The trilobites *Mitroplax* gen. nov. and *Spiniscutellum* (Scutelluidae) from the Lower Devonian of Victoria, Australia

David J. Holloway

The new scutelluid trilobite genus *Mitroplax*, with type species *M. enormis* (Etheridge, 1894), occurs in Pragian to early Emsian strata at several localities in Victoria, Australia. The genus is characterized by a remarkably long and flat anterior cephalic border, a glabella that expands almost uniformly forward from the occipital furrow, a subcircular S2 discrete from S1, and a pygidium with the well-rounded paired pleural ribs and the posterior bifurcations of the postaxial rib tapering almost to a point distally. The type species grew to exceptional size, as indicated by the dimensions of the largest pygidia. Another scutelluid from the Lochkovian of Victoria, '*Goldius*' *greenii* Chapman, 1914, is revised and assigned to *Spiniscutellum* Šnajdr, 1960. This species and a related one from the Lochkovian of the Bungonia district of south-eastern New South Wales are the first records of *Spiniscutellum* from eastern Gondwana. *Spiniscutellum* (*Lochkovopeltis*) Hörbinger, 2004 is regarded as a junior synonym of *Spiniscutellum*. • Key words: Trilobita, Scutelluidae, Lower Devonian, Australia, taxonomy.

Holloway, D.J. 2023. The trilobites *Mitroplax* gen. nov. and *Spiniscutellum* (Scutelluidae) from the Lower Devonian of Victoria, Australia. *Bulletin of Geosciences 98(2)*, 181–198 (8 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received April 4, 2023; accepted in revised form May 27, 2023; published online June 30, 2023; issued June 30, 2023.

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A very large, strongly deformed and flattened trilobite pygidium said to be collected from Delatite, Victoria, was described by Etheridge (1894) who stated that it represented the largest trilobite hitherto discovered from Australia. The specimen came from the private collection of George Sweet, a brickmaker and amateur geologist in Melbourne, who recorded the locality as 'Loyola lime kilns, Wappan, near Mansfield'. The Loyola district, in the County of Delatite, is about 10 km south-south-west of the township of Mansfield and about 120 km north-east of Melbourne (Fig. 1A). Etheridge was uncertain of both the precise age of the specimen and, because of the poor preservation, its taxonomic affinities. However, after considering the Asaphidae, Illaenidae and Bronteidae (= Scutelluidae) as possible families for it, he concluded that the last was most likely and proposed the name *Bronteus*? *enormis* for the species. Etheridge's uncertainty in determining the taxonomic affinities of the specimen was partly due to the fact that the axial part of the pygidium was obscured by rock matrix, which he was unable to remove. The assignment to the Scutelluidae was accepted by later authors and has been confirmed by recent removal of the matrix covering the axis. The holotype and several other strongly deformed and fragmentary pygidia of the species in the collections of Museums Victoria, all from the same locality, occur in siltstones of the Early Devonian Norton Gully Sandstone. Similar but much better preserved large pygidia occur in calcareous siltstones of the contemporaneous Woori Yallock Formation in the Seville–Woori Yallock district, about 6 km east of the outskirts of Melbourne (Fig. 1). More complete material including cranidia and librigenae apparently belonging to the same species are also present in siltstones of the Early Devonian Humevale Formation in the Lilydale district on the eastern outskirts of Melbourne. The species represents a new genus which is here named *Mitroplax*.

Another scutelluid from the Humevale Formation in the Lilydale district was described by Chapman (1915) as *Goldius greenii*. The species is herein revised based on the type and additional material and assigned to *Spiniscutellum* Šnajdr, 1960. This species and a related one from the Early Devonian of the Bungonia district of south-eastern New South Wales are the first records of *Spiniscutellum* from eastern Gondwana.

Stratigraphy and age

Siltstones and sandstones of the Humevale Formation (Fig. 2) are widely distributed in central Victoria, north of Melbourne and on its eastern outskirts. North of Melbourne, the formation extends down into the upper

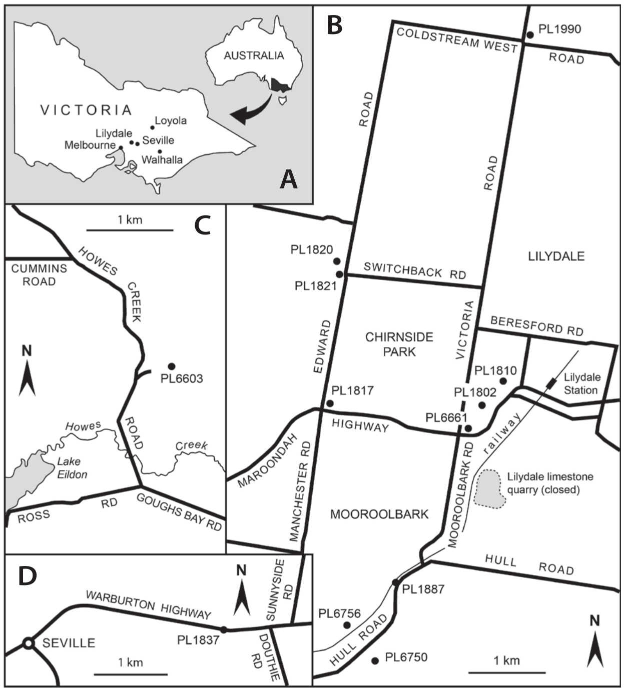


Figure 1. Locality maps. • A – Victoria, showing location of the Lilydale, Seville, Loyola and Walhalla districts. • B – collection localities in the Lilydale district. • C – locality PL6603 at Loyola. • D – locality PL1837 on Warburton Highway east of Seville.

Silurian, but in the Lilydale district on the eastern outskirts of Melbourne, where it has been referred to by the obsolete term 'Ruddock Siltstone' (Gill 1965a), it contains a very diverse Early Devonian shelly fauna generally regarded as ranging in age from Lochkovian to Pragian (*e.g.* Garratt 1983; Garratt & Wright 1988; Talent & Gratsianova 2003, p. 619; Sandford 2003). Three brachiopod assemblage zones spanning this stratigraphic range were recognized in the formation in the Lilydale district by Garratt (1983) and Garratt & Wright (1988): the *Boucotia janaea* Assemblage Zone (lowest), *B. australis* Assemblage Zone, and *B. loloyolensis* Assemblage Zone (= *Boucotia loyolensis–Nadiastrophia* Assemblage Zone of Garratt & Wright 1988). A conflicting opinion on the age of the strata at one locality in this area was presented by Garratt & Rickards (1987) who identified a graptolite from PL6750, where *Mitroplax enormis* also occurs (see following list of localities and Fig. 1B), as *Monograptus* cf. *mironovi* Koren', said to indicate a Přídolí age. Garratt & Rickards (1987) did not mention that brachiopods from this locality had previously been assigned by Garratt (1983, fig. 5; his locality G100) to the *Boucotia loyolensis* Assemblage Zone, ranging in age from Pragian to early Emsian (see following discussion on the Norton Gully Sandstone). Although Garratt & Rickards (1987, p. 138, text-fig. 2b) referred to the sicula of the graptolite specimen, and illustrated it in their drawing, that structure is not preserved because the rhabdosome is incomplete proximally. From examination of photographs of the two counterparts of the specimen, Professor Michael Melchin has advised (personal communication 2022) that, in the absence of the proximal thecae, the species is indeterminate, but that the distal thecal form, width and spacing are consistent with a number of different species of *Uncinatograptus* and *Neomonograptus*, including *U. prognatus* and *N. yukonensis*, indicating a total age range of early Ludlow to early Emsian. The specimen is not accepted here as reliable evidence for a Přídolí age.

At or close to the top of the Humevale Formation at Lilydale is the lenticular Lilydale Limestone, about 220 m thick and traceable along strike for about 1.6 km (VandenBerg 1971, p. 6). The relationship of the limestone to the surrounding siliciclastics is problematic, the boundary between them not being exposed and its nature therefore unknown. The limestone was traditionally regarded as part of a conformable stratigraphic sequence, and either overlying the siliciclastics of the Humevale Formation or as coeval with its uppermost strata (*e.g.* Gill 1965a, Talent 1965, Gill *et al.* 1966), but VandenBerg (1975, p. 35) suggested that the limestone is an allochthonous megaclast. More recently, there has been a return to the traditional view (VandenBerg 1988, p. 110). Conodonts from the Lilydale Limestone were assigned to the *Eognathodus kindlei* and *Polygnathus pireneae* biozones of the middle and upper Pragian by Wall *et al.* (1995), who also noted (their p. 377) that dolomites above the sampled sequence could extend into the *Polygnathus dehiscens* Biozone of the lowermost Emsian. The siliciclastics of the uppermost Humevale Formation are either stratigraphical equivalents of the Lilydale Limestone (Wall *et al.* 1995, p. 372) or, if the limestone is allochthonous, they could be somewhat younger. Unconformably overlying the Lilydale Limestone is the Cave Hill Sandstone, containing moulds of undescribed spiriferid brachiopods that were said by VandenBerg (1971, p. 6) to be indeterminable.

Also widely distributed in Victoria, east and northeast of Melbourne, is the Norton Gully Sandstone. It was traditionally considered to overlie the Wilson Creek Shale conformably, but the intervening Easts Lookout Formation with transitional lithologies of siltstone, sandstone and shale was recognised in an area to the west of Loyola by VandenBerg *et al.* (2006). In the Walhalla district (Fig. 1A), the Norton Gully Sandstone directly overlies the Wilson Creek Shale (VandenBerg *et al.* 2006, pp. 98, 116) which there ranges in age from early Pragian to earliest Emsian, based on conodonts of the *Eognathodus sulcatus* and *Polygnathus dehiscens* biozones recovered from thin calcareous beds within the formation (Carey & Bolger 1995). The graptolite *Neomonograptus thomasi*, indicative of the *N. yukonensis* Biozone of the Pragian to lower

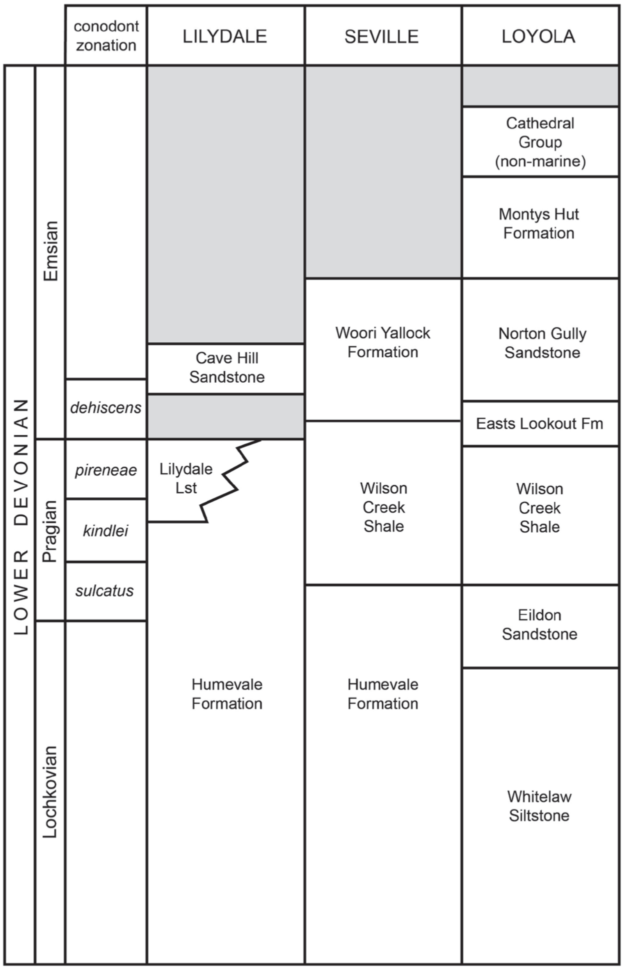


Figure 2. Correlation chart of Early Devonian strata in the Lilydale, Seville and Loyola districts of Victoria.

Emsian, occurs in the Wilson Creek Shale (commonly in association with the early land plant *Baragwanathia*), the Easts Lookout Formation (Earp 2012) and the lowermost part of the Norton Gully Sandstone (VandenBerg *et al.* 2006, p. 115). This evidence indicates that the Norton Gully Sandstone is of early Emsian age, consistent with a radiometric date of 403.8 ± 3.2 Ma derived from zircons in a tuff layer within the formation (Morand & Fanning 2006). At Loyola, several lenses of allochthonous limestones occurring within the Norton Gully Sandstone are older than the enclosing siliciclastics, yielding conodonts that were considered to represent the mid-Pragian *Eognathodus kindlei* Biozone by Mawson (1987, p. 284) but the late Pragian *Polygnathus pireneae* Biozone by Mawson *et al.* (1992, p. 41). The siliciclastics of the formation at Loyola contain a diverse but mostly undescribed shelly fauna including *Mitroplax enormis*. Brachiopods from the siliclastics were assigned by Garratt (1983) to his *Boucotia loyolensis* Assemblage Zone (*Boucotia loyolensis–Nadiastrophia* Assemblage Zone of Garratt & Wright 1988), previously regarded as ranging through the Pragian but which must be extended into the Emsian. Conformably overlying the Norton Gully Sandstone are sandstones, siltstones and shales of the Montys Hut Formation, which VandenBerg *et al.* (2006, p. 117) said had yielded no useful fossils, but a low-diversity brachiopod fauna including *Boucotia australis* and *B. loyolensis* was described from the formation by Earp (2012, 2015) who assigned it a mid- to late Emsian age.

In the Seville–Woori Yallock district east of Melbourne, the sandstones, siltstones and shales of the Woori Yallock Formation of Morand (2010) (= the Yeringberg Formation of VandenBerg 1988) are said to overlie the Wilson Creek Shale conformably, and to be stratigraphical equivalents of the Norton Gully Sandstone. The Woori Yallock Formation includes the so-called 'Seville Limestone' of Gill (1945, p. 184), an obsolete term applied to calcareous siltstones exposed in a former quarry about 2 km east of Seville, now obliterated by road realignment; this is locality PL1837 (Fig. 1D) that has yielded pygidia of *Mitroplax enormis*. The stratigraphical position of the Woori Yallock Formation above the Wilson Creek Shale indicates that it is early Emsian in age. Brachiopods from the diverse shelly fauna of the Woori Yallock Formation were assigned by Garratt (1983, fig. 5; localities G32–35, G37) to his *Boucotia loyolensis* Assemblage Zone.

Localities

PL prefix to locality numbers refers to the invertebrate palaeontology locality register of Museums Victoria; most of these localities are no longer accessible.

Humevale Formation, Lilydale district (Fig. 1B)

PL1802 and PL1810 (localities 2 and 10 respectively of Gill 1940, pp. 257, 259, fig. 1), temporary excavations in Albert Hill Road, Lilydale; as the road runs more or less parallel to regional strike, these localities are assumed to represent a similar stratigraphic level; *Boucotia loyolensis* brachiopod assemblage zone of Garratt (1983) and *P. loyolensis–Nadiastrophia* Assemblage Zone of Garratt & Wright (1988); Pragian.

PL1817 (locality 17 of Gill 1940, pp. 251, 259, fig. 1), gutter on north side of Maroondah Highway at intersection of Edward Road, Chirnside Park; brachiopod assemblage zone and age as for PL1802.

PL1820 (locality 20 of Gill 1940, p. 259, fig. 1), the former Ruddock's Quarry, on the hill slope west of Edward Road and 100 m north of the intersection of Switchback Road, Chirnside Park; *Boucotia janaea* brachiopod assemblage zone of Garratt (1983) and Garratt & Wright (1988), Lochkovian.

PL1821 (locality 21 of Gill 1940, p. 260, fig. 1), 'Ruddock's Corner', intersection of Edward and Switchback roads, Chirnside Park, Victoria; brachiopod assemblage zone and age as for PL1820.

PL1887, temporary pipeline excavation in Hull Road about 400 m west of intersection of Mooroolbark Road, Mooroolbark; brachiopod assemblage zone and age as for PL1802.

PL1990, cutting in Victoria Road just north of intersection with Coldstream West Road, Coldstream; not assigned to a brachiopod assemblage zone but age is Pragian.

PL6661, north-east corner of Victoria Road and Maroondah Highway, Lilydale; not assigned to a brachiopod assemblage zone but age is Pragian.

PL6750 (locality G100 of Garratt 1983, fig. 5, and M100 of Garratt & Rickards 1987, p. 138), corner of Taylor and Williams roads, Mooroolbark; brachiopod assemblage zone and age as for PL1802.

PL6756, temporary excavation on corner of Winyard Drive and Baradine Road, Mooroolbark, Victoria; not assigned to a brachiopod assemblage zone but age is Pragian.

Woori Yallock Formation, Seville–Woori Yallock district (Fig. 1D)

PL1837 (locality 37 of Gill 1945, fig. 2), former quarry on south side of Warburton Highway about 2 km east of Seville and 620 m west of intersection of Douthie Road; quarry now obliterated due to realignment of highway; brachiopod assemblage zone as for PL1802, early Emsian.

Norton Gully Sandstone, Loyola (Fig. 1C)

PL6603, former Griffith's Quarry (= 'Loyola lime kilns', locality LL of George Sweet collection in NMV), 350 m east of Howes Creek Road and about 10 km south-west of Mansfield township; marked on the map of Cooper (1973, fig. 1); brachiopod assemblage zone as for PL1802, early Emsian.

Systematic palaeontology

Terminology and repository. – Morphological terminology follows Whittington & Kelly (1997) and Holloway & Lane (2012, p. 420); the latter authors clarified the homology of the cephalic borders and border furrows in scutelluids, and introduced the term 'bolus' for the swelling that is enclosed by S1 in most members of the family. All specimens are housed in the invertebrate palaeontological collections of Museums Victoria (NMV).

Genus *Mitroplax* gen. nov.

LSID. – urn:lsid:zoobank.org:act:8ACD2771-7831-4542-81B9-096E84ACBE86

Type species. – *Bronteus*? *enormis* Etheridge, 1894, from the Norton Gully Sandstone (early Emsian), Loyola near Mansfield, Victoria.

Etymology. – Greek *mitra*, a headband, and *plax*, something flat and wide, referring to the anterior and lateral cephalic borders; gender feminine.

Diagnosis. – Anterior cephalic border exceptionally long (sag., exsag.) and flat, comprising one-third sagittal length of cephalon. Glabella gently convex, narrowing strongly forwards across occipital ring, expanding moderately and rather uniformly in front of occipital furrow, broadly rounded in outline around lateral extremity of frontal lobe. L1 very short (exsag.) abaxially and expanding strongly adaxially; S1 enclosing gently inflated bolus of moderate size; S2 circular, situated in weak longitudinal depression joining inner ends of S1 and S3, and about half way between them; S3 wide (tr.), meeting axial furrow more or less distinctly; median node on glabella situated between S2 and inner end of S3. Anterior fixigena very broad (tr.) in front of strong eye ridge. Pygidial axis strongly trilobate longitudinally; interpleural furrows and sagittal furrow in postaxial rib expanding very strongly in outer pleural region above doublure and becoming flat-bottomed; paired pleural ribs and posterior bifurcations of postaxial rib tapering almost to a point distally, dying out close to pygidial margin.

Remarks. – Other scutelluids having a notably long (sag., exsag.) anterior cephalic border are *Platyscutellum* Šnajdr, 1958 and *Poroscutellum* Šnajdr, 1958, regarded by Šnajdr (1960) and Přibyl & Vaněk (1971) as closely related to each other, and both known mainly from the various limestone facies of the Praha Formation (Pragian) of the Prague Basin where numerous species have been recognized (*e.g.* Šnajdr 1960; Vaněk 1970; Chlupáč & Šnajdr 1989; Vaněk *et al.* 1992; Vaněk 1999, 2000; Hörbinger 2006), some of them possibly being synonyms, and some in which the anterior cephalic border is not greatly expanded in length; also see discussion on *Poroscutellum* (*Ottoaspis*) Vaněk *et al.*, 1992 in the remarks on *Spiniscutellum*. *Platyscutellum* and *Poroscutellum* both differ from *Mitroplax* in that the anterior cephalic border is not as exceptionally long (sag., exsag.); the glabella is more expanded in width (tr.) across the frontal lobe, the lateral extremity of which is more strongly rounded in outline; L1 is not as short (exsag.) abaxially; S2 is situated farther posteriorly and is united with the inner end of S1 rather than being separate from it;

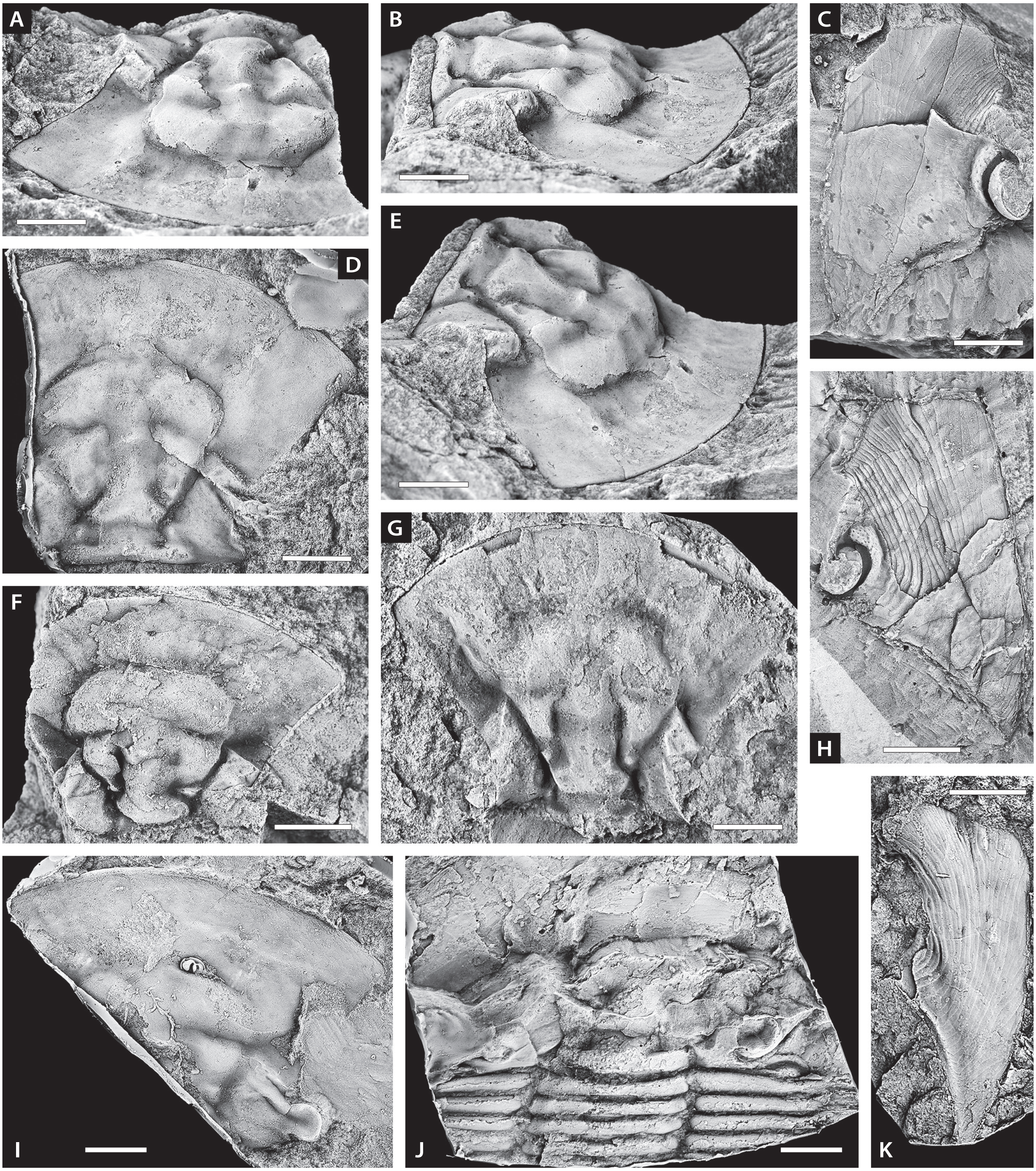


Figure 3. *Mitroplax enormis* (Etheridge, 1894), Pragian strata of the Humevale Formation, Lilydale district, Victoria; dorsal views unless stated otherwise. A, B, D, E – cranidium NMV P313647, locality PL1810; A, B, E – internal mould, anterodorsal, dorsolateral and oblique views; D – latex cast of external mould. C – librigena NMV P313653, internal mould with external mould of doublure partly exposed, locality PL1887. F – cranidium, NMV P313660, locality PL6756. G – cranidium NMV P313730, internal mould, locality PL1990. H – librigena NMV P313652, internal mould with external mould of doublure partly exposed, locality PL1887. I – cranidium NMV P313648, latex cast of external mould with beyrichiid ostracod lying in preglabellar furrow, locality about 50 m south-west of PL1810. J – incomplete cephalothorax NMV P313650, latex cast of external mould with posteriorly displaced rostral plate, locality PL1887. K – librigena P313656, latex cast of external mould, ventral view, locality PL1990. Scale bars represent 5 mm in A–G, I, J; 10 mm in H, K.

and the pygidial pleural ribs do not taper to a point distally where the inter-rib furrows are correspondingly narrower. Other differences are that S2 is markedly elongated exsagittally in *Poroscutellum*; and in *Platyscutellum* the bolus is larger, the glabella lacks a median node, L2+L3 is distinctly circular in outline and deflects the adjacent part of the axial furrow outwards, and the anterior margin of the pygidium is typically deflected more strongly backwards abaxially beyond the fulcrum. The union of S2 with S1 in *Platyscutellum*, *Poroscutellum* and many other Devonian scutelluids is a more derived character state than the discrete S2 in *Mitroplax* (*e.g.* see Šnajdr 1960, pp. 20, 230).

***Mitroplax enormis* (Etheridge, 1894)**
Figures 3–6

1894 *Bronteus*? *enormis*, Eth. fil; Etheridge, p. 194, pl. 9, figs 1, 2.
1914 (?) cf. *Bronteus enormis* Etheridge (*sic*). – Chapman, pp. 302, 312, 313.
1938 *Goldius enormis*. – Gill, p. 170.
1963 *Scutellum enorme* (Etheridge). – Talent, p. 105.
? 1963 *Scutellum* sp. – Talent, p. 105, pl. 74, fig. 4.
? 1966 *Scutellum* (*Scabriscutellum*) sp. – Gill *et al.*, p. 359 (listed only).
1971 *Scutellum enorme* (Etheridge). – VandenBerg, tab. 1, p. 5.
2006 ‘*Bronteus*’ *enormis* Etheridge, 1894. – Sandford, pp. 385, 390.

Holotype. – By monotypy, a very poorly preserved external mould of a very large, deformed pygidium, together with two fragments of the counterpart internal mould, NMV P24251, originally from the George Sweet collection; figured by Etheridge (1894, pl. 11, figs 1, 2), Fig. 5F herein.

Type horizon and locality. – Norton Gully Sandstone (early Emsian), locality PL6603, Griffith’s Quarry, Loyola district, Victoria.

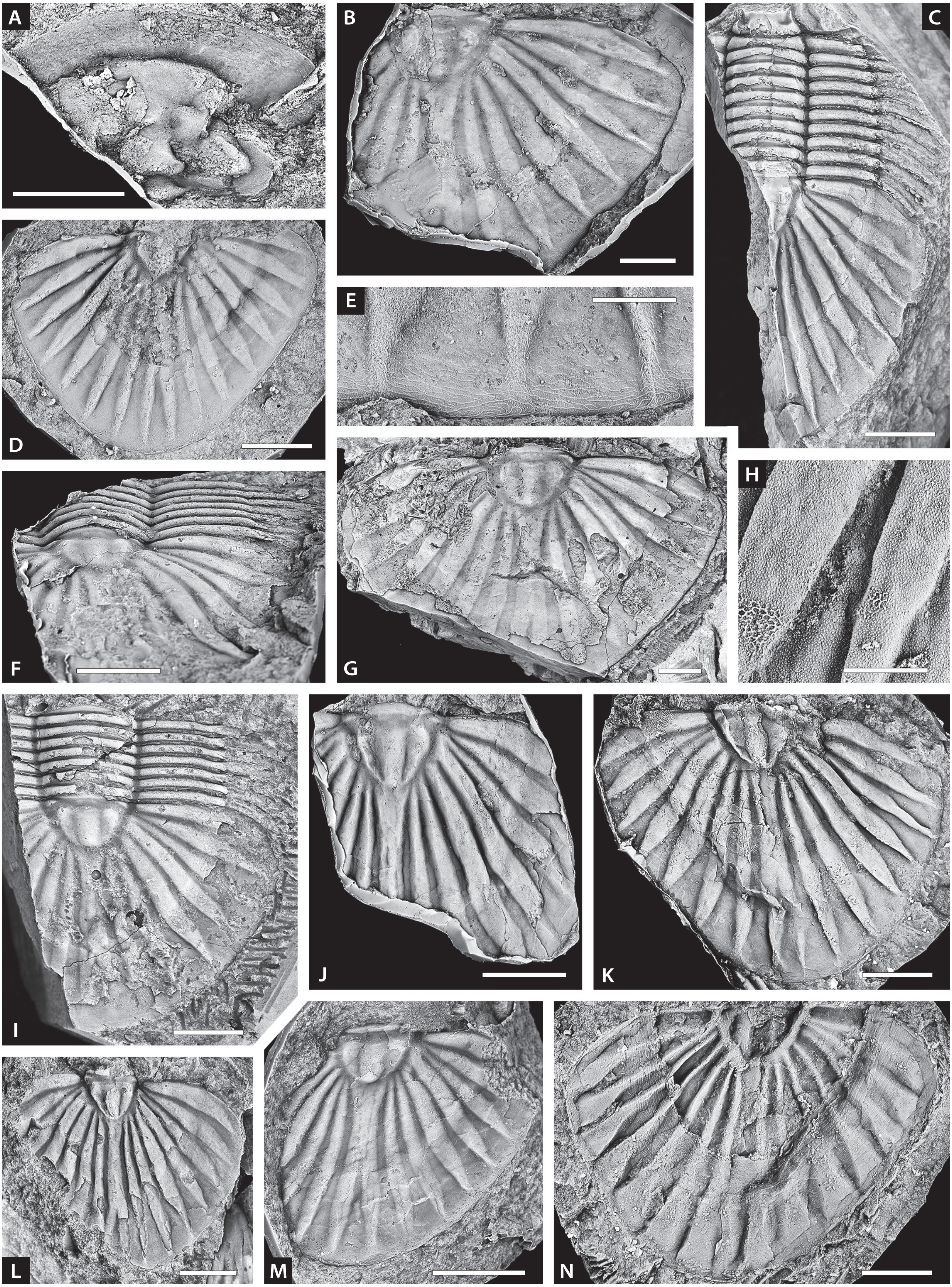
Other material. – From the type horizon and locality: three fragmentary and strongly deformed pygidia, NMV P33965, P33967, P33968. From Pragian strata of the Humevale Formation, Lilydale district: two cranidia NMV P313647–P313648, an incomplete thoracopygon NMV P315033, and an incomplete pygidium NMV P486, from localities PL1802 and PL1810; incomplete pygidium NMV P313649, from vicinity of locality PL1817; incomplete, poorly preserved cephalothorax NMV P313650, incomplete, poorly preserved small cranidium NMV P313651, two librigenae NMV P313652–P313653, incomplete dorsal exoskeleton NMV P313654, and pygidium NMV P313655, from locality PL1887; cranidium NMV P313730, librigenal doublure NMV P313656, and four pygidia NMV P313657–P313659, P313731, from PL1990; cranidium NMV P313660, from PL6756; small pygidium NMV P313661, from PL6661; incomplete pygidium NMV P313662, from PL6750. From Woori Yallock Formation (early Emsian), Seville–Woori Yallock district: four very large pygidia NMV P648, P16411, P16412, P33966, from PL1837.

Tentatively assigned to the species. – A fragmentary internal mould of a large pygidium NMV P61130, from the Kilgower Member of the Tabberabbera Formation (*Polygnatus pireneae* to lower *P. dehiscens* conodont biozones, late Pragian to earliest Emsian; Talent & Gratsianova 2003, p. 620), Tabberabbera district, eastern Victoria.

Diagnosis. – As for genus.

Description. – Cranidium with maximum width across anterior fixigena about 1.5 times sagittal length and twice width at γ–γ; anterior outline evenly curved. Glabella comprising about 40% cranidial width posteriorly; width at outer end of S3 twice that across L1; width across frontal lobe a little less than sagittal length. Occipital ring gently arched (tr.), narrowing strongly forwards, of uniform length (sag., exsag.) adaxial to node-like swelling situated at anterolateral extremity; posterior half of ring raised and convex (sag., exsag.), bearing large median node; anterior half weakly concave (sag., exsag.) and sloping forwards adaxial to occipital muscle scar which deepens backwards into a large pit (Fig. 3D). L1 shorter (exsag.) than occipital ring and narrower (tr.) than anterior width of ring; posterior branch of S1 well impressed, meeting

Figure 4. *Mitroplax enormis* (Etheridge, 1894), Pragian strata of the Humevale Formation, Lilydale district, Victoria; dorsal views unless stated otherwise. A – small cranidium NMV P313651, latex cast of external mould, locality PL1887. B, E, G – pygidium NMV P486, locality PL1802; B, E – latex cast of external mould, dorsal view, and detail of right pleural region showing sculpture of terrace ridges on margin; G – internal mould. C – incomplete dorsal exoskeleton NMV P313654, locality PL1887. D – pygidium NMV P313657, latex cast of external mould, locality PL1990. F, I – incomplete thoracopygon NMV P315033, locality 1802; F – latex cast of internal mould, posterodorsal view; I – internal mould. H – pygidium NMV P313649, latex cast of external mould, detail of right pleural region showing granulose sculpture and encrusting bryozoan, locality in vicinity of PL1817. J – pygidium NMV P313662, latex cast of external mould, from locality PL6750. K, N – pygidium NMV P313658, latex casts of external moulds, dorsal and ventral views, locality PL1990. L – small pygidium NMV P313661, internal mould, from locality PL6661. M – pygidium NMV P313655, latex cast of external mould, locality PL1887. Scale bars represent 5 mm in A, E, H, L; 10 mm in B–D, F, G, I–K, M, N.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axial furrow opposite midlength (exsag.) of lunette, directed anteromedially, anterior branch almost transverse and apparently of variable depth. S2 subcircular, situated about opposite glabellar midlength (sag.). S3 oblique, inner part deep, outer part apparently of variable depth. Median glabellar node situated almost equidistant from transverse lines through S2 and inner end of S3. Axial furrow deeper adjacent to posterior half of occipital ring than to anterior half, very deep adjacent to lunette, thereafter gradually shallowing as far as inner end of eye ridge; lateral part of preglabellar furrow shallow (Fig. 3D) to very poorly defined (Fig. 3I), median part even shallower, but furrow appears deeper in some specimens due to deformation (see remarks). Fixigena behind eye ridge gently convex (exsag., tr.), lunette subcircular in least deformed cranidium (Fig. 3D); in front of eye ridge, fixigena slopes steeply downwards into broad (exsag.), shallow and poorly defined anterior border furrow (Fig. 3B, E); anterior border weakly concave (sag., exsag.), half as long as glabella sagittally and increasing slightly in radial length abaxially. Palpebral lobe rather small in large cranidia, its posterior edge lying opposite posterior half of occipital ring, anterior edge opposite middle (exsag.) of bolus, palpebral margin very strongly curved; eye ridge meeting axial furrow opposite anterior part of L2+L3. Anterior branch of facial suture diverging forwards at about 43° to sagittal line, more strongly than adjacent part of axial furrow, meeting anterior cranidial margin slightly behind a transverse line through front of glabella; posterior branch sigmoidal. Librigena with very broad, weakly concave lateral border comprising most of its width; librigenal field largely reduced to a strongly raised eye socle that increases in width and convexity anteriorly, and is surrounded adaxially by a deep, trench-like subocular furrow; outer edge of socle coincides in position with inner margin of doublure, except anteriorly and posteriorly; broad genal spine apparently variable in length (Fig. 3H, K). Rostral plate of characteristic scutelluid form, with acute, dorsally curved posterolateral projections bounded by transversely arched hypostomal suture and connective suture that diverges backwards towards inner edge of doublure (Fig. 3J). Sculpture of sparse granules on frontal lobe of glabella and anterior border, interspersed with anastomosing terrace ridges on outer part of border in large cranidia, but terrace ridges more extensive on smallest cranidium (Fig. 4A); several rows of subparallel terrace ridges present on outer edges of anterior border and palpebral lobe; remainder of cranidium appears to lack sculpture; external sculpture not preserved on dorsal surface of librigena but inner surface of eye socle bears low, subcircular swellings anteriorly (dimples on internal mould; Fig. 3C, H); cephalic doublure with terrace ridges.

Thorax of 10 segments; axis expanding strongly backwards across first segment, subparallel-sided on segments 2–6 after which it progressively narrows slightly; small median spines present on axial rings of ninth and tenth segments (Fig. 4F) and apparently also on fourth; articulated portion of pleurae adaxial to fulcrum successively increasing in width (tr.) on segments 1–3, thereafter of more or less constant width; free spinose portion of pleurae beyond fulcrum about as wide (tr.) as articulated portion in posterior half of thorax, width in anterior half of thorax unknown.

Pygidium semielliptical in outline, width:length ratio varying considerably from about 1.2 to about 1.6 (estimated) but not related to specimen size (see remarks), length about twice that of thorax. Anterior pleural margin deflected backwards abaxial to outer end of articulating flange, situated about half way between axial furrow and exsagittal line through lateral extremity of pygidium; maximum pygidial width lies slightly farther back than axial terminus. Axis semielliptical in outline, comprising one-quarter or a little less of both maximum width and sagittal length of pygidium; small but prominent lateral remnant of first axial ring merges adaxially into medially expanded, concave (sag., exsag.) region that is differentiated from very narrow (sag., exsag.) articulating furrow immediately in front (*e.g.* Fig. 4B, F, G, I–K); remainder of axis subdivided by longitudinal furrows into anteriorly inflated lateral lobes and posteriorly inflated median lobe; median lobe narrows weakly backwards, in some specimens bearing faint traces of several axial rings (Figs 4B, G; 5E). Pleural region weakly vaulted in inner half and weakly concave in outer half, pleural ribs rounded in cross section; ribs 1 and 4–5 wider than other ribs proximally and more elevated than them adaxial to fulcrum; rib 4 expands only weakly from axial furrow to fulcrum; postaxial rib much wider anteriorly than median lobe of axis, narrowing backwards as far as about one-quarter its length and expanding thereafter, bifurcated in posterior half, distal width about twice its minimum width; a pair of narrow, very weak and discontinuous longitudinal grooves on postaxial rib, possibly representing an incipient pair of interpleural furrows, meet axial furrow anteriorly in line (exsag.) with longitudinal furrows on axis and run subparallel to rib margins (Figs 4J, M; 5D, E), but whether they extend posteriorly beyond bifurcation of rib is unclear. Interpleural furrows rounded in cross section adaxial to fulcrum, flat-bottomed beyond fulcrum and expanding to exceed maximum width of pleural ribs; sagittal furrow in postaxial rib similar in form to outer parts of interpleural furrows. Doublure comprising a little more than half postaxial length of pygidium. Sculpture of fine, dense granules on outer parts of pleural ribs, apparently also present on inner parts of ribs and on lateral and median lobes of axis but not well preserved there; granules intermingled with anastomosing terrace ridges on distal ends of ribs and interpleural furrows, remainder

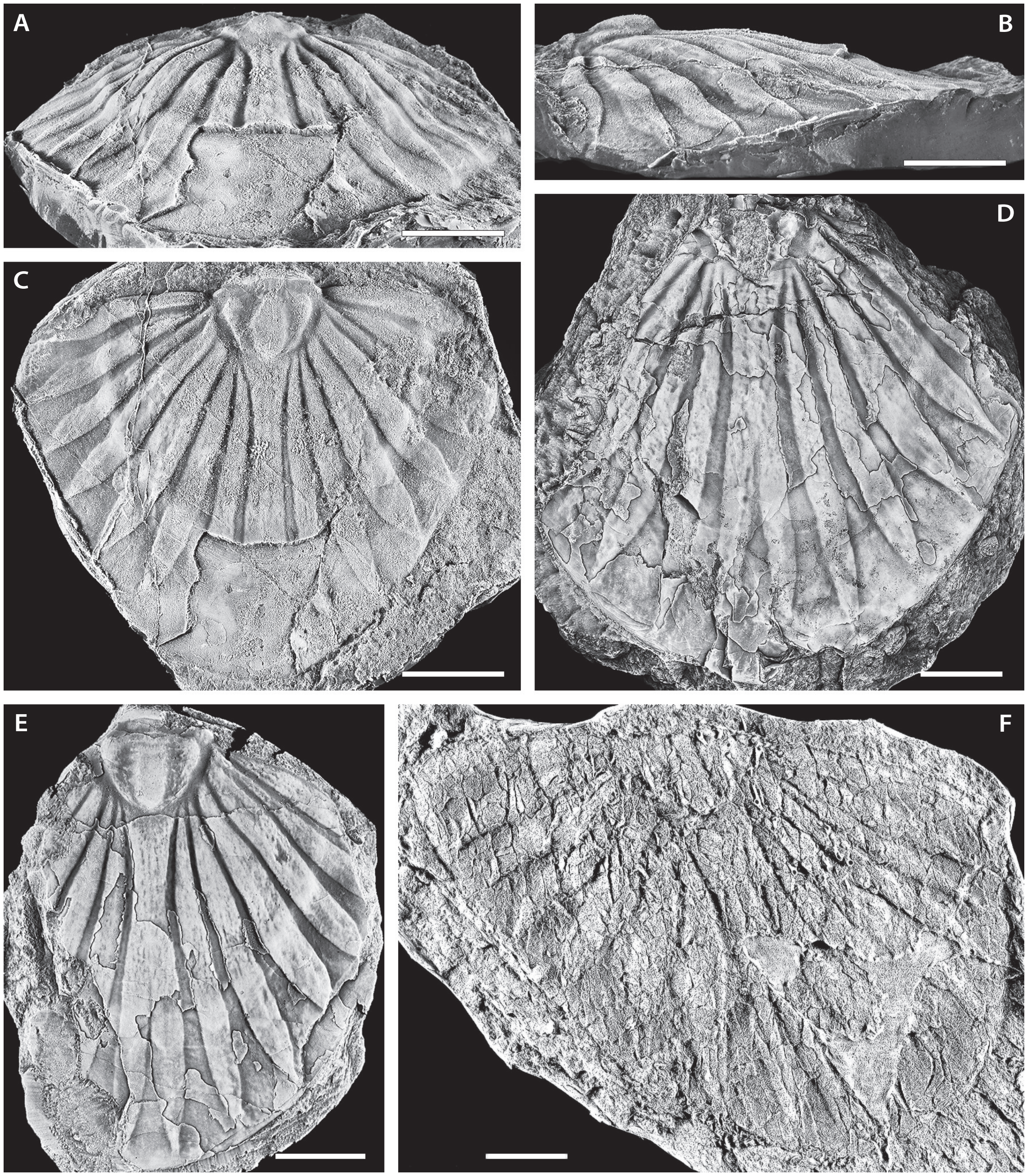

Figure 5. *Mitroplax enormis* (Etheridge, 1894), very large pygidia, all except F from Woori Yallock Formation (early Emsian), locality PL1837, Seville district, Victoria; dorsal views unless stated otherwise. A–C – NMV P33966, silicon rubber cast of external mould with testiferous doublure preserved posteromedially. D – NMV P16412, internal mould with fragments of exoskeleton adhering. E – NMV P16411, internal mould with fragments of exoskeleton adhering. F – holotype, NMV P24251, Norton Gully Sandstone (early Emsian), 'Loyola Lime Kilns' (= Griffith's Quarry), Loyola, Mansfield district, Victoria, silicon rubber cast of poorly preserved and deformed external mould. Scale bars represent 20 mm.

of interpleural furrows apparently smooth; terrace ridges present on doublure.

Remarks. – The cranidia range in length from about 9 mm to 24 mm, and the pygidia from about 18 mm to about 110 mm. Judging from the relative proportions of the cranidium, thorax and pygidium in three incomplete articulated exoskeletons (Figs 3J; 4C, I), the largest pygidium is estimated to have come from an individual at least 210 mm long. The specimens have been deformed tectonically to varying degrees, affecting the appearance of certain features in some specimens. In cranidium P313730 (Fig. 3G), transverse compaction has resulted in exaggeration of the depth of the weak longitudinal depression running between the inner ends of S1 and S3, and in the elongation of the pit-like S2 which is still separately distinguishable. In cranidium P313660 (Fig. 3F) and the smallest cranidium P313651 (Fig. 4A), longitudinal compaction has exaggerated the depth of the preglabellar furrow, and in the smallest cranidium has also resulted in the frontal lobe appearing wider (tr.) and more strongly curved in outline at its lateral extremity. The palpebral lobe of the smallest cranidium is relatively larger than in other cranidia, suggesting that the lobe decreased in size during ontogeny. In pygidium P313658 (Fig. 4K, N), dorsoventral compaction has resulted in strong imprinting of the ribs and furrows of the dorsal surface onto the doublure. The marked variation in the proportions of pygidia cannot be attributed entirely to deformation, nor is it due to ontogenetic change as the width/length ratio is about 1.2 in both the smallest pygidium (Fig. 4L) and very large ones (*e.g.* Fig. 5C), but in pygidia of intermediate size it varies from about 1.3 to 1.6 (Fig. 4D, G, I, M, N).

An unusual feature of the cranidium of *Mitroplax enormis* is a small node-like swelling situated at the anterolateral extremity of the occipital ring, and apparently associated with the occipital muscle scar (Fig. 3D). Similar swellings are developed to varying degrees in some species of *Meridioscutellum* Feist, 1970 but are not present in other species (see Feist 1974, pls 10, 11); however, the occipital muscle scars are larger in that genus than in *Mitroplax*. The variable development of the feature in a genus not closely related to *Mitroplax* indicates that the feature is not of taxonomic significance above the species level, and its relationship with the occipital muscle scar suggests that it may be related functionally to insertion of muscles.

A fragmentary internal mould of a large scutelluid pygidium from the Kilgower Member of the Tabberabbera Formation (late Pragian to possibly earliest Emsian) in the Tabberabbera district of eastern Victoria was documented as *Scutellum* sp. by Talent (1963, p. 105, pl. 74, fig. 4.) who compared its size with the holotype of *Mitroplax enormis*. The specimen preserves the distal parts of three pleural ribs and a much smaller, less distinct portion of a fourth rib. Though fragmentary, the specimen may be assigned to *Mitroplax* with confidence based on the distal tapering of the ribs almost to a point, and the very wide, flat-bottomed interpleural furrows. As in *M. enormis*, the pleural ribs are more sharply defined posteriorly than anteriorly. The ribs retain traces of widely spaced, coarse terrace ridges, whereas in *M. enormis* the pygidial pleural ribs are predominantly granulose with finer terrace ridges present only distally; there is insufficient evidence to judge whether this apparent difference in sculpture is a result of intraspecific variation within *M. enormis* or whether the Tabberabbera specimen belongs to a separate species. The sharply defined posterior edges of the pleural ribs and the orientation of the terrace ridges, which generally run more or less transversely on pygidia of scutelluids, indicate that the fragment represents the left posterolateral part of the pygidial pleural region.

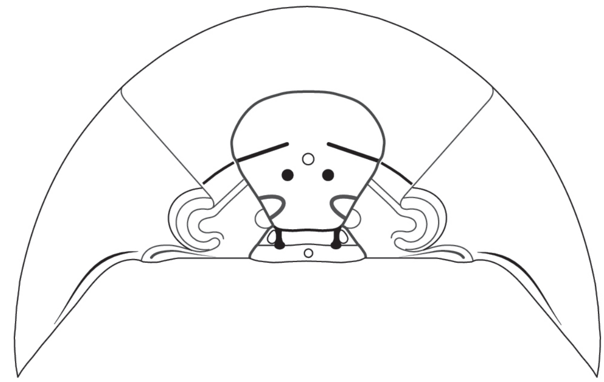

Figure 6. *Mitroplax enormis* (Etheridge, 1894); diagrammatic reconstruction of cephalon.

Genus *Spiniscutellum* Šnajdr, 1960
[= *Spiniscutellum* (*Lochkovopeltis*) Hörbinger, 2004]

Type species. – *Bronteus umbellifer* Beyrich, 1845, p. 35, from late Lochkovian strata of the Lochkov Formation (Radotín Limestone facies), Prague Basin, Czechia; by original designation. The holotype by monotypy is a pygidium from Prague-Lochkov in the Museum für Naturkunde, Berlin, figured by Beyrich (1845, pl. 1, fig. 13) and Přibyl & Vaněk (1975, pl. 3, fig. 7); the designation of an incomplete thoracopygon from Slivenec as neotype by Šnajdr (1960, p. 113) is consequently invalid.

Other species and subspecies. – *Spiniscutellum greenii* (Chapman, 1915), Lochkovian strata of the Humevale Formation, Victoria, Australia; *S*. aff. *greenii*, Efflux Siltstone Member, Frome Hill Formation (Lochkovian), New South Wales; *S. larviferum* Haas, 1968, 'upper Soğanlı beds' (Lochkovian, see Haas 1982; = Kaynarca Member, İstinye Formation of Yalçin & Yilmaz 2010; Soğanlık Limestone Member, Pelitli Formation of Özgül 2012), north-west Türkiye; *S. plasi plasi* (Šnajdr, 1960), uppermost Lochkov Formation (late Lochkovian–earliest Pragian), Prague Basin; *S. plasi alterum* Hörbinger, 2004, lower Lochkov Formation (early Lochkovian), Prague Basin; *S*.? *umbelliferum coquandi* Feist, 1991 *in* Durand-Delga & Feist (1991), late? Lochkovian, northern Morocco.

Diagnosis. – Glabella with S1–S3 shallow to moderately impressed; S1 enclosing bolus of small to moderate size; S2 subcircular to elongated exsagittally, discrete from S1 but may be very close to it, and joined to it and S3 by very weak to shallow longitudinal depression; S3 wide (tr.), commonly joined to axial furrow by shallower depression; glabella adaxial to S2 with median node or broad, low swelling. Preglabellar furrow continuous medially; anterior border concave with gently upturned margin. Pygidial axis semielliptical to parabolic in outline, strongly trilobate longitudinally; pleurae with interpleural furrows expanding weakly to moderately towards margin; postaxial rib bifurcated distally.

Remarks. – Šnajdr (1960) considered *Spiniscutellum* to be most closely related to *Decoroscutellum* Šnajdr, 1958, and to be descended from it or from a common ancestor, probably the latter. *Decoroscutellum* has a stratigraphic range of Wenlock to Pragian, whereas *Spiniscutellum* is known from the Lochkovian to lowermost Pragian. The two genera are certainly very similar morphologically, and for most species of *Spiniscutellum* the differences from *Decoroscutellum* are not striking. *Spiniscutellum* differs in that S2 is generally more elongated exsagittally and, though discrete from S1, is joined to it and more weakly to S3 by shallow longitudinal depressions; S3 is wider (tr.) and more or less distinctly joined to the axial furrow; the preglabellar furrow is continuous instead of being interrupted or very weak medially; and the anterior border is longer (sag., exsag.) and concave, with a narrow upturned marginal rim rather than being rolled downwards at the margin. Other supposed differences in *Spiniscutellum* listed by Šnajdr (1960, p. 112), who assigned only the type species to the genus, are the less expanded (tr.) frontal glabellar lobe, the absence of the median glabellar node adaxial to S2, the reduction in the occipital and palpebral spines, and the more elongated pygidium. These supposed differences are not supported by the additional species of *Spiniscutellum* now known, as discussed by Holloway & Lane (2012, p. 434).

The subgenus *Spiniscutellum* (*Lochkovopeltis*) was proposed by Hörbinger (2004), with type species '*Kosovopeltis*' *plasi* Šnajdr, 1960 from the uppermost Lochkov Formation (Radotín Limestone facies, late Lochkovian–earliest Pragian), together with the new subspecies *S.* (*L.*) *plasi alterum* from the lower Lochkov Formation (Kotýs Limestone facies) as well as '*Poroscutellum* (*Ottoaspis*)' *sessor* Vaněk, 1999 from the basal Praha Formation (Slivenec Limestone facies); the last species, and *Poroscutellum* (*Ottoaspis*) Vaněk *et al.*, 1992, are discussed below. '*Kosovopeltis*' *plasi* was originally based only on several pygidia but was revised from additional material including cranidia and an articulated exoskeleton by Chlupáč (1986, pl. 2, figs 1–6) who assigned it with question to *Spiniscutellum*; the species was also illustrated by Chlupáč *et al.* (1985, pl. 4, figs 6, 7) and Hörbinger (2004, pl. 3, figs 3, 4). Characters mentioned by Hörbinger (2004) as distinguishing *Lochkovopeltis* from *Spiniscutellum* (*s.s.*) were the glabella that is laterally extended anteriorly and has a distinct median node, the wider thoracic axis, the semielliptical pygidial outline, the narrower pygidial interpleural furrows, the short distal bifurcation of the postaxial rib, the smaller 'central part of pygidium' (the region inside the doublure) and the broader pygidial doublure; the last two characters are obviously mutually related. These characters, and a few others including the absence of tubercular sculpture, were listed as differentiating *S. plasi* from *S. umbelliferum* by Chlupáč (1986, p. 207), who stated that the presence of the median glabellar node and the broader thoracic axis do not comply with the diagnosis of *Spiniscutellum* given by Šnajdr (1960). However, a median glabellar node is present in some cranidia of *S. umbelliferum* illustrated by Šnajdr (1960, pl. 8, figs 1, 4, 18, 19) and a cranidium illustrated by Haas (1968, text-fig. 3g), and also in *S. larviferum* Haas (1968, pl. 26, figs 4, 5, 9). Some other specimens of *S. umbelliferum* have a prominent median glabellar swelling in a similar position (Chlupáč *et al.* 1985, pl. 4, fig. 4; Chlupáč 1998, pl. 49, fig. 3), as does *S. greenii* (Figs 7, 8). Comparison of *S. greenii*, *S. larviferum*, *S. plasi* and *S. umbelliferum* shows that there is considerable variation in the characters mentioned by Hörbinger (2004) as diagnostic of *Lochkovopeltis*, and there is even variation in the degree of lateral expansion of the frontal glabellar lobe within *S. umbelliferum* itself (compare Whittington 1999, fig. 3.1, 3.4). I therefore consider that these characters are not of significance at the generic or subgeneric level, and regard *Lochkovopeltis* as a junior synonym of *Spiniscutellum*.

Poroscutellum (*Ottoaspis*) was proposed by Vaněk *et al.* (1992) to include two new species from the Praha Formation, *P.* (*O.*) *peki* (type species) from the Loděnice Limestone facies and *P.* (*O.*) *carum* from the Slivenec Limestone facies. An anteriorly incomplete cranidium and two pygidia of *peki* were illustrated but only a cranidium of *carum*. Vaněk (1999) added the new species *P.* (*O.*) *sessor* from the Slivenec Limestone facies, illustrating only a cranidium, and he also included *Spiniscutellum plasi* in the subgenus and illustrated a pygidium that he assigned to *P.* (*O.*) *carum*. He did not compare the cranidium of *sessor* with that of *carum*, and no appreciable differences are evident in the illustrations of them, so these two names may be synonyms. Vaněk *et al.* (1992, p. 101) stated that *Poroscutellum* (*Ottoaspis*) differs from *Poroscutellum* (*s.s.*) in having a shorter 'preglabellar depression' (referring to the entire preglabellar area) and shallower, wider S1 and S2. As other supposed diagnostic features the authors also mentioned a median glabellar node, weakly vaulted pygidium of short semielliptical outline, a prominent, blunt posterior projection on the median lobe of the pygidial axis, weakly vaulted pygidial pleural ribs, narrow interpleural furrows and a punctate exoskeletal sculpture. Most of these characters are either present in many scutelluids or are variable in development within other genera; exoskeletal sculpture in particular may be very variable, even changing throughout ontogeny in a single species (Holloway & Lane 2012). A blunt posterior projection on the median lobe of the pygidial axis, as present in *peki* (Vaněk *et al.* 1992, pl. 4, fig. 4), does not appear to be present in *carum* though its pygidium was illustrated only in dorsal view by Vaněk (1999, pl. 1, fig. 1). It is not possible to assess the taxonomic independence of *Ottoaspis* from the few illustrated specimens and I draw no conclusions, though there are similarities with *Spiniscutellum* as well as *Poroscutellum*. In particular, the incomplete cranidium of *P.* (*O.*) *peki* (Vaněk *et al.* 1992, pl. 2, fig. 2) bears a very strong resemblance to that of the cephalon of *Spiniscutellum plasi* illustrated by Chlupáč (1986, pl. 2, fig. 1), probably influencing the assignment of *plasi* to *Ottoaspis* by Vaněk (1999).

Internal moulds of a cranidium and two pygidia of the species here designated *Spiniscutellum* aff. *greenii* were illustrated by Jones *et al.* (1981, fig. 3a–c) as *Scabriscutellum* sp. cf. *scabrum*, and additional specimens were illustrated by McTackett (2002, pl. 6, figs a–i). The specimens came from the Bungonia district of south-eastern New South Wales, from a stratigraphic unit now known as the Efflux Siltstone Member of the Frome Hill Formation (Bauer 1994), for which Jones *et al.* (1981) suggested a Lochkovian age based on their identification of the conodont *Spathognathodus* (now *Zieglerodina*) sp. cf. *remscheidensis* from 5 m higher in the sequence than the trilobite. Mawson (1986, p. 44) questioned the identification of the trilobite which she said would be better assigned to *Scutellum* (*Scutellum*) and to be consistent with a Přídolí age, the age she determined for the unit based on her re-identification of the conodont as *Ozarkodina eosteinhornensis*; however, *Scutellum* is not known to range down into the Silurian. From *Scabriscutellum*, a genus largely or entirely restricted to the Middle Devonian, the Bungonia species differs in that the S2 glabellar furrows are discrete, shallow and subcircular, rather than deep, elongated exsagittally and united with S1. The species cannot be assigned to *Scutellum* either on account of the rather long, flattened to gently concave anterior cephalic border, the shallow longitudinal furrow on the glabella joining S2 to the inner ends of S1 and S3, and the long distal bifurcation of the pygidial postaxial rib. Its similarity to *Spiniscutellum greenii*, with which it is compared in the remarks on that species, suggests that the Bungonia species is Lochkovian in age, like most other occurrences of the genus. Additional evidence that the Přídolí age advocated for the Efflux Siltstone Member by Mawson (1986) is unlikely comes from a phacopid trilobite illustrated by McTackett (2002, pl. 3, figs f–k) as *Lochkovella* sp., from several hundred metres lower in the Bungonia sequence, in the Cardinal View Shale conformably underlying the Frome Hill Formation. That species is here assigned to *Denckmannites rutherfordi* Sherwin, 1968, the type locality of which is in the Wallace Shale, ranging in age from Přídolí to earliest Devonian (Holloway & Lane 2012, p. 415) in the Orange–Molong district of New South Wales, some 200 km north-north-west of Bungonia. If the conodont from the Efflux Siltstone Member at Bungonia re-identified by Mawson (1986) is indeed *Ozarkodina eosteinhornensis*, it presumably was reworked from lower in the sequence.

Spiniscutellum? *umbelliferum coquandi* Feist in Durand-Delga & Feist, 1991 from northern Morocco is based only on a single pygidium and consequently is here assigned to the genus with question, though the specimen does closely resemble pygidia of *S. umbelliferum* from the Prague Basin. Maksimova (1979, p. 25, pl. 1, figs 8, 9) proposed the new species *Spiniscutellum*? *belaensis* [*sic*] on the basis of three fragmentary pygidia from the Pragian of the River Bela on the western slopes of the Urals, but the two specimens illustrated are too incomplete for assignment to a genus. *Spiniscutellum umbelliferum* has been reported from the Lower Devonian of the Altai-Sayan region of south-western Siberia (Maksimova 1980, p. 484), but as no specimens have been described or illustrated from there the record cannot be substantiated.

***Spiniscutellum greenii* (Chapman, 1915)**
Figures 7, 8

1915 *Goldius greenii* sp. nov.; Chapman, p. 158, pl. 14, figs 1, 2.
1929 *Goldius greenii* Chapm. – Chapman, p. 29, fig. 32.
1962 *Scutellum greenii* (Chapman). – Gill *et al.*, pp. 91, 92.
1965b *Scutellum greenii* (Chapman). – Gill, pl. 6, fig. 2.
2016 *Goldius greeni* Chapman, 1915. – Basse *et al.*, p. 68 and tab. 3 (= Genus indet.)

Holotype. – Internal and external moulds of a dorsal exoskeleton lacking the librigenae, NMV P12667; figured by Chapman (1915, pl. 14, fig. 1), Gill (1965b, pl. 6, fig. 2), Fig. 7E, H herein.

Type horizon and locality. – Lochkovian strata of the Humevale Formation, locality PL1820, Ruddock's Quarry, Chirnside Park, Victoria.

Paratype. – Internal mould of pygidium with partly exposed external mould of doublure, NMV P12668; figured by Chapman (1915, pl. 14, fig. 2), Fig. 7G herein; from locality PL1820.

Other material. – Four cranidia, NMV P313681–P313684; two librigenae, P313686, P313687; and six pygidia, P12681, P313685, P313688–P313691; from locality PL1820. A cranidium, NMV P313692; from locality PL1821.

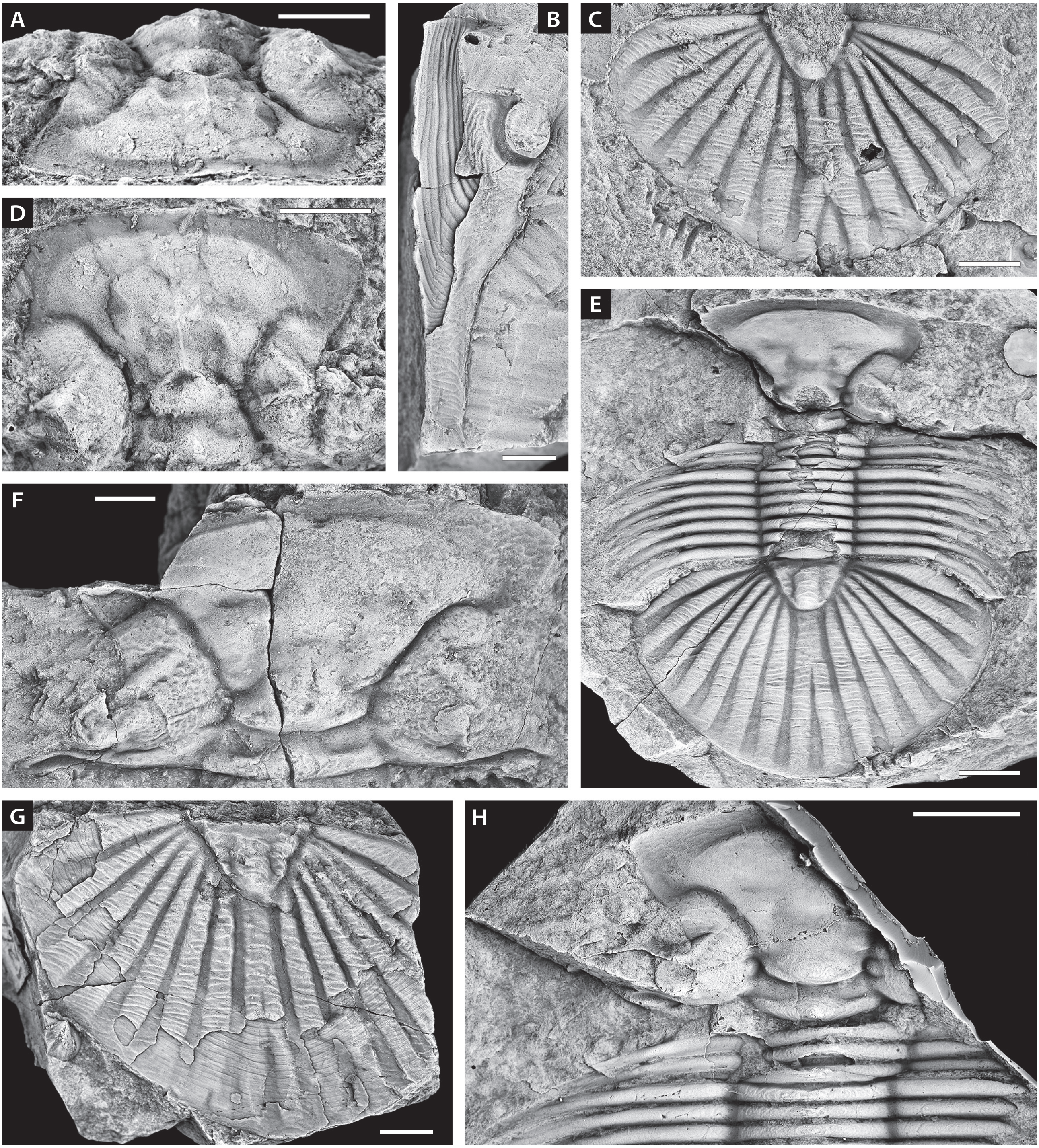

Figure 7. *Spiniscutellum greenii* (Chapman, 1915), Lochkovian strata of Humevale Formation, locality PL1820, Lilydale district, Victoria; dorsal views unless stated otherwise. A, D – cranidium NMV P313684, latex cast of external mould, anterodorsal and dorsal views. B – librigena NMV P313686, part internal and external moulds. C – teratological pygidium NMV P313689, internal mould. E, H – holotype, dorsal exoskeleton lacking librigenae NMV P12667, internal mould, and latex cast of external mould of cranidium and anterior part of thorax. G – paratype, pygidium NMV P12668, internal mould. Scale bars represent 5 mm.

Diagnosis. – Cranidium with anterior outline almost transverse medially; anterior border rather long for genus, about 66% as long sagittally as occipital ring, expanding strongly abaxially in front of lateral extremity of frontal lobe. Glabella markedly expanded laterally across frontal lobe where width is about twice that across occipital ring; low median swelling or weak node present between levels of S2 and S3; S3 not distinctly joined to axial furrow.

Anterior border furrow well defined on front of fixigena lateral to intersection with axial furrow; fixigena opposite δ about as wide as glabella across L1. Genal spine very long. Pygidium approximately 1.4–1.6 times as wide as long; postaxial rib expanding strongly backwards, about 2.5 times as wide posteriorly as anteriorly, with sagittal furrow extending forwards more or less to midlength; interpleural furrows and sagittal furrow on postaxial rib expanding strongly in distal half, furrow alongside postaxial rib wider than other interpleural furrows in proximal half. Dorsal sculpture of coarse terrace ridges.

Description. – Cranidium about as wide at ω–ω as at β–β or a little wider, width at δ–δ about 85% that at ω–ω; anterior outline gently curved, almost transverse medially. Glabella gently convex, comprising 35% to almost 40% cranidial width posteriorly, narrowing moderately forwards across occipital ring, subparallel-sided across L1, expanding at a gradually increasing rate from front of L1 to a point transversely opposite S3 where width increases abruptly; widths at posterior margin, L1 and frontal lobe approximately in ratio 1:0.67:1.8. Posterior half of occipital ring well rounded (sag., exsag.); anterior half sloping forwards in medial third, lateral third deeply indented by large occipital muscle impression; in transverse profile, strongest curvature of ring is at sagittal line; medial swelling or node present on highest point of ring (Figs 7A, D, H; 8B, E, G); occipital furrow relatively long (sag., exsag.) medially, merging laterally with occipital muscle impression, with rather abrupt anterior slope across entire glabellar width. L1 about half as long (exsag.) abaxially as occipital ring, inflated medially; a small, subcircular auxiliary muscle impression is present on lateral part of L1 (Fig. 8A, B, G); S1 semielliptical, gently impressed directly behind bolus, shallowing adaxial to bolus, very weak in front of it; bolus weakly inflated. S2 indistinct, subcircular (Figs 7E; 8A, B), joined to inner ends of S1 and possibly S3 by very weak longitudinal depression though its connection to S3 is accentuated by deformation in some specimens (Fig. 8E, G). S3 shallow but more distinct than S2, more or less transversely oriented, situated about its own width (tr.) from sagittal line, not meeting axial furrow; L2+L3 gently inflated. Central area of glabella between S2 and S3 weakly inflated, not differentiated anteriorly from frontal lobe but bounded behind by broad (sag.), very shallow and poorly defined transverse depression situated at about cranidial midlength (sag.) (Fig. 7E, H). Axial furrow well impressed except adjacent to occipital muscle impression, deepest adjacent to lunette; preglabellar furrow shallow, poorly defined beside lateral extremity of frontal lobe, in some specimens with a deeper, backward deflection medially (Fig. 7E, F). Anterior border decreasing in length adaxially, concave (sag., exsag.), with narrow, slightly upturned outer rim; fixigenal field weakly convex transversely, moderately convex exsagittally; posterior border furrow most distinct in largest cranidium, crossing fixigena obliquely from behind palpebral lobe towards posterior end of lunette but fading adaxially (Fig. 7F). Palpebral lobe with posterior edge opposite middle (sag.) of occipital ring and anterior edge opposite back of bolus; small, upwardly directed spines or node-like swellings present anteriorly and posteriorly on palpebral lobe; eye ridge prominent, directed towards axial furrow opposite anterior part of L2+L3; anterior branch of facial suture mostly runs subparallel to segment of axial furrow adjacent to L2+L3 but curves inwards slightly across outer part of anterior border. Visual surface surrounded on librigena by broad, deep, subocular furrow; librigenal field abaxial to subocular furrow narrow (about twice as wide as subocular furrow), arcuate, gently convex (tr.) anteriorly and weakening posteriorly; lateral border furrow shallow anteriorly and fading posteriorly; lateral border very broad, concave; proximal part of genal spine weakly concave (tr.) in outer half and weakly convex in inner half, distal part flattened. Prominent terrace ridges on median and posterior parts of occipital ring and median part of L1 arranged roughly concentrically; weaker terrace ridges on anterior and lateral margins of frontal lobe run subparallel to preglabellar furrow; anastomosing terrace ridges present on anterior border and on librigenal and fixigenal fields, except on eye ridge, with interspersed pits on fixigenal field; terrace ridges become reticulate abaxially on anterior border and on lateral border and genal spine; closely spaced, parallel and continuous terrace ridges present on outer rim of anterior border; librigenal doublure with coarse, prominent and widely spaced terrace ridges.

Thorax of 10 segments; axis moderately arched, subparallel-sided from first to sixth segment, thereafter narrowing slightly backwards; axial furrow well impressed; pleura on first segment narrower (tr.) than on remaining segments; fulcrum situated successively farther abaxially on first and second segments, farther still on later segments where articulated portion comprises about half total width of pleura; free spines abaxial to fulcrum successively curving a little more strongly backwards on more posterior segments. Terrace ridges developed more strongly on thoracic axial rings than on pleurae.

Pygidium with maximum width situated at outer end of first interpleural furrow and just behind level of axial terminus. Axis subtriangular in outline, about 133% as wide as long, comprising 23–26% maximum pygidial width anteriorly and 27–30% pygidial length; lateral remnant of first axial ring narrows (exsag.) adaxially and merges with depressed region that incorporates articulating furrow; longitudinal furrows of axis subparallel, aligned with anterior end of seventh interpleural furrow; median

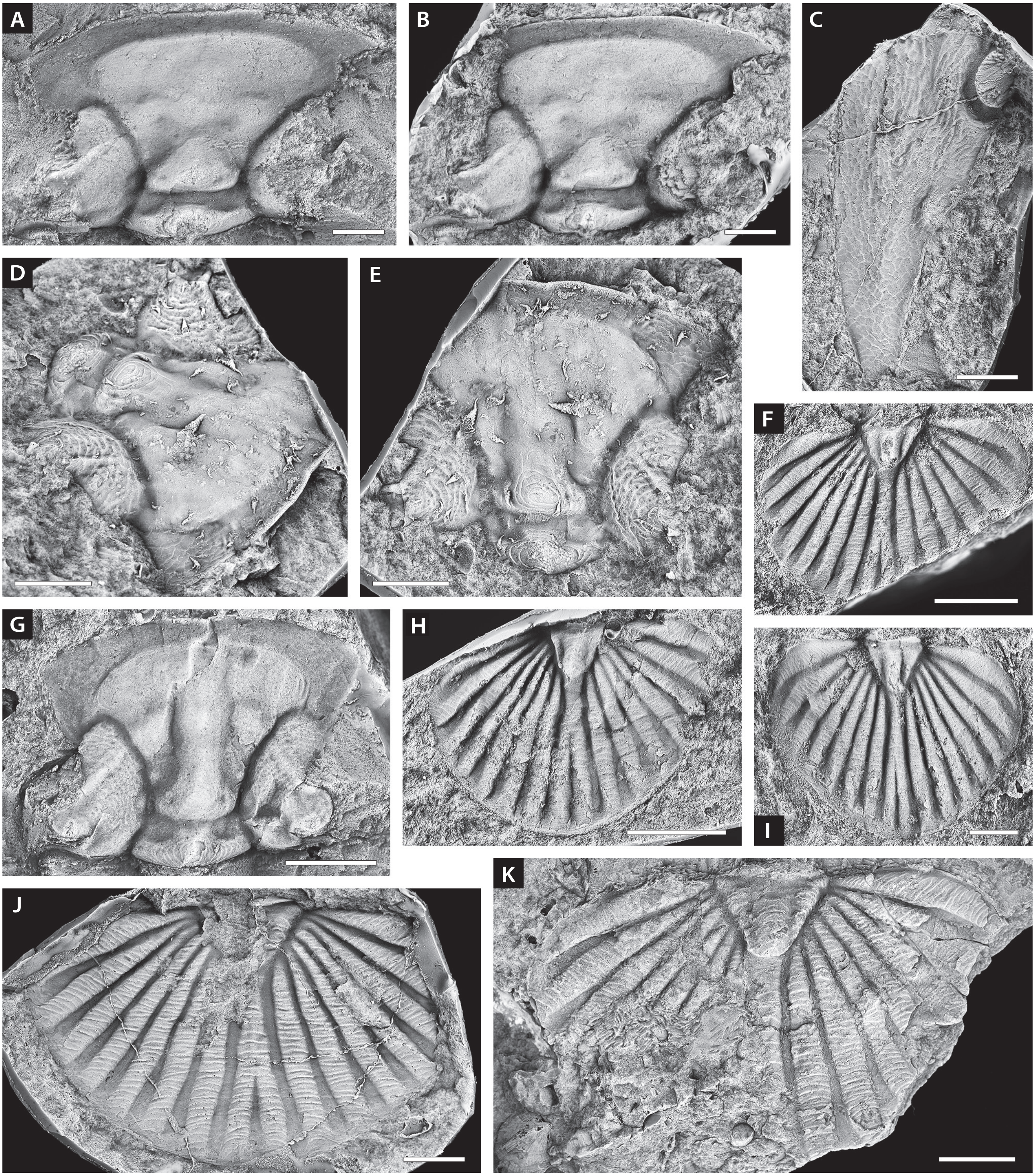

Figure 8. *Spiniscutellum greenii* (Chapman, 1915), Lochkovian strata of Humevale Formation, Lilydale district, Victoria; all except A, B from locality PL1820; dorsal views unless stated otherwise. A, B – cranidium NMV P313692, internal mould and latex cast of external mould, locality PL1821. C – librigena NMV P313687, latex cast of external mould. D, E – cranidium NMV P313682, latex cast of external mould, oblique and dorsal views. F – pygidium NMV P313691, internal mould. G – cranidium NMV P313683, internal mould. H – pygidium NMV P12681, latex cast of external mould. I – pygidium NMV P313690, latex cast of external mould. J – pygidium NMV P313688, latex cast of external mould. K – pygidium NMV P313685, internal mould. Scale bars represent 2 mm in A, B, I; 5 mm in C–F, G, H, J; 10 mm in K.

lobe of axis strongly inflated posteriorly. Pleural region gently convex in inner half and gently concave in outer half; anterior margin curving posterolaterally from about half way between axial furrow and exsagittal line through lateral extremity of pygidium; pleural ribs rounded in cross section, more strongly adaxially than abaxially; first rib narrowing in outer third so that it is about as wide distally as proximally, second rib narrowing less strongly than first in outer third, remaining paired ribs subparallel-sided or narrowing only very weakly in outer third; interpleural furrows expanding most strongly in outer half to one-third and becoming flat-bottomed, about two-thirds as wide as pleural ribs distally; posterior branches of postaxial rib as wide distally as paired pleural ribs, and sagittal furrow as wide distally as interpleural furrows. Doublure comprising half postaxial length of pygidium, narrowing slightly anterolaterally. Terrace ridges on axis and pleural ribs more or less transversely aligned except on anterior and lateral parts of pleural region where they curve anterolaterally; doublure with widely spaced, coarse terrace ridges between which are several fine terrace ridges.

Remarks. – The specimens have been somewhat deformed by flattening and shearing, affecting the appearance of some features of the cephalon in particular. The appearance in some specimens of a deep longitudinal glabellar furrow joining the inner ends of S1 and S3, and incorporating S2 (*e.g.* Fig. 8E, G), is a result of this deformation, and in other specimens S1–S3 are seen to be discrete, with S2 only weakly joined to S1 by a slight depression (*e.g.* Figs 7E, H; 8A, B). Differences in the definition of the shallow transverse depression adaxial to S2 may also be attributed to deformation (*e.g.* compare Fig. 7E, H with Fig. 8E, G).

Spiniscutellum umbelliferum, *S. larviferum* and *S. plasi* all differ from *S. greenii* in their shorter (sag., exsag.) anterior cephalic border (though the border varies in length in *S. umbelliferum*; see Whittington 1999, fig. 3.1, 3.4); deeper S2; very short genal spines; shorter sagittal furrow on the postaxial rib; and the sculpture of the dorsal surface – a combination of granules, fine tubercles and fine terrace ridges in *S. umbelliferum* and *S. larviferum*, the terrace ridges in *umbelliferum* being concentrated in more marginal regions of cranidia and pygidia, and weak terrace ridges in *S. plasi* (Chlupáč 1986, p. 206). *Spiniscutellum umbelliferum* and *S. plasi* also differ from *S. greenii* in that their pygidia are relatively longer compared with large pygidia of *S. greenii*; and in *S. plasi* the thorax has a relatively wider axis and correspondingly narrower pleural region, and the pygidial interpleural furrows and the sagittal furrow on the postaxial rib expand only weakly distally.

Spiniscutellum aff. *greenii* (see Jones *et al.* 1981, fig. 3a–c) from the Lochkovian of the Bungonia district of south-eastern New South Wales is very similar to *S. greenii* in the strongly laterally expanded frontal lobe of the glabella and the relatively long anterior cephalic border. However, it differs in having a prominent posterior node on the median lobe of the pygidial axis and more strongly distally expanded interpleural furrows. In addition, casts of external moulds of a cranidium (counterpart of Jones *et al.* 1981, fig. 3a) and several pygidia illustrated by McTackett (2002, pl. 6, figs c, e, f, h) show traces of tuberculate sculpture, in contrast to the coarse terrace ridges present in *S. greenii*.

Acknowledgements

I thank Michael Melchin (St Francis Xavier University, Nova Scotia) for his advice on the graptolite from the Humevale Formation at locality PL6750; Tony Wright (University of Wollongong, New South Wales) for providing a copy of the thesis by McTackett (2002); Francis Holmes and the late Enid Holmes for assistance in collecting specimens of *Mitroplax enormis* at Lilydale; and the reviewers Raimund Feist (Université Montpellier II) and Allart Van Viersen (Natuurhistorisch Museum Maastricht), whose helpful suggestions improved the manuscript.

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