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Structural Features of Female Genitalia in Some Species of Histerid Beetles (Coleoptera, Histeridae)

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Abstract—The ovipositor morphology in 12 species of Histeridae is considered, including the previously undescribed structures of the gonocoxites, stylus, and sclerotized sections of the wall of abdominal segment IX. The female genitalia of the studied species vary in the shape and degree of sclerotization of the gonocoxites and articular sclerites, the presence and position of the apical notch on the gonocoxites, the width and degree of sclerotization of the gonocoxite border, the position of the articular membrane, the presence and number of setae on the articular membrane, the length and shape of the stylus, and the shape of the ventromedian plate.

Keywords: Histeridae, *Hister*, *Margarinotus*, *Saprinus*, *Hypocaccus*, *Acritus*, female genitalia, ovipositor

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Histeridae is a widespread family of beetles, represented on all continents except Antarctica (Reichardt, 1941). The morphology of male genitalia is commonly used in identification of beetle species, while that of the ovipositor is quite rarely studied, despite the numerous publications devoted to the structure of the female genital apparatus. Reichardt (1941) published schematic drawings of the terminal abdominal segments in *Saprinus aeneus* (Fabricius, 1775) and *S. immundus* (Gyllenhal, 1827) but did not mark their constituent parts. Kryzhanovsky (1976) mentioned the potential usefulness of the female genitalia traits in clarifying the taxonomic position of histerid species. Mazur and Kaszab (1980) described and illustrated the gonocoxites of three closely related species of the genus *Saprinus* Erichson, 1834. Degallier (1981) described the gonocoxites in species of the genus *Euspilotus* Lewis, 1907 and used their structural traits as additional diagnostic characters. De Marzo and Vienna (1982) described the morphology of the spermatheca in 30 histerid species and noted its high variability.

A great contribution to the study of genital morphology in Histeridae was made by Ôhara (1989a, 1989b), who described the spermatheca in 11 species and designated the main elements of the ovipositor. He also distinguished six structural types of the spermatheca and proposed a scheme of their evolutionary transformations (Ôhara, 1994).

In their paper on the phylogeny of Histeridae, Ślipiński and Mazur (1999) considered two distinct states of the ovipositor: with sclerotized, scoop-shaped gonocoxites and strongly reduced, desclerotized ones. Caterino and Vogler (2002) distinguished three character states of the valvifers and four states of the spermatheca. Illustrations of the ovipositors of *Saprinus quadriguttatus* (Fabricius, 1798), *Gnathoncus vietnamicus* Kryzhanovskij, 1972, some species of the tribe Platysomatini, and *Saprinus subustus* Marseul, 1855 were published (Ôhara and Mazur, 2000; Mazur and Ôhara, 2003; Mazur et al., 2005), but their main structural elements were not indicated.

In 2013, a new species of the genus *Omalodes* Erichson, 1834 was described based on the features of ovipositor morphology (Moura and Almeida, 2013), but the ovipositor elements were not marked in the drawings.

Table 1. Terms used by different authors to describe the main elements of the female genitalia in Histeridae

Ôhara, 1989b	Caterino and Tishechkin, 2015	Lackner and Tarasov, 2019	This paper
segment VIII			
vagina	–	–	vagina
–	basal baculi of eighth sternite	basal baculi of eighth sternite	–
–	median plate of eighth sternite	–	–
–	spermatheca gland	spermatheca gland	–
spermatheca	spermatheca	spermatheca	spermatheca
–	–	spermatheca duct	–
bursa copulatrix	bursa copulatrix	bursa copulatrix	bursa copulatrix
–	common oviduct	–	–
segment IX			
vulva	–	–	–
coxite	coxite	gonocoxite	gonocoxite
stylus	gonostylus	gonostylus	stylus
–	–	–	border
–	–	–	apical notch
–	–	–	articular membrane
–	–	–	ventromedian plate
valvifer	valvifer	valvifer	valvifer
–	basal attachment of ninth sternite	–	–
–	coxite articulating sclerite	articulating sclerite	articular sclerite
–	paraproct	–	–

Caterino and Tishechkin (2015) used 31 characters of the ovipositor along with other external and internal morphological characters in a phylogenetic study of the tribe Exosterini and over 50 taxa from other genera and tribes of Histerinae. Arriagada (2015) described a new species of the genus *Euspilotus* and gave a brief description of its gonocoxites. In 2015, a new species of the genus *Hister* Linnaeus, 1758 was described based on the features of the female genitalia (Leivas et al., 2015) without designating their main elements. Seung and Lee (2019a, 2019b, 2019c, 2019d) illustrated the ovipositors of some Histeridae species from Korea, also without marking their main elements. In their phylogenetic analysis, Lackner and Tarasov (2019) used the structure of ovipositor sclerites in the type species of most genera and subgenera of the subfamily Saprininae. The new phylogenetic tree based on the features of ovipositor morphology agreed with the previous phylogenetic scheme of the subfamily (Lackner, 2015). The description of a new species of the genus *Eucurtiopsis* Silvestri, 1926 included a brief characteristic of its ovipositor (Théry, 2021).

In spite of quite extensive literature devoted to the ovipositor structure in Histeridae, the female genitalia of these beetles are still incompletely studied and remain undescribed in most species. Since the available descriptions of the ovipositor are incomplete and its main structural elements are not indicated in most publications, it is difficult to establish the homologies of these elements.

This paper presents the results of studying the structure and homologies of the ovipositor elements in representatives of different subfamilies of Histeridae.

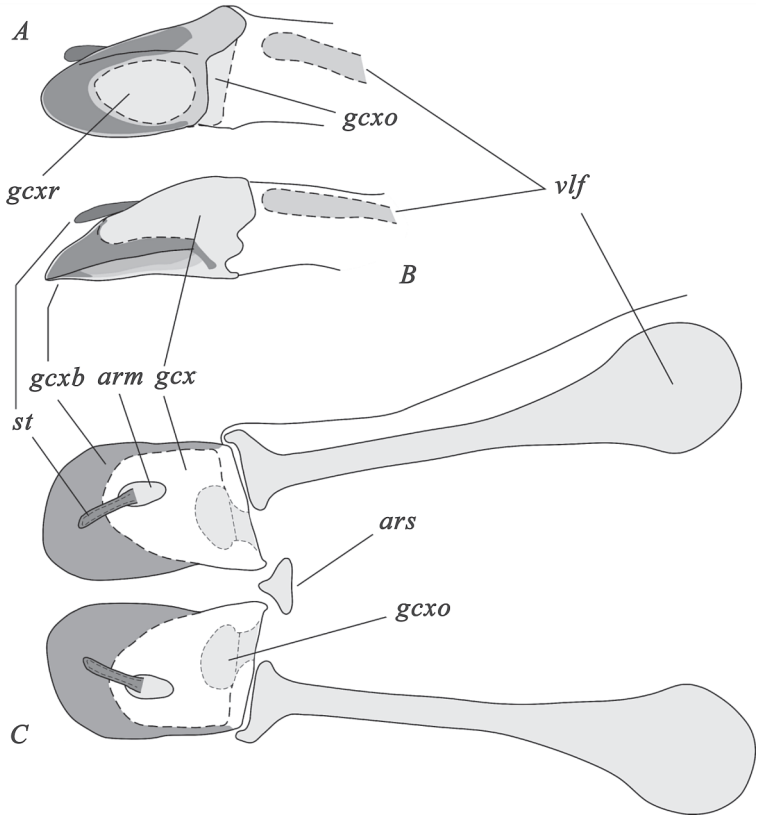

Fig. 1. Main elements of the ovipositor in *Saprinus maculatus* Rossi: (*A*) dorsal view; (*B*) lateral view; (*C*) ventrolateral view; *gcxr*, gonocoxite recess; *vlf*, valvifer; *gcx*, gonocoxite; *gcxb*, gonocoxite border; *gcxo*, opening of gonocoxite cavity; *arm*, articular membrane; *ars*, articular sclerite; *st*, stylus. Some setae on gonocoxites are not shown in Figs. 1, 2, 3, 5–9.

MATERIALS AND METHODS

Preparations of female genitalia were made by the technique described by Prosvirov and Savitsky (2011). After maceration, the genitalia were documented with a Levenhuk M500 BASE digital camera installed in place of the microscope eyepiece, and manually traced using the Inkscape graphics editor. The terms used to describe the main elements of the female genital apparatus in the previous publications and in this paper are summarized in Table 1.

All the collected material is kept in my private collection. The specimens collected by me are listed below without indication of the collector's name.

Morphology of Female Genitalia in Histeridae

"The terminal segments retracted into the cloacal cavity, together with the intersegmental membranes, form a rather long ovipositor" (Reichardt, 1941). The weakly sclerotized plates and longitudinal threads discernible in the ovipositor walls are rudimentary sternites and tergites of segments VIII and IX.

The cavity of segment VIII contains the bursa copulatrix and spermatheca.

The cavity of segment IX contains paired rod-shaped valvifers (Fig. 1), previously interpreted as derivatives of the sternite or tergite of segment IX (Reichardt, 1941; Kryzhanovsky and Reichardt, 1976; Ôhara, 1989a). The valvifers are usually dilated at the base, and their distal ends are articulated with the gonocoxites, i.e., sternites of segment IX.

The gonocoxites are paired structures, usually shaped as hollow pyramids with an obliquely truncated base. "During oviposition, they serve as the main organs forcing apart fragments of the substrate" (Kryzhanovsky and Reichardt, 1976). The cavity of the gonocoxites is

connected to that of segment IX by an opening, which is visible in dorsal view as a light basal oval.

The gonocoxites usually have a thin edge forming a characteristic border. The latter can be visible as a continuous dark stripe, alternating dark and light stripes, or an entirely light stripe; in some species the border is covered with cuticular wrinkles or bulges. The gonocoxite apex often has a notch, to which the articular membrane may adjoin on one side. This apical notch apparently serves to accommodate the stylus; when these structures are examined, the apical notch is usually obscured by the stylus and may be difficult to detect.

The stylus is a sclerotized element of segment IX, connected on one end to the gonocoxite via the articular membrane. The apex of the stylus bears setae. The homology of this element was not discussed in the literature on Histeridae and clearly requires additional research. No data on the apical setae of the stylus were reported in previous publications. My analysis has shown that the taxa of histerid beetles can be differentiated by the structure and topography of these setae.

The articular membrane connects the gonocoxite to the stylus. Its cuticle is much thinner than that of gonocoxites, so that the membrane has a lighter coloration. The articular membrane bears one or several setae, their number sometimes varying between conspecific individuals. This membrane was not considered in previous publications and is discussed here for the first time. The shape of the articular membrane, as well as the presence and number of setae provide important characters for identification of histerid species.

The articular sclerite is an unpaired sclerite located at the base of the gonocoxites above the vaginal opening. Fibers staining well with Chlorosol Black E extend from this sclerite into the gonocoxite cavities and seem to reinforce the connection between the gonocoxite bases and the sclerite. The unpaired articular sclerite may correspond to tergite X (Reichardt, 1941).

The wall of segment IX in some species is quite strongly sclerotized in the apical part, forming a ventromedian plate.

Thus, the ovipositor of histerid beetles has a complex structure. Its detailed study has revealed new structures that have not been used before in phylogenetic analysis of this family.

RESULTS

Subfamily HISTERINAE Gyllenhal, 1808

Hister illigeri Duftschmid, 1805 (Fig. 2, *A*–*C*)

Material. Russia. *Crimea*, Simferopol District, env. of Perevalnoe, Kizil-Koba area, VI.2011 (V. Shaporinsky), 2 ♀.

Gonocoxites short-oval, with considerable field of setae on the side facing vaginal opening (Fig. 2, *B*). Border of gonocoxites narrow, inconspicuous, lighter than body of gonocoxites. Stylus short, not reaching edge of gonocoxite. Articular membrane oval, with 1 seta. Articular sclerite diamond-shaped. Ventromedian plate in some specimens oval or emarginated, as shown in Fig 2, *C*.

Hister quadrimaculatus Linnaeus, 1758 (Fig. 2, *D*–*G*)

Material. Russia. *Volgograd Province*: Ilovlinskii District, Trekhostrovskaya, 15.VI.2014–20.VI.2019, 6 ♀; Volgograd: Tsentralnyi District, 15.V.2014, 12.VI.2019, 2 ♀; Dzerzhinskii District, narrow valley of Tsaritsa River, 31.V–18.VI.2020, 1 ♀.

Gonocoxites elongate-oval (Fig. 2, *E*), with apical notch, with considerable field of setae on the side facing vaginal opening (Fig. 2, *G*). Border narrow, lighter than body of gonocoxites, covered with inconspicuous bulges along its very edge. Stylus oblong, gradually dilating toward apex, reaching edge of gonocoxites, with dense apical cluster of setae. Articular membrane elongate, with 1 seta. Articular sclerite diamond-shaped, well visible in ventral view.

Margarinotus brunneus (Fabricius, 1775) (Fig. 3, *A*–*C*)

Material. Russia. *Volgograd Province*, Svetloyarskii District, Chapurnikovskaya ravine, 27.IV–28.V.2018, 6 ♀.

Gonocoxites elongate-oval with apical notch. Border narrow, lighter than body of gonocoxites, covered with inconspicuous cuticular bulges (Fig. 3, *A*). Stylus short, ending far short of edge of gonocoxites, with dense apical cluster of setae. Articular membrane oval, with 1 seta, differing from membrane of *M. obscurus* in complex pattern on ventromedian plate (Fig. 3, *C*). Articular sclerite diamond-shaped (Fig. 3, *B*).

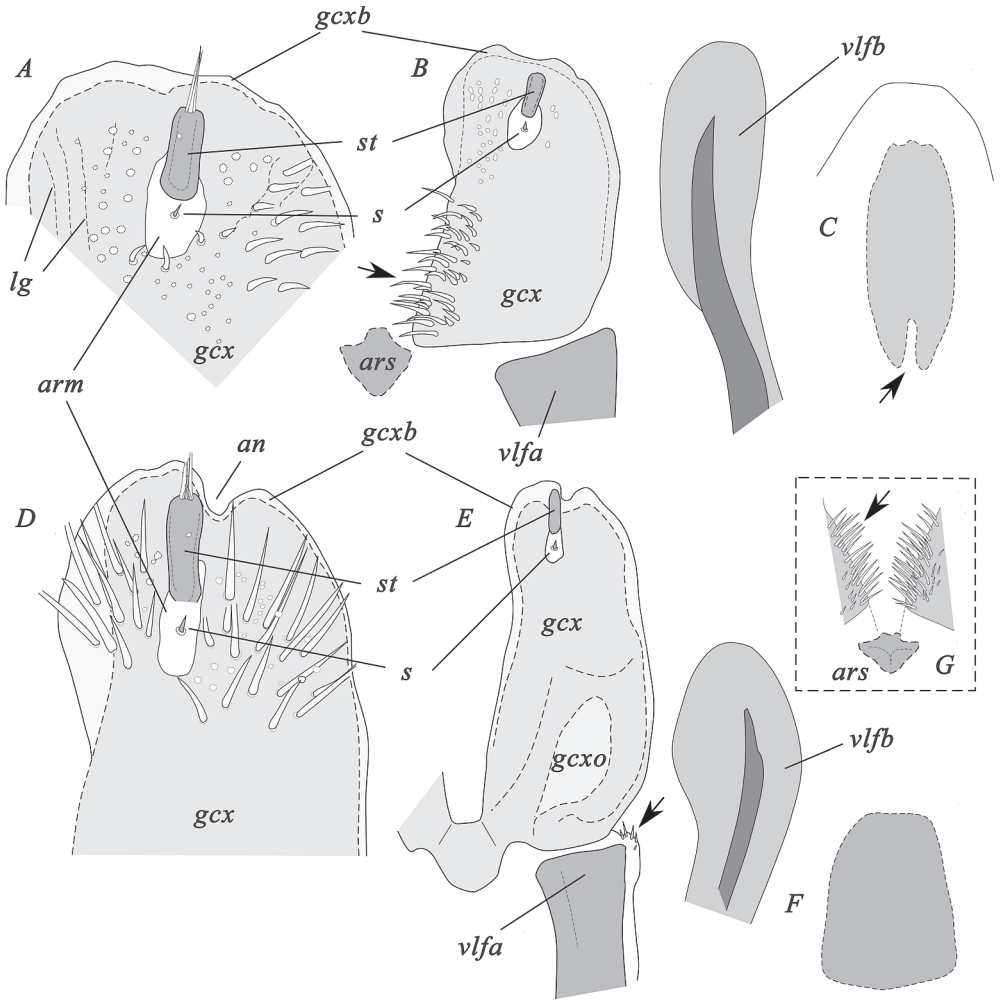

Fig. 2. Elements of the ovipositor: (*A*–*C*) *Hister illigeri* Duftschmid; (*D*–*G*) *Hister quadrimaculatus* Linnaeus: (*A*, *D*) apex of gonocoxite; (*B*, *E*) gonocoxite; (*C*, *F*) ventromedian plate of segment IX; (*G*) articular sclerite in ventral view; *an*, apical notch; *vlfa*, valvifer apex; *vlfb*, valvifer base; *lg*, longitudinal grooves; *s*, seta; other designations as in Fig. 1.

Margarinotus obscurus (Kugelann, 1792)
(Fig. 3, *D*–*F*)

Material. Russia. *Saratov Province*, Rovenskii District, 7.5 km N of Lugovskoe, bank of Bizyuk River, 4–9.V.2010 (I.A. Zabaluev), 1 ♀. *Volgograd Province*, Volgograd, Dzerzhinskii District, narrow valley of Tsaritsa River, 24.IV–31.V.2020, 1 ♀.

Gonocoxites elongate-oval (Fig. 3, *E*), with deep apical notch (Fig. 3, *D*). Border lighter than body of gonocoxites, with vesicular bulges of cuticle forming distinct complex patterns. Stylus of regular barrel-like shape, reaching apical notch on gonocoxite border, with dense apical cluster of at least 5 setae of varying length. Articular membrane elongate-obovate, narrowing toward gonocoxite base, with 1 seta. Articular sclerite diamond-shaped, with pointed beak-like apex. Ventromedian plate poorly developed, without pattern (Fig. 3, *F*).

Subfamily SAPRININAE Blanchard, 1845

Saprinus maculatus (Rossi, 1792) (Fig. 1; Fig. 4)

Material. Russia. *Volgograd Province*, Volgograd, Dzerzhinskii District, narrow valley of Tsaritsa River, 31.V–18.VI.2020, 4 ♀.

Gonocoxites wide, of regular spatulate shape, with smooth edge (Fig. 4, *A*, *B*). Border much darker than body of gonocoxites, its apex smooth or with small notch. Stylus elongate, gradually dilating toward apex,

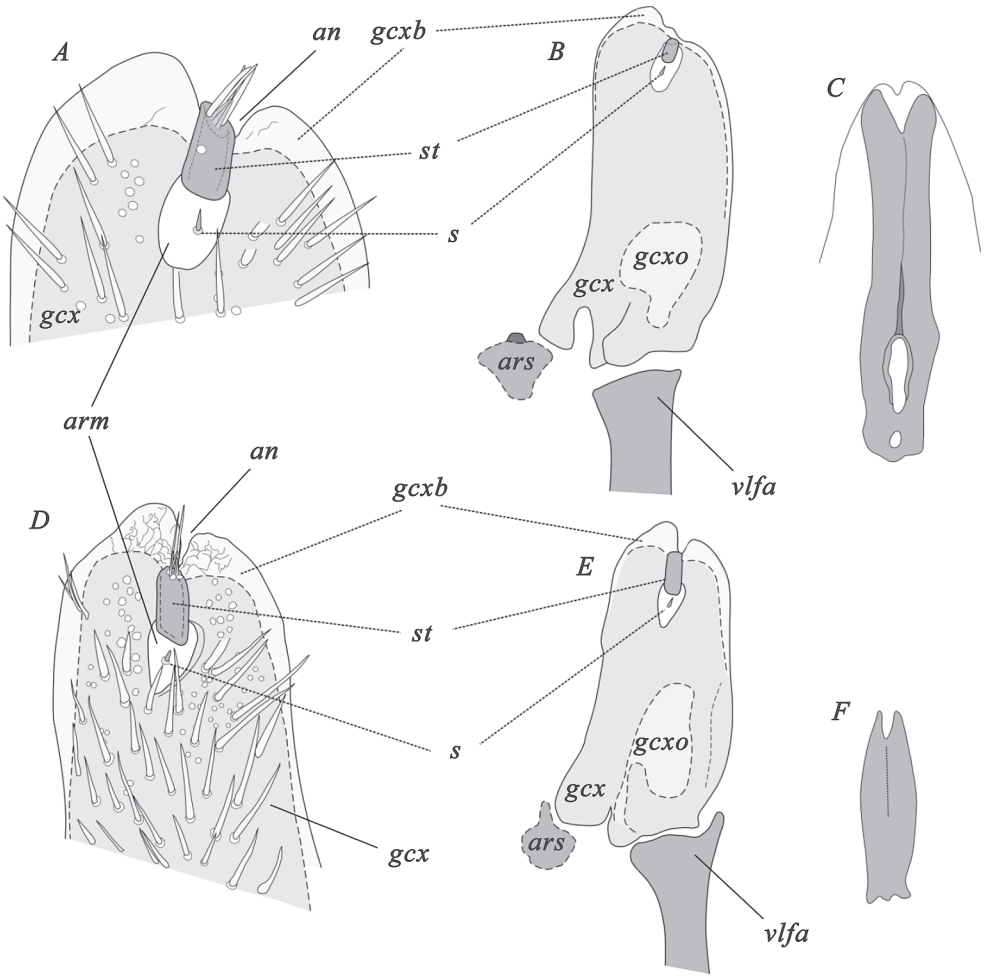

Fig. 3. Elements of the ovipositor: (*A–C*) *Margarinotus brunneus* (Fabricius); (*D–F*) *M. obscurus* (Kugelann): (*A*, *D*) apex of gonocoxite; (*B*, *E*) gonocoxite; (*C*, *F*) ventromedian plate of segment IX. Designations as in Figs. 1, 2.

reaching edge of gonocoxites, with up to 11 apical setae of varying length (Fig. 4, *D*). Articular membrane located in middle portion of gonocoxite, far from its border. Articular membrane bears 3 to 5 setae, as opposed to only 1 seta in *S. bimaculatus* (Fig. 5, *C*). Articular sclerite triangular.

Saprinus caerulescens (Hoffmann, 1803) (Fig. 5, *A*, *B*)

Material. Russia. *Volgograd Province*, Volgograd, Sovetskii District, Oroshaemoe agronomy farm, 13–25.IX.2019, 1 ♀.

Gonocoxites wide, of regular spatulate shape, with smooth edge. Border lighter than body of gonocoxites, its apex smooth or with small notch. Stylus elongate, gradually dilating toward apex, reaching edge of gonocoxites, with several apical setae of varying length. Articular membrane oval, located in middle portion of gonocoxite, near its border, bears 1 seta. Gonocoxites laterally with longitudinal depressions. Articular sclerite triangular.

Saprinus bimaculatus Dahlgren, 1964 (Fig. 5, *C*, *D*)

Material. Kazakhstan. *Turkestan Province*, Otyrar District, 3.5 km W of Baltakol, 13–14.VI.2016 (I.A. Zabaluev), 1 ♀.

Very similar to *S. maculatus*, differing in only 1 seta on articular membrane (Fig. 5, *C*) and narrow base of valvifers (Fig. 5, *E*).

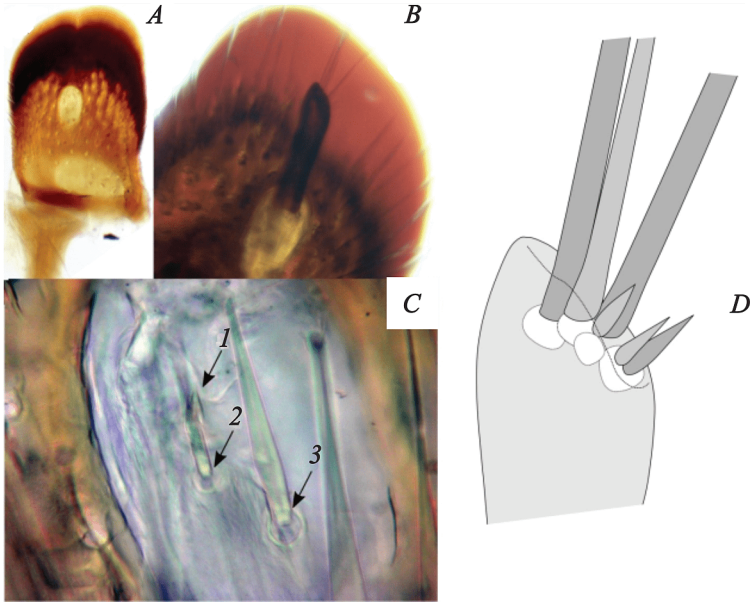

Fig. 4. Main elements of the ovipositor in *Saprinus maculatus* (Rossi): (*A*) left gonocoxite (with stylus removed); (*B*) apex of gonocoxite; (*C*) surface of articular membrane; (*D*) apex of stylus with apical setae; *1–3*, basal setae.

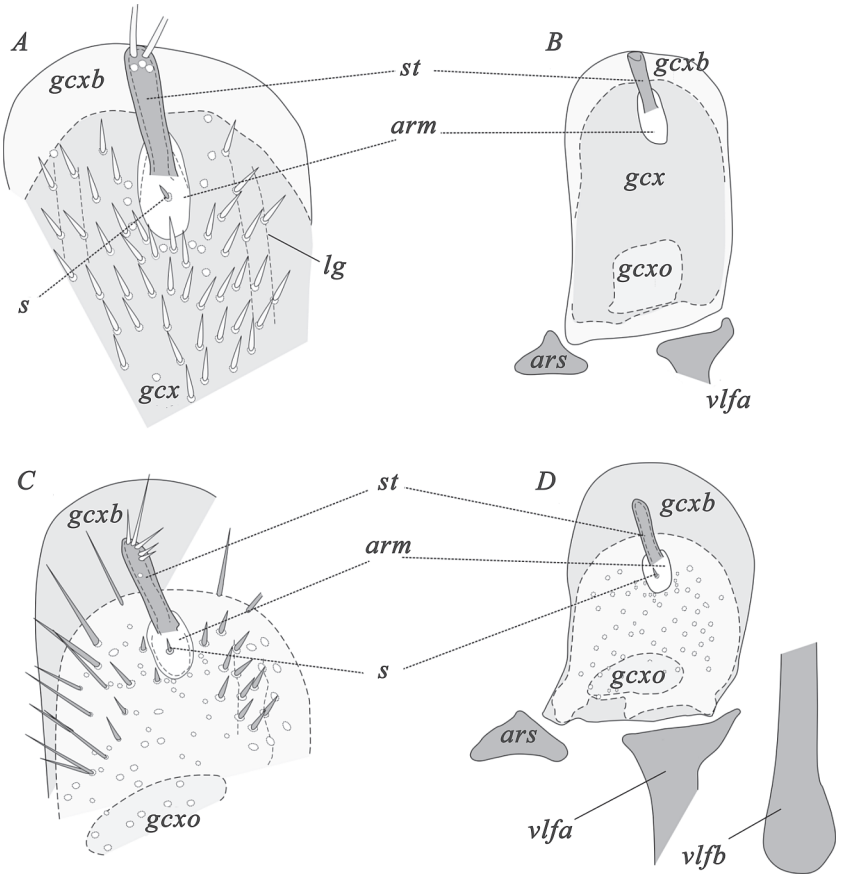

Fig. 5. Elements of the ovipositor: (*A*, *B*) *Saprinus caerulescens* (Hoffmann); (*C*, *D*) *S. bimaculatus* Dahlgren: (*A*, *C*) apex of gonocoxite; (*B*, *D*) gonocoxite. Designations as in Figs. 1, 2.

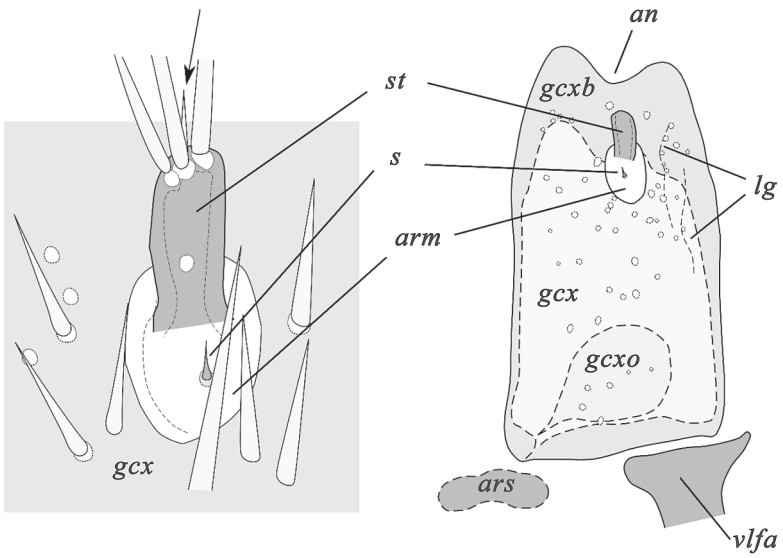

Fig. 6. Elements of the ovipositor in *Chalcionellus amoenus* (Erichson). Designations as in Figs. 1, 2.

Chalcionellus amoenus (Erichson, 1834) (Fig. 6)

Material. Russia. *Volgograd Province*, Volgograd, Sovetskii District, Oroshaemoe agronomy farm, 13–25.IX.2019, 1 ♀.

Gonocoxites wide, with wide apical notch. Body of gonocoxites non-uniformly punctate. Border slightly darker than body of gonocoxites. Stylus short, not reaching edge of gonocoxites, with 4 apical setae, 1 of them much shorter than others. Articular membrane rounded, slightly shifted toward body midline, with 1 seta. Articular sclerite terete.

Hypocaccus* (*Nessus*) *rubripes (Erichson, 1834) (Fig. 7)

Material. Russia. *Volgograd Province*, Volgograd, Sovetskii District, bank of Volga River, 15.VI.2020, 3 ♀.

Gonocoxites elongate (as compared with those of *Saprinus*), parallel-sided, with shallow apical notch. Border smooth, without rugosity, slightly lighter than body of gonocoxites. Base of stylus located on convex surface of articular membrane. Stylus short, of regular barrel-like shape, extending beyond edge of gonocoxites, with 4 apical setae (1 short and 3 long ones). Articular membrane without setae.

Hypocaccus* (*Hypocaccus*) *rugifrons (Paykull, 1798) (Fig. 8, *A–C*)

Material. Russia. *Volgograd Province*, Volgograd, Sovetskii District, bank of Volga River, 5.VI.2020, 2 ♀.

Gonocoxites considerably elongate, parallel-sided, with deep apical notch. Articular membrane strongly shifted toward apex of gonocoxite, merging with its border on one side. Border rugose, lighter than body of gonocoxites. Stylus short, of regular barrel-like shape, extending beyond edge of gonocoxites, with 6 apical setae, 2 of them much shorter than others. Articular membrane without setae. Articular sclerite triangular.

Hypocaccus* (*Hypocaccus*) *rugiceps (Duftschmid, 1805) (Fig. 8, *D–F*)

Material. Russia. *Volgograd Province*, Uryupinsk District, 28.VII–2.VIII.2018, 1 ♀.

Gonocoxites considerably elongate, parallel-sided, with shallow apical notch. Articular membrane obovate, strongly shifted toward apex of gonocoxite. Border smooth, slightly lighter than body of gonocoxites, its ventral surface with large pores discernible as light dots in dorsal view. Border of gonocoxite gradually continuing to its body. Stylus short, of regular barrel-like shape, extending beyond border of gonocoxites, with at least 6 apical setae. Articular sclerite terete, without grooves.

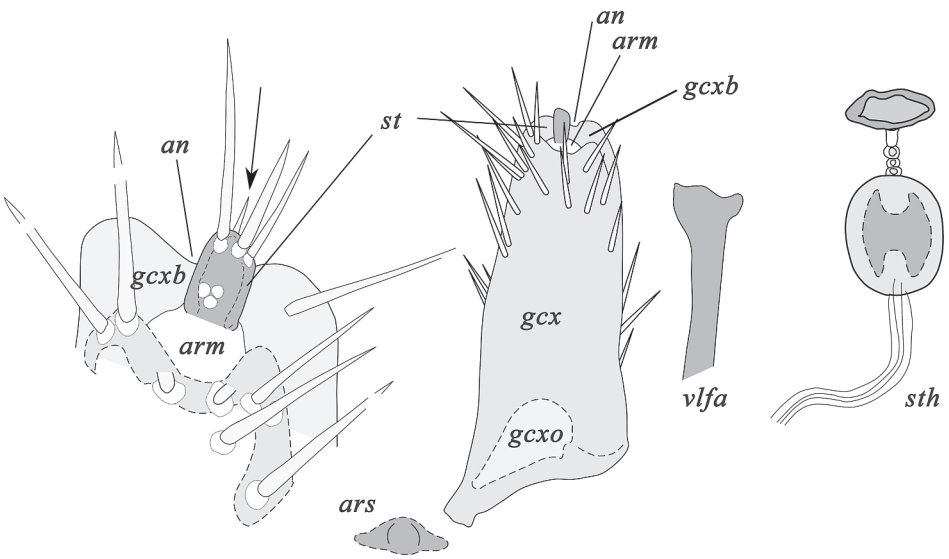

Fig. 7. Elements of the ovipositor in *Hypocaccus rubripes* (Erichson): *sth*, spermatheca; other designations as in Figs. 1, 2.

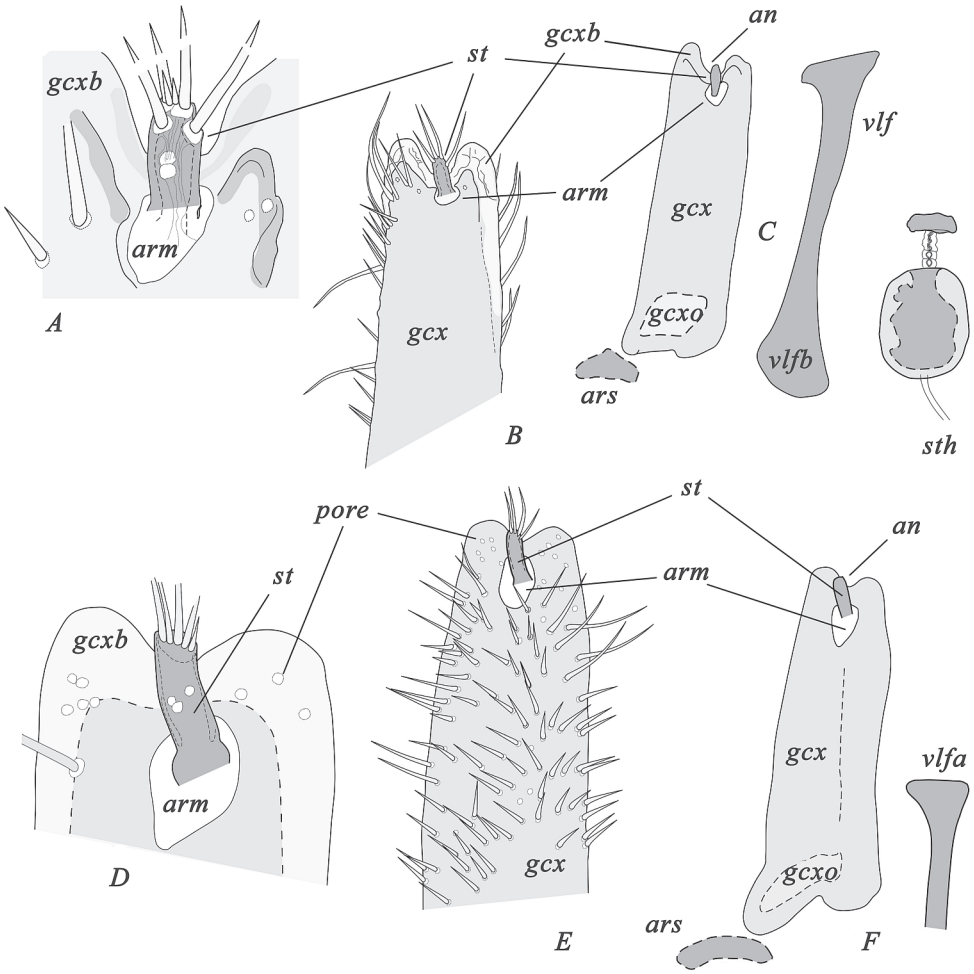

Fig. 8. Elements of the ovipositor: (*A–D*) *Hypocaccus rugifrons* (Paykull); (*E–G*) *H. rugiceps* (Duftschmid). Designations as in Figs. 1, 2, 7.

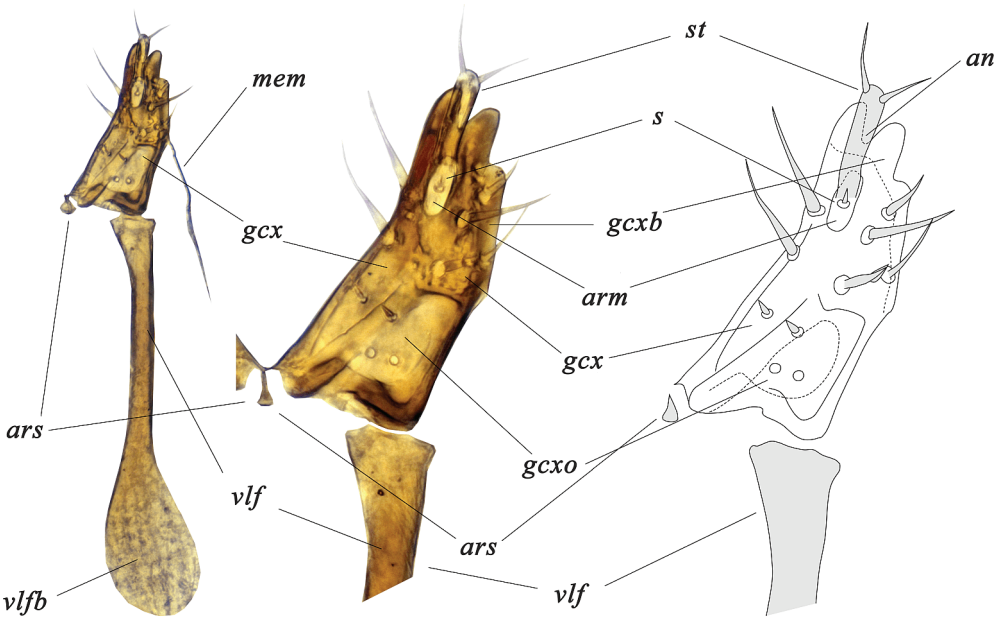

Fig. 9. Elements of the ovipositor in *Acritus minutus* (Herbst): *mem*, membrane; other designations as in Figs. 1, 2.

Subfamily ABRAEINAE Marseul, 1857

Acritus minutus (Herbst, 1791) (Fig. 9)

Material. Russia. *Volgograd Province*, Volgograd, Sovetskii District, bank of Volga River, 17.III.2020, 1 ♀.

Gonocoxites pyramidal, gradually narrowing toward deeply notched apex, with long digitiform processes of gonocoxite border located lateral to apex. Border slightly lighter than body of gonocoxites. Stylus long, extending far beyond edge of gonocoxites, with 2 lateral setae on its apex. Articular membrane rounded, close to middle portion of gonocoxite border, with 1 seta. Articular sclerite small, teardrop-shaped with its apex pointing anteriad.

DISCUSSION

Arriagada (2015) noted a bifurcation of the distal edge ("… bifurcación … sobre el borde distal") of the gonocoxites in *Euspilotus ater* Arriagada, 2015. The same structure was described as denticles on the gonocoxite apex by Lackner and Tarasov (2019), who considered its presence a basal character for the subfamily Saprininae.

According to the data of S. Mazur and M. Ôhara (Mazur and Ôhara, 2003; Mazur et al., 2005), the gonocoxites of *Saprinus quadriguttatus* (Fabricius, 1798) and *S. subustus* Marseul, 1855 have neither apical notch nor additional denticles on their border. An illustration of the ovipositor of *Gnathoncus vietnamicus* Kryzhanovskij, 1972 shows both additional denticles and a notch at the gonocoxite apex (Mazur and Ôhara, 2003). A subsequent study of the ovipositor in species from three subfamilies of Histeridae has shown that the presence of denticles on the gonocoxite apex is correlated with the presence of an apical notch.

The presence of a seta on the articular membrane in species of three subfamilies (Histerinae, Saprininae, and Dendrophilinae) suggests that the seta was also present in the common ancestor of all histerid beetles.

The genus *Hypocaccus* is characterized by specific morphology of the strongly elongate, parallel-sided gonocoxites and the specific position of the articular membrane. Species of the genera *Margarinotus* and *Hister* are united by the presence of a dense apical cluster of setae on the stylus, a diamond-shaped articular sclerite, and non-uniform distribution of setae over the gonocoxites. *Chalcionellus amoenus* shows some features typical of the studied Saprininae species, namely the triangular articular sclerite and numerous setae not forming a dense cluster on the stylus apex. Of all the studied species, *Acritus minutus* has the most peculiar

Table 2. States of morphological characters of female genitalia in the studied histerid beetle species

Species	Character				
	stylus with dense cluster of apical setae	articular sclerite diamond-shaped	border of gonocoxite smooth	articular membrane strongly shifted toward apex of gonocoxite	articular membrane without setae
Hister illigeri Duftschmid, 1805	+	+	−	−	−
H. quadrimaculatus Linnaeus, 1758	+	+	−	−	−
Margarinotus brunneus (Fabricius, 1775)	+	+	−	−	−
M. obscurus (Kugelann, 1792)	+	+	−	−	−
Saprinus maculatus (Rossi, 1792)	−	−	+	−	−
S. caerulescens (Hoffmann, 1803)	−	−	+	−	−
S. bimaculatus Dahlgren, 1964	−	−	+	−	−
Chalcionellus amoenus (Erichson, 1834)	−	−	−	−	−
Hypocaccus rubripes (Erichson, 1834)	−	−	−	+	+
H. rugifrons (Paykull, 1798)	−	−	−	+	+
H. rugiceps (Duftschmid, 1805)	−	−	−	+	+
Acritus minutus (Herbst, 1791)	−	−	−	−	−

ovipositor structure, with pyramidal gonocoxites, the unusually shaped outgrowths of the gonocoxite border, and the position of apical setae on the stylus (Table 2).

The ovipositors of *Ch. amoenus* and *A. minutus* have not revealed any shared characters that could unite *Chalcionellus* and *Acritus* with the other genera.

The studied species vary considerably in a number of features of their female genitalia, which can serve as diagnostic characters: the shape and degree of sclerotization of the gonocoxites and the articular sclerite, the presence and shape of the apical notch on the gonocoxites, the width and color of the gonocoxite border, the position of the articular membrane, the presence and number of setae on this membrane, the length and shape of the stylus, and the shape of the ventromedian plate.

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COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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