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Review

Reconciling morphology with phylogenomics in Chelicerata (Arthropoda)

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ABSTRACT

Whereas traditional morphology-based analyses have most often recovered horseshoe crabs as early branching chelicerates, nearly all phylogenomic analyses instead place this lineage as nested within Arachnida. Although this repositioning is not yet widely accepted, it resolves several important problems: (i) the placement of sea spiders (Pycnogonida) among fossil taxa; (ii) the questionable status of *Mollisonia* and *Sanctacaris* as chelicerates (herein rejected); (iii) the absence of any convincing crown group chelicerates from the Cambrian, whereas large-bodied and well armoured taxa are abundant in Ordovician deposits. The earliest chelicerates are hypothesized to have been minute-bodied inhabitants of interstices, hence their absence from the Cambrian fossil record. Tagmosis is also questioned as a useful concept for Chelicerata because the two main defining features of tagmata, somitic consolidation and the evolution of specialized functions in different body regions, are uncoupled in this lineage. A prosomal head is potentially a synapomorphy that unites only a portion of arachnids, including horseshoe crabs.

Keywords: Arachnida; head; horseshoe crabs; prosoma; tagmosis; Xiphosura

INTRODUCTION

In recent years, the early evolution of Chelicerata, one of the two main extant lineages of arthropods (the other is Mandibulata), has become controversial. It is traditionally held that Xiphosura (horseshoe crabs) form the sister group to a monophyletic Arachnida, with extinct groups like Eurypterida placed in between them. The morphologically aberrant sea spiders (Pycnogonida) are understood to be the sister group to the remaining chelicerates. Whereas most morphological analyses have placed horseshoe crabs (Xiphosura) outside Arachnida and as one of the early branches of Chelicerata (Wheeler and Hayashi 1998, Weygoldt and Paulus 1979, Legg 2014), the vast majority of phylogenomic analyses have instead recovered this lineage as nested within Arachnida (Sharma *et al.* 2014, Ballesteros *et al.* 2019, 2022, Ballesteros and Sharma 2019, Ontano *et al.* 2022). Earlier Sanger sequencing studies also recovered a derived position (Wheeler and Hayashi 1998, Giribet *et al.* 2001, Mastra *et al.* 2010, Pepato *et al.* 2010). Despite the now strong support for Xiphosura as nested within Arachnida (Sharma *et al.* 2021, Ballesteros *et al.* 2022), a number of authors still hold to the traditional hypothesis that Xiphosura and scorpions are early branching (Aria 2022, Lustri *et al.* 2023, 2024, Palacios *et al.* 2026, Strausfeld *et al.* 2025), partly because of the discrepancy with morphological analyses and partly because of the difficulty of reconciling the early appearance of Xiphosura and Scorpiones in the fossil record (from Ordovician and Silurian deposits, respectively) with a late-branching position (Aria 2022).

Closing the gap between fossils and molecules requires a reassessment of major morphological character systems whose evolutionary transformation series were predicated on the assumption that Xiphosura falls outside Arachnida. The major feature of the chelicerate Bauplan, which also defines the subphylum, is the division of the somites into two tagmata: the prosoma and the opisthosoma. The provisional definition of the prosoma is an anterior group of somites that bears feeding, sensory, and/or locomotory appendages, i.e. all the limb-bearing somites. The prosoma is generally considered to represent the consolidation of these somites into one tagma (but see below), so that the tergites are visibly

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fused. Because the consolidation of the first five or six somites is treated as a 'head' (or cephalon) in many stem-group arthropods, the prosoma is often recognized as the expansion of the head to include more posterior somites (Aria and Caron 2017, 2019). The opisthosoma, in turn, is composed of a posterior group of segments and (if present) reduced or specialized appendage derivatives such as respiratory organs, mechanoreceptory appendages, gonopores, and (in spiders) spinnerets. A second trait of significance is the chelicera, the anterior-most appendage of the chelicerates, which is ancestrally chelate (subchelate or jack-knife shaped in pantetrapulmonates) and composed of two to four articles in extant groups.

THE PROSOMA

The relocation of Xiphosura to a nested position within Arachnida solves the important problem of the uncertain placement of Pycnogonida (sea spiders) among fossil taxa, including putative chelicerates from Cambrian deposits. In a number of recent morphological analyses aimed at placing these fossil taxa, pycnogonids have been excluded because they are considered to have an incongruent combination of characters (Aria and Caron 2017, 2019, O'Flynn *et al.* 2023, Lustri *et al.* 2024). The pycnogonid head is formed from the consolidation of the first five somites (0 and I–IV): ocular (0), cheliceral (I), palpal (II), ovigeral (III), and first walking leg (IV) (Fig. 1A) (Dunlop and Lamsdell 2017, Petrova and Bogomolova 2025). This five-somite head formation may be symplesiomorphic with Megacheira and Artiopoda, which would suggest pycnogonids are the earliest branching chelicerates (Aria and Caron 2017). On the other hand, pycnogonids have uniramous limbs, which potentially indicates a more derived position (Aria and Caron 2017). This is because the biramous limbs of Offacolidae (including *Dibasterium* and *Offacolus*) and two putative chelicerate taxa, Habeliida (including *Sanctacaris*) and *Mollisonia*, are thought to be plesiomorphic (Aria and Caron 2017, 2019, Garwood and Dunlop 2023). In these biramous limbed taxa, the five-somite head has expanded to be seven or eight somites owing to consolidation with more posterior somites, up to somite VII (Dunlop and Lamsdell 2017). This interpretation of the biramous condition as being necessarily plesiomorphic is therefore consistent with the traditional hypothesis that a consolidated prosoma (prosomal head) is a synapomorphy uniting all chelicerates or at least all euchelicerates (all chelicerates except Pycnogonida). Accordingly, it has been suggested that Pycnogonida reverted back to a five-somite head (Aria and Caron 2017), but the case that has been made for this appears to rest entirely on an Ordovician fossil species assigned to Pycnogonida (Rudkin *et al.* 2013). This diagnosis is questionable (Sharma and Gavish-Regev 2025), and this species has been interpreted as having had a six-somite head (five limb bearing segments) (Rudkin *et al.* 2013) rather than a prosomal head.

The prosomal head of the Cambrian fossil taxa Habeliida and *Mollisonia* has been used to support their diagnosis as chelicerates

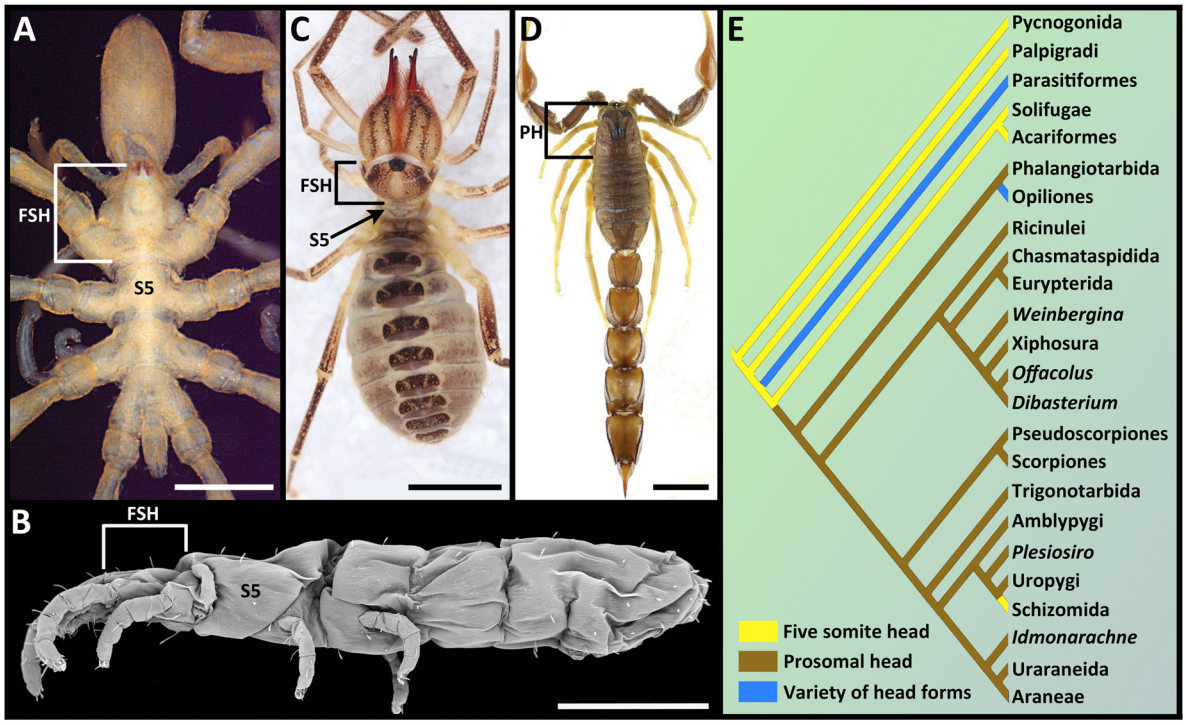

Figure 1. The head forms of chelicerates. A, Pycnogonida (*Ammothella biunguiculata* (Dohrn)) sourced from Lehmann *et al.* (2014) under the creative commons license (scale bar: 0.5 mm). B, Acariformes (*Proteonematalycus wagneri* Kethley, 1989) sourced from Bolton (2022) under the creative commons license (scale bar: 0.1 mm). C, Solifugae (*Karschia shigatse* Fan, Zhang and Zhang, 2024) sourced from Fan *et al.* (2024) under the creative commons license (scale bar: 5 mm). D, Scorpiones (*Androctonus tihamicus* Alqahtani, Yağmur and Badry, 2023) sourced from Alqahtani *et al.* (2023) under the creative commons license (scale bar 10 mm). E, maximum likelihood tree from a total evidence (morphological data and 152 slowly evolving genes) analysis of taxa (Ballesteros *et al.* 2022). Merostomata: Chasmataspidida, Eurypterida, Weinbergina, Xiphosura, *Offacolus*, *Dibasterium*. Arachnopulmonata: Pseudoscorpiones, Scorpiones, Trigonotarbida, Amblypygi, *Plesiosiro*, Uropygi, Schizomida, *Idmonarachne*, Uraraneida, Araneae. Branches colour coded (see legend) for head form. Abbreviations: FSH, five somite head (0 and I–IV); PH, prosomal head (0 and I–VI); S5, somite V.

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(Legg 2014, Aria and Caron 2017, 2019). When Pycnogonida are included in morphological analyses, their five somite head most often places them in an earlier branching position, causing Habeliida and *Mollisonia* to be recovered as crown-group chelicerates (Legg 2014, Aria and Caron 2017, 2019). However, repositioning Xiphosura to be in a clade with Arachnopulmonata (Tetrapulmonata, Scorpiones, etc.), in accordance with most phylogenomic analyses, causes Habeliida and *Mollisonia* to be pulled into a highly derived position (Supporting Information, Files S1–S3). This is incompatible with a Cambrian association, weakening the case for their placement within crown-group Chelicerata. This placement was already considered tentative because these two taxa lack convincing evidence for chelicerae or proto-book gills (Bousfield 1995, Budd 2021). Furthermore, the pygidial structure in *Mollisonia* bears a close resemblance to that in Trilobita, which is potential evidence of a closer affiliation with Artiopoda than Chelicerata (Lerosey-Aubril *et al.* 2020).

It has also recently been hypothesized that *Mollisonia* belongs within Arachnida (Strausfeld *et al.* 2025), but the phylogenetic analysis supporting this placement was heavily based on a very narrow selection of characters (mostly neuroanatomical). This analysis also failed to support the monophyly of Tetrapulmonata, one of the most strongly supported clades in both morphological (Garwood and Dunlop 2014) and molecular analyses (Ballesteros *et al.* 2019, 2022). The case for moving *Mollisonia* into Arachnida therefore seems weak (see also Bolton *et al.* 2026).

Xiphosura belongs within the broader group Merostomata, which includes Eurypterida (sea scorpions), Chasmataspidida, and Synziphosurina. Total evidence analyses (molecular and morphological data) recover all of Merostomata within Arachnida (Ballesteros *et al.* 2022) (Fig. 1E), so that fossil Merostomata are pulled into Arachnida with Xiphosura. This also happens when a molecular-based partial constraint for a clade including Xiphosura and Arachnopulmonata is added to a morphological analysis of fossil taxa that was originally constrained to place Xiphosura outside Arachnida (Aria and Caron 2019) (Supporting Information, Files S1–S3). With Merostomata nested within Arachnida, Pycnogonida is no longer a problematic taxon. All crown-group chelicerates outside of Merostomata have uniramous limbs, and pycnogonids share a five-somite head with several other early branching chelicerate taxa (Fig. 1E), namely Acariformes, Solifugae, and Palpigradi (Dunlop and Lamsdell 2017, Bolton 2022). Note that Pycnogonida was not a problem taxon in an earlier analysis of fossil taxa that excluded Habeliida and *Mollisonia* (Cotton and Braddy 2003). Moreover, the idea that a five-somite head may be plesiomorphic to arachnids is not new and it was previously hypothesized that the sejugal furrow in Acariformes and Solifugae delimits a plesiomorphic margin between a five-somite head and somite V (Dunlop *et al.* 2012). Accordingly, the division of the dorsum of the prosomal region in Solifugae and Palpigradi into a propeltidium (somites 0 and I–IV), mesopeltidium (somite V), and metapeltidium (somite VI) may represent no more than the retention of the ancestral state. Under this reconstruction, the mesopeltidium and metapeltidium would represent tergites that have remained part of the trunk rather than having ever consolidated with the head (Fig. 1). The nested placement of Merostomata close to Arachnopulmonata would then be supported by the consolidation of all the prosomal (limb-bearing) somites.

In Arachnopulmonata and Merostomata, one or more somites behind the prosomal region (somites VII onwards) have undergone narrowing (Dunlop and Lamsdell 2017), allowing the trunk to articulate against the expanded head. In two early branching chelicerate taxa (i.e. taxa that fall outside the large Merostomata-Arachnopulmonata clade in Fig. 1E), Solifugae and Palpigradi, the manoeuvrability of the trunk is conferred by the narrowing of somites V and VI in addition to subsequent segments (Fig. 1C). A Solifugae-Palpigradi clade has been recovered in phylogenomic analyses (Ballesteros *et al.* 2019, 2022), and these two taxa are also united by the architecture of the coxal glands (Ballesteros *et al.* 2019).

There are various states of somitic consolidation in Opiliones and Parasitiformes (Evans 1992, Pinto-da-Rocha *et al.* 2007, Klompen *et al.* 2015). Opilioacarida (Parasitiformes) has a six somite head (Klompen *et al.* 2015), whereas in many mesostigmatid taxa the entire body is consolidated, with no visible trace of a head tagma (Evans 1992). The whole body can be consolidated in several acariform taxa, so that a head tagma is weakly if at all discernible, but most taxa (including early branching taxa) have a distinct sejugal furrow (Dunlop *et al.* 2012). Although there are various states of consolidation in Opiliones, Phalangiotarbida—recovered as sister to Opiliones in total evidence analyses (Ballesteros *et al.* 2022)—appear to exhibit a prosomal head (Pollitt *et al.* 2003). Therefore, the ancestral state of Opiliones may be a prosomal head, but this is contingent upon an uncertain sister relationship with Phalangiotarbida.

Based on this distribution of head forms among chelicerates, total evidence analyses recover the prosomal head as a synapomorphy that unites a clade comprising Phalangiotarbida, Opiliones (lost or elaborated to additional somites in many members), Ricinulei, Arachnopulmonata (lost in Schizomida), and Merostomata (Fig. 1E), whereas the five-somite head of Pycnogonida, Acariformes, Solifugae, and Palpigradi is potentially symplesiomorphic with Megacheira, which are often interpreted as all having a five-somite head (Dunlop 2005, Dunlop *et al.* 2012, Dunlop and Lamsdell 2017). However, in a recent study, some megacheirans have been interpreted as having a six-somite head, which is thought to represent the plesiomorphic state for this group because of its occurrence in earlier branching taxa (O'Flynn *et al.* 2023). Megacheirans are commonly hypothesized to be paraphyletic to Chelicerata (Chen *et al.* 2004, Dunlop 2005), and a phylogenetic analysis has already recovered this result (Cotton and Braddy 2003). Therefore, a five-somite head may unite one or more sublineages of Megacheira with Chelicerata. If a five-somite head is plesiomorphic to chelicerates, this would further undermine the case that has been made for Habeliida or *Mollisonia* representing stem chelicerates based on the possession of a prosomal head (seven or eight somites), which could have evolved independently in these taxa.

A close relationship between Megacheira and Chelicerata has been inferred from the shared presence of a reduced labrum (Liu *et al.* 2020) and raptorial deutocerebral (somite I) appendages (Chen *et al.* 2004). Some doubt has been raised about the deutocerebral association of the raptorial 'great appendages' in Megacheira (Budd 2021), but the repositioning of *Mollisonia* to be further from Chelicerata strengthens the case for this homology because a close relationship between Megacheira and Chelicerata is supported by several very conserved characters pertaining

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to neuroanatomical organization (Ortega-Hernández *et al.* 2022). Moreover, based on the phylogenetic affinity of megacheirans with early branching euarthropods, large frontal appendages are likely to be associated with the deutocerebrum in many stem-group arthropods, including Radiodonta (O'Flynn *et al.* 2023), and the alternative hypothesis that the appendages of radiodonts are protocerebral is inconsistent with observations on neuroanatomy (Moysiuk and Caron 2022).

The derived position of Merostomata (including Offacolidae) may seem problematic because it means that biramous limbs and gnathobases must have independently re-evolved after being lost (Howard *et al.* 2020, Garwood and Dunlop 2023) if they did not persist as cryptic homologues. But this is not unrealistic or without precedent. Appendages, including their exites and endites, are among the most evolutionarily plastic structures across all of Arthropoda (Wills *et al.* 1998, Liu *et al.* 2021), as demonstrated by the evolution of wings, gin traps, armature (e.g. treehopper helmets), and larval tracheal gills in insects (Clark-Hachtel *et al.* 2013, Linz and Tomoyasu 2018, Hu *et al.* 2019, Bruce and Patel 2020, Fisher *et al.* 2020, Prokop *et al.* 2022), and also by the tremendous variety of different mouthpart morphologies across arthropods (Labandeira 1997, Pavlopoulos *et al.* 2009). In morphology-based analyses, the homoplasy of various appendicular characters, among others, may have caused long branch attraction between Merostomata and the putative chelicerates Habeliida and *Mollisonia*. This is certainly consistent with the heavy and selective use of molecular based constraints used in several analyses to reach what are subjectively deemed sensible results (Aria and Caron 2017, 2019, Lustri *et al.* 2024).

THE PROBLEM WITH TAGMOSIS IN CHELICERATES

The nested position of Merostomata within Arachnida has important implications with respect to tagmosis. Tagmata are distinct body regions, usually discernible via morphological boundaries, comprising somites with the same general form and function, e.g. feeding, locomotion and respiration (Chipman 2025). Therefore, a case can be made that there are two main defining components to tagmata: (i) shared form and function of constituent somites, including their associated appendages; (ii) consolidation of somitic regions, resulting in visible boundaries where articulations either remain or have become more pronounced (e.g. the division between the head and thorax in insects). An early branching Merostomata, outside of Arachnida, accommodates the origin of tagmosis in Chelicerata via the evolution of this combination of features. Accordingly, prosomal-opisthosomal tagmosis would either have united Euchelicerata (Merostomata + Arachnida) or all of Chelicerata if extant pycnogonids represented a reversion to a five-somite head (Aria and Caron 2017). For this reason, the proterosoma in Solifugae, Acariformes, and Palpigradi has been viewed not as a primitive five-somite head but as the anterior part of a subdivided prosoma (Gainett *et al.* 2024). However, by recovering a prosomal head (i.e. consolidation of the limb bearing somites) as nested within Arachnida (see above), phylogenomic analyses instead suggest that the two main defining features of tagmosis are uncoupled. The number of somites that have consolidated into a head can vary independently of the number of appendages or their form and function. For example, the reduction of the limb-bearing somites to only six in Arachnida (Megacheira and Pycnogonida possess a larger number) did not co-evolve with a change in the number of head somites, which remained at five.

The uncoupling of somitic consolidation with the presence, form, and function of appendages has been evident for some time (Dunlop and Lamsdell 2017). In order to accommodate this discrepancy, prosomal-opisthosomal tagmosis has sometimes been more or less exclusively defined by the latter, so that articulations and consolidations that diverge from a prosomal head are viewed as pseudotagmata (Lamsdell 2013, Dunlop and Lamsdell 2017). However, in this representation of tagmosis, the prosoma is treated as the entire limb-bearing region despite differences among appendages in form (chelicerae, palps, and legs) and function (feeding and locomotion) (Dunlop and Lamsdell 2017). Following the same treatment, in which consolidation and articulation are ignored, insects have a single anterior tagma (much like a prosoma) formed from the head and thorax. The other problem with this treatment is that the number of prosomal limbs (and therefore the prosomal-opisthosomal boundary) is not fixed (e.g. *Weinbergina* has seven rather than six pairs of limbs).

Furthermore, this modified representation of tagmosis has not diminished the central and overemphasized role that somitic consolidation has played in diagnosing taxa as putative chelicerates. The consolidation of seven to eight somites (with six to seven limb-bearing segments) into a prosomal head is a key diagnostic trait for Chelicerata (Legg 2014, Aria and Caron 2017, 2019). Therefore, the recovery of a prosomal head as apomorphic within Arachnida is not compatible with one of the main characters that has been used to diagnose *Mollisonia* and Habeliida as early branching chelicerates.

But note that if prosomal-opisthosomal tagmosis were instead exclusively defined through consolidations and articulations along the body, this would also be problematic because tagmosis is seldom, if ever, represented this way rather than as the division of the body into functional units (Chipman 2025). The expansion of the five-somite head to form a prosomal head in a subset of arachnids (Fig. 1E), in which all limb-bearing somites are consolidated, appears to have had no effect on the associated appendages (legs III and IV), which have retained both their form and function. Therefore, the concept of tagmosis, at least in how it is generally discussed in relation to other arthropod taxa, especially insects, does not provide a very useful way to characterize the body of chelicerates.

INTERSTITIAL ORIGIN

One of the main arguments against the acceptance of the nested position of Merostomata within Arachnida is that this result seems irreconcilable with the fossil record (Aria 2022). But this apparent discrepancy may only be because the fossil record is heavily biased towards large-bodied and well armoured arthropods. The earliest crown group chelicerates may be undetectable in the fossil record if they were minute (< 3.00 mm long) and also in an unsuitable environment for fossilization, paralleling the absence of fossils documenting the remipede-insect transition (Schwentner *et al.* 2017). In the most taxonomically comprehensive phylogenomic analyses (Ballesteros *et al.* 2022, Ontano *et al.* 2022), lineages that are predominantly or exclusively minute-bodied (Acariformes,

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Parasitiformes, and Palpigradi) are consistently clustered near the root of Chelicerata. Although Pseudoscorpiones are minute-bodied and sometimes recovered as an early branching lineage, a whole genome duplication strongly suggests that they instead belong within Arachnopulmonata (Ballesteros *et al.* 2022). The earliest branching lineage of Pycnogonida, Austrodecidae, is also minute-bodied, and despite its marine habitat, efforts to estimate the divergence timing of Pycnogonida have concluded that numerous ghost lineages must be present in the crown group to explain the stratigraphic distribution of sea spider fossils (Ballesteros *et al.* 2021, Nava *et al.* 2025).

This phylogenetic arrangement of micro-bodied chelicerates is compatible with the origin of chelicerates in interstices. Many members of two early branching lineages, Palpigradi and Acariformes, are known to inhabit the interstices of terrestrial sands, including beaches (van der Hammen 1977, McDaniel and Bolen 1981, André *et al.* 1994, Russell and Alberti 2010, Bolton *et al.* 2015), and it has long been hypothesized that these lineages followed an interstitial pathway onto land via sand (Monniot 1966, van der Hammen 1977, Walter and Proctor 1999). Early branching members of Acariformes [Endeostigmata *sensu* Walter *et al.* (2011)], including Nanorchestidae and Nematalycidae, are extremely abundant in sands (André *et al.* 1994, Russell and Alberti 2010, Bolton *et al.* 2015). Palpigradi provide a slightly less convincing case for an interstitial pathway onto land because they are more often recovered from caves. However, Prokoeneniidae, the sister group to the larger family Eukoneniidae (Giribet *et al.* 2014), has been recovered from soil (Silvestri 1913), and it should be noted sands are rarely sampled because technically complex flotation techniques are usually needed to efficiently extract microarthropods (André *et al.* 1994). It is possible that denser phylogenetic sampling of Prokoeneniidae or Eukoneniidae, together with intensive investigation of palpigrade ecology, may point to sand as the ancestral habitat of Palpigradi.

The derived position of Merostomata strongly suggests that arachnids underwent multiple terrestrialization events (Sharma *et al.* 2021); the alternative hypothesis that Merostomata radiated after a return to water is unlikely because of their relatively early appearance in the fossil record (Tihelka *et al.* 2022). In either case, a complex history of chelicerate terrestrialization is already substantiated by molecular phylogenetic studies of water mites (Pepato *et al.* 2022), as well as the incidence of Devonian scorpion fossils with external and filamentous gills (Poschmann *et al.* 2008), which are either interpreted as a secondary recolonization of aquatic habitats or the persistence of a gilled scorpion stem group.

A scenario of multiple land colonizations is easier to explain if several of these terrestrializations arose via an interstitial pathway (Fig. 2), accommodating a physiologically simple route to land. Minute body size permits the loss of gills, so that the basic mode of respiratory exchange is the same on land and in water, via diffusion across the integument, as exemplified by all extant pycnogonids. Tracheae (notably absent in Palpigradi and most lineages of Endeostigmata) are a later adaptation for body enlargement rather than terrestrialization. An interstitial pathway also allows for a gradual transition to land owing to the porosity and associated capillary action of sand (the pores of finer sediments are too small to accommodate microarthropods), which results in damp zones, thus intermediate humidity, between water-filled and dry macropores (Little 1990).

Minute body size and the inhabitation of a coarse-grained mineral matrix such as sand would have greatly reduced the likelihood of fossilization, especially because sand is a high-oxygen and high-energy depositional environment that hinders delicate preservation. Meiobenthic metazoan lineages are known to be largely absent from the fossil record (Harvey and Butterfield 2017), although trace fossils are known from finer-grained sediments (Löhr and Kennedy 2015). The coarse-grained matrix of sand (the medium for interstitial terrestrialization) even precludes the formation of trace fossils. Cambrian fossils of any form have yet to be found that can be confidently assigned to crown-group Chelicerata. Although a Cambrian fossil has been hypothesized to be the larval stage of a pycnogonid (Waloszek and Dunlop 2002), this is far from a certain assignment (Sharma and Gavish-Regev 2025). And if the earliest chelicerates exclusively moved within the interstices of sands

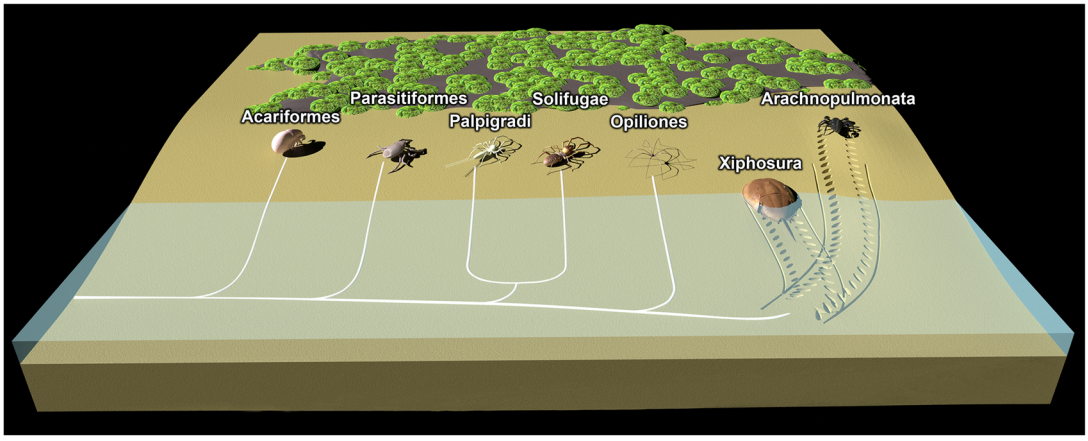

Figure 2. A scenic and simplified version of a tree produced from maximum likelihood analysis of the 152 most slowly evolving loci, with morphological data excluded (Ballesteros *et al.* 2022). White ducting represents the hypothesized interstitial pathway of early branching arachnids onto land, whereas the starting point of the locomotory tracks represents a switch to an epibenthic lifestyle in larger bodied arachnids (including Merostomata), based on the presence of book gills or book lungs. Early branching arachnids likely remained in terrestrial interstices for a long period, hence their late appearance (post-Silurian) in the fossil record.

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rather than burrowing through muds, convincing chelicerates may never be recovered from the Cambrian fossil record.

The appearance of Merostomata in the Ordovician fossil record, which is before any early branching chelicerates, is most easily explained by an early exit from interstices, leading to an enlarged body, made possible through the evolution of book gills. Earlier branching chelicerates appear to have remained in interstices longer, both on land and in the ocean (Garwood and Dunlop 2023) (Fig. 2). For example, the earliest known fossil that can be feasibly assigned to Solifugae dates to the Carboniferous (Dunlop & Rössler 2003), which is much later than various lineages within the Merostomata-Arachnopulmonata clade. The earliest unambiguous record of Pycnogonida, the most deeply rooted crown-group chelicerate, dates to the Silurian (Siveter *et al.* 2004, Sharma and Gavish-Regev 2025).

MAKING PEACE WITH HOMOPLASY IN MORPHOLOGICAL DATA

The principal challenge of reconciling morphology with phylogenomics in chelicerate biology is accepting that a swathe of morphological traits must be rendered homoplastic under any phylogenomic hypothesis. For example, the placement of scorpions within Arachnopulmonata renders the stomotheca (preoral chamber formed of fused coxapophyses) of Scorpiones and Opiliones—long held to be sister groups on the basis of this putative complex character—as homoplastic (Sharma *et al.* 2014, Ballesteros *et al.* 2019, Ballesteros and Sharma 2019). A suite of eight traits drawn from seemingly independently evolving character systems that are shared by Solifugae and Pseudoscorpiones were similarly rendered homoplastic when pseudoscorpions were established as members of the arachnopulmonates (Ontano *et al.* 2021, Gainett *et al.* 2024). Indeed, no obvious and unreversed morphological synapomorphy unites Arachnopulmonata as it is currently defined, and even book lungs are not present throughout this lineage based on their loss in Pseudoscorpiones and miniaturized spiders (e.g. Symphytognathoidea).

An examination of possible phylogenomic tree topologies suggests that this trend is bound to continue as more branches in the chelicerate tree of life are resolved. As an example, four traits—the presence of a chelate pedipalp (found in Xiphosura, non-spider arachnopulmonates, and Ricinulei), a sperm cell with a coiled flagellum (Tetrapulmonata, Pseudoscorpiones, and Ricinulei, but not scorpions), aflagellate sperm (Acariformes, Parasitiformes, Solifuges, Palpigradi, and Opiliones), and a hexapodous larva (Acariformes, Parasitiformes, and Ricinulei)—all appear to be phylogenetically informative and lend themselves to clear and reliable discretization for character state coding. Yet some subset of these four traits must exhibit homoplastic evolution, as they cannot define compatible taxon subsets. The chelicerate literature is filled with morphological trait distributions that follow this pattern.

Even characters thought to be invariant across much of Chelicerata may turn out to be somewhat homoplastic. An example is provided by the synganglion, which was recently represented by Strausfeld *et al.* (2025) as recurved throughout Arachnida. Accordingly, the more linear arrangement of the synganglion in Xiphosura is treated as support for a traditional early branching placement outside of Arachnida. However, the plesiomorphic shape of the synganglion in chelicerates may not be linear but instead upwardly curved, based on the latter form being present in Pycnogonida (Frankowski *et al.* 2022) and also Mandibulata (Kenning and Harzsch 2013). Upward curvature is also present in many arachnids (Fig. 3A); not all of them have a recurved synganglion (Bolton *et al.* 2026). The modification of Xiphosura to a linear arrangement can be reconciled with a highly modified head morphology. The foregut in this taxon is U-shaped, so that the oesophagus runs anteriorly rather than posteriorly (Fig. 3B). The plesiomorphic position of the mouth is anterior in Arthropoda, which is the state in most chelicerates, including pycnogonids. Xiphosura therefore represent a dramatic divergence from this morphology because the anterior appendages (palps and chelicerae) and mouth have migrated to the venter of the body. The mouth has migrated so far back as to be between the leg coxae, which would appear to explain the re-evolution of gnathobases. Because of their ventral location, the chelicerae are dorsoventrally aligned with the other appendages rather than being in a more

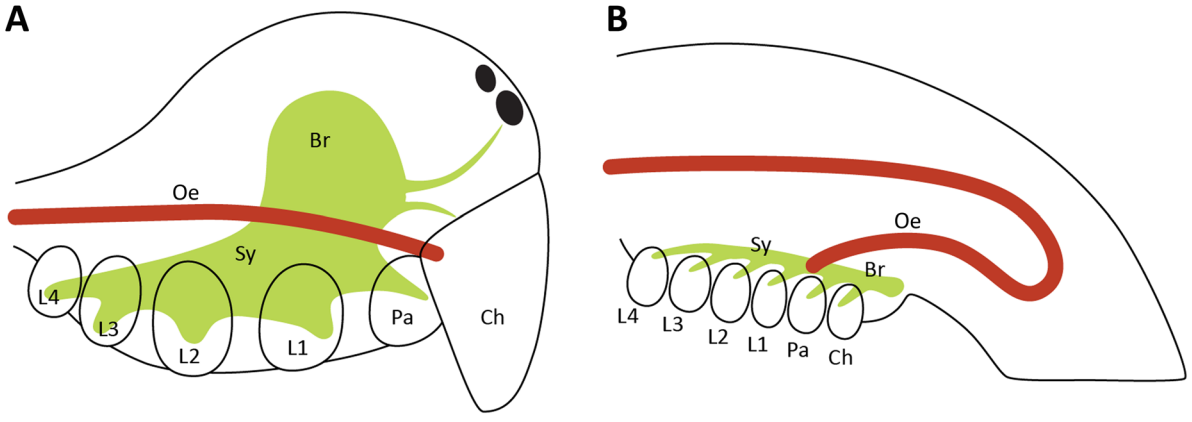

Figure 3. Schematic representations of the gut and synganglion in the prosomal head. A, Araneae, based on Propistsova *et al.* (2023: fig. 5C). B, Xiphosura, based on Roorda *et al.* (2020: fig. 5). In arthropods the gut always runs through the synganglion, at the ventral or posterior part of the brain. Neuromeres are close to their appendages. Changes in the positions of the appendages can therefore dramatically alter the arrangement of the head region. Abbreviations: Br, brain (protocerebrum, deutocerebrum and tritocerebrum); Ch, chelicera; Oe, oesophagus; L1, leg I; L2, leg II; L3, leg III; L4, leg IV; Pa, palp; Sy, synganglion (the entire green area).

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dorsal position. Accordingly, the synganglion, which often closely follows the positions of the appendages, has become more linear.

Xiphosura therefore has a head morphology that is very different from early branching chelicerates, including Pycnogonida and all megacheirans, in which the mouth has remained in an anterior position (Liu *et al.* 2020). Based on the U-shaped foregut, the mouth must have previously been anterior in position and the synganglion could have originally bent upwards, accommodating the dorsal position of the chelicerae. The shape of the synganglion in Xiphosura can therefore be explained through the dramatic rearrangement of the head rather than as a plesiomorphy that places it outside Arachnida.

The downstream implication of high levels of homoplasy in chelicerate morphological matrices is that numerous morphological character systems may not be reliable readouts of phylogenetic placement, or may not be informative within certain temporal windows. Reconciling the gap between structure and sequence requires measured reconsideration of long-held premises, including relaxing long-held assumptions about which characters (and character systems) are phylogenetically informative (Gainett *et al.* 2024), re-examining historically defined putative synapomorphies with fresh eyes (Bolton 2025), and accepting that some nodes may never be defined by unambiguous and unreversed morphological traits (e.g. the sister group relationship of Remipedia + Hexapoda, Chaetopteridae + Sipuncula, or Myriazoa), even in a fossil- and character-rich taxon such as Arthropoda.

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SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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