

SUPPLEMENTARY DISCUSSION

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SYSTEMATIC PALEONTOLOGY

Panarthropoda Nielsen, 1995

Euarthropoda Lankester, 1904

Heptopodomera Aria et al., 2015

Order Hymenocarina Clarke, 1882 (emended Raymond 1935)

Type genus. *Canadaspis* Walcott, 1912.

Included taxa. Canadaspidida Novozhilov (in Orlov) [inc. Canadaspididae Novozhilov (in Orlov), Odaraiidae Simonetta & Delle Cave], Protocarididae Miller (emended hereafter). Other putative members are: Perspicarididae Briggs, *Nereocaris* Legg et al., *Jugatacaris* Fu & Zhang, *Plenocaris* Walcott and Waptidae Walcott.

Emended diagnosis. Euarthropods with bivalved carapace covering cephalothoracic region up to a large portion of post-cephalothoracic tagma; plesiomorphically, cephalothorax bearing well-developed antennules and enditic endopod podomeres with well-developed terminal claws; limb basis segmented; posterior tagma with tergo-pleural rings; tailpiece a rounded telson bearing well-developed caudal rami.

Protocarididae Miller, 1889

Type genus and species. *Protocaris marshi* Walcott, 1884 (by original designation).

Included genera. *Branchiocaris* Resser (*sensu* Briggs 1976), *Tokummia* gen. nov. (infra), *Protocaris* Walcott, *Loricicaris* Legg and Caron.

Emended diagnosis. Hymenocarine euarthropods with body enclosed for ca. 5/7 of its length in a bipartite dorsal carapace whose valves are sub-elliptical in shape, presenting an overall transverse sub-symmetry, with long axis ca. 1.85 times longer than short axis, and with convex antero-posterior and ventral margins and sub-straight dorsal margin; in dorso-ventral view, angle between posterior lobes of valves more acute than in anterior; short antero- and postero-dorsal extremities of carapacial valves produced into short, blunt spinose processes; margin of valves made of an undulated frieze-like rim; post-thoracic body poly-segmented, composed of ca. 40 tergo-pleural rings, with length and width of segments gradually tapering over the anterior half of its length; posterior tergo-pleural rings much wider than long (14 times); tailpiece with rounded, short tergal plate whose tergite covers several terminal body segments; pair of caudal rami attached to anal segment beneath tergal plate; appendages defining three distinct body tagmata; tagma I (head) comprising six somites: small eyes likely present; pre-oral sub-triangular anterior process composed of a dorsal sclerite covering a bilobed structure with both soft and sclerotized elements; antennules ca. 20-segmented, strong proximo-distal tapering coupled with an increase of segment length; post-antennular appendage undeveloped; third appendage with endopod and exopod reduced and gnathal base forming a large mandible with masticatory process; fourth appendage with reduced ?four-segmented endopod; tagma II ?11-segmented: first appendage a pair of clawed maxillipeds; remaining appendages long and robust, with basipod six-“segmented” (arthrodization unknown) bearing five spinose endites plus slightly larger proximal endite (“coxa”); endopod stout, seven-segmented, ending in a pair of long claws; exopod much shorter than endopod, stenopodous, ?seven-segmented, ending in rounded setose segment; tagma III ca. 50-segmented: appendages composed of increasingly reduced stenopodous endopod and large phyllopodous exopod; intestine a simple tube (2/9th of trunk diameter).

Tokummia katalepsis gen. et sp. nov.

Life Science Identifiers (LSIDs). urn:lsid:zoobank.org:act:EAC748D1-9FF5-49C4-917B-C015AABDCD1F (genus); urn:lsid:zoobank.org:act:9BF24AC0-424D-4314-8780-3AC1D9E8159C (species).

Etymology. *Tokumm* (Stoney Indian), “red fox,” name of the river running through Marble Canyon, close to the deposit where the holotype was found; *katalepsis* (Greek), “seizing, grasping, holding, assaulting,” by reference to the large, chelate maxillipeds of the animal.

Holotype. ROM 63823; paratypes ROM 63014, 63081, 63824–63827, 63736 (7 specimens)

Other material. ROM 63014, 63709, 63825, 63826(x1), 63827, 63829, 63840–63846, 63848, 63849 from Marble Canyon (“Thick” Stephen Formation).

Locality. Marble Canyon, Kootenay National Park, British Columbia, Canada.

Horizon. Upper “thick” Stephen Formation, Cambrian Series 3, Stage 5.

Diagnosis. Large (great axis of valve: 7.31 ± 1.47 cm; N=17) protocaridid arthropod with strongly developed maxillipeds (distal portion ca. 0.65 times carapace length); peduncle large cylindrical, to which articulate two elongate sub-opposing articles; outer element ending in a pair of unmovable spines; inner element curved distally, with tip abruptly turned inward and adorned with four teeth along curvature; caudal rami ca. 12-segmented, arched, tubular and ?setose.

Description (for references to figures, see main text and following section). *Habitus.* Posteriorward tapering, stout poly-segmented body enclosed for 5/7 of its length in a carapace divided into two distinct sub-elliptical valves; pair of antennules and large maxillipeds protruding anteriorly; thoracic tagma bearing strong endopods with well-developed claws; furcate tailpiece.

Carapace. Thick and large carapace (great axis of valve: 7.31 ± 1.47 cm; N=17) tightly jointed along the dorsal margin forming two sub-elliptical transversally sub-symmetrical valves truncated dorsally, with ventral and antero-posterior margins convex; long axis of valve ca. 1.85 times longer than short axis, and with convex antero-posterior and ventral margins and sub-straight dorsal margin; in dorso-ventral view, angle between posterior lobes of valves more acute than anterior; short antero- and postero-dorsal extremities of carapacial valves produced into short, blunt spinose processes; ventral extension of the carapace fully covering trunk limbs; strip of cuticle layering the underside of the carapacial joint, serving as hinge; internal surface of valves covered with a doublure; margin of valves made of an undulated frieze-like rim.

Anteriormost structure. Large rostral structure composed of two elements: a sclerotic plate and a likely bilobed, partly fleshy protrusion. Sclerotic plate with sub-triangular anterior extension and lateral “shoulders” with convex margins; lateral parts of sclerite bulgy and mostly covered by carapace in dorsal view, possibly attached to anterior extremity of body; posterior margin of sclerite uncertain. Protrusion placed underneath sub-triangular extremity of sclerite; dark traces at the base of these protrusions suggest presence of more strongly sclerotized elements; posteriorly, protrusion likely attached to anterior extremity of body.

Eyes. Pair of eyes possibly indicated by highly reflective spots located on the dorsal equivalent of the outer margin of the mandibular area.

Antennules. ca. 20-segmented. Stout aspect, with segments dramatically tapering and elongating proximally (from width ca. 10 times length to width 1/3 of length). Nine terminal segments commonly jutting out from under carapace in dorsal view. Additional distal-most segment minute and rounded, inserted laterally just posterior to the labrum and adjacent to the insertion of mandibles.

Mouth and stomodeal area. Mouth elongate, flanked by lip-like cuticular elevations where the masticatory margins of the mandibles may have been attached.

Mandible. Large (slightly more than half of anterior body width), ovoid, with masticatory (molaris) margin bearing a row of stout teeth.

Maxillule and maxilla. Exact limb morphology uncertain; maxillule possibly a much-reduced limb; proximal portion made of an elongate gnathobase with short masticatory margin with few, stout teeth and with rounded basis bearing spinose process attached interno-mesially; likely presence of a second proximal-most process with rounded, toothed endite and basal spine, similar to enditic outgrowths of posterior appendages.

Maxilliped. Long (about half of carapacial length), composed of a five-segmented proximal portion and a distal chelate portion with an enlarged basal article (=peduncle, or manus) and two claw elements; chelate part slightly longer than the three distalmost proximal segments altogether. First two proximal segments (p1, p2) forming lateral attachment to body and with limited flexibility; other proximal segments (p3 to p5) allowing for bending of appendage ventrally under the body; p3 to p5 as cylinders gently tapering proximalward, equally sized and jointed

by conspicuous arthrodial membranes. Manus (p6) with ellipsoidal longitudinal section, containing two spherical reflective spots possibly connected. Outer/dorsal element (p7), or pollex, an elongate article ending in strong bifid claw; claw elements triangular; lower claw element slightly longer than lower one; outer margin concave; spacing and size of distal claw elements identical in all specimens; fixed situation assumed, separation between lower element and ramus possibly of taphonomic origin; likewise, whole pollex commonly separated from manus by cuticular line interpreted as compressional fold, and fixed condition assumed based on the consistent position of the pollex in all specimens. Inner/ventral article (p8), or dactyl, gently curved outward in the first 2/3 of its length, and ending in a strong inward curvature so that the tip points outward and quasi laterally; ventral margin (facing dorsally) adorned just posteriorly to the distal curvature by four triangular teeth; dactyl movable, with base inserting in a cuticular notch at the base of pollex.

Trunk. Trunk composed of ca. 50 segments progressively tapering posteriorward; segments forming tergo-pleural rings; first eleven segments bearing biramous limbs with strong endopods ending in well-developed terminal claws; first eight exopods much shorter, exopods of trunk limbs 9 to (at least) 11 larger and morphologically similar to posterior exopods; posterior trunk segments (?12 and posteriorward) much wider than long throughout (up to 10 times); sternites well sclerotized and strongly expressed all along trunk.

Thoracic appendages. Appendages 6 to (at least) 11 biramous, with multi-partite basipod and strong, clawed endopods; appendages 6 and 7 ca. 1/3 thinner than following appendages; terminal claw gradually reduced in size from appendage 8. Thick arthrodial membrane at the base of the limb. Transition thorax (tagma II)/post-thorax (tagma III) unclear.

Basipod. Large (ca. 1/3 of limb length), enditic, 5-segmented. Four equally-sized distal endites known, proximal endite incompletely preserved. Enditic structure bipartite, composed of a rounded, toothed, setose dorsal element, and of a ventral spine with enlarged basis.

Endopod. Endopod seven-segmented (terminal claw included). Four first proximal podomeres gradually reduced in size; fifth podomere slightly longer than fourth, its interno-distal margin produced into a pair of spines, long as ca. the length of the segment proper; sixth podomere much reduced (ca. 1/2 of podomere 4); terminal podomere a pair of long and strong claws (length ca. 1/5 of endopod). Outer margin of podomere segments concave; inner margin straight to convex; podomeres 1 to 4 with small rounded projections on their interno-distal margins.

Exopod. Post-cephalic appendages 1 to 8: proximal portion elongate; remaining morphology unclear. Post-cephalic appendages 9 to (at least) 11: proximal portion elongate, distal portion soft and lobate, as long or longer than distance between limb attachment and ventral margin of carapace.

Post-thoracic appendages. Appendages ?12 and posteriorward gradually reduced in size; biramous, with dominant lobate phyllopodous exopod.

Basipod. Based on specimens preserved laterally, morphology similar to thoracic exopods. Morphology of terminal limbs in *Branchiocaris* suggests basipod becomes much reduced posteriorly and may retain fewer segments.

Endopod. Unclear in *Tokummia*. Known stages of reduction in *Branchiocaris* include an intermediate segmented limb retaining some of the podomere differentiation and a terminal series of vestigial segmented buds.

Exopod. Posterior exopods broad and soft, prone to multiple and irregular folding; no outstanding surfacial features observed; stacking of prominent material basally suggests the presence of a proximal lobe.

Gut. Gut a simple but rather large (1/3 of body diameter) intestine with no hindgut differentiation; foregut differentiation uncertain; no visible alimentary glands along the body.

Tailpiece. Tailpiece a rounded, bud-like telson with a pair of segmented (ca. 12 annuli) caudal rami attached to the latero-ventral articulation with the last segment of the trunk proper; attachment of caudal rami with telson covered by tergal plate possibly extending over additional pre-telson segments.

SYSTEMATICS AND SIGNIFICANCE OF MORPHOLOGY

Tokummia katalepsis gen. et sp. nov. is described based on 21 specimens (see Methods) assigned to Heptopodomera³² based on the presence of exopods in tagmata II and III and of endopods with seven podomeres in at least tagma II (Figs 1–3 and Extended Data Fig. 2). This species is also placed under Hymenocarina (emended above) based notably on the presence of a large bivalved carapace and multi-segmented enditic basipod; whether those segments are in fact arthrodized is presently unclear. *Tokummia* differs from *Branchiocaris*³³ in the larger size of its maxillipeds, the more distinct identity of its thorax by reduction of the exopods, and the segmentation of its

caudal rami. *Tokummia* also differs from *Protocaris*³³ in its overall size, as well as in its large maxillipeds. The assignment of *Protocaris* to Protocarididae as diagnosed here (see above) is provisional, as a study of this taxon and its relatives is currently in preparation by the authors. The erection of *Loricicaris*³⁴ in particular lacked justification with respect to the morphological differences between this new genus and *Protocaris*, and awaits revision.

Laterally preserved specimens (Fig. 1b–e and Extended Data Figs 2, 3) show that the body plan of *Tokummia* is composed of three tagmata: an anterior “head” tagma (tagma I), including five appendages plus an anteriormost bilobed structure; an intermediate “thorax” (tagma II) composed of up to 11 biramous appendages with strong endopods and small exopods; and a terminal “post-thorax” (tagma III) made of ca. 40 biramous appendages with gradually reduced endopods and dominant lobate exopods—we reserve the term abdomen for limbless portions of the trunk. The transition from tagma II to tagma III, and therefore the relative sizes of these tagmata, is unclear, but probably occurs around thoracic limb number 8. As suggested by the anatomy of *Branchiocaris*, in which stout endopods are identifiable but present in association with lobate exopods showing no clear reduction in size (Fig. 2l and Extended Data Fig. 7), the thorax of *Tokummia* and protocaridids in general may not be as strictly a defined tagma as, for instance, the pereion of malacostracan crustaceans³⁵.

Tokummia exhibits a prominent anterior sub-triangular structure between the antennules, (Figs 1e, f; 2a–e and Extended Data Figs 3a, 5a, b). Such a structure is also present in *Branchiocaris pretiosa* (Fig. 2a, c and Extended Data Figs 6, 7a–d, 8a–d). These specimens corroborate the pre-oral position of the structure and the likely presence of a bilobation underneath the main triangular component. *Tokummia* (Figs 1e, 2b, d and Extended Data Figs 3a, 5a, b) and *Branchiocaris* (Extended Data Fig. 6) also show latero-basal “shoulders” behind the pair of lobes. These were likely part of the frontal triangular element, forming a relatively large sclerotic plate which corresponds to the “anterior sclerite” identified in other stem panarthropods^{36–38}.

Although the nature and orientation of lateral eyes are likely different in protocaridids, the bilobed organ and its associated sclerite occupy the same frontalmost position as the inter-ocular sclerite present in other stem arthropods, such as *Canadaspis*³⁹. It may be distinct from the adjacent inter-ocular lobes, as both sclerite and lobes are clearly disconnected structures in *Canadaspis* (Extended Data Fig. 9a–f). Accordingly, we interpret the so-called “anterior sclerite” as the ocular/protocerebral tergite. The pre-oral topology of these frontal structures corresponds with the upper lip of extant arthropods, the labrum, which is often associated with dorsal and antero-ventral sclerites, as in *Tokummia* and *Canadaspis*. Whether an equivalent of a pre-oral sternite, i.e., a hypostome, was present in protocaridids remains unclear to us.

The labral complex of paratype ROM 63825 (Figs 1e, f, 2b, c and Extended Data Fig. 3a) constitutes one of the best evidence for the bilobed nature of the body protrusion underneath the protocerebral tergite or sclerite of the ocular somite (TOS). On the part (Fig. 2b, c), preserved in dorsal aspect, a complex split of the TOS followed the mesial margin of the labral protrusion beneath, onto which the right side of the sclerite was compressed (additional cracks make it difficult to differentiate the sclerite from the protrusion distally). This interpretation comes from the fact that this margin is symmetrical to that of an imprint on the left side, which belongs to another, lower lamina and hence should be the remains of the body protrusion seen in other specimens (e.g. Fig. 2a, e, Extended Data Fig. 6). Such infill of sediment between the left and right lobes would not be expected with a sclerite alone or if the fossil had split through that sclerite. Thick carbonaceous remains similar to those seen inside adjacent appendages (Fig. 1f) possibly represent protocerebral tissues connecting the labral complex to the central nervous system (see below).

The topology of the labral protrusions (Fig. 3) in protocaridids is in fact surprisingly reminiscent of the epistemo-labral complex described in solifuges, scorpions and mites⁴⁰. The latter structure is likewise composed of a plate—the possible equivalent of the “anterior sclerite”—covering paired lips with fleshy and sclerotized components. Those structures in chelicerates and mandibulates could therefore have a common origin. There is evidence that the chelicerate labrum is in general bilobed in the early stages of development⁴¹.

A frontalmost position of the labrum in protocaridids also suggests that its posterior migration post-dated the evolution of the mandibulate head. Since the labral complex in protocaridids includes the inter-ocular sclerite that we interpret as the protocerebral tergite (Fig. 2a, e and Extended Data Figs 5a, b, 7a–d, 8a–d), the hymenocarine labrum was likely innervated by the protocerebrum—the anterior part of the panarthropod brain. Traces of neural tissue in *Lyrarapax* were presented as evidence for the protocerebral identity of the anomalocaridid appendage⁴², which would have then been fused and reduced to become the euarthropod labrum. However, the anomalocaridid affinities of the frontalmost appendage of *Surusicaris*, in conjunction with a ground-pattern cephalic configuration typical of euarthropods in this taxon⁴³, conflicts with this hypothesis. Our phylogenetic results further suggest that the frontal appendages of *Occacaris oviformis*⁴⁴ and *Clypeacaris serrata*⁴⁵ may well illustrate remainders of “great appendage” morphologies among hymenocarine/stem mandibulate relatives. Thus, to us, the time and circumstances of the proto- to deutocerebral appendage transition in panarthropods and the origin of the labrum remain a conundrum.

Alternatively, the frontal complex of protocaridids could generally correspond to that of hymenocarines, with paired structures being appendicular or sensorial projections of the ocular somite⁴³, as recently discussed in a review of this topic⁴⁶. In that paper, however, the examples chosen by the authors to illustrate homologous or convergent frontal projections in extant taxa are almost exclusively immature specimens. This illustrates either that the comparison with the adults of extinct species should implicitly assume heterochronic differences (in that case, a peramorphic trend), or that these structures may not be comparable at all (as the authors themselves recognize). In that later case, the argument that none of these structures are appendicular and/or related to the labrum is difficult to hold, notably because of the problematic origin of the labrum described in the previous paragraph. Several of the “Orsten” larval taxa (e.g. *Rehbachella*, *Bredocaris*, *Agnostus*, *Oelandocaris*) also show bilobed pre-labral structures interpreted originally as median eyes (interestingly fused to what could be the labrum in *Agnostus*). Given their phylogenetic distribution (Fig. 4 and Extended Data Fig. 10), these structures may well represent a general characteristic of larval anatomy across several clades. If, on the contrary, they correspond to the structures seen in adult hymenocarines (in which labral structures would be unknown) and some trilobitomorphs, both their common origin implied by this hypothesis and their general absence in the adults of extant lineages would remain unexplained. The evolution of labral structures in crown euarthropods may also have been more complex than previously thought, and the hypostome-labrum may have formed in the various lineages from different combinations of sclerites and projections ultimately originating from the protocerebrum.

A pair of large, rounded sclerotic elements is present posterior to the insertion of the antennules, in the area of the stomodaeum in both *Tokummia* (Fig. 1c, 2d, f and Extended Data Fig. 5a) and *Branchiocaris* (Fig. 2e, k and Extended Data Figs 6–8). This structure is much larger than posterior gnathal outgrowths and is never associated with an endopod or an exopod. A long distal dentate margin is clear in both *Tokummia* (Fig. 2d, f) and *Branchiocaris* (Fig. 2e and Extended Data 7a–c, 8), which, together with their shape and topology, identifies these plates as mandibles in the mandibulate sense, with at least a well-developed *pars molaris*. In *Branchiocaris* specimens from Utah (Fig. 2k and Extended Data Fig. 8), the gnathal edge is broad, ellipsoid, and covered in a multitude of aligned ridges. The association of a rounded mandible without a distinct *pars incisivus* and such a gnathal configuration is, in particular, reminiscent of the mandibular condition of branchiopod crustaceans^{47–49}. Because these gnathal elements are placed directly behind the antennules, they should belong to the appendages of the second segment (the crustacean A2), but their typical mandibular morphology, the absence of similar gnathal pieces on the antenna of crustaceans and the remaining anatomy of the cephalon has led us instead to invoke the presence of an intercalary segment (see main text). Lateral to the mandibles are highly reflective spots that may correspond to lateral eyes (Fig. 1a), which would be atypically posterior in protocaridids.

Characteristically strong chelate appendages, whose peduncles protrude in front of the animal, are inserted well behind the mandibles (Fig. 1 and Extended Data Figs 1–5). *Branchiocaris* specimens show two pairs of small appendages present in the area between the mandibles and the chelate appendages (Fig. 2j, k and Extended Data Fig. 8e, f); the gnathobases of these smaller limbs are preserved immediately posterior to the mandibles in *Tokummia* (Fig. 2d, f and Extended Data Fig. 5a). These appendages bring the number of head pairs, excluding the labrum, to five, which is a mandibulate synapomorphy, and can, therefore, be called maxillule and maxilla, whereas the chelate appendages constitute the first pair of maxillipeds.

The chelate appendages differ in the morphology of the chela proper but share the same number of podomeres with *Branchiocaris*, that is, seven instead of the five originally described. In *Tokummia*, the peduncle articulates with two elongate articles: a movable inner/upper article, or dactyl, with curved, dented tip; and an outer/lower article, or pollex, ending in a pair of strong teeth (Fig. 1a, e–g and Extended Data Figs 3–5). Dark carbonaceous impressions similar to those described in the appendages of *Yawunik*³² are present in both the peduncle of the chela—branching into each article—and the antennules (Fig. 1a, e–g and Extended Data Figs 1, 3, 4). Their presence in both appendages (as well as at the base of the labral complex) suggests that their interpretation as nerves and possibly ganglia is correct³².

The maxillipede chelae, particularly large in *Tokummia*, are surprisingly convergent with the chelifores of certain early pycnogonid larvae, including *Pycnogonum*⁵⁰, *Achelia*⁵¹ and *Nymphon*⁵². Reasons for this resemblance, other than parallelism, would be difficult to justify unless there were dramatic appendage losses or gains at the origin of chelicerates or mandibulates. This is not directly suggested by Hox gene alignments⁵³, despite a strong difference in overlap of anteriorly expressed Hox genes between the clades. The contrasting presence of annulated exopods, annulated caudal rami, and post-oral gnathobases in the larva of the Cambrian pycnogonid *Cambropycnogon*⁵⁴, point rather to the existence of a radiative event that included the co-occurrence of cheliceromorph and crustaceomorph characters. Convergences of both body plans, well illustrated by the “Arachnomorpha” versus “Antennulata” debate³², are also due to the fact that typically crustaceomorph features are tied to an aquatic lifestyle and likely pre-dated the rise of panmandibulates. Bipartite tailpieces, for instance, such as

caudal rami and uropod-like modified posterior limbs, may be found in arachnomorphs (e.g. *Sidneyia*⁵⁵), and megacheirans (e.g. *Fortiforceps*³⁶), as well, even if likely analogous to those known in extant taxa. To some extent, the ancestral nature of aquatic adaptations also applies to enditic outgrowths on trunk limbs, as they are involved in current-based types of food processing and are present in all euarthropod clades containing aquatic taxa.

The following appendages are biramous. The basipods of tagma II are five-segmented, with each segment bearing a spinose endite (Fig. 2d, f, g and Extended Data Fig. 5a). As noted by Walossek⁵⁶, an endite-bearing segmented basipod is also present in *Canadaspis* and most likely in *Odaraia* (Extended Data Fig. 9g, h). A basipod with multiple endites is also a feature of certain crustaceans and crustaceomorphs, and characterizes notably the phyllopodous limb of branchiopods and phyllocarids. Branchiopod larvae and especially those of notostracans⁵⁷ display trunk limbs that, in the very early stage of their formation, are composed of rows of rounded, spinose endites very similar to those on the basipods of *Tokummia*. Within tagma II, the endopods are composed of seven strong podomeres, thus the interpretation of poly-segmented endopods in those taxa⁵⁸ is a misinterpretation of the basipod. These limbs are heptopodomeran *sensu* Aria et al.³². Whether a multi-segmented basipod also exists in fuxianhuiids, euthycarcinoids and multi-segmented megacheirans could be difficult to determine if the supernumerary podomeres arose by the effacement of distinctive basipod margins.

Distally, the endopods of tagma II form a complex made of the pair of distalmost claws and the pair of claws borne by the antepenultimate podomere. Paired elongate spines produced from the upper distal podomere endites characterize *Sidneyia*^{55,59} and *Canadaspis*³⁹, but also leanchioliids^{32,60}, *Agnostus* in its meraspis stage⁶¹, and the walking legs of certain eurypterids⁶². In *Sanctacaris*, such claws are complemented by a third, median spine⁶³. In laterally-preserved *Tokummia* specimens (Fig. 1b, d and Extended Data Figs 1, 2), posterior exopods abruptly cease jutting out below the carapace ventral margin at the posterior end of tagma II, which suggests a distinct reduction in exopod size. The attachment margin of the exopods in this area is distinct, but the distal morphology remains uncertain.

Posterior appendages (tagma III), gradually reduced in size so as to become minute, have a dominant exopod whose folding during preservation and absence of structure is reminiscent of the phyllopodous exopod of branchiopod crustaceans. A large basis similar to appendages of tagma II is present at the base of those limbs within at least the first third of tagma III (Figs 1e, 2m and Extended Data Fig. 1). *Branchiocaris* (Fig. 1n) illustrates the presence of frail stenopodous endopods associated with these exopods.

The tailpiece is composed of a tergal plate that seems to cover additional segments (Fig. 1b and Extended Data Figs 1, 2) and the base of two annulated rami attached underneath the plate to the anal segment (Fig. 1a, b and Extended Data Figs 1a, b). These rami are therefore caudal rami in the pancrustacean sense, as defined by Schram³⁵.

OTHER TAXA POSSIBLY RELATED TO HYMENOCARINA AND THE SIGNIFICANCE OF FOSSIL LARVAE

Archaeostracans represent another prominent group of large bivalved arthropods during the Palaeozoic that have so far been considered as relatives to phyllocarid malacostracans⁶⁴. Our phylogenetic resolution of two of the best known archaeostracans, *Cinerocaris* and *Nahecaris*, supports a close affinity of at least some archaeostracans with leptostracans and other malacostracans (Extended Data Fig. 10). This result means that phyllocarid crustaceans, such as *Nebalia* have retained or converged on plesiomorphic characteristics of the hymenocarine body plan (e.g. bivalved carapace, tergo-pleural rings). Notostracan branchiopods show the greatest similarities with protocaridids in their multisegmented trunks, annulated caudal rami and arrangement of trunk limbs—giving to the trunks of *Tokummia* and *Branchiocaris* preserved ventrally a typical notostracan aspect. Striations on the masticatory margin of the mandibles in *Branchiocaris* is another characteristic documented in branchiopods⁶⁵. Other details of the stomodeal area, maxillule and maxilla in protocaridids, however, are insufficiently known to make further comparisons. The proximal morphology of maxillule and maxilla (dentate coxae), the morphology of the antennules (short, robust, annulated, uniramous) and absence of antenna constitute nonetheless considerable differences between protocaridids and branchiopods/leptostracans.

As in hymenocarines, limbs with a high number of podomeres in general also characterize Euthycarinoidea *sensu lato*, a clade including fuxianhuiids, which here represent the mandibulate stem, even if the distinction between basipod and endopod is not clear in either euthycarcinoids *sensu stricto* or fuxianhuiids (fuxianhuiids are generally considered lacking a basipod^{36,66}). Since they were first described, fuxianhuiids have been considered by many to be basalmost arthropods^{37,58,67}, even in the absence of polarization among dinocaridids or isoxyids for their alleged plesiomorphic traits, i.e. “two-segmented” heads and poly-segmented trunk limbs. The five endopods and tergites following the chelate appendage in fuxianhuiids are in fact clearly differentiated from

those of the trunk^{37,66} (being shorter, uniramous, or both), and hence arguably belong to the cephalic tagma. Following this interpretation, our phylogenetic result reinforces previous views⁶⁸ comparing fuxianhuiids with euthycarcinoids, despite the lack of mandibles and peculiar head configuration of the former³⁷. The presence of three nested optic neuropils in *Fuxianhuia*⁶⁹ also supports a more derived placement for this group⁷⁰. Euthycarcinoids *s.s.* have traditionally been difficult to resolve systematically, but multipodomorous, uniramous endopods and mandibles are now well-documented characters, as well as the presence of antennular frontal appendages^{71–73}. Importantly, several euthycarcinoid species show a decoupling between sternite (and appendages) and tergite numbers, a trait seen in myriapods and notostracans but also in fuxianhuiids (see char. 150 and 151 below). The Argentinian *Apankura* described by Vaccari et al.⁷³ also seems to possess smaller post-mandibular appendages that could be part of the cephalon.

We do not find support for other taxa to constitute the mandibulate stem. Contrary to a previous study⁷⁴, we find here that *Marrella* has no clear character diagnostic of total-group Mandibulata. Instead, we find that *Marrella* is sister taxon to Mandibulata *sensu lato*+Chelicerata *sensu lato* (Extended Data Fig. 10). As such, marrellomorphs could be representatives of the early differentiation of the tritocerebral (=post-antennular) appendage. By contrast, most Orsten-type larval taxa resolve as crown tetraconates, in accordance with a previous study⁷⁵, but some of these species, such as *Bredocaris*⁷⁶ or *Rehbachella*⁷⁷, show extensive morphological similarities with protocaridids (and hymenocarines in general). These include the bivalved carapace, the tergo-pleural rings, the bipartite tailpieces, the annulated antennules, the mandibles, and most notably their subdivided, enditic basipods. The ontogeny of *Rebachella*⁷⁷ in particular revealed a mandible that was not only “gnathobasic” in a broad sense—this hypothesis received developmental support via the study of *Distal-less* expression patterns⁷⁸—but also originated from a pre-basal, or coxal segment homologized with reduced pre-basal elements, termed “proximal endites”⁷⁷. Limb morphology in adult protocaridids and other hymenocarines (i.e. subdivided basipod with heptopodomeran endopod) thus corroborates that a subdivided basis was the plesiomorphic condition that allowed for the evolution of the coxa and the mandible, possibly via the fusion of several basal endites. The antero-posterior morphology of appendages in *Bredocaris*⁷⁶ is also consistent with this view. These interpretations support to a great extent the hypothesis⁷⁹ that one or more of these additional basal segments were to become the proximal pleurites of myriapods, malacostracans and insects⁸⁰.

Other larval taxa, however—*Agnostus*’ meraspis, *Oelandocaris* and other leanchiiliidomorph larvae (Extended Data Fig. 10)—are retrieved among stem groups. They all represent early ontogenetic stages that display morphological differences from the adults of related taxa, and all likewise exhibit features interpreted as crustaceomorph⁸¹. Those morphological traits are mainly antennulate frontal appendages, stenopodous exopods and large, anterior labral structures. Given that at least those fossil larvae are unlikely to be directly related to crustaceans, this means that the concerned clades (leanchiiliid megacheirans and artiopods) had developed ontogenetic niches from which crustacean-like morphologies evolved. This situation further suggests that some mandibulate traits may have later emerged through paedomorphosis, and, overall, that the separation of niches occupied by adults and juveniles played a role in the accelerated evolution taking place at the origin of extant clades⁸². Heterochrony could have been a strong evolutionary driver, especially if the development of stem arthropods was less canalized than that of crown ones^{83,84}.

PHYLOGENETIC ANALYSIS—METHODOLOGICAL NOTES

General comments

The following list of characters and corresponding dataset (Supplementary Dataset 1) are part of a work on panarthropod morphology started in 2010 and continuously updated. It was initially based on the works of Briggs and Fortey⁸⁵, Waggoner⁸⁶, Fortey et al.⁸⁷, Wills^{88,89}, Edgecombe and Ramsköld⁹⁰, Budd⁶⁷, Cotton and Braddy⁹¹, Hendricks and Lieberman⁹², Kühl et al.⁹³, and Daley et al.⁹⁴. It has been modified and updated to include the works of Stein and Selden⁹⁵, Legg et al.⁵⁸, Briggs et al.⁹⁶, Ortega-Hernández et al.⁹⁷, and Lamsdell⁹⁸. Additional morphological information on extant taxa was gathered from other sources^{35,99–103}, especially Rota-Stabelli et al.¹⁰⁴ (RS2011 hereafter), which itself relies heavily on the works of Edgecombe et al.¹⁰⁵, Giribet et al.¹⁰⁶, and Edgecombe¹⁰⁷. Contrary to, e.g. Legg et al.⁵⁸, we have not implemented the entire dataset of RS2011 in our matrix, in order to avoid a massive addition of uncertainties in fossils. It has been shown that the effect of missing data was a factor of missing entry proportion as well as total taxon number (e.g. Prevosti and Chemisquy¹⁰⁸), which mostly generates polytomies by collapsing nodes on the basis of an excess of possible, equally valid states. Although the issue of taxon incompleteness can be circumvented by character exhaustiveness¹⁰⁹, this does not apply to our matrix because of its relatively small size, and would only be worsened by adding quantities of extant-only characters

coded as missing entries for fossils. We limited the input of characters difficult or impossible to code for fossils to the major synapomorphies supporting the topology of Rota-Stabelli et al., including a large portion of the neurological evidence that has recently become available through pioneering work on Cambrian taxa¹¹⁰. It should also be noted that certain characters in RS2011 pertain to different changes to the same morphological structures, and it is not always clear whether those changes were the results of different evolutionary events—possibly creating redundancy. We complemented our analysis by adding phylogenetic signals from molecular data, in the form of a “backbone constraint,” based on the topology from Regier et al.¹¹¹. In keeping with previous observations of the behavior of phylogenetic analyses of panarthropods³², we treated inapplicable states as missing data but tried to optimize the dataset by creating a sovereign³² character for each multistate character describing a different homologous structure.

We have limited our sample of large bivalved arthropods from the Cambrian to the best known taxa—*Branchiocaris*, *Canadaspis*, *Odaraia* and, now, *Tokummia*. Two other well-preserved taxa in particular were not included due to revisions needed or ongoing. *Nereocaris*, first, was presented as providing evidence on the origin of arthrodization, but very little was in fact shown from its limb morphology (see fig. S2 in Legg et al.⁵⁸), and most of its anatomy, especially cephalic, remains unresolved. This taxon will have to be revised in light of the information provided here, and its phylogenetic position retested accordingly. The second of these taxa, *Waptia*, could have reinforced the placement and monophyly of Hymenocarina, as it has recently been interpreted as a mandibulate with an intercalary segment¹¹², but the study was based on a limited number of specimens and left the exact morphology of some features as conjectural. A reexamination of *Waptia* using all material available is currently in progress.

We have implemented larval taxa based on the morphology of the latest developmental stage known (in *Pycnogonum*⁵⁰, we took into account the presence of the reduced appendages 2 and 3, even if they are lost in later stages). We acknowledge the general criticism of Sharma et al.¹¹³ that the implementation of a selection of semaphoronts at different life stages altogether with adult morphologies may not be ideal from a Hennigian point of view. However, without discussing the issue further here, our results are consistent either with previous analyses⁷⁵ (Orsten crustaceomorphs) or with the original identification of these larvae (leanchoiliid larvae, *Cambropycnogon*), and otherwise illustrate our point about the importance to consider possible differences in morphology between larvae and adults (*Agnostus* meraspis stage). We do recognize the weight of heterochronic effects on such an approach and we leave here the case of Orsten-type larvae resolved as crustaceans to be ambiguous: it remains possible that they represent larvae of much more ancestral taxa which would display overall morphologies optimized as derived.

The disparity of our sources forced us to often use several representative genera for higher taxonomic levels, rather than just one genus per major group. This is also the reason why we did not include the individual genera in our analysis. The list of representative taxa is as follows:

Nematoda: *Caenorhabditis*
 Priapulida: *Priapulius*
 Tardigrada: *Stygarcus*, *Hypsibius*, *Milnesium*
 Onychophora: *Peripatus*, *Euperipatoides*
 Leanchoiliidae: *Alalcomenaeus*, *Leanchoilia*, *Yawunik*.
 Pycnogonida: *Pycnogonum*, *Flagellopantopus*, *Endeis*, *Colossendeis*, *Ammotheidae*
 Araneae: *Cupiennius*, Mygalomorphae
 Scorpiones: *Scorpio*, Scorpionidae
 Opiliones: *Phalangium*, *Siro*, *Nipponopsalis*, *Equitius*
 Euthycarcinoidea: *Synastrus*, *Apankua*, *Kottixerxes*, *Sottixerxes*
 Pauropoda: *Pauropus*, Pauropodinae
 Symphyla: *Scutigera*
 Chilopoda: *Lithobius*, *Scutigera*, *Scolopendra*
 Diplopoda: *Illacme*, *Glomeris*, *Proteroiulus*, *Polyxenus*
 Copepoda: *Mesocyclops*, *Archimisophria*
 Cephalocarida: *Hutchinsoniella*
 Remipedia: *Speleonectes*, *Lasionectes*
 Isopoda: *Porcellio*, *Phreatoicus*, *Oniscidea*
 Euphausiacea: *Meganocyphus*, *Euphausia*, *Bentheuphausia*, *Stylocheiron*
 Anaspidacea: *Anaspides*
 Stomatopoda: *Squilla*, *Harpisquilla*, *Erugosquilla*

Leptostraca: *Nebalia*, *Paranebalia*
 Zygentoma: *Thermobia*, Lepismatidae
 Odonata: *Libellula*
 Coleoptera: *Tribolium*
 Diptera: *Drosophila*
 Hymenoptera: *Pseudomyrmex*

Comparison of topologies

Topologies complementary to the cladogram in the main text (Fig. 4) are provided in Extended Data Fig. 10.

When removing the larval/juvenile taxa (Extended Data Fig. 10D), the topology remains largely unchanged, but all most parsimonious trees retrieve in this case monophyletic Hymenocarina and Euthycarcinoidea s. l. clades as sister groups to mandibulates. The fact that the consensus tree of the total dataset (Extended Data Fig. 10C) resolves hymenocarines as a polytomy is therefore a likely consequence of the addition of larval taxa, which provide, as expected, a phylogenetic signal conflicting with adult species.

Under an unconstrained analysis (without backbone; see Extended Data Fig. 10E), the general basal topology remains the same but hexapods and myriapods are resolved together as Atelocerata within mandibulates. As a result, Orsten-type crustaceomorph taxa are resolved as a stem-mandibulate grade, similarly to a recent phylogenetic analysis using implied weighting¹¹⁴, although the latter supported Tetraconata owing to its use of the full dataset in Rota-Stabelli et al.¹⁰⁴. Interestingly such a configuration also optimizes hymenocarines as allied to ostracods and branchiurans in Oligostraca, and, therefore, as pancrustaceans, while fuxianhuiids become sister group to chelicerates. That hymenocarines group here with some other bivalved crustaceans would cause an even greater contrast with recent interpretations and come much closer to the originally suspected crustacean affinities, but given, first, that this topology is not consistent with Tetraconata and, second, that the unconstrained topology is still very susceptible to changes in the matrix, we leave this result to further research.

Due to the fact that we separated many characters in arthropods and lobopodians by coding them as inapplicable to one another, the very base of the tree is inconsistent between cladograms, and nodes are poorly supported within the same analysis. We therefore refrain from discussing lobopodian/onychophoran/tardigrade relationships in this study, although these taxa, as well as dinocaridids, are important for the polarization of some characters.

CHARACTER LIST

GENERAL CHARACTERS

[1] Limbs

- 0. Absent
- 1. Present

[2] External cuticular segmentation

- 0. Absent
- 1. Present

[3] Type of segmentation

- 0. Sclerotized
- 1. Arthrodized (=tergal)

Remark: The integumental subdivision of anomalocaridid bodies remains unclear beyond the absence of tergites. Based on *Opabinia*¹¹⁵, but also *Schinderhannes*⁹³ and isoxyids⁴³, it seems that external segmentation is present, replacing annulation, but that these segments are not articulating tergites. Arthrodization throughout refers to the presence of sclerites articulating via arthrodial membranes.

[4] Calcified cuticle

- 0. Absent
- 1. Present

[5] Calcification type

- 0. Calcium phosphate
- 1. Calcium carbonate

[6] Holometaboly

- 0. Absent
- 1. Present

Remark: Apomorphy of Holometabola/Endopterygota. Inapplicable outside hexopods.

LOBOPODIAN CHARACTERS

[7] External anteriorization restricted to a single pair of ocular appendages

- 0. Absent
- 1. Present

Remark: Various lobopodians, such as luolishaniids and “hallucigeniids,” had evolved the differentiation of more than one pair of anterior limbs, which contrasts with the primary involvement of the first axial pair in *Aysheaia*, *Onychodictyon*, large forms such as *Megadictyon* and dinocaridids. We coded 0 for isoxyids and euarthropods, given that these taxa display a head tagma involving several limbs pairs (see char. 31).

[8] Lobopodous limbs

- 0. Absent
- 1. Present

Remark: This character codes for the presence of any annulated limbs in the onychophoran sense, defining the “lobopodian” group of taxa. There has been a debate regarding the presence of lobopodous limbs in *Opabinia*¹¹⁵⁻¹¹⁷. Consistently with some of our earlier observations⁴³, we regard the striated

traces interpreted as lobopods in *Opabinia* as partially internal structures that connect to the gill blades. Lobopodous limbs are also coded as present in *Surusicaris*.

[9] Type of main lobopodous trunk limb

- 0. Short, conical, subequal or shorter than trunk width
- 1. Elongated, slender, longer than trunk width

Remark: The existence of long-legged morphotypes, as opposed to short-legged morphotypes, has been recognized before among lobopodians, e.g. Haug et al.¹¹⁸. We concur with this distinction, regardless of limb differentiation along a single body plan. However, while *Hallucigenia* spp. and onychophorans most clearly characterize those two different states, *Onychodictyon* and *Aysheaia* represent the limits of the dichotomous separation, as differences in length and shape in these taxa are greatly reduced. A morphometric analysis of lobopod shape across genera could help redefine this *a priori* important character.

[10] Flap-like lateral limbs

- 0. Absent
- 1. Present

Remark: Soft, lobate flaps are diagnostic of dinocaridids. We assume here that phyllopodous exopods are unrelated to them, and remain agnostic about their relation to lobopods proper.

[11] Nodes/tubercles/dermal papillae

- 0. Absent
- 1. Present

Remark: We consider the tubercles on the integument of onychophorans and a number of lobopodians to be homologous. We code them as absent in hallucigeniids, as there is not, to our knowledge, clear evidence of nodes or tubercles on the annuli/plicae of these taxa. At the very least, these structures are sufficiently reduced or modified to justify the coding of a different state.

[12] Differentiation at limb insertion

- 0. Absent
- 1. Present

Remark: This character is applicable only to lobopodians because it is incompatible with segmentation. It designates in these taxa any differentiation of the integument at the location of limb insertions (and the corresponding body ring, but not necessarily the entire metamere), whether an interruption in the annulation pattern or the presence of cuticular outgrowths. Although there is evidence for differentiation at limb insertion in the form of anastomosing plicae in certain onychophorans¹¹⁹, the interruption of the annulation pattern is only partial, and we therefore code 0 for all onychophorans.

[13] Dorso-lateral sclerites above limb insertion

- 0. Absent
- 1. Present

Remark: This character and all following dependencies are applicable only to lobopodians. It could be hypothesized that lobopodian sclerites are developmentally and evolutionarily related to arthropod sclerites¹²⁰. We opted here for a neutral coding and differentiated this character from the possession of tergites/sternites proper.

[14] Median spine above limb insertions

- 0. Absent
- 1. Present

Remark: Armoured luolishaniids possess an additional row of median spines¹²¹⁻¹²³.

[15] Lobopod tip (main trunk limb)

- 0. Double claw
- 1. Juxtaposed series of claws
- 2. Pad

Remark: As previously stated¹²³, the pad/foot of onychophorans is a very peculiar autapomorphy of this group. The arrangement in multiple juxtaposed claws of tardigrades, however, is also observed in *Aysheaia* and *Diania*. The condition in *Luolishania* has been the subject of debate^{121,124-126}, and we code it here as uncertain.

[16] Posterior-most single claws

- 0. Absent
- 1. Present

Remark: Yang et al. 2015¹²³ noted that single claws seem to characterize the posterior limbs of a number of luolishaniids and hallucigeniids. After reevaluation of the available evidence, we largely concur with the validity of this character, in spite of the taphonomic uncertainty related to the exact count of claws. The evidence is particularly strong in *Hallucigenia sparsa*¹²⁷, with dozens of specimens corroborating the observation.

[17] Posterior claws pointing anteriad

- 0. Absent
- 1. Present

Remark: As discussed by various authors^{128,129}, a number (to us, a majority) of lobopodians share with tardigrades an anterior orientation of the posteriormost claws. It is especially clear and consistent across specimens of *Aysheaia*¹³⁰ and *Hallucigenia*¹²⁷, rejecting a taphonomic origin of this condition.

VISUAL ORGANS

[18] Ocelli as primary ocular units

- 0. Absent
- 1. Present

Remark: We have grouped all ocular features known in lobopodians under the single denomination of ocelli, grouping all types made of one or several visual units¹³¹. Euarthropod ocelli or median eyes as secondary visual organs are coded in character 18.

[19] Median eyes

- 0. Absent
- 1. Present

Remark: We code phosphatocopines and ostracods with median eyes instead of lateral eyes. In ostracods in particular, molecular studies have suggested that their compound eyes were not homologous to the lateral eyes of other arthropods¹³².

[20] Number of median eyes

- 0. 2
- 1. 3
- 2. 4

[21] Rhabdomeric lateral eye

- 0. Absent
- 1. Present

[22] Type of lateral eyes

- 0. Simple lens with cup-shaped retina
- 1. Faceted (compound)
- 2. Stemmata

Remark: Character from RS2011 #95.

[23] Type of corneagenous cells

- 0. Many
- 1. Two

Remark: Character from RS2011 #101.

[24] Tetraconate condition

- 0. Absent
- 1. Present

Remark: This character codes for the tetrapartite crystalline cone forming the ommatidia of crustaceans and insects. Tetraconata is a synonym for Pancrustacea.

[25] Number of nested optic neuropils

- 0. 1
- 1. 2
- 2. 3

[26] Multi-layered rhabdomeres

- 0. Absent
- 1. Present

Remark: This character is diagnostic of chilopods and diplopods¹³³.

[27] Eyes embedded within tergal shield

- 0. Absent
- 1. Present

[28] Ophthalmic ridges

- 0. Absent
- 1. Present

[29] Lateral eyes pedunculate

- 0. Absent
- 1. Present

[30] Pedunculate eyes projecting frontalward, large and ovate

- 0. Absent
- 1. Present

Remark: The pedunculate lateral eyes of a number of euarthropods are distinctly ovoid and protruding forward, with their peduncles attaching to the anteriormost portion of the head, sometimes semi-detached from the remainder of the cephalon (as in fuxianhuiids¹³⁴, euthycarcinoids⁷³, *Odaraia*¹³⁵ and generally in anostracans¹³⁶).

HEAD AND CEPHALIC CHARACTERS

[31] Somital head (as tagma I) defined by series of appendages and/or external segmentation

- 0. Absent (only anteriormost defines head)
- 1. Present

Remark: It has not always been accepted that the euchelicerate prosoma could be called a head, as opposed to a cephalothorax¹³⁷, but since such a condition would be an apomorphy equivalent to coding a state for six pairs of prosomal limbs in the anteriormost tagma, we adopt the latter approach. The fact that a cephalon with six pairs appendages could not be called a head, however, seems contradicted by *Sanctacaris*^{43,63,138}. Lobopodians with a prominent pair of anterior appendages lack a head tagma per se, in contrast to e.g. *Surusicaris*. The presence of head tagmata in dinocaridids is uncertain.

[32] Somites defining anteriormost tagma

- 0. 5
- 1. 6
- 2. 7
- 3. 9

Remark: This character codes for the traditional conception of the arthropod head in fossils and extant taxa. State 3 (9 somites) is reserved as an autapomorphy for the specific case of the *Pycnogonum* larva. *Sanctacaris* and fuxianhuids are coded as uncertain. Note that we coded state 1 for all mandibulates, although certain taxa such as crustaceans with cephalothoraces transcend this plesiomorphic condition. Their condition is addressed in char. 38.

[33] Tergal sclerotization of the post-ocular somite

- 0. Absent
- 1. Present

Remark: This character accounts for the presence a post-ocular tergite, whether a shield or carapace, excluding “anterior sclerites” (see char. 127).

[34] Tergal sclerotization type

- 0. Tergites with posterior expansion, some cephalic tergites can be freely articulating (carapace)
- 1. Tergites with limited expansion, cephalic tergites fused (shield)

[35] Carapacal valves

- 0. Bivalved
- 1. One plate

Remark: State 1 applies to univalved crustaceans but also to *Burgessia*. The bivalved condition is represented by a medial fold with a variable separation of the valves per se (see char. 35).

[36] Bivalved configuration

- 0. Unfused along most of dorsal margin
- 1. Fused along most of dorsal margin

Remark: The state of fusion of the carapacal valves has been briefly discussed in different papers (e.g. ¹³⁹), but a review of this character is in progress. We consider the valves of *Canadaspis* and *Waptia* to be loosely attached to one another relative to, e.g., the protocaridid carapace.

[37] Covering of the bivalved carapace (when body fully extended antero-posteriorly)

- 0. At least two thirds of body length
- 1. Cephalothorax

[38] Cephalothorax

- 0. Absent
- 1. Present

Remark: The term cephalothorax designates the association of posterior appendages with the somital head in different arthropod clades to form a coherent functional unit.

[39] Articulation of posterior margin of shield with first trunk segment

- 0. Tergal overlap
- 1. Closure

Remark: In general, shields either articulate with the first trunk segment through overlapping tergites or form a closed occipital margin with limited freedom of movement.

[40] Segmental impression in shield

- 0. Absent
- 1. Present

[41] Occipital lobe

- 0. Absent
- 1. Present

[42] Pair of occipital carinae

- 0. Absent
- 1. Present

[43] Anterior reduction of segments and/or appendages

- 0. Absent
- 1. Present

Remark: The length of anteriormost tergites and appendages can be dramatically reduced compared to posterior segments. This is a feature shared notably among mandibulates.

[44] Cephalic compaction

- 0. Absent
- 1. Present

Remark: In addition to the reduction of segments and appendages, cephalization is sometimes associated with the extreme reduction of the cephalic shield in a distinct anteriormost unit. This condition characterizes, for instance, insects, but also isopods. We implement it for its potential importance as a “local” synapomorphy.

[45] Doublure

- 0. Absent
- 1. Present

[46] Cephalic kinesis

- 0. Absent
- 1. Present

Remark: From RS2011, char. 88.

BRAIN CHARACTERS

[47] Ganglia of post-oral appendages fused into single nerve mass

- 0. Absent
- 1. Present

Remark: From RS2011, char. 64. We do not regard the condition of leanchoiids¹⁴⁰ to be equivalent to that of euchelicerates, owing to the difference in head configuration and development of trunk limbs. We code 0 for fuxianhuiids following Yang et al.¹⁴¹.

[48] Contiguity of the first two post-protocerebral ganglia

- 0. Absent
- 1. Present

Remark: Deuto- and tritocerebral ganglia in a number of mandibulates are generally forming a contiguous mass, separate from more posterior ganglia^{142,143}, which suggested the notion of “tripartite” brain in these taxa (see, e.g. Edgecombe et al.¹⁰⁵, char. 44). This appears to be the case also in leanchoiids¹⁴⁰, despite the fact that Tanaka et al. identified this mass as the single ganglion of the “great appendage.”

[49] Fan-shaped body in brain

- 0. Absent
- 1. Present

Remark: From RS2011, char. 66. See also Strausfeld¹⁴⁴.

[50] Position of midline neuropil

- 0. Superficial to protocerebrum
- 1. Embedded within protocerebral matrix

Remark: From RS2011, char. 69.

[51] Olfactory lobes linked to a lateral component of protocerebrum by olfactory globular tract

- 0. Absent
- 1. Present

Remark: From RS2011, char. 73.

[52] Deutocerebral olfactory lobe with glomeruli

- 0. Absent
- 1. Present

Remark: From RS2011, char. 80.

[53] Protocerebral bridge

- 0. Absent
- 1. Present

Remark : From RS2011, char. 78.

STERNITES (CEPHALON)

[54] Sternites

- 0. Absent
- 1. Present

Remark: We made this character dependent upon evidence for segmentation. Some have claimed that sternites were absent in fuxianhuiids, see e.g. supplemental material in Yang et al.¹²³, but they are clearly present in *Shankouia*⁶⁶, Fig. 1E and likely present in *Fuxianhuia* (Chen et al.¹³⁴ and fig1F,L in Bergström et al.¹⁴⁵). Yang et al.¹²³ cite Chen et al.¹³⁴ as supporting their view that sternites are absent in

fuxianhuiids, whereas Chen et al. in fact describe “abdominal sternites [that] connect with the tergites laterally, producing a closed casing for the abdominal soft parts.”

[55] Endosternum

- 0. Absent
- 1. Present

Remark: From RS2011, char. 259. The endosternum is a strong euchelicerate apomorphy. The condition in pycnogonids¹⁴⁶ is left as uncertain.

[56] Hypostome

- 0. Absent
- 1. Present

Remark: There has been much discussion about hypostomes^{147,148}, as they arguably represent an evolutionary benchmark along the arthropod tree. In crustaceans, the hypostome, or pre-oral sternite, can be associated with an outgrowth called the labrum. The labrum develops as a pre-oral fold, with its Anlage sometimes developed ontogenetically into a pair of buds¹³⁷. Some (e.g. ¹⁴⁹) have insisted on the distinct nature of the labrum; this distinction is correct, even if both structures belong to the same pre-oral area and are sometimes difficult to discriminate. We emphasize here the nature of the hypostome as a sclerotic plate. In malacostracans, this structure forms a distinctly bipartite complex called the epistome-labrum, and can extend significantly posteriorly behind the second antennal pair. In chelicerates, the terms labrum, hypostome and epistome have been regularly used interchangeably to designate the pre-oral sclerite, but Dunlop⁴⁰ specifically designated the labrum as a lip-like structure belonging to the Solifugae, Pseudoscorpiones, Acari and possibly Opiliones; in this case, however, the sclerotic element associated with the labrum is more likely a tergite than a sternite, as in the composite “labrum” of scorpions (see char. 110). In myriapods and insects, the hypostome-labrum complex is usually referred to as a “clypeo-labrum,” “epipharynx,” or likewise “epistome-labrum.” We construe that the clypeus of terrestrial mandibulates integrates the epistome (in crustaceans) and hypostome. In this study, we homologize pre-oral plates as sternites of the second segment, and we use the word labrum to refer to structures originating from the anteriormost somite. Further studies are needed to determine whether the hypostomes of stem arthropods are always sternites of the second head segment or whether they can be sternites of the first segment. The current scenario implies events of migration of the ocular labrum from ventrally anterior to ventrally posterior to the pre-oral sternite.

Starting with the description of *Fuxianhuia protensa*³⁶, there have been numerous claims about the presence of a hypostome in fuxianhuiids, including in a recent study of the head of these animals³⁷. However, we have found no evidence for the presence of a hypostome in any of the available documentation, including in the description of *Shankouia*¹⁵⁰ and the high quality imagery of the anterior cephalic area in the brain study of *Fuxianhuia*⁶⁹. In Yang et al. ³⁷, lines labeled “hyp” never point to a clear structure or a structure distinct from the inter-ocular sclerite. Chen et al. ¹³⁴ made a better case for a post-frontal plate, but since the area under the cephalic shield in specimen 19255b is a negative imprint, it is questionable whether the “anteroventral plate” is a remainder of the carapace. It seems likely, however, that the “specialized post-antennal appendages” had corresponding sternites, and their para-oral insertion would imply that these sternites would form a plate covering the mouth. For these reasons, we code “?” in fuxianhuiids.

As discussed in a previous study³², the presence of a hypostome in adult megacheirans is uncertain. Liu et al. ¹⁵¹ labeled a rounded, anteriormost structure in a leanchoiid larva from China as a hypostome. This is consistent with the presence of a pre-oral structure called a labrum in *Oelandocaris*⁸¹, proposed as a megacheiran larva³² and resolved as such in this study. In the absence of evidence for a plate-like structure, we shall consider that leanchoiid larvae possess a labrum.

No pre-oral structure has been described in isoxyids.

[57] Hypostome type

- 0. Conterminant
- 1. Natant
- 2. Fused with doublure

Remark: An overview of this character was provided by Cotton and Braddy¹⁵².

[58] Labrum (as a distinct, partly soft structure)

- 0. Absent
- 1. Present

[59] Hypostome-labrum covering mouth

- 0. Absent
- 1. Present

[60] Labium

- 0. Absent
- 1. Present

Remark: The labium is the differentiation of the maxilla (=second maxilla) involving sternitic elements, and is homologous across mandibulates.

[61] Post-hypostomal sternites externally developed within segments 2–4

- 0. Absent
- 1. Present

Remark: Sternites have not received consistent attention in the arthropod literature. Cephalic sternites in particular are less documented overall, as they may be difficult to access, reduced, weakly sclerotized or internalized. Following their work on the arthropods from Orsten-type localities, Müller and Walossek^{153,154} defended the existence of a group called the Labrophora¹⁵⁵. This group, which was to include Eucrustacea and Phosphatocopina, was based notably on the presence of a post-oral plate (“sternum”) made of the fused mandibular and maxillular sternites—a trait allegedly present in the nauplii of crown crustaceans. To our knowledge, the universality of this apomorphy has not been clearly demonstrated; in fact, there seems to be considerable variation in larvae and adults alike (e.g. these sternites are distinct in the early stages of *Nebalia*¹⁵⁶). In Euphausiacea¹⁵⁷, the mandibular sternite is limited to its invaginated bridge-like apodeme, and joined to the paragnathal sternite, all distinct from maxillular and maxillary sternites, which, in turn, can be either fused or unfused. In other cases, such as in the Cephalocarida, clarification may be needed, as photographic evidence of fusion (Fig 3A in Edgecombe et al.¹⁰⁵) conflicts with reconstructions of separate sclerites (Fig. 3 in Bitsch and Bitsch¹⁵⁸). In the present study, cephalic sternites were considered to be developed in the presence of paragnaths—and in many of these taxa, the reduced development of other cephalic sclerites is often assumed to be a reversal—but we never assumed the fusion of mandibular and maxillular sternites in crustaceans.

[62] Fusion of post-hypostomal sternites externally developed within segments 2–4

- 0. Absent
- 1. Present

[63] Metasternite

- 0. Absent
- 1. Present

Remark: The metasternite is a large sternum typically found in the prosoma of chelicerates, which then differs from the post-cephalic sternum of, e.g., decapod crustaceans.

[64] Coxosternite

- 0. Absent
- 1. Present

Remark: The coxosternite, typically in myriapods, is the gnathobasic plate of the maxilliped resulting from the fusion of a limb basis and its corresponding half-sternite.

[65] Both larval and imaginal head has tendention to form a hypostomal bridge

- 0. Absent
- 1. Present

Remark: Panzygothoracan apomorphy, *sensu* Kluge¹⁵⁹ (2004). Inapplicable outside hexopods.

FRONTALMOST APPENDAGES

[66] Arthrodization of first axial appendage

- 0. Absent
- 1. Present

[67] Ocular lobes

- 0. Absent
- 1. Present

Remark: A number of fossil and extant arthropods have vestigial anteriormost appendages, often inserted between the eyes and likely belonging to the ocular somite. The identity of frontal inter-ocular lobes in taxa such as *Canadaspis* is considered protocerebral here, but a more detailed study is needed.

[68] Bipartite labrum

- 0. Absent
- 1. Present

Remark: This condition applies to all arthropods with paired pre-oral lips or lobes, including protocaridids, *Agnostus* (tentatively) and *Archezogetes*.

[69] Branching frontalmost appendage

- 0. Absent
- 1. Present

Remark: We refrain here from using the term “multiramous” to avoid the confusion with biramous appendages. Based notably on musculature, Boxshall¹⁶⁰ discussed how known antennules were composed of a single true axis. We construe that this condition is similar in “great appendages.”

[70] Rami of branching frontalmost appendage originating from different podomeres

- 0. Absent
- 1. Present

Remark: This character differentiates the typically bipartite antennule of malacostracans from types involving a more complex branching pattern (typically megacheiran). Stomatopods are coded 0 since flagellae originate from the same podomere.

[71] Frontalmost appendage with flagellate extensions

- 0. Absent
- 1. Present

[72] Frontalmost appendage chelate

- 0. Absent
- 1. Present

[73] Orientation of first axial appendage

- 0. Ventro-frontal
- 1. Dorsal

[74] Segmentation of frontalmost arthrodized appendage

- 0. Multi-segmented
- 1. Reduced

Remark: We considered the reduced state to be inferior to six segments. Artiopod antennules are considered segmented, and not annulated, following e.g. Boxshall⁷⁹.

[75] Arthrodized frontalmost appendage, multi-segmented type

- 0. Robust, thick branch
- 1. Long antennular

[76] Inner spinose outgrowths on arthrodized frontalmost appendage

- 0. Absent
- 1. Present

Remark: For a more detailed review of the “inner” and “outer” spine characters, see Aria and Caron⁴³. In this analysis, inner and outer spines in the dinocaridid sense are coded as absent in euarthropods.

[77] Type of inner spinose outgrowths on frontalmost appendage

- 0. Sub-equal length or tapering gradually along entire margin
- 1. Elongate mid-margin

[78] Secondary spines on inner spinose outgrowths of frontalmost appendage

- 0. Absent
- 1. Present

[79] Outer spinose outgrowths on arthrodized frontalmost appendage

- 0. Absent
- 1. Present

[80] Outer spinose outgrowth on arthrodized frontalmost appendage with elongate terminal spine

- 0. Absent
- 1. Present

Remark: A differentiation by elongation of the distal outer spines is characteristic of the *Anomalocaris* group and isoxyids⁴³.

OTHER CEPHALIC LIMBS

[81] All cephalic endopods posterior to second pair well-developed

- 0. Absent
- 1. Present

Remark: This character primarily differentiates artiopods and chelicerates from mandibulates, in which some or all cephalic endopods are partially or totally reduced, at least in adults. The well-developed endopods are considered to be based on a heptopodomeran morphology; palps are considered sufficiently modified to depart from this definition.

[82] Endopod of second appendage pair

- 0. Developed
- 1. Reduced

[83] Endopod of third appendage pair

- 0. Developed
- 1. Reduced

[84] Endopod of fourth appendage pair

- 0. Developed
- 1. Reduced

[85] Endopod of fifth appendage pair

- 0. Developed
- 1. Reduced

[86] Some cephalic endopods are walking limbs

- 2. Absent
- 3. Present

[87] Repeated appendage morphology in tagma I

- 0. Absent
- 1. Present

Remark: This character codes for the presence of “duplicate” appendages within the somatic head, that is, successive appendage pairs that display identical or nearly identical morphologies. Thus, in taxa coded for 0, any successive pairs are differentiated from each other, which likely is the derived condition and is characteristic of most mandibulates and certain eurypterids, such as megalograptidae (see Lamsdell et al.¹⁶¹).

[88] Dichotomy in appendage morphology between tagma I and tagma II

- 0. Absent
- 1. Present

Remark: Most extant taxa but also some fossils show an abrupt change in limb morphology between the anterior series of appendages, or the last pair of this series, and the following ones.

[89] Proximo-distal differentiation of endopod podomeres in head (tagma I)

- 0. Absent
- 1. Present

Remark: This character refers to the relative elongation of certain podomeres, as opposed to uniform podomeres in the endopod.

[90] Podomere number in head (tagma I)

- 0. 7
- 1. <7
- 2. >7

Remark: The condition of seven endopodial podomeres (six segments and a terminal claw) is an especially well-constrained state across stem and extant arthropod groups. Notwithstanding variations, including the loss or subdivision of existing podomeres, this character has been found to have a strong influence on phylogenetic reconstructions, and has, for that reason, been associated with an entire euarthropod clade, the Heptopodomera Aria et al.³². Whenever there is variation between head limbs, we code “1” if at least one endopod shows seven podomeres.

[91] Post-antennular appendage expressed

- 0. Absent
- 1. Present

Remark: Post-antennular is here used a generic term for post-frontalmost, whether the frontalmost appendage is an antennule, a chelicera or a “great appendage”. We refrain from using the brain-based “deutocerebral” and “tritocerebral” terms, because most of the matrix is still coded based on external topological observations. The absence of expression implies here the presence of an intercalary segment in larvae, as in hexapods and myriapods.

[92] Post-antennular appendage differentiated

- 0. Absent
- 1. Present

Remark: The pair of appendages following the frontalmost appendages in euarthropods—presumably, the tritocerebral appendage—can be either identical to the morphology of posterior head limbs or have a morphology of its own.

[93] Chelate or sub-chelate termination of post-antennular appendage

- 0. Absent
- 1. Present

Remark: The alignment of the arthropod head and, in particular, of the homology of the chelicerae with the antennules of mandibulates, has been the subject of a long lasting debate¹⁴⁸. Although there is now a growing consensus that the chelicera is deutocerebral and has the same origin as antennules¹⁶², we remain here agnostic; this character in particular codes only for chelate pedipalps and therefore does not affect taxa other than chelicerates. For the same reason, we code “?” in *Offacolus* and *Dibasterium* for characters 95 and 96 below.

[94] Post-antennular appendage reduced, terminating in a strong claw

- 0. Absent
- 1. Present

Remark: The post-antennular appendage of fuxianhuiids, sometimes called the specialized post-antennal appendage (SPA)³⁷, is segmentally reduced and curved under the head, apparently ending in a single claw.

[95] Ramification of post-antennular appendage

- 0. Uniramous
- 1. Biramous

[96] Developed endites on endopod of post-antennular appendage

- 0. Absent
- 1. Present

[97] Endopod of post-antennular appendage annulate or flagellate

- 0. Absent
- 1. Present

[98] Podomere number of endopod of post-antennular appendage

- 0. <7
- 1. 7

[99] Coxa on post-antennular appendage

- 0. Absent
- 1. Present

Remark: Many euarthropod taxa have a well-developed proximalmost segment on the post-antennular appendage in addition to the basis. We call this a coxa, as per its use in crustaceans. In *Martinssonina*¹⁶³, this coxa is present on this appendage in a vestigial form, as a “proximal endite” (see Walossek⁷⁷).

[100] Exopod of post-antennular appendage, type

- 0. Stenopodous
- 1. Annulate
- 2. Rodiform
- 3. Paddle
- 4. Tripartite

Remark: The post-antennular exopods of the early leanchioid larva described by Liu et al.¹⁵¹ appear very similar to those of *Oelandocaris*, and are considered stenopodous here.

[101] Exopods on cephalic appendages excluding two anteriormost pairs

- 0. Absent
- 1. Present

[102] Exopod of cephalic appendages excluding two anteriormost pairs, type

- 0. Stenopodous
- 1. Annulate
- 2. Rodiform
- 3. Paddle
- 4. Tripartite

[103] Multisetose, rounded tip on cephalic exopods

- 0. Absent
- 1. Present

Remark: This type of limb termination is encountered in a variety of euarthropods, including copepods, Orsten crustaceomorphs *Offacolus* and *Dibasterium*. The setose appendage identified in the head of *Sanctacaris* is different from what has been described as the exopods¹³⁸. We are currently revising the description of *Sanctacaris* and its relatives.

[104] Enditic outgrowths on cephalic endopods excluding two anteriormost pairs

- 0. Absent
- 1. Present

[105] Endopod of third cephalic appendage chelate or subchelate

- 0. Absent
- 1. Present

[106] Third cephalic appendage with a well-developed gnathobase

- 0. Absent
- 1. Present

Remark: A gnathobase is a strongly developed basal (i.e., corresponding to the basis) podomere with dentate proximal margin.

[107] Third cephalic appendage a mandible

- 0. Absent
- 1. Present

Remark: Although the gnathobasic mandible of mandibulates has sometimes been homologized with the gnathobases of euchelicerates (e.g. Popadic et al.¹³⁷), other views based on the evolution of the

“proximal endite”^{77,164}, as well as this study argue that a pre-basal, coxal segment at least contributed to the formation of the mandible. We therefore separate the mandible from the coding of gnathobases of the third cephalic appendage in other taxa, namely in non-multi-segmented megacheirans and arachnomorphs.

[108] Telognathic mandible

- 0. Absent
- 1. Present

Remark: From RS2011, char. 170.

[109] Mandibular gnathal edge

- 0. Consisting of molar and incisor process
- 1. Only ellipsoid *pars molaris* present
- 2. Row of parallel teeth
- 3. Shovel with terminal teeth
- 4. Group of paired teeth and hair pad

Remark: From RS2011, char. 172; see also Richter⁴⁸.

[110] Mandibular lamellate combs

- 0. Absent
- 1. Present

Remark: Lamellate combs on the distal process of mandibles are diagnostic of diplopod and chilopod myriapods¹³³.

[111] Hypopharynx

- 0. Absent
- 1. Present

Remark: The hypopharynx of myriapods and insects is a complex sternal structure partly composed of the paragnaths¹⁶⁵ and possibly of the sternites of the maxillula.

[112] Fourth cephalic appendage

- 0. Reduced exopod
- 1. Exopod and endopod vestigial

Remark: Those conditions are mutually exclusive among known arthropods. Other possible states for this character are coded in separate characters, and therefore relevant taxa are inapplicable here.

[113] Palp on fourth cephalic appendage

- 0. Absent
- 1. Present

Remark: This character codes for the presence of an endopod modified into a palp, i.e. a slender, smaller appendage that has become secondary to a relatively large and often enditic coxa-basis complex.

[114] Palp on fourth cephalic appendage, type

- 0. Reduced
- 1. Well developed

Remark: This character codes for the well-developed maxillular palps of insects, but was also coded for the phyllopod-like arthropod *Cinerocaris*.

[115] Post-mandibular plate formed by the fusion of the maxilla and the intermaxillary sternum

- 0. Absent
- 1. Present

Remark: Following char. 51 in Edgecombe¹⁰⁷, the gnathochilarium of chilognath diplopods is homologized with the condition seen in pauropods, where the maxillule is fused with the intermaxillary sternum, based on the view that the gnathochilarium also, and exclusively, derives from the maxillular limbs and sternites^{78,166}.

[116] Cephalic appendages 4 and 5 ending with chelate termination

- 0. Absent
- 1. Present

[117] Fifth cephalic appendage

- 0. Integrated to gnathal plate (labium)
- 1. Reduced, enditic

Remark: As noted above for the fourth appendage (char. 112), only taxa showing relative differentiation are coded for this character.

[118] Fifth cephalic appendage vestigial

- 0. Absent
- 1. Present

Remark: In certain branchiopod crustaceans, the maxilla is reduced to only a vestigial apparatus; in diplopod and pauropod myriapods, the branches of the maxillar appendage are fully reduced.

[119] Fifth cephalic appendage with developed palp

- 0. Absent
- 1. Present

[120] Internalization of mouthparts

- 0. Absent
- 1. Present

Remark: Entognathy is a diagnostic trait of the Collembola, Diplura and Protura, but some authors (Manton¹⁶⁷) consider the mouthparts of pauropod and chilopod myriapods to be internalized as well. We restrict the character to the entire withdrawal of mouthparts within the cephalic compartment formed anteriorly by the clypeo-labrum and posteriorly by the labium. We also excluded the internalized jaws of onychophorans from the coding.

[121] Oral cone

- 0. Absent
- 1. Present

Remark: This character codes for the formation of circumoral complex of reduced appendages neatly distinct from more posterior limbs and independent from the structure of the head tagma.

[122] Atrium oris

- 0. Absent
- 1. Present

Remark: The atrium oris exclusively refers here to the recession of the stomodaeum so as to form an oral cavity, usually accommodating appendages differentiated as mouthparts.

MOUTH AND STOMODAEAL AREA

[123] Mouth opening anteriorly (as opposed to ventrally or dorso-ventrally)

- 0. Absent
- 1. Present

[124] Type of circumoral structures

- 0. Toothed lips
- 1. Lamellae
- 2. Plates
- 3. Hypostome-labrum complex

Remark: This character has been the focus of a recent analysis in early panarthropods¹²⁷. Although it is not clear whether the small oblong juxtaposed sclerotic elements in *Hallucigenia sparsa* form a full circumoral ring, we follow the authors and homologize them with those of dinocaridids. Although “peytoia-like mouthparts” have been described from *Megadictyon*¹⁶⁸, we doubt their authenticity based on published evidence¹⁶⁹. The circumoral lips of onychophorans are morphologically akin to those of tardigrades, in which they can be more or less plate-like¹⁷⁰. We consider that the condition is homologous in *Aysheaia*. Although the onychophoran circumoral papillae are likely autapomorphic, as secondarily formed around the deutocerebral appendage¹⁷¹ and involving innervation from all brain ganglia¹⁷², at least some of these papillae are still connected to the protocerebrum, as is the case in tardigrades¹⁷³, and likely represent the ancestral condition. We thus depart from the approach taken by Yang et al.¹²⁹ in regarding circumoral papillae in both taxa as analogous only.

[125] Circumoral structures sclerotized

- 0. Absent
- 1. Present

[126] Proboscis

- 0. Absent
- 1. Present

PROTOCEREBRAL TERGITE

[127] Tergite of the ocular (protocerebral) somite

- 0. Absent
- 1. Present

Remark: An inter-ocular tergite has been found in dinocaridids and fossil euarthropods^{38,174}, and is widespread in extant euarthropods. In stem arthropods, this structure has most often been referred to as the “anterior sclerite”³⁶. As the sclerite dorso-anterior to the labrum, the inter-ocular tergite could be integrated with the clypeus-frons of terrestrial mandibulates, and would then to a greater or lesser extent be fused to the pre-oral sternite (hypostome) and labrum. In chelicerates, this sclerite is sometimes distinct from the labral tissue proper (see hypostome character 56, but otherwise may form a coherent structure with the labrum *sensu strictu* as part of the “labrum-epistome”¹⁷⁵.

[128] Tergite of the ocular (protocerebral) somite, type

- 0. Rounded
- 1. Rostral

ALIMENTARY TRACT AND OTHER INTERNAL CHARACTERS

[129] Stomach

- 0. Absent
- 1. Present

Remark: The euarthropod main digestive tract is typically subdivided into three sections: foregut (or sometimes stomodaeum), midgut (or intestine or mesenteron) and hindgut (or proctodaeum). The foregut comprises the oesophagus and pharynx, which we consider plesiomorphic. The midgut can be subdivided primarily into a stomach, i.e. an anterior inflation of the tract often delimited by diagnostic constrictions (e.g. proventriculus), and further into a second stomach and one or two intestines. The hindgut can be differentiated into a rectum, which in insects is often inflated with respect to the intestine, but most of the time constitutes a neat diametrical reduction of the duct. In insects also, the post-oesophageal system is deported posteriorly towards the “abdomen,” a plasticity resulting from the decoupling between mesodermal somatization and the development of the endoderm (although there are developmental exceptions to this; see e.g. Brusca and Wilson¹⁷⁶). Given the post-stomodaeal attachment of the ramified caeca in many stem arthropods, we construe that these glands were originally cephalic and we therefore use this terminology. Insects have evolved very sophisticated alimentary tracts, and not all of their peculiarities are covered here. This character and the following ones refer exclusively to visible morphological differentiations of the digestive tract.

[130] Stomach in a frontal position

- 0. Absent
- 1. Present

Remark: In certain arthropods, the stomach occupies a very anterior position under the cephalic shield, so that the esophagus is either very short or directed posteriorward towards the posteriorly directed mouth.

[131] Stomach—additional pouch

- 0. Absent
- 1. Present

Remark: In decapod crustaceans and other eumalacostracans, as well as in (all?) insects, there are two post-oesophageal pouches. In decapods, they are called cardiac and pyloric stomachs; in insects, they are called crop and stomach.

[132] Secondary organs connected to the central digestive duct

- 0. Absent
- 1. Present

Remark: This is a sovereign character for all variations below describing secondary digestive structures, and refers to blind caeca or tubules adjoining the gut. All types of glands present in euarthropods are excluded, as they either originate from and open at the tips of the limbs or within the cephalic space and open next to the mouth opening, that is, they are not connected to the gut. Notable exceptions are the pharyngeal and post-pharyngeal glands in social hymenopterans; the presence of these foregut-related organs is coded accordingly, even if it is convergent, although they may have homologous developmental origins. It is also not rare that larvae possess caeca that may not be retained in adults, such as in the case of *Drosophila*¹⁷⁷—we have not considered ontogenetic variations in this dataset and have coded the imaginal state only (when known). Malpighian tubules are not included in this dataset, as they are likely plesiomorphic in Euarthropoda and otherwise extremely difficult to assess in fossils.

[133] Secondary digestive organs serially repeated along the post-cephalic portion of the gut

- 0. Absent
- 1. Present

Remark: This is a sovereign character character for the next three characters (134–136). In some instances, particularly in early arthropods¹⁶⁹, single-branch diverticulae are also repeated in head segments. As there is no case of serially repeated glands in the post-cephalic area co-existing with a

cephalon devoid of digestive glands, we make this state implicit here but explicitly dichotomous in character 138

[134] Shape of post-cephalic secondary digestive structures

- 0. Reniform
- 1. Bulgy triangles
- 2. Caeca

[135] Striations on post-cephalic secondary digestive structures

- 0. Absent
- 1. Present

[136] Branching of post-cephalic secondary digestive structures

- 0. Absent
- 1. Present

[137] Differentiation of cephalic secondary digestive structures

- 0. Absent
- 1. Present

[138] Ramification of cephalic secondary digestive structures

- 0. Absent
- 1. Present

Remark: This character codes for the sharing of a single base for all caeca/diverticulae, not branch ramification (termed branching here; see character 139).

[139] Branching of cephalic secondary digestive structures

- 0. Absent
- 1. Present

[140] Peritrophic membrane

- 0. Absent
- 1. Present

Remark: From RS2011, char. 238. Shared by mandibulates and onychophorans.

[141] Metameric ganglia on nerve cord

- 0. Absent
- 1. Present

Remark: Strong homology has been established between the nerve cord of tardigrades and that of euarthropods^{141,173}, and potentially constitutes a synapomorphy of Tactopoda^{129,178}.

[142] Metanephridia with sacculus containing podocytes

- 0. Absent
- 1. Present

Remark: From RS2011, char. 29. Shared by onychophorans and euarthropods.

[143] Segmental invaginations of neuroectoderm giving rise to ventral organs

- 0. Absent
- 1. Present

Remark: From RS2011, char. 48. Shared by chelicerates and myriapods.

TRUNK

[144] Thorax

- 0. Absent
- 1. Present

Remark: A thorax is a post-cephalic tagma mainly recognizable because of limb differentiation, but also sometimes because of tergo-sternal differentiation, with respect to both cephalon and posterior tagma, the latter possibly being an abdomen. Part or all of the thorax can be structurally incorporated into the head tagma as a cephalothorax, as coded by character 44. Although most likely homoplastic, we expect this character to be optimized locally and to provide information on the possible affinities of thoracic tagma in stem arthropods.

[145] Number of thoracic somites

- 0. 11
- 1. 5
- 2. 8
- 3. 3

Remark: This character is applicable only to taxa sharing a number of thoracic segments with at least one other taxon in the matrix. It is currently restricted to crustaceans and hexapods.

[146] Abdomen

- 0. Absent
- 1. Present

Remark: We here define the abdomen as a differentiated posterior tagma partially or totally limbless. The presence of a thoracic region does not itself determine the presence of an abdomen if the posterior tagma is limbed. Likewise, we coded this trait as absent in taxa with one or two posteriormost limbless segments if they were not structurally differentiated from anterior ones.

[147] Number of core trunk segments

- 0. >14
- 1. 12–14
- 2. 9
- 3. 7–8
- 4. <7

Remark: The pattern of 12 core trunk segments, with variations of generally one segment, is remarkably well constrained across many stem arthropods and chelicerates. We tentatively added non-leptostracan malacostracans to that group, as their fourteen-segmented trunk may originate from a similar ground pattern. This character is inapplicable to taxa coded as “polysegmented” (char. 149).

[148] Seventh appendage integrated into the cephalon and highly differentiated

- 0. Absent
- 1. Present

Remark: This character codes for the xiphosuran chilarium and its equivalents.

[149] Multisegmentation

- 0. Absent
- 1. Present

Remark: This character refers to the presence of a large number of segments (>20).

[150] Tergo-sternal decoupling

- 0. Absent
- 1. Present

Remark: In the Notostraca and Progoneata (non-chilopod myriapods), the number of tergites is known to differ from the number of sternites and appendages. In all but symphylans, this condition is called diplo- or polysegmentation, meaning that there are more sternites and appendages than tergites. In symphylans, there are supernumerary tergites. In *Chengjiangocaris*³⁶, there is possible polypody without increase in sternite number, as accounted for in character 131. We here restrict the coding to instances of such decoupling. For clarity, we use “multisegmentation” to describe segment number only (see char. 149).

[151] Tergo-sternal decoupling, type

- 0. Polypody
- 1. Polypody and “polysternity”
- 2. “Polytergity” (autapomorphy of symphylan myriapods)

[152] Pleurae

- 0. Reduced or fused
- 1. Developed

Remark: Pleurae (sometimes “pleurites”) are lateral sclerites on the body of arthropods that can be part of the tergites or independent, as in insects and some crustaceans, e.g., in which pleurae are developed internally in the cephalothorax¹⁷⁹. Since the independence of pleurae is useful in differentiating insect orders, this character codes exclusively for pleurae that are extensions of the tergites.

[153] Tergo-pleural rings

- 0. Absent
- 1. Present

Remark: Tergites and pleurae can be fused and form ring-shaped trunk segments closing on small sternites characteristic of a number of crustaceomorphs and hexapods.

[154] Pleural orientation

- 0. Horizontal
- 1. Around body

Remark: Sub-horizontal pleurae are usually characteristic of flattened, crawling taxa such as trilobitomorphs.

[155] Pleural length

- 0. Short, i.e. equal or inferior to body diameter
- 1. Long, i.e. exceeding body diameter

[156] Articulating ridge

- 0. Absent
- 1. Present

[157] Articulating ridge, type

- 0. Single
- 1. Antero-posterior

Remark: Pleurae can bear two dorsal carinae, creating a superstructure resembling two pleurae superimposed.

[158] Transverse stipital muscle

- 0. Absent
- 1. Present

Remark: The loss of the transverse stipital muscle has been regarded as a potential apomorphy of Neoptera excluding Plecoptera¹⁸⁰. Inapplicable outside hexopods.

TRUNK APPENDAGES AND GENERAL APPENDICULAR CHARACTERS

[159] Proximo-distal differentiation of endopod podomeres in tagma II

- 0. Absent
- 1. Present

[160] Podomere number in tagma II

- 0. 7
- 1. <7
- 2. >7

[161] Maxillipeds

- 0. Absent
- 1. Present

Remark: Maxillipeds are defined as thoracic appendages recruited by the gnathal, masticatory portion of the cephalon, and usually modified into stout clawed or sub-chelate legs.

[162] Tergites of maxilliped segments fused to head shield

- 0. Absent
- 1. Present

[163] Single main maxilliped

- 0. Absent
- 1. Present

Remark: Certain mandibulate taxa (e.g. chilopods, isopods) have a single dominant pair of maxillipeds associated with, but not necessarily fused to, the head shield.

[164] Slit sensilla

- 0. Absent
- 1. Present

Remark: From RS2011, char. 46.

[165] Basis (basipod)

- 0. Absent
- 1. Present

Remark: A basis/basipod, also called protopodite, is generally recognized as the enlarged basal podomere to which attach endopod and exopod. In uniramous limbs of mandibulates, reductions, fusions and subdivisions of podomeres may render the identification of the original coxal and basal segments difficult, however, we consider that all those limbs share a basis plesiomorphically.

[166] Basipod formed of at least two elements

- 0. Absent
- 1. Present

Remark: This is a general character for all taxa with limb bases composed of more than one structure, excluding epipods and exites. This includes pleurites and separate proximal endites. Consequently, this character is equivalent to coding presence or absence of a “coxa” defined as a separate element—but not necessarily a podomere—proximal to the basis (see characters 167 and 168 for further discussion of homology and choice of coding).

[167] Basipod multi-segmented

- 0. Absent
- 1. Present

Remark: Somewhat overlooked in recent analyses, though pointed out by Walossek⁵⁶, *Canadaspis*, but also *Odaraia* (Extended Data Fig. 9), have a seven-segmented distal portion of the limb and a proximal portion with endites, which we consider a segmented basis. This character codes only for basipods with a proximo-distal subdivision made up of more than three segments.

[168] Multiple endites on basipod

- 0. Absent
- 1. Present

[169] Proximal endite

- 0. Absent
- 1. Present

Remark: Müller and Walossek^{61,76,181} and Walossek⁷⁷ have documented the existence, in some crustaceomorphs and crustaceans, of a proximal endite that they construe to be homologous with the pre-basal structure called the coxa, and that would constitute a synapomorphy of Crustacea. We believe, like Boxshall⁷⁹, that this is more generally the detached proximalmost endite of the basis, which may not homologize with the pre-basal coxa when further proximal differentiations exist. The proximal endite is also unlikely to be diagnostic of mandibulates, because a proximal, movable endite has been described in xiphosurans^{167,182} (the “epicoxite” or precoxa of Størmer¹⁸³) as well as in eurypterids (see e.g. Lamsdell et al.¹⁶¹), and even in *Sidneyia*^{55,59,79}.

[170] Coxa as entire pre-basal podomere

- 0. Absent
- 1. Present

Remark: We use here the term coxa in the restricted sense of a fully formed segment proximal to the basis, as used among crustaceans. The nomenclatural history has otherwise differed between major mandibulate phyla, and there are still some uncertainties regarding homology among basal limb portions. In hexapods and myriapods, limb bases are surrounded by two sets of sclerites, namely, the outer eupleurites and inner trochantinopleurites¹⁸⁴, a condition that appears similar to the complex of sclerotic elements surrounding the base of malacostracan pleopods¹⁸⁵. In hexapods, however, it has been shown that those coxal sclerites originate developmentally from one precoxal (“subcoxa”) podomere⁸⁰, which was used as an argument to support homology between the crustacean coxa basis and the hexapod subcoxa and coxa. This conflicts with the hypothesis⁷⁹ that the documented “precoxa” of crustaceans^{186,187} is homologous to the equivalent precoxa of myriapods and insects, that is, the outer ring of pleurites (eupleurites). It is conceivable that the larval subcoxa identified in *Tribolium* represents two fused segments, but it is equally probable that the “coxa” itself is a structure the becomes subdivided when partially integrated into the body wall, as seems to be the case in *Speleonectes*¹⁸⁸ and as the complex scleritic patterns in malacostracan pleopods suggests¹⁸⁵. Further complications arise from *Arthropleura*, which displays a seemingly homologous condition of coxal pleurites—albeit likely autapomorphic in their arrangement—with a number of leg podomeres exceeding those of extant myriapods, thus suggesting that the transformation of a proximalmost segment into a set of supporting sclerites may be convergent within the same phylum. In this study, we nonetheless emphasized the homologous presence and arrangement of pleurites across mandibulates,

while otherwise restricting “coxa” and “precoxa” characters to taxa in which they were clearly expressed as podomeres in the adults. See further discussion on the importance of this character for arthropod evolution in main text. The “coxa” of chelicerates is considered synonymous to limb basis/basipod (see character 165).

[171] Precoxa as whole pre-coxal podomere

- 0. Absent
- 1. Present

[172] Pleurites formed by several sclerotic elements surrounding limb insertion

- 0. Absent
- 1. Present

[173] Arrangement of pleurites

- 0. Outer/proximal and distal/inner sets
- 1. Multiple sclerotic pieces

[174] Gnathobases

- 0. Absent
- 1. Present

Remark: Gnathobases are considered to be strong differentiations of the basipod involving lateral expansion and development of marginal teeth. This character applies to all tagma.

[175] One or more gnathobase(s) reduced in tagma I

- 0. Absent
- 1. Present

Remark: This mostly differentiates the plesiomorphic arachnomorph condition from the loss of most gnathobases in the arachnid prosoma.

[176] Secondary appendicular outgrowths on trunk

- 0. Absent
- 1. Present

Remark: It has been hypothesized¹¹⁵ that the biramous limb in euarthropods originated from the fusion of two branches along the trunk axis, a view supported by recent paleontological findings^{43,189}. In contrast, a developmental study¹⁹⁰ shows that, in certain crustaceans, the exopods could form as a division of the endopodial axis rather than as a distinct cell lineage from the basis, as would be expected from a plesiomorphic fusion of the rami. Accordingly, secondary branches in stem- and crown-group arthropods could be analogous. The morphology of trunk appendages in *Surusicaris*⁴³ as currently interpreted, with a long basis bearing two very similar rami, suggests that the ground pattern of the secondary appendicular branch was not exitic (rather than exopodial), at least not exclusively. Moreover, the example of Wolff and Scholtz¹⁹⁰ applies to a particular type of biramous limb where endopods and exopods are not morphologically differentiated—very much as is the case in *Surusicaris*. We therefore favour the hypothesis that developmental differences in the formation of exopods in extant taxa are secondary to a common origin of the biramous limb, an approach that could be supported by observations of variability in limb formation (although in that case the enditic origin of the stenopodous limb remains to be tested phylogenetically, see Olesen et al.¹⁹¹). We agree, however, on the distinct nature of proximal lamellae in xiphosurans, which we discuss in char. 178.

[177] Secondary appendicular outgrowths on trunk, type

- 0. Lobopodous
- 1. Sclerotized

[178] Proximal lamellae

- 0. Absent
- 1. Present

Remark: Suzuki and Bergström¹⁹² have built a case for the differentiation of the “protopod” lamellae in xiphosurans and the exopod ornamentation of trilobites and other lamellipedians. Redescriptions of xenopod limb morphology have shown that proximal and distal ornamentations, including proximal lamellae, could co-exist on a single, multi-partite exopod^{59,95}. The existence of proximal lamellae is also a possible feature of megacheirans, as we illustrated in *Alalcomenaeus*⁴³ (fig. 9E of that work). We therefore support the distinction between distal and proximal lamellae. Likewise, the dinocaridid lanceolate blades, attached to the lobes’ surface^{94,117}, are more likely to correspond to proximal lamellae than to exopodial adornment. A detailed study of the morphology and origin of such proximal lamellae is currently in progress.

[179] Proximal lamellae internalized

- 0. Absent
- 1. Present

Remark: This character groups scorpions and tetrapulmonates.

[180] Trunk endopod reduced posterior to somatic head

- 0. Absent
- 1. Present

[181] Limb arthrodization in trunk

- 0. Absent
- 1. Present

[182] Main sclerotized trunk exopod type

- 0. Paddle/lobe
- 1. Multipartite
- 2. Rodiform
- 3. Annulate
- 4. Reduced
- 5. Three-segmented
- 6. Phyllopodous

Remark: The “multi-partite” and “three-segmented” conditions differ in that the first designates the xenopod condition with a triangular middle podomere (e.g. *Sidneyia*⁵⁹), whereas the second refers to the three-segmented exopod branch of nectiopod and copepod crustaceans³⁵. The “pleon-type lobe” condition refers to the simple condition of an undivided exopod branch typically found on the pleon of certain malacostracan crustaceans. We tentatively code the exopod of opisthosomal appendages in xiphosurans as multi-partite: although they lack the clear tripartite division of xenopods, they show a similar division between laterally extended plates, the proximal one bearing lamellae.

[183] Endopod strongly developed in thorax

- 0. Absent
- 1. Present

Remark: Independently of the relative differentiation of podomeres, certain arthropods have distinct thoracic walking limbs.

[184] Phyllopodous-type limbs anywhere on body

- 0. Absent
- 1. Present

Remark: Certain crustaceomorphs do not have phyllopodous trunk limbs, but may have similar limbs, with extensive fusion of basis, endopod and exopod, as part of the head. The condition of the maxillar appendages in *Rehbachella* with the fusion of endopod and basis with well-developed endites is here considered phyllopodous.

[185] Terminal endopod stenopodous

- 0. Absent
- 1. Present

Remark: This character typifies body plans with articulated endopods along the entire length of their posterior tagma.

[186] Symmetrical pleopods

- 0. Absent
- 1. Present

Remark: Certain crustaceans have very typical biramous appendages on their posteriormost tagma whose endopods and exopods are almost identical. The formation of these appendages has been shown to differ developmentally from the typical biramous appendage¹⁹⁰.

[187] Annulation of at least one pair of exopods

- 0. Absent
- 1. Present

[188] Sub-segmentation of at least one pair of exopods

- 0. Absent
- 1. Present

Remark: For the structural difference between annulation and segmentation of arthropod appendages, see Boxshall⁷⁹.

[189] Attachment segment in lobate exopod

- 0. Absent
- 1. Present

Remark: The triangular proximal segment of the exopod allowing for the movement of the distal, lobate part⁶⁰, is considered homologous between megacheirans and xenopods.

[190] Exopod ornamentation type

- 0. Setae
- 1. Lamellae

[191] Epipod

- 0. Absent
- 1. Present

Remark: An epipod is a typically broad, ramus-like protrusion attached to the basis on the side of the exopod.

[192] Endite as a latero-distal projection on endopod podomeres

- 0. Absent
- 1. Present

Remark: This is a characteristic shared notably by eurypterids, *Sanctacaris*, *Waptia* and other bivalved arthropods.

[193] Pusher legs with paddle tips

- 0. Absent
- 1. Present

Remark: Although the last pair of cephalic limbs is commonly called pusher legs in *Limulus*, we only homologize here the conditions of chasmataspidids and eurypterids.

[194] Developed endites on endopod podomeres in trunk (tagma II and III)

- 0. Absent
- 1. Present

[195] Paired spines on endopod podomere

- 0. Absent
- 1. Present

Remark: This character and characters 196 and 198 are coded separately as they partially co-occur and are not mutually exclusive. This approach is preferred to coding polymorphism so as to both preserve the polarization and avoid creating a sovereign character unifying all taxa with one of the described types of ornament.

[196] Short spines on endopod podomere

- 0. Absent
- 1. Present

[197] Multiple setae on endopod podomere

- 0. Absent
- 1. Present

[198] Paired elongate spines distally on endopod

- 0. Absent
- 1. Present

Remark: Whether or not paired spines are the main adornment of podomeres or endites on those podomeres, some taxa display distinct pairs of slender spines on their distal endopodial podomeres. Other taxa with paired spines have them expressed mostly proximally.

[199] Limb tip

- 0. Pad
- 1. Juxtaposed claws
- 2. Trident of claws
- 3. Chelate or sub-chelate
- 4. Double claw
- 5. Multiple spines
- 6. Single claw

POSTERIOR TERMINATION

[200] Sclerotization of termination

- 0. Absent
- 1. Present (telson)

[201] Telson developed

- 0. Absent
- 1. Present

- [202] Telson type
- 0. Spine
 - 1. Plate
 - 2. Spatula

Remark: The terminal unit of pycnogonids is sometimes called a telson (e.g. Vilpoux and Waloszek⁵⁰), but it is clearly of metameric origin, as the anus is terminal in sea spiders.

- [203] Anus location
- 0. Terminal, last segment
 - 1. Base of telson

- [204] Caudal rami
- 0. Absent
 - 1. Present

Remark: For this character as well as for the furca and uropods, we follow the definition of Schram³⁵. According to this definition, caudal rami are the appendages of the anal segment or the base of the telson, and the furca is an unsegmented pair of telsonal “extensions”¹⁹³. For those two features specifically, we find such descriptions robust and applicable to fossil taxa.

- [205] Additional caudal processes
- 0. Absent
 - 1. Present

Remark: *Yicaris*, *Rehbachella* and *Lepidocaris* bear an additional pair of caudal processes on the anal segment in addition to caudal rami. This seems to also be the case in *Canadaspis*.

- [206] Furca
- 0. Absent
 - 1. Present

- [207] Uropods *sensu stricto*
- 0. Absent
 - 1. Present

Remark: In malacostracans, uropods have been precisely defined as the appendages of the sixth pleonic segment¹⁹⁴, which could conform to a definition of uropods as modified appendages of the pre-anal segments. It remains quite ambiguous, however, whether uropod-like structures in taxa such as *Fortiforceps* or *Sidneyia* could be homologous to one another and to malacostracan uropods. We therefore restrict the coding to malacostracans.

- [208] Caudal rami, type
- 0. Spinose
 - 1. Rounded
 - 2. Filamentous
 - 3. Annulate

- [209] Pygidium
- 0. Absent
 - 1. Present

Remark: A pygidium is typically a fusion of the terminal trunk tergites. Such fusion can be more or less complete so that segment boundaries can remain visible.

[210] Type of pygidial fusion

- 0. Partial
- 1. Complete

Remark: This character codes for the condition of naraoiids. We also coded *Limulus* with state 1, as the mesosomal tergites are similarly fused.

[211] Axial elevation of pygidium

- 0. Absent
- 1. Present

[212] Pygidial ornamentation

- 0. Smooth
- 1. Spinose

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