

# On the Significance of Genital Characters in Supraspecific Systematics of the Elaterid Subfamily Agrypninae (Coleoptera, Elateridae)

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**Abstract**—The genital characters of some click beetles from the tribes Agrypnini and Conoderini of the subfamily Agrypninae are reviewed. The structural features of male sternite IX, aedeagus, and bursa copulatrix are shown to have great diagnostic value for supraspecific taxa. Based on these characters, the distinctness of the genus *Compsoleacon* Rtt. is confirmed and the taxonomic position of some species from the tribe Conoderini is clarified. *Agrypnus cordicollis* (Cand.) is recorded for the Russian fauna for the first time.

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The subfamily Agrypninae is one of the most ancient and primitive in the family Elateridae (Gurjeva, 1969; Dolin, 1978a). It unites a considerable number of species most of which inhabit the tropical regions of the Old and New World. Despite the publication of reviews devoted to the taxonomy of the entire subfamily (Hayek, 1973, 1979) and its individual tribes (Arnett, 1952; Costa, 1975; Casari, 2008), the taxonomy of Agrypninae is still insufficiently developed due to the fact that most external characters which are used to establish genus-level taxa in more advanced subfamilies of click beetles show very high variability within Agrypninae, both at the genus and at the species level. At the same time, according to a number of authors (Hayek, 1979; Calder, 1996) some taxa of this subfamily are characterized by a peculiar morphology of the male and female genitalia. It is therefore possible that the taxonomic position of some species and genera could be characterized more precisely by using the genital characters together with characters of external morphology, including those which have not been used before in the taxonomy of the subfamily Agrypninae.

The taxonomic significance of the morphological features of the genitalia and terminalia in Elateridae was discussed by many authors. Most experts (Binaghi, 1941a; Becker, 1958; Dajoz, 1962, 1963; Mardjanian, 1977, 1987; Gurjeva, 1979, 1989a, etc.) believed that the male genital morphology could only be used for identification at the species level, whereas the morphology of sclerotized structures in the female

bursa copulatrix might provide important genus-level characters. Kishii (1987) and Dolin (1982) supposed that the genitalia of either sex had features characterizing both species and genera. Gurjeva (1995) concluded in one of her latest publications that the characters pertaining to the aedeagus and the bursa copulatrix were particularly important for establishment of natural supraspecific groups of the Palaearctic Conoderini (= Monocrepidiini, = Oophorini).

Publications devoted to the taxonomy of Elateridae usually cover only the morphology of the male and female genitalia proper, whereas the structural traits of the terminalia are either ignored or considered very briefly. An exception to this rule is the series of papers of Mardjanian (1976, 1980, 1987), in which these structures are considered in sufficient detail.

Our comparative analysis of the morphology of the male genitalia and terminalia in elaterid species from the fauna of Russia and adjacent countries (Prosvirov, 2009) showed that morphological features of sternite IX and the aedeagus could characterize not only genera but also taxa of higher ranks. The morphological traits of the male genitalia and terminalia can be most efficiently used to establish supraspecific taxa within more primitive subfamilies of click beetles (Agrypninae, Cardiophorinae, and Negastrinae). In this communication we will consider in greater detail the genital morphology of some representatives of the tribes Agrypnini and Conoderini (subfamily Agrypninae) and discuss their taxonomic position in view of these data.

The material examined included the authors' collections, some interesting specimens provided by colleagues, and specimens of rare species kept at the Zoological Institute of the Russian Academy of Sciences (ZIN, St. Petersburg), the Zoological Museum of the Moscow State University (ZMMU), and the Department of Entomology of the Moscow State University. The list of material examined includes only those specimens whose genital apparatus was studied. *Agrypnus cordicollis* (Cand.) is reported for the first time from the fauna of Russia.

#### MATERIALS AND METHODS

The preparations of terminalia and genitalia were made using the following method. The structures dissected from the abdomen were cleared in 10% KOH for one day, rinsed in water, and placed for one day in 96% ethanol. Then the genitalia and terminalia were stored in microvials with glycerol. All the drawings were made from glycerol preparations.

The parts of the genital apparatus are described below using the terminology of Zacharuk (1958), Mardjanian (1987), Calder (1996), and Prosvirov (2009). According to these authors, the genital apparatus of Elateridae consists of genitalia proper and terminalia.

The aedeagus consists of the basal plate, parameres, and penis (Figs. 1–20). The penis can be subdivided into the penial tube and the apophyses originating on it. The male terminalia are represented by modified abdominal segments VIII and IX, forming a chamber that conceals the aedeagus. Sternite IX is a moderately sclerotized, oval or elongated plate. It can be subdivided into the sternite proper and its processes forming the sternite frame (Figs. 21–26, 30–34), to which the vertical processes of tergite IX are articulated. The weakly sclerotized dorsal plate lies on the dorsal surface of sternite IX.

The female terminalia are represented by modified abdominal segment VIII whose cavity conceals the ovipositor. The proximal part of the ovipositor is formed by strongly modified segment IX with a moderately or weakly sclerotized base. Two strongly sclerotized strands originate on the lower surface of the base and continue proximally as elongate, gradually dilating apodemes. The distal part of the ovipositor is formed by the coxites, often bearing apical or preapical styli (Figs. 35–38). The bursa copulatrix often possesses heavily sclerotized spines, denticles, or plates (Figs. 39–44).

The following material was examined.

#### Tribe *Agrypnini* Candèze, 1857

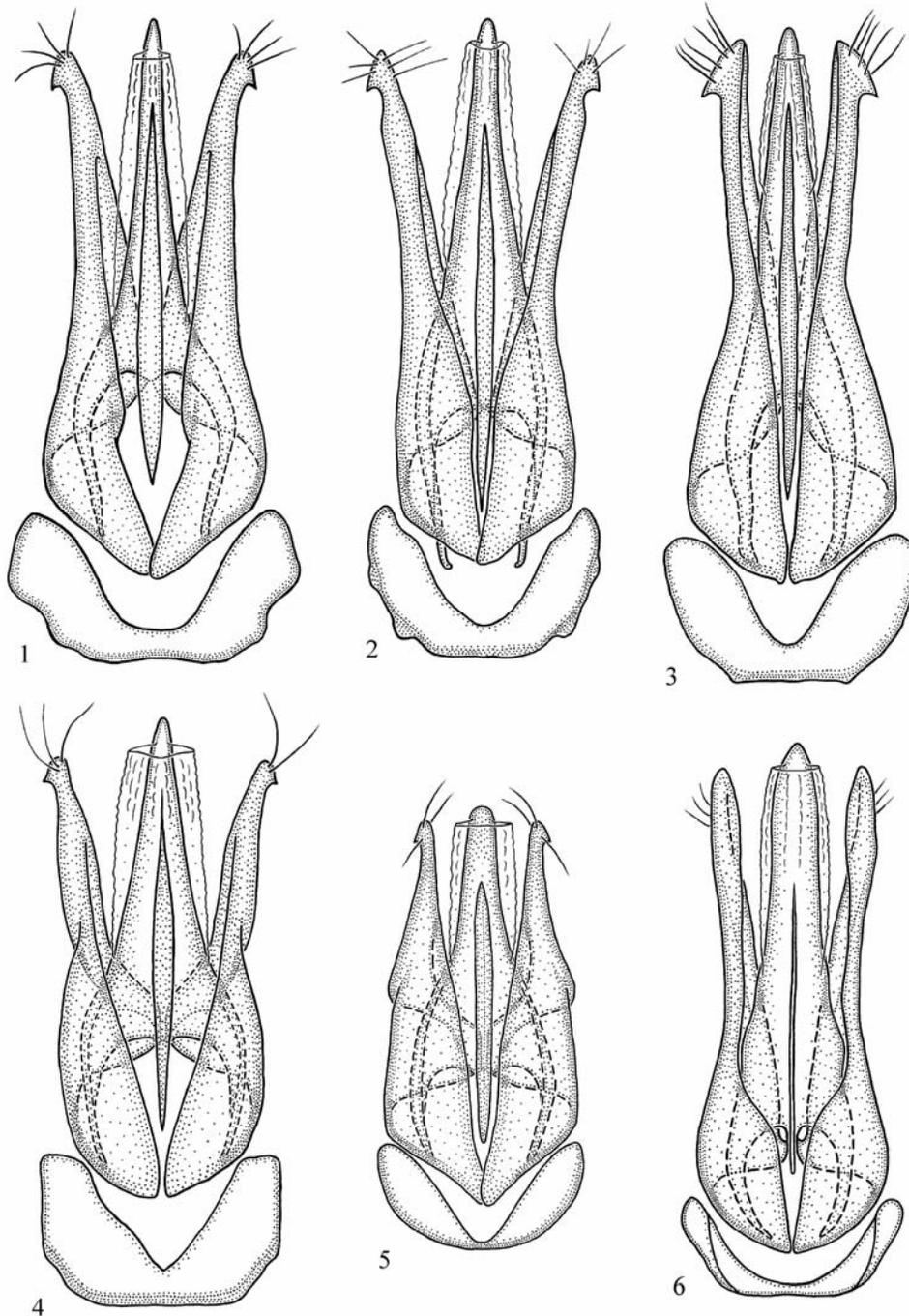
*Compsolacon crenicollis* (Ménétriés, 1832). 12 ♂, 2 ♀. **Russia**. *Krasnodar Territory*: 20 km NE of Tuapse, the Pshekakho River valley, 200–400 m, 15.VI.1993 (V.Yu. Savitsky), 3 ♂, 1 ♀; env. of Krasnaya Polyana, W part of the Aigba Range, 1400–1800 m, 24.VIII.1995 (V.Yu. Savitsky, M.Yu. Savitsky), 1 ♂. *Adygea*: env. of Novopokhladnoe, the Sakhray River valley, 700–900 m, 15.VIII.1999 (V.Yu. Savitsky, M.Yu. Savitsky), 3 ♂. *Dagestan*: the Nukatl Range, the Avar Koisu River valley near the Temiror outfall, 1150–1200 m, 30.VII.1997 (V.Yu. Savitsky, M.Yu. Savitsky), 1 ♂, 1 ♀. **Abkhazia**. The Gagra Range, the Gega River valley, 400–750 m, 8.VII.2006 (V.Yu. Savitsky, M.Yu. Savitsky), 1 ♂. **Azerbaijan**. N of Mt. Kutkashen [now Gabala], upper course of the Damir-Aparanchai, 1800–1400 m, 15.VII.1994 (V.Yu. Savitsky), 3 ♂.

*Compsolacon turkestanicus* Schwarz, 1902. 3 ♂, 4 ♀. **Tajikistan**. Kondara, 10.V.1974, 1 ♀; Khorugh, Botanical gardens, 27.V.1956, 1 ♀; the Darvaz Range, Viskharv, 1600–1700 m, 5.06 (A.V. Bogachev), 2 ♂; “Pamir,” 1 ♂, 2 ♀.

*Compsolacon lapideus* (Candèze, 1857). **Vietnam**. Ha Son Binh Prov., env. of Hoa Binh, 2.X.1979 (A.V. Kompantsev), 1 ♀.

*Compsolacon sinensis* (Candèze, 1857). 3 ♂, 1 ♀. **Vietnam**. The upper course of the Song Da, 20.XII.1961 (Izokh), 1 ♂; NW part of the Tam Dao Range, Shon Zuong, 200 m, 22.III.1962 (O.N. Kabakov), 1 ♂; NW Bai Tuong Mts., near Lang Tianh, 18.IV.1963 (O.N. Kabakov), 1 ♂; Thanh Hoa Prov., SW of Bai Tyong, 5.I.1963 (O.N. Kabakov), 1 ♀.

*Agrypnus murinus* (Linnaeus, 1758). 10 ♂, 10 ♀. **Ukraine**. *Zakarpattia Prov.*, Velikoberezinskii District, env. of Zhornava, 48.972°N, 22.627°E, 15–21.V.2007 (I.V. Mel'nik), 1 ♂. **Russia**. *Moscow Prov.*, Klin District, ~ 25 km NW of Klin, Elgozino, 28.VI.2007 (A.S. Prosvirov), 1 ♂. *Vladimir Prov.*, Kirzhach District, Pershino, 10.VI–16.VII.2004 (A.S. Shmakov), 1 ♂. *Voronezh Prov.*, ~ 10 km NNW of Borisoglebsk, 51°28'35"N, 42°01'40"E, 1.VI.2007 (A.S. Prosvirov), 1 ♂. *Tambov Prov.*, env. of Michurinsk, 53°02'15"N, 40°33'35"E, 31.V.2007 (A.S. Prosvirov), 1 ♂. *Saratov Prov.*, Tatishchevo District, ~ 2 km SW of Yagodnaya Polyana, 51°57'30"N, 45°35'45"N, 15.VI.2007 (A.S. Prosvirov), 1 ♂, 5 ♀.

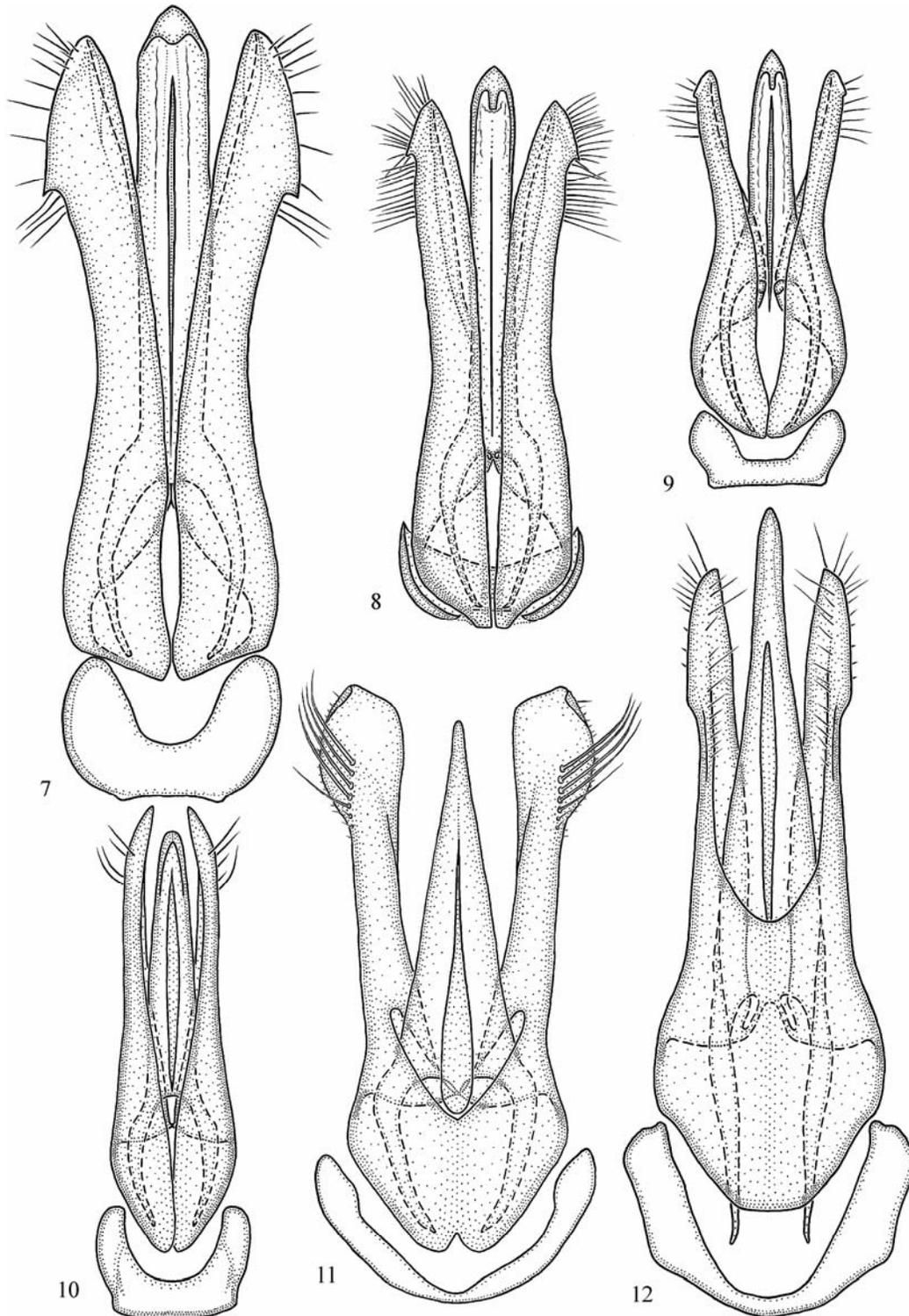


**Figs. 1–6.** *Agrypnus* Eschscholtz and *Colaulon* Arnett, aedeagus, ventral view: (1, 2) *A. murinus* (L.); (3) *A. argillaceus* (Sols.); (4) *A. binodulus* Motsch.; (5) *A.* sp. aff. *gypsatus* (Candèze); (6) *C. rectangularis* (Say).

Krasnoarmeiskii District, ~ 5 km W of Belogorskoe, 50°38'45"N, 45°33'45"E, 15.VI.2007 (A.S. Prosvirov), 4 ♂, 3 ♀. *Volgograd Prov.*, Archedinsk-Don sands, ~ 10 km SW of Frolovo, 49°41'55"N, 43°32'25"E, 2.VI.2007 (A.S. Prosvirov), 2 ♀.

*Agrypnus binodulus* (Motschulsky, 1861). 9 ♂, 3 ♀. **Russia.** *Primorskii Territory*, Lazo Reserve, env. of Lazo, 7–13.VIII.2005 (V.P. Shokhrin), 2 ♂;

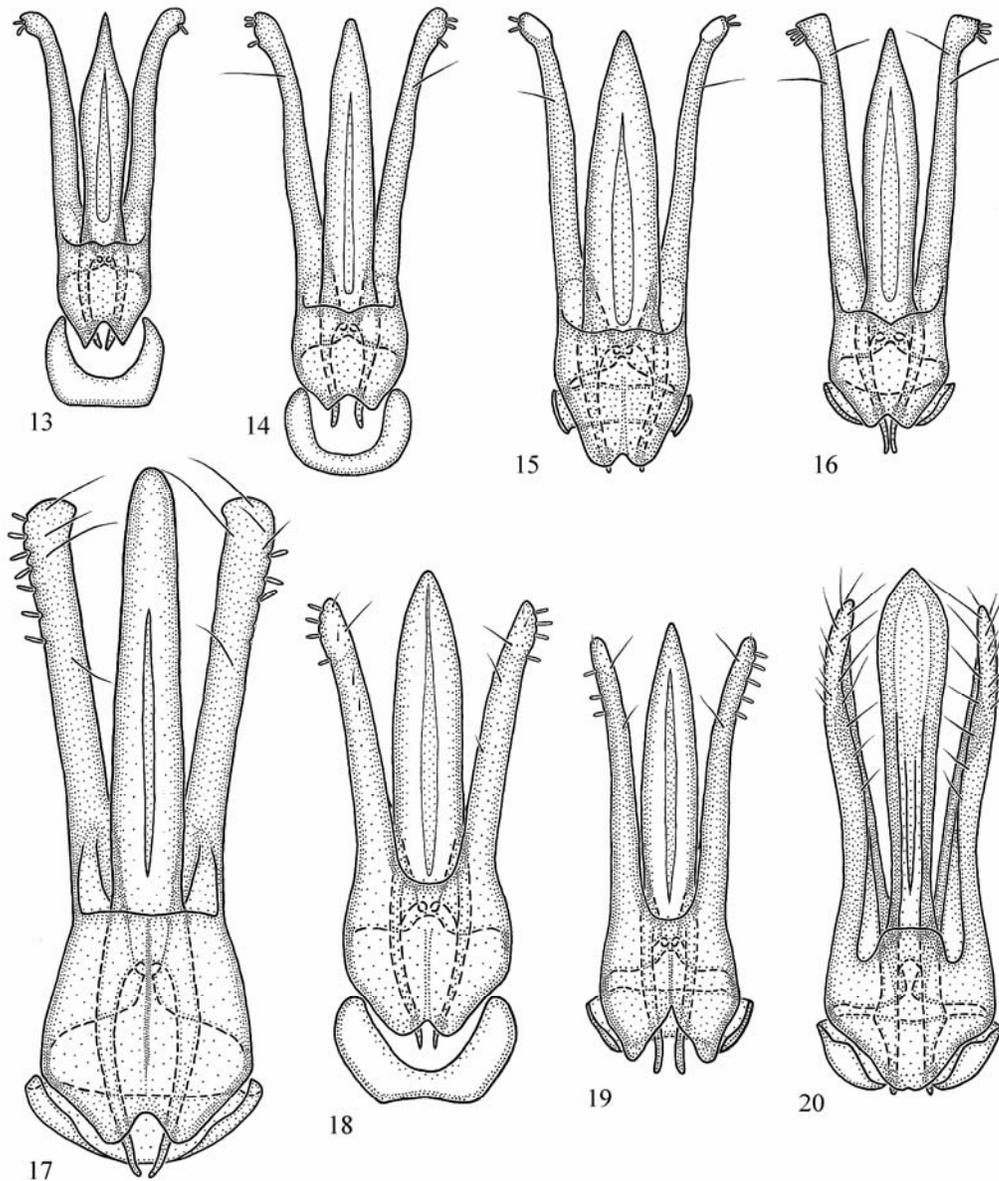
same locality, 1–3.VI.2007 (V.P. Shokhrin), 2 ♂; 43°22'43"N, 133°54'01"E, 6.VII.2005 (K.V. Makarov), 1 ♀; same locality, 29.VII.2005 (K.V. Makarov), 1 ♀; same locality, 13.VIII.2007 (K.V. Makarov, A.A. Zaitsev), 2 ♂; cordon Proselochnyi, 43°00'34"N, 134°07'43"E, 17–21.VIII.2007 (K.V. Makarov, A.A. Zaitsev), 1 ♂; cordon Korpad', 43°15'17"N, 134°07'59"E, 14.VII.2005 (K.V. Makarov), 1 ♂;



**Figs. 7–12.** Aedeagus, ventral view: (7) *Compsolacon turkestanicus* Schwarz; (8) *Com. crenicollis* (Mén.); (9) *Com. sinensis* (Candèze); (10) *Heteroderes* sp. aff. *albicans* Candèze; (11) *Conoderus* sp. aff. *malleatus* (Germ.); (12) *Con.* sp. aff. *scalaris* (Germ.).

same locality, 12–13.VII.2006 (S.K. Kholin), 1 ♀;  
N of Preobrazhenie, 12.VIII.2007 (K.V. Makarov,  
A.A. Zaitsev), 1 ♂.

*Agrypnus argillaceus* (Solsky, 1871). 9 ♂, 5 ♀.  
**Russia.** Primorskii Territory, Lazo Reserve, env. of  
Lazo, 43°22'43"N, 133°54'01"E, 24.VII–5.VIII.2006



**Figs. 13–20.** Aedeagus, ventral view: (13) *Aeoloderma agnata* (Candèze); (14) *Aeoloderma crucifer* (Rossi); (15, 16) *Aeolosomus rossi* (Germ.); (17) *Drasterius heydeni* (Rtt.); (18) *D. figuratus* (Germ.); (19) *D. bimaculatus* (Rossi); (20) *Aeoloides grisescens* (Germ.).

(V.P. Shokhrin), 1 ♂; same locality, Gerasimov Klyuch spring, 43°24'08"N, 133°53'25"E, 11.VI.2006 (Yu.N. Sundukov), 1 ♂; cordon Korpad', 43°15'17"N, 134°07'59"E, 17.VII.2005 (K.V. Makarov), 1 ♂; same locality, 16–18.VI.2005 (Yu.N. Sundukov, V.P. Shokhrin), 1 ♀; Glazkovka, 21.VI.2005 (V.P. Shokhrin), 1 ♀; cordon Amerika, 43°16'16"N, 134°03'01"E, 18–24.VI.2005 (Yu.N. Sundukov, V.P. Shokhrin), 3 ♂, 3 ♀; cordon Proselochnyi, 43°00'34"N, 134°07'43"E, 12.VII.2005 (K.V. Makarov), 1 ♂; same locality, 1–7.VII.2006 (Yu.N. Sundukov), 1 ♂; same locality, 3–5.VII.2007 (Yu.N. Sundukov, V.P. Shokhrin), 1 ♂.

*Agrypnus cordicollis* (Candèze, 1865). 1 ♂, 2 ♀. **Russia.** *Sakhalin Prov.*: Kunashir Island, Tretyakovo, 4.VIII.1973 (I.M. Kerzhner), 1 ♂; same locality, 29.VI.1973 (I.M. Kerzhner), 1 ♀; same locality 21.VII.1985 (Yu. Makarov), 1 ♀.

*Agrypnus* sp. aff. *gypsatus* (Candèze, 1891). **Vietnam.** Ha-Nung, Song Lang, 60 km N of An Khe, 8–27.11.1979 (A.V. Kompantsev), 4 ♂, 3 ♀.

*Colaulon rectangularis* (Say, 1825). "Amer. c., Texas," 2 ♂.

*Colaulon miyamotoi miyamotoi* (Nakane et Kishii, 1955). **Japan.** Takarajima, 2.VII.1960 (M. Sato), 2 ♂.

Tribe **Conoderini** Fleutiaux, 1919

*Aeoloides grisescens* (Germar, 1844). 8 ♂, 3 ♀. **Russia.** *Astrakhan Prov.*: Dosang railway station, antiplague station, 22–29.VII.1996 (V.Yu. Savitsky), 2 ♂; E of Basinskaya station, 46°08'05"N, 47°14'40"E, 2–4.VII.2010 (A.S. Prosvirov), 5 ♂, 3 ♀. **Turkmenistan.** 180 km NE of Ashgabat, near Dushak, 10.V.1995 (V.Yu. Savitsky), 1 ♂.

*Aeoloderma agnata* (Candèze, 1873). 1 ♂, 1 ♀. **Russia.** *Primorskii Territory*: Lazo District, env. of Lazo, 43°22'43"N, 133°54'01"E, 30.VII.2005 (K.V. Makarov), 1 ♂; same locality, 13.VIII.2007 (K.V. Makarov, A.A. Zaitsev), 1 ♀.

*Aeoloderma crucifer* (P. Rossi, 1790). 3 ♂, 3 ♀. **Turkmenistan.** 1 ♂. **Uzbekistan.** Golodnaya Steppe, 12.VI.1920, 2 ♂, 3 ♀.

*Aeolosomus rossii* (Germar, 1844). 16 ♂, 7 ♀. **Russia.** *Volgograd Prov.*: Volgograd, El'shanka, 26.VI.1996 (V.Yu. Savitsky), 4 ♂; W of Volgograd, ~ 3 km E of Vodnyi, Peschanaya Balka, 48°36'35"N, 44°13'55"E, 13.VI.2007 (A.S. Prosvirov), 1 ♀; NW of Elton, near Elton Lake, 17.V.1992 (V.Yu. Savitsky, M.Yu. Savitsky), 1 ♂, 2 ♀; same locality, 15.VI.1999 (V.Yu. Savitsky), 2 ♂; 20 km SW of Volzhskii, Tumak, 1–5.VI.2005 (A.S. Ukrainskii), 2 ♂, 1 ♀. **Astrakhan Prov.**: W coast of Baskunchak Lake, 22.V.2007 (A.S. Prosvirov), 2 ♂, 2 ♀. **Kazakhstan:** *Zapadno-Kazakhstanskaya Prov.*: SW of Dzhanybek, 15–28.VII.1998 (V.Yu. Savitsky, M.Yu. Savitsky), 1 ♂, 1 ♀. **Turkmenistan.** 180 km NE of Ashgabat, near Dushak, 10.V.1995 (V.Yu. Savitsky), 4 ♂.

*Drasterius bimaculatus* (P. Rossi, 1790). 3 ♂, 6 ♀. **Russia.** *Volgograd Prov.*: 20 km SW of Volzhskii, Tumak, 9.VI.2005 (A.S. Ukrainskii), 2 ♀. **Turkmenistan.** 180 km NE of Ashgabat, near Dushak, 10.X.1993 (V.Yu. Savitsky), 3 ♂; same locality, 10.V.1995 (V.Yu. Savitsky), 4 ♀.

*Drasterius figuratus* (Germar, 1844). 7 ♂. **Turkmenistan.** 180 km NE of Ashgabat, near Dushak, 10.X.1993 (V.Yu. Savitsky), 1 ♂; same locality, 10.V.1995 (V.Yu. Savitsky), 6 ♂.

*Drasterius atricapillus* (Germar, 1824). **Uzbekistan.** Env. of Termez, Kumkurgan, Kattakum sands, 27.V.2004 (O.G. Legezin), 1 ♂, 5 ♀.

*Drasterius heydeni* (Reitter, 1891). **Tajikistan.** Ti-grovaya Balka Reserve, 14.V.1988 (A.V. Kompantsev), 1 ♂.

*Drasterius* sp. aff. *sulcatulus* Candèze, 1859. **India.** *Bengalia*, Shiliguri Distr., Sevoke Vill., 7.VI.2008 (V. Patrikeev), 1 ♂.

*Conoderus* sp. aff. *malleatus* (Germar, 1824). **Argentina.** Jujuy, 24.I.2008 (M. Boilly), 2 ♂.

*Conoderus* sp. aff. *scalaris* (Germar, 1824). **Argentina.** Alemania, Salta, 26.I.2008 (M. Boilly), 3 ♂.

*Conoderus* sp. 3. **Australia.** Env. of Broome, 25–27.III.1996 (P.S. Tomkovich), 1 ♂.

*Heteroderes* sp. aff. *albicans* Candèze, 1878. **Vietnam.** *Dong Nai Prov.*, Cat Tien National Park, 11°25'N, 107°25'E, 7.IV.2009 (A.A. Polilov), 1 ♂.

*Heteroderes* sp. 2. **Vietnam.** Exact locality not specified (A.V. Kompantsev), 1 ♂.

## SUBFAMILY AGRYPNINAE CANDÈZE, 1857

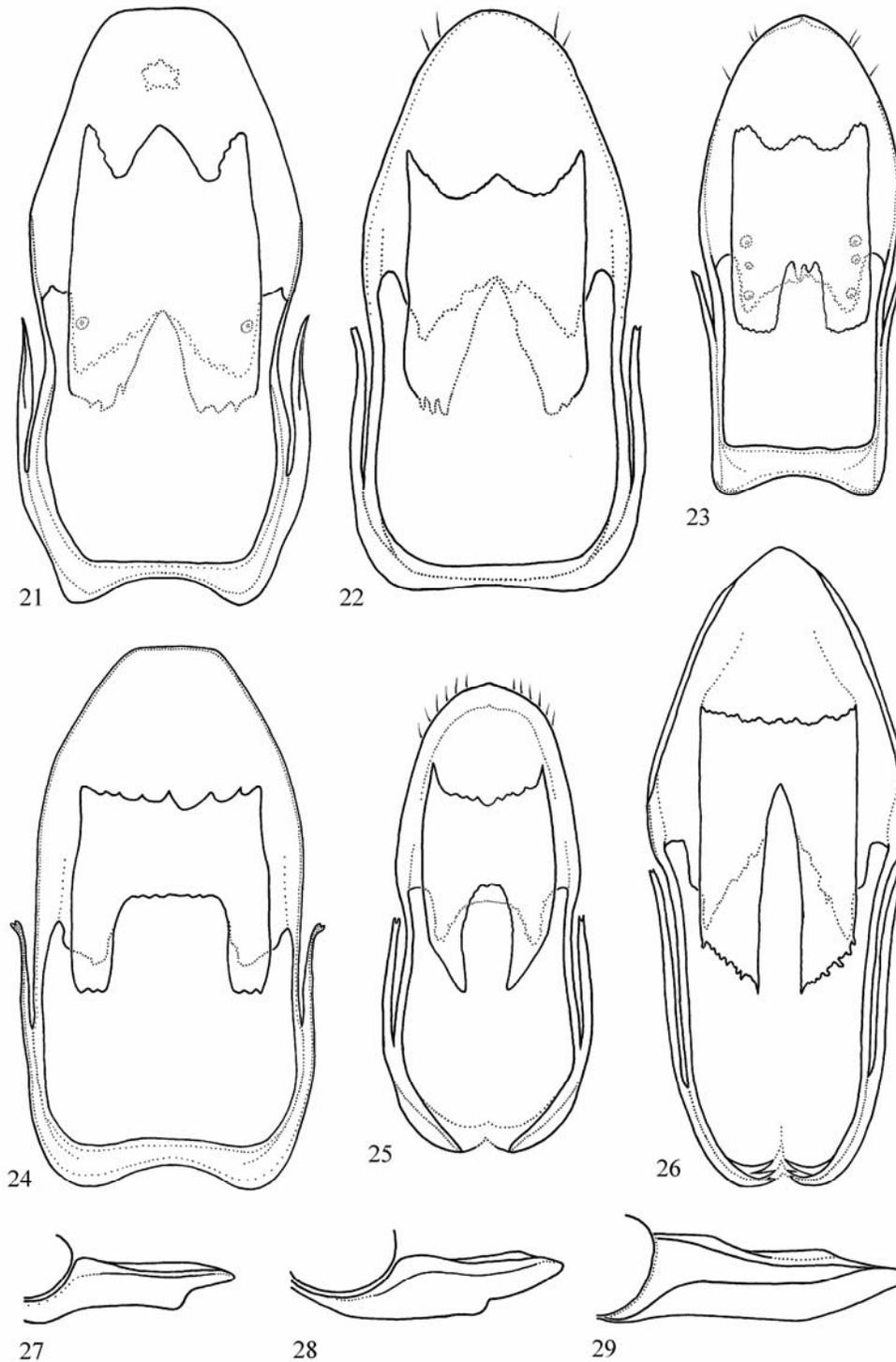
Tribe **Agrypnini** Candèze, 1857Genus *Compsolacon* Reitter, 1905

Reitter, 1905 : 6; Fleutiaux, 1918 : 189 (= *Lacon* auct., nec Laporte, 1838); Winkler, 1925 : 579 (*Compsolacon*); Van Zwaluwenburg, 1966 : 298 (*Adelocera* (*Compsolacon*) auct., nec. Latreille, 1829); Hayek, 1973 : 113 (*Agrypnus*); Gurjeva, 1977 : 794 (*Compsolacon*); Dolin, 1978b : 10 (*Compsolacon*); Mardjanian, 1980 : 260 (*Compsolacon*); Dolin, 1982 : 86 (*Compsolacon*); Mardjanian, 1987 : 39 (*Compsolacon*); Agaev, 1988 : 35 (*Compsolacon*); Gurjeva, 1989b : 497 (*Agrypnus* (*Campsolacon*)); Calder, 1996 : 53 (*Agrypnus*); Cate et al., 2007 : 96 (*Agrypnus*).

Type species *Elater crenicollis* Ménériés, 1832, by monotypy.

The genus includes about 35 species, mostly from Southeast Asia, Australia, and Oceania. The members of the genus are externally similar to species of the genus *Agrypnus* Eschscholtz (type species *Agrypnus murinus* (L.)) but differ from them in the flattened pronotum with serrate lateral margins and long keels extending from its posterior angles almost to the anterior margin. Van Zwaluwenburg (1966) considered *Compsolacon* as a subgenus within the genus *Adelocera* auct., which in his interpretation corresponded to the presently accepted genus *Agrypnus*.

The independent status of the genus *Compsolacon* was questioned by a number of researchers. Fleutiaux (1918) synonymized *Compsolacon* with *Lacon* auct., which in his interpretation corresponded to the present



**Figs. 21–29.** Sternite IX of male, dorsal view (21–26) and prothoracic process, lateral view (27–29): (21) *Agrypnus murinus* (L.); (22, 28) *A. argillaceus* (Sols.); (23) *A. sp. aff. gypsatus* (Candèze); (24, 27) *Colaulon rectangularis* (Say); (25) *Compsolacon sinensis* (Candèze); (26) *Com. crenicollis* (Mén.); (29) *Com. turkestanicus* Schwarz.

genus *Agrypnus*. Hayek (1973, 1979) in her revision of the genus-group taxa of the subfamily Agrypninae also considered *Compsolacon* as a synonym of *Agrypnus*, and so did some other researchers (Calder, 1996; Cate

et al., 2007). This conclusion of Hayek was mostly based on analysis of external characters in Agrypninae. Many characters previously used to establish genera within this subfamily were regarded by Hayek to

be unsuitable for this purpose since they can be found in clearly unrelated representatives of Agrypninae or vary strongly even at the intraspecific level. At the same time, Hayek (1979) noted that the morphological features of the bursa copulatrix could be used to distinguish several groups of genera within the subfamily. The works of the cited author provide almost no information on the male genital apparatus, whereas the genitalia of both sexes in species of the genus *Compsolacon* were not studied at all.

Gurjeva (1977) studied the morphology of the larvae and the female genital apparatus in the genera *Agrypnus* and *Compsolacon* and concluded that *Compsolacon* should be regarded as a separate genus. Later, however, Gurjeva (1989b) considered *Compsolacon* as a mere subgenus of *Agrypnus*, including the species *Agrypnus argillaceus* (Sols.). The independent status of the genus *Compsolacon* was also supported by Dolin (1982) and Mardjanian (1980, 1987). Although the works of these authors contained schematic drawings of the male genital apparatus of *C. crenicollis*, no comment was made on the taxonomic significance of the morphology of the aedeagus and terminalia of the species.

Species of the genus *Compsolacon* clearly differ from representatives of the genus *Agrypnus* in the male and female genital morphology. In members of *Compsolacon* the parameres are weakly dilated at the base and have 1 row of long setae in the apical and preapical portion below the denticle; the penis is almost parallel-sided, narrowing only in the apical part where it has a well-developed lamella protruding towards the preputial field (Figs. 7–9). In species of the genus *Agrypnus* the parameres are strongly dilated at the base and bear only several setae in the apical part above the denticle; the penis narrows gradually towards the apex and has no distinct lamella, its membranous ventral wall noticeably or considerably extending beyond the heavily sclerotized lateral parts of the penial tube (Figs. 1–5). The basal plate in species of *Compsolacon* is often completely bent on the dorsal side of the aedeagus (Fig. 8), which never occurs in the examined representatives of *Agrypnus*.

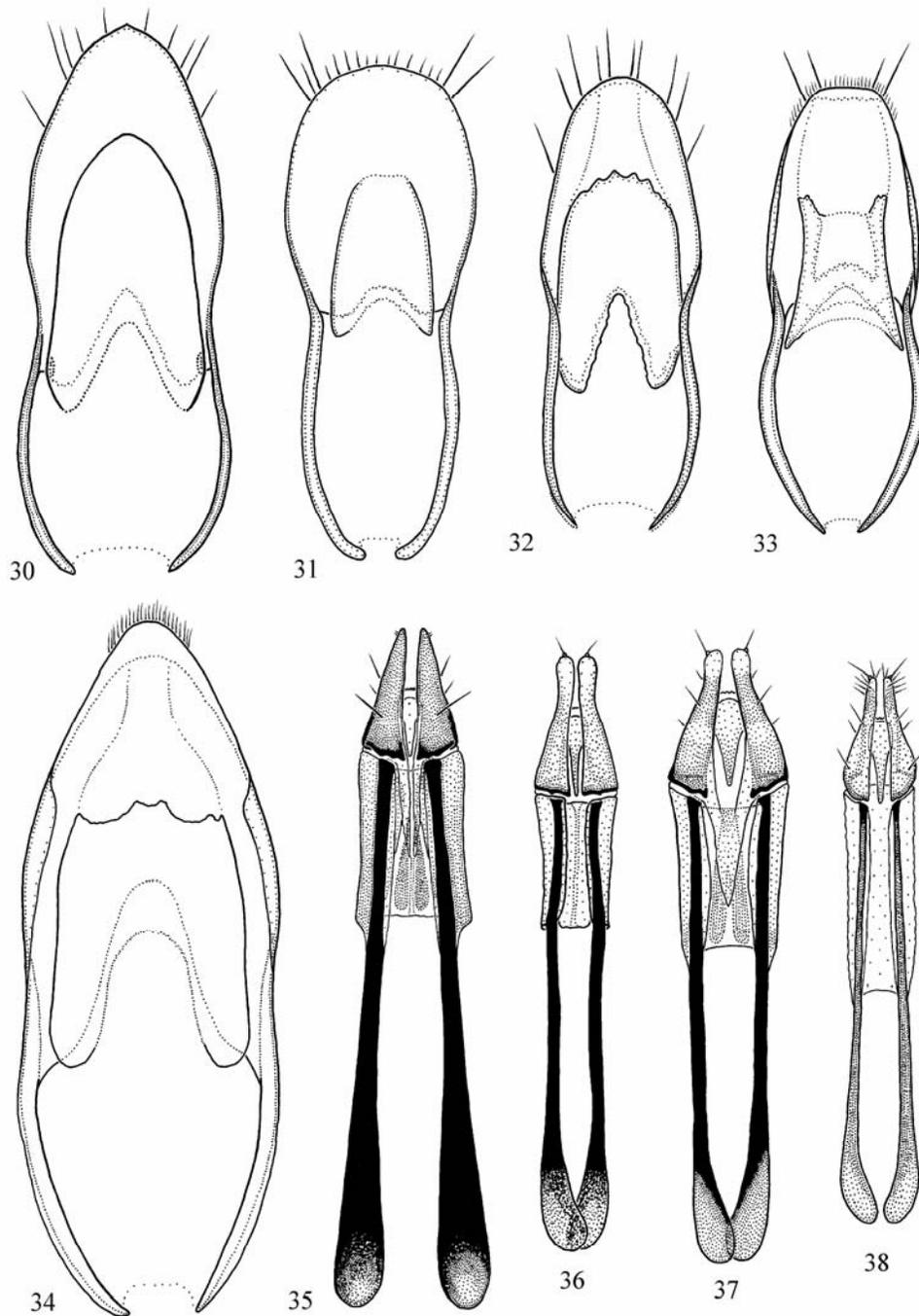
The frame of sternite IX in males is entire in all the examined species of *Agrypnus* (Figs. 21–23) and distinctly divided at the base in all the species of *Compsolacon* for which such data are available (Figs. 25, 26). In this feature species of the genus *Compsolacon* resemble those of the tribe Conoderini, in which the

frame of sternite IX is broadly subdivided at the base (Fig. 30–34).

Species of the genus *Compsolacon* have a relatively narrow, weakly sclerotized ovipositor. The coxites bear several short and long setae in the apical part and small apical styli. The apodemes are weakly sclerotized, approximately as long as the main part of segment IX (Fig. 38). The ovipositor of species of the genus *Agrypnus* is strongly or moderately sclerotized; it has wider coxites with fewer setae and heavily sclerotized apodemes which are much longer than the main part of segment IX (Figs. 35–37). The coxites of *A. murinus*, *A. binodulus* (Motsch.), and *A. sp. aff. gypsatus* (Candèze) are heavily sclerotized, have no styli, and often bear short, probably basiconical sensilla in the lateral preapical region. The coxites of *A. cordicollis* and *A. argillaceus* are moderately sclerotized and bear small apical styli, like those of *Compsolacon*.

The bursa copulatrix of *A. murinus*, *A. binodulus*, *A. sp. aff. gypsatus*, and *A. cordicollis* bears numerous elongate spinules arranged in 2 parallel helical bands. On one end these bands are noticeably dilated and separated by a wider gap, whereas on the other end they are connected forming a U-shaped loop (Fig. 39). At the bend of this loop there is a funnel-shaped sclerotized structure that enforces the distal part of the duct connecting the spermatheca and the bursa copulatrix. The bursa copulatrix of *A. argillaceus* has basically the same equipment consisting of shorter bands of elongate spinules; the funnel-shaped structure is weakly sclerotized and almost indistinct (Fig. 40). The bursal sclerotizations are even less developed in *C. crenicollis* and *C. turkestanicus* Schwarz, being represented by a moderately sclerotized funnel-shaped structure enveloped by a U-shaped band of shorter spinules (Figs. 41, 42). The bursa copulatrix of *C. lapideus* (Cand.) has 3 curved bands with spinules of variable size and a sclerotized funnel-shaped structure (Fig. 43), while that of *C. sinensis* (Cand.) has a moderately sclerotized plate with fine denticles, three plates with densely packed, heavily sclerotized long spines, and a strongly modified funnel-shaped structure with a thin duct (Fig. 44).

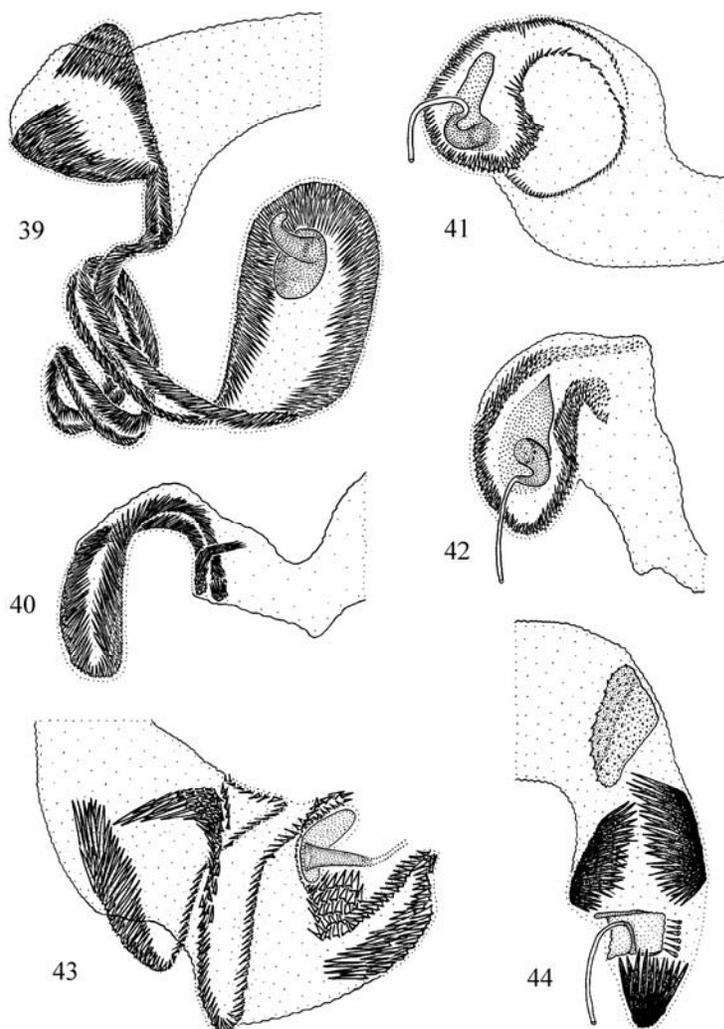
According to most authors, the diagnostic characters of the genus *Compsolacon* include only the flattened pronotum with serrated lateral margins and well-developed keels at posterior angles. However, the lateral margins of the pronotum may also be slightly



**Figs. 30–38.** Sternite IX of male, dorsal view (30–34) and ovipositor, ventral view (35–38): (30) *Drasterius bimaculatus* (Rossi), (31) *Aeoloderma crucifer* (Rossi), (32) *Aeoloides grisescens* (Germ.), (33) *Heteroderes* sp. aff. *albicans* Candèze, (34) *Conoderus* sp. aff. *scalaris* (Germ.), (35) *Agrypnus murinus* (L.), (36) *A. cordicollis* (Candèze), (37) *A. argillaceus* (Sols.), (38) *Compsolacon crenicollis* (Mén.).

serrated in some individuals of *A. argillaceus* and a number of tropical species of *Agrypnus*. It may be for this reason that Gurjeva (1989b) included *A. argillaceus* into *Compsolacon*. At the same time, the members of *Compsolacon* differ from species of the genus *Agrypnus* in other external characters as well, for ex-

ample, in the morphology of the prothoracic process (Gurjeva, 1977). In particular, this process is straight or weakly curved and has no ventral preapical protrusion in all the *Compsolacon* species in our material (Fig. 29), whereas in all the members of *Agrypnus* known to us, including *A. argillaceus*, the prothoracic



**Figs. 39–44.** *Agrypnus* Eschscholtz and *Compsolacon* Rtt., sclerotization of the bursa copulatrix: (39) *Agrypnus murinus* (L.), (40) *A. argillaceus* (Sols.), (41) *Compsolacon turkestanicus* Schwarz, (42) *C. crenicollis* (Mén.), (43) *C. lapideus* (Candèze), (44) *C. sinensis* (Candèze).

process has a more or less distinct ventral protrusion (Fig. 28). It should be noted that according to Gurjeva (1979), the presence of a protrusion or a denticle on the prothoracic process characterizes more advanced taxa of click beetles.

The lateral margin of elytra is distinctly serrated in the anterior part in species of the genus *Compsolacon*; it is smooth and carinate in *A. murinus*, *A. binodulus*, *A. sp. aff. gypsatus*, and *A. cordicollis*, and has a wide gap above the metathorax in *A. argillaceus*. Besides this, the epipleura of elytra in most species of *Agrypnus* have smooth, non-pubescent impressions at the level of hind coxae; these impressions are usually delimited by a distinct anterior transversal keel and serve to accommodate the genual parts of the hind legs. The epipleura of *A. argillaceus* and species of the genus

*Compsolacon* are uniformly pubescent along the entire length and have no such impressions. Based on this character, Reitter (1905) placed *A. argillaceus* into a separate genus *Paralaccon* Rtt. which, together with many other genera, was later synonymized with *Agrypnus* by Hayek (1973).

The larval morphology of *Compsolacon* and *Agrypnus* also shows a number of essential differences (Dolin, 1978b). For example, in the larvae of *Compsolacon* the posterior lobe of the frontal plate is considerably narrower, the base of the plate of the caudal segment is smooth, and the inner branches of the urogomphi are directed towards each other, partly closing the incision on the posterior margin of the terminal segment. In the larvae of *Agrypnus* the posterior lobe of the frontal plate is much wider, the base of

the plate of the caudal segment has two or three pairs of well-developed sclerotized tubercles, and the inner branches of the urogomphi are almost parallel-sided.

Thus, the independent status of the genus *Compsolacon* is confirmed by specific morphological features of both adults and larvae. In addition, the representatives of *Compsolacon* and *Agrypnus* differ considerably in their biology. The larvae of *Agrypnus* species develop in soil, forest litter, or under tree bark (Dolin and Gusakova, 1979), whereas the adults occur on herbaceous and arboreal vegetation. The larvae and adults of species of the genus *Compsolacon* inhabit pebble patches along the river and lake shores (Hayek, 1973; Gurjeva, 1977; Dolin, 1982; original observations). Heavy sclerotization of the ovipositor in *Agrypnus* appears to be related to the need of piercing soil or rotten wood during oviposition. The elongated and weakly sclerotized ovipositor of *Compsolacon* serves for laying eggs into natural cavities and fissures in the ground, where the larvae of these species develop.

It is interesting that long keels at the posterior angles of the pronotum, typical of *Compsolacon*, are also present in other periaquatic representatives of Elateridae, such as *Quasimus* Gz., *Yukoana* Kishii, and *Thurana* Stibick from the subfamily Negastrinae (Stibick, 1971). The periaquatic species of the subfamilies Negastrinae and Hypnoidinae also have elongated and weakly sclerotized ovipositors. Dolin (1982) regarded the periaquatic groups as the most primitive among Elateridae. Considering the morphological and ecological specificity of species of the genus *Compsolacon* and its broad geographic distribution, it may be assumed that this genus is one of the most archaic in the tribe Agrypnini.

Attention is drawn to the extreme similarity between the larvae of *Compsolacon* species and those of *Colaulon scrofa* (Cand.) (Ôhira, 1962; Gurjeva, 1977). The genus *Colaulon* Arnett was established to include the Nearctic species previously assigned to the genus *Lacon* auct. (= *Agrypnus*); these species differ from *A. murinus*, the type species of *Agrypnus*, by a serrated lateral margin of the pronotum and sparser but longer pale squamuliform setae forming regular rows on the elytra (Arnett, 1952). The genus *Colaulon* was synonymized with *Agrypnus* by Hayek (1973). Gurjeva (1977) regarded *Colaulon* as a synonym of *Compsolacon* based on the similar morphology of the larvae. We examined *Colaulon rectangularis* (Say),

the type species of this genus, and found it to be close to representatives of the genus *Agrypnus* in a number of characters. In particular, the species in question has an entire frame of sternite IX and a smooth or weakly serrated lateral margin of the pronotum; the keels at the posterior angles of the pronotum are absent, the prothoracic process has a distinct denticle (Fig. 27), and the epipleura of elytra have a smooth impression at the level of the hind coxae. In the structure of the aedeagus *C. rectangularis* resembles both *Compsolacon* and *Agrypnus* (Fig. 6). *Colaulon* occupies an intermediate position between these two genera, being closer to the latter on the strength of all the characters.

Besides *C. rectangularis*, we also examined *C. miyamotoi miyamotoi* (Nakane et Kishii) from Japan. The species is very close to representatives of the genus *Compsolacon* in external characters and morphology of the male genital apparatus. In particular, the lateral margin of the pronotum and most of the lateral margin of the elytra in *C. m. miyamotoi* are serrated, the epipleura are uniformly pubescent along their entire length and have no impression at the level of the hind coxae, the prothoracic process has no ventral protrusion, the frame of sternite IX is distinctly subdivided at the base, the penis is almost parallel-sided, and the parameres have setae both in the apical and in the preapical part, below the denticle. Judging by the publications of Kishii (1964) and Ôhira (2004), other Japanese species of *Colaulon* are also similar to representatives of *Compsolacon* in the morphology of the prothoracic process and the male and female genital apparatus. Thus, the taxonomic position of the Japanese members of *Colaulon* still needs to be elucidated. They appear to be unrelated to the Nearctic *Colaulon* species and should be assigned to a separate genus.

It should also be noted that the genus *Agrypnus* in the interpretation of modern authors (Hayek, 1973; Calder, 1996; Cate et al., 2007, etc.) appears to be a compound taxon. For example, *A. argillaceus* noticeably differs from *A. murinus* and close species by the morphology of the lateral margin and epipleura of the elytra, a more strongly bent apex of the penis, and the sclerotization of the bursa copulatrix. It is therefore possible that *Paralacoon* and *Compsolacon* were wrongfully synonymized with *Agrypnus*. Moreover, *Compsolacon* in its traditional interpretation may also be a compound group. For example, *C. sinensis* differs from *C. crenicollis* and *C. turkestanicus*, the typical representatives of this genus, by long penial apophyses, the shape of the parameres, and particularly the

sclerotization of the bursa copulatrix. However, additional material should be studied in order to solve the problem of the taxonomic composition of *Agrypnus*, *Compsolacon*, and related genera.

#### Tribe **Conoderini** Fleutiaux, 1919

The tribe Conoderini includes 17 genera and about 800 species (Dolin, 1982; Kishii, 1987, 1996; Ôhira, 1994; Johnson, 1995; Calder, 1996). About 90 species from 13 genera of this tribe are present in the Palaearctic (Cate et al., 2007).

Most researchers have used only the external morphological features of the adults as genus-level diagnostic characters within the tribe Conoderini. The most popular characters are the presence or absence of keels at the posterior angles of the pronotum, its punctation pattern (dual or simple), the specific features of the antennae, and also the presence or absence of a lobule on the 4th tarsomere and the shape of this segment. The taxonomic significance of these characters was differently evaluated by different researchers, because of which some species, for example *Aeoloderma agnata* (Cand.), *Drasterius heydeni* (Rtt.), and *D. figuratus* (Germ.) were assigned to different genera. Some authors (Calder, 1996; Platia and Gudenzi, 1997) attach much importance to the pronotal punctation pattern when distinguishing genera within the tribe Conoderini, whereas other experts consider this character to be unsuitable for supraspecific taxa (Van Dyke, 1932; Gurjeva, 1995).

At the same time, Gurjeva (1995) showed the morphology of the aedeagus and the bursa copulatrix to be of great significance for establishing natural supraspecific groups of Palaearctic Conoderini. The use of such features combined with external morphological characters allows one to make more adequate conclusions about the taxonomic position of dubious species.

Our comparative morphological study of the aedeagus in representatives of the tribe Conoderini from the fauna of Russia and adjacent countries showed that some genera of this tribe could be adequately characterized by the structure of their parameres and the penis shape, which confirmed the previous conclusions of Gurjeva (1995).

For example, in species of the genera *Aeoloderma* Fleutiaux and *Aeolosomus* Dolin the parameres are thickened apically, curved outwards, and bear 2 or 3 rod-like spinules on the outer side (Figs. 13–16). In species of the genus *Drasterius* Eschscholtz the pa-

rameres are almost straight and have several rod-like spinules on the outer side in the apical quarter (Figs. 17–19). Species of the genus *Aeoloides* Schwarz are characterized by inward-curved parameres lacking rod-like spinules but bearing numerous setae, which are long on the inner side and shorter on the outer side (Fig. 20). The penis in representatives of the genera *Aeoloderma*, *Aeolosomus*, and *Drasterius* narrows more or less uniformly from the base or only in the apical third, whereas in species of the genus *Aeoloides* the apical third of the penis dilates in a peculiar way.

According to the data of Gurjeva (1995), the bursa copulatrix in species of the genus *Aeoloides* has 2 elongated sclerotized plates, whereas in *Drasterius* the bursa either lacks sclerotized structures or has numerous fine spinules. Representatives of the genus *Aeoloderma* have 1 sclerotized plate in the bursa copulatrix (Calder, 1996).

Comparison of the details of genital morphology in the species examined and the external characters used for establishing genera in the tribe Conoderini has shown that the genus *Aeolosomus* is characterized by a dilated 1st antennal segment, the absence of keels at the posterior angles of the pronotum, and a strongly tapered 4th hind tarsomere without a lamella. In species of the genus *Aeoloderma* the 1st antennal segment is simple or weakly dilated, the keels at the posterior angles of the pronotum are absent or strongly smoothed, the 4th hind tarsomere is strongly tapered and has a lamella. Representatives of the genera *Drasterius* and *Aeoloides* have a simple 1st antennal segment and a weakly tapered 4th hind tarsomere without a lamella. The posterior angles of the pronotum have 2 keels in *Aeoloides* and 1 keel or, less frequently, no keels in *Drasterius*.

The genera *Aeoloderma* and *Drasterius*, characterized by the complex of external and genital characters described above, include species with both simple (*Ae. agnata*, *D. bimaculatus*) and dual (*Ae. crucifer*, *D. atricapillus*, *D. heydeni*, *D. figuratus*) punctation of the pronotum. Therefore we agree with some previous researchers (Van Dyke, 1932; Gurjeva, 1995) that the nature of pronotal punctation should not be used as a principal diagnostic character for supraspecific taxa within the tribe Conoderini. This opinion was probably shared by Dolin (1978b) who assigned *D. bimaculatus* and *D. figuratus* to the same genus based on the similarity of their larval morphology, even though the adults of these species have different types of pronotal punctation.

Besides the representatives of the genera *Aeoloderma*, *Aeolosomus*, *Drasterius*, and *Aeoloides*, we performed a comparative study of some non-Palaeartic species of the genera *Conoderus* Eschscholtz and *Heteroderes* Latr.

The frame of sternite IX is more or less divided at the base in all the examined species of the tribe Conoderini (Figs. 30–34). This feature appears to be characteristic of the tribe and to have a considerable taxonomic weight, since it is very rarely observed in other groups of Elateridae. In our material, a similar structure of the frame of sternite IX was found only in *Colaulon miyamotoi*, species of the genus *Compsolacon*, and representatives of the subfamily Diminae.

In addition, the parameres in all the examined species of the tribe Conoderini except *Heteroderes* sp. aff. *albicans* Candèze (Fig. 10) are broadly merged at their base on the lower side (Figs. 11–20). According to Calder (1996), such merging of the parameres is typical of most of the Australian Conoderini, excluding the genus *Pseudaolus* Candèze and some species of *Heteroderes*. This character was not mentioned in most of the available publications (Binaghi, 1941b; Gurjeva, 1995; Platia and Gudenzi, 1997, etc.) where the aedeagi of various species of Conoderini were depicted with separate parameres. Broad basal merging of the parameres was shown only in the monographs of Mardjanian (1987) and Calder (1996), in the drawings pertaining to representatives of different genera of this tribe. However, this character is typical of most species of Conoderini; it seems to have a considerable taxonomic significance since this particular type or other types of paramere merging are quite rare in other groups of Elateridae. In particular, during a comparative morphological study of the aedeagus in 400 species from 133 genera of click beetles, various types of paramere merging were recorded (besides Conoderini) only in representatives of the genera *Calais* Laporte (Agrypninae), *Prokraerus* Rtt. (Elaterinae), *Melanotus* Eschscholtz (Melanotinae), *Ascoliocerus* Méquignon, *Berninelsonius* Leseigneur (Hypnoidinae), *Cardiophorus* Eschscholtz, and *Dicronychus* Brullé (Cardiophorinae). According to Calder (1996), the parameres are also merged in representatives of the genera *Austrocalais* Neboiss, *Paracalais* Neboiss (Agrypninae), *Wynarka* Calder (Pityobiinae), *Anilicus* Candèze, *Melanoxanthus* Eschscholtz, *Simodactylus* Candèze (Elaterinae), *Paracardiophorus* Schwarz, *Patriciella* Van Zwaluwenburg (Cardiophorinae), and *Rivulicola* Calder (Negastrinae).

The rod-like spinules in the apical parts of the parameres seem to be present only in species of the tribe Conoderini.

Thus, at least 3 specific morphological features of the male genital apparatus can be considered to be typical of the tribe Conoderini: the basally subdivided frame of sternite IX, the parameres broadly merged at base, and the presence of rod-like spinules in the apical parts of the parameres. The first two characters are typical of all or most members of Conoderini but may be found in representatives of other groups of click beetles as well. The rod-like spinules are not present in all the genera of Conoderini but they seem to be lacking in the rest of Elateridae.

It should be noted that the genus *Conoderus*, including over 300 species from Southeast Asia, Australia, North and South America, is clearly a compound taxon. In particular, significant differences in the structure of the aedeagus and in external morphology between the South American species *C.* sp. aff. *malleatus* (Germ.) and *C.* sp. aff. *scalaris* (Germ.) (Figs. 11, 12) suggest that these species may actually belong to different supraspecific taxa.

Below we consider the taxonomic position of some Palaeartic representatives of the tribe Conoderini.

#### *Aeoloderma agnata* (Candèze, 1873) (Fig. 13)

Candèze, 1873 : 8 (*Aeolus*); Winkler, 1925 : 580 (*Conoderus*); Dolin, 1978b : 15 (*Aeoloderma*); Kishii, 1987 : 66 (*Aeoloderma*); Gurjeva, 1989b : 498 (*Aeoloderma*); Ôhira, 1994 : 229 (*Prodrasterius*); Cate et al., 2007 : 105 (*Drasterius*).

By the presence of the lamella on the 4th tarsomere, *Ae. agnata* resembles the representatives of the genera *Aeolus*, *Conoderus*, and *Aeoloderma* but differs from species of the genera *Prodrasterius* and *Drasterius* in which the 4th tarsomere is simple. The absence of distinct keels at the posterior pronotal angles in *Ae. agnata* places this species close to *Aeoloderma crucifer* (Rossi), the type species of the genus *Aeoloderma*. Species of the genera *Aeolus*, *Conoderus*, *Prodrasterius* and most species of *Drasterius* have well-developed keels at the posterior angles of the pronotum (Kishii, 1987; Calder, 1996).

The structure of the aedeagus in *Ae. agnata* is typical of the genus *Aeoloderma* (Fig. 13) and reliably distinguishes this species from representatives of the genera *Drasterius*, *Conoderus*, *Prodrasterius*, and

*Aeolus*. For example, according to the published data, the parameres of *Aeolus* lack rod-like spinules, whereas those of *Prodrasterius* and *Drasterius* have a row of rod-like spinules in the apical part (Ôhira, 1994; Calder, 1996). The shape and equipment of the parameres vary considerably in species of the compound genus *Conoderus* (Figs. 11, 12) but differ from those of *Aeoloderma* (Calder, 1996).

Thus, both the external characters and the specific features of the aedeagus suggest that *Ae. agnata* should be included into the genus *Aeoloderma*.

***Aeolosomus rossii*** (Germar, 1844) (Figs. 15, 16)

Germar, 1844 : 148 (*Cryptohypnus*); Candèze, 1859 : 381 (*Heteroderes*); Reitter, 1891 : 146 (*Aeolus*); Winkler, 1925 : 580 (*Heteroderes*); Dolin, 1978b : 15 (*Aeoloides*); Dolin, 1982 : 108 (*Aeolosomus*); Mardjanian, 1987 : 42 (*Aeoloderma*); Cate et al., 2007 : 104 (*Aeolosomus*).

This species was originally included in different genera within Conoderini and finally placed into a separate monotypic genus *Aeolosomus* by Dolin (1982). The absence of keels at the posterior angles of the pronotum, a strongly slanted 4th hind tarsomere, and the structure of the aedeagus (Fig. 15, 16) make *Ae. rossii* similar to species of the genus *Aeoloderma*. In addition, the larva of this species most closely resembles the described larvae of the genus *Aeoloderma* (Dolin, 1978b). These two genera are therefore the most closely related within the tribe Conoderini. Mardjanian (1987) even included *Aeolosomus rossii* into the genus *Aeoloderma* and, correspondingly, regarded *Aeolosomus* as a synonym of *Aeoloderma*. However, unlike species of the genus *Aeoloderma*, the adults of *Aeolosomus* lack a lamella on the 4th tarsomere and have a strongly dilated 1st antennal segment. It should be noted that a strongly slanted 4th tarsomere is not characteristic of other representatives of Conoderini that have no tarsal lamella. Considering the peculiar morphology of the 4th tarsomere and the 1st antennal segment in *Aeolosomus rossii*, we believe that *Aeolosomus* should be considered a separate genus. It may also be assumed that the slanted shape of the 4th tarsomere in *Aeolosomus* is a result of complete reduction of the lamella that was present in the ancestral form.

***Drasterius figuratus*** (Germar, 1844) (Fig. 18)

Germar, 1844 : 148 (*Cryptohypnus*); Winkler, 1925 : 582 (*Drasterius*); Binaghi, 1941b : 183 (*Dra-*

*sterius*); Cate et al., 2002 : 33 (*Aeoloides*); Cate et al., 2007 : 104 (*Aeoloides*).

—*turkomanus* Candèze, 1889 : 95 (*Heteroderes*); Dolin, 1978b : 16 (*Drasterius*); Agaev, 1988 : 40 (*Drasterius*); Gurjeva, 1995 : 616 (*Drasterius*).

—*candezei* Reitter, 1891 : 146 (*Aeolus*); Mardjanian, 1987 : 43 (*Aeoloderma*).

*Cryptohypnus figuratus* cannot be placed into *Heteroderes* or *Aeoloderma* because of the structure of its tarsi: the 4th tarsomere of *C. figuratus* is simple whereas in species of the above genera it has a lamella. *C. figuratus* resembles species of the genus *Aeoloderma* in the structure of strongly smoothed keels at the posterior angles of the pronotum; at the same time, it most closely resembles representatives of the genus *Drasterius* and well differs from species of *Aeoloides*, *Aeoloderma*, and *Heteroderes* (Fig. 10) in the structure of the aedeagus (Fig. 18). It should be noted that the Australian species of the genus *Heteroderes* have small spinules at the preapical part of the parameres (Calder, 1996). In details of the larval morphology *C. figuratus* also most closely resembles species of the genus *Drasterius* (Dolin, 1978b).

Thus, considering the larval and adult morphological traits, we suggest that *C. figuratus* should be placed into the genus *Drasterius*.

***Drasterius heydeni*** (Reitter, 1891) (Fig. 17)

Reitter, 1891 : 148 (*Aeolus*); Schwarz, 1906 : 106 (*Heteroderes*); Winkler, 1925 : 581 (*Oophorus*); Dolin and Atamuradov, 1994 : 33 (*Aeoloides*); Gurjeva, 1995 : 617 (*Drasterius*); Cate et al., 2002 : 33 (*Heteroderes*); Cate et al., 2007 : 106 (*Heteroderes*).

—*sericeus* Reitter, 1887 : 512 (*Aeolus*, nom. praecoc., non Candèze, 1859).

Cate and co-authors (2002, 2007) included *D. heydeni* into the genus *Heteroderes* since this species is characterized by dual punctuation of the pronotum. However, the 4th tarsomere is simple in *D. heydeni* but bears a lamella in species of the genus *Heteroderes*. The placement of *D. heydeni* in the genus *Aeoloides* is also insufficiently justified because species of *Aeoloides* are characterized by two keels at the posterior angles of the pronotum, whereas only one keel is present in *D. heydeni*. The simple 4th tarsomere and the presence of one keel at the posterior angles of the pronotum make this species similar to most representatives of the genus *Drasterius*. In the structure of

the aedeagus *D. heydeni* (Fig. 17) also most closely resembles species of this genus.

Thus, considering the external characters and the morphology of the aedeagus, we support the opinion of Gurjeva (1995) that *D. heydeni* should be placed into the genus *Drasterius*.

#### DISCUSSION

The results of comparative morphological studies of the genital apparatus of species of the subfamily Agrypninae demonstrate that characters pertaining to genitalia and terminalia can be used in supraspecific taxonomy of this group of click beetles. It was possible to determine some features of the male genital apparatus characterizing not only individual genera but the tribe Conoderini as a whole. These data refute the common notion that morphology of the male genital apparatus can only be used for identification at the species level (Binaghi, 1941a; Becker, 1958; Dajoz, 1962, 1963; Mardjanian, 1977, 1987; Gurjeva, 1979, 1989a, etc.).

Our previous comparative analysis of the male genitalia and terminalia in Elateridae (Prosvirov, 2009) also revealed the characters describing the subfamilies Agrypninae, Cardiophorinae, Negastriinae, Melanotinae, and Pleonominiae and the tribe Denticollini of the subfamily Denticollinae (= Athoinae). The subfamily Agrypninae was shown to be characterized by a greater diversity of genital morphology than Elaterinae and Denticollinae. The latter subfamilies (with the exception of the tribe Denticollini) have no distinct group characters in the structure of the male genitalia and terminalia. It was only natural that Gurjeva (1979, 1989a), who studied these particular subfamilies in detail, considered the male genital characters to be of little importance for supraspecific taxonomy of Elateridae. However, later, having studied species of the tribe Conoderini, Gurjeva (1995) concluded that morphological characters of the aedeagus and the bursa copulatrix were particularly important for establishing the natural supraspecific groups within this tribe.

The general diversity and existence of group-specific features in the male genital apparatus of representatives of the subfamily Agrypninae probably reflects a more ancient origin of this group as compared to the relatively young subfamilies Elaterinae and Denticollinae. Similar trends can be observed in the orthopteran superfamily Acridoidea (Dirsh, 1956, 1961), where the relatively young subfamilies are

characterized by a more uniform genital morphology. At the same time, in relatively primitive acridoid groups, not only species but also genus- and family-level taxa can be successfully established based on specific traits of the genitalia.

It was shown by the example of the tribes Agrypnini and Conoderini that some traits of genital morphology may be correlated with certain external characters of the adults and larvae. However, many researchers consider such characters (for example, the structure of the lateral margin of the elytra and the presence or absence of impressions on the epipleura at the level of hind coxae in species of the tribe Agrypnini) to be of small taxonomic significance or do not use them at all to diagnose supraspecific taxa. On the contrary, supraspecific taxa are often established based on such external traits that are weakly correlated not only with genital characters but also with other external features (e.g., simple or dual pronotal punctation in species of the tribe Conoderini).

It should be borne in mind that the structure of the male genital apparatus less strictly depends on the environment than the external morphological features (Dirsh, 1961; Gorokhov, 1986). The evolution of the male genital apparatus, unlike that of the external structures and physiological or behavioral characters, is not so strictly determined by adaptive changes in the organism reflecting changes in the environment. Therefore, similarity in the structure of the genital apparatus may better reflect the phylogenetic closeness of taxa than similarity in the external characters; moreover, the external characters correlated with traits of genital morphology may be more suitable for establishment of supraspecific taxa. Thus, the specific structural traits of the male genitalia and terminalia may serve as indicators of taxonomic significance of the external characters. Of course, this approach can be successfully used only for groups characterized by a relatively complex genital apparatus and sufficient variation of its elements. By applying this method to Caucasian weevils of the genus *Otiorhynchus*, the natural species groups were outlined and the composition of several subgenera was reassessed (Davidian and Savitsky, 2006; Savitsky and Davidian, 2007). Our data indicates that this approach can be also used for establishing supraspecific taxa in some groups within the family Elateridae.

Among the elements of the female genital apparatus, only sclerotizations of the bursa copulatrix are

considered by most experts to be suitable for describing the genus-group taxa. Indeed, in our material of species of the genera *Agrypnus* and *Compsolacon*, sclerotizations of the bursa copulatrix showed much better correlation with both external characters and the male genital traits than the characters pertaining to the ovipositor. The evolution of the bursa copulatrix, unlike that of the ovipositor, appears to be weakly dependent on changes in the environmental conditions. Therefore, the well-developed sclerotizations of the bursa copulatrix may represent important taxonomic characters, especially in those taxa of Elateridae where the male genital morphology is quite uniform.

Attention is drawn to the similarity in the structure of sternite IX in *Colaulon miyamotoi*, species of the genus *Compsolacon*, and members of the tribe Conoderini. In addition, the genera *Calais*, *Austrocalais*, and *Paracalais* of the tribe Hemirhipini are characterized by broad basal merging of the parameres resembling that of Conoderini. These facts may additionally support the inclusion of Conoderini in the subfamily Agrypninae.

The basally subdivided frame of sternite IX, broad basal merging of the parameres, and the presence of rod-like spinules in the apical part of the parameres, typical of Conoderini, appear to be apomorphic characters. Most of Agrypninae demonstrate the plesiomorphic states: the entire frame of sternite IX, free parameres, and the absence of rod-like spinules. The same plesiomorphic characters can be observed in most other members of Elateridae; in our material, the rod-like spinules on the parameres were found only in Conoderini. It may therefore be concluded that the tribe Conoderini is the most specialized in the subfamily Agrypninae. This conclusion is confirmed by ecological data. In particular, unlike the rest of Agrypninae, many species of the tribe Conoderini inhabit deserts, steppes, and other open landscapes, which is generally typical of more advanced and specialized taxa of Elateridae.

To summarize, the genital morphology of representatives of the subfamily Agrypninae reveals various combinations of plesiomorphic and apomorphic characters and shows a greater diversity of variants than in other subfamilies of click beetles. Thus, both the external morphological characters of the adults and larvae (Dolin, 1978a) and the structure of the genital apparatus demonstrate mosaic evolution, typical of the subfamily Agrypninae.

Finally, we shall address some methodological problems of studying the genital apparatus of click beetles. As mentioned above, the drawings of the aedeagus of species of the tribe Conoderini published by many authors (Binaghi, 1941b; Gurjeva, 1995; Platia and Gudenzi, 1997, etc.) do not reflect some important features of its morphology, such as the broad basal merging of the parameres. This may result from some drawbacks of the preparation technique: some structural details may become indistinct or obscured in dry preparations or in material embedded in Canada balsam. In particular, the merging of the parameres may be impossible to observe if the aedeagus is positioned in the preparation with its dorsal side up. Such drawbacks can be avoided by using glycerol-embedded material, in which the object of interest can be examined from any side. It should also be noted that a drawing of the elaterid aedeagus in ventral view is generally better suited for diagnostic purposes than a drawing showing the dorsal side.

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