Supplementary Note 1 | Character coding

In order to employ a self-consistent approach to character coding, we have coded all fossil and extant taxa according to a single model of head segmental organization that is informed by developmental studies on extant Onychophora, Tardigrada and Euarthropoda. We thus interpret the segmental affinity of anterior appendages in fossil taxa based on strict topological criteria alongside, where applicable, recent data on the neurological organization of exceptionally preserved fossils. Characters are thus coded after the following premises:

- The brain of Onychophora includes two neuromeres, the proto- and deuto-cerebrum (Mayer et al. 2010; Whittington and Mayer 2011), which are respectively associated with a pair of ‘primary antennae’ and a set of jaws integrated into the oral cavity (Eriksson and Budd 2000; Eriksson et al. 2003, 2009, 2010, 2013; Steinmetz et al. 2010). The ‘primary antennae’ and jaws each represent modified limbs (Mayer and Koch 2005; Eriksson et al. 2009; de Sena Oliveira and Mayer 2013). The mouth is ventral, and displays a complex pattern of innervation; although the jaws are deuto-cerebral, the lip papillae that surround the mouth opening receive nervous terminals from the anterior most three segments of the body, and display a bilaterally symmetrical organization (Eriksson and Budd 2000; Eriksson et al. 2003; Mayer et al. 2010; Martin and Mayer 2014).

- The brain of Tardigrada comprises a single neuromere, the protocerebrum (Zantke et al. 2007; Mayer et al. 2013b), which is associated with the stylet apparatus. This apparatus represents a modified pair of appendages (Nielsen 2001; Halberg et al. 2009). The stomatogastric nerves in the tardigrade mouth originate from the protocerebrum, forming a distinct ring-like arrangement associated with the lamellae in the mouth cone (Persson et al. 2012; Mayer et al. 2013b). The first and second pairs of walking legs are serially homologous to the deuto- and tritocerebrum of crown-group Euarthropoda (Ou et al. 2012; Mayer et al. 2013b). See discussion in transformation series 18 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 (Eriksson et al. 2010) and is typified by the possession of appendage-like features; these include the morphogenetic formation from paired anlages (Kimm and Prpic 2006; Liu et al. 2009, 2010) and the expression of limb patterning genes (Browne et al. 2005; Scholtz and Edgecombe 2006; Posnien et al. 2009). The deuto-cerebrum is associated with the first pair of appendages in Euarthropoda, which are
expressed as antennae in Mandibulata and as chelicerae in Chelicerata (Mittmann and Scholtz 2003; Harzsch et al. 2005; Scholtz and Edgecombe 2006). 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) and an ‘intercalary segment’ that lacks appendages (Myriapoda, Hexapoda). The mouth of Euarthropoda is ventral, faces posteriad, and is typically innervated by the deuto cerebrum (Mittmann and Scholtz 2003; Harzsch et al. 2005; Scholtz and Edgecombe 2006).

- The most anterior appendage pair of all lobopodian taxa, including ‘gilled lobopodians’, is interpreted as having a protocerebral segmental affinity (Budd 1993, 1997, 1998, 2002; Ou et al. 2012); consequently the second and third appendages are interpreted as serial homologues to the deuto- and tritocerebral segments of crown-group Panarthropoda. Anomalocaridid ‘great appendages’ treated as protocerebral on the basis their pre-ocular position (as in gilled-lobopodians), their association with the radially arranged Peytoia-type mouthpart, and palaeoneurological data (Budd 1997, 1998, 2002; Chen et al. 2004; Waloszek et al. 2005; Stein 2010; Haug et al. 2012b; Cong et al. 2014).

- The (protocerebral) euarthropod labrum is intimately associated with the mouth opening, both during embryogenesis and in the adult (Scholtz and Edgecombe 2006; Liu et al. 2009, 2010; Posnien et al. 2009; Steinmetz et al. 2010). A subset of Palaeozoic euarthropods are characterized by the presence of a sclerotized plate located anteriad of the mouth, including Fuxianhuiida (Chen et al. 1995c; Waloszek et al. 2005; Yang et al. 2013), Artiopoda (Edgecombe and Ramsköld 1999; Scholtz and Edgecombe 2005; Eriksson and Terfelt 2012; Ortega-Hernández et al. 2013) and Cambrian bivalved euarthropods (Budd 2008). Given the intimate association between these structures, we contend that the presence of a hypostome strongly insinuates the presence of an underlying labrum.

- Our coding of fuxianhuiid head organization follows recent data on the brain structure of Fuxianhua protensa (Ma et al. 2012). The antennae are interpreted as deutocerebral based on their attachment site relative to the protocerebral hypostome/labrum complex (Chen et al. 1995c; Waloszek et al. 2005; Yang et al. 2013); the specialized post-antennal appendages are correspondingly interpreted as tritocerebral.

- The ‘short great appendages’ of leanchoiliids are considered deutocerebral (Chen et al. 2004; Stein 2010; Haug et al. 2012b) in light of the neurological organization in Alalcomenaeus cambricus (Tanaka et al. 2013).
The antennae of Artiopoda are coded as deutocerebral in origin based on their position relative to the hypostome/labrum complex (Scholtz and Edgecombe 2005, 2006) and follows evidence that the ancestral euarthropod bore a antenniform deutocerebral appendage pair (Waloszek et al. 2005; Legg et al. 2013; Yang et al. 2013).

<table>
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<tr>
<th>General organization</th>
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<tr>
<td>1. Paired appendages</td>
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<td>(0) absent</td>
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<td>(1) present</td>
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<th>Head region</th>
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<tr>
<td>2. Anterior region covered by sclerites</td>
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<td>(0) absent</td>
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<tr>
<td>(1) present</td>
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Numerous lobopodians have been considered to have cephalic sclerites (see Ma et al. 2014, trans. ser. 37), but in some cases this interpretation requires revision or confirmation through new material. Following recent data presented by Liu and Dunlop (2014), we score this transformation series as absent in Hallucigenia fortis (contra Hou and Bergström 1995), Onychodictyon ferox (contra Ou et al. 2012) and Cardiodictyon (see Hou and Bergström 1995). We code it as uncertain where the anterior region is ambiguously preserved, as in Onychodictyon gracilis (Liu et al. 2008) and Hallucigenia hongmeia (Steiner et al. 2012). An uncertain coding is also applied to Luolishania, as their apparent presence is only documented by a single specimen (Ma et al. 2009) whose ‘sclerites’ worryingly resemble features in other lobopodians whose original interpretation as sclerites has since been overthrown. Taxa with an incomplete anterior region are coded as uncertain.
3. Head shield formed by fused cephalic segments

(0) absent
(1) present
(−) inapplicable: head sclerites (transformation series 2) absent

We score this transformation series as absent for fuxianhuiids, because the cephalic shield is not derived from fused segments (Chen et al. 1995c; Waloszek et al. 2005; Bergström et al. 2008; Yang et al. 2013), and in anomalocaridids, because the carapace-like structure on the head seems not to cover multiple cephalic segments (e.g. Daley et al. 2009; Daley and Edgecombe 2014).

4. Arcuate anterior sclerite associated with eye-stalks

(0) absent
(1) present
(−) inapplicable: head sclerites (trans. ser. 2) or stalked eyes (trans. ser. 24) absent

We score this transformation series as present in anomalocaridids because the dorsal carapace-like structure covering their heads is associated with eye-stalks (e.g. Daley et al. 2009; Daley and Edgecombe 2014). Anterior sclerites are widespread among Palaeozoic euarthropods including fuxianhuiids (Budd 2008; Yang et al. 2013), and artiopodans (e.g. Edgecombe and Ramsköld 1999; Ortega-Hernández et al. 2013). Only the leanchoiliids are coded as absent.

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

(0) lobopodous
(1) arthropodized (sclerotized; arthrodial membranes present)
(−) inapplicable: paired appendages (trans. ser. 1) absent
6. **Sclerotization of pre-ocular (protocerebral) limb pair**

(0) not sclerotized  
(1) sclerotized  
(−) inapplicable: paired appendages (trans. ser. 1) absent

We code this transformation series as present in any taxon with sclerotized pre-ocular (protocerebral) limbs, including the podomeres in anomalocaridid ‘great appendages’ (Daley and Edgecombe 2014) and the hypostome that covers the euarthropod labrum (e.g. Edgecombe and Ramsköld 1999; Yang *et al.* 2013). We score this transformation series as uncertain in taxa where the presence of a hypostome is suggested, but not verified (e.g. *Alalcomenaeus*), and in the Siberian ‘Orsten’ tardigrade (Maas and Waloszek 2001), where (assuming its modification to a stylet, as in modern tardigrades) it cannot be directly observed.

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

(0) absent  
(1) present  
(−) inapplicable: protocerebral limbs (trans. ser. 6) not sclerotized

This transformation series distinguishes the arthropodized ‘great appendages’ of anomalocaridids (Daley and Edgecombe 2014) from the hypostome of Euarthropoda (e.g. Edgecombe and Ramsköld 1999; Yang *et al.* 2013) and the stylet of Tardigrada (e.g. Halberg *et al.* 2009), both of which are sclerotized but lack soft arthrodial membranes.

8. **Nature of post-ocular lobopodous inner branch**

(0) cylindrical/subconical appendage  
(1) laterally expanded swimming flap  
(−) inapplicable: post-ocular limbs, if present, are arthropodized (trans. ser. 5 = 1)

The cylindrical ambulacral lobopodous leg characteristic of lobopodians is also found in *Opabinia* (Budd 1996; Budd and Daley 2012), *Kerygmachela* (Budd 1993, 1998) and *Pambdelurion* (Budd 1997). Van Roy *et al.* (2013) recently reported that anomalocaridids possess two sets of lateral flaps that are likely 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.
9. Nature of first post-ocular (deutocerebral) appendage

0. lobopodous limb
1. sclerotized jaw
2. arthropodized antenniform with distinct podomeres
3. arthropodized short great-appendage

(–) inapplicable: paired appendages (trans. ser. 1) absent

This character is coded as a single transformation series with four states because each state is seemingly independent.

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

(0) undifferentiated, or differentiated in size only
(1) structurally differentiated

(–) inapplicable: paired appendages (trans. ser. 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 Liu and Dunlop 2014). For example, Antennacanthopodia has a second set of antenna-like limbs that are morphologically distinct from the walking legs (Ou et al. 2011). On the other hand, the second appendage pair of Cardiodictyon is not differentiated from the trunk appendages (Liu and Dunlop 2014). Daley and Edgecombe (2014) 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, we score the deutocerebral limbs as undifferentiated in Anomalocaris.

The first pair of legs in Tardigrada is serially homologous with the deutocerebral segment of Euarthropoda (Mayer et al. 2013b), 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 (Eriksson et al. 2010; de Sena Oliveira and Mayer 2013). In Euarthropoda, this morphological differentiation is generally expressed in the presence of an antenniform (e.g. Edgecombe and Ramsköld 1999; Ma et al. 2012; Yang et al. 2013) or raptorial (Chen et al. 2004; Haug et al. 2012b; Tanaka et al. 2013) deutocerebral appendage.
11. Position of pre-ocular (protocerebral) appendage pair

(0) lateral
(1) ventral
(2) terminal
(−) inapplicable: paired appendages (trans. ser. 1) absent

We score a ventral position in Euarthropoda given that the reduced protocerebral appendage pair, transformed into the labrum, occupies a ventral position in association with the mouth (e.g. Scholtz and Edgecombe 2006). The forward-facing stylet apparatus of Eutardigrada is internalized into the mouth cone (Halberg et al. 2009), and is thus considered as having a terminal position relative to the body; in Heterotardigrada, however, the mouth is oriented ventrally and the stylet apparatus is coded as having a ventral position.

12. Pre-ocular (protocerebral) appendage pair fused

(0) not fused
(1) fused
(−) inapplicable: paired appendages (trans. ser. 1) absent

Modified from transformation series 16 in Ma et al. (2014) to reflect the posited homology between the anterior appendages of lobopodians and the euarthropod labrum (cf. Eriksson and Budd 2000; Budd 2002); specifically, the euarthropod labrum is coded as a fused pair of appendages (Scholtz and Edgecombe 2006; Liu et al. 2009, 2010; Posnien et al. 2009). The stylet apparatus of Tardigrada is not coded as fused, as each stylet within the buccal tube remains independent despite significant modification (Dewel and Eibye-Jacobsen 2006; Halberg et al. 2009; Guidetti et al. 2012). Jianshanopodia is coded uncertain due to unclear preservation (Liu et al. 2006).

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

(0) basal only, with separate distal elements
(1) fused into a reduced labrum
(−) inapplicable: protocerebral appendages not fused (trans. ser. 12 = 0)

In lobopodians, appendage fusion is restricted to the proximal component (cf. Budd 1993, 1998; Daley et al. 2009; Dzik 2011; Daley and Edgecombe 2014). Per transformation series 12 above, the euarthropod labrum is coded as a set of fully fused appendages.
14. Spines/spinules on pre-ocular (protocerebral) appendage

(0) absent
(1) present (anomalocaridids, gilled lobopodians, certain lobopodians)
(−) inapplicable: paired appendages (trans. ser. 1) absent

This transformation series refers to the spines/spinules present in the most anterior appendage pair of anomalocaridids (Daley et al. 2009; Daley and Edgecombe 2014), gilled lobopodians (Kerygmachela, see Budd 1993, 1998; Pambdelurion, see Budd 1997; Opabinia, see Budd 1996) and certain lobopodians (e.g. Aysheaia, see Whittington 1978; Jianshanopodia, see Liu et al. 2006; Megadictyon, see Liu et al. 2007; Onychodictyon ferox, see Ou et al. 2012).

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

(0) one series (e.g. Aysheaia, Kerygmachela, Opabinia) (Whittington 1978; Budd 1993, 1996, 1998)
(1) two series (e.g. anomalocaridids, Onychodictyon ferox) (Daley and Budd 2010; Ou et al. 2012; Daley and Edgecombe 2014)
(−) inapplicable: spines/spinules on the protocerebral appendage (trans. ser. 14) absent

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

(0) no (as in Radiodonta)
(1) yes (as in Onychodictyon ferox)
(−) inapplicable: spine/spinules, if present, in single series (trans. ser. 15 = 0)

This transformation series distinguishes the coplanar spinules found in Onychodictyon ferox (Ou et al. 2012) from those of anomalocaridids (Daley et al. 2009; Daley and Budd 2010; Daley and Edgecombe 2014), where both spine rows face in the same direction.

17. Multifurcate distal termination of protocerebral appendage

(0) absent
(1) present
(−) inapplicable: spines/spinules not present on the protocerebral appendage (trans. ser. 14 = 0)

This transformation series describes the multifurcate termination observed in the protocerebral appendages of dinocaridids (Budd 1996; Daley et al. 2009; Daley and Budd 2010; Budd and Daley...
2012; Daley and Edgecombe 2014) and certain lobopodians – such as *Aysheaia* (Whittington 1978), *Megadictyon* (Liu et al. 2007) and *Kerygmachela* (Budd 1993, 1998) – but absent in *Onychodictyon ferox* (Ou et al. 2012).

### Oral structures

#### 18. Mouth opening orientation

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

Most lobopodian taxa possess an anterior mouth – for example *Aysheaia* (Whittington 1978), *Onychodictyon ferox* (Ou et al. 2012) and *Kerygmachela* (Budd 1993, 1998) – as do Eutardigrada (e.g. Halberg et al. 2009; Persson et al. 2012). We code *Hallucigenia sparsa* and *Microdictyon* as having a ventrally facing mouth because the putative head regions are consistently preserved facing ventrally (Ramskölöd 1992; Chen et al. 1995b; Caron et al. 2013), indicative of an authentic life habit rather than post-mortem alteration. A ventrally facing mouth is evinced by the gut tract of *Hallucigenia fortis*, but the mouth position in *Cardiodictyon* is ambiguous (Liu and Dunlop 2014). We score this transformation series as uncertain in *Megadictyon* as it is difficult to determine whether the mouth was originally ventral (cf. Liu et al. 2007) or whether this appearance results from compaction; the position of the mouth in *Antennacanthopodia* is unclear (Ou et al. 2011). The mouth opening is ventrally oriented in *Pambdelurion* (Budd 1997), *Opabinia* (Budd 1996), anomalocaridids (Daley et al. 2009; Daley and Edgecombe 2014), Onychophora and Heterotardigrada (Eriksson and Budd 2000; Ou et al. 2012; de Sena Oliveira and Mayer 2013; Mayer et al. 2013b; Persson et al. 2014); it faces posteriad in euarthropods (Edgecombe and Ramskölöd 1999; Haug et al. 2012b; Yang et al. 2013).

#### 19. 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, anomalocaridids and various lobopodians (e.g.
Aysheaia, Megadyction, Kerygmachela, Pambdelurion) by virtue of their similar position around the mouth (e.g. Daley et al. 2009; Liu et al. 2011; Legg et al. 2013; Ma et al. 2014). Recent data on the morphogenesis of the onychophoran lip papillae indicate that these 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 (Martin and Mayer 2014; see also Eriksson and Budd 2000). As such, the onychophoran lip papillae do not reflect the symplesiomorphic organization of the anterior region that is observed in cycloneuralians (e.g. Storch 1991; Telford et al. 2008; Edgecombe 2009; Rothe and Schmidt-Rhaesa 2010). There is no evidence that the scalids of Priapulida and the oral lamellae of Tardigrada have a similarly complex morphogenetic origin; moreover, it is impossible to discern whether the circumoral structures of Palaeozoic lobopodians and anomalocaridids are homologous to onychophoran papillae. We therefore treat these structures as potentially homologous based on the distinct radial symmetry in their arrangement around the mouth opening. The case in onychophorans is distinctly different: although their lip papillae do surround the mouth, they have a fundamentally bilateral symmetry (Eriksson and Budd 2000; Martin and Mayer 2014), and we score radial symmetry as absent. Jianshanopodia is coded as present following a recent revision of its anterior morphology (Vannier et al. 2014).

20. Nature of radial circumoral structures

(0) scalids
(1) oral papillae or lamellae
(2) radial plates organized as a mouth apparatus
(–) inapplicable: radial circumoral structures (trans. ser. 19) absent

Panarthropods express a considerable diversity of circumoral structures, which represent a symplesiomorphic feature of Ecdysozoa as a whole (e.g. Edgecombe 2009). Various lobopodians bear oral papillae/lamellae (e.g. Aysheaia (Whittington 1978); Kerygmachela (Budd 1993, 1998); Opabinia (Whittington 1975)); a similar feature occurs in the oral cone of Tardigrada (Dewel and Eibye-Jacobsen 2006; Guidetti et al. 2012). Pambdelurion (Budd 1997) and anomalocaridids (e.g. Daley et al. 2009; Daley and Edgecombe 2014) exhibit radially arranged plates that together form a mouth apparatus (Daley and Bergström 2012). We code the nature of the circumoral structures in Megadictyon and Jianshanopodia (Liu et al. 2006, 2007; Vannier et al. 2014) 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. The transformation series is coded as inapplicable in Onychophora because the bilaterally symmetrical lip papillae are demonstrably not homologous.
with the radially symmetrical structures of other taxa (Eriksson and Budd 2000; Martin and Mayer 2014; see notes on previous transformation series)

21. 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 (trans. ser. 20 ≠ 2)

This transformation series distinguishes the somewhat indistinct organization of the mouth apparatus in *Pambdelurion* (Budd 1997) from the radially arranged mouthparts of anomalocaridids (Daley et al. 2009; Daley and Bergström 2012; Daley and Edgecombe 2014). We score *Megadictyon* and *Jianshanopodia* as uncertain to reflect their mouthparts’ poor preservation (Liu et al. 2006, 2007).

22. Inner rows of teeth within mouthpart

(0) absent
(1) present

(–) inapplicable: circumoral structures, if present, are not radial plates (trans. ser. 20 ≠ 2)

Transformation series 9 in Daley et al. (2009).

**Ocular structures**

23. Eyes

(0) absent
(1) present

Transformation series 10 in Daley et al. (2009) and 25 in Ma et al. (Ma et al. 2014). Eyes as treated as present in *Onychodictyon ferox* (cf. Ou et al. 2012) and *Hallucigenia fortis* (cf. Liu and Dunlop 2014).
24. Eye attachment

(0) eye sessile
(1) eye stalked
(–) inapplicable: eyes (trans. ser. 23) absent

Transformation series 26 in Ma et al. (2014).

25. Type of eyes

(0) ocellus-like or pigment spots
(1) multiple visual units (including compound eyes)
(–) inapplicable: eyes (trans. ser. 23) absent

Transformation series 27 in Ma et al. (2014). This transformation series is coded as uncertain in Luolishania because the fragmentary preservation of its visual units does not allow full resolution of the level of structural organization (see Ma et al. 2009)

Trunk region

26. Epidermal segmentation

(0) absent
(1) present

Transformation series 25 in Daley et al. (2009). Epidermal segmentation is a distinguishing feature of Euarthropoda (e.g. Budd 2001a; Edgecombe 2009). Although the body of Onychophora and Tardigrada is metamerically organized, both at the level of segment polarity gene expression (Gabriel and Goldstein 2007; Eriksson et al. 2009) and musculature (e.g. Halberg et al. 2009; Marchioro et al. 2013), this pattern is not expressed on the epidermis: we thus score it as absent in these phyla. We code Opabinia as present since has discrete body segments separated by furrows (Budd 1996; Zhang and Briggs 2007; Budd and Daley 2012). Epidermal segmentation is not evident in anomalocaridids (e.g. Daley and Edgecombe 2014), which we score absent. Hurdia is the exception: because the only complete specimen is partly disarticulated (Daley et al. 2009), we consider the presence of epidermal segmentation to be ambiguous.
27. 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 (e.g. Edgecombe and Ramsköld 1999; Haug et al. 2012b; Yang et al. 2013). Although some heterotardigrades possess dorsal plates (e.g. Nelson 2002; Marchioro et al. 2013; Persson et al. 2014), these are not connected by arthrodial membranes and thus score the heterotardigrade terminal Actinarctus as absent for this transformation series.

28. Sternites connected by arthrodial membranes

(0) absent
(1) present

(–) inapplicable: dorsal sclerotized integument (trans. ser. 27) absent

Sternites – ventral sclerotized plates – are a key feature of most Euarthropoda, and are well documented in Artiopoda (e.g. Whittington 1993; Edgecombe and Ramsköld 1999; Ortega-Hernández and Brena 2012). Sternites are notably absent in Fuxianhuiida (Chen et al. 1995c; Waloszek et al. 2005; Bergström et al. 2008; Yang et al. 2013), even though these taxa have a sclerotized dorsal exoskeleton. We code sternites as uncertain in leanchoiliids.

29. Annulations

(0) absent
(1) present

(–) inapplicable: sclerotized dorsal integument with arthrodial membranes (trans. ser. 27) present

Transformation series 26 in Daley et al. (2009). Annulations are repeated superficial integument rings.
30. Annulation distribution

(0) limbs only
(1) trunk and limbs
(−) inapplicable: annulations (trans. ser. 29) or paired limbs (trans. ser. 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 (Budd 1997). The same is true in *Antennacanthopodia* (cf. Ou et al. 2011), where the effaced preservation of the trunk may obscure trunk annulations.

31. Organization of trunk annulation

(0) homonomous
(1) heteronomous
(−) inapplicable: annulations (trans. ser. 29) not present

Transformation series 29 in Liu et al. (2011); trans. ser. 27 in Daley et al. 2009. This transformation series 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. We code *Pambdelurion* as uncertain, reflecting the poor preservation of the trunk (Budd 1997).

32. Paired dorsolateral epidermal specializations associated with lobopodous trunk limbs

(0) absent
(1) present
(−) inapplicable: trunk limbs (trans. ser. 5), if present, not lobopodous

This new transformation series refers to the differentiated epidermal regions found in most lobopodians. The epidermal specialization is usually conspicuous, as in the paired nodes of *Xenusion* (Dzik and Krumbiegel 1989), *Hadranax* (Budd and Peel 1998) and *Kerygmachela* (Budd 1993, 1998); the sclerotized plates of *Onychodictyon* (Zhang and Aldridge 2007; Ou et al. 2012); and the spines of *Hallucigenia* (Ramsköld 1992; Hou and Bergström 1995; Steiner et al. 2012) and *Orstenotubulus* (Maas et al. 2007). *Paucipodia* (Chen et al. 1995a), and *Aysheaia* (Liu and Dunlop 2014 fig. 1) bear subtle sub-circular specializations. *Diania* is coded as present based on the shield-like specializations associated with each leg pair (Ma et al. 2014, fig. 2). The transformation is also
coded as present in the modern 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 (e.g. Halberg et al. 2009; Marchioro et al. 2013); the epidermal specializations of lobopodians have also been interpreted as muscle attachment sites (Budd 2001a; Zhang and Aldridge 2007). This transformation series is independent of the presence of heteronomous or homonomous annulation (trans. ser. 31); it occurs in taxa with homonomous (e.g. Paucipodia and Aysheaia) and heteronomous (Hadranax and Kerygmachela) annulations.

33. Nature of paired epidermal specialization

(0) epidermal depressions
(1) epidermal evaginations
(–) inapplicable: epidermal specializations (trans. ser. 32) absent

The nodes, plates and spines of lobopodian taxa (trans. ser. 32) represent epidermal evaginations; the paired sclerotized dorsal plates of Actinarctus (Heterotardigrada) are also interpreted as epidermal evaginations (e.g. Nelson 2002; Marchioro et al. 2013; Persson et al. 2014). Halobiotus (Eutardigrada) has epidermal depressions, represented by the paired pits that serve as muscle attachment sites (Halberg et al. 2009; Marchioro et al. 2013). We code Paucipodia, Diania and Aysheaia as uncertain; their preservation is insufficient to establish whether the paired specializations are node-like evaginations or pit-like depressions (Chen et al. 1995a; Liu and Dunlop 2014; Ma et al. 2014).

34. Proportions of epidermal trunk evaginations

(0) wider than tall (e.g. nodes or plates)
(1) taller than wide (e.g. spines)
(–) inapplicable: epidermal evaginations (trans. ser. 33) absent

Lobopodians’ epidermal evaginations fall into two geometric categories: flat nodes or plates (token 0) and tall spines (token 1). Although the distal portions of the evaginations of Orstenotubulus are not preserved (Maas et al. 2007), we infer a spine-like habit from the proportions of the spine stubs.
35. Trunk epidermal evaginations with acute distal termination

(0) absent
(1) present
(–) inapplicable: epidermal evaginations (trans. ser. 33) absent

This transformation series refers solely to the shape of the trunk evaginations’ apices. It is independent from the evaginations’ proportions (trans. ser. 34), as demonstrated by Onychodictyon ferox, where sclerites are wider than tall (i.e. plates) but display an acute distal termination (Zhang and Aldridge 2007; Ou et al. 2012; Topper et al. 2013). O. gracilis is coded as uncertain due to its ambiguous preservation (Liu et al. 2008).

36. Acute distal termination in epidermal evagination is curved

(0) absent
(1) present
(–) inapplicable: epidermal evaginations, if present, lack an acute distal terminus (trans. ser. 35)

The spines of Hallucigenia fortis (Hou and Bergström 1995), H. hongmeia (Steiner et al. 2012), Luolishania (Ma et al. 2009) and the Emu Bay ‘Collins Monster’ (García-Bellido et al. 2013) are distinctively curved, whereas those of H. sparsa (Conway Morris 1977) and Onychodictyon ferox (Topper et al. 2013) are essentially straight.

37. Sclerotization of epidermal evaginations

(0) absent
(1) present
(–) inapplicable: epidermal evaginations (trans. ser. 33) absent

The epidermal evaginations of ‘armoured’ lobopodians are substantially sclerotized (Hou and Bergström 1995; Steiner et al. 2012; Caron et al. 2013), in contrast to those of Xenusion (Dzik and Krumbiegel 1989), Hadranax (Budd and Peel 1998) and Kerygmachela (Budd 1993, 1998).
38. Dorsal trunk sclerite ornament

(0) net-like
(1) scaly
(−) inapplicable: sclerotized epidermal evaginations (trans. ser. 37) absent

We code this transformation series as uncertain in taxa that are not well enough preserved for the ornament to be apparent. *Hallucigenia sparsa* has a scaly ornament (Caron et al. 2013) whereas *H. hongmeia* bears a net-like pattern (Steiner et al. 2012) shared with *Onychodictyon* and *Microdictyon* (e.g. Topper et al. 2013); *Cardiodictyon* specimens show a comparable ornament (Liu and Dunlop 2014 fig. 4f). *Actinarctus* sclerites also exhibit a net-like ornament (Marchioro et al. 2013).

39. Sclerites consist of a stack of constituent elements

(0) absent
(1) present
(−) inapplicable: sclerites absent

This transformation series 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 *Euperipatoides*, see main text), not just during ecdysis (as in *Onychodictyon*, see Topper et al. 2013). *Aysheaia* does not have stacked elements (Extended Data Fig. 4f). Where sclerites are not preserved in sufficient detail to assess their construction, this transformation series is coded as uncertain.

40. Maximum number of dorsal epidermal specializations above each leg pair

(0) one
(1) two
(2) three
(3) four
(−) inapplicable: epidermal specializations (trans. ser. 32) absent

We score *Cardiodictyon* as having two epidermal specializations (token 1), following suggestions that the apparently single dorsal sclerite is formed by the fusion of a pair of elements (Liu and Dunlop 2014).
41. Papillae on trunk annulations

(0) absent
(1) present

(−) inapplicable: annulations (trans. ser. 29) absent

Transformation series 41 in Ma et al. (2014). We code Orstenotubulus as uncertain as its papillae are not clearly observed throughout the trunk region (Maas et al. 2007).

42. Dorsal bands of lanceolate blades

(0) absent
(1) present

Transformation series 41 in Daley et al. (2009). A series of parallel-oriented lanceolate blades that are attached at one end and free-hanging towards the posterior of each trunk segment.

43. Serially repeated mid-gut glands

(0) absent
(1) reniform, submillimetric lamellar

Transformation series 42 in Ma et al. (2014); transformation series 16 in Daley et al. (2009). Coded as uncertain in Antennacanthopodia (Ou et al. 2011) because the dark infilling of the type material may represent decayed internal organs. The nature of the mid-gut glands of Megadicton, Jianshanopodia, Pambdelurion and Opabinia is elucidated by Vannier et al. (2014).

Trunk appendages

44. Trunk exites

(0) absent
(1) present

(−) inapplicable: paired appendages (trans. ser. 1) absent

Transformation series 31 in Daley et al. (2009).
45. Form of exite

(0) lanceolate blades in association with lateral lobes
(1) simple oval paddle with marginal spines
(2) bipartite shaft with lamellar setae
(−) inapplicable: trunk exites (trans. ser. 44) absent

46. Exite and endopod fused (biramy)

(0) not fused
(1) fused
(−) inapplicable: exites (trans. ser. 44) absent

We follow Daley et al. (2009, trans. ser. 34) in considering the lanceolate blades and lateral lobes of lobopodians and anomalocaridids as exites, and trunk walking legs as endopods. *Anomalocaris* is coded as unfused (token 0) based on the recently reported presence of a second set of lateral flaps (Van Roy et al. 2013). *Peytoia* and *Hurdia* (Daley et al. 2009) are coded as uncertain as the possible presence of a second pair of lateral flaps has not been explicitly discounted.

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

(0) absent
(1) present
(−) inapplicable: limbs (trans. ser. 5) not arthropodized

Transformation series 8 of Ma et al. (2014), 35 in Daley et al. (2009). Gnathobasic appendages are absent in fuxianhuiids (Chen et al. 1995c; Waloszek et al. 2005; Bergström et al. 2008; Yang et al. 2013) but present in Artiopoda (Edgecombe and Ramsköld 1999; Ortega-Hernández et al. 2013) and megacheirans (Chen et al. 2004; Haug et al. 2012a, b).
48. Secondary structures on lobopodous limbs

(0) absent
(1) present
(–) inapplicable: limbs (trans. ser. 5) not lobopodous

This transformation series is modified from transformation series 9 in Ma et al. (2014). We code as O. gracilis as uncertain as its longitudinal series of dot-like structures (Liu et al. 2008, fig. 2A6). 2A6 could indicate an organization of appendicules similar to those of O. ferox (see Ou et al. 2012, fig. 2a). Siberion is coded as uncertain because its limbs are poorly preserved (Dzik 2011). Hurdia and Peytoia are coded as uncertain pending new data on the structure of the second set of flaps and their morphology (see Van Roy et al. 2013).

49. Nature of secondary structure

(0) spines/setae
(1) appendicules
(–) inapplicable: no secondary structures on the lobopodous limbs (trans. ser. 48)

Spines and setae taper to sharp point, whereas appendicules have a uniform length and a flattened terminus.

50. Papillae on lobopodous limbs

(0) absent
(1) present
(–) inapplicable: limbs (trans. ser. 5) not lobopodous

Transformation series 10 in Ma et al. (2014). In contrast to appendicules and spines, papillae are short projections associated with the annulations.
51. **Finger-like elements in distal tip of limbs**

(0) absent  
(1) present  
(−) inapplicable: paired appendages (trans. ser. 1) absent

The finger-like projections in the legs of tardigrades can bear sets of terminal claws or sucking discs (Schuster *et al.* 1980; Nelson 2002).

52. **Terminal claws on trunk limbs**

(0) absent  
(1) present  
(−) inapplicable: paired appendages (trans. ser. 1) absent

We score terminal claws as absent in *Opabinia* following Budd and Daley (2012). *Hurdia* and *Peytoia* are coded as uncertain as there is no definitive information on the presence of lobopodous limbs or a second set of flaps (Van Roy *et al.* 2013). *Jianshanopodia* (Liu *et al.* 2006) and *Megadictyon* (Liu *et al.* 2007) are also 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 coded as uncertain, as it is difficult to distinguish possible terminal claws from its myriad accessory spines (Liu *et al.* 2011; Ma *et al.* 2014).

53. **Terminal claws with multiple branches**

(0) absent  
(1) present  
(−) inapplicable: terminal claws (trans. ser. 52) absent

Complex claws are present in Eutardigrada (Schuster *et al.* 1980; Nelson 2002; Halberg *et al.* 2009) and the Siberian Orsten-type tardigrade (Maas and Waloszek 2001), but not in heterotardigrades or any Palaeozoic lobopodian.
54. Number of claws on trunk limbs

(0) one
(1) two
(2) three
(3) four
(4) seven
(–) inapplicable: terminal claws (trans. ser. 52) absent

Modified from transformation series 18 in Ma et al. (2014) to better reflect the diversity of claw number in Cambrian lobopodians. Cardiodictyon unambiguously has two claws (Ramsköld and Chen 1998). Leanchoilia is coded as ambiguous for tokens 0 and 2 (one or three claws) to reflect the conflicting interpretations of García-Bellido and Collins (2007) and Haug et al. (2012a).

55. External branch expressed as lateral flaps (body extends laterally into imbricated, unsclerotized flaps)

(0) absent
(1) present
(–) inapplicable: exites (trans. ser. 44) absent

Transformation series 31 in Ma et al. (2014); trans. ser. 36 in Daley et al. (2009). The definition has been slightly modified reflect the presence of two pairs of lateral flaps in anomalocaridids (Van Roy et al. 2013).

56. Longitudinal ("gill-like") wrinkling on distal part of (outer branch) flaps

(0) absent
(1) present
(–) inapplicable: lateral flaps (trans. ser. 55) not present

Transformation series 38 in Daley et al. (2009).
57. Strengthening rays in lateral flaps

(0) absent

(1) present

(−) inapplicable: lateral flaps (trans. ser. 55) not present

Transformation series 37 in Daley et al. (2009)

58. Posterior tapering of lateral flaps

(0) absent

(1) present

(−) inapplicable: lateral flaps (trans. ser. 55) not present

Transformation series 40 in Daley et al. (2009)

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

(0) absent

(1) present

(−) inapplicable: limbs (trans. ser. 5) not lobopodous

Transformation series 38 in Ma et al. (2014).

60. Appendages comprise 15 or more podomeres

(0) Fewer than 15 podomeres

(1) 15 or more podomeres

(−) inapplicable: limbs (trans. ser. 5) not arthropodized

The endopods of certain taxa in the euarthropod stem-group, such as fuxianhuiids, bear 15 or more podomeres and are considered ‘multipodomerous’ (Chen et al. 1995c; Waloszek et al. 2005; Bergström et al. 2008; Yang et al. 2013).
61. Limbless posterior extension of the lobopodous trunk

(0) absent
(1) present: tubular portion of the body extends beyond the last observable appendage pair
(−) inapplicable: trunk stem not lobopodous

This transformation series has been modified by that of previous analyses (e.g. trans. ser. 34 in Ma et al. 2014) to reflect the fact that, in extant onychophorans, the posterior extension of the lobopodous trunk (i.e. anal cone) corresponds to a segment that has lost its appendage pair – evinced by the prevalence of nephridia in this region (Mayer and Koch 2005). As it is not possible to determine whether the posterior extension of the trunk in Palaeozoic lobopodians arises through the loss of the last appendage pair (as in Onychophora) or as an elongation of the trunk, we code this transformation series as present in all taxa where the trunk extends posteriad of the last observable pair of limbs. We code this transformation series as absent in Kerygmachela (Budd 1993, 1998), Jianshanopodia (Liu et al. 2006) and Anomalocaris (Daley and Edgecombe 2014) as their tails likely represent modified appendages (see transformation series 63 and 64). There is possible, but inconclusive, evidence for a small posterior extension in Opabinia (Whittington 1975; Budd 1996; Budd and Daley 2012), which is thus coded as uncertain. Siberion is coded as uncertain as it is difficult to distinguish the possible body termination from a posterior leg or pair of legs (Dzik 2011). Hallucigenia sparsa is also coded as uncertain; the posterior part of its body is poorly known (Ramsköld 1992). It is present in other species of Hallucigenia (e.g. Hou and Bergström 1995).

62. Posterior tagma composed of three paired lateral flaps

(0) absent
(1) present
(−) inapplicable: lateral flaps (trans. ser. 55) absent

Transformation series 42 in Daley et al. (2009).
63. Posteriormost pair of trunk appendages structurally differentiated

(0) undifferentiated
(1) differentiated
(–) inapplicable: paired appendages (trans. ser. 1) absent

We score Jianshanopodia (Liu et al. 2006) as present because the lateral extensions of the tail fan likely correspond to a modified pair of appendages. Onychophora are coded as undifferentiated: their posteriormost region does not express appendages (Mayer and Koch 2005), but the appendages are lost (not structurally differentiated); the posteriormost appendage pair that are expressed are not structurally differentiated. See also transformation series 35 in Ma et al. (2014).

64. Nature of differentiated posteriormost appendages

(0) appendicular tail
(1) partially fused/reduced walking legs
(–) inapplicable: posterior appendages unmodified (trans. ser. 63 = 0)

In fuxianhuiids, the posteriormost appendage pair is modified into a tail fan or tail flukes (e.g. Chen et al. 1995c; Yang et al. 2013); a similar condition is also observed in Opabinia (Whittington 1975; Budd 1996; Budd and Daley 2012), Anomalocaris (Daley and Edgecombe 2014) and Hurdia (Daley et al. 2009). The paired tail rami of Kerygmachela (Budd 1993, 1998) 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 (Liu et al. 2006). Partial fusion of the last pair of legs occurs in Aysheaia (Whittington 1978), Onychodictyon gracilis (Liu et al. 2008), O. ferox (Ou et al. 2012) and Tardigrada (e.g. Halberg et al. 2009; Marchioro et al. 2013); in these taxa, this characteristic is expressed as an incipient fusion of the medioproximal bases of the posteriormost appendage pair. The Siberian Orsten tardigrade is coded as having a reduced posteriormost appendage pair based on the vestigial rudiment present on its posteroventral body region (Maas and Waloszek 2001). We score Pambdelurion as uncertain because its posterior trunk is poorly known (Budd 1997).
65. Nature of appendicular tail

(0) tail rami
(1) tail flaps
(–) inapplicable: appendicular tail not present (trans. ser. 64 ≠ 0)

This transformation series distinguishes the long tail rami of *Kerygmachela* (Budd 1993, 1998) from the flaps observed in *Jianshanopodia* (Liu et al. 2006), *Opabinia* (Budd 1996; Budd and Daley 2012), anomalocaridids (Daley et al. 2009; Daley and Edgecombe 2014), and fuxianhuiids (e.g. Yang et al. 2013).

66. Direction of claws on posteriormost appendage pair

(0) Same direction as claws on other appendages
(1) rotated anteriad
(–) inapplicable: posterior appendages lack claws (trans. ser. 52 = 0)

The last pair of legs are rotated anteriad in tardigrades (e.g. Marchioro et al. 2013), *Aysheaia* (Whittington 1978), *Onychodictyon gracilis* (Liu et al. 2008) and *O. ferox* (Ou et al. 2012), but not in *Cardiodictyon, Hallucigenia fortis* or *Microdictyon* (Hou and Bergström 1995). *Hallucigenia sparsa* is coded as uncertain owing to the poor preservation of its posterior end. We score the Siberian Orsten tardigrade (Maas et al. 2007) as uncertain.

### Soft tissue organization

67. Ventral nerve cord with paired ganglia

(0) absent
(1) present

Transformation series 2 in Tanaka et al. (2013). Tardigrada and Euarthropoda have a ganglionated ventral nerve cord (Schulze et al. 2014), in contrast to the ladder-like ventral nerve cord in Onychophora (Mayer et al. 2013a). Priapulida have an unpaired nerve cord associated with a net-like system of neural connectives (Storch 1991; Rothe and Schmidt-Rhaesa 2010). Recent data on the neurological organization of stem-euarthropods indicate that paired ganglia are present in *Chengjiangocaris* (Yang et al. 2013) and *Alalcomenaeus* (Tanaka et al. 2013). Hou et al. (2004,
figs 2f, 4f) reported faint paired structures adjacent to the gut of *Paucipodia*, which were interpreted as potential nerve ganglia. We nevertheless code *Paucipodia* as uncertain: the structures cannot be observed in the figured material, and are described as ‘faintly preserved with a pink colour’ in contrast to the conspicuously dark colouration of unambiguous nervous tissue in Chengjiang-type fossils (see Ma *et al.* 2012; Tanaka *et al.* 2013; Yang *et al.* 2013).

68. **Dorsal condensed brain**

(0) absent  
(1) present

Whereas typical cycloneuralians have a circumoesophageal nerve ring (e.g. Storch 1991; Telford *et al.* 2008; Edgecombe 2009; Rothe and Schmidt-Rhaesa 2010), Panarthropoda is characterized by dorsal condensed brain neuromeres (Eriksson *et al.* 2003; Mittmann and Scholtz 2003; Harzsch *et al.* 2005; Mayer *et al.* 2010, 2013b). Recent studies have pioneered the study of palaeoneurology in fossil taxa, and a dorsal condensed brain has been described in *Fuxianhuia* (Ma *et al.* 2012) and *Alalcomenaeus* (Tanaka *et al.* 2013).

69. **Number of neuromeres integrated into the dorsal condensed brain**

(0) one  
(1) two  
(2) three  
(–) inapplicable: dorsal condensed brain (trans. ser. 68) absent

See the introductory statements above.

70. **Mouth innervation relative to brain neuromeres**

(0) protocerebral innervation  
(1) deutocerebral innervation  
(2) innervation from multiple neuromeres  
(3) tritocerebral innervation  
(–) inapplicable: dorsal condensed brain (trans. ser. 68) 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 (Ma *et al.*
2012; Tanaka et al. 2013), which is congruent with the organization found in phylogenetically basal extant euarthropods such as Chelicerata and Myriapoda (e.g. Mittmann and Scholtz 2003; Harzsch et al. 2005; Scholtz and Edgecombe 2005, 2006). Tritocerebral innervation is observed in Pancrustacea, but not among the taxa included in this study. Onychophora are coded with token 2 to reflect their complex neurological organization: although the jaws have a deutocerebral segmental affinity and innervation, the lip papillae that delineate the oral opening are formed as epidermal derivatives of the three anteriormost body segments, and thus receive nervous terminals from the protocerebrum, deutocerebrum and part of the ventral nerve cord (Eriksson and Budd 2000; Martin and Mayer 2014). The tardigrade mouth cone is innervated from the protocerebrum (e.g. Mayer et al. 2013b).

71. Nerve cord lateraled

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

Transformation series 1 in Tanaka et al. (2013). This transformation series distinguishes the organization of the ventral nerve cord in Onychophora (e.g. Mayer et al. 2013a) from that in other phyla.

72. Heart

(0) absent
(1) present

Ma et al. (2014) described a dorsal heart in Fuxianhuia; all other fossil taxa are coded as uncertain. Budd (2001b) discussed the difficulty of interpreting the absence of a circulatory system in Tardigrada as ancestral or derived, given that a circulatory system is unnecessary in a miniaturized organism; he concluded that the most methodologically sound way to address this issue in a cladistic context is to score the character as inapplicable. We follow this approach in our primary analysis, but explored the impact of this decision by repeating the analysis with tardigrades coded as ‘heart: absent’. The results under this condition were identical to those of the main analysis for all \( k > 2 \) (including equal weights).
Supplementary Note 2 | Character transformations

This list details the transformations implied by the tree topology that is most parsimonious under all values of \( k > 2 \) (including equal weights). The information provided is descriptive rather than interpretative: it simply describes the most parsimonious reconstruction(s) of each transformation series, as inferred from the series’ distribution on the optimal tree, with notes on the distribution where appropriate.

**General organization**

1. **Paired appendages**
   
   *Present in ancestral panarthropod. No extra steps.*
   
   i. Absent to present in common ancestor of ingroup. (Secondary loss in Priapulida is discounted based on the absence of appendages in other all ecdysozoans).

2. **Anterior region covered by sclerites**
   
   *Absent in ancestral panarthropod. One extra step.*
   
   i. Absent to present in common ancestor of anomalocaridids and euarthropods
   
   ii. Absent to present in heterotardigrades (independent origin)

3. **Head shield formed by fused cephalic segments**
   
   *Inapplicable in ancestral panarthropod; absent in ancestral paneuarthropod. No extra steps.*
   
   i. Absent to present in common ancestor of leanchoiliids and artiopodans

4. **Arcuate anterior sclerite associated with eye-stalks**
   
   *Inapplicable in ancestral panarthropod; present in ancestral paneuarthropod. No extra steps.*
   
   i. Present to absent in common ancestor of leanchoiliids
5. Nature of post-ocular (post-protocerebral) body appendages
Lobopodous in ancestral panarthropod. No extra steps.
i. Lobopodous to arthropodized in common ancestor of euarthropods + fuxianhuiids

6. Sclerotization of pre-ocular (protocerebral) limb pair
Absent in ancestral panarthropod. One extra step.
i. Absent to present in common ancestor of anomalocaridids + euarthropods
ii. Absent to present in common ancestor of tardigrades (independent gain)
i.e. the sclerotization of the tardigrade stylet was independent from the sclerotization of the pre-ocular arthropod appendages.

7. Pre-ocular (protocerebral) limb pair with arthrodial membranes
Inapplicable in ancestral panarthropod; absent in ancestral tardigrade and ancestral paneuarthropod. No extra steps.
i. Absent to present in common ancestor of anomalocaridids

8. Nature of post-ocular lobopodous inner branch
Cylindrical/subconical in ancestral panarthropod. No extra steps.
i. Cylindrical/subconical to laterally expanded swimming flap in Anomalocaris

9. Nature of first post-ocular (deutocerebral) appendage
Lobopodous limb in ancestral panarthropod. No extra steps.
i. Lobopodous limb to sclerotized jaw in Euperipatoides
ii. Lobopodous limb to arthropodized antenniform with distinct podomeres in common ancestor of euarthropods + fuxianhuiids
iii. Arthropodized antenniform with distinct podomeres to arthropodized short great appendage in leanchoiliids
10. Deutocerebral appendage structurally differentiated from rest of trunk appendages

Not differentiated in ancestral panarthropod. Two extra steps.

i. Not differentiated to differentiated in euarthropods + fuxianhuiids

ii. Not differentiated to differentiated in common ancestor of *Hallucigenia* spp. and *Euperipatoides* (independent gain)

iii. Differentiated to not differentiated in *Luolishania* (secondary loss). This taxon was coded as ‘not differentiated’ because some anterior trunk appendages are morphologically similar to the deutocerebral appendage. In light of this topology, it is more parsimonious to recognize the differentiated posterior appendages as having undergone differentiation equivalent to the differentiation of the deutocerebral appendage.

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

Lateral in ancestral panarthropod. One extra step.

i. Lateral to ventral in common ancestor of *Pambdelurion* and euarthropods

ii. Lateral/ventral to terminal in eutardigrades

iii. Lateral/terminal to ventral in heterotardigrades

Heterotardigrades’ ventral position presumably arose from a terminal position, as in Eutardigrada, in concert with a reorientation of the mouth opening.

12. Pre-ocular (protocerebral) appendage pair fused

Unfused in ancestral panarthropod. No extra steps.

i. Unfused to fused in common ancestor of euarthropods and *Siberion*

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

Inapplicable in ancestral panarthropod. Basal fusion in common ancestor of *Siberion* and euarthropods. No extra steps.

i. Transformation from basal fusion to reduced labrum in euarthropods + fuxianhuiids.

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

Present in ancestral panarthropod. Two extra steps.

i. Present to absent in common ancestor of euarthropods + fuxianhuiids

ii. Present to absent in common ancestor of tardigrades (independent loss)

iii. Present to absent in common ancestor of *Diania* and onychophorans (independent loss)
15. Number of spine/spinule series on pre-ocular (protocerebral) frontal appendage

Absent in ancestral panarthropod. One extra step.

i. Absent to present in anomalocaridids

ii. Absent to present in Onychodictyon ferox (independent origin)

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

Inapplicable in ancestral panarthropod. Ancestrally present in Onychodictyon ferox. Ancestrally absent in anomalocaridids. No transformations implied; parsimony-uninformative.

17. Multifurcate distal termination of protocerebral appendage

Present in ancestral panarthropod. Parsimony-uninformative.

i. Present to absent in Onychodictyon ferox

Oral structures

18. Mouth opening orientation

Anterior in ancestral panarthropod. Three extra steps.

i. Anterior to ventral in common ancestor of Pambdelurion and euarthropods

ii. Ventral to posterior in euarthropods

iii. Anterior to ventral in heterotardigrades (independent change)

iv. Anterior to ventral in ancestor of Microdictyon and Onychophora (independent change)

v. Ventral to anterior in Luolishania (secondary reversal)

19. Radially symmetrical circumoral structures

Present in ancestral panarthropod. Two extra steps.

i. Present to absent in common ancestor of Onychodictyon gracilis and onychophorans

ii. Present to absent in common ancestor of euarthropods + fuxianhuiids (independent loss)

iii. Present to absent in Onychodictyon ferox (independent loss)

The most parsimonious character distribution homologizes the circumoral structures of priapulids with those of the most stemward lobopodians in the tactopod lineage, Aysheaia and Siberion. These features are lost at the base of total-group Onychophora. Our results confirm that the onychophoran lip papillae are not homologous with the circumoral structures observed in other cycloneuralians.
20. Nature of radial circumoral structures

*Oral papillae or lamellae in ancestral panarthropod. One extra step.*

i. Transition between scalids and oral papillae or lamellae (direction unresolved) between priapulids and common ancestor of panarthropods + *Aysheaia*

ii. Transition from oral papillae or lamellae to radial plates in common ancestor of *Pambdelurion* and anomalocaridids

iii. Transition from radial plates to oral papillae or lamellae in *Opabinia* (secondary reversal) This character could equally mapped as having two independent origins (in *Pambdelurion* and in anomalocaridids), but given the esoteric nature of *Opabinia*’s feeding apparatus we choose to reconstruct a single origin with a secondary reversal in *Opabinia*.

21. Structure of mouth apparatus

*Variable number of undifferentiated plates in Pambdelurion; 32 plates with differentiation of four enlarged plates in a cross arrangement in anomalocaridids. No transformations implied. Parsimony-uninformative.*

If radial plates of *Pambdelurion* and anomalocaridids are homologous (being secondarily lost in *Opabinia*), a transformation of ambiguous polarity occurs near the common ancestor of *Pambdelurion* and anomalocaridids. If the plates evolved independently, no transformation is implied.

22. Inner rows of teeth within mouthpart


i. Absent to present in *Hurdia*

23. Ocular structures

23. Eyes

*Absent in ancestral panarthropod. Two extra steps.*

i. Absent to present in common ancestor of *Cardiodictyon* and onychophorans

ii. Absent to present in tardigrades (independent origin)

iii. Absent to present in common ancestor of dinocaridids and euarthropods (independent origin)
24. Eye attachment

*Inapplicable in ancestral panarthropod. Sessile in common ancestor of tardigrades + Onychodictyon ferox, and in common ancestor of Cardiodictyon and onychophorans; stalked in common ancestor of euarthropods. No transitions implied.*

25. Type of eyes

*Inapplicable in ancestral panarthropod. Ocellus-like in common ancestor of tardigrades and Onychodictyon ferox. Ambiguous in common ancestor of Hallucigenia fortis and onychophorans. Multiple visual units in common ancestor of euarthropods. No extra steps.*

i. Transformation between multiple visual units and ocellus-like or pigment spots between *Hallucigenia fortis* and common ancestor of *Antennacanthopodia* and *Euperipatoides*

**Trunk region**

26. Epidermal segmentation

*Absent in ancestral panarthropod. One extra step.*

i. Absent to present in common ancestor of euarthropods + fuxianhuiids

ii. Absent to present in *Opabinia* (independent origin)

27. Dorsal integument sclerotized and connected by arthrodial membranes

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of euarthropods + fuxianhuiids

28. Sternites connected by arthrodial membranes

*Inapplicable in ancestral panarthropod. Ambiguous in common ancestor of euarthropods + fuxianhuiids. No extra steps.*

i. Transition from absent to present (polarity uncertain) between fuxianhuiids and artiopodans

29. Annulations

*Present in ancestral panarthropod. Two extra steps.*

i. Present to absent in common ancestor of dinocaridids (inapplicable in euarthropods)

ii. Present to absent in common ancestor of tardigrades (independent loss)

iii. Present to absent in *Hallucigenia sparsa* (independent loss)
30. Annulation distribution

*Trunk and limbs in ancestral panarthropod. Invariant character; no transformations implied.*

31. Organization of trunk annulation

*Heteronomous in ancestral panarthropod. Three extra steps.*

i. homonomous to heteronomous in common ancestor of Onychophora, Tardigrada and Arthropoda
ii. heteronomous to homonomous in common ancestor of *Euperipatoides* and *Ilyodes* (secondary reversal)
iii. heteronomous to homonomous in *Siberion* (secondary reversal)
iv. heteronomous to homonomous in *Paucipodia* (secondary reversal)

32. Paired dorsolateral epidermal specializations associated with lobopous trunk limbs

*Present in ancestral panarthropod. Two extra steps.*

i. Present to absent in common ancestor of *Antennacanthopodia*, *Euperipatoides* and *Ilyodes*
ii. Present to absent in common ancestor of *Siberion* and *Jianshanopodia* (secondary loss)
iii. Present to absent in common ancestor of dinocaridids (secondary loss)

33. Nature of paired epidermal specialization

*Epidermal evaginations in ancestral panarthropods. No extra steps; parsimony-uninformative.*

i. Evaginations to depressions in eutardigrades

34. Proportions of epidermal trunk evaginations

*Wider than tall in ancestral panarthropod. No extra steps.*

i. Wider than tall to taller than wide in common ancestor of hallucigeniids and *Orstenotubulus*

35. Trunk epidermal evaginations with acute distal termination

*No acute distal termination in ancestral panarthropod. One extra step.*

i. Absent to present in common ancestor of hallucigeniids and *Orstenotubulus*
ii. Transition between absent (in heterotardigrades) and present (in *Onychodictyon ferox*) – assuming homology between their epidermal evaginations. The independent gain of this character in *Onychodictyon ferox* is consistent with the distinct nature of the spines, which arise as processes of a shield-like plate.
36. Acute distal termination in epidermal evagination is curved

*Inapplicable in ancestral panarthropod. Ambiguous in common ancestor of hallucigeniids and Orstenotubulus. No extra steps.*

i. Transition between absent and present (polarity ambiguous) near common ancestor of *Hallucigenia sparsa* and other hallucigeniids

37. Sclerotization of epidermal evaginations

*Present in ancestral panarthropod. One extra step.*

i. Present to absent in common ancestor of *Xenusion* and *Diania*

ii. Present to absent in common ancestor of *Hadranax* and *Kerygmachela* (inapplicable in euarthropods, in jianshanopodians and elsewhere)

38. Dorsal trunk sclerite ornament

*Inapplicable in ancestral panarthropod. Net-like in Onychodictyon ferox, in heterotardigrades, and in common ancestor of Microdictyon and onychophorans. No extra steps.*

i. Net-like to scaly in *Hallucigenia sparsa*

39. Sclerites consist of a stack of constituent elements

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of hallucigeniids and onychophorans

40. Maximum number of dorsal epidermal specializations above each leg pair

*Two in ancestral panarthropod. No extra steps.*

i. Modified from two to three in common ancestor of luolishaniids

ii. Modified from two to one in *Diania*

iii. Modified from two to four in common ancestor of *Hadranax* and *Kerygmachela*

41. Papillae on trunk annulations

*Present in ancestral panarthropod. Three extra steps.*

i. Present to absent in common ancestor of *Paucipodia* and onychophorans

ii. Absent to present in *Luolishania* (secondary reversal)

iii. Absent to present in common ancestor of *Ilyodes* and *Euperipatoides* (secondary reversal)

iv. Present to absent in jianshanopodians (independent loss)
42. Dorsal bands of lanceolate blades

*Absent in ancestral panarthropod. One extra step.*

i. Absent to present in common ancestor of dinocaridids
ii. Present to absent in common ancestor of euarthropods (secondary loss)

A single step is implied if dinocaridids are monophyletic.

43. Serially repeated mid-gut glands

*Absent in ancestral panarthropod. One extra step.*

i. Absent to present in common ancestor of *Jianshanopodia* and euarthropods
ii. Present to absent in common ancestor of fuxianhuiids (secondary loss)

**Trunk appendages**

44. Trunk exites

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of *Kerygmachela* and euarthropods

45. Form of exite

*Inapplicable in ancestral panarthropod; lanceolate blades in common ancestor of Kerygmachela and euarthropods. No extra steps.*

i. Lanceolate blades to simple oval paddle in common ancestor of euarthropods + fuxianhuiids
ii. Simple oval paddle to bipartite shaft in artiopods

46. Exite and endopod fused (biramy)

*Inapplicable in ancestral panarthropod; absent in common ancestor of Kerygmachela and euarthropods. No extra steps.*

i. Absent to present in common ancestor of euarthropods + fuxianhuiids

47. Antero-posteriorly compressed protopodite with gnathobasic endites in post-deuterocerebral appendage pair

*Inapplicable in ancestral panarthropod; ambiguous in common ancestor of euarthropods + fuxianhuiids. No extra steps.*

i. Transformation between absent and present (polarity ambiguous) near common ancestor of euarthropods + fuxianhuiids
48. Secondary structures on lobopodous limbs

Present in ancestral panarthropod. Three extra steps.

i. Present to absent in common ancestor of Paucipodia and onychophorans

ii. Absent to present in common ancestor of luolishaniids (secondary gain)

iii. Present to absent in common ancestor of tardigrades (independent loss)

iv. Present to absent in common ancestor of Hadranax and euarthropods (independent loss)

49. Nature of secondary structure

Spines/setae in ancestral panarthropod. No extra steps.

i. Spines/setae to appendicules in common ancestor of Onychodictyon ferox and jianshanopodians (inapplicable in euarthropods)

50. Papillae on lobopodous limbs

Absent in ancestral panarthropod. Three extra steps.

i. Present to absent in last common ancestor of panarthropods (or absent to present in Aysheaia)

ii. Absent to present in Luolishania (independent gain)

iii. Absent to present in common ancestor of onychophorans and Orstenotubulus (independent gain)

iv. Absent to present in Hadranax (independent gain)

This character seems rather trivial and its multiple origin is unsurprising.

51. Finger-like elements in distal tip of limbs

Absent in ancestral panarthropod. Nil to one extra steps.

i. Absent to present in common ancestor of extant tardigrades

ii? Present to absent in Siberian Orsten tardigrade

52. Terminal claws on trunk limbs

Present in ancestral panarthropod. Two extra steps.

i. Present to absent in or before common ancestor of Kerygmachela and euarthropods

ii. Absent to present in common ancestor of leanchoiliids and artiopodans (secondary gain)

iii. Present to absent in Antennacanthopodia (independent loss – or preservational artefact?)

The loss of terminal claws presumably corresponds to swimming habit of taxa that lack them.
53. Terminal claws with multiple branches  
Absent in ancestral panarthropod. Nil to one extra steps.  
i. Absent to present in common ancestor of eutardigrades and Siberian Orsten tardigrade 
ii? Present to absent in heterotardigrades 

54. Number of claws on trunk limbs  
Two in ancestral panarthropod. Inapplicable in common ancestor of euarthropods + Kerygmachela; one in common ancestor of leanchoiliids and artiopodans. One extra step.  
i. Two to one in common ancestor of Hallucigenia hongmeia and ‘Emu Bay Collins monster’.  
ii. One to four in Luolishania  
iii. Two to four in heterotardigrades (independent change)  
iv. Two to seven in Aysheaia  
v. One to three in Kuamaia  
Note that it is most parsimonious to interpret Leanchoilia (ambiguous: one claw or three) as having single claw (see García-Bellido and Collins 2007; Haug et al. 2012a). No transformation is reconstructed between euarthropods and Onychodictyon ferox because the intervening taxa lack terminal claws. 

55. External branch expressed as lateral flaps (body extends laterally into imbricated, unsclerotized flaps)  
Inapplicable in ancestral panarthropod; present in common ancestor of Kerygmachela and euarthropods. No extra steps.  
i. Present to absent in common ancestor of euarthropods + fuxianhuiids 

56. Longitudinal ("gill-like") wrinkling on distal part of (outer branch) flaps  
Inapplicable in ancestral panarthropod; present in common ancestor of Kerygmachela and euarthropods. No extra steps.  
i. Present to absent in common ancestor of dinocaridids 

57. Strengthening rays in lateral flaps  
Inapplicable in ancestral panarthropod; absent in common ancestor of Kerygmachela and euarthropods. No extra steps.  
i. Absent to present in common ancestor of anomalocaridids
58. Posterior tapering of lateral flaps

Inapplicable in ancestral panarthropod; absent in common ancestor of Kerygmachela and euarthropods. No extra steps.
i. Absent to present in common ancestor of Anomalocaris and Peytoia

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

Absent in ancestral panarthropod. No extra steps.
i. Absent to present in common ancestor of luolishaniids

60. Appendages comprise 15 or more podomeres

Inapplicable in ancestral panarthropod; ambiguous in last common ancestor of euarthropods. No extra steps.
i. Transition between few and many podomeres (polarity ambiguous) near last common ancestor of euarthropods and fuxianhuiids

**Posterior termination**

61. Limbless posterior extension of the lobopodous trunk

Absent in ancestral panarthropod. No extra steps.
i. Absent to present in last common ancestor of onychophorans and Onychodictyon gracilis

In onychophorans this extension represents a ‘segment’ where limbs are no longer expressed (Mayer and Koch 2005). Parsimony would suggest a similar situation in the fossil taxa, although of course developmental data are unavailable.

62. Posterior tagma composed of three paired lateral flaps

Inapplicable in ancestral panarthropod; ambiguous in common ancestor of Kerygmachela and euarthropods. One extra step.
i. Absent to present in Opabinia
ii. Absent to present in Anomalocaris
63. Posteriormost pair of trunk appendages structurally differentiated

*Differentiated in ancestral panarthropod. Two extra steps.*

i. Differentiated to undifferentiated in common ancestor of *Xenusion, Paucipodia* and onychophorans

ii. Differentiated to undifferentiated in *Peytoia* (independent loss)

iii. Differentiated to undifferentiated in common ancestor of leanchoiliids and artiopodans (independent loss)

64. Nature of differentiated posterior appendages

*Walking legs rotated anteriad in ancestral panarthropod. No extra steps.*

i. Transformed from walking legs rotated anteriad into tail in last common ancestor of *Jianshanopodia* and euarthropods

65. Nature of appendicular tail

*Inapplicable in ancestral panarthropod; tail flaps in common ancestor of Jianshanopodia and euarthropods. Parsimony-uninformative.*

i. Tail flaps to tail rami in *Kerygmachela*

66. Direction of claws on posteriormost appendage pair

*Rotated anteriad in ancestral panarthropod. No extra steps.*

i. Rotated to non-rotated in common ancestor of onychophorans and *Microdictyon*

**Soft tissue organization**

67. Ventral nerve cord with paired ganglia

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of tactopods

68. Dorsal condensed brain

*Present in ancestral panarthropod. No extra steps.*

i. Transformation between absent and present (polarity ambiguous) near common ancestor of panarthropods and priapulids

The brain can be recognized as a panarthropod synapomorphy with reference to other Cycloneuralia, where it is absent.
69. Number of neuromeres integrated into the dorsal condensed brain

*Ambiguous in ancestral panarthropod; taken here as one for illustrative purposes, though two or three are both equally parsimonious. No extra steps.*

i. One to two in onychophorans

ii. One to three in euarthropods

70. Mouth innervation relative to brain neuromeres

*Ambiguous innervation in ancestral panarthropod, taken here as deutocerebral for illustrative purposes. No extra steps.*

i. Deutocerebral to protocerebral innervation in tardigrades

ii. Deutocerebral innervation to innervation from multiple neuromeres in onychophorans

71. Nerve cord lateralized

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in onychophorans

72. Heart

*Present in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of panarthropods

A transition from present to inapplicable (or absent) in tardigrades reflects the secondary loss of a circulatory system due to miniaturization (Budd 2001b).
Supplementary references


between the segments of the chelicerae and of the (first) antennae of Mandibulata. *Development Genes and Evolution,* 213, 9–17.


