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Reply to: Embracing the taxonomic and topological stability of phylogenomics

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REPLYING TO: M. Koch; *Scientific Reports* <https://doi.org/10.1038/s41598-024-54208-4> (2024).

We would like to re-emphasize our contribution on re-classification of Scutelliformes based on our new findings and appreciate the valid criticism raised by Koch¹. In his reply to our work², Koch¹ criticized the use of a dataset based on four molecular markers (two mitochondrial loci: *Cox1* and *16S*, and two nuclear ones: *28S* and *H3*) for a reassessment of the classification of sand dollars. Koch¹ pointed out the incongruence of certain deeper level splits in the tree published in our recent work² with those based on their genome-scale datasets³. One of the taxonomic disagreements is the position of Laganiformes. In the original paper where Mongiardino Koch et al.² proposed the new clade Luminacea, Laganiformes are represented by only two taxa that form a sister group to Scutelliformes. The position of Laganiformes appears more closely related to Clypeasteroidea in our study². In the classic morphological classification in Kroh and Smith⁴, these three clades are closely related. Luminacea, however, includes the fourth clade Cassiduloida, which is morphologically distinct from the other three sand dollar clades. In fact, there is no morphological synapomorphy for Luminacea; instead, it is based on molecular evidence. We tested the taxonomic stability within the clade Luminacea by increasing taxon sampling (from 15 taxa in Mongiardino Koch et al.³ to 25 taxa) with new sand dollar data from Taiwan and other countries.

Koch¹ argue that the data presented in our study² cannot fully resolve deep branching patterns of the major luminacean clades, and we fully agree with that. Perhaps, the best alternative is to present the inter-relationships among Cassiduloida, Laganiformes, Scutelliformes, and Clypeasteroidea, as polytomies in our original study². This is one of the reasons why we presented the novel classification (Lee et al.²) in a way that is restricted to the scutelliform clade of Luminacea which is well supported by both analyses. A full phylogenetic reassessment of Luminacea addressing deep splits within that clade was neither the subject of Lee et al.² nor was any of the sister-group relationship contested by Koch¹ used to propose a novel classification in conflict with previous results. Publication of data and results that are in conflict with previous analyses does not create a state of taxonomic instability or chaos. It is well established that gene trees differ from species trees⁵. As such, it comes as no big surprise that the number of markers applied and taxonomic sampling effort affect the results of individual analyses, and deeper level splits in particular. We argue that for the progress of science it is necessary to report results even if they are in conflict with other datasets. From this point we can discuss potential reasons for the observed relationships and what the next steps are to improve our understanding of the relationships.

The main concern expressed by Koch¹, namely the sister-group relationship between laganids and clypeasteroids as outlined in the tree of our work², was only briefly addressed in that study. We did not consider the matter further in the conclusions or novel classification, because the respective nodes were poorly supported in the

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reconstructed tree. Moreover, the authors were well aware (and in part involved) in the genomic-scale studies of Mongiardino Koch et al.^{3,6}. We regret that this has not been expressed more clearly in our work² and acknowledge Koch¹ for rectifying this omission. The main finding of our study², namely, the relationship of the three main clades composing the Scutelliformes (Astriclypeoidea, Mellitoidea, and Taiwanasteroidea) remains valid. These clades, corresponding to the so named superfamilies, are well supported also in the trees provided by Koch¹ in Figure S2.C and S2.D and S2.A and S2.B, if the incorrectly placed spatangoids are ignored in the latter two trees.

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Author contributions

A.K., J.-P.L., D.J., H.L., K.-S.L., O.B. wrote the initial draft. H.L., O.B. checked and analyzed original data. All authors contributed to the writing of the manuscript, reviewed, and approved the final version.

Competing interests

The authors declare no competing interests.

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