
Supplementary information

A chelicera-bearing arthropod reveals the Cambrian origin of chelicerates

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A chelicera-bearing arthropod reveals the Cambrian origin of chelicerates

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SUPPLEMENTARY NOTE 1: THE ELUSIVE CAMBRIAN FOSSIL RECORD OF CHELICERAE-BEARING ARTHROPODS

The hypothesis that the Cambrian oceans were home to arthropods with chelicerae *sensu stricto* (i.e., uniramous, unichelate deutocerebral appendages) has gained wide acceptance over time (e.g.^{68,69}). This assumption finds apparent support from molecular timetrees estimating that pycnogonids and euchelicerates had diverged by the end of the Cambrian (53,70–73). These results are not surprising though, as most of these timetrees were calibrated using Cambrian fossils with presumed chelicerate affinities. For example, Lozano-Fernandez et al.⁵³ and Benavides et al.⁷³, following Wolfe et al.⁷⁴, used the early Cambrian *Wisangocaris barbarahardyae* as the oldest occurrence of euchelicerates, even though chelicerae have never been documented in this species or in any other sanctacaridid¹².

In fact, the fossil evidence supporting the hypothesis of Cambrian chelicerae-bearing arthropods was largely uncertain until the discovery of *Megachelicerax*. Raasch⁷⁵ described putative chelicerae in the Cambrian aglaspidid *Aglaspis spinifer* from the Furongian St. Lawrence Formation in Wisconsin. However, a subsequent restudy of the only known specimen with preserved limbs did not confirm the presence of chelate appendages, and redescribed it as preserving four, possibly five pairs of cephalic appendages, instead of six⁷⁶ (see Supplementary Note 4 below).

More recently, the Furongian strata of Sweden have yielded half a dozen phosphatized microfossils interpreted as pycnogonid larval stages³. These fossils were regarded as the oldest chelicerate body fossils (e.g.⁶⁸) and were subsequently used for timetree calibrations^{71,72}. Boxshall⁴⁴ accepted the chelicerate affinities of these larvae but disputed the presence of pre-cheliceral appendages. In contrast, Bamber⁷⁷ cited these pre-“cheliceral” structures as evidence against their assignment to Pycnogonida. Dunlop⁶⁸ refuted this argument and reaffirmed their pycnogonid affinities, a view that has prevailed in the recent years (e.g.,^{78,79}, but see ¹).

Resting trace fossils from the upper Miaolingian Hickory Sandstone in Texas have also been regarded as direct evidence of Cambrian euchelicerates^{39,68,74,80}. These ichnofossils were originally assigned to chasmataspidids, Ordovician–Devonian marine arthropods

typically retrieved well-nested within the Euchelicerata in morphological phylogenetic analyses⁸¹, despite the uncertain possession of chelicerae³⁹. These ichnofossils were recently re-interpreted as phyllocarid resting traces by Braddy⁸², who identified imprints of antennae. The discovery of similar fossils in shallow-water Furongian deposits of the Verkholensk Group, Siberia, was recently reported by Naimark et al.⁸³ and Naimark & Sizov⁸⁴. Regarded by these authors as the oldest representatives of euthycarcinoids (stem-group Myriapoda), and of chasmataspids and synziphosurines (total-group Chelicerata), these fossils remain extremely challenging to interpret. The preservation of appendages – especially the chelicerae – in these specimens is uncertain, and their body organization is open to alternative interpretations, such as that of Braddy⁸², who proposed reassigning them all to phyllocarid crustaceans.

Lastly, Aria & Caron¹⁴ argued for the presence of chelicerae in the arthropod *Mollisonia plenovenatrix* from the Wuliuan Burgess Shale in Canada. These appendages are only visible in two specimens, and only one of them actually shows a possible chela at its tip, a feature that could easily result from incomplete preservation of a non-chelate appendage. These forward-facing ‘chelicerae’ of *M. plenovenatrix* are exceedingly small relative to the other cephalic structures (e.g., cephalic shield, eyes, appendages) and are positioned far from the laterally splayed ‘post-chelicerai’ appendages, prompting doubts about their ability to manipulate food¹⁵. On the other hand, the size of chelicerae relative to the body greatly varies in extant chelicerates¹⁶, and even if the number and morphology of the cephalic appendages in this taxon are not as clear to us as claimed by Aria & Caron¹⁴, this set of appendages includes tubuliaceous exopodal rami and strong gnathobases, characters present in a variety of stem-group chelicerates including *Megachelicerax*. This indicates that, independent of whether its frontalmost appendages are legitimately chelate or not, *Mollisonia*, and more generally mollisoniids, most certainly belongs to the chelicerate lineage.

The discovery of unequivocal and massive chelicerae in *Megachelicerax*, along with an appendicular prosomal and opisthosomal differentiation diagnostic of chelicerates, removes the last remaining doubt regarding the Cambrian origins of these key features of the chelicerate body plan.

SUPPLEMENTARY NOTE 2: SYSTEMATIC PALAEONTOLOGY

Terminology. The terminology used hereafter is chelicerate-specific (e.g., prosoma/opisthosoma) and broadly follows Dunlop & Lamsdell³⁹ when referring to taxa with documented chelicerae. For members of the order Habeliida ('habeliids' hereafter), whose deutocerebral appendages are either non-chelate or of uncertain morphology, a more phylogenetically neutral terminology (e.g., cephalic region/trunk region) is adopted, following Lerosey-Aubril & Skabelund⁸⁵ and Lerosey-Aubril et al.⁸⁶.

The term *pseudobiramicity* is introduced to describe the association of an exopodal ramus and an endopodal ramus with close, but apparently distinct insertion sites on the body, rather than connected to one another via a protopodite (*biramicity* sensu stricto). This pseudobiramous condition was first described in the post-cheliceran prosomal appendages of the Silurian synziphosurine *Dibasterium*²⁶.

We also propose the term *tubuliaceous* (Latin, 'resembling a tube or a series of tubes') to refer to the unique morphology of the cephalic/prosomal exopodal rami of habeliids and some offacolid synziphosurines (see detailed comparisons below). Exopods of this type are *multi-segmented*, *elongate*, and *cylindrical* and therefore markedly differ from the foliaceous type of exopods found in early diverging stem-group chelicerates (e.g., megacheirans) and non-chelicerate arthropods³⁰. *Tubuliaceous* was preferred over *stenopodous* (Greek, 'narrow foot, appendage'), as the latter term is typically used by opposition to phyllopodous in the context of the whole appendage, not a ramus alone (e.g.⁸⁷). *Stenopodous* describes a usually walking, uniramous appendage solely composed of the endopod (e.g., the legs of insects or crabs).

Lastly, we propose using the term *megacheira* (no capital; plural, megacheirae) to refer to the 'short great appendage' of megacheiran arthropods, as this concise term aptly describes this type of deutocerebral appendages (from Greek *mega*, great or large, and *cheira*, hand or claw) and allows a parallel with the situation in chelicerates and their chelicerae. Note that this term is restricted to megacheirans and related taxa, and refers specifically to deutocerebral appendages with well-formed chelae and relatively few podomeres. As such, it should not be confused with the concept of 'cheira(e)' recently

proposed by Aria⁴¹, which encompasses the anteriormost paired arthropodized appendages of a wide diversity of early arthropods (including megacheirans), with or without raptorial function, and of uncertain homology.

The nomenclature of *Megachelicerax cousteau* gen. et sp. nov. has been registered in ZooBank (urn:lsid:zoobank.org:pub:0F9A12CA-06A7-416C-B89E-E014AFA1363E).

Abbreviations. en, prosomal endopodal ramus, ex, prosomal exopodal rami, exs., exsagittally, sag, sagittally, tr., transverse.

Phylum Arthropoda

Subphylum Chelicerata Heymons⁸⁸

Genus *Megachelicerax* gen. nov.

LSID. urn:lsid:zoobank.org:act:40631BDF-FECD-4A1C-BE3E-ABAF6BC563.

Type species. *Megachelicerax cousteau* sp. nov. (by monotypy).

Etymology. From the Greek ‘mega’, ‘khele’, and ‘keras’, meaning ‘large’, ‘claw’, and ‘horn’ respectively, in reference to the massive chelicerae of this taxon.

Diagnosis. Dorsal exoskeleton with a strongly arched axial region, composed of a semi-circular prosomal shield with short genal spines and at least nine opisthosomal tergites, most with well-developed, widely spaced, acute pleurae. Prosomal appendages include a pair of long, robust, three-segmented chelicerae and five pairs of pseudobiramous limbs with tubulaceous exopods bearing crowns of short spines at podomere boundaries. At least seven

pairs of plate-like opisthosomal appendages, each bearing on its outer third c. 35 elongate and imbricated lamellae that extend abaxially under the tergopleura.

Discussion. The pair of large three-segmented chelicerae supports a confident assignment of *Megachelicerax* gen. nov. to the subphylum Chelicerata⁸⁸, as it is regarded as the most defining character of the group (e.g., ^{39,43,89}). The new taxon also shares several characters with non-pycnogonid chelicerates, the Euchelicerata (*sensu*⁹⁰), namely the presence of a primarily seven-segmented prosoma and a morphological and functional differentiation between prosomal (feeding/walking, and sensory?) and opisthosomal (respiratory/swimming) limbs. However, *Megachelicerax* differs from all extant chelicerates in the absence of dorsal eyes and its pseudobiramous, rather than uniramous post-chelicerall prosomal appendages, hence its position on the stem of the chelicerate lineage along with habeliids and synziphosurines as resolved in our phylogenetic analyses.

Megachelicerax shares several similarities with members of the Cambrian family Sanctacarididae Legg & Pates²³ (see also¹¹ and emended diagnosis in⁸⁵): a strongly vaulted axial region, which is particularly wide (tr.) and extends to the shield anterior margin in the cephalic/prosomal region; a clustering of the five pairs of post-chelicerall/post-deutocerebral endopods ('limb-basket' of ³⁴), the significant size increase of these rami posteriorly, and the presence of multiple strong claws at their tips; seta-/spine-bearing tubuliaceous exopods; and a progressive, but significant narrowing (tr.) of the pleural regions posteriorly. However, we refrain from assigning the new genus to this family, as chelicerae remain undocumented in sanctacaridids. Additionally, there is no evidence for the presence of paired ventral eyes in *Megachelicerax*, and it is unknown whether its trunk region comprises eleven tergites and a paddle-shaped telson, two characteristics diagnostic of sanctacaridids.

Likewise, *Megachelicerax* is not assigned to the order Habeliida Aria and Caron¹³ – a group uniting the genera *Habelia*, *Messorocaris* and the family Sanctacarididae – despite some shared characters (i.e., a vaulted axis, sub-triangular pleurae, and five pairs of tubuliaceous exopods in the cephalic region). Indeed, the large chelicerae (reduced or non-

chelate deutocerebral appendages in habeliids), the plate-like trunk appendages bearing wide imbricated lamellae (lobate exopod fringed with setae in habeliids), and the absence of eye notches (and possibly eyes) in *Megachelicerax* are clear departure from the morphology typifying the order, as presently defined.

Three habeliid or habeliid-like taxa have been described from the Drumian strata of western Utah: *Dicranocaris* and *Messorocaris* from the Wheeler Formation in the Drum Mountains and the House Range, respectively, and *Nettapezoura* from the Marjum Formation^{85,86,91}. *Megachelicerax* and *Dicranocaris* can be easily distinguished from each other by the presence of genal spines and acute opisthosomal pleurae in the former and rounded genal angles and rather blunt trunk pleurae in the latter⁹¹. In *Megachelicerax*, these pleurae also seem wider (tr.) relative to the whole body than in *Dicranocaris*. *Megachelicerax* can also be differentiated from *Messorocaris* by its semi-circular, rather than lenticular prosomal/cephalic shield⁸⁵. The pleurae of the opisthosomal/trunk tergites are rather similar in the two taxa, except that their sickle shape is less pronounced and their spacing narrower (exs.) in *Megachelicerax*. Additionally, these pleural regions broaden (exs.) posteriorly in the new genus, while they apparently narrow (exs.) in the sole specimen of *Messorocaris* preserving the posterior trunk region⁸⁶. *Megachelicerax* and *Nettapezoura* share a semi-circular prosomal/cephalic outline, and the presence of tubuliaceous prosomal/cephalic exopodal rami and lamellae-bearing opisthosomal/trunk appendages. However, the Marjum genus lacks genal spines and features more narrowly spaced, sub-triangular trunk pleurae compared to *Megachelicerax*. Its trunk appendages are also equipped with long ‘inner leaf-like’ rami that have no equivalents in the new genus.

Megachelicerax cousteau gen. et sp. nov.

Figure 1, Extended Data Figures 1, 2, 3e, 4a–n, 5a–g

LSID. urn:lsid:zoobank.org:act:A1CAB82A-C6EF-45B4-B19B-52F265B1D0FD.

Etymology. In honour of the French explorer Jacques-Yves Cousteau for making millions of people around the world aware of the beauty and vulnerability of the undersea.

Holotype. Holotype (KUMIP314091), part and counterpart of a partial, dorso-ventrally flattened dorsal exoskeleton, including a prosomal shield and the remains of nine opisthosomal tergites, and associated appendages.

Locality. ‘Red Wheeler’ site, southern flank of Antelope Mountains, House Range, Utah, USA.

Horizon. Ochre shale of the upper part (c. 30 m) of the Wheeler Formation, *Bolaspidella* Zone (polymerid trilobites), *Ptychagnostus atavus* Zone (agnostoids), lower Drumian, Cambrian Series 3.

Diagnosis. As for genus.

Description. See main text.

Remarks. The holotype and sole available specimen of *Megachelicerax cousteau* gen. et sp. nov. was donated to the Biodiversity Institute of the University of Kansas (KUMIP) by Lloyd Gunther in November 1981. The full scientific significance of this fossil was only revealed after a long (>50h) and meticulous preparation by RL-A. We are particularly thankful to L. Gunther for his donation and to Bruce Lieberman and Julien Kimmig (KUMIP) for curatorial assistance.

SUPPLEMENTARY NOTE 3: DETAILED COMPARISONS WITH RELEVANT FOSSIL TAXA

Dorsal exoskeleton. Although incompletely preserved, the dorsal exoskeleton of *Megachelicerax cousteau* combines a strongly arched axial region and well-developed and distinctly differentiated pleural regions, characters shared with most representatives of the order Habeliida ('habeliids' hereafter; Fig. 1a, c, f; Extended Data Figs. 1, 2). The pronounced vaulting of the axial region in KUMIP314091 is evidenced by the fact that the counterpart preserves almost exclusively the axial region, indicating that even after compaction, this part of the body remained on a different topographical plane from the rest. In *M. cousteau*, each pleural region represents nearly a third of the body width (tr.); this significant development of the pleural region and the preservation of KUMIP314091 parallel to bedding suggest a relatively flat body morphology, despite the pronounced arching of the axial region.

This general body shape contrasts with the morphology of offacolid synziphosurines, which exhibit little to no differentiation of the pleural regions, and a strong arching of the whole dorsal exoskeleton that appears semi-circular in transverse section^{25,26}. A continuous arching of the dorsal exoskeleton also typifies mollisoniids, despite a better differentiation of the pleural regions (e.g.¹⁴). Additionally, mollisoniids have contiguous trunk pleurae and lack a posterior narrowing (tr.) of the body, two features that contrast with the body morphology of *Megachelicerax*.

Lastly, a reduced first opisthosomal tergite (T1) is a character repeatedly observed in chelicerates with uniramous prosomal limbs (i.e., clade Prosomapoda), where it may be associated with appendicular differentiation^{39,43}. However, a similar reduction of T1 is also common in early Palaeozoic stem-group chelicerates, having been inferred or documented in some habeliids (e.g., *Habelia*¹³), habeliid-like arthropods (e.g., *Dicranocaris*⁹¹), mollisoniids (e.g., *Thelxiope*⁶⁷), and offacolid synziphosurines (e.g., *Bunaia*⁹², *Dibasterium*²⁶). This sporadic distribution within the chelicerate lineage suggests that the feature evolved convergently in these taxa, most likely as an adaptation facilitating flexion at the prosomal–opisthosomal boundary. Accordingly, the presence of a reduced T1 in *Megachelicerax* is not regarded as phylogenetically significant.

Eyes. No eyes are apparent in KUMIP314091, suggesting that *M. cousteau* was blind, similar to synziphosurines (e.g. ^{20,25,26}). In contrast, mollisoniids typically possess a pair of well-developed stalked ventral eyes (e.g.⁶⁷), which can even be hypertrophied in *Mollisonia* (e.g.^{14,21}). Paired ventral eyes are also documented in most habeliids^{10,12,13,23}. These ventral eyes are typically preserved partially exposed along the anterior margin of the cephalic shield, which sometimes, but not always (*contra*¹³) forms broad notches to accommodate them. Critically, this partial exposure is not observed in all specimens of a given taxon (e.g. ^{10,12,13}), which warrants caution when interpreting *Megachelicerax* as a blind arthropod.

Chelicera. *M. cousteau* possesses robust three-segmented chelicerae (Fig. 1a–d, Extended Data Fig. 3e). The great length of these appendages relative to the body (c. 80% of prosomal shield, sag.) and their far anterior insertion beneath the prosomal shield suggest that they could reach far beyond the anterior margin of the body to catch and/or manipulate food. In this regard, they are reminiscent of the chelicerae of horseshoe crabs (Extended Data Fig. 3i) or some pycnogonids, mites, and opiliones (Extended Data Fig. 3c, g and j, and h, respectively). This markedly contrasts with the condition in *Mollisonia plenovenatrix*, where the putative chelicerae hardly project beyond the prosomal shield margin anteriorly¹⁴.

In *M. cousteau*, the chela proper represents c. 15% of the total length of the chelicera and is composed of distally curved fingers with smooth inner edges (Fig. 1b, d). This small size and simple morphology may indicate that the chela was used to hold prey or carcasses, and perhaps to pick off small pieces, while having crushing and cutting ability. Indeed, it lacks the robust construction and the spines or teeth characteristic of the chelae of pycnogonids and arachnids used to crush prey (Extended Data Fig. 3d, k–o), and the scissor-like morphology associated with cutting in harvestmen and horseshoe crabs (Extended Data Fig. 3h, i)¹⁶.

Post-chelicer al prosomal limbs. These five pairs of appendages (Fig. 1f, Extended Data Fig. 4a–n) are strongly reminiscent of the post-chelicer al appendages of habeliids, some early synziphosurines, and possibly *Mollisonia* regarding two aspects: the apparently independent

insertions of the endopodal and exopodal rami on the body – a condition here referred to as *pseudobiramicity* – and the tubuliaceous (i.e., non-foliaceous) morphology of the exopodal rami.

First described in *Dibasterium* and *Offacolus* by Briggs et al.²⁶, a pseudobiramous condition of at least some post-deutocerebral cephalic appendages has been subsequently suggested in the habeliid *Sanctacaris*¹¹ and *Habelia*¹³, and the mollisoniid *Mollisonia*¹⁴. It has also been hypothesized that pseudobiramicity represents a transitional stage towards the uniramicity of most prosomal appendages in the evolution of chelicerate body plan²⁶. *Setapedites*, the oldest (Early Ordovician) synziphosurine described to date, was recently reconstructed as having basipodites and therefore, truly biramous post-chelicerate prosomal appendages²⁰. This observation was considered by the latter authors as supporting evidence to Briggs et al.'s hypothesis²⁶. However, the seemingly distinct insertions of the endopodal and exopodal rami on the body in earlier diverging stem-group chelicerates – such as habeliids, mollisoniids, and now *M. cousteau*, suggests that pseudobiramicity may predate the evolution of synziphosurines.

The morphology of the exopodal rami of the post-deutocerebral cephalic appendages is also highly informative regarding the phylogenetic placement of *Megachelicerax* (Extended Data Fig. 4a–l). Boxshall³⁰ noted that a ‘well-developed, articulated cylindrical exopodite’ markedly differs from the foliaceous exopodal morphotype observed in most Palaeozoic arthropods. This non-foliaceous exopodal morphotype is almost exclusively observed in Cambrian to Silurian representatives of the chelicerate lineage: habeliids^{11,13,44}, mollisoniids¹⁴, and offacolid synziphosurines^{25,26} (*sensu*²⁰) (see³⁰ for a couple of exceptions). If Boxshall's aforementioned description³⁰ captures well the morphological uniqueness of these exopodal rami, no consensus has been reached as to how to refer to them (Table 1). A reason for that is the morphological diversity exhibited by the exopodal rami in all these taxa, both within the series of prosomal limbs of a given taxon and between those of different taxa. We believe the new term *tubuliaceous* (Latin, ‘resembling a tube or a series of tubes’) aptly captures the unique morphology of these disparate exopodal rami, while highlighting their difference from the foliaceous type characteristic of most aquatic Palaeozoic arthropods.

Taxon	Terms
Habeliida	Antenna-like limb/structure/ramus/rami ¹⁰ ; antenna-like exopods, pre-oral appendage ³⁴ ; antenniform pre-oral appendage ⁹³ ; filamentous or antenniform exopods ²⁵ ; outer ramus of cylindrical segments, flagelliform exopodite ⁴⁴ ; pediform exite(s) ¹¹ ; antennule-like/antennular exopods/appendages ¹³ ; filiform exopod ³⁹ ; exopodial branch ¹⁴ ; stenopodous prosomal exopods ⁹² .
Offacolidae	Robust setose exopods ²⁵ ; robust/well-developed, multisegmented/ six-segmented exopodite ^{30,44} ; outer ramus ²⁶ ; well-developed, articulated cylindrical exopodite ³⁰ ; pediform exopod, setiferous exopods ⁹⁴ ; stenopodous exopods, exopodial branches ¹³ ; pediform exopod ³⁹ ; exopodial branch ¹⁴ ; brush-like exopods ²⁰ ; stenopodous exopods ^{20,92} .
Mollisoniidae	Exopodial branch, small exopods with short podomeres and setose termination ¹⁴ .

Table 1. Non-exhaustive list of terms used to refer to the post-chelicerai exopods/exopodal rami of early chelicerates. We propose the new term *tubulaceous* to describe the unique morphology (i.e., multi-segmented, elongate, and cylindrical) of these exopodal rami/exopods.

Lustri et al.²⁰ recently regarded the presence of a ‘brush-like group of long and radially arranged setae on the distalmost podomere’ as a diagnostic character for the synziphosurine family Offacolidae. None of the exopodal rami of *M. cousteau* display a brush-like tip (Fig. 1, Extended Data Fig. 4a–l), but somewhat similar features are observed in some cephalic rami of habeliids (fig. 2b in ¹¹; Extended Data Fig. 4o) and mollisoniids (fig. 2g and extended data fig. 3f in ¹⁴). In the new taxon, the exopodal rami are of similar width, but they considerably increase in length posteriorly, which is unknown in offacolids. Ex5 and ex6 are particularly elongated in *Megachelicerax*, a morphology as-yet only documented in *Habelia*¹³ (Extended Data Fig. 4p) and *Sanctacaris*¹¹ (Extended Data Fig. 4o). The podomeres of these exopodal rami are much longer than wide in the new taxon and these two habeliid taxa, and spines project from their distal margins (Extended Data Fig. 4i–l), a character also known in (at least) *Habelia* (fig. 2c in ¹³).

The endopodal anatomy of the post-chelicerai prosomal appendages of *M. cousteau* is not fully known, owing to incomplete preservation distally and/or cover by the prosomal shield proximally (Fig. 1f, Extended Data Fig. 4m–n). Unlike in offacolids, these endopodal rami are robust and considerably increase in size posteriorly in the new taxon, a morphology more evocative of the cephalic endopodal condition in *Sanctacaris* (Extended Data Fig. 4o). Yet, they do not seem to possess the clustered spines projecting from podomere boundaries that characterize *Sanctacaris* and to a lesser extent, *Habelia* (Extended Data Fig. 4o, p);

instead, they apparently bear two stout spines distally (only one in habeliids), which may or may not form a chela.

Lastly, we reconstruct *Megachelicerax* as likely possessing prosomal gnathobases, as suggested by the preservation of series of tiny teeth-like structures under the central part of the prosoma (Fig. 1e, f). Gnathobases are well-documented in habeliids, such as *Habelia*¹³ and *Wisangocaris*¹², and may also occur in mollisoniids¹⁴ and the offacolid *Dibasterium*²⁶.

Opisthosomal limbs. *Megachelicerax cousteau* exhibits a unique post-cephalic appendicular anatomy, characterized by: 1) plate-like exopods bearing long, overlapping lamellae; and 2) the absence of endopods (Fig. 1a, c, g, Extended Data Fig. 5a–g). If confirmed by additional specimens, the latter absence would mark a significant departure from the Habeliida, where all species with known appendicular data possess post-cephalic endopodal rami^{10–13,23}. In *Habelia*, endopods are absent in the posterior trunk but particularly well-developed in the anterior trunk¹³ (Extended Data Fig. 7). In *Sanctacaris*, they are short (fig. 2h in ¹¹; Extended Data Fig. 7), a reduction that may represent an early evolutionary stage toward the complete loss of the post-cephalic endopods observed in early chelicerates, such as *Mollisonia*¹⁴, offacolid synziphosurines^{25,26}, and now *Megachelicerax*.

The post-cephalic exopods in habeliids and offacolid synziphosurines are plate-like (or flap-like) structures. In habeliids, they are splayed laterally under the tergopleurae and feature thin, marginally inserted setae^{10,11,13} – a condition reminiscent of megacheirans (e.g., ^{8,95}) – whereas in offacolids they are restricted to the axial region and bear broad, overlapping lamellae²⁶, resembling the sheath-like gill lamellae of xiphosurids (Extended Data Fig. 5h–j). The structures borne by the trunk exopods of *M. cousteau* differ from the gill lamellae of offacolids and xiphosurids by their elongate morphology (Fig. 1g, Extended Data Fig. 5a–g). However, the facts that they broadly overlap one another, and cover at least the outer third of the exopodal plate rather than insert marginally, suggest that they could represent an intermediate condition between habeliid marginal setae and synziphosurine gill lamellae.

The post-cephalic exopods of *Mollisonia* are essentially of the habeliid-type: large flaps fringed with thin setae. However, it also includes two smaller lobes, which led Aria & Caron¹⁴ to describe it as a "proto-book gill." While physical connections between these smaller structures and the main exopodal plate were convincingly illustrated, the precise nature of these additional exopodal elements remain unclear. For instance, instead of gill lamellae, these structures could be homologues of other lobes composing the xiphosurid operculum (Extended Data Fig. 5i), or to exites similar to those recently documented in various Cambrian arthropods⁴⁹.

Internal organs. We interpret the complex structures preserved as dark red stains in KUMIP314091 (Fig. 1a, c, Extended Data Figs. 1, 2, 5d, e) as the remains of a bilaterally symmetrical organ system, most likely – but maybe not exclusively – the circulatory system.

The internal anatomy of stem-group chelicerates is generally poorly understood, which limits the anatomical inferences that can be drawn about the new taxon through comparisons with related taxa. Digestive structures (and gut contents) have been documented in various habeliids^{10,12,23,96}, with the most complete description to date being that of *Habelia*¹³. In this taxon, the digestive system consists of a large, multi-chambered, yet essentially tubular tract running medially from the anterior cephalic region to the anterior part of the telson. Importantly, no paired structures comparable to the digestive glands of mollisoniids were observed flanking the digestive tract in any of the 41 specimens of *Habelia* studied by Aria & Caron¹³ or any other habeliid species. This is a significant difference between the digestive systems of habeliids and mollisoniids. Considering the habeliid-like body organization of *Megachelicerax*, the paired red stains in KUMIP314091 are unlikely to represent elements of the digestive system.

Briggs & Collins¹⁰ described two types of traces under the axis of the cephalic region in *Sanctacaris*: a large trace, possibly bilobed anteriorly, which they tentatively interpreted as stomach contents (their pl. 73, fig. 3, 5 and text-fig. 4, 5); and traces in slightly more abaxial positions relative to the large trace, forming either two rows of individualized spots (their pl. 73, fig. 2 and text-fig. 3) or two streaks (their pl. 71, fig. 3 and text-fig. 1B), which they compared to the muscle scars occasionally observed on the cephalic shields of

synziphosurine and xiphosurid chelicerates, as well as trilobites (e.g., ⁹⁷ and references therein). Whether these traces correspond to distinct structures or represent preservational variants of the same organ is uncertain. However, none of these traces are elongate and radially disposed, like the structures preserved in this prosomal region of KUMIP314091, so they likely belong to a different organ system.

The presence of gut glands in mollisoniids was documented in two specimens of *Mollisonia* by Ortega-Hernández et al.²¹ (fig. 1b, sup. fig. 4). These paired structures laterally flank the digestive tract in the cephalic, thoracic, and pygidial regions. They are elliptical in outline, differing noticeably from the elongate, radially arranged structures in KUMIP314091. One of these *Mollisonia* specimens appears to preserve three, possibly four, radially arranged digitiform structures on one side of its cephalic region (sup. fig. 1b in ²¹), structures more reminiscent of those observed in the holotype of *M. cousteaui*. This radial organization is similar to the arrangement of prosomal appendages in synziphosurines (e.g., ^{92,98}), which is sometimes mirrored dorsally by swellings or ridges on the cephalic shield in both mollisoniids⁹⁹ and synziphosurines (e.g., ¹⁰⁰). The alignment of the dark red elongate stains and the proximal parts of some exopodal rami is evident in the prosoma of KUMIP314091. However, their strong distal tapering suggests that these stains represent structures within the limbs, rather than the limbs themselves, unlike in synziphosurines and possibly mollisoniids.

Tagmosis. Both the dorsal exoskeleton and appendicular anatomy indicate the differentiation of two tagmata in *Megachelicerax cousteaui*: a prosoma, characterized by a dorsal shield and six pairs of feeding appendages, and an opisthosoma, consisting of articulated trunk tergites, each associated with respiratory and probably swimming appendages (Extended Data Fig. 7). It remains uncertain whether the opisthosoma includes a posterior region lacking appendages.

The presence of six pairs of cephalic appendages, distinctly differentiated from post-cephalic appendages – a hallmark of crown-group chelicerates³⁸ (e.g., eurypterids in Extended Data Fig. 7) – is unique to *Megachelicerax* among Cambrian arthropods. The head

region in megacheirans is a pseudotagma, consisting of a dorsal shield that dorsally covers up to five pairs of ventral appendages^{37,42} (e.g., *Yohoia* and *Haikoucaris* in Extended Data Fig. 7). Except for the deutocerebral megacheirae, these cephalic appendages are morphologically identical to the trunk appendages. A *Megachelicerax*-like body tagmosis has been repeatedly hypothesized in the habeliid *Sanctacaris*, although the precise number of head appendages in this taxon remains uncertain^{10,11,13,34,44} (Extended Data Fig. 7). Most recent studies have proposed a pair of chelicerae followed by five pairs of (pseudo)biramous limbs beneath the cephalic shield, but these hypothetical chelicerae have yet to be confirmed^{11,13,44}.

An additional cephalic appendage pair was suggested for *Sanctacaris* following the description of seven cephalic limbs in *Habelia*, a taxon that features two post-cephalic tagmata¹³ (Extended Data Fig. 7). The Cambrian mollisoniid *Mollisonia* was similarly reconstructed with seven cephalic appendages¹⁴, though their small size makes corroborating this observation challenging (Extended Data Fig. 7). Post-cephalic appendages in *Mollisonia* are homonomous, despite differentiation of the dorsal exoskeleton into a thorax and a pygidium. Lastly, *Megachelicerax* differs from offacolids regarding body tagmosis, as these synziphosurines exhibit three tagmata^{20,25} (*Offacolus* and *Dibasterium* in Extended Data Fig. 7).

SUPPLEMENTARY NOTE 4: CHELICERATE CLOSEST RELATIVES

The question of the origins of chelicerates is intimately connected to that of their closest (extinct) relatives. Three groups of marine arthropods present in the Cambrian have been repeatedly regarded as the most likely candidates: artiopods, habeliids (Order Habeliida), and megacheirans (e.g., ¹⁰¹). Mollisoniids are now relevant to this discussion as well, following the publication of Aria & Caron¹⁴.

Artiopoda

The modern concept of Artiopoda encompasses a wide variety of antenna-bearing Palaeozoic arthropods and includes two main groups: trilobitomorphs (e.g., trilobites, concilitergans, xandarellids/petalopleurans, nektaspidids) and vicissicaudates (e.g., aglaspidids, chelionellids) (e.g., ^{102,103} and references therein). Comprehensive literature reviews already exist on the long-debated hypothesis that chelicerates derived from trilobites, and more specifically the early diverging olenellids (e.g., ^{101,104}). Accordingly, we focus on vicissicaudates, and more specifically aglaspidids, as they have often been regarded as evolutionary intermediates between trilobitomorphs and chelicerates, and are still occasionally recovered as closely related to chelicerates in recent phylogenies.

The hypothesis that aglaspidids are related to chelicerates originates in the first description of aglaspidid fossils by Hall¹⁰⁵, who, although referring to them as crustacean remains, noted their strong resemblance to *Limulus* and even *Eurypterus*. Billings¹⁰⁶ reinterpreted these fossils as trilobites, a view shared by Miller¹⁰⁷, when establishing the family Aglaspidae (now Aglaspididae), but contradicted by Beecher¹⁰⁸, who unambiguously regarded them as merostomes. Clarke¹⁰⁹ may have been the first to formally assign aglaspidids to the Chelicerata (his 'Acerata'), uniting the family Aglaspididae with broadly similar synziphosurines within a merostome order 'Synxiphorura' (see also¹¹⁰). Walcott¹¹¹ essentially expressed a similar view regarding the merostome (i.e., chelicerate) affinities of aglaspidids with the establishment of a new order, Aglaspina (now Aglaspidida¹¹²), which he defined, among other traits, by the presence of five pairs of cephalic appendages. Conversely, Raymond¹¹³ proposed transferring the Aglaspididae from the Merostomata to the Crustacea

based on the putative presence of antennae in Burgess Shale-type taxa assigned to this family by Walcott¹¹¹, namely *Habelia* and *Molaria*. However, no appendicular data were available for *Aglaspis*, the sole true aglaspidid genus then included in the family Aglaspididae. Somewhat confusingly, Resser¹¹⁴ used the expression ‘merostome crustacean’ to describe a new aglaspidid genus *Beckwithia*, which he characterized as possessing a pygidium, rather than a telson/tailspine.

In 1939, Raasch⁷⁵ published what remains to this day one of the most comprehensive studies on aglaspidids, in which he: 1) proposed a new order, Aglaspida, which excludes all the Burgess Shale taxa associated with *Aglaspis* in the Walcott’s¹¹¹ order Aglaspina; 2) documented a highly diverse aglaspidid fauna, establishing seven new genera and 16 new species; 3) provided the first data on the appendicular anatomy of these arthropods, describing a pair of chelicerae followed by five pairs of uniramous, non-chelate walking legs in the cephalic region; 4) reviewed in detail the previous attempts at classifying aglaspidids; and 5) argued strongly that aglaspidids represent ‘by far the most primitive group of Arachnida’ (p. 81), and are unrelated to the independently evolved trilobite-crustacean lineage. The appendicular data presented by Raasch⁷⁵ were almost unanimously considered as decisive evidence that aglaspidids belonged to the Chelicerata, until the single specimen on which they were based was re-examined forty years later by Briggs et al.⁷⁶ (see references therein). This restudy, along with that of Hesselbo¹¹⁵, concluded: 1) that the evidence supporting the presence of chelate appendages in this specimen was inconclusive; and 2) that a maximum of five (most likely four) pairs of appendages occurred in the cephalic region. Both studies also emphasized, however, that aglaspidid limbs are uniramous and only five-segmented – features highly atypical within Artiopoda – and thus refrained from assigning the order Aglaspidida to any higher taxon.

Despite this clear demonstration of non-chelicerate appendicular anatomy in aglaspidids, a sister relationship between vicissicaudates and chelicerates, or between vicissicaudates and antenna-lacking arthropods (i.e., chelicerates + megacheirans and/or habeliids) has continued to be proposed over the last 45 years (e.g., ^{116–118}), often supported by phylogenetic analyses (e.g., ^{4–6,11,23,25,119,120}). Legg¹¹ provided a list of the few morphological characters supporting such a grouping, emphasizing those pertaining to the

trunk region, which is supposedly composed of 12 segments, including a differentiated three-segmented ‘abdomen’.

Habeliida

Aria and Caron¹³ established the order Habeliida to unite *Habelia* Walcott¹¹¹ (restricted to *H. optata*), *Messorocaris* Lerosey-Aubril & Skabelund⁸⁵, and the family Sanctacarididae²³, which includes *Sanctacaris*¹⁰, *Utahcaris*⁹⁶, and *Wisangocaris*¹². Although recent phylogenetic analyses have supported the placement of these taxa along the chelicerate stem^{13,14,20,92}, their systematic histories reveal a more complex picture.

Chelicerate affinities for these arthropods can be traced to Walcott’s¹¹¹ description of *Habelia optata*, which he assigned to the Merostomata (order Aglaspina). Walcott’s concept of Aglaspina, closer to the modern concept of Vicissicaudata^{112,121}, grouped *Aglaspis* with several taxa then believed to possess antennae. He described *H. optata* as having five pairs of cephalic appendages, including “antennules” and “antennae,” though his terminology was ambiguous. Raymond¹¹³ also reported five cephalic appendage pairs, including two pairs of antennae (see also ¹²²), and, while retaining the species within Aglaspidae, transferred this family from Merostomata (i.e., Chelicerata) to Crustacea (see also ¹²³). Raasch’s⁷⁵ description of putative chelicerae in *Aglaspis* later revived the idea that aglaspids were chelicerates. Simonetta¹²⁴ and Simonetta & Delle Cave^{125,126} accepted this relationship and maintained the chelicerate assignment of *H. optata*. Whittington¹²⁷ provided the first detailed redescription of *H. optata*, recognizing only three pairs of cephalic appendages (one pair of antennae and two pairs of biramous limbs) and rejecting the presence of an anal plate. Because this plate had linked *Habelia* to aglaspids, its absence undermined both aglaspid and chelicerate affinities for the Burgess Shale taxon. Whittington did not propose an alternative placement for *H. optata*, effectively leaving the species as a problematicum.

Sanctacaris was originally described as the first unequivocal Cambrian chelicerate¹⁰, largely based on its six pairs of raptorial cephalic appendages and their morphological and functional differentiation from post-cephalic limbs. This taxon lacks chelicerae, although it remains unclear whether they are genuinely absent or simply unpreserved, and bears only

biramous appendages, two traits regarded as plesiomorphic for chelicerates by Briggs & Collins¹⁰. The assignment of *Sanctacaris* to Chelicerata was initially well received (e.g.,^{116,128,129}) but later challenged after phylogenetic analyses failed to recover close relationships with chelicerates (e.g.,¹¹⁶ and references therein). Alternative interpretations of its head appendages soon followed. Bousfield³⁴ regarded the supposed sixth cephalic appendage as a pair of biramous antennae and the anterior five pairs as a “raptorial basket,” rejecting any chelicerate affinity and assigning the species to the antenna-bearing Trilobitoidea. He also synonymized *Utahcaris* with *Sanctacaris*. Dewel & Dewel¹³⁰ reinterpreted the six raptorial appendages as rami of a single pre-antennal (protocerebral) pair and recovered *Sanctacaris* as a basal arthropod, stemward of artiopods, chelicerates, and mandibulates, a view echoed by Budd⁹³.

Boxshall⁴⁴ offered a contrasting reconstruction inspired by comparison with the Silurian synziphosurine *Offacolus*²⁵. He argued that chelicerae were present but indistinct, followed by five pairs of homonomous appendages with robust endopods and tubuliaceous exopods, and that the prosoma bore seven limb pairs in total. Legg¹¹ fully adopted this model, proposing pseudobiramous post-cheliceral limbs and recovering *Sanctacaris* as a crown-group chelicerate. His analysis also positioned chelicerates within Artiopoda as sister to the antenna-bearing Vicissicaudata. Using Legg’s dataset, Jago et al.¹² placed *Wisangocaris*, a *Sanctacaris*-like early Cambrian form from Australia, in a similar position. Legg & Pates²³ subsequently erected Sanctacarididae to unite *Sanctacaris*, *Wisangocaris*, and *Utahcaris*, defining the family primarily by non-appendicular features such as a paddle-shaped telson. Lerosey-Aubril & Skabelund⁸⁵ later emended the diagnosis of this family and tentatively added *Messorocaris* to it.

Aria & Caron¹³ substantially revised *Habelia optata*, revealing strong anatomical similarities between *Habelia* and sanctacaridids and thus establishing the order Habeliida. They emphasized shared features of the prosomal limbs among *Habelia*, *Sanctacaris*, and (to a lesser extent) offacolid synziphosurines (e.g., pseudobiramous post-cheliceral appendages with tubuliaceous exopodal rami). They also convincingly illustrated the presence of uniramous, non-chelate deutocerebral appendages, a trait shared with *Sanctacaris* that likely explains the recovery of the two taxa as the earliest-branching chelicerates in their analysis.

Lastly, Leroosey-Aubril et al.⁸⁶ showed that *Messorocaris* possesses a forked, rather than paddle-shaped (Sanctacarididae) or spiniform (*Habelia*) telson. This supported Aria & Caron's¹³ suggestion that *Messorocaris* may warrant placement in its own family within Habeliida, potentially alongside *Dicranocaris*, from the Cambrian of Utah⁸⁶.

Restudies of *Sanctacaris*¹¹ and *Habelia*¹³ have reinforced the hypothesis that habeliids are closely related to chelicerates^{69,131,132}. Since then, habeliids have consistently been recovered within the chelicerate stem (e.g.,^{14,20,31,92,133}), although our results suggest that they may represent a grade rather than a clade (Extended Data Fig. 6).

Megacheira

The first hint at a close affinity between chelicerates and megacheirans can be found in Briggs & Fortey's¹³⁴ pioneering attempt to use cladistics to investigate the relationships of Cambrian arthropods. In their analysis, megacheirans such as *Alalcomenaeus*, *Leancoilia*, and *Yohoia* formed a clade with chelicerates and two Burgess Shale taxa (including an antenna-bearing one). Surprisingly, this interesting result was not discussed in this contribution and only brief comments about it were provided in their follow-up study¹¹⁹. It was only a few years later, with the work of Bousfield³⁴, that the hypothesis of a megacheiran origin of chelicerates was explicitly formulated. Bousfield³⁴ regarded *Jianfengia* and *Yohoia* (his "protochelicerates") as early diverging representatives of a chelicerate lineage rooted in Radiodonta (his fig. 10), and described an evolutionary scenario in which chelicerae arose from multichelate megacheirae through podomere reduction and appendage rotation (his fig. 3). However, in Bousfield's evolutionary scheme, megacheirans with flagellum-bearing megacheirae (i.e., Leancoiliidae) were depicted as belonging to separate lineages of antennae-bearing arthropods (his fig. 10).

Chen et al.⁷ (see also¹³⁵) developed essentially similar views as Bousfield³⁴ about the megacheiran origin of chelicerates and the evolution of chelate deutocerebral appendages in this lineage, which they again regarded as deriving from radiodonts. However, they included leancoiliids within their 'Chelicerata sensu lato' (i.e., total-group Chelicerata) and tentatively proposed extending this concept to two additional, then incompletely known

megacheirans (*Fortiforceps* and *Tanglangia*), and even to radiodonts. In their redescription of *Yohoia*, Haug et al.⁸ provided new data on *Fortiforceps* and *Tanglangia* that confirmed their megacheiran affinities, and otherwise reiterated Chen et al.'s arguments, albeit in greater detail, supporting the Radiodonta–Megacheira–Chelicerata evolutionary scenario. To our knowledge, no phylogenetic analysis has ever recovered a clade regrouping these three groups, but any analyses retrieving megacheirans in positions stemward to a clade [Chelicerata + antenna-bearing arthropods (e.g., Artiopoda, Mandibulata, or both)] remain essentially consistent with a derivation of chelicerae from megacheirae (e.g.,^{20,136}).

Cotton and Braddy's⁴ phylogenetic investigation of the origin of chelicerates provided strong support for a clade uniting megacheirans and chelicerates (their "Clade 4"). This clade was defined by the presence of flap-shaped, rounded exopods and cephalic appendages differentiated into spinose raptorial organs. These appendages correspond to the megacheirae and chelicerae, which were regarded by the authors as the second pair of cephalic appendages following the original description of putative antennae in *Fortiforceps*¹¹⁷. With the exception of that taxon, antennae were thought to have been secondarily lost in these forms, whereas they remain present in their sister clade – now referred to as Vicissicaudata – as well as in all the other arthropod taxa included in the analysis. Since then, the deutocerebral identity of the megacheirae and chelicerae (i.e., their positional homology with antennae) and the associated evolutionary scenario deriving the latter appendages from the former have received strong support from anatomical, developmental, and palaeontological data (e.g.,¹⁰⁴ and references therein;^{9,21,35}), and a clade uniting megacheirans and chelicerates – sometimes also including habeliids and/or mollisoniids – has been repeatedly recovered in phylogenetic analyses (e.g.,^{9,31,33,36,43,137–140}).

Mollisoniidae

Mollisoniidae (*sensu*⁸⁶) is a low-diversity group of Cambro-Ordovician arthropods whose phylogenetic significance has only recently been recognized, following the description of appendicular data suggesting close relationships with chelicerates¹⁴. *Mollisonia*, the first described mollisoniid, was classified by Walcott¹¹¹ in a new trilobite order, Hypoparia,

characterized by the putative presence of a hypoparian cephalic suture. Similarly, Raymond¹⁴¹ suggested affinities with antenna-bearing trilobites and isopod crustaceans. Simonetta & Delle Cave¹²⁵ (see also ¹²⁴) were the first to propose the inclusion of mollisoniids (*Mollisonia* and *Thelxiope*) – together with *Habelia* and the vicissicaudates *Emeraldella* and *Molaria* (their superorder Emeraldellidea) – within Chelicerata (including Aglaspidida). Although acknowledging that all these taxa possessed antennae (supposedly reduced in *Mollisonia* and *Thelxiope*), rather than chelicerae, they highlighted similarities with Aglaspidida as well as Eurypterida (e.g., the presence of anal plates; p. 27 in ¹²⁵). Their arguments, however, were not adopted by Bousfield³⁴, who instead derived *Mollisonia* and *Thelxiope* (including *Ecnomocaris*⁶⁷) from two distinct lineages of antenna-bearing arthropods (his fig. 7). Likewise, Briggs et al.⁹¹ tentatively regarded mollisoniids as arachnomorphs, but also strongly emphasized that the lack of appendicular data precluded a more precise phylogenetic placement.

The description of appendicular data in the Burgess Shale species *Mollisonia plenovenatrix*¹⁴ has brought mollisoniids into focus. Many aspects of the appendicular anatomy of this taxon remain unknown or unconvincingly demonstrated (e.g., the number of cephalic appendages or whether most of them are truly uniramous, the natures of the different lobes composing the post-cephalic appendages; Extended Data Fig. 7), with some even contested (e.g., the presence of chelicerae or of four pairs of pygidial appendages^{15,67}). This uncertainty explains why mollisoniids were only tentatively placed within Chelicerata in Lerosey-Aubril et al.^{67,86}, a view still followed in Kimmig et al.¹⁴². On the other hand, features such as the large ocular notches on the head shield, the crowding of the cephalic appendages, and the morphology of the best-preserved cephalic and post-cephalic appendages (including the likely presence of gnathobases) confer to these arthropods an anatomy reminiscent to habeliids, or even synziphosurines (e.g., the morphology of the sole preserved cephalic exopodal ramus), supporting their inclusion within total-group Chelicerata. This view was shared by Ortega-Hernández et al.²¹, who presented new neuroanatomical data on *Mollisonia* suggestive of a simple nervous system organization, likely plesiomorphic within total-group Chelicerata. Such simplicity contrasts with the more

complex architectures documented in megacheirans and chelicerates, as well as with the elaborate appendicular anatomy described by Aria & Caron¹³.

In the recent years, the hypothesis that mollisoniids belong to the chelicerate lineage has progressively gained traction (e.g.,^{20,92,131,143}), their most recent reinterpretation even suggesting they belong to stem-group Arachnida¹⁴⁴). However, this controversial claim rests on putatively previously unrecognized neurological remains – most likely appendicular instead – in a single specimen already documented by Ortega-Hernández et al.²¹, and, in our view, requires further investigation to be substantiated.

SUPPLEMENTARY NOTE 5: DID CHELICERAE DIRECTLY EVOLVE FROM ANTENNA-LIKE APPENDAGES?

The origin of chelicerae (i.e., uniramous, unichelate deutocerebral appendages) and their evolutionary relationship with their positional homologues in mandibulates – the antennae (i.e., antennulae of crustaceans) – are central yet contentious topics in arthropod research. In extant chelicerates, chelicerae typically possess two or three podomeres, with the three-segmented condition widely regarded as the plesiomorphic state for the clade^{27,145–147}. However, it has been repeatedly hypothesized that chelicerae have directly evolved from multi-segmented, antenna-like appendages (e.g., ^{6,11,13,44}), which implies a significant reduction in the number of podomeres composing these deutocerebral appendages. The presence of four-segmented chelicerae ('cheliformes') in rare pycnogonids and descriptions of elongate multisegmented (i.e., four-segmented or more) chelicerae in a handful of Palaeozoic representatives may be regarded as supporting evidence for this evolutionary scenario, which is otherwise based primarily on phylogenetic inferences (e.g., ^{6,11}). We argue that a critical review of (1) these two lines of evidence, (2) the appendicular anatomy of *Habelia*, *Mollisonia*, and, crucially, *Megachelicerax*, and (3) recent phylogenetic analyses provides little to no support for the hypothesis that chelicerae evolved directly from antenna-like appendages. Conversely, all these elements are consistent with, and in some cases strongly supportive of, a derivation of these unichelate appendages from the multichelate megacheirae of megacheirans.

The chelicerae of pycnogonids

Chelicerae/cheliformes are always present in newly hatched pycnogonids^{79,148}, but they may be lost in adults. When present, adult chelicerae comprise one to four podomeres²⁸, a number that may differ in closely related species or even in males and females within a given species. Crucially, fully functional three-segmented chelicerae are present in the larval and/or post-larval instars of all pycnogonids, and in adults of the overwhelming majority of them^{28,79}. Both the addition of a podomere or conversely, the partial or complete atrophy of the appendage during development are changes affecting a primarily three-segmented

functional chelicera^{28,148–150}. Four podomeres is the maximum number ever documented in extant pycnogonid chelicerae. Four-segmented chelicerae are rare but found in representatives of four out of eleven pycnogonid families, which are widely distributed within the pycnogonid tree²⁸. They are not known in the earliest diverging pycnogonids (Austrodecidae, Pycnogonidae), but these taxa lack chelicerae in adults entirely²⁸. Accordingly, it remains unclear how many podomeres composed the chelicerae of the last common ancestor of crown group pycnogonids, and if some authors (e.g., ²⁸) favoured the four-segmented chelicera hypothesis, it is solely based on palaeontological evidence.

Four podomeres were tentatively identified in the chelicerae of two Palaeozoic pycnogonids – the Silurian *Haliestes*¹⁵¹ and the Early Devonian *Pentapantopus*¹⁵². Bergström et al.¹⁵³ described chelicerae that ‘may consist of five podomeres’ in the Early Devonian pycnogonid *Palaeoisopus* from the Hunsrück Slate Lagerstätte, but only after acknowledging that wrinkling and deformation make the counting of the chelicer segments difficult. The two photographs they provide do not convincingly show the presence of so many podomeres in the chelicera, which only appear in tentative interpretative drawings (figs. 4 and 6 in ¹⁵³). The recent restudy of *Palaeoisopus* by Sabroux et al.²⁹ stressed the difficulty in counting the number of chelicer segments in this Devonian taxon, before concluding that a count of four segments appears more likely.

In the light of these observations, we consider that the claims that some fossil pycnogonids possessed five-segmented chelicerae²⁸, and that *Palaeoisopus* “may bridge the gap between the megacheiran condition and the three chelicer podomeres of euchelicerates”³⁹, are unsupported by the available data. The hypothesis that four-segmented chelicerae are plesiomorphic in pycnogonids remains plausible. However, the discovery of a middle Cambrian arthropod with three-segmented chelicerae (i.e., *Megachelicerax*), combined with the particularly crownward position of pycnogonids – especially relative to the chelicerae-bearing synziphosurines – in most trees resulting from our phylogenetic analysis, suggests that this hypersegmented condition is autapomorphic for pycnogonids or evolved secondarily within this group. The fact that the four-segmented chelicerae condition in some extant pycnogonids results from the late ontogenetic splitting

of a podomere further supports the interpretation that this condition is derived for these chelicerates, rather than ancestral for total-group Chelicerata.

Multisegmented chelicerae in fossil taxa

The fossil record of euchelicerates provides rare examples of multisegmented (i.e., four-segmented or more) chelicerae, which some authors have regarded as possible evidence supporting a hypothetical ‘antenniform phase’ in the early evolution of this appendage³⁰. The most compelling example is the Silurian synziphosurine *Dibasterium*, which possesses long and slender chelicerae with at least three podomere boundaries, or four if one considers that a finger of the chela was mobile²⁶. As acknowledged by Briggs et al.²⁶, the great length and strong curvature of these appendages suggest that they might comprise even more than five podomeres – we tentatively count as many as seven in their virtual reconstruction (Extended Data Figure 3a). Interestingly, the chelicerae of the closely related and contemporaneous *Offacolus* appear to have fewer podomeres. According to Sutton et al.²⁵, they are probably composed of three ‘units’, which would amount to a total of four podomeres if one finger of the terminal chela was mobile (Extended Data Figure 3b). For completeness, it is worth noting the hypothesis that eurypterids possessed four-segmented chelicerae, a view championed by Kjellesvig-Waering^{154,155} but one that has lost all support in modern literature^{156,157}. Similarly, the Jurassic scorpion *Liassoscorpionides* was originally described as possessing four-segmented chelicerae, rather than three-segmented chelicerae as in all modern and fossil scorpions¹⁵⁸. However, a re-examination of the sole available specimen concluded that these putative ‘chelicerae’ are more likely pedipalpal coxae¹⁵⁹, restricting the confirmed occurrences of multisegmented chelicerae in the fossil record to post-Cambrian offacolids and pycnogonids.

There is no evidence that this condition was present in older fossil chelicerates. The phosphatized Furongian pycnogonid larvae described by Waloszek & Dunlop³ all exhibit three-segmented chelicerae. While this does not exclude the possibility that adults of this taxon bore four-segmented chelicerae, no such evidence currently exists. The number of podomeres composing the putative chelicerae of *Mollisonia* is unknown, but these

appendages are minute and were described as extending only a short distance posteriorly beneath the cephalic shield¹⁴, suggesting that three podomeres would be the maximum. The non-chelate deutocerebral appendages of *Habelia* – the only members of the order Habeliida in which these appendages are known – are also short¹³. With their terminal claws, they more closely resemble the endopodal rami following them under the cephalon than putative multisegmented, sensory antenniform appendages (contra¹³).

The discovery of *Megachelicerax* provides definitive evidence for the presence of three-segmented chelicerae as far back as the middle Cambrian. Unlike the chelicerae of the Silurian *Dibasterium*, their morphology offers no indication of derivation from elongate, sensory appendages composed of numerous podomeres.

Phylogenetic analyses

The ‘antenniform phase’ hypothesis has received support in a few phylogenetic analyses that retrieved Chelicerata sensu stricto (i.e., chelicerae-bearing arthropods) nested within antennae-bearing Artiopoda, usually vicissicaudates (e.g.,^{6,11,12,25,120,160}). More recent studies, however, have recovered megacheirans in positions consistent with the evolution of chelicerae from megacheiran great appendages: either as sister to Chelicerata (e.g.,^{31,33,36}), as sister to a clade [Artiopoda+Chelicerata] (e.g.,¹³⁶), or as sister to a clade [[Artiopoda+Mandibulata]+Chelicerata] (e.g.,^{14,20,133}). Our own cladistic analysis retrieves megacheirans as a grade comprising the earliest diverging members of total group Chelicerata (Fig. 3, Extended Data Fig. 6), a position supporting a direct evolutionary relationship between these two types of grasping appendages.

In summary, multisegmented chelicerae rarely occur in extinct and extant chelicerates, the most extreme case being the Silurian synziphosurine *Dibasterium* (possibly up to seven podomeres). Other documented examples do not exceed four podomeres, and all post-date the three-segmented chelicerae of *Megachelicerax* by tens of millions of years. This pattern suggests that chelicerate multisegmentation is a derived condition that evolved convergently in post-Cambrian offacolid synziphosurines and pycnogonids. Even if four-segmented chelicerae were eventually documented in a Cambrian taxon, this would not provide

substantial support for the 'antenniform phase' hypothesis, particularly since most recent phylogenetic analyses do not back it. Rather, such a discovery would refine our understanding of the transformation of megacheiran megacheirae into chelicerae, suggesting that the reduction in the number of chelae (from three to one) was achieved before the reduction in the number of podomeres (six to three).

SUPPLEMENTARY NOTE 6: TAXA INCLUDED IN THE PHYLOGENETIC ANALYSES

TAXA	REFERENCES
<i>Chengjiangocaris kunmingensis</i>	161,162
<i>Alacaris mirabilis</i>	162
<i>Fortiforceps foliosa</i>	117,133
<i>Jianfengia multisegmentalis</i>	42,117,133
<i>Sklerolibyon maomima</i>	133
<i>Haikoucaris ercaeiensis</i>	7
<i>Yohoia tenuis</i>	8
<i>Alalcomenaeus cambricus</i>	9,163
<i>Leancoilia superlata</i>	95
<i>Leancoilia illecebrosa</i>	35,164
<i>Yawunik kootenayi</i>	140
<i>Acanthomeridion anacanthus</i>	165
<i>Acanthomeridion serratum</i>	117,165
<i>Australimicola spriggi</i>	166
<i>Zhiwenia coronata</i>	167
<i>Emeraldella brockii</i>	168
<i>Sidneyia inexpectans</i>	169,170
<i>Aglaspis spinifer</i>	115
<i>Glypharthrus magnoculus</i>	171
<i>Glypharthrus simplex</i>	115
<i>Glypharthrus trispinicaudatus</i>	102
<i>Brachyaglaspis singularis</i>	112
<i>Tremaglaspis unite</i>	115
<i>Tremaglaspis vanroyi</i>	172
<i>Eoredlichia intermedia</i>	173
<i>Olenoides serratus</i>	174
<i>Misszhouia longicaudata</i>	175
<i>Naraoia compacta</i>	175,176
<i>Naraoia spinosa</i>	177
<i>Sinoburius lunaris</i>	178
<i>Cindarella eucalla</i>	179
<i>Xandarella spectaculum</i>	117
<i>Helmetia expansa</i>	180,181
<i>Kuamaia muricata</i>	117
<i>Saperion glumaceum</i>	117
<i>Skioldia alata</i>	117
<i>Tegopelte gigas</i>	182,183
<i>Kwanyinaspis maotiashanensis</i>	184
<i>Retifacies abnormalis</i>	185
<i>Thelxiope holmani</i>	67

<i>Mollisonia symmetrica</i>	21
<i>Mollisonia plenovenatrix</i>	14
<i>Sanctacaris uncata</i>	10,11
<i>Habelia optata</i>	13
<i>Utahcaris orion</i>	23
<i>Wisangocaris barbarahardya</i>	12
<i>Megachelicerax cousteau</i> nov.	This study
<i>Pycnogonum litorale</i>	186
<i>Haliestes dasos</i>	151,187
<i>Palaeoisopus problematicus</i>	29,153
<i>Flagellopantopus blocki</i>	29,188
<i>Offacolus kingi</i>	25
<i>Setapedites abundantis</i>	20
<i>Dibasterium durgae</i>	26
<i>Weinbergina opitzi</i>	40
<i>Venustulus waukeshanesis</i>	100
<i>Lunataspis aurora</i>	189
<i>Lunataspis borealis</i>	190
<i>Limulus polyphemus</i>	191,192
<i>Tachypleus gigas</i>	193,194
<i>Yunnanolimulus luopingensis</i>	66
<i>Adelophthalmus pyrrhae</i>	143
<i>Slimonia acuminata</i>	156
<i>Eramoscorius brucensis</i>	195
<i>Proscorpius osborni</i>	196

SUPPLEMENTARY NOTE 7: CHARACTER CODING

The phylogenetic dataset includes 65 taxa and 112 morphological characters. Data incorporated from previously published studies are referenced with the following symbol key: OH_2013¹²¹, L_2016⁸¹, and LA_2017¹⁰².

CEPHALIC/PROSOMAL APPENDAGES

1. Nature of first (deutocerebral) cephalic/prosomal appendages

(0) raptorial / grasping appendage

(1) antennae

Remarks: see char. 1 in OH_2013. This character encompasses the deutocerebral raptorial / grasping appendage pair expressed in crown-group chelicerates^{192,197}, as well as stem-group representatives such as megacheirans based on the availability of preserved neuroanatomical data^{9,198}. *Megachelicerax* is unique among known Cambrian taxa by virtue of having extremely well-developed pincer-like chelicerae that extend prominently beyond the prosomal shield margins (Fig. 1; Extended Data Fig. 3). By contrast, this character is scored as uncertain for several taxa that have been considered as stem-group chelicerates but for which this structure has not been directly observed, namely *Sanctacaris uncata*¹¹, *Habelia optata*¹³, *Utahcaris orion*²³, and *Wisangocaris barbarahardya*¹². The presence of chelicerae in *Mollisonia plenovenatrix* follows the morphological interpretation proposed by Aria and Caron¹⁴, although these structures are minute and lack fine anatomical details. The mollisoniids *Mollisonia symmetrica* and *Thelxiope holmani* are also scored as uncertain since they lack appendicular data^{21,67}. We score the presence of a raptorial / grasping appendage in the pycnogonid *Flagellopantopus blocki* as it most likely has chelifores, although the terminal tips are not preserved²⁹.

2. Number of spine-bearing podomeres in raptorial appendage

(0) four

(1) three

(2) two

(-) inapplicable: nature of first (deutocerebral) appendage (Char. 1) antenniform

Remarks: see char. 2 in OH_2013.

3. Number of peduncular podomeres in raptorial appendage

(0) two

(1) one

(-) inapplicable: nature of first (deutocerebral) appendage (Char. 1) antenniform

Remarks: The short great appendages of megacheirans are characterized by the presence of a two-segmented peduncle (e.g., ^{8,42,95,133}); this condition is also observed in pycnogonids such as *Haliestes* and *Palaeopantopus* (e.g. ^{8,29,187}). By contrast, the chelicerae of *Megachelicerax* and xiphosurans have a single-segmented peduncle (Fig. 1; Extended Data Fig. 3). This character is scored as uncertain for the synziphosurine *Dibasterium* because it has remarkably elongate chelicerae with at least four segmental boundaries, but the precise number of peduncular podomeres cannot be resolved with confidence²⁶.

4. Number of raptorial cephalic/prosomal appendages

(0) one, deutocerebral appendages only

(1) two or more

(-) inapplicable: nature of first (deutocerebral) appendage (Char. 1) antenniform

Remarks: A single set of raptorial cephalic/prosomal appendages is ancestrally expressed in megacheirans (megacheirae), *Megachelicerax* (chelicerae) and Pycnogonida (cheliformes), whereas the presence of additional raptorial appendages in the prosoma represents a more derived condition observed in both extinct (e.g. *Dibasterium*, *Offacolus*, *Setapedites*) and extant crown-group euchelicerates (e.g. Xiphosura).

5. Orientation of elbow-joint articulation in deutocerebral raptorial appendages

(0) elbow-joint articulation orientated dorsally with forward-facing raptorial appendages

(1) elbow-joint articulation orientated ventrally with ventral-facing raptorial appendages

(-) inapplicable: nature of first (deutocerebral) appendage (Char. 1) antenniform

Remarks: This character distinguishes between the raptorial appendage configuration observed in megacheirans, in which the elbow joint is orientated dorsally resulting in forward facing appendages (e.g., ^{8,42,133}), and that of *Megachelicerax* and other more derived chelicerates (e.g. synziphosurines, xiphosurans, pycnogonids) in which the joint is orientated ventrally resulting in ventral-facing chelicerae^{25,26}.

6. Distal spines of raptorial appendages terminating in annulated flagella

(0) absent

(1) present

(-) inapplicable: nature of first (deutocerebral) appendage (Char. 1) antenniform

Remarks: see char. 3 in OH_2013. This character is exclusive to the distal flagella found in leanchoiliid megacheirans such as *Leanchoilia*^{35,95}, *Alalcomenaeus*¹⁶³ and *Yawunik*¹⁴⁰.

7. Length of distal spines on terminal podomeres of first (deutocerebral) appendages

(0) absent or shorter than podomere

(1) subequal to length of podomeres

(2) longer than entire podomere series

Remarks: see char. 4 in OH_2013.

8. Number of appendage-bearing post-ocular segments incorporated into the head/prosoma

(0) zero

(1) one

(2) two

(3) three

- (4) four
- (5) five
- (6) six
- (7) seven

Remarks: see char. 5 in OH_2013. This character embodies the variable number of observable appendage bearing segments on the head region. For consistency, character states vary from zero (0) to seven (7) post-ocular segments, although character state (0) and (3) are not represented in our sample. The range actually varies from a single appendage-bearing cephalic segment in *Sidneyia* (antennae only), two in fuxianhuiids (antennae and specialized post-antennal appendages), four or five as observed in several megacheirans and artiopods (uniramous appendage followed by biramous post-antennal appendages), six in *Megachelicerax*, synziphosurines, xiphosurids, eurypterids and arachnids (chelicerae and five prosomal appendages) and seven in Pycnogonida and possibly in taxa with an uncertain count such as *Habelia* and *Weinbergina*.

9. Nature of second (tritocerebral) cephalic/prosomal appendage

- (0) biramous
- (1) uniramous

Remarks: see char. 6 in OH_2013.

10. Nature of uniramous second (tritocerebral) cephalic/prosomal appendage

- (0) stenopodous limb
- (1) specialized post-antennal appendage
- (-) inapplicable: second cephalic appendage (Char. 9) biramous

Remarks: The uniramous second cephalic appendage fuxianhuiids is modified as the so-called specialized post-antennal appendage^{161,162}, whereas this condition is not found in any of the ingroup taxa considered in our analysis.

11. Nature of third (first post-tritocerebral) cephalic appendage

(0) biramous

(1) uniramous

Remarks: see char. 7 in OH_2013. The presence of uniramous third (first post-tritocerebral) cephalic/prosomal appendages is exclusive to crown-group Chelicerata in the context of the present analysis, namely members of Pycnogonida and Xiphosura. Notably, Ordovician–Devonian chelicerates retain the ancestrally (pseudo)biramous organization observed in Cambrian representatives^{20,25,26,40}.

12. Differentiation of sixth appendage pair relative to anterior appendages

(0) absent

(1) present

Remarks: This character reflects the unique morphological differentiation of the sixth appendage pair relative to the anterior limbs observed in euchelicerates, particularly expressed as the pusher leg of xiphosurans⁴⁵ as well as the swimming paddle of eurypterine eurypterids^{143,156}. This character is absent in scorpions^{195,196} as all the prosomal walking legs are morphologically and functionally similar.

13. Nature of sixth appendage pair differentiation

(0) pusher leg

(1) swimming paddle

(-) inapplicable: differentiation of sixth appendage pair (Char 12) absent.

14. Differentiation of seventh appendage pair relative to anterior appendages

(0) absent

(1) present

Remarks: This character reflects the morphological differentiation of the seventh appendage pair relative to the anterior limbs observed in *Habelia*¹³, *Megachelicerax* (Extended Data Fig. 1), synziphosurids^{20,25,26,40} and xiphosurans (e.g. *Limulus*, *Tachypleus*^{193,194}). This character is scored as present in Eurypterida based on direct morphological evidence from *Adelophthalmus pyrrhae*¹⁴³ that the seventh appendage pair is modified as internalized book gills within the opisthosoma. This character is also scored as present in the Silurian *Proscorpius*¹⁹⁶ and *Eramoscorpius*¹⁹⁵ based on their morphological similarity with extant scorpions.

15. Nature of morphologically differentiated seventh appendage pair

(0) biramous

(1) uniramous or with reduced endopod

(-) inapplicable: seventh appendage pair (Char. 14) not differentiated

Remarks: This character can be expressed as either a biramous appendage, as observed in *Habelia optata*¹³, or a uniramous appendage consisting mostly of the exopod with a highly reduced/absent endopod as observed in *Megachelicerax* (Extended Data Figs. 1, 2), synziphosurines, xiphosurans, eurypterids, and arachnids.

16. Nature of uniramous seventh appendage pair

(0) elongate uniramous pediform limb

(1) gill opercula/plate

(2) chilaria

(3) metastoma or sternum

(-) inapplicable: seventh appendage pair (Char. 14) not differentiated; seventh appendage pair (Char. 15) biramous

Remarks: The differentiated seventh appendage pair demonstrates a significant degree of morphological diversity, which can be expressed as either an elongate pediform limb (*Weinbergina*), a flattened gill plate (*Dibasterium*, *Megachelicerax*, *Offacolus*, *Setapedites*), or

greatly reduced chilaria (Xiphosura) , or the plate-like metastoma of Eurypterida and the sternum of Scorpiones which are considered a pair of highly modified appendages³⁹.

17. Nature of exopod on cephalic/prosomal biramous appendages

(0) simple flap with marginal setae

(1) exopod differentiated into proximal and distal lobes the proximal lobe bearing lamellae, the distal lobe bearing short setae

(2) lamellae-bearing broad flap

(3) tubulaceous with or without multiple spines per podomere

(-) inapplicable: second appendages (Char. 9) uniramous; third appendages (Char. 11) uniramous

Remarks: The exopod in the cephalic/prosomal appendages is highly variable depending on the taxonomic group. Most Cambrian representatives feature either a simple flap with marginal setae (e.g. fuxianhuiids, megacheirans) or a bilobed exopod with lamellae (e.g. trilobitomorphs). However, the presence of tubulaceous exopods is comparatively more restricted to *Megachelicerax* (Fig. 1; Extended Data Fig. 1, 4), *Mollisonia*¹⁴, *Habelia*¹³, sanctacaridids^{11,12} and synzhiphosurines^{25,26,40}. Among trilobitomorphs, *Sinoburius lunaris* is unique in having elongate tubulaceous-like cephalic exopods without spines¹⁷⁸.

18. Gnathobasic limbs

(0) absent

(1) present

Remarks: see char. 17 in OH_2013.

19. Proboscis

(0) absent

(1) present

Remarks: see char. 47 in L_2016

TRUNK/OPISTHOSOMAL APPENDAGES

20. Functional trunk/opisthosomal endopods

(0) absent or reduced

(1) present

Remarks: modified from char. 9 in OH_2013. Functional trunk endopods are present in most Cambrian arthropods, including fuxianhuiids, megacheirans, trilobitomorphs and habeliids. The loss of functional endopods characterizes the evolution of the opisthosomal tagma in early chelicerates, such as *Megachelicerax* (Fig. 1; Extended Data Fig. 1, 5), *Mollisonia plenovenatrix*¹⁴, synziphosurines^{25,26,40}, and some members of Xiphosura^{66,193,194}, Eurypterida¹⁴³, and Scorpiones^{39,195,196}.

21. Appendages of first trunk/opisthosomal segment underneath the cephalic/prosomal articulation

(0) absent

(1) present

Remarks: modified from char. 8 in OH_2013.

22. Trunk/opisthosomal exopods

(0) absent or reduced

(1) present

Remarks: Trunk/opisthosomal exopods are expressed in most arthropods in our analysis with sufficiently high quality of appendage preservation, with the notable exception of pycnogonids in which the opisthosoma is greatly reduced. Presence of opisthosomal exopods is scored as present in Eurypterida based on direct morphological evidence from *Adelophthalmus pyrrhae*¹⁴³. This character is also scored as present in the Silurian

*Proscorpius*¹⁹⁶ and *Eramoscorpius*¹⁹⁵ based on their morphological similarity with extant scorpions.

23. Trunk/opisthosomal exopod structure

- (0) simple flap with marginal setae
- (1) exopod differentiated into proximal and distal lobes the proximal lobe bearing lamellae, the distal lobe bearing short setae
- (2) lamellae-bearing broad flap or operculum
- (3) internalized book lungs
- (-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced

Remarks: modified from char. 10 in OH_2013. Given the discrepancy in exopod morphology expressed between the prosoma and opisthosoma in *Megachelicerax* (Fig 1; Extended Data Fig. 1, 2, 4, 5), *Habelia*¹³, *Dibasterium*²⁶, *Offacolus*²⁵, and *Setapedites*²⁰, this character is treated separately from the exopod morphology of the cephalon/prosoma (Char. 15). The presence of fully internalized book lungs is found in Scorpiones^{39,196}, whereas Eurypterida feature a moveable ventral operculum that accommodates the book gills¹⁴³.

24. Proximal lobe of trunk/opisthosomal exopod

- (0) flattened lobe
- (1) slender shaft
- (-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced; exopod structure (Char. 23) not differentiated into proximal and distal lobes

Remarks: see char. 11 in OH_2013.

25. Distal lobe of trunk/opisthosomal exopod

- (0) small to moderate sized flap
- (1) large teardrop shaped lobe with wide attachment
- (-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced; exopod structure (Char. 23) not differentiated into proximal and distal lobes

Remarks: see char. 12 in OH_2013.

26. Distal articulations in trunk/opisthosomal exopod lobe

(0) absent

(1) present

(-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced; exopod structure (Char. 23) not differentiated into proximal and distal lobes

Remarks: modified from char. 13 in OH_2013.

27. Imbricate trunk/opisthosomal exopod lamellae

(0) absent

(1) present

(-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced

Remarks: see char. 14 in OH_2013.

28. Lamellae organization

(0) thick, flat paddle-like lamellae

(1) delicate, comb-like lamellae

(-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced: lamellae (Char. 27) absent

Remarks: see char. 15 in OH_2013.

29. Non-overlapping marginal exopod setae

(0) absent

(1) present

(-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced

Remarks: see char. 16 in OH_2013.

30. Length of non-overlapping marginal exopod setae

(0) short

(1) elongate

(-) inapplicable: trunk/opisthosomal exopods (Char. 22) absent or reduced; marginal exopod lamellae (Char. 29) absent.

Remarks: see char. 16 in OH_2013.

31. Genital appendage

(0) absent

(1) present

Remarks: The genital appendage is a key character of Eurypterida^{39,157} and is regarded as the modified eighth endopodite associated with the corresponding genital operculum in the opisthosoma.

OCULAR STRUCTURES

32. Lateral eyes

(0) absent

(1) present

Remarks: see char. 18 in OH_2013.

33. Nature of lateral eyes

(0) stalked

(1) sessile

(-) inapplicable: lateral eyes (Char. 32) absent

Remarks: see char. 19 in OH_2013. aria

34. Lateral eye doublets

(0) absent

(1) present

(-) inapplicable: lateral eyes (Char. 32) absent

Remarks: Lateral eye doubles are expressed in Cambrian leanchoiliids^{9,95,140,198}, but no other megacheirans (e.g., ^{7,42,133}).

35. Visual surface with calcified lenses

(0) absent

(1) present

(-) inapplicable: lateral eyes (Char. 32) absent

Remarks: see char. 21 in OH_2013.

36. Dorsal bulge in exoskeleton accommodating drop-shaped ventral eyes

(0) absent

(1) present

(-) inapplicable: lateral eyes (Char. 32) absent; nature of lateral eyes (Char. 33) stalked

Remarks: see char. 22 in OH_2013.

37. Eye slits

(0) absent

(1) present

(-) inapplicable: lateral eyes (Char. 32) absent

Remarks: see char. 23 in OH_2013.

38. Dorsal median eyes

(0) absent

(1) present

Remarks: see char. 24 in OH_2013.

CEPHALIC/PROSOMAL EXOSKELETON

39. Head shield

(0) absent

(1) present

Remarks: modified char. 25 in OH_2013. We use head shield to refer to the expanded dorsal exoskeletal plate/tergite that covers the head region in most Palaeozoic arthropods groups, regardless of whether it is fused to the appendage-bearing segments (e.g., artiopods, megacheirans, habeliids) or not (e.g., fuxianhuiids). Pycnogonids are notable in lacking a head shield altogether.

40. Nature of head shield

(0) unfused to anterior segments, attached by anterior sclerite (e.g. fuxianhuiids)

(1) fused with anterior appendage-bearing segments into a cephalon

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 25 in OH_2013. The head shield of fuxianhuiids differs from that of other Palaeozoic arthropods in that it is not fused to the cephalic appendages as indicated by instances of disarticulation observed in the Xiaoshiba Biota, particularly *Chengjiangocaris kunmingensis*¹⁶¹.

41. First (deutocerebral) cephalic appendages elongate and projecting beyond head shield

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 115 in L_2016. The pterygotoid *Slimonia acuminata* demonstrates that early branching members of this clade ancestrally bore small chelicerae¹⁵⁶, whereas the massive chelicerae observed in well-known taxa such as *Pterygotus* are a secondarily derived condition. The chelicerae of *Proscorpius*¹⁹⁶ and *Eramoscorpius*¹⁹⁵ are clearly visible beyond the prosomal margins, so this character is scored as present for Scorpiones.

42. Expanded cephalic doublure

(0) absent

(1) present

(-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 27 in OH_2013.

43. Anteromedian margin of cephalon notched, accommodating strongly sclerotized plate (anterior sclerite)

(0) absent

(1) present

(-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 28 in OH_2013.

44. Hypostome

(0) absent

(1) present

Remarks: see char. 29 in OH_2013. As deuteropods¹⁹⁹, most taxa in our analyses either possess a confirmed embryonic labrum (e.g., *Limulus*¹⁹²) or likely did so (for most extinct forms), a structure homologous to the ancestral protocerebral frontal appendages of lower stem-group arthropods (e.g., radiodonts). The only notable exception is Pycnogonida, for

which a labrum has not been identified¹⁸⁶. Given their phylogenetic position, the labrum of all non-pycnogonid taxa in the analysis is expected to be expressed as a cover of the mouth opening, as exemplified by recent fossil data on Cambrian megacheirans^{35,42} and trilobites²⁰⁰. The present character refers specifically to the hypostome as a sclerotized ventral plate covering the labrum and the mouth opening²⁰¹.

45. Nature of hypostome

- (0) median extension of the doublure without suture
- (1) natant, hypostome not in contact with doublure
- (2) hypostome with narrow overlap with anterior sclerite
- (3) narrow attachment to doublure at hypostomal suture
- (4) butterfly-shaped with anterior margin delimited by lateral slits (e.g. fuxianhuiids)
- (-) inapplicable: hypostome (Char. 44) absent

Remarks: see char. 29 in OH_2013.

46. Reduced labrum

- (0) absent
- (1) present

Remarks: The labrum is a fundamental component of the arthropod head from a developmental and embryological perspective, and so it can be assumed that all members of Deuteropoda will have a homologue of the labrum, whether visible or not¹⁹⁹. Pycnogonida are a notable exception in this regard, but it has been hypothesized that the labrum might be incorporated as part of the proboscis¹⁸⁶. The presence of a developed hypostome implies the presence of an underlying labrum²⁰¹, which has been recently confirmed by the preservation of Cambrian trilobites in Morocco²⁰⁰. Exceptional data from Cambrian arthropods also demonstrate that in the absence of a sclerotized hypostome, it is still possible to resolve the presence of a labrum in pyritized macrofossils with soft tissue preservation such as the megacheirans *Jianfengia multisegmentalis*⁴² and *Leancoilia illecebrosa*³⁵. The recognition of a reduced labrum in *L. illecebrosa* establishes a link with crown-group chelicerates, in which

this structure has a similarly cryptic morphology¹⁹². In the context of our analysis, the presence of a hypostome (Character 44) implies the existence of a labrum, but the absence of a hypostome does not negate the existence of the underlying labrum.

47. Anterior sclerite

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 30 in OH_2013.

48. Dorsal ecdysial sutures

(0) absent

(1) present

Remarks: modified from char. 31 and 32 in OH_2013.

49. Elevated marginal rim

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 33 in OH_2013.

50. Marginal rim ornamented

(0) absent

(1) present

(-) inapplicable: marginal rim (Char. 49) absent

Remarks: see char. 34 in OH_2013.

51. Morphologically differentiated cephalic/prosomal axial region

(0) absent

(1) present – differentiation expressed in axial furrows, glabellar region or inflated axis

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 33 in OH_2013.

52. Morphologically differentiated cephalic/prosomal axial region with abrupt constriction on anterior margin

(0) absent

(1) present

(-) inapplicable: morphologically differentiated cephalic/proximal axial region (Char. 51) absent

Remarks: The character is recognized in the axial region of most habeliids (e.g. *Habelia*, *Sanctacaris*, *Utahcaris*^{11,13,23}) but absent in *Wisangocaris*¹² as there is no anterior constriction. Although the differentiated axial region of various artiopods is narrowed anteriorly, this character is scored as absent if the change is gradual rather than abrupt (e.g. aglaspidids).

53. Posterior width of morphologically differentiated cephalic/prosomal axial region

(0) equal or lesser width than pleural region

(1) wider than pleural region

(-) inapplicable: morphologically differentiated cephalic/proximal axial region (Char. 51) absent

Remarks: The posterior region of the differentiated prosomal axial region in habeliids and *Megachelicerax* is broader than the corresponding pleural region of the trunk. In all other taxa with axial differentiation, the posterior region is less pronounced.

54. Dorsal eyes confined to anterior half of cephalon

(0) absent

(1) present

(-) inapplicable: sessile eyes (Char. 33) absent; fused cephalon (Char. 40) absent

Remarks: see char. 82 in LA_2017. This character is scored as uncertain in the eurypterid *Adelophthalmus pyrrhae* as the preservation of the type material does not clearly show the preservation of ocular features¹⁴³, although these are well known in other species of the genus.

55. Dorsal eyes abutting glabella anteriorly

(0) absent

(1) present

(-) inapplicable: sessile eyes (Char. 33) absent; differentiated axial region (Char. 51) absent

Remarks: see char. 83 in LA_2017.

56. Dorsal eyes progressively merge with rest of cephalon/prosoma anteriorly

(0) absent

(1) present

(-) inapplicable: sessile eyes (Char. 33) absent; fused cephalon (Char. 40) absent

Remarks: see char. 84 in LA_2017.

57. Anterolateral cephalic notches accommodating lateral eyes

(0) absent

(1) present

(-) inapplicable: cephalic shield (Char. 39) absent

Remarks: Anterolateral cephalic notches that accommodate the lateral eyes are expressed in various taxa, including jianfengiids^{42,133}, *Habelia*¹³, *Mollisonia*^{14,21}, *Sanctacaris*^{10,11}, *Sidneyia*¹⁶⁹, and *Zhiwenia*¹⁶⁷.

58. Head shield outline

- (0) genal spines
- (1) acute genal angles
- (2) rounded genal angles
- (3) broad subtriangular lateral flanks
- (-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 36 in OH_2013. Habeliids^{11-13,23} and *Megachelicerax* (Fig. 1; Extended data Fig. 1) share the presence of broad lateral flanks on the genal region that are substantially more developed than conventional genal spines observed in trilobitomorphs or Aglaspididae^{102,115}, and entirely absent in synziphosurines^{20,25,26,40}.

59. Posterior cephalic band

- (0) absent
- (1) present
- (-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 37 in OH_2013.

60. Cephalic furrows

- (0) absent
- (1) present
- (-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 38 in OH_2013.

61. Sagittal keel on head shield

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 7 in L_2016.

62. Ophthalmic ridges on head shield

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent

Remarks: see char. 17 in L_2016.

63. Interophthalmic ridges on head shield

(0) absent

(1) present

(-) inapplicable: head shield (Char. 39) absent; ophthalmic ridges (Char. 62) absent

Remarks: see char. 24 in L_2016.

TRUNK/OPISTHOSOMAL EXOSKELETON

64. Cuticle sculpture

(0) absent

(1) present

Remarks: see char. 39 in OH_2013.

65. Biomineralized cuticle

(0) absent

(1) present

Remarks: see char. 40 in OH_2013.

66. Nature of trunk/opisthosomal tagmosis

- (0) trunk/opisthosoma with biramous appendages (at least exopod) throughout
- (1) trunk/opisthosoma divided into anterior biramous appendage-bearing region (pre-abdomen or mesosoma) and posterior biramous appendage-less region (post-abdomen or metasoma)
- (2) trunk/opisthosoma entirely devoid of appendages

Remarks: modified from char. 59 in OH_2013. Most taxa have a full set of biramous appendages throughout the trunk. Among Cambrian and Ordovician representatives, aglaspidids differ in the presence of paired post-ventral plates underneath the last two or three segments, which would occupy the position of the biramous appendages^{102,112,121}. Thus, the presence of the postventral plates effectively divides the trunk into an appendage-bearing region and an appendage-less posterior region. A post-abdomen-like differentiation is also expressed in the vicissicaudatans *Emeraldella*¹⁶⁸ and *Sidneyia*¹⁶⁹, and is widespread among synziphosurines^{20,25,26}. A trunk/opisthosoma entirely devoid of appendages is characteristic of Pycnogonida. Eurypterids are scored as having an opisthosoma divided into an appendage-bearing anterior region and an appendage-lacking posterior region based on the presence of the book gills and the widespread evidence of the genital appendages^{39,143}. Although the morphology of *Lunataspis* species suggests that this character is present^{189,190}, we conservatively score it as uncertain owing to the absence of appendicular information.

67. Trunk/opisthosomal tergites with expanded tergopleurae covering biramous appendages dorsally

- (0) absent
- (1) present

Remarks: see char. 41 in OH_2013. This character is expressed in most arthropods in our analysis, with the exception of pycnogonids as they lack expanded tergopleurae.

68. Free trunk/opisthosomal tergites

(0) absent

(1) present – at least one functional articulation within trunk/opisthosoma

Remarks: see char. 42 in OH_2013. This character is scored as present for *Lunataspis* species^{189,190}, as they uniquely combine the presence of freely articulating tergites on the anterior opisthosoma, followed by a fused thoracetron, and also an appendage-less posterior region with free tergites (see below).

69. Decoupling of trunk/opisthosomal tergites and appendage-bearing segments

(0) absent

(1) present

(-) inapplicable: trunk/opisthosomal region (Char. 66) without biramous appendages

Remarks: see char. 43 in OH_2013.

70. Articulation types within trunk/opisthosoma

(0) tergites non-overlapping

(1) extensive overlap of tergites

(2) edge to edge pleural articulations

(-) inapplicable: free trunk/opisthosomal tergites (Char. 68) absent

Remarks: see char. 44 in OH_2013.

71. Dorsal trunk/opisthosomal effacement/fusion

(0) tergites with defined (separate or fused) tergite boundaries

(1) tergite boundaries laterally effaced

(2) tergite boundaries completely effaced

Remarks: see char. 45 in OH_2013.

72. Cephalic/prosomal articulation fused

(0) absent

(1) present

(-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 46 in OH_2013.

73. Head shield overlap of trunk/opisthosomal tergites

(0) overlap absent or identical between thoracic tergites

(1) head shield covers first thoracic tergite only

(2) head shield covers multiple anterior trunk tergites

(-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 47 in OH_2013.

74. Cephalon articulates with first trunk/opisthosomal reduced tergite

(0) absent

(1) present

(-) inapplicable: fused cephalon (Char. 40) absent

Remarks: see char. 48 in OH_2013.

75. Degree of first trunk/opisthosomal tergite reduction

(0) first tergite with reduced tergopleurae compared to rest of trunk/opisthosoma

(1) microtergite without tergopleurae

(-) inapplicable: fused cephalon (Char. 40) absent; first trunk/opisthosomal tergite reduced (Char. 73) absent

76. Boundaries of anterior trunk/opisthosomal tergites reflexed anterolaterally

(0) absent

(1) present

Remarks: see char. 50 in OH_2013.

77. Joints between posterior trunk/opisthosomal tergites functional, anterior ones variably fused

(0) absent

(1) present

Remarks: see char. 51 in OH_2013.

78. Posterior trunk/opisthosomal tergite bearing axial spine

(0) absent

(1) present

Remarks: see char. 52 in OH_2013.

79. Raised axial region in trunk/opisthosoma

(0) absent

(1) present

Remarks: see char. 54 in OH_2013.

80. Anterior tergal processes

(0) absent

(1) present

Remarks: see char. 55 in OH_2013.

81. Tuberculation of posterior margin of tergites

(0) absent

(1) present

(-) inapplicable: cuticle sculpture (Char. 64) absent

Remarks: see char. 56 in OH_2013.

82. Articulating half rings

(0) absent

(1) present

Remarks: see char. 80 in OH_2013.

83. Axial furrows on trunk

(0) absent

(1) present

Remarks: see char. 81 in OH_2013.

POSTERIOR BODY

84. Axial dorsal cuticular extensions

(0) absent

(1) present

Remarks: see char. 57 in OH_2013.

85. Number of axial dorsal cuticular extensions

(0) single row of spines/nodes/carinae

(1) paired row of spines/nodes/carinae

(2) three rows of spines/nodes/carinae

(-) inapplicable: axial dorsal cuticular extensions (Char. 84) absent

Remarks: The extant Indo-Pacific horseshoe crab *Tachypleus* features three rows of spines¹⁹³, which differentiate it from the smooth surface of the Atlantic horseshoe crab *Limulus polyphemus*¹⁹⁴. Dorsal cuticular extensions are variably expressed in Palaeozoic arthropods in the present analysis, including aglaspidids, habeliids, megacheirans, mollisoniids, synziphosurines, and xiphosurans. *Flagellopantopus blocki* is scored as having a single row of nodes following Sabroux et al.²⁹.

86. Nature of dorsal extensions

(0) carinae or nodes

(1) well-developed axial spines

(-) inapplicable: dorsal cuticular extensions (Char. 84) absent

Remarks: Developed axial spine series are expressed in *Mollisonia plenovenatrix*¹⁴, *Thelxiope holmani*⁶⁷ and *Habelia optata*¹³, whereas in other taxa these features are expressed as more delicate carinae or raised nodes (e.g. *Leancoilia*, *Sanctacaris*, *Wisangocaris*). The presence of well-developed axial spines is one of the exoskeletal characters that differentiate the extant *Tachypleus gigas*^{193,194} from *Limulus polyphemus*, the latter of which has a smooth dorsal surface.

87. Subaxial nodes

(0) absent

(1) present

(-) inapplicable: axial cuticular extensions (Char. 84) absent

Remarks: see char. 108 in L_2016

88. Dorsal exoskeletal differentiation of posterior appendage-less region of trunk/opisthosoma

(0) absent – posterior tergites morphologically undifferentiated, albeit smaller

(1) present – elongate cylindrical posterior tergite with greatly reduced or absent pleural spines

(-) inapplicable: trunk/opisthosoma with biramous appendages (at least exopod) throughout (Char. 66) present

Remarks: This character differentiates the morphology of the posterior appendage-less region of the body, which may simply be expressed as having slightly smaller segments (e.g. *Megachelicerax*, *Sanctacaris*, *Yohoia*) in contrast with the presence of modified posterior cylindrical tergites (e.g. aglaspidids, *Emeraldella*, *Sidneyia*, synziphosurines, eurypterids and scorpions). Despite the absence of appendicular data, this character is scored as present in *Lunataspis* species based on the presence of cylindrical posterior tergites without extended pleurae.

89. Nature of morphologically differentiated cylindrical pre-terminal tergite

(0) preterminal tergite freely articulating

(1) preterminal tergite fused resulting in anterior expansion of tailspine base

(-) inapplicable: cylindrical posterior tergites without pleurae (Char. 88) absent

Remarks: modified from char. 86 in LA_2017.

90. Number of segments in posterior region without biramous appendages

(-) inapplicable: trunk/opisthosoma with biramous appendages (at least exopod) throughout (Char. 66) present

Remarks: This character embodies the variable number of observable appendage-lacking segments in the posterior region. The range varies from a single appendage-lacking segment of *Emeraldella* and *Sanctacaris*), two or three in several aglaspidids with preserved posterior ventral plate (e.g., *Aglaspis*, *Glypharthrus*, *Brachyaglaspis*), three in synziphosurines, four in some extinct pycnogonids, and five in eurypterids and scorpions.

91. Posterior tergites strongly curved in dorsal aspect compared to anterior tergites in trunk/opisthosoma

(0) absent

(1) present

(-) inapplicable: trunk tergites with expanded tergopleurae (Char. 67) absent; free tergites (Char. 68) absent

Remarks: see char. 61 in OH_2013.

92. Multisegmented trunk

(0) absent

(1) present

Remarks: The jianfengioid megacheirans *Jianfengia*⁴² and *Sklerolibyon*¹³³ share the presence of elongate trunk with over 30 appendage-bearing segments.

93. Fused posterior tergal shield in terminal position

(0) absent

(1) present

(-) inapplicable: trunk tergites with expanded tergopleurae (Char. 67) absent

Remarks: modified from char. 62 in OH_2013. This character is expressed as either the pygidium of trilobitomorpha, the posterior shield of *Mollisonia*, or the thoracetrone of Xiphosura. The unfused mesosoma of synzyphosurines and the xiphosuran *Lunataspis* are scored as absent because there is no fusion into a single posterior tergal shield; furthermore, *Lunataspis* species demonstrate the presence of cylindrical tergites in a posterior position relative to the fused thoracetrone that covers the mid-section of the opisthosoma^{189,190}.

94. Posterior tergal shield with broad median spine

(0) absent

(1) present

(-) inapplicable: posterior tergal shield in terminal position (Char. 93) absent

Remarks: see char. 65 in OH_2013.

95. Posterior tergal shield with lateral spines

(0) absent

(1) present

(-) inapplicable: posterior tergal shield in terminal position (Char. 93) absent

Remarks: modified from char. 66 in OH_2013.

96. Nature of lateral spines on posterior tergal shield

(0) fixed

(1) moveable and socketed

(-) inapplicable: posterior tergal shield in terminal position (Char. 93) absent; lateral spines on posterior shield (Char. 95) absent

Remarks: modified from char. 66 in OH_2013. This character differentiates the fixed spines formed as a direct extension of the pygidium of trilobitomorphs and mollisoniids, from the moveable/socketed spines in the thoracetron of xiphosurans.

97. Thoracetron

(0) absent

(1) present

Remarks: The presence of a thoracetron in xiphosurids is considered a unique mode of tergal fusion because it is possible for taxa to combine a thoracetron and have anterior freely articulating trunk tergites, and also a freely articulating posterior metasoma region without appendages, as observed in *Lunataspis*^{189,190}.

98. Tailspine

(0) absent

(1) present

Remarks: see char. 67 in OH_2013. Although not preserved in the type material¹⁴³, a tailspine is scored as present for the eurypterid *Adelophthalmus pyrrhae* as this is a widespread character in Eurypterida; however, more detailed aspects of the tailspine morphology and organization are conservatively scored as uncertain for this taxon.

99. Tailspine shape

(0) spinose

(1) paddle-shaped

(-) inapplicable: tailspine (Char. 98) absent

Remarks: see char. 68 in OH_2013.

100. Length of tailspine

(0) shorter than half length of trunk/opisthosoma

(1) longer than half length of trunk/opisthosoma

(-) inapplicable: tailspine (Char. 98) absent

Remarks: see char. 70 in OH_2013.

101. Numerous accessory marginal spines or setae on tailspine

(0) absent

(1) present

(-) inapplicable: tailspine (Char. 98) absent

Remarks: see char. 71 in OH_2013.

102. Paddle-shaped tailspine with thickened lateral flange

(0) absent

(1) present

(-) inapplicable: tailspine shape (Char. 99) spinose

Remarks: Scored as present in *Alalcomenaeus* following He et al. (2017).

103. Transverse articulation (functional or ankylosed) in tailspine

(0) absent

(1) present

(-) inapplicable: tailspine (Char. 98) absent

Remarks: Several taxa feature an articulation, or more, in the tailspine that is variable according to their morphology, including *Emeraldella*¹⁶⁸, *Retifacies*¹⁸⁵, sanctacaridids^{11–13,23}, *Offacolus*²⁵ and some extinct pycnogonids²⁰².

104. Transverse articulation in tailspine extending into short lateral spines

(0) absent

(1) present

(-) inapplicable: tailspine (Char. 98) absent; transverse articulations in tailspine (Char. 103) absent

Remarks: this character is expressed in all sanctacaridids^{11,12,23}.

105. Number of transverse articulations tailspine

(0) single articulation

(1) multiple articulations

(-) inapplicable: tailspine (Char. 98) absent; transverse articulations in tailspine (Char. 103) absent

106. Nature of spinose tailspine termination

(0) single pointed/blunt termination

(1) bifid termination

(2) trifid termination

(-) inapplicable: tailspine (Char. 98) absent; tailspine shape (Char. 99) paddle

107. Ventral sclerotized plate covering anal region

(0) absent

(1) present

Remarks: see char. 73 in LA_2017.

108. Nature of ventral sclerotized plate covering anal region

(0) single anal plate

(1) paired postventral plates

(-) inapplicable: ventral anal sclerite (Char. 107) absent

Remarks: see char. 85 in LA_2017.

109. Paired postventral plate medial attachment

(0) narrow attachment by central portion

(1) wide longitudinal

(-) inapplicable: ventral anal plate (Char. 108) is single

Remarks: see char. 82 in OH_2013.

110. Paired modified appendages attached to a cylindrical pre-terminal segment

(0) absent

(1) present

(-) inapplicable: cylindrical posterior tergites without pleurae (Char. 88) absent

Remarks: see char. 75 in OH_2013.

111. Nature of paired modified appendages

(0) flattened uropods

(1) furca

(-) inapplicable: preterminal modified appendages (Char. 110) absent

Remarks: see char. 76 in OH_2013.

112. Length of thorax relative to posterior tergal shield in terminal position

(0) longer than posterior tergal shield

(1) shorter than posterior tergal shield

(-) inapplicable: fused posterior shield in terminal position (Char. 93) absent

Remarks: see char. 79 in OH_2013.

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