Detailed answers to reviewers

Dupichaud *et al.* combined review file: round 1

We would like to thank the two reviewers, Elise NARDIN (Reviewer 1) and Maggie LIMBECK (Reviewer 2), as well as the editors of *Open Palaeontology*, for their very helpful and constructive comments, which really helped improving our MS.

Most suggested changes have been made; the colors used for our answers indicate whether we fully agree, partially agree or disagree with the reviewers' comments. All changes to the text and figures are also listed below. Comments are in blue. Lines numbers indicated in brackets refer to those in the (clean) revised version of the MS (without tracked changes).

Dear Christophe Dupichaud, Bertrand Lefebvre, Ninon Allaire, Enzo Birolini, Malo Meyruey, Martina Nohejlová

We have reached a decision regarding your submission, "*Respiratory structures in cornute stylophorans (Echinodermata)*", to *Open Palaeontology*.

Our decision is to: **Request Revisions**.

Thank you for your submission, and for your patience while we collected the reviews.

Two reviewers have provided constructive comments on your submission. In general they praised the large data set that was used in this work and feel it offers a compelling contribution to the field. They also noted that it was on a topic that is often complicated and that a holistic investigation in one manuscript will be of value to future researchers. Both, however, commented that revisions should be made to the phrasing and organisation of the manuscript. In particular, they suggest clarifications around the introduction, measurement methods, and more separation of results and discussion. In my personal reading of the manuscript I felt as if the introduction could benefit from a table that associated each organism discussed with the relevant morphology and that the final section of the discussion could be broken up into more manageable sections.

> We agree with all these suggestions, and consequently, the introduction has been modified; results and discussion are better separated; a table listing the different types of respiratory structures, their characteristics and associated taxa has been added; and the discussion has been separated into several shorter parts. All sections dealing with the quantitative analysis of respiratory structures in cornutes and rhombiferans have been removed.

Upon receiving your revisions, our editorial team will decide if another round of reviews is required. In general, I think that the reviewers did not have many issues with the content and academic quality of the work.

The reviews are available in the Review Files section of our submission platform and are appended to the bottom of this email.

When you submit a revised version of your manuscript, please provide:

- a revised editable version of the manuscript with tracked changes,

> DONE: attached file "Dupichaud et al. corrected with tracked changes.docx"

- a 'clean' version of the manuscript (with no tracked changes) as a pdf,

> DONE: attached file Dupichaud et al. corrected clean.pdf

- a point by point explanation of how you have addressed the reviewers' comments,

> DONE: this document (attached file Dupichaud et al. answers to reviewers.pdf)

- updates to any figures or new figures included in this revision

> DONE: see below; the revised version of the MS now contains 9 figures and 1 table, instead of 11 figures in the original version of the MS, with:
> Fig. 1 (revised) = Fig. 1 (original)
> Fig. 2 (revised) = Fig. 10 (original)
> Fig. 3 (revised) = Fig. 8 (original)
> Fig. 4 (revised) = Fig. 3 (original)
> Fig. 5 (revised) = Fig. 4 (original)
> Fig. 6 (revised) = Fig. 5 (original)
> Fig. 7 (revised) = Fig. 6 (original)
> Fig. 8 (revised) = Fig. 7 (original)
> Fig. 9 (revised) = Fig. 11 (original)
> Original figures 2 and 9 have been suppressed.

- please also be sure to double check that all references are included

> DONE, we have double-checked that all references cited in the MS are included.

Please remember that we operate a transparent peer review process at *Open Palaeontology*.

This means that we will publish unblinded peer review reports along with any accepted articles.

You will be able to resubmit you work for further consideration by logging in to the OJS platform or from this URL: https://www.openpalaeo.org/workflow/index/8440/3

We encourage preprinting of your work where possible. If you have not already done so but would like to post a preprint we encourage you to do so, but please let us know.

Thank you again for your submission to *Open Palaeontology*. If you have any queries, please do not hesitate to contact us.

Best wishes
David Cordie
Phone David R Cordie
dcordie@edgewood.edu

On behalf of the Open Palaeontology team

Reviewer 1: Elise Nardin

Dear authors,
I was pleased to review your manuscript on the respiratory structures in cornute stylophorans and the numerous comparisons you make with other echinoderms. I particularly appreciate the perspective of the paper. The manuscript is well-structured, clearly written, and richly illustrated. The results are based on an extensive review of numerous specimens, following a well-defined approach, which robustly supports both the identification of the respiratory structures and their new interpretation. The breadth of the reference list is justified by the large dataset and the complex history of interpretations regarding these unusual echinoderms. The drawings are clear, accurate, and informative.
Overall, I consider this study a valuable contribution for all echinoderm researchers, and an interesting work that should be published pending minor revisions. Please find my detailed remarks below.
All the best
Elise Nardin

> We are very thankful to Elise Nardin for her very relevant and constructive comments on the MS.

Abstract.
You state that you discuss "their similarities and differences with other deuterostome respiratory structures." The comparison with other deuterostomes appears minimal; most of the comparisons are with other echinoderms (which is entirely appropriate and sufficient). You may wish to reconsider this part of the sentence to better reflect the content.
> we agree; we have modified this sentence in the introduction to: "their similarities and differences with the respiratory structures of other echinoderms";

Although I acknowledge the importance of the last sentence of the abstract, it feels somewhat abrupt, as the preceding text focuses on the diversity of respiratory structures in cornutes. A brief transition explaining why *Thoralicystis* is reinstated—directly in the abstract—would help readers understand the relevance of this point, as it is clearly explained later in the manuscript.
> we agree and have therefore added two sentences to the end of the abstract: "Similar respiratory structures (conjunct cothurnopores) are present in the type species of the two scotiaecystid genera *Thoralicystis* Chauvel, 1971 and *Proscotiaecystis* Ubaghs, 1994. Therefore, *Thoralicystis* is reinstated here as valid, while *Proscotiaecystis* is considered a junior synonym".

Methods.
You state that the measurement protocol follows Paul (1968). While the method is indeed similar, Paul (1968) expressed measurements in mm, not mm^{-2} as shown in Fig. 9. I could not find an explanation in the manuscript for how and why raw measurements were transformed into WL and Ws in mm^{-2}. Please include this information.
> Actually, in Fig. 9, the measurements were expressed in mm^{-2} (*not* mm^2), i.e. 10^{-2} mm: for example, the value "4" on the diagram corresponds to 4 x 10^{-2} mm, i.e. 0.04 mm. In any case, Fig. 9 has been removed (see below).

- Line 501**:** You mention a test computed to compare the metrics of lamellae and dichopores in *Cheirocystella* and *Homocystites*, but the type of test is neither named

nor described. Please clarify this either in the methods section or directly within the brackets in line 501.

> The entire section dealing with the quantitative analysis of cornutes and rhombiferans has been removed from the MS (see further explanations below).

Terminology and orientation

Although you refer to Lefebvre et al. (2022) for terminology and homologies, it would be helpful to define the terms “abmarginal” and “admarginal” explicitly, as they appear frequently in the text.

> We agree with Reviewer 1 that the terms "abmarginal" and "admarginal" are not defined in Lefebvre et al. (2022). We have therefore slightly modified the text to include another reference (Lefebvre and Vizcaïno 1999), where these terms are defined: "The morphological terminology follows closely that used in the *Treatise of Invertebrate Paleontology* (Ubaghs, 1968b), and its updates (e.g. Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022)." [lines 269-272]. Furthermore, in order to avoid any ambiguity, the meaning of these terms is explained several times in the text, e.g. on lines 164 ["abmarginal (posterior)"], 397 ["anterior (admarginal)"], 399 ["posterior (abmarginal)"], 533 ["anterior (admarginal)"], 534 ["posterior (abmarginal)"], and 552-553 ["anteriorly (admarginally) and posteriorly (abmarginally)"]. Finally, admarginal and abmarginal U-shaped elements are clearly designated on Figs 2C and 7.

In addition, Figure 1A could be annotated to indicate “anterior” and “posterior,” to ensure all readers have this orientation clearly in mind.

> we agree; "anterior" and "posterior" have been added to Fig. 1A.

Results

Morphology or respiratory structures in cornutes

Your descriptions of the various pores and organs are well-supported by numerous examples and detailed observations. However, some points could be clarified:

- Pustulipores and cornuthopores: You state that pustulipores can occur within cornuthopores (line 357) and describe them as an autapomorphy of *Phyllocystis crassimarginata*. Yet they also occur in *blayaci* (lines 684–703). By contrast, slit-like cornuthopores of proto-lamellate organs lack pustulipores. This may cause confusion for readers. One option would be to add a descriptive adjective when referring to cornuthopores with pustulipores, as you did for slit-like cornuthopores, to distinguish them clearly. Alternatively, you could consider whether the cornuthopore–pustulipore association warrants definition as a distinct organ.

> This is an excellent point raised by Reviewer 1. To clarify the distinction between these two types of cothurnopores, we proposed the terms "disjunct cothurnopores" for isolated cothurnopores with pustulipores, and "conjunct cothurnopores" for laterally sutured cothurnopores without pustulipores. Furthermore, the main differences between these two types of respiratory structures are now presented in Table 1. In the literature, the two descriptive terms "conjunct" and "disjunct" are also used to distinguish two main types of rhombs in rhombiferan "cystoids".

- Measurements: While you provide size ranges for sutural pores and pustulipores, there is no such information for cornuthopores. Including length and width measurements would aid in their recognition and provide consistent data for all pore types.

> It is not possible to provide such information, as the width and length of disjunct cothurnopores vary considerably within the same individual: the smallest (=formed last) are located at the anterior and posterior extremities of the crescent-shaped area. Conversely, the largest disjunct cothurnopores are found more or less in the middle of this crescent-shaped area. Their size and number both increase with growth. This point is explained in the MS: "In a single individual, the first disjunct cothurnopores formed are located in the middle of this elongated region, while later and smaller openings are added at both ends" [lines 388-390]. Therefore measurements/values could not be provided for disjunct cothurnopores. On the other hand, the size of pustulipores and sutural pores, as well as the width of lamellae (in lamellate organs), vary very little during the ontogeny.

- Terminological clarification: It may be useful to clarify the similarities and differences between the "sutural pores" you describe and the "epispires" reported in other echinoderm groups.

> The terms "epispires" and "sutural pores" are often considered equivalent by many authors. However, in this MS we have followed the definitions provided in the *Treatise on Invertebrate Paleontology* (Ubaghs, 1968a), where sutural pores correspond to the rounded orifices occurring along the sutures of adjacent thecal plates, while the term "epispires" refers to the (probably soft, papulae-like) respiratory structures associated with the sutural pores. The difference is subtle, but meaningful. See Ubaghs (1968a, S474): "**epispire**: Epithecal structure, open or covered, associated with sutural pore or slit, and presumably serving for respiration", and "**sutural pore**: Any diminutive opening in theca, generally very numerous, distributed along sutures in many eocrinoids".

Apart from this problem of definition, the differences and similarities between the sutural pores (and associated epispires) of cornutes and those found in other Palaeozoic echinoderms are addressed in the section entitled "Sutural pores are the plesiomorphic condition in cornutes" of the Discussion [lines 573-610].

Minor points

- Lines 242–243: Use the same order for formations and basins (e.g., "Jince Formation, Jince Basin") for consistency.

> done, we have modified the text to: "Buchava and Jince formations, Drumian; Skryje-Týřovice and Jince Basins, Czech Republic".

- Lines 251–252: The information in brackets may be unnecessary since you already provide a measurement range.

> we have kept the information in brackets, because the orifices are slightly elliptical, and it is important to distinguish between the measurements provided for their maximum length and width.

<u>Quantitative analysis</u>

This section is valuable, but currently mixes results with discussion, and its link to the general discussion is limited. It could be strengthened by:

- Adding a short introduction to explain why this analysis is relevant and what it contributes to the study.
- Making a clearer connection between the identification and naming of stylophoran respiratory structures and the quantitative analysis of folded structures.
- Incorporating measurements from Álvarez-Armada et al. (2022) and/or Jackson (2024) into Figure 9 (when possible), to broaden the comparative framework with other echinoderms.

- Moving the discussion elements from this section into the general discussion, where they could be integrated into a broader consideration of convergent evolution of respiratory structures among echinoderms.

> We really thank Reviewer 1 for these insightful comments. We fully agree that it would be beneficial to incorporate the measurements of Álvarez-Armada et al. (2022) and/or Jackson (2024) into Figure 9 to broaden the comparative framework with other echinoderms. However, this task is not directly feasible or would require considerable work, including a new campaign of measurements using different techniques (3D imagery). The main difficulty lies in the fact that Álvarez-Armada et al. (2022) and Jackson (2024) acquired three distinct sets of measurements from CT-scans: the width of the lamellae, the spacing between two lamellae, and the depth of the lamellae. In this work, the measurements were made on two-dimensional latex casts, which only allowed us to estimate the width of the lamellae and the spacing between two lamellae, but not the depth of the lamellae. Therefore, we decided to remove the quantitative analysis from the MS (and the two associated figures, Figs 2 and 9), as the results are not directly comparable to those obtained by Álvarez-Armada et al. (2022) and Jackson (2024).

Removing the section devoted to the quantitative analysis helps to increase the homogeneity of the MS, and resolves the issues rightfully raised by Reviewer 1 concerning the significance of this section, and the mixing between results and discussion.

Conclusions

Consider adding one or two sentences summarising the insights gained from the quantitative analysis of folded structures.

> Good point, but useless with the removal of the section devoted to the quantitative analysis of folded structures in cornutes and rhombiferans.

References

The reference “Jefferies 1969” (cited at lines 569, 572, 623, 630, 653, 658, 663) is missing from the reference list. Please add it.

> This publication is now listed in the references; thank you for noticing its absence!

Figures

- The use of bright red rectangles in the figures, particularly in combination with blue (as in Fig. 9), creates a strong contrast that may be visually distracting for some readers. You might consider testing alternative, colour-blind–friendly palettes that still provide clear differentiation.

> we agree, but this is no longer necessary: the original Fig. 9 has been removed.

- Annotating some photographs to highlight key features could further assist readers in distinguishing between the different respiratory structures and their associated plating.

> done: annotations on photographs have been added to highlight sutural pores (Fig. 1C) disjunct cothurnopores (Figs 1C, 5B), pustulipores (Fig. 5D, F, G), conjunct cothurnopores (Fig. 6B, D, E, G, H), and lamellae (Fig. 8B, D, E, G).

Recommendation: Revisions Required

Reviewer 2: Maggie Limbeck

This paper will be very important given the much needed investigation and review of echinoderm respiratory structures – it is great to see cornutes being included in this ongoing review by the community.

> We thank Reviewer 2 for these positive comments.

I am recommending this paper undergo major revisions, because I do have several major concerns about how this article is currently presented. As the paper is currently presented, the main findings (and main drivers) of your study are not clear until the last few paragraphs of the discussion, which does create confusion for the reader. Additionally, there is a lot that is being addressed in this paper, and currently, a lof of topics are only mentioned briefly and are never brought up again in the discussion or conclusions. My major recommendations all revolve around restructuring the paper (suggestions below) and adding a few tables and figures to help readability and highlight your findings more successfully.

> We would like to thank Reviewer 2 again for her valuable feedback. Her comments were essential and, thanks to her review, we have significantly modified the structure of the MS.

Introduction: You do a good job summarizing the importance of respiratory structures in echinoderms and that there is a long history of studying Paleozoic echinoderm respiratory structures in particular.

> Thank you.

What is missing here (but is included as the first half of the discussion) is the introduction to these structures in cornutes and what previous interpretations are that led you to develop this study. This is briefly covered, but the more in-depth explanations from lines 531-595 set up your motivations more clearly. If length is an issue, the introduction to echinoderm respiratory structures can more than likely be shortened. If it is not an issue, some of the discussion of echinoderm respiratory structures could likely fit well in the discussion.

> This is a very good point from Reviewer 2. We agree that it is advisable to present the previous interpretations earlier in the MS. Therefore, this section has been moved from the discussion (located at the very end of the MS) and placed immediately after the introduction. This move necessitated the rewriting of some sentences (as many descriptive terms are now explained later).

Results: The sections on cothurnopores, proto-lamellate organ, and lamellate organ are really hard to follow. I was left uncertain about what defines a cothurnopore, which made the constant referral to them in the sections on the proto-lamellate organ and lamellate organ hard to interpret. As written, I interpreted the cothurnopores to be structures that were large, elliptical orifices that open at a suture between two U-shaped plates and based on exceptionally preserved specimens, are filled with pustulipores. This interpretation then led to a lot of confusion in the following sections because you describe the proto-lamellate organ as having cothurnopores that are covered by platelets but not all have pustulipores. This confusion is perpetuated in the section on the lamellate organ because this is now an organ composed of cothurnopores that are closed.

> We acknowledge that distinguishing between these different types of (related) respiratory structures was not always straightforward. Reviewer 1 also noted this difficulty. Therefore, the differences between all the main types of cornute respiratory structures are now summarized in a table (Table 1), which lists their main characteristics and some examples of taxa in which they are found. We have also revised the terminology to better distinguish the

different types of respiratory structures, notably by introducing the terms "disjunct cothurnopores" and "conjunct cothurnopores".

In addition to reworking these descriptions, a figure or line drawing demonstrating these structures in comparison to each other may be helpful to the reader.
> we thank Reviewer 2 for this excellent suggestion. A figure illustrating these respiratory structures in comparison was indeed created: Fig. 11 in the original version of the MS, now Fig. 9 in the revised version of the MS. We are pleased that Reviewer 2 recognized the usefulness of such a figure (which has no equivalent in the literature).

In the discussion you mention that the proto-lamellate and lamellate organs are collections of cothurnopores – I would mention that in their respective sections in the results as well to clear up some of that confusion.
> we share the opinion of Reviewer 2, and this point was (and still is) mentioned in the section on proto-lamellate ("confirms their identification as cothurnopores [...]. However, [...] the pairs of U-shaped plates are particularly numerous and are laterally sutured to one another, forming an elongate proto-lamellate organ" [lines 478-480]) and lamellate organs ("lamellate organs correspond to strongly folded thecal structures resulting from the adjoining of numerous hollow, sutured lamellae [...] each lamella corresponds to a pair of opposite, strongly laterally compressed U-shaped plates, homologous to those occurring in conjunct cothurnopores" [lines 557-569]). This point is now also clearly mentioned in Table 1.

Based on the description of the proto-lamellate organ and the lamellate organ, I was left wondering how cothurnopores on their own do not make up a proto-lamellate organ or if there is a distinction defined by number of cothurnopores present or width of the cothurnopores. One suggestion that may help the reader, in addition to re-examining the wording, is to include a table (similar to Sheffield et al., 2022 Table 1) that would list the included taxa and what kinds of structures they have and whether or not they are organized into a proto-lamellate or lamellate organ.
> To clarify this point, a table (Table 1) listing all types of cornute respiratory structures (and their characteristics) has been added.

I am also unclear on the part of the study that was done measuring the width and spacing of the lamellae. Was this only done for specimens that have a lamellate organ? Was this done to test homology between morphologically similar respiratory structures? This part of the study is never mentioned in the discussion and I think it could be an interesting tie in to some of the introduction where you discuss respiration in other early echinoderms.
> We agree with Reviewer 2 that the link between this section on the quantitative analysis of folded respiratory structures and the rest of the MS was not very clear. This problematic part of the MS has been removed (see above).

Discussion: The discussion under the heading “Implications of new observations on cornute respiratory structures” is well done and has the answers to many of the questions that I had while reading the manuscript.
> Thank you!

However, as discussed above, some of this information should be introduced earlier to help with clarity up to this point.
> Moving the section on previous interpretations to the beginning of the MS, now allows the discussion (and interpretation) of cornute respiratory structures to immediately follow the

results (and their description). This change in the structure of the MS should help to better link the descriptions to their interpretations.

Additionally, since you mention the results of the measurement study, this should be discussed again here with what the implications are for understanding cornute respiratory structures in relation to other echinoderm respiratory structures.
> The section related to quantitative analyses has been removed.

After reading this paper, I am left wondering if the authors do interpret these openings as respiratory structures based on this paper. Even though the title of the paper refers to respiratory structures in cornute stylophorans, the consistent usage of orifices, accessory orifices, accessory structures, and putting quotations around these terms throughout the article vs calling them respiratory structures leads the reader to infer that the function of these structures is still uncertain.
> We are surprised by this comment. The title, abstract, discussion, and conclusions are relatively clear regarding the respiratory function of these thecal openings in cornutes. This impression might stem from the placement of the section on previous interpretations at the end of the MS, within the discussion. For example, "accessory orifices" was a historical term coined by Ubaghs (1968b) to refer to these structures in general, which are present in several (but not all) cornutes, and completely absent in other stylophorans (hence their designation as "accessory"). We hope that moving this section to the beginning of the MS will clarify the differences between previous interpretations and those presented in the MS.

In the discussion and the conclusion, we clearly state that: "detailed morphological analysis of "accessory structures" present on the upper thecal surface of cornutes does not confirm their interpretation as multiple mouths (no evidence of ambulacral cover plates), gonopores, or gill openings (they are not constructed as outlet valves, and there is no evidence of any flap)" [lines 777-780]. In accordance with Reviewer's 2 comment, we have added the following two sentences to the end the conclusion, in order to remove any ambiguity in our interpretations and conclusions: "Like the diplopores of "cystoids" (...), cornute respiratory structures thus originated from sutural pores, which represent the plesiomorphic condition at the phylum scale (...). This implies that disjunct cothurnopores, pustulipores, proto-lamellate and lamellate organs, derived from standard echinoderm respiratory structures, are not homologous to the gill slits of other deuterostomes". [lines 791-796].

Have the authors considered looking at the construction of epispires in other echinoderm groups and comparing them to cothurnopores? That could be outside the scope of this paper but would certainly be interesting and could give more evidence to congruence in respiratory structures along with some discussion of evolution of respiratory structures in these groups.
> We thank Reviewer 2 for this interesting comment. In fact, we have carefully examined the structure of sutural pores in other echinoderm groups (e.g. eocrinoids) and compared it to that of disjunct cothurnopores: "These observations demonstrate that disjunct cothurnopores were (...) highly specialized covered sutural pores more closely resembling those found in some eocrinoids (e.g. *Alanisicystis andalusiae*, *Rhopalocystis destombesi*; ...). However, while the thecal respiratory orifices are protected by a simple layer of thin plates in *Alanisicystis* and *Rhopalocystis*, they are covered by a more complex arrangement of skeletal elements forming numerous small perforated cones in cornutes (...). Disjunct cothurnopores therefore most likely represent exothecal respiratory structures, probably analogous to the covered epispires of eocrinoids, and derived from classical sutural pores comparable to those present in *Ceratocystis* and many other Cambrian echinoderms" [lines 652-664].

Additionally, a figure that maps these different kinds of epispires (and other respiratory structures) on a phylogeny would be really interesting to see given the discussion of these structures.
> We agree that this would be really interesting, but mapping the diversity of sutural pores and all types of respiratory structures (e.g. cataspires, coronal canals, cothurnopores, cryptorhombs, diplopores, humatipores, humatirhombs, hydrospires, pectinirhombs, pustulipores) on a phylogeny of blastozoans (i.e. a dozen classes of echinoderms) is far beyond the scope of this MS, which focuses on respiratory structures present in one order of stylophorans.

Lines 17 & 25: Remove “” around accessory orifices
> We prefer to keep the "", because it is a historical, neutral term coined by Ubaghs (1968b) in the *Treatise on Invertebrate Paleontology*, and still widely used in the literature. However, for us, these structures are better defined as respiratory structures.

Line 20: Recommend removing deuterostome, you only discuss echinoderm respiration in this article
> We agree; "deuterostome" was replaced by "echinoderm";

Line 42: Recommend changing situation to condition. Condition is more frequently used to describe a feature that is seen in animal groups.
> done: "situation" was replaced by "condition";

Line 44: Do you mean employing highlight specialized respiratory structures?
> no, we simply mean "highly";

Line 58: remove “” around sutural pores
> done

Line 70: What are the two types of respiratory structures?
> no change; the two (main) types of respiratory are listed and explained in the lines immediately below, i.e. endothecal respiratory structures [lines 75-79] and exothecal respiratory structures [79-85]

Lines 82- 84: Rephrase for clarity.
> no change; the meaning of the sentence "Although respiratory structures have long been used to define taxonomic groups within blastozoans (e.g. Diploporita and Rhombifera), phylogenetic analyses have suggested that they can occur in different clades" is clear, and we do not see what needs to be changed.

Lines 99-103: This sentence, as currently written, seems to suggest that the inclusion of cornutes within Echinodermata is disputed, with the main argument for that dispute being the lack of five-fold symmetry. Surely that isn’t the case. There are numerous blastozoan echinoderms that are asymmetric and lack what is commonly thought as the characteristic five-fold symmetry. The actual bauplan that is used to join echinoderms is a bilateral symmetry with a secondary pentaradial symmetry (as is exemplified in groups such as the Eublastoids and many eleutherozoans).
> We are in complete agreement with Reviewer 2!!! Unfortunately, some colleagues do not share this opinion, and consider stylophorans to be basal members of the echinoderm stem-

group, which never acquired the five-fold symmetry as adults (apomorphy of more crownward taxa) (see e.g. Smith 2005, 2008; Bottjer et al. 2006; Rahman and Zamora, 2024).

Lines 106-114: Which is the main objective of the paper? Determining if these orifices are homologous to gill slits or respiratory structures or reviewing the diversity of the orifices.
> As stated in the text, the main objective of the paper is to study the nature and function of cornute "accessory orifices". To do this, it is necessary to review and redescribe their morphology: "The main objective of this contribution is to review the diversity of accessory orifices in cornutes, based on the detailed examination of previously described and new material, in order to discuss their similarities and differences with other respiratory structures present in echinoderms. Such a sample-based approach is necessary, as highly contrasting descriptions of the same structures, leading to widely divergent interpretations, have been published in the literature. In this context, the priority is therefore to provide a set of fundamental and reproducible observations and descriptions" [lines 114-121].

Lines 146-143: I highly recommend removing this list and putting it in a table format that is presented with the paper rather than only included in the supplement. Within a table you can easily indicate which are the specimens that were utilized in the measurement study vs ones that were only used for morphological comparison. This makes it easier for readers to reference the taxa used and to refer to while reading, especially if they are not cornute specialists. You could easily summarize in text the geographic locations that the taxa come from if that is important to the text.
> No change; in a paper covering such a large number of taxa examined, it is important to indicate the collections visited. This information is routinely provided in palaeontological studies. Furthermore, the list of acronyms is useful for locating all the specimens figured in the MS. There is no special interest to presenting this list in a table: including the registration numbers of hundreds of examined specimens in such a table would make no sense. Apparently, Reviewer 2 did not understand whether the list of visited collections and the list of specimens measured for the quantitative analysis were linked. They are not: the list of institutions (lines 130-145) refers directly to the list of taxa examined for their respiratory structures, which appears just below, on lines 147-163. Only 11 specimens of cornutes were originally measured, and the quantitative part of the MS is now removed from the revised version of the MS.

Lines 185-186: It is unclear what you mean by “the largest number of measurements was taken…”. Does this refer to taking multiple measurements to collect an average, you looked for the largest width to record, or there was a threshold in size of the pectinirhomb or lamellate organ to record the measure so that it was large?
> this paragraph, and all other sections related to the quantitave analysis have been removed.

Lines 209-212: In the methodology section you refer to examining 37 specimens and in the results you mention looking at hundreds of specimens. Again, I think the clarity of putting the studied taxa and taxa selected for quantitative study in a table would make this differentiation more clear.
> Hundreds of cornute specimens were observed for their respiratory structures; 11 of them (and 26 rhombiferans) were measured. This ambiguity(?) is now resolved by removing all sections related to the quantitative analysis of folded respiratory structures.

Line 212: List which taxa are missing respiratory structures, or if you include a table that lists the studied taxa and which respiratory structures they have, mark it there.

> Done; Table 1 summarizes all types of cornute respiratory structures, along with their morphological charateristics, and examples of taxa that possess them. Cornutes without respiratory structures are also listed in this table.

Line 231: I would call the sutural pores epispires. There is already a lot of confusing terminology that has been developed surrounding echinoderm morphology and respiratory structures, if that can be limited in the literature that will reduce confusion for future research and those new to the field. How you have them described in the text as well as the provided figures, it is reasonable to refer to these as epispires (they are visually and structurally similar to those seen in blastozoan echinoderms).
> We do not share this opinion for the same reason already mentioned above (see answer to Reviewer 1 on the same topic). The terms "epispires" and "sutural pores" are often considered equivalent by many authors (including, it seems, Reviewer 2). However, in this MS we have followed the definitions in the *Treatise on Invertebrate Paleontology* (Ubaghs, 1968a), where the sutural pores correspond to rounded orifices present along the sutures of adjacent thecal plates, while the term "epispires" refers to the (probably soft, papulae-like) respiratory structures associated with the sutural pores. The difference is subtle, but significant. See Ubaghs (1968a, S474): "**epispire**: Epithecal structure, open or covered, associated with sutural pore or slit, and presumably serving for respiration", and "**sutural pore**: Any diminutive opening in theca, generally very numerous, distributed along sutures in many eocrinoids".

Line 257: remove apparently
> we have changed "apparently" to "very likely", in order to express that the situation in *Protocystites* is not clear, because of the strong tectonic distortion of the specimens, which makes it difficult to clearly identify the existence of sutural pores in this taxon.

Lines 279-280: Consider rephrasing, are these pustulipores in *P. crassimarginata* truly unique if pustulipores are also present in cothurnopores?
> agreed; the sentence has been modified to: "The existence of such pores opening **directly through the supracentral area**, at the top of large, numerous, multi-plated chimneys or volcanoes is unique to *P. crassimarginata*". Pustulipores opening "directly through the supracentral area" is a unique characteristic of *P. crassimarginata*. The smaller pustulipores present in other cornutes are always associated with disjunct cothurnopores and form small clusters surrounded by pairs of opposite U-shaped plates.

Line 327: A figure is needed to show this spike-like process.
> we do not think that an additional figure is necessary to illustrate morphological variability of the outlines of the posterior U-shaped plates. However, we have added a reference in the text, so that the readers can consult the original figure: "The posterior end of the abmarginal U-shaped element may sometimes be elongated into a spike-like process (e.g. *Persiacarpos*? *fellinensis* from the late Tremadocian Saint-Chinian Formation; Montagne Noire, France**; see Ubaghs, 1969, fig. 20.2**)".

Line 350: Remarkably similar or the same construction?
> no change: "remarkably similar", as the general morphology is comparable; however, the construction is not exactly the same, as the (larger) isolated pustulipores of *P. crassimarginata* are constructed by the upturned edges of several (two to five) supracentrals, while the smaller pustulipores found in disjunct pustulipores are generally made of only two plates.

Line 360: How are proto-lamellate organs different from cothurnopores. Is this based on number/size of cothurnopores and once a threshold is reached it is considered a proto-lamellate organ?
> This point is explained in the text, but is further clarified in Table 1, which summarizes the main characteristics of all types of cornute respiratory structures. We have also modified the terminology (introducing the terms "disjunct" and "conjunct"), to highlight the similarities and differences between these orifices. Disjunct cothurnopores are wider, not in contact with each other, and they are covered by (small) pustulipores, while conjunct cothurnopores are narrower, laterally sutured (thus forming a proto-lamellate organ), and they are closed by a thin layer of integument without any pustulipore.

Lines 369-372: Figure 6 needs updating to show the thin layer of platelet that cover the cothurnopores. Are these the same platelets that would create the pustulipores?
> The original Fig. 6 (now Fig. 7 in the revised MS) does not require updating, because it is not an idealized reconstruction of the proto-lamellate organ of *Thoralicystis melchiori*, but rather a camera-lucida observation drawing of the holotype of this taxon. On this original specimen, the thin integumentary layer covering the conjunct cothurnopores is absent on most of them; however, the presence of platelets above and/or near some cothurnopores (e.g. cothurnopores n°4, 8, 10, and 18, from the left) suggests that this thin layer was originally present on all of them.

Line 381: Should this refer to a proto-lamellate organ in *B. zagoraensis*?
> yes, this and the following lines clearly indicate that "*Bohemiaecystis*" *zagoraensis* does not possess (as previously suggested by all authors) a lamellate, but a proto-lamellate organ: "did not confirm the presence of a lamellate organ in this taxon, but did reveal the occurrence of more than 25 closely packed pairs of opposite U-shaped plates surrounding slit-like cothurnopores covered with minute smooth platelets, with no evidence of cone-shaped structures" [lines 461-464].

Line 385: remove yet
> done, "yet" removed

Lines 396-402: Based on the previous sections of the article, cothurnopores have pustilipores present, are these proto-lamellate organs still made of cothurnopores if they do not have pustilipores? Please re-examine your classification and descriptions of and revisit this paragraph.
> This is now clarified in the text, with different terms coined for cothurnopores with pustulipores (disjunct cothurnopores) and without pustulipores (conjunct cothurnopores); see also Table 1 summarizing all types of cornute respiratory structures and their characteristics.

Line 404: You describe both scotiaecystids and *Bohemiaecystis* as having proto-lamellate organs and now are discussing them again and stating they have lamellate organs. Which kind of organ do these taxa have?
> This is detailed in Table 1, which lists all valid scotiaecystid genera (*Thoralicystis*, *Bohemiaecystis*, *Thoralicarpus*, and *Scotiaecystis*). Within scotiaecystids, only *Thoralicystis* possesse proto-lamellate organs, while lamellate organs are found exclusively in the three other genera. A precise definition of all scotiaecystid genera is provided on lines 753-774.

Lines 437-439: Are the cothurnopores still present if they are closed? If yes, please provide a figure where that is observable.
> In Table 1, lamellipores are defined as "slit-like thecal orifices opening internally at the base of hollow, closed lamellae formed by laterally strongly compressed, opposite U-shaped plates"; this definition fits that of the closed conjunct cothurnopores of lamellate organs. That is clearly observable on Fig. 3B (see also Fig. 9C).

Line 457: Remove more or less, replace with approximately
> done, "more or less" replaced by "approximately".

Lines 456-471: Please revise for clarity, I am not certain what is being discussed in this paragraph. Coloring the figure differently may enhance the visualization of internal vs external views. The following paragraph (lines 472-477) does convey what I believe is trying to come across in this paragraph.
> This is actually a complex folded morphology, with external grooves corresponding to internal ridges, and vice versa. We have done our best to describe this morphology the best we could, and do not see really how to improve clarity in our text. The associated new Fig. 3 (=Fig. 8 in the original version) really helps to better understand the text. In that figure, we have been careful to suggest the relief, with darker colors for deeper zones, and brighter ones for higher areas. Fig. 9C also illustrates this complex folded structure. We believe that these two figures, along with the text, provide a relatively good description of the morphology of the lamellate organ.

Line 476-477: “separated from each other by more or less deep grooves” I’m not sure what this is referring to. Please revise for clarity.
> no change. This sentence describes the actual morphology of lamellate organs, with numerous elongated and regularly spaced transverse ridges (= the lamellae), separated by grooves (i.e. furrows) and not by open slits. The expression "more or less deep grooves" refers to the variations observed among scotiaecystid taxa: grooves are particularly deep in *Bohemiaecystis*, but shallow in *Scotiaecystis*. This morphology is clearly visible in Fig. 3 and Fig. 9C.

Line 494: Consider the inclusion of Sheffield et al., 2022.
> we agree, but this section of the MS on the data analysis of folded respiratory structures in cornutes and glyptocystitids has been removed.

Line 497: Similar or the same respiratory structures?
> they belong to the same type of respiratory structures (conjunct pectinirhombs with confluent dichopores), but this section on the data analysis of folded respiratory structures in cornutes and glyptocystitids has been removed in the revised version of the MS.

Lines 506-520: Can you plot your data that you collected with the studies included here? It would be helpful to see the comparison of these data sets as well, especially since the studies you mention have very different results than you found with respect to similarity of lamellate construction.
> the same suggestion was made by Reviewer 1 (see above). We fully agree that it would be entirely relevant to integrate the measurements from Álvarez-Armada et al. (2022) and/or Jackson (2024) into Figure 9, in order to broaden the comparative framework with other echinoderms. However, this task is not directly feasible or would require considerable work including a new measurement campaign using different techniques (3D imagery). The main

difficulty lies in the fact that three separate sets of measurements were acquired from CT-scans in the analyses by Álvarez-Armada et al. (2022) and Jackson (2024): the width of the lamellae, the spacing between two lamellae, and the depth of the lamellae. In this study, measurements were taken on two-dimensional latex casts, which only allowed for the estimation of the width of the lamellae and the spacing between two lamellae, but not the depth of the lamellae. For this reason, we decided to remove the quantitative analysis from the MS (and the two associated figures, Figs 2 and 9), as the results are not directly comparable to those obtained by Álvarez-Armada et al. (2022) and Jackson (2024).

Line 519-520: Consider changing "the disjunct pectinirhombs of *Strobilocystites* were clearly away from them" to …clearly plot further away from similarly folded respiratory structures
> we agree, but this section on the data analysis of folded respiratory structures in cornutes and glyptocystitids has been removed in the revised version of the MS.

Lines 521-527: This paragraph is more interpretation of results than results
> we agree, but this section has been removed in the revised version of the MS.

Line 597: Following text doesn't ever explicitly address the hypothesis from the introduction – the debate is still ongoing, whether these orifices are homologous to gill slits or homologous to echinoderm respiratory structures. An explicit statement here from the authors about what these orifices are (and changing language in text to consistently refer to these openings based on their structure) will reduce confusion.
> we partially agree with this comment. In the discussion, it is clearly stated that the sutural pores of cornutes are morphologically equivalent (homologous) to those found in other echinoderms. This strong and unambiguous statement clearly refutes other interpretations. Then, the interpretation of other cornute respiratory structures as derived from sutural pores clearly implies that they are not homologous to gill slits. To remove any ambiguity (if any) in our MS, we have added two sentences to the end of the conclusion: "Like the diplopores of "cystoids" (...), cornute respiratory structures thus originated from sutural pores, which represent the plesiomorphic condition at the phylum scale (...). This implies that disjunct cothurnopores, pustulipores, proto-lamellate and lamellate organs, derived from standard echinoderm respiratory structures, are not homologous to the gill slits of other deuterostomes" [lines 792-797].

Line 743: Have you looked into the construction of these respiratory structures and determined that they are not homologous? The use of the word analogy here may not be best since without knowing if these structures are homologous, they could also be analogous. I may consider switching analogy to similarity?
> We do not agree with this suggestion. In this MS, we have demonstrated that the lamellate organs of scotiaecystid cornutes are folded respiratory structures deriving from the amalgation and compaction of numerous cothurnopores. The acquisition of cothurnopores is an apomorphy of cornute stylophorans, while the presence of pectinirhombs represents an apomorphy of glyptocystitoid rhombiferans. Although they possibly share a common Cambrian eocrinoid-like ancestor, cornute stylophorans and glyptocystitoid rhombiferans are not closely related phylogenetically. In this context, their folded respiratory structures can hardly be considered homologous, as they were acquired independently, through different ways, in these two lineages (morphological convergence).

Lines 747-752: This should be much earlier in the paper, it would resolve a lot of confusion about the different structures.

> Thank you; we believe that, in the new version of the MS, the "confusion" is now largely clarified earlier in the MS, with the more precise terminology, and also Table 1.

Line 756: There should be a figure that illustrates the morphology of these organisms to clarify and help justify the reclassification.
> we fully agree with Reviewer 2 that it is important to illustrate these organisms (i.e scotiaecystid cornutes) on a figure. This is precisely what was done in the original version of the MS reviewed by Reviewer 2: *Thoralicystis melchiori* was illustrated on Figs 5A-E and 6 (=Figs 6A-E and 7 in the revised version), *Thoralicystis zagoraensis*, on Fig. 5F-H (=revised Fig. 6F-H), *Bohemiaecystis griffei*, on Fig. 7A-D (=revised Fig. 8A-D), *Bohemiaecystis bouceki*, on Fig. 7F-G (=revised Fig. 8F-G), and *Scotiaecystis curvata*, on Fig. 7E (=revised Fig. 8E). These five scotiaecystid taxa exhibiting all the respiratory structures known in this cornute family are also illustrated in the new, revised version of the MS (see above). Furthermore, as notes in the MS, the family Scotiaecystidae has been recently thoroughly revised by Lefebvre et al. (2022), with numerous illustrations and detailed descriptions: "In their revision of scotiaecystid systematics, Lefebvre et al. (2022) identified four main morphotypes based on the morphology of their respiratory structures and the number of posterior thecal spines" [lines 755-757].

Lines 776-779: Does not confirm implies to the reader that you also are not rejecting these hypotheses. Consider rephrasing for clarity on what these openings are.
> we felt that demonstrating that a hypothesis is not confirmed implied that it cannot be considered valid. For the sake of clarity, we replaced "does not confirm their interpretation" with "does not support their interpretation".

Recommendation: Revisions Required

Review Round 2 Authors Response

Dear Editorial Team,

We would like to thank you for your careful review of our reply to reviewers, and we are grateful that you pointed out the following discrepancies. Here is our response point by point.

1. Both of the reviewers commented that the terminology of epispires and sutural pores is a bit confusing. You did fully address this in the responses to the reviewers, but I felt that since both reviewers pointed out this confusion it may also be confusing to other readers as well. I also know that you follow the terminology of Ubaghs throughout, however, since this is a major point of the paper a clarification in the manuscript itself I think is important. I would suggest using the phrasing in your responses to reviewers in the (namely that epispires are papulate-like associated *with* sutural pores, or something to that effect) around line 59 of the manuscript will satisfy this concern.
> Thank you very much for pointing this out, and we totally agree with you. Accordingly, we have modified the sentence "They were probably analogous to the papulae of extant asteroids, and were housed within rounded to oval sutural pores, i.e. orifices located across the boundaries between two (or three) adjoining skeletal elements" (lines 60-63) into: "They were soft, papulate respiratory structures probably analogous to the papulae of extant asteroids, and associated with sutural pores, i.e. rounded to oval orifices located across the boundaries between two (or three) adjoining skeletal elements" (lines 60-63). We hope this clears the confusion.

2. Can you confirm how many specimens were studied? Reviewer 2 pointed out that there was not a very clear list and you did address it in the response. But on line 231 you said "several hundreds" were studied. I think it would improve the manuscript to:
> state clearly how many species and approximately how many specimens (I understand this might be an estimate) were studied,
> We have modified the text, so as to provide a better and more realistic estimate of the number of examined specimens: "This material represents several hundreds of specimens comprising the type series of most cornute taxa" (line 231) has been modified into "This material represents over 2,000 specimens comprising the type series of most cornute taxa" (line 231) ; the precise list of all investigated taxa is provided in the text. We believe that a more precise and extensive list would be too tedious to provide, while not serving the point of our manuscript

> a reference in the body text of the manuscript to the online data where readers can find the full list (I know it is in the bottom materials, but just to be clear to a reader that doesn't go all the way to the bottom of the document), and
> The original version of the manuscript contained a section on quantitative analysis based on 11 cornute specimens and 26 rhombiferan individuals. These 27 measured specimens are those which were listed in the online supplementary data. In the revised version of the manuscript, the section on quantitative analysis was deleted. However, you are absolutely correct in pointing out that we should also have suppressed the link to the corresponding online dataset of 27 specimens, as this file no longer serve any purpose in the absence of any quantitative analysis in the manuscript. We have now deleted the link to the online dataset in the section "Data availaibility" and replaced it by this sentence: "All examined specimens are housed in public collections and accessible upon request" (lines 803-804). We apologize for this overlook and are grateful that you pointed it out.

> please confirm that the online list of specimens is up to date.

For example, I did not see any specimens listed in the supplemental materials from USA despite that being mentioned in the methods section about museums visited. Please ensure that this paragraph and the supplemental materials are aligned. Ideally, an individual wishing to double check your work should know specifically all of the specimens you studied and where they are houses. I think the IDs in the supplementary material accomplish this, but it seems to me to be an incomplete list or at the least one that does not align with the paragraph in the methods.
> The online list is not up-to-date (see above). It is no longer mentioned in the new revised version of the manuscript. Again, this was an overlook on our part, and we are thankful for your vigilance.

Please find the latest version of our manuscript as a clean document under the name "Dupichaud et al corrected clean.pdf", as well as a document with tracked changes under the name "Dupichaud et al corrected tracked changes.docx". No new figures have been uploaded as no modifications were done on that part.