pygidial morphology is also distinctive: *Otarion* (*Otarion*) and *O.* (*Aulacopleura*) have narrow axes and very broad pleural areas, while in *Cyphaspis* and *Harpidella* the axis is as broad as the pleural area (compare Pl. 7, figs. 3, 4*b*). Topotype material of *O. diffractum* is figured here (Pl. 7, figs. 1–3, 5, 6) and this shows the following important features: palpebral lobe small, placed about one-third of the way along the cephalon from the posterior margin; faint eye ridge visible only on internal moulds with a series of further faint ridges behind it (Pl. 7, fig. 2*a*); glabella about as long as wide, subparallel sided; L1 suboval, elongated exsagittally; S1 directed adaxially backwards at first, then parallel to the sagittal line; no distinct S2; anterior border narrow, barely widened sagittally; preocular facial sutures weakly divergent; thorax of 13–15 segments (up to 17 if *O. halli* (Barrande, 1852) is synonymous as Prantl and Přibyl (1951, p. 453) suggest); axial spine on sixth thoracic

segment; pygidium with 5–8 axial rings, distinct narrow pygidial border. We consider that the nominate subgenus of *Otarion* should be reserved for forms which closely resemble the type species in these respects. One such is *O. latum* Alberti, 1967 (see Alberti 1969, pl. 34, figs. 5, 6). Other species placed by Alberti in *O.* (*Otarion*) differ in the form of the glabella and length of the preglabellar field.

The type species of *Malayaproetus*, *M. bulbus* Kobayashi and Hamada, 1971*b*, has a long convex preglabellar field, an isolated L1, no occipital lobe, and the poorly segmented pygidium is much wider than long. All these features suggest that the species is an aulacopleurid rather than a proetid. *M. bulbus* is not well known but the general morphology (see Kobayashi and Hamada 1971*b*, pl. 23, figs. 4–6, 8–11) is not unlike that of *O.* (*Otarion*) species, and we tentatively place *Malayaproetus* in the synonymy of that subgenus.

Subgenus OTARION (AULACOPLEURA) Hawle and Corda, 1847

Type species. Arethusa koninckii Barrande, 1846; from Silurian (Wenlock Series), Reporyje, Ohrada, Prague district, Czechoslovakia; by monotypy.

Diagnosis. Otarion with prominent eye ridge; 18–22 thoracic segments, no axial spine.

Stratigraphical range. Ordovician (Tremadoc Series) to middle Devonian.

Remarks. Chaubet (1937, p. 196) erected the subgenus *Paraaulacopleura*, type species *P. roquemaillerensis* Chaubet, 1937 from the Wenlock of the Montagne Noire, southern France. There are no features by which this species can be separated at the subgeneric level from *A. koninckii* (compare Pl. 7, figs. 9 and 10), and *Paraaulacopleura* is therefore a subjective junior synonym of *Aulacopleura*. In Moore (1959), the type species of *Paraaulacopleura* is not illustrated, the figure given (fig. 309.6, p. O405) being of *A. beyrichi*. This species differs considerably from *roquemaillerensis* in having rather large palpebral lobes and a short preglabellar field—features more typical of

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EXPLANATION OF PLATE 7

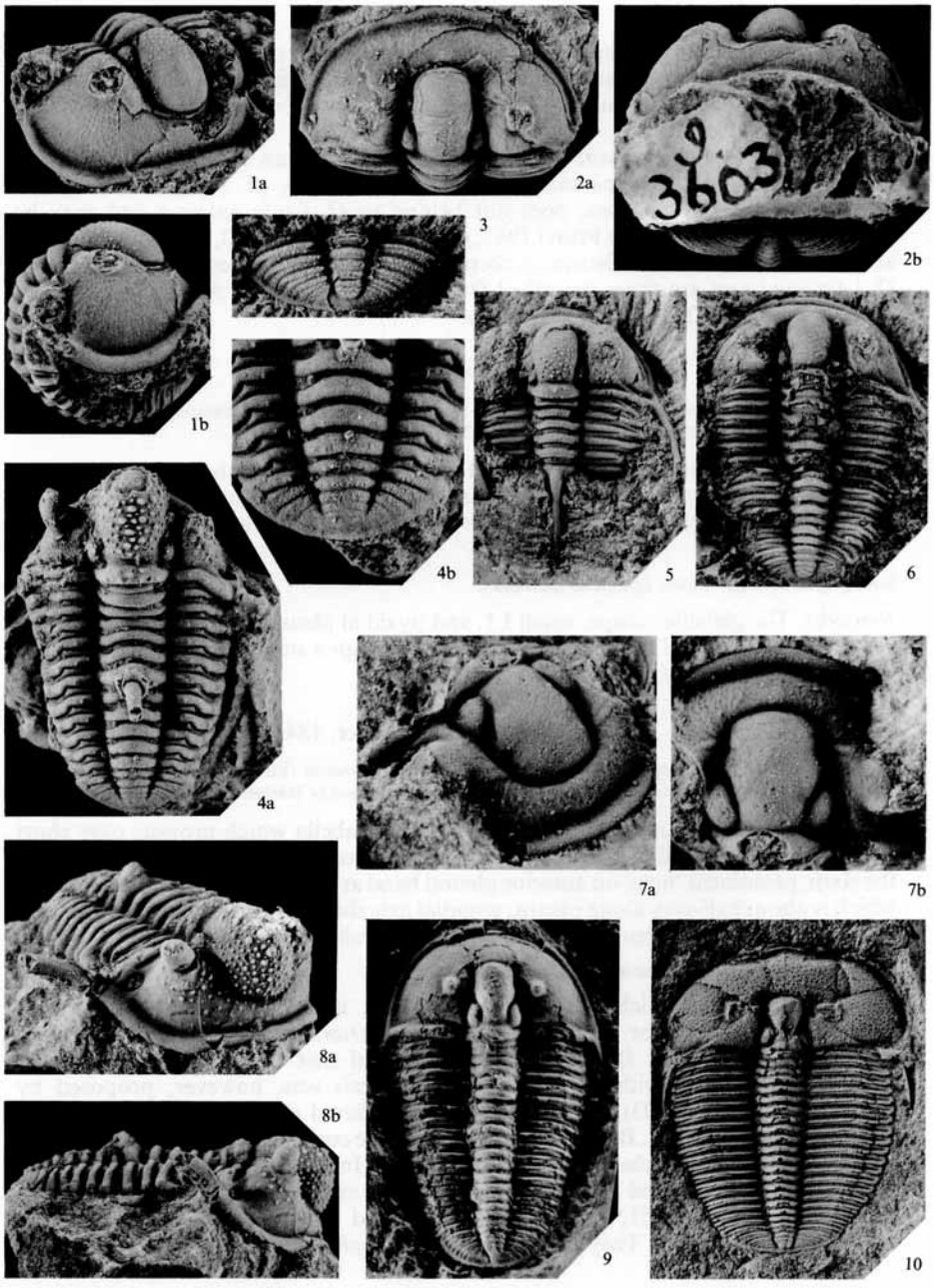
Figs. 1–3, 5, 6. *Otarion* (*Otarion*) *diffractum* Zenker, 1833. Kopanina Formation (Ludlow Series), Dlouhá hora, near Beroun, Czechoslovakia, 1*a–b*, BM It 14144, complete, enrolled, partly exfoliated specimen, oblique antero-lateral and lateral views, ×3. 2*a–b*, BM It 14149, complete, partly enrolled specimen, palpebral and anterior views, ×3. 3, BM It 14148, partly exfoliated pygidium, dorsal view, ×5. 5, BM It 14143, incomplete thorax and downwardly flexed cephalon, dorsal view, ×4. 6, SM A49357, complete specimen (cephalon flexed downwards), dorsal view, ×3.

Figs. 4, 8. *Cyphaspis ceratophthalma* (Goldfuss, 1843). Devonian (Eifelian), Gees, near Gerolstein, Eifel district, BDR. 4*a–b*, NMW 72.47G.4, complete specimen, dorsal view, ×3, and enlarged dorsal view of pygidium and part of thorax, ×5. 8*a–b*, NMW 72.47G.3, complete specimen, oblique antero-lateral and lateral views, ×3.

Fig. 7*a–b*. *Harpidella* (*Harpidella*) *novella* (Barrande, 1852). Silurian (exact horizon unknown), Lochkov, Czechoslovakia. BM It 14146, cranidium, antero-lateral and dorsal views, ×8.

Fig. 9. *Otarion* (*Aulacopleura*) *roquemailerensis* Chaubet, 1937. Wenlock Series, Roquemaillère, Montagne Noire, southern France. University of Montpelier collection, unnumbered, complete specimen, dorsal view, ×2. Original of Chaubet 1937, plate 6, fig. 1.

Fig. 10. *Otarion* (*Aulacopleura*) *koninckii* (Barrande, 1846). Silurian (probably Litĕn Formation, late Wenlock), Loděnice, Czechoslovakia. SM A49395, complete, partly exfoliated specimen, dorsal view, ×3.



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Harpidella. Most authors appear to have interpreted *Paraaulacopleura* in terms of *beyrichi* rather than *roquemaillerensis*. Species presently assigned to *Paraaulacopleura* can be accommodated in *Aulacopleura* (e.g. *A. ignorata* Alberti, 1969, pl. 36, figs. 14–16), or in *Harpidella* s.l.

Species of *O.* (*Aulacopleura*) are widespread in the Silurian and Devonian but rare in the Ordovician. *Aulacopleura*? *sola* Reed, 1935 (p. 43, pl. 1, fig. 16), from the Caradoc of the Girvan area, does not belong to *O.* (*Aulacopleura*) and may be a dimeropygid. *A. reedi* (see Přibyl 1947, p. 541; Reed 1904, p. 83, pl. 11, figs. 14–15), also from the Caradoc of Girvan, is correctly assigned. The oldest known species of *O.* (*Aulacopleura*) are those described from the Tremadoc and Arenig of China by Lu (1975, pp. 392–395, pl. 34, figs. 8–12).

Genus CYPHASPIDES Novák, 1890

Type species. Cyphaspides scuticauda Novák, 1890; from middle Devonian, Greifenstein, German Federal Republic; by subsequent designation of Vogdes 1925.

Diagnosis. Aulacopleurine with forward-expanding clavate glabella, L1 small and inconspicuous; thorax of 11–12 segments, no thoracic axial spine; pygidium with posterior pleural bands elevated above anterior; cephalic and pygidial margins crenulate.

Stratigraphical range. Lower to middle Devonian.

Remarks. The glabellar shape, small L1, and pygidial pleural rib structure make this genus distinct from all other aulacopleurids, although a similar type of rib structure is seen in *Namuropyge* (see below).

Genus CYPHASPIS Burmeister, 1843

Type species. Phacops ceratophthalmus Goldfuss, 1843; from Devonian (Eifelian), Gees, near Gerolstein, Eifel district, German Federal Republic; by subsequent designation of Burmeister 1846.

Diagnosis. Aulacopleurine with strongly inflated glabella which projects over short (sag.) preglabellar field in dorsal view; thorax of eleven segments with axial spine on the sixth, prominent 'boss' on anterior pleural band at inner edge of articulating facet, which is about half-way along pleura; pygidial axis short and wide, anteriorly as wide as pleural areas; interpleural furrows only very weakly developed.

Stratigraphical range. Lower to middle Devonian.

Remarks. Following Richter and Richter (1926), most authors have considered *Cyphaspis* to be a junior subjective synonym of *Otarion*. The Richters attributed *Cyphaspis* to Barrande, 1846 and rightly indicated that *C. burmeisteri* Barrande, 1846 is synonymous with *O. diffractum*. *Cyphaspis* was, however, proposed by Burmeister (1843, p. 103) for specimens he considered conspecific with *Calymene clavifrons* Dalman, 1827. Burmeister's specimens are conspecific with those described as *Phacops ceratophthalmus* by Goldfuss (1843). In 1846 (pp. 98–99) Burmeister corrected his mistake and listed *C. ceratophthalma* as the type species of *Cyphaspis*. Prantl and Přibyl (1951, pp. 444–445) discussed the nomenclatural confusion surrounding *Cyphaspis*. They considered *C. ceratophthalma* and *O.* (*O.*) *diffractum*

to be congeneric and therefore listed *Cyphaspis* as a synonym of *Otarion*. We have examined topotype material of *C. ceratophthalma* (see Pl. 7, figs. 4*a–b*, 8*a–b*) and this differs from *O.* (*O.*) *diffractum* in its shorter preglabellar field, greater glabellar convexity, stalked eye, deep sulcus at the base of the genal spine, thorax of eleven segments, and thoracic and pygidial characters listed in the remarks under *O.* (*Otarion*) (p. 67). We consider that these differences, which are shared by several species, suffice to separate *Cyphaspis* from *Otarion* at generic level. There are several species which are like the type and closely related species of *Cyphaspis*, but which differ in various details; these range from the late Ordovician to the Devonian, and may require new genera or subgenera. Until they are better known, we refer them to '*Cyphaspis* s.l.'

Genus HARPIDELLA M'Coy, 1849

Type species. Harpes? *megalops* M'Coy, 1846; Silurian (upper Llandovery), Boocaun, Cong, Co. Galway, Ireland; by monotypy.

Diagnosis. Aulacopleurine with rather weakly inflated glabella, wider posteriorly than long, subparabolic in outline; S2 distinct; eye ridge developed; palpebral lobe large, backwardly placed; thorax of 12 segments, axial spine (when present) developed on the sixth segment, inner edge of articulating facet half-way along pleura; pygidial axis weakly defined, as wide anteriorly as pleural areas, with 2–4 rings; pleural areas with 1–2 pairs of ribs with scalloped profile.

Remarks. Many authors, such as Salter (1853), Richter, Richter, and Schmidt (*in* Moore 1959), and Whittington and Campbell (1967), considered *Harpidella* to be synonymous with *Otarion*. We agree with Přibyl (1960), who considered the two to be distinct. The type species of *Harpidella* is known only from cranidia. The holotype and topotype specimens have been figured by Whittington and Campbell (1967, pl. 19, figs. 1–14) and other specimens examined by us. These show the following important features: glabella wider (tr.) posteriorly than long, subparabolic in outline; L1 subtriangular, S1 not strongly curved; S2 short, distinct on both internal and external surfaces; palpebral lobe large, extending back from a point opposite the outer end of S1 to a point opposite mid-L1; distinct eye ridge. In both *H. novella* and *O.* (*O.*) *diffractum* a ridge is developed which arises at the adaxial tip of the eye ridge and curves forwards and outwards across the preglabellar field (Pl. 7, figs. 2*a*, 7*a–b*). The significance of this structure is unknown.

Hawle and Corda (1847, p. 80) selected *Proetus elegantulus* Lovén, 1846 as type species of their genus *Goniopleura*—a generic name preoccupied by Westwood *in* Cuvier (1832, p. 149). Because the cranidium of *P. elegantulus* shares many of the features of *H. megalops* (differing principally in that the anterior border is distinctly longer sagittally than exsagittally—see Lovén 1846, pl. 1, fig. 4*a*) this species can be considered to belong to *Harpidella*. *H. elegantula* has twelve thoracic segments and the pygidial axis is weakly defined and poorly segmented (see Lovén op. cit.). *H. christyi* (see Hall 1879, pl. 32, figs. 5–7) and a *Harpidella* species from the British Wenlock also have a cranidium like that of *H. megalops* and the thorax and pygidium like those of *H. elegantula*. Whittington and Campbell (1967, p. 461) noted several differences between *H. megalops* and *O.* (*O.*) *diffractum* but argued that *Harpidella*

should not be used since *H. novella* (Barrande, 1852), while similar in other respects to *H. megalops*, has a small palpebral lobe which is similarly placed to that of *O.* (*O.*) *diffractum*. Topotype material of *H. novella* (Pl. 7, fig. 7*a–b*) shows that while the palpebral lobe is somewhat smaller than that of *megalops*, it is more posteriorly placed than that of *O.* (*O.*) *diffractum*. Since the other cranidial features of *H. novella* are so similar to those of *H. megalops*, we assign it to *Harpidella*.

Alberti, having first used *Harpidella* (1967, p. 500) for a group of species close to *H. elegantula*, later (1969, p. 383) accepted Whittington and Campbell's (1967, p. 461) arguments for regarding *Harpidella* as a junior subjective synonym of *Otarion* and erected a new subgenus, *Maurotarion*, to accommodate the species previously referred to *Harpidella*. His diagnosis (1969, p. 383) shows that *Maurotarion* differs from *O.* (*O.*) *diffractum* in the same ways as *H. megalops*. We therefore regard *Maurotarion* as a junior subjective synonym of *Harpidella*.

Although the type species of *Harpidella* is not well known, enough features are seen to distinguish it from *O.* (*O.*) *diffractum* and to demonstrate affinities with several other aulacopleurid species. We therefore regard *Harpidella* and *Otarion* as distinct genera.

Subgenus HARPIDELLA (HARPIDELLA) M'Coy, 1849

Type species. As for genus.

Diagnosis. Harpidella with no median spine on anterior cephalic border; rostral plate triangular.

Stratigraphical range. Ordovician (Ashgill) to lower Devonian.

Remarks. Chatterton (1971, p. 74) stated that the most distinctive feature of his *Tricornotarion* is the presence of prominent single spines (instead of paired ones) on the glabellae of meraspide cranidia, and considered this feature to be of subgeneric importance. We consider that much more information on aulacopleurid ontogeny is necessary to evaluate the significance of this feature. In other respects *T. struzi* (see Chatterton 1971, pl. 18, figs. 1–18, 33, pl. 19, figs. 13–34), the only known species, is very similar to *H.* (*Harpidella*) species and we therefore place it in the synonymy of that subgenus.

Many Ordovician and Devonian aulacopleurids show similarities to *H.* (*Harpidella*) species. New genera or subgenera will eventually be necessary to accommodate these, but until they are better known, we recommend that they be referred to '*Harpidella* s.l.'

Subgenus HARPIDELLA (RHINOTARION) Whittington and Campbell, 1967

Type species. Rhinotarion sentosum Whittington and Campbell, 1967; from Silurian (late Wenlock/lower Ludlow), Baker Pond, Maine, U.S.A.; by original designation.

Diagnosis. Harpidella with median part of anterior border drawn forward into projection; rostral plate shaped like an inverted T.

Stratigraphical range. As for type species.

Remarks. The anterior projection of this subgenus is unique in the Aulacopleuridae, and its functional significance is unknown. In other respects the cephalon of *H.* (*Rhinotarion*) is exceedingly like those of species of the nominate subgenus

(Whittington and Campbell 1967, pl. 4; pl. 5, figs. 1–4). All the material of the type species is disarticulated and occurs in association with *H.* (*Harpidella*) species. The pygidium is not, therefore, known with certainty but all the pygidia described by Whittington and Campbell (1967, pp. 464–465, pls. 8, 9) are of similar type. Hence the anterior spine and form of the rostral plate appear to be the only distinctive features of *Rhinotarion*—we do not consider these to be of more than subgeneric importance.

Genus NAMUROPYGE Richter and Richter, 1939

Type species. Namuropyge demaneti Richter and Richter, 1939; from Carboniferous (Viséan, CuIII), Bioul, Belgium; by original designation. [Note: Richter and Richter (1939, pp. 3, 8) gave the horizon of this species as basal Namurian. Dr. P. Sartenaer (pers. comm. to R.M.O., 1975) informs us that the horizon is late Viséan.]

Diagnosis. Aulacopleurine with ankylosed facial sutures; two rows of spines on cephalic margin; rostral plate occupying most of doublure; thorax of 6(?) segments, median spine on fifth (?); pygidial axis with 9–13 rings; pleural ribs with posterior pleural band much elevated above anterior; margin spinose.

Stratigraphical range. Carboniferous, Viséan.

Remarks. The aulacopleurids *Namuropyge* and *Coignouina* Reed, 1943 were based on a pygidium and a cephalon respectively, but discovery of a complete specimen has confirmed that they belong to the same genus (Miller 1977). *Coignouina* is thus a junior subjective synonym of *Namuropyge*.

Genus OTARIONELLA Weyer, 1965

Type species. Cyphaspis davidsoni Barrande, 1852; from Devonian (Eifelian), Koněprusy, Prague district, Czechoslovakia; by original designation.

Diagnosis. Cephalon like that of *Cyphaspis*, but with single row of spines on margin, less strongly inflated glabella, eye not stalked, and sulcus at base of genal spine smaller.

Stratigraphical range. Middle Devonian.

Remarks. The type species of this genus has been included in *Coignouina* (= *Namuropyge*) [e.g. Moore (1959, p. O405, fig. 309.1a)] but differs from the latter in having only one row of cephalic spines and functional dorsal facial sutures. Species with spinose cephalic margins and functional facial sutures are currently included in *Otarionella* (e.g. see Alberti 1969), but it is probable that spinosity has developed independently in several lineages. Some species, for instance, *O. magnificum* (see Alberti 1969, pl. 35, fig. 2*a*), have a glabella and preglabellar field similar to those of *Cyphaspis* species while others (e.g. *O. tafilaltense*—see Alberti 1969, pl. 35, figs. 6*a*, 7*a*) are much more similar to *Otarion* (*Otarion*) *diffractum*.

Only the cephalon of *Otarionella* is known. A full evaluation of the genus must await the availability of more complete material.

Genus OTARIONIDES Alberti, 1969

Type species. Otarion (Otarionides) franconicus Alberti, 1969; from lower Devonian, Oberfranken, Bavaria, German Federal Republic; by original designation.

Diagnosis. Fixed cheek broad, facial suture nearly straight, gently concave adaxially; palpebral lobe absent (?).

Stratigraphical range. As for type species.

Remarks. This genus was founded on two cranidia, one badly preserved, the other incomplete (Alberti 1969, pl. 34, figs. 8, 9). From these, it is difficult to judge whether or not *Otarionides* possessed eyes.

Genus PSEUDOTRINODUS Kobayashi and Hamada, 1971*a*

Type species. Pseudotrinodus aenigma Kobayashi and Hamada, 1971*a*; from Devonian (late lower/early middle), Kroh, Upper Perak, Malaysia; by monotypy.

Diagnosis. Aulacopleurine with dorsal facial suture ankylosed; blind; rostral plate occupying most of cephalic doublure.

Stratigraphical range. As for type species.

Remarks. Kobayashi and Hamada (1971*a*) described disarticulated remains of a blind Devonian trilobite as an 'agnostoid'. Later (1972, p. 13) they proposed the family Pseudotrinodidae to accommodate it, and concluded (p. 14) that 'The Agnostida is the best order for this family'. The best-preserved figured specimen is an internal mould of a cephalon (Kobayashi and Hamada 1971*a*, p. 398, fig. 2). A reconstruction alongside shows dorsal facial sutures. These are not detectable on the photograph though a crack is present on the left-hand side of the cephalon. Their fig. 4 shows three articulated thoracic segments, the possible remains of a fourth, a detached doublure (= rostral plate) and another cephalon. This cephalon was interpreted by Kobayashi and Hamada as a pygidium—which they used in their reconstruction (1972, p. 14, fig. 3). This also shows a 'median suture' on the underside of the cephalon (an interpretation followed by Bergström 1977), but their 1971*a* fig. 4 clearly shows that the 'suture' is a compression crack.

The *Pseudotrinodus* cephalon, while having some resemblance to those of agnostids, also resembles those of certain aulacopleurids—especially species such as *Cyphaspis* (s.l.) *stigmatophthalmus* Richter, 1914, from the Devonian of Sessacker, Germany (see Richter and Richter 1926, pl. 7, figs. 11–15). If the eyes and facial sutures of such a species were to be lost the result would closely resemble *P. aenigma*. Aulacopleurids such as *Namuropyge*, and brachymetopids such as *Brachymetopus*, have developed rostral plates occupying the entire cephalic doublure in association with ankylosis of the dorsal facial sutures, and this has occurred in *Pseudotrinodus*. We therefore regard *Pseudotrinodus* as an aulacopleurid, and consider this association with a contemporaneous family much more likely than association with the agnostids, the known record of which ends with the Ordovician.

Bergström (1973, p. 37) considered *Pseudotrinodus* to be a proetacean, but did not elaborate further; he later (1977, pp. 97, 102) stated it to be a proetid but gave no

reasons for doing so. Since *Pseudotrinodus* probably has at least four thoracic segments (see above), Bergström's (1977, p. 102) statement that it has 'only 3' cannot be substantiated.

Subfamily SCHARYIINAE Osmólska, 1957

Diagnosis. Glabella weakly inflated, triangular or trapezoidal; S1 sometimes shallow or effaced; facial suture normal opisthoparian or cedariiform (in *Scharyia* only); rostral plate small and triangular; thorax of 6–9 segments, median thoracic axial spine absent.

Genera. Scharyia Přibyl, 1946; *Panarchaeogonus* Öpik, 1937; *Isbergia* Warburg, 1925; *Cyamops* Owens, 1977.

Remarks. Bergström (1977, p. 102) objected to the inclusion of *Scharyia* in the Aulacopleuridae because of its triangular glabella, large eye, small number of thoracic segments, large pygidium, and because it probably enrolled sphaeroidally, unlike the spiral enrolment 'typical' of aulacopleurids. On the basis of these characters he implied that *Scharyia* was a proetid but did not suggest to which genera it might be related, nor did he comment on *Panarchaeogonus*—the aulacopleurid from which *Scharyia* is believed to have been derived (Owens 1974, p. 687; 1977; Thomas and Owens, this paper).

We can refute all of Bergström's objections to *Scharyia* being an aulacopleurid. Several Ordovician aulacopleurids have a triangular glabella and large eyes (e.g. *Panarchaeogonus whittardi*, see Owens 1974, p. 688, text-fig. 2B), and both *Isbergia* and *Cyamops* have a comparatively small number of thoracic segments and a large pygidium. It is not difficult to derive a comparatively larger pygidium and reduce the number of thoracic segments by tagmosis. We do not consider that the differing styles of enrolment (spiral in such genera as *Otarion* and *Harpidella*, and probably sphaeroidal in *Scharyia*) preclude familial relationship. In the undoubtedly monophyletic Homalonotinae, for example, early species display the spiral enrolment typical of calymenaceans. Later homalonotines have a relatively larger pygidium which renders spiral enrolment impracticable, and here enrolment is sphaeroidal.

Panarchaeogonus appears to be the root stock of the Scharyiinae and shows comparatively few differences from its inferred aulacopleurine ancestors. Owens (1974, 1977) suggested that *Panarchaeogonus* gave rise to *Scharyia* on the one hand, and to *Isbergia* and *Cyamops* on the other. Hence the four genera constitute a discrete phyletic unit which we regard as a subfamily—they display a considerable range of morphology, however, which makes subfamily diagnoses difficult to compose.

For further discussion of this subfamily and its constituent genera see Owens (1974, 1977).

Genus SCHARYIA Přibyl, 1946

Type species. Proetus micropygus Hawle and Corda, 1847; from Silurian (Ludlow Series), Klodeník, near Beroun, Prague district, Czechoslovakia; by original designation.

Diagnosis. Scharyiine with triangular glabella, with or without shallow lateral furrows; preglabellar field weakly convex in longitudinal profile; facial suture

cedariiform; thorax of 6 segments; pygidium with or without border, margin entire or crenulate; axis with 5–9 rings, pleural areas with 4–6 pairs of ribs; small granule on adaxial end of each thoracic and pygidial posterior pleural band.

Genus PANARCHAEOGONUS Öpik, 1937

Type species. Panarchaeogonus parvus Öpik, 1937; from Ordovician (Llandeilo–Caradoc Series), Kukruse Stage, Kohtla-Jarve, Estonia; by original designation.

Diagnosis. Scharyiine with triangular glabella with distinct L1; palpebral lobe large, close to glabella; weak eye ridge present; three sulci commonly present on posterior part of preglabellar field; thorax of 9 segments; pygidium without border; pygidial axis narrow with 5–9 rings; pleural areas broad, with 5–6 pairs of ribs.

Genus ISBERGIA Warburg, 1925

Type species. Isbergia planifrons Warburg, 1925; from Ordovician (Ashgill Series), Kallholn, Siljan district, Sweden; by original designation.

Diagnosis. Scharyiine with strongly vaulted cephalon; glabella trapezoidal with weak, non-incised furrows; preglabellar field and cheeks strongly declined; no genal spine or eye ridge; thorax of 8 segments; pygidial axis with 5–6 poorly defined rings, pleural areas with 5–6 pairs of ribs; dorsal exoskeleton smooth.

Genus CYAMOPS Owens, 1977

Type species. Cyamops stensioei Owens, 1977; from Ordovician (Ashgill Series), Kallholn, Siljan district, Sweden; by original designation.

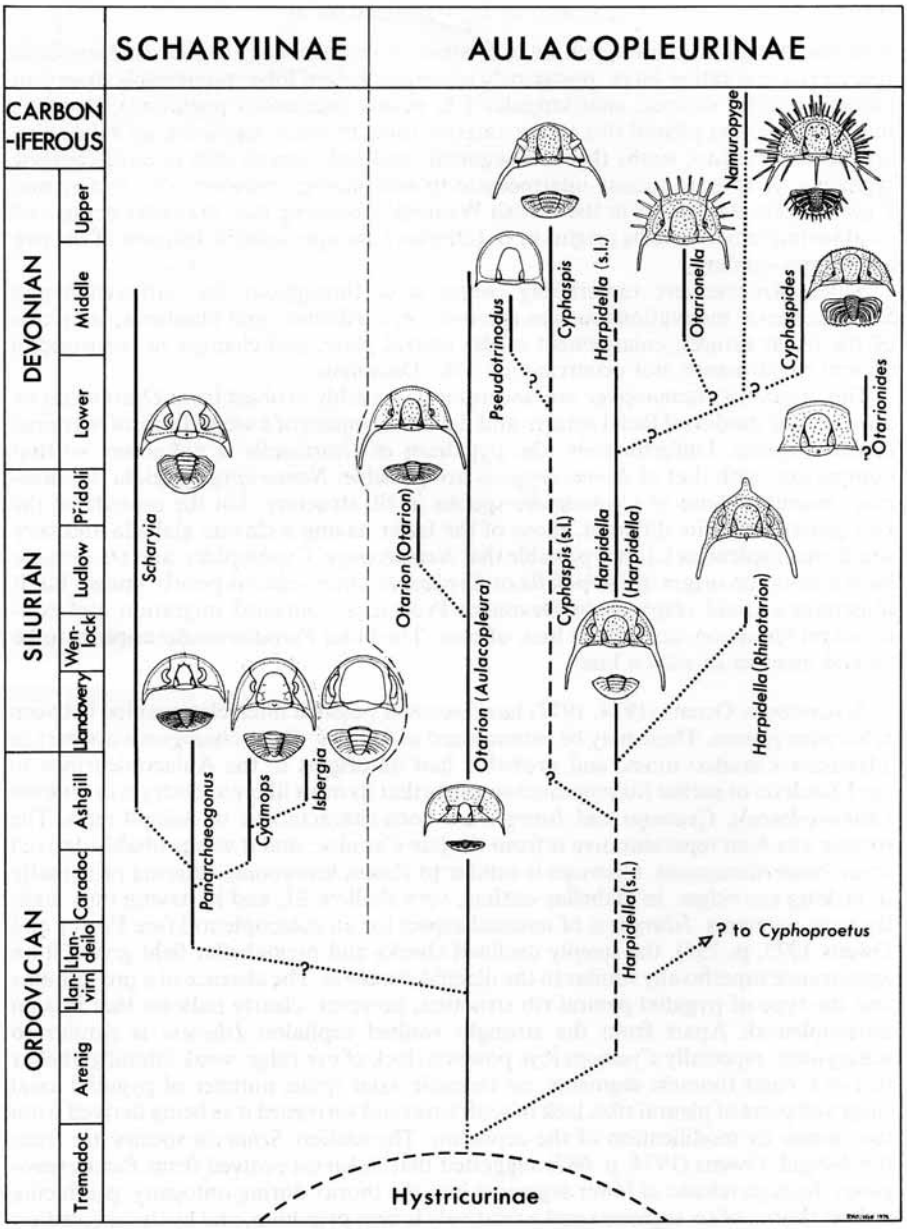
Diagnosis. Scharyiine with trapezoidal glabella, with weakly impressed lateral furrows; preglabellar field sigmoidal or straight in longitudinal section; no eye ridges; thorax of 8 segments; pygidium with conical axis with 6–7 rings; pleural areas broad with 5–6 pairs of ribs, pleural and interpleural furrows reach margin; exoskeleton smooth.

PHYLOGENY OF AULACOPLEURIDAE

Origins. Aulacopleurids occur only rarely in the early Ordovician and almost certainly evolved in the Tremadoc from hystricurine species (for detailed discussion see Fortey and Owens 1975, pp. 230–231).

Aulacopleurinae. A species of *Otarion* (*Aulacopleura*) occurs in the Tremadoc, the morphology of this subgenus remaining remarkably constant throughout its long range. Fortey and Owens (1975, p. 237) considered that *O.* (*Aulacopleura*) lived in a deep-water environment similar to that previously inhabited by olenids.

Other aulacopleurines occur sporadically in the Ordovician, but their relationships are difficult to determine, principally because most of the material is so fragmentary. A cranidium figured by Whittington (1965, pl. 19, figs. 13, 14, 18) is almost intermediate in morphology between aulacopleurines and *Cyphoproetus* (see Fortey and Owens 1975, p. 229). This suggests that proetines were derived from the Aulacopleurinae in the early Ordovician (see Owens 1973, p. 85). *O. tridens* Ingham, 1970,



TEXT-FIG. 1. Known ranges of aulacopleurid genera, with suggested phylogenetic relationships.

from the Ashgill of the English Lake District, is in some ways similar to *Harpidella* species (having rather large, posteriorly placed palpebral lobe; moderately divergent preocular facial sutures; subtriangular L1; poorly segmented pygidium). It differs in having pointed pleural tips to the anterior three thoracic segments, an axial spine on the seventh (not sixth) thoracic segment, and only eleven (not twelve) thoracic segments. A species almost intermediate in morphology between '*O.*' *tridens* and *Cyphaspis* species occurs in the British Wenlock indicating that the latter genus and its allies might not have its origins in *O.* (*Otarion*), though cephalic features of the two are closely similar.

Aulacopleurines are remarkably conservative throughout the Ordovician and Silurian, major innovations such as spinosity, eye reduction and blindness, ankylosis of the facial sutures, enlargement of the rostral plate, and changes in the pygidial pleural rib structure, not occurring until the Devonian.

The origins of *Namuropyge* are uncertain. It possibly evolved from *Otarionella* by ankylosis of the dorsal facial sutures and the development of a second row of marginal cephalic spines. Unfortunately, the pygidium of *Otarionella* is unknown, so that comparison with that of *Namuropyge* is not possible. *Namuropyge* pygidia do, however, resemble those of *Cyphaspides* species in rib structure, but the cephala of the two genera are quite different, those of the latter having a clavate glabella and very small, inconspicuous L1. It is possible that *Namuropyge*, *Cyphaspides*, and *Otarionella* have a common origin in *Harpidella* or *Cyphaspis*. *Otarionides* is poorly known but it illustrates a trend common in Devonian Proetacea—outward migration and concomitant reduction, and finally loss, of eyes. The blind *Pseudotrinodus* appears to be an end member of such a line.

Scharyiinae. Owens (1974, 1977) has discussed possible interrelationships between scharyiine genera. These may be summarized as follows: *Panarchaeogonus* appears in Llandeilo–Caradoc times, and probably had its origins in the Aulacopleurinae in the Llandeilo or earlier (its pygidium suggests that its most likely ancestry is in *Otarion* (*Aulacopleura*)). *Cyamops* and *Isbergia* are both characteristic of Ashgill reefs. The former's earliest representative is from the late Caradoc, and it was probably derived from *Panarchaeogonus*. *Cyamops* is similar to *Panarchaeogonus*, differing principally in lacking eye ridges, in glabellar outline, very shallow S1, and in having only eight thoracic segments. *Isbergia* is of unusual aspect for an aulacopleurid (see Fortey and Owens 1975, p. 236), the steeply declined cheeks and preglabellar field giving it an appearance superficially similar to the illaenid *Panderia*. The absence of a pre-annulus and the type of pygidial pleural rib structure, however, clearly indicate that it is an aulacopleurid. Apart from the strongly vaulted cephalon *Isbergia* is similar to scharyiines, especially *Cyamops* (eye position, lack of eye ridge, weak lateral glabellar furrows, eight thoracic segments, no thoracic axial spine, number of pygidial axial rings and pairs of pleural ribs, lack of sculpture) and we regard it as being derived from that genus by modification of the cephalon. The earliest *Scharyia* species are from the Ashgill. Owens (1974, p. 687) suggested that *Scharyia* evolved from *Panarchaeogonus* through release of fewer segments into the thorax during ontogeny, producing a short thorax of six segments and a relatively longer pygidium, and by the acquisition of a cedariiform facial suture.

Repositories. BM—British Museum (Natural History), London; NMW—National Museum of Wales, Cardiff; SM—Sedgwick Museum, Cambridge.

Acknowledgements. Professor H. B. Whittington, F.R.S. and Dr. P. D. Lane critically read the manuscript and made useful suggestions for its improvement. Dr. R. Feist provided the negative from which Plate 7, fig. 9 was made. Dr. R. A. Fortey and Mr. S. F. Morris (BM) and Dr. R. B. Rickards (SM) kindly gave access to specimens in their care. A. T. T. acknowledges a N.E.R.C. Research Fellowship.

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Typescript received 6 December 1976
Revised typescript received 1 February 1977