



Legacy molecular phylogenetics suggests restricting the concept of Melandryidae and resurrecting Osphyidae (Coleoptera: Tenebrionoidea)

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<https://zoobank.org/AAD7917A-D042-43A5-8C73-1D4635BA116A>

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Received 10 July 2023

Accepted 26 August 2024

Published 4 November 2024

Academic Editors André Nel, Marianna Simões

Citation: Cosandey V, Konvička O, Toussaint EFA (2024) Legacy molecular phylogenetics suggests restricting the concept of Melandryidae and resurrecting Osphyidae (Coleoptera: Tenebrionoidea). Arthropod Systematics & Phylogeny 82: 621–627. <https://doi.org/10.3897/asp.82.e131738>

Abstract

The superfamily Tenebrionoidea is one of the most challenging clades in the beetle tree-of-life owing to its vast species richness and complex taxonomic history. Within this group, the family Melandryidae has long been overlooked and its systematics remains poorly known. Using available sequence data, we infer the most comprehensive phylogeny of Melandryidae to date. Our results support the polyphyly of Melandryidae with three independent clades spread across Tenebrionoidea. To accommodate these results, we restrict the status of Melandryidae and resurrect the family Osphyidae **stat. rev.** The third clade corresponding to the tribe Serropalpini pro parte is placed as incertae sedis within Tenebrionoidea pending further investigation and additional taxon sampling to resolve its phylogenetic placement.

Keywords

Beetle evolution; false darkling beetles; Melandryinae; Osphyinae; Serropalpini; Tenebrionoidea systematics

1. Introduction

The superfamily Tenebrionoidea has a worldwide distribution, encompasses 28 families and comprises over 33,000 species in more than 3,000 genera, approximately two thirds of which belong to the family Tenebrionidae (Barclay and Bouchard 2023). Tenebrionoidea exhibits a wide array of ecologies with saproxylic, saprophagous, mycetophagous, predatory and ectoparasitic taxa. Members of Tenebrionoidea are characterized by their tarsomere formula: 5-5-4, rarely 3-3-3 or 3-4-4 in males but never 5-5-5. In molecular analyses, the monophyly of Tenebrionoidea is not supported by all studies. They are

sometimes inferred as monophyletic (Hunt et al. 2007; Gunter et al. 2014; Cai et al. 2022), but in most recent phylogenomic treatments are recovered as paraphyletic due to the placement of Lymexyloidea as a derived lineage in this group (McKenna et al. 2015, 2019; Batelka et al. 2016). Despite recent developments in the phylogenomics of beetles, higher-level phylogenetic relationships in the Tenebrionoidea remain uncertain (Gunter et al. 2014). Studies focusing on intra-Tenebrionoidea relationships are scarce and have often resulted in poorly supported backbones preventing a better understanding

of the group evolution. The most comprehensive molecular phylogeny of Tenebrionoidea was inferred by Kergoat et al. (2014). Of the 18 families of Tenebrionoidea included in this study, five were found to be paraphyletic or polyphyletic. Some cases such as the Rhipiphoridae are well-documented, these beetles being known to form a paraphyletic family due to the placement of the monophyletic Mordellidae (Kergoat et al. 2014; Batelka et al. 2016).

Another interesting case within Tenebrionoidea is the family Melandryidae. Previously named Serropalpidae, it is represented by more than 420 species classified in ca. 60 genera (Nikitsky and Pollock 2010). Most of them are placed in Melandryinae, one of the two recognized subfamilies of Melandryidae, itself divided into eight tribes: Anisoxiellini, Dircaeini, Hypulini, Melandryini, Orchesiini, Serropalpini, Xylitini, and Zilorini. Melandryidae have a great variety of morphologies (Fig. 1) and a wide range of sizes, from 1.1 mm to 22 mm (Nikitsky and Pollock 2010). They are vaguely characterized by the last maxillary palpomere which is usually triangular and securiform or hook-shaped, markedly large. Their antennae have 11 antennomeres (excepted in *Conopalpus*, which has 10 antennomeres), filiform or serrate, sometimes dilated apically. The abdomen consists of five visible ventrites (exceptionally six ventrites) where at least the first two are fused. The tarsal formula is 5-5-4 in both sexes. Basal metatarsomeres are elongate (Lawrence 1982; Pollock 2002). Because of their cryptic habits, the ecology of many species remains unknown, especially outside of the Holarctic region. They are mostly referred to as mycophagous or saproxylic beetles linked with dead or decaying wood or associated with fungi on wood or in the soil litter (Hammond and Lawrence 1989; Nikitsky and Pollock 2010; Konvička 2016a; Evans 2021).

The English common name of the family ‘false darkling beetles’ illustrates well the definition of the family as tenebrionid-like but not tenebrionid beetles. Indeed, it has always included various genera difficult to place and

has always ‘lost’ some genera or subfamilies due to revisions pointing to the incoherence of their placement. The delimitation and definition of the family have markedly changed through time with the distinction of multiple families (Stenotrachelidae, Synchronidae, Tetratomidae) and with the placement of some species/genera in other families (e.g. *Pseudeucinetus* in Limnichidae, *Sphalma* in Pythidae) (Nikitsky and Pollock 2010).

Crowson (1966) followed by Lawrence (1982, 1991) considered the Melandryidae to be divided into three subfamilies: Eustrophinae, Melandryinae and Osphyinae, based on the combination of larval and imaginal features. Later, Nikitsky (1998) transferred the Eustrophinae to Tetratomidae. The subfamilial division within Melandryidae has not changed since then. Currently two subfamilies of Melandryidae are recognized: Melandryinae and Osphyinae (Nikitsky and Pollock 2010). These two taxa have fundamentally different imaginal morphologies: Melandryinae have simple claws and a head not notably narrowed behind the eyes, while Osphyinae have claws with distinct basal teeth and a distinctly narrowed head behind the eyes (Pollock 2002; Nikitsky and Pollock 2010; Crowson 1966). Crowson (1966) himself questioned the reliability to keep Osphyinae within the Melandryidae. Recently, Melandryidae have repeatedly been shown to be polyphyletic (Kergoat et al. 2014; Liu et al. 2023), highlighting the fact that some taxa are still erroneously included in this family. A renewed interest in the taxonomy and systematics of Melandryidae prompts a better understanding of high-level phylogenetic relationships and an updated classification of the different constituent groups (Nikitsky and Saitô 2014; Konvička 2016b; Recalde Irurzun et al. 2017; Konvička and Brustel 2021; Choi et al. 2020; Cosandey 2023a, b, c, 2024). Based on an exhaustive compilation of available Melandryidae sequence data and of a selection of neighboring clades, we investigated the phylogeny of Melandryidae with a special attention on the relatedness of Melandryinae and Osphyinae.

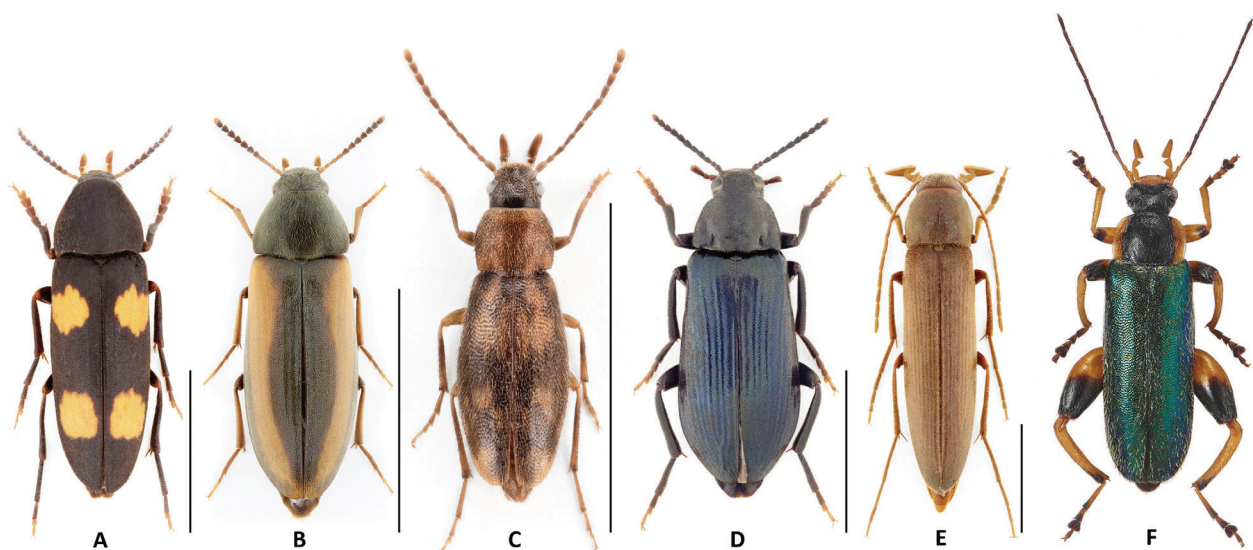


Figure 1. Morphological diversity of Melandryidae. **A** *Dircaea australis* **B** *Dolotarsus lividus* **C** *Marolia alicantina* **D** *Melandrya caraboides* **E** *Serropalpus barbatus* **F** *Osphyia aeneipennis*. Scale bars: 5 mm. (Pictures: **A**, **F** Vít Kabourek **B–E** Aleš Sedláček)

2. Material and Methods

2.1. Taxon sampling

We gathered available sequence data from GenBank. We included all closely related families to Melandryidae to test the monophyly of the group and as many species of Melandryidae as possible to reconstruct the most comprehensive phylogeny of the family to date. The longhorn beetle *Saperda tridentata* (Coleoptera, Cerambycidae) was used as an outgroup following McKenna et al. (2019). Most data came from the studies of Batelka et al. (2016), Buder et al. (2008), Gunter et al. (2014) and Kergoat et al. (2014). All data were curated in Geneious Prime 2023.2.1 (<https://www.geneious.com>). Individual locus alignments were generated using MAFFT 7.490 (Katoh et al. 2013) and the E-INS-I algorithm. Locus trees were inferred using FastTree 2.1.12 (Price et al. 2009) and visually inspected for problematic sequences. Finally, a multilocus matrix comprising 117 terminals was assembled in Geneious by concatenating all curated gene fragments. The matrix was composed of two mitochondrial gene fragments (CO1, 1380 bp and 16S, 549 bp) and two nuclear ribosomal gene fragments (18S, 2031 bp and 28S, 759 bp) for a total of 4719 aligned nucleotides. The final matrix used for phylogenetic inference is available in supplementary files (Zenodo: <https://zenodo.org/records/14002625>).

2.2. Phylogenetic inference

The phylogeny of Tenebrionoidea with a focus on Melandryidae was inferred in IQ-TREE 2.0.3 (Minh et al. 2020) as implemented on Pyrgus, the bioinformatic cluster of the Natural History Museum of Geneva. The final matrix was partitioned a priori by locus and for the CO1 by codon position to search for an optimal partitioning scheme using ModelFinder (Kalyaanamoorthy et al. 2017) (Available as a supplementary file in the Zenodo repository). We performed 100 independent tree searches to avoid local optima and branch support was estimated using SH-aLRT and ultrafast bootstrap (UFBoot) calculations (Guindon et al. 2009; Hoang et al. 2018). We used the option -bnni to optimize each bootstrap tree with a hill-climbing nearest neighbor interchange (NNI) search based directly on the corresponding bootstrap alignment, thereby reducing the risk of branch support overestimation. We also used the -allnni option to consider all possible NNI moves instead of only those in the vicinity of previously applied NNI moves.

3. Phylogenetic results

The best maximum likelihood tree inferred in IQ-TREE is shown in Figure 2 (Available as a supplementary file in the Zenodo repository). Branch support across the phy-

logeny is moderate in particular for the deeper nodes of the tree; however, the monophyly of most families is inferred with varying levels of branch support. The only three families that are not recovered as monophyletic are the Melandryidae, Ripiphoridae and Tetratomidae. The inferred phylogeny recovers Melandryidae as polyphyletic and divided in three clades: 1) Osphyinae (clade I), 2) *Mikadonius* and *Enchodes* (clade II), and 3) Melandryinae without *Mikadonius* and *Enchodes* (clade III). Clade I is recovered as sister to Scaptiidae with moderate branch support. Despite low branch support for the relationships between families in this part of the tree, the placement of Clade I in a larger clade comprising Mycteridae, Salpingidae, Scaptiidae and Trictenomidae is recovered with moderate branch support (SH-aLRT = 92, UFBoot = 30). Within the robustly supported Clade I (SH-aLRT = 100, UFBoot = 100), we recover *Osphyia* as paraphyletic due to the placement of *Conopalpus testaceus* as sister to a clade comprising *O. orientalis* and *O. sinensis* with moderate branch support (SH-aLRT = 80, UFBoot = 64). Clade II is inferred as sister to Aderidae, Synchronidae and most of Tetratomidae with moderate branch support (SH-aLRT = 83, UFBoot = 34). We infer that clade III is sister to *Tetratoma*, the placement of which results in Tetratomidae being polyphyletic with low branch support. Clade II and III are placed with moderate branch support (SH-aLRT = 80, UFBoot = 44) in a larger clade comprising Aderidae and Tetratomidae. Within Clade III, the relationships between major clades are poorly supported. The genera *Melandrya* and *Phloiortya* are recovered as paraphyletic with moderate to strong branch support due to the respective placements of *Phryganophilus ruficollis* as sister to *Melandrya dubia* and *M. pictipennis*, and of the genus *Abdera* as sister to *Phloiortya planiuscula*. We infer a moderately to strongly supported sister relationship between *Dircaea* and a monophyletic *Microtonus*, between a monophyletic *Hypulus* and (*Phloiortya* + *Abdera* + *Anisoxya*), and between *Microscapha* and a monophyletic *Orchesia*.

4. Discussion: Systematics

4.1. Melandryidae Leach, 1815

The type genus is *Melandrya* Fabricius, 1801: 163. The type species is *Helops serratus* Fabricius, 1775: 257 (now synonym of *Melandrya caraboides* (Linnaeus, 1760)).

In previous studies, the subfamily Melandryinae was scattered in three clades (Gunter et al. 2014; Kergoat et al. 2014; Kanda 2017) with Orchesiini forming a clade by itself. Our results show that Melandryinae is composed of two distinct lineages, the tribe Serropalpini in Clade II (represented by the genera *Enchodes* and *Mikadonius*) and the rest of the subfamily in Clade III. The placement of Serropalpini outside of Melandryinae was inferred by Kergoat et al. (2014)

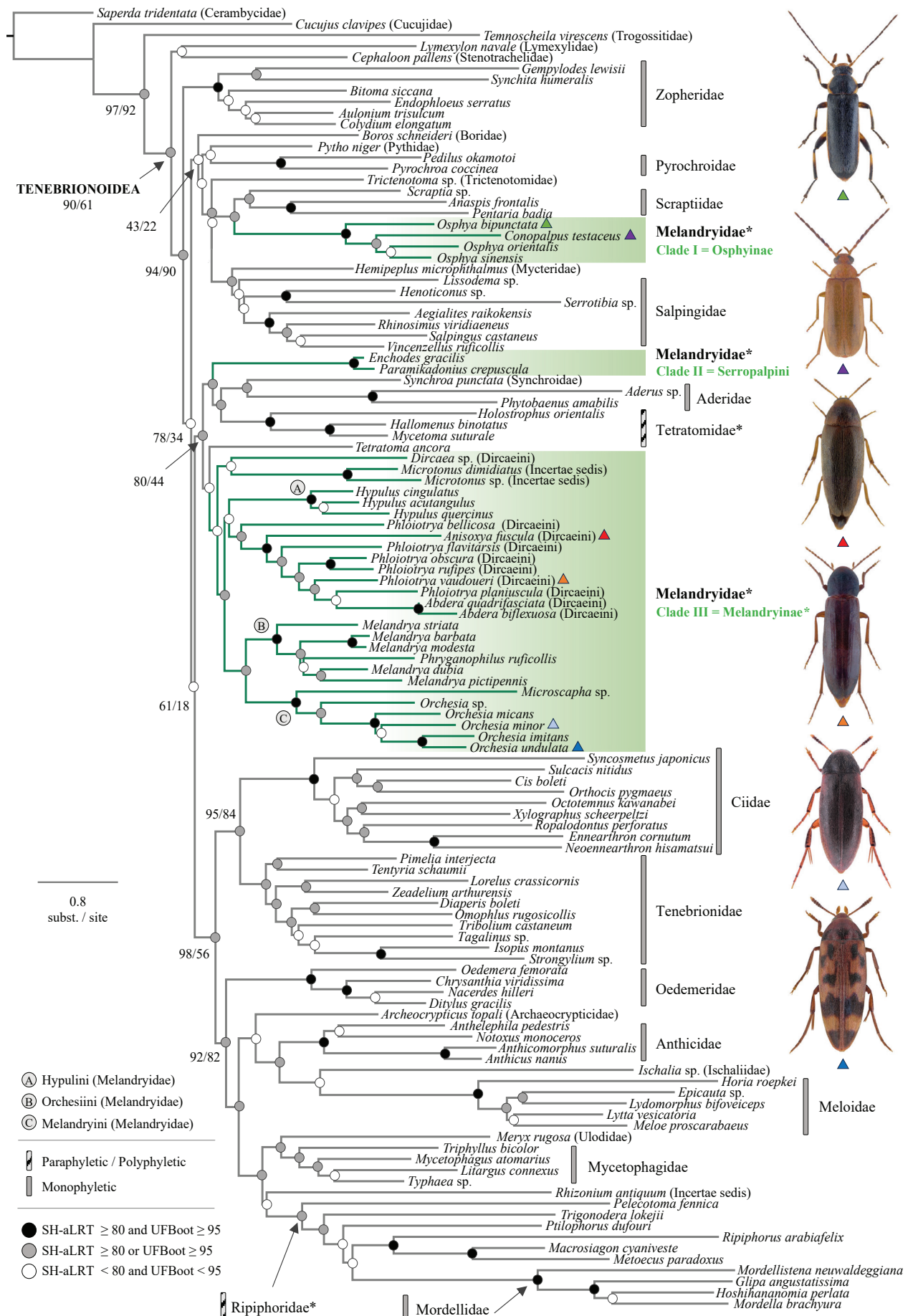


Figure 2. Best maximum likelihood tree inferred in IQ-TREE for Melandryidae including closely related families. The polyphyletic Melandryidae s.l. are shown in green. Habitus of selected species are indicated with colored triangles. (Pictures: Udo Schmidt)

Adults of Melandryidae can be distinguished from Osphyidae by the following combination of characters: head not notably narrowed behind eyes, labrum simple, tarsal claws simple, front coxal cavities internally closed. The larvae can be identified using the following features: labial palpi parallel and very close together, head with distinct median epicranial suture and no endocarina (Crownson 1966).

4.2. Melandryidae: Anisoxiellini Nikitsky, 1989

We could not incorporate any sequence data of a representative of this tribe in the phylogeny. This tribe includes only the single genus *Anisoxiella*. Knowing its placement as a clade nested or not in another tribe of Melandryidae is necessary to confirm its taxonomic validity. Further studies should focus on this topic.

4.3. Melandryidae: Dircaeini Mulsant, 1856

This tribe is recovered as polyphyletic in our analyses. The type-genus of the tribe Dircaeini, *Dircaea*, was found within the Melandryinae, contrarily to the results of Kergoat et al. (2014), who found it grouped with Osphyinae and Scaptiidae. In our analysis, *Dircaea* groups with *Microtonus*, currently considered as incertae sedis and not assigned to any Melandryidae tribe. These two genera form the basal lineage of all Melandryidae. Further studies will have to focus on the placement of the genus *Dircaea*. Being the type-genus of the tribe Dircaeini, it is possible that taxonomic and nomenclatural changes will be required to reflect the evolutionary history of these genera in the classification of Melandryidae.

The genus *Phloiотrya* is also recovered as polyphyletic in our analysis, with a monophyletic *Abdera* nested inside as well as *Anisoxya fuscula*. This genus requires more attention and a global revision is needed to clarify its systematics.

4.4. Melandryidae: Hypulini Seidlitz, 1875

This tribe is found as a monophylum with Dircaeini pro parte as sister.

4.5. Melandryidae: Melandryini Leach, 1815

This tribe forms a monophylum in our analyses. However, the genus *Melandrya* is recovered as paraphyletic due to the placement of *Phryganophilus*. Interestingly, Melandryini is reported as a sister clade of Orchesiini.

4.6. Melandryidae: Orchesiini Mulsant, 1856

The monophyly of the tribe Orchesiini is supported by our analyses: all *Orchesia* as well as *Microscapha* group together. This indicates that the features used to characterize this group are likely real apomorphies. Orchesiini are characterized by their saltatory hind legs bearing long metatarsal spurs and their bilobate aedeagus. Orchesiini are known to be able to jump up to 300x their body length (Fairmaire and Germain 1863; Sasaji 1995). Some genera are winged and distributed almost worldwide (*Orchesia*, *Microscapha*), while others (*Eucinetomorphus*, *Lederia*, *Lederina*, *Lyperocharis*, *Parvapila*) are wingless and more restricted geographically. For now, it is not known if the wingless genera form monophyletic lineages or if they are specialized groups of species nested in paraphyletic groups including winged genera (Cosandey 2023c).

4.7. Melandryidae: Serropalpini Latreille, 1829

Due to the lack of quality sequences, the only Serropalpini genera included in our analyses were *Enchodes* and *Mikadonius*. Both these genera must be excluded from Melandryidae (see next incertae sedis section). Further studies should focus on the placement of Serropalpini. Indeed, they could be excluded from the Melandryidae and form their own family, restoring Serropalpidae.

4.8. Melandryidae: Incertae sedis

The genera *Enchodes* and *Mikadonius* were not found to be part of Melandryidae. Therefore, we suggest to consider them as Tenebrionoidea incertae sedis. Our findings are in adequation with those of Kergoat et al. (2014) as expected from the analysis of largely overlapping datasets. Further work focusing on the phylogeny of this superfamily should be carried out to better understand the placement of these two genera and, more widely the placement of Serropalpini.

4.9. Osphyidae Mulsant, 1856 stat. rev.

The type genus is *Osphya* Illiger: 370. The type species is *Cantharis bipunctata* Fabricius, 1775: 206 (now placed in *Osphya*).

The great morphological differences between Osphyidae and Melandryidae are supported by the molecular data. Osphyidae was found as a monophylum and it did not group with the rest of the Melandryidae. Osphyidae have Scaptiidae as a sister clade, both taxa being monophyletic. Contrarily to what Gunter et al. (2014) observed, we did not find a relationship between Osphyidae and Myce-

toma suturale. This latter species is placed in Hallome-ninae (Tetratomidae), a former member of Melandryidae.

Osphyidae should no more be considered as a subfam-ily of Melandryidae but as a distinct family. The diagno-sis to identify this family is given in the next section.

Adults of Osphyidae can be distinguished from those of Melandryidae s.str. by the following combination of characters: head considerably narrowed behind eyes, tar-sal claws strongly toothed or split, front coxal cavities internally open, a very short prosternum and prosternal process, and the penultimate tarsomere with distinct lobe, extended under last tarsomere, labrum with ventral pouches opening outwardly at its posterior angles (Pol-lock 2002; Nikitsky and Pollock 2010; Crowson 1966). Larvae of Osphyidae can be identified with the following morphological features: labial palpi more or less separat-ed and not parallel, head without median epicranial suture (Crowson 1966).

4.10. Stenotrachelidae, Synchronidae, Tetratomidae

These families were previously classified as Melandry-idae. While Synchronidae and Tetratomidae were recov-ered as sister groups of Melandryidae, Stenotrachelidae grouped with Lymexylidae as a basal lineage of Tene-brionoidea.

5. Conclusion

This study presents the first phylogenetic work specifical-ly focusing on Melandryidae. Our results are largely in adequation with those of studies focusing on beetle phy-logenomics (McKenna et al. 2015; Cai et al. 2022) or Tene-brionoidea in particular (Gunter et al. 2014; Kergoat et al. 2014); all of them inferred Melandryidae s.l. as a polyphy-letic family with Osphyidae and Melandryidae s.str. form-ing distinct clades. Crowson (1966) already doubted the placement of Osphyidae inside of the Melandryidae. Our results demonstrate clearly that Osphyidae forms a family on its own. A third clade of Melandryidae s.l. was present. It contained *Mikadonius* and *Enchodes*, two Serropalpini genera already pointed out to display unusual morpho-logical features (Nikitsky and Pollock 2010). Moreover, *Enchodes crepusculus* was previously placed in the genus *Synchroa* (now placed in Synchronidae) before being trans-ferred to *Mikadonius* by Crowson (1966), illustrating once more the ambiguity of the relatedness of this species (and genus). The placement of these two genera is still unclear and they should be considered as Tenebrionoidea incertae sedis since they apparently do not belong to Melandryidae but they cannot be placed in another family. One possi-bility is that the tribe Serropalpini forms a distinct family Serropalpidae that needs to be resurrected. However, fur-ther analyses including more Serropalpini taxa are need-ed to confirm or reject this hypothesis. Taxa previously

considered as part of Melandryidae – Synchronidae and Tetratomidae – were found as sister clades to Melandry-idae with Tetratomidae being polyphyletic. Stenotrache-lidae, also previously placed in Melandryidae was recov-ered as a basal lineage of Tenebrionoidea as in McKenna et al. (2015). This family grouped with Lymexylidae, a taxon considered as part of the Tenebrionoidea or form-ing its own superfamily depending on the authors. Further studies focusing on Tenebrionoidea should try to elucidate the placement of Stenotrachelidae and its relationships with Lymexylidae. The present work is a further step in the comprehension of the systematics of Tenebrionoidea, a clade known for its complex taxonomy and also in the global knowledge of evolutionary relatedness of beetles. This refinement of the Melandryidae classification will be useful in the framework of ongoing taxonomic and phylo-genetic efforts (Nikitsky and Saitō 2014; Konvička 2016b; Recalde Irurzun et al. 2017; Konvička and Brustel 2021; Choi et al. 2020; Cosandey 2023a, b, c, 2024).

6. Acknowledgments

We would like to thank Gaël Kergoat for his advices in an early stage in this work. We acknowledge Vít Kabourek, Aleš Sedláček and Udo Schimdt for letting us use their pictures. We thank the reviewers and the editorial board for their comments that helped improve this article. Finally, we thank all the people contributing to genetic databases, thus permitting studies like ours.

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Jahr/Year: 2024

Band/Volume: [82](#)

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Artikel/Article: [Legacy molecular phylogenetics suggests restricting the concept of Melandryidae and resurrecting Osphyidae \(Coleoptera: Tenebrionoidea\) 621-627](#)