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Early Silurian phacopide trilobites from central Victoria, Australia

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Abstract

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A diverse component of trilobite faunas in lower Silurian marine strata of central Victoria are members of the suborder Phacopina, here assigned to 19 species within the Phacopidae, Dalmanitidae and Acastidae. New genera are represented by the blind acastid *Berylacaste berylae* gen. et sp. nov. and the phacopid *Ivops wallanensis* gen. et sp. nov. Other new species are the phacopids *Acernaspis georgei* and *Ananaspis kenleyi*, and the dalmanitids *Preodontochile springfieldensis* and *Struveria*? *plinthourgos*. Two previously described species, *Ananaspis typhlagogus* Öpik, 1953 and *Dalmanites athamas* Öpik, 1953 [= '*Dalmanitina* (*Eudolatites*)' *aborigenum* Öpik, 1953], are revised. Other species are assigned to *Bessazoon*, *Phacopidella*? and indeterminate phacopid and dalmanitid genera. These trilobites are a significant representation of early Silurian Phacopina on the world scale.

Keywords Trilobita, Silurian, Phacopidae, Dalmanitidae, Acastidae, Victoria, Australia, systematics, new taxa

Introduction

Trilobite assemblages occur in lower Silurian (Llandovery and Wenlock) sedimentary sequences at various localities in central Victoria, between Costerfield in the north and Camberwell in metropolitan Melbourne in the south (fig. 1). Despite the occurrence in these sequences of at least 45 trilobite taxa, 19 of which are members of the Phacopina, only nine species have been described previously (Table 1). These include '*Phacops*' *typhlagogus* Öpik, 1953, *Dalmanites athamas* Öpik, 1953, *D. wandongensis* Gill, 1948 and '*Dalmanitina* (*Eudolatites*)' *aborigenum* Öpik, 1953. Fossil collections in Museum Victoria permit the revision of Öpik's poorly known species and the description of the 16 other species of Phacopina recorded.

Strata and ages

Stratigraphic terminology employed here follows Rickards and Sandford (1998), and differs significantly from that of VandenBerg et al. (2000) and VandenBerg (2003, figs 5.2, 5.7).

Trilobites of the suborder Phacopina occur at many horizons in the Llandovery and Wenlock strata of central Victoria. The stratigraphically lowest, and one of the earliest recorded trilobites from Victoria (as *Asaphus*, see Selwyn, 1863), is *Phacopidella*? sp. from a siltstone underlying the Lintons Creek Conglomerate Member of the Springfield Formation at Keilor, at a similar horizon to beds yielding graptolites of the late Llandovery (Telychian) *Spirograptus turriculatus–Monograptus crispus* biozones (Rickards and Sandford, 1998). Further north, on Deep Creek at Springfield, the uppermost part of the Springfield Formation, which is correlated with beds containing graptolites of the *Monoclimacis crenulata* Biozone, has yielded a low diversity deep water fauna of Phacopina dominated by *Preodontochile springfieldensis* sp. nov. The overlying sandstones of the Chintin Formation contain several more diverse trilobite faunas including three representatives of the Phacopina, *Acernaspis georgei* sp. nov., *Ananaspis typhlagogus*? (Öpik, 1953) and *Bessazoon* sp., suggesting an age range for the unit of latest Llandovery–early Wenlock.

Known from a single specimen from Camberwell, *Struveria*? *plinthourgos* sp. nov. is part of a poorly sampled trilobite fauna occurring high in the Anderson Creek Formation in the eastern suburbs of Melbourne, at similar horizons to those yielding graptolites of the late Wenlock (early Homerian) *Cyrtograptus lundgreni–Testograptus testis* Biozone (Rickards and Sandford, 1998). The only other trilobites known from the formation are three specimens of the blind illaenid *Thomastus jutsoni* (Chapman, 1912) and one of an undescribed homalonotid.

Öpik (1953) documented a trilobite fauna from concretion-bearing mudstones of the so-called '*Illaenus* band' in the Costerfield area. Following Thomas (1937) this unit was traditionally regarded as defining the base of the Wapentake Formation, but Edwards et al. (1998) placed the '*Illaenus* band' at the top of the underlying Costerfield Siltstone. Although

Table 1. List of trilobite taxa in the Llandovery and Wenlock beds of central Victoria. Taxa from the Yan Yean Formation marked with † occur only in the upper horizons of the unit, which are earliest Ludlow in age.

Yan Yean Formation (late Wenlock-earliest Ludlow)
Proetidae indet.
Decoroproetus sp.†
Maurotarion euryceps (McCoy, 1876)
Encrinuridae indet.
Sthenarocalymene sp. †
Trimerus (*Trimerus*) *vomer* (Chapman, 1912) †
Ananaspis kenleyi sp. nov. †
Phacopidae gen. indet 1. †
Dalmanites wandongensis Gill, 1948
Kettneraspis hollowayi Sandford, 2000 †

Anderson Creek Formation (Wenlock)
Thomastus jutsoni (Chapman, 1912)
Trimerus? sp.
Struveria? plinthourgos sp. nov.

Bylands Siltstone (Wenlock)
Thomastus aops Sandford and Holloway, 1998
Proetidae indet.
Homalonotid indet.
Ananaspis sp. 1
Ivops wallanensis gen. et sp. nov.
Ananaspis typhlagogus? (Öpik, 1953)
Struveria sp. 2
Berylacaste berylae gen. et sp. nov.
Dicranurus sp.
Selenopeltinae sp.
Odontopleuridae indet.

Wapentake Formation (Wenlock)
Thomastus thomastus Öpik, 1953
Maurotarion sp.
Trimerus (*Ramiotis*) *tomczykowae* Sandford, 2005
Ananaspis typhlagogus (Öpik, 1953)
Acernaspis? sp..

Wapentake Formation (cont.)
Dalmanites athamas Öpik, 1953
Struveria sp. 2
Odontopleuridae indet.

Chintin Formation (latest Llandovery–early Wenlock)
Proetidae sp.
Decoroproetus sp.
Radnoria sp.
Encrinuridae indet.
Calymene sp.
Calymenella sp. 1
Trimerus (*Ramiotis*) *rickardsi* Sandford, 2005
Acernaspis georgei sp. nov.
Ananaspis typhlagogus (Öpik, 1953)
Bessazoon sp.
Odontopleuridae indet.

Springfield Formation (mid-late Llandovery)
Encrinuridae indet.
Hadromeros? sp.
Calymenella sp. 2
Phacopidella? sp.
Phacopidae gen. indet. 2
Phacopidae gen. indet. 3
Preodontochile springfieldensis sp. nov.

Costerfield Siltstone (late Llandovery?)
Dalmanitidae indet.

Deep Creek Siltstone (early-mid Llandovery)
Calymenidae indet.

Uncertain stratigraphic assignment
Ananaspis sp. 2
Struveria sp. 1

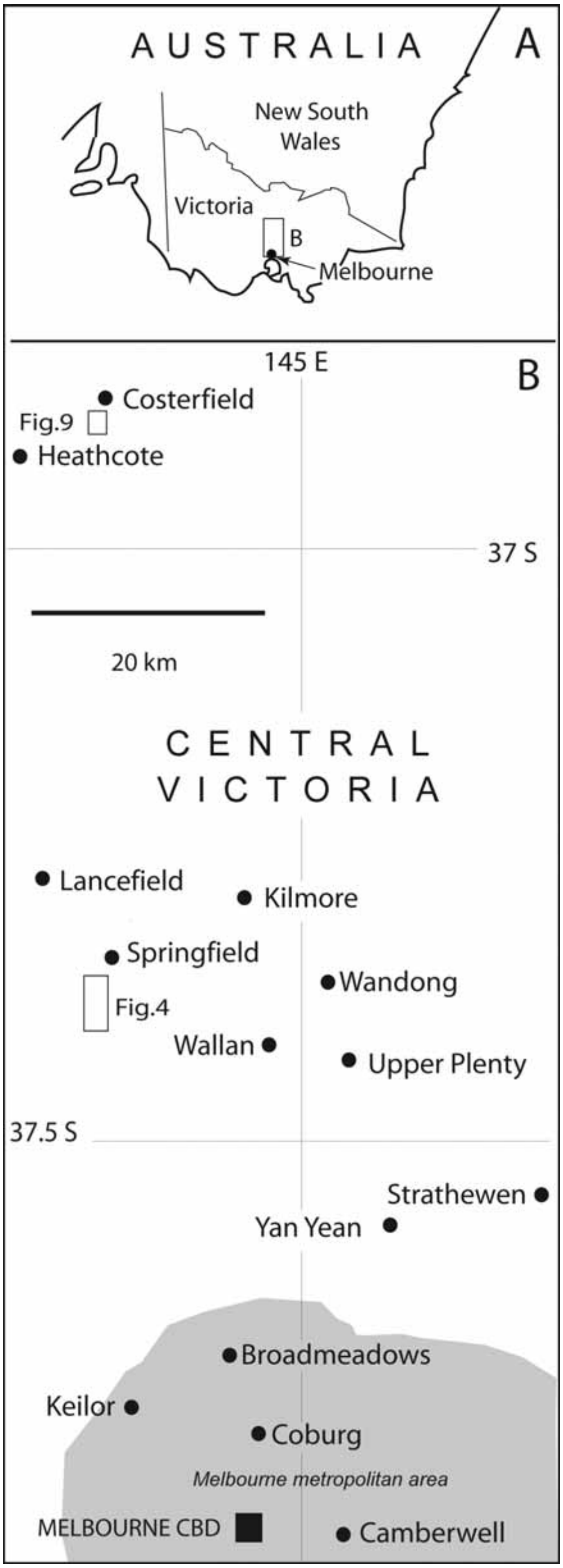

Figure 1. A, map of south-eastern Australia; approximate area of fig. 1B is indicated by a rectangle. B, map of central Victoria showing localities cited in the text; the areas covered by maps in figs. 4 and 9 are indicated.

Thomas (1940, 1941, 1956) mapped the '*Illaenus* band' as a distinct horizon extending around most of the Costerfield Dome, Edwards et al. (1998: 50) stated that it is not an extensive mappable unit. As noted by Rickards and Sandford (1998), fossils are not confined to a narrow horizon in this part of the sequence; indeed at localities on the western side of the Heathcote–Nagambie road both *Thomastus* (attributed to *Illaenus* by Thomas, 1937) and concretions occur 200 m stratigraphically below and 100 m above the band as mapped by Thomas (see fig. 9). Hence several concretion-rich beds seem to be present over a fairly wide stratigraphical interval, and as there is otherwise no distinct lithological change in this part of the sequence it seems an inappropriate level to define a lithostratigraphical boundary. Rickards and Sandford (1998) defined the base of the Wapentake Formation at the top of sandstones lower in the sequence (the Costerfield Sandstone of Reeder, 1990), and that is the boundary accepted here. We do not recognise the '*Illaenus* band' as a distinct unit of the Wapentake Formation, and we use the former term only when referring to poorly localised material from old collections.

The fauna of the Wapentake Formation is dominated by the illaenid *Thomastus thomastus* (see Sandford and Holloway, 1998) but Öpik also described three species of Phacopina, namely '*Phacops*' *typhlagogus*, *Dalmanites athamas* and '*Dalmanitina* (*Eudolatites*)' *aborigenum*. Öpik considered that shelly elements of the fauna indicated a late Llandovery age but noted the post-Llandovery aspect of certain elements including *D. athamas*. From a sandy concretion within the beds Thomas in Öpik (1953: 12) identified the graptolites *Monograptus* cf. *jaculum* and *Climacograptus hughesi*; however, these identifications cannot be confirmed as the specimens are lost, so the postulated late Llandovery age cannot be verified. Rickards and Sandford (1998) considered that the presence of *Ananaspis* indicated a Wenlock age for the fauna, and noted the similarity of the trilobite assemblage to that of the Wenlock Anderson Creek Formation, with both faunas having *Thomastus* as the dominant element and also containing dalmanitid and homalonotid species.

At Wallan Rickards and Sandford (1998) distinguished a massive siltstone from the underlying Chintin Formation and named it the Bylands Siltstone. The unit contains several species of Phacopina including the blind acastid *Berylacaste berylae* gen. et sp. nov., the phacopids *Ivops wallanensis* gen. et sp. nov. and *Ananaspis typhlagogus*?, the dalmanitid *Struveria* sp. and, at a slightly higher horizon, *Ananaspis* sp. 1. As in the case of the Wapentake Formation assemblage, the presence of *Ananaspis* and the similarity of the Wallan fauna to that of the Anderson Creek Formation indicates a Wenlock age for the unit.

Dalmanites wandongensis dominates a low diversity trilobite fauna from the middle horizons of the Yan Yean Formation at Wandong and Kilmore. Graptolites from these horizons belong to the latest Wenlock *Colonograptus ludensis* Biozone. *D. wandongensis* ranges into the upper horizons of the Yan Yean Formation, of earliest Ludlow age (*Neodiversograptus nilssoni* Biozone), where it dominates a more diverse fauna including the phacopid *Ananaspis kenleyi* sp. nov. Farther south at Strathewen the upper beds of the Yan Yean Formation have yielded a single specimen of a phacopid

(Phacopidae gen. indet. 1 herein) with small eyes, a condition that may be associated with life in a deep-water environment (Fortey and Owens, 1997: 267; Whittington, 1997: 163).

Faunal comparisons

Trilobites are poorly represented in the Victorian Llandovery (Table 1). None are known from Rhuddanian strata, and only *Hadromeros, Phacopidella*?, an indeterminate flexicalymenine and an indeterminate encrinurid from the Aeronian–lower Telychian, making comparison difficult with faunas from this interval elsewhere. Trilobites are more abundant in upper Telychian strata. *Calymenella* occurs in the Calton Hill Sandstone Member of the Springfield Formation. The low diversity *Preodontochile* fauna from the uppermost beds of the Springfield Formation on Deep Creek compares only to the monospecific *Preodontochile* fauna from the Llandovery of Spain. These *Preodontochile* faunas are interpreted as atheloptic assemblages representing a deep water biofacies whose relationship to other Llandovery deep water assemblages is unclear. Edgecombe and Sherwin (2001) interpreted the *Aulacopleura–Raphiophorus* Biofacies as inhabiting cold, deep-water, offshore environments, and Chatterton and Ludvigsen (2004) regarded the *Maurotarion*–dalmanitid Biofacies as a deep water fauna representing depths not as great as the *Aulacopleura–Raphiophorus* Biofacies. The latter is represented in Australia by a low-diversity fauna from the early Telychian Cotton Formation in central New South Wales (Edgecombe and Sherwin, 2001), containing *Aulacopleura*, *Raphiophorus* and *Odontopleura* (*Sinespinaspis*), and bears no similarity to the Llandovery faunas of central Victoria. The late Telychian to Sheinwoodian Chintin Formation yields the oldest diverse trilobite faunas in the Silurian of central Victoria. Eleven taxa are present including *Acernaspis georgei* sp. nov., *Ananaspis typhlagogus*? (Öpik, 1953), *Bessazoon* sp., *Trimerus* (*Ramiotis*) *rickardsi* Sandford, 2005, *Radnoria* sp., *Calymene* sp., *Decoroproetus* sp. and *Calymenella* sp. In composition the Chintin fauna is closely comparable to that of the late Telychian Richea Siltstone in south-west Tasmania (Holloway and Sandford, 1993), which also contains species of *Acernaspis, Bessazoon, Trimerus* (*Ramiotis*) and *Decoroproetus*. Taxa represented in the Richea fauna but not known from the Chintin fauna include *Maurotarion, Dicranurus, Gravicalymene, Anacaenaspis* and *Latiproetus*?

The only other Llandovery trilobite faunas known from Australia occur in the Broken River region of north Queensland. The early Telychian fauna of the Poley Cow Formation contains *Gaotania, Gravicalymene*?, *Prostrix, Batocara, Coronocephalus*, *Kosovopeltis*, *Proetus, Warburgella*?, *Otarion, Maurotarion, Scharyia, Youngia, Sphaerexochus, Sphaerocoryphe* and *Ceratocephala* (Holloway, 1994). From the laterally equivalent Quinton Formation, Lane and Thomas (1978) described *Rhaxeros, Sphaerexochus, Encrinurus*?, a possible warburgelline and an indeterminate calymenid, and Öpik (in White, 1965: 43) listed *Encrinurus*, *Proetus*?¸ *Onycopyge* or *Sphaerexochus*, and undetermined scutelluids. These faunas thus show little similarity in generic composition to the Llandovery faunas of Victoria and Tasmania, and they further differ in lacking phacopids, homalonotids and dalmanitids, and in the presence of scutelluids and illaenids. These differences may reflect biogeographical provincialism or environmental preferences. Rickards, Wright and Sherwin (*in* Pickett et al., 2000: 131) noted an analogous contrast between the Llandovery graptolite faunas of north Queensland and those of central Victoria, the latter having much stronger European affinities (98% of species) than the Queensland faunas (75% of species). Rickards et al. considered that the composition of the Victorian graptolite faunas indicate stronger interaction with the Americas rather than with the Uralian-Cordilleran Province.

Trilobites represented in the lower and middle Wenlock of central Victoria include species of *Thomastus, Maurotarion, Decoroproetus*, *Trimerus* (*Ramiotis*), *Ivops* gen. nov., *Ananaspis*, *Dalmanites, Struveria*, *Berylacaste* gen. nov., *Dicranurus*, and indeterminate Encrinuridae and Odontopleuridae. Faunas of similar age are present in the Rosyth Limestone and the laterally equivalent Boree Creek Formation in the Orange district, central western New South Wales, but of the 29 genera from those formations listed by Holloway (*in* Pickett et al., 2000: 163) only *Ananaspis*, *Decoroproetus* and *Dicranurus* also occur in central Victoria, and dalmanitids, homalonotids and acastids are conspicuously absent from the New South Wales faunas.

Differences in faunal composition between central Victoria and more northerly regions continued into the late Wenlock and earliest Ludlow. The only trilobite genus in common between the Yan Yean Formation and the Walker Volcanics of the Canberra area (see Holloway *in* Pickett et al., 2000: 164) is *Sthenarocalymene* (= *Gravicalymene*? of Holloway's list), and the latter fauna lacks phacopids and dalmanitids but includes scutelluids, illaenids, harpetids, cheirurids and staurocephalids that are absent from the Yan Yean. Diverse trilobite faunas of mid-Wenlock to early Ludlow or possibly even late Ludlow age occur in the Orange–Molong district in limestone bodies within the Mirrabooka Formation, and in the laterally equivalent Borenore and Molong limestones. Illaenids and scutelluids dominate the fauna, which otherwise resembles that from the underlying Boree Creek Formation except that phacopids are absent (Holloway and Lane, 1998).

The general absence of phacopid and dalmanitid trilobites in the Wenlock faunas of the Canberra and Orange districts (apart from the occurrence of *Ananaspis* in the Boree Creek Formation and Rosyth Limestone) is at least partly due to environmental preferences. The Silurian sequences of those districts were deposited on a series of offshore highs and troughs whereas those of central Victoria were deposited on the continental margin. The fauna of the Borenore Limestone and its stratigraphical equivalents is similar to those occurring in lithologically similar pure limestones of Silurian age elsewhere in the world (see Lane, 1972; Thomas and Lane, 1998). Mikulic (1981) reported that in middle and late Silurian reef limestones of North America the reef core is dominated by illaenids, scutelluids, lichids and cheirurids, and the reef fringes are characterised by assemblages of cheirurids, calymenids and encrinurids. He interpreted rare phacopid and dalmanitid trilobites in the reef fringes as temporary migrants from non-reef areas.

After the Wenlock members of the Phacopina were a significant component of trilobite faunas in New South Wales as in Victoria. The fauna of the late Ludlow Rosebank Shale in the Yass district includes both phacopids and dalmanitids [*Ananaspis crossleii* (Etheridge and Mitchell, 1896), *Dalmanites meridianus* (Etheridge and Mitchell, 1896)]. In the Early Devonian, *Echidnops*, *Paciphacops, Lochkovella, Odontochile*, several genera not belonging to the Phacopina, and at least one species (*Sthenarocalymene* sp. A, see Chatterton, Johnson and Campbell, 1979; Holloway and Neil, 1982) were present in both central Victoria and New South Wales; however, continuing limitations on faunal exchange is evident in the absence of homalonotids and acastids in New South Wales, and in the absence of harpetids in central Victoria.

Systematic palaeontology

With the exception of the partly mineralized exoskeletons preserved in concretions of the Wapentake Formation, all trilobite specimens figured here are preserved in mudstones and sandstones as internal and external moulds. For photography, internal moulds were coated with colloidal graphite, latex peels were made from external moulds, and all were whitened with ammonium chloride. Specimens housed in Museum Victoria are registered with the prefix NMV P, and those housed in the collections of Geoscience Australia, Canberra, are registered with the prefix CPC. Two missing specimens of *Ananaspis typhlagogus* are documented with registration numbers of the old Geological Survey of Victoria collection, prefixed GSV. Trilobite localities with the prefix PL are documented in the Museum Victoria invertebrate palaeontology locality register.

Order **Phacopida** Salter, 1864
Suborder **Phacopina** Richter, Richter and Struve, 1959
Superfamily **Phacopoidea** Hawle and Corda, 1847
Family **Phacopidae** Hawle and Corda, 1847

Remarks. In his seminal review of the Phacopidae in which he established the genera *Acernaspis* and *Ananaspis*, Campbell (1967) proposed a classification of the family that he considered to be ‘horizontal’ in the sense of Simpson (1961). His approach was criticised by some workers (e.g. Eldredge, 1973: 292) as creating paraphyletic and polyphyletic taxa, an outcome that was acknowledged by Campbell (1977: 26). Nevertheless, *Acernaspis* and *Ananaspis* have been universally recognised, and the former has come to be accepted as monophyletic (Ramsköld and Werdelin, 1991: 61).

Ananaspis continues to present more problems than *Acernaspis* because it embraces greater variability in characters such as the width of the cheeks in relation to that of the glabella, the relative lengths (exsag.) of L2 and L3, the size of the eye and the position of its lower margin in respect to the lateral border furrow, the depth of the vincular furrow medially and the strength of its notching laterally, the glabellar sculpture (but in relation to this character see remarks on *Acernaspis* below), and the width and degree of taper of the pygidial axis. These characters, many of which were regarded by Campbell (1967) and later workers as diagnostic of *Ananaspis*, are expressed to differing degrees and in a variety of combinations in the species assigned. Ramsköld and Werdelin (1991) restricted *Ananaspis* to a small number of species of Ludlow and Lochkovian ages [*A. orientalis* (Maksimova, 1968), to which Ramsköld and Werdelin ascribed a possible Ludlow age, is from the Kokbaital Horizon of Central Kazakhastan, now known to be early Lochkovian; Talent et al., 2001: 61]. Several other species previously assigned to *Ananaspis*, and of late Llandovery–late Wenlock age, were referred to by Ramsköld and Werdelin as ‘*Ananaspis*’ or *incertae sedis*, and said to represent ‘…a number of monospecific (or nearly so) genera … between *Acernaspis* and *Ananaspis*’ (Ramsköld and Werdelin, 1991: 56). We are not in complete agreement between ourselves on the relationships of these species which include ‘*Phacops*’ *typhlagogus* Öpik, 1953, redescribed below. However, it is difficult to identify any consistently developed characters that could be used to distinguish such species from others assigned to *Ananaspis* s.s. by Ramsköld and Werdelin, or to be sure that the latter species are more closely related to each other than to some of the species excluded from *Ananaspis* by those authors. Consequently *Ananaspis* is more broadly conceived herein than by Ramsköld and Werdelin.

Acernaspis Campbell, 1967

=*Eskaspis* Clarkson et al., 1977; =*Murphycops* Lespérance, 1968

Type species. *Phacops orestes* Billings, 1860 from the Jupiter Formation (Llandovery), Anticosti I., Quebec, by original designation.

Remarks. Chatterton and Ludvigsen (2004: 39) discussed the possible synonymy of *Acernaspis* with *Portlockia* McCoy, 1846 (type species *P. sublaevis*) from the Wenlock of western Ireland and gave notice of their intention to apply to the International Commission of Zoological Nomenclature to suppress the latter generic name as a *nomen oblitum*. We would support such an application as being in the best interests of nomenclatural stability.

Chatterton and Ludvigsen (2004) considered *Acernaspis mimica* Lespérance and Letendre, 1982 to be a synonym of *A. orestes*, and also noted that *A. superciliexcelsis* Howells, 1982 differs only in very minor respects from *orestes* and might be considered synonymous. These conclusions are in accord with the cladistic analysis of *Acernaspis* presented by Ramsköld and Werdelin (1991, fig. 5), in which these three taxa are grouped together. Curtis and Lane (1998) considered a number of other species to be synonyms of *orestes* including *A. quadrilineata* (Angelin, 1851), *A. konoverensis* Männil, 1970, *A. elliptifrons* (Esmark, 1833) and *A. sororia* Ramsköld, 1985; however, Ramsköld and Werdelin’s cladistic analysis shows these species and *orestes* grouped quite separately. Chatterton and Ludvigsen arrived at a similar conclusion, rejecting Curtis and Lane’s synonymy and listing a number of characters distinguishing *orestes* and *quadrilineata*, emphasising minor differences in the lens formula and the proportions of the glabella.

Acernaspis rubicundula Ramsköld, 1985, from the lower Wenlock of Sweden, was interpreted by Ramsköld as intermediate between *Acernaspis* and *Ananaspis* with respect to morphological trends that he recognised between his late Llandovery species *Acernaspis sororia* and *Ananaspis stokesii* (Milne Edwards, 1840) from the British Wenlock. He emphasised the glabellar width, the short (exsag.) L2 and the glabellar tuberculation as characters of *rubicundula* typical of *Ananaspis*, and remarked that *stokesii* differs from *rubicundula* in few features of which only the strongly forwardly expanding glabella and deep lateral border furrow (on the fixigena) were mentioned. Neotenic changes significant in the evolution of *Ananaspis* from *Acernaspis*, including a decrease in the length (exsag.) of L2 and the development of glabellar tuberculation, were outlined by Ramsköld (1988). In this context he interpreted *rubicundula* as a sister-taxon to all other *Acernaspis* species, exhibiting the first of these neotenic changes. In their cladistic analysis of *Acernaspis*, Ramsköld and Werdelin (1991) discovered that their consensus tree was essentially unresolved with the inclusion of *rubicundula* but on its removal an almost fully resolved consensus tree was obtained. Nevertheless they retained *rubicundula* in *Acernaspis*, and we agree that the majority of its characters clearly ally the species with that genus. However, in view of its unusual features, we assign *rubicundula* to *Acernaspis* with question, together with a somewhat similar species described below as *A.*? sp.

Acernaspis georgei sp. nov.

Figures 2, 3A–B, D–E, H–I

Acernaspis.—Rickards and Sandford, 1998: 750.

Type material. Holotype NMV P515 (cephalon) from PL1964, Geological Survey locality B25, Springfield. Paratypes NMV P138259 (cephalon), NMV P138262 (pygidium), NMV P138278 (pygidium), NMV P147765 (cephalon), NMV P147766 (cephalon), NMV P147796 (pygidium), NMV P312816 (cephalon) from PL256, Wallan. Paratype NMV P138271 (cephalon) from PL598, type section of the Chintin Formation, Springfield.

Other material. NMV P138260–P138261, NMV P147764, NMV P147767–P147768, NMV P147788–P147795, NMV P147797–P147806 from PL256, Wallan. NMV P139447–P139453 from ‘Lancefield’ (unknown locality in the Parish of Goldie). For localities see Thomas (1960), VandenBerg (1991), Sandford and Rickards (1999) (fig. 1), Sandford (2005) (fig. 11) and (fig. 4).

Derivation of name. After ACS’s late father.

Diagnosis. Anterior cephalic border comprising 2.5% sagittal cephalic length in dorsal view. Lateral glabellar furrows moderately impressed, S2 extending close to axial furrow, posterior branch of S3 weakly convex forward, anterior branch placed posteriorly, with midlength opposite anterior margin of palpebral lobe. Palpebral furrow moderately to deeply impressed, distinct palpebral rim furrow, eye length (exsag.) 45% sagittal cephalic length, postocular area with length (exsag.) 5% sagittal cephalic length, visual surface with 15 files of lenses with up to 6 (mostly 5) lenses per file. Genal angle obtusely angular, lacking prominent point or genal spine. Second and third pygidial pleural furrows moderately impressed.

Description. Cephalon semicircular, in frontal view with anterior margin weakly arched. Glabella weakly convex (sag., tr.), not reaching anterior cephalic margin in dorsal view, maximum width across frontal lobe approximately equal to cephalic length, 50% maximum cephalic width and 160% occipital width (tr.). Axial furrow wide and very deep, weakly converging between posterior margin and L1, diverging at 60° between L1 and a point opposite midlength of palpebral lobe, thereafter diverging forward at 20°. Anterior margin gently rounded in front of glabella, forming arc centred on posterior margin. Occipital ring with length (sag.) 15% cephalic length and width (tr.) 33% cephalic width, with exsagittal furrow impressed in anterior margin defining obliquely directed lateral lobes. Occipital furrow deeply impressed. L1 high, lateral node isolated by deep exsagittal furrow. S1 deep laterally, weak across median part of glabella. S2 and S3 moderately impressed on external surface. S2 directed at about 10° to transverse, straight, its inner end situated more or less opposite 40% glabellar length from posterior. Posterior branch of S3 with anteriormost point more or less opposite 55% sagittal glabellar length from posterior. Anterior branch of S3 oriented at 40° to exsagittal line, weakly sigmoidal. L2 and L3 equal in length (exsag.). Anterior border furrow moderately impressed. Anterior border wide. Eye placed with midlength opposite 38% sagittal cephalic length from posterior. Palpebral area high, convex. Palpebral lobe steeply inclined, flat (tr.), raised above palpebral area. Visual surface large, with up to 71 lenses, formula (NMV P138259, fig. 2D, H) 5 5 6 5 5 5 5 5 5 5 4 5 5 4 3. Posterior border furrow deep adaxially, terminating abruptly abaxially at a point in line (exsag.) with distal margin of eye. Posterior border narrow adaxially, widening slightly abaxially. Librigenal field concave below eye, not distinctly differentiated from lateral border furrow. Posterior branch of facial suture skirting posterior margin of eye abaxially, crossing genal area directed anterolaterally at about 25° to transverse, reaching a point opposite 33% sagittal cephalic length, deflected backwards at same angle abaxially. Cephalic doublure with vincular furrow deep throughout and strongly notched laterally. Cephalic sculpture finely granulate.

Pygidium lenticular in dorsal outline. Axis comprising 85% sagittal pygidial length and 30% maximum pygidial width anteriorly, with 6 rings that are well defined in anterior part of axis and poorly defined in posterior part, terminal piece merging with postaxial region. Pleurae with 5 pleural furrows, anterior one narrow (exsag.), deep, reaching 75% distance to margin, remaining pleural furrows successively shallower, posteriormost one very weak. Interpleural furrows very shallow. Border and furrow not defined.

Remarks. *Acernaspis georgei* occurs at several localities in the Chintin Formation, although its relative abundance, faunal associates, preservation and associated lithology vary markedly. In Slab Hut Creek at PL256, Wallan, the species is common (relative abundance 44%) and together with *Calymene* (relative abundance 35%) dominates the fauna preserved almost entirely as fragmentary cephala and pygidia. The trilobites at PL256 occur within bioclastic sandstone coquinas which contain abundant disarticulated crinoid elements, gastropods, bryozoans and clasts of siltstone incorporated into the coquina in the plastic

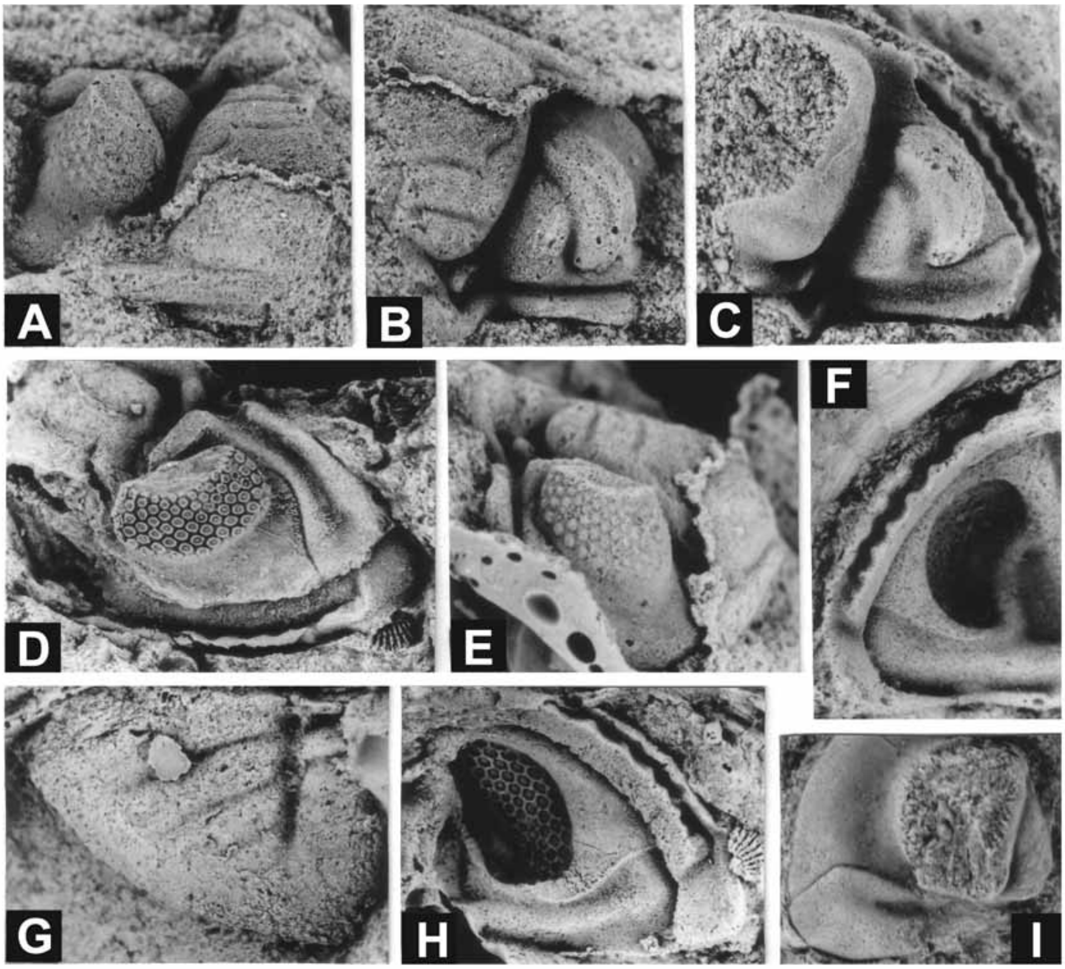

Figure 2. *Acernaspis georgei* sp. nov. A–C, E–F, holotype NMV P515, cephalon (fragment), from PL1964, Springfield; A–C, × 5; E, × 6.5; F, × 6. D, H, paratype NMV P138259, cephalon, from PL256, Wallan; D, × 5; H, × 4. G, paratype NMV P138261, pygidium, × 8, from PL256, Wallan. I, paratype NMV P138271, cephalon (fragment), × 7, from PL598, Springfield. (C, D are internal moulds).

state, presumably as rip-up clasts. The coquinas are bedded but form large irregular bodies within massive siltstones, with which they have sharp contacts. At 'Lancefield' the species occurs (relative abundance 14%) in a fauna dominated by *Bessazoon* sp. and *Calymene* sp., preserved as isolated and generally undamaged exoskeletal elements in medium-grained sandstone.

The species can be confidently assigned to *Acernaspis*. Significant characters in this assignment include the low glabellar profile, non-tuberculate cephalic ornament, long (exsag.) L2 (equal in length to L3), wide anterior border visible in dorsal view, poorly defined lateral cephalic border furrow, short postocular area, strong notching of the vincular furrow laterally and the weak expression of the pygidial interpleural furrows and the fourth and fifth pleural furrows.

A poorly known, unnamed species of *Acernaspis* was described by Holloway and Sandford (1993) from the late Llandovery Richea Siltstone of Tasmania. The present species differs from the Tasmanian one in having a longer postocular area, a deeper palpebral furrow and a longer anterior cephalic border. '*Phacops*' *macdonaldi* Fletcher, 1950, from the upper Llandovery to lower Wenlock of the Orange district, New South Wales, was tentatively assigned to *Acernaspis* by Sherwin (1971), but is now assigned to *Ananaspis* along with its junior subjective synonym '*Acernaspis*?' *oblatus* [*sic*] Sherwin (see discussion of *Ananaspis typhlagogus*).

Acernaspis georgei is most similar to the type species *A. orestes*. The two species share a relatively long (sag.) anterior cephalic border, a long postocular area and a non-spinose genal angle. *A. georgei* has one fewer lens file in the eye but otherwise shares a similar lens formula to small-eyed morphs of *orestes*, which have 16 files of up to six (mostly five) lenses per file. The species differ most notably in the arrangement of the lateral glabellar furrows and in the deeper palpebral furrows of *georgei*.

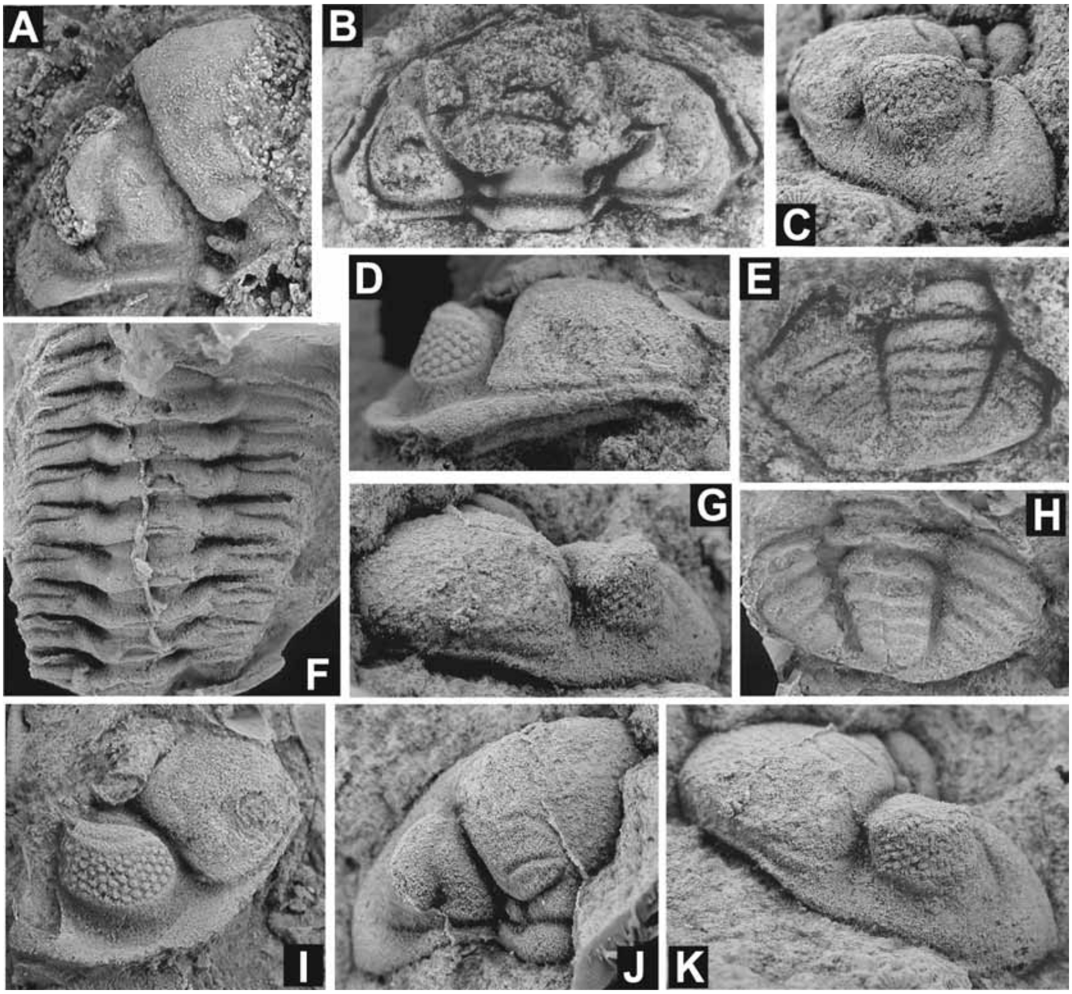

Figure 3. A–B, D–E, H–I, *Acernaspis georgei* sp. nov. A, paratype NMV P147766, incomplete cephalon, × 4, from PL256, Wallan. B, NMV P139448, damaged cephalon with cephalic doublure exposed, × 3.25, from 'Lancefield'. D, I, paratype NMV P312816, incomplete cephalon from PL256; D, × 5; I, × 4.5. E, NMV P139451, pygidium, × 4, from 'Lancefield'. H, paratype NMV P138262, pygidium, × 5, from PL256, Wallan. C, F–G, J–K, *Ananaspis typhlagogus* (Öpik, 1953) from PL6361, Springfield. C, G, J–K, NMV P312813, cephalon; C, J, K × 3.75, G × 4.75. F, NMV P312814, thorax, × 5. (A–B, H are internal moulds).

Species less closely related to *A. georgei* and *A. orestes* include Männil's (1970) Estonian species *A. semicircularis*, *A. estonica*, *A. sulcata*, *A. rectifrons* and *A. incerta*, and the Scottish *A. xynon* Howells, 1982, all of which are easily distinguished in having acutely angular genal angles or short genal spines. In the depth and lateral extension of S2 (to a point close to the axial furrow), *A. georgei* resembles *A. besciensis* Lespérance and Letendre, 1982 from the Rhuddanian of Anticosti Island, Canada (=*A. salmoensis* Lespérance, 1988 *fide* Chatterton and Ludvigsen, 2004), the oldest known species of the genus. *A. besciensis* differs from *A. georgei* in many other features, notably in having fewer lenses per file but more files in the eye (up to four lenses in 16 files), a shorter (tr.) and more forwardly convex S3, a narrow preoccipital ring and a shallower preglabellar furrow.

***Acernaspis*? sp.**

Figures 5A–D

Material. NMV P139804 (incomplete cephalon) from PL385, Costerfield. Wapentake Formation. For locality see fig. 9.

Description. Anterior and anterolateral cephalic margins moderately arched upwards medially in anterior view. Glabella weakly convex (sag., tr.), low anteriorly, sides of composite lobe diverging at about 55° between level of S2 and outer end of preglabellar furrow. S1 curving forward adaxially, connected medially by wide (sag.), shallow depression. S2 moderately impressed, convex forwards, subparallel to posterior branch of S3, its inner end connected to S1 by shallow exsagittal furrow. L2 about 75% length (exsag.) of L3 adaxially. S3 distinctly shallower than S2; posterior branch of S3 not extending as far

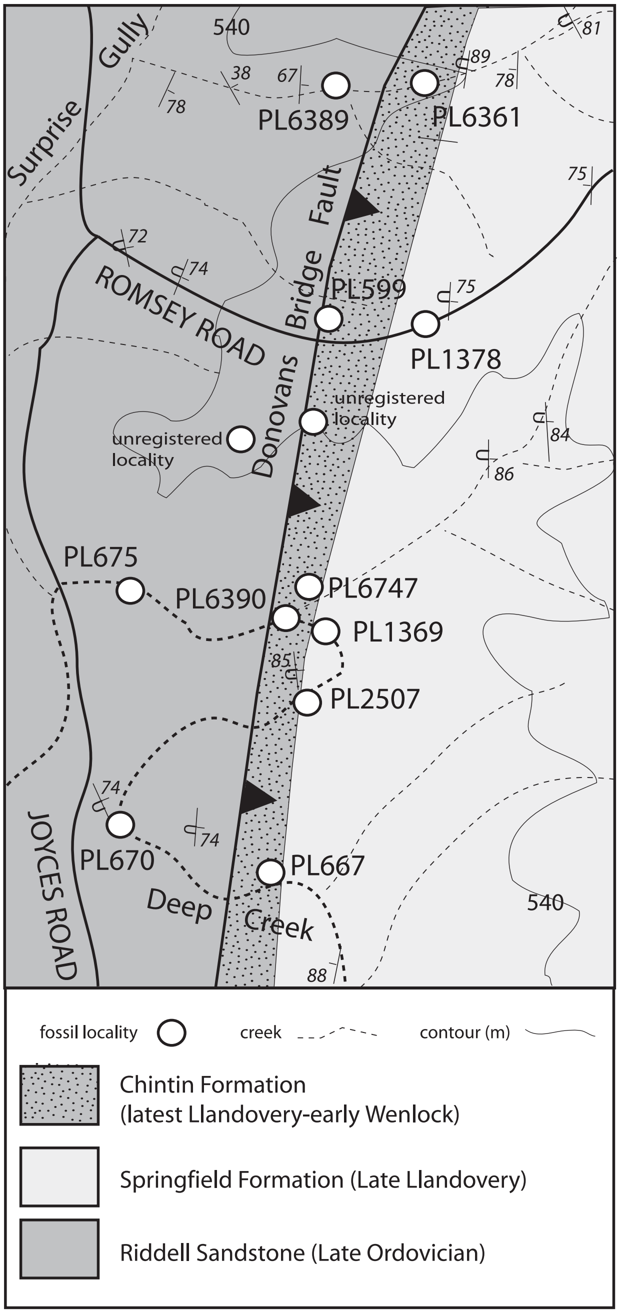

Figure 4. Fossil localities of the Springfield Formation, Chintin Formation and Riddell Sandstone in the Springfield area, 65 km NNE of Melbourne; the area covered by the map is indicated on fig. 1. The geology of this area given by Rickards and Sandford (1998) (fig. 6) is incorrect. The presumed faunal similarities with the Bylands Siltstone are not substantiated on description of the fauna herein. On lithological and apparent faunal similarities Rickards and Sandford erroneously correlated the siltstone at PL1369 with the Bylands Siltstone and showed the Chintin Formation underlying it. Additional field observations show that the Chintin Formation crops out upstream from and hence overlies PL1369, which lies in the uppermost beds of the Springfield Formation, as mapped by VandenBerg (1991).

adaxially and abaxially as S2; anterior branch not quite meeting posterior branch, oriented at about 60° to sagittal line and very weakly curved, meeting axial furrow anteriorly. Preglabellar furrow moderately impressed, continuous medially. Anterior cephalic border of almost uniform length (sag., exsag.) except abaxially. Preserved portion of eye (more than anterior half) with 12 files of lenses, formula (from anterior) 4 5 6 7 6 7 6 6 6 6 7 6 …, sclera depressed. Palpebral lobe raised high above palpebral area, with shallow but distinct rim furrow; anterior part of palpebral furrow deep and narrow. Librigenal field concave below eye and merging with lateral border furrow. Anterior branch of facial suture cutting across anterolateral corner of glabella (fig. 5B–C). Vincular furrow moderately impressed medially, deep laterally with strong notching. Medial part of cephalic doublure not raised as high above vincular furrow anteriorly as posteriorly, giving doublure a step-like profile or 'bevelled' morphology. Composite glabellar lobe with sculpture of low, perforate tubercles of small to moderate size.

Remarks. The species is represented by a single, incomplete cephalon lacking the posterior portion more or less behind a transverse line through the medial part of S1. The specimen differs from *Ananaspis typhlagogus* from the same formation in that the glabella is much more weakly convex, not as strongly curved in anterior outline and does not overhang the anterior border; the anterior border is wider (sag., exsag.); S2 is deeper, more strongly curved (not transverse adaxially), runs subparallel to the posterior branch of S3, and is connected to S1 adaxially by a shallow exsagittal furrow; the posterior branch of S3 is narrower (tr.) and the anterior branch longer; the preglabellar furrow and preserved portion of the palpebral furrow are deeper; and the visual surface does not overhang the lateral border as strongly in dorsal view and is higher, with more lenses per file (up to seven instead of five as in *typhlagogus*). Although it could be suggested that the low glabellar profile of the specimen is due to tectonic flattening, we consider that this is unlikely because of the other differences from *typhlagogus* listed, especially those in the eyes.

Acernaspis? sp. differs from most species of *Acernaspis* except *A.*? *rubicundula* Ramsköld, 1985, from the lower Wenlock of Sweden, in having tuberculate sculpture on the composite glabellar lobe (see discussion above under genus). *A.*? *rubicundula* differs from *A.*? sp. in that S2 is not as curved, does not extend as close to the sagittal line and is not connected to S1 adaxially by a weak longitudinal furrow; L2 is much shorter (about half length of L3 adaxially); S3 is deeper, with a shorter anterior branch not extending as close to the posterior branch; and S2 and S3 have weakly raised rims. These differences suggest that the Victorian species may not be most closely related to *rubicundula*, despite the similarity in glabellar sculpture.

Ananaspis Campbell, 1967

Type species. *Phacops fecundus* Barrande, 1846 from the Kopanina Formation (Ludlow), Koledník, Bohemia, by original designation.

Diagnosis. Glabella moderately to strongly convex (sag., tr.), vertical or slightly overhanging anteriorly in dorsal view.

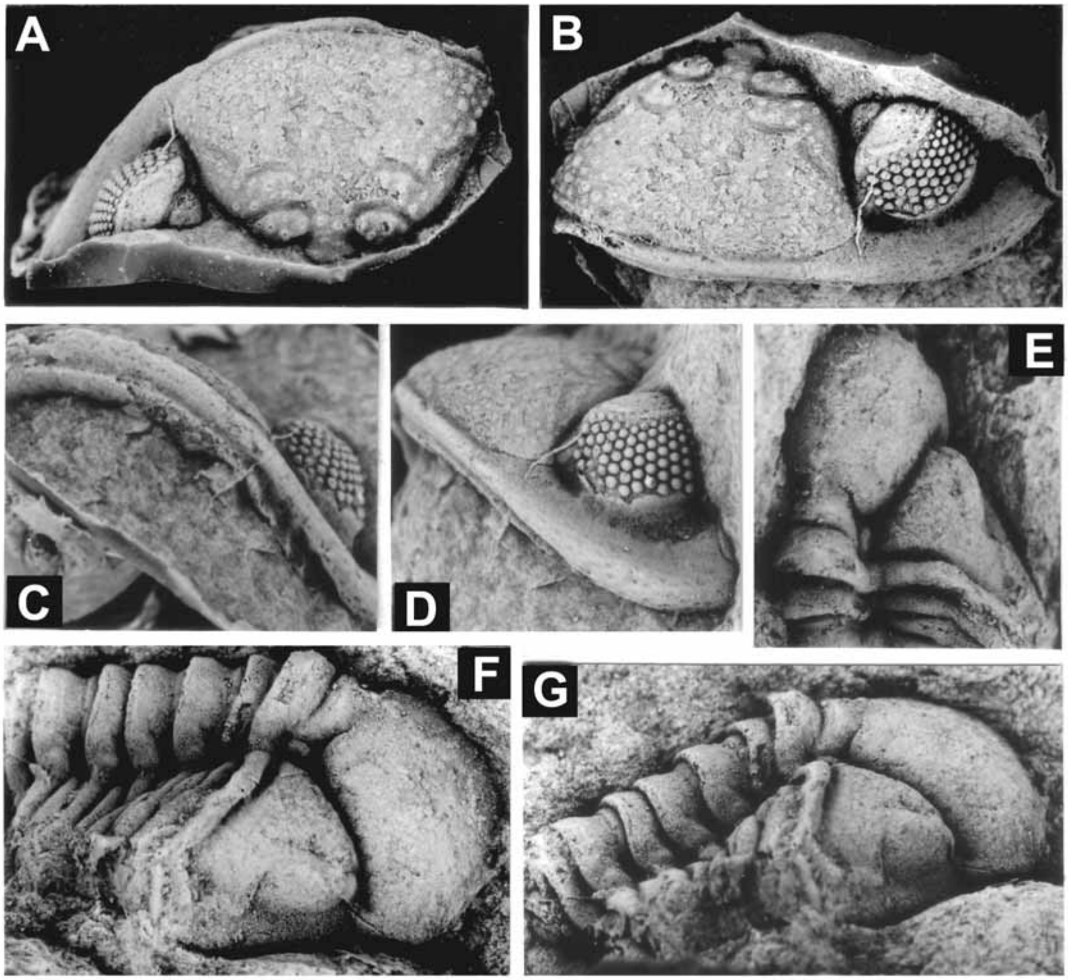

Figure 5. A–D, *Acernaspis*? sp., NMV P139804, cephalon, × 4, from PL385, Costerfield. E–G, Phacopidae gen. indet. 3, NMV P139353, enrolled exoskeleton from PL1369, Springfield; E, × 4.0; F, × 4.5.

Composite lobe expanding strongly forward, maximum width twice width at L1 or a little more. L2 commonly significantly shorter (exsag.) than L3. Eye of moderate to large size, lower edge situated in or slightly above lateral border furrow anteriorly and distant from lateral border furrow posteriorly, visual surface lacking strongly raised sclera (may be slightly thickened dorsally). Palpebral area as high as or higher than palpebral lobe. Fixigenal portion of lateral border furrow deep and continuous with posterior border furrow. Vincular furrow shallow to moderately impressed medially, commonly rather weakly notched laterally. Glabellar sculpture of bimodal tubercles lacking perforations and with superimposed and interspersed granules, doublure finely and densely granulate. Hypostome with short (sag.) posterior border having 3 angular points on margin. Pygidial pleural furrows deep and wide (exsag.), interpleural furrows distinct.

Remarks. This diagnosis distinguishes *Ananaspis* from a number of closely related genera recognised since the work of Campbell (1967). *Echidnops* Sandford, 2002 is the closest to *Ananaspis* but differs not only in having characteristic occipital and thoracic axial spines but also a much more deeply incised vincular furrow medially. *Paciphacops* Maksimova, 1972 is distinguished especially by the strongly raised sclera on the visual surface and the perforate glabellar tubercles, but in addition L1 is more depressed medially, the glabella is more raised and subquadrate in anterior profile, and the vincular furrow is deep medially. *Lochkovella* Chlupáč, 1972 (see also Sandford, 2004) differs from *Ananaspis* in that the cephalic tuberculation is finer and of more uniform size, the eye is situated very low on the cheek with its lower edge indenting the lateral cephalic border, the hypostome has a long (sag.) posterior border with five marginal denticles, the pygidial interpleural furrows are not as deep, and the pygidial granulation is coarser. Similar distinctions can be made with *Nephranomma* Erben, 1952 (see Sandford, 2003) which further differs from *Ananaspis* in lacking a vincular furrow medially and in having a distinctive scaly sculpture on the cephalic doublure. See the remarks on *Ivops* gen. nov. for comparison of that genus with *Ananaspis*.

Ananaspis kenleyi sp. nov.

Figures 6A–H, I?, J–K

> *Ananaspis*.—Rickards and Sandford, 1998: 753.
> '*Ananaspis*' sp. nov.—Sandford, 2000: 199.

Type material. Holotype NMV P136821 (cephalon) from PL375, Kilmore East. Paratype NMV P136815 (cephalon) from PL377, Kilmore East. Paratypes NMV P136819 (cephalon), NMV P136820 (pygidium), NMV P140154 (enrolled thoracopygon), NMV P140155 (cephalon), NMV P140156 (cephalon) from PL375, Kilmore East. Yan Yean Formation.

Other material. NMV P137165 from PL286, Williams locality F22, Wandong. NMV P136801, NMV P137142 from ''Wandong'' (exact locality unknown). NMV P136816 from PL377, Kilmore East. NMV P136802, NMV P138648 from PL380, Geological Survey locality Bb18, Wandong. NMV P137146 from PL1692, Wandong. NMV P140403 from PL1691, Kilmore East. NMV P139409 from PL1342, Kilmore East. NMV P140598 from PL1699, Upper Plenty. Yan Yean Formation. For localities see Taylor (1864), Williams (1964) (fig. 2) and Sandford (2006) (figs 2–3).

Derivation of name. After Peter Kenley, formerly of the Geological Survey of Victoria, who made valuable fossil collections from the Silurian of central Victoria.

Diagnosis. Eye large, length (exsag.) 44% sagittal cephalic length, placed with midlength opposite 45% sagittal cephalic length from posterior, visual surface with about 20–21 files of up to 7 lenses, postocular fixigenal field short, 7% sagittal cephalic length. Posterior border furrow narrowing and shallowing abaxially behind eye, terminating almost in line (exsag.) with lateral extremity of visual surface. Lateral border furrow indistinct, especially on librigena. Vincular furrow wide and shallow medially. Glabella with low tubercles of moderate size and density. Pygidium with 6–7 axial rings, 2nd to 5th ones with successively diminishing pseudo-articulating half rings. Five distinct pygidial pleural furrows, first 3 much deeper than remainder, last one very shallow, interpleural furrows very weak.

Description. Glabella narrow, maximum width approximately 80% sagittal length and 175% occipital width, placed level with 70% sagittal length from posterior. Axial furrow weakly converging forward adjacent to occipital ring and L1, wide and deep in front of occipital ring, diverging forward at about 65° adjacent to composite lobe. Occipital ring comprising 12% cephalic length sagittally, with small notch in anterior margin defining obliquely oriented lateral lobe. Occipital furrow deep, transverse medially. Medial part of L1 as high as composite lobe, lateral node small, depressed, isolated by deep exsagittal furrow. Glabellar width at L1 85% occipital width. S1 shallowing rapidly adaxial to inner edge of L1 node, expanding forwards to become a wide (sag.), triangular depressed area. S2 and S3 variably impressed. S2 weakly arcuate, reaching axial furrow, oriented at about 15° to transverse, anteriormost point opposite 38% sagittal cephalic length from posterior. Posterior branch of S3 strongly arcuate, anteriormost point opposite 55% sagittal glabellar length. Anterior branch of S3 sinusoidal, reaching axial furrow anteriorly. Length of L2 (exsag.) 70% length of L3 and 11% sagittal cephalic length. Front of glabella very high, strongly convex (tr.) in anterior view, in dorsal view forming strongly rounded arc centred at glabellar midlength (sag.) and overhanging anterior border. Preglabellar furrow shallow and wide. Palpebral area high, of low convexity, palpebral furrow moderately impressed, continuous with wide, moderately impressed sutural furrow behind eye. Palpebral lobe arcuate, of uniform width, raised above palpebral area. Lens formula from anterior (NMV P140136) 3 5 6 7 6 7 7 6 7 6 6 7 6 ? ? ? ? ? ? ? ? , about 120 lenses, visual surface without raised sclera. Librigenal field below eye concave, not distinctly separated from border. Medial part of cephalic doublure 30% sagittal cephalic length, anterior half very weakly convex (sag.) and posterior half weakly concave, vincular furrow running adjacent to anterior margin and separated from it by narrow (sag.) rim. Hypostomal suture transverse medially.

Thoracic axis narrowing weakly backwards, comprising about 30% segmental width (tr.). Axial rings with strong lateral nodes defined by posteriorly divergent furrows that notch front of segments. Pleurae horizontal and transverse adaxial of fulcrum, steeply inclined lateral to fulcrum and widening to well-rounded tips. Deep pleural furrow situated at midlength (exsag.) of segment at fulcrum, on anterior segments terminating distally at edge of articulating facet but extending onto facet on posterior segments.

Pygidium lenticular in dorsal view. Axis comprising 80% sagittal pygidial length and 25% maximum pygidial width anteriorly, tapering uniformly backwards. Axial rings strongly raised anteriorly, decreasing in height, length and definition posteriorly. First 5 rings comprise 72% axial length. Posterior end of axis broadly rounded and well defined. Pleural field weakly convex with weakly defined border. Anteriormost pleural furrow deep and wide, posterior furrows successively narrower (exsag.) and shallower.

Remarks. *Ananaspis kenleyi* occurs in the uppermost beds of the Yan Yean Formation at a number of localities between Upper Plenty and Kilmore but is nowhere common. It occurs together with the abundant *Dalmanites wandongensis*, and the rare *Trimerus* (*Trimerus*) *vomer* Chapman, 1912 and *Sthenarocalymene* sp.

Sandford (2000) considered *Ananaspis kenleyi* (as '*Ananaspis*' sp. nov.) to be most closely related and possibly ancestral to the distinctive *A. woiwurrungi* from the overlying Melbourne Formation. Sandford listed differences between the two species, *kenleyi* having stronger glabellar tuberculation that extends further posteriorly, shorter eyes, a deeper medial section of the vincular furrow and deeper pygidial pleural furrows (in *woiwurrungi* only the first to third pleural furrows are distinct on the external surface). Other differences in *kenleyi* are the narrower glabella (cf. maximum glabellar width 90% maximum cephalic width and 200% occipital width in *woiwurrungi*), shorter L2 (length 80% length of L3 and 15% sagittal cephalic length in *woiwurrungi*), fewer lenses in the eye (cf. 22 files with up to 8 lenses per file in *woiwurrungi*), slightly longer postocular fixigenal field (cf. length 5% sagittal cephalic length in *woiwurrungi*), indistinct lateral border furrow (shallow in *woiwurrungi*), shorter pygidial axis and less distinct interpleural furrows.

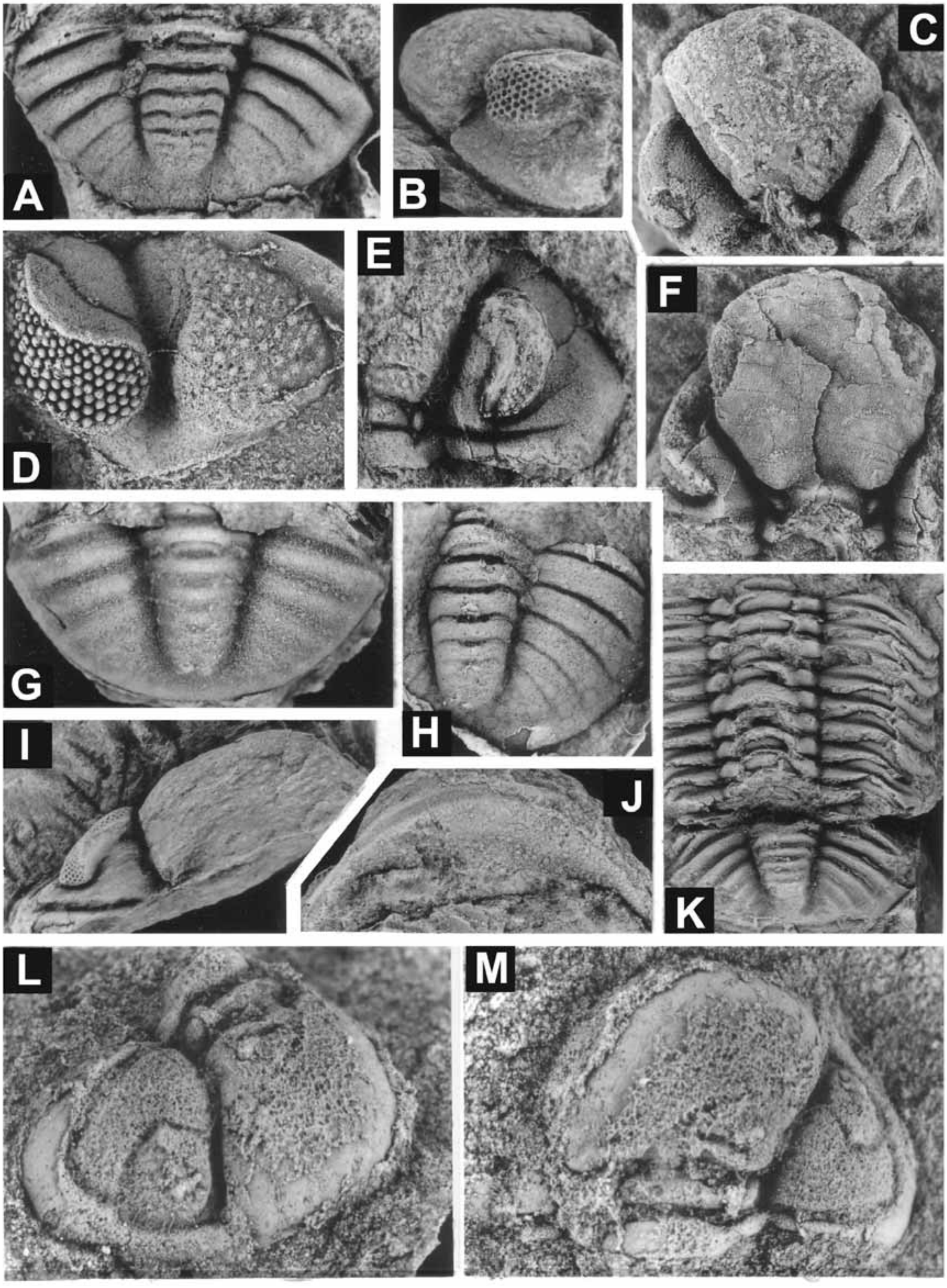

Figure 6. A–H, I?, J–K, *Ananaspis kenleyi* sp. nov. A, holotype NMV P136802, pygidium, × 6, from 'Broadhursts Creek', Wandong. B–C, paratype NMV P136821, cephalon × 4, from PL375, Kilmore East. D, paratype NMV P140156, cephalon, × 4.5, from PL375, Kilmore East. E, paratype NMV P140403, cephalon (fragment), × 2.5, from PL1691, Kilmore East. F, paratype NMV P137165, cephalon, × 3.5, from PL286, Wandong. G, paratype NMV P140154, thoracopygon with pygidium displaced and inverted, view of pygidium, × 4.5. H, paratype NMV P136820, pygidium with circular textural markings, × 4, from PL375, Kilmore East. I, paratype NMV P136815 cephalon, × 3, PL377, Kilmore East. J, paratype NMV P136819, exoskeleton with displaced cephalon, view of doublure, × 4, PL375, Kilmore East. K, paratype NMV P138648, thoracopygon, × 2.5, from 'Broadhursts Creek', Wandong. L–M, Phacopidae gen. indet. 1, NMV P136136 cephalon, × 5, from PL1368, Strathewen. (B–C, F–G, I–K are internal moulds).

Many of the differences between *kenleyi* and *woiwurrungi* can be interpreted in the context of ontogenetic and heterochronic processes. Chlupáč (1977) and Ramsköld (1988) discussed a number of features in the ontogeny of phacopids. Chlupáč noted that juvenile phacopids exhibit wider, more inflated glabellae with deeper S2 and S3, continuous S1, fewer lenses in the eye, deeper vincular furrows, stronger tuberculation and deeper pygidial pleural and interpleural furrows. Ramsköld's more detailed study showed that many of the characters of *Ananaspis* could be recognised in the ontogeny of *Acernaspis*. He noted that, compared with adults, juvenile *Acernaspis* exhibit a narrower, longer occipital ring with a median node, a longer (sag., exsag.) and less depressed L1, shorter L2, deeper and straighter S2 and S3 with S2 extending closer to the axial furrow, a smaller and more anteriorly placed palpebral lobe with deeper palpebral furrows, stronger tuberculation on the glabella and cheeks, deeper lateral border furrows, and the presence of genal spines.

Arguing that most of the juvenile characters are primitive for phacopids (where this could be determined), Ramsköld (1988) concluded that *Ananaspis* was a paedomorphic genus descended neotenically from *Acernaspis*. The opposite can be said for the *kenleyi–woiwurrungi* lineage. *Ananaspis kenleyi* exhibits a more paedomorphic or *Ananaspis*-like appearance compared to the more *Acernaspis*-like *woiwurrungi*, the significant differences being the stronger glabellar tuberculation, deeper vincular furrow, smaller eye, shorter L2 and deeper pygidial pleural furrows of *kenleyi*. The *kenleyi–woiwurrungi* lineage represents a reversal from the *Acernaspis–Ananaspis* morphocline and indicates that the radiation of phacopines in the Silurian was more complex than supposed by Campbell (1967) or Ramsköld (1988).

The relationships of the *kenleyi–woiwurrungi* lineage to other *Ananaspis* species remains uncertain although, as noted by Sandford (2000), there are similarities with the Wenlock species *Ananaspis stokesii* from Britain, *A. nuda* (Salter, 1864) (= '*Ananaspis* sp. aff. *A. stokesii*' of Siveter, 1989, pl. 19, figs 1–27, pl. 20, figs 8–10) from Ireland, and *A. amelangi* from Sweden (note that although the name *amelangi* was originally incorrectly derived, under the Code it cannot be corrected and its proposed change to *amelangorum* by Ramsköld and Werdelin, 1991: 70 is an unjustified emendation; ICZN Articles 32.2, 32.3, 32.5.1). Of these species *A. kenleyi* is most like *nuda*, exhibiting similar glabellar tuberculation and pygidial pleural furrows. However, the indistinct lateral border furrow on the fixigena and the shallower pygidial interpleural furrows distinguish the *kenleyi–woiwurrungi* lineage from these northern hemisphere species and others assigned to *Ananaspis*.

Ananaspis typhlagogus (Öpik, 1953)

Figures 3C, F–G, J–K, 7–8, ?10E–G, ?10J

Phacops typhlagogus.—Öpik, 1953: 26, pl. 10, figs 81–84.—Talent, 1964: 50.—Sherwin, 1971: 94.

Ananaspis typhlagogus.—Campbell, 1967: 32.—Ramsköld, 1988: 312, 313.—Rickards and Sandford, 1998: 751.—Sandford and Holloway, 1998: 915.

'*Phacops*' *typhlagonus* [*sic*].—Chlupáč, 1977: 77.

'*Ananaspis*' *typhlagoga* [*sic*].—Ramsköld and Werdelin, 1991: 72, 74.

Type material. Holotype CPC 686 (incomplete and partially enrolled exoskeleton), figured Öpik (1953: pl. 10, figs 81–84), figs 7C–E, from the '*Illaenus* band' (exact locality unknown), Costerfield. Wapentake Formation.

Other material. NMV P138228, NMV P138234–P138238, GSV36558 (missing), GSV46658 (missing), unregistered Geoscience Australia collection specimen from the '*Illaenus* band' (exact locality unknown), Costerfield. NMV P138229 from PL385, Costerfield. NMV P138279–P138289, NMV P140039, NMV P147835–P147837 from PL1460 (Thomas locality F43A), Costerfield. NMV P140152 from PL390, Costerfield. NMV P147049 from PL2263, Costerfield. Wapentake Formation. NMV P312813–P312815 from PL6361, Springfield. Chintin Formation. A single crushed cephalon NMV P147055 (figs. 10E–G, J) from PL206, Wallan, in the Bylands Siltstone, is tentatively assigned to the species.

Diagnosis. Glabella comprising a little more than 33% maximum cephalic width posteriorly and about 58% across frontal lobe. L2 not markedly shorter (exsag.) than L3 adaxially, S2 transverse adaxially and curving backwards abaxially. Composite lobe with densely and evenly distributed tubercles, larger ones of moderate size. Eye large, posterior edge very close to posterior border furrow, lower edge separated from lateral border furrow anteriorly by narrow band of librigenal field, visual surface with 16–18 rows of up to 5 lenses each. Fixigenal lateral border furrow shallow and wide. Pygidium with 6 axial rings and 4–5 pleural furrows.

Description. Exoskeleton of estimated maximum length 40 mm. Cephalon semi-elliptical in outline, length (sag.) approximately 58% maximum width, in frontal view anterior margin broadly arched upward adaxially with very weak downward sag medially. Glabella of moderate to strong convexity (sag., tr.), slightly overhanging anterior cephalic border in dorsal view, anterior margin forming arc centred approximately level with inner ends of S2. Width of glabella across frontal lobe almost twice width across L1 and approximately equal to sagittal cephalic length. Axial furrow shallow opposite occipital ring, very deep in front of occipital furrow and diverging forward at 55°–70° in front of S1. Occipital ring of uniform length (sag. exsag.) except distally where it is contracted, deflected slightly obliquely forward and bears weak lateral lobes. Occipital furrow very deep behind lateral node on L1, transverse and moderately impressed medially. L1 about 60% as long as occipital ring medially, with small, subquadrate, depressed lateral nodes. S1 deflected slightly forward adaxial to lateral node on L1, expanding and shallowing medially but continuous across glabella. L2 with maximum length (exsag.) 70%–80% maximum length of L3. S2 placed opposite midlength of eye, not reaching axial furrow. Posterior branch of S3 oriented transversely but gently convex forwards, inner end level with glabellar midlength (sag.). Anterior branch of S3 oriented diagonally, weakly convex forward. Preglabellar furrow moderately impressed. In anterior view anterior border narrow medially, wider laterally. Eye 45% sagittal cephalic length, distance of posterior edge from posterior border furrow less than or equal to length (exsag.) of posterior border directly behind. Visual surface on NMV P138236 (figs 7F–H, K) with lens formula 3? 5? 5 4? 5 4? 4 4? 4 5 4 4 4 4 3? 4 3 2; NMV P140152 (fig. 8J) with formula 2? 3? 4? 4 5 4 5 5? 5? 5? 4 5 5 5 4 3? Palpebral area weakly convex (tr., exsag.), palpebral furrow

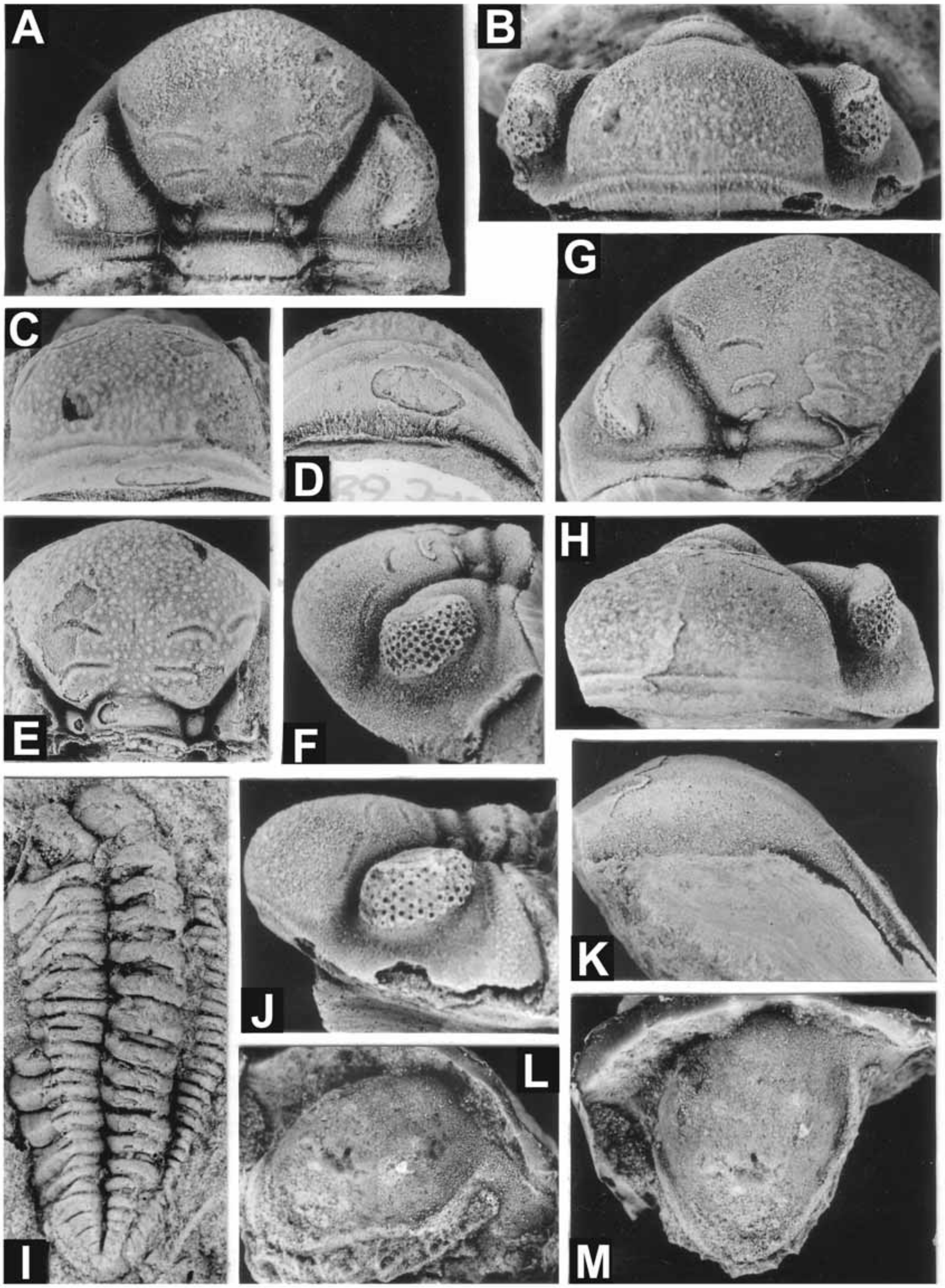

Figure 7. *Ananaspis typhlagogus* (Öpik, 1953). A–B, J, NMV P138229, cephalon × 7, from PL385, Costerfield. C–E, holotype CPC 686, dorsal exoskeleton, views of cephalon, × 3, from the '*Illaenus* band', Costerfield. F–H, K, NMV P138236, cephalon, × 4, from the '*Illaenus* band', Costerfield. I (and fig. 10C), NMV P138237, dorsal exoskeleton, × 4.5, from the '*Illaenus* band', Costerfield. L–M, unregistered specimen in AGSO collection, cephalon, view of hypostome, × 2.5, from the '*Illaenus* band', Costerfield. (I, L–M are latex casts).

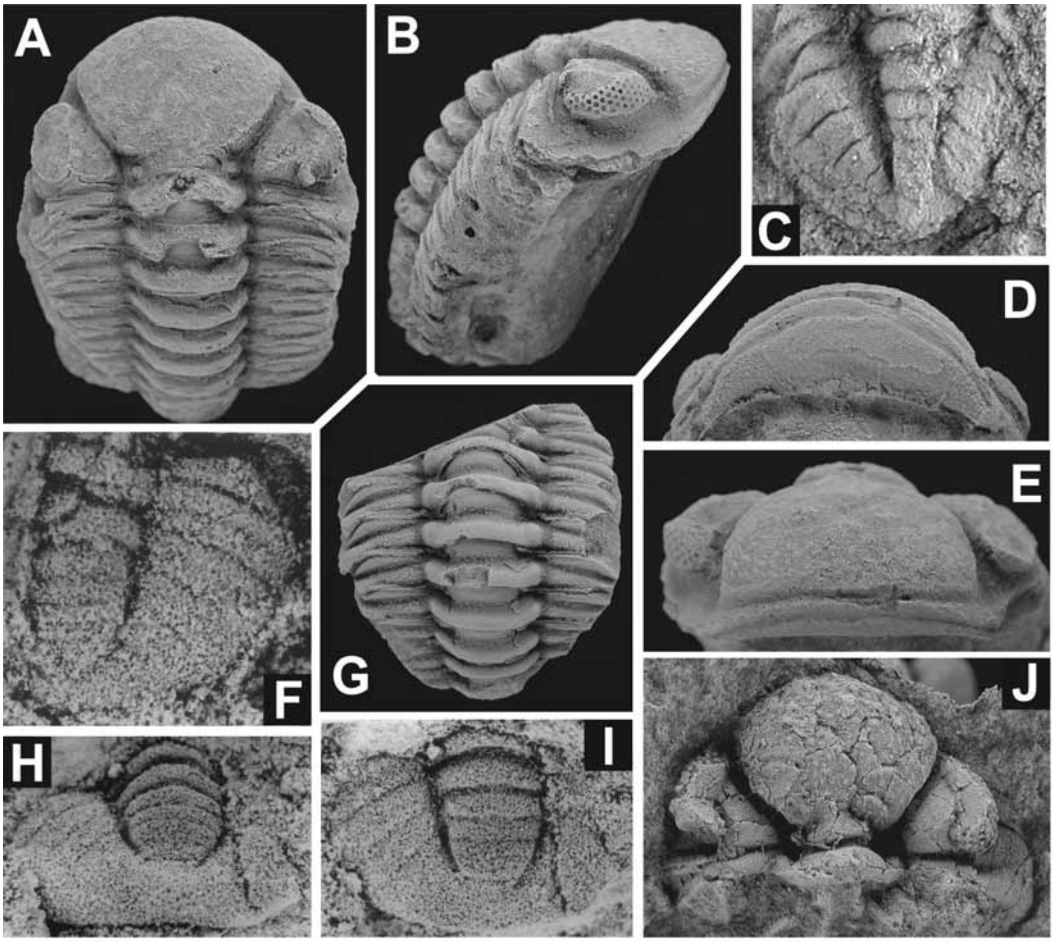

Figure 8. *Ananaspis typhlagogus* (Öpik, 1953). A–B, D–E, NMV P147049, partially enrolled exoskeleton from PL2263, Costerfield; A, × 2.8; B, × 3; D–E, × 3.5. C, NMV P138237, view of pygidium, × 9. F, NMV P138287, pygidium, × 4.3, from PL1460, Costerfield. G, NMV P138233, thorax, × 2.5, from the '*Illaenus* band', Costerfield. H–I, NMV P138285, pygidium, × 4.5, from PL1460, Costerfield. J, NMV P140152, cephalon, × 3.9, from PL390, Costerfield. (C, F, H–J are latex casts).

moderately impressed. Palpebral lobe crescentic in outline, very weakly convex (tr.), slightly elevated above palpebral area, with distinct rim furrow. Posterior border furrow deep, posterior border expanding (exsag.) backward adaxially so that genal angle is produced posteriorly. Librigenal field weakly concave below eye, steeply inclined, indistinctly separated from very weakly convex lateral border. Posterior branch of facial suture directed slightly obliquely forward across genal field and deflected backward across border to meet cephalic margin approximately level with median part of occipital furrow. Medial part of cephalic doublure steeply inclined backwards, weakly concave (sag.) in posterior part and weakly convex anteriorly. Hypostomal suture transverse medially. Vincular furrow moderately impressed, separated from anterior margin by narrow band, lateral notching moderately expressed.

Hypostome about 150% as wide anteriorly as long (sag.), parabolic in outline behind large, equilaterally-triangular anterior wings, with weakly defined shoulder opposite midlength (sag.). Middle body ovate in outline, moderately and evenly convex (sag., tr.), middle furrow and maculae indistinct. Lateral border narrow, in lateral view sloping gently dorsally from anterior wing to shoulder where it is gently deflected ventrally. Posterior border expanding slightly medially, posterior border furrow shallower than lateral border furrow.

Thorax of 11 segments. Axis wider (tr.) than pleurae, strongly convex (tr.), rings with lateral lobes weakly defined by slight expansion, by shallow notch in anterior margin, and by slightly oblique orientation of articulating furrow. Pleurae steeply inclined beyond fulcrum, well rounded distally, with deep pleural furrow terminating distally at edge of articulating facet, approximately 25% distance from fulcrum to tip.

Pygidia all incomplete or poorly preserved, with large, strongly oblique articulating facet and broadly rounded posterior margin. Axis gently tapering backwards and decreasing in height, bluntly rounded posteriorly, 1st ring standing higher than remainder and with shallow medial embayment in posterior

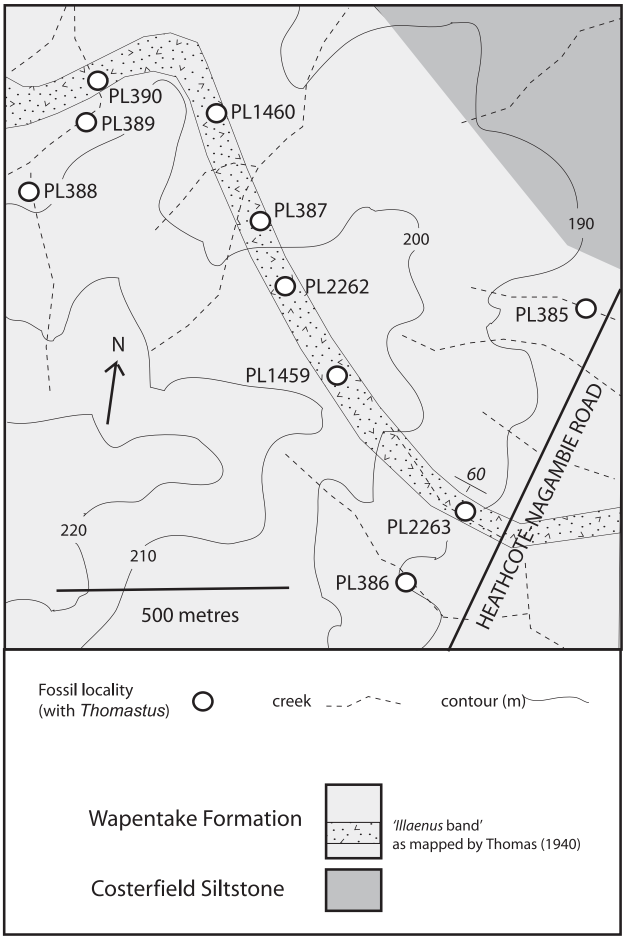

Figure 9. Fossil localities about 1 km south of Costerfield township; the area covered by the map is indicated on fig. 1.

edge to accommodate pseudo-articulating half ring on 2nd segment, 2nd and 3rd inter-ring furrows slightly expanded sagittally but without pseudo-articulating half-rings, 6th and 7th inter-ring furrows very poorly defined close together. Axial furrow deeper alongside axis than behind it. Pleural furrows short (exsag.) and rather sharply incised, 1st interpleural furrow shallow but distinct, remaining interpleural furrows very weak. Border very poorly defined.

Remarks. *Ananaspis typhlagogus* is not very common in the Wapentake Formation. Öpik (1953) reported that he had numerous fragments of the species but that only the holotype was well enough preserved to be used for description. Specimens such as the holotype that are preserved in the siliceous nodules of the Wapentake Formation are undeformed and the exoskeleton may be partly preserved as a mineralised crust (see Sandford and Holloway, 1998: 921). In contrast, moulds from mudstones of the Wapentake are crushed and fractured (fig. 8J), and those from a sandstone clast are fragmentary (figs 8F, H–I).

Öpik (1953) placed *typhlagogus* with the *Phacops orestes* group (i.e. *Acernaspis*) but noted that the latter species differs in 'many important points' including the lower glabellar profile and stronger vincular notching. Campbell (1967) assigned *typhlagogus* to *Ananaspis* on the basis of its glabellar tuberculation and the bevelled profile of the cephalic anterior margin and doublure.

Ananaspis typhlagogus is very closely related to *A. macdonaldi* Fletcher, 1950 [=*Acernaspis*? *oblatus* [*sic*] Sherwin, 1971; see Holloway, 1980: 64; Ramsköld and Werdelin, 1991:73], from the upper Llandovery to lower Wenlock of central-western New South Wales, and to '*Ananaspis*' sp. of Waisfeld and Sánchez, 1993, from strata of presumed similar age in Argentina. Sherwin (1971) stated that *typhlagogus* has more definite tuberculation and a more strongly inflated glabella than *macdonaldi*. However, the significance of the latter difference is difficult to assess in view of the wide variation in glabellar profile in *typhlagogus*, and we cannot see any clear difference between the species in sculpture. Ramsköld and Werdelin (1991) regarded *macdonaldi* and *typhlagogus* as possible synonyms, but we consider that *typhlagogus* can be distinguished by a higher visual surface of the eye with a greater number of lenses (five in the longest file instead of four in *macdonaldi*), a lower eye socle, a larger L1, and a more strongly curved posteromedial outline of the hypostome. '*Ananaspis*' sp. from Argentina, known only from an internal mould of a single cephalon (Waisfeld and Sánchez, 1993, pl. 1, figs 7–10), is difficult to distinguish from *typhlagogus* but it has an eye with up to six lenses per file and a vincular furrow that appears to be slightly deeper medially and has a distinct flexure anterolaterally.

Also similar morphologically to *A. typhlagogus* is *A. aspera* (Hawle and Corda, 1847) from the Ludlow of the Czech Republic (see Chlupáč, 1977, pl. 5, figs 9–25). The similarities include: relatively narrow (tr.) cheeks; L2 not markedly shorter (exsag.) than L3; adaxial half of S2 transverse; lower edge of eye situated above lateral border furrow anteriorly; visual surface very steeply inclined; and first order glabellar tubercles of moderate size. *A. aspera* differs from *A. typhlagogus* in that the cheeks are approximately as wide as the glabella posteriorly instead of slightly narrower than it; the eyes are much shorter (exsag.); the palpebral furrow is deeper; the lateral border furrow is deeper on the fixigena; and the pygidium has a greater number of more strongly defined segments and a narrower, subparallel-sided axis.

Ananaspis sp. 1

Figures 10A, 10D, 10I

Material. NMV P139354 (partly disarticulated cephalothorax), NMV P139355 (cephalon), NMV P139356 (right cheek) from PL1338, Wallan. Bylands Siltstone. For locality see Sandford and Rickards (1999: fig. 1).

Description. Cephalon subsemicircular, length 50% width. Glabella strongly convex (tr.), with maximum width situated at about 66% sagittal glabellar length and equal to 56% maximum cephalic width, 110% sagittal cephalic length and 170% occipital width. Outline of front of glabella forming arc centred at 33% sagittal cephalic length from posterior. Axial furrow wide and very deep in front of occipital ring, diverging strongly at about 75° between S1 and anterior end of palpebral furrow, thereafter diverging forward at about 45° to widest part of

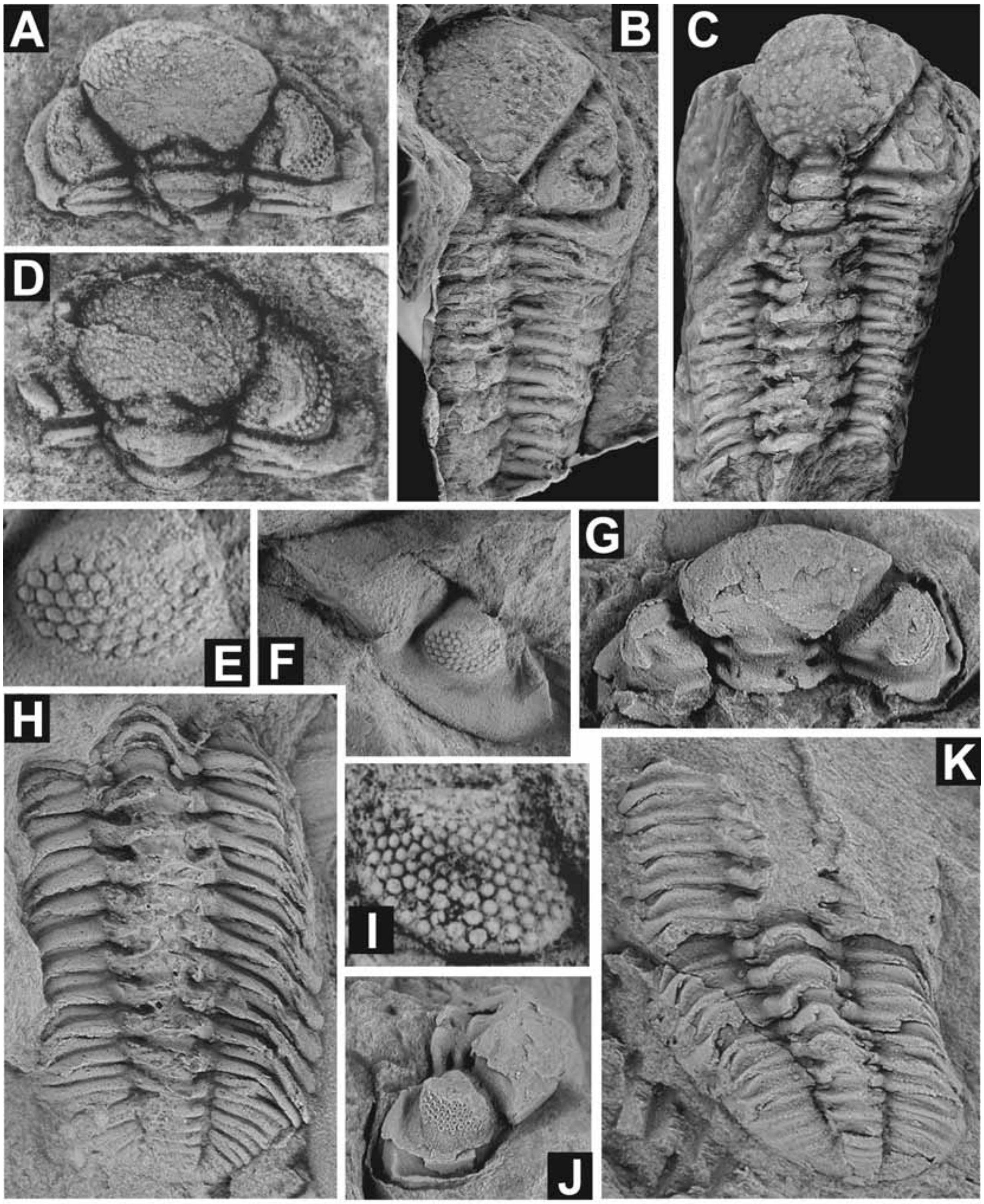

Figure 10. A, D, I, *Ananaspis* sp. 1 from PL1338, Wallan. A, D, NMV P139354, cranidium, × 6.5. I, NMV P139356 cephalon (fragment), enlargement of eye, × 9. B–C, *Ananaspis* sp. 2, NMV P136142, damaged cephalothorax, from PL1371, Coburg; B, × 1.4; C, × 1.2. E–G, J, *Ananaspis typhlagogus*? (Öpik, 1953), NMV P147055, cephalon (crushed) from PL206, Wallan; E–G, × 3; J, × 2.5. H, *Ivops wallanensis* gen. et sp. nov., paratype NMV P139326, thoracopygon, × 3, from PL206, Wallan. K, Phacopidae gen. indet. 3, NMV P312077, partly disarticulated thoracopygon, × 4.5, from PL1369, Springfield. (A, C, E–H, J–K are internal moulds).

frontal lobe. Occipital ring 30% maximum cephalic width, short, 10% glabellar length sagittally and slightly shorter laterally, lacking lateral lobes defined by notches in anterior margin. Occipital furrow deep, transverse. L1 as high as composite lobe medially, lateral node of moderate size and height, isolated by deep exsagittal furrow from preoccipital ring, width of glabella across L1 75% occipital width. S1 deep, directed anteromedially from inner end of lateral node on L1, at about 22° to transverse, connected medially by a shallower, wide (sag.), transverse furrow. L2 65% length (exsag.) of L3 and 11% sagittal cephalic length. S2 and S3 moderately impressed. S2 directed at 45° distally, curving abruptly to transverse direction proximally, anteriormost point opposite 40% sagittal glabellar length from posterior. Posterior branch of S3 weakly convex forward, oriented transversely opposite glabellar midlength (sag.). Anterior branch of S3 straight, not connected to posterior branch, placed anteriorly opposite anterior margin of eye, directed anterolaterally at 60° to exsagittal line. Frontal lobe high. Preglabellar furrow very shallow. Anterior border very short (sag.). Eye large, 50% sagittal cephalic length, placed with midlength of eye opposite 33% sagittal glabellar length, occupying entire length of genal field. Palpebral area low, weakly convex, palpebral furrow moderately impressed. Palpebral lobe steeply inclined, raised above palpebral area, with shallow rim furrow. Visual surface large, higher anteriorly than posteriorly, with more than 18 files of up to 7 lenses each, without raised sclera. Posterior border short (exsag.) adaxially, approximately 300% as long distally. Posterior border furrow deep and wide, continuous with deep and wide fixigenal lateral border furrow. Genal angle obtuse, with small point at angle. Lateral border moderately convex, wide (tr.) posteriorly, narrowing strongly anteriorly. Librigenal lateral border furrow moderately impressed. Posterior branch of facial suture skirting back of eye to lateral border furrow, strongly convex forward across lateral border, anteriormost point opposite 25% cephalic length. Cephalic doublure with extremely shallow vincular furrow anteriorly, very shallow and very weakly notched laterally. Cephalic tubercles variable in size from small to moderate, with superimposed granules, densely distributed on composite lobe of glabella, L1 and palpebral area, remainder of exoskeleton with granulose sculpture.

Remarks. *Ananaspis* sp. 1 is the only trilobite known from PL1338. Stratigraphically, the locality is about 50 m above PL206, which lies 750 m further to the south and yields a more diverse fauna.

Although the above description is based only on one complete cephalon and two fragments, the material is sufficient to distinguish the species from other Victorian Silurian phacopids. The species is most easily distinguished by its fine, dense cephalic tuberculation, by the large size of the eye which extends the entire length of the genal field, and by the very shallow vincular furrow medially. Assignment to *Ananaspis* is indicated by features including short L2 (relative to the length of L3), a narrow glabella, the variably sized glabellar tubercles, a deep lateral border furrow continuous with the posterior border furrow and the obtuse genal angle with a small point. The eye is larger than those of other *Ananaspis*, although eye length is a character that varies significantly between species here assigned to the genus (eye length up to about 47% sagittal cephalic length in *A. amelangi*, 45% in *A. fecunda* and *A. crossleii,* 40% in *A. decora*, 37% in *A. calvescens*, 30% in *A. aspera*). *Ananaspis* sp. 1 most closely resembles *amelangi*, sharing large eye size, similar cephalic ornament and cephalic proportions. The species differ in that *amelangi* has a glabella that does not always extend to the anterior margin of the cephalon, the occipital ring has more strongly defined lateral lobes, the visual surface has only six lenses per file and 15–16 files, the preglabellar and vincular furrows are deeper and the vincular notching is deeper. *Ananaspis* sp. 1 differs from the type species in having finer cephalic tuberculation, a larger eye and fewer lens files in the visual surface (19–21 in *fecunda*). In lens formula *A.* sp. 1 is most similar to *A. guttulus* (16 files of up to seven lenses per file) and *decora* (16–17 files of seven, rarely eight, lenses per file).

Ananaspis sp. 2

Figures 10B–C

Material. NMV P136142 (cephalothorax) from PL1371, about 50 m SW of corner of Murray Road and Elizabeth Street, Coburg. Dargile Group, precise stratigraphic horizon uncertain.

Description. Glabella wide, maximum width 110% sagittal length and 65% maximum cephalic width, overhanging anterior border. Axial furrow very shallow and slightly convergent forwards adjacent to occipital ring, very deep adjacent to composite lobe, straight and diverging forwards at about 65°. Occipital ring 50% maximum glabellar width, medial section raised, separated from short (exsag.) lateral section by deep notch in anterior margin. Occipital furrow transverse medially, deep. L1 short (exsag.) 13% sagittal cephalic length, lateral node low, globular, isolated from remainder of L1. S1 deep laterally, shallower medially where it forms posterior edge of a slightly depressed triangular area between L1 and composite lobe. Length of L2 16% sagittal cephalic length. S2 and posterior branch of S3 of moderate depth, wide, uniformly arcuate, almost reaching axial furrow. S2 directed obliquely inwards-forwards at about 15° to transverse. Posterior branch of S3 oriented transversely opposite glabellar midlength (sag.), anterior branch directed parallel to axial furrow. Posterior border furrow deep and wide (exsag.), widening abaxially, continuous with wide and deep lateral border furrow on fixigena. Postocular area 14% sagittal cephalic length. Glabellar tubercles large to very large, low and flat-topped, distributed irregularly with moderate density. Tuberculation subdued on genal field.

Remarks. The formation to which the strata at PL1371 belong is difficult to determine as the site is no longer exposed. Fossils are uninformative in this respect as the trilobite is the only fossil known and is not known from elsewhere.

The glabellar tuberculation, depth and placement of the lateral glabellar furrows, depth of the posterior and lateral cephalic border furrows and length of the postocular area are comparable to Eastern European and Central Asian species of *Ananaspis.* In the greater width of the glabella the Coburg species is closest to *A. crossleii* from the Yass district of New South Wales (maximum glabellar width 60% maximum cephalic width; see Sherwin, 1971, pl. 2, figs 6–9, pl. 3, figs 1–7). The Coburg specimen differs from *crossleii* in having a wider glabella with larger, flat and less densely distributed tubercles, and a longer (exsag.) postocular area (postocular length 14% sagittal cephalic length versus 10% in *crossleii*).

Ivops gen. nov.

Type species. *Ivops wallanensis* sp. nov. from the Bylands Siltstone (Wenlock), central Victoria.

Derivation of name. After the late Professor Ivo Chlupáč, Charles University, Prague. Gender masculine.

Diagnosis. L1 with lateral node very small and depressed, L2 short (exsag.). S2 containing deep pit adjacent to axial furrow, forming a notch in side of glabella. Anterior branch of S3 long, subparallel to axial furrow. Front of glabella overhanging anterior border. Eye relatively small, length (exsag.) approximately 30% sagittal cephalic length, its lower edge lying just above lateral border furrow anteriorly, visual surface without raised sclera. Lateral border furrow on fixigena continuous with posterior border furrow. Vincular furrow with weak notching laterally. Pygidium with weakly tapering axis constituting about 30% maximum pygidial width anteriorly, and with deep pleural and shallow but distinct interpleural furrows. Dense sculpture of bimodal tubercles on glabella.

Remarks. *Ivops* is known only from the type species. The genus closely resembles *Ananaspis* in glabellar and pygidial proportions, the short L2 (exsagittal length 80% that of L3), the continuity of the posterior border furrow with the lateral border furrow on the fixigena, the weak notching in the lateral part of the vincular furrow, and the depth of the pygidial pleural and interpleural furrows. The relatively small eye with its lower edge placed a short distance above the lateral border furrow and with a small number of lenses in the dorsoventral files are features comparable with species such as *A. aspera* and *A. calvescens*. Despite these shared features *Ivops* is unlike *Ananaspis* and other known Silurian phacopines in that S2 is deep laterally and contains an apodemal pit where it meets the axial furrow. This feature contrasts with the more typical phacopine morphology of a shallow S2 that is isolated from the axial furrow. A laterally deep S2 similar to that of *Ivops* is present in '*Paciphacops*' *microps* Chatterton, Johnson and Campbell, 1979 (type species of *Kainops* Ramsköld and Werdelin, 1991), from the upper Lochkovian to lower Pragian of New South Wales, but in that species S2 does not contain an apodemal pit and does not meet the axial furrow in all specimens. The relatively small eye of *Ivops* (the smallest of known Wenlock phacopids) is interpreted as an adaptation to a deep-water environment; see discussion in remarks on *Berylacaste berylae* gen. et sp. nov.

Ivops wallanensis sp. nov.

Figure 11

Ananaspis.—Rickards and Sandford, 1998: 752.
Ananaspis.—Sandford and Holloway, 1998: 915.

Type material. Holotype NMV P139323 (enrolled cephalothorax). Paratypes NMV P139324 (dorsal exoskeleton, pygidium displaced), NMV P139325 (enrolled cephalothorax), NMV P139326 (thoracopygon), NMV P139328 (partly enrolled dorsal exoskeleton), NMV P138230 (dorsal exoskeleton), NMV P138231 (incomplete cephalothorax). All from PL206, Wallan. Bylands Siltstone.

Other material. NMV P138232, NMV P139327, P147056 from PL206, Wallan. For locality see Sandford and Holloway (1998: text-fig. 1).

Derivation of name. In reference to the type locality.

Diagnosis. As for genus.

Description. Exoskeleton of known maximum length 30 mm. Cephalon about 60% as long (sag.) as wide, anterior outline with greatest curvature medially and in front of anterior extremity of eye. In frontal view anterior margin moderately arched upward medially, glabella strongly convex and evenly rounded. Glabella comprising about 30% maximum cephalic width posteriorly, width across frontal lobe about twice width at occipital ring and equal to sagittal length. Axial furrow diverging forward at about 70° from S1 to anterior end of palpebral furrow, thereafter diverging slightly more weakly to widest part of frontal lobe. Occipital ring high medially and with small, well-developed, obliquely oriented lobe laterally. Occipital furrow deep, transverse medially. L1 slightly narrower (tr.) than occipital ring, as high medially as composite lobe, lateral node smaller than lateral lobe of occipital ring. S1 expanding (exsag.) adaxially or bifid, posterior section transverse and weakly continuous medially, anterior section curving forward and rapidly dying out. L2 almost as short (exsag.) laterally as L1 and about 60% length of L3. S2 meeting axial furrow more or less opposite posterior edge of palpebral lobe, directed anteromedially and shallowing rapidly, weakly arcuate. S3 with anterior and posterior branches confluent opposite about 40% glabellar length (sag.) from posterior, anterior branch extending forward to opposite about 60% glabellar length (sag.) from posterior. Preglabellar furrow distinct across entire width (tr.) of glabella on internal moulds, decreasing in length (exsag.) adaxially in front of lateral part of frontal lobe. Posterior border and border furrow deflected rather strongly backward beyond fulcrum to genal angle. Palpebral lobe narrow (tr.), lenticular in outline, raised above palpebral area, palpebral furrow weakly curved. Visual surface with lenses arranged regularly in files anteriorly but less regularly posteriorly, lens formula (NMV P139328, figs 11H–I, K) from front 4566525654?3?. Librigenal field subvertical below eye, lateral border steeply inclined. Posterior branch of facial suture transverse across genal field and deflected backward at about 45° across border. Cephalic doublure flat sagittally, vincular furrow forming distinct bevelled edge anteriorly, deep posterolaterally. Hypostomal suture transverse medially.

Thorax of 11 segments. Axis comprising 30% segmental width (tr.), strongly convex, rings transverse medially, with short exsagittal incisions in anterior margin defining obliquely forwardly directed lateral lobes. Pleurae with well-rounded tips and deep pleural furrows that are situated at midlength (exsag.) of segment at fulcrum and terminate distally at edges of articulating facets.

Pygidium lenticular, length (sag.) about 60% maximum width. Axis with 5 well defined rings and 1 or 2 very short (sag.) and weak ones posteriorly, axial terminus well rounded. Pleurae weakly convex (tr.), with 4 distinct pleural furrows and 2 very weak ones posteriorly. Border not present.

Remarks. The above description is based mainly on the least deformed specimens (e.g. figs 11B–C, E, J). S2 and S3 appear to vary markedly in depth, being very weak on most specimens

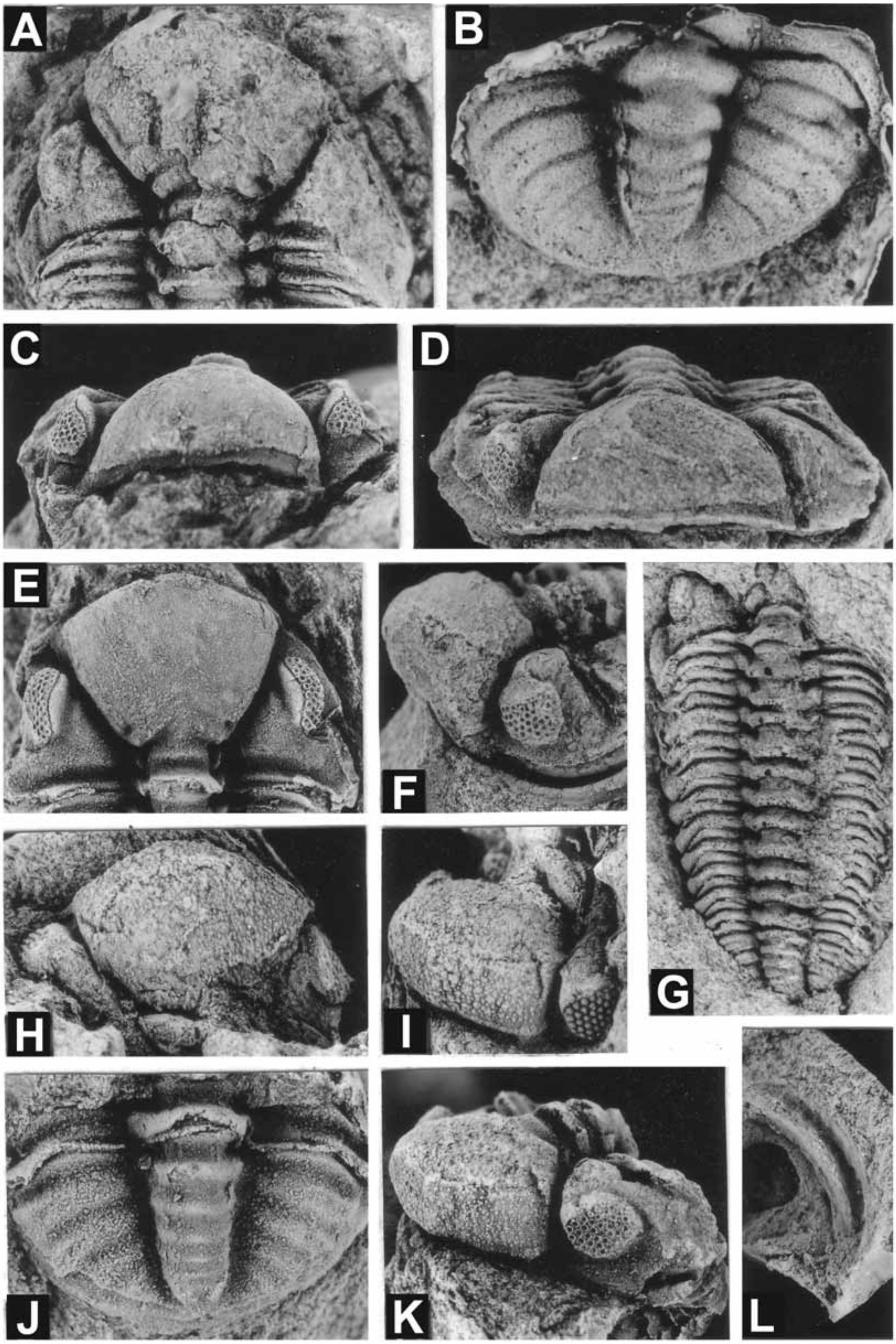

Figure 11. *Ivops wallanensis* gen. et sp. nov., from PL206, Wallan. A, G, paratype NMV P138230, dorsal exoskeleton; A, × 4.3; G, × 3.2. B, F, J, L, paratype NMV P139324, exoskeleton with displaced pygidium; B, view of pygidium, × 6.5; F, view of cephalon, × 3.8; J, view of pygidium, × 5.4; L, view of cephalic doublure, × 3.8. C, E, holotype NMV P139323, enrolled exoskeleton, view of cephalon, × 3.8. D, paratype NMV P139325, cephalon, × 3.8. H–I, K, paratype NMV P139328, partly enrolled exoskeleton, view of cephalon, × 4.3. (A, C–F, J–K are internal moulds).

but moderately impressed on both internal and external moulds of NMV P138230 (figs 11A, G). However, the apodemal pit in the lateral part of S2 is always present.

Phacopidella Reed, 1905

Type species. *Phacops glockeri* Barrande, 1846 from the upper part of the Motol Formation (upper Wenlock), Czech Republic, by original designation.

Phacopidella? sp.

Figure 12A

Asaphus.—Selwyn, 1863: map note.

Phacops crosslei.—Chapman, 1913: 210, 229.—Chapman, 1915: 169.

Phacopidella?.—Rickards and Sandford, 1998: 749.

Material. NMV P1218 (dorsal exoskeleton with displaced cephalon), probably from PL1393, Geological Survey locality Ba5, Keilor. Springfield Formation, in siltstone underlying the Lintons Creek Conglomerate Member; late Llandovery, Telychian (*Spirograptus turriculatus*–*Monograptus crispus* biozones). For locality see Selwyn (1863), Rickards and Sandford (1998) (fig. 5).

Description. Exoskeleton, of estimated original length about 35 mm, has been flattened tectonically and slightly sheared. The preserved portion of the cephalon consists of the glabella behind about the middle (sag.) of the frontal lobe together with the posteromedian part of cheeks. The glabella is slightly narrower across L1 than across the occipital ring and expands gently forwards in front of L1, the axial furrow here diverging at about 40°. The occipital ring is almost twice as long sagittally as exsagittally, with lateral lobes defined by very short exsagittal incisions in the anterior edge. The median portion of the occipital furrow is arched forward. L1 has large, quadrate nodes laterally and is slightly shorter (sag., exsag.) than the occipital ring medially. S1 is deep laterally, is deflected forwards adaxial to the short exsagittal furrow defining the lateral node of L1 and shallowing rapidly, becoming indistinct medially. S2 is short (exsag.), very faint and weakly convex forward, directed slightly obliquely backward laterally. L2 is about as long (exsag.) as L1. The posterior branch of S3 is indistinctly preserved on the left side of the glabella, running subparallel to S2. Axial furrow deep. Left palpebral lobe possibly partly preserved, seemingly relatively long (exsag.) and obliquely oriented. Thorax with 11 segments. Axial rings with short, deep exsagittal incisions in anterior margin defining large, quadrate lateral lobes. Pleurae with deep pleural furrow situated at middle (exsag.) of segment at fulcrum; distal parts of pleurae not preserved but overall width of pleural lobe appears not to exceed width of axis. Pygidium large, approximately 160% as wide as long (sag.). Axis about 30% maximum pygidial width anteriorly and about 66% sagittal pygidial length, with 5 well defined rings and weak 6th ring. Pleurae with 5 deep pleural furrows and 2 weak ones posteriorly; interpleural furrows moderately impressed. Dorsal surface of pleurae not intact abaxially on internal mould, so appearance of wide, smooth border is largely an artefact.

Remarks. The lithology of this specimen is identical to that of a specimen of *Hadromeros* from Keilor, one of two trilobites collected by C.D. Aplin in the 1850s that were noted on the geological quarter sheet by Selwyn (1863) as *Cheirurus* and *Asaphus*. NMV P1218 is apparently the second trilobite collected by Aplin, and that recorded by Chapman (1913) as *Phacops crossleii* Etheridge and Mitchell, 1896 from Keilor. However, the museum label with the specimen records the locality as ‘Saltwater River, one mile west of Gisborne’, as published by Chapman (1915). Chapman (1915) noted the lithology of the trilobite specimen as ‘bearing a strong resemblance to the Keilor...mudstones’. Chapman, the museum palaeontologist at the time, appears to have confused Gisborne with Keilor. Only Early to Middle Ordovician graptolitic beds outcrop in the Gisborne area, with a lithology quite unlike that of the trilobite specimen.

The low pygidial convexity (largely a result of tectonic flattening) and well defined pygidial segmentation explain Selwyn’s (1863) preliminary assignment of the specimen to *Asaphus*. The glabellar segmentation, especially S1 that is continuous though very weak medially and the shallowness and orientation of S2 and the posterior branch of S3, as well as the overall form of the pygidium, indicate that the specimen belongs to the Phacopidae. The gentle forward expansion of the glabella, the relatively long (sag., exsag.) L1 with large lateral nodes, the well-defined nodes on the occipital ring and thoracic axial rings, and the relatively large and well-segmented pygidium are all consistent with assignment to *Phacopidella*. A characteristic feature of *Phacopidella* (and of *Eophacops*) is the abrupt shallowing and adaxial flexure of the axial furrow at the anterolateral extremity of L3. This part of the glabella is not preserved in the specimen; however, so that the presence of this feature and assignment to *Phacopidella* cannot be confirmed. This uncertainty aside, the specimen differs from the type species of *Phacopidella, P. glockeri,* in having a wider axis on the thorax and pygidium, the pygidial axis extends closer to the posterior margin, and the pygidial pleural and interpleural furrows are deeper.

Phacopidae gen. indet. 1

Figures 6L–M

Lochkovella?.—Rickards and Sandford, 1998: 753.

Material. NMV P136136 (cephalon) from PL1638, Williams locality W25, Strathewen. Yan Yean Formation. The locality occurs in strata mapped just below the boundary of the Anderson Creek Formation and the Dargile Formation (Garratt, 1972). Strata mapped at this horizon in some areas around Melbourne were reassigned by Rickards and Sandford (1998) to the Yan Yean Formation. The presence of a distinctive encrinurid at PL1638 that otherwise occurs in the upper beds of the Yan Yean Formation at Heathcote (at PL2259, Thomas locality F41, Parish of Heathcote) and at Upper Plenty (PL1697, PL1699) supports the assignment of strata at PL1638 to the Yan Yean Formation. For localities see Thomas (1940), Williams (1964) (fig. 2) and Sandford (2006) (figs 2, 4).

Description. Cephalon semi-elliptical in outline, sagittal length about 60% maximum width. Glabella gently to moderately convex (sag., tr.), frontal lobe low, width across frontal lobe approximately twice width across L1 and a little more than sagittal length. Axial furrow wide and very deep, diverging at

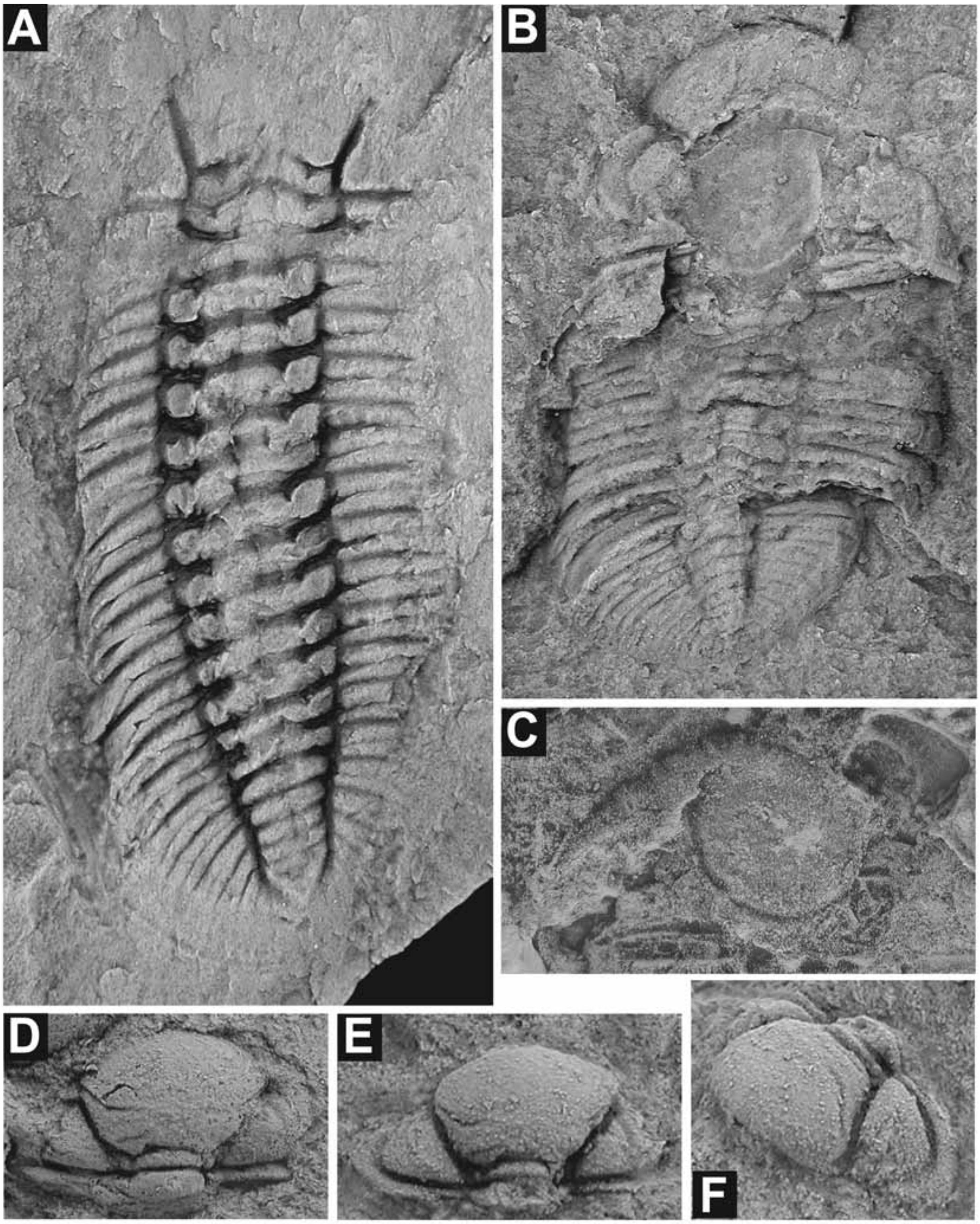

Figure 12. A, *Phacopidella*? sp., NMV P1218, dorsal exoskeleton, × 2.7, from PL1393, Keilor. B–C, *Struveria* sp. 1, NMV P139357, partly disarticulated exoskeleton with hypostome and cephalic doublure exposed, from PL1386, Broadmeadows; B, × 3.4; C, × 4. D–F, Phacopidae gen. indet. 2, NMV P312076, cephalon, × 8, from PL1369, Springfield. (A, E–F are internal moulds).

about 60° in front of S1. Occipital ring comprising 40% maximum cephalic width, raised high medially, shorter (exsag.) and obliquely directed laterally but without well defined lateral lobes. Occipital furrow deep. L1 of almost uniform length (sag., exsag.) across glabella, high medially, inner edge of lateral node obscured. S1 very deep and wide laterally, directed slightly forward of transverse, shallowing abruptly close to sagittal line. S2 deep, weakly convex forward, its outer end opposite posterior edge of eye, running parallel to S1 and very close to it. S3 not clear but posterior branch apparently directed posteromedially at about 30° to transverse and with inner end more or less level with glabellar midlength (sag.) and close to

S2. Eye small and obliquely oriented, situated almost its own length (exsag.) from posterior border furrow and with midlength opposite glabellar midlength (sag.). Palpebral furrow moderately impressed, weakly arcuate, continuous with postocular furrow that is of similar depth and reaches lateral border furrow. Palpebral lobe not raised above palpebral area. Visual surface not well preserved but appears greatly reduced, ovate in outline with lower edge distant from lateral border furrow, and with about 10 lenses. Posterior border furrow deep adaxially, continuous with wide, deep lateral border furrow. Posterior border uniformly short (exsag.) except distally. Genal angle rounded. Lateral border weakly convex, wider behind intersection of postocular furrow than in front. Sculpture obscured by preservational pitting covering most of cephalic surface.

Remarks. Tentative assignment of this specimen to *Lochkovella* by Rickards and Sandford (1998) was based on the small and forwardly placed eye, the deep and continuous posterior and lateral cephalic border furrows, the deep postocular furrow, and the apparent absence of coarse tuberculation on the glabella. These characters as well as the narrow cheeks invite comparison with the Czech Early Devonian (Pragian) species ‘*Phacops* (*Phacops*?)’ *hanusi* Chlupáč, 1977 and ‘*P.* (*P.*?)’ *veles* Chlupáč, 1972, which were assigned to *Lochkovella* by Sandford (2004). However, other characters of the specimen are incompatible with assignment to *Lochkovella*. Such characters include the glabella of low convexity that does not overhang anteriorly, and the very small, elliptical visual surface of the eye with its lower edge distant from the lateral border furrow. It is possible that the specimen belongs to an undescribed genus.

The monotypic *Orygmatos* Sandford, 2000, from a slightly higher stratigraphic horizon low in the Melbourne Formation at Yan Yean, 10 km to the north-east, also has very small eyes with an elliptical visual surface. Compared with the present specimen from Strathewen, *Orygmatos* has an occipital ring that is more expanded (sag., exsag.) and prominent medially, L1 is very short (sag., exsag.) and markedly depressed, the composite glabellar lobe expands more strongly forward and is coarsely tuberculate, the palpebral furrow meets the postocular furrow in an broad curve rather than an abrupt angle, and the posterior border furrow and fixigenal portion of the lateral border furrow are very wide. *Denckmannites* Wedekind, 1914 has even more greatly reduced eyes than the Strathewen specimen, much weaker palpebral and postocular furrows, a more elongated glabella, wider cheeks, and a longer anterior border. The small-eyed *Denckmannites rutherfordi* Sherwin, 1968 from the Ludlow–Přídolí of central western New South Wales was assigned to *Lochkovella* by Chlupáč (1977) but Sandford (2004) noted that the presence of strong notching in the lateral part of the vincular furrow excluded the species from that genus, a conclusion supported by the apparent absence of granular sculpture on the exoskeleton. The very low cephalic profile (sag., tr.), the more pentagonal outline of the glabella, the subparallel alignment of S2 and S3, and the broadly arcuate union of the palpebral and postocular furrows distinguish *rutherfordi* from the Strathewen specimen.

Phacopidae gen. indet. 2

Figures 12D–F

Material. NMV P312076 (cephalon) from PL1369, Deep Creek, Springfield. Springfield Formation. For locality see fig. 4.

Remarks. This very small cephalon (3 mm in length), and two other small specimens documented below as Phacopidae gen. indet. 3, are the only phacopids known from PL1369. The cephalon undoubtedly belongs to a juvenile individual, and its size is in the range of late meraspides and early holaspides of *Acernaspis* (cephalic lengths 1.3 mm to 3.3 mm) documented by Ramsköld (1988). It is characterised by a strongly convex glabella that overhangs anteriorly, a short (exsag.) L2, a very large eye occupying almost the entire length of the genal field, a well defined fixigenal lateral border furrow joining the posterior border furrow, and a granulose sculpture. The glabellar convexity, length of L2 and distinct lateral border furrow suggest assignment to *Ananaspis*, but the last two characters could also be attributed to the small size of the specimen as Ramsköld (1988) observed that in juveniles of *Acernaspis* L2 is shorter and the lateral border furrow deeper than in adults. The glabella lacks the tuberculation characteristic of *Ananaspis*, whereas the sculpture is normally relatively coarser in juveniles than adults.

Phacopidae gen. indet. 3

Figures 5E–G, 10K

Material. NMV P139353 (partially enrolled exoskeleton), NMV P312077 (partly disarticulated thoracopygon) from PL1369, Springfield. Springfield Formation.

Remarks. These two small specimens are considered to belong to the same species because of similarities in the pygidia, which have six axial rings, two pseudo-articulating half rings (although the third ring is damaged in the thoracopygon), four distinct pleural furrows, and well-defined interpleural furrows extending almost to the margin. The partially enrolled exoskeleton has a cephalon with a moderately convex (sag.) glabella that does not overhang the preglabellar furrow and anterior border in dorsal view, very weak S2 and S3, a shallow fixigenal border furrow, an eye of moderate size situated well in front of the posterior border furrow, a weakly curved palpebral lobe, and a finely granulose sculpture. Compared to the cephalon described above as Phacopidae gen. indet. 2, which is from the same locality, the present specimen represents a larger individual (cephalic length 7.5 mm as opposed to 3 mm) and has a more weakly convex glabella and much smaller eye. The difference in the eyes cannot be attributed to ontogenetic changes as eye size increases during ontogeny rather than decreases, as documented by Ramsköld (1988) in *Acernaspis*. We therefore conclude that Phacopidae gen. indet. 2 and Phacopidae gen. indet. 3 belong to different taxa.

Superfamily **Dalmanitoidea** Vodges, 1890
Family **Dalmanitidae** Vodges, 1890

Dalmanites Barrande, 1852

Type species. *Trilobus caudatus* Brünnich, 1781 from the Coalbrookdale Formation (Wenlock) of England.

Dalmanites athamas Öpik, 1953

Figures 13A–K

Dalmanites sp.—Thomas, 1937: 66.

Dalmanites athamas Öpik, 1953: 28, pl. 10, figs 88–91; text-fig. 9 (IV).—Holloway and Sandford, 1993: 97.—Sandford and Holloway, 1998: 916.—Rickards and Sandford, 1998: 751.

Dalmanitina (*Eudolatites*) *aborigenum* Öpik, 1953: 26 (*partim.*), pl. 10, fig. 85, text-fig. 9 (III) (*non* pl. 10, figs 86–87 = *Struveria*? sp.).

Dalmanites? *athamas*.—Talent, 1964: 50.

'*Dalmanitina*' *aborigenum*.—Talent, 1964: 50.

Type material: Holotype NMV P52484 (pygidium, figured Öpik, 1953: pl. 10, fig. 88) and paratype NMV P52485 (fragment of cephalon, figured Öpik, 1953: pl. 10, fig. 89) from PL2262, Thomas locality F43, Costerfield. Paratype NMV P52486 (fragment of cephalon, figured Öpik, 1953: pl. 10, figs 90–91) from PL2269, Thomas locality F51, Costerfield. Wapentake Formation.

Other material. NMV P138215–P138216 from the '*Illaenus* band' (exact locality unknown), Costerfield. NMV P138217 from PL389, Costerfield. NMV P52482 (holotype of '*Dalmanitina* (*Eudolatites*)' *aborigenum*), P138218–P138219, NMV P138223 from PL2269, Costerfield. NMV P138220 from PL2263, Thomas locality F44, Costerfield. NMV P139805 from PL386, Costerfield. Wapentake Formation. For localities see Thomas (1940) and fig. 9.

Diagnosis. *Dalmanites* with very short (sag., exsag.) anterior cephalic border lacking median expansion or process. Glabella about 77% as wide across frontal lobe as long (sag.), frontal lobe comprising a little more than half sagittal length of glabella. Pygidium with 14–15 axial rings and 10 pleural furrows. Axis narrow, comprising 23% maximum pygidial width anteriorly, with apodemes on 1st 10–12 segments. Pleural furrows flat-bottomed, as long (exsag.) as or longer than preceding anterior pleural band, posterior bands much shorter except adaxially and dying out distally on more posterior segments, pleural nodes absent.

Description. Glabella with widths across L1, L3 and frontal lobe approximately in ratio 1:1.6:1.8. Occipital ring, L1 and L2 of equal length, together comprising 35% sagittal glabellar length. S1 and S2 transverse, S1 with apodemal pit extending almost to axial furrow, S2 with slightly narrower (tr.) apodemal pit and shallow extension to axial furrow. L3 as long (exsag.) adaxially as L1 and L2, twice as long at axial furrow. S3 deepest proximally, expanding abaxially and subsequently contracting again toward axial furrow. Frontal lobe transversely elliptical, width 150% length, with short longitudinal depression in posterior half and forwardly expanding median field of muscle scars occupying slightly more than anterior half. Anterior border slightly shorter sagittally than laterally, weakly concave. Anterior branch of facial suture running slightly closer to preglabellar furrow than to anterior cephalic margin. Posterior border furrow lanceolate in outline, gently deflected backward distally, not meeting lateral border furrow.

Thoracic axis weakly convex (tr.), gently tapering backward. Axial rings very weakly convex (sag., exsag.), slightly bowed forward medially. Axial furrow deep. Pleural furrows expanding (exsag.) abaxially to fulcrum, deep, anterior slope much steeper than posterior slope. Anterior pleural bands strongly convex (exsag.), posterior bands becoming flattened toward fulcrum and inclined, poorly differentiated from posterior slope of pleural furrow. Pleural bands with sculpture of small, sparse granules.

Pygidium triangular in outline, shape of posterior termination unknown. Axis with length about 70% maximum pygidial width, tapering uniformly backward, 1st ring with subrectangular medial embayment in posterior edge accommodating pseudo-articulating half ring on 2nd segment, inter-ring furrows shallowing medially and expanded (sag.) except towards back of axis where they become increasingly more poorly defined. Axial furrow narrow but distinct on external surface. 1st pleural furrow straight except distally where it is deflected strongly backwards, subsequent furrows successively more evenly curved and more posteriorly directed, 10th furrow directed exsagittally. 7th pleural rib with distinct forward deflection proximally. Interpleural furrows sharply impressed externally. Doublure narrow, moderately convex abaxially and with a low upturned lip adaxially, with densely distributed small granules.

Remarks. The synonymy of '*Dalmanitina* (*Eudolatites*)' *aborigenum* with *Dalmanites athamas* was discussed by Sandford and Holloway (1998: 916). The paratype of *aborigenum*, a pygidial fragment, is not congeneric with the holotype and we assign it to *Struveria* sp. 2.

New material of *athamas* has become available since Öpik's (1953) original description but no cephala that are more complete. Öpik considered the species to be close to and possibly a subspecies of *Dalmanites wandongensis* from the overlying Dargile Formation, but comparison of the available material indicates that the two species are distinct. *D. wandongensis* was revised by Sandford (2006) and differs from *D. athamas* in that L1 is shorter than L2 instead of equal in length; the pygidial pleural furrows are shorter (exsag.) and not as flat-bottomed in cross section but form a continous slope with the succeeding posterior pleural band; and the interpleural furrows are weaker.

Ramsköld (1985) recognised a closely related group of European and North American Wenlock–early Ludlow species of *Dalmanites* including the type species, *D. caudatus* (Brünnich, 1781), as well as *D. corrugatus* (Reed, 1901), *D. limulurus* (Green, 1832), *D. myops* (König, 1825), *D. nexilis* Salter, 1864, *D. obtusus* (Lindström, 1885) and *D. platycaudatus* Weller, 1907. These species share prominent lateral nodes on the first, sixth and seventh thoracic axial rings, and nodes on the pygidial pleural ribs. *D. athamas* lacks the thoracic and pygidial nodes characterising this group, which also differs from *athamas* in having a medially expanded anterior cephalic border, and pygidia with shorter (exsag.) pleural furrows and longer (exag.) posterior pleural bands that are subequal in length to the anterior bands.

Bessazoon Curtis and Lane, 1998

Type species. *Dalmanites weaveri* var. *tenuimucronata* Whittard, 1938 from the Hughley Shales (upper Llandovery) of Shropshire, England, by original designation.

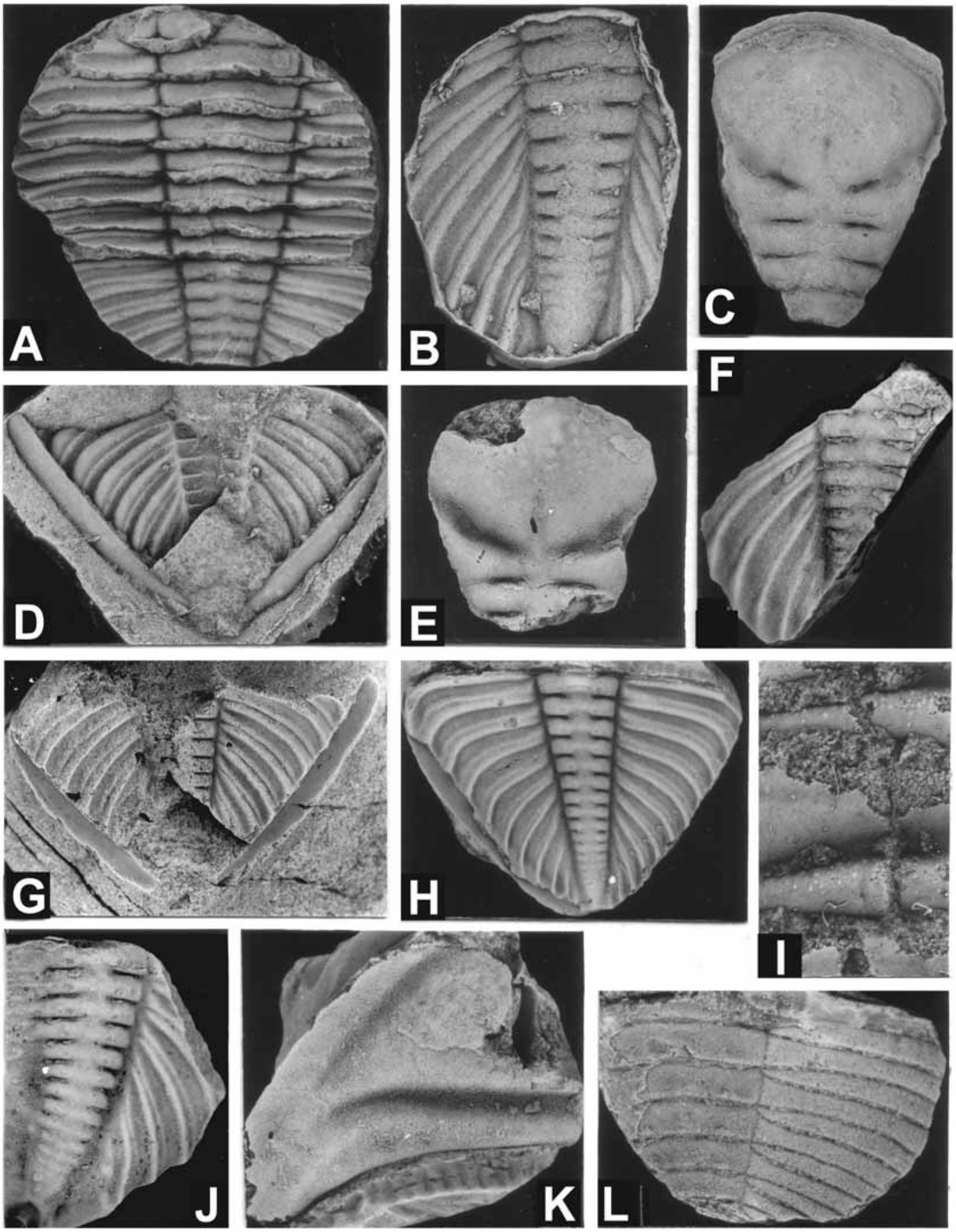

Figure 13. A–K, *Dalmanites athamas* Öpik, 1953. A, NMV P138215, thoracopygon, × 1.5, from the '*Illaenus* band', Costerfield. B, NMV P138219, pygidium, × 3.5, from PL2269, Costerfield. C, paratype NMV P52485, cranidium, × 2, from PL2262, Costerfield. D, G, NMV P138217, pygidium, × 2, from PL389, Costerfield. E, paratype NMV P52486, cranidium, × 2, from PL2269, Costerfield. F, NMV P138218 pygidium, × 2, from PL2269, Costerfield. H, holotype NMV P52484, pygidium, × 1.5, from PL2262, Costerfield. I, NMV P138223, thorax, enlargement showing granulation, from PL2269, Costerfield. J, NMV P139805, teratological pygidium, × 2, from PL386, Costerfield. K, NMV P52482, incomplete fixigena, holotype of '*Dalmanitina* (*Eudolatites*) *aborigenum*' Öpik, 1953, × 2, from PL2269, Costerfield. L, *Struveria* sp. 2, NMV P52483, pygidium, paratype of '*Dalmanitina* (*Eudolatites*) *aborigenum*' Öpik, 1953, × 3, from PL2269, Costerfield. (B, D are latex casts)

Remarks. Of the characters regarded by Curtis and Lane (1998: 62) as diagnostic of *Bessazoon*, Chatterton and Ludvigsen (2004: 47) questioned the taxonomic value of the size of the eyes and the loss of the pygidial mucro in large specimens. In the type species and *B. tigerense* (Holloway and Sandford, 1993) the eyes are very large and occupy almost the entire length of the genal field, but in Curtis and Lane's species *B. buttingtonense* and the cephalon they illustrated as *B*. cf. *B. tenuimucronatum* (their pl. 9, fig. 1) the eyes are smaller and do not extend very close to the border furrows anteriorly and/or posteriorly. In regard to the loss of the mucro, Curtis and Lane illustrated three pygidia assigned to *B. tenuimucronatum* with the posterior termination preserved. Two of these (Curtis and Lane's pl. 8, figs 6, 8) have a mucro, that on the larger specimen being considerably shorter than the one on the smaller specimen. The third pygidium, which is very much larger that the others (Curtis and Lane's 'type 2' pygidium, pl. 8, fig. 2), does not have 'a shorter mucral spine' as stated by Chatterton and Ludvigsen (2004) but an embayment in the margin posteromedially. Because of this difference, as well as the differences in size and the much greater number of axial rings and pleural furrows, it is not possible to be confident that this pygidium is correctly assigned to *B. tenuimucronatum*. However, we note that it has a distinctive pleural structure in which the posterior bands expand distally and the anterior bands are pinched out, and that this structure appears to be shared by the smaller pygidium in pl. 8, fig. 6 (the structure is not clear in the third pygidium as the dorsal surface is broken away distally to reveal the doublure). Although we believe that these pygidia are correctly assigned to the Dalmanitidae, their pleural structure is unusual for Silurian and Devonian representatives of the family, in most of which it is the anterior rather than the posterior pleural band that is dominant distally (Holloway, 1981: 710), as is also the case in *B. buttingtonense* (Curtis and Lane, 1998, pl. 9, figs 2, 4, 7), *B. tigerense* (Holloway and Sandford, 1993, fig. 6) and in the unnamed species from Victoria described below. The only pygidium of *B. buttingtonense* with the posterior termination preserved (Curtis and Lane, pl. 9, fig. 2a, b) is of about the same size as the 'type 2' pygidium of *B. tenuimucronatum* but has neither a mucro nor a posteromedian embayment; instead the margin is rather truncated in dorsal view and arched upwards in posterior view. There is no evidence that the mucro is lost in *B. tigerense* but all known pygidia are smaller than that of *buttingtonense* and the 'type 2' pygidium of *tenuimucronatum*.

Some of the other characters listed by Curtis and Lane as diagnostic of *Bessazoon* cannot in our view be used to distinguish *Bessazoon* either. The size of the palpebral area is determined by the size of the eye, and thus in comparison with other Silurian and Devonian dalmanitids is not particularly large in *B. buttingtonense* and *B*. cf. *B. tenuimucronatum*. We can see no difference from *Dalmanites* and other closely related genera in the form of the palpebral lobe, which rises steeply from the palpebral furrow and becomes flat towards the outer margin. Finally, a posterior cephalic border furrow that fails to meet the lateral border furrow distally, an epiborder furrow on the lateral cephalic borders and genal spine, and a straight-sided pygidial axis are not unusual features for dalmanitids but are present in most Silurian and Devonian representatives. The discrimination and composition of *Bessazoon* are in need of review, but in the meantime we apply the name here to dalmanitids differing from species commonly assigned to *Dalmanites* (e.g. see Ramsköld, 1985) in lacking a well-developed anterior cephalic process (although in *B. tenuimucronatum* the cephalic margin is deflected slightly forwards medially) and tubercles on the glabella, and in having a pygidium with a curved posterolateral outline, a slender, narrow-based mucro merging anteriorly with a strong postaxial ridge, and a very wide doublure extending adaxially beyond the distal ends of the pleural and interpleural furrows.

Bessazoon sp.

Figures 14, 17D–F

Dalmanites.—Rickards and Sandford, 1998: 750.

Material. NMV P139427–P139439, NMV P138276 from PL1452, Goldie. NMV P139470–P139487 from 'Lancefield' (exact locality unknown). NMV P147769–P147770 from PL256, Wallan. NMV P312817 from PL6361, Springfield. Chintin Formation. For locality PL1452 see Thomas (1960), marked as 'shelly fossils, *Dalmanites*'.

Description. Anterior cephalic margin parabolic in outline (fig. 14I). L1 about 75% length of L2. S1 deflected forwards slightly at adaxial end, S2 more or less transverse; S3 shallow, oriented at about 65° to sagittal line, expanding (exsag.) abaxially. Inner ends of S1–S3 in line (exsag.). Palpebral lobe large, length (exsag.) about 40% sagittal glabellar length, almost semicircular in dorsal outline, anterior margin opposite anterior margin of L3 and posterior margin reaching almost as far back as occipital furrow. Palpebral furrow weak (fig. 17E), palpebral area wide (tr.) and weakly concave.

Hypostome approximately as wide across anterior wings as long (sag.), subparallel sided from back of anterior wing to outer end of posterior border furrow, thereafter narrowing backward and parabolic in outline. Anterior wings small, triangular, length (exsag.) about 15% sagittal length of hypostome. Middle body comprising 80% sagittal length of hypostome, weakly convex transversely and flat sagittally. Maculae indistinct swellings behind weak depressions placed opposite 40% hypostomal length from posterior and halfway between sagittal line and lateral border furrow. Lateral border narrow, approximately 6% width of hypostome at midlength (sag.), lateral border furrow weak in anterior half and moderately impressed in posterior half. Posterior border long, 15% hypostomal length sagittally, posterior border furrow semicircular in outline.

Pygidium triangular in outline, relatively undeformed specimens with length (excluding mucro) approximately 75% estimated maximum width. Axis about 25% maximum pygidial width anteriorly, tapering uniformly backward, with 14 axial rings of which last 6 are poorly defined. Inter-ring furrows 1–9 with deep apodemes extending approximately. 33% width, all inter-ring furrows very shallow medially. Axis continuous posteriorly with postaxial ridge and mucro. Axial furrow deep. Mucro slender, at least 75% length (sag.) of remainder of pygidium. 10 pleural furrows that are directed

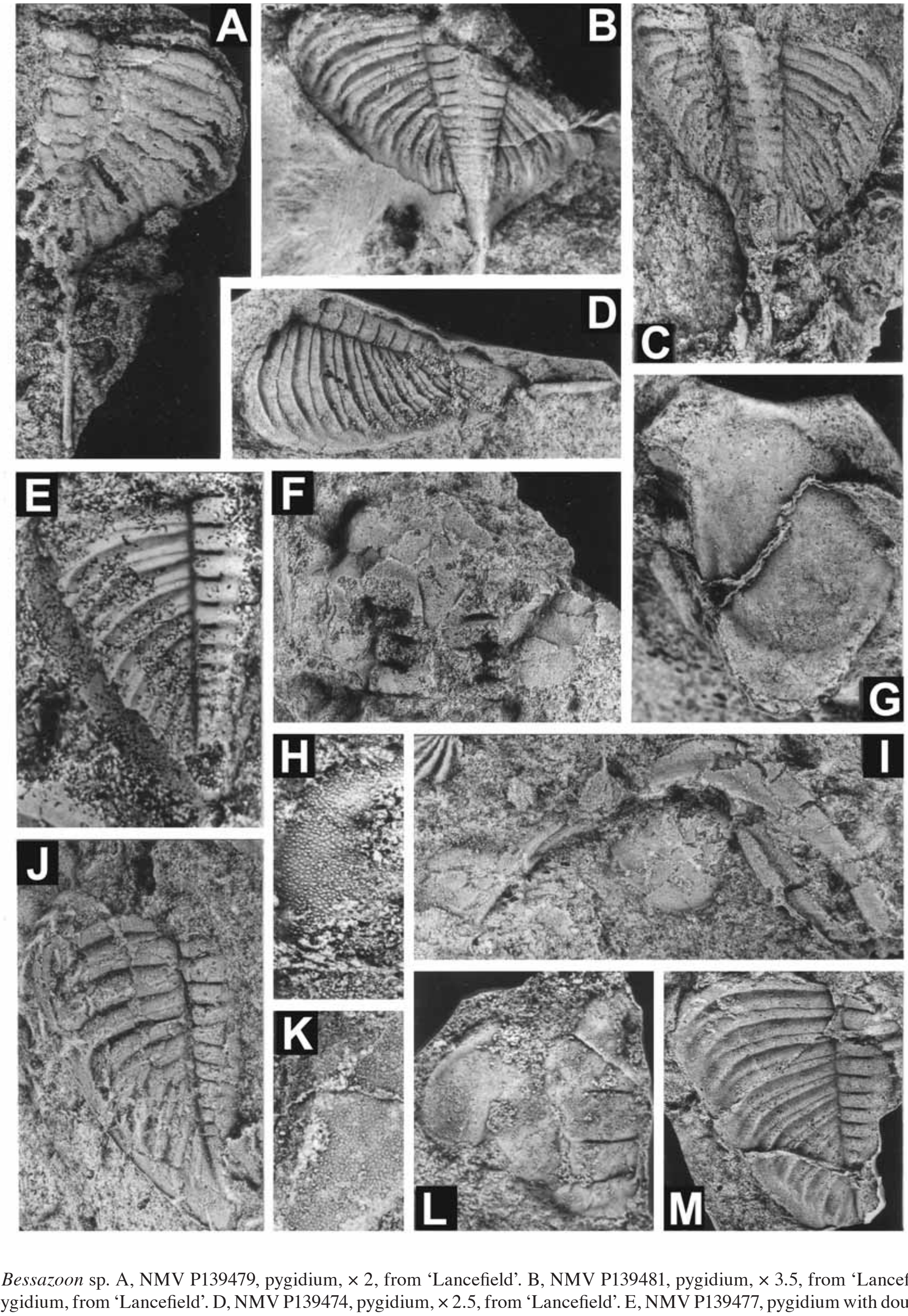

Figure 14. *Bessazoon* sp. A, NMV P139479, pygidium, × 2, from 'Lancefield'. B, NMV P139481, pygidium, × 3.5, from 'Lancefield'. C, NMV P139475, pygidium, from 'Lancefield'. D, NMV P139474, pygidium, × 2.5, from 'Lancefield'. E, NMV P139477, pygidium with doublure exposed, × 6, from 'Lancefield'. F, NMV P139471, crushed cephalon, × 2, from 'Lancefield'. G, NMV P139427, hypostome, × 3, from PL1452, Lancefield. H, J, NMV P139438, pygidium, from PL1452, Lancefield; H, enlargement of anterolateral region showing granular sculpture, × 8; J, × 2. I, NMV P139439, crushed cephalic doublure, × 1.9, from PL1452, Lancefield. K, thoracic segment, enlargement showing granulose ornament on pleural tip, × 8, from 'Lancefield'. L, NMV P139470, fragment of cephalon, × 3, from 'Lancefield'. M, NMV P139473, pygidium, × 2, from 'Lancefield'. (E–F are internal moulds).

successively more strongly backward, last one parallel to sagittal axis. Interpleural furrows moderately incised, widening distally. Anterior pleural bands expand slightly and very gradually abaxially, at fulcrum approximately as long (exsag.) as succeeding pleural furrow, slightly elevated above posterior bands distally. Posterior pleural bands subparallel sided except distally where they taper, at fulcrum comprising about 75% length (exsag.) of anterior bands.

Densely distributed small granules present on preserved parts of external surface including occipital ring, thoracic pleural tips and doublure, dorsal surface of pygidium and pygidial doublure.

Remarks. This species can be distinguished from other Silurian dalmanitids from central Victoria by its pygidial pleural morphology, with relatively narrow, trench-like pleural furrows, and anterior bands that are slightly longer (exsag.) than the posterior bands at the fulcrum and only slightly elevated above the posterior bands distally. *Dalmanites athamas* differs in having longer (exsag.) pleural furrows and anterior pleural bands that are much longer than the posterior bands, whereas *D. wandongensis* has anterior bands that are slightly shorter (exsag.) than the posterior bands at the fulcrum and strongly elevated above the posterior bands distally. *D. wandongensis* also differs from the present species in having a pygidium with a well defined axial terminus and a shorter mucro that is very broad at the base, and a hypostome with deeper middle, lateral border and posterior border furrows, and a posterior margin that is transverse in outline medially instead of parabolic.

The specimens are poorly preserved and mostly fragmentary, especially the cephala. Assignment to *Bessazoon* is based on the finely granulose cephalic ornament, the entire anterior cephalic margin, the curved posterolateral pygidial margin and the long, slender mucro merging with the axial terminus. The type species *B. tenuimucronatum* differs from the present one in having slightly inflated lateral glabellar lobes, a more strongly curved (exsag.) palpebral lobe, a deeper palpebral furrow, and the posterior pleural bands on the pygidium more expanded and prominent distally than the anterior bands rather than the reverse. *B. tigerense* from the upper Llandovery of Tasmania has a more strongly curved palpebral lobe, a deeper palpebral furrow, and less robust postaxial ridge and mucro.

Preodontochile Degardin and Pillet, 1984

Type species. *Dalmanites* (*Preodontochile*) *camprodonensis* Degardin and Pillet, 1984 from the central Pyrenees, Spain, by original designation. The precise age of *D.* (*P.*) *camprodonensis* is uncertain, as Degardin and Pillet stated (p. 87) that the species occurs with graptolites of the early Wenlock *Monograptus riccartonensis* Biozone, but elsewhere (fig. 4) they showed its stratigraphical range as lying in the upper Llandovery.

Remarks. Degardin and Pillet (1984) erected the monotypic *Dalmanites* (*Preodontochile*) for a poorly known species represented by few and poorly preserved specimens including a single crushed cranidium, an isolated thoracic segment and a number of pygidia that are mostly incomplete posteriorly. The material permits only a limited assessment of *Preodontochile*, but as diagnostic of their subgenus Degardin and Pillet listed the small eye, the course of the anterior branch of the facial suture, and the multisegmented pygidium with a short, blunt mucro. They likened the facial suture both to that of *Dalmanites* in being situated in close proximity to the glabella and to that of *Odontochile* in being separated from the glabella by the preglabellar furrow and a narrow band of the anterior cephalic border. However, as noted by Whittington and Campbell (1967), the distinction between *Dalmanites* and *Odontochile* on the basis of the anterior cephalic morphology is not as clear-cut as stated by Richter, Richter and Struve (1959). Several Wenlock–Ludlow species of *Dalmanites*, including the Swedish *D. imbricatulus* (Angelin, 1851) (see Ramsköld, 1985), the North American *D. puticulifrons* Whittington and Campbell, 1967 and *D. rutellum* Campbell, 1967, and the Australian *D. wandongensis*, have a narrow band of the anterior border enclosed by the facial suture on the cranidium. This condition is also present in the Victorian Llandovery dalmanitid described below as *Preodontochile springfieldensis* (see Fig. 16A), which further resembles *P. camprodonensis* in the greatly reduced eye situated far forwards opposite L3, the robust genal spine, the short, bluntly pointed mucro and the finely granulose sculpture. We consider this combination of characters to be of generic significance. With better understanding of *P. camprodonensis* other cephalic features of *P. springfieldensis* may also prove to be diagnostic of the genus, such as the uniformly narrow (sag., exsag.) anterior border that is less than half the width of the lateral border and lacks a median projection. In its pygidium with a large number of segments and narrow axis, *P. camprodonensis* resembles late Silurian–Devonian species assigned to *Odontochile* and closely related genera. Degardin and Pillet (1984) considered a large number of pygidial segments as diagnostic of *Preodontochile*, but in view of the otherwise close similarity of the type species with the more poorly segmented *P. springfieldensis* the number of pygidial segments is here regarded as only of specific significance.

Other dalmanitid genera known from the Llandovery include *Bessazoon* (see above), *Daytonia* Holloway, 1981 and *Prodontochile* Kobayashi and Hamada, 1971, all of which are easily distinguished from *Preodontochile* by their much larger eyes. In addition, *Bessazoon* differs from *Preodontochile* in having the facial suture tightly enclosing the glabella, and a long, slender mucro connected to the pygidial axis by a postaxial ridge; *Daytonia* has the occipital ring markedly reduced in length abaxially, S1 bifurcate adaxially and converging slightly with S2 abaxially, the anterior cephalic border as wide as the lateral border, short and slender genal spines, and a pygidium with parabolic outline and a tiny mucro joined to the axis by a postaxial ridge; and *Prodontochile* has a narrower lateral cephalic border and slender genal spines.

Wenlock–early Ludlow species of *Dalmanites* assigned by Ramsköld (1985) to his group around the type species *D. caudatus* differ from *Preodontochile* in having a large eye extending from opposite L3 to opposite L1, an anterior cephalic border with a well-developed medial process, tuberculate sculpture on the glabella, prominent lateral nodes on some thoracic axial rings, pleural nodes on some pygidial segments, and a long pygidial mucro.

Preodontochile springfieldensis sp. nov.

Figures 15, 16

Type material. Holotype NMV P312070 (cephalon with broken and displaced genal field). Paratypes NMV P312071 (incomplete cephalothorax showing damage to genal field), NMV P139350 (incomplete and partly disarticulated cephalothorax showing cephalic doublure and hypostome), NMV P312074 (incomplete pygidium), NMV P312075 (incomplete and partly disarticulated thoracopygon). All from PL1369, Springfield.

Other material. NMV P139350–P139352, NMV P312072–P312073, from PL1369, Springfield.

Diagnosis. *Preodontochile* with eye oriented slightly obliquely to exsagittal line and visual surface having approximately 40 lenses arranged in about 15 files of up to 4 lenses each. Posterior cephalic border markedly expanding (exsag.) abaxially, genal spine very broad proximally and tapering strongly distally. Pygidial axis about 25% maximum pygidial width anteriorly, with 10 axial rings, first 5 well defined by inter-ring furrows that contain apodemal pits laterally and are shallow medially, posterior rings poorly defined by shallow inter-ring furrows that are not continuous medially. Pleurae with about 7 shallow pleural furrows and very weakly impressed interpleural furrows. Mucro with length (measured from terminus of axis) comprising about 25% sagittal pygidial length. Pygidial doublure wide.

Description. Cephalon (excluding genal spines) semi-circular in outline, anterior margin with very weak convex-downward medial flexure in anterior profile. Glabella weakly convex, slightly narrower across L1 than across occipital ring, thereafter expanding moderately forward, a little more strongly in front of S3 than behind, width across frontal lobe 170–180% occipital width and about 80% sagittal length of glabella. Occipital ring raised slightly higher than remainder of glabella, width (tr.) about 30% cephalic width across same transverse line, length about 12% cephalic length sagittally, shorter (exsag.) laterally. Median section of occipital furrow gently convex forward and very shallow, lateral section (approximately 30% total width) with arcuate, slit-like apodemal pit not quite reaching axial furrow distally. S1 and S2 defined only by slit-like apodemal pits that are equal in width (tr.) to occipital apodemal pit and placed directly in front of it; S1 gently arcuate, equidistant from occipital furrow and S2; S2 transverse, situated at 33% cephalic length from posterior. L3 as long (exsag.) as L1 and L2 adaxially, 160% as long abaxially. Adaxial portion of S3 oriented at about 20° to transverse, abaxial portion very wide, lenticular in outline, oriented at about 35° to transverse. Frontal lobe comprising half sagittal length of glabella, elliptical in outline, with short, shallow sagittal depression in posterior half. Axial furrow moderately impressed, preglabellar furrow shallow. Anterior cephalic border of uniform length (sag., exsag.), comprising about 8% sagittal cephalic length, subhorizontal, weakly concave. Lateral border furrow defined mainly by change in slope, lateral border very wide (tr.), twice width of anterior border, gently sloping, weakly concave. Posterior border furrow deep, adaxial portion transverse, abaxial portion directed posterolaterally, terminating before reaching lateral border furrow. Genal spine long, with longitudinal furrow dividing horizontal lateral portion from steeply sloping adaxial portion. Eye with length about 20% sagittal cephalic length, anterior edge placed opposite front of L3 and posterior edge just in front of level of S2. Palpebral lobe not greatly raised above palpebral area, crescentic in outline, narrow (tr.). Palpebral furrow weak. Visual surface with lower margin subtending an angle of about 80° in dorsal view. Anterior branch of facial suture diverging gently forward towards widest part of frontal lobe, posterior branch weakly sinusoidal, meeting lateral cephalic margin more or less opposite posterior edge of eye. Librigenal field weakly convex, about 66% width of lateral border.

Cephalic doublure flat anteromedially, approximately 33% sagittal cephalic length, crossed by weak arcuate furrow defining crescentic area adjacent to hypostomal suture. Lateral to hypostomal suture, doublure with upturned inner flange that is continuous posteriorly with adaxial surface of genal spine. Only available hypostome is incomplete posteriorly. Anterior wing small, middle body with parabolic posterior outline, middle furrow indistinct, posterior portion of lateral border furrow and posterior border furrow shallow.

Anterior part of thoracic axis subparallel-sided and comprising about 33% segmental width (tr.) (fig. 15A–B, D, F), posterior part of axis relatively narrower (fig. 16G). Axial rings weakly convex (sag.), with indistinct lateral lobes that lack nodes. Axial furrow moderately impressed. Pleural furrows sigmoidal, short (exsag.) and sharply impressed, at fulcrum dividing segment into anterior and posterior bands of equal length (exsag.) and height. Distal ends of pleurae rounded anteriorly and angular posteriorly.

Pygidium moderately convex transversely, subtriangular in outline with weakly convex sides converging posteriorly at about 60°. Axis tapering uniformly backward, 2nd segment with broad, subrectangular pseudo-articulating half ring, much smaller and weaker pseudo-articulating half rings possibly present on next two segments. Mucro triangular, postaxial ridge absent.

Exoskeleton finely granulate, lacking tubercles.

Remarks. The poor preservation of the only available cranidium of *P. camprodonensis* does not permit detailed comparison with *P. springfieldensis*, but the latter differs in the less obliquely oriented eye and the greater abaxial expansion of the posterior border. Differences in the form of S1 and S2, which in *springfieldensis* are isolated and very narrow (exsag.) but in *camprodonensis* appear wider (exsag.) and deeper, with S1 said to be connected medially (Degardin and Pillet, 1984, p. 87, fig. 5), can be attributed to crushing in the latter. The most striking difference between *P. springfieldensis* and *P. camprodonensis* is in pygidial segmentation. Pygidia of the type species have about 20 axial rings, at least 15 deep and medially continuous inter-ring furrows, at least 11 wide and deep pleural furrows, and very strongly incised interpleural furrows. In contrast, pygidia of *springfieldensis* have only ten axial rings, five continuous inter-ring furrows that are shallow medially, seven narrow (exsag.), shallow to moderately impressed pleural furrows, and very weak interpleural furrows.

The occurrence of *P. springfieldensis* at PL1369 together with another relatively small-eyed form (Phacopidae gen. indet. 3) is significant. Eye reduction in phacopids and other

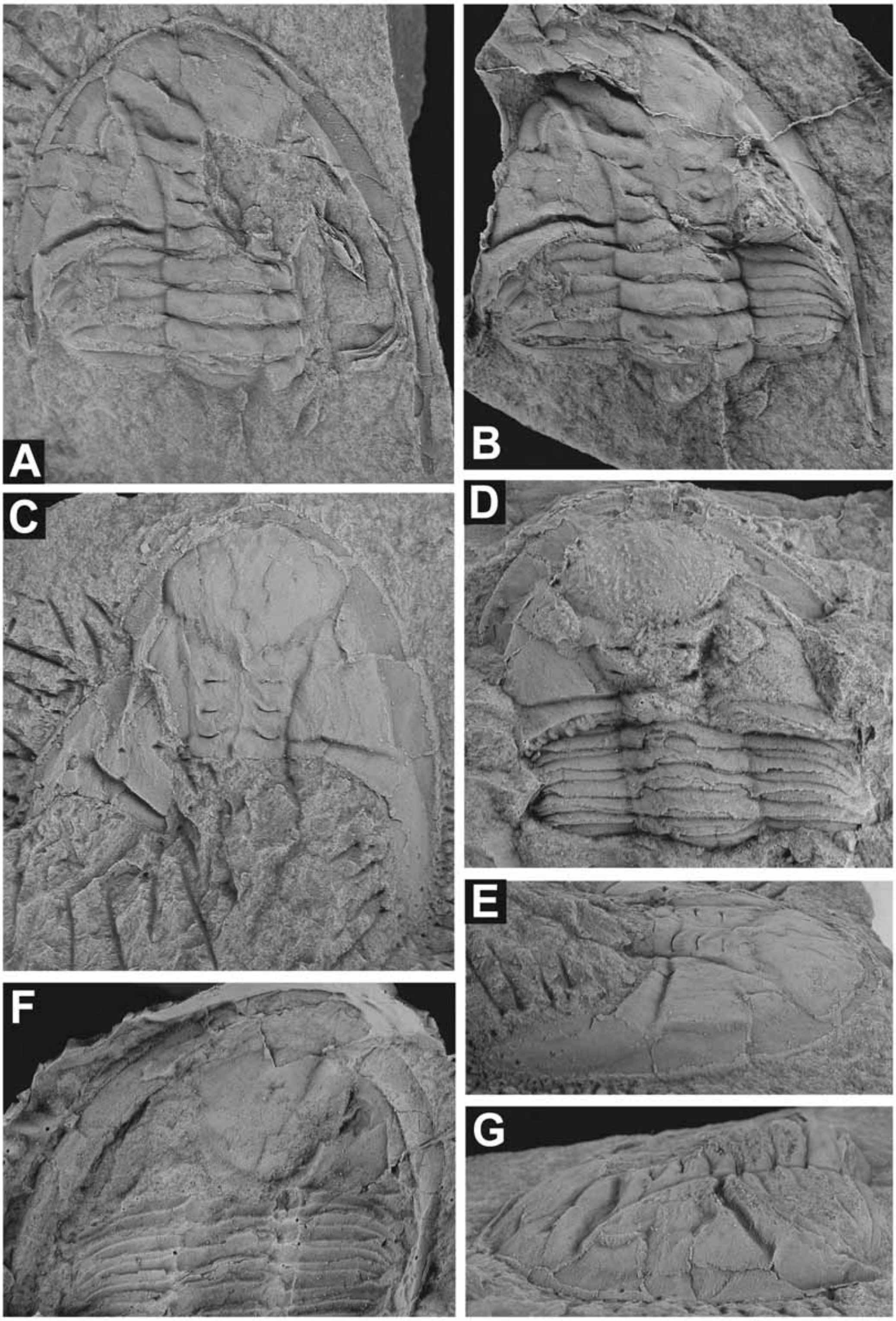

Figure 15. *Preodontochile springfieldensis* sp. nov., from PL1369, Springfield. A–B, G, paratype NMV P312071, incomplete cephalothorax with damaged genal field; A–B, × 2.2; G, × 2.7. C, E (and figs 16A, E–F), holotype NMV P312070, cephalon with left cheek broken and displaced; C, × 2; E, × 1.8. D, F (and fig. 16H), paratype NMV P139350, cephalothorax; D, × 1.8, with glabella showing tool marks from preparation; F, × 2.0, showing cephalic doublure and hypostome. (A, C, E, G are internal moulds).

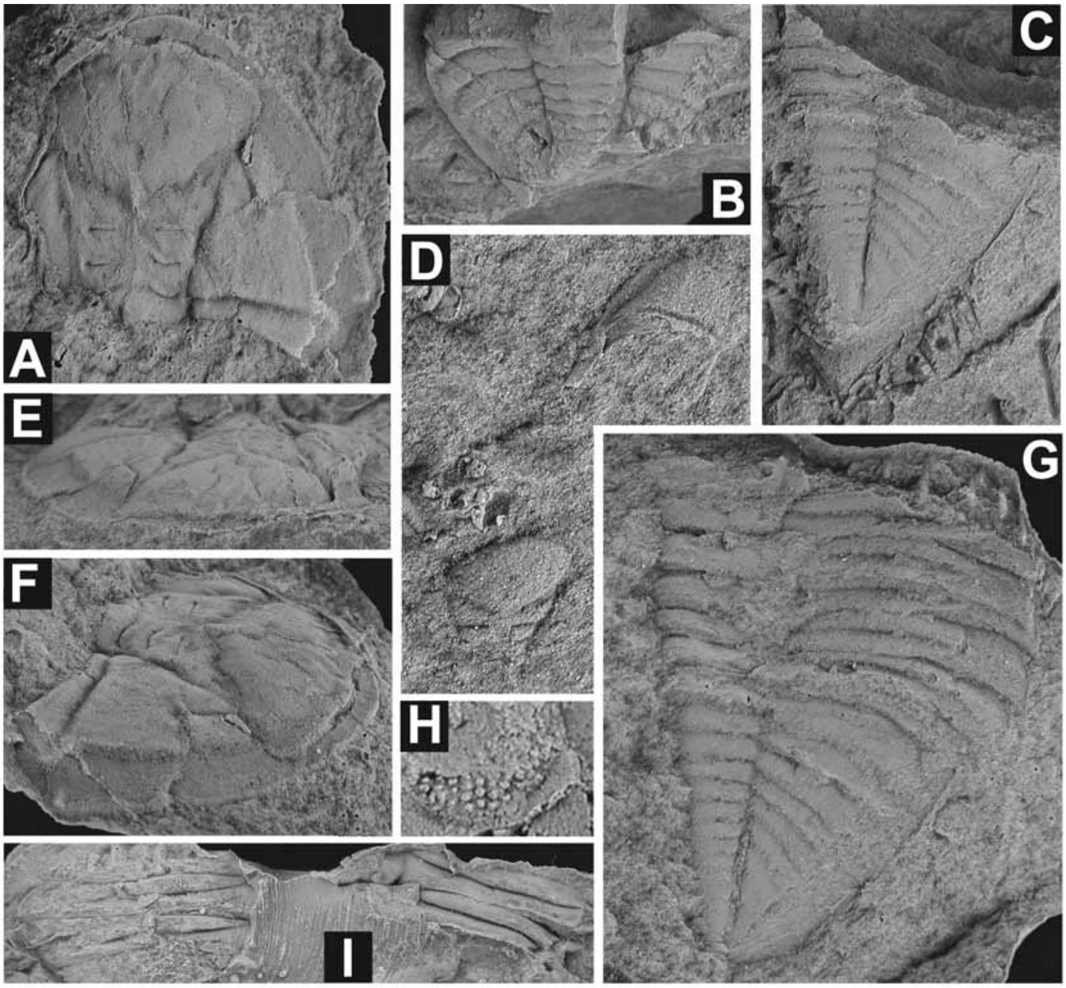

Figure 16. *Preodontochile springfieldensis* sp. nov., from PL1369, Springfield. A, E–F, holotype NMV P312070, × 2. B, paratype NMV P312074, pygidium, × 2. C, G, paratype NMV P312075, thoracopygon; C, × 3; G, × 2.7. D, paratype NMV P312072, cranidium and displaced cheek, × 5. H, paratype NMV P139350, enlargement of eye, × 8. I, NMV P139351, three thoracic segments, × 1.5. (B–C, E are internal moulds).

trilobites has been widely interpreted as an adaptation to deep water, subphotic environments, although Álvaro and Vizcaïno (2003) noted that high turbidity may create subphotic environments in shallower settings. The taphonomy of the Deep Creek trilobite population is indicative of a deep water facies rather than turbid conditions. The degree of articulation is high (isolated tergites 40%), and although there are no fully articulated exoskeletons, specimens have been found with the hypostome only slightly displaced along the hypostomal suture (fig. 15F), and with incomplete thoraces attached to the cephalon or only slightly detached from it or from the pygidium (figs 15A–B, D, G, 16G). This evidence suggests deposition at depths below normal wave base where bottom current activity is negligible, preventing displacement, winnowing and concentration or reworking of the exoskeletal elements. These deep water beds correlate in age with the late Telychian (mid *Monoclimacis crenulata* Biozone) eustatic highstand (event 4) documented from six palaeocontinents by Johnson (1996). The abrupt transition from these beds to the shallower water facies of the overlying Chintin Formation may reflect the influence of an extensive latest Telychian Gondwanan glaciation event documented from Brazil (Grahn and Caputo, 1992). Otherwise, the Chintin Formation appears to correspond closely in age to the subsequent regressive phase that culminated in an earliest Wenlock lowstand.

Struveria Rickards, 1965

Type species. *Struveria howgillensis* Rickards, 1965 from the upper Wenlock–lower Ludlow of northern England and North Wales, by original designation.

Remarks. Apart from the type species and the Victorian specimens described below, *Struveria* includes *S. orba* (Barrande, 1852) from the upper Wenlock of the Czech Republic, and *S. simrica* (Hede, 1915) from the upper

Llandovery?–Wenlock of southern Sweden (see Laufeld et al., 1975) and the upper Wenlock of Poland (Tomczykowa, 1991). *S. howgillensis* is the most completely known species (Rickards, 1965: pl. 85, figs 1–6) but neither this nor the other representatives have been extensively illustrated, and most are rather poorly preserved. Consequently the genus is not very well known morphologically, but distinctive characters include: a very short (sag., exsag.) anterior cephalic border; almost transverse S1 and S2, both containing apodemal pits; a moderately large eye extending very close to the lateral border furrow anteriorly and laterally; a long, flattened genal spine; a pygidium that is curved in outline posterolaterally and lacks a convex border or mucro; pygidial axial rings bearing oblique muscle impressions laterally, except for the last few; a narrow, rather sharp postaxial ridge; short (sag., exsag.), sharply impressed pygidial pleural and interpleural furrows, the pleural ones terminating distally a short distance from the margin whereas the interpleural ones reach the margin; and posterior pleural bands that are slightly more raised distally than the anterior bands towards the back of the pygidium.

Struveria orba was tentatively assigned to *Delops* by Šnajdr (1982), but the lectotype cranidium and other specimens figured by Šnajdr (1982: pl. 2, figs 5–10) resemble the type species of *Struveria* in the strongly transverse frontal lobe and distinctly concave lateral outline of the glabella behind a transverse line through the inner end of S3, and they lack the tuberculate sculpture and expanded (exsag.) pygidial pleural furrows characteristic of *Delops*. Two pygidia assigned to *orba* by Barrande, one of them a paralectotype (Barrande 1852: pl. 26, fig. 38; Šnajdr 1982: pl. 2, fig. 1), are not conspecific with the lectotype but belong to *Delops dermolac* (see also Budil, 1996). '*Calymene*? *daviesii* Salter, 1865, known only from an internal mould of a pygidium from the upper Wenlock of Wales, was tentatively assigned to *Struveria* by Morris (1988: 223) but we cannot assess this assignment from the woodcut illustration of Salter (1865) (fig. 23).

As pointed out by Rickards (1965: 549) and Bergström (in Laufeld et al., 1975: 219), *Struveria* shows similarities to *Eudolatites*, a genus largely restricted to the Caradoc apart from the late Ashgill subgenus *E.* (*Deloites*) Destombes, 1972, which was regarded as an independent genus by Tomczykowa (1991) and Vaněk and Vokáč (1997). *Eudolatites* differs from *Struveria* in that S1 is more obliquely oriented; S2, though commonly rather deep, seems to lack an apodemal pit (Destombes, 1972: pl. 3, fig. 1a, pl. 4, fig. 1a); the librigenal field is much broader anterior and lateral to the eye; there is either no genal spine present, or it is short, strongly tapered, and rounded in cross section distally rather than flattened (see Rábano *in* Gutierrez Marco and Rábano, 1987: pl. 1, fig. 1c); and the pygidium lacks a sharply defined postaxial ridge.

Struveria sp. 1

Figures 12B–C

Material. NMV P139357 (partly disarticulated dorsal exoskeleton with displaced hypostome, thorax and pygidium) from PL1386, Geological Survey locality B3 (exact locality unknown), Moonee Ponds Creek, Broadmeadows. Precise stratigraphic horizon uncertain.

Remarks. The cephalon of the specimen has the glabella except for the anteriormost part obscured by the displaced hypostome and medial part of the doublure. Much of the left fixigena is preserved, including the large palpebral lobe and the posterior border, the latter curving backwards abaxially to the base of the genal spine. The pygidium is more completely preserved than the cephalon, is almost twice as wide as long (sag.), with six or seven axial rings and pleural furrows, and the axis comprising a little more than 25% maximum pygidial width anteriorly. The specimen can be assigned to *Struveria* with confidence on the basis of the pygidial morphology.

The hypostome of *Struveria* has not previously been illustrated. That of the present specimen is similar to hypostomes of other dalmanitids (e.g. see Ramsköld, 1985, pl. 10, fig. 12).

Struveria sp. 2

Figures 13L, 17A, 17C

Dalmanitina (*Eudolatites*) *aborigenum* Öpik, 1953: 26 (*partim.*), pl. 10, figs 86–87 (*non* pl. 10, fig. 85 = *Dalmanites athamas* Öpik, 1953).

Material. NMV P52483 (fragmentary pygidium), from PL2269, Thomas locality F51, Costerfield. Wapentake Formation. For locality see Thomas (1960). NMV P139337 (cranidium), NMV P138209 (pygidium), from PL206, Wallan. Bylands Siltstone.

Remarks. Compared to the pygidium of *Struveria* sp. 1 from Broadmeadows, the pygidium from Wallan (fig. 17A) is longer (maximum width about 150% sagittal length), with a wider axis (almost 33% maximum pygidial width anteriorly) and a greater number of axial rings (nine or ten) and pleural furrows (ten or 11). It is unlikely that these differences can be explained by the larger size of the Wallan pygidium, and we therefore consider it to belong to a separate species. The cranidium from Wallan (fig. 17C) is small and indifferently preserved but its morphology is consistent with assignment to *Struveria*.

The paratype of '*Dalmanitina* (*Eudolatites*)' *aborigenum* is a fragmentary pygidium from Costerfield, consisting of the anterior part of the axis and the adjacent part of the right pleural lobe (fig. 13L). It differs from pygidia of *Dalmanites athamas*, to which the holotype of *aborigenum* belongs, in that the inter-ring furrows do not shallow markedly medially but are deeply impressed across the entire width of the axis; the pleural furrows are not expanded but are short (exsag.), sharply impressed and similar in appearance to the interpleural furrows; and the anterior and posterior pleural bands are flat-topped. These characters suggest that the specimen belongs to *Struveria*, and it may be conspecific with the Wallan specimens which come from a similar stratigraphical level.

Struveria? *plinthourgos* sp. nov.

Figure 18

Eudolatites sp.—Rickards and Sandford, 1998: 751.

Type material. Holotype NMV P79125 (internal mould of dorsal exoskeleton) from PL1374, old Camberwell brick pit, Rose Street, Camberwell. Anderson Creek Formation.

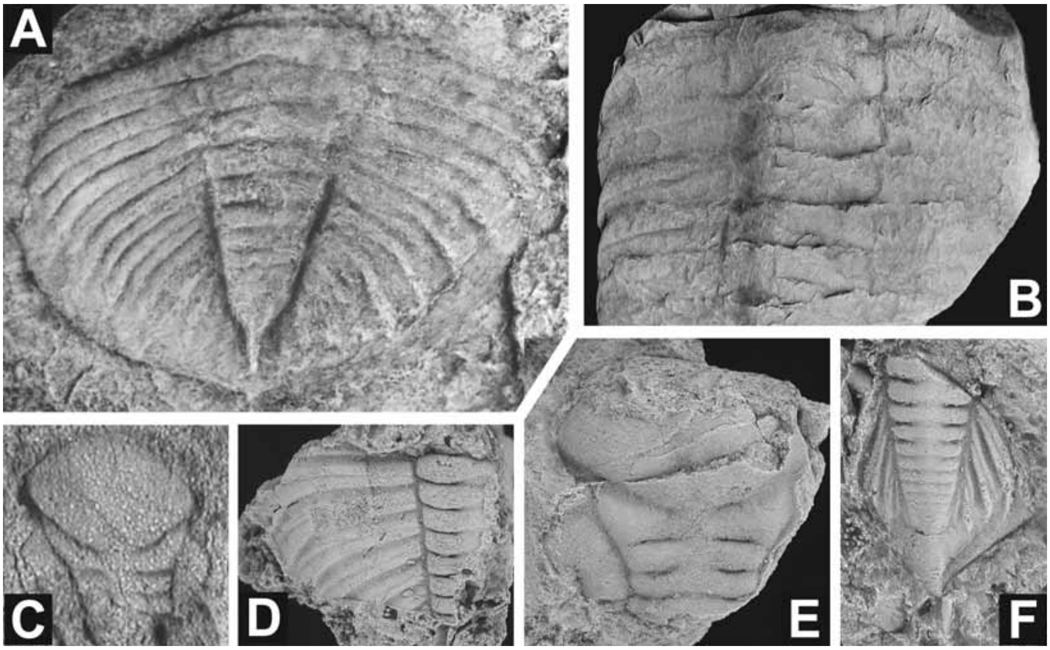

Figure 17. A, C, *Struveria* sp. 2, from PL206, Wallan. A, NMV P138209, pygidium, × 2. C, NMV P139337, cranidium, × 5.5. B, Dalmanitidae indet., NMV P127957, partial view of incomplete thorax, × 0.9, from old Costerfield Antimony Mine, Costerfield. D–F, *Bessazoon* sp. D, NMV P147769, pygidium (fragment), × 1.8, from PL256, Wallan. E, NMV P312817, cranidium (fragment), × 2.2, from PL6361, Springfield. F, NMV P147770, pygidium (fragment), × 2.4, from PL256, Wallan.

Derivation of name. Greek, 'brickmaker', in reference to the type locality.

Diagnosis. Glabella subpentagonal in outline, expanding strongly and rather uniformly forward, width across frontal lobe about twice width across occipital ring and approximately equal to sagittal length. Eye short (exsag.), with posterior edge opposite S3. Pygidium with strongly convex (tr.) axis of 10 or 11 rings, 9 pleural furrows, and relatively broad, concave border on which pleural and interpleural furrows are very weakly expressed.

Description. Cephalon with length (sag.) about 60% maximum width. Glabella comprising a little less than 30% cephalic width posteriorly. Occipital furrow shallowing and deflected forward medially. S1 and S2 transverse, meeting axial furrow distinctly, adaxial portions with slit-like apodemal pits situated in line exsagittally, S2 comprising 33% glabellar width at this level and with apodemal pit occupying half width (tr.) of furrow. L1 approximately 80% length (exsag.) of L2 laterally. S3 diverging forward at about 125°, shallow adaxially and deepening slightly abaxially but not expanding appreciably. L3 a little more than twice as long (exsag.) abaxially as adaxially. Frontal lobe comprising approximately half sagittal length of glabella, rhombic in outline, apparently with short (exsag.) longitudinal depression at about midlength. Eyes and palpebral lobes not preserved, palpebral furrow apparently shallow, weakly curved and oriented slightly oblique to exsagittal line. Posterior branch of facial following gently sigmoidal course, directed slightly forward across most of genal field and deflected backward laterally. Posterior border furrow deeply impressed, apparently deflected forward slightly abaxially and dying out distally before reaching lateral border furrow. Backward deflection of posterior cephalic margin distally indicates that genal spine was present (fig. 18D) but its length is unknown. Fixigenal field densely pitted.

Thorax of 11 segments. Axis strongly convex (tr.), increasing slightly in width from 1st to 4th or 5th segment and thereafter narrowing at similar rate, width on 1st segment equal to that on 8th segment and almost 120% that on last segment. Axial rings gently convex (sag., exsag.), without lateral lobes. Axial furrow deeply impressed. Pleural lobe slightly wider (tr.) than axis in anterior half of thorax and becoming increasingly wider towards back. Pleurae strongly downturned beyond fulcrum, with large articulating facets and pointed tips becoming backwardly deflected towards back of thorax. Pleural furrows very deep, extending weakly onto articulating facets distally where they curve slightly forward.

Posterior termination of pygidium unknown; if it is rounded rather than mucronate or angular, pygidium is about 150% as wide as long (sag.) with parabolic posterior outline; anterolateral corner well-rounded. Axis strongly convex (tr.), width 25% maximum pygidial width anteriorly, possibly not tapering uniformly backward but a little more strongly across first 3 segments than next 2 or 3, thereafter at similar rate as initially. 1st ring with broad, shallow median excavation in posterior margin for pseudo-articulating half ring on 2nd segment, much weaker excavations present on 2nd and 3rd rings. Inter-ring furrows 1–6 with apodemal pits laterally,

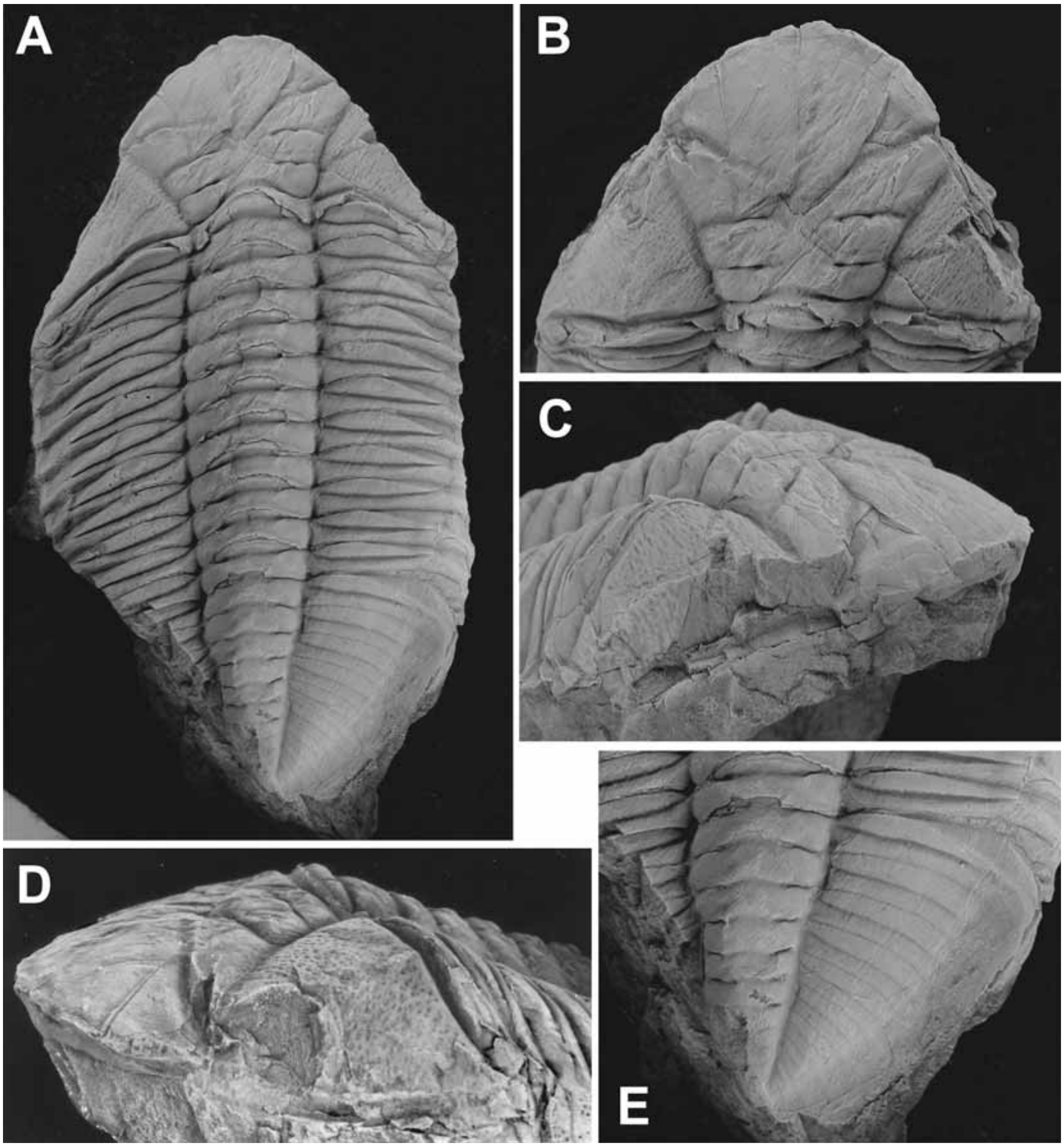

Figure 18. *Struveria*? *plinthourgos* sp. nov., holotype NMV P79125, internal mould of dorsal exoskeleton, from PL1374, Camberwell; A, × 1; B–E, × 1.25.

remaining inter-ring furrows very weak. Pleural field rather strongly convex (tr.), 1st segment with wide articulating facet extending 66% width of pleura and with deep pleural furrow not extending onto facet distally, subsequent segments with successively shallower pleural furrows more closely approaching interpleural furrows in depth and length (exsag.). Concave border comprising almost 33% pleural width anteriorly, not bounded adaxially by distinct border furrow, outer margin not rolled in transverse section.

Remarks. The only known specimen is an internal mould of a very large and substantially complete dorsal exoskeleton almost 130 mm long (assuming the pygidium lacks a mucro). The cephalon is crushed, especially the frontal lobe of the glabella which bears radiating fractures, so that its flattened profile is not indicative of the original convexity. The anterior outline of the glabella in dorsal view is formed by an arcuate fracture, below which the cephalon slopes steeply downward to a lower margin that is a smoothly curved line (figs 18C–D); it is not clear whether this line is the facial suture or the hypostomal suture, but the former is more likely. The lateral part of the right cheek has been pushed downward and inward along a posterolaterally-directed fracture that has destroyed the palpebral lobe, and of the right librigena only the border and possibly a small portion of the adjacent field are preserved. On the left cheek the palpebral lobe has been broken off along the palpebral furrow, the flattened appearance of the genal spine base may not be indicative of its original shape in cross-section, and all that remains of the librigena is the lateral outline (fig. 18D). The distal parts of the last few thoracic segments are missing on the left side, together with most of the left pleural lobe and posterior termination of the pygidium.

Generic assignment of the species is problematic, partly because certain important characters cannot be determined, including the form of the cephalic borders and genal spine, and the nature of the pygidial termination. The specimen was assigned to *Eudolatites* by Rickards and Sandford (1998), although that genus is not known to range above the Ordovician, but features such as the transverse orientation of S1 and the presence of an apodemal pit in S2 are incompatible with such an assignment. On the basis of these characters and the form of the pygidial pleural and interpleural furrows we tentatively assign *plinthourgos* to *Struveria*. The species differs from other members of the genus in that the glabella is subpentagonal in outline rather than club-shaped (i.e. it is not concave in lateral outline behind a transverse line through the inner end of S3), the eye is shorter (exsag.) and does not extend as far backward, the palpebral furrow is more weakly curved, the genal spine appears to be smaller at its base, and the pygidium has a concave border; however ,we can not be certain that the last feature is not caused by compression of the dorsal exoskeleton onto the doublure.

Dalmanitidae indet.

Figure 17B

Dalmanitina sp. cf. *Dalmanitina* (*Eudolatites*) *aborigenum*.—Öpik, 1953: 28, pl. 10, fig. 92.

Trilobita *indet*.—Talent, 1964: 51 (pars).

Material. NMV P127957 (incomplete thorax) from old Costerfield Antimony Mine, Costerfield. Costerfield Siltstone. Locality marked Thomas (1941).

Remarks. This poorly preserved thorax with seven or possibly eight segments distinguishable is the only fossil recorded from the Costerfield Siltstone. Based on its large size (about 60 mm wide) and the form of the pleural furrows, Öpik (1953, p. 29) suggested that it probably belongs to *Dalmanitina*, a genus then interpreted more broadly than now, and that it may be related to his species ‘*Dalmanitina* (*Eudolatites*)’ *aborigenum* from beds higher in the sequence. However, Talent (1964), regarded the specimen as too poorly preserved for identification even to family level.

We agree with Öpik that the specimen probably belongs to the Dalmanitidae, and that the short (exsag.), sharply incised pleural furrows preclude assignment to *Dalmanites* or its close allies. However, the holotype of ‘*Dalmanitina* (*Eudolatites*)’ *aborigenum*, the species to which he thought it may be related, belongs to *Dalmanites athamas* (see above), and the fragmentary pygidium also included in *aborigenum* by Öpik is here assigned to *Struveria* sp. 2. In size, the abaxially subquadrate outline of the axial rings and the form of the pleural furrows, the poorly preserved thorax from Costerfield is not unlike *Struveria*? *plithourgos* described above, and it is possible that the two forms are related.

Superfamily **Acastoidea** Delo, 1935
Family **Acastidae** Delo, 1935

Berylacaste gen. nov.

Type species. *Berylacaste berylae* gen. et sp. nov.

Derivation of name. After ACS’s mother. Gender feminine.

Diagnosis. Glabella expanding strongly forward, about twice as wide across frontal lobe as across occipital ring, strongly inflated, overhanging anterior cephalic border. L1 almost as long (exsag.) as L2, S2 and S3 very shallow. Visual surface absent, palpebral lobe very small, situated towards front of genal field, merging with eye ridge that reaches axial furrow, palpebral suture straight and obliquely oriented. Genal spine very small, thorn-like. Thoracic pleural tips with small posterolaterally directed spines. Pygidial axis with 3 rings and poorly segmented posterior part, pleurae with 4 pleural furrows and poorly defined border furrow, posteromedian margin rounded, lacking spine or point.

Remarks. *Berylacaste* gen. nov. is known only from the type species. The genus is distinguished from others in the Acastoidea most notably by the strong forward expansion of the glabella, the frontal lobe that overhangs the anterior cephalic border, the vestigial palpebral lobe situated far forward, and the absence of a visual field. Other distinctive characters are the very weak impression of S2 and S3, the presence of genal and thoracic terminal pleural spines, and the very weak pygidial segmentation.

Edgecombe (1993) recognised the monophyletic superfamily Acastoidea *s.s.* comprising the Calmoniidae and the Acastidae, but excluding more primitive genera such as *Phacopidina*, *Baniaspis* and *Kloucekia* which he referred to as Acastoidea *s.l.* without familial assignment. *Berylacaste* gen. nov. can be assigned to his Acastoidea *s.s.* as it exhibits a ‘shouldered’ anterior cephalic margin (i.e. the median part of the margin in front of the glabella projects in front of the outline of the cheeks) and an abrupt change in depth between the anterior and posterior inter-ring furrows in the pygidial axis. The Acastidae was considered by Edgecombe (1993) to consist of a monophyletic Acastidae *s.s.* together with some other loosely related genera (*Llandovacaste* and *Australoacaste*) that were assigned to Acastidae *s.l.* He gave a brief diagnosis for the Acastidae *s.s.* that included the following synapomorphies: S1 transverse or anteromedially directed, lacking proximal bifurcation; L1 much shorter (exsag.) than L2; S2 transverse. *Berylacaste* conforms to this diagnosis in the orientation of S1 and S2, but S1 appears to be slightly expanded or incipiently bifurcate at its proximal end in some specimens (e.g. figs 19F–G), and L1 is not markedly shorter than L2. We note, however, that there is some variation in the length of L1 within the Acastidae *s.s.*, and that it may be almost as long as L2 (e.g. see Richter and Richter, 1954, pl. 3, fig. 37; Tomczykowa, 1991, pl. 7, fig. 23, pl. 9, figs 7–12, 14, 16–17).

Ramsköld and Edgecombe (1993: 265) identified a ‘Wenlock group’ of acastid genera including *Acaste, Acastoides* and *Acastocephala*, some species of which persist into the late Silurian. *Berylacaste* is contemporaneous with most members of that group but shares few of their stated characteristics, such as a distinctly convex forward S2, a deep sagittal impression at the back of the glabellar frontal lobe, a deep preglabellar furrow, and a genal angle that is rounded or bears a tiny node. The wide glabella considered characteristic of the 'Wenlock group' is not as strongly expanded as that of *Berylacaste*. In the form of the genal spine and the apparent lack of a sagittal impression on the frontal glabellar lobe *Berylacaste* is more similar to Ludlow–Přídolí species of *Acastella*, but in the other cephalic characters listed above *Berylacaste* is easily distinguished from those species, which also differ in having a strongly segmented pygidium with a spine or blunt point posteriorly. *Scotiella* (see Shergold, 1967, pl. 2, figs 1–8, pl. 3, figs 1–8) and *Ewacaste* Ramsköld and Edgecombe, 1993 (see Schrank, 1972, pl. 21, figs 6–9; Tomczykowa, 1991, pl. 7, figs 21–24) are like *Berylacaste* in the very weak S2 and S3 but have less inflated glabellae that expand only weakly forward and large eyes, and *Scotiella* also has a mucronate pygidium. *Berylacaste* cannot be considered primitive; rather, it is a highly derived form evolved independently of and along different lines to other Acastidae.

Reduction of the visual surface and palpebral lobe also occurs in the Devonian calmoniid genera *Typhloniscus* (see Cooper, 1982), *Punillaspis* Baldis and Longobucco, 1977 and *Tormesiscus* Waisfeld et al., 1994. The eye of *Berylacaste* most closely resembles that of *Tormesiscus*, in which it is also reduced to a laterally directed palpebral ridge placed anteriorly on the genae. The glabella of *Tormesiscus* is similarly expanded strongly forward and is inflated anteriorly, overhanging the anterior border. The genera differ in thoracic and pygidial features, the depth of the glabellar axial furrows and the course of the facial suture, the latter apparently being submarginal in *Tormesiscus*.

Berylacaste berylae gen. et sp. nov.

Figures 19–20

Acastidae n. gen.—Rickards and Sandford, 1998: 752.

Type material. Holotype NMV P138224 (dorsal exoskeleton) and paratypes NMV P138225 (dorsal exoskeleton), NMV P138226 (cephalon), NMV P139330 (dorsal exoskeleton), NMV P139331 (thoracopygon with displaced pygidium), NMV P139332 (cephalon with displaced librigena), NMV P139333 (cephalon), NMV P139334. All from PL206, Bylands Siltstone.

Other material. NMV P138227 from PL206, Wallan. Bylands Siltstone.

Derivation of name and diagnosis. As for genus.

Description. Exoskeleton elliptical in outline, estimated maximum length 20 mm. Cephalon strongly convex (sag., tr.), about twice as wide as long (sag.), anterior margin with maximum curvature medially in dorsal view and with outline interrupted anteromedially by slightly protruding glabella. Glabella rounded-pentagonal in dorsal view, about as wide across frontal lobe as long (sag.), maximum width situated at approximately 66% sagittal glabellar length from posterior. Axial furrows deep, diverging forward at about 55°. Occipital ring comprising about 30% maximum glabellar width, approximately twice as long sagittally as distally, with median node situated close to posterior edge. Occipital furrow moderately impressed medially and forming convex forward arc, increasing in depth abaxially and curving slightly forward distally. L1 about as long (exsag.) distally as occipital ring, apparently with weakly defined lateral node. S1 very deeply impressed laterally and directed slightly obliquely inward and backward, shallowing abruptly adaxially and curving forward slightly subparallel to occipital furrow, apparently very weakly impressed medially. S2 and S3 more distinct on internal moulds than on exterior of exoskeleton, S2 transverse, reaching axial furrow, S3 directed obliquely inwards and backwards from axial furrow in concave-forward curve, inner end situated opposite glabellar midlength (sag.). Frontal lobe transversely elliptical or rhombic, lacking sagittal furrow. Anterior border subvertical. Genal field moderately convex (tr.), steeply sloping laterally and in front of palpebral lobe. Palpebral lobe slightly raised, placed opposite anterior half of L3, palpebral furrow shallow, oblique and weakly curved, continuous adaxially with weak furrow behind eye ridge. Anterior branch of facial suture diverging forward in gentle curve subparallel with axial furrow, not cutting across anterolateral corner of glabella, posterior branch directed posterolaterally across genal field and inner part of lateral border, deflected sharply backward across outer part of border to meet cephalic margin opposite L1. Librigena lenticular in outline with long posterior projection. Posterior border narrow proximally, gently widening abaxially to about midpoint (tr.), thereafter uniform in width and gently curving forward. Posterior border furrow deep proximally, moderately impressed distally and continuous with shallower lateral border furrow. Lateral border weakly convex, steep and poorly defined anteriorly. Genal spine diverging slightly from line of lateral margin. Cephalic doublure strongly convex laterally, widening and flattening medially, no vincular furrow.

Hypostome unknown.

Thorax of 11 segments. Axis weakly tapering backward, comprising about 30% segmental width at front of axis and about 25% toward the back. Axial rings strongly convex (sag.), flexed forward distally, lateral lobes not defined. In transverse profile pleurae convex adaxially, concave abaxially. In dorsal view pleurae convex forward adaxially, concave forward abaxially, posterior edge of segment curving slightly forward distally to spinose tip. Pleural furrows short (exsag.) and deep, extending onto articulating facet distally. Anterior pleural band approximately as long (exsag.) as posterior band at fulcrum.

Pygidium lenticular, about twice as wide as long (sag.). Axis as wide as pleura anteriorly, comprising about 75% sagittal pygidial length, weakly tapering backwards and broadly rounded posteriorly. 1st axial ring high, 2nd ring well defined, 3rd ring poorly defined. Pleurae moderately convex (tr., exsag.), comprising at least 5 segments, 1st 4 four with posterior pleural bands slightly more raised than anterior bands on internal moulds and extending onto border distally. Only 2 pleural furrows distinct, 1st sharply incised, not extending onto articulating facet distally, 2nd reaching halfway to margin. 1st 2 interpleural furrows weaker than pleural ones. Pygidial margin smooth on exterior of exoskeleton, weakly scalloped on internal mould. Pygidial doublure narrow, convex.

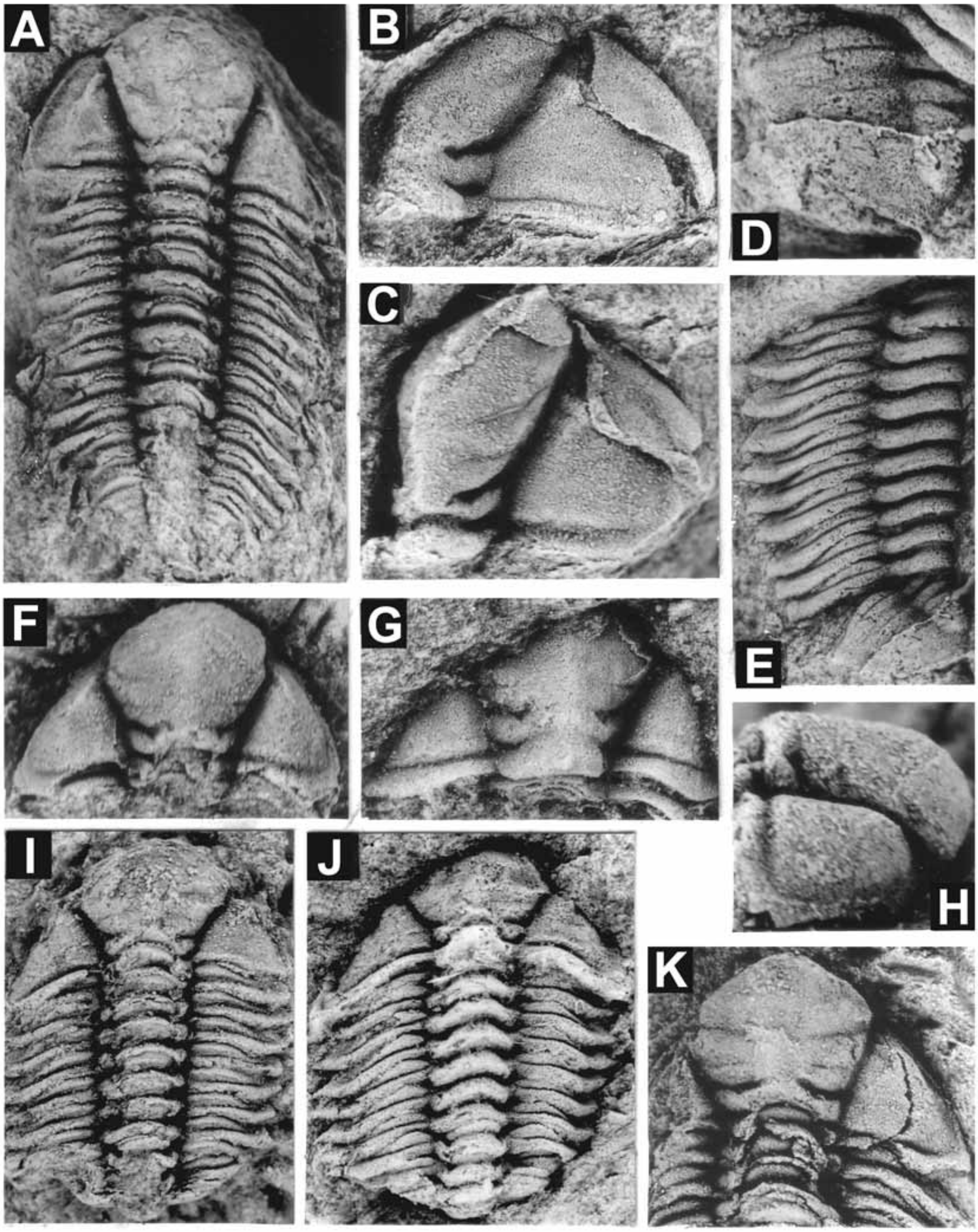

Figure 19. *Berylacaste berylae* gen. et sp. nov., from PL206, Wallan. A, paratype NMV P138224, dorsal exoskeleton, × 4. B–C, paratype NMV P139332, cephalon with displaced librigena, × 5. D–E (and fig. 20D), paratype NMV P139331, thoracopygon; D, × 8; E, × 4. F–H, paratype NMV P139333, cephalon, × 4. I–J (and fig. 20C), paratype NMV P138225, dorsal exoskeleton with down-flexed pygidium, × 5. K, holotype NMV P138224, cephalothorax, × 5. (A, C, F, H, I, K are internal moulds).

Remarks. The specimens are rather poorly preserved and affected by compression, shearing and fracturing. As a result there is apparent variation in the depth of some furrows, such as the medial part of S1 (compare fig. 19A with 19B–C, G) and the lateral cephalic border furrow (compare figs 19B–C with 19H). Some other morphological features are unclear, such as the extent to which lateral nodes are defined on L1 by adaxial expansion and/or bifurcation of S1 (compare figs 19F–G with 19K).

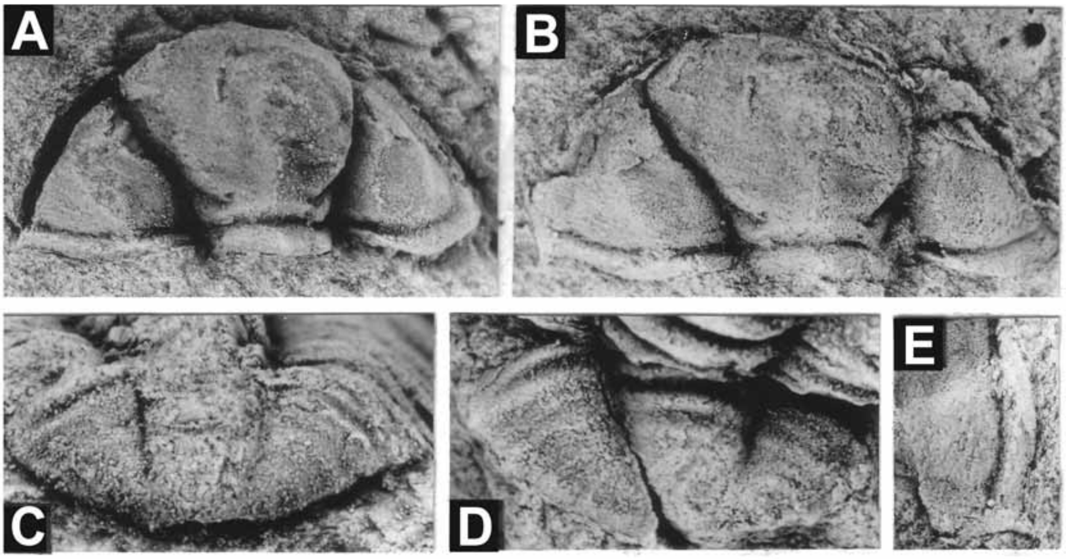

Figure 20. *Berylacaste berylae* gen. et sp. nov., from PL206, Wallan. A–B, E, paratype NMV P138226, cephalon; A–B, × 4; E, enlargement of genal angle showing thorn-like genal spine. C, paratype NMV P138225, enlargement of pygidium, × 10. D, paratype NMV P139331, enlargement of pygidium, × 8.

The blind condition of *Berylacaste* reinforces other evidence for a deep-water, possibly sub-photic environmental setting for the trilobite fauna at PL206, Wallan. *Berylacaste berylae* is well-represented, but the fauna is dominated by the blind, effaced styginid *Thomastus aops* Sandford and Holloway, 1998. Together these blind trilobites represent 63% of the trilobite population and 22% of the faunal diversity. Furthermore *Ivops wallanensis*, representing 19% of the trilobite population, bears an eye markedly smaller than other Wenlock phacopids. The taphonomy of the fauna at PL206 contains a high proportion of partly articulated exoskeletons (60%) and indicates assignment to trilobite taphofacies TIV (see Sandford, 2002), considered to represent depths below maximum storm wave base. Exoskeletons of *T. aops* showing partly displaced librigenae may be moult assemblages characteristic of taphofacies TIV, although as the amount of displacement is small it is more likely due to post-depositional compaction.

Four other acastids are known from central Victoria, all in the Lower Devonian. *Acaste lokii* Edgecombe, 1993 and *Acastella frontosa* Shergold, 1968 are from the Humevale Siltstone at Lilydale, and *Acastella* sp. was recorded by Holloway and Neil (1982) from the Mt Ida Formation at Heathcote. These species are easily distinguished from *Berylacaste berylae* by their large eyes and deeply impressed S2 and S3. A distinctive, as yet undescribed acastid with long occipital and thoracic axial spines occurs in the Humevale Siltstone at Yarra Junction and at Kinglake West.

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