A Late Devonian xiphosuran from near Parkes, New South Wales

JOHN PICKETT

The ecdysed carapace of a xiphosuran from the Late Devonian Mandagery Sst. of central western New South Wales is described as *Kasibelinurus amicorum* gen. et sp. nov., and the Kasibelinuridae established to receive it and three other Late Devonian species from Europe and North America. Interrelationships of later Palaeozoic suprafamilial groups are discussed.

Keywords: Xiphosura, Late Devonian, Famennian, New South Wales, new taxon, *Kasibelinurus*, classification.

J. W. Pickett, Specialist Services Section, Geological Survey of New South Wales, P. O. Box 76, Lidcombe 2141, Australia; received 8 February 1993.

XIPHOSURANS are rare fossils, and reports from Australia are few (Pickett,1984). Since 1984 Ewington *et al.* (1989) described but did not name a *Paleolimulus* from the Late Permian Jackey Shale in Tasmania, and Jago & Baillie (1992) reported a Late Cambrian aglaspid from that state's northwest.

Aglaspids are no longer placed among the chelicerates (Briggs *et al.*, 1979), so the *Paleolimulus* of Ewington *et al.* (1989) is the oldest known Australian xiphosuran. The Australian specimens, including the form described here, and the Early Devonian Bolivian material (Eldredge,1974) are the only known fossil xiphosurans from Gondwana continents.

The specimen described here was discovered by workmen splitting flagstones, and was offered for sale to the Australian Museum. Many friends and colleagues made personal contributions to the purchase fund, and donations were forthcoming from the Fossil Club of Victoria and the Australian Museum Society; the generosity of all is acknowledged in the specific epithet.

Selden & Siveter (1987) advised careful distinction between divisions of the arthropod body (somites) and their dorsal meromes (tergites), and on the difficulty of relating these to external segmentation. Their usage of 'segment' as a general term, not implying relationship to a particular somite, is followed here. I also accept their classification of Xiphosura, slightly modified from that of Eldredge (1974).

Starobogatov (1990) disregarded older names of higher taxa and recent works (Fisher,1982; Briggs *et al.*,1979; Selden & Siveter,1987; references therein) in presenting a classification for the Chelicerata, including the Aglaspida, for which he needlessly introduced the superorder Strabopiformii. His various xiphosuran groups and those of Selden & Siveter (1987) appear identical (Table 1), with the single exception that the Euproopoidea is grouped with the Limuloidea (or possibly the Bellinuroidea). Structurally also there is the single difference that whereas the chasmataspids are considered separate from all other xiphosurans by Selden & Siveter, Staro-

Class **Xiphosura** Latreille 1802	Subclass **Limuliones** Starobogatov 1986
Order **Chasmataspida** Caster & Brooks 1956	Superorder **Chasmataspidiformii** Caster & Brooks 1956
Order **Xiphosurida** Latreille 1802	[same as subclass Limuliones]
Suborder **Synziphosurina** Packard 1886	Superorder **Bunodiformii** Zittel & Eastman 1913
Suborder **Limulina** Richter & Richter 1929	Superorder **Limuliformii** Richter & Richter 1929
Infraorder **Pseudoniscina** Eldredge 1974	Order **Pseudonisciformes** Starobogatov 1990
Infraorder **Limulicina** Richter & Richter 1929	Order **Limuliformes** Richter & Richter 1929
Superfamily **Bellinuroidea** Zittel & Eastman 1913	Suborder **Belinuroidei** Bergström 1975
Superfamily **Euproopoidea** Eller 1938	[included in ?Limuloidei]
Superfamily **Limuloidea** Zittel 1885	Suborder **Limuloidei** Richter & Richter 1929

Table 1. Comparison of taxa in the classifications of Selden & Siveter (1987) (left) and Starobogatov (1990) (right). The composition of the taxonomic units is identical, or at least very similar, in the two cases.
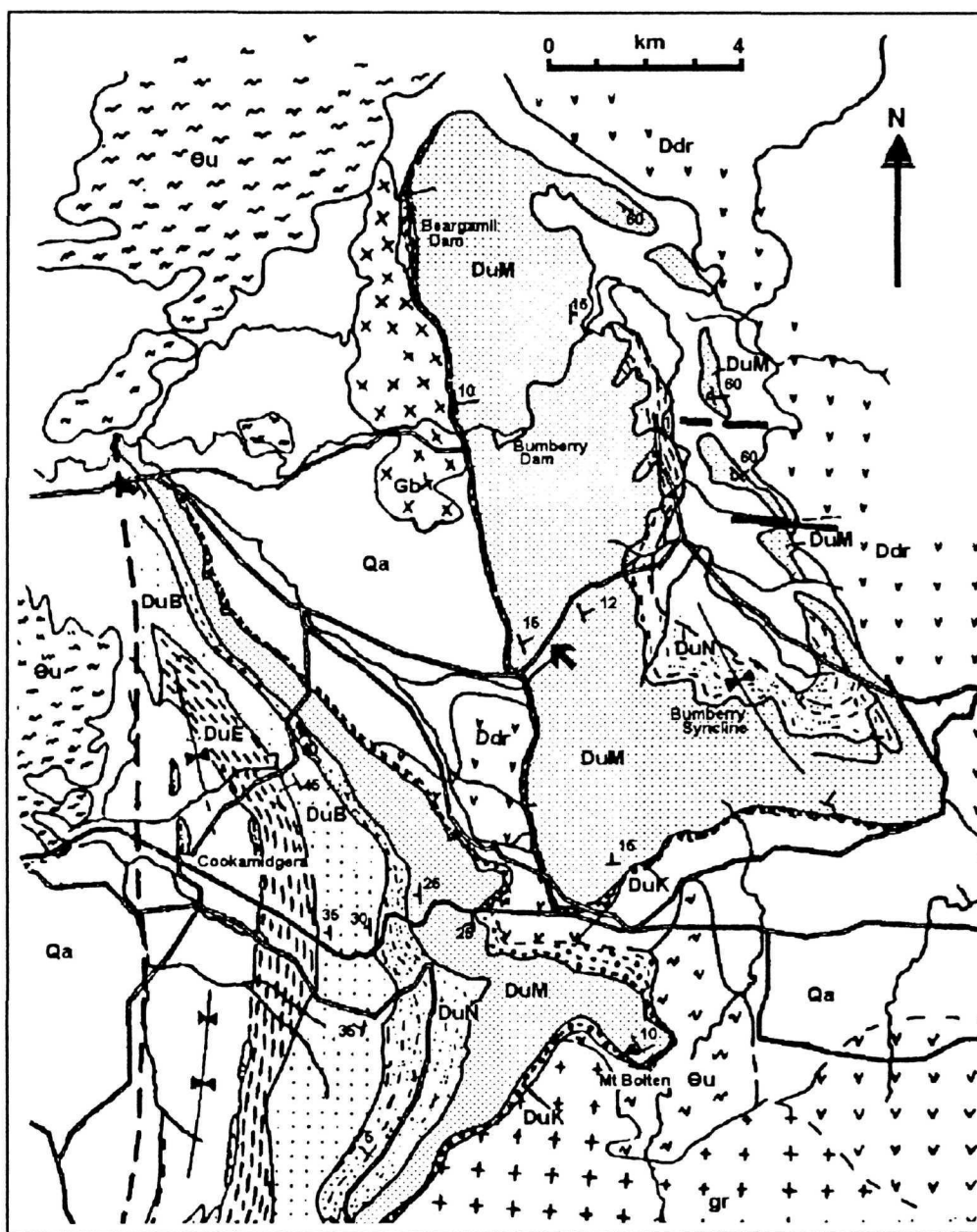
Fig.1. Geological map of the Bumberry Syncline and adjacent area, after Conolly (1965, fig.8). The type locality of *Kasibelinurus amicorum* is marked with an arrow near the centre of the figure. Qa - alluvium; DuE - Eurow Fmn; DuB - Bumberry Fmn; DuN - Pipe Fmn; DuM - Mandagery Sst.; DuK - Kadina Fmn; Ddr - Early Devonian volcanics; gr - Eugowra Granite; Gb - Bindogandri Granite; Θu - undifferentiated Ordovician sediments and metasediments.

bogatov includes them as a superorder at the same level and in the same higher group as the pseudo-niscines and limulicines. Starobogatov does not give his reasons for grouping taxa at this level, but discusses various features in a general way and presents the classification in tabular form. Since the arguments in support of the classification adopted by Selden & Siveter (1987), via the careful analyses of Eldredge (1974) and Fisher (1982,1984), are convincing, I can see no reason

for adopting either the structure or the new names suggested by Starobogatov.

Locality and age

The specimen was found a few metres south of the Orange – Parkes road, on the western slope of the Bumberry Ridges, at GR 630100 6329200, Parkes 1:50,000 sheet (8351-1-S), about 22 km E

of Parkes (148° 21' 49" E, 33° 10' 0" S) (Fig.1). The locality lies on the western flank of the Bumberry Syncline, in the lower part of the Mandagery Sst. (Conolly,1965, fig.8). The Mandagery Sst. forms part of the redbed sequence of the Hervey Group, and in this area is the second lowest of 5 formations, only the lower 3 occurring in the Bumberry Syncline. At the collecting locality are fine sandstones, siltstones and red shales. Ripple marks and mud clasts are common; plant fragments are common on some horizons, but, apart from the lepidodendroid lycopod *Leptophloeum australe* (MMF32489), none is identifiable (MMF30812–30826, Geological Survey of N.S.W. collections).

Age control on the Mandagery Sst. is poor. Conolly (1965:56) reported *Leptophloeum australe* from the overlying Pipe Fmn, c.200 m above its base; this form is typical of Late Devonian strata elsewhere in the state, although only its upper limit is well documented (Mory,1981:216) as within the late Famennian *costatus* Zone. Elsewhere the Mandagery Sst. has yielded lingulids (Etheridge,1901), and from the southern end of the same ridge an exceptional assemblage of fish (Fletcher,1956) including the arthrodire *Groenlandaspis*, the antiarchs *Bothriolepis* and *Remigolepis* (Alex Ritchie pers. comm. 1993), and the crossopterygian *Canowindra grossi* Thomson,1973. Williams (1977) described the lingulid *Apsilingula* Williams,1977 from the lowest Mandagery Sst. (Kadina Fmn of Conolly's mapping) accepting the Frasnian age proposed by Webby (1972, table 2). Samples from the limulid locality have not produced palynomorphs.

Ritchie *et al.* (1992) described the antiarch *Grenfellaspis branagani* from the Hunter Siltstone at several localities 10–15km NW of Grenfell, and listed a number of other forms from that formation. These localities lie 70km S of the limulid locality in a separate area of outcrop of Hervey Group sediments. Whereas the Mandagery Sst. east of Parkes is underlain by the Kadina Fmn, in the Grenfell area it is underlain by the Hunter Siltstone. Consequently age discussion for the fish assemblage (Ritchie *et al.*,1992) is highly relevant to the age of *Kasibelinurus*, assuming that the lithostratigraphy can be used as a basis for correlation, since they claim that '[the fauna from] the Hunter Siltstone is considerably younger than the stratigraphy indicates, and indeed may be one of the youngest Devonian vertebrate faunas known from eastern Australia' (Ritchie *et al.*,1992:363). Ritchie *et al.* (1992:363) drew on evidence from: 1, comparison of the Grenfell assemblage with that of the Worange Point Fmn, which have certain forms in common (a new species of *Groenlandaspis*, and *Bothriolepis* and *Remigolepis*). Absence of *Grenfellaspis* and presence of a crossopterygian different from that at Grenfell lead them to conclude that the Worange Point assemblage may be 'slightly older'. 2, neither assemblage includes phyllolepid placoderms, so that they are both younger than the upper limit of *Phyllolepis*. In Europe this is regarded as a reliable index for the late Famennian. 3, 'Evidence from borehole data [source unstated] in western New South Wales suggests that the *Bothriolepis – Remigolepis* assemblage approximates to the *Retispora lepidophyta* palynofloral zone of Playford (1976, 1982), which crosses the Devonian-Carboniferous boundary'.

The Worange Point Fmn conformably overlies the marine Bellbird Creek Fmn which is almost certainly part of 'a widespread Frasnian marine incursion characterized by a low-diversity *Cyrtospirifer* fauna ... recorded from many otherwise non-marine sequences in eastern Australia. Conodont data from Ettrema in southeast New South Wales (Pickett,1972 [*recte* 1973]) and the Dee Volcanics near Mt Morgan in central east Queensland (Druce,1970) confirm this transgression as *gigas* Zone, specifically upper or uppermost *gigas* Zone. We therefore connect it with the eustatic rise initiating the Johnson *et al.* (1985) T-R cycle IId' (Talent & Yolkin, 1987:242). Young (1983, fig.2) placed the Worange Point Fmn at the base of the Famennian, and this conclusion appears soundly based. If this assemblage is indeed 'slightly older' than that from Grenfell, then a latest Famennian age for the latter appears improbable, and a Carboniferous age untenable. It may well be that the *Apsilingula* locality of Williams (1977) represents the westernmost extent of the late Frasnian marine event, as Williams suggested, but for the present this is not fully substantiated.

Conclusions based on the absence of a particular form are notoriously unreliable, and there is as yet no firm indication that the European ranges of *Phyllolepis* are also valid in Australia.

A reliable correlation of the *Retispora lepidophyta* palynofloral zone and the *Bothriolepis – Remigolepis* assemblage appears unlikely, in view of the presence of *Leptophloeum australe*, which in eastern Australia ranges into the Mandagery Sst. and overlying formations (Conolly,1965). In any case, the *Retispora lepidophyta* Zone does not extend into the Carboniferous, since its upper levels are Strun-ian (Tn1a,Tn1b), now considered latest Devonian.

Further to considerations by Ritchie *et al.* (1992) *Phyllolepis, Bothriolepis, Striacanthus* and *Holoptychius* from Gingham Gap in the Her-
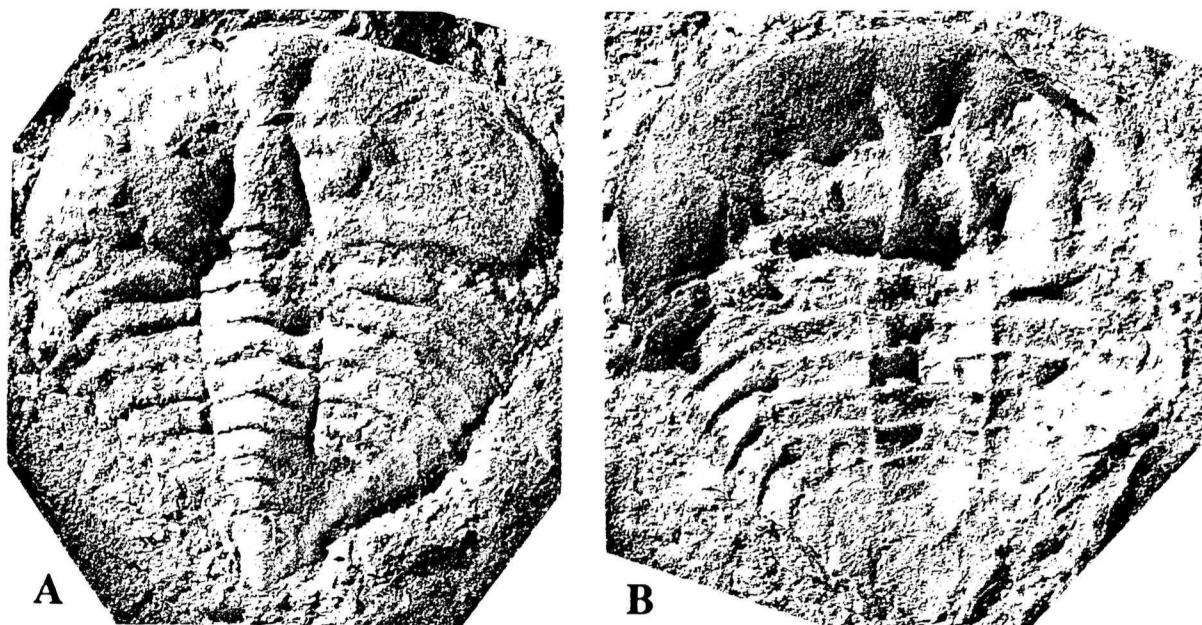
Fig.2. Kasibelinurus amicorum gen. et sp. nov., holotype, latex casts of mould of ecdysed carapace. A, external. B, internal. x1.

vey Range, 40 km north of the limulid locality (Hills,1932,1936), occur in the Caloma Sst. (Conolly,1965:51); in this area the stratigraphic succession is (oldest to youngest) Kadina Fmn, Mandagery Sst., Pipe Fmn, Caloma Sst.. Hills' determinations may no longer be regarded as up to date, but the aspect of the assemblage is nonetheless decidedly Devonian. Extrapolating from thicknesses quoted by Conolly (1965), this horizon must be at least 350m above the limulid locality, and more than that above the level of the *Grenfellaspis* assemblage.

Alex Ritchie (pers. comm. 1993) indicated that a locality high in the Bumberry Fmn, overlying the Mandagery Sst. and in the same succession NE of Grenfell as the *Grenfellaspis* assemblage, yielded a Devonian assemblage - a large antiarch and the arthrodire *Groenlandaspis*. Once again extrapolating from thicknesses given by Conolly (1965), this locality is separated by a stratigraphic interval of possibly 1000m from the limulid level, and even more from the *Grenfellaspis* level.

Consequently there can be no doubt of the Famennian age of the Mandagery Sst. and at least some of its overlying formations. An early or mid Famennian age is considered most likely for *Kasibelinurus*.

Systematic palaeontology

Order XIPHOSURIDA Latreille,1802
Suborder LIMULINA Richter & Richter,1929

Infraorder LIMULICINA Richter & Richter, 1929

Family KASIBELINURIDAE nov.

Diagnosis. Limulicina with subequal prosoma and opisthosoma; cardiac lobe defined by a strongly impressed cardiac furrow which meets the posterior margin of the prosoma opposite the anterior point of the opisthosomal axial furrow; widest point of axis posterior of first opisthosomal segment.

Remarks. In his Infraorder Pseudoniscina Eldredge (1974:37) included a group of taxa 'species of *"Bellinurus"* in which axis of opisthosoma is broader than posterior width of cardiac lobe'. The group was not listed, but is here interpreted to include *'Bellinurus' carterae* Eller,1940 (not *carteri*; Eller stated he named the species for Mrs A.L. Carter), *'B.' alleganyensis* Eller,1938a and *Bellinuroopsis rossicus* Chernyshev,1933; these forms and *Kasibelinurus amicorum* are included in the family.

Eldredge also cited as characters of the infraorder: 'axial furrows aligned with ophthalmic ridges' and 'all free opisthosomal segments with well-defined articulating half-rings'. In kasibelinurids the axial furrows are not aligned with the ophthalmic ridges, but instead with the cardiac furrows, and in *Kasibelinurus* at least there does not appear to be any development of articulating halfrings.

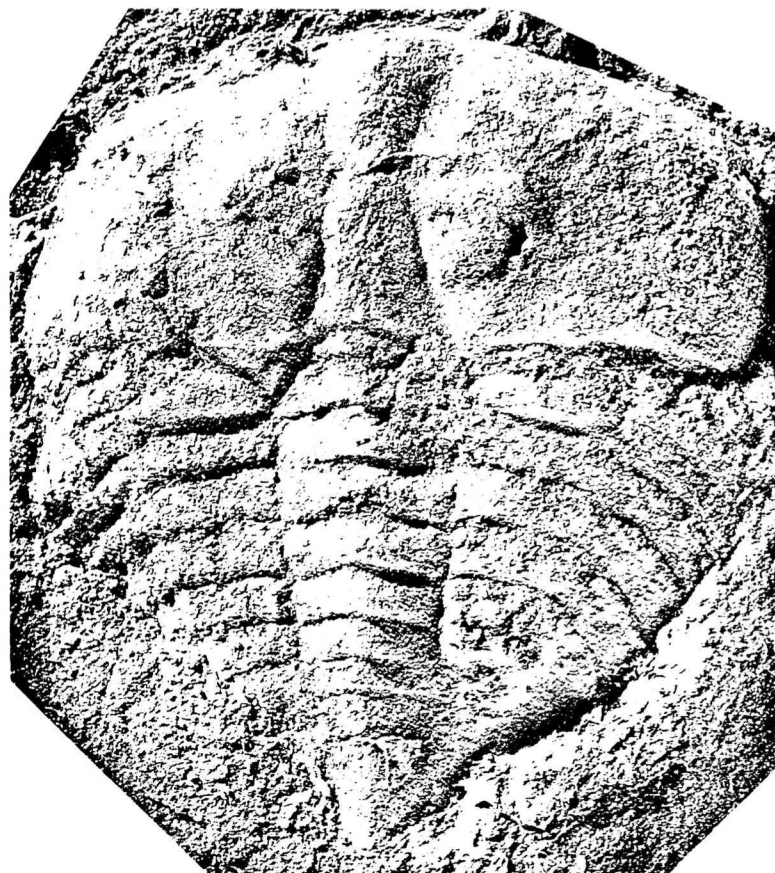In Fisher's phylogeny (1982, text-fig. 1) my Kasibelinuridae lies at the divergence of two

Fig.3. *Kasibelinurus amicorum* gen. et sp. nov., holotype, latex cast of mould of ecdysed carapace, external surface, lighting less oblique than in Fig. 2A, showing outer right pleurae in more detail. x1.5.

been newly derived from the Greek, and is not subject to this change.

Diagnosis. Ophthalmic ridges effaced; precardiac field defined by anterior prolongations of the cardiac furrows; opisthosomal pleurae with distinct inner and outer zones.

Kasibelinurus amicorum sp. nov. (Figs 2–6)

Material. The holotype and only specimen, part and counterpart, AMF68969a (lower) and b (upper); Australian Museum, Sydney.

Derivation of name. Latin *amicus*, friend, in gratitude to all contributors to the purchase fund.

Description. Prosoma and opisthosoma present but not telson. Overall length (without telson) 63mm. The genal angles of the prosoma and parts of the marginal area of the opisthosoma are not preserved, and the specimen appears to have undergone slight erosion prior to burial. There is no trace of any appendages or other features of the ventral surface, not even the doublure, and the counterpart is highly arched, indicating that the specimen is the dorsal carapace only. There is some dislocation between prosoma and opisthosoma, the former covering most of the first segment of the latter. The right pleura of the first segment seems to have been lost altogether. The left side is less well preserved than the right; there is a significant fracture running from the anterior edge of the cardiac lobe obliquely to the left lateral margin of the prosoma; a second fracture along the left lateral margin of the opisthosoma has obscured detail and caused the shortening of the pleurae by up to 3mm. There is no indication of any kind of spines, either lateral or dorsal.

Prosoma smooth, semicircular, strongly arched, steepest anteriorly, without demarcated borders. Present dimensions 60mm wide, 24mm long at the axis, at least 12mm high. Cardiac lobe elongate, subtriangular, defined by a conspicuous cardiac furrow, narrowest anteriorly, and a posterior margin which curves slightly forward. In front of the cardiac lobe is a subtriangular field (here termed the precardiac field) which broadens anteriorly, and is defined by conspicuous furrows continuous with those around the cardiac lobe. Ocelli, if present, were presumably borne on the

major clades, one leading to the modern limuloids, and the other to the euproopoids via the bellinuroids. On this basis the Kasibelinuridae would be more logically placed with the Bellinuroidea in the Infraorder Limulicina, as adopted by Fisher (1982, explanation of text-fig.1). Although placed in the Limulicina the Kasibelinuridae remains the limulicine family nearest to the pseudoniscines.

Neither '*Bellinurus*' *alleganyensis* nor '*B.*' *carterae* rests comfortably in *Bellinurus*. However, since a re-examination of the material and of *Bellinuroopsis rossicus* is necessary to evaluate their family affinities no re-assignment is undertaken here.

Kasibelinurus gen. nov.

Type species. Kasibelinurus amicorum sp. nov.

Derivation of name. Greek *kasis*, sibling; *belos*, dart; *oura*, tail, referring to the relationship to *Bellinurus*. Not: The prioity of the spelling *Bellinurus* over *Belinurus* was pointed out by Morris (1980), in which he was followed by Selden & Siveter (1987). All names of higher taxa based on *Bellinurus* require this spelling. The name *Kasibelinurus* However, has
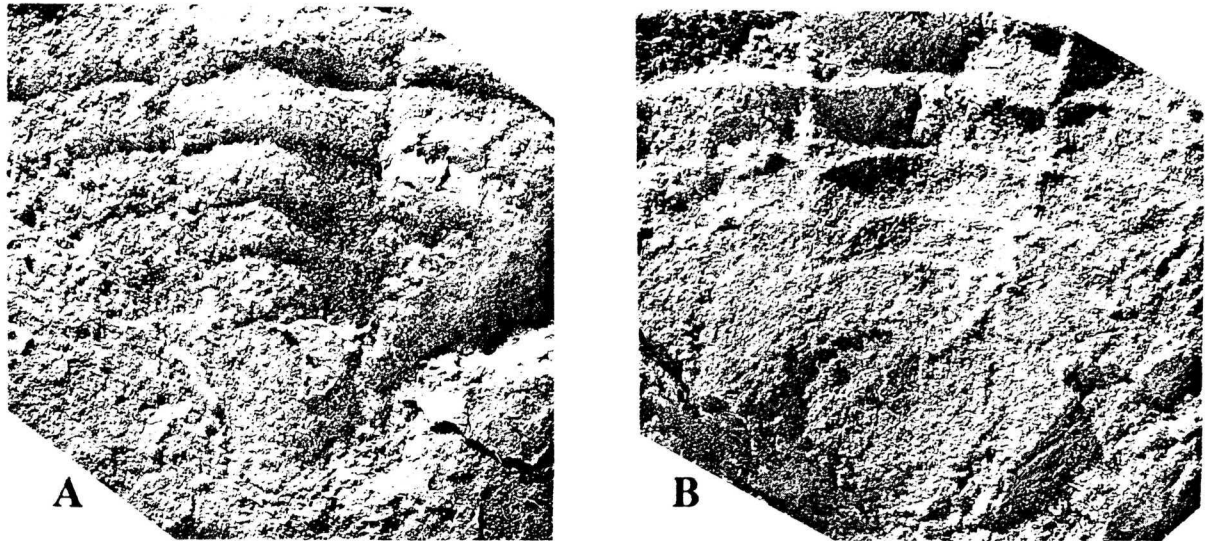
Fig.4. Kasibelinurus amicorum gen. et sp. nov., holotype, latex cast of mould of ecdysed carapace. Details of posterior segments of opisthosoma, showing crack producing the impression of a tenth segment. A, external. B, internal. x2.4.

precardiac field, but no trace of them is apparent. The compound eyes are halfway between anterior and posterior borders, 9mm from the furrow defining the cardiac lobe, and level with the front of it. The area on the axial side of the eyes is slightly higher than the rest of the cheek, and
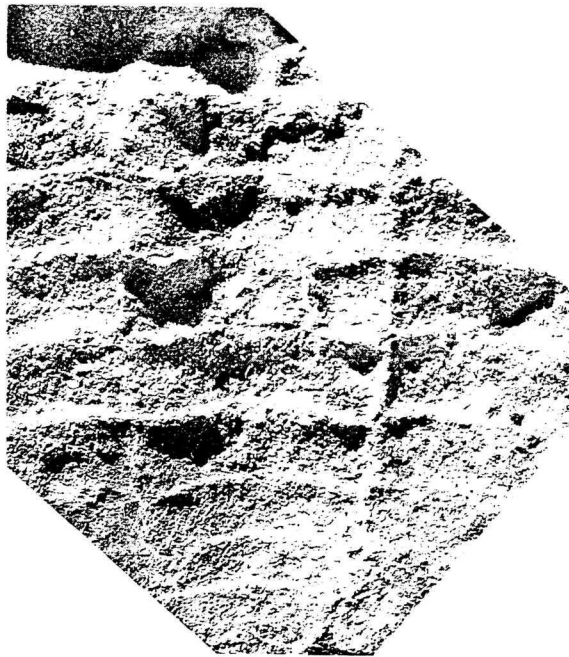

Fig.5. Kasibelinurus amicorum gen. et sp. nov., holotype, latex cast of mould of ecdysed carapace. Anterior portion of opisthosomal axis, internal view, showing short paired apodemes and absence of articulating half-rings. x2.3.

forms the highest points of the entire carapace. The compound eye lies at the anterolateral angle of an indistinctly triangular raised area, whose anterior margin lies at 90° to the sagittal direction, which gradually fades posteriorly vanishing well in front of the posterior margin, and whose inner edge is the furrow around the cardiac lobe. It is doubtful whether the margin of this raised area can be considered homologous with the limulid ophthalmic ridge, which in most taxa runs from the posterior prosomal margin and unites with its symmetrical counterpart in front of the cardiac lobe, near which point the ocelli are usually found.

Details of the visual surfaces are not preserved. The posterior margin is initially straight laterally, but with increasing curvature towards the lateral margins. Genal angles not preserved, but the remaining portions suggest that pronounced genal spines were not developed. The [biological] left genal angle on the lower counterpart is best preserved, and indicates an acute termination of slightly over 60°.

The opisthosoma is subtriangular, divided into axis and pleurae, and consists of 9 articulated segments. The posterior segment bears a transverse depression across the axis, which initially suggested an ankylosis of segments 9 and 10; however, on the lower counterpart this depression is seen to be a crack (Fig.4), so the apparent 10th segment is an artefact. Maximum left-right dimensions of axis and pleurae are 14mm and 24mm on opisthosomal segment 2. The axial segments are curved forward at the midline, with a curved profile which is highest
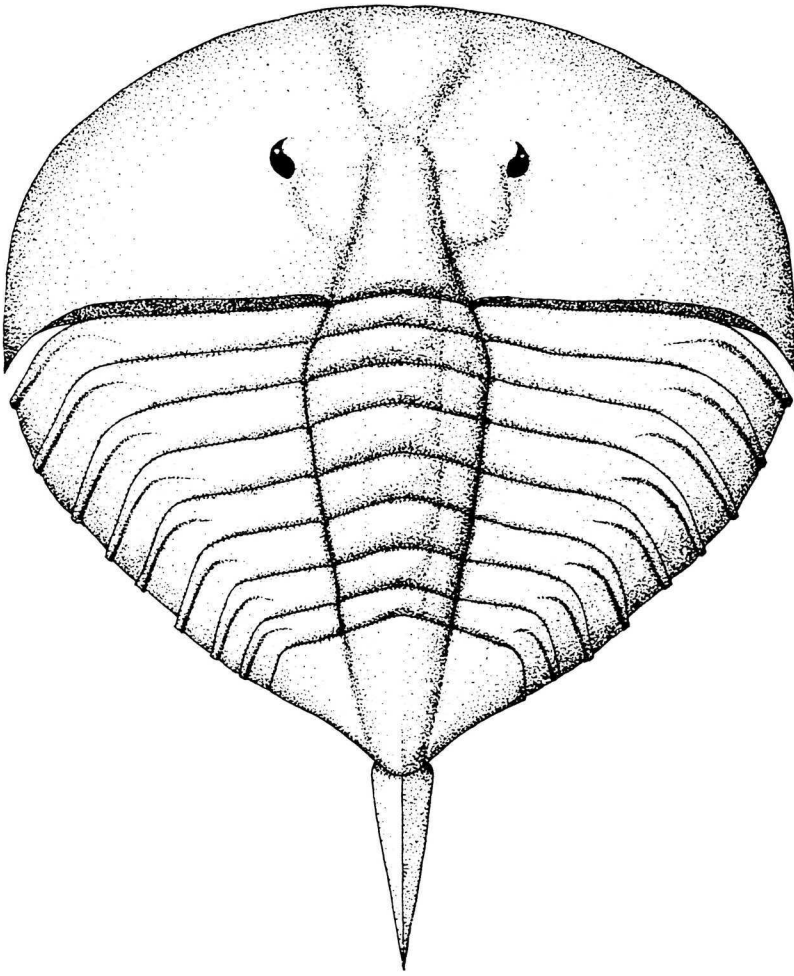
The lower counterpart indicates paired apodemes on the anterior margins of the opisthosomal segments, c. 1mm inside the axis on the largest segments, and c. 1mm in width (Fig.5). Details of their morphology are not preserved. There appear to be no articulating halfrings (Figs 4B,5).

Remarks. Restricted movement of the telson and lack of fusion in posterior segments of the opisthosoma represent the primitive condition of a functionality-driven evolutionary mechanism (Fisher, 1981,1982); Fisher proposed that the fusion of opisthosomal segments was associated with greater versatility of movement of the telson, since it allowed attachment of muscles controlling the telson in more anterior segments of the opisthosoma. A successful righting mechanism for overturned animals has been important in development of most xiphosuran clades.

The ridged final segment of the opisthosoma of *K. amicorum* hints at a telson with squat triangular cross section, either of the type considered primitive by Fisher (1982:178, text-fig.2A) or that illustrated for 'advanced Belinuracea' (text-fig.2D). The shape of the posterior end of the opisthosoma suggests that the telson was restricted in its movability, any upward movement being precluded by the blunt point on the axis. In contrast, articulating facets of the pleurae on the opisthosoma indicate that Kasibelinurus was capable of a fair degree of enrollment (ventroflexion. This means that the righting strategies of co-aptative forms such as *Euproops* or similarly ankylosed forms (all the limuloids), which require a large cone of movement for the telson, are not of major importance in the activities of *Kasibelinurus*. The bluntly pointed termination of the final opisthosomal segment indicates reduced movability of the telson, and this, together with the flexibility of the opisthosoma, suggests that there was little require-

Fig.6. Kasibelinurus amicorum gen. et sp. nov., reconstruction of animal, x1.5. Telson is hypothetical. Drawn by Roger Springthorpe, Australian Museum, Sydney.

nearer the posterior margin. The final axial segment develops a low median angulation on its posterior half, which is not otherwise raised above the rest of the segment. The final segment appears to have terminated in a blunt point, without any embayment to accommodate the telson. There is no suggestion that any part of the carapace is missing in this area. The pleurae are divided into distinct inner and outer zones of subequal width, demarcated in the outer zone by a downward flexure of the dorsal surface, an increase in posterior deflexion of the segments, and an articulating facet on the posterior margin. In the inner zone their profile is flat anteriorly, rising evenly to the highest point near the posterior margin; the second opisthosomal segment differs from those behind it in its symmetrical and slightly greater curvature.

ment for an elongated telson. The differing profiles of prosoma (semicircular) and opisthosoma (triangular) indicate that in the enrolled condition there was not a close coincidence of their margins. The opisthosoma is roughly 1.5 times the length of the prosoma, and its final segment is longer than all the others; allowing for most of the movement to be taken up on the more anterior segments of the prosoma, the more posterior segments would have been capable of covering most of the ventral surface of the prosoma, though it is unlikely that the ends of all appendages would have been concealed during flexure.

Affinities. Apart from the Early Devonian synziphosurines *Weinbergina opitzi* Richter & Richter and *Legrandella lombardi* Eldredge, the only known Devonian xiphosurans are *Bellinurus kiltorkensis* Baily 1869, '*B.*' *alleganyensis* Eller 1938a, '*B.*' *carterae* Eller 1940, *Bellinuroopsis rossicus* Chernyshev 1933, *Elleria morani* (Eller 1938b) and *Paleolimulus randalli* (Beecher 1902). The first of these is a minute form, the published illustrations of which suggest that the type material might include two genera. The prosoma has a well marked border, thus differentiating it from *K. amicorum*; details of the opisthosoma are not preserved. In *Elleria* the opisthosoma is fused to a thoracetron. The opisthosoma of *P. randalli* is not known, but if Fisher's (1982) placement in *Paleolimulus* is correct (? following Størmer, 1955), it too must have had fused segments. In '*Bellinurus*' *alleganyensis*, '*B.*' *carterae* and *Bellinuroopsis rossicus* the cardiac lobe is defined by a pronounced furrow, the dominant feature of the prosoma, which diverges to meet the posterior edge of the prosoma opposite the axial furrows of the opisthosoma. In all these species the ophthalmic ridges are recognisable, in the case of '*B.*' *alleganyensis* and *B. rossicus* quite pronounced, meeting in front of the cardiac lobe. Thus a cardiac lobe defined by a strong furrow is a common feature of Late Devonian limulicines, though none of those so far described has the precardiac field of *Kasibelinurus*. '*B.*' *alleganyensis* and '*B.*' *carterae* both have the genal angles produced into broad spines which extend posteriorly for at least half the length of the opisthosoma. Of these forms, only *B. rossicus* appears to have the two distinct zones of pleurae shown by *K. amicorum*. Published photographs of the holotype of *B. rossicus* (Chernyshev,1933, pl.1, fig.1 was reproduced by Eller,1938a, pl.14, fig.8) appear to indicate articulating facets on the posterolateral margins of the pleurae, at least superficially similar to those of *K. amicorum*, so that there is some differentiation across the

pleurae in the former. In *K. amicorum* this differentiation is related to the strong profile of the animal, as is probably also the case in the Russian species (deep shadow on right of figures). It is possible that the long, broad pleural spines of '*B.*' *carterae* could be homologous with the outer pleural zone of *K. amicorum*. However, if this homology were valid a doublure would be expected to extend to the inner edge of the outer pleural zone of *K. amicorum* but this has not been observed (but see discussion below).

The 9 segments on the opisthosomal axis in *Kasibelinurus* appears to be the primitive number for kasibelinurids, and the apparent absence of fusion in *Kasibelinurus* is also considered a primitive condition. (A critical review of these features, re-interpreting the original material, could prove useful in defining lines of descent in this group and the Carboniferous bellinuroids). Eller reported that the opisthosoma of '*B.*' *alleganyensis* consists of 6 free and 2 fused segments. However, his illustrations (Eller,1938a, pl.9, figs 1,2) suggest that there could be 9 segments; these seem to be clear along the axis, but I cannot comment on the degree of fusion. The last 3 segments of the holotype appear to be partly enrolled. '*B.*' *carterae* seems to have had 8, so there may have been fusion of two segments. The first opisthosomal segment is broader than the others, but if this indicates ankylosis then the species is unusual among bellinuroids, in which it occurs typically in the posterior segments. The opisthosoma of *B. rossicus* has 8 axial segments, of which the last seems to represent a double segment (cf. Selden & Siveter,1987, fig.1E).

Absence of doublure. The prosoma is highly vaulted and its cracking rather than folding during compression suggests that it was strongly sclerotised. In comparison to the opisthosoma it gives the impression of solidity. If, therefore, a doublure had been present on such a solid structure, it seems unlikely that it could have been eroded to leave a clean margin, on both prosoma and opisthosoma. In *Limulus* ecdysis proceeds via an anterior marginal ecdysial suture, and a similar suture of much greater extent could explain the apparent absence of doublure in *Kasibelinurus*. Complete absence of doublure seems unlikely, from anatomical necessity.

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