

Original Article

Cite this article: Bicknell RDC, Hecker A, and Heyng AM (2021) New horseshoe crab fossil from Germany demonstrates post-Triassic extinction of Austrolimulidae. *Geological Magazine* 158: 1461–1471. <https://doi.org/10.1017/S0016756820001478>

Received: 13 October 2020
Revised: 2 December 2020
Accepted: 29 December 2020
First published online: 11 February 2021

Keywords:

Xiphosurida; Pechgraben; Hettangian; horseshoe crab; *Franconiolimulus*

Author for correspondence:

Russell D. C. Bicknell,
Email: rdcbicknell@gmail.com

New horseshoe crab fossil from Germany demonstrates post-Triassic extinction of Austrolimulidae

Russell D. C. Bicknell¹ , Andreas Hecker² and Alexander M. Heyng³

¹Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales, 2351, Australia; ²Jura Museum, 85072 Eichstätt, Germany and ³amh-Geo, 84168 Aham, Germany

Abstract

Horseshoe crabs within Austrolimulidae represent the extreme limits to which the xiphosurid *Bauplan* could be modified. Recent interest in this group has uncovered an unprecedented diversity of these odd-ball xiphosurids and led to suggestions that Austrolimulidae arose during the Permian Period and had become extinct by the end of the Triassic Period. Here, we extend the temporal record of Austrolimulidae by documenting a new horseshoe crab from the Lower Jurassic (Hettangian) Bayreuth Formation, *Franconiolimulus pochankei* gen. et sp. nov. The novel specimen displays hypertrophied genal spines, a key feature indicative of Austrolimulidae, but does not show as prominent accentuation or reduction of other exoskeletal sections. In considering the interesting family, we explore the possible origins and explanations for the bizarre morphologies exhibited by the Austrolimulidae and present hypotheses regarding the extinction of the group. Further examination of horseshoe crab fossils with unique features will undoubtedly continue to increase the diversity and disparity of these curious xiphosurids.

1. Introduction

Horseshoe crabs (Chelicerata, Xiphosurida) are extant marine chelicerates that have a fossil record extending back to the Ordovician Period (Rudkin *et al.* 2008; Van Roy *et al.* 2010, 2015). This fossil record, coupled with apparent evidence for evolutionary stasis and the co-called ‘living fossil’ condition, has resulted in examination of the group somewhat sporadically over the last two centuries (Bicknell & Pates, 2020). However, over the past five years, a modern renaissance in xiphosurid research has occurred. This explosion of research is concurrent with the development of a new phylogenetic framework for Xiphosurida and the synthesis of taxonomy with geometric morphometric methods (Lamsdell & McKenzie, 2015; Lamsdell, 2016, 2020; Lerner *et al.* 2016, 2017; Błażejowski *et al.* 2017; Naugolnykh, 2017, 2020; Zuber *et al.* 2017; Bicknell *et al.* 2018, 2019a, b, c, d, e, 2020, *in press*; Haug & Rötzer, 2018; Shpinev, 2018; Shpinev & Vasilenko, 2018; Bicknell, 2019; Bicknell & Pates, 2019, 2020; Tashman *et al.* 2019; Haug & Haug, 2020; Lamsdell *et al.* 2020 represent the majority of key publications). The taxonomic component of this renaissance has seen re-examination of both historically important and new specimens; a crucial direction for organizing oversplit groups (such as *Euproops* Meek, 1867 and *Paleolimulus* Dunbar, 1923) while simultaneously increasing the diversity of previously under-represented groups, such as Austrolimulidae. As a result, the austrolimulid diversity has increased from one genus to at least six genera (see Bicknell *et al.* 2020; Lamsdell, 2020). Continued examination of this family has demonstrated the origin of these extreme xiphosurid forms in the Permian Period (Bicknell, 2019; Bicknell *et al.* 2020), followed by a Triassic diversification event and apparent extinction by the end of the Triassic Period (Lamsdell, 2020). New xiphosurid fossils need to be identified to thoroughly understand the timing of this extinction event. To align with this direction, here we assess a new horseshoe crab specimen from the lowermost Jurassic deposits of Upper Franconia, Bavaria, that represents the youngest austrolimulid, the third genus of the family known from German deposits, and increases the already diverse German xiphosurid fossil record (Table 1, Fig. 1).

2. Institutional acronyms

AM F: Australian Museum, Sydney, New South Wales, Australia; GZG INV: Geowissenschaftliches Zentrum der Georg-August-Universität Geowissenschaftliches Museum, Göttingen, Germany; MMF: Geological Survey of New South Wales, Londonderry, New South Wales, Australia; SSN: Paläontologisches Museum Nierstein, Nierstein, Germany; UCM: University of Colorado Museum of Natural History, Boulder, Colorado, USA; USNM: United

Table 1. Records of named Palaeozoic and Mesozoic xiphosurids from German deposits. Order by Family, then time periods

| Species | Family | Formation | Relevant publications | Period | Series | Stage | Reference for age constraints |
|--|-----------------|--|---|-------------------|--------------------------------|------------------------|--|
| <i>Bellinurus</i> cf. <i>truemani</i> Dix & Pringle, 1929 | Belinuridae | Sprockhövel Formation, Germany | Schultka (1994) | Carboniferous | Lower Pennsylvanian | Bashkirian | Martha et al. (2014) |
| <i>Euproops bifidus</i> Seigfried, 1972 | Belinuridae | ? Ibbenbüren Formation | Siegfried (1972) | Carboniferous | Middle Pennsylvanian | Moscovian | Wuestefeld et al. (2014) |
| <i>Euproops</i> (“Piesproops”) sp. | Belinuridae | Osnabrück Formation | Haug et al. (2012), Bicknell et al. (2019b), Haug & Haug (2020) | Carboniferous | Middle Pennsylvanian | Moscovian | Haug et al. (2012) |
| <i>Liomesaspis laevis</i> Raymond, 1944 | Belinuridae | Meisenheim Formation | Malz & Poschmann (1993), Schindler & Poschmann (2012) | Permian | Cisuralian | Sakmarian | Witzmann & Brainerd (2017) |
| <i>Psammolimulus gottingensis</i> Lange, 1923 | Austrolimulidae | Solling Formation | Lange (1923), Meischner (1962), Kustatscher et al. (2014), Bicknell et al. (2019b), Bicknell & Pates (2019) | Triassic | Early Triassic | Olenekian (Spathian) | Lerner et al. (2017) |
| “ <i>Paleolimulus</i> ” <i>fuchsbergensis</i> Hauschke & Wilde, 1987 | Austrolimulidae | Exter Formation | Hauschke & Wilde (1987), Hauschke (2014) | Triassic | Late Triassic | Rhaetian | Hauschke & Kozur (2011) |
| <i>Limulitella henkeli</i> (von Fritsch, 1906) | Limulidae | Jena Formation | von Fritsch (1906) | Triassic | Early Triassic | Anisian | Knaust (2019) |
| <i>Limulitella liasokeuperinus</i> (Braun, 1860) | Limulidae | ?Exter Formation – ?Bayreuth Formation | Braun (1860), Hauschke & Wilde (1984) | Triassic–Jurassic | Late Triassic – Early Jurassic | ?Rhaetian–Hettangian | Hauschke & Kozur (2011), Kohli et al. (2016) |
| <i>Franconiolimulus pochankei</i> gen. et sp. nov. | Austrolimulidae | Bayreuth Formation | — | Jurassic | Early Jurassic | Hettangian | Kohli et al. (2016) |
| <i>Mesolimulus walchi</i> (Desmarest, 1822) | Limulidae | Solnhofen Limestone | Desmarest (1822), Koenig (1825), Zittel (1885), Shuster (2001), Shuster & Anderson (2003), Briggs et al. (2005), Rudkin & Young (2009), Sekiguchi & Shuster (2009), Haug et al. (2011), Ebert et al. (2015), Hauschke & Mertmann (2016), Bicknell et al. (2019b, d) | Jurassic | Late Jurassic | Kimmeridgian–Tithonian | Odin et al. (2019) |

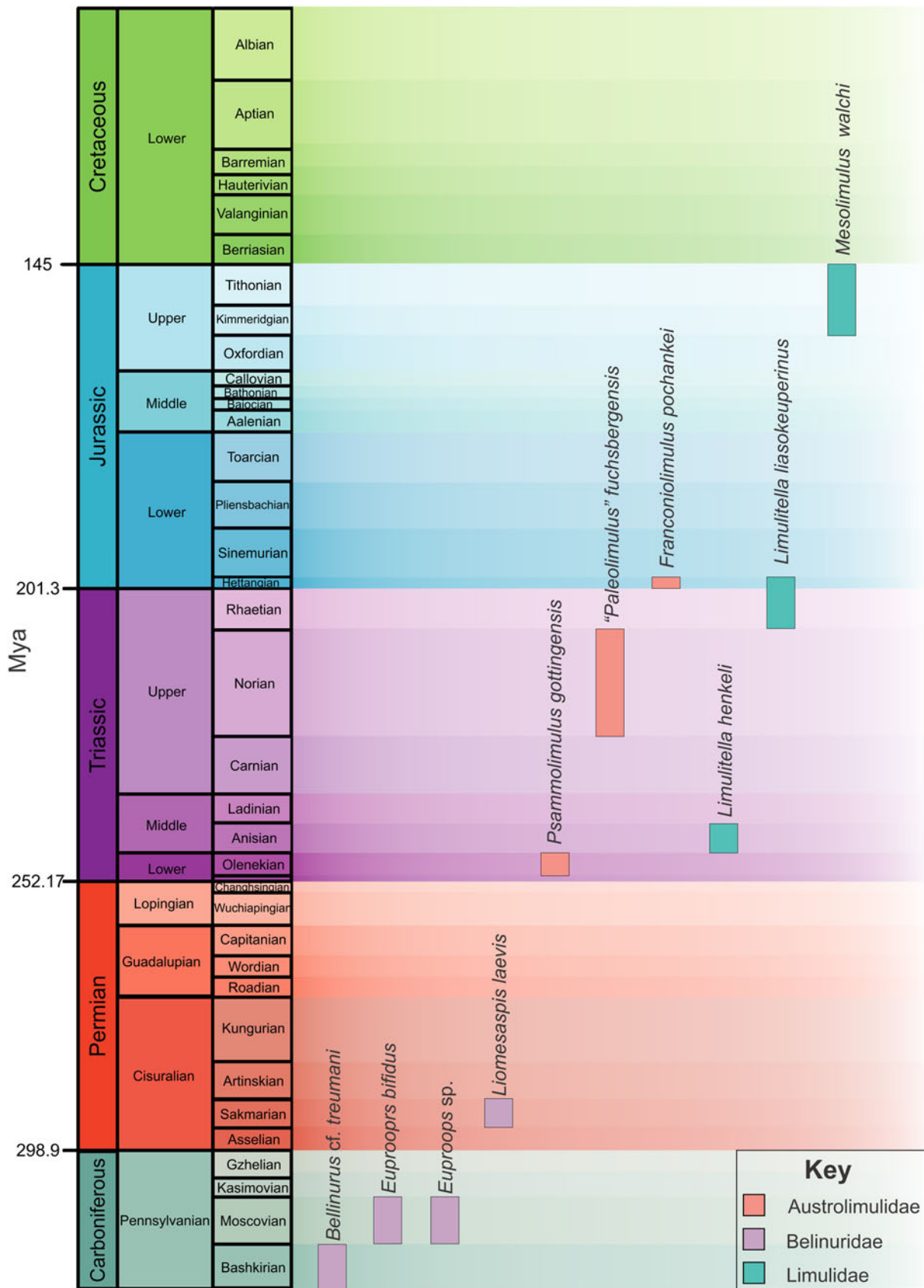


Fig. 1. (Colour online) Temporal ranges of Palaeozoic and Mesozoic xiphosurids from German deposits. See Table 1 for further information.

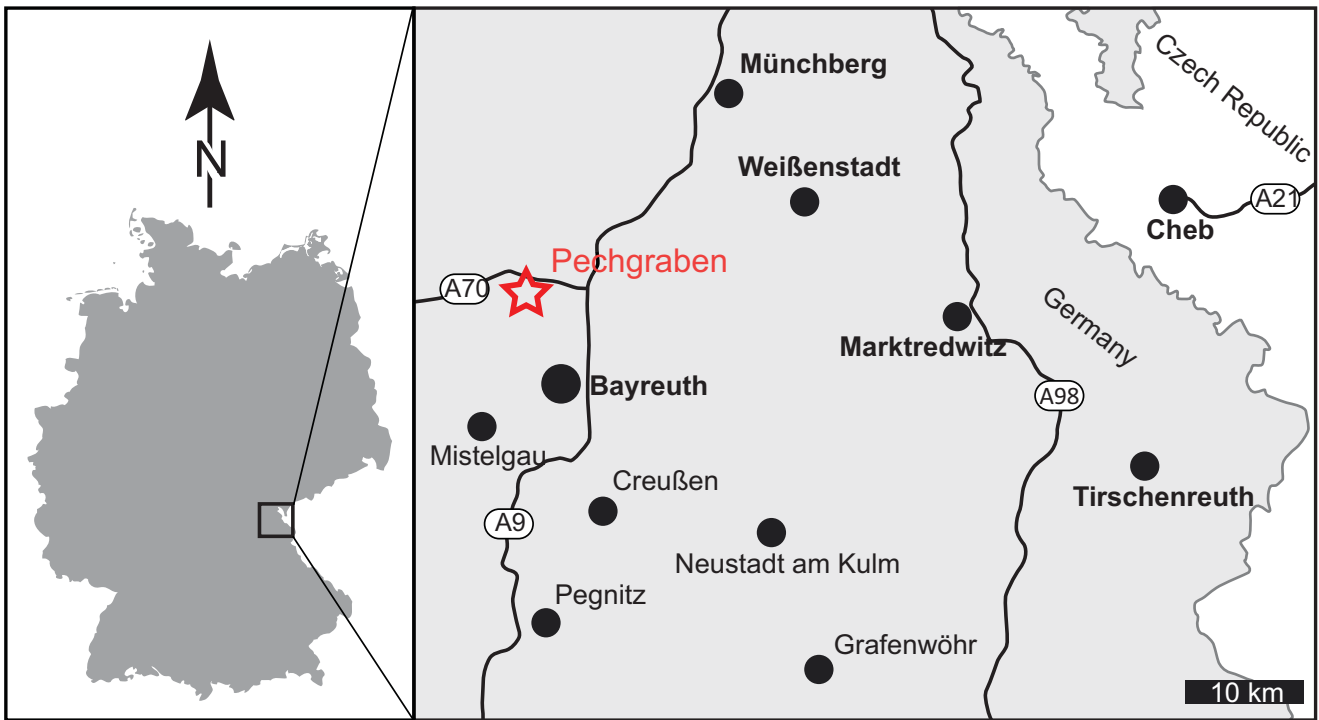


Fig. 2. (Colour online) Map of Germany showing close-up of specimen locality at Pechgraben (red star).

| System | Series | Stage | Stratigraphic correlation chart | |
|------------------------|----------------|---------------|---------------------------------|------------------------------|
| | | | W | E |
| Jurassic | Lower Jurassic | Pliensbachian | Amaltheenton Formation | |
| | | | Numismalismergel Formation | |
| | | Sinemurian | Obtususton Formation | Gryphaeensandstein Formation |
| | | | Arietenkalk Formation | |
| | | Hettangian | Angulatensandstein Formation | Bayreuth Formation |
| Pilonotenton Formation | | | | |
| Triassic | Upper Triassic | Rhaetian | Exter Formation | |

Fig. 3. (Colour online) Simplified correlation of Triassic–Jurassic sequences in the Bayreuth region. Stratigraphic position of units containing *Franconiolimulus pochankei* gen. et. sp. nov. highlighted (red star).

States National Museum, Washington, DC, USA; UTGD: Geology Department, University of Tasmania, Tasmania, Australia.

3. Geological context

The specimen considered here was collected in 1999 by Harald Stapf from a clay lens at the Pechgraben locality; a sand pit of the Bocksrück Sandgrube GmbH & Co. KG, situated near Neudrossenfeld, Franconia, Bavaria, Southern Germany (TK 1:25 000, No. 5935 Marktschorgast, 50° 00' 08.1" N, 11° 32' 26.2" E; Fig. 2). Following Kohli *et al.* (2016), the Pechgraben material likely represents an outcrop of the Bayreuth Formation. The Bayreuth Formation is considered temporally contiguous with the Pilonotenton Formation (lower Hettangian) and the overlying Angulatussandstein Formation (upper Hettangian; Fig. 3); however, these formations cannot be confidently discerned at Pechgraben (Bloos *et al.* 2006). The Bayreuth Formation is largely composed of sandstones with intercalated clay lenses, the latter locally rich in exceptionally preserved terrestrial plant fossils indicative of a fluvial-limnic to brackish environment with limited coastal influence (Bloos *et al.* 2006).

The Bayreuth Formation at Pechgraben shows an extraordinary level of preservation (suggesting it may represent a *Konservat Lagerstätte*) and, as such, has been examined variably over the last 160 years (Braun, 1860; Weber, 1968; van Konijnenburg-van Cittert & Schmeißner, 1999; Bauer *et al.* 2015). In particular, a variety of distinct plant groups have been described from the locality (van Konijnenburg-van Cittert *et al.* 2001; van Konijnenburg-van Cittert, 2010; Bauer *et al.* 2015; Kustatscher *et al.* 2016). Curiously, animal remains are rarely identified at Pechgraben (Braun, 1860; Weber, 1968; Emmert, 1977; Bloos *et al.* 2006; Kohli *et al.* 2016). Aside from horseshoe crabs, animal fossils include eggs from freshwater hybodont sharks *Palaeoxyris alterna* Fischer *et al.* 2011 and *Palaeoxyris muensteri* (Presl, 1838) (Fischer *et al.* 2011), a freshwater mussel – *Anoplophora* (Syn. *Anodonta*) *liasokeuperina* (Braun, 1860) – and rare dragonfly fossils (Bechly, 2015; Kohli *et al.* 2016). Taken together, the Pechgraben site likely preserves a low-energy freshwater environment (possibly an oxbow lake) that was surrounded by dense vegetation (Weber, 1968; Schmeissner & Hauptmann, 1998; van Konijnenburg-van Cittert *et al.* 2001).

4. Methods

The studied specimen is housed in the Paläontologisches Museum Nierstein, Nierstein, Rhineland-Palatinate, Germany and was assigned specimen number SSN 8PG35. The specimen was photographed using a Canon EOS 800D with a Canon EFS 35 mm macro lens under normal and low-angle halogen light to highlight all features. The camera was controlled by Capture One Pro 12.1. Measurements were digitally obtained from photographs using ImageJ. For comparison, photographs of other austrolimulids were requested from collections or gathered by the authors. We follow the systematic taxonomy of Bicknell & Pates (2020) and the anatomical terms presented in Bicknell (2019) and Bicknell *et al.* (2019c, 2020).

5. Systematic palaeontology

Subphylum Chelicerata Heymons, 1901

Class Xiphosura Latreille, 1802

Order Xiphosurida Latreille, 1802

Suborder Limulina Richter & Richter, 1929

Superfamily Limuloidea Zittel, 1885

Family Austrolimulidae Riek, 1955

Genus *Franconiolimulus* gen. nov.

Etymology. Generic name combines the Upper Franconian origin of the specimen with the generic name of the iconic American horseshoe crab; *Limulus*.

Type and only species. *Franconiolimulus pochankei* gen. et sp. nov. type and only species.

Diagnosis. An austrolimulid with kinked genal spines that terminate over half way along the thoracetron, an anteriorly effaced, keeled cardiac lobe, and a medial thoracetric lobe without pronounced keeling.

Franconiolimulus pochankei sp. nov.

Figures 4–6

Diagnosis. Same as for genus.

Etymology. The species name *pochankei* honours Hartmut Pochanke, whose knowledge of the Pechgraben geology and aid in specimen collection resulted in the identification of the studied specimen.

Holotype specimen. SSN 8PG35

Location. 95521 Neudrossenfeld, district Pechgraben, owner Bocksrück Sandgrube GmbH & Co. KG (50° 00' 08.1" N, 11° 32' 26.2" E)

Formation, type locality, age. Bayreuth Formation, Pechgraben, Early Jurassic, Hettangian.

Distribution. Limited to the Pechgraben fossil-bearing clay lenses.

Preservation. SSN 8PG35 is preserved as a slightly vaulted, cream- to orange-coloured prosoma and thoracetron on a slab of light-brown-coloured clay.

Description. SSN 8PG35 is a slightly deformed articulated prosoma and thoracetron (Fig. 4). The specimen is 48.8 mm long. Prosoma is completely preserved, has a parabolic outline, is 30.1 mm long at midline and is 47.0 mm wide at the widest section. A thin prosomal rim is preserved, with a maximum width of 1.3 mm. Slight deformation of the exoskeleton is noted about the anterior right margin of the prosoma (Fig. 5). Both ophthalmic ridges are preserved. Left ophthalmic ridge is 19.4 mm long and lacks concavity. Right ophthalmic ridge is 21.2 mm long and is slightly concave. Ophthalmic ridges do not converge anteriorly. Lateral compound eyes are preserved on the ophthalmic ridges, c. 7.5 mm anteriorly from prosoma–thoracetron border (Fig. 4d). A cardiac lobe is present. The cardiac lobe is 8.0 mm wide posteriorly, tapering anteriorly into an apparently triangular shape. A pronounced cardiac ridge is noted, 20.1 mm long (Fig. 5). The ridge becomes less pronounced anteriorly. Ocelli are not observed. Both genal spines are preserved and splay laterally from the thoracetron. Genal spines extend posteriorly to terminate over half way along thoracetron. Kinks are observed approximately half way along the genal spine length. Left genal tip is 24.2 mm from the organismal midline. Angle between the left genal spine and left side of the thoracetron is 65.2°. Right genal spine is 19.0 mm from the organismal midline. Angle between the right genal spine and right side of the thoracetron is 66.9°. An occipital band is preserved along the left genal spine. Band starts at the lateral-most section of prosoma–thoracetron

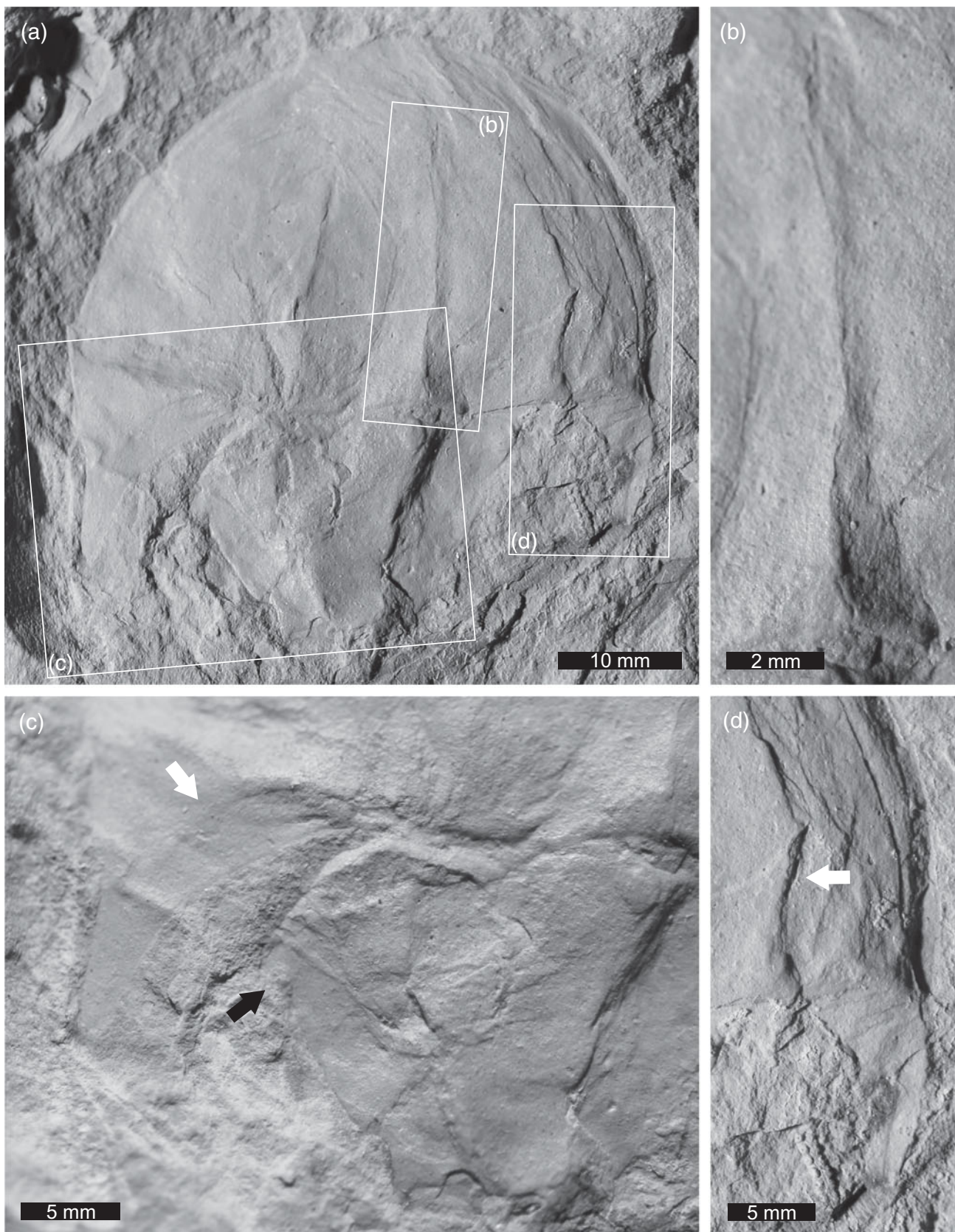


Fig. 4. *Franconiolimulus pochankei* gen. et. sp. nov., holotype (SSN 8PG35). (a) Complete specimen. Boxes indicate close-up of the specimen in (b–d). (b) Close-up of cardiac lobe and associated ridge. (c) Close-up of left side of posterior prosoma and thoracetreron. Occipital band (white arrow) is effaced distally. Thoracetrone border shows a small free lobe (black arrow) and notable tapering of the thoracetreron. (d) Close-up of right genal spine. Ophthalmic ridge with lateral compound eye is prominent (white arrow). Images are converted to greyscale. Image credit: Andreas Hecker.

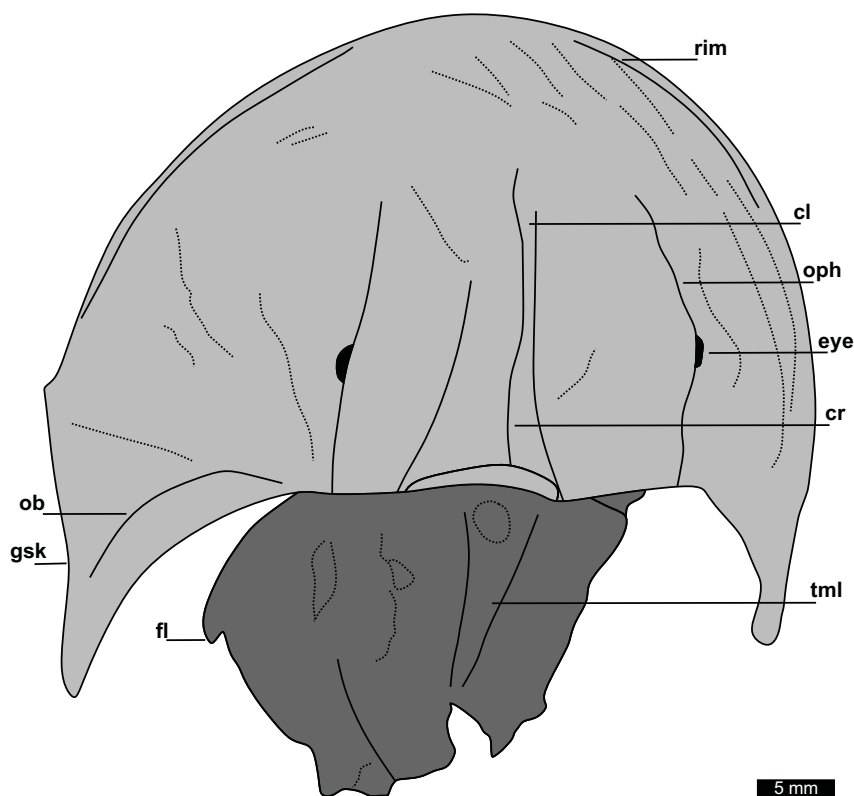


Fig. 5. Interpretative drawing of *Franconiolimulus pochankei* gen. et. sp. nov., holotype (SSN 8PG35) showing key morphological features. Abbreviations: cl – cardiac lobe; cr – cardiac ridge; eye – lateral compound eye; fl – free lobe; gsk – genal spine kink; ob – occipital band; oph – ophthalmic ridge; rim – prosomal rim; tml – thoracetrone medial lobe. Dotted lines indicate deformation of the exoskeleton.

joint and extends along the genal spine, becoming effaced towards spine terminus (Fig. 4c). Prosoma–thoracetrone hinge is pronounced, 21.3 mm wide and 1.8 mm long. No prosomal appendages are preserved.

The thoracetrone is partly preserved: the left side is completely preserved and the proximal section of the right side is preserved (Figs 4, 5). As such, width measurements will not represent life-size. Shape of the left side suggests the thoracetrone would be strongly trapezoidal (see Fig. 6). It is 17.8 mm long, 23.2 mm wide anteriorly, increasing to a width of 25.6 mm at 5.8 mm posteriorly from the prosoma–thoracetrone joint, tapering to 10.7 mm wide posteriorly. At the maximum width, the thoracetrone is c. 50% narrower than the prosoma. A medial lobe is visible, slightly domed, but poorly defined. The lobe is slightly triangular, tapering from 8.3 mm to becoming effaced posteriorly. No segmentary furrows are present. The left pleural lobe is not segmented, 17.8 mm long, 12.4 mm wide, tapering to the posterior specimen edge (Fig. 4c). No marginal rim is preserved on the left side. A reduced free lobe is present on anterior section of pleural lobe (Fig. 4c). Left pleural lobe truncates markedly towards the posterior-most region. The right pleural lobe is poorly preserved, and appears to have been injured as the edge seems slightly cicatrized. The thoracetrone–telson articulation and telson are not preserved.

Remarks. Austrolimulids represent the extreme morphological limitations of the xiphosurid *Bauplan* (Fig. 7). This is manifested in hypertrophied genal spines (hypertrophy here refers to overdeveloped spines, often with a marked splay when compared with limulid genal spines; see *Austrolimulus fletcheri* Riek, 1955, *Psammolimulus gottlingensis* Lange, 1923, *Tasmaniolimulus patersoni* Bicknell, 2019 and *Vaderlimulus tricki* Lerner et al. 2017)

and decreased size of major exoskeletal sections (*Dubbolimulus peetae* Pickett, 1984). The hypertrophied genal spines of the Pechgraben horseshoe crab indicates an austrolimulid alignment (Fig. 6). The lack of an extreme lateral genal spine splay excludes SSN 8PG35 from *A. fletcheri* and *V. tricki* (Fig. 7a, h) and the lack of an inflated free lobe excludes SSN 8PG35 from *Ps. gottlingensis* (Fig. 7c, d). The kinks along the genal spines are comparable to *T. patersoni* and *Panduralimulus babcocki* Allen & Feldmann, 2005 (Fig. 7b, e, f). However, SSN 8PG35 lacks the M-shaped ophthalmic ridge joint known from *T. patersoni* and the strongly keeled medial thoracetrone lobe of *Pa. babcocki*. Finally, as SSN 8PG35 lacks a highly reduced thoracetrone, the material is excluded from *D. peetae* (Fig. 7g). As such, we assert that the placement of the Pechgraben horseshoe crab into a new genus and species is a valid taxonomic conclusion. *Franconiolimulus pochankei* gen. et sp. nov. therefore represents the youngest austrolimulid and illustrates that the family survived into the Jurassic Period.

Consideration must be given to *Limulitella liasoqueuperinus* (Braun, 1860) as this taxon is known from Upper Triassic (? Rhaetian) through to the lowermost Jurassic (?Hettangian) deposits of Franconia. There is poor stratigraphic control on the taxon; however, it seems that the material is from either the Exter Formation or Bayreuth Formation (Hauschke & Wilde, 1984). Assuming that *L. liasoqueuperinus* is from the Bayreuth Formation, it is imperative that we demonstrate how SSN 8PG35 is distinct from *L. liasoqueuperinus*. Considering the original work in Braun (1860, fig. 1; note that, according to Hauschke & Wilde, 1984, the holotype has since been lost), the line drawing shows the ophthalmic ridges forming an M-shaped joint anterior to a well-defined cardiac lobe. Both of these features are unknown

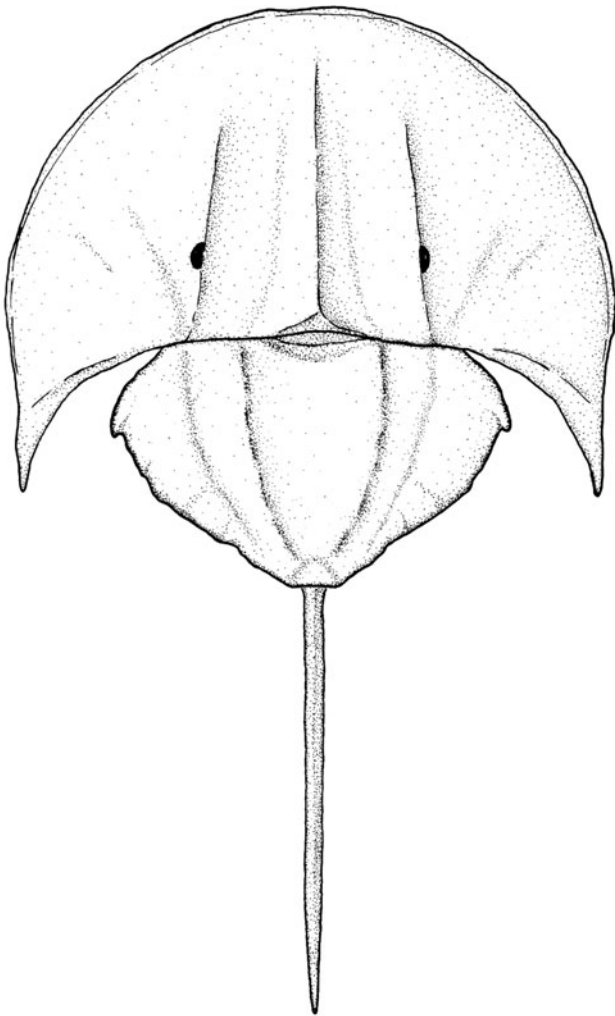


Fig. 6. Idealized reconstruction of *Franconiolimulus pochankei* gen. et. sp. nov. Reconstruction credit: Andreas Hecker.

to SSN 8PG35. The only other comparative material from Franconia ascribed to *L. cf. liasoikeuperinus* was presented in Hauschke & Wilde (1984, exemplar 1). This partial prosoma shows pronounced cardiac lobe furrows, ophthalmic ridges joining anteriorly and an elongate diamond-shaped feature along the cardiac lobe ridge. These features are not observed in SSN 8PG35. To this end, we assert that SSN 8PG35 is distinct from *L. liasoikeuperinus*. Possible evidence for two xiphosurids in the Bayreuth Formation suggests that the depositional environment of the formation may have represented an ideal habitat for freshwater horseshoe crabs that also allowed for preservation of cuticular exoskeletons. Such taxonomic abundance is known to the Bear Gulch Limestone (Mississippian, Serpukhovian), Montana, USA; the Mazon Creek *Lagerstätte* within the Francis Creek Shale Member of the Carbondale Formation (Pennsylvanian, Moscovian), Illinois, USA; the Wellington Formation (Cisuralian, Wolfcampian), Oklahoma, USA; and the Alcover Limestone Formation (Middle Triassic, Ladinian), Spain (Bicknell & Pates, 2020). Further examination of the Exter and Bayreuth formations is needed to determine the true xiphosurid diversity of these interesting deposits.

6. Discussion

The identification of a Jurassic austrolimulid genus demonstrates that the family had survived the supposed end-Triassic austrolimulid extinction and are now known from the time period when horseshoe crabs are considered representative of evolutionary stasis (Kin & Błażejowski, 2014). Comparing *Franconiolimulus pochankei* gen. et sp. nov. with the Triassic austrolimulids, an extreme genal spine splay and a reduction of exoskeletal sections are not observed in *F. pochankei*. This observation prompts two questions: (1) Why were austrolimulid morphologies so diverse during the Triassic? (2) Why are austrolimulids unknown after *F. pochankei*? The extreme morphological diversity of Triassic austrolimulids is often ascribed to habitation of freshwater conditions (Lerner *et al.* 2017; Bicknell, 2019; Bicknell & Pates, 2019, 2020; Bicknell *et al.* 2020). The prevalence of overdeveloped genal spines may have decreased the impact of uni-directional freshwater currents (Bicknell, 2019), potentially allowing them to be anchored and avoid being transported downstream. This evolutionary transition therefore resulted in notable innovations and extreme morphological variation within the group (Bicknell, 2019; Bicknell & Pates, 2019; Bicknell *et al.* 2020). Interestingly, Permian and Jurassic forms lack the notable genal splay common to Triassic austrolimulids (Compare *Tasmaniolimulus patersoni* and *F. pochankei* to *Dubbolimulus peetae* and *Austrolimulus fletcheri*). This may reflect habitation of more brackish conditions, or the lack of morphological stock that would have permitted and maintained such forms. An explanation for why freshwater conditions were explored by non-belurid xiphosurids remains somewhat nebulous. A likely explanation is associated with freshwater niches that were left vacant after the end-Permian extinction (Hu *et al.* 2011; Chen & Benton, 2012). Permian-aged, freshwater xiphosurids with hypertrophied genal spines may have diversified during the Triassic Period to fill the vacant niches, capitalizing on freshwater conditions. This does not address why these forms are unknown after Early Jurassic time. Lamsdell (2020) recently tackled xiphosurid evolutionary dynamics and considered how primarily marine Limulidae was descendant from non-marine ancestors (Błażejowski *et al.* 2017; Lamsdell, 2020). This may be possible. However, this hypothesis is contradicted by the record of Triassic-aged marine limulids, such as *Sloveniolimulus rudkini* Bicknell *et al.* 2019e from the Strelovec Formation (Middle Triassic, Anisian), Slovenia and *Heterolimulus gadeai* Vía & De Villalta, 1966 from the Alcover Limestone Formation. It is therefore more likely that the divergence of austrolimulids from the more standard limulid morphology resulted in forms that were not optimized for palaeoenvironmental and palaeoecological changes. As such, austrolimulids were likely outcompeted by other freshwater organisms leading into the rest of the Jurassic Period.

Acknowledgements. This research was supported by funding from an Australian Postgraduate Award (to RDCB), a University of New England Postdoctoral Research Fellowship (to RDCB), a Charles Schuchert and Carl O Dunbar Grants-in-Aid award (to RDCB), and a James R Welch Scholarship (to RDCB). We thank Allan Lerner, David Barnes, Gerhart Hundertmark, and Josh White for photographs of specimens. We thank Harald Staf, Isabella von Lichten, Mark Florence, Matthew McCurry, and Yong-Yi Zhen for help with collections. We thank Jan Fischer, Joachim M Rabold, and Ulrike Albert for discussions regarding the Pechgraben ecology. Finally, we thank the two anonymous reviewers for their constructive comments that improved the direction and use of the text.

Conflict of interest. None.

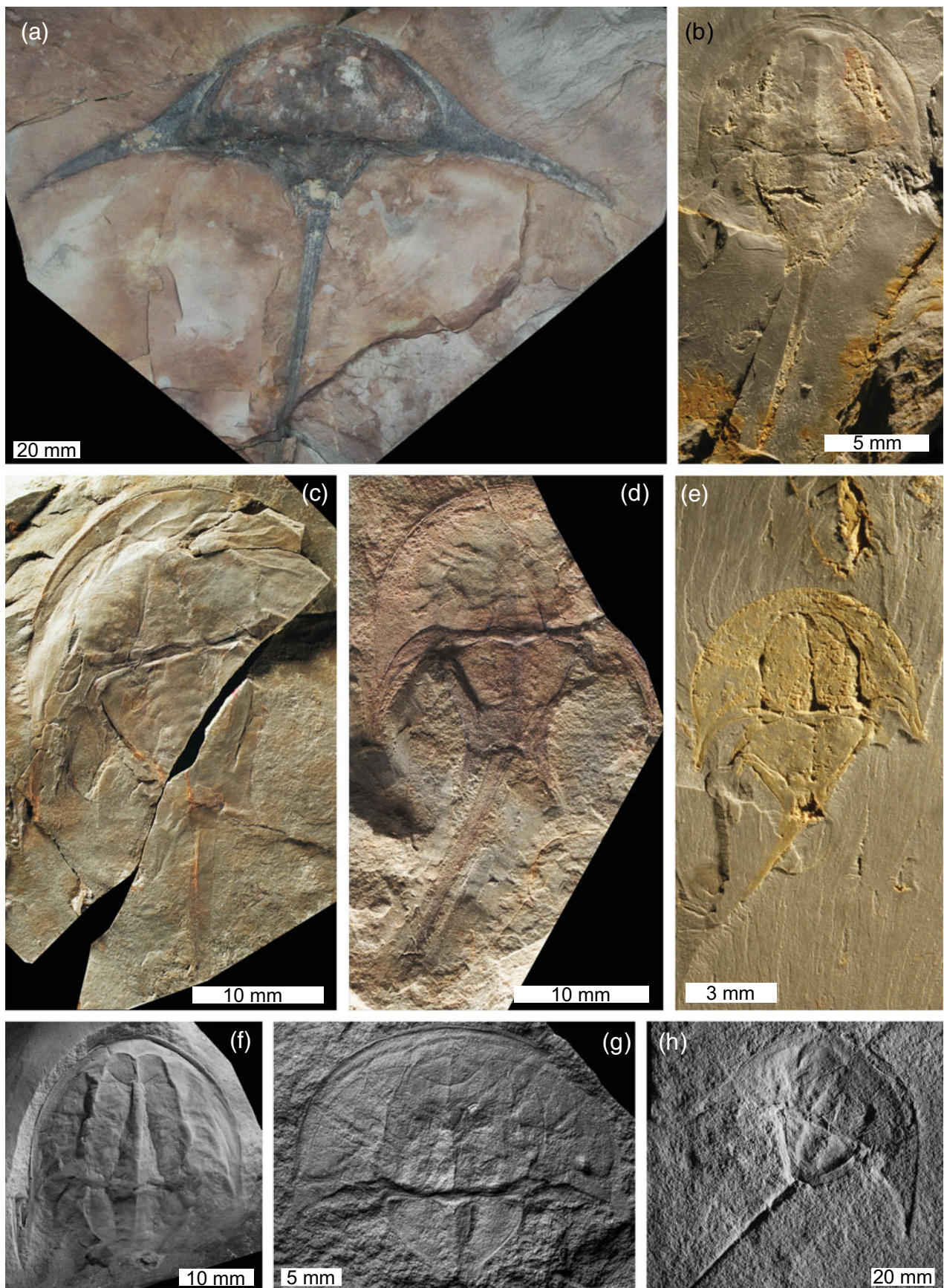


Fig. 7. (Colour online) Other representatives of Austroliimulidae. (a) *Austroliimulus fletcheri* from the Beacon Hill Formation (Middle Triassic, Ladinian), New South Wales, Australia. AM F38274, holotype. (b, e) *Panduralimulus babcocki* from the Maybelle Limestone, Lueders Formation (Permian, Cisuralian, Kungurian), Texas, USA: (b) USNM 520723, holotype and (e) USNM 520724, paratype. (c, d) *Psammolimulus gottingensis* from the Solling Formation (Lower Triassic, Olenekian, Spathian), Lower Saxony, Germany: (c) GZG INV 15376a and (d) GZG INV 45730a. (f) *Tasmaniolimulus patersoni* from the Jackey Shale (Permian, Lopingian), Tasmania, Australia. UTGD 123979, holotype. (g) *Dubbolimulus peetae* from the Ballimore Formation (Middle Triassic, Ladinian), New South Wales, Australia. MMF 27693, holotype. (h) *Vaderlimulus tricki* from the lower shale unit, Thaynes Group (Lower Triassic, Olenekian, Spathian), Idaho, USA. UCM 140.25, holotype. Image credit: (a) Josh White; (b, e, f) Russell Bicknell; (c, d) Gerhart Hundertmark; (g) David Barnes; and (h) Allan Lerner. (f) Coated in ammonium chloride sublimate.

References

- Allen JG and Feldmann RM (2005) *Panduralimulus babcocki* n. gen. and sp., a new Limulacean horseshoe crab from the Permian of Texas. *Journal of Paleontology* **79**, 594–600.
- Bauer K, Kustatscher E, Dütsch G, Schmeißner S, Krings M and van Konijnenburg-van Cittert JHA (2015) *Lepacyclotes kirchneri* n. sp. (Isoetales, Isoetaceae) aus dem unteren Jura von Oberfranken, Deutschland. *Berichte der Naturwissenschaftlichen Gesellschaft Bayreuth* **27**, 429–43.
- Bechly G (2015) Fossile Libellennachweise aus Deutschland (Odonoptera). *Libellula Supplement* **14**, 423–64.
- Bicknell RDC (2019) Xiphosurid from the Upper Permian of Tasmania confirms Palaeozoic origin of Austrolimulidae. *Palaeontologia Electronica* **22**(3), 1–13.
- Bicknell RDC, Amati L and Ortega-Hernández J (2019a) New insights into the evolution of lateral compound eyes in Palaeozoic horseshoe crabs. *Zoological Journal of the Linnean Society* **187**(4), 1061–77.
- Bicknell RDC, Błażejowski B, Wings O, Hitij T and Botton ML (in press) Critical re-evaluation of Limulidae reveals limited *Limulus* diversity. *Papers in Palaeontology*, <https://doi.org/10.1002/spp2.1352>
- Bicknell RDC, Brougham T, Charbonnier S, Sautereau F, Hitij T and Campione NE (2019b) On the appendicular anatomy of the xiphosurid *Tachypleus syriacus* and the evolution of fossil horseshoe crab appendages. *The Science of Nature* **106**, 38.
- Bicknell RDC, Klinkhamer AJ, Flavel RJ, Wroe S and Paterson JR (2018) A 3D anatomical atlas of appendage musculature in the chelicerate arthropod *Limulus polyphemus*. *PLoS One* **13**, e0191400.
- Bicknell RDC, Lustrri L and Brougham T (2019c) Revision of ‘*Bellinurus*’ *carteri* (Chelicerata: Xiphosura) from the Late Devonian of Pennsylvania, USA. *Comptes Rendus Palevol* **18**, 967–76.
- Bicknell RDC, Naugolnykh SV and Brougham T (2020) A reappraisal of Paleozoic horseshoe crabs from Russia and Ukraine. *The Science of Nature* **107**, 46.
- Bicknell RDC and Pates S (2019) Xiphosurid from the Tournaisian (Carboniferous) of Scotland confirms deep origin of Limuloidea. *Scientific Reports* **9**, 17102.
- Bicknell RDC and Pates S (2020) Pictorial atlas of fossil and extant horseshoe crabs, with focus on Xiphosurida. *Frontiers in Earth Science* **8**, 60.
- Bicknell RDC, Pates S and Botton ML (2019d) *Euproops danae* (Belinuridae) cluster confirms deep origin of gregarious behaviour in xiphosurids. *Arthropoda Selecta* **28**(4), 549–55.
- Bicknell RDC, Žalohar J, Miklavc P, Celarc B, Križnar M and Hitij T (2019e) A new limulid genus from the Strelovec Formation (Middle Triassic, Anisian) of northern Slovenia. *Geological Magazine* **156**, 2017–30.
- Błażejowski B, Niedzwiedzki G, Boukhalfa K and Soussi M (2017) *Limulitella tejraensis*, a new species of limulid (Chelicerata, Xiphosura) from the Middle Triassic of southern Tunisia (Saharan Platform). *Journal of Paleontology* **91**, 960–67.
- Bloos G, Dietl G and Schweigert G (2006) Der Jura Süddeutschlands in der Stratigraphischen Tabelle von Deutschland 2002. *Newsletters on Stratigraphy* **41**, 263–77.
- Braun KFW (1860) Die Thiere in den Pflanzenschiefern der Gegend von Bayreuth. *Jahresbericht von der König. Kreis-Landwirtschafts- und Gewerbschule zu Bayreuth für das Schuljahr 1859/60*, 1–11.
- Briggs DEG, Moore RA, Shultz JW and Schweigert G (2005) Mineralization of soft-part anatomy and invading microbes in the horseshoe crab *Mesolimulus* from the Upper Jurassic Lagerstätte of Nusplingen, Germany. *Proceedings of the Royal Society of London B: Biological Sciences* **272**, 627–32.
- Chen Z-Q and Benton MJ (2012) The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* **5**, 375–83.
- Desmarest A-G (1822) Les crustacés proprement dits. In *Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et géologiques* (eds A Brongniart and A-G Desmarest). pp. 67–142. Paris: F-G Levrault.
- Dix E and Pringle J (1929) On the fossil Xiphosura from the South Wales Coalfield with a note on the myriapod *Euphoberia*. *Summary of Progress of the Geological Survey of Great Britain* **1928**(II), 90–113.
- Dunbar CO (1923) Kansas Permian insects, Part 2, *Paleolimulus*, a new genus of Paleozoic Xiphosura, with notes on other genera. *American Journal of Science* **5**, 443–54.
- Ebert M, Kölbl-Ebert M and Lane JA (2015) Fauna and predator-prey relationships of Ettling, an actinopterygian fish-dominated Konservat-Lagerstätte from the Late Jurassic of Southern Germany. *PLoS ONE* **10**, e0116140.
- Emmert U (1977) Geologische Karte von Bayern, 1:25000, Erläuterungen zum Blatt Nr. 6035 Bayreuth. Bayerisches Geologisches Landesamt, Prinzregentenstraße 28, 8000 München 2.
- Fischer J, Voigt S, Schneider JW, Buchwitz M and Voigt S (2011) A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries. *Journal of Vertebrate Paleontology* **31**, 937–53.
- Haug C and Haug JT (2020) Untangling the Gordian knot—further resolving the super-species complex of 300-million-year-old xiphosurids by reconstructing their ontogeny. *Development Genes and Evolution* **230**, 13–26.
- Haug C and Rötzer MAIN (2018) The ontogeny of the 300 million year old xiphosuran *Euproops danae* (Euchelicerata) and implications for resolving the *Euproops* species complex. *Development Genes and Evolution* **228**, 63–74.
- Haug C, Van Roy P, Leipner A, Funch P, Rudkin DM, Schöllmann L and Haug JT (2012) A holomorph approach to xiphosuran evolution—a case study on the ontogeny of *Euproops*. *Development Genes and Evolution* **222**, 253–68.
- Haug JT, Haug C, Waloszek D and Schweigert G (2011) The importance of lithographic limestones for revealing ontogenies in fossil crustaceans. *Swiss Journal of Geosciences* **104**, 85–98.
- Hauschke N (2014) Conchostraken als Zeitmarken und Faziesanzeiger in kontinentalen Ablagerungen der Trias: Fallbeispiele aus Sachsen-Anhalt und dem östlichen Niedersachsen. *Abhandlungen und Berichte für Naturkunde* **34**, 19–55.
- Hauschke N and Kozur HW (2011) Two new conchostracan species from the Late Triassic of the Fuchsberg, northern foreland of the Harz Mountains northeast of Seinstedt (Lower Saxony, Germany). In *Fossil Record 3* (eds R Sullivan, S Lucas and J Spielmann), pp. 187–94. Albuquerque: New Mexico Museum of Natural History and Science.
- Hauschke N and Mertmann D (2016) Ausgewählte Fossilfunde aus den Geologisch-Paläontologischen Sammlungen der Martin-Luther-Universität in Halle (Saale): Deutschland. *der Aufschluss* **67**, 325–53.
- Hauschke N and Wilde V (1984) Limuliden-Reste aus dem unteren Lias Frankens. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **24**, 51–56.
- Hauschke N and Wilde V (1987) *Paleolimulus fuchsbergensis* n. sp. (Xiphosura, Merostomata) aus der oberen Trias von Nordwestdeutschland, mit einer Übersicht zur Systematik und Verbreitung rezenter Limuliden. *Paläontologische Zeitschrift* **61**, 87–108.
- Heymons R (1901) Die Entwicklungsgeschichte der Scolopender. *Zoologica* **13**, 1–244.
- Hu S-X, Zhang Q-Y, Chen Z-Q, Zhou C-Y, Lü T, Xie T, Wen W, Huang J-Y and Benton MJ (2011) The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2274–82.
- Kin A and Błażejowski B (2014) The horseshoe crab of the genus *Limulus*: living fossil or stabilomorph? *PLoS ONE* **9**, e108036.
- Knaust D (2019) *Rhizocorallites* Müller, 1955 from the Triassic and Jurassic of Germany: burrow, coprolite, or cololite? *PalZ* **94**, 769–85.
- Koenig CDE (1825) *Icones fossilium sectiles: Centuria prima*. London: GB Sowerby.
- Kohli MK, Ware JL and Bechly G (2016) How to date a dragonfly: Fossil calibrations for odonates. *Palaeontologia Electronica* **19**.1.FC, 1–14.
- Kustatscher E, Franz M, Heunisch C, Reich M and Wappler T (2014) Floodplain habitats of braided river systems: depositional environment, flora and fauna of the Solling Formation (Buntsandstein, Lower Triassic) from Bremke and Fürstenberg (Germany). *Palaeobiodiversity and Palaeoenvironments* **94**, 237–70.
- Kustatscher E, van Konijnenburg-van Cittert JHA, Bauer K and Krings M (2016) Strobilus organization in the enigmatic gymnosperm *Bernettia inopinata* from the Jurassic of Germany. *Review of Palaeobotany and Palynology* **232**, 151–61.
- Lamsdell JC (2016) Horseshoe crab phylogeny and independent colonizations of fresh water: ecological invasion as a driver for morphological innovation. *Palaeontology* **59**, 181–94.

- Lamsdell JC (2020) A new method for quantifying heterochrony in evolutionary lineages. *Paleobiology* 1–22.
- Lamsdell JC and McKenzie SC (2015) *Tachypleus syriacus* (Woodward)—a sexually dimorphic Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. *Organisms Diversity & Evolution* 15, 681–93.
- Lamsdell JC, Tashman JN, Pasini G and Garassino A (2020) A new limulid (Chelicerata, Xiphosurida) from the Late Cretaceous (Cenomanian–Turonian) of Gara Sbaa, southeast Morocco. *Cretaceous Research* 106, 104230.
- Lange W (1923) Über neue Fossilfunde aus der Trias von Göttingen. *Zeitschrift der deutschen geologischen Gesellschaft* 74, 162–68.
- Latreille PA (1802) *Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes*. Paris: Dufart.
- Lerner AJ, Lucas SG and Lockley M (2017) First fossil horseshoe crab (Xiphosurida) from the Triassic of North America. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 286, 289–302.
- Lerner AJ, Lucas SG and Mansky CF (2016) The earliest paleolimulid and its attributed ichnofossils from the Lower Mississippian (Tournaisian) Horton Bluff Formation of Blue Beach, Nova Scotia, Canada. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 280, 193–214.
- Malz H and Poschmann M (1993) Erste Süßwasser-Limuliden (Arthropoda, Chelicerata) aus dem Rotliegenden der Saar-Nahe-Senke. *Osnabrücker naturwissenschaftliche Mitteilungen* 19, 21–24.
- Martha SO, Taylor PD, Matsuyama K and Scholz J (2014) A brief history of misidentification and missing links: the Jurassic cyclostome *Kolophos* Gregory, 1896 and a new genus from the Cretaceous. In *Bryozoan Studies 2013: Proceedings of the 16th International Bryozoology Association Conference*, Catania, Sicily: Studi Trentini di Scienze Naturali pp. 169–79.
- Meek FB (1867) Notes on a new genus of fossil Crustacea. *Geological Magazine* 4, 320–21.
- Meischner K-D (1962) Neue Funde von *Psammolimulus göttingensis* (Merostomata, Xiphosura) aus dem Mittleren Buntsandstein von Göttingen. *Paläontologische Zeitschrift* 36, 185–93.
- Naugolnykh SV (2017) Lower Kungurian shallow-water lagoon biota of Middle Cis-Urals, Russia: towards paleoecological reconstruction. *Global Geology* 20, 1–13.
- Naugolnykh SV (2020) Main biotic and climatic events in Early Permian of the Western Urals, Russia, as exemplified by the shallow-water biota of the early Kungurian lagoons. *Palaeoworld* 29, 391–404.
- Odin GP, Charbonnier S, Devillez J and Schweigert G (2019) On unreported historical specimens of marine arthropods from the Solnhofen and Nusplingen Lithographic Limestones (Late Jurassic, Germany) housed at the Muséum national d'Histoire naturelle, Paris. *Geodiversitas* 41, 643–62.
- Pickett JW (1984) A new freshwater limuloid from the middle Triassic of New South Wales. *Palaeontology* 27, 609–21.
- Presl KB (1838) Restiacites. In *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt* (ed K Strenberg), p. 189. Leipzig: Deutschen Museum.
- Raymond PE (1944) Late Paleozoic xiphosurans. *Bulletin of the Museum of Comparative Zoology* 94, 475–508.
- Richter R and Richter E (1929) *Weinbergina opitzi* n. g. n. sp., ein Schwerträger (Merost., Xiphos.) aus dem Devon (Rheinland). *Senckenbergiana* 11, 193–209.
- Riek EF (1955) A new xiphosuran from the Triassic sediments at Brookvale, New South Wales. *Records of the Australian Museum* 23, 281–82.
- Rudkin DM and Young GA (2009) Horseshoe crabs—an ancient ancestry revealed. In *Biology and Conservation of Horseshoe Crabs* (eds JT Tanacredi, ML Botton and DR Smith), pp. 25–44. New York: Springer.
- Rudkin DM, Young GA and Nowlan GS (2008) The oldest horseshoe crab: a new xiphosurid from Late Ordovician Konservat-Lagerstätten deposits, Manitoba, Canada. *Palaeontology* 5, 1–9.
- Schindler T and Poschmann M (2012) Das jüngste Vorkommen von Pfeilschwanzkrebse (Xiphosurida, Euproopidae) im Saar-Nahe-Becken, mit Anmerkungen zur Paläoökologie der Fundschichten (Perm, Südwestdeutschland). *Mainzer Geowissenschaftliche Mitteilungen* 40, 23–38.
- Schmeissner S and Hauptmann S (1998) Ein Blattschopf von *Nilsonia acuminata* (Presl) Goeppert aus dem unteren Lias Oberfrankens. *Documenta naturae* 117, 1–11.
- Schultka S (1994) *Bellinurus* cf. *truemanii* (Merostomata) aus dem tiefen Oberkarbon (Namur B/C) von Fröndenberg (Nordrhein-Westfalen, Deutschland). *Paläontologische Zeitschrift* 68, 339–49.
- Sekiguchi K and Shuster CN Jr (2009) Limits on the global distribution of horseshoe crabs (Limulacea): lessons learned from two lifetimes of observations: Asia and America. In *Biology and Conservation of Horseshoe Crabs* (eds JT Tanacredi, ML Botton and DR Smith), pp. 5–24. Dordrecht: Springer.
- Shpinev ES (2018) New data on Carboniferous xiphosurans (Xiphosura, Chelicerata) of the Donets Coal Basin. *Paleontological Journal* 52, 271–83.
- Shpinev ES and Vasilenko DV (2018) First fossil xiphosuran (Chelicerata, Xiphosura) egg clutch from the Carboniferous of Khakassia. *Paleontological Journal* 52, 400–4.
- Shuster CN Jr (2001) Two perspectives: horseshoe crabs during 420 million years, worldwide, and the past 150 years in the Delaware Bay area. In *Limulus in the Limelight* (ed JT Tanacredi), pp. 17–40. New York: Springer.
- Shuster CN Jr and Anderson LI (2003) A history of skeletal structure: Clues to relationships among species. In *The American Horseshoe Crab* (eds CN Shuster Jr, RB Barlow and HJ Brockmann), pp. 154–88. Cambridge: Harvard University Press.
- Siegfried P (1972) Ein Schwertschwanz (Merostomata, Xiphosurida) aus dem Oberkarbon von Ibbenbüren/Westf. *Paläontologische Zeitschrift* 46, 180–85.
- Tashman JN, Feldmann RM and Schweitzer CE (2019) Morphological variation in the Pennsylvanian horseshoe crab *Euproops danae* (Meek & Worthen, 1865) (Xiphosurida, Euproopidae) from the lower Mercer Shale, Windber, Pennsylvania, USA. *Journal of Crustacean Biology* 39, 396–406.
- van Konijnenburg-van Cittert JHA (2010) The Early Jurassic male ginkgoalean inflorescence *Stachyopitys preslii* Schenk and its *in situ* pollen. *Scripta Geologica Special Issue* 7, 141–49.
- van Konijnenburg-van Cittert JHA and Schmeißner S (1999) Fossil insect eggs on Lower Jurassic plant remains from Bavaria (Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology* 152, 215–23.
- van Konijnenburg-van Cittert JHA, Schmeißner S and Dütsch G (2001) A new *Rhaphidopteris* from the Lower Liassic of Bavaria, Germany. *Acta Palaeobotanica* 41, 107–13.
- Van Roy P, Briggs DEG and Gaines RR (2015) The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society* 172, 541–49.
- Van Roy P, Orr PJ, Botting JP, Muir LA, Vinther J, Lefebvre B, El Hariri K and Briggs DEG (2010) Ordovician faunas of Burgess Shale type. *Nature* 465, 215–18.
- Vía L and De Villalta JF (1966) *Hetrolimulus gadeai*, nov. gen., nov. sp., représentant d'une nouvelle famille de Limulacés dans le Trias d'Espagne. *Comptes Rendues Sommaire Séances Société Géologique France* 8, 57–59.
- von Fritsch KWG (1906) Beitrag zur Kenntnis der Tierwelt der deutschen Trias. *Abhandlungen der naturforschender Gesellschaft Halle* 24, 220–85.
- Weber R (1968) Die fossile Flora der Rhät-Lias-Übergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. *Erlanger Geologische Abhandlungen* 72, 1–73.
- Witzmann F and Brainerd E (2017) Modeling the physiology of the aquatic temnospondyl *Archegosaurus decheni* from the early Permian of Germany. *Fossil Record* 20, 105–27.
- Wuestefeld P, Hilgers C, Koehrer B, Hoehne M, Steindorf P, Schurk K, Becker S and Bertier P (2014) Reservoir heterogeneity in Upper Carboniferous tight gas sandstones: Lessons learned from an analog study. In *SPE/EAGE European Unconventional Resources Conference and Exhibition*, pp. 1–10. European Association of Geoscientists & Engineers.
- Zittel KA (1885) *Handbuch der Palaeontologie. I. Abteilung, Palaeozoologie*. München: R. Oldenbourg.
- Zuber M, Laaf M, Hamann E, Kretschmer S, Hauschke N, Van De Kamp T, Baumbach T and Koenig T (2017) Augmented laminography, a correlative 3D imaging method for revealing the inner structure of compressed fossils. *Scientific Reports* 7, 41413.