

An unusual euchelicerate linking horseshoe crabs and eurypterids, from the Lower Devonian (Lochkovian) of Yunnan, China

PAUL A. SELDEN, JAMES C. LAMSDELL & LIU QI

Submitted: 18 March 2015

Accepted: 12 May 2015

doi:10.1111/zsc.12124

Selden, P.A., Lamsdell, J.C. & Qi, L. (2015). An unusual euchelicerate linking horseshoe crabs and eurypterids, from the Lower Devonian (Lochkovian) of Yunnan, China. —*Zoologica Scripta*, 44, 645–652.

Two new specimens of the xiphosuran *Kasibelimurus yueya* Lamsdell, Xue & Selden, 2013 are described, from the same horizon and locality as the type. The new specimens are conspecific with the type, but show ventral morphology, which considerably alters interpretation of the species. It can no longer be referred to *Kasibelimurus* Pickett, 1993, and a new genus, *Houia* n. gen., is erected. *Houia* shows a unique combination of xiphosurid and chasmataspidid/eurypterid characteristics such as lack of opisthosomal pleura and possession of a large, ventral metastomal plate. Phylogenetic analysis of all the major chelicerate orders suggests that *Houia* branched from the main euchelicerate lineage prior to the divergence of the three constituent clades of the Dekatriata Lamsdell, 2013 (Eurypterida, Arachnida, Chasmataspidida). Together with bunodids and pseudoniscids, *Houia* provides evidence for basal dekatriatans persisting into the middle Palaeozoic alongside eurypterids and arachnids and that the morphological diversity of these basal forms was greater than previously thought.

Corresponding author: Paul A. Selden, Department of Geology, University of Kansas, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA. E-mail: selden@ku.edu

Paul A. Selden, Department of Geology, University of Kansas, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA and Natural History Museum, Cromwell Road, London, SW7 5BD UK. E-mail: selden@ku.edu

James C. Lamsdell, Department of Geology and Geophysics, Yale University, PO Box 208109, New Haven, CT 06520, USA. E-mail: james.lamsdell@yale.edu

Liu Qi, School of Earth Sciences, China University of Geosciences, Wubao, 430074 Hubei, China. E-mail: cambrianlq@yahoo.com

Introduction

Xiphosurans are aquatic chelicerate arthropods traditionally defined by the possible synapomorphies of ophthalmic ridges and an axial region of the opisthosoma (Dunlop & Selden 1997), although they have recently been suggested to comprise a paraphyletic group (Lamsdell 2013a). The four extant species belong to the monophyletic order Xiphosurida, united by their large, crescentic prosomal shield and the fusion of opisthosomal tergites into a thoracetrone. The xiphosurid fossil record extends back to the Ordovician (Rudkin *et al.* 2008; Van Roy *et al.* 2010), while that of their supposed stem lineage ranges from Ordovician to Carboniferous (Moore *et al.* 2006; Van Roy *et al.* 2010). Previously, this stem lineage was regarded as a monophyletic clade with

subordinal status (Eldredge 1974), but is now considered a paraphyletic grade, informally termed ‘synziphosurines’ (Anderson & Selden 1997). It consists of xiphosurans with freely articulating opisthosomal segments.

The Australian late Devonian synziphosurine *Kasibelimurus* Pickett, 1993 has been retrieved as sister taxon to Xiphosurida (Anderson & Selden 1997), united with that order by the reduction of the number of opisthosomal segments to nine. A new species of *Kasibelimurus*, *K. yueya* Lamsdell *et al.*, 2013b; was described from a single specimen from the Devonian (Lochkovian) Xishancun Formation of Yunnan, China. This was only the second record of a horseshoe crab body fossil from China (the other being *Yunnanolimulus luopingensis*, from the Triassic of Luoping, Yunnan: Zhang *et al.* 2009). Here, we describe new mate-

rial of *K. yueya*, from the same locality as the holotype, which shows that the original description was erroneous, and that the species does not belong to *Kasibelinurus*. *Houia yueya* n. gen. exhibits a unique combination of xiphosuran and eurypterid characteristics. The dorsal carapace and ventral doublure are typical of xiphosurids, and lack of opisthosomal pleura and possession of a large, ventral, metastomal plate are characteristics of the Dekatriata (Lamsdell 2013a): arachnids, eurypterids and chasmataspidids. The large size of the metastoma of *Houia*, together with its stratigraphic age, indicates that the genus likely branched off the main euchelicerate lineage prior to the divergence of the three constituent dekatratan clades.

Material and methods

The specimens come from a locality south of the Shangxi-shan Reservoir, near Qujing city, Yunnan, China (25°30.43'79"N 103°42.12'71"E; see Fig. 1 of Xue 2012), from the lower part of the Xishancun Formation, a thin bed of greenish grey mudstone in which axes of the marine dasycladalean alga *Uncatoella verticillata* have also been found. The specimens are in a fine sandy matrix with abundant plant remains; eurypterid fragments were also collected along with the specimens described here. See Lamsdell *et al.* (2013b) for more detailed description of the locality, stratigraphy, sedimentology and associated biota. The more complete specimen (NIGP161923) is preserved ventral side

uppermost (part and counterpart: the specimen has split more or less through the cuticle). On the part, the ventral carapace is broken away medially to reveal the interior of the dorsal carapace and a pair of eyes (Figs 1B, 2). To trace the posterior part of the carapace on the part, and the telson on the counterpart, some preparation was carried out using a compressed air tool (Figs 1C,D, 4C,D). The isolated carapace (NIGP161924, Fig. 3) presents a dorsal surface to view.

The specimens were photographed both dry (with low-angle illumination; Figs 1A,C, 4A,C) and immersed in 70% ethanol (to increase contrast; Figs 1B,D, 2, 4B,D) with a Canon EOS 5D MkIII camera mounted on a Leica MZ16 stereomicroscope using cross-polarized illumination (Selden 2014). Drawings were made with the aid of a drawing tube attachment on the microscope and by tracing photographs using iDraw (indeo.com). Measurements were taken using iDraw and are in millimetres. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China (NIGP).

We use the term ‘pleuron’ (pl. pleura) to refer to the pleural region of arthropod segments, visible dorsally as pleura (syn. epimera) separated from the axial region by a furrow. Pleura are not present in *Houia*. Note that pleura are synonymous with tergopleura *sensu* Lamsdell (2013a), except that there is some confusion regarding the singular and plural forms of these terms in the literature. Pleuron is



Fig. 1 A–D. *Houia yueya* gen. nov. NIGP161923, part. —A. Photograph of specimen dry, before preparation. —B. Photograph of specimen under ethanol, before preparation. —C. Photograph of specimen dry, after preparation on the left side of metastoma. —D. Photograph of specimen under ethanol, after preparation on the left side of metastoma. Scale bars are 5 mm.

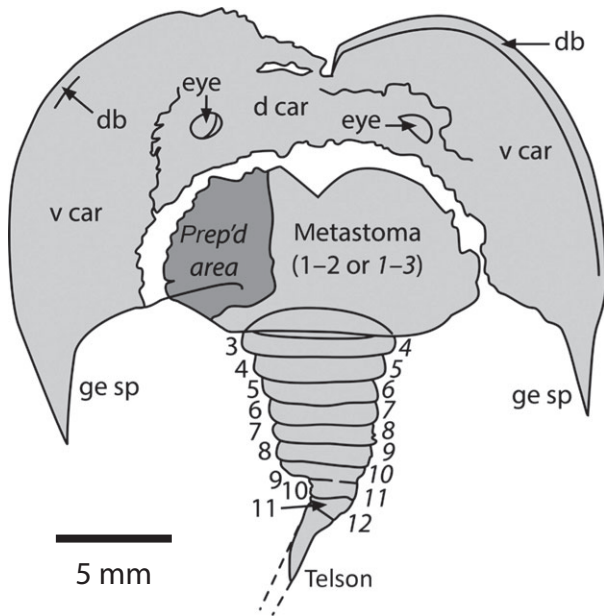


Fig. 2 *Houia yueya* gen. nov. NIGP161923, part. Explanatory drawing. 1-12, inferred opisthosomal segments (italicized in alternative interpretation); d car, dorsal carapace; db, doublure; ge sp, genal spine; v car, ventral carapace.

Greek and means the side of an animal; its plural is pleura. Commonly, these terms are transliterated into Latin as pleura (s.) and pleurae (pl.), which begs confusion and is not used here. However, the meaning of the term pleuron is different in different branches of zoology. For example, in mammals (esp. medicine), the pleura (s.) is the membrane lining the lung, while in arthropod anatomy it refers to the lateral side of the body and may be a membrane or one or more sclerites (pleurites), as in insect pleura (pro-, meso- and metapleuron for each of the thoracic segments) and in myriapods. By virtue of the fact that these regions in trilobites are lateral, they gained the name pleural lobes. Here, we use the term pleuron to mean a lateral extension of the segment, beyond a pleural furrow. These can be seen in the opisthosoma of basal chelicerates such as xiphosurans, chasmataspids and eurypterids (mesosoma). However, the lateral plates on the dorsal surface of arachnids such as ricinuleids and trigonotarbid are most likely divisions of the dorsal tergites, and not pleurites.

To test the relationship of *Houia* to other chelicerates, the phylogenetic analysis of Lamsdell (2013a) was expanded to include 67 more taxa and 101 new characters, resulting in a matrix comprising 215 characters coded for 104 taxa which can be found as a NEXUS file and a character list in supplementary information. The majority of these additions consist of arachnids, eurypterids and chasmataspidids, which are now represented by 40, 26 and eight taxa, respectively.

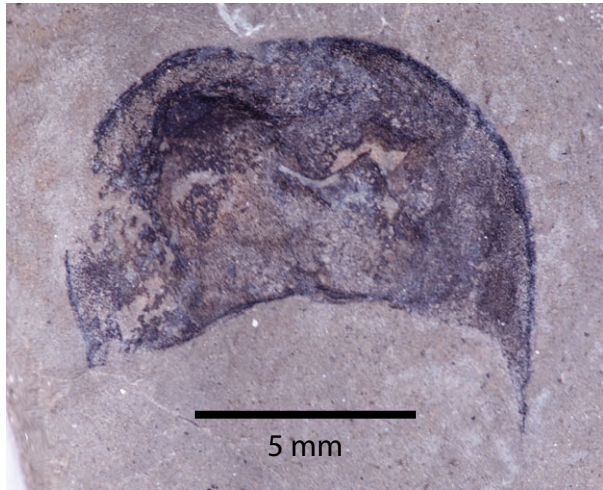


Fig. 3 *Houia yueya* gen. nov. NIGP161924 (isolated carapace). Photograph of specimen under ethanol.

Characters for these groups were largely derived from the analyses of Shultz (2007), Lamsdell *et al.* (2010) and Lamsdell & Selden (2013). Also, the synziphosurine taxa *Dibasterium durgae* and *Andarella parva* were included to afford a more comprehensive sampling of these stem euchelicerates. *Houia* was recorded for the analysis based on the new material presented here. No revisions have been made to previously coded taxa, with the exception of *Weinbergina opitzi*. Re-evaluation of this species suggests that the structure of the prosomal appendages may be more similar to those of *Dibasterium* and *Offacolus*, each limb being biramous with a potentially chelate endopod and a pediform exopod. Support for this interpretation stems from Fig. 6 of Stürmer & Bergström (1981) and Fig. 4 of Moore *et al.* (2005), which show the endopods curving ventrally on the specimen, while the supposed terminations of these limbs project outward from the carapace; these terminations may, in fact, represent the distal portions of the exopods, while the distal podomeres of the endopods have not been preserved. Fig. 7 of Stürmer & Bergström (1981) and Fig. 2 of Moore *et al.* (2005) also both show specimens with a series of potentially chelate appendages contracted and curving inwards on the prosoma while a second series of appendages more closely resembling the setiferous exopods of *Offacolus* and *Dibasterium* originate dorsally from the insertion point of the inwardly angling appendages and project outwards from the prosoma. It is possible that the first set of appendages represents the endopods, while the second set represents the exopods. Further study of *Weinbergina* will be required to ascertain the exact situation of the prosomal limbs, but it is worth noting that coding *Weinbergina* according to this revised interpretation results in no change to its position within the tree.

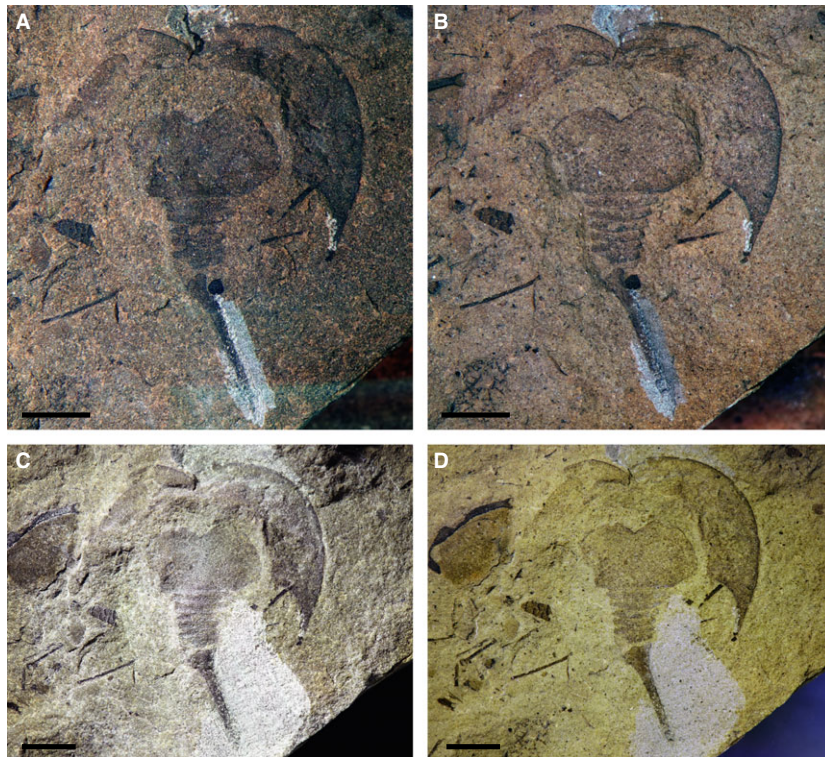


Fig. 4 A–D. *Houia yueya* gen. nov. NIGP161923, counterpart. —A. Photograph of specimen dry, before preparation. —B. Photograph of specimen under ethanol, before preparation. —C. Photograph of specimen dry, after preparation of right-hand side of telson. —D. Photograph of specimen under ethanol, after preparation of right-hand side of telson.

The analysis was performed using TNT (Goloboff *et al.* 2008) (made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by tree bisection–reconnection (TBR) branch swapping (the mult command in TNT) with 100 000 repetitions with all characters unordered and of equal weight. Jackknife (Farris *et al.* 1996), bootstrap (Felsenstein 1985) and bremer (Bremer 1994) support values were calculated in TNT, and the ensemble Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 3.02 (Maddison & 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. The analysis resulted in 12 mpts with a tree length of 660 steps, an ensemble Consistency Index of 0.475, an ensemble Retention Index of 0.835 and a Rescaled Consistency Index of 0.397.

Systematic palaeontology

Subphylum Chelicerata Heymons, 1901

Superclass Euchelicerata Weygoldt & Paulus, 1979

Genus Houia gen. nov. (Figs 1–5)

Type species. *Houia yueya* (Lamsdell *et al.*, 2013b).

Included species. Only the type species.

Etymology. From the Chinese 蟹 (hòu), meaning horseshoe crab.

Stratigraphical range and distribution. Devonian (Lochkovian) of China.

Material. NIGP161923 (part and counterpart) and NIGP161924 (part only, isolated carapace).

Emended diagnosis. Euchelicerate with large, subsemicircular carapace; bearing large ventral metastomal plate; lacking opisthosomal pleura.

Description

Carapace subsemicircular in outline, with nearly straight anterior margin, evenly curved lateral margins, posterior margin recurved medially, straightening, then curving gently, to genal angles laterally; genal angle produced into narrow, isosceles triangle (genal spine), clearly set off from posterior margin of carapace. Narrow doublure around anterior and lateral carapace margins. Ventral carapace anterior margin with marked, backward-pointing angle (as in *Limulus*). Pair of small, suboval eyes, each situated slightly less than one-third of carapace width (at that point) from lateral margin and two-fifths of distance from anterior

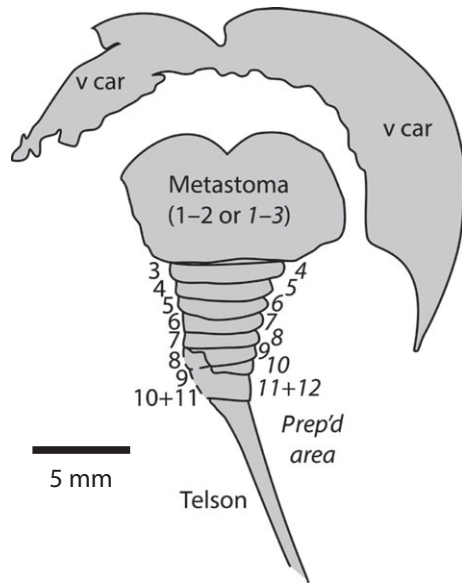


Fig. 5 *Houia yueya* gen. nov. NIGP161923, counterpart. Explanatory drawing. 1-12, inferred opisthosomal segments (italicized in alternative interpretation); v car, ventral carapace.

to posterior margin of carapace. Isolated carapace shows distinct, backward-pointing angle centrally placed, connecting laterally with gently inward-curving lines running to posterior margin, meeting margin at about one-third of width from lateral margins, outlining a median area. Dorsal cuticle minutely spiculate (Fig. 3). Ventral cuticle tuberculate (Fig. 4B), clearly seen on left and right sides of metastoma. Ventral metastoma nearly twice as wide as long, suboval in general outline, anterior margin with marked, backward-pointing, anterior angle, similar to that of ventral carapace margin. Ventral tergites 8 in number, lacking epimera, narrow gently and evenly from anterior to posterior, all about similar length. Telson narrows slightly, then straight, converging sides, presumably to pointed tip. Telson cuticle minutely spiculate (Fig. 1D).

Measurements of NIGP161923 (part and counterpart): carapace width 18.7, length (anterior margin to base of genal angle) 10.4; genal spine length 3.0, width at base 1.5; eyes approximately 1.2×1.0 ; metastoma width 10.0, length 5.4; opisthosomal tergite width (anteriormost to posteriormost) 4.8, 4.1, 3.6, 3.4, 3.2, 3.0, 2.6, 1.9, 1.3; lengths approximately 0.7; telson length >6.7 .

Measurements of NIGP161924 (isolated carapace): carapace width 12.5, length (anterior margin to base of genal angle) 18.1; genal spine length 2.8, width at base 1.0; approximate width of median area 6.0, length 4.8.

Remarks. The new specimens are clearly conspecific with *Kasibelinurus yueya*, which lies between the two specimens

described here in terms of size. The carapace is of a similar shape, and the opisthosoma (dorsal only preserved in the holotype) is similarly narrow and lacking pleura (they were originally interpreted as not preserved in the holotype (Lamsdell *et al.* 2013b)). However, the lack of opisthosomal pleura, which are prominent in *Kasibelinurus*, precludes its assignment to this genus, and so a new one is proposed.

Discussion

The number of body segments in *Houia* is equivocal, while the new specimens show that the elongated pretelson used by Lamsdell *et al.* (2013b) to assign the species to *Kasibelinurus* in fact represents two individual segments, it is unclear whether there are 11 or 12 tergites in total. This is because the large metastoma overlaps possibly two or three opisthosomal segments ventrally. Its identification as a metastoma is based on its position towards the posterior of the carapace, and the general morphology of the plate, with an overall rounded outline and angular anterior notch. An opercular affinity for the structure can be discounted as all genital opercula in xiphosurids, chasmataspidids and eurypterids are unfused medially and occur as separate left and right plates (Lamsdell 2011). Furthermore, the genital operculum is derived from the opisthosomal appendages and, as such, has a flattened anterior margin where the limbs insert into the body wall; a median notch, as seen in *Houia*, is present in all known metastomae but is unknown from any genital operculum. The presence of sternites posterior to the plate also indicates that the structure has not been displaced forwards. The large size of the metastoma is unusual for chelicerates; only the aberrant mycteropoids exhibit a plate similar in size (Waterston 1958), but even these do not encompass as much of the ventral prosomal structures as that in *Houia*. The shape of the metastoma is roughly similar to that in the Ordovician eurypterid *Megalograptus*, with curved lateral margins and a deep, broad anterior notch (Caster & Kjellesvig-Waering 1964). However, unlike *Megalograptus*, the metastoma in *Houia* has a straight posterior margin; a similar morphology is seen in mycteropoids, although they also exhibit a median posterior cleft that is absent in *Houia* (Lamsdell *et al.* 2009; Lamsdell 2013b).

The metastoma has been considered homologous to the fused chilaria of xiphosurids and the sternum of scorpions (Lamsdell 2013a). Chilaria represent the appendages of the first opisthosomal segment which have become incorporated within the prosoma, hence the intermediate position of the plate in *Houia*. As well as the median cleft exhibited in mycteropoids, a number of eurypterids show a median line, which suggests that the metastoma may be the result of fusion of paired structures. The metastoma may also exhibit a gnathobasic edge within the anterior notch which

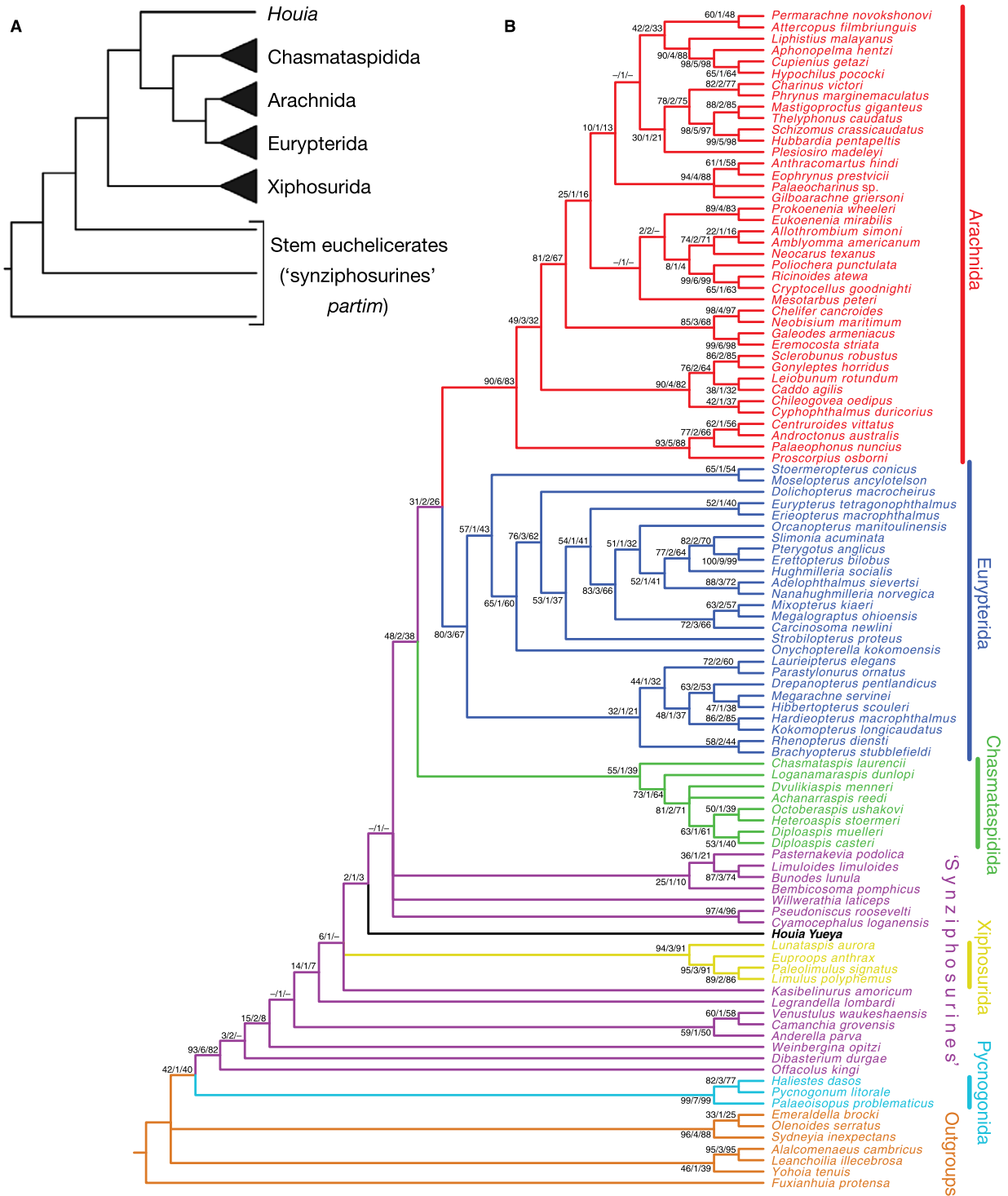


Fig. 6 Results of phylogenetic analysis. —A. Summary cladogram showing the position of *Houia* within Chelicerata. —B. Strict consensus of 12 mpts retrieved from analysing the data matrix of supplementary information. Branch supports are shown alongside the node in the following format: jackknife support/bremer support/bootstrap support. The composition of traditional chelicerate higher taxa is denoted by colour (online version); pycnogonids are shown in cyan, synziphosurines in purple, xiphosurids in yellow, chasmataspidids in green, eurypterids in blue and arachnids in red. All traditional higher taxa are shown to be monophyletic with the exception of synziphosurines. *Houia* is shown in black, with the taxon label in bold.

likely represents the remnants of the chilarial spines; the cuticular margin within the metastomal notch of *Houia* is heavily sclerotized, and it is possible that gnathobasic spines were also present in life. The metastoma consistently exhibits the same ornamentation as the body cuticle, and this is also true in *Houia*; it is possible that this ornamentation is derived from the setal hairs which cover the chilaria in xiphosurids; eurypterid scales have been shown to terminate in setal follicles (Caster & Kjellesvig-Waering 1964), and likely occur wherever setae are present on the external cuticle.

In eurypterids (and presumably chasmataspids), the metastoma aided in food mastication, forming the rear part of the oral cavity and supporting food while the teeth of the gnathobases broke it up, at the same time acting as a base about which the coxae of appendage VI could rotate (Selden 1981). It shares this latter function with the chilaria of xiphosurids, and it is likely that the metastoma of *Houia* also had a similar role. However, it is probable that the form of the metastoma in *Houia* is relatively derived because the lineage must have diverged from the dekatratan stem prior to the Middle Ordovician (Lamsdell *et al.* 2013a), so the ancestral form of the metastoma cannot be known with certainty. The enlargement of the plate in *Houia* could be linked to the width of the carapace, which is much broader than in any eurypterid or chasmataspid. The metastoma may have also had a more direct role in feeding than in eurypterids. Eurypterids show a marked enlargement of the gnathobasic teeth, with those of the sixth appendage being particularly robust, but in xiphosurans these teeth are less pronounced, and the thickened and enlarged metastoma of *Houia* may have acted to crush harder prey.

Phylogenetic analysis has suggested that xiphosurans, as traditionally defined, were not monophyletic (Lamsdell 2013a), instead retrieving a number of synziphosurines as stem euchelicerates, while bunodids and pseudoniscids appear to show closer affinities to eurypterids, arachnids and chasmataspids (Dekatriata). A subsequent phylogenetic analysis failed to retrieve the same exact relationships (Legg 2014) and appeared to treat the chilaria and metastoma as non-homologous (but no data matrix was provided). Our phylogenetic analysis retains the majority of synziphosurines as a paraphyletic lineage of stem euchelicerates, while bunodids, pseudoniscids and *Houia* resolve as intermediate between xiphosurids and Dekatriata (Fig. 6). The ventral morphology of *Houia* provides a clear link to Dekatriata irrespective of chilarial/metastomal homology.

Thus, *Houia yueya* exhibits a unique combination of xiphosurid and eurypterid characteristics. The dorsal carapace and ventral doublure are typically xiphosurid in form, yet the lack of opisthosomal pleura and the possession of a

metastoma are observed only in eurypterids, chasmataspids and scorpions. The large size of the metastoma and the stratigraphic age of *Houia* indicate that it branched from the main euchelicerate lineage prior to the divergence of the dekatratan clades. Together with the bunodids and pseudoniscids, *Houia* provides evidence for basal dekatratan persisting into the middle Palaeozoic alongside eurypterids and arachnids and that the morphological diversity of these basal forms was greater than previously thought. Anderson (1996) suggested that the sudden appearance of weinberginid synziphosurines (which retain an extreme number of plesiomorphic morphological features) during the early Devonian was due to their radiation from a Gondwanan refuge. *Houia* confirms that derivatives of the euchelicerate stem lineage were present on the satellite palaeocontinents surrounding Gondwana during the time period. The prevalence of relict populations of plesiomorphic euchelicerates among the Gondwanan continents may suggest that the group has its origins in Gondwana (Lamsdell *et al.* 2013a), a possibility further supported by the occurrence of some of the clade's earliest representatives on the continent during the Ordovician (Van Roy *et al.* 2010).

Acknowledgements

We thank Dave Burnham (University of Kansas Natural History Museum, Division of Vertebrate Paleontology) for the use of preparatory equipment, and Huang Diying (NIGP) for accessioning the specimens to the Nanjing Institute of Geology and Palaeontology collections.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. NEXUS file.

Data S2. Character list.