REVIEW ARTICLE

The origin and early evolution of arthropods

Cédric Aria[1]* iD

[1] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences – Nanjing, P. R. China

* Current address: Shaanxi Key Laboratory of Early Life and Environments, Northwest University – Xi'an, P.R. China

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Abstract

The rise of arthropods is a decisive event in the history of life. Likely the first animals to have established themselves on land and in the air, arthropods have pervaded nearly all ecosystems and have become pillars of the planet's ecological networks. Forerunners of this saga, exceptionally well-preserved Palaeozoic fossils recently discovered or re-discovered thanks to new approaches and techniques have elucidated the precocious appearance of extant lineages at the onset of the Cambrian explosion, and pointed to the critical role of the plankton and hard integuments in early arthropod diversification. Despite new interpretative challenges, phylogenetic advances based on palaeontological evidence open the prospect of finally using the full potential of the most diverse animal phylum to investigate macroevolutionary patterns and processes.

Introduction

Arthropods constitute a central and colossal component of Earth's biosphere, at both the macroscopic and microscopic levels. Since the beginning of the Phanerozoic, these hyperdiverse, articulated animals have shaped most terrestrial and marine ecosystems, and their pivotal roles in trophic networks often have a direct and considerable impact on our industries and economy—be it vital or detrimental. The war on insects, prominently, waged in the name of a wasteful and profit-driven agriculture, has led to catastrophic consequences for the survivability of these animals worldwide, and the loss of pollinators to cascading ecosystem breakdowns [1]. The agro-economical peril to arthropods, in conjunction with other environmental crises caused by unbridled resource exploitation and consumption, such as global warming, threatens to irremediably pauperize the planet's landscapes [2, 3].

This waning and fragility stand in stark contrast to more than half-a-billion years of exceptional resilience to mass extinctions. Although trilobites, vanishing at the end of the Permian, are a notable exception, the body plans (which can be broadly defined based on morphoanatomy, see e.g. Aria [4]) of all other four largest and traditional arthropod groups—chelicerates, myriapods, "crustaceans" and insects—, all present by at least by the Late Devonian [5–8], diversified through all of the five major pre-Anthropocene biodiversity crises. Likely since the Jurassic [9], insects have become by a large margin the most diversified and abundant of arthropods [10], but all main lineages have characteristically experienced explosive radiations and have shown extended stability of their families and genera.

The search for the causes and mechanisms surrounding the origin of the highly modular architecture that has been certainly determinant in the success and expansion of the arthropod phylum has therefore focused on the earliest Phanerozoic, and specifically the Cambrian explosion [11]. Starting with the Burgess Shale, a variety of Cambrian Fossil Lagerstätten across the world have yielded a wealth of non-biomineralizing species informing early diversity and character transitions leading to arthropods and to their ramifications [12, 13]. In this context, arthropods have famously initiated discussions about shifts in evolutionary tempo and mode at the macroevolutionary scale (that is, at the inter-specific taxonomic level and above [14]), and in particular the heterogeneity of disparity patterns and their possible meaning for body plan evolution [15–17].

The insights and developments following these studies have been marked by debates about the deep phylogenetic relationships between arthropods, to which fossil taxa contributed in increasingly significant ways [18–20], in the context of a still seemingly intractable phylogeny of extant lineages. In the last ten years, broad-scale combined morphological and molecular phylogenetics and phylogenomics have broken the systematic deadlock by achieving strong branch support and topological convergence for major extant clades [21–24], even if the resolution of certain internal nodes remains a salient issue [25]. There is now robust evidence that all extant arthropods can be divided into two main lineages: Chelicerata and Mandibulata, the latter including Myriapoda as well as Pancrustacea (also called Tetraconata), a broad grouping according to which Hexapoda (including insects) arose from a paraphyletic crustacean group [21, 22, 26].

The inclusion of fossils to one of these total-evidence datasets—key to a contextualized macroevolutionary perspective—has been shown to be consistent with these topologies [13, 27]. While summarizing certain solid advances in this field, this result did not mean, however, that the palaeontological understanding itself was complete, and recent findings, catalysed in part by the discovery of new fossil sites [28–30] or the use of new technologies [31, 32], have since rewritten the significance of many extinct taxa. This, in turn, has changed our perspective on early body plan evolution in these animals, introducing new fundamental questions to current research [33]. Conversely, a series of exceptional discoveries involving preserved neural tissues [34] have lately been followed by broad scenarios describing the evolution of arthropod heads [35]. However, some of these challenging new data have arguably been overinterpreted,

emphasizing the importance of maintaining consistency with the information provided by external morphology [36]. Beyond genes and morphoanatomy, an integrated palaeobiological and palaeoecological picture and its role in the early radiation of arthropods is also starting to take shape [37–39].

We certainly are at a decisive turn where converge an unprecedented amount of often seemingly conflicting evidence from revised fossils, new fossils, new types of preserved tissues, genes, development, genetic networks, new technologies, and new phylogenetic methods. This review aims to provide a simple but critical guide to current knowledge, and to lay out a synthesis of persisting or emerging challenges in early arthropod evolution, to serve as foundation for future studies. The stakes are high, for the elucidation of the early diversification of the largest animal phylum may also provide the richest insight into the biological principles governing macroevolution.

The panarthropod cradle and a "Cambrian planktonic revolution"

Arthropoda is now recognized as a monophyletic phylum within Ecdysozoa, the moulting animals [12, 13, 23] (see Box 1 for a glossary of terms used in this paper). Ecdysozoa is composed of the cycloneuralian 'worms'—including priapulids and nematodes—usually considered to be a mono- or paraphyletic grouping next to the Panarthropoda, an expanded systematic definition of Arthropoda also including, among extant forms, onychophorans (velvet worms) and tardigrades (water bears) [40].

There is an ongoing debate about whether onychophorans or tardigrades are the sister taxa of Arthropoda. Evidence coming from neuroanatomy [41] and other internal organs favours either a sistergroup relationship with tardigrades (e.g. presence of metameric ganglia along the ventral nerve cord; a grouping also called Tactopoda [42]) or with onychophorans (e.g. presence of sacculus and podocytes on metanephridia), and in a number of cases are ambiguous, their presence or absence varying also among arthropods (e.g. presence of a peritrophic membrane or Malpighian tubules) [43]. A recent fossil-inclusive analysis found Tardigrada to be the sister group to Onychophora + Arthropoda [37], consistent with most other phylogenetic studies [40]. This result is influenced by the fact that, in spite of their dramatic developmental contraction [44], tardigrades display the plesiomorphic condition of a truncated posterior termination bearing a limb pair with claws pointing anteriorly—possibly inherited from the pool of adaptations acquired by suspension-feeding lobopodians, which includes an anchoring function of posterior lobopods [45]. The plesiomorphic presence of more trunk somites and the presence of several elongate, curved claws on their limbs are consistent with a sister-group relationship with the Burgess Shale lobopodian *Aysheaia pedunculata* [37]. However, while providing detailed genetic and phenotypic information, tardigrades and onychophorans are also typified by a number of outstandingly autapomorphic characters (onychophorans appear to have independently evolved a ventral mouth opening and internalized mouthparts [37, 45] and, like many tardigrades, are largely terrestrial), which urges caution when attempting to extrapolate shared derived conditions.

By contrast, fossils called lobopodians, mostly found in Cambrian rocks, have directly enriched our understanding of the early evolution of panarthropods [46] (Figs 1g, l, 2). Although specimens are characteristically rare across assemblages, these worm-like taxa bearing paired metameric, annulated and lightly sclerotized limbs (the lobopods) have revealed that a broad diversity of organisms had in fact initially evolved from cycloneuralian ancestors. Fossil-inclusive phylogenetic analyses find tardigrades to be well nested within Panarthropoda [37, 42, 47], and show that the surviving Onychophora and Tardigrada are, indeed, but offshoots with highly autapomorphic traits from this initial radiation associated with the Cambrian explosion. Other lobopodians survived through the Silurian [48] up to at least the Carboniferous [49], however, which means that they represented much more than an "experimental" body plan and had eventually reached a relatively stable (if cryptic) adaptive zone within Palaeozoic marine ecosystems.

Box 1

Glossary

- **Antennula**: Frontal (deutocerebral) arthrodized appendage, stenopodous or flagellate, fulfilling a sensory function, typically monoramous and elongate, with undifferentiated distalmost podomere. Also called "first antenna" in crustaceans, in which the antenniform appendage of the following segment is called the "second antenna", or, under this nomenclature, simply the antenna.

- **Arthrodization**: The articulation of two sclerotized cuticular elements by an arthrodial membrane. The word "arthropodization" is sometimes used to apply specifically to limb podomeres, developmentally different from body segments (see below).

- **Arthropod**: An ecdysozan protostome with arthrodized appendages.

- **Basipod**: The proximal unit of the biramous limb, to which are connected its two defining rami: endopod and exopod. The basipod is commonly modified as a feeding device in euarthropods, either through its development into a masticatory gnathal plate (a characteristic of arachnomorphs) or its subdivision into endite-bearing units (a characteristic of mandibulates). Whether the basipod originated from a single limb Anlage inherited from early panarthropods or formed by fusion of two separate appendicular branches corresponding to endopod and exopod is a matter of debate. Often called the 'protopodite' in the crustacean jargon.

- **Cheira (pl. cheirae)**: Frontal multichelate appendage of the first arthropods. Typically bears claws differentiated according to various feeding functions. Shortened and directed upward in megacheiran euarthropods, confined to a prehensile predatory role.

- **Chelicera**: Frontal (deutocerebral) arthrodized appendage with chelate or sub-chelate termination characteristic of Chelicerata. Commonly considered homologous to the "chelifores" of sea spiders.

- **Coxa**: A proximalmost podomere usually fulfilling a masticatory function in pancrustaceans' heads, and from which mandibles are thought to be derived. Coxae would be derived from the proximal endite of subdivided basipods in early members of the mandibulate lineage.

- **Endopod**: One of the two rami defining the biramous arthropod appendage, usually stenopodous and used for locomotion.

- **Endite**: Outgrowth on the ventral side of a limb, usually associated with a particular podomere. Commonly bearing spines or setae.

- **Euarthropod**: Arthropod with arthrodized body segments and biramous arthrodized appendages.

- **Exite**: Outgrowth on the dorsal side of a limb, usually associated with a particular podomere. Common among crustaceans, especially on the coxae and basipods. Would be developmentally distinct from the exopod by developing as a growth axis secondary to the main cell lineage forming the arthrodized limb.

- **Exopod**: One of the two rami defining the biramous arthropod appendage, often used for swimming.

- **Gnathobasipod**: A basipod differentiated into a large masticatory gnathal plate, often fringed with teeth.

- **Great appendage**: See 'cheira'.

- **Heptapodomerous**: Composed of seven podomeres.

- **Mandible**: Coxal podomere (proximal to the basipod) of the third segment (or fourth somite) developed as a masticatory device.

- **Multipodomerous**: Composed of a great number of podomeres, usually 15 or more.

- **Multisegmented**: Composed of a great number of segments, usually 20 or more.

- **Podomere**: Unit of an arthropod limb as defined externally by an arthrodized sclerotic ring and internally by muscular attachment.

- **Segment**: Sclerotized metameric unit (somite) separated from adjoining units by clear margins.

- **Somite**: Constitutive body unit containing an arrangement of organs serially repeated in other somites.

- **Stenopodous**: Qualifies an elongate appendage articulated by a series of well-defined podomeres.

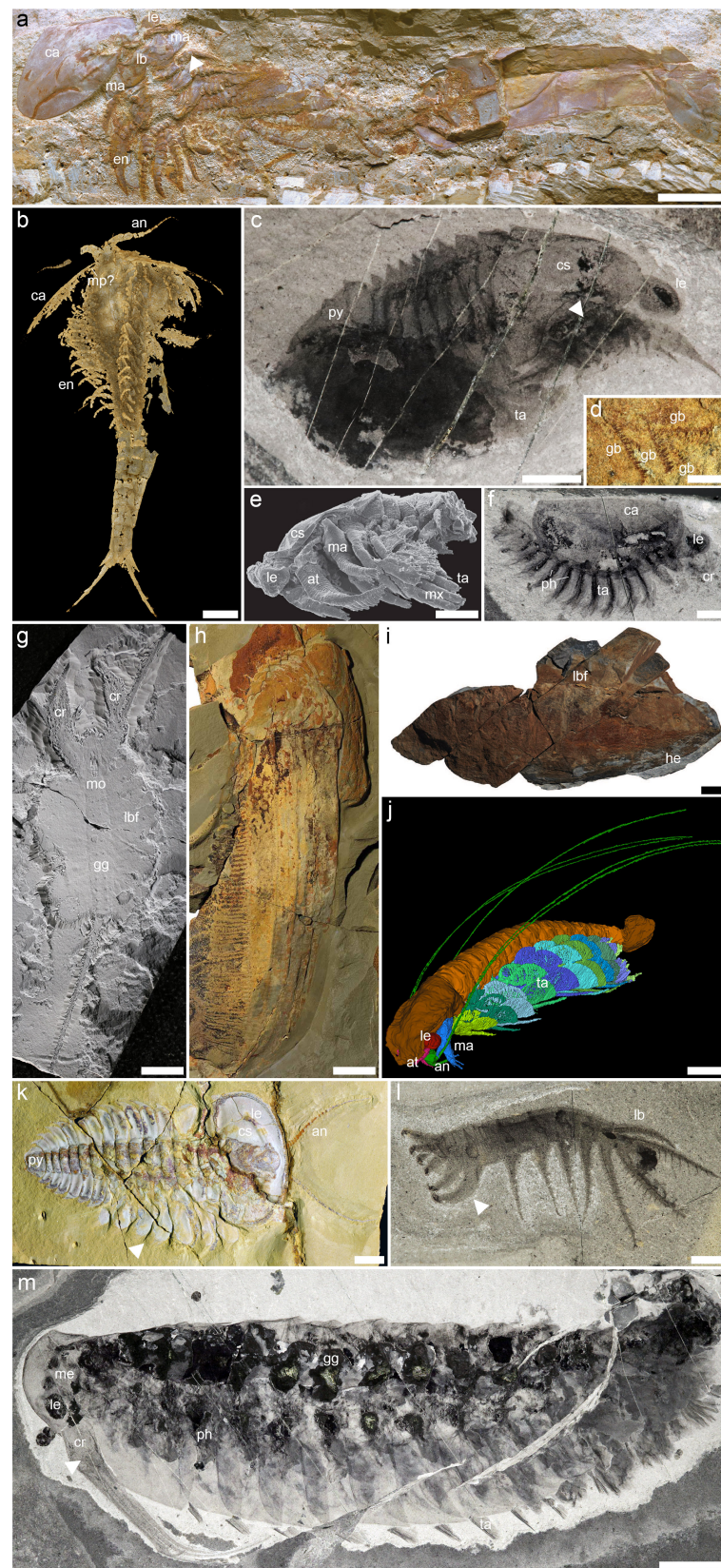- **Tergite**: Dorsal segmental sclerite, usually arthrodized.

Perhaps the most important aspect of lobopodians put forward in the recent years is their arguably common adaptation, at various degrees, to suspension-feeding [37, 50]. Most striking among the luolis-haniids, which possess stout anchoring back limbs and frontal arms adorned with pairs of thin spinules [37, 50, 51] (Fig. 1l), this ecology also possibly characterizes the famed hallucigeniids [37, 47], and would thereby apply to a majority of lobopodians with diagnostically elongate appendages. These are distinct from a series of other taxa, including much larger and stouter forms [52, 53] (termed herein 'xenusiids'), that bear short and conical lobopods, as they are known in onychophorans and tardigrades, and which would lie closer to the common arthropod ancestor (Fig. 2). Whether arthropods and their closest relatives arose from a paraphyletic lineage of suspension-feeders or whether suspension-feeding triggered a separate, monophyletic radiation depends on the evolutionary scenario considered [e.g., 37, 45], but it appears that the distinction between an ambulatory or semi-sessile feeding lifestyle was determinant in the primordial diversification of panarthropods.

Parallel studies on the first arthropods, the radiodontans (I use here a definition of Arthropoda based on the presence of an arthrodized appendage [64]; see also Box 1), add even greater significance to suspension-feeding, broadly defined, in the rise of this phylum. A filter-feeding strategy, more precisely (which uses a filtration structure and captures food particles below a precise size threshold [65]), has indeed been shown to be present in several relatives of the iconic predator *Anomalocaris*, having evolved multiple times within the group and led to gigantism in the Ordovician [39, 60, 65] (Fig. 1h, i). Contrary to long-legged lobopodians, however, filter-feeding in radiodontans was entirely carried out by the extensive modification of a single pair of appendages—the frontal, arthrodized appendages, characteristic of this group which otherwise lacks any body or limb arthrodization. These appendages are coined here "cheirae" (see Box 1).

This evidence further emphasizes the central role of small macro- to microscopic organisms in Cambrian sea waters, and notably larvae. It should be in fact questioned whether the "planktonic revolution" thought to characterize the Great Ordovician Biodiversification Event [66] should not be placed within the Cambrian instead, correlated to a massive and sudden expansion of suspension-feeding strategies born during the Ediacaran [67, 68]. Cases of suspension-feeding cited above among Cambrian panarthropods have been expanded to more derived fossil taxa [69], and thoroughly spread across all Metazoa, in sponges, cnidarian polyps, echinoderms, brachiopods and a variety of other animals [70, 71]. Certain localities, like Marble Canyon, were arguably even built on suspension-feeding [72]. Although the fossil evidence for small meso- to microplankton is still largely indirect [39], Small Carbonaceous Fossils (SCFs) [73] and "Orsten" taxa from different localities around the world [57, 74, 75] directly document the existence of abundant, planktonic crustaceomorph faunas that may be related to known mandibulate macrofossils (see below). Burgess Shale-type (BST) deposits do not preserve well micrometric fossils simply because of grain resolution limit, but there is plentiful evidence of tiny arthropod-like fossils, which, for the most part, are undescribable (pers. obs.), although several post-hatchling stage larvae have already been published [31, 76], some of them differing somewhat in morphology from their adult counterparts, pointing to ontogenetic niche differences. Arthropods being already the most diverse and abundant of animals by the early Cambrian, their larvae must therefore have constituted an important part of planktonic life forms, even if there were plenty of benthic direct developers [77].

Radiodontans, nonetheless, also developed a much broader diversity of specializations involving the cheirae of radiodontans, which also includes sediment sifting [78], for instance. Similar observations can be made about the variety of shapes realized by other arthrodized limbs and arthropod body segments, by comparison with the rather conservative morphology of lobopodians. Arthrodization, as a structural innovation, was therefore decisive in the early success of arthropods by providing a modular medium with both developmental flexibility and structural rigidity, a "sculpting material" that worked particularly

Figure 1. (Caption next page)

Figure 1. (Previous page) Variety of preservations and fossils that have recently reshaped or challenged our views on early arthropod evolution. a, *Alacaris multinoda* Yang et al. [54], specimen YKLP 12268 (holotype), from the Xiaoshiba biota; a fuxianhuiid. Image courtesy of Xiguang Zhang. **b**, *Ercaicunia multinodosa* Zhai et al. [32], specimen YKLP 16201, from the Chengjiang biota; a hymenocarine. X-ray computed tomography, image courtesy of Dayou Zhai. **c**, *Mollisonia plenovenatrix* Aria and Caron [55], specimen ROMIP 65262, from the Burgess Shale (Marble Canyon); an early chelicerate. Image courtesy of Jean-Bernard Caron. **d**, Gnathobases of *Wisangocaris barbarahardyae* Jago et al. [56], specimen SAM P45629, from the Emu Bay Shale; a habeliidan. Image courtesy of Jim Jago. **e**, *Yicaris dianensis* Zhang et al. [57], specimen YKLP 10844, from the Yu'anshan "Orsten" biota; a larval crustaceomorph. Scanning electron microscopy, image courtesy of Xiguang Zhang. **f**, *Surusicaris elegans* Aria and Caron [58], specimen ROMIP 62976 (holotype), from the Burgess Shale (Marble Canyon); an isoxyid. Image courtesy of Jean-Bernard Caron. **g**, *Kerygmachela kierkegaardi* Budd [59], specimen MGUH 32048a, from Sirius Passet; a swimming lobopodian. Image courtesy of Jakob Vinther. **h, i**, *Aegirocassis benmoulae* Van Roy et al. [60], from the Fezouata biota; a radiodontan. Images courtesy of Derek Briggs. **h**, Specimen YPM 527123, filter-feeding frontal appendages. **i**, Specimen YPM 237172, whole body, three-dimensional. **j**, *Cascolus ravitis* Siveter et al. [61], specimen OUMNH C.29698, from the Herefordshire biota; a possible malacostracan. Digital reconstruction from serial photography, image courtesy of David Siveter, Derek Briggs, Derek Siveter, Mark Sutton and David Legg. **k**, *Hongshiyanaspis yiliangensis* Zhang and Lin *in* Zhang et al. [62], specimen NIGPAS 164503, from the Xiazhuang biota; a trilobite. Image courtesy of Han Zheng. **l**, *Ovatiovermis cribratus* Caron and Aria [37], specimen ROMIP 52707, from the Burgess Shale (Walcott Quarry); a suspension-feeding lobopodian. Image courtesy of Jean-Bernard Caron. **m**, *Yawunik kootenayi* Aria et al. [63], specimen ROMIP 63066, from the Burgess Shale (Marble Canyon); a leanchoiliid megacheiran. Image courtesy of Jean-Bernard Caron. Arrowheads point to: subdivided, enditic basipod (a), raptorial and sensory complex of appendages (c), tripartite exopods (k), stout lobopods for anchoring (l) and robust basis of cheira (m). Abbreviations: an, antennule(s); at, antenna(e); ca, carapace; cr, cheira(e); cs, cephalic shield; en, endopod(s); gn, gnathobasipod; he, h-element "carapace"; la, labrum; lb, lobopod(s); lbf, lobopodous flaps; le, lateral eye(s); ma, mandible(s); me, median eye(s); mo, mouth apparatus; mp, mandibular palp; mx, maxillula and maxilla; ph, peri-intestinal hemocoelic cavity; py, pygidium; ta, trunk appendage(s). Scale bars, 10mm (**a, g, m**), 1mm (**b, j**), 3mm (**c, f, k, l**), 2mm (**d**), 100μm (**e**), 20mm (**h**), 100mm (**i**).

well as a rapid driver of phenotypic evolution, notwithstanding the anatomical and genetic trade-offs that later stabilized a number of well-defined body plans [4].

Assembly of the arthropod body plan

One of the most interesting and well-documented sequences of phenotypic evolution from cycloneuralians to arthropods is that of the mouth and its associated structures [47]. Some basal lobopodians possessed an eversible pharynx lined with teeth, similar to that of priapulids [37]; others, like *Hallucigenia*, had also independently evolved circumoral sclerotic plates [47], reminiscent of radiodontans (but expressed internally). The dented pharynx is a plesiomorphy of arthropods, and has been retained by extant taxa. The location of the mouth was terminal from cycloneuralians through xenusiids [45, 79–81]; however, the first midgut glands only appear in xenusiids [53], suggesting an evolution in the mode of feeding and/or diet in these animals, possibly associated with the introduction of predation or irregular scavenging [82, 83]. From a xenusiid-like ancestor emerged peculiar lobopodians, such as *Kerygmachela* (Fig. 1g) and *Pambdelurion* (long endemic to the early Cambrian Greenland locality of Sirius Passet, but possibly present elsewhere [84]), apparently bearing flap-like swimming appendages, in addition to lobopods. By contrast to xenusiid ancestors, *Pambdelurion* displays a circumoral sclerotic mouth apparatus clearly placed on the ventral side of the body, although it was argued that the animal also retained an eversible pharynx [84]. The rotation of the mouth opening, which in extant lineages is characteristically ventral with posteroventral orientation and connected to an anteriorly-looped esopha-

gus, therefore occurred during the xenusiid-radiodontan transition (Fig. 2). *Kerygmachela* may document a transitional morphological state in which the mouth opening is ventral but directed anteriorly [85].

A circumoral sclerotized apparatus, giving its name to radiodontans (*radius* (Latin) – *odoús* (Greek) meaning literally radial-teeth), exemplified by *Anomalocaris* [86] or *Hurdia* [87], is therefore not exclusive to this group. A 'peytoia' type of outer sclerotized ring (or its derivatives [88]) composed of differentiated plates (by their size), also commonly called the "oral cone", would unite radiodontans, but resemblances with *Pambdelurion* are extensive, to the point that some isolated radiodontan-like mouthparts from the Chengjiang biota were proposed to belong to a relative of *Pambdelurion* [84]. The numerous inner teeth of *Pambdelurion* are found in radiodontans in the form of an inner row of smaller dented plates, which could be derived from the symplesiomorphic pharyngeal teeth. Interestingly, a comparable set of elements are also found in dissociation in amplectobeluid radiodontans from the Chengjiang biota, never forming the typical oral cone [89, 90]. A single specimen of *Amplectobelua symbrachiata* shows overlapping gnathobase-like differentiated plates associated with alleged reduced flaps [89]. An interpretation as structures homologous to gnathobasipods is difficult to reconcile at present with the known early evolution of euarthropods (Figs 2, 3), and is also at odds with the circumoral identity of similar sclerites in other radiodontans, but this intriguing evidence undoubtedly designates a crucial area of investigation at both the palaeontological and developmental level for the near future.
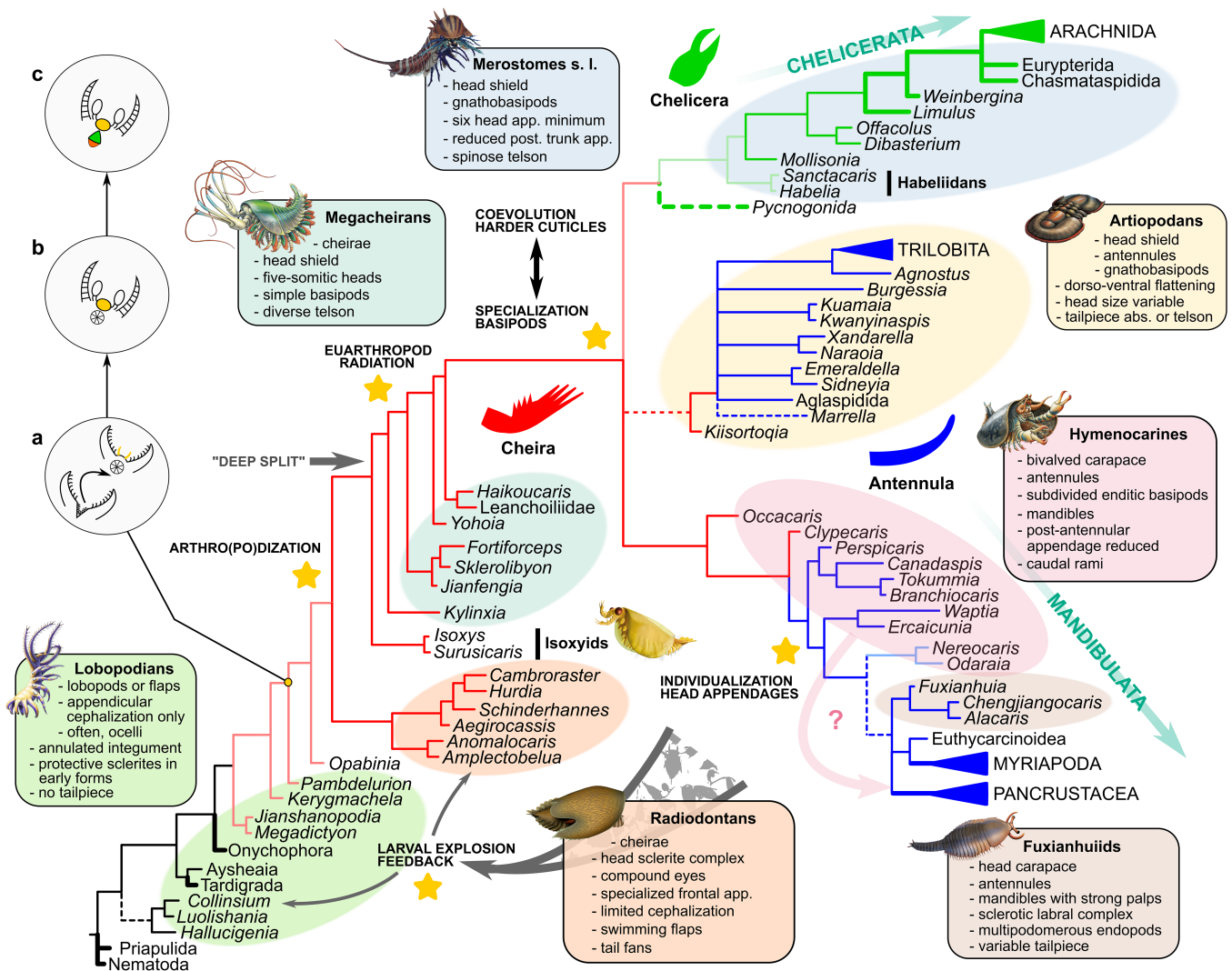
As mentioned previously, the emergence of radiodontans as earliest members of Arthropoda is otherwise characterized by the evolution of an arthrodized pair of appendages (see below and Fig. 3a for considerations regarding the somitic identity of the frontal appendage). By contrast to the oral complex, there is no known sequence of character change leading to arthro(po)dization: this condition seems to appear rather suddenly in radiodontans, even if the cheirae themselves are likely homologous to the similar stout and purportedly raptorial appendages of *Pambdelurion*, *Kerygmachela* and xenusiids (which lack subdivisions into podomeres). Another important trait associated with the appearance of radiodontans is the presence of well-developed compound eyes, which in these taxa are stalked [91] (but see [92]), whereas lobopodians only possess simple ocelli [93], when present (Fig. 2).

However, stalked compound eyes could in fact be plesiomorphic to Arthropoda, depending on the phylogenetic placement of *Opabinia regalis*. To this day, the iconic "weird wonder" from the Burgess Shale [94, 95] remains an oddity, albeit less so than when it was redescribed by Harry Whittington. Although clearly related to radiodontans with its gill-bearing lateral flaps and stalked eyes, the single, unpaired frontal appendage with soft, annulated stem and terminal 'jaw'—a unique morphology among all panarthropods—, together with the absence of sclerotized mouthparts, make its affinity within Arthropoda ambiguous. The presence of typical stacked midgut glands with radial folds identical to those of *Kerygmachela* and *Pambdelurion* [96] on the one hand, and *Isoxys* [97], leanchoiliid euarthropods [63, 98] and even the trilobite-like *Kiisortoqia* [99], on the other hand, shows nonetheless a broad evolutionary contiguity of this feature across these taxa. Quasi-identical digestive glands with radial folds or diverticulate pattern are found in xenusiids [53] and anomalocaridids [86] (in which these phosphatized structures were possibly misinterpreted as muscle tissues—but see [100]), yet are not stacked.

Opabinia also serves as a point of reference for the two most critical lines of discussion pertaining to the origin of "true" arthropods (Euarthropoda), as defined by the presence of arthrodized body segments and biramous limbs [64]. While irregularities in length between visible somites suggests that there were no articulating tergites, all authors who have studied *Opabinia* have recognized the presence of some form of external segmentation [95], which is, by contrast, more difficult to detect in complete radiodontan specimens [78, 86, 101] (perhaps due to the absence of lateral preservation). There does not seem to be any comparable form of externalization of somite boundaries in more basal lobopodians, although there exist differentiations at limb insertions and different annulation patterns [37, 102]. Body arthrodization is unclear in isoxyids (arthropods with bivalved carapaces sharing affinities with ra-

diodontans; Figs 1f, 2), which places *Kylinxia* [103] and megacheirans—historically, the so-called "great appendage" euarthropods—as the earliest unambiguous euarthropod representatives [36] (Figs 1m, 2). Details about the formation of tergite articulation are not documented.

It has been debated whether *Opabinia* combined both lateral flaps and lobopods [95, 104]. Although any developmental remnants of lobopodous limbs in *Opabinia* seems fully internalized and associated with the circum-intestinal haemocoelic cavity [58], such combination is arguably well evidenced at least

Figure 2. Relationships and characteristics of the main fossil panarthropod groups. Summarized phylogenetic framework of panarthropod relationships, with main fossil groups highlighted. Boxes contain combinations of defining but overlapping character states for these fossil groups, which can be para- or monophyletic. Insets (**a**, **b**, **c**) represent crucial steps of ocular, mouth and external protocerebral evolution at the onset of the arthropod radiation: (**a**) mouth is ventralized and accommodates circumoral plates, frontal sensory organs derived from protocerebrum (yellow); (**b**) compound eyes born by stalks, arthrodization, complex of frontalmost organs protected by a sclerite (yellow); (**c**) later, formation of the hypostome-labrum complex, with pre-oral sternal plate (red) protecting the mouth instead of circumoral plates, and a fleshy extension (green) possibly derived from the same Anlage as those of the anteriormost sclerotic/sensory complex (yellow; see Fig. 3). Yellow stars on tree mark important morphological innovations or evolutionary events. Coloured branches indicate the frontalmost appendage type (red, cheira; green, chelicera; blue, antennula). The arrow and question mark associated with the hymenocarine morphogroup represent the uncertainty as to whether some of these taxa lay in fact closer to pancrustaceans. Extant lineages are represented by bold branches. Dashed lines represent grouping uncertainties. Palaeo-art by Marianne Collins and Danielle Dufault ©Royal Ontario Museum, except the *Fuxianhuia* by Nobu Tamura.
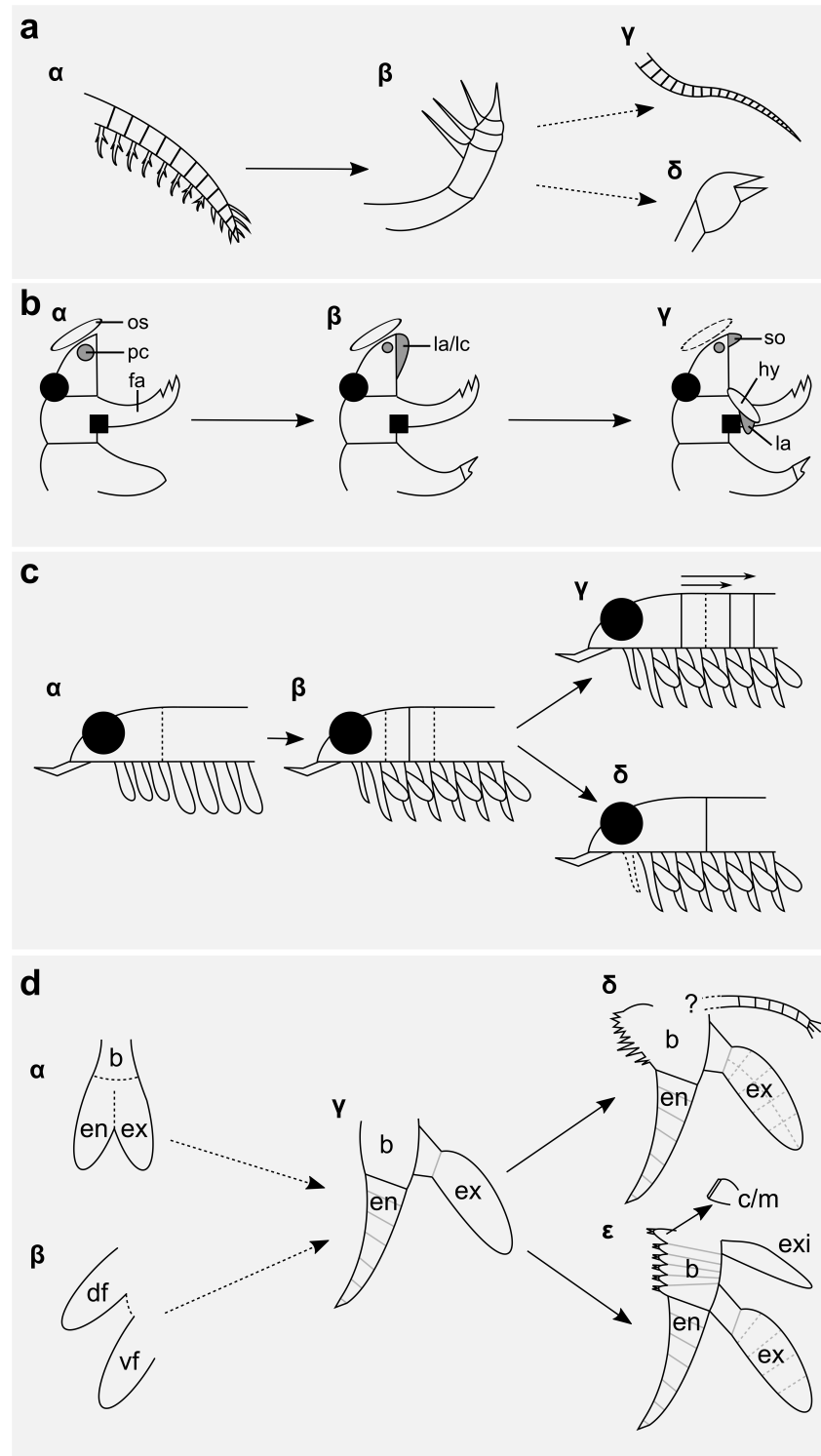
in *Pambdelurion* [96]. Two separate rows of lateral flaps were otherwise described in the massive *Aegirocassis* from the Lower Ordovician Fezouata Lagerstätte in Morocco (Fig. 1h, i), and as possibly present in other radiodontans [60]. This evidence would suggest that the typical biramous limbs of euarthropods formed by fusion of separate limb Anlagen (Fig. 3d). This is at odds with some other fossil evidence, such as in the isoxyid *Surusicaris* [58], which shows broadly attached and morphologically similar endopods and exopods (Fig. 3d), as well as with developmental data also supporting that both rami originated by splitting of a single limb axis [105]. Complicating this matter, early members of the chelicerate lineage (Fig. 1c) display an intriguing separation of the exopod branch from the main basipod-endopod limb axis [55, 106–108] (Fig. 3d; see below), likely related to the derived loss of exopods in the euchelicerate head (the prosoma), and also supporting the view that the exopod might belong to a separate limb Anlage. Further developmental data could help shed light on this issue, but we must be cautious about our interpretation of extant models, for their external morphology may sometimes hide derived developmental complexity. Olesen et al. [109] have shown for instance that, in certain branchiopods, podomeres in stenopodous limbs were likely derived from the endites of phyllopodous appendages, and therefore that using developmental data from these stenopodous limbs to extrapolate podomere origin in crustacean stenopodous appendages in general would be misleading.

The journey towards Euarthropoda also involves the formation of a broad sclerite protecting the head, taking the form of a carapace or head shield. Various head sclerites are known in "long-legged" lobopodians, but a basal phylogenetic position of these taxa speaks against any direct homology with arthropod tergites [37]. A variety of antero-dorsal and paired ventro-lateral sclerites mark the early evolution of arthropods, and unique lateral elements ("p-elements") may even constitute one of the strongest apomorphies of Radiodonta [60, 78, 89, 110]. The continuity of these distinct sclerites with arthropod carapaces and head shields is not entirely clear, but there is some evidence [36] to posit that at least the antero-dorsal element, despite spanning a very large size range in radiodontans [78], corresponds to the socalled "anterior/ocular sclerite" identified across early arthropods [111, 112], including megacheirans [36] (Fig. 3b).

Isoxyids (Fig. 1f), now retrieved by different large phylogenetic datasets as sister taxa to all other euarthropods [27, 112] (Fig. 2, Box 2; although this bears partly on uncertainties, including body arthrodization) bear bivalved carapaces, as defined by tergites of the anteriormost somites extending dorsally over other tergites and thus having a free posterior range of motion (Box 1). By comparison, euarthropods such as arachnomorphs are typically identified by the presence of a head shield, which represents the fusion of all cephalic tergites and has limited posterior overlap over trunk tergites. This tagma evolved into the chelicerate prosoma [55, 106].

In reality, the morphological ranges of these structures overlap, as is clearly documented by crustaceans [113]. In general, shields and carapaces could be seen as different phases of an evolutionary continuity based on the integration of additional segments into the head tagma, but their homology also depends on the precise somite from which they originate. For instance, the lateral "carapace-like" p-elements of radiodontans are likely analogous with euarthropod carapaces because they arguably originate from the protocerebral somite [78, 114], instead of a deutocerebral—as seems to be case in isoxyids and *Kylinxia* based on the post-ocular location of the carapace/shield [58, 103]—or more posterior affinity—notably, in crustaceans, with the maxillary somite [113]. Yet bivalved carapaces enclosing a part or the entire body laterally are easily recognizable in a wide range of Cambrian taxa, despite showing shape variations [69], and possibly being modified into a flat 'shield' in fuxianhuiids (Fig. 1a). Hence carapaces may constitute an ancestral diagnostic feature of mandibulates, at least in adults, contrasting with the more restrictive head shield of arachnomorphs (Fig. 2). The lack of broad protecting carapaces in arachnomorphs is further associated with greater cuticular developments of post-cephalic segments, in

Figure 3. Understanding and challenges of the early evolution of key arthropod features. a, Frontalmost appendage. The robust, raptorial frontal appendage of xenusiids and radiodontans (α) is known to transition to the megacheiran cheira (β), adopting a dorsal orientation, and sometimes coupling differentiated grasping and sensory functions (as in leanchoiliids). The cheira supposedly diversifies into an exclusively sensory (the antennula, γ) or predatory, manipulating form (the chelicera, δ) in extant taxa, but these transitions are not yet documented clearly by the fossil record—except perhaps in *Kiisortoqia*. **(Continued on next page)**

Figure 3. **(Continued from previous page) b**, Labrum. The black square represents the mouth, the black dot is the eye. The labrum presumably originates in early panarthropods from a protocerebral Anlage that could have served a sensory function (α), then forming an externalized sensory organ commonly covered by an "anterior" or "ocular" sclerite (β). In more derived forms, frontalmost sensory features co-exist with the hypostome-labrum complex (γ), in which a pre-oral sclerite also bears a fleshy protrusion—the latter is the labrum in the traditional sense. The labrum of the hypostome-labrum being known as protocerebral in origin, the question is to know if it derives evolutionarily from the frontalmost pre-oral organs seen in some fossils. **c**, Head tagma. The head tagma is poorly defined in stem euarthropods, but in some cases appendage differentiations seem to delimit a five-somitic head (α); in megacheirans, this five-somitic configuration is clearly delimited by the head shield in cheiromorphs, but the ancestral jianfengiids appear to display variability in the length of the cephalon and a possible decoupling between the tergal and appendicular head tagmata (β). From the plesiomorphic five-somitic head arose the diagnostic six-somitic mandibulate cephalon (δ, although the tritocerebral somite independently became limbless in some groups, and, beyond the larval, stage crustaceans evolved the more inclusive cephalothorax), but also the more variable cephala of arachnomorphs. In these taxa, the five-somitic tagma transitions directly to possibly six-, -seven and even eight-somitic heads, the latter representing the ancestral condition of panchelicerates (γ). **d**, Biramous appendage. There exist two scenarios for the origin of biramicity, both supported by different fossil evidence: the split of the main limb axis, as suggested by isoxyids (α), and the fusion of separate limb axes, as interpreted in radiodontans with double rows of swimming flaps (β). Either of these initial conditions led to the archetypal biramous appendage with basipod, endopod and exopod (γ), as expressed in megacheirans. The differentiation of the basipod plays a critical role in the emergence of cenocondylans. The arachnomorphs are distinguished by a gnathobasipod (δ), while early members of the mandibulate lineage evolved subdivisions of the basipod that later gave rise to coxal features, including the mandible (ε). From a developmental point of view, the "true" exopod could a priori be recognized by attaching to the original basipod, that is, the distalmost segment of the entire basipod complex, or basipodite; by contrast, exites arise from other basal segments (ε). Early members of the chelicerate lineage possess "semi-detached" stenopodous exopods whose affinity as exopods or exites is unclear (δ). Abbreviations: b, basipod; c/m, coxa/mandible; df, dorsal flap; en, endopod; ex, exopod; exi, exite; fa, frontal appendage; hy, hypostome; la, labrum; lc, labral complex; os, ocular sclerite; pc, protocerebrum; so, sensorial organ; vf, ventral flap.

particular in the form of pleural extensions, fusion of posterior segments (the pygidium, but see [115]) and other ornamentations.

Although the presence of tergites is unclear in isoxyids, but would have to co-exist with radiodontan-like soft tail flaps [116], the genus *Isoxys* in particular possesses trunk endopods with distinct podomere boundaries [117, 118]. A form of post-frontal metameric limb arthrodization may therefore have appeared in these animals, prior to taking a more conventional leg-like aspect in megacheirans. Most remarkably, megacheirans and arachnomorphs point to a ground pattern of seven podomeres ("heptapodomerous" condition [63], see Box 1) for post-frontal endopods (notwithstanding minor variations in certain species), which was possibly already present in *Isoxys* [117, 118].

Megacheirans (Figs 1m, 2) represent archetypes of the first 'true' arthropods: they possess both arthrodized limbs and fully arthrodized bodies, including the tailpiece, but lack elaborate limb differentiations. Their basipods bear teeth but their margins are not produced into expanded masticatory surfaces and, as such, cannot be regarded as gnathobases as they are known in arachnomorphs [119] (Fig. 3d). Megacheirans therefore essentially relied on their cheirae for morpho-functionality, sometimes cumulating both raptorial and differentiated sensory functions on this single limb (Fig. 1m)—a unique combination of the frontalmost appendage among all adult arthropods, and likely an evolutionary solution coping with the lack of "division of labour" across other limbs [63]. Jianfengiids, the earliest members of this paraphyletic group, show decoupling of dorsal and ventral cephalization, possibly reflecting a greater initial variability of the cephalon in euarthropods [36]. Decoupling of dorsal and ventral (specifically, appendicular) tagmatization is an important phenomenon to consider across euarthropod groups
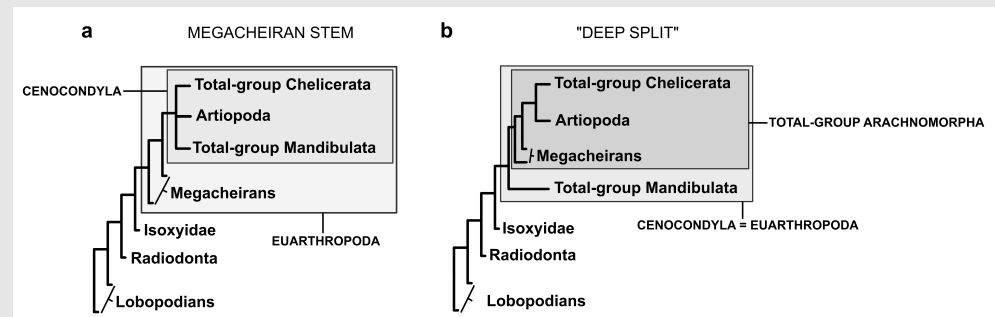
[120, 121], and its mechanism has been documented developmentally [122], but will not be covered in detail herein.

The recently-described *Kylinxia* beautifully documents the homologous continuity of the cheirae across arthropods and euarthropods and anchors the basal position of megacheirans in the euarthropod tree [103]. The animal bears two large lateral as well as three smaller median eyes, thus also importantly shedding light on the long-puzzling quintet of eyes in *Opabinia*, now possibly present in the common euarthropod ancestor. However, owing to the numerous characters (dinocaridid-like tailfan, non-arthrodized head limbs, absence of clear body arthrodization) still indicating a basal position of isoxyids, *Kylinxia* is here resolved either simply as a basalmost megacheiran in the more classic topology (Fig. 2), or as sister to total-group Arachnomorpha under a "deep split" scenario—that is, the early separation of the total-group Mandibulata and Arachnomorpha close to the origin of Euarthropoda itself (Box 2).

Rare Cambrian arthropods with bivalved carapaces have also been described bearing cheirae. It would therefore appear that the presence of these elaborate frontal appendages was contiguous across two separate lineages, one of them also possibly retaining the bivalved carapace of isoxyids (Fig. 2; see also [103]). Although relatively simple in principle, the plausibility of the "deep split" evolutionary scenario [4] (bluerefBox 2)—which would also settle the lengthy dispute about the phylogenetic position of trilobites (Box 3)—is only made possible by recent reassessments of critical Cambrian taxa and, in particular, their relation to extant clades.

Box 2

Competing new evolutionary scenarios

Arthropod phylogenies, with or without fossils, have long represented seemingly intractable problems and never-ending debates. In the last ten years or so, however, considerable progress has been made towards a consensus, in no small part due to the improvement and expansion of molecular analyses, even if true difficulties remain, for instance internal chelicerate relationships [123]. Disagreements do persist regarding the placement of early fossil groups [24], but cumulative evidence from redescriptions and new discoveries has arguably constrained the broad panarthropod topology as presented in (**a**): lobopodians, radiodontans, isoxyids and megacheirans forming the stem of a clade containing both extant lineages (Chelicerata and Mandibulata) as well as trilobites and their relatives (Artiopoda), and which is called Cenocondyla [64]. This configuration, however, leads to conflicts when attempting to place taxa that have long been considered as "oddballs" but whose significance may now be understood, such as fossils with both bivalved carapaces and cheirae (e.g. *Occacaris*), or megacheirans bearing gnathobasipods (e.g. *Parapeytoia*). An alternative topology accommodating these issues is presented in a recent work [4] as well as this paper (**b**) and is called "deep split," owing to the early branching of total-group Mandibulata and Arachnomorpha lineages. In this scenario, megacheirans are closer to chelicerates than they are to mandibulates, while hymenocarines are brought closer to the common euarthropod ancestor. In part, this view reconciles hypotheses previously seen as conflicting, in which authors posited the chelicerate affinity of megacheirans [124] or the basal position of bivalved taxa [125]. Some authors have recently proposed a variant of the "deep split" scenario with derived isoxyids [103]. The stability of the "deep split" topology requires further testing, however, hence the more consensual topology in (**a**) is used in Figure 2.

Deep Cambrian origins of extant lineages

Numerous morphotypes from the Burgess Shale have long been included in or compared to crustaceans [126], although these interpretations were challenged in the 21st century [18, 125]. Since the stabilization of Mandibulata [21, 22], it became paramount to re-examine crustacean-like species in this new light. Recently, new palaeontological evidence, made possible notably thanks to the discovery of the new Burgess Shale locality of Marble Canyon [30], provided support for the mandibulate affinity of a *Branchiocaris* relative, *Tokummia* [112], and also shed light on the affinities of Cambrian bivalved arthropods as a whole, coined—in the exclusion of isoxyids, ostracods and bradoriids—the hymenocarines (Fig. 1b). These taxa would in fact resolve as basal mandibulates, branching before myriapods and pancrustaceans (Fig. 2), rather than derived pancrustaceans. These observations were largely corroborated and completed by the redescription of one of the first-found and best-preserved Burgess Shale arthropods, *Waptia fieldensis* [33]. Aside from the presence of mandibles with a surprisingly derived morphology, these studies illustrated and clarified some hypotheses concerning arthropod limb evolution and the origin of proximal features in mandibulates [74, 127]; namely, the role of subdivided basipods bearing multiple differentiated endites in the formation of the coxa, sub-coxa and features derived from them—notoriously, the mandibles [128, 129] (Fig. 3d).

This evidence from the fossil record nicely complemented the observation that articulating pleurites in terrestrial arthropods also derived from supernumerary proximal limb elements [130]. Recently reevaluated evidence from the renowned Rhynie Chert Lagerstätte has also illuminated the morphoanatomy of the enigmatic euthycarcinoids, placing them on the myriapod lineage [131]. This represents a crucial find that helps link myriapods with their marine ancestors, and will therefore help elucidate plesiomorphic characters at the divergence between Myriapoda and Pancrustacea. The reconstruction of ancestral character states in both marine stem pancrustaceans and stem myriapods is a necessary condition to resolving the placement of hymenocarines as either stem mandibulates or stem pancrustaceans—for instance to resolve whether antennae (or "second antennae") really are a pancrustacean synapomorphy [33] (Fig. 2; see below). Correlative to this finding, and elaborating on previous phylogenetic results [33, 36], the iconic fuxianhuiids of the Chengjiang fauna (Figs 1d, 2) have been described as mandibulates with strong morphological affinities with euthycarcinoids and myriapods [132].

However, there also exists a more cryptic yet rich diversity of Cambrian "crustaceomorphs". First, the famous "Orsten" biotas, originally from Sweden, but now known more generally around the world since the early Cambrian [57] (Fig. 1e) as a type of exceptional three-dimensional preservation by secondary phosphatisation, have yielded a wealth of micro- to meso-planktonic crustacean-like taxa which have been associated with the origin of "crustaceans" [74] before the phylogenetic concepts of Mandibulata and Pancrustacea / Tetraconata had gained wider support. Owing to their small size, these forms, however, are most likely all larval, and ontogeny-based phylogenetic analyses retrieved them nested among diverse extant crustacean lineages [133]. Second, "small carbonaceous fossils" (SCFs) from western Canada have revealed disarticulated assemblages of decidedly modern-looking appendages, including mouthparts, found mostly nowadays in anostracans and copepods [73], and in certain cases reaching likely adult sizes [134]. Interestingly, the mouthparts of the Orsten 'full-bodied' crustaceomorphs are different, and more plesiomorphic, than the disarticulated SCF elements, implying the co-existence of two separate planktonic crustacean-like faunas, representing different levels of the pancrustacean phylogeny. It seems highly probable that at least one of these faunas is related to hymenocarines, either as larvae, or, for SCFs, simply as disarticulated mouthparts, which have already been shown to display derived features in taxa from BST deposits [112].

The diversification of larvae in the water column with potentially different phenotypes is here considered to be fundamental to the early evolution of arthropods for two main reasons. First, they reasonably

constituted an immediate evolutionary feedback on the radiation of suspension-feeders as discussed above ("larval explosion feedback", Fig. 2). Second, from an evo-devo perspective, the creation of larval niches different from adult ones serves as a catalyst for the emergence of new morphological features during development [112, 135], potentially accelerating evolution in a way similar to that of the emergence of holometaboly (i.e., complete metamorphosis and morpho-functionally separate immature and adult stages) in insects [136].

One of the main features placing hymenocarines outside of Pancrustacea is the lack of second antennae [33, 112], which was legitimately regarded as puzzling [137], especially when appendages arguably corresponding to second antennae are present in Orsten crustaceomorphs. Thanks to an unprecedented quality of computed tomographic rendering for this type of fossils, a small hymenocarine, *Ercaicunia* (Fig. 1b), was since documented with three-dimensional preservation of appendages, including a pair of post-antennular 'hooks' interpreted as differentiated second antennae [32]. Problematically, however, other cephalic appendages are arguably not as clearly preserved as the authors claim, and the shape or location of the mandibles appears rather uncertain. In *Waptia*, for instance, which remains much more finely preserved, and in which no trace of post-antennular appendages can be found, it is known that mandibles and their palps occupy a very anterior position, with these palps usually projecting forward [33]. One may therefore wonder whether these short and curved appendages are not simply mandibular palps. Alternatively, it is also possible that these hooks are akin to other comparable post-antennular appendages, such as those of the exotic *Cascolus* (see below), suggesting a plasticity in the expression of the hymenocarine post-antennular segment. This limbless segment remains nonetheless a characteristic of other hymenocarines [115], and is accompanied by other unusual appendicular reductions in *Odaraia* and its allies, which seemingly also lack antennules altogether. The fact that the cephala of both fuxianhuiids and euthycarcinoids are also characterized by intercalary segments [132] further testifies of the prevalence of this trait in marine taxa articulating the origin of mandibulate lineages, even if the causes of this segmental reduction remain unexplained.

By contrast to the mandibulates, the Burgess Shale fossil *Sanctacaris* had long represented the first and only relative of chelicerates from the Cambrian [138, 139], although megacheirans have also been considered by some authors as possible members of this lineage [76, 124, 140]. The formerly unclassified *Habelia optata*, originally described by Charles D. Walcott, came to demonstrate that *Sanctacaris* was not a lonely offshoot, and that, although numerically rare, chelicerate precursors had already diversified in Cambrian seas [106]. *Habelia* also clarified the thought-provoking complexity of the head of *Sanctacaris*, both taxa displaying an unparalleled alignment of seven fully-developed cephalic appendage pairs (which forms the basis of the extant chelicerate prosoma), most of which being multifunctional appendages combining sensory, grasping and crushing abilities. Although stemming from a different appendicular architecture, this evolutionary solution mimicked the morphofunctional head of mandibulates, but combined into single appendages, and became relatively simplified further up the chelicerate tree—other merostome and arachnid legs can fulfill additional grinding and sensory functions, but not in such combination and degree of morphological differentiation in a single limb [106]. It appears that this adaptation fitted the predation of small crawling animals with hard integuments—in essence, trilobite juveniles. No gut content, however, has so far been found to verify this hypothesis.

Habelia and *Sanctacaris*, now grouped in Habeliida, also allowed a direct connection with horseshoe crab-like taxa from the Silurian thought to represent basal euchelicerates [107, 108] through a particularly unwieldy character. Cephalic exopods in these taxa are leg- or antenna-like and seem to be somehow 'detached' from the basipod [106, 139]. The alternative location of attachment of these exopods to the body is not known, but there is evidence that they moved independently from the rest of the main limb axis. This condition would hence be intermediary to the later loss of this limb ramus in chelicerates and would provide support to the developmental hypothesis that the "exopod" of basal euarthropod taxa

developed in fact as a separate limb axis [60]—which would be called an exite instead of exopod [105] (Fig. 3d).

Chelicerates being diagnosed by the eponymous chelicerae (Box 1), it is not clear whether habeliidans belong to this group because the frontal appendages potentially homologous to chelicerae in these taxa are very small and not evidently chelate or sub-chelate. *Mollisonia*, another typical taxon first introduced by Walcott, very recently grounded the origination of chelicerates per se from at least the middle Cambrian, also thanks to new material found at Marble Canyon [55] (Fig. 1c). In addition to chelicerae, *Mollisonia* sports sets of overlapping "gills" reminiscent of the merostome book gills, albeit with a much-reduced number of constitutive elements. Because of this, *Mollisonia* resolves as the sister taxon to Euchelicerata, further pointing to the early Cambrian origination of extant lineages.

Box 3

The trilobites of Buridan

In order to illustrate the paradox of indecision and the human ability to choose without motive, French philosopher Jean Buridan used a fable in which a donkey would let itself starve to death, incapable of choosing between two identical buckets filled with oat. An equally staggering indecision has long affected the placement of trilobites in the arthropod phylogeny [19, 20, 63, 106, 141–143]. Trilobites possess antennules, an a priori strong character to associate them with mandibulates, especially since the ancestral euarthropod appendage is the cheira. They can also have setae on their exopods, like crustaceans often do, have large plate-like hypostomes, and it was shown recently that their eyes had a crystalline structure comparable to that of mandibulates [143]. However, trilobites also sport gnathobasipods, sets of fully-developed cephalic endopods and, importantly, tripartite apoteles (i.e. claws) that constitute robust apomorphies of Arachnomorpha [106]. The retrieval of the "deep split" topology (see Fig. 2 and Box 2) in which artiopodans are deeply nested within total-group Arachnomorpha shows that the mandibulate-like characters can reasonably be interpreted as convergences, in some cases perhaps related to a more pelagic lifestyle [144]. The eye structure of trilobites would thus illustrate the problem of extrapolating evolutionary scenarios based on the association of an extant character with a few fossils, without considering that the absence of information in most other fossil forms could in fact hide a polarization of this character as plesiomorphic—as is the case, for instance, of the "cone in cone growth" character previously presented as the apomorphy of a clade grouping hallucigeniids and onychophorans [42].

Head problems and fossil brains

A series of groundbreaking studies interpreting neurological and other rare internal remains in Cambrian fossils, at first from the Chengjiang biota [114, 140, 145, 146], have attracted a lot of attention recently and delivered thought-provoking new evidence in the context of early arthropod evolution [35]. One of these studies revealed the existence of complex visual systems in the iconic Chinese arthropod *Fuxianhuia* [145], a find recently supplemented by the arguably distantly-related *Mollisonia* from the Burgess Shale [112]. These fossils suggest that the presence of multiple optical neural centers originated early in euarthropods and were later repeatedly simplified in more derived taxa, for instance in arachnids and myriapods [147]. This scenario could serve in turn an example that even complex and a priori generally advantageous structures such as efficient eyes remain governed by evolutionary trade-offs [148].

Other studies also attempted to use neural remains in order to elucidate historical disputes about appendage homology in both extinct and extant arthropods [114, 140]. Central in this debate is the labrum, a generally pre-oral ventral structure found in a variety of shapes across extinct and extant arthropods [20], typically associated with a sclerotic plate called a hypostome, and shown to originate from an appendicular protocerebral Anlage [149, 150]. The Cambrian palaeoneurological evidence was considered as supportive of the hypothesis that the frontal appendage of radiodontans was not homologous to that of early euarthropods, being instead reduced to form the labrum [18, 35, 151]. This view was con-

tested, however, based on the alignment of anterior panarthropod metameres and the homologization of onychophoran antennae with similar protocerebral structures in euarthropods [121], but also on the argument that external morphoanatomy and phylogenetic analyses strongly support a continuous evolutionary history of the cheirae across early arthropods [36] (Fig. 3a).

It follows that the labrum more likely has a complex history across early arthropods, potentially involving the posterior migration of part, but not all the ancestral "labral complex" (Fig. 3b). It has been shown that leanchoiliid juveniles possessed a well-developed labral protrusion [76, 152], confirming the predicted presence of this structure in megacheiran based on a reinterpretation of *Oelandocaris oelandica* from the Swedish "Orsten" deposit [63, 153]. This suggests that the ostracod-like frontal complex (including sensory organs and the labrum) observed in hymenocarines [33, 112, 115] may have already dissociated from a posterior labrum, or perhaps that the individualization and posterior migration of the labrum occurred convergently in total-group Mandibulata and Panchelicerata/total-group Arachnomorpha (Fig. 3b).

Perhaps the directed effort in homologizing the tripartite brain (protocerebrum, deutocerebrum, tritocerebrum) in fossil taxa [35] is misguided by the assumption that this brain is visibly tripartite in all fossils. It should be considered that the morphoanatomy of the brain itself has evolved, and therefore that brain subdivisions in fossils (in the form of fused and emerging ganglia) could mislead topological alignments based on extant taxa [121]. A current investigation may provide evidence to support this view by showing that pre-gnathal segments have different developmental properties compared to trunk segments, which is extrapolated into considering that the former originated from a single somite during the rise of euarthropods [154]. This is by far the best and most innovative explanation to the conundrum of "proto- to deutocerebral transition" of the cheira in panarthropods [36], and implies that single anterior connectives to the cheirae [85, 114] are not protocerebral in an extant sense, but "metaprotocerebral," as they connect in fact to an undivided neural mass that later is to separate into proto-, deuto- and tritocerebrum as defined in cenocondylans.

Some authors have also generally rejected palaeoneurological evidence based on the frailty of such internal tissues as ganglions and nerves and their high susceptibility to decay [155]. Taphonomic and decay patterns these authors document seem to show convincingly that the published reconstruction of a vascular system in *Fuxianhuia* is dubious, and in general that peri-intestinal and haemocaelic structures are often neglected yet occupy a central importance in the understanding of arthropods from BST deposits [33, 58, 63, 156]. This cautionary approach is not trivial because the general taphonomic shrinking of the peri-intestinal cavity as well as appendicular hemocoelic cavities has led some authors to misinterpret these remains or even the gut as part of the central nervous system [103, 157].

The presence of neural tissues in Cambrian fossils, however, remains supported by a solid line of evidence, as these also occur in areas not overlapping with other body parts and away from the gut, such as eye stalks, and where they are known to constitute a large portion of the organic mass [33, 55, 145]. The selective resistance of nerves to decay has also been demonstrated experimentally [158]. In general, a temporal decay-based approach in experimental taphonomy is not applicable to fossils of BST deposits, because the selective taphonomy of tissues is based on idiosyncratic environmental and diagenetic conditions leading to this mode of preservation, as is generally the case for all Konservat Lagerstätten [159]. Nonetheless, as of yet, we still lack a full causal understanding of specific tissue preservation in these deposits, which is why reports of this kind must remain particularly cautious [121].

Weird wonders of the post-Cambrian

Although existing collections and further discoveries from the Cambrian certainly hold more surprises (*Kylinxia* being a recent example), it is also evident that the majority of Cambrian arthropods now fall within definite lineages, be it radiodontans, isoxyids, megacheirans, fuxianhuiids, hymenocarines, artiopodans, or the stem of extant groups (Fig. 2). In parallel to that, Silurian fossils from the Herefordshire biota in Wales, have, for a number of years, and alongside very modern-looking forms [160, 161], revealed many arthropods with challenging morphologies, despite being three-dimensionally-preserved animals generally yielding an impressive amount of morphological details (Fig. 1j). *Enalikter*, for instance, was presented as a megacheiran [162], but this interpretation was nothing straightforward, for *Enalikter* arguably lacks any megacheiran apomorphy, and its frontal appendages are not clearly distinct from some tripartite crustacean antenna; yet, this is also clearly not a crustacean, and some authors went as far as interpreting it as a polychaete [163]. This is the type of stories the "weird wonder" days of the Burgess Shale were full of. Taxa such as *Cascolus*, *Aquilonifer*, *Tanazios* or *Xylokorys* are similar in this regard: although they possess characters linking them with some known extinct or extant arthropod group, their morphoanatomies also show significant differences hampering their stable phylogenetic placement and inciting to place them in their own group. This may be a combination of the fact that they are Silurian, with much less soft-bodied data on arthropods from this period than there is from the Cambrian BST deposits, and from the discrepancies between types of preservation: with information provided by the Herefordshire material that a BST deposit lacks, and vice versa, differences between fossils may appear greater than they are. The effort made by attempting to dissect fossils [112] and obtain three-dimensional information from typically two-dimensional preservation [32] promises to harmonize our morphoanatomical understanding. As a synthesis emerges and these data are better integrated, "oddities" from the Herefordshire biota, but also from other exceptional Palaeozoic deposits yielding stem-group arthropods and euarthropods, such as the Hunsrück slate in Germany [164, 165], may prove to be more significant contributions to our understanding of the arthropod tree of life, and draw another dimension to the breadth of arthropod body plans after the Cambrian explosion.

Temporal constraints

The accumulation of evidence in recent years that the origination of both mandibulates and chelicerates occurred deep within the Cambrian necessarily represents a strong timing constraint on the arthropod evolutionary tree. On the other hand, the first appearance datum (FAD) of trilobites is well constrained to the base of Cambrian Stage 3 [166], and is documented also by the distribution of trilobite and lobopodian (*Microdictyon*) fragments among small shelly fossils (SSF), which show relatively few discontinuities and have stratigraphic significance across the Lower Cambrian [167]. A wealth of traces that arguably only arthropod appendages can produce have been described from older sediments, deep into the Fortunian, but there is no solid evidence to date that would suggest the presence of arthropods before the Cambrian [168]. Most of the panarthropod basic phenotypic pool would have appeared within 20 million years, with the presence of mineralized elements from Stage 3 then likely being an accelerating evolutionary factor in the specialization of masticatory appendages. The palaeontological evidence therefore points to an even more dramatic radiative event than was assumed thus far, as is corroborated by well-calibrated molecular clocks [17, 166]. This necessarily has important implications for genetic and phenotypic evolution early in this group [17], not the least being that parsimony is likely to be an oversimplistic approach to reconstruct relationships between basal taxa, owing to widespread parallelism and changing variability [166], explaining in part historical conflicts using this method [63].

Very recent studies have also completed the ichnological record [168] with morphological evidence to constrain the timing of terrestrialization in both total-group mandibulates, through euthycarcinoids [131], and total-group chelicerates, or arachnomorphs, through aerial breathing in eurypterids [169]. The oldest known euthycarcinoids are from the middle Cambrian [170] and the first eurypterids are from the middle Ordovician [171]. Although both groups remained primarily aquatic, this suggests that excursions onto land were well underway by the end of the Cambrian for both of the extant euarthropod lineages, raising the question of what advantages these first land dwellers might have found on generally barren grounds.

Macroevolutionary perspectives

The manifestations of evolutionary mechanisms on long time scales and among species involve asymmetrical patterns due in part to the latency between genetic regulation and phenotypic expression [14]. This asymmetry between disparity and diversity is particularly obvious in arthropods, emphasising clearly that their high-level systematics have been shaped by evolutionary constraints and trade-offs at least as much as by phenotypic innovations [4]. In that sense, the "sculpting material" metaphor of the arthropod body should be more interestingly approached from the perspective of what composed, and what can deform this material rather than simply the wealth of its possible shapes. Wills and colleagues have long worked on quantifying heterogeneous disparity patterns using arthropods as models, especially early disparity bursts among lineages [16, 172, 173]. They have also explored the promising and far-reaching avenue of defining persistent evolutionary trends, in that case increasing morpho-functional complexity [174]. This is of particular interest to our understanding of arthropod evolution, because this phenomenon appears early on as a driver of selection [58, 175]. Updating these analyses in the context of Mandibulata and expanding them to other groups could reveal a powerful explanatory factor for overall phenotypic evolution in Arthropoda.

Owing to their strong biomineralization, which correlates to their known abundance and diversity through the Palaeozoic, trilobites have generally been pioneering models to identify macroevolutionary patterns in arthropods and the fossil record as a whole [176]. They also have been used to investigate early burst models of high Cambrian disparity preceding phenotypic canalization [177, 178], a view that was later refined to point out the variable relaxation of constraints on segment number across lineages, often associated with the co-evolution of adaptive features on a large scale [179–181]. Reference ontogenetic work on trilobites, especially to reconstruct heterochronic trends [182], should inspire research on softbodied larvae [75, 77, 152], because heterochrony is another potentially highly significant explanatory variable of arthropod morphoanatomy over time.

In general, however, comparative studies on fossil arthropods are lacking. A preliminary top-down approach investigating disparity in euarthropods as a whole [4] finds evidence that a "displaced-optimum model" of evolution (that is, with swift but increasingly smaller translations from one adaptive peak to another [183]) characterizes the rise of body plans in these animals, and that this phenomenon was associated with the fast build-up of genetic regulatory networks, as suggested by others for all metazoans [184]. The next step is to link these patterns to morphological characters, notably through studying covariations in the context of heterochrony and developmental plasticity, as was done for trilobites. Although this integrated information will serve to refine our evolutionary models for phylogenetic analyses, now that a phylogenetic framework appears to be broadly stabilizing for fossil and extant arthropods [4, 24, 103], we should look beyond the sole genealogy and use these uniquely rich data to elucidate the many persistent mysteries of macroevolution.

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Institutional abbreviations

MGUH, Geological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; NIGPAS, Nanjing Institute of Geology and Palaeontology, Nanjing, China; OUMNH, Oxford University Museum of Natural History, Oxford, United Kingdom; ROMIP, Royal Ontario Museum, Invertebrate Palaeontology collection, Toronto, Canada; SAM, South Australian Museum, Adelaide, Australia; YKLP, Yunnan Key Laboratory for Palaeobiology, Kunming, China; YPM, Yale Peabody Museum of Natural History, New Haven, USA.

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