

I enjoyed reading this MS that presents an excellent updated and critical review of the early evolution of arthropods. In the recent decades, numerous papers were published on Cambrian arthropods mainly from exceptional fossil sites. The author succeeded in digesting and analyzing this huge amount of information to propose a credible evolutionary scenario as seen in Fig. 2. This review will be useful to specialists of the group but more generally to scientists working on animal evolution and will make a perfect teaching material as well. For these reasons, I strongly recommend this MS for publication. Some paragraphs need minor adjustments (e.g. make the text easier to understand; see remarks below)

**Line 55-60**

Perhaps it would be better here to stress on the vital importance of insects as pollinating organisms and crustaceans (copepods, krill) as key-elements of the marine ecosystem instead of embarking into controversial subjects (e.g. “waged in the name of a wasteful and profit-driven agriculture”) ? It is true that human activities are threatening biological diversity (not only arthropods).

**Line 98-100**

*“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).”*

Fossil from Lagerstätten provide key information on both internal (e.g. organs, digestive, nervous, reproductive system) and external (e.g. appendages) morphology. These are complementary sources of information that cannot be dissociated. Comparative morphology based on external features (especially concerning arthropods) is not conservative at all. Please rephrase and avoid terms like “in reality”.

**Line 129-130**

*“bearing a limb pair with claws pointing anteriorly (inherited from the pool of suspension-feeding adaptations).”*

I don't see any direct relation between the orientation of claws and suspension-feeding adaptations. Please clarify or delete.

**Line 156** – There are good images of such conical stout lobopods in Vannier et al. 2014 (Nat Comm) also.

**Line 158-161**

*“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”*

Arthropods seem to have evolved from lobopodians via the arthrodization of their limbs and body (cuticular thickenings + arthropodial membranes + associated muscles). These assumed lobopodian ancestors were certainly mobile animals (just like onychophorans; not semi-sessile). It is true that some lobopodians bear a filtering apparatus but it is far from being the rule. I find no reason to suppose that arthropods would derive from filter-feeding lobopodian ancestors. The animal radiation (in each group) is associated with the colonization of various niches and ecological specialization through various feeding strategies. It is true for lobopodians and more advanced panarthropod groups.

**Line 175-178**

*“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).”*

Perhaps I would avoid “revolution” here. Simply 1) numerous early Cambrian animals (e.g. arthropods) seem to have developed through larval stages that probably swam within the water column and were a potential food source for other animals; and 2) some groups (e.g. chaetognaths, some anomalocaridids) lived permanently within the water column and took part in the construction of early pelagic food chain.

**Line 178 +**

*“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.”*

Why a rapid expansion of suspension-feeding in the Cambrian? Many other feeding strategies co-occurred (scavenging, predation, etc..)and seem to have appeared virtually at the same time.

In the Ediacaran (e.g. White Sea) suspension feeding was not largely represented. Instead numerous organisms probably fed via osmotrophy (see Laflamme) or external digestion of microbial mats (some of them may have been grazers). I agree that the water column contained suspended material (e.g. marine snow, phytoplankton) but I don't see many organisms capable of feeding on it.

So stating that *"the rapid expansion of the suspension-feeding niche in the Cambrian, however, is clearly the continuation of an adaptation already largely present in the Ediacaran"* does not sound correct to me. Please revise this part.

There is a huge gap between the Ediacaran and the Cambrian ecosystem. I would avoid "continuation" here.

To me one of the most important event of this period (early Cambrian) would concern the development mode of early animals. Indirect development through swimming larval stages created a new potential source of food that favoured filter-feeding and possibly the ecological shift (pelagic) of some groups

*"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."*

It is not very clear- Please rephrase.

#### **Line 196-197**

The dented pharynx is a plesiomorphy of arthropods, and has been retained by extant taxa.

Extant arthropods don't have a pharynx. They have an oesophagus and a foregut that functions as a triturating stomach. Please clarify here

#### **Line 198**

"although" sounds a bit odd here. Please write the sentence.

#### **Line 356-360**

In Fig. 2 Euthycarcinoids appear as a sister-group of Myriapoda. Is it based on Edgecombe et al. 2020 ? The last part of the sentence is quite unclear to me. Please reformulate.

#### **Line 381**

*Diversification of larvae*

Zhang et al. (2010) described an assumed eucrustacean metanauplius larva in the early Cambrian of China. Why not mention it here ?

#### **Line 386**

*Holometaboly*

Please define. Not all readers know what it means.

#### **Line 452-455**

*"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."*

Why do you think that these ancestral multiple neural centers simplified in the course of evolution ? Please give examples. The last sentence is uneasy to understand. It is clear that the increasing capacity to analyze, process and respond to sensory signals (via complex brains) revolutionized the relationships between animals (e.g. vision: see and be seen), accelerated evolutionary pressure and triggered responses. If I were you, that's what I would emphasize here. Why evolutionary trade-offs here ?

#### **Line 456-464**

These sentences extremely difficult to follow for non-specialists (e.g. "subtle and complex history parallel to the diversification of arthropod"- what on earth does that mean ?). Please rewrite and present more clearly the competing hypotheses and define what the labrum is. Your text here gives the impression of endless and boring academic disputes whereas the present review aims to clarify arthropod evolution.

A continuous evolution of cheirae is convincing to me.

**Line 464-469**

[Idem here](#)

**Line 470-474**

*“Perhaps the zealousness 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).”*

Please avoid “zealousness” and such understatements in general. Do you mean that the basic features (broad subdivisions) of extant arthropod brains have equivalents in Cambrian forms ? Why ? Please explain more clearly why Lev and Chipman (2020) warn about possible misleading interpretations.

**Line 475-480**

Yes , the vascular system of Fuxianhuia is also very dubious to me. Yes, the head of numerous arthropods is occupied by digestive glands (perhaps you can cite Zacai et al. for Sidneyia) that are often phosphatized. The assumed fossil brains seem to have a different chemical composition. Eyes are clearly connected to brain ganglia (even in Waptia) which would support the brain hypothesis in Cambrian fossils.

**Line 484**

Do you mean experimental taphonomy ? It is true that laboratory conditions may not faithfully reproduce those of the Cambrian depositional environments but experimental taphonomy do provide valuable information on the chronology of decay processes and the mineralization of soft tissues (including embryos).

**Line 504**

Another example to be cited here are the ostracodes from Herefordshire. They are almost identical to modern ones (including swimming appendages, specialized limbs, reproductive organs). See paper by Siveter and coll.

**Line 533-537**

*“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).”*

This paragraph is perfectly clear up to “Lee et al. 2013”. However, the last sentence is obscure. Please explain

**Line 547 +**

What does “sculpting material” metaphor means ? Meccano-kit rather than sculpture ? Why trade-off here ? To me morphology is an evolutionary response to biological and environmental factors that recruits the best-fitted genetic tools and regulatory networks for optimal viability.

**Line 558-560**

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).

I am afraid that most readers will not follow here. Your MS is a review that will be read by non-specialists. Please, wherever it is possible, try to use a simple and clear expression.

**Line 561**

*“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.”*

[Idem here.](#)

**BOX 2**

[You write the following](#)

*“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 (Artiopoda), and which is called Cenocondyla (Aria 2019)”.*

This is scenario a) in BOX 2 and also in Figure 2. Right ?

Then

*“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.”*

OK, this alternative scenario is shown in b) BOX 2. If you give more credit to this scenario why didn't you choose it in Figure 2 ? “Deep Split” appears in Figure 2 where as it is supposed to belong to scenario b). There is something unclear here. Please check consistency.

Somewhere in the text, indicate what you mean by “big slit” (important)

#### **FIG. 1**

It looks a bit too small and quite heterogenous (reconstructions mixed with fossils). I would recommend to make one figure for each key group (e.g. lobopodians, radiodonts, megacheirans, hymenocarines, Artiopodans)

#### **FIG. 2**

If possible, use a reconstruction for fuxianhuiids and artiopodans

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