Abstract. A taxonomic review of tenebrionid platyopoid genera of the subfamily Pimeliinae from Eastern Europe, Central Asia, Afghanistan, Iran and Pakistan is given. This group of taxa was known before 1994 as the tribe Platyopini Motschulsky, 1849, which is now interpreted as a junior synonym of Pimeliini Latreille, 1802. The group is different from other Pimeliini in having dorso-lateral eyes, located above the level of the genae, and it includes the following ultrapsammophilic genera at least from Central and Southern Asia: Apatopsis Semenov, 1891, Habrochiton Semenov-Tjan-Shansky, 1907, Habrobates Semenov, 1903 [= Kawiria Schuster, 1935 syn. nov.], Dietomorpha Reymond, 1938, Przewalskia Semenov, 1893, Mantichorula Reitter, 1889, Platyope Fischer von Waldheim, 1820 [= Homopsis Semenov, 1893 syn. nov.], Earophanta Semenov, 1903. These genera are distributed in almost all large deserts of Palaeartic Asia: Karakum, Kyzylkum, Muyunkum, Taklamakan, Gobi, Registan, Dasht-e-Kawir, Dasht-e-Lut, as well as in other arid and semi-arid sandy landscapes from European Russia to the south of Eastern Siberia. The group of platyopoid genera is polyphyletic. We propose at least two monophyletic branches: the Habrobates genus group (the first four genera mentioned above), which represents the subtribe Habrobatina Nabozhenko & S. Chigray subtrib. nov. and the Platyope genus group (latter four genera) within the nominotypical subtribe. A new species is described from

**Keywords.** Tenebrionidae, Pimeliini, new taxa, synonymy, nomenclature.


**Introduction**

Pimeliini is a large tenebrionid tribe in the subfamily Pimeliinae Latreille, 1802 with 64 genera distributed mainly in the Palaearctic and transition biogeographic zones of the Afrotropic and the Indo-Malayan regions (Gebien 1937; Iwan et al. 2020). The majority of genera is distributed in deserts of Central Asia, Iran, Pakistan, Afghanistan, the Near East and North Africa. Many authors hypothesised that the ecological diversification of the tribe took place since the Pleistocene (Kryzhanovsky 1965) or no later than the Pliocene (Medvedev 2005; Abdurakhmanov & Nabozhenko 2016; Abdurakhmanov et al. 2016a; Abdurakhmanov et al. 2016b) in Central Asia. Kwieten (1981) proposed an Iranian origin of Pimeliini.

Various groups of Pimeliini in Central Asia and Iran were mainly revised by Russian entomologists starting with the works of the German-Russian scientist Fischer von Waldheim (1820, 1822, 1837). Solsky (1876) erected two genera from the Tian Shan and surrounding deserts. Semenov-Tjan-Shansky (Semenov 1889, 1891, 1893, 1903a, 1903b; Semenov-Tjan-Shansky 1907) described several ultrasammophilic genera from Karakum and Taklamakan Deserts. Reitter (1887, 1893, 1889, 1900) also added three genera of Pimeliini from Central Asia, Iran and Mongolia and completed a key to the Palaearctic Pimeliini (Reitter 1893). Bogachev (1949, 1960a, 1960b) described three unusual genera from Tajikistan and Iran and revised the species of the genus *Pachyseles* Solier, 1836 occurring in Turkmenistan (Bogachev & Nepesova 1980). Skopin made the greatest contribution to the study of Pimeliini. He described many larvae of species of this tribe, several new genera (Skopin 1959, 1960, 1961, 1962, 1964, 1968a, 1968b, 1971, 1972, 1973, 1974), revised the group of genera *Diesia* Fischer von Waldheim, 1820 – *Platesyesia* Skopin, 1971 (Skopin 1971) and *Sternoplas* J. Frivaldszky, 1890 – *Trigonoscelis* Dejean, 1834 (Skopin 1973), as well as the genera *Stalagmoptera* Solsky, 1876 (Skopin 1972) and *Pterocoma* Dejean, 1834 (Skopin 1974). Schuster & Reymond (1937) and Chinese authors (Ren et al. 1993; Ren & Yu 1999; Ren & Dong 2001; Wu et al. 2005) reviewed part of Chinese-Mongolian genera with a key to taxa, and described several species of *Platyope* Fischer von Waldheim,

The classification of genera within the tribe is discussed by Semenov (1893), Skopin (1962), Pierre (1964), Koch (1969), Kwieton (1981), Kaszab (1982) and Doyen (1993). Semenov (1893) erected the subtribe Platyopina (written originally as “Platyopidae”) on the basis of dorsally located eyes, unlike the laterally located eyes in other pimeliine genera. Skopin (1962) was the first to question the need for this tribe and treated it as a junior synonym of Pimeliini. He studied larval structures (Skopin 1959, 1962) and concluded that larvae of Pimeliini and Platyopini have no fundamental differences. Pierre (1964) erected the tribe Leucolaephini for six Sahara-Arabian genera mainly on the basis of structures of antennae, profemora and the sub-cylindrical prothorax, but Koch (1969) challenged this decision and suggested that Leucolaephini does not differ from Platyopini and cannot be retained, while considering that even representatives of the tribes Pimeliini and Platyopini do not always clearly differ. Later, Kwieton (1981) synonymized the tribe Leucolaephini with Platyopini without any comments. Doyen (1994) studied adult structures of Pimeliinae and placed Platyopini as a junior synonym of Pimeliini as a result of cladistic analysis. Despite this, some authors continued to interpret Pimeliini and Platyopini as separate tribes (Ren & Yu 1999; Ren & Dong 2001; Lillig & Pavlíček 2003; Medvedev 2005; L. Soldati 2009).

Despite such abundance of works on Central Asian Pimeliini, the morphological basis to build a balanced classification of the tribe is very poor. The current classification of the genera is based mainly on the external morphology of adults, especially on the structure of eyes, legs, antennae, pronotal and elytral structures. Internal structures (genitalia) are briefly presented in the work of Doyen (1994), who figured the ovipositor of *Lasioptola* and the female genital ducts of *Ocnera* and *Sternoplox*. Some figures of male genitalia and ovipositor for species of the genera *Platyope* and *Ocnera* are presented in the works of Chinese authors mentioned above. Leo (2016) photographed the ovipositor of the species *Spectrocnera anguliceps* Kwieton, 1981 from the Arabian Peninsula. Svetlana Chigray (2019) figured male and female genitalia of *Podhomala* Solier, 1836. The majority of Central Asian genera have not been studied since the original descriptions.

The aim of this work is to compare the Asian genera of Pimeliini with dorso-lateral eyes, which were previously united in the tribe Platyopini. Kaszab (1982) listed 15 genera of this group, three of which (*Leucoleaephus* Lucas, 1859, *Pseudoplatyope* Pierre, 1964, *Pseudostorthocnemis* Gridelli, 1953) are distributed in North Africa, including the Afrotropical regions (Pierre 1964), two occur in the Near East, including the Arabian Peninsula (*Paraplatyope* Löbl, Bouchard, Merkl & Bousquet, 2020, *Astorthocnemis* Lillig & Pavlíček, 2003) and one genus *Storthocnemis* Karsch, 1881 is Saharo-Arabian. Species of all the genera mentioned above have lateral eyes located on the level of the genae and have ovipositors that are typical for the subtribe Platyicina. The mentioned genera were erroneously interpreted as members or relatives of the former tribe Platyopini.

Below, we give morphological characteristics and diagnoses of genera from Central Asia, Iran, Afghanistan and Pakistan, analyse addition characters supporting polyphylly of genera with dorso-lateral eyes, discuss the classification of the tribe Pimeliini and morphological adaptations to arid environments and sandy soils. In addition, a new species, new synonyms and new combinations are given. This work
is only part of a revision of the Central Asian Pimeliini, therefore a phylogenetic analysis is not provided here.

**Material and methods**

The specimens were primarily studied at the Department of Applied Ecology at St. Petersburg State University and in the Laboratory of the Insect Systematics of Zoological Institute of the Russian Academy of Sciences. The study was carried out using the equipment of the Resource Center “Microscopy and Microanalysis” (Research Park of St. Petersburg State University, St. Petersburg, Russia). We used High-vacuum carbon sputter with a turbomolecular pump Q150T E (Quorum Technologies Ltd, Great Britain) and Hitachi TM 3000 Tabletop Scanning Electron Microscope (SEM) for electron scanning microscopy. We used Leica DM4500P and Micromed MC-4-Zoom LED light microscopes with the camera ToupCam 14.0 MP, a Canon DS 126171 camera with a Canon MPE EF 65 mm 1:2.8 macrophoto lens for photographing details of structures. Helicon FocusPro ver. 7.6.4 and ToupTek ToupView ver. 4.7.14088 software were used for digital image processing.

Also, we use photographs provided by David Gonzales (Saint-Laurent-du-Pape, France) of species of his private collection.

Andrey Semenov and Andrey Semenov-Tjan-Shansky are the same person. The honorary title “Tjan-Shansky” was added to the surname of his father and all his family in 1906. Here, we use Semenov for papers before 1906 and Semenov-Tjan-Shansky for papers published after 1906 (just as the author himself did).

The aedeagus of Pimeliini is inverted at 180°. Below ventral and dorsal sides of the tegmen of the aedeagus and median lobe is interpreted excluding inversion.

The genera below are listed in order of morphological similarity within a subtribe and a genus group. Countries for each taxon are listed in the alphabetic order. Square brackets in material for each species are used for modern names of localities and translations of Cyrillic labels.

**Institutional abbreviations**

<table>
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<th>Abbreviation</th>
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<tr>
<td>BMNH</td>
<td>Natural History Museum (NHMUK) (formerly British Museum of Natural History), London, UK</td>
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<tr>
<td>CMN</td>
<td>private collection of M.V. Nabozhenko, Rostov-on-Don, Russia</td>
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<tr>
<td>HNHM</td>
<td>Hungarian Natural History Museum, Budapest, Hungary</td>
</tr>
<tr>
<td>MNHP</td>
<td>Muséum national d'Histoire naturelle, Paris, France</td>
</tr>
<tr>
<td>NMB</td>
<td>Naturhistorisches Museum Basel, Basel, Switzerland</td>
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<tr>
<td>ZIN</td>
<td>Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia</td>
</tr>
<tr>
<td>ZMMU</td>
<td>Zoological Museum of Moscow State University</td>
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<tr>
<td>ZMSFU</td>
<td>Zoological Museum of Southern Federal University, Rostov-on-Don, Russia</td>
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**Abbreviations for morphological terms used in illustrations**

- **Male genitalia**
  - da = dorsal apophyses of the apical lobe of the aedeagus
  - gVIII = gland of the inner sternite VIII
  - mlb = median lobe baculi
  - va = ventral apophyses of the apical lobe of the aedeagus

- **Ovipositor**
  - aspcl = additional sclerotized projection of the coxite lobe I
Female genitalic ducts

Female genital ducts

<table>
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<th>Abbreviation</th>
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<tr>
<td>bpar</td>
<td>baculi of the paraproct</td>
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<tr>
<td>bptg</td>
<td>baculi of proctiger</td>
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<tr>
<td>cl, cII, cIII, cIV</td>
<td>lobes of the coxite</td>
</tr>
<tr>
<td>dbpar</td>
<td>dorsal baculi of the paraproct</td>
</tr>
<tr>
<td>par</td>
<td>paraproct</td>
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<tr>
<td>pttg</td>
<td>proctiger</td>
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<tr>
<td>sv</td>
<td>median sclerotization of vulva</td>
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The figures are grouped in the following order (for the convenience of comparison of the same structures in different genera):

1. Habitus and details of thorax (Figs 1–7)
2. Surface and sculpture of integument, SEM images (Figs 8–13)
3. Genitalia (Figs 14–22)
4. Female genital tubes (Figs 23)
5. Apical part of antennae (Fig 24)
6. Legs (Figs 25–28)

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Family Tenebrionidae Latreille, 1802
Subfamily Pimeliinae Latreille, 1802
Tribe Pimeliini Latreille, 1802

Subtribe Habrobatina Nabozhenko & S. Chigray subtrib. nov.

Type genus

Habrobates Semenov, 1903.

Diagnosis

Body entirely covered with dense scales. Pronotum and elytra without large tubercles or strong sculpture, or only with small sparse tubercles. Eyes rounded or weakly oval, dorsoventrally placed above genal level. Legs thin, slender, long, not fossorial, with long sparse setae. Ovipositor very short and weakly sclerotized, transverse or of subequal length and width; paraproct very short, often with reduced or very short baculi; proctiger strongly widened, with very wide weakly sclerotized baculi; lobes 4 of coxite membraneous, rounded, with long, very dense hair brush. Spiculum ventrale very short, strongly widened and without common stem. Aedeagus with strongly sub-angurally curved apical piece.
Etymology
From the Ancient Greek ‘ἁβρός’ (‘habros’ = delicate or splendid) and ‘βατίς’ (plural inflection of ‘batis’ = a plant, samphire; genitive = ‘batis’; stem = ‘bat’).

Genera included

Distribution and bionomics
The representatives of the new subtribe are distributed in the deserts of Central and South Asia (Turkmenistan, Iran, Afghanistan, Pakistan, China): Karakum, Dasht-e Lut, Dasht-e Kewir, Registan, Taklamakan. Species of the mentioned genera inhabit non-fixed barchan sand dunes.

Comparison
The subtribe Habrobatina Nabozhenko & S. Chigray subtrib. nov. can be distinguished from the nominotypical one by the following key:

Key to the subtribes of Pimeliini Latreille, 1802
1. Combination of characters: eyes located dorsoventrally, above genal level; body completely covered with scales; ovipositor very short and weakly sclerotized, with membranous rounded and densely pubescent apical lobes of coxite; spiculum ventrale very wide and short, without or with very short common stem. Apical piece of aedeagus strongly sub-angulally curved ............................................. subtribe Habrobatina Nabozhenko & S. Chigray subtrib. nov.
   – Combination of characters: eyes located dorsoventrally above genal level and body without scales (Platyope genus group) or eyes located laterally on genal level (body can be without or rarely with scales); ovipositor long, with fossorial, bare, strongly sclerotized apical lobes of coxite. Apical piece of aedeagus weakly or moderately (not sub-angulally) curved ....subtribe Pimeliina Latreille, 1802

Genus Apatopsis Semenov, 1891
Figs 1A, 8A–D, 14, 23A, 26F, 27A–B

Apatopsis Semenov, 1891: 368, 370.

Type species
Apatopsis grombczewskii Semenov, 1891, by subsequent designation (Semenov 1903a).

Species included
Apatopsis grombczewskii Semenov, 1891 [= A. conradti Semenov, 1891, syn. resurr.].

Notes
Semenov described two species in this genus but did not designate a type species. Later, he placed Apatopsis conradti Semenov, 1891 as a junior synonym of A. grombczewskii Semenov, 1891 (Semenov 1903a; Semenov-Tjan-Shansky 1907) and clearly indicated that the genus Apatopsis includes only the one latter species. This indication (Semenov 1903a) corresponds to the subsequent designation of the type species of the genus according to article 69.1.1 of ICZN (1999). Gebien (1937) also listed Apatopsis
as monotypical genus. We do not know why these two species of *Apatopsis* were given as valid in both editions of the Palaearctic Catalogue (Löbl *et al.* 2008; Iwan *et al.* 2020) and we here resurrect the synonymy after the examination of the lectotypes of these conspecific taxa: *A. grombcewskii* Semenov, 1891 = *Apatopsis conradti* Semenov, 1891, syn. resurr.

**Diagnosis**

Body brown, elongate-oval (Fig. 1A–B), completely covered with goldish, lanceolate, longitudinally striated scales (Fig. 8A–D) and sparse, long, erected, yellowish setae (Fig. 8C–D), body length 10–12 mm. Eyes small, circular, located almost dorsally; surface behind eyes not covered by anterior margin of pronotum. Head covered with short, sparse projecting thin setae.

![Fig. 1. Species of the genera *Apatopsis* Semenov, 1891, *Habrochiton* Semenov Tjan-Shansky, 1907 and *Habrobates* Semenov, 1903, habitus. A. *A. grombcewskii* Semenov, 1891, ♀, paralectotype (ZIN), dorsal view. B. Ditto, ventral view. C. *Habrochiton vernus* Semenov-Tjan-Shansky, 1907, ♀, paralectotype (ZIN), dorsal view. D. Ditto, ventral view. E. *Habrobates vernalis* Semenov, 1903, ♂, paralectotype (ZIN), dorsal view. F. Ditto, ventral view.](image-url)
Pronotum transverse (width $1.8 \times$ length). Anterolateral angles of pronotum weakly projecting, obtuse, not extending to posterior margin of eyes. Disc of pronotum (Figs 1A, 8A) moderately convex, with suture-like longitudinal median line, surface of pronotum without depressions. Prothorax almost cylindrical. Prosternum without transverse triangular depression along anterior margin, short, $1.8 \times$ as long as transverse diameter of one procoxa. Prosternal process short (ratio of length of prosternal process to its maximum width: 3:2), not raised between procoxae.

Elytra translucent (see in transmitted light), with wide, oval depressions on lateral sides, surface of depressions densely covered with very long yellowish setae (Fig. 1A). Surface of elytra with longitudinal rows of very small sparse granules; each granule with long, erect, yellowish setae (Fig. 8D). Scutellar...
shield almost concealed by base of pronotum. Transverse length of metacoxae 1.2 × as long as intercoxal process of abdominal ventrite 1.

Trochanters with long sparse setae. Meso- and metafemora weakly curved outward, protibiae straight, meso- and metatibiae weakly curved outward, covered with short, yellowish setae. Protibiae (Figs 26F, 27A–B) widened at apex, outer anterior margin forms projecting process with outer apical tooth. Outer margin of protibiae covered with conical spinose tubercles, ventral surface of protibiae with long dense setae. Protibial terminal spurs elongated, extending to base of protarsomere 5, mesotibial terminal spur extending to apex of mesotarsomere 2, metatibial terminal spurs extending to midlength of

metatarsomere 1. Outer and inner protibial terminal spurs subequal in length, inner meso- and metatibial terminal spurs longer than outer ones, spurs flattened, acutely angulate at apex. Tarsi elongated, flattened from sides, protarsi with short spinose setae ventrally and more elongate fine dense setae dorsally, mesotarsi with very long erected setae dorsally and shorter setae ventrally, metatarsi with very long and dense suberected setae dorsally and very short recumbent setae ventrally. Tarsal claws elongated, thin, weakly curved outward.

Fig. 4. Species of the genera Przewalskia Semenov, 1893, Mantichorula Reitter, 1889 and Platyope Fischer von Waldheim, 1820, habitus. A. Przewalskia dilatata (Reitter, 1887), ♀ (ZIN), dorsal view. B. Ditto, ventral view. C. M. semenowi Reitter, 1889, ♂ (ZIN), dorsal view. D. Ditto, ventral view. E. Platyope leucogramma (Pallas, 1773), ♂ (ZIN), dorsal view. F. Ditto, ventral view.
Fig. 5. Species of the genus *Platyope* Fischer von Waldheim, 1820, details of structure and habitus.  
A. *P. leucogramma* (Pallas, 1773), ♂ (ZIN), prosternal process, ventral view.  
B. Ditto, ventral view.  
C. Ditto, dorso-lateral view.  
D. *P. grumi* (Semenov, 1893), ♂, paralectotype (ZIN), prosternal process, ventral view.  
E. Ditto, lateral view.  
F. Ditto, dorso-lateral view.  
G. Ditto, habitus, dorsal view.  
H. Ditto, ventral view.  
I. *P. granulata* Fischer von Waldheim, 1820, ♂ (ZIN), habitus, dorsal view.
Male genitalia
Inner sternite VIII (Fig. 14H) weakly sclerotized on lateral margins and membranous in middle, densely covered with short setae; setae longer along posterior margin; anterior margin arcuately emarginated; gland absent (at least was not observed).

Rods of spiculum gastrale (Fig. 14G) arcuately connected at apex; derivatives of inner sternite IX ladle-shaped covered with sparse setae.

Basal piece of tegmen (Fig. 14A–C) 1.2–1.4 × as long as apical piece, rounded at base, widest in basal third. Apical piece bare, rounded at apex, strongly curved (Fig. 14C), ventral apophyses of apical piece very short (Fig. 14A), projecting and elevated, dorsal apophyses long (Fig. 14B), triangular, acutely angulate at apex, not merged; median lobe (Fig. 14D–F) strongly curved, bifurcated at base, membrane between baculi weakly sclerotized in basal third, baculi at apex dorsally rolled into tube, not merged, apex narrowly rounded.

Female genitalia
Spiculum ventrale (Fig. 14I) very short and thickened, with short common stem, rods connected by membranous plate at apex; apophyses of sternite VIII long, acutely angulate at apex.

Ovipositor (Fig. 14J–L) weakly sclerotized, very short, transverse. Paraproct short, with narrow baculi; coxite lobes not merged; lobe IV transformed into weakly sclerotized and very densely pubescent pair plate, rounded at apex; lobe III forms additional elongate apical process, similar to lobe IV; lobes I–II with shorter setae; lobe I with oblique, narrow baculi, widened at apices. Proctiger wide, with straight apical margin and densely pubescent middle, baculi of proctiger strongly widened along all length.

Fig. 6. Species of the genus Platyope Fischer von Waldheim, 1820, habitus, dorsal view. A. P. proctoleuca proctoleuca Fischer von Waldheim, 1820, ♂ (ZIN). B. P. ordossica Semenov-Tjan-Shansky, 1907, ♂ (ZIN).
Female genital ducts (Fig. 23A)
Vagina sacciform, narrower before oviduct and after spermatheca, apical part of vagina elastically curved. Spermatheca consists of six tubes: two tubes flow into vagina independently, other four tubes combined into bundle with common base; two tubes (one independent, one in bundle) bifurcated. Accessory gland with four constrictions, one (as narrow tube) at base and three others in middle.

Distribution
China (Taklamakan Desert).

Fig. 7. Species of the genus *Earophantha* Semenov, 1903, habitus, details of structure. A. *E. collaris* (Fischer von Waldheim, 1844), ♂ (ZIN), dorsal view. B. *E. planidorsis* (Reitter, 1889), ♂ (ZIN), dorsal view. C. *E. serrata* (Semenov, 1893), ♂ (ZIN), dorsal view (ZIN). D. Ditto, ventral view. E. *E. beludzhistanica* Bogatchev, 1957, ♂, holotype (ZIN), dorsal view (ZIN). F. Ditto, right protibia, not to scale.
Apatopsis grombczewskii Semenov, 1891
Figs 1A, 8A–D, 14, 23A, 26F, 27A–B


Material examined

Lectotype of Apatopsis grombczewskii designated here
CHINA • 1 ♂; “М. Керей и Ней, 8.III.90, Громбчевскй” [Xinjiang: between Keriya and Niya]; 8 Mar. 1890; B.L. Grombchevsky leg.; “Apatopsis Grombczewskii m. Typ. XI.02. A. Semenov det.”; ZIN.

Paralectotype of Apatopsis grombczewskii
CHINA • 1 ♀; same collection data as for lectotype; ZIN • 1 ♀; “М. Хотаном и Керей (бл. последн.), X.89, Пѣвцов” [Xinjiang: between Hotan and Keriya, near the latter]; Oct. 1889; M.V. Pevtsov leg.; ZIN.

Lectotype of Apatopsis conradti designated here
CHINA • 1 ♀; “М. Керей и Ней, 8.III.90, Громбчевскй.” [Xinjiang: between Keriya and Niya]; 8 March 1890; B.L. Grombchevsky leg.; ZIN.

Additional material
CHINA • 1 ♂; “Kara-Kosh” [Karakax County], “Pudshia” [Puji]; 36°55’ N, 79°24’ E; alt. 2450 m; 21 Feb. 1890; S. Conradt leg.; ZIN • 3 ♂♂, 1 ♀; same collection data as for preceding; B.L. Grombchevsky leg.; ZIN • 1 ♂; between Keriya and Niya; 8 Mar. 1890; B.L. Grombchevsky leg.; ZIN • 15 ♂♂, 19 ♀♀; Yasumun; 8 Mar. 1890; B.L. Grombchevsky leg.; ZIN.

Distribution
China (Xijiang, Taklamakan Desert).

Genus Habrochiton Semenov Tjan-Shansky, 1907
Figs 1C–D, 10, 15, 26A, 27E


Type species
Habrochiton vernus Semenov-Tjan-Shansky, 1907, by original designation.

Species included
Habrochiton vernus Semenov-Tjan-Shansky, 1907, H. primaeveris Semenov-Tjan-Shansky, 1907.

Diagnosis
Body (Fig. 1C–D) brown, slender, elongate-oval, completely covered with moderately dense short (H. vernus) or long (H. primaeveris) longitudinally striated scales, sparse scale-like and simple setae (Fig. 10). Body length 7–12 mm. Eyes small circular, moderately convex in dorsal view; surface behind eyes concealed under anterior margin of pronotum.

Pronotum weakly transverse (1.4 × as wide as long). Anterolateral angles not expressed. Prosternum without transverse triangular depression along anterior margin. Prosternal process short and narrow
Fig. 8. *Apatopsis* Semenov, 1891 and *Habrobates* Semenov, 1903, details of structure. 

A. *A. grombchewskii* Semenov, 1891, ♂ (ZIN), pronotum. 

B. Ditto, scales and seta on pronotum. 

C. Ditto, elytral scales, setation and granulation. 

D. Ditto, granule, seta and scales on elytra. 

E. *H. vernalis* Semenov, 1903, ♂, paralectotype (ZIN), pronotum. 

F. Scales and spinulose setation on pronotum.
Fig. 9. *Habrobates* Semenov, 1903 and *Dietomorpha* Kühnelt, 1957, details of structure. 

A. *H. vernalis* Semenov, 1903, ♂, paralectotype (ZIN), left elytron. 
B. Ditto, elytral scales and rows of setae. 
D. Ditto, scales, setae and granules in middle of pronotum. 
E. Ditto, base of left elytron. 
F. Ditto, scales, spine-like tubercle and seta on elytron.
CHIGRAY S.N. et al., A revision of the Palaearctic Pimeliini (Coleoptera: Tenebrionidae)

Length 1.7 × width, not raised above procoxae, not protruding. Prosternum very short, near 2 × as long as longitudinal diameter of one procoxa.

Elytra elongate-oval (H. vernus) or triangular, almost wedge-shaped (H. primaeveris). Scutellar shield completely (H. vernus) or partially concealed (H. primaeveris) by elytral base; surface around scutellar shield without triangular depression. Transverse length of one metacoxa less than intercoxal process of abdominal ventrite 1 (Fig. 1D).

Trochanters with very short dense setae. Meso- and metafemora curved outward along elytral lateral vertical side. Pro- and metatibiae weakly curved outward, protibiae (Figs 26A, 27E) widened at apex, outer margin of protibia projecting into short rounded process at apex with one (H. primaeveris) or several acutely angulate and closely located (H. vernus) short spines; outer margin armed with very short tubercles with long and thin spines and additionally with long and sparse setae (Fig. 27E). Protibial terminal spurs strongly elongated, extending to base of protarsomere 5, mesotibial terminal spurs extending to base of mesotarsomere 3, metatibial terminal spurs extending to midlength of metatarsomere 1. Outer and inner protibial terminal spurs subequal in length, inner meso- and metatibial terminal spurs longer than outer one; spurs flattened, outer spur moderately narrowed to apex, acutely angulate at apex. Protarsi laterally not flattened, covered with short strong setae. Meso- and metatarsi flattened from sides, covered with long fine setae dorsally and short and stronger setae ventrally. Tarsal claws elongated, thin, weakly curved outward.

**Male genitalia**

Male genitalia identical to those in *Apatopsis*.

**Ovipositor** (Fig. 15J–L)

Very short, paraproct slightly longer than coxite. Paraproct with thin baculi, indistinct at apical third. Coxite lobe baculi short, more sclerotized in apical part, with additional sclerotized projection on ventral side; lobe II very narrow (Fig. 15L); lobe III slightly longer, conical, without additional projecting apical processes; lobe IV membranous, conical, rounded at apex, densely pubescent with long setae.

**Female genital ducts**

Destroyed during preparation.

**Distribution**

China (Taklamakan Desert).

*Habrochiton vernus* Semenov Tjan-Shansky, 1907
Figs 1C–D, 10, 15, 26A, 27E

**Material examined**

**Lectotype** designated here

CHINA • 1 ♂; “Оаз. Ниа, Вост. Турк., 3/3 II. 2/3.III.-90, Пѣвцов” [Xinjiang: Niya oasis, Eastern Turkestan, 38°01′17″, 82°44′15.4″], “*Habrochiton vernus* Sem. 1973 N. Skopin det.”; Feb.–Mar. 1890; M.V. Pevtsov leg.; ZIN.

**Paralectotype**

CHINA • 1 ♀; “Оаз. Ниа, Вост. Турк., 3/3 II. 2/3.III.-90, Пѣвцов” [Xinjiang: Niya oasis, Eastern Turkestan, 38°01′17″, 82°44′15.4″], “*Habrochiton vernus* Sem. 1973 N. Skopin det.”; Feb.–Mar. 1890; M.V. Pevtsov leg.; “*Habrochiton vernus* Typ 11.07 A. Semenow det.”; ZIN.
**Distribution**

China (Xijiang, Taklamakan Desert).

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**Fig. 10.** *Habrochiton vernus* Semenov-Tjan-Shansky, 1907, ♀, paralectotype (ZIN), covers and setation.  
A. Covers of pronotum. B. Ditto, larger scale. C. Elytral covers. a = simple setae; b = scale-like setae; c = scales.
Material examined

Habrochiton primaeveris Semenov Tjan-Shansky, 1907

Holotype
CHINA • ♂; “Ня (пески), 23.1.90, Пѣвцов” [Xinjiang, Niya ruins, sands, 38°01’17″, 82°44’15.4″]; 23 Jan. 1890, M.V. Pevtsov leg.; ZIN.

Notes
This species was originally described from a single specimen. The name ‘primaeveris’ is incorrectly written as ‘primaeverris’ in both editions of the catalogue of Palaearctic Coleoptera (Löbl et al. 2008; Iwan et al. 2020). Semenov Tjan-Shansky used the original epithet ‘primae-veris’.

Distribution
China (Xijiang: Taklamakan Desert).

Genus Habrobates Semenov, 1903

Habrobates Semenov, 1903a: 12 (type species Habrobates vernalis Semenov, 1903, by monotypy).


Kawiria – Kühnelt, 1957: 86.

Species included

Diagnosis
Body slender, elongate-oval, brown (Fig. 1E–F) or dark brown to black (Fig. 2A, E), completely densely covered with creamy to reddish (Fig. 1E–F) or brown (Fig. 2D–E) to black (Fig. 2A–C), flat, longitudinally striated scales (Figs 8F, 9B); body length from 6.5–8 mm (H. vejisovi) to 9–13 mm (H. vernalis, H. gabrieli comb. nov., H. agnesae). Body also covered with sparse small granules with yellowish or black setae. Eyes small, circular, convex in dorsal view; surface behind eyes not concealed by anterior margin of pronotum.

Pronotum transverse (Figs 1E, 2A, D, 8E). Anterolateral angles not expressed. Disc of pronotum moderately convex (Fig. 2C, E), with wide, transverse depression in basal third (Fig. 1E) or two longitudinal lateral depressions (Fig. 2A, D). Prosternum short (longitudinal length 2.8 × as short as longitudinal length of one procoxa), without transverse triangular depression along anterior margin. Prosternal process (1.5 × as long as wide), not raised and not protruding (Fig. 1F) or raised and protruding beyond procoxae as in H. gabrieli comb. nov. (Fig. 2B–C, E).

Elytra egg-shaped, convex, with 10 longitudinal rows of sparse granules, each granule with short seta (Figs 1E, 2A, D, 9A). Scutellar shield completely or partly hidden by base of pronotum; surface around
scutellar shield without distinct triangular depression. Transverse length of metacoxae 1.6× as long as intercoxal process of abdominal ventrite 1 (Figs 1F, 2B).

Trochanters with brush of dense long setae. Meso- and metatibiae curved outward along lateral vertical side of elytra. All tibiae weakly curved outward. Protibiae weakly widened at apex, outer margin of protibiae with small, spinose granules and long, erected setae along all length and projecting apical process (Figs 26B, 27C–D). Protibial terminal spurs more or less widened and flattened, extending to base of protarsomere 4, mesotibial terminal spurs extending to apex of mesotarsomere 1, metatibial terminal spurs extending to midlength of metatarsomere 1. Outer and inner protibial terminal spurs subequal in length, inner meso- and metatibial terminal spurs longer than outer ones. Protarsi not flattened from lateral sides, completely covered with spinose setae ventrally and simple setae dorsally. Meso- and metatarsi flattened from lateral sides, covered with long, fine setae dorsally and shorter, stronger setae ventrally. Tarsal claws long, thin, curved outward.

**Male genitalia**

Inner sternite VIII (Fig. 16I) weakly sclerotized along lateral margins and in middle, densely setose, especially at outer margin; anterior margin with short median emargination; pair gland present.

Rods of spiculum gastrale (Fig. 16G–H) widely spaced, arcuately connected at apex; derivatives of inner sternite IX ladel-shaped, evenly weakly sclerotized; apical margin of these derivatives covered with dense short setae.

Aedeagus thickened, robust (Fig. 16A–C). Basal piece of tegmen slightly longer than apical one, rounded apically, widest in basal half. Apical piece strongly curved, glabrous, narrowly rounded at apex; ventral apophyses not expressed, dorsal apophyses thin and short, like furca. Median lobe (Fig. 16D–F) fusiform, curved, bifurcated basally, basal third of membrane weakly sclerotized, apex narrowly rounded.

**Female genitalia**

Spiculum ventrale (Fig. 16G) very short and widened, without common stem; sternite VIII strongly transverse, evenly weakly sclerotized, with long, acutely angulate lateral apophyses, anterior margin rounded, covered with very long dense setae.

Ovipositor (Fig. 16K–M) very short and weakly sclerotized. Paraproct very short, with reduced baculi (with only weakly sclerotized inner apices); lobe I of coxite with very short baculi (in form of short sclerotization of inner apices); lobe II weakly sclerotized, transverse; lobe III conical, slightly stronger sclerotized; lobe IV not paired and not sclerotized, membranous, rounded at apex, densely pubescent by long setae. Proctiger very wide, widely emarginate at apex, sparsely pubescent on lateral margins and with very wide triangular baculi.

**Female genital ducts** (Fig. 23B)

Vagina strongly widened, saciform, narrower before oviduct and after spermatheca, apical part of vagina elastically, sharply curved. Spermatheca short, single-tube. Accessory gland widened at apical ⅔, with thick basal canal and one short constriction between gland and vagina.

**Distribution**

Turkmenistan (Karakum Desert) and Iran (Dasht-e Lut and Dasht-e Kavir deserts).

**Notes**

Only one character, the protruding and raised prosternal process, distinguishes *Kawiria* from *Habrobates*. This character cannot be used as the main character for diagnostics of genera within Pimeliini, because
Fig. 11. *Przewalskia* Semenov, 1893 and *Mantichorula* Reitter, 1889, details of structure. A. *P. dilatata* (Reitter, 1887), ♂ (ZIN), pronotum. B. Ditto, hemispherical large tubercles on pronotum. C. Ditto, base of left elytron. D. Ditto, pubescence of elytron. E. *M. semenowi* Reitter, 1889, ♂ (ZIN), pronotum. F. Ditto, tubercles and setation on sides of pronotum.
it is often used for diagnosis of different species within one genus, for instance, in Diesia Fischer von Waldheim, 1820, Sternoplax, Lasiostola. A complex of other characters shows that the type species of both Habrobates and Kawiria are congeneric: body completely covered by flattened scales without central ridge, head with erect sparse setae, pronotum with microgranules for scales and slightly small granules for short setae, elytra with 10 longitudinal rows of small granules (each granule with short seta) and dense granules along apical margin, width of intercoxal process of abdominal ventrite 1 less than width of one metacoxa, outer margin of protibiae with thin short spines, sparse long setae and projecting process at apex. Characters such as body colour and density of setation of meso- and metatibiae are of species level. Consequently, the following synonymy is proposed: Habrobates Semenov, 1903 = Kawiria Schuster, 1935 syn. nov. So, the following new combination is established: Habrobates gabrieli (Schuster, 1935) comb. nov. (from Kawiria).

It is interesting that Schuster did not compare Kawiria with Habrobates in the original description (but he compared it with Mantichorula and Homopsis), although he noted that his new genus is very similar to Habrochiton. In addition, he interpreted scales on the body as microwrinkles, which give a silky shine (Schuster 1935).

In general, early authors gave unjustifiably high importance to the prosternal process and used this species-level character for descriptions of genera. The same situation with the prosternal process is observed in two species of Dietomorpha and discussed below in the case of the synonymy of the genera Platypoe and Homopsis.

Bionomics
Detailed bionomics, behaviour and adaptations of Habrobates vernalis were described by Medvedev (1965b) and Kaplin (2019). Brief information about bionomics of H. agnesae and H. gabrieli comb. nov. was given by Schuster (1935, 1938). Species of this genus inhabit non-fixed barchans sand dunes, but often climb bushes and trees (usually Haploxylon) for thermoregulation. Schuster noted that Kawiria was described from a salt desert, and Habrobates is known from sand deserts (Schuster 1938). However, two collectors, Dr Alfons Gabriel and his wife Agnes, informed him via the privy councillor Professor Meinhard v. Pfaunder, that they collected these beetles (Kawiria) on saxaul barchan sand dunes near Halvan village (South Khorasan Province), without getting off their camels. So, Habrobates gabrieli comb. nov. has very similar behaviour and bionomics to other species of Habrobates, and it is not associated with salt marshes.

Habrobates agnesae Schuster, 1938

Material examined

Syntype

Additional material
IRAN • 2 specs; Desert du Lut; Mar. 1970; Ab. Khoran leg.; HNHM.
Material examined

**Lectotype** designated here
TURKMENISTAN • 1 ♂; “Уч-аджи, 5.IV.900, Гермс” [Uch-Aji, now Bagtyýarlyk in Mary Province]; “Syntypus”; “*Habrobates vernalis* m. Typ. ♂, XI.02, A. Semenov det.”; “Coll. Semenov-Tian-Shansky”; 5 Apr. 1900; Germs leg.; ZIN.

**Paralectotype**
TURKMENISTAN • 1 ♂; same collection data as for lectotype; ZIN.

**Additional material**
TURKMENISTAN • 1 spec.; Karakum, Repetek; 6 Mar. 1958; G.S. Medvedev leg.; HNHM • 1 spec.; Karakum, Repetek; 6 Mar. 1958; G.N. Medvedeva leg.; HNHM • 1 spec.; Uzboy River coast, sands near Yaskhan Lake, on saxaul; 19 Apr. 1951; Steinberg leg.; HNHM.

**Distribution**
Turkmenistan (Karakum Desert).

*Habrobates vejisovi* Kelejnıkova, 1977

Material examined

**Paratypes**
TURKMENISTAN • 2 ♀♀; “Репетек, 23–24.IV.1974, Кузнецов” [Repetek]; “22-IV-74, гол. барх.” [bare barchans dunes]; “Paratypus, ♀, *Habrobates vejisovi* Kelejn 19.II.1977”; 23–24 Apr. 1974; N.Ya. Kuznetsov leg.; ZIN • 1 ♀; same collection data as for preceding; HNHM.

**Additional material**
TURKMENISTAN • 1 ♂; Karakum, Repetek; 27 Jan. 1957; N.G. Skopin leg.; ZIN • 7 ♂♂, 6 ♀♀♀; same collection data as for preceding; 6 Mar. 1958; G.S. Medvedev leg.; ZIN • 1 ♂, 1 ♀; same collection data as for preceding; 12 Apr. 1972; Begov leg.; ZIN • 2 ♂♂, 3 ♀♀♀; same collection data as for preceding; 16 Apr. 1980; B.A. Korotyaev leg.; ZIN.

**Distribution**
Turkmenistan (Karakum Desert, east).

*Habrobates gabrieli* (Schuster, 1935) comb. nov.
Figs 2, 26B

Material examined

**Lectotype** designated here
IRAN • 1 spec. (sex unknown); “Kawiria n. g. Gabrieli n. sp. Schuster”; “Pers Halwan” [Alwand or Halwan River]; “TYPUS”; “gabrieli; Pfaundler”; NMB.

**Paralectotyopes**
IRAN • 1 spec.; “Pers. G. Kawir S.” [Dasht-e Kavir Desert]; “4”; “COTYPUS”; NMB • 1 spec.; “Kawiria gabrieli”; “Pers Halwan” [Alwand or Halwan River]; “COTYPUS”; “Paratypus 1935 Kawiria Gabrieli Schuster”; HNHM.
Additional material
IRAN • 2 specs; Yazd, Riq-e Dion, 32 km of Chah Malek 33°46’ N, 52°42’ E versus Chupunum 33°31’ N, 54°19’ E, alt. 800 m; 16 May 1975; W. and F.C. Rechinger leg.; HNHM • 1 spec.; Yazd, Sudrand, Kavir desert, between Tabas and Anarak; 15 May 1975; W. and F.C. Rechinger leg.; HNHM • 1 spec.; “Persia Centr.”; 1948; N. Alexandrov leg; ZMMU.

Fig. 12. Manticorula Reitter, 1889 and Platyope Fischer von Waldheim, 1820, details of structure. A. M. semenowi Reitter, 1889, ♂ (ZIN), base of left elytron. B. Ditto, pubescence of elytron. C. P. leucogramma (Pallas, 1773), ♂ (ZIN), pronotum. D. Ditto, hemispherical tubercles and pubescence of pronotum. E. Ditto, basal half of left elytron. F. Ditto, pubescence of elytron.
Distribution
Iran (Dasht-e Kavir Desert).

Genus *Dietomorpha* Reymond, 1938
Figs 3, 17, 23C, 26C

*Dietomorpha* Reymond, 1938: 143.

*Dietomorpha* – Kühnelt 1957: 86, fig. 4.
*Kawiria* – Kaszab 1957: 295–296 (erroneous interpretation of *Dietomorpha pardalis*).

Type species
*Dietomorpha pardalis* Reymond, 1938, by monotypy.

Species included
*Dietomorpha pardalis* Reymond, 1938, *Dietomorpha gonzalesi* S. Chigray & Nabozhenko sp. nov.

Diagnosis
Body robust (Fig. 3), completely covered with lanceolate longitudinally striated, creamy scales (each scale with median longitudinal ridge at middle) (Fig. 9D, F), with spotted (Fig. 2A) or striped (Fig. 3C, E–G) pattern of dark scales on elytra and dark spots on pronotum. Body under scales black or dark-brown. Body length 9–14 mm. Epistoma and frons covered with sparse, erected yellowish setae. Eyes large, circular, convex in dorsal view; surface behind eyes concealed by anterior margin of pronotum.

Pronotum slightly transverse (1.4–1.7 × as wide as long); lateral margins and partly prothoracic hypomera basally with bare and smooth black spot. Disc of pronotum (Fig. 52) convex, with two triangular deep impressions at base. Pronotum covered with sparse, erect, conical tubercles becoming larger along lateral margins, each tubercle with spine at apex. Prosternum without transverse triangular depression along anterior margin, longitudinal length 2.2 × as short as longitudinal length of one procoxa. Prosternal process elongated and narrow (length 3 × width), raised or not raised between procoxae, strongly (*D. pardalis*) (Fig. 3B) or weakly (*D. gonzalesi* S. Chigray & Nabozhenko sp. nov.) (Fig. 3D) protruding, not touching with mesoventrite.

Elytra oval or widely oval, with one (*D. gonzalesi* S. Chigray & Nabozhenko sp. nov.) or double in middle (*D. pardalis*) humeral rib; with strong, acute spinose tubercles (with spine in base of each tubercle) (Fig. 9E–F) on dark spots (*D. pardalis*) or with five longitudinal rows of spinose tubercles (*D. gonzalesi* S. Chigray & Nabozhenko sp. nov.). Scutellar shield completely or partly concealed by base of pronotum; surface around scutellar shield with triangular depression. Transverse length of metacoxae subequal to intercoxal process of abdominal ventrite 1.

Trochanters with elongate, sparse setae. Meso- and metafemora curved outward. Protibiae with projecting process at apex of outer margin, armed with tuft of spines (Fig. 26B). Lateral margins of protibiae with long, fine setae and short spines. Protibial terminal spurs elongated, extending to base of protarsomere 4; mesotibial terminal spurs extending to apex of mesotarsomere 2; metatibial terminal spurs extending to midlength of metatarsomere 1. Outer and inner protibial terminal spurs subequal in length, inner meso- and metatibial terminal spurs longer than outer ones, spurs flattened from sides. All tarsi flattened from sides, covered with long setae dorsally and short setae ventrally. Tarsal claws elongated, thin, weakly curved outward.
**Male genitalia** (Fig. 17A–H)
Inner sternite VIII (Fig. 17H) weakly sclerotized on margins, densely covered with long, dense setae; anterior margin deeply emarginated in middle; gland is absent (or at least, was not observed).

Rods of spiculum gastrale (Fig. 17G) widely spaced, thickened, arcuately connected at apex, with wide membrane along this connection and near derivatives of inner sternite IX; these derivatives elongated, ladle-shaped, evenly sclerotized in middle and slightly more sclerotized terminally; apical margin of derivatives covered with short dense setae.

Tegmen of aedeagus thickened, obtuse (Fig. 17A–C). Basal piece of tegmen much shorter and wider than apical piece, with tubercle-shaped apex (Fig. 17A–B). Apical piece strongly curved, narrowly rounded at apex, covered with short setae in apical half; ventral apophyses not expressed, dorsal apophyses moderately long, triangular. Median lobe (Fig. 17D, F) widened in basal ⅔ and narrowed in apical third, with weakly separated apex, strongly curved; basal part with additional four sclerotized armatures; baculi not merged at apex.

**Female genitalia**
Spiculum ventrale (Fig. 17I) very short and strongly widened, sternite VIII with long acutely angulate curved apophyses.

Ovipositor (Fig. 17G–L) short, weakly sclerotized. Coxite with four distinct not merged lobes. Baculi of coxite lobe I short, shorter than paraproct baculi; lobe II small, sclerotized; lobe III larger, conical, sclerotized; lobe IV membranous (only at apex slightly sclerotized), conical, with dense pubescence of long setae. Paraproct V-shaped on each side ventrally, baculi sharply widened in base and narrow in apical third. Vulva with narrow sclerotization in the middle of ventral side. Apical margin of proctiger with deep V-shape emargination, baculi of proctiger strongly widened.

**Female genital ducts** (Fig. 23C)
Vagina moderately widened, saciform, narrower before oviduct and after spermatheca, apical part of vagina not elastically curved. Spermatheca very short, single-tube. Accessory gland long, with two tube-like constrictions, short in base and long in middle. Basal part between two constrictions not saciform.

**Distribution**
Iran and Pakistan (Balochistan region), Afghanistan (Registan Desert).

**Notes**
Koch (1964) synonymized *Dietomorpha pardalis* and *Kawiria szekessyi* Kaszab, 1957 (junior synonym). Koch also noted that Reymond (1938) should be considered as the author of the genus *Dietomorpha* and the species *Dietomorpha pardalis*, because he presented figures for this species. Kaszab (1957) noted that Reymond (1938) did not give a description or a differential diagnosis of the genus, and the author of *Dietomorpha pardalis* should therefore be Kühnelt (1957), who distinctly described, compared and figured this taxon. Later Kweton (1982) cited Koch’s work but incorrectly established the following synonymy: *Kawiria pardalis* Reymond, 1938, comb. n. = *Kawiria szekessyi* and *Dietomorpha* Reymond, 1938 = *Kawiria* Schuster, 1957. Medvedev (2005) was not aware of these works and re-established the synonymy previously proposed by Koch, and he also recognised the author of the binomen *Dietomorpha pardalis* Kühnelt, 1957.
Dietomorpha pardalis Reymond, 1938
Figs 3A–B, 17, 23C, 26C

Kawiriia szekessyi Kaszab, 1957: 295 (original description).

Material examined

Paratypes of Kawiriia szekessyi Kaszab, 1957

Additional material
AFGHANISTAN • 2 ♂♂; Registan, Malekdokun; 5 Mar. 1973; O.N. Kabakov leg.; ZIN • 2 ♂♂, 2 ♀♀; SW Registan Desert; alt. 1000 m; 15 Mar. 1973; O.N. Kabakov leg.; ZIN.

PAKISTAN • 2 ♂♂; Balochistan Province, 20 km of W Nushki; 25–29 Dec. 1918; ZIN.

Distribution
Iran and Pakistan (Balochistan region in both countries), Afghanistan. Medvedev (2005) listed D. pardalis for Registan Desert (Afghanistan) and adjacent areas of Pakistan, but this record was omitted from the Palaearctic Catalogue (Iwan et al. 2020).

Dietomorpha gonzalesi S. Chigray & Nabozhenko sp. nov.
Fig. 3B–G

Etymology
The new species is named after David Gonzales (Saint-Laurent-du-Pape, France), who made a great contribution to the Tenebrionidae of the New and Old Worlds.

Material examined

Holotype
PAKISTAN • ♀; Balochistan, Khuzdar; May 2009; Hafiz Akhtar leg.; V.2009; coll. David Gonzales; MNHP.

Paratypes

Notes on paratypes (Maxwell Barclay, personal communication)
Ernest Vredenburg (the donor of the specimens, Superintendent of the Geological Survey of India) and Captain Frank C. Webb Ware (the collector of the paratypes, at Quetta, ‘Political Assistant’ at Chagai and who was working on the Sistan-Quetta caravan route) went to Quetta together. It is likely that the
beetles were collected at Quetta in 1899, given the Indian Museum registration in 1914, and eventually given the BMNH registration in 1973.

**Description**

**Female**

Body oval, covered by creamy scales, with striped pattern of dark spots on pronotum and elytra; scales lanceolate, longitudinally striated. Anterior margin of epistoma widely emargined. Epistoma and frons sparsely covered with erected, yellowish setae. Genae rounded. Eyes large, circular, convex in dorsal view; surface behind eyes covered by anterior margin of pronotum. Ratio of head width across eyes to interocular distance on frons is 1.3. Antennae long, with ultimate antennomere extending elytral base. Ratio of length (width) of 2nd–11th antennomeres: 0.5(0.5), 2.4(0.5), 0.9(0.4), 0.8(0.5), 0.8(0.5), 0.8(0.5), 0.7(0.8), 0.7(0.8), 0.2(0.1), 0.3(0.4). Head covered with fine, sparse spinose granules (granule diameter 2–3× less than intergranular spaces).

Pronotum transverse (1.7× as wide as long), widest before middle, where it 1.2× as wide as head, with two dark, broad fields and pale spot in middle; lateral margins at base together with contiguous part of prothoracic hypomera with glabrous and smooth black spot. Ratio of width of pronotum at anterior margin to its maximum width and to width at base: 8:8.5:8. Anterior margin and base of pronotum widely weakly emarginated at middle. Lateral margins rounded, emarginated at base. Anterolateral angles not expressed, posteralateral angles obtuse, widely rounded. Disc of pronotum transversely convex, with two triangular depressions at base. Apical half and middle of pronotum covered with projecting spine-like spinose tubercles (mainly on sides of pronotal disc). Prosternal process narrow, elongated (3× as long as wide), not raised between procoxae, slightly protruding beyond procoxae.

Elytra weakly elongate (1.2× as wide as long), 3.4× as long and 1.8× as wide as pronotum, 2.1× as wide as head. Each elytron with five brown, longitudinal stripes on creamy background. Elytra without humeral ribs, with four longitudinal rows of spine-like tubercles: one row on each lateral vertical side, one humeral row and four discal rows. Apex of elytra with dense tubercles. Scutellar shield not concealed by base of elytra; surface around scutellar shield with triangular depression. Metepisterna, meso- and metaventrites with fine sparse spinose granules. Transverse length of one metacoxa subequal to intercoxal process of abdominal ventrite 1.

Abdominal ventrites covered with fine, sparse granules (granule diameter 1.5–3× as short as intergranular spaces).

Trochanters with elongated, sparse, yellowish setae. Meso- and metafemora curved outward. Protibiae sharply widened at apex, outer margin with row of short, acutely angulate spines and several sparse, long setae; spines closely spaced at apex. Outer and inner margins with row of long, thin setae. Tibial terminal spurs flattened, straight, acutely angulate at apex (except for metatibial terminal spurs), widened to apex and rounded apically. Pro- and mesotibial terminal spurs moderately elongated, extending base of tarsomere 2, metatibial terminal spurs extending to midlength of metatarsomere 1. Meso- and metatibiae slightly curved outward, with similar spines and dorsal setae as on protibiae. All tarsi flattened from sides, protarsi only with spines, meso- and especially metatarsi with dense, long setae dorsally and spines ventrally. Tarsal claws large, thin, visibly curved outward. Length ratio for femur, tibia, and tarsus: 6.5:4:2 in fore leg, 7.5:5.5:3.5 in middle leg, 8.5:8:6 in hind leg.

Body length 12 mm, width 7.5 mm.
Comparative diagnosis

This new species differs from *D. pardalis* by the more elongated body, the slightly protruding prosternal process (strongly protruding beyond procoxae in *D. pardalis*), the striped pattern (spotted in *D. pardalis*), the longitudinal rows of spine-like setae on elytra (the tubercles located only in spots in *D. pardalis*), the absence of elytral humeral ribs and not concealed scutellar shield.

Subtribe **Pimeliina** Latreille, 1802

**Type genus**


**Platyope** genus group


Genus **Przewalskia** Semenov, 1893

Figs 4A–B, 11A–D, 18, 23D, 24B, 26E, 28A–B

*Przewalskia* Semenov, 1893: 262, nota.


**Type species**

*Platyope dilatata* Reitter, 1887, by original designation.

**Species included**

*Platyope dilatata* (Reitter, 1887), *P. lineata* (Reitter, 1887), *P. trinkleri* Gebien, 1940.

**Diagnosis**

Body (Fig. 4A–B) from pale brown to dark brown, robust, elytra rounded (semispherical), sometimes slightly flattened dorsally, completely covered with recumbent, white or yellowish and brown setae, with longitudinally striped pattern on elytra. Body length 7–18 mm. Eyes small, circular, convex in dorsal view; surface behind eyes concealed by anterior margin of pronotum.

Pronotum almost square (width subequal to length) (Fig. 3A), with lateral margins straight or weakly emarginated basally. Anterolateral angles strongly projecting, acutely angulated (but rounded at apex), visibly raised above level of eyes. Disc of pronotum moderately convex, with rounded, deep depression in middle and two triangular, deep depressions at base, surface around depressions densely covered with very large semispherical tubercles with seta (Fig. 11A–B), with setae between them. Prosternum long, 1.8 times as short as longitudinal diameter of one procoxa (Fig. 4B), without depression along anterior margin. Prosternal process narrower between middle level of coxae and strongly widened to apex (1.5 times as long as wide), not raised between procoxae and not protruding beyond procoxae.

Elytra semispherical (2 or more times as wide as pronotum), humeral rib weakly expressed, not strongly elevated, with row of sparse tubercles. Elytral pubescence has longitudinally striped pattern (from 3 in *P. trinkleri* to 7 in *P. dilatata*) of recumbent, yellowish setae (Fig. 4A) as a result of presence of denser or sparser setae (Fig. 11C–D). *Przewalskia trinkleri* has glabrous anterior half and striped apical and lateral parts of elytra. Each elytron with three (*P. trinkleri*) to 4–6 longitudinal rows of very small granules with
long seta in denser pubescent (light) striae. Scutellar shield not hidden under base of pronotum, widened to apex; surface around scutellar shield without depression. Transverse length of one metacoxa subequal to intercoxal process of abdominal ventrite 1.

At least pro- and mesotrochanters with very long setae. Meso- and metafemora curved along elytral lateral vertical side. Protibiae widened from proximal to distal part, weakly curved outward, with strong, short spines (on outer margin) and very dense, long setae (Figs 26E, 28A–B); spines denser at apex. Mesotibiae curved outward, with smaller and sparser spines and dense pubescence on inner margin. Metatibiae straight, with small, sparse spines and dense pubescence at least in apical part. Protibial terminal spurs usually lanceolate (at least outer spur), large, widened and flattened, slightly curved inward, subequal in length, extending to base of protarsomere 3; meso- and metatibial terminal spurs different in length, narrowed from base to apex, mesotibial terminal spurs extending to base of mesotarsomere 2, the latter ones extending to apex of metatarsomere 1. Pro- and mesotarsi flattened from lateral sides, covered with long fine setae dorsally and shorter, stronger setae ventrally; metatarsi also flattened from lateral sides, with long setae dorsally and very short ones ventrally; setae form dense, flattened brushes. Tarsal claws elongate, narrow, weakly curved outward.

**Male genitalia** (Fig. 18A–H)
Inner sternite VIII (Fig. 18H) weakly, widely sclerotized, except for narrow, membranous median part in middle, densely covered with long setae (setae much longer and denser along posterior margin); posterior margin with deep V-shaped median emargination; gland absent (or at least, not observed). Spiculum gastrale (Fig. 18G) without common stem, with weakly sclerotized membrane, rods roundly connected; derivatives of inner sternite IX elongate-oval, evenly sclerotized, with long setae apically.

Tegmen of aedeagus (Fig. 18A–C) long, slender, with basal piece slightly shorter than apical one; apical piece bare, slightly curved, acutely angulate at apex ventral apophyses not expressed, dorsal apophyses long, merged in triangular plate; basal piece with narrowly rounded apex; median lobe with wide sclerotization in apical and basal parts and small membranous area in middle, base narrowly rounded, not bifurcate, apex acutely angulate (Fig. 18D–F).

**Female genitalia**
Spiculum ventrale (Fig. 18I) with long common stem, rods narrow, anterior margin of sternite VIII nearly straight, with long, dense setae, apophyses of sternite VIII short, narrow, narrowly rounded at apex.

Ovipositor (Fig. 18J–L) moderately sclerotized, elongate. Coxite with four distinct, not merged lobes. Baculi of coxite lobe I well expressed, but much shorter than paraproct baculi; lobe II short, transverse; lobe III elongate; lobe IV strongly sclerotized, transformed into curved spatulate structure. Paraproct elongate, with narrow, long baculi. Proctiger also elongate and with narrow baculi, anterior margin rounded. Vulva with pair of sclerotized ‘spicula’ in the middle on ventral side. Paraproct in base, coxite and proctiger with very dense and long pubescence.

**Female genital ducts** (Fig. 23D)
Vagina elongated, with longitudinal wrinkles and separated anterior part. Spermatheca as short single tube. Accessory gland long, sacciform, with one thick constriction at base.

**Distribution**
China (Qinghai, Xinjiang): Taklamakan Desert.
Przewalskia dilatata (Reitter, 1887)
Figs 4A–B, 11A–D, 18, 23D, 24B, 26E, 28A–B

Material examined

Lectotype of Platyope dilatata designated here
CHINA • 1 ♂; “Prj 85” [green label]; “(Przewalsky) Nördlichen Tibet”; “Typus Platyope dilatata Rtt. Coll. Reitter”; “Platyope dilatata m.”; N.M. Przewalsky leg.; HNHM.

Paralectotype
CHINA • 1 spec.; “IV” [green label]; “Prj 85”; “Typus Platyope dilatata Rtt. Coll. Reitter”; HNHM.

Additional material
CHINA • 10 ♂♂, 7 ♀♀; Niya; 3 Mar. 1890; M.V. Pevtsov leg.; ZIN • 10 ♂♂, 6 ♀♀; same collection data as for paralectotype; 1–20 Apr. 1890; ZIN • 21 ♂♂, 40 ♀♀♀; between Keriya and Niya; 8 Mar. 1890; B.L. Grombchevsky leg.; ZIN • 1 ♂, 1 ♀; Keriya; 5 Mar. 1890; B.L. Grombchevsky leg.; ZIN • 1 ♀; same collection data as for preceding; 6–11 Apr. 1890; ZIN • 15 ♂♂, 10 ♀♀♀; Karasay; May 1890; M.V. Pevtsov leg.; ZIN • 7 ♂♂, 15 ♀♀♀; Niya; 1891; V.I. Robarovsky leg.; ZIN • 1 spec.; Turk. Chin. [Turkestanian China], Keria; 5 Mar. 1890; B.L. Grombchevsky leg.; HNHM • 1 spec.; Sinkiang [Xinjiang]; 5 May 1960; unknown collector; HNHM.

Distribution
China (Xinjiang: Taklamakan Desert; Qinghai).

Genus Mantichorula Reitter, 1889
Figs 4C–D, 11E–F, 12A–B, 19, 23E, 24C, 26D, 27F–G

Mantichorula Reitter, 1889: 695.


Type species
Mantichorula semenowi Reitter, 1889, by monotypy.

Species included
M. semenowi Reitter, 1889; M. grandis Semenov, 1893; M. mongolica Schuster, 1940.

Diagnosis
Body black, wide, dorsoventrally flattened, disc-shaped, without dense pubescence dorsally, only some parts of pronotum and head with setae, elytra dorsally and laterally with very short, fine, sparse spines (Fig. 4C–D) and sometimes with small area of setation along apical part of suture. Body length 10–20 mm. Eyes large, circular, moderately convex dorsally.

Pronotum strongly transverse (more than 2 × as wide as long). Anterolateral angles weakly projecting. Base of pronotum strongly widely emarginated, and posterolateral angles deeply protruding and impressed into elytral base (Figs 4C, 11E). Disc of pronotum with one medial and two lateral longitudinal stripes of recumbent, moderately dense, short setae and coarse, semispherical tubercles on lateral sides (Fig. 11E–F); base widely, sharply depressed and flattened. Prosternum before procoxae near 2 × shorter
than longitudinal diameter of one procoxa. Prosternal process very large and broad, raised between procoxae, strongly protruding beyond procoxae, extending to mesoventrite (Fig. 4D).

Scutellar shield not concealed by base of pronotum, triangular. Elytra short, oval, with (Fig. 11E) or without depressions around scutellar shield, apical part abducted. Elytra with double humeral rib. Ventral side of body covered with short, dense setae. Metaventrite much shorter, than mesoventrite. Intercoxal process 1.2–1.24 × as wide as one metacoxa (Fig. 4D).

Protrochanters and inner side of profemora covered with very long, dense setae. Femora robust, weakly curved outward. All tibiae weakly curved outward. Protibiae strongly gradually widened to apex, triangular, flattened, without projecting process at apex of outer margin, with dense, short, strong spines, but with longer and finer spines and dense, long setae along lateral margins (more recumbent on inner side) (Figs 26D, 27F–G); strong spines denser at apex of outer margin. Meso- and metatibiae with similar structures, but not dorsoventrally flattened and widened, often additionally covered with cream coloured scales. Protibial terminal spurs large and widened, not lanceolate (Fig. 27F–G), subequal in length, extending to base of protarsomere 5. Meso- and metatibial terminal spurs different in length, inner tibial terminal spurs longer than outer ones, extending to protarsomere 3 and half length of metatarsomere 1 subsequently. Protarsi with long, recumbent spines dorsally and ventrally and short setae laterally; meso- and metatarsi flattened from sides, with very dense, long setae on dorsal side.

**Male genitalia** (Fig. 19A, H)
Inner sternite VIII (Fig. 19H) sclerotized on margins and membranous in middle, densely pubescent; posterior margin deeply emarginated medially; gland absent (at least, not observed). Spiculum gastrale (Fig. 19G) with roundly connected rods and rounded derivatives of inner sternite IX with short pubescence terminally.

Tegmen of aedeagus (Fig. 19A–C) elongate, slender, with subequal basal and apical pieces. Basal piece weakly wider than apical piece, both fusiform. Apical piece glabrous, weakly curved, ventral apophyses not expressed, dorsal apophyses short, merged in triangular plate. Basal piece with sub-acutely angulate apex. Median lobe acutely angulate apically, with narrow baculi and wide, membranous area at middle, slightly bifurcated at base (Fig. 19D–F).

**Female genitalia**
Spiculum ventrale with elongate common stem and narrow rods (Fig. 19I). Sternite VIII narrow, strongly transverse, with moderately short apophyses.

Ovipositor (Fig. 19J–L) is very similar to that in Przewalskia, but differs in the absence of sclerotization on vulva, apical lobes turned to dorsal side and widely weakly rounded proctiger.

**Female genital ducts** (Fig. 23E)
Vagina elongated, tube-shaped, not widened, with short primary bursa copulatrix at apex. Spermatheca absent. Accessory gland of spermatheca very short, tube-shaped, not modified, without constrictions.

**Distribution**
Mongolia, China (Inner Mongolia, Ningxia, Gansu, Shanxi provinces).

**Notes**
Schuster (1940) believed that all three species of Mantichorula should be regarded as valid, and that M. grandis distinctly differs from M. semenowi and M. mongolica because of their short antennae, which do not extend far beyond the base of the pronotum. Medvedev (1990) interpreted the genus
Mantichorula as monotypic. We studied the type series of *M. grandis* and discovered that this species and some specimens standing as *M. semenowi* in the ZIN collection do indeed have shorter antennomeres. Studies of the type specimens of *M. semenowi* and *M. mongolica*, as well as a detailed examination of male and female genitalia, are necessary to revise this genus.

*Mantichorula semenowi* Reitter, 1889
Figs 4C–D, 11E–F, 12A–B, 19, 23E, 24C, 26D, 27F–G

Material examined

Lectotype designated here
CHINA • 1 ♂; “Kan-ssu 1886 G. Patanin”; “Typus Mantichorula Semenovi Rtt. Coll. Reitter”; “Mantichorula Semenovi m. 1889”; 1886; G.N. Potanin leg.; HNHM.

Paralectotypes
CHINA • 1 spec.; “Kan-ssu 1886 G. Patanin”; “Cotypus Mantichorula Semenovi Rtt. Coll. Reitter”; “Mantichorula Semenovi m. 1889”; 1886; G.N. Potanin leg.; HNHM • 1 spec.; “Ordos 1884 Patanin 5.VIII”; “Cotypus Mantichorula Semenovi Rtt. Coll. Reitter”; “Mantichorula m. semenovi m. 1888”; 5 Aug. 1884; G.N. Potanin leg.; HNHM.

Additional material
CHINA – Inner Mongolia Province • 3 ♂♂, 3 ♀♀; Ordos; 1884; G.N. Potanin leg.; ZIN • 5 ♂♂, 8 ♀♀; Alashan, Tain-Ula; 16–19 Apr. 1908; M.A. Kozlov leg.; ZIN • 15 ♂♂, 9 ♀♀, Sogo-Nur; 9 May 1926; M.A. Kozlov leg.; ZIN. – Gansu Province • 1 ♂; Gansu; 1886; G.N. Potanin leg.; ZIN • 1 ♂; same collection data as for preceding; 3–6 Jul. 1908; M.A. Kozlov leg.; ZIN • 2 ♂♂, 5 ♀♀; Gan River; 25 Apr. 1990; Martin leg.; ZIN.

MONGOLIA • 1 ♂; Tengri-elisu Desert; 3 Sep. 1901; M.A. Kozlov leg.; ZIN • 4 ♂♂, 6 ♀♀; Gojco; 1–2 Apr. 1908; M.A. Kozlov leg.; ZIN • 4 ♂♂, 4 ♀♀; Dyn-yuan-in, Utzur-huduk; 20–22 Apr. 1908; M.A. Kozlov leg.; ZIN • 6 ♂♂, 4 ♀♀; Bain-huduk; 2–4 Apr. 1909; M.A. Kozlov leg.; ZIN • 4 ♂♂, 2 ♀♀; Hayry-huduk; 22–23 May 1909; M.A. Kozlov leg.; ZIN • 2 ♂♂, 1 ♀; Bordzon-Gobi 80 km SSE of Nomgona; 5–8 Aug. 1967; V.F. Zaytsev leg.; ZIN.

Distribution
Mongolia, China (Inner Mongolia, Xinjiang, Gansu, Ningxia, Shaanxi provinces).

*Mantichorula grandis* Semenov, 1893

Material examined

Lectotype designated here
MONGOLIA • 1 ♂; “Алашанск. горы, Пржевальский, 20.VI.1873” [Alashan Mountains]; “Mantichorula grandis Typ. Φ Алашанские горы Н.М. Пржевальский”; 20 Jun. 1873; N.M. Przhevalsky leg.; ZIN.

Paralectotypes
MONGOLIA • 2 ♂♂, 2 ♀♀; same collection data as for lectotype; “Mantichorula grandis Typ. ♂” [for males]; ZIN.

Distribution
China (Inner Mongolia: Alashan).
Fig. 13. *Platyope* Fischer von Waldheim, 1820 and *Earophanta* Semenov, 1903, details of structure. **A.** *P. grumi* (Semenov, 1893), paralectotype (ZIN), pronotum. **B.** Ditto, hemispherical large tubercles and pubescence of pronotum. **C.** Ditto, base of left elytron. **D.** Ditto, tubercles and setae on elytron. **E.** *E. serrata* (Semenov, 1893) (ZIN), basal half of left elytron. **F.** Ditto, sculpture and setation of elytron.
Genus *Platyope* Fischer von Waldheim, 1820


*Platyope* Fischer von Waldheim, 1820: fig. 15.

*Homopsis* Semenov, 1893: 258 (type species *Homopsis grumi* Semenov, 1893, by monotypy).


**Type species**

*Tenebrio leucographa* Pallas, 1781 (= *Tenebrio leucogramma* Pallas, 1781), by monotypy.

**Species included**


**Diagnosis**

Body black, elongate-oval (Figs 4E–F, 5G–I, 6), weakly flattened dorsally, densely covered with recumbent grey, yellowish, cream or white setae; elytra often with striped or mixed spotted and striped pattern partly or completely. Sometimes (*P. ordosicola*) body dorsally glabrous (Fig. 6B). Body completely or partly granulated, each granule with spine or strong seta. Body length 9–15 mm. Eyes circular, very weakly convex in dorsal view; surface behind eyes partly concealed by anterior margin of pronotum.

Pronotum transverse (1.7–2.3 × as wide as long) (Figs 4E–F, 5G–I, 6, 12C, 13A), usually widest before middle, covered by coarse, moderate (Fig. 12C–D) or large (Fig. 13A–B) semispherical tubercles. Anterolateral angles from weakly (*P. leucogramma*) (Fig. 4E–F) to strongly (*P. grumi*) (Fig. 5G–H) projecting. Disc of pronotum distinctly and deeply (Figs 4E, 5G, I, 6A) or weakly (Fig. 6B) depressed in middle, or pronotum without wide depression in middle (*P. granulata*) (Fig. 5I). Prosternum short before procoxae, with deep (*P. grumi*) or weak and wide triangular depression along anterior margin. Prosternal process not raised between procoxae (Fig. 5A–C), sometimes slightly protruding beyond procoxae (*P. grumi*) (Fig. 5D–F). Procoxal cavities externally open, postcoxal bridge discontinuous in middle (Fig. 25A).

Scutellar shield not concealed by pronotum, triangular or rounded, elytra unspotted triangular or oval impression around scutellar shield. Elytral humeral ribs consist of two or three confused rows of conical large (Figs 4E, 5G, 6A, 13C), small (*P. granulata*) (Fig. 5I) or combined (Fig. 6B) tubercles. Dorsal surface of elytra with several longitudinal rows of granules, sometimes granules located on slightly elevated ribs (*P. granulata, P. grumi*) (Fig. 5G, I), which connected by short transverse elevations.
Therefore, a spotted pattern of dense setae in depressions between elevations is formed (Figs 12E–F, 13C–D).

Intercoxal process of the first abdominal ventrite 1.2–1.3 × wider than one metacoxa (Figs 4F, 5H).

Protibia wide and flattened, triangular, without projecting process at apex of outer margin, with strong teeth on outer margin (Figs 26H, 28D–E). Maximal length of teeth much shorter than maximal width of protibia. Teeth spinose or not, often spines abraded. Meso- and often metatibiae curved outward, with conical, coarse granules bearing spines and dense or sparse, long setae. Protibial terminal spurs moderately elongated, extending to protarsomere 4, subequal; longest mesotibial terminal spurs extending to or slightly not extending to apex of mesotarsomere 1; longest metatibial terminal spur not extending to apex of metatarsomere 1. Tarsal claws comparatively (compared to other genera) short, weakly curved outward.

**Male genitalia** (Figs 20A–H, 21A–I)

Inner sternite VIII (Figs 20H, 21I) widely sclerotized on margins, V-shaped emarginated medially, densely pubescent; gland moderately long, sclerotized in apical third.

Spiculum gastrale (Figs 20F–G, 21G–H) arcuately connected at apex, slightly curved in lateral view; derivatives of inner sternite IX large, weakly oval, unevenly sclerotized, with membranous C-shaped area along outer margins; apical margins of these derivatives pubescent with long sparse setae.

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**Fig. 15.** *Habrochiton vernus* Semenov-Tjan-Shansky, 1907 (ZIN), genitalia. **A.** Tegmen of aedeagus, ventrally. **B.** Ditto, dorsally. **C.** Ditto, laterally. **D.** Median lobe, ventrally. **E.** Ditto, dorsally. **F.** Ditto, laterally. **G.** Spiculum gastrale. **H.** ♂, inner sternite VIII. **I.** ♀, inner sternite VIII and spiculum ventrale. **J.** Ovipositor, ventrally. **K.** Ditto, dorsally. **L.** Ditto, laterally. Not to scale. Abbreviations: see Material and methods.
Tegmen of aedeagus long and slender (Figs 20A–C, 21A–C), basal piece more or less longer than apical piece. Apical piece bare, weakly curved, fusiform, acutely angulate at apex; ventral apophyses presented, short; dorsal apophyses long, triangular, not merged. Basal piece slightly wider than apical piece. Median lobe with baculi not distinct, bifurcate or narrowly rounded apex and sub-acutely angulate base (Figs 20D–E, 21D–F).

**Female genitalia**

Spiculum ventrale (Figs 20I, 21J) long, with long common stem. Inner sternite VIII can be with long or short acutely angulate apophyses.

Ovipositor long, moderately sclerotized (Figs 20J–L, 21K–M). Coxite with not merged lobes. Baculi of lobe I transverse, narrow, strongly sclerotized only near middle of ovipositor; pair of lobe I forms cruciform sclerotization area ventrally together with median sclerotization of vulva; lobes I and II membranous; lobe III widely sclerotized; apical lobes fossorial, strongly sclerotized, flattened, sub-acutely angulate or widely rounded at apex. Coxite laterally and on inner side of apical lobe densely

covered with very long setae. Apical margin of proctiger narrowly or densely rounded. Paraproct basally, proctiger and coxite densely pubescent with long setae.

**Female genital ducts** (Fig. 23F–G)

Vagina strongly widened, saciform, sometimes with poorly expressed bursa copulatrix, sometimes in apical third elastically turned back. Spermatheca short, single-tube (Fig. 23F) or with thick basal tube with tuft of small tubes at apex (*P. grumi*) (Fig. 23G). Accessory gland of spermatheca elongate, shortly constricted at base and with narrow basal duct, saciform after this duct.

**Notes**

The genus *Homopsis* was described by Semenov (1893) based on the structure of the prosternal process, which is slightly raised and slightly protruding beyond the posterior margin of procoxae, in contrast with *Platyope*, which has the vertically rounded prosternal process, not raised in ventral aspect and not protruding beyond procoxae. Semenov (1893) placed *Homopsis* and *Mantichorula* in one couplet, as genera having protruding and raised prosternal process, in contrast to other genera of ‘Platyopidae’. In our opinion, the prosternal process in the latter genera is strongly different from each other. *Mantichorula* has a process that is strongly protruding, extending to mesoventrite and horizontally (in lateral view) flattened, while *Homopsis* has only a slightly protruding, angularly rounded prosternal process. *Homopsis* is very similar to *Platyope* and differs only by some species-rank characters, including the prosternal process, the structure of the pronotum, the elytra, the male and female genitalia (especially the ovipositors are similar). On the other hand, a single species of *Homopsis* has peculiarities in the structure of the female genital ducts: vagina elastically V-curved and spermatheca multi-tubed at the apex. However, the main congeneric character of *Platyope* and *Homopsis* is externally open procoxal cavities (postcoxal bridge is discontinuous in the middle). As a result, the following synonymy is proposed: *Platyope* Fischer von Waldheim, 1820 = *Homopsis* Semenov, 1893 syn. nov. Consequently, the following combination is proposed: *Platyope grumi* Semenov, 1893 comb. nov. (from *Homopsis*).

**Distribution**

Russia (south of the European part, Southern Siberia), North Kazakhstan, China (from Xinjiang to Inner Mongolia).

*Platyope leucogramma* (Pallas, 1781)

Figs 4E–F, 5AC, 12C–F, 20, 23F, 24D, 26H, 28D

**Material examined**

KAZAKHSTAN • 6 ♂♂, 4 ♀♀; Bol’shiye Barsuki; 28 Apr. 1904; V.A. Dubyansky leg.; ZIN • 4 ♂♂, 3 ♀♀; same collection data as for preceding; 20 May 1906; L. Berg leg.; ZIN • 2 ♂♂, 1 ♀; near Temir; 1 May 1905; B.P. Uvarov leg.; ZIN • 1 ♀; Temir, Kumkuduk; 30 May 1908; D.N. Borodin leg.; ZIN • 1 ♀; same collection data as for preceding; B.P. Uvarov leg.; ZIN • 8 ♂♂, 6 ♀♀; near Shalkar [Chelkar], Bol’shiye Barsuki; N.V. Androsov leg.; ZIN • 8 ♂♂, 4 ♀♀; Petrovo, Embulatovka River; 2–3 June 1949; K.G. Romadina leg.; ZIN • 5 ♂♂, 2 ♀♀; Yanvarcevo, right bank of Ural River; 23 Jun. 1949; L.V. Arnol’di leg.; ZIN • 2 ♂♂, 1 ♀; sands of Atyrau [= Guryev]; 3 May 1951; L.V. Arnol’di leg.; ZIN • 1 ♂, 1 ♀; same collection data as for preceding; K.G. Romadina leg.; ZIN • 3 ♂♂, 6 ♀♀; Kzyl-Chachyl; 9 Jun. 1952; L.V. Arnol’di leg.; ZIN • 1 ♂, 2 ♀♀; Karaagach 60 km NW of Zhanaarka; 19 May 1962; L.V. Arnol’di leg.; ZIN • 4 ♂♂, 7 ♀♀; sands 12 km N of Kensus; 28 May 1962; L.V. Arnol’di leg.; ZIN • 4 ♂♂, 2 ♀♀; Zaysan; ZIN • 4 specs; Atyrau Region, Akkiztologay; 9 Jun. 1980, 20 June 1980; E.A. Khachikov leg.; CMN.
RUSSIA • 8 ♂♂, 9 ♀♀; “Sibir. occ.” [Eastern Siberia]; ZIN • 2 ♂♂, 3 ♀♀; Volgograd Region, Sarepta; 13 Jun. 1891; A.K. Becker leg.; ZIN • 1 ♂, 3 ♀♀; same collection data as for preceding; G.L. Suvorov leg.; ZIN • 3 ♂♂, 2 ♀♀; Volgograd Region, Volzhsky; 30 Apr. 2016; M.V. Mokrousov leg.; ZIN • 2 ♀♀; Kalmykia, Artezian, 26 Apr.–2 May 1998; I.V. Shokhin leg. ZMSFU • 1 spec.; Kalmykia, Artezian, Kuma

River bank; 18 May 2013; I.V. Shokhin leg.; CMN • 3 ♂♂, 2 ♀♀; Astrakhan Region, Selitrennoye; 2 Feb. 1910; Chernavin leg.; ZIN • 2 specs; Rostov Region, Nizhnkundryuchenskaya; 1 May 1997; CMN • 11 specs; Rostov Region, Tsymlansk sands near Nizhnegnutov; 7–10 May 1998; M.V. Nabozhenko, D.A. Dubovikoff, L.V. Markitan leg.; ZMSFU, CMN.

**Distribution**

South of the European part of Russia (Rostov, Stavropol, Volgograd, Astrakhan regions, Kalmykia, Chechnya, Dagestan,), North Kazakhstan from Volga River to Zaysan Lake.

**Platyope unicolor** Zubkov, 1829  
Fig. 25A

**Material examined**

KAZAKHSTAN • 1 ♂; Temir, Kumkuduk; 29 May 1908; D.N. Borodin, B.P. Uvarov leg.; ZIN • 1 ♂, 3 ♀♀; near Yanvarcevo; 21 May 1949; K.G. Romadina leg.; ZIN • 2 ♂♂, 3 ♀♀; Petrovo, Embulatovka River; 2–3 Jun. 1949; K.G. Romadina leg.; ZIN • 5 ♂♂, 7 ♀♀; Yanvarcevo, right bank of Ural River; 13 May 1950; K.G. Romadina leg.; ZIN.

RUSSIA • 2 ♂♂, 1 ♀; “Russia merid.”; Reitter leg.; ZIN • 1 spec.; Kalmykia, Utta; 24 May 1975; I.A. Fomichev leg.; CMN • 10 specs; Kalmykia, Rybachiy, 14–16 May 1974, 20 May 1978; A. Fomichev leg.; ZMSFU • 3 specs; Kalmykia, Rybachiy, 15 May 1978; Yu.G. Arzanov leg.; ZMSFU • 2 specs; Dagestan, Nogayskiy Distr., Kuma River sands; 10 May 1990; Yu.G. Arzanov leg.; CMN.

**Distribution**

South of the European part of Russia (Kalmykia, Dagestan), Western Kazakhstan (Aktobe, Atyrau regions).

**Platyope granulata** Fischer von Waldheim, 1820  
Fig. 5I

**Material examined**

KAZAKHSTAN • 32 ♂♂, 25 ♀♀; Kumtobe sands; 19 Jun. 1910; G.G. Jacobson leg.; ZIN • 2 ♂♂, 4 ♀♀; Zaysan, Aggyrkum; 8 Jun. 1958; N.G. Skopin leg.; ZIN • 2 ♂♂, 4 ♀♀; same collection data as for preceding; 9 Jun. 1958; ZIN • 2 ♂♂, 4 ♀♀; same collection data as for preceding; 10 Jun. 1958; ZIN • 1 ♂; Karatal sands; 16 Jun. 1964; P.Yu. Gorbunov leg.; ZIN.

RUSSIA • 2 ♂♂; “Sibir.”; ZIN.

**Distribution**

Eastern Kazakhstan (new record for the country), China (Xinjiang).

**Platyope proctoleuca proctoleuca** Fischer von Waldheim, 1820  
Fig. 6A

**Material examined**

KAZAKHSTAN • 1 ♂; Zaysan valley, Aggy-kum; 10 Jun. 1968; N.G. Skopin leg.; ZIN.

RUSSIA • 1 ♂, 4 ♀♀; “Sibir.”; ZIN • 2 ♂♂, 3 ♀♀; “Sibir. occ.”; ZIN.
Distribution

Russia (Altai: Kulunda Steppe). Kazakhstan (Zaysan Depression, Irtysh River and Black Irtysh River valleys). This species was listed only for Zaysan Depression in Kazakhstan in the Palaearctic Catalogue (Iwan et al. 2020), but Medvedev (1990) recorded *P. proctoleuca proctoleuca* also for Russian Altai and the Irtysh valley in Kazakhstan.

Platyope proctoleuca chinensis Kaszab, 1962

Material examined
MONGOLIA • 3 ♂, 3 ♀; Gobi-Altai Prov., 5 km SE of Bulgan, between Bijiin-gol und Bodoncijn-gol rivers; alt. 1500 m; 1 Jul. 1966; Z. Kaszab leg.; ZIN.

Distribution
Mongolia, China (Xinjiang).

Platyope mongolica Faldermann, 1835

Material examined
CHINA • 1 ♂; Manchuria; 10–28 May 1905; A.V. Serebryan leg.; ZIN.

MONGOLIA • 5 ♂, 10 ♀; Khovd [Kobdo]; 16 Jun. 1911; K.V. Yurganova leg.; ZIN • 2 ♂; near Orog Lake, Gobi Desert; 30 May 1926; M.A. Kozlov leg.; ZIN • 1 ♂; Böön Tsagaan Lake; 6 Jun. 1962; Tsendsuren leg.; ZIN • 15 ♂, 23 ♀; 55 km SE of Airag [Hara-Ayrag]; 12 Jun. 1971; I.V. Emel’yanov leg.; ZIN • 16 ♂, 13 ♀; 12 km NE of Mandakh; 15 Jun. 1971; I.M. Kerzhner leg.; ZIN • 15 ♂, 23 ♀; 60 km ESE of Manlay; 15 Jun. 1971; G.S. Medvedev leg.; ZIN • 30 ♂, 25 ♀; 25 km ESE of Manlay; 16 Jun. 1971; G.S. Medvedev leg.; ZIN • 3 ♂, 8 ♀; 60 km SSE of Manlay; 17 Jun. 1971; M.A. Kozlov leg.; ZIN • 9 ♂, 5 ♀; SW Tahlga-Ula; 15 Jun. 1973; G.S. Medvedev leg.; ZIN • 26 ♂, 38 ♀; 10 km SW of Huh-Mor’t; 21 Aug. 1971; K.V. Arnol’di leg.; ZIN • 8 ♂, 3 ♀; Bayankhongor, 60 km NNE of Orog Lake; 4 Jul. 1973; G.S. Medvedev leg.; ZIN.

Distribution
Russia (Tuva), Mongolia, China (Jilin, Inner Mongolia, Liaoning, Ningxia).

Platyope ordosica Semenov-Tjan-Shansky, 1907

Material examined
Holotype
CHINA • ♂; “Ordos 1884 G. Patanin” [Inner Mongolia]; “Platyope ordosica A. Semenow det.”; “Coll. Semenov-Tian-Shansky”; “Holotype”; 1884; G. Patanin leg.; ZIN.

Additional material
CHINA • 4 ♂, 5 ♀; Alashan, 15 May 1908; M.A. Kozlov leg.; ZIN • 4 ♂, 6 ♀; Dyn-Kou; 28–30 May 1908; M.A. Kozlov leg.; ZIN • 9 ♂, 7 ♀; Alashan, Dyn-yuan-in; 17–22 Jun. 1908; M.A. Kozlov leg.; ZIN • 2 ♂, 1 ♀; Southern Alashan, Bain-huduk; 2–4 Apr. 1909; M.A. Kozlov leg.; ZIN • 10 ♂, 5 ♀; near Linzhou; 24 Apr. 1909; M.A. Kozlov leg.; ZIN.

Distribution
China (Gansu, Ningxia, Inner Mongolia).
**Platyope grumi** (Semenov, 1893) comb. nov.
Figs 5D–H, 13A–D, 21, 23G, 28E

**Material examined**

**Lectotype** designated here

CHINA • 1 ♂; bronze circle; “Кульджа 1879. А. Регель” [Kul’dzha; now Yining]; “*Homopsis Grumi* m. AS. II.92.”; “104726”; 1879; A. Regel’ leg.; ZIN.

**Paralectotypes**

CHINA • 19 ♂♂, 14 ♀♀♀; same collection data as for lectotype; ZIN.

**Additional material**

CHINA • 1 spec.; “Джинго” [Jinghe]; 13 April 1889; G.E. Grum-Grzhimaylo leg.; ZIN • 1 spec. “Dzungarische Wüste Z.T.” [Dzungarian Desert]; 16 April 1926; S.G. Beick leg.; ZIN.

**Distribution**

China (Xinjiang: Yining).

Genus *Earophanta* Semenov, 1903
Figs 7, 13E, F, 22, 23H, 24E, 25B, 26G, 28C

*Earophanta* Semenov, 1903b: 172 (replacement name for the elimination of the homonymy).

*Earophila* Semenov, 1903a: 9 (type species: *Platyope serrata* Semenov, 1893, by original designation; as subgenus of *Platyope*; homonym, nec *Earophila* Gumpenberg, 1887).

*Earophilina* Strand, 1917: 99 (unnecessary replacement name for the elimination of the homonymy).


**Type species**

*Platyope serrata* Semenov, 1893, by original designation.

**Species included**


**Diagnosis**

Body black, robust, wide, oval, completely or partially covered with dense white, grey or yellowish recumbent setae, elytra with moderate or large tubercles and serrate lateral margins (Fig. 7A–D). Body length 7.5–17 mm. Eyes circular, convex in dorsal view.

Pronotum transverse (1.7–2.25 × as wide as long) (Fig. 7A–D). Lateral margins usually strongly rounded in dorsal view. Disc of pronotum strongly or moderately convex, with triangular depressions in base, with strong, acute, spinose tubercles. Prosternum without depression along anterior margin. Procoxae usually very large and protornum before procoxae very short (15 × as short as longitudinal diameter of procoxae in *E. serrata*) (Fig. 7D). Prosternal process wide between procoxae and sharply narrowed at
apex, not raised between procoxae or protruding beyond procoxae. Procoxal cavities closed, postcoxal bridges complete (Fig. 25B).

Elytra with double or simple humeral ribs consisting of longitudinal row/rows of very coarse, strong, acute, spine-like tubercles and seems serrate (Fig. 13E). Dorsal surface of elytra with 2–4 longitudinal lines (sometimes irregular) of moderate or large shining spine-like tubercles (Fig. 7F) and dense setation.

between them, forming striped or spotted pattern. Each tubercle with very long, erected seta. Surface between tubercles densely or sparsely microgranulated (some setae located on microgranules).

Scutellar shield almost concealed by base of pronotum (Fig. 7A–C), but sometimes open (E. beludzhistana) (Fig. 7E); elytral surface around scutellar shield usually weakly depressed. Ventral side densely pubescent. Intercostal process of abdominal ventrite 1 wide, near 1.7–2 × as wide as one metacoxa (Fig. 7D).

Pro- and mesotrochanters usually with long, dense pubescence. Pro- and mesofemora weakly curved outward, protibiae straight, meso- and metatibiae curved along elytral lateral vertical side. Outer margin of protibiae with 5–7 very large and long sparse teeth and sometimes with several small teeth, widened to apex, sub-triangular, without projecting process at apex of outer margin (Figs 26G, 28C). Protibiae of Earophanta beludzhistana have four teeth in basal part and flattened undulate lamina (merged teeth) in distal part (Fig. 7F). Length of largest teeth is at least one third of width of protibia at apex. Tibial terminal spurs as in Platyope. Protibiae often curved outward (Fig. 7A, C–F), but sometimes straight (E. planidorsis) (Fig. 7B). Mesotibiae always curved outward, metatibiae straight. Tarsi as in Platyope.

**Male genitalia** (Fig. 22A–H)
Inner sternite VIII (Fig. 22H) widely sclerotized, except for weakly sclerotized median part, densely covered with long setae; anterior margin with round, wide median emargination, with extremely dense pubescence; gland straight, very long and completely sclerotized. Rods of spiculum gastrale (Fig. 22G) narrowly connected at apex; derivatives of inner sternite IX elongate, more or less evenly sclerotized.

Tegmen of aedeagus long, slender, fusiform, with apical piece longer than basal piece (Fig. 22A–C). Apical piece weakly curved, ventral apophyses unclear, dorsal apophyses usually very short and merged. Basal piece with small, separated apex. Median lobe (Fig. 22D–F) weakly curved, with clear narrow baculi, merged basally; base not bifurcated, apex acutely angulate.

**Female genitalia**
Spiculum ventrale (Fig. 22I) with long and sharply widened at apex common stem, thin rods and often with weak sclerotized area between them, apophyses of sternite VIII comparatively short, acutely angulate at apex.

**Fig. 25.** Closure of procoxal cavities of Platyope Fischer von Waldheim, 1820 and Earophanta Semenov, 1903, posterior view. A. Externally open procoxal cavities of Platyope unicolor Zubkov, 1829 (ZMSFU). B. Externally closed procoxal cavities of Earophanta serrata (Semenov, 1893), ♂ (ZIN). Arrows indicate postcoxal bridge. Not to scale.
Ovipositor (Fig. 22J–L) long and moderately sclerotized. Coxite lobe I with baculi, strongly sclerotized distally; lobes II and III merged into one moderately sclerotized plate; apical lobe fossorial, transformed to strongly sclerotized and rounded apically scoop-like plates. Paraproct with long and narrow ventral baculi and very short additional dorsal baculi. Vulva without sclerotized areas. Only coxite with sparse pubescence of moderately long and short setae; paraproct with very short setae on margins near coxite. Proctiger with long, narrow baculi and rounded apical margin.

**Female genital ducts** (Fig. 23H)
Very similar to those in *Platyope*, with single-tube long spermatheca and long, constricted basally accessory gland.

**Distribution**
Turkmenistan (Karakum Desert), Uzbekistan (Kyzylkum Desert), South-Eastern Kazakhstan (Muyunkum Desert), China (Xinjiang), North Afghanistan, Pakistan.

*Earophanta serrata* (Semenov, 1893)

**Material examined**

**Lectotype designated here**
TURKMENISTAN • 1 ♂; “Ашхабад, 12.IV.28, Е. Щещеринов” [Ashgabat]; “Earophanta serrata m. ♂ A. Semenov-Tian-Shansky det. IV.31”; “Paratypus”; 12 Apr. 1928; E.L. Shestoperov leg.; ZIN.

**Additional material**
TURKMENISTAN • 2 ♂♂, 2 ♀♀; “TransCaspi, Eylanadt.”; ZIN • 6 ♂♂, 10 ♀♀; Kushka River; 4 May 1908; I. Ivanov leg.; ZIN • 3 ♂♂, 4 ♀♀; same collection data as for preceding; 22 Apr. 1957; G.S. Medvedev leg.; ZIN • 2 ♂♂, Nokhur; 22 Jul. 1926; Moritz leg.; ZIN • 3 ♂♂, 3 ♀♀; Ashgabat; 12 March 1937; Ya.P. Vlasov leg.; ZIN • 1 ♂, 1 ♀; same collection data as for preceding; 25 Mar. 1964; L. Freyberg leg.; ZIN • 3 ♀♀; near Ashgabat 20 km NO; 27 Mar. 1952; Il’ichev leg.; ZIN • 2 ♂♂, 4 ♀♀; 20 km NW of Ashgabat; 27 Mar. 1952; O.L. Kryzhanovsky leg.; ZIN • 2 ♀♀; Badhyz State Nature reserve; 11 Apr. 1952; Z. Yudina leg.; ZIN • 1 ♂, 1 ♀; May 1986; V.A. D’yakov leg.; CMN • 2 ♂♂, 1 ♀; Badhyz State Nature reserve; Kepele cordon; 11 Apr. 1990; A. Napolov leg.; CMN • 2 ♂♂; 40 km W of Yasga [Yaskhan]; 22 Apr. 1952; O.L. Kryzhanovsky leg.; ZIN • 13 ♂♂, 7 ♀♀; Badhyz, 8 km of Galaymor; 28 Mar. 1957; G.S. Medvedev leg.; ZIN • 6 ♂♂, 3 ♀♀; Badhyz, 12 km W of Galaymor; 21 Mar. 1957; G.S. Medvedev leg.; ZIN • 3 ♂♂, 2 ♀♀; same collection data as for preceding; 9 Apr. 1957; ZIN.

**Distribution**
Turkmenistan.

*Earophanta collaris* (Fischer von Waldheim, 1844)

**Material examined**
KAZAKHSTAN • 2 ♂♂, 1 ♀; Kapchagay, Kokbasta: 27 Jun. 1952; P. Ler leg.; ZIN • 4 ♂♂, 2 ♀♀; near Ili; 22 Jun. 1950; N.G. Skopin leg.; ZIN • same collection data as for preceding; 6 Jul. 1954; ZIN • 1 ♂, 2 ♀♀; Ili River; 8 Jun. 1952; P. Ler leg.; ZIN • 1 ♀; Kapchagay; 15 Apr. 1962; G. Nikolaev leg.; ZIN.

CHINA • 45 ♂♂, 70 ♀♀; Yining [Qulja]; 1879; A. Regel’ leg.; ZIN.
Distribution
South Eastern Kazakhstan, China (Xijiang).

*Earophanta planidorsis* (Reitter, 1889)

Fig. 7B

*Earophanta autumnalis* Semenov, 1903a: 9 (original description).

Material examined

Lectotype of *Platyope planidorsis* designated here

TURKMENISTAN • 1 spec.; “Sary-jasy 30.9.87”; “Turkmenien Leder, Reitter”; “Typus *Platyope planidorsis* Rtt. Coll. Reitter”; “*Platyope planidorsis*”; 30 Sep. 1887; leg. H. Leder; HNHM.

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Paralectotype
TURKMENISTAN • 1 spec.; “Turcmenia Sary-jasi”; “Cotypus Platyope planidorsis Rtt. Coll. Reitter”; HNHM.

Holotype of Earophanta autumnalis

Additional material
AFGHANISTAN • 1 ♂; Maymana; 17 Mar. 1964; O. Jakes leg.; ZIN.

TURKMENISTAN • 2 ♂; Zaunguz Karakum, Aqsaqal; A. Zatoka leg.; ZIN • 2 ♂♂, 6 ♀♀; 53 km of Bayramali; 10 Apr. 1984; A. Sabirova leg.; ZIN.

Distribution
Turkmenistan, Afghanistan.

Earophanta pilosissima (Reitter, 1895)

Earophanta loudoni Semenov, 1903a: 11 (original description).

Material examined

Holotype of Earophanta loudoni
TURKMENISTAN • ♂; goldish circle; “Уч-Аджи 6.III.01 бар. Г. Лоудон” [Uch-Adzhi – now Bagtyýarlyk in Mary Prov.]; “Platyope Loudoni m. Typ un. (♂?) XI.02 A. Semenow det.”; “coll. Semenov-Tian-Shansky”; “Holotype”; 6 Mar. 1901; Baron G. Loudon leg.; ZIN.

Additional material
AFGHANISTAN • 4 specs; Maymana Prov., Andkhoy; alt. 350–400 m; 17 Mar. 1964; O. Jakeš leg.; ZIN.

TURKMENISTAN • 1 spec.; Berkarar [Ravnina railway station]; 8 Mar. 1908; Baron G. Loudon leg.; ZIN • 11 specs; Repetek; 6–14 Mar. 1958; inter-barchan depression with black saxaul; G.S. Medvedev leg.; ZIN • 3 specs; Karakum channel, Nichki; 25 Apr. 1968; G.S. Medvedev leg.; ZIN • 3 specs; Repetek; 19 Feb. 1973; V.G. Kaplin leg.; ZIN • 1 ♂, 1 ♀; Karakum channel, Chaloy; 10 Apr. 1983; E.A. Khachikov leg.; CMN.

Distribution
Turkmenistan, Afghanistan.

Notes
Earophanta loudoni was described from a single specimen and was synonymised by Medvedev (2005). The specimens from Turkmenistan, which were standing in the collection of ZIN as E. loudoni, differ from the specimens from Afghanistan (determined by Z. Kaszab as E. pilosissima) by much more pubescent elytra and visibly smaller smooth tubercles on the elytra. A larger series of specimens is necessary to establish the status of these populations.
**Fig. 28.** Protibiae of Pimeliini, SEM. **A.** *Przewalskia dilatata* (Reitter, 1887), ♂ (ZIN), dorsal view. **B.** Ditto, ventral view. **C.** *Earophanta serrata* (Semenov, 1893), ♂ (ZIN), dorsal view. **D.** *Platyope leucogramma* (Pallas, 1773), ♂ (ZIN), dorsal view. **E.** *Platyope grumi* (Semenov, 1893), ♂, paralectotype (ZIN), dorsal view.
CHIGRAY S.N. et al., A revision of the Palaeartic Pimeliini (Coleoptera: Tenebrionidae)

**Earophanta tomentosa** (Semenov, 1893)

**Material examined**

**Lectotype** designated here according to Articles 61.1 and 74.1 of ICZN (1999)

UZBEKISTAN • 1 ♂; “Kisil-Kum, mer. Sarybai-Bulysch, Glasunov, 1892” [Kyzykum Desert]; “*Platyope tomentosa* m. ♂ Typ. Aes. II.93”; “Holotypus”; 1892; D.K. Glasunov leg.; ZIN.

**Paralectotypes**

UZBEKISTAN • 1 ♀; “Trkst. mnt. NURATA, Temir-Kauk, Glasunov, 1892” [Turkestan mountains]; “*Platyope tomentosa* m. ♂ Typ. II.93, A. Semenow det.”; “Allotypus”; 1892; D.K. Glasunov leg.; ZIN • 1 ♀; “Kisil-Kum, mer. Kalma-Tai, Glasunov, 1892” [Kyzykum Desert]; “*Platyope tomentosa* m. ♀ Typ. Aes. II.93”; “Paratypus”; 1892; D.K. Glasunov leg.; ZIN.

**Distribution**

Uzbekistan (Kyzykum Desert).

**Earophanta pubescens** Skopin, 1960

**Material examined**

**Holotype**

KAZAKHSTAN • 1 ♂; “Ю.З. Прибалхашье, Колшенгил, 25.04.1951, М. Мальховский” [SW Balkhash region, west of Muyunkum Desert, Kolshengil]; “Holotypus, *Europhanta pubescens* 1959 N. Skopin det.”; 25 Apr. 1951; M. Mal’khovskiy leg.; ZIN.

**Paratypes**

KAZAKHSTAN • 2 ♂; same geographic labels as for holotype; “Paratypus, *Earophanta pubescens* 1959, N. Skopin det.”; ZIN.

**Additional material**

KAZAKHSTAN • 1 spec.; Muyunkum; 26 Apr. 1954; M. Serкова leg.; “*Earophanta pubescens* sp. n. Typ. 1959 N. Skopin”; “Holotypus 1960 *Earophanta pubescens* Skopin” (curator’s label); HNHM • 1 spec.; same collection data as for preceding; “*Earophanta pubescens* sp. n. paratyp. 1959 N. Skopin”; “Paratypus 1960 *Earophanta pubescens* Skopin” (curator’s label); HNHM • 6 ♂, 1 ♀; 18 km E of Kokozech [Kok-uzek]; 5 Oct. 1961; Kunitsky leg.; ZIN • 1 ♂, 1 ♀; same collection data as for preceding; 8 May 1962; ZIN • 2 ♂, Karatal; 30 Jun. 1965; N.G. Skopin leg.; ZIN • 1 ♂; Karatal; 100 km below Ushtobe; 28 Apr. 1965; N.G. Skopin leg.; ZIN • 3 ♂, 4 ♀; Muyunkum Desert; 23 Mar. 1963; N.G. Skopin leg.; ZIN

**Distribution**

Kazakhstan (Balchash region, Muyunkum Desert) (Skopin 1960, 1968).

**Note**

Skopin and curators marked two specimens of *E. pubescens* from HNHM as a holotype and a paratype, respectively. However, Skopin (1960) did not include these specimens in the type series.
*Earophanta beludzhistanica* Bogatchev, 1957

Fig. 7E–F

**Material examined**

**Holotype**

PAKISTAN • ♂; “Quetta, Rost”; “Holotype”; “*Earophanta anglorossica* sp. n., A. Semenow-Tian-Shansky det.”; “*Ear. beludzhistanica* sp. n. typ A. Bog. A. Bogačev det.”; ZIN.

**Note**

This species was originally described from a single specimen and known only from the type locality.

**Key to genera of Pimeliini with dorso-lateral eyes from Central Asia, Iran, Afghanistan and Pakistan**

1. Pronotum without large semispherical or conical tubercles or granules, with fine cuticular microgranules or smooth, sometimes with short spines on surface. Body completely covered with scales. Ovipositor very short and weakly sclerotized, with membranous, rounded and densely pubescent apical lobes; spiculum ventrale wide and short, without or with very short common stem (subtribe Habrobatina) ................................................................. 2
   - Pronotum with large semispherical or conical tubercles or granules. Body without scales. Ovipositor long, with well-expressed long paraproct and many sclerotized parts, and fossorial, strongly sclerotized, glabrous apical lobes; spiculum ventrale long, with long common stem and narrow rods (subtribe Pimeliina, the *Platyope* genus group) ........................................... 5
2. Elytra dorsally with bronze scales and pubescent with erect, yellow setae, especially dense and long in wide longitudinal depression on sides of each elytron. Protibiae with strong, conical granules on outer margin, each granule with strong spine at apex ........................................ *Apatopsis* Semenov, 1891
   - Elytra dorsally with reddish-brown or creamy scales, or with combination of creamy and brown scales; sometimes with eight longitudinal lines (elytra all together) of short palesetae, but without dense long setae and wide longitudinal depression on sides. Outer margin of protibiae with very short tubercles bearing long thin spines ............................................................. 3
3. Prothorax with black, clearly visible, small spines and callus-like smooth shiny areas on dorsolateral sides near base. Scales on elytra form spotted or striped creamy-brown colour pattern ...................
   - Prothorax without small, black spines and callus-like smooth shiny areas on dorsolateral sides. Elytra with monochromatic scales, without colour pattern ................................................................. 4
4. Head, pronotum and elytra with reddish scales and white spine-like setae (clearly visible among scale cover); setae form eight longitudinal lines on elytra. Width of intercoxal process of the first abdominal ventricle shorter than width of one metacoxa ............................................................ *Habrobates* Semenov, 1903
   - Head, pronotum and elytra with creamy scales, without spine-like setae. Width of intercoxal process of the first abdominal ventricle broader than width of one metacoxa ............................................................ *Habrochiton* Semenov-Tjan-Shansky, 1907
5. Elytra spherical, more than twice as wide as pronotum. Lateral margins of pronotum widely completely emarginated in dorsal view. Prosternum before procoxae long, its length between procoxae and anterior margin 1.6× as short as transverse diameter of one procoxa. Elytra with alternating longitudinal stripes of pale dense recumbent setae and dark, weakly pubescent lines, without coarse granules or large smooth tubercles ..................................... *Przewalskia* Semenov, 1893
   - Elytra oval, not more than 1.7× as wide as pronotum. Lateral margins of pronotum weakly or strongly rounded in dorsal view. Prosternum before procoxae short, its length between procoxae and anterior margin 1.8–14× as short as transverse diameter of one procoxa. Elytra smooth and bare or with large, smooth granules, tubercles or elevations and pale pubescence between them .................. 6
6. Elytra smooth and glabrous, only with very small, sparse granules and one elevated line of slightly larger granules along granulated lateral margin. Pronotum with strongly arcuately emarginated base, posterolateral angles protruding far into impressed base of elytra. Prosternal process very broad, weakly narrowed between procoxae, slightly raised between procoxae and horizontally flattened (lateral view), strongly protruding beyond posterior margin of procoxae to mesoventrite. Protibiae with dense, long, thin spines and setae along outer margin. .............................................. Manticorula Reitter, 1889
- Elytra with coarse granules or smooth tubercles completely or at least on sides and pubescence between them or at least apical striped pubescence (sometimes elytra without pubescence as in Platyope ordosica Semenov-Tjan-Shansky, 1907). Pronotum with straight or very weakly emarginated base, posterolateral angles not protruding. Prosternal process broad, but usually visibly narrowed between procoxae, not raised between procoxae, not protruding or very weakly protruding beyond posterior margin of procoxae, rounded down. Protibiae with teeth on outer margin. .......................... Mantichorula Reitter, 1889
- Elytra with coarse granules and smooth tubercles completely or at least on sides and pubescence between them or at least apical striped pubescence (sometimes elytra without pubescence as in Platyope ordosica Semenov-Tjan-Shansky, 1907). Pronotum with straight or very weakly emarginated base, posterolateral angles not protruding. Prosternal process broad, but usually visibly narrowed between procoxae, not raised between procoxae, not protruding or very weakly protruding beyond posterior margin of procoxae, rounded down. Protibiae with teeth on outer margin. .......................... Mantichorula Reitter, 1889

7. Procoxal cavities externally closed. Protibiae with large teeth or teeth partly merged into thin entire lamella (as in Earophanta beludzhistana Bogatchev, 1957); length of largest teeth is at least one third of width of protibia at apex. Lateral rib of elytron with strong acute “serrate” teeth. ............................................................................................................ Earophanta Semenov, 1903
- Procoxal cavities externally open, postcoxal bridges discontinuous at middle. Protibiae with small teeth; length of largest teeth one-sixth to one-eighth of width of protibiae at apex. Lateral rib of elytron with large or small, wound or conical and acute, but not serrate tubercles. ............................................................................................................ Platyope Fischer von Waldheim, 1820

Discussion

Status of the former tribe Platypini

The family name “Platyopes” was originally established by Motschulsky (1849) to hold two Iberian genera Morica Dejean, 1834 and Akis Herbst, 1799 (Herbst 1799: 125) and five unknown (Herbst 1799: 58) genera from “à Astrabad en Perse” (in Astrabad in Persia). Bouchard et al. (2005, 2011) listed Platyope as the type genus of “Platyopes” according to Article 29.1 of ICZN (1999), but Motschulsky did not include this genus in the mentioned family because no species of Platyope occur in Iran and adjacent countries.

The subtribe “Platyopidae” (original spelling) was secondarily erected on the base of dorso-lateral eyes, located above the level of the genae (Semenov 1893). Later, Semenov-Tjan-Shansky (1907) raised its rank to a tribe. Pierre (1961, 1964) erected from Pimeliini the additional tribe Leucolaephini (correct name Leucolaephusini according to Bouchard et al. (2011)) on the base of callus-like swellings on the inner side of male profemora and the structure of antennae with 3-segmented club and very small antennomere 11 with the basal part placed into the penultimate antennomere. Koch (1969) noted that both these characters occur in different genera of Pimeliini and Platypini, therefore Leucolaephusini is a doubtful tribe. Later Leucolaephusini was synonymized with Platypini (Kwieton 1981). It should be noted that Koch (1969), in an endeavor to analyse the relationships between Pimeliini, Platypini and Leucolaephusini and to establish a status of these tribes, used the structure of the protibiae, which has an adaptive function and cannot be used as a basis for classification.

Many subsequent authors did not consider other structures and were guided by this single character of the location of eyes for Platypini. Only Skopin (1962) did not accept the tribe Platypini after the analysis of structures of the larvae of Platyope and Earophanta. He concluded that it cannot be saved even as a subtribe because larvae are identical to those of Pimeliini. Doyen (1994) also proposed the Platypini as a junior synonym of Pimeliini and concluded that these two groups only slightly differ in the structure of mouthparts and antennae, but he included only one species of Platypini (Platyope) and three species of Pimeliini in his analysis. He also figured the structures of the ovipositor and the female genital ducts, but only for two species of Pimeliini. We analysed a comprehensive complex of external
and internal structures and found that the former Platyopini (s. str., excluding Saharo-Arabian genera) is a polyphyletic group and includes two branches, which were previously united in one tribe on the basis of the adaptive character of dorso-lateral eyes, which appeared independently in their evolution.

The first group (subtribe Habrobatina) united related ultrapsammophilic genera, which sharply differ from other Pimeliini by the structure of ovipositor and aedeagus. The second group (Platyope genus group) forms a separate subgroup within the tribe, differing in the dorso-lateral eyes, the large hemispherical tubercles on the pronotum and the absence of the uncus on the lacinia (Medvedev 1959), but it has no significant differences in the structure of the male genitalia and the ovipositor. Thus, the tribe Platyopini with the type genus Platyope was correctly synonymized with Pimeliini by Skopin (1962) and Doyen (1994).

Since both groups inhabit sandy deserts with the dominance of Arenosols – soils with very initial features of pedogenesis and alteration of the mineral part (IUSS Working Group WRB 2015), they have acquired a number of similar adaptations. Below, we analyse adaptive structures, which originated independently in psammophilic Pimeliini, and characters suitable for a future phylogeny.

**Structural transformations and adaptations to life in sandy deserts**

**Surface of integument**

Many desert darkling beetles have a waxy coating pigmentation or various structures on the surface of the integument, partially to protect the body from overheating (Pierre 1958; Cloudsley-Thompson & Chadwick 1964; Edney 1971; Medvedev & Nepesova 1985; Medvedev 1990; Abushama 1990). Pale colouration can lower the temperature of the corresponding parts of the body by several degrees (Edney 1971). Turner & Lombard (1990) argue that colouration only partially affects the beetle’s body temperature. Black tenebrionids heat up much more than white-black ones, at least at direct absorption of visible light warms, and “a black beetle is also warmed more by reflected visible radiation than the white beetle” (Turner & Lombard 1990: 311). In Pimeliini, the protective structures of the integument are usually pale, white, yellow, pale brown, pale grey. We can observe several directions for the formation of pale colouration among diurnal Pimeliini: white waxy coating (*Trigonoscelis* Dejean, 1834, *Sternoplax*, *Pisterotarsa* Motschulsky, 1860, *Sternodes* Fischer von Waldheim, 1837), setae, spines and coarse elytral and pronotal sculpture for the formation of a non-natural covering (clay crust) (*Lasiostola* Dejean, 1834, often *Pimelia* Fabricius, 1775), entire or partial cover of pale felt setae (*Pterocoma* Dejean, 1834, *Platylesia* Skopin, 1971, the *Platyope* group of genera, some *Pimelia*), scale cover (*Leucolaephus*, *Paraplatyope*, some *Storthocnemis*, *Pimelia senegalensis* Olivier, 1795, Habrobatina). A combination of bristles and scales is also not uncommon. In Habrobatina and platyopoid genera, the latter two types of integument are shown. Leaf-like scales with micro-grooves in the form of venation (Figs 8B, D, 9B, 10) or scales with medial elevated ridge (Figs 9D, F) cover the integument of species of Habrobatina. These scales originated from setae as it is well illustrated on fig. 10A(b) with intermediate scale-like setae. The pubescence of tomentose recumbent white, pale grey, and yellow setae is characteristic for the *Platyope* genus group (Figs 4A, E, 5G, I, 6A), and it can either be entire or between tubercles (*Earophanta*) (Figs 7A–C). It should be noted that the covering of hairs and scales also provides the function of protective colouration. Many species hide in the shade of desert vegetation, and the pattern on the elytra is often associated with the pattern of this shade. Thus, the spotted pattern on the dorsal side of the body of *Dietomorpha pardalis* (Fig. 3A) is probably associated with dappled shadows, as in the ground beetle genus *Graphipterus* Latreille, 1802, which becomes completely invisible in the shade of plants with small rounded leaves (personal observations of M.V. Nabozhenko in Morocco). Structures on the elytra of many species of *Earophanta* apparently have a similar function of protective colouration, combining a dark smooth large round tubercles and a grey or yellow tomentose cover of hairs (Fig. 7E, C). *Platyope leucogramma* with a striped pattern (Fig. 4E) is hardly visible among the elongated shadows of cereals (personal observations of M.V. Nabozhenko in the Rostov Region of
Russia). A similar camouflage effect was noted for Zophosini from the Namib Desert (Matthews et al. 2010). Some species of Platyope have mixed camouflage with spotted and striped patterns (Fig. 5G, I). Species of some genera (for example Mantichorula, some Platyope) have the bare body or dorsal surface (Figs 4C, 6B), covered with dark-brown scales (Habrobates gabrieli comb. nov.) (Fig. 2A–E), and probably their adaptations to the high temperatures in deserts are associated with behaviour, diurnal activity, and phenology, as in other black-coloured desert darkling beetles (Matthews et al. 2010).

Some features of the structure of the head
The most characteristic feature for Habrobatina and platyopoid genera is the eyes, located dorso-lateral, above the level of genae (Figs 2C, E, 3, 3E, G). Such location of eyes is associated with general compaction of the body and transformation of the head from prognathous to sub-hypognathous.

Mouthparts are tenebrionoid, the mentum is slightly enlarged but does not hide the cardo and stipes, unlike many other desert Pimeliinae (Erodini, Zophosini, the majority of Tentyriini, etc.) with a large mentum (Medvedev 1959). Antennae with a weak 3-segmented club, moreover the antennomere 11 looks like deeply with the basal part placed into the penultimate antennomere (Fig. 24). Habrobatina and platyopoid genera, like all other Pimeliini (Skopin 1964, 1971), have a distinct border between the apical sensorial area and the remaining antennomeres, which are bare. The difference from other Pimeliini is that the antennomere 11 is always very small, and its apex is hemispherical, not acutely angulate. A similar structure of the apical antennomere occurs among other Pimeliini, in the genus Pimelia Fabricius, 1775. Only Habrobates gabrieli comb. nov. has the intermediate structure of antennomere 11, which is slightly smaller than the penultimate one and has a large sensorial area with a sub-acutely angulate apex. In general, there are no clear differences in the antennal structures between different groups of Pimeliini, as it was noted by Koch (1969).

The structure of the thorax
Doyen (1993) noted that at least Platyope (Fig. 25A) and Ocnera Fischer von Waldheim, 1822 of the tribe Pimeliini have externally open procoxal cavities, which is a secondary condition. However, species of Ocnera have procoxal cavities closed by thin postcoxal bridge, which can be broken near the prosternal process in collection specimens (we studied 10 specimens of two species of Ocnera and postcoxal bridge was broken and discontinuous in some specimens). Probably, he examined such a specimen. Doyen associates the secondarily open procoxal cavities in some groups of Tenebrionidae with the close association of the pro- and pterothoraces, unlike the primary internally and externally open ones in Zolodininae (Doyen 1993; Matthews & Bouchard 2008) and Kuhitangiinae (Medvedev 1962; Nabozhenko & Sadeghi 2017) (Doyen erroneously wrote that one species of the tribe Kuhitangiini has internally closed procoxal cavities). However, he noted that the prothorax in Pimeliini is relatively free but internally closed procoxal cavities indicate the secondary reduction of the postcoxal bridge in Platyope. In fact, the prothorax is fixed in relation to the pterothorax (although the pro- and mesothorax are joined by a thickened membrane rather than fused through various mechanisms as in Edrotini, Adesmiini, Erodini, and Cryptochilini, see Doyen 1994), which is associated with the general compaction of the thoracic region. All at least platyopoid genera have an identical fusion of the pro- and pterothorax, but within Pimeliini only Platyope has the discontinuous postcoxal bridge (Fig. 25A). Therefore, the open procoxal cavities in Platyope can not be explained by the close association of the pro- and pterothorax. Probably, this is associated with the strengthening of the muscles of the fossorial protibiae and, accordingly, an increase in the area of the inner surface of the procoxae for attaching this musculature (and, accordingly, an increase of the size of the procoxae). Thus, the procoxae are increased due to the reduction of the postcoxal bridge. In contrast, an increase in the size of the procoxae in some Earophanta is achieved by a strong shortening of the sternum before procoxae (Fig. 7D).
The pterothorax in all Pimeliini is characterized by mesocoxal cavities that are partially closed by the mesepimeron, by the large trochanters and the very wide distance between the coxae, which is associated with the increase of the volume of the subelytral cavity. Doyen (1994) noted that mesocoxal cavities that are externally closed by the mesepimeron, certainly represents the primitive condition, which occurs in the non-pimeliine lineages, while the majority of pimeliines has mesocoxal cavities closed by meso- and metaventrites.

The structure of protibiae

Various structures of protibiae are closely associated with adaptations to locomotion in sandy soils. All the genera of Pimeliini in this study inhabit sand deserts and have different adaptations to moving on sandy soil. Medvedev (1965b) analysed in detail the adaptations of legs of the Central Asian darkling beetles and indicated several directions of tibial and tarsal transformations in association with the structure of sandy soils. Two types of specialization (with some intermediate types) are observed in the tribe Pimeliini in general and in platyopoid genera and Habrobatina in particular:

1. Inhabitants of migratory sands. Sand dunes are characterised by a weak development of the root system of plants and an extremely low aggregation of textured grains of fine sand; therefore, protibiae in species living on such sands are adapted to sand sweeping, which is accompanied by an increase of the tibial speed (when digging) in some groups, such as *Habrobates* (Medvedev 1965b). The following directions of adaptation of non-fossorial protibiae can be observed among genera with dorso-lateral eyes:

a) Protibiae narrow, with the sharp, projecting process at the apex of outer margin (Fig. 26A–C). This process can by reinforced by longer merged spines at the protibial apex (*Habrochiton*) (Figs 26A, 27E) or with a series of shorter strong spines (*Habrobates, Dietomorpha*) (Figs 26C, 27C–D) or large, but not reinforced additionally (*Apatopsis*) (Figs 26F, 27A–B). The outer margin of protibiae bears sparse, long setae and sparse, spinose tubercles. Combinations can be from very short narrow tubercles and thin, long spines (*Habrochiton*) (Fig. 27E) to the similar tubercles, but stronger and shorter spines (*Habrobates, Dietomorpha*) (Figs 26C, 27C–D) and to large tubercles with short, strong spines (*Apatopsis*) (Fig. 27A). Spines can be abraded during the lifetime of the adults (Fig. 27B).

b) Protibiae strongly gradually widened to the apex, flattened, with a weak, rounded process at the apex of the outer margin and with dense, thin, long spines and long setae along the outer margin (*Mantichorula*) (Figs 26D, 27F–G). Spines can be of two types: stronger and slightly shorter mainly dorsally (Fig. 27F) and finer and longer ventrally (Fig. 27G).

*Przewalskia* has the intermediate type of protibiae, with long and very dense setae, two types of dense spines, but protibiae are thin and not flattened as in the version a) (Fig. 28A–B).

Thus, the adaptive transformation of protibiae in Habrobatina and platyopoid genera living on sand dunes is accompanied by an increase of the surface area of the protibiae due to the development of long setae and long thin spines on the outer margin, necessary for the displacement of dry moving sand. Spines can be reinforced for digging in deeper and denser sand layers.

*Mantichorula* and *Sternodes* Fischer von Waldheim, 1837, which have a more flattened strongly widened body and a very similar structure of tibiae, share the same life form and therefore they probably have similar bionomics and move on the sand as described by Medvedev (1965b) for the latter genus.

2. Inhabitants of fixed or wet (in early spring periods of rains) sands have widened and flattened tibiae with various teeth or tubercles with strong spines, as well as the apex of the protibiae often sharply...
projecting outward. All these adaptations are necessary for digging in the sand with high particle adhesion, which is achieved in different ways (in order of increasing complexity of specialization):

a) Protibiae curved and moderately widened to the apex, that is compensated by very large and sparsely spaced teeth on the outer margin (Figs 26G, 28C), which (teeth) sometimes merged into an entire undulate lamina (Fig. 7F); the outer margin is without a protruding process at the apex (*Earophanta*);

b) Protibiae strongly widened to the apex and have dense, strong, but much shorter teeth on the outer margin than *Earophanta*; the outer margin is not projecting as the process at apex (*Platyope*) (Figs 26H, 27F–G).

Thus, the strengthening of the fossorial function of protibiae occurs due to the increase of their area at the apex of the outer margin or the development of various spines and teeth on the outer margin.

**The structure of the abdomen**

Habrobatina and platyopoid genera, as well as other Pimeliini, have intersegmental membranes between abdominal ventrites 3–5, in contrast with other Pimeliinae. Doyen (1994) believes that these membranes in Pimeliini are secondary exposed, because they do not have defensive glands, as in all other Pimeliinae. The correlation between the presence of intersegmental membranes and defensive glands was noted by Doyen (1972) himself, therefore reasons for this “possibly secondarily evolved specialization” (Doyen, 1994: 470) are unclear.

**Male genitalia**

The aedeagus in genera with dorso-lateral eyes is typical for Pimeliini, inverted 180°, and the apical piece without a long ventral apophysis. Species of the subtribe Habrobatina differ from species of the other Pimeliini by their strongly sub-angularly curved apical piece of the tegmen (Figs 14C, 15C, 16C, 17C). Other characters of the aedeagus can help to differentiate genera and generic sub-groups. *Apatopsis* and *Habrochiton* have small elevated sclerotized ventral apophyses of the apical piece (Figs 14A, 15A). The majority of genera of Habrobatina have more or less long, triangular, not merged dorsal apophyses of the apical piece (Figs 14B, 15B, 17B), excluding *Habrobates* with Y-like, thin, merged apophyses (Fig. 16B). The apical piece consists of paired lobes, which are usually merged, therefore the merged apophyses can be interpreted as the advanced state. The apical piece of species in *Dietomorpha* are covered with short, fine spines apically (Fig. 17A–B), while species of other Habrobatina and Pimeliini, in general, have a bare apical piece. The median lobe is more or less uniform in the subtribe, only *Apatopsis* and *Habrochiton* have a rolled baculi at the apex (Figs 14E, 15E), which is not typical for other pimeliine genera, and *Habrobates* has rod-like baculi that are fused apically (Fig. 16D–E). Other genera we studied have rod-like baculi that are separated, this character state is probably a symplesiomorphy within Tenebrionidae, as it is also shown for the evolution of the median lobe in Heleini (Matthews 1993).

The aedeagus in platyopoid genera is characterized by a weakly curved and glabrous apical piece (Figs 18A–C, 19A–C, 20A–C, 21A–C, 22A–C), usually with merged (Figs 18B, 19B, 22B) dorsal apophyses. Only species of *Platyope* have separated dorsal apophyses (Figs 20B, 21B); species of this genus have short but clear ventral apophyses (Figs 20A, 21A).

The inner sternite VIII is similar in all Pimeliini, having a V-shaped or roundly-emarginate anterior margin. The most important is the structure of the gland of the sternite. This gland is well expressed among darkling beetles of the tribe Blaptini (Medvedev 2001; I. Chigray *et al.* 2018, 2019; I. Chigray & Ivanov 2020; etc.) and some Helopini (Nabozenko & Ando 2018; Nabozenko & Grimm 2019; Nabozenko & Purchart 2019; etc.), but it has not been imaged or discussed for other Tenebrionidae. We did not find this gland in some samples because it often dissolves when boiled in alkali, but several
species have a well-expressed gland. *Habrobates*, for example, has paired short gland of the sternite VIII with separate ducts weakly sclerozited at the apex (Fig. 16I). *Platyope* and *Earophanta* have long not paired ducts of the gland, whereas the gland in *Platyope* is shorter and sclerotized only in the apical part (Figs 20H, 21I), while *Earophanta* has a very long and completely strongly sclerotized gland (Fig. 22H). The paired duct of glands, as well as its extension and sclerotization can be interpreted as advanced states.

The structure of the spiculum gastrale is similar in all pimeliine genera and differs only at the species level (sclerotization and form of derivatives of inner sternite IX).

**Ovipositor**

The Pimeliini is distinctly divided into two groups by the structure of the ovipositor. The majority of Pimeliini (subtribe Pimeliina) has an ovipositor that is partly transformed into a fossorial structure (Doyen 1994; Ren & Ba 2009; Leo 2016; S. Chigray 2019): the paraproct and proctiger are long and armed with long distinct baculi, apical lobe of coxite strongly sclerotized and transformed into glabrous shovel-like derivatives of inner sternite IX (Figs 18J–L, 19J–L, 10J–L, 21K–M, 22J–L). Species of the subtribe Habrobatina have the ovipositor transformed to a structure for sweeping away sand: paraproct and proctiger short, with reduced baculi, apical lobe of coxite sub-conical, membranous, with a brush of dense, long setae (Figs 14J–L, 15J–L, 16K–M, 17J–L). The coxite lobe III is the most transformed structure in Habrobatina. The ovipositor of *Apatopsis* has four apices with hair brushes (apomorphic state): two of these are on pair coxite lobe IV and two additional ones are formed from a strongly projecting apical part of pair coxite lobe III on the ventral side of the ovipositor (Fig. 14J–K). The coxite lobe III is conical in other genera, without additional processes apically, very short in *Habrochiton* (Fig. 15L) and much longer and larger than lobes II and IV in *Habrobates* (Fig. 16K) and *Dietomorpha* (Fig. 17J).

The ovipositor of the *Platyope* genus group does not differ from that in other Pimeliina, but many species have very dense pubescence of the coxite, which combines fossorial and the sand brushing functions (Figs 18J–L, 19J–L, 20J–L, 21K–M). The characters of the ovipositor of the ultrapsammophilic group Habrobatina are regarded as the advanced state.

**Female genital ducts**

The most simple structure (plesiomorphic state) is presented in the genus *Mantichorula*, species of which do not have the spermatheca (instead, only a short primary bursa copulatrix), and accessory gland of spermatheca short, thin, not branched and not modified (without constriction and the basal narrow part or duct) (Fig. 23E). The further ways of specialization are associated with an increase in the volume of the spermatheca due to the lengthening of the single duct as in *Earophanta* (Fig. 23H) or by increasing the number of short ducts flowing directly into the vagina as in *Apatopsis* (Fig. 23A) like those in Edrotini (Doyen 1994; S. Chigray 2018), or branched at the apex of the thickened basal duct of the spermatheca as in *Platyope grumi* (Fig. 23G). The complication of the accessory gland is achieved by increasing its volume and the formation of constrictions, similar to those in some Tentyriini (S. Chigray et al. 2018; S. Chigray & Abakumov 2019): one basal in *Habrobates, Przewalskia, Platyope, Earophanta* (Fig. 23B, D, F–H,), two in *Dietomorpha* (Fig. 23C) or four in *Apatopsis* (Fig. 23A).

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