

1 *Review*

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4 **The origin and early evolution of arthropods**

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14 **Abstract**

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

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51 **Introduction**

52 Arthropods constitute a central and colossal component of Earth's biosphere, at both the macroscopic and
53 microscopic levels. Since the beginning of the Phanerozoic, these hyperdiverse, articulated animals have
54 shaped most terrestrial and marine ecosystems, and their pivotal roles in trophic networks often have a
55 direct and considerable impact on our industries and economy—be it vital or detrimental. The war on
56 insects, in particular, waged in the name of a wasteful and profit-driven agriculture, has led to catastrophic
57 consequences for the survivability of these animals worldwide (Sánchez-Bayo and Wyckhuys 2019),
58 which, cumulated to other environmental crises caused by unbridled resource exploitation and
59 consumption, such as global warming, is threatening to irremediably pauperize the planet's landscapes
60 (Dirzo *et al.* 2014; Newbold *et al.* 2016).

61 This waning and fragility stand in stark contrast to more than half-a-billion years of exceptional
62 resilience to mass extinctions. Although trilobites, vanishing at the end of the Permian, are a notable
63 exception, the **body plans** of all other **four largest and traditional arthropod groups—chelicerates,**
64 **myriapods, crustaceans and insects**—, all present by at least by the Late Devonian (Garrouste *et al.* 2012;
65 Siveter *et al.* 2014b; Waddington *et al.* 2015; Suarez *et al.* 2017), diversified through all of the five major
66 pre-Anthropocene biodiversity crises. Likely since the Jurassic (Labandeira and Sepkoski 1993), insects
67 have become by a large margin the most diversified and abundant of arthropods (Grimaldi and Engel 2005),
68 but all main lineages have characteristically experienced explosive radiations and have shown extended
69 **longevity of their families and genera.** The search for the causes and mechanisms surrounding the origin of
70 the highly modular architecture that has been certainly determinant in the success and expansion of the
71 arthropod phylum has therefore focused on the earliest Phanerozoic, and specifically the Cambrian
72 explosion (Erwin and Valentine 2013). Starting with the Burgess Shale, a variety of Cambrian Fossil
73 Lagerstätten across the world have yielded a wealth of non-biomineralizing species informing early
74 diversity and character transitions leading to arthropods and to their ramifications (Budd and Telford 2009;
75 Edgecombe and Legg 2014). In this context, arthropods have famously initiated discussions about shifts in
76 evolutionary tempo and mode at the **macroevolutionary scale,** and in particular the heterogeneity of

77 disparity patterns and their possible meaning for body plan evolution (Gould 1989; Briggs *et al.* 1992; Lee
78 *et al.* 2013).

79 However, the insights and developments following these studies have been hindered by enduring
80 debates about the phylogenetic relationships between arthropods, which fossil taxa have often more fueled
81 than resolved (Budd 2002; Cotton and Braddy 2004; Scholtz and Edgecombe 2006). In the last ten years
82 and in the case of extant taxa, broad-scale combined morphological and molecular phylogenetics and
83 phylogenomics have broken this deadlock by achieving strong branch support and topological convergence
84 for major clades (Regier *et al.* 2010; Rota-Stabelli *et al.* 2011; Giribet and Edgecombe 2019; Edgecombe
85 2020), even if the resolution of certain internal nodes remains a salient issue (Sharma *et al.* 2014). There is
86 now robust evidence that all extant arthropods can be divided into two main lineages: Chelicerata and
87 Mandibulata, the latter including Myriapoda as well as Pancrustacea, a broad grouping according to which
88 Hexapoda (including insects) arose from a paraphyletic crustacean lineage.

89 The inclusion of fossils to one of these total-evidence datasets—key to a contextualized
90 macroevolutionary perspective—has been shown to be consistent with these topologies (Edgecombe and
91 Legg 2014; Legg *et al.* 2013). While summarizing certain solid advances in this field, this result did not
92 mean, however, that the palaeontological understanding itself was complete, and recent findings, catalysed
93 in part by the discovery of new fossil sites (Caron *et al.* 2010; Yang *et al.* 2013; Caron *et al.* 2014) or the
94 use of new technologies (Zhai *et al.* 2019), have since rewritten the significance of many extinct taxa. This,
95 in turn, has changed our perspective on early body plan evolution in these animals, introducing new
96 fundamental questions to current research (Vannier *et al.* 2018). Conversely, a series of exceptional
97 discoveries involving preserved neural tissues (Strausfeld *et al.* 2016b) have lately prompted reassessments
98 of the evolution of arthropod heads (Ortega-Hernández *et al.* 2017), but, in reality, these interpretations of
99 a relatively new and challenging palaeontological medium may not yet replace the strength of more
100 conservative hypotheses based on external morphology (Aria *et al.* 2020). Beyond genes and morpho-
101 anatomy, an integrated palaeobiological and palaeoecological picture and its role in the early radiation of

102 arthropods is also starting to take shape (Bicknell and Paterson 2017; Caron and Aria 2017; Lerosey-Aubril
103 and Pates 2018).

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

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112 **The panarthropod cradle and the “Cambrian planktonic revolution”**

113 Arthropoda is now recognized as a monophyletic phylum within Ecdysozoa, the moulting animals (Budd
114 and Telford 2009; Edgecombe and Legg 2014; Giribet and Edgecombe 2019) (see Box 1 for a glossary of
115 terms used in this paper). Ecdysozoa is composed of the cycloneuralian ‘worms’—including priapulids and
116 nematodes—usually considered to be a mono- or paraphyletic grouping sister to the Panarthropoda, an
117 expanded definition of Arthropoda also including, among extant forms, onychophorans (velvet worms) and,
118 most likely, tardigrades (water bears) (Giribet and Edgecombe 2017).

119 There is an ongoing debate about whether onychophorans or tardigrades are the extant
120 panarthropods closest to the common arthropod ancestor. Evidence coming from neuroanatomy (Mayer *et*
121 *al.* 2013) and other internal organs favours either a sister-group relationship with tardigrades (e.g. presence
122 of metameric ganglia along the ventral nerve cord; a grouping also called Tactopoda (Smith and Ortega-
123 Hernandez 2014)) or with onychophorans (e.g. presence of sacculus and podocytes on metanephridia), and
124 in a number of cases are ambiguous, their presence or absence varying also among arthropods (e.g. presence
125 of a peritrophic membrane or Malpighian tubules) (Edgecombe *et al.* 2000). A recent fossil-inclusive
126 analysis found tardigrades to be ancestral (Caron and Aria 2017), consistent with most other phylogenetic
127 studies (Giribet and Edgecombe 2017). This result is influenced by the fact that, in spite of their dramatic

128 developmental contraction (Smith *et al.* 2016), tardigrades retain the plesiomorphic condition of a truncated
129 posterior termination bearing a limb pair with claws pointing anteriorly (inherited from the pool of
130 suspension-feeding adaptations). The loss of many trunk somites—pointing to a longer ancestral body—
131 and the presence of several elongate, curved claws on their limbs are consistent with a sister-group
132 relationship with the Burgess Shale lobopodian *Aysheaia pedunculata* (Caron and Aria 2017). However,
133 while providing detailed genetic and phenotypic information, tardigrades and onychophorans are also
134 outstandingly autapomorphic (onychophorans have independently evolved a ventral mouth opening and
135 internalized mouthparts and, not the least, are terrestrial), which urges caution when attempting to
136 extrapolate shared derived conditions.

137 By contrast, fossils called lobopodians, mostly found in Cambrian rocks, have greatly enriched our
138 understanding of the early evolution of panarthropods (Liu and Dunlop 2014) (Figs 1g, 1, 2). Although
139 specimens are characteristically rare across assemblages, these worm-like taxa bearing paired metameric,
140 annulated and lightly sclerotized limbs (the lobopods) have revealed that a broad diversity of organisms
141 had in fact initially evolved from cycloneuralian ancestors, composing the foundation of the arthropod
142 megaclade. Fossil-inclusive phylogenetic analyses find tardigrades to be well nested within Panarthropoda
143 (Smith and Ortega-Hernandez 2014; Smith and Caron 2015; Caron and Aria 2017), and show that the
144 surviving Onychophora and Tardigrada are but highly autapomorphic offshoots of this initial radiation
145 associated with the Cambrian explosion. Other lobopodians survived through the Silurian (Siveter *et al.*
146 2018) up to at least the Carboniferous (Haug *et al.* 2012a), however, which means that they represented
147 much more than an “experimental” body plan and had eventually reached a relatively stable (if cryptic)
148 adaptive zone within Palaeozoic marine ecosystems.

149 Perhaps the most important aspect of lobopodians put forward in the recent years is their arguably
150 common adaptation, at various degrees, to suspension-feeding (Yang *et al.* 2015; Caron and Aria 2017).
151 Most striking among the luolishaniids, which possess stout anchoring back limbs and frontal arms adorned
152 with pairs of thin spinules (Ma *et al.* 2009; Yang *et al.* 2015; Caron and Aria 2017) (Fig. 11), this ecology
153 also possibly characterizes the famed hallucigeniids (Smith and Caron 2015; Caron and Aria 2017), and

154 would thereby apply to a majority of lobopodians with diagnostically elongate appendages. These are
155 distinct from a series of other taxa, including much larger and stouter crawling forms (Dzik 2011) (termed
156 herein ‘xenusiids’), that bear short and conical lobopods, as they are known in onychophorans and
157 tardigrades, and which would lie closer to the common arthropod ancestor (Fig. 2). Whether arthropods and
158 their closest relatives arose from a paraphyletic lineage of suspension-feeders or whether suspension-
159 feeding triggered a separate, monophyletic radiation is not entirely clear, but it appears that the distinction
160 between an ambulatory or semi-sessile feeding lifestyle was determinant in the primordial diversification
161 of panarthropods.

162 Parallel studies on the first arthropods, the radiodontans (I use here a definition of Arthropoda based
163 on the presence of an arthrodized appendage (Aria 2019); see also Box 1), add even greater significance to
164 suspension-feeding, broadly defined, in the rise of this phylum. A filter-feeding strategy, more precisely
165 (which uses a filtration structure and captures food particles below a precise size threshold (Vinther *et al.*
166 2014)), has indeed been shown to be present in several relatives of the iconic predator *Anomalocaris*, having
167 evolved multiple times within the group and led to gigantism in the Ordovician (Vinther *et al.* 2014; Van
168 Roy *et al.* 2015; Lerosey-Aubril and Pates 2018) (Fig. 1h, i). Contrary to long-legged lobopodians, however,
169 filter-feeding in radiodontans was entirely carried out by the extensive modification of a single pair of
170 appendages—the frontal, arthrodized appendages, characteristic of this group which otherwise lacks any
171 body or limb arthrodization. These appendages are coined here “cheirae” (see Box 1).

172 This evidence further emphasizes the central role of small macro- to microscopic organisms in
173 Cambrian sea waters, and particularly larvae. When put into the overall metazoan perspective, alongside
174 sponges, cnidarian polyps, echinoderms, brachiopods and a variety of other animals (Nanglu *et al.* 2016;
175 Moysiuk *et al.* 2017), it seems that a “planktonic revolution” was as much a driver of the Cambrian
176 explosion as it was of the Great Ordovician Biodiversification Event (Servais *et al.* 2008), even if the fossil
177 evidence for small meso- to microplankton is still largely (but decreasingly so, see below) indirect (Lerosey-
178 Aubril and Pates 2018) (Fig. 2). This rapid expansion of the suspension-feeding niche in the Cambrian,
179 however, is clearly the continuation of an adaptation already largely present in the Ediacaran (Wood and

180 Curtis 2015; Gibson *et al.* 2019), and it seems therefore that the presence of arthropods and their larvae
181 represent one of the major distinctions between the two stages of this process.

182 Radiodontans, nonetheless, also developed a much broader diversity of specializations involving
183 the cheirae of radiodontans, which also includes sediment sifting (Moysiuk and Caron 2019a), for instance.
184 Similar observations can be made about the variety of shapes realized by other arthrodized limbs and
185 arthropod body segments, by comparison with the rather conservative morphology of lobopodians.
186 Arthrodization, as a structural innovation, was therefore decisive in the early success of arthropods by
187 providing a modular medium with both developmental flexibility and structural rigidity, a “sculpting
188 material” that worked particularly well as a rapid driver of phenotypic evolution, notwithstanding the
189 anatomical and genetic trade-offs that later stabilized a number of well-defined body plans.

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191 **Assembly of the arthropod body plan**

192 One of the most interesting and well-documented evolutionary sequences from cycloneuralians to
193 arthropods is that of the mouth and its associated structures (Smith and Caron 2015). Some basal
194 lobopodians possessed an eversible pharynx lined with teeth, similar to that of priapulids (Caron and Aria
195 2017); others, like *Hallucigenia*, had also independently evolved circumoral sclerotic plates (Smith and
196 Caron 2015), reminiscent of radiodontans (but expressed internally). The dented pharynx is a plesiomorphy
197 of arthropods, and has been retained by extant taxa. The location of the mouth was terminal from

198 cycloneuralians through xenusiids (Liu *et al.* 2006, 2007), although the first midgut glands only appear in
199 xenusiids (Vannier *et al.* 2014), suggesting an evolution in the mode of feeding and/or diet (possibly
200 associated with the introduction of predation or irregular scavenging (Chen *et al.* 1997; Vannier and Chen
201 2002)). From a xenusiid-like ancestor emerged peculiar lobopodians, such as *Kerygmachela* (Fig. 1g) and
202 *Pambdelurion* (long endemic to the early Cambrian Greenland locality of Sirius Passet, but possibly present
203 elsewhere (Vinther *et al.* 2016)), bearing flap-like swimming appendages, in addition to lobopods—at least
204 in *Pambdelurion* (Budd 1997). By contrast to xenusiid ancestors, *Pambdelurion* displays a circumoral
205 sclerotic mouth apparatus clearly placed on the ventral side of the body, although it was argued that the

206 animal also retained an eversible pharynx (Vinther *et al.* 2016). The rotation of the mouth opening, which
207 in extant lineages is characteristically ventral with postero-ventral orientation and connected to an
208 anteriorly-looped esophagus, therefore occurred during the xenusiid-radiodontan transition (Fig. 2).
209 *Kerygmachela* may document a transitional morphological state in which the mouth opening is ventral but
210 directed anteriorly (Park *et al.* 2018).

211 A circumoral sclerotized apparatus, giving its name to radiodontans (radius (Latin) – odoús (Greek)
212 meaning literally radial – teeth), exemplified by *Anomalocaris* (Daley and Edgecombe 2013) or *Hurdia*
213 (Daley *et al.* 2013), is therefore not exclusive to this group. A ‘peytoia’ type of outer sclerotized ring (or its
214 derivatives (Daley and Bergström 2012)) composed of differentiated plates (by their size), also commonly
215 called the “oral cone”, would unite radiodontans, but resemblances with *Pambdelurion* are extensive, to the
216 point that some isolated radiodontan-like mouthparts from the Chengjiang biota were proposed to belong
217 to a relative of *Pambdelurion* (Vinther *et al.* 2016). Similarities include the presence of numerous inner
218 teeth. A number of radiodontans also possess such an inner row of smaller dented plates, which could be
219 derived from the symplesiomorphic pharyngeal teeth. Interestingly, a comparable set of elements are found
220 in dissociation in amplexobeluid radiodontans from the Chengjiang biota, never forming the typical oral
221 cone (Cong *et al.* 2017, 2018). A single specimen of *Amplectobelua symbrachiata* shows overlapping
222 gnathobase-like differentiated plates in association with alleged reduced flaps (Cong *et al.* 2017). An
223 interpretation as structures homologous to gnathobasipods is difficult to reconcile at present with the known
224 early evolution of euarthropods (Figs 2, 3), and is also at odds with the circumoral identity of similar
225 sclerites in other radiodontans, but this intriguing evidence undoubtedly designates a crucial area of
226 investigation at both the palaeontological and developmental level for the near future.

227 As mentioned previously, the emergence of radiodontans is otherwise fundamentally defined by
228 the evolution of an arthrodized pair of appendages, although this is obviously not an autapomorphy of the
229 group (see below and Figs 3a for considerations regarding the somitic identity of the frontal appendage).
230 By contrast to the oral complex, there is no known sequence of character change leading to
231 arthro(po)dization: this condition seems to appear rather suddenly in radiodontans, even if the cheirae

232 themselves are likely homologous to the similar stout and purportedly raptorial appendages of
233 *Pambdelurion*, *Kerygmachela* and xenusiids (which lack subdivisions into podomeres). Another important
234 and seemingly sudden evolutionary step marking the appearance of radiodontans is the presence of well-
235 developed stalked compound eyes (Paterson *et al.* 2011), whereas lobopodians only possess simple ocelli
236 (Ma *et al.* 2012a), when present (Fig. 2).

237 To this day, the iconic *Opabinia regalis* from the Burgess Shale (Whittington 1975; Briggs 2015)
238 remains an oddity. Although clearly related to radiodontans with its gill-bearing lateral flaps and stalked
239 eyes, the single, unpaired frontal appendage with soft, annulated stem and terminal ‘jaw’—a unique
240 morphology among all panarthropods—together with the absence of sclerotized mouthparts make its
241 affinity within Arthropoda ambiguous. The presence of typical stacked midgut glands with radial folds
242 identical to those of *Kerygmachela* and *Pambdelurion* (Budd 1997) on the one hand, and *Isoxys* (Vannier
243 *et al.* 2009), leanchoilid euarthropods (Butterfield 2002; Aria *et al.* 2015) and even the trilobite-like
244 *Kiisortoqia* (Stein 2010), on the other hand, shows nonetheless a broad evolutionary contiguity of this
245 feature across these taxa. Quasi-identical digestive glands with radial folds or diverticulate pattern are found
246 in xenusiids (Vannier *et al.* 2014) and anomalocaridids (Daley and Edgecombe 2013) (in which these
247 phosphatized structures were possibly misinterpreted as muscle tissues (but see Young and Vinther (2017)),
248 but are not stacked.

249 *Opabinia* can, however, serve as a point of reference for the two most critical lines of discussion
250 pertaining to the origin of “true” arthropods (Euarthropoda), as defined by the presence of arthrodized body
251 segments and biramous limbs (Aria 2019). While irregularities in length between visible somites suggests
252 that there were no articulating tergites, all authors who have studied *Opabinia* have recognized the presence
253 of some form of external segmentation (Briggs 2015), which is, by contrast, more difficult to detect in
254 complete radiodontan specimens (Chen *et al.* 1994; Daley and Edgecombe 2013; Moysiuk and Caron
255 2019a) (perhaps due to the absence of lateral preservation). There does not seem to be any comparable form
256 of externalization of somite boundaries in more basal lobopodians, although there exist differentiations at
257 limb insertions and different annulation patterns (Budd 2001; Caron and Aria 2017). Body arthrodization

258 is unclear in isoxyids, which places megacheirans—historically, the so-called “great appendage”
259 euarthropods—, and more precisely jianfengiids, as the earliest unambiguous euarthropod representatives
260 (Aria *et al.* 2020) (Figs 1m, 2). Details about the formation of tergitic articulation are not documented.

261 It has been debated whether *Opabinia* combined both lateral flaps and lobopods (Briggs 2015).
262 Although any developmental remnants of lobopodous limbs in *Opabinia* seems fully internalized and
263 associated with the circum-intestinal haemocoelic cavity (Aria and Caron 2015), such combination is
264 arguably well evidenced at least in *Pambdelurion* (Budd 1997). Two separate rows of lateral flaps were
265 otherwise described in the massive *Aegirocassis* from the Lower Ordovician Fezouata Lagerstätte in
266 Morocco, and as possibly present in other radiodontans (Van Roy *et al.* 2015). This evidence would suggest
267 that the typical biramous limbs of euarthropods formed by fusion of separate limb Anlagen (Fig. 3d). This
268 is at odds with some other fossil evidence, such as in the isoxyid *Surusicaris* (Aria and Caron 2015)
269 (isoxysids are arthropods with bivalved carapaces sharing traits with radiodontans; Figs. 1f, 2), showing
270 broadly attached and morphologically similar endopods and exopods (Fig. 3d), as well as with
271 developmental data also supporting that both rami originated by splitting of a single limb axis (Wolff and
272 Scholtz 2008). Complicating this matter, early members of the chelicerate lineage (Fig. 1c) display an
273 intriguing separation of the exopod branch from the main basipod-endopod limb axis (Sutton *et al.* 2002;
274 Briggs *et al.* 2012; Aria and Caron 2017b, 2019) (Fig. 3d), likely related to the derived loss of exopods in
275 the euchelicerate head (the prosoma), and also supporting the view that the exopod might belong to a
276 separate limb Anlage. Further developmental data could help shed light on this issue, but we must be
277 cautious about our interpretation of extant models, for their external morphology may sometimes hide
278 derived developmental complexity (Olesen *et al.* 2001).

279 The journey towards Euarthropoda also involves the formation of a broad sclerite protecting the
280 head, taking the form of a carapace or head shield. Various head sclerites are known in “long-legged”
281 lobopodians, but a basal phylogenetic position of these taxa speaks against any direct homology with
282 arthropod tergites (Caron and Aria 2017). A variety of antero-dorsal and paired ventro-lateral sclerites mark
283 the appearance of radiodontans, and their unique lateral elements may even constitute one of their strongest

284 apomorphies (Van Roy *et al.* 2015; Moysiuk and Caron 2019a; Cong *et al.* 2017; Zeng *et al.* 2018). Their
285 continuity with arthropod carapaces and head shields is not entirely clear, but there is some evidence (Aria
286 *et al.* 2020) to posit that at least the antero-dorsal element, despite spanning a very large size range in
287 radiodontans (Moysiuk and Caron 2019a), corresponds to the so-called “anterior/ocular sclerite” identified
288 across early arthropods (Ortega-Hernández 2015; Aria and Caron 2017a), including megacheirans (Aria *et*
289 *al.* 2020) (Fig. 3b).

290 Isoxyids (Figs 1f), now retrieved by different large phylogenetic datasets as sister taxa to all other
291 euarthropods (Legg *et al.* 2013; Aria and Caron 2017a) (Fig. 2, Box 2; although this bears partly on many
292 uncertainties, including body arthrodization) bear bivalved carapaces, as defined by tergites of the
293 anteriormost somites extending dorsally over other tergites and thus having a free posterior range of motion
294 (Box 1). By comparison, euarthropods such as arachnomorphs are typically identified by the presence of a
295 head shield, which represents the fusion of all cephalic tergites and has limited posterior overlap over trunk
296 tergites. In reality, the morphological ranges of these structures overlap, as is clearly documented by
297 crustaceans (Olesen 2013), and, in general, it might be better to see shields and carapaces as different phases
298 of an evolutionary continuity based on the integration of additional segments into the head tagma. Yet these
299 bivalved carapaces enclosing a part or the entire body laterally are easily recognizable in a wide range of
300 Cambrian taxa, despite showing shape variations (Izquierdo-López and Caron 2019), and possibly being
301 modified into a flat ‘shield’ in fuxianhuiids (Figs 1a). These carapaces may constitute an ancestral
302 diagnostic feature of mandibulates, at least in adults, contrasting with the more restrictive head shield of
303 arachnomorphs (Fig. 2). The lack of broad protecting carapaces in arachnomorphs is further associated with
304 greater cuticular developments of post-cephalic segments, in particular in the form of pleural extensions,
305 fusion of posterior segments (the pygidium) and other ornamentations.

306 Although the presence of tergites is unclear in isoxyids (and somewhat incompatible with an
307 interpretation of their tailpiece as composed of radiontan-like soft flaps (Legg and Vannier 2013)), the
308 genus *Isoxys* in particular possesses trunk endopods with distinct podomere boundaries (Fu *et al.* 2011,
309 2014). A form of post-frontal metameric limb arthrodization may therefore have appeared in these animals,

310 prior to taking a more conventional leg-like aspect in megacheirans. Most remarkably, megacheirans and
311 arachnomorphs point to a ground pattern of seven podomeres (“heptapodomerous” condition (Aria *et al.*
312 2015)) for post-frontal endopods (notwithstanding minor variations), which was possibly already present
313 in *Isoxys* (Fu *et al.* 2011, 2014).

314 Megacheirans (Figs 1m, 2) represent archetypes of the first ‘true’ arthropods: they possess both
315 arthrodized limbs and fully arthrodized bodies, including the tailpiece, but lack elaborate limb
316 differentiations, except perhaps for their toothed basipods which remain of simple architecture and,
317 arguably, cannot be regarded as gnathobases as they are known in arachnomorphs (Ortega-Hernandez *et al.*
318 2013) (Fig. 3d). They therefore essentially relied on their cheirae for morpho-functionality, sometimes
319 cumulating both raptorial and differentiated sensory functions on this single limb (Fig. 1m)—a unique
320 combination of the frontalmost appendage among all adult arthropods, and likely an evolutionary solution
321 coping with the lack of “division of labour” across other limbs (Aria *et al.* 2015). The recently described
322 *Kylinxia* beautifully documents the homologous continuity of the cheirae across arthropods and
323 euarthropods as well as the very basal position of megacheirans in the euarthropod tree (Zeng *et al.* 2020).
324 The animal also importantly sheds light on the long-puzzling quintet of eyes in *Opabinia*, now arguably
325 present in the common euarthropod ancestor. However, owing to the numerous characters (dinocaridid-like
326 tailfan, non-arthrodized head limbs, absence of clear body arthrodization) still indicating a basal position
327 of isoxyids, *Kylinxia* is here resolved either simply as a basalmost megacheiran in the more classic topology
328 (Fig. 2), or as sister to total-group Arachnomorpha under a “deep split” scenario (result not shown).

329 However, rare Cambrian arthropods with bivalved carapaces have also been described displaying
330 cheirae. It would therefore appear that these elaborate frontal appendages were retained through two
331 separate lineages, one of them also possibly retaining the bivalved carapace of isoxyids (Fig. 2; see also
332 Zeng *et al.* 2020). Although relatively simple in principle, the plausibility of this evolutionary scenario (Box
333 2)—which would also settle the lengthy dispute about the phylogenetic position of trilobites (Box 3)—is
334 only made possible by recent reassessments of critical Cambrian taxa and, in particular, their relation to
335 extant clades.

336

337 **Deep Cambrian origins of extant lineages**

338 Numerous morphotypes from the Burgess Shale have long been included in or compared to crustaceans
339 (Briggs 1978), although these interpretations were challenged in the 21st century (Budd 2002; Legg *et al.*
340 2012). Since the stabilization of Mandibulata (Regier *et al.* 2010; Rota-Stabelli *et al.* 2011), it became
341 paramount to re-examine crustacean-like species in this new light. Recently, new palaeontological evidence
342 made possible notably thanks to the discovery of the new Burgess Shale locality of Marble Canyon (Caron
343 *et al.* 2014) provided support for the mandibulate affinity of a *Branchiocaris* relative, *Tokummia* (Aria and
344 Caron 2017a), and also shed light on the affinities of Cambrian bivalved arthropods as a whole, coined—
345 in the exclusion of isoxyids, ostracods and bradoriids—the hymenocarines (Fig. 1b). These taxa would in
346 fact resolve as basal mandibulates, branching before myriapods and pancrustaceans (Fig. 2), rather than
347 derived pancrustaceans. These observations were largely corroborated and completed by the redescription
348 of one of the first-found and best-preserved Burgess Shale arthropods, *Waptia fieldensis* (Vannier *et al.*
349 2018). Aside from the presence of mandibles with a surprisingly derived morphology, these studies
350 illustrated and clarified some hypotheses concerning arthropod limb evolution and the origin of proximal
351 features in mandibulates (Walossek and Müller 1998; Boxshall 2004); namely, the role of subdivided
352 basipods bearing multiple differentiated endites in the formation of the coxa, sub-coxa and features derived
353 from them—notably the mandibles (Popadić *et al.* 1998) (Fig. 3d).

354 This evidence from the fossil record nicely complemented the observation that articulating pleurites
355 in terrestrial arthropods also derived from supernumerary proximal limb elements (Coulcher *et al.* 2015).
356 Recently reevaluated evidence from the renowned Rhynie Chert Lagerstätte has also illuminated the
357 morpho-anatomy of the enigmatic euthycarcinoids, placing them on the myriapod lineage (Edgecombe *et*
358 *al.* 2020); a crucial find that will help link myriapods with their marine ancestors and therefore elucidate
359 plesiomorphic characters at divergence between Myriapoda and Pancrustacea—a necessary condition to
360 resolving the placement of hymenocarines as either stem mandibulates or stem pancrustaceans (Fig. 2).
361 Correlative to this finding, and elaborating on previous phylogenetic results (Vannier *et al.* 2018; Aria *et*

362 *al.* 2020), the iconic fuxianhuiids of the Chengjiang fauna (Figs 1, 2) have been described as mandibulates
363 with strong morphological affinities with euthycarcinoids and myriapods (Aria *et al.* 2021).

364 However, there also exists a more cryptic yet rich diversity of Cambrian ‘crustaceomorphs’. First,
365 the famous “Orsten” biotas, originally from Sweden, but now known more generally around the world since
366 the early Cambrian (Zhang *et al.* 2007) (Fig. 1e) as a type of exceptional three-dimensional preservation by
367 secondary phosphatisation, have yielded a wealth of micro- to meso-planktonic crustacean-like taxa which
368 have been associated with the origin of “crustaceans”(Walossek and Müller 1998) before the phylogenetic
369 concepts of Mandibulata and Pancrustacea / Tetraconata had gained wider support. Owing to their small
370 size, these forms, however, are most likely all larval, and ontogeny-based phylogenetic analyses retrieved
371 them nested among diverse extant crustacean lineages (Wolfe and Hegna 2014). Second, “small
372 carbonaceous fossils” (SCFs) from western Canada have revealed disarticulated assemblages of decidedly
373 modern-looking appendages, including mouthparts, found mostly nowadays in anostracans and copepods
374 (Harvey *et al.* 2012), and in certain cases reaching arguably adult sizes (Harvey and Butterfield 2008).
375 Interestingly, the mouthparts of the Orsten ‘full-bodied’ crustaceomorphs are different, and more
376 plesiomorphic, than the disarticulated SCF elements, implying the co-existence of two separate planktonic
377 crustacean-like faunas, representing different levels of the pancrustacean phylogeny. It seems highly
378 probable that at least one of these faunas is related to hymenocarines, either as larvae, or, for SCFs, simply
379 as disarticulated mouthparts, which have already been shown to display derived features in taxa from **BST**
380 deposits.

381 The diversification of larvae in the water column is here considered to be fundamental to the early
382 evolution of arthropods for two main reasons. First, they reasonably constituted an immediate evolutionary
383 feedback on the radiation of suspension-feeders as discussed above (“larval explosion feedback”, Fig. 2).
384 Second, from an evo-devo perspective, the creation of larval niches different from adult ones serves as a
385 catalyst for the emergence of new morphological features during development (Aria and Caron 2017a;
386 Wolfe 2017), potentially accelerating evolution in a way similar to that of the emergence of holometaboly
387 in insects (Rainford *et al.* 2014). Although some have already been described (Liu *et al.* 2016; Fu *et al.*

388 2018), certain Cambrian biotas such as the Chengjiang contain an opulence of fossil larvae known since
389 early excavations but remained understudied (pers. obs.); as demonstrated notably with trilobites (Hughes
390 2007), their study could be invaluable to understanding early arthropod evolution beyond one-dimensional
391 phylogenetic relationships, informing heterochronic trends and providing another perspective on a still
392 elusive Cambrian morphological variability.

393 One of the main features placing hymenocarines outside of Pancrustacea is the lack of second
394 antennae (Aria and Caron 2017a; Vannier *et al.* 2018), which was legitimately regarded as puzzling
395 (Edgecombe 2017), especially when appendages arguably corresponding to second antennae are present in
396 Orsten crustaceomorphs. Thanks to an unprecedented quality of computed tomographic rendering for this
397 type of fossils, a small hymenocarine, *Ercaicunia* (Fig. 1b), was since documented with three-dimensional
398 preservation of appendages, including a pair of post-antennular ‘hooks’ interpreted as differentiated second
399 antennae (Zhai *et al.* 2019). Problematically, however, other cephalic appendages are arguably not as
400 clearly preserved as the authors claim, and the shape or location of the mandibles is in fact uncertain. In
401 *Waptia*, for instance, which remains much more finely preserved, and in which no trace of post-antennular
402 can be found, it is known that mandibles and their palps occupy a very anterior position, with these palps
403 usually projecting forward (Vannier *et al.* 2018). One may therefore wonder whether these short and curved
404 appendages are not simply mandibular palps. Alternatively, it is also possible that these hooks are akin to
405 other such post-antennular appendages, such as those of the exotic *Cascolus* (see below), suggesting a
406 plasticity in the expression of the hymenocarine post-antennular segment. This limbless segment remains
407 nonetheless a characteristic of other hymenocarines, and is accompanied by other unusual appendicular
408 reductions in *Odaraia* and its allies, which seemingly also lack antennules altogether. The fact that the
409 cephalae of both fuxianhuiids and euthycarcinoids are also characterized by intercalary segments (this issue)
410 further testifies of the prevalence of this trait in marine taxa articulating the origin of mandibulate lineages,
411 even if the causes of this segmental reduction remain unexplained.

412 By contrast to the mandibulates, the Burgess Shale fossil *Sanctacaris* had long represented the first
413 and only relative of chelicerates from the Cambrian (Briggs and Collins 1988; Legg 2014), although

414 megacheirans have also been considered by some authors as possible members of the chelicerate lineage
415 (Haug *et al.* 2012b; Tanaka *et al.* 2013; Liu *et al.* 2020). The formerly unclassified *Habelia optata*,
416 originally described by Charles D. Walcott, came to demonstrate that *Sanctacaris* was not a lonely offshoot,
417 and that, although numerically rare, chelicerate precursors had already diversified in Cambrian seas (Aria
418 and Caron 2017b). *Habelia* also clarified the thought-provoking complexity of *Sanctacaris*' head, these
419 taxa displaying an unparalleled alignment of seven cephalic appendage pairs (which forms the basis of the
420 extant chelicerate prosoma), most of which being multifunctional appendages combining sensory, grasping
421 and crushing abilities. Although stemming from a different appendicular architecture, this evolutionary
422 solution mimicked the appendage differentiation characteristic of mandibulates, and, interestingly, became
423 simplified further up the chelicerate tree (Aria and Caron 2017b). It appears that this adaptation fitted the
424 predation of small crawling animals with hard integuments—in essence, trilobite juveniles. No gut content,
425 however, has so far been found to verify this hypothesis.

426 *Habelia* and *Sanctacaris*, now grouped in Habeliida, also allowed a direct connection with
427 horseshoe crab-like taxa from the Silurian thought to represent basal euchelicerates (Sutton *et al.* 2002;
428 Briggs *et al.* 2012) through a particularly unwieldy character. Cephalic exopods in these taxa are leg- or
429 antenna-like and seem to be somehow 'detached' from the basipod (Legg 2014; Aria and Caron 2017b).
430 The location of attachment of these exopods to the body is not known, but there is evidence that they moved
431 independently from the rest of the main limb axis. This condition would hence be intermediary to the later
432 loss of exopods in chelicerates and would provide support to the developmental hypothesis that the exopod
433 of basal euarthropod taxa developed in fact as a separate limb axis (Van Roy *et al.* 2015) (which would be
434 called an exite instead of exopod (Wolff and Scholtz 2008)), directly at odds with the appendage
435 morphology of isoxyids (Fig. 3d).

436 Chelicerates being defined by the eponymous chelicerae (Box 1), it is not clear whether habeliidans
437 belong to this group because the frontal appendages potentially homologous to chelicerae in these taxa are
438 very small and not evidently chelate or sub-chelate. *Mollisonia*, another typical taxon first introduced by
439 Walcott, very recently grounded the origination of chelicerates *per se* from at least the middle Cambrian,

440 also thanks to new material found at Marble Canyon (Aria and Caron 2019) (Fig. 1c). In addition to
441 chelicerae, *Mollisonia* sports sets of overlapping “gills” reminiscent of the merostome book gills, albeit
442 with a much-reduced number of constitutive elements. Because of this, *Mollisonia* resolves as the sister
443 taxon to Euchelicerata, further pointing to the early Cambrian origination of extant lineages.

444

445 **Head problems and fossil brains**

446 A series of groundbreaking studies interpreting neurological and other rare internal remains in Cambrian
447 fossils, at first from the Chengjiang biota (Ma *et al.* 2012b, 2014; Tanaka *et al.* 2013; Cong *et al.* 2014),
448 have attracted a lot of attention recently and delivered thought-provoking new evidence in the context of
449 early arthropod evolution (Ortega-Hernández *et al.* 2017). One of these studies revealed the existence of
450 complex visual systems in the iconic Chinese arthropod *Fuxianhuia* (Ma *et al.* 2012b), a find recently
451 corroborated by the arguably distantly related *Mollisonia* from the Burgess Shale (Aria and Caron 2017a),
452 suggesting that the presence of multiple neural centers originated early in euarthropods and were later
453 repeatedly simplified in more derived taxa (Strausfeld *et al.* 2016a). This phenomenon particularly
454 emphasizes the fact that even complex and a priori generally advantageous structures such as efficient eyes
455 remain governed by evolutionary trade-offs.

456 Other studies also attempted topological reconstructions of neural remains in order to elucidate
457 historical disputes about appendage homology in both extinct and extant arthropods (Tanaka *et al.* 2013;
458 Cong *et al.* 2014); the evidence presented allegedly supported the hypothesis that the frontal appendage of
459 radiodontans was analogous to that of early euarthropods, evolving instead into the originally appendicular
460 and protocerebral structure called the labrum (Budd 2002; Ortega-Hernández *et al.* 2017), generally located
461 in front of the mouth. This evidence was contested, however, showing that external morpho-anatomy and
462 phylogenetic analyses strongly supported a continuous evolutionary history of the cheirae across early
463 arthropods (Aria *et al.* 2020) (Fig. 3a), hence also implying that the labrum has a more subtle and complex
464 history parallel to the diversification of arthropods (Fig. 3b). It has been shown that leanchoiliid juveniles
465 possessed a well-developed labral protrusion akin to that of extant lineages (Liu *et al.* 2016, 2020),

466 suggesting that the ostracod-like frontal complex observed in hymenocarines (Aria and Caron 2017a;
467 Vannier *et al.* 2018) may have already dissociated from the labrum, or perhaps that the individualization
468 and posterior migration of the labrum occurred convergently in total-group Mandibulata and
469 Panchelicerata/total-group Arachnomorpha.

470 Perhaps the zealotness in homologizing the tripartite brain (protocerebrum, deutocerebrum,
471 tritocerebrum) in fossil taxa (Ortega-Hernández *et al.* 2017) could also be mitigated by the consideration
472 that the morpho-anatomy of the brain itself has evolved, and therefore that brain subdivisions in fossils (in
473 the form of fused and emerging ganglia) could mislead topological alignments based on extant taxa. A
474 current investigation may provide developmental evidence to support this view (Lev and Chipman 2020).

475 Some authors have also generally rejected the palaeoneurological evidence based on the frailty of
476 such internal tissues as ganglions and nerves and their high susceptibility to decay (Liu *et al.* 2018).
477 Taphonomic and decay patterns these authors document seem to show convincingly that the published
478 reconstruction of a vascular system in *Fuxianhuia* is dubious, and in general that peri-intestinal and
479 haemocoelic structures are often neglected yet occupy a central importance in the understanding of
480 arthropods from BST deposits (Aria and Caron 2015; Aria *et al.* 2015; Vannier *et al.* 2018; Mayers *et al.*
481 2019). The presence of neural tissues in Cambrian fossils, however, remains supported by a solid line of
482 evidence, as these also occur in areas not overlapping with other body parts and away from the gut, such as
483 eye stalks, and where they are known to constitute a large portion of the organic mass, while the selective
484 resistance of nerves to decay has also been demonstrated experimentally (Edgecombe *et al.* 2015). In
485 general, a temporal decay-based approach is not applicable to fossils of BST deposits, because the selective
486 taphonomy of tissues is based on idiosyncratic environmental and diagenetic conditions leading to this
487 mode of preservation, as is generally the case for all Konservat Lagerstätten (Parry *et al.* 2018).
488 Nonetheless, as of yet, we still lack a full causal understanding of specific tissue preservation in these
489 deposits, which is why reports of this kind must remain particularly cautious, especially considering that
490 studies are published in which guts in poorly preserved, partially decayed specimens are misinterpreted as
491 nerve cords (Ortega-Hernández *et al.* 2019).

492

493 **Weird wonders of the post-Cambrian**

494 Although existing collections and further discoveries from the Cambrian certainly hold more surprises, it
495 is also evident that the majority of Cambrian arthropods now fall within definite lineages, be it radiodontans,
496 isoxyids, megacheirans, fuxianhuids, hymenocarines, artiopodans, or the stem of extant groups (Fig. 2). In
497 parallel to that, Silurian fossils from the Herefordshire biota in Wales, have, for a number of years, revealed
498 many arthropods with challenging morphologies, despite being three-dimensionally-preserved animals
499 generally preserving an impressive amount of morphological details (Fig. 1j). *Enalikter*, for instance, was
500 presented as a megacheiran (Siveter *et al.* 2014a), but this interpretation was nothing straightforward, for
501 *Enalikter* arguably lacks in fact any megacheiran apomorphy, and its frontal appendages are not clearly
502 distinct from some tripartite crustacean antenna; yet, this is also clearly no crustacean, and some authors
503 went as far as interpreting it as a polychaete (Struck *et al.* 2015). This is the type of stories the “weird
504 wonder” days of the Burgess Shale were full of. Taxa such as *Cascolus*, *Aquilonifer*, *Tanazios* or *Xylokorys*
505 are similar in this regard: although they possess characters linking them with some known extinct or extant
506 arthropod group, their morpho-anatomies also show significant differences hampering their stable
507 phylogenetic placement and inciting to place them in their own group. This may be a combination of the
508 fact that they are Silurian, with much less soft-bodied data on arthropods from this period than there is from
509 the Cambrian BST deposits (also considering fossil reconstructions from the Herefordshire biota are time-
510 consuming and published taxa are selected from a still vast quantity of unstudied material, D. Briggs, pers.
511 comm.) and from the discrepancies in types of preservation: with information provided by the Herefordshire
512 material that a BST deposit lacks, and vice versa, differences between fossils may appear greater than they
513 are. The effort made by attempting to dissect fossils (Aria and Caron 2017a) and obtain three-dimensional
514 information from typically two-dimensional preservation (Zhai *et al.* 2019) promises to harmonize our
515 morpho-anatomical understanding. As a synthesis emerges and these data are better integrated, “oddities”
516 from the Herefordshire biota, but also from other exceptional Palaeozoic deposits yielding stem-group
517 arthropods and euarthropods, such as the Hunsrück slate in Germany (Kühl and Rust 2012), may prove to

518 be more significant contributions to our understanding of the arthropod tree of life, and provide another
519 dimension to the breadth of arthropod body plans after the Cambrian explosion.

520

521 **Temporal constraints**

522 The accumulation of evidence in recent years that the origination of both mandibulates and chelicerates
523 occurred deep within the Cambrian necessarily represents a strong timing constraint on the arthropod
524 evolutionary tree. On the other hand, the first appearance datum (FAD) of trilobites is well constrained to
525 the base of Cambrian Stage 3 (Paterson *et al.* 2019), and is documented also by the distribution of trilobite
526 and lobopodian (*Microdictyon*) fragments among small shelly fossils (SSF), which show relatively few
527 discontinuities and have stratigraphic significance across the Lower Cambrian (Steiner *et al.* 2007). A
528 wealth of traces that arguably only arthropod appendages can produce have been described from older
529 sediments, deep into the Fortunian, but there is no solid evidence to date that would suggest the presence
530 of arthropods before the Cambrian (Daley *et al.* 2018). Most of the panarthropod basic phenotypic pool
531 would have appeared within 20 million years, with the presence of mineralized elements from Stage 3 then
532 likely being an accelerating evolutionary factor in the specialization of masticatory appendages. The
533 palaeontological evidence therefore points to an even more dramatic radiative event than was assumed thus
534 far, as is corroborated by well-calibrated molecular clocks (Lee *et al.* 2013; Paterson *et al.* 2019). This
535 necessarily has important implications for genetic and phenotypic evolution early in this group (Lee *et al.*
536 2013), not the least being that **parsimony is likely to be an oversimplistic evolutionary model** to reconstruct
537 relationships between basal taxa, explaining in part historical conflicts using this method (Aria *et al.* 2015).

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

543 *et al.* 2015), and although both groups remained primarily aquatic, this suggests that excursions onto land
544 were well underway by the end of the Cambrian for both of the extant euarthropod lineages.

545

546 **Macroevolutionary perspectives**

547 When considered in its genetic and developmental context, the “sculpting material” metaphor of the
548 arthropod body is evidently a simplification, for, in fact, the story of evolution is first that of constraints:
549 any given feature or shape is the result of a trade-off between the content of the genetic toolkit, the control
550 of its expression, and the sum of biological and environmental factors integrating its viability into a whole,
551 including other features of the same organism. Arthropods are archetypes of the paradox opposing
552 morphological constraint and variability, as illustrated by a tremendous diversity of secondary traits
553 associated with exceptionally stable and long-lasting body architectures. Fossils offer insight into the rise
554 of these body plans, and thus they are crucial to understanding these morphological transitions, which in
555 turn permit to apprehend key – yet still mechanistically elusive – macroevolutionary concepts such as
556 canalization, stasis or modularity. Owing to their abundance and diversity, trilobites have served as model
557 organisms for such investigations, and “early bursts” models of high Cambrian disparity preceding
558 canalization (Hughes 1991; Webster 2007) were refined to point out the relaxation of segmental constraints
559 often through the co-evolution of adaptive features on a large scale (Hughes *et al.* 1999; Hughes 2003;
560 Webster and Zelditch 2011). However, comparative studies on other fossil arthropods are lacking. A top-
561 down approach investigating disparity in euarthropods as a whole (Aria 2020) finds evidence that a
562 canalized displaced-optimum model of evolution (that is, with swift but increasingly smaller translations
563 from one adaptive peak to another) characterizes the rise of body plans in these animals, and that this
564 phenomenon was associated with the fast build-up of genetic regulatory networks. The next step is to link
565 these patterns to morphological characters, notably through studying co-variations in the context of
566 heterochrony and developmental plasticity, as was done for trilobites. Although this integrated information
567 will serve to refine our evolutionary models for phylogenetic analyses, now that a phylogenetic framework

568 is already stabilizing for fossil and extant arthropods, we should look beyond the sole genealogy and use
569 these uniquely rich data to elucidate the many persistent mysteries of macroevolution.
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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 "cheliformes" 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.

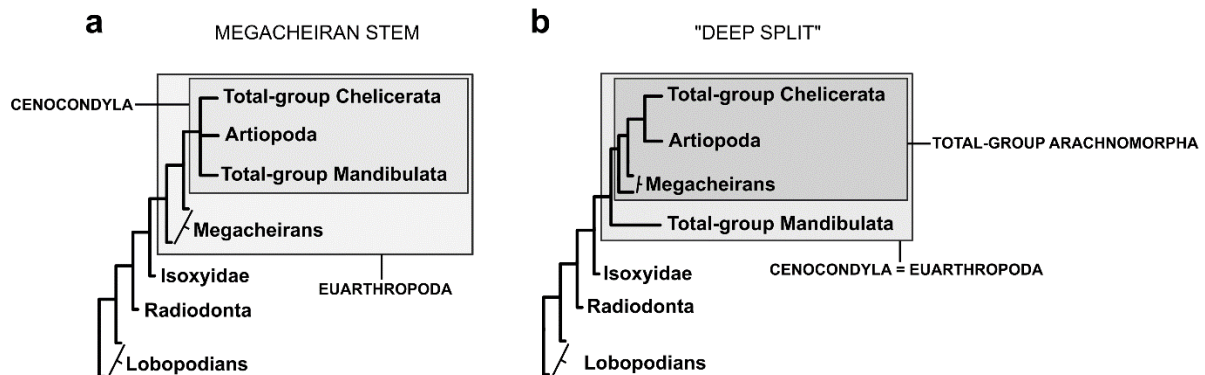
Stenopodous: Qualifies an elongate appendage articulated by a series of podomeres.

Tergite: Dorsal segmental sclerite, usually arthrodized.

582

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 (Giribet 2018). Disagreements do persist regarding the placement of early fossil groups (Edgecombe 2020), but cumulative evidence in the past decades from redescrptions 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 (Arthropoda), 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).

583

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).

584

585 **Figure 1. Variety of preservations and fossils that have recently reshaped or challenged our views on**

586 **early arthropod evolution. a, *Alacaris multinoda* Yang et al. 2018, specimen YKLP 12268 (holotype),**

587 **from the Xiaoshiba biota; a fuxianhuiid. Image courtesy of Xiguang Zhang. b, *Ercaicunia multinodosa***

588 **Zhai et al. 2018, specimen YKLP 16201, from the Chengjiang biota; a hymenocarine. X-ray computed**

589 **tomography, image courtesy of Dayou Zhai. c, *Mollisonia plenovenatrix* Aria and Caron 2019, specimen**

590 **ROMIP 65262, from the Burgess Shale (Marble Canyon); an early chelicerate. Image courtesy of Jean-**

591 **Bernard Caron. d, Gnathobases of *Wisangocaris barbarahardyae* Jago et al. 2016, specimen SAM P45629,**

592 **from the Emu Bay Shale; a habeliidan. Image courtesy of Jim Jago. e, *Yicaris dianensis* Zhang et al. 2007,**

593 **specimen YKLP 10844, from the Yu’anshan “Orsten” biota; a larval crustaceomorph. Scanning electron**

594 **microscopy, image courtesy of Xiguang Zhang. f, *Surusicaris elegans* Aria and Caron 2015, specimen**

595 **ROMIP 62976 (holotype), from the Burgess Shale (Marble Canyon); an isoxyid. Image courtesy of Jean-**

596 **Bernard Caron. g, *Kerygmachela kierkegaardi* Budd 1993, specimen MGHU 32048a, from Sirius Passet;**

597 **a swimming lobopodian. Image courtesy of Jakob Vinther. h, i, *Aegirocassis benmoulae* Van Roy et al.**

598 **2015, from the Fezouata biota; a radiodontan. Images courtesy of Derek Briggs. h, Specimen YPM 527123,**

599 **filter-feeding frontal appendages. i, Specimen YPM 237172, whole body, three-dimensional. j, *Cascolus***

600 ***ravitis* Siveter et al. 2017, specimen OUMNH C.29698, from the Herefordshire biota; a possible**

601 malacostracan. Digital reconstruction from serial photography, image courtesy of David Siveter, Derek
602 Briggs, Derek Siveter, Mark Sutton and David Legg. **k**, *Hongshiyanaspis yiliangensis* Zhang and Lin in
603 Zhang et al. 1980, specimen NIGPAS 164503, from the Xiazhuang biota; a trilobite. Image courtesy of Han
604 Zheng. **l**, *Ovatiovermis cribratus* Caron and Aria 2017, specimen ROMIP 52707, from the Burgess Shale
605 (Walcott Quarry); a suspension-feeding lobopodian. Image courtesy of Jean-Bernard Caron. **m**, *Yawunik*
606 *kootenayi* Aria et al. 2015, specimen ROMIP 63066, from the Burgess Shale (Marble Canyon); a
607 leanchoilid megacheiran. Image courtesy of Jean-Bernard Caron. Arrowheads point to: subdivided, enditic
608 basipod (a), raptorial and sensory complex of appendages (c), tripartite exopods (k), stout lobopods for
609 anchoring (l) and robust basis of cheira (m). Scale bars, 10mm (**a**, **g**, **m**), 1mm (**b**, **j**), 3mm (**c**, **f**, **k**, **l**), 2mm
610 (**d**), 100µm (**e**), 20mm (**h**), 100mm (**i**).

611

612 **Figure 2. Relationships and characteristics of the main fossil panarthropod groups.** Summarized
613 phylogenetic framework of panarthropod relationships. Insets (a, b, c) represent crucial steps of ocular,
614 mouth and external protocerebral evolution at the onset of the arthropod radiation: (a) mouth is ventralized
615 and accommodates circumoral plates, frontal sensory organs derived from protocerebrum (yellow); (b)
616 compound eyes born by stalks, arthrodization, complex of frontalmost organs protected by a sclerite
617 (yellow); (c) later, formation of the hypostome-labrum complex, with pre-oral sternal plate (red) protecting
618 the mouth instead of circumoral plates, and a fleshy extension (green) possibly derived from the same
619 Anlage as those of the anteriormost sclerotic/sensory complex (yellow; see Fig. 3). Yellow stars on tree
620 mark important morphological innovations or evolutionary events. Coloured branches indicate the
621 frontalmost appendage type (red, cheira; green, chelicera; blue, antennula). The arrow and question mark
622 associated with the hymenocarine morphogroup represent the uncertainty as to whether some of these taxa
623 lay in fact closer to pancrustaceans. Extant lineages are represented by bold branches. Dashed lines
624 represent grouping uncertainties. Palaeo-art by Marianne Collins and Danielle Dufault © Royal Ontario
625 Museum.

626

627 **Figure 3. Understanding and challenges of the early evolution of key arthropod features. a,**
628 Frontal-most appendage. The robust, raptorial frontal appendage of xenusiids and radiodontans (α) is known
629 to transition to the megacheiran cheira (β), adopting a dorsal orientation, and sometimes coupling
630 differentiated grasping and sensory functions (as in leanchoiliids). The cheira supposedly diversifies into
631 an exclusively sensory (the antennula, γ) or predatory, manipulating form (the chelicera, δ) in extant taxa,
632 but these transitions are not yet documented clearly by the fossil record—except perhaps in *Kiisortoqia*. **b,**
633 **Labrum.** The labrum presumably originates in early panarthropods from a protocerebral Anlage that could
634 have served a sensory function (α), then forming an externalized sensory organ commonly covered by an
635 “anterior” or “ocular” sclerite (β). In more derived forms, frontal-most sensory features co-exist with the
636 hypostome-labrum complex (γ), in which a pre-oral sclerite also bears a fleshy protrusion—the latter is the
637 labrum in the traditional sense. The labrum of the hypostome-labrum being known as protocerebral in
638 origin, the question is to know if it derives evolutionarily from the frontal-most pre-oral organs seen in some
639 fossils, and whether the various “labral” features in chelicerates and mandibulates correspond to one of
640 these externalized protocerebral features, or both. The black square represents the mouth. **c, Head tagma.**
641 The head tagma is poorly defined in stem euarthropods, but in some cases appendage differentiations seem
642 to delimit a **four-segmented (i.e., five-somitic) head** (α); in megacheirans, this five-somitic configuration is
643 clearly delimited by the head shield in cheiromorphs, but the ancestral jianfengiids appear to display
644 variability in the length of the cephalon and a possible decoupling between the tergal and appendicular head
645 tagmata (β). **From the plesiomorphic five-somitic head arose the diagnostic** six-somitic mandibulate
646 cephalon (γ , although beyond the larval stage crustaceans evolved the more inclusive cephalothorax), but
647 also the more variable cephalon of arachnomorphs. In these taxa, the five-somitic tagma transitions directly
648 to possibly six-, -seven and even eight-somitic heads, the latter representing the ancestral condition of
649 panchelicerates (δ). **d, Biramous appendage.** There exist two scenarios for the origin of biramicity, both
650 supported by different fossil evidence: the split of the main limb axis, as suggested by isoxyids (α), and the
651 fusion of separate limb axes, as interpreted in radiodontans with double rows of swimming flaps (β). Either
652 of these initial conditions led to the archetypal biramous appendage with **basipod**, endopod and exopod (γ),

653 as expressed in megacheirans. The differentiation of the basipod plays a critical role in the emergence of
654 cenocondylans. The arachnomorphs are distinguished by a gnathobasipod (δ), while early members of the
655 mandibulate lineage evolved subdivisions of the basipod that later gave rise to coxal features, including the
656 mandible (ϵ). From a developmental point of view, the “true” exopod could a priori be recognized by
657 attaching the original basipod, that is, the distalmost segment of the entire basipod complex, or basipodite;
658 by contrast, exites arise from other basal segments (δ). Early members of the chelicerate lineage possess
659 “semi-detached” stenopodous exopods whose affinity as exopods or exites is unclear (ϵ). b, basipod; c/m,
660 coxa/mandible; df, dorsal flap; en, endopod; ex, exopod; exi, exite; vf, ventral flap.

661

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665

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