Supporting Information

Yang et al. 10.1073/pnas.0000000000

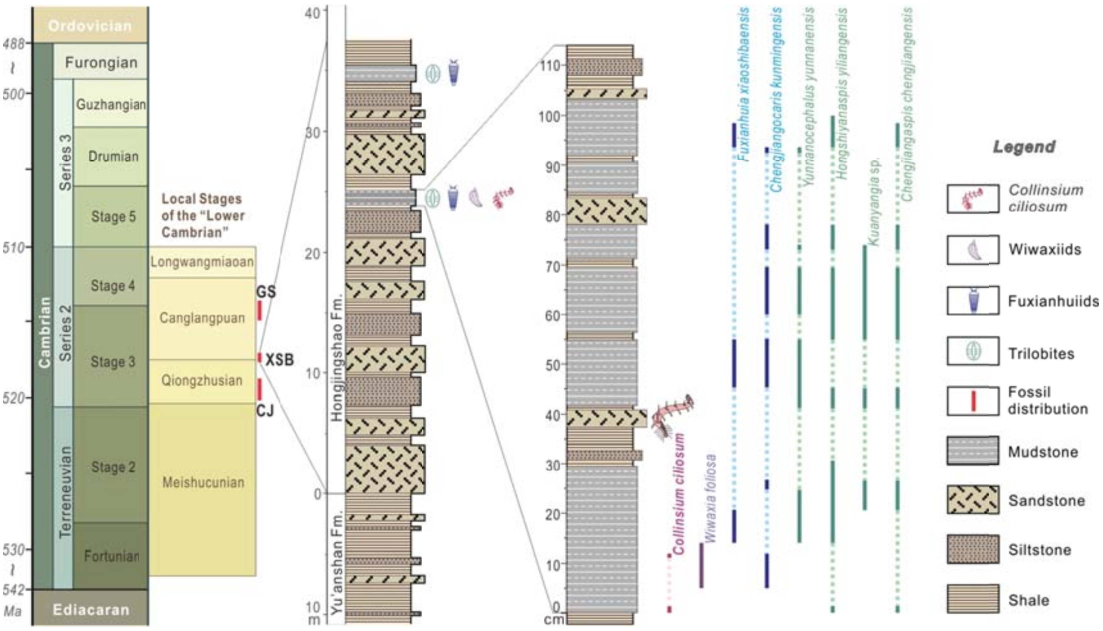

Fig. S1. Stratigraphic column and fossil distribution within the lower portion of the Hongjingshao Formation (Cambrian Stage 3) at the Xiaoshiba section in Kunming. The soft-bodied fossil assemblage is mainly found in multilayers of mudstone ca. 1.15 m in total thickness; *Collinsium ciliosum* occurs within the lowest bed, approximately 10 cm thick. Based on the co-occurring trilobites, this fossil assemblage of the Xiaoshiba Lagersttäte is located within the uppermost of the Qiongzhusian, above the Chengjiang biota (CJ) and below the Guanshan biota (GS) whereas the Hongjingshao Formation is diachronous (1).

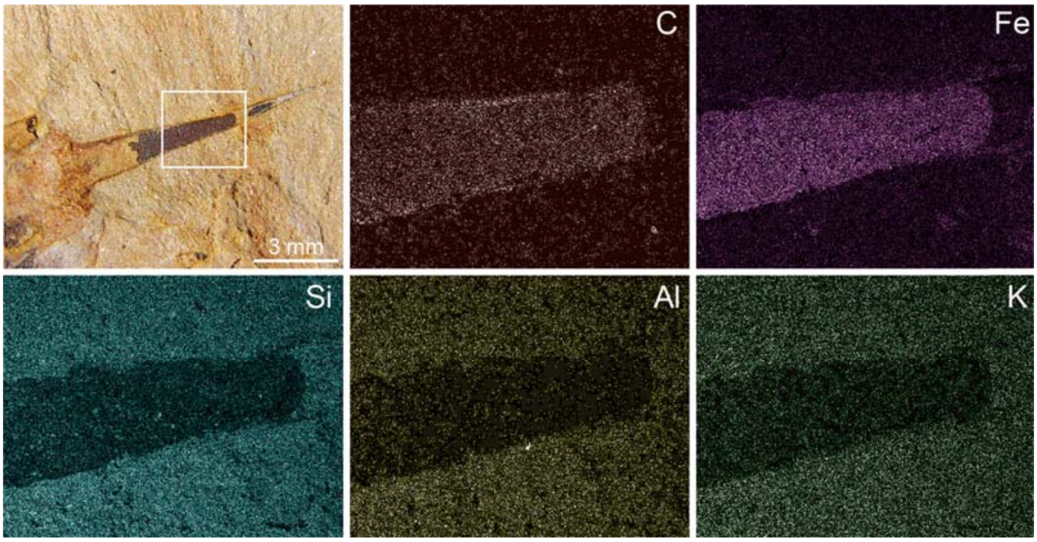

Fig. S2. Elemental analysis of well-preserved dorsal spine of *Collinsium ciliosum* (YKLP 12154). Tested area is framed, showing elemental distributions of carbon (C); iron (Fe); silicon (Si); aluminium (Al) and potassium (K).

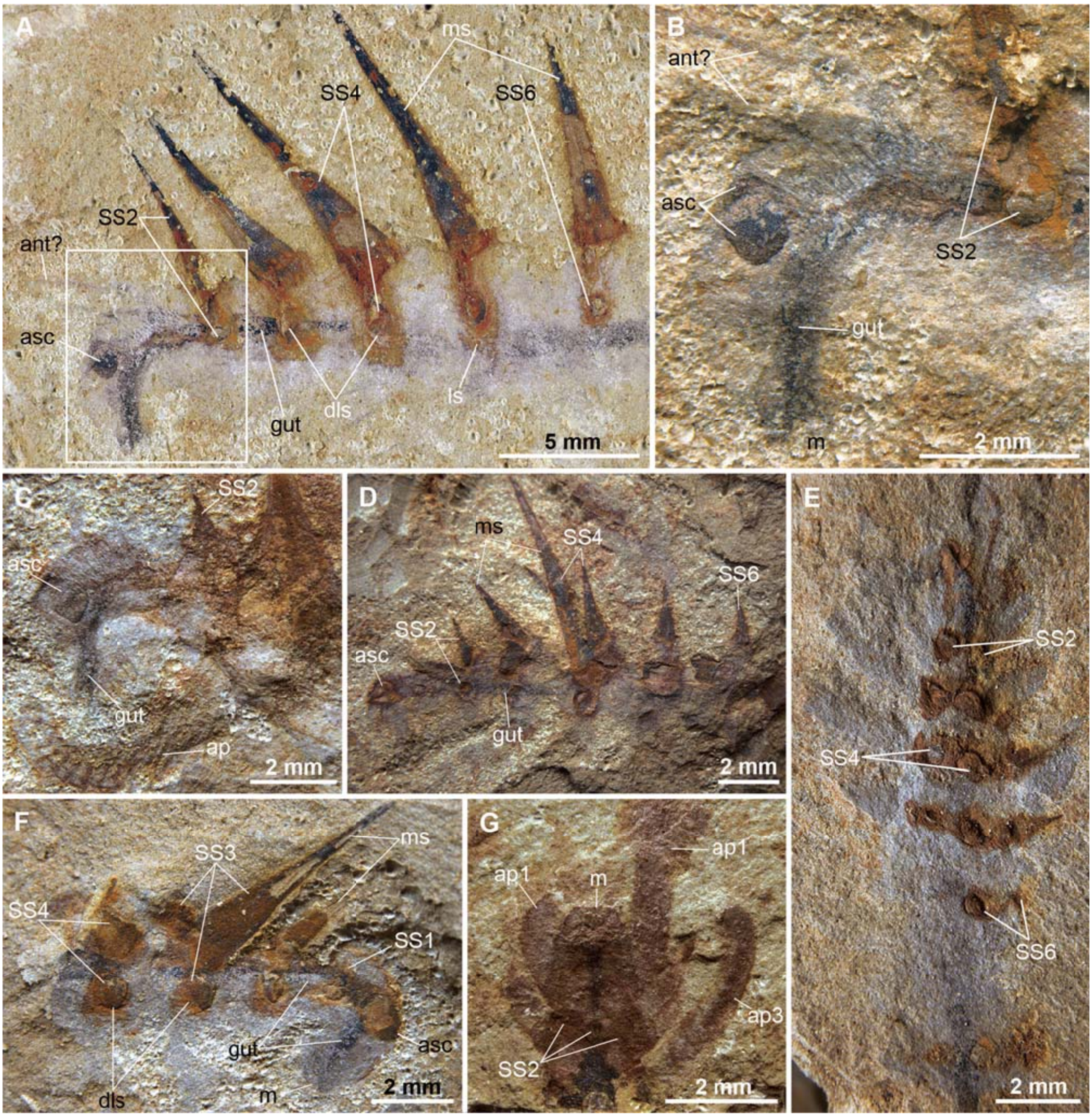

Fig. S3. Cephalic morphology of *Collinsium ciliosum*. (*A*) YKLP 12131, anterior portion of an incomplete specimen in lateral view with sclerotized spines (SS2-SS6) and anterior sclerites (asc) preserved. (*B*) Detail of (A) showing antennae—like appendages (ant), mouth opening (m), paired anterior sclerites (asc) and gut. (*C*) YKLP 12132, an incomplete specimen in lateral view with fragmentary appendages and anteriormost dorsal spines. (*D*) YKLP 12142, fragmentary specimens preserved dorsoventrally showing sclerites series on anterior region of the body. (*E*) YKLP 12142a, dorsal view of an incomplete specimen showing distribution of sclerite series. (*F*) YKLP 12140, anterior portion of an incomplete specimen in lateral view showing four sets of dorsal spines, mouth, gut and the right anterior sclerite. (*G*) YKLP 12152, dorsoventrally preserved fragmentary specimen showing only three most anterior pairs of appendages, mouth, gut and the second set of dorsal spines.

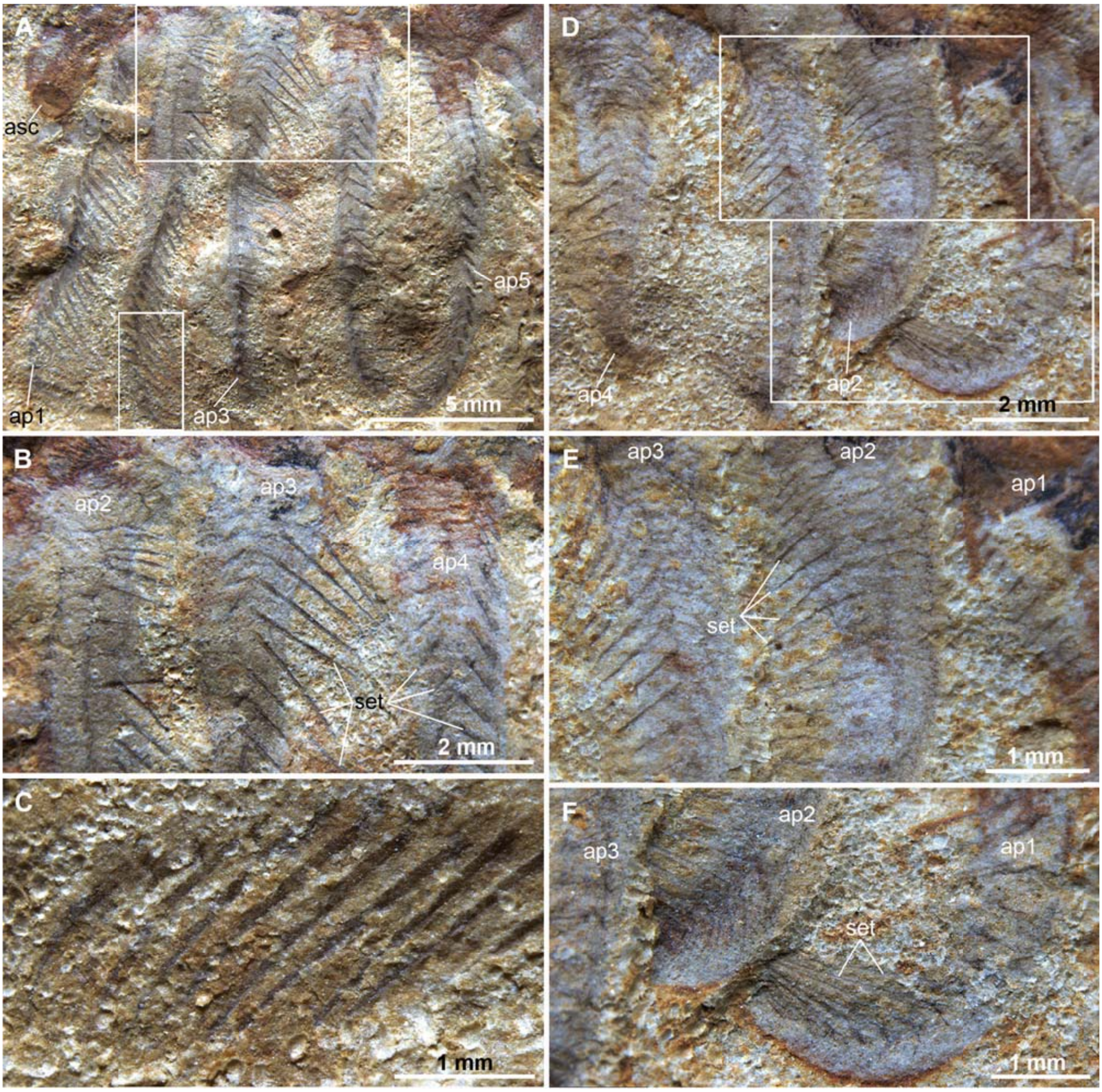

Fig. S4. Anterior setiferous appendages of *Collinsium ciliosum*. (*A*) YKLP 12127, lateral view of specimen showing the five pairs of anterior differentiated appendages. (*B*) Detail of (A), showing the proximal portion of the appendages with paired elongate setae (arrowed). (*C*) Distal portion of the second appendage (SS2) in (A). (*D*) YKLP 12128, anterior four pairs of specialized appendages. (*E*) Detail of (D) showing long elongate setae. (*F*) Distal portions of the differentiated appendages showing concentration of the setae when the limbs are curved posteriorly.

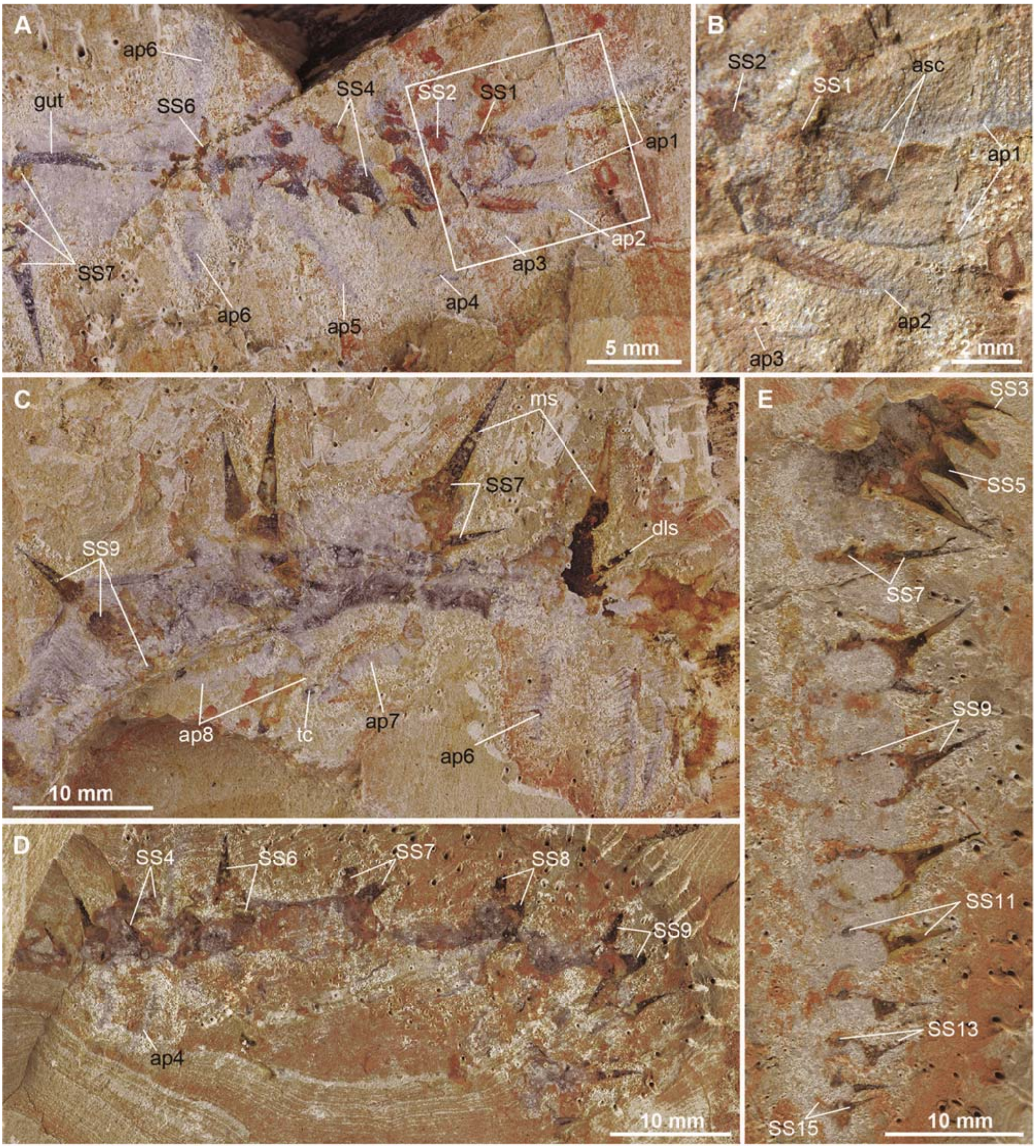

Fig. S5. Nearly complete specimens of *Collinsium ciliosum*. (*A*) YKLP 12151, dorsal view showing paired appendages on both sides and sets of dorsal spines. (*B*) Detail of (A), showing first pair of differentiated appendages (tap1) and paired anterior sclerites (asc). (*C*) YKLP 12135, fragmentary specimen with some appendages and dorsal spines. (*D*) YKLP 12150, fragmentary, irregularly curved specimen. (*E*) YKLP 12137, showing proportions of sclerite series throughout the trunk.

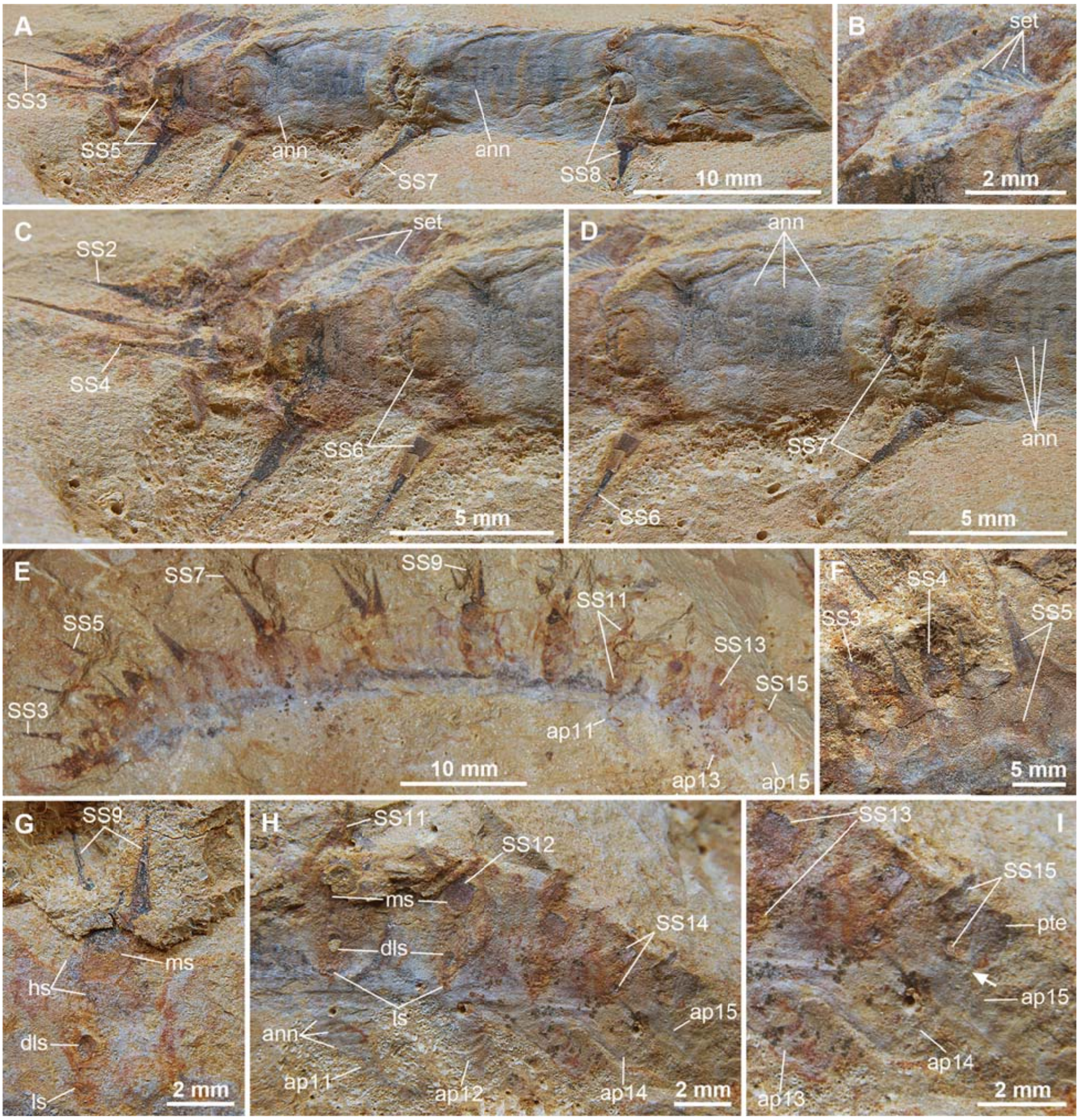

Fig. S6. Dorsal spines and annulations of *Collinsium ciliosum*. (*A–D*) YKLP 12155: (*A*) incomplete individual in dorsal view showing overall organization of sclerotized spine series; (*B*) detail of (A) showing setae on the anterior appendages preserved in separate layers; (*C*) detail of anterior portion in (A), showing overlapped spines and appendages following burial pattern; (*D*) detail of middle portion in (A) showing transverse trunk annulations. (*E–I*) YKLP 12154: (*E*) lateral view of a nearly complete specimen; (*F*) detail of (E) showing overlapped dorsal spines due to burial (SS3-SS5); (*G*) detail of (E) showing medial, dorsal lateral and lateral spines of SS9 on the left side of trunk and fine hair; (*H*) detail of (E) showing posterior portion of the trunk including the annulations on the limbs and the medial, dorsal lateral and lateral spines of SS11 and SS12; (*I*) detail of the last three spine sets and corresponding limbs, as well as the boundary between the last leg and the posterior extension (pte) of the lobopodous trunk (arrowed).

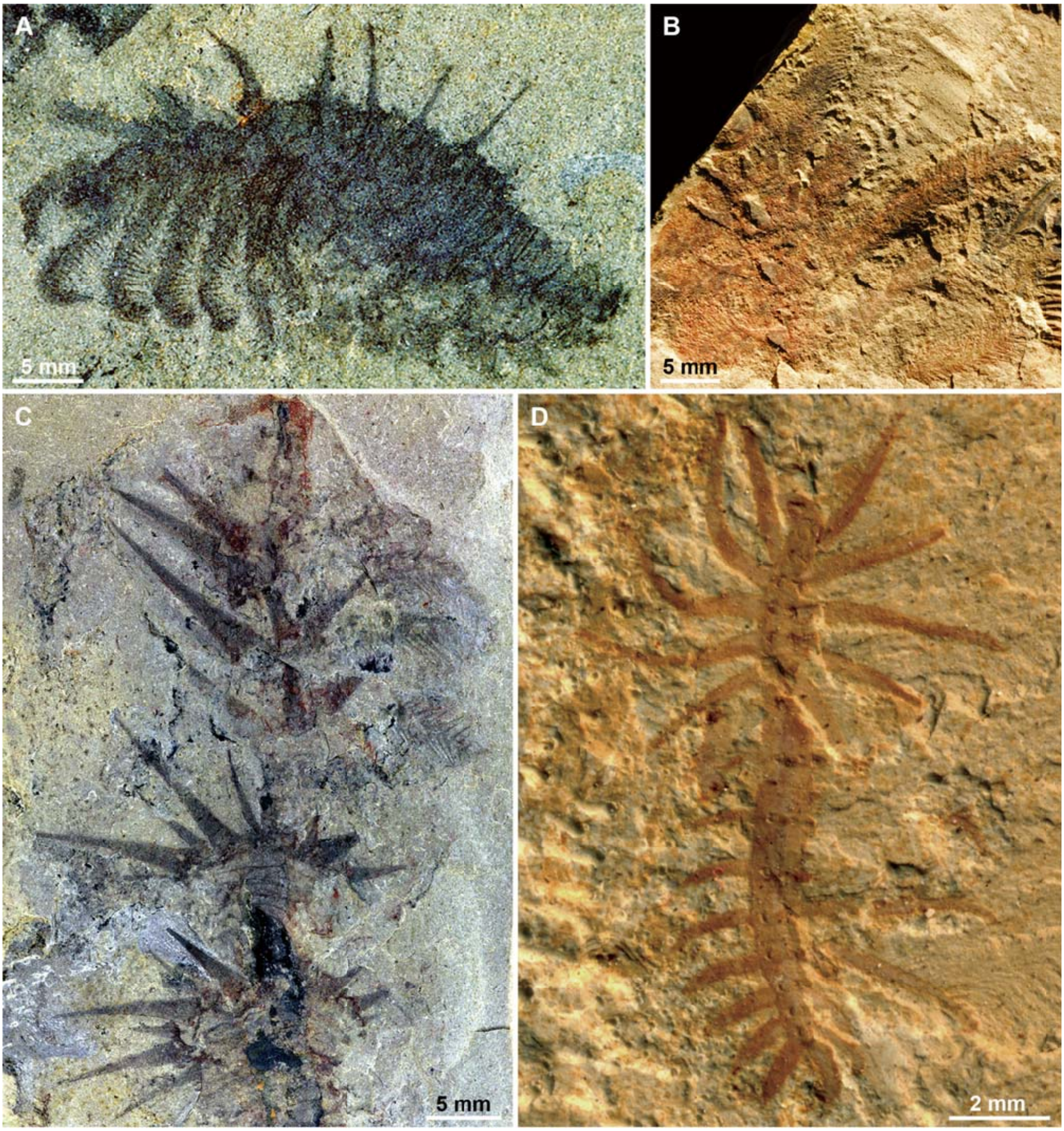

Fig. S7. Diversity within Luolishaniidae Hou and Bergström, 1995. (*A*) Unnamed Collins' monster from the middle Cambrian Burgess Shale (2); (*B*) Unnamed Collins' monster from the early Cambrian Emu Bay Shale (3), South Australian Museum P14848Aa (holotype); courtesy of John Paterson, University of New England, Armidale). (*C*) *Acinocricus stichus* from the middle Cambrian Spence Shale (4), Kansas Museum of Invertebrate Paleontology 204353 (holotype) *(D*) *Luolishania longicruris* from the early Cambrian Chengjiang (5).

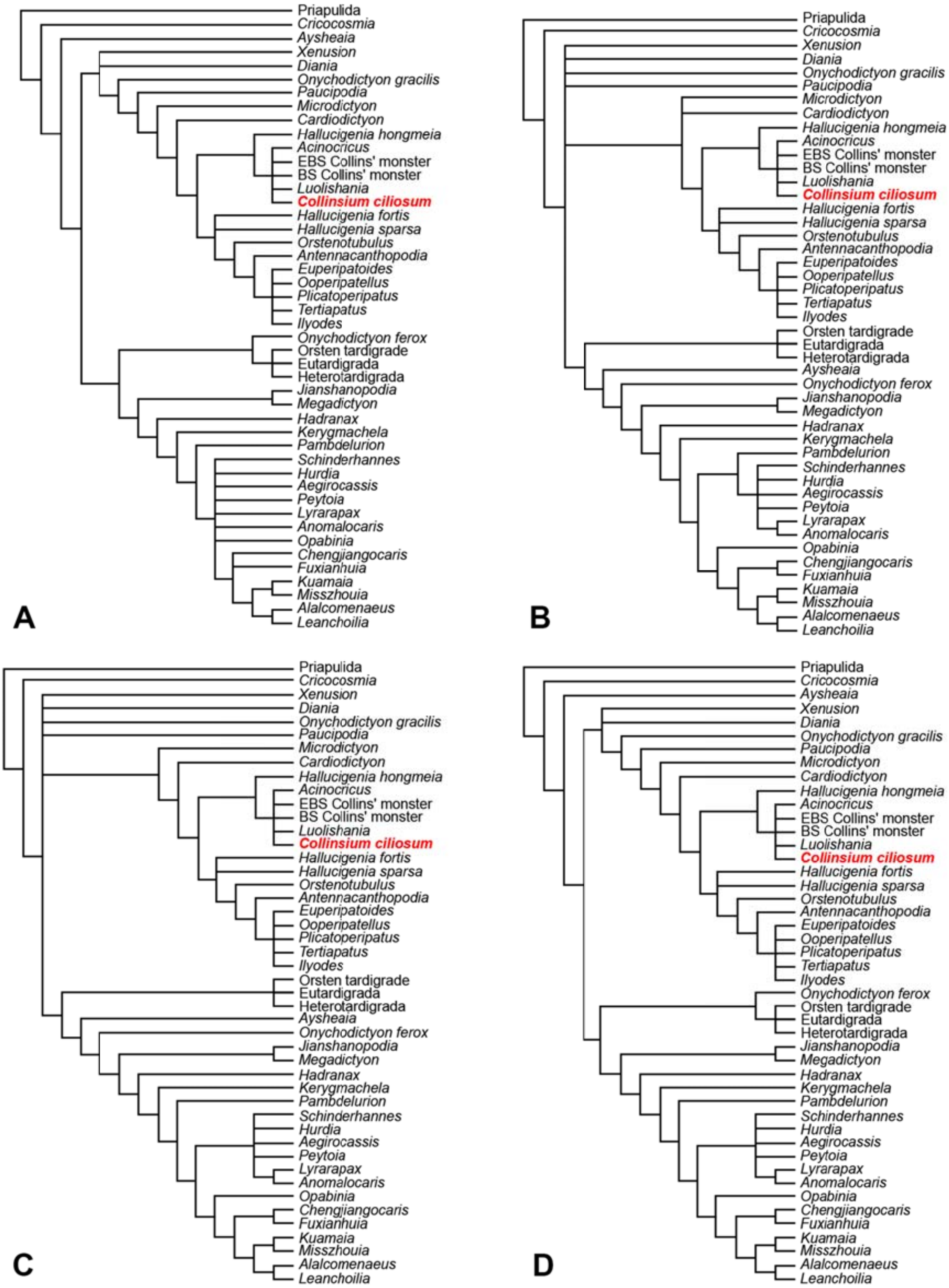

Fig. S8. Summary of results from phylogenetic analyses. (*A*) Strict consensus of 350 most parsimonious trees (MPTs) under equal weights (157 steps, CI=0.65, RI=0.87). (*B*) Strict consensus of 198 MPTs under implied weights ($k = 1$). (*C*) Strict consensus of 208 MPTs under implied weights ($k = 3$). (*D*) Strict consensus of 123 MPTs under implied weights ($k = 4$); this topology is stable when $k \rightarrow \infty$, with minimal variation in number of MPTs (see also Fig. 4 *A*).

Note S1. Methods

Photography

Digital images for all specimens were captured under bright-field illustration using a Leica DFC 500 digital camera mounted to a Stereoscope Leica M205-C. All images were processed in Adobe Photoshop CS 4. The elemental composition of the dorsal biomineralized spines was analyzed with an FEI XL30 FEGSEM electronic microscope with Oxford instruments using ATM Sili spectrometer and running INCA software.

Phylogenetic analysis

The data matrix includes 46 taxa and 86 characters (Dataset S1, Note S2). The analysis was run in TNT (6) under New Technology Search, using Driven Search with Sectorial Search, Ratchet, Drift, and Tree fusing options activated in standard settings (7, 8). The analysis was set to find the minimum tree length 100 times and to collapse trees after each search. All characters were treated as unordered. For an initial analysis, all characters were treated as equally weighted (Fig. S8 *A*); subsequent repetitions with variable concavity values (*k*) were used to explore the effect of different degrees of homoplasy penalization to test the robustness of the dataset (Fig. 4 *A* and Fig. S8 *B*–*D*).

Morphospace analysis

Morphospace analyses were based on the phylogenetic dataset (Dataset S1), and thus the morphospace is the discrete character space represented by the cladistic matrix. This approach has become commonplace in morphospace and disparity studies of extinct and extant clades (e.g. refs. 9, 10). In this context, the morphology of each taxon is represented as a combination of character states, and the morphological dissimilarity between any two taxa is measured as the number of mismatches between their character states divided by the number of characters compared (mean character difference; e.g. refs 11, 12). Because the focus of this study is on total-group Onychophora, the maximum number of applicable characters is 61 and corresponds to the character subset {1–4, 8, 9, 11–17, 19, 23–25, 29–33, 35–53, 59–67, 72, 73, 75, 77, 80–86}. The average percentage of missing data per taxon is 38.79 ± 15.90.

A principal coordinate analysis (PCoA) was performed on this matrix of morphological dissimilarity in order to visualize the main features of the onychophoran morphospace (Fig. 5 *A*). The first two principal coordinate axes summarize 76.4% of the original variance (53.5% and 22.9%, respectively) and provide a synthetic and informative depiction of the relative dissimilarity among taxa (Spearman's $rho = 0.89$, $p < 0.0001$).

Subsequent disparity analyses were carried out from the original dissimilarity matrix. Morphological disparity within each group was calculated as the mean pairwise dissimilarity (e.g. refs. 12, 13). The contribution of Luolishaniidae to the disparity of stem- and total-group Onychophora was assessed by partial disparity analysis (13). This approach decomposes the overall disparity of a clade into its subclade components. Given the discrete nature of the morphospace, the contribution of a subclade was calculated from the summed pairwise dissimilarities (divided by the size of the total clade) between the taxa constitutive of the subclade and the clade centroid, the latter being defined as the vector of median character states. Subclade components sum up to the mean pairwise dissimilarity to the clade centroid. This approach was preferred over performing the analysis in the principal coordinate space with the mean coordinates of the distribution as the centroid, because the latter might not correspond to any actual location in the discrete space (i.e. a possible combination of character states).

Limb tagmosis analysis

Measures of limb complexity were calculated using the coefficient of limb tagmosis proposed by Cisne (14) and based on Brillouin's expression (15):

$$h = (\ln N! - \textstyle\sum_i \ln n_i\ !)/N$$

Where N is the total number of limb pairs and n the number of limb pairs of the ith type (14, 15). For comparison, the known range of limb differentiation in extant Onychophora was added on the plot. The two species defining this range, *Plicatoperipatus jamaicensis* and *Ooperipatellus nanus*, can be described as the 4-tuples (1,1,1,43) and (1,1,1,13), and correspond to h values of 0.2482499 and 0.507481, respectively.

Based on the available developmental data that allows homologizing the 'frontal appendage' of various Palaeozoic lobopodians (e.g. *Aysheaia*), gilled lobopodians (e.g. *Kerygmachela, Opabinia*) and radiodontans (e.g. *Anomalocaris*) with the pre-ocular derived hypostome/labrum complex of stem-Euarthropoda (e.g. fuxianhuiids), it is assumed that all members of the latter group have a reduced protocerebral appendage pair (i.e. labrum) regardless of whether it is observable or not in the fossils (see Note S3). Scoring for individual taxa is provided in Dataset S1 and discussed in Note S4.

Note S2. Character coding

The dataset used for the phylogenetic analysis has been updated from that presented by Smith and Ortega-Hernández (16), including the formulation of new morphological characters to resolve lobopodian relationships. In addition to *Collinsium ciliosum,* other new fossil taxa incorporated to the analysis include an outgroup paleoscolecid (*Cricocosmia jinningensis* [17]), lobopodians (Burgess Shale Collins' monster [2], *Acinocricus stichus* [4], *Tertiapatus dominicanus* [18]) and radiodontans (*Schinderhannes bartelsi* [19], *Lyrarapax unguispinus* [20], *Aegirocassis benmoulae* [21]). The lobopodian *Siberion lenaicus* (22) was included in initial iterations of the analysis, but subsequently removed in order to improve the resolution of the results given the excess of uncertain morphological data in this rogue taxon. Fossil and extant taxa are scored according to a single model of head segmental organization that is informed by developmental studies on extant Onychophora, Tardigrada and Euarthropoda. The segmental affinity of anterior appendages in fossil taxa is thus interpreted based on strict topological criteria alongside recent data on the neurological organization of exceptionally preserved fossils. Characters are coded after the following premises:

- The brain of Onychophora includes two neuromeres, the proto- and deutocerebrum (23, 24), which are respectively associated with a pair of 'primary antennae' and a set of jaws integrated into the oral cavity (25, 26–30). The 'primary antennae' and jaws each represent modified limbs (28, 31, 32). The mouth is ventral, and displays a complex pattern of innervation; although the jaws are deutocerebral, the lip papillae that surround the mouth opening receive nervous terminals from the anteriormost three segments of the body, and display a bilaterally symmetrical organization (23, 26, 27, 33).
- The brain of Tardigrada comprises a single neuromere, the protocerebrum (34, 35), which is associated with the stylet apparatus. This apparatus represents a modified pair of appendages (36, 37). The stomatogastric nerves in the mouth of Tardigrada originate from the protocerebrum, forming a distinct ring-like arrangement associated with the lamellae in the mouth cone (35, 38).

The first and second pairs of walking legs are serially homologous to the deutocerebrum and tritocerebrum of crown-group Euarthropoda (39, 35). See discussion in Character 19 on mouth orientation in Tardigrada.

- The brain of Euarthropoda consists of three neuromeres. The protocerebrum is associated with the labrum, which has a pre-ocular origin during embryogenesis (25, 30) and is typified by the possession of appendage-like features; these include the morphogenetic formation from paired anlages (40–42), and the expression of limb patterning genes (43–45). The deutocerebrum is associated with the first pair of appendages in Euarthropoda, which are expressed as antennae in Mandibulata and chelicerae in Chelicerata (44, 46, 47). The tritocerebrum is associated with a diverse range of limbs among the major groups that comprise Euarthropoda, including pedipalps (Chelicerata), an additional set of antennae (Crustacea) or with an ‘intercalary segment’ that lacks appendages (Myriapoda, Hexapoda). The mouth of Euarthropoda is ventral, faces posteriad, and is typically innervated by the deutocerebrum in phylogenetically basal groups (44, 46, 47).
- The most anterior appendage pair of all lobopodian taxa, including ‘gilled lobopodians’, is interpreted as having a protocerebral segmental affinity (cf. refs. 39, 48–51); consequently the second and third appendages are interpreted as serial homologues to the deutocerebral and tritocerebral segments of crown-group Panarthropoda. Because radiodontan ‘great-appendages’ are pre-ocular (as in gilled-lobopodians) and associated with the radially arranged Peytoia-type mouthpart, these too are treated as protocerebral (cf. refs. 70, 49–51; *contra* refs. 52–55); furthermore, recent paleoneurological data strongly support a protocerebral affinity for the radiodontan great appendages (20).
- The (protocerebral) euarthropod labrum is intimately associated with the mouth opening, both during embryogenesis and in the adult (30, 41, 42, 44, 45). A subset of Paleozoic euarthropods are characterized by the presence of a sclerotized plate located anteriad of the mouth, including Fuxianhuiida (1, 53, 56), Artiopoda (57–60) and Cambrian bivalved euarthropods (61). Given the intimate association between these structures, the presence of a hypostome strongly insinuates the presence of an underlying labrum.
- Coding of fuxianhuiid head organization follows recent data on the brain structure of *Fuxianhuia protensa* (62). The antennae are interpreted as deutocerebral based on their attachment site relative to the protocerebral hypostome/labrum complex (1, 53, 56); the specialized post-antennal appendages are correspondingly interpreted as tritocerebral.
- The ‘short great appendages’ of leanchoiliids are considered deutocerebral (52, 54, 55) in light of the neurological organization in *Alalcomenaeus* sp. (63).
- The antennae of Artiopoda are coded as deutocerebral in origin based on their position relative to the hypostome/labrum complex (44, 58) and follows evidence that the ancestral euarthropod bore a antenniform deutocerebral appendage pair (1, 53, 64).

General organization

1. Paired appendages

(0) absent
(1) present

Head region

2. Anterior region covered by sclerites

(0) absent
(1) present

Numerous lobopodians have been considered to have cephalic sclerites (see ref. 65, character 37), but in some cases this interpretation requires revision or confirmation through new material. Following recent data presented by Liu and Dunlop (66), this character is scored absent in *Hallucigenia fortis* (*contra* ref. 67), *Onychodictyon ferox* (*contra* ref. 39) and *Cardiodictyon* (see ref. 67). An uncertain scoring is used where the anterior region is ambiguously preserved, such as in *H. hongmeia* (68). This character is scored as present in for the sclerotized structures observed in the head region of *Luolishania* (5) and the Emu Bay Shale Collins' monster (ref. 3, fig. 1c), as the morphological similarity with *Collinsium* strengthens the likelihood that the cephalic sclerites represent a legitimate feature in the former taxon (*contra* ref. 3). *Collinsium* bears a pair of discrete subrectangular sclerites on the anterior region (Fig. 1). Taxa with an incomplete anterior region (e.g. *Acinocricus*, *Hadranax, Orstenotubulus*) are coded as uncertain. This character is coded as uncertain for the Burgess Shale Collins' monster (2) as the only photograph of this taxon does not allow the presence of head sclerites to be distinguished.

3. Head shield formed by fused cephalic segments

(0) absent
(1) present
(–) inapplicable: head sclerites (Character 2) absent

This character is scored as absent for fuxianhuiids, because the cephalic shield is not derived from fused segments (1. 53, 56, 69), and in radiodontans, because the carapace-like structure on the head seems not to cover multiple cephalic segments (20, 70, 71, 72). This character is scored as absent in the Emu Bay Shale Collins' monster based on the close morphological similarities with the anterior organization in *Luolishania* (5, 73) and *Collinsium* (Fig. 1).

4. Isolated dorsal sclerite associated with eye-stalks

(0) absent
(1) present
(–) inapplicable: head sclerites (Character 2)

This character is scored as present in radiodontans because the dorsal carapace-like structure covering their heads is associated with eye-stalks, regardless of its shape or size (e.g. 20, 71, 72). Anterior sclerites are widespread among Paleozoic euarthropods including fuxianhuiids (1, 61), and artiopodans (57, 60). Recent palaeoneurological data support the homology of the dorsal carapace-like plate in Radiodonta with the anterior sclerite of upper-stem and crown-group Euarthropoda (74). This character is scored as absent in *Collinsium* and *Luolishania* (5) given that the isolated sclerites on the head region are not associated with stalked lateral eyes; an uncertain score is coded for the Emu Bay Shale Collins' monster as it is not possible to discern the anterior organization of the only available specimen, despite the presence of a well-defined isolated sclerite (3).

5. Shape of dorsal isolated sclerite

(0) semicircular/rounded
(1) well-developed and elongate
(–) inapplicable: isolated dorsal sclerite (Character 4) absent

See Van Roy *et al.* (ref. 21, char. 59).

6. Extent of coverage of dorsal isolated sclerite on head

(0) broad attachment to cephalic region
(1) narrow attachment with anterior edge of cephalic region
(–) inapplicable: isolated dorsal sclerite (Character 4) absent

The dorsal isolated sclerite is broadly attached in Radiodonta (20, 21, 71, 72, 75), whereas the euarthropod anterior sclerite is only narrowly attached to the anterior end of the body in upper-stem and crown group euarthorpods (1, 57, 61, 74).

7. Isolated lateral sclerites, forming tri-partite carapace

(0) absent
(1) present
(–) inapplicable: isolated dorsal sclerite (Character 4) absent; cephalic shield (Character 3) present

This character refers to the lateral elements that typify the anterior scleritome of hurdiid radiodontans (21, 72, 75).

Cephalic/anterior appendages

8. Nature of post-ocular (post-protocerebral) body appendages

(0) lobopodous
(1) arthropodized (sclerotized; arthrodial membranes present)
(–) inapplicable: paired appendages (Character 1) absent

Schinderhannes (19) is coded as having lobopodous post-protocerebral appendages based on the presence of a pair of enlarged lateral body flaps resembling those of the recently described radiodontan *Lyrarapax* (20). Although Liu *et al.* (76) described the appendages of the lobopodian *Diania* as having an arthropodized organization, a recent revision of this taxon by Ma *et al.* (65) concluded that the podomere-like structures on the legs are the result of taphonomic artifacts during burial; *Diania* is thus scored as having lobopodous appendages.

9. Sclerotization of pre-ocular (protocerebral) limb pair

(0) not sclerotized
(1) sclerotized
(–) inapplicable: paired appendages (Character 1) absent

This character is scored as present in any taxon with sclerotized pre-ocular (protocerebral) limbs, including the podomeres in radiodontan 'great appendages' (71) and the hypostome that covers the euarthropod labrum (1, 57, 61). This character is scored as uncertain in taxa where the presence of a hypostome is suggested, but not verified (e.g. *Alalcomenaeus*), and in the Siberian 'Orsten' tardigrade (77), where (assuming its modification to a stylet, as in modern tardigrades) it cannot be directly observed.

10. Pre-ocular (protocerebral) limb pair with arthrodial membranes

(0) absent
(1) present
(–) inapplicable: protocerebral limbs (Character 9) not sclerotized

This character distinguishes the arthropodized 'great appendages' of radiodontans (71) from the hypostome of Euarthropoda (1, 57) and the stylet apparatus of Tardigrada (37), both of which are sclerotized but lack soft arthrodial membranes.

11. Nature of post-ocular lobopodous inner branch

(0) cylindrical/subconical appendage
(1) laterally expanded swimming flap
(–) inapplicable: post-ocular limbs, if present, are arthropodized (Character 8)

Van Roy *et al.* (ref. 21, char. 49). The cylindrical ambulacral lobopodous leg characteristic of lobopodians is also found in *Opabinia* (78, 79), *Kerygmachela* (48, 50) and *Pambdelurion* (49). Van Roy *et al.* (21, 80) recently described the radiodontan *Aegirocassis benmoulae*, which indicates that some representatives of this group possess two sets of lateral flaps that are homologous to the outer and inner branches of the appendages in euarthropods, and thus represent a derived state relative to the presence of cylindrical ambulatory legs. This character is scored for most radiodontans following the data presented by Van Roy *et al.* (21, 80, rectified from ref. 16); an uncertain score is coded only for *Schinderhannes* given the uncertainty regarding the morphological interpretation of this taxon (19, 70).

12. Nature of first post-ocular (deutocerebral) appendage

(0) lobopodous ambulatory limb
(1) lobopodous sensorial limb
(2) loboodous limb with sclerotized jaw
(3) arthropodized antenniform with distinct podomeres
(4) arthropodized short great-appendage
(–) inapplicable: paired appendages (Character 1) absent

Although it is highly likely that this character corresponds to a lobopodous limb with sclerotized jaw in *Tertiapatus* and *Ilyodes*, this is scored as uncertain in both species as it is not possible to observe directly the nature of the deutocerebral appendage pair due to the preservation (18, 81). *Schinderhannes* is scored as having a lobopodous ambulatory limb based on the structure of the enlarged body flap, which is the first observable post-ocular appendage pair (19). *Antennacanthopodia* is scored as having a lobopodous sensorial limb based on the morphology of the deutocerebral “second antennae” (82). A lobopodous sensorial limb is also scored for the corresponding deutocerebral appendages in *Hallucigenia sparsa* (83) and *H. fortis* (84), as they are more slender than the more posterior walking legs.

13. Inner blade of deutocerebral jaw with diastema

(0) absent
(1) present
(–) inapplicable: deutocerebral jaw (Character 12) absent

The presence of a diastema on the inner blade in the jaws of Onychophora is autapomorphic for Peripatidae (32), and thus is scored present for *Plicatoperipatus* and *Ooperipatellus*; this character is absent in *Euperipatoides* (16).

14. Deutocerebral limb pair structurally differentiated from rest of trunk appendages

(0) undifferentiated, or reduced in size only
(1) structurally differentiated
(–) inapplicable: paired appendages (Character 1) absent

There are various taxa in which the deutocerebral appendage pair is morphologically differentiated from the rest of the trunk appendages (see references in ref. 66). For example, *Antennacanthopodia* has a second set of antenna-like limbs that are morphologically distinct from the walking legs (82). Although the deutocerebral appendage in *Collinsium* and other Luolishaniidae is morphologically specialized (2–5), this is expressed on the anterior five or six legs; consequently, this character is scored as absent given that the deutocerebral limb pair is not uniquely differentiated relative to other trunk appendages. Daley and Edgecombe (71) recently redescribed *Anomalocaris canadensis* and reported the presence of a smaller set of flaps in proximity with the putative head region; given that this differentiation is expressed in size, rather than structural identity, the deutocerebral limbs are scored as undifferentiated in *Anomalocaris*. This character is scored as uncertain for *Schinderhannes* (21) as the preservation does not allow identifying the occurrence of limbs on the anterior region. The first pair of legs in Tardigrada is serially homologous with the deutocerebral segment of Euarthropoda (35), and thus is not structurally different from the rest of the trunk appendages. The deutocerebral jaws of Onychophora are significantly modified relative to the rest of the appendages in the body (25, 32). In Euarthropoda, this morphological differentiation is generally expressed in the presence of an antenniform (1, 57, 62) or raptorial (52, 55, 63) deutocerebral appendage. *Ilyodes* and *Tertiapatus* are scored as uncertain as the preservation does not allow observing the presence of possible jaws as in extant onychophorans (18, 81).

15. Nature of second post-ocular (tritocerebral) appendage

(0) undifferentiated lobopodous limb
(1) specialized papillae
(2) arthropodized ambulatory limb with distinct podomeres
(3) arthropodized specialized post-antennal appendage
(-) inapplicable: paired appendages (Character 1) absent

State 3 applies to the condition observed in fuxianhuiids in which the tritocerebral appendage pair is reduced for a sweep-feeding function (1). *Ilyodes* is scored as having specialized papillae based on the morphological interpretations presented by Haug *et al.* (81); *Tertiapatus* is also scored as possessing paired oral papillae (18). *Schinderhannes* is coded as lobopodous based on the presence of the hypertrophied body flap appendage pair, suggesting that other trunk appendages had a similar non-arthropodized construction as observed in the similarly organized *Lyrarapax* (20). This character is scored as uncertain in *Hadranax* (85), *Orstenotubulus* (86) and *Hallucigenia hongmeia* (68), as it is not possible to observe the structure of the second post-ocular appendage pair in the available material.

16. Position of pre-ocular (protocerebral) appendage pair

(0) lateral
(1) ventral
(2) terminal
(–) inapplicable: paired appendages (Character 1) absent

This character is scored as ventral in Euarthropoda given that the reduced protocerebral appendage pair, transformed into the labrum, occupies a ventral position in association with the mouth (44). The forward-facing stylet apparatus of Eutardigrada is internalized into the mouth cone (37), and is thus considered as having a terminal position relative to the body; in Heterotardigrada, however, the mouth is orientated ventrally, and thus the stylet apparatus is also scored as having a ventral orientation. The antennae-like limbs on the head region of *Collinsium* and *Luolishania* (5) are scored as having a lateral position. Coding for a ventral position of the frontal appendages in *Pambdelurion* follow Budd (49).

17. Pre-ocular (protocerebral) appendage pair fused

(0) not fused
(1) fused
(–) inapplicable: paired appendages (Character 1) absent

Modified from character 16 in Ma *et al.* (87) to reflect the posited homology between the anterior appendages of lobopodians and the euarthropod labrum (26, 51): specifically, the euarthropod labrum is coded as a fused pair of appendages (41, 42, 44, 45). The stylet apparatus of Tardigrada is not coded as fused, as each stylet within the buccal tube remains independent despite significant modification (37, 88, 89). *Megadictyon* is coded as having unfused protocerebral appendages as there is no indication that the bases of these limbs are in contact with each other (90, 91), unlike the case in *Kerygmachela* (48, 50), *Pambdelurion* (49) and Radiodonta (71). *Jianshanopodia* is scored as uncertain as the preservation does not allow resolving this aspect of the morphology (91, 92). This character is scored as uncertain in *Hurdia* (72) and *Aegirocassis* (21) as the well-developed dorsal cephalic plate does not allow to directly observe the proximal potions of the frontal appendages.

18. Nature of pre-ocular (protocerebral) appendage fusion

(0) basal only, with separate distal elements
(1) fused into a reduced labrum
(–) inapplicable: protocerebral appendages (Character 17) not fused

In gilled-lobopodians and radiodontans, appendage fusion is restricted to the proximal component of the frontal appendages (48, 50, 71, 72). Per character 17 above, the euarthropod labrum is coded as a set of fully fused appendages (see also introductory statements).

19. Spines/spinules on pre-ocular (protocerebral) appendage

(0) absent
(1) present (radiodontans, gilled lobopodians, certain lobopodians)
(–) inapplicable: paired appendages (Character 1) absent; protocerebral appendages fused into labrum (Character 18)

This character refers to the spines/spinules present in the most anterior appendage pair of radiodontans (20, 21, 71, 72), gilled lobopodians (*Kerygmachela*, see refs. 48, 50; *Pambdelurion*, see ref. 49; *Opabinia*, see ref. 78, 79) and certain lobopodians (e.g. *Aysheaia*, see ref. 93; *Jianshanopodia*, see ref. 92; *Megadictyon*, see ref. 90; *Onychodictyon ferox,* see ref. 39).

20. Number of spine/spinule series on pre-ocular (protocerebral) frontal appendage

(0) one series (e.g. Aysheaia, Kerygmachela, Opabinia*)* (48, 50, 79, 93)
(1) two series (e.g. Anomalocaris canadensis, Onychodictyon ferox, Schinderhannes bartelsi*)* (19, 39, 71, 94)
(–) inapplicable: protocerebral appendages fused into labrum (Character 18); spines/spinules on the protocerebral appendages (Character 19) absent

21. Coplanar spine/spinule series in pre-ocular (protocerebral) frontal appendages

(0) no
(1) yes
(–) inapplicable: protocerebral appendages fused into labrum (Character 18); spine/spinules, if present, in single series (Character 20)

This character distinguishes the coplanar spinules found in *Onychodictyon ferox* (39), in which the spines attach at opposite sides of the protocerebral first appendage, from those of *Anomalocaris canadensis* (71, 94) and *Schinderhannes bartelsi* (19).

22. Multifurcate distal termination of protocerebral appendage

(0) absent
(1) present
(–) inapplicable: protocerebral appendages fused into labrum (Character 18); spines/spinules on the protocerebral appendages (Character 19) absent

This character describes the multifurcate termination observed in the protocerebral appendages of dinocaridids (71, 72, 78, 79, 94) and certain lobopodians – such as *Aysheaia* (93), *Megadictyon* (90) and *Kerygmachela* (48, 50) – but absent in *Onychodictyon ferox* (39).

Oral structures

23. Mouth opening orientation

(0) anterior
(1) ventral
(2) posterior

Most lobopodian taxa possess an anterior mouth – for example *Aysheaia* (93), *Onychodictyon ferox* (39) and *Kerygmachela* (48, 50) – as do Eutardigrada (37, 38). The mouth opening is ventrally oriented in *Pambdelurion* (49), radiodontans (71, 72), Onychophora and Heterotardigrada (26, 32, 35, 39, 95); it faces posteriad in *Opabinia* (79) and upper stem-group euarthropods (1, 55, 57, 70). The mouth is orientated ventrally in *Collinsium*, as evinced by the distinctive curvature of the head region and the trace of the anterior parts of the gut. A similar organization is observed in other lobopodians, including *Hallucigenia sparsa*, *H. fortis* (84, 67), *Microdictyon* (96), and *Luolishania* (5). Murdock *et al.* (97) have recently recommended that the orientation of the mouth should be interpreted with caution in fossil lobopodians based on decay experiments of extant onychophorans. With this consideration, the mouth orientation has been scored as ventral (state 1) in those taxa in which there is direct evidence of mouth orientation in combination with a well-preserved gut, as Murdock *et al.* (ref. 97, p. 6) concede that the preservation of more labile structures is a good indicator of limited decay and thus authentic biological signal. The mouth is scored as ventral in *Tertiapatus* based on the observations by Poinar (18). This character is scored as uncertain in *Cardiodictyon* as the preservation does not allow the position of the mouth to be resolved.

24. One or more pairs of appendages located anteriorly relative to the mouth opening

(0) absent
(1) present
(-) innaplicable; paired appendages (Character 1) absent

This character refers to the condition observed in Onychophora, upper stem-Euarthropoda and Euarthropoda, in which either protocerebral or deutocerebral appendages are actually displaced forward relative to the mouth opening such that they occupy a pre-oral position. This character is absent in various lobopodians in which the mouth opening is located anterior to the first appendage pair, including *Aysheaia* (93), *Cardiodictyon* (66), *Hallucigenia* (84, 67), *Onychodictyon ferox* (39), *Paucipodia* (98) and *Antennacanthopodia* (82); *Collinsium* also displays this anterior organization. Although the preservation of *Jianshanopodia* (91, 92) and *Megadictyon* (90) obscures the most proximal morphology of the frontal appendages, there is no indication that the body wall extends beyond the bases of these limbs and the mouth; thus the presence of additional anterior limb pairs is highly unlikely. This character is scored as present in *Tertiapatus* as the position of the mouth is clearly not anterior, but most likely on the ventral side of the body (18), thus leaving the protocerebral antennae in a forward position.

25. Radially symmetrical circumoral structures

(0) absent
(1) present

Previous studies have considered the lip papillae of Onychophora as homologous to the circumoral structures observed in Priapulida, Tardigrada, various lobopodians (e.g. *Aysheaia*, *Megadictyon*, *Kerygmachela*, *Pambdelurion*) and radiodontans by virtue of their similar position around the mouth (64, 72, 76, 87). Recent data on the morphogenesis of the onychophoran lip papillae, however, indicate that the latter structures have a complex developmental patterning, and receive nervous terminals from the dorsal part of the brain associated with the anteriormost three-segments of the body (26, 33); thus, the onychophoran papillae do not reflect the symplesiomorphic organization of the anterior region as observed in cycloneuralians (99–102). Given that there is no evidence that the scalids of Priapulida and the oral lamellae of Tardigrada have a similarly complex morphogenetic origin, and that it is impossible to discern whether the circumoral structures of Paleozoic lobopodians and radiodontans are analogous to the onychophoran papillae, these structures are scored as potentially homologous based on their distinctly radially symmetric arrangement around the mouth opening. Onychophorans differ considerably on this regard, as the lip papillae are circumoral but have a fundamentally bilaterally symmetrical organization (26, 33); thus this character is scored as absent. This character is scored as present in *Jianshanopodia* (92) following a recent revision of the anterior morphology of this taxon by Vannier *et al.* (91). Scored as uncertain in *Tertiapatus* as the ventral mouth is obscured by the body curvature in the only known specimen (18). Mouthparts are unknown in *Aegirocassis* (21).

26. Nature of radial circumoral structures

(0) scalids
(1) oral papillae or lamellae
(2) radial plates organized as a mouth apparatus
(–) inapplicable: radial circumoral structures (Character 25) absent

Panarthropods express a considerable diversity of circumoral structures, which represent a symplesiomorphic feature of Ecdysozoa as a whole (101). Various lobopodians bear oral papillae/lamellae (e.g. *Aysheaia*, see ref. 93; *Kerygmachela*, see refs. 48, 50; *Opabinia*, see ref. 79); a similar feature occurs in the oral cone of Tardigrada (88, 89). *Pambdelurion* (49) and radiodontans (71, 72) exhibit radially arranged plates that together form a mouth apparatus (75). The nature of the circumoral structures in *Megadictyon* and *Jianshanopodia* (90–92) are scored as uncertain; in the former case, the type material does not unequivocally exhibit a plate-like nature; in the latter, the documentation of the plates is inconclusive. This character is scored as inapplicable in Onychophora given that the bilaterally symmetrical lip papillae are demonstrably not homologous with the radially symmetrical circumoral structures of other taxa based on their developmental origin and neurological organization (26, 33; see also Character 25).

27. Structure of mouth apparatus

(0) variable number of undifferentiated plates (e.g. Pambdelurion*)*
(1) plates with differentiation of three or four enlarged plates (i.e. Radiodonta)
(–) inapplicable: circumoral structures, if present, are not radial plates (Character 26)

This character distinguishes the somewhat indistinct organization of the mouth apparatus in *Pambdelurion* (49) from the radially arranged mouthparts of radiodontans (71, 72, 75). *Megadictyon* and *Jianshanopodia* are scored as uncertain to reflect their mouthparts' poor preservation (90–92).

28. Inner rows of teeth within mouthpart

(0) absent
(1) present
(–) inapplicable: circumoral structures, if present, are not radial plates (Character 26)

Character 9 in Daley *et al.* (72). This character is scored as uncertain in *Schinderhannes* (19) and *Lyrarapax* (20) due to the state of preservation of these taxa.

Ocular structures

29. Eyes

(0) absent
(1) present

Character 10 in Daley *et al.* (72) and 25 in Ma *et al.* (65) (see also ref. 73). Eyes as treated as present in *Onychodictyon ferox* (39) and *Hallucigenia fortis* (66). Eyes are scored as absent in *Aysheaia* (*contra* ref. 39) following the original description by Whittington (93). There is no evidence that *Collinsium* possess eyes. Although the paired sclerites on the head region superficially resemble ocular structures, the lack of individual lenses or other structural organization suggestive of visual units provide no indication that these sclerites were involved in photoreception; the evidence for overlap of these structures in laterally preserved complete specimens (e.g. Fig. 1H) indicates that these structures are more comparable with the laterodorsal sclerites in the trunk region of *Collinsium*.

30. Eye attachment

(0) eye sessile
(1) eye stalked
(–) inapplicable: eyes (Character 29) absent

Character 26 in Ma *et al.* (65).

31. Type of eyes

(0) single lens eye or pigment spots
(1) multiple visual units (including compound eyes)
(–) inapplicable: eyes (Character 29) absent

Character 27 in Ma *et al.* (65). This character is scored as uncertain in *Luolishania* and *Hallucigenia fortis* given that it is not possible to fully resolve the level of structural organization of the visual units due to their fragmentary preservation (5, 73).

Trunk region

32. Epidermal segmentation

(0) absent
(1) present

Character 25 in Daley *et al.* (72). Epidermal segmentation is a distinguishing feature of Euarthropoda (101, 103). Although the body of Onychophora and Tardigrada is metamerically organized, both at the level of segment polarity gene expression (28, 104) and musculature (37), this pattern is not expressed on the epidermis: this character is thus score as absent in these phyla. *Opabinia* is scored as present since has discrete body segments separated by furrows (78, 105). Epidermal segmentation is not evident in radiodontans (20, 71, 106), and thus is scored as absent. *Hurdia* is the exception: because the only complete specimen is partly disarticulated (72), the presence of epidermal segmentation is scored as ambiguous. *Schinderhannes* is scored as uncertain as the ventral perspective of the only available specimen does not allow resolving this character (19).

33. Dorsal integument sclerotized and connected by arthrodial membranes

(0) absent
(1) present

The development of sclerotized tergal plates connected by arthrodial membranes is distinctive of body arthrodization, and thus exclusive to Euarthropoda (1, 55, 57). Although some heterotardigrades possess dorsal plates (36, 95, 107), these are not connected by arthrodial membranes and thus score the heterotardigrade *Actinarctus* as absent for this character. *Schinderhannes* is scored as uncertain as the ventral perspective of the only available specimen does not allow resolving this character (19).

34. Sternites connected by arthrodial membranes

(0) absent
(1) present
(–) inapplicable: dorsal sclerotized integument (Character 29) absent

Sternites – ventral sclerotized plates – are a key feature of most Euarthropoda, and are well documented in Artiopoda (57, 108, 109). Sternites are notably absent in fuxianhuiids (1, 53, 56, 69), even though these taxa have a sclerotized dorsal exoskeleton. Sternites are scored as uncertain in leanchoiliids. Given that it is unknown whether *Schinderhannes* displays epidermal segmentation due to its preservation, and the fact that sternites are not observable on the ventral side (19), this character is scored as uncertain.

35. Neck-like constriction on lobopodous trunk

(0) absent
(1) present
(–) inapplicable: sclerotized dorsal integument with arthrodial membranes (Character 33) present

This character is distinctive of the radiodontans *Anomalocaris* (71, 106) and *Lyrarapax* (20). This feature is scored as absent in *Hurdia*, *Peytoia* (72, 106), *Schinderhannes* (19) and *Aegirocassis* (21).

36. Annulations

(0) absent
(1) present
(–) inapplicable: sclerotized dorsal integument with arthrodial membranes (Character 33) present

Character 26 in Daley *et al.* (72). Annulations are repeated superficial integument rings that do not reflect any pattern of body segmentation. This character is scored as uncertain for *Ilyodes* as preservation does not allow observing fine details of the morphology (81).

37. Annulation distribution

(0) limbs only
(1) trunk and limbs
(–) inapplicable: annulations (Character 36) or paired limbs (Character 1) absent

Most taxa have annulations on the trunk and limbs. Whereas the limbs of *Pambdelurion* unambiguously exhibit annulations, preservation makes it unclear whether the structures also occurred on the trunk (49). The same applies to *Antennacanthopodia* (82), where the effaced preservation of the trunk may obscure trunk annulations.

38. Organization of trunk annulation

(0) homonomous
(1) heteronomous
(–) inapplicable: annulations (Character 36) absent

Character 29 in Liu *et al.* (76), and character 27 in Daley *et al.* (72). This character distinguishes between annulation patterns that are uniform along the length of the trunk (homonomous) from those which display serially-repeated differentiated fields (heteronomous), usually associated with the location of limbs. *Pambdelurion* is scored as uncertain, reflecting the poor preservation of the trunk (49).

39. Metamerically arranged dorsolateral epidermal specializations

(0) absent
(1) present

This character refers to the differentiated epidermal regions found on the dorsal side of most lobopodians. This character has been modified from the definition used by Smith and Ortega-Hernández (16) to reflect the hypothesis that the epidermal specializations of lobopodians may be homologous to those observed in numerous paleoscolecid taxa known from Cambrian deposits, such as

Cricocosmia (17, 110). Consequently, this character is scored as absent, rather than inapplicable, for *Tubiluchus*. The epidermal specialization is usually conspicuous, as in the paired nodes of *Xenusion* (110), *Hadranax* (85) and *Kerygmachela* (48, 50); the sclerotized plates of *Onychodictyon* (39, 111); the spines of *Hallucigenia* (67, 68, 83) and *Orstenotubulus* (104); as well as the elaborate armature of Luolishaniidae (2–5), including *Collinsium*. *Paucipodia* (98, 112) bears subtle sub-circular specializations. This character is scored as present in *Diania* based on the shield-like specializations associated with each leg pair (ref. 65, fig. 2). The character is also coded as present in extant tardigrades, denoting the paired pit-like structures associated with each pair of legs. These have been described as sites for muscular attachment in the visceral side of the body wall (37, 107, 113); the epidermal specializations of lobopodians have also been interpreted as muscle attachment sites (103, 111). *Schinderhannes* (19) is scored as uncertain as the only available specimens are preserved from a ventral perspective. The coding for *Aysheaia* has also been modified from that used in Smith and Ortega-Hernández (ref. 16, char. 32) based on direct observations of type fossil material by JOH; contrary to the interpretation by Liu and Dunlop (ref. 66, fig. 1), the putative subcircular specializations of *Aysheaia* actually represent the insertion of the lobopodous limbs on the opposite side of the body wall (93). This character has also been scored as absent for *Paucipodia* (*contra* ref. 16), as the structures previously identified as possible epidermal specializations also correspond to the insertion site of the appendages on the body wall (98).

40. Nature of paired epidermal specializations

(0) epidermal depressions
(1) epidermal evaginations
(–) inapplicable: epidermal specializations (Character 39) absent

The nodes, plates and spines of *Cricocosmia* and lobopodians (Character 41) represent epidermal evaginations; the paired sclerotized dorsal plates of *Actinarctus* (Heterotardigrada) are also interpreted as epidermal evaginations (36, 95, 107). *Halobiotus* (Eutardigrada) has epidermal depressions, represented by the paired pits that serve as muscle attachment sites (37, 107, 113). The nodes in *Paucipodia* (98, 112) and flattened plates in *Diania* (65, 66, 76) are scored as epidermal evaginations.

41. Proportions of epidermal trunk evaginations

(0) wider than tall (e.g. nodes or plates)
(1) taller than wide (e.g. spines)
(–) inapplicable: epidermal evaginations (Character 40) absent

Epidermal evaginations fall into two geometric categories: flat nodes or plates (state 0) and tall spines (state 1). Although the distal portions of the evaginations of *Orstenotubulus* are not preserved (86), a spine-like habit is inferred from the proportions of the dorsal stubs. Although the epidermal evaginations in *Hallucigenia hongmeia* change slightly in their proportions throughout the trunk region (68), this character is scored as state 1 based on the prevalence of spine-like dorsal sclerites.

42. Trunk epidermal evaginations with acute distal termination

(0) absent
(1) present
(–) inapplicable: epidermal evaginations (Character 40) absent

This character refers solely to the shape of the trunk evaginations' apices. It is independent from the evaginations' proportions (Character 40), as demonstrated by *Onychodictyon ferox*, where sclerites are wider than tall (i.e. plates) but display an acute distal termination (39, 111, 114). *O. gracilis* is coded as uncertain due to its ambiguous preservation (115). *Orstenotubulus* is also scored as uncertain given the incomplete preservation of the distal components of the epidermal evaginations (86).

43. Acute distal termination in epidermal evagination is curved

(0) absent
(1) present
(–) inapplicable: epidermal evaginations, if present, lack an acute distal terminus (Character 42)

The spines of *Hallucigenia fortis* (67), *H. hongmeia* (68), *Luolishania* (5), the Burgess Shale and Emu Bay Collins' Monster (5, 3), *Acinocricus* (4) and *Collinsium* are distinctively curved, whereas those of *H. sparsa* (116) and *Onychodictyon ferox* (114) are essentially straight. Following the results presented by Murdock et al. (97) on the durability against decay of jaws and claws in onychophorans, the curvature in the dorsolateral sclerites can be regarded as an original biological signal given their substantial degree of sclerotization, and also possible light phosphatic biomineralization (117).

44. Sclerotization of epidermal evaginations

(0) absent
(1) present
(–) inapplicable: epidermal evaginations (Character 40) absent

The epidermal evaginations of several 'armored' lobopodians are substantially sclerotized (67, 68, 117), in contrast to those of *Xenusion* (110), *Hadranax* (85) and *Kerygmachela* (48, 50).

45. Dorsal trunk sclerite ornament

(0) net-like
(1) scaly
(–) inapplicable: sclerotized epidermal evaginations (Character 44) absent

This character is scored as uncertain in taxa that are not well enough preserved for the ornament to be apparent. *Hallucigenia sparsa* has a scaly ornament (16, 117) whereas *H. hongmeia* bears a punctate to net-like pattern (68) shared with *Onychodictyon* and *Microdictyon* (114); *Cricocosmia* (17) and *Cardiodictyon* specimens show a comparable surface ornament (ref. 66, fig. 4f). *Actinarctus* sclerites also exhibit a net-like ornament (107). The dorsolateral spines of *Collinsium* have a distinctive punctate-like ornamentation similar to that of *H. hongmeia*.

46. Sclerites consist of a stack of constituent elements

(0) absent
(1) present
(–) inapplicable: sclerotized epidermal evaginations (Character 44) absent; terminal claws on limbs (Character 64) absent

This character is coded as present in any taxon where exoskeletal elements (claws or epidermal evaginations) comprise stacked constituent elements at all stages of growth (as in *Hallucigenia sparsa* and onychophorans, see ref. 16), not just during ecdysis (as in *Onychodictyon*, see ref. 114). Where sclerites are not preserved in sufficient detail to assess their construction (e.g. *Luolishania*), this character is coded as ambiguous. This character is scored as present in *Collinsium*, as the structural organization of the dorsal spines indicates the presence of several constituent elements expressed as the cone-in-cone organization (Fig. 2G) (117). This character is scored as inapplicable in taxa that in addition to lacking dorsal sclerites, also lack terminal claws that could indicate the presence of stacked constituent elements (16).

47. Maximum number of primary dorsal epidermal specializations above each leg pair

(0) one
(1) two
(2) three
(3) four
(4) five
(5) seven
(–) inapplicable: epidermal specializations (Character 39) absent

Cricocosmia is scored as having paired epidermal specializations (17). *Cardiodictyon* is also coded with two epidermal specializations (state 1), following suggestions that the apparently single dorsal sclerite is formed by the fusion of a pair of elements (66). The sclerite-series in *Collinsium* consist of five epidermal specializations, including a long dorsal spine, two shorter dorsolateral spines, and two smaller lateral spines. The sclerite series in *Acinocricus* consists of seven primary sclerotized spines, which are intercalated with several additional secondary spines (ref. 4, see Character 20). This character is scored as uncertain in Heterotardigrada given the complex integration of dorsal plates in these organisms.

48. ‘Secondary’ sclerotized dorsolateral spines

(0) absent
(1) present
(–) inapplicable: epidermal specializations (Character 39) absent; epidermal evaginations (Character 40) absent

This character refers to the unique condition observed in *Acinocricus* (4), in which the sclerotized dorsolateral spine series are typified by the presence of ‘primary’ spines (i.e. those that decrease gradually in size throughout the dorsoventral axis of the lobopodous body), and ‘secondary’ spines (i.e. those that maintain a similar length throughout the dorsoventral axis of the lobopodous body).

49. Dorsal sclerotized spine-like evaginations of variable length along the body

(0) similar length along body
(1) variable length along the body
(-) inapplicable: epidermal evaginations (Character 40) absent; epidermal evaginations taller than wide (Character 41) absent

The dorsolateral spines in most armored lobopodians maintain a similar length throughout the body (e.g. *Hallucigenia sparsa*). Spines with variable length are observed in *Collinsium*, *H. hongmeia* (68), *Luolishania* (5), the Emu Bay Shale Collins' monster (3) and *Acinocricus* (4). This character is scored as uncertain on the Burgess Shale Collins' monster as it is not possible to distinguish the presence or structure of spines on the posterior part of the body (2). *Orstenotubulus* is also scored as uncertain given the incomplete preservation of the distal portions of the dorsal spines (86).

50. Spacing between dorsolateral epidermal specializations along longitudinal body axis

(0) epidermal specializations regularly spaced
(1) epidermal specializations irregularly spaced
(–) inapplicable: epidermal specializations (Character 39) absent

The epidermal specializations present in most lobopodian taxa follow a regular spacing between them along the long axis of the body. In *Collinsium* and *Luolishania* (5), however, the anteriormost and posteriormost thirds of the dorsolateral spines are spaced at regular intervals, but the spines on the middle region of the body are positioned further apart relative to each other. This character is scored as uncertain for the Emu Bay Shale Collins' monster (3) and the Burgess shale Collins' monster (2) given that the incomplete preservation of the only known specimens does not allow this condition to be verified. Although Ramsköld and Chen (ref. 84, p. 128) described the spine series of *Acinocricus* (ref. 4, fig. 6) as being 'regularly spaced', this character is scored as uncertain given that the available photographs of the holotype do not allow to clearly identify this condition.

51. Papillae on trunk annulations

(0) absent
(1) present
(–) inapplicable: annulations (Character 36) absent

Character 41 in Ma *et al.* (65). *Orstenotubulus* is scored as uncertain as its papillae are not clearly observed throughout the trunk region (86).

52. Serially repeated mid-gut glands

(0) absent
(1) reniform, submillimetric lamellar

Character 42 in Ma *et al.* (65); character 16 in Daley *et al.* (72). The presence of this character for lobopodians has been scored following a conservative approach based on decay experiments in onychophorans indicating that the detachment between the procuticle and epicuticle can produce taphonomic artefacts that superficially resemble gut diverticulae (97). Therefore, this character is scored as uncertain in *Antennacanthopodia* (82) as the dark infilling of the type material may represent decayed internal organs. This character is scored as absent in *Collinsium* given that the gut displays a consistently simple morphology throughout the body. The presence of this character for the lobopodians *Megadictyon*, *Jianshanopodia*, *Pambdelurion* and *Opabinia* follows new information presented by Vannier *et al.* (91). Unlike other radiodontans, paired midgut glands seem to be absent in *Lyrarapax* (20). This character is scored as absent for *Acinocricus* based on the putative preservation of a straight gut on the holotype specimen (see "central zone" in ref. 4). Scored as absent in *Ilyodes* based on specimens showing a preserved straight gut (81).

Trunk appendages

53. Trunk exites

(0) absent
(1) present
(–) inapplicable: paired appendages (Character 1) absent

Character 20 in Van Roy *et al.* (21). *Schinderhannes* (19) is scored as uncertain as the only available specimen is preserved from a ventral perspective.

54. Exite organization

(0) lanceolate dorsal blades
(1) simple oval paddle with marginal spines
(2) bipartite shaft with lamellar setae
(–) inapplicable: trunk exites (Character 53) absent

The recent description of *Aegirocassis* (21) clarifies the relationship of the dorsal lanceolate blades in gilled lobopodians and radiodontans, and their homology with the exites of upper-stem Euarthropoda.

55. Exites/lanceolate dorsal blades associated with dorsolateral flaps

(0) absent
(1) present
(-) inapplicable: post-ocular limbs biramous (Character 57) present
Character 21 in Van Roy *et al.* (21). This character reflects the diversity observed in Radiodonta, in which the dorsolateral flaps may be lost in some taxa, such as *Anomalocaris* (71) and *Lyrarapax* (20). The coding of this character differs slightly from that used by Van Roy *et al.* (21) in that it is coded as inapplicable for taxa with fused biramous limbs and completely body arthrodization and limb arthropodization (i.e. Deuteropoda cf. ref. 70).

56. Exite/setal blade distribution

(0) confined laterally
(1) present dorsally
(-) inapplicable: exites (Character 53) absent; dorsal integument sclerotized (Character 33) present.
Character 51 in Van Roy *et al.* (21).

57. Dorsal flaps/exites fused with endopod into biramous appendage

(0) not fused
(1) fused
(–) inapplicable: trunk exites (Character 53) absent

See Van Roy *et al.* (ref. 21, char. 57).

58. Antero-posteriorly compressed protopodite with gnathobasic endites in post-deutocerebral appendage pair

(0) absent
(1) present
(–) inapplicable: limbs (Character 8) not arthropodized

Character 8 of Ma *et al.* (65), 35 in Daley *et al.* (72). Gnathobasic appendages are absent in fuxianhuiids (1, 53, 56, 69) but present in Artiopoda (57, 60) and megacheirans (52, 55, 118).

59. Secondary structures on lobopodous limbs

(0) absent
(1) present
(–) inapplicable: limbs (Character 8) not lobopodous

Modified from character 9 in Ma *et al.* (65). *Onychodictyon gracilis* is coded as uncertain as its longitudinal series of dot-like structures (ref. 115, fig. 2A6) could indicate an organization of appendicules similar to those of *O. ferox* (see ref. 39, fig. 2a). *Collinsium* and other members of Luolishaniidae are typified by the presence of conspicuous secondary structures on the lobopodous limbs that are expressed as long setae (see Characters 60 and 61).

60. Nature of secondary structures

(0) spines/setae
(1) appendicules
(–) inapplicable: secondary structures on the lobopodous limbs (Character 59) absent

Spines and setae taper to sharp point, whereas appendicules have a uniform length and a flattened terminus. *Xenusion* is scored as uncertain as the preservation of the material does not allow distinguishing fine details of the morphology (110).

61. Length of spines on lobopodous limbs

(0) short (*e.g.* Aysheaia, Diania)
(1) long (*i.e. Luolishaniidae*)
(–) inapplicable: spines on lobopodous limbs (Character 60) absent or inapplicable

Luolishaniidae are typified by long setiform spines on the anterior trunk appendages (2–5), which contrast with the short spines of *Diania* (65, 76) and *Aysheaia* (93).

62. Papillae on lobopodous limbs

(0) absent
(1) present
(–) inapplicable: limbs (Character 8) are not lobopodous

Character 10 in Ma *et al.* (65). In contrast to appendicules and spines, papillae are short projections associated with the annulations.

63. Finger-like elements in distal tip of limbs

(0) absent
(1) present
(–) inapplicable: paired appendages (Character 1) absent

The finger-like projections in the legs of tardigrades can bear sets of terminal claws or sucking discs (36, 119, 120). *Antennacanthopodia* is scored as uncertain as the preservation of the available material is not good enough to distinguish fine detail of the distal portion of the limbs (82).

64. Terminal claws on trunk limbs

(0) absent
(1) present
(–) inapplicable: paired appendages (Character 1) absent

Terminal claws are scored as absent in *Opabinia* following Budd and Daley (78). *Jianshanopodia* (109), *Megadictyon* (90) and *Tertiapatus* (18) are coded as uncertain as the preservation of the type material does not allow the presence or absence of terminal claws to be confirmed. *Diania* too is scored as uncertain, as it is difficult to distinguish possible terminal claws from its myriad accessory spines (65, 76). This character is scored as present in *Luolishania* (5) based on the presence of robust curved claws on the posterior appendages (see Character 61). This character is scored as absent in fuxianhuiids as the limb terminates in a conical tip rather than a differentiated claw element (1). Claws are scored as present in *Ilyodes* based on the observations by Thompson and Jones (121).

65. Terminal claws with multiple branches

(0) absent
(1) present
(–) inapplicable: terminal claws (Character 64) absent

Complex claws are present in Eutardigrada (36, 37, 119, 120) and the Siberian Orsten-type tardigrade (77), but not in heterotardigrades or any Paleozoic lobopodian known to date.

66. Number of claws on trunk limbs

(0) one
(1) two
(2) three
(3) four
(4) seven
(–) inapplicable: terminal claws (Character 64) absent

Modified from character 18 in Ma *et al.* (65) to better reflect the diversity of claw number in Cambrian lobopodians. *Cardiodictyon* unambiguously has two claws (84). *Leanchoilia* is coded as ambiguous for states 0 and 2 (one or three claws) to reflect the conflicting interpretations of García-Bellido and Collins (134) and Haug *et al.* (118). *Luolishania* is scored as having a single strongly curved claw based on the well preserved sclerites on the posterior legs; the interpretation of this taxon as having four claws on the anterior elongated limbs is questioned given that it is not possible to distinguish between terminal spines and the elongate setae that characterize the appendages (ref. 5, fig. 10). The condition of *Luolishania* is closely reminiscent to those found in *Collinsium* and the Emu Bay Collins' monster (3). The Burgess Shale Collins' monster (2) and *Acinocricus* (4) are scored as uncertain as the available photographic material does not allow such fine morphological detail to be resolved.

67. Differentiated distal foot in lobopodous trunk limbs

(0) absent
(1) present
(–) inapplicable: paired appendages (Character 1) absent; post-ocular appendages sclerotized (Character 8); inner branch modified as lateral flaps (Character 11).

The presence of a moveable foot is a synapomoprhic feature of crown-group Onychophora (18, 32, 121). *Tertiapatus* lacks a moveable foot (18). A foot is not clearly preserved in *Ilyodes* (81, 121), and thus is scored as uncertain.

68. Hypertrophied set of anterior body flaps

(0) absent
(1) present
(–) inapplicable: inner branch is not a lateral flap (Character 11) and dorsolateral flaps (Character 55) absent

This character applies to the enlarged pair of body flaps observed in the Hünsruck radiodontan *Schinderhannes* (19) and in the recently described *Lyrarapax* from the Chengjiang (20).

69. Strengthening rays in lateral flaps

(0) absent
(1) present
(–) inapplicable: : inner branch is not a lateral flap (Character 11) and dorsolateral flaps (Character 55) absent

Character 37 in Daley *et al.* (72).

70. Posterior tapering of lateral flaps

(0) absent
(1) present
(–) inapplicable: : inner branch is not a lateral flap (Character 11) and dorsolateral flaps (Character 55) absent

Character 40 in Daley *et al.* (72).

71. Anterior sets of reduced lateral flaps

(0) absent
(1) present
(–) inapplicable: : inner branch is not a lateral flap (Character 11) and dorsolateral flaps (Character 55) absent

This character applies to the presence of a series of reduced flaps in the anterior trunk region of various radiodontans (2, 20, 71, 72, 106). The presence of reduced lateral flaps is independent from the presence of a neck-like constriction, as *Peytoia* features the former but not the latter character. Scored as uncertain in *Aegirocassis* (21) and *Schinderhannes* (19) as the preservation of these taxa does not allow recognizing this feature.

72. Lobopodous limbs differentiated into two batches of multiple anterior/long and posterior/short limbs

(0) absent
(1) present
(–) inapplicable: limbs (Character 8) not lobopodous

Character 38 in Ma *et al.* (65). This condition is distinctive of all members of Luolishaniidae (2–5, 84), including *Collinsium*. This character is scored as absent for *Hadranax* as a significant portion of the body is preserved (85) and shows no indication of limb differentiation.

73. Number of anterior morphologically differentiated elongated limbs

(0) five (Luolishania, Acinocricus, *Collins' monster EBS*)
(1) six (Collinsium*, Collins' monster BS*)
(–) inapplicable: paired appendages (Character 1) absent; morphologically distinct appendage batches (Character 72) absent

Following the interpretation of Ramsköld and Chen (84) *Acinocricus* is scored as having five morphologically distinct anterior appendages.

74. Appendages comprise 15 or more podomeres

(0) Fewer than 15 podomeres
(1) 15 or more podomeres
(–) inapplicable: limbs (Character 8) not arthropodized

The endopods of certain taxa in the euarthropod stem-group, such as fuxianhuiids, bear 15 or more podomeres and are considered 'multipodomerous' (1, 53, 56, 69).

Posterior termination

75. Limbless posterior extension of the lobopodous trunk beyond last appendage pair

(0) absent
(1) present
(–) inapplicable: paired appendages (Character 1) absent; dorsal trunk covered by sclerotized plates (Character 33) present

This character has been altered from that utilized on previous analyses (e.g. Character 34 in ref. 65) to reflect the fact that, in extant Onychophora, the posterior extension of the lobopodous trunk (i.e. anal cone) corresponds to a segment that has lost its appendage pair as evinced by the prevalence of nephridia in this region (31). Since it is not possible to determine whether the posterior extension of the trunk in Paleozoic lobopodians originates from the loss of the last appendage pair – as in Onychophora – or as a true elongation of the trunk, this character is scored as present in all taxa that possess an appendage-less posterior extension beyond the last observable pair of limbs. This character is scored as absent in *Kerygmachela* (48, 50), *Jianshanopodia* (92) and *Anomalocaris* (71) as their tails likely represent modified appendages (see Characters 69 and 70). There is possible, but inconclusive, evidence for a small posterior extension in *Opabinia* (78, 79), which is thus coded as uncertain. *Hallucigenia sparsa* is also coded as uncertain; the posterior part of its body is poorly known (83). It is present in other species of *Hallucigenia* (67, 68). Similarly to other armored lobopodians with dorsal spines (e.g. *H. hongmeia, Luolishania*), this character is present in *Collinsium* (Fig. S6 *I*).

76. Posterior tagma composed of three paired lateral flaps

(0) absent
(1) present
(–) inapplicable: inner branch is not a lateral flap (Character 11) and dorsolateral flaps (Character 55) absent

Character 42 in Daley *et al.* (72).

77. Posteriormost trunk appendage pair structurally differentiated

(0) undifferentiated
(1) differentiated
(–) inapplicable: paired appendages (Character 1) absent

Jianshanopodia (92) is coded as present because the lateral extensions of the tail fan likely correspond to a modified pair of appendages. This character is scored as absent in Onychophora given that the last appendage pair is completely lost (31), rather than structurally modified. See also character 35 (65). Unlike *Onychodictyon ferox,* the posterior legs in *O. gracilis* are not consistently rotated forwards (39, 115), and thus this character is scored as absent for the former taxon. Ou *et al.* (82) described a pair of filiform-like structures seemingly attached to the posterior body extension of *Antennacanthopodia*; however, these features are not scored as appendicular as it is uncertain whether they actually belong to the fossil rather than being a superimposed filament. *Hurdia* (72) and *Schinderhannes* (19) bear a single flap-like appendage on the posterior end.

78. Nature of differentiated posterior appendages

(0) appendicular tail
(1) partially fused/reduced walking legs
(–) inapplicable: posterior appendages undifferentiated (Character 77)

In fuxianhuiids, the posteriormost appendage pair is modified into a tail fan or tail flukes (1, 56); a similar condition is also observed in *Opabinia* (78, 79), *Anomalocaris* (71), *Hurdia* (72), and *Lyrarapax* (20). The paired tail rami of *Kerygmachela* (48, 50) likely represent modified appendages. The last appendage pair of *Jianshanopodia* is modified into a set of lateral flaps, which form a tail fan together with the flattened terminal portion of the body (92). Partial fusion of the last pair of legs occurs in *Aysheaia* (93), *Onychodictyon gracilis* (115), *O. ferox* (39) and Tardigrada (37, 107); in all of these taxa, this character is expressed as an incipient fusion of the medioproximal bases of the posteriormost pair of limbs. The Siberian Orsten tardigrade is also coded as having a reduced posteriormost leg pair based on the morphological interpretation of Maas and Waloszek (77) for a vestigial rudiment on the posteroventral body region of this taxon. *Pambdelurion* is scored as uncertain because its posterior trunk is poorly known (49).

79. Nature of appendicular tail

(0) tail rami
(1) tail flaps
(–) inapplicable: appendicular tail (Character 78) absent

This character distinguishes the long tail rami of *Kerygmachela* (48, 50) from the flaps observed in *Jianshanopodia* (92), *Opabinia* (78, 79), radiodontans (71, 72), and fuxianhuiids (1).

80. Claws on posterior appendages directed anteriad

(0) normal orientation (claws pointing posteriad)
(1) rotated anteriad
(–) inapplicable: appendages lack terminal claws (Character 64); appendicular tail (Character 78) present

The last pair of legs are rotated anteriad in tardigrades (107), *Aysheaia* (93), *Onychodictyon ferox* (39), but not in *Cardiodictyon*, *Hallucigenia fortis* or *Microdictyon* (67). Although Liu *et al.* (ref. 115, p. 289) report that the claws on the 8th leg of a specimen of *O. gracilis* point in opposite directions, this refers to the fact that the two claws within the same limb are orientated in such a conformation, rather than suggesting that the claws point anteriad relative to the other clawed appendages. *Hallucigenia sparsa* is coded as uncertain owing to the poor preservation of its posterior end. The Siberian Orsten tardigrade (77) is coded as uncertain as the claws seem to be absent from the last pair of legs, although this could be an artifact of preservation.

Soft tissue organization

81. Ventral nerve cord with paired ganglia

(0) absent
(1) present

Character 2 in Tanaka *et al.* (63). Tardigrada and Euarthropoda have a ganglionated ventral nerve cord (136), in contrast to the ladder-like ventral nerve cord in Onychophora (124). Priapulida have an unpaired nerve cord associated with a net-like system of neural connectives (99, 102). Recent data on the neurological organization of stem-euarthropods indicate that paired condensed ganglia are present in *Chengjiangocaris* (1) and *Alalcomenaeus* (63). Hou *et al.* (ref. 98, figs 2f, 4f) reported the presence of paired faint structures adjacent to the gut that were interpreted as potential nerve ganglia on *Paucipodia*; however, this character is scored as uncertain for *Paucipodia* given that these structures cannot be observed in the material illustrated, and their description as ‘faintly preserved with a pink color” is contrary to unambiguous reports of nervous tissue preserved in Chengjiang-type fossils that display a conspicuous dark coloration (1, 62, 63). This character is scored as uncertain in *Lyrarapax* (20) as the preservation of this taxon does not allow the organization of the ventral nerve cord to be resolved.

82. Dorsal condensed brain

(0) absent
(1) present

Within the constituent groups of Ecdysozoa, Cycloneuralia is typified by the presence of a circumoesophageal nerve ring (99-102), whilst Panarthropoda is characterized by dorsal condensed brain neuromeres observed in Panarthropoda (23, 26, 27, 35, 46, 47). Recent studies have pioneered the study of paleoneurology in fossil taxa, and a dorsal condensed brain has been described in *Fuxianhuia* (62) and *Alalcomenaeus* (63).

83. Number of neuromeres integrated into the dorsal condensed brain

(0) one
(1) two
(2) three
(–) inapplicable: dorsal condensed brain (Character 82) absent

See the introductory statements above.

84. Mouth innervation relative to brain neuromeres

(0) protocerebral innervation
(1) deutocerebral innervation
(2) innervation from multiple neuromeres
(–) inapplicable: condensed dorsal brain (Character 82) absent

Recent fossil data suggest a likely deutocerebral innervation for the mouth in *Fuxianhuia* and *Alalcomenaeus* based on the position of the oesophageal foramen relative to the brain (62, 63), which is congruent with the organization found in phylogenetically basal extant Euarthropoda such as

Chelicerata and Myriapoda (44, 46, 47, 58); note that although the stomatogastric nerves around the mouth in Pancrustacea originate from the tritocerebrum, this character state is not included given that none of the taxa analyzed display this organization. State 2 reflects the complex neurological organization present in Onychophora; although the jaws have a deutocerebral segmental affinity and innervation, the lip papillae that delineate the mouth opening are formed as epidermal derivates of the three anteriormost body segments, and thus receiver nervous terminals from the protocerebrum, deutocerebrum and part of the ventral nerve cord (26, 33). The tardigrade mouth cone is innervated from the protocerebrum (35). The mouth innervation is coded as protocerebral in *Lyrarapax* (20) based on the position relative to the dorsal brain, and the lack of additional neuromeres integrated into the central nervous system.

85. Nerve cord lateralized

*(0) absent (*Alalcomenaeus*,* Fuxianhuia*, Tardigrada)*
(1) present (Onychophora)

Character 1 in Tanaka *et al.* (63). This character distinguishes the organization of the ventral nerve cord in Onychophora (124) from that in other phyla.

86. Dorsal heart

(0) absent
(1) present

Ma *et al.* (65) recently described the presence of a dorsal heart in an exceptionally preserved specimen of the stem-euarthropod *Fuxianhuia protensa* from the Chengjiang biota; this character is scored as uncertain in all other fossil taxa included in the analysis. Budd (125) discussed the problematic case of interpreting the absence of a circulatory system in Tardigrada as either ancestral or derived given the inherent physical properties associated with a miniaturized body organization, and concluded that a methodologically sound way of addressing this issue in a cladistic analysis is to score this character as inapplicable. In acknowledgement of this issue, the dorsal heart was scored as inapplicable in a secondary iteration of the analysis; however, this resulted in the loss of resolution. Given that there is no fundamentally correct method for scoring the dorsal heart of Tardigrada due to the incomplete understanding of their evolution and overall physiology, this character is scored as absent in order to improve the resolution of the taxa that represent the focus of this study.

Note S3. Comments on the results of the phylogenetic analysis

The results of the phylogenetic analysis support the overall topology found by Smith and Ortega-Hernández (16), albeit with minor alterations due to the inclusion of additional data in terms of taxa and characters studied. The most striking feature of the resulting topology lies in its substantial degree of stability to several degrees of homology penalization (Fig. 4 *A* and Fig. S8), and the support for a monophyletic group including Tardigrada and Euarthropoda (i.e. Tactopoda *sensu* refs. 103, 125; see also ref. 70), unlike the more conventional relationship of Onychophora and Euarthropoda supported by molecular data (64, 126, 127). The overall relationships between analyzed representatives of Tactopoda demonstrate stable phylogenetic positions. The only taxa that show important variability at relatively low concavity (k) values are *Aysheaia pedunculata* (94) and *Onychodictyon ferox* (39, 115). Under equal weights and concavity values of $k > 4$, these taxa are recovered as members of stem-

Panarthropoda and stem-Tardigrada respectively (Fig. 4 *A* and Fig. S8 *A, D*); however, concavity values of $k < 4$ recover both lobopodians as basal stem-Euarthropoda (Figs. S8 *B, C*). This variability is most likely associated with the position of *Aysheaia* and *O. ferox* as potentially basal representatives of the stem-lineages of Panarthropoda, Euarthropoda and Tardigrada, resulting in alternative character polarities that makes resolving their precise affinities difficult without the input of additional data (125, 128). The paraphyly of the genus *Onychodictyon* supported by this study (16) can be attributed to this phenomenon, and also suggest that the morphology of the dorsolateral sclerites is not necessarily the most informative character for making systematic classifications of lobopodian taxa (39, 115).

The relationships between lobopodians with spinose frontal appendages (*Jianshanopodia*, *Megadictyon*), gilled-lobopodians (*Kerygmachela*, *Pambdelurion*, *Opabinia*) and radiodontans are in accordance with previous results (16, 70, 65, 64, 76). Interestingly, the gilled-lobopodian *Opabinia* was found consistently as sister-group to Deuteropoda; this is likely a result of several derived characters in *Opabinia*, such as the presence of epidermal segmentation and a posteriorly-oriented mouth opening (78, 79). The problematic taxon *Schinderhannes* was recovered as a member of a monophyletic Radiodonta (20, 21, 64), as opposed to as sister-taxon to Euarthropoda (65, 19). Although the results of the analysis consistently indicated a sister-group association between *Lyrarapax* (20) and *Anomalocaris* (71), it was not possible to resolve the internal relationships within other analyzed members of Radiodonta.

Some of the variability observed from the analyses focuses on the relationships of basal members of stem-group Onychophora. The taxa that evince substantial motility include *Xenusion* (110, 129), *Paucipodia* (98, 112), *Onychodictyon gracilis* (115) and *Diania* (65, 76). Under equal weights (Fig. S8 *A*) and concavity values of $k \geq 4$ (Fig. 4 *A* and Fig. S8 *D*), these taxa are recovered as stem-Onychophora; however, concavity values of $k < 4$ (Fig. S8 *B, C*) produce a polytomy between these taxa relative to total-group Onychophora and Tactopoda. These observations mirror the motility of *Aysheaia* and *O. ferox*, and are likely caused by their position as basal representatives within either stem-group Onychophora or Panarthropoda. Given the stability and resolution of the equally weighted and implied weighted analysis with $k \geq 4$, it is considered that these topologies are the most informative regarding the phylogenetic relationships of total-group Panarthropoda in this study; in particular, the topology obtained under a concavity value of $k = 4$ offers the best balance between strength of homology penalization and tree resolution (see Fig. *4 A*). Within unambiguous members of total-group Onychophora, all iterations of the analysis provided unambiguously support for the monophyly of Luolishaniidae Hou and Bergström 1995, indicating that the presence of supernumerary dorsal spines and plumose differentiated appendages have a single origin. *Hallucigenia hongmeia* (68) represents closest reconstruction of the ancestral luolishaniid before the evolution of the autapomorphic characters that define this group; this result provides further support for the paraphyly of the genus *Hallucigenia* (3). Despite the extraordinary preservation of *Collinsium*, and to an approximately similar degree *Luolishania* (5), it was not possible to resolve the internal relationships within Luolishaniidae given the poorly known morphology of the Burgess Shale Collins' monster (2), the Emu Bay Shale Collins's monster-like lobopodian (3) and *Acinocricus* (4). Although a sister-group relationship between *Collinsium* and the Burgess Shale Collins' monster was found among some of the most parsimonious trees based on the possession of six pairs of differentiated appendages, it was not possible to obtain this result in the strict consensus. Finally, the analysis was unable to resolve a polytomy including *Illyodes* (81, 121), *Tertiapatus* (18) and extant onychophorans, suggesting that these fossil species are extremely close to the crown-group despite uncertainty on some crucial characters, such as the presence of a moveable foot or identifiable slime papillae; this lack of resolution likely stems from the large amount of missing data in these fossil taxa, coupled with conflict of the available characters.

Note S4. Scoring of limb tagmosis data used for calculation of Brillouin index

Tubiluchus troglodytes Todaro and Shirley 2003 (129)
Priapulids and other cycloneuralians lack paired appendages, and thus it is not possible to calculate a coefficient of limb tagmosis for the outgroup.

Cricocosmia jinningensis Hou and Sun 1988 (130)
Paleoscolecids and other cycloneuralians lack paired appendages, and thus it is not possible to calculate a coefficient of limb tagmosis for the outgroup.

Aysheaia pedunculata Whittington 1978 (93)
Aysheaia is characterized by a pair of anteriormost, spinose frontal appendages, followed by 10 pairs of ventrolateral lobopodous limbs. The last two limb pairs, however, are differentiated in that they are rotated so that the claws face anteriorly rather than posteriorly as in the other trunk appendages (93), a condition that is also present in *Onychodictyon ferox* (39, 115) and Tardigrada. The present scoring of limb tagmosis in *Aysheaia* differs from that used in previous studies in that the presence of two pairs of posterior differentiated legs are acknowledged (*contra* 137).

Onychodictyon ferox Hou *et al.* 1991 (131)
The recent redescription of *O. ferox* (39) clearly shows the presence of a feathery-like antenniform first limb pair, followed by 12 pairs of lobopodous limbs. Similarly to *Aysheaia*, however, the last limb pair of *O. ferox* is differentiated by the rotation of the appendages so that the claws face anteriorly.

Onychodictyon gracilis Liu *et al.* 2008 (115)
Liu *et al.* (115) report that *O. gracilis* lacks a 'pair of antennae' on the head region, but report that the first pair of trunk limbs is significantly more robust that the rest of the trunk appendages; however, based on the figured specimens, (e.g. ref. 115, fig. 2A1, 3), it does not appear that this first trunk appendage if any different from some of the more posterior ones, and thus it is considered that this species has only one type of limb morphotype. Finally, although some authors have regarded the last limb pair of *O. gracilis* as being rotated anteriorly (as in *O. ferox*; e.g. ref. 107), Liu *et al.* (ref. 115, p. 289) report that this orientation is variable and depend of the preservation of the trunk region, and thus it is likely to represent a taphonomic artifact.

Diania cactiformis Liu *et al.* 2011 (76)
Diania is characterized by 10 pairs of lobopodous legs with a dense coverage of short spines (65, 76). Although some of the legs are bent in various directions, the changes in size and shape throughout the trunk are negligible.

Xenusion auerswaldae Pompeckj 1927 (132)
The studies describing the morphology of *Xenusion* consistently report fragmentary material (110, 133), and thus it is not possible to determine the total number of appendage pairs in this taxon; because of this, the limb tagmosis index cannot be calculated for *Xenusion*. Despite these problems, the close relationship found between *Xenusion* and *Diania* in the cladistic analysis suggests that the better-known morphology of the latter is representative of both taxa.

Paucipodia inermis Chen *et al.* 1995 (112)
The trunk appendages of *Paucipodia* comprise nine limb pairs of nearly identical construction and dimensions (98, 112).

Microdictyon sinicum Chen *et al.* 1995 (96)
The limbs of *Microdictyon* consist of 10 pairs of homopodous appendages of similar size and shape throughout the body (67, 96).

Cardiodictyon catenulum Hou et al. 1991 (131)
The limbs of *Cardiodictyon* consist of 25 pairs of homopodous appendages of similar size and shape throughout the body (66, 131).

Hallucigenia sparsa (Walcott 1911) (134)
The limbs of *H. sparsa* consist of three significantly reduced and slender anteriormost appendage pairs, followed by seven pairs of elongate lobopodous clawed legs (83).

Hallucigenia fortis Hou and Bergström 1995 (67)
The first and second appendage pairs of *H. fortis* are differentiated from the other trunk limbs by its more elongate construction and the absence of claws (84, 66). The remaining limbs consist of eight pairs of walking legs.

Hallucigenia hongmeia Steiner *et al.* 2012 (68)
H. hongmeia is only known from incomplete specimens that lack details of the anterior and posterior ends of the body, and thus it is not possible to calculate the limb tagmosis index for this species. Although the complete appendage count may be similar to that of other *H. sparsa* and *H. fortis* – both of which display 10 limb pairs – this information is not included given the variable patterns of limb differentiation observed in the these taxa.

Luolishania longicruris Hou and Chen 1989 (135)
Ma *et al.* (5) have provided the most comprehensive account of the morphology of *Luolishania*. The head possesses a pair of small antennae-like limbs. The trunk region is subdivided into two major tagma based on their limb morphology: the anteriorst five pairs of trunk limbs are elongated and bear paired rows of fine setae, whereas the remaining limbs consist of nine walking legs with a single terminal claw.

Collinsium ciliosum nov.
The pattern of limb tagmosis in *Collinsium* is similar to that of *Luolishania* and other Collins' monster-type lobopodians, with the major distinction being the presence of six pairs of setulose anterior trunk limbs. Together with the antenna-like first appendage pair and the nine pairs of clawed posterior walking legs, *Collinsium* has a total of 16 pairs of limbs.

Burgess Shale Collins' monster (2)
The Burgess Shale Collins' monster is currently known from a single photograph published by Collins (2). This figured specimen shows the presence of six sets of anterior differentiated limbs with setae similar to those of *Collinsium* and other luolishaniids, followed by six pairs of shorter – presumably walking – legs.

Emu Bay Collins' monster (3)
García-Bellido *et al.* (3) reported a fragmentary Collins' monster type lobopodian that includes information of five anterior differentiated appendages with fine setae, and one lobopodous walking leg with a single claw. Although this morphological information is enough to recognize the overall affinities of this organism, the paucity of appendicular information makes it not possible to calculate the limb tagmosis index.

Acinocricus stichus Conway-Morris and Robison 1988 (4)
The holotype of *Acinocricus* is the only nearly complete specimen known. Ramsköld and Chen (84) compared this taxon extensively to the Burgess Shale Collins' monster, and drew several parallels in terms of number preserved limbs and overall segmental organization. Unfortunately the number of legs on the posterior region, as well as the presence of anterior differentiated limbs, remains obscure in the type material. Due to these issues *Acinocricus* it is not possible to calculate the limb tagmosis index for this taxon.

Orstenotubulus evamuellerae Maas *et al.* 2007 (86)
Orstenotubulus is only known from fragmentary material and thus it is impossible to calculate the limb tagmosis index for this taxon.

Antennacanthopodia gracilis Ou *et al.* 2011 (82)
The head region in *Antennacanthopodia* is typified by two elongate anterior limb pairs that display slightly different morphologies, with the first being significantly longer than the second; the trunk includes nine pairs of short lobopodous limbs (82). The holotype of *Antennacanthopodia* is described as having a pair of long and flexible "cirriform structures". However, is uncertain whether these structures are highly modified appendages or actually represent a superimposed exogenous fragment that is not actually part of the morphology of this taxon. The cirriform structures are treated as non-appendicular in the limb tagmosis analysis as such structure is not known from any other closely related taxa.

Megadictyon haikouensis Luo *et al.* 1999 (136)
The early Cambrian lobopodian *Megadictyon* bears a pair of robust frontal appendages. Although the trunk region of *Megadictyon* is incomplete in the available fossil material, Liu *et al.* (ref. 90, p. 282) estimate that there may be as many as 13 leg-bearing segments. This number is tentatively used for calculating the limb tagmosis index, but caution is exercised in the interpretation of the resulting data.

Jianshanopodia decora Liu *et al.* 2006 (92)
As with *Megadictyon, Jianshanopodia* displays a pair of differentiated frontal appendages followed by numerous trunk limbs. However, *Jianshanopodia* is also known from well-preserved but fragmentary material, and it is estimated that the trunk bore a total of up to 12 ambulatory legs (92); this number is tentatively used for calculating the limb tamosis index, but caution is exercised in the interpretation of the resulting data. The posterior region of *Jianshanopodia* terminates in a tail flap that most likely has an appendicular origin.

Hadranax augustus Budd and Peel 1998 (85)
Hadranax is only known from fragmentary material and thus it is impossible to calculate the limb tagmosis index for this taxon.

Kerygmachela kierkegaardi Budd 1993 (48)
The overall organization of *Kerygmachela* includes a pair of large frontal appendages with forward-facing spines, 11 sets of homonomous gill-bearing lateral lobes, and a pair of terminal multisegmeted cerci-like appendages (48, 50). The present scoring of *Kerygmachela* is identical to that of see ref. 137.

Pambdelurion whittingtoni Budd 1997 (49)

The morphology of *Pambdelurion* is similar to that of *Kerygmachela* in that both possess a well-developed pair of frontal appendages, as well as 11 sets of lateral body flaps. However, Budd (49) reports the possible presence of three smaller occipital flaps on the anteriormost part of the trunk region; based on the presence of reduced body flaps in radiodontans (71, 72), the presence of similar structures in *Pambdelurion* is tentatively scored in the analysis. The posterior region of *Pambdelurion* is not well known (49), and thus it is uncertain whether terminal appendages were present or not. Given the uncertainty on some aspects of this taxon's morphology, caution is exercised in the interpretation of the data resulting from these calculations.

Opabinia regalis Walcott 1912 (138)

The morphology of *Opabinia* consists of a first appendage pair fused into a clawed nozzle-like proboscis, followed by fifteen pairs of gilled body flaps, and terminating on three pairs of appendicular tail flukes (79). The present scoring of *Opabinia* is modified from a previous analysis in which the first pair of trunk body flaps was considered as a distinct specialized appendage due to the putative absence of dorsal gills (see ref. 137).

Hurdia victoria Walcott 1912 (138)

The preservation of the most complete *Hurdia* specimens allows the identification of some sets of differentiated limbs. There is a single pair of spinose frontal appendages, followed by three pairs of reduced setal blades; the main portion of the body however, has been described as having between six and ten segments bearing body flaps, which likely results from post-mortem disarticulation (72). Finally, the posterior termination of the body possesses a single pair of lobe-like flaps (72).

Peytoia nathorsti Walcott 1911 (134)

Peytoia shares with other radiodontans the presence of a first pair of spinose frontal appendages and a trunk region with two sets of specialized body flaps. The first four pairs of body flaps are reduced, and followed by 10 pairs of flaps that vary in size gradually throughout the body (72, 106, 139). There is no evidence for the presence of caudal appendages.

Anomalocaris canadensis Whiteaves 1892 (140)

A. canadensis is typified by a pair of well developed frontal appendages, followed ventrally by three reduced body flaps, 14 gilled-body flaps of variable size, and three posterior tail flukes (71, 106, 139).

Schinderhannes bartelsi Kühl *et al.* 2009 (19)

Schinderhannes is characterized the presence of spinose frontal appendages, followed by a hypertrophied set of body flaps, 10 segments with homopodous limbs, and a pair of tail flukes on the posterior region. There is no evidence for the presence of a neck-like construction or reduced flaps as observed in other radiodontans (20, 72).

Lyrarapax unguispinus Cong *et al.* 2014 (20)

In addition to a pair of well-developed spinose frontal appendages, *Lyrarapax* is similar to *Anomalocaris* in the presence of a neck-like constriction of the anterior trunk region, in this case consisting of four segments with reduced body flaps. The first trunk segment after the neck bears a set of hypertrophied body flaps, followed by up to 11 flaps (including a hypertrophied set of anterior flaps) that taper posteriorly (20); similarly to *Anomalocaris*, the posterior part of the trunk of *Lyrarapax* possesses three-paired caudal flaps.

Aegirocassis benmoulae Van Roy *et al.* 2015 (21)

In addition to a pair of well-developed spinose frontal appendages, *Aegirocassis* has a total of 11 segments attaining maximum width at the third segment and tapering to a blunt tip. There is no morphological variation on the dorsal and ventral body flaps apart from a slight change in size towards the posterior end. *Aegirocassis* lacks appendicular specializations.

Ilyodes inopinata Thompson and Jones 1980 (121)

Following the revision of the morphology of *Ilyodes* by Haug *et al.* (81) and its similarity with extant onychophorans, this taxon is scored as having a pair of antenniform first appendages, the possible presence of jaws, a set of reduced slime papillae, and a trunk with at least 20 lobopodous short walking legs. Caution should be followed with the interpretation of the resulting tagmosis index given that the presence of jaws is not confirmed in the fossil material.

Tertiapatus dominicanus Poinar 2000 (18)

Based on the similarity between *Tertiapatus* and extant onychophorans, particularly the ventral position of the mouth (18), this taxon is scored as having antenniform first appendages, putative jaws, slime papillae and 19 walking legs. Caution should be followed with the interpretation of the resulting tagmosis index given that the presence of jaws is not confirmed in the fossil material.

Euperipatoides kanangrensis Reid 1996 (141)

Euperipatoides is representative of the overall limb specialization of Onychophora, consisting of a pair of protocerebral antennae-like limbs, a pair of modified and internalized jaws, a set of slime papillae, and a trunk with 15 pairs of homopodous walking legs with terminal claws. Although developmental evidence indicates that the anal cone includes the remains of a lost pair of appendages (31), this condition is not reflected in the scoring as it does not qualify as functional differentiation of the limb itself.

Plicatoperipatus jamaicensis Grabham and Cockerell 1892 (142)

Plicatoperipatus jamaicensis shares the same basic cephalic organization with *Euperipatoides*, consisting of antennae, jaws and slime papillae, but differs in the number of walking legs. Grabham (143) reported the presence of up to 43 pairs of legs in this species, the largest number of legs recorded in Onychophora (144).

Ooperipatellus nanus Ruhberg 1985 (145)

Ooperipatellus nanus shares the same basic cephalic organization with *Euperipatoides*, consisting of antennae, jaws and slime papillae, but differs in the number of walking legs. *O. nanus* possesses only 13 pairs of walking legs, the lowest leg count recorded in Onychophora (144).

Orsten Siberian tardigrade Maas and Waloszek 2001 (77)

The tardigrade-like taxon described from the middle Cambrian of Siberia by Maas and Waloszek (77) bears three identical clawed limbs, followed posteriorly by a vestigial structure that is interpreted as a reduced fourth leg pair. Based on the similarity of this taxon to extant Tardigrada, including the presence of oral papillae, it is assumed that a protocerebral stylet apparatus was present even if not observable on the fossil material.

Actinarctus doryphorus Schulz 1935 (146)

The appendicular organization of tardigrades is remarkably conserved, consisting of a set of internalized protocerebral appendages that form a stylet apparatus (37, 147), followed by four pairs of unarticulated lobopodous legs. The only legs that show a degree of differentiation are those of the 4th segment, which differ in that they are turned anteriorly and fused to a variable degree in different groups.

Halobiotus crispae Kristensen 1983 (148)
The appendicular organization of tardigrades is remarkably conserved, consisting of a set of internalized protocerebral appendages that form a stylet apparatus (37, 147), followed by four pairs of unarticulated lobopodous legs. The only legs that show a degree of differentiation are those of the 4th segment, which differ in that they are turned anteriorly and fused to a variable degree in different groups.

Chengjiangocaris kunmingensis Yang *et al.* 2013 (1)
C. kunmingensis reflects the fundamental limb organization of the anterior region of fuxianhuiids, including a hypostome/labrum complex, a pair of deutocerebral antennae, and a set of specialized post-antennal appendages. The following two limb pairs consist of greatly reduced biramous walking legs, each of which corresponds to a single reduced anterior tergite. The following three reduced tergites also bear a single pair of well-developed briamous limbs. The remaining trunk tergites are polypodous, and bear between three and four sets of biramous legs. Given that the trunk of *C. kunmingensis* consists of 21 'normal' tergites, the total number of legs on the main trunk is scored as 66, that is three legs on the anterior reduced segments, and an average of three legs from the 6th to 26th tergite. The tailspine is associated with paired tail flukes.

Fuxianhuia xiaoshibaensis Yang *et al.* 2013 (1)
F. xiaoshibaensis reflects the basic fuxianhuiid head organization similarly to *C. kunminensis*, but differs in the pattern of trunk tagmosis. The first three pairs in *F. xiaoshibaensis* are associated with each one of the anteriormost three reduced tergites, whereas there are two or three limb pairs below the 4th to 20th tergites; the number of total limbs is scored as 37, including three limbs for the reduced tergites, and two for each of the remaining 17 tergites. Based on comparisons with *F. protensa* (67, 69, 96), the presence of paired tail flukes is also scored for *F. xiaoshibaensis*.

Alalcomaneus sp. (Tanaka *et al.* 2013) (63)
The limb organization of *Alalcomenaeus* sp. from the Chengjiang biota (63) incorporates a pair of 'short great appendages', followed by three sets of biramous cephalic appendages (*contra* two pairs of limbs in *A. cambricus*, see ref. 149), and 11 pairs of identical trunk limbs; there is no significant change in morphology between the cephalic and trunk appendages. The presence of a reduced protocerebral segment in to a labrum-like anlage is assumed based on the phylogenetic position of *Alalcomenaeus*.

Leanchoilia superlata Walcott 1912 (138)
Leanchoilia is similar to *Alalcomenaeus* in the presence of a pair of short great appendages, but differs in the presence of cephalic limb differentiation. Haug *et al.* (55) recently reported the presence of a significantly reduced biramous pair of appendages posterior to the short great appendages, which together with two additional 'normal sized' limb pairs are located under the cephalic shield. The biramous limbs on the trunk region are of a nearly identical construction, although they decrease in size posteriorly.

Misszhouia longicaudata (Zhang and Hou 1985) (150)
Zhang et al. (151) provided the most recent update on the morphology of the nektaspidid *Misszhouia*. The limb organization includes a hypostome/labrum complex, a pair of well-developed antennae, and up to 30 pairs of trilobite-like biramous limbs with a similar construction in adult specimens.

Kuamaia lata Hou 1987 (152)
In addition the hypostome/labrum complex, *Kuamaia* bears a pair of antennae followed by at least 14 biramous limbs of similar construction throughout the body, with only subtle differences in size. Based on the information available from figured specimens in Hou and Bergström (ref. 153, fig. 59) and Edgecombe and Ramsköld (ref. 57, fig. 6), the *Kuamaia* is scored as having three post-antennal cephalic limbs, followed by at least 11 additional limb pairs in the trunk region.

1. Yang J, Ortega-Hernández J, Butterfield NJ, Zhang X-G (2013) Specialized appendages in fuxianhuiids and the head organization of early euarthropods. *Nature* 494:468–71.

2. Collins D (1986) Paradise revisited. *Rotunda* 19:30–39.

3. García-Bellido DC, Edgecombe GD, Paterson JR, Ma X-Y (2013) A 'Collins' monster'-type lobopodian from the Emu Bay Shale Konservat-Lagerstätte (Cambrian), South Australia. *Alcheringa* 37:474–478.

4. Conway Morris S, Robison RA (1988) More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. *Univ Kans Paleontol Contrib* 122:1–48.

5. Ma X-Y, Hou X-G, Bergström J (2009) Morphology of *Luolishania longicruris* (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic relationships within lobopodians. *Arthropod Struct Dev* 38:271–91.

6. Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24:415–428.

7. Goloboff PA (1999) Analyzing large datasets in reasonable times: solutions for composite optima. *Cladistics* 15:415–428.

8. Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15:407–414.

9. Brusatte SL, Benton MJ, Ruta M, Lloyd GT (2008) Superiority, competition and opportunism in the evolutionary radiation of dinosaurs. *Science* 321:1485–1488.

10. Wills MA, Gerber S, Ruta M, Hughes M (2012) The disparity of priapulid, archaeopriapulid and palaeoscolecid worms in the light of new data. *J Evol Biol* 25:2056–2076.

11. Sneath PH, Sokal RR (1973) *Numerical Taxonomy* (Freeman, San Francisco).

12. Foote MJ (1992) Paleozoic record of morphological diversity in blastozoan echinoderms. *Proc Natl Acad Sci USA* 89:7325–7329.

13. Foote MJ (1993) Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19:403–419.

14. Cisne JL (1974) Evolution of world fauna of aquatic free-living arthropods. *Evolution* 28:337–366.

15. Brillouin L (1962) *Science and information theory*, 2nd ed (Academic Press).

16. Smith MR, Ortega-Hernández J (2014) *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. *Nature* 514:363–366.

17. Han J, Liu J-N, Zhang X-L, Shu D-G (2007) Trunk ornament on the palaeoscolecid worms *Cricocosmia* and *Tabelliscolex* from the Early Cambrian Chengjiang deposits in China. *Acta Palaeontol Pol* 52:423–431.

18. Poinar G Jr (2000) Fossil onychophorans from Dominican and Baltic amber: *Tertiapatus dominicanus* n.g., n.sp. (Tertiapatidae n. fam. and *Succinipatopsis balticus* n.g., n.sp. (Succinipatopsidae n. fam.) with a proposed classification of the Subphlylum Onychophora. *Invert Biol* 119:104–109.

19. Kühl G, Briggs, DEG, Rust, J (2009) A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany. *Science* 323:771–773.

20. Cong PY, Ma X-Y, Hou X-G, Edgecombe GD,Strausfield NJ (2014) Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513:538–542.

21. Van Roy P, Daley AC, Briggs DEG (2015) Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature* (doi. 10.1038/nature14256).

22. Dzik J (2011) The xenusian-to-anomalocaridid transition within the lobopodians. *Bollettino della Società Paleontologica Italiana* 50:65–74.

23. Mayer G, Whitinton P, Sunnuks P, Pflüger H-J (2010) A revision of brain composition in Onychophora (velvet worms) suggests that the tritocerebrum evolved in arthropods. *BMC Evol Biol* 10:255.

24. Whitington PM, Mayer G (2011) The origins of the arthropod nervous system: insights from the Onychophora. *Arthropod Struct Dev* 40:193–209.

25. Eriksson BJ, Tait NN, Budd GE, Janssen R, Akam M (2010) Head patterning and Hox gene expression in an onychophoran and its implications for the arthropod head problem. *Dev Genes Evol* 220:117–122.

26. Eriksson BJ, Budd GE (2000) Onychophoran cephalic nerves and their bearing on our understanding of head segmentation and stem-group evolution of Arthropoda. *Arthropod Struct Dev* 29:197–209.

27. Eriksson BJ, Tait NN, Budd GE (2003) Head development in the onychophoran *Euperipatoides kanangrensis* with particular reference to the central nervous system. *J Morphol* 255:1–23.

28. Eriksson BJ, Tait NN, Budd GE, Akam M (2009) The involvement of *engrailed* and *wingless* during segmentation in the onychophoran *Euperipatoides kanangrensis* (Peripatopsidae: Onychophora) (Reid 1996). *Dev Genes Evol* 219:249–64.

29. Eriksson BJ, Samadi L, Schmid A (2013) The expression pattern of the genes *engrailed*, *pax6*, *otd* and *six3* with special respect to head and eye development *Euperipatoides kanangrensis* Reid 1996 (Onychophora: Peripatopsidae). *Dev Genes Evol* 223:237–46.

30. Steinmetz PRH et al. (2010) *Six3* demarcates the anterior-most developing brain region in bilaterian animals. *EvoDevo* 1:14.

31. Mayer G, Koch M (2005) Ultrastructure and fate of the nephridial anlagen in the antennal segment of *Epiperipatus biolleyi* (Onychophora, Peripatidae)—evidence for the onychophoran antennae being modified legs. *Arthropod Struct Dev* 34:471–480.

32. De Sena Oliveira I, Mayer G (2013) Apodemes associated with limbs support serial homology of claws and jaws in Onychophora (velvet worms). *J Morphol* 274:1180–1190.

33. Martin C, Mayer G (2014) Neuronal tracing of oral nerves in a velvet worm - implications for the evolution of the ecdysozoan brain. *Front Neuroanatomy* 8:1–13.

34. Zantke J, Wolff C, Scholtz G (2007) Three-dimensional reconstruction of the central nervous system of *Macrobiotus hufelandi* (Eutardigrada, Parachela): implications for the phylogenetic position of Tardigrada. *Zoomorphology* 127:21–36.

35. Mayer G, Kauschke S, Rüdiger J, Stevenson PA (2013) Neural markers reveal a one-segmented head in tardigrades (water bears). *PloS One* 8:e59090.

36. Nelson DR (2002) Current status of the Tardigrada: evolution and ecology. *Integr Comp Biol* 42:652–659.

37. Halberg KA, Persson D, Mobjerg N, Wanninger A, Kristensen RM (2009) Myoanatomy of the marine tardigrade *Halobiotus crispae* (Eutardigrada: Hypsibiidae). *J Morphol* 270:996–1013.

38. Persson DK, Halberg K, Jørgensen A, Møbjerg N, Kristensen RM (2012) Neuroanatomy of *Halobiotus crispae* (Eutardigrada: Hypsibiidae): Tardigrade brain structure supports the clade Panarthropoda. *J Morphol* 273:1227–1245.

39. Ou Q, Shu D-G, Mayer G (2012) Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. *Nat Commun* 3:1261.

40. Kimm MA, Prpic N-M (2006) Formation of the arthropod labrum by fusion of paired and rotated limb-bud-like primordia. *Zoomorphology* 125:147–155.

41. Liu Y, Maas A, Waloszek D (2009) Early development of the anterior body region of the grey widow spider *Latrodectus geometricus* Koch, 1841 (Theridiidae, Araneae). *Arthropod Struct Dev* 38:401–416.

42. Liu Y, Maas A, Waloszek D (2010) Early embryonic development of the head region of *Gryllus assimilis* Fabricius, 1775 (Orthoptera, Insecta). *Arthropod Struct Dev* 39:382–395.

43. Browne WE, Price AL, Gerberding M, Patel NH (2005) Stages of embryonic development in the amphipod crustacean, *Parhyale hawaiensis*. *Genesis* 42:124–49.

44. Scholtz G, Edgecombe, GD (2006) The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Dev Genes Evol* 216:395–415.

45. Posnien N, Bashasab F, Bucher G (2009) The insect upper lip (labrum) is a nonsegmental appendage-like structure. *Evol Dev* 11: 480–488.

46. Mittmann B, Scholtz G (2003) Development of the nervous system in the "head" of *Limulus polyphemus* (Chelicerata: Xiphosura): morphological evidence for a correspondence between the segments of the chelicerae and of the (first) antennae of Mandibulata. *Dev Genes Evol* 213:9–17.

47. Harzsch S, Wildt M, Battelle B, Waloszek D (2005) Immunohistochemical localization of neurotransmitters in the nervous system of larval *Limulus polyphemus* (Chelicerata, Xiphosura): evidence for a conserved protocerebral architecture in Euarthropoda. *Arthropod Struct Dev* 34:327–342.

48. Budd GE (1993) A Cambrian gilled lobopod from Greenland. *Nature* 364:709–711.

49. Budd GE (1997) Stem-group arthropods from the Lower Cambrian Sirius Passet fauna of North Greenland. *In* Fortey RA, Thomas RH (eds.) *Arthropod Relationships*, Chapman and Hall, London, 125–138 pp.

50. Budd GE (1998) The morphology and phylogenetic significance of *Kerygmachela kierkegaardi* Budd (Buen Formation, Lower Cambrian, N Greenland). *Trans R Soc Edinburgh: Earth Sci* 89:249–290.

51. Budd GE (2002) A palaeontological solution to the arthropod head problem. *Nature* 417:271–275.

52. Chen J-Y, Waloszek D, Maas A (2004) A new “great-appendage” arthropod from the Lower Cambrian of China and homology of chelicerate chelicerae and raptorial antero-ventral appendages. *Lethaia* 37:3–20.

53. Waloszek D, Chen J-Y, Maas A, Wang X (2005) Early Cambrian arthropods—new insights into arthropod head and structural evolution. *Arthropod Struct Dev* 34:189–205.

54. Stein M (2010) A new arthropod from the Early Cambrian of North Greenland, with a “great appendage”-like antennula. *Zool J Linnean Soc* 158:477–500.

55. Haug JT, Waloszek D, Maas A, Liu Y, Haug C (2012) Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* 55:369–399.

56. Chen J-Y, Edgecombe G, Ramsköld L, Zhou G (1995) Head segmentation in Early Cambrian *Fuxianhuia*: implications for arthropod evolution. *Science* 268:1339–43.

57. Edgecombe GD, Ramsköld L (1999) Relationships of Cambrian Arachnata and the systematic position of Trilobita. *J Paleontol* 73:263–287.

58. Scholtz G, Edgecombe, GD (2005) Heads, Hox and the phylogenetic position of trilobites. *Crustacean Issues 16: Crustacea and Arthropod Relationships*, eds Koenemann S, Jenner RA (CRC Press, Boca Raton), pp 139–165.

59. Eriksson ME, Terfelt F (2012) Exceptionally preserved Cambrian trilobite digestive system revealed in 3D by synchrotron-radiation X-ray tomographic microscopy. *PloS One* 7:e35625.

60. Ortega-Hernández J, Legg D, Braddy S (2013) The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* 29:15–45.

61. Budd GE (2008) Head structure in upper stem-group euarthropods. *Palaeontology* 51:561–573.

62. Ma X-Y, Hou X-G, Edgecombe GD, Strausfeld NJ (2012) Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490:258–261.

63. Tanaka G, Hou X-G, MA X-Y, Edgecombe GD, Strausfeld NJ (2013) Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature* 502:364–367.

64. Legg DA, Sutton MD, Edgecombe GD (2013) Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nat Commun* 4: 2485.

65. Ma X-Y, Edgecombe GD, Legg DA, Hou X-G (2014) The morphology and phylogenetic position of the Cambrian lobopodian *Diania cactiformis*. *J Syst Palaeontol* 12:445–457.

66. Liu J-N, Dunlop JA (2014) Cambrian lobopodians: A review of recent progress in our understanding of their morphology and evolution. *Palaeogeogr Palaeoclimatol Palaeoecol* 398:4–15.

67. Hou X-G, Bergström J (1995) Cambrian lobopodians – ancestors of extant onychophorans. *Zool J Linn Soc* 114:3–19.

68. Steiner M, Hu S-X, Liu J-N, Keupp H (2012) A new species of Hallucigenia from the Cambrian Stage 4 Wulongqing Formation of Yunnan (South China) and the structure of sclerites in lobopodians. *Bull Geosci* 87:107–124.

69. Bergström J, Hou, X-G, Zhang X-G, Clausen S (2008) A new view of the Cambrian arthropod Fuxianhuia. *GFF* 130:189–201.

70. Ortega-Hernández, J. (2014). Making sense of “lower” and “upper” stem-group Euarthropoda, with comment on the strict use of the name Arthropoda von Siebold, 1848. *Biol Rev* early view online (doi: 10.1111/brv.12168).

71. Daley AC, Edgecombe GD (2014) Morphology of Anomalocaris canadensis from the Burgess Shale. *J Paleontol* 88:68–91.

72. Daley AC, Budd GE, Caron J-B, Edgecombe GD, Collins D (2009) The Burgess Shale anomalocaridid Hurdia and its significance for early euarthropod evolution. *Science* 323:1597–1600.

73. Ma X-Y, et al. (2012) Morphology of Cambrian lobopodian eyes from the Chengjiang Lagerstätte and their evolutionary significance. *Arthropod Struct Dev* 41:495–504.

74. Ortega-Hernández J. (2015) Homology of head sclerites in Burgess Shale euarthropods. *Curr Biol* early view online (doi: 10.1016/j.cub.2015.04.034).

75. Daley AC, Bergström J (2012) The oral cone of *Anomalocaris* is not a classic “peytoia”. *Naturwissenschaften* 99: 501–4.

76. Liu J-N, Steiner M, Dunlop JA, Keupp H, Shu D-G, OU Q, Han J, Zhang Z-F, Zhang X-L (2011) An armoured Cambrian lobopodian from China with arthropod-like appendages. *Nature* 470:526–530.

77. Maas A, Waloszek D (2001) Cambrian derivatives of the early arthropod stem lineage, pentastomids, tardigrades and lobopodians – an “Orsten” perspective. *Zool Anz* 240:451–459.

78. Budd GE, Daley AC (2012) The lobes and lobopods of *Opabinia regalis* from the middle Cambrian Burgess Shale. *Lethaia* 45:83–95.

79. Whittington HB (1975) The enigmatic animal *Opabinia regalis*, Middle Cambrian, Burgess Shale, British Columbia. *Phil Trans R Soc Lond B* 271:1–43.

80. Van Roy P, Daley AC, Briggs DEG (2013) Anomalocaridids had two sets of lateral flaps. *57th Palaeontol Assoc Annu Meeting*, *Abst booklet* p. 58.

81. Haug JT, Mayer G, Haug C, Briggs DEG (2012) A Carboniferous non-onychophoran lobopodian reveals long-term survival of a Cambrian morphotype. *Curr Biol* 22:1673–1675.

82. Ou Q, et al. (2011) A rare onychophoran-like lobopodian from the lower Cambrian Chengjiang Lagerstätte, southwestern China, and its phylogenetic implications. *J Paleontol* 85:587–594.

83. Ramsköld L (1992) The second leg row of Hallucigenia discovered. *Lethaia* 25:221–224.

84. Ramsköld L, Chen J-Y (1998). Cambrian lobopodian: morphology and phylogeny. *Arthropod Fossils and Phylogeny*, ed Edgecombe, GD (Columbia Univ Press, New York), pp 107–150.

85. Budd GE, Peel J (1998) A new xenusiid lobopod from the Early Cambrian Sirius Passet fauna of North Greenland. *Palaeontology* 41:1201–1213.

86. Maas A, Mayer G, Kristensen RM, Waloszek D (2007) A Cambrian micro-lobopodian and the evolution of arthropod locomotion and reproduction. *Chinese Sci Bull* 52:3385–3392.

87. Ma X-Y, Cong P-Y, Hou X-G, Edgecombe GD, Strausfeld NJ (2014) An exceptionally preserved arthropod cardiovascular system from the early Cambrian. *Nat Commun* 5:3560.

88. Dewel RA, Eibye-Jacobsen J (2006) The mouth cone and mouth ring of Echiniscus viridissimus Peterfi, 1956 (Heterotardigrada) with comparisons to corresponding structures in other tardigrades. *Hydrobiologia* 558: 41–51.

89. Guidetti R, et al. (2012) Form and function of the feeding apparatus in Eutardigrada (Tardigrada). *Zoomorphology* 131:127–148.

90. Liu J-N, Shu D, Han J, Zhang Z-F, Zhang X-L (2007) Morpho-anatomy of the lobopod *Magadictyon* cf. *haikouensis* from the Early Cambrian Chengjiang Lagerstätte, South China. *Acta Zool* 88:279–288.

91. Vannier J, Liu J-N, Lerosey-Aubril R, Vinther J, Daley AC (2014) Sophisticated digestive systems in early arthropods. *Nat Commun* 5:3641.

92. Liu J-N, Shu D, Han J, Zhang Z-F, Zhang X-L (2006) A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte. *Acta Palaeontol Pol* 51:215–222.

93. Whittington HB (1978) The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Phil Trans R Soc Lond B* 284:165–197.

94. Daley AC, Budd GE (2010) New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* 53: 721–738.

95. Persson DK, Halberg K, Jørgensen A, Møbjerg N, Kristensen RM (2014) Brain anatomy of the marine tardigrade Actinarctus doryphorus (Arthrotardigrada). *J Morphol* 275:173–190.

96. Chen J-Y, Zhou G-Q, Ramsköld L (1995) The Cambrian lobopodian *Microdictyon sinicum* and its broader significance. *Bull Natl Mus Nat Sci* 5:1–93.

97. Murdock DJE, Gabbot SE, Mayer G, Purnell MA (2014) Decay of velvet worms (Onychophora), and bias in the fossil record of lobopodians. *BMC Evol Biol* 14:222.

98. Hou X-G, Ma X-Y, Zhao J, Bergström J (2004) The lobopodian *Paucipodia inermis* from the Lower Cambrian Chengjiang fauna, Yunnan, China. *Lethaia* 37:235–244.

99. Storch V (1991) Priapulida. *Microscopic Anatomy of Invertebrates Volume 4*, eds Harrison FW, Rupert EE (Wiley-Liss Inc, New York), pp 333–350.

100. Telford MJ, Bourlat SJ, Economou A, Papillon D, Rota-Stabelli O (2008) The evolution of the Ecdysozoa. *Phil Trans R Soc Lond B* 363:1529–1537.

101. Edgecombe GD (2009) Palaeontological and molecular evidence linking arthropods, onychophorans, and other Ecdysozoa. *Evol: Education Outreach* 2:178–190.

102. Rothe B H, Schmidt-Rhaesa A (2010) Structure of the nervous system in *Tubiluchus troglodytes* (Priapulida). *Invertebr Biol* 129:39–58.

103. Budd GE (2001) Why are arthropods segmented? *Evol Dev* 3:332–342.

104. Gabriel WN, Goldstein B (2007) Segmental expression of Pax3/7 and Engrailed homologs in tardigrade development. *Dev Genes Evol* 217:421–33.

105. Zhang X-L, Briggs DEG (2007) The nature and significance of the appendages of *Opabinia* from the Middle Cambrian Burgess Shale. *Lethaia* 40:161–173.

106. Whittington HB, Briggs DEG (1985) The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Phil Trans R Soc Lond B* 309:569–609.

107. Marchioro T, Rebecchi L, Cesari M, Hansen JG, Viotti G, Guidetti R (2013) Somatic musculature of Tardigrada: phylogenetic signal and metameric patterns. *Zool J Linnean Soc* 169:580–603.

108. Whittington HB (1993) Anatomy of the Ordovician trilobite *Placoparia*. *Phil Trans R Soc B* 339:109–118.

109. Ortega-Hernández J, Brena C (2012) Ancestral patterning of tergite formation in a centipede suggests derived mode of trunk segmentation in trilobites. *PloS One* 7:e52623.

110. Dzik J, Krumbiegel G (1989) The oldest "onychophoran" *Xenusion*: a link connecting phyla? *Lethaia* 22:169–181.

111. Zhang X-G, Aldridge RJ (2007) Development and diversification of trunk plates of the Lower Cambrian lobopodians. *Palaeontology* 50:401–415.

112. Chen J-Y, Zhou G, Ramsköld L (1995) A new Early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China. *Trans R Soc Edinburgh: Earth Sci* 85, 275–282.

113. Smith FW, Jockusch EL (2014) The metameric pattern of *Hypsibius dujardini* (Eutardigrada) and its relationship to that of other panarthropods. *Front Zool* 11:66.

114. Topper TP, Skovsted CB, Peel JS, Happer DAT (2013) Moulting in the lobopodian *Onychodictyon* from the lower Cambrian of Greenland. *Lethaia* 46:490–495.

115. Liu J-N, Shu D, Han J, Zhang Z-F, Zhang X-L (2008) The lobopod *Onychodictyon* from the lower Cambrian Chengjiang lagerstätte revisited. *Acta Palaeontol Pol* 53:285–292.

116. Conway Morris S (1977) A new metazoan from the Cambrian Burgess Shale of British Columbia. *Palaeontology* 20:623–640.

117. Caron J-B, Smith MR, Harvey THP (2013) Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. *Proc R Soc B* 280:20131613.

119. Bertolani R, Biserov VI (1996) Leg and claw adaptations in soil tardigrades, with erection of two new genera of Eutardigrada, Macrobiotidae: *Pseudohexapodibius* and *Xerobiotus*. *Invertebr Biol* 115:299–304.

120. Schuster R, Nelson DR, Grigarick, AA, Christenberry D (1980) Systematic criteria of the Eutardigrada. *Trans Am Microscop Soc* 99:284–303.

121. Thompson I, Jones DS (1980) A possible onychoporan from the Middle Pennsylvanian Mazon Creek Beds of northern Illinois. *J Paleontol* 54:588–596.

122. García-Bellido DC, Collins DH (2007) Reassessment of the genus *Leanchoilia* (Arthropoda, Arachnomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Palaeontology* 50:693–709.

123. Haug JT, Briggs DEG, Haug C (2012) Morphology and function in the Cambrian Burgess Shale megacheiran arthropod *Leanchoilia superlata* and the application of a descriptive matrix. *BMC evol biol* 12:162.

123. Schulze C, Neves RC, Schmidt-Rhaesa A (2014) Comparative immunohistochemical investigation on the nervous system of two species of Arthrotardigrada (Heterotardigrada, Tardigrada). *Zool Anz* 253:225–235.

124. Mayer G, et al. (2013) Selective neuronal staining in tardigrades and onychophorans provides insights into the evolution of segmental ganglia in panarthropods. *BMC Evol Biol* 13:230.

125. Budd GE (2001) Tardigrades as 'stem-group arthropods': the evidence from the Cambrian fauna. *Zool Anz* 240:265–279.

126. Dunn CW, et al. (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452:745–749.

127. Campbell LI, et al. (2011) MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. *Proc Natl Acad Sci USA* 108:15920–15924.

128. Budd GE, Jensen S (2000) A critical reappraisal of the fossil record of the bilaterian phyla. *Biol Rev* 75:253–295.

129. Todaro MA, Shirley TC (2003) A new meiobenthic priapulid (Priapulida, Tubiluchidae) from a Mediterranean submarine cave. *Italian J Zool* 70:79–87.

130. Hou X-G, Sun W-G (1988) Discovery of Chengjiang fauna at Meishucun, Jinning, Yunnan [in Chinese, with English abstract]. *Acta Palaeontol Sin* 27:1–12.

131. Hou X-G, Ramsköld L, Bergström J (1991) Composition and preservation of the Chengjiang fauna - a lower Cambrian soft-bodied biota. *Zool Scr* 20:395–411.

132. Pompeckj JF (1927) Ein neues Zeugnis uralten Lebens. *Paläontol Zeitschrift* 9: 287–313.

133. Jaeger H, Martinsson A (1967) Remarks on the problematic fossil *Xenusion auerswaldae. GFF* 88:435–452.

134. Walcott CD (1911) Cambrian geology and paleontology. II. 5. Middle Cambrian annelids. *Smithson Miscell Collect* 57:109–144.

135. Hou X-G, Chen J-Y (1989) Early Cambrian arthropod-annelid intermediate sea animal, *Luolishania* gen. nov. *Acta Palaeontol Sin* 28:207–213.

136. Luo H-L, Hu S-X, Chen L-Z, Zhang S-S, Tao Y-H (1999) *Early Cambrian Chengjiang fauna from Kunming region, China.* (Yunnan Sci Technol Press, Kunming), pp 1–129 (In Chinese with English summary).

138. Walcott CD (1912) Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merotomata. Cambrian Geology and Paleontology II. *Smithson Miscell Collect* 57:145–228.

139. Collins D (1996) The "evolution" of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). *J Paleontol* 280:280–293.

140. Whiteaves JF (1892) Description of a new genus and species of Phyllocarid Crustacea from the middle Cambrian of Mount Stephen, B. C. *Can Record Sci* 5:205–208.

141. Reid AL (1996) Review of the Peripatopsidae (Onychophora) in Australia, with comments on peripatopsid relationships. *Invert Systematics* 10:663–936.

144. Grabham M, Cockerell TDA (1892) *Peripatus* rediscovered in Jamaica. *Nature* 46:514.

143. Grabham M (1893) *Peripatus*. *J Inst Jamaica* 5:217–219.

144. Mayer G (2007) *Metaperipatus inae* sp. nov. (Onychophora: Peripatopsidae) from Chile with a novel ovarian type and dermal insemination. *Zootaxa*, 1440:21–37.

145. Ruhberg H (1985) Die Peripatopsidae (Onychophora). Systematic, Ökologie, Chorologie und phylogenetische Aspekte. *Zoologica, Helft 137*, ed Schaller F (E. Schweizerbart' sche Verlagsbuchhandlung Stuttgart).

146. Schulz E (1935) *Actinarctus doryphorus* nov. gen., nov. spec. ein merkwurdiger Tardigrad aus der Nordsee. *Zool Anz* 111:285–288.

147. Nielsen C (1995) *Animal Evolution: Interrelationships of the Living Phyla*. (Oxford Univ Press, Oxford), pp 1–563.

148. Kristensen RM (1983) The first record of cyclomorphosis in Tardigrada based on a new genus and species from Arctic meiobenthos. *J Zool Syst Evol Res* 20:249–270.

149. Briggs DEG, Collins D (1999) The arthropod *Alalcomenaeus cambricus* Simonetta, from the Middle Cambrian Burgess Shale of British Columbia. *Palaeontology* 42:953–977.

150. Zhang W-T, Hou X-G (1985) Preliminary notes on the occurrence of the unusual trilobite Naraoia in Asia. *Acta Palaeontol Sin* 24:591–595.

151. Zhang X-L, Shu, DG, Erwin DH (2007) Cambrian naraoiids (Arthropoda): morphology, ontogeny, systematics, and evolutionary relationships. *J Paleontol* 81 (sp68), 1–52.

152. Hou X-G (1987) Three new large arthropods from Lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeontol Sin* 26:271–285 (In Chinese with English summary).

153. Hou X-G, Bergström J (1997) Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils Strata* 45:1–116.