

Late Ordovician and early Silurian trilobites from Tasmania

DAVID J. HOLLOWAY, MAXWELL R. BANKS† & DORIS M. BANKS



Thirteen species of trilobites are described from two different faunas in late Katian and Rhuddanian strata respectively of the Arndell Sandstone in the Florentine Valley of southern Tasmania. The late Katian fauna includes the trinucleid *Auritolithus corbetti* gen. et sp. nov., the calymenids *Salterocoryphe? bailliei* sp. nov. and *Vietnamia hyron* sp. nov., and limited material of the lichid *Amphilichas?* and two indeterminate asaphids. *Auritolithus*, characterized by the markedly subpentagonal outline of the cephalon, cannot be assigned to any of the existing trinucleid subfamilies but seems closely related to forms occurring in the Upper Ordovician of the Precordillera Basin of Argentina. *Salterocoryphe? bailliei*, the first record of a member of the Colpocoryphinae from Australia, is considerably younger stratigraphically than other occurrences of that genus in the middle to upper Darriwilian of France and the Iberian Peninsula. The Rhuddanian fauna from the Arndell Sandstone includes the illaenid *Pepodes agrestis* gen. et sp. nov., the scutelluid *Japonoscutellum senectum* sp. nov., the brachymetopid *Niuchangella agastor* sp. nov., the encrinurids *Arndellaspis oryxis* gen. et sp. nov. and *Cromus?*, the calymenid *Gravicalymene clarkei* sp. nov. and the homalonotid *Brongniartella calveri* sp. nov. *Niuchangella* is accepted as a senior synonym of *Radnorina*. *Arndellaspis* is not closely related to other members of the Encrinurinae from Australia but shares unique derived characters of the pygidium with *Encrinurus* (*s.s.*) and *Wallacia*, occurring in Laurentia, Avalonia and Baltica, and *Arndellaspis* may share common ancestry with *Encrinurus*. The commonly broadly interpreted *Gravicalymene* is revised and restricted to a smaller number of closely related species from the Darriwilian to middle Telychian. The faunal affinities of the trilobites suggest links with terranes that lay along the north-western margin of Gondwana and with South America in the Late Ordovician, and with South China and possibly Laurentia in the early Silurian. • Key words: Trilobita, late Katian, Rhuddanian, Tasmania, new taxa, palaeobiogeography.

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The Arndell Sandstone crops out in the Florentine Valley and Tiger Range of southern Tasmania, about 80km west-north-west of Hobart (Fig. 1). The formation contains at several levels a diverse fauna of shelly fossils including corals, bryozoans, brachiopods, bivalves, gastropods and trilobites, of which only the brachiopods have been described previously (Sheehan & Baillie 1981, Laurie 1991). Graptolites have been recorded from the upper part of the formation. The trilobite fauna, described herein, differs markedly in composition between lower and upper parts of the formation, with no genera in common. The lower fauna includes six species belonging to the trinucleid *Auritolithus* gen. nov., the calymenids *Salterocoryphe?* and *Vietnamia*, the lichid *Amphilichas?* and two indeterminate genera of the Asaphidae. The upper fauna includes seven species belonging to the illaenid *Pepodes* gen. nov., the scutelluid *Japonoscutellum*, the brachymetopid *Niuchangella*,

the encrinurids *Arndellaspis* gen. nov. and *Cromus?*, the calymenid *Gravicalymene* and the homalonotid *Brongniartella*.

The Arndell Sandstone was named by Baillie (1979) to incorporate the Westfield Beds of Corbett & Banks (1974) though that unit as originally conceived did not include the uppermost strata now assigned to the formation. The older term was retained by some authors, as Westfield Sandstone (*e.g.* Banks 1988, Laurie 1991), but the name Arndell Sandstone has prevailed (Banks & Burrett 1989, Calver *et al.* 2014). The lithology and stratigraphic relations of the formation were summarized by Calver *et al.* (2014, p. 256). It consists of about 250 m of buff-coloured micaceous siltstone and fine-grained sandstone, with coarser sandstones towards the top. Bioturbation and vertical feeding burrows are common, and the presence in places of herringbone crossbedding is said to be indicative of

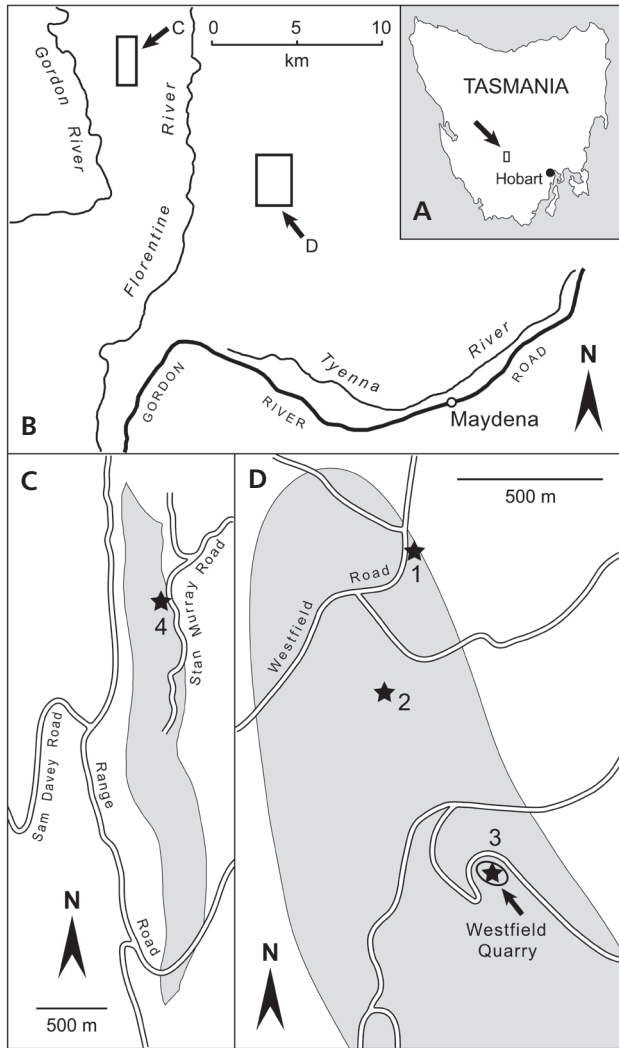


Figure 1. Locality maps. • A – Tasmania; approximate location of the Florentine Valley indicated by arrow. • B – Florentine Valley and surrounding region, showing approximate areas of maps C and D. • C – location of Locality 4 in Tiger Range on western flank of Florentine Valley. • D – Westfield Quarry area, showing location of localities 1–3. C and D modified from Banks (1988, fig. 1); surface distribution of the Arndell Sandstone indicated by shading.

shallow-water deposition in tidal channels (Baillie & Clarke 1976, p. 1; unit TR1 therein). The Arndell Sandstone conformably overlies the Benjamin Limestone, the uppermost unit in an Early–Late Ordovician carbonate sequence. Trilobites from the Benjamin Limestone, described by Edgecombe *et al.* (1999, 2004), include species of *Amphilichas*, *Basiliella*, *Ceraurinella*, *Eokosovopeltis*, *Erratencrinurus*, *Pliomerina* and *Vietnamia* (= *Sarrabesia* of those authors). Conformably overlying the Arndell Sandstone is the unfossiliferous Gell Quartzite, which is of Llandovery age and considered to have been deposited in very shallow water, probably on a sandy tidal flat (Calver *et al.* 2014, p. 263).

Age of the Arndell Sandstone

Opinions on the age of the Arndell Sandstone have varied, in particular on whether it spans the Ordovician–Silurian boundary, as believed by Baillie (1979, p. 5), Banks (1988), Banks (in Banks & Burrett 1989, p. 201), Laurie (1991) and Calver *et al.* (2014, fig. 5.2), based on identifications of graptolites (see below) and brachiopods. Laurie (1991) assigned brachiopods in the upper part of the formation to his *Isorthis (Ovalella) arndellensis* (lower) and *Onniella? perplexa* (upper) assemblages, regarded by him as Silurian, but he stated (1991, p. 25) that the basal part of the formation contains rare brachiopods that he did not describe but considered to belong to his *Dinorthis holdenoides* assemblage, of Ordovician age and also represented at the top of the underlying Benjamin Limestone. From both the *Onniella? perplexa* and *Isorthis (Ovalella) arndellensis* assemblages Laurie recorded *Hirnantia*, and from an uncertain stratigraphic level in relation to them he recorded the globally widely distributed Hirnantian species *Kinnella kielanae*. Subsequently, brachiopods from the upper part of the formation, including *Eospirifer tasmaniensis* Sheehan & Baillie, 1981 and *Eospirifer? sp.* of those authors, have been variously assigned to the Hirnantian (Rong *et al.* 1994, p. 768; Cocks & Cooper 2004, p. 74; Rong *et al.* 2013, p. 127; Wang *et al.* 2019, p. 20) or to the Rhuddanian (Zhan *et al.* 2011, p. 642; 2012, p. 1433; Cocks 2019, p. 135). Cocks & Rong (2007, p. 298) considered that specimens illustrated by Laurie (1991) as *Hirnantia* do not belong to that genus, and Rong *et al.* (2020, p. 7) noted that brachiopods in the upper Arndell Sandstone do not represent a *Hirnantia* Fauna. Laurie (1991, p. 48) stated that his identification of *Kinnella kielanae* in the upper part of the formation was based on only a few, mostly fragmentary specimens, so it may also be questionable. A different view from that of other authors on the age of the Arndell Sandstone was proposed by Zhen & Percival (2017, fig. 5 and p. 16) who, citing Laurie (1991), assigned the entire formation to the Silurian, with a large stratigraphic gap separating it from the underlying Benjamin Limestone. However, this view is incompatible with the occurrence in the lower part of the Arndell Sandstone of trilobites belonging to the exclusively Ordovician Asaphidae, Trinucleidae, Colpocoryphinae and Reedocalymeninae.

Graptolites from the upper part of the Arndell Sandstone, from the same strata yielding the *Onniella? perplexa* assemblage of Laurie (1991) and our upper trilobite fauna, were identified by Rickards (*in* Baillie *et al.* 1978), as *Metabolograptus persculptus*, *M. cf. persculptus*, *Normalograptus normalis*, and rare *Atavograptus sp.* and *Akidograptus? sp.*, said to indicate a horizon in either the *M. persculptus* Biozone or low in the *Parakidograptus acuminatus* Biozone, more likely the latter. At that time

these were the lowermost zones of the Silurian; however, with the redefinition of the base of the Silurian as coinciding with the base of the *acuminatus* Biozone (Cocks 1985), subsequently revised to the base of the *Akidograptus ascensus* Biozone (Rong et al. 2008), the question arises as to whether the graptolites indicate a late Hirnantian or Rhuddanian age. Professor Michael Melchin has kindly reviewed the identifications for us, based on the illustrations of the specimens provided by Baillie et al. (1978), and he advised (personal communication 2022) that the presence of *Atavograptus* indicates the Silurian, as would the questionably identified *Akidograptus* which, however, was not illustrated. He noted that the specimen illustrated as *M. persculptus* is somewhat narrower than previously reported in this species and that the identification is therefore questionable. On the other hand, he stated that the illustrated specimen of *Atavograptus* is wider than in any species of that genus known from lower than the *Cystograptus vesiculosus* Biozone of the Rhuddanian. On this evidence, he considered the graptolites to be clearly Silurian, and suggested a mid-Rhuddanian age as most likely. The trilobites from the upper fauna in the Arndell Sandstone provide some support for an early Silurian age for this part of the formation. *Japonoscutellum* is widely distributed in the Silurian, both geographically and stratigraphically (see Holloway & Lane 2012, 2016), but the oldest known occurrences elsewhere are in the upper Aeronian or possibly upper Rhuddanian of South China (see remarks on *J. senectum* sp. nov.). *Niuchangella* (= *Radnorina*) is also widely distributed geographically and stratigraphically, ranging from the upper Sandbian or lower Katian to the Ludfordian (Pereira et al. 2015), but *N. agastor* sp. nov. from the Arndell Sandstone is very similar to the type species *N. meitanensis* from the lower–middle Rhuddanian of South China.

No evidence for the upper age limit of the Arndell Sandstone is provided by the conformably overlying Gell Quartzite from which no fossils have been recorded though a Silurian age is accepted (e.g. Calver et al. 2014). Conformably overlying the Gell Quartzite is the Richea Siltstone, containing graptolites of the mid-Telychian *Monoclimacis griestoniensis* or *M. crenulata* biozones (Rickards in Baillie 1979) and of possible mid- or late Wenlock age at a higher level (Rickards 1989), as well as a diverse early Silurian trilobite fauna (Holloway & Sandford 1993).

Conodonts from the uppermost part of the Benjamin Limestone, conformably underlying the Arndell Sandstone, were said by Burrett (reported in Corbett & Banks 1974, p. 225) to suggest an Edenian–early Maysvillian age in terms of the North American stages. Corals from the uppermost Benjamin Limestone were assigned by Banks & Burrett (1980, p. 372) to faunal assemblage OT19 in their Tasmanian biostratigraphic scheme, equated by them with coral/stromatoporoid fauna C/S IV of Webby (1972), but by Webby (1989, p. 20) with his (Webby 1969) C/S

Fauna III. The latter fauna, formally named the *Favistina–Halysites–Plasmoporella* Assemblage Zone by Pickett & Percival (2001, p. 19), is of late Eastonian (Ea3–Ea4) age in terms of the Australasian regional zonation. The uppermost Benjamin Limestone is thus mid-Katian in age, suggesting a late Katian (early Bolindian) age for the lower part of the Arndell Sandstone (e.g. Banks & Burrett 1980, tab. 3; Webby et al. 1981; Calver et al. 2014, fig. 5.2). Trilobites in the lower part of the formation do not provide more accurate information on its age. *Vietnamia* is known (as the junior synonym *Sarrabesia*) from the late Katian of Sardinia (Hammann & Leone 1997) but Turvey (2002, p. 61) stated that the stratigraphic occurrence of the genus at Asian localities, representing most known species, is poorly understood. In Tasmania the genus, and possibly the same species (Edgecombe et al. 1999, fig. 3a, b, c), occurs in the Benjamin Limestone below the Arndell Sandstone, as low as assemblage OT14 (early Eastonian, early Katian). Trinucleids, represented in the lower part of the Arndell Sandstone by *Auritolithus* gen. nov., range as high as the Hirnantian in North America, England, Wales and the Baltic region but are very uncommon above the Katian (Lespérance 1988, p. 369; Owen 2007, pp. 46, 47). The possible occurrence of *Salterocoryphe* in the Arndell Sandstone is very late for that genus which is otherwise known from the Darriwilian to possibly earliest Sandbian of France and the Iberian Peninsula.

In summary, the available evidence indicates that the Arndell Sandstone ranges in age from late Katian to Rhuddanian, probably mid-Rhuddanian. The only other formation in Australia that is known to span the Ordovician–Silurian boundary, based on fossil evidence, is the Deep Creek Siltstone in Victoria, which contains graptolites of the *persculptus* Biozone in its lower beds and of the *acuminatus*, *triangulatus* and *magnus* biozones in its higher parts (Vandenberg et al. 1984, Rickards & Sandford 1998).

Faunal affinities

The faunal affinities of the trilobites from the Arndell Sandstone suggest various palaeobiogeographical links. Of the genera present in the lower assemblage (late Katian), the trinucleid *Auritolithus* seems to be most closely related to forms from the Upper Ordovician of the Precordillera Basin of Argentina, part of the Cuyania Terrane which is considered to have been originally part of Laurentia but rifted from it and subsequently accreted to the south-eastern margin of Gondwana (e.g. Astini 2003, Thomas & Astini 2003). There has been debate about the timing of these events, with estimates on the docking with South America ranging from Middle Ordovician to as late as between the end of the Silurian and the early Carboniferous (Benedetto 2003, p. 102), with consequent implications for the route

of any faunal exchange with Tasmania. However, Domeier (2015) considered that Cuyania had rifted from Laurentia by the mid-Cambrian and accreted to Gondwana in the Middle Ordovician, thus prior to the deposition of the Arndell Sandstone (also see palaeogeographic maps of Torsvik & Cocks 2017, figs 6.1a, b, 6.2a). *Salterocoryphe*, if the Arndell Sandstone species belongs to that genus, is otherwise known only from Iberia and Armorica (Armorican Terrane Assemblage) where, however, the occurrences (middle and upper Darriwilian) are considerably older than in the Arndell Sandstone. *Vietnamia* is known from regions that were situated along the north-western margin of Gondwana or were closely associated with it, from Sardinia (situated east of the Armorican Terrane Assemblage in the map of Torsvik & Cocks 2017, fig. 6.2b) in the west to Indochina (Annamia) and South China in the east. *Amphilichas* is very widely distributed around the world in the Upper Ordovician but the Arndell species, tentatively assigned to the genus, appears to be most closely related to a stratigraphically older form from the upper Sandbian to lower Katian of western Tasmania.

Of the genera present in the upper assemblage (Rhuddanian) of the Arndell Sandstone, the illaenid *Pepodes* and encrinurid *Arndellaspis* are unknown elsewhere, but if *Arndellaspis* shares common ancestry with *Encrinurus* (*s.s.*), as we speculate, it provides a link to Laurentia where the stratigraphically earliest (Aeronian) species of the latter occur. *Japonoscutellum*, as noted above, was very widely distributed in the Silurian, from Laurentia in the west to eastern Gondwana (Holloway & Lane 2012, p. 417), but in the strong effacement of the glabellar furrows *J. senectum* is similar to *J. yichangense* (Zhang, 1974) and the poorly known *J. fenxiangense* (Yi, 1978) and *J. niuchangense* (Zhang, 1974) from the upper Rhuddanian and upper Aeronian of South China, these also being closest in age to the Arndell Sandstone species. The palaeogeographically widely distributed *Niuchangella* is known from southern and northern Laurentia, Avalonia, Perunica, South China and eastern Gondwana in the Silurian, but as noted above *N. agastor* from the Arndell Sandstone is very similar morphologically to the type species *N. meitanensis* Zhang, 1974 from the lower to middle Rhuddanian of South China. *Brongniartella* and *Gravicalymene* (the latter as restricted herein) are both widely distributed in the Upper Ordovician but other Silurian records are very limited – for *Brongniartella* from Avalonia and northern Gondwana, and for *Gravicalymene* only from Tasmania, higher in the same sequence as the Arndell Sandstone.

Localities

Localities at which trilobites were collected from the Arndell Sandstone are as follows (Fig. 1; they are also shown on

the map of Banks 1988, fig. 1). Localities 1–3 are in the Westfield Syncline, and Locality 4 is in the Tiger Syncline 10–11 km to the north-north-west of the others.

- (= Locality 15 of Corbett & Banks 1974, fig. 4; C & B 15 of Banks 1988, fig. 1b.) Cutting on Westfield Road about 3 km east of junction with Florentine Road; *ca* –42.6355°, 146.4916°; close to the base of the Arndell Sandstone (Corbett & Banks 1974, p. 226; Banks 1988, p. 191); late Katian. Trilobites present are Asaphidae indet., *Vietnamia hyron* and *Amphilichas?* sp.
- (= Locality 16 of Corbett & Banks 1974, fig. 4; C & B 16 of Banks 1988, fig. 1b.) Approximately 500 m south-south-west of Locality 1; *ca* –42.6400°, 146.4907°; stratigraphically higher than Locality 1 (Corbett & Banks 1974, p. 226) but the occurrence of the same trilobites as at Locality 4 suggests that it lies towards the base of the formation; late Katian. Trilobites present are Isotelinae indet., *Auritolithus corbetti* and *Salterocoryphe? bailliei*.
- (= Locality 18 of Corbett & Banks 1974, fig. 4; F2 of Baillie & Clarke 1976, p. 2; locality 11 of Laurie 1991, fig. 10.) Westfield Quarry and immediate vicinity; *ca* –42.6455°, 146.4950°; said by Baillie (1979, p. 7) to be situated some 150 m above the base of the Arndell Sandstone; *i.e.* upper half of the formation; Rhuddanian. Trilobites present are *Pepodes agrestis*, *Japonoscutellum senectum*, *Niuchangella agastor*, *Arndellaspis oryxis*, *Cromus?* sp., *Gravicalymene clarkei* and *Brongniartella calveri*.
- (= Locality F3 of Baillie & Clarke 1976, p. 2; Banks 1988, fig. 1a.) Cutting on Stan Murray Road; *ca* –42.5670°, 146.4107°; close to the base of the Arndell Sandstone (Baillie & Clarke 1976, fig. 1, ‘TR1’ = Arndell Sandstone; Baillie 1979, fig. 2); late Katian. Trilobites present are *Auritolithus corbetti* and *Salterocoryphe? bailliei*.

Material and methods

The specimens are preserved as internal and external moulds in rather soft, orange-yellow siltstone or fine sandstone. They are housed in the School of Earth Sciences, University of Tasmania, Hobart (UTGD), and in the invertebrate palaeontological collections of Museums Victoria, Melbourne (NMV).

Morphological terminology follows Whittington & Kelly (1997) with the following exceptions and additions. The independently convex portion of the glabella between the occipital furrow and S1 in trinucleids is referred to as the preoccipital ring rather than the occiput, as we consider the latter term to be inappropriate because it does not refer to part of the occipital ring. The region of the gena inside the fringe was called the ‘genal lobe’ by Hughes *et al.* (1975, fig. 1) but this term was regarded as a synonym of ‘gena’ by Whittington & Kelly (1997). As the trinucleid fringe

is apparently homologous with the anterior and lateral cephalic borders in other trilobites, we refer to the region of the gena inside the fringe as the genal field. ‘Omphalus’ and ‘anterolateral internal pit’, defined by Holloway & Lane (1998, pp. 863–864), refer respectively to a socketed boss and a pit on the interior of the cranidium of bumastines, the former lying at the anterior end of the axial furrow or in line with its projected course, and the latter situated a little farther forward. Terminology applied to scutelluids follows Holloway & Lane (2012, 2016) in relation to the homology of the cephalic borders and border furrows, and the use of ‘bolus’ for the swelling enclosed by S1, and ‘rib’ or ‘pleural rib’ for the portion of the pygidial pleural region between successive interpleural furrows rather than pleural furrows, the latter furrows being absent in scutelluids. The term ‘plan view’ in taxonomic descriptions and figure captions indicates that the specimen is oriented so that the maximum sagittal length is shown; this may differ from ‘dorsal view’, which in the case of cephalia or cranidia indicates that the specimen is oriented with the posterior edge of the occipital ring vertical.

Systematic palaeontology

Family Asaphidae Burmeister, 1843
Subfamily Isotelinae Angelin, 1854

Isotelinae indet.

Figure 2A–C, F

Material. – Three cranidia, UTGD 81408, 81411, 81416, from Locality 2; late Katian.

Remarks. – These small, strongly effaced and uniformly convex (sag.) cranidia range in length from 7 mm to about 10 mm. Axial, preglabellar and posterior border furrows are not defined, but the position of the articulating processes on the posterior margin indicate that the glabella is here very wide, comprising about 66% cranial width across ω – ω and a little wider than width across ε – ε . A median glabellar node is not distinguishable on either internal or external moulds. The cranidium is approximately equal in width across δ – δ and β – β , and about 80% as wide at β – β as at ε – ε . The palpebral lobe is large, its length about 33% sagittal cranial length and with its midlength opposite 60% cranial length from anterior. The anterior branch of the facial suture diverges very strongly from γ to β , and the suture meets the midline in a marked flexure. One of the cranidia, preserved as an external mould, shows a sculpture of fine, dense pits (Fig. 2A).

In their extreme effacement, posteriorly very wide glabella, palpebral lobes situated with their midlength opposite or just behind the cranial midlength (sag.), and

very strong divergence of the facial suture from γ to β , these cranidia resemble those of *Anataphrus* Whittington, 1954, *Homotelus* Raymond, 1920, *Nahannia* Chatterton & Ludvigsen, 1976, *Protopresbynileus* Hintze, 1954 and *Vogdesia* Raymond, 1910. Those genera, mostly from the Lower–Upper Ordovician of North America but with a few representatives from Greenland, Russia and Spitsbergen, have been regarded as comprising a closely related group (Chatterton & Ludvigsen 1976, p. 25; Amati 2014, p. 25). It has been suggested that the glabella in these genera extends to the anterior margin of the cranidium (e.g. Amati 2014, p. 25). However, in some species of all of them a weak preglabellar furrow is present very close to the margin (*Anataphrus*, see Amati 2014, pl. 23, fig. 1, pl. 30, figs 1, 2 (meraspid cranidia); *Homotelus*, see Whittington 1950, pl. 73, fig. 9; *Nahannia*, see Chatterton & Ludvigsen 1976, pl. 3, figs 2, 3; *Protopresbynileus*, see Adrain et al. 2009, fig. 10aa); *Vogdesia*, see Shaw & Bolton 2011, fig. 7.12). It is likely that a very short but undefined preglabellar region is also present in the cranidia from the Arndell Sandstone.

Similar to the present cranidia in degree of effacement are those of some species of *Liomegalaspides* Lu, 1975, from the Floian–Darriwilian of South China [e.g. *L. usuii* (Yabe, 1920) in Yabe & Hatasaka (1920), see Lu 1975, pl. 13, figs 1–6; *L. hupeiensis* (Sun, 1931), see Turvey 2007, pl. 2, figs 1–3, 6] and from the Darriwilian of Iran [*L. winsnesi* (Bruton, 2004) in Bruton et al. (2004), their pl. 5, figs 2, 5, 9, 10, 13; for assignment of the species to *Liomegalaspides* see Ghobadi Pour et al. 2006]. Turvey (2007) expanded the concept of *Liomegalaspides* to include Chinese species previously assigned to *Megalaspides* Brögger, 1886, and assigned the former genus and several others to the resurrected Nobiliasaphinae Balashova, 1971 based on the morphology of the hypostome. Compared to the cranidia from the Arndell Sandstone, those of *Liomegalaspides* are more elongated, the anterior branch of the facial suture does not diverge as strongly from γ to β , and the glabella is less expanded posteriorly, there comprising about 50% cranial width or less rather than about 66%. We do not consider the present cranidia to be closely related to *Liomegalaspides*.

We have considered whether the present cranidia might belong to a member of the Nileidae, but believe that this is less likely as the glabella is more strongly expanded posteriorly than is generally the case in that family, and the anterior suture is strongly flexed medially rather than broadly rounded.

Subfamily Uncertain

Asaphidae indet.

Figure 2D, E

Material. – Two pygidia, UTGD 81369, 81375, from Locality 1; late Katian.

Remarks. – These poorly preserved pygidia are probably not closely related to the cranidia of *Isotelinae* indet., which come from a different locality and stratigraphic horizon. If the affinities of the cranidia lie with *Anataphrus* and its allies, these pygidia differ from those of such forms in their longer proportions and parabolic rather than broadly rounded posterior outline, the narrow and prominent axis, the well-defined concave border, and the extremely wide doublure that is markedly indented by the end of the axis. It is not possible to assign these pygidia to an asaphid subfamily with any confidence.

Family Trinucleidae Hawle & Corda, 1847

Genus *Auritolithus* gen. nov.

LSID. – urn:lsid:zoobank.org:act:89F0DA70-57D9-4FB1-A2FE-EACC16939DCF

Type species. – *Auritolithus corbetti* gen. et sp. nov. from the lower part of the Arndell Sandstone (late Katian), south-western Tasmania.

Etymology. – Latin *auritus*, eared, together with the common suffix *-lithus* for trinucleid genera, referring to the strong lateral expansion of the fringe; gender masculine.

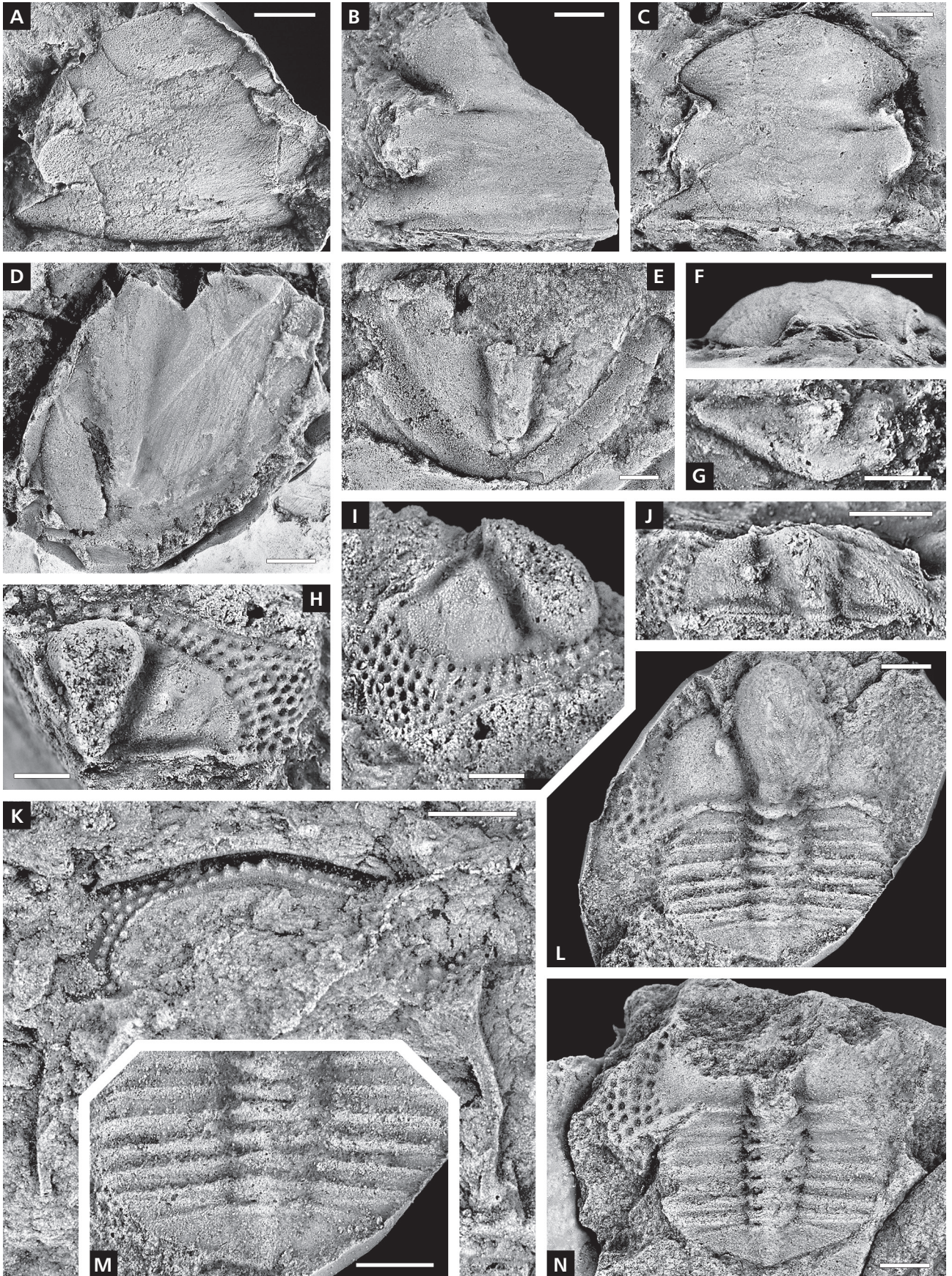
Diagnosis. – Cephalon excluding genal spines sub-pentagonal in dorsal outline; fringe short (sag., exsag.) frontally, markedly expanded in width laterally where it is strongly rounded to subangular in outline; two pit arcs present in front of glabella, progressively increasing to five regularly arranged arcs laterally where they are aligned diagonally to curvature of outer margin of fringe at its widest part, less complete arcs lying external to more complete ones; pits in two arcs frontally and inner three arcs anterolaterally and laterally arranged in about 15–17 radial rows (half fringe, excluding posterior row); pits in outer two regular arcs on lateral part of fringe out of phase with those in inner three arcs and with each other; pits external to these arcs on lateral extremity of fringe, including marginal pits, mostly small and mostly lacking regular arrangement; no F pits apart from posterior fossula. Glabella with convex (sag., exsag.) preoccipital ring;

occipital ring without medial spine. No preglabellar field. Lateral eye tubercles situated relatively close to glabella. Reticulate sculpture on glabella and pitted sculpture on genal field. Pygidium very short, only first segment clearly defined on axis and pleural region.

Remarks. – The conventional notation for trinucleid fringe pits (Ingham 1970, Hughes *et al.* 1975) cannot readily be applied to *Auritolithus*, and we have avoided doing so. Correct identification of the girder, a concentric ridge on the lower lamella continuous posteriorly with a median longitudinal ridge on the genal spine, is required to distinguish I arcs of pits situated internally to the girder, and E arcs situated externally to the girder. New I arcs were added to the fringe during ontogeny on the outside of the innermost arc, I_n , and new E arcs were said by Bancroft (1929, p. 69) to be added externally to the outermost arc. That this is true for the addition of E arcs is shown by silicified small cephalons of *Tretaspis sagenosa* with one, two and three E arcs, illustrated by Whittington (1959, pl. 28, figs 2, 8 and pl. 26, fig. 14 respectively), the outmost arc in the cephalon with three E arcs being less complete posteriorly, indicating that it was added last. The girder may be lost secondarily, as shown by species of *Bancroftolithus* Baldis & Pöthe de Baldis, 1995 from the Sandbian of Argentina, illustrated by Waisfeld *et al.* (2011, figs 2, 5, 8, 9). In the type species *B. hughesi* the girder is complete, but in *B. pozoensis* and *B. alki* it cannot be unambiguously identified. Loss of the girder may make the discrimination of I and E pit arcs difficult or impossible.

The lower lamella of *Auritolithus* has a prominent concentric ridge anteriorly and anterolaterally, situated submarginally and separated from the marginal suture by a furrow (Fig. 3L). Farther laterally, this furrow seems to disappear, and the ridge abruptly decreases in prominence more or less in line (exsag.) with the base of the genal spine, thereafter continuing around the widest part of the fringe to reach the base of the spine. This submarginal/marginal ridge may be the girder, perhaps only anteriorly and anterolaterally but dying out laterally, or it may in its entirety be the external rim of the lower lamella; its relationship posteriorly to the median longitudinal ridge on the genal spine is not clear in the only available lower lamella with the external surface preserved. We consider

Figure 2. Asaphid and trinucleid trilobites from the lower Arndell Sandstone (late Katian), Florentine Valley, southern Tasmania; all except D, E, L–N from Locality 2. • A–C, F – *Isotelinae* indet. A – cranidium UTGD 81416, latex cast of external mould, dorsal view. B – cranidium UTGD 81411, internal mould, dorsal view. C, F – cranidium UTGD 81408, internal mould, dorsal and lateral views. • D, E – *Asaphidae* indet., Locality 1, Westfield Road. D – pygidium UTGD 81375, internal mould with external mould of doublure exposed, dorsal view. E – pygidium UTGD 81369, internal mould, dorsal view. • G–N – *Auritolithus corbetti* gen. et sp. nov. G – small pygidium UTGD 81418B, internal mould, dorsal view. H, I – cranidium UTGD 81400, internal mould, dorsal and oblique views. J – very small (meraspid?) cranidium UTGD 81405A, internal mould, dorsal view. K – fringe lower lamella UTGD 81399, latex cast of external mould of dorsal surface, dorsal view. L–N – dorsal exoskeleton lacking lower lamella UTGD 126263/126266 (counterparts), from Locality 4, Stan Murray Road; L, M – UTGD 126266, latex cast of external mould, dorsal view, and detail of thorax and pygidium dorsal view; N – UTGD 126263, internal mould, dorsal view. Scale bars represent 2 mm in A–C, E, F, K–N; 5 mm in D; 1 mm in G–J.



it most likely that this ridge is the external rim, and the concentric furrow surrounding it anteriorly and anterolaterally is the furrow that separates the external rim from the marginal suture on the dorsally deflected outer edge of the lower lamella; *i.e.* on the marginal band (see Whittington 1959, pl. 24, figs 3, 4; Hunda *et al.* 2003, pl. 11, fig. 14).

It is not clear whether in *Auritolithus* the outermost pits on the frontal part of the fringe belong to the same arc as the outermost pits on the widest part of the fringe, or whether they are part of a more internal arc laterally; if the latter is true, there is an abrupt change in alignment of the arc laterally. The small size and irregular arrangement of the pits outside the regular concentric arcs on the widest part of the fringe suggest that these pits were not added on the outside of I_n early in the meraspid period, as would be the case if they are I pits, but were added outside the concentric arcs later in the meraspid period, as the cephalic outline changed from subelliptical to subpentagonal, assuming a similar ontogenetic change in outline as in other trinucleids with subrectangular to subpentagonal cephalae (see following discussion on *Marrolithus bureau*). These small and irregularly arranged outer pits on the lateral part of the fringe may therefore be E pits, and if so this would confirm that a girder is not present in *Auritolithus*, at least on this part of the fringe.

The strong expansion of the fringe laterally, resulting in the subpentagonal cephalic outline, is the most striking feature of *Auritolithus*. Other trinucleids in which the fringe is conspicuously expanded laterally compared to frontally and posterolaterally include *Ningkianolithus* within the Hanchungolithinae, *Marrolithus* Bancroft, 1929 and to a lesser extent *Marrolithoides* Williams, 1948 within the Marrolithinae, *Telaemarrolithus* Williams, 1948 within the Trinucleinae, and the bizarre *Fantasticolithus* Fortey & Gutiérrez-Marco, 2022. In those genera, the pits occupy the increased width of the lateral part of the fringe by one or more modifications including an increase in the size of the pits in the outer arcs (excluding E arcs in some cases), an increase in pit spacing, and insertion of additional, incomplete pit arcs. Such modifications also occur, however, in some other trinucleids in which the fringe is not significantly expanded laterally. In *Telaemarrolithus* and *Fantasticolithus*, pits do not occupy the entire width of the fringe laterally, where the outermost part is devoid of pits (Hughes *et al.* 1975, pl. 3, figs 36, 37; Fortey & Gutiérrez-Marco 2022, figs 2, 3). In *Ningkianolithus*, the increased numbers of pits on the lateral part of the fringe inside the outer arcs of enlarged pits generally have an irregular arrangement (*e.g.* Lu & Zhang 1974, pl. 51, figs 7, 8; Lu 1975, pl. 37, figs 5–9). In *Marrolithus*, *Marrolithoides* and *Telaemarrolithus*, incomplete pit arcs occur on the inner part of the fringe laterally, and successively shorter arcs are situated successively closer to the I_n arc (*e.g.* Hughes *et al.* 1975, pl. 3, figs 36, 37, pl. 7, fig. 89, pl. 8, figs 97, 99). Delabroye & Crônier (2008) showed that in

Marrolithus bureau short pit arcs ('mini-arcs' of those authors) were inserted successively on the outside of the I_n arc during ontogeny, as the cephalic outline changed from subelliptical to subrectangular or subtrapezoidal with the development of the lateral expansion of the fringe. In contrast to all these genera, in *Auritolithus* the outer pits laterally are smaller than those elsewhere, and successively shorter pit arcs are situated successively farther from the I_n arc instead of successively closer to it.

In the fringe that is relatively narrow frontally but wide laterally, where the outer pits are commonly small and rather irregularly arranged, *Auritolithus* resembles *Guandacolithus* Harrington & Leanza, 1957 (see also Hughes *et al.* 1975, p. 569, pl. 6, figs 70, 71; Waisfeld & Vaccari 2003, p. 309, pl. 12, figs 7–9) and 'un-named reedolithine genus' of Hughes *et al.* (1975, pl. 6, figs 72–74), both from the Precordillera Basin of Argentina, the former from the Las Plantas Formation (*Climacograptus bicornis* Biozone, upper Sandbian) and the latter said to be from the 'Empozadense Beds' (= Empozada Formation, Upper Ordovician; Astini 2003, p. 15, text-fig. 1.16). Other similarities with those forms include the absence of I_n cut-off and F pits apart from the posterior fossula, the presence of a convex preoccipital ring, and lateral eye tubercles situated rather close to the glabella. In neither of the Argentinian forms is the lower lamella known, so the presence or absence of a girder cannot be confirmed, nor can the previous tentative identification of the outermost complete pit arc as E_1 . The Argentinian forms differ from *Auritolithus* in that the fringe is not as expanded laterally, so the cephalon is not markedly subpentagonal in outline, and the progressively less complete arcs anterolaterally and laterally lie successively closer to I_n rather than successively farther from it. Also, in *Guandacolithus* there is a greater number of concentric pit arcs frontally (four), and the pits in the outer three regularly arranged arcs laterally are not offset in relation to the inner three arcs and themselves; in 'un-named reedolithine genus' there are fewer regularly-arranged concentric arcs laterally (three); and in 'un-named reedolithine genus' and possibly also in *Guandacolithus* an occipital spine is present. Hughes *et al.* (1975) assigned the Argentinian forms to the Reedolithinae based on the glabellar morphology, the prominent lateral eye tubercles, and similarity in overall proportions of the fringe. However, *Reedolithus* Bancroft, 1929 and its presumed relative, the poorly known *Eirelithus* Lamont, 1941, differ from *Auritolithus* and the Argentinian forms in the arrangement of the fringe pits, the outer arcs (E_1 and I_1 in *Reedolithus*; E_{1-2} and I_n in *Eirelithus*) being complete and composed of enlarged pits. In addition, in *Reedolithus* the inner I arcs contain very small pits, and between these and I_1 the pits are rather irregularly arranged.

Despite their differences, *Auritolithus* and the Argentinian forms share unique characters of the fringe, as well

as the other similarities mentioned above, and are probably closely related. However, we consider that it is premature to propose a new subfamily for them, in view of the lack of information on the lower lamella of the Argentinian forms, and in particular on whether a girder is present in them. Another Argentinian species, '*Onnia*' *verrucosa* Rusconi, 1956 from the Empozada Formation, also seems to be related and was assigned to *Guandacolithus* by Hughes *et al.* (1975, p. 569), and tentatively so by Waisfeld & Vaccari (2003, p. 309), based on the original, rather poor illustration. Two other species from the Empozada Formation, '*Cryptolithus*' *emposadensis* Rusconi, 1953 and '*C.*' *stelarusconii* Rusconi, 1954, mentioned by Hughes *et al.* (1975) in connection with their 'un-named reedolithine genus', cannot be assessed from the original, diagrammatical illustrations; however, they may be synonyms of each other, if not also of *verrucosa*.

Parkesolithus Campbell & Durham, 1970, represented in the upper Eastonian (middle Katian) of New South Wales by the type species *P. gradyi* and *P. dictyotos* Webby, 1974, is similar in age to *Auritolithus* but is very different morphologically and not closely related, despite the suggestion to the contrary by Webby & Edgecombe (*in* Webby *et al.* 2000, p. 85). Differences in *Parkesolithus* include: the fringe is not expanded laterally so the cephalon is not subpentagonal in outline; a girder is present; there are two complete E arcs of pits, with a very strong list between E₁ and E₂ on the upper lamella; there are two to five I arcs frontally and up to two more I arcs anterolaterally, but the arrangement of I pits becomes irregular posterolaterally; both I and E pits are smaller with a much greater number of radial rows where these are defined; alae are retained in large holaspides, though not mentioned by previous authors; and the pygidium is relatively longer, more rounded in outline posterolaterally, and more distinctly segmented. Waisfeld *et al.* (2011) regarded *Parkesolithus* as closely related to *Bancroftolithus* Baldis & Pöthe de Baldis, 1995 from the lower Sandbian of the Precordillera of Argentina, the two genera probably belonging to a new subfamily which, however, those authors declined to name until phylogenetic relationships within the Trinucleidae are better understood.

Auritolithus corbettii sp. nov.

Figures 2G–N, 3

- 1974 *Ninkiangolithus* (*sic*) sp. – Corbett & Banks, p. 226, pl. 4, fig. 6 (*recte* *Ningianolithus*).
 1976 cf. *Ninkiangolithus* (*sic*). – Baillie & Clarke, p. 2.
 1979 cf. *Guandacolithus* sp. – Baillie, fig. 2.
 1980 cf. *Guandacolithus* sp. – Banks & Burrett, p. 369.
 1980 cf. *Guandacolithus* sp. 2. – Banks & Burrett, tab. 2.
 1981 cf. *Guandacolithus* sp. – Sheehan & Baillie, p. 252, text-fig. 3.

- 1988 cf. *Guandacolithus* sp. – Banks, tab. 1.
 2007 *Guandacolithus*? sp. – Ross & Ross, p. 215.
 2014 cf. *Guandacolithus*. – Calver *et al.*, p. 256.

LSID. – urn:lsid:zoobank.org:act:97F65F58-A004-4C16-8E49-2CC00EB838AA

Holotype. – Cranidium UTGD 126264A (Fig. 3A, B); Locality 4; late Katian.

Paratypes. – Articulated dorsal exoskeleton lacking lower lamella UTGD 126263/126266 (counterparts); cranidia UTGD 126261, UTGD 126264A, UTGD 126265/126267 (counterparts); Locality 4. Cranidia UTGD 81397, UTGD 81400, UTGD 81405A, UTGD 81405C; fringe lower lamellae UTGD 81399, UTGD 81405B, UTGD 81406, UTGD 81418A; small pygidium UTGD 81418B; Locality 2. Fringe lower lamella UTGD 90903A, B; locality uncertain (either 2 or 4). The questioned record by Banks (1988, tab. 1) of this species, as cf. *Guandacolithus*, from Westfield Quarry (Locality 3 herein) is erroneous.

Etymology. – After Keith D. Corbett, formerly of the Tasmanian Department of Mines.

Diagnosis. – As for genus.

Description. – Cephalon with maximum width across lateral extremity of fringe about 2.6 times sagittal length and about 1.1–1.3 times width at base of genal spine; anterior margin almost straight between broad median flexure and a point more or less in line (exsag.) with base of genal spine, beyond which it curves back to widest part of fringe; posterolateral margin diverging strongly forwards from base of genal spine and concave in outline. Glabella clavate, strongly inflated, especially frontally where it overhangs posterior edge of fringe; occipital ring prominent, occipital furrow containing apodemal pit distally; preoccipital ring narrower (tr.) than occipital ring, much less elevated and about twice as long (sag.), comprising almost 20% of sagittal glabellar length excluding occipital ring; S1 directed anteromedially on flanks of glabella and rapidly shallowing adaxially but continuous medially (Figs 2L; 3B, D); S2 and S3 not definitely identified, but position of S3 may be indicated by slight deepening of axial furrow behind anterior fossula and immediately in front of likely anterior end of eye ridge (Fig. 3B). Axial furrow broad, shallower in front of anterior fossula which is situated at usual position adjacent to maximum width of glabella. Genal field roughly as wide posteriorly as frontal lobe of glabella, gently inflated; eye tubercle situated at or just behind midlength (exsag.) of genal field, almost at summit of steeply sloping anterior and lateral regions of genal field; eye ridge weak, directed

anteromedially (Fig. 3G, right side). Posterior border with fulcrum situated at about 60% distance between posterior end of axial furrow and posterior fossula; border about as long (exsag.) adaxial to fulcrum as occipital ring, and lateral to fulcrum expands gently abaxially. Fringe steeply inclined frontally; laterally, it decreases in slope abaxially and expands rapidly to reach maximum width more or less opposite cephalic midlength (sag.); maximum radial width of fringe more than three times its sagittal length; upper lamella with low inter-radial ridges crossing two arcs present in front of glabella, all three arcs present in front of adaxial part of genal field, and four inner arcs laterally; on posterior part of fringe, very short arc of only a few pits present on outside of inner arc in some specimens (Figs 2H, L, N; 3A, B, K); eight or nine radial rows of pits present in front of glabella, between forward projections of axial furrows; posterior row probably with six pits (Fig. 3I, innermost pit in row covered by matrix). Genal spine longer than sagittal length of cephalon, tapering uniformly, initially diverging and gradually curving backwards distally, with marked longitudinal ridge on both dorsal and ventral surfaces (Fig. 3C, F, J–L).

Thorax of six segments, widest across third and/or fourth. Axis subparallel-sided on segments 1–4, comprising about 25% maximum width of thorax, successively narrower on segments 5 and 6. Pleurae with raised posterior bands and flattened anterior bands, and poorly differentiated pleural furrows; posterior bands of uniform length (exsag.) adaxial to fulcrum; anterior band on first segment almost twice as long as posterior band, anterior bands on following segments successively shorter.

Pygidium triangular in outline, about four times as wide as long excluding steep outer face of posterior border; axis comprising about 20–25% pygidial width anteriorly, narrowing strongly backwards, extending to inner edge of border; pleural region flat inside border, its anterior margin with transverse ridge; first pleural furrow shallow, expanding backwards abaxially at a uniform rate; in dorsal view border is a narrow ridge along which it is sharply downturned, its outer face increasing in height and convexity posteromedially.

Remarks. – The coarseness of the matrix is not favourable to the preservation of sculpture, but traces of reticulate

sculpture on the glabella and pits on the genal field are distinguishable on some external moulds (Figs 2L; 3E). The specimens show variation in the shape of the lateral extremity of the fringe, ranging from broadly and strongly rounded (Figs 2H, I; 3K, L) to subangular (Fig. 3J), with other specimens apparently showing an intermediate condition (Fig. 3C, M). The differences are not related to collection localities, and we attribute them to intraspecific variation. A very small cranidium with the glabella about 1.2 mm long may belong to a meraspis (Fig. 2J). Only the posterior part of the fringe is preserved on the left side and it is incomplete, showing a maximum of four arcs of pits, those in the fourth arc from the innermost one apparently out of phase with the others as in larger cephalo and cranidia. The specimen differs from larger cephalo and cranidia, on which the preceding description is based, in that alae are present, extending forwards to about the level of the posterior edge of the eye, and the eye ridge is more distinct.

Family Illaenidae Hawle & Corda, 1847

Subfamily Illaeninae Hawle & Corda, 1847

Genus *Pepodes* gen. nov.

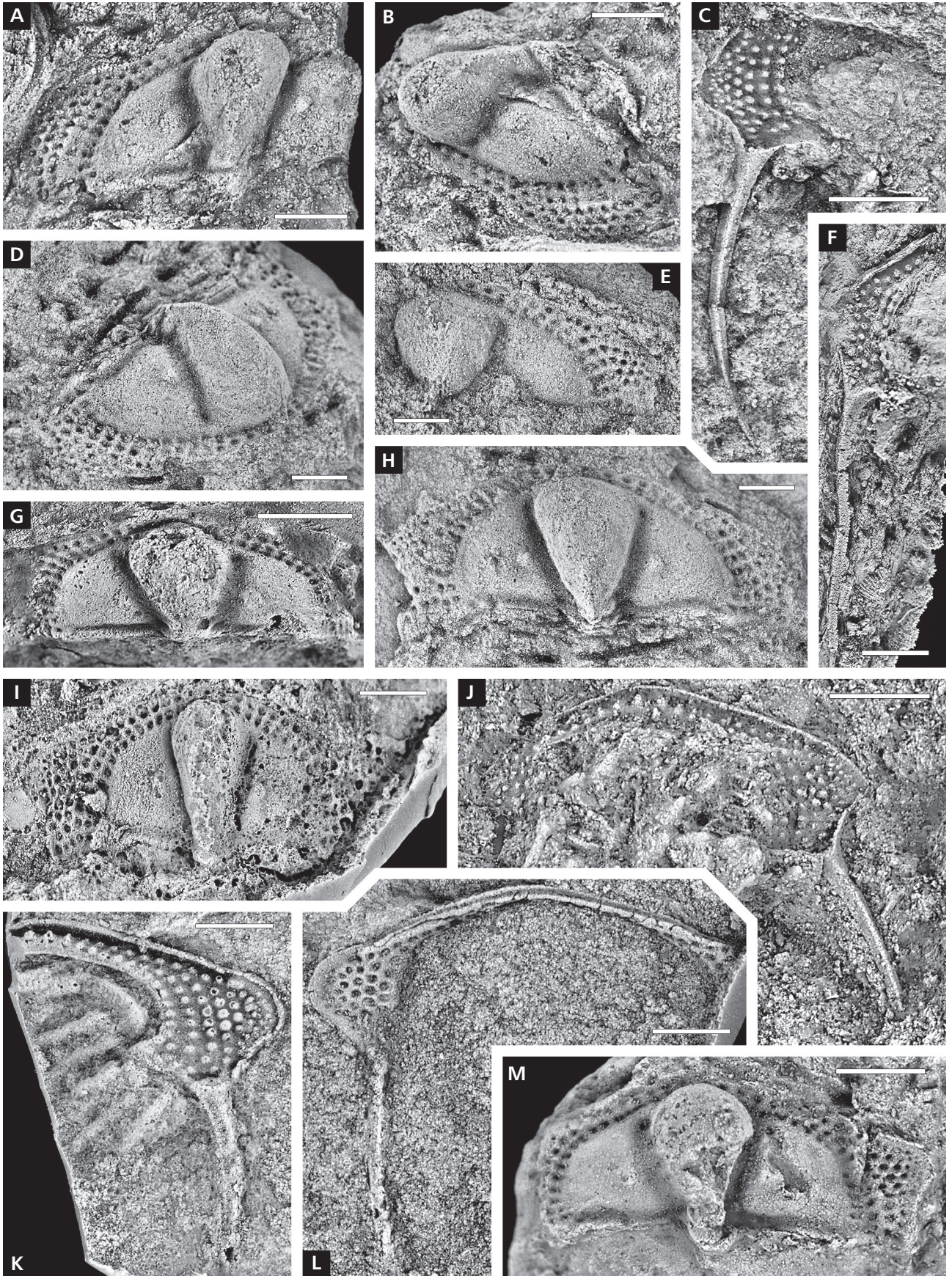
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Type species. – *Pepodes agrestis* gen. et sp. nov. from the upper part of the Arndell Sandstone (Rhuddanian) of Tasmania.

Etymology. – Greek, *pepon*, a melon, together with the suffix *-odes*, denoting likeness, referring to the smooth dorsal exoskeleton; gender masculine.

Diagnosis. – Cephalon of low convexity (sag., exsag., tr.). Glabella very wide posteriorly, there comprising about 75% cranial width, narrowing forwards abruptly for short distance immediately in front of posterior margin, thereafter narrowing less strongly as far as lunette, expanding at similar rate in front of lunette as far as axial furrow is distinguishable. Palpebral lobe of moderate size, situated its own length or less from posterior cephalic margin; anterior branch of facial suture diverging moderately

Figure 3. *Auritolithus corbetti* gen. et sp. nov., lower Arndell Sandstone (late Katian), Florentine Valley, southern Tasmania; all except C, F, G, J–M from Locality 4, Stan Murray Road. A, B – holotype, cranidium UTGD 126264A, internal mould, dorsal and oblique views. C – fringe lower lamella UTGD 81406, latex cast of external mould of dorsal surface, dorsal view; Locality 2. D, E, H – cranidium UTGD 126265/126267 (counterparts); D, H – UTGD 126265, internal mould, dorsal and oblique views; E – UTGD 126267, latex cast of external mould, dorsal view. F – fringe lower lamella UTGD 81405B, latex cast of external mould of dorsal surface, dorsal view; Locality 2. G – cranidium UTGD 81397, internal mould, dorsal view; Locality 2. I – cranidium UTGD 126261, latex cast of external mould, dorsal view. J – fringe lower lamella UTGD 81418A, latex cast of external mould of dorsal surface, dorsal view; Locality 2. K, L – fringe lower lamella 90903A, B (counterparts), from uncertain locality; K – UTGD 90903A, latex cast of external mould of dorsal surface, dorsal view; L – UTGD 90903B, latex cast of external mould of ventral surface, ventral view. M – cranidium UTGD 81405C, internal mould, dorsal view; Locality 2. Scale bars represent 2 mm.



strongly forwards from γ to β . Librigena with posterior margin curving gently backwards to strongly rounded genal angle, and with very weak vincular furrow running close to and subparallel with inner edge of doublure adaxial to genal angle. Rostral plate lenticular in ventral view, gently convex (sag., exsag.). Hypostome parabolic in outline behind large anterior wings, without shoulders; anterior lobe of middle body elliptical in outline, posterior lobe with prominent maculae. Thorax nonfulcrate, with very wide axis comprising most of segmental width (tr.); axial furrow indistinct. Pygidium more convex than cranidium, subelliptical in outline, as wide or a little wider than long, maximum width well in front of midlength (sag.); axis very wide anteriorly, there comprising about 60% maximum pygidial width, otherwise undefined; anteriormost pleural furrow impressed; doublure increasing in width posteromedially, its inner margin with a bifid forward projection medially.

Remarks. – *Pepodes* is known only from the type species. The absence of the omphalus and anterolateral internal pit on the cranidium, and the presence of a forward projection on the inner margin of the pygidial doublure, suggest that the affinities of the genus lie with the Illaeninae rather than with the Bumastinae (see subfamily diagnoses in Ludvigsen & Chatterton 1980, p. 476). Other than *Pepodes*, the only member of the Illaeninae having a thorax with very broad axis and nonfulcrate pleural region is *Bumastoides* Whittington, 1954, recorded from the Darriwilian–Hirnantian of North America and Greenland (see Carlucci *et al.* 2012 for illustrations of many of these species), and from the lower Eastonian (lower Katian) of Tasmania (Edgecombe *et al.* 2006). Reported occurrences of *Bumastoides* from Scotland and South China have been either dismissed (Carlucci *et al.* 2012) or questioned (Zhou *et al.* 1984), and we agree that they do not represent this genus. *Bumastoides* differs from *Pepodes* in many characters. The cephalon is more strongly vaulted (sag., exsag.), even allowing for likely tectonic flattening of the Tasmanian specimens; the palpebral lobe and lunette are situated more posteriorly; the anterior branch of the facial suture converges forward over its entire length instead of initially diverging; the librigena is broadly rounded at the genal angle rather than backwardly deflected and acutely rounded; and the librigenal margin is deflected upwards anteriorly in a dorsal arch, into which the lateral extremity of the pygidium fitted on enrolment (Carlucci *et al.* 2012, fig. 11c, d). The hypostome of *Bumastoides* has prominent shoulders, a shorter anterior lobe of the middle body that is trapeziform in outline rather than elliptical, and indistinct maculae (Hunda *et al.* 2003, pl. 1, figs 10, 11). The maximum width of the pygidium is situated much farther posteriorly in *Bumastoides*, due to the longer articulating facets that are directed more strongly

backwards; the first pleural furrow of the pygidium is not impressed; the pygidial doublure is wider, especially laterally, as the inner margin lies only a little farther back medially than abaxially; and the inner margin has a pair of widely-spaced forward projections (cusps) rather than a bifid median projection, except in *B. tricuspoidatus* from Tasmania which apparently has a simple median cusp as well as lateral ones (Edgecombe *et al.* 2006, fig. 4c).

Also easily distinguished from *Pepodes* is *Eastonillaenus* Edgecombe & Webby, 2007, known from two species from the upper Eastonian (Ea3–4, mid-Katian) of New South Wales, *E. goonumblaensis* Edgecombe & Webby (type species) and *E. incertus* (Webby, 1973). Most obviously, the thoracic axis in *Eastonillaenus* is not as wide and the thoracic pleurae are fulcrate. Other differences in *Eastonillaenus* include: the axial furrow converges forwards only weakly as far as the lunette, and the glabella here is more convex (tr.); the palpebral lobe and lunette are situated more posteriorly; the genal angle is broadly rounded and not deflected backwards; the rostral plate is subtrapeziform in outline rather than lenticular, concave (sag.) medially in its posterior half, and the connective suture is strongly sigmoidal in outline; and the pygidial doublure is narrower, its inner margin being subparallel to the pygidial margin and lacking a forward projection medially.

***Pepodes agrestis* sp. nov.**

Figures 4, 5

- 1976 *Bumastus*. – Baillie & Clarke, p. 2.
- 1978 *Bumastoides* sp. – Baillie *et al.*, p. 46.
- 1979 *Bumastoides* sp. – Baillie, fig. 2.
- 1980 *Bumastoides* sp. f. – Banks & Burrett, tab. 2.
- 1981 *Bumastoides* sp. – Sheehan & Baillie, p. 252, text-fig. 3.
- 1988 *Bumastoides* sp. – Banks, p. 193, tab. 1.
- 1991 *Bumastoides* sp. – Laurie, p. 26.

LSID. – urn:lsid:zoobank.org:act:B07E2EEF-D6A6-4C26-9411-408DCAAEA511

Holotype. – Cranidium UTGD 98386 (Fig. 4A–C); Locality 3; Rhuddanian.

Paratypes. – Cranidia UTGD 126162, UTGD 126174/126179 (counterparts), UTGD 126177, NMV P313693–P313694; librigenae UTGD 126159/126170 (counterparts), NMV P313696–P313699; hypostomes UTGD 126183, NMV P313695 (with rostral plate attached); partial thorax UTGD 126175; pygidia UTGD 126160/126161 (counterparts), UTGD 126163–126165, UTGD 126169/126176 (counterparts), UTGD 126172, UTGD 126173, UTGD 126178, UTGD 126184, NMV P313700–P313701; all from Locality 3.

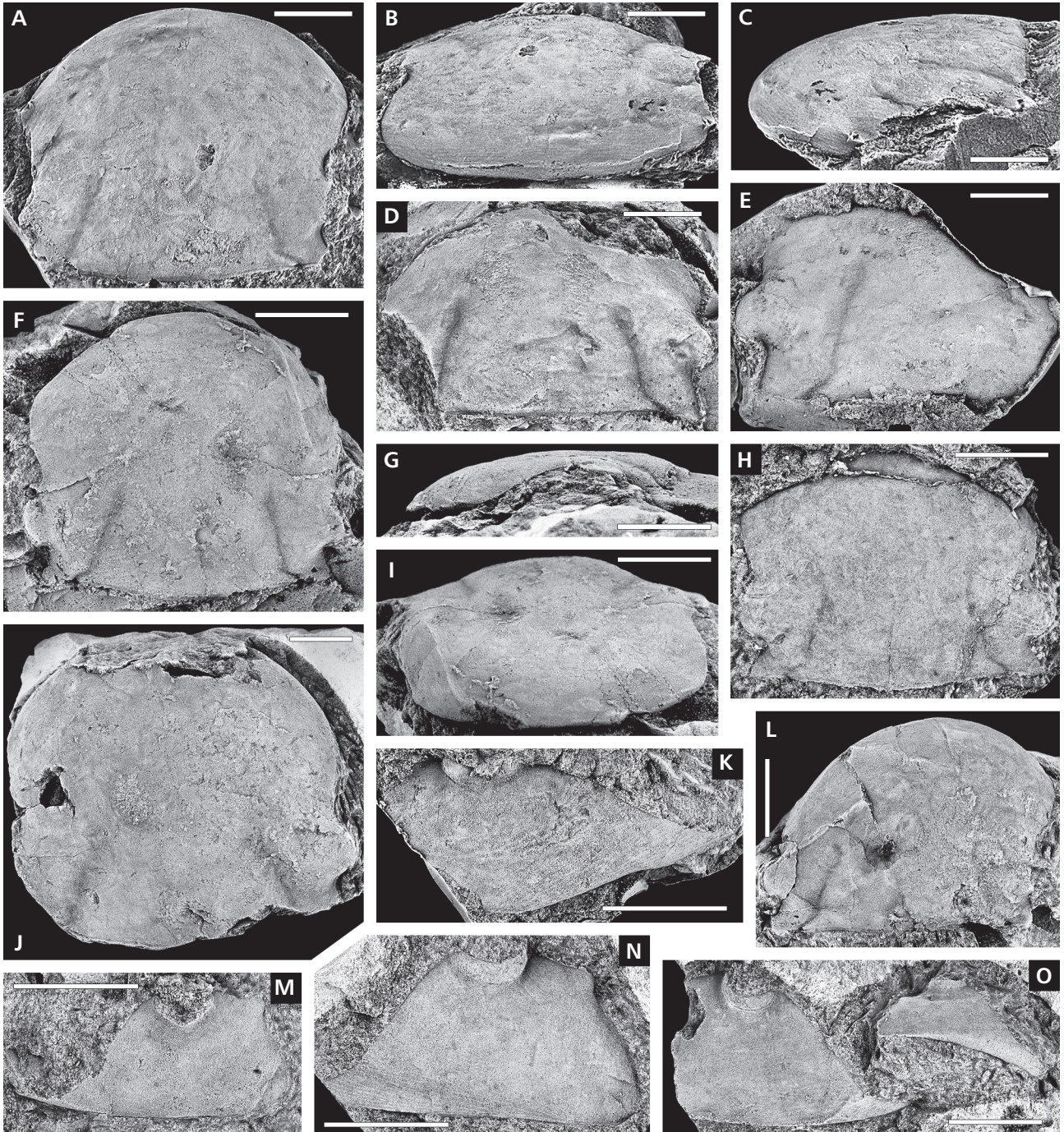


Figure 4. *Pepodes agrestis* gen. et sp. nov., upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. A–C – holotype, cranidium UTGD 98386, internal mould, plan, anterodorsal and lateral views. D, E – cranidium UTGD 126174/126179 (counterparts); D – UTGD 126174, internal mould, dorsal view; E – UTGD 126179, latex cast of external mould, dorsal view. F, G, I – flattened cranidium UTGD 126162, internal mould, plan, lateral and anterodorsal views. H – cranidium NMV P313694, latex cast of external mould, plan view. J – large cranidium UTGD 126177, internal mould, plan view. K – librigena NMV P313698, latex cast of external mould, oblique view. L – cranidium NMV P313693, internal mould, dorsal view. M – librigena NMV P313699, internal mould, oblique view. N – librigena UTGD 126170B, internal mould, oblique view. O – librigenae NMV P313728 (left) and NMV P313729 (right), internal moulds, oblique views. Scale bars represent 10 mm.

Etymology. – Latin, ‘of the fields’, referring to the Westfield Syncline and Westfield Quarry where the species occurs.

Diagnosis. – As for genus.

Description. – Exoskeleton reaching large size, largest measurable cranidium and pygidium having sagittal lengths of *ca* 50 mm and *ca* 73 mm respectively. Cranidium slightly wider across γ – γ and ϵ – ϵ than long (sag.) in plan

view, width across palpebral lobes slightly greater than across β - β and ω - ω (Fig. 4D–F, H, J); posterior margin transverse or slightly convex backwards behind glabella in dorsal view, directed slightly obliquely backwards from posterior end of axial furrow to ω ; anterior margin almost evenly curved. Glabella about 66% as wide at lunette as posteriorly, with low independent convexity (tr.) from fixigenae behind lunette; posteromedian pit on inner surface of glabella not observed and may be absent; only glabellar muscle scar distinguishable is very large G1, defined on internal mould of one specimen as elongated area with reticulate appearance extending forward from about opposite midlength of lunette in dorsal view, weaker on external surface (Fig. 4D, E). Axial furrow very shallow, its marked decrease in forward convergence situated about half-way (exsag.) between posterior cranial margin and posterior edge of palpebral lobe, straight or describing a weakly abaxially convex curve from this point as far as lunette. Small apodeme (circular pit on internal moulds; Fig. 4A, F) present at posterior end of axial furrow. Lunette weak on interior of exoskeleton and even weaker externally, situated with midlength opposite front of palpebral lobe in dorsal view. Palpebral lobe situated with midpoint roughly opposite 75% cranial length (sag.) from anterior; fixigena opposite palpebral lobe sloping gently abaxially, slightly more downturned around palpebral margin; palpebral furrow not defined. Anterior branch of facial suture with γ - β gently curved, β - α converging very strongly forwards and forming almost uniform curve with rostral suture; posterior branch of suture almost straight and diverging backwards. Front of cranidium with terrace ridge reflected on internal mould, running subparallel to anterior margin and extending backwards to palpebral lobe posterolaterally (Fig. 4B, C).

Librigena roughly triangular in outline, tapering to slender point anteriorly; posterior margin variably but gently concave in outline adjacent to facial suture (Figs 4M, N; 5H, M). Dorsal surface gently concave (tr.) around eye, gently convex (tr., exsag.) elsewhere. Eye situated in posterior half, not borne on socle. Doublure broad and flat posterolaterally, increasing in convexity anteriorly and narrowing at first, expanding gently forwards in front of about midlength. Terrace ridges on dorsal surface most distinct laterally, converging towards a point on margin in front of genal angle; terrace ridges on doublure subparallel to inner and outer margins, dying out towards broad posterior region.

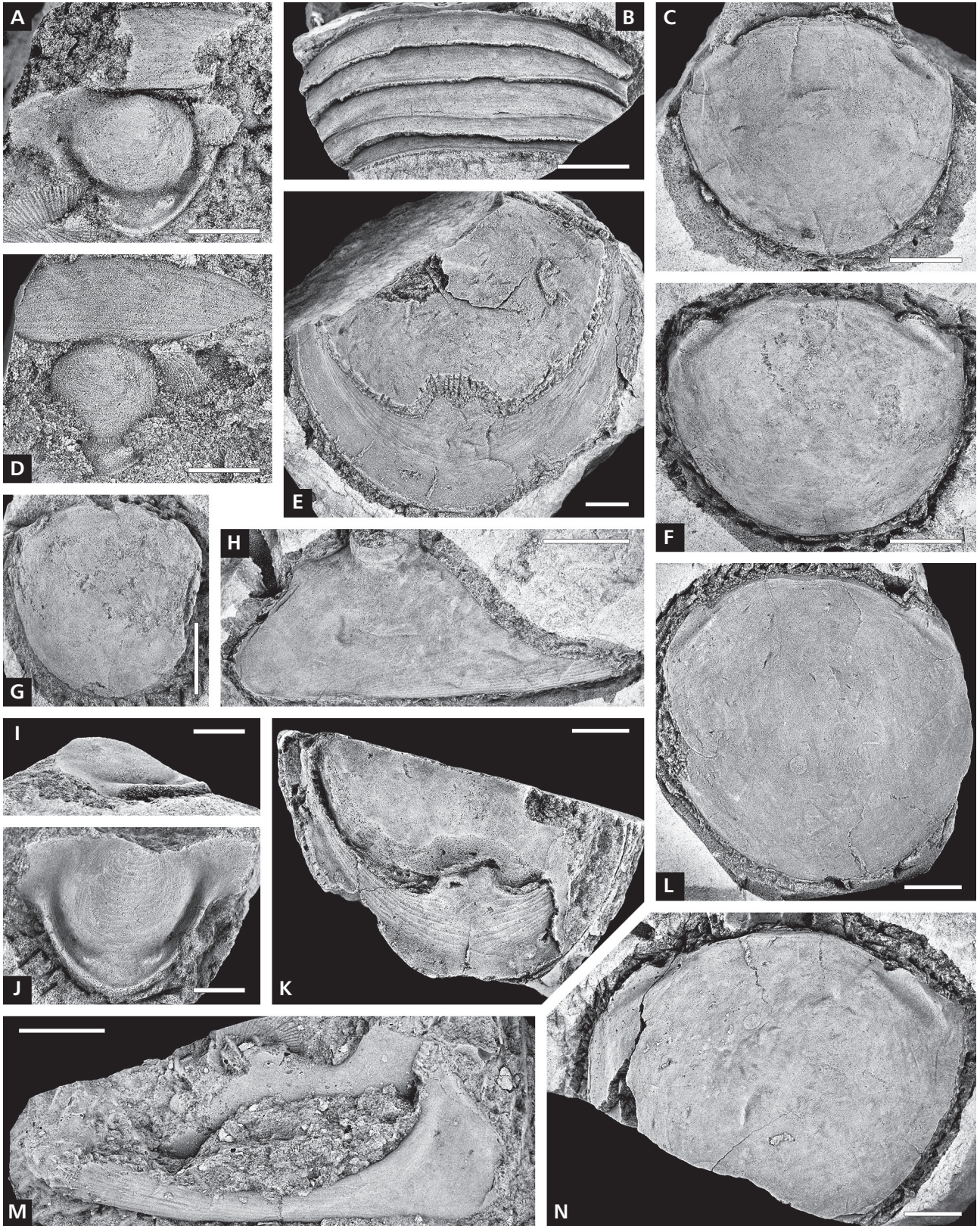
Rostral plate (Fig. 5A, D) excluding posterior flange roughly 260% as wide as long (sag.), widest slightly behind midlength; connective suture very gently convex backwards in outline, intersection with hypostomal suture not clear but apparently more or less in line (exsag.) with widest part of middle body of hypostome; rostral flange obscured in only available specimen. Terrace ridges on anterior half of rostral plate subparallel to anterior margin, becoming more transverse in posterior half.

Hypostome more than 175% wider across anterior wings than long (sag.), without shoulder. Anterior lobe of middle body subelliptical, a little wider than long, slightly pointed in outline anteromedially, strongly inflated; middle furrow shallowing adaxially in front of maculae; posterior lobe crescentic, depressed, approximately 25% sagittal length of anterior lobe, weakly convex sagittally and gently convex transversely; maculae situated towards anterolateral extremities of posterior lobe. Lateral and posterior borders narrow and strongly rounded in cross section; border furrow decreasing in width and depth behind maculae. Sculpture of terrace ridges reflected on internal mould, on anterior lobe of middle body arranged in ellipses with their centres situated successively farther back.

Only thorax available consists mainly of axial part of five segments, last segment mostly overlapped by previous one (Fig. 5B). Axial rings weakly convex in sagittal profile, gently arched in transverse profile and arched forwards in dorsal view, decreasing in length (exsag.) abaxially; very short (sag., exsag.) ridge present across anterior edge of rings; weak axial furrow (preserved on left side of second segment) strongly oblique.

Pygidium of moderate convexity, varying in proportions from about as wide as long (Fig. 5G, L) to 125% as wide as long (Fig. 5F), maximum width situated at about 40% sagittal length, just behind posterior edge of articulating facet. Lateral extent of axis defined anteriorly by forward arching of margin between a pair of notches on internal moulds (*i.e.* moulds of apodemes; Fig. 5C, F, N); anterior edge of axis thickened (expressed as furrow on internal moulds). Notches at outer extremity of axis are separated from inner end of articulating facet by an extremely narrow, transverse section of anterior pleural margin. Anteriormost pleural furrow shallow, originating at a point just behind and adaxial to notches in anterior margin, expanding abaxially and converging gradually with posterior edge of articulating facet. Doublure (Fig. 5E, K) with convex outer portion and concave inner portion, both (but mainly inner

Figure 5. *Pepodes agrestis* gen. et sp. nov., upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. A, D – hypostome with attached rostral plate NMV P313695, internal mould and latex cast of external mould, ventral view. B – fragmentary thorax UTGD 126175, internal mould, dorsal view. C – pygidium UTGD 126176, internal mould, dorsal view. E – pygidium NMV P313700, internal mould with external mould of doublure exposed, dorsal view. F – pygidium NMV P313701, internal mould, dorsal view. G – pygidium UTGD 126163,



internal mould, dorsal view. H – librigena NMV P313697, internal mould, oblique view. I, J – hypostome UTGD 126183, internal mould, lateral and ventral views. K – pygidium UTGD 126173, internal mould with external mould of doublure exposed, dorsal view. L – pygidium UTGD 126160, internal mould, dorsal view. M – librigena NMV P313696, latex cast of external mould, ventral view. N – pygidium UTGD 126184A, internal mould, dorsal view. Scale bars represent 5 mm in A, D, I, J; 10 mm in B, C, E–H, K–N.

portion) expanding posteromedially so that radial width of doublure at outer edge of posteromedian projection is about three times anterior width; notch between cusps on bifid projection not extending as far backwards as inner margin of doublure lateral to projection. Internal moulds of dorsal surface of pygidium with no trace of sculpture; doublure with terrace ridges subparallel to inner and outer margins, except on forward projection.

Remarks. – The considerable variation in pygidial proportions, ranging from about as wide as long to about 125% as wide as long, is not related to the size of the specimens, as the smallest and one of the largest are relatively longest.

Family Scutelluidae Richter & Richter, 1955

Genus *Japonoscutellum* Přibyl & Vaněk, 1971

Type species. – *Scutellum* (Subgenus nov.) *japonicum* [sic] Kobayashi & Hamada, 1965, from the Fukata Formation (late Wenlock to early Ludlow) of Gomi, Yokokurayama, Kôchi Prefecture, Shikoku, Japan, by original designation.

Diagnosis. – See Holloway & Lane (2012, p. 449).

Remarks. – Holloway & Lane (2012) thoroughly discussed the genus and gave a comprehensive list of species, to which should be added *J. drakton*, *J. fractum* and *J. mawsonae*, described by Holloway & Lane (2016) from the Telychian to possibly lowermost Sheinwoodian of north Queensland, and possibly ‘*Planiscutellum*’ *niuchangensis* [sic] Zhang, 1974 from the upper Rhuddanian of South China (see following remarks on *Japonoscutellum senectum*).

Japonoscutellum senectum sp. nov.

Figure 6

- 1976 *Heptabronteus*. – Baillie & Clarke, p. 2.
- 1978 *Eokosovopeltis* sp. – Baillie *et al.*, p. 46.
- 1979 *Eokosovopeltis* sp. – Baillie, fig. 2.
- 1980 *Eokosovopeltis* sp. i. – Banks & Burrett, tab. 2.

1981 *Eokosovopeltis* sp. – Sheehan & Baillie, p. 252, text-fig. 3.

1988 *Eokosovopeltis* sp. – Banks, p. 191, tab. 1.

1991 *Eokosovopeltis* sp. nov. – Laurie, p. 26.

2000 *Kosovopeltis*. – Holloway, p. 163.

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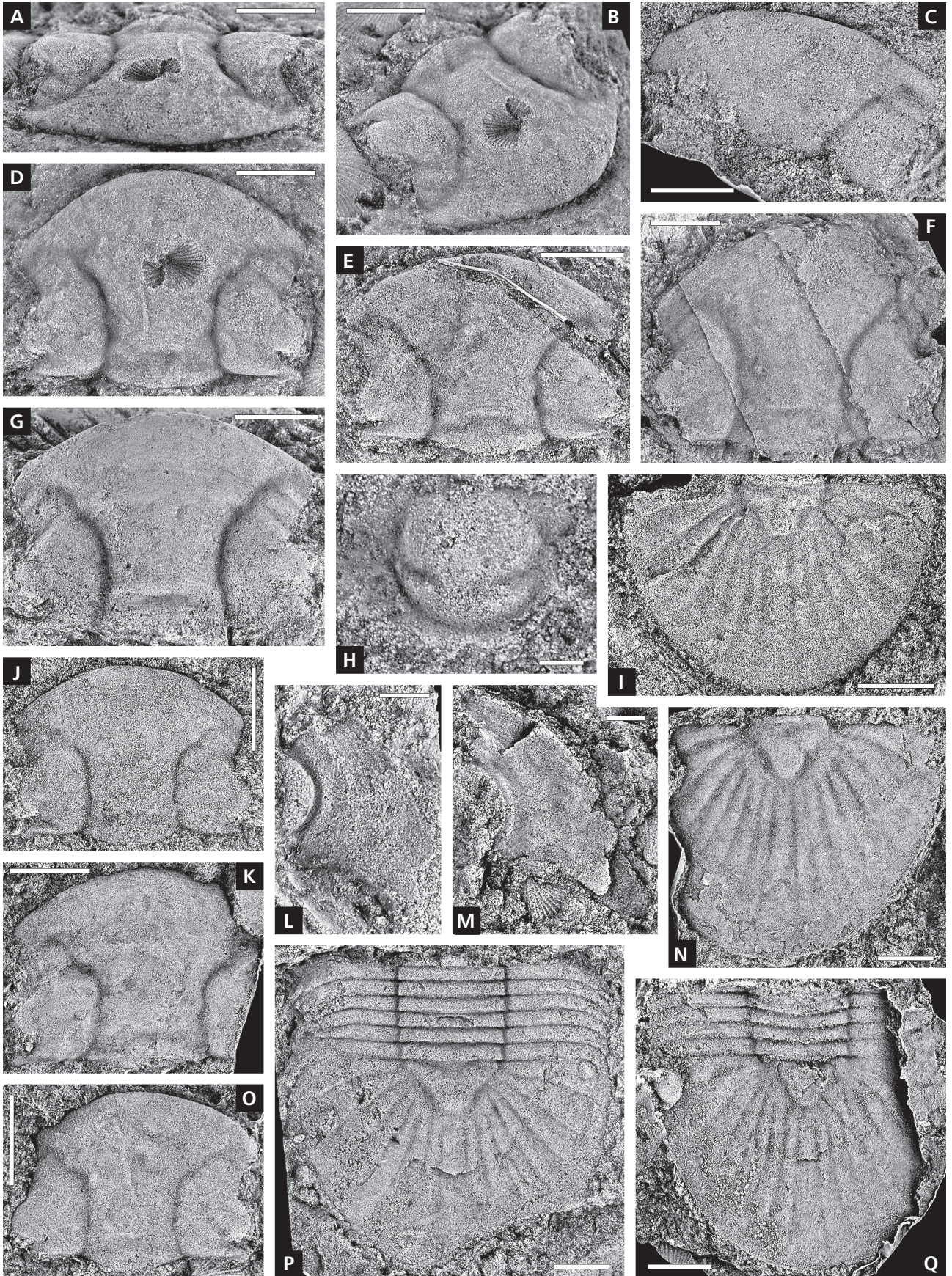
Holotype. – Cranidium NMV P313717 (Fig. 6A, B, D); Locality 3; Rhuddanian.

Paratypes. – Cranidia UTGD 126159, UTGD 126189/126197 (counterparts), UTGD 126190, UTGD 126194, UTGD 126196A, UTGD 126196B, UTGD 126198, UTGD 126200, UTGD 126222A, UTGD 126223, NMV P313718–P313724; librigenae UTGD 126227A, NMV P313727; hypostome NMV P313725; pygidia with incomplete thoraces UTGD 126201A, UTGD 126201B; pygidia UTGD 126204/126207 (counterparts), UTGD 126210, UTGD 126211/126219 (counterparts), UTGD 126215, NMV P313726; all from Locality 3.

Etymology. – Latin *senectus*, very old, aged, referring to this being the stratigraphically oldest known species of the genus.

Diagnosis. – Glabella in front of occipital ring subparallel-sided in posterior half, increasing very strongly in width in anterior half with marked increase in rate of expansion across frontal lobe; S1–S3 effaced, bolus generally indistinguishable. Fixigena broad (tr.) at palpebral lobe, almost as wide as adjacent part of glabella; anterior branch of facial suture diverging more weakly forward than anterior portion of axial furrow. Pygidium 1.3–1.5 times as wide as long; axis markedly bell-shaped in outline, approximately 0.3 times maximum pygidial width anteriorly and slightly less than 0.3 times sagittal pygidial length; paired pleural ribs distinctly imbricate in profile abaxially; postaxial rib wider anteriorly than adjacent paired ribs, expanding a little more strongly backwards in posterior half than in anterior half, 2–2.75 times as wide posteriorly as anteriorly.

Figure 6. *Japonoscutellum senectum* gen. et sp. nov., upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. A, B, D – holotype, cranidium NMV P313717, internal mould, anterodorsal, oblique and dorsal views. C – cranidium UTGD 126222A, latex cast of internal mould, dorsal view. E – cranidium NMV P313718, internal mould, dorsal view. F – cranidium UTGD 126200, internal mould, dorsal view. G – cranidium UTGD 126198, internal mould, dorsal view. H – hypostome NMV P313725, internal mould, ventral view. I – pygidium UTGD 126210A, internal mould, dorsal view. J – cranidium NMV P313720, latex cast of external mould, dorsal view. K – cranidium UTGD 126223A, latex cast of external mould, dorsal view. L – librigena NMV P313727, internal mould, dorsal view. M – librigena UTGD 126227A, internal mould, dorsal view. N – pygidium UTGD 126211, latex cast of external mould, dorsal view. O – cranidium NMV P313722, latex cast of external mould, dorsal view. P – incomplete thoracopygon UTGD 126201B, internal mould, dorsal view. Q – incomplete thoracopygon UTGD 126201A, latex cast of external mould, dorsal view. Scale bars represent 5 mm in A–G, I–K, N–Q; 2 mm in H, L, M.



Description. – Cranium with width at β - β equal to or slightly greater than widths at δ - δ and ω - ω , and 1.3–1.4 times sagittal length. Glabella weakly convex, comprising a little less than half cranial width posteriorly, gently narrowing forwards across occipital ring, frontal lobe indistinctly differentiated laterally from portion of anterior border in front of epiborder furrow (Fig. 6C); ratio of glabellar widths at posterior margin, at intersection of axial and anterior border furrows, and across frontal lobe approximately 1:1.5:2. Occipital ring more strongly convex (tr.) than remainder of glabella, flattened and gently sloping forwards in sagittal profile, posterior edge convex backwards; occipital furrow shallow in medial third, effaced laterally by expanded (exsag.) occipital muscle scar that is poorly differentiated from L1. S1 and bolus generally indistinguishable, but position of bolus indicated in some specimens by weak outward deflection of axial furrow opposite anterior half of palpebral lobe (Fig. 6E, F, K). Axial furrow shallow, weakest adjacent to frontal lobe; preglabellar furrow faint in front of lateral extremity of frontal lobe, fading altogether adaxially (Fig. 6G). Fixigena gently sloping adaxially opposite weakly upturned palpebral lobe; lunette faintly defined, situated with midlength opposite δ (Fig. 6G), its position also indicated in some specimens by slight deepening of axial furrow (Fig. 6E). Palpebral lobe with posterior edge opposite median part of occipital furrow and anterior edge just behind cranial midlength (sag.); palpebral furrow faint (Fig. 6K). Weak eye ridge directed obliquely forwards at ca 45° to sagittal axis, anterior end situated half-way between point of divergence of axial furrow and intersection of axial and anterior border furrows. Fixigena in front of eye ridge sloping anterolaterally to weak anterior border furrow situated slightly closer to eye ridge than to cranial margin; anterolateral border wide (exsag.), with shallow epiborder furrow that is much broader than border furrow (Fig. 6C, G). Posterior part of fixigena sloping backwards to articulating furrow. Anterior branch of facial suture sigmoidal, greater part diverging forwards at 25–35° to sagittal axis; posterior branch diverging very strongly from back of eye, flexed sharply backwards distally. Librigena with eye bounded below by incised furrow and surrounded by very narrow, rounded (tr.), ridge-like librigenal field that expands only weakly anteriorly; very broad, shallow and poorly defined lateral border furrow runs adjacent to this ridge (Fig. 6L, M). Lateral border comprises most of librigenal width, expanding posteriorly; epiborder furrow broad, shallow and poorly defined, fading posteriorly toward base of acute genal spine; librigenal doublure gently convex.

Hypostome a little wider across shoulders as long (sag.), about 1.5 times this width across anterior wings. Middle body subcircular in outline, anterior lobe moderately inflated, posterior lobe flattened medially and gently

inflated abaxially; middle furrow directed obliquely backwards from border furrow opposite midlength (sag.) of middle body, dying out medially; maculae not identified. Border furrow shallow, wider opposite anterior wing than farther back. Posterior border apparently not greatly elongated medially.

Thorax known only from last six segments. Axis gently convex (tr.), narrowing very slightly on last two segments, otherwise subparallel-sided and approximately equal in width (tr.) to pleural lobe. Inner part (about two-thirds) of pleurae horizontal, outer part beyond fulcrum weakly downturned and curving backwards in sickle-like spines.

Pygidial axis gently convex, 1.4–1.6 times as wide anteriorly as long (sag.), markedly concave in posterolateral outline at inner ends of pleural ribs 4–6, broadly to rather sharply rounded posteromedially, with no trace of axial rings or longitudinal furrows; axial furrow shallowest behind axial terminus. Seven paired pleural ribs weakly convex adaxially, becoming progressively more flattened and imbricate abaxially, first two ribs expanding more strongly abaxially than remainder, ribs 4–7 narrower than remainder; postaxial rib non-bifurcate distally. Interpleural furrows shallow, first one or two curving convex forwards, next almost straight, remainder concave forwards, furrows 4–6 fading close to axis. Doublure extending forwards approximately half sagittal length of pygidium, inner edge with maximum curvature medially.

Sculpture of terrace ridges on dorsal surface of exoskeleton, librigenal and pygidial doublure and hypostome.

Remarks. – *Japonoscutellum senectum* is distinguished from most other species of the genus by the complete or almost complete effacement of S1–S3 and the bolus. Nevertheless, assignment of the species to *Japonoscutellum* is supported by the occipital muscle scar that appears attached to the back of L1, and is bounded behind by a distinct convex-backwards furrow that joins the occipital furrow adaxially; the strongly laterally-expanded frontal lobe of the glabella that is poorly differentiated from the outer part of the lateral border in front of the epiborder furrow; the preglabellar furrow that is faint laterally and absent medially; the narrow, ridge-like librigenal field surrounding the eye; the bell-shaped pygidial axis; and the flattened and imbricate profile of the outer portions of the paired pygidial pleural ribs. The last two features are particularly characteristic of *Japonoscutellum* though in some species they are not strongly developed.

Japonoscutellum senectum is the stratigraphically oldest species of the genus. Other stratigraphically early species that were assigned to *Japonoscutellum* by Holloway & Lane (2012, p. 449) include *J. yichangense* (Zhang, 1974) and possibly *J. fenxiangense* (Yi, 1978), both from the upper Aeronian of Hubei Province, South China, and

like *J. senectum* having cranidia with weak or effaced S1–S3. *Japonoscutellum yichangense* (see Zhang 1974, pl. 80, fig. 2; also Yi 1978, pl. 91, figs 1–4) differs from *J. senectum* in that the glabella does not expand as strongly forwards in its anterior half, as far as the anterior border furrow; the axial furrow is entirely effaced in front of its intersection with the anterior border furrow; the anterior border furrow is very deep on the front of the fixigena, and the border here lacks an epiborder furrow; the fixigena is narrower at γ – γ and ε – ε , and the palpebral lobe is wider; the anterior branch of the facial suture diverges more strongly forwards, subparallel to the axial furrow; and the pygidial postaxial rib is parallel-sided instead of expanding backwards. The affinities of *J. fenxiangense* cannot be assessed reliably from the only illustrated specimen, a rather poorly preserved cranidium (Yi 1978, pl. 92, fig. 9), but it may be conspecific with the specimens illustrated by that author as *J. yichangense*. Older than these species is the poorly known ‘*Planiscutellum niuchangensis* [sic] Zhang, 1974 (p. 173, pl. 80, fig. 1), based on a cranidium from the upper Rhuddanian of Guizhou Province, South China. The holotype shows weakly developed S1–S3 but is fractured and somewhat flattened by crushing, so the species is difficult to interpret from this specimen. Two additional cranidia were each illustrated by Wei & Zhan (2017, fig 6j; 2018, fig. 5.12) who assigned the species to *Kosovopeltis*, this assignment being accepted by Holloway (2021, p. 19) based on the cranidium from 2017. Both of these cranidia are strongly effaced, with S1–S3 and the bolus indistinguishable. However, the cranidium from 2018 shows a weakly defined border furrow and epiborder furrow on the anterior fixigena, and this specimen appears to belong to *Japonoscutellum*. Better preserved specimens are needed to assess the generic assignment of the species with more confidence, but it differs from *J. senectum* in that the glabella in front of the occipital ring is not subparallel sided in its posterior half and expands less strongly forwards in its anterior half, without an abrupt increase in the rate of expansion across the frontal lobe, and the fixigenal field is narrower.

Of the three species of *Japonoscutellum* described by Holloway & Lane (2016) from the Telychian to possibly earliest Sheinwoodian of the Broken River region of north Queensland, *J. senectum* is most similar to *J. mawsonae*. The cephalon of that species is not effaced like that of *J. senectum*, so that the glabellar, axial, border and epiborder furrows are deeper, and the bolus and lunette are better defined. In addition, in *J. mawsonae* the glabella expands forwards from farther back, opposite the middle (exsag.) of the palpebral lobe instead of the front; there is not such a marked increase in the width of the glabella across the frontal lobe; the fixigena is narrower (tr.) overall; the ridge-like librigenal field lateral to the eye expands distinctly anteriorly; the genal spine is shorter;

the hypostome has more prominent shoulders; and the pygidial interpleural furrows are deeper.

Family Brachymetopidae Prantl & Přibyl, 1951

Genus *Niuchangella* Zhang, 1974

[= *Radnorina* Owens & Thomas, 1975]

Type species. – *Niuchangella meitanensis* Zhang, 1974, from early–middle Rhuddanian strata (*Parakidograptus acuminatus* and *Cystograptus vesiculosus* biozones) of the Wulipo Beds, Meitan County, Guizhou, China, by original designation.

Remarks. – The affinities of *Niuchangella* have long been a matter of contention, largely because the only available illustration of the type species was that of the holotype (Zhang 1974, pl. 80, fig. 11). Yin *in* Yin & Li (1978) included the genus in the Proetidae, but Kobayashi (1985) placed it in the Brachymetopidae, noting similarities with *Radnorina* Owens & Thomas, 1975. Owens (*in* Owens & Hammann 1990) assigned *Niuchangella* to the Roringtoniidae but Adrain & Chatterton (1993) transferred it to the Scharyiidae, mentioning as evidence a few characters including the apparent lateral displacement of L1 (actually a lateral constriction of the glabella in front of L1) in the type species, though that feature is not generally characteristic of members of that family. Assignment to the Scharyiidae was maintained by Jell & Adrain (2003), Owens & Fortey (2009), Adrain (2013) and Pereira *et al.* (2015), the last acknowledging that there were difficulties in assessing the affinities of the genus based on the only illustration of *N. meitanensis*. Additional specimens of the type species have since been illustrated by Wei & Zhan (2018, fig. 4.1–4.4), and these support the views of Zhou & Zhou (2008, pp. 218, 240) and Zhou *et al.* (2016, p. 279) that *Niuchangella* is a senior synonym of *Radnorina*. Specimens illustrated by Wei & Zhan (2018) have only a very weak lateral constriction of the glabella in front of L1 (at a faint S2), in contrast to the marked constriction that seems to be present in the holotype. Although Pereira *et al.* (2015, p. 546) suggested that the holotype may have eight thoracic segments, it does appear to have nine as stated tentatively by Zhang (1974, p. 176), the axis of the last segment being partly broken medially and exposing the articulating half ring of the pygidium. This is the same number of thoracic segments present in other species of *Niuchangella* for which the full number is known with certainty: *N. bretti* (Adrain & Tetreault, 2005), *N. carlsi* (Owens & Hammann, 1990), *N. guyi* (Pereira *et al.*, 2015) and *N. loredensis* (Thadeu, 1947). The report by Hammann & Leone (1997) of at least 10 segments in specimens they assigned to *N. simplex* (Kolobova, 1978) cannot be confirmed from their illustrations.

***Niuchangella agastor* sp. nov.**

Figure 7

1978 new proetid genus. – Baillie *et al.*, p. 46.

1981 new proetid genus. – Sheehan & Baillie, p. 252.

2000 *Radnorina*. – Holloway, p. 163, left column.

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Holotype. – Cranidium UTGD 126260/126268 (counterparts) (Fig. 7C, G, J); Locality 3; Rhuddanian.

Paratypes. – Cranidia UTGD 121121, UTGD 126256, UTGD 126271; pygidia UTGD 126258, NMV P313715; Locality 3.

Etymology. – Greek, ‘near kinsman’, referring to the similarity to the type species; noun in apposition.

Diagnosis. – Cranidium moderately vaulted. Glabella comprising 70% sagittal length of cranidium, narrowing moderately forwards in front of occipital ring, with slight lateral constriction about 30% glabellar length from broadly rounded anterior; width across L1 about 80% sagittal length. L1 large, 75% as wide as adjacent median part of glabella, not depressed; S1 gently curved. Anterior branch of facial suture diverging forwards at about 65–75° to sagittal axis. Preglabellar field comprises about half sagittal cranial length in front of glabella; anterior border furrow not impressed. Pygidium about twice as wide as long; axis extending close to posterior margin of pygidium, with more than seven weakly rounded (sag., exsag.) rings, axial terminus steeply declined; pleural region with about eight pleural furrows, a narrow, rather weakly defined border, and with posterior pleural bands only slightly elevated above anterior bands abaxially.

Description. – Cranidium wider across β – β than long (sag.). Glabella gently convex, longer than wide, width across frontal lobe about 75% maximum width across occipital ring and back of L1. Occipital ring decreasing in length abaxially behind L1, deflected slightly forwards distally; median section of occipital furrow longer (sag., exsag.) and shallower than lateral section. L1 subtriangular, with slight independent convexity; S1 shallow, meeting axial furrow just behind glabellar midlength, decreasing in depth posteriorly but extending to occipital furrow. S2 and S3 not observed (S2 probably corresponds with lateral constriction of glabella). Axial and preglabellar furrows shallow but well defined. Anterior part of cranidium between preglabellar and epiborder furrows sigmoidal in longitudinal profile and sloping forwards; posterior, gently convex portion comprises preglabellar field, and anterior,

weakly concave portion comprises inner part of anterior border behind epiborder furrow (see remarks following); outer part of anterior border weakly rounded (sag., exsag.). Palpebral lobe upturned from adaxially sloping fixigena, backwardly placed, with posterior edge opposite occipital furrow.

Pygidium almost twice as wide as long, lenticular in dorsal outline. Axis strongly convex (tr.), slightly more than 25% maximum pygidial width anteriorly, narrowing gently backwards; axial rings flattened (sag., exsag.) on external surface of exoskeleton, second ring with well-developed pseudo-articulating half ring (Fig. 7K); first inter-ring furrow more distinct than remainder. Axial furrow shallow around terminal lobe of axis. Pleural field gently convex; pleural furrows longer (exsag.) and deeper than interpleural furrows; both gently curved, directed successively more strongly backwards, almost exsagittally directed towards back of pygidium, extending virtually to pygidial margin; anterior pleural bands on segments 2 and 3 slightly wider distally than posterior bands; border flattened, rather steeply inclined posteriorly; border furrow very shallow.

Sculpture on cranidium and pygidium not preserved.

Remarks. – *Niuchangella agastor* is very similar to the type species. *Niuchangella meitanensis* differs in that the glabella tapers more strongly forwards and is slightly longer, about 75% sagittal cephalic length as opposed to 70%; L1 is narrower, about 50% of the width of the adjacent median part of the glabella instead of about 75%; the anterior branch of the facial suture possibly diverges a little more strongly forwards, though there seems to be some variation in this character in the Tasmanian specimens; the pygidial axial rings are more convex (sag., exsag.) and the inter-ring furrows deeper; and the pygidium lacks a border.

The anterior border furrow is not impressed in either *N. meitanensis* or *N. agastor*. However, in the cranidium of *N. meitanensis* illustrated by Wei & Zhan (2018, fig. 4.2) the inner edge of the anterior border, and thus the position of the border furrow, is indicated by the anterior extent of the pitted sculpture of the preglabellar field and anterior fixigena. It is likely that in *N. agastor* the anterior border furrow occupies a similar position, marked by the change from the gently convex (sag., exsag.) preglabellar field to the weakly concave inner portion of the anterior border behind the epiborder furrow.

Family Encrinuridae Angelin, 1854

Genus *Arndellaspis* gen. nov.

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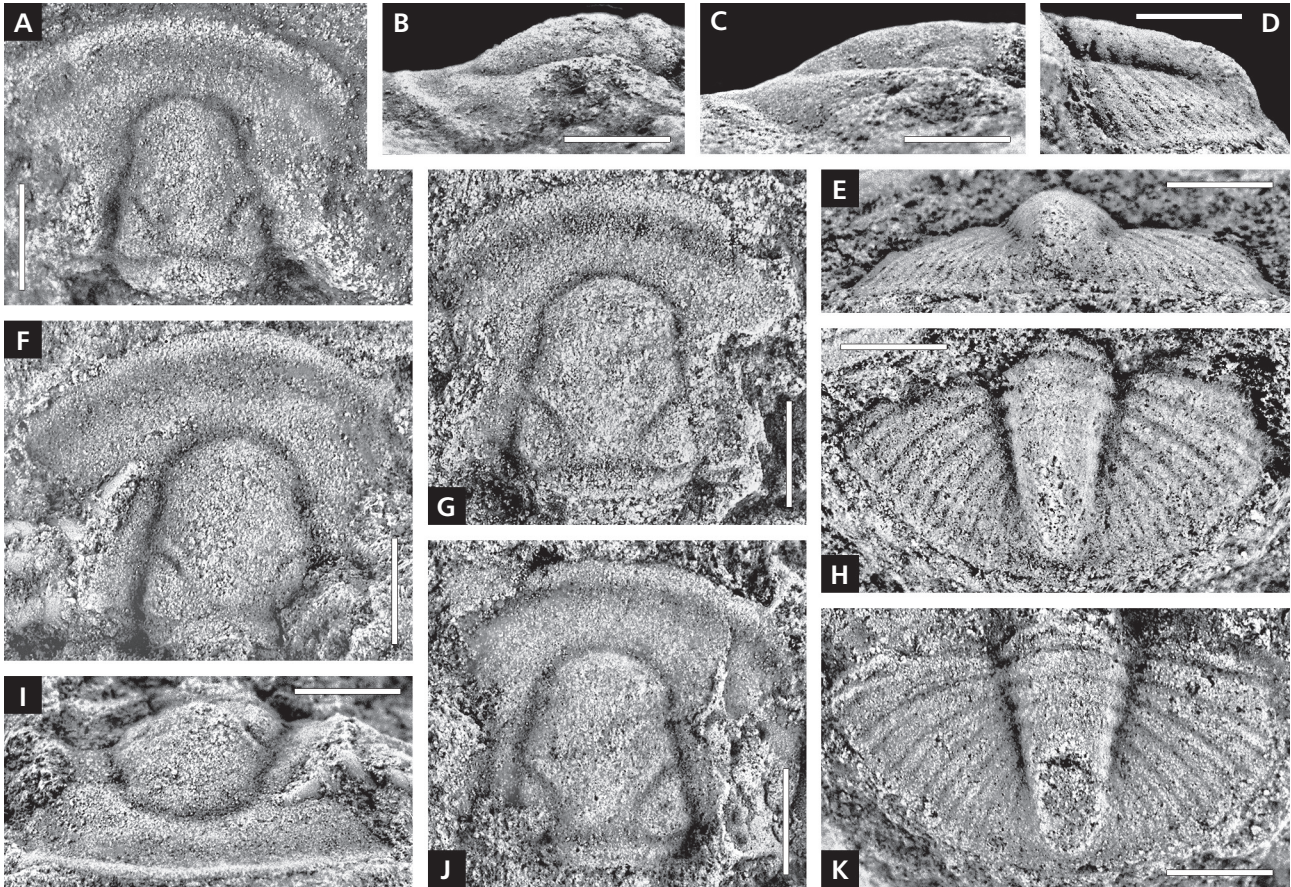


Figure 7. *Niuchangella agastor* sp. nov., upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. A, B – cranium UTGD 126271, internal mould, dorsal and lateral views. C, G, J – holotype, cranium UTGD 126260/126268 (counterparts); C, G – UTGD 126260, internal mould, lateral and dorsal views; J – UTGD 126268, latex cast of external mould, dorsal view. D, E, H, K – pygidium UTGD 126258A, B (counterparts); D, E, H – UTGD 126258B, latex cast of external mould, lateral, posterior and dorsal views; K – UTGD 126258A, internal mould, dorsal view. F, I – cranium UTGD 121121, latex cast of external mould, dorsal and anterodorsal views. Scale bars represent 2 mm.

Type species. – *Arndellaspis oryxis* gen. et sp. nov., from the upper part of the Arndell Sandstone (Rhuddanian), south-western Tasmania.

Etymology. – After the Arndell Sandstone, together with Greek *aspis*, shield; gender feminine.

Diagnosis. – Glabella not strongly constricted across L2, almost as wide here as across occipital ring; L1 ridge-like, continuous across glabella; L2–L4 not tuberculiform, L2 and L3 rounded subquadrate in outline laterally; S1–S3 slit-like laterally; strong sagittal furrow present on anterior of frontal lobe. Preglabellar furrow well defined medially as well as laterally. Palpebral lobe situated far back, with posterior edge opposite medial part of occipital furrow and anterior edge opposite L3; genal angle with strong spine. Librigenal field about as wide as lateral border; eye not pedunculate. Glabellar tubercles relatively small and sparse except for closely spaced arc bordering preglabellar furrow; L1 with a pair of tubercles medially, tubercles on L2 in a slightly irregular row; anterior border of cranium with

a row of at least 14 tubercles; fixigena lacking a distinct row of coarse tubercles adjacent to axial furrow. Pygidium elongated, mucronate, concave in outline posterolaterally; axis with more than 20 rings and a weak sagittal band, a few rings with indistinct median tubercles; pleural region with 8 paired ribs, ribs 1–7 ending in free projections, eighth merging with base of mucro; anterior as well as posterior ribs with long, backwardly-deflected abaxial portions.

Remarks. – *Arndellaspis* is known only from the type species. Its mucronate pygidium with seven pairs of pleural ribs ending in free projections and the eighth rib merging with the base of the mucro are characters otherwise known only in *Encrinurus* Emmrich, 1844 (= *E. punctatus* group as defined by Holloway 1980 and *Encrinurus (Encrinurus)* of Ramsköld 1986) and *Wallacia* Lamont, 1978, and were regarded as synapomorphies of those genera by Ramsköld & Edgecombe (1994, p. 93) who, however, also included in *Wallacia* three species lacking these characters; those species were subsequently assigned by Chatterton & Ludvigsen (2004) to the new genus *Rielaspis*. Other

similarities *Arndellaspis* shares with *Encrinurus* (*s.s.*) and *Wallacia* include the presence of genal spines; the relatively high ratio of axial rings to pleural ribs in the pygidium; the weakly segmented sagittal band on all but the anterior part of the pygidial axis; and the presence of median tubercles on the pygidial axial rings. However, some of these latter characters are primitive for the Encrinurinae (genal spines) or shared with other genera, for example *Distyrax* Lane, 1988 (which is closely related to *Encrinurus*, see Edgecombe & Chatterton 1992, p. 53) and *Erratencrinurus* Krueger, 1972, amongst others.

In contrast to the derived characters of the pygidium, the cephalon of *Arndellaspis* features primitive character states, namely the relatively small glabellar tubercles mostly lacking a symmetrical arrangement; the ridge-like and medially continuous L1; the abaxially deep and slit-like S1–S3; the non-tuberculiform L2–L4; the well-defined preglabellar furrow; the deep sagittal furrow on the anterior cranial border and front of the glabella; the lack of an adaxial row of enlarged tubercles on the fixigena adjacent to the axial furrow; and the long genal spines referred to above. Some or all of these primitive characters are present in genera from the Ordovician and Silurian such as *Cromus* Barrande, 1852, *Perryus* Gass & Mikulic, 1982 (see Edgecombe & Chatterton 1992 for illustrations of both), *Curriella* Lamont, 1978 and the problematic *Encrinuroides* Reed, 1931 (see Edgecombe & Chatterton 1990 for illustrations of the former and discussion on the latter), *Frenocrinuroides* Lespérance & Desbiens, 1995, *Prophysemataspis* Lespérance & Desbiens, 1995 and *Walencrinuroides* Lespérance & Desbiens, 1995.

The presence in *Arndellaspis* of a mucronate pygidium with seven pairs of pleural ribs ending in free points raises the question of whether the genus shares common ancestry with *Encrinurus* and *Wallacia* that uniquely share these derived characters, or whether *Arndellaspis* acquired these pygidial characters independently. *Encrinurus* was endemic to Laurentia, Baltica and Avalonia, the stratigraphically earliest species being from the Aeronian of Laurentia (*E. deomenos* Tripp, 1962 and *E. jini* Chatterton & Ludvigsen, 2004 from Anticosti Island; *E. confusevarus* and *E. stateratus*, both of Howells 1982, from south-western Scotland), and that is probably where the genus arose. Its ancestry was considered by Evitt & Tripp (1977, p. 120), Strusz (1980, text-fig. 9) and Ramsköld (1986, p. 531) to lie close to ‘*Encrinuroides*’ *uncatus* Evitt & Tripp and/or ‘*Encrinuroides*’ *neuter* Evitt & Tripp from the lower Katian of Virginia. Those species were regarded as sister taxa by Edgecombe *et al.* (1988, p. 794) and Edgecombe & Chatterton (1990, pp. 824, 825, fig. 1), and were assigned by Lespérance & Desbiens (1995) to their new genus-group taxon *Prophysemataspis*. *Wallacia* occurs in the Telychian and lower Sheinwoodian of Laurentia and Baltica, and presumably had its origins in a species of *En-*

crinurus; if so, recognition of *Wallacia* as a separate genus renders *Encrinurus* paraphyletic. A close relationship between *Arndellaspis* and *Encrinurus* may seem unlikely, based on palaeobiogeographical evidence, but if the two indeed share common ancestry, *Arndellaspis* may have originated in Laurentia and migrated to eastern Gondwana by dispersal of larvae across the Palaeo-Pacific Ocean (see Late Ordovician and early Silurian palaeogeographic reconstructions in Torsvik & Cocks 2017, figs 6.2b, 7.1a). Although *Arndellaspis* would have had protaspides of adult-like type, as do other encrinurids (Edgecombe *et al.* 1988, Chatterton & Speyer 1989), and these are presumed to have been benthic, it may have had a planktonic non-sclerotized pre-protaspis larval stage (life-history strategy type IIIa of Speyer & Chatterton 1990 and Chatterton & Speyer 1997). Dispersal of larvae across the Palaeo-Pacific Ocean would have been facilitated by westward-flowing equatorial currents, as depicted in the oceanic circulation maps of Wilde *et al.* (1991, text-fig. 4) and Servais *et al.* (2014, fig. 1, 430 Ma map).

Arndellaspis is not closely related to *Batocara* Strusz, 1980 to which most Silurian encrinurid species from Australia belong. *Batocara* is part of the ‘coronocephaline’ radiation (Strusz 1980, p. 48, text-fig. 12; Edgecombe & Ramsköld 1992, p. 261; Holloway 2000, p. 144) which attained its greatest diversity in the late Llandovery to Ludlow of China. Its origins are to be found amongst Chinese Ordovician species assigned to ‘*Encrinuroides*’, such as ‘*E.*’ *zhenxiogensis* Sheng, 1964, ‘*E.*’ *yanheensis* Yin, 1978 in Yin & Li (1978) (see also Zhou *et al.* 2016, pl. 20, figs 13–15, 17), ‘*E.*’ *minor* Ju, 1983 in Qiu *et al.* (1983) and ‘*E.*’ *qijiangensis* Xiang & Ji, 1988. Therefore, regardless of whether *Arndellaspis* was an immigrant to eastern Gondwana, it failed to establish a lineage there.

***Arndellaspis oryxis* sp. nov.**

Figures 8, 9

- 1974 *Encrinurus*. – Corbett & Banks, p. 226.
- 1976 *Encrinurus*. – Baillie & Clarke, p. 2.
- 1978 *Encrinuraspis* n. sp. – Baillie *et al.*, p. 46.
- 1979 *Encrinuraspis* sp. – Baillie, fig. 2.
- 1981 *Encrinuraspis* sp. – Sheehan & Baillie, p. 252, text-fig. 3.
- 1988 *Encrinuraspis* sp. – Banks, p. 191, tab. 1.
- 1988 *Encrinurus* sp. – Banks, tab. 1.
- 1991 ?*Encrinurus* sp. – Laurie, p. 26.
- 1992 *Cromus* n. sp. – Edgecombe & Chatterton, p. 67, tab. 2.

LSID. – urn:lsid:zoobank.org:act:0D0F263B-A6AF-404A-9460-835B666B5374

Holotype. – Cranium UTGD 126242 (Fig. 8A, E); Locality 3; Rhuddanian.

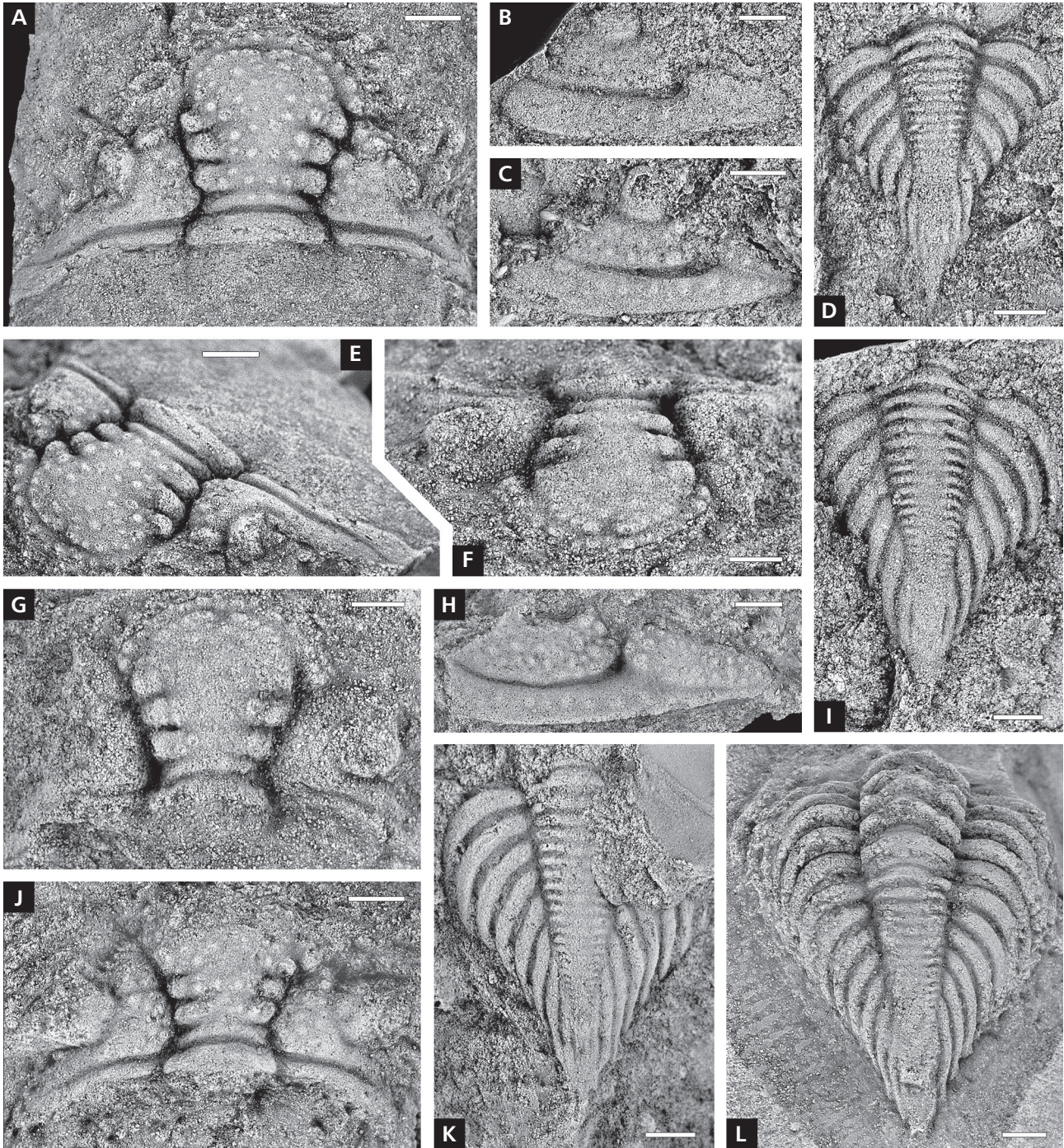


Figure 8. *Arndellaspis oryxis* gen. et sp. nov., upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. A, E – holotype, cranidium UTGD 126242, internal mould, dorsal and oblique views. B – librigena NMV P313705, latex cast of external mould, oblique view. C – librigena NMV P313708, latex cast of external mould, oblique view. D – pygidium UTGD 126224, latex cast of external mould, dorsal view. F, G – cranidium UTGD 126250, internal mould, anterodorsal and dorsal views. H – librigena UTGD 126241, internal mould, oblique view. I – pygidium NMV P313709, latex cast of external mould, dorsal view. J – cranidium UTGD 126249, internal mould, dorsal view. K – pygidium UTGD 126226, latex cast of external mould, dorsal view. L – incomplete, partly enrolled thoracopygon UTGD 126245, internal mould, dorsal view of pygidium. Scale bars represent 2 mm.

Paratypes. – Cranidia UTGD 126235, UTGD 126238, UTGD 126250, NMV P313704; librigenae 126237/126243 (counterparts), UTGD 126241, NMV P313705–P313708; thora-

copygon UTGD 126245; pygidia UTGD 126224, UTGD 126226, UTGD 126227B, UTGD 126229–126230, UTGD 126234, UTGD 126253, NMV P313709–P313713; Locality 3.

Etymology. – Greek, ‘a digging’, referring to the type locality adjacent to Westfield Quarry; noun in apposition.

Diagnosis. – As for genus.

Description. – Glabella of moderate convexity; width across frontal lobe about 1.5 times width at L1 and approximately equal to sagittal length excluding occipital ring; width across occipital ring approximately equal to width at L3. Occipital ring with weak node distally (Fig. 9A). L1 approximately half as long sagittally as occipital ring, convex (sag., exsag.), not tuberculate abaxially; S1 shallow but distinct medially; L2 approximately twice as long sagittally as L1; L3 as long (exsag.) as L2 abaxially but increasing to about 1.5 times this length adaxially, with tubercles arranged two deep on median part. Small, discrete tubercles present abaxially on L2–L4. Frontal lobe with sagittal length approximately equal to that of L2+L3, semicircular in outline. Anterior cranial border decreasing slightly in length (sag., exsag.) adaxially (Figs 8F; 9A). Palpebral lobe gently upturned, flap-like, situated less than its own length from posterior border furrow and with its anterior edge relatively far from glabella; palpebral furrow obliquely aligned, with shallow, pit-like lateral expansion at midlength (Fig. 8J, right side); a furrow directed anteromedially from front of palpebral lobe towards outer end of S3 defines posterior edge of eye ridge. Posterior border deflected backwards beyond fulcrum and expanding gently towards base of weakly curved genal spine of moderate length. Posterior branch of facial suture crosses border so close to base of genal spine that no part of lateral border furrow is present on fixigena (Fig. 9E). Tubercles on inner part of fixigenal field fade posterolaterally, lateral part of field behind posterior branch of suture apparently lacking tubercles.

Librigena with globose eye borne on high, gently convex socle; tubercles on librigenal field arranged roughly in 2–4 concentric rows, strongest anteriorly and fading posteriorly, dying out close to posterior branch of suture; small pits present between tubercles. Lateral border behind precranial lobe weakly convex (tr.), with a single row of weak tubercles on inner part; border furrow narrow, sharply impressed, increasing greatly in depth and slightly in width anteriorly. Precranial lobe almost as long as field, with numerous tubercles; furrow below precranial lobe shallow, not interrupted by tubercles anteriorly. Librigenal margin with broad, weak embayment towards front of precranial lobe (Figs 8H; 9D).

Only last five thoracic segments known; presence or absence of median axial spine on second last segment indeterminate due to breakage (Fig. 8L).

Pygidium about 75% to 90% as wide as long, apparently longer in large ones though many specimens are incomplete posteriorly; maximum width situated at

about 33–40% sagittal length from anterior and more or less opposite sixth to eighth axial ring. Axis 30% to almost 40% maximum pygidial width anteriorly, gently convex (tr.); up to 23 axial rings distinguishable, but axis is seen to extend farther posteriorly as converging line of apodemal pits not resolvable into inter-ring furrows (Fig. 9H); first ring standing higher than remainder and longer (exsag.) than them abaxially, decreasing in length adaxially and gently arched forwards; inter-ring furrows successively weaker medially but distinguishable across axis for most of its length; weak sagittal tubercles present on rings 4 or 5, 8 and possibly 13 (Figs 8I, L; 9C, I). First pleural rib extends backwards to at least 60% length of axis; postaxial ridge may carry a weak sagittal furrow in some specimens, and possibly represents an undivided ninth pleural rib (Fig. 9C); no trace of tubercles on pleural ribs. More anterior inter-rib furrows rather wide, at fulcrum almost half width of preceding rib, posterior few inter-rib furrows narrower.

Remarks. – In pygidia having the mucro preserved to some extent it appears to be rather variable in size. In some specimens it is of moderate width and length (Fig. 8D, I) whereas in others it appears to be more slender and possibly shorter (Figs 8L; 9I). In one pygidium it is very slender and, although incomplete distally, is apparently very short (Fig. 8K); in this specimen the narrowness of the mucro is due to the eighth pleural rib being strongly deflected adaxially towards its distal end.

The report by Edgecombe & Chatterton (1992, tab. 2) of *Cromus* n. sp. from the early Llandovery of Tasmania was based on the reference by Baillie *et al.* (1978, p. 46) to ‘a new species of *Encrinuraspis*’ from the Arndell Sandstone, the latter genus generally being regarded as a junior synonym of *Cromus*. Edgecombe & Chatterton’s report thus refers to *Arndellaspis oryxis* and not to the taxon represented by the pygidium documented below.

Genus *Cromus* Barrande, 1852

Type species. – *Trilobites intercostatus* Barrande, 1846, from the Kopanina Formation (Ludlow) of Lochkov, Bohemia, by subsequent designation of Vogdes (1890, p. 85).

Cromus? sp.

Figure 9F

2000 *Cromus*. – Holloway, p. 163.

Material. – Pygidium NMV P313716 from Locality 3; Rhuddanian.

Remarks. – This small (about 5 mm long), rather poorly preserved encrinurid pygidium is easily distinguished

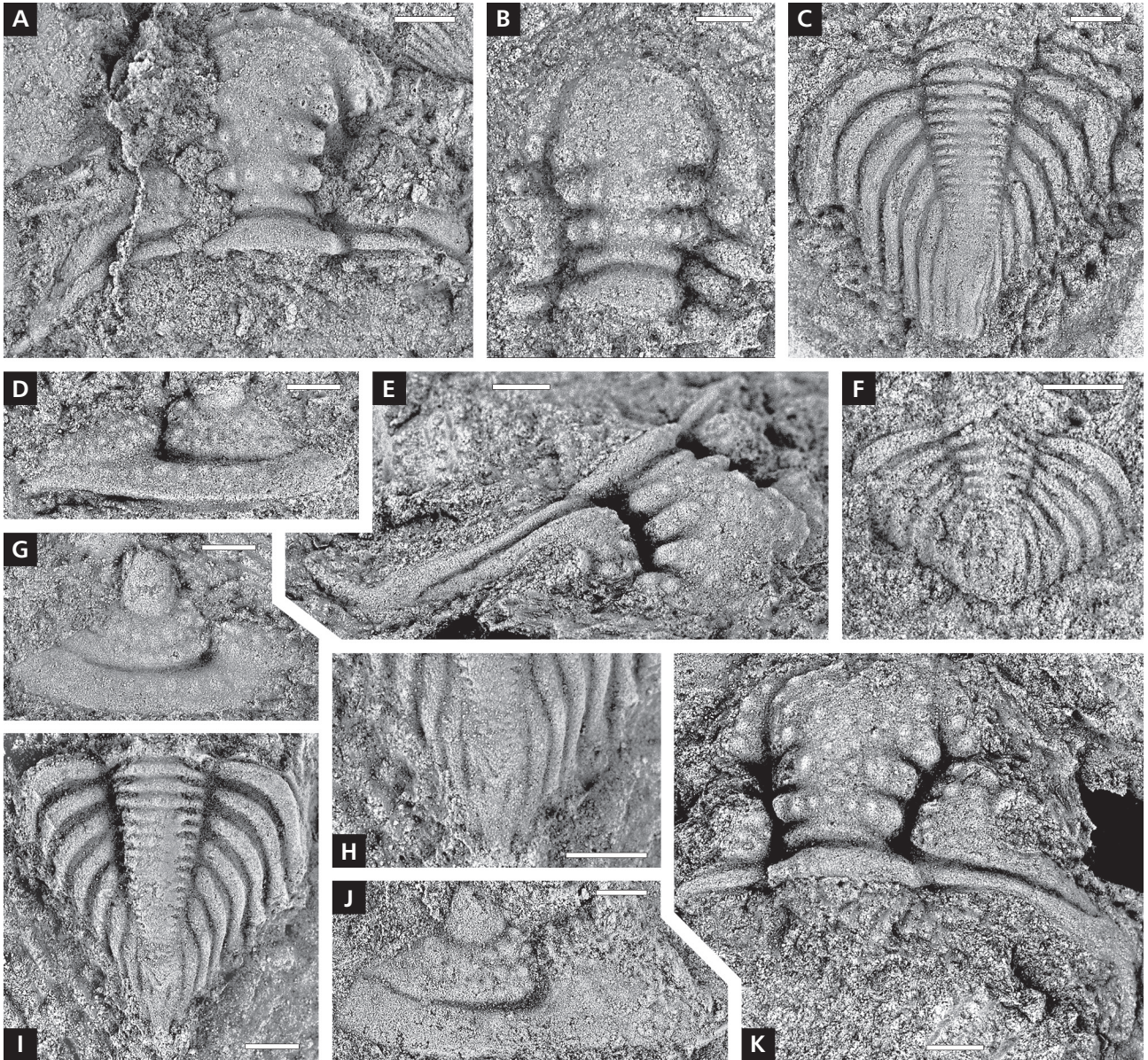


Figure 9. Encrinurid trilobites from the upper Arndell Sandstone (Rhuddanian), Florentine Valley, southern Tasmania; all from Locality 3, Westfield Quarry. • A–E, G–K – *Arndellaspis oryxis* gen. et sp. nov. A – cranium UTGD 126238, latex cast of external mould, dorsal view. B – cranium UTGD 126222B, internal mould, dorsal view. C – pygidium UTGD 126230, internal mould, dorsal view. D – librigena NMV P313707, internal mould, oblique view. E, K – cranium NMV P313704, internal mould, oblique and dorsal views. G – librigena NMV P313706, internal mould, oblique view. H, I – pygidium UTGD 126227B, internal mould, detail of posterior end, and whole specimen, dorsal view. J – librigena UTGD 126243, latex cast of external mould, oblique view. • F – *Cromus?* sp., pygidium NMV P313716, latex cast of external mould, dorsal view. Scale bars represent 2 mm.

from that of *Arndellaspis oryxis* from the same locality. It is about 140% as wide as long, non-mucronate, with the axis comprising a little more than 33% of the maximum pygidial width, and with the pleural region having at least eight ribs (a very small ninth rib may be present). The rings are not preserved in the posterior portion of the axis, so the full number is indeterminate, but the ratio of rings to pleural ribs is much lower than in *A. oryxis*. The specimen shows similarities to that of *Cromus optimus* (Webby *et al.*, 1970) from near the base

of the Malongulli Formation (late Eastonian, Ea3, early Katian) of New South Wales, and may be congeneric. It is also similar to the pygidium from early Eastonian strata of the Gordon Group of Tasmania illustrated by Edgecombe *et al.* (1999, fig. 7f) as encrinurid gen. indet. though it is not clear whether median axial tubercles are present as in that specimen. Edgecombe *et al.* considered that the affinities of their specimen lay with forms previously assigned to the paraphyletic ‘*Encrinuroides?*’.

Family Calymenidae Milne Edwards, 1840
Subfamily Calymeninae Milne Edwards, 1840

Remarks. – Following Holloway *et al.* (2020), the subfamily Flexicalymeninae Siveter, 1977 is not utilised here.

Genus *Gravicalymene* Shirley, 1936

Type species. – *Gravicalymene convolva* Shirley, 1936 from the Birdshill Limestone (Katian), Birdshill Quarry near Llandeilo, South Wales, by original designation. The statement by Morris (1988, p. 100) that the type horizon and locality are the Crûg Limestone about 2.5 km east of Birdshill Quarry is apparently incorrect. Although Shirley (1936) gave descriptions of the cranidium and pygidium of *G. convolva* he illustrated only the holotype cranidium, preserved as internal and external moulds. A latex cast of the external mould of the holotype and a topotype cranidium and pygidium were illustrated by Owens *et al.* (2001, pl. 2, figs 5–9).

Other species and occurrences. – (With original generic assignment.) *Calymene abbreviata* Foerste, 1910 (= *Gravicalymene truncata* Ross, 1979; see Brandt & Davis 2007, p. 44), upper Lexington Limestone and Kope Formation (Katian), Kentucky; *Gravicalymene asperula* Vaněk, 1965, Králův Dvůr Formation (late Katian), Czechia, revised by Shaw (2000, p. 381, pl. 4, figs 3–8); *G. capitovata* Siveter, 1977, Heggen Member, Elnes Formation (late Darriwilian), Norway, refigured by Hansen (2009, pl. 26, figs 5–8); *G. clarkei* sp. nov., upper part of Arndell Sandstone (Rhuddanian), Tasmania; *G. deani* Ingham, 1977, Cautleyan age strata of the Cautley Mudstone Formation (late Katian), northern England; *Calymene* [*sic*] *granulosa* Foerste, 1909, Kope Formation (Katian), Ohio and Kentucky, figured by Hughes & Cooper (1999, figs 1.1–1.19, 2.1–2.13) as *Flexicalymene* aff. *granulosa*; *G. hagani* Ross, 1967, Perryville Member, Lexington Limestone (early Katian), Kentucky, additional specimens illustrated by Ross (1979, pl. 2, figs 18, 19, pl. 3, figs 1–9); *G. inflata* Dean, 1963, Onnian Stage (middle Katian), Shropshire, England; *G. jugifera* Dean, 1962, Pusgillian strata of the Dufton Shale Formation (middle Katian), northern England, revised by Ingham (1977, p. 94, pl. 20, figs 6–15); *Calymene magnotuberculata* Ruedemann, 1926, Trenton Group (Katian), New York, illustrated by Whiteley *et al.* (2002, pls 71, 72) (= ? *Gravicalymene* sp. of Ross 1967, pl. 3, figs 18–23; unnamed species in pl. 4, figs 7–10 of same author possibly not conspecific); *Gravicalymene pontilis* Price, 1982, Rawtheyan Stage (late Katian), Wales; *Diacalymene praecox* Bancroft, 1949, Smeathen Wood Formation (middle Sandbian), Shropshire, England, revised by Dean (1963, p. 225, pl. 39, figs 1, 3, 9, 12–14); *Gravicalymene* cf. *praecox* of Dean

(1963, pl. 39, figs 4, 5, 7, 8) and Owen & Ingham (1996, pl. 29, figs 4, 5), Wistanstow Member, Acton Scott Formation (middle Katian), Shropshire, England; *Flexicalymene praelongicephala* Stumm & Kauffman, 1958, Bills Creek Formation equivalent (late Katian), Michigan; *Flexicalymene quadricapita* Stumm & Kauffman, 1958, Bills Creek Formation (late Katian), Michigan, holotype refigured by Ross (1967, pl. 2, fig. 23); *Gravicalymene* aff. *G. quadricapita* of Ross (1967, pl. 4, figs 14, 15), lower Maquoketa Group (late Katian), Iowa; *G. susi* McNamara, 1979, Applethwaite Member, Kirkley Bank Formation (late Katian), northern England; *Flexicalymene* sp. of Ross (1979, pl. 3, fig. 10), Gilbert Member, Ashlock Formation (middle Katian), Kentucky; *Gravicalymene* spp. 2–4 of Ross (1967, pl. 2, figs 19, 20, 24–27, pl. 3, figs 14–17), Grier Limestone Member, Lexington Limestone, and Clays Ferry Formation (both Katian), Kentucky; *Gravicalymene* sp. of Holloway & Sandford (1993, fig. 4q), Richea Siltstone (middle Telychian), Tasmania.

Diagnosis. – Glabella markedly bell-shaped due to strongly abaxially protruding L1; width across L1 generally about 1.4 times width across L2; preglabellar furrow deep and trench-like with abrupt anterior slope, meeting anterior border furrow laterally at a marked change in direction; anterior border relatively long, about as long sagittally as occipital ring or slightly longer, its upper surface flattened or weakly convex and rising forwards or roughly horizontal; posterior edge of anterior border with slight swellings laterally in front of intersection of preglabellar and anterior border furrows.

Remarks. – A large number of species from upper Darriwilian to Emsian strata have been assigned to *Gravicalymene*, a very long stratigraphic range that has led to concerns about the taxonomic coherence of this grouping (e.g. see Whittington 1971, pp. 472, 473). Some of the Silurian and Devonian species were included by Chatterton & Campbell (1980) in their new genus *Apocalymene*, with type species *A. coppinsensis* from the Wenlock of the Canberra district of south-eastern Australia. Subsequently, there has been considerable debate on the discrimination between *Gravicalymene*, *Apocalymene* and *Sthenarocalymene* Siveter, 1977 (type species *S. lirella* from the upper Darriwilian–lower Sandbian of the Oslo Region, Norway; see also Hansen 2009, p. 140, pl. 26, figs 9–12), and on the viability of the latter two genera which have been regarded variously as synonyms or possible synonyms of *Gravicalymene* and/or of each other; for discussion of the various views see Smith & Ebach (2020, pp. 498, 499).

When proposing that *Apocalymene* is a junior synonym of *Sthenarocalymene*, Holloway (1980) expressed unease because of the large stratigraphic gap between the re-

spective type species, and the apparent widespread homoeomorphy amongst calymenids. *Apocalymene* was regarded as a synonym of *Gravicalymene* rather than of *Sthenarocalymene* by Smith & Ebach (2020), who restricted *Sthenarocalymene* to the type species and *S. aldonensis* (Reed, 1935) from the basal Superstes Mudstone Formation (earliest Sandbian) of south-western Scotland. Illustrated cranidia of these two species are mostly very small, those of *S. lirella* ranging in length from 3.5 mm to 5.7 mm (Siveter 1977, p. 388), and those of *S. aldonensis* figured by Tripp (1976, pl. 7, figs 8, 9) being about 4–5 mm long; the lectotype cranidium of *S. aldonensis* is larger, almost 10 mm long (Reed 1935, pl. 1, fig. 14). Both species require revision on the basis of more mature specimens.

We here restrict *Gravicalymene* to those species listed above, with a stratigraphic range of upper Darriwilian to middle Telychian. These species share the characters traditionally regarded as distinguishing the genus – the strongly bell-shaped glabella, and the anterior border with flattened or gently convex upper surface that rises forwards or is subhorizontal – as well as the trench-like preglabellar furrow and the slight swellings on the posterior edge of the anterior border in front of where the preglabellar and anterior border furrows meet in a distinct change of direction (e.g. see *G. hagani*, Ross 1967, pl. 3, fig 1; *G. cf. praecox* of Owen & Ingham 1996, pl. 29, fig. 4). Ross (1967, p. 9) stated that the break between the anterior margin of the trench-like preglabellar furrow and the upper surface of the anterior border is a remarkably consistent feature of *Gravicalymene*. Although doubts have been raised by some workers (e.g. Price 1982, p. 58) about the taxonomic usefulness of the anterior border at the generic level, we consider that in combination with other characters it is of value in recognising closely related groups of species. The significance of the anterior border in the discrimination of *Diacalymene* Kegel, 1928 was discussed by Holloway (1980, p. 55), Edgecombe & Adrain (1995, p. 10) and Siveter & Chatterton (1996, p. 46), and Dean (1962, p. 114) noted similarities with *Gravicalymene* in this feature; however, *Gravicalymene* is easily distinguished from *Diacalymene* by the lack of genal buttresses. The appearance of the anterior border and the shape of the glabella in calymenids is strongly affected by tectonic deformation. This is especially so for specimens that are compressed longitudinally, in which the anterior border may appear shorter and more strongly upturned than is actually the case, and the glabella may appear more bell shaped; for example, see ‘*Gravicalymene?*’ *vaccina* Holloway (1994, fig. 9a–c, e, f, h, t, u), which we here assign to *Apocalymene* (see below). Also, in specimens preserved as internal moulds the preglabellar area generally differs significantly in appearance from its form on the external surface, the preglabellar furrow appearing

longer (sag., exsag.) and the anterior border shorter on internal moulds (e.g. compare Ingham 1977, pl. 20, figs 16, 17). Both these factors should be taken into account when assessing these characters.

The diagnosis for *Gravicalymene* provided by Smith & Ebach (2020) is broader in scope than ours, as they assigned to the genus many species that we exclude from it, including their species *G. bakeri* from the Eastonian (Ea3, Katian) of northern Tasmania. Also, their diagnosis includes characters that we consider of significance only at the species level (e.g. width of the cranidium across β – β , axial furrow fading around terminal piece of pygidial axis) or present in many calymenids (e.g. S2 transverse to posteromedially directed, posterior border furrow widening abaxially, thorax with 12 or 13 segments, pygidium lenticular in dorsal view and with faint to distinct pleural ribs).

Most of the species originally included in *Gravicalymene* but here excluded from the genus can be assigned to *Apocalymene*. These species, some of which were listed as belonging to *Apocalymene* by Chatterton *et al.* (1979) and Chatterton & Campbell (1980), include: *Calymene* (*Gravicalymene*) *cootamundrensis* Gill, 1940; *Gravicalymene bakeri* Smith & Ebach, 2020; *G. eunoa* Haas, 1968; *G. hamlagdadica* Alberti, 1981; *G. hornyi* Šnajdr, 1981 (illustrated by Šnajdr 1982, pl. 2, figs 2–4); *G. kilmorensis* Gill, 1945 (= *G. hetera* Gill, 1945; see Holloway & Neil 1982, p. 143; Sandford 2000); *G. longmenshanensis* Li, 1978; *G. maura* Alberti, 1969; *G. pola* Šnajdr, 1982; *G. quadrilobata* Chatterton, 1971; *G. teddersensis* Alberti, 1969; *G.?* *vaccina* Holloway, 1994; and *G. yamakoshii* Kobayashi & Hamada, 1977. ‘*Calymene*’ *australis* Etheridge & Mitchell, 1917 was included in *Gravicalymene* by Chatterton (1971, pp. 84, 85) but is not assigned to a genus here pending its revision, as Chatterton noted that the type specimens belong to two different genera. *Apocalymene* is distinguished from *Gravicalymene* by the following characters: the glabella is not markedly bell-shaped but is trapeziform, narrowing forwards from the widest part of L1 at a more or less uniform rate; the width of the glabella across L1 is about 1.2 times that across L2 rather than about 1.4 times; and the anterior border is shorter, evenly rounded in sagittal profile, and lacks slight swellings on its posterior edge in front of the intersection of the preglabellar and anterior border furrows, those furrows being more or less aligned instead of meeting in a distinct change of direction.

Two other species previously assigned to *Gravicalymene* are here excluded from the genus, namely ‘*Calymene*’ *quadrata* King, 1923 and ‘*Gravicalymene*’ *arcuata* Price, 1982, both from the upper Katian of North Wales. Opinions on the relationships of ‘*C.*’ *quadrata* have varied. It was referred to *Flexicalymene* with question by Price (1974, p. 856) and to *Sthenarocalymene* by Siveter

(1977). Price (1982) assigned it to *Gravicalymene* and regarded it and ‘*G.* *arcuata* as closely related to his new species *G. pontilis*, partly because of the similarity of all three in age and provenance, and in their having 12 thoracic segments instead of the 13 usual for calymenids. However, the presence of 12 thoracic segments may not be evidence for the close relationship of these three species. *Alcymene puellaris* (Reed, 1920) has 12 thoracic segments whereas other species of that genus have 13 (Siveter 1983; Ramsköld *et al.* 1994); and Siveter (1973) recorded 12 segments in *Calymene frontosa* Lindström, 1885 from the uppermost Llandoverly of Gotland but 13 segments in a related form from the same horizon and localities, and Clarkson & Howells (1981) reported 13 segments in specimens they assigned to *C. frontosa* from Scotland. This evidence suggests that, though the presence of 12 segments is rare amongst calymenines, this character did appear occasionally in unrelated stocks. Although ‘*G.* *quadrata* and ‘*G.* *arcuata* have bell-shaped glabellae, more marked in the former than in the latter, in both species the anterior border is very short, abruptly upturned and strongly rounded (sag.), the preglabellar and anterior border furrows do not meet at a distinct change in direction but are more or less aligned, and consequently the posterior edge of the anterior border lacks slight swellings in front of the intersection of these furrows. We tentatively assign these species to *Sthenarocalymene*, pending revision of that genus.

The single poorly preserved calymenid pygidium from the Lochkovian of south-eastern Turkey documented by Crônier & Hoşgör (2022, fig. 3a–d) as *Gravicalymene?* sp. indet. cannot be assigned to a genus without knowledge of the cephalon or cranidium of the species.

***Gravicalymene clarkei* sp. nov.**

Figure 10A–I

- 1978 *Gravicalymene* sp. – Baillie *et al.*, p. 46.
- 1979 *Gravicalymene* sp. – Baillie, fig. 2.
- 1981 *Gravicalymene* sp. – Sheehan & Baillie, p. 252, text-fig. 3.
- 1988 *Gravicalymene* sp. – Banks, p. 193, tab. 1.
- 2000 *Gravicalymene*. – Holloway, p. 163.

LSID. – urn:lsid:zoobank.org:act:53AB3DE3-94C7-44AD-AB7D-E272A7653768

Holotype. – Cranidium UTGD 126273 (Fig. 10B, C, F); Locality 3; Rhuddanian.

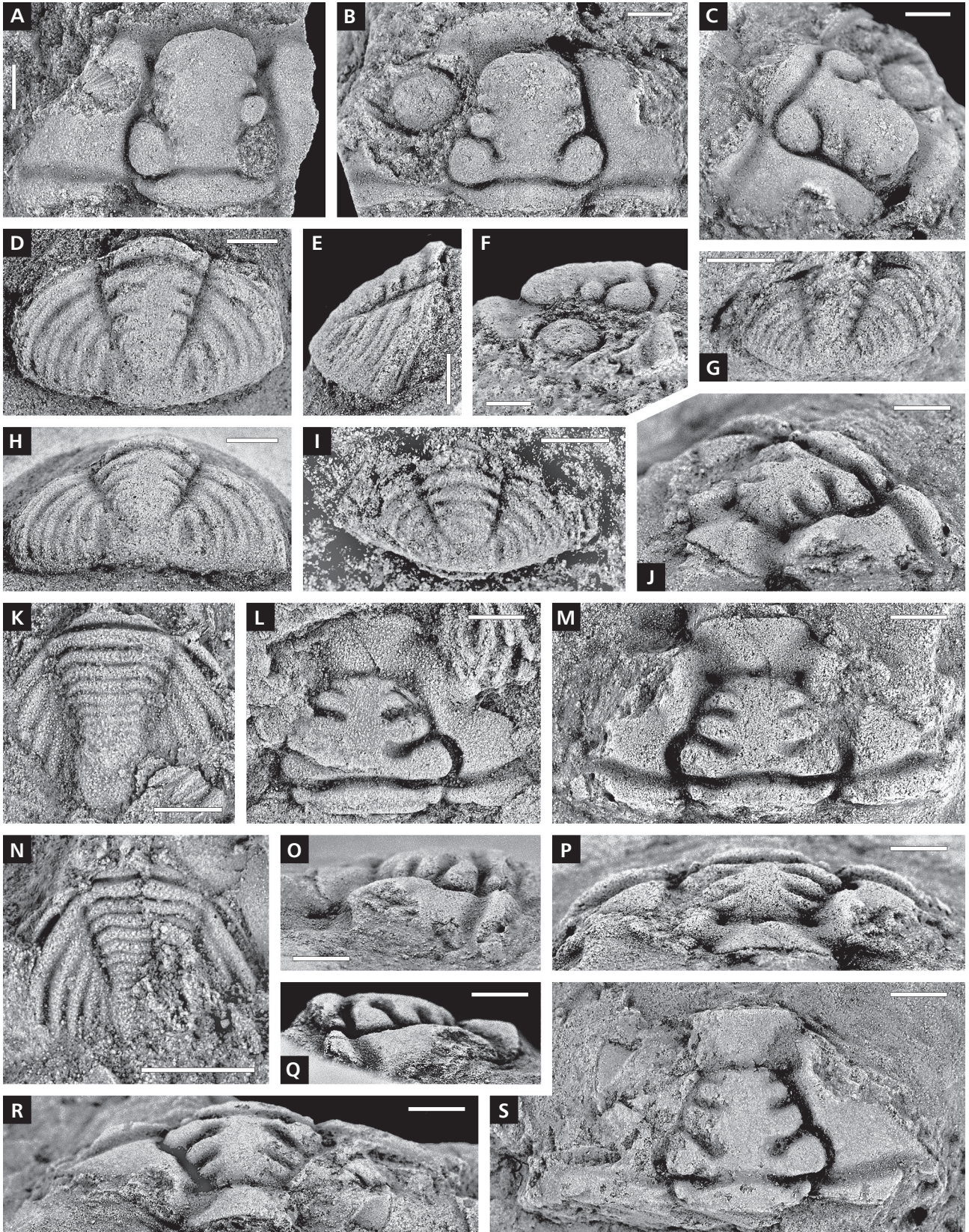
Paratypes. – Cranidium NMV P313702; pygidia UTGD 126269, UTGD 126270 (with several incomplete articulated thoracic segments), UTGD 126272; Locality 3.

Etymology. – After Michael J. Clarke, formerly of the Tasmanian Department of Mines.

Diagnosis. – Glabella comprising a little more than 33% cranial width posteriorly; anterior border furrow relatively shallow on fixigena; upper surface of anterior border gently convex (sag., exsag.) and more or less horizontal overall; pygidial axis with 5 rings and terminal piece, comprising about 40% maximum pygidial width anteriorly, narrowing strongly backwards, width across fifth ring about 60% that across first; axial furrow weak behind axis; fifth pleural furrow expanded in width.

Description. – Glabella bell-shaped, width across L1 slightly less than sagittal length and *ca* 1.6 times width across frontal lobe, anterior margin broadly rounded in outline and lying transversely opposite front of fixigenal field or projecting slightly farther forwards. Occipital ring gently convex (sag., exsag.), decreasing in length abaxially behind L1 and curving forwards distally; occipital furrow transverse medially, deflected backwards behind L1 and increasing in depth. L1 ovate, narrower than adjacent median part of glabella, anterior edge opposite glabellar midlength; S1 very deep where it curves around anteromedial edge of L1, abruptly shallowing opposite widest part of L1 but extending backwards weakly to occipital furrow. L2 subcircular, half as long (exsag.) and wide as L1; S2 subparallel to outer part of S1 but shallower, meeting axial furrow opposite one-third sagittal length of glabella, connected posteriorly with shallow furrow extending forwards from S1 around posteromedial edge of L2. L3 smaller than L2, not isolated from median part of glabella; S3 shallow, notching side of glabella. S4 very small and weak on paratype (Fig. 10A), not evident on holotype. Axial furrow wider in front of S1 than behind, containing shallow anterior pit opposite S4; preglabellar furrow with posterior slope slightly recessed beneath front of glabella. Anterior border not upturned, with faint swelling in front of intersection of preglabellar and anterior border furrows. Fixigenal field convex (exsag., tr.), about three times as wide posteriorly as anteriorly; palpebral lobe gently upturned, anterior edge situated opposite S3 and posterior edge opposite back of L2. Anterior branch of facial suture converging gently in front of palpebral lobe,

Figure 10. Calymenid trilobites from the Arndell Sandstone, Florentine Valley, southern Tasmania. • A–I – *Gravicalymene clarkei* sp. nov., from Locality 3, Westfield Quarry (Rhuddanian). A – cranidium NMV P313702, internal mould, dorsal view. B, C, F – holotype, cranidium UTGD 126273, internal mould, dorsal, oblique and lateral views. D, E, H – pygidium UTGD 126269, internal mould, dorsal, lateral and posterior views. G – small pygidium with a few fragmentary thoracic segments UTGD 126270, internal mould, dorsal view. I – pygidium, UTGD 126272, internal mould, dorsal view. • J–S – *Vietnamia hyron* sp. nov., from Locality 1, Westfield Road (late Katian). J, L, M, O, P – holotype, cranidium UTGD 81374/81378



(counterparts); J, M, O, P – UTGD 81374, internal mould, oblique, dorsal, lateral and anterior views; L – UTGD 81378, latex cast of external mould, dorsal view. K – pygidium UTGD 81385A, latex cast of external mould, dorsal view. N – pygidium UTGD 81385B, latex cast of external mould, dorsal view. Q–S – cranium UTGD 81381, internal mould, lateral, anterior and dorsal views. Scale bars represent 2mm.

curving more strongly inwards across anterior border; posterior branch directed laterally from posterior edge of palpebral lobe, deflected obliquely backwards abaxially and curving more strongly backwards across distal part of posterior border. Posterior border expanding gently from axial furrow to fulcrum, more strongly abaxial to fulcrum; posterior border furrow expanding abaxially to a point beyond fulcrum, thereafter contracting and dying out very close to posterior branch of suture.

Pygidium lenticular in plan view, *ca* 1.5 times as wide as long, maximum width level with posterior end of axis; posterior margin curving upwards adaxially in subangular median arch. Axis with first three inter-ring furrows containing apodemal pits distally, fifth inter-ring furrow very weak; postaxial region poorly differentiated from axial terminus in lateral profile. Pleural region with very narrow (tr.) horizontal portion adaxial to fulcrum, steeply downturned abaxial to fulcrum, lacking vincular furrow on outer portion. Pleural and interpleural furrows curving evenly backwards abaxially; pleural furrows wider and deeper than interpleural, expanded fifth pleural furrow incorporates posterior pleural band of same segment; anterior pleural band of sixth segment more or less exsagittally aligned; interpleural furrows slightly deeper abaxially than adaxially.

Remarks. – The slight swelling on the posterior edge of the anterior border at the junction of the preglabellar and anterior border furrows is not as obvious in *G. clarkei* as in other species of the genus. We attribute this to the somewhat shallower preglabellar and anterior border furrows, and the fact that the only specimens available are internal moulds. The pygidium of *G. clarkei* is also distinctive amongst most species of the genus in having the axial furrow fading behind the axis and the fifth pleural furrow apparently expanded in width beyond its proximal end. The second feature, which results from the merging of the last pleural furrow (usually the fifth but in rare cases the sixth) with the depressed posterior pleural band on the same segment, is widely developed in calymenines (see discussion in Holloway 1980, pp. 57, 59), and is present in at least some species of *Calymene*, *Diacalymene*, *Flexicalymene*, *Apocalymene* and *Alcymene*. The feature is clearly not of significance taxonomically at the generic level, and its function is uncertain; although it is commonly associated with the development of a strongly protuberant postaxial region that on enrolment fitted into the concave doublure sector of the rostral plate, this is not always the case (*e.g.* Edgecombe & Adrain 1995, pl. 4, figs 5, 6, 8), so the two structures do not appear to be related functionally. In most species of *Gravicalymene* for which the pygidium is known the axial furrow is distinctly impressed behind the axis, and the fifth or sixth pleural furrow is either not expanded in width (*e.g.* *G. capitovata*, see Siveter

1977, fig. 12a, f, i; *G. hagani*, see Dean 1967, pl. 3, figs 7, 12; *G. quadricapita*, see Stumm & Kauffman 1958, pl. 124, figs 2, 3, 16) or its expansion is variably developed, with the posterior band on the same segment still being distinguishable (*e.g.* *G. granulosa*, see Hughes & Cooper 1999, figs 1, 2; *G. magnotuberculata*, see Whiteley *et al.* 2002, pl. 71). Species of *Gravicalymene* in which the fifth pygidial furrow is expanded in width include *G. asperula* (see Vaněk 1965, pl. 1, figs 1, 2; Shaw 2000, pl. 4, figs 3–8), *G. jugifera* (see Ingham 1977, pl. 20, figs 6–15) and *G. susi* (see McNamara 1979, pl. 10, figs 1–13). These species are distinguished from *C. clarkei* in having deeper preglabellar and anterior border furrows and a more upturned anterior border; in addition, the glabella of *G. asperula* is not as strongly bell shaped, the axial furrow is distinctly impressed behind the pygidial axis in *G. jugifera*, and the glabella of *G. susi* has a smaller L2.

Gravicalymene sp. of Holloway & Sandford (1993, fig. 4q), from a stratigraphically higher level in the Florentine Valley sequence than the Arndell Sandstone, differs from *G. clarkei* in that the glabella is more elongated and projects forwards well in front of the fixigenal field; the anterior border is flattened and slopes upwards; the preglabellar furrow meets the anterior border furrow at a very marked change in direction; and the posterior edge of the palpebral lobe is situated slightly farther back.

Subfamily Colpocoryphinae Hupé, 1955

Genus *Salterocoryphe* Hammann, 1977

Type species. – *Calymene salteri* Rouault, 1851 from the Schistes d'Angers (Llandeilo, late Darriwilian) of Brittany, by original designation.

Diagnosis. – See Hammann (1977, p. 94).

Remarks. – *Salterocoryphe salteri*, of which *S. lusitanica* (Thadeu, 1949) is a synonym (see Romano 1991, pp. 343, 355), has been reported in France and the Iberian Peninsula from the Llanvirn as well as the Llandeilo, in the historical sense of those 'series', equivalent to the Oretanian and lower Dobrotivian stages of the Iberian–Bohemian regional chronostratigraphic scale (Gutiérrez-Marco *et al.* 2017); however, Sofia Pereira (pers. comm.) has advised us that the species is restricted to the Dobrotivian. The only other named species is *S. sampelayoi* Hammann, 1977, recorded by Hammann (1983) from the *Didymograptus murchisoni* Biozone in Spain (upper Oretanian in the regional scale), but *S. cf. sampelayoi* was illustrated by Sá *et al.* (2006, pp. 120–125) and Gutiérrez-Marco *et al.* (2009, fig. 4d) from the lower Oretanian of northern Portugal. *Salterocoryphe* thus occurs in the middle and upper Darriwilian in Europe where it is considerably older

stratigraphically than *Salterocoryphe? bailliei* sp. nov. in the upper Katian of Tasmania. Waisfeld & Vaccari (2003, p. 311, pl. 15, fig. 14) reported an unnamed species of *Salterocoryphe* from the upper Floian of Argentina, based on a single, rather deformed cranidium, but it may belong to a calymenine.

***Salterocoryphe? bailliei* sp. nov.**

Figure 11

1976 *Flexicalymene*. – Baillie & Clarke, p. 2.

1988 *Flexicalymene*. – Banks, tab. 1.

LSID. – urn:lsid:zoobank.org:act:10761242-D6C6-47F9-87CD-27B25CB079FB

Holotype. – Cephalon UTGD 126277/126278 (counterparts) (Fig. 11A, B, E–H); Locality 4; late Katian.

Paratypes. – Cephalon with incomplete thorax UTGD 81417A, B; Locality 2. Incomplete cephalon UTGD 126264C; small cephalo UTGD 126264B, UTGD 126275/126276 (counterparts); Locality 4.

Etymology. – After Peter W. Baillie, formerly of the Tasmanian Department of Mines.

Diagnosis. – Cephalon moderately vaulted transversely, genal field not overhanging lateral border in dorsal view; glabella markedly narrower across L2 than across L1, thereafter narrowing rather weakly forwards; S1 not curving backwards adaxially or extending close to occipital furrow, L1 wider than adjacent median part of glabella; anterior border longer (sag.) than occipital ring, gently upturned, flattened posterodorsally; eye situated opposite L2, at summit of strongly swollen region of gena extending from opposite front of L1 to anterior and lateral border furrows; broad paraglabellar area present on interior of fixigena; lateral border furrow broad and shallow on large cephalo, deeper on smaller ones, weakening posteriorly on both.

Description. – Cephalon subtrapezoidal to semielliptical in dorsal outline; maximum width approximately 170% sagittal length, situated a little farther forward than outer end of posterior border furrow. Glabella comprising about 80% sagittal cephalic length and about 45% maximum cephalic width posteriorly, a little longer than wide, slightly narrower across L1 than across occipital ring, gently concave in lateral outline in front of S1, anterior outline transverse or very weakly indented medially, width across frontal lobe about 55% width at L1. Occipital furrow firmly impressed, median third gently convex forwards and slightly expanded (sag., exsag.), lateral third deeper and occupied by apodemal pit (Fig. 11K). L1 gently

inflated, subtriangular to ovate, as wide as long, wider than adjacent median part of glabella; S1 deep, directed obliquely backwards from axial furrow opposite glabellar midlength (sag.) at roughly 55–65° to an exsagittal line, not extending to occipital furrow. S2 meeting axial furrow equidistant from S1 and S3, shorter (tr.) and shallower than S1 and directed slightly less strongly backwards. S3 shorter (tr.) than S2, weak, almost transverse. Axial furrow shallowest adjacent to occipital ring, containing small anterior pit adjacent to frontal lobe (Fig. 11K, Q); preglabellar furrow well defined. Anterior border about 150% as long (sag.) as occipital ring, sharply bent downwards along anterior margin (Fig. 11A, N), strongly arched medially in anterior profile (Fig. 11B, C). Inflated area of genal field exceeding height of adjacent part of glabella; posterior fixigena behind inflated region only slightly longer (exsag.) than posterior border, with large paraglabellar area on interior of exoskeleton, extending abaxially about 30% genal width in dorsal view (Fig. 11G). Eye rather small, apparently lacking socle (Fig. 11A, L), palpebral lobe strongly curved in outline (Fig. 11L); anterior branch of facial suture converging progressively more strongly forwards in a curve, crossing anterior border at about 45° to sagittal line, meeting rostral suture on outer edge of border; transverse curvature of rostral suture accords with arch of border (Fig. 11C); posterior branch of facial suture runs from back of eye across posterior slope of inflated genal region (Fig. 11L), curving forwards slightly until just beyond inflated region, thereafter curving backwards to cross lateral margin a little farther forward than outer end of posterior border furrow (Fig. 11E, G, left side). Lateral border narrow at midlength, expanding anteriorly and posteriorly, weakly convex dorsally but with well-rounded (tr.) outer edge; lateral border furrow broad and shallow on librigena of larger cephalo. Posterior border rounded (exsag.), crest horizontal between axial furrow and fulcrum, where it stands higher than genal field just in front, strongly downturned beyond fulcrum; posterior border furrow deeper and more sharply impressed than lateral border furrow. Genal angle rounded.

Hypostome elongated, anterior margin gently convex in outline and flexed ventrally, anterior border furrow very long (sag., exsag.) and poorly defined; posterior margin with a pair of broad, flattened spines separated by a rounded notch; shoulder rounded in outline, lying opposite posterior lobe of middle body. Middle furrow continuous across middle body, meeting lateral border furrow more or less opposite hypostomal midlength (sag.), strongly oblique laterally, transverse medially. Anterior lobe of middle body elliptical, gently inflated; posterior lobe crescentic, inflated anterolaterally.

Only first four thoracic segments known; axis strongly convex, rings well rounded (sag., exsag.); pleurae about 66% as wide as axis in dorsal view, strongly downturned

beyond fulcrum; axial and pleural furrows deep, pleural furrows more sharply impressed than axial furrow.

Remarks. – The cephalon range in length from about 3.5 mm to about 10.5 mm. The preceding description of the cephalon is based mainly on the three largest specimens, which include the holotype. Smaller cephalon (Fig. 11I, J, N–P) differ from the larger ones in being relatively wider, with the maximum width situated more posteriorly, opposite the end of the posterior border furrow; the glabella is less elongated, does not narrow as strongly forwards, especially from L1 to L2, is not as concave in lateral outline in front of L1, and is more rounded in outline anteriorly; L1 is shorter (exsag.) and S1 is not directed as strongly backwards; the cheek slopes more steeply forwards in front of the eye; the anterior border is not as strongly arched transversely; and the lateral border furrow is deeper. Some of these differences may be due to deformation rather than to changes during ontogeny.

In features such as the glabella that narrows strongly forwards and, at least in larger cephalon, tends to be concave in outline in front of L1, the upturned and posterodorsally flattened anterior cephalic border, and the eyes elevated on swellings of the genal field, *Salterocoryphe? bailliei* resembles European species of the genus (see Hammann 1977, pl. 1, figs 4–8; Henry 1980, pl. 9, figs 3–9, pl. 11, fig. 4, pl. 45, figs 1–4; Hammann 1983, pls 10, 11, pl. 21, figs 203, 204; Rábano 1989, pls 20, 21; Romano 1991, pl. 2, figs 4–6, 9, 10, 12, pl. 3, fig. 9). The European species differ considerably in the following respects: the cephalon is more strongly vaulted transversely with a higher anterior arch; the librigenal field is wider and overhangs the lateral border in dorsal view; the anterior border is shorter; S1 is directed more strongly backwards, extends closer to the occipital furrow adaxially, and L1 is narrower than the adjacent median part of the glabella instead of wider; the eye is situated farther forward, the midlength of the palpebral lobe lying opposite L3 instead of L2; a broad paraglabellar area is apparently not present but instead the axial furrow is expanded adjacent to S1; and the lateral border furrow is almost effaced on the librigena. In light of some of these morphological differences, especially the longer preglabellar region and presence of broad paraglabellar areas in *S.? bailliei*, as well as the difference in stratigraphical and palaeogeographical occurrence, we have considered whether the Tasmanian species might belong to the Reedocalymeninae rather than to the Colpocoryphinae, possibly being related to *Calymenesun Kobayashi*, 1951 though it lacks an anterior cephalic spine as present in that genus. However, the preglabellar region in *S.? bailliei* comprises only the anterior border, whereas in reedocalymenines it comprises a convex preglabellar field and a short, upturned anterior border, though the two may not be distinctly differentiated; and S1 is straight in

S.? bailliei whereas in reedocalymenines it tends to be sigmoidal due to the presence of a large muscle impression adaxially. In addition, the available hypostomes of *S.? bailliei*, though very poorly preserved, appear to be more like those of *Colpocoryphe* and *Salterocoryphe* than those of reedocalymenines, in the subangular rather than broadly rounded outline of the shoulder and in the very long pair of posterior spines (e.g. see Hammann 1983, text-fig. 14).

Subfamily Reedocalymeninae Hupé, 1955

Genus *Vietnamia* Kobayashi, 1960

Type species. – *Calymene douvillei* Mansuy, 1908, from the Na Mo Formation (Middle–Late Ordovician) of northern Vietnam, by original designation.

Diagnosis. – See Turvey (2005, p. 564).

Remarks. – *Vietnamia* was revised by Turvey (2005) who regarded it as a senior synonym of *Sarrabesia* Hammann & Leone, 1997. The type species of *Sarrabesia*, *S. teichmuelleri* from the Katian of southern Sardinia, lacks one of the features that has been considered diagnostic of *Vietnamia*, namely well-developed intermediate lobes at the inner ends of S1. The presence or absence of these lobes reflects the development of muscle insertion areas on the interior of the exoskeleton as either concave or raised features, expressed externally as intermediate lobes or impressed areas respectively. Turvey (2005, p. 565) noted that intermediate lobes are variably developed or absent in some other species he assigned to *Vietnamia*, and also in *Neseuretus*. His concept of *Vietnamia* is accepted here.

Vietnamia hyron sp. nov.

Figure 10J–S

- 1974 *Neseuretus* cf. *birmanicus*. – Corbett & Banks, p. 226, pl. 4, figs 7, 8.
- 1980 cf. *Calymene birmanica* Reed. – Banks & Burrett, pp. 369, 372, tab. 2 (species name misspelled ‘*birmanica*’ in tab. 2).
- 1980 ‘calymenid close to *C. nivalis*’. – Banks & Burrett, p. 372.
- 1988 cf. *Calymene birmanicus*. – Banks, tab. 1.
- 1999 *Sarrabesia?* sp. – Edgecombe *et al.*, p. 236, fig. 3a, b, d.
- 2007 *Calymene birmanica*. – Ross & Ross, p. 215.

LSID. – urn:lsid:zoobank.org:act:CC851794-127C-48B8-B992-1D212AC3A869

Holotype. – Cranidium UTGD 81374/81378 (counterparts), (Fig. 10J, L, M, O, P); also figured by Corbett & Banks (1974, pl. 4, figs 7, 8); Locality 1; late Katian.

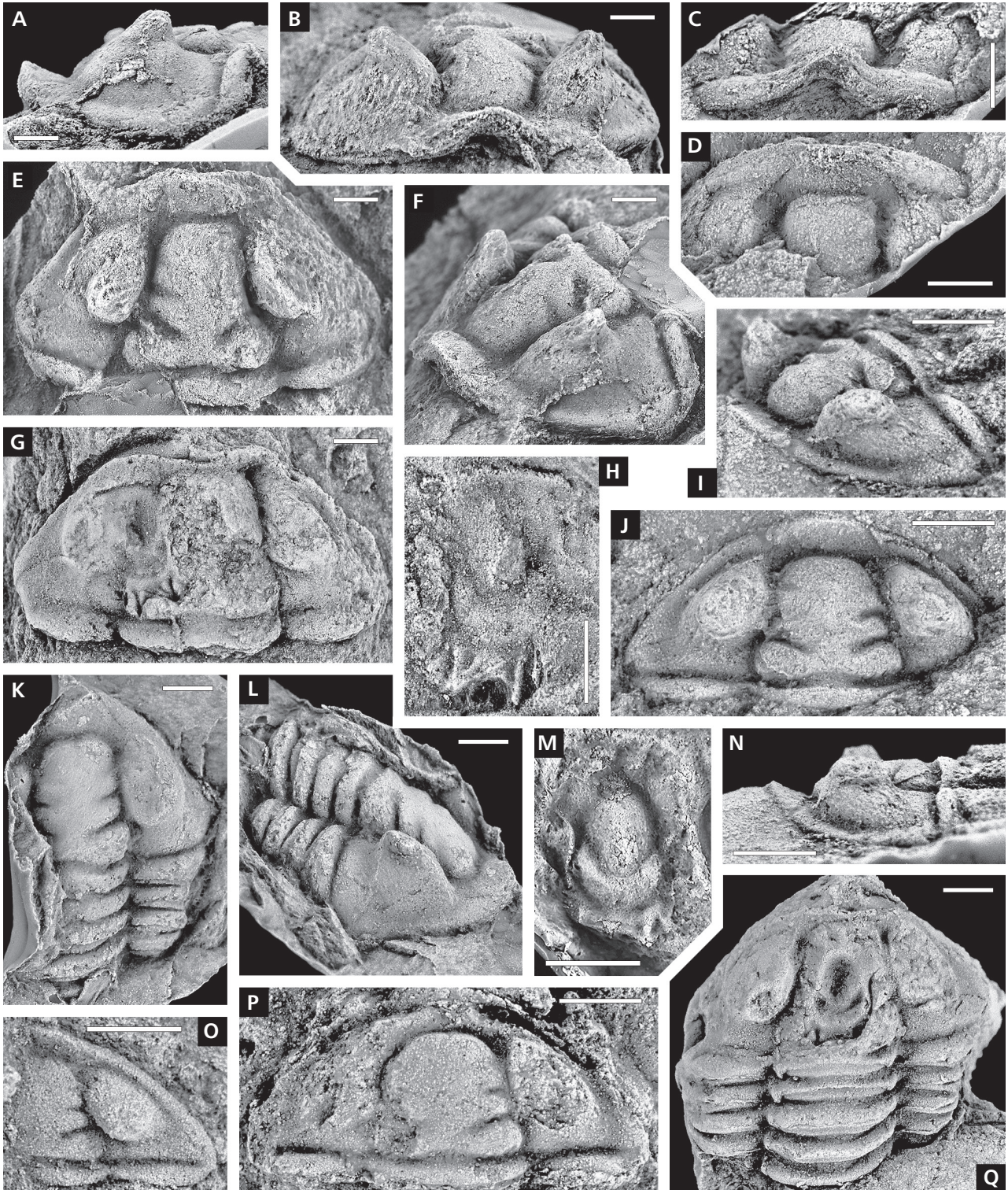


Figure 11. *Salterocoryphe? bailliei* sp. nov., lower Arndell Sandstone (late Katian), Florentine Valley, southern Tasmania; all except K–M, Q from Locality 4, Stan Murray Road. A, B, E–H – holotype, cephalon UTGD 126277/126278 (counterparts); A, B, E, F – UTGD 126278, latex cast of external mould, lateral, anterior, dorsal and oblique views; glabella in front of L1 appears unnaturally constricted on right side due to damage; G, H – UTGD 126277, internal mould with external mould of displaced hypostome, dorsal view, and latex cast of hypostome, ventral view. C, D – fragmentary cephalon, UTGD 126264B, latex cast of external mould, anterior and dorsal views. I, J, N – cephalon UTGD 126275, latex cast of external mould, oblique, dorsal and lateral views. K–M, Q – cephalon and partial thorax UTGD 81417A, B (counterparts), Locality 2; K, L – UTGD 81417A, latex cast of external mould, dorsal and oblique views; M, Q – UTGD 81417B, internal mould with external mould of hypostome, latex cast of hypostome, ventral view, and whole specimen, dorsal view. O – small cephalon UTGD 126264C, latex cast of external mould, dorsal view. Scale bars represent 2 mm.

Paratypes. – Cranidium UTGD 81381; pygidia UTGD 81385A, UTGD 81385B; Locality 1.

Etymology. – Greek, ‘beehive’, referring to the shape of the glabella; noun in apposition.

Diagnosis. – Glabella comprising about 33% cranial width posteriorly; width across L1 about 115% width across occipital ring, twice width across frontal lobe, and 115–125% sagittal length; occipital ring with distinct lateral lobes; no intermediate lobe at inner end of S1; frontal lobe very short (sag., exsag.), less than length of occipital ring abaxially. Preglabellar area inverted-subtriangular in outline, comprising about 30% sagittal length of cranidium, transverse in outline anteriorly. Pygidium with 9 or 10 axial rings in front of bulbous terminal piece and at least 6 pleural furrows.

Description. – Cranidium approximately twice as wide posteriorly as long (sag.). Glabella weakly bell-shaped, gently convex, widths across L1, L2 and L3 approximately in ratio 1.4:1:0.75, anterior outline transverse. Occipital ring gently rounded (sag., exsag.), decreasing gradually in length (sag., exsag.) abaxially, deflected slightly forwards distally where lateral node is bounded adaxially by shallow, oblique depression extending forwards from notch in posterior edge of ring; weak, transverse depression extends across posterior part of ring adaxial to notch (Fig. 10L); small median granule present on anterior half of occipital ring but difficult to distinguish amongst general granulation (Fig. 10L); occipital furrow deep, median part weakly convex forwards, outer part containing transverse apodemal pit. L1 ovate, wider than long, about as wide as adjacent median part of glabella, anterior edge opposite glabellar midlength (sag.); S1 deep, directed backwards at 60–65° to sagittal axis, at adaxial end expanding and shallowing in impressed muscle scar, not connected to occipital furrow. L2 subrectangular; S2 meeting axial furrow opposite 25% sagittal length of glabella from anterior, almost as deep as S1 and slightly less oblique. L3 similar in form to L2 but much smaller; S3 meeting axial furrow close to front of glabella, subparallel to S2 but shorter (exsag.) and shallower. Axial furrow deep, expanded in width adjacent to L1 where outer slope is very steep, containing anterior pit opposite front of glabella; slight shallowing of axial furrow immediately behind anterior pit is probably adaxial end of eye ridge (Fig. 10M); preglabellar furrow containing shallow pit medially (Fig. 10J, M). Preglabellar area arched transversely but flattened in sagittal profile, bounded laterally by broad, shallow, well-rounded (tr.) depressions directed anterolaterally from lateral part of preglabellar furrow; slightly raised anterior edge of preglabellar area forms short (sag., exsag.) anterior cephalic border. Palpebral

lobe strongly upturned, situated far forward and obliquely on cheek, anterior edge opposite front of glabella and posterior edge opposite posterior part of L3. Anterior branch of facial suture converging strongly forwards, with slight adaxially convex deflection across oblique depression bounding preglabellar region; posterior branch directed outwards and slightly backwards from palpebral lobe, deflected more strongly backwards part way across cheek, at about 50° to exsagittal line. Fixigenal field sloping adaxially opposite and in front of palpebral lobe, sloping abaxially and gently convex (tr.) behind palpebral lobe. Posterior border well rounded (exsag.), expanding abaxially, increasing in height above fixigenal field as far as fulcrum beyond which it is strongly downturned; posterior border furrow directed slightly obliquely forwards abaxially, with rounded base.

Pygidial axis moderately convex (tr.), narrowing strongly backwards, width across first ring about twice that across bulbous terminal lobe and much greater than maximum width of pleural region; terminal lobe appears segmented in smaller pygidium (Fig. 10N); axial rings convex (sag., exsag.), transverse or weakly convex backwards medially, deflected backwards laterally. Anterior pleural margin deflected sharply backwards close to axial furrow (Fig. 10K); pleural furrows successively directed more strongly backwards, more posterior ones subparallel to exsagittal line, first furrow much deeper and wider than remainder; interpleural furrows not defined.

Cranidium and pygidium with sculpture of dense granules.

Remarks. – Also assigned to this species are specimens illustrated as *Sarrabesia?* sp. by Edgecombe *et al.* (1999, fig. 3a, b, d), consisting of a cranidium and pygidium from the Benjamin Limestone underlying the Arndell Sandstone in the Florentine Valley, and a cranidium from the uppermost Sandbian–lowermost Katian of Gunn’s Plains, north-western Tasmania. These specimens were assigned to *Vietnamia* by Turvey (2005, p. 565), and we agree with Edgecombe *et al.* that they are indistinguishable from those from the Arndell Sandstone.

The type species *V. douvillei*, revised by Turvey (2005, p. 565, pl. 3, pl. 4, figs 1–5) based on the rather strongly deformed type specimens, is easily distinguished from *V. hyron*. The glabella is much more expanded laterally across L1, which is much larger and more inflated; the occipital ring apparently lacks distinct lateral lobes; there is a large intermediate lobe at the inner end of S1; the preglabellar region is trapeziform in outline rather than subtriangular, the anterior border and border furrow are better defined, and the preglabellar field is more convex (sag.); and the posterior branch of the facial suture is initially directed strongly backwards from the palpebral lobe and approaches the front of L1 before curving

posterolaterally. It is not possible to compare the pygidial internal moulds of *V. douvillei* reliably with the latex casts of the incomplete pygidial external moulds of *V. hyron*.

The best known species of the genus is *V. yushanensis* Lee, 2013 from the upper Katian of Jiangxi Province, South China (see his figs 8, 9A–J, N, ?11R–U). Specimens documented by Lee as *Vietnamia* spp. A–E, *Vietnamia*? sp. and possibly *Neseuretinus*? sp. and cf. *Reedocalymene* sp. probably belong to *V. yushanensis*, the stated differences being due to deformation and/or intraspecific variation. *Vietnamia yushanensis* is very similar to *V. douvillei* and differs from *V. hyron* in the same characters, except that *V. yushanensis* shares with *V. hyron* the presence of lateral lobes on the occipital ring. Other characters in which *V. yushanensis* differs from *V. hyron* are that the anterior cranial margin is more curved in outline and is pointed medially; the palpebral lobe is situated farther back, its posterior edge opposite the posterior part of L2 instead of opposite S2; the anterior branch of the facial suture converges more strongly forwards, so the preglabellar region is narrower (tr.); the pygidium has fewer axial rings and pleural furrows, 7 and 5 respectively instead of 9–10 and at least 6; the pygidium has a marked vincular furrow; and the pygidial pleural furrows are shallower in front of the vincular furrow.

Similar to *V. hyron* in lacking intermediate lobes are *V. pamirica* (Balashova, 1966) (her pl. 2, figs 12–15) from the ‘middle Ordovician’ of Tadzhikistan and *V. teichmuelleri* (Hammann & Leone, 1997) (their pl. 29) from the middle Katian of southern Sardinia. *Vietnamia pamirica* was regarded as a possible junior synonym of *V. nivalis* (Salter, 1865), from the central Himalayas of India, by Turvey (2005; see his pl. 4, figs 6–12), but the former is distinguished by its very wide (tr.) lateral glabellar furrows extending close to the sagittal axis, and the deep S3. The illustrations of *pamirica* are inadequate, however, for worthwhile comparison with *V. hyron*. *Vietnamia teichmuelleri* differs from *V. hyron* in that the glabella is more elongated; the occipital ring lacks lateral lobes; the frontal lobe is longer (sag., exsag.) and more rounded in outline anteriorly; the preglabellar region is shorter, about 25% of the sagittal cranial length, roughly anvil-shaped rather subtriangular in outline, its anterior margin convex rather than transverse; the fixigenae are narrower; and the posterior border furrow is more sigmoidal in outline.

Family Homalonotidae Chapman, 1890

Subfamily Homalonotinae Chapman, 1890

Genus *Brongniartella* Reed, 1918

Type species. – *Homalonotus bisulcatus* M^cCoy in Sedgwick & M^cCoy, 1851 from the Alternata Limestone

Formation (early Katian) of Shropshire, England, by original designation. The type species was revised by Dean (1961, p. 346, pl. 54, figs 1, 2, 4, 8, 9, pl. 55, figs 1, 4, 7).

Remarks. – Based on a cladistic analysis of Ordovician homalonotids, Congreve & Lieberman (2008) considered that *Brongniartella* is paraphyletic, being ancestral to both *Trimerus* and *Platycoryphe*, and they proposed restricting *Brongniartella* to the type species. The validity of their analysis was questioned by Adrain (2013, p. 310) who noted that it was based on only a small number of species constituting a polyphyletic in-group that included two species of the calymenid *Colpocoryphe*. Also included in the in-group were two species of another calymenid, *Calymenella*. The two species of *Brongniartella* included in the analysis, *B. bisulcata* and *B. trentonensis* (Simpson, 1890) (the latter revised by Whitcomb 1930), are so similar morphologically that we consider them to be closely related. Consequently, we do not accept Congreve & Lieberman’s proposal to restrict *Brongniartella* to the type species. Although Congreve & Lieberman alleged that *Platycoryphe* had its origins in *Brongniartella*, the reverse was suggested by Whittington (1966a, text-fig. 13) and Thomas (1977, p. 172), and is supported by the presence of certain less-derived character states in *Platycoryphe* (see following discussion), and by the ages of the stratigraphically oldest known species of each genus – *Brongniartella caradociana* Dean, 1961 from the Sandbian of Shropshire, and several species attributed to *Platycoryphe* by Henry (1971, 1980) from the ‘Grès armoricain supérieur’ (upper Floian; Vidal *et al.* 2011, p. 19, fig. 9) of western France. We agree that *Brongniartella* was likely ancestral to *Trimerus*, and we follow Thomas (1977) in assigning the former to the Homalonotinae rather than, as some authors have advocated, to the Eohomalonotinae (Sdzuy 1957, 1959; Dean 1966, 1967, who regarded the Eohomalonotinae as of family rank; Wolfart in Wolfart *et al.* (1968); Tomczykowa 1975) or the Kerfornellinae (Henry 1980, 1996; Hammann 1983, 1985).

Brongniartella is generally regarded as differing from *Platycoryphe* in the absence of lateral glabellar furrows, but several authors have commented that variation in the development of the furrows may cause difficulties in differentiating the two genera (*e.g.* see Thomas 1977, p. 172). Other features cited by Whittington (1965, pp. 487, 488; 1966b, p. 64) as distinguishing *Brongniartella* were the distinct lateral constriction of the anterior part of the glabella, the wider thoracic axis, and the shallowness or absence on the external surface of the occipital and articulating furrows, which are, however, deep on internal moulds. Ingham (1977, p. 109) also stated that in *Platycoryphe* the pleural furrows and the distally impressed interpleural furrows reach the pygidial margin, though we cannot see consistent differences from *Brongniartella*

in these features. We add that in *Brongniartella* the rostral suture runs on the dorsal surface, though close to the anterior margin of the cephalon (Kielan 1960, pl. 19, fig. 3; Dean 1961, p. 347), whereas in *Platycoryphe* it is marginal (Whittington 1965, pl. 39, fig. 13); L1 tends to be weakly concave in lateral outline in *Platycoryphe* but not in *Brongniartella*; and in *Brongniartella* the thoracic and pygidial axis tends to lack marked independent convexity from the pleural regions, except for the posterior part of the pygidial axis (e.g. see *B. platynota marocana* Destombes, 1966; his pl. 1). There appear to be exceptions to at least some of these criteria, so they cannot be applied uncritically; for example, Kielan (1960, pl. 19, fig. 1) illustrated a cranidium of *Brongniartella platynota* (Dalman, 1828) with shallow glabellar furrows; the anterior part of the glabella does not seem to be constricted laterally in specimens of *Brongniartella minor* (Salter, 1852) figured by Whittington (1966b, pls 19, 20) but is weakly constricted in *Platycoryphe dentata* Dean, 1961 (his pl. 53, figs 1, 3, 5, 9); the thoracic axis does not appear wider or less convex in those specimens of *B. minor* than in *Platycoryphe christyi* (Hall, 1860) (see Whittington 1965, pl. 64, figs 8, 11); and Ingham (1977, p. 108) described the pygidial axis of his species *B. bulbosa* as having strong independent convexity.

Henry (1996, pp. 336, 337) contrasted the morphology of the occipital and thoracic axial rings and thoracic articulating structures of *Platycoryphe* with those of *Brongniartella* and other homalonotids, and on this basis argued that *Platycoryphe* is a calymenid. Briefly, in *Platycoryphe*, as in calymenids, the occipital and thoracic axial rings are rounded at their distal ends rather than being obliquely truncated and narrowing strongly forwards; the axial furrow on the thorax is continuous from each segment to the following one instead of being offset adaxially because of its oblique orientation (see *Brongniartella platynota marocana* in Hammann 1985, fig. 4f); and the articulating processes and sockets on the pleurae are situated relatively distant from the axial furrow rather than adjacent to the posterior ends of the axial furrow on each segment. However, the hypostome of *Platycoryphe* is like that of homalonotids rather than calymenids (see Apollonov 1974, pl. 11, fig. 6; 1980, pl. 28, fig. 12; Lu & Wu 1982, pl. 2, fig. 8, pl. 3, figs 9–11), and we therefore retain the genus in the Homalonotidae. We attribute the differences from other homalonotids in the structure of the occipital ring and thoracic segments to the retention of primitive character states from the common ancestor of calymenids and homalonotids.

Following from the preceding discussion, we reassign '*Platycoryphe*' *dyaulax* Thomas, 1977 from the Aeronian of Saudia Arabia to *Brongniartella*, based on the occipital ring that is obliquely truncated distally and narrows strongly forwards, the similar thoracic axial rings with

the axial furrow offset from one segment to the next (Thomas's pl. 24, fig. 11, left side), the very wide thoracic axis, and the weak independent convexity (tr.) of the axis on thorax and pygidium. This species was included by Sandford (2005) in his new subgenus *Trimerus* (*Ramiotis*), but the type and other species included differ in the more triangular pygidium with a more protuberant axial terminus that merges with a convex postaxial region. Silicified specimens belonging to an ontogenetic series documented by Chatterton *et al.* (1990, fig. 12) as *Brongniartella* n. sp. A, from the Late Ordovician Martinsburg Formation of Virginia, belong to *Platycoryphe*, as evidenced by the well impressed glabellar furrows and the narrow, strongly convex pygidial axis in holaspides.

Apart from the occurrence of *Brongniartella dyaulax* in the Aeronian, there have been several other reports of the genus in the Silurian, two of them based on solitary pygidia, from the Haverford Mudstone Formation (Rhuddanian) of South Wales (Temple 1975, pl. 27, fig. 9; Curtis & Lane 1998), and from Telychian strata of the Richea Siltstone above the Arndell Sandstone in the Florentine Valley of south-west Tasmania (Sandford 2005, p. 21). The first of these shows features consistent with assignment to *Brongniartella* but in the absence of cephalae or cranidia the identification must be regarded as tentative. The pygidium referred to by Sandford is small and deformed, and together with additional specimens from the same locality was previously illustrated by Holloway & Sandford (1993, fig. 4l) as *Trimerus* sp. The other specimens from the Richea Siltstone were assigned by Sandford (2005, p. 47, fig. 19.1–19.4, 19.6) to the new species *Trimerus* (*Ramiotis*) *iani*, but features he cited to support separation of the small pygidium from the others and assign it to *Brongniartella* include its elongate outline, and the narrow and strongly raised axis with concave sides. However, these features are not characteristic of *Brongniartella*, and in any case are probably the result of deformation. We consider it most likely that the pygidium is a deformed pygidium of *Trimerus iani*. From strata in southern Jordan tentatively ascribed a Llandovery age, Wolfart (in Wolfart *et al.* 1968), described *Brongniartella benderi* and two pygidia he assigned to the genus in open nomenclature, but he stated that the age may actually be Ordovician. Considered a junior synonym of *Brongniartella* by Thomas (1977, p. 160) is the monotypic *Pamirotellus* Balashova, 1968 (*nomen novum* for the preoccupied *Pamirites* Balashova, 1966), from strata assigned a Wenlock age in eastern Pamir, Tajikistan. The reasons for the stated Wenlock age are not clear, but the fact that Balashova (1966, tab. 1) apparently correlated the strata with others elsewhere in eastern Pamir containing her subspecies '*Dalmanitina*' *subduplicata zorabata*, which we assign to *Mucronaspis* or *Songxites*, suggests that a Late Ordovician age may be more likely.

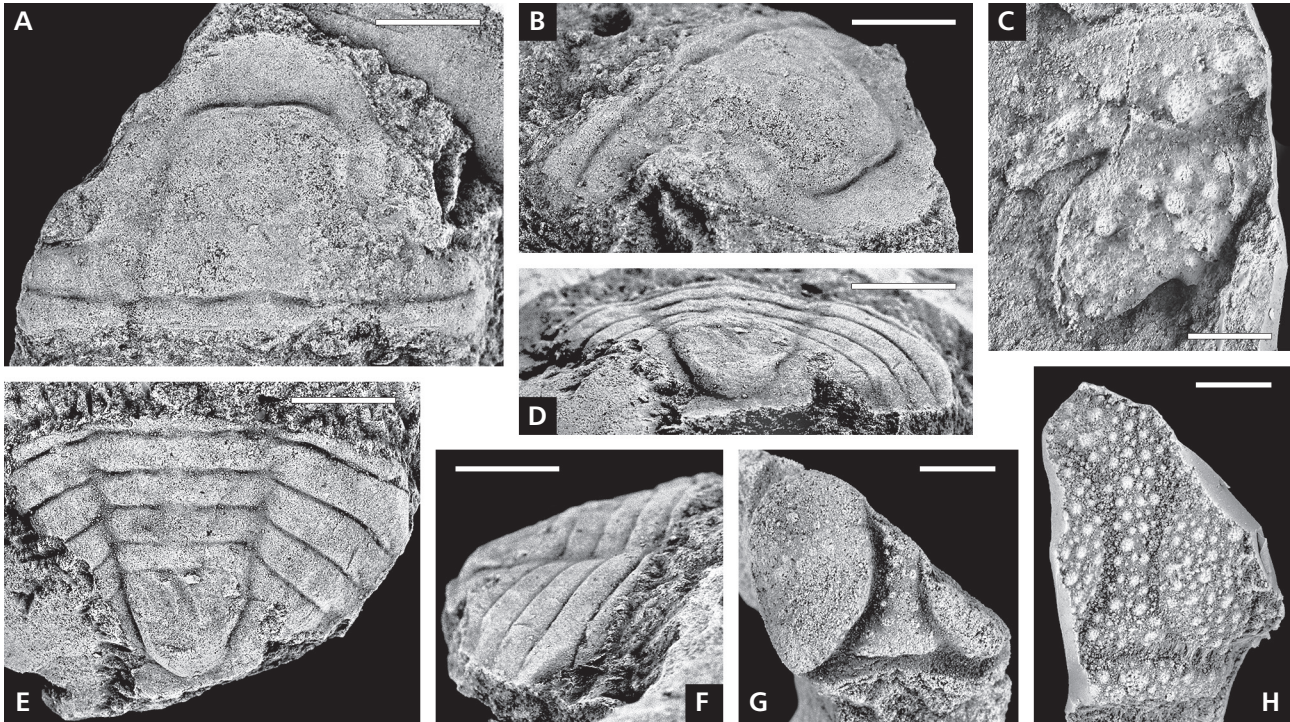


Figure 12. Homalonotid and lichid trilobites from the Arndell Sandstone, Florentine Valley, southern Tasmania. • A, B, D–F – *Brongniartella calveri* sp. nov., from Locality 3, Westfield Quarry (Rhuddanian). A, B – holotype, cranidium UTGD 126181, internal mould, dorsal and oblique views. D–F – pygidium NMV P313703, internal mould, posterior, dorsal and lateral views. • C, G, H – *Amphilichas?* sp., from Locality 1, Westfield Road (late Katian). C – fragmentary pygidium UTGD 81372, latex cast of external mould, dorsal view. G, H – fragmentary cranidium UTGD 81387A, B (counterparts), dorsal view; G – UTGD 81387B, internal mould; H – UTGD 81387A, latex cast of external mould. Scale bars represent 5 mm in A, B, D–F; 2 mm in C, G, H.

***Brongniartella calveri* sp. nov.**

Figure 12A, B, D–F

- 1976 *Brongniartella*. – Baillie & Clarke, p. 2.
- 1978 *Brongniartella* sp. – Baillie et al., p. 46.
- 1979 *Brongniartella* sp. – Baillie, fig. 2.
- 1981 *Brongniartella* sp. – Sheehan & Baillie, p. 252, text-fig. 3.
- 1988 *Brongniartella* sp. – Banks, p. 191, tab. 1.
- 2000 *Brongniartella?* – Holloway, p. 163.

LSID. – urn:lsid:zoobank.org:act:E31352B8-2424-444D-A6AF-6D03966327AD

Holotype. – Cranidium UTGD 126181 (Fig. 12A, B); Locality 3; Rhuddanian.

Paratype. – Pygidium NMV P313703; Locality 3.

Etymology. – After Clive R. Calver, formerly of the School of Earth Sciences, University of Tasmania.

Diagnosis. – Glabella a little wider posteriorly than long (sag.); axial furrow very weak alongside glabella but preglabellar furrow deep and sharply impressed; palpebral

lobe situated far back, its posterior edge level with front of paraglabellar area; cranial portion of preglabellar area long, more than twice as long (sag.) as occipital ring; anterior branches of facial suture converging more strongly forwards than anterior part of axial furrow; rostral suture with broadly subangular outline medially. Pygidium with four axial rings, long unsegmented terminal lobe of axis, and five pleural furrows.

Description. – Cranidium about 160% as wide across posterior border as long (sag.). Glabella of low convexity (sag., tr.), outline subtrapezoidal with weak lateral constriction just in front of midlength, width across occipital ring about 110% sagittal length and about half posterior width of cranidium, width across frontal lobe about 66% posterior width. Axial furrow weakest in posterior half; preglabellar furrow with small backward deflection medially, indenting front of glabella. Occipital ring flattened (sag., exsag.), wider than glabella immediately in front; occipital furrow deeper than axial furrow, deepest between 50% and 85% distance to sagittal line, median third arched gently forwards. Lateral glabellar furrows not impressed. Cranial part of preglabellar area about 225% as long (sag.) as occipital ring, flat in sagittal profile and faintly concave in transverse profile. Palpebral lobe

situated approximately its own length in front of posterior border furrow, and with midlength more or less opposite midlength of glabella. Anterior branch of facial suture converging forwards at about 40° to sagittal line across genal field, converging a little less strongly on posterior part of anterior border, deflected strongly adaxially across front of border; posterior branch of suture directed laterally from posterior edge of eye, curving backwards abaxially. Fixigena in front of palpebral lobe sloping gently forwards, separated from anterior border by broad, shallow, poorly defined oblique depression. Fixigena behind palpebral lobe sloping abaxially, more or less continuous with convexity (tr.) of glabella; paraglabellar area indistinct; posterior border expanding abaxially, gently convex (exsag.) beyond fulcrum; posterior border furrow similar in depth to occipital furrow.

Pygidium gently vaulted (tr.), approximately 160% as wide as long, with broadly rounded posterior margin; axial furrow weak on first segment, progressively increasing slightly in depth posteriorly; axial rings and pleural ribs flattened (sag., exsag.). Axis about 40% maximum pygidial width anteriorly, narrowing evenly backwards to strongly rounded terminus, lacking appreciable independent convexity (tr.) from pleural regions except posteriorly; first three rings approximately equal in length (sag., exsag.), fourth slightly shorter; unsegmented terminal lobe comprising 40% sagittal length of axis. Outer part of pleural region becoming gently concave towards axial terminus; pleural furrows weakly curved, narrow (exsag.) and sharply incised, first extending onto articulating facet distally, next three extending to margin but shallowing distally, fifth incompletely preserved; interpleural furrows almost imperceptible.

Remarks. – This species is assigned to *Brongniartella* rather than to *Platycoryphe* based on the absence of glabellar furrows; the distinctly convex lateral outline of the pre-occipital part of the glabella adjacent to the paraglabellar area; the lateral constriction of the glabella opposite the palpebral lobe; the rostral suture that apparently runs on the dorsal surface rather than marginally, because the anterior border is not downturned towards the suture; and the broad pygidial axis with weak independent convexity (tr.). Other species of *Brongniartella* are easily distinguished by at least several of the following characters: the glabella is more elongate, the cephalic axial furrow is more distinct, the preglabellar furrow is shallower, the palpebral lobe is situated farther forward, the anterior border is shorter, the rostral suture is not subangular in outline medially, and there are a greater number of pygidial axial rings. In the short and broad glabella, *B. calveri* resembles *B. caradociana* Dean, 1961 (his pl. 53, fig. 12, pl. 54, figs 3, 5, 7, 10, pl. 55, fig. 2), from the Sandbian of Shropshire, but that species differs in that the cephalic axial furrow is

deeper, the lateral constriction of the glabella is situated farther forward, the palpebral lobe is placed more anteriorly and farther from the glabella, the anterior fixigena is wider, the anterior border is weakly concave (sag.), the rostral suture is evenly curved medially, there is a greater number of pygidial axial rings, and the pygidial pleural furrows are weaker except for the first.

In the proportions of the glabella, the weak axial furrow alongside the glabella, the deep preglabellar furrow, and the palpebral lobe situated close to the glabella with its posterior edge opposite the front of the paraglabellar area, the cranium of *B. calveri* bears a resemblance to that illustrated by Chatterton & Ludvigsen (2004, pl. 85, figs 1, 2) as *Platycoryphe* sp., from the Hirnantian Ellis Bay Formation of Anticosti Island. However, for reasons stated above we exclude the Tasmanian species from *Platycoryphe* and consequently do not consider the similarities with the cranium from Canada as indicating relationship.

Family Lichidae Hawle & Corda, 1847
Subfamily Tetralichinae Phleger, 1936

Genus *Amphilichas* Raymond, 1905

Type species. – *Platymetopus lineatus* Angelin, 1854 from late Katian strata of the Boda Limestone, Dalarna, Sweden, by monotypy.

Amphilichas? sp.
Figure 12C, G, H

Material. – Fragments of a cranium UTGD 81387, and pygidium UTGD 81372, both from Locality 1; late Katian.

Remarks. – The fragmentary cranium consists of a glabella that is incomplete anteriorly. Distinctive features include the inflated composite lobe with its long axis exsagittally aligned, the longitudinal furrow that diverges strongly backwards in its posterior part, and the markedly constricted median lobe that at its narrowest is only one-third the maximum width of the composite lobe. Based on these characters the specimen might be compared with some members of the Platyllichinae and Homollichinae, as those subfamilies were revised by Holloway & Thomas (2002), especially *Allolichas* Krueger, 1992 (e.g. see Thomas & Holloway 1988, pl. 9, figs 188–190) and some species of *Conolichas* Dames, 1877 (e.g. Thomas & Holloway 1988, pl. 7, figs 129–133, 135) from the Sandbian and Katian, but the absence of L1a, which consequently is incorporated in the composite lobe, precludes assignment to those subfamilies. In most or all of its features the cranium also resembles certain species that have been assigned to the tetralichine *Amphilichas*,

including *Amphilichas? periformis* Warburg, 1925 from the Boda Limestone of Sweden (see discussion and illustrations in Thomas & Holloway 1988, p. 217, pl. 11, figs 241–243), *Amphilichas* sp. of Romano & Owen (1993, p. 713, text-fig. 5d) from the lower Katian of Ireland, *Amphilichas* sp. nov. A of Edgecombe *et al.* (2004, p. 75, fig. 12a–f) from the upper Gisbornian–lower Eastonian (upper Sandbian–lower Katian) of western Tasmania, and *Amphilichas* sp. of Zhou & Zhou (2006, fig. 3f) from the Sandbian–Katian of Inner Mongolia. However, the marked posterior divergence of the longitudinal furrow and the constricted median lobe are unusual in that genus, and indeed in other members of the Tetralichinae. The pygidial fragment from the Arndell Sandstone represents the left anterolateral pleural region, with two short, broad marginal spines and an indication of a third spine behind a notch in the margin. The first interpleural furrow is broad and shallow but there is no evidence of pleural furrows which, if present, must have been confined to more adaxial regions. The preserved morphology of the pygidium is consistent with assignment to *Amphilichas* but because of the unusual features of the cranidium we include the species in the genus with question, together with the other species mentioned above. The present species may be descended from the older Tasmanian species documented by Edgecombe *et al.* (2004).

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