

HORSESHOE CRAB PHYLOGENY AND INDEPENDENT COLONIZATIONS OF FRESH WATER: ECOLOGICAL INVASION AS A DRIVER FOR MORPHOLOGICAL INNOVATION

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Abstract: Xiphosurids are an archaic group of aquatic chelicerate arthropods, generally known by the colloquial misnomer of ‘horseshoe crabs’. Known from marine environments as far back as the early Ordovician, horseshoe crabs are generally considered ‘living fossils’ – descendants of a bradytelic lineage exhibiting little morphological or ecological variation throughout geological time. However, xiphosurids are known from freshwater sediments in the Palaeozoic and Mesozoic; furthermore, the contention that xiphosurids show little morphological variation has never been tested empirically. Attempts to test this are hampered by the lack of a modern phylogenetic framework with which to explore different evolutionary scenarios. Here, I present a phylogenetic analysis of Xiphosurida and explore patterns of morphospace and environmental occupation of

the group throughout the Phanerozoic. Xiphosurids are shown to have invaded non-marine environments independently at least five times throughout their evolutionary history, twice resulting in the radiation of major clades – bellinurines and austrolimulids – that occupied novel regions of morphospace. These clades show a convergent ecological pattern of differentiation, speciation and subsequent extinction. Horseshoe crabs are shown to have a more dynamic and complex evolutionary history than previously supposed, with the extant species representing only a fraction of the group’s past ecological and morphological diversity.

Key words: bradytely, convergence, ecology, morphospace, niche conservatism, Xiphosurida.

XIPHOSURIDS are aquatic chelicerate arthropods with a fossil record extending back to the Ordovician (Rudkin *et al.* 2008; Van Roy *et al.* 2010). Four species exist today, all limited to the marine realm with occasional excursions into marginal, brackish environments, and are considered ecological generalists (Sekiguchi and Shuster 2009). The apparent conservation of body form exhibited by xiphosurids has led to their classification as ‘living fossils’ (Eldredge 1976), bradytelic archetypes (Fisher 1984) and stabilomorphs (Kin and Błażejowski 2014). Despite this, fossil xiphosurids are known to exhibit extremely aberrant morphologies (Riek 1955; Anderson 1997) and to have established populations in freshwater ecosystems (Anderson and Horrocks 1995; Racheboeuf *et al.* 2002; Riek and Gill 1971). Studies of xiphosurids are hampered, however, by the lack of a phylogenetic framework with which to test the distribution of xiphosurid ecology through geological time. Such a framework would allow for evolutionary scenarios, such as whether all freshwater occurrences of xiphosurids are derived from a single

invasion and subsequent radiation, to be explored. The existing taxonomic framework, largely derived from that of Størmer (1952), is out of date and was compiled in a pre-cladistic age. Furthermore, the tree presented by Fisher (1984) suggested a number of Størmer’s taxa were paraphyletic; however, Fisher presented no data matrix alongside his tree and so the analysis is irreproducible. Previous phylogenetic analyses of Xiphosura (equivalent to total group Xiphosurida) have included only a handful of xiphosurid taxa, either focusing on the relationships of the supposed synziphosurine stem lineage (Anderson and Selden 1997; Lamsdell 2013; Lamsdell *et al.* 2015; Selden *et al.* 2015), or including xiphosurans as part of a broader analysis of chelicerate phylogeny (Shultz 2007; Garwood and Dunlop 2014). One recent phylogenetic analysis did include a number of xiphosurids (Lamsdell and McKenzie 2015), but limited itself only to a subset of Mesozoic and Cenozoic taxa. A number of these analyses have suggested that synziphosurines are an unnatural grouping of stem euchelicerates and stem dekatratiatans (Lamsdell 2013;

Lamsdell *et al.* 2015; Selden *et al.* 2015) and should be excluded from Xiphosura; this would result in a significant reduction in the order's Palaeozoic diversity and demonstrates the importance of a phylogenetic framework for evaluating macroevolutionary and macroecological trends.

Here, I present a more comprehensive phylogeny of the Xiphosura and utilize the resulting tree to explore patterns of ecological specialization and morphospace occupation throughout the Phanerozoic. The resulting phylogenetic tree reveals a more nuanced view of horseshoe crab evolutionary history beyond their simple categorization as 'living fossils' and forms the core of a revised taxonomy of Xiphosurida.

METHOD

The phylogenetic analysis of Xiphosura presented herein represents an expanded version of the matrix presented in Lamsdell (2013), Lamsdell *et al.* (2015) and Selden *et al.* (2015), combined with that of Lamsdell and McKenzie (2015). The resulting matrix comprises 252 characters

coded for 105 taxa and is available in MorphoBank (Lamsdell 2015). Sampling of Xiphosurida is increased from 5 taxa to 50, 17 of which are bellinurines and 26 of which are limulines, with the remaining 6 representing stem taxa. Environmental data for these taxa were taken from the primary literature (Tables 1–3). Morphological terminology follows Selden and Siveter (1987) and Lamsdell (2013) throughout.

The analysis was performed using TNT (Goloboff *et al.* 2008; made available with the sponsorship of the Willi Hennig Society). The search strategy employed 100 000 random addition sequences with all characters unordered and of equal weight, each followed by tree bisection-reconnection (TBR) branch swapping (the *mult* command in TNT). Jackknife (Farris *et al.* 1996), bootstrap (Felsenstein 1985) and Bremer (Bremer 1994) support values were also calculated in TNT, and the ensemble consistency, retention and rescaled consistency indices were calculated in Mesquite 3.02 (Maddison and Maddison 2015). Bootstrapping was performed with 50% resampling for 1000 repetitions, while jackknifing was performed using simple addition sequence and tree bisection-reconnection branch swapping for 1000 repetitions with 33% character deletion.

TABLE 1. Environmental affinities of Palaeozoic Xiphosura.

| Taxon | Environment | Reference |
|---------------------------------|---------------------------|---------------------------------|
| <i>Alanops magnifica</i> | Freshwater/Brackish | Racheboeuf <i>et al.</i> (2002) |
| <i>Anacontium brevis</i> | Freshwater/Brackish | Raymond (1944) |
| <i>Anacontium carpenter</i> | Freshwater/Brackish | Raymond (1944) |
| <i>Bellinuroopsis rossicus</i> | Marine | Chernyshev (1933) |
| <i>Bellinurus arcuatus</i> | Freshwater/Brackish | Dix and Pringle (1929) |
| <i>Bellinurus bellulus</i> | Freshwater/Brackish | Dix and Pringle (1930) |
| <i>Bellinurus lunatus</i> | Freshwater/Brackish | Filipiak and Krawczyński (1996) |
| <i>Bellinurus reginae</i> | Freshwater/Brackish | Copeland (1957) |
| <i>Bellinurus trilobitoides</i> | Freshwater/Brackish | Anderson <i>et al.</i> (1997) |
| <i>Bellinurus truemanii</i> | Freshwater/Brackish | Dix and Pringle (1929) |
| <i>Euproops anthrax</i> | Freshwater/Brackish | Prestwich (1840) |
| <i>Euproops danae</i> | Freshwater/Brackish | Anderson (1994) |
| <i>Euproops mariae</i> | Freshwater/Brackish | Crônier and Courville (2005) |
| <i>Euproops rotundatus</i> | Freshwater/Brackish | Filipiak and Krawczyński (1996) |
| <i>Euproops</i> sp. | Freshwater/Brackish | Haug <i>et al.</i> (2012) |
| <i>Kasibelinurus amoricum</i> | Marine | Pickett (1993) |
| <i>Kasibelinurus randalli</i> | Marine | Babcock <i>et al.</i> (1995) |
| <i>Limulitella bronni</i> | Freshwater | Schimper (1853) |
| <i>Liomesaspis laevis</i> | Freshwater/Brackish | Anderson (1997) |
| <i>Liomesaspis leonardensis</i> | Freshwater/Brackish | Tasch (1961) |
| <i>Lunataspis aurora</i> | Marine | Rudkin <i>et al.</i> (2008) |
| <i>Paleolimulus longispinus</i> | Marginal Marine/Brackish? | Hagadorn (2002) |
| <i>Paleolimulus signatus</i> | Marine | Babcock <i>et al.</i> (2000) |
| <i>Panduralimulus babcocki</i> | Freshwater/Brackish? | Allen and Feldmann (2005) |
| <i>Pringlia birtwelli</i> | Freshwater/Brackish | Raymond (1944) |
| <i>Rolfeia fouldenensis</i> | Marine | Waterston (1985) |
| <i>Valloisella lievinensis</i> | Freshwater/Brackish | Anderson and Horrocks (1995) |
| <i>Xaniopyramis lindseyi</i> | Marine | Siveter and Selden (1987) |

TABLE 2. Environmental affinities of Mesozoic Xiphosura.

| Taxon | Environment | Reference |
|------------------------------------|-------------|----------------------------------|
| <i>Austrolimulus fletcheri</i> | Freshwater | Riek (1955) |
| <i>Casterolimulus kletti</i> | Freshwater | Holland <i>et al.</i> (1975) |
| <i>Crenatolimulus paluxyensis</i> | Marine | Feldmann <i>et al.</i> (2011) |
| <i>Dubbolimulus peetae</i> | Freshwater | Pickett (1984) |
| <i>Limulitella henkeli</i> | Marine | Fritsch (1906) |
| <i>Limulitella vicensis</i> | Marine | Bleicher (1897) |
| <i>Limulus? darwini</i> | Marine | Kin and Błażejowski (2014) |
| <i>Limulus coffini</i> | Marine | Reeside and Harris (1952) |
| <i>Mesolimulus crispelli</i> | Marine | Vía (1987) |
| <i>Mesolimulus walchi</i> | Marine | Briggs <i>et al.</i> (2005) |
| <i>Paleolimulus fuschbergensis</i> | Freshwater | Hauschke and Wilde (1987) |
| <i>Psammolimulus gottingensis</i> | Freshwater | Meischner (1962) |
| <i>Tachypleus gadeai</i> | Marine | Vía Boada and De Villalta (1966) |
| <i>Tachypleus syriacus</i> | Marine | Lamsdell and McKenzie (2015) |
| <i>Tarracolimulus riei</i> | Marine | Romero and Vía Boada (1977) |
| <i>Victalimulus mcqueeni</i> | Freshwater | Riek and Gill (1971) |
| <i>Yunnanolimulus luopingensis</i> | Marine | Hu <i>et al.</i> (2011) |

TABLE 3. Environmental affinities of Cenozoic Xiphosura.

| Taxon | Environment | Reference |
|-------------------------------------|-------------|--------------------------------|
| <i>Carcinoscorpius rotundicauda</i> | Marine | Tanacredi <i>et al.</i> (2009) |
| <i>Limulus polyphemus</i> | Marine | Tanacredi <i>et al.</i> (2009) |
| <i>Tachypleus decheni</i> | Marine | Hauschke and Wilde (2004) |
| <i>Tachypleus gigas</i> | Marine | Tanacredi <i>et al.</i> (2009) |
| <i>Tachypleus tridentatus</i> | Marine | Tanacredi <i>et al.</i> (2009) |

Disparity measures were calculated from the cladistic character data (which have been shown to converge on a common signal with other forms of morphometric data, e.g. morphological landmarks (Foth *et al.* 2012; Hetherington *et al.* 2015)) using standard methods (Wills *et al.* 1994; Wills 1998). Pairwise (taxon to taxon) Euclidean distance matrices were calculated and subjected to PCO using scripts in R (Hughes *et al.* 2013) from which morphospace plots were produced. Taxa were then assigned to period-level time bins and separated into groups based on the possession of either a marine or freshwater/brackish environmental affinity. One taxon, *Paleolimulus longispinus*, is of uncertain environmental affinity and was excluded from

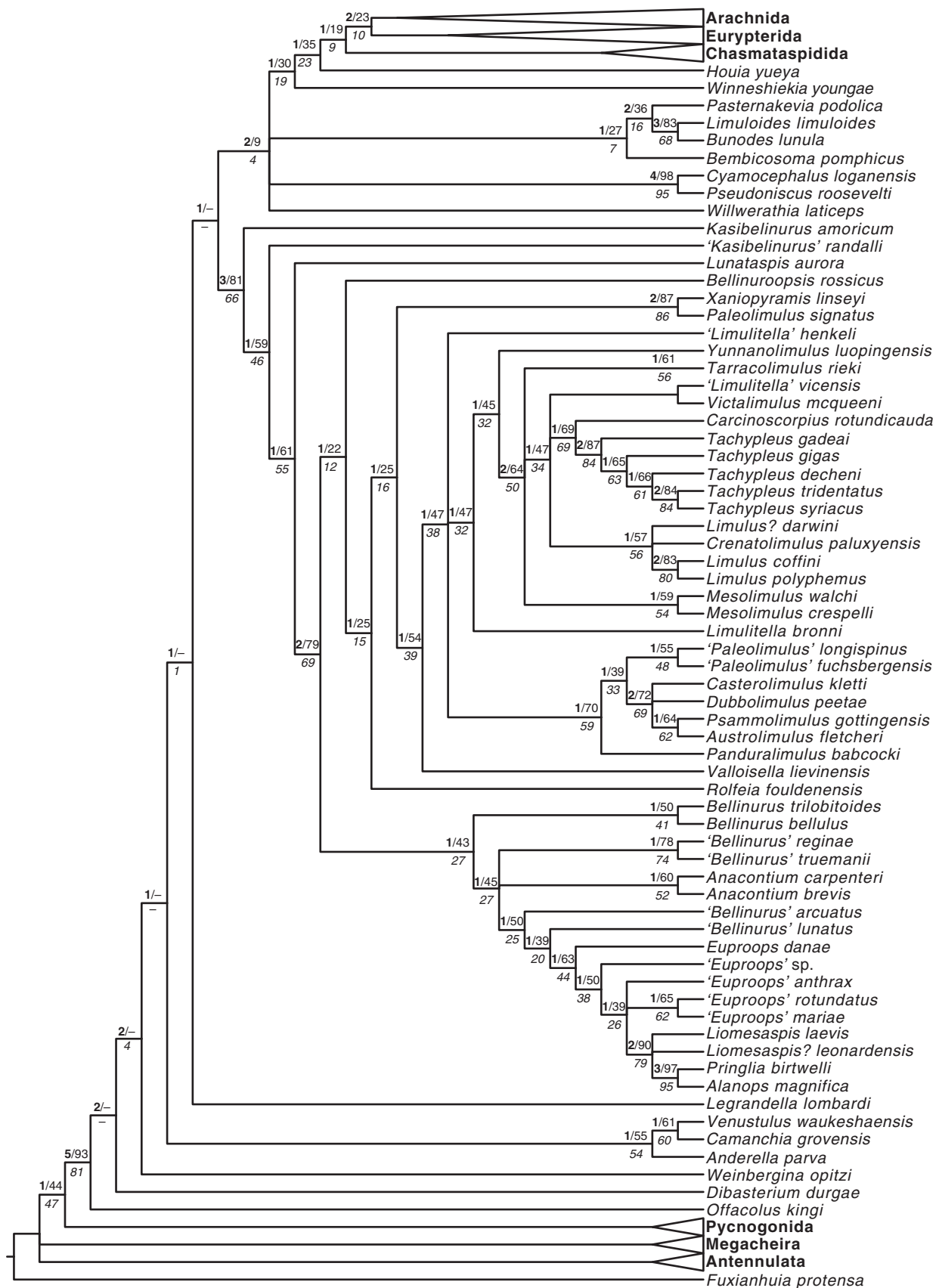
the ecological study. Assigning it to either group made no difference to the results obtained.

Multivariate statistical tests (NPMANOVA using the Euclidean distance measure) were performed to ascertain the statistical significance of overlap and separation of morphospace between these environmental groups. Significance was estimated by permutation across groups with 10 000 replicates, with Bonferroni correction.

RESULTS

Analysis of the phylogenetic data resulted in nine most parsimonious trees with a tree length of 730 steps, an ensemble Consistency Index of 0.482, an ensemble Retention Index of 0.879, and a Rescaled Consistency Index of 0.424. The strict consensus of these nine trees is illustrated (Fig. 1). The tree topology is congruent with that from previous analyses (Lamsdell 2013; Lamsdell and McKenzie 2015; Lamsdell *et al.* 2015; Selden *et al.* 2015), with synziphosurines resolving as a mixture of stem euchelicerates and stem dekatrarians; Xiphosura therefore comprises solely xiphosurids and their kasibelinurid stem lineage, defined by the possession of a cardiac lobe extending anterior to the posterior half of the carapace and segments VIII–XIV fused into a thoracetron. ‘Kasibelinurids’ are found to be paraphyletic, as is the genus *Kasibelinurus* as currently defined (Babcock *et al.* 1995). These taxa, along with *Lunataspis*, comprise the xiphosurid stem lineage.

Xiphosurida is defined as xiphosurans possessing a sagittal keel on the prosomal shield and having a postabdomen composed of only a single segment, which is subsequently merged with the thoracetron in some taxa. The internal topology of Xiphosurida proposed here is also congruent with that of Anderson and Selden (1997), with a basal split between Belinurina and Limulina. Within Belinurina, however, the genera *Belinurus* and *Euproops* are both found to be paraphyletic, with *Belinurus* grading into *Euproops* which in turn grades into a clade comprising *Liomesaspis*, *Pringlia* and *Alanops*. This supports previous suggestions that belinurines are over-split at the generic level (Anderson 1997). It could be argued that the clade should be reduced to consisting of a single genus; however, no taxonomic change is currently proposed pending further study of the group. Limulina encompasses all the remaining xiphosurids, the relationships of which are in agreement with that of Anderson and Selden (1997). *Bellinuroopsis* resolves at the base of the clade with *Rolfeia* representing the sister taxon to a clade comprising Paleolimulidae and Limuloidea. The genus *Paleolimulus* has frequently been suggested to represent an unnatural group in the past (Anderson and Selden 1997; Babcock and Merriam 2000; Allen and Feldmann 2005), a contention supported by the



current topology. *Paleolimulus* here comprises only the type species, *Paleolimulus signatus*, with the remaining species assigned to the Austrolimulidae. *Paleolimulus* proper is united with *Xaniopyramis* through the possession of a pyramidal cheek node and interopthalmic ridges on the prosomal shield.

Limuloidea, defined by the thoracetrone exhibiting no lateral expression of individual tergites, resolves with *Valloisella* at its base and a prominent split between Austrolimulidae and Limulidae. The topology of Limulidae is unchanged from Lamsdell and McKenzie (2015), with *Limulitella* resolving as polyphyletic and the genera *Carcinoscopus*, *Crenatolimulus*, *Limulus* and *Tachypleus* forming the xiphosurid crown group. Austrolimulidae is composed of Australian xiphosurids and taxa previously assigned to *Paleolimulus*. The clade is united by the thoracetrone lacking tergopleural fixed spines, with the exception of the posteriormost which are swept back and elongated to form a 'swallowtail', and by a trend for the genal spines to splay outward, a condition that becomes most pronounced in *Austrolimulus* (Riek 1955).

Colonization of the freshwater realm is shown to have occurred at least five times independently within Xiphosurida (Fig. 2), and twice this shift is associated with the origination of a major clade. Belinurina is the more speciose of the two, even though a number of species have been synonymized in recent years (Anderson 1994, 1997; Haug *et al.* 2012), and is a common component of Carboniferous freshwater/brackish coal swamps; bellinurines were so successful that they are by far the most speciose group in the Palaeozoic xiphosurid record. The second clade, Austrolimulidae, comprises taxa known predominantly from fluvial environments. Austrolimulids also have a Palaeozoic origin but radiated during the early Mesozoic. The Palaeozoic representatives are known from marginal marine, fluvially influenced environments, with *Panduralimulus* closely associated with terrestrial components that suggest it had been transported into the delta from upstream (Allen and Feldmann 2005). '*Paleolimulus*' *longispinus*, however, is known from a shallow marine basin with freshwater influence along its margin. *Euproops* is also known from these marginal regions, and it is possible that '*Paleolimulus*' *longispinus* is also derived from a more brackish environment; at present, its environmental affinities are unclear (Hagadorn 2002). Given the current tree topology, a marine habitat for '*Paleolimulus*' *longispinus* would suggest that an austrolimulid returned to the marine realm from a brackish/freshwater environment. Aside from these two clades, xiphosurids are shown to

have invaded the freshwater realm twice in the Palaeozoic (Schimper 1853; Anderson and Horrocks 1995) and once in the Mesozoic (Riek and Gill 1971). These, however, appear to be isolated events and do not result in any subsequent radiations.

Principal coordinates analysis of the Euclidean distance matrix derived from the phylogenetic character matrix reveals marine and non-marine taxa to be clustered in empirical morphospace (Fig. 3A). Dividing the taxa according to period-level time bins and comparing the rarefied sum of ranges (SOR) and sum of variances (SOV) calculated from all axes shows that variance has decreased through time while the range (area of morphospace occupation) has remained relatively unchanged (Fig. 3B). Separating out marine and non-marine taxa reveals that the SOR of marine taxa has increased through time, whereas the SOR of non-marine taxa has decreased. SOV also decreases through time for non-marine taxa; however, it remains constant for marine taxa, resulting in the overall observed decrease. Morphospace occupation is, however, shown to shift between the period-level time bins, with Palaeozoic taxa (Fig. 4A) occupying a region of morphospace adjacent to, and distinct from, that occupied by Mesozoic (Fig. 4B) and Cenozoic (Fig. 4C) taxa, with changes in morphospace occupation between the Mesozoic and Cenozoic appearing to be due to a contraction of occupied space rather than a directional shift. This is borne out statistically through NPMANOVA (Table 4); Palaeozoic taxa are shown to occupy a statistically distinct morphospace compared with Mesozoic and Cenozoic taxa, while the Mesozoic and Cenozoic time bins show no statistical difference in morphospace occupation. Separating the taxa out according to environmental affinity reveals that non-marine taxa are driving this difference in morphospace occupation, with non-marine taxa inhabiting a statistically significant different morphospace between the Palaeozoic and the Mesozoic, while marine taxa exhibit no statistical difference in morphospace occupation throughout the Phanerozoic.

SYSTEMATIC PALAEONTOLOGY

Subphylum CHELICERATA Heymons, 1901

Class XIPHOSURA Latreille, 1802

(= MEROSTAMATA Dana, 1852)

Included taxa. 'Kasibelinuridae' Pickett, 1993; Xiphosurida Latreille, 1802.

FIG. 1. Strict consensus of the nine most parsimonious trees from analysis of the dataset in TNT as detailed under Method above. Numbers in branches represent: Bremer support values/jackknife values (above branch) and *bootstrap values* (beneath branch). The internal topology for the Antennulata, Megacheira, Pycnogonida, Chasmatspidida, Eurypterida and Arachnida clades is identical to previous analyses and is not the focus of the current study and so has been collapsed here for ease of representation.

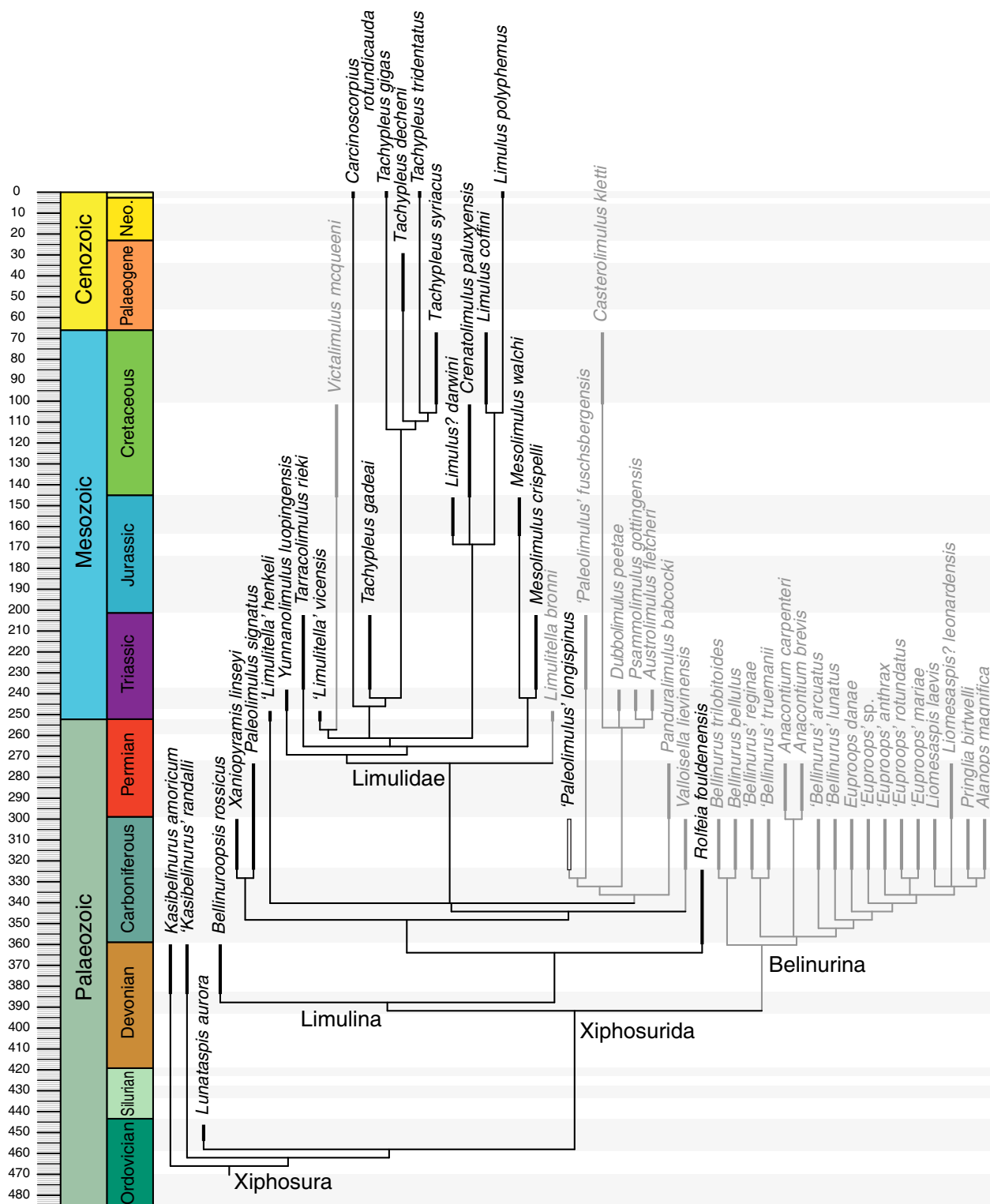


FIG. 2. Xiphosurid phylogeny plotted onto the geological timescale using the *strap* package in R (Bell and Lloyd 2015). Environmental affinities of taxa are shown, with the names and range bar of marine taxa in black and non-marine taxa in grey. *'Paleolimulus' longispinus*, with its uncertain environmental affinity, is shown by a hollow range bar. Colour online.

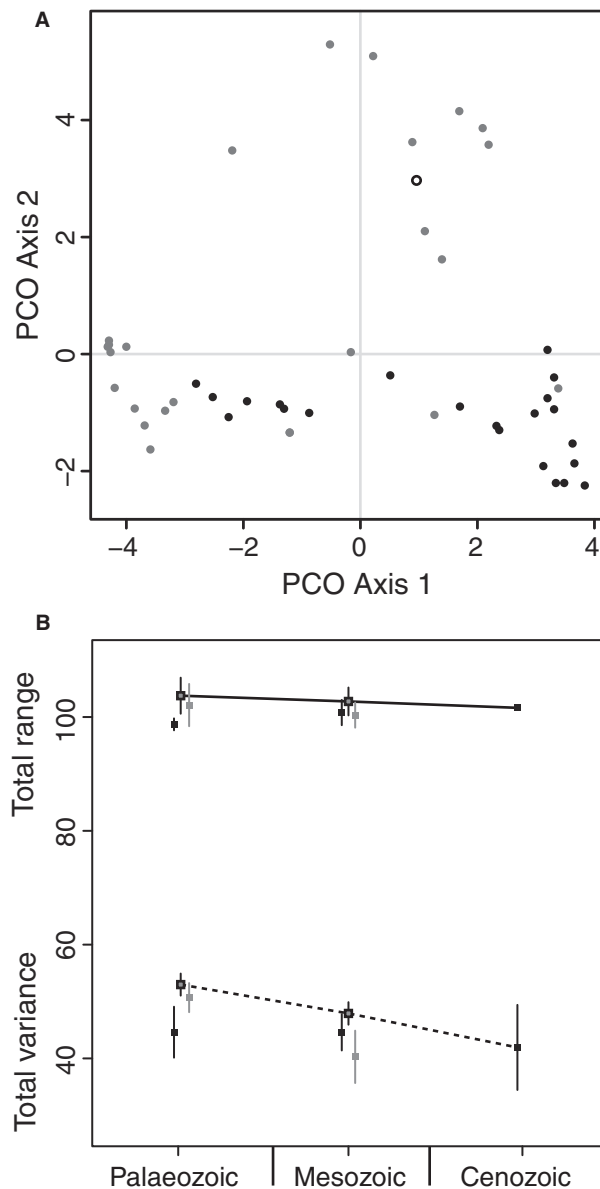


FIG. 3. Results of analysis of xiphosurid disparity derived from the discrete character matrix. A, morphospace occupation of Xiphosurida as indicated by the first two PCO axes; marine taxa are indicated by black circles, non-marine taxa by grey circles; the position of '*Paleolimulus longispinus*' is shown by the hollow circle. B, sum of ranges (SOR, shown by total range) and sum of variances (SOV, shown by total variance) for Xiphosurida in the Palaeozoic, Mesozoic and Cenozoic; black squares are values for marine taxa, grey squares for non-marine taxa; hollow squares represent combined values for all taxa in a given time bin; error bars are 95% confidence intervals.

Diagnosis. Chelicerata with unfused appendage VII; cardiac lobe extending anteriorly beyond the posterior half of carapace; width of prosomal axis equal to that of cardiac lobe; vaulted prosomal shield covering appendages

dorsally and laterally; segments VIII–XIV fused into thoracetrone.

Remarks. Xiphosura here is limited to those chelicerates with a thoracetrone, thereby excluding the majority of synziphosurines from the group as suggested by Lamsdell (2013).

Family 'KASIBELINURIDAE' Pickett, 1993

Type genus. *Kasibelinurus* Pickett, 1993.

Included genera. *Elleria* Raymond, 1944; *Lunataspis* Rudkin *et al.*, 2008.

Remarks. The genus *Kasibelinurus*, as defined by Babcock *et al.* (1995), is paraphyletic and needs to be redefined so as to be monophyletic. This also renders the family 'Kasibelinuridae' paraphyletic. The family is here used to denote stem xiphosurids, with quote marks denoting paraphyly (Wiley 1979).

Order XIPHOSURIDA Latreille, 1802

Included taxa. Belinurina Zittel *in* Zittel and Eastman, 1913; Limulina Richter and Richter, 1929.

Diagnosis. Xiphosura with sagittal keel on prosomal shield; postabdomen comprising a single segment.

Suborder BELINURINA Zittel *in* Zittel and Eastman, 1913

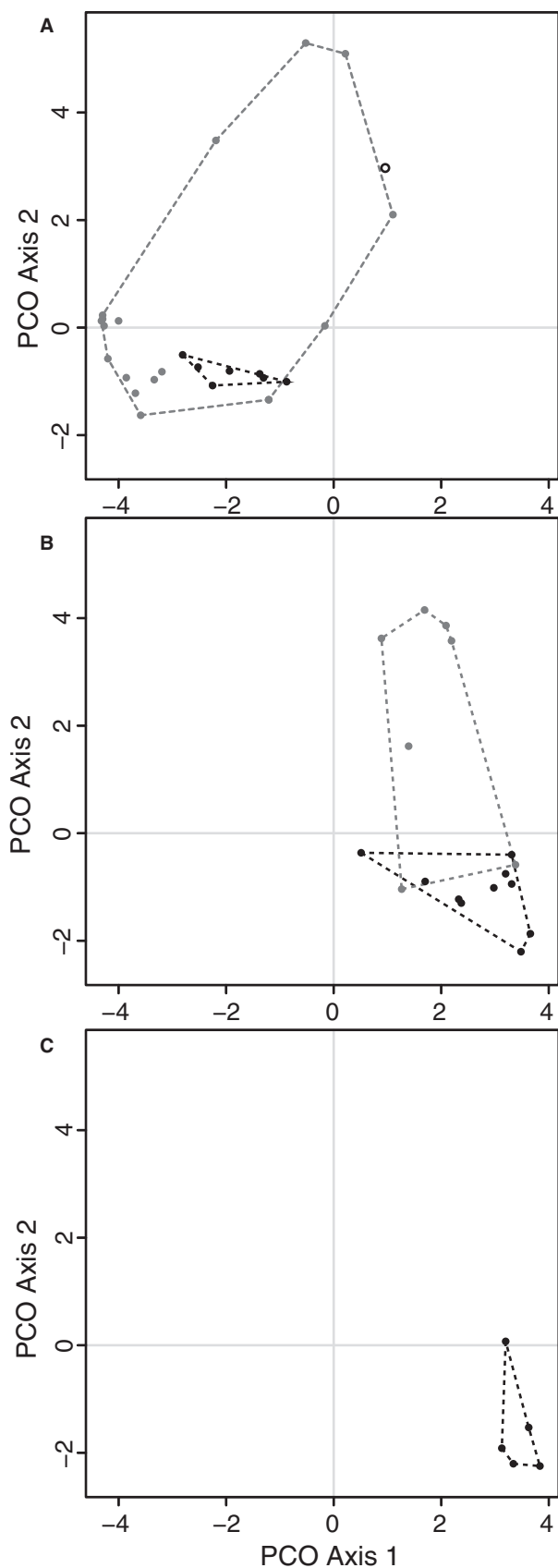
Included taxa. Belinuridae Zittel *in* Zittel and Eastman, 1913.

Diagnosis. Xiphosurida with trunk doublure dorsally delineated by furrow; tergopleurae present on posterior tergites; thoracetrone lacking moveable spines; tergites expressed dorsally on thoracetrone; ophthalmic ridges bowing towards the axis posterior to the lateral eyes.

Family BELINURIDAE Zittel *in* Zittel and Eastman, 1913 (= EUPROPIDAE Eller, 1938a syn. nov.; = LIOMESASPIDAE Raymond, 1944)

Type genus. *Bellinurus* Pictet, 1846 (= *Belinurus* König, 1851; = *Steropsis* Bailly, 1969; = *Koenigiella* Raymond, 1944).

Included genera. *Alanops* Racheboeuf *et al.*, 2002; *Anacontium* Raymond, 1944; *Euproops* Meek, 1867 (= *Prestwichia* Woodward, 1867; = *Prestwichianella* Cockerell, 1905); *Liomesaspis* Raymond,



1944; *Pringlia* Raymond, 1944) (= *Palatinaspis* Malz and Poschmann, 1993); *Prolimulus* Fric, 1899.

Diagnosis. As for *Belinurina*.

Remarks. *Bellinurus* is here suggested to be paraphyletic with respect to *Euproops*, which is in turn paraphyletic with regard to *Liomesaspis*, *Alanops*, and *Pringlia*. The only taxonomic solutions to this issue involve either synonymizing all five genera or the erection of multiple monotypic genera, and so no action is taken pending further study of the group.

Suborder LIMULINA Richter and Richter, 1929

Included taxa. *Bellinuroopsis* Chernyshev, 1933 (= *Neobelinuropsis* Eller, 1938b); Rolfeidae Selden and Siveter, 1987; Paleolimulidae Raymond, 1944; Limuloidea Zittel, 1885.

Diagnosis. Xiphosurida with the tergites of somites XIV–XV fused; articulating flange present on lateral region of prosomal/opisthosomal joint.

Family ROLFEIIDAE Selden and Siveter, 1987

Type and only genus. *Rolfeia* Waterston, 1985.

Diagnosis. Limulina with transverse ridge nodes present on prosomal shield; thoracetron with moveable lateral spines.

Family PALEOLIMULIDAE Raymond, 1944 (= MORAVURIDAE Příbyl, 1967 syn. nov.)

Type genus. *Paleolimulus* Dunbar, 1923.

Included genera. *Moravurus* Příbyl, 1967; *Xaniopyramis* Siveter and Selden, 1987.

Diagnosis. Limulina with pyramidal cheek node; interopthalmic ridges on prosomal shield; thoracetron with free lobes; moveable

FIG. 4. Xiphosurid morphospace occupation throughout geological time as indicated by the first two PCO axes. A, Palaeozoic. B, Mesozoic. C, Cenozoic. Marine taxa are indicated by black circles, non-marine taxa by grey circles. The position of '*Paleolimulus*' *longispinus* is shown by the hollow circle. Minimum morphospace occupation polygons indicating the boundaries of the ecological groups are shown with dashed lines.

TABLE 4. NPMANOVA test results for statistical differences between all taxa, freshwater taxa and marine taxa for each of the three period-level time bins based on PCO analysis, after Bonferroni correction.

| | All taxa | | Non-marine taxa | Marine taxa | |
|------------|---------------|----------|-----------------|-------------|----------|
| | Palaeozoic | Mesozoic | Palaeozoic | Palaeozoic | Mesozoic |
| Palaeozoic | — | — | — | — | — |
| Mesozoic | 0.0009 | — | 0.038 | 0.214 | — |
| Cenozoic | 0.0189 | 0.783 | — | 0.089 | 1 |

Significant p-values (indicating significant difference between time bins) shown in bold

lateral spines present on thoracetrone; transverse ridge nodes present on prosomal shield.

Remarks. *Paleolimulus* is resolved in the present analysis as polyphyletic. The type species, *Paleolimulus signatus*, forms a clade with *Xaniopyramis* which is here considered to represent Paleolimulidae. The other ‘*Paleolimulus*’ species are placed within the Austrolimulidae and should be removed from the genus.

Superfamily LIMULOIDEA Zittel, 1885

Included taxa. *Valloisella* Racheboeuf, 1992; Austrolimulidae Riek, 1955; Limulidae Zittel, 1885.

Diagnosis. Limulina with thoracetrone showing no lateral expression of individual tergites; moveable spines present on thoracetrone; thoracetrone with free lobes.

Family AUSTROLIMULIDAE Riek, 1955 (= DUBBOLIMULIDAE Pickett, 1984)

Type genus. *Austrolimulus* Riek, 1955.

Included genera. *Casterolimulus* Holland *et al.*, 1975; *Panduralimulus* Allen and Feldmann, 2005; *Dubbolimulus* Pickett, 1984; *Psammolimulus* Lange, 1922; ‘*Paleolimulus*’ Dunbar, 1923.

Diagnosis. Limuloidea with apodemal pits present on thoracetrone; thoracetrone lacking tergopleural fixed spines; posteriormost thoracetrone tergopleurae swept back and elongated to form ‘swallowtail’; axis of thoracetrone bearing dorsal keel.

Remarks. As previously noted, the ‘*Paleolimulus*’ assigned to Austrolimulidae do not resolve with the type species and should be removed from the genus. *Dubbolimulus*, previously considered to be a synonym of *Paleolimulus*, is also shown to be a valid taxon.

Family LIMULIDAE Zittel, 1885 (= MESOLIMULIDAE Størmer, 1952)

Type genus. *Limulus* Müller, 1785.

Included genera. *Carcinoscorpius* Pocock, 1902; *Crenatolimulus* Feldmann *et al.*, 2011; *Limulitella* Størmer, 1952 (= *Limulites* Schimper, 1853); *Mesolimulus* Størmer, 1952; *Tachypleus* Leach, 1819 (= *Heterolimulus* Vía Boada and De Villalta 1966); *Taraccolimulus* Romero and Vía Boada, 1977; *Victalimulus* Riek and Gill, 1971; *Yunnanolimulus* Zhang *et al.*, 2009.

Diagnosis. Limuloidea with thoracetrone showing no expression of individual tergites; axis of thoracetrone bearing dorsal keel; apodemal pits sometimes present.

Remarks. The internal topology of Limulidae is identical to that presented in Lamsdell and McKenzie (2015).

DISCUSSION

Xiphosurids have long been considered ideal examples of bradytely (Fisher 1984), a concept often linked to their apparent ecological role of marine generalists (Kin and Błażejowski 2014). The results here show that, in terms of both morphological and ecological stability, this traditional view of xiphosurids is an over-simplification. Belinurines have frequently been recognized as aberrant in comparison with other xiphosurids and were excluded from Fisher’s (1984) treatment of xiphosurid bradytely. The traditional view that xiphosurids are indicative of purely marine environments (Caster 1957) has also been restricted to apply only to limulines (Holland *et al.* 1975), again removing belinurines from consideration. However, while marine xiphosurids consistently occupy the same regions of the morphospace, limulines independently colonized non-marine environments at least four times throughout their evolutionary history and are therefore not as ecologically conservative as previously supposed. Furthermore, inva-

sion of the non-marine realm appears to have coincided with the occupation of new regions of the morphospace. Although not explicitly stated, this pattern has been noted before; all the aberrant morphologies cited by Fisher (1984) belong to taxa known from non-marine environments and were considered ecological specialists.

Simpson (1944) argued that shifts between 'adaptive zones' (equivalent to the modern ecological niche or a set of similar niches depending on the hierarchical scope of the study) are tied to shifts in morphology and rapid evolutionary radiations. Invasions of the brackish/fresh-water realm by otherwise marine lineages constitute such a shift, requiring extreme physiological changes in salinity tolerance (Little 1990), and have been observed to result in morphological radiations (Lee and Bell 1999). Such changes in evolutionary regime are likely due to the change in niche habitation; different environments have been suggested to result in the differential prevalence of evolutionary processes (Sheldon 1996) and the genealogical and ecological hierarchies are known to interact to define the trajectory of evolutionary lineages (Eldredge and Salthe 1984; Eldredge 2003). For xiphosurids, the transition to non-marine environments likely resulted in a change in population structure. Modern horseshoe crabs show a substantial gene flow between neighbouring populations (King *et al.* 2005). However, becoming restricted to non-marine environments would likely result in an overall decrease in effective population sizes and a greater degree of isolation, as has been observed in modern fish (DeWoody and Avise 2000). As well as increasing the likelihood of allopatric speciation through geographic isolation, this change in population structure would reduce genetic diversity, resulting in a greater probability of establishing morphological novelties (Eldredge *et al.* 2005). These factors combined would explain the proliferation of belinurines during the Carboniferous and the manner by which both bellinurines and austrolimulids occupied previously unexplored regions of morphospace.

The specialization that led to this relatively short-term evolutionary success may have also lead to the eventual downfall of these non-marine clades. Evolutionary trends tied to a reduction of population density and increased trophic specialization have been shown to correlate with increased extinction risk (Van Valkenburgh *et al.* 2004) as evolution proceeds along a trajectory that favours individual fitness but results in a lineage less likely to persist (Stanley 1979). The observed phenomenon of niche conservatism within phylogenetic lineages (Wiens 2004; Wiens *et al.* 2010) means that a return to the marine realm was incredibly unlikely for these taxa and, as a result, they were severely impacted by the loss of habitat caused by events such as the Kasimovian rainforest

collapse in the Carboniferous (Sahney *et al.* 2010) and the climatic upheaval following the Chicxulub asteroid impact at the end Cretaceous (Schulte *et al.* 2010).

Given niche conservatism and paucity of examples of non-marine taxa returning to the marine realm, it would seem exceptional that xiphosurids have independently repeatedly invaded non-marine environments. Furthermore, while modern horseshoe crabs exhibit a broad range of salinity tolerances, none can remain in fresh water for extended periods of time (Sekiguchi and Shuster 2009), suggesting that the environmental shifts observed here cannot be explained by a contraction in niche occupation. However, as ecologically widespread populations are more likely to seed new populations than restricted populations are (Vermeij and Dietl 2006), it is likely that there is simply a greater likelihood that marine taxa will colonize non-marine environments than vice versa through sheer weight of numbers.

CONCLUSIONS

The results of the phylogenetic analysis presented herein have some interesting implications for xiphosurid evolution. The realization that horseshoe crabs have independently invaded the non-marine realm at least five times during the Palaeozoic and Mesozoic, with two of these events linked to the origin of major clades, indicates that the long-held view that xiphosurids are a lineage exhibiting no innovation or experimentation in basic organization (Eldredge 1976) is over simplistic. Instead, horseshoe crabs have a complex evolutionary history of repeated shifts in niche occupation from marine generalists to specialist non-marine offshoots. These non-marine taxa occupy novel regions of morphospace and exhibit a repeated, convergent ecological pattern of differentiation, speciation and subsequent extinction.

It is unclear why xiphosurids have not re-invaded the non-marine realm since the end of the Mesozoic. One potential reason is the reduction of species ranges relative to those in the Palaeozoic and Mesozoic, resulting in reduced potential for isolation and speciation. Alternatively, Cenozoic fossils of non-marine taxa may yet await discovery. Either way, it is clear that the four modern species of horseshoe crab represent only a fraction of the lineage's past ecological diversity.

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DATA ARCHIVING STATEMENT

Data for this study are available in Morphobank: <http://morphobank.org/permalink/?P1221>

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REFERENCES

- ALLEN, J. G. and FELDMANN, R. M. 2005. *Panduralimulus babcocki* n. gen. and sp., a new limulacean horseshoe crab from the Permian of Texas. *Journal of Paleontology*, **79**, 595–600.
- ANDERSON, L. I. 1994. Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois. *Proceedings of the Geologists' Association*, **105**, 265–275.
- 1997. The xiphosuran *Liomesaspis* from the Montceau-les-Mines Konservat-Lagerstätte, Massif Central, France. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **204**, 415–436.
- and HORROCKS, C. 1995. *Valloisella lievinensis* Racheboeuf, 1992 (Chelicerata: Xiphosura) from the Westphalian B of England. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1995**, 647–658.
- and SELDEN, P. A. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia*, **30**, 19–31.
- DUNLOP, J. A., HORROCKS, C. A., WINKELMANN, H. M. and EAGAR, R. M. C. 1997. Exceptionally preserved fossils from Bickershaw, Lancashire UK (Upper Carboniferous, Westphalian A (Langsettian)). *Geological Journal*, **32**, 197–210.
- BABCOCK, L. E. and MERRIAM, D. F. 2000. Horseshoe crabs (Arthropoda: Xiphosurida) from the Pennsylvanian of Kansas and Elsewhere. *Transactions of the Kansas Academy of Science*, **103**, 76–94.
- WEGWEISER, M. D., WEGWEISER, A. E., STANLEY, T. M. and MCKENZIE, S. C. 1995. Horseshoe crabs and their trace fossils from the Devonian of Pennsylvania. *Pennsylvania Geology*, **26**, 2–7.
- MERRIAM, D. F. and WEST, R. R. 2000. Paleolimulus, an early limuline (Xiphosurida), from Pennsylvanian-Permian Lagerstätten of Kansas and taphonomic comparison with modern *Limulus*. *Lethaia*, **33**, 129–141.
- BAILY, W. H. 1969. On fossils obtained at Kiltorcan Quarry, Co. Kilkenny. *British Association Report*, 73–75.
- BELL, M. A. and LLOYD, G. T. 2015. *strap*: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology*, **58**, 379–389.
- BLEICHER, M. 1897. Sur la découverte d'une nouvelle espèce de limule dans les marnes irisées de Lorraine. *Bulletin de la Société des Sciences de Nancy*, **14**, 116–126.
- BREMER, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.
- BRIGGS, D. E. G., MOORE, R. A., SHULTZ, J. W. and SCHWEIGERT, G. 2005. Mineralization of soft-part anatomy and invading microbes in the horseshoe crab *Mesolimulus* from the Upper Jurassic Lagerstätte of Nusplingen, Germany. *Proceedings of the Royal Society B*, **272**, 627–632.
- CASTER, K. E. 1957. Problematica. 1025–1032. In LADD, H. S. (ed.). *Treatise on marine ecology and paleoecology. Volume 2, Paleoecology*. The Geological Society of America Memoire, **67**, 1077 pp.
- CHERNYSHEV, B. I. 1933. Arthropoda from the Urals and other regions of the USSR. *Materials of the Central Scientific and Prospecting Institute Paleontology and Stratigraphy, Magazine*, **1**, 15–25. [in Russian]
- COCKERELL, T. D. A. 1905. Two Carboniferous genera of xiphosurans. *American Geologist*, **36**, 330.
- COPELAND, M. J. 1957. The arthropod fauna of the Upper Carboniferous rocks of the maritime provinces. *Geological Survey of Canada Memoir*, **286**, 1–110.
- CRÔNIER, C. and COURVILLE, P. 2005. New xiphosuran merostomata from the Upper Carboniferous of the Graissessac Basin (Massif Central, France). *Comptes Rendus Palevol*, **4**, 123–133.
- DANA, J. D. 1852. United States exploring expedition during the years 1838, 1839, 1840, 1841, 1942. *Under the command of Charles Wilkes, U.S.N. Volume 13. Crustacea. Part 1*. Sherman, Philadelphia, 685 pp.
- DEWOODY, J. A. and AVISE, J. C. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. *Journal of Fish Biology*, **56**, 461–473.
- DIX, E. and PRINGLE, J. 1929. On the fossil Xiphosura from the South Wales Coalfield with a note on the myriapod *Euphoberia*. *Summary of Progress of the Geological Survey of Great Britain*, **1928**, 90–113.
- 1930. XIII.—Some coal measure arthropods from the South Wales Coalfield. *Annals and Magazine of Natural History*, **6**, 136–144.
- DUNBAR, C. O. 1923. Kansas Permian insects, Part 2. *Paleolimulus*, a new genus of Paleozoic Xiphosura, with notes on other genera. *American Journal of Science*, 5th Series, **5**, 443–454.
- ELDREDGE, N. I. 1976. Differential evolutionary rates. *Paleobiology*, **2**, 174–177.
- 2003. The sloshing bucket: how the physical realm controls evolution. 3–32. In CRUTCHFIELD, J. and SCHUSTER, P. (eds). *Evolutionary dynamics. Exploring the interplay of selection, accident, neutrality, and function. SFI studies in the sciences of complexity series*. Oxford University Press, New York, 488 pp.
- and SALTHER, S. N. 1984. Hierarchy and evolution. *Oxford surveys in evolutionary biology*, **1**, 184–208.
- THOMPSON, J. N., BRAKEFIELD, P. M., GAVRILETTS, S., JABLONSKI, D., JACKSON, J. B. C., LENSKI, R. E., LIEBERMAN, B. S., MCPEEK, M. A. and MILLER, W. III 2005. The dynamics of evolutionary stasis. *Paleobiology*, **31**, 133–145.
- ELLER, E. R. 1938a. A new xiphosuran, *Euproops morani*, from the Upper Devonian of Pennsylvania. *Annals of the Carnegie Museum*, **27**, 152–153.
- 1938b. A review of the xiphosuran genus *Belinurus* with the description of a new species, *B. alleganyensis*. *Annals of the Carnegie Museum*, **27**, 129–150.
- FARRIS, J. S., ALBERT, V. A., KÄLLERSJÖ, M., LIPSCOMB, D. and KLUGE, A. G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, **12**, 99–124.

- FELDMANN, R. M., SCHWEITZER, C. E., DATTILO, B. and FARLOW, J. O. 2011. Remarkable preservation of a new genus and species of limuline horseshoe crab from the Cretaceous of Texas, USA. *Palaeontology*, **54**, 1337–1346.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.
- FILIPIAK, P. and KRAWCZYŃSKI, W. 1996. Westphalian xiphosurans (Chelicerata) from the Upper Silesia Coal Basin of Sosnowiec, Poland. *Acta Palaeontologica Polonica*, **41**, 413–425.
- FISHER, D. C. 1984. The Xiphosurida: archetypes of bradytely? 196–213. In ELDREDGE, N. I. and STANLEY, S. M. (eds). *Living fossils*. Springer Verlag, New York, 291 pp.
- FOTH, C., BRUSATTE, S. L. and BUTLER, R. J. 2012. Do different disparity proxies converge on a common signal? Insights from the cranial morphometrics and evolutionary history of Pterosauria (Diaspida: Archosauria). *Journal of Evolutionary Biology*, **25**, 904–915.
- FRIČ, A. 1899. On *Prolimulus woodwardi*. *Geological Magazine*, **6** (Decade IV), 57–58.
- FRITSCH, K. 1906. Beitrag zur Kenntnis der Tierwelt der Deutschen Trias. *Abhandlungen der naturforschenden Gesellschaft Halle*, **24**, 220–285.
- GARWOOD, R. J. and DUNLOP, J. A. 2014. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. *PeerJ*, **2**, 1–33.
- GOLOBOFF, P. A., FARRIS, J. A. and NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.
- HAGADORN, J. 2002. Bear Gulch: an exceptional Upper Carboniferous Plattenkalk. 167–184. In BOTTJER, D. J. and BAMBACH, R. K. (eds). *Exceptional fossil preservation: a unique view on the evolution of marine life*. Columbia University Press, New York, NY, 424 pp.
- HAUG, C., VAN ROY, P., LEIPNER, A., FUNCH, P., RUDKIN, D. M., SCHÖLLMANN, L. and HAUG, J. T. 2012. A holomorph approach to xiphosuran evolution—a case study on the ontogeny of *Euproops*. *Development Genes & Evolution*, **222**, 253–268.
- HAUSCHKE, N. and WILDE, V. 1987. *Paleolimulus fuchsbergensis* n. sp. (Xiphosura, Merostomata) aus der oberen Trias von Nordwestdeutschland, mit einer Übersicht zur Systematik und Verbreitung rezenter Limuliden. *Paläontologische Zeitschrift*, **61**, 87–108.
- 2004. Palaeogene limulids (Xiphosura) from Saxony-Anhalt (Germany) – systematics and palaeobiogeography. *Hallesches Jahrbuch für Geowissenschaften Reihe B*, **18**, 161–168.
- HETHERINGTON, A. J., SHERRATT, E., RUTA, M., WILKINSON, M., DELINE, B. and DONOGHUE, P. C. J. 2015. Do cladistic and morphometric data capture common patterns of morphological disparity? *Palaeontology*, **58**, 393–399.
- HEYMONS, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica*, **13**, 1–244.
- HOLLAND, F. D., ERICKSON, J. M. and O'BRIEN, D. E. 1975. *Casterolimulus*: a new Late Cretaceous generic link in limulid lineage. *Studies in Paleontology and Stratigraphy. Bulletin of American Paleontology*, **62**, 235–249.
- HU, S.-X., ZHANG, Q.-Y., CHEN, Z.-Q., ZHOU, C.-Y., LÜ, T., XIE, T., WEN, W., HUANG, J.-Y. and BENTON, M. J. 2011. The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proceedings of the Royal Society B*, **278**, 2274–2282. doi:10.1098/rspb.2010.2235
- HUGHES, M., GERBER, S. and WILLS, M. A. 2013. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences*, **110**, 13875–13879.
- KIN, A. and BŁAŻEJOWSKI, B. 2014. The horseshoe crab of the genus *Limulus*: living fossil or stabilomorph? *PLoS One*, **9**, 1–11.
- KING, T. L., EACKLES, M. S., SPIDLE, A. P. and BROCKMANN, H. J. 2005. Regional differentiation and sex-biased dispersal among populations of the horseshoe crab *Limulus polyphemus*. *Transactions of the American Fisheries Society*, **134**, 441–465.
- KÖNIG, C. 1851. *Icones fossilium sectiles*. G. B. Sowerby, London, 19 pp.
- LAMSDALL, J. C. 2013. Revised systematics of Palaeozoic 'horseshoe crabs' and the myth of monophyletic Xiphosura. *Zoological Journal of the Linnean Society*, **167**, 1–27.
- 2015. Data from: Horseshoe crab phylogeny and independent colonizations of freshwater: ecological invasion as a driver for morphological innovation. *MorphoBank*, P1221. doi:10.7934/P1221
- and McKENZIE, S. C. 2015. *Tachypleus syriacus* (Woodward) – a sexually dimorphic Cretaceous crown limulid reveals underestimated horseshoe crab divergence times. *Organisms Diversity & Evolution*, first published online 1 August 2015. doi:10.1007/s13127-015-0229-3
- BRIGGS, D. E. G., LIU, H. P., WITZKE, B. J. and McKAY, R. M. 2015. A new Ordovician arthropod from the Winneshiek Lagerstätte of Iowa reveals the ground plan of eurypterids and chasmataspids. *The Science of Nature*, **102**, doi:10.1007/s00114-015-1312-5
- LANGE, W. 1922. Über neue fossilfunde aus der Trias von Göttingen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **74**, 162–168.
- LATREILLE, P. A. 1802. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*, Vol. 3. Dufart, Paris.
- LEACH, W. E. 1819. Entomostracés. 524–543. In CUVIER, F. G. (ed.). *Dictionnaires des Sciences Naturelles*, Vol. 14. F. G. Levrault, Paris, 571 pp.
- LEE, C. E. and BELL, M. A. 1999. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology & Evolution*, **14**, 284–288.
- LITTLE, C. 1990. *The terrestrial invasion: an ecophysiological approach to the origins of land animals*. Cambridge University Press, 304 pp.
- MADDISON, W. P. and MADDISON, D. R. 2015. Mesquite: a modular system for evolutionary analysis. <http://mesquiteproject.org/>
- MALZ, H. and POSCHMANN, M. 1993. Erste Süßwasser-Limuliden (Arthropoda, Chelicerata) aus dem Rotliegenden der Saar-Nahe-Senke. *Osnabrücker Naturwissenschaftliche Mitteilungen*, **19**, 21–24.

- MEEK, F. B. 1867. Notes on a new genus of fossil Crustacea. *Geological Magazine*, **4**, 320–321.
- MEISCHNER, K.-D. 1962. Neue Funde von *Psammolimulus gottingensis* (Merostomata, Xiphosura) aus dem Mittleren Buntsandstein von Göttingen. *Paläontologische Zeitschrift*, **36**, 185–193.
- MÜLLER, O. F. 1785. *Entemostraca, seu, Insecta testacea quae in aquis Daniae et Norvegie reperiuntur, descripsit et iconibus illustravit*. J. G. Müller, London, 135 pp.
- PICKETT, J. W. 1984. A new freshwater limuloid from the Middle Triassic of New South Wales. *Palaeontology*, **27**, 609–621.
- 1993. A Late Devonian xiphosuran from near Parkes, New South Wales. *Memoir of the Association of Australasian Palaeontologists*, **15**, 279–287.
- PICTET, F. J. 1846. *Traité élémentaire de paléontologie*, Vol. 4. Langlois et Leclercq, Paris, 458 pp.
- POCOCK, R. F. 1902. The taxonomy of Recent species of *Limulus*. *Annals and Magazine of Natural History*, **9**, 256–266.
- PRESTWICH, J. 1840. Memoir on the geology of the Coalbrook Dale. *Transactions of the Geological Society of London*, **5**, 413–495.
- PŘÍBYL, A. 1967. *Moravurus* gen. n. eine neue Xiphosurida Gattung aus dem mährisch-schlesischen Oberkarbon. *Časopis pro Mineralogii a Geologii*, **12**, 457–460.
- RACHEBOEUF, P. R. 1992. *Valloisella lievinensis* n. g. n. sp.: nouveau Xiphosure carbonifère du nord de la France. *Neues Jahrbuch für Geology und Paläontologie Monatshefte*, **1992**, 336–342.
- VANNIER, J. and ANDERSON, L. I. 2002. A new three-dimensionally preserved xiphosuran chelicerate from the Montceau-les-Mines Lagerstätte (Carboniferous, France). *Palaeontology*, **45**, 125–147.
- RAYMOND, P. E. 1944. Late Paleozoic xiphosurans. *Bulletin of the Museum of Comparative Zoology*, **94**, 475–508.
- REESIDE, J. B. and HARRIS, D. V. 1952. A Cretaceous horseshoe crab from Colorado. *Journal of the Washington Academy of Science*, **42**, 174–178.
- RICHTER, R. and RICHTER, E. 1929. *Weinbergina opitzi* n. g., n. sp., ein Schwerträger (Merost. Xiphos.) aus dem Devon (Rheinland). *Senckenbergiana*, **11**, 21–39.
- RIEK, E. F. 1955. A new xiphosuran from the Triassic sediments at Brookvale, New South Wales. *Records of the Australian Museum*, **23**, 281–282.
- and GILL, E. D. 1971. A new xiphosuran genus from Lower Cretaceous freshwater sediments at Koonwarra, Victoria, Australia. *Palaeontology*, **14**, 206–210.
- ROMERO, A. and VÍA BOADA, L. 1977. *Tarracolimulus riei*, nov. gen., nov. sp., nuevo limulido del Triásico de Mont-ral-Alcover (Tarragona). *Cuadernos de Geología Ibérica*, **4**, 239–246.
- RUDKIN, D. M., YOUNG, G. A. and NOWLAN, G. S. 2008. The oldest horseshoe crab: a new xiphosurid from Late Ordovician Konservat-Lagerstätten deposits, Manitoba, Canada. *Palaeontology*, **51**, 1–9.
- SAHNEY, S., BENTON, M. J. and FALCON-LANG, H. J. 2010. Rainforest collapse triggered Carboniferous tetrapod diversification. *Geology*, **38**, 1079–1082.
- SCHIMPER, W. P. 1853. *Paleontologica alsatica ou fragments paléontologiques des différents terrains stratifiés qui se rencontrent en Alsace. Mémoires de la Société du Muséum d'Histoire Naturelle de Strasbourg*, **4**, 1–10.
- SCHULTE, P., ALEGRET, L., ARENILLAS, I., ARZ, J. A., BARTON, P. J., BOWN, P. R., BRALOWER, T. J., CHRISTESON, G. L., CLAEYS, P., COCKELL, C. S., COLLINS, G. S., DEUTSCH, A., GOLDIN, T. J., GOTO, K., GRAJALES-NISHIMURA, J. M., GRIEVE, R. A. F., GULICK, S. P. S., JOHNSON, K. R., KIESLING, W., KOEBERL, C., KRING, D. A., MACLEOD, K. G., MATSUI, T., MELOSH, J., MONTANARI, A., MORGAN, J. V., NEAL, C. R., NICHOLS, D. J., NORRIS, R. D., PIERAZZO, E., RAVIZZA, G., REBOLLEDO-VIEYRA, M., REIMOLD, W. U., ROBIN, E., SALGE, T., SPEIJER, R. P., SWEET, A. R., URRUTIA-FUCUGAUCHI, J., VAJDA, V., WHALEN, M. T. and WILLUMSEN, P. S. 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science*, **327**, 1214–1218.
- SEKIGUCHI, K. and SHUSTER, C. N. 2009. Limits on the global distribution of horseshoe crabs (Limulacea): lessons learned from two lifetimes of observations: Asia and America. 5–24. In TANACREDI, J. T., BOTTON, M. L. and SMITH, D. R. (eds). *Conservation of horseshoe crabs*. Springer, Dordrecht, 662 pp.
- SELDEN, P. A. and SIVETER, D. J. 1987. The origin of the limuloids. *Lethaia*, **20**, 383–392.
- LAMSDELL, J. C. and LIU, Q. 2015. An unusual euchelicerate linking horseshoe crabs and eurypterids, from the Lower Devonian (Lochkovian) of Yunnan, China. *Zoologica Scripta*, **44** (6), 645–652. doi:10.1111/zsc.12124
- SHELDON, P. R. 1996. Plus ça change – a model for stasis and evolution in different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **127**, 209–227.
- SHULTZ, J. W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society*, **150**, 221–265.
- SIMPSON, G. G. 1944. *Tempo and mode in evolution*. Columbia University Press, New York, 237 pp.
- SIVETER, D. J. and SELDEN, P. A. 1987. A new, giant xiphosurid from the lower Namurian of Weardale, County Durham. *Proceedings of the Yorkshire Geological Society*, **46**, 153–168.
- STANLEY, S. M. 1979. *Macroevolution: pattern and process*. Freeman, San Francisco, 370 pp.
- STØRMER, L. 1952. Phylogeny and taxonomy of fossil horseshoe crabs. *Journal of Paleontology*, **26**, 630–639.
- TANACREDI, J. T., BOTTON, M. L. and SMITH, D. R. 2009. *Biology and conservation of horseshoe crabs*. Springer, Heidelberg, 662 pp.
- TASCH, P. 1961. Paleolimnology: Part 2: Harvey and Sedgwick Counties, Kansas: stratigraphy and biota. *Journal of Paleontology*, **35**, 836–865.
- VAN ROY, P., ORR, P. J., BOTTING, J. P., MUIR, L. A., VINTHER, J., LEFEBVRE, B., EL HARIRI, K. and BRIGGS, D. E. G. 2010. Ordovician faunas of Burgess Shale type. *Nature*, **465**, 215–218.

- VAN VALKENBURGH, B., WANG, X. and DAMUTH, J. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, **306**, 101–104.
- VERMEIJ, G. J. and DIETL, G. P. 2006. Majority rule: adaptation and the long-term dynamics of species. *Paleobiology*, **32**, 173–178.
- VÍA, L. 1987. Artropodos fosiles Triasicos de Alcover-Montral. II. Limulidos. *Cuadernos Geología Ibérica*, **11**, 281–282.
- VÍA BOADA, L. and VILLALTA, J. F. DE. 1966. *Heterolimulus gadeai* nov. gen., nov. sp., representante de una nueva familia de Limulacea, en el Triásico español. *Comptes Rendues Sommaire Séances Société Géologique France*, **1966**, 57–59.
- WATERSTON, C. D. 1985. Chelicerata from the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **76**, 25–33.
- WIENS, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, **58**, 193–197.
- ACKERLY, D. D., ALLEN, A. P., ANACKER, B. L., BUCKLEY, L. B., CORNELL, H. V., DAMSCHEN, E. I., DAVIES, T. J., GRYNES, J.-A., HARRISON, S. P., HAWKINS, B. A., HOLT, R. D., MCCAIN, C. M. and STEPHENS, P. R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.
- WILEY, E. O. 1979. Annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Systematic Zoology*, **28**, 308–337.
- WILLS, M. A. 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnean Society*, **65**, 455–500.
- BRIGGS, D. E. G. and FORTEY, R. A. 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology*, **20**, 93–130.
- WOODWARD, H. 1867. On some points in the structure of the Xiphosura, having reference to their relationship with the Eurypteridae. *Quarterly Journal of the Geological Society of London*, **23**, 28–37.
- ZHANG, Q.-Y., HU, S.-X., ZHOU, C.-Y., IV, T. and BAI, J.-K. 2009. New occurrence of Xiphosura in China. *Progress in Nature Science*, **19**, 1090–1093.
- ZITTEL, K. A. 1885. *Handbuch der Palaeontologie, Part 1. Palaeozoologie*, Vol. 2. R. Oldenbourg, Munich & Leipzig, 893 pp.
- and EASTMAN, C. R. 1913. *Text-book of palaeontology*, 2nd edn, Vol. 1. Macmillan, London, 839 pp.