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Segmentation in early Xiphosura and the evolution of the thoracetron

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Non-technical Summary.—Horseshoe crabs are characterized by the fusion of their body segments into a thoracetron; however, it has been debated whether this fusion happened once or multiple times during their evolutionary history. By looking at many species of fossil horseshoe crab for which juvenile and adult specimens are known, this study demonstrates that the thoracetron evolved once in the shared horseshoe crab ancestor. The loss of visible segment boundaries, however, has occurred multiple times within horseshoe crab evolution. This research shows that the loss of segment boundaries in three lineages of horseshoe crabs represents cases of parallel evolution, where these lineages independently lost their segment boundaries by progressing along the same shared developmental pathway. In one group, however, the segment boundaries are not expressed due to the retention of juvenile characteristics into adulthood, which indicates a case of convergent evolution.

Abstract.—Xiphosuran chelicerates, also known as horseshoe crabs, are a long-lived clade characterized by a highly distinctive morphology and are a classic example of supposed evolutionary stasis. One key feature of horseshoe crabs is the fusion of the opisthosomal segments into a single sclerite referred to as a thoracetron. There has been historical uncertainty as to whether the thoracetron originated once or multiple times within the clade. Here we review criteria for determining whether segments are fused and apply them to a broad census of taxa for which their ontogeny is known or the adult status of specimens can be reasonably asserted to explore the evolution of the thoracetron within a developmental framework. Our findings indicate that the thoracetron evolved once in the common ancestor to Xiphosura. However, subsequent independent loss of the thoracetron segment boundaries is identified and shown to be the result of heterochronic processes acting on a shared developmental pathway. The multiple cases of effacement of the thoracetron within Limuloidea are cases of peramorphically driven parallelism, while the effacement of the thoracetron in the pedomorphic Belinurina is a case of convergence. Xiphosurids therefore represent an interesting case study for recognizing parallelism and convergence on the same structure within closely related lineages. We also demonstrate that somite VII has been incorporated into the prosoma multiple times within the chelicerate lineage, which has implications for interpreting the ground pattern of the group.

Introduction

With a known evolutionary history spanning approximately 480 million years (Van Roy et al., 2010), horseshoe crabs (Xiphosura Latreille, 1802) are often referred to as “living fossils” due to apparent superficial similarities between modern and fossil representatives. Further examination of their fossil record, however, reveals a hidden morphological and ecological diversity (Lamsdell, 2016, 2021a, b). One of the most easily recognizable sources of variation across the evolutionary history of Xiphosura is the expression of visible tergite boundaries on the thoracetron, or lack thereof. The thoracetron (Fig. 1), formed by the external fusion of the opisthosoma (Størmer, 1955; Anderson and Selden, 1997), is a morphological character unique to Xiphosura (Lamsdell, 2013, 2020).

Characterizing the evolution and segmental composition of the thoracetron has been integral to our understanding of xiphosuran taxonomy and phylogeny (Selden and Siveter, 1987; Anderson and Selden, 1997; Lamsdell, 2013, 2020). Notoriously segmented, the arthropod body is composed of serially homologous units known as somites or metameres (Lankester, 1904). Lankester (1904) further divided somites into eight meromes, although four are of primary focus: the tergite (dorsal sclerite), sternite (ventral sclerite), appendages, and musculature. The modification of meromes, and therefore the corresponding somite, to form specialized regions of the body that are distinctive from those preceding and succeeding is referred to as tagmosis (Lankester, 1904). The differentiation of somites is the underlying mechanism behind the evolution of morphological complexity and specialization in arthropods; therefore, characterizing the evolutionary history behind patterns of tagmosis in a clade is a fundamental underpinning of arthropod paleobiology.

Xiphosura are generally recognized as ancestrally comprising 18 somites (Lankester, 1881; Anderson and Selden, 1997;

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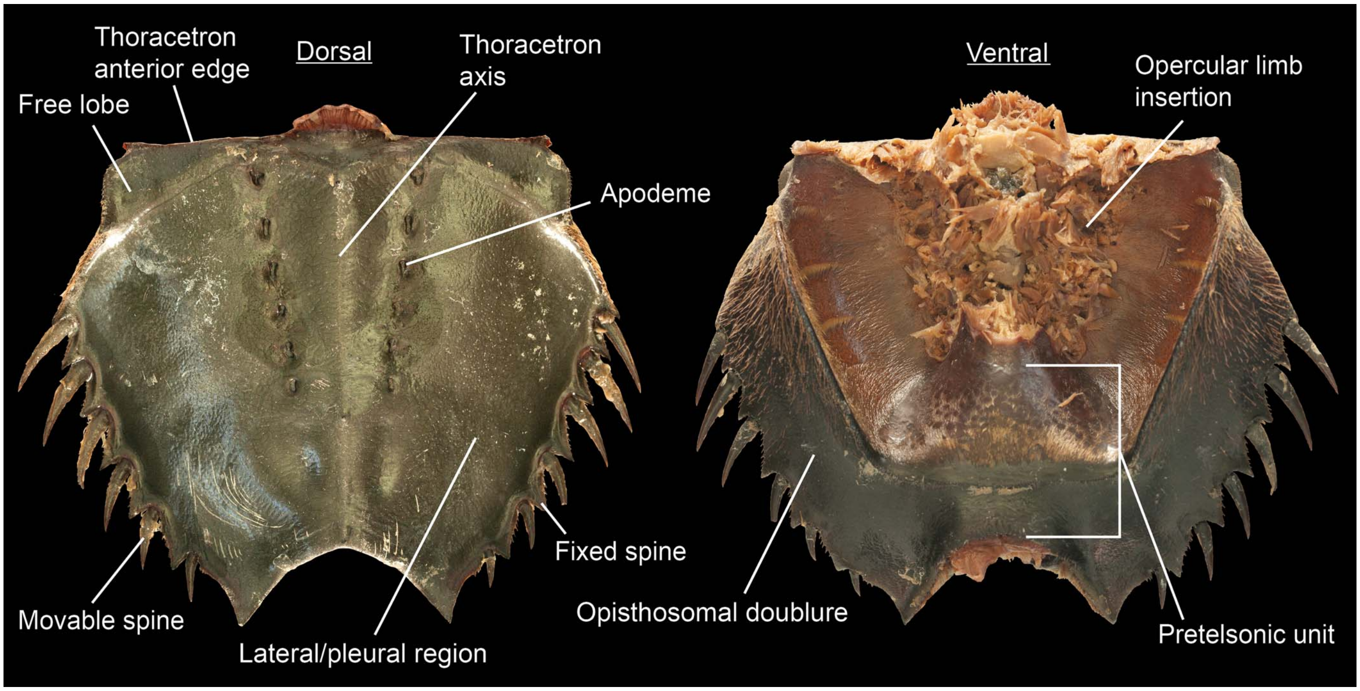

Figure 1. Anatomy and terminology of an anatomically modern thoracetron.

Lamsdell, 2013), although recent reports of lunataspids with an opisthosoma consisting of 12 tergites (Lamsdell et al., 2023) indicates that the ancestral condition for xiphosurans may in fact be 19 somites. Anatomically modern limulines (as exemplified by *Limulus*) exhibit 16 clear somites, the last somite consisting of an unspecified number of suppressed or completely merged somites (Shultz, 2001; Dunlop and Lamsdell, 2017). The preocular somite is numbered 0, followed by somites I–XVII (Anderson and Selden, 1997). In terms of tagmata, somites I–VI comprise the prosoma, VII–XIII comprise the mesosoma, and XIV–XVII form the metasoma, following Lamsdell (2013). The opisthosoma is a pseudotagma composed of all post-cephalic somites. Previously, the fusion of somites IX–XVII (Anderson and Selden, 1997) or VIII–XIV (Lamsdell, 2013) have been variably considered to constitute the formation of the thoracetron. In actuality, either scheme results in the exclusion of taxa with a thoracetron from being considered as possessing one, with, for example, *Rolfeia* exhibiting a freely articulating 8 (Waterston, 1985) and *Lunataspis* retaining a freely articulating postabdomen of somites XV–XVII (Rudkin et al., 2008). The thoracetron therefore consists of somites IX–XIV and later expands to comprise somites VIII–XVII.

The tagmatic affinity of somite VII, which bears the chilaria, is of some controversy. During development, somite VII and part of somite VIII, the opercular tergite, are integrated into the prosoma (Scholl, 1977). Stürmer and Bergström (1981) and Haug et al. (2012) therefore argued that somite VII should be considered prosomal in nature, contra the conventional view that it is inherently opisthosomal in nature (Snodgrass, 1952). The definition of tagmata used herein explicitly addresses that tagmata are defined at the earliest ontogenetic stage (Lamsdell, 2013); therefore, we consider somite VII to be originally opisthosomal in nature.

In past iterations of xiphosuran taxonomy, the presence of unfused opisthosomal tergites was used to differentiate the superfamily Belinuroidea Packard, 1886—comprising *Belinurus* and *Bellinuroopsis*—from other Paleozoic xiphosurids with a thoracetron, namely the superfamilies Limuloidea Leach, 1819 and Euproopoidea Eller, 1938 (see Størmer, 1955; Selden and Siveter, 1987; Anderson and Selden, 1997). Belinuroids were suspected to have a variable number of freely articulating tergites located anteriorly to a partially fused opisthosoma (Størmer, 1955; see Anderson and Selden, 1997 for a review); however, a reexamination of *Belinurus* Bronn, 1839 material determined that the anterior opisthosomal tergites were indeed fused in belinuroid taxa and established the thoracetron as a synapomorphy for Xiphosurida (Anderson and Selden, 1997). Anderson and Selden (1997) also included Synziphosurina Packard, 1886 within Xiphosura as a paraphyletic grade of stem xiphosurids lacking a thoracetron; further work by Lamsdell (2013) determined that synziphosurines were a polyphyletic grouping of basal aquatic chelicerates and defined a monophyletic Xiphosura united by the possession of a thoracetron (Lamsdell, 2013, 2016, 2020), thereby rendering Xiphosura and Xiphosurida broadly synonymous.

The timing of opisthosomal fusion in Xiphosura is still undetermined. Anderson and Selden (1997) speculated that it had to have occurred before the late Devonian. The surprising discovery of *Lunataspis aurora* Rudkin, Young, and Nowlan, 2008 from the Ordovician of Canada prompted a reevaluation of this timeline and demonstrated that a thoracetron was present in the earliest xiphosurans (Rudkin et al., 2008). Further reports of Ordovician xiphosurids have confirmed that a thoracetron was ubiquitous among these taxa (Van Roy et al., 2010; Lamsdell et al., 2023). This narrative is challenged, however, by conflicting interpretations of a variety of Devonian taxa that resolve phylogenetically crownward of *Lunataspis* according to prosomal characteristics (Lamsdell, 2020, 2021a) but have been interpreted as possessing an unfused opisthosoma (Pickett, 1993; Bicknell et al., 2019; Bicknell and Smith, 2021), indicating either: (1) that the thoracetron developed independently multiple times within Xiphosura (a scenario previously suggested by Raymond [1944] and Fisher [1981]), (2) that the Devonian taxa diverged from the main xiphosuran lineage before *Lunataspis*, or (3) that the interpretations of an unfused opisthosoma in these taxa are erroneous. Complicating matters further, xiphosurids appear to exhibit conflicting patterns of segment boundary effacement within the thoracetron, with tergite expression occurring variably within Belinurina, Paleolimulidae, and Austrolimulidae, potentially suggesting a high degree of plasticity within the thoracetron or further support for its convergent development.

Here we review the opisthosomal morphology of Xiphosura across their evolutionary history. Patterns of opisthosomal fusion and segment effacement are documented in each of the major horseshoe crab clades, and a revised scenario for the evolution of the thoracetron is suggested. We focus particularly on Ordovician and Devonian taxa that represent the earliest records of thoracetron evolution and for which interpretations of the opisthosoma have proven contentious, as well as the Belinurina, a group for which interpreting the condition of the prosomal/opisthosomal articulation has been historically problematic. We also consider the development of the thoracetron during ontogeny where possible. While we have attempted to be as accurate and comprehensive as possible, we stress that this is a preliminary review and that a number of our interpretations are tentative; our goal here is to challenge prevailing assumptions about opisthosomal fusion and thoracetron evolution and to stress the need for further detailed descriptive work on key taxa, especially those for which a large number of individuals are known.

Materials and methods

We use the distinction between segments and somites employed by Selden and Siveter (1987) and Lamsdell (2013): segments are demarcated by the external expression of a tergite or sternite and are referred to using Arabic numerals, while somites (numbered using roman numerals) may not always be externally differentiated, as exemplified by the fusion of the prosoma in chelicerates. In addition, we follow the distinction between pseudotagma and tagma as originally proposed by van der Hammen (1963, 1986a, b) and elaborated on by Lamsdell (2013), from which we draw additional associated morphological terminology. Morphological terminology for xiphosurids follows Selden and Siveter (1987) and Lamsdell (2013, 2016, 2020, 2021a).

One major challenge in interpreting trends in xiphosuran morphology is determining whether the individuals being considered represent adults or juveniles, an important concern when species undergo marked morphological changes during their development (as is the case in modern horseshoe crabs; Sekiguchi et al., 1982, 1988a, b; Sekiguchi, 1988; Shuster and Sekiguchi, 2003) and when heterochronic processes underlie periods of evolution within a group (a scenario also supported in Xiphosura; Lamsdell, 2021a, b). Adult forms may be more readily distinguished in the fossil record among taxa that undergo metamorphosis as part of their development (Haug and Haug, 2012; Zippel et al., 2022; Prokop et al., 2023) but can be more difficult to determine in arthropod groups that undergo anamorphic or more gradualistic development, in part because arthropods generally lack a reliable size-independent indication of age (Higgins and Rankin, 1996) without detailed descriptive and comparative work. Adults have been determined in fossil taxa known from a large number of individuals where ontogenetic sequences are known, determined either by their terminal position on a size regression (e.g., Andrews et al., 1974; Kues and Kietzke, 1981; Wagner et al., 2017) or by a stabilization in their expressed morphology (utilized predominantly in trilobites as determined by their segmental expression; see, e.g., Hughes et al., 2006; Dai and Zhang, 2013a, b; Holmes et al., 2021). A number of fossil horseshoe crab species are known from a large number of specimens for which size regression has been plotted (Haug et al., 2012; Haug and Rötzer, 2018a; Tashman et al., 2019; Bicknell et al., 2022; Naugolnykh and Bicknell, 2022). In combination with developmental data from extant species, these studies support previous observations that the majority of Paleozoic and Mesozoic horseshoe crabs were smaller than their modern counterparts (Siveter and Selden, 1987) and, critically for our purposes, that any ontogenetic changes in opisthosomal fusion and segmental expression occur in the earliest post-hatching instars (see also Haug and Haug, 2020; Lamsdell, 2021a), suggesting that even if individuals are subadults, the condition of their thoracetron is likely representative of the adult morphology.

We take a relatively conservative approach to inferring the adult condition of specimens and focus only on taxa for which we consider the available material to likely represent adult individuals. Therefore, we focus mainly on species for which a large number of specimens—with associated ontogenetic data—are known (adulthood determined on the basis of primary criteria). We also consider species known from a limited number of individuals where those individuals are an equivalent size or larger than the adults of closely related species within their own or a closely related clade (adulthood determined on the basis of secondary criteria). In total, we directly consider 23 species from across all xiphosuran clades. Of these, eleven (*Lunataspis aurora*, the undescribed Fezouata xiphosurid, *Belinurus trilobitoides* [Buckland, 1837], *Euproops danae* Meek and Worthen, 1865, *Liomesaspis laevis* Raymond, 1944, *Alanops magnificus* Racheboeuf, Vannier, and Anderson, 2002, *Paleolimulus signatus* [Beecher, 1904], *Boeotiaspis longispinus* [Schram, 1979], *Mesolimulus walchi* Desmarest, 1822, *Tachypleus syriacus* [Woodward, 1879], and *Limulus polyphemus* [Linnaeus, 1758]) include adult representatives as determined from primary criteria, while the remaining twelve (*Lunataspis borealis* Lamsdell et al., 2023, *Patesia randalli* [Beecher, 1902], *Kasibelinurus amicorum* Pickett, 1993, *Pickettia carterae* [Eller, 1940], *Bellinuroopsis rossicus* Chernyshev, 1933, *Rolfeia fouldenensis* Waterston, 1985, *Xaniopyramis linseyi*, *Norilimulus woodae* [Lerner, Lucas, and Mansky, 2016], *Tasmaniolimulus patersoni* Bicknell, 2019, *Vaderlimulus tricki* Lerner, Lucas, and Lockley, 2017, *Austrolimulus fletcheri* Riek, 1955, and *Victalimulus mcqueeni* Riek and Gill, 1971) include adults as determined through secondary criteria—although *Lunataspis borealis* is also known from juvenile material, and *Patesia randalli* is represented by several specimens.

Of equal importance for exploring the evolution of the thoracetron is discriminating between freely articulating and fused tergites. Anderson and Selden (1997) set out four criteria for determining when opisthosomal tergites were unfused: (1) distinct anterior and posterior boundaries to the opisthosomal tergites should be visible in the fossils; (2) dorsoventral compression of the tergites should result in the asymmetrical disposition of the lateral spines in the fossils; (3) on enrollment, the axial portions of the opisthosomal tergites should show some degree of flexure in the vertical plane; (4) fully or partially disarticulated free tergites should be found in the rock matrix. We largely follow this scheme but recognize some limitations and biases in the original criteria and present updated guidelines for determining tergite fusion here. First, we note that Anderson and Selden (1997) were considering fusion of the entire opisthosoma and not a smaller subsection of tergites within it; their original criteria are therefore likely to not be clearly fulfilled if only one or two tergites are free within the opisthosoma, as is the case in *Rolfeia*, *Euproops*, and *Belinurus*, which were considered to have a freely articulating somite VIII (in *Rolfeia*) and microtergite of somite VII (in *Euproops* and *Belinurus*) but met none of the stated criteria. Size may also bias the likelihood of several of the criteria occurring or being detected. Asymmetrical disposition of the lateral spines due to compression (criterion 2) is caused by the original three-dimensionality of the fossil; this can be reduced in smaller individuals with less convexity–the cited examples of aglaspidids are all significantly larger than most fossil Xiphosura (Hesselbo, 1992)—and similar displacement is not seen in eurypterids with even large epimeral spines, likely due to their shallower cross section in life (e.g., Wills, 1965; Lamsdell et al., 2020a). Similarly, the occurrence of disarticulated tergites (criterion 4) will be less common if only one or a couple of the tergites are freely articulating and may be extremely difficult to detect in smaller individuals where their length may be measured in millimeters; for example, chasmataspidids (which are generally small and of a similar size to Paleozoic xiphosurans) are not found in association with disarticulated tergites even when specimens occur in large concentrations (e.g., Størmer, 1972; Marshall et al., 2014), likely due to their difficulty to detect and fragile nature rather than a lack of occurrence.

We recognize six possible criteria for determining whether opisthosomal tergites exhibit fusion. While ideally free tergites would be indicated by the co-occurrence of several criteria, it is important to accept that free tergites may in some cases be indicated by only a single criterion (or none; tergites are, after all, freely articulating—or not—irrespective of our ability to identify them). Our revised criteria are, in order of decreasing unambiguity: (1) free tergites occur disarticulated, as indicated by their occurrence as isolated sclerites, their absence from a detached but otherwise complete thoracetron, or their attachment to a prosomal carapace from which the thoracetron has become detached; (2) free tergites exhibit flexure at the axis during enrollment, with the degree of enrollment indicative of the number of free segments located anterior to the thoracetron; (3) the pleural spines of free tergites overlap with those of other segments; (4) free tergites show clear anterior and posterior boundaries across their entire width as determined by the degree of incision between segments; (5) free tergites are separated from the thoracetron doublure; (6) free tergites exhibit some form of physical differentiation, in the form of a change in tergite shape, a change in pleural angle, or a change in the distribution of thoracic nodes.

Phylogenetic analysis of Xiphosura was conducted on the basis of a modified matrix derived from Lamsdell (2021a), which is itself an evolution of the matrices presented in Lamsdell (2013, 2020), Lamsdell and McKenzie (2015), Selden et al. (2015), and Lamsdell et al. (2015). Five taxa (*Belinurus lunatus* [Baldwin, 1905], *Belinurus arcuatus* [Baily, 1859], *Belinurus reginae* Baily, 1863, *Belinurus truemanii* [Dix and Pringle, 1929], and *Belinurus bellulus* König, 1851) were removed from the analysis as they have been shown to represent synonyms of *Belinurus trilobitoides* (Lamsdell and Clapham, 2021; Lamsdell, 2022). The outgroup taxa included in the analysis were also revised on the basis of recent reinterpretations of a variety of Cambrian taxa as putative stem chelicerates (Aria and Caron, 2017, 2019); as such, *Fuxianhuia protensa* Hou, 1987, *Leanchoilia illecebrosa* Hou, 1987, *Alalcomenaeus cambricus* Simonetta, 1970, *Emeraldella brocki* Walcott, 1912, *Sydneyia inexpectans* Walcott, 1911, and *Olenoides serratus* (Rominger, 1887) were removed from the matrix, with *Yohoia tenuis* Walcott, 1912 retained as the new outgroup taxon and *Sanctacaris uncata* Briggs and Collins, 1988, *Habelia optata* Walcott, 1912, and *Mollisonia plenovenatrix* Aria and Caron, 2019 included to aid in resolving character polarity at the base of Xiphosura. The treatment of the thoracetron in the matrix is also modified, with the thoracetron considered to be present when the fusion of somites XI to XIV occurs, rather than somites VIII to XIV as in a previous version of the matrix. The fusion of somites VIII, IX, and X into the thoracetron are therefore coded as separate, distinct characters. The revised matrix compromises 259 characters coded for 156 taxa. Tree inference was performed through maximum parsimony analysis performed using TNT (Goloboff et al., 2008). The search strategy employed 100,000 random addition sequences with all characters unordered and of equal weight (Congreve and Lamsdell, 2016), each followed by tree bisection–reconnection (TBR) branch swapping. Most parsimonious trees were summarized through a strict consensus. Jackknife (Farris et al., 1996), Bootstrap (Felsenstein, 1985), and Bremer (Bremer, 1994) support values were also calculated in TNT. Bootstrapping was performed with 50% resampling for 1,000 repetitions, while jackknifing was performed using simple addition sequence and TBR branch swapping for 1,000 repetitions with 33% character deletion.

Repositories and institutional abbreviations.—AM, Australian Museum, Sydney, New South Wales, Australia; BMS, Buffalo Museum of Science, Buffalo, New York, USA; CCMGE, Chernyshev Central Museum of Geological Exploration, Saint Petersburg, Russia; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GIUS, Silesian University Faculty of Earth Sciences, Sosnowiec, Poland; KUMIP, University of Kansas Biodiversity Institute, Lawrence, Kansas, USA; MM, Manitoba Museum, Winnipeg, Manitoba, Canada; MNHN, Museum National d'Histoire Naturelle, Paris, France;

NHMUK, Natural History, London, England, UK; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico, USA; NMS, National Museums of Scotland, Edinburgh, Scotland, UK; NMV, Museums Victoria, Carlton, Victoria, Australia; NMW, National Museum of Wales, Cardiff, Wales, UK; NSM, Nova Scotia Museum, Halifax, Nova Scotia, Canada; OUM, Oxford University Museum of Natural History, Oxford, England, UK; ROM, Royal Ontario Museum, Toronto, Canada; USNM, National Museum of Natural History, Washington, DC, USA; UTGD, Rock Library and Geological Museum of the University of Tasmania, Hobart, Tasmania, Australia; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Results

Analysis of the character matrix retrieved one most parsimonious tree resulting in a phylogenetic framework congruent with those of previous analyses (Lamsdell, 2020, 2021a, b), differing solely in the position of bunodids, which resolve here as stem chelicerates diverging before the origin of Xiphosura, and of *Patesia*, which here resolves as sister taxon to *Pickettia*—united by the shared possession of an inflated axis of the anterior tergites—within a monophyletic Kasibelinuridae. Kasibelinurids as a whole maintain their position as the sister group to the Belinurina/Limulina clade. Taxa are considered within the context of their clades as defined here.

Lunataspidae and Fezouata xiphosurid.—Within the Lunataspidae, adults of both *Lunataspis aurora* and *Lunataspis borealis* have a thoracetron with six tergites expressed axially but not laterally on the dorsal surface (Fig. 2.1, 2.2). Posterior to the thoracetron is a freely articulating postabdomen comprising four segments, the last of which is an elongated pretelson. Anterior to the thoracetron are two freely articulating tergites as demarcated by clear, deeply incised segmental boundaries across their entire breadth, the thoracic doublure terminating before the two anterior tergites, and the tergites being differentiated by an anterolateral flexure (fulfilling criteria 4–6 for determining the state of tergite articulation). An isolated juvenile thoracetron of *Lunataspis aurora* (Fig. 2.3) also shows that these two tergites can become disarticulated from the thoracetron (thereby fulfilling the first criterion also). Articulated juvenile specimens for *Lunataspis aurora* (see Rudkin et al., 2008) and *Lunataspis borealis* (Fig. 2.4, 2.5) demonstrate that these free tergites are present in earlier ontogenetic stages. These juveniles also exhibit lateral expression of the tergite boundaries in the thoracetron, indicating that the effacement of the lateral segment boundaries in the thoracetron occurs during ontogeny in these species.

Study of a limited number of specimens (Fig. 2.6–2.11) of the undescribed xiphosurid from the lower Ordovician of Fezouata, Morocco, indicates marked ontogenetic change within the thoracetron during the species' development. Adults exhibit faint axial segmentation in the thoracetron (indicating the presence of maybe six segments; Fig. 2.9) with no evidence of laterally expressed tergite boundaries. Anterior to these six segments, the thoracetron possesses a dorsally inflected lip that articulates directly with a flange on the posterior of the prosomal carapace (Fig. 2.7), although this articulation is generally obscured in dorsal view by the overlapping of the carapace posterior over the anterior regions of the thoracetron (Fig. 2.6). Posterior to the thoracetron are freely articulating postabdominal segments. In juveniles the thoracetron clearly expresses segment boundaries both axially and laterally (Fig. 2.8) with the postabdomen shown to comprise four segments. The anterior of the opisthosoma is again obscured dorsally by the prosomal carapace posterior; however, one specimen shows two deeply incised anterior tergites posterior to the prosomal carapace (Fig. 2.10), and another preserved in an oblique dorsolateral view shows the presence of two freely articulating tergites anterior to the thoracetron (Fig. 2.11). The free nature of these tergites is demonstrated by flexure of the tergites and clear, deeply incised anterior and posterior boundaries (criteria two and four). These tergites appear absent in adults, and so it seems that the species undergoes a loss of the anterior free tergites and the lateral expression of segment boundaries in the thoracetron alongside the development of the prosomal flange and anterior thoracetron lip over the course of its ontogeny.

Kasibelinuridae.—*Kasibelinurus amicorum*, *Pickettia carterae*, and *Patesia randalli* all exhibit a similar thoracetron structure. The thoracetron of *Kasibelinurus amicorum* comprises six segments expressed both axially and laterally with an enlarged pretelsonic unit incorporated into the thoracetron to their posterior (Fig. 3.1). These segments are all considered fused because of the shallow nature of the segmental boundaries and the lack of gaps between the distal pleural regions. Anterior to the thoracetron are two freely articulating tergites, determined as such by the deeper incision of the segment boundaries and the presence of articulation facets on the pleurae (criteria four and six, with the third criterion filled indirectly). A small anterior projection of the first free tergite is also present, mostly obscured by the posterior of the prosomal carapace.

Pickettia carterae possesses a thoracetron comprising six segments with boundaries expressed axially and laterally and an elongated pretelsonic unit incorporated into its posterior (Fig. 3.2). Fusion of the thoracetron is indicated by the presence of a continuous ventral doublure and the shallow nature of the segment boundary incisions. Two freely articulating tergites are located in front of the thoracetron, their articulating nature indicated by deeply incised anterior and posterior boundaries, their separation from the thoracetron doublure, and differentiation of the sclerites through enlarged pleurae bearing articulating facets and an inflated axial region (fulfilling criteria 4–6). Once again, a small projection from the first tergite is observed partially covered by the prosomal carapace. A similar opisthosomal configuration is observed in *Patesia randalli* (Fig. 3.3–3.6). The thoracetron—again comprising six segments and an enlarged pretelson—is indicated to be fused through the shallow divisions between segments and the lack of axial flexion within the thoracetron in enrolled specimens. The boundaries of the thoracetron segments are expressed axially and laterally. Two freely articulating tergites are located anterior to the thoracetron. These segments show clear axial flexure, facilitating the partial

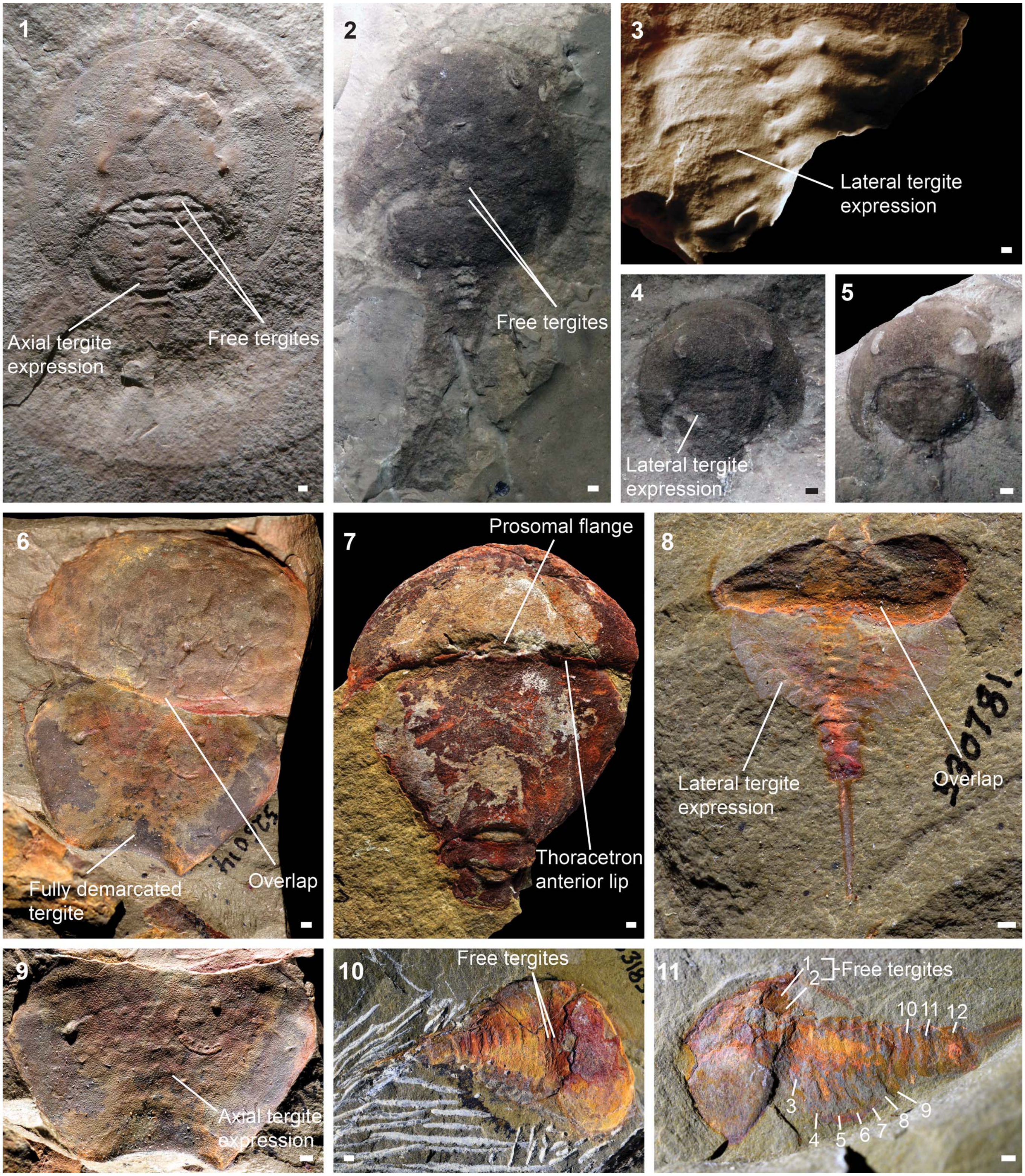
1
Axial tergite expression
Free tergites
2
Free tergites
3
Lateral tergite expression
4
Lateral tergite expression
5
6
Fully demarcated tergite
Overlap
7
Prosomal flange
Thoracetron anterior lip
8
Lateral tergite expression
Overlap
9
Axial tergite expression
10
Free tergites
11
1
2
Free tergites
3
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Figure 2. Representatives of Lunataspidae and an undescribed Moroccan Ordovician taxon. (**1, 3**) *Lunataspis aurora*; (**2, 4, 5**) *Lunataspis borealis*; (**6–11**) Undescribed xiphosurid species. (**1**) *Lunataspis aurora* (MM I-4583), Upper Ordovician (Katian), Churchill River Group, Canada, adult or subadult. (**2**) *Lunataspis borealis* (ROM IP 64616), Upper Ordovician (Sandbian), Gull River Formation, Canada, adult or subadult. (**3**) *Lunataspis aurora* (MM I-3990), Upper Ordovician (Katian), Churchill River Group, Canada, juvenile thoracetron. (**4**) *Lunataspis borealis* (ROM IP 64617), Upper Ordovician (Sandbian), Gull River Formation, Canada, juvenile. (**5**) *Lunataspis borealis* (ROM IP 64618), Upper Ordovician (Sandbian), Gull River Formation, Canada, juvenile. (**6**) Undescribed xiphosurid (YPM IP 526014), Lower Ordovician (Floian), Fezouata Formation, Morocco, adult. (**7**) Undescribed xiphosurid (YPM IP 532152), Lower Ordovician (Floian), Fezouata Formation, Morocco, adult. (**8**) Undescribed xiphosurid (YPM IP 530781), Lower Ordovician (Floian), Fezouata Formation, Morocco, juvenile. (**9**) Undescribed xiphosurid (YPM IP 526014), Lower Ordovician (Floian), Fezouata Formation, Morocco, detail of adult thoracetron. (**10**) Undescribed xiphosurid (YPM IP 531837), Lower Ordovician (Floian), Fezouata Formation, Morocco, large juvenile showing the two free tergites under the prosomal carapace posterior. (**11**) Undescribed xiphosurid (YPM IP 531656), Lower Ordovician (Floian), Fezouata Formation, Morocco, juvenile lateral view. Lunataspids possess two free tergites anterior to the thoracetron, with juveniles exhibiting both axial and lateral expression of the tergites within the thoracetron (**3–5**) while the adults express tergites within the axis only (**1, 2**). The undescribed Lower Ordovician xiphosurid exhibits two anterior free tergites and fully expressed tergites within the thoracetron (**10, 11**). In adults, the first free tergite appears to be incorporated into the prosomal carapace as a prosomal flange while the second tergite fuses onto the thoracetron as an anterior lip (**7**). The thoracetron itself greatly reduces the tergite expression, so they are only faintly visible in the axis (**9**). In both juveniles and adults, the degree of overlap between the prosoma and thoracetron generally obscures the articulation (**6, 8**). Scale bars = 1 mm.

enrollment of individuals, the anterior and posterior boundaries of the two anterior tergites are deeply incised, and the tergites are differentiated from those of the thoracetron by inflation of the axis and pleural articulating furrows (criteria 2, 4, and 6). Data for earlier ontogenetic stages are currently unknown for any of these species.

Belinurina.—Belinurines exhibit significant variation in the thoracetron. The morphology in basal forms, as exemplified by *Belinurus trilobitoides* (Fig. 4.1–4.3), comprises seven segments with their boundaries expressed both axially and laterally. Anterior to the thoracetron, a single free tergite may be present (Fig. 4.3), indicated by a deeper expression of the segment boundaries and a change in angle of the pleurae (criteria 4 and 6). Juvenile individuals exhibit a greater number of free tergites—up to three—in front of the thoracetron. The freely articulating nature of these tergites is demonstrated by their occurrence attached to the posterior of the prosomal carapace in some specimens where the thoracetron has become detached (Fig. 4.1), flexure of the axial region and overlap of the pleurae in specimens exhibiting enrollment (Fig. 4.2), and clear and deeply incised anterior and posterior segment boundaries (criteria 1–4). The thoracetron of juveniles with an increased number of free tergites comprises six segments, indicating that the reduction of free tergites in adults occurs via the incorporation of at least one of these tergites into the thoracetron during ontogeny. Adults also exhibit a posterior prosomal flange that appears absent in juveniles.

Euproops (Fig. 4.4–4.9) possess a thoracetron consisting of seven segments, the boundaries of which are expressed axially and laterally. Anterior to the thoracetron is a microtergite or anterior projection that appears to be fused onto the thoracetron in larger adults (Figs. 4.8, 5.4) but is freely articulating in smaller adults or subadults (Figs. 4.7, 4.9, 5.2, 5.3). Adults also possess a posterior flange to the prosomal carapace that becomes more heavily sclerotized laterally in a manner similar to the anteriormost tergite of the thoracetron and may be free of the carapace at its extremities (Fig. 5.2–5.4). Juveniles exhibit a broader free tergite as opposed to a microtergite (Figs. 4.6, 5.1) that is clearly differentiated from the rest of the thoracetron by a deep furrow, with the sclerite separated from the doublure and the pleurae deflected anteriorly (fulfilling criteria 4–6). The articulation of the microtergite in subadults is demonstrated by the degree of enrollment observed in subadults (Fig. 6.1, 6.3) compared with the partial enrollment in adults (Fig. 6.2). While the extreme folding in the smaller specimens is likely due in part to compression, the cross-sectional view of the microtergite in combination with the thoracetron oriented parallel to the prosomal carapace indicates that the sclerite must have an articulation with both the prosoma and thoracetron.

Among the more-derived belinurines, *Liomesaspis laevis* has a thoracetron comprising seven segments that are expressed only axially (Fig. 4.10); no freely articulating tergites are apparent in any specimens of the species. *Alanops magnificus* also lacks freely articulating tergites, with the thoracetron articulating with the prosoma via a microtergite that is fully fused to the thoracetron anterior. The thoracetron itself does not express any segment boundaries and exhibits an undifferentiated axial region (Fig. 4.11); this highly effaced condition is observed in the earliest known instars and maintained throughout the species' ontogeny (Racheboeuf et al., 2002).

Rolfeiidae and Bellinuroopsis.—These basal Limulina exhibit a similar overall thoracetron structure, although with some key differences. *Bellinuroopsis rossicus* Chernyshev, 1933 is interpreted as possessing a fused thoracetron consisting of at least five and potentially six segments, the last of which is an enlarged pretelson that may or may not be freely articulating. The fusion of the thoracic segments is determined by the fact that the boundaries between these segments in the lateral regions of the thoracetron express as fused, raised ridges rather than incisions. The pleural nodes on these segments also occur across the boundaries, which also indicates that these segments did not articulate (Fig. 7.1). Anterior to the thoracetron are two tergites that are here considered to be freely articulating, as indicated by the partial overlap of the pleurae, the deeply incised anterior and posterior segment boundaries, and the differentiation of the tergites in lacking pleural nodes (criteria 3, 4, and 6).

Rolfeia fouldenensis has a thoracetron composed of seven fused segments (Waterston, 1985), including an elongated pretelson, which express their segment boundaries both axially and laterally. A single freely articulating tergite is located anterior to the thoracetron (Fig. 7.2), marked as such by the deeply incised boundary between the tergite and the thoracetron, the separation of the tergite from the thoracetron doublure, and the differentiation of the pleural region of the tergite—which forms an elongated projection that may be homologous to the free lobes of other taxa—from those within the thoracetron

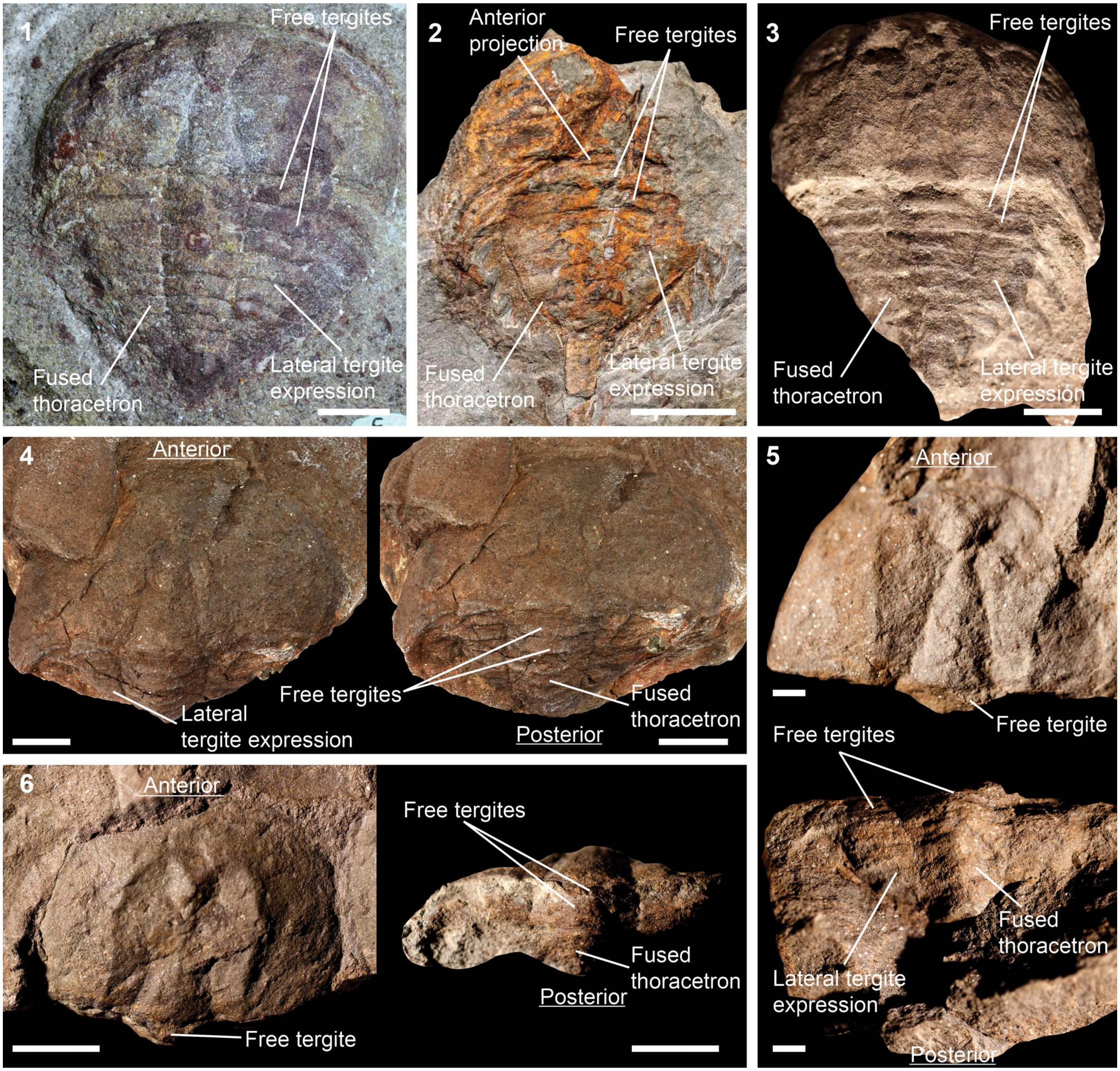

Figure 3. Representatives of Kasibelinuridae. (**1**) *Kasibelinurus amicorum* (AM F68969), Upper Devonian (Famennian), Mandagery Sandstone, Australia, presumed adult or subadult. (**2**) *Pickettia carterae* (BMS E9644), Upper Devonian (Famennian), Cattaraugus Formation, Pennsylvania, USA, presumed adult or subadult. (**3–6**) *Patesia randalli*: (**3**) *Patesia randalli* (FMNH PE56581), Upper Devonian (Famennian), Chadakoin Formation, Pennsylvania, USA, apparent adult or subadult; (**4**) *Patesia randalli* (USNM PAL 4845), Upper Devonian (Famennian), Chadakoin Formation, Pennsylvania, USA, apparent adult or subadult; (**5**) *Patesia randalli* (FMNH PE57077), Upper Devonian (Famennian), Chadakoin Formation, Pennsylvania, USA, apparent adult or subadult; (**6**) *Patesia randalli* (FMNH PE56589), Upper Devonian (Famennian), Chadakoin Formation, Pennsylvania, USA, apparent adult or subadult. All taxa exhibit a small sclerite located partially underneath the prosomal carapace posterior and two free articulating tergites anterior to the thoracetron. The thoracetron itself shows lateral and axial dorsal expression of the tergites. Scale bars = 10 mm. (**1**) Reproduced from Bicknell and Pates (2020) under a CC BY 4.0 license.

(criteria 4–6). Data for earlier ontogenetic stages are currently unknown for either of these species.

Paleolimulidae.—Despite being a relatively small group, paleolimulids exhibit a degree of variation within the thoracetron. The basalmost forms, exemplified here by *Norilimulus woodae* (Lerner et al., 2016), express segmental boundaries both axially and laterally in the thoracetron. The thoracetron comprises at least five segments, although the posterior margin is not preserved and so it is unclear whether a pretelson is present. Two anterior segments show differentiation in having deeply incised anterior and posterior boundaries, especially in the axis, and in the angle of the pleural margins, which are inflected anteriorly (Fig. 8.2). This may indicate that these segments were freely articulating in front of the thoracetron, although the first tergite is overlapped

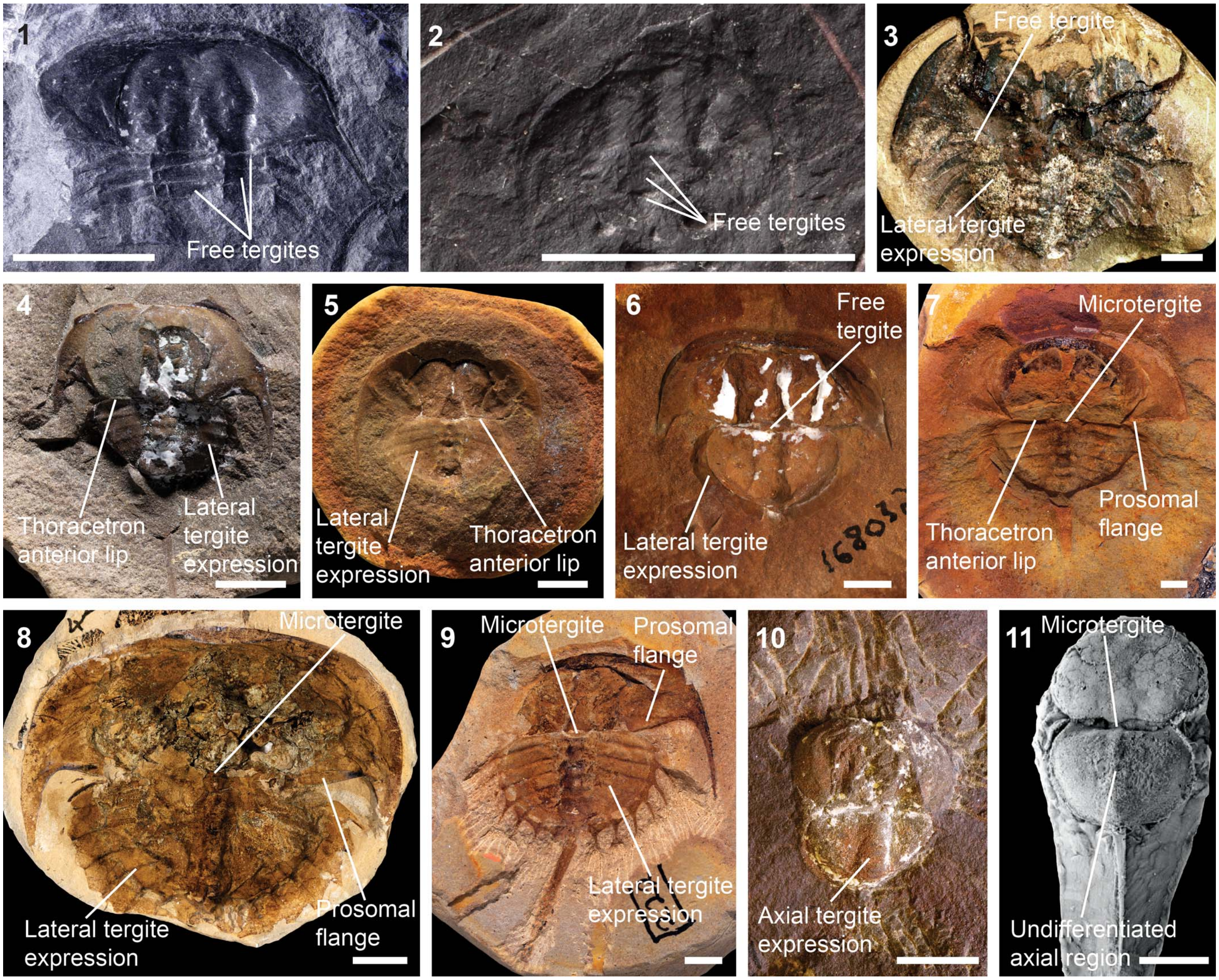

Figure 4. Representatives of Belinurina. (**1–3**) *Belinurus trilobitoides*: (**1**) *Belinurus trilobitoides* (NMW 70.17G.9), Carboniferous (Bashkirian), South Wales Lower Coal Measures Formation, Wales, UK, apparent adult or subadult, juvenile; (**2**) *Belinurus trilobitoides* (NMW 29.197.G1), Carboniferous (Bashkirian), South Wales Lower Coal Measures Formation, Wales, UK, juvenile; (**3**) *Belinurus trilobitoides* (GIUS 5-845/7), Carboniferous (Moscovian), Orzesze Beds, Poland, adult. (**4–9**) *Euproops danae*: (**4**) *Euproops danae* (YPM IP 255613), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, juvenile; (**5**) *Euproops danae* (YPM IP 168054), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, juvenile; (**6**) *Euproops danae* (YPM IP 168032), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, subadult or adult; (**7**) *Euproops danae* (YPM IP 50754), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, subadult or adult; (**8**) *Euproops danae* (YPM IP 428963), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, presumed adult; (**9**) *Euproops danae* (YPM IP 168011), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, subadult or adult. (**10**) *Liomesaspis laevis* (YPM IP 18050), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA, presumed adult. (**11**) *Alanops magnificus* (MNHN SOT 1951), Carboniferous (Kasimovian), Great Seams Formation, France, adult. Basal-most belinurines as exemplified by *Belinurus* exhibit three freely articulating tergites in front of the thoracetron (**1–3**), which display both axial and lateral expression of the constituent tergites. The thoracetron of *Euproops* also expresses individual tergites axially and laterally, with juveniles exhibiting an upwardly inflected anterior lip of the thoracetron (**4, 5**) and an anterior free tergite (**6**). More-mature *Euproops* develop a broad posterior prosomal flange that resembles a tergite fused to the prosomal carapace, the lateral margins of which are more differentiated than the axial region (**8**), while the anterior free tergite reduces to a microtergite (**9**) and eventually fuses into the thoracetron (**7**). More-derived belinurines show a progressive decrease in tergite expression on the thoracetron, with *Liomesaspis* having tergites expressed only in the axis (**10**) and *Alanops* having a completely undifferentiated axial region devoid of tergite expression (**11**). Scale bars = 5 mm. (**3**) Reproduced from Bicknell and Pates (2020) under a CC BY 4.0 license.

laterally by free lobes, which indicates the presence of a tergite anterior to these two that is largely suppressed or incorporated into the prosoma axially. Free lobes that are fused with and overlap the succeeding segment are otherwise observed only at the anterior of a fused thoracetron, and so it is unclear whether these anterior segments in *Norilimulus* are freely articulating or simply differentiated but otherwise fully incorporated into the thoracetron (in which case the thoracetron would comprise eight segments, including that of the free lobes laterally). Another possibility is that the known specimens of *Norilimulus* are those of juveniles or early subadults, and that these anterior segments are freely articulating but fuse into the thoracetron over the course of their later ontogeny.

Xaniopyramus linseyi Siveter and Selden, 1987, a member of the group that resolves as the sister clade to *Paleolimulus*, expresses segmental boundaries both axially and laterally within the thoracetron. Longitudinal pleural ridges running the length

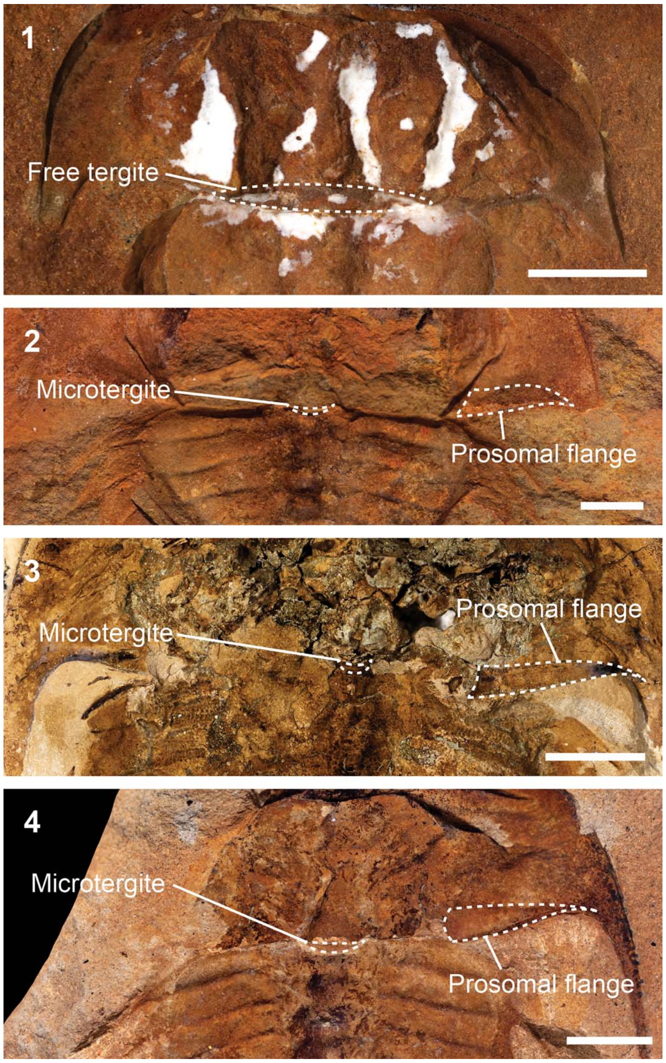

Figure 5. Detailed view of the prosomal/opisthosomal joint in *Euproops danae*. (**1**) YPM IP 168032, juvenile exhibiting free tergite. (**2**) YPM IP 50754, subadult or adult exhibiting microtergite and prosomal flange. (**3**) YPM IP 168011, subadult or adult exhibiting microtergite and prosomal flange. (**4**) YPM IP 428963, presumed adult exhibiting microtergite and prosomal flange. Scale bars = 5 mm.

of the thoracetron, punctuated by pleural nodes that occur across the segment boundaries, indicate that all visible segments were fully fused into the thoracetron (Fig. 8.1). The posterior of the thoracetron is not preserved, so it is unclear whether a pretelsonic sclerite was present either fused to the thoracetron or articulating. The anteriormost segment of the thoracetron is produced laterally into free lobes derived from the lateral portions of an anterior segment that is either incorporated in the prosoma or largely suppressed axially.

Paleolimulus signatus exhibits change in the thoracetron over the course of its ontogeny. Juveniles possess a thoracetron composed of seven segments, including free lobes, which are expressed both laterally and axially (Fig. 8.3). Posterior to the thoracetron is an elongated pretelson that is freely articulating as indicated by its occasional disarticulation from the thoracetron, the clear and deeply incised boundary between the two sclerites, and the total separation of the pretelson from the thoracetron doublure (criteria 1, 4, and 5). Adults also possess a thoracetron of seven segments with free lobes; however, the segment boundaries are greatly effaced and clearly expressed only axially (Fig. 8.4). The pretelsonic sclerite is less clearly defined in adults and may become fused to the thoracetron during development, although the presently available material of the species does not show this with clarity.

Austrolimulidae.—Austrolimulids also exhibit interspecific variation in the thoracetron. *Boeotiaspis longispinus*, an apparent basal form, has a thoracetron comprising eight segments that are expressed only axially (Fig. 9.3), the posteriormost of which is a pretelson that is somewhat more differentiated than the preceding segments. No free lobes are visible on the thoracetron, and the anteriormost segment has more deeply incised anterior and posterior margins as well as anteriorly inflected pleural margins, indicating that it may potentially be freely articulating (criteria 4 and 6). These traits are unusual and potentially unique among Austrolimulidae, however, and *Boeotiaspis* may have affinities outside of the clade (see Discussion). *Tasmaniolimulus pattersoni* Bicknell, 2019 is more representative of the general morphology among basal species, with a thoracetron comprising at least six segments (the posterior margin is not preserved). The segmental boundaries are expressed axially but not laterally on the thoracetron, and free lobes are present at the anterolateral margins (Fig. 9.1).

Among more-derived austrolimulids, as exemplified here by *Vaderlimulus tricki*, the thoracetron lacks clear dorsal segment demarcations in either the axial or pleural regions, although the presence of small moveable spines indicates that the thoracetron is composed of six segments and a pretelson that is fully incorporated into the thoracetron doublure (Fig. 9.2). Free lobes are also present on the thoracetron, indicating the presence of an additional segment that is suppressed or partially incorporated into the prosoma axially. Another derived austrolimulid, *Austrolimulus fletcheri*, is less well preserved, so the details of the thoracetron are somewhat tentative. The thoracetron is largely devoid of visible segmentation and does not preserve either fixed or movable spines, so the number of segments within the thoracetron is unknown. Free lobes are apparent at the thoracetron anterior, however, as is an elongated pretelson with an apparent anterior demarcation where it connects to the thoracetron, although it is unclear whether the pretelson was freely articulating or fused onto the thoracetron.

Limulidae.—The overall morphology of the thoracetron is consistent across Limulidae as demonstrated by exemplars across both the major constituent clades. *Mesolimulus walchi* possesses a thoracetron lacking tergite demarcations with free lobes at its anterior (Fig. 10.1). This thoracetron morphology is shared in the freshwater representative *Victalimulus mcqueeni* (Fig. 10.2). The presence of apodemes and movable spines indicates the thoracetron to comprise six segments in addition to the free lobes and a fused pretelson composed of an undetermined number of segments. *Tachypleus syriacus*, representative of the other major limulid clade, exhibits a fundamentally identical thoracetron composition (Fig. 10.3). *Limulus polyphemus* (Linnaeus, 1758) demonstrates the

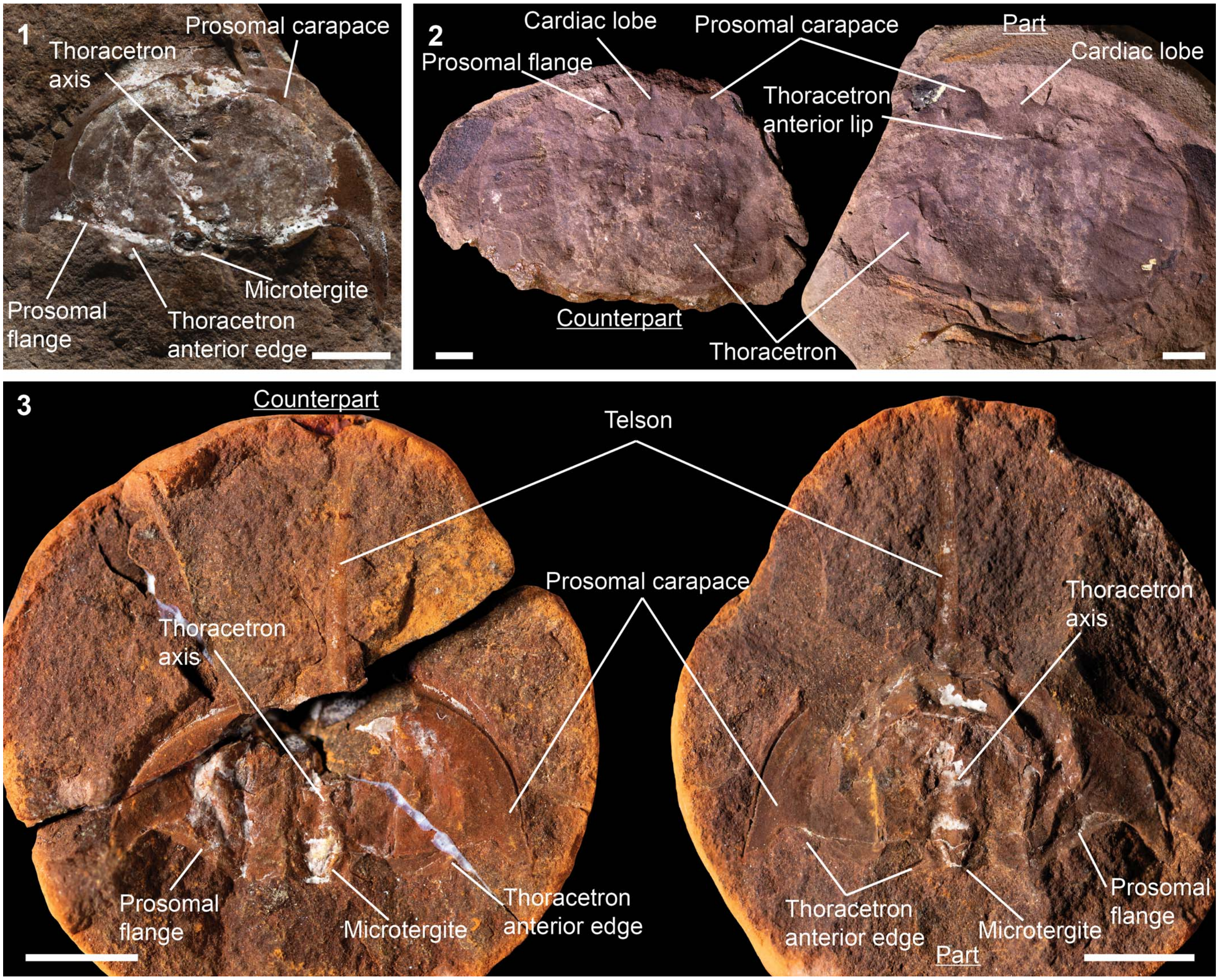

Figure 6. Specimens of *Euproops* exhibiting folding. (**1**) *Euproops danae* (YPM IP 50813), Carboniferous (Moscovian), Carbondale Formation, Illinois, USA. (**2**) *Euproops danae* (YPM IP 50951) part and counterpart, Carboniferous (Moscovian), Carbondale Formation, Illinois, USA. (**3**) *Euproops danae* (YPM IP 50863) part and counterpart, Carboniferous (Moscovian), Carbondale Formation, Illinois, USA. Smaller juveniles or early subadults (**1, 3**) exhibit a greater degree of enrollment, with the axis of the thoracetron compressed directly against the prosomal carapace indicating that the thoracetron is lying directly beneath the prosoma with the telson projecting anteriorly. The microtergite and anterior margin of the thoracetron are visible end-on at the prosomal carapace posterior, however, suggesting that the thoracetron in juveniles may have had some anterior flexibility. Larger subadults or adults are preserved only partially enrolled (**2**) and preserve the main body of the thoracetron in line with the microtergite. Scale bars = 5 mm.

ontogeny of the group, with pre-hatchling embryos first developing a topographic expression of segments without clear boundaries and with no differentiated free lobes or defined axial region (Fig. 10.4) before developing clearly demarcated tergites in the axis (Fig. 10.5). Post-hatchling instars first exhibit both lateral and axial tergites expression as well as clear free lobes (Fig. 10.6) before progressively effacing first the lateral tergite boundaries (Fig. 10.7) and later the axial tergite boundaries as the thoracetron matures into the typical adult morphology (Fig. 10.8).

Discussion

The thoracetron is recognized to have originated once early in the evolution of Xiphosura; however, subsequent convergent evolution of the thoracetron morphology is prevalent across the clade (Fig. 11). When the Fezouata species is considered to represent the sister taxon to all other xiphosurans (suggested by the Early Ordovician age of the taxon and the lack of clear lateral eyes or raised cardiac lobe on the prosomal carapace), lateral tergite expression is considered to be suppressed in the xiphosuran ancestor, as indicated by their absence in adults within Lunataspidae and the Fezouata taxon. Under this scheme, xiphosurids are considered to have undergone a reversal in expression of the thoracetron lateral segment boundaries that occurred before the divergence of Kasibelinuridae from the main xiphosurid lineage. Alternatively, if the Fezouata taxon resolves in a clade with the lunataspid species, the ancestral condition of the thoracetron is for the segments to be fully expressed, and their lateral suppression in the Ordovician species would represent another case of convergence.

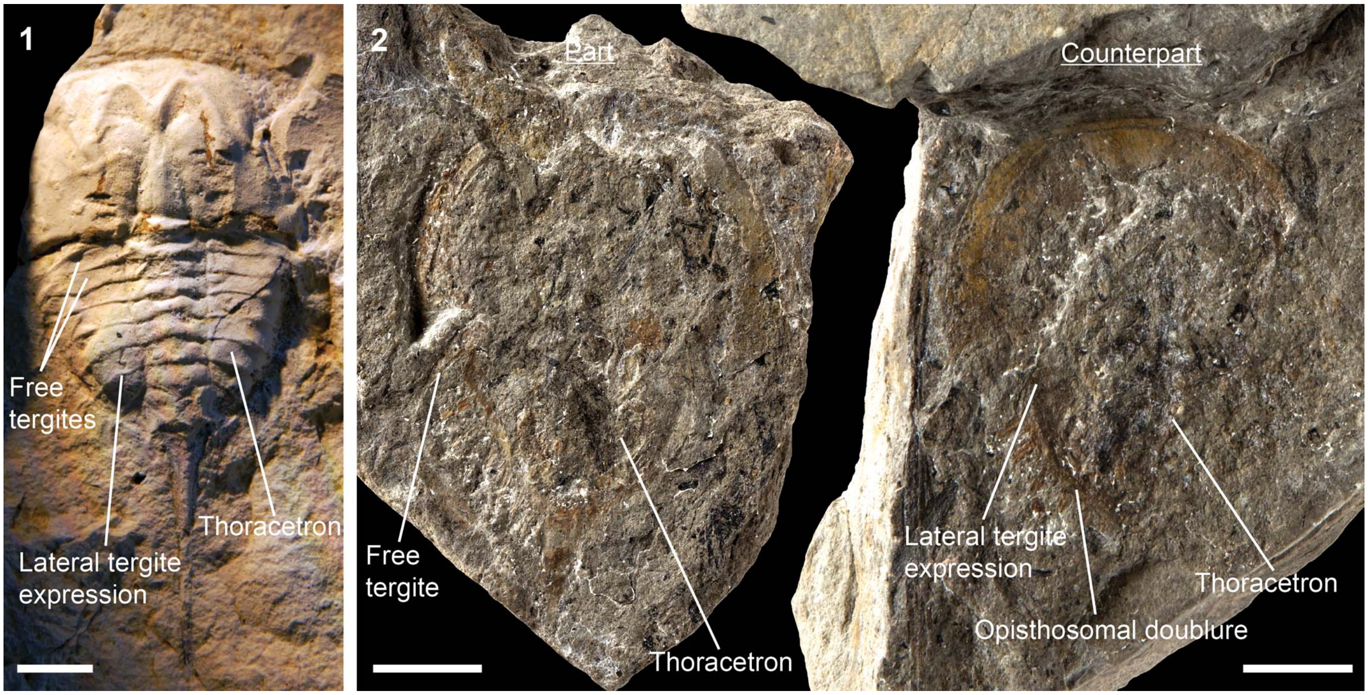

Figure 7. Representatives of the Limulina stem lineage. (**1**) *Bellinuroopsis rossicus* (CCMGE 1/3694), Upper Devonian (Famennian), Lebedjan Formation, Russia, adult or mature subadult. (**2**) *Rolfeia fouldenensis* (NMS G.1984.67.1) part and counterpart, Carboniferous (Tournaisian), Cementstones Group, Scotland, UK, adult or mature subadult. *Bellinuroopsis* exhibits lateral and axial expression of the tergites within the thoracetron and two anterior free tergites. While *Rolfeia* also displays lateral and axial tergite expression, only the first tergite is freely articulating. Scale bars = 10 mm. (**1**) Reproduced from Bicknell and Pates (2020) under a CC BY 4.0 license. (**2**) Made available under a CC BY-NC-SA 3.0 license courtesy of the GB3D type fossils database.

The xiphosurid thoracetron exhibits convergent patterns of evolution between Belinurina and Limulina as well as within Limulina across Paleolimulidae, Austrolimulidae, and Limulidae; suppression of the tergite boundaries laterally, suppression of the tergite boundaries axially, incorporation of somite VII into the prosoma, and incorporation of somite VIII into the thoracetron are all interpreted to have occurred at least three separate times. Suppression of the lateral segment boundaries occurs independently in Belinurina and Paleolimulidae and at the base of Limuloidea, while suppression of the axial segment boundaries occurs in Belinurina, Austrolimulidae, and the base of Limulidae. Somite VII is interpreted as becoming fully incorporated into the prosoma in the Fezouata xiphosurid, within Belinurina, and before the divergence of Rolfeiidae within Limuloidea, and somite VIII is interpreted as being fully incorporated into the thoracetron in the Fezouata xiphosurid and within Limulidae before the divergence of Paleolimulidae.

The convergent changes within the thoracetron generally follow a consistent pathway, with the lateral expression of segmentation becoming suppressed before that of the axis, and the somite of segment VII generally being incorporated into the prosoma before segment boundaries begin to become effaced. This pattern is seen clearly in Belinurina. Both *Belinurus* (Filipiak and Krawczyński, 1996) and *Euproops* (Anderson, 1994) exhibit full axial and lateral expression of the segments; the lateral segment margins are largely effaced in more-derived taxa such as *Liomesaspis* (Malz and Poschmann, 1993; Anderson, 1997). Subsequently, the axial segment boundaries are suppressed in *Alanops* (Rachebeouf et al., 2002) and *Prolimulus* (Lustri et al., 2021). The tergite of somite VII is considered to be free in *Belinurus* but incorporated into the prosoma of *Euproops*—with the pleural margins clearly delineated at the prosomal carapace posterior (Fig. 4.8, 4.9)—and all other belinurines. Somite VIII is interpreted to be a free tergite in *Belinurus* and a reduced microtergite fused onto the thoracetron in *Euproops* (Anderson, 1994; Anderson and Selden, 1997) and *Alanops* (Rachebeouf et al., 2002).

The trend in Limulina begins with the incorporation of somite VII into the prosoma in *Rolfeia* (Waterston, 1985) and continues with the full incorporation of the tergite of somite VIII into the thoracetron before the divergence of Paleolimulidae and Limuloidea. Within paleolimulids, the full segment boundaries are expressed in the basal taxa *Moravurus* (Přibyl, 1967), *Xaniopyramis* (Selden and Siveter, 1987), and *Norilimulus* (Lerner et al., 2016) but are suppressed laterally in *Paleolimulus* (Babcock et al., 2000; Bicknell et al., 2022; Naugolnykh and Bicknell, 2022). The lateral segment boundaries are independently suppressed in Limuloidea, the earliest offshoot of which—*Valloisella*—exhibits axial but not lateral tergite expression (Anderson and Horrocks, 1995). Limulidae subsequently undergoes suppression of the axial tergite boundaries before the divergence of the group, as evidenced by the lack of any segmental expression within the thoracetron across the clade, including the most basal offshoots such as *Yunnanolimulus* (Hu et al., 2017). The condition is ubiquitous among both the large clade of stem limulids that includes *Mesolimulus*—as further demonstrated by *Guangyanolimulus* (Hu et al., 2022) and *Ostenolimulus* (Lamsdell et al., 2021)—and the extant species with their close extinct relatives such as *Crenatolimulus* (Feldmann et al., 2011; Kin and Błażejowski, 2014).

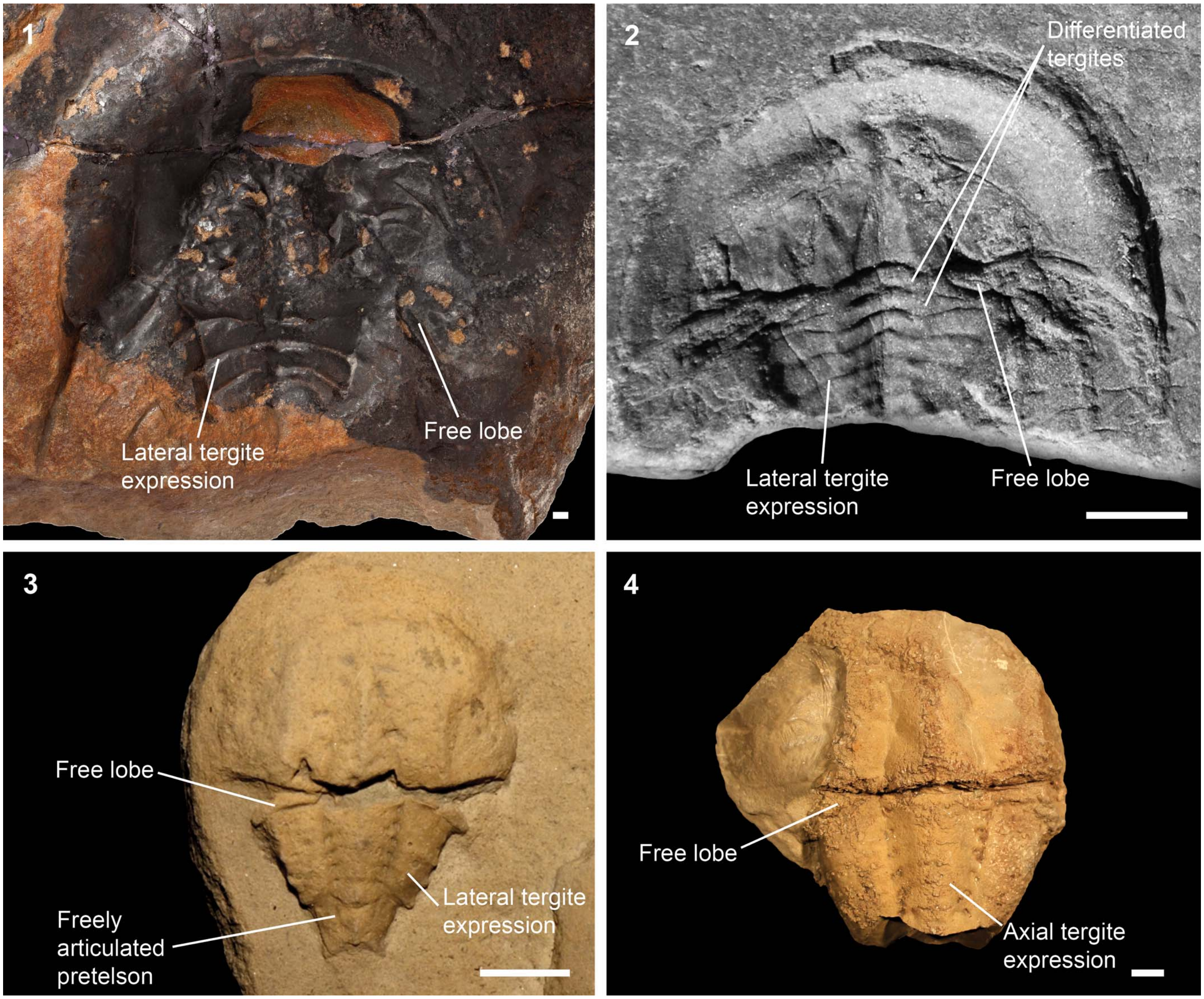

Figure 8. Representatives of Paleolimulidae. (**1**) *Xaniopyramis linseyi* (OUM E.03994), Carboniferous (Mississippian), Upper Limestone Group, England, UK, apparent adult. (**2**) *Norilimulus woodae* (NSM 005GF045.374), Carboniferous (Tournasian), Horton Bluff Formation, Canada, potential adult. (**3, 4**) *Paleolimulus signatus*: (**3**) *Paleolimulus signatus* (KUMIP 399929), Carboniferous (Gzhelian), Wood Siding Formation, Kansas, USA, juvenile; (**4**) *Paleolimulus signatus* (KUMIP 399962), Carboniferous (Gzhelian), Wood Siding Formation, Kansas, USA, subadult or adult. More-basal taxa, such as *Xaniopyramis* and *Norilimulus*, exhibit lateral and axial expression of the tergites within the thoracetron. *Norilimulus* also shows differentiation of the two anterior-most tergites by an anterior angling of their lateral expression as in lunataspids, although it is unclear whether these tergites are freely articulating or whether they are an adult trait. More-derived taxa within the clade, as exemplified by *Paleolimulus,* display clear lateral and axial expression of the tergites within the thoracetron in juveniles while the lateral tergite expression is largely effaced in adults. Scale bars = 5 mm. (**1**) Made available under a CC BY-NC-SA 3.0 license courtesy of the GB3D type fossils database.

The axial segmentation of the thoracetron is lost independently in Austrolimulidae, as several more-basal forms such as *Tasmaniolimulus* and *Panduralimulus* (Allen and Feldmann, 2005) exhibit axial segmentation, while derived forms such as *Vaderlimulus* and *Austrolimulus* do not. The condition of segmentation in the thoracetron of *Psammolimulus* is unclear; originally interpreted as exhibiting no segmentation, the thoracetron seems to have segmentation within the axial region (Meischner, 1962). The distribution of axial segmentation in austrolimulids may indicate it was lost multiple times, as *Limulitella*—the sister taxon to *Psammolimulus*—is definitively devoid of segmentation (Błażejowski et al., 2017; Klompmaker et al., 2023). The exact affinities of *Limulitella* are uncertain, however, as some species are potentially diagnosed from specimens representing multiple different species, and the genus may in actuality resolve outside of Austrolimulidae. *Boeotiaspis*, a supposed basal form, is also unusual for an austrolimulid as it potentially has a freely articulating tergite of somite VIII. Previous authors have suggested the species comprising the genus may show affinities to *Rolfeia* (Anderson and Selden, 1997); the species needs redescription. Other derived austrolimulid taxa lacking segmentation—*Batracholimulus* (Hauschke and Wilde, 1987) and *Dubbolimulus* (Pickett, 1984)—also have a poorly defined axial region and may represent juveniles. Nonetheless, these uncertainties do not invalidate the overall trend in axial effacement within austrolimulids, or the fact that it

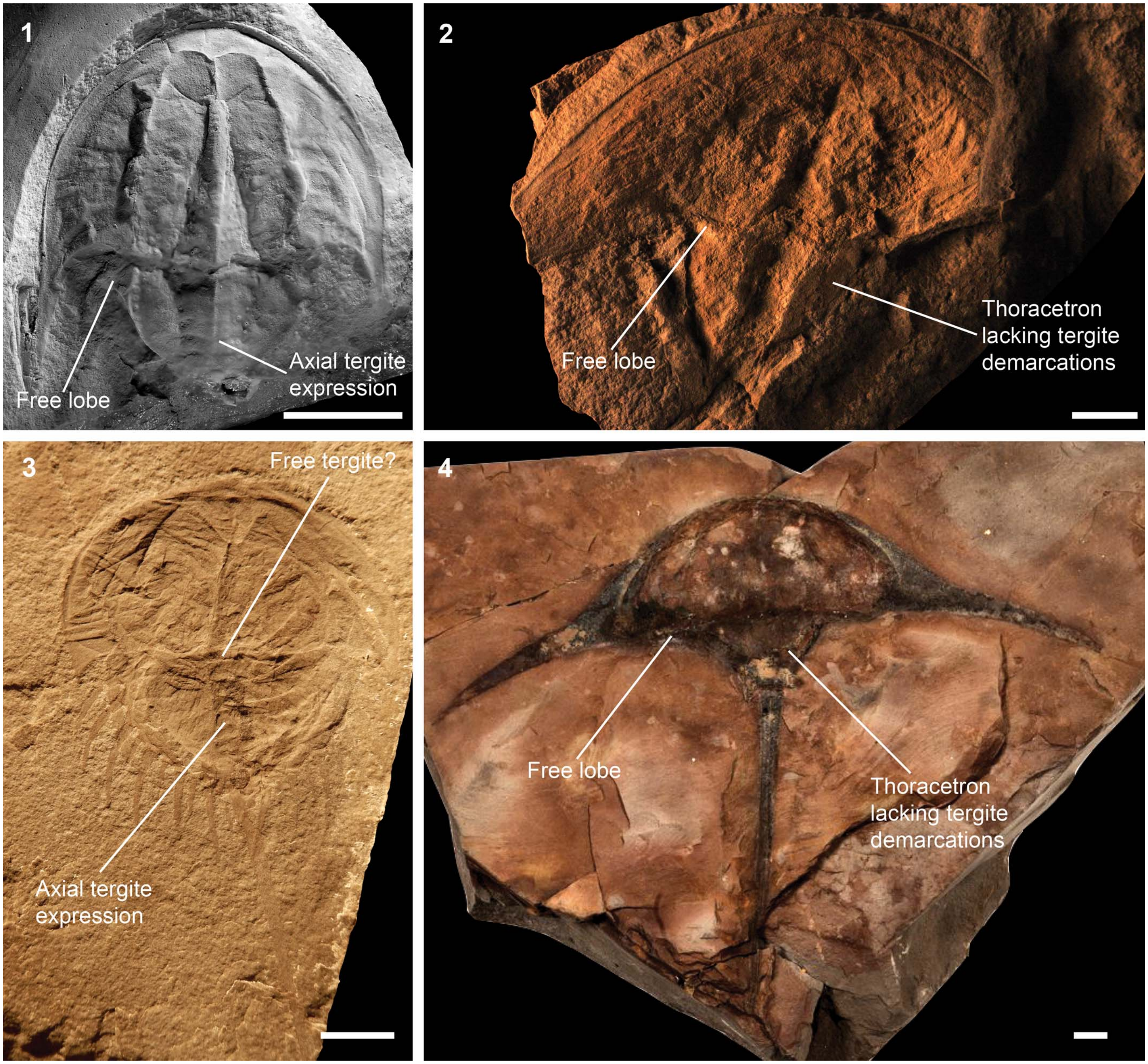

Figure 9. Representatives of Austrolimulidae. (**1**) *Tasmaniolimulus patersoni* (UTGD 123979), Early Triassic (Induan), Jackey Shale, Tasmania, Australia. (**2**) *Vaderlimulus tricki* (NMMNH P-81445), Early Triassic (Olenekian), Thaynes Group, Idaho, USA, adult or mature subadult. (**3**) *Boeotiaspis longispinus* (ROM IP 49769), Carboniferous (Bashkirian), Bear Gulch Limestone, Montana, USA, adult or mature subadult. (**4**) *Austrolimulus fletcheri* (AM F38274), Middle Triassic (Anisian), Beacon Hill Shale, Australia, adult or mature subadult. More-basal taxa within the clade, such as *Tasmaniolimulus* and potentially *Boeotiaspis*, retain the axial expression of tergites within the thoracetron. This is lost in more-derived taxa such as *Austrolimulus* and *Vaderlimulus*, the thoracetrons of which lack any expression of the tergites. Scale bars = 10 mm. (**1**) Reproduced from Bicknell (2019) under a CC BY-NC-SA 4.0 license.

occurred independently from the same trend observed in Limulidae.

Developmental mechanisms of opisthosomal fusion.—The evolution of the thoracetron within Limulina broadly recapitulates the development of the tagma as seen in modern species. Our understanding of developmental mechanisms underlying thoracetron evolution in fossil limulines is limited by the paucity of detailed ontogenetic descriptions in the literature. Although several extinct species are known from multiple ontogenetic stages or subadult material (Gall, 1971; Kin and Błażejowski, 2014; Lamsdell and McKenzie, 2015; Lamsdell, 2021a), most of our understanding of development in limulines is based on modern representatives. Further documentation of ontogeny in extinct taxa, especially that focusing on descriptions of morphological change rather than quantitative measurement-based surveys, would be enlightening. In *Limulus polyphemus* and *Tachypleus tridentatus* Leach, 1819, the two species for which development is best known (Scholl, 1977; Sekiguchi et al.,

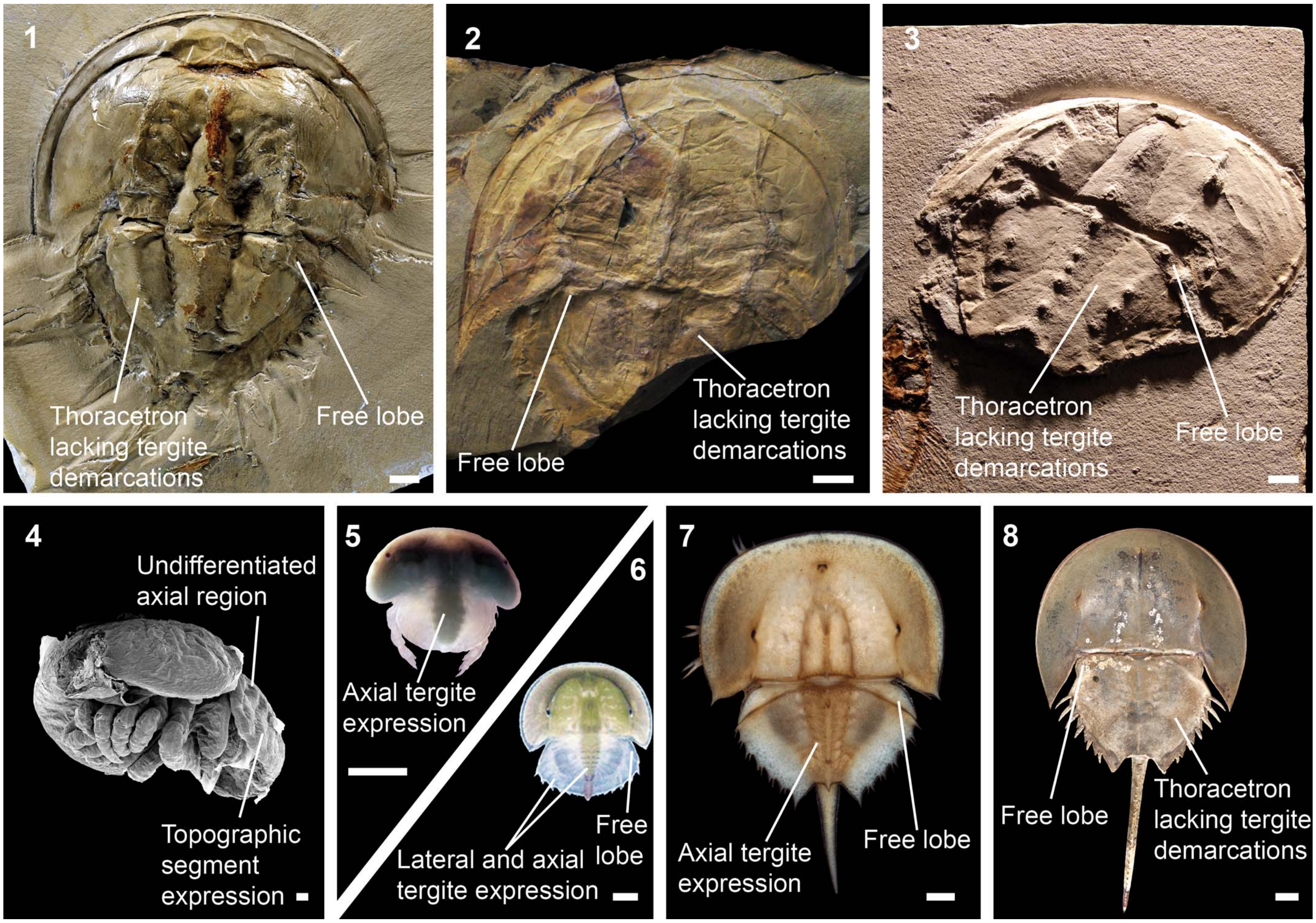

Figure 10. Representatives of Limulidae. (**1**) *Mesolimulus walchi* (MNHN F.A33516), Upper Jurassic (Tithonian), Altmühltal Formation, Germany, adult. (**2**) *Victalimulus mcqueeni* (NMV P22410B), Early Cretaceous (Aptian), Korumburra Group, Australia, adult. (**3**) *Tachypleus syriacus* (NHMUK IA 188), Late Cretaceous (Cenomanian), Hjoûla Konservat-Lagerstätten, Lebanon, adult. (**4–8**) *Limulus polyphemus*: (**4**) *Limulus polyphemus*, recent, United States of America, pre-hatchling larva imaged under SEM; (**5**) *Limulus polyphemus*, recent, United States of America, later pre-hatchling larva; (**6**) *Limulus polyphemus*, recent, United States of America, fourth-molt hatchling; (**7**) *Limulus polyphemus* (YPM IZ 070174), recent, United States of America, twelfth-molt juvenile; (**8**) *Limulus polyphemus*, recent, United States of America, adult. Adults across all taxa possess a thoracetron lacking tergite demarcations; however, the earlier developmental stages of *Limulus* exhibit varying degrees of tergite expression within the thoracetron, with the pre-hatchling phase showing lateral expression of the tergites, the hatchling showing an undifferentiated thoracetron without a clear axis, and the juvenile exhibiting axial tergite expression. (**1–3, 8**) Scales bars = 10 mm; (**4**) scale bar = 100 µm; (**5–7**) scale bars = 1 mm. (**1**) Made available as part of the RECOLNAT (ANR-11-INBS-0004) program.

1982, 1988a, b; Sekiguchi, 1988; Shuster and Sekiguchi, 2003; Farley, 2010; Haug and Rötzer, 2018b; Lamsdell, 2021a), the embryo first develops faint segmentation through topographic expression of the segments without incisions at the anterior or posterior margins before developing a differentiated axial region with the segment boundaries within the thoracetron being more deeply incised. After hatching, the larval horseshoe crabs undergo an effacement of first the lateral and later axial segment margins within the thoracetron. The segment of somite VII and the axial region of somite VIII are incorporated into the prosoma during the embryonic stage, with the lateral portions of VIII forming the free lobe on the thoracetron.

At the base of Limulina, both somites VII and VIII are considered to be freely articulating anterior to the thoracetron but soon become integrated into the prosoma and thoracetron as in the extant species. The lateral tergite expression is then suppressed independently in Paleolimulidae and Limuloidea, with the axial tergite expression subsequently suppressed independently in Austrolimulidae and Limulidae. This progression along the developmental trajectory seen in modern taxa fits with the general peramorphic heterochronic trend observed in these clades, which is most strongly expressed in Austrolimulidae (Lamsdell, 2021a). *Paleolimulus*, for which juvenile specimens are known, exhibits a similar developmental trajectory to the modern species, including a weakly expressed axis and lack of deep incisions at the segment boundaries of larval forms. The juveniles exhibit a freely articulating pretelson, however, and maintain the lateral segment boundaries well into subadulthood (Naugolnykh and Bicknell, 2022). Juveniles of *Mesolimulus*, meanwhile, have already effaced the tergite boundaries in the thoracetron (Lamsdell et al., 2020b); these species are also larger than those of *Paleolimulus*, suggesting that these morphological changes may have been achieved by either lengthening the time or increasing the rate of development.

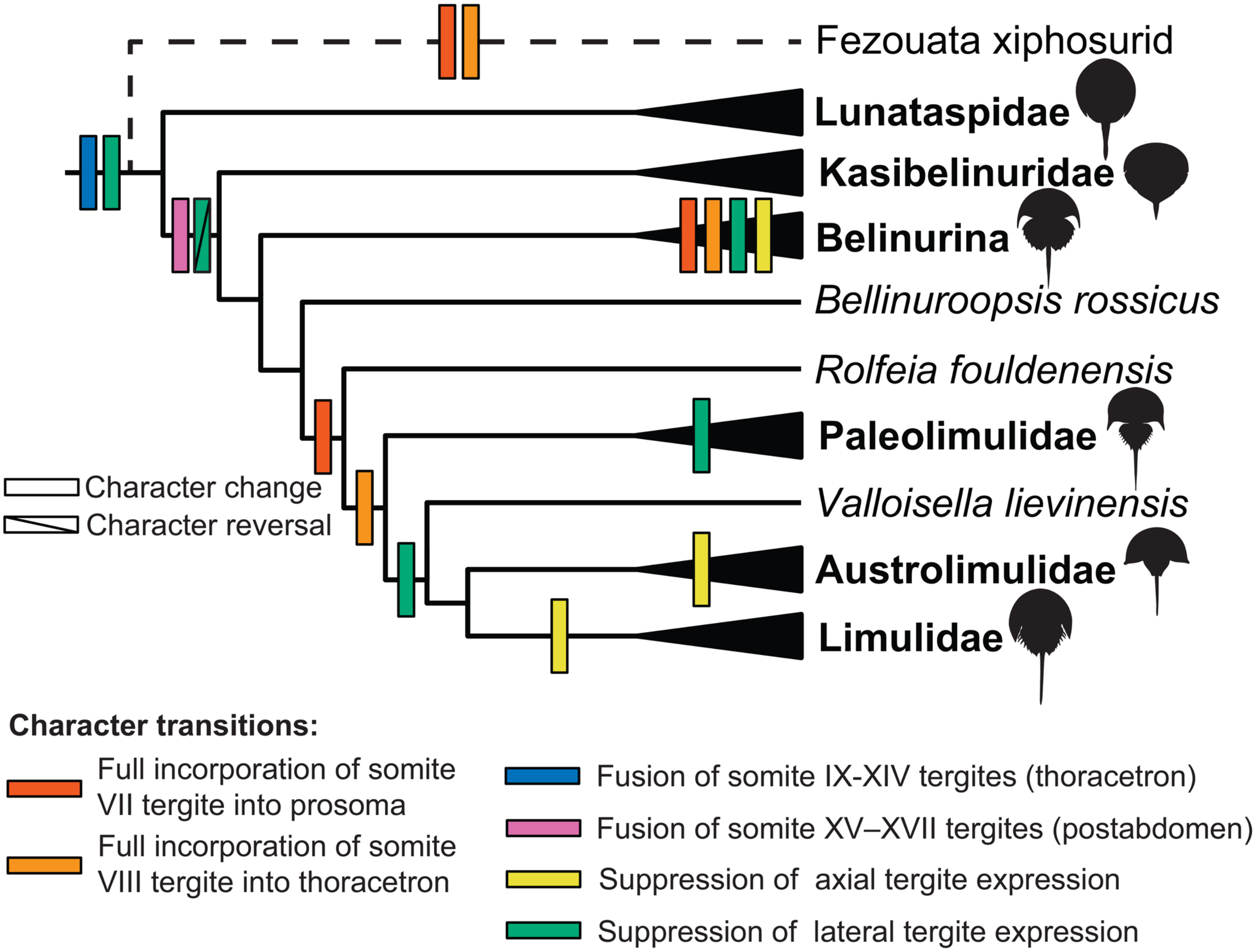

Figure 11. Phylogeny of Xiphosura derived from analysis of the character matrix as described in the Materials and methods section, strict consensus of two most parsimonious trees with clades collapsed for ease of display. Character transitions for the thoracetron in adults are shown. Where multiple transitions are shown within a collapsed clade, they are presented in the order in which they occur. Widespread convergence in thoracetron evolution is apparent, interpreted as being driven by developmental parallelism. Incorporation of somite VII into the prosoma and somites VIII and IX into the thoracetron is interpreted as having occurred independently in the Fezouata xiphosurid, Belinurina, and Limulina; suppression of the tergites laterally in the thoracetron occurs independently in Belinurina, Paleolimulidae, and Limuloidea; and the suppression of tergite expression within the thoracetron axis occurs independently in Belinurina, Austrolimulidae, and Limulidae. Importantly, a single reversal is inferred near the base of Xiphosura in the expression of tergites laterally within the thoracetron, which likely represents the retention of juvenile traits into adulthood (pedomorphosis).

The pattern of thoracetron consolidation through ontogeny is maintained basally within Belinurina. *Belinurus* appears to exhibit a more-extreme degree of anterior tergite fusion into the thoracetron over the course of its development, with potentially as many as three free tergites being progressively incorporated into the thoracetron beginning with the posteriormost. This is interesting in that it provides a mechanism by which the posterior “pygidium” of the Silurian basal prosomapod *Offacolus* (Sutton et al., 2002) could develop into the xiphosurid thoracetron and is diametrically opposite to the ontogeny of trilobites, which develop and release segments from the pygidium as they grow (Hughes et al., 2006). The earliest available instars of *Euproops* have two free tergites between the prosoma and thoracetron; later instars have a free tergite and small sclerite (microtergite) located posterior to the prosoma. By adulthood, these two tergites are incorporated into the prosoma and opisthosoma, although incompletely as indicated by the free lateral margins of segment VII within the prosomal carapace. The tergite of somite VIII decreases in size progressively to a reduced tergite then microtergite before suturing onto the thoracetron in adults. *Euproops* also exhibits a reduced degree of enrollment as it matures (Fig. 6), likely due to the progressive fusion of free segments into the prosoma and thoracetron through development. This could potentially be the explanatory mechanism behind the variable types of enrollment seen in *Euproops* (see Anderson, 1994; Anderson and Selden, 1997; Haug et al., 2012) and could indicate some degree of ontogenetic niche partitioning. It is unclear from the description of the highly derived belinurine *Alanops* whether juveniles exhibit any free tergites as the description focused on adult morphology (Rachebeouf et al., 2002). The species is known from some 140 specimens, including juveniles, however, and an evaluation of the earlier instars would be illuminating. It is also unclear whether juvenile *Alanops* exhibit any clear segmental boundaries within the thoracetron. *Belinurus* and *Euproops* exhibit axial and lateral segment boundaries within the thoracetron throughout their development, and juvenile material has not been reported from any derived belinurine aside from *Alanops*. *Liomesaspis* exhibits axial but not lateral segmental expression in adults, although some species do exhibit faint evidence of lateral segmentation in the form of undulations or topographic expression (e.g., Tasch, 1961), while *Prolimulus* and *Alanops* have the axial as well as the lateral segment margins effaced, although in *Alanops* faint evidence of the axial segmentation may sometimes be seen in the form of topographic expression (Rachebeouf et al., 2002), in a manner similar to the lateral segmentation in *Liomesaspis.*

The independent development of similar forms or structures in organisms is known as convergent evolution (McGhee, 2011; Pearce, 2012). Convergent evolution may be the result of distinct developmental or genetic pathways—sometimes resulting in the co-option of different aspects of anatomy to develop similar structure— or the independent expression of the same developmental or genetic pathways in (usually closely related) lineages (McGhee, 2011; Pearce, 2012). When convergent change has a shared developmental or genetic cause, it is referred to as parallelism, or parallel evolution (Arendt and Reznick, 2008; Scotland, 2011; Hall, 2012). Critically, while convergence is generally considered to be an adaptational response to similar environmental or mechanical pressures, parallel evolution may be the result of developmental (as opposed to functional) constraints (Mahler et al., 2017). Developmental constraints may also shape broad heterochronic trends within a lineage, so it is possible for a suite of morphological characters to exhibit nonselective parallel patterns of evolution due to selection favoring a heterochronically derived condition within a single trait. Differentiating between convergence and parallelism in closely related taxa—such as is the case here—therefore requires an assessment of not only whether changes are due to a shared developmental pathway, but also whether these changes progress along the same trajectory within those pathways (i.e., whether the observed changes are consistently pedomorphic or peramorphic in nature). Within Paleolimulidae, Austrolimulidae, and Limulidae, the effacement of the thoracetron segment boundaries progresses along the general developmental trajectory that remains relatively conserved within Xiphosura (Lamsdell, 2021a; Bicknell et al., 2022; Lamsdell et al., 2023), fitting with the prevalence of peramorphic changes within these lineages (Lamsdell, 2021a, b) and indicating that the shared changes observed within the thoracetron represent cases of parallel evolution within these groups. The evolutionary changes in the thoracetron of Belinurina appear to follow the same trend in reducing the expression of the lateral followed by the axial boundaries and so at first may appear to represent another case of parallelism within the group; however, belinurines are known to exhibit a pedomorphic heterochronic trend (Lamsdell 2021a, b; Lustri et al., 2021) as opposed to the general peramorphic condition across Limuloidea. As noted in the preceding discussion, belinurines with largely suppressed segmental boundaries may still exhibit a topographic expression of the segments as seen in the earliest larvae of modern limulids. Belinurina are therefore interpreted here as exhibiting a retrograde trend along the common developmental trajectory, as extant larvae develop incised margins along the axis before incisions develop in the lateral segments. The pedomorphic nature of the thoracetron is further supported by the reduced number of opisthosomal opercula in *Alanops*, which is a condition also seen in larval extant limulids that increase the number of opercula in successive molts up to their full complement (Dunlop, 1998). The extreme effacement of the prosomal carapace of *Alanops*, *Prolimulus*, and *Stilpnocephalus* is also a condition seen only in larvae; that these represent adult individuals with larval traits rather than larvae or juveniles themselves is confirmed by the large size of *Stilpnocephalus* (Selden et al., 2019). The progressive effacement of thoracetron segmentation in belinurines is therefore the result of truly independent convergence rather than parallelism.

Conclusions

The xiphosuran thoracetron is present within the earliest known representatives of the group (Anderson and Selden, 1997; Lamsdell, 2013, 2020) and therefore is a key synapomorphy of the clade. Previous suggestions that the thoracetron originated independently in disparate xiphosurid clades are here disproven; however, convergent and parallel trends are present within the subsequent development of this functional pseudotagma. Evolutionary trends in xiphosurids are, however, obfuscated by a variety of biotic and abiotic processes; these challenges reinforce the critical necessity for a consideration and understanding of both taphonomy and ontogeny when interpreting fossils. Further documentation of ontogeny in fossil Xiphosura is integral to our understanding of developmental macroevolutionary mechanisms. Presently, the identification of parallelism and convergence within the development of the thoracetron by progression and retrogression along a shared developmental trajectory represents an important case study into the significance of developmental macroevolutionary mechanisms in morphological evolution and provides further support for the role of heterochronic processes in xiphosuran evolution. This work also further elucidates the highly conserved developmental pathway within Xiphosura and the heterochronic push and pull toward endmember morphologies along the same shared pathway of development while still conserving the overall trajectory.

Finally, it is interesting to note that juveniles of the Fezouata xiphosurid have two freely articulating tergites anterior to a fused thoracetron, whereas adults possess a prosomal flange and anterior lip on the thoracetron. These features are possibly formed from the fusion of the two freely articulating segments seen in juveniles onto the posterior edge of the prosoma and anterior edge of the thoracetron, respectively, paralleling the fusion of somites VII and VIII to the prosoma and thoracetron during the development of modern *Limulus* embryos (Scholl, 1977). Somite VII is considered to be represented by a freely articulating tergite in kasibelinurids and basal members of both Belinurina and Limulina, which would indicate its consolidation has occurred independently a number of times within Xiphosura. Expanding to view Chelicerata more generally, somite VII is considered to be consolidated into the prosoma in arachnids and potentially eurypterids (Dunlop, 1998), while it is retained as an opisthosomal microtergite in chasmataspidids (Marshall et al., 2014); the incorporation of somite VII into the prosoma is clearly a somewhat plastic trait among basal chelicerates, and this realization should be enlightening for discussions regarding the ground pattern of the clade and whether the consolidation of somite VII into the prosoma in the stem chelicerate *Mollisonia* (Aria and Caron, 2019) represents the plesiomorphic condition for the group.

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Declaration of competing interests

The authors declare no competing interests.

Data availability statement

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.2fqz612z2

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