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REVIEW OF THE PHD DISSERTATION

Doctoral Candidate:	Aleksandra Tokareva, M.Sc.
PhD dissertation:	A comprehensive genus-level phylogeny of Paederinae (Coleoptera: Staphylinidae) based on combined genomic and morphological data
Supervisor:	Prof. dr hab. K. Wioletta Tomaszewska (MIIZ PAN, Warszawa)
Supervisor:	dr Dagmara Żyła (Leibniz Institute for the Analysis of Biodiversity Change, Hamburg)
Reviewer:	Dr hab. Agnieszka Soszyńska, prof. UŁ

Dissertation characteristics:

The dissertation submitted for review by Aleksandra Tokareva, consists of three original research articles in English (Chapters 1–3) with appendices, as well as two additional chapters presented as a submitted manuscript (Chapter 4) and a submission-ready manuscript (Chapter 5). The thesis chapters are prefaced by an abstract in Polish and English, an Introduction, a Materials and methods, Results, Conclusions, and References. At the very end, in Chapter 6, the PhD student presents *Further Plans and perspectives*. The entire dissertation is written in English and comprises 293 pages, including supplementary materials. The five appendices related to phylogenetic analyses have been provided in electronic form only.

In two published articles, the PhD student is the second author, while in one, she is the first and corresponding author. In both unpublished manuscripts, she is listed as the first and corresponding author. Declarations of the contributions of all co-authors to the individual papers and manuscripts are included in the documentation.

The articles included in the dissertation were published in English-language journals indexed in *Journal Citation Reports* (Web of Science) and the *Scopus* database. These journals are highly regarded in their field: *European Journal of Taxonomy* (IF: 1.6; 70 ministerial points) and *Scientific Reports* (IF: 3.8; 140 ministerial points). The declarations of author contributions, along with the PhD student's first-author position in one publication and two final manuscripts, confirm her leading role in conceptualisation, study design, data collection, analysis, interpretation of results, and manuscript preparation, as well as her significant contribution to the other two publications.

Published papers:

Żyła D.*, Tokareva A., Koszela K. 2022. Phylogenetic position of genera *Acrostilicus* Hubbard and *Pachystilicus* Casey (Staphylinidae, Paederinae) and their redescription. *European Journal of Taxonomy* 819: 1–22

Tokareva A.*, Koszela K., Ferreira V.S., Yamamoto S., Żyła D. 2023. The oldest case of paedomorphosis in rove beetles and description of a new genus of Paederinae from Cretaceous amber (Coleoptera: Staphylinidae). *Scientific Reports* 13: 5317.

GUZMAN Y.C.*, TOKAREVA A., KOSZELA K., ŻYŁA D. 2023. Twenty-one new species of the Neotropical rove beetle genus *Neolindus* Scheerpeltz (Coleoptera, Staphylinidae, Paederinae). *European Journal of Taxonomy* 942: 1–76.

Manuscripts:

Tokareva A.*, Żyła D. (submitted) Comparative morphology of mesoventrite in Paederine: insights for subtribal-level phylogenetic reconstruction.

Tokareva A.*, Koszela K., Sarmiento Y.C.G., Żyła D. A comprehensive genus-level phylogeny of paederinae (Coleoptera: Staphylinidae) based on combined genomic and morphological data.

Substantive value of the dissertation

The main objective of the PhD thesis submitted for evaluation was to revise the beetles of the family Staphylinidae, specifically the subfamily Paederinae, at the generic level, based on a phylogeny integrating both molecular and morphological data.

The challenge undertaken by the PhD student was significant. Paederinae, the most numerous subfamily within Staphylinidae—the most diverse beetle family and one of the largest known animal groups (67,000 species)—comprises approximately 8,000 species grouped into more than 230 genera. This subfamily remains poorly understood and under-recognized, with old taxa requiring revision and redescription, making research in this field particularly complex. Consequently, Paederinae has not yet been the subject of a comprehensive study.

The greatest challenge of the research was obtaining representative material for both molecular and morphological analyses. Specimens were acquired through loans from museums across Europe and the USA, as well as from field expeditions to Armenia, Georgia, Ecuador, and the USA.

The PhD student pursued the main objective through several specific goals, including the description of fossil taxa, the redescription of historical type specimens, the identification of new species to update the morphological data matrix, and the analysis of new morphological characters to enrich the dataset. The final task involved designing molecular studies and conducting bioinformatics analyses to process raw sequencing data and generate a genomic alignment ready for further analysis.

In publication I (Żyła et al. 2022), the Nearctic genera *Acrostilicus* and *Pachystilicus*, described more than 100 years ago, were re-examined to clarify their phylogenetic position. Their taxonomic placement had remained uncertain due to insufficient descriptions and their weak differentiation from the genus *Rugilus*. A total-evidence dataset, integrating both

molecular and morphological data, confirmed for the first time that these taxa belong to the tribe Lathroiini and the subtribe Stilicina.

In Publication II (Tokareva et al. 2023), the PhD student described a new genus of fossil Paederinae found in Burmese amber from Kachin, dated to the mid-Cretaceous (~99 My). This discovery not only provided new morphological data but also yielded important insights into the life history strategies of *Paederinae*. The newly described genus, *Midinudon* Tokareva & Żyła, 2023, along with a second genus, forms a clade distinct from other *Paederinae* within the tribe *Scopaeina*. These genera represent the oldest known examples of miniaturization and paedomorphosis (understood as a set of morphological features) in this group. The paper well discusses the significance of these unique morphological traits in the context of the palaeoenvironment and life history strategies, including inquilinism. Additionally, phylogenetic analyses were conducted to determine the placement of this taxon within the evolutionary tree of the subfamily.

In Publication III (Guzman et al. 2024), the PhD student contributed to the redescription of the genus *Neolindus*, the description of 21 new species, and the development of an updated key to 60 species of the genus. Additionally, genomic data—applied for the first time to this group—and molecular data obtained from museum collections were incorporated into the study. The publication is supported by high-quality documentation of trichobothria and pseudosensillia on head, utilizing Scanning Electron Microscopy (SEM) imaging techniques, as well as photographs and drawings of 21 species. This work, based on museum material, significantly enhances the understanding of genus *Neolindus*, its geographical distribution, and highlights the importance of museum collections for studying biodiversity.

Manuscript I (Chapter 4), which has been submitted for publication, presents a morphological study of the subfamily Paederinae. In this work, the PhD student undertook meticulous research to identify new morphological characters crucial for determining phylogenetic relationships within different subfamilies and genera of Paederinae. The author addressed the longstanding issue of the lack of a consistent homologous nomenclature for an essential structural feature of Pterygota—the mesoventral plates on the mesothorax. The study demonstrates modifications in the structure of this feature within related groups such as Staphylininae and Xantholininae and clarifies the homology of its various components. The research was based on representatives of 155 genera of Paederinae and two related subfamilies. The *mesoventrite* was classified into 23 distinct types, each of which was described in detail and illustrated with drawings and SEM microphotographs. The genera characterized by each *mesoventrite* morphotype were also identified.

Manuscript II (Chapter 5) represents a significant achievement, fulfilling the stated final objective. As the leading author, the PhD student conducted the first comprehensive phylogenetic analysis of the entire subfamily Paederinae, integrating genomic and morphological data, including information from 16 fossil species. Notably, this study marks the first application of ultraconserved elements (UCEs) in the phylogenetic analysis of beetles within the family Staphylinidae. The analyses were based on molecular data from 205 species representing 180 genera of Paederinae, while the morphological dataset included 204 characters. Many existing taxonomic concepts within the family were confirmed; however, systematic revisions were introduced at the tribal and subtribal levels. These revisions included the elevation of the subtribe Sphaeronina to the status of the tribe Sphaeronini and the designation of a new subtribe, Scymbaliina. Several subtribes (Lathrobiini, Scopaeina, Astenina, Stilicopsina, and Echiasteina) were revised, with updated

diagnoses and a newly proposed generic composition. Additionally, the study confirmed the non-monophyly of the two largest subtribes, Lathrobiina and Medonina.

In conclusion, the PhD student has demonstrated both courage and determination in undertaking the ambitious task of studying the phylogeny of a group comprising approximately 8,000 species. She has effectively applied modern molecular, bioinformatic, and phylogenetic methods, which are widely accepted in contemporary integrative taxonomy, while also utilizing traditional taxonomic techniques that are essential for establishing the foundation for such advanced methods.

The work of Aleksandra Tokareva, represents a significant contribution to the taxonomy of the family Staphylinidae, particularly through major revisions within the subfamily Paederinae based on the results of a total-evidence analysis, which integrates molecular, morphological, and fossil taxa.

Editorial Correctness of the Dissertation

The layout of the dissertation follows the standard structure of a doctoral thesis in the "Manuscript Series". The dissertation is written in English at a very high level, which is expected given that the PhD student has passed an English exam at the highest proficiency level. The illustrative quality of the individual papers and manuscripts is very good, featuring high-quality microscope images and very well-prepared SEM images. There are only a few minor inconsistencies in literature citations, a few typos and minor shortcomings.

Critical comments/questions

- I am confused by the differences in the reported number of species and genera, and I am curious about the correct numbers. In Publication I, it states that "the subfamily Paederinae includes about 7,600 species grouped into 225 genera"; in Publication II, it states "the subfamily Paederinae includes 7,400 species in 230 genera"; in Publication III, it mentions "the subfamily Paederinae includes 8,000 species grouped into 238 genera"; and in Manuscript II (Chapter 5), it states "the subfamily Paederinae includes 7,900 species in 230 genera."
- Assuming a figure of approximately 8,000 species grouped into more than 230 genera, I find it lacking that the dissertation does not address what percentage of these taxa have already been redescribed or sorted out, and what percentage are still awaiting revision. Considering the vast number of species in the subfamily, these three published papers represent only "a drop in the ocean of diversity" within this group. I am aware that a PhD project is time-limited, making it impossible to address everything. However, in my opinion, it would be useful to outline the scale of work that still needs to be done to fully revise this subfamily. Perhaps this dissertation already covers the entirety of the subject matter.
- Manuscript II (Chapter 5), I do not understand why the updated diagnosis was not included in the Results section but was instead placed in the Discussion.
- In the morphological data matrix (Manuscript II), I notice that fossil species are almost entirely described by states of characters, with only a dozen or so characters missing out of a total of 204. This is puzzling to me, in my experience, even well-preserved inclusions usually present challenges in coding most features. What's more, as I looked at the list of features I was amazed to find that this large list of

features (204 morphological characters) seems to only include external features that are easily visible. Does this mean that characters related to internal structural elements are not considered in morphological analysis, e.g. the copulatory organs. Perhaps there is a simple answer to this question that I don't know due to the nature of the group.

- The PhD student is conducting research under an NCN grant that explores the impact of the Paleocene-Eocene Thermal Maximum (PETM) on the diversification of the Staphylinidae. It is unfortunate that this broader context was not mentioned in the introduction.

Final Conclusion

In summary, I conclude that the dissertation of Aleksandra Tokareva, M.Sc., is an original work that meets the criteria required for the a doctoral degree in the field of natural sciences, specifically in the discipline of biological sciences. My critical remarks in no way diminish the substantive value of the dissertation.

In view of the above, I conclude that the evaluated doctoral dissertation of Alexandra Tokareva fully meets the conditions specified in art. 187 of Act of 20 July 2018, Law on Higher Education and Science (Journal of Laws of 2018, item1668, as amended). I therefore request the Scientific Council of the Museum and Institute of Zoology of the Polish Academy of Sciences to admit Alexandra Tokareva to the further stages of the doctoral dissertation.

Dr hab. Agnieszka Soszyńska, prof. UŁ