Zoomorphology (2016) 135:453–485
DOI 10.1007/s00435-016-0328-5

ORIGINAL PAPER

Toward a natural classification of opatrine darkling beetles: comparative study of female terminalia

Dariusz Iwan[1] · **Marcin Jan Kamiński**[1]

Received: 1 September 2016 / Revised: 16 September 2016 / Accepted: 19 September 2016 / Published online: 5 October 2016

Abstract The opatrine darkling beetles (Coleoptera: Tenebrionidae: Opatrini) are a worldwide radiation of ~1200 described species, with many more still awaiting discovery. This paper presents results of the first comparative morphological study of the female terminalia of this group. The structure of ovipositor and female genital tubes proved to be extremely useful for delimiting phylogenetic relationships within Opatrini. The following new lineages are recovered: *Opatrum* (basal parts of paraprocts equipped with claws constituted of baculi) and *Sclerum* (middle part of coxites soft and extended, apical lobe small and located laterally) generic complexes. Moreover, the analysis revealed that Heterotarsini and Heterocheirini share a unique vagina modification (presence of dual sclerites). Based on this observation, Heterocheirini is placed as a synonym of Heterotarsini. An additional comparative analysis of chosen external characters was performed to test hypotheses mentioned above. This investigation not only supports the conclusions derived from the female reproductive system analysis (*Opatrum* and *Sclerum* generic complexes; homogeneity of Heterotarsini and Heterocheirini), but also leads to the recovery of other presumably monophyletic groups (e.g., *Blapsitnus* generic complex). Finally, to test the explicitness of the current autapomorphy and determine the status of the whole studied group, a comparative morphological analysis of protrochanters among different tribes of Tenebrioninae was performed. All opatrine genera exhibit a unique protrochanter structure, which is characterized by the elongate base. This feature is unique for Opatrini among Tenebrioninae. Based on the above-mentioned results, the subtribal classification of the Opatrini is revised. Seven following subtribes are recognized: Ammobiina **stat. restit.**, Blapstinina **stat. restit.**, Heterotarsina (=Heterocheirini **syn. nov.**), Neopachypterina, Opatrina, Sclerina **stat. restit.** and Stizopina. Additionally, *Wolladrus* **nom. nov.** is proposed as a replacement name for *Hadrus* (Opatrini), which is a junior homonym of a dipteran genus.

Keywords Classification · Morphology · Ovipositor · Genital tubes · Darkling beetles

Introduction

Comparative morphological studies of the female terminalia have proved to be extremely useful for determining phylogenetic relationships among members of the superfamily Tenebrionoidea (e.g., Watt 1974; Tschinkel and Doyen 1980; Marcuzzi 1989; Bouchard and Yeates 2001; Iwan 2002; Banaszkiewicz 2006; Matthews and Bouchard 2008; Smith 2013; Kamiński 2015b). Twenty out of 73 adult characters used by Doyen and Tschinkel (1982) to reconstruct the phylogeny of Tenebrionidae concerned the ovipositor and female genital tubes. Despite this fact, the morphology of these structures is often omitted by taxonomists during species descriptions and generic revisions.

According to the hitherto accepted classification, Opatrini Brullé (1832) is one of the 29 tribes within the subfamily Tenebrioninae (Bouchard et al. 2005, 2011). The

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Electronic supplementary material The online version of this article (doi:10.1007/s00435-016-0328-5) contains supplementary material, which is available to authorized users.

✉ Marcin Jan Kamiński
mkaminski@miiz.waw.pl

[1] Zoological Museum, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland

monophyly of this taxon is grounded in the unique structure of the protrochanter (for details see below) and male terminalia (Iwan 2004). Currently, over 1200 species representing 118 genera in Opatrini have been described from different biogeographic realms around the world (present estimation).

Five subtribes are currently recognized within Opatrini (Bouchard et al. 2005, 2011; Iwan and Schimrosczyk 2009; Kamiński 2015a): Heterocheirina Koch (1956) (Afrotropical, Australian, Indomalayan and Palearctic realms), Heterotarsina Blanchard (1845) (Afrotropical, Indomalayan, and Palearctic realms), Opatrina (worldwide distribution), Neopachypterina Bouchard et al. (2007) (Afrotropical, Indomalayan, and Palearctic realms) and Stizopina Lacordaire (1859) (southern Africa). The fossil record indicates that Opatrini species were already present in the Lowermost Eocene (Kirejtshuk et al. 2008). A phylogenetic analysis of this tribe has never been conducted.

There are significant gaps in accessible knowledge concerning the structure of female terminalia within Opatrini. Until now, the most comprehensive study was conducted by Marcuzzi (1987). In his paper on the Neotropical darkling beetles, he included the descriptions of ovipositors of 18 species representing the following genera: *Austrocaribius* Marcuzzi, 1954, *Blapstinus* Sturm, 1826, *Diastolinus* Mulsant & Rey, 1859, and *Trichoton* Hope, 1840. Additional information on the structure of coxites and paraprocts has been included in a few alpha-taxonomic and revisionary papers (e.g., Ferrer 2000; Kamiński 2015a). On the other hand, female genital tube morphology within Opatrini is almost entirely unknown (e.g., Tschinkel and Doyen 1980; Iwan 2008), and their significance in relation to the phylogeny of Opatrini could not be assessed.

To address this problem, the structure of the female terminalia (ovipositor, vagina, bursa copulatrix, and spermatheca) in most of the extant opatrine genera is investigated. In order to test the homology hypotheses formed during this analysis, a supporting comparative analysis of selected external morphological features (e.g., eyes, prothoraces, and legs) is performed. Moreover, to verify the status of Iwan's (2004) autapomorphy for Opatrini, a comparative analysis of protrochanter morphology using representatives of all current Tenebrioninae tribes is conducted. The classification of the opatrine darkling beetles is revised based on the obtained results.

Taxonomic history

The family-group name based on the genus *Opatrum* Fabricius, 1775, was established by Brullé (1832) as Opatroides and has been made available under Art. 11.7.2 of the International Code of Zoological Nomenclature (ICZN 1999).

In 1956, Koch performed the first comprehensive revision of this phylogenetic group. Taking into account the information provided by previous authors (e.g., Reichardt 1936; Gebien 1938; Español 1945), he interpreted this taxonomic entity as a subfamily and designated the following tribes: Dendarini Mulsant and Rey (1854), Heterocheirini, Heterotarsini, Leichenini Mulsant (1854), Litoborini Antoine (1941), Loensini Koch (1956), Melanimini Seidlitz (1894), Oncotini Koch (1953), Opatrini, Pedinini Eschscholtz (1829), Platynotini Mulsant and Rey (1853) and Pythiopini Koch (1953). Moreover, within Opatrini he recognized five subtribes: Opatrina, Stenolamina Koch (1956), Stizopina, Emmallina Koch (1956) and Sclerina Lacordaire (1859). In his paper, Koch did not provide any morphological concepts or a clear description of the characters that delimit Opatrinae.

A similar concept of Opatrinae was presented by Medvedev (1968), who summarized the information provided by previous authors (e.g., Reichardt 1936; Gebien 1938; Español 1945; Koch 1953, 1955, 1956) and proposed the following morphological definition for the subfamily: (1) anterior margin of clypeus emarginated, (2) eyes narrow, (3) antenna with 11 segments, (4) submentum small, (5) mesotrochantin present, (6) epimeron of mesothorax protruding to mesocoxal cavities, (7) wing venation of cantharoid type, and (8) last abdominal sternites with intersegmental membrane exposed.

Doyen (1972) presented a new classification of Tenebrionidae. Based on the structure of the abdominal sternites, aedeagal tegmen and defensive glands he divided this family into four subfamilies: Allecullinae, Lagriinae, Nilioninae and Tenebrioninae. However, he did not propose a new classification for the taxa previously classified as Opatrinae. Therefore, presumably the taxonomic rank of this entity was decreased, while Koch's (1956) subtribes were merged with their parental tribes (see Bouchard et al. 2005, 2011).

Watt (1974) revised the above-mentioned classification concept. He defined Opatrinae sensu Koch (1956) as Blapimorpha sensu Skopin (1964) with a deeply emarginated clypeus in imagines. He included this group within the subfamily Tenebrioninae.

In 1982, Tschinkel and Doyen conducted the only morphologically based cladistic analysis of the family Tenebrionidae to date. One of the analyzed operational taxonomic units (OTUs) was "Opatrini". According to the provided description, this taxon was composed of Gebien's (1938) tribes: Eleodiini Blaisdell (1909), Helopinini Lacordaire (1859), Opatrini and Pedinini. The performed analysis revealed a close relationship of this OTU with Ulomini. Tschinkel and Doyen did not give this clade any formal taxonomic rank and referred to it as the "opatrinae lineage". This concept was adopted by some subsequent authors (e.g., Aalbu and Triplehorn 1985).

Iwan (2001, 2004) performed a morphological comparative study of the protrochanter and male terminalia within Opatrinae sensu Medvedev (1968). Based on his results he divided this subfamily into two groups: (1) Opatrini, with elongate base of trochanter (opatrinoid type), aedeagus with ventral apophyses, well-developed inflexed alae of basal part of tegmen; (2) Pedinini, with reduced trochanter (pedinoid type), aedeagus without ventral apophyses, and narrow inflexed alae of basal part of tegmen. Because Iwan (2001, 2004) did not extend his analysis to the other tribes of Tenebrionidae, he could not evaluate the appropriateness of maintaining Opatrinae at the subfamily level. However, he stated that the characters used to group Opatrini and Pedinini together (e.g., deeply emarginated clypeus) display too much variation to be treated as autapomorphies.

This assumption was supported by more recent studies which focused on the taxonomy of particular genera among Opatrini (e.g., Kamiński 2015c). Furthermore, the results of a phylogenetic analysis based on molecular markers suggest that Opatrini and Pedinini occupy different places on the Tenebrionidae phylogenetic tree (Kergoat et al. 2014).

Additionally to the above-mentioned classification problems, with a few exceptions (e.g., Schawaller 2013; Iwan and Matthews 2015; Iwan and Schimrosczyk 2015), Opatrini suffers from a lack of systematic studies concerning particular genera or generic groups. Presumably, the main reason why most of the researchers working on Opatrini focus only on the alpha-taxonomy of this group is the high level of diversity of the known species (Iwan et al. 2010, 2011). Comprehensive analyses of any kind were probably inhibited by the lack of clearly distinguished evolutionary lineages within the subtribe Opatrina, which currently contains nearly 75 % of the known genera in the tribe.

Materials and methods

Terminology

Morphological terminology follows Tschinkel and Doyen (1980) and Matthews et al. (2010). Conveniently, the cuticular structures of the female reproductive system are divided into the ovipositor and the female genital tube with associated structures.

Ovipositor (Fig. 1)

The ovipositor is constituted of two pairs of sclerites—the apical coxites and the proximal paraprocts. The coxites are usually subdivided into four lobes. The proximal lobes (valvifers) are stiffened by a pair of rod-like baculi, while the terminal lobes bear the gonostyli. The latter structure is often equipped with sensory setae. The paraprocts are usually aligned with the coxites and carry a baculus. The ovipositor bears the vulva at its posterior end. The dorsal portion of the ovipositor is partially covered by the proctiger, which carries the anus at its posterior margin.

Female genital tube (Fig. 2)

The female genital tube consists of two sequentially arranged structures: the vagina and bursa copulatrix. The vagina is treated here as the most distal part of the female genital tube (viewing from the scutellum), which transform into the bursa copulatrix at the level of the basal tip of paraprocts. Therefore, according to some other authors like Tschinkel and Doyen (1980) and Matthews et al. (2010), the structure referred here as the bursa copulatrix would be considered to be the anterior part of the vagina.

In some cases, genital tubes might have partial sclerotizations. The oviduct usually opens into the bursa copularix in the basal half of this structure. The spermatheca and the spermathecal accessory gland are located at the proximal apex of the bursa copulatrix.

Material

This study is based on material from the following collections: Hungarian Natural History Museum, Budapest, Hungary (HNMN); Instituto Argentino de Investigaciones de Zonas Áridas Mendoza, Argentina (IADIZA); Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland (MIZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (RBINS); Ditsong National Museum of Natural History in Pretoria, South Africa (TMNH); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Zoological Museum, Academy of Sciences, Sankt Petersburg, Russia (ZMAS).

In order to analyze the morphology of female terminalia, 177 adult females, representing 105 species of 102 genera of Opatrini, were dissected (Table 1). To confront the hypotheses obtained during these considerations with the ones based on external characters, the morphology of the above-mentioned females and separately that of select male specimens was studied. Label data for voucher specimens are provided in Appendix 1 in Supplementary material.

To test the status of Iwan's (2004) autapomorphy for Opatrini, a comparative analysis of protrochanter morphology within the Tenebrioninae was performed. The representatives of all known tribes of this subfamily were investigated (see Bouchard et al. 2011).

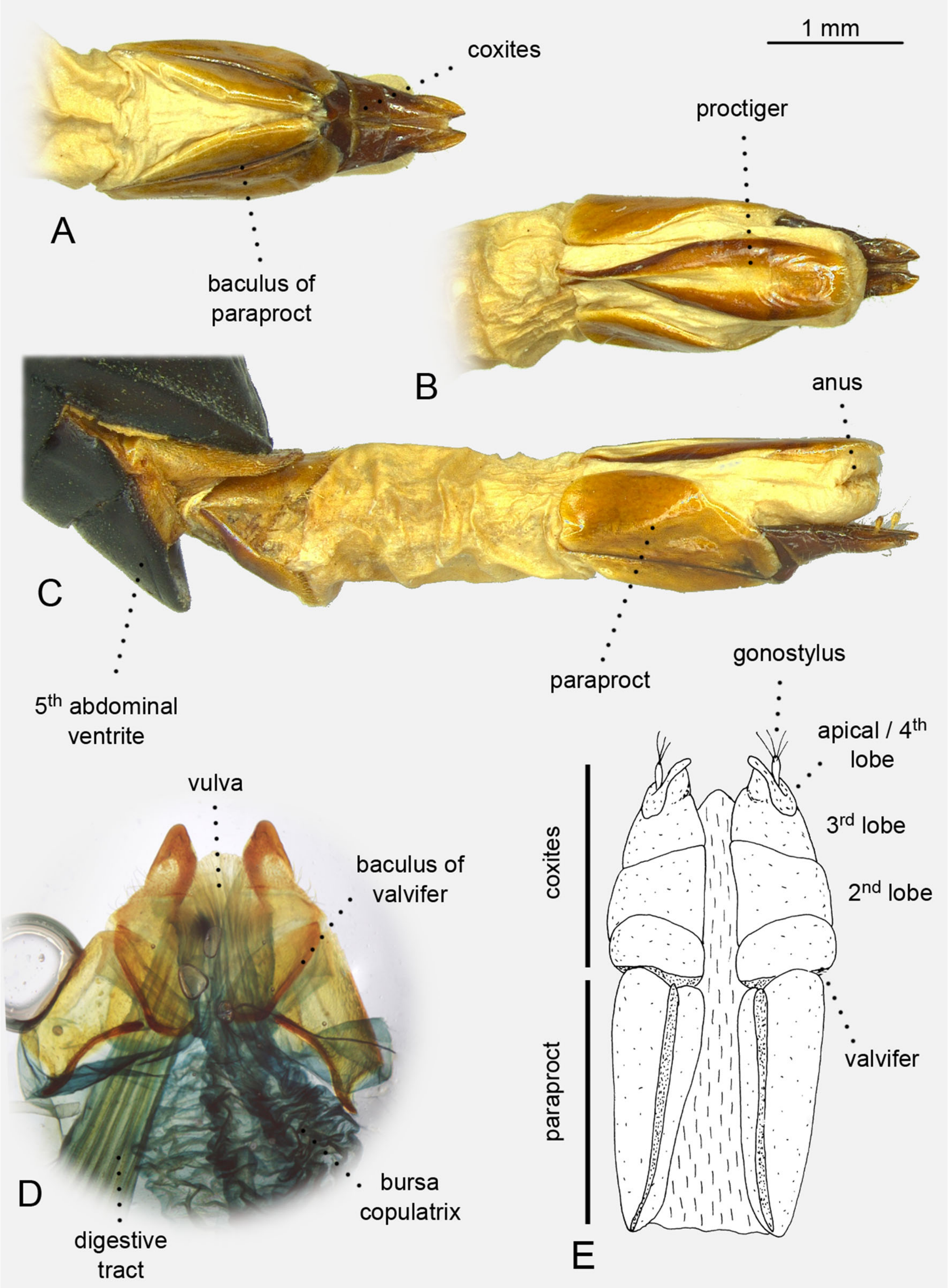

Fig. 1 Morphology of the ovipositor of chosen Tenebrionidae representatives. Dorsal (**b**), lateral (**c**) and ventral (**a**, **d**, **e**) views. *Zidalus latipes*, Pedinini (**a**–**c**), *Socotropatrum*, Opatrini (**d**) and *Sellio tibidens*, Opatrini (**e**)

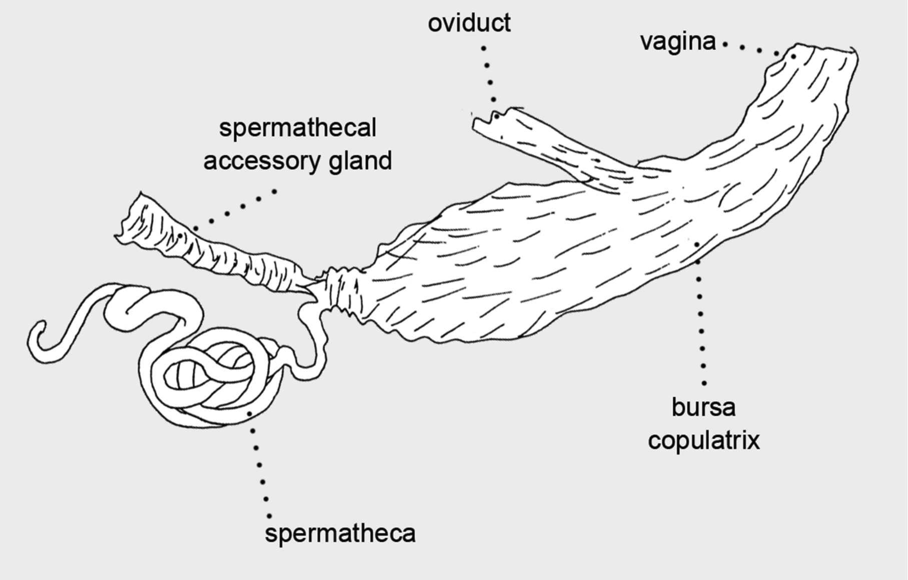

Fig. 2 Morphology of the genital tube of Tenebrionidae (*Sobas australis*, Opatrini)

Methods

In order to isolate the female terminalia, the abdomens of specimens to be studied were removed and cleared overnight in 10 % potassium hydroxide. After that, the reproductive systems were dissected by manipulating with entomological needles and scalpels. To increase the visibility of certain features, the samples were stained with Chlorazol Black dissolved in glycerin. The dissected structures were then transferred to a drop of glycerin on a microscope slide for drawing. In order to sustain the original structure of the studied body parts, cover slips were not used. The analyzed material was preserved in microtubes filled with glycerin and pinned beneath the specimens. Due to the condition of the studied material (dried, museum specimens), the ovary structure was not investigated.

Photographs were taken using a Canon 1000D body and Canon EF 100 mm f/2.8 Macro USM lens. Drawings and measurements were made using a dissecting microscope (Olympus SZH10) with attached camera lucida. SEM images were acquired with a Hitachi S-3400 N in the Museum and Institute of Zoology (Polish Academy of Sciences).

Body length of the studied females was measured from the anterior margin of the labrum to the elytral apex. Total coxite length was recorded by taking measurements from the apex of the 4th lobe of the coxite to the apical part of the paraproct (baculus). The following abbreviations are used: total length of coxites (tc); breadth (bc1); and length (lc1) of the valvifer.

The R language and environment was employed for morphometric analyses (R Core Team 2013). Plots were generated with the ‘ggplot2’ package (Wickham 2010).

Results

The results are presented using the hitherto accepted classification proposed by Bouchard et al. (2005, 2011), with an update concerning Stizopina suggested by Iwan and Schimrosczyk (2009) (see Table 1).

Female terminalia

Female terminalia morphology varied across the studied taxa. The modifications concern all of the analyzed structures, i.e., ovipositor and genital tubes (Table 1).

Morphometric data

Ovipositor length across the studied species increases linearly with the total body size (Fig. 3a). However, in a few cases, reductions of certain parts of the first variable are observed (e.g., due to the different number of lobes of coxites). Therefore, the longest ovipositor is reported for *Heterotarsus* (Fig. 3a).

The highest value of tc/2bc index is reported for *Dilamus* (Opatrina), while the lowest is for *Stizopus* of Stizopina (Fig. 3b; Table 1). The coxites of the latter genus are strongly reduced and composed only of the strongly

Table 1 Female terminalia morphology of the studied Opatrini genera

Subtribe	Morphometrics				
Studied genus	b.l. (mm)	o.l. (mm)	tc/2bc	bc1/lc1	Egg size (mm)
Heterocheirina (3/3)					
Diphyrrhynchus Fairmaire, 1849	5.0	1.2	0.9	1.9	–
Heterocheira Lacordaire, 1859	7.4	1.1	0.8	3.6	–
Scymena Pascoe, 1866	6.9	1.3	1.0	2.1	–
Heterotarsina (1/1)					
Heterotarsus Latreille, 1829	14.0	3.1	0.8	2.2	1.9 × 1.2
Neopachypterina (1/1[a])					
Neopachypterus Bouchard et al. 2007	10.5	1.6	0.9	6.8	–
Opatrina (80/90)					
Aconobius Casey, 1895	6.1	0.7	0.8	2.6	–
Adavius Mulsant & Rey, 1859	9.6	2.2	0.8	2.0	–
Amblysphagus Fairmaire, 1896	9.5	1.3	1.0	7.0	–
Ammidium Erichson, 1843	5.3	0.7	0.6	3.4	–
Ammobius Guérin-Méneville, 1844	2.8	1.1	0.9	2.3	–
Ammodonus Mulsant & Rey, 1859	5.5	0.4	0.8	2.5	–
Amphithrixoides Bouchard & Löbl, 2008	3.6	0.4	0.7	2.8	–
Anatrum Reichardt, 1936	11.5	1.1	0.6	2.6	–
Asiocaedius Medvedev & Nepesova, 1985	6.9	0.6	0.8	2.0	–
Blapstinus Sturm, 1826	5.8	0.5	0.7	2.2	–
Brachyidium Fairmaire, 1883	7.2	1.6	1.0	2.0	–
Bycrea Pascoe, 1868	7.2	1.2	0.7	2.7	–
Caediexis Lebedev, 1932	4.4	0.4	0.7	3.0	–
Caedius Mulsant & Rey, 1859	4.1	0.6	0.6	3.5	–
Cenophorus Mulsant & Rey, 1859	6.1	0.7	0.7	3.5	–
Clitobius Mulsant & Rey, 1859	6.5	1.0	0.6	2.6	–
Coeloecetes Blair, 1929	7.9	0.6	0.7	2.5	1.6 × 1.1
Conibiosoma Casey, 1890	3.8	0.5	0.9	1.6	–
Conibius LeConte, 1851	7.3	1.1	0.8	3.0	–
Corinta Koch, 1950	3.0	0.4	0.7	3.0	–
Cornopterus Koch, 1950	4.5	0.6	0.7	2.5	–
Ctesicles Champion 1896	10.3	0.7	0.8	2.8	–
Cybotus Casey, 1890	4.8	0.8	0.8	2.6	–
Cyptus Gerstaecker, 1871	8.8	1.4	0.8	2.8	–
Diastolinus Mulsant & Rey, 1859	10.0	1.2	0.9	2.7	–
Dilamus Jacquelin du Val, 1861	2.7	0.9	1.4	2.3	–
Emmallus Erichson, 1843	13.3	1.4	0.9	2.3	–
Ephalus LeConte, 1862	8.2	1.3	0.9	2.6	–
Eumylada Reitter, 1904	10.0	1.0	0.6	2.6	–
Eurycaulus Fairmaire, 1868	5.0	0.7	0.7	2.8	–
Falsammidium Koch, 1960	7.7	0.9	0.7	1.8	–
Falsocaedius Español, 1943	5.2	0.6	0.7	2.3	–
Falsolobodera Kaszab, 1967	6.6	0.8	0.7	3.0	–
Freyula Koch, 1959	3.2	0.3	0.6	2.3	–
Gonocephalum Chevrolat, 1849	10.2	1.4	0.7	3.0	2.0 × 1.2
Helenomelas Ardoin, 1972	9.5	2.0	0.6	3.0	–
Mateuina Español, 1944	9.5	2.0	0.9	3.1	–
Mecysmus Horn, 1870	7.3	1.2	1.2	2.5	–

Table 1 continued

Subtribe	Morphometrics				
Studied genus	b.l. (mm)	o.l. (mm)	tc/2bc	bc1/lc1	Egg size (mm)
Melanesthes Dejean, 1833	11.6	1.6	0.7	2.8	–
Melanocoma Wollaston, 1867	14.5	2.2	0.8	2.2	–
Mesomorphus Seidlitz, 1893	7.0	1.1	0.6	2.0	–
Messoricolum Koch, 1960	4.3	0.5	0.7	2.2	–
Moragacinella Español, 1954	11.4	1.9	0.7	2.5	–
Myladina Reitter, 1889	9.5	1.1	0.6	2.3	–
Nesocaedius Kolbe, 1915	7.2	0.8	0.8	3.0	–
Nocibiotes Casey, 1895	6.1	1.3	0.6	3.2	–
Notibius LeConte, 1851	5.2	0.7	0.8	3.7	–
Opatroides Brullé, 1832	8.3	1.3	0.9	1.6	–
Opatrum Fabricius, 1775	8.0	1.2	0.7	3.2	–
Penthicinus Reitter, 1896	7.2	1.0	0.7	2.2	–
Penthicus Faldermann, 1836	12.2	2.1	0.8	2.0	–
Phelopatrum Marseul, 1876	12.4	1.6	0.6	2.3	–
Platylus Mulsant & Rey, 1859	11.1	1.2	1.1	2.5	–
Platyprocnemis Español & Lindberg, 1962	10.2	2.1	0.7	2.8	–
Platysum Mulsant & Rey, 1859	2.9	0.5	0.7	3.0	–
Plesioderes Mulsant & Rey, 1860	5.1	0.9	0.6	3.3	–
Polycoelogastridion Reichardt, 1936	5.7	0.5	0.6	3.2	–
Prodilamus Ardoin, 1969	4.7	0.8	1.0	3.3	–
Proscheimus Desbrochers des Loges, 1881	3.7	0.7	0.8	2.0	–
Psammestus Reichardt, 1936	4.2	0.7	0.6	3.2	–
Pseudephalus Casey, 1924	6.2	0.7	0.8	2.6	–
Pseudolamus Fairmaire, 1874	4.7	1.0	0.9	6.9	–
Pseudoleichenum Ardoin, 1972	5.8	1.0	0.8	1.6	–
Raynalius Chatanay, 1912	7.5	0.9	0.7	3.5	–
Reichardtiellina Kaszab, 1982	14.7	1.7	0.6	3.0	–
Scleropatroides Löbl & Merkl, 2003	6.7	0.7	0.9	2.5	–
Scleropatrum Reitter, 1887	11.1	1.7	0.7	3.4	–
Sclerum Dejan, 1834	6.6	0.5	0.8	3.6	–
Sellio Mulsant & Rey, 1859	7.7	1.6	1.1	1.6	–
Sinorus Mulsant & Revelière, 1860	9.1	1.1	0.7	4.0	–
Sobas Pascoe, 1863	4.4	0.7	0.7	2.6	–
Socotropatrum Koch, 1970	9.6	1.1	0.6	2.3	–
Tarphiophasis Wollaston, 1877	8.8	1.2	0.7	1.4	–
Tonibius Casey, 1895	5.7	0.8	0.7	3.6	–
Trichosternum Wollaston, 1861	10.2	1.2	0.7	1.4	
Trichoton Hope, 1840	11.1	1.2	0.8	2.6	–
Trigonopoda Gebien, 1914	7.2	0.9	0.6	4.2	–
Ulus Horn, 1870	11.4	2.1	0.7	2.1	–
Weisea Semenov, 1890	6.6	1.1	0.7	2.8	–
Wolladrus **nom. nov.**	11.6	2.0	0.8	2.7	–
Stizopina (18/22)					
Adoryacus Koch, 1963	8.8	0.5	0.9	3.2	–
Amathobius Gebien, 1920	9.4	0.4	0.6	3.1	–
Blacodatus Koch, 1963	5.2	0.8	0.7	3.1	–
Blenosia Laporte de Castelnau, 1840	6.1	0.3	0.7	3.0	–

Table 1 continued

Subtribe	Morphometrics				
Studied genus	b.l. (mm)	o.l. (mm)	tc/2bc	bc1/lc1	Egg size (mm)
Eichleria Kamiński, 2015	6.7	0.5	0.9	3.2	–
Ennychiatus Koch, 1963	9.4	0.5	0.7	2.8	–
Eremostibes Koch, 1963	7.2	1.4	0.7	2.8	–
Helibatus Mulsant et Rey, 1859	6.7	0.5	0.7	2.5	–
Luebbertia Koch, 1963	6.7	1.0	0.8	3.9	–
Namazopus Koch, 1963	8.3	0.4	0.7	1.6	–
Parastizopus Gebien, 1938	20.0	2.0	0.7	2.0	–
Periloma Gebien, 1938	5.0	0.9	0.7	6.0	1.6 × 0.9
Planostibes Gemminger et Harold, 1870	6.2	0.4	0.8	2.5	–
Psammogaster Koch, 1953	4.1	0.6	0.8	3.5	–
Sphaerostibes Koch, 1963	3.1	0.4	0.7	3.0	–
Stizopus Erichson, 1843	10.1	0.1	0.4	3.5	–
Sulpius Fairmaire, 1906	9.3	1.0	0.8	2.3	–
Syntyphlus Koch, 1953	2.5	0.1	0.5	3.0	–

Subtribe	Ovipositor								Genital tube			
Studied genus	1	2	3	4	5	6	7	8	9	10	11	12
Heterocheirina (3/3)												
Diphyrrhynchus Fairmaire, 1849	1	2	0	0	0	0	0	0	1	0	0	3
Heterocheira Lacordaire, 1859	1	4	0	0	0	0	0	0	1	0	0	3
Scymena Pascoe, 1866	0	2	0	0	1	0	0	0	1	0	0	3
Heterotarsina (1/1)												
Heterotarsus Latreille, 1829	1	3	0	0	0	0	0	0	1	0	0	1
Neopachypterina (1/1[a])												
Neopachypterus Bouchard et al. 2007	1	4	0	0	0	1	0	1	0	1	0	1
Opatrina (80/90)												
Aconobius Casey, 1895	1	4	0	0	0	0	0	1	0	0	0	1
Adavius Mulsant & Rey, 1859	0	3	1	0	0	0	0	0	0	0	0	1
Amblysphagus Fairmaire, 1896	1	4	0	0	0	1	0	1	0	1	0	1
Ammidium Erichson, 1843	1	4	0	0	0	0	0	0	0	0	0	1
Ammobius Guérin-Méneville, 1844	1	3	0	0	0	0	0	0	0	0	0	2
Ammodonus Mulsant & Rey, 1859	0	2	0	0	0	0	0	0	0	0	0	2
Amphithrixoides Bouchard & Löbl, 2008	1	3	0	0	0	0	0	0	0	1	0	1
Anatrum Reichardt, 1936	1	3	0	0	0	0	1	0	0	0	0	1
Asiocaedius Medvedev & Nepesova, 1985	0	2	0	0	0	0	0	0	0	0	0	1
Blapstinus Sturm, 1826	1	4	1	0	0	0	0	1	0	0	0	1
Brachyidium Fairmaire, 1883	0	3	0	0	0	0	0	0	0	1	0	1
Bycrea Pascoe, 1868	1	4	0	0	0	0	0	0	0	0	0	1
Caediexis Lebedev, 1932	1	4	0	0	0	0	0	0	0	0	0	1
Caedius Mulsant & Rey, 1859	0	4	0	0	0	0	0	0	0	1	0	2
Cenophorus Mulsant & Rey, 1859	1	4	1	0	0	0	0	0	0	1	0	1
Clitobius Mulsant & Rey, 1859	1	4	0	0	0	0	0	0	0	0	0	1
Coeloecetes Blair, 1929	0	2	0	0	0	0	0	0	0	0	0	1
Conibiosoma Casey, 1890	1	4	0	0	0	0	0	0	0	0	0	1
Conibius LeConte, 1851	1	4	0	0	0	0	0	0	0	0	0	1
Corinta Koch, 1950	1	4	0	0	0	0	0	0	0	0	0	1
Cornopterus Koch, 1950	0	4	0	0	0	0	0	0	0	0	0	1

Table 1 continued

Subtribe	Ovipositor								Genital tube			
Studied genus	1	2	3	4	5	6	7	8	9	10	11	12
Ctesicles Champion 1896	1	4	1	0	0	0	0	1	0	0	0	1
Cybotus Casey, 1890	1	4	0	0	0	0	0	0	0	0	0	0
Cyptus Gerstaecker, 1871	0	4	0	0	0	0	0	0	0	0	0	1
Diastolinus Mulsant & Rey, 1859	1	4	1	0	0	0	0	1	0	0	0	1
Dilamus Jacquelin du Val, 1861	1	4	0	0	0	0	0	0	0	0	0	1
Emmallus Erichson, 1843	1	4	0	0	0	0	0	0	0	0	0	1
Ephalus LeConte, 1862	0	3	0	0	0	0	0	0	0	0	0	1
Eumylada Reitter, 1904	1	3	0	0	0	0	1	0	0	0	0	1
Eurycaulus Fairmaire, 1868	1	3	0	0	0	0	0	0	0	0	0	2
Falsammidium Koch, 1960	1	3	0	0	0	0	0	0	0	0	0	2
Falsocaedius Español, 1943	1	3	0	0	0	0	0	0	0	0	0	2
Falsolobodera Kaszab, 1967	1	3	0	0	0	0	1	0	0	0	0	1
Freyula Koch, 1959	1	3	0	0	0	0	0	0	0	0	0	1
Gonocephalum Chevrolat, 1849	1	4	0	0	0	0	1	0	0	0	0	1
Helenomelas Ardoin, 1972	0	4	0	0	0	0	0	0	0	0	0	1
Mateuina Español, 1944	0	4	1	0	0	0	0	0	0	0	0	1
Mecysmus Horn, 1870	1	4	1	0	0	0	0	1	0	0	0	1
Melanesthes Dejean, 1833	1	3	0	0	1	0	1	0	0	0	0	1
Melanocoma Wollaston, 1867	1	4	0	0	0	0	1	0	0	1	0	1
Mesomorphus Seidlitz, 1893	1	4	0	0	1	0	1	0	0	0	1	1
Messoricolum Koch, 1960	1	3	0	0	0	0	0	0	0	0	0	2
Moragacinella Español, 1954	1	3	0	0	0	0	0	0	0	1	0	2
Myladina Reitter, 1889	1	3	0	0	1	0	0	0	0	0	0	1
Nesocaedius Kolbe, 1915	1	4	0	0	0	0	0	0	0	0	0	1
Nocibiotes Casey, 1895	1	4	1	0	0	0	0	0	0	0	0	2
Notibius LeConte, 1851	1	4	0	0	0	0	0	0	0	0	0	1
Opatroides Brullé, 1832	1	4	0	0	0	0	1	0	0	0	0	1
Opatrum Fabricius, 1775	1	3	0	0	0	0	1	0	0	0	0	1
Penthicinus Reitter, 1896	0	2	0	0	0	0	1	0	0	0	0	1
Penthicus Faldermann, 1836	0	4	0	0	0	0	1	0	0	0	0	1
Phelopatrum Marseul, 1876	1	3	0	0	0	0	1	0	0	0	0	1
Platylus Mulsant & Rey, 1859	1	4	1	0	0	0	0	0	0	0	0	1
Platyprocnemis Español & Lindberg, 1962	1	3	0	0	0	0	0	0	0	0	0	1
Platysum Mulsant & Rey, 1859	1	3	0	0	0	0	0	0	0	0	0	2
Plesioderes Mulsant & Rey, 1860	1	3	0	0	0	0	0	0	0	0	0	1
Polycoelogastridion Reichardt, 1936	1	3	0	0	0	0	1	0	0	0	0	1
Prodilamus Ardoin, 1969	1	4	0	0	0	0	0	0	0	0	0	1
Proscheimus Desbrochers des Loges, 1881	0	3	0	0	0	0	0	0	0	?	0	?
Psammestus Reichardt, 1936	0	3	0	0	0	0	0	0	0	1	0	0
Pseudephalus Casey, 1924	0	3	0	0	0	0	0	0	0	0	0	1
Pseudolamus Fairmaire, 1874	1	4	0	0	0	1	0	1	0	1	0	1
Pseudoleichenum Ardoin, 1972	1	4	0	0	0	0	0	0	0	0	0	1
Raynalius Chatanay, 1912	0	4	0	0	0	0	0	0	0	0	0	2
Reichardtiellina Kaszab, 1982	0	3	0	0	0	0	1	0	0	0	0	1
Scleropatroides Löbl & Merkl, 2003	1	3	0	0	0	0	1	0	0	0	0	1
Scleropatrum Reitter, 1887	1	3	0	0	0	0	1	0	0	0	0	1
Sclerum Dejan, 1834	1	3	0	0	0	0	0	0	0	0	0	2

Table 1 continued

Subtribe	Ovipositor								Genital tube			
Studied genus	1	2	3	4	5	6	7	8	9	10	11	12
Sellio Mulsant & Rey, 1859	1	4	1	1	0	0	0	0	1	0	0	2
Sinorus Mulsant & Revelière, 1860	1	3	0	0	0	0	1	0	0	0	0	1
Sobas Pascoe, 1863	0	3	0	0	0	0	0	0	0	0	0	1
Socotropatrum Koch, 1970	1	3	0	0	0	0	1	0	0	0	0	1
Tarphiophasis Wollaston, 1877	1	4	0	0	0	0	0	0	0	0	0	1
Tonibius Casey, 1895	1	4	0	0	0	0	0	0	0	0	0	1
Trichosternum Wollaston, 1861	1	4	0	0	0	0	0	0	0	0	0	1
Trichoton Hope, 1840	0	4	1	0	0	0	0	0	1	0	0	1
Trigonopoda Gebien, 1914	0	3	0	0	0	0	0	0	0	1	0	1
Ulus Horn, 1870	1	4	1	0	0	0	0	0	?	0	0	2
Weisea Semenov, 1890	0	4	0	0	0	0	0	0	0	0	0	1
Wolladrus **nom. nov.**	1	4	0	0	0	0	1	0	0	0	0	0
Stizopina (18/22)												
Adoryacus Koch, 1963	1	3	0	0	1	0	0	0	0	0	0	1
Amathobius Gebien, 1920	1	4	0	0	0	0	0	0	0	0	0	1
Blacodatus Koch, 1963	1	3	0	0	0	0	0	0	0	0	0	1
Blenosia Laporte de Castelnau, 1840	1	3	0	0	0	0	0	0	0	0	0	1
Eichleria Kamiński, 2015	1	2	0	0	1	0	0	0	0	0	0	1
Ennychiatus Koch, 1963	1	4	0	0	0	0	0	0	0	0	0	1
Eremostibes Koch, 1963	1	3	0	0	0/1	0	0	0	0	0	0	1
Helibatus Mulsant et Rey, 1859	1	3	0	0	1	0	0	0	0	0	0	1
Luebbertia Koch, 1963	1	4	0	0	1	0	0	0	0	0	0	1
Namazopus Koch, 1963	1	3	0	0	1	0	0	0	0	0	0	1
Parastizopus Gebien, 1938	1	3	0	0	1	0	0	0	0	0	0	1
Periloma Gebien, 1938	1	2	0	0	1	0	0	0	0	0	0	1
Planostibes Gemminger et Harold, 1870	1	2	0	0	1	0	0	0	0	0	0	1
Psammogaster Koch, 1953	1	4	0	0	1	0	0	0	0	0	0	1
Sphaerostibes Koch, 1963	1	3	0	0	1	0	0	0	0	0	0	1
Stizopus Erichson, 1843	1	2	0	0	0	0	0	0	0	0	0	1
Sulpius Fairmaire, 1906	1	4	0	0	0	0	0	0	0	0	0	2
Syntyphlus Koch, 1953	1	1	0	0	0	0	0	0	0	0	0	1

Classification follows Bouchard et al. (2011) and Iwan and Schimrosczyk (2009). Numbers in brackets near the subtribe names indicate ratio of studied to currently known genera

Character descriptions: *Ovipositor*—(**1**) Gonostyli [0—absent; 1—present]; (**2**) Number of coxites lobes [1—single lobe; 2—two lobes; 3—three lobes; 4—four lobes present]; (**3**) Length of coxites greater than paraprocts [0—no; 1—yes]; (**4**) Baculi of paraprocts and coxites [0—arranged diagonally; 1—arranged perpendicularly]; (**5**) Paraprocts rotated laterally [0—no; 1—yes]; (**6**) Paraprocts rotated dorsolaterally [0—no; 1—yes]; (**7**) Base of paraproct hook-like [0—no; 1—yes]; (**8**) Proctiger [0—short; 1—elongated, reaching the tip of the second lobe]; Genital tube—(**9**) Vagina with sclerite [0—no; 1—yes]; (**10**) Bursa copulatrix with sclerite [0—no; 1—yes]; (**11**) Bursa copulatrix with an bifurcation of its apical part [0—no; 1—yes]; (**12**) Ducts of spermatheca [1—thin; 2—wide; 3—sac-like]; *b.l.* body length; *o.l.* ovipositor length; *tc/2bc* ratio of coxites length to double breadth of first coxite lobe; *bc1/lc1* ratio of breadth to length of first coxite lobe

[a] Neopachypterina is also represented by an extinct genus *Eupachypterus* (Kiirejtshuk, Nabozhenko & Nel, 2010)

sclerotized valvifer and gonostyli. The remaining lobes are soft and shapeless (Fig. 14a).

The highest value of bc1/lc1 index is reported for *Amblysphagus* (Opatrina), *Neopachypterus* (Neopachypterina), *Prodilamus* (Opatrina) and *Periloma* (Stizopina), while the lowest for *Tarphiophasis* and *Trichosternum* of Opatrini (Fig. 3a; Table 1). The coxites of *Amblysphagus*, *Neopachypterus* and *Prodilamus* are strongly elongate, yet simultaneously the valvifer is relatively broad (Fig. 3b). This character seems to correspond with elongation of the spiculum ventrale (Fig. 9a, b).

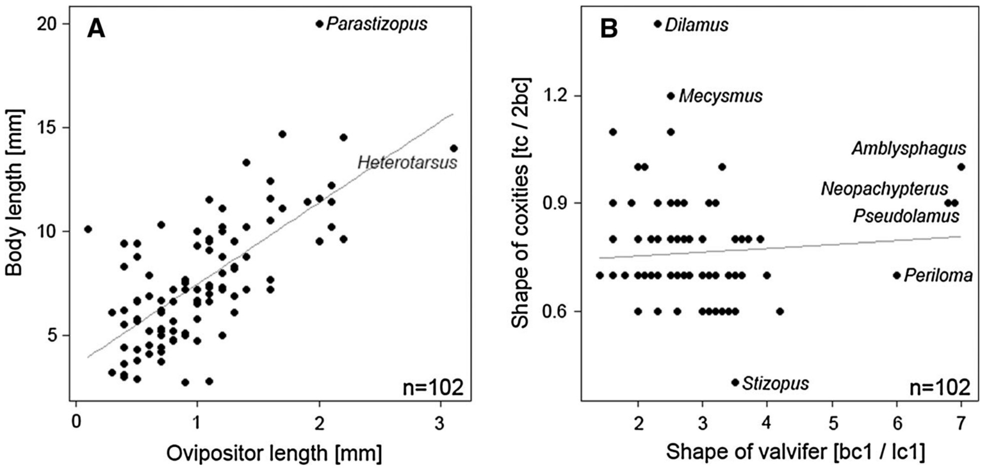

Fig. 3 Morphometric characteristics of the studied terminalia: relative lengths (**a**), and shape (**b**) of ovipositors. *tc/2bc* ratio of coxites length to double breadth of first coxite lobe, *bc1/lc1* ratio of breadth to length of first coxite lobe

Gonostyli

Gonostyli are present in 79 out of 102 of the studied genera (Table 1). These structures were observed in all of the analyzed subtribes. Most frequently the gonostyli are situated on the dorsal part of the apical coxite lobe—e.g., *Helonomelas*, *Moragacinella*, *Nocibiotes* and *Planostibes* (Figs. 7d, 13b). On the other hand, *Dilamus*, *Heterotarsus* and *Prodilamus* are the only genera with apically located gonostyli (e.g., Figs. 5e, 8a), while the gonostyli of *Diphyrrhynchus* are positioned internally (Fig. 8b).

The disappearance of gonostyli does not seem to be related to the length of the ovipositor. It is reported in the case of both very small and large species (Table 1). In most cases when the gonostyli are absent, they are replaced by a tuft of sensory setae, e.g., *Ammodonus*, *Asiocaedius*, *Scymena* (Figs. 4b, 8d).

Coxites

Only *Syntyphlus* was observed to lack the valvifer's baculi (Fig. 14b). However, in most of the studied genera, the valvifer's baculi are not aligned (e.g., Figs. 10a, 11a, 12a, 14d).

In 50 of the studied genera, four lobed coxites are present (e.g., Figs. 6a, 10d), while three lobes occur in 43 of analyzed taxa (e.g., Figs. 4a, 10a; Table 1). The coxites of the following genera are constituted of two lobes: *Ammodonus*, *Diphyrrhynchus*, *Periloma*, *Planostibes*, *Stizopus* and *Scymena* (e.g., Figs. 4b, 8b, d, 13b, d, 14a). Only *Syntyphlus* was observed to have a single lobed ovipositor (Fig. 14b). On the other hand, *Adoryacus*, *Nemanes* and *Plesioderes* are characterized by the partially fused lobes 3 and 4 (Fig. 13a, c). *Eurycaulus*, *Platysum* and *Sclerum* exhibit two fully sclerotized lobes (valvifers, and 4th lobes), and a soft lobe between them (Fig. 12a).

The highest variability concerning the number of visible lobes (1, 2, 3, 4 lobes) was observed in Stizopina, followed by Opatrina (2, 3, 4 lobes) and Heterocheirina (2, 4 lobes). Within the monogeneric subtribes Heterotarsina (Fig. 8a) and Neopachypterina (Fig. 9b), three and four lobed coxites are present, respectively.

In case of *Dilamus* and *Prodilamus*, all lobes of a single coxite are aligned (Fig. 5e). The second and third lobes of *Amblysphagus*, *Neopachypterus* and *Pseudolamus* are elongate (Fig. 9). Moreover, all of these taxa share a similar structure of the valvifers. Apical coxite lobes are strongly sclerotized and elongate in the following genera: *Adoryacus*, *Diphyrrhynchus*, *Nemanes*, *Planostibes*, *Periloma*, *Proscheimus* and *Scymena* (e.g., Figs. 8d, 13a, d).

Paraprocts

Paraproct length is variable across the studied taxa. In approximately 90 % of the studied taxa the length of this morphological structure is greater than the length of the combined coxite lobes (Table 1). In all analyzed specimens, the paraprocts are equipped with baculi, which in most cases are at an obtuse angle relative to each other.

In most of the studied taxa, the paraprocts are situated proximally to the coxites and are in contact with the valvifers along their whole apical surface (e.g., Figs. 6b, 7e, 8b). However, three types of deviation from this configuration can be observed: (1) lateral rotation of paraprocts, (2) laterodorsal rotation of paraprocts, and (3) shape modification. The common feature of all these transitions is that the paraprocts shield some/all of the coxites.

The first type of modification is present in the following genera of Stizopina: *Adoryacus*, *Eichleria*, *Helibatus*, *Namazopus*, *Nemanes*, *Periloma* and *Planostibes* (e.g., Fig. 13a–c). On the other hand, a similar structure of paraprocts can be found in *Scymena* (Fig. 8d). However, in

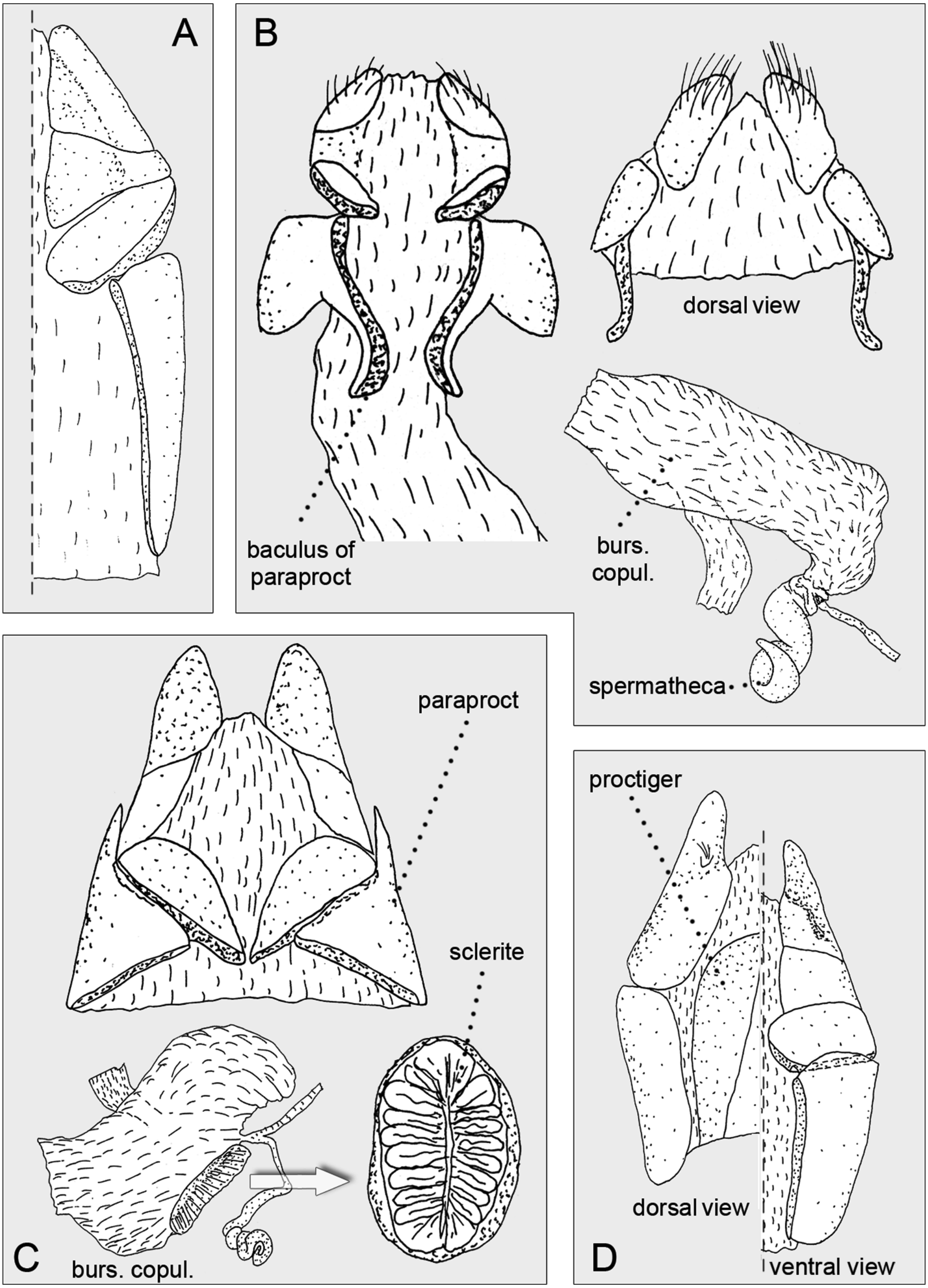

Fig. 4 Morphology of the ovipositor (**a–d**) and genital tube (**b**, **c**) of Ammobiina **stat. restit**. *Adavius nodieri* (**a**), *Ammodonus dermestiformis* (**b**), *Amphithrixoides peyerimhoffi* (**c**) and *Brachyidium demeyeri* (**d**)

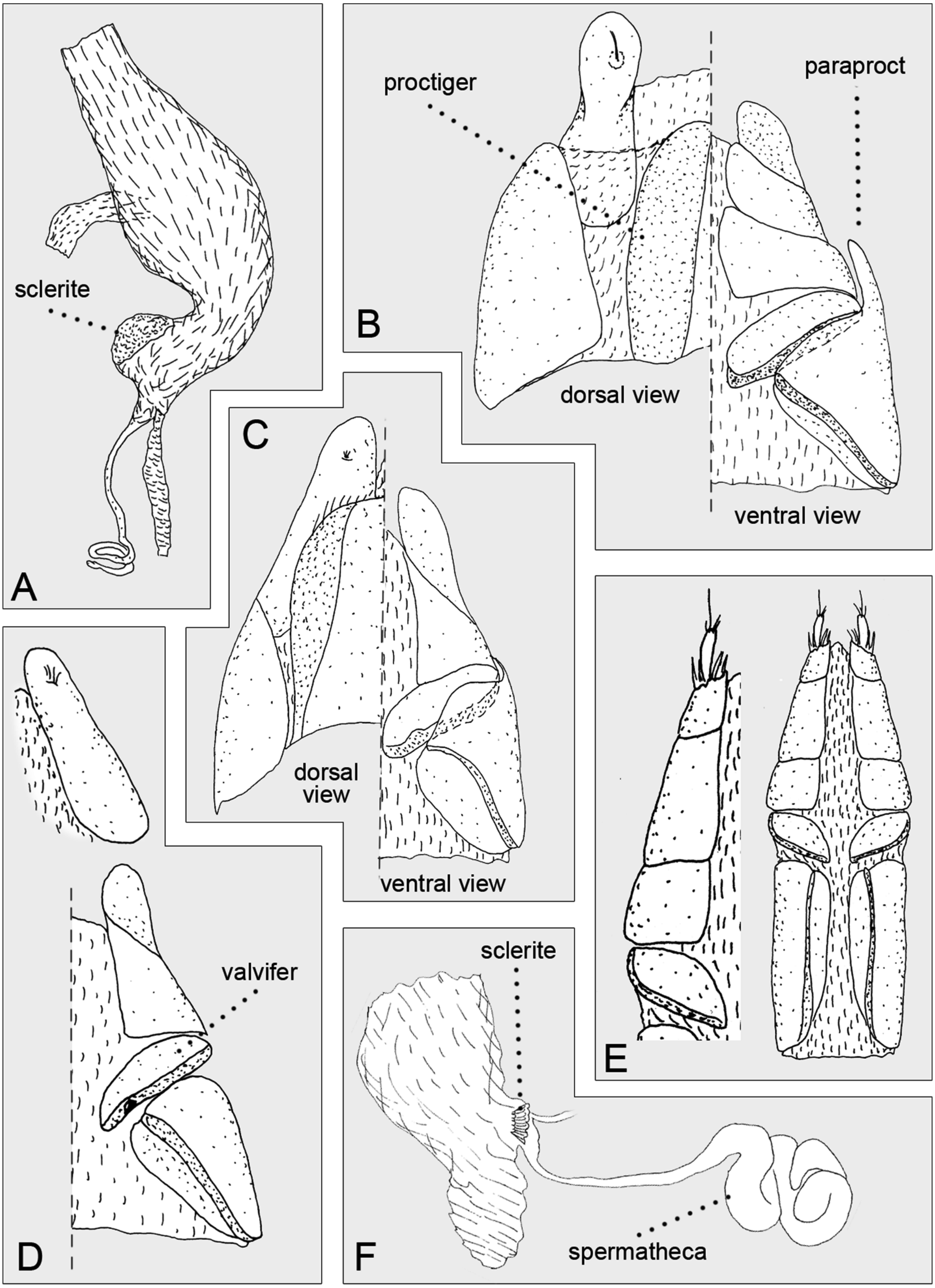

Fig. 5 Morphology of the ovipositor (**b–e**) and genital tube (**a**, **f**) of Ammobiina **stat. restit**. *Cornopterus wykehami* (**a**), *Cyptus scabrosus* (**b**), *Pseudephallus brevicornis* (**c**), *Ephalus latimanus* (**d**), *Dilamus rufipes* (**e**) and *Trigonopoda bengalensis* (**f**)

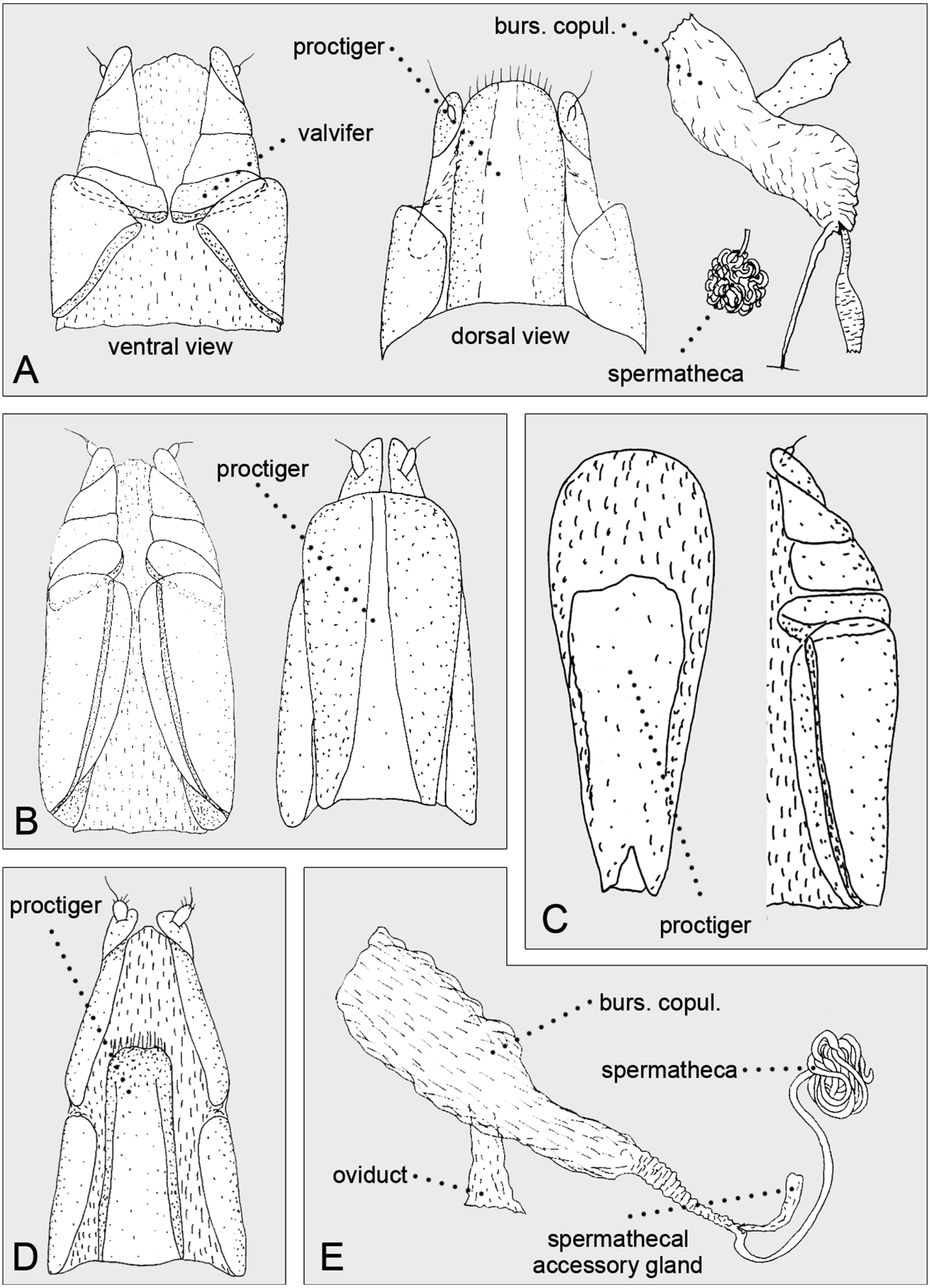

Fig. 6 Morphology of the ovipositor (**a–d**) and genital tube (**a**, **e**) of Blapstinina **stat. restit**. *Aconobius nigripes* (**a**), *Blapstinus dilatatus* (**b**), *Diastolinus perforatus* (**c**), *Mecysmus angustus* (**d**) and *Platylus dilatatus* (**e**)

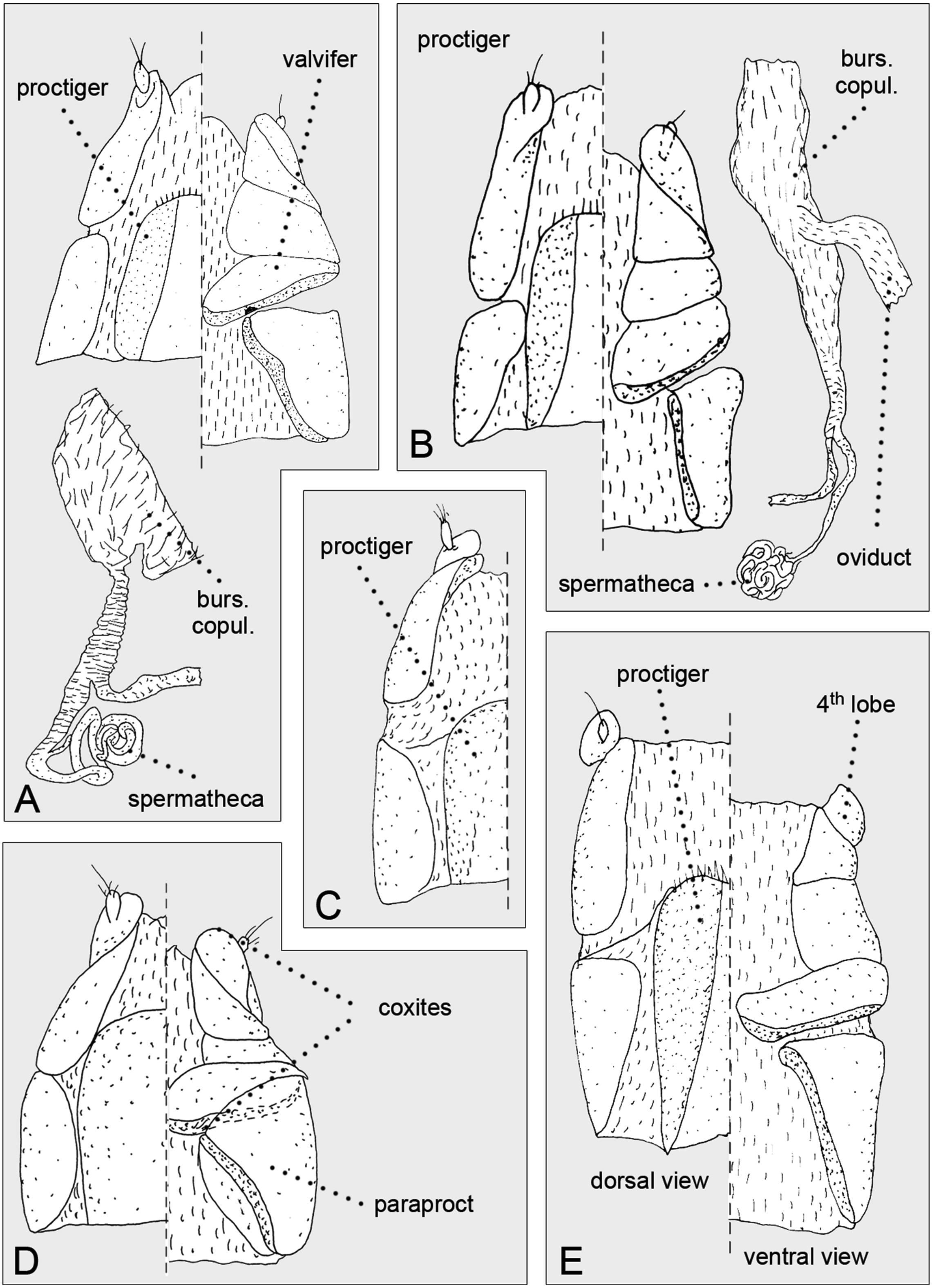

Fig. 7 Morphology of the ovipositor (**a–e**) and genital tube (**a**, **b**) of Blapstinina **stat. restit**. *Bycrea villosa* (**a**), *Conibiosoma elongatum* (**b**), *Tonibius sulcatus* (**c**), *Nocibiotes granulatus* (**d**) and *Cybotus estriatus* (**e**)

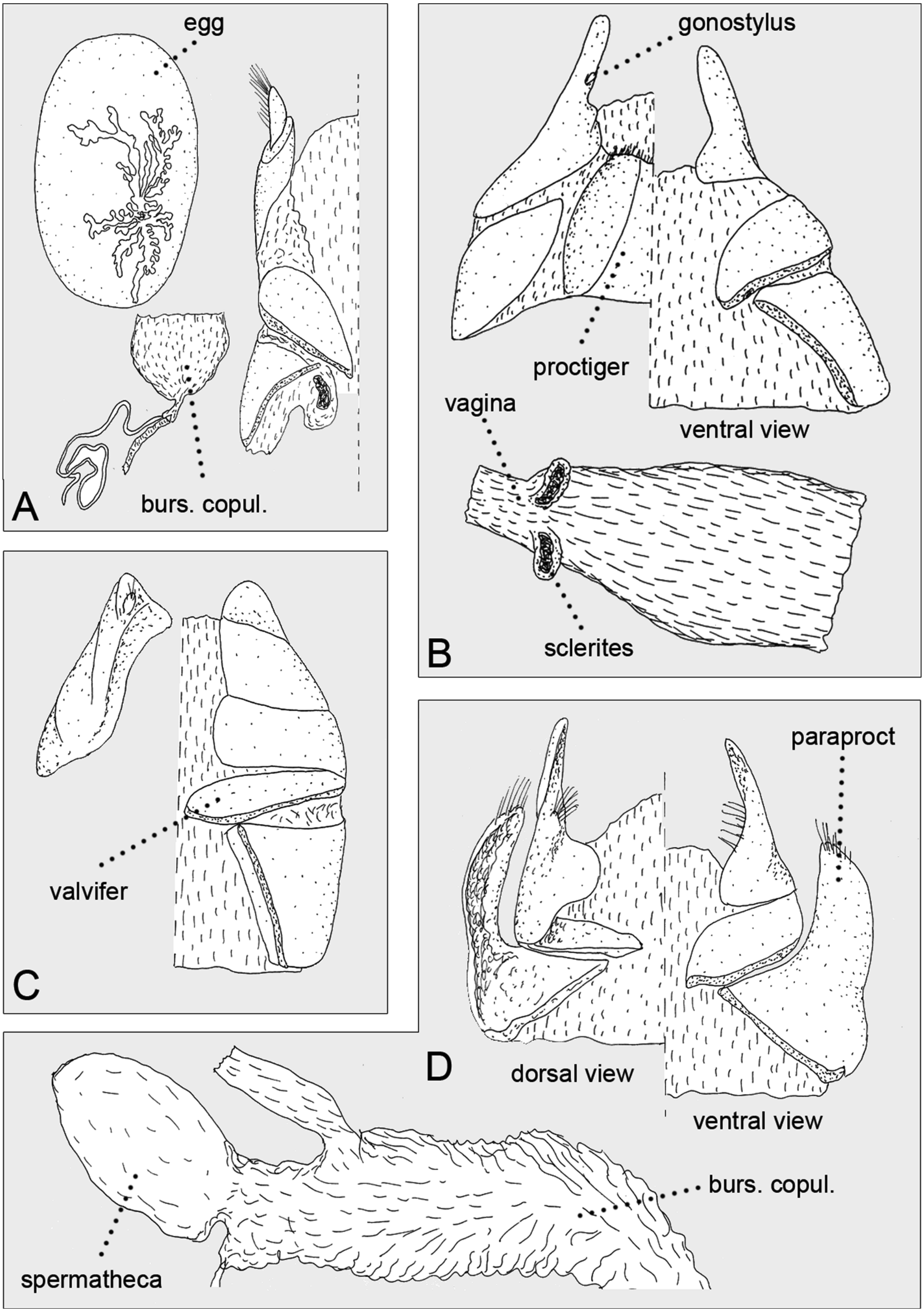

Fig. 8 Morphology of the ovipositor (**a**–**d**), genital tube (**a**, **b**, **d**) and egg (**a**) of Heterotarsina **sens. nov**. *Heterotarsus inflatus* (**a**), *Diphyrrhynchus chalceus* (**b**), *Heterocheira australis* (**c**) and *Scymena variabilis* (**d**)

the latter case, the baculi of valvifers and paraprocts are not fully aligned. Moreover, in *Scymena*, the apically extended parts of the paraprocts contain a tuft of setae. Within Opatrini, a similar rotation of the paraprocts occurs in the following genera: *Melanesthes*, *Myladina*, *Reichardtiellina* (e.g., Fig. 10e). However, in this case, the basal parts of the paraprocts are equipped with claws constituted of baculi. Similar claws are reported for several genera representing Opatrina (Table 1)—e.g., *Gonocephalum*, *Opatrum* and *Socotropatrum* (Figs. 1d, 10d, 11c).

Amblysphagus, *Neopachypterus* and *Pseudolamus* exhibit laterodorsally rotated paraprocts (Fig. 9). This feature seems to be associated with various modifications in coxites and specula ventrale (see above).

Unique modifications concerning the apex of the paraprocts are present in *Amphithrixoides* and *Cyptus* (Figs. 4c, 5b). In both of these cases, the lateral part of this morphological structure is elongate and forms thin spines. *Ammodonus* exhibits a unique paraproct modification. In this case the paraprocts are reduced in the basal part, while the baculi remain (Fig. 4b).

Proctiger

In most of the analyzed specimens, the length of the proctiger is slightly greater than that of the paraprocts (e.g., Figs. 4d, 5b). However, in some New World genera, the proctiger is more elongate (Fig. 6). In the most extreme cases, namely *Blapstinus* and *Diastolinus*, the proctiger completely covers the ovipositor on the dorsal side (Fig. 6b, c). Proctigers of *Amblysphagus*, *Neopachypterus* and *Pseudolamus* are also elongate; however, in this case they cover only the basal half of the coxites, due to the extension of the second and third coxites lobes.

Vagina

Presence of sclerites in vaginae is exclusively restricted to the following genera *Diphyrrhynchus*, *Heterocheira*, *Heterotarsus*, *Scymena* (e.g., Fig. 8a, b). Vaginae of all other studied taxa do not exhibit such modifications.

Bursa copulatrix

In most of the studied cases, this morphological feature had a sac-like structure and did not show any modifications (Table 1). However, approximately 10 % of the studied genera have sclerotizations located in different parts of the bursa copulatrix (Table 1). Only Heterocheirina, Heterotarsina and Stizopina lacked any taxa with sclerites in the bursa copulatrix (Table 1).

Bursae of *Corinta*, *Trigonopoda* and *Proscheimus* exhibits small circular sclerites near the spermatheca opening (e.g., Fig. 5f). On the other hand, unique rounded sclerites are present near the apex of bursa copulatrix in *Amphithrixoides* (Fig. 4c), and a cap-like one in *Cornopterus* (Fig. 5a). Sclerites discovered in bursae of *Amblysphagus*, *Neopachypterus* and *Pseudolamus* are of irregular shape (Fig. 9c). Other reported modifications of the bursa copulatrix concern bifurcation of its apical part. Such structures are present in *Polycoelogastridion* and *Trichopodus.*

Spermatheca

Three types of spermathecae can be observed: “narrow duct” (e.g., Fig. 9b), “wide duct” (e.g., Fig. 5f) and “sac-like” (e.g., Fig. 8d). The first type occurs in the majority of the studied species (Table 1). The wide duct spermathecae are present in some Opatrina species (e.g., *Ammobius*, *Ammodonus*, *Falsammidium*, *Falsocaedius*) and a single Stizopina representative—*Sulpius*. The “sac-like” spermathecae occur exclusively in Heterocheirina (e.g., Fig. 8d).

Corinta exhibits a unique spermatheca modification. In this case duct near the opening is narrow and strongly expands in the further part.

All studied taxa exhibit spermathecal accessory glands (e.g., Figs. 6e, 7b, 9c).

Eggs

In case of *Coeloecetes*, *Gonocephalum*, *Heterotarsus* and *Periloma* eggs located in the bursa copulatrix were observed. They are of ovoid shape (Fig. 8a) and measure, respectively: 1.6 mm × 1.1 mm, 2.0 mm × 1.2 mm, 1.9 mm × 1.2 mm, 1.6 mm × 0.9 mm. The highest ratio of egg length to female body length was reported for *Periloma* (31.2 %), then for *Coeloecetes* (20.2 %), *Hasticollum* (19.4 %), and *Heterotarsus* (15.3 %).

External morphology: supporting analysis

The Blapstinus generic complex

The complete division of the eye into the upper and lower parts is present in several genera within Opatrini (e.g., *Ammodonus*, *Blapstinus*, *Cornopterus*, *Gonocephalum*, *Mesomorphus*, *Opatrum*, *Penthicus*, *Socotropatrum*, *Wolladrus* nom. nov.). However, in some of these cases, the canthal suture is either situated more apically or basally (Fig. 15a, e). In the first case, the eyes are evidently divided by expanding temples (Fig. 15a–d), while in the second by genae (Fig. 15e–h). The eyes divided by the extending temples are unique for the following group of the New World genera named herein as the *Blapstinus* generic complex (for generic composition see classification section, under Blapstinina).

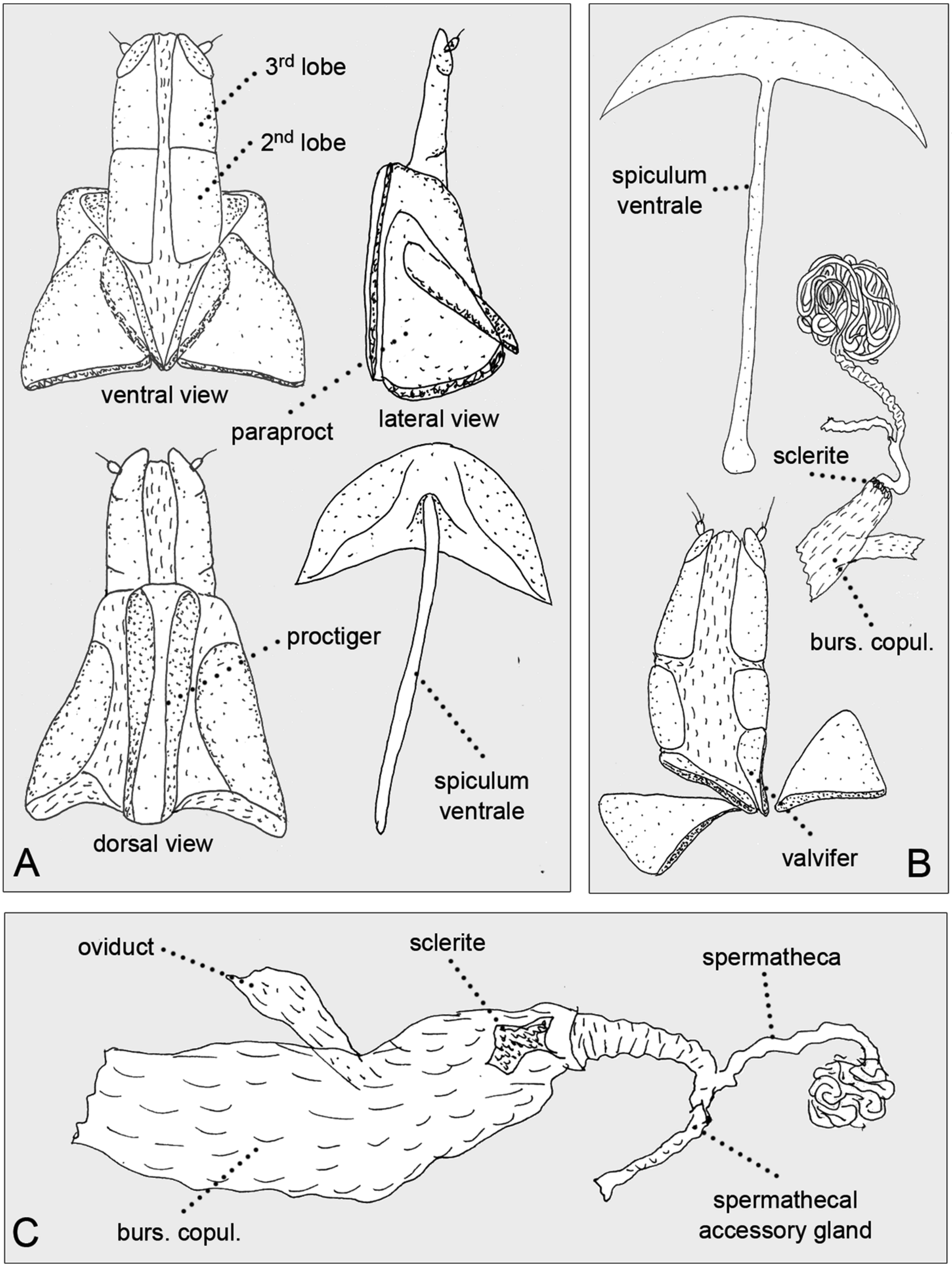

Fig. 9 Morphology of the ovipositor (**a**, **b**), genital tube (**b**, **c**) and spiculum ventrale (**a**, **b**) of Neopachypterina **sens. nov**. *Amblysphagus pachyderus* (**a**), *Neopachypterus elongatus* (**b**) and *Pseudolamus seriatoporus* (**c**)

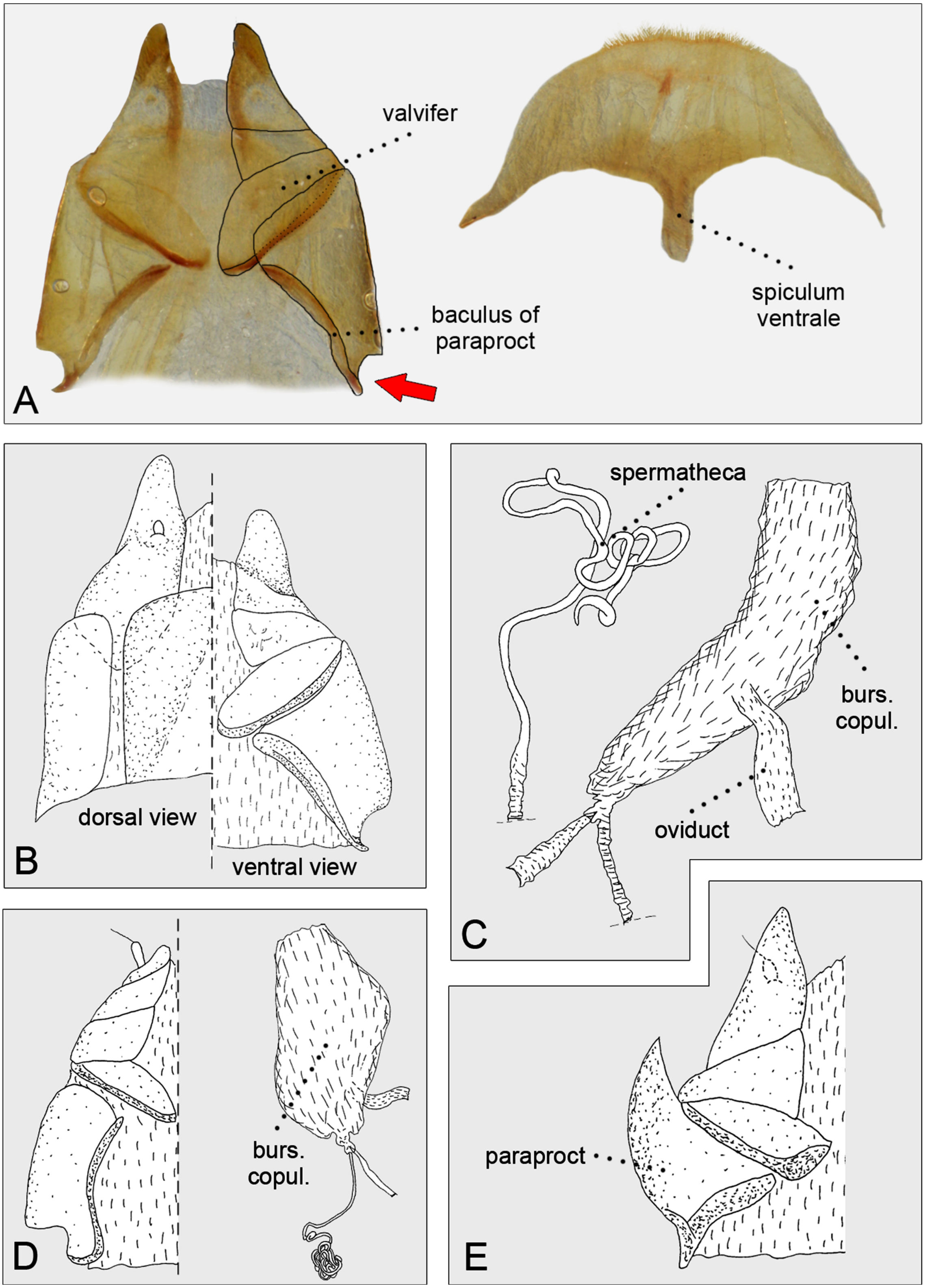

Fig. 10 Morphology of the ovipositor (**a**, **b**, **d**, **e**), genital tube (**c**, **d**) and spiculum ventrale (**a**) of Opatrina **sens. nov**. *Phelopatrum scaphoides* (**a**), *Anatrum songoricum* (**b**), *Falsolobodera skopini* (**c**), *Gonocephalum pygmaeum* (**d**) and *Melanesthes belawskyi* (**e**)

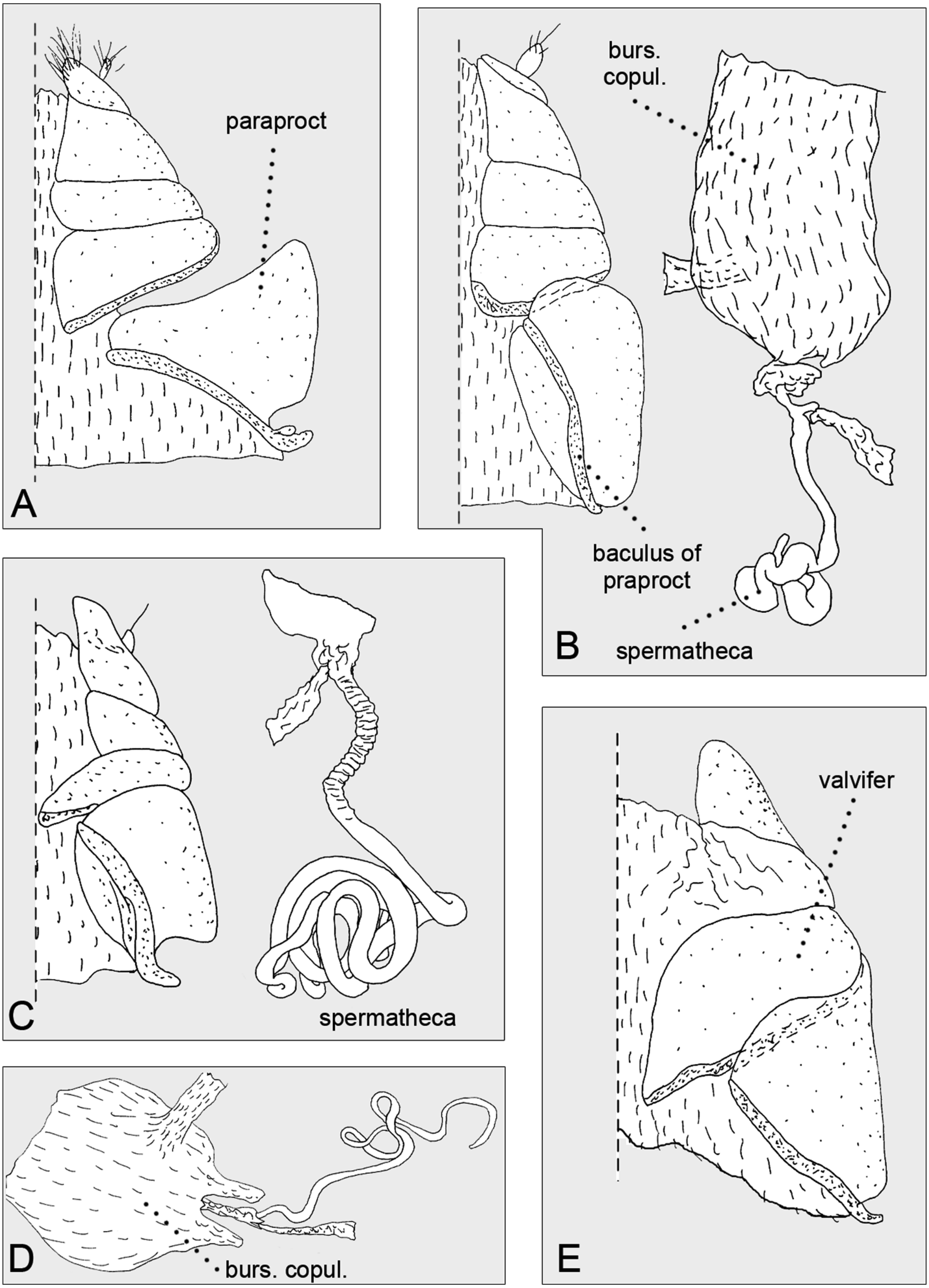

Fig. 11 Morphology of the ovipositor (**a**–**c**, **e**) and genital tube (**b**–**d**) of Opatrina **sens. nov**. *Mesomorphus villiger* (**a**), *Opatroides punctulatus* (**b**), *Opatrum sabulosum* (**c**), *Polycoelogastridion tenuipes* (**d**) and *Penthicinus pedinoides* (**e**)

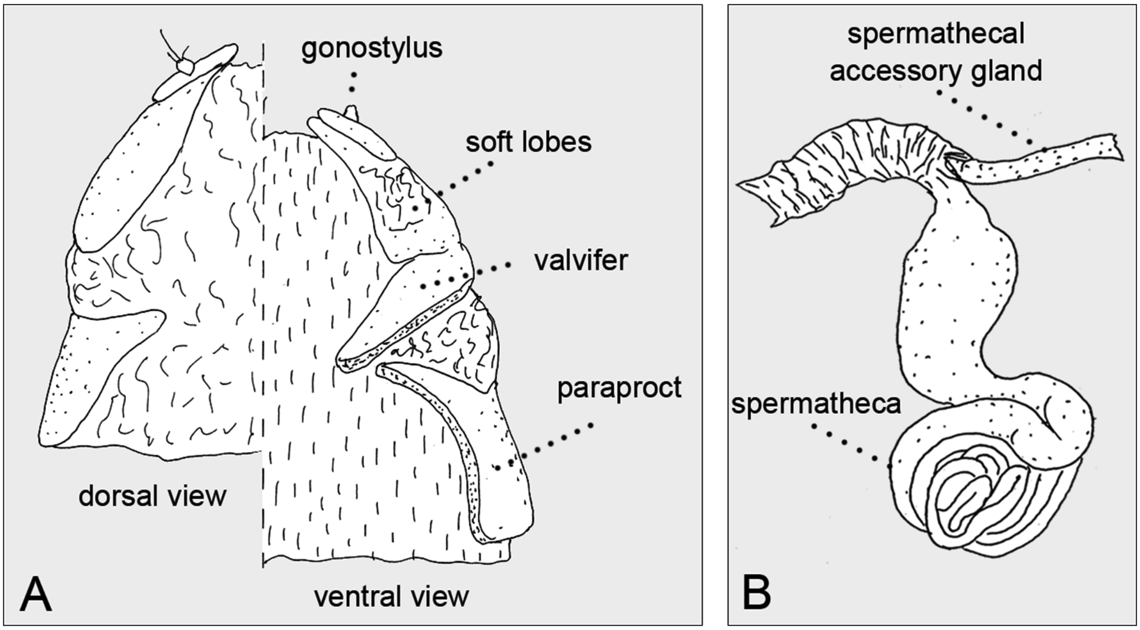

Fig. 12 Morphology of the ovipositor (**a**) and spermatheca (**b**) of Sclerina **stat. restit**. *Sclerum orientale* (**a**) and *Eurycaulus henoni* (**b**)

The Opatrum generic complex

According to the results of a comparative analysis of the ovipositor morphology (Table 1), several genera classified within Opatrina share a similar structure of the paraprocts—presence of claws constituted of baculi on the proximal ends (e.g., Fig. 10a). Additionally, the species representing this group exhibit a unique pronotal morphology. In all of these cases, basal depressions on pronotal disks are present. The visibility of this feature depends on the convexity of the pronotal disk (Fig. 16g, h). However, similar depressions are not present in other analyzed genera. The above-mentioned group is named here as the *Opatrum* generic complex (for generic composition see classification section, under Opatrina) (Fig. 11).

The Sclerum generic complex

The genera *Eurycaulus*, *Platysum* and *Sclerum* share a similar configuration of the coxite lobes. The middle part is soft and extended, apical lobe is small and located laterally (Fig. 12a). These taxa are also characterized by unique prothoracic and protibial characters. All exhibit the apical portion of the prosternal process strongly raised and the protibiae strongly expanded toward the apex (Fig. 16d–f). The above-mentioned group is named here as *Sclerum* generic complex (for details see classification section, under Sclerina) (Fig. 13).

Heterotarsini and Heterocheirini

The genera currently classified within Heterotarsini and Heterocheirini share a unique structure of the vagina—presence of dual sclerites in proximal part (Fig. 8a, b). Moreover, these taxa exhibit a unique structure of protarsi, which are considerably dilated, at least in males; preapical segment is reduced (Fig. 16a–c).

Protrochanter: Opatrini within Tenebrioninae

All of the studied Opatrini genera exhibit a unique protrochanter structure (oparinoid type) (Fig. 17a). The base of this morphological structure is elongate. However, several modifications of this type are observed. They might be ordered to form a morphocline with the following sequence: (1) opened type: process of the trochanter with narrow base, process of the coxa and acetabulum of trochanter well visible (Fig. 18a, b); (2) semi-opened type: process of the coxa and acetabulum of trochanter poorly visible, gradually covered by the widened process of trochanter's base (Fig. 18c, d); (3) closed type: process of the trochanter with wide base; very strongly widened, process of trochanter base overlaps the acetabulum of trochanter and covers it practically or entirely (Fig. 18e, f).

The opatrinoid protrochanter type was not observed in any of the other studied Tenebrioninae tribes (Figs. 17b, 18g–i). In all of these cases, the base of femur is longer than the trochanter's base (without the process). The protrochanter is narrower than the base of the femur (in some

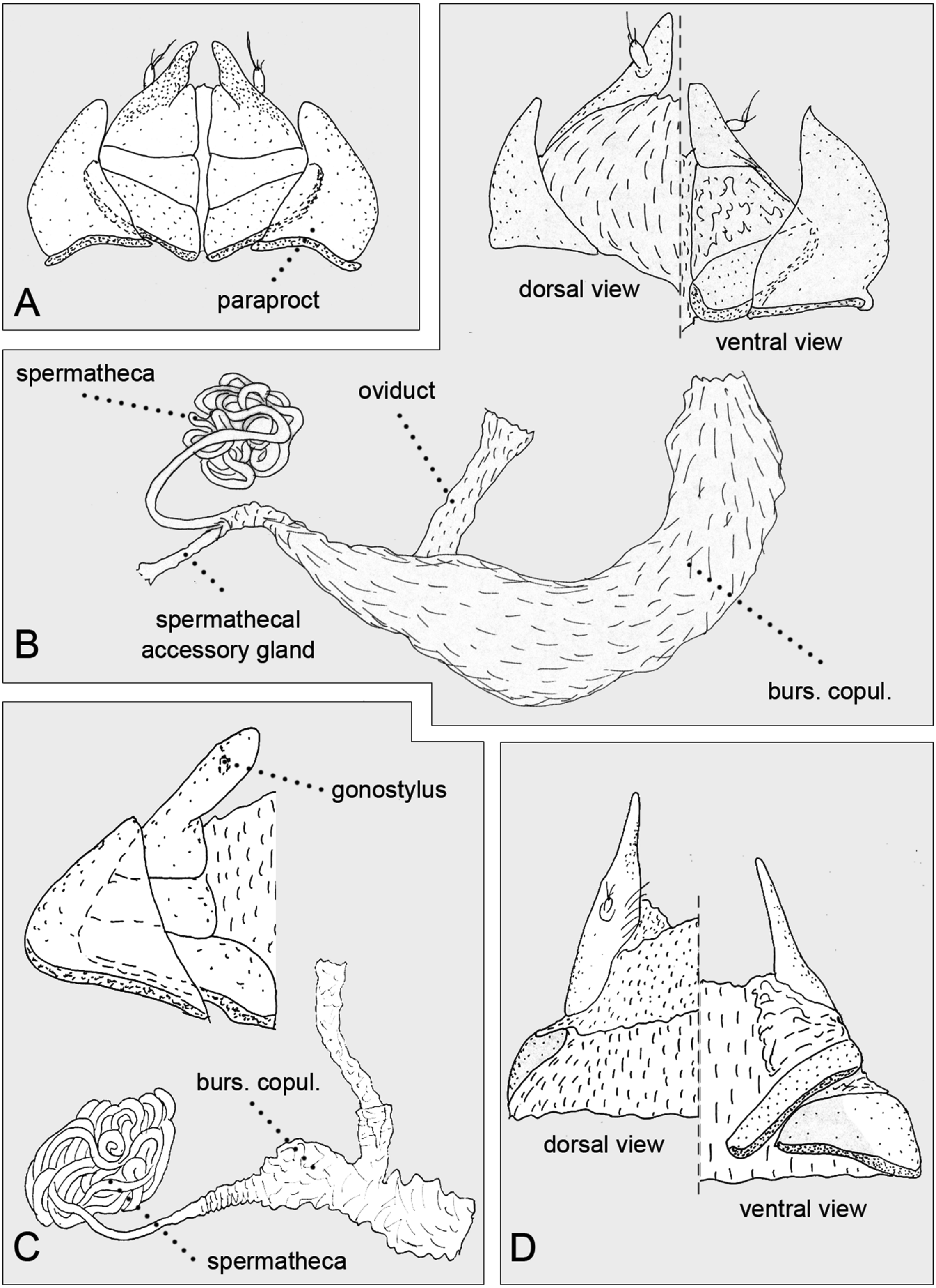

Fig. 13 Morphology of the ovipositor (**a**–**d**), genital tube (**b**, **c**) of Stizopina. *Adoryacus bidens* (**a**), *Planostibes cribricollis* (**b**), *Nemanes expansicollis* (**c**) and *Periloma alfkeni* (**d**)

cases reduced, e.g., *Leichenum*). The protrochanter acetabulum is most often exposed.

Discussion

Female terminalia: classification of Opatrini

The tribe Opatrini comprises about 5 % of the total darkling beetle species diversity. Despite this fact, up to now our knowledge of female terminalia morphology within this group has remained scarce. The most comprehensive study concerning this issue focused exclusively on a few Neotropical taxa (Marcuzzi 1987). Moreover, the author of this publication and the subsequent researchers (e.g., Marcuzzi 1989; Tschinkel and Doyen 1980) did not have the possibility to discuss their results within a modern classification frame of Tenebrionidae (Bouchard et al. 2005, 2011). For example, Tschinkel and Doyen (1980) treated *Blapstinus* as a representative of Pedinini. Therefore, all these publications suffer from a "Pedinini-Opatrini" bias. However, the female terminalia of both of those tribes seems to be convergent in many aspects (Banaszkiewicz 2006). Therefore, the data acquired in the present study are consistent with the general findings of Tschinkel and Doyen (1980), who reported a variation of "opatrinae" ovipositors from "*Tenebrio*-like" (laterally located gonostyles; subequal and apparent lobation of coxites, paraprocts and coxites simply abut) to the more specialized types (e.g., dorsolaterally oriented gonostyles; lobation reduced or absent; paraprocts enclose coxites). Moreover, the structure of the female genital tubes revealed here for Opatrini agrees with the "single, bursa-derived spermatheca" model presented by those authors.

Tschinkel and Doyen (1980) were the first to notice the differences in baculi orientation within "opatrinae". According to their hypothesis, baculi of paraprocts and coxites become obliquely oriented in more specialized ovipositors. Unfortunately, as mentioned before their interpretation of "opatrinae" referred to the Pedinini-Opatrini clade, which is currently considered as a polyphyletic entity (Kergoat et al. 2014). In general, present study shows that the baculi of paraprocts and coxites within Opatrini are in most cases X-oriented (e.g., Fig. 10a), while within Pedinini T-oriented (Banaszkiewicz 2006). The diagonally oriented baculi of Opatrini might even be observed in more plesiomorphic "*Tenebrio*-like" ovipositors (Table 1). This evolutionary tendency supports the hypothesis about the phylogenetic heterogeneity of Opatrini and Pedinini (Iwan 2001, 2004; Kergoat et al. 2014).

This study revealed significant differences in the female terminalia morphology among the investigated taxa (e.g., number of coxites lobes, orientation of paraprocts, and presence of sclerites in genital tubes). A major part of this variability may be associated with the differing ovipositioning strategies/behaviors of the taxa. For example, within Stizopina the modifications of the ovipositor are probably caused by edaphic drivers, which are directly linked to particular oviposition strategies. Within this group, genera occurring in or near the Namib Desert (Iwan and Schimrosczyk 2015; Kamiński 2015a) show reductions of coxites and paraprocts (e.g., *Syntyphlus*, Fig. 14b). Due to the short ovipositor, females have to directly reach the oviposition substrate to provide suitable conditions for developing larvae. Some species of Stizopina were observed to construct burrows or dive directly in sand (Penrith 1984; Rasa 1994, 1996; Rasa and Endrödy-Younga 1997; Geiselhardt et al. 2006). Moreover, the reduction in the length of the ovipositor might allow desert species to lay larger eggs containing more developed embryos (Tschinkel 1978; Iwan 2000).

On the other hand, current study revealed several modifications of the female terminalia which seem to be stable across different genera (e.g., presence of apical "claws" of paraprocts—Fig. 10; presence of dual sclerites in vaginae—Fig. 8b). Confrontation of this information with the data obtained during the comparative analysis of the external morphology enabled us to form hypotheses concerning the existence of several evolutionary informative characters. This information was used to propose a new classification of the studied group.

Up to know, the subtribe Opatrina contained 88 of the 118 known opatrine genera. Information concerning evolutionary relationships within this heterogeneous subtribe was scarce and incomplete (e.g., Koch 1956; Ferrer 2002; Iwan 2004). Moreover, a part of this information was blurred with the decrease of the taxonomic rank of Opatrinae to Opatrini, as the subtribes were merged with their parent tribes (Bouchard et al. 2005, 2011). This study has revealed two main types of Opatrina female terminalia, which differ in the structure of the paraprocts. The first one is characterized by the presence of claw-like structures on the apical part of paraproct baculi (e.g., Fig. 1d). This type of ovipositor was reported for a complex of 25 widely distributed genera (*Opatrum* generic complex). Moreover, the results of a comparative analysis using external morphology show that all of the representatives of this group share a similar structure of pronotum (Fig. 16g, h). Therefore, the *Opatrum* generic complex should be treated as an monophyletic entity. In its current interpretation, it is by far the most species-rich lineage of Opatrini (Iwan et al. 2010, 2011). Unfortunately, no morphological characters to further clarify relationships within this group were presently discovered. However, some of the genera might be associated into presumably monophyletic groups (e.g., *Scleropatroides* generic complex; Iwan and Matthews 2015).

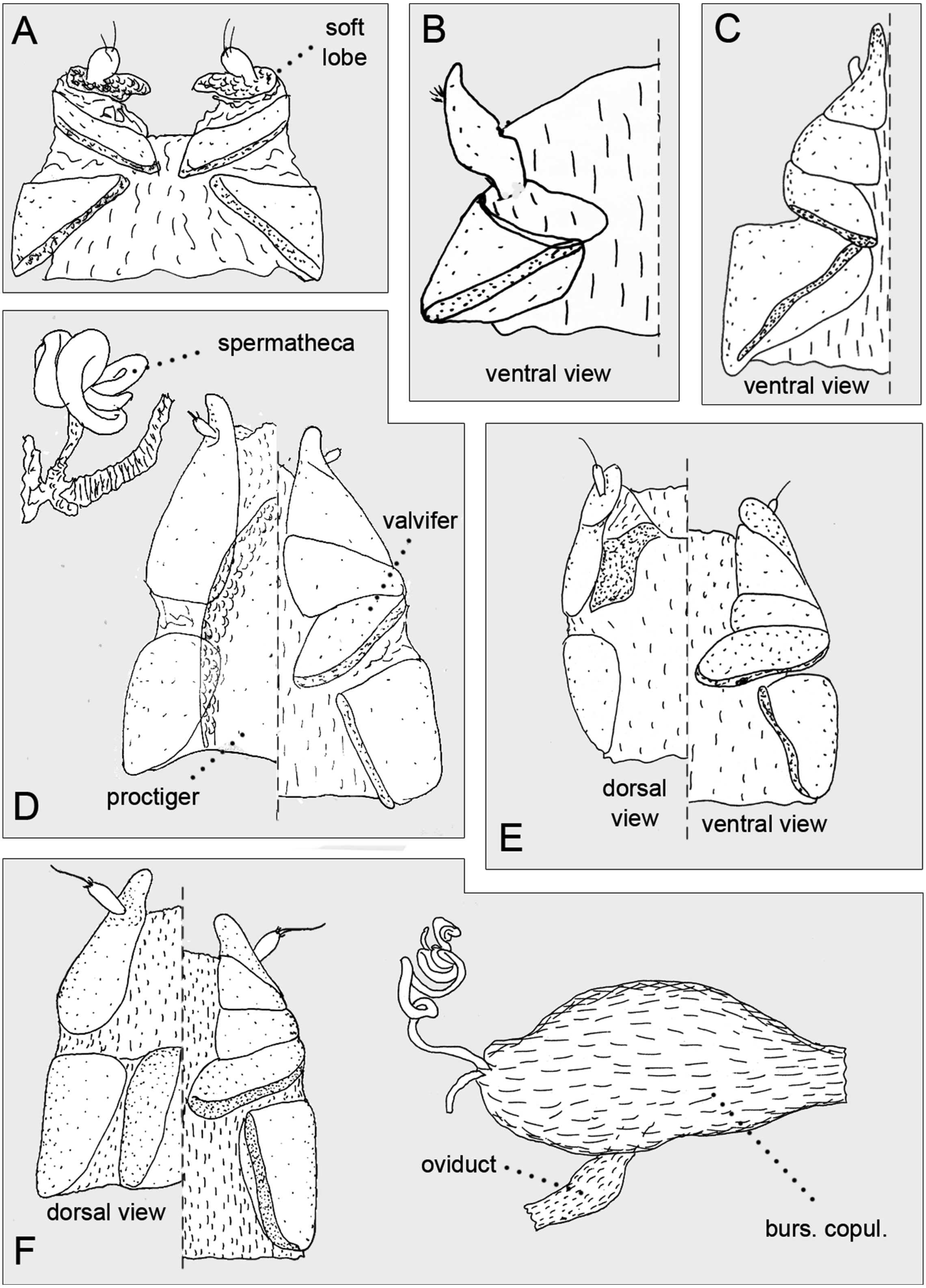

Fig. 14 Morphology of the ovipositor (**a**–**f**), genital tube (**d**, **f**) of Stizopina. *Stizopus laticollis* (**a**), *Syntyphlus namaquaensis* (**b**), *Eremostibes bushmanicus* (**c**), *Sulpius oblongulus* (**d**), *Amathobius glyptopterus* (**e**) and *Ennychiatus caraboides* (**f**)

The second type of ovipositor is simply characterized by the lack of claw-like structures at the tips of the paraprocts. Within the genera which share this type of female terminalia, a group that exhibits a unique structure of coxites was recognized—two fully sclerotized lobes (valvifers, and fourth lobes), and a soft lobe between them (Fig. 12). Similarly, as in the above-mentioned generic complex, external morphological features unique for these genera were found (e.g., Fig. 16d–f). Therefore, *Eurycaulus*, *Platysum* and *Sclerum* form a monophyletic entity within Opatrini (*Sclerum* generic complex). Historically, a family-group name based on genus *Scleron* Hope, 1840, synonym of *Sclerum* Dejean, 1834 (Bouchard et al. 2011), was already proposed by Lacordaire (1859). However, his interpretation was different from the one presented here.

Moreover, within the group of genera with "clawless" paraprocts, several New World entities with extended proctigers were reported (Fig. 6b, c). However, during the study of external morphology, it was impossible to find any clear autapomorphies for this group of genera. On the other hand, it was shown that some of the New World genera are characterized by a unique type of eye division (Fig. 15a–d). An idea that some of the Western Hemisphere genera form a separate phylogenetic group is relatively old, and reaches back into the nineteenth century (Mulsant and Rey 1853; LeConte 1862). However, in more modern classifications, this lineage was not recognized as a different family-group taxon (e.g., Aalbu and Triplehorn 1985; Bouchard et al. 2011). Nevertheless, in all of the above-mentioned cases, the morphological concepts of this group were mainly based on the presence of completely divided eyes, without any specifications concerning the type of this division. During this study, it was revealed that eye division occurs in several different genera within Opatrini. However, there are at least two not homologous types of division within this group—eyes divided by expanding temples (Fig. 15a–d) or genae (Fig. 15e–h). The first type is unique for certain New World genera (*Blapstinus* generic complex), while the second one probably evolved independently within other groups of Opatrini (and other Tenebrionidae, see Antoine 1956; Koch 1956; Kamiński 2012). In conclusion, it is hypothesized that *Blapstinus* generic complex is a separate entity, whose monophyly is based in the unique type of eye division found within these genera.

During this study, no other female terminalia characters were found to divide the remaining genera of Opatnina into phylogenetic entities. Therefore, it is proposed to group them together (*Ammobius* generic complex), despite the potentially polyphyletic nature of the grouping. During the primary morphology analysis of the representatives of this group, it was noticed that genera distributed on Saint Helena (*Helenomelas*, *Pseudoleichenum* and *Tarphiophasis*) share a unique structure of the prosternum (intercoxal process strongly depressed apically) and epipleuron (extremely widened at the level of the 5th ventrite). The latter character might be an evidence of a close phylogenetic relationship of these genera with Stizopina (Koch 1963). On the other hand, the *Ammobius* generic complex also contains the genus *Emmallus*, which in some of the previous classifications was distinguished as a separate family-group taxon named Emmallina (Koch 1956; Ferrer 2002).

Relationships within the subtribe Opatrina should be further studied within a phylogenetic framework, which ought to include more comprehensive studies of external morphology. However, the phylogenetic information gathered on the basis of the female terminalia and associated external morphological characters is sufficient to propose a new status for this group. Hopefully, a revised classification scheme based on the results presented here will accelerate alpha-taxonomic studies within this diverse group of species.

The obtained results suggest a close phylogenetic relationship between Heterocheirina and Heterotarsina. This affinity is supported by a unique structure of the vagina (Fig. 8b), protarsi (Fig. 16a–c) and protrochanter (Iwan 2004). According to the initial description of Heterocheirina (Koch 1956), the uniqueness of this taxonomic entity is based on the "tri-partite" aedeagal tegmen. However, this hypothesis was not supported during the comprehensive study of male terminalia made by Iwan (2001, 2004), which showed that the "tripartite" tegmen is actually an artifact caused by incorrect homology assessments of the structures. As such, it is proposed to merge Heterocheirina and Heterotarsina into a single taxon.

Acquired results suggest a close phylogenetic relationship between *Amblysphagus*, *Neopachypterus* and *Pseudolamus*. All of these genera have similar ovipositor, bursa copulatrix and spiculum ventrale morphology (Fig. 9). Therefore, it is hypothesized that this generic complex represents a monophyletic entity, formally named Neopachypterina (see also Medvedev 1968). Additionally, the extinct genus *Eupachypterus* is presumably closely related to the above-mentioned genera (Kirejtshuk et al. 2010).

Protrochanter: Opatrini within Tenebrioninae

Many researchers do not recognize the phylogenetic heterogeneity of Opatrini in relation to Pedinini. This phenomenon is most likely caused by the external morphological similarity of these two taxonomic tribes, which is possibly a result of xerophylic adaptations within both groups. Additionally, some of the characters used to define Opatrini (e.g., subquadrate labrum) are considered to be plesiomorphic among Tenebrionidae (Matthews et al. 2010). Moreover, this tribe is customarily defined by the

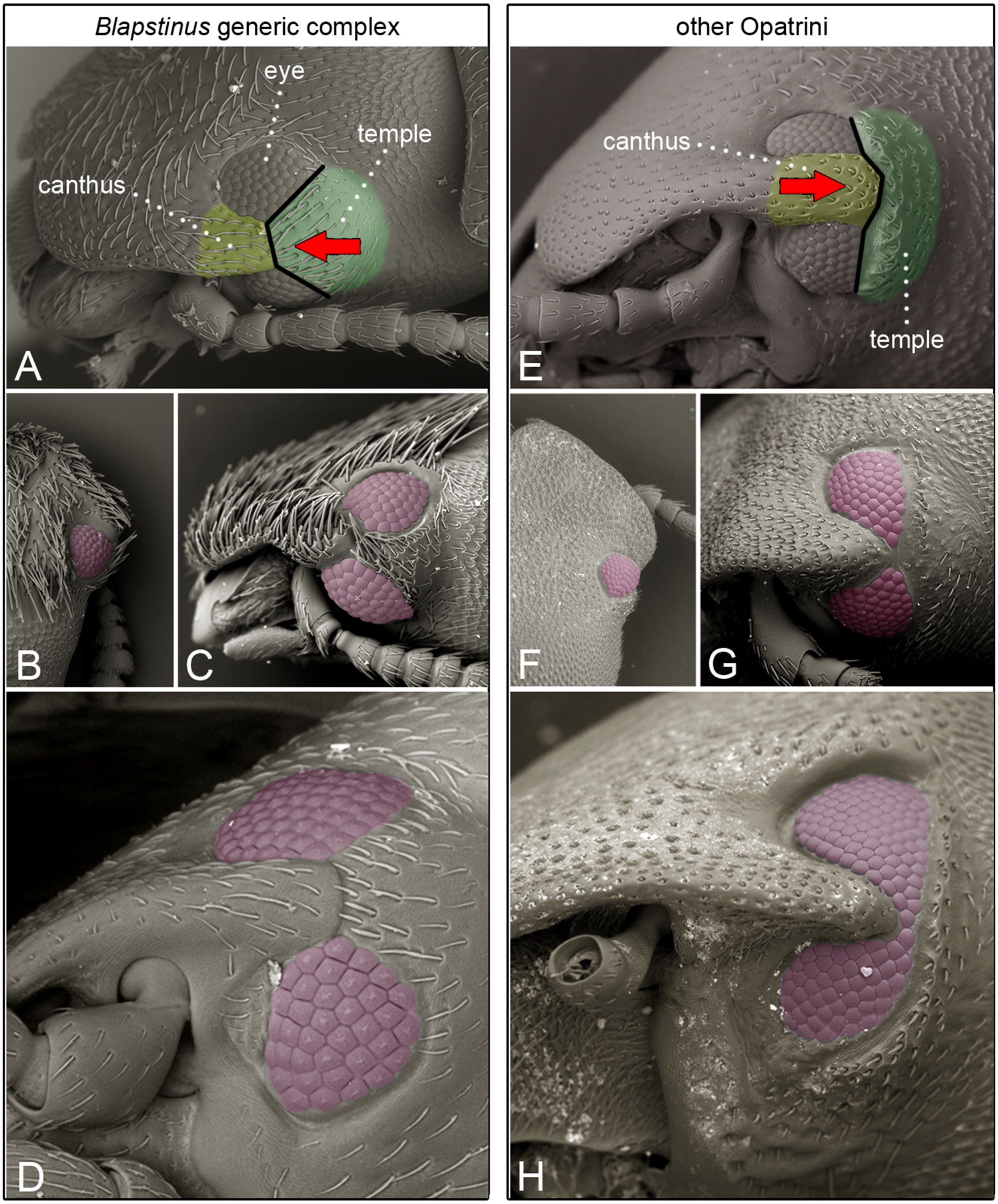

Fig. 15 Different types of eye division in Opatrini: eyes divided by expanding temples (**a–d**), and genae (**e–h**). *Blapstinus dilatatus* (**a**), *Bycrea villosa* (**b**, **c**), *Diastolinus perforatus* (**d**), *Opatroides punctulatus* (**e**), *Wolladrus carbonarius* (**f**, **g**), *Penthicus dilectans* (**h**)

excised clypeus, which can be misleading because this feature is shared by several Pedinini genera, e.g. *Doyenus*, *Styphacus* (Iwan 2010) or *Zadenos* (Kamiński 2015c).

In 2004, Iwan highlighted the differences in the male terminalia of the tribes. He stated that in contrast to Pedinini, Opatrini are characterized by aedeagi with ventral apophyses and well-developed inflexed basal alae. As an additional result to his comparative study of male terminalia, Iwan noticed differences in protrochanter structure of these two tribes. Based on the results of both above-mentioned analyses, Opatrini and Pedinini likely represent two evolutionally distinct lineages. This assumption was later supported by the result of a molecular study (Kergoat et al. 2014). The material studied by Iwan (2004) was

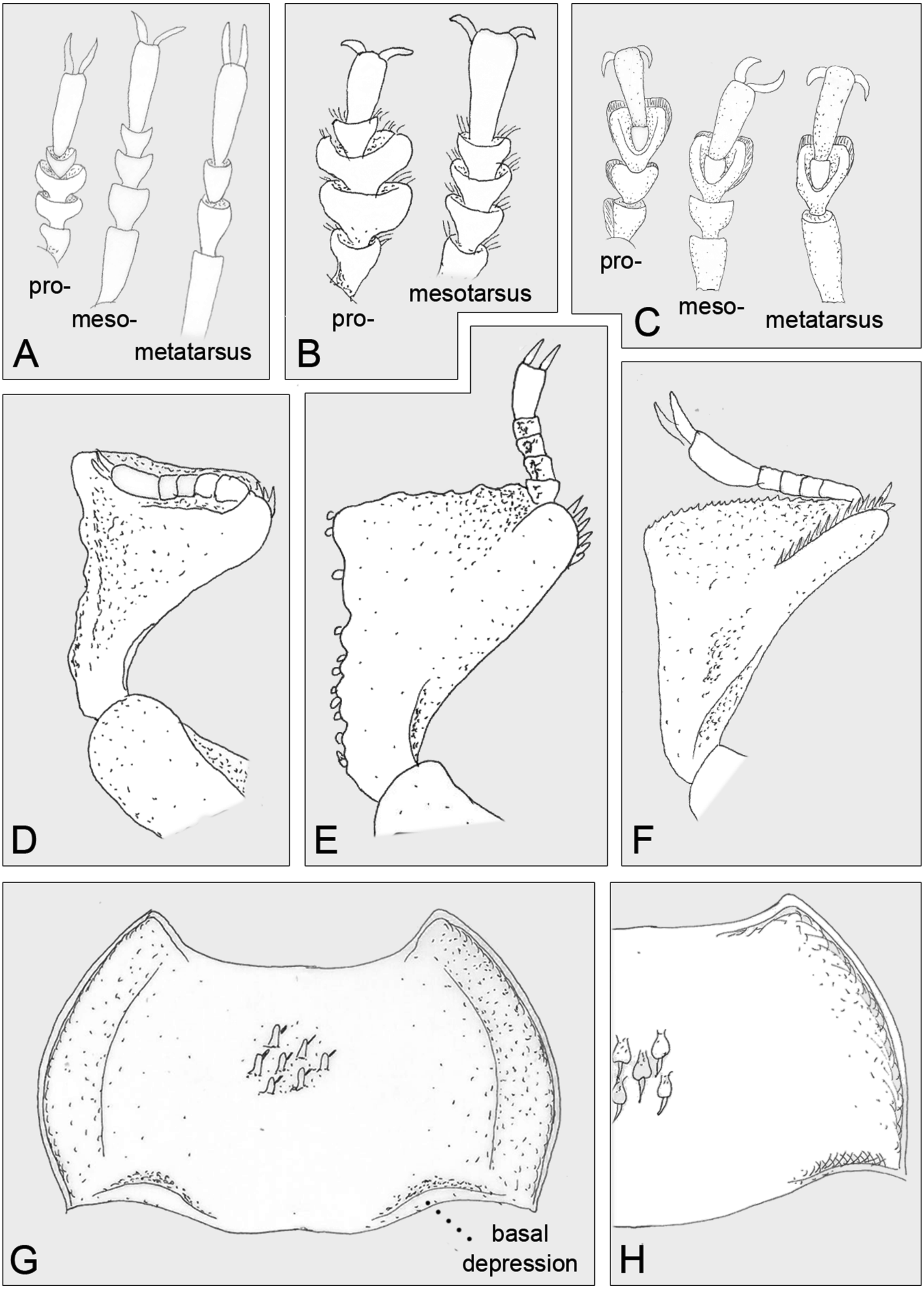

Fig. 16 Morphological autapomorphies for chosen tribes of Opatrini: Heterotarsina **sens. nov**. (**a**–**c**), Sclerina **stat. restit**. (**d**–**f**), and Opatrina **sens. nov**. (**g**, **h**). *Heterocheira australis* (**a**), *Scymena variabilis* (**b**), *Heterotarsus inflatus* (**c**), *Platysum paulinae* (**d**), *Eurycaulus henoni* (**e**), *Sclerum armatum* (**f**), *Scleropatrum prescotti* (**g**, **h**)

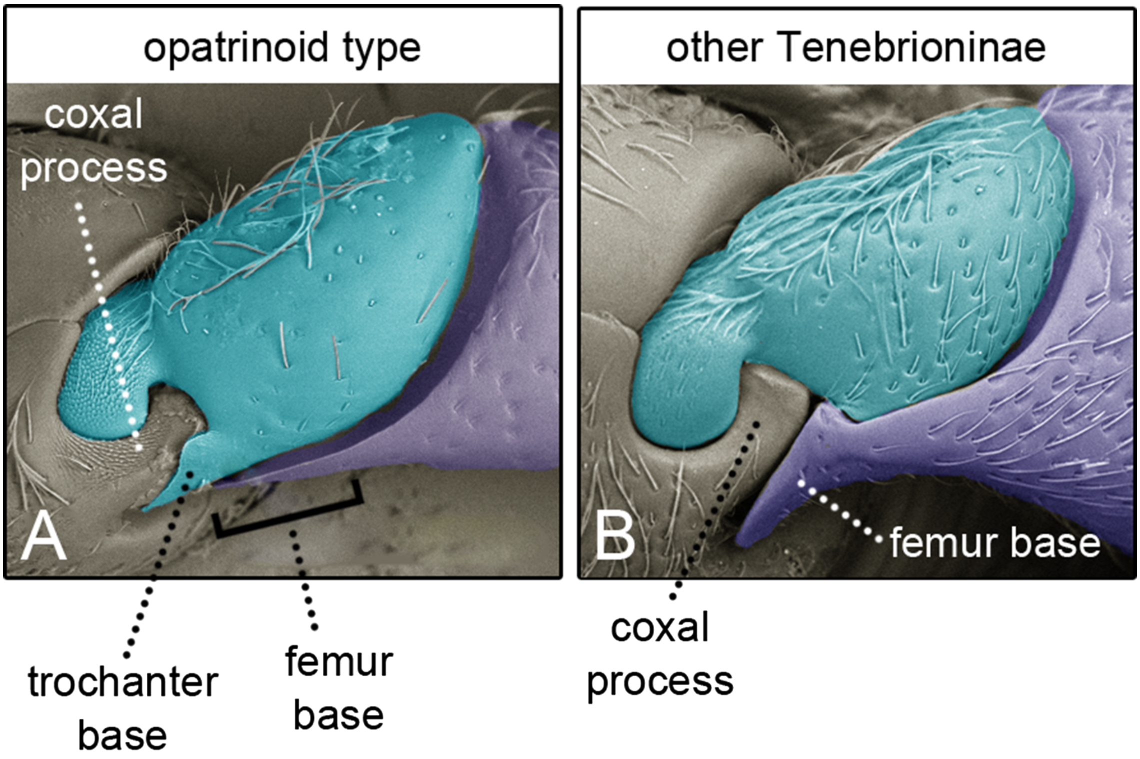

Fig. 17 Morphological characteristics of the opatrinoid protrochanter. *Heterotarsus inflatus* (**a**), *Ectateus crenatus* (Fabricius, 1792), Pedinini (**b**)

taxonomically limited and lacked the information from other groups of Tenebrionidae. Therefore, he was not equipped with any data to evaluate whether the rank of Opatrinae sensu Medvedev (1968) should be maintained. The results acquired in the present study show that the opatrinoid type of protrochanter (Fig. 17a) is unique for Opatrini within the whole Tenebrioninae. Therefore, this feature should be used as a paramount diagnostic character for this taxonomic group.

The subfamily Tenebrioninae is considered to be a polyphyletic assemblage (Matthews and Bouchard 2008; Matthews et al. 2010; Lawrence et al. 2011; Kergoat et al. 2014; Matthews and Merkl 2015), while the evidence presented in this paper suggests that Opatrini is clearly a monophyletic lineage.

All of the above-mentioned taxonomic decisions are summarized in the next section.

Revised classification and key to subtribes of Opatrini

The phylogenetic placement of uninvestigated genera was determined on the basis of available diagnoses published in the literature.

Classification

Tribe **Opatrini** Brullé 1832

Type genus *Opatrum* Fabricius, 1775.

Diagnostic characters Opatrini can be distinguished from other tribes of Tenebrioninae based on the following characters: protrochanter with the elongate base (Figs. 17a, 18a–f), aedeagus with ventral apophyses and well-developed inflexed alae on basal part, and in most cases diagonally oriented baculi of paraprocts and coxites.

Subtribes included (7) Ammobiina, Blapstinina, Heterotarsina, Neopachypterina, Opatrina, Sclerina, Stizopina.

Subtribe **Ammobiina** Desbrochers des Loges, 1902 **stat. restit.**
(Referred in text as *Ammobius* generic complex)

Type genus *Ammobius* Guérin-Méneville, 1844.

Genera included (40) *Adavius* Mulsant & Rey, 1859, *Ammidium* Erichson, 1843, *Ammobius* Guérin-Méneville, 1844, *Ammodonus* Mulsant & Rey, 1859, *Amphithrixoides*

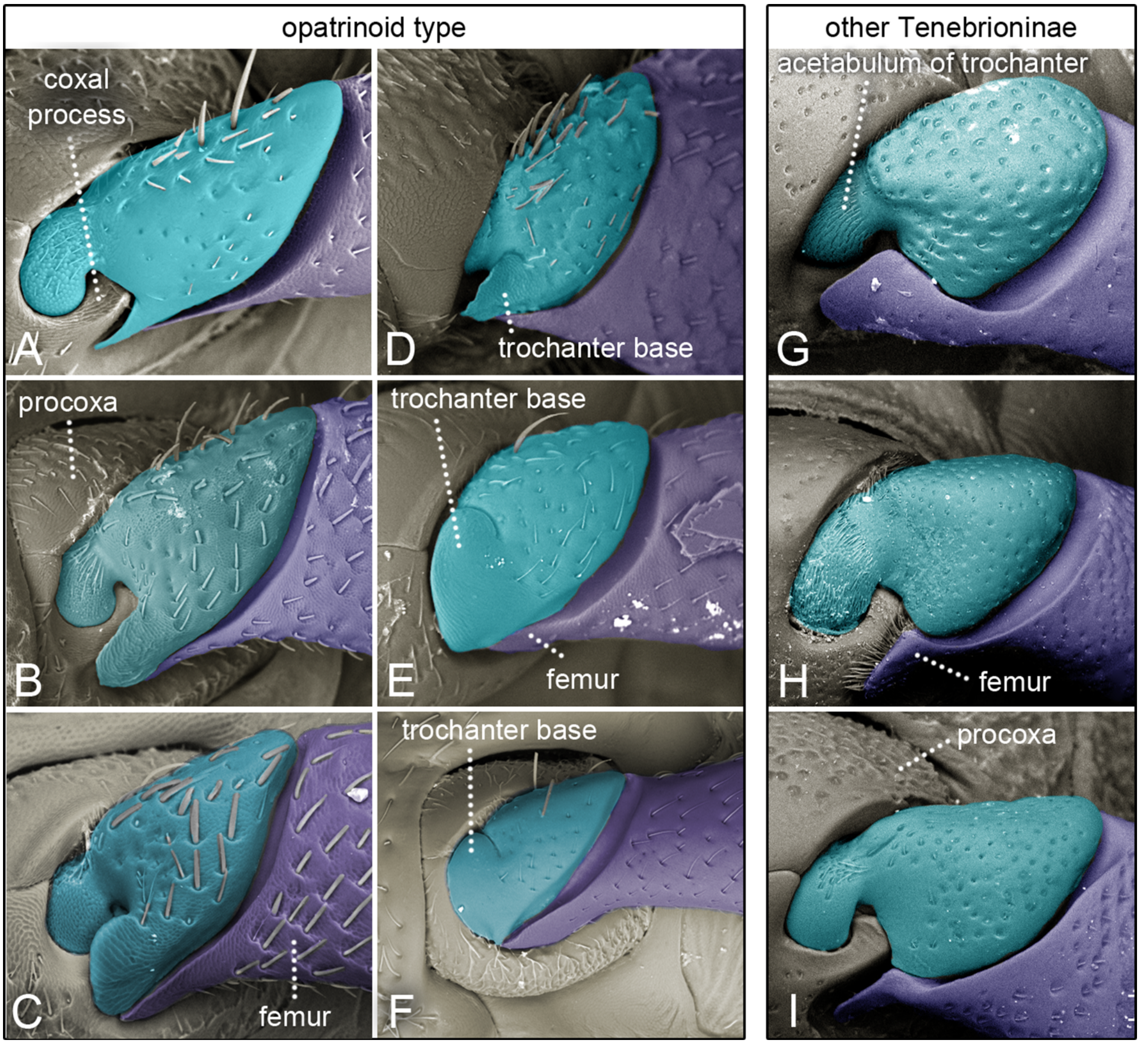

Fig. 18 Comparison of the opatrinoid (**a**–**f**) and tenebrionoid protrochanters (**g**–**i**). Morphological variability of the protrochanters within Opatrini (**a**–**f**): opened type—process of the trochanter with narrow base, process of the coxa and acetabulum of trochanter well visible (**a**, **b**), semi-opened type—process of the coxa and acetabulum of trochanter poorly visible, gradually covered by the widened process of trochanter's base (**c**, **d**), closed type (**e**, **f**). *Diphyrrhynchus chalceus* (**a**), *Opatrum sabulosum* (**b**), *Scleropatrum prescotti* (**c**), *Stizopus laticollis* (**d**), *Diastolinus perforatus* (**e**), *Blapstinus dilatatus* (**f**), *Scaurus* sp. (**g**), *Blaps* sp. (**h**) and *Tenebrio molitor* (**i**)

Bouchard & Löbl, 2008, *Asiocaedius* Medvedev & Nepesova, 1985, *Brachyidium* Fairmaire, 1883, *Caediexis* Lebedev, 1932, *Caediomorpha* Blackburn, 1887, *Caedius* Mulsant & Rey, 1859, *Clitobius* Mulsant & Rey, 1859, *Coeloecetes* Blair, 1929, *Corinta* Koch, 1950, *Cornopterus* Koch, 1950, *Cyptus* Gerstaecker, 1871, *Diaderma* Koch, 1960, *Dilamus* Jacquelin du Val, 1861, *Emmallus* Erichson, 1843, *Ephalus* LeConte, 1862, *Falsammidium* Koch, 1960, *Falsocaedius* Español, 1943, *Freyula* Koch, 1959, *Helenomelas* Ardoin, 1972, *Mateuina* Español, 1944, *Messoricolum* Koch, 1960, *Moragacinella* Español, 1954, *Nesocaedius* Kolbe, 1915, *Perithrix* Fairmaire, 1879, *Platyprocnemis* Español & Lindberg, 1962, *Plesioderes* Mulsant & Rey, 1860, *Prodilamus* Ardoin, 1969, *Proscheimus* Desbrochers des Loges, 1881, *Psammestus* Reichardt, 1936, *Pseudephalus* Casey, 1924, *Pseudoleichenum* Ardoin, 1972, *Raynalius* Chatanay, 1912, *Sobas* Pascoe, 1863, *Tarphiophasis* Wollaston, 1877, *Trigonopoda* Gebien, 1914, *Weisea* Semenov, 1890.

Distribution (Fig. 19) Representatives of this subtribe were collected in the following biogeographic realms: Afrotropic, Australasia, Indomalaya, Neotropic, Palearctic and Nearctic.

Subtribe **Blapstinina** Mulsant and Rey, 1853 **stat. restit.** (Referred in text as *Blapstinus* generic complex)

Type genus *Blapstinus* Sturm, 1826.

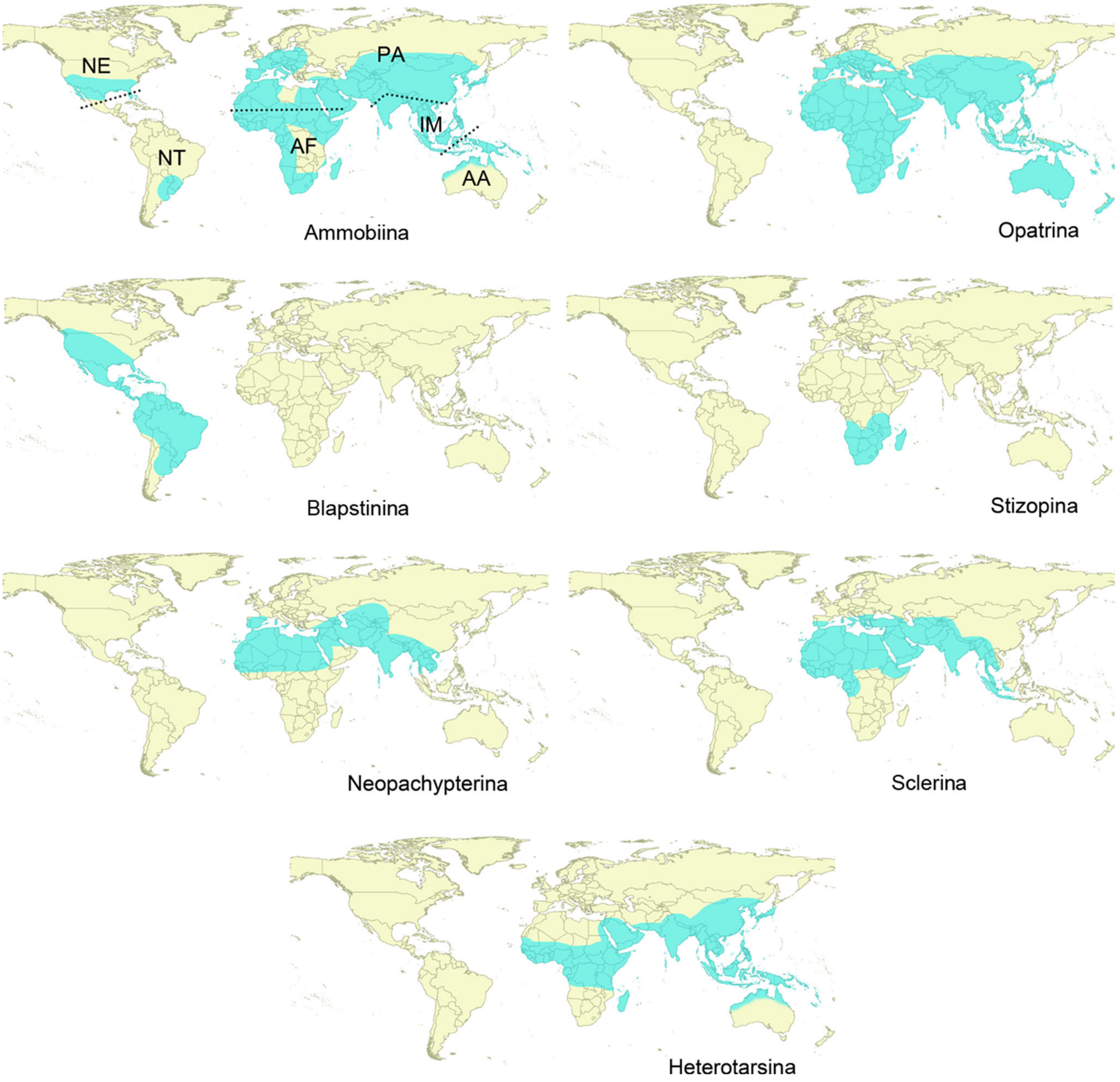

Fig. 19 General distribution of the revised subtribes of Opatrini. Biogeographic realms: Afrotropical (AF), Australasian (AA), Indomalaya (IM), Nearctic (NE), Neotropic (NT), Palearctic (PA)

Genera included (20) *Aconobius* Casey, 1895, *Austrocaribius* Marcuzzi, 1954, *Blapstinus* Sturm, 1826, *Bycrea* Pascoe, 1868, *Cenophorus* Mulsant & Rey, 1859, *Conibiosoma* Casey, 1890, *Conibius* LeConte, 1851, *Ctesicles* Champion 1896, *Cybotus* Casey, 1890, *Diastolinus* Mulsant & Rey, 1859, *Hummelinckia* Marcuzzi, 1954, *Mecysmus* Horn, 1870, *Nocibiotes* Casey, 1895, *Notibius* LeConte, 1851, *Platylus* Mulsant & Rey, 1859, *Sellio* Mulsant & Rey, 1859, *Tonibius* Casey, 1895, *Tonibiastes* Casey, 1895, *Trichoton* Hope, 1840, *Ulus* Horn, 1870.

Distribution (Fig. 19**)** Representatives of this subtribe were collected in the following biogeographic realms: Neotropic and Nearctic.

Subtribe **Heterotarsina** Blanchard, 1845
=Heterocheirini Koch (1956) **syn. nov.**

Type genus *Heterotarsus* Latreille, 1829.

Genera included (4) *Diphyrrhynchus* Fairmaire, 1849, *Heterocheira* Lacordaire, 1859, *Heterotarsus* Latreille, 1829, *Scymena* Pascoe, 1866.

Distribution (Fig. 19) Representatives of this subtribe were collected in the following biogeographic realms: Afrotropic, Australasia, Indomalaya and Palearctic.

Subtribe **Neopachypterina** Bouchard et al. 2007

Type genus *Neopachypterus* Bouchard et al. 2007.

Genera included (4) *Amblysphagus* Fairmaire, 1896, † *Eupachypterus* Kiirejtshuk, Nabozhenko & Nel, 2010, *Neopachypterus* Bouchard et al. 2007, *Pseudolamus* Fairmaire, 1874.

Distribution (Fig. 19) Representatives of this subtribe were collected in the following biogeographic realms: Afrotropic, Indomalaya and Palearctic.

Subtribe **Opatrina** Brullé, 1832
(Referred in text as *Opatrum* generic complex)

Type genus *Opatrum* Fabricius, 1775.

Genera included (25) *Anatrum* Reichardt, 1936, *Brachyesthes* Fairmaire, 1868, *Eumylada* Reitter, 1904, *Falsolobodera* Kaszab, 1967, *Gonocephalum* Solier, 1834, *Hadrophasis* Ferrer, 1992, *Jintainum* Ren, 1999, *Melanesthes* Dejean, 1834, *Melanocoma* Wollaston, 1867, *Mesomorphus* Miedel, 1880, *Myladina* Reitter, 1889, *Opatroides* Brullé, 1832, *Opatrum* Fabricius, 1775, *Penthicinus* Reitter, 1896, *Penthicus* Faldermann, 1836, *Phelopatrum* Marseul, 1876, *Polycoelogastridion* Reichardt, 1936, *Reichardtiellina* Kaszab, 1982, *Scleropatroides* Löbl & Merkl, 2003, *Scleropatrum* Reitter, 1887, *Sinorus* Mulsant & Revelière, 1860, *Socotropatrum* Koch, 1970, *Trichosternum* Wollaston, 1861, *Tidiguinia* Español, 1959, *Wolladrus*[1] **nom. nov**.

Distribution (Fig. 19) Representatives of this subtribe were collected in the following biogeographic realms: Afrotropic, Australasia, Indomalaya and Palearctic.

Subtribe **Sclerina** Lacordaire, 1859 **stat. restit.**
(Referred in text as *Sclerum* generic complex)

Type genus *Scleron* Hope, 1840, synonym of *Sclerum* Dejean, 1834.

Genera included (3) *Eurycaulus* Fairmaire, 1868, *Platysum* Mulsant & Rey, 1859, *Sclerum* Dejan, 1834.

Distribution (Fig. 19) Representatives of this subtribe were collected in the following biogeographic realms: Afrotropic, Indomalaya and Palearctic.

Subtribe **Stizopina** Lacordaire, 1859

Type genus *Stizopus* Erichson, 1843.

Genera included (22) *Adoryacus* Koch, 1963, *Amathobius* Gebien, 1920, *Blacodatus* Koch, 1963, *Blenosia* Laporte de Castelnau, 1840, *Calaharena* Koch, 1963, *Crististibes* Koch, 1963, *Eichleria* Kamiński, 2015, *Ennychiatus* Koch, 1963, *Eremostibes* Koch, 1963, *Helibatus* Mulsant & Rey, 1859, *Luebbertia* Koch, 1963, *Microstizopus* Koch, 1963, *Namazopus* Koch, 1963, *Nemanes* Fairmaire, 1888, *Parastizopus* Gebien, 1938, *Periloma* Gebien, 1938, *Planostibes* Gemminger et Harold, 1870, *Psammogaster* Koch, 1953, *Sphaerostibes* Koch, 1963, *Stizopus* Erichson, 1843, *Sulpius* Fairmaire, 1906, *Syntyphlus* Koch, 1953.

Distribution (Fig. 19) Representatives of this subtribe were collected exclusively in the Afrotropic realm.

Key to the subtribes of Opatrini

1	Eyes divided by the extending temples (Fig. 15a). The canthal suture situated more apically in the anterior–posterior body axis (Fig. 15b–d). New World taxa (Fig. 19) …	**Blapstinina**
	Eyes divided by the extending genae (Fig. 15e). The canthal suture situated more basally in the anterior–posterior body axis (Fig. 15f–h) …	**(2)**
2	Pronotum with a pair of basal depressions (Fig. 16g, h). Proximal tips of paraprocts equipped with claws (e.g., Fig. 10a) …	**Opatrina**
	Pronotum without basal depressions. Proximal tips of paraprocts simple (e.g., Figs. 5, 8, 9, 13) …	**(3)**
3	Apical portion of the prosternal process strongly raised. Protibiae strongly expanded toward the apex (Fig. 16d–f). Middle part of coxites soft and extended, apical lobe small and located laterally (Fig. 12a) …	**Sclerina**
	Apical portion of the prosternal process flat or depressed. Protibiae slightly expanded toward the apex. Coxites of different structure (e.g., Figs. 5, 8, 13, 14) …	**(4)**
4	Elytral epipleuron strongly developed in its apical part. Madagascan and southern African taxa …	**Stizopina**
	Elytral epipleuron evenly narrowing toward apex …	**(5)**
5	Protarsi considerably dilated, at least in males; preapical segment reduced (Fig. 16a–c). Vagina with dual sclerites in proximal part (Fig. 8a, b) …	**Heterotarsina**

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[1] This name is proposed here as replacement name for *Hadrus* Wollaston, 1854 (Tenebrionidae: Opatrini), junior homonym of *Hadrus* Perty, 1833 (Insecta: Diptera). We dedicate this name to Thomas Vernon Wollaston (9th March 1822–4th January 1878), the author of the taxonomic conception of this genus.

	Protarsi relatively narrow, with preapical segment not reduced. Vagina simple, without sclerites (Figs. 4, 5, 9)…	**(6)**
6	Second and third lobes of coxites elongate (Fig. 9). Paraprocts rotated laterodorsally. Spiculum ventrale elongate (Fig. 9) …	**Neopachypterina**
	Middle coxites not elongate. Paraprocts not rotated laterodorsally. Spiculum ventrale short …	**Ammobiina**

Acknowledgments This research was founded by the SONATA 7 Project (Number 2014/13/D/NZ8/02428) from the National Science Centre, Poland. For valuable comments on the manuscript, the authors thank Aaron D. Smith (Northern Arizona University) and the anonymous reviewers assigned by the Editor.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study.

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