Review

The origin and early evolution of arthropods

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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 epopee, exceptionally-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, in particular, waged in the name of a wasteful and profit-driven agriculture, has led to catastrophic consequences for the survivability of these animals worldwide (Sánchez-Bayo and Wyckhuys 2019), which, cumulated to other environmental crises caused by unbridled resource exploitation and consumption, such as global warming, is threatening to irremediably pauperize the planet’s landscapes (Dirzo et al. 2014; Newbold et al. 2016).

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 of all other four largest and traditional arthropod groups—chelicerates, myriapods, crustaceans and insects—, all present by at least by the Late Devonian (Garrouste et al. 2012; Siveter et al. 2014b; Waddington et al. 2015; Suarez et al. 2017), diversified through all of the five major pre-Anthropocene biodiversity crises. Likely since the Jurassic (Labandeira and Sepkoski 1993), insects have become by a large margin the most diversified and abundant of arthropods (Grimaldi and Engel 2005), but all main lineages have characteristically experienced explosive radiations and have shown extended longevity 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 (Erwin and Valentine 2013). 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 (Budd and Telford 2009; Edgecombe and Legg 2014). In this context, arthropods have famously initiated discussions about shifts in evolutionary tempo and mode at the macroevolutionary scale, and in particular the heterogeneity of
disparity patterns and their possible meaning for body plan evolution (Gould 1989; Briggs et al. 1992; Lee et al. 2013).

However, the insights and developments following these studies have been hindered by enduring debates about the phylogenetic relationships between arthropods, which fossil taxa have often more fueled than resolved (Budd 2002; Cotton and Braddy 2004; Scholtz and Edgecombe 2006). In the last ten years and in the case of extant taxa, broad-scale combined morphological and molecular phylogenetics and phylogenomics have broken this deadlock by achieving strong branch support and topological convergence for major clades (Regier et al. 2010; Rota-Stabelli et al. 2011; Giribet and Edgecombe 2019; Edgecombe 2020), even if the resolution of certain internal nodes remains a salient issue (Sharma et al. 2014). 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, a broad grouping according to which Hexapoda (including insects) arose from a paraphyletic crustacean lineage.

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 (Edgecombe and Legg 2014; Legg et al. 2013). 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 (Caron et al. 2010; Yang et al. 2013; Caron et al. 2014) or the use of new technologies (Zhai et al. 2019), 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 (Vannier et al. 2018). Conversely, a series of exceptional discoveries involving preserved neural tissues (Strausfeld et al. 2016b) have lately prompted reassessments of the evolution of arthropod heads (Ortega-Hernández et al. 2017), but, in reality, these interpretations of a relatively new and challenging palaeontological medium may not yet replace the strength of more conservative hypotheses based on external morphology (Aria et al. 2020). Beyond genes and morpho-anatomy, an integrated palaeobiological and palaeoecological picture and its role in the early radiation of
arthropods is also starting to take shape (Bicknell and Paterson 2017; Caron and Aria 2017; Lerosey-Aubril and Pates 2018).

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, new phylogenetic methods, and this review aims at providing a simple guide to current knowledge as well as to 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 the “Cambrian planktonic revolution”

Arthropoda is now recognized as a monophyletic phylum within Ecdysozoa, the moulting animals (Budd and Telford 2009; Edgecombe and Legg 2014; Giribet and Edgecombe 2019) (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 sister to the Panarthropoda, an expanded definition of Arthropoda also including, among extant forms, onychophorans (velvet worms) and, most likely, tardigrades (water bears) (Giribet and Edgecombe 2017).

There is an ongoing debate about whether onychophorans or tardigrades are the extant panarthropods closest to the common arthropod ancestor. Evidence coming from neuroanatomy (Mayer et al. 2013) and other internal organs favours either a sister-group relationship with tardigrades (e.g. presence of metameric ganglia along the ventral nerve cord; a grouping also called Tactopoda (Smith and Ortega-Hernandez 2014)) 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) (Edgecombe et al. 2000). A recent fossil-inclusive analysis found tardigrades to be ancestral (Caron and Aria 2017), consistent with most other phylogenetic studies (Giribet and Edgecombe 2017). This result is influenced by the fact that, in spite of their dramatic
developmental contraction (Smith et al. 2016), tardigrades retain the plesiomorphic condition of a truncated posterior termination bearing a limb pair with claws pointing anteriorly (inherited from the pool of suspension-feeding adaptations). The loss of many trunk somites—pointing to a longer ancestral body—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* (Caron and Aria 2017). However, while providing detailed genetic and phenotypic information, tardigrades and onychophorans are also outstandingly autapomorphic (onychophorans have independently evolved a ventral mouth opening and internalized mouthparts and, not the least, are terrestrial), which urges caution when attempting to extrapolate shared derived conditions.

By contrast, fossils called lobopodians, mostly found in Cambrian rocks, have greatly enriched our understanding of the early evolution of panarthropods (Liu and Dunlop 2014) (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, composing the foundation of the arthropod megaclade. Fossil-inclusive phylogenetic analyses find tardigrades to be well nested within Panarthropoda (Smith and Ortega-Hernandez 2014; Smith and Caron 2015; Caron and Aria 2017), and show that the surviving Onychophora and Tardigrada are but highly autapomorphic offshoots of this initial radiation associated with the Cambrian explosion. Other lobopodians survived through the Silurian (Siveter et al. 2018) up to at least the Carboniferous (Haug et al. 2012a), 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.

Perhaps the most important aspect of lobopodians put forward in the recent years is their arguably common adaptation, at various degrees, to suspension-feeding (Yang et al. 2015; Caron and Aria 2017). Most striking among the luolishaniids, which possess stout anchoring back limbs and frontal arms adorned with pairs of thin spinules (Ma et al. 2009; Yang et al. 2015; Caron and Aria 2017) (Fig. 1l), this ecology also possibly characterizes the famed hallucigeniids (Smith and Caron 2015; Caron and Aria 2017), 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 crawling forms (Dzik 2011) (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 is not entirely clear, 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 (Aria 2019); 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
(evolved multiple times within the group and led to gigantism in the Ordovician (Vinther et al. 2014)), has indeed been shown to be present in several relatives of the iconic predator Anomalocaris, having
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 particularly larvae. When put into the overall metazoan perspective, alongside
sponges, cnidarian polyps, echinoderms, brachiopods and a variety of other animals (Nanglu et al. 2016;
Moysiuk et al. 2017), it seems that a “planktonic revolution” was as much a driver of the Cambrian
explosion as it was of the Great Ordovician Biodiversification Event (Servais et al. 2008), even if the fossil
evidence for small meso- to microplankton is still largely (but decreasingly so, see below) indirect (Lerosey-
Aubril and Pates 2018) (Fig. 2). This rapid expansion of the suspension-feeding niche in the Cambrian,
however, is clearly the continuation of an adaptation already largely present in the Ediacaran (Wood and
Curtis 2015; Gibson et al. 2019), and it seems therefore that the presence of arthropods and their larvae represent one of the major distinctions between the two stages of this process. Radiodontans, nonetheless, also developed a much broader diversity of specializations involving the cheirae of radiodontans, which also includes sediment sifting (Moysiuk and Caron 2019a), 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 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.

Assembly of the arthropod body plan

One of the most interesting and well-documented evolutionary sequences from cycloneuralians to arthropods is that of the mouth and its associated structures (Smith and Caron 2015). Some basal lobopodians possessed an eversible pharynx lined with teeth, similar to that of priapulids (Caron and Aria 2017); others, like Hallucigenia, had also independently evolved circumoral sclerotic plates (Smith and Caron 2015), 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 (Liu et al. 2006, 2007), although the first midgut glands only appear in xenusiids (Vannier et al. 2014), suggesting an evolution in the mode of feeding and/or diet (possibly associated with the introduction of predation or irregular scavenging (Chen et al. 1997; Vannier and Chen 2002)). 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 (Vinther et al. 2016)), bearing flap-like swimming appendages, in addition to lobopods—at least in Pambdelurion (Budd 1997). 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 (Vinther et al. 2016). The rotation of the mouth opening, which
in extant lineages is characteristically ventral with postero-ventral orientation and connected to an
anterio-ly-looped esophagus, 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 (Park et al. 2018).

A circumoral sclerotized apparatus, giving its name to radiodontans (radius (Latin) – odoús (Greek)
meaning literally radial – teeth), exemplified by Anomalocaris (Daley and Edgecombe 2013) or Hurdia
(Daley et al. 2013), is therefore not exclusive to this group. A ‘peytoia’ type of outer sclerotized ring (or its
derivatives (Daley and Bergström 2012)) 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 (Vinther et al. 2016). Similarities include the presence of numerous inner
teeth. A number of radiodontans also possess such an inner row of smaller dented plates, which could be
derived from the symplesiomorphic pharyngeal teeth. Interestingly, a comparable set of elements are found
in dissociation in amplectobeluid radiodontans from the Chengjiang biota, never forming the typical oral
cone (Cong et al. 2017, 2018). A single specimen of Amplectobelua symbrachiata shows overlapping
gnathobase-like differentiated plates in association with alleged reduced flaps (Cong et al. 2017). 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 is otherwise fundamentally defined by
the evolution of an arthrodized pair of appendages, although this is obviously not an autapomorphy of the
group (see below and Figs 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 and seemingly sudden evolutionary step marking the appearance of radiodontans is the presence of well-developed stalked compound eyes (Paterson et al. 2011), whereas lobopodians only possess simple ocelli (Ma et al. 2012a), when present (Fig. 2).

To this day, the iconic *Opabinia regalis* from the Burgess Shale (Whittington 1975; Briggs 2015) remains an oddity. 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* (Budd 1997) on the one hand, and *Isoxys* (Vannier et al. 2009), leanchoiliid euarthropods (Butterfield 2002; Aria et al. 2015) and even the trilobite-like *Kiisortoqia* (Stein 2010), 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 (Vannier et al. 2014) and anomalocaridids (Daley and Edgecombe 2013) (in which these phosphatized structures were possibly misinterpreted as muscle tissues (but see Young and Vinther (2017)), but are not stacked.

*Opabinia* can, however, serve 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 (Aria 2019). 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 (Briggs 2015), which is, by contrast, more difficult to detect in complete radiodontan specimens (Chen et al. 1994; Daley and Edgecombe 2013; Moysiuk and Caron 2019a) (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 (Budd 2001; Caron and Aria 2017). Body arthrodization
is unclear in isoxyids, which places megacheirans—historically, the so-called “great appendage” euarthropods—, and more precisely jianfengiids, as the earliest unambiguous euarthropod representatives (Aria et al. 2020) (Figs 1m, 2). Details about the formation of tergitic articulation are not documented.

It has been debated whether Opabinia combined both lateral flaps and lobopods (Briggs 2015). Although any developmental remnants of lobopodous limbs in Opabinia seems fully internalized and associated with the circum-intestinal haemocoelic cavity (Aria and Caron 2015), such combination is arguably well evidenced at least in Pambdelurion (Budd 1997). Two separate rows of lateral flaps were otherwise described in the massive Aegirocassis from the Lower Ordovician Fezouata Lagerstätte in Morocco, and as possibly present in other radiodontans (Van Roy et al. 2015). 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 (Aria and Caron 2015) (isoxyids are arthropods with bivalved carapaces sharing traits with radiodontans; Figs. 1f, 2), showing 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 (Wolff and Scholtz 2008). 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 (Sutton et al. 2002; Briggs et al. 2012; Aria and Caron 2017b, 2019) (Fig. 3d), 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. 2001).

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 (Caron and Aria 2017). A variety of antero-dorsal and paired ventro-lateral sclerites mark the appearance of radiodontans, and their unique lateral elements may even constitute one of their strongest
apomorphies (Van Roy et al. 2015; Moysiuk and Caron 2019a; Cong et al. 2017; Zeng et al. 2018). Their continuity with arthropod carapaces and head shields is not entirely clear, but there is some evidence (Aria et al. 2020) to posit that at least the antero-dorsal element, despite spanning a very large size range in radiodontans (Moysiuk and Caron 2019a), corresponds to the so-called “anterior/ocular sclerite” identified across early arthropods (Ortega-Hernández 2015; Aria and Caron 2017a), including megacheirans (Aria et al. 2020) (Fig. 3b).

Isoxyids (Figs 1f), now retrieved by different large phylogenetic datasets as sister taxa to all other euarthropods (Legg et al. 2013; Aria and Caron 2017a) (Fig. 2, Box 2; although this bears partly on many 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. In reality, the morphological ranges of these structures overlap, as is clearly documented by crustaceans (Olesen 2013), and, in general, it might be better to see shields and carapaces as different phases of an evolutionary continuity based on the integration of additional segments into the head tagma. Yet these bivalved carapaces enclosing a part or the entire body laterally are easily recognizable in a wide range of Cambrian taxa, despite showing shape variations (Izquierdo-López and Caron 2019), and possibly being modified into a flat ‘shield’ in fuxianhuiids (Figs 1a). These 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 particular in the form of pleural extensions, fusion of posterior segments (the pygidium) and other ornamentations.

Although the presence of tergites is unclear in isoxyids (and somewhat incompatible with an interpretation of their tailpiece as composed of radiodontan-like soft flaps (Legg and Vannier 2013)), the genus Isoxys in particular possesses trunk endopods with distinct podomere boundaries (Fu et al. 2011, 2014). 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 (Aria et al.
2015)) for post-frontal endopods (notwithstanding minor variations), which was possibly already present
in Isoxys (Fu et al. 2011, 2014).

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, except perhaps for their toothed basipods which remain of simple architecture and,
arguably, cannot be regarded as gnathobases as they are known in arachnomorphs (Ortega-Hernandez et al.
2013) (Fig. 3d). They 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 (Aria et al. 2015). The recently described
Kylinxia beautifully documents the homologous continuity of the cheirae across arthropods and
euarthropods as well as the very basal position of megacheirans in the euarthropod tree (Zeng et al. 2020).
The animal also importantly sheds light on the long-puzzling quintet of eyes in Opabinia, now arguably
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 (result not shown).

However, rare Cambrian arthropods with bivalved carapaces have also been described displaying
cheirae. It would therefore appear that these elaborate frontal appendages were retained through two
separate lineages, one of them also possibly retaining the bivalved carapace of isoxyids (Fig. 2; see also
Zeng et al. 2020). Although relatively simple in principle, the plausibility of this evolutionary scenario (Box
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.
Deep Cambrian origins of extant lineages

Numerous morphotypes from the Burgess Shale have long been included in or compared to crustaceans (Briggs 1978), although these interpretations were challenged in the 21st century (Budd 2002; Legg et al. 2012). Since the stabilization of Mandibulata (Regier et al. 2010; Rota-Stabelli et al. 2011), 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 (Caron et al. 2014) provided support for the mandibulate affinity of a Branchiocaris relative, Tokummia (Aria and Caron 2017a), and also shed light on the affinities of Cambrian bivalved arthropods as a whole, coined—in the exclusion of isoxys, 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 (Vannier et al. 2018). 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 (Walossek and Müller 1998; Boxshall 2004); namely, the role of subdivided basipods bearing multiple differentiated endites in the formation of the coxa, sub-coxa and features derived from them—notably the mandibles (Popadić et al. 1998) (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 (Coulcher et al. 2015). Recently reevaluated evidence from the renowned Rhynie Chert Lagerstätte has also illuminated the morpho-anatomy of the enigmatic euthycarcinoids, placing them on the myriapod lineage (Edgecombe et al. 2020); a crucial find that will help link myriapods with their marine ancestors and therefore elucidate plesiomorphic characters at divergence between Myriapoda and Pancrustacea—a necessary condition to resolving the placement of hymenocarines as either stem mandibulates or stem pancrustaceans (Fig. 2). Correlative to this finding, and elaborating on previous phylogenetic results (Vannier et al. 2018; Aria et
the iconic fuxianhuiids of the Chengjiang fauna (Figs 1, 2) have been described as mandibulates with strong morphological affinities with euthycarcinoids and myriapods (Aria et al. 2021).

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 (Zhang et al. 2007) (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” (Walossek and Müller 1998) 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 (Wolfe and Hegna 2014). 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 (Harvey et al. 2012), and in certain cases reaching arguably adult sizes (Harvey and Butterfield 2008). 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.

The diversification of larvae in the water column 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 (Aria and Caron 2017a; Wolfe 2017), potentially accelerating evolution in a way similar to that of the emergence of holometaboly in insects (Rainford et al. 2014). Although some have already been described (Liu et al. 2016; Fu et al. 2020), the iconic fuxianhuiids of the Chengjiang fauna (Figs 1, 2) have been described as mandibulates with strong morphological affinities with euthycarcinoids and myriapods (Aria et al. 2021).
2018), certain Cambrian biotas such as the Chengjiang contain an opulence of fossil larvae known since early excavations but remained understudied (pers. obs.); as demonstrated notably with trilobites (Hughes 2007), their study could be invaluable to understanding early arthropod evolution beyond one-dimensional phylogenetic relationships, informing heterochronic trends and providing another perspective on a still elusive Cambrian morphological variability.

One of the main features placing hymenocarines outside of Pancrustacea is the lack of second antennae (Aria and Caron 2017a; Vannier et al. 2018), which was legitimately regarded as puzzling (Edgecombe 2017), 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 (Zhai et al. 2019). Problematically, however, other cephalic appendages are arguably not as clearly preserved as the authors claim, and the shape or location of the mandibles is in fact uncertain. In *Waptia*, for instance, which remains much more finely preserved, and in which no trace of post-antennular can be found, it is known that mandibles and their palps occupy a very anterior position, with these palps usually projecting forward (Vannier et al. 2018). 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 such 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, and is accompanied by other unusual appendicular reductions in *Odaraia* and its allies, which seemingly also lack antennules altogether. The fact that the cephal of both fuxianhuiids and euthycarcinoids are also characterized by intercalary segments (this issue) 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 (Briggs and Collins 1988; Legg 2014), although
megacheirans have also been considered by some authors as possible members of the chelicerate lineage (Haug et al. 2012b; Tanaka et al. 2013; Liu et al. 2020). 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 (Aria and Caron 2017b). Habelia also clarified the thought-provoking complexity of Sanctacaris’ head, these taxa displaying an unparalleled alignment of seven 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 appendage differentiation characteristic of mandibulates, and, interestingly, became simplified further up the chelicerate tree (Aria and Caron 2017b). 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 (Sutton et al. 2002; Briggs et al. 2012) through a particularly unwieldy character. Cephalic exopods in these taxa are leg- or antenna-like and seem to be somehow ‘detached’ from the basipod (Legg 2014; Aria and Caron 2017b). The 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 exopods 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 (Van Roy et al. 2015) (which would be called an exite instead of exopod (Wolff and Scholtz 2008)), directly at odds with the appendage morphology of isoxyids (Fig. 3d).

Chelicerates being defined 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 (Aria and Caron 2019) (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.

**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 (Ma *et al.* 2012b, 2014; Tanaka *et al.* 2013; Cong *et al.* 2014), have attracted a lot of attention recently and delivered thought-provoking new evidence in the context of early arthropod evolution (Ortega-Hernández *et al.* 2017). One of these studies revealed the existence of complex visual systems in the iconic Chinese arthropod *Fuxianhuia* (Ma *et al.* 2012b), a find recently corroborated by the arguably distantly related *Mollisonia* from the Burgess Shale (Aria and Caron 2017a), suggesting that the presence of multiple neural centers originated early in euarthropods and were later repeatedly simplified in more derived taxa (Strausfeld *et al.* 2016a). This phenomenon particularly emphasizes the fact that even complex and a priori generally advantageous structures such as efficient eyes remain governed by evolutionary trade-offs.

Other studies also attempted topological reconstructions of neural remains in order to elucidate historical disputes about appendage homology in both extinct and extant arthropods (Tanaka *et al.* 2013; Cong *et al.* 2014); the evidence presented allegedly supported the hypothesis that the frontal appendage of radiodontans was analogous to that of early euarthropods, evolving instead into the originally appendicular and protocerebral structure called the labrum (Budd 2002; Ortega-Hernández *et al.* 2017), generally located in front of the mouth. This evidence was contested, however, showing that external morpho-anatomy and phylogenetic analyses strongly supported a continuous evolutionary history of the cheirae across early arthropods (Aria *et al.* 2020) (Fig. 3a), hence also implying that the labrum has a more subtle and complex history parallel to the diversification of arthropods (Fig. 3b). It has been shown that leanchoiliid juveniles possessed a well-developed labral protrusion akin to that of extant lineages (Liu *et al.* 2016, 2020).
suggesting that the ostracod-like frontal complex observed in hymenocarines (Aria and Caron 2017a; Vannier et al. 2018) may have already dissociated from the labrum, or perhaps that the individualization and posterior migration of the labrum occurred convergently in total-group Mandibulata and Panchelicerata/total-group Arachnomorpha.

Perhaps the zealously in homologizing the tripartite brain (protocerebrum, deutocerebrum, tritocerebrum) in fossil taxa (Ortega-Hernández et al. 2017) could also be mitigated by the consideration that the morpho-anatomy 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. A current investigation may provide developmental evidence to support this view (Lev and Chipman 2020).

Some authors have also generally rejected the palaeoneurological evidence based on the frailty of such internal tissues as ganglions and nerves and their high susceptibility to decay (Liu et al. 2018). 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 (Aria and Caron 2015; Aria et al. 2015; Vannier et al. 2018; Mayers et al. 2019). 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, while the selective resistance of nerves to decay has also been demonstrated experimentally (Edgecombe et al. 2015). In general, a temporal decay-based approach 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 (Parry et al. 2018). 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, especially considering that studies are published in which guts in poorly preserved, partially decayed specimens are misinterpreted as nerve cords (Ortega-Hernández et al. 2019).
Weird wonders of the post-Cambrian

Although existing collections and further discoveries from the Cambrian certainly hold more surprises, 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, revealed many arthropods with challenging morphologies, despite being three-dimensionally-preserved animals generally preserving an impressive amount of morphological details (Fig. 1j). *Enalikter*, for instance, was presented as a megacheiran (Siveter *et al.* 2014a), but this interpretation was nothing straightforward, for *Enalikter* arguably lacks in fact any megacheiran apomorphy, and its frontal appendages are not clearly distinct from some tripartite crustacean antenna; yet, this is also clearly no crustacean, and some authors went as far as interpreting it as a polychaete (Struck *et al.* 2015). 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 morpho-anatomies 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 (also considering fossil reconstructions from the Herefordshire biota are time-consuming and published taxa are selected from a still vast quantity of unstudied material, D. Briggs, pers. comm.) and from the discrepancies in 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 (Aria and Caron 2017a) and obtain three-dimensional information from typically two-dimensional preservation (Zhai *et al.* 2019) promises to harmonize our morpho-anatomical 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 (Kühl and Rust 2012), may prove to
be more significant contributions to our understanding of the arthropod tree of life, and provide 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 (Paterson et al. 2019), 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 (Steiner et al. 2007). 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 (Daley et al. 2018). 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 (Lee et al. 2013; Paterson et al. 2019). This
necessarily has important implications for genetic and phenotypic evolution early in this group (Lee et al.
2013), not the least being that **parsimony is likely to be an oversimplistic evolutionary model** to reconstruct
relationships between basal taxa, explaining in part historical conflicts using this method (Aria et al. 2015).

Very recent studies have also completed the ichnological record (Daley et al. 2018) with
morphological evidence of aerial breathing to constrain the timing of terrestrialization in both total-group
mandibulates, via euthycarcinoids (Edgecombe et al. 2020), and total-group chelicerates, or
arachnomorphs, via eurypterids (Lamsdell et al. 2020). The oldest euthycarcinoids are from the middle
Cambrian (Collette and Hagadorn 2010) and the first eurypterids are from the middle Ordovician (Lamsdell
et al. 2015), and 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.

Macroevolutionary perspectives

When considered in its genetic and developmental context, the “sculpting material” metaphor of the arthropod body is evidently a simplification, for, in fact, the story of evolution is first that of constraints: any given feature or shape is the result of a trade-off between the content of the genetic toolkit, the control of its expression, and the sum of biological and environmental factors integrating its viability into a whole, including other features of the same organism. Arthropods are archetypes of the paradox opposing morphological constraint and variability, as illustrated by a tremendous diversity of secondary traits associated with exceptionally stable and long-lasting body architectures. Fossils offer insight into the rise of these body plans, and thus they are crucial to understanding these morphological transitions, which in turn permit to apprehend key – yet still mechanistically elusive – macroevolutionary concepts such as canalization, stasis or modularity. Owing to their abundance and diversity, trilobites have served as model organisms for such investigations, and “early bursts” models of high Cambrian disparity preceding canalization (Hughes 1991; Webster 2007) were refined to point out the relaxation of segmental constraints often through the co-evolution of adaptive features on a large scale (Hughes et al. 1999; Hughes 2003; Webster and Zelditch 2011). However, comparative studies on other fossil arthropods are lacking. A top-down approach investigating disparity in euarthropods as a whole (Aria 2020) finds evidence that a canalized displaced-optimum model of evolution (that is, with swift but increasingly smaller translations from one adaptive peak to another) characterizes the rise of body plans in these animals, and that this phenomenon was associated with the fast build-up of genetic regulatory networks. The next step is to link these patterns to morphological characters, notably through studying co-variations 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
is already stabilizing for fossil and extant arthropods, we should look beyond the sole genealogy and use these uniquely rich data to elucidate the many persistent mysteries of macroevolution.

Box 1

Glossary

**Arthrodization:** The articulation of two sclerotized body 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 raptorial 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 podomere.

**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 podomeres.

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

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**Box 2**

**Competing new evolutionary scenarios**

| A | B |
|---|---|
| ![MEGACHEIRAN STEM](image1) | !["DEEP SPLIT"](image2) |

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 chelicere relationships (Giribet 2018). Disagreements do persist regarding the placement of early fossil groups (Edgecombe 2020), but cumulative evidence in the past decades 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 (Aria 2019). 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 (Aria 2020) 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 (Haug et al. 2012b) or the basal position of bivalved taxa (Legg et al. 2012). Some authors have recently proposed a variant of the “deep split” scenario with derived isoxyids (Zeng et al. 2020).

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 (Edgecombe and Ramsköld 1999; Cotton and Braddy 2004; Aria et al. 2015; Aria and Caron 2017b; Zeng et al. 2017; Scholtz et al. 2019). 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, and it was shown recently that their eyes had a crystalline structure comparable to that of mandibulates (Scholtz et al. 2019). However, trilobites also sport gnathobasipods, sets of fully-developed cephalic endopods and, importantly, tripartite apoteles (i.e. claws) that constitute robust
apomorphies of Arachnomorpha (Aria and Caron 2017b). 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 (Moysiuk and Caron 2019b). 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 (Smith and Ortega-Hernandez 2014).

Figure 1. Variety of preservations and fossils that have recently reshaped or challenged our views on early arthropod evolution. a, Alacaris multinoda Yang et al. 2018, specimen YKLP 12268 (holotype), from the Xiaoshiba biota; a fuxianhuiid. Image courtesy of Xiguang Zhang. b, Ercaicunia multinodosa Zhai et al. 2018, specimen YKLP 16201, from the Chengjiang biota; a hymenocarine. X-ray computed tomography, image courtesy of Dayou Zhai. c, Mollisonia plenovenatrix Aria and Caron 2019, 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. 2016, specimen SAM P45629, from the Emu Bay Shale; a habeliidan. Image courtesy of Jim Jago. e, Yicaris dianensis Zhang et al. 2007, 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 2015, specimen ROMIP 62976 (holotype), from the Burgess Shale (Marble Canyon); an isoxyd. Image courtesy of Jean-Bernard Caron. g, Kerygmachela kierkegaardi Budd 1993, specimen MGUH 32048a, from Sirius Passet; a swimming lobopodian. Image courtesy of Jakob Vinther. h, i, Aegirocassis benmoulae Van Roy et al. 2015, 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. 2017, 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, *Hongshiyanspis yiliangensis* Zhang and Lin in Zhang et al. 1980, specimen NIGPAS 164503, from the Xiazhuang biota; a trilobite. Image courtesy of Han Zheng. l, *Ovatiovermis cribratus* Caron and Aria 2017, 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. 2015, 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). Scale bars, 10mm (a, g, m), 1mm (b, j), 3mm (c, f, k, l), 2mm (d), 100μm (e), 20mm (h), 100mm (i).

**Figure 2. Relationships and characteristics of the main fossil panarthropod groups.** Summarized phylogenetic framework of panarthropod relationships. 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.
Figure 3. Understanding and challenges of the early evolution of key arthropod features. a, Frontal most appendage. The robust, raptorial frontal appendage of xenusiiids 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. b, Labrum. 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, frontal most 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 frontal most pre-oral organs seen in some fossils, and whether the various “labral” features in chelicerates and mandibulates correspond to one of these externalized protocerebral features, or both. The black square represents the mouth. c, Head tagma. The head tagma is poorly defined in stem euarthropods, but in some cases appendage differentiations seem to delimit a four-segmented (i.e., five-somatic) head (α); in megacheirans, this five-somatic 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-somatic head arose the diagnostic six-somatic mandibulate cephalon (γ, although beyond the larval stage crustaceans evolved the more inclusive cephalothorax), but also the more variable cephalas of arachnomorphs. In these taxa, the five-somatic tagma transitions directly to possibly six-, seven and even eight-somatic heads, the latter representing the ancestral condition of panchelicerates (δ). 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 cenocodylans. 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 the original basipod, that is, the distalmost segment of the entire basipod complex, or basipodite; by contrast, exites arise from other basal segments (δ). Early members of the chelicerate lineage possess “semi-detached” stenopodous exopods whose affinity as exopods or exites is unclear (ε). b, basipod; c/m, coxa/mandible; df, dorsal flap; en, endopod; ex, exopod; exi, exite; vf, ventral flap.

Acknowledgements
I thank Gregory Edgecombe and Joe Moysiuk for various discussions and early comments on this version of the manuscript.

Ethics declaration
This work was supported by a President’s International Fellowship Initiative grant (#2018PC0043) and a China Postdoctoral Science Foundation Grant (#2018 M630616). The author declares having no competing interests.

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