Review of “An earliest Triassic age for *Tasmaniolimulus* and comments on synchrotron tomography of Gondwanan horseshoe crabs” (#67956)

Horseshoe crabs are an iconic clade of euarthropods with a long evolutionary history, and the only extant fully aquatic chelicerates. While currently only four species are in existence, their taxonomic diversity and morphological disparity used to be much greater in the Paleozoic and Mesozoic. Therefore, any paper dealing with fossil xiphosurids is of considerable interest to palaeobiologists and invertebrate and evolutionary biologists.

The current manuscript revises the age of *Tasmaniolimulus*, previously believed to be Permian, to the Triassic, which has implications for our understanding of the timing of the radiation of the family Austrolimulidae. In addition, it discusses the results of synchrotron CT scanning of four specimens of fossil Australian horseshoe crabs. The extremely high energies, brilliance and almost monochromatic character of synchrotron light allow a penetration and resolution unequalled by classical X-ray tomography. Therefore, synchrotron tomography is quickly becoming established as an extremely valuable technique in the study of fossil specimens. However, so far, synchrotron tomography had only been applied to one fossil horseshoe crab specimen. The four specimens scanned for this paper therefore represent a welcome addition, and provide some additional morphological data over what was known previously from more classical studies of the material using imaging in visible wavelengths. Consequently, this paper is of interest, and deserves to be published. There are, however, a number of issues that need to be addressed first.

On p. 14, line 221, the authors state that *“... a limited portion of the spine was cuticularised.*” What is this supposed to mean? What is “cuticularised”? Xiphosurids are euarthropods. Euarthropods are Ecdysozoa. Ecdysozoans, as one of their primary defining characters, have an external cuticle. In euarthropods, most of this cuticle (except for arthrodial membrane) is at least to some degree sclerotised to form an exoskeleton. So, a euarthropod, by definition, is externally encased in a sclerotised cuticle. I suppose the authors may be trying to say to say that the degree of sclerotisation varied along the spine, or that the whole spine was less sclerotised compared to the rest of the prosomal shield? This sentence does need rephrasing to make sense – talking about a portion of the external surface of an ecdysozoan being “cuticularised” is akin to talking about a portion of a mammalian spine being “notochordised”.

On p. 15, lines 227-228, it is stated that “*The reconstruction of Victalimulus mcqueeni reveals evidence for the thoracetronic doublure, moveable spines and notches, and appendage impressions.*”

- First, after reviewing both Fig. 4 and the supplemental image, I fail to see the moveable spines – I can only make out the fixed spines of the thoracetron, and the intervening notches that accommodated the moveable spines, not the moveable spines themselves. Indeed, the caption to Fig. 4 itself states: “*... X-ray tomographic slice showing* ***fixed spines and moveable spine notches*** *(white arrows) and thoracetronic doublure*”; so the caption itself does not mention the presence of the actual moveable spines either. If the moveable spines are indeed visible anywhere, they should be indicated.

- Second, the statement is somewhat misleading, considering that the original description by Riek & Gill (1971) already commented on the thoracetronic doublure, the presence of fixed spines and notches, and the impressions of the prosomal walking limbs. Therefore, these do not exactly represent new findings.

On p. 16, the authors talk about "dorsal preservation", and "ventral preservation". It is not entirely clear what they mean by this:

- Does it mean that only the dorsal (or ventral) exoskeleton is *preserved*?
- Or, do the authors intend to say that the fossils are *exposed* from the dorsal (or ventral) side?
- Or, do they intend to convey that the *original orientation* in which the specimens were preserved was with the dorsal (or ventral) side up?

These are not trivial differences in meaning. The authors comment that "dorsal preservation" is more common than "ventral preservation" in horseshoe crabs. If they are referring to the surface of the fossil that is exposed, this is not surprising: the dorsal surface represents a relatively smooth, convex surface, whereas the concave ventral surface is much less regular. As such, the dorsal surface will represent a plane of weakness along which the matrix containing the fossil will preferentially fracture. It therefore makes sense for the majority of xiphosurid specimens to be exposed from the dorsal side – as is observed for most other dorso-ventrally flattened euarthropods. However, the fact that these specimens are *exposed* on the dorsal side does not necessarily mean that they have been preserved dorsal side up: it is common for specimens which have been embedded dorsal side down to still crack out along the dorsal surface, because of the aforementioned reasons. Hence, if it is the intention of the authors to make the case that most horseshoe crab fossils were *preserved* with the dorsal side up, they need to provide additional arguments for the original orientation of the specimen – either from sedimentological characteristics of the surrounding matrix that allow polarity to be deduced, or from data documenting the original orientation of the fossil when collected.

On the same page, the authors also comment that *"... a ventral orientation has a lower preservational protentional*". Again, if they are just referring to the side of the fossil that is *exposed*, it makes sense, as explained above, that the majority of fossils exposes the dorsal side. However, if the argument is that specimens being preserved with their ventral side up stand a lesser chance of preservation, this also makes sense: the ventral exoskeleton is considerably less sclerotised than the dorsal side. So, if a carcass is lying on the sea floor upside down, with its ventral side exposed, scavengers and currents will have free reign to tear it up. If, on the other hand, the carcass is not overturned, the heavy dorsal exoskeleton will to some extent help protect the more fragile ventral anatomy from being destroyed, allowing time for the carcass to be buried, potentially helping it to enter the fossil record. In this respect, a dorsal-side-up orientation may actually aid preservation of limbs and soft anatomy, rather than "damage" it, as the authors suggest. In that case, the overlying dorsal exoskeleton would obscure any underlying preserved parts, making it harder for them to be studied, but in itself would not "damage" them; in this respect, it is also important to note that at least in the case of non-biomineralising arthropods, flattening of carcasses mostly results from decay-induced collapse of the carcass onto itself, rather than from compaction by the surrounding sediment.

On p. 19, lines 317-319, it is claimed that the Winterswijk *Limulitella* shows "*extensive soft tissue traces*". At least based on the information provided in the paper by Zuber *et al.* (2017), this claim is entirely incorrect: the authors of that study only identified exoskeletal morphological features of this fossil. They do refer to the presence of "muscular markings", but as is clear from their figures, by this they do not mean actual muscle tissue, but rather the depressions on the prosomal shield associated with internal apodemes to which muscles would have attached. Hence, the only thing visible in their scans was the sclerotised, exoskeletal cuticle, which is neither soft, nor a tissue!

Apart from these issues, I have added some further small remarks and (mainly typographical) corrections as sticky notes to the attached annotated manuscript.

In conclusion, this manuscript does present some interesting data, and does merit to be published in *PeerJ*. However, before it can be published, the authors do need to rectify the several issues raised here.

Peter Van Roy
23 December 2021

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An earliest Triassic age for *Tasmaniolimulus* and comments on synchrotron tomography of Gondwanan horseshoe crabs

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Constraining the timing of morphological innovations within horseshoe crab evolution is cardinal for understanding when and how such a long-lived group exploited vacant ecological niches over the majority of the Phanerozoic. To expand the knowledge on the evolution of select extreme xiphosurid forms, we consider the four Australian taxa: *Austrolimulus fletcheri*, *Dubbolimulus peetae*, *Tasmaniolimulus patersoni*, and *Victalimulus mcqueeni*. In revisiting these taxa, we determine that, contrary to previous suggestion, *T. patersoni* arose after the Permian and the origin of over-developed genal spine structures within Austrolimulidae is exclusive to the Triassic. To increase the availability of morphological data pertaining to these unique forms, we also examined the holotypes of the four horseshoe crabs using synchrotron radiation X-ray tomography (SRXT). Such non-destructive *in-situ* imaging of the internal structures of palaeontological specimens aids in the identification of novel morphological data by obviating the need for potentially extensive preparation of fossils from the surrounding rock matrix, which is particularly important for rare and/or delicate holotypes. Here, SRXT revealed additional data regarding cardiac lobe morphologies of *A. fletcheri* and *T. patersoni*, and novel anatomical information for *V. mcqueeni*, including the prominence of the thoracetronic doublure, appendage impressions, and moveable spine notches. Unfortunately, the strongly compacted *D. peetae* precluded the identification of any internal structures, but appendage impressions were observed. The application of computational fluid dynamics to high-resolution 3D reconstructions are proposed to understand the hydrodynamic properties of divergent genal spine morphologies of austrolimulid xiphosurids.

An earliest Triassic age for *Tasmaniolimulus* and comments on synchrotron tomography of Gondwanan horseshoe crabs

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Abstract

Constraining the timing of morphological innovations within horseshoe crab evolution is cardinal for understanding when and how such a long-lived group exploited vacant ecological niches over the majority of the Phanerozoic. To expand the knowledge on the evolution of select extreme xiphosurid forms, we consider the four Australian taxa: *Austrolimulus fletcheri*, *Dubbolimulus peetae*, *Tasmaniolimulus patersoni*, and *Victalimulus mcqueeni*. In revisiting these taxa, we determine that, contrary to previous suggestion, *T. patersoni* arose after the Permian and the origin of over-developed genal spine structures within Austrolimulidae is exclusive to the Triassic. To increase the availability of morphological data pertaining to these unique forms, we also examined the holotypes of the four horseshoe crabs using synchrotron radiation X-ray tomography (SRXT). Such non-destructive *in-situ* imaging of the internal structures of palaeontological specimens aids in the identification of novel morphological data by obviating the need for potentially extensive preparation of fossils from the surrounding rock matrix, which is particularly important for rare and/or delicate holotypes. Here, SRXT revealed additional data regarding cardiac lobe morphologies of *A. fletcheri* and *T. patersoni*, and novel anatomical information for *V. mcqueeni*, including the prominence of the thoracetronic doublure, appendage impressions, and moveable spine notches. Unfortunately, the strongly compacted *D. peetae* precluded the identification of any internal structures, but appendage impressions were observed. The application of computational fluid dynamics to high-resolution 3D reconstructions are proposed to understand the hydrodynamic properties of divergent genal spine morphologies of austrolimulid xiphosurids.

Keywords: Euchelicerate, Xiphosurida, Austrolimulidae, Australia, Synchrotron radiation X-ray tomography

Introduction

The increasing availability of three-dimensional (3D) data in the preceding two decades has revolutionised the acquisition of morphological data from both biological (Hita Garcia et al., 2017; Parapar et al., 2017; Landschoff et al., 2018; Marcondes Machado et al., 2019) and palaeontological specimens (Sutton, 2008; Pardo & Anderson, 2016; Liu et al., 2017, 2019; Forel et al., 2021). Traditional lab-based micro-CT, along with more sophisticated synchrotron radiation X-ray tomography (SRXT) with neutron micro-tomography (NCT) have permitted non-destructive visualisation of previously unknown and inaccessible morphological features for taxa across all of Animalia (Donoghue et al., 2006; Tafforeau et al., 2006; Sutton, 2008; Metscher, 2009; Motchurova-Dekova & Harper, 2010; Faulwetter et al., 2013, 2014; Herrera et al., 2020; Snyder et al., 2020). This precludes the need for physical dissection and/or preparation of specimens, which is relevant when describing structures from rare or fragile material (e.g., Metscher, 2009; Haszprunar et al., 2011; Deans et al., 2012; Beutel et al., 2019; Willsch et al., 2020). In palaeontology, 3D data has been used widely in the visualisation of fossils preserved in amber (Lak et al., 2008; Perrichot et al., 2008; Riedel et al., 2012; Xing et al., 2016a, b, 2018; Daza et al., 2020; Bolet et al., 2021) and also in the examination of fossils that are still surrounded in their original rock matrix (Moreau et al., 2014; Schwarzhans et al., 2018; Reid et al., 2019; Mayr et al., 2020).

Research into fossil arthropods has benefitted greatly from the availability of non-destructive 3D imaging techniques (Deans et al., 2012; Liu et al., 2016, 2020; Hegna et al., 2017; Wesener, 2019; Zhai et al., 2019a, b; Liu et al., 2020), particularly the diverse array of insects preserved within resins (Tafforeau et al., 2006; Lak et al., 2008; Pohl et al., 2010; Henderickx et al., 2012; Riedel et al., 2012). In stark contrast, extinct members of Xiphosurida (i.e., horseshoe crabs) have received comparatively limited 3D examination. The anatomy of two extant xiphosurids, the American horseshoe crab [*Limulus polyphemus* (Linnaeus, 1758)] and the mangrove horseshoe crab [*Carcinoscorpius rotundicauda* (Latreille, 1802)] have been documented using micro-CT (Göpel & Wirkner, 2015; Bicknell et al., 2018a, b, 2021c, d). Magnetic resonance imaging has also been used in studies of the Japanese horseshoe crab [*Tachypleus tridentatus* (Leach, 1819)] (Kutara et al., 2019; Yuen et al., 2019). However, as Bicknell & Pates (2020) highlighted, there are over 80 extinct xiphosurids that have not been explored using 3D data and most 3D data collected from fossil xiphosurids have been surface scans (Schimpf et al., 2017). A recent study combined CT and computed laminography (Zuber et al., 2017) to image *Limulitella* Størmer, 1952 from the Winterswijk quarry complex, Middle Triassic (Anisian) Vossenfeld Formation, Muschelkalk, Netherlands (Klompmaker & Fraaije, 2011; Klein, 2012; Sander et al., 2016; Zuber et al., 2017). These techniques revealed previously unknown morphological information that was not visible due to compression and ventral preservation of the specimen. However, no other fossil xiphosurids have been examined using comparable methods. Here we address this lack of data by presenting the first application of SRXT to holotypes of four Australian xiphosurids. In doing so, we also reconsider the temporal range of these four taxa. This revision uncovers a younger age for one genus, pushing the rise of Austrolimulidae within Australia into exclusively the Triassic.

Institutional acronyms

AM F: Australian Museum, Sydney, New South Wales, Australia. MMF: Geological Survey of New South Wales, Londonderry, New South Wales, Australia. NMV P: Museums Victoria, Carlton, Victoria, Australia. UTGD: Geology Department, University of Tasmania, Tasmania, Australia.

Methods

We examined four of the five fossil horseshoe crabs known from Australia using SRXT: *Austrolimulus fletcheri* Riek, 1955 from the Hawkesbury Sandstone (Middle Triassic, Anisian), New South Wales (NSW); *Dubbolimulus peetae* Pickett, 1984 from the Napperby Formation (Middle Triassic, Ansian), NSW; *Tasmaniolimulus patersoni* Bicknell, 2019 from the Jackey Shale (Early Triassic, Induan), Tasmania; and *Victalimulus mcqueeni* Riek & Gill, 1971 from Koonwarra Fossil Bed (Early Cretaceous, Aptian), Victoria. All four taxa therefore fall within the distinct xiphosurid families Limulidae and Austrolimulidae (Bicknell, 2019; Bicknell et al., 2021a; Lamsdell, 2021).

Non-destructive X-ray microtomographic measurements were conducted using the Imaging and Medical Beamline at the Australian Nuclear Science and Technology Organisation's (ANSTO) Australian Synchrotron, Clayton, Victoria, Australia.
A monochromatic beam energy of 70 keV was used for *Dubbolimulus peetae* and *Victalimulus mcqueeni*, with a sample-to-detector distance of 50 cm. X-rays were converted to visible photons and detected using the "Ruby detector", a 20 µm thick Gadox/CsI(Tl)/$CdWO_4$ scintillator screen coupled with a PCO.edge sCMOS camera (16-bit, 2560 x 2160 pixels) and a Nikon Makro Planar 50 mm lens to achieve a pixel size of 24.8 x 24.8 µm. A total of 1800 equal angle shadow-radiographs were obtained (i.e., one radiograph every 0.10°) with an exposure length of 0.070 seconds each as the samples were continuously rotated 180° about their vertical axes. Due to the restricted beam height and field-of-view, this radiograph capture procedure was repeated after lowering the specimen with respect to the beam after a full rotation. This produced a series of overlapping vertical radiographs capturing the full height of each specimen, which were then stitched together into a single set of radiographs prior to reconstruction into 3D volumes. For *V.*

mcqueeni the reconstructed data was binned to voxels of 49.6 µm for visualisation. *Tasmaniolimulus patersoni* and *Austrolimulus fletcheri* were similarly scanned with a pixel size of 40.29 x 40.29 µm. An incident monochromatic beam energy of 80 keV was used for *T. patersoni* and a broad range of higher energy X-rays (pink beam, peak energy of 220 keV) was used for *A. fletcheri* due to the high attenuation of available monochromatic X-rays.

The raw 16-bit radiographs were normalised relative to the beam calibration files, stitched using the in-house software IMBL Stitch, and reconstructed with CSIRO's X-TRACT (Gureyev et al., 2011) software available on Australian Synchrotron Computing Infrastructure (ASCI). The filtered-back projection reconstruction method was used to form a 16-bit, three-dimensional volume image of the sample.

The reconstructed slices for each fossil were imported into Mimics version 23.0 (Materialise, Leuven, Belgium) and digitally prepared. Any artefacts in the tomographic slices were removed using the 'Segmenting' tool and the remaining components were segmented out. and converted to .STL files in Mimics, and imported into Geomagic Studio (3D Systems, North Carolina, USA) to be smoothed. The smoothed .STL files were used to generate 3D PDFs using Terta4D (Adobe Systems; see Supplemental Figures 1–4 found at https://osf.io/at528/?view_only=78985d12aca941dda8ac95a2cc191d93) Raw radiograph data associated with this research was uploaded to MorphoSource. Photographs of each specimen were taken either by the authors or by collection managers for comparison to the 3D reconstructions.

Geological context

The oldest Australian xiphosurid, *Tasmaniolimulus patersoni*, was found in the Jackey Shale of the Upper Parmeener Supergroup, Tasmania (Bicknell, 2019). This formation is largely composed of cross-bedded quartz and feldspathic sandstones, laminated dark grey shales and thin coal lenses (Pike, 1973). Stratigraphically, the fossil was located near the very top of the formation, ~3 m below the base of the overlying Ross Formation, exposed alongside a cliff on the Poatina Highway (41°48'05"S, 146°53'06"E) (Ewington et al., 1989; Bicknell, 2019). Based on the lithology, the unit likely represents deposition of lake and river sediments in a non-marine swamp with limited coastal influence (Banks, 1973; Ewington et al., 1989). While the Jackey Shale at the stratigraphic level of the collection locality lacks age diagnostic fossils, palynomorphs from other, temporally contiguous sites can be assigned to the *Protohaploxypinus microcorpus* Zone, equivalent to upper APP6 (see Price, 1997) and restricted to the Griesbachian substage, early Induan (Early Triassic) based on previous studies in the Sydney Basin (Laurie et al., 2016; Mays et al., 2020). This contradicts previous interpretations of latest Permian that used now outdated chronostratigraphic ages for this palynomorph zone An Early Triassic age is further supported by the vertebrate fauna and macro- and microflora of the *Protohaploxypinus samoilovichii* Zone from the overlying Ross Formation which pertains to the younger Smithian substage of the Olenekian (Early Triassic; Forsyth, 1989). The presence of abundant latest Permian macroflora at stratigraphic levels below the level of *T. patersoni* in the Jackey Shale does suggest that, at least at some locations, the formation does extend into the latest Permian (Ewington et al., 1989). Nonetheless, given the high stratigraphic position of *T. patersoni*, it appears more likely that this specimen is of Early Triassic age.

Slightly younger is *Dubbolimulus peetae*, which was collected from the Napperby Formation (previously the "Ballimore Formation") of the Gunnedah Basin in central New South Wales (Pickett, 1984). The only known specimen, with an associated counterpart, was found just south of Western Plains Zoo, Dubbo (at approximately 32°17'30.8"S 148°34'35.8"E). The

Napperby Formation consists of white, fine–medium grain, quartz-rich, ferruginous sandstone with occasional cross bedding. Thin horizons of grey to red brown shale and minor conglomerate lenses are interbedded with this sandstone. The stratigraphic horizon within which the specimen was found is a red brown, slightly micaceous shale. This lithology indicates a high-energy braided river system or lacustrine deposits (Tadros, 1993), possibly part of the same Triassic delta system that continues into the Sydney Basin to the east. The finer grained shale horizons likely represent lower-energy conditions which presumably occurred in quiet, cut-off river channels or small ponds. The possible presence of acritarchs (McMinn, 1982) suggest the unit may have experienced a slight coastal influence occasionally. A diverse macroflora assemblage has been described from both the fossil site itself (Pickett, 1984) and a nearby locality (Holmes, 1982) which broadly correlate to the *Dicroidium zuberi* Zone (Helby, 1973, 1987; Retallack, 1977, 1980; Helby et al., 1987) of the Ansian (earliest Middle Triassic) in the Sydney Basin. Palynomorphs from core within the Dubbo area, at Mirrie DOH I (McMinn, 1982) and Pibbon DOH 1 (McMinn, 1984), support this age interpretation with placement in the *Aratrjsporites parvispinoslis* Zone which correlates to the middle to upper *Dicroidium zuberi* Zone (Young & Laurie, 1966). A middle *D. zuberi* Zone stratigraphic position, which indicates an earliest Ansian age, is most likely given palynomorphs from other locations in the Gunnedah Basin suggest an age range between the upper *Aratrisporites tenuispinosus* Zone and lower *Aratrjsporites parvispinoslis* Zone.

Of a similar age is *Austrolimulus fletcheri*, from Beacon Hill Quarry, near the suburb of Brookvale, Sydney, New South Wales (Riek, 1955). The exact co-ordinates of the original collection site are unknown, however, is considered to be 33°45'11.2"S, 151°15'55.5"E. The specimen originates from a thin (8 m) shale lens in the Hawkesbury Sandstone. This lens mostly consists of numerous thin, recessive, grey-red mudrock laminations with little bioturbation (Webby, 1970) and small amounts of rippling (Herbert, 1983). Overall, the Hawkesbury Sandstone was likely formed in a vast coastal floodplain made up of high energy braided rivers, scour channels, lakes, and sand dunes (Conaghan, 1980 and references therein). Shale lenses, like those at the *A. fletcheri* site, likely represent lower-energy regimes consisting of shallow water bodies disconnected from a main river channel as isolated shallow pools of water (Herbert, 1980, 1997; Rust & Jones, 1987). Unfortunately, none of the diverse fossil fauna and flora found at Brookvale (see Bicknell & Smith in press for a recent overview) are insufficiently diagnostic for relative age estimation. However, the Hawkesbury Sandstone is well constrained within the *Aratrisporites parvispinosus* Zone and upper *Dicroidium zuberi* Zone based on palynomorphs and macroflora (Helby, 1973; Retallack, 1977, 1980; Helby et al., 1987). Similar to the Napperby Formation, this places it within the Anisian (earliest Middle Triassic) and likely within the earliest Anisian. Recent high-precision U-Pb CA-TIMS obtained from the Garie Formation, which underlies the Newport Formation and succeeding Hawkesbury Sandstone, is dated to the latest Olenekian (248.23±0.13 Ma and 247.87±0.11Ma; Metcalfe et al., 2015). This further supports an Anisian age for the Hawkesbury Sandstone as there is an unconformity in the Sydney Basin between Newport Formation and Hawkesbury Sandstone (Helby, 1973; Herbert, 1980).

Victalimulus mcqueeni from Koonwarra Fossil Bed of the Strzelecki Group (Riek & Gill, 1971), is the youngest xiphosurid known from Australia. A single partial specimen was found at a road cutting along the South Gippsland Highway, approximately 2.4 km east of Koonwarra (38°33'48.9"S 145°57'33.9"E). The unit at this location consists of a thick (~7–8 m) lower and upper feldspathic sandstone bracketing a grey-green, fossiliferous mudstone (Waldman, 1971;

Jell & Roberts, 1986). The mudstone is made up of extremely fine alternating layers of a clay- and silt-dominated matrix. A freshwater lacustrine environment was originally suggested for the Koonwarra Fossil Bed, with the finely laminated mudstones representing a rhythmic varve formed under freezing conditions (Waldman, 1971, 1973, 1984). However, the highly diverse fossil fauna and flora (see overview in Poropat et al. 2018), instead suggests a cold, but not freezing, swamp or a lacustrine environment with seasonal flooding causing overbank-type deposits (Douglas & Williams, 1982; Jell & Roberts, 1986). Presence of the palynomorphs *Clavatipollenite hughesii* Couper, 1957 and *Foraminisporis asymmetricus* Dettmann, 1963 from the Koonwarra Fossil Bed, and absence of other palynomorphs from younger zones, indicate an age within Upper *Cyclosporites hughesii* subzone (Jell & Roberts, 1986; Seegets-Villiers & Wagstaff, 2016; Korasidis & Wagstaff, 2020; Wagstaff et al., 2020). This places the unit entirely within the Aptian Stage (Early Cretaceous). Fission track dating of volcanoclastic sediments in the Koonwarra Fossil Beds suggests an age of 118 ± 5–115 ± 6 Ma, which correlates to the mid-Aptian (Gleadow & Duddy, 1980; Lindsay, 1982).

Results

The reconstructed tomographic volumes revealed additional morphological data that could not be observed from the external expression of the fossils. The density of the matrix surrounding *Austrolimulus fletcheri* precluded the unambiguous identification of many internal structures (Figure 1). However, the cardiac lobe can be more readily distinguished in the reconstructed volume and more depth is observed than exposed on the dorsal surface of the fossil (Figure 1C). Furthermore, the composition of the genal spines is less dense than the prosoma, suggesting a limited portion of the spine was cuticularized (Figure 1D). *Dubbolimulus peetae* shows no evidence of preserved internal structures, reflecting the strong dorsoventral compression of the specimen (Figure 2). However, an examination of the surface reconstruction reveals impression of the walking legs. The cardiac lobe of *Tasmaniolimulus patersoni* is the most prominent feature visible in the reconstruction (Figure 3), and which has been previously described in this taxon (Ewington et al., 1989; Bicknell, 2019). However, no internal structures are visible. The reconstruction of *Victalimulus mcqueeni* reveals evidence for the thoracetronic doublure, moveable spines and notches, and appendage impressions (Figure 4).

Discussion

Age of *Tasmaniolimulus patersoni*

The revised earliest Triassic age of *Tasmaniolimulus patersoni* has important implications for austrolimulid evolution. *Tasmaniolimulus patersoni* was originally considered to be of latest Permian age (Ewington et al., 1989; Lerner et al., 2017; Bicknell, 2019; Lamsdell, 2020) which indicated the first appearance of hypertrophied genal spines within Austrolimulidae at this time (Bicknell et al., 2020). However, the revised date shifts the first appearance of this trait to the earliest Triassic. Furthermore, *T. patersoni* is now either the oldest Triassic austrolimulid, or contemporaneous with *Vaderlimulus tricki* Lerner et al., 2017 and *Psammolimulus gottingensis* Lange, 1923—taxa that all have overdeveloped genal spine morphologies (Meischner, 1962; Lerner et al., 2017; Bicknell et al., 2021b).

The SRXT examination of the Australian xiphosurid fossils did not reveal much novel anatomy, nor traces of soft tissues. The aforementioned specimens were preserved primarily in sand- and siltstones which limits the preservation potential of fine, delicate structures. This is in contrast to the tomographic and laminographic reconstructions of xiphosurids described by Zuber et al. (2017) and which were preserved in fine grained, Muschelkalk-type limestones. These sediments tend to preserve soft-bodied anatomical details in exceptional detail (Vía et al., 1977; Briggs & Gall, 1990; Cartañà i Martí, 1994; Klug et al., 2005). Another limiting factor influencing the relatively poorer preservation of the Australian xiphosurids is differences in preservation orientation. Specifically, the Vossenfeld Formation *Limulitella* is preserved in ventral view and the Australian specimens are preserved dorsally. This difference may have limited the observable internal and ventral structures as ventral features would have been compressed and likely damaged by the dorsum. As such, any appendage data in the observed specimens is recorded in impressions in the prosoma. Interestingly, there are limited examples of horseshoe crabs preserved ventrally (Tschernyshev, 1933; Racheboeuf et al., 2002; Lamsdell & McKenzie, 2015; Hu et al., 2017; Zuber et al., 2017; Bicknell et al., 2019a). This limited record suggests that a ventral orientation has a lower preservational potential.

Comments on application of synchrotron tomography to the study of fossil xiphosurids

Palaeontological and biological collections house a wealth of specimens with academic and historic value. Digitisation of holotype specimens is a salient direction for recording and transferring fundamental anatomical information. These records are traditionally conducted by taking photographs or making line drawings. However, two-dimensional data and views cannot (by definition) display all characteristics needed for modern taxonomic and phylogenetic studies (Mathys et al., 2015; Bicknell et al., 2018a). As such, researchers often need to visit collections to examine specimens in person. This process can be prohibitive for logistic, cost, and policy reasons, to name a few. This complication can be circumvented by producing scans of taxonomically important and unique specimens. Such data is becoming a means of transferring important anatomical data to researchers across the globe and provide interested individuals with another medium with which to examine unique material.

Non-destructive three-dimensional imaging using SRXT will continue to play a central role in anatomical studies of fossil horseshoe crabs, following the rapid adoption of this imaging modality across palaeontology. In particular, techniques that can more readily distinguish areas with very small differences in radiopacity, such as phase-contrast enhanced imaging, hold out the promise for more detailed examination of muscles and other internal structures in suitably well-preserved specimens. For example, study of specimens of *Mesolimulus walchi* (Desmarest, 1822) from the Nusplingen Lithographic Limestone (Upper Jurassic, Kimmeridgian), Germany indicates that phosphatised muscle traces were likely to be preserved under the carapace (Briggs et al., 2005). Muscle traces have also been described from specimens of *Euproops danae* from the Upper Pennsylvanian (Virgilian) Lawrence Formation, Kansas (Feldman et al., 1993; Babcock & Merriam, 2000; Bicknell et al., 2021f). Further examination of the Lawrence Formation specimens would determine if the muscles exhibit moldic preservation—as is common for Mazon Creek fossils (Clements et al., 2019; Bicknell et al., 2021e)—or if there are additional, unexpressed anatomical features. More recently, neutron micro-tomography (NCT) is undergoing a renaissance in palaeontology, owing to the ability of neutrons to penetrate through typically radiopaque minerals such as iron pyrite, a high sensitivity to hydrogenous material, and thus to residual organic remains, (Gee et al., 2019a; Gee et al., 2019b; Na et al., 2021; Smith et al., 2021), and to increasing availability of high-quality neutron imaging facilities at nuclear research reactors and spallation neutron sources around the world (see list https://www.isnr.de/index.php/facilities/user-facilities). The collection of novel soft anatomy from these and other fossil xiphosurids are vitally important in presenting and revising hypotheses regarding homology with extant xiphosurids (*sensu* Briggs et al., 2005; Bicknell et al., 2021f) and resolving conflicts between phylogenetic hypotheses (e.g., Ballesteros & Sharma, 2019; Bicknell et al., 2019b, 2020; Lamsdell, 2020). More broadly, this same approach can be applied to the as-of-yet unnamed xiphosuran specimens from the Fezouata Shale *Lagerstätte* (Lower Ordovician, Morocco; Van Roy et al., 2010), previous micro-CT imagery has yielded useful results and allowed for specimens to be differentiated in 3D (Kouraiss et al., 2019).

Three-dimensional reconstructions are increasingly used in computational fluid dynamics (CFD) analyses to study the hydrodynamic properties of extinct aquatic taxa (Rahman et al., 2015a; Darroch et al., 2017; Rahman, 2017; Gibson et al., 2019; Ferrón et al., 2020; Hebdon et al., 2020; Song et al., 2021). The majority of CFD studies have focused on enigmatic Ediacaran taxa (Rahman et al., 2015a; Rahman, 2017; Gibson et al., 2019), echinoderms (Rahman et al., 2015b, 2020; Waters et al., 2017), and vertebrate groups (Dec, 2019; Troelsen et al., 2019; Ferrón et al., 2020, 2021). While fossil arthropods have received comparatively less attention than the aforementioned taxa (e.g., Pates et al., 2021; Song et al., 2021). CFD studies have modelled lift and drag experienced by modern horseshoe crabs (Bicknell & Pates, 2019; Davis et al., 2019). Extending CFDA studies to fossil xiphosurids will facilitate comparative studies of the hydrodynamic properties of the carapaces of extinct members of the clade, in addition to elucidating the effects of bizarre morphologies, such as the hypertrophied genal spines, on fluid flow. Such spines have been hypothesised to represent an adaptation to movement through unidirectional fluid flow in primarily freshwater or marginal marine environments (Lamsdell, 2016, 2021; Bicknell & Pates, 2019; Bicknell & Shcherbakov, 2021); CFD provides the most compelling method for evaluating the likelihood of this hypothesis.

Conclusion

Reconsidering the four Australian horseshoe crabs here, we have highlighted the rise of Austrolimulidae in the Gondwanan record began just after the end-Permian extinction. This timing also suggests that, globally, the development of hypertrophied spines within non-belinurid xiphosurids began after the end-Permian. We demonstrate that limited novel anatomical data were obtained for *Austrolimulus fletcheri*, *Dubbolimulus peetae*, *Tasmaniolimulus patersoni*, and *Victalimulus mcqueeni*. This is in contrast to extensive soft tissue traces revealed in 3D reconstructions a xiphosurid from the Vossenfeld Formation, a result of burial in a more favourable environment and a ventral preservation aspect. Future directions include examining similar fossils with NCT, an additional method that achieves an alternative and complementary contrast to XCT, and may resolve features that conventional lab-based- and synchrotron X-rays are unable to reveal. Future applications of these scan data include informing reconstructions needed for computational fluid dynamic analyses; a direction that may uncover the morpho-functional use of overdeveloped spines common to Australian horseshoe crabs.

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Author contributions

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References

Babcock LE, Merriam DF. **2000**. Horseshoe crabs (Arthropoda: Xiphosurida) from the Pennsylvanian of Kansas and elsewhere. *Transactions of the Kansas Academy of Science* **103 (1)**: 76–94.

Ballesteros JA, Sharma PP. **2019**. A critical appraisal of the placement of Xiphosura (Chelicerata) with account of known sources of phylogenetic error. *Systematic Biology* **68 (6)**: 896–917.

Banks MR. **1973**. General geology. In: Banks MR, ed. *The Lake Country of Tasmania*. Hobart: Royal Society of Tasmania, 25–33.

Beutel RG, Yan E, Yavorskaya M, Büsse S, Gorb SN, Wipfler B. **2019**. On the thoracic anatomy of the Madagascan *Heterogyrus milloti* and the phylogeny of Gyrinidae (Coleoptera). *Systematic Entomology* **44 (2)**: 336–360.

Bicknell RDC. **2019**. Xiphosurid from the Upper Permian of Tasmania confirms Palaeozoic origin of Austrolimulidae. *Palaeontologia Electronica* **22 (3)**: 1–13.

Bicknell RDC, Błażejowski B, Wings O, Hitij T, Botton ML. **2021a**. Critical re-evaluation of Limulidae reveals limited *Limulus* diversity. *Papers in Palaeontology* **7 (3)**: 1525–1556.

Bicknell RDC, Brougham T, Charbonnier S, Sautereau F, Hitij T, Campione NE. **2019a**. On the appendicular anatomy of the xiphosurid *Tachypleus syriacus* and the evolution of fossil horseshoe crab appendages. *The Science of Nature* **106 (7)**: 38.

Bicknell RDC, Hecker A, Heyng AM. **2021b**. New horseshoe crab fossil from Germany demonstrates post-Triassic extinction of Austrolimulidae. *Geological Magazine* **158 (8)**: 1461–1471.

Bicknell RDC, Holmes JD, Edgecombe GD, Losso SR, Ortega-Hernández J, Wroe S, Paterson JR. **2021c**. Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy. *Proceedings of the Royal Society of London B: Biological Sciences* **288 (1943)**: 20202075.

Bicknell RDC, Klinkhamer AJ, Flavel RJ, Wroe S, Paterson JR. **2018a**. A 3D anatomical atlas of appendage musculature in the chelicerate arthropod *Limulus polyphemus*. *PLoS ONE* **13 (2)**: e0191400.

Bicknell RDC, Ledogar JA, Wroe S, Gutzler BC, Watson III WH, Paterson JR. **2018b**. Computational biomechanical analyses demonstrate similar shell-crushing abilities in modern and ancient arthropods. *Proceedings of the Royal Society of London B: Biological Sciences* **285 (1889)**: 20181935.

Bicknell RDC, Lustri L, Brougham T. **2019b**. Revision of '*Bellinurus*' *carteri* (Chelicerata: Xiphosura) from the Late Devonian of Pennsylvania, USA. *Comptes Rendus Palevol* **18 (8)**: 967–976.

Bicknell RDC, Melzer RR, Schmidt M. **2021d**. Three-dimensional kinematics of euchelicerate limbs uncover functional specialisation in eurypterid appendages. *Biological Journal of the Linnean Society*: DOI: 10.1093/biolinnean/blab1108.

Bicknell RDC, Naugolnykh SV, Brougham T. **2020**. A reappraisal of Paleozoic horseshoe crabs from Russia and Ukraine. *The Science of Nature* **107**: 46.

Bicknell RDC, Ortega-Hernández J, Edgecombe GD, Gaines RR, Paterson JR. **2021e**. Central nervous system of a 310-million-year-old horseshoe crab: expanding the taphonomic window for nervous system preservation. *Geology* **49 (11)**: 1381–1385.

Bicknell RDC, Pates S. **2019**. Xiphosurid from the Tournaisian (Carboniferous) of Scotland confirms deep origin of Limuloidea. *Scientific Reports* **9 (1)**: 17102.

Bicknell RDC, Pates S. **2020**. Pictorial atlas of fossil and extant horseshoe crabs, with focus on Xiphosurida. *Frontiers in Earth Science* **8**: 98.

Bicknell RDC, Shcherbakov DE. **2021**. New austrolimulid from Russia supports role of Early Triassic horseshoe crabs as opportunistic taxa. *PeerJ* **9**: e11709.

Bicknell RDC, Smith PM. **in press**. The first fossil scorpion from Australia. *Alcheringa*: DOI: 10.1080/03115518.03112021.01983874.

Bicknell RDC, Tashman JN, Edgecombe GD, Paterson JR. **2021f**. Carboniferous horseshoe crab musculature suggests anatomical conservatism within Xiphosurida. *Papers in Palaeontology*: 10.1002/spp1002.1403.

Bolet A, Stanley EL, Daza JD, Arias JS, Čerňanský A, Vidal-García M, Bauer AM, Bevitt JJ, Peretti A, Evans SE. **2021**. Unusual morphology in the mid-Cretaceous lizard Oculudentavis. *Current Biology* **31 (15)**: 3303–3314.e3303.

Briggs DEG, Gall J-C. **1990**. The continuum in soft-bodied biotas from transitional environments: a quantitative comparison of Triassic and Carboniferous Konservat-Lagerstätten. *Paleobiology* **16 (2)**: 204–218.

Briggs DEG, Moore RA, Shultz JW, 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 (1563)**: 627–632.

Cartañà i Martí J. **1994**. Noves aportacions paleontologiques al Muschelkalk superior de les Muntanyes de Prades el cas del Pinetell. *Quaderns de Vilaniu* **25**: 67–93.

Clements T, Purnell M, Gabbott S. **2019**. The Mazon Creek Lagerstätte: a diverse late Paleozoic ecosystem entombed within siderite concretions. *Journal of the Geological Society* **176**: 1–11.

Conaghan PJ. **1980**. The Hawkesbury Sandstone: gross characteristics and depositional environment. In A Guide to the Sydney Basin (eds., C. Herbert and R. Helby). *Geological Survey of New South Wales Bulletin* **26**: 188–253.

Couper RA. **1957**. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica Abteilung B*: 75–179.

Darroch SAF, Rahman IA, Gibson B, Racicot RA, Laflamme M. **2017**. Inference of facultative mobility in the enigmatic Ediacaran organism. *Biology Letters* **13 (5)**: 20170033.

Davis AL, Hoover AP, Miller LA. **2019**. Lift and drag acting on the shell of the American horseshoe crab (*Limulus polyphemus*). *Bulletin of Mathematical Biology* **81 (10)**: 3803–3822.

Daza JD, Stanley EL, Bolet A, Bauer AM, Arias JS, Čerňanský A, Bevitt JJ, Wagner P, Evans SE. **2020**. Enigmatic amphibians in mid-Cretaceous amber were chameleon-like ballistic feeders. *Science* **370 (6517)**: 687–691.

Deans AR, Mikó I, Wipfler B, Friedrich F. **2012**. Evolutionary phenomics and the emerging enlightenment of arthropod systematics. *Invertebrate Systematics* **26 (3)**: 323–330.

Dec M. **2019**. Hydrodynamic performance of psammosteids: New insights from computational fluid dynamics simulations. *Acta Palaeontologica Polonica* **64 (4)**: 679–684.

Desmarest A-G. **1822**. Les crustacés proprement dits. In: Brongniart A, and Desmarest A-G, eds. *Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et geologiques*. Paris: F.-G. Levrault, 67–142.

Dettmann ME. **1963**. Upper Mesozoic microfloras from south-eastern Australia. *Proceedings of the Royal Society of Victoria* **77**: 1–148.

Donoghue PCJ, Bengtson S, Dong X-p, Gostling NJ, Huldtgren T, Cunningham JA, Yin C, Yue Z, Peng F, Stampanoni M. **2006**. Synchrotron X-ray tomographic microscopy of fossil embryos. *Nature* **442 (7103)**: 680–683.

Douglas JG, Williams GE. **1982**. Southern polar forests: the Early Cretaceous floras of Victoria and their palaeoclimatic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **39 (3-4)**: 171–185.

Ewington DL, Clarke MJ, Banks MR. **1989**. A Late Permian fossil horseshoe crab (*Paleolimulus*: Xiphosura) from Poatina, Great Western Tiers, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **123**: 127–131.

Faulwetter S, Dailianis T, Vasileiadou K, Kouratoras M, Arvanitidis C. **2014**. Can micro-CT become an essential tool for the 21st century taxonomist? An evaluation using marine polychaetes. *Microscopy and Analysis* **28 (2)**: S9–S11.

Faulwetter S, Vasileiadou A, Kouratoras M, Dailianis T, Arvanitidis C. **2013**. Micro-computed tomography: Introducing new dimensions to taxonomy. *ZooKeys* **263**: 1–45.

Feldman HR, Archer AW, Kvale EP, Cunningham CR, Maples CG, West RR. **1993**. A tidal model of Carboniferous Konservat-Lagerstätten formation. *Palaios* **8 (5)**: 485–498.

Ferrón HG, Martínez-Pérez C, Rahman IA, de Lucas VS, Botella H, Donoghue PCJ. **2020**. Computational fluid dynamics suggests ecological diversification among stem-gnathostomes. *Current Biology* **30 (23)**: 1–6.

Ferrón HG, Martínez-Pérez C, Rahman IA, Selles de Lucas V, Botella H, Donoghue PCJ. **2021**. Functional assessment of morphological homoplasy in stem-gnathostomes. *Proceedings of the Royal Society of London B: Biological Sciences* **288 (1943)**: 20202719.

Forel M-B, Poulet-Crovisier N, Korat L. **2021**. Ostracods like ghosts in their shells: input of X-ray computed tomography for taxonomy and taphonomy of Early Triassic *Hollinella*. *Revue de Micropaléontologie* **72**: 100528.

Gee BM, Bevitt JJ, Garbe U, Reisz RR. **2019a**. New material of the 'microsaur' *Llistrofus* from the cave deposits of Richards Spur, Oklahoma and the paleoecology of the Hapsidopareiidae. *PeerJ* **7**: e6327.

Gee BM, Bevitt JJ, Reisz RR. **2019b**. Dissorophid diversity at the early Permian cave system near Richards Spur, Oklahoma, USA. *Palaeontologia Electronica* **22 (2)**: 1-32.

Gibson BM, Rahman IA, Maloney KM, Racicot RA, Mocke H, Laflamme M, Darroch SAF. **2019**. Gregarious suspension feeding in a modular Ediacaran organism. *Science Advances* **5 (6)**: eaaw0260.

Gleadow AJW, Duddy IR. **1980**. Early Cretaceous volcanism and the early breakup history of south-eastern Australia: evidence from fission-track dating of volcanoclastic sediments. In: Cresswell MM, and Vella P, eds. *Proceedings of the Fifth International Geological Symposium, Wellington, New Zealand*. Rotterdam: Balkema, 295–300.

Göpel T, Wirkner CS. **2015**. An “ancient” complexity? Evolutionary morphology of the circulatory system in Xiphosura. *Zoology* **118 (4)**: 221–238.

Gureyev TE, Nesterets Y, Ternovski D, Thompson D, Wilkins SW, Stevenson AW, Sakellariou A, Taylor JA. **2011**. Toolbox for advanced X-ray image processing. *Advances in Computational Methods for X-Ray Optics II* **8141**: 81410B.

Haszprunar G, Speimann E, Hawe A, Heß M. **2011**. Interactive 3D anatomy and affinities of the Hyalogyrinidae, basal Heterobranchia (Gastropoda) with a rhipidoglossate radula. *Organisms Diversity & Evolution* **11 (3)**: 201–236.

Hebdon N, Ritterbush KA, Choi Y. **2020**. Computational fluid dynamics modeling of fossil ammonoid shells. *Palaeontologia Electronica* **23 (1)**: a21.

Hegna TA, Martin MJ, Darroch SAF. **2017**. Pyritized *in situ* trilobite eggs from the Ordovician of New York (Lorraine Group): implications for trilobite reproductive biology. *Geology* **45 (3)**: 199–202.

Helby R. **1973**. Review of Late Permian and Triassic palynology of New South Wales. *Special Publications of the Geological Society of Australia* **4**: 141–155.

Helby R, Morgan R, Partridge AD. **1987**. A palynological zonation of the Australian Mesozoic. *Memoir of the Association of Australasian Palaeontologists* **4**: 1–94.

Henderickx H, Tafforeau P, Soriano C. **2012**. Phase contrast synchrotron microtomography reveals the morphology of a partially visible new *Pseudogarypus* in Baltic amber (Pseudoscorpiones: Pseudogarypidae). *Palaeontologia Electronica* **15 (2)**: 1–11.

Herbert C. **1980**. Depostional development of the Sydney Basin. In A Guide to the Sydney Basin (eds., C. Herbert and R. Helby). *Geological Survey of New South Wales Bulletin* **26**: 11–25.

Herbert C. **1983**. Sydney Basin stratigraphy. In: Herbert C, ed. *Geology of the Sydney Basin 1:100,000 Sheet 9130*. Sydney: New South Wales Department of Natural Resources.

Herbert G. **1997**. Sequence stratigraphic analysis of early and middle Triassic alluvial and estuarine fades in the Sydney Basin, Australia. *Australian Journal of Earth Sciences* **44 (1)**: 125–143.

Herrera F, Shi G, Mays C, Ichinnorov N, Takahashi M, Bevitt JJ, Herendeen PS, Crane PR. **2020**. Reconstructing *Krassilovia mongolica* supports recognition of a new and unusual group of Mesozoic conifers. *PLoS ONE* **15 (1)**: e0226779.

Hita Garcia F, Fischer G, Liu C, Audisio TL, Alpert GD, Fisher BL, Economo EP. **2017**. X-Ray microtomography for ant taxonomy: An exploration and case study with two new *Terataner* (Hymenoptera, Formicidae, Myrmicinae) species from Madagascar. *PLoS ONE* **12 (3)**: e0172641.

Holmes WBK. **1982**. The Middle Triassic flora from Benolong, near Dubbo, central-western New South Wales. *Alcheringa* **6 (1)**: 1–33.

Hu S, Zhang Q, Feldmann RM, Benton MJ, Schweitzer CE, Huang J, Wen W, Zhou C, Xie T, Lü T, Hong S. **2017**. Exceptional appendage and soft-tissue preservation in a Middle Triassic horseshoe crab from SW China. *Scientific Reports* **7 (1)**: 14112.

Jell PA, Roberts J. **1986**. Plants and invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* **3**: 1–77.

Klein N. **2012**. Postcranial morphology and growth of the pachypleurosaur *Anarosaurus heterodontus* (Sauropterygia) from the Lower Muschelkalk of Winterswijk, The Netherlands. *Paläontologische Zeitschrift* **86 (4)**: 389–408.

Klompmaker AA, Fraaije RHB. **2011**. The oldest (Middle Triassic, Anisian) lobsters from the Netherlands: taxonomy, taphonomy, paleoenvironment, and paleoecology. *Palaeontologia Electronica* **14 (1)**: 1–16.

Klug C, Hagdorn H, Montenari M. **2005**. Phosphatized soft-tissue in Triassic bivalves. *Palaeontology* **48 (4)**: 833–852.

Korasidis VA, Wagstaff BE. **2020**. The rise of flowering plants in the high southern latitudes of Australia. *Review of Palaeobotany and Palynology* **272**: 104126.

Kouraiss K, El Hariri K, El Albani A, Azizi A, Mazurier A, Lefebvre B. **2019**. Digitization of fossils from the Fezouata Biota (Lower Ordovician, Morocco): Evaluating computed tomography and photogrammetry in collection enhancement. *Geoheritage* **11 (4)**: 1889–1901.

Kutara K, Une Y, Fujita Y. **2019**. Morphological assessment of horseshoe crabs (*Tachypleus tridentatus*) by using magnetic resonance imaging. *Journal of Zoo and Wildlife Medicine* **50 (3)**: 742–748.

Lak M, Néraudeau D, Nel A, Cloetens P, Perrichot V, Tafforeau P. **2008**. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microscopy and Microanalysis* **14 (3)**: 251–259.

Lamsdell JC. **2016**. Horseshoe crab phylogeny and independent colonizations of fresh water: ecological invasion as a driver for morphological innovation. *Palaeontology* **59 (2)**: 181–194.

Lamsdell JC. **2020**. The phylogeny and systematics of Xiphosura. *PeerJ* **8**: e10431.

Lamsdell JC. **2021**. A new method for quantifying heterochrony in evolutionary lineages. *Paleobiology* **47 (2)**: 363–384.

Lamsdell JC, McKenzie SC. **2015**. *Tachypleus syriacus* (Woodward)—a sexually dimorphic Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. *Organisms Diversity & Evolution* **15 (4)**: 681–693.

Landschoff J, Komai T, Du Plessis A, Gouws G, Griffiths CL. **2018**. MicroCT imaging applied to description of a new species of *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae), with selection of three-dimensional type data. *PLoS ONE* **13 (9)**: e0203107.

Lange W. **1923**. Über neue Fossilfunde aus der Trias von Göttingen. *Zeitschrift der deutschen geologischen Gesellschaft* **74**: 162–168.

Latreille PA. **1802**. *Histoire naturelle, générale et particulière, des crustacés et des insectes*. Paris: Dufart.

Laurie JR, Bodorkos S, Nicoll RS, Crowley JL, Mantle DJ, Mory AJ, Wood GR, Backhouse J, Holmes EK, Smith TE. **2016**. Calibrating the middle and late Permian palynostratigraphy of Australia to the geologic time-scale via U–Pb zircon CA-IDTIMS dating. *Australian Journal of Earth Sciences* **63 (6)**: 701–730.

Leach WE. **1819**. Entomostraca. In: Levrault F, ed. *Dictionaire des Science Naturelles*. Paris.: Levrault and Schoell, 524–543.

Lerner AJ, Lucas SG, Lockley M. **2017**. First fossil horseshoe crab (Xiphosurida) from the Triassic of North America. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **286 (3)**: 289–302.

Lindsay NM. **1982**. *The Burial History of the Strzelecki Group Sandstones, S.E. Australia: A Petrographic and Fission Track Study. Unpublished M.Sc. thesis.* Melbourne: University of Melbourne.

Linnaeus C. **1758**. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentius Salvius, Holmiae.

Liu T, Duan B, Zhang H, Cheng G, Liu J, Dong X-p, Waloszek D, Maas A. **2019**. Soft-tissue anatomy of an Orsten-type phosphatocopid crustacean from the Cambrian Furongian of China revealed by synchrotron radiation X-ray tomographic microscopy. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **294**: 263–274.

Liu W, Rühr PT, Wesener T. **2017**. A look with µCT technology into a treasure trove of fossils: The first two fossils of the millipede order Siphoniulida discovered in Cretaceous Burmese amber (Myriapoda, Diplopoda). *Cretaceous Research* **74**: 100–108.

Liu Y, Melzer RR, Haug JT, Haug C, Briggs DE, Hörnig MK, He Y-y, Hou X-g. **2016**. Three-dimensionally preserved minute larva of a great-appendage arthropod from the early Cambrian Chengjiang biota. *Proceedings of the National Academy of Sciences* **113 (20)**: 5542–5546.

Liu Y, Ortega-Hernández J, Chen H, Mai H, Zhai D, Hou X. **2020**. Computed tomography sheds new light on the affinities of the enigmatic euarthropod Jianshania furcatus from the early Cambrian Chengjiang biota. *BMC Evolutionary Biology* **20**: 1–17.

Marcondes Machado F, Passos FD, Giribet G. **2019**. The use of micro-computed tomography as a minimally invasive tool for anatomical study of bivalves (Mollusca: Bivalvia). *Zoological Journal of the Linnean Society* **186 (1)**: 46–75.

Mathys A, Brecko J, Vandenspiegel D, Cammaert L, Semal P. **2015**. Bringing collections to the digital era three examples of integrated high resolution digitisation projects. 2015 Digital Heritage: IEEE. p 155–158.

Mayr G, De Pietri VL, Love L, Mannering AA, Bevitt JJ, Scofield RP. **2020**. First complete wing of a stem group sphenisciform from the Paleocene of New Zealand sheds light on the evolution of the penguin flipper. *Diversity* **12 (2)**: 46.

Mays C, Vajda V, Frank TD, Fielding CR, Nicoll RS, Tevyaw AP, McLoughlin S. **2020**. Refined Permian–Triassic floristic timeline reveals early collapse and delayed recovery of south polar terrestrial ecosystems. *Geological Society of America Bulletin* **132 (7-8)**: 1489–1513.

McMinn A. **1982**. Early Permian-Early Jurassic palynology of DM Mirrie DDH 1, northwest of Dunedoo. *Geological Survey of New South Wales, Report* **GS1982/289 (unpublished)**:

McMinn A. **1984**. Palynology of DM Pibbon DDH 1, Goulburn River-Binnaway area. *Geological Survey of New South Wales, Report* **84/4, GS1984/052 (unpublished)**:

Meischner K-D. **1962**. Neue Funde von *Psammolimulus gottingensis* (Merostomata, Xiphosura) aus dem Mittleren Buntsandstein von Göttingen. *Paläontologische Zeitschrift* **36 (1)**: 185–193.

Metcalfe I, Crowley JL, Nicoll RS, Schmitz M. **2015**. High-precision U-Pb CA-TIMS calibration of Middle Permian to Lower Triassic sequences, mass extinction and extreme climate-change in eastern Australian Gondwana. *Gondwana Research* **28 (1)**: 61–81.

Metscher BD. **2009**. MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiology* **9 (1)**: 11.

Moreau J-D, Cloetens P, Gomez B, Daviero-Gomez V, Néraudeau D, Lafford TA, Tafforeau P. **2014**. Multiscale 3D virtual dissections of 100-million-year-old flowers using X-ray synchrotron micro-and nanotomography. *Microscopy and Microanalysis* **20 (1)**: 305–312.

Motchurova-Dekova N, Harper DAT. **2010**. Synchrotron radiation X-ray tomographic microscopy (SRXTM) of brachiopod shell interiors for taxonomy: preliminary report. *Annales Géologiques de la Péninsule Balkanique* **71**: 109–117.

Na Y, Sun C, Wang H, Huang T, Bevitt J, Li Y, Li T, Zhao Y, Li N. **2021**. Application of neutron tomography in studying new material of *Ixostrobus* Raciborski from the Middle Jurassic of Inner Mongolia, China. *Geological Journal* **56 (9)**: 4618-4626.

Parapar J, Candás M, Cunha-Veira X, Moreira J. **2017**. Exploring annelid anatomy using micro-computed tomography: A taxonomic approach. *Zoologischer Anzeiger* **270**: 19–42.

Pardo JD, Anderson JS. **2016**. Cranial morphology of the Carboniferous-Permian tetrapod *Brachydectes newberryi* (Lepospondyli, Lysorophia): new data from µCT. *PLoS ONE* **11 (8)**: e0161823.

Pates S, Daley AC, Legg DA, Rahman IA. **2021**. Vertically migrating *Isoxys* and the early Cambrian biological pump. *Proceedings of the Royal Society of London B: Biological Sciences* **288 (1953)**: 20210464.

Perrichot V, Marion L, Neraudeau D, Vullo R, Tafforeau P. **2008**. The early evolution of feathers: fossil evidence from Cretaceous amber of France. *Proceedings of the Royal Society of London B: Biological Sciences* **275 (1639)**: 1197–1202.

Pickett JW. **1984**. A new freshwater limuloid from the middle Triassic of New South Wales. *Palaeontology* **27 (3)**: 609–621.

Pike GP. **1973**. Quamby, Tasmania. Geological Atlas 1 Mile Series Explanatory Report, Sheet 46 (8219N). Tasmanian Department of Mines, Hobart.

Pohl H, Wipfler B, Grimaldi D, Beckmann F, Beutel R. **2010**. Reconstructing the anatomy of the 42-million-year-old fossil *Mengea tertiaria* (Insecta, Strepsiptera). *Naturwissenschaften* **97** **(9)**: 855–859.

Poropat SF, Martin SK, Tosolini A-MP, Wagstaff BE, Bean LB, Kear BP, Vickers-Rich P, Rich TH. **2018**. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. *Alcheringa* **42** **(2)**: 157–229.

Price PL. **1997**. Permian to Jurassic palynostratigraphic nomenclature of the Bowen and Surat Basin. In: Green PM, ed. *The Surat and Bowen Basins, south-east Queensland*: Queensland Minerals and Energy Review Series, 137–178.

Racheboeuf PR, Vannier J, Anderson LI. **2002**. A new three-dimensionally preserved xiphosuran chelicerate from the Montceau-les-Mines Lagerstätte (Carboniferous, France). *Palaeontology* **45** **(1)**: 125–147.

Rahman IA. **2017**. Computational fluid dynamics as a tool for testing functional and ecological hypotheses in fossil taxa. *Palaeontology* **60** **(4)**: 451–459.

Rahman IA, Darroch SAF, Racicot RA, Laflamme M. **2015a**. Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. *Science Advances* **1** **(10)**: e1500800.

Rahman IA, O'Shea J, Lautenschlager S, Zamora S. **2020**. Potential evolutionary trade-off between feeding and stability in Cambrian cinctan echinoderms. *Palaeontology* **63** **(5)**: 689–701.

Rahman IA, Zamora S, Falkingham PL, Phillips JC. **2015b**. Cambrian cinctan echinoderms shed light on feeding in the ancestral deuterostome. *Proceedings of the Royal Society of London B: Biological Sciences* **282** **(1818)**: 20151964.

Reid M, Bordy EM, Taylor WL, le Roux SG, du Plessis A. **2019**. A micro X-ray computed tomography dataset of fossil echinoderms in an ancient obrution bed: a robust method for taphonomic and palaeoecologic analyses. *GigaScience* **8 (3)**: giy156.

Retallack GJ. **1977**. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* **1 (3)**: 247–277.

Retallack GJ. **1980**. Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In A Guide to the Sydney Basin (eds., C. Herbert and R. Helby). *Geological Survey of New South Wales Bulletin* **26**: 385–430.

Riedel A, Dos Santos Rolo T, Cecilia A, Van de Kamp T. **2012**. Sayrevilleinae Legalov, a newly recognised subfamily of fossil weevils (Coleoptera, Curculionoidea, Attelabidae) and the use of synchrotron microtomography to examine inclusions in amber. *Zoological Journal of the Linnean Society* **165 (4)**: 773–794.

Riek EF. **1955**. A new xiphosuran from the Triassic sediments at Brookvale, New South Wales. *Records of the Australian Museum* **23 (5)**: 281–282.

Riek EF, Gill ED. **1971**. A new xiphosuran genus from Lower Cretaceous freshwater sediments at Koonwarra, Victoria, Australia. *Palaeontology* **14 (2)**: 206–210.

Rust BR, Jones BG. **1987**. The Hawkesbury Sandstone south of Sydney, Australia; Triassic analogue for the deposit of a large, braided river. *Journal of Sedimentary Research* **57 (2)**: 222–233.

Sander PM, Wintrich T, Schwermann AH, Kindlimann R. **2016**. Die paläontologische Grabung in der Rhät-Lias-Tongrube der Fa. Lücking bei Warburg-Bonenburg (Kr. Höxter) im Frühjahr 2015. *Geologie und Paläontologie in Westfalen* **88**: 11–37.

Schimpf L, Isaak S, Hauschke N, Gossel W. **2017**. Computer-generated 3D models and digital storage for use in palaeontological collections, tested for xiphosurans of Eocene age from Saxony-Anhalt, Germany. *Hallesches Jahrbuch für Geowissenschaften* **40**: 1–16.

Schwarzhans W, Beckett HT, Schein JD, Friedman M. **2018**. Computed tomography scanning as a tool for linking the skeletal and otolith-based fossil records of teleost fishes. *Palaeontology* **61 (4)**: 511–541.

Seegets-Villiers DE, Wagstaff BE. **2016**. Morphological variation of stratigraphically important species in the genus *Pilosisporites* Delcourt & Sprumont, 1955 in the Gippsland Basin, southeastern Australia. *Memoirs of Museum Victoria* **74**: 81–91.

Smith HE, Bevitt JJ, Zaim J, Rizal Y, Puspaningrum MR, Trihascaryo A, Price GJ, Webb GE, Louys J. **2021**. High-resolution high-throughput thermal neutron tomographic imaging of fossiliferous cave breccias from Sumatra. *Scientific Reports* **11 (1)**: 1-16.

Snyder AJ, LeBlanc ARH, Jun C, Bevitt JJ, Reisz RR. **2020**. Thecodont tooth attachment and replacement in bolosaurid parareptiles. *PeerJ* **8**: e9168.

Song H, Song H, Rahman IA, Chu D. **2021**. Computational fluid dynamics confirms drag reduction associated with trilobite queuing behaviour. *Palaeontology* **64 (5)**: 597–608.

Størmer L. **1952**. Phylogeny and taxonomy of fossil horseshoe crabs. *Journal of Paleontology* **26 (4)**: 630–640.

Sutton MD. **2008**. Tomographic techniques for the study of exceptionally preserved fossils. *Proceedings of the Royal Society of London B: Biological Sciences* **275 (1643)**: 1587–1593.

Tadros NZ. **1993**. Gunnedah Basin, New South Wales. *Geological Survey of New South Wales, Memoir (Geology)* **12**: 1–649.

Tafforeau P, Boistel R, Boller E, Bravin A, Brunet M, Chaimanee Y, Cloetens P, Feist M, Hoszowska J, Jaeger J-J. **2006**. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A* **83 (2)**: 195–202.

Troelsen PV, Wilkinson DM, Seddighi M, Allanson DR, Falkingham PL. **2019**. Functional morphology and hydrodynamics of plesiosaur necks: does size matter? *Journal of Vertebrate Paleontology* **39 (2)**: e1594850.

Tschernyshev BI. **1933**. Arthropoda from the Urals and other regions of the USSR. *Materials of the Central Scientific and Prospecting Institute Paleontology and Stratigraphy* **1**: 15–25.

Van Roy P, Orr PJ, Botting JP, Muir LA, Vinther J, Lefebvre B, El Hariri K, Briggs DEG. **2010**. Ordovician faunas of Burgess Shale type. *Nature* **465 (7295)**: 215–218.

Vía L, De Villata FJ, Esteban Cerdá M. **1977**. Paleontología y Paleoecología de los yacimientos fosilíferos del Muschelkalk superior entre Alcover y Mont-Ral (Montañas de Prades, provincia de Tarragona). *Journal of Iberian Geology* **4**: 247–258.

Wagstaff BE, Gallagher SJ, Hall WM, Korasidis VA, Rich TH, Seegets-Villiers DE, Vickers-Rich PA. **2020**. Palynological-age determination of Early Cretaceous vertebrate-bearing beds along the south Victorian coast of Australia, with implications for the spore-pollen biostratigraphy of the region. *Alcheringa* **44 (3)**: 460–474.

Waldman M. **1971**. Fish from the freshwater Lower Cretaceous of Victoria, Australia, with comments on the palaeoenvironment. *Special Papers in Palaeontology* **9**: 1–124.

Waldman M. **1973**. The fossil lake-fauna of Koonwarra, Victoria. *Australian Natural History* **17**: 317–321.

Waldman M. **1984**. The fossil lake-fauna of Koonwarra, Victoria. In: Archer M, and Clayton G, eds. *Vertebrate Zoogeography & Evolution in Australasia (Animals in Space and Time)*. Sydney: Hesperian Press, 231–233.

Waters JA, White LE, Sumrall CD, Nguyen BK. **2017**. A new model of respiration in blastoid (Echinodermata) hydrospires based on computational fluid dynamic simulations of virtual 3D models. *Journal of Paleontology* **91 (4)**: 662–671.

Webby BD. **1970**. *Brookvalichnus*, a new trace fossil from the Triassic of the Sydney Basin, Australia. *Geological Journal Special Issue* **3**: 527–530.

Wesener T. **2019**. The oldest pill millipede fossil: a species of the Asiatic pill millipede genus *Hyleoglomeris* in Baltic amber (Diplopoda: Glomerida: Glomeridae). *Zoologischer Anzeiger* **283**: 40–45.

Willsch M, Friedrich F, Baum D, Jurisch I, Ohl M. **2020**. A comparative description of the mesosomal musculature in Sphecidae and Ampulicidae (Hymenoptera, Apoidea) using 3D techniques. *Deutsche Entomologische Zeitschrift* **67 (1)**: 51–67.

Xing L, Caldwell MW, Chen R, Nydam RL, Palci A, Simões TR, McKellar RC, Lee MSY, Liu Y, Shi H. **2018**. A mid-Cretaceous embryonic-to-neonate snake in amber from Myanmar. *Science Advances* **4 (7)**: eaat5042.

Xing L, McKellar RC, Wang M, Bai M, O'Connor JK, Benton MJ, Zhang J, Wang Y, Tseng K, Lockley MG. **2016a**. Mummified precocial bird wings in mid-Cretaceous Burmese amber. *Nature Communications* **7 (1)**: 1–7.

Xing L, McKellar RC, Xu X, Li G, Bai M, Persons IV WS, Miyashita T, Benton MJ, Zhang J, Wolfe AP. **2016b**. A feathered dinosaur tail with primitive plumage trapped in mid-Cretaceous amber. *Current Biology* **26 (24)**: 3352–3360.

Young GC, Laurie JR. **1966**. *An Australian Phanerozoic Timescale*. Melbourne: Oxford University Press.

Yuen AHL, Kwok DHC, Kim SW. **2019**. Magnetic resonance imaging of the live tri-spine horseshoe crab (*Tachypleus tridentatus*). *Arthropoda Selecta* **28 (2)**: 247–251.

Zhai D, Edgecombe GD, Bond AD, Mai H, Hou X, Liu Y. **2019a**. Fine-scale appendage structure of the Cambrian trilobitomorph *Naraoia spinosa* and its ontogenetic and ecological implications. *Proceedings of the Royal Society of London B: Biological Sciences* **286 (1916)**: 20192371.

Zhai D, Ortega Hernández J, Wolfe JM, Hou X, Cao C, Liu Y. **2019b**. Three-dimensionally preserved appendages in an early Cambrian stem-group pancrustacean. *Current Biology* **29 (1)**: 171–177.

Zuber M, Laaß M, Hamann E, Kretschmer S, Hauschke N, Van De Kamp T, Baumbach T, Koenig T. **2017**. Augmented laminography, a correlative 3D imaging method for revealing the inner structure of compressed fossils. *Scientific Reports* **7**: 41413.

Figure captions

Figure 1: *Austrolimulus fletcheri* from the Hawkesbury Sandstone (Middle Triassic, Anisian). AM F38275 counterpart of holotype. (A) Specimen under plain light. (B) 3D reconstruction of specimen, see Supplemental Figure 1. (C) X-ray tomographic slice showing pronounced cardiac lobe (white arrows). (D) X-ray tomographic slice showing difference in density between prosoma (red dotted line) and hypertrophied genal spine (blue lines). Image credit: (A) Joshua White.

Figure 2: *Dubbolimulus fletcheri* from the Napperby Formation (Middle Triassic, Ansian). MMF 27693, holotype. (A) Specimen under plain light. (B) 3D reconstruction of specimen showing appendage impressions (white arrows), see Supplemental Figure 2. Image credit: (A) David Barnes.

Figure 3: *Tasmaniolimulus patersoni* from the Jackey Shale (Early Triassic, Induan). UTGD 123979, holotype. (A) Specimen under plain light. (B, C) 3D reconstruction of specimen, see Supplemental Figure 3. (B) Dorsal view. (C) Oblique view. (D, E) X-ray tomographic slices showing pronounced cardiac lobe (white arrows). (A) Coated in ammonium chloride sublimate and image converted to greyscale. Image credit: (A) Russell Bicknell.

Figure 4: *Victalimulus mcqueeni* from the Koonwarra Fossil Bed (Early Cretaceous, Aptian). NMV P22410B, holotype. (A) Specimen under plain light. (B) 3D reconstruction of specimen, see Supplemental Figure 4. (D) X-ray tomographic slice showing cardiac lobe (white arrows). (E) X-ray tomographic slice showing walking leg impressions (white arrows). (F) X-ray

tomographic slice showing fixed spines and moveable spine notches (white arrows) and thoracetronic doublure (black arrow). Image credit: (A) Frank Holmes.

Supplemental Figure 1: 3D interactive model of *Austrolimulus fletcheri*, AM F38275 as modelled from SXCT. 3D PDF found at https://osf.io/at528/?view_only=78985d12aca941dda8ac95a2cc191d93.

Supplemental Figure 2: 3D interactive model of *Dubbolimulus fletcheri*, MMF 27693 as modelled from SXCT. 3D PDF found at https://osf.io/at528/?view_only=78985d12aca941dda8ac95a2cc191d93.

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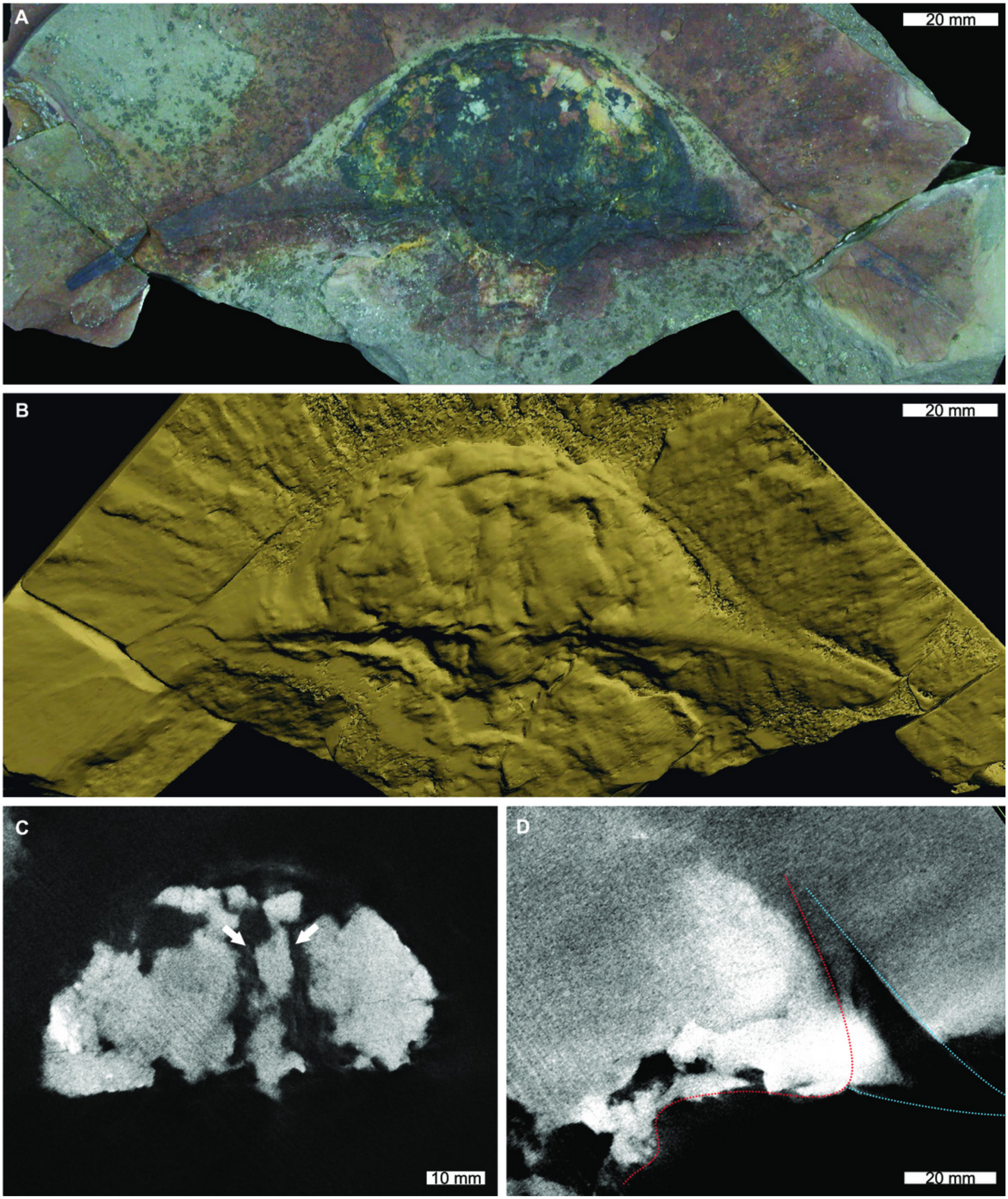
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Figure 2

Dubbolimulus fletcheri from the Napperby Formation (Middle Triassic, Ansian). MMF 27693, holotype.

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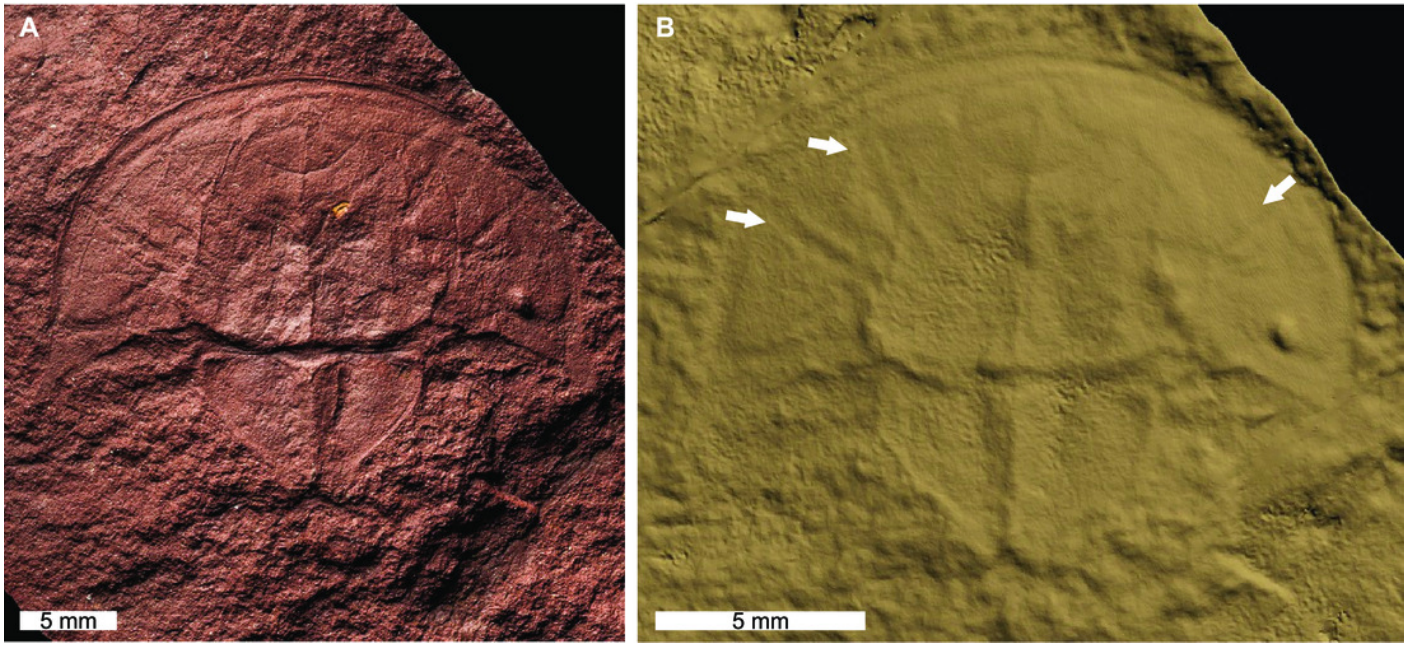

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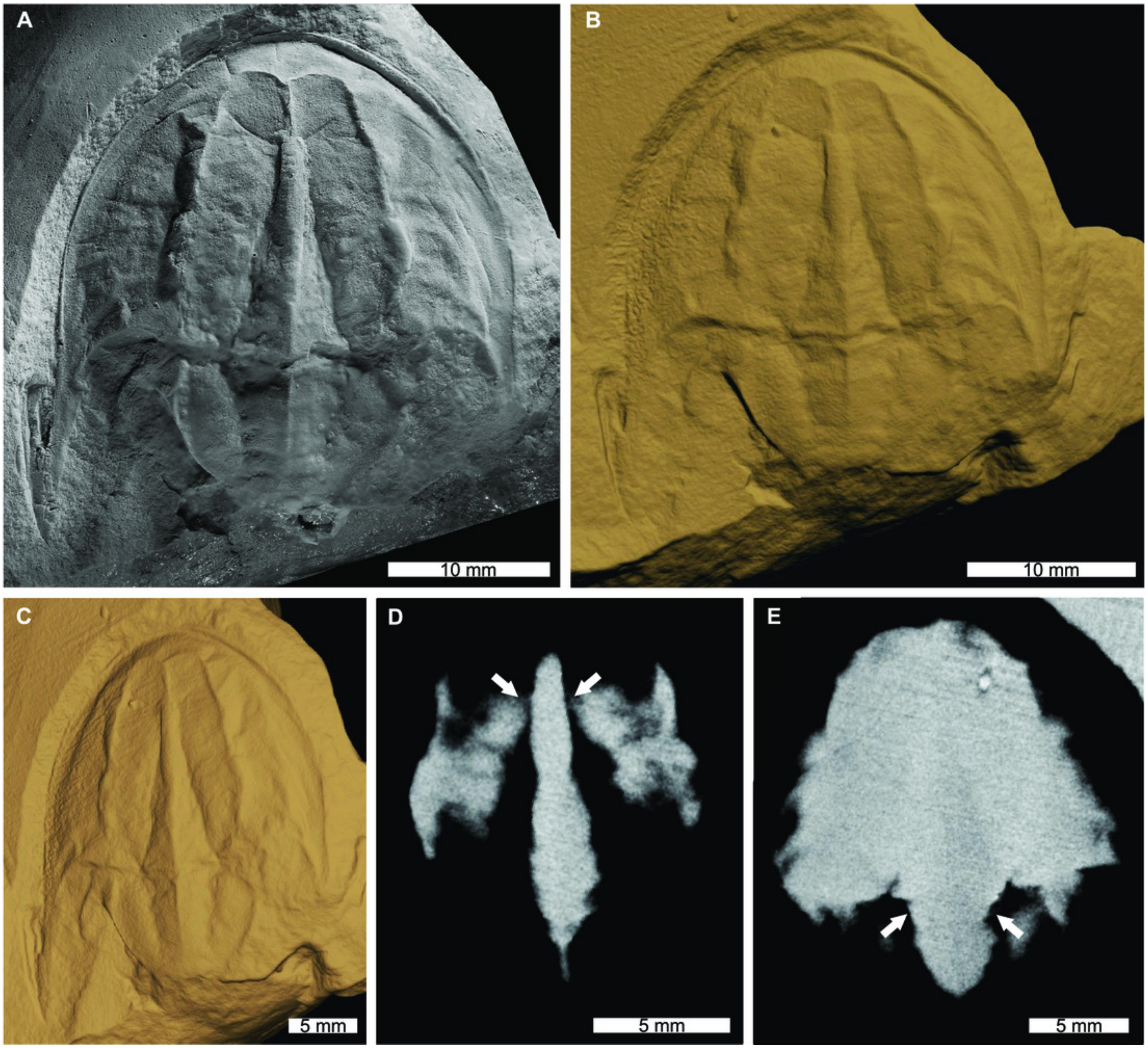
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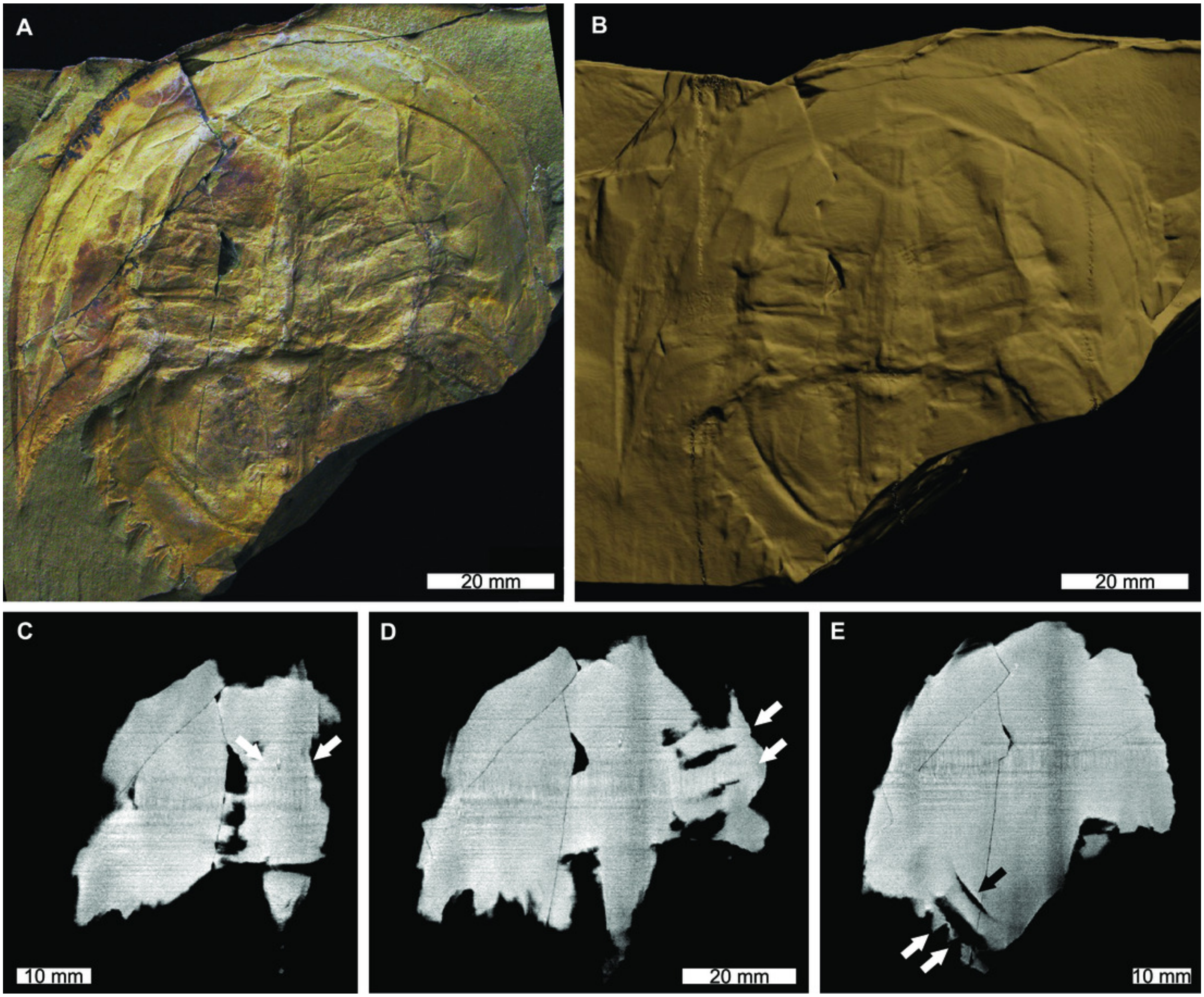
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