

Xiphosurid from the Upper Permian of Tasmania confirms Palaeozoic origin of Austrolimulidae

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ABSTRACT

Representatives of Austrolimulidae exhibit the most extreme morphological variation documented within true horseshoe crabs. Relative to the more standard morphologies of paleolimulids and limulids, austrolimulids have been described as oddball taxa. Despite their unique morphologies, austrolimulid diversity is somewhat understated. A horseshoe crab specimen from the Upper Permian Jackey Shale of Tasmania described in Ewington et al. (1989) is reconsidered here to develop the recent increased interest in the family. The specimen was originally assigned to *Paleolimulus* sp., but an array of unique features suggests it belongs within Austrolimulidae and *Tasmaniolimulus patersoni* gen. et sp. nov. is erected herein. Parsimony-based phylogenetic analyses support such a placement of *T. patersoni* in Xiphosurida and show that the new taxon is located at the base of Austrolimulidae. Furthermore, landmark-based geometric morphometric analyses corroborate the erection of the new taxon and illustrate a more extensive occupation of morphospace by austrolimulids than previously observed. Further studies of the paraphyletic genus *Paleolimulus* are needed to highlight the true diversity of austrolimulids and paleolimulids.

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INTRODUCTION

Horseshoe crabs are one of the most wellstudied marine chelicerate groups. The interest in xiphosurids reflects their unique array of biological and physiological features (Shuster Jr., 1982; Bicknell et al., 2018a–c), an exceptional fossil record that spans the Lower Ordovician to today (Rudkin and Young, 2009; Van Roy et al., 2010, 2015; Bick-

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nell et al., 2019a), and the exhibition of evolutionary conservation since the Jurassic (Kin and Błażejowski, 2014; Bicknell et al., 2019b, c; d). Curiously, fossil horseshoe crab species numbers remained generally low across the Phanerozoic. However, there were two pulses of expansion, the first during the Pennsylvanian (Moore et al., 2007; Rudkin and Young, 2009) and a second during the Triassic (Bicknell et al., 2019a). During the Triassic, a family of xiphosurids with extreme morphologies-Austrolimulidae-diversified. Lamsdell (2016) suggested that the group had a mid to late Palaeozoic origin. As such, further examples of these oddball taxa may help fill in the gap between the Palaeozoic onset and the Triassic diversification event.

Australian fossil horseshoe crabs are currently represented by five taxa: Kasibelinurus amicorum Pickett, 1993, from the Upper Devonian Mandagery Sandstone, New South Wales (NSW); Paleolimulus sp. Ewington Clarke, and Banks, 1989, from the Upper Permian Jackey Shale, Tasmania; Austrolimulus fletcheri Riek, 1955, from the Middle Triassic Beacon Hill Shale, NSW; Dubbolimulus peetae Pickett, 1984, from the Middle Triassic Ballimore Formation, NSW and Victalimulus mcqueeni Riek and Gill, 1971, from the Lower Cretaceous Korumburra Group, NSW. Recent phylogenetic analyses highlighted that both A. fletcheri and D. peetae are austrolimulids (Lamsdell, 2016) and that Paleolimulus Dunbar, 1923, was a paraphyletic group (also see comments in Anderson and Selden, 1997, Babcock and Merriam, 2000, and Allen and Feldmann, 2005), such that select Paleolimulus species were austrolimulids. In light of these recent developments, I have reconsidered Paleolimulus sp. from the Jackey Shale to determine if this taxon is an austrolimulid, as suggested in Lerner et al. (2017). I remove the taxon from the family Paleolimulidae and the genus Paleolimulus, instead treating it as Tasmaniolimulus patersoni gen. et sp. nov.-a representative of Austrolimulidae.

MATERIAL AND METHODS

The single studied fossil specimen was originally described by Ewington et al. (1989) from an outcrop of the Jackey Shale. This is a formation within the Upper Parmeener Supergroup that preserves non-marine swamp, lake, and river deposits that may have experienced limited coastal influence (Banks, 1973; Ewington et al., 1989). The specimen was found close to the top of the Jackey Shale, 3 m from the base of the overlying Ross Sandstone at Poatina (Figure 1, 41°48'05"S 146°53'06"E; Ewington et al., 1989). The specimen (UTGD 123979) is housed at the Rock Library and Geological Museum of the University of Tasmania (UTGD), Hobart, Tasmania, Australia. The fossil is preserved as a slightly domed internal mould without cuticle or a counterpart, on a slab of dark-yellow shale. UTGD 123979 was coated with ammonium chloride sublimate and photographed under LED lighting with a Canon EOS 5DS housed at the University of New England, Armidale, NSW, Australia. Images were stacked using Helicon Focus 7 (Helicon Soft Limited) stacking software. Description of UTGD 123979 hereinfollows the systematic taxonomy of Lamsdell (2013, 2016) and anatomical terms presented in Bicknell et al. (2018a, 2019a) and Bicknell and Pates (2019). The specimen was measured using the measuring tool in ImageJ. This approach was used to derive the most accurate length and width values of the specimen.

A geometric morphometric analysis using the method in Bicknell et al. (2019a) was conducted to quantitatively assess where UTGD 123979 is located in morphospace relative to other taxa. Contrasting Bicknell et al. (2019a) who used semilandmarks and landmarks, here only a landmark analysis of 21 specimens was conducted. The species considered are from the families Austrolimulidae and Paleolimulidae (sensu Lamsdell, 2016 and Lerner et al., 2017). Landmarking was conducted using the Thin-Plate Spline (TPS) suite (http:// life.bio.sunysb.edu/morph/index.html). A TPS file was constructed using tpsUtil64 (v.1.7). The TPS file was imported into tspDig2 (v.2.26), which was used to place nine landmarks on the right cephalothorax (Supplementary Figure 1, Supplementary Table 1). Points are digitised as xy coordinates. Where the right side was poorly preserved, the left side was used instead, and the data mirrored. These points populated the TPS file with landmark data (Supplementary Information 1). The TPS file was imported into R. The 'geomorph' package (Adams and Otárola-Castillo, 2013) conducted the Procrustes Superimposition and Principal Components Analysis (PCA) of the data. Procrustes Superimposition standardises for size and orientation so that only shape variation was assessed. Only the first two Principal Components (PCs) were considered as they explain 69.9% of the variation in the data (Supplementary Information 2). It is important to note that results of geometric morphometric analyses can be impacted by taphonomy. However, Bicknell et al. (2019a) highlighted



FIGURE 1. Position of the fossil locality (yellow star) within the Jackey Shale at Poatina (41°48'05"S 146°53'06"E). **1.** Outline map of Australia. **2.** Outline map of Tasmania, red box shows studied area. **3.** Area about the specimen locality. Geological data based on the map presented in Blake et al. (1956).

that the preservational mode of fossil horseshoe crabs does not impact the distribution of specimens in PC space. Finally, the generic and family assignment follows notes in Lamsdell (2016) and Lerner et al. (2017).

To evaluate the phylogenetic position of Tasmaniolimulus patersoni gen. et sp. nov., the taxon was coded into the matrix of Lamsdell (2016). This matrix contains a range of fossil and extant euchelicerates (Supplementary Information 3). The analwas performed under ysis equal-weights parsimony in TNT 1.5 (Goloboff and Catalano, 2016) and the "New Technology" tree search strategy using the default settings for searches, tree fusing, and drifting, together with 1000 iterations of the parsimony ratchet. All multistate characters were considered unordered, just as in the original analysis.

SYSTEMATIC PALAEONTOLOGY

Subphylum CHELICERATA Heymons, 1901 Order XIPHOSURIDA Latreille, 1802 Suborder LIMULINA Richter and Richter, 1929

Family AUSTROLIMULIDAE Riek, 1955 Genus *Tasmaniolimulus* gen. nov.

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Etymology. Generic name *Tasmaniolimulus* is suggested as the specimen is from the Australian state of Tasmania and *Limulus* is the genus of the iconic extant North American horseshoe crab.

Type species. *Tasmaniolimulus patersoni*, type and only species.

Diagnosis. Austrolimulid with genal spines extending posteriorly to the terminus of the thoracetron, without substantial splay; a prominent M-shaped terminus to the ophthalmic ridges, and thoracetron smaller than cephalothorax.

> *Tasmaniolimulus patersoni* sp. nov. Figures 2 and 3

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1989	<i>Paleolimulus</i> sp. Ewington et al., p. 128, fig. 1.
1993	Paleolimulus sp. Selden, p. 12.
2003	Paleolimulidae Itow et al., fig. 7.
2005	Paleolimulus sp. Allen and Feldmann, p. 594.

2013 *Paleolimulus* sp. Lamsdell et al., p. 344.



FIGURE 2. *Tasmaniolimulus patersoni* gen. et sp. nov., holotype (UTGD 123979). **1.** Complete specimen. **2.** Close-up of the left side of the cephalothorax showing the two cephalothoracic appendages preserved as impressions (white arrows), enlarged anterolateral spine on the free lobe (black arrow), and indentation in genal spine (grey arrow). Only the distal sections of the appendages are preserved. **3.** Close-up of right side of cephalothorax showing indentation along the genal spine (white arrow). **4.** Close-up of cephalothorax showing prominent interophthalmic and ophthalmic ridges, and 'M'-shaped terminus of ophthalmic ridges. **5.** Close-up of thoracetron showing expression of apodemal pits and pronounced axial ridge. Specimen was coated with ammonium chloride.



FIGURE 3. Reconstruction of *Tasmaniolimulus patersoni* gen. et sp. nov. Telson length is based on length preserved in other taxa. Reconstruction credited to Katrina Kenny.

2017 *"Paleolimulus"* sp. Lerner et al., p. 294.

Diagnosis. Same as for genus.

Etymology. The trivial name *patersoni* was chosen in recognition of John R. Paterson who has contributed extensively to Australian arthropod palaeontology and xiphosurid research across his career. **Holotype.** UTGD 123979. The specimen is preserved on a slab of dark-yellow shale as an internal mould with a small degree of relief.

Description. UTGD 123979 is an articulated cephalothorax and partial thoracetron without a telson preserved as an internal mould (Figures 2, 3). Specimen is 24.14 mm long, slightly domed, with a prominent axial ridge. Cephalothorax preserved well on both sides, parabolic in shape, and 16.9 mm long at midline. Cephalothoracic width across the posterior margin of lateral rims 23.8 mm. A cephalothoracic rim is preserved along margins and attains a greatest width of 0.83 mm. Left side of cephalothoracic doublure is partly preserved and visible. Ophthalmic ridges 14 mm long, pronounced, with slight concavity towards lateral borders, converging anteriorly to form an 'M'-shaped terminus (Figure 2.1, 2.4). A putative lateral compound eye is discerned on the left ophthalmic ridge, 4.46 mm anteriorly from the posterior cephalothoracic boarder. A pronounced cardiac lobe is noted. Lobe is 5.55 mm wide posteriorly, tapering anteriorly into a triangular shape with a width of 1.37 mm. Cardiac lobe has a medial ridge that is 13.9 mm long. Interophthalmic ridges bordering the cardiac lobe are 11.43 and 11.31 mm long (left and right, respectively). Ocelli are not observed. Both genal spines are preserved, but the posterior edge of right genal spine is broken. Left genal spine is 11.24 mm long and terminates posteriorly of the thoracetron end. Genal spine tip is 12.4 mm from the sagittal line. Angle between the left genal spine and left side of the thoracetron is 59°. Inner margin of the left genal spine is curved slightly anteriorly, with a small indentation in the first fifth of the spine length (Figures 2.2, 3). Right genal spine 4.7 mm long, terminating at rock edge, half way along thoracetron (Figure 2.3). Angle between right genal spine and right side of thoracetron 64°. Inner margin of the right genal spine is curved slightly anteriorly, with small indentation within the first fifth of the spine length (Figure 2.3). Hinge between cephalothorax and thoracetron is pronounced, 12.4 mm wide and has a thickness of 0.3 mm. Impressions of distal sections of walking legs, likely the tibiotarsus and dactylopodite, are preserved on the left side of the cephalothorax (Figure 2.2).

Thoracetron trapezoidal, at least 6.74 mm long and 9.96 mm wide anteriorly, increasing to a width of 12.7 mm at 2 mm along the thoracetron (Figure 2.5). Increase in width is associated with a possible anterolateral spine and extension of a free lobe (Figure 2.2). Thoracetron then tapers to at least 3.65 mm posteriorly. Thoracetron is less wide and shorter than cephalothorax. Right side of the thoracetron preserved more completely than left. Axial lobe present, triangular in shape, tapering from 5.59 mm anteriorly to 3.14 mm posteriorly. At least five segmentary axial furrows are visible, ranging between 0.98 and 1.3 mm in length. At least five, possibly six, pairs of apodemal pits are visible (Figure 2.5). Medial ridge present, 6.61 mm in length. Left pleural lobe has limited relief and no segments, 3.16 mm wide anteriorly, tapering to 1.16 mm posteriorly. Marginal rim not preserved. Right pleural lobe wider than the left, 3.6 mm wide anteriorly, tapering to 1.16 mm posteriorly. No segmentation noted. Marginal rim present and is 0.55 mm wide along its length. No evidence of movable or fixed spines. Telson not preserved.

Remarks. UTGD 123979 was originally considered a paleolimulid by Ewington et al. (1989). They compared UTGD 123979 to Paleolimulus and Limulitella Størmer, 1952, and noted that the parabolic cephalothorax was twice as long as the thoracetron, a condition unique to the taxon and potentially indicative of a new genus. Advances in horseshoe crab taxonomy, morphometrics, and phylogeny highlight that this specimen is indeed representative of a unique genus as explored in Lerner et al. (2017). The feature that excludes UTGD 123979 from Paleolimulidae, and relates the specimen to Austrolimulidae, is the overdevelopment of the genal spines that terminate near the level of the telson (Lerner et al., 2017). Such genal spine development is not known in limulids or paleolimulids, but is observed in select belinurids (Haug et al., 2012; Haug and Rötzer, 2018). However, the completely fused thoracetron and lack of ophthalmic spines precludes the assignment of UTGD 123979 to Belinuridae. Additional characteristics that UTGD 123979 exhibits supporting an austrolimulid assignment are pronounced apodemal pits and absence of fixed spines. Furthermore, the thoracetron in UTGD 123979 is half the size of the cephalothorax, a feature known in Dubbolimulus peetae and Austrolimulus fletcheri. This difference in cephalothorax and thoracetronic size is related to the austrolimulid tendency towards reduction or accentuation of the xiphosurid body plan. Finally, UTGD 123979 has an array of unique characteristics relative to other austrolimulids that warrant the erection of Tasmaniolimulus patersoni gen. et sp. nov. These features are the posteriorly projected genal spines with a slight indentation, comparable to Sloveniolimulus rudkini Bicknell, Žalohar, Miklavc, Celarc, Križnar, and Hitij, 2019, and the notable absence of the swallowtail feature, the condition where posteriormost fixed thoracetronic spines "are swept back and elongated" into a swallowtaillike morphology (Lamsdell, 2016, p. 185). Finally, the assignment of UTGD 123979 to the new genus and to Austrolimulidae is supported by geometric morphometric results (discussed below).



FIGURE 4. Xiphosurids in PCA space. Austrolimulids occupying almost all parts of PC space, except the most positive PC1 space. *Tasmaniolimulus patersoni* gen. et sp. nov. falls at the extreme edge of the convex hull occupied by Austrolimulidae.

Occurrence. The species is known only from its type locality: Jackey Shale at Poatina, 41°48'05"S 146°53'06"E, 3 m below the Ross Sandstone; Upper Permian.

GEOMETRIC MORPHOMETRICS

The PCA plot shows how PC1 (45% shape variation) describes the posterior extension of the most distal genal spine point (Landmark 3, see Supplementary Figure 1) relative to the cephalothorax (Figure 4). Austrolimulus fletcheri is therefore located in distinctly negative PC1 space. PC2 (24.9% shape variation) describes the lateral extent of the outer-most cephalothoracic edge relative to the sagittal line (Landmark 2, see Supplementary Figure 1) and the lateral extent of the posterior edge of the ophthalmic ridge relative to the sagittal line (Landmark 8, see Supplementary Figure 1). UTGD 123979 is located in a PC1 space of ~0 (PC1 = -0.01) and a slightly negative PC2 space (PC2 = -0.14) (Figures 4, 5). The genus falls within the outer limits of the shape space occupied

by austrolimulids (as defined by the convex hull around austrolimulid specimens in PC space) (Figure 4) and outside the limits of the other genera when considering the generic distribution of specimens (Figure 5).There is an overlap between *Paleolimulus* taxa and *Limulitella*. Furthermore, *Dubbolimulus peetae* is located within the *Paleolimulus* convex hull.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis resulted in five most parsimonious trees (CI: 0.473, RI: 0.880). The topology of the strict consensus tree is similar to those in Selden et al. (2015), Lamsdell (2016) and Bicknell et al. (2019d) (Figure 6). *Tasmaniolimulus patersoni* gen. et sp. nov. is resolved as the earliest diverging representative of a monophyletic Austrolimulidae (sensu Lamsdell, 2016), superseding *Panduralimulus babcocki* Allen and Feldmann, 2005, at the base of the clade. No other changes are noted.



FIGURE 5. PCA plots showing morphospace occupied by xiphosurid genera. Xiphosurid genera are bound by convex hulls. *Tasmaniolimulus patersoni* gen. et sp. nov. is not bound by any convex hull, excluding the specimen from other genera.

DISCUSSION

The morphometric, phylogenetic, and systematic assessments presented here confirm that Tasmaniolimulus patersoni gen. et sp. nov. is a valid taxon and as such represents the oldest described Gondwanan austrolimulid (Lerner et al., 2017), increasing the diversity of Australian austrolimulid genera, and indeed species, to three. These results have also built on Lamsdell (2016) and Lerner et al. (2017) to confirm that Paleolimulus has been somewhat treated as a waste-basket genus. Taxa within this paraphyletic genus that exhibit accentuated or diminished features (see discussion in Lerner et al., 2017) are therefore in need of revision. This research effort will undoubtedly impact the phylogenetic construction of Austrolimulidae and, more broadly, Xiphosurida.

The erection of *Tasmaniolimulus patersoni* gen. et sp. nov. confirms the thesis that austrolimulids had a Palaeozoic origin and diversified during the Triassic—an event that occurred concurrently with the limulid diversification (Lamsdell, 2016; Lerner et al., 2017; Bicknell et al., 2019a). The austrolimulid radiation likely reflects the exploration and exploitation of freshwater environments (Lamsdell, 2016). It seems plausible that the larger genal spines characteristic of the family might have reduced the impact of uni-directional currents in freshwater flow regimes (Anderson, 1996), but may

also have aided in sub-aerial activity or selfdefence (Fisher, 1979). In the case of *T. patersoni* gen. et sp. nov., the austrolimulid would have experienced an extreme limit of freshwater conditions by inhabiting the glacial climatic regime of Tasmania in the Late Palaeozoic (Ewington et al., 1989).

Geometric morphometric analyses have previously been applied effectively to explore horseshoe crab evolution (Bicknell et al., 2019a). The preliminary geometric morphometric results of Bicknell et al. (2019a) illustrated mathematically how extreme the austrolimulid morphologies are when compared to other xiphosurid families. This same study also noted that if the definition of austrolimulids was changed, for example to follow definitions in Lamsdell (2016) and Lerner et al. (2017), the morphospace occupied by the family would require reconsideration. Here, I have shown that with a broader definition of the family, austrolimulids are far more diverse than previously considered. This broader definition has highlighted that geometric morphometric analyses of horseshoe crabs produce far more complex results than Bicknell et al. (2019a) had originally suggested and a degree of caution is needed when interpreting these outcomes. Alternatively, the exclusion of semi-landmarks in my analysis resulted in more overlap between groups. Future research should exploit both landmarks and semi-landmarks. Nonetheless,



FIGURE 6. Xiphosurid phylogeny colour coded for major families. *Tasmaniolimulus patersoni* gen. et sp. nov. (in bold) is located at the base of Austrolimulidae. Other clades coded into this phylogenetic matrix were not presented as they are not changed from Lamsdell (2016) and do not relate directly to the research presented herein. Abbreviation: Pal.=Paleolimulidae. Reconstructions courtesy of Stephen Pates.

the overlap with Paleolimulidae and Austrolimulidae confirms that a careful reconsideration of paleolimulids is needed, as discussed above. In this context, one consideration is given to Dubbolimulus peetae. Originally placed into its own genus, Dubbolimulus, the species has also been placed within Paleolimulus (sensu Hauschke and Wilde, 1987, and Dunlop et al., 2019) but has been resolved within Austrolimulidae in phylogenetic analyses (Lamsdell, 2016). The geometric morphometric results presented here show that the taxon falls within the Paleolimulus morphospace, suggesting that the taxon could indeed be a paleolimulid. However, D. peetae has a much smaller thoracetron compared to the cephalothorax (see comments in Lerner et al., 2017). This reduction of body elements is typical of Austrolimulidae and, as such, D. peetae is most likely an austrolimulid (sensu Lamsdell, 2016, Figure 6). An extension of the geometric morphometric analyses that might highlight and explore this distinction is the inclusion of thoracetron data, an area of future research in the taxonomy of Xiphosurida. This new direction may also produce more distinct differentiations in morphospace and potentially uncover even more interesting evolutionary patterns exhibited by this iconic group of marine chelicerates.

CONCLUSIONS

Revision of a horseshoe crab specimen from the Late Permian of Tasmania has highlighted the need for a new taxon. The combination of systematic palaeontology, phylogenetic analyses, and geometric morphometrics was therefore used to erect *Tasmaniolimulus patersoni*. This taxon confirms the Palaeozoic origin of Austrolimulidae and illustrates new examples of curious morphologies for which the family is known. Further revision of *Paleolimulus* will undoubtedly result in the description of more austrolimulids. This research direction is key for uncovering the true diversity of these oddball xiphosurids.

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SUPPLEMENTARY MATERIAL

SUPPLEMENTARY FIGURE 1. Depiction of landmark placement. Reconstruction courtesy of Stephen Pates.



SUPPLEMENTARY TABLE 1. Table of landmarks used for the geometric morphometric analysis. When the right cephalothoracic side was not preserved, the left side of the cephalothorax was digitised and the data were reflected.

Landmark number	Description
Number 1	Most anterior section of cephalothorax
Number 2	Most lateral extent of right cephalothoracic edge
Number 3	Most distal point of genal spine
Number 4	Most posterior point of right ophthalmic ridge
Number 5	Most anterior point of right ophthalmic ridge
Number 6	Most anterior point of right interophthalmic ridge
Number 7	Most right lateral extent of cephalothoracic-thoracetronic hinge
Number 8	Most posterior point of right interophthalmic ridge
Number 9	Most posterior point of cephalothoracic midline

SUPPLEMENTARY INFORMATION 1. The TPS file of analysed specimens (available at https://palaeo-electronica.org/content/2019/2731-a-permian-austrolimulid).

SUPPLEMENTARY INFORMATION 2. CSV file of PCA results, family and generic assignment of specimens (available at https://palaeo-electronica.org/content/2019/2731-a-permian-austro-limulid).

SUPPLEMENTARY INFORMATION 3. NEXUS file of the analysed phylogenetic matrix. Originally presented in Lamsdell (2016) (available at https://palaeo-electronica.org/content/2019/2731-a-permian-austrolimulid).