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Lower Devonian trilobites from Cobar, New South Wales

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Abstract – A Lower Devonian (Lochkovian-Pragian) trilobite fauna from the Biddabirra Formation near Cobar, New South Wales, Australia includes 11 previously undescribed species (*Alberticoryphe* sp., *Cornuproetus* sp., *Gerastos sandfordi* sp. nov., *Cyphaspis mcnamarai* sp. nov., *Kainops* cf. *ekphymus*, *Paciphacops* sp., *Acanthopyge* (*Lobopyge*) *edgecombei* sp. nov., *Crotalocephalus* sp. and *Leonaspis* sp., a styginid sp., and a harpetid sp.). Three species belonging to the genera *Paciphacops*, *Kainops*, *Acanthopyge* (*Lobopyge*), and *Leonaspis* are preserved with sufficient detail to provide enough information to be coded and analysed by two cladistic analyses. The resulting cladograms provide justification for the monophyly of *Paciphacops* and further support for *Kainops*. *Leonaspis* sp. is placed as the most plesiomorphic species within the monophyletic *Leonaspis*.

INTRODUCTION

The Lochkovian-Pragian Biddabirra Formation (Glen 1987) has yielded a trilobite fauna containing twelve species, of which eleven have previously been undescribed. The species include the fragmentary material of a styginid and harpetid, internal and external moulds of *Alberticoryphe* sp., *Cornuproetus* sp., *Gerastos sandfordi* sp. nov., *Cyphaspis mcnamarai* sp. nov., *Kainops* cf. *ekphymus*, *Paciphacops* sp., *Acanthopyge* (*Lobopyge*) *edgecombei* sp. nov., *Crotalocephalus* sp., *Leonaspis* sp and *Cordania buicki* Ebach and Edgecombe, 1999. The taxonomic compostion of the fauna is similar to other preserved clastic faunas (Jones *et al.* (1986), Wright and Chatterton (1988), Wright and Haas (1990)) and silicified faunas (Chatterton (1971), Chatterton *et al.* (1979) and Chatterton and Wright (1986)) in New South Wales, with the exception of *Cordania buicki*, the first record of *Cordania* Clarke, 1892 in Australia.

The Cobar fauna was previously recorded by Sherwin (1978b unpubl.), Sherwin (1980a unpubl.) and Sherwin in Glen (1987), as containing seven species.

Cladistic analyses are undertaken for three species (*Kainops* cf. *ekphymus*, *Paciphacops* sp. and *Leonaspis* sp.). The first analysis of *Paciphacops*-*Kainops*, employs characters used by Ramsköld and Werdelin (1991). Input data include species not used in the original analysis (*Paciphacops argentinus*, *P. crawfordae*, *P. waisfeldae* and *P.* sp.). The *Leonaspis* analysis, using Ramsköld and Chatterton's (1991) characters, includes *Leonaspis* sp. from Cobar. The analysis will attempt to use species with more than 45% of their characters coded.

All photographed and type specimens are held in the Australian Museum (prefix number AMF).

AGE

The Biddabirra Formation has a thickness of about 1.5 km, and lies stratigraphically between the lower Amphitheatre Group and the upper Amphitheatre Group within the Cobar Supergroup. The Biddabirra Formation is a sandy sequence above the C.S.A Siltstone and the lower Amphitheatre Group and below the upper Amphitheatre Group (Glen 1987). It consists of poorly outcropping, medium to thick bedded sandstones. Due to the lack of marker beds, the trilobite fauna cannot be accurately placed within the Biddabirra Formation. The presence of the brachiopod *Howellella jaqueti* Dun (1898) in the Biddabirra Formation was regarded as evidence for a Pragian age, possibly extending down into the Lochkovian (Sherwin, in Glen 1987). A more recent assessment of brachiopods in the Cobar Supergroup (Sherwin 1995) recognises the occurrence of *H. jaqueti* as probably Lochkovian. Trilobites in the Cobar fauna are consistent with a Lochkovian age, as close comparisons can be made with species recognised as Lochkovian in other parts of New South Wales (eg. *Kainops ekphymus* and *Crotalocephalus* sp. from the lower part of the Tangerang Formation in the Windellama district; Jones *et al.* (1986). *Cordania buicki* Ebach and Edgecombe 1999 constrains the age to the Lochkovian-Pragian interval, the most species closely related to the Cobar *C. buicki* being Lochkovian. *Alberticoryphe* sp. is the only indicator of a post-Lochkovian age, with its closest comparison being *A. marshalli* from the Jesse Limestone (Emsian) at Limekilns, New South Wales (Wright and Chatterton 1988).

SYSTEMATIC PALAEONTOLOGY AND CLADISTIC ANALYSES

Order Corynexochida Kobayashi, 1935

Suborder Illenina Jaanusson, 1959

Superfamily Illenacea Hawle and Corda, 1847

Family Styginidae Vogdes, 1890

styginid gen. and sp. indet.
Figure 1 A, F & H

Material examined
Cranidium AMF 106635, free cheek AMF 106637 and pygidium AMF 106636.

Remarks
Few Devonian species of styginids have been described in Australia. These include *Scutellum (Scutellum)* sp. (Strusz 1964), *S. calvum* Chatterton, 1971, *S. droseron* Holloway and Neil, 1982, *S. hollandi* Wright and Chatterton, 1988, *S. sudorum*, *Xyoeax eponcus* and styginidae gen. and sp. indet. (Holloway 1996), *Dentaloscutellum hudsoni* Chatterton, 1971 and two unnamed styginid species (Wright and Chatterton 1988). A styginid from the Biddabirra Formation cannot be confidently assigned to a genus due to the lack of a complete crandium and pygidium. However, the Cobar specimens do not compare especially closely with any of the described species. The sparsely granulated surface in the Cobar styginid contrasts with *Dentaloscutellum hudsoni* Chatterton, 1971, *Scutellum droseroni* and *S. calvum*, which all have tuberculated surfaces. *Scutellum hollandi* is distinguished from the Cobar styginid by a pair of tubercles located submedially in front of S1. The pygidium in *Scutellum hollandi* and *S. sudorum* is heavily ornamented, versus finely granulated in the Cobar styginid, and the doublure of the free cheek is densely terraced in the Cobar styginid versus more sparsely terraced in *Scutellum hollandi*. The Silurian *Australoscutellum* from New South Wales shares the smooth ornament of the Cobar styginid, but differs in possessing a median rib with partial subdivision into three ribs.

Order Ptychopariida Swinnerton, 1915

Suborder Harpina Whittington, 1959

Family Harpetidae Hawle and Corda, 1847

Genus harpetid gen. and sp. indet.
Figure 1E & G

Material examined
Cephalon AMF 106638

Remarks
The present material is too fragmentary to confidently assign it at the generic and species level. The Cobar species differs from other described Devonian harpetids found in New South Wales (Etheridge and Mitchell 1917; Fletcher 1975; Chatteron and Campbell 1980) by its developed caeca on the genal roll that anastomose to the wide external rim. A combination of both these characters are present in several species of *Scotoharpes* Lamont, 1948 and *Hibbertia* Jones and Woodward, 1898 and cannot be considered to be a defining feature of either genus. The well developed caeca on the genal roll and wide rim are absent from *Scotoharpes trinucleoides* (Etheridge and Mitchell 1917) from Yass, New South Wales, *Lioharpes nymageensis* Fletcher, (1975) from near Cobar, New South Wales and, present in the Silurian *Scotoharpes molongloensis* Chatteron and Campbell, 1980 from the Yass Basin, New South Wales.

Order Proetida Fortey and Owens, 1975

Superfamily Proetoidea Hawle and Corda, 1847

Family Proetidae Salter, 1864

Subfamily Tropidocoryphinae Přibyl, 1946

(= Prionopeltiinae Přibyl, 1946; Proetidellinae Hupé, 1953;

Decoroproetinae Erben, 1966)

Genus *Alberticoryphe* Erben, 1966

Type Species
Astycoryphe cogneyi Alberti, 1964; Lower Devonian (Pragian), Morocco.

***Alberticoryphe* sp.**
Figure 1 B, C, D & I

Material Examined
Cranidium AMF 106639, free cheeks AMF 106640, AMF 106646 and pygidium AMF 106641.

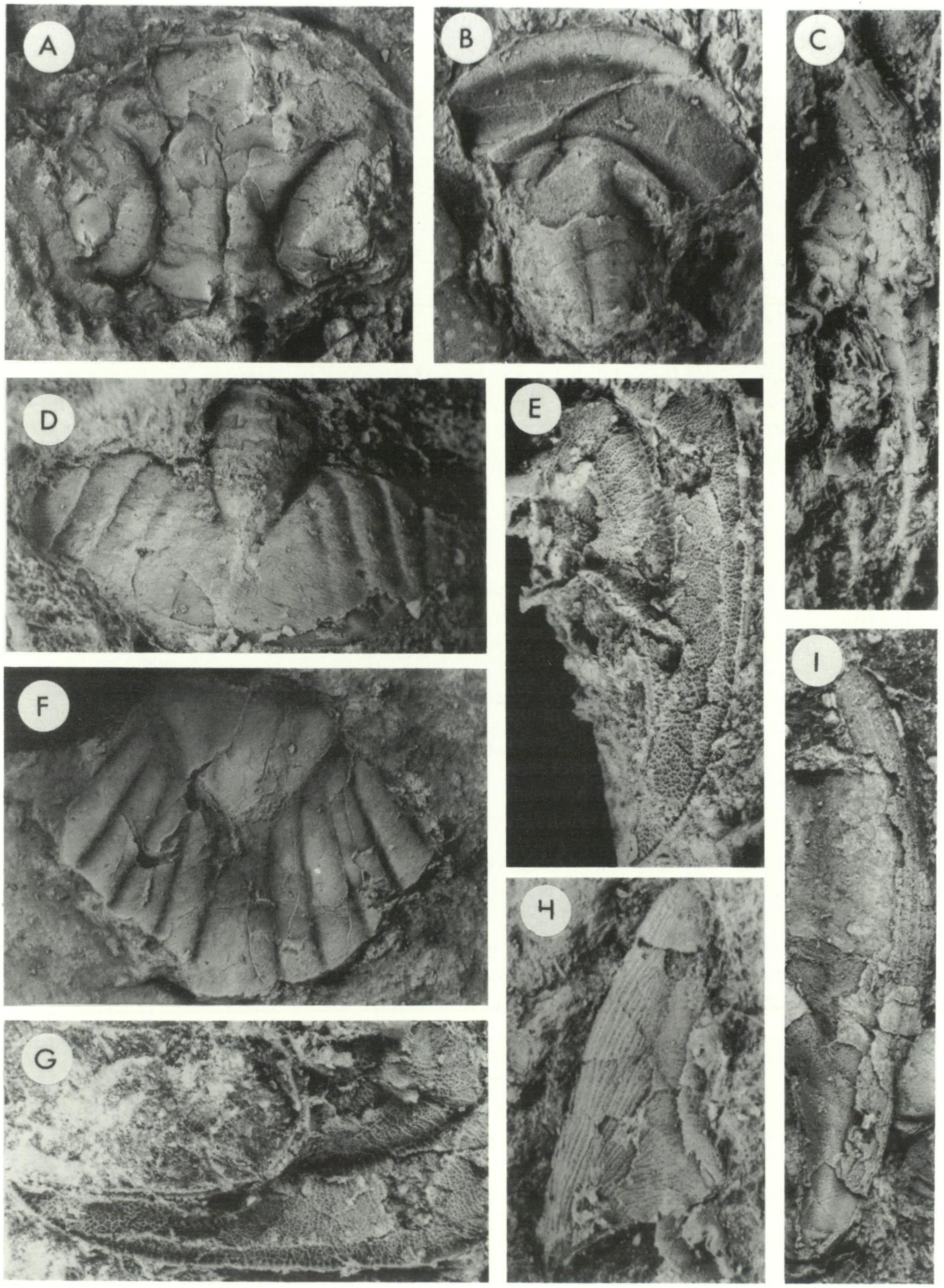

Figure 1 Styginid gen. and sp. indet, A. Dorsal view of crandium (internal mould), X 4.2, AMF 106635; F. Dorsal view pygidium (internal mould), X 4.5, AMF 106636; H. Dorsal view of free cheek (internal mould), X 4.5, AMF 106637; E & G Harpetid gen. and sp. indent, E. Dorsal view of cephalon (internal mould), X 4, AMF 106638; G. Dorsolateral view of cephalon (internal mould), X 4, AMF 106638; B, C, D & I *Alberticoryphe* sp., B. Dorsal view of cranidium (internal mould), X 4.5, AMF 106639; C. Dorsal view of free cheek (internal mould), X4.5, AMF 106640; D. Dorsal view of pygidium (external mould), X 4.5, AMF 106641; I. Dorsal view of free cheek (internal mould), X4.5, AMF 106646.

Description

Glabella weakly inflated, elongate, longer (sag.) than wide (tr.), tapering forward to rounded frontal lobe; glabellar furrows weakly defined; preglabellar furrow deep and short medially, lengthening abaxially; prominent tropidium located close to the preglabellar furrow; border furrow wide (sag.) and gently concave in front of ridge. Anterior border roll convex, widest (sag.) medially. Glabellar ornament of fine granules; preglabellar furrow and anterior border furrow perforated by fine pits; anterior border roll with fine terrace lines. Wide (exsag.) border furrow continues onto free cheek, half way (tr.) across gena. Lateral border gently convex and wide (tr.), joined to convex short (exsag.) posterior border; genal spine long and strongly terraced. Free cheek sculpture smooth, with pits on posterior margin and genal spine; lateral border with terrace lines, continuing onto genal spine. Facial sutures not preserved.

Hypostome and thorax unknown.

Pygidium apparently subtriangular, with six axial rings. Axis tapering posteriorly, with a faint and long postaxial ridge effacing in front of posterior extremity. Interpleural furrows subdued, pleural furrows strong, posterior pair converging backwards, reaching posterior margin; three well defined pleural furrows, fourth very faint; border furrow absent. Pygidium covered with numerous transversely, distinct, thin terrace lines, anteriorly directed towards axis.

Remarks

The cranidium of this species is typical of *Alberticoryphe* in its forward tapering glabella, relatively short preglabellar field for a tropidocoryphine, wide anterior border furrow and short anterior border. The pygidium displays anteromedially directed pleural furrows posteriorly and strong terracing.

Of Australian species, *Alberticoryphe* sp. most closely resembles *A. marshalli* Wright and Chatterton, 1988 from the Jesse Limestone, Limekilns, New South Wales. It differs in possessing a wider (sag.), non-terraced anterior border. The North African species *A. cogneyi* (Alberti, 1964) and *A. stirps* Alberti, 1966 differ in having a pronounced pygidial border, a shorter (sag.) area behind the terminal piece, and no postaxial ridge. *Alberticoryphe* sp., like *A. marshalli* (see Wright and Chatterton 1988) shows greater similarities to the Bohemian *A. chemazur* Šnajdr, 1980 in having pronounced pleural ridges and shallow interpleural furrows. The pleural ridges are considerably deeper in *Alberticoryphe tauron* Šnajdr, 1980. Both Bohemian species differ from the Australian *Alberticoryphe* by having a wider (tr.) pygidial axis.

Subfamily Cornuproetinae Richter and Richter, 1919

Genus *Cornuproetus* Richter and Richter, 1919

Type Species

Gerastos cornutus Goldfuss, 1843; Middle Devonian; Germany.

Cornuproetus. sp.

Figure 2

Material Examined

Cranidia AMF 106647, AMF 106649, AMF 107920, and pygidia AMF 106652, AMF 106653.

Description

Glabella elongate, subquadrate, gently tapering forwards, inflated, with a distinct constriction in front of mid length. Frontal lobe rounded anteriorly. Preglabellar furrow narrow, shortest medially (sag.); anterior border furrow short (sag.), anterior border twice the length of anterior border furrow medially, convex forwards in lateral view with a prominent roll. Occipital ring long (sag.), ¼ length (sag.) of glabella and equal in length medially and distally; large, triangular lateral occipital lobes defined by faint furrows, S0 narrow (sag.) and deep. Axial furrows narrow and deep; palpebral lobe steeply inclined and convex outwards between γ and δ. Sculpture of fine granules and terracing on anterior border and pitting on the lateral margins of the preglabellar field (exsag.).

Hypostome, free cheek and thorax unknown.

Pygidium semi-circular except for slightly transverse posteromedial margin, with sagittal length (including articulating half ring) 80 percent of width (tr.), axial width (tr.) 46–50 percent pygidial width (tr.); axial furrows wide, shallowing posteriorly, first ring furrow longest (sag.); seven axial rings plus a short, vaulted terminal piece. four pleural furrows present, with distinct, narrow interpleural furrows; pleural furrows wide, shallowing medially, effacing abaxially. Pleural and interpleural furrows shallow behind border furrow; border wide, slightly lengthening posteromedially; border furrow shallow, prominent along whole pygidial margin, continuous with axial furrows, shallowing slightly behind terminal piece. Whole pygidium evenly granulated.

Remarks

Cornuproetus sp. displays many similarities to the broken specimens from Mudgee, N.S.W., assigned to *Cornuproetus* by Chatterton and Wright (1986). Both share a strongly terraced anterior border, which is longer (sag.) in the Mudgee species. The Victorian species described by Talent (1963, p108, Figure 76 D) has a longer (sag.) anterior border

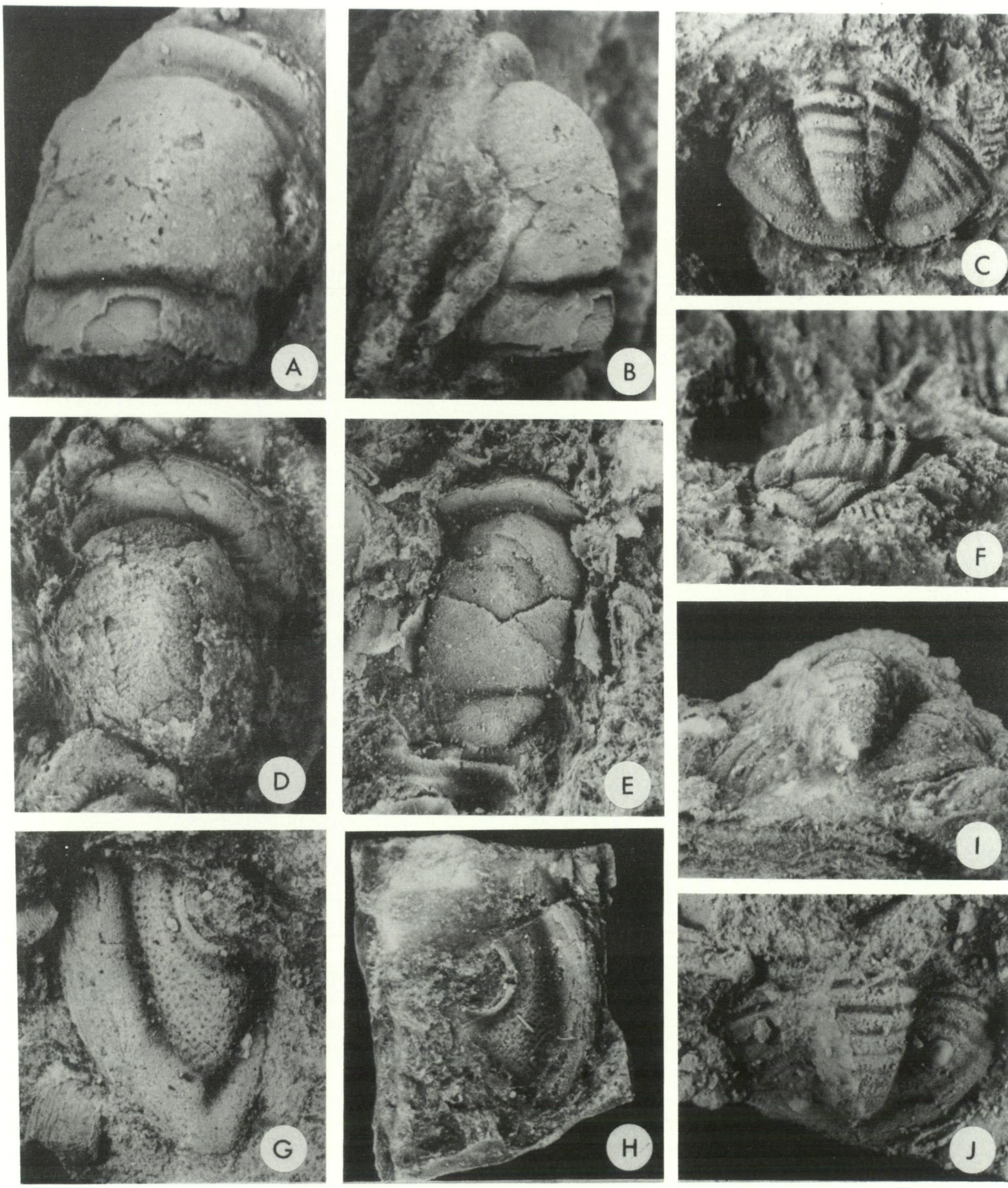

Figure 2 *Cornuproetus* sp., A, B. Dorsal and left lateral views of crandium (internal mould), X 4.5, AMF 106647; C. Dorsal view of pygidium (internal mould), X 4.5, AMF 106652; D. Dorsal view of cranidium (internal mould), X 4.2, AMF 106649; E. Dorsal view of cranidium (external mould), X 4.2, AMF 107920; F. Right lateral view of pygidium (external mould), X 4.5, AMF 106652; I. Posterior view of pygidium (external mould), X 4.5, AMF 106653; J. Dorsal view of pygidium (external mould), X 4.5, AMF 106653; G. Dorsal view of free cheek (external mould), X 4, AMF 106650; H. Dorsal view of free cheek (external mould), X 4, AMF 106651.

than the Mudgee species. Talent's (1963, Figure 77 C 15) is regarded herein as *Coniproetus* Alberti, 1966, based on its wide anterior border (sag.), strongly tapering glabella and narrow occipital ring. *Interproetus albertii* Chatterton and Campbell, 1980 (see Siveter 1989 for discussion of *Interproetus*) from the Wenlockian near Canberra, ACT, has a heavily tuberculated glabella and wide preglabelllar field, both absent in the Cobar *Cornuproetus*.

Genus *Gerastos* Goldfuss, 1843

Type Species

Proetus cuvieri Steininger, 1831; Middle Devonian, Germany.

Gerastos sandfordi sp. nov.

Figures 3 and 4

Material Examined

Holotype

Crandium AMF 106655

Paratypes

Cranidia AMF 106648, AMF 106654 free cheek AMF 106656 and pygidia AMF 106658 and AMF 106657.

Diagnosis

Glabella strongly inflated, triangular (in lateral view), over-hanging wide anterior border with prominent roll. Anterior border furrow wide, continuous with lateral glabellar furrows; anterior area of fixigena inflated. Librigena tapering posteriorly to form small, thorn-like genal spine. Pygidium with seven axial rings; pygidial border wide, doublure strongly terraced; shallow border furrow around whole pygidial margin.

Description

Glabella strongly inflated, tapering forward with rounded, tapered frontal lobe; in lateral view, cranidium equal in width (sag.) and height; preglabellar field absent, anterior border wide (sag.) with prominent roll; anterior border furrow short (sag.) medially, widening distally. Glabella posteriorly inflated, markedly higher in front of S0 and occipital ring; in dorsal view L0 short (sag.), 25 percent of glabella and occipital length (sag.), lengthening distally, with subdued anterior notch exsagittally; S1 weakly impressed distally, effacing posteromedially. S0 deep and wide, approximately equal across width (sag.); facial suture convergent in front of palpebral lobes, lateral border wide (tr.), thinning posteriorly, with a prominent roll; anterior border furrow narrow. Posterior border furrow deep; γ to ε subovate, ε to ξ outwardly concave, adaxially directed to ω. Sculpture on cranidium granulated; terracing on lateral border and pitting on eye furrow.

Librigenal width (tr.) half of maximum length (exsag.); field inflated with small granules distributed evenly on internal and external moulds, rising steeply anteriorly to subocular furrow. Subocular furrow wide (tr.) and continuous around eye; posterior border short (exsag.), visual surface unknown. Lateral border wide and deeply incised with posterior outward convexity, shallowing posteriorly near genal angle. Lateral border wide (tr.) and inflated, tapering posteriorly to form small, thorn-like genal spine. Posterior border furrow deeply incised, narrow.

Hypostome and thorax unknown.

Pygidium with sagittal length (including articulating half ring) 90 percent of width; axial width (tr.) 45 percent of pygidial width (tr.); axial furrow wide, deflected laterally around first axial ring, then gently posteriorly convergent. Second axial ring with gentle "W" shape along posterior and anterior edges; seven axial rings and terminal piece, ring furrows shallowing and narrowing posteriorly, last furrow distinct; axis strongly raised above pleural field. Five pleural ribs, pleural furrows shallow and wide, shallowing posteriorly; interpleural furrows narrow, first two variably distinct on internal mould. Border wide, and doublure strongly terraced; shallow border furrow prominent around whole pygidial margin, confluent with axial furrows directly behind terminal piece. Sculpture consisting of granules concentrated medially on axial rings.

Remarks

The Cobar species possesses a distinctive inflated glabella that tapers forward, lack of a preglabellar field, a prominently rolled (sag.) anterior border, and reduced genal spine that are characteristic of *Gerastos* (Adrain 1997). The discovery of *Gerastos* from the Cobar region of New South Wales extends the generic range from the Canadian Arctic, Europe, Turkey and North Africa to Australia. Lütke (1990) assigned *Devonoproetus* Lütke, 1990 as a subgenus of *Gerastos*. However, Adrain (1997) doubted that it had any potential apomorphic affinities to *Gerastos* and placed *Devonoproetus* as a subjective synonym of *Proetus* s.s. (see Adrain 1997 pp. 25–27). Feist and Talent (2000) reject Adrain's (1997) synonymy believing a 'direct ancestor-descendant relationship between both taxa' justifies *Devonoproetus* as a subgenus of *Proetus* (Feist and Talent 2000). Establishing a subgenus based on a tenuous ancestor-descendant relationship between two species is unwarranted. The synonymy of Adrain (1997) is supported herein.

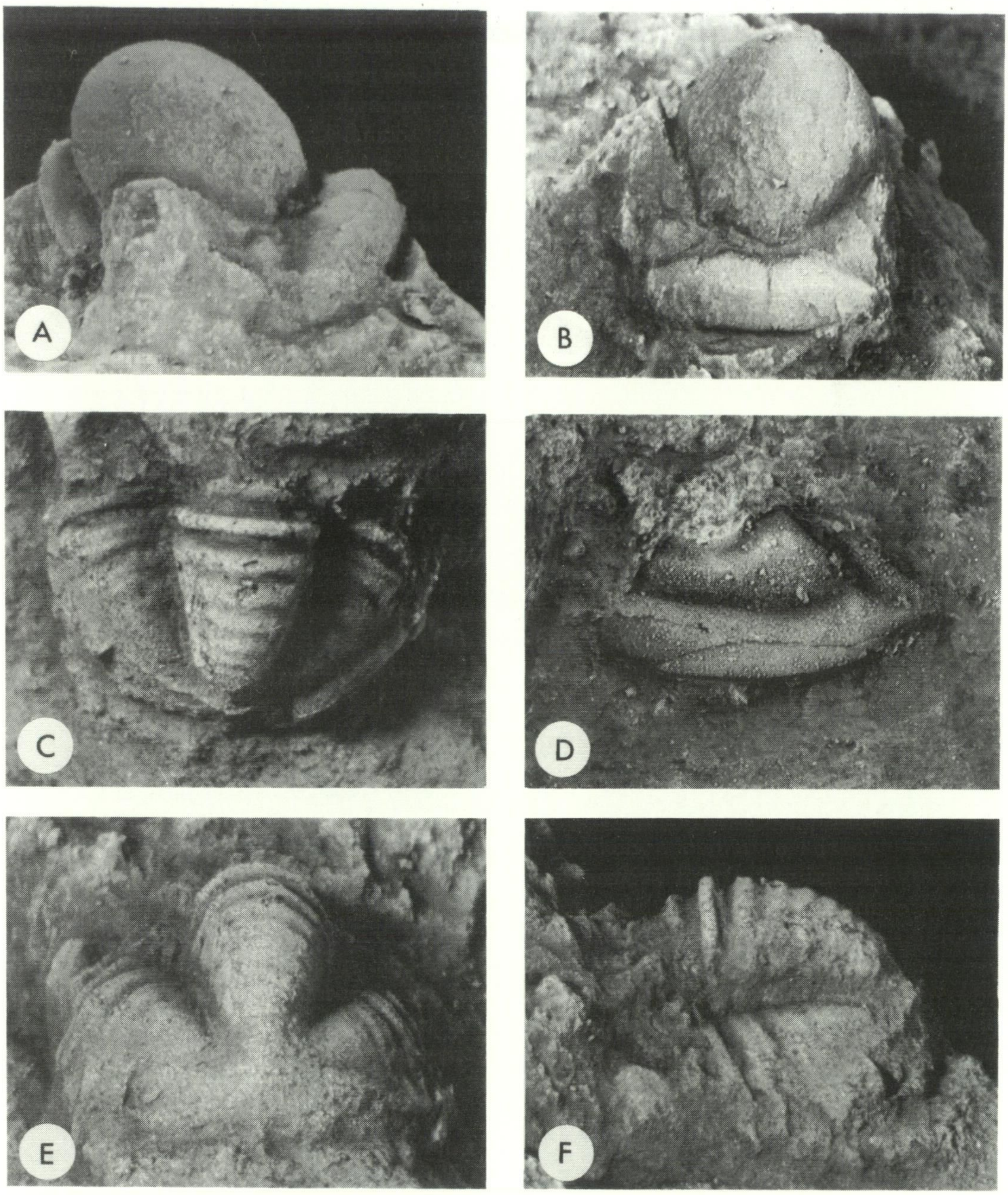

Figure 3 *Gerastos sandfordi* sp. nov., A, B. Left lateral and anterior view of cranidium (internal), X 4, AMF 106648; C, E, F. Dorsal, posterior and left lateral view of pygidium (internal), X 4, AMF 106657; D. Lateral view of free cheek (internal), X 4.5, AMF 106656.

Gerastos sandfordi is unusual in having a prominent pygidial border furrow, which is also seen in all Bohemian species with the exception of the *G. retroflexus* (Barrande 1852) group, but is absent in all Arctic Canadian Silurian species described by Adrain (1997). *Gerastos sandfordi* has many similarities with the Bohemian species *G. kazan* Šnajdr, 1980, including a granulose glabella and wide anterior border. The prominent, deep anterior border furrow present in *G. sandfordi* is absent from *G. kazan*. *Gerastos sandfordi* differs from all Bohemian *Gerastos* (with the exception of *G. gagis* (Šnajdr 1980), *G. expectatus* (Přibyl 1964) and *G. confusus* (Hawle and Corda 1847) group) by its triangular glabellar (in lateral view) and prominent wide (sag.) anterior border. The predominant overhanging glabella and the anterior inflation of the fixigena in *G. sandfordi* are absent in each of the Bohemian species.

Etymology

After Andrew C. Sandford.

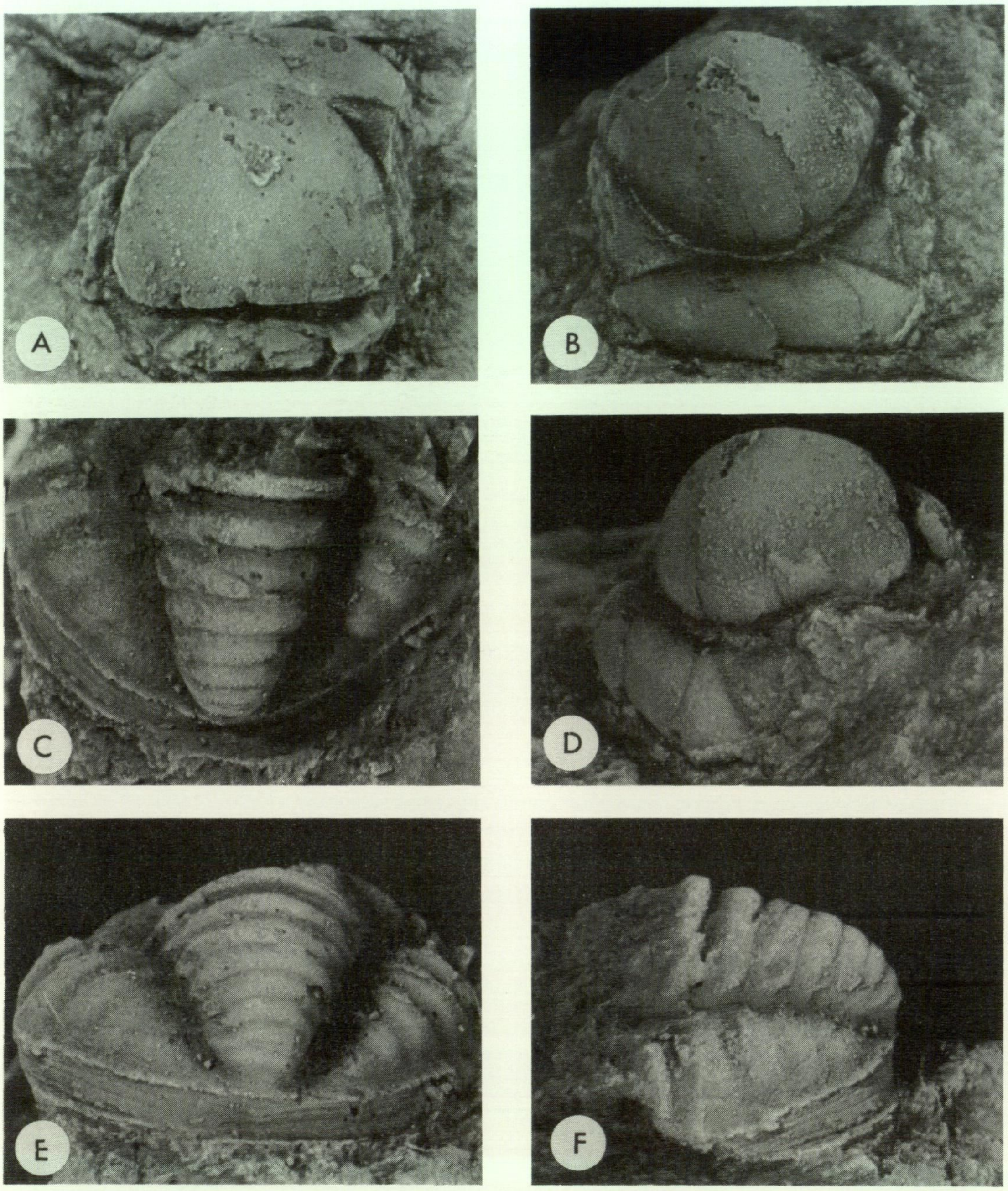

Figure 4 *Gerastos sandfordi* sp. nov., A, B, D. Dorsal, anterior and left lateral views of cranidium (internal), X4 AMF 106655; C, E, F. Dorsal, posterior and left lateral views of pygidium (internal), X4.5, AMF 106658.

Family Aulacopleuridae Angelin, 1854

Subfamily Otarioninae Richter and Richter, 1926

Tribe Otarionini Richter and Richter, 1926

Genus *Cyphaspis* Burmeister, 1843

Type Species

Phacops ceratophthalmus Goldfuss, 1843; Eifelian, Germany.

Remarks

Cyphaspis was defined by Adrain and Chatterton (1994) as possessing a short, inflated glabella, a short preglabellar field, strong tuberculation, eleven thoracic segments and three pygidial axial rings (Adrain and Chatterton 1994). These characters justify the assignment of a Cobar species to the genus.

Cyphaspis mcnamarai sp. nov.

Figure 5

Material Examined

Holotype

Cranidium AMF 106659.

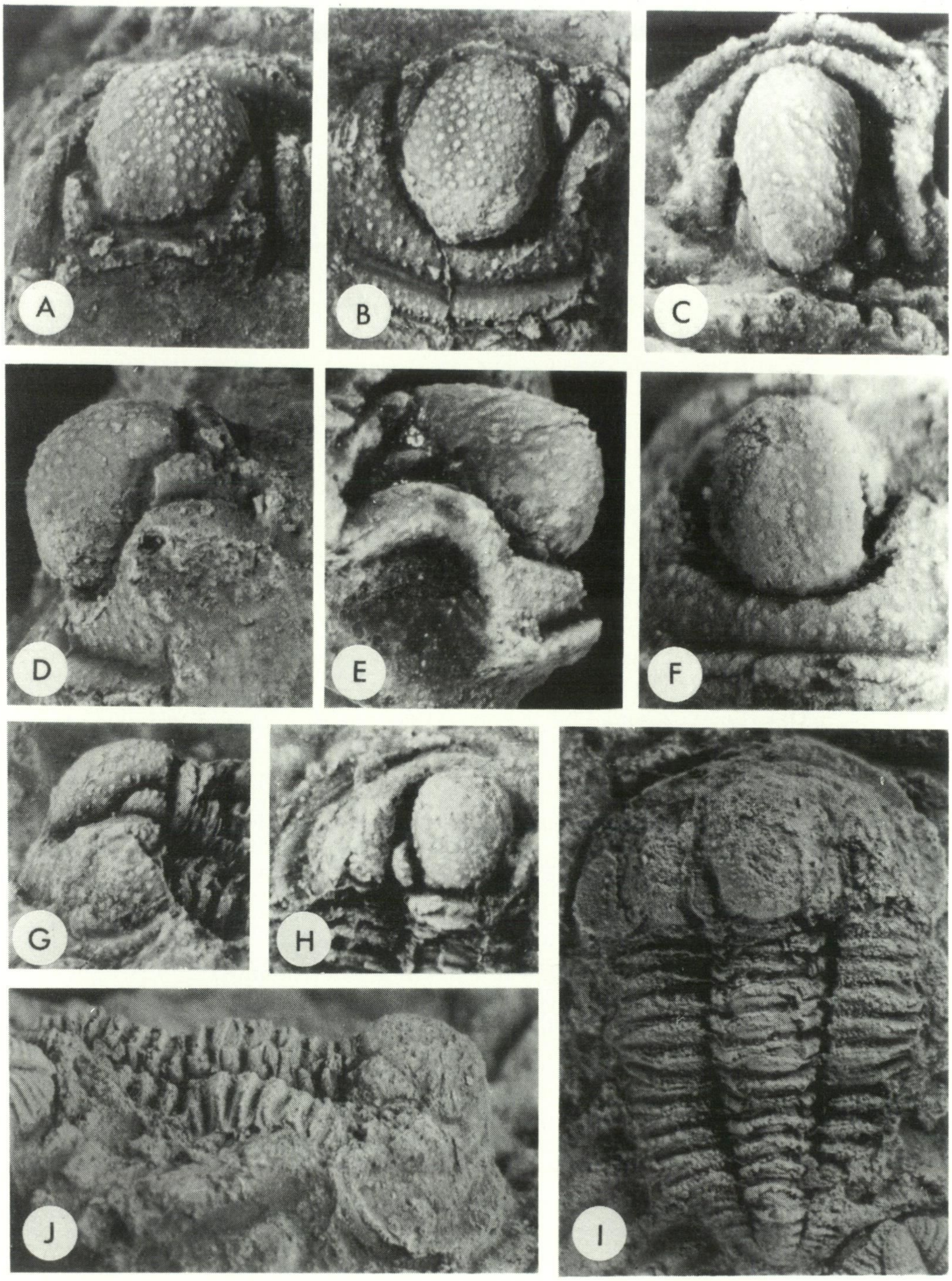

Figure 5 *Cyphaspis mcnamari* sp. nov., A. Dorsal view of cranidium (internal), X 4, AMF 106659; B. Anterior view of cranidium (internal), X 4, AMF 106659; C. Dorsal view of cranidium (internal), X 4, AMF 106660; D. Left lateral view of cranidium (internal), X 4, AMF 106659; E. Right lateral view of cranidium (internal), X 4, AMF 106660; F. Anterior view of cranidium (internal), X 4, AMF 106660; G. Left lateral view of cephalon and part of thorax, X 5, AMF 106661; H. Dorsal view of cephalon and part of thorax, X 5, AMF 106661, I. Dorsal view of complete exoskeleton, X 4.5, AMF 106662; J. Right lateral view of complete exoskeleton, X 4.5, AMF 106662.

Paratypes

Cranidium AMF 106660, cephalon with thorax attached AMF 106661 and complete exoskeleton AMF 106662.

Diagnosis

Glabella inflated anteriorly, over-hanging wide anterior border and deep anterior border furrow; S1 wide and deep, continuous with S0; L1 inflated. Pygidium small, with four axial rings.

Description

Cranidial length subequal to width across palpebral lobes; anterior border of equal length sagittally and exsagittally, with prominent dorsal convexity; anterior border furrow deep and narrow, short (sag.). Anterior sections of facial suture running approximately straight forward in front of palpebral lobes. In lateral view suture forming an asymmetrical inverted "U" shape; preglabellar field with gentle dorsal convexity. Preglabellar furrow prominent, semi circular in outline, short sagittally and subequal in width. Glabella inflated anteriorly, anterior part overhanging anterior border (when anterior border is held horizontal); in lateral view, glabella more than 50 percent of cephalic height, 1/3 of cephalic width (tr.); in lateral view, preglabellar field approximately twice the length of anterior border. L1 reniform, prominent, convex outward. Glabellar ornament of even, densely scattered, small to moderate sized tubercles, less numerous on preglabellar field; anterior border bearing abundant coarse granules. Axial furrows shallow, wide, converging anteriorly into preglabellar furrow. S1 deep and wide, forming a steep side on glabella. S2 shallow, effacing posteromedially, S3 indistinct. S0 moderately deep and wide, with glabella rising steeply (sag.). Palpebral area strongly convex, high, eye unknown. Librigenae steep (exsag.), with a line of evenly spaced tubercles on lateral border; genal spine unknown.

Hypostome unknown.

Thorax of 11 segments, axial spine not preserved on sixth segment but margin broken in sole complete specimen. Axial rings and pleurae narrowing (tr.) posteriorly, with fulcrum set midway between axial furrow and lateral margin. Axial furrow shallow; pleural furrows shallow and wide, tapering laterally. In lateral view last four axial rings with preannulus. Pleurae wide (tr.); pleural tip with small articulating facet, longest (exsag.) on sixth pleural band, absent on first pleural band. Tubercles present on axial rings and pleurae, forming irregular rows.

Pygidium small, axial furrows moderately deep, remain constant around whole axis. Axis with four distinct rings; last ring merged with terminal piece. Ring furrows deep, narrow; the first with a pseudo-articulating half ring. Pleural furrows deep and confluent with axial furrow; pleural furrows becoming shallow posteriorly; interpleural furrows, narrow and distinct. Rows of irregular tubercles on most anterior axial rings and pleural ribs.

Remarks

The glabella in *Cyphaspis mcnamarai* differs from that of other NSW species of *Cyphaspis* as it overhangs the anterior cranidal border (in lateral view) and expands anteriorly. *Cyphaspis mcnamarai* also has a wide anterior border (sag.) and an inflated L1, absent in both *Cyphaspis dabrowni* (Chatterton, 1971) from the Emsian Taemas Limestone, and *Cyphaspis horani* (Etheridge and Mitchell, 1893) from the Ludlow Yarwood Siltstone Member, near Yass.

There are no unique features that unite New South Wales *Cyphaspis*, however the considerable differences in age (Ludlow to Emsian) may indicate a large number of missing species, or suggest several separate migrations, possibly from Laurentia. Support for the later is seen in the closer resemblances between *C. dabrowni* and species from England and northwestern Canada (see Adrain and Chatterton 1996), than species from New South Wales.

Etymology

After Dr. Kenneth J. McNamara.

Order Phacopida Salter, 1864

Suborder Cheirurina Harrington and Leanza, 1957

Family Cheiruridae Salter, 1864

Subfamily Cheirurinae Salter, 1864

Genus *Crotalocephalus* Salter, 1853

Type Species

Cheirurus pengellyi Whidbourne, 1889; Middle Devonian (Givetian), England; see Lane (1971).

Crotalocephalus sp.

Figure 6 D & E

Material Examined

Cranidium AMF 106642 and hypostome AMF 106643.

Remarks

Crotalocephalus sp. from the Cobar fauna displays characters typical of the genus (*sensu* Chatterton and Wright 1986), such as the continuation of S1 with S0, wide fixigenae and the presence of a genal spine, all absent from the somewhat similar Victorian genus *Azyptyx* Holloway, 1991. *Crotalocephalus* sp. is distinct from all described Victorian and New South Wales species.

Crotalocephalus sp. differs from *Crotalocephalus oxina* Holloway and Neil, 1982 from Lochkovian strata in the Mount Ida Formation of Victoria by its medially subdued S2, medially effaced S3 and squat hypostome with a concave inwards lateral border. *Crotalocephalus silverdalensis* Etheridge and Mitchell, 1917 is alleged to occur both in Victoria (Phillip 1962) and New South Wales (Fletcher 1975), although Holloway and Neil (1982) questioned the conspecificity of the material. It is distinguished from *Crotalocephalus* sp. by a distinctly shallow S1 that is continuous with the occipital ring. *Crotalocephalus struszi* Chatterton and Wright, 1986,

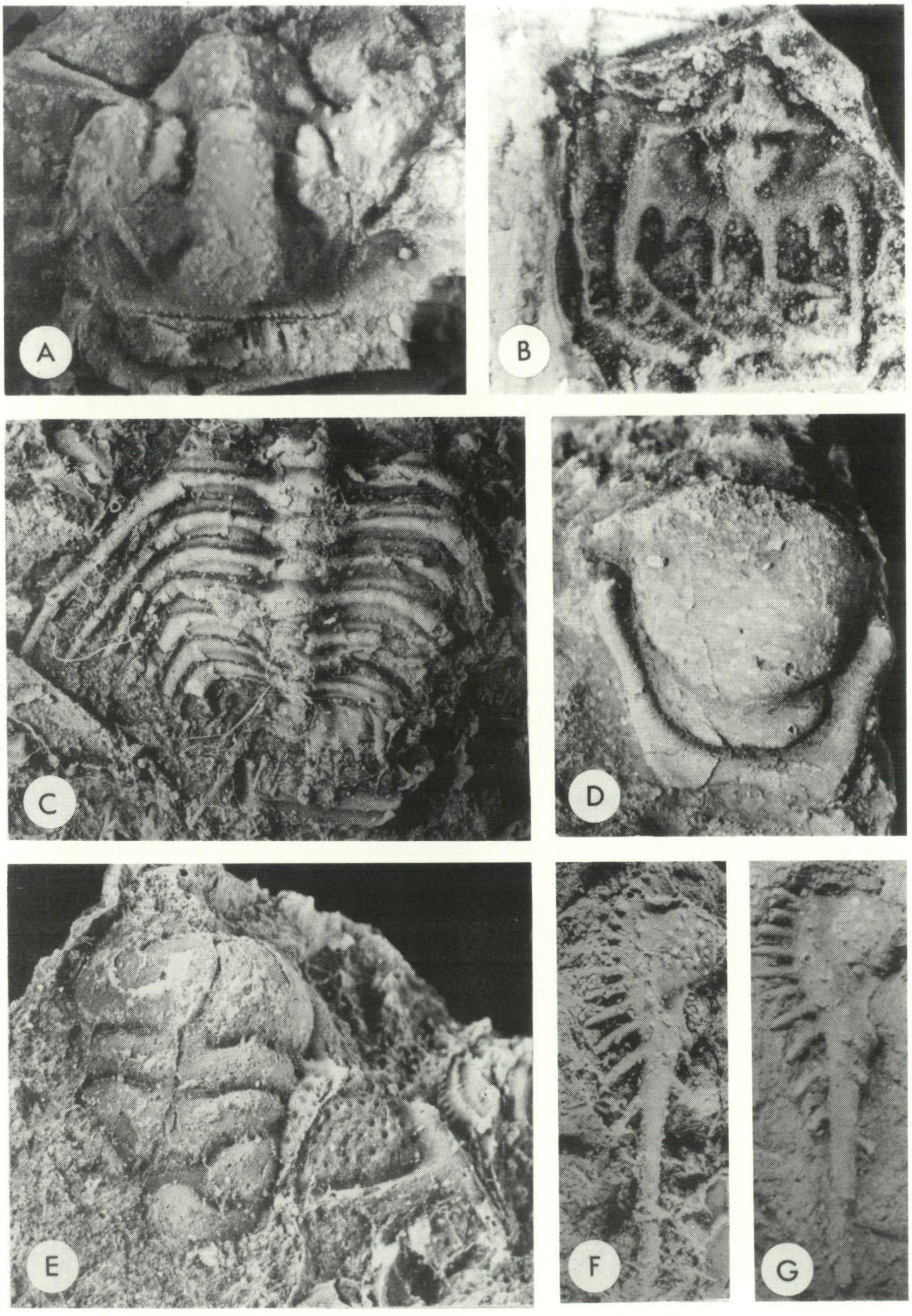

Figure 6 *Crotalocephalus* sp., D. Dorsal view of hypostome (internal), X 3.5, AMF 106643; E. Dorsal view of cephalon (external), X 3, AMF 106642;. *Leonaspis* sp., A. Anterior-dorsal view of cephalon (internal), X 10, AMF 106644; B. Dorsal view of pygidium (external), X10, AMF 106645; C. Dorsal view of thorax attached to pygidium (external), X 8.5, AMF 106685; F. Left lateral view of free cheek (external), X 8.5, AMF 106683; G. Left lateral view of free cheek (external), X 8.5, AMF 106684.

Crotalocephalus packhami Strusz, 1964, *Crotalocephalus sculptus* Etheridge and Mitchell, 1917 and *Crotalocephalus regius* Foldvary, 1970 have continuous S2 and S3 furrows, absent from the Cobar species. Similarities between the Cobar *Crotalocephalus* and *Crotalocephalus* sp. of Jones *et al.* 1986, from the Lochkovian Tangerang Formation, Windellama District, include a subdued S2 and long S0 medially. However the Tangerang species has a continuous S3 and more tuberculate glabella. The

Victorian *Crotalocephalus* sp. of Talent (1963) was described as "a juvenile [and therefore] no attempt [was] made to determine its specific affinities". However, it differs from the Cobar species in having a continuous S3 furrow, a secondary sagittal furrow that dissects L3 medially, S1 not converging with S0 medially and a greatly expanded frontal glabellar lobe.

Suborder Phacopina Struve, 1959

Family Phacopidae Hawle and Corda, 1847

Genus *Kainops* Ramsköld and Werdelin, 1991

Type species

Paciphacops (*Paciphacops*) *microps* Chatterton *et al.*, 1979; Lower Devonian (late Lochkovian - early Pragian), New South Wales, Australia.

Remarks

Kainops Ramsköld and Werdelin, 1991, included *K. ekphymus* Jones *et al.*, 1986, "*K*". *invius* (Campbell, 1977) "*K*". *guttulus* (Campbell, 1967), "*K*". *raymondi* (Delo, 1935) and *K. veles* (Chlupáč, 1972) in addition to the type. "*Ananaspis*" sp. from the Wenlockian St. Clair Limestone of Arkansas, USA (Holloway, 1980), excluded from Ramsköld and Werdelin's (1991) analysis, was tentatively placed in *Kainops* (Ramsköld and Werdelin, 1991) but is herein considered *incertae sedis.*

Kainops cf. *ekyphmus* (Jones *et al.*, 1986)

Figure 7 and Figure 8 A & B

Material Examined

Cephala AMF 105636, AMF 105637, AMF 105639 and AMF 105643. Pygidia AMF 105638, 105640 and 105644, thorax articulated to pygidium AMF 105635. Unfigured material consists of 10 cephala and seven pygidia.

Description

Length (sag.) of cephalon about half of its width (tr.). Glabella inflated, inclined anteriorly, not overhanging anterior cephalic border. Axial furrows deep [Character 14:2 of Ramsköld and Werdelin 1991], diverging at 60 degrees in front of L1. L1 large, equal in length (sag.) to occipital ring, but wider (tr.), with a large, distinct adaxial ridge [Character 5:2 of Ramsköld and Werdelin 1991]. Intercalating ring defined sagittally. S2 impressed across most of glabella; S3 well defined. Length between S1 and S2 equal to that between S2 and S3. Occipital ring wide, tapering strongly laterally (tr.) behind L1 lateral lobe. Eye greater in height than in length (exsag.), situated anteriorly, mid length (exsag.) of palpebral lobe opposite posterior edge of S3. 18 files of lenses, with a maximum of nine lenses per file; lens count (anterior to posterior) is 678 ?89 877 776 ??? ???, sclera are thin, slightly thickened dorsally. Palpebral area inflated, higher than visual surface [Character 13:2 of Ramsköld and Werdelin 1991]; palpebral furrow deep and distinct [Character 15:2 of Ramsköld and Werdelin 1991] continuous across palpebral area (exsag.); deepest and widest posteriorly. Genal field slopes steeply to lateral border furrow; palpebral area gently convex (exsag.). Posterior border furrow evenly deep and wide, weakly directed backwards across distal half, reflected at 90 degrees to lateral border furrow retaining the same width and depth; beneath eye lateral border furrow narrows anteriorly. Genal angle wide, rounded, without spine or node. Posterior border short (exsag.), abruptly widening distal to fulcrum, forming a "J" curve. Tubercles of similar, moderate size, evenly spread over glabella [Character 8:4 of Ramsköld and Werdelin 1991], palpebral area and genal field, large granules on ventral margin and doublure, becoming smaller anteriorly. Granulation on cephalic border becomes finer toward the ventral edge of the lateral border; no granulation in furrows.

Hypostome unknown.

Thorax of 11 segments, tapering posteriorly between the fifth and 11th segment. Axis does not taper posteriorly; axial furrow narrow. Abaxial notches present on axial rings, rings arched (tr.) and inclined posteriorly. Pleurae narrow (tr.) distal to fulcrum. Posterior margin of pleurae behind the articulating facet with a posteriorly aligned, rounded tip. Pleural furrows narrow and deep (exsag.), pleural ribs and pleural furrows granulated on internal mould; little granulation on axial rings and furrows.

Pygidium semi-oval, with nine axial rings and terminal piece of up to 3–4 axial rings. In lateral view the axis inclines at 50 degrees, and the pleurae 40 degrees posteriorly. Axis tapers posteriorly to form a blunt terminal piece. Anterior ring highly arched, becoming less so posteriorly; first two or three rings furrows with prominent pseudo-articulating half ring, anterior four axial rings with shallow "W" shape. Five congruent pleural segments [30:2] with six distinct, deep, pleural furrows faintly widening abaxially; seventh pleural furrow narrow (tr.). Interpleural furrows thin, first four distinctly impressed across most of pleural field, fifth weak [Character 31:2 of Ramsköld and Werdelin 1991]. Axial ring furrows shallowing medially, becoming moderately deep and continuous between first and ninth axial ring. Border distinct, defined by termination of the pleural furrows to form a high, steep area that narrows posteriorly. No postaxial ridge. Pygidium evenly covered with large granules, except in pleural and axial furrows. Four likely bands of large

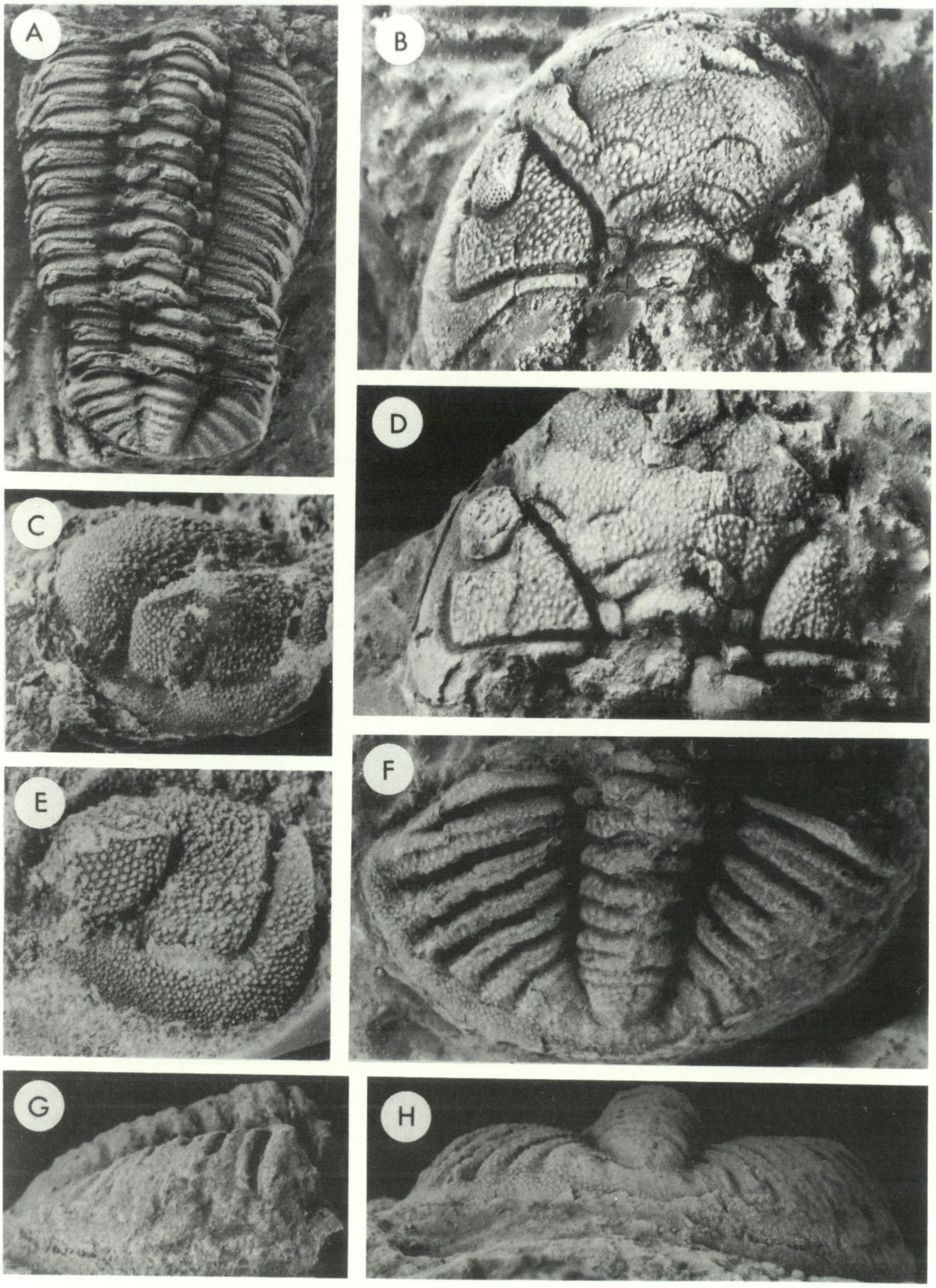

Figure 7 *Kainops* cf. *ekphymus*, A. dorsal view of thorax and pygidium, internal mould, AMF 105635; B, D. dorsal view of cephala, internal moulds, AMF 105639 and AMF 105643; C, E. left lateral views of cephala, external moulds, AMF 105636 and AMF 105637; F–H. dorsal, posterior-lateral view and lateral view of pygidium, external and internal moulds, AMF 105640 and AMF 105638. All specimens X2.5 magnification.

granules present on each pleura, and two on each axial ring

Remarks

Character coding for *Kainops* cf. *ekphymus* using the 32 characters of Ramsköld and Werdelin (1991), is as follows: 30312 124?0 22222 311?? ??0?? 22002 23. *Kainops ekphymus* codes identically except for characters [1:0], [8:5], [9:0], [12:4], [13:0] and [19:3].

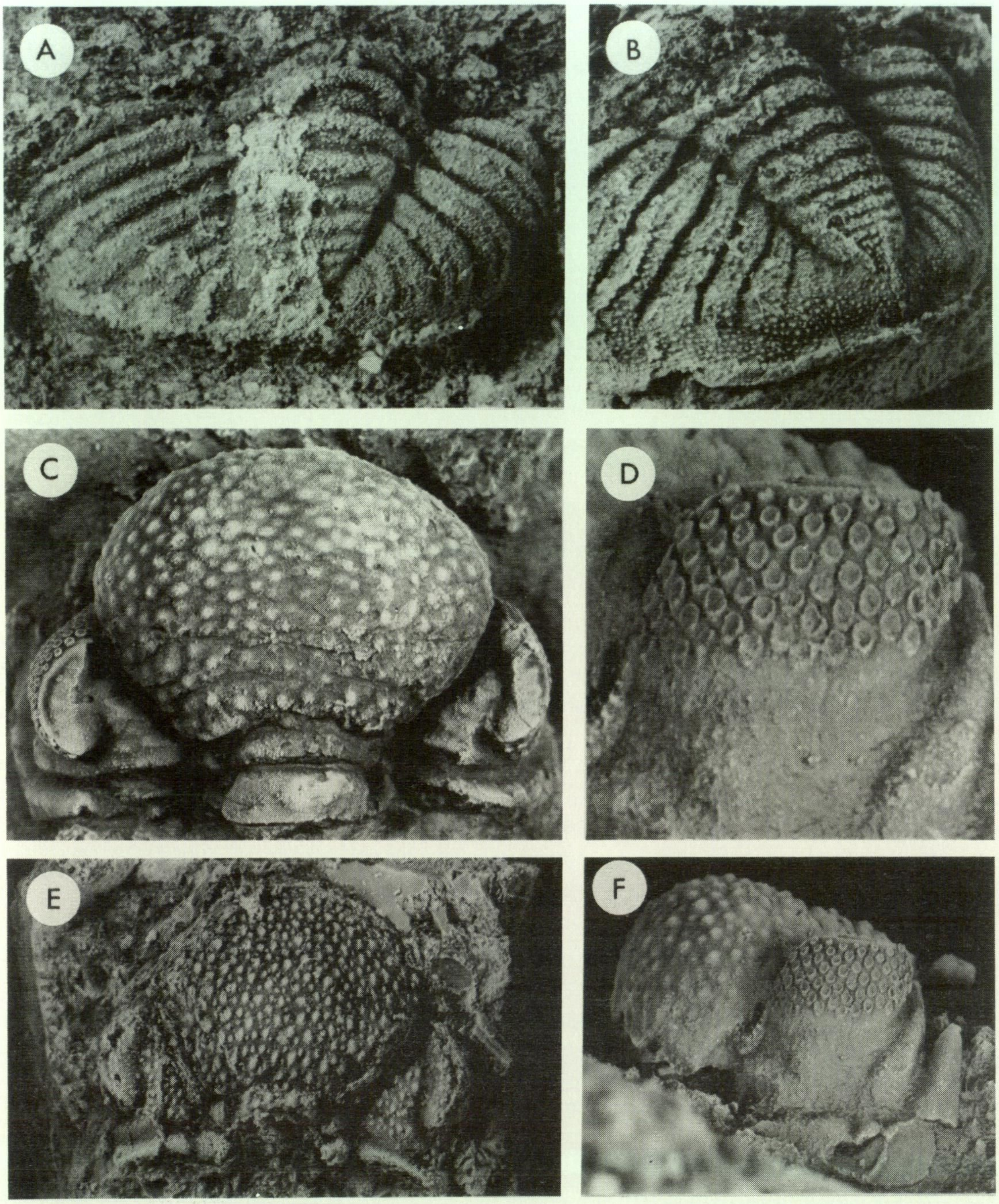

Figure 8 *Kainops* cf. *ekphymus*, A & B. dorsolateral and dorsal view of pygidium, external mould, AMF 105644; C–F. *Paciphacops* sp.; C and F internal dorsal and left lateral of cephalon, AMF 105641; D lateral view of left eye, AMF 105641 and E external dorsal of cephalon, AMF 105642. All specimens X 2.5 magnification.

Assignment of the pygidium

The pygidium shares many characteristics with that of the small-eyed Australian *Paciphacops* and *Kainops* species, in particular, *K. microps* and *K. ekphymus*. Similarities include faint to absent posterior pleural and interpleural furrows and a wide (sag.) border behind the terminal piece. Both these characters are absent from the large eyed Australian *Paciphacops* species, thus justifying the association of the only phacopid pygidium in the Biddabirra Formation to *K.* cf. *ekphymus* rather than to the co-occurring *Paciphacops* sp.

Discussion

Kainops microps and *K.* cf. *ekphymus* are very similar apart from a wider (sag.) occipital ring and fainter S2 and S3 in *K. microps*, and a far more heavily tuberculate glabella in *K.* cf. *ekphymus*. The eye is set lower in elevation, and the palpebral areas are more inflated in *K. microps*. The pygidial axis in *K.* cf. *ekphymus* has a distinctive 'W' formation, not as pronounced in *K. microps*, and a widened anterior furrow is absent in *K.* cf. *ekphymus*. *Kainops* cf. *ekphymus* is distinguished from *K. ekphymus* by its narrow (tr.) and long (sag.) glabella and, its weak and short (tr.) S2 and S3 furrows. *K. ekphymus* was considered a junior synonym of *K. microps* by Ramsköld and Werdelin (1991), as they regarded all differences in morphology to be due to the preservation (*K. ekphymus* is preserved as distorted moulds and *K. microps* as undistorted silicified material). I consider that several coding differences (listed above) justify specific distinctness.

Genus *Paciphacops* Maksimova, 1972

Type species

Phacops logani Hall, 1861; Lower Devonian (Lochkovian), New York.

Paciphacops sp.

Figure 8 C–F

Material Examined

Cephala AMF 105642 and 105641.

Description

Length (sag.) of cephalon about 70 percent of its width (tr.). Frontal lobe strongly inflated, wide, almost twice width (tr.) of occipital ring (tr.). Axial furrows diverging at 60 to 70 degrees, deep and wide [14:2], forming a vertical wall along glabella and an inclined wall against cheek. In lateral view the glabella overhangs anterior cephalic border. Occipital ring wide, highly arched, with anterior incision (exsag.) near abaxial edge, dissected by lateral groove (tr.) to form a lower step posteriorly, raised well above L1 medially; occipital node weak. L1 wide, with deep adaxial incisions. S0 deep, confluent with axial furrows. L1 distinct, wide (sag.) at mid line with distinct adaxial edge; S1 well impressed distally, becoming shallow medially, forming a small intercalating ring, distinctly inclined posteriorly [4:1]. S2 shallow and wide (tr.), S3 lightly impressed; maximum length between S1 and S2 nearly equal to length between S2 and S3; no rims present along S2 and S3. Eyes long (exsag.), reniform, extending from anterior border furrow almost to posterior border furrow. 53 lenses in 14 files, with a maximum of five lenses in a file; lens count (anterior to posterior) 345 554 545 443 2; sclera wide [23:1]. Palpebral lobe raised well above palpebral area [13:0]. Palpebral furrow wide, shallowing medially [15:2], parallel to axial furrow posteriorly, curving adaxially anteriorly. Post-ocular area short [11:1], bordered by wide and shallow posterior furrow. Cheek concave outwardly beneath eye. Posterior border equal in height to distinctly arched palpebral area, flattens and widens laterally towards the rounded genae [16:3]. Posterior border furrow deep and wide (exsag.), widens abruptly, curving at 95 degrees into the lateral border furrow; anterior border furrow narrow.

Granulated tubercles strong and even on glabella [8:4], intermittent with smaller tubercules. Palpebral area bearing numerous small, subdued tubercles. Smaller tubercles on occipital ring; posterior border evenly granulated; smaller granules on lateral border.

Hypostome, thorax and pygidium unknown.

Remarks

Character coding using Ramsköld and Werdelin's (1991) characters for *Paciphacops* sp.: 30412 51410 13022 3?12? 2?3?? ????? ??. *Paciphacops* sp. shares similarities with the Australian *P. serratus* (Foerste, 1888), *P. crosslei* and *P. latigenalis* (Etheridge and Mitchell, 1895) in eye length (exsag.) and width (tr.), and the small post-ocular area. Compared with *P. crosslei* (Etheridge and Mitchell, 1895), it possesses fainter S2 and S3 furrows, a wider occipital ring [3:4], large L1 with distinct adaxial edge [5:2], a palpebral area lower than the palpebral lobe [13:0]. Compared with *P.* sp., *P. latigenalis* has a shorter eye and hence a longer (exsag) post-ocular area [11:2]. *P. serratus* possesses deep S1 and S2, a wide (tr.) palpebral area behind a smaller eye compared to *P.* sp. *Paciphacops* sp. 1 (Ramsköld and Werdelin 1991), has an inflated palpebral area, higher than the eye, absent in *P.* sp. *P. crawfordae* Wright and Haas, 1990 differs in possessing a large post-ocular area, and small, anteriorly set eye. *Paciphacops* sp. does show features similar to North American taxa, such as a large eye, small post-ocular area, heavy tuberculation on the glabella, and a prominent (sag.) occipital ring with anterior incisions (exsag.). Compared to the North American, South American and European species, the Cobar *Paciphacops* has a wide glabella ornamented with large tubercules. The long (tr.) L1 with small adaxial nodes, deep S1, and occipital ring with a transverse groove of the Cobar species are not apparent in *P. logani* (Hall, 1861). The heavily tuberculated palpebral area, with wide and deep palpebral furrows of *P.* sp from Cobar is not present in *P. eldredgei* Ramsköld and Werdelin, 1991. L1 is shorter (tr.) in *P. birdsongensis* (Delo, 1940) and *P. campbelli* Ramsköld and Werdelin, 1991 with 2–3 lenses per row is shorter, compared to the 4 to 5 in *P.* sp. The palpebral area is inflated and markedly higher than the eye in *P. hudsonicus* (Hall, 1861), but deflated and below the eye in *P.* sp. In the South American species *P. argentinus* (Thomas, 1905) and *P. waisfeldae* Edgecombe and Ramsköld, 1994, the palpebral area is inflated and higher than the eye and L1 is attached to an intercalating ring, without a long, deep S1 furrow as in *P.* sp.

Cladistic Analysis of *Kainops* and *Paciphacops*

Ramsköld and Werdelin (1991) erected *Kainops* on the basis that it formed a clade separate from

Paciphacops. However, *Kainops* was based on one homoplastic character state [25:1] (Ramsköld and Werdelin 1991, Figure 3a & b) on one node, and *Paciphacops* on two character states [5:2] and [6:4] (their Figure 3a & b). The present analysis is restricted to *Kainops* and *Paciphacops*, hence more closely related outgroups than those used by Ramsköld and Werdelin (1991), *Podowrinella* Clarkson, Eldredge and Henry, 1977 and *Acernaspis* Campbell 1967, should be used. In the broader analyses of Ramsköld and Werdelin (1991), *Ananaspis* and *"Ananaspis"* proved to be the nearest outgroups to *Paciphacops* and *Kainops*, thus the most fully coded species of each of these groups, *Ananaspis decora* Mänill, 1987 and *"Ananaspis" amelangorum* Ramsköld, 1985 have been selected as outgroups.

Data

The only alterations made to the original data set of Ramsköld and Werdelin are the additions of *Paciphacops crawfordae* Wright and Haas, 1990 of the late Pragian from the Limekilns Formation, New South Wales, Australia, (character coding is as follows: ?0012 5?310 23222 21?1? ?12?3 2?220 02), *P. waisfeldae* Edgecombe and Ramsköld, 1994 of the early Lochkovian from the Catavi formation, Bolivia and *P. argentinus* (Thomas, 1905) of the Pridolian or early Lochkovian Los Espejos Formation, San Juan, Argentina (see Edgecombe and Ramsköld 1994, for character coding of both of these species), as well as *Kainops* cf. *ekphymus* and *Paciphacops* sp. from the Biddabirra Formation, New South Wales.

Computer analysis

Three analyses were run using the original 32 characters of Ramsköld and Werdelin on *PAUP* version 3.11 (Swofford 1993). The heuristic search option and the TBR and ACCTRAN algorithms and characters were subject to sucessive reweighting (using the rescaled consistency index (RCI) scaled to a base weight of 1000) to find greater resolution amongst equally parsimonious cladograms. All species that have been designated as *Paciphacops* and *Kainops* have been used in this analysis. All trees are rooted keeping the ingroup monophyletic.

The sets of outgroups included in these analyses are *Ananaspis decora* as outgroup, *"Ananaspis" amelangorum* as outgroup and a combination of both *A. decora* and *"A". amelangorum* as outgroups.

Results

The unweighted using *Ananaspis decora* produced 21 trees, 121 steps in length (CI 0.504, RI 0.520), compared to reweighting which found 63 trees (CI 0.636, RI 0.680) (Figure 9). Figure 10 shows characters optimised on the first tree. The unweighted run using *"Ananaspis" amelangorum* as an outgroup retrieved an 12 trees of 120 steps (CI 0.525, RI 0.544), the reweighted run yielded a single most parsimonious tree (CI 0.639, RI 0.694) (Figure 11). The combined run (using both outgroups) yielded 411 trees, 127 steps in length (CI 0.496, RI 0.540) in the unweighted run and 3 trees (CI 0.581, RI 0.628) (Figure 12) in the reweighted run. Figure 13 shows characters optimised on the first tree.

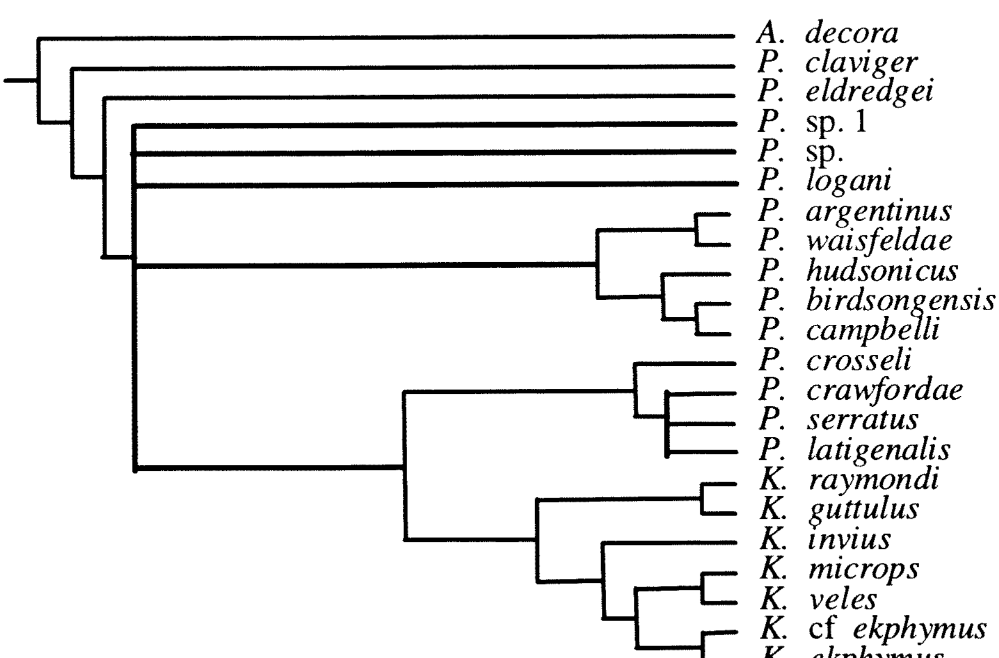

Figure 9 Cladogram for phacopids using *Ananaspis decora* as an outgroup. Strict consensus of 63 reweighted trees.

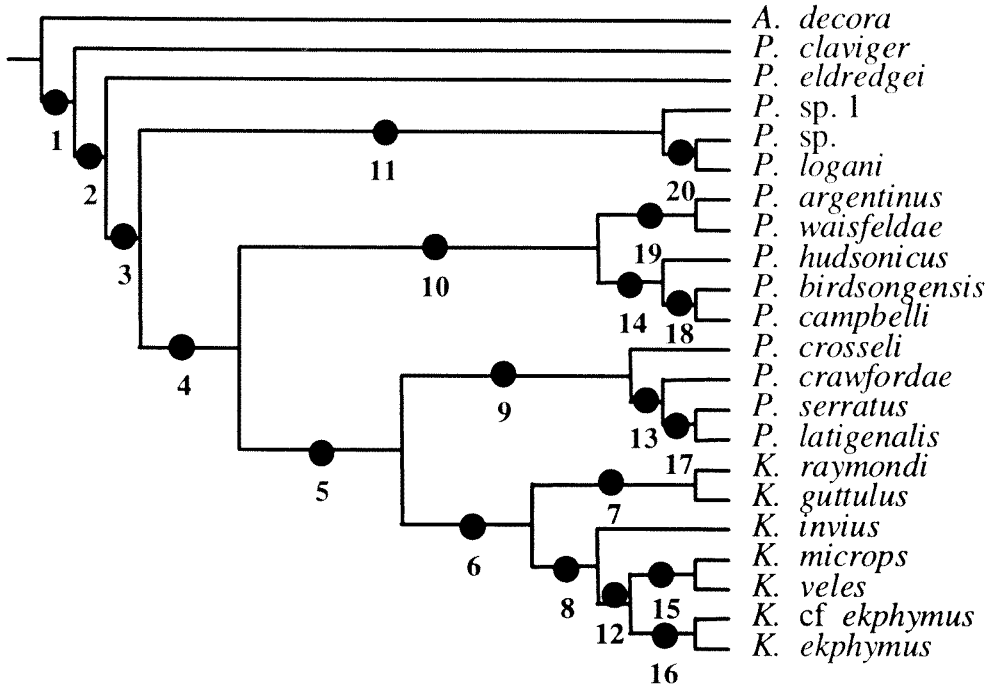

Figure 10 Cladogram for phacopids using *Ananaspis decora* as an outgroup. Character state changes on tree No 1 of 63 reweighted trees; Node 1 [6:3], [8:4], [17:1], [24:3], 26:2], [27:3], [28:2], [30:2]; Node 2 [1:3], [3:4], [5:2], [6:4], [16:3], [32:2]; Node 3 [12:3], [13:2], [29:3]; Node 4 [3:2], [27:2]; Node 5 [8:3], [12:2], [25:1], [29:1]; Node 6 [19:1], [22:0], [23:1], [24:2]; Node 7 [1:2], [6:3]; Node 8 [3:3]; Node 9 [6:5], [31:], [32:3]; Node 10 [17:1], [19:3]; Node 11 [20:2], [26:3]; Node 12 [6:0], [11:2], [19:3], [28:0]; Node 13 [11:2]; Node 14 [3:3], [26:4]; Node15 [zero length branch]; Node 16 [6:1], [7:2], [8?:4], [9:0], [20:0], [23:0], [29:0]; Node 17 [31:3]; Node 18 [15:3], [24:4], [32:3]; Node 19 [1:2]; and Node 20 [13:0], [29:2], [30:1], [32:3].

Remarks

In the *Ananaspis decora* run, *Kainops* is nested in *Paciphacops* in the reweighted consensus (Figure 9). Within *Paciphacops* an Australian clade consists of *P. serratus*, *P. crawfordae* and *P. latigenalis* forming a polytomy above *P. crosslei.* A North and South American *Paciphacops* clade, consisting of the North American species *P. hudsonicus*, *P. campbelli* Ramsköld and Werdelin 1991 and *P. birdsongensis* group as sister taxa to the South American species *P. argentinus* and *P. waisfeldae*. All *Kainops* species fall into a monophyletic clade supported by [19:1, 22:0, 23:1 and 24:2], as opposed to the single character state [25:1], on which the genus was erected in Ramsköld and Werdelin's (1991) analysis.

In the *"Ananaspis" amelangorum* run (Figure 11), most of *Kainops* again forms a distinct clade, consisting of *K. microps*, *K. invius*, *K. veles*, *K. ekphymus* and *K.* cf. *ekphymus* supported by four character states [1:3, 3:3, 24:2 and 26:1]. Within *Paciphacops*, *P. hudsonicus*, *P. campbelli* and *P. birdsongensis*, *P. argentinus* and *P. waisfeldae* form a sister group to *P. claviger*, *P. eldredgei*, *P.* sp. 1 and *P.* sp. and these together form a sister clade to the Australian *P. serratus*, *P. crosslei* and *P. latigenalis.* The sister grouping of *P. crawfordae and P. guttulus* is unusual (although supported by four character states), and is not seen in the *A. decora* or combined runs (see below). The type species of *Paciphacops*, *P. logani* lies outside the large group of species normally assigned to that genus. In the combined run with both outgroups (Figure 12), *Kainops* is restricted to four taxa, *K. microps*, *K. veles*, *K. ekphymus*, and *K.* cf. *ekphymus*, and is supported by three characters [6:0, 11:2 and 28:0]. The Australian *Paciphacops* group consists of *P. crosslei*, *P. latigenalis* and *P. serratus* and *P.* sp. However the inclusion of *P. claviger* (Haas 1969) from Nevada, deeply nested with *P. crosslei* and *P. serratus* from New South Wales, is probably due to homoplasy rather than true homology. Another unusual grouping is that of *P.* sp.1 from the Birdsong Shale of Tennessee and *P.* sp. of the Biddabirra Formation of New South Wales. This clade is supported by five character states using ACCTRAN, but since only one is based on the cephalon [3:4], the significance of the others is doubtful (i.e., missing data are extended down tree by ACCTRAN). A predominantly American *Paciphacops* clade consists of two groupings; the two sister taxa *P. eldredgei* Ramsköld and Werdelin 1991, and *P. logani* and the North American *P. campbelli*, *P. hudsonicus*, *P. birdsongensis* together with the South American *P. waisfeldae* and *P. argentinus*.

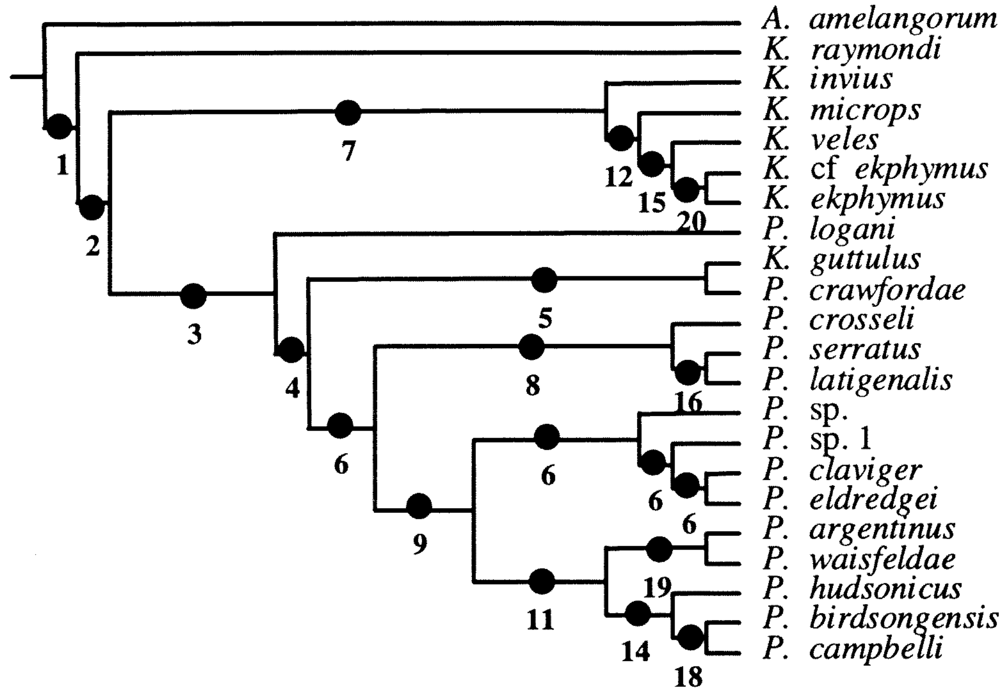

Figure 11 Cladogram for phacopids using *"Ananaspis" amelangorum* as an outgroup. Character state changes on single reweighted tree; Node 1 [3:2], [6:3], [13:2], [16:3], [17:1], [20:1], [30:2], [31:2] ; Node 2 [5:2], [6:4], [22:2]; Node 3 [8:4], [12:3]; Node 4 [6:5], [26:2], [29:1]; Node 5 [8:3], [20:0], [25:2], [31:0]; Node 6 [1:3], [19:2], [23:3]; Node 7 [1:3], [3:3], [24:2], [26:1]; Node 8 [12:2], [31:3], [32:3]; Node 9 [25:3], [29:3]; Node 10 [3:4], [20:2],.[27:3]; Node 11 [6:4], [17:0], [19:3]; Node 12 [6:0], [11:2], [19:3], 28:0], [29:1]; Node 13 [6:3], [9:0]; Node 14 [3:3], [6:3], [9:0], [26:4]; Node 15 [20:0], [26:2]; Node 16 [8:3], [11:2]; Node 17 [12:2], [13:1]; Node 18 [15:3], [24:4], [32:3]; Node 19 [1:2] and Node [6:1], [7:2], [8:4], [9:0], [23:0], [29:0].

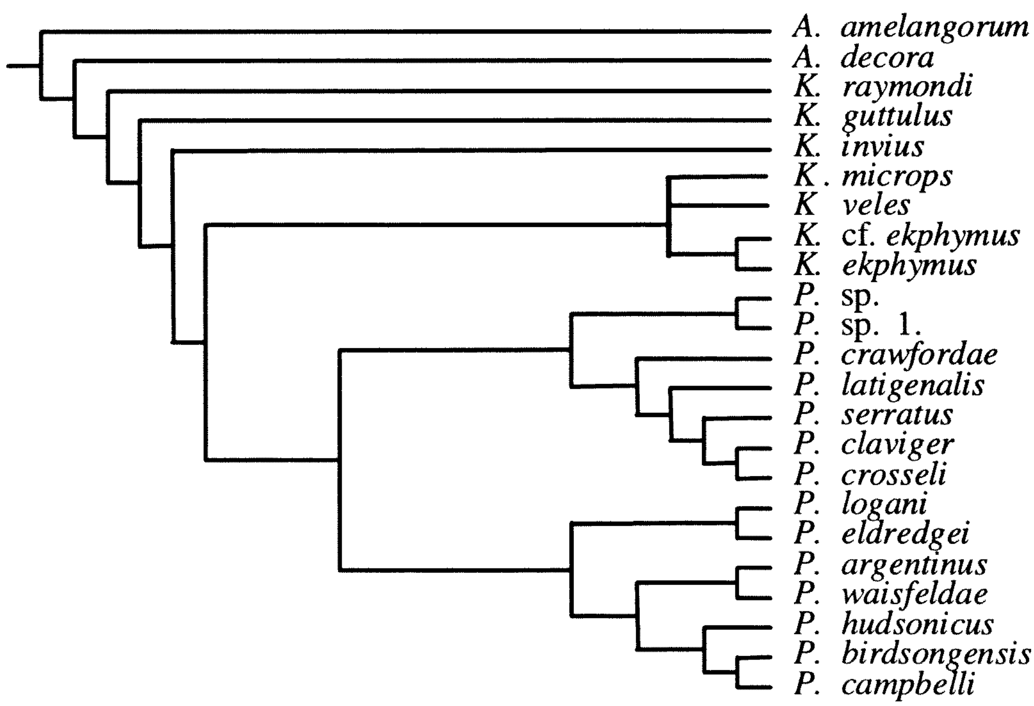

Figure 12 Cladogram of *Ananaspis decora* and *"Ananaspis" amelangorum* as outgroups. Strict consensus of 3 reweighted trees.

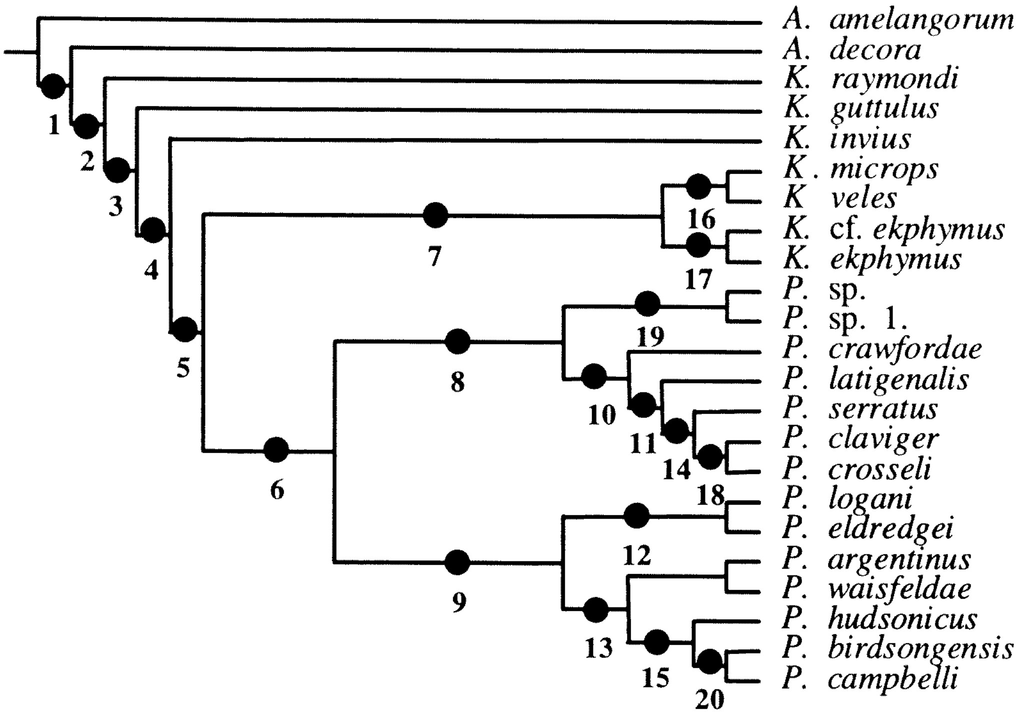

Figure 13 Cladogram of *Ananaspis decora* and *"Ananaspis" amelangorum* as outgroups. Character state changes mapped on tree No 1 of 3 reweighted trees; Node 1 [20:1], [30:1], [31:2]; Node 2 [3:2], [6:3], [13:2], [16:3], [17:1], [25:1, [30:2]; Node 3 [5:2], [26:2], Node 4 [1:3], [3:3], [6:4], [22:2], Node 5 [8:4], [19:3]; Node 6 [3:2], [12:3], [23:3]; Node 7 [28:0], [11:2], [6:0]; Node 8 [6:5, [19:2], [20:2]; Node 9 [25:3]; Node 10 [8:3], [11:2], [31:0]; Node 11 [12:2], [31:3], [32:3]; Node 12 [13:0], [15:1], [26:3], [27:3]; Node 13 [17:0], [29:3]; Node 14 [9:2]; Node 15 [3:3], [26:4]; Node 16 [8:3]; Node 17 [6:1], [7:2], [9:0], [20:0], [23:0], [29:0]; Node 18 [5:1], [8:4], [11:0], [29:2]; Node 19 [3:4], [22:1], [26:5], [27:3], [29:0]; Node 20 [15:3], [24:4], [32:3]; and Node 21 [1:2].

Taxonomic Implications

Because it accommodates more taxa, the analysis using both outgroups is considered to be the methodologically superior interpretation of both *Paciphacops* and *Kainops*. The combined result of all three trees show:

1. *Kainops* and *Paciphacops* are monophyletic.
2. the possibility of a unique American *Paciphacops* clade consisting of North American *P. eldredgei, P. logani, P. hudsonicus, P. campbelli* and *P. birdsongensis* and South American *P. waisfeldae* and *P. argentinus*. The American *Paciphacops* clade (with the exception of newly added South American taxa), has been noted by Ramsköld and Werdelin (1991, Figure 2a & b);
3. a distinct Australian clade consisting of *P. serratus*. *P. crosslei, P. latigenalis,* which Ramsköld and Werdelin (1991) resolved as a clade, but also including *P. crawfordae* and *P.* sp., and;
4. the recognition of unconstrained species, *P. claviger, P. logani, P. crawfordae* and *K. guttulus,* that will only be resolved with the addition of complete specimens of known species, new taxa and new characters.

Order Lichidae Moore, 1959

Superfamily Lichoidea sensu Fortey, 1997

Family Lichidae Hawle and Corda, 1847

Subfamily Trochurinae Phleger, 1936

Genus *Acanthopyge* Hawle and Corda, 1847

Subgenus *Lobopyge* Přibyl and Erben, 1952

Type Species

Lichas Branikensis Barrande, 1872; Lower Devonian (Pragian), Czech Republic.

Acanthopyge (*Lobopyge*) *edgecombei* sp. nov.
Figure 14

Material Examined

Holotype
Cranidium AMF 106418

Paratypes
Cranidia AMF 106417, AMF 106070, hypostome

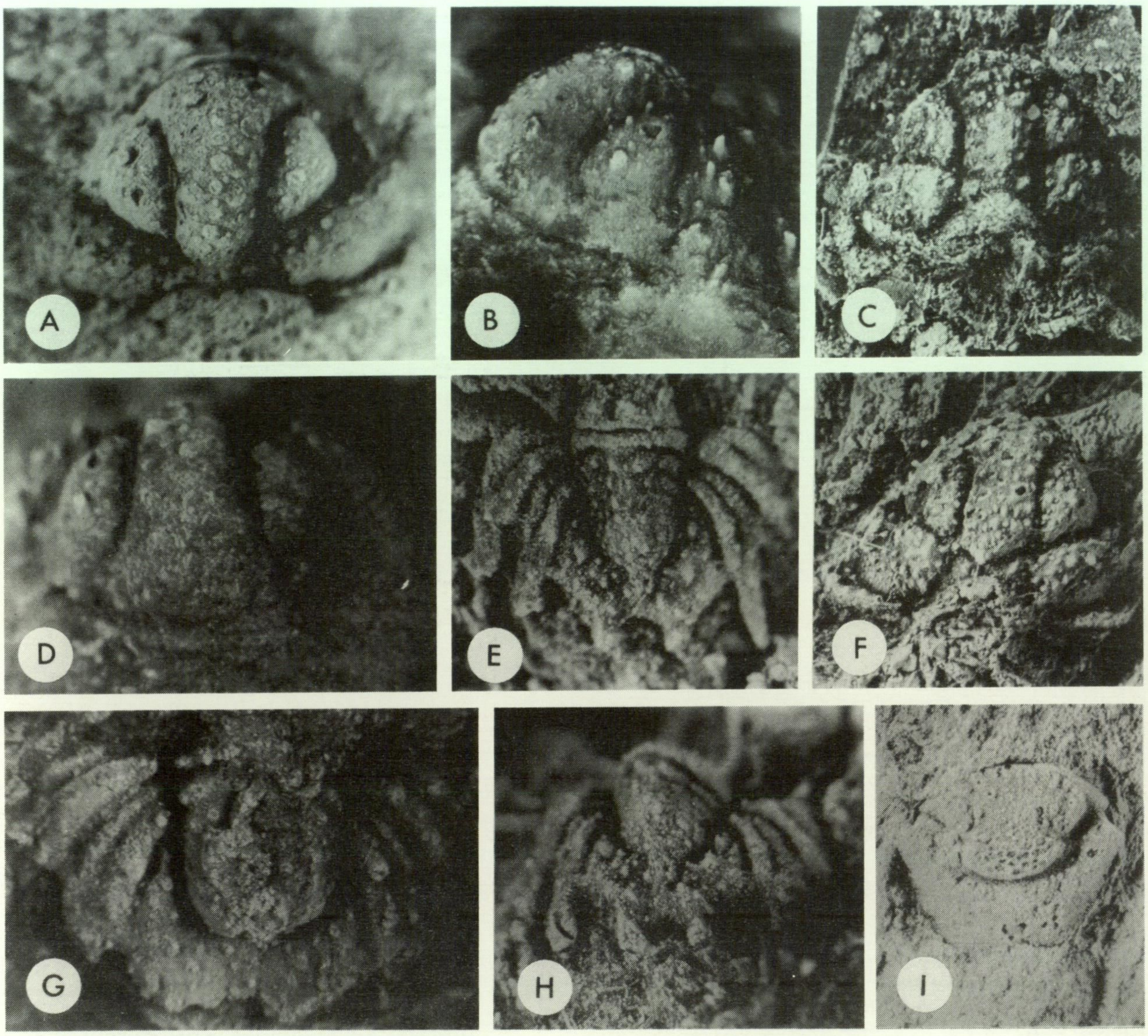

Figure 14 *Acanthopyge* (*Lobopyge*) *edgecombei* sp. nov., A, B & D. Paratype AMF 106070 external dorsal view, lateral view and frontal view of cranidium; C. AMF 106417 external dorsal view of crandium; E, H. AMF 106069 external dorsal and lateral view of pygidium; F. AMF 106418 external dorsal view of cranidium; G. AMF 106072 internal dorsal view of pygidium; I. AMF 106070 external dorsal view of hypostome. All specimens X 9 magnification.

AMF 106071 and pygidia AMF 106069 and AMF 106472.

Diagnosis

Posterolateral cranidial lobe triangular, bullar lobes angular in shape, not rounded as in most Devonian species (*Acanthopyge* (*Lobopyge*) *campbelli* Chatterton and Wright, 1986, *A.* (*L.*) *australiformis* Chatterton *et al.*, 1979 and *A.* (*L.*) *sinuata* (Ratte, 1886)). Sculpture on hypostomal middle body tuberculate and pitted. Marginal pygidial spine long, thin and outwardly directed.

Description

Cranidium trapezoidal, wider (tr.) than long (sag.). Bullar and posterolateral cranidal lobes inflated, and median glabellar lobe strongly inflated. Anterior margin convex medially, converging posteriorly to bound a highly arched and strongly inflated glabella medially. Sagittal region of median glabellar lobe the highest point on the cranidium. S1 converges to meet S0 medially, forming a short (sag.) and wide (tr.) occipital furrow; median tubercle between two prominent nodes on preoccipital glabellar region. Bullar lobes triangular, asymmetrically arched, sloping abaxially, distinctly larger than the trapezoidal posterolateral cranidial lobes. Posterolateral cranidial lobes convex. L0 shortens distally; S0 shallow medially, becoming deeper abaxially. Cranidium strongly tuberculate, with several large paired tubercles on glabella; tuberculation sparse on L0.

Hypostome squat, with long posterior border, posterior margin concave backward, with straight lateral margins. Border furrow widest and deepest opposite shoulder, shallowing medially, with uneven tubercles scattered on furrow margin. Posterior furrow on middle body effaces adaxially; wing short. Middle body with uneven tubercles concentrated anteriorly, coarsely pitted posteromedially.

Thorax unknown.

Pygidial axis inflated, longer (sag.) than wide (tr.), gently tapering, forming a blunt terminal piece with a prominent postaxial ridge. Distinct incision of first ring furrow abaxially, second ring furrow incomplete. Two distinct pairs of prominent pleurae with well defined interpleural and pleural furrows, form the two pairs of major pygidial spines. Major pygidial spines outwardly directed, evenly long (exsag.), tapering at extremities to form sharp tip. Posterior pleural region (behind second rib) lacks furrows, heavily ornamented with evenly scattered tubercles. Weak posterior border fused with posterior pleurae and postaxial ridge. Pair of posterior marginal spines, blunt and shorter than the major pygidial pleural spines, extend from raised margin. Distance between posterior marginal spines equal in width (tr.) to pygidial axis at second axial ring. Axial rings strongly tuberculate; evenly scattered tubercles on pleural ribs.

Remarks

A recent cladistic analysis of *Acanthopyge* (*Lobopyge*) found a consensus of 18 trees Ebach and Ahyong (2001; Figure 4) in which *A. (L.) edgecombei* and *A. (L.) erinacea* (Haas, 1968) are sister taxa in an unresolved clade consisting of the Australian species *A. (L.) australis* (McCoy, 1876), *A. (L.) sinuata* (Ratte, 1886), *A. (L.) pustulosa* Morzadec, 1983, *A. (L.) campbelli* Chatterton and Wright, 1986 and *A. (L.) australiformis* Chatterton *et al.*, 1979.

Acanthopyge (*Lobopyge*) *edgecombei* is distinguished from *A. (L.) erinacea* (Haas, 1968) by longer posterior pygidial spines. The second posterior spines are posteriorly directed in *A. (L.) australis* (McCoy, 1876), *A. (L.)* sp. 1 NSW Chatterton *et al.*, 1979, *A. (L.) campbelli* Chatterton and Wright, 1986 versus outwardly directed in *A. (L.) edgecombei*. A subdued node present on the pygidial posterior border in *A. (L.) sinuata* (Ratte, 1886) is absent in *A. (L.) edgecombei* and a shorter pygidial ring furrow (tr.) in *A. (L.) pustulosa* Morzadec, 1983. The area between the posterior spine pair is larger in *A. (L.) edgecombei* than in *A. (L.) australiformis* Chatterton *et al.*, 1979 and *A. (L.) sinuata*. S0 is sagittally wide in *A. (L.)* of Jones *et al.*, 1986, but narrower with a median tubercle in *A. (L.) edgecombei*. *A. (Lobopyge)* sp. of Holloway and Neil, 1982, from the Mt Ida Formation in Victoria, has an inwardly directed posterior pygidial spine pair and wide (tr.) pygidial axis, both absent in *A. (L.) edgecombei*.

Etymology

After Dr. Gregory D. Edgecombe.

Order Odontopleurida Whittington, 1959

Family Odontopleuridae Burmeister, 1843

Subfamily Odontopleurinae Burmeister, 1843

Genus *Leonaspis* Richter and Richter, 1917

Type Species

Odontopleura leonhardi Barrande, 1846; Silurian (Ludlow), Bohemia, Czech Republic.

Leonaspis sp.

Figure 6 A–C and F & G

Material Examined

Cranidium AMF 106644, free cheeks AMF 106683, AMF 106684, thoraco-pygidium AMF 106685 and pygidium AMF 106645.

Remarks

Ramsköld and Chatterton (1991), in their classification of the Odontopleuridae, diagnosed *Leonaspis* as possessing four marginal spines between the pygidial major border spines and nine thoracic segments, compared to the two marginal spines found on the pygidium in *Kettnerapsis* Prantl and Přibyl (1949).

Compared to the Cobar *Leonaspis*, *L. jenkinsi* (Etheridge and Mitchell, 1896, see Chatterton (1971)) from Lochkovian strata in the Yass district possesses shallower S1, a wider (tr.) glabella and a tuberculated pygidium. Bohemian *Leonaspis* mainly possess sparsely tuberculated glabella, as seen in *L. confluens* Přibyl and Vaněk, 1966 and *L. truncata* Hawle and Corda, 1847. Axial furrows and the terminal piece are distinct and present in *L. confluens*, *L. leonhardi* Barrande, 1846 and *L. truncata*, versus subdued and absent, respectively in *Leonaspis* sp. The Moroccan *L. maura* Alberti, 1969 possesses a wide and deep S0, wide and shallow in *L.* sp. *Leonaspis belisarius* Haas, 1968 from Turkey is similar to the Cobar species, but differs in possessing subdued axial furrows.

Cladistic Analysis

Ramsköld and Chatterton (1991) revised the Odontopleurinae Burmeister, 1843 in a series of cladistic analyses. The analyses included *Leonaspis*, *Kettneraspis* Prantl and Přibyl , 1949 and their newly erected genus *Exallaspis* Ramsköld and Chatterton, 1991. A separate clade of eight *Kettneraspis* species was later separated as *Edgecombeaspis* by Adrain and Ramsköld, 1997.

Computer treatment of data

The analyses were run using PAUP 3.11 with the same settings in the above *Paciphacops-Kainops* analysis. All characters were treated as unordered, and reweighted based on the rescaled consistency index using a base weight of 1000. Multistate taxa are treated as 'uncertain'. All analyses were run using the branch and bound search. All consistency (CI) and retention (RI) indices listed are from the shortest trees. All trees were rooted keeping the ingroup (*Leonaspis*) monophyletic.

Of the 14 coded *Leonaspis* species (13 in Ramsköld and Chatterton 1991), only nine had less 45 percent their characters missing and therefore were used in the analysis. Results from similar approaches (see Ebach and Ahyong 2001 and Kitching *et al.* 1998) conclued that an increase in the number of missing data led to more equally parsimonious trees and generated ambiguous results in some cladistic computer programs. In the *Leonaspis* analysis, 45 percent of the data represent up to two whole regions. Thus, deleted taxa are based on on a combination of missing cranial, hypostomal, thoracic or pygidal features.

Outgroup Selection

Kettneraspis jaanussoni Chatterton and Perry, 1983 was suggested to be among the closest relatives of *Leonaspis* by Ramsköld and Chatterton (1991). They considered that *Leonaspis* was not directly derived from *Kettneraspis* but rather that *Leonaspis* originated from a taxon similar to that giving rise to

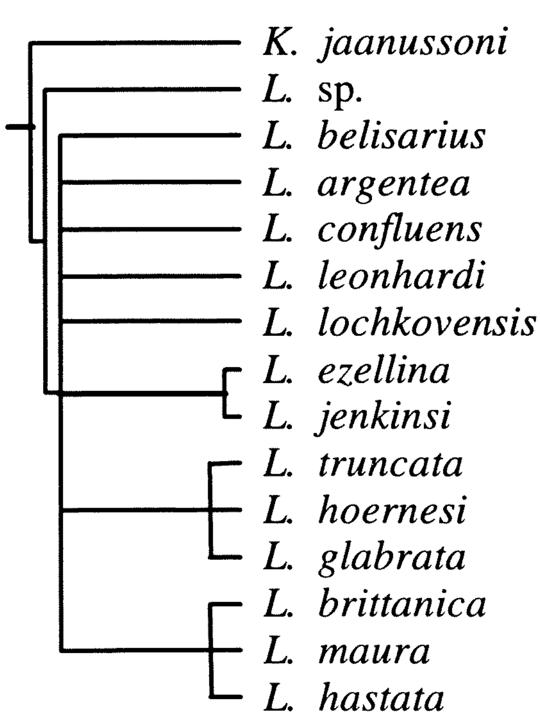

Figure 15 Reweighted consensus tree of the *Leonaspis* fourteen taxon run.

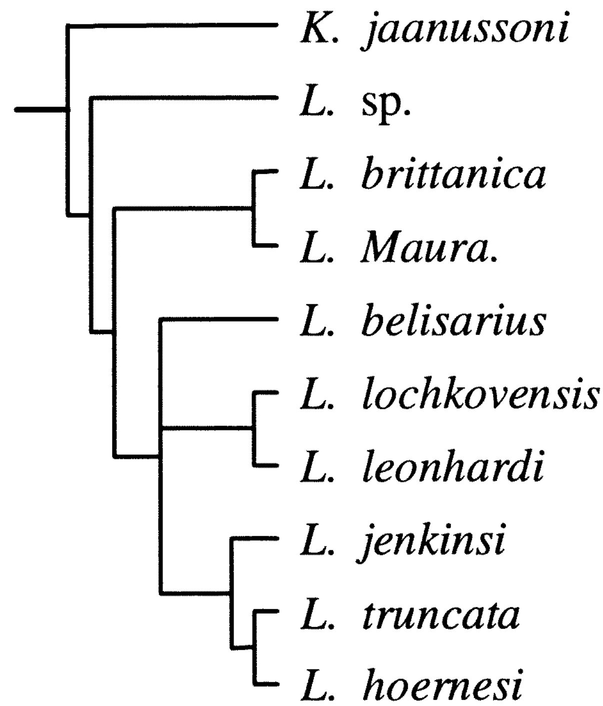

Figure 16 Reweighted consensus tree of the *Leonaspis* nine taxon run.

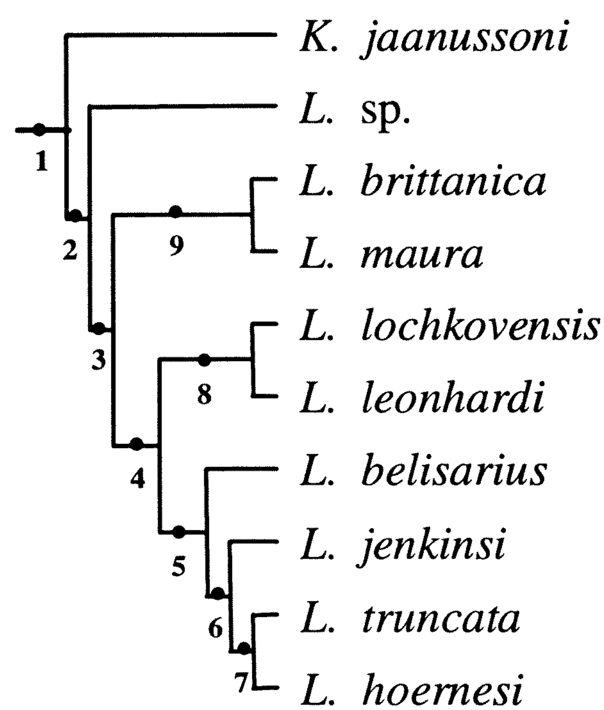

Figure 17 First tree of the reweighted consensus tree of *Leonaspis* nine taxon run; Node 1 [1:2], [2:1], [4:1], [31:1], [32:2], [33:1]; Node 2 [8:1], [10:1], [11:1], [17:2], [20:0], [21:1], [27:0], [29:2]; Node 3 [13:1], [14:2], [22:1], [24:2], [28:1], [32:2], [35:0]; Node 4 [1:0], [18:0], [25:1], [26:1]; Node 5 [5:1], [9:2], [28:1], [32:1]; Node 6 [10:0], [12:0], [16:1], [23:0]; Node 7 [9:1]; Node 8 [10:0], [17:1], [23:0]; Node 9 [7:0], [9:1], [24:0].

Kettneraspis. Hence, *Kettneraspis jaanussoni* is used as the outgroup for *Leonaspis* in this analysis.

Data

All characters used in this analysis are from Ramsköld and Chatterton's (1991) analysis. That work should be consulted for character definitions and codings.

The only alteration made to the original data set of Ramsköld and Chatterton is the addition of *Leonaspis* sp. from the Cobar fauna (character coding is as follows: 2000{0/1}0110001???121000?110?1?201110{0/1}).

Results

Fourteen Taxon Run

The fourteen taxon run includes all 13 coded *Leonaspis* species from Ramsköld and Chatterton (1991) and *Leonaspis* sp. The reweighted analysis found 720 trees (CI 0.892, RI 0.827) (Figure 15).

Remarks

Using all coded taxa with equal weights yielded an unresolved consensus, regardless of its high consistency and retention indices (CI 0.762, RI 0.667). A reweighted run yielded two trichotomous clades, with *Leonaspis brittanica* Morzadec, 1969, *L. hastata* (Alberti, 1967) and *L. maura* (Alberti, 1969) forming one clade and *L. glabrata* (Roemer, 1843), *L. hoernesi* (Barrande, 1846) and *L. truncata* (Hawle and Corda, 1847) forming another.

Nine Taxon Run

The unweighted run found 3 trees of 40 steps, (CI 0.800, RI 0.636). Reweighting yielded 2 trees (CI 0.929, RI 0.851) (Figure 16 and Figure 17).

Remarks

In the rewieghted run, *Leonaspis brittanica* from the Upper Emsian of France and the Upper Emsian Moroccan *L. maura* are grouped as sister taxa. A trichotomy is formed between the Turkish *Leonaspis belisarius* Haas, 1968, a clade containing the Bohemian *L. hoernesi*, *L. truncata* and Australian *L. jenkinsi* Etheridge and Mitchell, 1895 and the Bohemian sister taxa *L. lochkovensis* Prantl and Přibyl, 1949 and *L. leonhardi* Barrande, 1846. *Leonaspis* sp. is the most plesiomorphic taxon within *Leonaspis*.

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