doi:10.1038/nature14573

## Supplementary Note 1 | Character coding

Character coding follows Smith and Ortega-Hernández (2014) [SOH]; new transformation series are marked. Three taxa have been added: the extant hexapod *Supella* allows comparison with euarthropod foregut armature, which can be ambiguously preserved in fossils; the Carboniferous lobopodian *Carbotubulus* (Haug *et al.* 2012*c*) improves the coverage of *Hallucigenia*-like lobopodians, providing the opportunity to improve phylogenetic resolution and extending the reach of the study; and the Cambrian palaeoscolecid *Cricocosmia* is included to reduce the scope for long-branch error with respect to the priapulid outgroup. Modifications of SOH transformation series are presented in orange type.

### *General organization*

**1. Paired appendages [SOH: 1]**

*(0) absent*
*(1) present*

### *Head region*

**2. Anterior region covered by sclerites [SOH: 2]**

*(0) absent*
*(1) present*

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*b*) 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' resemble features in other lobopodians whose original interpretation as sclerites has since been overthrown. *Actinarctus* is coded as absent as a single dorsal sclerites covers the entire body; this structure does not seem to correspond directly to the anterior sclerites of other taxa (Boesgaard and Kristensen 2001). Fossil taxa with an incomplete anterior region are coded as uncertain.

### 3. Head shield formed by fused cephalic segments [SOH: 3]

*(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.* 1995*c*; 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 [SOH: 4]

*(0) absent*
*(1) present*
*(–) inapplicable: head sclerites (trans. ser. 2) or stalked eyes (trans. ser. 17) 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. Anterior trunk flexure in coronal plane [NEW]

*(0) orientation of mouth is fixed relative to main trunk*
*(1) flexible anterior trunk allowing mouth's dorsal-ventral orientation to be independent of main trunk axis*

The terminal mouths of *Hallucigenia sparsa* (Ramsköld 1992; Caron *et al.* 2013), *H. fortis* (Liu and Dunlop 2014), *Microdictyon* and *Cardiodictyon* (Chen *et al.* 1995*b*; Liu and Dunlop 2014) are consistently oriented ventrally, perpendicular to the main trunk axis; the anteriormost trunk (or, colloquially, ‘head’) can be manoeuvred independently of the main trunk. In other taxa (e.g. priapulids), the orientation of the mouth is fixed relative to the main trunk.

### 6. Swelling of anteriormost trunk [NEW]

*(0) anteriormost trunk contiguous with posterior trunk; no swollen ‘head’*
*(1) anteriormost trunk elliptical, substantially wider than adjacent trunk*
*(–) inapplicable: head comprises externally differentiated segments.*

Certain lobopodians (*Cardiodictyon*, *Hallucigenia fortis*, *Luolishania*) have a differentiated anteriormost trunk that forms a wide ellipse or ‘head’ (Liu and Dunlop 2014). In *Hallucigenia sparsa*, the ‘head’ is denoted by a slight increase in the width of the anteriormost trunk, which is most prominent in smaller specimens. In other taxa (*Aysheaia*, *Onychodictyon ferox*, *Megadictyon*, *Jianshanopodia*, *Ilyodes*), the anteriormost trunk is not differentiated in this way (Thompson and Jones 1980; Ou *et al.* 2012; Vannier *et al.* 2014).

## *Oral structures*

### 7. Mouth opening orientation [SOH: 18]

*(0) terminal*
*(1) ventral*
*(2) posterior*

Most lobopodian taxa possess a terminal anterior mouth – for example *Aysheaia* (Whittington 1978), *Onychodictyon ferox* (Ou *et al.* 2012) and *Kerygmachela* (Budd 1993, 1998*a*) – as do Eutardigrada (e.g. Halberg *et al.* 2009; Persson *et al.* 2012). Hallucigeniids also have a terminal mouth, even if it has a ventral orientation in most specimens due to the flexible neck (trans. ser. 5). 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 mouth opening is ventrally oriented in *Pambdelurion* (Budd 1998*b*), 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.* 2013*b*; Persson *et al.* 2014); it faces posteriad in euarthropods (Edgecombe and Ramsköld 1999; Haug *et al.* 2012*b*; Yang *et al.* 2013) and *Opabinia* (Whittington 1975; Budd 1996; Budd and Daley 2012). The mouth of *Luolishania* is to some extent turned ventrally; we score it as ambiguous for anterior/ventral (Ma *et al.* 2009). *Antennacanthopodia* is coded as ambiguous as there is no direct evidence for the location of the mouth (Ou *et al.* 2011).

### 8. Pre-oral chamber [NEW]

*(0) absent*
*(1) present*

We define a pre-oral ('buccal') chamber as a region enclosing the mouth and formed by the outgrowth of surrounding body tissue – as observed in modern onychophorans (Martin and Mayer 2014). Taking the circumoral structures of *Hallucigenia sparsa* to represent the position of the true mouth, the mouth is located in a chamber within the anteriormost trunk (i.e. 'head'). The transformation series is coded as absent where the oral region is clearly displayed externally, as in Tardigrada, euarthropods from *Kerygmachela* crownwards (where the position of the mouth is marked by the expression of an 'oral cone'), *Jianshanopodia* (Vannier *et al.* 2014), *Aysheaia* (Whittington 1978), and *Siberion* (Dzik 2011). It is coded as ambiguous in other taxa, as the location of the original mouth is unclear. In *Supella*, the 'buccal cavity' represents part of the foregut rather than a pre-oral chamber (Elzinga and Hopkins 1994).

### 9. Radially arranged circumoral structures [SOH: 19]

*(0) absent*
*(1) present*

The mouth of many ecdysozoans is surrounded by radially-arranged cuticular or sclerotized structures. In priapulids and other cycloneuralians these are typically conical spines, arranged centripetally when the pharynx is contracted and centrifugally when the pharynx is everted (Conway Morris 1977). In basal panarthropods such as *Aysheaia*, *Kerygmachela* and *Jianshanopodia*, the structures are regular non-sclerotized lamellae or plates (Whittington 1978; Budd 1998*a*; Vannier *et al.* 2014); among anomalocaridids the plates are sclerotized and differentiated (Daley and Bergström 2012; Daley *et al.* 2013*a*, *b*). (Although the three or four prominent plates in the anomalocaridid oral cone are differentiated to give rise to bilateral symmetry (Daley and Bergström 2012), the underlying radial arrangement of these plates is clear: some plates straddle the midline, and if rotated by 90° the smaller plates are equivalent to their counterparts.) Tardigrades bear circumoral lamellae (Budd 2001*a*; Guidetti *et al.* 2012; Mayer *et al.*

2013*b*). *Antennacanthopodia* is coded as ambiguous as there is no direct evidence for the location of the mouth. *Opabinia* has been changed from present to ambiguous; radial structures around the mouth are drawn by Whittington (1975) but not interpreted, and further study is needed to confirm their status. Coded as present in *Hallucigenia sparsa* based on the new observations presented herein. The cuticular ring reported in the head of *Microdictyon* (Liu and Dunlop 2014) requires detailed study before its interpretation can be considered secure. Other lobopodians are coded as ambiguous; euarthropods are coded as absent.

On a more fundamental level, homology between ecdysozoan mouths is indicated by their shared embryological origin; the homology of ecdysozoan pharynxes is demonstrated by their common construction and their lining with ectodermally-derived, periodically moulted cuticle (Dewel *et al.* 1973). As such, homology between the radially arranged cuticular structures can be defended based on their location (along the boundary between the head and the pharynx), their equivalent (elongate, flat) shape, their robust sclerotized constitution, and their radial arrangement. Ultimately, of course, this cladistic analysis serves to test the homology proposed in this transformation series.

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*, *Megadictyon*, *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). Moreover, the onychophoran lip papillae do not express a radial arrangement: individual papillae correspond to their bilaterally-opposite neighbours, and no papillae occupy the midline of symmetry. As such, the onychophoran 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).

### 10. Differentiated circumoral structures [SOH: 21]

*(0) undifferentiated plates (e.g.* Pambdelurion*)*
*(1) differentiation of three or four enlarged plates (i.e. Radiodonta)*
*(–) inapplicable: radially symmetrical circumoral structures absent (trans. ser. 9 = 0)*

This transformation series distinguishes the somewhat indistinct organization of the mouth apparatus in *Pambdelurion* (Budd 1998*b*) from the more complex 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).

This transformation series was formerly contingent on 'Nature of radial circumoral sclerites = radial plates arranged as a mouth apparatus' [SOH 20]. That transformation series was removed in this study: token 0 (scalids) was invalid as scalids are features of the trunk/introvert, not the mouth; and there is no consistent morphological basis to distinguish between token 1 (oral papillae or lamellae) and token 2 (radial plates organized as a mouth apparatus). As such, the revised transformation series is contingent on the presence of radially symmetrical circumoral structures (trans. ser. 9). Taxa whose circumoral structures were coded as 'oral papillae or lamellae' under SOH 20, token 1, were formerly scored as inapplicable but are now scored as 'undifferentiated plates'.

### 11. Pharynx differentiated from midgut [NEW]

*(0) not differentiated*
*(1) differentiated*

Coded as differentiated in taxa where the pharynx (foregut) is distinct from the midgut. This may reflect a change in width (as in extant onychophorans), structural differentiation (as in priapulids and *Anomalocaris* (Daley and Edgecombe 2014)), or the presence of cuticular teeth in the foregut but not midgut (as in *Jianshanopodia*).

### 12. Pharynx eversible [NEW]

*(0) permanently inverted*
*(1) completely eversible*
*(–) inapplicable: pharynx not differentiated (trans. ser. 11)*

The pharynx of priapulids and palaeoscolecids can be everted (Conway Morris 1977), whereas the panarthropod foregut is permanently inverted. No lobopodians exhibit complete eversion of the pharynx, even if some taxa display a certain degree of flexibility: as perhaps evident in the proboscis of *Onychodictyon ferox* (Ou *et al.* 2012) or the presumed suction-feeding mouthparts of anomalocaridids (Daley and Bergström 2012). Taxa whose mouth region is unknown or is known from a limited sample size are coded ambiguous to reflect the possibility that eversion was possible but not displayed in the available material.

### 13. Sclerotized pharyngeal ‘teeth’ [SOH: 22]

*(0) absent*

*(1) present*

*(–) inapplicable: pharynx not differentiated (trans. ser. 11)*

In many taxa the pharynx is lined with cuticular sclerites or ‘pharyngeal teeth’. Priapulids have an eversible pharynx lined with pharyngeal teeth (van der Land 1970; Conway Morris 1977). *Hallucigenia sparsa* has a structurally differentiated (narrower) pharynx lined with acicular teeth (this study). *Jianshanopodia* bears a series of pharyngeal teeth with multiple cusps (Liu *et al.* 2006; Vannier *et al.* 2014). This fossil, perhaps alongside *Omnidens* (Hou *et al.* 2006), resembles a longitudinally extended *Hurdia* mouthpart; the inner rows of teeth in *Hurdia* are correspondingly interpreted as pharyngeal teeth (Daley *et al.* 2009, 2013*a*). Sclerotized teeth have also been reported in the foregut of *Paucipodia* (Hou *et al.* 2004), although the nature and distribution of the teeth is not clear from the fossil material. *Supella* bears pharyngeal teeth (‘microspines’), uniformly distributed about the pharynx (Elzinga and Hopkins 1994). Onychophorans bear a differentiated pharynx with an oesophageal constriction, but this is unornamented (Elzinga 1998). Most tardigrade taxa exhibit two to five rows of buccopharyngeal teeth (= mucrones) caudally to their circumoral lamellae (Pilato 1972; Schuster *et al.* 1980; Dastych *et al.* 2003; Guidetti *et al.* 2012); a further row of sclerotized transverse ridges (=baffles) may also correspond to pharyngeal teeth. Coded as ambiguous in all other taxa due to inadequate preservation.

### 14. Nature of pharyngeal teeth or aciculae [NEW]

*(0) spinose/acicular: each tooth has a single point*

*(1) multiple cusps: each tooth has multiple tips, perhaps expressed as denticles or serrations*

*(–) inapplicable: pharyngeal teeth or aciculae absent (trans. ser. 13)*

Priapulids’ pharyngeal teeth exhibit a range of morphologies but always bear multiple cusps (van der Land 1970; Smith *et al.* in press). *Hallucigenia sparsa* has acicular teeth that come to a single point (this study). The teeth of *Hurdia*, *Jianshanopodia* and *Supella* have multiple cusps (Elzinga and Hopkins 1994; Daley *et al.* 2009, 2013*a*; Vannier *et al.* 2014); tardigrade teeth do not (Pilato 1972; Schuster *et al.* 1980; Dastych *et al.* 2003).

### 15. Arrangement of pharyngeal teeth or aciculae [NEW]

*(0) uniform distribution around pharynx*

*(1) limited number of longitudinal rows or series*

In contrast to the uniform distribution of sclerites in priapulids and total-group euarthropods, the pharyngeal teeth in *Hallucigenia sparsa* seem to occupy one or two longitudinal rows and do not cover the entire surface of the pharynx.

## *Ocular structures*

### 16. Eyes [SOH: 23]

*(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), *Hallucigenia fortis* (cf. Liu and Dunlop 2014), and *Hallucigenia sparsa* (this study).

### 17. Eye attachment [SOH: 24]

*(0) eye sessile*

*(1) eye stalked*

*(–) inapplicable: eyes (trans. ser. 16) absent*

Transformation series 26 in Ma *et al.* (2014). Eyes are sessile in *Hallucigenia sparsa* (this study).

### 18. Type of eyes [SOH: 25]

*(0) ocellus-like or pigment spots*

*(1) multiple visual units (including compound eyes)*

*(–) inapplicable: eyes (trans. ser. 16) absent*

Transformation series 27 in Ma *et al.* (2014). This transformation series is scored 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). In dorsoventral view, *Luolishania* is convincingly shown to have a pair of pit-type eyes (Schoenemann *et al.* 2009). In lateral view, these eyes are compressed to lie one above the other, and in our view these correspond to two of the three carbonaceous spots evident in laterally preserved specimens (Ma *et al*. 2012*a*). The third spot is clearly different in composition, reflectivity and relief; the fact that it is only preserved in a single specimen suggests that it is an artefact, possibly representing a separate biological or abiogenic entity adpressed onto the fossil specimen. We therefore reconstruct *Luolishania* as having pit-type eyes. *Hallucigenia sparsa* does not exhibit multiple visual units (this study). We code *Hallucigenia fortis* as uncertain, as in our view the various carbonaceous regions and pigmented patches (Ma *et al*. 2012*a*) likely represent a degraded but originally continuous carbon film.

## *Cephalic / anterior appendages*

### 19. Sclerotized post-ocular (post-protocerebral) body appendages with arthrodial membranes [SOH: 5]

*(0) not sclerotized; arthrodial membranes absent ('lobopodous')*
*(1) sclerotized; arthrodial membranes present ('arthropodized')*
*(–) inapplicable: paired appendages (trans. ser. 1) absent*

Note that we use the term 'lobopodous' to refer to limbs that are not sclerotized and that lack arthrodial membranes, but with no other implication with respect to limb morphology.

### 20. Pre-ocular (protocerebral) limb pair, structurally differentiated from trunk appendages [NEW]

*(0) pre-ocular limb pair absent or not differentiated from other limbs*
*(1) distinct pre-ocular limb pair*
*(–) inapplicable: paired appendages (trans. ser. 1) absent*

In most panarthropods, the first pair of limbs is pre-ocular (at least developmentally), is associated with the protocerebral segment, and is structurally differentiated from other limb pairs. In hallucigeniids, however, the first limb pair is not structurally differentiated from its neighbour; moreover, the great distance between the head and the first limb pair in *Hallucigenia sparsa* (this study) argues against a pre-ocular or indeed cerebral identity of these appendages. Whether or not the first appendage pair truly corresponds to the pre-ocular appendage of other groups, the absence of a differentiated pre-ocular appendage characterizes a number of armoured lobopodians: *Xenusion* (Dzik and Krumbiegel 1989), *Diania* (Ma *et al.* 2014), *Microdictyon* (Chen *et al.* 1995*b*), *Paucipodia* (Chen *et al.* 1995*a*; Hou *et al.* 2004), *H. fortis* (Ramsköld and Chen 1998), and *H.*

*sparsa* (this study). A distinct structure is evident in onychophorans, *Antennacanthopodia Ilyodes*, and luolishaniids (antennae); tardigrades (the stylet apparatus); anomalocaridids (great appendages) (Cong *et al.* 2014); *Opabinia* (proboscis); and euarthropods and basal panarthropods (various). Coded as ambiguous in *Cardiodictyon*, where the detailed morphology of the head is unclear, and in taxa where the head is not preserved (including *Carbotubulus*).

### 21. Sclerotization of pre-ocular (protocerebral) limb pair [SOH: 6]

*(0) not sclerotized*
*(1) sclerotized*
*(–) inapplicable: pre-ocular (protocerebral) appendages (trans. ser. 20) 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.

### 22. Pre-ocular (protocerebral) limb pair with arthrodial membranes [SOH: 7]

*(0) absent*
*(1) present*
*(–) inapplicable: protocerebral limbs (trans. ser. 21) 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.

### 23. Nature of post-ocular lobopodous inner branch [SOH: 8]

*(0) cylindrical/subconical appendage*

*(1) laterally expanded swimming flap*

*(–) inapplicable: post-ocular limbs, if present, are arthropodized (trans. ser. 19 = 1)*

The cylindrical ambulacral lobopodous leg characteristic of lobopodians is also found in *Opabinia* (Budd 1996; Budd and Daley 2012), *Kerygmachela* (Budd 1993, 1998*a*) and *Pambdelurion* (Budd 1998*b*). The anomalocaridids *Peytoia* and (probably) *Hurdia* 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 (Van Roy *et al.* 2015). The presence of dorsal flaps in *Anomalocaris* is ambiguous (Van Roy *et al.* 2015).

### 24. Deutocerebral limb pair structurally differentiated from trunk appendages [SOH: 10]

*(0) undifferentiated, or differentiated in size only*

*(1) structurally differentiated*

*(–) inapplicable: pre-ocular appendages (trans. ser. 20) not differentiated*

This transformation series is now coded as inapplicable if the pre-ocular appendage pair are not differentiated, as we consider it unlikely that a deutocerebral appendage would be differentiated if the protocerebral appendage was not. 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). 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.* 2013*b*), 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*b*; Yang *et al.* 2013) or raptorial (Chen *et al.* 2004; Haug *et al.* 2012*b*; Tanaka *et al.* 2013) deutocerebral appendage. The second leg pair of *Luolishania* and *Hallucigenia sparsa* are not differentiated from their neighbours (Ramsköld and Chen 1998) and are therefore coded as undifferentiated; the trunk limbs are instead divided into two morphological zones (trans. ser. 51). The second appendage pair of *Cardiodictyon* does not seem to be differentiated (Liu *et al.* 2008*a*). Because the head of *Carbotubulus* is not preserved (Haug *et al.* 2012*c*), the identity of the limbs is unclear and this transformation series is coded as ambiguous.

### 25. Nature of first post-ocular (deutocerebral) appendage [SOH: 9]

*(0) lobopodous*
*(1) sclerotized jaw*
*(2) arthropodized antenniform with distinct podomeres*
*(3) arthropodized short great-appendage*
*(–) inapplicable: deutocerebral appendage (trans. ser. 24) not differentiated*

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

### 26. Position of pre-ocular (protocerebral) appendage pair [SOH: 11]

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

We score this transformation series as ventral 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 thus scored as having a ventral position. The first pair of appendages in *Ilyodes* are lateral (Thompson and Jones 1980; Haug *et al.* 2012*c*).

### 27. Pre-ocular (protocerebral) appendages directly adjacent to one another [SOH: 12]

*(0) pre-ocular appendages not directly adjacent*

*(1) pre-ocular appendages adjacent to one another, with or without physical fusion*

*(–) 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* and *Megadictyon* are coded uncertain due to unclear preservation (Liu *et al.* 2006, 2007). The first pair of appendages in *Ilyodes* are not directly adjacent (Thompson and Jones 1980; Haug *et al.* 2012*c*).

### 28. Pre-ocular (protocerebral) appendages mechanically fused [NEW]

*(0) pre-ocular appendages adjacent but not mechanically fused*

*(1) pre-ocular appendages are mechanically fused to form a single element*

*(–) inapplicable: pre-ocular appendages not adjacent to one another (trans. ser. 27 = 0)*

In *Kerygmachela*, *Pambdelurion* and *Siberion*, the appendages have migrated into an adjacent position but are not mechanically connected (Budd 1993, 1998*a*, *b*; Dzik 2011); this also seems to be the case in anomalocaridids (Daley *et al.* 2009; Daley and Edgecombe 2014). In *Opabinia* and euarthropods, the appendages exhibit a degree of fusion (see trans. ser. 28).

### 29. Extent of pre-ocular (protocerebral) appendage fusion [SOH: 13]

*(0) locational basal only, with separate distal elements*

*(1) fused into a reduced labrum*

*(–) inapplicable: protocerebral appendages not mechanically fused (trans. ser. 28 = 0)*

The pre-ocular appendages of *Opabinia* are fused basally but have separate distal elements, whereas the euarthropod labrum (per trans. ser. 12) is coded as a set of fully fused appendages.

### 30. Spines/spinules on pre-ocular (protocerebral) appendage [SOH: 14]

*(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). Coded as inapplicable in tardigrades due to the extremely modification of the pre-ocular appendage into a stylet apparatus, which poses challenges to the identification of homologues of appendicular features, and absent in *Ilyodes* (Haug *et al.* 2012*c*).

### 31. Number of spine/spinule series on pre-ocular (protocerebral) frontal appendage [SOH: 15]

*(0) one series (e.g.* Aysheaia, Kerygmachela, Opabinia, Hurdia, Peytoia*)* (Whittington 1978; Budd 1993, 1996, 1998*a*; Daley and Budd 2010)

*(1) two series (e.g.* Anomalocaris, Onychodictyon ferox*)* (Daley and Budd 2010; Ou *et al.* 2012; Daley and Edgecombe 2014)

*(–) inapplicable: spines/spinules on the protocerebral appendage (trans. ser. 30) absent*

### 32. Coplanar spine/spinule series in pre-ocular (protocerebral) frontal appendages [SOH: 16]

*(0) no (as in Radiodonta)*

*(1) yes (as in* Onychodictyon ferox*)*

*(–) inapplicable: spine/spinules, if present, in single series (trans. ser. 31= 0)*

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

### 33. Multifurcate distal termination of protocerebral appendage [SOH: 17]

*(0) absent*
*(1) present*
*(–) inapplicable: spines/spinules not present on the protocerebral appendage (trans. ser. 30 = 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*a*) – but absent in *Onychodictyon ferox* (Ou *et al.* 2012).

## *Trunk region*

### 34. Epidermal segmentation [SOH: 26]

*(0) absent*
*(1) present*

Transformation series 25 in Daley *et al.* (2009). Epidermal segmentation is a distinguishing feature of Euarthropoda (e.g. Budd 2001*b*; 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.

**35. Dorsal integument sclerotized and connected by arthrodial membranes [SOH: 27]**

*(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.* 2012*b*; 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.

**36. Sternites connected by arthrodial membranes [SOH: 28]**

*(0) absent*
*(1) present*
*(–) inapplicable: dorsal sclerotized integument (trans. ser. 35) 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.* 1995*c*; 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.

**37. Annulations [SOH: 29]**

*(0) absent*
*(1) present*
*(–) inapplicable: sclerotized dorsal integument with arthrodial membranes (trans. ser. 35) present*

Transformation series 26 in Daley *et al.* (2009). Annulations are repeated superficial integument rings. Absent in *Hallucigenia sparsa* (this study). Coded as absent in *Carbotubulus*; a taphonomic absence can be discounted because annulations are preserved in co-occurring specimens of *Ilyodes* (Haug *et al.* 2012*c*).

### 38. Annulation distribution [SOH: 30]

*(0) limbs only*

*(1) trunk and limbs*

*(–) inapplicable: annulations (trans. ser. 37) 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 1998*b*). The same is true in *Antennacanthopodia* (cf. Ou *et al.* 2011), where the effaced preservation of the trunk may obscure trunk annulations.

### 39. Anterior projection of trunk lacking annulations [NEW]

*(0) annulations continue for full length of trunk*

*(1) differentiated anterior region of trunk lacking annulations*

*(–) inapplicable: trunk lack annulations (trans. ser. 37)*

The anterior trunk of *Aysheaia* and *Onychodictyon ferox* is differentiated into a stout ‘proboscis’, distinct from the trunk by virtue of its shape and its lack of annulations (Ou *et al.* 2012). The anterior introvert of *Tubiluchus* and *Cricocosmia* is differentiated in a similar fashion, to a greater or lesser (Calloway 1975; Kirsteuer 1976; Han *et al.* 2007). The bulbous heads of *Hallucigenia fortis, Microdictyon, Cardiodictyon* and *Luolishania* also lack annulations (Chen *et al.* 1995*b*; Ma *et al.* 2009, 2012*a*; Liu and Dunlop 2014). In contrast, annulations continue to the tip of the head in *Paucipodia*, *Onychodictyon gracilis*, and *Diania* (whichever end of *Diania* is interpreted as anterior) (Chen *et al.* 1995*a*; Hou *et al.* 2004; Liu *et al.* 2008*b*; Ma *et al.* 2014). Annulations are not clearly preserved in the anterior region of *Jianshanopodia* and *Megadictyon* (Liu *et al.* 2006, 2007), making this transformation series difficult to score with confidence. Annulations in the pharynx of *Kerygmachela* continue to the terminal mouth (Budd 1998*a*); given the position of the prominent annulated appendages, it seems likely that the head also expressed external annulations. Annulations continue to the anterior extremity of the onychophoran trunk.

### 40. Organization of trunk annulation [SOH: 31]

*(0) homonomous*
*(1) heteronomous*
*(–) inapplicable: annulations (trans. ser. 37) 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 1998*b*).

### 41. Regularly spaced paired dorsolateral epidermal specializations [SOH: 32]

*(0) absent*
*(1) present*
*(–) inapplicable: sclerotized exoskeleton (trans. ser. 35) present*

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*a*); 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.* 1995*a*), 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 2001*b*; Zhang and Aldridge 2007). This transformation series is independent of the presence of heteronomous or homonomous annulation (trans. ser. 37); it occurs in taxa with homonomous (e.g. *Paucipodia* and *Aysheaia*) and heteronomous (*Hadranax* and *Kerygmachela*) annulations. Ambiguous in *Carbotubulus* as the dorsal surface is not visible in the available material (Haug *et al.* 2012*c*). We have re-coded *Aysheaia* as absent (formerly present), as observation confirms that the reported ‘specializations’ (Liu and Dunlop 2014) represent the imprints of the opposite legs (Whittington 1978). The transformation has been renamed to remove the association of sclerites with trunk limbs, reflecting the presence of net-like sclerites on *Cricocosmia* that potentially correspond to lobopodian sclerites (Han *et al.* 2007; Steiner *et al.* 2012).

### 42. Nature of paired epidermal specialization [SOH: 33]

*(0) epidermal depressions*
*(1) epidermal evaginations*
*(–) inapplicable: epidermal specializations (trans. ser. 41) absent*

The nodes, plates and spines of *Cricocosmia* and lobopodian taxa (trans. ser. 38) 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* and *Diania* as uncertain; their preservation is insufficient to establish whether the paired specializations are node-like evaginations or pit-like depressions (Chen *et al.* 1995*a*; Liu and Dunlop 2014; Ma *et al.* 2014).

### 43. Proportions of epidermal trunk evaginations [SOH: 34]

*(0) wider than tall (e.g. nodes or plates)*
*(1) taller than wide (e.g. spines)*
*(–) inapplicable: epidermal evaginations (trans. ser. 42) absent*

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.

### 44. Trunk epidermal evaginations with acute distal termination [SOH: 35]

*(0) absent*
*(1) present*
*(–) inapplicable: epidermal evaginations (trans. ser. 42) absent*

This transformation series refers solely to the shape of the trunk evaginations' apices. It is independent from the evaginations' proportions (trans. ser. 43), 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* and *Orstenotubulus* are coded as uncertain due to its ambiguous preservation (Liu *et al.* 2008*b*). *Cricocosmia* plates lack an acute distal termination.

### 45. Acute distal termination in epidermal evagination is curved [SOH: 36]

*(0) straight*
*(1) curved*
*(–) inapplicable: epidermal evaginations, if present, lack an acute distal terminus (trans. ser. 44)*

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 *Onychodictyon ferox* (Topper *et al.* 2013) are essentially straight. The spines of *Hallucigenia sparsa* (formerly 'straight') are gently curved (this study).

### 46. Sclerotization of epidermal evaginations [SOH: 37]

*(0) epidermal evaginations not sclerotized*
*(1) epidermal evaginations sclerotized*
*(–) inapplicable: epidermal evaginations (trans. ser. 42) absent*

The epidermal evaginations of *Cricocosmia* and 'armoured' lobopodians are substantially sclerotized (Hou and Bergström 1995; Han *et al.* 2007; Steiner *et al.* 2012; Caron *et al.* 2013), in contrast to those of *Xenusion* (Dzik and Krumbiegel 1989), *Hadranax* (Budd and Peel 1998), *Diania* (Ma *et al.* 2014) and *Kerygmachela* (Budd 1993, 1998*a*).

### 47. Dorsal trunk sclerite ornament [SOH: 38]

*(0) net-like*
*(1) scaly*
*(–) inapplicable: sclerotized epidermal evaginations (trans. ser. 46) 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*, *Microdictyon* and *Cricocosmia* (Han *et al.* 2007; 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).

### 48. Sclerites consist of a stack of constituent elements [SOH: 39]

*(0) sclerites comprise single element*
*(1) sclerites comprise stacked elements*
*(–) 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. 1p–q). Whereas the dorsal sclerites of *Microdictyon* and *Onychodictyon* do not express constituent elements, the detailed construction of their claws is not known; as such these taxa are coded as ambiguous. Where sclerites are not preserved in sufficient detail to assess their construction, this transformation series is coded as ambiguous.

### 49. Maximum number of dorsal epidermal specializations above each leg pair [SOH: 40]

*(0) one*

*(1) two*

*(2) three*

*(3) four*

*(–) inapplicable: epidermal specializations (trans. ser. 41) 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). The plates of *Cricocosmia* occur in pairs (Han *et al.* 2007).

### 50. Papillae on trunk annulations [SOH: 41]

*(0) absent*

*(1) present*

*(–) inapplicable: annulations (trans. ser. 37) 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), and *Antennacanthopodia* as uncertain as its trunk annulations are not clearly apparent (Ou *et al.* 2011).

### 51. Dorsal bands of lanceolate blades [SOH: 42]

*(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.

### 52. Skeletal musculature [NEW]

*(0) peripheral longitudinal and circular muscle*

*(1) metamerically arranged skeletal muscle*

Budd (2001*a*) proposes the distribution of musculature as a key phylogenetic character. The musculature of tardigrades, *Pambdelurion*, *Anomalocaris* and more derived euarthropods is metamerically arranged and runs through the body cavity, whereas muscles in cycloneuralians, onychophorans and *Kerygmachela* are seemingly dominated by longitudinal and circular structures (Budd 1998*c*, 2001*a*). A longitudinal arrangement of musculature is suggested by the longitudinal wrinkling present in *Carbotubulus* (Haug *et al.* 2012*c*). The metameric distribution of musculature in artiopodans is inferred by comparison with *Campanamuta* (Budd 2011).

**53. Serially repeated mid-gut glands [SOH: 43]**

*(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 *Megadictyon*, *Jianshanopodia*, *Pambdelurion* and *Opabinia* is elucidated by Vannier *et al.* (2014). Gut glands are present in *Anomalocaris* (Daley and Edgecombe 2014). The range of preservation modes observed in this study allows us to establish that midgut glands were biologically, rather than taphonomically, absent in *Hallucigenia sparsa*.

**54. Differentiated anterior trunk [SOH: 59]**

*(0) trunk of uniform construction*
*(1) anterior trunk differentiated from posterior trunk by abrupt change in thickness, armature and appendage construction*

This transformation series has been reformulated to reflect the pronounced differentiation of the posterior and anterior trunk – not just the trunk appendages – in certain lobopodians. In *Hallucigenia sparsa*, the region of the trunk anterior of the third appendage pair is narrower, lacks dorsal armature, and expresses differentiated appendages (this study). The short constricted region anterior of the first spine pair in *H. fortis* is associated with two differentiated appendage pairs (Ramsköld and Chen 1998) and apparently corresponds with the 'neck' of *H. sparsa*. In luolishaniids, the anterior body bears elongate limbs with accentuated armature (Ma *et al.* 2009; García-Bellido *et al.* 2013). The portion of the trunk in *Carbotubulus* corresponding to the first two or three leg pairs is substantially narrower than the posterior trunk and its associated appendages are narrower and less prominent than the posterior appendages, indicating trunk differentiation (Haug *et al.* 2012*c*). Although the width of the trunk narrows gradually towards the front of *Paucipodia*, this tapering is gradual and does not correspond to the differentiation of the anterior trunk (Chen *et al.*

1995*a*; Hou *et al.* 2004). Coded ambiguous in *Orstenotubulus, Hallucigenia hongmeia*, and *Ilyodes* due to incomplete preservation (Thompson and Jones 1980; Maas *et al.* 2007; Steiner *et al.* 2012).

## *Trunk appendages*

### 55. Trunk exites [SOH: 44]

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

Transformation series 31 in Daley *et al.* (2009). Absent in *Supella*.

### 56. Form of exite [SOH: 45]

*(0) lateral lobes*
*(1) simple oval paddle with marginal spines*
*(2) bipartite shaft with lamellar setae*
*(–) inapplicable: trunk exites (trans. ser. 55) absent*

### 57. Exite and endopod fused (biramy) [SOH: 46]

*(0) not fused*
*(1) fused*
*(–) inapplicable: exites (trans. ser. 55) 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. *Peytoia* and *Hurdia* are coded as unfused (token 0) based on the presence of a second set of lateral flaps (Van Roy *et al.* 2015). *Anomalocaris* is coded as uncertain as the possible presence of a second pair of lateral flaps has not been discounted.

### 58. Antero-posteriorly compressed protopodite with gnathobasic endites in post-deutocerebral appendage pair [SOH: 47]

*(0) absent*
*(1) present*
*(–) inapplicable: limbs (trans. ser. 19) 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.* 1995*c*; 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.* 2012*a*, *b*).

### 59. Secondary structures on non-sclerotized (lobopodous) limbs [SOH: 48]

*(0) absent*
*(1) present*
*(–) inapplicable: limbs (trans. ser. 19) 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*b*, 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* as scored as absent, and *Anomalocaris* as uncertain (Van Roy *et al.* 2015).

### 60. Nature of secondary structure [SOH: 49]

*(0) spines/setae*
*(1) appendicules*
*(–) inapplicable: no secondary structures on the lobopodous limbs (trans. ser. 59)*

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

### 61. Papillae on non-sclerotized (lobopodous) limbs [SOH: 50]

*(0) absent*

*(1) present*

*(–) inapplicable: limbs (trans. ser. 19) not lobopodous*

Transformation series 10 in Ma *et al.* (2014). In contrast to appendicules and spines, papillae are short projections associated with the annulations. The preservation of papillae in *Ilyodes* indicates that the absence of papillae in *Carbotubulus* is not taphonomic (Haug *et al.* 2012*c*).

### 62. Finger-like elements in distal tip of limbs [SOH: 51]

*(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).

### 63. Terminal claws on trunk limbs [SOH: 52]

*(0) absent*

*(1) present*

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

We score terminal claws as absent in *Opabinia* following Budd and Daley (2012). *Anomalocaris* is coded as ambiguous as there is no definitive information on the presence of lobopodous limbs or a second set of flaps (Van Roy *et al.* 2015). *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 scored as uncertain, as it is difficult to distinguish possible terminal claws from its myriad accessory spines (Liu *et al.* 2011; Ma *et al.* 2014).

### 64. Terminal claws with multiple branches [SOH: 53]

*(0) absent*
*(1) present*
*(–) inapplicable: terminal claws (trans. ser. 63) absent*

Present in Eutardigrada (Schuster *et al.* 1980; Nelson 2002; Halberg *et al.* 2009) and the Siberian Orsten-type tardigrade (Maas and Waloszek 2001). Absent in heterotardigrades and Palaeozoic lobopodians, which express simple concavo-convex claws.

### 65. Number of claws on undifferentiated trunk limbs [SOH: 54]

*(0) one*
*(1) two*
*(2) three*
*(3) four*
*(4) seven*
*(–) inapplicable: terminal claws (trans. ser. 63) 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.* (2012*a*). *Luolishania* is coded with token 0 (one claw) as this represents the state of its typical trunk limbs. Spinose elements on its anterior limbs do not exhibit a claw-like morphology and may represent cirri rather than claws. *Hallucigenia sparsa* is coded with token 3 (two claws) as this is the state on most trunk limbs, even if a second claw is not evident on the posteriormost appendages.

### 66. Nature of claws on each trunk limb [NEW]

*(0) claws on single limb all identical*
*(1) claws on single limb differentiated*
*(–) inapplicable: fewer than two claws on trunk limbs (trans. ser. 65)*

All seven claws in *Aysheaia* are identical (Whittington 1978). *Euperipatoides* claws are identical on trunk limbs, although the jaw elements are differentiated (Smith and Ortega-Hernández 2014). *Paucipodia* claws are not visibly differentiated (Hou *et al.* 2004); neither are those of *Hallucigenia* *sparsa* (this study). *Onychodictyon ferox* has a large and a small claw (Steiner *et al.* 2012 fig. 8). The nature of other lobopodians' claws has not been described in detail.

**67. External branch expressed as lateral flaps (body extends laterally into imbricated, unsclerotized flaps) [SOH: 55]**

*(0) absent*
*(1) present*
*(–) inapplicable: exites (trans. ser. 55) 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 *Peytoia* and *Hurdia*, and the uncertain number of lateral flaps in *Anomalocaris* (Van Roy *et al.* 2015).

**68. Longitudinal ('gill-like') wrinkling on distal part of (outer branch) flaps [SOH: 56]**

*(0) absent*
*(1) present*
*(–) inapplicable: lateral flaps (trans. ser. 67) not present*

Transformation series 38 in Daley *et al.* (2009).

**69. Strengthening rays in lateral flaps [SOH: 57]**

*(0) absent*
*(1) present*
*(–) inapplicable: lateral flaps (trans. ser. 67) not present*

Transformation series 37 in Daley *et al.* (2009)

**70. Posterior tapering of lateral flaps [SOH: 58]**

*(0) absent*
*(1) present*
*(–) inapplicable: lateral flaps (trans. ser. 67) not present*

Transformation series 40 in Daley *et al.* (2009)

### 71. Nature of lobopodous limbs on differentiated anterior trunk [NEW]

*(0) slender, simple*

*(1) cirrate*

*(–) inapplicable: trunk not differentiated into posterior and anterior regions (trans. ser. 54)*

The anterior limbs of *Hallucigenia sparsa* are simple and lack cirri; the anterior limbs of luolishaniids bear multiple cirri. The trunk is not differentiated into distinct anterior and posterior components in any other taxon.

### 72. Appendages comprise 15 or more podomeres [SOH: 60]

*(0) Fewer than 15 podomeres*

*(1) 15 or more podomeres*

*(–) inapplicable: limbs (trans. ser. 19) 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.* 1995*c*; Waloszek *et al.* 2005; Bergström *et al.* 2008; Yang *et al.* 2013).

## *Posterior termination*

### 73. Limbless posterior extension of the lobopodous trunk [SOH: 61]

*(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. transformation series 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, as 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*a*), *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 scored as uncertain as it is difficult to distinguish the possible body termination from a posterior leg or pair of legs (Dzik 2011). *Carbotubulus* is coded as absent (Haug *et al.* 2012*c*). *Hallucigenia sparsa* is coded as absent (this study); *H. hongmeia* and *H. fortis* are coded as ambiguous, as the preservation is insufficiently clear to determine whether possible 'posterior extensions' correspond to the trunk or to legs (Hou and Bergström 1995; Steiner *et al.* 2012; Liu and Dunlop 2014). Although *Luolishania* is described as bearing a protruding posterior termination, this is not unambiguously evident in specimens or camera lucida images; this taxon is thus coded as ambiguous (Liu *et al.* 2008*a*; Ma *et al.* 2009). A posterior extension is present in *Microdictyon* (Chen *et al.* 1995*b*).

### 74. Posterior tagma composed of three paired lateral flaps [SOH: 62]

*(0) absent*
*(1) present*
*(–) inapplicable: lateral flaps (trans. ser. 67) absent*

Transformation series 42 in Daley *et al.* (2009)

### 75. Posteriormost pair of trunk appendages structurally differentiated [SOH: 63]

*(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 scored 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). Coded as ambiguous in *Carbotubulus* due to poor preservation (Haug *et al.* 2012*c*).

### 76. Nature of differentiated posteriormost appendages [SOH: 64]

*(0) appendicular tail*

*(1) partially fused/reduced walking legs*

*(–) inapplicable: posterior appendages unmodified (trans. ser. 75 = 0)*

In fuxianhuiids, the posteriormost appendage pair is modified into a tail fan or tail flukes (e.g. Chen *et al.* 1995*c*; 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*a*) 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*b*), *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 scored 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 1998*b*).

### 77. Nature of appendicular tail [SOH: 65]

*(0) tail rami*

*(1) tail flaps*

*(–) inapplicable: appendicular tail not present (trans. ser. 76 $\neq$ 0)*

This transformation series distinguishes the long tail rami of *Kerygmachela* (Budd 1993, 1998*a*) 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).

### 78. Direction of claws on posteriormost appendage pair [SOH: 66]

*(0) Same direction as claws on other appendages*
*(1) rotated anteriad*
*(–) inapplicable: posterior appendages lack claws (trans. ser. 63 = 0)*

The last pair of legs are rotated anteriad in tardigrades (e.g. Marchioro *et al.* 2013), *Aysheaia* (Whittington 1978) and *O. ferox* (Ou *et al.* 2012), but not in *Cardiodictyon*, *Hallucigenia fortis* or *Microdictyon* (Hou and Bergström 1995). The claws of *Hallucigenia sparsa* seem to be oriented in the same direction on all appendage pairs (this study). We score the Siberian Orsten tardigrade (Maas *et al.* 2007) and *Onychodictyon gracilis* (Liu *et al.* 2008*b*) as uncertain.

## *Soft tissue organization*

### 79. Ventral nerve cord with paired ganglia [SOH: 67]

*(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.* 2013*a*). 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 ambiguous: 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*b*; Tanaka *et al.* 2013; Yang *et al.* 2013).

### 80. Dorsal condensed brain [SOH: 68]

*(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, 2013*b*). 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*b*) and *Alalcomenaeus* (Tanaka *et al.* 2013).

### 81. Number of neuromeres integrated into the dorsal condensed brain [SOH: 69]

*(0) one*
*(1) two*
*(2) three*
*(–) inapplicable: dorsal condensed brain (trans. ser. 80) absent*

See the introductory statements above.

### 82. Mouth innervation relative to brain neuromeres [SOH: 70]

*(0) protocerebral innervation*
*(1) deutocerebral innervation*
*(2) innervation from multiple neuromeres*
*(3) tritocerebral innervation*
*(–) inapplicable: dorsal condensed brain (trans. ser. 80) 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*b*; 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 as state 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 (Mayer *et al.* 2013*b*).

**83. Nerve cord lateralized [SOH: 71]**

*(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.* 2013*a*) from that in other phyla.

**84. Heart [SOH: 72]**

*(0) absent*
*(1) present*

Ma *et al.* (2014) described a dorsal heart in *Fuxianhuia*; all other fossil taxa are scored as ambiguous. Budd (2001*a*) 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 scored 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 with *k* between 0.46 and 211. 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. The most parsimonious reconstruction represents the reconstruction that best explains the observed data, but of course is not guaranteed to recover the 'true' evolutionary history; alternative explanations that explain similarities as separate innovations rather than a shared inheritance are possible, but require the invocation of additional evolutionary steps for which the data provide no evidence.

### *General organization*

**1. Paired appendages**

*Present in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of panarthropods. (Secondary loss in priapulids and palaeoscolecids is discounted based on the absence of appendages in other all ecdysozoans.)

### *Head region*

**2. Anterior region covered by sclerites**

*Absent in ancestral ecdysozoan. One extra step.*

i. Absent to present in common ancestor of anomalocaridids and crown euarthropods

ii. Present to absent in *Opabinia*

**3. Head shield formed by fused cephalic segments**

*Inapplicable in ancestral ecdysozoan; 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 ecdysozoan; present in ancestral paneuarthropod. No extra steps.*

i. Present to absent in common ancestor of leanchoiliids

**5. Neck flexure in coronal plane**

*Fixed relative to trunk in ancestral ecdysozoan. No extra steps.*

i. Fixed to flexible in common ancestor of *Microdictyon* and *Hallucigenia*

**6. Swelling of anteriormost trunk**

*No swelling in ancestral ecdysozoan. No extra steps.*

i. No swelling to swollen anterior trunk in ancestor of *Cardiodictyon* and *Hallucigenia*

## *Oral structures*

**7. Mouth opening orientation**

*Anterior in ancestral ecdysozoan. Two extra steps.*

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

ii. Ventral to posterior in common ancestor of *Opabinia* and euarthropods

iii. Anterior to ventral in onychophorans (independent change)

iv. Anterior to ventral in heterotardigrades (independent change)

**8. Pre-oral chamber**

*Absent in ancestral panarthropod. No extra steps.*

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

**9. Radially arranged circumoral structures**

*Present in ancestral ecdysozoan. One extra step.*

i. Present to absent in onychophorans

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

The most parsimonious character distribution homologizes the circumoral structures of priapulids and cycloneuralians with those of tardigrades, stem-group euarthropods, and *Hallucigenia*. The independent innovation of circumoral structures in cycloneuralians and panarthropods would require a second evolutionary gain, for which there is no evidence, and would imply that the features were absent in the ancestral ecdysozoan. The independent innovation of the structures in each panarthropod lineage as well as cycloneuralians would require three further steps, and would imply the absence of such features in early crown-group panarthropods.

### 10. Differentiated circumoral structures

*Undifferentiated in ancestral panarthropod. No extra steps.*

i. Undifferentiated to differentiated in common ancestor of anomalocaridids

### 11. Pharynx differentiated from midgut

*Differentiated in ancestral panarthropod. No transitions implied.*

### 12. Pharynx eversible

*Eversible in cycloneuralians; not eversible in panarthropods. No extra steps.*

i. Eversible to not eversible in common ancestor of panarthropods.

This reconstruction interprets *Cricocosmia* as a stem-group panarthropod, implying cycloneuralian paraphyly (per Garey 2001; Mallatt and Giribet 2006; Campbell *et al.* 2011; Borner *et al.* 2014). An eversible proboscis has elsewhere been considered a cycloneuralian synapomorphy (Telford *et al.* 2008).

### 13. Sclerotized pharyngeal teeth

*Present in ancestral ecdysozoan. No extra steps.*

i. Present to absent in onychophorans

### 14. Nature of pharyngeal teeth or aciculae

*Ancestral condition unresolved. One extra step.*

i. spinose to multiple cusps in priapulids

ii. spinose to multiple cusps in common ancestor of *Jianshanopodia* and euarthropods

This reconstruction is presented rather than the equally-parsimonious inverse (i.e. multiple cusps to spinose in tardigrades and *Hallucigenia*) in order to interpret the simpler morphology as ancestral.

### 15. Arrangement of pharyngeal teeth or aciculae

*Uniform distribution in ancestral panarthropod. No extra steps.*

i. Uniform to isolated longitudinal rows in *Hallucigenia sparsa*

## *Ocular structures*

**16. Eyes**

*Absent in ancestral ecdysozoan. Three extra steps.*

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

ii. Absent to present in common ancestor of *Antennacanthopodia* and onychophorans (independent origin)

ii. Absent to present in common ancestor of *Onychodictyon ferox* and tardigrades (independent origin)

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

**17. Eye attachment**

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

**18. Type of eyes**

*Inapplicable in ancestral ecdysozoan. Ocellus-like in common ancestor of tardigrades and Onychodictyon ferox, in Hallucigenia, and in common ancestor of Antennacanthopodia and onychophorans. Multiple visual units in common ancestor of euarthropods. No transitions implied.*

## *Cephalic/anterior appendages*

**19. Sclerotized post-ocular (post-protocerebral) body appendages with arthrodial membranes**

*Not sclerotized in ancestral panarthropod. No extra steps.*

i. Not sclerotized (lobopodous) to sclerotized (arthropodized) in common ancestor of euarthropods + fuxianhuiids

**20. Pre-ocular (protocerebral) limb pair, structurally differentiated from trunk appendages**

*Differentiated in common ancestor of panarthropods. One extra step.*

i. Differentiated limb pair present to absent or not differentiated in common ancestor of *Diania* and *Hallucigenia*

ii. Absent or not differentiated to present in *Luolishania* (secondary reversal)

Our new topology allows the protocerebral appendages to be homologous with those of tardigrades and euarthropods, which represents a less surprising conclusion than that presented in Smith & Ortega Hernández (2014). It is worth noting that our new tree implies that onychophoran antennae are not homologous to the antenniform appendages of *Luolishania*.

**21. 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.

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

*Inapplicable in ancestral panarthropod; absent in ancestral tardigrade. Ambiguous in ancestral paneuarthropod. No extra steps.*

i. Absent to present in common ancestor of anomalocaridids, OR present to absent in common ancestor of *Fuxianhuia* and euarthropods.

The Fitch algorithm interprets an absence of arthrodial membranes in the sclerotized pre-ocular limb pair in the common ancestor of tardigrades and euarthropods, indicating that arthrodial membranes were added to a sclerotized limb pair in the ancestor of anomalocaridids. However, the pre-ocular limbs (stylets) of tardigrades were sclerotized independently of the pre-ocular limbs (great appendages) in euarthropods (trans. ser. 21); as such it is also possible that when the pre-ocular limbs of anomalocaridids + euarthropods evolved, they expressed arthrodial membranes, and arthrodial membranes were lost in the common ancestor of fuxianhuiids and euarthropods. The Fitch algorithm erroneously disregards this possibility as a consequence of the way that it handles the inapplicable token (Brazeau 2011).

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

*Cylindrical/subconical in ancestral panarthropod. No extra steps.*

i. Cylindrical/subconical to laterally expanded swimming flap in common ancestor of anomalocaridids

**24. Deutocerebral appendage structurally differentiated from rest of trunk appendages**

*Not differentiated in ancestral panarthropod. One extra step.*

i. Not differentiated to differentiated in euarthropods + fuxianhuiids

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

**25. Nature of first post-ocular (deutocerebral) appendage**

*Inapplicable in ancestral ecdysozoan. No extra steps.*

i. Lobopodous limb to sclerotized jaw in *Euperipatoides*

ii. Arthropodized antenniform with distinct podomeres to arthropodized short great appendage in leanchoiliids

**26. 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.

**27. Pre-ocular (protocerebral) appendage pair directly adjacent to one another**

*Not directly adjacent in ancestral panarthropod. No extra steps.*

i. Not directly adjacent to adjacent in common ancestor of euarthropods and *Siberion* – possibly earlier, if the appendages of *Jianshanopodia* and *Megadictyon* are indeed adjacent

**28. Pre-ocular (protocerebral) appendages mechanically fused**

*Inapplicable in ancestral panarthropod. Not mechanically fused in common ancestor of Siberion and euarthropods. No extra steps.*

i. Not fused to mechanically fused in common ancestor of *Opabinia* and euarthropods.

**29. Nature of pre-ocular (protocerebral) appendage fusion**

*Inapplicable in ancestral panarthropod. Ambiguous (presumably basal only) in common ancestor of Opabinia and euarthropods. No extra steps.*

i. Transition between basal fusion and complete fusion to reduced labrum between *Opabinia* and common ancestor of euarthropods + fuxianhuiids.

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

*inapplicable in ancestral ecdysozoan; ambiguous in ancestral panarthropod. One extra step.*

i. Transition between present and absent at divergence of Tactopoda and Onychophora.

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

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

*inapplicable in ancestral ecdysozoan. One series in ancestral tactopod. One extra step.*

i. One series to two series in *Onychodictyon ferox*

ii. One series to two series in *Anomalocaris* (independent origin)

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

*Inapplicable in ancestral ecdysozoan. Ancestrally present in Onychodictyon ferox. Ancestrally absent in anomalocaridids. No transitions implied.*

**33. Multifurcate distal termination of protocerebral appendage**

*inapplicable in ancestral ecdysozoan. Present in ancestral tactopod. No extra steps.*

i. Present to absent in *Onychodictyon ferox*

## *Trunk region*

**34. Epidermal segmentation**

*Absent in ancestral ecdysozoan. No extra steps.*

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

**35. Dorsal integument sclerotized and connected by arthrodial membranes**

*Absent in ancestral ecdysozoan. No extra steps.*

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

### 36. Sternites connected by arthrodial membranes

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

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

### 37. 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 common ancestor of *Carbotubulus* and *Hallucigenia sparsa* (independent loss)

### 38. Annulation distribution

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

### 39. Anterior projection of trunk lacking annulations

*Differentiated anterior region of trunk lacking annulations in ancestral ecdysozoan. Two extra steps.*

i. Present to absent in common ancestor of *Paucipodia* and onychophorans
ii. Absent to present in common ancestor of *Microdictyon* and *Hallucigenia* (reversal)
iii. Present to absent in *Kerygmachela*

The latter loss may simply reflect the prominence of the annulated frontal appendages in *Kerygmachela* (and *Jianshanopodia* and *Megadictyon*?); could these enclose a non-annulated head?

### 40. Organization of trunk annulation

*Heteronomous in ancestral ecdysozoan. Four extra steps.*

i. Homonomous to heteronomous in common ancestor of Panarthropoda
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 *Aysheaia* (secondary reversal)
v. Heteronomous to homonomous in *Paucipodia* (secondary reversal)

This character does not appear to carry a great deal of phylogenetic weight. This reconstruction assumes that *Paucipodia* is closer to *Microdictyon* than to *Xenusion* and *Diania*; alternative resolutions of this polytomy would lead to a different transformation reconstruction.

**41. Regularly spaced paired dorsolateral epidermal specializations**

*Absent in ancestral ecdysozoan. Four extra steps.*

i. Absent to present in common ancestor of *Cricocosmia* and panarthropods
ii. Present to absent in *Aysheaia* (secondary loss)
iii. Present to absent in common ancestor of *Antennacanthopodia*, *Euperipatoides* and *Ilyodes* (secondary loss)
iv. Present to absent in common ancestor of *Siberion* and dinocaridids (secondary loss)
v. Absent to present in *Kerygmachela* (secondary reversal)

Although paired epidermal specializations seem to have a single origin in the panarthropod stem lineage, they are frequently lost. The lump-like nodes in *Kerygmachela* (Budd 1998*a*) apparently, and quite believably, have a separate origin from the sclerotized plates on other lobopodians.

**42. Nature of paired epidermal specialization**

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

i. Evaginations to depressions in eutardigrades

**43. 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*

**44. 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 (trans. ser. 45), which arise as processes of a shield-like plate.

**45. Acute distal termination in epidermal evagination is curved**

*Inapplicable in ancestral panarthropod. Present in common ancestor of Hallucigenia and luolishaniids. Absent in Onychodictyon ferox. No transformations implied.*

**46. 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)

**47. Dorsal trunk sclerite ornament**

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

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

**48. Sclerites consist of a stack of constituent elements**

*Single constituent element in ancestral panarthropod. No extra steps.*

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

**49. 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*

**50. Papillae on trunk annulations**

*Present in ancestral panarthropod. Two extra steps.*

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

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

iv. Present to absent in jianshanopodians (independent loss)

**51. 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 and fuxianhuiids (secondary loss)

**52. Skeletal musculature**

*Peripheral longitudinal and circular in ancestral panarthropod. One extra step.*

i. Peripheral to metameric in common ancestor of tardigrades

ii. Peripheral to metameric in common ancestor of euarthropods and *Pambdelurion* (independent gain)

This reconstruction is considered more plausible than the secondary reversal to peripheral musculature in *Kerygmachela*, though each scenario is equally parsimonious.

**53. Serially repeated mid-gut glands**

*Absent in ancestral ecdysozoan. 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)

**54. Differentiated anterior trunk**

*Uniform construction in ancestral panarthropod. No extra steps.*

i. Uniform construction to differentiated anterior trunk in common ancestor of *Hallucigenia* and luolishaniids

## *Trunk appendages*

**55. Trunk exites**

*Absent in ancestral panarthropod. One extra step.*

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

ii. Present to absent in *Supella* (secondary loss)

**56. Form of exite**

*Inapplicable in ancestral ecdysozoan; 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

**57. Exite and endopod fused (biramy)**

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

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

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

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

i. Transformation between absent and present (polarity ambiguous) near common ancestor of euarthropods + fuxianhuiids

**59. Secondary structures on non-sclerotized (lobopodous) limbs**

*Present in ancestral panarthropod. Three (or four) 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)

An additional gain is implied if *Jianshanopodia* and *Megadictyon* plot crownwards of *Hadranax*.

**60. Nature of secondary structure**

*Inapplicable in ancestral panarthropod. No extra steps.*

Secondary structures evolved multiple times (see trans. ser. 59) so should not be treated as homologous across Panarthropoda. As a result, this transformation series may lead to artefacts resulting from the Fitch algorithm's incorrect handling of inapplicable tokens (Brazeau 2011).

**61. Papillae on non-sclerotized (lobopodous) limbs**

*Absent in ancestral panarthropod. Four extra steps.*

i. Absent to present in *Aysheaia*

ii. Absent to present in *Luolishania* (independent gain)

iii. Absent to present in *Orstenotubulus* (independent gain)

iv. Absent to present in last common ancestor of onychophorans and *Antennacanthopodia* (independent gain)

v. Absent to present in *Hadranax* (independent gain)

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

**62. Finger-like elements in distal tip of limbs**

*Absent in ancestral panarthropod. Zero to one extra steps.*

i. Absent to present in common ancestor of extant tardigrades

ii? Present to absent in Siberian Orsten tardigrade

**63. 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.

**64. Terminal claws with multiple branches**

*Absent in ancestral panarthropod. Zero to one extra steps.*

i. Absent to present in common ancestor of eutardigrades and Siberian Orsten tardigrade

ii? Present to absent in heterotardigrades

**65. 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. No extra steps.*

i. Two to one in common ancestor of *Hallucigenia hongmeia* and *Luolishania*.

ii. Two to four in heterotardigrades

iii. Two to seven in *Aysheaia*

iv. 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.* 2012*a*). No transformation is reconstructed between euarthropods and *Onychodictyon ferox* because the intervening taxa lack terminal claws.

**66. Nature of claws on each trunk limb**

*Inapplicable in ancestral ecdysozoan, and in taxa lacking claws. Identical in ancestral panarthropod and in Supella. Differentiated in Kuamaia. No extra steps.*

i. Identical to differentiated in common ancestor of *Onychodictyon ferox* and tardigrades

**67. External branch expressed as lateral 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

**68. 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

**69. 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

**70. 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*

**71. Nature of lobopodous limbs on differentiated anterior trunk**

*Inapplicable in ancestral panarthropod; slender and simple in last common ancestor of Hallucigenia and luolishaniids. No extra steps.*

i. Slender and simple to cirrate in common ancestor of luolishaniids

**72. 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*

**73. Limbless posterior extension of the lobopodous trunk**

*Absent in ancestral panarthropod. One extra step.*

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

ii. Present to absent in common ancestor of *Carbotubulus* and *Hallucigenia sparsa*

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.

**74. 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*

**75. 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)

**76. Nature of differentiated posterior appendages**

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

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

**77. Nature of appendicular tail**

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

i. Tail flaps to tail rami in *Kerygmachela*

**78. 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*

**79. Ventral nerve cord with paired ganglia**

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in common ancestor of tactopods

**80. 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.

**81. 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

**82. 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

**83. Nerve cord lateralized**

*Absent in ancestral panarthropod. No extra steps.*

i. Absent to present in onychophorans

**84. 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 2001*a*).

## Supplementary references

BERGSTRÖM, J., HOU, X., ZHANG, X.-G. and CLAUSEN, S. 2008. A new view of the Cambrian arthropod *Fuxianhuia*. *GFF*, **130**, 189–201.

BOESGAARD, T. M. and KRISTENSEN, R. M. 2001. Tardigrades from Australian marine caves. With a redescription of *Actinarctus neretinus* (Arthrotardigrada). *Zoologischer Anzeiger*, **240**, 253–264.

BORNER, J., REHM, P., SCHILL, R. O., EBERSBERGER, I. and BURMESTER, T. 2014. A transcriptome approach to ecdysozoan phylogeny. *Molecular Phylogenetics and Evolution*, **80**, 79–87.

BRAZEAU, M. D. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*, **104**, 489–498.

BUDD, G. E. 1993. A Cambrian gilled lobopod from Greenland. *Nature*, **364**, 709–711.

———. 1996. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia*, **29**, 1–14.

———. 1998*a*. The morphology and phylogenetic significance of *Kerygmachela kierkegaardi* Budd (Buen Formation, Lower Cambrian, N Greenland). *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **89**, 249–290.

———. 1998*b*. Stem group arthropods from the Lower Cambrian Sirius Passet fauna of north Greenland. *In* FORTEY, R. A. and THOMAS, R. H. (eds.) *Arthropod Relationships*, Vol. 55 Chapman and Hall, London, 125–138 pp.

———. 1998*c*. Arthropod body-plan evolution in the Cambrian with an example from anomalocaridid muscle. *Lethaia*, **31**, 197–210.

———. 2001*a*. Tardigrades as ‘stem-group arthropods’: the evidence from the Cambrian fauna. *Zoologischer Anzeiger*, **240**, 265–279.

———. 2001*b*. Why are arthropods segmented? *Evolution & Development*, **3**, 332–342.

———. 2002. A palaeontological solution to the arthropod head problem. *Nature*, **417**, 271–275.

———. 2008. Head structure in upper stem-group euarthropods. *Palaeontology*, **51**, 561–573.

———. 2011. *Campanamuta mantonae* gen. et. sp. nov., an exceptionally preserved arthropod from the Sirius Passet Fauna (Buen Formation, lower Cambrian, North Greenland). *Journal of Systematic Palaeontology*, **9**, 217–260.

——— and DALEY, A. C. 2012. The lobes and lobopods of *Opabinia regalis* from the middle Cambrian Burgess Shale. *Lethaia*, **45**, 83–95.

BUDD, G. and PEEL, J. 1998. A new xenusiid lobopod from the Early Cambrian Sirius Passet fauna of North Greenland. *Palaeontology*, **41**, 1201–1213.

CALLOWAY, C. B. 1975. Morphology of the introvert and associated structures of the priapulid *Tubiluchus corallicola* from Bermuda. *Marine Biology,* **31**, 161–174.

CAMPBELL, L. I., ROTA-STABELLI, O., EDGECOMBE, G. D., MARCHIORO, T., LONGHORN, S. J., TELFORD, M. J., PHILIPPE, H., REBECCHI, L., PETERSON, K. J. and PISANI, D. 2011. MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 15920–15924.

CAMPIGLIA, S. and LAVALLARD, R. 1990. On the ecdysis at birth and intermoult period of gravid and young *Peripatus acacioi* (Onychophora, Peripatidae). *In* MINELLI, A. (ed.) *Proceedings of the 7th International Congress of Myriapodology*, E. J. Brill, Lieden, Netherlands, 461 pp.

CARON, J.-B., SMITH, M. R. and HARVEY, T. H. P. 2013. Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. *Proceedings of the Royal Society B: Biological Sciences,* **280**, 20131613.

CHEN, J., ZHOU, G. and RAMSKÖLD, L. 1995*a*. A new Early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **85**, 275–282.

CHEN, J.-Y., ZHOU, G.-Q. and RAMSKÖLD, L. 1995*b*. The Cambrian lobopodian *Microdictyon sinicum*. *Bulletin of the National Museum of Natural Science,* **5**, 1–93.

———, WALOSZEK, D. and 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.

———, EDGECOMBE, G., RAMSKÖLD, L. and ZHOU, G.-Q. 1995*c*. Head segmentation in Early Cambrian *Fuxianhuia*: implications for arthropod evolution. *Science,* **268**, 1339–1343.

CONG, P., MA, X., HOU, X., EDGECOMBE, G. D. and STRAUSFELD, N. J. 2014. Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature*, **513**, 538–542.

CONWAY MORRIS, S. 1977. Fossil priapulid worms. *Special Papers in Palaeontology*, **20**.

DALEY, A. C. and BUDD, G. E. 2010. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology,* **53**, 721–738.

DALEY, A. C. and BERGSTRÖM, J. 2012. The oral cone of *Anomalocaris* is not a classic ‘peytoia’. *Naturwissenschaften,* **99**, 501–504.

DALEY, A. C. and EDGECOMBE, G. D. 2014. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology*, **88**, 68–91.

———, BUDD, G. E. and CARON, J.-B. 2013*a*. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology*, **11**, 743–787.

———, ———, ———, EDGECOMBE, G. D. and COLLINS, D. H. 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science*, **323**, 1597–1600.

———, PATERSON, J. R., EDGECOMBE, G. D., GARCÍA-BELLIDO, D. C. and JAGO, J. B. 2013*b*. New anatomical information on *Anomalocaris* from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits. *Palaeontology*, **56**, 971–990.

DASTYCH, H., KRAUS, H. and THALER, K. 2003. Redescription and notes on the biology of the glacier tardigrade *Hypsibius klebelsbergi* Mihelčič, 1959 (Tardigrada), based on material from the Ötztal Alps,. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, **100**, 77–100.

DE SENA OLIVEIRA, I. and MAYER, G. 2013. Apodemes associated with limbs support serial homology of claws and jaws in Onychophora (velvet worms). *Journal of Morphology*, **274**, 1180–1190.

DEWEL, R. A. and 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.

———, CLARK, W. H. J. and DEWELL, R. A. 1973. Studies on the tardigrades. II. Fine structure of the pharynx of *Milnesium tardigradum* Doyère. *Tissue and Cell*, **5**, 147–159.

DZIK, J. 2011. The xenusian-to-anomalocaridid transition within the lobopodians. *Bollettino della Società Paleontologica Italiana*, **50**, 65–74.

DZIK, J. and KRUMBIEGEL, G. 1989. The oldest 'onychophoran' *Xenusion*: a link connecting phyla? *Lethaia*, **22**, 169–181.

EDGECOMBE, G. D. 2009. Palaeontological and molecular evidence linking arthropods, onychophorans, and other Ecdysozoa. *Evolution: Education and Outreach*, **2**, 178–190.

EDGECOMBE, G. and RAMSKÖLD, L. 1999. Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology*, **73**, 263–287.

ELZINGA, R. J. 1998. Microspines in the alimentary canal of Arthropoda, Onychophora, Annelida. *International Journal of Insect Morphology and Embryology*, **27**, 341–349.

ELZINGA, R. J. and HOPKINS, T. L. 1994. Foregut microspines in four families of cockroaches (Blattaria). *International Journal of Insect Morphology and Embryology*, **23**, 253–260.

ERIKSSON, B. J. and BUDD, G. E. 2000. Onychophoran cephalic nerves and their bearing on our understanding of head segmentation and stem-group evolution of Arthropoda. *Arthropod Structure & Development*, **29**, 197–209.

ERIKSSON, B. J., TAIT, N. N. and BUDD, G. E. 2003. Head development in the onychophoran *Euperipatoides kanangrensis* with particular reference to the central nervous system. *Journal of Morphology*, **255**, 1–23.

ERIKSSON, B. J., TAIT, N. N., BUDD, G. E. and AKAM, M. 2009. The involvement of *engrailed* and *wingless* during segmentation in the onychophoran *Euperipatoides kanangrensis* (Peripatopsidae: Onychophora) (Reid 1996). *Development Genes and Evolution*, **219**, 249–264.

———, ———, BUDD, G. E., JANSSEN, R. and AKAM, M. 2010. Head patterning and Hox gene expression in an onychophoran and its implications for the arthropod head problem. *Development Genes and Evolution*, **220**, 117–122.

GABRIEL, W. N. and GOLDSTEIN, B. 2007. Segmental expression of Pax3/7 and Engrailed homologs in tardigrade development. *Development Genes and Evolution*, **217**, 421–433.

GARCÍA-BELLIDO, D. C. and COLLINS, D. H. 2007. Reassessment of the genus *Leanchoilia* (Arthropoda, Arachnomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Palaeontology*, **50**, 693–709.

GARCÍA-BELLIDO, D. C., EDGECOMBE, G. D., PATERSON, J. R. and MA, X. 2013. A ‘Collins’ monster’-type lobopodian from the Emu Bay Shale Konservat-Lagerstätte (Cambrian), South Australia. *Alcheringa*, **37**, 474–478.

GAREY, J. R. 2001. Ecdysozoa: the relationship between Cycloneuralia and Panarthropoda. *Zoologischer Anzeiger*, **240**, 321–330.

GUIDETTI, R., ALTIERO, T., MARCHIORO, T., SARZI AMADÈ, L., AVDONINA, A. M., BERTOLANI, R. and REBECCHI, L. 2012. Form and function of the feeding apparatus in Eutardigrada (Tardigrada). *Zoomorphology*, **131**, 127–148.

HALBERG, K. A., PERSSON, D., MØBJERG, N., WANNINGER, A. and KRISTENSEN, R. M. 2009. Myoanatomy of the marine tardigrade *Halobiotus crispae* (Eutardigrada: Hypsibiidae). *Journal of Morphology*, **270**, 996–1013.

HAN, J., LIU, J., ZHANG, Z.-F., ZHANG, X.-L. and SHU, D. 2007. Trunk ornament on the palaeoscolecid worms *Cricocosmia* and *Tabelliscolex* from the Early Cambrian Chengjiang deposits of China. *Acta Palaeontologica Polonica*, **52**, 423–431.

HARVEY, T. H. P., ORTEGA-HERNÁNDEZ, J., LIN, J.-P., ZHAO, Y.-L. and BUTTERFIELD, N. J. 2012. Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China. *Acta Palaeontologica Polonica*, **57**, 423–436.

HARZSCH, S., WILDT, M., BATTELLE, B. and 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 Structure & Development*, **34**, 327–342.

HAUG, J. T., BRIGGS, D. E. and HAUG, C. 2012*a*. Morphology and function in the Cambrian Burgess Shale megacheiran arthropod *Leanchoilia superlata* and the application of a descriptive matrix. *BMC Evolutionary Biology*, **12**, 162.

HAUG, J. T., WALOSZEK, D., MAAS, A., LIU, Y. U. and HAUG, C. 2012*b*. Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology*, **55**, 369–399.

HAUG, J., MAYER, G., HAUG, C. and BRIGGS, D. E. G. 2012*c*. A Carboniferous non-onychophoran lobopodian reveals long-term survival of a Cambrian morphotype. *Current Biology*, **22**, 1673–1675.

HOU, X., BERGSTRÖM, J. and YANG, J. 2006. Distinguishing anomalocaridids from arthropods and priapulids. *Geological Journal*, **41**, 259–269.

HOU, X.-G. and BERGSTRÖM, J. 1995. Cambrian lobopodians–ancestors of extant onychophorans? *Zoological Journal of the Linnean Society*, **114**, 3–19.

———, MA, X.-Y., ZHAO, J. and BERGSTRÖM, J. 2004. The lobopodian *Paucipodia inermis* from the Lower Cambrian Chengjiang fauna, Yunnan, China. *Lethaia*, **37**, 235–244.

———, ALDRIDGE, R., BERGSTRÖM, J., SIVETER, D. J., SIVETER, D. J. and FENG, X.-H. 2003. *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. Wiley-Blackwell, 248 pp.

KIRSTEUER, E. 1976. Notes on adult morphology and larval development of *Tubiluchus corallicola* (Priapulida), based on in vivo and scanning electron microscopic examinations of specimens from Bermuda. *Zoologica Scripta*, **5**, 239–255.

LEGG, D. A., SUTTON, M. D. and EDGECOMBE, G. D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications*, **4**, 2485.

LIU, J. and DUNLOP, J. A. 2014. Cambrian lobopodians: a review of recent progress in our understanding of their morphology and evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **398**, 4–15.

LIU, J., SHU, D., HAN, J. and ZHANG, Z.-F. 2008*a*. Comparative study of Cambrian lobopods *Miraluolishania* and *Luolishania*. *Chinese Science Bulletin*, **53**, 87–93.

LIU, J., SHU, D., HAN, J., ZHANG, Z.-F. and ZHANG, X.-L. 2006. A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte. *Acta Palaeontologica Polonica*, **51**, 215–222.

———, ———, ———, ——— and ———. 2007. Morpho-anatomy of the lobopod *Magadictyon* [sic] cf. *haikouensis* from the Early Cambrian Chengjiang Lagerstätte, South China. *Acta Zoologica*, **88**, 279–288.

———, ———, ———, ——— and ———. 2008*b*. The lobopod *Onychodictyon* from the lower Cambrian Chengjiang Lagerstätte revisited. *Acta Palaeontologica Polonica*, **53**, 285–292.

———, STEINER, M., DUNLOP, J. A., KEUPP, H., SHU, D., OU, Q., HAN, J., ZHANG, Z.-F. and ZHANG, X.-L. 2011. An armoured Cambrian lobopodian from China with arthropod-like appendages. *Nature*, **470**, 526–530.

LIU, Y., MAAS, A. and WALOSZEK, D. 2009. Early development of the anterior body region of the grey widow spider *Latrodectus geometricus* Koch, 1841 (Theridiidae, Araneae). *Arthropod Structure & Development*, **38**, 401–416.

———, ——— and ———. 2010. Early embryonic development of the head region of *Gryllus assimilis* Fabricius, 1775 (Orthoptera, Insecta). *Arthropod Structure & Development*, **39**, 382–395.

MA, X., HOU, X. and BERGSTRÖM, J. 2009. Morphology of *Luolishania longicruris* (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic relationships within lobopodians. *Arthropod Structure & Development*, **38**, 271–291.

———, EDGECOMBE, G. D., LEGG, D. A. and HOU, X. 2014. The morphology and phylogenetic position of the Cambrian lobopodian *Diania cactiformis*. *Journal of Systematic Palaeontology*, **12**, 445–457.

———, HOU, X., ALDRIDGE, R. J., SIVETER, D. J., SIVETER, D. J., GABBOTT, S. E., PURNELL, M. a, PARKER, A. R. and EDGECOMBE, G. D. 2012*a*. Morphology of Cambrian lobopodian eyes from the Chengjiang Lagerstätte and their evolutionary significance. *Arthropod Structure & Development*, **41**, 495–504.

MA, X.-Y., HOU, X.-G., EDGECOMBE, G. D. and STRAUSFELD, N. J. 2012*b*. Complex brain and optic lobes in an early Cambrian arthropod. *Nature,* **490**, 258–261.

MAAS, A. and WALOSZEK, D. 2001. Cambrian derivatives of the early arthropod stem lineage, pentastomids, tardigrades and lobopodians – an ‘Orsten’ perspective. *Zoologischer Anzeiger*, **240**, 451–459.

MAAS, A., MAYER, G., KRISTENSEN, R. M. and WALOSZEK, D. 2007. A Cambrian micro-lobopodian and the evolution of arthropod locomotion and reproduction. *Chinese Science Bulletin*, **52**, 3385–3392.

MALLATT, J. and GIRIBET, G. 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Molecular Phylogenetics and Evolution*, **40**, 772–794.

MARCHIORO, T., REBECCHI, L., CESARI, M., HANSEN, J. G., VIOTTI, G. and GUIDETTI, R. 2013. Somatic musculature of Tardigrada: phylogenetic signal and metameric patterns. *Zoological Journal of the Linnean Society*, **169**, 580–603.

MARTIN, C. and MAYER, G. 2014. Neuronal tracing of oral nerves in a velvet worm—implications for the evolution of the ecdysozoan brain. *Frontiers in Neuroanatomy*, **8**, 7.

MAYER, G., MARTIN, C., RÜDIGER, J., KAUSCHKE, S., STEVENSON, P. A., POPRAWA, I., HOHBERG, K., SCHILL, R. O., PFLÜGER, H. and SCHLEGEL, M. 2013*a*. Selective neuronal staining in tardigrades and onychophorans provides insights into the evolution of segmental ganglia in panarthropods. *BMC Evolutionary Biology*, **13**, 230.

——— and 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 Structure & Development*, **34**, 471–480.

———, KAUSCHKE, S., RÜDIGER, J. and STEVENSON, P. A. 2013*b*. Neural markers reveal a one-segmented head in tardigrades (water bears). *PLoS ONE*, **8**, e59090.

———, WHITINGTON, P. P. M., SUNNUKS, P., PFLÜGER, H.-J. and SUNNUCKS, P. 2010. A revision of brain composition in Onychophora (velvet worms) suggests that the tritocerebrum evolved in arthropods. *BMC Evolutionary Biology*, **10**, 255.

MITTMANN, B. and 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. *Development Genes and Evolution*, **213**, 9–17.

NELSON, D. R. 2002. Current status of the Tardigrada: evolution and ecology. *Integrative and Comparative Biology*, **42**, 652–659.

ORTEGA-HERNÁNDEZ, J. and BRENA, C. 2012. Ancestral patterning of tergite formation in a centipede suggests derived mode of trunk segmentation in trilobites. *PLoS ONE*, **7**, e52623.

ORTEGA-HERNÁNDEZ, J., LEGG, D. and BRADDY, S. 2013. The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics*, **29**, 15–45.

OU, Q., SHU, D. and MAYER, G. 2012. Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. *Nature Communications*, **3**, 1261.

———, LIU, J., SHU, D., HAN, J., ZHANG, Z.-F., WAN, X. and LEI, Q. 2011. A rare onychophoran-like lobopodian from the lower Cambrian Chengjiang Lagerstätte, southwestern China, and its phylogenetic implications. *Journal of Paleontology*, **85**, 587–594.

PERSSON, D. K., HALBERG, K. A., JØRGENSEN, A., MØBJERG, N. and KRISTENSEN, R. M. 2012. Neuroanatomy of *Halobiotus crispae* (Eutardigrada: Hypsibiidae): Tardigrade brain structure supports the clade Panarthropoda. *Journal of Morphology*, **273**, 1227–1245.

———, HALBERG, K. A., JØRGENSEN, A., MØBJERG, N. and KRISTENSEN, R. M. 2014. Brain anatomy of the marine tardigrade *Actinarctus doryphorus* (Arthrotardigrada). *Journal of Morphology*, **275**, 173–190.

PILATO, G. 1972. Structure, intraspecific variability and systematic value of the buccal armature of eutardigrades. *Zeitschrift fur Zoologische Systematik und Evolutionsforschung*, **10**, 65–78.

POSNIEN, N., BASHASAB, F. and BUCHER, G. 2009. The insect upper lip (labrum) is a nonsegmental appendage-like structure. *Evolution & Development*, **11**, 480–488.

RAMSKÖLD, L. 1992. The second leg row of *Hallucigenia* discovered. *Lethaia*, **25**, 221–224.

——— and CHEN, J.-Y. 1998. Cambrian lobopodians: morphology and phylogeny. *In* EDGECOMBE, G. D. (ed.) *Arthropod Fossils and Phylogeny*, Columbia University Press, New York, 107–150.

RAUP, D. M. 1966. Geometric analysis of shell coiling; general problems. *Journal of Paleontology*, **40**, 1178–1190.

ROTHE, B. H. and SCHMIDT-RHAESA, A. 2010. Structure of the nervous system in *Tubiluchus troglodytes* (Priapulida). *Invertebrate Biology,* **129**, 39–58.

SCHOENEMANN, B., LIU, J., SHU, D., HAN, J. and ZHANG, Z.-F. 2009. A miniscule optimized visual system in the Lower Cambrian. *Lethaia*, **42**, 265–273.

SCHOLTZ, G. and EDGECOMBE, G. . D. 2005. Heads, Hox and the phylogenetic position of trilobites. *In* KOENEMANN, S. and JENNER, R. A. (eds.) *Crustacean Issues 16: Crustacea and Arthropod Relationships*, CRC Press, Boca Raton, FL, 139–165.

SCHOLTZ, G. and EDGECOMBE, G. D. 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Development Genes and Evolution*, **216**, 395–415.

SCHULZE, C., NEVES, R. C. and SCHMIDT-RHAESA, A. 2014. Comparative immunohistochemical investigation on the nervous system of two species of *Arthrotardigrada* (Heterotardigrada, Tardigrada). *Zoologischer Anzeiger*, **253**, 225–235.

SCHUSTER, R., NELSON, D., GRIGARICK, A. A. and CHRISTENBERRY, D. 1980. Systematic criteria of the Eutardigrada. *Transactions of the American Microscopical Society,* **99**, 284–303.

SMITH, M. R. and ORTEGA-HERNÁNDEZ, J. 2014. *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. *Nature,* **514**, 363–366.

———, HARVEY, T. H. P. and BUTTERFIELD, N. J. 2015. The macro- and microfossil record of the Cambrian priapulid *Ottoia*. *Palaeontology,* advanced online publication. doi: 10.1111/pala.12168

STEINER, M., HU, S.-X., LIU, J. and 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. *Bulletin of Geosciences,* **87**, 107–124.

STORCH, V. 1991. Priapulida. *In* HARRISON, F. W. and RUPERT, E. E. (eds.) *Microscopic Anatomy of Invertebrates Volume 4*, Wiley-Liss, Inc., New York, 333–350 pp.

TANAKA, G., HOU, X., MA, X., EDGECOMBE, G. D. and STRAUSFELD, N. J. 2013. Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature,* **502**, 364–367.

TELFORD, M. J., BOURLAT, S. J., ECONOMOU, A., PAPILLON, D. and ROTA-STABELLI, O. 2008. The evolution of the Ecdysozoa. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* **363**, 1529–1537.

THOMPSON, I. and JONES, D. 1980. A possible onychophoran from the Middle Pennsylvanian Mazon Creek beds of northern Illinois. *Journal of Paleontology*, **54**, 588–596.

TOPPER, T. P., SKOVSTED, C. B., PEEL, J. S. and HARPER, D. A. T. 2013. Moulting in the lobopodian *Onychodictyon* from the lower Cambrian of Greenland. *Lethaia*, **46**, 490–495.

VAN DER LAND, J. 1970. Systematics, zoogeography, and ecology of the Priapulida. *Zoologische Verhandelingen*, **112**, 1–118.

VAN ROY, P., DALEY, A. C. and BRIGGS, D. E. G. 2015. Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature*, **522**, 77–80.

VANNIER, J., LIU, J., LEROSEY-AUBRIL, R., VINTHER, J. and DALEY, A. C. 2014. Sophisticated digestive systems in early arthropods. *Nature Communications*, **5**, 3641.

WALOSZEK, D., CHEN, J.-Y., MAAS, A. and WANG, X. 2005. Early Cambrian arthropods—new insights into arthropod head and structural evolution. *Arthropod Structure & Development*, **34**, 189–205.

WHITTINGTON, H. B. 1975. The enigmatic animal *Opabinia regalis*, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **271**, 1–43.

WHITTINGTON, H. B. 1978. The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **284**, 165–197.

WHITTINGTON, H. B. 1993. Anatomy of the Ordovician trilobite *Placoparia*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **339**, 109–118.

YANG, J., ORTEGA-HERNÁNDEZ, J., BUTTERFIELD, N. J. and ZHANG, X.-G. 2013. Specialized appendages in fuxianhuiids and the head organization of early euarthropods. *Nature*, **494**, 468–471.

ZHANG, X.-G. and ALDRIDGE, R. J. 2007. Development and diversification of trunk plates of the lower Cambrian lobopodians. *Palaeontology*, **50**, 401–415.

ZHANG, X.-L. and BRIGGS, D. E. G. 2007. The nature and significance of the appendages of *Opabinia* from the Middle Cambrian Burgess Shale. *Lethaia*, **40**, 161–173.