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Genus *Apterocuris* Jacobson, 1901 (Coleoptera: Chrysomelidae) in the Subfamily Chrysomelinae with Description of a New Species and Remarks on Significance of Preimaginal Characters [†]

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urn:lsid:zoobank.org:act:F60292B6-1F0C-49B5-9AB9-4978B9AEA0CB.

Abstract: For *Apterocuris* Jacobson, 1901, formerly considered a monotypic genus endemic to South Siberia, a second congener is described from the Central Sikhote-Alin' Mountains in the Far East of Russia. *Apterocuris brinevi* sp. n. differs from *A. sibirica* Jacobson, 1901 in the rather convex body, shining smooth dorsum, absence of rectangular projecting basilateral angles of elytra, and only two or three distinct striae of elytral punctures. For *Apterocuris sibirica*, the pupa is first described, imago redescribed, and the revised distribution is mapped. The place of *Apterocuris* in the tribe Chrysomelini is discussed and its similarity to the genus *Sclerophaedon* Weise, 1882 considered. Both genera have pupae with two urogomphi that should place them into the subtribe Entomoscelina, but their adults with open anterior coxal cavities do not fit the subtribe diagnosis. Therefore, re-establishment of the subtribe Sclerophaedonina Steinhausen, 1996 is proposed to place the genera *Sclerophaedon*, *Apterocuris*, *Colaphellus* Weise, 1916 and *Colaspidema* Laporte, 1833. A triple key to the genera of the tribe Chrysomelini based on the combination of larval, pupal and imaginal characters is presented.

Keywords: leaf beetles; pupa; tribal diagnoses; key to larvae; key to pupae; combined key to genera; Russian Far East

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1. Introduction

Apterocuris was proposed by Jacobson [1] as a monotypic genus with *Chrysomela sibirica* Gebler, 1830 as a type species. Up to now it had been restricted to the mountains of South Siberia. The first specimen (female) of the new species described herein was found by Dr. Alexei Brinev in Central Sikhote-Alin' in 2007. The second specimen, again female, was obtained by the same collector in 2018. When the larva of *Apterocuris sibirica* was described by Dolgin and Medvedev [2], its similarity was first mentioned to the genus *Sclerophaedon* Weise, 1882, known at that time only from the mountains of Central Europe. Moreover, for several species described not long ago from China, such as *Sclerophaedon kabaki* Daccordi and Ge, 2013, *S. orientalis* Daccordi and Ge, 2013, and *S. rufipes* Daccordi and Ge, 2013, only female holotypes are known, while for *S. murzini* Daccordi and Ge, 2013, only holotype and paratype, both females, are known. Similarly, in the case of *Apterocuris*, females have enough characters to distinguish species.

Daccordi [3] regarded the taxon *Apterocuris* as a subgenus of *Sternoplatys* Motschulsky, 1860. However, Medvedev [4] restored the generic status of *Apterocuris* based mainly on larval characters clearly different from those of *Sternoplatys*. Here, the pupa of *Apterocuris* is first described and this description gives further evidence of its place in the tribe Chrysomelini.

2. Materials and Methods

This paper is based on an examination of the collections from several museums, specimens collected by Dr. Alexei Brinev in Khabarovsk Province, and materials collected by Dr. Roman Dudko and the author in the mountains of South Siberia. The examined material is housed in the following collections: ISEA—Zoological Museum of the Institute of Systematic and Ecology of Animals, Novosibirsk, Russia; MFNB—Museum für Naturkunde, Berlin, Germany; ZIN—Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; YMC—Y.E. Mikhailov personal collection, Yekaterinburg, Russia; AKC—A.G. Koval personal collection, St. Petersburg, Russia.

All measurements were made using an ocular grid mounted on MBS-10 stereomicroscope. Total body length was measured from the anterior edge of the pronotum to the elytral apex, and body width was measured in the broadest part of the elytra. Pupae have never been described in Russian publications before; the description plan follows Takizawa [5] and Steinhausen [6]. As the underside of the body does not show any useful characters [7], only the dorsal side is depicted and described. Morphological terminology of life cycle stages was checked after Reid [8].

The exact label data are cited for type and historical specimens only. Separate labels are divided with "|", and separate lines of one label with "/".

3. Results

3.1. Genus Apterocuris Jacobson, 1901

Apterocuris Jacobson, 1901: 85 (type species *Chrysomela sibirica* Gebler, 1830, by original designation); [9], p. 165; [10], p. 115; [11], p. 90; [12], p. 236; [13], p. 425;

Sternoplatys (*Apterocuris*): [3], p. 80; [14], p. 394; generic status resurrected by Medvedev [4], p. 476.

The original description of the genus was made by Jacobson [1] in Latin. Short redescriptions were given by Lopatin and Kulenova [10] and Lopatin [12] in Russian. The main and distinguishing characters will be given here in the detailed descriptions of constituting species and in the keys.

Chrysomela sibirica was described by Gebler [15] from the Salair Mountains ("in sylva Salairensi") based on two syntypes. Later on, Gebler [16] transferred it to the genus *Phaedon*. Jacobson [1], after the studies of Gebler's types and specimens collected by his brother Alexei from the Shaman Mountain Range, described the new monotypic genus *Apterocuris* to place *Chrysomela sibirica*. In the diagnosis, Jacobson [1] compared *Apterocuris* with *Prasocuris* Latreille, 1802 (and separately its subgenus *Hydrothassa* C. Thomson, 1859), *Oreothassa* Jacobson, 1901, *Sternoplatys* Motschulsky, 1860 and *Sclerophaedon* Weise, 1882. In the same work, the key was given for determination of these and some other genera.

Daccordi and coauthors [17,18] elaborated the set of characters for the description of genera and species including the genera, where *Apterocuris* was compared by Jacobson [1]. Some characters are essential for understanding the phylogeny, but not mentioned in the previous descriptions. That is why the redescription of *Apterocuris sibirica* is needed.

3.2. Apterocuris sibirica (Gebler, 1830)

Chrysomela sibirica Gebler, 1830: 218 ("in sylva Salairensi", syntypes in ZIN, were studied by Jacobson [1] for description of the genus);

Phaedon sibiricus: [16], p. 620;

Apterocuris sibirica: [1], p. 86; [9], p. 165; [10], p. 115; [11], p. 112; [12], p. 236; [13], p. 425;

Sternoplatys (*Apterocuris*) *sibiricus*: [14], p. 394;

Chrysomela puncticollis Gebler, 1833: 308 ("prope Ustkamenogorsk", type deposition unknown); synonymised by Jacobson [1], p. 86.

Phaedon puncticollis: [16], p. 620.

3.2.1. Material Examined

RUSSIA:

Altai Province:

49825 | Phaedon sibiricum Gebl./Kolywan, Gebl.—1♂♂, 4♀♀ (MFNB); "Kolyvanskij zavod, Zmeinogorsk. uezda, 22.IV—22.V.1919"—1♀♀ (ISEA); Korgonskie Belki Mts.: upper Sentelek River, Gor'ky Belok Mt., 1850–1950 m, subalpine-alpine, 51°04.5′ N, 83°35′ E, 26 June 2011, Yu. Mikhailov—1♂♂, 4♀♀ (YMC); Inskoye Lake and upper Belogolosov Korgon River, 1750–1950 m, subalpine meadows, 50°58′ N, 83°40–41′ E, 29 June 2011, Yu. Mikhailov—2♀♀ (YMC).

Altai Republic:

Iolgo Mt. Range: Karakol'skie Lakes, 30 June 1993, F.V. Melyakh—1♀♀ (YMC); Bagatash pass, h = 1500 m, on Asteraceae, 17 September 1993, Yu. Mikhailov—1♂♂, 2♀♀ (YMC); Teletskoye Lake, Artybash, 23 May 1970, M.M. Dolgin—1♀ (ISEA); the same locality, 26 May 1971, M.M. Dolgin—1♀♀(ISEA); Teletskoye Lake, Iogach, mixed forest, 4.06.1970, 3 August 1970, M.M. Dolgin—2♂♂, 2♀♀ (ISEA); Kholzun Mt. Range: near upper course of Malaya Kolbina River, N 50°16′38″, E 84°36′46.1″, h = 2000–2100 m, 14–16 June 2005, A.G. Koval—1♀♀ (AKC); pass near source of Antshigar River, N 50°10′54.8″, E 84°41′45.3″, h = 2000 m, 21 June 2005, A.G. Koval—1♀♀ (AKC); NE spurs of Kholzun Mt. Range, right tributary of Poperechnaya Krasnoyarka River, h = 1750–1850 m, 1 July 2021, R. and E. Dudko—2♂♂, 1♀♀ (YMC); upper Poperechnaya Krasnoyarka River, h = 2150–2350 m, 4 July 2021, R. and E. Dudko—2♂♂, 2♀♀ (ISEA); watershed of Bystraya River and Poperechnaya Krasnoyarka River, h = 2350–2450 m, 3–4 July 2021, R. and E. Dudko—2♂♂, 8♀♀ (YMC); 5 km SSW Ust'-Kan, Kutergen River valley, h = 1300 m, forest, 7 June 1999, A. and R. Dudko—2♂♂, 7♀♀ (ISEA, YMC); 25 km SSW Ust'-Koksa, Kabanukha Mt., h = 1880 m, subalpine meadows, 28–29 May 2005, Yu. Mikhailov—2♂♂, 2♀♀ (YMC); 32 km SSW Ust'-Koksa, upper Petrushkina River, 1500 m, forest clearings, 50°03′ N, 85°21′ E, 31 May 2005, Yu. Mikhailov—1♀♀ (YMC); 32 km SW Ust'-Koksa, eastern slope of Krasnaya Mt., 1850–2000 m, subalpine and alpine tundra, 50°3–4′ N, 85°15–16′ E, 3–4 June 2005, Yu. Mikhailov—2♀♀ (YMC); Korgonskij Mt. Range: upper Antonov Korgon River, 27 km SW Ust'-Kumir, 1900–2100 m, alpine meadow, 50°51.9′ N, 84°00.2′E–50°53.3′ N, 84°02.9′ E, 3–4 July 2019, A. Gurina, R. and E. Dudko—1♀♀ (YMC); Tigiretskij Mt. Range, eastern end, upper Kytma River, 1900–2200 m, 50°49.5′ N, 83°55.2′ E, 4 July 2019, A. Gurina, R. and E. Dudko—1♀♀ (YMC).

Kemerovo region:

Kuznetsky Alatau Mts.: Skalistye Gory Mts., subalpine meadows, 12 July 1995, Yu. Mikhailov—2♂♂, 1♀♀ (YMC); slopes of Dvuglavaya Mt., 17 July 1995, Yu. Mikhailov—1♀♀ (YMC); Amzas River valley, tall herbage meadows, 23–24 July 1996, Yu. Mikhailov—1♀♀ (YMC); Gornaya Shoriya: Bolshoi Unzas River valley, 12 km NNE Sheregesh, h = 500–700 m, 7–27 June 1999, D. Lomakin—1♀♀ (YMC).

Republic of Khakassia:

Kuznetsky Alatau Mts.: 10 km S Priiskovy village, Bobrovaya Mt., alpine tundra, h = 1200–1600 m, 15–25 June 2003, D. Lomakin—3♂♂, 7♀♀ (YMC); Western Sayan Mts.: Shaman Mt. Range: Tomsk Gouv., Schaman/A. Jacobson | Apterocuris sibirica Gebl./G. Jacobson det.—1♀♀ (MFNB); Choochek Mt. Range, 20 km SSE Mrassu village, alpine tundra, h = 1600–1800 m, 7–19 July 1999, D. Lomakin—3♀♀ (YMC).

Krasnoyarsk Province:

Western Sayan Mts., Stan-Taskyl Mt. Range, upper Big Kazanashka River, h = 1700–1900 m, alpine tundra, 27 June –2 July 2010, A. Brinev—1♀♀ (YMC).

KAZAKHSTAN:

East Kazakhstan region:

Ivanovsky Mt. Range: Prokhodnoy Belok Mts., h = 1700 m, subalpine meadows, 6–7 June 2000, Yu. Mikhailov—12♂♂, 15♀♀ (YMC); Kholzun Mt. Range: Kozlushka, 4 June 1925, V.N. Lebedev—2♂♂, 2♀♀ (ISEA); "Pass Khamir–Krasnoyarka 4.VII.1925"—4♀♀ (ISEA); Ulbinsky Mt. Range: Studenukha Mt., 18 km NW Turgusun village, h = 1600–1700 m, 49°51′ N, 83°48′ E, 5–6 June 2019, A. Gurina and R. Dudko—1♂♂, 2♀♀ (YMC).

3.2.2. Redescription

Body elongate, moderately convex, in males oval, in females slightly egg-shaped (Figure 1). Body length: 3.7–4.0 mm (males), 4.0–4.8 mm (females); body width: 1.9–2.1 mm (males), 2.2–2.4 mm (females). Dorsum slightly shining, usually greenish blue or bluish green, sometimes coppery (var. *aurichalcea* Jacobson), purplish bronze (var. *purpurea* Jacobson), dark blue (var. *cyanea* Jacobson), bronze with violet tinge or bluish violet (var. *violacea* Jacobson). The mentioned colour varieties were described in the work containing also subspecies [1] and later on, they were not used in another status; therefore, these names are infrasubspecific (Art 45.6.4 of ICZN 1999). Underside, legs and antennomeres 1 black with metallic luster; tarsi and antennae (except antennomere 1) dark brown.

Figure 1. *Apterocuris sibirica* Jacobson, 1901, female (East Kazakhstan, Prokhodnoy Belok Mts.): habitus in dorsal, dorsolateral and lateral view. Scale bar—1 mm.

Head: clypeus almost flat or slightly convex, with dense coarse punctures except the outer margin; frons slightly depressed, with dense coarse punctures, frontal suture absent, epicranial suture slightly deepened along antennal sockets. Apical segment of maxillary palpi slender and pointed, longer than penultimate segment. Antennae short, antennomere 1 distinctly inflated (1.3× longer than wide), third antennomere 1.2–1.3× longer than antennomere 2, antennomeres 7–11 broader than preceding and with dense pubescence. Mandibles with two dents.

Pronotum: distinctly narrower at base than elytra; transverse (1.8× broader than long); with maximum width before middle; lateral margins evenly-rounded in anterior 2/3, straightly narrowed or incised in basal third (narrowed at base in females more distinctly than in males); at anterior angles, 1.4× narrower than at base; anterior margin not emarginate with projecting anterior angles; posterior angles obtuse or rectangular; lateral and posterior edges finely bordered. Disc moderately convex and finely-shagreened, unevenly covered with punctures, in the middle with sparse, large, slightly-deepened ones and at lateral sides with dense, coarse and deep punctures; interspaces with scattered, very fine punctures. Scutellum: wide (1.7–1.8× broader than long), half-rounded, impunctate.

Elytra: distinctly broader at base (1.1×) than pronotum, which is especially visible due to rectangular projecting basilateral angles (Figure 1); elongate (2.8–2.9× longer than wide), slightly broadened before middle in both sexes (1.17–1.2× broader than base); humeral callus absent. Primary punctures dense, large or moderately large, not deepened. They form short scutellar row from 5–6 punctures and from presumably nine striae, only 1–4 and 8–9 (or 1–5 and 9) are usually regular or slightly irregular, while 5–7 or 6–8 are completely confused (Figure 1); striae 8 and 9 near lateral margin complete, reaching apex of elytra. Rarely in males all nine striae are almost regular (Figure 2a). Interspaces between traceable elytral striae subequal in width and apically tapering; flat, smooth, impunctate, but each bearing thin longitudinal wrinkle. Epipleura inclined outside, with long row or medium-sized punctures along inner margin (reaching abdominal ventrite 3) and short row of punctures along outer margin (reaching metaventrite). Hind wings narrow, reduced, not longer than metaventrite. Pygidium with deep longitudinal median groove.

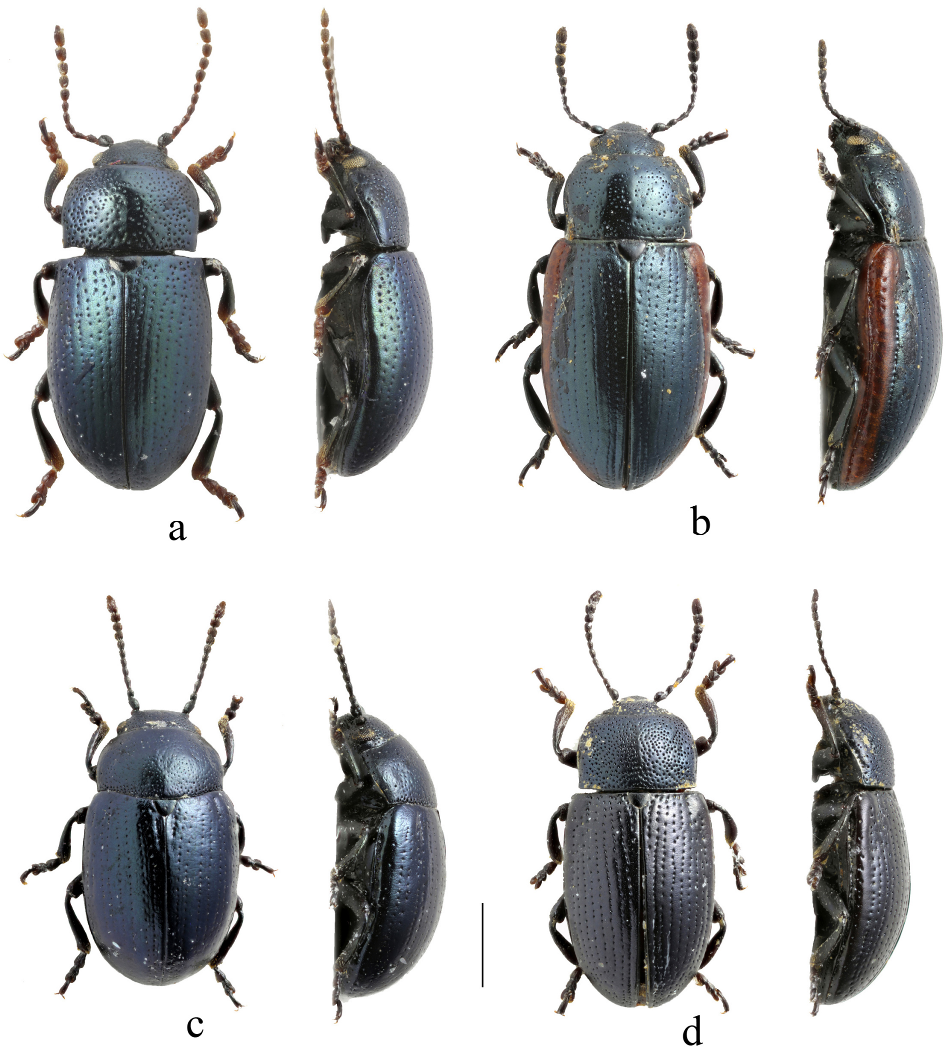

Figure 2. Habitus of adult beetles in dorsal and lateral view: (**a**)—*Apterocuris sibirica* Jacobson, 1901, male (East Kazakhstan, Prokhodnoy Belok Mts.); (**b**)—*Oreothassa martjanowi* Jacobson, 1901, female (Russia, Kemerovo Region, Kuznetsky Alatau Mts.); (**c**)—*Sternoplatys clementzi* Jacobson, 1901, male (Russia, Tyva Republic, Mongun-Taiga Massif); (**d**)—*Oreothassa weisei* (Reitter, 1901), male (Russia, Altai Republic, Iolgo Mt. Range). Scale bar—1 mm.

Underside: prothoracic hypomera almost flat and shagreened, densely covered with coarse punctures; prosternal process broad, apically widened and truncate, with coarse and dense punctures. Metaventrite with dense and coarse punctures; abdominal ventrite

1 with large punctures in anterior half, its posterior half and ventrites 2–5 with dense fine punctures. Last ventrite slightly convex in the middle and depressed at sides.

Legs: femurs robust; tibiae slender, slightly curved with dense pubescence at apex. Female tarsi narrow, male fore and middle tarsi slightly broadened, tarsomere 3 is the widest. All tarsi in both sexes with entire sole beneath.

Aedeagus: in dorsal view moderately broadened to middle, tapered to truncate and broadly-rounded apex; in lateral view bent at middle; flagellum visible, tubular, turned upwards. Spermatheca absent.

3.2.3. Differential Diagnosis

Among the genera of similar habitus and size, uniformly-coloured dorsum easily distinguishes *A. sibirica* (Figure 2a) from the bicolour species *Prasocuris* (*Hydrothassa*) *marginella* (Linnaeus, 1758) and *Oreothassa martjanowi* Jacobson, 1901 (Figure 2b). It differs from similarly uniformly-coloured *Sternoplatys clementzi* Jacobson, 1901 (Figure 2c) by elongate body and confused punctation on dorso-lateral portions of elytra. The most similar is *Oreothassa weisei* (Reitter, 1901) (Figure 2d)–both species may occur in sympatry and are therefore confused, but *O. weisei* has all elytral puncture rows distinct and base of elytra margined (see also a key to imagines below).

3.2.4. Distribution

Encompasses North-Western and North-Eastern Altai, Kuznetsky Alatau, and extreme West of Western Sayan. The most detailed map of known localities is given in Figure 3. The record from the environs of Almaty in South-East Kazakhstan [10] is unreliable and not proved by examined material.

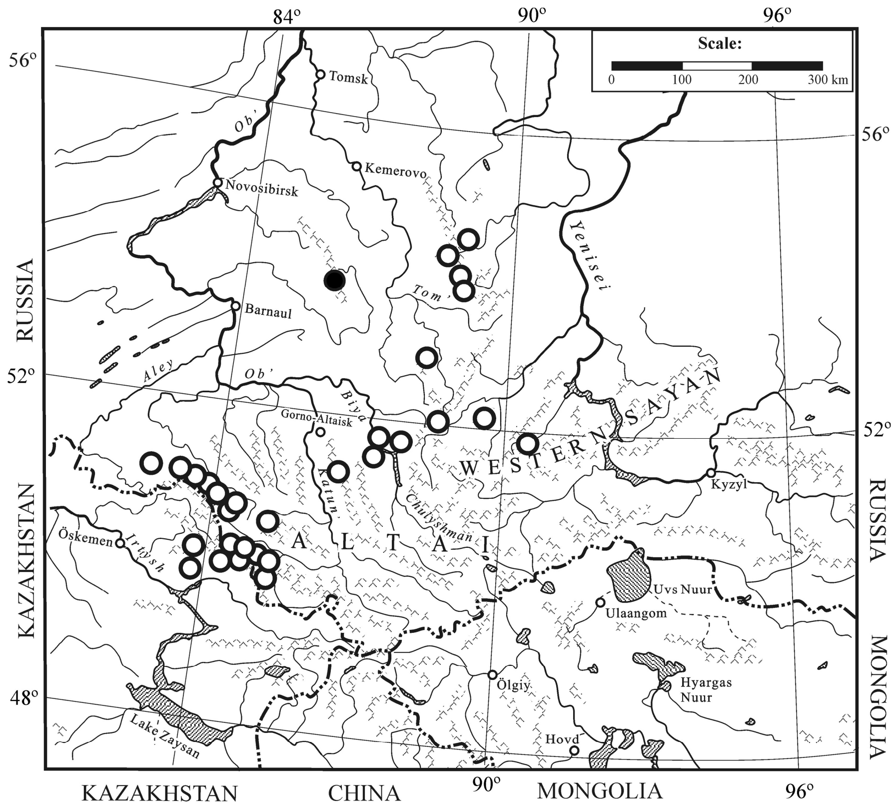

Figure 3. Distribution of *Apterocuris sibirica* in the mountains of South Siberia and East Kazakhstan. White circles—known localities, black circle—*locus typicus*.

3.2.5. Biotopes

Inhabits tall grass clearings in mountain forests, subalpine meadows and alpine tundra (mainly near springs).

3.2.6. Host Plants

Delphinium elatum (Ranunculaceae), *Geranium* sp. (Geraniaceae) [11]. In Ivanovsky Mountain Range, I recorded feeding on *Anemone* sp. and, in Korgonsky Mountain Range, on *Aquilegia* sp. (Ranunculaceae).

3.2.7. Larva

Larva was described by Dolgin and Medvedev [2]. Body light grey, head capsule, sclerites and legs brown. Distinguishing features are given in the key to larvae below.

3.2.8. Pupa

Material Examined: three pupae (ISEA, YMC) were obtained from larvae hatched by two females collected from *Aquilegia* sp. (Ranunculaceae) in Altai Province, Korgonskie Belki Mts., Inskoye Lake and upper Belogolosov Korgon River, 1750–1950 m, subalpine meadows, 50°58′ N, 83°40–41′ E, 29 June 2011, Yu. Mikhailov leg. These beetles and later on their larvae were reared on *Aquilegia* spp. in cage.

Description. Body elongate (Figure 4a), uniformly light yellow, setae and abdominal stigmae brown; length 6.0 mm, width 2.2 mm. Head with five pairs of setae (Figure 4b); pronotum with 17 pairs of setae. Meso- and metathoraces with three pairs of setae forming four longitudinal rows. Dorsally abdominal segment 1 with five pairs of setae, segments 2–6 with seven pairs including microsetae; segments 7 and 8 with five pairs of setae only on distal margin. Setae on abdominal segments form 6 longitudinal rows. Stigmae on abdominal segments 1–5 chitinized, on abdominal segments 6–7 reduced. Last segment produced, chitinized, with a pair of urogomphi. Urogomphi with one pair of long and one pair of short setae (Figure 4c).

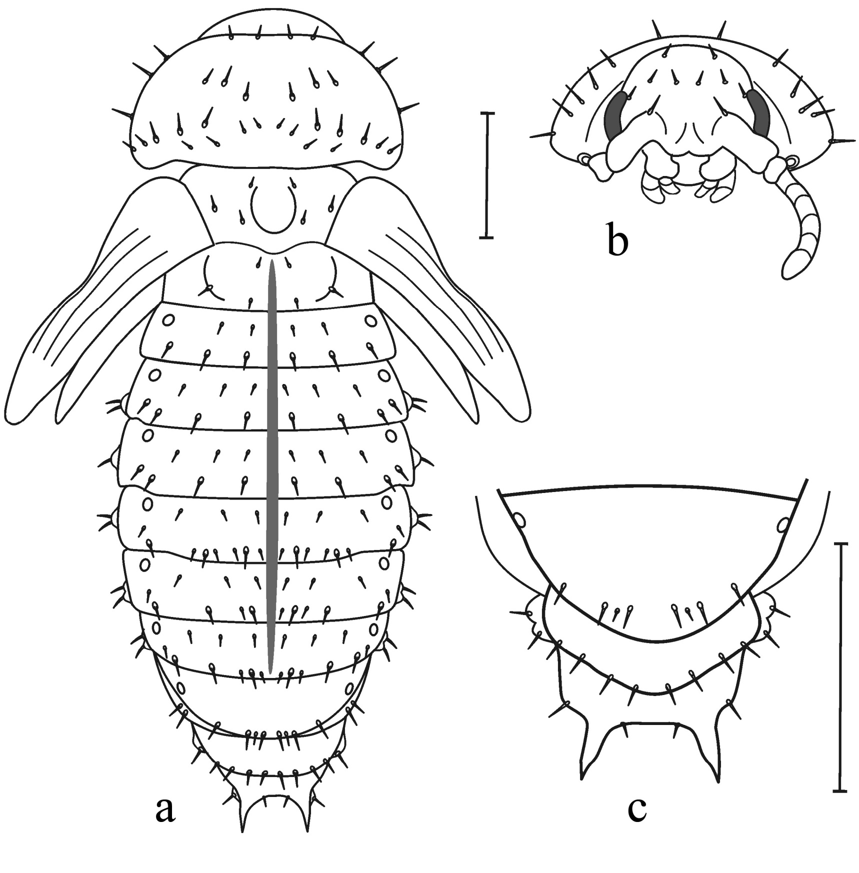

Figure 4. Pupa of *Apterocuris sibirica:* (**a**)—dorsal view, (**b**)—head, (**c**)—abdominal segments 7–9 with urogomphi. Scale bar—1 mm.

Belongs to a group of soil-pupating species.

3.3. *Apterocuris brinevi* sp. n.

urn:lsid:zoobank.org:act:F60292B6-1F0C-49B5-9AB9-4978B9AEA0CB.

3.3.1. Type Material

Holotype: female with labels: юг Хабаровского края,/р-н им. Лазо, Центр./Сихоте-Алинь, г. Ко,/h = 1700 м./25–28 July 2018/А. Бринев leg. [south of Khabarovsk Province, district named after Lazo, Central Sikhote-Alin', Ko Mountain, h = 1700 m, 25–28 July 2018, A. Brinev leg.] | HOLOTYPUS/*Apterocuris*/*brinevi* sp. n./Yu. Mikhailov design. 2021 [red label] (ZIN). Paratype, female with labels: юг Хабаровского края,/р-н им. Лазо, Центр./Сихоте-Алинь, г. Ко,/h = 1500 м./1–5 July 2007/А. Бринев leg. [south of Khabarovsk Province, district named after Lazo, Central Sikhote-Alin', Ko Mountain, h = 1500 m 1–5 July 2007, A. Brinev leg.] | PARATYPUS/*Apterocuris*/*brinevi* sp. n./Yu. Mikhailov design. 2021 [red label] (YMC).

The combination of characters including oblong body outline, reduced hind wings, pronotum narrower than base of elytra, and elytral punctures mostly confused and arranged in rows only along suture and lateral margins, corresponds well with the original description of the genus *Apterocuris* [1] and therefore justifies the assignment of the species described below to this genus.

3.3.2. Description

Female (holotype) (Figure 5). Body elongate, distinctly egg-shaped and rather convex. Body length: 4.7 mm (5.0 mm with head); body width: 2.4 mm. Dorsum shining, especially elytra with lacquer shine, head and pronotum bronze, elytra blackish blue. Underside, legs and antennomere 1 black with metallic luster; tarsi and antennomeres 7–11 reddish brown.

Figure 5. *Apterocuris brinevi* sp. n., holotype (Russia, Khabarovsk Province, Central Sikhote-Alin' Mts)-habitus in dorsal, dorsolateral and lateral view of. Scale bar—1 mm.

Head: clypeus flat, with dense coarse punctures except the outer margin; frons slightly depressed, with dense coarse punctures, frontal suture absent, epicranial suture slightly deepened along antennal sockets. Apical segment of maxillary palpi slender and pointed, longer than penultimate segment. Antennae short, antennomere 1 distinctly inflated (1.3× longer than wide), antennomere 3 1.3× longer than antennomere 2, antennomeres 7–11 broader then preceding and with dense pubescence. Mandibles with two dents.

Pronotum: narrower at base than elytra; transverse (1.9× broader than long); with maximum width before middle; lateral margins evenly-rounded in anterior 2/3, straightly narrowed in basal third; at anterior angles 1.5× narrower than at base; anterior margin not emarginate with projecting anterior angles; posterior angles obtuse; lateral and posterior edges finely bordered. Disc moderately convex, smooth, unevenly punctured: in the middle covered with sparse, large, slightly deepened punctures, at lateral sides covered with dense, coarse, deep punctures; interspaces with scattered very fine punctures. Scutellum: wide (1.9× broader than long), half-rounded, impunctate.

Elytra: broader at base (1.08×) than pronotum, with obtuse basilateral angles; elongate (2.8× longer than wide), distinctly broadened before middle (1.29× broader than base); humeral callus absent. Primary punctures dense, medium-sized, not deepened; they form short scutellar row from 7–8 punctures, striae 1, 2 and 9 almost regular, 3 and 4 irregular and hardly traced because of doubled punctures; rest of punctures completely confused (Figure 5); stria 9 near lateral margin complete, reaching apex of elytra. Interspaces between traceable elytral striae subequal in width and apically tapering; flat, lacquer smooth, impunctate, but each bearing thin longitudinal wrinkle (Figure 5). Epipleura inclined outside, with long row or medium-sized punctures along inner margin (reaching abdominal ventrite 3) and short row of punctures along outer margin (reaching metaventrite). Hind wings narrow, reduced, not longer than metaventrite. Pygidium with deep longitudinal median groove.

Underside: prothoracic hypomera almost flat and smooth, densely covered with coarse punctures; prosternal process broad, apically widened and truncate, with coarse and dense punctures. Metaventrite with dense and coarse punctures; abdominal ventrites with large dense punctures. Last ventrite slightly convex in the middle and depressed at sides.

Legs: femurs robust; tibiae slender, slightly curved with dense pubescence at apex. Tarsi narrow, 2.2× longer than wide, tarsomere 3 is the widest. All tarsi with entire sole beneath. Spermatheca absent.

Paratype (female). Body length: 4.3 mm (4.7 mm with head); body width: 2.3 mm. Dorsum shining, especially elytra with lacquer shine, head and pronotum greenish blue, elytra dark blue. Elytra with short scutellar row from 3–6 punctures, striae 1 and 2 mainly regular, striae 3 and 4 irregular and hardly traced because of doubled punctures; rest of punctures completely confused. Other characters as in holotype.

3.3.3. Etymology

Dedicated to Dr. Alexei Brinev (Moscow Pedagogical State University), who collected the type specimens.

3.3.4. Differential Diagnosis

Among the genera of similar habitus and size and similarly uniformly-coloured, the new species differs from *Sternoplatys fulvipes fulvipes* Motschulsky, 1860 (Figure 6) by elongate body and confused punctation of elytra. It differs from the species of *Phratora* Chevrolat, 1836 by reduced hind wings.

From *Apterocuris sibirica* (Figure 1) with moderately convex or almost-flattened body, slightly broadened before middle in both sexes, with slightly shining finely-shagreened dorsum, the new species differs by rather convex body, distinctly broadened before middle, shining smooth dorsum and elytra with lacquer shine (Figure 5). In addition, the elytra in *A. sibirica* are distinctly broader at base than pronotum, especially visible due to rectangular projecting basilateral angles; elytral punctures form four or five usually regular striae, while the rest are confused. In new species, elytra broader at base than pronotum, with obtuse basilateral angles; elytral punctures form only two or three regular striae and are confused on the remainder elytral integument.

Figure 6. *Sternoplatys fulvipes fulvipes* Motschulsky, 1860, female (Russia, Primorye Province, env. of Kamenushka)—habitus in dorsal and lateral view. Scale bar—1 mm.

3.3.5. Distribution

Known only from the Ko Mountain in the Central Sikhote-Alin'.

4. Discussion

Daccordi [3] downgraded *Apterocuris* to a subgenus of *Sternoplatys* and this treatment was supported in the Catalogue of Palaearctic Coleoptera [14]. In fact, *Apterocuris* and *Sternoplatys* are usually placed together in the keys of adult beetles [11–13] as both have reduced hind wings, tarsomere 3 entire apically or shallowly emarginated, and elytral punctures arranged in rows. The main differences in adults are made up of body outline (oval or oblong) and elytral puncture rows (all regular or irregular at the sides). Aedeagus structure of *Sternoplatys* and *Apterocuris* has never been illustrated in the keys [11–13], although it is clearly different (Figure 7). *Sternoplatys* has quite flat aedeagus without flagellum (Figure 7a), while in *Apterocuris*, flagellum is tubular and turned upwards (Figure 7b). The similar aedeagus structure with tubular flagellum is known in the species of *Sclerophaedon* (Figure 7c,d).

Two species of *Oreothassa* (Figure 2) are habitually very similar to *Apterocuris*, also have reduced hind wings and occur in the mountains of South Siberia, but they are readily distinguished from *Apterocuris sibirica* in the keys to adult beetles due to distinctly incised tarsomere 3 and base of elytra with distinct convex margin [11–13].

The treatment of *Apterocuris* as a subgenus of *Sternoplatys* based solely on external morphology of adults was rejected by Medvedev [4], who restored the generic status of *Apterocuris* based on the difference with *Sternoplatys* in imaginal and especially larval characters. In the description of larva of *Apterocuris sibirica* [2] it was clearly stated that the absence of dorsal glands distinguished it from the larvae of *Prasocuris* and *Phaedon*, but made it similar to those of *Sclerophaedon*.

Hennig [19] and then Steinhausen [20] pointed out that larvae of Chrysomelinae Latreille, 1802 are divided into well-defined groups with or without dorsal openings of defensive glands. The larvae with defensive glands arranged segmentally in nine pairs along the back can release droplets of secretions from the everted reservoirs (Figure 8). The major components in the secretion of the ancestral leaf beetle group (members of *Phaedon*, *Gastrophysa* and *Phratora* (but not *Ph. vitellinae*) are iridoid monoterpenes. The larvae of the more advanced genus *Chrysomela* and *Ph. vitellinae* display secretions with salicylaldehyde as the sole or major component [21].

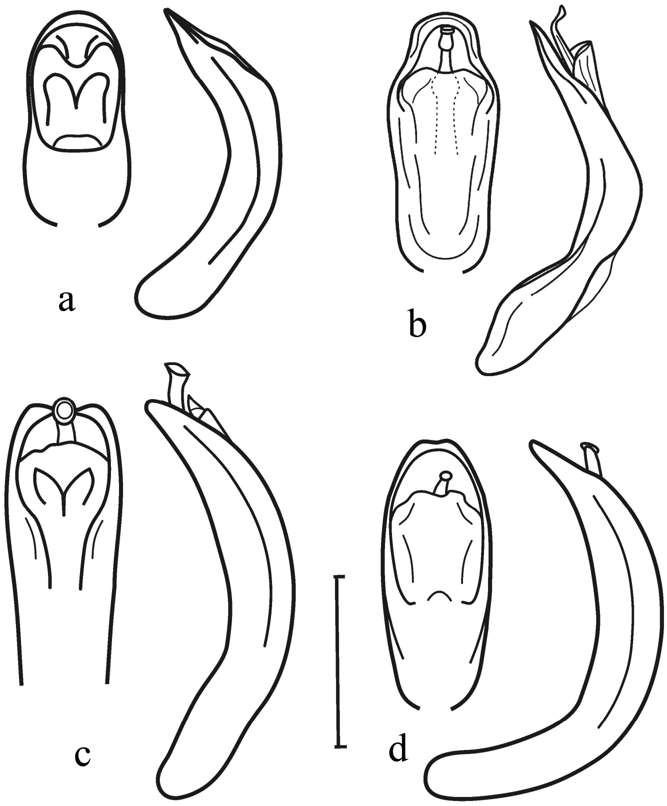

Figure 7. Aedeagus in dorsal and lateral view: (**a**)—*Sternoplatys clementzi* Jacobson, 1901 (Russia, Tyva Republic, Mongun-Taiga Massif); (**b**)—*Apterocuris sibirica* Jacobson, 1901 (Russia, Kemerovo Region, Kuznetsky Alatau Mts.); (**c**)—*Sclerophaedon carniolicus* Germar, 1824 (Austria, Bubenberg, Spielfeld); (**d**)—*Sclerophaedon carpathicus* (Ukraine, Transcarpathia, Marmarosh Massif). Scale bar—0.5 mm.

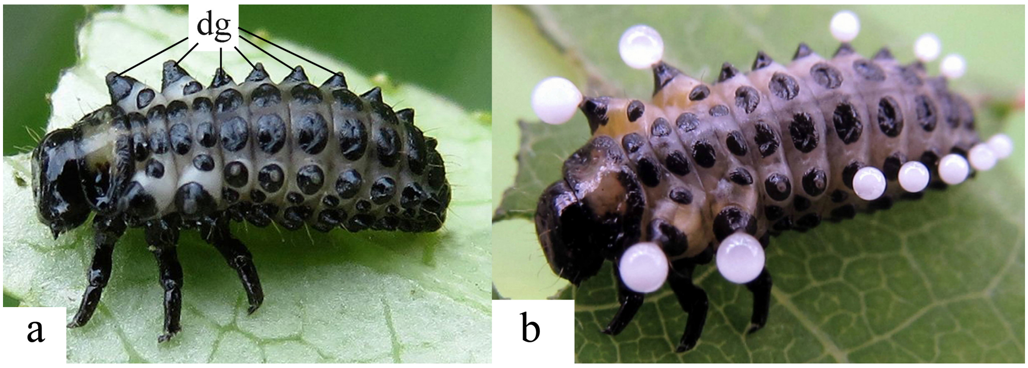

Figure 8. Larva of *Chrysomela tremula* Fabricius, 1787: (**a**)—everted reservoirs of dorsal defensive glands (dg) are indicated; (**b**)—defensive glands release droplets of secretions.

Steinhausen [20] indicated *Sclerophaedon*, *Entomoscelis* and *Colaphellus* as the genera that have larvae without dorsal defensive glands and abdominal segments 6 and 7 with pseudopodia. *Apterocuris* and *Sternoplatys* are absent in the European keys to larvae, but both genera are included in the key to larvae of the leaf beetles of Russia [22]. They are placed far away from each other as *Apterocuris* has pseudopodia on abdominal segments 6 and 7 and no openings of defensive glands, while *Sternoplatys* has dorsal glands on wing sclerites. Larvae of *Oreothassa* have not been described so far [22], although both larva and pupa of *O. martjanowi* are at my disposal as they were reared in parallel with those of *A. sibirica*. They are still pending proper description but for the purpose of including in the key below it is enough to indicate that the larva of *O. martjanowi* has dorsal glands and its pupa has no urogomphi.

The genus *Sclerophaedon* was proposed by Weise [23], with *Chrysomela carniolica* Germar, 1824 as a type species. For a long time, this genus was restricted to Central Europe and included three species only. However, Daccordi and Medvedev [24] discovered five more species of *Sclerophaedon* in Nepal and Northern India and included them in the separate subgenus *Tantraedon* Daccordi and Medvedev, 2000. The first species in China, *S. daccordii*, was discovered by Lopatin [25], then Ge, Daccordi et al. [18] described six new species of *Sclerophaedon* s. str. and reviewed eight Chinese species known so far and distributed mainly in Gansu and Sichuan. As a result, the genus *Sclerophaedon* includes 16 known species in three isolated mountainous areas: Central Europe, Nepal and China. Now we can see a similarity with *Apterocuris* that proves to be distributed in two isolated mountainous areas, Altai in South Siberia and Sikhote-Alin' in the Far East.

Sclerophaedon and *Colaspidema* Laporte, 1833 were usually regarded in the subtribe Chrysomelina of the tribe Chrysomelini Latreille, 1802 based on the morphology of adult beetles [3,26]. However, their larvae have no dorsal defensive glands, and the pupae of both genera have paired urogomphi (urogomphi-like two-pointed projection) on the last abdominal segment [6,7]. The mentioned combination of preimaginal characters made Steinhausen [7] first to gather the genera *Colaphellus*, *Sclerophaedon* and *Colaspidema* in one group with *Gonioctena* (Group 4—Gonioctenina) separated from Chrysomelina, Chrysolinina and Entomoscelina (all these subtribes were provisional). Later on, *Colaphellus*, *Sclerophaedon* and *Entomoscelis* were placed [6] in the tribe Entomoscelini sensu Steinhausen, 2001. The placement of *Sclerophaedon* and *Colaspidema* in the tribe Entomoscelini was adopted in the Catalogue of Palaearctic Coleoptera [14] and furthermore, the East Palaearctic genera *Suinzona* Chen, 1931, *Taipinus* Lopatin, 2007 and *Yunnaedon* Daccordi and Medvedev, 1999 were also placed in this tribe as "closely related to *Sclerophaedon*". This is notwithstanding that the pupae of the three mentioned genera have not been described yet.

The tribe level of Entomoscelini proposed by Steinhausen [6] in his system of five tribes (Timarchini, Doryphorini, Chrysomelini, Gonioctenini and Entomoscelini), instead of only two (Timarchini and Chrysomelini), is not recognised by other experts in Chrysomelinae [12,27]. In the revised and updated edition of the Catalogue of Palaearctic Coleoptera [28], the system of two tribes (Timarchini and Chrysomelini) is restored and Entomoscelina is a subtribe of the latter.

As regards essential distinguishing features, the species belonging to the subtribe Entomoscelina have adults with anterior coxal cavities closed posteriorly [12,13] and pupae with two urogomphi [6]. The species from the subtribe Chrysomelina have adults with anterior coxal cavities open [12,13] and pupae without urogomphi [6]. The genera *Sclerophaedon* and *Colaphellus* have pupae with two urogomphi and based on that, were placed in the tribe Entomoscelini by Steinhausen [6], although their adults have anterior coxal cavities open [12,18]. *Colaspidema* has the same situation [27]. *Apterocuris* with open anterior coxal cavities was usually placed in the subtribe Chrysomelina [3,12], but its pupa described herein demonstrates a pair of urogomphi (Figure 4). It is clear now that the mentioned genera do not fully meet the definitions of the subtribes, which they were previously placed in [6,14]. That is why the new subtribe Colaspidemina Petitpierre, 2019 was proposed [27] for the genera *Colaspidema*, *Colaphellus* and *Sclerophaedon*. The latter genus was included in Colaspidemina with a doubt [27].

Before the system of tribes based on the pupal characters [6], the same author compared imaginal and larval characters in one double key [7] and proposed subtribe Sclerophaedonina Steinhausen, 1996 for the genus *Sclerophaedon*. Taking into account the similar combination of adults with anterior coxal cavities open and pupae with two urogomphi, it is possible to place the genera *Sclerophaedon*, *Apterocuris*, *Colaphellus* and *Colaspidema* in the subtribe Sclerophaedonina. In this case, it has priority for Colaspidemina. It is possible also to place only *Sclerophaedon* and *Apterocuris* in Sclerophaedonina, while *Colaphellus* and *Colaspidema* place in the subtribe Colaspidemina.

Steinhausen [7] demonstrated that the simultaneous treatment of the characters of adult beetles and larvae in one double key is better for understanding phylogenetic relationships of genera and tribes. He also tried to make a triple key adding the characters of pupae [29], but it included only a limited number of Central European genera and was published in hardly-accessible source. Here, I make a new attempt to create the triple key, taking into account the division of the larvae into groups with or without dorsal openings of defensive glands and the division of the pupae into groups with or without urogomphi (Table 1). To complete this triple key, the existing keys to larvae [22], pupae [6] and imagines [12,13,27] were combined.

Table 1. Triple key for the Palaearctic genera of Chrysomelini combining the characters of larvae, pupae and adult beetles (includes only genera with known immature stages).

	Larvae	Pupae	Imagines
1	Dorsolateral sclerites of thoracic and abdominal terga with large openings of dorsal defensive glands (Figures 8 and 9a,b)	Last abdominal segment without any appendages (Figure 9e,f)	Labial palps are attached to mentum close to each other (Figure 9j) 2
–	Dorsolateral sclerites without openings of dorsal defensive glands (Figure 9c,d)	Last abdominal segment with one or a pair of urogomphi (Figure 9g–i) . . .	Labial palps are attached to mentum at larger distance from each other . . . 7
2	Anterior margin of labrum with well-pronounced median incisure (Figure 9k). Claws with large tooth (dendrophagous genera of subtribe Chrysomelina)	Dorsum completely coloured or with brown markings, especially thoracic and abdominal terga. Leaf-pupating species of Chrysomelina	Tarsomere 3 entire apically or shallowly emarginated (Figure 9m), rarely deeply incised (Figure 9n). Elytra without sutural stria on apical slope, tibiae without triangular process at apex 3
–	Anterior margin of labrum with or without median incisure (Figure 9l). Claws with or without tooth at base . . .	Dorsum almost white, conspicuously setose. Soil-pupating species of subtribe Chrysomelina	Tarsomere 3 deeply incised, bilobed (Figure 9n). Elytra with sutural stria on apical slope, tibiae with triangular process at apex 4
3	Antennae short, antennomere 2 transverse, antennomere 3 short, not longer than preceding, maximum twice longer than wide	–	Hind wings developed. Elytral punctures confused . . . . *Plagiodera* Chevrolat, 1836, *Plagiosterna* Motschulsky, 1860, *Chrysomela* Linnaeus, 1758, *Gastrolina* Baly, 1859
–	Antennae long, antennomere 2 of equal length and width, antennomere 3 long, 3–4 times longer than wide . . .	Pupae unknown	Hind wings reduced. Elytral punctures arranged in regular rows . . . . . . *Sternoplatys* Motschulsky, 1860
4	Anterior margin of labrum without median incisure. Claws with or without tooth at base	Abdominal segments without post-stigmal setae	Claws with tooth at base . . . . *Phratora* Chevrolat, 1836
–	Anterior margin of labrum with well-pronounced median incisure (Figure 9k). Claws without tooth at base	Abdominal segments with post-stigmal setae	Claws without tooth at base 5
5	Frontal arms first parallel at base, then diverge (Figure 9k). Abdominal terga without pre-tergal sclerites or with their rudiments	Body elongate. Length to width ratio more than 2.0	Body elongate. Pronotum base and base of elytra with distinct convex margin (Figure 2). Prosternal appendix wide . . . . *Prasocuris* Latreille, 1802, *Oreothassa* Jacobson, 1901
–	Frontal arms diverge from the very base, not parallel at any distance (Figure 9l). Post-tergal sclerites of abdominal terga with two setae . . .	Body short, oval. Length to width ratio less than 2.0	Body outline oval. Pronotum base narrowly margined, base of elytra not margined. Prosternal appendix narrow 6

Table 1. *Cont.*

	Larvae	Pupae	Imagines
6	Microsculpture of chitinous body surface (tubercles and spikes) covers not only interspaces but also sclerites. Mesothorax with two pretergal sclerites bearing two setae each . . .	Outer setae of dorsal pairs at segments 7 and 9 very short, inner setae large and long; rarely outer setae completely absent	Punctation of elytra arranged in regular rows . . . . *Phaedon* Megerle von Muhlfeld, 1823, *Neophaedon* Jacobson, 1901
–	Microsculpture of body surface visible only between sclerites and does not cover the latter. Mesothorax with four pretergal sclerites bearing one seta each or tergal sclerites unclear and their situation is indicated by setae	Abdominal terga with a pair of setae at posterior side, from which inner setae slightly longer and at apex of last segment bent inwards	Punctation of elytra confused . . . . *Gastrophysa* Chevrolat, 1836
7	Body convex. Sclerites hardly visible or absent	Last abdominal segment with one sharply pointed urogomphus (Figure 9g) . . . subtribe Chrysolinina	Elytral epipleura with setae at interior border at least in apical part . . . *Chrysolina* Motschulsky, 1860, *Oreina* Chevrolat, 1836, *Ambrostoma* Motschulsky, 1845
–	Body weakly convex. Sclerites clearly visible and well-defined	Last abdominal segment with a pair of urogomphi (Figures 4 and 9h,i) . . .	Elytral epipleura without setae . . . 8
8	A pair of eversible glands is between abdominal segments 7 and 8 (Figure 9o)	A pair of urogomphi at last abdominal segment only slightly separated at base from each other, divergent (Figure 9h)	Last maxillary palpomere transversely shortened . . . . . . *Gonioctena* Chevrolat, 1836 (subtribe Gonioctenina)
–	No eversible glands between abdominal segments 7 and 8. Mesoterga and metaterga with two rows of sclerites	A pair of urogomphi at last abdominal segment distinctly separated at base from each other by concave line and placed in parallel (Figures 4 and 9i)	Last maxillary palpomere sharpened 9
9	Head capsule with numerous secondary setae similar in length with primary setae. Thoracic and abdominal terga with three transverse rows of sclerites	A pair of urogomphi separated from each other at base by distance twice of their length	Hind wings developed. Elytral punctures confused 10
–	Head capsule with primary setae only or vertex with few secondary setae. Thoracic and abdominal terga with two transverse rows of sclerites (sometimes reduced). Claws with tooth at base	A pair of urogomphi separated from each other at base by distance equal to their length	Hind wings reduced. Elytral punctures arranged in regular rows (at least partly) 11
10	Second transverse row of sclerites on meso-, metaterga and abdominal segments consists of 6 sclerites of equal size. All setae light-coloured, 5 to 10 on each sclerite	Frons with 1 pair of setae, vertex with 10 pairs of short setae	Anterior coxae with closed cavities . . . . *Entomoscelis* Chevrolat, 1836 (subtribe Entomoscelina)
–	Second transverse row of sclerites on meso-, metaterga and abdominal segments consists of 2 sclerites much larger than others. All setae dark, 10 to 20 on each sclerite	Frons and vertex both with 10 pairs of setae	Anterior coxae with open cavities . . . *Colaphellus* Weise, 1916

Table 1. *Cont.*

	Larvae	Pupae	Imagines
11	Meso- and metathorax bear two post-tergal sclerites each. All sclerites of abdominal terga bear one long seta	Body short, oval. Length to width ratio less than 2.0. Urogomphi with two pairs of setae outside (Figure 9i)	Body outline oval. Pronotum as broad as base of elytra, its hind angles acute. Elytral punctures large and sparse, elytral striae (usually striae 6–7) may be irregular at the sides (Figure 10) . . . *Sclerophaedon* Weise, 1882
–	Dorsal setae short, always shorter than length of sclerites. On abdominal terga each pretergal sclerite bears one seta and each post-tergal sclerite bears two or three setae	Body elongate. Length to width ratio more than two. Urogomphi with one pair of setae outside (Figure 4)	Body outline oblong. Pronotum narrower than base of elytra, its hind angles right. Elytral punctures mostly confused and arranged in rows only along suture and lateral margins (Figures 1 and 5) . . . *Apterocuris* Jacobson, 1901

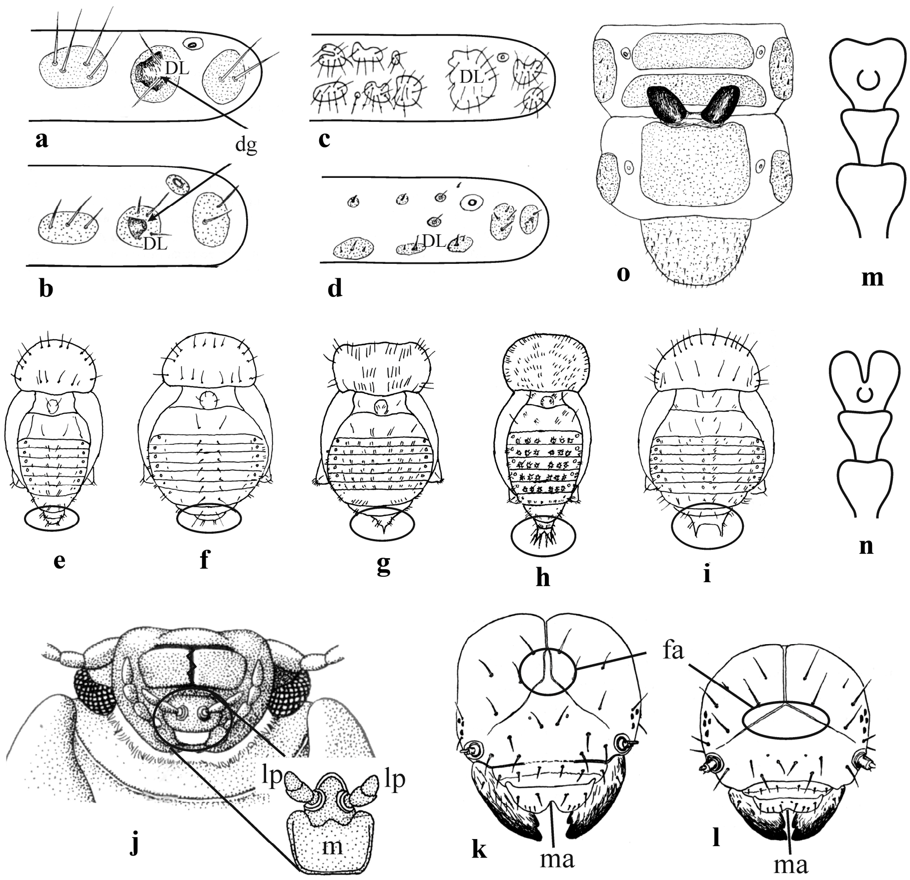

Figure 9. Morphological details of larvae, pupae and adult leaf beetles: (**a**)—abdominal tergum 2 of larva of *Sternoplatys clementzi* Jacobson, 1901 (DL—dorsolateral sclerite; dg–dorsal defensive glands); (**b**)—idem of *Phratora laticollis* (Suffrian, 1851); (**c**)—idem of *Chrysolina carnifex* (Fabricius, 1792); (**d**)—idem of *Apterocuris sibirica* Jacobson, 1901; (**e**)—dorsal view of pupa of *Gastrophysa viridula* (De Geer, 1775); (**f**)—idem of *Phaedon concinnus* Stephens, 1834; (**g**)—idem of *Chrysolina carnifex*; (**h**)—idem of *Gonioctena gobanzi* (Reitter, 1902); (**i**)—idem of *Sclerophaedon carniolicus* Germar, 1824; (**j**)—mentum (m) and labial palpi (lp) of adult *Chrysomela populi* Linnaeus, 1758; (**k**)—head of larva of *Sternoplatys fulvipes* Motschulsky, 1860; (**l**)—idem of *Gastrophysa mannerheimi* Stål, 1858 (fa—frontal arms, ma—median incisure of labrum); (**m**)—tarsus of adult beetle with tarsomere 3 entire apically; (**n**)—idem with tarsomere 3 deeply incised; (**o**)—eversible glands between abdominal segments 7 and 8 of *Paropsides soriculata* Swartz, 1808 (**a**–**d**,**k**,**l**,**o** —modified from Zaitsev and Medvedev [22], **e**–**i**—from Steinhausen [6], **j**—from Chen [30], others—orig.).

Figure 10. Sclerophaedon carpathicus Weise, 1875, male (Ukraine, Transcarpathia, Marmarosh Massif)—habitus in dorsal view. Scale bar—1 mm.

5. Conclusions

The research of the preimaginal phases of leaf beetles are now not as active as before, although for many species and whole genera, our knowledge is far from complete. Here the pupa of *Apterocuris sibirica* was described and this made it possible to find the true position of this genus in the tribe Chrysomelini. It is also a good example how the separate use of imaginal and preimaginal characters may cause incorrect placement of genera in exact tribes or subtribes. The integrative systematic of the subfamily Chrysomelinae shown in the triple comparison of larval, pupal and imaginal characters underlines the most important character states. For larvae, this is the division into groups with or without dorsal openings of defensive glands, while for pupae, these are the groups with no projections on the last abdominal segment or with urogomphi-like single or two-pointed projections (paired urogomphi). For adult beetles, labial palps proved to be the most important character connected with the division of larvae into groups with or without defensive glands. In subtribe Chrysomelina, tarsomere 3 may be either entire apically or distinctly incised. The anterior coxal cavities closed or open posteriorly are also important, especially for distinguishing adults of the subtribe Entomoscelina. The developed or reduced hind wings and elytral punctures, confused or arranged in rows, proved to be less important, secondary features.

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