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A New Early Devonian Spinose Phacopid Trilobite from Limekilns, New South Wales: Morphology, Affinities, Taphonomy and Palaeoenvironment

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ABSTRACT. *Paciphacops (Paciphacops) crawfordae* n.sp. is a distinctive spinose phacopid trilobite of late Pragian (Early Devonian) age from the deepwater, dysaerobic Rosedale Shale, Limekilns district, New South Wales. It is characterised by short occipital, genal and intergenal spines on the cephalon, and short thoracic spines on the axial rings and pleurae. Various combinations of such spines are developed in *P. (Paciphacops) serratus* Foerste (Lochkovian, New South Wales; Ludlovian, Kazakhstan?) and *P. (Paciphacops) claviger* Haas (Siegenian, Nevada), but the three species cannot be shown to be related.

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In 1969, Elizabeth Crawford collected shelly fossils from temporary exposures of shales belonging to the Rosedale Shale in the Limekilns district, near Bathurst, New South Wales (Fig. 1). This collection included the eight known specimens of the new trilobite species which is the focus of this paper.

Setting **and Stratigraphy**

The stratigraphic succession in the Limekilns district (Table 1), where the Devonian strata between the

Merrions Tuff and the Winburn Tuff (Table 1) have been assigned to the Limekilns Group by Packham (1968), was first mapped and studied by the late L.V. Hawkins (1953) . The stratigraphic terminology was established by Packham (1968) and the age of the succession was discussed by Wright & Chatterton (1988). The area lies just inside the eastern margin of the Hill End Trough of Packham (1968), as indicated by the deepwater sedimentary rocks of the Limekilns sequence.

Devonian fossils occur in three units in the sequence, as summarised by Wright & Chatterton (1988, Table 1). The lowest fossils (?late Lochkovian; Wright &

Fig.1. Map showing the trilobite locality in relation to limestones of the Diamond Creek and Fernbrook belts and Merrions Tuff as mapped by Stone (1973); base after Bathurst 1: 100,000 topographic map 8831 (1st edition, 1975).

Chatterton, 1988; Garratt & Wright, 1988) occur at Paling Yards at the top of the Crudine Group, which is overlain by the unfossiliferous Merrions Tuff.

In the basal unit of the overlying Limekilns Group, the Rosedale Shale (late Pragian; see discussion herein and **in** Garratt & Wright, 1988), there are scattered fossils, possibly at different levels, and mostly from the Fernbrook belt. Rich faunas occur in the next highest unit, the Jesse Limestone, from the Diamond Creek belt in the western part of the area; the youngest conodonts from this formation indicate a Zlichovian to early Dalejan (late Emsian; discussed herein) age. Trilobites from a level high in the Jesse Limestone were described by Wright & Chatterton (1988). No age-significant fossils are known from the topmost sedimentary unit, the Limekilns Shale which, according to Packham (1968), overlies the Jesse Limestone. Packham (1968) recognised a volcanic unit, the Winburn Tuff, above the Limekilns Group (Table 1).

Despite this apparently simple sequence, some qualifying comments are necessary. At Limekilns, there are two belts of limestone (Fig. 1). These are the western or Diamond Creek belt, containing well-preserved and rich faunas, and the eastern or Fernbrook belt, more renowned forits 'marble' quarries (now defunct) than forits well-preserved fossils. These limestone belts outcrop on either side of an expanse of shale $(Fig. 1)$; the general structure is believed to be a syncline, but limestone exposures cannot be mapped around the nose of the inferred syncline; as the exposures of the underlying and overlying shales are poor, there are no objective data to prove that the limestones constitute a single formation or occur at a single horizon. In fact, Crawford (1969) recognised limestones at a number of horizons. More recently, studies in the Diamond Creek area by Voorhoeve (1986) indicated that the limestones of the Diamond Creek belt are olistoliths.

Rosedale Shale: Faunas and Age

The Rosedale Shale yields a mostly pelagic fauna (graptolites, tentaculitids, hyolithids, conulariids) and plant fragments; benthic faunas, mostly brachiopods (notanopliids being possibly epiplanktonic) with some corals, rare bivalves and trilobites, also occur. Strusz (1972) reported *Monograptus yukonensis* (identified by G.H. Packham) from this formation, and inferred a Pragian age.

As stratigraphic control within the poorly exposed Limekilns Group is poor, the relative position and relative age of the trilobite-bearing horizon in the Fernbrook belt and the Jesse Limestone (the source of all the conodont data at hand) in the Diamond Creek belt cannot be established on the basis of mapping. Further, there is the possible need to amend the stratigraphic terminology for the Limekilns district, so that the predominantly shaley sequence (currently termed the Limekilns Group) could be relegated to formation status (Limekilns Formation), containing unnamed limestone olistoliths.

Several palaeontological lines of evidence indicate a late Pragian age for the Rosedale Shale trilobites from the Fernbrook belt: 1) If the trilobites from the Rosedale Shale are at about the *Monograptus yukonensis* level, this would indicate a late Pragian age for the trilobites, according to Lenz (1987, 1988). The occurrence of *M. yukonensis* in the early Zlichovian (see Wright & Chatterton, 1988 *after* Jaeger, 1979) is thus not yet agreed; 2) Most important of all, tenaculitids occurring with the trilobites have been determined by one of us (W.H.) as *Nowakia acuaria,* the well-known Pragian index fossil (e.g. Liitke, 1979); 3) Garratt & Wright (1988) reported the conodont *Polygnathus* cf. *dehiscens* from basal beds of the Jesse Limestone in the Diamond Creek belt, and Wright & Chatterton (1988) referred to this specimen as *P. dehiscens.* Drs R. Mawson and J. Pickett (personal communication, 1987) consider the specimen more likely to be *P. pirenae* Boersma, and it could therefore indicate a late Pragian age for the lower beds of the Jesse Limestone. *Polygnathus pirenae* has been recorded from Limekilns by Mawson *et al.* (1988). Present conodont data from the Jesse Limestone do not conflict with faunal age data from the Rosedale Shale.

The conodont fauna from the upper beds of the Jesse Limestone in the Diamond Creek belt includes (Wright & Chatterton, 1988) *Polygnathus* sp. cf. *P. inversus* and

Table 1. Limekilns sequence (after Packham, 1968) showing approximate positions of fossiliferous horizons and their correlation, as suggested herein and by Wright & Chatterton (1986) and Garratt & Wright (1988).

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Polygnathus sp. cf. *laticostatus,* of late Zlichovian or early Dalejan age. This did suggest the possibility in the Jesse Limestone of the *pirenae, dehiscens, perbonus* (= *gronbergi)* and *laticostatus* (= *inversus)* conodont zones of Klapper & Ziegler (1979); however, detailed conodont studies in the district are being carried out by Dr Ruth Mawson and Professor John Talent of Macquarie University, and speculations are clearly hazardous until these studies are further advanced.

Preservation of Fauna, and Palaeoenvironment

In addition to the eight trilobite specimens, the trilobite locality has yielded only a few benthonic species including several brachiopod taxa (in particular a notanopliid [possibly epiplanktonic] and a leptocoeliid), a few corals and rare bivalves, as well as the 'pelagic' tentaculitids, conulariids andhyolithids.

The closest comparisons appear to be with certain parts of the Siluro-Devonian Melbourne Trough sequence. For instance, the Pragian Wilson Creek Shale contains a pelagic plant-graptolite assemblage; according to Garratt (1983) this lithofacies is restricted to the basin floor in his 'shale lithofacies' which is occasionally pyritic. In the Humevale and Boola Formations Garratt (1983) recognised the *Notanoplia* community of Savage (1974), which may be closer to the Rosedale fauna than is the fauna from the Wilson Creek Shale.

Taphonomy. One specimen of *Pac. (Paciphacops) crawfordae* (AMF 73417) is found as a Salterian moult (Fig.4A) with its thoracopygon intact but slightly disturbed, the hypostoma inverted and displaced (rotated by about 130°) and located under the cephalon which is inverted. The holotype (AMF 73411) consists of a thoracopygon with cephalon nearby (not inverted), and there is another thoracopygon (AMF 73415). All specimens are, to some extent, crushed and deformed by soft-sediment processes, but are not broken or abraded by turbidity or traction currents. Salterian molts cannot to be transported intact by any common mechanism, so the trilobites must be preserved near to their living environment (Speyer, 1985; Speyer & Brett, 1986) and cannot be carcasses of individuals killed by anaerobic or dysaerobic currents.

Pyritisation. The trilobite-bearing rocks contain pyrite close to the recrystallised trilobite tests, most of the pyrite being altered to a limonitic (?) mineral. The pyrite is believed to be derived from bacterial decomposition of organic material (Raiswell & Bemer, 1985; Dick & Brett, 1986); some oxygenation of the sediments and high initial levels of organic material in the Rosedale Shale are indicated by the abundant bioturbation (e.g. Raiswell *et al.,* 1988). The environment indicated is similar to the dysaerobic one inferred by Thompson & Newton (1987) for the well-preserved, low-diversity *in situ* Late Devonian *Leiorhynchus*

fauna of New York which occurs in generally poorly fossiliferous pyritic black shales. Thompson & Newton (1987: 279) argue for "... abundant calcareous fauna..." at ... lower oxygen levels..." than those set by Rhodes & Morse (1971); that is, down to 0.3 ml/l O₂.

Depth. The sparse assemblage dominated by pelagic elements which occurs at places in laminated or bioturbated shales in the formation, together with rare graded sandy turbidites, strongly suggests a deepwater muddy 'outer shelf' or 'continental slope' environment. The shales are occasionally finely bedded and lack the chaotic structure indicative of deposition as slumps. Thus, aspects of both the restricted fauna and the sedimentary rocks demonstrate that the environment was deep and dysaerobic (perhaps episodically, see Wignall & Myers, 1988). If the dysaerobic (see above) interpretation is correct, ponding or some other mechanism may be indicated to account for the reduced oxygenation.

Similar trilobites from similar environments have not yet been described from Australia. The only other Pragian phacopid trilobite described from New South Wales is *Phacops microps* Chatterton, Johnson & Campbell, 1979, but this is a clearly different form from a different biofacies, being from shallow marine carbonates of the Garra Formation. A restricted trilobite fauna of Zlichovian age from the top of the Jesse Limestone described by Wright & Chatterton (1988) not only lacks phacopids, but has a distinctly 'European' aspect.

Systematic Palaeontology

Phylum Trilobita

Suborder Phacopina Struve, 1959

Family Phacopidae Hawle & Corda, 1847

Paciphacops (Paciphacops) Maximova, 1972

Type species. *Phacops logani* Hall, 1861 by original designation.

Paciphacops (Paciphacops) crawfordae n.sp.

Figs2,3A-K,4A-H

Material examined. HOLOTYPE, AMF 73411a-b; PARATYPES, AMF 7341Oa-b, AMF 73412a-b, AMF 73413, AMF 73414a-b, AMF 73415, AMF 73416a-b, AMF 73417a-b. All are from the late Pragian Rosedale Shale, at Limekilns, New South Wales. Grid reference 581185, Bathurst 1:100,000 topographic sheet 8831. All material is deposited in the Australian Museum, Sydney.

Derivation of name. The species is named for

Elizabeth Crawford, collector of the described material.

Diagnosis. *Paciphacops (Paciphacops)* with short, stout occipital, genal and intergenal spines on cephalon, and spines on thoracic axial rings and pleurae. Axial furrow in front of S1 diverging at 75° -90°. Small, anteriorlyplaced eye with 11 or 12 vertical files and from 48-57 lenses. Pygidium with about 8 axial rings and up to 5 straight pleural furrows.

Description. Cephalon transverse, with prominent overhanging SUb-pentagonal glabella. Axial furrows deep and diverge at 75°-90° in front of SI, so that ratio of maximum to minimum glabellar width (tr.) is up to 1:2.25. L1 not as long (exsag.) as median part of occipital ring; L2 at least as long (sag.) as occipital ring. Occipital furrow shallow medially, SI almost absent medially; both are incised laterally and swing forward laterally; posterior branch of S3 arcuate, anterior branch straight and almost parallel to axial furrow. Facial suture indistinguishable. Sculpture of glabella and posterior parts of fixigenae poorly preserved, consisting of tubercles. Posterior border furrow long (exsag.), shallow and basally rounded, swinging anteromedially well inside genal angle, deepening lateral to eye and again at junction with axial furrow; very shallow but persistent preglabellar furrow. Cephalic doublure broad (sag.) anteriorly. Vincular furrow well defined beneath border, becoming deeper and notched on both sides laterally, with about 8 notches. Short, stout occipital, intergenal and genal spines present.

Palpebral furrow faint to absent; deep furrow below elevated, reniform eye developed posteriorly; weak furrow developed just above the lenses. Eyes small and low, with 11 or 12 files; posterior end located just anterior of S2, anterior end located just in front of abaxial end of S3 and very close to both axial and border furrows. Sclera depressed and narrow below lenses, and thin where seen in internal moulds. Lens composition (Fig.3)

can be confidently interpreted in only a few specimens, asfollows:-

AMF 73410 (Fig.3J) and AMF 73416 have irregular lens arrangement at about midlength of eye. The difference in lens number between AMF 73411 (Fig.3A) and AMF 73416 (Fig.4G) does not appear to be size related, as the specimens are of similar size. AMF 73410 has 54 (?plus 2) lenses and 11 or 12 files, but is deformed and difficult to interpret. Hypostoma rather broad, with wide, gently convex forward anterior margin, acute anterior wings, convex, relatively short (sag.) oval middle body with posterior median depression of possible tectonic nature; border furrow present; 3 small posterior spines.

Thorax with prominent spines on axial rings, and on posterior pleural band just lateral to articulation point. Pleural furrows narrow (exsag.), trend obliquely across the pleurae, and extend from near wide (tr.) but poorly defined axial nodes (not completely isolated by notches) to upper part of spatulate facet. Pleurae apparently taper steadily in width (tr.) from cephalon to pygidium.

Pygidium transverse, with about 8 axial rings and a terminal piece, and up to 5 pleural furrows. Axis high and narrow, tapering slightly to ring 5, then tapering more rapidly towards the terminal piece. Axial rings longer (sag.) than narrow (sag.) ring furrows, only 5 of which are developed. Axial furrow weak over anterior few pleurae; strong concentric-forwards apodemes on the first few segments extend from axial furrow on to side of axis. Pleural furrows shallower and narrower than interpleural furrows, producing a smaller posterior portion of the pleurae which expand weakly and curve only slightly, so that the posterior pair of pleurae make an angle of about $30^{\circ} - 40^{\circ}$ with the axis. Doublure narrow (sag.), almost horizontal. Border wide (sag.) and smooth, width constant.

Fig.2. Pattern of lenses in eyes of 3 specimens of *Paciphacops (Paciphacops) crawfordae* (see Campbell, 1977: fig.11).

Fig.3. A-K: *Paciphacops (Paciphacops) crawfordae* n.sp., all from Rosedale Shale (late Pragian), Limekilns district, New South Wales. A-D, holotype AMP 73411. A, latex cast of cephalon showing occipital and intergenal spines, x2.5. B, latex cast of eye (anterior to right), xlO. C, latex cast of thorax (showing spines) and pygidium, x2.5. D, latex cast'~f pygidium, x3. E, paratype thoracopygon AMP 73415, internal mould, x2. P, paratype partly testiferous thorax AMP 73413, x1.5. G, paratype pygidium AMP 73414, latex cast, x3. H-K, paratype cephalon AMP 73410. H, latex cast, dorsal view, x2. I, cephalon in anterolateral view, x3. J, internal mould of eye (anterior to right), x8. K, doublure showing continuous vincular furrow, x3.

Dimensions (approximate):-

Generic assignment. Although this material is poorly preserved by comparison with many Silurian and Devonian phacopids and details of the sculpture are obscure, a firm generic assignment can be made. One of the characteristics of *Paciphacops (Paciphacops)* is the presence of perforated glabellar tubercles in large-eyed forms (Campbell, 1977), but perforations are not visible in the glabellar tubercles in this small-eyed form. Campbell (1977) placed emphasis on the continuous vincular furrow, the thickened sclera in small-eyed forms (in particular) and the straight or slightly convex hypostomal suture as diagnostic characters of this subgenus. Chlupac (1971, 1972, 1977) synonymised *Paciphacops (Paciphacops)* and *Paciphacops (Viaphacops),* treating *Paciphacops* as a subgenus of *Phacops*, but noted the importance of the continuous vincular furrow. Chlupac (1977) further considered that, in *Phacops (Paciphacops),* SI is weak or interrupted medially, and genal spines are commonly developed; these latter features can be seen in both *Pac. (Pac.) logani* (Campbell, 1977) and *Pac. (Pac.) crawfordae.* Holloway (1980) regarded *Paciphacops* as a synonym of *Ananaspis,* and *Viaphacops* as an independent genus. Holloway & Neil (1982) stated that the only features distinguishing *Paciphacops* from *Ananaspis* are the perforated glabellar tubercles in large-eyed morphs, and the thickened sclera in all small-eyed morphs and most large-eyed morphs. *Paciphacops (Angulophacops)* Maximova, 1978, based on *Phacops angulatus* Maximova (1968: 66, p1.20, figs 1-4), was differentiated from *Pac. (Paciphacops)* by Maximova (1978: 120) on the basis of the "...triangular sub-cranidial (= vincular) furrow and the corresponding pygidial outline..."

This Limekilns species is assigned to *Paciphacops (Paciphacops)* because of the anteriorly continuous and posteriorly notched vincular furrow, the wide and gently convex anterior border and three posterior spines of the hypostoma, and the medially weak S1.

The generic assignment of comparable species should now be discussed. *Phacops claviger* Haas, 1968 was assigned to *Ananaspis* by Holloway & Neil (1982), but the perforated glabellar tubercles (which can be seen on calcareous specimens but not on silicified specimens) and other characteristics (listed in the previous paragraph) suggest that it belongs to *Pac. (Paciphacops). Phacops serratus* Foerste, 1888 was assigned to *Ananaspis* by Campbell (1967) and Holloway & Neil (1980), and to *Pac. (Paciphacops)* by Campbell (1977). In our opinion this species falls outside *Ananaspis* as it possesses a vincular furrow which is clearly continuous across the anterior part of the doublure, and the species is here assigned to *Pac. (Paciphacops).*

Comparisons. Few other phacopids have spines developed to a significant degree. The most striking of these are *Pac. (Paciphacops) serratus* and *Pac. (Paciphacops) claviger.* Spines are also developed in the *cristata* group (Eldredge, 1973; Campbell, 1977) where they "... are variably developed in related taxa and *may not* (our italics) be of much taxonomic value...(and) are probably sexually dimorphic features..." (Campbell, 1977: 33). The *cristata* group belongs to *Paciphacops (Viaphacops)* which is not closely related to the species from Limekilns. There are no substantial differences between the eyes of Limekilns specimens which might suggest dimorphism as discussed for other phacopids by (Clarkson,1966; Campbell,1977).

Paciphacops (Paciphacops) claviger differs from *Pac. (Pac.) crawfordae* in having a greater number of pygidial pleural furrows, pseudo-half rings on the pygidial axis, spines on alternating thoracic axial rings, larger eyes with 17 vertical files, granules on the tubercles, and a prominent facial suture.

Paciphacops (Paciphacops) serratus differs from *Pac. (Pac.) crawfordae* in many features, including the posterior location of the large eye $(14-17$ files, 61 lenses), the strong palpebral furrow, the facial suture described by Sherwin (1972), the moderately deep anterior vincular furrow, the spines on some pygidial axial rings, and the absence of genal and intergenal spines. There is some suggestion that the anterior 3 or 4 pygidial axial rings in *Pac. (Pac.) crawfordae* bear transverse elevations, but no nodes or spines have been observed.

Balashova (1968: 206-207, p1.54, figs 1a,b, 2) erected *Reedops serratus spiniferus* for a Ludlovian form from central Kazakhstan. The illustrated material has a small anteriorly placed eye having about 12 vertical files each having six lenses, a stubby occipital spine and apparently a short genal spine as seen in *Pac. (Pac.) crawfordae,* but no definite intergenal spine. This taxon is probably best viewed as another spinose *Paciphacops* but it may be close to *Pac. (Pac.) crawfordae;* as *Pac. (Pac.) serratus* lacks a genal spine, Balashova's specific assignment of this material is suspect. Many described Russian and Chinese phacopids are apparently known only from internal moulds, and external surfaces are crucial for the recognition of spines. A second Russian form, described by Maximova (1968: 84--85, pl.12, figs 7, 8a) as *Reedops* aff. *sternbergi,* appears to have an intergenal spine.

A further *Pac. (Paciphacops)* specimen (AMF73418a-b) has recently been collected at Queens Pinch, near Mudgee, NSW, from the Warratra Mudstone (Wright, 1966; Offenberg *et al.,* 1968) which is a deepwater unit dominated by a pelagic fauna (of slightly different aspect to that of the Rosedale Shale) and overlain by the mid-Zlichovian Sutchers Creek Formation yielding

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Polygnathus perbonus. The generic assignment is based on the weakly continuous anterior vincular furrow and a few apparently perforated glabellar tubercles; SI is poorly preserved. This incomplete and crushed specimen (Fig.5A-C) differs *fromPac. (Pac.) crawfordae* in having a genal spine placed more medially, a possible intergenal node, and a distinct facial suture. The eye has 11 vertical files and 54 lenses (ant. 3,5,5,6,6,6,6,5,5,4,2), a similar number to *Pac. (Pac.) crawfordae.* This specimen is different from Pac. *(Pac.) crawfordae*, but seemingly similar to it, and offers some support for the contention that the spinose condition of these phacopids was an

Fig.4. A-G: *Paciphacops (Paciphacops) crawfordae* n.sp., all from the Rosedale Shale (late Pragian), Limekilns district, New South Wales. A-E, Paratype AMF 73417A, A, dorsal view of Salterian molt, with cephalon and hypostoma inverted, x2. B, latex cast of cephalon, showing genal and intergenal spines, x3. C, latex cast of hypostoma, x6. D, latex cast of eye (anterior to right), xlO. E, latex cast of thorax showing spines, x2. F-G, paratype cephalon AMF 73416. F, internal mould showing genal spine and vincular furrow, x3. G, latex cast showing occipital and intergenal spines, x3. H. Paratype cephalon AMF 73412, latex cast showing glabellar furrows, x3.

adaptation to a deepwater environment. Available conodont data indicate different ages (Zlichovian, contrasted with late Pragian) for the two occurrences. However, both are in deepwater muds overlain by calcareous units containing abundant allochthonous limestone blocks; thus, reworked blocks could be yielding conodonts indicating only maximum ages.

General comments on some Australian phacopids. One of the above species *(Phacops serratus)* was revised by Sherwin (1972) along with other species described from New South Wales by Etheridge & Mitchell (1896) and Fletcher (1950). Victorian species of ?Siluro-Devonian age include the poorly known forms *Phacops sweeti* (Etheridge & Mitchell, 1896: 487, pl.38, fig.9; pl.39, figs 1-2; pl.40, fig.1O) and *Phacops mansfieldense* (Etheridge & Mitchell, 1896: 501, pl.39, fig.12). Other Phacopidae described from eastern Australia, with ages suggested herein or by the original authors, include *Phacops* n.sp. (Talent, 1963: 106, pl.75, figs 1-6; pl.76, figs 1-8), Pragian; *Phacops* n.sp. B (Talent, 1963: pl.76, fig.1O), Pragian; *Denckmannites rutherfordi* Sherwin (1969), Pridolian; *Phacops spedeni* Chatterton (1971), early Zlichovian; *Paciphacops (Paciphacops)*

Fig.5. A-C: *Paciphacops (Paciphacops)* sp., Warratra Mudstone (Zlichovian), Queens Pinch district *via* Mudgee, New South Wales, AMF 73418. A, latex cast of exterior showing genal spine, x3. B, latex cast of eye (anterior to right), xlO. C, internal mould of eye (anterior to right), xlO.

microps Chatterton, Johnson & Campbell (1979), Pragian; *Phacops serratus* (Foerste, 1888); (Holloway & Neil, 1980; Talent, 1965), latest Pridolian to early Lochkovian; *Reedops* n.sp., Jell & Holloway (1983), Pridolian; *Phacops (Phacops)* sp., Chatterton & Wright (1986), Zlichovian; and *Ananaspis ekphyma* Wright *in* Jones *et al. (1986),* Lochkovian. For the Late Silurian species, in particular, there is considerable disagreement concerning generic and subgeneric assignment (Sherwin, 1972; Campbell, 1976: fig.6); Strusz, fig.20 *in* Jenkins, 1986).

It is possible that *Pac. (Pac.) serratus* (Pridolian-Lochkovian), *Pac. (Pac.) claviger* (Siegenian), *Pac. (Pac.) crawfordae* (Pragian) and the form from the Warratra Mudstone discussed and figured here are related, and form a compact group which is spinose to a degree not seen in other stocks of phacopids. With so few occurrences a new genus cannot be justified, especially as some of the differences between the three taxa are substantial. Both Eldredge (1973) and Campbell (1977) caution that such spines are of uncertain taxonomic value, and we have no reason to dispute this. For instance, a prominent occipital spine is developed in a probably unrelated Middle Devonian species *(Geesops battidohmi* Struve, 1982).

With regard to a pattern in East Australian Early Devonian phacopids, Chatterton, Johnson & Campbell (1979) stated that *Phacops spedeni* is a 'late *Paciphacops'* transitional to true *Phacops* in having a long Ll and perforated tubercles, and a similar doublure ornament to *Pac. (Pac.) microps.* If so, spinosity may have been an early random trend seen in the Lochkovian *Pac. (Pac.) serratus* and the Pragian *Pac. (Pac.) crawfordae* which was reversed or at least absent in the Pragian *Pac. (Pac.) microps* (which has juvenile genal spines and an adult genal node) and the Zlichovian *Pac. (Pac.) spedeni* (no spines). Preservation does not permit evaluation of the position of *crawfordae* in any morphocline based on criteria relating to tubercles or ornament, as discussed by Chatterton, Johnson & Campbell (1979: 819). Dimorphism is not known in *Pac. (Pac.) microps* or *Pac. (Pac.) spedeni,* but may be present in the *serratus-crosslei* complex (Etheridge & Mitchell, 1896), as the latter two taxa differ only in the absence of thoracic and pygidial axial spines in *Pac. (Pac.) serratus.*

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