Peer Review File

Earliest siphuncle-bearing cephalopod from the early Cambrian

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Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)
Song et al. present new phosphatized shelly fossils with internal septa connected by an internal tube. This tube exhibits all the characteristics of the siphuncle, which is perhaps the most convincing synapomorphy of the cephalopods. The most obvious interpretation for this fossil material is thus as the earliest antecedents of the cephalopods, extending the fossil range of this group by some millions of years. This stratigraphic extension is significant insofar as it informs the timing and sequence of the early stages of molluscan evolution.

This material therefore has substantial intrinsic interest. However, the implications of the finding are not yet sufficiently developed or coherent to achieve the reach I would expect of a Nature publication. The current taxonomic treatment also requires further explanation in the text, to demonstrate that its potential for confusion is justified.

FOSSIL MATERIAL

The authors present a good number of specimens preserved under a complementary set of preservational conditions; CT scans and SEM images provide a rather complete view of the original anatomy and microstructure, even if it was not always easy to interpret the full distribution of microstructural details from the figures (perhaps a schematic cartoon would help to visualize the relationship between the different fabrics and features?).

The images convincingly characterize the ‘segmented’ (perhaps a loaded term - as cephalopods are not segmented organisms, might e.g. ‘modular’ be a wiser choice?) tube connecting the chambers. The secondarily shrunken terminal component supports the interpretation of this tube as an organ. No interpretation other than a siphuncle presents itself to me. A convergent origin is of course plausible given the functional value of such a connecting tube, the presence of other camerate taxa in the Cambrian, and the frequent occurrence of convergent structures in the Cambrian. To mention the possibility of convergence - even if to articulate briefly why it can be dismissed - would provide a more complete evaluation of the significance of the structure.

SYSTEMATIC TAXONOMY

The authors do not provide a rationale for assigning this material to Cupitheca; nor is there any formal taxonomic treatment.

I find the case for inclusion in Cupitheca hard to follow. The authors assert that their material belongs in the genus; then go on to argue that the genus must be polyphyletic because Cupitheca sp. contains a siphuncle. If including a monophyletic genus becomes paraphyletic when a new species is added to it, this feels like a strong signal that the species does not belong in the genus. I view the presence of a siphuncle as a clear distinction from Cupitheca and a sufficient diagnostic criterion to justify the erection of a new genus and am unclear why the authors have not done this.

From a broader perspective, the morphology of the shells is difficult to square with a hyolith affinity (which is conclusively shown for Cupitheca). Assigning the material to Cupitheca implies that the authors interpret the new material as a derived hyolith. I am not aware of any hyoliths whose aperture has a comparable shape or such an oblique orientation. No opercula are reported as occurring in the conch-bearing samples; and I am not aware of any isolated opercula whose shape matches the shape of the aperture. The potential relationship of the new material to hyoliths is of great consequence for the implications of the material and for the reconstruction of cephalopod evolution (and the affinity of hyoliths); it therefore warrants an in-depth exploration. Perhaps (as hinted later) the authors are not in fact advocating the "hyoliths are ancestral cephalopods" viewpoint alluded to in line 51. Here and throughout, a clear exposition of the authors' perspective is essential in order for a reader to understand the framework of relationships that is being advocated.

INTERPRETATIVE CONTEXT

In turn, the manuscript would benefit from a meaningful comparison between the new material and other contemporary shelly taxa; particularly those that have been linked to cephalopods. Without such a discussion, the implications of the new material cannot be evaluated or contextualized

The manuscript hints throughout that the new material connects hyoliths with the origins of cephalopods, but never presents a meaningful evaluation of the similarities between the new material and bona fide hyoliths. The rich microstructural data available seems particularly pertinent to potential relationships with other taxa; how does this compare with other molluscs and hyoliths? My personal view is that microstructure is prone to convergence, but given that microstructure is one of the main arguments linking hyoliths to molluscs, it is surely salient to the authors' interpretation. The schematic portrait of cephalopod evolution presented in lines 255 onwards is not implausible, but doesn't go far beyond a "join the dots" exercise; to be convincing, it needs to be clear that the reference taxa are not just cherry picked for the purposes of story-telling, but are unequivocally linked by specific morphological and stratigraphic arguments; and that alternative hypotheses can be unequivocally rebutted.

The material is also compared briefly to other molluscan material and other potential cephalopod precursors. It would be useful to summarise this other material in its stratigraphic context, perhaps in Fig. 4, which implies substantial stratigraphic gaps, both before and after 'cupitheca'. I would like to see the authors evaluate whether gaps of this magnitude are plausible, given the richness of the Cambrian SSF record. In turn, a more robust treatment of other imperforate septate taxa in the figure and their relationship to the new material would provide a more complete view of how the authors think the new fossil rewrites our understanding of early cephalopod evolution; are these other taxa now irrelevant to molluscan evolution; can they be reconciled with the new specimens; or does the new material actually not help us to interpret them at all? As a specific example, I'm unclear from line 275 whether Cupitheca decollata should still be considered a hyolith (and if not, why it is associated with opercula); whether it should be considered congeneric with the new material; and how hyoliths can simultaneously represent stem-group cephalopods and sit outside the conchiferan crown group.

Another aspect that is underdeveloped is the fossil's role in 'fixing a mismatch' between the fossil record and molecular clocks. Budd & Mann have indicated that molecular clock results often simply return the prior distribution, rather than being informed by molecular data. To understand what we have learned in the context of a molecular clock, the reader needs to evaluate whether the clock is simply reflecting the known pattern of the fossil record (expressed in the effective priors), or whether there was a genuine mismatch between the molecular evidence and the fossil record (and how far the new specimens genuinely close this gap).

SUGGESTED CLARIFICATIONS

L36: "a mollusc with key cephalopod characters": This is slightly misleading. Strictly, only one diagnostic cephalopod character is presented (the siphuncle; many lineages exhibit septate tubes). Aside from this, no evidence demonstrates that the taxon is a mollusc (and/or not a hyolith).

L60: "nearly all >skeletonized< metazoan phyla" would be more accurate

L66: There's potential for confusion here between the molecular clock (which aims to assign absolute divergences to nodes) and molecular phylogenetics (which use molecular data to produce tree topologies). Whilst acknowledging the overlap between these methods, it's perhaps worth being clear that the early divergence of cephalopods is a common (if not universal) topological result that is independent of using a clock model.

L75–6 currently reads as if SEM/CT data revealed the homology of the siphuncle with that of modern cephalopods. This should be reworded to clearly separate the observation (i.e. tube passing through perforate septa) from the interpretation (i.e. status as siphuncle; homology with cephalopods).

L100 If the apical end is an exposed septum, I expect it to be perforated – but I don't see evidence of this in the specimens. Is it the case that the siphuncle does not pass through all septa?

L210 reads as if the absence of a siphuncle disqualifies shelly taxa from the cephalopod stem lineage; please evaluate whether these taxa may instead be stem-cephalopods that diverged before "Cupitheca" and the siphuncle.

L280. Please explain why you "think it likely" that hyoliths are molluscan. If shell microstructure is a key factor, how do the new observations complement this argument?

Fig. 1. The "anterior - posterior" / "dorsal - ventral" axes do not correspond to the body axes of a cephalopod with an embryologically dorsal valve.

Referee #2

(Remarks to the Author)

This manuscript reports an exciting finding and is fully worth to be published in Nature, because the authors convincingly make the case that this is indeed the oldest conchiferan mollusc with a siphuncle, and hence a cephalopod.
The fossil occurrence and the morphological features of the specimens are very well described, with methods and documentation making the finding reproducible and convincing. The illustrations are beautiful and appropriate for a Nature publication.
That said I have three main points of criticism:
(1) I believe, the description needs to be improved: To me, it seems quite imprecise and ambiguous in several paragraphs, with mixed terminology, with interpretation and description mixed, and partly with clumsy wording (see my detailed comments and suggestions in the annotated pdf). For instance, it is not clear why sometimes apertural / apical and sometimes anterior / posterior is used for describing the positions of e.g. the septa… This is confusing. Sometimes the descriptions use present tense and sometimes past tense. Regarding the wording: There is at least one native English speaker within the group of authors. I suggest that he carefully goes through the descriptions and improves wording and consistency of descriptive terms. The sometimes-awkward wording makes me wonder if all authors carefully read this paper and contributed to the text.
(2) The specimens are assigned to the genus Cupitheca. However, a formal systematic description of the specimens is lacking in this manuscript. As far as I see it in the literature, there are several species of Cupitheca described. Several of them are cyrtoconic. In what ways do these known species (and the type species) differ from or compare with the specimens described herein? Please add a formal systematic description and then make an argument: why do you place these specimens into Cupitheca?
(3) In this context it appears to me important to discuss in more detail previous descriptions and interpretations of Cupitheca (e.g. Bengtson 1990, Skovsted et al. 2016). Notably, Skovsted et al. 2016 described opercula from a Cupitheca holocyclata and other characters that "unequivocally" demonstrates to them a hyolith affinity. A crossed-lamellar microstructure has been observed in Cupitheca sp. previously, and from it, a molluscan affinity was concluded: (Li et al., 2022: doi: 10.1111/pala.12620). etc. In my opinion, here (e.g. in line 277) the careful work of Skovsted et al. 2016 is brushed off too quickly. What if they are right and C. holocyclata is a hyolith? What, if C. holocyclatha had a siphuncle? What if our Cupitheca sp. is not a Cupitheca? How do these previously published interpretations relate to your interpretation of your specimens of Cupitheca as a cephalopod? How, can one species of Cupitheca be a hyolith and another species be a cephalopod? What if your specimens really belong to Cupitheca, what does this tell about the hyolithid – cephalopod phylogenitic relationship. In the last years great progess has been made to understand the biology of hyoliths (e.g., Li et al. 2020, Liu et al. 2021; Dzik 2025). This problem is in my opinion not sufficiently discussed by the authors. In the manuscript, a chapter is called "Caphalopod affinity of Cupitheca". In my opinion the possible hyolithid affinity of Cupitheca should be also critically reviewed in this context. In the context of a Nature paper, this might appear as just a side aspect. But I think it is important to put the finding into proper context and not only superficially report the finding of "a siphuncle in a hyolithid like conch". May be then, this would be something to put as a discussion in supplementary material.

An interesting aspect (just as a side note) is the concave shape of the siphuncle in the specimens described: This is similar to the Ellesmerocerida, Plectronocerida, and Yanhericerida (they were previously seen as the oldest cephlaopods; see Kröger, https://doi.org/10.1111/j.1475-4983.2007.00644.x; Pohle et al. https://doi.org/10.1186/s12915-022-01284-5). I see this as supporting the argument of the authors.

Here are some of my comments from the annotated pdf that I consider important:
Line 195: No! They are similar to simple orthoconic ellesmerocerid cephalopods, such as Paleoceras, see e.g. Flower 1964, not to endocerids. Endocerids are cephalopods with highly specialised siphuncles with complex internal structures and with very specific septal neck structures. This is a poor comparison. They are much better compared with nearly orthoconic Plectronocerids.
Line 221: Although the story is a bit hidden in this monograph, but I think a much better and more up to date reference to the Ascocerid evolutionary history and morphology is: Kröger 2013: http://dx.doi.org/10.5852/ejt.2013.41
Line 221: What is a "siphuncular displacement canal"? I am not aware of any description of this in ascocerids or elsewhere in the cephalopod literature. Also, in the references cited at the end of this sentence, such a canal is not mentioned.
Lines 255-265: Tannuella, as far as I know, is interpreted as a Helcionellid. C. holocyclata and the closely related type of the genus, C. mira previously have been interpreted as hyolithids. Both opinions are not explicitly mentioned in this paragraph. For me as a non SSF specialist this seems to be quite confusing. I don't understand how all this comes together in a phylogeny to become a cephalopod in Cupitheca sp. How do these stages of proposed hyolithids / helcionellids become to be cephalopod? More precise explanation would be good.
Line 277: In my opinion here the careful work of ref. 50 (Skovsted et al. 2016) is brushed off too quickly. What if they are right and C. holocyclata is a hyolith? What, if C. holocyclatha had a siphuncle? What if your Cupitheca is not Cupitheca?

Refs:

Bengtson, S. (1990). Early Cambrian fossils from south Australia. Association of Australasian Palaeontologists.
Dzik, J. (2025). Early ontogeny and other possible molluscan traits in hyolith biology and anatomy. Lethaia, 58(2), 1-16.
Li, L., Skovsted, C. B., Yun, H., Betts, M. J., & Zhang, X. (2020). New insight into the soft anatomy and shell microstructures of early Cambrian orthothecids (Hyolitha). Proceedings of the Royal Society B: Biological Sciences, 287(1933).
Liu, F., Skovsted, C. B., Topper, T. P., & Zhang, Z. (2021). Soft part preservation in hyolithids from the lower Cambrian (Stage 4) Guanshan Biota of South China and its implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 562, 110079.
Skovsted, C. B., Pan, B., Topper, T. P., Betts, M. J., Li, G., & Brock, G. A. (2016). The operculum and mode of life of the lower Cambrian hyolith Cupitheca from South Australia and North China. Palaeogeography, Palaeoclimatology, Palaeoecology, 443, 123-130.

Referee #3

(Remarks to the Author)
The authors use SEM and micro-CT scanning to image hitherto undescribed structures in small conical fossils. These structures are suggested to be primitive siphuncles and septa, which would infer that these shells were created by early cephalopods (rather than hyoliths). If these are indeed cephalopods, this work would be topical and significant, pushing the first appearance of cephalopod fossils back by ~30 Ma. Most of my comments are minor and concern improving clarity, fixing grammatical issues, and the addition of a few references.

Line by line comments are listed below:

Line 32: Regarding the “segmented” tube. The next sentence states that this feature enabled connection with all chambers, which would be unlikely if they were entirely segmented (closed off). Are there any features that suggest the septa would have been perforated? (e.g., pore canals, restricted connecting rings and inflated intra-cameral siphuncles, etc.). Or does this feature reflect a primitive condition, unlike cephalopods with septal foramina?

Line 40: Noun-verb agreement issue. Please consider changing “Cephalopods” to “Cephalopoda” or “includes” to “include”. The use of “its” in the following phrase, and next sentence points towards a singular noun, thus both issues can be fixed by using “Cephalopoda”.

Line 47: Consider citing a recent paper about cephalopod cameral deposits here (Peterman et al., 2025; DOI:10.1017/pab.2025.10085). This paper explores the functional opportunities among a wide variety of orthocone cephalopods with various cameral deposit configurations. I also suggest citing this chapter of the ammonoid paleobiology, which summarizes research on the early shell coiling of the ammonoids (Naglik et al., 2015; DOI:10.1007/978-94-017-9630-9_17).

Figure 1 caption and elsewhere:
The anterior portion of the shell is referred to as an “aperture”. The siphuncle runs up to this region, suggesting that the figured specimen is mostly, or all phragmocone, with no body chamber preserved. Does the highly oblique, concave feature reflect the shape of the last preserved septum? If so, how was the soft body attached to the shell? If this is only a phragmocone with no body chamber, I would not suggest using the term aperture here. An aperture should denote the anterior-most opening of the shell, and the site of shell growth.
Why are different colors used for the siphuncle between different figure panels? I suggest keeping this feature color-coded within, and between, images.

Line 101: I suggest using the term “adoral” instead of the “apertural”. Please see my comment above. Those will familiarity of ectocochleates will question why the siphuncle runs up to the “aperture” rather than terminating into a posterior mantle.

Line 110: “Internal chambers of the siphuncle”. Is phragmocone meant here instead?

Line 121: Consider changing “endodeposits” to “endosiphuncular deposits”. I also recommend citing Peterman et al. (2019) here, who quantitatively explored how these features influenced stability and hydrostatics (doi.org/10.26879/884).

Line 133: I suggest being cautious calling this a prismatic layer. Perhaps “ … an intervening layer, possibly analogous to the prismatic layer of ectocochleates…”. There may be diagenetic affects that produce similar perpendicular crystal arrangements.

Line 141: Something is wrong with this sentence. The shell and septa are secreted by mantle epithelium. The siphuncle is broadly a vascularized structure that grows with the soft body, rather than being secreted by a “gland”.

Line 145: All septa are internal. Consider simply deleting some of this sentence. E.g., “….interpret the posterior-most septum as a younger septum, exposed as the result of post-mortem….”.

Figure 3: The red arrows are very small. I suggest doubling their size, at least.

Line 195: The term “nautiloid” no longer has much taxonomic value. I suggest something like this “… most similar to those of younger, orthoconic stem group cephalopods (Endocerid and Orthocerida)…”.

Line 196: How do we know that this is the ventral side? Ectocochleates had variable siphuncular positions depending on the clade (Aturidae and Clymeniida are dorsal, most ammonoids are ventral, nautilds and many stem group cephalopods are central to ventral). Is this based on the aperture/lirae obliquity? There are examples of orthocones with dorsally tilted apertures (e.g., Sciponoceras) .

Line 215: Ever since seeing Fig. 1, I was wondering about how the chambers were connected since the septa appear to lack siphuncular foramina. I suggest making this more apparent earlier in the abstract and figure 1 caption. The abstract states that the siphuncle is a segmented tube, then later indicates there was contact between earlier chambers. Clearly stating, early on, that the siphuncle appears to bridge septa through minute canals would be considerably improve clarity for those reading chronologically.

Line 221: A “siphuncular displacement canal” is an unusual term. I’ve never heard of this being applied to the ascocerids. I also cannot find this term in the two references at the end of this sentence. Also the Ascocerida are best known for syn vivo truncation of the shell rather than post-mortem breakage. I’m not sure what is being implied here.

Line 234: Grammer issues. I suggest rewriting this sentence.

Line 242: Based on the proportion of the soft body to phragmocone, I suspect managing positive buoyancy would be the issue. If these chambers were all emptied, the living animal would likely weigh much less than the water it displaced (air is ~1000 times less dense than any other organismal component). Very generally speaking, cephalopods with a body chamber ratio less than 40% to 30% (depending on shell thickness) would have required cameral liquid or mineral deposits to reduce positive buoyancy. See Peterman et al. (2019; doi.org/10.26879/884) and (2025; DOI:10.1017/pab.2025.10085). That is, this extra space near the posterior mantle probably wasn’t necessary, unless there was a considerable amount of fluid in earlier chambers.

Line 247: “living chamber” is a less-used term today. I suggest using “body chamber” to be consistent throughout.

Supplementary video: I am having issues playing this video in AVI format. I suggest saving as an MP4, which is generally more accessible.

Extended Data Fig. 4: Consider changing “animal mass” on the legend and caption to “soft body”. Also, the key suggests the siphuncle is denoted by a blue outline. This blue outline also highlights the rest of the soft body in the body chamber, which is confusing. The soft body and siphuncle should be distinct from one another.

Referee #4

(Remarks to the Author)
Dear authors,
I greatly appreciate your extraordinarily thorough presentation of the earliest cephalopod. It is without doubts a milestone in molluscan research.

I find your manuscript well written, your methods highly topical, your descriptions concise, and your conclusions intelligible.

I could not find any major inconsistency in your manuscript. One minor open question concerns the evolution of the cephalopod funnel that you do not discuss, though it is added in Extended Data figure 4f. The development of a funnel is closely associated with the ability of jetting and thus with a nektonic life style and this contradicts your assumption that Cuspitheca lived mainly benthic.

Congratulations!
Dirk

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)
I thank the authors for the improvements; the erection of a new genus has greatly simplified the systematic aspects of the paper, and the simpler evolutionary framework is clearer and more clearly tied to the novel data.

There are however many aspects of the manuscript that remain unclear and whose strengthening would clarify the evidential support for aspects of the description that remain at present less than convincing.

Caption to Fig 1 - it would be helpful to spell out whether light or dark greyscale values correspond to high X-ray attenuation.

Due to the blue colouration, it is difficult to determine whether the siphuncle in 1a is a void or a sediment-infilled structure. It is also difficult to see whether it displays contrast with the rest of the internal infill. The presence of a high[?] attenuation film over the aperture also invites comment – is this because the specimen has been gold-coated for SEM, or was the aperture originally covered by a high-attenuation layer in life (??).

Fig 2 - it remains unclear how the various greys in the "Type X" column correspond to the pinks purples. The key does not contain an entry corresponding to the dark grey. It's not clear from the figure what evidence implies the presence of phosphatized sediments within Type I, and why the internal structure is visible in Type 2 if the shell is preserved in its entirety. It's not clear whether the shell is preserved in types 1 and 2, or whether we are seeing only an infill of the shell septa. None of the preservation modes shown leave an obvious pathway for the preservation of complete septa.

Fig 3: The septal pores/canals are not convincingly documented; it's not clear that they represent originally open structures rather than an aspect of the columnar microstructure, such as an originally organic scaffold that facilitated the growth of prisms. I don't see any evidence to support the claim of permeability or osmosis (line 225).

ED Fig 4. Specimen a has the largest body cavity, but is interpreted as the youngest specimen; it's not clear that an ontogenetic sequence is the most convincing explanation for specimens that are all approximately the same size.

ED Fig 6. The position of the siphuncle on these septa is not clear; the siphuncle seems not to pass through them, which seems to contradict the interpretation presented elsewhere.

Even if "Anterior/Posterior" is sometimes used in cephalopod terminology, it has potential for confusion, particularly when talking about the derivation of cephalopods from molluscs. The terms "apertural / apical" are suitable unambiguous alternatives. At a minimum, it is essential that the same orientation terminology is used throughout; on line 56, "dorsally" is used where the orientation scheme used later in the manuscript requires "posteriad".

The definition on Line 479 would be more helpful if it (i) were presented to the reader before the first use of orientation terminology; and (ii) stipulated in the text how the terms were used, rather than requiring the reader to look up another reference before they can understand the rest of the manuscript.

56 - "predating" could potentially be misread as meaning "that preyed upon"; suggest "preceding" or "earlier than"

267. It would be useful to mention here what evidence of osmoregulation exists in Tannuella.

268–272 - The argument against Cupitheca and Tchuranitheca being cephalopod relatives is inscrutable; osmoregulation is not convincingly demonstrated in Eosceras, and it seems that there's a plausible argument that it's present anyway in Cup. and Tch. Even if it's not, its absence would not preclude Cup. and Tch. from being members of the stem group that diverged before osmoregulation arose.

282 - this is clearly articulated and seems well supported

284. Why would a benthic organism be keen to reduce ballast?

286. "The small size of this species is an artefact" – as written this implies that taphonomy has shrunk the species; please be clear whether you mean "only juveniles are preserved" or something else.

288. "a more efficient buoyancy apparatus" – the efficiency of the buoyancy apparatus is nowhere discussed or quantified; it has not been established that the Eosceras apparatus is (or is not) inefficient.

The manuscript would benefit from a careful copyedit throughout to correct its numerous grammatical errors (notably misuse of 'that' and commas).

Systematic palaeontology.
As a new genus and a new species are being described, there should be a separate definition of each, per the ICZN; the new species must be formally defined as the type species of the genus.

I'm not up to date with the ICZN position on defining new species in supplementary appendices – worth confirming that the registration of the SI material will comply with the current Code.

Under "Referred material" it would be helpful to provide a count of the number of specimens in each category, as this information is difficult to eyeball from the list.

The statement that "gross anatomical similarities … are superficial" is itself superficial; it should either be expanded to describe the similarities and to explain why they are not considered consequential. If the similarities are spurious, then it's not clear what purpose there is in mentioning them at all.

Referee #2

(Remarks to the Author)
This is a much-improved revised manuscript. I am in particular happy to see that the authors now added a formal taxonomic description of the specimens they describe. This will help in the future to disentangle the confusion of different potential groups currently subsumed under Cupitheca sp. The description itself is now also much clearer and ambiguous wording resolved. The improvements and removal of redundancies in the figures improved the quality of the manuscript.
I also noted the improvements in grammar and writing style.

I found only some small grammar issues. After these issues are resolved I would recommend this manuscript for publication. (I did not cross check the references).

In the long sentence lines 60-64: I don't understand the last part of the sentence part "possible intermediate for,s preceding those still lacking".
In lines 100-101 I would place (Types I-II) behind "taphonomic types".
In lines 280-282: Is the word "polarized" here correct? Please consider rewording.
In line 283-286: Something is wrong with this sentence. I don't understand what "as much" refers to.

Referee #3

(Remarks to the Author)
The new version of the manuscript is rewritten for enhanced clarity. Major improvements involve fixing grammar, using softer/cautious language when referring to uncertainties, and adding a systematics section in the SI. My points from the first review have generally been addressed. I only have a few minor suggestions (see below).

Regarding name "Eosceras": Please doublecheck the etymological rules for having an "s" and a "c" next to each other in a separate prefix and root. Often, the "s" will become assimilated into the root. Therefore, I think "Eoceras" would be more appropriate. E.g., the historical term "Eocarboniferous", lacks an "s" after "eo". But please double-check this.

Line 27: Consider getting rid of the text "through jet propulsion". Jet propulsion is already mentioned earlier in this sentence, so it is redundant.

Line 72: consider changing "siphuncular" to "siphunculate". I.e., siphuncle-bearing.

Line 201: consider using the term "in vivo" (i.e., during life) instead of "real life".

Line 280: the plural form of "foramen" should be "foramina".

Referee #4

(Remarks to the Author)
Dear authors,
you adequately addressed my recommendations. Thank you for that!
I find your ms is now acceptable for publication.
I´m largely conform with your interpretation Eosceras is - due to the possession of a phragmocone-like shell apparatus a representative of the cephalopod stem lineage. Chambers interconnected by a complex arrangment of septa and siphuncular-like segments absolutely allow such an affiliation. We are now closer to the origin of cephalopods than ever before.
The weak point in your contribution is - from my point of view - the referred "developmental sequence" (extended fig. 4), because I think your argumentation about the septum/siphuncle formation cycle is still too sketchy, leaving some open questions. In its present state it is difficult to comprehend your idea. E.g. you state there is no septal foramen, but in Fig. 4, phase 5 it seems as if the soft body passes through the newly build septum (in orange). Is it possible that the foramen was secondarily closed?
good luck and with best wishes
Dirk

Version 2:

Reviewer comments:

Referee #1

(Remarks to the Author)
I thank the authors for their careful attention to my previous comments, which have been addressed to my satisfaction.

There is one remaining issue: In Fig. 2, the legend is somewhat clearer, but the Type I schematic is still confusing. By drawing the phosphatized infillings “on top of” the phosphatized shell wall, the schematic gives the impression that a distinct siphuncular infilling is preserved and differentiated from other infill, which I do not see evidence of in the fossil material.

I think that the entire inner region of the shell should be coloured light grey (for “phosphatized infillings”, representing the infill of the shell and the infill of the siphuncle - with the structure distinguishing the two invisible, as already denoted with the dotted lines) and the dark grey “shell wall” should only surround the margins of the specimen. If the desire is to depict an external view rather than a cross-section, then the ‘infillings’ of the siphuncle should be covered by the shell wall and not be visible in the schematic (as indeed they are not visible on the associated SEMs).

Referee #2

(Remarks to the Author)
The revised manuscript looks good now. I have only very few things to comment:
In the abstract and in the Systematic palaeontology section the new species is described as Eoceras shaanxiense gen. et sp. nov.. However, in the main text, in the figure captions, and in section headings the species is listed and mentioned as “Eoceras gen. nov.” or simply as “Eoceras”. I am not sure what is the rational behind that. I would suggest a consistent reference here, such as “E. shaanxiense gen. et sp. nov..” in the main text and figure captions and “Eoceras gen. nov.” in the headings.
The new genus (Eoceras) is missing in the systematic palaeontology section. Currently, this section is a mix of genus (e.g. lines 433) and species part (lines 434-438). I would suggest have first a genus section with paragraphs: “Type species. […], by monotypy”, “Diagnosis. As for type species, by monotypy”, etc. and then, in the species section place the full diagnosis and comparison etc.

Line 283-284: Some ending is missing in this sentence: “Although, the truncation of the embryonic shell would reduce energy consumption, improve mobility and increase buoyancy.” May be something like this: .. “, suggesting an adaptive value of this feature for a swimming life-style.”

Referee #3

(Remarks to the Author)
The authors have addressed each of my comments. I'd like to thank them for their careful consideration throughout each round of review. I recommend acceptance if the other reviewer comments are satisfactorily addressed.

Version 3:

Reviewer comments:

Referee #1

(Remarks to the Author)
The authors have addressed my comments.

Referee #2

(Remarks to the Author)
The authors have addressed each of my few remaining comments. I thank them for the careful consideration of all of my previous comments. The manuscript improved much and I will be happy to see it published now. This will advance discussions on the origin of cephalopods significantly!

Response to Reviewers' Comments

Manuscript Title: **Earliest siphuncle-bearing cephalopod from the early Cambrian**

Manuscript ID: 2026-02-04042

To the Editor Dr Henry Gee,

Please find a revised version of our manuscript "**Earliest siphuncle-bearing cephalopod from the early Cambrian**", which we are resubmitting for publication in *Nature*.

We very appreciate the comments and suggestions provided by the four referees. We have worked diligently to incorporate their suggested changes and we believe their suggestions have improved the overall quality of our manuscript.

Here we provide a point-by-point response describing how we have addressed their comments. The original comments are listed in black and our reply, along with a description of changes we have made to the manuscript text in blue, follows immediately after. We also have included the references cited in our responses to the referees at the end.

We thank you very much for taking the time to consider our manuscript for publication in *Nature* and we hope our manuscript will be ready for acceptance after we made these changes to our paper. If you have any further questions about our revised manuscript, please do not hesitate to get in contact. Thank you very much for your time and consideration.

Your Sincerely,
Junfeng Guo and Zuchen Song
(on behalf of all co-authors)
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Referees' comments:

Referee #1 (Remarks to the Author):

Song et al. present new phosphatized shelly fossils with internal septa connected by an internal tube. This tube exhibits all the characteristics of the siphuncle, which is perhaps the most convincing synapomorphy of the cephalopods. The most obvious interpretation for this fossil material is thus as the earliest antecedents of the cephalopods, extending the fossil range of this group by some millions of years. This stratigraphic extension is significant insofar as it informs the timing and sequence of the early stages of molluscan evolution.

This material therefore has substantial intrinsic interest. However, the implications of the finding are not yet sufficiently developed or coherent to achieve the reach I would expect of a Nature publication. The current taxonomic treatment also requires further explanation in the text, to demonstrate that its potential for confusion is justified.

FOSSIL MATERIAL

The authors present a good number of specimens preserved under a complementary set of preservational conditions; CT scans and SEM images provide a rather complete view of the original anatomy and microstructure, even if it was not always easy to interpret the full distribution of microstructural details from the figures (perhaps a schematic cartoon would help to visualize the relationship between the different fabrics and features?).

Response:

Thank you for your suggestion. Due to preservation limitations, we had to combine morphological features visible in specimens with different preservation to reconstruct the original shell morphology and internal structures. As you suggested, we have redrawn the three different preservation type of Figure 2 to more clearly and neatly illustrate these features. The microstructural details of the possibly prismatic layer and canals are shown in Figure 4a.

The images convincingly characterize the ‘segmented’ (perhaps a loaded term - as cephalopods are not segmented organisms, might e.g. ‘modular’ be a wiser choice?) tube connecting the chambers. The secondarily shrunken terminal component supports the interpretation of this tube as an organ. No interpretation other than a siphuncle presents itself to me.

Response:

Thank you for your positive comments. We use the term “segmented” based on descriptions of early cephalopod (e.g. Plectronocerida) siphuncle morphology, consistent with “siphuncular segments” in previous studies (e.g., ref.[7], Mutvei, 2020, https://doi.org/10.1080/11035897.2020.1739742 ; Pohle et al., 2024, https://doi.org/10.7717/peerj.17003).

A convergent origin is of course plausible given the functional value of such a connecting tube, the presence of other camerate taxa in the Cambrian, and the frequent occurrence of convergent structures in the Cambrian. To mention the possibility of convergence - even if to articulate briefly why it can be dismissed - would provide a more complete evaluation of the significance of the structure.

Response:

Thank you for your comments.

We have added a brief discussion on this issue below, please refer to the main text in Future assessment of tubular SSFs: "Indeed, the cephalopod *Eosceras* bears some strikingly resemblance to hyoliths within the genus *Cupitheca*[42,44,49] in having an orthoconic or slightly cyrtoconic, septate shell and a truncated apex. While the affinities of hyoliths have been debated, they share unique shell microstructures with molluscs, suggestive of some close relationship[50]. One scenario could be that these comparable shell features evolved independently in hyoliths and cephalopods, but from a shared ancestral biomineralization pathway and a similarly organized shell secreting gland or mantle. Alternatively, hyoliths or certain members of this clade (i.e. *Cupitheca*), if polyphyletic, are stem cephalopods within crown Conchifera in which *Eosceras* evolved from diminutive cupithecid molluscs exhibiting orthoconic, septate shells lacking a functional siphuncle. Future discoveries and anatomical studies may eventually resolve these competing scenarios or refute them both."

SYSTEMATIC TAXONOMY

The authors do not provide a rationale for assigning this material to Cupitheca; nor is there any formal taxonomic treatment.

Response:

Thank you for your critical comments. We have now erected a new genus and species, ***Eosceras shaanxiense***, and added a complete chapter on Systematic Paleontology in the Supplementary Information.

I find the case for inclusion in Cupitheca hard to follow. The authors assert that their material belongs in the genus; then go on to argue that the genus must be polyphyletic because Cupitheca sp. contains a siphuncle. If including a monophyletic genus becomes paraphyletic when a new species is added to it, this feels like a strong signal that the species does not belong in the genus. I view the presence of a siphuncle as a clear distinction from Cupitheca and a sufficient diagnostic criterion to justify the erection of a new genus and am unclear why the authors have not done this.

Response:

Thank you for your critical comments again. We agree that the presence of a siphuncle as a sufficient diagnostic criterion to allow us to erect a new genus and species, ***Eosceras shaanxiense.*** Please refer to the Systematic Palaeontology section in the Supplementary Information for details.

We initially assigned the new material to the genus *Cupitheca* and identified it as *Cupitheca* sp., primarily because its external morphology—including the orthoconic, barrel-shaped shell and bluntly conical apical end—is largely consistent with the generic diagnosis of *Cupitheca*. Specifically, we used the indeterminate species designation “sp.” because a siphuncle was observed in these specimens.

Indeed, we must acknowledge that most small shelly fossils preserve only external shell morphology. The absence of internal soft tissues implies that numerous genera and species erected in previous studies could instead represent morphological species as a possibility, lacking clear biological taxonomic features comparable to those in extant organisms—such as the cephalopod siphuncle and molluscan radula. This represents a common challenge in traditional palaeontological research, particularly for studies focusing on SSFs from the terminal Ediacaran to early Cambrian.

From a broader perspective, the morphology of the shells is difficult to square with a hyolith affinity (which is conclusively shown for Cupitheca). Assigning the material to Cupitheca implies that the authors interpret the new material as a derived hyolith. I am not aware of any hyoliths whose aperture has a comparable shape or such an oblique orientation. No opercula are reported as occurring in the conch-bearing samples; and I am not aware of any isolated opercula whose shape matches the shape of the aperture. The potential relationship of the new material to hyoliths is of great consequence for the implications of the material and for the reconstruction of cephalopod evolution (and the affinity of hyoliths); it therefore warrants an in-depth exploration. Perhaps (as hinted later) the authors are not in fact advocating the "hyoliths are ancestral cephalopods" viewpoint alluded to in line 51. Here and throughout, a clear exposition of the authors' perspective is essential in order for a reader to understand the framework of relationships that is being advocated.

Response:

Thanks again for these very constructive comments!

We agree that although *Eosceras* shares some similar shell features with *Cupitheca*, the absence of an operculum, the opposite dorsoventral orientation, a highly oblique aperture, and the diagnostic siphuncle in *Eosceras* all preclude a hyolith affinity. The morphological similarities—including the orthoconic, barrel-shaped shell with a bluntly conical apical end (where shell truncation exposes the septa)—between the hyolith *Cupitheca* and the cephalopod *Eosceras* are now interpreted as the possible result of independent evolution while we have discussed these similarities a bit further also.

Please see the detailed revisions in the Future reassessment of tubular SSFs section.

INTERPRETATIVE CONTEXT

In turn, the manuscript would benefit from a meaningful comparison between the new material and other contemporary shelly taxa; particularly those that have been linked to cephalopods. Without such a discussion, the implications of the new material cannot be evaluated or contextualized.

Response:

Thank you for your comments! We have added the brief discussion of *Eosceras* and contemporary shelly taxa including *Cupitheca* cf. *C. mira* and *Tchuranitheca* sp. in Orthoconic shell origin of cephalopods section. The relevant text reads: “Other septate orthoconic fossils, such as *Cupitheca* cf. *C. mira* (Cambrian Stage 3 of Mexico)[42] and *Tchuranitheca* sp. (Cambrian Stage 3 of Siberia)[43], may be rejected as potential cephalopod precursors on account of their two-layered septum which may not have been capable of osmoregulation, although canals are also documented within the septa in these that may have functioned in osmotic water transport[44].".

Detailed comparisons please also see the systematic palaeontology section provided in the supplementary information.

The manuscript hints throughout that the new material connects hyoliths with the origins of cephalopods, but never presents a meaningful evaluation of the similarities between the new material and bona fide hyoliths. The rich microstructural data available seems particularly pertinent to potential relationships with other taxa; how does this compare with other molluscs and hyoliths? My personal view is that microstructure is prone to convergence, but given that microstructure is one of the main arguments linking hyoliths to molluscs, it is surely salient to the authors' interpretation. The schematic portrait of cephalopod evolution presented in lines 255 onwards is not implausible, but doesn't go far beyond a "join the dots" exercise; to be convincing, it needs to be clear that the reference taxa are not just cherry picked for the purposes of story-telling, but are unequivocally linked by specific morphological and stratigraphic arguments; and that alternative hypotheses can be unequivocally rebutted.

Response:

Thank you for your critical and constructive comments.

The microstructures of *Eosceras* mainly include preserved prismatic layer (shown well, especially in Extended data Fig. 3g) and minute canal structure connecting the siphuncle and septa. The shell stratification of *Eosceras*, particularly the possible prismatic layer, may support it as a conchiferan mollusc. And, the siphuncle and septa interconnected by minute penetrating canals further support it as a cephalopod (although, we are also familiar with the documented canals in hyolith taxa for good measure). Shell microstructures (aragonite/calcite arrangements) are not preserved. The septum of *Cupitheca decollata* and *Cupitheca* cf. *C. mira* differs from that of *Eosceras* in being two-layered, and the distribution of minute canals is also different. We acknowledge, this further indicate that *Eosceras* and *Cupitheca* are two separate taxa.

Regarding the early cephalopod evolution, as you suggest, we have added the brief discussion about certain orthoconic septate taxa: "Other septate orthoconic fossils, such as *Cupitheca* cf. *C. mira* (Cambrian Stage 3 of Mexico)[42] and *Tchuranitheca* sp. (Cambrian Stage 3 of Siberia)[43], may be rejected as potential cephalopod precursors on account of their two-layered septum which may not have been capable of osmoregulation, although canals are also documented within the septa in these that may have functioned in osmotic water transport[44].".

The material is also compared briefly to other molluscan material and other potential cephalopod precursors. It would be useful to summarise this other material in its stratigraphic context, perhaps in Fig. 4, which implies substantial stratigraphic gaps, both before and after 'cupitheca'. I would like to see the authors evaluate whether gaps of this magnitude are plausible, given the richness of the Cambrian SSF record. In turn, a more robust treatment of other imperforate septate taxa in the figure and their relationship to the new material would provide a more complete view of how the authors think the new fossil rewrites our understanding of early cephalopod evolution; are these other taxa now irrelevant to molluscan evolution; can they be reconciled with the new specimens; or does the new material actually not help us to interpret them at all? As a specific example, I'm unclear from line 275 whether Cupitheca decollata should still be considered a hyolith (and if not, why it is associated with opercula); whether it should be considered congeneric with the new material; and how hyoliths can simultaneously represent stem-group cephalopods and sit outside the conchiferan crown group.

Response:

Thank you for your critical and constructive comments. Following your suggestions, we have revised Figure 4b by adding a basal lineage, possibly represented by *Tannuella*?, and incorporating the key synapomorphies.

In fact, many proposed cephalopod precursors have now been tentatively refuted, as mentioned in the main text. Our new material (now *Eosceras*) currently supports only septate orthoconic *Tannuella*. Please see our response above. A comparison of *Eosceras* with hyolith *Cupitheca* has been provided in the section Future reassessment of tubular SSFs: "Indeed, the cephalopod *Eosceras* bears some strikingly resemblance to hyoliths within the genus *Cupitheca*[42,44,49] in having an orthoconic or slightly cyrtoconic, septate shell and a truncated apex. While the affinities of hyoliths have been debated, they share unique shell microstructures with molluscs, suggestive of some close relationship[50]. One scenario could be that these comparable shell features evolved independently in hyoliths and cephalopods, but from a shared ancestral biomineralization pathway and a similarly organized shell secreting gland or mantle. Alternatively, hyoliths or certain members of this clade (i.e. *Cupitheca*), if polyphyletic, are stem cephalopods within crown Conchifera in which *Eosceras* evolved from diminutive cupithecid molluscs exhibiting orthoconic, septate shells lacking a functional siphuncle. Future discoveries and anatomical studies may eventually resolve these competing scenarios or refute them both.".

Substantial stratigraphic gaps also exist between the other lineages and their common fossil record and their earlier first occurrences. Therefore, although the record of early Cambrian SSFs is exceptionally rich, the greatest challenge is linking these to discoveries of soft tissues with definitive taxonomic significance or discoveries of additional internal anatomy or shell microstructures like in this study. Furthermore, the progressive closure of phosphatic preservation windows during the middle to late Cambrian leaves significant gaps in tracing and linking shelly taxa through the early Palaeozoic. Finally, advances in techniques and methods have also improved researchers' understanding and identification of fossils. Collectively, we suggest that such large stratigraphic gaps are plausible.

We agree that *Cupitheca decollata* is a hyolith, with its diagnostic opercula and other soft tissues. And we therefore will leave the questions about the affinities and natural grouping of hyoliths more open in our revised text.

Another aspect that is underdeveloped is the fossil's role in 'fixing a mismatch' between the fossil record and molecular clocks. Budd & Mann have indicated that molecular clock results often simply return the prior distribution, rather than being informed by molecular data. To understand what we have learned in the context of a molecular clock, the reader needs to evaluate whether the clock is simply reflecting the known pattern of the fossil record (expressed in the effective priors), or whether there was a genuine mismatch between the molecular evidence and the fossil record (and how far the new specimens genuinely close this gap).

Response:

Thanks for your comments.

We will leave this an open question. It is outside our scope to engage with molecular clocks in this study beyond mentioning their findings. Our findings do not disagree with recent molecular clock studies in terms of establishing the timing of when different molluscan classes evolved. Placing all hyoliths within crown Conchifera and stem cephalopods would, however given their relatively old appearance that likely precede most conchiferan taxa, occurring in the *Protohertzina* levels in which only siphogonuchitids (candidate stem molluscs) are known. Again, this is not a necessary rabbit hole to dive into with the word and page constraints and also a great departure in our narrative that wouldn't bear novel insights or bearing to the significance to the findings presented.

As a note, a recent molecular clock study (ref.[3], https://doi.org/10.1073/pnas.2302361120), did indicate that the molecular evidence had significant weight to bear on the resulting ages for conchiferan molluscs. The molecular clock ignored a calibration point in this study and based the inferred ages on the molecular data. When *Watsonella* was used as a Diasome minimum calibration due to its proposed affinity as a stem bivalve (530 Ma), the clock ignored it and instead placed the diasome split at 520 Ma, which coincides with more widely agreed stem bivalves (*Fordilla* and *Pojetaia*), indicating that the diasome split must be younger and many laterally compressed univalved conchiferans debated to be either stem scaphopods or stem bivalves instead may be stem diasomes, which had not been entertained previously. But that is an entirely reasonable scenario to entertain also. So, just from that observation, molecules do seem to inform the ages inferred and the overall consistencies observed is due to the agreement between molecules and fossil calibrations, not due to fossils only informing the inferred ages as highlighted as a concern by the referee.

SUGGESTED CLARIFICATIONS

L36: "a mollusc with key cephalopod characters": This is slightly misleading. Strictly, only one diagnostic cephalopod character is presented (the siphuncle; many lineages exhibit septate tubes). Aside from this, no evidence demonstrates that the taxon is a mollusc (and/or not a hyolith).

Response:

Thanks for your comments. As we have now established the new genus *Eosceras*, we have revised this sentence to "Collectively, these features identify the segmented tube in *Eosceras* as a candidate primordial cephalopod siphuncle, extending the known range of stem cephalopods back to the Early Cambrian and also revealing the early stages in the evolutionary assembly of a chambered phragmocone employed in buoyancy regulation." Please see lines 35-39 in the clean version of revised manuscript.

L60: "nearly all >skeletonized< metazoan phyla" would be more accurate

Response:

Thanks. We have added this word into the sentence. Please see line 67 in the clean version.

L66: There's potential for confusion here between the molecular clock (which aims to assign absolute divergences to nodes) and molecular phylogenetics (which use molecular data to produce tree topologies). Whilst acknowledging the overlap between these methods, it's perhaps worth being clear that the early divergence of cephalopods is a common (if not universal) topological result that is independent of using a clock model.

Response:

Thanks for your suggestions. Now these sentences are "Molecular phylogenies and associated molecular clock estimates place the divergence of cephalopods in the early Cambrian, identifying them as one of the deepest branches within conchiferan molluscs[3,4]. This creates a substantial temporal gap before their first appearance in the fossil record in the Late Cambrian, represented by *Plectronoceras cambria*[2].". Please see lines 72-76 in the clean version.

L75–6 currently reads as if SEM/CT data revealed the homology of the siphuncle with that of modern cephalopods. This should be reworded to clearly separate the observation (i.e. tube passing through perforate septa) from the interpretation (i.e. status as siphuncle; homology with cephalopods).

Response:

Thanks for your rigorous comments. We have revised it to "Scanning electron microscopy (SEM) and micro-computed tomography (micro-CT) (Fig. 1) reveal the presence of multiple transverse septa within the shell, traversed by an internal segmented tube. This tube is interpreted as a siphuncle—homologous to that of living cephalopods.". Please see lines 81-84 in the clean version.

L100 If the apical end is an exposed septum, I expect it to be perforated – but I don't see evidence of this in the specimens. Is it the case that the siphuncle does not pass through all septa?

Response:

Yes. Unlike the truncated apical end of *Plectronoceras*, which is perforated by a siphuncle, the apical end (basal exposed septum) of *Eosceras*—like its internal septa—was not perforated. The bottom of each siphuncle segment is closed off and connected to the septum via canals.

L210 reads as if the absence of a siphuncle disqualifies shelly taxa from the cephalopod stem lineage; please evaluate whether these taxa may instead be stem-cephalopods that diverged before "Cupitheca" and the siphuncle.

Response:

This sentence has been revised to "For example, even though the helcionellid *Tannuella* from the early Cambrian of South Australia and the hypseloconid *Knightoconus* from the late Cambrian of Antarctica possess a septate shell, the absence of diagnostic siphuncle obscures their precise phylogenetic position within or outside total group Cephalopoda although an affinity on the stem cephalopod could still be envisioned, if a camerate shell preceded the evolution of a siphuncle." Please see lines 209-214 in the clean version.

In fact, the views held in previous studies that these two septate shelly taxa represent primitive cephalopods is merely speculative, and the absence of a diagnostic siphuncle indeed makes it hard to reach a definitive conclusion. Following your and another referee's suggestions, and based on possibly permeable septa of *Eosceras*, we have added a brief discussion: "The initial stages of cephalopod evolution, therefore, presumably involved the development of osmoregulation through the septa, that could be exemplified by camerate taxa lacking a siphuncle, such as the slightly younger genus *Tannuella*[1,17,26] (Cambrian Stage 4 of Australia). Other septate orthoconic fossils, such as *Cupitheca* cf.

C. mira (Cambrian Stage 3 of Mexico)[42] and *Tchuranitheca* sp. (Cambrian Stage 3 of Siberia)[43], may be rejected as potential cephalopod precursors on account of their two-layered septum which may not have been capable of osmoregulation, although canals are also documented within the septa in these that may have functioned in osmotic water transport[44].". Please see lines 264-272 in the clean version.

In our view, if the septa of these shelly taxa are widely distributed throughout the shell, extremely thin and possibly perform an osmotic function, it is highly likely that these taxa represent stem-group cephalopods that diverged before the siphuncle. Furthermore, the possible earlier evolutionary sequence may have been: septa initially restricted to the apical region → septa becoming widespread throughout the shell; the septa gradually thin and even develop perforations. Therefore, future studies should focus on fossil taxa that exhibit these possibly intermediate evolutionary characteristics.

L280. Please explain why you "think it likely" that hyoliths are molluscan. If shell microstructure is a key factor, how do the new observations complement this argument?

Response:

Thanks! We agree that hyoliths might belong to total-group Mollusca in view of biominerals and shell structure (ref.[21]). And, the evolution of specific features, such as the siphuncle in cephalopods and the diagnostic opercula and tentacle-bearing structures in hyoliths, separate the original argument from being us being able to erect a new genus species with clear synapomorphies affiliating it with cephalopods and instead we discuss the fact that some hyoliths appear to share some features with our taxon, such as the truncated shell closed off with a septum. Please see the revised section of Future Reassessment of tubular SSFs: "Indeed, the cephalopod *Eosceras* bears some strikingly resemblance to hyoliths within the genus *Cupitheca*[42,44,49] in having an orthoconic or slightly cyrtoconic, septate shell and a truncated apex. While the affinities of hyoliths have been debated, they share unique shell microstructures with molluscs, suggestive of some close relationship[50]. One scenario could be that these comparable shell features evolved independently in hyoliths and cephalopods, but from a shared ancestral biomineralization pathway and a similarly organized shell secreting gland or mantle. Alternatively, hyoliths or certain members of this clade (i.e. *Cupitheca*), if polyphyletic, are stem cephalopods within crown Conchifera in which *Eosceras* evolved from diminutive cupithecid molluscs exhibiting orthoconic, septate shells lacking a functional siphuncle. Future discoveries and anatomical studies may eventually resolve these competing scenarios or refute them both." (Lines 295-305 in the clean version).

In our view, just given the high similarity in shell morphology between certain hyoliths and the newly described cephalopod *Eosceras*, we suspect that some so-called other "orthothecid hyoliths" lacking critical diagnostic features such as opercula, musculature and other soft tissues, may be molluscs also and possibly related to *Eosceras*. But again, this demands closer scrutiny and we just need to highlight this possibility for future corroboration or rejection.

In fact, shell microstructures (aragonite/calcite arrangements) are not preserved in our materials. The microstructures of *Eosceras* mainly consist of poorly preserved prismatic layer and canal structure connecting the siphuncle and septa. The shell stratification of *Eosceras*, particularly the possible prismatic layer, may supports it as a conchiferan mollusc. And, the siphuncle and septa interconnected by minute penetrating canals further indicate it is a cephalopod.

Fig. 1. The “anterior - posterior” / “dorsal - ventral” axes do not correspond to the body axes of a cephalopod with an embryologically dorsal valve.

Response:

The dorsal valve represents an embryological orientation, which is mainly used in embryogenesis studies. Here we use the anterior–posterior / dorsal–ventral axes, which reflect the physiological orientation in adult cephalopod studies and commonly used when discussing cephalopod anatomy (please see Body Plans of Nautilus Hatchlings section in ref.[12], Shigeno et al., 2008 https://doi.org/10.1002/jmor.10564).

References not cited in the main text:

Pohle A, Jell P, Klug C. 2024. Plectronoceratids (Cephalopoda) from the latest Cambrian at Black Mountain, Queensland, reveal complex three-dimensional siphuncle morphology, with major taxonomic implications. *PeerJ* 12:e17003 https://doi.org/10.7717/peerj.17003

Referee #2 (Remarks to the Author):

This manuscript reports an exciting finding and is fully worth to be published in Nature, because the authors convincingly make the case that this is indeed the oldest conchiferan mollusc with a siphuncle, and hence a cephalopod.

The fossil occurrence and the morphological features of the specimens are very well described, with methods and documentation making the finding reproducible and convincing. The illustrations are beautiful and appropriate for a Nature publication.

That said I have three main points of criticism:

(1) I believe, the description needs to be improved: To me, it seems quite imprecise and ambiguous in several paragraphs, with mixed terminology, with interpretation and description mixed, and partly with clumsy wording (see my detailed comments and suggestions in the annotated pdf). For instance, it is not clear why sometimes apertural / apical and sometimes anterior / posterior is used for describing the positions of e.g. the septa… This is confusing. Sometimes the descriptions use present tense and sometimes past tense. Regarding the wording: There is at least one native English speaker within the group of authors. I suggest that he carefully goes through the descriptions and improves wording and consistency of descriptive terms. The sometimes-awkward wording makes me wonder if all authors carefully read this paper and contributed to the text.

Response:

Thanks for your critical comments. Following the suggestions you provided in the annotated pdf, we have carefully revised the descriptions and improved the consistency of terminology throughout the manuscript. All authors have carefully reviewed and revised the manuscript.

(2) The specimens are assigned to the genus Cupitheca. However, a formal systematic description of the specimens is lacking in this manuscript. As far as I see it in the literature, there are several species of Cupitheca described. Several of them are cyrtoconic. In what ways do these known species (and the type species) differ from or compare with the specimens described herein? Please add a formal systematic description and then make an argument: why do you place these specimens into Cupitheca?

Response:

Thanks for your critical comments. We agree with the comments you and another referee have provided. Considering that the siphuncle is a sufficient diagnostic character, we now establish a new genus and species of cephalopod, *Eosceras shaanxiense*. Please see the systematic palaeontology in Supplementary Information. By the way of explanation, we initially assigned the new material to the genus *Cupitheca* and identified it as *Cupitheca* sp., primarily because its external morphology—including the orthoconic, barrel-shaped shell and bluntly conical apical end—is largely consistent with the generic diagnosis of *Cupitheca*. Specifically, we used the indeterminate species designation "sp." because a siphuncle was observed in these specimens.

Now we think the absence of the diagnostic operculum of hyoliths, the completely opposite dorsoventral orientation, a highly oblique aperture and the occurrence of diagnostic siphuncle of cephalopods, refute a strict hyolith affinity of our new material. And, the morphological similarities of the orthoconic barrel-shaped shells with bluntly conical apical end (shell truncation resulting in exposed septum) to the hyoliths *Cupitheca*, are now discussed as possibly independent evolution.

Several known species possessing diagnostic opercula, such as the *Cupitheca mira*, *C. decollate* and *C. holocyclata*, can be unequivocally assigned to hyoliths. Our new material suggests that the taxonomic assignment of fossils originally identified as hyoliths—possessing only orthoconic or slightly cyrtoconic shells with or without transverse single-layered septa—requires further security.

Actually, we must acknowledge that most small shelly fossil taxa only preserve their external shell morphology; the absence of internal soft tissues means that plenty of genera and species established by previous studies could be morphological species, lacking clear biological taxonomic structures (e.g. siphuncle of cephalopod; molluscan radula and foot) that can be compared with extant organisms can render some of these open to revision upon future discoveries. This is a common challenge in traditional paleontological research, especially in studies of SSFs from the terminal Ediacaran to early Cambrian.

(3) In this context it appears to me important to discuss in more detail previous descriptions and interpretations of Cupitheca (e.g. Bengtson 1990, Skovsted et al. 2016). Notably, Skovsted et al. 2016 described opercula from a Cupitheca holocyclata and other characters that "unequivocally" demonstrates to them a hyolith affinity. A crossed-lamellar microstructure has been observed in Cupitheca sp. previously, and from it, a molluscan affinity was concluded: (Li et al., 2022: doi: 10.1111/pala.12620). etc. In my opinion, here (e.g. in line 277) the careful work of Skovsted et al. 2016 is brushed off too quickly. What if they are right and C. holocyclata is a hyolith? What, if C. holocyclatha had a siphuncle? What if our Cupitheca sp. is not a Cupitheca? How do these previously published interpretations relate to your interpretation of your specimens of Cupitheca as a cephalopod? How, can one species of Cupitheca be a hyolith and another species be a cephalopod? What if your specimens really belong to Cupitheca, what does this tell about the hyolithid – cephalopod phylogenitic relationship. In the last years great progess has been made to understand the biology of hyoliths (e.g., Li et al. 2020, Liu et al. 2021; Dzik 2025). This problem is in my opinion not sufficiently discussed by the authors. In the manuscript, a chapter is called "Caphalopod affinity of Cupitheca". In my opinion the possible hyolithid affinity of Cupitheca should be also critically reviewed in this context. In the context of a Nature paper, this might appear as just a side aspect. But I think it is important to put the finding into proper context and not only superficially report the finding of "a siphuncle in a hyolithid like conch". May be then, this would be something to put as a discussion in supplementary material.

Response:

Thanks for your comments! Please see above. We agree that most taxa assigned to *Cupitheca* must be hyoliths, with their diagnostic opercula and other soft tissues. We have left this issue more open due to us being able to establish our taxon in a new genus *Eosceras* due to its unique features not exhibited by *Cupitheca*, which leaves the issue as to how hyoliths may or may not relate to stem-group cephalopods or other crown-group Conchifera more open, which we still discuss. But we cannot resolve this debate with our discovery.

We agree that hyoliths may have a close phylogenetic relationship with molluscs from the perspective of biomineralization and aspects of conch morphologies, and hyoliths may belong somewhere in total-group Mollusca or Conchifera. Please see the main text in section Future reassessment of tubular SSFs: "Indeed, the cephalopod *Eosceras* bears some strikingly resemblance to hyoliths within the genus *Cupitheca*[42,44,49] in having an orthoconic or slightly cyrtoconic, septate shell and a truncated apex. While the affinities of hyoliths have been debated, they share unique shell microstructures with molluscs, suggestive of some close relationship[50]. One scenario could be that these comparable shell features evolved independently in hyoliths and cephalopods, but from a shared ancestral biomineralization pathway and a similarly organized shell secreting gland or mantle."

An interesting aspect (just as a side note) is the concave shape of the siphuncle in the specimens described: This is similar to the Ellesmerocerida, Plectronocerida, and Yanhericerida (they were previously seen as the oldest cephlaopods; see Kröger, https://doi.org/10.1111/j.1475-4983.2007.00644.x; Pohle et al. https://doi.org/10.1186/s12915-022-01284-5). I see this as supporting the argument of the authors.

Response:

Thank you for your suggestions!

Although we reconstructed a concave siphuncle based on the majority of specimens, the organic nature of the siphuncle makes it highly susceptible to taphonomic deformation. Therefore, its similarity to the concave shape of the siphuncles in Ellesmerocerida, Plectronocerida, and Yanhericerida may be considered as an important issue for future research.

Here are some of my comments from the annotated pdf that I consider important:

Response:

Thank you very much for detailed annotations. All of the annotations in the provided PDF have been carefully reviewed and revised.

Line 195: No! They are similar to simple orthoconic ellesmerocerid cephalopods, such as Paleoceras, see e.g. Flower 1964, not to endocerids. Endocerids are cephalopods with highly specialised siphuncles with complex internal structures and with very specific septal neck structures. This is a poor comparison. They are much better compared with nearly orthoconic Plectronocerids.

Response:

Thanks for your professional suggestions. We have revised it to "Shells of *Eosceras* exhibit a number of features aligning them with cephalopods, specifically orthoconic ellesmerocerid cephalopods[28], such as *Paleoceras*, with less specialized and a ventrally displaced siphuncle.". Please see lines 198-200 in the clean version of revised manuscript.

We have also added this reference (ref.[26]) "Flower, R.H. *The Nautiloid Order Ellesmeroceratida (Cephalopoda)* (New Mexico: Socorro, 1964)".

Line 221: Although the story is a bit hidden in this monograph, but I think a much better and more up to date reference to the Ascocerid evolutionary history and morphology is: Kröger 2013: http://dx.doi.org/10.5852/ejt.2013.41

Response:

Thanks. We have changed into this reference (ref.[35]) "Kröger, B. The cephalopods of the Boda Limestone, Late Ordovician, of Dalarna, Sweden. *Eur. J. Taxon.* **41**, 1–110 (2013)".

Line 221: What is a “siphuncular displacement canal”? I am not aware of any description of this in ascocerids or elsewhere in the cephalopod literature. Also, in the references cited at the end of this sentence, such a canal is not mentioned.

Response:

Thanks. We have removed it. Now this sentence is “Additionally, the exposed apical end of *Eosceras,* truncated to expose a septum, is reminiscent of Ordovician–Silurian Ascocerida (Subclass Nautiloidea)[1,35], which has no phylogenetic significance, but may attest to structural and developmental similarities in how the phragmocone can be modulated during ontogeny.” Please see lines 227-231 in the clean version.

Lines 255-265: Tannuella, as far as I know, is interpreted as a Helcionellid. C. holocyclata and the closely related type of the genus, C. mira previously have been interpreted as hyolithids. Both opinions are not explicitly mentioned in this paragraph. For me as a non SSF specialist this seems to be quite confusing. I don’t understand how all this comes together in a phylogeny to become a cephalopod in Cupitheca sp. How do these stages of proposed hyolithids / helcionellids become to be cephalopod? More precise explanation would be good.

Response:

Thank you for your comments. Please see our response above. The establishment of *Eosceras* now breaks the necessity to directly invoke or assume hyoliths as stem-group cephalopods or crown-group Conchifera and is left more open. And, as we mentioned in main text “The earlier stage presumably involved development of osmoregulation through the septa, enabling relatively limited control of shell buoyancy”, the septate orthoconic *Tannuella*—though previously regarded as a helcionellid—is therefore considered a possible cephalopod precursor here.

Line 277: In my opinion here the careful work of ref. 50 (Skovsted et al. 2016) is brushed off too quickly. What if they are right and C. holocyclata is a hyolith? What, if C. holocyclatha had a siphuncle? What if your Cupitheca is not Cupitheca?

Response:

Thanks for your critical comments. Please see our response about the relation between *Eosceras* and *Cupitheca* above. We agree the work of Skovsted et al. about the hyolith affinity of *Cupitheca*, based on the diagnostic opercula. And, the establishment of *Eosceras* (rather than *Cupitheca* sp.) now breaks the phylogenetic relationship that hyoliths as stem-group cephalopods or the potentially crown-group Conchifera.

Refs:

Bengtson, S. (1990). Early Cambrian fossils from south Australia. Association of Australasian Palaeontologists.

Dzik, J. (2025). Early ontogeny and other possible molluscan traits in hyolith biology and anatomy. Lethaia, 58(2), 1-16.

Li, L., Skovsted, C. B., Yun, H., Betts, M. J., & Zhang, X. (2020). New insight into the soft anatomy

and shell microstructures of early Cambrian orthothecids (Hyolitha). Proceedings of the Royal Society B: Biological Sciences, 287(1933).
Liu, F., Skovsted, C. B., Topper, T. P., & Zhang, Z. (2021). Soft part preservation in hyolithids from the lower Cambrian (Stage 4) Guanshan Biota of South China and its implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 562, 110079.
Skovsted, C. B., Pan, B., Topper, T. P., Betts, M. J., Li, G., & Brock, G. A. (2016). The operculum and mode of life of the lower Cambrian hyolith Cupitheca from South Australia and North China. Palaeogeography, Palaeoclimatology, Palaeoecology, 443, 123-130.

Referee #3 (Remarks to the Author):

The authors use SEM and micro-CT scanning to image hitherto undescribed structures in small conical fossils. These structures are suggested to be primitive siphuncles and septa, which would infer that these shells were created by early cephalopods (rather than hyoliths). If these are indeed cephalopods, this work would be topical and significant, pushing the first appearance of cephalopod fossils back by ~30 Ma. Most of my comments are minor and concern improving clarity, fixing grammatical issues, and the addition of a few references.

Line by line comments are listed below:

Line 32: Regarding the “segmented” tube. The next sentence states that this feature enabled connection with all chambers, which would be unlikely if they were entirely segmented (closed off). Are there any features that suggest the septa would have been perforated? (e.g., pore canals, restricted connecting rings and inflated intra-cameral siphuncles, etc.). Or does this feature reflect a primitive condition, unlike cephalopods with septal foramina?

Response:

Thanks for your comments. As a primitive cephalopod, the base of the siphuncle segment is closed off and only connected to the septum via canal structure (please see Fig. 3b, c and Extended Fig. 6). As mentioned in our manuscript, these pore canals reflect a primitive condition and may be homologous to the connecting rings in later cephalopods.

Line 40: Noun-verb agreement issue. Please consider changing “Cephalopods” to “Cephalopoda” or “includes” to “include”. The use of “its” in the following phrase, and next sentence points towards a singular noun, thus both issues can be fixed by using “Cephalopoda”.

Response:

Thanks for your comments. We have changed “Cephalopods” to “Cephalopoda”. Please see line 40 in the clean version of revised manuscript.

Line 47: Consider citing a recent paper about cephalopod cameral deposits here (Peterman et al., 2025; DOI:10.1017/pab.2025.10085). This paper explores the functional opportunities among a wide variety of orthocone cephalopods with various cameral deposit configurations. I also suggest citing this chapter of the ammonoid paleobiology, which summarizes research on the early shell coiling of the ammonoids (Naglik et al., 2015; DOI:10.1007/978-94-017-9630-9_17).

Response:

Thanks for your suggestions. Given that our study does not focus on the evolution of conch curvature, and considering the reference limit for Nature, we have only included the recent paper by Peterman et al. (please see ref.[27]).

Figure 1 caption and elsewhere:

The anterior portion of the shell is referred to as an “aperture”. The siphuncle runs up to this region, suggesting that the figured specimen is mostly, or all phragmocone, with no body chamber preserved. Does the highly oblique, concave feature reflect the shape of the last preserved septum? If so, how was the soft body attached to the shell? If this is only a phragmocone with no body chamber, I would not suggest using the term aperture here. An aperture should denote the anterior-most opening of the shell, and the site of shell growth.

Why are different colors used for the siphuncle between different figure panels? I suggest keeping this feature color-coded within, and between, images.

Response:

Thanks for your suggestions. The last segment of the siphuncle shown in Fig. 1 is indeed connected to the aperture. This segment represents the shrunken body chamber lining, which is flush with the original, flaring anterior-most segment (body chamber) illustrated in Figs. 2k–p and 3a. And, the specimen illustrated in Extended Fig. 5 shows growth lines parallel to the oblique aperture, indicating that the oblique aperture is a primary structure.

Fig.1b and 1c–f are processed differently: the former shows the original CT slice of the specimen, while the latter are rendered to more clearly visualize the siphuncle. Accordingly, we used different colors to highlight this structure.

Line 101: I suggest using the term “adoral” instead of the “apertural”. Please see my comment above. Those will familiarity of ectocochleates will question why the siphuncle runs up to the “aperture” rather than terminating into a posterior mantle.

Response:

Thanks. As we responded above, this anterior-most segment represents the shrunken body chamber lining (mantle membrane). We have revised the note of Figure 1f to clarify this point.

Line 110: “Internal chambers of the siphuncle”. Is phragmocone meant here instead?

Response:

No. Our new material possesses a relatively wide siphuncle. In type II specimens, severe abrasion occurred on both the ventral side of shell and the siphuncle wall, exposing the internal chambers of the siphuncle segments.

Line 121: Consider changing “endodeposits” to “endosiphuncular deposits”. I also recommend citing Peterman et al. (2019) here, who quantitatively explored how these features influenced stability and hydrostatics (doi.org/10.26879/884).

Response:

Thanks for your suggestions. We have revised it. Please see lines 123-124 in the clean version. Given the reference limit in Nature, we have only included the latest study by Peterman et al. (2026) (ref.[27]).

Line 133: I suggest being cautious calling this a prismatic layer. Perhaps “ … an intervening layer, possibly analogous to the prismatic layer of ectocochleates…”. There may be diagenetic affects that produce similar perpendicular crystal arrangements.

Response:

Thanks! We have revised it as your suggestions. Now this sentence is “an intervening layer containing poorly preserved fibrous bundles (Fig. 3d, j–k), possibly similar to the prismatic layer of ectocochleate cephalopods”. Please see lines 137-139 in clean version. In fact, we consider it highly likely that the intervening layer represents a primarily prismatic layer, as this structure is common and stable among our specimens, and can be clearly observed especially in Extended Fig. 3f, g.

Line 141: Something is wrong with this sentence. The shell and septa are secreted by mantle epithelium. The siphuncle is broadly a vascularized structure that grows with the soft body, rather than being secreted by a “gland”.

Response:

Thanks. We have revised it to “The clear differences in composition between the septa, phragmocone and siphuncle suggest that the former two were secreted by the mantle epithelium and was mineralized, while the latter was organic and more plastic in morphology during ontogeny”. Please see lines 144-147 in the clean version.

Line 145: All septa are internal. Consider simply deleting some of this sentence. E.g., “….interpret the posterior-most septum as a younger septum, exposed as the result of post-mortem….”.

Response:

Thanks. Here, the internal septa are mainly relative to the exposed septa.

Figure 3: The red arrows are very small. I suggest doubling their size, at least.

Response:

Thanks. We have revised it.

Line 195: The term “nautiloid” no longer has much taxonomic value. I suggest something like this “… most similar to those of younger, orthoconic stem group cephalopods (Endocerid and Orthocerida)…”.

Response:

Thanks. As you and another referee suggested, now we revised it to “… those of younger, simple orthoconic ellesmerocerid cephalopods, such as *Paleoceras*, …”. Please see lines 198-200 in the clean version.

Line 196: How do we know that this is the ventral side? Ectocochleates had variable siphuncular positions depending on the clade (Aturidae and Clymeniida are dorsal, most ammonoids are ventral, nautilds and many stem group cephalopods are central to ventral). Is this based on the aperture/lirae obliquity? There are examples of orthocones with dorsally tilted apertures (e.g., Sciponoceras) .

Response:

Thanks for your comments. We base this on the orientation of the oblique aperture assuming it flared dorsally and hence the siphuncle is then placed ventrally (Fig. 1).

Line 215: Ever since seeing Fig. 1, I was wondering about how the chambers were connected since the septa appear to lack siphuncular foramina. I suggest making this more apparent earlier in the abstract and figure 1 caption. The abstract states that the siphuncle is a segmented tube, then later indicates there was contact between earlier chambers. Clearly stating, early on, that the siphuncle appears to bridge septa through minute canals would be considerably improve clarity for those reading chronologically.

Response:

Thanks for your suggestions. We have added "The segmented tube appears to bridge septa through minute canals." into abstract. Please see line 33 in the clean version.

Line 221: A "siphuncular displacement canal" is an unusual term. I've never heard of this being applied to the ascocerids. I also cannot find this term in the two references at the end of this sentence. Also the Ascocerida are best known for syn vivo truncation of the shell rather than post-mortem breakage. I'm not sure what is being implied here.

Response:

Thanks for your critical comments. We have removed this term. Now this sentence is "Additionally, the exposed apical end of *Eosceras,* truncated to expose a septum, is reminiscent of Ordovician–Silurian Ascocerida (Subclass Nautiloidea)[1,35], which has no phylogenetic significance, but may attest to structural and developmental similarities in how the phragmocone can be modulated during ontogeny." Please see lines 227-231 in the clean version.

We refer to the truncation in Ascocerida because they also possess exposed septa. However, it remains difficult to determine from our material whether the exposed septa resulting from truncation represent a biological process or a taphonomic outcome (Although we prefer a taphonomic explanation). And, *Cupitheca decollata*, a hyolith with an apical end similar to that of our new material, is interpreted to exhibit active shell decollation (ref. 44, Sun et al., 2020, doi: 10.1111/pala.12463).

Line 234: Grammer issues. I suggest rewriting this sentence.

Response:

Thanks. We have revised this sentence to "As in later cephalopods, the soft body moved anteriorly within the shell during development. This positional shift, accompanied by periodic formation of septa, connected by a segmented siphuncle extending through the phragmocone (Extended Data Fig. 4f).". Please see lines 238-241 in clean version.

Line 242: Based on the proportion of the soft body to phragmocone, I suspect managing positive buoyancy would be the issue. If these chambers were all emptied, the living animal would likely weigh much less than the water it displaced (air is ~1000 times less dense than any other organismal component). Very generally speaking, cephalopods with a body chamber ratio less than 40% to 30% (depending on shell thickness) would have required cameral liquid or mineral deposits to reduce positive buoyancy. See Peterman et al. (2019; doi.org/10.26879/884) and (2025; DOI:10.1017/pab.2025.10085). That is, this extra space near the posterior mantle probably wasn't necessary, unless there was a considerable amount of fluid in earlier chambers.

Response:

Thanks for your professional and constructive comments. This is consistent with our preliminary interpretation: primitive cephalopods likely possess limited buoyancy control, although our specimens do show the presence of extra space near the posterior mantle. With additional specimens collected in future studies, further research on buoyancy control will be conducted.

Line 247: "living chamber" is a less-used term today. I suggest using "body chamber" to be consistent throughout.

Response:

Thanks. We have revised all "living chamber" to "body chamber".

Supplementary video: I am having issues playing this video in AVI format. I suggest saving as an MP4, which is generally more accessible.

Response:

OK. We have converted the supplementary video from AVI format to MP4.

Extended Data Fig. 4: Consider changing "animal mass" on the legend and caption to "soft body". Also, the key suggests the siphuncle is denoted by a blue outline. This blue outline also highlights the rest of the soft body in the body chamber, which is confusing. The soft body and siphuncle should be distinct from one another.

Response:

Thanks! We have made these changes, and the soft body is now highlighted with a green outline.

Referee #4 (Remarks to the Author):

Dear authors,
I greatly appreciate your extraordinarily thorough presentation of the earliest cephalopod. It is without doubts a milestone in molluscan research.

I find your manuscript well written, your methods highly topical, your descriptions concise, and your conclusions intelligible.

I could not find any major inconsistency in your manuscript. One minor open question concerns the evolution of the cephalopod funnel that you do not discuss, though it is added in Extended Data figure 4f. The development of a funnel is closely associated with the ability of jetting and thus with a nektonic life style and this contradicts your assumption that Cuspitheca lived mainly benthic.

Congratulations!
Dirk

Response:

Thanks for your positive comments! We have now removed the inferred funnel structure in Extended Data figure 4f. Granted, we cannot establish if such a structure was present. Sometimes there are hints at its presence as a notch in the shell aperture of some ectocochleate cephalopods, which we do not see. We cannot speculate on whether this taxon had evolved such a structure yet, like for many other fossil cephalopods.

Response to Reviewers' Comments

Manuscript Title: **Earliest siphuncle-bearing cephalopod from the early Cambrian**

Manuscript ID: 2026-02-04042A

To the Editor Dr Henry Gee,

Please find an updated revised version of our manuscript "**Earliest siphuncle-bearing cephalopod from the early Cambrian**", which we are resubmitting for publication in *Nature*.

We very much appreciate the comments and suggestions provided by you and the four referees. We have worked diligently to incorporate these suggested changes, which have improved the overall quality and significance of our manuscript.

Here we provide a point-by-point response describing how we have addressed these comments. The original comments are listed in black and our reply, along with a description of changes we have made to the manuscript text in blue, follows immediately after.

We thank you very much for taking the time to consider our manuscript for publication in *Nature* and we hope our manuscript will be ready for acceptance after we made these changes to our paper. If you have any further questions about our revised manuscript, please do not hesitate to get in contact. Thank you very much for your time and consideration.

Your Sincerely,
Junfeng Guo and Zuchen Song
(on behalf of all co-authors)
School of Earth Science and Resources, Chang'an University, Xi'an 710054, China
junfengg@chd.edu.cn and songzuchen@chd.edu.cn

Referees' comments:

Referee #1 (Remarks to the Author):

I thank the authors for the improvements; the erection of a new genus has greatly simplified the systematic aspects of the paper, and the simpler evolutionary framework is clearer and more clearly tied to the novel data.

There are however many aspects of the manuscript that remain unclear and whose strengthening would clarify the evidential support for aspects of the description that remain at present less than convincing.

Caption to Fig 1 - it would be helpful to spell out whether light or dark greyscale values correspond to high X-ray attenuation. Due to the blue colouration, it is difficult to determine whether the siphuncle in 1a is a void or a sediment-infilled structure. It is also difficult to see whether it displays contrast with the rest of the internal infill. The presence of a high[?] attenuation film over the aperture also invites comment – is this because the specimen has been gold-coated for SEM, or was the aperture originally covered by a high-attenuation layer in life (??).

Response: Thanks for your valuable comments! Following your suggestion, we have added a clear explanation in the caption of Figure 1 regarding the correspondence between greyscale brightness and X-ray attenuation values. Specifically, light greyscale values (high attenuation) represent biological structures with secondary phosphatization or phosphatic infillings within camera (intermediate grey values), while dark greyscale values (low attenuation) indicate void spaces. Please see lines 91-93 in clean version.

In addition, the bright, high-attenuation film at the aperture corresponds to the original biological structure that underwent secondary phosphatization, which can be correlated with the apertural membrane shown in ED Figure 3. We have further clarified this point in the Micro-computed tomography (micro-CT) method section: "Micro-CT scanning was performed on **a single gold-coated specimen CUBar297-1, and two uncoated specimens CU(CT-Eoceras)-7 and CU(CT-Eoceras)-11** with the Zeiss Xradia 520…". Please see lines 509-510 in clean version. We should note that the gold coating is too thin to contribute to the bright values observed in the gold coated holotype specimen, given that similar bright value is present within the enclosed void.

Fig 2 - it remains unclear how the various greys in the "Type X" column correspond to the pinks purples. The key does not contain an entry corresponding to the dark grey. It's not clear from the figure what evidence implies the presence of phosphatized sediments within Type I, and why the internal structure is visible in Type 2 if the shell is preserved in its entirety. It's not clear whether the shell is preserved in types 1 and 2, or whether we are seeing only an infill of the shell septa. None of the preservation modes shown leave an obvious pathway for the preservation of complete septa.

Response:

Thanks for your comments! We have revised the greyscale color of Type II to light grey to match the siphuncle color used in Types I and III, and added the corresponding dark grey entry "phosphatized shell wall" in the figure legend. We also revised the caption of Type II to "…exposed "septa" **that**

formed by secondarily infilling and thickening of the cavities between adjacent siphuncular segments…". Please see lines 166-167 in clean version.

In this updated version, light grey indicates camerae (type II) and the internal cavities of siphuncle (pinks) (types I and III) infilled by secondarily phosphatized infillings (i.e. steinkerns). Dark grey denotes only original shell walls (purples) replaced by secondary phosphatization, therefore, the interior of Type I specimens is not infilled by phosphatized infillings, or is only partially infilled. Notably, the internal cavities of the siphuncle show some different preservation: some only partially infilled (Fig. 1), whereas others are largely infilled (ED Fig. 3). For consistency, we adopt a uniform light-grey color for the siphuncle in both Type I and Type III.

Regarding Type II, as stated in the figure caption, these specimens do not represent completely preserved shells. This type corresponds to individuals whose ventral side was abraded or damaged after death; subsequently, the camerae were infilled by secondary phosphatized sediments during taphonomic process. We also revised the caption of type II to "…consisting of **broken ventral phragmocones with phosphatized infillings of the camerae** and…". Please see lines 165-166 in clean version.

Regarding the preservation of septa: indeed, aside from several possible septa relic preserved in Type III, the structures appearing as septa in Type II are actually artefacts formed by secondary infilling and thickening of the cavities between adjacent siphuncular segments. Their morphology and position resemble those of in-situ preserved septa (Fig. 3b, c). We have added quotation marks around the term septa and explanation in the figure caption.

Fig 3: The septal pores/canals are not convincingly documented; it's not clear that they represent originally open structures rather than an aspect of the columnar microstructure, such as an originally organic scaffold that facilitated the growth of prisms. I don't see any evidence to support the claim of permeability or osmosis (line 225).

Response:

Thanks for your critical comments. We agree that these canal structures may alternatively serve a certain supportive or scaffolding function. However, these canals are not spaced with a frequency or density expected of any organic shell matrix we are familiar with. Furthermore, they are hollow and connect the septa to adjacent chambers and the siphuncle (Fig. 3b, c; ED Fig. 6c–h), indicating the possibility of a transport function worth highlighting in this context. *Cupitheca decollata* from the same period has similar structures, which are considered to provide a means for secondary periostracal material secretion (Sun et al., 2020, ref[44], https://doi/10.1111/pala.12463), although the diameter of its canals are only ~1 μm with no evidence of being hollow (the canals in *Eoceras* are ~5μm).

Regarding the evidence for septal permeability, we have revised the text to "**the extremely thin central portion of the septa (specimen BM-05; Extended Data Fig. 6a, b) may have facilitated permeability**, allowing…". Please see lines 227-228 in clean version. Compared with the septal thickness of *Cupitheca decollata* (upper septa ~4.8 μm; lower septa ~12.2 μm) (Sun et al., 2020, ref[44]), the septal central portion (excluding the columnar zone) thickness of our materials is ~ 2 μm (ED Fig. 6h). This, together with the semi-transparent appearance of the septa under an ultra-depth-field microscope, enhances the possibility of an osmotic function. However, it is indeed true that there is no strict logical connection between extremely thin septa and osmotic function. Taking this into account, a question mark at the septa in Fig. 4a indicates this uncertainty. And we have removed the "osmotic" in the septa label.

ED Fig 4. Specimen a has the largest body cavity, but is interpreted as the youngest specimen; it's not clear that an ontogenetic sequence is the most convincing explanation for specimens that are all approximately the same size.

Response:

Thank you very much for your valuable comments. We agree that the specimen (ED Fig. 4a) represents adult stage rather than initial stage. We originally regarded only the number of segments as the criterion for distinguishing growth stages. We acknowledge that it is premature to speculate about an ontogenetic sequence in this study, and thus have removed the discussion of ontogenetic sequence in our paper. And now, we only show these specimens indicating the siphuncle development via mantle membrane condensation. Perhaps further discovery of juvenile specimens may reconstruct a complete ontogenetic sequence of *Eoceras*.

ED Fig 6. The position of the siphuncle on these septa is not clear; the siphuncle seems not to pass through them, which seems to contradict the interpretation presented elsewhere.

Response:

Thank you very much for your comments.

Following your suggestion, we have removed the caption text regarding the position of the siphuncle. Now the ED fig.6 specimens mainly reveal the radial canals structure on the transitional marginal corner of septa. And Fig. 3b, c provides compelling evidence for a connection between the siphuncle and septa.

Indeed, each segment of the siphuncle is closed and completely separated by septa, with fluid exchange seemly achieved only through these connecting canal structures. We have also revised the main text to maintain consistency with this interpretation.

Even if "Anterior/Posterior" is sometimes used in cephalopod terminology, it has potential for confusion, particularly when talking about the derivation of cephalopods from molluscs. The terms "apertural / apical" are suitable unambiguous alternatives. At a minimum, it is essential that the same orientation terminology is used throughout; on line 56, "dorsally" is used where the orientation scheme used later in the manuscript requires "posteriad".

Response:

Thank you very much for your constructive comment. We agree with your suggestion that the orientation terminology of cephalopods is indeed prone to confusion. We have now uniformly adopted the terms apertural/apical to replace the original anterior/posterior throughout the manuscript.

The definition on Line 479 would be more helpful if it (i) were presented to the reader before the first use of orientation terminology; and (ii) stipulated in the text how the terms were used, rather than requiring the reader to look up another reference before they can understand the rest of the manuscript.

Response:

Thank you for the constructive suggestion. We have added a brief definition on Cephalopod affinity of *Eoceras* section: "**Given that cephalopods may have evolved from monoplacophoran-like molluscs, that modified the original body axes through dorsal elongation[1], we employ the unambiguous orientation terminology "apertural/apical" and define "ventral/dorsal" mainly on the basis of peripherally situated siphuncle and the oblique apertural margin.**". Please see lines

204-208 in clean version and the orientational definition in schematic anatomy in Fig. 4a.

56 - “predating” could potentially be misread as meaning “that preyed upon”; suggest “preceding” or “earlier than”

Response:

Thanks! We have changed “predating” to “preceding”.

267. It would be useful to mention here what evidence of osmoregulation exists in Tannuella.

Response:

Thank you for this helpful suggestion. Existing literatures on *Tannuella* does not provide any evidence for osmotic permeability. This genus is regarded as a potential cephalopod ancestor mainly based on the morphological characteristics of its septate shell. We already discuss the issue with all of these taxa having apparent thicker and two-layered septal walls at the end of this paragraph.

268–272 - The argument against Cupitheca and Tchuranitheca being cephalopod relatives is inscrutable; osmoregulation is not convincingly demonstrated in Eosceras, and it seems that there’s a plausible argument that it’s present anyway in Cup. and Tch. Even if it’s not, its absence would not preclude Cup. and Tch. from being members of the stem group that diverged before osmoregulation arose.

Response:

Thank you for your constructive comments. We agree that these septate taxa with two-layered or relatively thick septa may also represent cephalopod stem-group members that diverged prior to the origin of siphuncular-osmoregulation. We have included this alternative evolutionary possibility in the revised text. Please see lines 263-269 in clean version.

282 - this is clearly articulated and seems well supported

Response:

Thanks for your positive comment!

284. Why would a benthic organism be keen to reduce ballast?

Response:

We think that the truncation of the embryonic shell may have taken place to reduce energy consumption and improve mobility, such as certain marine and terrestrial gastropods. However, as the text reads, we are open to the possibility of this taxon having been more nektonic in its mode of life—if the specimens represent juveniles, given the taphonomic biases existing with SSF preservation.

286. “The small size of this species is an artefact” – as written this implies that taphonomy has shrunk the species; please be clear whether you mean “only juveniles are preserved” or something else.

Response:

Thank you for your comments. We have revised this sentence to “**It is also possible that the small size of available specimens is a consequence of the preferential preservation of juvenile specimens in the SSF taphonomic window, as has been observed in other conchiferan taxa**[44].” Please see lines 284-286 in clean version.

288. “a more efficient buoyancy apparatus” – the efficiency of the buoyancy apparatus is nowhere discussed or quantified; it has not been established that the Eosceras apparatus is (or is not) inefficient.

Response:

Thanks. We have deleted this part.

The manuscript would benefit from a careful copyedit throughout to correct its numerous grammatical errors (notably misuse of ‘that’ and commas).

Response:

Thank you for your helpful comment. We fully agree that the manuscript requires careful copyediting to address grammatical issues. We have thoroughly revised the entire text to correct numerous grammatical errors.

Systematic palaeontology.

As a new genus and a new species are being described, there should be a separate definition of each, per the ICZN; the new species must be formally defined as the type species of the genus.

Response:

Thank you for this important observation. We have added this section to comply with the ICZN.

I’m not up to date with the ICZN position on defining new species in supplementary appendices – worth confirming that the registration of the SI material will comply with the current Code.

Response:

Thanks! Following your and the editor’s advice, we have relocated this section to after the main text and before the Methods.

Under “Referred material” it would be helpful to provide a count of the number of specimens in each category, as this information is difficult to eyeball from the list.

Response:

Thanks! We have added specimen counts for each category in the referred material list.

The statement that “gross anatomical similarities … are superficial” is itself superficial; it should either be expanded to describe the similarities and to explain why they are not considered consequential. If the similarities are spurious, then it’s not clear what purpose there is in mentioning them at all.

Response:

Thanks! We have added the detailed comparison among *Eoceras* and other taxa with similar morphology. Please see lines 461-477 in clean version. Several taxa, such as *Cupitheca* cf. *C. mira, Tchuranitheca* sp. and *C. mira* resemble *Eoceras* in external shell morphology but differ distinctly in internal septa and siphuncle. Notably, specimens referred to as *Inflatatheca* (Liu et al., 2024, ref.[48], https://doi.org/10.1002/spp2.1554) show high similarity to *Eoceras* in first segment of the siphuncle. But here we consider *Inflatatheca* a nomen dubium; detailed reasoning is provided in the main text. Collectively, aside from cloudinid cnidarian *Mianxiantubus*, these hyolith taxa are indeed morphologically comparable and most likely related to *Eoceras*.

Referee #2 (Remarks to the Author):

This is a much-improved revised manuscript. I am in particular happy to see that the authors now added a formal taxonomic description of the specimens they describe. This will help in the future to disentangle the confusion of different potential groups currently subsumed under Cupitheca sp. The description itself is now also much clearer and ambiguous wording resolved. The improvements and removal of redundancies in the figures improved the quality of the manuscript.
I also noted the improvements in grammar and writing style.

I found only some small grammar issues. After these issues are resolved I would recommend this manuscript for publication. (I did not cross check the references).

In the long sentence lines 60-64: I don't understand the last part of the sentence part "possible intermediate forms preceding those still lacking".

Response:

Thanks for your comments! We have revised this sentence to: "**Irrespective, how a simple conical shell with septa evolved into a chambered buoyancy apparatus remains unresolved due to the significant gaps in the fossil record between the relatively complex siphunculate cephalopods known from the late Cambrian and the current lack of older unequivocal records of intermediate forms**[7,8]." Please see lines 60-64 in clean version.

In lines 100-101 I would place (Types I-II) behind "taphonomic types".

Response:

Thanks for your suggestions! We have changed it.

In lines 280-282: Is the word "polarized" here correct? Please consider rewording.

Response:

Thanks for your comment. We have changed this word to "inferred". Now this sentence is "**Given the possession of a siphuncle but complete septa of *Eoceras* gen. nov., the evolutionary polarization of key buoyancy-regulating elements in the cephalopod phragmocone can therefore be inferred**.". Please see lines 278-280 in clean version.

In line 283-286: Something is wrong with this sentence. I don't understand what "as much" refers to.

Response:

Thanks for your comment. Following you and another referee's comments, now we break this long sentence into "**Considering its very small body size, simpler system for osmotic fluid exchange, and relatively thick shell walls**[43]**, *Eoceras* gen. nov. may have had a mostly benthic mode of life (Fig. 4c). Although, the truncation of the embryonic shell would reduce energy consumption, improve mobility and increase buoyancy**[35,42].". Please see lines 281-284 in clean version.

Referee #3 (Remarks to the Author):

The new version of the manuscript is rewritten for enhanced clarity. Major improvements involve fixing grammar, using softer/cautious language when referring to uncertainties, and adding a systematics section in the SI. My points from the first review have generally been addressed. I only have a few minor suggestions (see below).

Regarding name “Eosceras”: Please doublecheck the etymological rules for having an “s” and a “c” next to each other in a separate prefix and root. Often, the “s” will become assimilated into the root. Therefore, I think “Eoceras” would be more appropriate. E.g., the historical term “Eocarboniferous”, lacks an “s” after “eo”. But please double-check this.

Response:

Thank you very much for your careful and valuable comment. We have removed the letter “s” and revised the generic name to *Eoceras* following the standard etymological rules.

Line 27: Consider getting rid of the text “through jet propulsion”. Jet propulsion is already mentioned earlier in this sentence, so it is redundant.

Response:

Thanks very much! We have removed them.

Line 72: consider changing “siphuncular” to “siphunculate”. I.e., siphuncle-bearing.

Response:

Thanks! We have changed it.

Line 201: consider using the term “in vivo” (i.e., during life) instead of “real life”.

Response:

Thanks! We have changed it, now this sentence is “**Isolated septa are very thin and semi-transparent under optical light (Extended Data Fig. 6a, b), reflecting their delicate, membranous nature within the shell in vivo**.”. Please see lines 156-158 in clean version.

Line 280: the plural form of “foramen” should be “foramina”.

Response:

Thanks! We have revised it.

Referee #4 (Remarks to the Author):

Dear authors,
you adequately addressed my recommendations. Thank you for that!
I find your ms is now acceptable for publication.
I´m largely conform with your interpretation Eosceras is - due to the possession of a phragmocone-like shell apparatus a representative of the cephalopod stem lineage. Chambers interconnected by a complex arrangment of septa and siphuncular-like segments absolutely allow such an affiliation. We are now closer to the origin of cephalopods than ever before.
The weak point in your contribution is - from my point of view - the referred "developmental sequence" (extended fig. 4), because I think your argumentation about the septum/siphuncle formation cycle is still too sketchy, leaving some open questions. In its present state it is difficult to comprehend your idea. E.g. you state there is no septal foramen, but in Fig. 4, phase 5 it seems as if the soft body passes through the newly build septum (in orange). Is it possible that the foramen was secondarily closed?
good luck and with best wishes
Dirk
Response:

Thank you very much for your valuable comment, Dirk!

All of the annotations in the provided PDF have been carefully reviewed and revised. Given your and another referee's concern, we have now removed the discussion of ontogenetic sequence in our paper. And we only show these specimens indicating the siphuncle development via mantle membrane condensation. Indeed, the detailed pattern of septum formation, growth and the subsequent closure of the siphuncle remains uncertain based solely on the currently available specimens. We agree that it leaves a few questions open and would be better addressed in a future independent study.

The isolated complete septa shown in Extended Figure 6 indicate that the septa of *Eoceras* were indeed fully closed, rather than secondarily closed.

Response to Reviewers' Comments

Manuscript Title: **Earliest siphuncle-bearing cephalopod from the early Cambrian**

Manuscript ID: 2026-02-04042B

To the Editor Dr Henry Gee,

Please find an updated revised version of our manuscript "**Earliest siphuncle-bearing cephalopod from the early Cambrian**", which we are resubmitting for publication in *Nature*.

We very much appreciate the comments and suggestions provided by you and the three referees. We have worked diligently to incorporate these suggested changes, which have further improved the overall quality of our manuscript.

Here we provide a point-by-point response describing how we have addressed these comments. The original comments are listed in black and our reply, along with a description of changes we have made to the manuscript text in blue, follows immediately after.

We thank you very much for taking the time to consider our manuscript for publication in *Nature* and we hope our manuscript will be ready for acceptance after we made these changes to our paper. If you have any further questions about our revised manuscript, please do not hesitate to get in contact. Thank you very much for your time and consideration.

Your Sincerely,
Junfeng Guo and Zuchen Song
(on behalf of all co-authors)
School of Earth Science and Resources, Chang'an University, Xi'an 710054, China
junfengg@chd.edu.cn and songzuchen@chd.edu.cn

Referees' comments:

Referee #1 (Remarks to the Author):

I thank the authors for their careful attention to my previous comments, which have been addressed to my satisfaction.

There is one remaining issue: In Fig. 2, the legend is somewhat clearer, but the Type I schematic is still confusing. By drawing the phosphatized infillings "on top of" the phosphatized shell wall, the schematic gives the impression that a distinct siphuncular infilling is preserved and differentiated from other infill, which I do not see evidence of in the fossil material.

I think that the entire inner region of the shell should be coloured light grey (for "phosphatized infillings", representing the infill of the shell and the infill of the siphuncle - with the structure distinguishing the two invisible, as already denoted with the dotted lines) and the dark grey "shell wall" should only surround the margins of the specimen. If the desire is to depict an external view rather than a cross-section, then the 'infillings' of the siphuncle should be covered by the shell wall and not be visible in the schematic (as indeed they are not visible on the associated SEMs).

Response:
Thank you for your detailed suggestions! We agree with your advice for the Type I schematic in Figure 2. To match an external view consistent with our SEM data, we have rendered the entire shell wall in dark grey (the internal siphuncle or infillings are invisible under SEM). The oblique apertural region is retained in light grey to denote the partially exposed internal cavity.

Referee #2 (Remarks to the Author):

The revised manuscript looks good now. I have only very few things to comment:
In the abstract and in the Systematic palaeontology section the new species is described as Eoceras shaanxiense gen. et sp. nov.. However, in the main text, in the figure captions, and in section headings the species is listed and mentioned as "Eoceras gen. nov." or simply as "Eoceras". I am not sure what is the rational behind that. I would suggest a consistent reference here, such as "E. shaanxiense gen. et sp. nov.." in the main text and figure captions and "Eoceras gen. nov." in the headings.
The new genus (Eoceras) is missing in the systematic palaeontology section. Currently, this section is a mix of genus (e.g. lines 433) and species part (lines 434-438). I would suggest have first a genus section with paragraphs: "Type species. […], by monotypy", "Diagnosis. As for type species, by monotypy", etc. and then, in the species section place the full diagnosis and comparison etc.

Response:
Thank you for your detailed suggestions! We have uniformly replaced all instances of *Eoceras* gen. nov. with *E. shaanxiense* gen. et sp. nov. throughout the main text and figure captions to maintain consistency; only section headings retain *Eoceras* gen. nov. We have also revised the Systematic Palaeontology section accordingly.

Line 283-284: Some ending is missing in this sentence: "Although, the truncation of the embryonic shell would reduce energy consumption, improve mobility and increase buoyancy." May be something like this: .. ", suggesting an adaptive value of this feature for a swimming life-style."

Response:
Thanks! We have revised this sentence. Now it is "…, although the truncation of the embryonic shell would reduce energy consumption, improve mobility and increase buoyancy[35,42], which suggests an adaptive value of this feature for a swimming lifestyle.". Please see lines 291-293 in revised version.

Referee #3 (Remarks to the Author):

The authors have addressed each of my comments. I'd like to thank them for their careful consideration throughout each round of review. I recommend acceptance if the other reviewer comments are satisfactorily addressed.

Response:
We greatly appreciate your positive evaluation and careful review of our manuscript.

Referees' comments:

Referee #1 (Remarks to the Author):

The authors have addressed my comments.
Response: We greatly appreciate your positive evaluation and careful review of our manuscript.

Referee #2 (Remarks to the Author):

The authors have addressed each of my few remaining comments. I thank them for the careful consideration of all of my previous comments. The manuscript improved much and I will be happy to see it published now. This will advance discussions on the origin of cephalopods significantly!
Response: Thanks for your positive comments! We greatly appreciate your positive evaluation and careful review of our manuscript.