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EARLY SILURIAN TRILOBITES FROM THE BROKEN RIVER AREA, NORTH QUEENSLAND

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Abstract

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A Late Llandovery (Telychian) trilobite fauna is described from the Poley Cow Formation in the Broken River Province of north Queensland. Taxa recorded are *Kosovopeltis*, *Proetus* (s.l.), *Warburgella*?, *Otarion*, *Maurotarion*, *Scharyia*, *Youngia*, *Sphaerexochus*, *Sphaerocoryphe*, *Coronocephalus*? aff. *urbis* Strusz, 1980, *Ceratocephala*, the new encrinurid genus *Prostrix*, and the new species *Prostrix amnicola*, *Batocara fritillum*, *Gravicalymene*? *vaccina* and *Gaotania bimusa*. *Youngia* and *Gaotania* are recorded from Australia for the first time. *Batocara* Strusz, 1980 is considered to be a senior subjective synonym of *Pacificurus* Ramsköld, 1986a.

Keywords: Trilobita, Early Silurian, Queensland, new taxa.

Introduction

The Poley Cow Formation (Withnall et al., 1988; Withnall, 1989) is part of the Early Silurian to earliest Devonian Graveyard Creek Group in the Broken River Province (Arnold and Henderson, 1976) of north Queensland. The formation, which consists of up to 550 m of feldspatholithic siltstones, mudstones and polymictic conglomerates, unconformably overlies Ordovician volcanics and clastic sediments of the Judea Formation, and is conformably overlain by limestones and clastic sediments of the Jack Formation (Fielding, 1993). Fossils are not common in the Poley Cow Formation, but a few scattered localities have yielded shelly faunas as well as graptolites and conodonts indicative of a Late Llandovery (Telychian) age (*turriculatus–griestoniensis* and *celloni* Biozones; Jell et al., 1988; Jell and Talent, 1989).

The trilobites described herein were collected from the Poley Cow Formation at Museum of Victoria (NMV) invertebrate fossil locality PL1906 (Fig. 1), situated in the bed of a creek approximately 1.2 km south-east of where the track from Jessey Springs to Wando Vale crosses the Broken River, and approximately 400 m due east of the track (grid reference 703434 on the Burges 1:100,000 sheet 7859). This is the locality reported to yield the richest fauna from the clastic sequence of the Graveyard Creek Group by Jell et al. (1988: 116), who gave a slightly different grid reference, and by Jell and Talent (1989: 200), who marked the locality as S2 on their fig. 144, not S1 as stated in the text. In addition to the trilobites, the fauna from PL1906 also includes brachiopods, bivalves, gastropods, nautiloids, ostracodes and abundant disarticulated crinoid remains, all preserved as

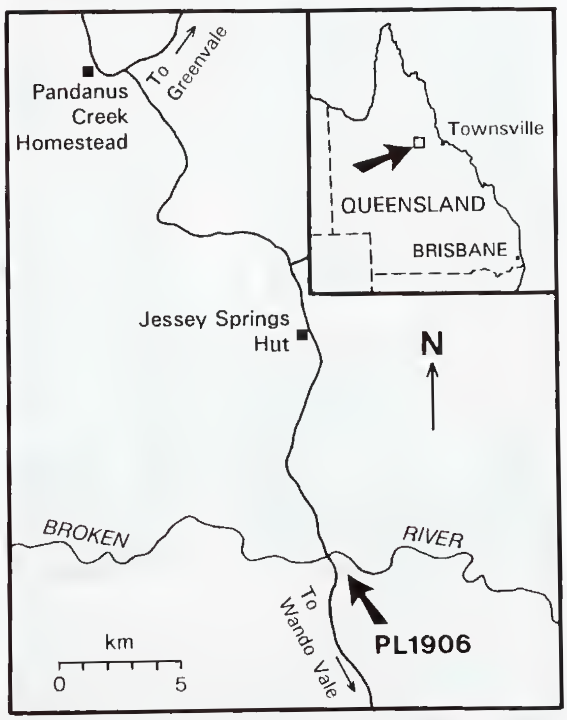


Figure 1. Locality map showing where trilobites were collected from the Poley Cow Formation near Broken River crossing, north Queensland.

internal and external moulds in thinly-bedded, fine micaceous siltstones. The trilobites are disarticulated and commonly broken, indicating that they are not preserved *in situ* but have been transported or reworked. All the faunal elements are represented by specimens of relatively small size, suggesting that sorting may have occurred. This evidence is consistent with the views of Withnall (1989) and Fielding (1993) that the Poley Cow Formation was deposited in a shallow, off-shore marine shelf environment affected by storm or wave activity.

The trilobite assemblage from PL1906 is consistent with the Late Llandovery age indicated by graptolites and conodonts. *Youngia* is not known to range above the Llandovery, and the species of *Kosovopeltis* and *Gaotania* are closely related to *K. yichangensis* Chang and *G. ovata* Chang, respectively, from the Upper Llandovery of China.

The only trilobites previously described from the Broken River Province are the effaced styginid *Rhaxeros pollinctrix*, the cheirurid *Sphaerexochus*, *Encrinurus*?, a possible warburgelline and an indeterminate calymenid (Lane and Thomas, 1978, 1980), from Late Llandovery strata of the Quinton Formation, a lateral equivalent of the Poley Cow Formation in the Gray Creek area, some 25 km north of the Broken River. Effaced styginids have not been found in the Poley Cow Formation, and the material of the other taxa recorded by Lane and Thomas is mostly too fragmentary for useful comparison. Öpik (in White, 1965: 43) identified *Encrinurus*, two species of undetermined scutelluids (= styginids), *Proetus*?, and *Sphaerexochus* or *Onycopyge* from the Quinton Formation in the same area, though the horizon was incorrectly given as the Wairuna Formation, which is of Ordovician age. Arnold and Henderson (1976) reported that the present whereabouts of these specimens are unknown, and a search of the collections in the Australian Geological Survey Organisation failed to locate them (D. L. Strusz, personal communication), so it is not possible to verify Öpik's identifications.

The only other Llandovery trilobite faunas previously described from Australia are those of the "*Illaenus*" band in the Heathcote district of central Victoria (Öpik, 1953), the Richea Siltstone in the Tiger Range of south-western Tasmania (Holloway and Sandford, 1993), and the Rosyth Limestone near Borenore in central western New South Wales (Fletcher, 1950; if the Rosyth Limestone correlates with the Quarry Creek Limestone and with the lower part of the Boree Creek Formation, as suggested by Pickett, 1982, this fauna may be of early Wenlock age; Bischoff, 1986). The first two of these faunas are very different from that of the Poley Cow Formation. The trilobite assemblage of the "*Illaenus*" band is dominated by the effaced styginid *Thomastus* together with dalmanitids and a phacopid, all of which are absent from the Poley Cow Formation. The Richea Siltstone fauna includes *Decoroproetus*, *Latiproetus*?, *Trimerus*, *Acernaspis*, *Dalmanites*, *Anacaenaspis* and *Dicranurus*, as well as *Maurotarion* and *Gravicalymene* which are shared with the Poley Cow Formation. The Rosyth Limestone contains *Ananaspis*, *Trochurus*, *Batocara* and *Youngia*, the last not being recorded by Fletcher (1950) though present in his collections; the last two genera are shared with the Poley Cow Formation, but the species of *Batocara* is not very similar to *B. fritillum* sp. nov.

Systematic palaeontology

Styginidae Vogdes, 1890

Kosovopeltis Šnajdr, 1958

Type species. Kosovopeltis svobodai Šnajdr, 1958, from the Ludlow of Bohemia; original designation.

Kosovopeltis sp.

Figure 2A

Material. An incomplete cranidium comprising the left part of the glabella and most of the fixigena.

Remarks. The low convexity of the cranidium, the preglabellar furrow that is very shallow laterally and appears to weaken further adaxially, and the rounded (exsag.) anterolateral border suggest assignment to *Kosovopeltis*. A distinctive feature is the deep and rather sharp furrow (lateral border furrow?) running subparallel to the cranidial margin on the front of the fixigena, and meeting the axial furrow just behind the widest part of the frontal lobe. This feature is also present in *K. yichangensis* Chang (1974, pl. 80, fig. 2) from the lower Upper Llandovery of south-west China, suggesting that the two species may be closely related. *K. yichangensis* differs from the present species in lacking a shallower furrow (epiborder furrow?) in front of the very deep one on the front of the fixigena, the axial furrow is more abaxially-concave in outline in front of the occipital furrow, the anterior branch of the facial suture diverges more strongly forwards, and the frontal lobe is poorly differentiated from the anterior and lateral borders.

Proetidae Salter, 1864

Proetinae Salter, 1864

Proetus Steininger, 1831

Type species. Calymmene concinna Dalman, 1827, from the Wenlock of Gotland; original designation.

Proetus (s.l.) sp.

Figure 2B–F, I

Material. A cranidium, a librigena and 2 pygidia.

Remarks. This species is characterised by an elongate, gently forwardly tapering glabella that is well rounded anteriorly; occipital lobes that are weak or absent; no preglabellar field; an apparently weakly forwardly diverging anterior branch of the facial suture; a librigenal field that is narrower than the lateral border; a short genal spine; and a pygidium with a poorly defined border that expands strongly posteromedially. The elongate shape of the glabella has probably been exaggerated by deformation. The weak or absent occipital lobes would exclude the species from *Proetus* (*Proetus*) *sensu* Owens (1973: 11). No similar species has previously been recorded from the Silurian of Australia.

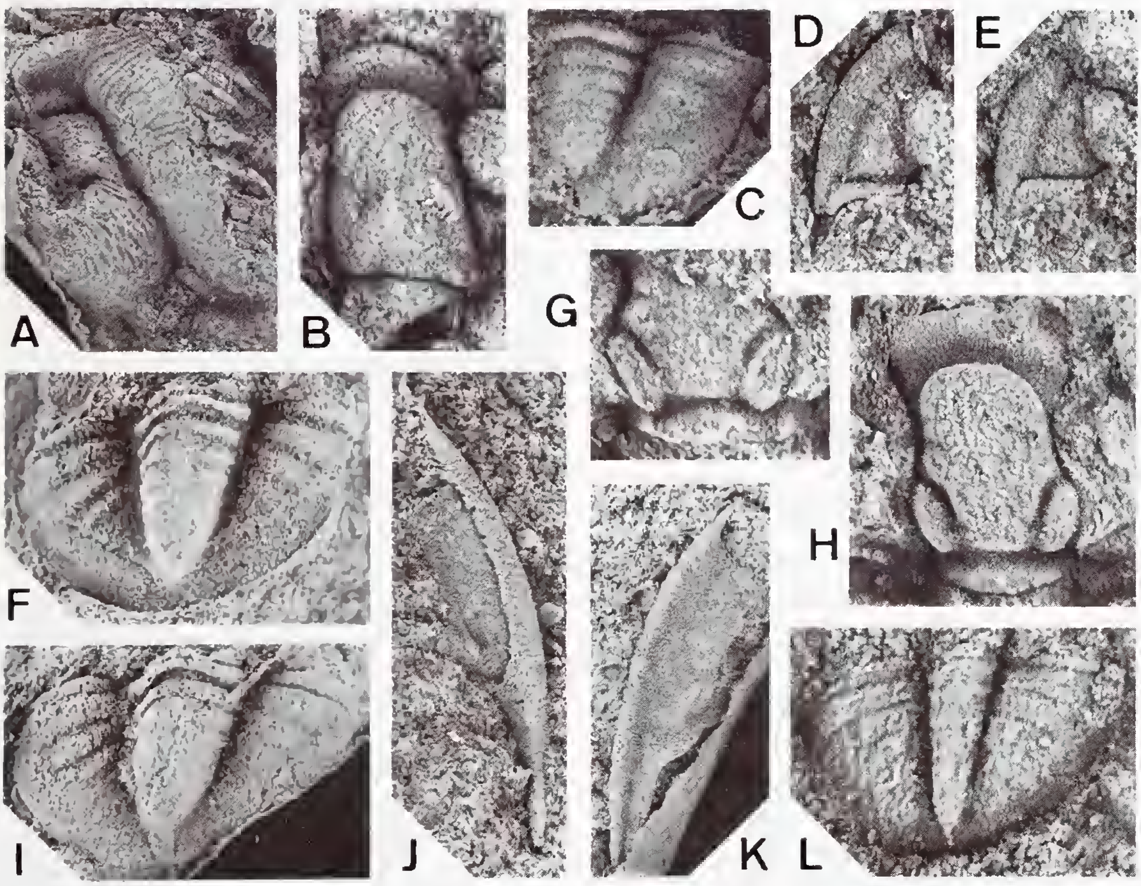


Figure 2. A, *Kosovopeltis* sp., cranidium NMV P134800, latex cast of external mould, dorsal view, × 4. B–F, I, *Proetus* (s.l.) sp. B, cranidium NMV P134801, latex cast of external mould, dorsal view, × 10. C, pygidium NMV P134805, latex cast of external mould, dorsal view, × 10. D, E, librigena NMV P134803, internal mould and latex cast of external mould, dorsal view, × 9. F, I, pygidium NMV P134804, internal mould and latex cast of external mould, × 7. G, H, J–L, *Warburgella* sp. G, cranidium NMV P134809, internal mould, dorsal view, × 8. H, cranidium NMV P134808, internal mould, dorsal view, × 8. J, K, librigena NMV P134810, latex casts of counterpart moulds, ventral and dorsal views, × 6. L, pygidium NMV P134811, internal mould, dorsal view, × 9.

Warburgellinae Owens, 1973

Warburgella Reed, 1931

Type species. Asaphus Stokesii Murchison, 1839, from the Wenlock of England; original designation.

***Warburgella*? sp.**

Figure 2G, H, J–L

Material. Two cranidia, a librigena and a pygidium.

Remarks. These specimens are tentatively assigned to *Warburgella* because of the strongly waisted glabella with deep S1 and shallow S2 and S3, the rather narrow, subparallel-sided L1 with long axis oblique to the sagittal line, the long palpebral lobe, and the comparatively long pygidium with narrow axis (the narrowness is possibly exaggerated by deformation). Features that are not typical of *Warburgella*, however, are the lack of occipital lobes; the absence of a preglabellar field, transverse preglabellar ridge and tropidium; and the weak forward divergence of the anterior branch of the facial suture. Some of these features are characteristic of *Warburgella* (*Anambon*) Landrum and Sherwin, 1976, a subgenus so far recorded only from the Lower Devonian (see also Chatterton and Perry, 1977). A distinctive feature of the librigena is a weak depression on the field, running subparallel to the lateral margin and curving adaxially posteriorly (Fig. 2K); a similar depression is present in some species of *Prantlia* (see *P. grindrodi* Owens, 1973, pl. 15, figs 3–5).

The present cranidia resemble the proetine *Cyphoproetus* but differ in the rather short (sag., exsag.) occipital ring with no lateral lobes and median tubercle not forwardly placed. If the librigena and pygidium are correctly associated with the cranidium, the poorly defined lateral border furrow, weak depression on the librigenal field and the long pygidium with narrow axis also suggest that this species does not belong to *Cyphoproetus*.

The present pygidium is too poorly preserved for comparison with the warburgelline pygidium figured by Lane and Thomas (1978, pl. 2, figs m, p) from the Quinton Formation in the Gray Creek area of the Broken River Province.

Aulacopleuridae Angelin, 1854

Remarks. Adrain and Chatterton (1993) included their new genus *Goodsiraspis* in the Rorringtoniidae Owens in Owens and Hammann, 1990 but acknowledged that it resembles members of the Aulacopleuridae in "general proportions", the prominent, fully isolated L1, the number of thoracic segments (14 as opposed to 8 or 9 in rorringtoniids), and the short, broad pygidium with only the first pairs of pleural and interpleural furrows well defined. Other similarities with aulacopleurids are the width of L1, which is much narrower than the adjacent median part of the glabella instead of being approximately the same width as in rorringtoniids; the distance of the palpebral lobe from the axial furrow, which is greater than it is in rorringtoniids; the median swelling on the posterior part of the preglabellar field, which is also developed in *Otarion* (see Adrain and Chatterton, 1994, fig. 12.5–12.7), *Songkania* (see Ludvigsen and Tripp, 1990, pl. 8, fig. 3) and more weakly in *Maurotarion* (see Thomas, 1978, pl. 8, fig. 1a, b); and the anterior border furrow that is flexed medially.

Reasons cited by Adrain and Chatterton (1993: 1637) for the assignment of *Goodsiraspis* to the Rorringtoniidae are the deep S2, the rostral plate that does not taper to a point posteriorly, the genal spine that is flattened at its base and carries extensions of the lateral and posterior border furrows, the absence of a "lobate" eye socle, and the apparent absence of posterior spines on the hypostome. None of these points provides grounds for exclusion of the genus from the Aulacopleuridae. S2 appears to be very variable in development in *Goodsiraspis*; in most specimens of the type species, *G. packardi*, it is certainly wider (tr.) and deeper than is normal for aulacopleurids, but in other specimens it is weak (e.g., Adrain and Chatterton, 1993, pl. 1, fig. 1, pl. 2, fig. 9). S2 is also very weak in "*Harpidella*" *butorus* Holloway and "*Cyphaspis*" *novella* Barrande, both of which were assigned to *Goodsiraspis* with question by Adrain and Chatterton, and which I consider to be undoubtedly congeneric with *G. packardi*. The rostral plate does not taper to a point posteriorly in all aulacopleurids; in *Rhinotarion* (see Whittington and Campbell, 1967, pl. 4, fig. 11) and possibly also in *Maurotarion axitiosum* (Campbell, 1977: 16, pl. 3, fig. 2c) the posterior ends of the connective suture are widely separated, as in *Goodsiraspis*. The flattening of the genal spine in *G. packardi* appears to be at least partly due to collapse under post-depositional compression, as shown by the presence of longitudinal fractures and/or depressions along most spines (e.g., Adrain and Chatterton, 1993, pl. 1, figs 1, 4, 5, 7, 8, pl. 2, figs 1, 4). Fracturing also seems to account for the apparent extension of the lateral border furrow onto the genal spine in Adrain and Chatterton's pl. 1, fig. 7; the true lateral border furrow is seen to meet the posterior border furrow in front of the spine base, and only a single furrow extends along the spine, as is common in aulacopleurids. Adrain and Chatterton (1993, 1994) did not explain their use of the terms "lobate" and "bilobate" for the eye socle of aulacopleurids, but "bilobate" apparently refers to a socle that is considerably wider and/or more convex anteriorly and posteriorly than at midlength (exsag.). The socle of *G. packardi* is poorly defined but does not appear to be bilobate. The socle in *Rhinotarion* is not bilobate either but parallel-sided (Whittington, 1992, pl. 102, figs A, C, D), indicating that a bilobate socle is not a synapomorphy of Aulacopleuridae as indicated by Adrain and Chatterton (1993, fig. 2) in their cladogram. Finally, the only hypostomes of *G. packardi* known are too incomplete to be certain that posterior spines are not present.

Goodsiraspis is consequently here assigned to the Aulacopleuridae and is considered to be most closely related to *Maurotarion*. Characters uniting these two genera, and collectively differentiating them from all other aulacopleurids, are the moderate cranidial convexity, the subtrapezoidal or parabolic glabella that is not markedly indented laterally at the front of L1, the relatively short (sag.) preglabellar field, the position of the eye with its midlength (exsag.) opposite the outer end of S1, and the pygidium with the axis as wide anteriorly as the pleurae.

Maurotarion Alberti, 1969

Type species. Harpidella maura Alberti, 1967, from the lower Ludlow of Morocco; original designation.

Diagnosis. See Holloway and Sandford (1993).

Maurotarion sp.

Figure 3A, B, E–G, I

Material. Four cranidia and 4 librigenae.

Remarks. In the subquadrate glabella with more or less transverse anterior outline, the small L1, the anterior border furrow that is uniformly curved in dorsal view instead of having maximum curvature medially, and the anterior border that is not expanded medially, the cranidia resemble those of *Maurotarion christyi* (Hall, 1864) from the Wenlock of Indiana (see Hall, 1879, pl. 32, figs 5–7), *M. hama* (Šnajdr, 1984) from the Wenlock of Bohemia and *M. plautum* (Whittington and Campbell, 1967) from the Upper Wenlock or Ludlow of Maine. Compared with those species, the anterior borders of the present cranidia are more convex (sag., exsag.) and upturned, especially medially, and the anterior border furrow is deeper, but these differences may be due to slight deformation by longitudinal compression. Librigenae assigned to this species differ from those assigned to *Otarion* sp. in having the lateral margin only weakly incurved at the base of the genal spine, and the facial suture crossing the posterior border farther from the genal spine.

Maurotarion rhaptomyosa (Sun, 1990) from the Rainbow Hill Marl Member (Ludlow) of the Yass Basin, New South Wales, differs from the present species in having a more elongated and anteriorly-rounded glabella, a larger L1, a less steeply inclined preglabellar field, a shallower anterior border furrow and a flatter anterior border. *M. bowningense* (Mitchell, 1887) from the Lochkovian of the Yass Basin appears to be similar to the present species but the published illustrations are very poor. *M. bowningense* was based on a single specimen (Mitchell, 1887: 438, pl. 16, fig 3; Chatterton, 1971, pl. 24, fig. 10), which is thus the holotype; the designation of a different specimen as lectotype by Chatterton (1971: 96) is invalid.

Otarion Zenker, 1833

Type species. Otarion diffractum Zenker, 1833, from the Ludlow of Bohemia; by monotypy.

Remarks. Adrain and Chatterton (1994) have revised *Otarion* and sought to distinguish it from the closely related *Cyphaspis* Burmeister, 1843. Evaluation of their concepts of both taxa must await publication of their forthcoming work on *Cyphaspis*.

Otarion sp.

Figure 3C, D, H, J–L

Material. Four cranidia and 4 librigenae.

Remarks. Distinctive features are the moderately inflated glabella that narrows weakly forwards in front of L1 and is broadly rounded anteriorly, the very small and laterally projecting L1, the weakly curved S1, the convex and steeply inclined preglabellar field that is approximately equal in length (sag.) to the anterior border plus anterior border furrow, the rather dense cranidial sculpture of fine tubercles, and the librigena with wide (tr.) field

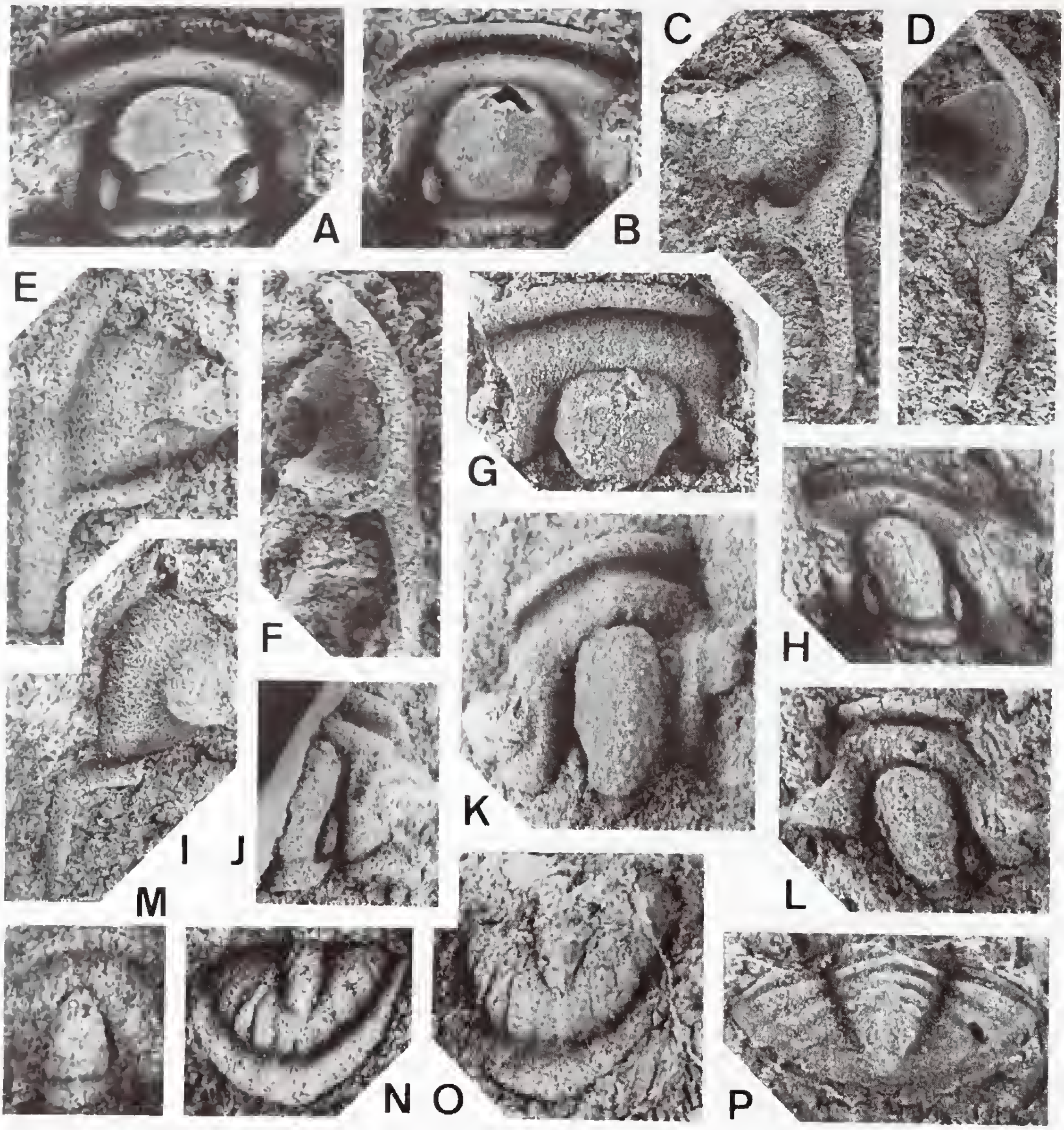


Figure 3. A, B, E–G, I, *Maurotarion* sp. A, cranidium NMV P134816, internal mould, dorsal view, × 6.5. B, G, cranidium NMV P134817, internal mould and latex cast of external mould, dorsal views, × 8. E, librigena NMV P134819, latex cast of external mould, dorsal view, × 10. F, librigena NMV P134835, latex cast of natural mould, ventral view, × 9. I, librigena NMV P134821, latex cast of external mould, dorsal view, × 8. C, D, H, J–L, *Otarion* sp. C, librigena NMV P134814, latex cast of external mould, dorsolateral view, × 8. D, librigena NMV P134815, latex cast of external mould, ventrolateral view, × 8. H, L, cranidium NMV P134812, internal mould and latex cast of counterpart mould, dorsal views, × 10 and × 11.5. J, cranidium NMV P134802, latex cast of external mould, dorsal view, × 9.5. K, cranidium NMV P134813, latex cast of external mould, dorsal view, × 9. M–O, *Scharyia* sp. M, cranidium NMV P134823, internal mould, dorsal view, × 12. N, pygidium NMV P134825, latex cast of external mould, dorsal view, × 12. O, pygidium NMV P134824, latex cast of external mould, dorsal view, × 12. P, Aulacopleuridae indet., pygidium NMV P134822, internal mould, dorsal view, × 9.

and with the lateral margin strongly incurved at the base of the genal spine. In these features there is a similarity to species such as *Otarion brauni* Perry and Chatterton, 1979 and *O. huddyi* Adrain and Chatterton, 1994, both from the Wenlock of Canada, and *O. coppinsensis* Adrain and Chatterton, 1994 from the Wenlock of the Australian Capital Territory. The present material, however, is inadequate for detailed comparison with other species.

Otarion coppinsensis was based on specimens considered by Chatterton and Campbell (1980: 87) to be closely related to or possibly conspecific with *Cyphaspis horani* Etheridge and Mitchell (see Chatterton, 1971: 95, pl. 24, figs 1–6; Chatterton and Campbell, 1980, pl. 11, figs 13, 14), from the Ludlow of the Yass district, New South Wales. Adrain and Chatterton (1994: 320) stated of *horani* that it "has 11 thoracic segments, a strongly inflated, but not elongate, glabella, and a pygidium which is narrow relative to its length, bears three axial rings, and has both rings and posterior pleural bands ornamented with single rows of relatively coarse tubercles. All of these make its assignment to *Cyphaspis* unambiguous, and serve to differentiate it from the older Coppins Crossing species" (i.e. *O. coppinsensis*). However, no complete (or even incomplete) thoraces of *coppinsensis* are known, so the number of thoracic segments is indeterminate; there is no appreciable difference from *horani* in the length and inflation of the glabella or in the width of the pygidium; the number of pygidial axial rings is the same as in *horani*; and rows of tubercles are present on the axial rings and posterior pleural bands of both species. Hence none of these features can be used to distinguish *horani* from *coppinsensis*, or to justify assignment of these species to separate genera.

Aulacopleuridae indet.

Figure 3P

Remarks. The only aulacopleurid pygidium found is transversely lenticular in outline, with an axis that is as wide anteriorly as the pleurae and narrows strongly backwards, six or possibly seven axial rings, four pleural furrows, and a poorly defined border. It is uncertain as to which of the two preceding species this pygidium belongs.

Scharyiidae Osmólska, 1957

Remarks. Thomas and Owens (1978) included the Scharyiinae in the Aulacopleuridae, but Owens (in Owens and Hammann, 1990) transferred it to the Brachymetopidae. I follow Adrain and Chatterton (1993) in regarding Scharyiidae as a separate family within the Aulacopleuroidea.

Scharyia Přibyl, 1946

Type species. Proetus micropygus Hawle and Corda, 1847, from the Ludlow of Bohemia; original designation.

Scharyia sp.

Figure 3M–O

Material. A cranidium and 2 pygidia.

Remarks. The conical glabella lacking furrows, the long preglabellar field, and the rather long pygidium indicate that these poorly preserved specimens belong to *Scharyia*. The pygidia resemble that of *S. redunzoi* Perry and Chatterton, 1979 from the Wenlock of Canada in having interpleural furrows that are much deeper than the pleural furrows (except for the first pleural furrow; see Fig 3O), a prominent border and a deep border furrow; *S. redunzoi* differs, however, in that the axis extends closer to the border furrow posteriorly, the border does not expand posteromedially, and the posterior margin is not subangular medially.

Cheiruridae Hawle and Corda, 1847

Acanthoparyphinae Whittington and Evitt, 1954

Youngia Lindström, 1885

Type species. Cheirurus trispinosus Young, 1868, from the Llandovery of Scotland; subsequent designation of Vogdes (1917: 115).

Remarks. Several species previously included in *Youngia* were reassigned by Ramsköld (1983) and Chatterton and Perry (1984) to *Hyrokybe* Lane, 1972. There has been confusion in the discrimination of these genera because they share similar cephalic morphology and because no pygidia are known for either type species. New diagnoses for *Youngia* and *Hyrokybe* were given by Chatterton and Perry (1984) on the basis of new material of a number of species, most represented by both cephala and pygidia. The pygidia of species they assigned to *Hyrokybe* have two pairs of marginal spines of almost equal size, and are very different from the pygidia assigned to *Youngia* which have the outer pair of spines greatly elongated and the inner pair very reduced in size. Although Chatterton and Perry did not list differences between the two genera, comparison of their diagnoses and discussion suggests that, in addition to the form of the pygidial spines, they considered *Hyrokybe* to differ from *Youngia* in that the occipital and genal spines are commonly shorter, there are two pairs of secondary spines on the lateral fixigenal border in front of the genal spine, the hypostome is commonly fused to the rostral plate, and the posterior margin of the hypostome has a series of blunt spines medially. Secondary spines on the lateral fixigenal border are apparently not present, however, in the type species of *Hyrokybe*, *H. pharanx* Lane (1972, pl. 64, figs 1–3). Species assigned by Chatterton and Perry to *Hyrokybe* also differ from those assigned to *Youngia* in that the glabella (excluding the occipital spine) is always wider than long in dorsal view (in *Youngia* the glabella is commonly as wide as long or slightly longer than wide, but in *Y. johnsoni* it is wider than long), and the middle furrow of the hypostome is weaker and directed transversely or slightly obliquely forwards rather than obliquely backwards. The differences in the cranidium are not always consistently developed, so that in the absence of hypostomes or pygidia unequivocal assignment to *Youngia* or *Hyrokybe* may not be possible.

Youngia sp.

Figure 4

Material. A cephalon, 6 cranidia, 3 isolated fixigenae, 3 librigenae, and a hypostome.

Remarks. S3 is distinguishable on only one of the cranidia (Fig. 4L), in which, however, S2 is obliterated by a fracture. S3 is more anteriorly directed than S1 and S2, and meets the axial furrow at the abaxial end of the preglabellar furrow.

This species, which in the absence of pygidia is not formally named, is assigned to *Youngia* rather than to *Hyrokybe* because the glabella is approximately as wide as long (sag.) in dorsal view, the occipital and genal spines are relatively large, the hypostome has a well-defined middle furrow that is directed obliquely backward, and the posterior margin of the hypostome is not spinose medially. The type species, *Y. trispinosa*, differs from the present one in having longer occipital and genal spines, the occipital spine is thicker at its base, the eye is situated farther forwards with its posterior edge opposite S1, and the lateral border furrow is indistinct near the genal angle (Lane, 1971, pl. 16, figs 1–4, 7–9, 11, 13).

Of the species assigned to *Youngia* by Chatterton and Perry (1984) from the Upper Llandovery of Canada, those most closely resembling the present one are *Y. boucoti*, *Y. kathyae* and *Y. steineri*. These three species, considered by Chatterton and Perry to belong to a single evolutionary lineage, differ from the Poley Cow species in that S1 does not meet the occipital furrow, the fixigenae are narrower so that the genal spine arises closer to the occipital ring, and the palpebral lobe is situated farther forwards with its posterior edge opposite S1. The hypostome of *Y. boucoti* is unknown, but those of *Y. kathyae* and *Y. steineri* differ from the hypostome of the Poley Cow species in having more pronounced tubercles on the anterior lobe of the middle body.

Sphaerexochinae Öpik, 1937

Sphaerexochus Beyrich, 1845

Type species. Spaerexochus [sic] *mirus* Beyrich, 1845, from the Wenlock of Bohemia; by monotypy.

Sphaerexochus sp.

Figure 5A–G, I, J

Material. Eight cranidia, a hypostome, an incomplete thoracic segment and a pygidium.

Remarks. Numerous *Sphaerexochus* species have been named from the Silurian but their discrimination is made difficult by conservatism in cephalic morphology (Holloway, 1980: 38) and variability in the pygidium. Pygidial variation has in some cases been attributed to dimorphism (Perry and Chatterton, 1977; Ramsköld, 1983; Chatterton and Perry, 1984) and in other cases to the type of preservation or to changes during ontogeny (Thomas, 1981). These factors, together with the poor preservation of the present material and the paucity of pygidia, make reliable comparison with other species impossible.

Nevertheless, several species resemble the present one in having a relatively broad pygidium with very short marginal projections and distinct pits in the axial furrow near the front of the terminal lobe. Such species include *S. britannicus* Dean, 1971 from the Wenlock of England (if this is distinct from *S. mirus*; see Thomas,

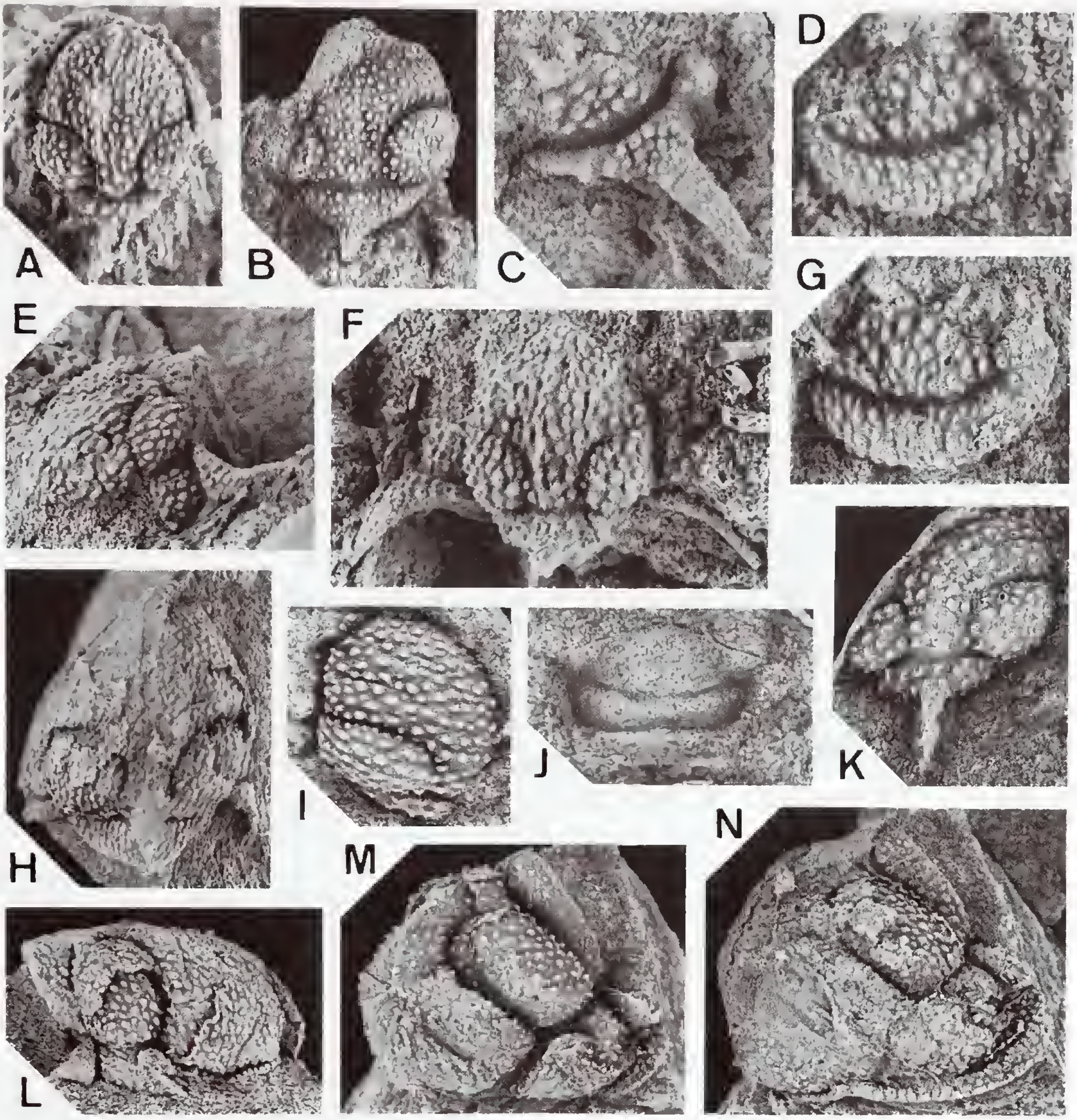


Figure 4. *Youngia* sp. A, cranidium NMV P134828, latex cast of external mould, external view, × 5. B, cranidium NMV P134830, internal mould, dorsal view, × 4. C, fixigena NMV P134834, latex cast of external mould, oblique view (posterior border at bottom of photograph), × 6. D, librigena NMV P134839, latex cast of external mould, oblique view, × 10. E, F, cranidium NMV P134827, latex cast of external mould, oblique and external views, × 6. G, librigena NMV P134838, latex cast of external mould, oblique view, × 6. H, L–N, incomplete cephalon NMV P134826; H, L, N, latex cast of external mould, dorsal, lateral and oblique views (anterior lateral glabellar furrow in L is S3), × 3; M, internal mould, oblique view, × 3. I, cranidium NMV P134832, latex cast of external mould, oblique view, × 4. J, hypostome NMV P134840, latex cast of external mould, ventral view, × 2. K, cranidium NMV P134829, latex cast of external mould, dorsal view, × 4.

1981), *S. glaber* Holloway, 1980 from the Wenlock of Arkansas and Oklahoma, *S. scabridus* Angelin, 1854 from the Wenlock of Gotland (see Ramsköld, 1983), and Ramsköld's (1983, pl. 28, figs 1a, b, 6a, b) pygidial dimorph B of *S. latifrons* Angelin, 1854, from the Ludlow of Gotland. The last of these is perhaps the most similar but, compared with the present species, the glabella of *S. latifrons* seems to be much wider adaxial to L1 (Ramsköld, 1983, pl. 27, fig. 12b). Pygidia of *S. britannicus* and *S. scabridus* have a more convex (sag.) axial terminal lobe that is semielliptical or bulbous rather than subtriangular, and the third marginal projection is longer. In addition, the hypostome of *S. scabridus* has a more convex anterior margin, a lateral border not expanding as strongly backwards, and a deeper, more concave-forwards posterior border furrow (Ramsköld, 1983, pl. 27, figs 7, 8). The pygidium of *S. glaber* has a more convex (sag.) terminal lobe, and the third pleural rib does not project distally at all.

Chatterton and Campbell (1980) described two Australian species, *Sphaerexochus molongloensis* from the Wenlock of Canberra and *S. lorum* from the Ludlow of the Yass Basin, New South Wales. The former is the more similar to the present species but appears to have a longer pygidium with a more distinct pseudo-articulating half ring on the second segment, and a longer third marginal projection.

Deiphoninae Raymond, 1913

Sphaerocoryphe Angelin, 1854

Type species. Sphaerocoryphe dentata Angelin, 1854, from the Upper Ordovician of Sweden; ICZN Opinion 614 (*Bulletin of Zoological Nomenclature* 18: 357).

Sphaerocoryphe sp.

Figure 5H, K

Material. Internal moulds of a cranidium and a pygidium, on the same piece of rock.

Remarks. Distinctive features are the glabellar bulb that is wider than long; the very short (sag.) L1; the widely divergent genal spine (very poorly preserved as an external mould of the ventral surface); the stout, downwardly directed profixigenal spine (preserved as a pit in Fig. 5H; the slightly smaller pit to the right of it is not another spine); the shallow subgenal notch; the relatively long and weakly curved first pygidial marginal spine; the second marginal spine that is flexed backwards distally; the narrow, transverse posterior pygidial margin between the second pair of spines; and the deep pygidial axial furrow behind the second ring. In the pygidial characters listed above there are similarities with *Deiphon*, a genus generally considered to have been derived from *Sphaerocoryphe* (Lane, 1971; Holloway and Campbell, 1974; Chatterton and Perry, 1984; Přibyl et al., 1985). The present species is assigned to *Sphaerocoryphe* rather than to *Deiphon* because the fixigena is not markedly reduced in size, there is a well developed posterior cephalic border, and the subgenal notch is only very shallow. Further assessment of relationships must await the availability of better material.

A short, third pair of pygidial spines is present in most, if not all, deiphonines (Holloway, 1980) but has not been seen on the present pygidium. In *Deiphon* and at least some species of *Sphaerocoryphe* these spines are ventrally directed and consequently are not visible unless the entire posterior margin of the pygidium is excavated. Such excavation was considered inadvisable in the case of the present pygidium because of likely damage to the internal mould of the dorsal surface.

The only previous record of *Sphaerocoryphe* from strata younger than Ashgill was by Thomas and Lane (1983: 62), who mentioned its occurrence at an unspecified horizon in the Silurian.

Encrinuridae Angelin, 1854

Encrinurinae Angelin, 1854

Prostrix gen. nov.

Etymology. Latin *pro*, forward, and *strix*, furrow, referring to the deep longitudinal median furrow on the frontal lobe of the type species. Gender feminine.

Type species. Prostrix amnicola sp. nov., from the upper Llandovery of north Queensland.

Diagnosis. Glabella of low convexity; L1 continuous across glabella; S1–S3 and preglabellar furrow deep and slit-like abaxially but weak medially; frontal lobe with deep longitudinal median furrow anteriorly. Glabellar tubercles weak on external surface but distinct internally, longitudinally paired on L2–L4; anterior cranidial border with a few small, weak tubercles. Palpebral lobe long (exsag.), situated close to glabella with posterior edge opposite median part of occipital furrow and anterior edge opposite

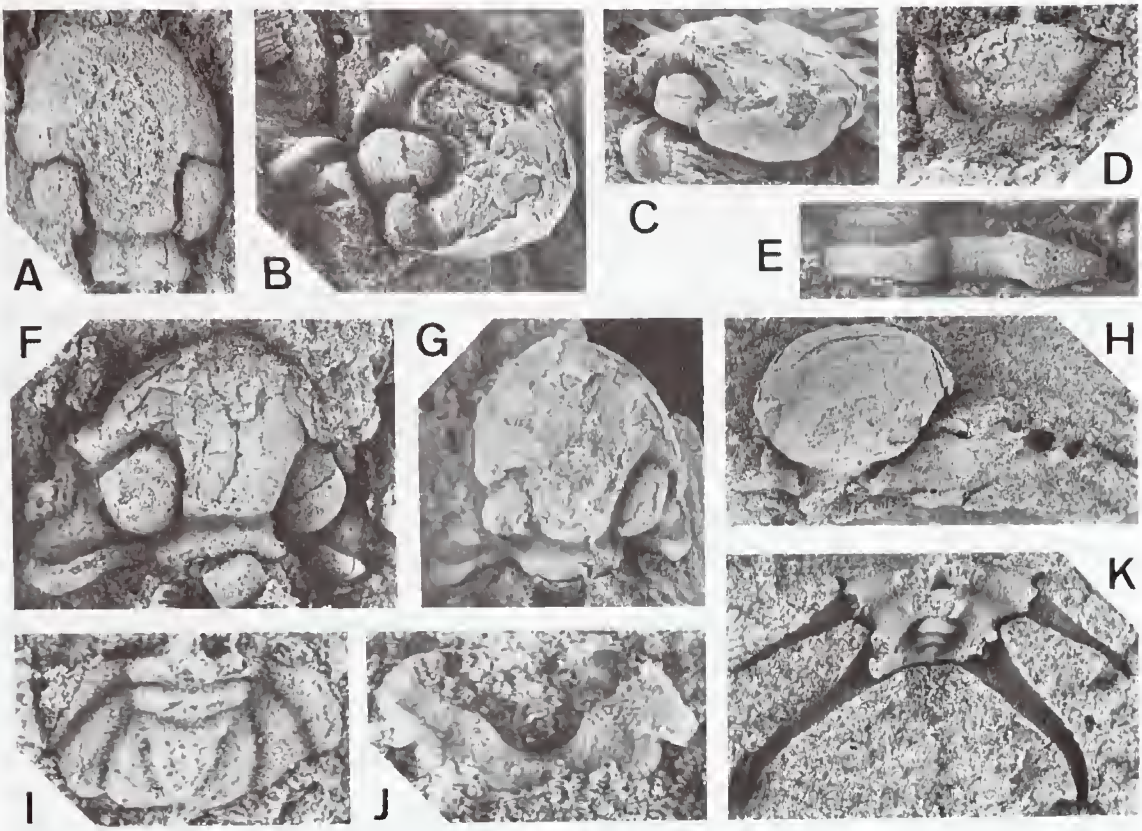


Figure 5. A–G, I, J, *Sphaerexochus* sp. A, cranidium NMV P134842, latex cast of external mould, dorsal view, × 5. B, F, cranidium NMV P134841, internal mould and latex cast of external mould, oblique and dorsal views, × 5.5. C, G, cranidium NMV P134843, internal mould, oblique and dorsal views, × 5. D, hypostome NMV P134849, latex cast of external mould, ventral view (ridge extending forward from median part of anterior margin is preparation mark), × 6. E, thoracic segment NMV P134850, internal mould, oblique view, × 6. I, J, pygidium NMV P134851, latex casts of counterpart moulds, dorsal and ventral views, × 9. H, K, *Sphaerocoryphe* sp. H, cranidium NMV P134853, internal mould, dorsal view, × 4. K, pygidium NMV P134854, broken internal mould, dorsal view, × 5.

S3, with small circular pit at midlength; palpebral furrow almost exsagittally aligned except anteriorly and posteriorly. Fixigenal field without distinct tubercles; genal spine absent. Hypostome with poorly defined rhynchos. Pygidium with 12+ axial rings and 9 or possibly 10 pleural ribs not projecting strongly distally. Doublure sloping steeply downwards and inwards towards front of pygidium.

Remarks. The genus is known only from the rather poorly preserved type species, whose relationship with other encrinurines is uncertain. With the discovery of additional species, some characters included in the preceding diagnosis may prove to be significant only at species level. Other characters included are primitive for Encrinurinae (e.g., presence of preglabellar furrow and longitudinal median furrow, abaxially slit-like lateral glabellar furrows, L1 continuous across glabella rather than obsolete medially, glabellar tubercles longitudinally paired on L2–L4), so that their presence in other taxa (e.g., *Cromus* Barrande, 1852, *Perryus* Gass and Mikulic, 1982; see Edgecombe and Chatterton, 1992) is not necessarily indicative of close relationship.

Prostrix differs from *Batocara* Strusz, 1980, to which most other Australian Silurian encrinurines are assigned herein (see below), in that the glabella is less convex, the glabellar and preglabellar furrows are wider (tr.) and slit-like abaxially, the longitudinal median furrow is well defined, L2–L4 are not tuberculiform but have longitudinally paired tubercles, the tuberculation is weak on the exterior of the glabella (Fig. 6A, K) and on the anterior cranidial border, the palpebral lobe is situated very close to the glabella and to the posterior border furrow, the fixigenal field lacks distinct tubercles, the hypostome has a poorly defined rhynchos, and there are fewer axial rings in relation to the number of pleural ribs.

Prostrix resembles some of the Chinese Llandovery encrinurine species that have been assigned to *Encrinuroides* Reed, 1931, but whose affinity with that genus was considered dubious by Edgecombe and Chatterton (1990a). The greatest similarity is with species such as "*Encrinuroides*" *abnormis* Chang, 1974, "*E.*" *enshiensis* Chang, 1974 (both revised by Chang, 1986), "*E.*" *guangyuanensis* Chang, 1986 and "*E.*" *renhuaiensis* Yin in Yin and Lee, 1978. Similarities include the abaxially slit-like glabellar and preglabellar furrows, the moderate-sized glabellar tubercles that in some species are longitudinally paired on L2–L4, and the absence of genal spines (in species with the genal angles preserved). The Chinese species differ from *Prostrix*, however, in having stronger tuberculation on the glabella and anterior cranidial border, the eye is situated farther from the glabella and from the posterior border furrow, there are prominent tubercles on the fixigenal field, and the pygidium has a greater number of axial rings in relation to the number of pleurae.

Langgonia Kobayashi and Hamada, 1971, known from three species (probably synonymous) from the upper Llandovery or lower Wenlock of West Malaysia, was originally placed in the Dalmanitidae but was transferred to the Encrinuridae by Holloway (1981). *Langgonia* resembles *Prostrix* in the abaxially slit-like glabellar and preglabellar furrows, the distinct longitudinal median furrow on the front of the glabella, L1 that is continuous across the glabella, the weak tuberculation on the glabellar exterior, the closeness of the eyes to the glabella, and the absence of genal spines. *Langgonia* differs from *Prostrix* in that the glabella is more convex across the frontal lobe, the palpebral lobe is situated farther forward and more obliquely on the cheek, there are nodular lobes on the posterior part of the fixigena adjacent to the axial furrow, and the pygidium is semi-elliptical rather than subtriangular in outline, with broader pleural lobes and fewer axial rings in relation to the number of pleural ribs.

Prostrix amnicola sp. nov.

Figure 6

Etymology. Latin *amnicola*, inhabitant of or by a river, referring to the proximity of the type locality to the Broken River; noun in apposition.

Type material. Holotype: cranidium NMV P134833A, B (counterparts), Fig. 6F, K.

Paratypes: NMV P134855, P134857, P134862 (cranidia); NMV P134859–P134861 (hypostomes); NMV P134863–P134865 (pygidia).

Diagnosis. As for genus.

Description. Glabella flat-topped in transverse profile and weakly convex in lateral profile, expanding gently forwards in front of occipital ring, approximately 1.5 times as wide at frontal lobe as at L1. Occipital ring decreasing slightly in length (exsag.) abaxially, with a slight node distally; occipital furrow deep and gently arched forwards. Preglabellar furrow not as deep as glabellar furrows abaxially, not defined medially on external surface. L1–L3 successively longer exsagittally; frontal lobe comprising half preoccipital length of glabella, lateral extremity partly isolated in holotype by short, weak depression directed forwards from S3 (Fig. 6F). Glabellar tubercles arranged in transverse row on medial part of L2 and posterior part of frontal lobe; arrangement on L3 apparently more variable (Fig. 6E, F). Palpebral lobe occupying most of fixigena, steeply upturned; palpebral furrow narrow and deep. Posterior cranidial margin deflected backwards at fulcrum and recurved forwards distally; posterior border furrow longer (exsag.) and deeper than occipital furrow adaxially, shallowing distally.

Hypostome with elliptical, moderately convex middle body; rhynchos poorly defined, projecting over anterior border furrow but not bounded laterally by furrow; macula distinct.

Pygidium approximately as wide as long (sag.), subtriangular, rounded posteriorly. Axis well-rounded (tr.), approximately as wide as pleural lobe anteriorly; ring furrows deep laterally, shallower medially; sagittal tubercle present on sixth and possibly third rings. Pleurae curving downwards abaxially from axial furrow; pleural ribs flat-topped, first one projecting slightly distally, remainder not projecting; interrib furrows much shorter (exsag.) than ribs. Doublure divided into a flattened, steeply inclined outer portion and an upwardly flexed

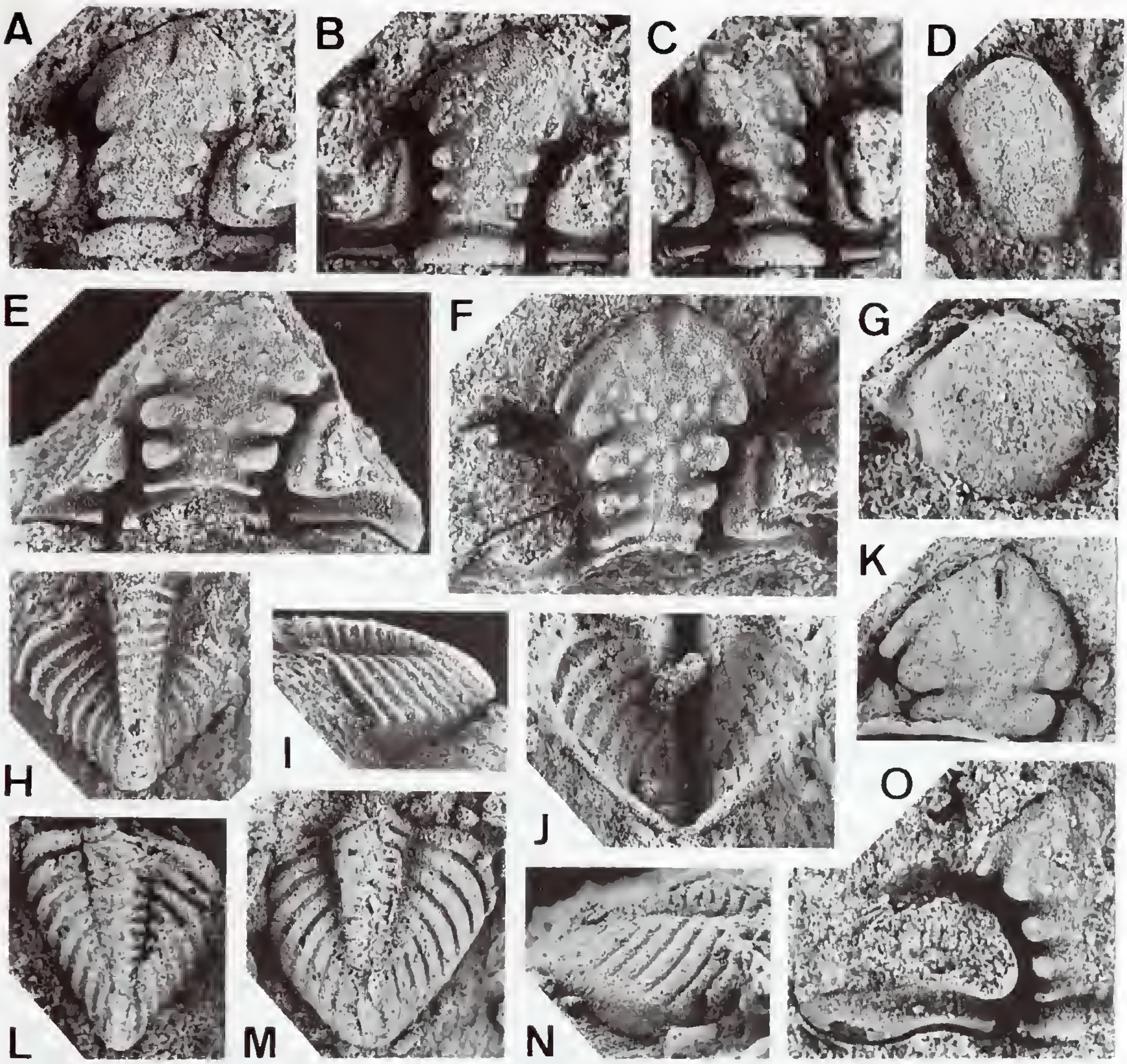


Figure 6. *Prostrix amnicola* gen. nov., sp. nov. A, B, cranidium NMV P134856, latex cast of external mould and internal mould, dorsal views, × 7. C, cranidium NMV P134862, internal mould, dorsal view, × 9. D, hypostome NMV P134860, latex cast of external mould, ventral view, × 7. E, cranidium NMV P134855, internal mould, dorsal view, × 4.5. F, K, cranidium NMV P134833, internal mould and latex cast of external mould, dorsal views, × 4.5. G, hypostome NMV P134861, latex cast of external mould, ventral view, × 8. H, I, pygidium NMV P134864, internal mould, dorsal and lateral views, × 7. J, M, N, pygidium NMV P134863, latex casts of counterpart moulds, ventral, dorsal and lateral views, × 4. L, pygidium NMV P134865, latex cast of external mould, dorsal view, × 6. O, cranidium NMV P134857, internal mould, dorsolateral view, × 6.

inner portion; outer portion very high anteriorly (Fig. 6I, N) but diminishing rapidly posteriorly; inner portion with shallow embayment posteriorly (Fig. 6J).

Batocara Strusz, 1980

(= *Pacificurus* Ramsköld, 1986a, *pro Australurus* Ramsköld, 1986b, *non* Jell and Duncan, 1986)

Type species. Encrinurus Bowningi Foerste, 1888, from the upper Ludlow of New South Wales; original designation.

Diagnosis. See Ramsköld (1986b: 559; diagnosis of *Encrinurus* (*Australurus*)).

Remarks. Strusz (1980) assigned most Australian and some Asian Silurian encrinurine species to his *Encrinurus mitchelli* plexus but excluded "*Encrinurus*" *bowningi*, for which he erected *Batocara* as a monotypic genus. Ramsköld (1986a, 1986b) subsequently proposed *Pacificurus* for the *mitchelli* plexus *sensu* Strusz. *Batocara* shares diagnostic characters of *Pacificurus* (L1 continuous across glabella, bearing tubercles adaxially and usually abaxially; L2–L4 tuberculiform and alternating with adaxial tubercles on fixigena; abundant tubercles on genal field and precranidial lobe of librigena; eyes not stalked; genal angle without spines; pygidium relatively large, non-mucronate, with broad pleural lobe), suggesting that *bowningi* shares a common ancestor with species of the *mitchelli* plexus rather than originating in a separate lineage as proposed by Strusz (1980, text-fig. 9). Strusz (1980) considered *Batocara* to be distinguished partly by the coarseness and crowding of the cranidial tuberculation, but amongst species included in *Pacificurus* this character is shared with "*Encrinurus*" *silverdalensis* Etheridge and Mitchell, which also resembles *bowningi* in the prominent median tubercles and well developed sagittal band on the pygidial axis (Strusz, 1980, pl. 5, figs 8–16, pl. 6, figs 5–14). As *bowningi* is evidently closely related to *silverdalensis* and the other Australian species, I consider its separation from them in a monotypic genus to be unjustified. Hence *bowningi* is here included in the *mitchelli* plexus, and *Pacificurus* is regarded as a junior subjective synonym of *Batocara*. The synonymy of *Batocara* and *Pacificurus* was also suspected by Edgecombe and Chatterton (1990b: 4), who listed similarities (some interpreted as synapomorphies) between the two genera, and concluded that *Batocara* is "sister group to *Pacificurus* (if not part of the ingroup)".

Batocara fritillum sp. nov.

Figure 7

Etymology. Latin *fritillus*, spotted, referring to the tuberculate cephalon.

Type material. Holotype: cranidium NMV P134868A, B (counterparts), Fig. 7B, E.

Paratypes: NMV P134869 (cephalon); NMV P134870, P134871 (cranidia); NMV P134872 (isolated fixigena); NMV P134884, P134885 (librigenae); NMV P134852, P134873–P134882 (pygidia).

Diagnosis. Glabella markedly constricted at L2, expanding very strongly forwards in front of L2; front of glabella and anterior cranidial border very steep. Tubercles on posterior part of glabella include I–1,(2); II–1,2; III–1,2,3; iv–1; distal tubercles on L2–L4 not significantly enlarged. Axial furrow wide. Fixigenal field strongly inflated adaxially, with tubercles adjacent to axial furrow not enlarged; 2–3 tubercles situated between posterior edge of palpebral lobe and axial furrow. Librigenal field apparently with only a few tubercles. Pygidium with up to 21 axial rings and 7–10 (usually 9) pleural ribs plus postaxial ridge.

Description. Glabella slightly narrower at L2 than at L1 and narrower at L3 than at occipital ring; widths at occipital ring, L2 and L4 approximately in ratio 1.7:1:2. Occipital ring well rounded (sag., exsag.), decreasing in length (exsag.) distally abaxial to L1; occipital furrow deep. S1–S3 continuous across glabella, S3 very shallow medially; distal tubercle on L1 (if present) small and low. Frontal lobe strongly inflated, comprising half sagittal length of glabella in dorsal view, bearing fairly dense tubercles that are of two sizes (Fig. 7B) and not arranged in distinct rows. Preglabellar furrow indistinct or undefined medially; anterior cranidial border complete only on holotype (Fig. 7E), lateral third with 5 tubercles that decrease in size adaxially, median third lacking distinct tubercles. Palpebral lobe upturned, anterior edge opposite L4 and posterior edge opposite L2; palpebral furrow shallow and broad. Eye ridge distinct on internal moulds (Fig. 7E), crossing axial furrow obliquely opposite L4 and with prominent tubercle at abaxial edge of axial furrow. Anterior branch of facial suture not converging as strongly forward as eye ridge; posterior branch transverse adaxially, thereafter flexed posterolaterally in concave-forward curve subparallel to part of posterior cranidial margin. Posteromedial part of fixigenal field standing higher than glabella opposite, with dense tubercles and intervening pits; largest tubercles adjacent to palpebral furrow; fixigenal tubercles very subdued on exterior of large specimens (Fig. 7A). Genal angle rounded.

Librigenal field wider (tr.) than height of lateral border, bearing only a few large tubercles. Base of eye socle higher than precranidial lobe, defined by rather deep furrow. Lateral border behind precranidial lobe with a single row of subdued tubercles; anterior furrow poorly defined; precranidial lobe shorter (exsag.) than librigenal field.

Pygidium slightly longer than wide, posterolateral margins weakly concave in outline. Axis 0.25–0.3 times maximum pygidial width anter-

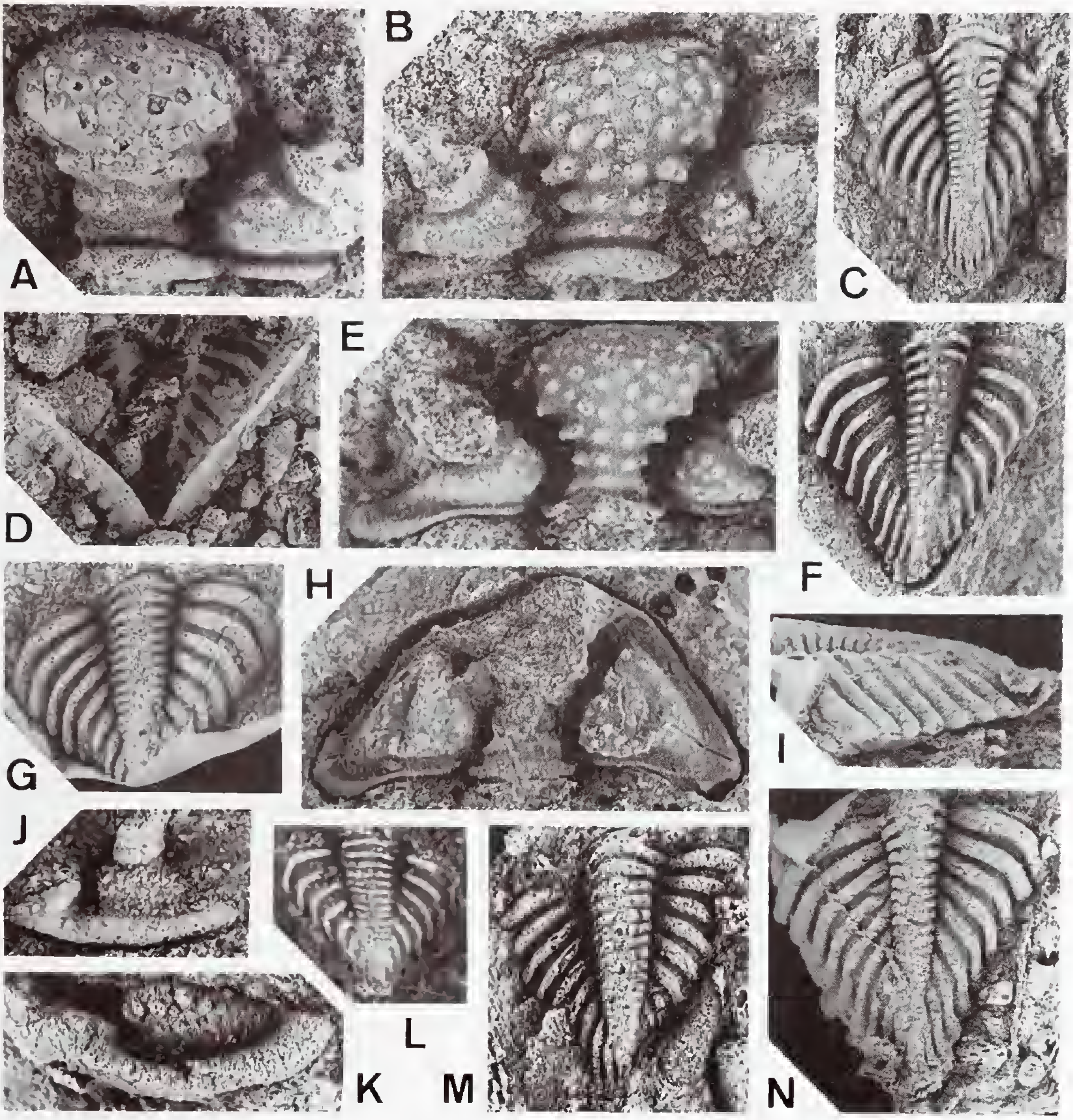


Figure 7. *Batocara fritillum* sp. nov. A, cranidium NMV P134870, latex cast of external mould, dorsal view, × 4.5. B, E, holotype, cranidium NMV P134868, latex cast of external mould and internal mould, dorsal views, × 6.5 and × 5.5. C, pygidium NMV P134873, latex cast of external mould, dorsal view, × 4. D, pygidium NMV P134874, latex cast of natural mould, ventral view, × 6. F, pygidium NMV P134875, internal mould, dorsal view, × 6. G, pygidium NMV P134852, latex cast of external mould, dorsal view, × 5. H, cephalon NMV P134869, internal mould, dorsal view, × 4. I, N, pygidium NMV P134876, latex cast of external mould, lateral and dorsal views, × 4. J, librigena NMV P134884, internal mould, exterior view, × 10. K, librigena NMV P134885, latex cast of external mould, exterior view, × 7. L, pygidium NMV P134877, internal mould, dorsal view, × 7. M, pygidium NMV P134878, latex cast of external mould, dorsal view, × 8.

iorly, tapering backwards rather strongly over first 2–3 segments, thereafter more gently; sagittal band distinct but crossed by shallow medial parts of ring furrows, especially anteriorly. Up to 3 median axial tubercles distinguishable on some pygidia but subdued on exterior; first tubercle on ring 3 or 4, second on third next ring, last on third or fourth next ring. Pleural ribs on anterior segments curving strongly backwards abaxially, on posterior segments becoming more exsagittally aligned and acquiring sigmoidal shape as distal ends turn outwards slightly; ends of ribs form blunt projections (Fig. 7D). Some internal moulds with sparse tubercles along ribs (Fig. 7F). Inter-rib furrows narrower than ribs on external surface. Pygidial doublure widening slightly posteriorly towards V-shaped notch (Fig. 7D).

Remarks. The librigena on a poorly preserved cephalon of *Batocara fritillum* has the tubercles on the field arranged in a single row close to the base of the eye (Fig. 7H), whereas two isolated librigenae lack this arrangement of tubercles on the field (Fig. 7J, K). Despite this difference, the isolated librigenae are assigned to *B. fritillum* rather than to *Prostrix amnicola* because the eye appears too small to match the palpebral lobe on the latter species.

Batocara fritillum is easily distinguished from most other species of the genus by the marked constriction of the glabella at L2, the inflated frontal lobe that is very steep anteriorly, the wide axial furrow not overhung by enlarged adaxial tubercles on the fixigena, and the sparse tuberculation on the librigenal field. *B. fritillum* resembles *B. bowningi* (see Strusz, 1980, pl. 6, figs 5–14) in the constriction of the glabella at L2, but there are so many other differences between the two species that they are not considered to be closely related.

"*Pacificurus*" *chilorhodus* Edgecombe and Ramsköld, 1992 from the Telychian (not Sheinwoodian; G. D. Edgecombe, personal communication) of Canada resembles *Batocara fritillum* in several respects, notably the constriction of the glabella across L2, the distal tubercles on L2–L4 that are not significantly enlarged, and the non-enlarged adaxial fixigenal tubercles. "*P.*" *chilorhodus* differs from *B. fritillum*, and from all other members of *Batocara*, in having S1 merging with the occipital furrow medially, a pygidium with a low ratio of axial rings to pleural ribs, and distinct paired tubercles on the pygidial axial rings. These characters are shared with *Balizoma* (*sensu* Holloway, 1980 and Ramsköld, 1986b), suggesting that *chilorhodus* may be more closely related to that genus (though not belonging to it) than to *Batocara*.

Coronocephalus Grabau, 1924

Type species. Encrinurus (Coronocephalus) rex Grabau, 1924, from the Upper Llandovery (Temple and Wu, 1990) of China; by monotypy.

***Coronocephalus*? aff. *urbis* Strusz, 1980**

Figure 8A–F, H–J, L–N

Material. Five cranidia, an isolated fixigena, 2 librigenae and 5 pygidia.

Remarks. Coronocephalus urbis, from the Wenlock of the Canberra district, was excluded from *Coronocephalus* by Chang (1983: 203, 223) because it has a distinct preglabellar furrow, a shallow longitudinal median furrow on the front of the glabella, and numerous small tubercles on the librigenal margin. However, these characters are primitive homologues of derived states present in most *Coronocephalus* species (preglabellar and longitudinal median furrows weak or effaced, single row of large denticles on librigenal margin) and do not preclude a close relationship with that genus. Consequently *urbis* is here assigned to *Coronocephalus* with question.

The present specimens resemble *Coronocephalus*? *urbis* in the long genal spine, the wide (tr.) anterior cranidial border with a double row of tubercles, the shallow longitudinal median furrow (Fig. 8L), the broad palpebral area, the densely tuberculate librigena with a narrow field, and the relatively short pygidium with distinct sagittal tubercles. The specimens differ from topotypes of *urbis* in having fewer pygidial axial rings (about 14 instead of about 20) and pleural ribs (9–10 instead of 10–11), a distinct anterior furrow on the librigena (Fig. 8C), and possibly in the glabellar tubercle pattern (e.g., the presence of tubercles ii-0 and iii-0 or iii-1 in some cranidia). The Poley Cow species thus appears distinct from *urbis* but the material (especially of cranidia) is considered inadequate for formal naming.

Coronocephalus? *thailandicus* (Kobayashi and Sakagami, 1989), from the upper Wenlock or lower Ludlow of Thailand, was considered by Edgecombe and Ramsköld (1992: 261) to be closely related to *urbis*, and shares many of the similarities between that species and the present

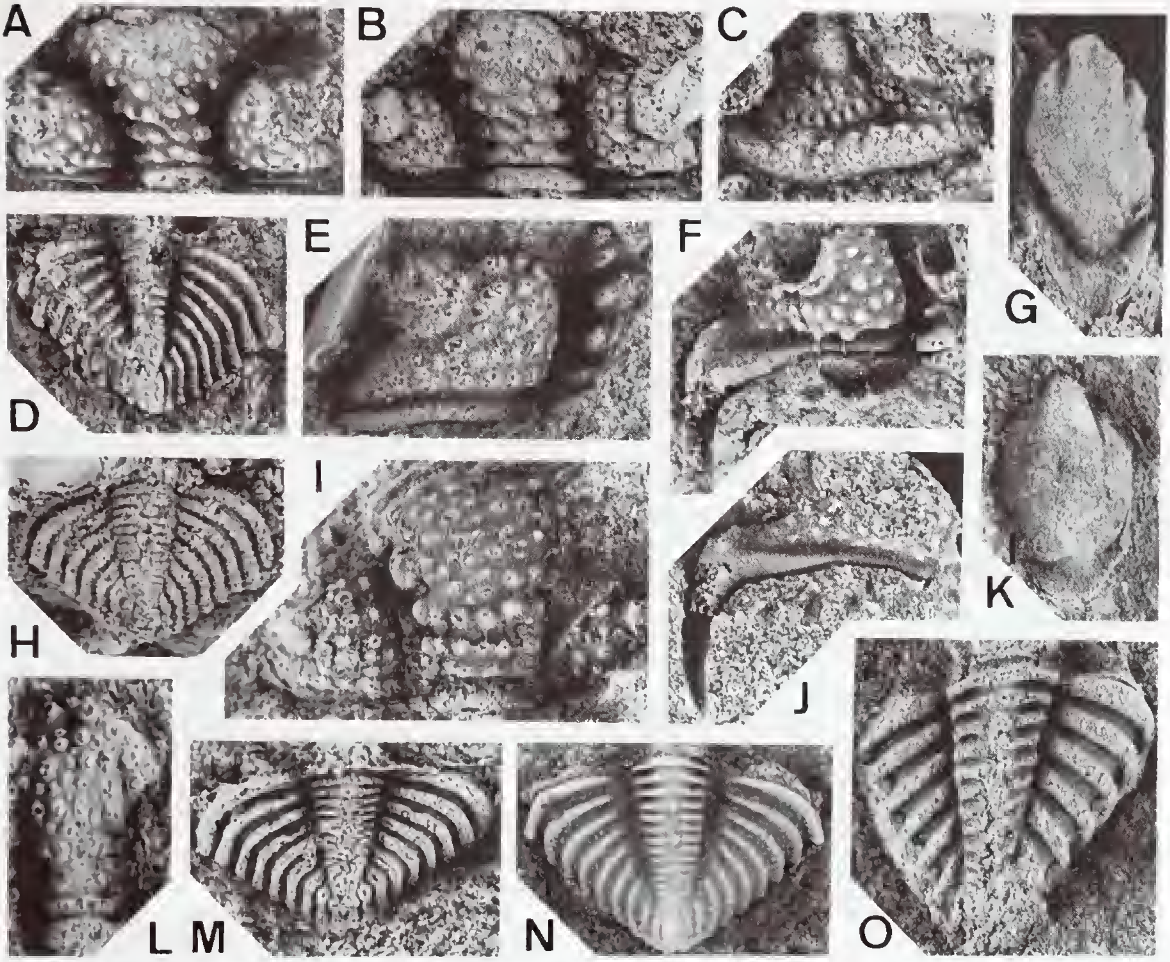


Figure 8. A–F, H–J, L–N, *Coronocephalus*? aff. *urbis* Strusz. A, B, cranidium NMV P134886, internal mould and latex cast of external mould, dorsal views, × 7. C, librigena NMV P134892, latex cast of external mould, exterior view, × 7. D, pygidium NMV P134893, internal mould, dorsal view, × 8. E, cranidium NMV P134887, latex cast of external mould, dorsal view, × 6. F, cranidium NMV P134888, internal mould, dorsal view, × 5. H, pygidium NMV P134894, latex cast of external mould, dorsal view, × 8. I, cranidium NMV P134889, latex cast of partly testiferous mould, dorsal view, × 5. J, fixigena NMV P134890, internal mould, dorsal view, × 5. L, small cranidium NMV P134891, latex cast of external mould, dorsal view, × 10. M, pygidium NMV P134895, latex cast of external mould, dorsal view, × 6.5. N, pygidium NMV P134896, internal mould, dorsal view, × 6. G, K, encrinurid hypostomes indet. G, NMV P134897, internal mould, ventral view, × 7. K, NMV P134898, latex cast of external mould, ventral view, × 6. O, encrinurid pygidium indet., NMV P134899, latex cast of external mould, dorsal view, × 4.

one. *C*? *thailandicus* is most readily distinguished from the present species by its longer pygidium with a greater number of axial rings.

encrinurid hypostomes indet.

Figure 8G, K

Remarks. These two hypostomes differ markedly from each other and clearly belong to separate taxa. Both hypostomes have a rhynchos that projects strongly anteriorly and is bounded laterally by deep furrows, but in one specimen the rhynchos is conical (Fig. 8K) whereas in the other it narrows weakly forwards, is broadly rounded anteriorly and slightly concave in outline laterally (Fig. 8G). The specimens also differ in the length (sag.) of the posterior border and the curvature of the posterior margin.

It is not possible confidently to match these hypostomes with the two preceding species. *Cor-*

onocephalus? urbis has a conical rhynchos, as do most species of *Batocara*. However, *Batocara silverdalense* (Etheridge and Mitchell) has a rather weakly tapering rhynchos (Strusz, 1980, pl. 5, fig. 14), suggesting that the present hypostome with this character may belong to *B. fritillum*.

encrinurid pygidium indet.

Figure 8O

Remarks. A single encrinurid pygidium, which is incomplete posteriorly, differs from the others known from the Poley Cow Formation. The specimen resembles pygidia of *Batocara fritillum* in overall proportions but has a wider and more strongly tapering axis, fewer axial rings and pleural ribs, ring furrows containing elliptical apodemal pits laterally, and wider (exsag.) inter-rib furrows.

Calymenidae Milne Edwards, 1840

Flexicalymeninae Siveter, 1977

(= Metacalymeninae Přibyl and Vaněk, 1977)

Remarks. Flexicalymeninae and Metacalymeninae are considered here to be synonymous. Although Přibyl and Vaněk's publication establishing Metacalymeninae is dated 1975, the date of issue given inside the front cover of the volume is December 1977. Dr Siveter has informed me that his publication was issued in April 1977. Flexicalymeninae thus has priority over Metacalymeninae.

Gravicalymene Shirley, 1936

Type species. Gravicalymene convolva Shirley, 1936, from the lower Ashgill of south Wales; original designation.

Remarks. The following species belongs to the group for which Chatterton and Campbell (1980) proposed the genus *Apocalymene*. The difficulty of classifying such species was discussed by Holloway (1980), who concluded that present knowledge of calymenid relationships does not enable the discrimination of *Apocalymene* from *Sthenarocalymene* Siveter, 1977. *Sthenarocalymene* was considered by Siveter (1977) and Holloway (1980) to differ from *Gravicalymene* in the form of the anterior cephalic border. Price (1982), however, presented evidence that the form of the anterior border is too variable to be used to distinguish between these two genera, lending support to doubts raised by other workers (e.g., see Price, 1982: 58) on the taxonomic usefulness of this character at the generic level. Price therefore placed *Sthenarocalymene* in synonymy with *Gravicalymene*. Until the relationships of calymenids of *Apocalymene* and *Sthenarocalymene* type are clarified, I prefer to assign such species to *Gravicalymene* with question.

Gravicalymene*? *vaccina sp. nov.

Figure 9

Etymology. Latin *vaccinus*, of cows, referring to the Poley Cow Formation.

Type material. Holotype: cranidium NMV P138830A, B (counterparts), Fig. 9A, B.

Paratypes: NMV P138831–P138838 (cranidia); NMV P134883, P138839–P138842 (librigenae); NMV P134867, P138843–P138847 (hypostomes); NMV P138848–P138856 (pygidia).

Diagnosis. Anterior cephalic border as long (sag.) as occipital ring, gently upturned. L1 large, almost as wide as adjacent median part of glabella, with anterior edge opposite glabellar midlength. Midlength of palpebral lobe opposite S2 or slightly farther forward. Hypostome with broad posterior border spines having abaxial and adaxial margins convex in outline, separated by sharp notch. Pygidium with narrow, gently taping axis of 6–7 rings, 5 sharply impressed pleural furrows, and no vincular furrow.

Description. Glabella bell-shaped, widest towards back of L1 and approximately 0.6 times as wide across frontal lobe; front of glabella flattened in outline medially, level with front of fixigenal field or projecting slightly farther forwards. Occipital ring decreasing in length abaxially behind L1, flexed forwards slightly distally; occipital furrow increasing greatly in depth behind L1. L1 ovate; posterior branch of S1 shallowing abruptly opposite middle (exsag.) of L1 but extending to occipital furrow. L2 subcircular or elliptical, half as long (exsag.) as L1 and not as distinctly separated from median part of glabella. L3 nodular, half as long (exsag.) as L2; S3 narrow (tr.), shallow and situated at 0.25 times glabellar length. Axial furrow containing anterior pit just behind anterolateral extremity of frontal lobe; preglabellar furrow not as deep as axial furrow but recessed slightly beneath front of glabella. Anterior border flattened (sag., exsag.) behind strongly rounded crest; anterior border furrow shallow and well-rounded in cross section. Fixigenal field convex (exsag.), sloping steeply forwards in front of palpebral lobe; anterior edge of palpebral lobe opposite S3, pos-

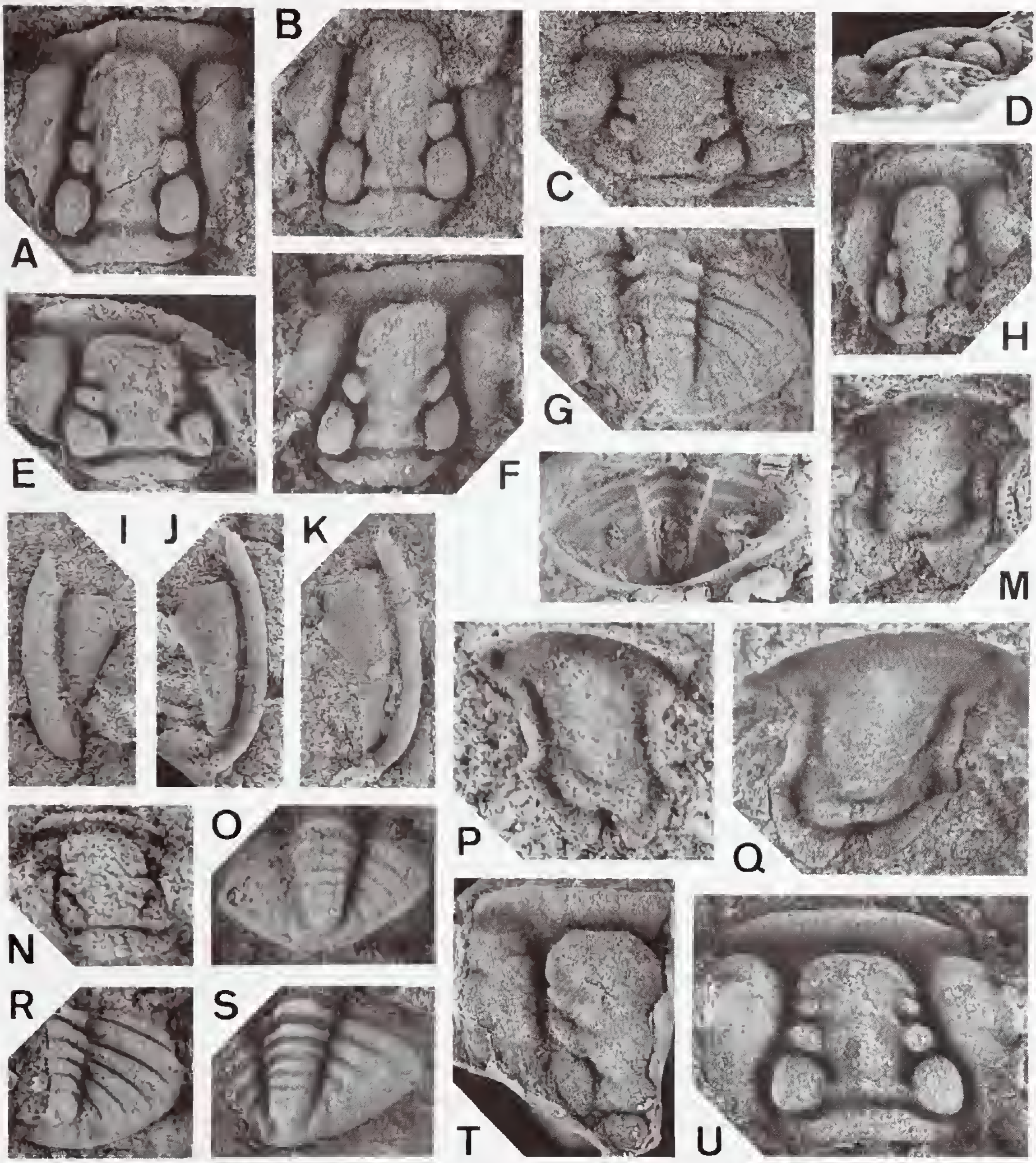


Figure 9. *Gravicalymene*? *vaccina* sp. nov. A, B, holotype, cranidium NMV P138830, internal mould and latex cast of external mould, dorsal views, × 3.5. C, cranidium NMV P138831, latex cast of external mould, dorsal view, × 5. D, H, cranidium NMV P138832, latex cast of external mould, lateral and dorsal views, × 5. E, cranidium NMV P138833, internal mould, dorsal view, × 5. F, cranidium NMV P138834, internal mould, dorsal view, × 5. G, pygidium NMV P138848, latex cast of external mould, dorsal view, × 3. I, J, left librigena NMV P138839, latex casts of counterpart moulds, dorsal and ventral views, × 3.5. K, left librigena NMV P138840, latex cast of natural mould, ventral view, × 3.5. L, pygidium NMV P138849, latex cast of natural mould, ventral view, × 3.5. M, hypostome NMV P134867, latex cast of external mould, ventral view, × 8. N, cranidium NMV P138835, internal mould, dorsal view, × 10. O, pygidium NMV P138850, internal mould, dorsal view, × 6. P, hypostome NMV P138843, latex cast of external mould, ventral view, × 7. Q, hypostome NMV P138844, internal mould, ventral view, × 7.5. R, pygidium NMV P138851, latex cast of external mould, dorsal view, × 3. S, pygidium NMV P138852, internal mould, dorsal view, × 3. T, cranidium NMV P138836, latex cast of external mould, dorsal view, × 4. U, cranidium NMV P138837, internal mould, dorsal view, × 4.5.

terior edge opposite outer end of S1. Anterior branch of facial suture mostly subparallel to sagittal line or converging weakly, curving strongly inwards across front of anterior border furrow; posterior branch of suture (interpreted from librigena) directed laterally or even slightly forwards from ε, flexed more strongly backwards about half way to lateral border furrow. Librigena with gently convex field, shallow lateral border furrow, and broad and well-rounded border; doublure flattened, inner edge lying close beneath inner part of border.

Hypostome approximately as wide across shoulders as long (sag.), about 1.5 times wider across anterior wings; anterior margin broadly rounded, lateral margin subparallel between anterior wing and shoulder; notch between posterior spines extending forwards to posterior border furrow. Anterior lobe of middle body elliptical, rising steeply to a central prominence; posterior lobe crescentic, slightly inflated, wider (tr.) than anterior lobe; middle furrow deepest abaxially and medially, median part lying opposite shoulder; maculae inconspicuous. Anterior border flexed ventrally to form a sharp flange separated from middle body by a long (sag., exsag.), poorly delimited depression; anterior wing with deep pit. Lateral border strongly convex (tr.), of uniform width except towards shoulder where it expands slightly; lateral border furrow firmly impressed. Posterior spines flattened; posterior border furrow increasing in depth abaxially and medially.

Pygidium 1.5–1.6 times as wide as long, lenticular to rhombic in outline. First axial ring flexed slightly forwards distally and with weak node; rings 2 and 3 with pseudo-articulating half rings medially; all except last ring furrow deepest abaxially. Axial furrow very shallow behind axis. Pleural lobes gently convex (tr.); posterior margin arched upwards towards sagittal line. Pleural furrows shallowing abaxially but distinguishable almost to margin; interpleural furrows weak, most distinct abaxially; posterior pleural band on fifth segment depressed abaxially, bounding gently convex (tr.) postaxial region. Doublure narrow and sharply rounded in cross section.

External surface of cranidium, librigena, hypostome and pygidium with traces of granulose sculpture.

Remarks. The preserved shape of the glabella of *Gravicalymene*? *vaccina* and the degree to which the anterior border is upturned vary due to deformation of the specimens (e.g., compare Fig. 9A, C, H). The holotype (Fig. 9A, B) appears to be the least deformed specimen. A very small cranidium (Fig. 9N), 1.9 mm in length, differs from larger cranidia in having a broader, more subquadrate glabella and a shorter (sag.), sharply upturned anterior border, although these differences could again be due to deformation. L1 is subtriangular; S1 is rather shallow at the axial furrow, the anterior branch is very weak and transverse, and the posterior branch is deep but dies out abruptly just in front of the occipital furrow. S2 and S3 are transverse and narrow, S3 being very shallow; L2 is not separated from the median part of the glabella. The cranidium is rather coarsely granulose and there is a median tubercle on the occipital ring.

Gravicalymene? *vaccina* is very similar to *G*? *hetera* Gill, 1945 and *G*? *kilmorensis* Gill, 1945, both from the Ludlow of central Victoria, and *G*? *coppinsensis* (Chatterton and Campbell, 1980) from the Wenlock of the Australian Capital Territory. *G*? *hetera* and *G*? *kilmorensis*, which are probably synonymous (Holloway and Neil, 1982), differ from *G*? *vaccina* in having a more upturned anterior cephalic border and slightly more posteriorly placed palpebral lobes, with their midlength opposite L2 rather than S2. *G*? *coppinsensis* has a smaller L1 than *G*? *vaccina*, slightly narrower posterior hypostomal spines separated by a broader median notch, a more strongly tapering pygidial axis, less sharply impressed pygidial pleural furrows (except the first), and interpleural furrows that are more distinct abaxially. *G*? *cootamundrensis* (Gill, 1940), from strata in New South Wales previously assigned a Late Silurian age but now known to be Early Devonian (Adrian, 1978), is also similar to *G*? *vaccina* but has a slightly more upturned anterior border, a somewhat smaller L1, coarser cranidial granulation, and pygidial pleural and interpleural furrows that are deeper abaxially.

Gravicalymene? *changyangensis* (Chang, 1974) from the Silurian of south-west China is distinguished from *G*? *vaccina* by its less bell-shaped glabella with much smaller L1.

The incomplete calymenid pygidium figured by Lane and Thomas (1978, pl. 2, fig. o), from the Quinton Formation in the Grey Creek area of the Broken River Province, differs from pygidia of *Gravicalymene*? *vaccina* in having longer (exsag.) pleural furrows that curve more strongly backwards abaxially and extend closer to the pygidial margin, and interpleural furrows that are deeper abaxially.

Odontopleuridae Burmeister, 1843

Odontopleurinae Burmeister, 1843

Remarks. A number of odontopleurid genera were assigned by Ramsköld and Chatterton (1991) to the Acidaspidinae Salter, 1864, a subfamily previously considered synonymous with the Odontopleurinae. Ramsköld and Chatterton stated that their concept of the Acidaspidinae is new but did not give a full diagnosis as details are to be presented elsewhere. Pending the publication of these details, the Acidaspidinae is not recognised here.

Gaotania Chang, 1974

Type species. Gaotania ovata Chang, 1974, from the upper Llandovery of south-west China; original designation.

Remarks. Gaotania is not well known, morphological information on the genus having been derived mostly from the cephalon and pygidium of the type species illustrated by Chang (1974, pl. 82, figs 7, 8). Another Chinese species, *G. pulchella* Chang, 1974, is based on a very poorly preserved dorsal exoskeleton, and has also been recorded from poorly preserved material by Wu (1977: 103, pl. 2, figs 15, 16; note that the numbering of figs 12 and 16 is transposed on Wu's plate 2). Poorly preserved specimens assigned to *G. ovata* by Chang and Meng (1986: 513, pl. 3, figs 8–12) apparently do not belong to that species, as the major border spines on the pygidium are not greatly inflated.

Ramsköld and Chatterton (1991) considered *Gaotania* to belong to a monophyletic group of genera that also includes *Globulaspis* Reed, 1931, *Stelckaspis* Chatterton and Perry, 1983 and *Uriarra* Chatterton and Campbell, 1980. *Gaotania* is extremely similar to *Stelckaspis* and was considered to be a senior synonym of that genus by Lane (1988). Characters shared by the two genera include: glabella narrower than the cheeks; frontal lobe not expanded laterally; L3 absent; L2 weakly separated from the median lobe; facial suture apparently fused in holaspides; eyes situated posteriorly and very close to the glabella; anterior and lateral cephalic border furrows joining in a curve; genal spines relatively short and stout; and pygidium with two pairs of median secondary border spines between the major spines. Ramsköld and Chatterton (1991: 356) stated that the pygidium of *Gaotania* differs from that of *Stelckaspis* in having the lateral pair of median secondary border spines partly fused with the major spine pair instead of being separate. Partial fusion of these spines is, however, variably developed within some other odontopleurid genera; among species assigned by Ramsköld and Chatterton to *Meadowtownella*, these spines are partly fused in *Primaspis ascita* Whittington (1956: 199, pls 1, 2) and *Acidaspis trentonensis* Hall (see Ross, 1979: D8, pl. 4, figs 8–11) but not in *Acidaspis girvanensis* Reed (1914: 33, pl. 5, figs 8–10, pl. 6, figs 1–3). This suggests that partial fusion of pygidial spines may develop independently within lineages and should be used with caution in adducing relationships. Species assigned to *Gaotania* also differ from those assigned to *Stelckaspis* in that the occipital lobes are very weak or absent and the pygidial pleural ridge is more poorly defined along its adaxial edge.

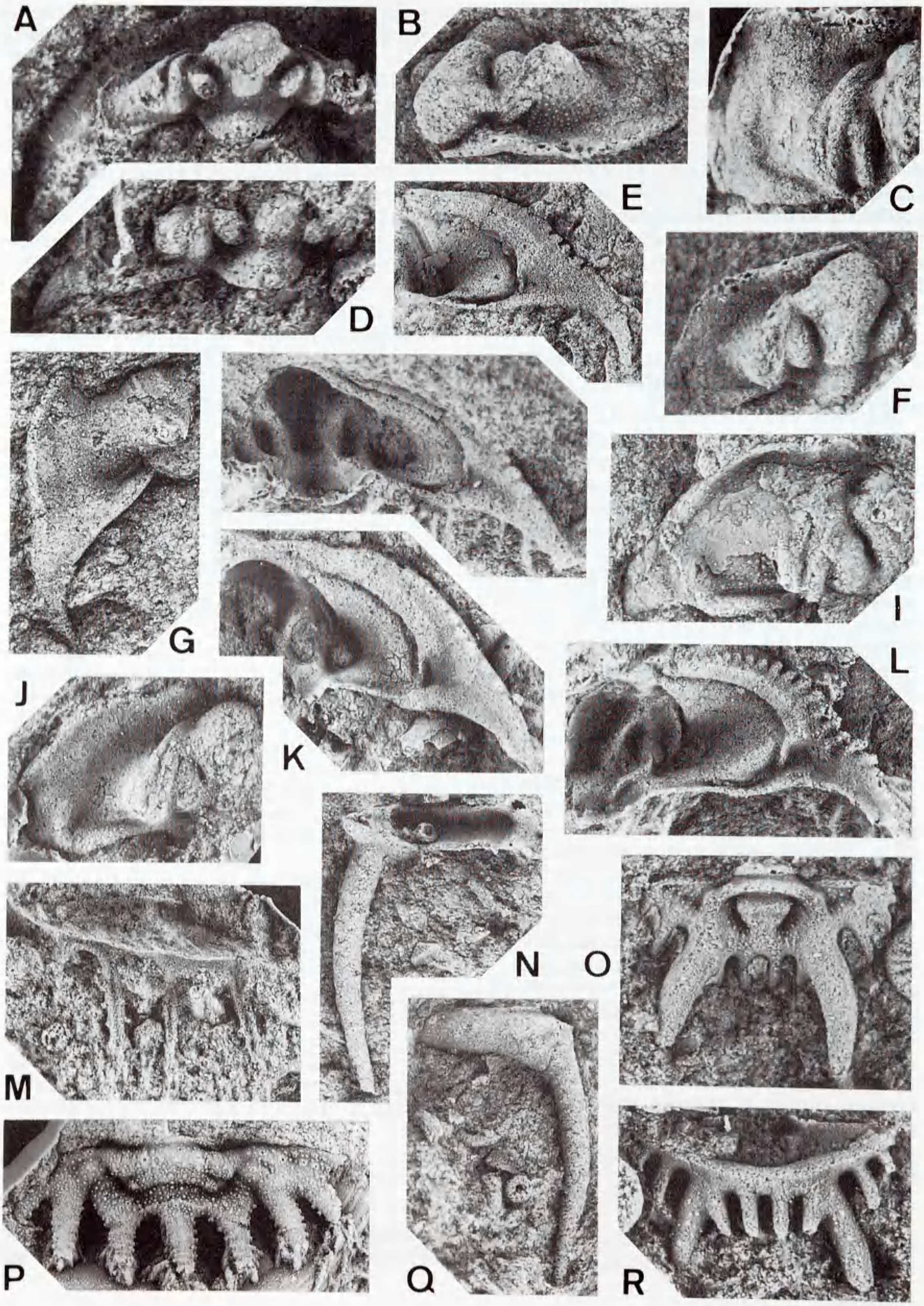
Globulaspis is even more poorly known than *Gaotania*, the type and only known species, *Globulaspis prominens* (Reed, 1931) from the lower Llandovery of Scotland, being represented only by several fragmentary cranidia (Howells, 1982, pl. 15, figs 8, 12, 13). The narrow frontal lobe, the absence of L3, the relatively weak isolation of S2 from the median glabellar lobe and the narrow, rather inflated part of the fixigena adaxial to the palpebral lobe and eye ridge are similarities with *Gaotania* and *Stelckaspis*, and the apparent absence of occipital lobes suggests a greater similarity with the former. *G. prominens* differs from species assigned to both *Gaotania* and *Stelckaspis* in having a functional facial suture. *Globulaspis* may eventually be judged to be a senior synonym of one or both of these genera, but until the discovery of more complete material of *G. prominens*, including pygidia, I consider that *Globulaspis* should be restricted to that species.

Uriarra, known only from the type species *U. kausi* Chatterton and Campbell, 1980 from the Wenlock of the Australian Capital Territory, resembles *Stelckaspis* and *Gaotania* in most of the cephalic characters shared by those genera but differs in having S2 strongly separated from the median glabellar lobe, a longer (sag.) occipital furrow, secondary spines along the dorsal edge of the genal spine and a pygidium with only one pair of median secondary border spines between the major spines.

Gaotania bimusa sp. nov.

Figure 10A–M, N, O, Q, R

Etymology. Latin *bi-*, two, together with the generic name of the banana, in reference to the


A
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major border spines on the pygidium. Noun in apposition.

Type material. Holotype: pygidium NMV P138857A, B (counterparts), Fig. 10O, R.

Paratypes: NMV P134837, P138858–P138868 (cephala); NMV P138869, P138870 (thoracic segments); NMV P134807, P138871 (pygidia).

Diagnosis. Pygidium with inflated major border spines having distinct backward flexure at mid-length, and with two pairs of secondary border spines lateral to major spines.

Description. Cephalon including genal spines crescentic in dorsal view; anterior margin apparently flexed forward slightly directly in front of eye, more or less transverse in outline medially (Fig. 10K). Glabella expanding slightly from occipital ring almost to front of L1, thereafter narrowing strongly. Occipital ring strongly arched (tr.), decreasing greatly in length abaxially behind L1; occipital furrow long (sag., exsag.) and shallow medially, deeper and more sharply impressed laterally. L1 elliptical to ovate, separated from median lobe by deep, oblique S1 and less-sharply impressed longitudinal furrow. L2 much smaller than L1, not separated from median lobe; S2 notching side of glabella. Axial furrow deep alongside posterior part of L1 and in front of S2, shallow elsewhere. Eye situated opposite L1, together with arcuate eye ridge isolating a narrow, inflated sliver of cheek adjacent to axial furrow; lateral and anterolateral to eye and eye ridge, cheek gently concave (tr.) and inclined. Lateral border flattened or weakly concave (Fig. 10B), very wide posteriorly and narrowing strongly forwards; lateral border furrow shallow. Genal spine broad proximally and tapering strongly distally. Cephalic margin with at least 16 blunt, downwardly-directed spines in a row extending from more or less directly in front of eye onto base of genal spine. Cephalic doublure with deep, exsagittally elongated depression situated adjacent to inner margin at base of genal spine (Fig. 10K).

Thoracic segments with long (exsag.), convex pleural ridge and very short (exsag.) anterior articulating flange abaxially (Fig. 10N, Q); anterior pleural spine short, blunt and downwardly directed; posterior spine long, stout and gently curved.

Pygidium excluding border spines approximately 2.7 times as wide as long. Axis with width across articulating half ring approximately 0.25 times maximum pygidial width, slightly narrower across second axial ring but much wider across first ring. First axial ring highly elevated and gently arched forwards; second ring much lower, weakly separated from terminal piece of axis, with a short (sag.), steeply inclined pseudo-articulating half ring lying beneath posterior edge of first ring and separated from remainder of second ring by a deep furrow. Axial furrow very deep lateral to second ring and terminal piece of axis, not impressed adjacent to first ring or behind axis. Pleural lobe with slightly raised anterior margin and broad, gently convex border that slopes backwards between major border spines. Pleural ridge short, extending obliquely backwards from first axial ring and merging with border in front of lateral part of major spine base. Major spines extending backwards more than twice sagittal length of pygidium; first (most anterior) secondary spine smaller than second, both curving backwards abaxially subparallel to proximal part of major spine but directed more ventrally than it; third and fourth secondary spines similar in size to second, directed posteroventrally, third spines converging slightly backwards, fourth spines subparallel (Fig. 10O). Doublure divided into inner and outer bands by an angular, transverse ridge; inner band expanding adaxially to a point in front of major spine base and thereafter increasing in slope.

Exterior of cephalon and pygidium with granulose sculpture.

Remarks. Gaotania bimusa is more closely related to *G. ovata* than to *G. pulchella*. Charac-

Figure 10. A–M, N, O, Q, R, *Gaotania bimusa* sp. nov. A, D, cephalon NMV P138858, internal mould and latex cast of external mould, dorsal view, × 8.5. B, F, H, cephalon NMV P138859, latex casts of counterpart moulds, oblique, dorsal and ventral views, × 8. C, cephalon NMV P138860, latex cast of external mould, dorsal view, × 7.5. E, cephalon NMV P138861, latex cast of natural mould, ventral view, × 5. G, cephalon NMV P138862, latex cast of external mould, dorsal view, × 5. I, cephalon NMV P138863, latex cast of external mould, dorsal view, × 7. J, cephalon NMV P138864, latex cast of external mould, dorsal view, × 7. K, cephalon NMV P138865, latex cast of natural mould, ventral view, × 6. L, cephalon NMV P138866, latex cast of natural mould, ventral view, × 5. N, Q, thoracic segment NMV P138869, latex casts of counterpart moulds, ventral and dorsal views, × 5. O, R, holotype, pygidium NMV P138857, latex casts of counterpart moulds, dorsal and ventral views, × 8. M, P, *Ceratocephala* sp. M, pygidium NMV P138872, latex cast of natural mould, ventral view, × 5. P, pygidium NMV P138873, latex cast of external mould, dorsal view, × 3.

ters in which the first two species differ from the last are the inflated major border spines on the pygidium, the secondary border spines that are much smaller than the major spines, and the distinct pygidial border abaxial to the major spines. The pygidium of *G. bimusa* differs from that of *G. ovata* in having only one secondary border spine lateral to the major spine rather than two, the major spine is not as distinctly flexed backwards at midlength, the posterior pair of secondary spines diverge backwards instead of being subparallel, and the pygidial granulation is apparently coarser. *G. bimusa* seems to have shorter, more strongly tapering genal spines than either of the Chinese species, but cephala of all three species are too poorly preserved for further useful comparison.

Ceratocephalinae Richter and Richter, 1925

Ceratocephala Warder, 1838

Type species. Ceratocephala goniata Warder, 1838, from the Silurian of Ohio; by monotypy.

Ceratocephala sp.

Figure 10M, P

Remarks. The more complete of two pygidia belonging to this genus lacks the left lateral extremity and the distal parts of the marginal spines (Fig. 10P). The specimen seems to have been deformed by upward flexing of the anterior portion along a transverse line passing between the second and third marginal spines. As a result, the axis appears to slope very steeply backwards with respect to the remainder of the pygidium.

Ceratocephala species with three, seven or nine marginal spines on the pygidium are known from the Silurian. In having seven spines and two axial rings, the present specimens most closely resemble *C. plummeri* Chatterton and Perry, 1983 from the lower Wenlock of Canada, but the first and second marginal spines are more laterally directed than in that species, the barbs on the marginal spines are finer (to judge from their broken bases), the exoskeletal granulation is less uniform in size, and there is a pair of small tubercles on the first axial ring. The second ring furrow appears to be much deeper and the terminal piece of the axis more depressed in the present material, but these differences can be attributed to deformation. Other Silurian species of *Ceratocephala* with seven pygidial marginal spines are *C. rhabdophora* (Hawle and Corda, 1847) (redescribed by Šnajdr, 1986) from the upper Ludlow to lowermost Přídolí of Bohemia, *C. vogdesi* Etheridge and Mitchell, 1897 from the upper Ludlow of the Yass Basin, New South Wales, and *Ceratocephala* n. sp. A of Chatterton and Campbell, 1980 from the Wenlock of Canberra. Pygidia of these species differ from the present specimen in having only one axial ring.

"*Ceratocephala*" *impedita* Etheridge and Mitchell, 1897, based on cranidia from the Ludlow of the Yass Basin and revised by Chatterton (1971), actually belongs to *Miraspis*, as shown by the S1 that is directed obliquely backwards from the longitudinal furrow instead of obliquely forwards, and the median glabellar lobe that is widest at the inner end of S1 instead of narrowing forwards from the occipital furrow.

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