

**I am grateful to both reviewers for the time they have spent on this lengthy paper and the fairness of their comments. It seems overall that there were no fundamental disagreements with the views expressed here, and I have otherwise responded to every single query to best of my ability, extensively emending the text and further improving the fluidity and simplicity of the language, as J. Vannier especially put emphasis on this issue (although jargony language is sometimes unavoidable). The idea of “Cambrian planktonic revolution” that I put forward had not been sufficiently argued, and I believe that I was able to make a much stronger case for it. I have also improved the figures according to the reviewers’ suggestions.**

- Especially I concur with Review 1 on your point about the ‘planktonic revolution.’ Although the manuscript acknowledged the evidence is still indirect, still it tries to expand the case into the arthropod larvae. As far as I know we yet to have enough evidence of ‘planktonic arthropod larvae’ in early Cambrian, except for Zhang et al. 2010 that Reviewer 2 mentioned. Earliest trilobites did not have larvae (protaspides) which undergo an indirect development, the first possibly planktonic trilobite larvae appeared in the Furongian. Those arthropod larvae documented from Chengjiang (Liu et al. 2016; Fu et al. 2018) were not indirect developers.

**>>> Admittedly this part was weakly argued. However, I still think the evidence for Cambrian waters brimming with arthropod larvae is overwhelming. My reasoning is the following:**

- **Suspension-feeding has grown to be a central ecological aspect of many Cambrian localities (see e.g. Nanglu et al. 2020 Palaeobiology).**
- **Arthropods since the early Cambrian are the most diverse and abundant of animals.**
- **There is direct evidence of meso-planktonic sized crustaceomorphs in the Cambrian from SCFs and Orsten.**

**It was also proposed that Orsten forms could be related to hymenocarines (Aria and Caron 2017, Nature). Agnostids also arguably showed morpho-anatomical differences between larvae and adults (Moysiuk and Caron 2019 Proc B), as well as leanchoiliids. I don’t think the taphonomic limitation on the preservation of larvae in BST deposits should overcome the rest of the evidence, even if the description of more indirect developers could be helpful (larvae of nektobenthic direct developers would have fed suspension feeders too).**

**The section has been rewritten to be more robust. See also my answer to J. Vannier.**

- The title of the manuscript has been already used by Edgecombe and Legg (2014). Rephrasing the title is recommended.

**>>> Budd and Telford used “The origin and evolution of arthropods” in 2009, then Edgecombe and Legg used “Origins and early evolution of arthropods” in 2014. I think the title used here makes sense both as part of this ca. five-year cycle (involving different authorship) and also perhaps as a better combination of both previous titles (there is a single origin of arthropods and the review only deals with early evolution).**

- Line 79-81. I worry that this sentence (especially 'often more fueled') could sound like depreciating the previous works. I think all those previous works were on a way toward better hypotheses.

**>>> This was rephrased in a more positive light.**

- Line 98-100. The same concern as above.

**>>> Rephrased, also according to J. Vannier’s comment. I think it should still be clear that there is an interpretational conflict.**

- Line 491. (Although I agree with you on this) You can still make your point without specifying (Ortega-Hernandez et al. 2019).

**>>> I think there is a need to formally contest this interpretation since this has remained unchecked so far. But to avoid singling out this study, I developed and placed my criticism early in this section, and cited Zeng et al. 2020 along with it.**

#### REVIEWER 1

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)

**>>> Thank you.**

Line 55-60 Perhaps it would be better here to stress on the vital of 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). **>>> It is admittedly political – however, is it really scientifically controversial that agriculture in a neo-liberal world is the cause of the war on insects? Cited literature directly relates to this. Your points are well understood, however, and I have emended these sentences accordingly.**

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”.

**>>> The cited paper (Aria et al. 2020 BMCEB) discusses how some recently published evidence of internal tissues across several studies has arguably been overinterpreted. Specifically, this study demonstrates how evidence from external anatomy had long been clear yet overshadowed by the attractiveness of neural palaeotissues. This is not to say of course that fossilized internal tissues are not important – they are, but should be evaluated more carefully. The sentence has been rewritten.**

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.

**>>> This was a shortcut. What is meant is that the posterior limb pair with claws pointing anteriorly is a character found more ancestrally in suspension-feeding lobopodians, in which it appeared as a way to facilitate anchoring to substrate. The sentence has been emended.**

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

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.

**>>> This idea was discussed in Caron and Aria (2017, 2020), because hallucigeniids were also interpreted as semi-sessile suspension-feeders based on their morphoanatomical characteristics. In a scenario where luolishaniids and hallucigeniids form a grade to xenusiids and Arthropoda, there would be at least a partially sessile common ancestor to the rest of the panarthropod tree. With both luolishaniids and hallucigeniids being suspension-feeders, the majority in fact of early lobopodians would have an obligatory or facultative sessile lifestyle. References added for clarity.**

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.

**>>> The GOBE is currently thought to be the stage of a “planktonic revolution”, a term widely used in the literature. The question is whether this planktonic revolution was really Ordovician. Lately, however, evidence for a widespread suspension-feeding lifestyle in the Cambrian has been plentiful, for instance in enteropneusts, lobopodians, radiodontans, in addition to what was already known in sponges, cnidarian polyps, echinoderms, brachiopods. Certain localities, like Marble Canyon, were arguably even built on suspension-feeding (Nanglu et al. 2020, Palaeobiology). So this is not simply about a few planktonic individuals – the water column was arguably full of them, albeit at different degrees between localities. BST deposits mostly don’t preserve the smallest fossils simply because of grain resolution limit, but there is plentiful evidence of tiny individual arthropod-like fossils, which for the most part are undescribable (pers. obs.) – although some exceptions have been published. As Reviewer 2 suggests, protists and algae could certainly have been part of these particles, but arthropods were already the most diverse and abundant of animals, and already there was an abundant cryptic crustaceomorph fauna as evidenced by SCFs and Orsten. That the GOBE planktonic revolution is actually Cambrian is not just a possibility to me... it is overwhelmingly consistent with all the available evidence. What makes the Ordovician stand out in that regard in the abundance of biomineralized plankton.**

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

>>> **Yes, continuation was not the best suited term. The idea was more simply that suspension-feeding actually originated in the Ediacaran (a point which was raised during a previous submission). The whole paragraph has been rewritten anyway.**

“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.

>>> **This sentence has been removed.**

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

>>> **The arthropod pharynx is identifiable in arthropods as part of the foregut and located between the mouth and the oesophagus. See e.g. Moore, R. C., and L. McCormick. 1969. General features of Crustacea. In: R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4. Geological Society of America and University of Kansas Press, Lawrence.**

Line 198 “although” sounds a bit odd here. Please write the sentence.

>>> **Emended for clarity.**

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.

>>> **Based on this paper and also Aria et al. 2021, JGS, cited just after. As discussed in Vannier et al. 2018, comparing marine stem groups is essential to addressing questions of character ancestry between pancrustaceans and myriapods, because terrestrialization events were associated with wide-reaching convergences. Emended.**

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 ?

>>> **Added.**

Line 386 Holometaboly. Please define. Not all readers know what it means.

>>> **Done.**

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 ?

>>> **This view simply follows the evolution of neuropils on the arthropod tree (see the Strausfeld citation), given what is said of the polarization of this character by fuxianhuiids and mollisoniids. Emended for examples. What is meant here is that, beyond the obvious fact that better vision was initially advantageous, it was actually traded back for different adaptive reasons – such as a wider**

**field of vision in arachnids or perhaps as simpler structures in myriapods as a reduction of energy cost. Those are possible trade-offs associated with the simplification of visual systems in derived euarthropods. I added the following to clarify what I mean: Alexander RM. Optima for animals. Revised edition. Princeton, N.J: Princeton University Press; 1996.**

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.

**>>> It is a review, but any review at a given time will face ongoing debates – this is perhaps truer for arthropods... Nonetheless, I have thoroughly rewritten this paragraph to try and make it more fluid.**

Line 464-469 Idem here

**>>> Emended for clarity.**

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.

**>>> “zealousness” removed and paragraph emended and expanded for clarity.**

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.

**>>> Whether the eyes connect to the brain or to the general peri-intestinal cavity is not always clear. Certain cases are stronger than others, because elements are isolated taphonomically and through the plan of splitting (like in Waptia). But in other cases, as for the relatively poorly-preserved Utah leanchiiliids in Ortega-Hernandez et al. 2019, the continuity between the eyes and the peri-intestinal cavity is the result of partial decay and the general taphonomic pathways characteristic of arthropods in BST deposits.**

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).

**>>> As the text says and Parry et al. 2018 argue, the issue is that the chronology of tissue decay obtained through experimental taphonomy does not generally apply to fossils from BST deposits, notably because tissue preservation is differently mediated by microbiomes. But I do agree obviously that these experimental approaches are essential to obtain a base line to which differential taphonomy can be compared, and perhaps explained.**

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.

**>>> I voluntarily focused on the more problematic taxa of the Herefordshire for the purpose of the argument, but, yes, indeed, this locality also holds many modern-looking taxa.**

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

**>>> Emended with citation.**

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.

**>>> The “sculpting metaphor” is introduced early in the manuscript and related to arthrodization, and therefore modularity. However this section needed thorough rewriting.**

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.

**>>> Emended. As you will see, the entire section has been rewritten.**

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.

**>>> Emended, slightly. I don’t think the formulation is particularly obscure – I referenced the displaced optimum model.**

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)

>>> **Deep split now defined at first use (in addition to definition and illustration in Box 2). I decided to use a more "agnostic" topology in Figure 1 because the "deep split" result is still relatively new and its stability requires further testing. This is now clarified in Box 2.**

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)

>>> **I believe the figure will be readable as full-page display and online – the aim is really to provide an overview of both fossil and taphonomic diversity at a glance, without going into too many morphological details. It is true that the text abundantly goes into morphological details, which are not otherwise illustrated, so I decided to also annotate the fossils for the most important features discussed in the manuscript. I don't think that it is necessary, given the summarization, to really expand into one figure for each group; the paper is already long as is, and this may cause length issues later on should this manuscript be sent to a journal. This would also make the figures more redundant with the ones in Edgecombe 2020. 2b is the tomographic reconstruction of Ercaicunia because the fossil itself doesn't show much. 2j is the computer model of the animal because this is the only representation of the fossil that is obtained from Herefordshire – the original fossil is only slices, which are destroyed when rendering the computer model.**

FIG. 2

If possible, use a reconstruction for fuxianhuiids and artiopodans

>>> **Done.**

REVIEWER 2 (pasted from PDF annotations)

This is a very controversial term. What do you mean here?

>>> **Macroevolution was used here as elsewhere in the literature, as evolution at the inter-specific level and above (because evolution at the population level is not the focus on this work). This was not trying to signify in particular that macroevolutionary processes were disconnected from microevolutionary ones (although I'd argue that patterns are different). Jablonski 2017 *Evolutionary Biology* is now cited for this.**

Body plan is a very vague term. I can imagine that the tagmatization of Chelicerata and Hexapoda is more or less reflected by this term. However, what is the body plan of diverse groups like myriapods and crustaceans? In particular, since the latter are not even monophyletic?

>>> **Yes, a "body plan" has flexible boundaries, which is why it is appealing to use when fossils are involved... However, arthropod body plans have also been quantified through disparity metrics and morphospaces – see e.g. Aria 2020, *Palaeobiology*. In that sense, a "body plan" is the sum of morpho-anatomical characteristics rather than just overall architecture as count of segments or tagmatic arrangement. I emended the sentence accordingly.**

As mentioned above, crustaceans do not form a group. Pancrustacea or Tetraconata would be more appropriate. But again what is the body plan of pancrustaceans? The ground pattern, or the apomorphies of this extremely heterogeneous group?

>>> See above. The reference to Crustacea is simply for a historical purpose. Quote marks added to emphasize crustaceans are not monophyletic, but Pancrustacea is clearly explained soon after in the text. Crustaceans form a distinct cluster in morphospace – at least when fossils are excluded (Aria 2020), which could be used as a way to circumscribe a crustacean body plan.

Categorical ranks such as genera and families are artificial constructs (logical classes) and have no life at all and thus no longevity. Only species and monophyletic groups can exist for a certain period.

>>> Indeed, but, on the other hand, supra-specific taxonomic levels are not entirely devoid of biological meaning either. What I intend to express here is the great morpho-anatomical stability of insect families and genera, upon which their tremendous species diversity is based. I replaced “longevity” with “stability”.

As mentioned above, what is meant by this?

>>> Precision of meaning added.

A "paraphyletic lineage" sound like a contradiction. Some references are needed here!

>>> Reworded. References added.

The pioneer work of Liu et al. 2015 When a 520 million-year-old... could be cited here.

>>> Added.

What is the meaning of this sentence? Does the authors doubt the validity of the brain and head data? Then he should say so (see Liu et al. 2018). Or does he mean that head and brain data are overrun by external morphology data if analysed together?

>>> This has been rephrased. Preservation potential of neural tissues is discussed later in this paper. It is meant here that fossilized brain data was partially overinterpreted and was taken as superseding external morphology when really there should be consistency of all data.

This is a very long sentence and something seems to be missing.

>>> The sentence was separated into two and modified.

a praphyletic grouping cannot be a sister!

>>> Modified.

What does the author mean by "definition"? The formation of a genealogical unit or a set of characters?

>>> The systematic definition. Modified.

why "most likely"?

>>> In several molecular analyses tardigrades are still resolved as cycloneuralians – see Giribet and Edgecombe 2017. However, it is true that the meaning could be misinterpreted, so I removed this bit.

Neither Onychophora nor Tardigrada are close to the common arthropod ancestor. One of these taxa or a taxon combing both groups together is the sister group of Arthropoda (or Euarthropoda).

>>> Modified.

A Recent monophyletic group cannot be ancestral to another Recent monophyletic group. In addition, it is not really clear to what tardigrades are ancestral. Does the author mean they are the sister group to Onychophora plus (Eu)Arthropoda?

>>> Modified.



This is circular reasoning. The loss of many somites does not indicate a longer ancestral body!  
Furthermore, the evidence for tardigrades being derived from a suspension feeder is pretty poor. The tardigrade claws are excellent for walking.

>>> **The study in question suggests that tardigrades plesiomorphically possessed many more somites – this is what I meant by “longer”. There is no evidence that tardigrades directly evolved from suspension-feeding lobopodians, but the character states mentioned can be traced back to earlier lobopodians which had developed them alongside other suspension-feeding adaptations – the type of claws are part of these adaptations, and it is therefore suggested here that their presence in tardigrades is co-opted from this ancestral phenotypic set.**

Taxa are not apomorphic, only characters

>>> **Modified.**

What is the evidence for this. A reference is necessary.

>>> **Lobopodians have terminal mouths – see e.g. Caron and Aria (2017, 2020).**

so are many tardigrades

>>> **Added.**

??

>>> **Removed.**

again, autapomorphic relates to characters not taxa.

>>> **Modified.**

This a very teleological view. Again, body plan is used in a problematic way.

>>> **The term is not ideal, which is why it is put between quote marks (it has been used in the Cambrian literature before). Please see above about body plans – arguably a fossil taxon can be identified as being or not a lobopodian, even if the group is paraphyletic, which means there is a morphospace that could define the lobopodian body plan.**

Suspension feeding is a very general term. What about a potential homology? Is there any clearly recognisable homologous structural correlate of the feeding behaviour to claim homology of suspension feeding in lobopodians and radiodontans. Otherwise this discussion is pretty speculative.

>>> **As the text clearly says, this is a broad ecological comparison between lobopodians and radiodontans – no homologous structures are involved. But active suspension-feeding habits are strongly supported by morphology and both sides, and distinct from deposit feeding, predation or scavenging in other panarthropod taxa.**

What about algae? The existence of small metazoan larvae is not necessary if there are enough planktic algae and protozoans.

>>> **As discussed later in the text, there are reasons to think based on evidence from certain Cambrian deposits (such as Orsten) that larvae were a substantial component of the macroplankton. “particularly” changed to “notably”.**

Very speculative!

>>> **This entire paragraph has been rewritten.**

But see onychophorans and possibly tardigrades. An opposing view was published by Nielsen 2019 Was the ancestral panarthropod mouth ventral or terminal?

>>> **The fossil evidence is quite clear: the ancestral panarthropod mouth was terminal, and remained so throughout the lobopodian radiation up to the origin of radiodontans (see text and figure 2). This is based on the entire lobopodian fossil evidence, not just one taxon. I would argue that tardigrades have a terminal mouth and that the ventral mouth in onychophorans is indeed autapomorphically derived. Even conflicting fossil-inclusive datasets all show that an ancestral ventral mouth would be either extremely unparsimonious or extremely unlikely. Ortega-Hernandez et al. had specifically replied to Nielsen about this: [The last common ancestor of Ecdysozoa had an adult terminal mouth - PubMed \(nih.gov\)](#). Reference added.**

Above the authors uses the arthrodized appendages for arthropods. Both together is not possible; apart from the problematic use of "define".

>>> **“fundamentally defined” replaced by “characterized”. As stated just below, the arthrodized appendage is not an apomorphy of the group, but of the common ancestor node of all Arthropoda, of which Radiodonta is a direct branching clade. The sentence has been emended.**

Again, is this a radiodontan or arthropod apomorphy? Moreover, should the occurrence of compound eyes not be seen independent of the question of the eyes being stalked. Stalked eyes are restricted to some arthropod groups and appeared independently in several lineages.

>>> **Considering compound eyes as an apomorphy of Arthropoda is complicated by the placement of Opabinia, as explained just after. The text has been emended for clarification.**

see Budd 1996 Opabinia (should be cited here)

>>> **Added slightly before.**

This needs slightly more explanation.

>>> **Emended.**

Again, it is not clear, whether this is considered as arthropod apomorphy or an apomorphy of Radiodonta.

>>> **Clarified.**

So, where does the head end? Is the prosoma identical to the head?

>>> **Yes, fossil evidence supports that the head tagma of chelicerates is the prosoma.**

Not clear. It depends on the fusion of the head shield/carapace with segments and the starting point, what was present in the last common ancestor of arthropods/euarthropods.

>>> **Correct. Arguably the origin of both carapaces and shield in isoxyids and euarthropods is deutocerebral. Paragraph emended.**

why not?

>>> **Sentence emended. The distinction is based on the fact that the megacheiran basipod essentially remains a large undifferentiated pseudo-cylindrical podomere.**

Why this? What is the evidence? Any references?

>>> **Sentence emended. This is from the reference cited in the previous sentence – Kylinxia has five stalked eyes, like Opabinia.**

see also Scholtz et al. 1998 The pattern of Distal-less expression in the mouthparts of crustaceans, myriapods and insects...

>>> **Added.**

BST: abbreviation not explained.

>>> **Added.**

"post-antennular" what? appendages?

>>> **Corrected.**

what does this refer to?

>>> **Obsolete. Removed.**

this is an oversimplification since the legs of *Limulus* are multifunctional as well and likewise the walking limbs of arachnids serve as sensory organs (also in mandibulates).

>>> **The sentence has been emended to reflect that fact. Arguably, however, there is nothing like a habeliidan head appendage in either merostomes or arachnids. The degree of morphological differentiation seen in basipod, endopod and exopod in habeliidans is closer to what is seen in mandibulates as mandible, palp and antenna, but combined into a single appendage.**

This is confusing, because then it would be no exopod (see text in brackets).

>>> **Sentence emended.**

see above

>>> **Replaced with “diagnosed”**

This is not a phenomenon but a speculation (hypothesis).

>>> **Modified.**

see Budd 2021 The origin and evolution of the euarthropod labrum

>>> **Added.**

for another line of argument see Scholtz 2016 Heads and brains in arthropods: 40 years after...

>>> **Indeed. Added.**

What is meant here? The frontal filaments of some crustaceans?

>>> **In ostracods, yes, as well as additional sensory organs, forming a coherent frontal structure also including the labrum – and as a whole similar to what is observed in certain Cambrian hymenocarines-although not all hymenocarines have protocerebral “filaments”. Emended.**

see Scholtz 2016, p. 407

>>> **Added here and below.**

parsimony is no model but a requirement of thought.

>>> **Replaced with “approach”.**

What did the look for? It was wasteland!

>>> **Emended. It is possible that the first land dwellers used the relatively barren environment as an advantage for safer reproduction and offspring. This is all very speculative, however, but the trace fossil evidence is clear.**

see above

>>> **As mentioned above, macroevolution is understood here as elsewhere in the literature simply as the study of evolution at the level of species and above, which also implies the geologic time scale.**

This view is too optimistic. The recent phylogenies including fossils differ to a high degree! See

>>> This would seem to be one of the most contentious aspects of this review. In reality, however, the phylogenetic scenarios presented here have been the most credible in the recent years (Edgecombe, 2020). Scenario advocated by Budd, Ortega-Hernández and colleague (Ortega-Hernández, Janssen & Budd, 2017) only found *some* phylogenetic support in the dataset by Legg (Legg, Sutton & Edgecombe, 2013), which needs to rely on highly contestable implied weighting (Congreve and Lamsdell 2016) to achieve any resolution, and which, even in its latest iterations (Yang et al., 2018), still hasn't integrated the mandibulate information regarding hymenocarines. The framework presented here has been used as the backbone of a recent review by Gregory Edgecombe (Edgecombe, 2020) as well as by a number of other researchers, which have or not compiled their own extensions of the data (Moysiuk & Caron, 2019; Izquierdo-López & Caron, 2019; Zeng et al., 2020).

Opabinia?

>>> As far as I know Opabinia has neither of those and therefore is not a euarthropod.

Scholtz & Edgecombe 2006;

>>> Added.

Explanation of characters in boxes???? Are they apomorphies, ground patterns or something else?

>>> These fossil (typically, stem) groups can be either para- or monophyletic, hence these sets of character states are not apomorphies, but combinations of defining traits for these groups. Some are overlapping. Because of the structure of the tree, only using monophyletic groups wouldn't help non specialists grasp the full breadth of fossil diversity in relation with the text. Caption emended.

This sequence needs more explanations. What is the labrum, what is the halo, what is the black dot, what is the grey dot?

>>> The diagram is now annotated.

??? what is the difference

>>> As you know, whether the ocular somite should be considered a "segment" is problematic, hence the double definition. Anyway, I just kept one.

The distinction between dorsal and ventral cephalisation would be helpful (see Scholtz 2016)

>>> Absolutely, it is just worded a bit differently here. There is also Lamsdell (2013, ZJLS) who discussed this in chelicerates. The main text has been emended with a couple of sentences mentioning this, although I cannot really afford to go into too many details about this, for it might bring confusion to non specialists.

protopod?

>>> Yes, the basipod is used here as a generalized equivalent of the protopod (see definitions)

I guess this should be a delta?

>>> Yes, corrected.

Incomplete references have been corrected.