

To the Systematics and Nomenclature of Tenebrionid Beetles of the Tribes Phaleriini, Lachnogyini, Klewariini, and Blaptini (Coleoptera, Tenebrionidae)

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Abstract—The following new synonymies are established: *Paranemia* Heyden, 1892 = *Taklamakania* Ferrer et Yvinec, 2004, **syn. n.**; *Paranemia schroederi* Heyden, 1892 = *P. argiropuloi* A. Bogačev, 1965 = *P. argiropuloi* A. Bogačev, 1967, **syn. n.**; *Paranemia bicolor* Reitter, 1895 = *Taklamakania lepetzi* Ferrer et Yvinec, 2004, **syn. n.**; *Lachnogyia squamosa* Ménériés, 1849 = *L. skopini* Ferrer et Yvinec, 2004, **syn. n.** Placement of the genus *Lachnodactylus* Seidl. in the tribe Lachnogyini and the distinctness of the tribe Klewariini are substantiated. The larva of *Agnaptoria anthracina* G. Medv. is described.

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In the communication concerned with the connections of Tenebrionidae faunas of the sand deserts of Middle Asia and Iran (Medvedev, 2005), main attention was given to the distribution of the tribes including only wingless forms (Erodiini, Tentyriini, Platypini, Pimeliini, and Blaptini). The lack of wings indicates a long-term association of these taxa with arid habitats. The present paper deals with the distribution, morphology, and biology of alate tenebrionid beetles (Phaleriini, Lachnogyini, and Klewariini) in the arid regions of Eastern Palaearctic. In addition, we discuss some nomenclatural issues concerning the tribe Lachnogyini, in relation to the erroneous inclusion of strange elements under new generic and specific names (Ferrer and Yvinec, 2004) and the attempt at reverting to the previously rejected view on the taxonomic position of the genus *Lachnodactylus* (see Ferrer, 2003; Ferrer and Yvinec, 2004).

This communication also includes the description of the larva of *Agnaptoria anthracina* G. Medv. from the subtribe Gnaptorinina (Blaptini). Analysis of larval characters of this species allowed us to describe in more detail the complex of characters specific to this developmental stage of the species included in Gnaptorinina. Previously, only the larva of *Asidoblaps kabaki* G. Medv., representing one of the largest genera in the subtribe, was studied (Medvedev, 2002).

TRIBE PHALERIINI

Most members of the tribe Phaleriini inhabit the supralittoral zone of warm seas and oceans. *Phaleria*

cadaverina F. extends along the coast of the Atlantic Ocean and adjacent seas as far northwards as Britain and Ireland, and along the southern Baltic coast, from Denmark to the Oder mouth. Species of this tribe occur on the Asian Pacific coast from Kamchatka (Kamchatka and Kronotskii Bays) to its southern extreme (Vietnam), as well as in Australia, Tasmania, and New Zealand. They are broadly distributed on the coasts of Southern Asia, Africa, and Madagascar. The American Pacific coast is inhabited by species of this tribe from Alexander Archipelago to northern Chile, and the American Atlantic coast, from Florida to Brazil. These data show the species of the tribe Phaleriini to be very closely associated with sea coasts. Their findings far from the sea are rare. In particular, *Phaleria pilifera* LeC. has been reported not only from the coasts of Mexico and California, but also from Arizona (Papp, 1961) having no sea borders. An exception from this rule is the genus *Paranemia* Heyd., whose species (*P. schroederi* Heyd. and *P. bicolor* Rtt.) have an inland distribution but occupy the stations somewhat resembling sea coasts in their abiotic conditions, such as salinity and humidity. For example, *P. schroederi* occurs on salt marshes overgrown with annual saltworts (Mynbulak Depression in Kyzyl Kum Desert). According to our observations, this species was very common in the ground areas exposed during the Aral Sea reliction from the eastern branch of Ust-Urt. The beetles were found on wet soil under the saltworts, together with the numerous larvae of *Centorus calcaroides* Rtt. and adults of *Scleropatroides hirtulus*

Baudi. The ancestor of the genus *Paranemia* probably inhabited the coasts of inner seas of the Thetis system, and, as these seas disappeared, switched to salt marshes, which represent a denser substrate as compared to the coastal sands. Consequently, beetles of the genus *Paranemia* have a dentiform lobe on the outer margin of fore tibia, clearly differing from other genera of the tribe Phaleriini, in which the outer apical angle of fore tibia is rounded. The Middle Asian lineage of the genus was separated from the Central Asian one during the mountain rise in the Neogene and Quaternary (Fig. 11). Even though the Caspian Sea was connected with the Black Sea before the middle Pliocene as well as during the later Akchagyl transgression, the Caspian supralittoral zone was not colonized by members of the Black Sea coastal fauna from the genera *Ammobius* Guerin, *Phaleria* Latr., and *Trachyscelis* Latr. This fact may be explained by the lower salinity of the Caspian Sea, especially in its northern part, and the effects of this factor upon the natural conditions, including the vegetation and soil. The presence of *P. schroederi* on the western coast of the Aral Sea and near Baku clearly depends on the development of salt marshes in these areas.

The antennal segments in members of the tribe Phaleriini typically bear multiconical sensilla resting in distinct cuticular depressions (Fig. 9) (Medvedev, 1977). These sensilla are most likely to act as hydroreceptors.

The development of these structures is explained by association of the species in question with sea coasts. They also remain important for the continental species of *Paranemia* that prefer stations with saline and wet soil, often isolated in desert areas.

The presence of large multiconical sensilla on antennal segments is typical of the genus *Phtora* Germ. from the tribe Cataphronetini. Species of this genus prefer saline soils in desert areas, while outside the deserts they occur along sea coasts, as does, for example, *Ph. reitteri* Seidl.

Being represented on all the continents and many islands, in particular Madagascar, the Galapagos, and New Zealand, the tribe Phaleriini comprises the genera strongly varying in individual characters but having similar biological features. The following morphological traits are common to all the adults: anterior margin of clypeus straight or almost straight; eyes transverse, without emargination at gena; elytral epipleura reaching sutural angle; outer apical angle of fore tibia

rounded (very rarely protruding, dentiform); abdominal glands present. Some other characters apply to most taxa of the tribe but still show a noticeable variability. In particular, the antennae are short, with 3–5-segmented dense or loose club, sometimes almost gradually dilating toward apex; base of pronotum laterally with short dash-like longitudinal impression, sometimes without any trace of this impression (*Choerodes* White); elytra with 9 intervals, with punctuation sometimes completely irregular (*Choerodes*); outer margin of fore tibia usually slightly arcuately concave, sometimes very deeply arcuately concave, with apical angle of tibia forming long and narrow lobe reaching the apex of 3rd tarsomere; fore and mid tarsomeres not dilated but becoming transverse in species with strongly shortened tarsi. The aedeagus in the resting state is not inverted, i.e., the tegmen is positioned dorsal to penis but can turn along its longitudinal axis during protrusion. In *Phaleria pontica* the basal outer margin of phallobase on one side forms a lobular protrusion on which a muscle from the spiculum gastrale is inserted. Contraction of this muscle rotates the aedeagus. The parameres in dorsal view are narrow or narrowing (Figs. 3, 5). The structure of the spiculum gastrale in the tribe Phaleriini is very specific: the rod-shaped sclerites extend to the apical lobes and form two branches enforcing the anterior and posterior margins of the lobes (*Paranemia*, see Figs. 6, 7; *Phaleria*). The styli of the apical lobes of the ovipositor are short (Fig. 8).

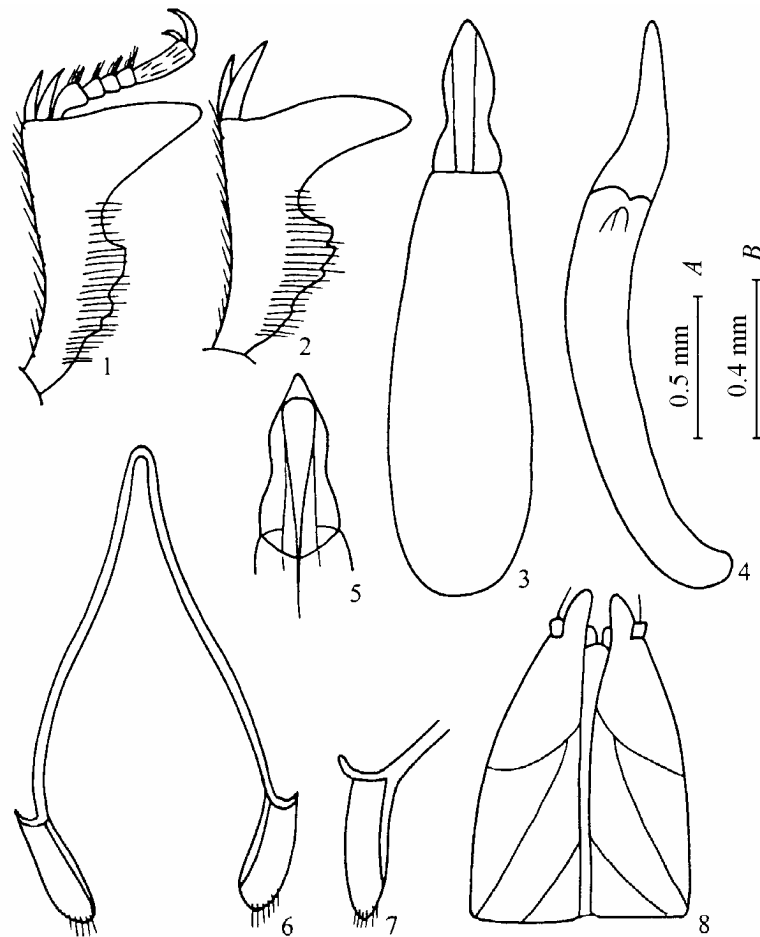
Genus *PARANEMIA* Heyd.

Heyden, 1892 : 103; Reitter, 1916 : 10; Medvedev, 1965 : 371; 1990 : 214; 1992 : 644; Medvedev and Nepesova, 1985 : 141.—*Taklamakania* Ferrer and Yvinec, 2004 : 42 (type species *T. lepetzi* Ferrer, Yvinec, 2004, by original designation), syn. n.

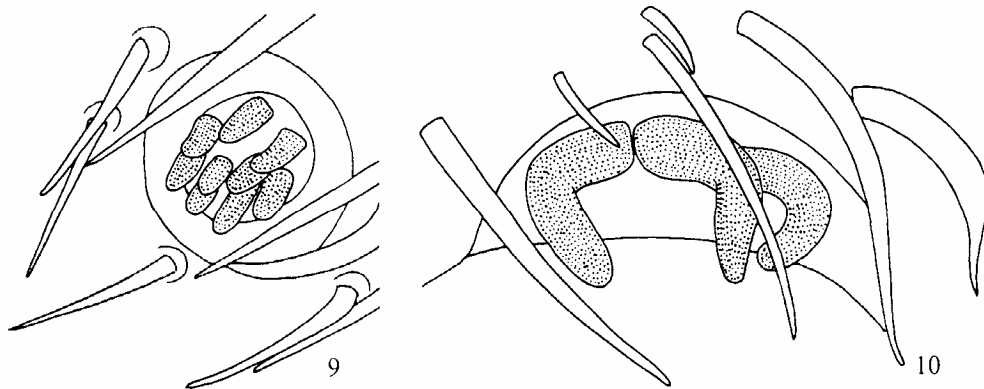
Type species *Paranemia schroederi* Heyden, 1892, by monotypy.

The genus includes two species: Middle Asian *P. schroederi* Heyd. and Central Asian *P. bicolor* Rtt.

Ferrer and Yvinec (2004) described the genus *Paranemia* for the second time under the name *Taklamakania* and included it in the tribe Lachnogyini as the genus closest to *Netuschilia* Rtt. (subtribe *Netuschiliina* Ferrer et Yvinec, 2004). Earlier (Ferrer, 2002), the tribe Lachnogyini was regarded as a member of the pimelioid complex. However, the genus



Figs. 1–8. (1, 3–8) *Paranemia schroederi* Heyd., (2) *P. bicolor* Rtt. [(1, 2) fore tibia; (3, 4) aedeagus, dorsal and lateral view; (5) parameres, ventral view; (6) spiculum gastrale; (7) lobe of spiculum gastrale, lateral view; (8) ovipositor, dorsal view]. Scale bars: A for Figs. 1, 2, 8; B for Figs. 3–7.



Figs. 9, 10. Sensilla on the 11th antennal segment: (9) *Paranemia schroederi* Heyd., $\times 3250$; (10) *Trachyscelis aphodioides* Latr., $\times 3250$.

Paranemia (= *Taklamakania*) is a typical representative of the tenebrioid complex: its ventral glands are well developed, the articulatory membranes between the 3rd and 4th, and also between the 4th and 5th visible abdominal sternites are distinct; the aedeagus in the resting state is not inverted; the antennal segments

bear multiconical sensilla (Fig. 9; Medvedev, 1977 : fig. 60).

***Paranemia schroederi* Heyd. (Figs. 1, 3–9, 11)**

Heyden, 1892 : 103 (type locality: “Alai”); Reitter, 1916 : 10; Medvedev and Nepesova, 1985 : 141.—

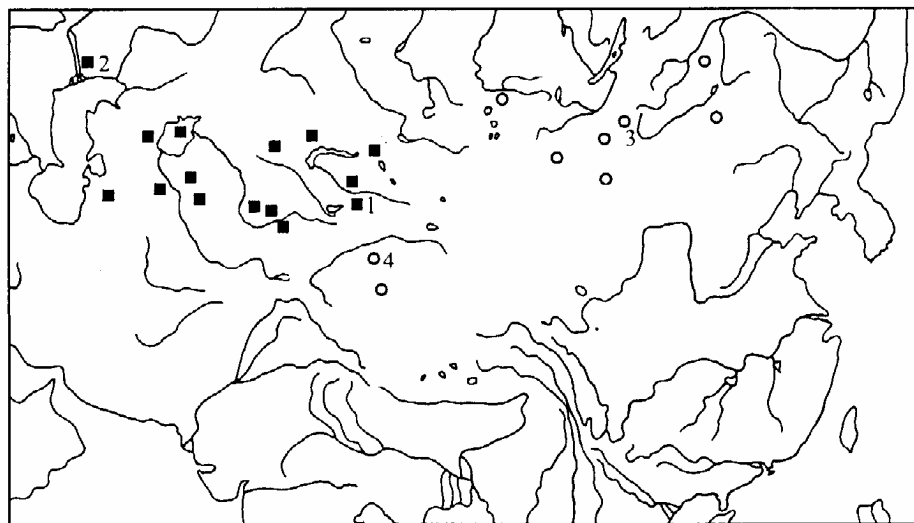


Fig. 11. Distribution of *Paranemia schroederi* Heyd. (squares) and *P. bicolor* Rtt. (circles). Type localities: (1) *P. schroederi*, (2) *P. argiropuloi* A. Bog., (3) *P. bicolor*, (4) *Taklamakania lepetzi* Ferrer et Yvinec.

argiropuloi A. Bogačev in Medvedev, 1965 : 372 (type locality: Astrakhan), syn. n.—*argyropuloi* A. Bogačev, 1967: 160 (type locality: Azerbaijan, Puta station, Baku), syn. n.

In the paper by Bogačev (1967), only two specimens of *P. argyropuloi* from Azerbaijan (Puta station, Baku) were designated as the “type” (holotype) and “cotype” (paratype), though specimens from Russia (Astrakhan—ZIN), Turkmenia (Lake Yaskhan area—ZIN), and Uzbekistan (Khiva—ZIN) were also listed. According to ICZN (2000: 72.4.6), these specimens do not belong to the type series.

Examination of the holotypes of *P. schroederi* (Deutsches Entomologisches Institut, Eberswalde, Germany) and *P. argiropuloi* (Zoological Institute, Russian Academy of Sciences, St. Petersburg—ZIN) showed them to be identical. The holotype of *P. schroederi* has the labels “Alai Schröder” and “Holotypus,” while the holotype of *P. argiropuloi* has the labels “Astrakhan. V. Yakovlev” and “Holotypus. *Paranemia argyropuloi* A. Bogačev.”

The differences between *P. argyropuloi* and *P. schroederi* in coloration of the body, morphology of the legs, and sculpture of the elytra, mentioned by Bogačev (1967), fall within the range of intrapopulation variation. In particular, in the beetles from Barsakelmes Island (64 specimens) and the western Aral Sea coast (20 specimens) body coloration varies from brown to nearly black, while the lobe in the middle part of the outer margin of fore tibia may be either dentate or almost rounded.

Examination of the specimens from Astrakhan, the Lake Yaskhan area, and Khiva, identified by Bogačev (1967) as *P. argyropuloi*, showed them to be *P. schroederi*.

Distribution (Fig. 11). Russia: Astrakhan. Kazakhstan: Barsakelmes Island (Aral Sea); central Betpak-Dala Desert; Balkhash; N coast of Lake Alakul; Almaty Prov., Ayak-Kalkan (middle course of Ili River). Turkmenia: Uzboi, Yaskhan. Uzbekistan: W coast of Aral Sea, 10 km E of Komsomolsk-on-Ustyurt; Khiva; Kyzyl-Kum Desert, Mynbulak Depression; Kuljuktai Mts., Ayak-Guzhumdy; Tashkent; Kokand; Ferghana [“Neu-Margelan”]. Azerbaijan: Puta station, Baku.

Biology. In Middle Asia, this species was found on saline soils, especially in depressions overgrown with annual saltworts, and also in basal hillocks of shrubs from the family Chaenopodiaceae, including the saxaul (*Haloxylon aphyllum*). On Apsheron Peninsula, the beetles were collected on a salt marsh, in wet saline sand near the roots of saltworts and glasswort (*Salicornia*) (Bogačev, 1967).

Paranemia bicolor Rtt. (Figs. 2, 11)

Reitter, 1895 : 157 (type locality: “Nördliche Mongolei, Urga, Changaigebirge”); 1916 : 10; Medvedev and Kaszab, 1973 : 107; Medvedev and Lobanov, 1990 : 199; Medvedev, 1990 : 215, 1992 : 643.—*lepetzi* Ferrer et Yvinec, 2004 : 42 (*Taklamakania*—type locality: “Taklamakan”), syn. n.

The collection of the Zoological Institute, RAS (St. Petersburg) includes one specimen of this species,

collected in Niya Oasis near the southern boundary of Takla Makan Desert. This specimen is very similar to the examined holotype of *P. bicolor* and specimens of this species from other localities. Thus, the name *Taklamakania lepetzi* Ferrer et Yvinec, 2004 is a junior synonym of *Paranemia bicolor* Reitter, 1895.

Distribution (Fig. 11). Mongolia: Urga [Ulaanbaatar]; Central Aymag [District], 6 km W of Undzhul; Eastern Aymag: Tamsag-Bulak; Bayan-Khongor Aymag, N coast of Lake Orog-Nur; Southern Gobi Aymag, Bulgan and 30 km S of Khurmen. Russia: Tuva, 40 km S of Kyzyl, Lake Chedyr; SE Chita Prov., Chindat Lake near Kharanor. China: Kashgar, Niya Oasis. Other material examined: 1 specimen of *P. bicolor* with labels: "Pecking," "Deyrolle," and "78."

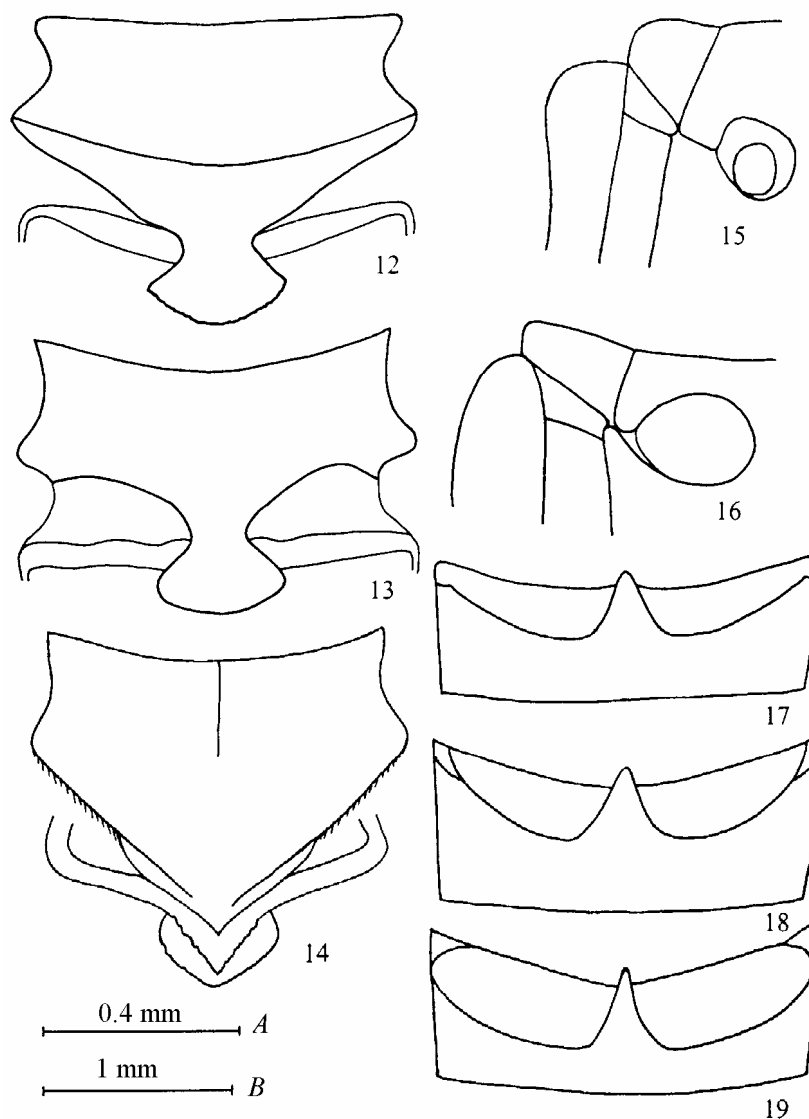
Biology. This species occurs on the coasts of salt lakes, inhabiting the areas overgrown with *Achnatherum* and *Nitraria*. In the sand desert of Takla Makan it was found in organic debris (Ferrer and Yvinec, 2004).

TRIBE LACHNOGYINI

The composition of the tribe Lachnogyini has been repeatedly reconsidered, reflecting the different views as to the taxonomic position of the genus *Lachnodactylus* Seidl. This genus was originally described under the name *Lachnopus* Seidl. in the subfamily Trachyscelinae. The name *Lachnopus* Seidl. was then changed by Seidlitz (1898) to *Lachnodactylus*, since it was found to have been preoccupied in the family Curculionidae. The genus *Lachnodactylus* was included in the subfamily Trachyscelinae based on the incomplete closure of meso- and metathoracic sternites lateral to mid-coxal cavities, and on the presence of the trochantin. Reitter (1904) first agreed with Seidlitz as to the position of *Lachnodactylus* in the tribe Trachyscelini, but, later (Reitter, 1916) placed the genera *Klewaria* Rtt. (subtribe Klewariina), *Lachnogyia* Mén. (subtribe Lachnogyina), *Lachnodactylus* Seidl., and *Netuschilia* Rtt. (subtribe Lachnodactylina) in the tribe Lachnogyini that concluded the pimelioid complex of the family Tenebrionidae. Ferrer (2002) and later Ferrer and Yvinec (2004) tried to justify the placement of *Lachnodactylus* in the tribe Trachyscelini by assuming the aedeagus of *Lachnodactylus digitatus* Seidl. to be non-inverted. However, my examination of the aedeagus in several specimens of this species showed its position to be the same as in species of the pimelioid complex. Evaluation of some other essential

characters clearly shows that the transfer of the genus *Lachnodactylus* was an error. For example, the apical antennal segments of *L. digitatus* bear only setae, whereas in members of Trachyscelini and closely related tribes (Phaleriini, Cataphronetini) these segments bear complex sensory structures, the multiconical sensilla (Figs. 9, 10), which are absent in species of the pimelioid complex.

The eyes of *L. digitatus*, as in other species of Lachnogyini, are strongly transverse, without an arcuate emargination of the anterior margin and with rigid hooked spinules between the facets; the epipleura reach apices of the elytra; the elytra are not striate; the process of prothoracic sternite is very narrow; the process of the 1st visible abdominal sternite between the hind coxae is also narrow, cuneiform, narrowing anteriorly (Figs. 17–19). By contrast with *L. squamosa* and *N. hauseri*, the outer processes of meso- and metathoracic sternites, embracing the mid-coxal cavities in *L. digitatus*, do not join completely, so that the cavities could be interpreted as open (Fig. 15); for this reason the genus *Lachnodactylus* was considered within the tribe Trachyscelini (Seidlitz, 1894, 1898). Weakening of the suture between the outer processes of meso- and metathoracic sternites has a secondary nature resulting from a high mobility of the pronotum, which in *L. digitatus* plays an essential role in locomotion in the loose substrate of the burrows, while the significance of the middle and hind legs and the associated sclerites has decreased. The genus *Klewaria* could also be placed in the tenebrioid complex on the same grounds as *Lachnodactylus*. Showing similarity in the essential characters, the genera of the tribe Lachnogyini have a certain degree of morphological specificity, and the combination of structural features of every genus makes it more or less similar to one of the others. For example, the genera *Netuschilia* and *Lachnodactylus* are similar in the structure of the strongly shortened antennae with a very dense 3-segmented club. Morphology of the dorsal surface of mesonotum, though being uniform in all genera of the tribe (Figs. 12–14), is more similar in *L. squamosa* and *N. hauseri* (Fig. 13) but noticeably different in *L. digitatus* (Fig. 14). The genera *Netuschilia* and *Lachnodactylus* differ from *Lachnogyia* in having larger lobes on the arms of metendosternite (Figs. 26–28). *L. squamosa* (Fig. 20) and *L. digitatus* (Fig. 22) are more similar in the shape of the epiproct. Morphology of abdominal sternite VIII in the male unites the genera *Lachnogyia* (Fig. 23) and *Netuschilia* (Fig. 24). *L. digi-*



Figs. 12–19. (12, 15, 17) *Lachnogyia squamosa* Mén., (13, 18) *Netuschilia hauseri* Rtt., (14, 16, 19) *Lachnodactylus digitatus* Seidl.: (12–14) sclerites of dorsal surface of mesothorax; (15, 16) mesothorax, ventral view; (17–19) 1st visible abdominal segment. Scale bars: A for Figs. 12–14; B for Figs. 15–19.

tatus differs from *L. squamosa* and *N. hauseri* in the absence of a clear suture between the parameres and the phallobase (Figs. 54, 55).

In the structure of the spiculum gastrale, *L. squamosa* manifests a trend to the development of a common stalk (Fig. 36), consisting in convergence of the anterior ends of the rod-like sclerites, whereas in *N. hauseri* (Fig. 48) and *L. digitatus* (Fig. 58) these sclerites are connected to an arcuate bridge. The latter state is typical of the pimelioid lineage (Erodiini, Pimeliini) and represents an initial condition for the tribe Lachnogyini. In this connection it should be noted that the bottom of the aedeagal sac of *L. squa-*

mosa has a V-shaped sclerite whose branches are directed toward the apex of abdomen. A similar structure consisting of two sclerites with separate bases is typical of the tribe Pimeliini (*Pisterotarsa gigantea* F.-W.).

Judging from the morphology of the ovipositor, all genera of the tribe Lachnogyini are rather well separated. In particular, the ovipositor of *L. squamosa* and *N. hauseri* has sclerotized apical lobes without any traces of styli; however, the basal portion of the ovipositor, occupied by the paraproct and proctiger, is long in the former species (Fig. 38) and short in the latter (Fig. 49). In *L. digitatus*, the lobes of the ovi-

positor are membranous narrowing outgrowths bearing tufts of long setae, whereas the basal portion of the ovipositor is very short (Fig. 55). It may be assumed that the tactile function during oviposition is more important in *L. digitatus* than the mechanical function (burrowing). The structure of the spiculum ventrale in the tribe Lachnogyini is also variable, the degree of its elongation being proportional to the length of the ovipositor. The spiculum ventrale of *L. squamosa* is very long and fused with abdominal sternite VIII (Fig. 39), very closely resembling speculum ventrale of Erodiini. The spiculum ventrale of *N. hauseri* is a Y-shaped sclerite whose lateral branches are not fused with the base of abdominal sternite VIII (Fig. 50). The spiculum ventrale of *L. digitatus* is very short, as in *N. hauseri*, Y-shaped, with the apices of lateral branches not fused with the base of abdominal sternite VIII.

Morphology of the ovipositor and associated structures most strongly emphasizes the specificity of each genus within the tribe Lachnogyini and justifies their grouping into the subtribes Lachnogyina, Netuschiliina, and Lachnodactylina. The first and second subtribes in this system are the most distant, whereas the subtribe Netuschiliina occupies an intermediate position. Such relationships are confirmed by the specific biological features of representatives of these taxa.

The common biological feature of members of the tribe Lachnogyini is the use of rodent burrows as shelters and habitats of the preimaginal stages. At the same time, the degree of association with these habitats varies between the genera. Species of the genus *Lachnogyia* (*L. squamosa*, *L. orientalis* Kasz.) exhibit less bothrophilic features in their biology and morphology (relatively long antennae with a weak trend toward the club development and the elongate ovipositor) than species of the other genera. It should be noted that *L. orientalis* was described from eastern India and central Myanmar, i.e., regions with tropical climate. Therefore, the ancestral form of the tribe Lachnogyini may have already existed in Middle and Central Asia when these areas were occupied by savannahs of varying humidity. *L. squamosa*, inhabiting sand deserts from the Caspian Lowland to the Southern Balkhash area (Fig. 42), is a common bothrophilic form, occurring in shelters under various objects lying on the soil surface. The presence of scaly cover on the body, antennae (Fig. 41), and legs of this species reflects a rather high degree of adaptation to diurnal activity in the desert. *N. hauseri* occurs mainly in rodent burrows, and *L. digitatus* has been found only in burrows.

Thus, the ancestral form of the tribe Lachnogyini most probably switched to living in organic-rich burrow habitats during the period when the warm climate predominated in Middle and Central Asia and the open territories were colonized by burrowing rodents. As the climate became more severe in the late Neogene and the Quaternary, the burrow-dwelling forms became more dependent on their shelters. Such factors as bothrophily and the presence of wings facilitated broad distribution of the tribe Lachnogyini over the deserts of Eastern Palaearctic.

Genus *LACHNOGYA* Mén.

Ménétriés, 1849 : 229.—*Lachnogyia* Reitter, 1904 : 34 (laps. cal.).

Type species *L. squamosa* Ménétriés, 1849, by monotypy.

The genus includes two species.

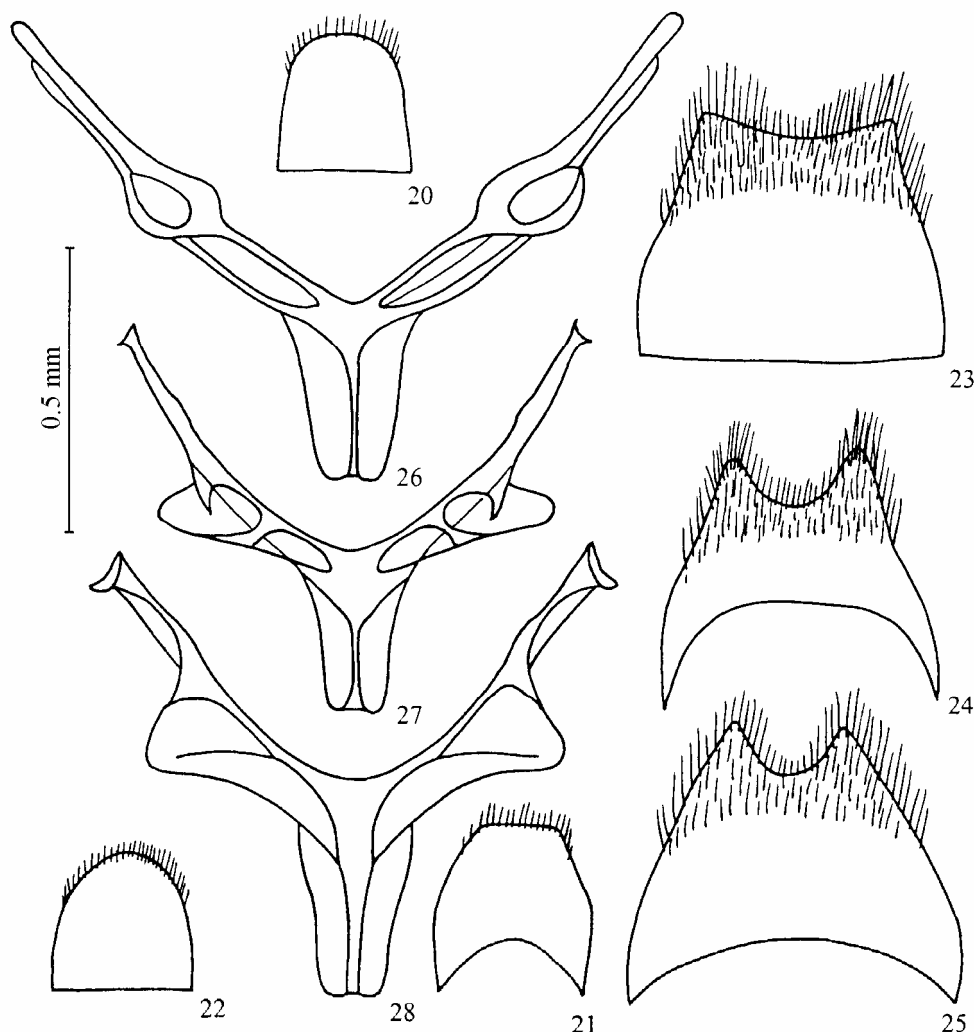
Lachnogyia squamosa Mén.

(Figs. 12, 15, 20, 23, 26, 29–42)

Ménétriés, 1849 : 229 (type locality: Central Kyzyl Kum, “Bakakum”).—*skopini* Ferrer et Yvinec, 2004 : 45 (type locality: “Afghanistan, Kushke”), syn. n.

L. squamosa was described from a single female collected by M. Lehman in the central Kyzyl Kum Desert. The holotype, kept in the collection of the Zoological Institute, RAS (St. Petersburg), has the label “*squamosa* Ménétr. Bakakum” and a golden square.

L. scopini was described from the vicinities of Kushka (SE Turkmenia). No specimen from the type locality of *L. squamosa*, or from other parts of the vast distribution area was examined by the authors. The differences between *L. scopini* and *L. squamosa* in the morphology of aedeagus, described by J. Ferrer and J.H. Yvinec (2004), fall within the narrow variation range of this structure in *L. squamosa* (Figs. 30–35). *L. squamosa* retains well-developed wings and therefore its differentiation into local forms is limited. At the same time, individuals in one sample may vary strongly in size: from 3.9 to 8.5 mm. Wide variation is also observed in body coloration, in particular, in the combination of pale and dark areas. Considering the variability of *L. squamosa*, the name *L. scopini* Ferrer et Yvinec, 2004 should be regarded as a junior synonym of *L. squamosa* Ménétriés, 1849.



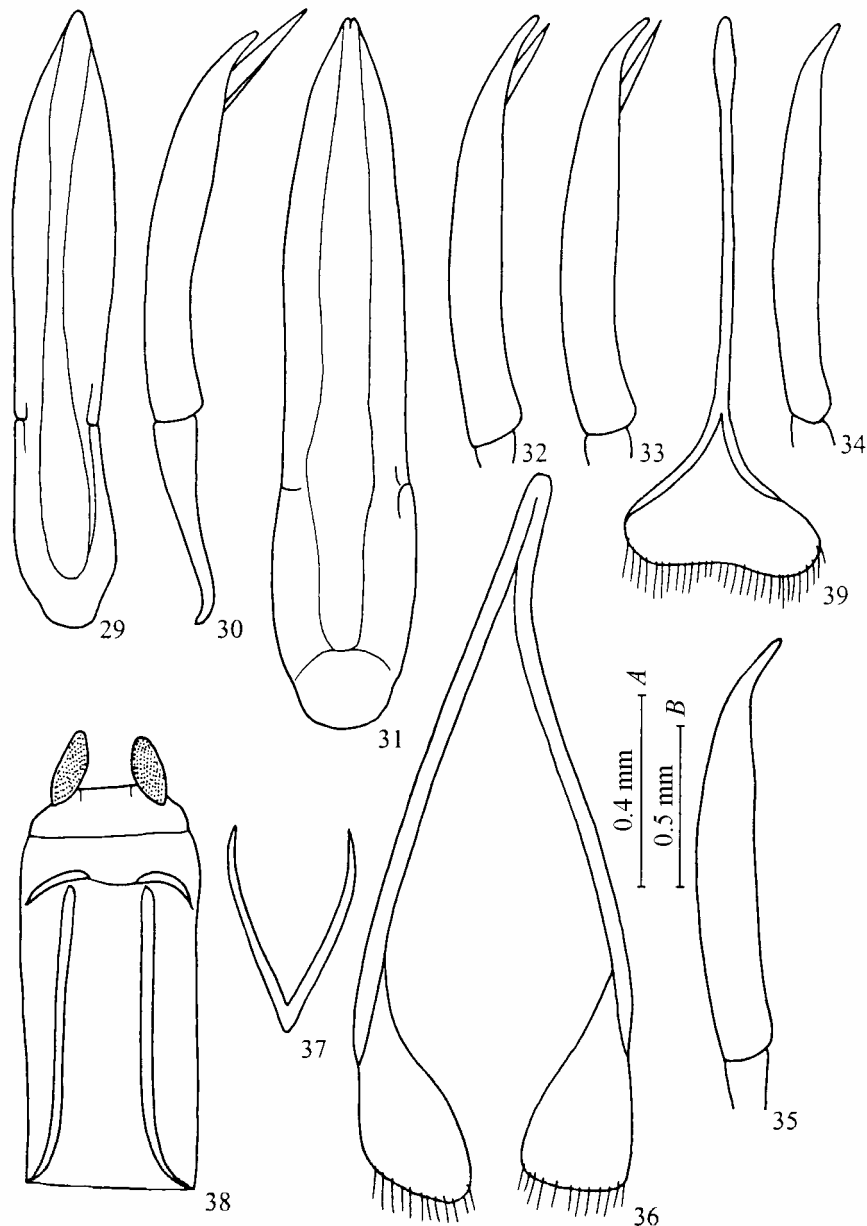
Figs. 20–28. (20, 23, 26) *Lachnogyia squamosa* Mén., (21, 24, 27) *Netuschilia hauseri* Rtt., (22, 25, 28) *Lachnodactylus digitatus* Seidl.: (20–22) epiproct; (23–25) abdominal segment VIII; (26–28) metendosternite, ventral view.

Distribution (Fig. 42). Russia: Kalmykia (Kaspiiskii, Komsomolskii, Rybachii, Chernozemelskii, Utta), Daghestan (Achikulak, Terekli-Mekteb). Kazakhstan: Western (20 km E of Kara-Nogai; 29 km SE of Novaya Kazanka; Kharkin, left bank of the Ural; right bank of the Ural opposite Indeborskii; 21 km SE of Koskol), Southern (Baigakum near Zhulek, Turkmenistan, 120 km W of Chu), and Southeastern (30 km SW of Lepsy station). Turkmenia: Shasenem (41°35'N, 58°41'E); 7 km W of Kun-Urgench; Bugdaili (100 km N of Kyzyl-Arvat); Akhcha-Kuima station; Lake Yashkan coast (50 km N of Kazanjik); 40 km W of Delan; Pereval station; Kirpili (100 km NE of Kyzyl-Arvat); Baskuduk Sands, 15 km WNW of Uchtagan; Ashgabat; 60 km N of Ashgabat; Badkhyz: 12 km W of Kala-I-Mor and the upper part of Kizyl-Dzhar Canyon; 5 km W of Kushka; Takhta-Bazar; Karabil',

10 km NE of Takhta-Bazar; SE Kara Kum Desert: Karamet-Niyaz, Nichka; 10 km NW of Karabek-Aul; Repetek; Charjou. Uzbekistan: "Bakakum" (42°00'N, 63°30'E); 5 and 7 km N of Tamdy-Bulak; 50 km NW of Jingildy; 25 km N of Ayak-Guzhumdy; 95 km NW of Gazli; Ferghana Valley, sands N of Yaz-Yavan. Tajikistan: lower course of the Vakhsh (Jilikul, "Tigrovaya Balka" Nature Reserve), 15 km SE of Shaartuz.

L. squamosa was recorded from eastern Pakistan (Kushalgar, Indus; Pusa Bengal) (Ferrer and Yvinec, 2004) and the Eastern Transcaucasia (Kalyuzhnaya, 1982). The specimens from "Pusa Bengal" may actually belong to *L. orientalis* Kasz.

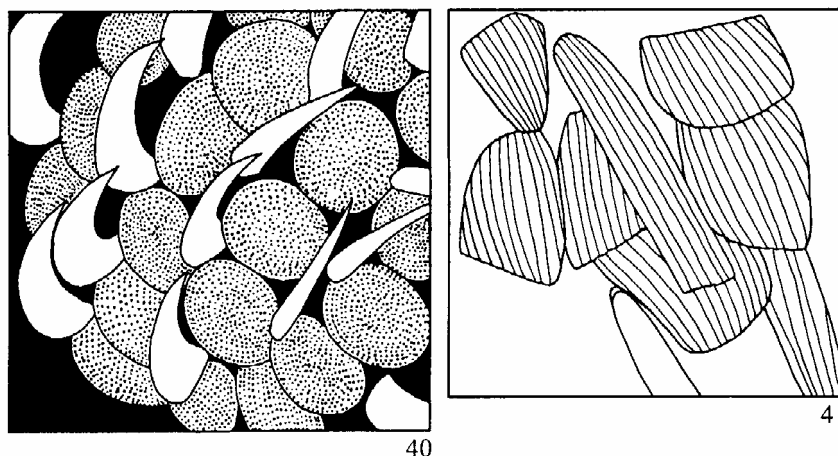
Biology. According to Kalyuzhnaya (1982), *L. squamosa* occurs on fixed and bare barchan sands. The beetles can be found under plant debris, in rodent



Figs. 29–39. *Lachnogyia squamosa* Mén.: (29–31) aedeagus [(29, 31) ventral; (30) lateral view]; (32–35) parameres, lateral view; (36) spiculum gastrale; (37) sclerite of aedeagal sac; (38) ovipositor, ventral view; (39) spiculum ventrale. (29, 30) Kyzyl Kum Sands, Tamdybulak; (31–33) Eastern Ciscaucasia, Terekli-Mekteb; (34, 37–39) lower course of Emba N of Kulsary Vill.; (35, 36) Tajikistan, lower course of Vakhsh River. Scale bars: A for Figs. 29–37; B for Figs. 38, 39.

burrows, and also, in the active state, in sandy barchan areas in the daytime. In the Kara Kum Desert, this species commonly occurs in depressions between the sand-hills, overgrown with saxaul (*Haloxylon aphyllum*); there, the beetles keep under the saltworts and leaves of *Rheum*, and can also be swept from flowering *Malcolmia* sp. According to my observations in early May, 1985, in the lower course of the Emba (15 km N of Kulsary), the beetles find shelter under the sandy crust raised by young stems of *Peganum*

harmala. The larvae develop in gerbil burrows. They differ from the larvae of other tenebrionid species in the following characters: upper surface of abdominal tergite IX flattened, medially covered with foveiform punctures; apex of this tergite raised, with 2 large hooked urogomphi; pygopods absent; pleural surface not delimited by sutures; body integument fulvous brown, hard, punctate, with almost no setae; mandibles distal of condylar pit with 2 setae; anterior margin of hypopharyngeal sclerite arcuately concave.



Figs. 40, 41. *Lachnogyia squamosa* Mén.: (40) lower portion of eye, $\times 900$; (41) scales on 1 antennal segment, $\times 1750$.

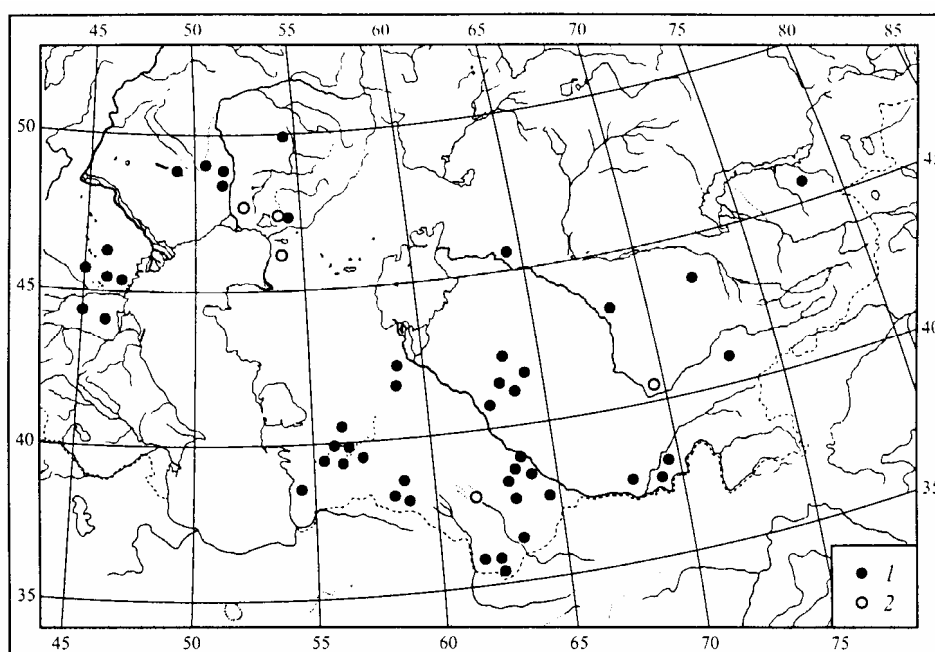


Fig. 42. Distribution of *Lachnogyia squamosa* Mén. (1) and *Lachnodactylus digitatus* Seidl. (2).

***Lachnogyia orientalis* Kasz.**

Kaszab, 1982 : 57 (type locality: India, Bengal).

Material examined. Holotype (“Vorder-Indien, Bengal”) and 1 paratype (“Paratypus. 1982. *Lachnogyia orientalis* Kaszab”).

Distribution. India: Bengal. Myanmar: Pagan.

Genus **NETUSCHILIA** Rtt.

Reitter, 1904 : 35; Ferrer and Yvinec, 2004 : 48.

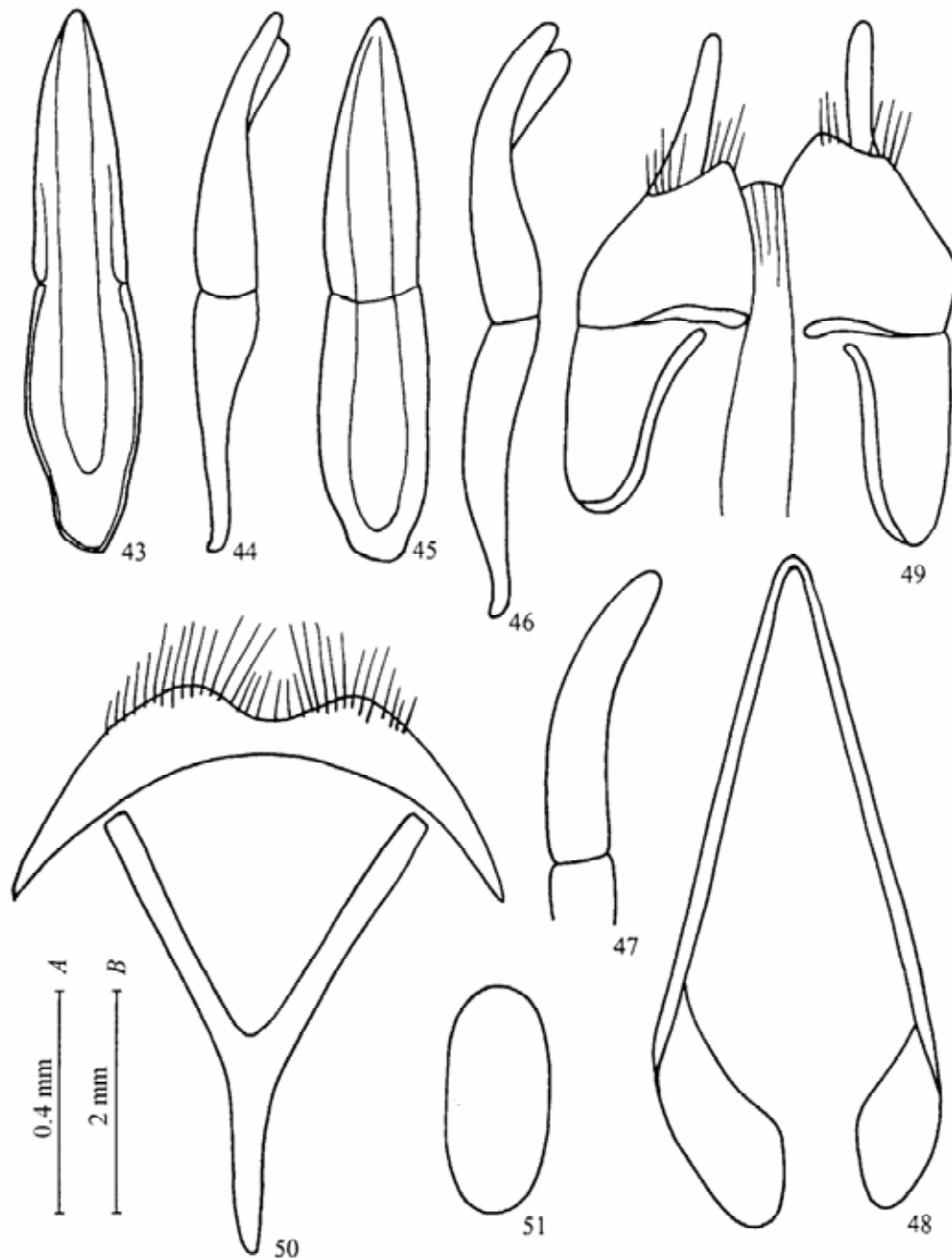
Type species *Lachnopus hauseri* Reitter, 1897, by monotypy.

The genus includes one species.

***Netuschilia hauseri* Rtt.** (Figs. 13, 18, 21, 27, 43–52)

Reitter, 1897 : 217 (*Lachnopus*) (type locality: Buchara, Repetek); 1904 : 35; Ferrer and Yvinec, 2004 : 45 (year of original description erroneously cited as Reitter, 1904).

Distribution (Fig. 52). Georgia (Tbilisi). Eastern Transcaucasia. Kazakhstan: Western (Iskine), Southern (Bala-Murun, 30 km E of Baigakum), Central (Balkhash District, Taspine locality), and Southeastern (Tau-Kum Sands; Uzen; Kurtagoi; Sarytagoi W of Chunji). Turkmenia: 4, 6, and 8 km N of Kara-Kala; Bakharden Cave S of Bakharden; Ashgabat; Karakhan; Iolotan; Repetek; Farab; Khalach; Kuhitangtau Range, Svintsovyi Rudnik). Uzbekistan: western Aral



Figs. 43–51. *Netuschilia hauseri* Rtt.: (43, 44) aedeagus, ventral and lateral view (Kara Kum, Repetek); (45, 46) aedeagus, ventral and lateral view (Kyzyl Kum Sands, Karabas-Koprik Vill.); (47) parameres, lateral view (Turkmenia, Karakhan); (48) spiculum gastrale (Karakhan); (49) ovipositor (Karabas-Koprik); (50) sternite VII and spiculum ventrale (Repetek); (51) egg (Repetek). Scale bars: A for Figs. 43–50; B for Fig. 51.

Sea coast E of Komsomolsk-on-Ustyurta; Kyzyl Kum Sands, Ayakagytna locality (64°25.8'N, 40°32.4'E); Bagaabzal, 48 km N of Bukhara; Kokand. Tajikistan: Kabadian, Obi-Kiik, Yavan, Sary-Chashma, Murav-Khurg N of Isfan, Rushan. China: Xinjiang (Turpan Zhan, 43°05'N, 88°51'E; Untubi Xian, 44°12'N, 86°54'E; Yining, 43°59'N, 81°36'E; Shache, 38°26'N, 77°13'E; Yutian, 36°52'N, 81°39'E; Qira Xian,

37°02'N, 80°46'E; Gansu (Dunhuang Shi, 40°08'N, 94°41'E), Inner Mongolia (Hanggin Houqi, 40°53'N, 107°08'E), Hopenh (Ji Xian, 40°02'N, 117°24'E).

Biology. This species occurs on sandy and clay soils. In the Kuhitang-Darya valley (easternmost Turkmenia) it commonly inhabits gerbil burrows made in loess soils, the beetles concentrating in slightly

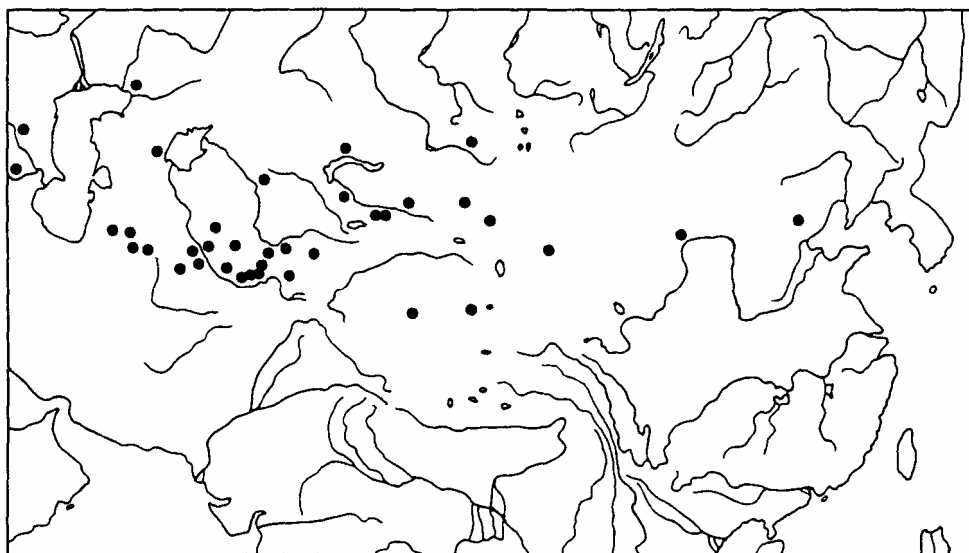


Fig. 52. Distribution of *Netuschilia hauseri* Rtt.

moist plant debris. Numerous remains of the beetles were collected from gerbil burrows in the sands exposed after the Aral Sea reliction in the area of the Ust-Urt eastern cliff. Findings of *N. hauseri* in gerbil burrows were reported by Ya.P. Vlasov and E.L. Shestoporov (1937). In the Bakharden Cave, the beetles were found on bat excrements (Vlasov, 1937), and in SW Tajikistan, in human dwellings and other buildings (collected by E.E. Gussakovskii and E.P. Lupova).

Genus *LACHNODACTYLUS* Seidl.

Seidlitz, 1898 : 837; Reitter, 1904 : 183; 1916 : 137; Ferrer, 2002 : 52; Ferrer and Yvinec, 2004 : 47, 48.—*Lachnopus* Seidlitz, 1894 : 476 (nom. praecoc.).

Type species *Lachnopus digitatus* Seidlitz, 1894, by monotypy.

The genus includes one species.

Lachnodactylus digitatus Seidl.

(Figs. 14, 16, 19, 25, 28, 42, 53–60)

Seidlitz, 1894 : 476 (*Lachnopus*; type locality: “Asia centralis”); Reitter, 1904 : 183; Ferrer and Yvinec, 2004 : 47.

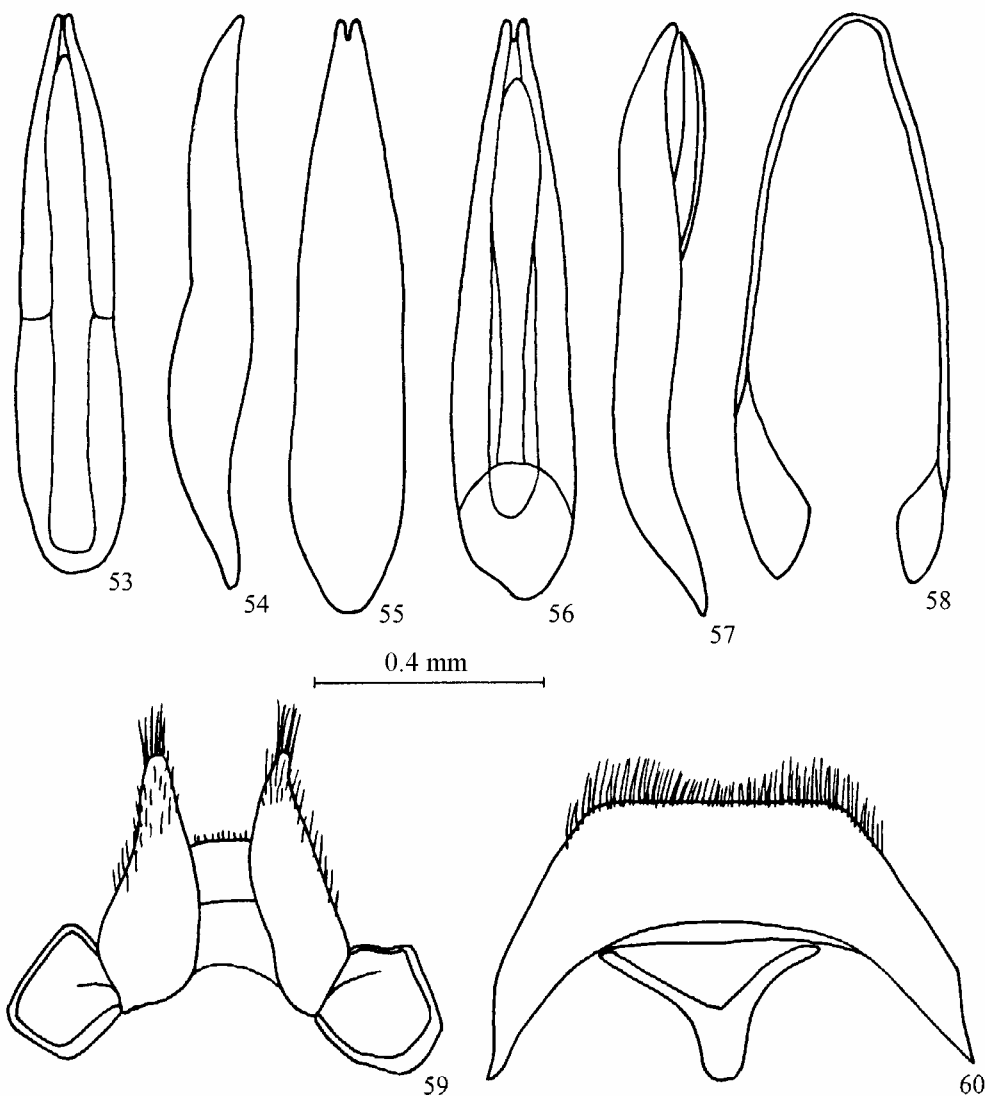
Distribution (Fig. 42). Western Kazakhstan: Iskine, Kainar–Emba landscape area, 10 km W of Akkiztogai (47°06'N, 54°19'E), Karaton (52°26'N, 53°34'E). Turkmenia: the Murgab valley. Tajikistan: Khujand.

Biology. In Gur'ev Prov. (Kazakhstan), the beetles were collected in the burrows of ground squirrels

(*Citellus* spp.) and the great gerbil (*Rhombomys opimus*).

TRIBE KLEWARIINI

The tribe Klewariini is closest to the tribe Lachnogyini and is considered a subtribe of the latter by a number of authors (Reitter, 1916; Ferrer and Yvinec, 2004). The two tribes share the following characters: epipleura reaching the sutural angle of elytra; intercoxal process of prothoracic sternite very narrow; antennae with 3-segmented club (though loose) (Fig. 61); fore tibia dilated; pronotum highly movable. The general morphology of *Klewaria colydiiformis* suggests that this species should differ considerably in its biology from members of the tribe Lachnogyini. In Tajikistan, *K. colydiiformis* was found on salt marshes in the daytime. Tenebrionid beetles living on salt marshes (for example, species of *Centorus*) typically find shelters in soil cavities, especially near plant stems. They are characterized by a somewhat flattened and elongate body, a movable pronotum, and narrow middle and hind tibiae. Since the fore tibiae of *K. colydiiformis* are noticeably dilated (Fig. 64), this species may find shelters not only in burrows but also in soil cavities. The strongly dilated fore femora (Fig. 64) indicate that the fore legs play an essential role in burrowing. A noticeable elongation of the basal portion of ovipositor (Figs. 67, 68), bearing long sclerotized outgrowths, suggests that during oviposition this structure actively penetrates the substrate. The eggs of *K. colydiiformis* are strongly elongate (Fig. 69), being 2.55 times as long as wide (1.15 × 0.45 mm; the adult body



Figs. 53–60. *Lachnodactylus digitatus* Seidl.: (53, 54) aedeagus, dorsal and lateral view (Ferghana Valley, Khujand); (55–57) aedeagus, ventral, dorsal, and lateral view (northern Caspian Sea area: Karaton); (58) spiculum ventrale; (59) ovipositor, ventral view (northern Caspian Sea area: Iskine); (60) abdominal sternite VII and spiculum ventrale (Iskine).

length 4.6 mm), whereas the eggs of *Netuschilia hauseri* are 2.28 times as long as wide (0.8×0.35 mm; the adult body length 5.6 mm).

All species of the tribe Lachnogyini share the following characters: eyes strongly transverse, with rigid hooked spines (Fig. 40); intercoxal process of 1st visible abdominal sternite narrowing, cuneiform; elytra with rows of setae, but without distinct striae. These characters clearly distinguish members of Lachnogyini from *K. colydiiformis*, since the latter has small eyes with straight setae between the facets; the intercoxal process of the 1st visible abdominal sternite is long and narrow but has a rounded apex; and the elytra are very clearly striate.

Thus, the genus *Klewaria* represents a distinct taxon (the tribe Klewariini), separated from the genera included in the tribe Lachnogyini.

Genus *KLEWARIA* Rtt.

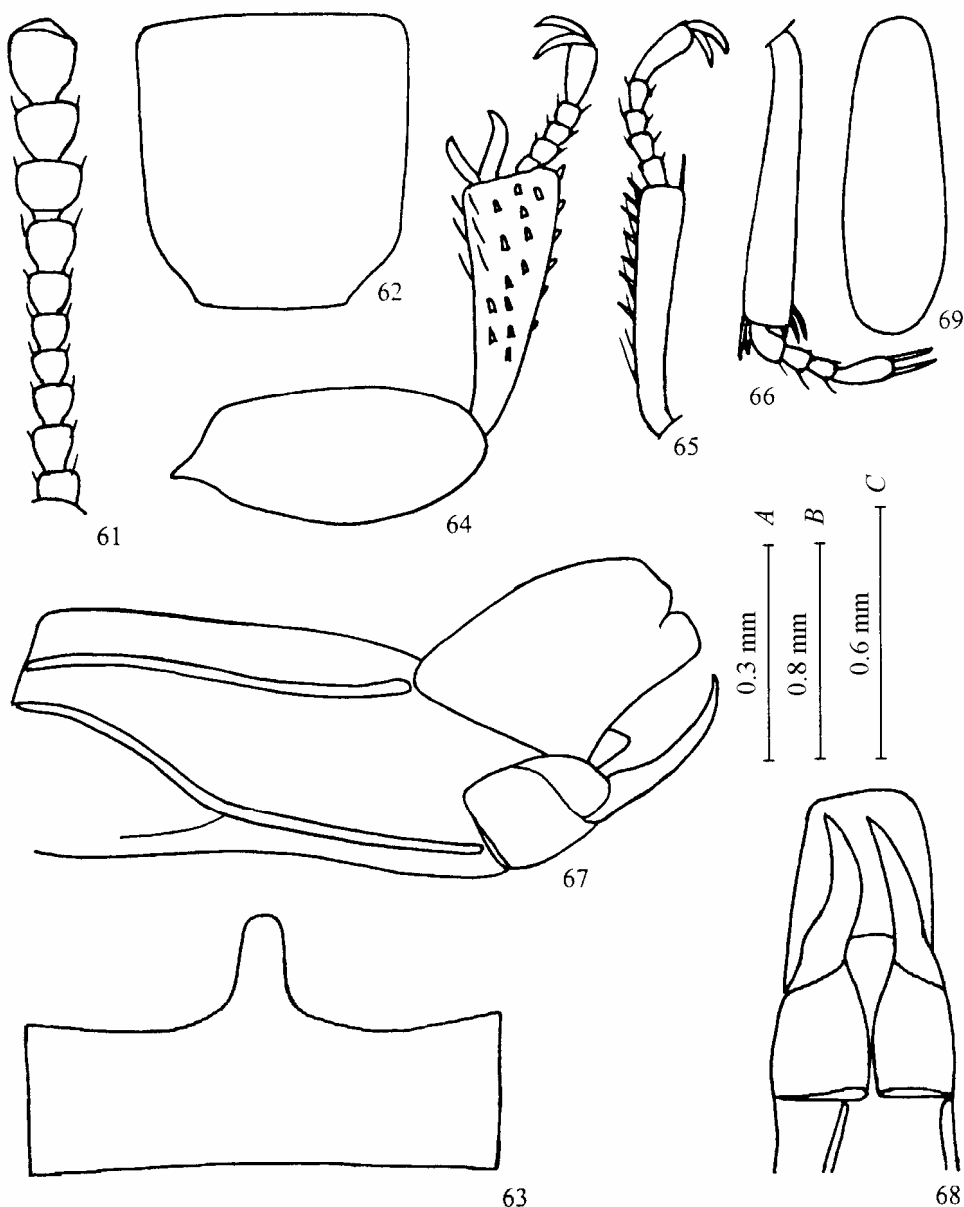
Reitter, 1910 : 21; 1916 : 136.

Type species *Klewaria colydiiformis* Reitter, 1910, by monotypy.

The genus includes one species.

Klewaria colydiiformis Rtt. (Figs. 61–69)

Reitter, 1910 : 21 (type locality: Turkmenia, Farab station); 1916 : 136.—*colydioides* Ferrer et Yvinec, 2004 (lap. cal.).



Figs. 61–69. *Klewaria colydiiformis* Rtt., female: (61) antenna; (62) pronotum; (63) 1st visible abdominal sternite; (64) fore leg, ventral view; (65) middle tibia, dorsal view; (66) hind tibia, dorsal view; (67, 68) ovipositor [(67) lateral, (68) ventral view]; (69) egg. Scale bars: A for Figs. 61, 67, 68; B for Figs. 62, 69; C for Figs. 63–66.

Distribution. Turkmenia: Farab station. SW Tajikistan: vicinities of Shaartuz, Beshkent Valley.

The holotype labeled “Transcasp.,” “St. Farab, S-Az. zh. d. 1.VI.05 G. Sumakov. Tr. 5.5.4 Gl. *Colydiiformis* m.,” and “Holotypus, 1916. *Klewaria colydiiformis* Reitter” has been examined.

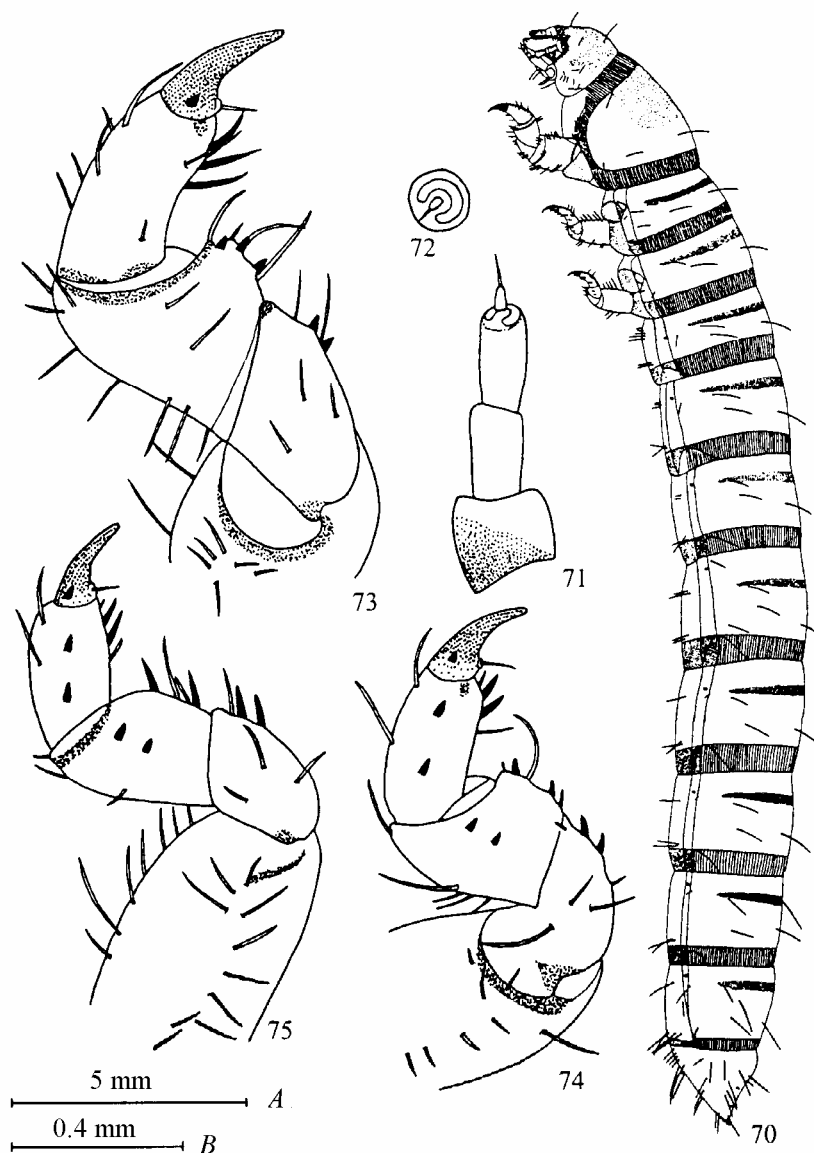
K. colydiiformis was described from a single specimen collected near Farab station, on the right bank of Amu Darya (eastern Turkmenia). In the paper by J. Ferrer and J.H. Yvinec (2004), this locality was

erroneously attributed to Azerbaijan. In the same publication, the date of original description was erroneously cited as 1916 instead of the correct 1910, and the name of the species was misspelled as *K. colydioides*.

TRIBE BLAPTINI

Agnaptoria anthracina G. Medv., larva (Figs. 70–94)

Description. Depending on sclerotization of integument, coloration of larva varying from pale to varyingly deep brown, with posterior margins of tho-



Figs. 70–75. *Agnaptoria anthracina* G. Medv., larva: (70) habitus, lateral view; (71) antenna and basal tubercle; (72) apical surface of 2nd antennal segment; (73–75) fore, middle, and hind legs, ventral view [(70–73) 4.VII.2005, (74, 75) 25.VI.2005]. Scale bars: A for Fig. 70; B for Figs. 71–75.

racic segments as well as abdominal segments I–VIII, apex of abdominal segment IX, base of clypeus, labrum, mentum, and prementum (Figs. 70, 90, 91, 94) darkest

Body length 6–8 times its width at level of metathorax (Fig. 70). Head capsule (Fig. 76) transverse-oval, its width 1.9 times distance from foramen magnum to frontoclypeal suture. Anterior margin of head capsule shallowly arcuately concave, occipital margin straight. Epicranial suture short, equal to 1/14 length of head capsule. Branches of frontal suture anteriorly entire or bifurcate (Fig. 76). Frontal sclerite campaniform, with 1 pair of short setae at anterior margin. Vertex with

2 pairs of short setae: antero-vertical ones, situated lateral to terminal branches of frontoclypeal suture, and postero-vertical ones, situated lateral to middle portions (sharp bends) of these branches. Head margin at base of antennal articulatory membrane with 4 very closely situated setae. Two longer setae situated on both sides at posterior margin of pit accommodating cardo of maxilla. Anterior half of ventrolateral surface of head capsule bearing 9 setae, their relative position varying between individuals and even between two sides of head in same specimen (3 rows of setae on one side and randomly arranged setae on other side). Ventral surface of head lateral to gular sutures covered



Figs. 76–88. *Agnaptoria anthracina* G. Medv., larva: (76) head capsule, dorsal view; (77, 78) head capsule (without mouthparts), lateral view; (79, 80) labrum in dorsal and ventral view; (81, 82) left and right mandibles in dorsal view; (83) left mandible, inside view; (84–87) spiracles [(84) of mesothorax, (85) of abdominal segments III, (86) V, (87) VIII]; (88) sclerite of hypopharynx; (76, 81–88) 4.V.2005; (77) 25.VI.2005; (78–80) 20.VI.2005. Scale bars: A for Figs. 76–78; B for Figs. 79–88.

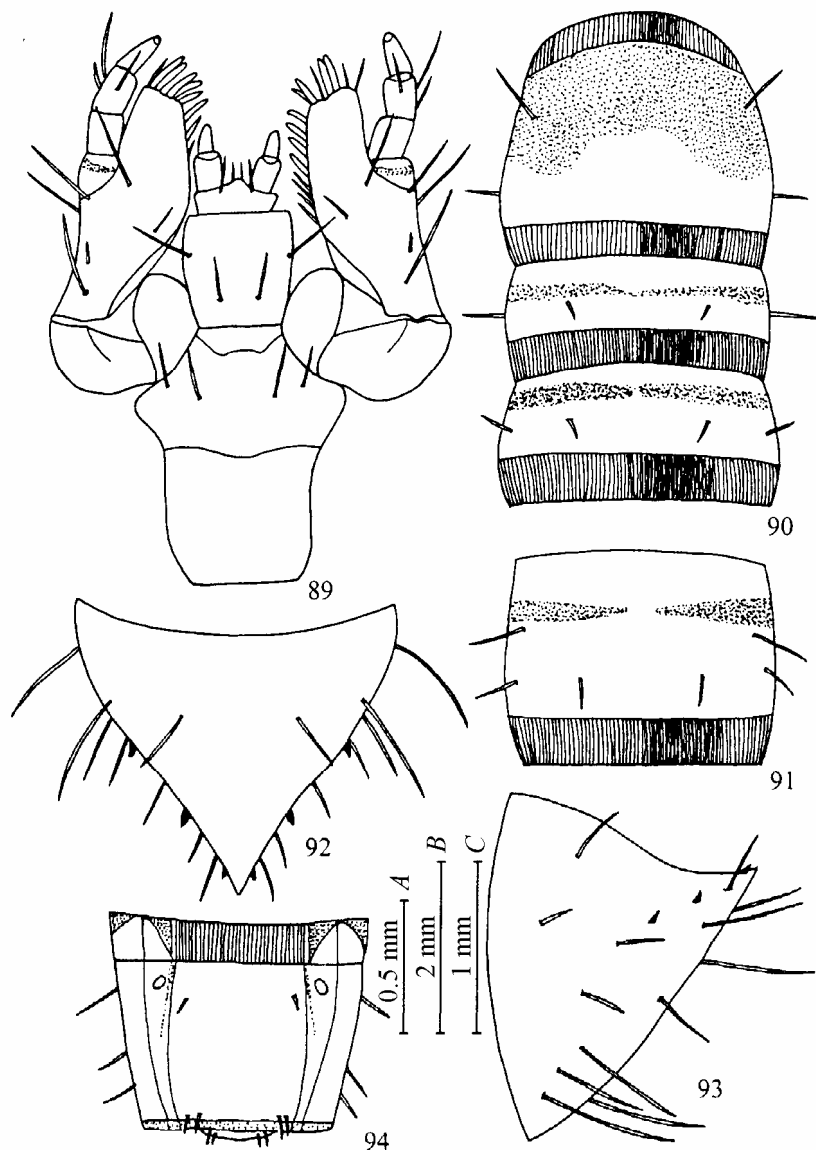
with minute setae. Ocelli either completely absent (with no visible traces), or present in form of 2 or 3 closely positioned oval pigmented spots on genae (Figs. 77, 78). All antennal segments elongate (Fig. 71); 2nd segment 1.2 times as long as 1st; 3rd segment rod-shaped, with apical seta. Apical surface of 2nd antennal segment bearing C-shaped seta (Fig. 72). Basal portion of articulatory antennal membrane partly sclerotized, resembling separate segment. Length (width) ratio of socket-shaped articulatory membrane and 1st–3rd antennal segments 15(19) : 18(12) : 20(12) : 6(3) (with 1 unit equal to 0.014 mm).

Clypeus inverted-trapezoid, transverse (2.5 times as wide as long), consisting of sclerotized basal part and membranous apical part. Basal part strongly transverse (3.57 times as wide as long), slightly asymmetrical, its

anterior corners with 1 long seta; 1 short spiniform seta situated somewhat behind and medially of long seta on each side.

Labrum (Figs. 79, 80) transverse (1.7 times as wide as long). Anterior margin slightly arcuately concave, upper surface with transverse row of 8 setae at mid-length and one row of 6 setae near anterior margin. Outer portions of anterior margin on each side with 3 shorter spiniform setae. Lower surface of labrum not setose; its central area with 2 short spines, in front of which group of up to 9 fine rounded sensilla present (Fig. 80). Tormae very short.

Mandibles (Figs. 81–83) stout, with 2 apical denticles. Left mandible more elongate than right one (1.6 and 1.17 times as long as wide, respectively). Mola noticeably shifted forwards from base (Fig. 12). Base



Figs. 89–94. *Agnaptoria anthracina* G. Medv., larva: (89) labio-maxillary complex; (90) pro- and mesothorax; (91) abdominal tergite VI; (92, 93) abdominal segment IX, dorsal and lateral view; (94) abdominal segment VIII, ventral view; (89–91, 94) 4.VII.2005; (92, 93) 3.VII.2005. Scale bars: A for Fig. 89; B for Figs. 90, 91, 94; C for figs. 92, 93.

of outer upper margin with small protrusion bearing 2 long setae; its surface at base of setae pale.

Inner margin of distal maxillary lobe (Fig. 89) with 2 rows of dentiform spinules and few finer setae. Lower surface of distal lobe with 6 setae, of which 1 short and 1 long one situated basally, 1 seta at middle of inner margin, and two setae at inner and outer margins of antennal articulatory membrane.

Submentum (Fig. 89) 1.46 times as wide as long, strongly dilated in middle, so that its outer margins lobiform protruding. Surface of submentum near its

articulation with mentum membranous. Middle portion of submentum with 2 pairs of setae, anterior pair situated at outer margins of submentum, and posterior pair somewhat closer to middle. Mentum only slightly longer than wide, with 2 pairs of setae. Bases of setae of anterior pair situated at outer margins of mentum in its anterior third, and bases of setae of posterior pair situated in its posterior third, at one-third of mentum width from its lateral margin. Prementum with 1 pair of setae inward of base of palpus and 1 pair on apex of glossa. Palpomeres without setae. Hypopharyngeal sclerite with tridentate anterior margin (Fig. 88).

Pharyngeal sclerite transverse, 1.23 times as wide as long.

Abdomen 3.3 times as long as thorax (larva, 4.VII.2005). All thoracic and abdominal segments transverse. Prothorax (Fig. 90) approximately twice as long as meso- or metathorax. Width (length) ratio of pro-, meso-, and metathorax 63(53) : 64(26) : 66(27); that of abdominal segments I–IX 67(44) : 67(46) : 68(46) : 65(45) : 64(45) : 62(48) : 59(46) : 56(40) : 38(28). Surface of thorax and abdomen appearing glabrous, with sparse setae dorsally. Prothoracic tergite widest at base; disk with 8 setae, of which 6 lying in front of posterior edge and 2 laterally behind anterior edge; about 5 long setae and 7 short ones present at lateral margin of tergite on either side. Tergite of meso- and metathorax with 4 or 5 setae on either side: 1 at outer end of transverse dark stripe, 2 between this stripe and posterior dark edge, and 1 or 2 at lateral margin of tergite. Surface of abdominal tergites I–VII on each side with 2 long setae between transverse dark stripe and posterior dark edge, and 1 seta at outer end of transverse dark stripe; in addition, 1 short seta occasionally present at inner end of this stripe (on tergites I, III, V, and VII). One short seta present at anterior margin of sides of abdominal tergites I–VIII, behind level of spiracle. Pleura without setae. Abdominal sternites with few setae at sides. Abdominal sternite I with up to 14 setae, other sternites with 6–8 setae. Inner and outer boundaries of pleural surface distinct, parallel on segments I–VII and converging posteriad in wedge-like pattern on segment VIII (Fig. 94). Posterior edge of segment VIII very thin, especially on sternite. Abdominal tergite VIII with 6 setae on either side: 1 at outer margin behind level of spiracle, 1 at posterior corner, 1 at outer end of dark transverse stripe, 1 above preceding one, and 2 in posterior third of tergite.

Abdominal segment IX (Fig. 92) helmet-shaped in dorsal view, with almost entire surface being of tergal origin. Posterior margin of sternite IX only slightly extending beyond posterior margin of sternite VIII (Fig. 94) and bearing 4 short setae. In lateral view, apical half of upper margin of segment IX arcuately concave, i.e., apex of segment slightly elevated, while lower margin only slightly arcuate in its basal third (Fig. 93). Apex of segment IX barely blunted, with 3 short spinules on sides in apical half (Fig. 92). Basal third of upper surface of segment IX with 4 long setae forming transverse row. Outer margin of segment IX with 1 seta situated in front of 3rd spinule, and 4 setae

on rest of its surface. Lower surface with 10 long setae and few fine ones.

Fore leg (Fig. 73) noticeably larger than middle (Fig. 74) and hind legs (Fig. 75). Outer (extensor) surface of all coxae without setae; upper and lower surfaces with sparse setae of moderate length. Lower surface of fore trochanter with 3 setae in transverse row in apical third and 3 setae at base of inner margin. Inner margin of fore trochanter with 2 short spines. Lower surface of fore femur with 1 seta in center and 1 seta somewhat closer to apical margin. Upper surface of fore femur much darker than lower one, with 4 coarse setae on inner half, 2 setae in middle, and 1 seta at apical margin. Inner margin of fore femur with 3 dark spiniform protrusions and 3–4 rigid setae. Fore tibia with beak-shaped claw accompanied by seta at base (on inner margin) and spinule (on lower surface). Lower surface of fore tibia with 2 spiniform setae along median line; inner margin with 3 large rigid setae in apical half; upper surface with 2 fine setae along median line; apical margin with 4 setae.

Middle and hind tibiae similar. Inner margin of trochanter, femur, and tibia with 2 spiniform setae accompanied by 1–3 finer ones. Lower surface of trochanter with 3 setae. Lower surface of femur and tibia medially with two short dark spines. Outer margin of femur with 2 setae: 1 in middle and 1 at apex. Outer margin of tibia with 1 seta slightly distal to middle and 1 seta at apex.

Spiracles (Figs. 83–87) oval, transverse and somewhat oblique, with posterior margins shifted slightly outwards relative to anterior ones. Spiracles of mesothorax and abdominal segments I–VIII lying in anterior 1/4 of pleural surface. Spiracles largest (0.18 × 1 mm) on mesothorax, their size slightly decreasing toward apex of abdomen from 0.14 mm (segment II) to 0.13 mm (segment VIII).

Body size of larvae: length and width (mm): 22.5 × 3.8 (20.VI.2005), 23.2 × 3.6, 19 × 3.2 (25.VI.2005), 20.8 × 3.2 (3.VII.2005), 27 × 3.4 (4.VII.2005).

Material. China, SE Gansu, 17 km S of Ling Village, 34°11'57"N, 104°31'44"E, 3475–3510 m, 20.VI.2005, 2 larvae, I. Belousov, I. Kabak; S Gansu, SSW of Kangle, 35°07'36"N, 103°28'01"E, 3823 m, 26.VI.2005, 2 larvae, I. Belousov, I. Kabak; S Gansu, 14.5 km WSW of Yelinguan, 34°55'03"N, 103°30'04"E, 3250 m, 3.VII.2005, 1 larva, I. Belousov, I. Kabak; S Gansu, WSW of Yelinguan, 34°53'16"N,

103°25'52"E, 3788 m, 4.VII.2005, I. Belousov, I. Kabak.

There are quite a few data on the larvae of tenebrionids of the subtribe Gnaptorinina. Until recently, the larva of only one species of the genus *Asidoblaps* Fairm. was described (Medvedev, 2002). Examination of the larva of a species representing the genus *Agnaptoria* Rtt. gives more detail as to the specific structural features of larvae in the subtribe Gnaptorinina. Judging from the morphology of the larvae of *Asidoblaps kabaki* G. Medv. and *Agnaptoria anthracina* G. Medv., the subtribe Gnaptorinina is characterized by such features as the absence of setiferous fields on the ventral surface of labrum; presence of distinct pleural sutures; presence of an angular membranous surface, facilitating free bending of the abdomen, at the junction of tergite and pleuron at the posterior margins of abdominal segments I–VIII; and strong development of the tergal surface of abdominal segment IX, because of which only the margin of sternite IX remains exposed.

Having the above features in common, the larvae of *A. kabaki* and *A. anthracina* differ sharply in the structure of the labrum, body integument, and abdominal segment IX. The anterior margin of labrum of *A. anthracina* is arcuately concave, similar to that of the known larvae of the tribe Blaptini (*Blaps*, *Dila*, *Prosodes*, *Tagona*), whereas that of *A. kabaki* is arcuate-convex. Tergites of all body segments of *A. kabaki* are covered with rounded, slightly submerged sensilla distinguished by their dark color against the general background, while the long setae rise from rounded elevations, slightly submerged into the integument and clearly delimited from the surrounding surface. In the larva of *A. anthracina* the body tergites bear only simple setae with barely submerged bases. The terminal process of abdominal segment IX of *A. anthracina* is pointed at the apex, whereas that of *A. kabaki* is slightly blunted, not extending beyond the base of apical pair of spinules.

Analysis of the larval characters of *A. kabaki* and *A. anthracina* indicates that the subtribe Gnaptorinina occupies the most isolated position in the tribe Blaptini. This conclusion is confirmed by morphological characters of the adults. In particular, the trend for strengthening of the 8th antennal segment, which provides support for the 9–11th segments bearing sensory structures, is not observed in the subtribe Gnaptorinina. In the subtribes Blaptina, Prosodina, and Gnaptorinina the 8th segment is more or less dilated, some-

times massive. It may be assumed that this feature was inherited from the common ancestor of these taxa.

ACKNOWLEDGMENTS

The author is very grateful to I.A. Belousov and I.I. Kabak who collected the larvae of *Agnaptoria anthracina* and *Asidoblaps kabaki* G. Medv. and donated this material to the Zoological Institute, RAS (St. Petersburg).

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