

Making sense of ‘lower’ and ‘upper’ stem-group Euarthropoda, with comments on the strict use of the name Arthropoda von Siebold, 1848

Javier Ortega-Hernández*

Department of Earth Sciences, University of Cambridge, Downing Site, Cambridge, CB2 3EQ, U.K.

ABSTRACT

The ever-increasing number of studies that address the origin and evolution of Euarthropoda – whose extant representatives include chelicerates, myriapods, crustaceans and hexapods – are gradually reaching a consensus with regard to the overall phylogenetic relationships of some of the earliest representatives of this phylum. The stem-lineage of Euarthropoda includes numerous forms that reflect the major morphological transition from a lobopodian-type to a completely arthropodized body organization. Several methods of classification that aim to reflect such a complex evolutionary history have been proposed as a consequence of this taxonomic diversity. Unfortunately, this has also led to a saturation of nomenclatural schemes, often in conflict with each other, some of which are incompatible with cladistic-based methodologies. Here, I review the convoluted terminology associated with the classification of stem-group Euarthropoda, and propose a synapomorphy-based distinction that allows ‘lower stem-Euarthropoda’ (e.g. lobopodians, radiodontans) to be separated from ‘upper stem-Euarthropoda’ (e.g. fuxianhuiids, Cambrian bivalved forms) in terms of the structural organization of the head region and other aspects of overall body architecture. The step-wise acquisition of morphological features associated with the origins of the crown-group indicate that the node defining upper stem-Euarthropoda is phylogenetically stable, and supported by numerous synapomorphic characters; these include the presence of a deutocerebral first appendage pair, multisegmented head region with one or more pairs of post-ocular differentiated limbs, complete body arthropodization, posterior-facing mouth associated with the hypostome/labrum complex, and post-oral biramous arthropodized appendages. The name ‘Deuteropoda’ nov. is proposed for the scion (monophyletic group including the crown-group and an extension of the stem-group) that comprises upper stem-Euarthropoda and Euarthropoda. A brief account of common terminological inaccuracies in recent palaeontological studies evinces the utility of Deuteropoda nov. as a reference point for discussing aspects of early euarthropod phylogeny.

Key words: Euarthropoda, Panarthropoda, Tardigrada, Onychophora, Deuteropoda nov., phylogeny, crown-group, lobopodian, arthropodization, Aiolopoda.

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* Address for correspondence (Tel: +44 (0) 1223 333416; E-mail: jo314@cam.ac.uk).

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I. INTRODUCTION

The application of stem- and crown-group concepts (Jefferies, 1979; see also Budd & Jensen, 2000) has led to an improved understanding of the evolutionary links between extinct and extant organisms, particularly with the widespread usage of parsimony-based cladistic methods for exploring phylogenetic relationships. Euarthropoda Lankester, 1904 (see Table 1) – the monophyletic group including Chelicerata (pycnogonids, xiphosurans, arachnids) and Mandibulata (myriapods, crustaceans and hexapods) – represents a classical example of the utility of this nomenclatural convention. Numerous studies produced in the last two decades indicate that total-group Euarthropoda is typified by a long and diverse stem-lineage that includes forms characterized by a lobopodian-like construction (i.e. lobopodians, gilled-lobopodians; Fig. 1A, B), partially arthropodized limb sets (i.e. radiodontans; Fig. 1C), and even fully arthropodized bodies (e.g. fuxianhuids, Cambrian bivalved euarthropods; Fig. 1D, E). Given that stem-Euarthropoda encompasses disparate types of body organization, a further categorization of these representatives is desirable for practical reasons, such as discussing the phylogenetic position of specific taxa relative to each other, and describing the sequential acquisition of major synapomorphies leading to evolutionary origins of the crown-group (e.g. Budd, 2002; Daley *et al.*, 2009; Kühl, Briggs & Rust, 2009; Liu *et al.*, 2011; Legg, Sutton & Edgecombe, 2013; Ma *et al.*, 2014; Smith & Ortega-Hernández, 2014). However, a formal sub-categorization of stem-Euarthropoda is lacking, likely due to the scarcity of clearly monophyletic clades within this stem-lineage and the unstable phylogenetic position of some of its constituent fossil taxa.

Budd (2002, 2008) is so far the only author that has suggested a potential categorization by introducing the concept of ‘upper stem-group Euarthropoda’; references to this term have been used by subsequent workers, which suggest that the utility of such a distinction is welcomed (e.g. Budd & Telford, 2009; Daley *et al.*, 2009; Edgecombe, 2009; Legg *et al.*, 2013). However, there is no clear definition of upper stem-Euarthropoda or its applicability, and thus it has been largely utilized as a non-descript term that embodies a superficial notion of body organization present in some Palaeozoic representatives. The aim of this contribution is to produce a formal distinction between ‘lower’

and ‘upper’ stem-Euarthropoda based on the results of recent phylogenetic analyses, and propose a clear synapomorphy-based definition that can be applied when discussing aspects of early euarthropod evolution. The suggested categorization is then compared to alternative models that seek to distinguish between different evolutionary stages and taxonomic levels in this phylum. The appropriate usage of systematic and phylogenetic nomenclature is addressed in light of these discussions in order to rectify recent terminological inaccuracies, and also to promote its correct application in future contributions.

II. ARTHROPODA, EUARTHROPODA, OR PANARTHROPODA? A NOTE ON NOMENCLATURE

The literature addressing the classification, morphology and evolution of Euarthropoda is rich and often convoluted, mainly as a result of its lengthy history and continuous growth. Given that using precise nomenclature is fundamental for an efficient communication, it is necessary to elucidate the origins and applicability of the more recurrent terminology. As a pre-emptive convention for clarity, Euarthropoda *sensu* Lankester (1904) is used throughout the discussion instead of its senior synonym, Condylropodes Bronn 1850 (see Table 1), given that the former term carries a greater familiarity in the recent literature (see also Hegna *et al.*, 2013).

The precise use of the name ‘Arthropoda’ – as well as the taxonomic scope it encompasses – have been the source of much nomenclatural confusion (Table 1). In a recent revision on the term’s authorship, Hegna *et al.* (2013, p. 72) drew attention to the original diagnosis of Arthropoda von Siebold, 1848; in addition to bilateral symmetry and jointed limbs, Arthropoda is characterized by the possession of a ring of ganglia around the oesophagus, followed by a chain-like (ganglionated) nerve cord. Based on this diagnosis, von Siebold (1848) utilized Arthropoda for a group comprising Crustacea (considered also to include Myriapoda), Hexapoda (listed as ‘classis Insecta’) and Chelicerata (listed as ‘classis Arachnida’). Significantly, von Siebold (1848, p. 586) classified Tardigrada (water bears) as a suborder under his ‘classis Arachnida’, and assigned the former group the same taxonomic rank as Pycnogonida (sea spiders). This context makes

Table 1. Different uses of the names ‘Arthropoda’, ‘Euarthropoda’ and ‘Panarthropoda’

Original name	Constituent groups	Junior synonyms/subsequent usage
Arthropoda von Siebold, 1848	Euarthropoda Lankester, 1904 + Tardigrada Spallanzani, 1777	Arthropodoidea de Haro, 1999 Tactopoda Budd, 2001 ^{a,b} Tritocerebra Grimaldi & Engel, 2005 Tactopoda <i>cf.</i> Mayer <i>et al.</i> (2013a)
§Arthropoda <i>cf.</i> Lankester (1904)	Euarthropoda Lankester, 1904 + Onychophora Grube, 1853	Arthropoda <i>cf.</i> Ax (1984, 1987) Arthropoda <i>cf.</i> Weygoldt (1986) Arthropoda <i>cf.</i> Schmidt-Rhaesa <i>et al.</i> (1998) Antennopoda de Haro, 1998 Arthropoda <i>cf.</i> Edgecombe (2010)
Gnathopoda Lankester, 1877	Euarthropoda Lankester, 1904 + Onychophora Grube, 1853 + Tardigrada Spallanzani, 1777	§Arthropoda <i>cf.</i> Lankester (1904) Lobopoda Boudreaux, 1979 Panarthropoda Nielsen (1995) Podophora Waggoner, 1996 Panarthropoda <i>cf.</i> Schmidt-Rhaesa <i>et al.</i> (1998) Lobopoda de Haro, 1998 Arthropoda <i>cf.</i> Budd (2001 ^b) Arthropoda <i>sensu lato</i> Maas & Waloszek, 2001 Panarthropoda <i>cf.</i> Grimaldi & Engel (2005) Aiolopoda Hou & Bergström, 2006 Panarthropoda <i>cf.</i> Dunn <i>et al.</i> (2008) Panarthropoda <i>cf.</i> Budd & Telford (2009) Panarthropoda <i>cf.</i> Edgecombe (2010) Panarthropoda <i>cf.</i> Campbell <i>et al.</i> (2011) Arthropoda <i>cf.</i> Rota-Stabelli <i>et al.</i> (2011) Panarthropoda <i>cf.</i> Rota-Stabelli <i>et al.</i> (2011) Panarthropoda <i>cf.</i> Mayer <i>et al.</i> (2013a)
Condylopoes Bronn, 1850	Chelicerata Heymons, 1901 + Mandibulata Snodgrass, 1935	Euarthropoda Lankester, 1904 Arthropoda <i>cf.</i> Boudreaux (1979) Euarthropoda <i>cf.</i> Ax (1984, 1987) Euarthropoda <i>cf.</i> Weygoldt (1986) Arthropoda <i>cf.</i> Nielsen (1995) Euarthropoda <i>cf.</i> Waggoner (1996) Arthropoda de Haro, 1999 Euarthropoda <i>cf.</i> Schmidt-Rhaesa <i>et al.</i> (1998) Euarthropoda <i>cf.</i> Budd (2001 ^b) Euarthropoda <i>cf.</i> Maas & Waloszek (2001) Arthropoda <i>cf.</i> Grimaldi & Engel (2005) Arthropoda <i>cf.</i> Hou & Bergström (2006) Arthropoda <i>cf.</i> Dunn <i>et al.</i> (2008) Euarthropoda <i>cf.</i> Budd & Telford (2009) Euarthropoda <i>cf.</i> Edgecombe (2010) Arthropoda <i>cf.</i> Rota-Stabelli <i>et al.</i> (2011) Euarthropoda <i>cf.</i> Rota-Stabelli <i>et al.</i> (2011) Arthropoda <i>cf.</i> Campbell <i>et al.</i> (2011) Arthropoda <i>cf.</i> Mayer <i>et al.</i> (2013a)

This summary is not exhaustive, as its aim is to convey the extent of the historically burdened use of conflicting nomenclature in the literature. Bold lettering in the right-hand column highlights common uses in recent literature. *cf.* denotes the secondary usage of nomenclature in the literature by third authors, regardless of original terminology (left column) or taxonomic scope (middle column) of the names. §, note that these alternative uses of ‘Arthropoda’ result from different interpretations of the systematic classification used by Lankester (1904). See text for details.

it clear that the original definition of Arthropoda (*sensu* von Siebold, 1848) includes the taxa that are now equivalent to Euarthropoda (*sensu* Lankester, 1904) and Tardigrada, even if their precise phylogenetic positions differ from those originally suggested. von Siebold’s (1848) broad classification is congruent with his proposed diagnosis and thus valid from a strictly apomorphy-based perspective, as Tardigrada

and Euarthropoda share various neurological characters, most notably the presence of condensed ganglia on the ventral nerve cord (e.g. Mayer & Whittington, 2009; Mayer *et al.*, 2013^{a,b}) (see Table 3). This insight is relevant for understanding the strict application of the name Arthropoda, as its original meaning has been practically abandoned in recent times; rather, Arthropoda is now widely – but imprecisely – used as



Fig. 1. Diversity of Palaeozoic lobopodians and stem-group Euarthropoda. (A) The lobopodian *Aysheia pedunculata* Walcott, 1911a, from the middle Cambrian Burgess Shale (USNM 365608, Smithsonian Institution Washington D.C.). (B) The gilled-lobopodian *Kerygmachela kierkegaardi* Budd, 1993, from the early Cambrian Sirius Passet (photograph courtesy of M. Stein). (C) The radiodontan *Anomalocaris canadensis* Whiteaves, 1892, from the Burgess Shale (ROM 51212, Royal Ontario Museum; photograph courtesy of J. B. Caron, ROM). (D) The fuxianhuiid *Fuxianhuia xiaoshibaensis* Yang *et al.*, 2013, from the lower Cambrian Xiaoshiba biota (YKLP 12031, Key Laboratory for Palaeobiology, Yunnan University; photograph courtesy of J. Yang, Yunnan University). (E) The bivalved stem-euarthropod *Lovicaris spinocaudatus* Legg & Caron, 2014, from the Burgess Shale (ROM 62145; photograph courtesy of D. A. Legg, University of Oxford). (F) The megacheiran *Leanchoilia superlata* Walcott, 1912, from the Burgess Shale (ROM 54215; photograph courtesy of J. B. Caron, ROM). Scale bars: A, B, D–F = 5 mm; C = 10 mm.

an interchangeable term with Euarthropoda (*sensu* Lankester, 1904) (Table 1). Additionally, various junior synonyms for Arthropoda (*sensu* von Siebold, 1848) have been proposed despite the clarity of its original diagnosis. Tactopoda Budd, 2001a, (p. 277) is arguably the most ubiquitous, and indeed this term has featured in recent neurological and palaeontological studies that support the close relationship between Tardigrada and Euarthropoda (Mayer *et al.*, 2013b; Smith & Ortega-Hernández, 2014). Other junior synonyms include Arthropeidea De Haro, 1999, and Tritocerebra Grimaldi & Engel, 2005, but none has received a wide application.

Subsequent uses of Arthropoda (*sensu* von Siebold, 1848) became somewhat distorted during the early 20th century as a result of the continuous growth of higher classification systems, further accentuated by the uncertain placement of Tardigrada. Gnathopoda Lankester, 1877, represents the earliest term used to encompass multiple groups associated with Arthropoda at the phylum level (Table 1); in its original iteration, Gnathopoda included Onychophora ('classis Peripatoidea'), Crustacea ('classis Crustacea'), Hexapoda ('classis Insecta Hexapoda'), Myriapoda ('classis Insecta Myriapoda') and Chelicerata ('classis Arachnida'). Similarly to von Siebold (1848), however, Lankester (1877) also classified Tardigrada as a subgroup within

'Arachnida'; therefore, Gnathopoda (*sensu* Lankester, 1877) is the first term actually to encompass Onychophora, Tardigrada and Euarthropoda within a single taxonomic unit. In his later work, Lankester (1904, p. 524) claimed that his Gnathopoda had a similar applicability to Arthropoda (*sensu* von Siebold, 1848); even writing '... *Arthropoda* might be better called the "*Gnathopoda*", since their distinctive character is that one or more pairs of appendages behind the mouth are densely chitinised and turned towards one another so as to act as jaws' (Lankester, 1904, p. 526). Lankester (1904, p. 527) also emphasized the presence of a dorsal blood vessel (heart) with ostiae in extant representatives of his interpretation of Arthropoda, which is a widely recognized morphological feature shared between Euarthropoda and Onychophora (e.g. Weygoldt, 1986, p. 28–29; see also Edgecombe, 2010, p. 75). Interestingly, Lankester (1904, p. 527) mentioned that the only exception to these observations is found among '... *minute degenerate forms where the heart has disappeared altogether*', referring specifically to Tardigrada and Pentastomida (tongue worms; actually parasitic crustaceans), which were assigned an *incertae sedis* status within his classification of Arthropoda (p. 530). Lankester's (1904, p. 529) treatment of Tardigrada, Onychophora and Euarthropoda within Arthropoda (*sensu* von Siebold, 1848) is problematic, as the original diagnosis of the former term is clearly exclusive to Tardigrada and Euarthropoda (see above).

With the removal of Tardigrada from Arachnida (*cf.* von Siebold, 1848; Lankester, 1877), and to an uncertain position relative to Euarthropoda and Onychophora (e.g. Lankester, 1904; Weygoldt, 1986), the use of the term Arthropoda acquired two different meanings during the late 20th century (Table 1). The first one is Arthropoda as the group including Euarthropoda and Onychophora (e.g. Ax, 1984, 1987; Weygoldt, 1986; Schmidt-Rhaesa *et al.*, 1998; Mayer, 2006; see also Edgecombe, 2010, p. 75), which most likely follows Lankester's (1904, p. 529) systematic classification emphasizing the morphological characters uniting these organisms (see Table 2). A second interpretation regards Arthropoda as a more inclusive term encompassing Euarthropoda, Onychophora and Tardigrada (e.g. Budd, 2001*b*, table 1; Maas & Waloszek, 2001, fig. 4; Rota-Stabelli *et al.*, 2011, p. 298, 299, 304, 305), and thus synonymous with Lankester's (1877) Gnathopoda; this usage likely originated from Lankester's (1904, p. 527) recognition of a general, but unresolved, affinity between Tardigrada and Euarthropoda and/or Onychophora.

This terminology became even more convoluted by the introduction of the term Panarthropoda Nielsen (1995, p. 149): '*Arthropoda, Onychophora and Tardigrada are often regarded as closely related, and the two latter phyla have sometimes been united in a group called Proarthropoda; this is not in accordance with the conclusions reached below.*

There seems to be no generally accepted collective name for the three phyla; Weygoldt (1986) and Ax (1987) used Arthropoda in a wide sense comprising Onychophora and Euarthropoda, but I have chosen to introduce the term Panarthropoda to maintain the accustomed sense of the term Arthropoda. From the present understanding of the name's history, it is clear that Nielsen's (1995) treatment of Arthropoda does not actually convey its 'traditional' or 'accustomed' usage in the strict sense (i.e. *sensu* von Siebold, 1848). Instead, Nielsen's intent was to recapture the widespread, but erroneous, use of Arthropoda as understood from most English-language sources (see Edgecombe, 2010, p. 75), which is as a synonym to Euarthropoda (*sensu* Lankester, 1904) (Table 1). Panarthropoda has since become deeply engraved in the literature, particularly among neontologists (e.g. Schmidt-Rhaesa *et al.*, 1998; Dunn *et al.*, 2008; Budd & Telford, 2009; Campbell *et al.*, 2011; Mayer *et al.*, 2013*b*). To complicate things even further, a number of additional junior synonyms referring to the same group (i.e. Euarthropoda, Tardigrada, Onychophora) have been put forward, most notably Arthropoda *sensu lato* (see Maas *et al.*, 2004; Waloszek *et al.*, 2005, 2007), and Aiolopoda (Hou & Bergström, 2006) (see Table 1). Aiolopoda was introduced in an attempt to alleviate the over-abundance of conflicting nomenclatural schemes, with the goal that this term would allow the use of Arthropoda '*in its traditional sense, i.e., excluding onychophorans...*' (Bergström *et al.*, 2008, p. 190; see also Legg & Vannier, 2013), strongly implying the restriction of this name to encompass Chelicerata and Mandibulata (i.e. Euarthropoda *sensu* Lankester, 1904). Unfortunately this assertion is erroneous, as the strictly traditional use of Arthropoda (*sensu* von Siebold, 1848) clearly incorporates Euarthropoda and Tardigrada, to the exclusion of Onychophora. The use of Arthropoda *sensu lato* (*cf.* Maas *et al.*, 2004; Waloszek *et al.*, 2005, 2007), and that of its derivative Arthropoda *sensu stricto*, is addressed in Section V.

(1) The status of 'Lobopodia Snodgrass, 1938'

The current understanding of the phylogenetic relationships between Euarthropoda, Tardigrada and Onychophora primarily supports an association between the former group with either of the latter clades (Table 3; but see Rota-Stabelli *et al.*, 2011). Some workers have suggested a sister-group relationship between Onychophora and Tardigrada, and the discussions on the affinities of these taxa have extended to include Palaeozoic lobopodians, a suite of soft-bodied extinct organisms resembling worms with legs; however, this has also led to the formulation of new clades leading to further confusion and inconsistent use (Table 2). Numerous studies have utilized 'Lobopodia Snodgrass, 1938' (alternatively spelled as 'Lobopoda'), as a vaguely defined higher taxonomic unit when addressing the systematics of Palaeozoic lobopodians (e.g. Dzik & Krumbiegel, 1989; Budd, 1993, 1997; Hou & Bergström,

Table 2. Different applications of the names ‘Lobopodia’ and ‘Protarthropoda’

Taxonomic unit	Constituent groups	Notes on taxonomic usage
Protarthropoda Lankester, 1904	Onychophora Grube, 1853	Lankester's (1904) classification subcategorizes Arthropoda into Protarthropoda (= Onychophora) and Euarthropoda (= Chelicerata + Mandibulata).
'Lobopodia/Lobopoda' Snodgrass, 1938	†Protonychophora Hutchinson, 1930 + †Protarthropoda <i>cf.</i> Snodgrass, 1938	Snodgrass (1938) used 'lobopod' only in reference to a type of limb construction distinguishing ancestors of onychophorans (†Protonychophora) and euarthropods (†Protarthropoda) from annelids. Although Snodgrass (1938) did not discuss the limb structure of Tardigrada, most subsequent uses of 'Lobopodia' also include this group.
'Lobopodia' <i>cf.</i> Dzik & Krumbiegel, 1989	†Xenusia Dzik & Krumbiegel, 1989 + Onychophora Grube, 1853 + Tardigrada Spallanzani, 1777	†Xenusia Dzik & Krumbiegel, 1989, refers to a clade including all Palaeozoic lobopodians. Dzik & Krumbiegel (1989, p. 178) included Tardigrada into 'Lobopodia' based on comparisons with some 'xenusians' (e.g. <i>Aysheaia</i>).
'Lobopodia' <i>cf.</i> Hou & Bergström, 1995 = Protarthropoda Lankester, 1904	†Xenusia Dzik & Krumbiegel, 1989 + Onychophora Grube, 1853	Hou & Bergström (1995) considered these names as taxonomically equivalent. Dzik & Krumbiegel (1989) group †Xenusia and Tardigrada under 'Lobopodia'; however, the position of tardigrades in Hou & Bergström's (1995) classification is not addressed.
Protarthropoda <i>cf.</i> Wägele <i>et al.</i> , 1999	Onychophora Grube, 1853 + Tardigrada Spallanzani, 1777	Protarthropoda has been occasionally used in reference to Onychophora + Tardigrada in some phylogenetic studies (Nielsen, 1995; Waggoner, 1996; Wägele <i>et al.</i> , 1999).
'Lobopodia' <i>cf.</i> Waggoner, 1996	Polylobopoda Waggoner, 1996 + Tardigrada Spallanzani, 1777	Polylobopoda Waggoner, 1996, includes †Xenusia Dzik & Krumbiegel, 1989, and Onychophora Grube, 1853). Waggoner (1996) uses 'Lobopodia' in a similar way to Dzik & Krumbiegel (1989). Poinar (2000) followed a similar classification, but did not employ Polylobopoda as a systematic unit.
'Lobopodia' <i>cf.</i> Budd & Peel, 1998	†Xenusia Dzik & Krumbiegel, 1989 + Onychophora Grube, 1853 + Tardigrada Spallanzani, 1777 + Euarthropoda Lankester, 1904	'Lobopodia' (<i>cf.</i> Budd & Peel, 1998) represents the closest derivation of the name relative to the original discussion by Snodgrass (1938) in terms of constituent taxa, including also extinct forms. Boudreaux (1979) and de Haro (1999) have used 'Lobopodia Snodgrass, 1938' in reference to a similarly inclusive group, essentially equivalent to Panarthropoda Nielsen, 1995 (see Table 1).

cf. indicates subsequent usage of nomenclature. † denotes extinct clades. See text for details.

1995; Waggoner, 1996; Budd & Peel, 1998; Liu *et al.*, 2006, 2007, 2008, 2011; Zhang & Aldridge, 2007; Zhang & Briggs, 2007; Ma, Hou & Bergström, 2009; Dzik, 2011); however, the origins of the term 'Lobopodia' differ significantly from such applications. Snodgrass

(1938, p. 134) never formulated 'Lobopodia' as a taxonomic unit, but instead used the term 'lobopod' for describing the appendage construction of hypothetical ancestors of Onychophora (Protonychophora Hutchinson, 1930) and Arthropoda (Protarthropoda; but see

comments below on Protarthropoda Lankester, 1904) (see also Whittington, 1978, p. 166; Steiner *et al.*, 2012, p. 110). Furthermore, Snodgrass (1938) discussed these taxa strictly in the context of the Articulata hypothesis, and considered that the presence of lobopod-type limbs distinguished the ancestral Onychophora and Arthropoda from ‘chaetae-bearing forms’ that gave rise to Chaetopoda (i.e. Annelida). Although it is clear that Snodgrass (1938) only made a distinction in terms of perceived functional morphology, subsequent authors have used ‘Lobopodia’ to refer to a monophyletic clade including aquatic Palaeozoic lobopodians (i.e. class Xenusia Dzik & Krumbiegel, 1989), and terrestrial extant onychophorans (i.e. class Onychophora Grube, 1853) (see also Hou & Bergström, 1995, pp. 12–18). To complicate things even further, there are significant inconsistencies over the constituent groups in ‘Lobopodia’ and its equivalence with previous terminology (Table 2). Dzik & Krumbiegel (1989, p. 181) considered that ‘Lobopodia Snodgrass, 1938’, should encompass Tardigrada in addition to Onychophora and Palaeozoic lobopodians; such a clade, however, has received extremely limited support from phylogenetic analyses (Waggoner, 1996; see also Wägele *et al.*, 1999), as it is currently accepted that lobopodians are paraphyletic relative to the three extant phyla (e.g. Liu *et al.*, 2007, 2011; Ma *et al.*, 2009, 2014; Smith & Ortega-Hernández, 2014). Hou & Bergström (1995, p. 12) considered ‘Lobopodia Snodgrass, 1938’, as taxonomically equivalent to Protarthropoda Lankester, 1904, and favoured the use of the former term due to its semantic familiarity with the groups it is supposedly meant to encompass (i.e. Palaeozoic lobopodians). However, this comparison is inadequate since Lankester (1904, p. 529) specifically formulated his Protarthropoda as a higher level of classification for Onychophora (Grade B. Protarthropoda; Class Onychophora), which together with Euarthropoda (Grade C. Euarthropoda; Classes Diplopoda, Arachnida, Crustacea and Chilopoda) constitute his rendition of Arthropoda (Tables 1 and 2). As a final example, Budd & Peel (1998, p. 1203) suggested that ‘Lobopodia Snodgrass, 1938’, should be considered to include all Palaeozoic lobopodians, Onychophora, Tardigrada and Euarthropoda, effectively synonymizing ‘Lobopodia’ with total-group Panarthropoda (*sensu* Nielsen, 1995) (see Tables 1 and 2).

Ultimately, the validity of any taxonomic unit should be judged on its informative potential and representation of a natural phylogeny. Given the substantial evidence that ‘Lobopodia Snodgrass, 1938’, as well as Xenusia Dzik & Krumbiegel, 1989, embody paraphyletic groupings as understood from the phylogenetic position of Palaeozoic lobopodians relative to onychophorans, tardigrades and euarthropods, it is suggested that their use as formal taxonomic units

should be abandoned. Instead, the higher affiliation of lobopodians and other closely related forms should be made with reference to the crown-groups whenever possible, and given the availability of supporting phylogenetic data (e.g. radiodontans as stem-Euarthropoda, see Daley *et al.*, 2009, p. 1597; hallucigeniids as stem-Onychophora, see Smith & Ortega-Hernández, 2014).

(2) Suggested taxonomic consensus

From this overview it is clear that there is no straightforward criterion for deciding which term is the most appropriate to refer collectively to, or to specific sub-groupings of, Euarthropoda, Onychophora and Tardigrada. With the improved understanding of the evolutionary relationships among these groups, the lay use of the term ‘arthropod’ has become ill defined, and is now no more informative about the precise phylogenetic affinities of its constituent taxa than ‘fish’ or ‘reptile’ in the field of vertebrate systematics. Given that the International Code for Zoological Nomenclature (ICZN) is inapplicable for taxonomic ranks above the family level, the principle of priority is inconsequential for resolving the most accurate utilization of any of the names discussed in this section. An alternative purist approach that relies exclusively on apomorphy-based terminology to convey a sense of phylogenetic affiliation through the name alone is also problematic (e.g. Liu *et al.*, 2011; Legg & Vannier, 2013; Legg *et al.*, 2013; see comments in Section VI), as it would require the continuous renaming of clades in order to satisfy such an inevitably narrow definition with every new discovery deviating from the *status quo*. Additionally, none of the original names that address the relationships between Euarthropoda (*sensu* Lankester, 1904) with Onychophora and Tardigrada have been widely utilized in the last decades, nor are they familiarly associated with their actual constituent taxa (Table 1). For the sake of clarity and in order to reach a unified nomenclatural convention, it is suggested that the terminology describing the possible associations between Euarthropoda, Onychophora and Tardigrada follows their most widespread current application as summarized in Table 3. A consistent application of this proposed nomenclature should help to dissipate the confusion that has accumulated since von Siebold (1848) first coined Arthropoda.

III. DIVERSITY IN STEM-GROUP EUARTHROPODA

It is widely acknowledged that Palaeozoic lobopodians include stem-group representatives of Onychophora, Tardigrada and Euarthropoda (e.g. Whittington, 1978; Budd, 1993, 1996, 2001*a*; Hou & Bergström, 1995;

Table 3. Suggested consensus for taxonomic nomenclature. Ω , note that these groups represent conflicting phylogenetic hypotheses, and thus only one of them is valid. The sister-group relationship between Onychophora and Tardigrada (e.g. Protarthropoda *cf.* Wägele *et al.*, 1999; see Table 2) is not depicted given the lack of recent molecular and/or morphological data supporting such an association

Higher groups	Constituent crown-groups	Synapomorphies in extant representatives
Ecdysozoa Aguinaldo <i>et al.</i> , 1997	Panarthropoda + Cycloneuralia	Growth through ecdysis Chitinous and trilaminar cuticle Terminal mouth with radial organization
Panarthropoda Nielsen, 1995	Euarthropoda + Onychophora + Tardigrada	Metameric organization Paired ambulatory appendages Condensed dorsal brain Terminal sclerotized claws on limbs Segmental leg musculature
Ω Tactopoda Budd, 2001a	Euarthropoda + Tardigrada	Stomatogastric 'tritocerebral' ganglion Ventral nerve ganglia Parasegmentally organized nerve cord Metameric longitudinal musculature
Ω Arthropoda <i>cf.</i> Lankester, 1904	Euarthropoda + Onychophora	Open haemocoelic circulatory system Dorsal heart with segmentally paired ostia Segmental nephridia
Euarthropoda Lankester, 1904	Chelicerata + Mandibulata	Sclerotized exoskeletal plates Arthropodized limbs Three-segmented brain Deutocerebral first appendage pair Posterior-facing mouth

Ω , note that these groups represent conflicting phylogenetic hypotheses, and thus only one of them is valid. The sister-group relationship between Onychophora and Tardigrada (e.g. Protarthropoda *cf.* Wägele *et al.*, 1999; see Table 2) is not depicted given the lack of recent molecular and/or morphological data supporting such an association.

Budd & Peel, 1998; Ramsköld & Chen, 1998; Waloszek *et al.*, 2005, 2007; Ma *et al.*, 2009, 2014; Liu *et al.*, 2011; Ou, Shu & Mayer, 2012; Smith & Ortega-Hernández, 2014) (Fig. 1A–C). Although the designation of particular lobopodian taxa to specific stem-lineages within these extant phyla has been historically problematic (e.g. Budd, 2001a; Edgecombe, 2009), recent studies evince an increasing agreement on the taxa that can be confidently assigned to the euarthropod stem-lineage, as well as the general character polarity expressed at this level (e.g. Edgecombe, 2010; Liu *et al.*, 2011; Legg *et al.*, 2013; Ma *et al.*, 2014; Smith & Ortega-Hernández, 2014) (Table 1; Fig. 2). Notable representatives include the early Cambrian Chengjiang species *Jianshanopodia* Liu *et al.*, 2006, and *Megadictyon* (Luo *et al.*, 1999; see also Liu *et al.*, 2007), and the lobopodian *Siberion* Dzik, 2011, from the early Cambrian of Siberia. The former taxa are distinguished from other lobopodians (e.g. hallucigeniids; see Hou & Bergström, 1995; Ramsköld & Chen, 1998) by the presence of spines on the frontal lobopodous appendages, the basal fusion of this pair of limbs (*Siberion*), the presence of an appendicular tail (*Jianshanopodia*), and paired gut diverticulae (Vannier *et al.*, 2014; see also discussion in Smith & Ortega-Hernández, 2014). The following nodes crownwards include a paraphyletic grade of so-called

'gilled-lobopodians' that feature sets of lateral flaps originating from the body wall in addition to ventral and annulated lobopodous limbs. These include the early Cambrian Sirius Passet taxa *Kerygmachela* Budd, 1993 (see also Budd, 1998) and *Pambdelurion* Budd, 1997. It is possible to observe a substantial change in the anterior organization of stem-Euarthropoda at this level, consisting of the migration of the anterior-facing mouth (e.g. *Jianshanopodia*, *Kerygmachela*) to the ventral side of the body (*Pambdelurion*) (e.g. Dewel *et al.*, 1999; see also Eriksson & Budd, 2000; Eriksson, Tait & Budd, 2003). Closer to the crown-group is *Opabinia* Walcott, 1912, from the middle Cambrian Burgess Shale (Whittington, 1975; Budd, 1996; Budd & Daley, 2011), which is distinguished from the former gilled-lobopodians by the possession of dorsal lanceolate blades, stalked and compound eyes, a posterior region with three 'tail' flaps, the peculiar fusion of the frontal appendage in a nozzle-like structure, well-defined dorsal trunk segments, and a posterior-facing mouth opening. The following node comprises the large nektonic predators in Radiodonta Collins, 1996, including well-known Burgess Shale forms such as *Anomalocaris* Whiteaves, 1892 (see also Whittington & Briggs, 1985; Daley & Edgecombe, 2014), *Hurdia* Walcott, 1912 (see also Daley *et al.*, 2009; Daley, Budd & Caron, 2013), and *Peytoia* (Walcott, 1911b; see also Daley & Bergström, 2012). Given that some Radiodonta

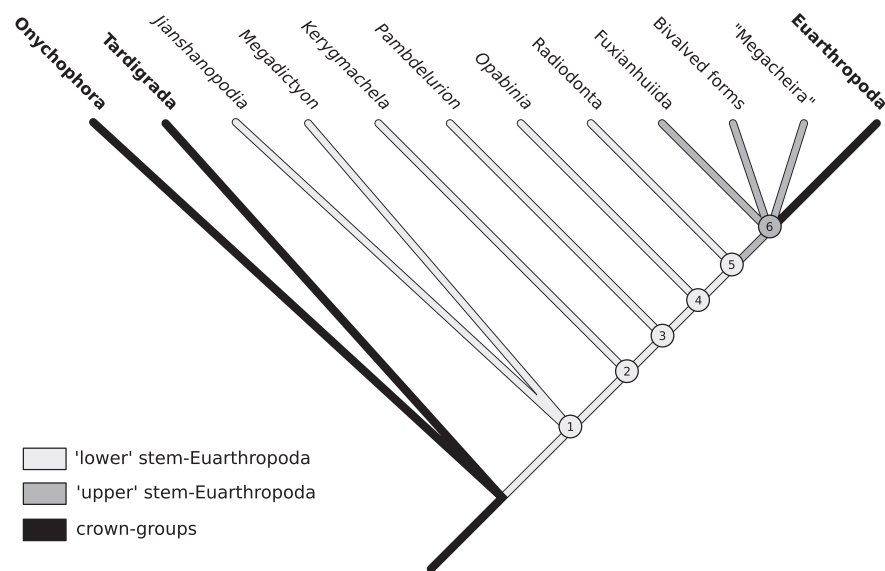


Fig. 2. Summary of character acquisition in the stem-lineage of Euarthropoda. Generalized topology based on the results of Daley *et al.* (2009), Legg *et al.* (2013), and Smith & Ortega-Hernández (2014); note that Radiodonta is depicted as monophyletic based on the results of Cong *et al.* (2014) and Vinther *et al.* (2014). The polytomy of the taxa comprising upper stem-Euarthropoda reflects the lack of consensus with regard to their phylogenetic positions relative to each other. Crown-groups are highlighted in bold. Sympleiomorphic characters not depicted on the tree include possession of annulated epidermis, anterior-facing mouth, radial mouthparts, lobopodous limbs, ambulatory legs, one-segmented head, protocerebral first limb pair and spinous frontal appendage (see Table 4). Character numbering: 1, frontal appendage fused basally, paired gut diverticulae, appendicular tail; 2, body flaps; 3, ventral-facing mouth, sclerotized oral plates; 4, dorsal lanceolate blades, stalked and compound eyes, posterior-facing mouth; 5, isolated cephalic sclerites, frontal appendages arthropodized, 'Peytoia'-type mouthpart; 6, complete dorsal arthropodization, post-oral biramous limbs, arthropodization of all limbs, multisegmented head, first limb pair (deutocerebral) structurally differentiated, hypostome/labrum complex.

share with *Opabinia* the presence of dorsal lanceolate blades, complex ocular structures and similar posterior flaps (except *Hurdia* that has only one pair of flaps, and *Peytoia* that has none), these taxa are sometimes resolved within a clade known as Dinocaridida Collins, 1996 (e.g. Wills *et al.*, 1998; Ma *et al.*, 2009). Radiodonta is significant within stem-Euarthropoda as it provides the first indications of limb arthropodization and body arthropodization, in the form of the spinose frontal appendages and isolated sclerites on the dorsal and lateral sides of the head respectively (e.g. *Hurdia*, see Daley *et al.*, 2009; *Anomalocaris*, see Daley & Edgecombe, 2014) (Fig. 1C). The putative radiodontan *Schinderhannes* Kühl *et al.*, 2009, from the Lower Devonian Hunsrück Slate has been described as having a sclerotized dorsum in addition to the frontal appendages. The former characters have made the precise position of *Schinderhannes* difficult to establish, as phylogenetic analyses have recovered it within Radiodonta (*cf.* Legg *et al.*, 2013; Cong *et al.*, 2014; Vinther *et al.*, 2014), but also as sister-group to other stem-euarthropods closer to the crown-group (*cf.* Kühl *et al.*, 2009; Liu *et al.*, 2011; Van Roy & Briggs, 2011; Ma *et al.*, 2014) (Fig. 3); the problematic morphology and wider evolutionary significance of *Schinderhannes* are addressed in detail in Section IV.1.

The transition between the taxa with a lobopodian/radiodontan-type of organization (Table 4) and those characterized by full body arthropodization, appendage arthropodization, multisegmented head region, biramous post-oral limbs, and a posterior-facing mouth covered by the hypostome/labrum complex arguably represents one of the major events in the evolutionary history leading to Euarthropoda. The stem-euarthropods that display all of these derived morphological traits are diverse and abundant in Palaeozoic deposits with exceptional preservation (e.g. Briggs, 1977, 1978; Hou & Bergström, 1997; Budd, 2002, 2008; Budd & Telford, 2009; Stein, 2010; Stein *et al.*, 2010; Fu & Zhang, 2011; Fu, Zhang & Shu, 2011; Legg & Vannier, 2013; Yang *et al.*, 2013; Legg & Caron, 2014), which makes it all the more problematic that there is a considerable disagreement over the precise position of these taxa and the polarity of character acquisition crownwards (Fig. 2). Notable representatives that possess this general structural organization in the stem-lineage include fuxianhuiids (e.g. Chen *et al.*, 1995; Hou & Bergström, 1997; Waloszek *et al.*, 2005, 2007; Bergström *et al.*, 2008; Yang *et al.*, 2013) (Fig. 1D), bivalved stem-euarthropods (e.g. Briggs, 1977, 1978; Budd, 2008; Stein *et al.*, 2010; Fu & Zhang,

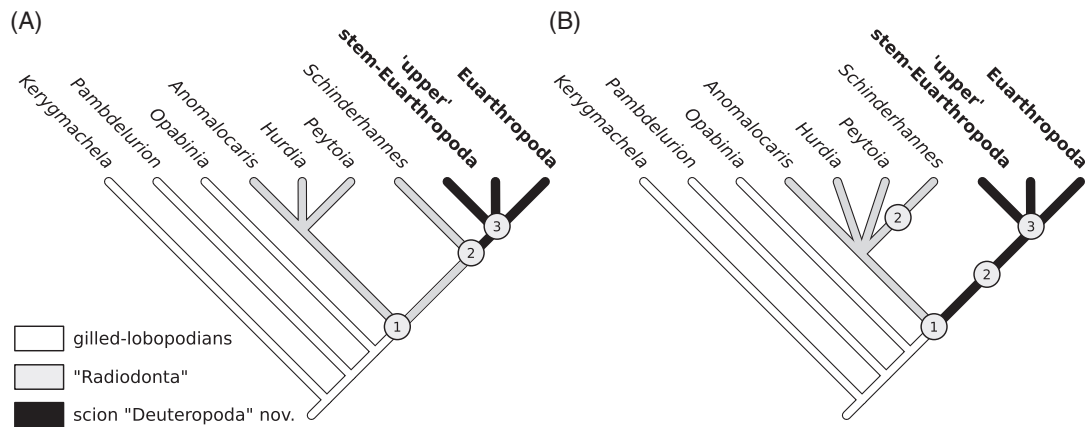


Fig. 3. Alternative phylogenetic positions of *Schinderhannes* Khl *et al.*, 2009, and their evolutionary implications. (A) *Schinderhannes* as sister group to scion Deuteropoda nov. (see text for discussion), implying paraphyly of Radiodonta (*cf.* Khl *et al.*, 2009; Liu *et al.*, 2011; Ma *et al.*, 2014). (B) *Schinderhannes* as a member of monophyletic Radiodonta (*cf.* Legg *et al.*, 2013; Cong *et al.*, 2014; Vinther *et al.*, 2014), indicating that the latter clade is the sister-group to scion Deuteropoda nov.; note that this topology implies multiple origins for dorsal body arthrodization and limb biramy based on the original morphological interpretation of *Schinderhannes* (Khl *et al.*, 2009). Character numbering: 1, isolated cephalic sclerites, frontal appendages arthropodized, 'Peytoia'-type mouthpart; 2, dorsal arthrodization, post-oral biramous limbs; 3, arthropodization of all limbs, multisegmented head, first limb pair (deutocerebral) structurally differentiated, hypostome/labrum complex.

2011; Fu *et al.*, 2011; Legg & Vannier, 2013; Legg & Caron, 2014) (Fig. 1E), and rather controversially, the megacheirans (Hou & Bergstrm, 1997; Chen, Waloszek & Maas, 2004; Haug *et al.*, 2012; see phylogenetic position recovered by Budd, 2002; Daley *et al.*, 2009; Legg *et al.*, 2013) (Fig. 1F); indeed, it has been suggested that the latter group may instead occupy a position within Euarthropoda, as potential stem-lineage representatives of Chelicerata (Fig. 4B) (*cf.* Chen *et al.*, 2004; Maas *et al.*, 2004; Waloszek *et al.*, 2007; Stein, 2010; Haug *et al.*, 2012; Tanaka *et al.*, 2013). Although resolving the interrelationships of these taxa is essential for understanding the origins of Euarthropoda (e.g. Budd & Telford, 2009; Daley *et al.*, 2009; Khl *et al.*, 2009; Legg & Vannier, 2013; Legg *et al.*, 2013), their significance for the present discussion stems from the fact that they share a fundamentally similar organization that is distinct from that of lobopodian-like stem-euarthropods (Fig. 1A–C).

IV. TRANSITION FROM 'LOWER' TO 'UPPER' STEM-EUARTHROPODA

The distinction between 'lower' and 'upper' stem-Euarthropoda (*cf.* Budd, 2002, 2008) is expressed in terms of the phylogenetic position of fossil taxa in the transition of a lobopodian-type body organization (Fig. 1A–C) to a fully arthropodized one (Fig. 1D–F). Given that radiodontans are widely recovered as the most derived stem-euarthropods typified by a predominantly lobopodian-like construction (e.g. Daley

et al., 2009; Khl *et al.*, 2009; Liu *et al.*, 2011; Van Roy & Briggs, 2011; Legg *et al.*, 2013; Ma *et al.*, 2014; Smith & Ortega-Hernndez, 2014) (Fig. 1C), the former have been used as a reference point within the stem-lineage. Thus, the upper stem-euarthropods are informally regarded as *those taxa in stem-Euarthropoda that occupy a crownwards position relative to Radiodonta*, whilst lower stem-euarthropods encompass all the remaining members of stem-Euarthropoda typified by a primarily lobopodian-like organization (Fig. 2; see discussion in Section VII.1). It should be stressed that such categorization does not carry specific connotations with regard to the interrelationships of the taxa in upper stem-Euarthropoda; a widely agreed topology has yet to be reached as evinced by the results of different data sets.

(1) The problem with *Schinderhannes*

The question now is identifying which are the autapomorphic characters that define upper stem-Euarthropoda. The extent of cuticle sclerotization (e.g. unsclerotized *versus* arthropodized body; lobopodous *versus* arthropodized limbs) and the presence of biramous post-oral limbs are easily recognizable characters in fossils, and competently distinguish between most taxa at either side of this major evolutionary transition (Figs 1 and 2). However, these criteria could have complications given that *Schinderhannes* has been described as combining a radiodontan-like organization (e.g. spinose frontal appendages, *Peytoia*-type mouthpart, enlarged anterior body flaps) with complete dorsal sclerotization and biramous trunk appendages (Khl

Table 4. Summary of morphological innovations associated with the evolution of stem-group Euarthropoda and their phylogenetic distribution

Category	Taxa	Morphological features	
		Synapomorphies	Symplesiomorphies
'Upper' stem-Euarthropoda	?megacheirans bivalved Cambrian forms Fuxianhuiida	Complete dorsal arthrodization Post-oral biramous limbs Arthropodization of all limbs Multisegmented head First limb pair (deutocerebral) structurally differentiated hypostome/labrum complex	Stalked eyes Compound eyes Posterior-facing mouth Isolated cephalic sclerites
'Lower' stem-Euarthropoda	Radiodonta (monophyly <i>cf.</i> Legg <i>et al.</i> , 2013; Cong <i>et al.</i> , 2014; Vinther <i>et al.</i> , 2014)	Isolated cephalic sclerites Arthropodization of frontal (protocerebral) appendages 'Peytoia'-type mouthpart	Ventral-facing mouth Sclerotized oral plates Stalked eyes Compound eyes Dorsal lanceolate blades
'Lower' stem-Euarthropoda	<i>Opabinia</i> <i>Pambdelurion</i> <i>Kerygmachela</i>	Body flaps Ventral-facing mouth (<i>Pambdelurion</i>) Sclerotized oral plates (<i>Pambdelurion</i>) Stalked eyes (<i>Opabinia</i>) Compound eyes (<i>Opabinia</i>) Posterior-facing mouth (<i>Opabinia</i>) Dorsal lanceolate blades (<i>Opabinia</i>)	Frontal appendage fused basally Appendicular tail Paired gut-diverticula
'Lower' stem-Euarthropoda	<i>Jianshanopodia</i> <i>Megadictyon</i> <i>Siberion</i>	Frontal appendage fused basally (<i>Siberion</i>) Appendicular tail (<i>Jianshanopodia</i>) Paired gut-diverticula (<i>Jianshanopodia</i> , <i>Megadictyon</i>)	Lobopodous limbs Ambulatory legs (endopod) Protocerebral first limb pair One-segmented head Spinous frontal appendage
Stem-group Panarthropoda	<i>Aysheaia</i> (position <i>cf.</i> Smith & Ortega-Hernández, 2014)	Lobopodous limbs Ambulatory legs (endopod) One-segmented head Protocerebral first limb pair Spinous frontal appendage	Annulated epidermis Anterior-facing mouth Radial mouthparts
Cycloneuralia	<i>Ottoia</i> <i>Priapulius</i>		Annulated epidermis Anterior-facing mouth Radial mouthparts

Characters restricted to specific taxa within each category are indicated with parentheses. Note that the symplesiomorphies listed accumulate throughout the phylogeny of stem-Euarthropoda. See text for discussion on the phylogenetic position of megacheirans.

et al., 2009), both features typical of taxa closer to the crown-group. This situation is further exacerbated by the contested phylogenetic position of *Schinderhannes* as either a derived representative within a monophyletic Radiodonta (Legg *et al.*, 2013; Cong *et al.*, 2014; Vinther *et al.*, 2014) (Fig. 3B), or at the base of upper stem-Euarthropoda – if the latter is defined by the presence of body arthrodization and limb biramy (Kühl *et al.*, 2009; Liu *et al.*, 2011; Ma *et al.*, 2014) (Fig. 3A).

The evolutionary scenario implied by the original description of *Schinderhannes* carries a number of unconventional implications (Fig. 3A). Some of the more controversial aspects of the morphology in this taxon, however, merit further scrutiny in terms of their interpretation and wider evolutionary significance. Although

Kühl *et al.* (2009, fig. 1) regard regularly spaced cuticular folds in the trunk of *Schinderhannes* as sclerotized tergites, the uneven appearance and degree of deformation observed on the posterior region of the body suggests that these features may represent artefacts caused by compaction of the unarmoured segments as observed ventrally; alternatively, it may be the case that *Schinderhannes* has discrete – but unsclerotized – dorsal segments similar to those found in *Opabinia* (Whittington, 1975; Budd, 1996; Zhang & Briggs, 2007; Budd & Daley, 2011; see also Daley *et al.*, 2009, character 25). The presence of putative biramous limbs in *Schinderhannes* is similarly problematic, as these structures bear no clear morphological correspondence with the limbs of phylogenetically basal upper stem-euarthropods (e.g.

fuxianhuiids; Chen *et al.*, 1995; Hou & Bergström, 1997; Waloszek *et al.*, 2005; Bergström *et al.*, 2008; Yang *et al.*, 2013). Instead, it is possible that these represent setal blades similar to those found in numerous anomalocaridids (e.g. Daley *et al.*, 2009, 2013; Daley & Edgecombe, 2014), or even metamericly arranged muscle strands such as those recently reported for the Chengjiang radiodontan *Lyrarapax* Cong *et al.*, 2014 (e.g. fig. 2e). The fact that recent cladistic analyses have favoured a position of *Schinderhannes* within a monophyletic Radiodonta (Legg *et al.*, 2013; Cong *et al.*, 2014; Vinther *et al.*, 2014), rather than in a node above the former clade (*cf.* Kühl *et al.*, 2009; Liu *et al.*, 2011; Ma *et al.*, 2014), suggests that a more conservative interpretation of the morphology of this problematic taxon is better supported by the available evidence. The data supporting the presence of euarthropod-like characters (i.e. body arthrodization, biramous limbs) in *Schinderhannes* is inconclusive at best. Given that *Schinderhannes* lacks other features that could suggest a crownwards position relative to other radiodontans (e.g. deutocerebral first appendage pair, multisegmented head; see Section IV.2), it is considered that most aspects of the morphology of this taxon are in agreement with its classification as a member of lower stem-Euarthropoda (Table 4).

(2) Insights from head segmentation

The transition from a lobopodous to a completely arthrodized overall body architecture is correlated with arguably the most significant evolutionary innovation that distinguishes Euarthropoda from Tardigrada and Onychophora, namely the formation of a discrete head region composed of multiple segments with functionally specialized appendages (e.g. Waloszek *et al.*, 2005, 2007). The interpretation of the anterior organization in stem-Euarthropoda within the context of recent developmental data on head segmentation in extant model organisms (e.g. Eriksson *et al.*, 2003; Harzsch *et al.*, 2005; Scholtz & Edgecombe, 2006; Mayer *et al.*, 2013a,b), allows a clear categorization of fossil taxa based on the position of their differentiated anterior appendages to be made. Lower stem-euarthropods are typified by a *single-segmented head bearing one pair of pre-ocular differentiated appendages (relative to the trunk limbs) in close association with the radially arranged mouth opening*, the pair of limbs most likely belonging to the protocerebral brain neuromere (see Eriksson & Budd, 2000; Budd, 2002; Eriksson *et al.*, 2003; Ou *et al.*, 2012; Cong *et al.*, 2014; Smith & Ortega-Hernández, 2014); conversely, taxa within upper stem-Euarthropoda can be identified by the presence of a *multisegmented head featuring one or more pairs of post-ocular differentiated limbs, the anteriormost of which has a pre-oral position and is serially homologous to the deutocerebral brain neuromere* (e.g. Chen *et al.*, 1995; Waloszek *et al.*, 2005, 2007; Ma *et al.*, 2012; Tanaka *et al.*, 2013; Yang *et al.*, 2013) (Fig. 2; Table 4). Additional characters that are exclusively observed

in known members of upper stem-Euarthropoda include the presence of complete body arthrodization, arthropodized post-oral biramous limbs, and the coverage of the posterior-facing mouth by a hypostomal plate (see discussion in Section VII.1). In particular, it has been suggested that the hypostome may incorporate the euarthropod labrum (i.e. hypostome/labrum complex, see Chen *et al.*, 1995; Budd, 2002; Scholtz & Edgecombe, 2005; Budd & Telford, 2009; Yang *et al.*, 2013), a problematic pre-ocular structure with limb-like attributes that is most likely homologous to the frontal appendage of lobopodian-like taxa occupying lower

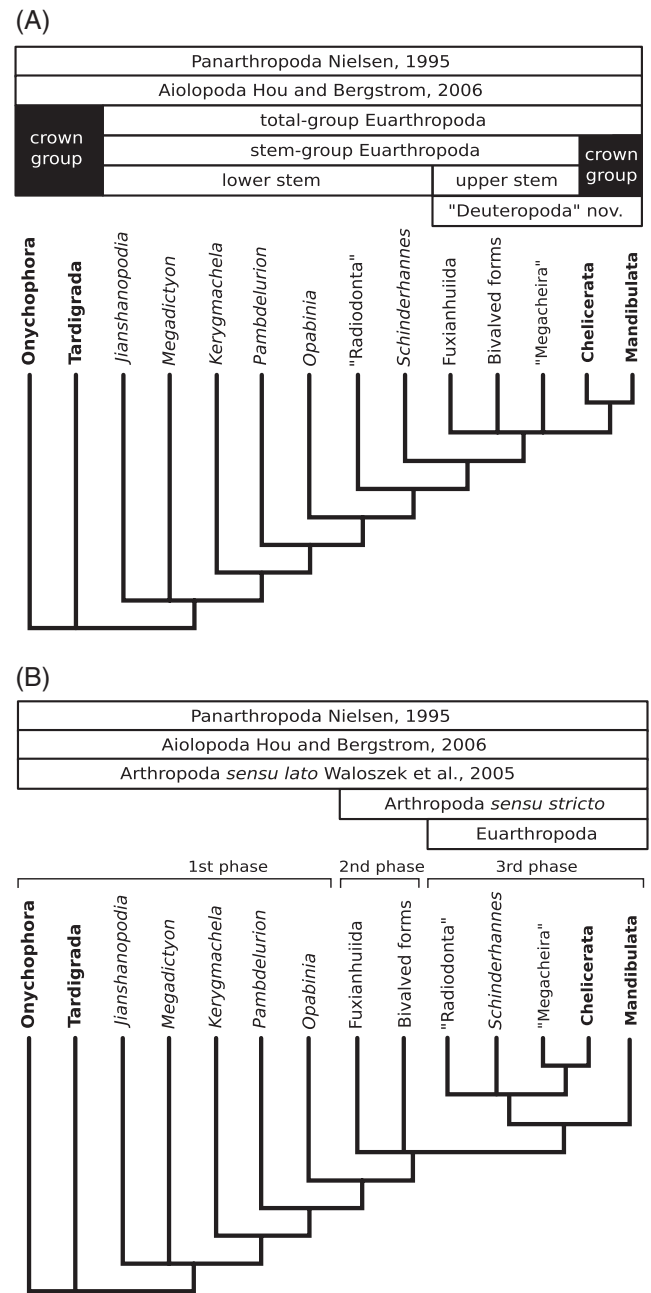


Fig. 4. Legend on next page.

stem-Euarthropoda (e.g. Eriksson & Budd, 2000; Eriksson *et al.*, 2003; Scholtz & Edgecombe, 2006; Liu *et al.*, 2007; Cong *et al.*, 2014; Smith & Ortega-Hernández, 2014). Thus, the fossil record reflects a major reorganization of the segmental architecture of the head region, in which the protocerebral frontal appendages of lower stem-Euarthropoda become significantly reduced, and are functionally replaced by the differentiated deutocerebral appendages that migrate anteriorly to become the first appendage pair in upper stem-Euarthropoda, a condition that is prevalent in extant Euarthropoda. These characters offer a set of robust criteria for categorizing stem-Euarthropoda based on fundamental aspects of their structural organization that reflect significant evolutionary innovations leading to the crown-group.

(a) *Considerations for taxa with unusual morphologies*

Given that the proposed scheme depends on the position of the first appendage pair relative to the eyes and the mouth in fossil taxa, as well as the possession of a multisegmented head region, its application requires further discussion for certain groups. For example, the distinctive morphology of Cambrian bivalved stem-euarthropods makes the site of limb attachment to the head difficult to assess in some cases due to the presence of an extensive carapace that obscures the body outline (e.g. Briggs, 1977, 1978; García-Bellido, Vannier & Collins, 2009; Fu & Zhang, 2011; Fu *et al.*, 2011; Legg & Vannier, 2013; Legg & Caron, 2014). Exceptional preservation of individuals in ventral view, however, allows detailed observations of the appendicular organization to be made, and indicates that the

first appendage pair is clearly attached posteriorly to the eyes in these forms, or alternatively on the anterior edge of the hypostome/labrum complex [e.g. *Branchiocaris* (Resser, 1929) see (Budd, 2008), figs 1, 2; *Isoxys* Walcott, 1890, see (Stein *et al.*, 2010), fig. 2], both of which are indicators of a deutocerebral segmental affinity (Scholtz & Edgecombe, 2005, 2006; Yang *et al.*, 2013). Legg & Vannier (2013, p. 544) regarded the first appendage pair of *Isoxys* as protocerebral based on its association with a putative anterior sclerite; however, the morphological interpretation of the latter structure is extremely dubious owing to unclear preservation, and most likely represents a taphonomic artefact resulting from decay or disarticulation of adjacent cuticle. Cambrian bivalved forms can thus be confidently identified as upper stem-euarthropods based on their cephalic structure, which evinces fundamental similarities with the anterior organization of fuxianhuids (Chen *et al.*, 1995; Hou & Bergström, 1997; Budd & Telford, 2009; Yang *et al.*, 2013).

Another complication stems from interpretations that the head region of some radiodontans incorporates a number of reduced anterior body flaps into a discrete 'neck' (e.g. *Anomalocaris*, see Daley & Edgecombe, 2014; *Hurdia*, see Daley *et al.*, 2009, 2013; *Peytoia*, see Whittington & Briggs, 1985; *Lyrarapax*, see Cong *et al.*, 2014), potentially suggesting a multisegmented organization that would imply an affiliation with upper stem-Euarthropoda as defined here. However, there are a number of arguments against these appendages being part of the head tagma in radiodontans. The reports of these reduced flaps indicate that they occupy a post-oral position; this contrasts with confirmed cases of multisegmented heads in Panarthropoda, in which at least the second (deutocerebral) limb pair inserts pre- or para-orally, and is usually modified for a sensorial (e.g. fuxianhuids, trilobites) or feeding function (e.g. megacheirans, onychophorans). Furthermore, given that radiodontans lack trunk tergites, it is impossible to determine whether the segments associated with the anterior reduced flaps are dorsally fused into a single head shield. Although the presence of a cephalic sclerite in radiodontans is well documented in various species (e.g. Daley *et al.*, 2009, 2013; Daley & Edgecombe, 2014), this structure is attached to the body only at the level of the frontal appendage pair and the eye stalks, and thus most likely represents an exclusive feature of the protocerebral segment (see also Cong *et al.*, 2014). Whilst it is clear that radiodontans display signs of progressive appendage differentiation, also expressed as enlarged body flaps in *Schinderhannes* (Kühl *et al.*, 2009) and *Lyrarapax* (Cong *et al.*, 2014), the available evidence suggests that these limb specializations are confined to the trunk tagma rather than the head. In conclusion, a multisegmented head region represents a diagnostic character of upper stem-Euarthropoda (Table 4).

Fig. 4. Comparison between alternative scenarios for understanding the evolutionary origins of Euarthropoda. Panarthropoda Nielsen, 1995, and Aiolopoda Hou & Bergström, 2006, are included as reference points; note that Radiodonta is depicted as monophyletic based on the results of Legg *et al.* (2013), Cong *et al.* (2014) and Vinther *et al.* (2014). Crown-groups are highlighted in bold. (A) Application of stem- and crown-group concepts to the results of parsimony-based phylogenetic analyses (topology and references as in Fig. 2), including the distinction between lower and upper stem-Euarthropoda discussed in this study; note that scion Deuteropoda nov. represents a monophyletic group encompassing upper stem-Euarthropoda and Euarthropoda (see text for details). (B) 'Three-phase model' including suggested terminology and correspondence with major evolutionary phases (*cf.* Maas & Waloszek, 2001; Waloszek *et al.*, 2005, 2007). This model suggests the alignment of Radiodonta and megacheirans within the stem-lineage of Chelicerata, thus making them crown-group representatives (e.g. Chen *et al.*, 2004; Maas *et al.*, 2004; Stein, 2010; Haug *et al.*, 2012). Note that this topology is not supported by the results of cladistic analyses, but rather based on hypothesis-based hand-drawn cladograms.

V. COMPARISON WITH ‘THREE-PHASE MODEL OF EUARTHROPOD EVOLUTION’

There is an alternative classification that outlines the major steps in euarthropod evolution in a phylogenetic context, summarizing the former into a ‘three-phase model’ that reflects the gradual acquisition of characters leading to the establishment of the crown-group (Fig. 4B) (Maas *et al.*, 2004; Waloszek *et al.*, 2005, 2007; Stein, 2010). The ‘first phase’ describes taxa typified by the possession of uniramous limbs, lack of body sclerotization and an undifferentiated head region (Waloszek *et al.*, 2007), and thus encompasses Palaeozoic lobopodians, as well as Onychophora and Tardigrada (Fig. 4B). Together with more crownwards representatives, all the former taxa characterized by a lobopodian-like construction are categorized under the name ‘Arthropoda *sensu lato*’ (Maas *et al.*, 2004; Waloszek *et al.*, 2005, 2007); this term is phylogenetically equivalent to Panarthropoda (Nielsen, 1995; see Tables 1 and 3) but lacks a direct correlation with the concepts of stem- and crown-group Euarthropoda due to its more inclusive nature (Fig. 4A). The ‘second phase’ describes the evolution of those taxa characterized by the presence of compound eyes, a ‘leg-shaped’ pair of anterior appendages, posterior-facing mouth, hypostome, body segmentation, dorsal arthrodization, appendage arthrodization, biramy, multipodomorous endopods, and a posterior tailspine (Waloszek *et al.*, 2007). Although fuxianhuids are the only taxa discussed directly as an example of such configuration (*cf.* Waloszek *et al.*, 2005, 2007), some bivalved Cambrian forms (e.g. *Branchiocaris*; see Briggs, 1977) can also be considered as representatives of this evolutionary phase based on their similar cephalic organization (e.g. Budd, 2002, 2008; Budd & Telford, 2009; Yang *et al.*, 2013). These arthrodized taxa, together with the crown-group, are identified under the name ‘Arthropoda *sensu stricto*’ (Fig. 4B); this category is similar to upper stem-Euarthropoda (as defined here), but also conflicts with the distinction between stem- and crown-groups in terms of the relative phylogenetic position of its suggested constituent taxa (Fig. 4A). Finally, the ‘third phase’ is embodied by taxa with a multisegmented head including the eyes, a set of antennae and at least three more segments with biramous limbs; additional characters include the coverage of the head by a fused dorsal shield, and the presence of an endopod composed of seven podomeres. This final phase corresponds to Euarthropoda, and at least in principle, is intended to be equivalent to the crown-group (Fig. 4); the fossil taxa that fall under this category (*cf.* Waloszek *et al.*, 2005, 2007), however, depend largely on the interpretation of their phylogenetic position relative to extant representatives.

Although this scheme has had a continuous presence in the literature for the past decade, it suffers from shortcomings that hinder its applicability in a

practical phylogenetic context, particularly when compared with the stem- and crown-group concepts. The major complication of the three-phase model is its ‘euarthropod-centric’ perspective of the evolution of Onychophora, Tardigrada and Euarthropoda; although it offers a detailed account of the acquisition of euarthropodian characters, there is little consideration of the origins of Onychophora and Tardigrada, and thus their evolution from lobopodian ancestors is largely ignored (e.g. Waloszek *et al.*, 2007, p. 279; but see Maas & Waloszek, 2001; Maas *et al.*, 2007). Another substantial problem is that this classification does not address the major evolutionary innovations that take place among lobopodian-like taxa (i.e. lower stem-Euarthropoda as defined here), namely the appearance of body flaps, dorsal gills, development of basally fused spinose frontal appendages, and independent ventral migration of the mouth opening in various lineages (e.g. Smith & Ortega-Hernández, 2014) (Table 4; Fig. 2). Although it is acknowledged that *Kerygmachela*, *Pambdelurion*, and possibly *Opabinia*, may belong to the Arthropoda *sensu lato* (Waloszek *et al.*, 2007, pp. 278–281), these taxa are excluded from the discussion based on the – rather unjustified – premise that their morphology is poorly known (but see Budd, 1993, 1996, 1997, 1998; Zhang & Briggs, 2007; Budd & Daley, 2011). A final major issue with this model is the fact that the characters that purportedly define some of the main phases fail actually to support the hypothesized evolutionary relationships of certain groups (Fig. 4B). This is best exemplified by the phylogenetic position of Radiodonta and megacheirans relative to extant euarthropods. In the three-phase model, the former groups are considered as part of Euarthropoda – as stem-lineage members of Chelicerata – based on the suggested homology between their spinose frontal appendages as deutocerebral, and the subsequent transformation of these limbs into the chelicerae (*cf.* Chen *et al.*, 2004; Maas *et al.*, 2004; Stein, 2010; Haug *et al.*, 2012). Indeed, there is evidence that supports the serial homology between the megacheiran ‘short great-appendages’ and the chelicerae as limbs of the deutocerebral segment (Haug *et al.*, 2012; Tanaka *et al.*, 2013). The anterior structural organization of Radiodonta, however, suggests a protocerebral origin for their (pre-ocular) frontal spinose appendages (see Budd, 2002; Smith & Ortega-Hernández, 2014), thus weakening the hypothesis of serial homology with the chelicerae; the recent discovery of well-preserved neurological material in *Lyrarapax* (Cong *et al.*, 2014) represents critical data in favour of the protocerebral nature of the frontal appendage pair in radiodontans. Furthermore, all parsimony-based cladistics analyses with a sufficiently comprehensive taxonomic sampling in the last decade have consistently resolved Radiodonta in the node below fuxianhuids (e.g. Budd, 2002; Daley *et al.*, 2009; Köhl *et al.*, 2009; Edgecombe, 2010; Liu *et al.*, 2011; Legg *et al.*, 2013; Ma *et al.*, 2014; Smith

& Ortega-Hernández, 2014), indicating that any close affinity with Chelicerata is extremely unlikely. Forcing radiodontans into stem-group Chelicerata would require numerous character reversals, including the loss of body sclerotization, loss of arthropodization on all limbs except for the raptorial appendages, and secondary evolution of body flaps. This scenario would also imply convergence of major characters observed in extant chelicerates and mandibulates, namely complete body arthropodization and arthropodized limbs with seven podomeres (Boxshall, 2004).

It is concluded that the three-phase model is not sufficiently informative for understanding the evolution of total-group Euarthropoda given its lack of compatibility with a rigorous cladistic-based phylogenetic framework, particularly when compared with the more methodologically sound stem- and crown-group concepts (Jeffries, 1979; Budd & Jensen, 2000). The former system of classification carries the advantage of making clear distinctions between the fossil taxa that belong to specific ancestral lineages (stem-groups) relative to extant representatives (crown-groups), whilst also maintaining a self-consistent terminology.

VI. ON NAMING CONFUSION AND PALAEOLOGICAL INACCURACIES

A lack of practical cohesiveness and overabundance of non-standardized classifications (Table 1; Fig. 4) has led to various incorrect applications of nomenclature when discussing specific regions of the total-group Euarthropoda evolutionary tree from a palaeontological perspective. Whilst many of these inaccuracies resulted from early studies incorporating the fossil record into analyses of the relationships among the different phyla (e.g. see references in Budd, 1998, fig. 35), the misleading use of terminology is still apparent in more recent times. For instance, the cladogram of Köhl *et al.* (2009, fig. 2) labels *Schinderhannes* as belonging to Euarthropoda, which implies a phylogenetic position within the crown-group. This is incorrect, as *Schinderhannes* is not in the direct phylogenetic lineage of any extant clade within Euarthropoda, but rather sits within lower stem-Euarthropoda regardless of its position relative to other Radiodonta (Fig. 3). In another example, Liu *et al.* (2011, fig. 4) use the name Arthropoda for a scion – that is a monophyletic group that is an extension of the crown-group down into the stem-group (see Budd, 2001a, p. 267) – that includes *Schinderhannes*, upper stem-Euarthropoda and Euarthropoda. Although it is clear that this represents an attempt to exercise an apomorphy-based definition of Arthropoda – given that the presence of jointed limbs support this node – this application is erroneous under any of the possible usages of the name since neither Tardigrada (*sensu* von Siebold, 1848) nor Onychophora

(*cf.* Lankester, 1904) are included (see Table 1). Since Liu *et al.* (2011) correctly use Euarthropoda to denote the clade of extant Mandibulata and Chelicerata in their phylogenetic tree (*cf.* Lankester, 1904), the application of Arthropoda in this case does not follow any congruent previous classification. Legg *et al.* (2013, fig. 4b) and Legg & Vannier (2013, fig. 6) also apply Arthropoda inappropriately for a scion including Radiodonta, upper stem-Euarthropoda and Euarthropoda. Indeed, Legg & Vannier (2013, p. 549; see also Lerosey-Aubril *et al.*, 2014) explicitly state that their use of Arthropoda follows an apomorphy-based definition that once again focuses on the presence limb arthropodization; similarly to Liu *et al.* (2011), however, this usage does not conform to any of the possible classifications of Arthropoda in a strict sense (see Table 1). In another comparable case, the cladogram of Ma *et al.* (2009, fig. 12b) uses Arthropoda for a scion including fuxianhuids, which belong to upper stem-Euarthropoda, and trilobites, which are most likely members of the crown-group (e.g. Scholtz & Edgecombe, 2005, 2006; Budd & Telford, 2009; Ortega-Hernández & Brena, 2012; Legg *et al.*, 2013; Ortega-Hernández, Legg & Braddy, 2013). Finally, the recent cladogram by Vinther *et al.* (2014, supplementary figs 1, 2) labels a clade including a fuxianhuid and a trilobite as Euarthropoda; this is incorrect as such grouping actually refers to a scion including upper stem-Euarthropoda and the crown-group, rather than the latter exclusively.

VII. A NEW CLASSIFICATION FOR SCION UPPER STEM-EUARTHROPODA+EUARTHROPODA

It only takes a glimpse of the appropriate palaeontological literature to recognize that highlighting the phylogenetic position of specific fossil groups relative to Euarthropoda is a common practice (e.g. Budd, 1998, 2002; Dewel *et al.*, 1999; Liu *et al.*, 2004, 2011; Maas *et al.*, 2004; Waloszek *et al.*, 2005, 2007; Zhang & Briggs, 2007; Daley *et al.*, 2009; Köhl *et al.*, 2009; Ma *et al.*, 2009; Edgecombe, 2010; Ortega-Hernández & Brena, 2012; Legg *et al.*, 2013; Cong *et al.*, 2014; Smith & Ortega-Hernández, 2014). The problem here is that there is no nomenclature that adequately encompasses those fossil taxa in upper stem-Euarthropoda – typified by a substantial suite of apomorphic characters shared with euarthropods (see Fig. 2; Table 4) – together with crown-group representatives; the reason for this being that a relatively stable topology for this part of the evolutionary tree of total-group Euarthropoda has only been reached in the last few years (Figs 2–4A).

Based on the identification of synapomorphic characters that distinguish fuxianhuids, bivalved Cambrian forms, and possibly megacheirans from the more basal representatives of this stem-lineage (Table 4; Fig. 2), it is considered that the scion including upper

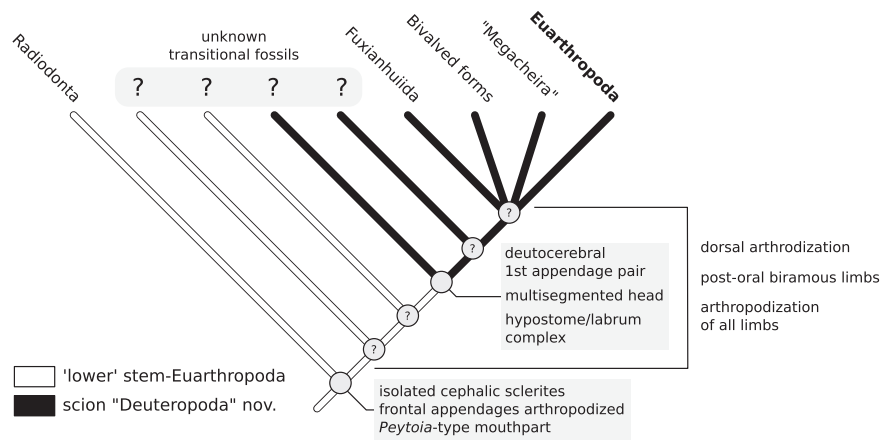


Fig. 5. Applicability of Deuteropoda nov. based on the current understanding of the evolution and fossil record of stem-group Euarthropoda. Question marks in nodes indicate uncertain character polarity. Future discoveries may provide new data on transitional fossil taxa that fill the gaps between known members of lower and upper stem-Euarthropoda, and thus clarify the polarity of some of the characters that are currently only observed in the latter (i.e. dorsal arthrodization, post-oral biramous limbs, arthrodization of all limbs). Note that scion Deuteropoda nov., and by implication upper stem-Euarthropoda, are strictly defined by the reorganization of the segmental organization of the head region relative to lobopodian-like ancestors (i.e. differentiated deutocerebral first appendage pair, multisegmented head, hypostome/labrum complex).

stem-Euarthropoda and Euarthropoda warrants a formal name given its critical position for understanding the evolution of this phylum. From a practical viewpoint, such classification would allow specific comparisons between taxa at either side of the transition of lobopodous-type to arthropodized body organization to be made without treading into terminological inaccuracies. I propose the name 'Deuteropoda' nov. for this scion (Figs 3, 4A, and 5), from the Greek *deutero* (second) and *poda* (foot), referencing the fact that the first appendage pair expressed in the adult anterior region of these organisms originates from the second head segment (i.e. deutocerebrum), as evinced from the post-ocular position of these limbs in all extant and extinct representatives.

(1) The applicability and fossil record of Deuteropoda nov.

The proposed character-based distinction between lower and upper stem-Euarthropoda, as well as the formalization of Deuteropoda nov., highlight an important gap in the fossil record of the euarthropod stem lineage. Despite the overall agreement on the polarity of character acquisition among lower stem-euarthropods (Fig. 2), the precise appearance of all the morphological features that typify known members of upper stem-Euarthropoda – and implicitly the base of Deuteropoda nov. – is more elusive. Current phylogenies indicate that radiodontans are the most crownwards lower stem-euarthropods, and that either fuxianhuiids (*cf.* Daley *et al.*, 2009; Liu *et al.*, 2011; Ma *et al.*, 2014; Smith & Ortega-Hernández, 2014), bivalved stem-euarthropods (*cf.* Legg & Vannier, 2013; Legg

et al., 2013; Legg & Caron, 2014) or megacheirans (*cf.* Budd, 2002) represent the most phylogenetically basal group within Deuteropoda nov. (Fig. 2); however, it is highly unlikely that the entire suite of synapomorphic characters observed in these upper stem-euarthropods evolved simultaneously (Table 4). Instead, phylogenetic gradualism suggests the existence of transitional fossil taxa that reflect the detailed step-wise accumulation of characters in the evolutionary continuum from lower to upper stem-Euarthropoda, but which have not been discovered yet given the lack of resolution in the known fossil record (Fig. 5). This context makes it clear that upper stem-Euarthropoda cannot be defined simply as 'those taxa in a position crownwards to Radiodonta', but rather that it is necessary to determine a specific combination of characters that support Deuteropoda nov., while also allowing accommodation of future fossil discoveries. Based on the evidence indicating a complex reorganization of the head region from lower to upper stem-Euarthropoda, the basal node of Deuteropoda nov. is defined here by the presence of a *structurally differentiated deutocerebral first appendage pair, reduced protocerebral appendages integrated into the labrum/hypostome complex, and a multisegmented head* (Fig. 5). This diagnosis includes characters that are intimately linked with each other functionally and developmentally, and thus offer a robust reference point to study the evolutionary transition between taxa with fundamentally distinct types of cephalic segmentation. By contrast, it is not possible to invoke the same level of developmental integration between the evolution of dorsal arthrodization, post-oral biramous appendages and the arthropodization of all the limbs. These characters are

certainly important for understanding the origins of the body organization that typifies extant euarthropods; however, some or all of these features may have evolved in taxa within lower stem-Euarthropoda but in a more crownwards position relative to radiodontans, or alternatively in upper stem-euarthropods that are phylogenetically basal to fuxianhuiids, bivalved forms and megacheirans (Fig. 5). Although these uncertainties will only be clarified through the input of new fossils, the present classification of the euarthropod stem lineage provides a clear context for scrutinizing the phylogenetic position, and evolutionary significance, of extinct taxa critical for reconstructing the deep origins of the euarthropod crown group.

VIII. CONCLUSIONS

(1) An overview of recent phylogenetic studies with broad taxon sampling within stem-Euarthropoda allows the step-wise acquisition of major morphological innovations to be followed (Fig. 2; Table 4). The accumulation of numerous synapomorphies associated with the evolution of the structural organization in Euarthropoda, particularly in the head region, leads to a formalized classification within the stem-lineage.

(2) Lower stem-Euarthropoda includes taxa characterized by a fundamentally lobopodian-type of body organization, protocerebral first appendages and a one-segmented head, such as lobopodians (e.g. *Siberion*, *Megadictyon*, *Jianshanopodia*), gilled-lobopodians (e.g. *Kerygmachela*, *Pambdelurion*, *Opabinia*) and radiodontans (e.g. *Anomalocaris*, *Hurdia*, *Schinderhannes*). Conversely, members of upper stem-Euarthropoda are typified by the possession of a multisegmented head region with a differentiated deutocerebral first appendage pair, as well as fully arthropodized bodies with arthropodized biramous appendages, and thus encompass fuxianhuiids, Cambrian bivalved forms (e.g. *Branchiocaris*) and possibly megacheirans. The definitive phylogenetic position of megacheirans as members of upper stem-Euarthropoda (cf. Budd, 2002; Daley *et al.*, 2009; Legg *et al.*, 2013) or stem-Chelicerata (cf. Chen *et al.*, 2004; Haug *et al.*, 2012; Tanaka *et al.*, 2013) is yet to be fully resolved.

(3) The systematic and phylogenetic terminology used for discussing the evolutionary relationships between Euarthropoda, Tardigrada, and Onychophora has been heavily burdened by a lack of consistency in its definition and application for over a century. This inevitably leads to the abandonment of the original meaning of Arthropoda *sensu* von Siebold (1848), as its strict diagnosis and taxonomic scope have become distorted in the recent literature (Table 1). A consensus that combines the more familiar usage of the terms Panarthropoda (*sensu* Nielsen, 1995) and Euarthropoda (*sensu* Lankester, 1904) may help to reduce terminological

confusion in the future (Table 3), but only if the scientific community adheres to a standardized nomenclatural scheme. Arthropoda (cf. Lankester, 1904) and Tactopoda (*sensu* Budd, 2001*a,b*) currently stand as equally valid names that reflect opposing hypotheses of evolutionary relationships between Onychophora and Tardigrada relative to Euarthropoda; only one will stand up to further phylogenetic scrutiny.

(4) The 'three-phase model of euarthropod evolution' (Waloszek *et al.*, 2005, 2007) is found to be less suitable for understanding the history and relationships among Onychophora, Tardigrada, and Euarthropoda than the stem- and crown-group concepts, at least in a cladistic-based phylogenetic framework (Fig. 4). Furthermore, the lack of support for some of its constituent hypotheses (e.g. radiodontans within stem-Chelicerata) weakens its wider applicability when compared with parsimony-informed quantitative analyses.

(5) Deuteropoda nov. is proposed for the scion including upper stem-Euarthropoda and Euarthropoda; this new term allows comparisons between different members of the stem-lineage, and relative to the crown-group, to be made whilst maintaining a nomenclature that is congruent with standard phylogenetic terminology. Abundant inaccuracies in the recent literature attest that Deuteropoda nov. fills an important terminological gap for describing the evolution of total-group Euarthropoda.

(6) Characters that define the basal node of Deuteropoda nov. include the presence of a differentiated deutocerebral first appendage pair, a multisegmented head, and reduced protocerebral appendages integrated into the labrum/hypostome complex. The incomplete fossil record of stem-group Euarthropoda suggests the existence of yet undiscovered intermediate forms that reflect the evolution of characters that are currently only known for members of Deuteropoda nov. (i.e. dorsal arthropodization, limb biramy, arthropodization of all limbs); these morphological features, however, are excluded from the diagnosis of Deuteropoda nov. in order to accommodate future discoveries.

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