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DISSONOMINI MEDVEDEV, 1968: THE EIGHTH TRIBE OF THE SUBFAMILY BLAPTINAE (COLEOPTERA: TENEBRIONIDAE)

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Abstract.— The phylogenetic placement of the tribe Dissonomini Medvedev, 1968 (Coleoptera: Tenebrionidae) is investigated using sequences from a historical museum specimen of *Dissonomus tibialis* Reitter, 1904, along with representative sequences and specimens from the subfamilies Blaptinae (tribes Amphidorini, Blaptini, Dendarini, Opatrini, Pedinini, Platynotini), Tenebrioninae (Bolitophagini, Helopini), Pimeliinae (Adesmini, Sepidiini, Tentyriini, Zophosini), Alleculinae (Alleculini), and Lagriinae (Lagriini). Maximum likelihood and Bayesian analyses were performed on a multi-loci dataset (548 loci spanning 178,309 amino acids). The resulting trees render Dissonomini as sister to Blaptini within Blaptinae with high support. This phylogenetic relation is further supported by morphological traits (e.g., lack ancorae, tenebrionoid protrochanters). As a result, Dissonomini is placed within Blaptinae.

Key words.— darkling beetles, museomics, classification, Blaptini, Platyscelidini

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Introduction

While assessing the polyphyletic subfamily Tenebrioninae Latreille, 1802, Kamiński *et al*. (2021) suggested the Central-Asian tribe Dissonomini Medvedev, 1968 (2 genera, 26 species, Iwan *et al*. 2020, Makhan 2018) as a potential member of the resurrected subfamily Blaptinae Leach, 1815. The inclusion of Dissonomini was suggested strictly based on morphological traits due to a lack of molecular data on the tribe at the time. Adult representatives in the tribe possess a reduced scutellar shield, aedeagal tegmen without ancorae (see Lumen & Kamiński 2023a), and 'blaptoid' habitus, all of which indicate a close morphological affiliation with the tribes Blaptini Leach, 1815 and Platyscelidini Lacordaire, 1859 (Medvedev 1968). Between these two tribes, Dissonomini appeared to share more adult morphological traits with Platyscelidini, such as widened pro- and mesotarsi (Medvedev 1968). However, when considering larval morphological characteristics, Dissonomini seemed to share more features in common with other Blaptinae, specifically Dendarini Mulsant & Rey, 1854, Pedinini Eschscholtz, 1829, and Platynotini Mulsant & Rey, 1853 (Medvedev 1968). Most larvae of those tribes are equipped with four enlarged apical spines on the terminal segment of the abdomen (Kamiński *et al*. 2019). As a result of conflicting morphology and the lack of molecular data, Kamiński *et al*. (2021) decided not to place Dissonomini within Blaptinae formally, pending additional data.

To investigate the phylogenetic position of Dissonomini, a historical museum specimen of *Dissonomus tibialis* Reitter, 1904 was sequenced using targeted enrichment with a hybridization capture probe set (after Swichtenberg et. al. 2023). Phylogenetic analyses were then conducted using the recovered genetic loci for this species and representatives from the current Blaptinae tribes, as well as taxa representing four additional tenebrionid subfamilies.

Material and methods

Newly sequenced material

Ethanol-preserved specimens used for extractions were collected by the authors (permits in acknowledgments) or contributed by collaborators (Table 1). Additionally, a single pinned museum specimen of *Dissonomus tibialis* (label data: "Turkest Ashabad" / "Tenebrionid Base Aaron D. Smith TB26594") was acquired from the Entomological Collection of the Museum and Institute of Zoology PAS (MIZ PAN).

DNA was extracted from the head capsules and pronota of specimens using a Qiagen DNeasy Blood & Tissue Kit following the manufacturer's protocols, except pipetting was used to mix samples during incubation instead of vortexing to reduce DNA shearing. Grinding of the cuticle was also avoided to preserve specimens for future morphological examination. Extractions were performed in a sterilized laminar flow hood to minimize contamination from non-target DNA (see Kanda *et al*. 2015). After DNA extraction, voucher specimens were rearticulated and card-mounted. Unique identifiers (TB, KKRNA, and MEL#s) were assigned to each voucher specimen for linking back to sequence data in the Sequence Read Archive (Table 1). All voucher specimens are preserved in the Purdue Entomological Research Collection (PERC) and the Entomological Collection of MIZ PAN.

Extracts were sent to Daicel Arbor Biosciences for library preparation and targeted enrichment using a MyBaits probe kit designed to capture 618 protein-coding genetic loci (see Kanda 2017 and Swichtenberg *et al*. 2023). Libraries were sequenced on a NovaSeq 6000 system using 150 bp paired-end runs.

Data acquired from NCBI-SRA

To increase the taxonomic coverage of Blaptinae and outgroups, additional sequences were downloaded from the Sequence Read Archive (NCBI-SRA) (Table 1). These additional data were generated and analyzed by Ragionieri *et al*. (2023) and Swichtenberg *et al*. (2023).

Sequence assembly and analysis

Read quality was assessed with FastQC v.0.11.9 (Andrews 2010). Reads with an average sequence quality across any 4 bases below 20 were removed with Trimmomatic (Bolger *et al*. 2014). HybPiper v. 2.0 pipeline (Johnson *et al*. 2016), operating in DIAMOND mode (Buchfink *et al*. 2015), was used to assemble reads using the set of orthologs designed by Kanda (2017). The implemented files contained sequence information for 618 protein-coding genetic loci acquired from transcriptomes of the following species: *Clamoris americana* (Horn, 1874) (voucher code: KKRNA00020) representing Phrenapatinae, *Eleodes delicata* Blaisdell, 1929 (KKRNA00086), and *Eulabis bicarinata* Eschscholtz, 1829 (KKRNA00037) both representing Tenebrioninae. This dataset is hereafter referred to as the Tenebrionidae bait probe markers (*Tps*). To ensure that mapped sequences of the museum sample were not biased by the reference (Smith *et al*. 2021), data acquired for *Dissonomus tibialis* were also mapped to a more phylogenetically distant probeset designed for the subfamily Pimeliinae (for details see Kanda 2017) – referred hereafter as *Pps*. All data

Table 1. Characteristics of samples analyzed in the present study.

Species	Higher classification	Voucher no.	NCBI-SRA no.	Reference	Genotyping success rate* [%]
Museum specimen					
Dissonomus tibialis Reitter, 1904	Blaptinae: Dissonomini	TB26594	SAMN40249083	present paper	2.5
Ethanol-preserved specimens					
Asiopus aciculatus (LeConte, 1858)	Blaptinae: Platynotini	MEL147	SAMN40249084	present paper	35.6
Blaps mucronata Latreille, 1804	Blaptinae: Blaptini	TB15113	SAMN40249085	present paper	62.8
Blapstinus fortis LeConte, 1878	Blaptinae: Opatrini	KKRNA0060	SAMN40249086	present paper	97.9
Byrsax sp.	Tenebrioninae: Bolitophagini	TB22621	SAMN40249087	present paper	58.4
Eleodes nigrina LeConte, 1858	Blaptinae: Amphidorini	KKRNA0025	SAMN40249088	present paper	98.5
Eurynotus capensis (Fabricius, 1794)	Blaptinae: Platynotini	MEL126	SAMN40249089	present paper	81.9
Namibomodes sp.	Pimeliinae: Sepidiini	TB23298	SAMN40249090	present paper	68.1
Rhipidandrus paradoxus (Palisot de Beauvois, 1818)	Tenebrioninae: Bolitophagini	TB16878	SAMN40249091	present paper	60.0
Sequences acquired from previous studies					
Allecula morio (Fabricius, 1787)	Alleculinae: Alleculini	*na*	SRS15779361	Ragionieri *et al*. 2023	97.9
Archinamibia peezi Koch, 1952	Pimeliinae: Tentyriini	TB18861	–	Swichtenberg *et al*. 2023	68.3
Blaps gibba Laporte de Castelnau, 1840	Blaptinae: Opatrini	*na*	SRR22314228	Ragionieri *et al*. 2023	97.6
Epiphysa flavicollis (Fabricius, 1794)	Pimeliinae: Adesmiini	TB19082	–	Swichtenberg *et al*. 2023	70.1
Lagria sp.	Lagriinae: Lagriini	*na*	SRS15779382	Ragionieri *et al*. 2023	93.7
Nalassus laevioctostriatus (Goeze, 1777)	Tenebrioninae: Helopini	*na*	SRS15779391	Ragionieri *et al*. 2023	98.2
Neoisocerus ferrugineus (Fabricius, 1798)	Blaptinae: Dendarini	*na*	SRS15779392	Ragionieri *et al*. 2023	98.4
Opatrum sabulosum (Linnaeus, 1760)	Blaptinae: Opatrini	*na*	SRS15779401	Ragionieri *et al*. 2023	98.4
Pedinus sp.	Blaptinae: Pedinini	na	SRS15779402	Ragionieri *et al*. 2023	98.4
Stenolamus reichenspergeri Koch, 1955	Blaptinae: Opatrini	TB26395	PRJNA1016168	Kamiński *et al*. 2023	69.7
Zophosis giessi (Koch, 1962)	Pimeliinae: Zophosini	TB19048	–	Swichtenberg *et al*. 2023	66.0
Cis sp.	Ciidae (outgroup)	*na*	SRS15779349	Ragionieri *et al*. 2023	90.5

* Percentage of total targeted loci (n = 618) for which >50% of sequence was recovered. Tenebrionidae bait probe markers (Tps) were used.

used in the mapping process are available as supplementary material (see Kamiński *et al*. 2024). The resulting amino acid sequences were then aligned using MAFFT with the L-INS-I algorithm (Katoh *et al*. 2005). Low-quality amino acid sequence sites were masked, and sequences with over 50% gaps per locus were trimmed using trimAl (Capella-Gutiérrez *et al*. 2009). SendSketch script, as implemented in BBMap/36.92, was used to characterize the metagenomic profile of assembled contigs. In the case of *Dissonomus tibialis*, data concerning two loci (OrthoMCL8004, OrthoMCL7212) were excluded from further analysis due to contamination detection. Surviving sequences were concatenated with FASConCAT (Kück and Meusemann 2010) into a single partitioned dataset including a total of 548 loci spanning 178,309 amino acids. All sequence assembly analyses were performed on Purdue University's Bell community cluster, within Rosen Center for Advanced Computing (McCartney *et al*. 2014).

Phylogenetic analysis

IQ-TREE 2 (Minh *et al*. 2020) was used to run maximum likelihood (ML) analyses using an edge-unlinked partition model (-Q), with the dataset partitioned by loci and the models for each locus applied from ModelFinder (Kalyaanamoorthy *et al*. 2017). Support for the resulting topology was assessed using 10,000 UltraFast Bootstrap (Hoang *et al*. 2018) iterations. The dataset, with the same partitions, was also analyzed using ExaBayes 1.5.1 (BI) (Aberer *et al*. 2014) run through the CIPRES portal (Miller *et al*. 2010). Two independent runs of 20 million generations, each with 1 cold chain and 2 heated chains, were performed with a burn-in fraction of 0.25.

Morphological data

Additional pinned specimens loaned from the Národní Muzeum of Prague, Czech Republic (NMPC) representing *Dissonomus* Jacquelin du Val, 1861, and *Bradyus* Dejean, 1834, were included for morphological examination.

Dissonomus label data: "Turkmen.23.IV.81 BAIRAM ALI Jelínek lgt.". "USSR Tadjikistan Aruk-Tau 20.4.(Garavuti) 1978 Mir. Dvořák lgt." / "ex coll. M. Dvořák National Museum Prague, Czech Republic". "USSR, Tadžikistan Aruk-Tau, 29.4. (Garavuti) 1978 Mir. Dvořák lgt." / "ex coll. M. Dvořák National Museum Prague, Czech Republic" (two specimens). "Kasakh SSR-8.V. UYUK NW Jambul Jelínek lgt, 1981". "USSR ARMENIA c. Garni-Gechard 24.-26.5.1982 Zd. Černý lgt.".

Bradyus label data: "Uzbekistan Buchara, Kyzyl-Kyr 4-5.5.1977 J.Pradáč leg." / "ex. coll. Pradáč Nat. Mus. Prague" (9 specimens).

Additionally, specimens of *Blaps putrida* Motschulsky, 1845, *Oodoscelis tibialis* Ballion, 1878, and *Platyscelis striatia* Motschulsky, 1859 from MIZ PAN were included for morphological comparison. *Blaps putrida* label data: "Ciscaucasia Athsi Kulak" / QR label "MIZ PAN WARSZAWA 38/1947 99261". *Oodoscelis tibialis* label data: "Platyscelis tibialis Ball. H. Gebien det. 1939" / "Platyscelis tibialis Ball" / Mus. Zool. Polonicum Warszawa 12/45" / "MIZ PAN COL047871". *Platyscelis striata* label data: "Turkestan" / "Platyscelis striata Mot. H.Gebien det.1939" / Mus. Zool. Polonicum Warszawa 12/45" / "Platyscelis striata Mot." / "striatus Motsch Turkest Faust" / QR label "MIZ PAN COL047854".

Results

Bioinformatic analysis did not reveal any obvious taxonomic sensitivity for the used probeset (Table 1). In particular, the genotyping success rates were relatively consistent between treated subfamilies, and seemed to be dependent on sample quality. This also included the outgroup (*Cis* sp.) for which more than 90% of targeted loci were at least partly (>50%) recovered (Fig. S1 in Kamiński *et al*. 2024). Furthermore, this study revealed a great degree of convergence between the molecular methodologies of Ragionieri *et al*. (2023) and Swichtenberg *et al*. (2023).

After sequence trimming and quality assessment, the final matrix contained a total of 548 loci (17,309 amino acids). Only a small portion of the total recovered loci for the matrix was recovered for *Dissonomus tibialis* (15 loci, 2047 amino acids) (Table S1 in Kamiński *et al*. 2024). The number of mapped reads for *Dissonomus tibialis* was similar regardless of the used bait probe markers in the bioinformatic analysis (Tps/Pps). In the case of the Tenebrionidae probes (Tps), 103,826 reads (12.0% of total recovered reads) were mapped, while 102,082 reads (11.8%) were mapped using Pimelinae probes (Pps). Overlapping sequences obtained in both mapping approaches were identical, indicating that they were not subject to the mapping bias (Fig. 1).

Regardless of the used bait probe markers and phylogenetic inference method (ML/BI), *Dissonomus tibialis* was recovered sister to both analyzed *Blaps* species, and clustered with *Eleodes nigrina* (Fig. 1). The *Dissonomus*+*Blaps*+*Eleodes* clade (*i.e.* 'blaptinoid clade') constitutes a sister grouping to the opatrinoid clade composed of members of Dendarini (*Neoisocerus ferrugineus*), Opatrini (*Opatrum sabulosum*, *Stenolamus reichenspergeri*), Pedinini (*Pedinus* sp.), and Platynotini (*Asiopus aciculatus*, *Eurynotus capensis*). All taxa above represent the subfamily Blaptinae, and statistical support for the majority of recovered clades was absolute (Fig. 1).

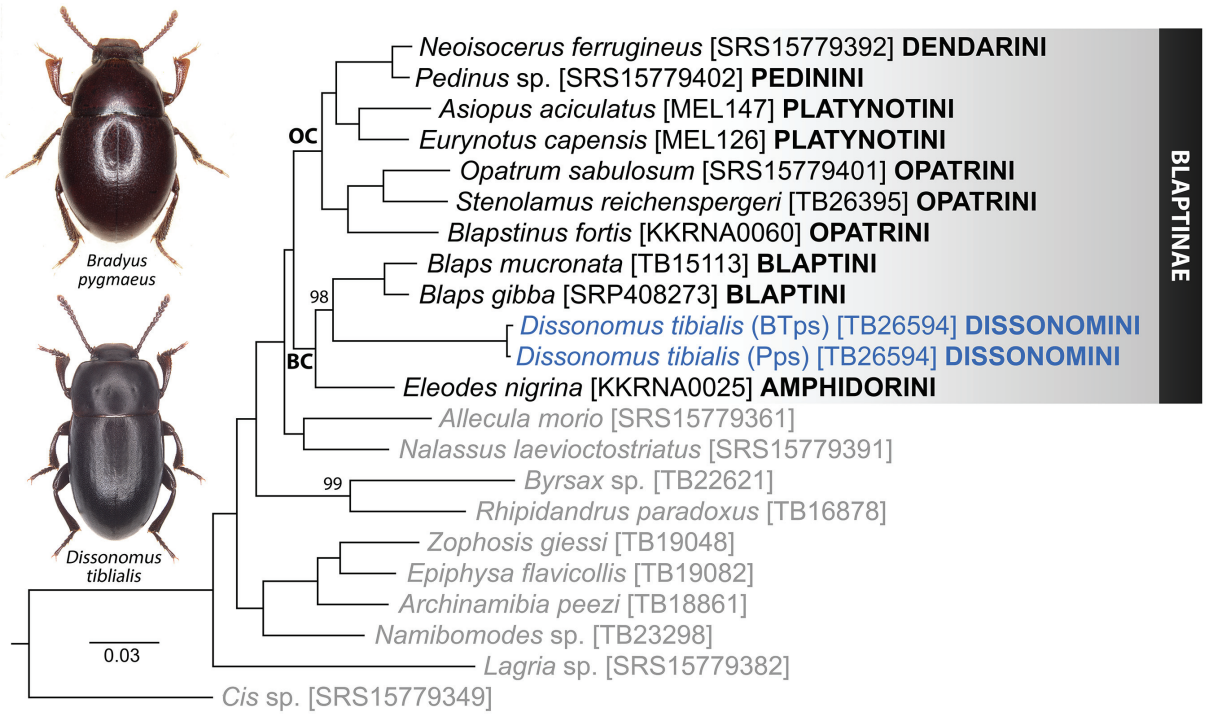

Figure 1. Phylogenetic placement of Dissonomini within the subfamily Blaptinae. Strict consensus tree derived from the maximum likelihood analysis of the concatenated matrix. Gray taxon names represent subfamilies outside Blaptinae, and Dissonomini representatives are blue. Branch support is displayed as an ultrafast bootstrap (above). Missing values indicate full branch support. All displayed nodes were fully supported in the Bayesian analysis (Posterior probability = 1.0). *Dissonomus tibialis* samples: Tps – sample mapped to Tenebrionidae probeset; Pps – sample mapped to Pimeliinae probeset. Abbreviations: BC – 'blaptinoid clade', OC – 'opatrinoid clade'.

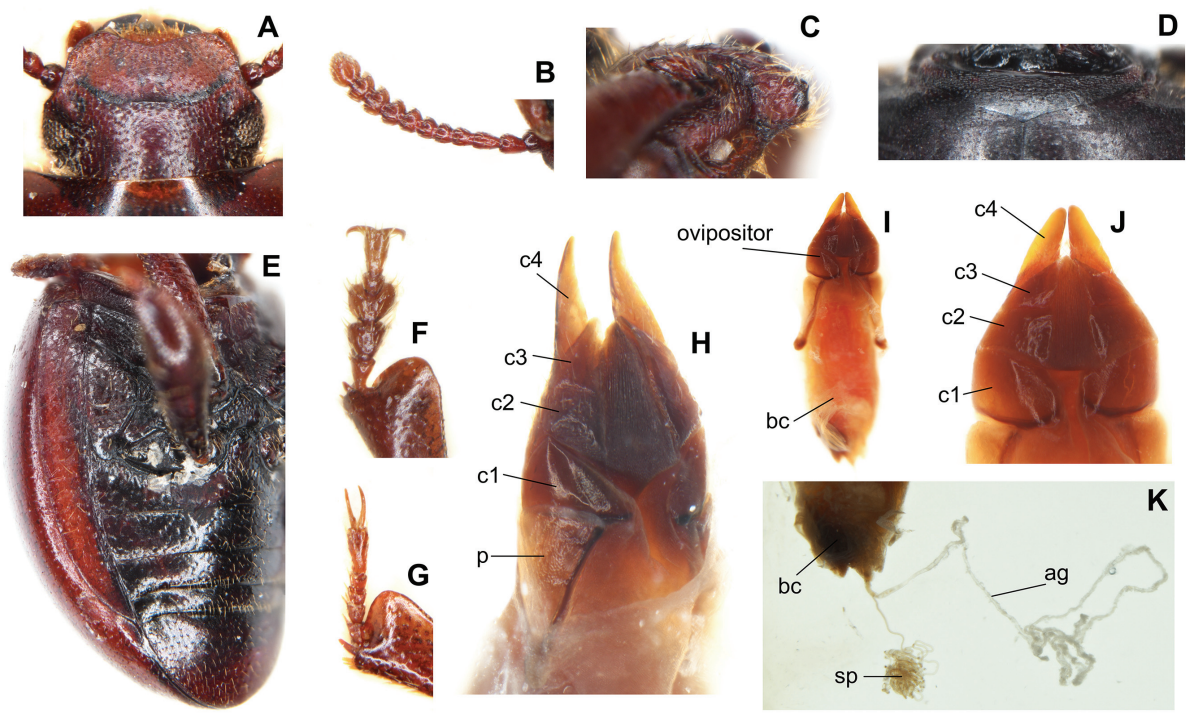

Figure 2. Morphology of species representing Dissonomini. (A–H) *Bradyus pygmaeus*, (I–K) *Dissonomus tibialis*. (A) dorsum of head, (B) antenna, (C) prosternal process in lateral view, (D) scutellum, (E) epipleuron, (F) male protarsus, (G) female protarsus, (H–J) ovipositor, (K) genital tubes. Abbreviations: bc – bursa copulatrix, c1–4 – coxites, p – paraproct, sp – spermatheca, ag – accessory gland.

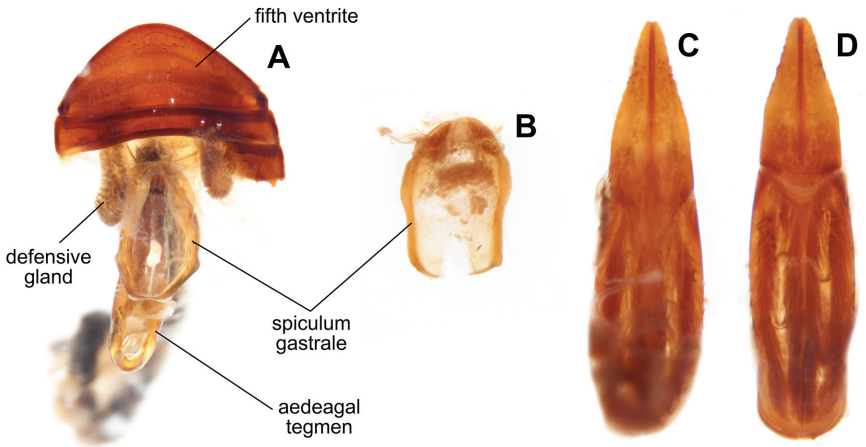

Figure 3. Male terminalia of (A) *Dissonomus tibialis* and (B, C, D) *Bradyus pygmaeus*. (B) Spiculum gastrale, (C) ventral and (D) dorsal views of tegmen.

Discussion

The analyses here provide novel data necessary to address the neglected phylogenetic position of Dissonomini, which were recovered deeply embedded within Blaptinae (Fig. 1). Their position close to Blaptini within the 'blaptinoid clade' appears to be morphologically justified, as representatives of Dissonomini lack ancorae (Lumen & Kamiński 2023a) and opatrinoid trochanters (Iwan & Kamiński 2016) – precluding a closer relationship with Dendarini, Pedinini, Platynotini, and Opatrini (Iwan & Kamiński 2016, Kamiński & Iwan 2017, Kamiński *et al*. 2021, Lumen & Kamiński 2023b). The lack of ancorae also distinguishes Dissonomini from the Nearctic tribe Amphidorini (Johnston *et al*. 2022), which also clustered within the 'blaptinoid clade'

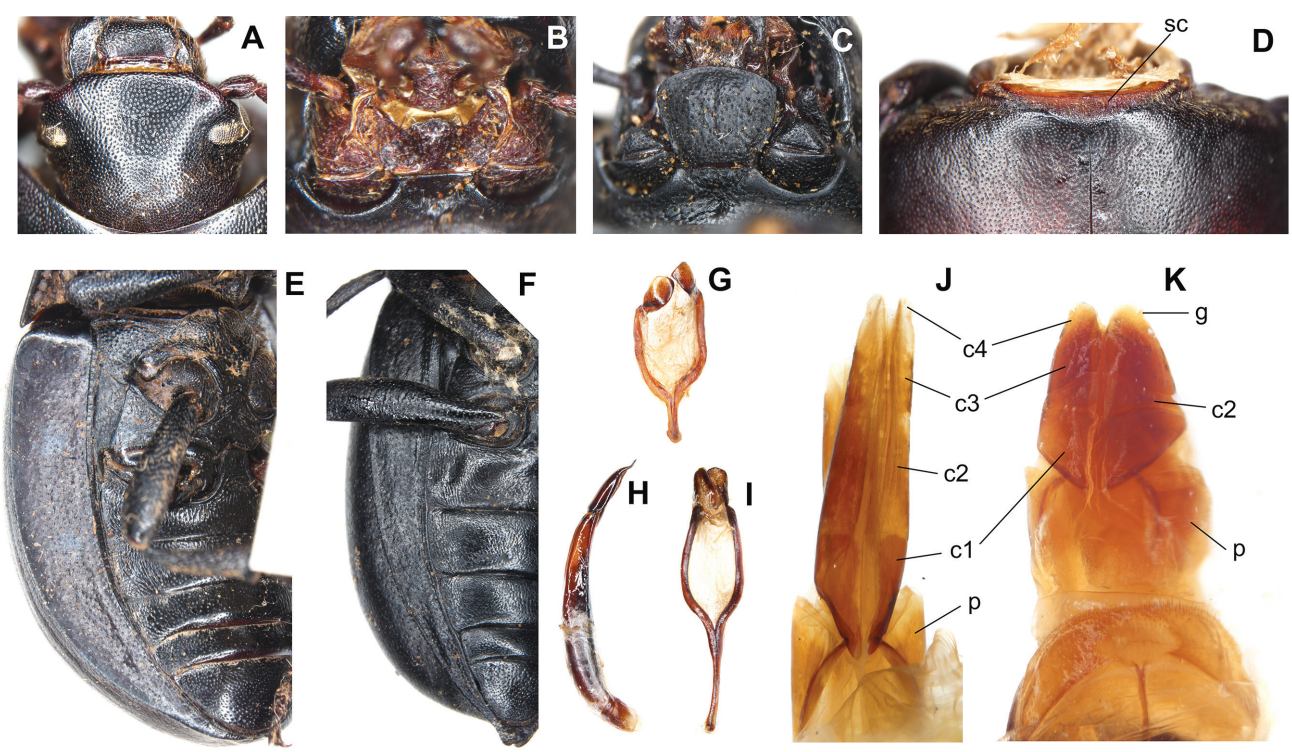

Figure 4. Morphology of selected representatives of Blaptini and Platyscelidini. (C, F) *Blaps putrida*, (A, B, D, I, J) *Oodoscelis tibialis*, and (E, G, H, K) *Platyscelis striata*. (A) Head in dorsal view, (B, C) mentum, (D) scutellum, (E, F) epipleura, (G, I) spiculum gastrale, (H) aedeagal tegmen, (J, K) ovipositor. Abbreviations: c1–4 – coxites, g – gonostylus, p – paraproct, sc – scutellum.

in these (Fig. 1), and previous analyses (Kamiński *et al*. 2021). Both tribes can be further separated by the ovipositor structure, which in Amphidorini is composed of fused apical coxites (4-lobed in Dissonomini, Fig. 2H–J).

Dissonomini is easily distinguished from Blaptini by the widened protarsi in males (Medvedev 1968, Chigray *et al*. 2020) (Fig. 2F). While this study lacked sequences of Platyscelidini, Dissonomini is morphologically separable *inter alia* by the notched epistoma (Fig. 2A). Dissonomini is also distinct from both Blaptini and Platyscelidini by their sharply keeled menta (flat in Blaptini or broadly keeled at most in Platyscelidini, Fig. 4B and C) and epipleura terminating at abdominal ventrite V (epipleura ending later in Platyscelidini and continuing to apex in Blaptini) (Figs 2E and 4E and F) (see also Egorov 2004).

Although the monophyly of Dissonomini was not tested here by molecular data, several unique morphological features strongly suggest that *Bradyus* and *Dissonomus* are linked (Figs 2, 3, Medvedev 1968): concealed scutellum (Figs. 1 and 2D), antennal shape (short, robust, with apical antennomeres forming a loose club (Fig. 2B); longer in Blaptini and Platyscelidini where the third antennomere is often also elongated,) termination of the epipleura (reaching the level of the base of fifth ventrite) (Fig. 2E), notched epistoma (Fig. 2A), configuration of the aedeagi (ventrally without clear opening for the penis) (Fig. 3C), formation of the spiculum gastrale (weakly sclerotized, U-shaped with reduced 'stem' (Fig. 3A and B); Platyscelidini and Blaptini both have strongly sclerotized spiculae with or without a long stem and large, paddle-shaped terminations of the 'arms') (Fig. 4G and I) (see also Chigray *et al*. 2020), and the structure of the ovipositor (4-lobed coxities, lack of gonostyli, and overlapping coxites 3 and 4) (Fig. 2I and J).

In conclusion, the molecular data recovered here are consistent with morphological data revealed for adult forms (Figs 1–4). The taxonomic distinctiveness of Dissonomini appears well-grounded, and its phylogenetic position regarding Platyscelidini should be investigated further (for recent treatments within Platyscelidini see Bai *et al*. 2019a, b, Bai & Ren 2019). Based on the results presented here, Dissonomini is incorporated within the borders of Blaptinae where it becomes the eighth tribe of the subfamily. The definition of Blaptinae remains unmodified (Kamiński *et al*. 2021): Adults: antennae lacking compound/stellate sensoria (except *Stenolamus* Gebien, 1920 – Kamiński *et al*. 2023); procoxal cavities externally and internally closed, intersternal membrane of abdominal ventrites 3–5 visible; paired abdominal defensive glands present, elongate, not annulated. Larvae: prolegs enlarged (adapted for digging); ninth tergite lacking urogomphi.

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