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ORIGINAL PAPER

A reappraisal of Paleozoic horseshoe crabs from Russia and Ukraine

Russell D. C. Bicknell[1] · **Serge V. Naugolnykh**[2] · **Sienna A. Birch**[1]

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Abstract

Xiphosura are extant marine chelicerates that have displayed apparent morphological conservatism and remarkable survivorship across their ~ 480 Ma fossil record. The easily recognisable features that are known to even the earliest xiphosurans—a crescentic prosoma and often trapezoidal thoracetron (opisthosoma)—have generated debate surrounding their origins and taxonomic significance. This interest resulted in the description of numerous horseshoe crab species during the early to mid-twentieth century, particularly in Russia, that have remained unrevised since their original publications and unconsidered in the light of recent phylogenetic hypotheses. Here, we re-examine the non-belinurid taxa housed within the Chernyshev Central Museum for Geological Exploration in Saint Petersburg. We present the first formal diagnosis of *Bellinuroopsis rossicus*, erect *Shpineviolimulus jakovlevi* (Glushenko and Ivanov, 1961) comb. nov., to contain the species formerly described as ‘*Paleolimulus*’ *jakovlevi* and refer *Paleolimulus juresanensis* to Paleolimulidae *incertae sedis*. Phylogenetic analysis places *S. jakovlevi* at the base of Limulina. This position, coupled with a prosomal shield that is notably larger than the thoracetron, and lack of hypertrophied genal spines, suggests that this morphology may represent the ancestral austrolimulid shape. As an extension of this revision, we assessed the general austrolimulid morphological characters and uncovered two possible groups of these bizarre xiphosurids.

Keywords Xiphosurida · *Bellinuroopsis* · *Shpineviolimulus* · Paleolimulidae · Austrolimulidae

Introduction

The evolutionary history and diversity of Russian xiphosurid fossils have recently been subject to renewed interest (Marshall et al. 2014; Naugolnykh 2017, 2018a; Shpinev and Vasilenko 2018; Shpinev 2018; Naugolnykh and Areshin 2019), a transition fuelled by an overall interest in Russian marine chelicerates (Naugolnykh and Shpinev 2018; Shpinev and Filimonov 2018) and xiphosurids and stem-xiphosurids globally (Dunlop 2010; Lamsdell 2016; Bicknell 2019; Bicknell et al. 2019a, c; Bicknell and Pates 2019; Selden et al. 2019; Lamsdell 2020). A significant proportion of the recent xiphosurid research has come from re-examining specimens in museum collections. These specimens have often been unstudied since their original descriptions and have not been considered in light of modern phylogenetic and taxonomic hypotheses. The Chernyshev Central Museum of Geological Exploration in Saint Petersburg contains a selection of xiphosurids, including two *Paleolimulus* Dunbar, 1923 species, and *Bellinuroopsis rossicus* Tschernyshev, 1933. These species require a revision given the Late Devonian age of *B. rossicus* (Bicknell and Pates 2020) and the possible austrolimulid affinities of the *Paleolimulus* taxa (Lerner et al. 2017). Here, we present a formal diagnosis for *B. rossicus*, erect *Shpineviolimulus jakovlevi* comb. nov., to contain the limuloid species formerly described as ‘*Paleolimulus*’ *jakovlevi* and discuss aspects of paleolimulid and austrolimulid evolution.

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✉ Russell D. C. Bicknell
rdcbicknell@gmail.com

[1] Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia

[2] Geological Institute, Russian Academy of Sciences, Moscow, Russia 119117

Methods

The Chernyshev Central Museum of Geological Exploration (CCMGE), Saint Petersburg, Russia, is the repository for the material considered in this study. Specimens were photographed with a Canon EOS 5DS under normal and low angle light. Measurements were obtained from photographs using ImageJ. We follow the systematic taxonomy of Lamsdell (2016) and anatomical terms presented in Bicknell et al. (2018, 2019b, c) and Bicknell (2019).

To evaluate the phylogenetic position of *Shpineviolimulus* gen. nov., it was coded as an additional taxon into the recently published matrix of Bicknell (2019), modified from Lamsdell (2016). This matrix contains a broad sampling of fossil and extant euchelicerates (Supplementary Information 1). The analysis was performed under equally weighted parsimony in TNT 1.5 (Goloboff and Catalano 2016) using the 100 replicates of the 'New Technology' tree search strategy using random and constrained sectorial searches, 100 iterations of the parsimony ratchet, 50 cycles of drifting, and 5 rounds of tree fusing. Searching was stopped after two such runs returned trees of the same minimum length. Nodal supports were calculated from 100 bootstrap and jackknife replicates using the strict consensus of the most parsimonious trees as the target and using the 'Group present/Contradicted' (GC; Goloboff et al. 2003) metric. Bremer support values were calculated using the BREMER.RUN script, saving trees up to 10 steps longer than the most parsimonious trees.. All multistate characters were considered unordered *sensu* the original analysis. *Fuxianhuia protensa* Hou, 1987 was the outgroup taxon, following Lamsdell (2013). Additionally, character codings for *Bellinuroopsis rossicus* were reviewed and adjusted based on the re-examination of the holotype. '*Paleolimulus juresanensis*' was not coded as there were limited characters that could be unambiguously scored (see "Systematic Palaeontology").

A line-tracing technique was used to prepare reconstructions of studied specimens. This method employs photographs of specimens made under direct and oblique light to highlight all aspects of the fossil. The outlines of the holotypes were marked in ink (by hand) or in digital contrast line. From this initial layer, the remainder of the drawing is processed separately in other layers or sheets of paper.

Stratigraphic details

Bellinuroopsis rossicus Tschernyshev, 1933

The *Bellinuroopsis rossicus* type locality is within the Late Devonian (Famennian)–aged Lebedjan Formation near Lebedjan, Lipetsk, Russia (Fig. 1). This formation consists of grey and yellowish-grey platy dolostones and mudstones, rarely interbedded with carbonate conglomerates, invertebrate-rich mudstones, and clays (Markovsky 1975). The Lebedjan Formation is 12–25 m thick, located below the Famennian-aged Mtsensk Formation (so-called Mtsensk layers) consisting of dolostones and sandstones, and above the Elets Formation consisting of mudstones and dolostones (Markovsky 1975).

Shpineviolimulus jakovlevi comb. nov. (Glushenko and Ivanov, 1961)

Detailed data on the holotype locality for *Shpineviolimulus jakovlevi* comb. nov. is unknown. However, considering the lithological and stratigraphic information that can be derived from the specimen, it likely came from the lowermost Cisuralian (Asselian)–aged Araukaritovaya Formation in the Donetsk Basin near Novopavlovka Village, Donetsk, Ukraine (former Stalin region) (Fig. 2). The Araukaritovaya Formation is characterised by permineralised coniferophyte attributed to *Dadoxylon amadokense* Zalessky, 1937 and an array of lower Permian callipterids (Boyarina 1994, 2010). These particular callipterids belong to taxa known in the Lower Permian of Europe (Augusta 1946), contradicting the Upper Carboniferous (Gzhelian) age suggested by Boyarina (2010).

Paleolimulus juresanensis Tschernyshev, 1933

Stratigraphic position and the source strata of *Paleolimulus juresanensis* have previously been considered Upper Carboniferous. However, the specimen is preserved on platy, tan-coloured marl, and rock that is atypical of Carboniferous deposits of the Ural Mountains. It is much likely that the specimen is from a Lower Permian deposit, likely Artinskian (see Naugolnykh 2018b) or lowermost Kungurian in age. Currently, there is no known formation name for this material.

Systematic palaeontology

Subphylum Chelicerata Heymons, 1901
Class Xiphosura Latreille, 1802
Order Xiphosurida Latreille, 1802
Genus *Bellinuroopsis* Tschernyshev, 1933
Type species: *Bellinuroopsis rossicus* Tschernyshev, 1933

Diagnosis: Xiphosurid with a pronounced 'M'-shaped cardiac ridge joint, pronounced lateral nodes on thoracetronic segments IX–XIII, potentially XIV, and large thoracetronic lateral spines.

Note: Tschernyshev (1933) did not present a formal diagnosis for *Bellinuroopsis rossicus*.

Bellinuroopsis rossicus Tschernyshev, 1933

1933, *Bellinuroopsis rossicus* Tschernyshev, 1933, Fig. 1

1938b, *Neobelinuropsis rossicus* (Tschernyshev); Eller, Plate XIV, Fig. 8

1938a, *Neobelinuropsis* Eller, p. 152

1952, *Neobelinuropsis rossicus* (Tschernyshev); Størmer, fig. 1h

1955, *Neobelinuropsis rossicus* (Tschernyshev); Størmer, fig. 14

1974, *Neobelinuropsis rossicus* (Tschernyshev); Eldredge, p. 35

1975, *Neobelinuropsis rossicus* (Tschernyshev); Bergström, p. 293

1982, *Neobelinuropsis rossicus* (Tschernyshev); Fisher, text fig. 1

1984, *Neobelinuropsis rossicus* (Tschernyshev); Fisher, fig. 2j

1985, *Neobelinuropsis rossicus* (Tschernyshev); Waterston, fig. 4

1987, *Neobelinuropsis* Eller, Siveter & Selden, p. 156

1987a, *Neobelinuropsis rossicus* (Tschernyshev); Selden & Siveter, p. 383

1987b, *Bellinuroopsis rossicus* Tschernyshev; Selden & Siveter, p. 1285

1990, *Neobelinuropsis* Eller, Beall & Labandeira, fig. 1

1993, *Bellinuroopsis rossicus* Tschernyshev; Pickett, p. 282

1994, *Bellinuroopsis rossicus* Tschernyshev; Schultka, p. 346

1997, *Bellinuroopsis rossicus* Tschernyshev; Anderson & Selden, fig. 2M

2007, *Bellinuroopsis rossicus* Tschernyshev; Moore et al., p. 1017

2014, *Bellinuroopsis rossicus* Tschernyshev; Tashman, p.12

2016, *Bellinuroopsis rossicus* Tschernyshev; Lamsdell, Table 1

2017, *Bellinuroopsis rossicus* Tschernyshev; Zuber et al., p. 6

2019c, *Bellinuroopsis rossicus* Tschernyshev; Bicknell et al., p. 973

2020, *Bellinuroopsis rossicus* Tschernyshev; Bicknell & Pates 2020, fig. 23A

Diagnosis: As for the genus.

Holotype and only specimen: CCMGE 1/3694.

Type locality and horizon: Lebedjan Formation, Lebedjan, Russia; Upper Devonian (Famennian).

Material: CCMGE 1/3694 is preserved as an internal impression on a slab of yellow plattenkalk-like dolomite.

Description: An articulated prosoma, thoracetron, and telson (Fig. 3a, b). Specimen is 80.5 mm long, including the telson. Prosoma is convex, mostly preserved, semi-circular, and 34.6 mm wide. There is no notable prosomal rim or prosomal doublure. Ophthalmic ridges are preserved, curving towards the lateral sides of the prosoma and forming a pronounced double-arched, 'M'-shaped anterior to the cardiac lobe (Fig. 3c). The left ophthalmic ridge is 17.0 mm long, and the partly preserved right ophthalmic ridge is 10.8 mm long. A lateral compound eye impression is present along the left ophthalmic ridge; this feature was identified by Tschernyshev (1933) as a 'tubercle'. Cardiac lobe is convex, cone-shaped, 14.5 mm long and 7.9 mm wide posteriorly, tapering to 1.9 mm anteriorly. Ocelli are not observed. Neither of the genal spines is completely preserved. The left spine is broken at the rock edge, and the right spine was broken through preparation.

Thoracetron is completely preserved, slightly trapezoidal with curved lateral sides, and is 25.2 mm long and 33.2 mm wide anteriorly, tapering to 5.9 mm at the thoracetron-telson joint. Thoracetron fully expresses tergites VIII–XV. Tergites appear to show varying degrees of fusion: tergites XIII–XV appear more fused than anterior sections (Fig. 3e). Tergite VIII is 36.8 mm wide and 3.6 mm long, and extends laterally ~ 2 mm from the thoracetron. This tergite has a 0.6-mm-thick anterior rim. Tergites IX–XIII are between 2.4 and 3.3 mm long and between 20.1 and 32.7 mm wide, taping posteriorly. Tergite XV has a maximum width of 15.2 mm and is 4.5 mm long, suggesting that it is a pretelson section. Thoracetronic axial lobe is approximately rectangular: 25.4 mm long, 11.2 mm wide anteriorly, tapering to 7.3 mm posteriorly. No apodemes or marginal rims are noted. Left pleural lobe is slightly domed, has minimal relief, and is segmented. Excluding tergite VIII, the left pleural lobe is 10.9 mm wide anteriorly, tapering to 3.8 mm posteriorly. The right pleural lobe is slightly domed with minimal relief and is segmented. Excluding tergite VIII, the right pleural lobe is 11.4 mm wide anteriorly, tapering to 2.6 mm posteriorly. Nodes are located two-thirds along the transverse ridge length of tergites IX–XIII (Fig. 3d) and are ~ 1.2 mm wide. Triangular fixed spines are present on tergites XII–XV (Fig. 3d). Spines are all 4.0–4.5 mm wide across the posterior margins (Fig. 3d).

The telson is lanceolate and articulated with the posterior thoracetron margin. The thoracetron-telson articulation is slightly concave towards the specimen anterior. Telson is completely preserved and 33.4 mm long. No axial ridge is noted along telson. Anterior section of telson is 5.9 mm wide, tapering to a point.

Remarks: *Bellinuroopsis rossicus* is one of the few xiphosurid fossils from pre-Carboniferous formations (Bicknell and Pates 2020). Due to its age and plesiomorphic features compared with other xiphosurid groups, *B. rossicus* has been considered an intermediate taxon between Belinuridae and synziphosurines (Bergström 1975) and a member of the stem xiphosurid grade formerly considered

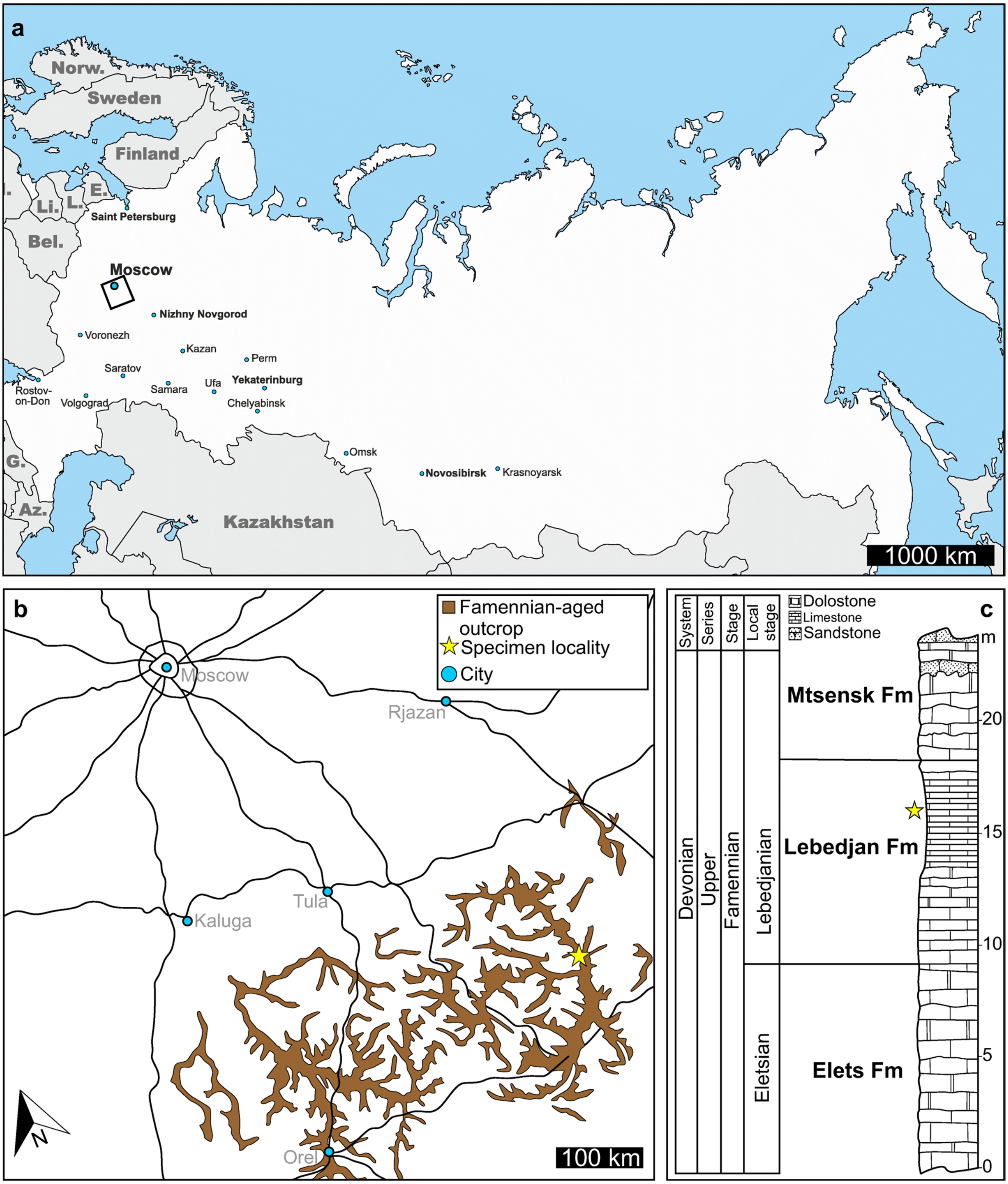


Fig. 1 Geological and geographical information for the type locality of *Bellinuroopsis rossicus*. **a** Map of Russia and other parts of Europe. Box shows close-up of **b**. **b** Close-up of specimen location (star) showing local outcrops of Late Devonian (Famennian) strata in the area. **c** Simplified stratigraphic column showing units above and below *B. rossicus*–bearing formation (star)

Kasibelinuridae (Pickett 1993; Bicknell et al. 2019c; Bicknell and Smith in press). Aligning with these positions, *B. rossicus* has been resolved phylogenetically close to the base of Xiphosurida over the past three decades (Fisher 1982;

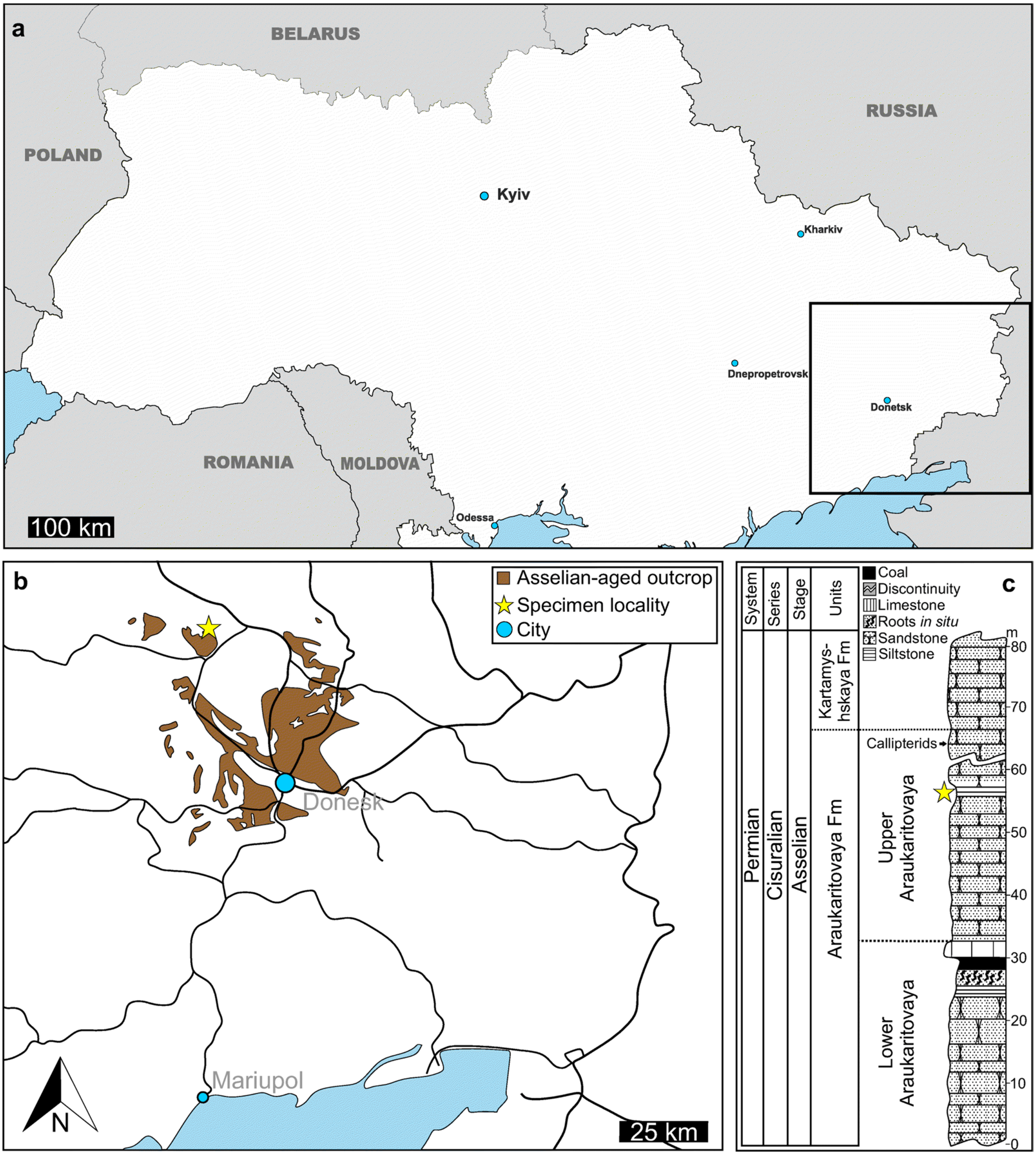


Fig. 2 Geological and geographical information for the type locality of *Shpineviolimulus jakovlevi* comb. nov. **a** Map of most Ukrainian borders and other parts of Europe. Box shows close-up of **b**. **b** Close-up of specimen location (star) showing local outcrops of Cisuralian (Asselian)–aged strata in the area. **c** Simplified stratigraphic column showing units above and below the section of the Araukaritovaya Formation bearing *S. jakovlevi* (star)

Anderson and Selden 1997; Lamsdell 2016; Bicknell 2019). Our re-examination confirms this placement (see “Results”). It is also important to note that our revised phylogenetic hypothesis places *B. rossicus* outside of Limulina (*sensu* Lamsdell, 2016) suggesting that it may represent a transitional form between stem xiphosurids and the crown group.

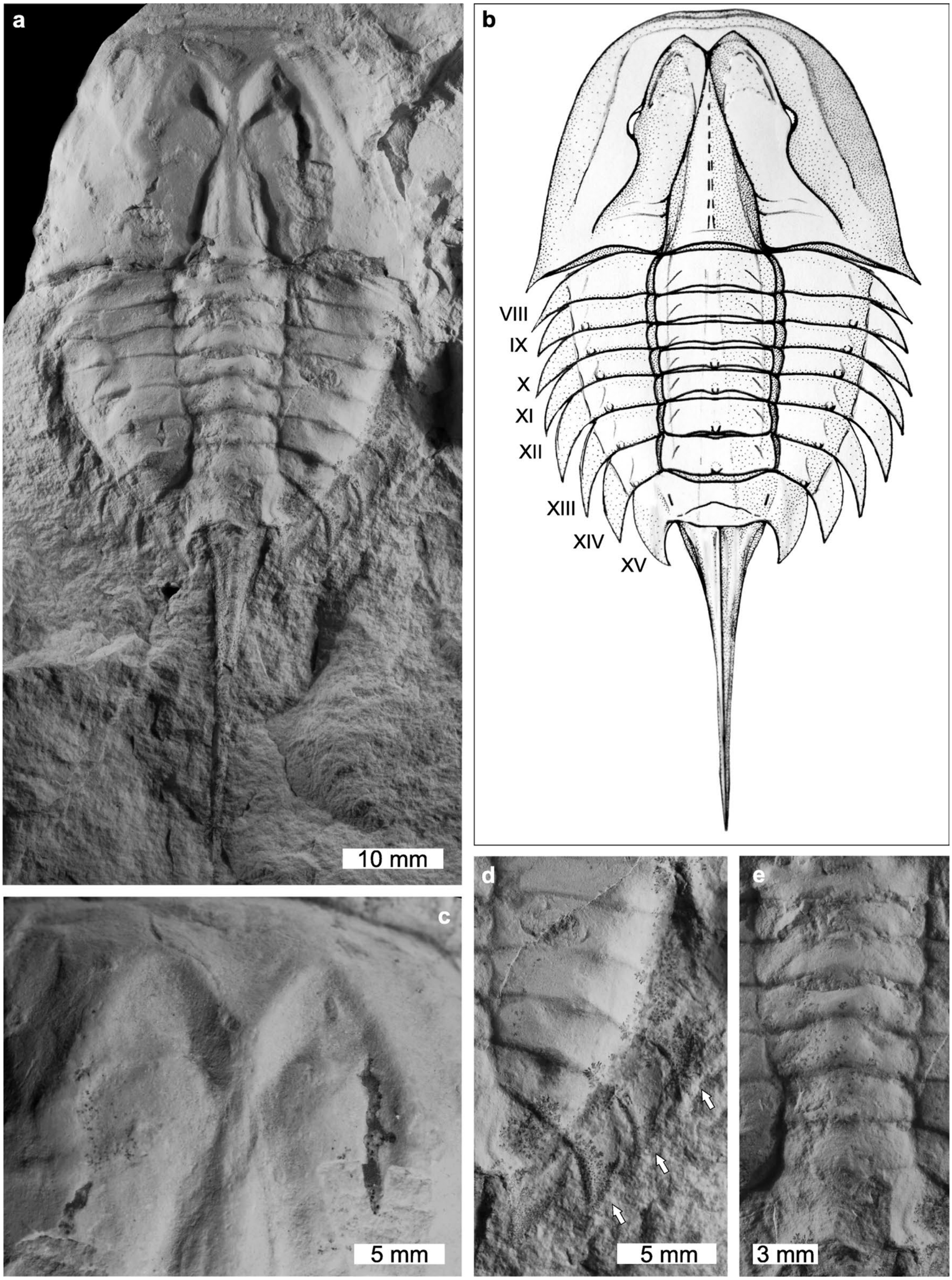


Fig. 3 Holotype and only specimen of *Bellinuroopsis rossicus* from the Famennian-aged Lebedjan Formation, Russia. **a** Complete specimen. CCMGE 1/3694. **b** Reconstruction of *B. rossicus*. Roman numerals indicate tergal sections. **c** Close-up of prosomal shield showing pronounced 'M'-shaped ophthalmic ridges. **d** Close-up of right posterior thoracetron showing transverse nodes and lateral spines (white arrows). **e** Close-up of axial lobe showing how posterior tergite appears more fused than anterior tergites. Images converted to greyscale

However, the non-crown group xiphosurids (*sensu* Lamsdell, 2016) contain *Lunataspis aurora* Rudkin et al., 2008, a highly derived horseshoe crab with a completely fused thoracetron, especially when compared with *B. rossicus*. Reconsidering and re-coding *L. aurora* may place it within Xiphosurida and help organise the supposed stem xiphosurids. In the light of these points, we have not placed *B. rossicus* in a monogeneric family or suborder to avoid introducing additional confusion as xiphosurid systematics rapidly continues to develop.

Our revised description of *Bellinuroopsis rossicus* differs from the original report in two key respects. Tschernyshev (1933) suggested that ocelli were preserved close to the anterior cardiac lobe. We cannot confirm this observation following re-examination of the holotype. Furthermore, Tschernyshev (1933) suggested that lateral fixed spines were present on all tergites. While this was likely the case in life—as is observed in similarly aged stem horseshoe crabs (Bicknell et al. 2019c)—such spines are not preserved on tergites IIX–XI.

Suborder Limulina Richter and Richter, 1929

Superfamily Limuloidea Zittel, 1885

Shpineviolimulus jakovlevi gen. nov.

Etymology: Generic name *Shpineviolimulus* is presented in honour of Evgeny Shpinev who contributed immensely to research on Russian Chelicerata combined with *Limulus*, the generic name of the extant North American horseshoe crab.

Diagnosis: Limuloid with a prosoma that is 79% wider than the thoracetron, inflated occipital lobes that extend to genal spines points, and a thoracetron with segmentary furrows.

Shpineviolimulus jakovlevi comb. nov.

Fig. 4

1961, *Paleolimulus jakovlevi* Glushenko & Ivanov, fig. 1

1987, *Paleolimulus jakovlevi* Glushenko & Ivanov; Hauschke & Wilde, p. 96

2014, *Paleolimulus jakovlevi* Glushenko & Ivanov; Tashman, p. 60

2017, ‘*Paleolimulus*’ *jakovlevi* Glushenko & Ivanov; Lerner et al., p. 299

2020, ?*Paleolimulus jakovlevi* Glushenko & Ivanov; Bicknell & Pates 2020, fig. 26E

Diagnosis: As for the genus.

Type and only species: *Paleolimulus jakovlevi* Glushenko & Ivanov, 1961

Holotype and only specimen: CCMGE 1/8886.

Type locality and horizon: Novoselovka locality, Donetsk region; Araukaritovaya Formation, lowermost Permian (Asselian, Lower Cisuralian).

Distribution: Cisuralian of the Donets Coal Basin.

Material: CCMGE 1/8886 is preserved as a mostly flat external impression on a slab of tan coloured, indurated limey mudstone.

Description: CCMGE 1/8886 is an articulated prosoma, thoracetron, and partial telson (Fig. 4a, b). The specimen is 55.6 mm long. Prosoma is mostly preserved, has a parabolic outline, and is 28.4 mm long at midline and 49.5 mm wide at the widest part. The left-most lateral edge of the specimen is broken. A prosomal rim is preserved and has a maximum width of 0.9 mm. Prosomal doublure is not preserved. Both ophthalmic ridges are preserved, ~ 14.5 mm long, and lacking any concavity. They do not appear to converge anteriorly. A lateral compound eye is preserved on the left ophthalmic ridge. The eye is located 8.0 mm anteriorly from prosoma-thoracetron border. A cardiac lobe is present but is no more domed than the rest of the specimen. The cardiac lobe is 12.6 mm wide posteriorly, tapering anteriorly into a triangular shape, which has a 14.4-mm-long medial ridge. Ocelli are not observed. Both genal spines are preserved and splay slightly out laterally beyond the thoracetron. Left genal tip is 20.2 mm from the organismal midline. Angle between the left genal spine and left side of the thoracetron is 84.4°. Right genal spine is 20.2 mm from the organismal midline. Angle between the right genal spine and right side of the thoracetron is 75.4°. Occipital lobes are observed along the genal spines, are inflated, and extend to spine terminus (Fig. 4c). Prosomal-thoracetronic hinge is pronounced, 23.5 mm wide, and 1.1 mm long. No prosomal appendages are preserved.

The thoracetron is completely preserved, strongly trapezoidal, 16.8 mm long, 23.6 mm wide anteriorly, increasing to a width of 27.6 mm at 3.8 mm along the thoracetron, then tapering to 6.7 mm posteriorly. The thoracetron is ~ 44% narrower than the prosoma. Under low angle light, an axial lobe is visible (Fig. 4d). The lobe is slightly triangular, tapering from 6.6 to 4.8 mm posteriorly. At least four segmentary axial furrows are present within the axial lobe and are all 3.6 mm wide. The left pleural lobe is not segmented, 18.6 mm long, 10.2 mm wide, tapering to a posteriorly directed terminal spine (Fig. 4d). The marginal rim is not preserved on the left side. The right pleural lobe is not segmented, 18.6 mm long, 10.1 wide anteriorly, tapering to a posteriorly directed terminal spine. A marginal rim is preserved on the right pleural lobe and is 0.8 mm wide along its length. Crenulations are preserved along this margin. These may be moveable spine notches (Fig. 4d). Anterior section of the telson is preserved and is 10.5 mm long, terminating at the rock edge. No axial ridge is noted along telson.

Remarks: *Paleolimulus* has functioned somewhat as a waste-basket genus for late Paleozoic xiphosurids that display non-limulid morphologies, such as a segmented thoracetron, or elongated genal spines. The erection of Austrolimulidae, and the realisation that taxa within Limulina can display ‘oddball’ morphologies (Eldredge 1976), has resulted in the placement of ‘*Paleolimulus*’ species in a revised taxonomic and phylogenetic framework (Lerner et al. 2017; Bicknell 2019; Bicknell and Pates 2020). *Shpineviolimulus jakovlevi* comb. nov. represents yet another taxon that was conservatively placed within Paleolimulidae, but belongs closer to Austrolimulidae

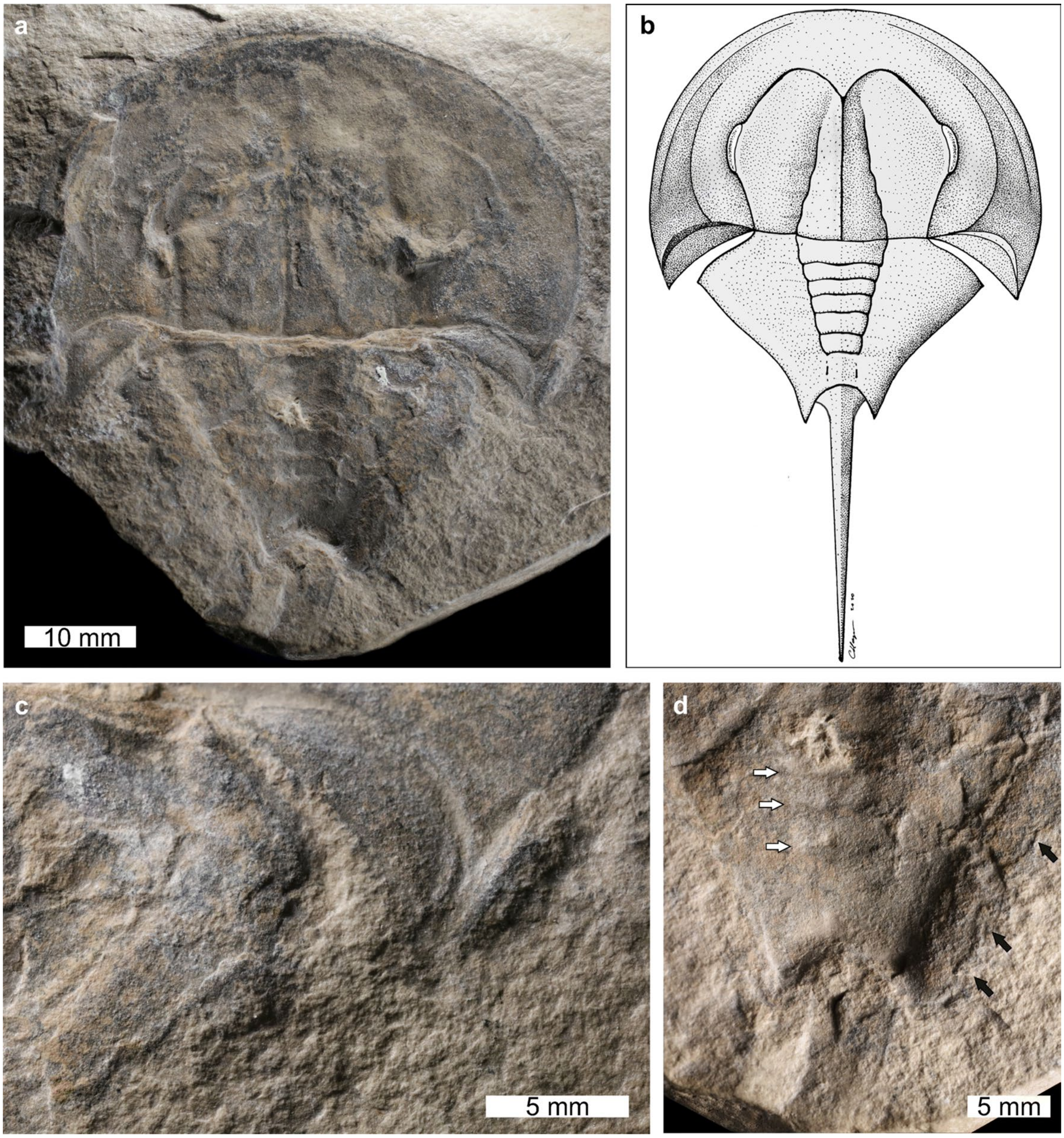


Fig. 4 Holotype and only specimen of *Shpineviolimulus jakovlevi* comb. nov. from the Asselian-aged Upper Araukaritovaya Formation, Ukraine. **a** Complete specimen. CCMGE 1/8886. **b** Reconstruction of *S. jakovlevi*. **c** Close-up of right genal spine showing inflated posterior margin. **d** Close-up of thoracetron under low angle light showing segmentary furrows (white arrows) and crenulated thoracetronic margin (black arrows)

(Lerner et al. 2017). The large prosoma relative to a slightly reduced thoracetron is similar to *Dubbolimulus peetae* Pickett, 1984. However, as *S. jakovlevi* lacks hypertrophied genal spines that extend up to the thoracetron terminus (such as *Austrolimulus fletcheri* Riek, 1955, *Tasmaniolimulus patersoni* Bicknell, 2019, *Vaderlimulus tricki* Lerner et al., 2017), and a swallow-tailed or highly reduced thoracetron, *S. jakovlevi* is not an austrolimulid *sensu stricto*.

Suborder Limulina Richter and Richter, 1929

Superfamily Limuloidea Zittel, 1885

Family Paleolimulidae Dunbar, 1923

Paleolimulidae *incertae sedis*

1933, *Paleolimulus juresanensis* Tschernyshev, fig. 2

1985, *Paleolimulus*? *juresanensis* Tschernyshev; Waterston, p. 26

1987, *Paleolimulus*? *juresanensis* Tschernyshev; Hauschke & Wilde, p. 96

2000, ?*Paleolimulus juresanensis* Tschernyshev; Babcock & Merriam, p. 87

2005, ?*Paleolimulus juresanensis* Tschernyshev; Allen & Feldmann, p. 596

2014, ?*Paleolimulus juresanensis* Tschernyshev; Tashman, p. 52

2016, *Paleolimulus juresanensis* Tschernyshev; Lerner et al., p. 200

2017, '*Paleolimulus*' *juresanensis* Tschernyshev; Lerner et al., p. 299

2018b, *Paleolimulus juresanensis* Tschernyshev; Naugolnykh, p. 50

2020, ?*Paleolimulus juresanensis* Tschernyshev; Bicknell & Pates 2020, fig. 22E

Referred specimen: CCMGE 2/3694; holotype and only specimen.

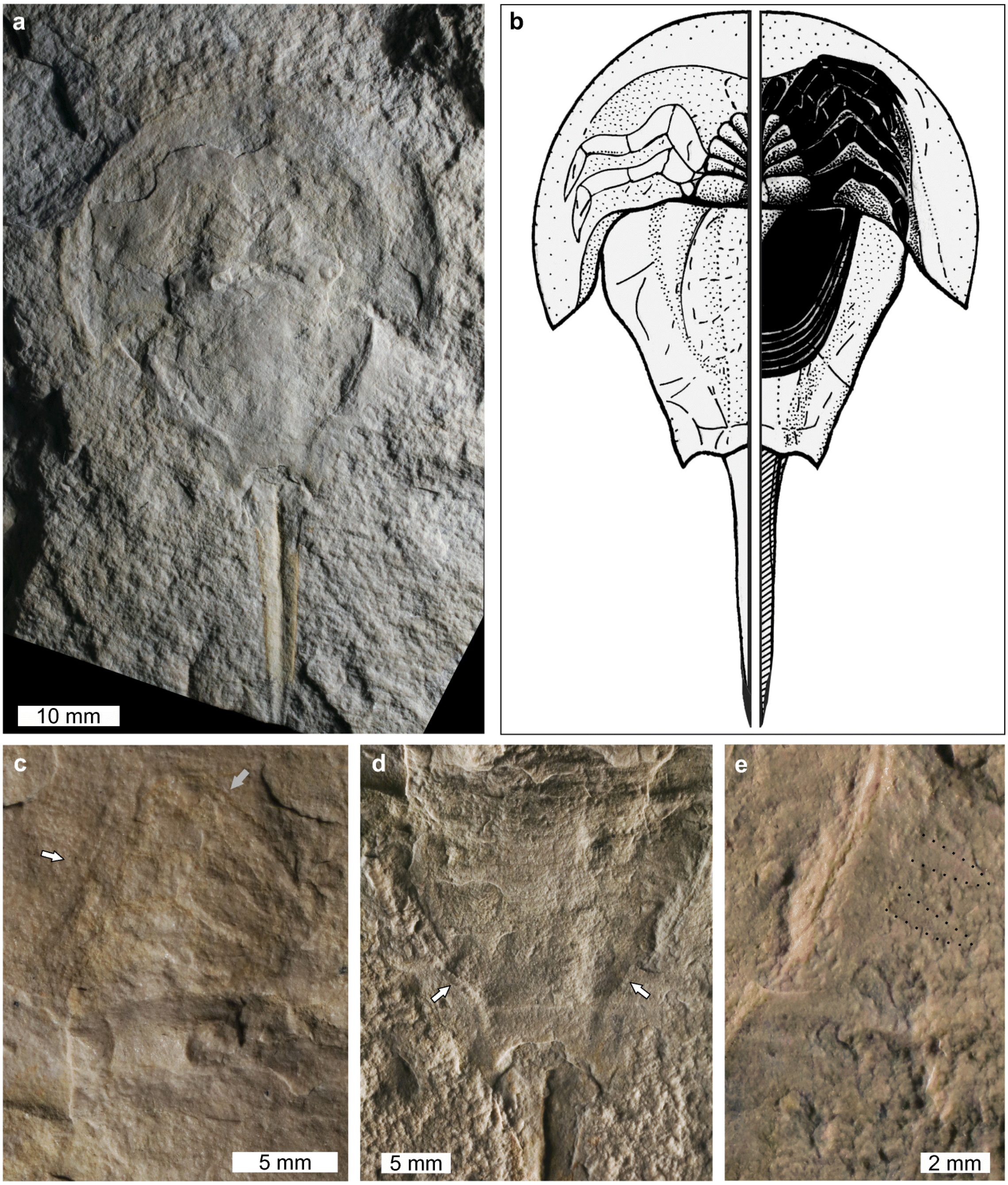


Fig. 5 Paleolimulidae *incertae sedis* from the Trubkino locality, Bashkortostan, likely Cisuralian, Russia. **a** Complete specimen. Holotype of *Paleolimulus juresanensis* CCMGE 2/3694. **b** Idealised reconstruction of specimen. **c** Close-up of most complete appendages on the left prosomal side showing patella (grey arrow) and tibiotarsus (white arrow). **d** Close-up of thoracetron under low angle light showing thoracetronic doublure (white arrows). **e** Close-up of right side of thoracetron, under low angle light, showing possible examples of faintly preserved lateral spines (dotted outlines)

Type locality and horizon: Formation indeterminate. Section along the left side of the Jurezan (= Juruzan) River, 1 km upstream of Trubkino village, Bashkortostan, Southern Urals, Russia. Artinskian to lowermost Kungurian.

Material. CCMGE 2/3694 is preserved in a ventral perspective on a slab of platy, tan-coloured marl.

Description. CCMGE 2/3694 is an articulated prosoma, thoracetron and telson in ventral view (Fig. 5). The specimen is completely flat and 68.0 mm long. Prosoma is completely preserved, has a horseshoe shape, and is 22.6 mm long and 37.1 mm wide along the posterior margin. A very thin prosomal rim is noted and has a maximum width of 0.5 mm. The right side of the prosomal doublure is slightly visible. No ophthalmic ridges, ocelli, lateral compound eyes, or cardiac lobes are visible. Both genal spines are preserved and not posteriorly extended. The left genal spine point is 17.8 mm from the organismal midline and the angle between the left genal spine and left thoracetron side is 68.8°. Although poorly preserved, the inner margin of the genal spine is curved slightly anteriorly. The right genal spine is ~ 17 mm from the organismal midline. Due to poor preservation, it is not possible to confidently determine the angle between the right genal spine and right side of the thoracetron. Prosomal-thoracetronic hinge is slightly preserved, ~ 0.7 mm long and 21.0 mm wide. At least three prosomal appendages are preserved as impressions radially about the prosomal medial line (Fig. 5c). Impressions are of the proximal sections of walking legs and more distal sections (likely the patella and tibiotarsus) of the left anterior-most prosomal appendage are preserved.

The thoracetron is trapezoidal, ~ 17.5 mm long and 24.2 mm wide anteriorly, tapering to 3.4 mm posteriorly. The thoracetron is completely preserved and a thoracetronic doublure is present (Fig. 5d). Due to the ventral preservational aspect, the axial lobe cannot be observed. Segmentary axial furrows and apodemal pits can also not be observed. A marginal rim is noted, with a maximum width of 0.9 mm. Possible evidence for four fixed spines is present on the right side (Fig. 5e). Terminal thoracetronic spines are noted and posteriorly directed. Telson is almost completely preserved and 26.6 mm long. A pronounced axial ridge of the telson is preserved as an external mould.

Remarks. The placement of CCMGE 2/3694 within *Paleolimulus* has been questioned by xiphosurid palaeontologists since its original description (Babcock and Merriam 2000; Tashman 2014; Lerner et al. 2017). This stems from the preservational aspect and lack of readily identifiable characteristics that would permit differential diagnoses of CCMGE 2/3694 with other horseshoe crabs. The age of CCMGE 2/3694 corresponds with those of other paleolimulids and true *Paleolimulus* (Babcock and Merriam 2000; Naugolnykh 2018a; Table 1; Fig. 6) and the preserved characters permit its referral to Paleolimulidae. However, more comparative specimens from the same locality are needed to confirm if CCMGE 2/3694 is a valid and unique taxon. Therefore, we refer this material to Paleolimulidae *incertae sedis* as suggested by Babcock and Merriam (2000).

Results

The phylogenetic analysis resulted in seven most parsimonious trees of length 741 (CI: 0.470; RI: 0.878). The topology of the strict consensus tree (Fig. 7) is similar to that presented in previous studies that have used this matrix (Lamsdell 2016; Bicknell 2019; Bicknell and Pates 2019). *Bellinuroopsis rossicus* resolves in a polytomy with Limulina and Belinurina, as opposed to at the base of Limulina, the suborder containing Rolfeiidae, Paleolimulidae, and Limuloidea (Lamsdell 2016). *Shpineviolimulus jakovlevi* comb. nov. resolves

Table 1 Geological and geographical information of paleolimulids (see Fig. 6)

Taxon	Geological formation	Age and relevant reference	Country
Paleolimulus woodae Lerner et al., 2016	Horton Bluff Formation	Tournaisian (Lerner et al. 2016)	Nova Scotia, Canada
Moravurus rehori Příbyl, 1967	Tichá Borehole NP 552. Hradec-Kyjovice Formation	Visean (Jirman et al. 2018)	Czech Republic
Xaniopyramis linseyi Siveter and Selden, 1987	Stainmore Formation (*sensu* Waters et al. 2014)	Serpukhovian-Bashkirian (Waters et al. 2014)	Durham County, England
Paleolimulus signatus (Beecher 1904)	Pony Creek Shale *Konservat-Lagerstätte*, Wood Siding Formation Wellington Shale Fort Riley Limestone Member, Barneston Limestone Crouse Limestone	Kasimovian (Wood Siding Formation) Artinskian (Barneston Limestone, Crouse Limestone) Kungurian (Wellington Shale Fort) (Babcock and Merriam 2000)	Kansas, USA
Paleolimulus kunguricus Naugolnykh, 2017	Philippovian Horizon, Shurtan Formation	Kungurian (Naugolnykh 2017)	Middle Cis-Urals, Russia

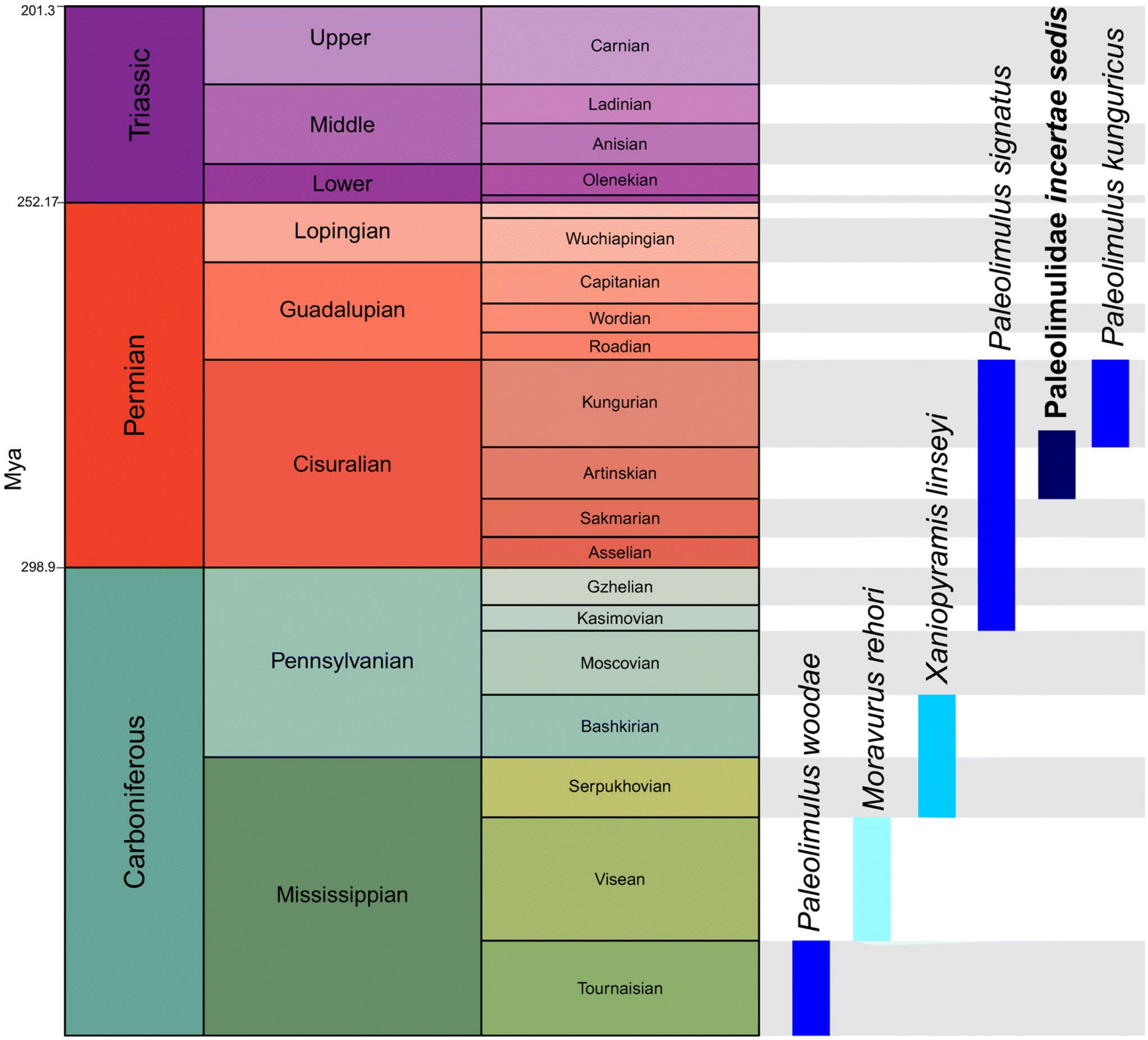
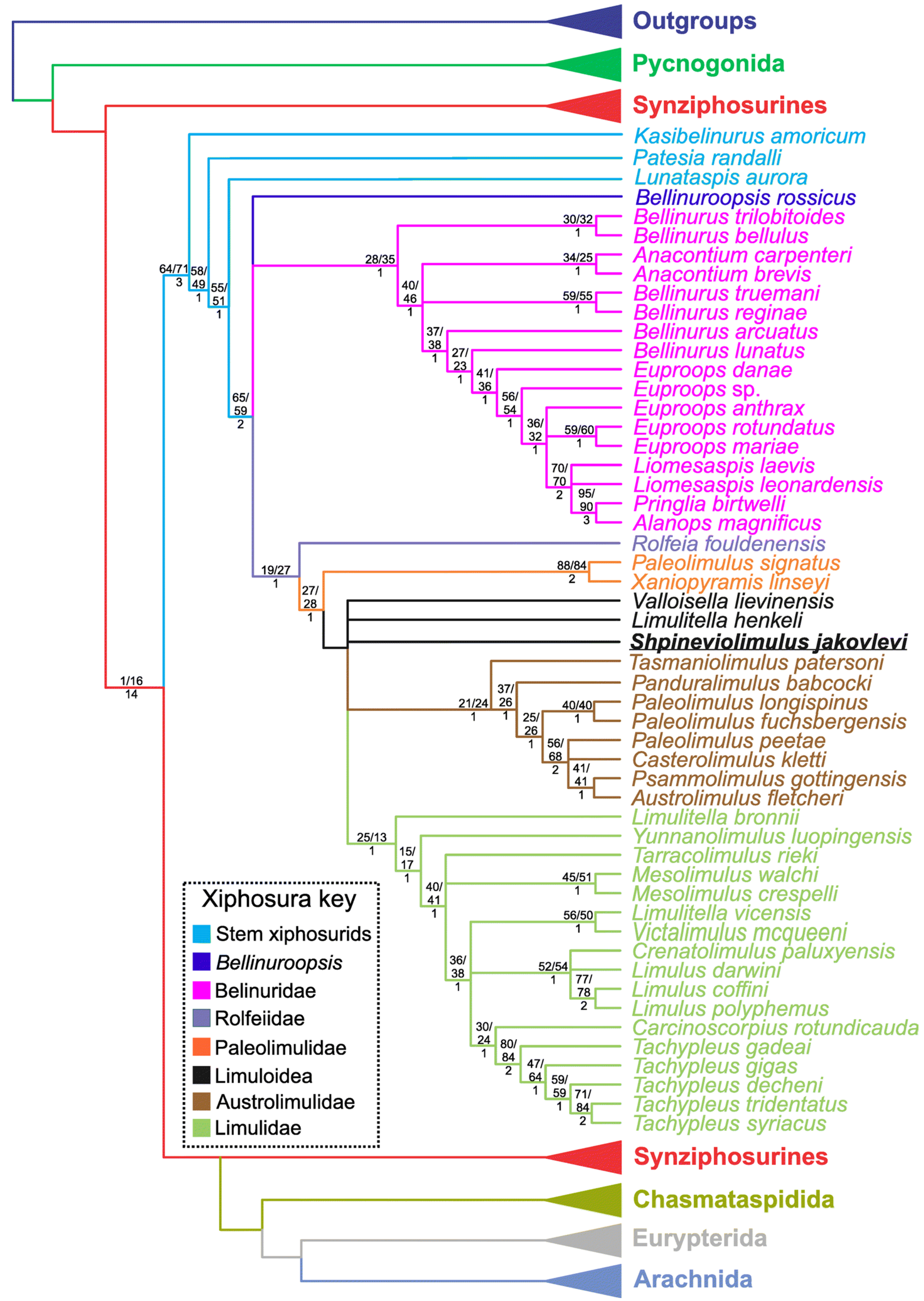


Fig. 6 Distribution of paleolimulids in time to demonstrate the temporal position of Paleolimulidae *incertae sedis*. Taxa are colour coded by genus. Consider with Table 1

within a polytomy containing *Limulitella henkeli* (von Fritsch, 1906) and *Valloisella lievinensis* Racheboeuf, 1992, outside of Austrolimulidae and Limulidae (*sensu* Lamsdell, 2016). This differs from the topology of Lamsdell (2016) in that only *L. henkeli* was resolved in a polytomy with Limulidae and Austrolimulidae.

Discussion

Austrolimulidae and Belinuridae represent the groups of xiphosurids that explored non-marine niches and likely derived extreme dorsal morphologies from inhabiting these fluvial conditions (Haug et al. 2012; Lerner et al. 2017; Bicknell 2019; Bicknell et al. 2019d). Curiously, although Austrolimulidae was erected in Riek (1955) to accommodate *Austrolimulus fletcheri*, the number of austrolimulid taxa remained low until phylogenetic work by Lamsdell (Lamsdell 2016; Lerner et al. 2017; Bicknell 2019; Bicknell and Pates 2020; Fig. 8; Table 2). Recent taxonomic studies, in the light of this new phylogenetic framework, have revealed that many supposed *Paleolimulus* species are more likely austrolimulids (Lamsdell 2016; Lerner et al. 2017; Bicknell 2019). The grouping of austrolimulid-like forms into the *Paleolimulus* likely reflects the historical nature of the genus. Furthermore, the lack of research formally organising all *Paleolimulus* species has


Outgroups
Pycnogonida
Synziphosurines
Kasibelinurus amoricum
Patesia randalli
Lunataspis aurora
Bellinuroopsis rossicus
Bellinurus trilobitoides
Bellinurus bellulus
Anacontium carpenteri
Anacontium brevis
Bellinurus truemani
Bellinurus reginae
Bellinurus arcuatus
Bellinurus lunatus
Euproops danae
Euproops sp.
Euproops anthrax
Euproops rotundatus
Euproops mariae
Liomesaspis laevis
Liomesaspis leonardensis
Pringlia birtwelli
Alanops magnificus
Rolfeia fouldenensis
Paleolimulus signatus
Xaniopyramis linseyi
Valloisella lievinensis
Limulitella henkeli
Shpineviolimulus jakovlevi
Tasmaniolimulus patersoni
Panduralimulus babcocki
Paleolimulus longispinus
Paleolimulus fuchsbergensis
Paleolimulus peetae
Casterolimulus kletti
Psammolimulus gottingensis
Austrolimulus fletcheri
Limulitella bronnii
Yunnanolimulus luopingensis
Tarracolimulus rieki
Mesolimulus walchi
Mesolimulus crespelli
Limulitella vicensis
Victalimulus mcqueeni
Crenatolimulus paluxyensis
Limulus darwini
Limulus coffini
Limulus polyphemus
Carcinoscorpius rotundicauda
Tachypleus gadeai
Tachypleus gigas
Tachypleus decheni
Tachypleus tridentatus
Tachypleus syriacus
Synziphosurines
Chasmataspidida
Eurypterida
Arachnida
30/32 1
28/35 1
34/25 1
64/71 3
58/ 49 1
55/ 51 1
40/ 46 1
59/55 1
37/ 38 1
27/ 23 1
41/ 36 1
65/ 59 2
56/ 54 1
36/ 32 1
59/60 1
70/ 70 2
95/ 90 3
19/27 1
88/84 2
27/ 28 1
1/16 14
37/ 26 1
21/24 1
40/40 1
25/ 26 1
56/ 68 2
41/ 41 1
25/13 1
15/ 17 1
45/51 1
40/ 41 1
56/50 1
36/ 38 1
52/54 1
77/ 78 2
30/ 24 1
80/ 84 2
47/ 64 1
59/ 59 1
71/ 84 2
Xiphosura key
🟦 Stem xiphosurids
🟦 Bellinuroopsis
🟪 Belinuridae
🟪 Rolfeiidae
🟧 Paleolimulidae
⬛ Limuloidea
🟫 Austrolimulidae
🟩 Limulidae

◂**Fig. 7** Results of the phylogenetic analysis, focussing specifically on xiphosurids and their immediate outgroups. Strict consensus of the 7 most parsimonious trees from the analysis of the data matrix in Supplementary Information 1. Node labels represent bootstrap, jackknife, and Bremer support values respectively. *Shpineviolimulus jakovlevi* is shown in bold and underlined. Pycnogonida, Synziphosurines, Chasmataspidida, Eurypterida, and Arachnida were collapsed and the phylogeny of Selden et al. (2015) (see Supplementary Fig. 1 for the full tree)

produced a polyphyletic distribution of the genus within Xiphosurida. True paleolimulids are therefore a sister group to Limuloidea, while *Paleolimulus* species with extreme morphologies being located within Austrolimulidae. The re-evaluation of *Shpineviolimulus jakovlevi* comb. nov. presented here further highlights the waste-basket nature of *Paleolimulus* and demonstrates that a thorough revision of the genus is needed.

Reconsidering austrolimulid morphology while describing *Shpineviolimulus jakovlevi* comb. nov. has highlighted two major groupings in the family. The less diverse group are those taxa with notably larger prosomal regions relative to the thoracetron, but lack genal spines that extend to the thoracetron terminus. This morphology is observed in *S. jakovlevi*, *Dubbolimulus peetae*, and *Panduralimulus babcocki* Allen and Feldmann, 2005, the latter two of which are true austrolimulids, *sensu* Lamsdell (2016). The second group of horseshoe crabs are those with hypertrophied genal spines that extend to the thoracetron terminus: *Austrolimulus fletcheri*, *Psammolimulus gottingensis* Lange, 1923, *Tasmaniolimulus patersoni*, and *Vaderlimulus tricki*. This morphology is potentially derived from the inflated prosomal morphology. The transition to taxa with these hypertrophied spines may have permitted for more effective motion through a freshwater unidirectional fluid flow that austrolimulids exploited (Bicknell 2019; Bicknell and Pates 2019).

In the light of the above discussion, consideration must be given to '*Paleolimulus*' *longispinus* Schram, 1979 from the Serpukhovian-aged Bear Gulch Limestone in the Heath Formation, MT, USA (Grogan and Lund 2002). Lamsdell (2016) suggested that '*P.*' *longispinus* was an austrolimulid. This notion was supported by Lerner et al. (2016, 2017) and, as we used the Lamsdell (2016) matrix, '*P.*' *longispinus* is resolved within Austrolimulidae in Fig. 6. An alternative perspective was presented by Anderson (1996): that '*P.*' *longispinus* belongs within *Rolfeia* Waterston, 1985 based on the presence of hypertrophied fixed and movable spines, a thesis supported by other authors (Anderson and Selden 1997; Babcock and Merriam 2000; Moore et al. 2007; Tashman 2014). Unfortunately, no formal taxonomic redescription has been presented beyond Anderson's thesis. In reconsidering Austrolimulidae here, we consider the placement of '*P.*' *longispinus* within Austrolimulidae unlikely as members of the family either completely lack lateral thoracetronic spines (e.g. *Austrolimulus fletcheri*, *Dubbolimulus peetae*, *Tasmaniolimulus patersoni*, *Vaderlimulus tricki*) or have strongly reduced moveable spines (e.g. *Panduralimulus babcocki* and *Psammolimulus gottingensis*). Furthermore, since *Rolfeia* is the only known xiphosurid genus with hypertrophied fixed spines, we favour the Anderson (1996) hypothesis. This discrepancy between the phylogenetic placement and morphological characteristics of this species highlights possible issues with the assessed phylogenetic matrix. To this end, a reconsideration of the phylogenetic framework in which xiphosurids are discussed is warranted (Bicknell et al. 2019c).

Table 2 Geological and geographical information of true austrolimulids (*sensu* Lamsdell 2016; Lerner et al. 2017) ordered temporally (excluding '*Paleolimulus*' *longispinus*, see comments in "Discussion") (see Fig. 8)

Taxon	Geological formation	Age and most recent reference	Country
Panduralimulus babcocki Allen and Feldmann, 2005	Maybelle Limestone, Lueders Formation	Kungurian (Lerner et al. 2017)	Texas, USA
Tasmaniolimulus patersoni Bicknell, 2019	Jackey Shale	Lopingian (no geological stage has been suggested; Banks and Clarke 1987)	Tasmania, Australia
Vaderlimulus tricki Lerner et al., 2017	Lower shale unit, Thaynes Group	Spathian (Lerner et al. 2017)	Idaho, USA
Psammolimulus gottingensis Lange, 1923	Solling Formation	Spathian (Lerner et al. 2017; Bicknell et al. 2019b)	Lower Saxony, Germany
Austrolimulus fletcheri Riek, 1955	Beacon Hill Formation	Ladinian (Lerner et al. 2017)	New South Wales, Australia
Dubbolimulus peetae Pickett, 1984	Ballimore Formation	Ladinian (Lerner et al. 2017)	New South Wales, Australia
'*Paleolimulus*' *fuchsbergensis* Hauschke and Wilde, 1987	Exter Formation (Seegis 2014)	Norian (Hauschke and Kozur 2011)	Lower Saxony, Germany
Casterolimulus kletti Holland et al., 1975	Fox Hills Formation	Maastrichtian (Lerner et al. 2017)	North Dakota, USA

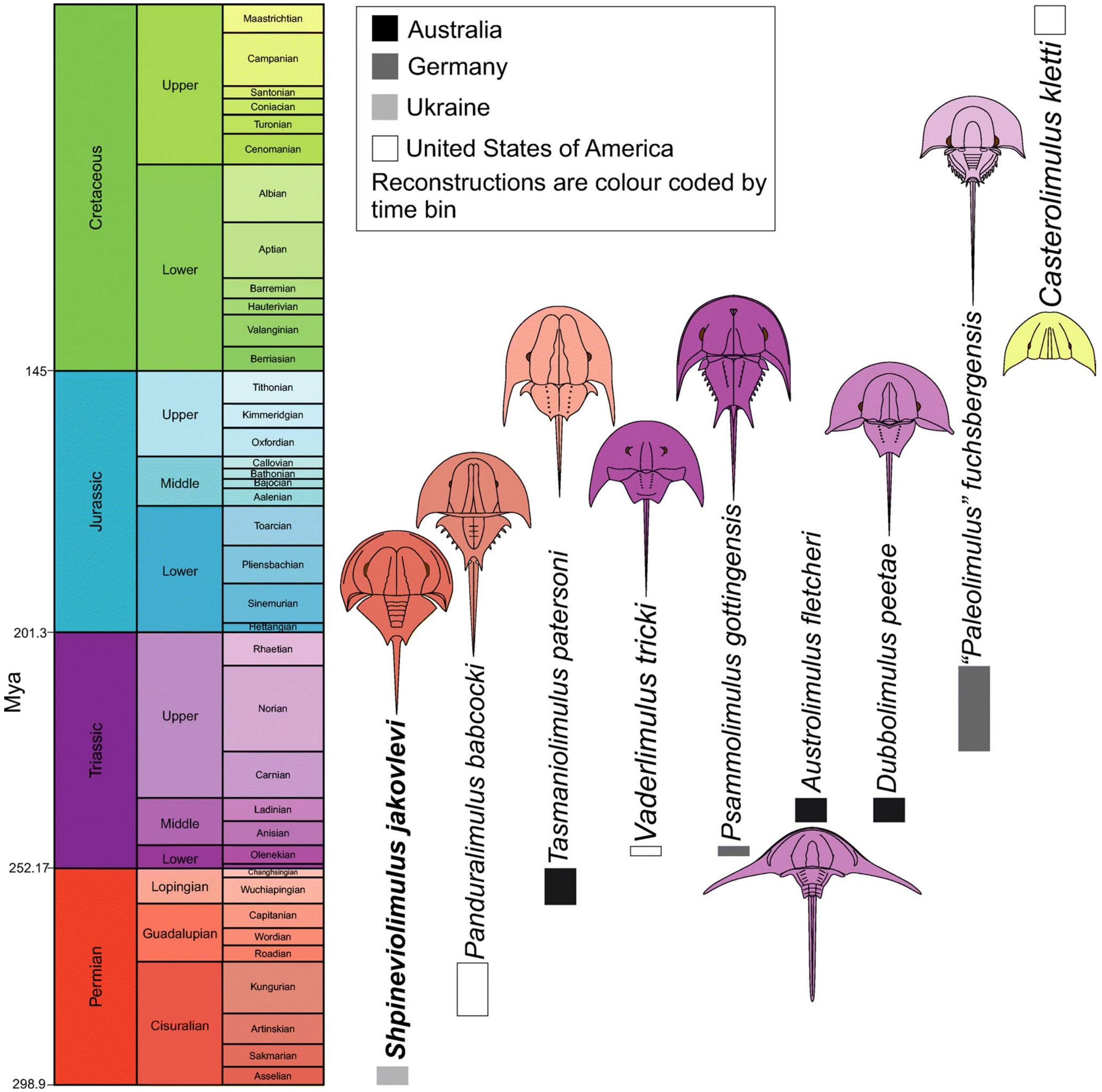


Fig. 8 Distribution of suggested austrolimulids in time and space relative to *Shpineviolimulus jakovlevi* comb. nov. (in bold). Majority of taxa with hypertrophied genal spines occur about the Permian-Triassic boundary. Reconstructions are colour coded to match stages, except *Tasmaniolimulus patersoni* that is coded to the epoch, as there is no stage division for the Jackey Shale. Consider with Table 2. Note that, in a recent revision of Xiphosurida, *Casterolimulus kletti* Holland et al., 1975 was considered a limulid (Lamsdell 2020). Further specimens of this taxon are needed to more accurately determine where this genus is located, as presently only a partially preserved prosoma is known (Bicknell and Pates 2020)

Conclusion

Re-examination of specimens from historically important collections is a salient approach for uncovering new morphological and taxonomic information on long-lived groups. Re-describing three horseshoe crab specimens from the Chernyshev Central Museum of Geological Exploration here has uncovered more morphological information on one of the oldest xiphosurids and prompted the naming of a new limuloid genus. Future research related to this should involve restudying supposed *Paleolimulus* species to uncover the true evolutionary record of both Paleolimulidae and Austrolimulidae.

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Authors' contributions RDCB designed the study, gathered images, and wrote most of the main text. SAB conducted analyses and helped develop the Methods. SVN produced species reconstructions and wrote the Stratigraphic details section. All authors reviewed the final draft.

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Data availability One supplemental phylogenetic matrix is accessible by downloading the Supplemental Documents associated with this publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Code availability Not applicable.

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