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The ground beetles of the subgenus *Caucasoharpalus* Kataev, 2023, genus *Harpalus* Latreille, 1802 (Coleoptera: Carabidae)

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Abstract. A taxonomic review of the *Caucasoharpalus* Kataev, 2023, the only subgenus of the genus *Harpalus* Latreille, 1802 (Coleoptera: Carabidae), endemic to the Caucasus, is presented. The subgenus includes three species, one of which, *H. belousovi* **sp. n.**, is newly described from the Svaneti and Racha-Lechkhumi regions (Georgia). This species is parapatric with *H. aeneipennis* (Faldermann, 1836) and forms two subspecies: the nominotypical one (the western part of the Svaneti Mountain Range) and *H. b. conterminus* **subsp. n.** (the southern slopes of the Main Caucasus Range, the eastern Svaneti Mountain Range and the Lechkhumi Mountain Range). The third species, *Harpalus chrysopus* Reitter, 1887 is treated as polytypical, with six subspecies, two of which are newly described, while the rest are presented in a new interpretation: *H. ch. chrysopus*, *H. ch. retowskianus* Reitter, 1887, **stat. n.**, *H. ch. abasinus* Rost, 1891, *H. ch. contumax* Lutshnik, 1933, *H. ch. chkhaltensis* **subsp. n.**, and *H. ch. kodorensis* **subsp. n.** The latter two subspecies are described from the Abkhazian and Kodor ranges, respectively. A key to species and subspecies is provided. Individual, altitudinal and geographical variability of colouration and structural characters of species and subspecies is discussed. It was found that leg colouration and pronotum shape of *H. chrysopus* depend significantly on altitude. A possible scenario for the main moments of formation and differentiation of the subgenus is also discussed. The following synonymy is proposed: *H. ch. retowskianus* Reitter, 1887 = *H. dinniki* Lutshnik, 1933, **syn. n.** The lectotypes are designated for *H. chrysopus* Reitter, 1887 and *H. abasinus* Rost, 1891.

***Key words*:** Caucasus, Harpalini, new species, new subspecies, new status, new synonym.

Жужелицы подрода *Caucasoharpalus* Kataev, 2023 рода *Harpalus* Latreille, 1802 (Coleoptera: Carabidae)

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Резюме. Представлен таксономический обзор *Caucasoharpalus* Kataev, 2023, единственного эндемичного для Кавказа подрода рода *Harpalus* Latreille, 1802 (Coleoptera: Carabidae). Подрод включает три вида, один из которых, *H. belousovi* **sp. n.**, описан из Сванетии и Рача-Лечхумского региона (Грузия). Этот вид является парапатрическим по отношению к *H. aeneipennis* (Faldermann, 1836) и формирует два подвида: номинативный (западная часть Сванетского хребта) и *H. b. conterminus* **subsp. n.** (южные склоны Главного Кавказского хребта, восток Сванетского хребта и Лечхумский хребет). Третий вид, *Harpalus chrysopus* Reitter, 1887, рассматривается как политипический с шестью подвидами, два из которых описаны как новые, а остальные представлены в новой интерпретации: *H. ch. chrysopus*, *H. ch. retowskianus* Reitter, 1887, **stat. n.**, *H. ch. abasinus* Rost, 1891, *H. ch. contumax* Lutshnik, 1933, *H. ch. chkhaltensis* **subsp. n.** и *H. ch. kodorensis* **subsp. n.** Два новых подвида описаны с Абхазского и Кодорского хребтов соответственно. Предложена определительная таблица для видов и подвидов. Обсуждается индивидуальная, высотная и географическая изменчивость окраски и структурных признаков. Показана значительная зависимость окраски ног и формы переднеспинки от высоты. Также обсуждается возможный сценарий основных моментов формирования и дифференциации подрода. Предложена следующая синонимия: *H. ch. retowskianus* Reitter, 1887 = *H. dinniki* Lutshnik, 1933, **syn. n.** Для *H. chrysopus* Reitter, 1887 и *H. abasinus* Rost, 1891 обозначены лектотипы.

***Ключевые слова*:** Кавказ, Harpalini, новый вид, новый подвид, новый статус, новый синоним.

Introduction

Caucasoharpalus Kataev, 2023 is the only subgenus of the genus *Harpalus* Latreille, 1802, endemic to the Caucasus. All representatives of the subgenus are obligatory wingless, live both in the foothills and in the mountains, and demonstrate extremely high morphological variability, not only individual and geographical, but also altitudinal. All this creates significant difficulties in recognizing distinct taxa within this group. Although the number of described species reached six in the first half of the last century, by the end of the century most of them had been downgraded to subspecies or their names were considered synonyms. Only two species, *H. aeneipennis* (Faldermann, 1836) and *H. chrysopus* Reitter, 1887, were then recognized, and the latter species was treated as polytypical with three subspecies: *H. ch. chrysopus*, *H. ch. abasinus* Rost, 1891 and *H. ch. contumax* Lutshnik, 1933, but no convincing justification was provided for this [Kataev, 1995b]. The study, which began 40 years ago, was delayed due to a number of unresolved issues. Further research, including additional route collections in various regions of the Caucasus, made it possible to clarify the variability, distribution, and status of many forms distingwished within this subgenus. The results of this study form the basis of this contribution, which presents a taxonomic review of the subgenus *Caucasoharpalus*, with description of a new species and three new subspecies.

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Material and methods

More than 1775 specimens of *Caucasoharpalus*, including most of the types, were examined.

Standard methods were applied for treating the material. A total of 190 specimens were measured. Measurements were made under the stereomicroscope LOMO MBS 10 using an ocular-micrometer and were taken as follows: body length (L), measured from the anterior margin of the clypeus to the elytral apex; maximum width of head (HWmax), measured as the maximum linear distance across the head, including the compound eyes; minimum width of head (HWmin), measured as the minimum linear distance across the head, which in this case corresponds to the neck constriction just behind the eyes; length of pronotum (PL), measured along its median line; length of elytra (EL), measured from the basal border near scutellum to the apex of the sutural angle; maximum width of pronotum (PWmax) and elytra (EW), both measured at their broadest points; apical width of pronotum (PWap), measured between the apical angles; basal width of pronotum (PWbas), measured between the hind angles; width and length of metepisternum, measured along its anterior and inner margins, respectively; *m* = mean; *n* = number of specimens.

Male and female genitalia were examined in glycerin and then either embedded in Euparal or dried and glued on a piece of hard paper pinned under the beetle. For ease of the location of certain structures of the internal sac of the aedeagus (basal spiny patches), they are conventionally designated in the figures by the letters *a* and *b*.

To assess the dependence of leg colouration in *Harpalus chrysopus* on altitude, a table was compiled listing all localities where it was found, their altitudes, and the numbers of individuals of each colour variant (reddish-brown legs, black legs, and black femora and reddish-brown tibiae). The analysis was performed using ordinal and multinomial logistic regression. The first approach assumes that the three colour states form an ordered sequence (implemented via the MASS package in R), whereas the second treats them as independent categories (implemented via the nnet package in R).

The drawings were prepared using an ocular grid (10 × 10 squares) attached to the above-mentioned stereomicroscope. Most of the photographs were taken with a Canon EOS 6 D camera with a Canon MPE 65 mm lens, and subsequently processed using the Helicon Focus 7.2 software and optimized with Photoshop® CS2; the habitus photograph of the syntype of *Omaseus aeneipennis* was taken with a Canon PowerShot A710 IS camera and also optimized with Photoshop® CS2. Maps were prepared in CorelDRAW X3 using OSM data in SAS.Planet ver. 141212.8406 as the cartographic basis. The maps also include some records from literary sources [Iablokoff-Khnzorian, 1976; Zamotajlov, 1992; Reck, Chaladze, 2004; Zamotajlov, Makaov, 2010].

The following abbreviations are used for the depositories of the specimens examined:

MFNB – Museum für Naturkunde Berlin (Germany);

MNHN – Muséum National d'Histoire Naturelle (Paris, France);

MPSU – Moscow Pedagogical State University (Moscow, Russia);

OÖLL – Oberösterreichisches Landesmuseum (Linz, Austria);

SMTD – Staatliches Museun für Tierkunde (Dresden, Germany);

TMB – Természettudományi Múzeum (Budapest, Hungary);

ZIN – Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia);

ZMMU – Zoological Museum at Moscow State University (Moscow, Russia);

cAA – collection of A.V. Anichtchenko (Daugavpils, Latvia);

cAK – collection of A.G. Koval (Saint Petersburg, Russia);

cAP – collection of A.V. Putchkov (Kiev, Ukraine);

cAPZ – collection of A. Pütz (Eisenhüttenstadt, Germany);

cAR – collection of A.I. Roubchenya (Minsk, Belarus);

cAT – collection of A.S. Tilli (Samara, Russia);

cAZ – collection of A.S. Zamotajlov (Krasnodar, Russia);

cFM – collection of F.V. Melyakh (Ekaterinburg, Russia);

cIAS – collection of I.A. Solodovnikov (Vitebsk, Belarus);

cIB – collection of I.A. Belousov (Saint Petersburg, Russia);

cIMS – collection of I.M. Sokolov (Washington, USA);

cMD – collection of M.L. Danilevsky (Moscow, Russia);

cMK – collection of M.Yu. Kalashian (Yerevan, Armenia);

cVK – collection of V.G. Knysh (Krasnodar, Russia);

cVM – collection of V.A. Matsyuk (Tiraspol, Pridnestrovian Moldavian Republic);

cVS – collection of V.A. Stolbov (Tyumen, Russia);

cVSH – collection of V.G. Shilenkov (Irkutsk, Russia);

cVZ – collection of V. Zieris (Pardubice, Czech Republic);

cWR – working coll. D.W. Wrase (part of Zoologische Staatssammlung München) (Gusow-Platkow, Germany).

Genus *Harpalus* Latreille, 1802
Subgenus *Caucasoharpalus* Kataev, 2023

Caucasoharpalus Kataev, 2023: 54 (type species *Omaseus aeneipennis* Faldermann, 1836, by original designation).

Diagnosis. Medium-sized (length 7.4–11.1 mm). Body slightly elongate, moderately convex, dark brown to black, with or without metallic luster. Head impunctate and glabrous. Pronotal basal edge glabrous. Elytra impunctate and glabrous, with glabrous basal border and prominent humeral denticle (Figs 1–3); preapical sinuation moderately to very deep, with more or less prominent denticle at its base (Figs 20–23, 38–41, 79–84, 136–139); intervals 7, 5 and 3 with or without preapical setigerous pores. Metepisternum short and wide, wider than long (Figs 1–3). Tarsi glabrous dorsally or, particularly male pro- and mesotarsomeres, with very short, sparse setae. Three last abdominal

sternites glabrous, only with obligatory setae. Median lobe of aedeagus with a moderately long terminal lamella and an oblique or botton-like apical capitulum; internal sac of aedeagus with two separate closely spaced macrospines apically, a group of small or medium-sized spines medially and a few spiny patches apically and/or basally.

Additional description. Head dorsally and elytra occasionally micro-punctate. Microsculpture on head absent; disc of pronotum either smooth, with fine, almost isodiametric meshes along lateral margin, or with fine, more or less obliterate, slightly transverse meshes almost throughout; elytra with isodiametric meshes, in female distinct, in male distinct or more or less strongly obliterate on inner intervals.

Eyes large and convex, separated from buccal fissure by distance slightly exceeding width of scapus. Supraorbital pore situated at level of posterior margin of eye at distance of approximately diameter of pore from supraorbital furrow. Postgenae with a few very fine and short setae. Mentum with prominent median tooth. Submentum with one pair of long lateral setae. Antennae extending beyond basal edge of pronotum or, especially in females, slightly shorter.

Pronotum widest before middle, moderately or deeply arcuately emarginate along apical margin and with prominent apical angles narrowly rounded at tip; basal margin almost straight, or emarginate along entire length, or concave at middle and oblique laterally; sides from rounded to sinuate basally, normally with one seta; basal angles from acute to widely rounded; disc more or less widely punctate at least basally, occasionally punctation restricted to basal foveae; lateral impressions at most present only at base, narrow and shallow; basal foveae somewhat shallow, separated from lateral margin and from each other by convexities. Pro-, meso- and metasternum with very fine and short setae.

Elytra more or less oval, rounded at sides; sutural angle almost right, in male often blunted at tip, in female occasionally elongate, forming an acute spine; basal border slightly sinuate or almost straight, forming an obtuse angle with lateral bead; parascutellar (abbreviate) striole moderately long, with or without basal setigerous pore; striae impunctate, deepened along entire length, in male more strongly and intervals correspondingly more convex than in female; in both sexes intervals only slightly narrowed at apex; interval 3 generally with one discal setigerous pore.

Legs comparatively slender and long for the genus. Metacoxa with only two obligarory setigerous pores, without additional pores. Metatrochanter with one setigerous pore. Metafemur with three or four setigerous pores along posterior margin and with one to four such pores on ventral surface at apical margin, more rarely without them. Protibia with one ventroapical spine and with three (occasionally four) preapical spines on outer margin, isolated from spines on ventral surface of protibia; ventroapical tubercle in male not developed. Male mesotibia without preapical callous thickening on inner margin. Metatarsi slender, with elongate tarsomeres. Tarsomere 5 with four, occasionally three pairs of lateral setae ventrally, male pro- and mesotarsomeres 1–4 markedly widened and with biseriate adhesive vestiture ventrally.

Abdominal visible sternite 2 between metacoxae and sternite 3 medially with very fine and short setae; other abdominal sternites glabrous, only with obligatory setae; last visible sternite without pronounced sexual dimorphism, its apex in both sexes more or less rounded and not swollen, at most subtruncate in male.

Female genitalia uniform (Figs 4–15): laterotergite almost symmetrical, with two or three (more rarely one or four) setae apically; gonosubcoxite widened apically, mostly with three very short setae on outer distal corner; gonocoxite strongly arcuate, with one or several very fine setae on dorsal outer edge.

Armament of the internal sac of the aedeagus is very similar in all taxa, with the exception of the small basal spiny patches (*a* and *b*), as indicated in Figs 24, 25, 42, 43, 109, 110, which (at least one of them) are constantly present in *H. aeneipennis* and *H. belousovi* **sp. n.** and variable in *H. chrysopus*.

Due to high individual and geographic variability, the body size and proportions are very similar among different species (Table 1).

These characters, common to all taxa of the subgenus, are not repeated in the descriptions of species and subspecies given below, which include mainly only distinctive characters.

Notes. The subgenus *Caucasoharpalus* belongs to the *Amblystus* subgroup sensu Kataev [2023], which comprises several Palaearctic subgenera with morphologically distinct, mountain wingless species, in some cases geographically distant from each other. For a long time, representatives of *Caucasoharpalus* were considered to constitute the majority of the former subgenus *Harpaloxys* Reitter, 1900, which originally also included the more distinct and geographically separated Iberian *Harpalus cardiaderus* Putzeys, 1872 (= *H. ebeninus* Heyden, 1870). The unnaturalness of such a combining was noted long ago, for example, by Lutshnik [1922], who insisted on the need to include Iberian and Caucasian species in different subgenera. Meanwile, after *H. cardiaderus* was designated by Noonan [1976] as the type species of *Harpaloxys*, a new subgenus, *Caucasoharpalus*, was subsequently erected for the Caucasian species [Kataev, 2023]. The designation of the Caucasian *H. aeneipennis* (Faldermann, 1836) as the type species of *Harpaloxys* by Iablokoff-Khnzorian [1976], made almost simultaneously with Noonan, but actually later, was invalid [Kataev, 1995a].

Caucasoharpalus is morphologically very similar to the subgenus *Epiharpalus* Reitter, 1900 (= *Harpaloxys*), which includes two species from the West Mediterranean, but differs from it in the narrower and more convex body shape, a deeper preapical sinuation of the elytra with a more prominent denticle at the base and the characteristic male genitalia. *Harpalus punctipennis* Mulsant, 1852, the type species of *Epiharpalus*, additionally differs in its coarsely punctate and pubescent elytra and finely pubescent abdominal sternites. The male genitalia of both species of *Epiharpalus* are illustrated in Kataev [2023: figs 32c, d, 32e, f]. Among the Caucasian *Harpalus*, the members of *Caucasoharpalus* are easily recognized by their very short, transverse metepisternum in combination with a glabrous basal pronotal edge and glabrous abdominal sternites. Similar shape of metepisternum is also characteristic of *H.* (*Brachyharpalus*) *reflexus* Putzeys, 1878 and *H.* (*B.*) *kazanensis* Jedlička, 1958, recorded from Transcaucasia, but they are easily distinguished by the presence of a fringe of short setae on the pronotal basal edge and additional long setae on the abdominal sternites.

The aberrant state of chaetotaxy on the pronotum (additional lateral setigerous pores) and elytra (additional discal setigerous pore on interval 3), known for many species of *Harpalus*, occurs in species of *Caucasoharpalus*, though rare, but more often than in species of most other subgenera. Such aberrations can be either unilateral or bilateral, more or less symmetrical (Fig. 37). In particular, an additional lateral pore before the basal angle of the pronotum is present in the syntype of *Omaseus aeneipennis* on the right

Table 1. Variation of length and body proportions (average value in brackets) in species and subspecies of the subgenus *Caucasoharpalus*, genus *Harpalus*.
Таблица 1. Длина и пропорции тела (в скобках среднее значение) видов и подвидов подрода *Caucasoharpalus* рода *Harpalus*.

Parameter Показатель	*H. aeneipennis*	*H. belousovi* **sp. n.**	*H. b. belousovi* **subsp. n.**	*H. b. conterminus* **subsp. n.**	*H. chrysopus*
Number of specimens measured / Количество измеренных экземпляров	7♂, 7♀	17♂, 9♀	8♂, 5♀	9♂, 4♀	81♂, 69♀
L (mm)	7.5–11.1 (9.7) ♂ 7.5–10.7 (10.1) ♀ 8.5–11.1 (9.3)	8–10.2 (8.9) ♂ 8–9.7 (8.8) ♀ 8.4–10.2 (8.9)	8–10.2 (8.8) ♂ 8–9.1 (8.6) ♀ 8.5–10.2 (9)	8.1–9.7 (8.9) ♂ 8.1–9.7 (8.9) ♀ 8.4–9.2 (8.8)	7.4–10.7 ♂ 7.4–10.7 ♀ 7.5–10.5
L/EW	2.23–2.61 (2.45) ♂ 2.49–2.61 (2.55) ♀ 2.23–2.43 (2.35)	2.16–2.55 (2.38) ♂ 2.22–2.55 (2.42) ♀ 2.16–2.41 (2.29)	2.27–2.55 (2.41) ♂ 2.35–2.55 (2.45) ♀ 2.27–2.41 (2.33)	2.16–2.52 (2.35) ♂ 2.22–2.52 (2.39) ♀ 2.16–2.32 (2.25)	2.17–2.61 (2.37) ♂ 2.18–2.58 (2.39) ♀ 2.17–2.61 (2.34)
HWmax/PWmax	0.69–0.76 (0.72) ♂ 0.69–0.72 (0.71) ♀ 0.72–0.76 (0.74)	0.69–0.81 (0.72) ♂ 0.69–0.81 (0.71) ♀ 0.71–0.76 (0.73)	0.69–0.81 (0.72) ♂ 0.69–0.81 (0.72) ♀ 0.71–0.76 (0.74)	0.7–0.74 (0.72) ♂ 0.7–0.72 (0.71) ♀ 0.72–0.74 (0.73)	0.67–0.79 (0.72) ♂ 0.67–0.77 (0.72) ♀ 0.68–0.79 (0.73)
HWmin/PWmax	0.55–0.62 (0.59) ♂ 0.55–0.61 (0.58) ♀ 0.60–0.62 (0.61)	0.56–0.65 (0.59) ♂ 0.56–0.65 (0.58) ♀ 0.58–0.65 (0.61)	0.56–0.65 (0.59) ♂ 0.56–0.65 (0.58) ♀ 0.58–0.63 (0.61)	0.56–0.65 (0.58) ♂ 0.56–0.58 (0.57) ♀ 0.6–0.65 (0.61)	0.54–0.68 (0.59) ♂ 0.54–0.68 (0.57) ♀ 0.56–0.66 (0.61)
HWmax/HWmin	1.18–1.26 (1.22) ♂ 1.18–1.26 (1.23) ♀ 1.19–1.25 (1.22)	1.15–1.28 (1.23) ♂ 1.20–1.28 (1.24) ♀ 1.15–1.24 (1.2)	1.18–1.27 (1.23) ♂ 1.2–1.27 (1.24) ♀ 1.18–1.24 (1.21)	1.15–1.28 (1.23) ♂ 1.22–1.28 (1.25) ♀ 1.15–1.21 (1.19)	1.03–1.31 (1.23) ♂ 1.03–1.31 (1.25) ♀ 1.14–1.29 (1.21)
PWmax/PL	1.45–1.56 (1.49)	1.36–1.58 (1.51)	1.49–1.58 (1.54)	1.36–1.56 (1.48)	1.41–1.64 (1.53)
PWmax/PWbas	1.11–1.3 (1.21)	1.18–1.27 (1.21)	1.18–1.24 (1.21)	1.18–1.27 (1.22)	1.13–1.35 (1.23)
PWmax/PWap	1.31–1.46 (1.39)	1.29–1.45 (1.38)	1.29–1.43 (1.36)	1.29–1.45 (1.39)	1.28–1.49 (2.38)
PWap/PWbas	0.83–0.94 (0. 87)	0.84–0.96 (0.88)	0.84–0.93 (0.89)	0.84–0.96 (0.88)	0.8–0.98 (0.89)
PWbas/HWmax	1.08–1.23 (1.15) ♂ 1.08–1.2 (1.15) ♀ 1.09–1.23 (1.16)	1.02–1.2 (1.15) ♂ 1.02–1.2 (1.15) ♀ 1.09–1.17 (1.14)	1.02–1.2 (1.14) ♂ 1.02–1.2 (1.15) ♀ 1.1–1.16 (1.14)	1.09–1.18 (1.15) ♂ 1.1–1.18 (1.15) ♀ 1.09–1.17 (1.14)	1.03–1.23 (1.13) ♂ 1.03–1.23 (1.13) ♀ 1.05–1.19 (1.12)
EL/EW	1.37–1.56 (1.44) ♂ 1.43–1.56 (1.49) ♀ 1.37–1.41 (1.39)	1.25–1.5 (1.41) ♂ 1.32–1.5 (1.43) ♀ 1.25–1.41 (1.36)	1.36–1.48 (1.42) ♂ 1.41–1.48 (1.45) ♀ 1.36–1.41 (1.39)	1.25–1.5 (1.39) ♂ 1.32–1.5 (1.42) ♀ 1.25–1.39 (1.33)	1.29–1.5 (1.41) ♂ 1.29–1.5 (1.42) ♀ 1.31–1.48 (1.39)
EL/PL	2.44–2.65 (2.55) ♂ 2.47–2.62 (2.53) ♀ 2.44–2.65 (2.56)	2.22–2.78 (2.53) ♂ 2.4–2.78 (2.53) ♀ 2.22–2.64 (2.54)	2.4–2.78 (2.6) ♂ 2.4–2.78 (2.58) ♀ 2.59–2.64 (2.62)	2.22–2.56 (2.46) ♂ 2.43–3.51 (2.48) ♀ 2.22–2.56 (2.43)	2.31–2.82 (2.59) ♂ 2.31–2.77 (2.57) ♀ 2.42–2.82 (2.61)
EW/PWmax	1.1–1.27 (1.19) ♂ 1.1–1.19 (1.15) ♀ 1.22–1.27 (1.24)	1.12–1.31 (1.2) ♂ 1.12–1.25 (1.17) ♀ 1.2–1.31 (1.25)	1.12–1.26 (1.19) ♂ 1.12–1.21 (1.16) ♀ 1.2–1.26 (1.23)	1.13–1.31 (1.2) ♂ 1.13–1.25 (1.17) ♀ 1.21–1.31 (2.27)	1.12–1.33 (1.21) ♂ 1.12–1.26 (1.19) ♀ 1.16–1.33 (1.23)
EW/HWmax	1.54–1.71 (1.65) ♂ 1.54–1.66 (1.61) ♀ 1.65–1.71 (1.68)	1.47–1.79 (1.66) ♂ 1.47–1.74 (1.64) ♀ 1.61–1.79 (1.71)	1.46–1.74 (1.64) ♂ 1.47–1.73 (1.62) ♀ 1.61–1.74 (1.68)	1.59–1.79 (1.68) ♂ 1.58–1.74 (1.65) ♀ 1.68–1.79 (1.74)	1.55–1.81 (1.67) ♂ 1.55–1.77 (1.66) ♀ 1.56–1.81 (1.68)

side (Fig. 18) and in the holotype of *H. contumax* on the left side (Fig. 75). These pores are apparently homologous to similar pores in *H.* (*Licinoderus*) *chobautianus* Lutshnik, 1922 and *Ophonus* (*Metophonus*) *laticollis* Mannerheim, 1825, as well as in some less related harpalines, for example *Progonochaetus* G. Müller, 1838, in which this character is constant.

The only key to this subgenus was published by Reitter [1900], which included four species recognized in that time, differring mostly in colour, the shape of the pronotum and preapical setation of the elytral intervals. Later, Lutshnik [1933] described two new species. All these species were based on very limited material. Lutshnik probably intended to continue studying the taxonomy of this group, since, judging by the determinational labels in his former collection (now in ZIN), he also designated for description, but did not publish, several intraspecific forms from Krasnodar Region of Russia as aberrations. Similarly, judging by the determinational labels in Schauberger's former collection (now in OÖLL), this author intended to describe several new species from Abkhazia and Georgia.

Composition. The subgenus includes three species: *H. aeneipennis*, *H. belousovi* **sp. n.**, and *H. chrysopus*; the latter two are polytypical: *H. belousovi* **sp. n.** with two subspecies (the nominotypical and *H. b. conterminus* **subsp. n.**),

and *H. chrysopus* with six subspecies (*H. ch. chrysopus*, *H. ch. retowskianus* Reitter, 1887b, **stat. n.**, *H. ch. abasinus*, *H. ch. contumax*, *H. ch. chkhaltensis* **subsp. n.**, and *H. ch. kodorensis* **subsp. n.**).

Distribution. Species of this subgenus are distributed in the North-West Caucasus and Transcaucasia: in the northwest to Krasny Les and Krasnodar in Russia, and in the east to the Kodori Pass on the southern slope of the Main Caucasus Range in Georgia. The southern border of the subgenus range reaches the southern slopes of the Meskheti Range in Georgia and the northern shore of Lake Sevan in Armenia. The species occur from the lower forest to the alpine zone; in the forest zone, both in forests and on forest edges.

Key to species and subspecies

1. Dorsum at least partially bright metallic, legs (at least femora and tibiae) black or dark brown. Pronotal disc impunctate anteriorly or with very fine, almost indistinct punctures between lateral margins and median line. Odd elytral intervals without preapical setigerous pores. Median lobe of aedeagus in lateral view relatively narrower (Figs 24–31, 42–52) 2
– Dorsum black, not metallic, at most with very light bluish green shine, legs black or reddish brown. Pronotal disc more or less distinctly punctate anteriorly between lateral margins and median line or punctation there very fine, almost indistinct. Odd elytral intervals with or without preapical setigerous pores. Median lobe of aedeagus in lateral view relatively wider (Figs 85–98, 107–117, 122–129, 140–145) ..... *H. chrysopus* (4)
2. Median lobe of aedeagus in lateral view less arcuate, its dorsal margin more or less sinuate at middle and apical capitulum botton-like (Figs 24–31). Basal pronotal angles more or less widely rounded (Figs 16–19). Transcaucasia, with exception of Svaneti and Racha-Lechkhumi regions ..... *H. aeneipennis*
– Median lobe of aedeagus in lateral view more arcuate, its dorsal margin rounded at middle and apical capitulum oblique (Figs 42–52). Basal pronotal angles rounded to more or less angulate (Figs 32–37). Central Caucasus: Svaneti and Racha-Lechkhumi regions .... *H. belousovi* **sp. n.** (3)
3. Aedeagus in lateral view with terminal lamella slightly curved ventrally, median lobe relatively wider in middle portion (Figs 42, 44, 45). Basal pronotal angles more or less angulate, blunted or narrowly rounded at tip (Figs 32, 33, 36). Svaneti Mountain Range, west of Latpari Pass ..... *H. belousovi belousovi* **subsp. n.**
– Terminal lamella of aedeagus in lateral view not curved ventrally, straight or slightly curved dorsally, median lobe relatively narrower in middle portion (Figs 46, 47, 49–51). Basal pronotal angles obtuse, more or less rounded at tip (Figs 34, 35, 37). Southern slopes of Main Caucasus Range from Mestia to Chiora, eastern Svaneti Mountain Range and southern Lechkhumi Mountain Range .... *H. belousovi conterminus* **subsp. n.**
4. Elytra generally without parascutellar pore (Fig. 135), and intervals 7 and 5 generally with preapical setigerous pores (as in Figs 136, 137). Body black, often with light greenish blue shine on dorsum, legs black or dark brown. Median lobe of aedeagus without basal spiny patches in internal sac on left side (Figs 140–143). Abkhazian and northeastern Chedym ranges .... *H. chrysopus chkhaltensis* **subsp. n.**
– Elytra with parascutellar pore (Fig. 134), intervals 7 and 5 with or without preapical setigerous pores. Body black, generally without light greenish blue shine on dorsum, legs black or reddish brown. Median lobe of aedeagus with or without basal spiny patches (*a* and *b*, as indicated in Figs 109, 110) in internal sac on left side 5
5. Median lobe of aedeagus generally with one or two small basal spiny patches (*a* and *b*) in internal sac on left side (Figs 107–117, 122–129), and elytral interval 7 in most specimens, often also 5 and rarely 3, with one or several (up to seven) preapical setigerous pores (Figs 81–84) 6
– Median lobe of aedeagus without small basal spiny patches in internal sac on left side (Figs 86, 88, 89, 91–98, 140–145). Elytra without preapical pores on intervals 7 and 5, or at most with one to three preapical setigerous pores, often only on one elytron 7
6. Aedeagus in lateral view with terminal lamella curved ventrally; ventral margin of median lobe generally with more or less distinct preapical sinuation (Figs 107, 109, 111, 113, 115, 116). Western Caucasus from Mzymta River to south of Abkhazian Mountain Range, with exception of southern part of Gagra Mountain Range ..... *H. chrysopus abasinus*
– Terminal lamella of aedeagus generally not curved ventrally, straight or slightly curved dorsally; ventral margin of median lobe generally without preapical sinuation (Figs 122, 124–128). Foothills and southern part of Gagra Mountain Range from Mzymta River to Bsyb River ..... *H. chrysopus contumax*
7. Pronotal basal angles obtuse, blunted or more or less rounded at tip (Figs 76–78). Body less elongate, with relatively wider elytra (Figs 132, 133). Legs black or dark brown. Terminal lamella of aedeagus in dorsal view slightly more widened apically (Fig. 145). Kodor Mountain Range ..... *H. chrysopus kodorensis* **subsp. n.**
– Pronotal basal angles almost right or slightly obtuse, at most slightly blunted at tip (Figs 64–69). Body more elongate, with relatively narrower elytra (Figs 60–63, 118). Legs reddish brown to black. Terminal lamella of aedeagus in dorsal view less widened apically (Figs 89, 93, 95). North-West Caucasus, north of Mzymta River 8
8. Aedeagus in lateral view with terminal lamella curved ventrally; ventral margin of median lobe generally with more or less distinct preapical sinuation (Figs 94, 96–98). North-West Caucasus between Achishkho and Bolshoy Tkhach ..... *H. chrysopus retowskianus*
– Terminal lamella of aedeagus not curved ventrally, straight or slightly curved dorsally; ventral margin of median lobe generally without ptreapical sinuation (Figs 85–88, 90–92). Foothills and mountains of the North-West Caucasus, north-west of Mzymta River .... *H. chrysopus chrysopus*

Harpalus (*Caucasoharpalus*) *aeneipennis* (Faldermann, 1836) (Figs 1, 4–7, 16–19, 20–31, 53)

Omaseus aeneipennis Faldermann, 1836: 54 (type locality: "Persico-Armeniaca" (inferred from title of the book)).

Harpalus aeneipennis: Chaudoir, 1846: 172; Marseul, 1880: 250; Csiki, 1932: 1151; Lutshnik, 1939: 194; Kryzhanovskij et al., 1995: 142; Reck, Chaladze, 2004: 148.

Harpalus (*Harpaloxys*) *aeneipennis*: Reitter, 1900: 95; Lutshnik, 1922: 61; Iablokoff-Khnzorian, 1976: 250, 262.

Harpalus (*Harpalus*) *aeneipennis*: Iablokoff-Khnzorian, 1961: 219; Lorenz, 1998: 344; Lorenz, 2005: 365; Kataev et al., 2003: 371; Kataev, Wrase, 2017: 521.

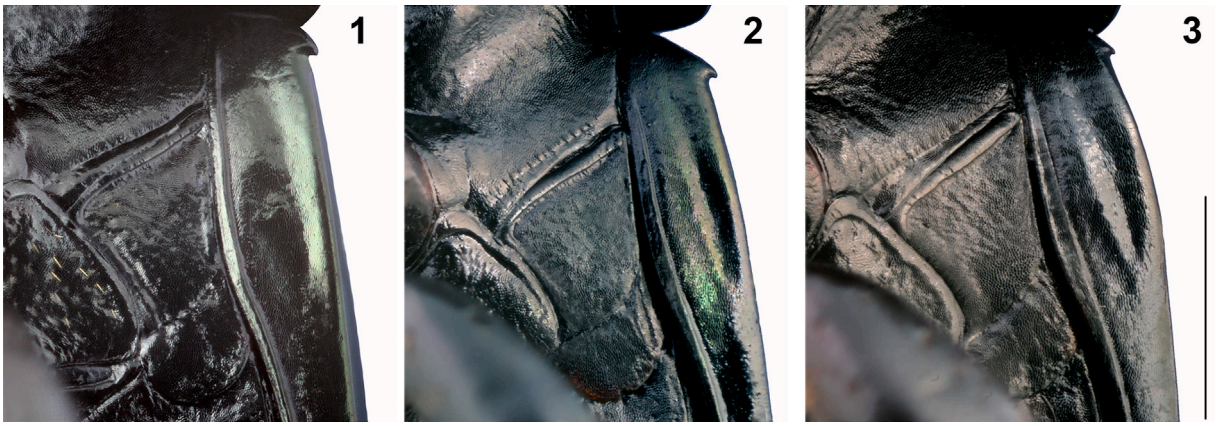
Harpalus (*Caucasoharpalus*) *aeneipennis*: Kataev, 2023: 54.

Type material. 1♀, syntype (MNHN (former Chaudoir's collection)) (Fig. 18), "*aeneipennis* Falderm. (*Omaseus*) Transcaucasie Bayern" (bottom label), "type de Faldermann".

Material. 1♂ (ZIN), with rectangular piece of golden paper, "Caucasus", "*metallicus* Chaud. ? Caucas." (Ménétriés' handwriting, this taxon was not described); 1♂, 2♀ (ZIN), "Kaukas Leder 119"; 1♂ (ZIN), "Transcaucasia"; 1♂ (OÖLL), "Caucasus", "*H. pseudaeneipennis* Schaub" (this taxon was not desribed).

Abkhazia. 1♂ (OÖLL), "G[?]omlja [18]88 K...", "*H. coortis* Schaub." (this taxon was not desribed); 1♂ (ZIN), "Abkhasia Rost. 1892"; 3♂, 4♀ (OÖLL), "Abchasien Ca. Carl Rost", "Anara [18]97", "*Harpalus abchasicus* Schaub." (this taxon was not described). Gagra Distr.: 1♂ (ZIN), "ур. Доулаквара, оз. Ридза, Сух. о., 8.IX.11. Н. Брянск" (isolated terrain feature Doulakvara, Lake Ritsa, Sukhum Province, 8.09.1911. N. Bryanskiy); 1♀ (MPSU), Pitsunda env., 17.09.1991 (V. Semenov). Gudauta Distr.: 1 ex. (MFNB), Mts near Otkhara (F. Hieke); 1♂ (cAK), Aapsta Valley, 350 m, soil tarps, 1.06–5.07.1985 (A.G. Koval); 1♀ (cAK), Otkhara env., forest, ca 500 m, 29.06–5.07.1985 (A.G. Koval); 1♂ (ZIN), Bzyb Mt. R., Khuap vill. env., forest, soil traps, 31.05–26.07.1986 (A.G. Koval); 1♂ (cAK), Gudauta Distr., Kaldakhvara env., soil traps, 1.06–26.07.1986 (A.G. Koval); 1 ex. (cAK), Mugudzyrkhva env., soil traps, 7.06–26.07.1987 (A.G. Koval); 1♂ (cIB), Bzyb Mt. R., N Khuap vill., 1800 m, 23–24.07.1987 (I.A. Belousov); 1♂, 1♀ (ZMMU), Bzyb Mt. R., W macroslope of Mt. Chibzhagra, 43°17′43″N / 40°24′40″E, beech forest, 395 m, 9.06.2004 (A.A. Gusakov). Gulripsh Distr.: 1 ex. (MFNB), Lake Amtkel env. (Schaarschmidt); 1♂ (ZIN), "Ажары у Чхатлы на Кодоре, Сухум. Калишевс. 21.07.1905" (Azhara near Chkhalta at Kodor, Sukhum. Kalishevskiy); 2♂, 1♀ (ZIN), "Ю скл. Клухора, красн. будка на ключе, 5–6.IX.09" (S slope of Klukhor Pass, red booth at spring, 5–6.09.1909); 2♂, 2♀ (ZIN), Abkhazian Mt. R., Chkhalta, soil traps, 1986 (A.S. Zamotajlov); 1♂, 1♀ (ZIN), Abkhazian Mt. R., Atsgara, soil traps, 1986 (A.S. Zamotajlov); 1♂ (ZIN), Abkhazian Mt. R., Dzhampal Gorge, ca 800 m, 1.09.1986 (V.N. Prasolov); 2♂, 2♀ (ZIN), Abkhazian Mt. R., Chamagvara, 1000–1300 m, forest zone, 6.06.1989 (B.M. Kataev); 1♂ (ZIN), Abkhazian Mt. R., Shoudidi River, forest zone, 12.06.1989 (B.M. Kataev); 3♂, 4♀ (ZIN), Chkhalta River valley from Shoudidi River to Pekh River, 12.06.1989 (B.M. Kataev); 1♂, 1♀ (ZIN), Kelasur River, 43°06′20.1″N / 41°11′11.6″E, 700 m, 05.2012 (E.E. Khomitskiy); 4♂ (ZIN), S env. of Lake Amtkel, 43°05′10.49″N / 41°17′46.92″E, 500 m, 19.05–17.07.2012 (D.D. Fominykh). Ochamchira Distr.: 1♀ (ZIN), Galidzga River valley, Khodzhal env., 960 m, 16.06.1982 (V.I. Drabkin); 4♂ (cAK, ZIN), Kodor Mt. R., Bolshoy Khodzhal River valley, ca 1200 m, 27.06.1986 (A.G. Koval); 2♂, 3♀ (cIB), Tkvarchal, Khodzhal, 15.07.1986 (I.A. Belousov). Tkvarchal Distr.: 6♂, 4♀ (cIB), Kodor Mt. R.,Tkvarchal, Mine 5, 1000 m, 16.07.1986 (I.A. Belousov); 4♂, 3♀ (ZIN), S spur of Akiba Mt. R., middle of Okumi River, 500–1000 m, 1.05.1989 (I.A. Belousov, B.M. Kataev); 8♂, 3♀ (ZIN, cIB), same data but 1000–1800 m, 2.05.1989 (I.A. Belousov, B.M. Kataev); 1♀ (ZIN), Akiba Mt. R., source of Tsarche River, upper forest zone, 10.05.1989 (I.A. Belousov, B.M. Kataev).

Georgia. Samegrelo-Zemo Svaneti: 19♂, 8♀ (ZIN), Akiba Mt. R., Mt. Akhachkhu (= Okhachkue), alpine and upper forest zone, 4.05.1989 (I.A. Belousov, B.M. Kataev); 2♂, 7♀ (ZIN, cIB), Akiba Mt. R., S slope of Mt. Akhachkhu (= Okhachkue), middle forest zone, 5.05.1989 (I.A. Belousov, B.M. Kataev); 3♂ (ZIN), Akiba Mt. R., NW slope of Mt. Akhachkhu (= Okhachkue), 8.05.1989 (I.A. Belousov, B.M. Kataev). Samegrelo-Zemo Svaneti: 1♂ (ZIN), Megrel (Egrisi) Mt. R., 1800 m, 10.09.1962 (Ya. Dzhambazishvili); 2♂, 2♀ (ZIN), Megrel (Egrisi) Mt. R., upper Intsira River, Mt. Khvira, 29.05.1988 (B.M. Kataev); 1♀ (cIB), W part of Egrisi Mt. R., SW slope of Mt. Khvira, subalpine zone, 1800–1900 m, 30.05.1988 (I.A. Belousov); 1♂ (cIB), Egrisi Mt. R., upper Magana River, subalpine zone, 1700–2100 m, 4.06.1988 (I.A. Belousov); 3♂, 1♀ (ZIN), Megrel (Egrisi) Mt. R., upper Magana River, alpine zone, 5.06.1988 (B.M. Kataev); 3♂, 3♀ (ZIN), Megrel (Egrisi) Mt. R., upper of right tributary of Khobi River, 6.06.1988 (B.M. Kataev); 1♂ (cIB), Egrisi Mt. R., right tributary of Khobitskali River, 2000–2400 m, 6.06.1988 (I.A. Belousov); 1♀ (ZIN), Megrel (Egrisi) Mt. R., upper Khobi River, 7.06.1988 (B.M. Kataev); 1♂ (cIB), N slope of Egrisi Mt. R., SE Khaishi, 6.06.1989 (I.A. Belousov); 1♂, 3♀ (cAK, ZIN), Egrisi Mt. R., Tekhuri River valley, near Doberazeni, ca 400 m, 28.06.1989 (A.G. Koval); 2♂, 2♀ (cAK, ZIN), Egrisi Mt. R., upper Tekhuri River, 2100 m, subalpine zone, 30.06.1989 (A.G. Koval); 1♂ (ZIN), S part of Askhi Plateau, N of Martvili, 2100–2400 m, alpine zone, 12.07.1990 (B.M. Kataev); 1♂ (ZIN), N slope of Egrisi Mt. R., near Tsikuri, upper Devash River, alpine zone, 16.07.1990 (B.M. Kataev); 4♂ (ZIN), Megrelian (Egrisi) Mt. R., upper Tekhuri River, 2000 m, 10.08.1990 (A.I. Roubchenya); 2♂ (ZIN), Egrisi Mt. R., Mt. Otepura-Dudi, 2500 m, 3–4.07.1991 (I.A. Belousov); 1♂ (MPSU), Abasha River valley, S slopes of Askhi Plateau, 7 km NNE Martvili, 42°29′17″N / 42°24′15″E, 3–11.07.2001 (A. Rubenyan); 2♂, 1♀ (MPSU), S spurs of Askhi Plateau, 18 km NE Martvili, 42°34′10″N / 42°31′58″E, 10–15.07.2001 (A. Rubenyan); 5♂, 1♀ (cAP, ZIN), Martvili Distr., W spurs of Askhi Plateau, 2000 m, 9.06.2005 (S.N. Shumov); 12♂, 3♀ (cAPK, ZIN), Martvili Distr., Lebarde, 1800–1900 m, 25–27.06.2005 (S.N. Shumov); 11♂, 2♀ (ZIN), Martvili Distr., 3 km NE Doberazeni vill., Tekhuri River, 250–300 m, 1–5.07.2008 (A.V. Putchkov); 6♂, 2♀ (ZIN), Samegrelo, N slopes of Ofitzari Mt. R., left bank of Shakvi River, 42°35′09.05″N / 42°24′02.77″E, 1300 m, 19–26.05.2013 (D.D. Fominykh); 4♂, 4♀ (ZIN), same data but

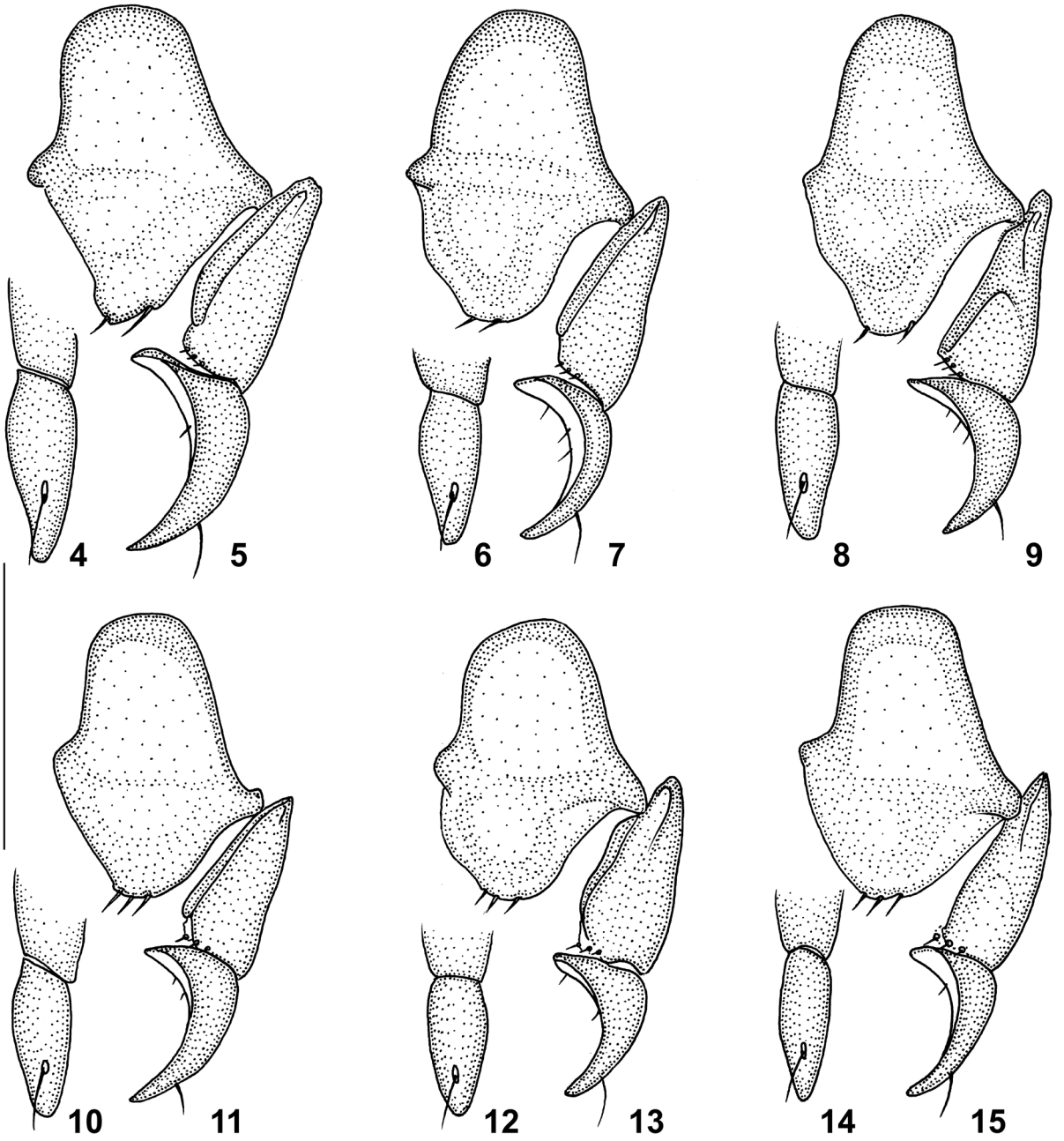


Figs 1–3. *Harpalus* (*Caucasoharpalus*) spp., elytral humeral angle and metepisternum, ventral view.

1 – *H.* (*C.*) *aeneipennis* (Lake Amtkel); 2 – *H.* (*C.*) *belousovi belousovi* **subsp. n.** (Goldash); 3 – *H.* (*C.*) *chrysopus contumax* (Kushonskiy Pass). Scale bar 1 mm.

Рис. 1–3. *Harpalus* (*Caucasoharpalus*) spp., плечевой угол надкрылий и метэпистерн, вид снизу.

1 – *H.* (*C.*) *aeneipennis* (озеро Амткел); 2 – *H.* (*C.*) *belousovi belousovi* **subsp. n.** (Гольдаш); 3 – *H.* (*C.*) *chrysopus contumax* (Кушонский перевал). Масштабная линейка 1 мм.



Figs 4–15. *Harpalus* (*Caucasoharpalus*) spp., female genitalia.

4–7 – *H.* (*C.*) *aeneipennis* (4–5 – Lake Amtkel; 6–7 – Gunzhi); 8–9 – *H.* (*C.*) *belousovi belousovi* **subsp. n.** (Goldash); 10–11 – *H.* (*C.*) *chrysopus chrysopus* (Ubinskaya); 12–13 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Kulamba); 14–15 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (Apshara). 4, 6, 8, 10, 12, 14 – gonocoxite, lateral view; 5, 7, 9, 11, 13, 15 – laterotergite, gonosubcoxite, and gonocoxite, ventral view. Scale bar 1 mm.

Рис. 4–15. *Harpalus* (*Caucasoharpalus*) spp., гениталии самки.

4–7 – *H.* (*C.*) *aeneipennis* (4–5 – озеро Амткел; 6–7 – Гунжи); 8–9 – *H.* (*C.*) *belousovi belousovi* **subsp. n.** (Гольдаш); 10–11 – *H.* (*C.*) *chrysopus chrysopus* (Убинская); 12–13 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Куламба); 14–15 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (Апшара). 4, 6, 8, 10, 12, 14 – гонококсит, вид сбоку; 5, 7, 9, 11, 13, 15 – латеротергит, гоносубкоксит и гонококсит, вид снизу. Масштабная линейка 1 мм.

42°35′14.48″N / 42°25′05.48″E, 1500 m, 20–26.05.2013 (D.D. Fominykh); 1♂, 1♀ (ZIN), Samegrelo, near Skuri vill., right bank of Tsenskari River, 42°41′51.00″N / 42°08′59.80″E, 600 m, 12.04–14.06.2017 (D.D. Fominykh); 9♂, 3♀ (ZIN), Samegrelo, Egrisi Mt. R., S slopes of Mt. Tsatskhibali, upper of Gunzhi River, 42°43′49.94″N / 42°15′21.61″E, 2300 m, 14–17.06.2018 (A. Zubov, B. Dubinin). Racha-Lechkhumi and Kvemo Svaneti: 1♂, 1♀ (ZIN), "Ущелье р. Везури Рачинск. у. 2400 м 18.VII.1928 А. Богачев" (gorge of Vezuri River, Racha District, 2400 m, A. Bogachev); 1♂ (ZIN), Racha Mt. R., alpine zone, 1987 (I.A. Belousov); 1♂ (cIB), Racha Mt. R., NW Signauri vill., 800–1500 m, forest, 14–15.08.1987 (I.A. Belousov); 2♂ (cIB, ZIN), S slope of Racha Mt. R., Mt. Lebiuristma, 1600–2200 m, 16–18.08.1987 (I.A. Belousov); 1♀ (ZIN), Racha Mt. R., Mt. Lebiuristma, 17.08.1987 (I.A. Belousov); 1♀ (ZIN), Racha Mt. R., 20.08.1987 (I.A. Belousov); 1♀ (ZIN), Racha, Racha Mt. R., left bank of Shaori reservour, near Haristvala vill., 42°24′42.40″N / 43°02′24.50″E, 1100 m, 24.04–9.06.2016 (D.D. Fominykh). Imereti: 1♂ (ZIN), Adjaria, Sairme, 20.06.1957 (V.N. Kurnakov); 2♂ (ZIN), Adjara-Imereti Mts, Sairme – Zekari Pass, 20.06.1957 (V.N. Kurnakov); 5♂, 1♀ (ZIN), Adjara-Imereti Mts, Sairme, 24.06.1958 (V.N. Kurnakov); 1 ex. (cMD), Zekari Pass, 2100 m, 1988 (M.L. Danilevsky); 6♂, 1♀ (cVZ, ZIN), Zekari Pass, Sairme env., 41°49′40″N / 42°51′44″E, 2182 m, 2–4.07.2016

(V. Zieris); 1 ex. (cIB), Makhtgila Mt. R., S of Mayakovskiy (= Bagdati), 1300 m, 1981 (I.A. Belousov); 1♂, 1♀ (ZIN), Meskhet Mt. R., Mayakovskiy (= Bagdati), 1700 m, 3.05.1981 (I.A. Belousov); 1♂ (cIB), Meskhet, Mayakovskiy (= Bagdati), 1300 m, 1.06.1981 (I.A. Belousov); 1♂ (MPSU), Sataplia Nature Reserve, beech forest, under stones, 26.01.1984; 1♂ (ZIN), "Prov. Kutais"; 1 ex. (MPSU), Kutaisi env.; 1 ex. (ZMMU), Chelaty, Kutaisi; 2♂, 1♀ (MPSU), Kutaisi env., Mt. Sataplia, beech forest, under stones, 2.02.1988 (N. Kozlov); 2♂, 1♀ (ZIN), Tkibuli env., 1200 m, 19.09.1989 (S. Zonshtein). Guria: 1♂ (ZIN), Mt. Bakhmaro, 13.08.1958 (Chintsadze); 3♂ (ZIN), Guria, N slopes of Adzharo-Imeretinskiy Mt. R., near Chkhakoura vill., E slopes of Mt. Dzegvila, right bank of Chkhakoura River, 41°53′30.10″N / 42°22′14.00″E, 1434 m, 9.04–4.06.2016 (D.D. Fominykh). Samtskhe-Javakheti: 1♀ (MNHN), "Akhaltzikhi [Akhaltsikhe]"; 1♂ (ZIN), Abastumani, 4.07.1895; 2♂ (ZIN), "Caucasus centr., Borzom [Borjomi], Dr. Lgocki"; 1♂ (ZIN), "Borzh[omi]. 1886"; 2♂, 1♀ (ZIN), Borjomi, 08.1894 (Purin); 1♀ (ZIN), Banis-Khevi near Borjomi (A.V. Bogachev); 1♀ (ZIN), Banis-Khevi gorge, near Borjomi, 22.06.1956 (V.N. Kurnakov); 1 ex. (cIB), NW slope of Meskhet Mt. R., 1700 m, 05.1981 (I.A. Belousov); 2♀ (cIB, ZIN), Meskhet Mt. R., Tsinubani, 2200 m, 5.05.1981 (I.A. Belousov); 1♀ (ZIN), Tsagveri Distr., Timotesubani env., meadow, 20.06.1981 (T.N. Vereshchagina); 1♂ (OÖLL), "Bakuriani (Transcauc.)", "*H. coortis* Schaub." (this taxon was not desribed); 1♂ (ZIN), Bakuriani, 19.07.1923 (Ya.D. Kirshenbladt); 2♂, 2♀ (ZIN), Bakuriani, upper forest zone, 10.06.1974 (N. Reck); 3♂, 3♀ (ZIN), Bakuriani, waterfall, near water, 21.06.1981 (T.N. Vereshchagina). Mtkheti-Mtianeti: 2♂ (ZIN), 2.5 km to NE of Passanauri vill., Mtiulet-Gudamakari Mt. R., right bank of Black Aragvi River, 42°21′50.50″N / 44°43′07.10″E, 1152 m, 2.05–30.06.2016 (D.D. Fominykh). Kakheti: 1♂, 1♀ (cIB, ZIN), Kvareli Distr., below Kodori Pass, ca 1500–1800 m, forest, 23.09.1984 (I.A. Belousov). Shida Kartli: 1♀ (ZIN), "Caucasus Lomis-Mta 7000′, E. König"; 1♂ (ZIN), Gori Distr., Alchashenta, 2000 m, 3.08.1928 (A.V. Bogachev); 1♂ (OÖLL), "Alchashenta, 2000 m, 3.08.[1]928 Dist. Gori, A. Bogatschev", "H. reitterianus" (this taxon was not desribed). Tbilisi: 1♂ (ZIN), "Тифлис 18–IV–912 Н.Л. Пастухов" (Tiflis 18–IV–1912 N.L. Pastukhov); 1♂ (ZIN), Tbilisi, Upper Tskneti, ca 1200 m, mixed forest, 9.06.1981 (T.N. Vereshchagina). Kvemo-Kartli: 1♂ (ZIN), Manglisi, 1.07.1971 (A.K. Zagulyaev).

South Ossetia. 1 ex. (ZMMU), "South Ossetia, Ermani"; 2♂, 3♀ (cIB, ZIN), N Kwaisi vill., S slope of Mt. Khalaza, 2300–2700 m, 21–22.08.1987 (I.A. Belousov).

Armenia. 1♀ (ZIN), 1 ex. (ZMMU), Dilizhan, nature reserve, beech-hornbeam forest; 1 ex. (cMK), "Dilizhan, Agartsin", "Чубухлы, Гокча с. бер. 11.VI.1902, Елачич, Клеман." (Chubukhly (Tsovagyugh), Gokcha (Sevan) N shore, Elachich, Kleman.); 1♂ (cMK), Tavush Prov., Haghartsin monastery, 1440 m, 40°48′N / 44°53′E, 20.06.1993 (M.Yu. Kalashian); 1♂ (cMK), Tavush Prov., 10 km E Dilijan, Lake Parzlich, soil traps, 2–24.07.2005 (M.Yu. Kalashian); 1♂ (ZIN), Tavush Prov., S env. of Teghut, 40.7629°N / 44.9328°E, 1310 m, soil traps, 9.07–22.08.2025 (M.Yu. Kalashian, N.M. Grigoryan).

Redescription. Habitus as in Figs 16–19. Dorsum at least partially bright metallic, legs black or dark brown, with tarsi in many specimens lighter; palpi reddish brown, occasionally slightly infuscate; antennae more or less markedly infuscate from antennomere 2. Pronotal sides from slightly rounded to slightly sinuate basally; basal margin in many specimens oblique laterally and concave medially; basal angles more or less widely rounded; pronotal disc impunctate anteriorly or with very fine, almost indistinct punctures between lateral margins and median line; microsculpture on disc absent medially, if present, very fine, obliterate in females, and almost indistinct in males. Elytra with parascutellar (basal) pore; odd intervals without preapical setigerous pores; preapical sinuation moderately deep, in male with comparatively faintly prominent basal denticle rounded or blunted at tip (Figs 20–23). Median lobe of aedeagus (Figs 24–31) in lateral view somewhat straight, slightly bent just behind basal bulb, its dorsal margin more or less sinuate at middle; terminal lamella not curved ventrally, straight or slightly curved dorsally, in dorsal view more or less widened at apex; apical capitulum in lateral view more or less botton-like; two macrospines in internal sac spaced very close to each other, usually at the same level; two small basal spiny patches (ventrolateral (*a*) and dorsal (*b*), as indicated in Figs 24, 25, occasionally only one of them) present.

Body size and proportions: see Table 1.

Comparative diagnosis. The most distinctive feature of *H. aeneipennis* is a peculiar shape of the median lobe of the aedeagus in lateral view: it is almost straight, with a dorsal margin more or less sinuate at middle and a botton-like apical capitulum. In two other species of the subgenus, the dorsal margin of the median lobe is rounded at middle, and the apical capitulum is oblique. The shape of the pronotum and the colouration of the body are variable, but the pronotal basal angles are always more or less widely rounded, and the dorsal surface of the body, like in *H. belousovi* **sp. n.** and unlike in *H. chrysopus*, is at least partially metallic – green, bronze or bluish violet (in *H. chrysopus*, the dorsum is black, not metallic, at most with very light bluish green shine). The legs of all specimens are black or dark brown. The preapical sinuation of the elytra is similar to that of *H. belousovi* **sp. n.** and is usually, particularly in male, shallower than that of *H. chrysopus*, and in male the denticle at its base much less prominent; the humeral denticle is usually larger (Fig. 1) than in the latter species.

Notes. The species was described from the "Persico-Armeniaco" region without additional information, based on collections by Ménétriés and Szovitz in 1827–1831. Faldermann [1836] originally included this species in the genus *Omaseus* Dejean, 1821, but later Chaudoir [1846], who examined the original and several additional specimens, transferred it to the genus *Harpalus*.

The species is morphologically variable, but does not appear to form distinct geographical forms that could be considered subspecies.

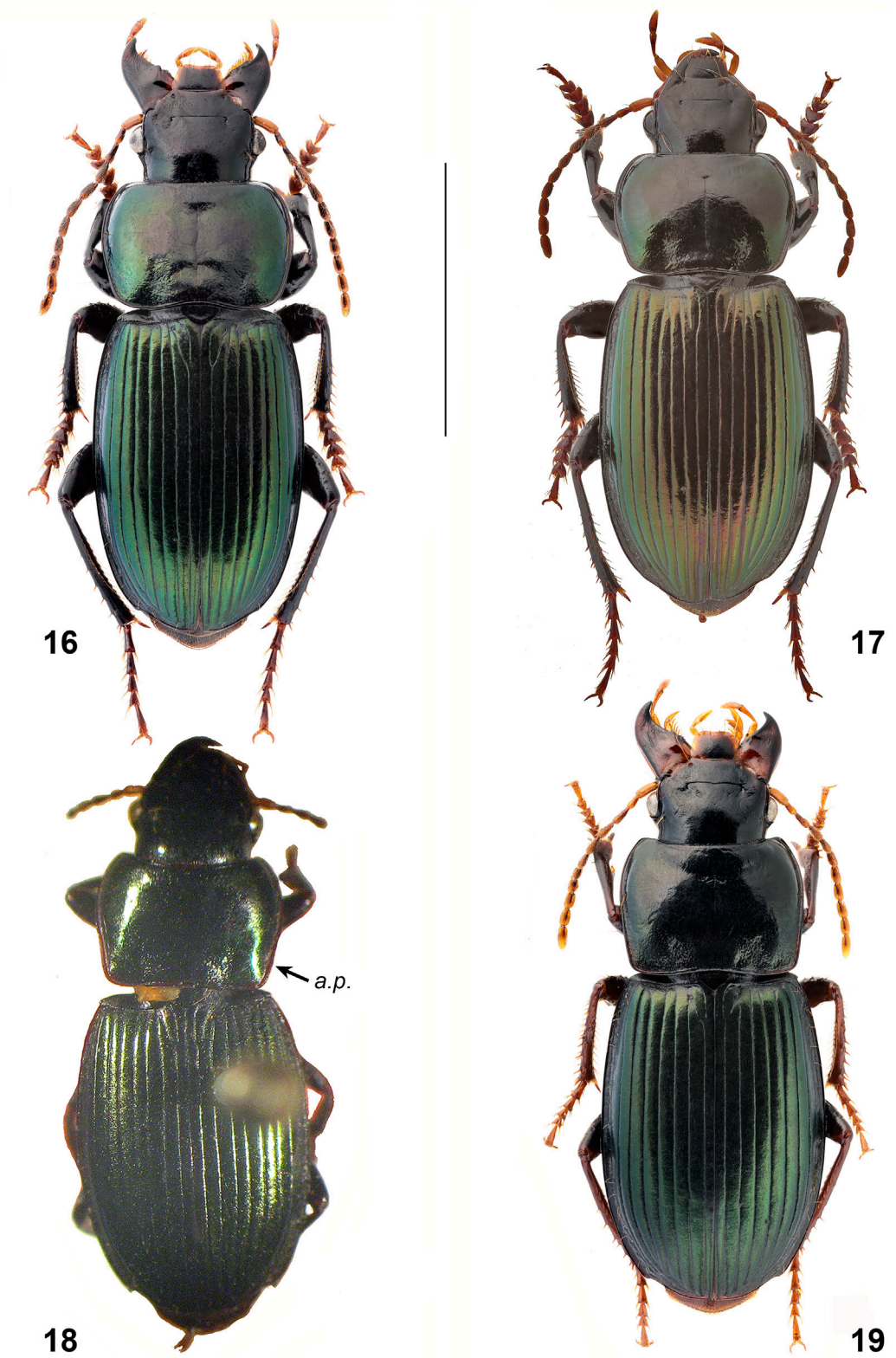
Distribution (Fig. 53). The mountains and foothills of Transcaucasia to Lake Ritsa in Abkhazia in the northwest and to the Kodori Pass on the southern slope of the Main Caucasus Range in Georgia in the east; in the south, to the southern slopes of the Meskheti Mountain Range (Akhaltsikhe) in Georgia and to the northern shore of Lake Sevan in Armenia. The species occurs from the lower forest to the alpine zone at altitudes from 300 to 2700 m. It is replaced in the Svaneti and Racha-Lechkhumi regions by the allopatric *H. belousovi* **sp. n.**

Harpalus (*Caucasoharpalus*) *belousovi* **sp. n.**
(Figs 2, 32–52, 53)

Material. See for *H. belousovi belousovi* Kataev, **subsp. n.**

Description. Habitus as in Figs 32–35. Dorsum at least partially bright metallic, legs black or dark brown, with tarsi in some specimens lighter; palpi reddish brown, occasionally slightly infuscate; antennae more or less markedly infuscate from antennomere 2. Pronotal sides straight or slightly sinuate basally; basal margin more or less straight; basal angles from more or less angulate to rounded; pronotal disc impunctate anteriorly or with very fine, almost indistinct punctures between lateral margins and median line; microsculpture on disc absent medially, if present, very fine, obliterate in females, and almost indistinct in males. Elytra with parascutellar (basal) pore; odd intervals without preapical setigerous pores; preapical sinuation moderately or markedly deep, in male with comparatively faintly prominent basal denticle rounded or blunted at tip (Figs 38–41). Median lobe of aedeagus (Figs 42–52) in lateral view slightly bent just behind basal bulb; its dorsal margin rounded at middle; terminal lamella straight or slightly curved ventrally or dorsally, in dorsal view more or less widened at apex; apical capitulum in lateral view oblique; two macrospines in internal sac usually located one after other; two small basal spiny patches (ventrolateral (*a*) and dorsal (*b*), as indicated in Figs 42, 43) present.

Body size and proportions: see Table 1.

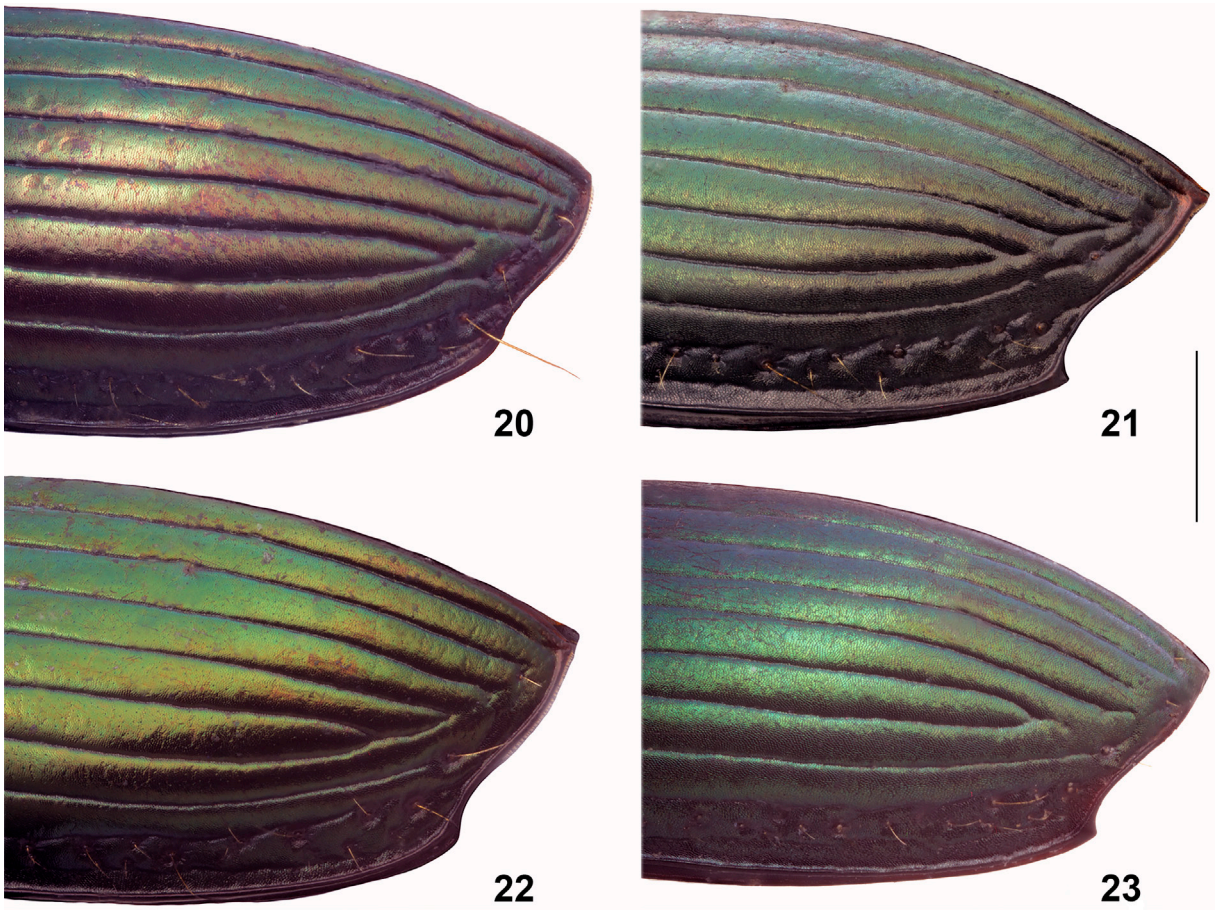


Figs 16–19. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, habitus, dorsal view.

16–17 – males; 18–19 – females (18 – syntype). Specimens: 16 – from Lebarde; 17 – from Zekari Pass; 19 – from Chkhalta. *a.p.* – additional setigerous pore. Scale bar 5 mm.

Рис. 16–19. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, габитус, вид сверху.

16–17 – самцы; 18–19 – самки (18 – синтип). Экземпляры: 16 – из Лебарде; 17 – с Зекарского перевала; 19 – из Чхалты. *a.p.* – дополнительная щетинконосная пора. Масштабная линейка 5 мм.



Figs 20–23. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, apical part of left elytron, dorsolateral view.
20, 22 – males; 21, 23 – females. Specimens: 20 – from Okhachkue; 21 – from Chkhalta; 22–23 – from Lebarde. Scale bar 1 mm.
Рис. 20–23. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, апикальная часть левого надкрылья, дорсолатеральный вид.
20, 22 – самцы; 21, 23 – самки. Экземпляры: 20 – с Охачкуе; 21 – из Чхалты; 22–23 – из Лебарде. Масштабная линейка 1 мм.

Comparative diagnosis. This new species is most similar in general habitus to *H. aeneipennis*, differing from it in having the aedeagus, like that of *H. chrysopus*, with a dorsal margin rounded at the middle in lateral view and with an oblique apical capitulum; in addition, body size is smaller on average. Like *H. aeneipennis*, the new species is characterized by the dorsal surface of the body at least partially metallic (green, bronze or bluish violet); the legs of all examined specimens are also black or dark brown; the preapical sinuation of the elytra, particularly in male, is also usually shallower than in *H. chrysopus* and humeral denticle in most specimens larger.

Notes. Although *H. belousovi* **sp. n.** is vicarious and apparently closely related to *H. aeneipennis*, the remarkable and constant differences in the male genitalia argue for treating the both as parapatric species.

This new species forms two subspecies.

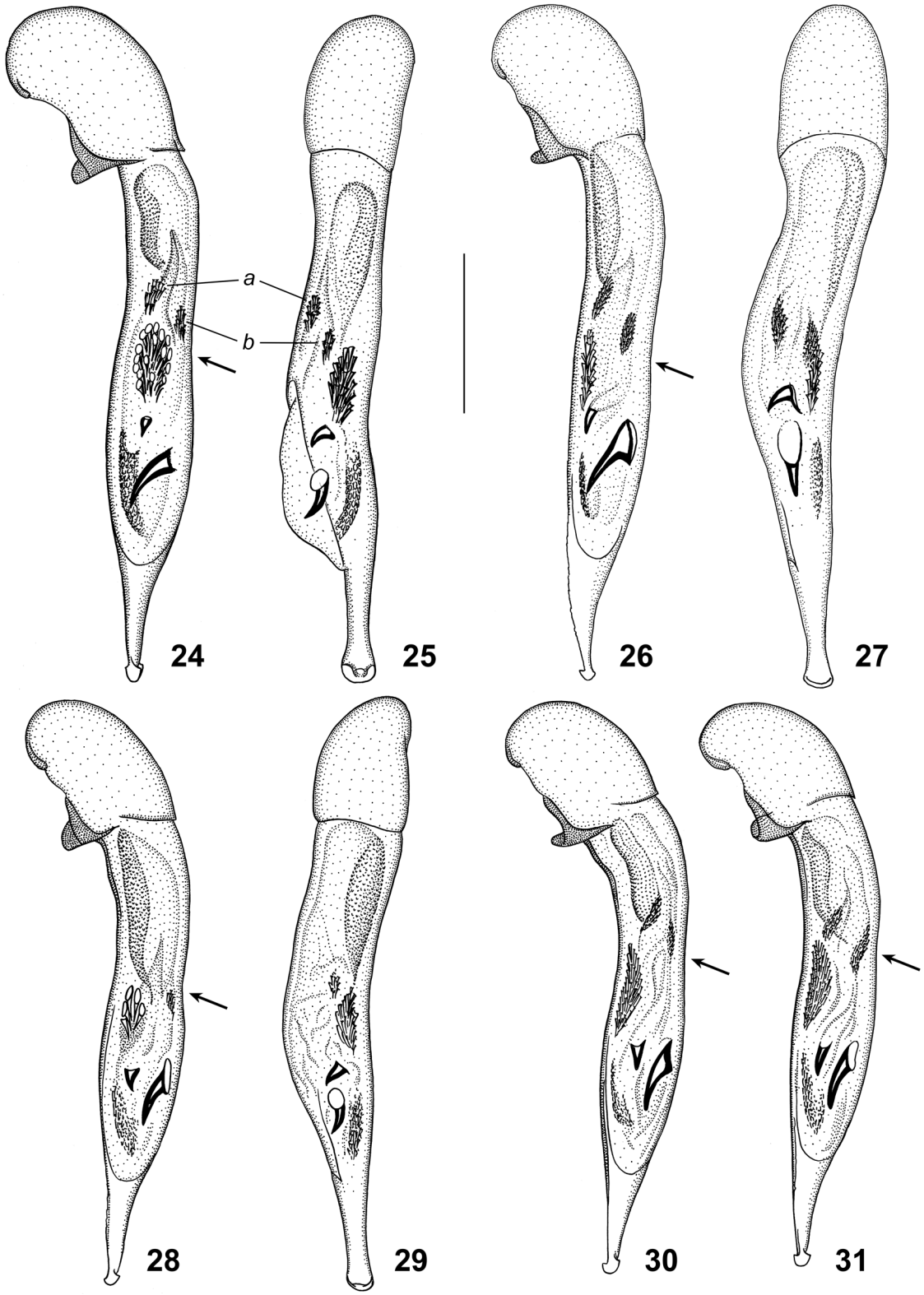
Distribution (Figs 53). Central Caucasus. The species is endemic to Svaneti and Racha-Lechkhumi regions (Georgia) where it replaces *H. aeneipennis*. The new species occurs from the upper forest to alpine zone at altitudes of about 1300–3300 m.

Etymology. The species is named after my friend and colleague Igor A. Belousov (Saint Petersburg, Russia), an outstanding specialist in ground beetles, my companion on many expeditions to the Caucasus.

Harpalus (*Caucasoharpalus*) *belousovi belousovi* **subsp. n.**
(Figs 2, 8, 9, 32, 33, 36, 38, 39, 42–45, 53)

Material. Holotype, ♂ (ZIN): "Svanetia, S slope of Svanetian Mt. R., S of Mt. Layla, Mananauri Riv., forest and alpine zones, 18.VII.1990, B. Kataev leg.". Paratypes: 10♂, 4♀ (ZIN), same data as holotype; 7♂, 6♀ (cIB, ZIN), same data but I. Belousov leg.; 10♂, 1♀ (cIB, ZIN), "Gruz. SSR Svanetia r. Khaledula, s-w mt. Laila, 27–28.07.1985 Belousov leg."; 7♂, 5♀ (cIMS, ZIN), "Svanetian Mt. R., S slope of Lashnil, upper edge of forest, 2200–2500 m, 28.VII.1985, I. Sokolov leg."; 5♂ (cIMS, ZIN), "Svanetian Mt. R., S slope, right trib. of Kheledula Riv., upper edge of forest, 2500 m, 28.VII.1985, I. Sokolov leg."; 1♂ (ZIN), "Svanetian Mt. R., S slope of Lashnil, alpine zone, 2700 m, 29.VII.1986, I. Sokolov leg."; 1♂ (ZIN), "Svanetia, S slope of Svanetian Mt. R., S of Mt. Layla, ~3300 m, alpine zone, 19.VII.1990, B. Kataev leg."; 1♀ (ZIN), "Svanetia, N slope of Svanetian Mt. R., W of Mt. Layla, upp. Khumpreri Riv., 20.VII.1990, I. Belousov leg."; 3♂ (cAP, ZIN), "Georgia, S slps of Swanetian rng., Lentekhi distr., 8 km NW Kheledy, H – 1800–1900, 8–11.07.[20]05"; 4♂ (ZIN), "Georgia: Kvemo-Svaneti, S slopes of Svanetskiy [Svaneti] Mt. R., near Lentekhi Vill., S slope of Mt. Goldash, 42°49′21.80″N 42°44′55.60″E, 2180 m, 18.VI–13.VII.2017, D. Fominykh leg."; 31♂, 7♀ (ZIN), same data but "42°50′00.10″N 42°45′16.90″E, 2615 m".

Description. Habitus as in Figs 32, 33. Median lobe of aedeagus (Figs 43–45) in lateral view with terminal lamella slightly curved ventrally, median lobe relatively wider in middle portion.



Figs 24–31. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, median lobe of aedeagus.

24, 26, 28, 30–31 – lateral view; 26, 27, 29 – dorsal view. *a* – ventrolateral basal spiny patch; *b* – dorsal basal spiny patch. The arrows indicate the sinuation of the dorsal margin. Specimens: 24–25 – from southern slope of Klukhor Pass; 26–27 – from Manglisi; 28–29 – from Khuap; 30–31 – from right tributary of Khobi. Scale bar 1 mm.

Рис. 24–31. *Harpalus* (*Caucasoharpalus*) *aeneipennis*, срединная доля эдеагуса.

24, 26, 28, 30–31 – вид сбоку; 26, 27, 29 – вид сверху. *a* – вентролатеральная базальная группа шипиков, *b* – дорсальная базальная группа шипиков. Стрелками показана изогнутость дорсального края. Экземпляры: 24–25 – с южного склона Клухорского перевала; 26–27 – из Манглиси; 28–29 – из Хуапа; 30–31 – с правого притока Хоби. Масштабная линейка 1 мм.

Basal pronotal angles of most specimens more or less angulate, blunted or narrowly rounded at tip (Fig. 36).

Body size and proportions: see Table 1.

Notes. The distinctive features of this subspecies, particularly in the shape of the median lobe of the aedeagus, although seemingly insignificant, are fairly constant in all the localities examined.

In its bright colouration and more or less distinct basal angles of the pronotum, this subspecies is somewhat similar to *H. honestus* (Duftschmid, 1812) of the subgenus *Amblystus* Motschulsky, 1864, but is easily distinguished from it by the short metepisternum and the glabrous basal edge of the pronotum.

Distribution (Fig. 53). Svaneti Mountain Range, west of Latpari Pass, at altitudes of about 1800–3300 m.

Harpalus (*Caucasoharpalus*) *belousovi conterminus* **subsp. n.** (Figs 34, 35, 37, 40, 41, 46–52, 53)

Material. Holotype, ♂ (ZIN): "Georgia: Ratcha, S slopes of Main Caucasus Mt. R., near Chiora Vill., upper of Khvargula R., 42°46′56.05″N 43°37′00.72″E, 2600 m, 12.VII.2017, D. Fominykh leg.". Paratypes: 3♂ (ZIN), same data as holotype; 1♂ (ZIN), "15 Muchali" (= Mukhli, ca 10 km NE Ambrolauri, Letskhumi Mt. R.); 1♀ (cIB), "Грузия Сванетия Цана 9/VIII-1979 г. Coll. Громов А.В." (Georgia Svanetia Tsana 9.08.1979 coll. Gromov A.V.); 1♂ (ZIN), "Грузин. ССР Местия 12.07.85 Мелях Ф.В." (Georgian SSR Mestia 12.07.1985 Melyakh F.V.); 1♂, 1♀ (cIB, ZIN), "Gruz. [Georgian] SSR S mountain range Letskhum, W Ambrolaury, 24.07.1985, Belousov leg."; 2♀ (cIB, ZIN), "Great Caucasus, Georgia, S slope of Mt. Banguriani, NE Mestia, more than 2000 m, 9.VIII.1988, I. Belousov leg."; 2♂ (cIB, ZIN), "Сванетский хр. С скл. Латпарского пер, ~2400 12 VIII.88, Белоусов" (Svaneti Mt. R., N slope of Latpari Pass, ~2400 m, 12.08.1988, Belousov); 1♂ (ZIN), "Сванетский хр., сев. скл. Латпарского пер., альпика H = 2200–2500 м, 12.08.988 Белоусов И.А." (Svaneti Mt. R., N slope of Latpari Pass, alpine zone, H = 2200–2500 m, 12.08.1988 Belousov I.A.; 1♀ (ZIN), "Georgia bor., MESTIA env. Cauc. c., Svaneti Range 1.vii.2015, 2150 +/– 50 m, r. si[?]. 43°10′10″N 42°43′55″E B. Zvarič lgt. S 38b/ 153"; 1♀ (ZIN), "Georgia: Ratcha, S slopes of Main Caucasus Mt. R., near Chiora Vill., W slopes of Mt. Chiora, 42°46′12.81″N 43°34′43.52″E, 2300 m, 19.V–12.VII.2017, D. Fominykh leg.".

Description. Habitus as in Figs 34, 35. Terminal lamella of aedeagus (Figs 46–52) in lateral view not curved ventrally, straight or slightly curved dorsally, median lobe relatively narrower in middle portion. Basal pronotal angles in most specimens obtuse, more or less rounded at tip (Fig. 37).

Body size and proportions: see Table 1.

Notes. In addition to the distinguishing characters listed in the description, the pronotum of *H. b. conterminus* **subsp. n.** is on average relatively slightly longer than that of the nominotypical subspecies.

The median lobe of the aedeagus of the male from the Lechkhumi Mt. Range (west of Ambrolauri) has a rounded dorsal margin and an oblique apical capitulum, as in other localities, but its terminal lamella is slightly curved dorsally (Fig 51, 52); in the male from Mukhli, collected probably in the Rioni Valley to the east of this locality, the terminal lamella is almost straight. The status of populations from the Lechkhumi Range requires further study based on additional material from there.

Distribution (Fig. 53). Southern slopes of the Main Caucasus Range from Mestia at least to Chiora, the eastern Svaneti Mountain Range (Latpari Pass) and the southern Lechkhum Mountain Range. This subspecies is found at altitudes of about 1300–2600 m. In the Main Caucasus, the eastern border probably reaches the Mamison Pass region at most, since the vicarious *H. aeneipennis* is known already from the southern slopes of Mount Khalatsa to the south of the Mamison Pass.

Etymology. The name of this subspecies is a Latin adjective meaning "adjacent" and referring to the distribution of this taxon relative to the nominotypical subspecies.

Harpalus (*Caucasoharpalus*) *chrysopus* Reitter, 1887 (Figs 3, 10–15, 54–146)

Harpalus chrysopus Reitter, 1887a: 246 (type locality: "Utsch-Dere in Circassien", Krasnodar Region, Russia).

Redescription. Habitus as in Figs 60–63, 99–106, 118–121, 130–133. Dorsum black, not metallic, at most with very light bluish green shine, legs from black to reddish brown; palpi and antennae reddish brown or more or less infuscate (correlating with legs colouration). Pronotum (Figs 64–78) with basal angles from acute to rounded; basal margin almost straight or emarginate; pronotal disc medially either more or less distinctly punctate anteriorly between lateral margins and median line or punctation there very fine, almost indistinct; microsculpture on disc absent or present very fine. Elytra with or without parascutellar (basal) pore and with or without preapical setigerous pores on odd intervals; preapical sinuation deep, particularly in females, in both sexes with prominent basal denticle, more or less sharp at apex (Figs 79–84, 136–139). Median lobe of aedeagus (Figs 85–98, 107–117, 122–129, 140–145) in lateral view somewhat arcuate, markedly bent before the middle; dorsal margin rounded (occasionally slightly sinuate before or behind middle); terminal lamella either curved or not curved ventrally; apical capitulum in lateral view oblique; internal sac with or without one or two small (additional) basal spiny patches on left side of median lobe: ventrolateral (*a*) and dorsolateral (*b*), as indicated in Figs 109, 110; size of spines in internal sac variable even within subspecies and populations.

Body size and proportions: see Tables 1, 2.

Comparative diagnosis. This species differs from *H. aeneipennis* and *H. belousovi* **sp. n.** in the dorsum black, not metallic, at most with very light bluish green shine, and the median lobe of the aedeagus in lateral view is relatively wider. In addition, it differs from *H. aeneipennis* in having the median lobe, like that of *H. belousovi* **sp. n.**, rounded at the middle in lateral view and with an oblique apical capitulum. On average, the preapical sinuation of the elytra of *H. chrysopus*, especially in males, is deeper, and the humeral denticle is smaller than in most *H. aeneipennis* and *H. belousovi* **sp. n.**

Notes. The species is highly variable and, against the background of the high individual (intrapopulation) variability, also demonstrates very pronounced, almost continuous geographical (interpopulation) variability in a number of several distinct characters, in particular, in the colour of the legs (Fig. 54), the shape of the pronotum (Fig. 55), the presence of the setigerous pores on the elytra (Figs 56, 57) and the male genitalia (Figs 58, 59). Different populations are distinguished significantly in these characters, and some were even described as separate species, but all of them are allopatric and connected by populations with intermediate characteristics that argue against their species status. Moreover, and this is the main problem, all these distinctive characters vary geographically almost independently of each other, without forming clear common boundaries, which creates great difficulties in recognizing even subspecies. In addition, it was found that

Table 2. Variation of length and body proportions (average value in brackets) in subspecies of *Harpalus* (*Caucasoharpalus*) *chrysopus*.
Таблица 2. Длина и пропорции тела (в скобках среднее значение) подвидов *Harpalus* (*Caucasoharpalus*) *chrysopus*.

Parameter Показатель	*H. ch. chrysopus*	*H. ch. retowskianus*	*H. ch. abasinus*	*H. ch. contumax*	*H. ch. chkhaltensis* **subsp. n.**	*H. ch. kodorensis* **subsp. n.**
Number of specimens measured / Количество измеренных экземпляров	13♂, 11♀	7♂, 9♀	26♂, 22♀	10♂, 10♀	15♂, 10♀	10♂, 7♀
L (mm)	7.7–10.3 (9.1) ♂ 7.8–9.6 (8.9) ♀ 7.7–10.3 (9.3)	8.1–9.6 (8.8) ♂ 8.1–9 (8.7) ♀ 8.1–9.6 (8.8)	8.1–10.7 (9.2) ♂ 8.1–10.7 (8.9) ♀ 8.3–10.5 (9.5)	9.1–10.5 (9.6) ♂ 9.1–10.2 (9.5) ♀ 9.4–10.5 (9.6)	7.4–9.7 (8.5) ♂ 7.4–9.4 (8.3) ♀ 7.5–9.7 (8.7)	7.8–9.7 (8.6) ♂ 8.2–9 (8.5) ♀ 7.8–9.7 (8.7)
L/EW	2.35–2.49 (2.41) ♂ 2.35–2.48 (2.41) ♀ 2.35–2.49 (2.4)	2.28–2.47 (2.38) ♂ 2.28–2.47 (2.4) ♀ 2.31–2.43 (2.37)	2.23–2.61 (2.38) ♂ 2.28–2.58 (2.41) ♀ 2.23–2.61 (2.35)	2.24–2.51 (2.38) ♂ 2.33–2.51 (2.43) ♀ 2.24–2.4 (2.33)	2.18–2.54 (2.34) ♂ 2.18–2.47 (2.36) ♀ 2.22–2.54 (2.32)	2.17–2.47 (2.32) ♂ 2.25–2.47 (2.35) ♀ 2.17–2.34 (2.28)
HWmax/ PWmax	0.7–0.76 (0.74) ♂ 0.7–0.75 (0.73) ♀ 0.73–0.76 (0.75)	0.72–0.77 (0.75) ♂ 0.72–0.77 (0.74) ♀ 0.72–0.77 (0.75)	0.67–0.75 (0.72) ♂ 0.67–0.75 (0.71) ♀ 0.68–0.76 (0.72)	0.7–0.76 (0.72) ♂ 0.7–0.73 (0.71) ♀ 0.7–0.76 (0.73)	0.67–0.75 (0.71) ♂ 0.67–0.75 (0.71) ♀ 0.69–0.75 (0.73)	0.7–0.79 (0.73) ♂ 0.7–0.73 (0.72) ♀ 0.72–0.79 (0.74)
HWmin/ PWmax	0.55–0.63 (0.6) ♂ 0.55–0.61 (0.58) ♀ 0.61–0.64 (0.63)	0.56–0.65 (0.61) ♂ 0.56–0.6 (0.59) ♀ 0.6–0.65 (0.63)	0.55–0.63 (0.58) ♂ 0.55–0.6 (0.57) ♀ 0.56–0.63 (0.60)	0.55–0.68 (0.59) ♂ 0.55–0.68 (0.58) ♀ 0.58–0.62 (0.6)	0.54–0.63 (0.58) ♂ 0.54–0.59 (0.56) ♀ 0.57–0.63 (0.6)	0.55–0.66 (0.6) ♂ 0.55–0.6 (0.58) ♀ 0.6–0.66 (0.62)
HWmax/ HWmin	1.17–1.29 (1.23) ♂ 1.21–1.29 (1.25) ♀ 1.17–1.22 (1.2)	1.14–1.31 (1.23) ♂ 1.24–1.31 (1.27) ♀ 1.14–1.24 (1.19)	1.15–1.3 (1.23) ♂ 1.2–1.3 (1.25) ♀ 1.15–1.29 (1.21)	1.03–1.3 (1.23) ♂ 1.03–1.3 (1.24) ♀ 1.2–1.26 (1.22)	1.19–1.3 (1.24) ♂ 1.2–1.3 (1.26) ♀ 1.19–1.27 (1.22)	1.15–1.3 (1.22) ♂ 1.2–1.3 (1.24) ♀ 1.15–1.23 (1.19)
PWmax/PL	1.45–1.64 (1.52)	1.46–1.55 (1.5)	1.41–1.64 (1.53)	1.44–1.6 (1.52)	1.47–1.64 (1.56)	1.42–1.58 (1.52)
PWmax/PWbas	1.13–1.3 (1.21)	1.17–1.24 (1.19)	1.15–1.35 (1.23)	1.18–1.31 (1.23)	1.19–1.32 (1.26)	1.15–1.28 (1.22)
PWmax/PWap	1.31–1.45 (1.37)	1.28–1.41 (1.34)	1.29–1.49 (1.38)	1.31–1.48 (1.4)	1.32–1.47 (1.39)	1.3–1.47 (1.37)
PWap/PWbas	0.81–0.94 (0.88)	0.83–0.93 (0.89)	0.82–0.98 (0.9)	0.8–0.96 (0.88)	0.84–0.98 (0.9)	0.84–0.96 (0.89)
PWbas/ HWmax	1.06–1.2 (1.13) ♂ 1.06–1.2 (1.13) ♀ 1.07–1.16 (1.12)	1.1–1.19 (1.13) ♂ 1.11–1.18 (1.14) ♀ 1.1–1.19 (1.13)	1.03–1.23 (1.14) ♂ 1.03–1.23 (1.14) ♀ 1.06–1.18 (1.13)	1.06–1.21 (1.13) ♂ 1.07–1.21 (1.13) ♀ 1.06–1.17 (1.13)	1.05–1.19 (1.12) ♂ 1.08–1.19 (1.12) ♀ 1.05–1.19 (1.11)	1.07–1.17 (1.13) ♂ 1.09–1.15 (1.13) ♀ 1.07–1.17 (1.13)
EL/EW	1.39–1.48 (1.43) ♂ 1.39–1.46 (1.43) ♀ 1.4–1.48 (1.43)	1.34–1.48 (1.42) ♂ 1.34–1.48 (1.43) ♀ 1.35–1.44 (1.4)	1.31–1.5 (1.41) ♂ 1.35–1.5 (1.42) ♀ 1.31–1.45 (1.39)	1.33–.1.48 (1.41) ♂ 1.38–1.48 (1.44) ♀ 1.33–1.42 (1.4)	1.29–1.47 (1.4) ♂ 1.29–1.47 (1.4) ♀ 1.33–1.44 (1.38)	1.32–1.41 (1.37) ♂ 1.34–1.41 (1.38) ♀ 1.32–1.39 (1.35)
EL/PL	2.46–2.82 (2.6) ♂ 2.46–2.77 (2.59) ♀ 2.55–2.82 (2.63)	2.47–2.73 (2.57) ♂ 2.47–2.73 (2.57) ♀ 2.49–2.68 (2.58)	2.31–2.73 (2.59) ♂ 2.31–2.72 (2.57) ♀ 2.42–2.73 (2.62)	2.49–2.7 (2.58) ♂ 2.49–2.63 (2.54) ♀ 2.54–2.7 (2.62)	2.45–2.73 (2.6) ♂ 2.45–2.67 (2.58) ♀ 2.47–2.73 (2.62)	2.4–2.71 (2.56) ♂ 2.4–2.62 (2.54) ♀ 2.51–2.71 (2.58)
EW/PWmax	1.16–1.26 (1.2) ♂ 1.16–1.22 (1.19) ♀ 1.17–1.26 (1.22)	1.15–1.25 (1.21) ♂ 1.15–1.22 (1.19) ♀ 1.2–1.25 (1.23)	1.13–1.28 (1.2) ♂ 1.13–1.23 (1.19) ♀ 1.18–1.28 (1.22)	1.12–1.27 (1.2) ♂ 1.12–1.22 (1.18) ♀ 1.2–1.27 (1.23)	1.14–1.28 (1.2) ♂ 1.14–1.26 (1.19) ♀ 1.16–1.28 (1.22)	1.15–1.33 (1.23) ♂ 1.15–1.26 (1.21) ♀ 1.21–1.33 (1.26)
EW/HWmax	1.56–1.71 (1.64) ♂ 1.58–1.71 (1.64) ♀ 1.56–1.68 (1.63)	1.55–1.69 (1.63) ♂ 1.55–1.69 (1.6) ♀ 1.59–1.68 (1.64)	1.57–1.81 (1.68) ♂ 1.57–1.75 (1.66) ♀ 1.62–1.81 (1.7)	1.59–1.75 (1.67) ♂ 1.59–1.71 (1.65) ♀ 1.62–1.75 (1.68)	1.6–1.77 (1.68) ♂ 1.6–1.77 (1.68) ♀ 1.64–1.77 (1.69)	1.57–1.8 (1.69) ♂ 1.57–1.73 (1.68) ♀ 1.65–1.8 (1.7)

leg colouration and pronotum shape depend significantly on altitude: red-legged specimens occur at lower altitudes than dark-legged specimens, and with increasing altitude the basal angles of the pronotum, although not as obvious as in the case of leg colouration, become more rounded; the body shape of many highland populations is also often less elongate than that of lowland populations. These patterns can be traced across various mountain ranges, and the changes occur in parallel. Both ordinal and multinomial logistic analyses confirmed a strong, significant effect of altitude on leg colouration. The two models produced remarkably congruent estimates, indicating that a 100 m elevation increase raises the odds of dark-legged forms by slightly more than 30% ($t > 19$, $p << 0.001$). Dimorphism in leg colouration is observed in many species of ground beetles, including Harpalini, but the reasons for this are still poorly understood and apparently varied. In many cases the both colour forms occur together throughout the whole or large part of the range of the species, as for example in *Anisodactylus binotatus* (Fabricius, 1787) [Noonan, 1996: figs 232, 233]; in other cases, especially in the mountains, they can form distinct distribution patterns. According to Kurnakov [1958, 1961], in species of the predominantly Caucasian subgenera *Myosodus* Fischer von Waldheim, 1823 (genus *Pterostichus* Bonelli, 1810) and *Lindrothius* Kurnakov, 1961 (genus *Calathus* Bonelli, 1810), the

colouration of the legs does not have an independent taxonomic significance, and red-femoral specimens form populations on the margins of the species ranges in less favorable conditions, which are evolutionarily younger than the dark-femoral populations. In the mountain-lowland *H. chrysopus*, the red-legged lowland populations also generally occupy a marginal position relative to the dark-legged highland populations.

Considering these data, six subspecies of *H. chrysopus* are recognized here, two of which are newly described, while the rest are presented in a new interpretation and differ mainly in the male genitalia and the elytral setation. The study of the intraspecific structure of this species should be continued.

Distribution (Fig. 146). The species ranges in the forest and alpine zones of the North-West Caucasus from Krasny Les and Krasnodar in Russia in the northwest to the Akiba Mountain Range (the spur of the Kodor Mountain Range) in Abkhazia in the southeast.

Harpalus (*Caucasoharpalus*) *chrysopus chrysopus* Reitter, 1887
(Figs 10, 11, 60–67, 79, 80, 85–93, 146)

Harpalus chrysopus Reitter, 1887a: 246 (type locality: "Utsch-Dere in Circassien", Krasnodar Region, Russia); Csiki, 1932: 1151; Reck, Chaladze, 2004: 148.

Harpalus (*Harpaloxys*) *chrysopus*: Reitter, 1900: 95; Lutshnik, 1922: 61; Zamotajlov, 1992: 46.

Harpalus chrysopus chrysopus: Kryzhanovskij et al., 1995: 142.

Harpalus (*Harpalus*) *chrysopus chrysopus*: Lorenz, 1998: 345; Kataev et al., 2003: 374; Lorenz, 2005: 366; Zamotajlov, Makaov, 2010: 51; Kataev, Wrase, 2017: 525.

Harpalus (*Caucasoharpalus*) *chrysopus chrysopus*: Kataev, 2023: 54.

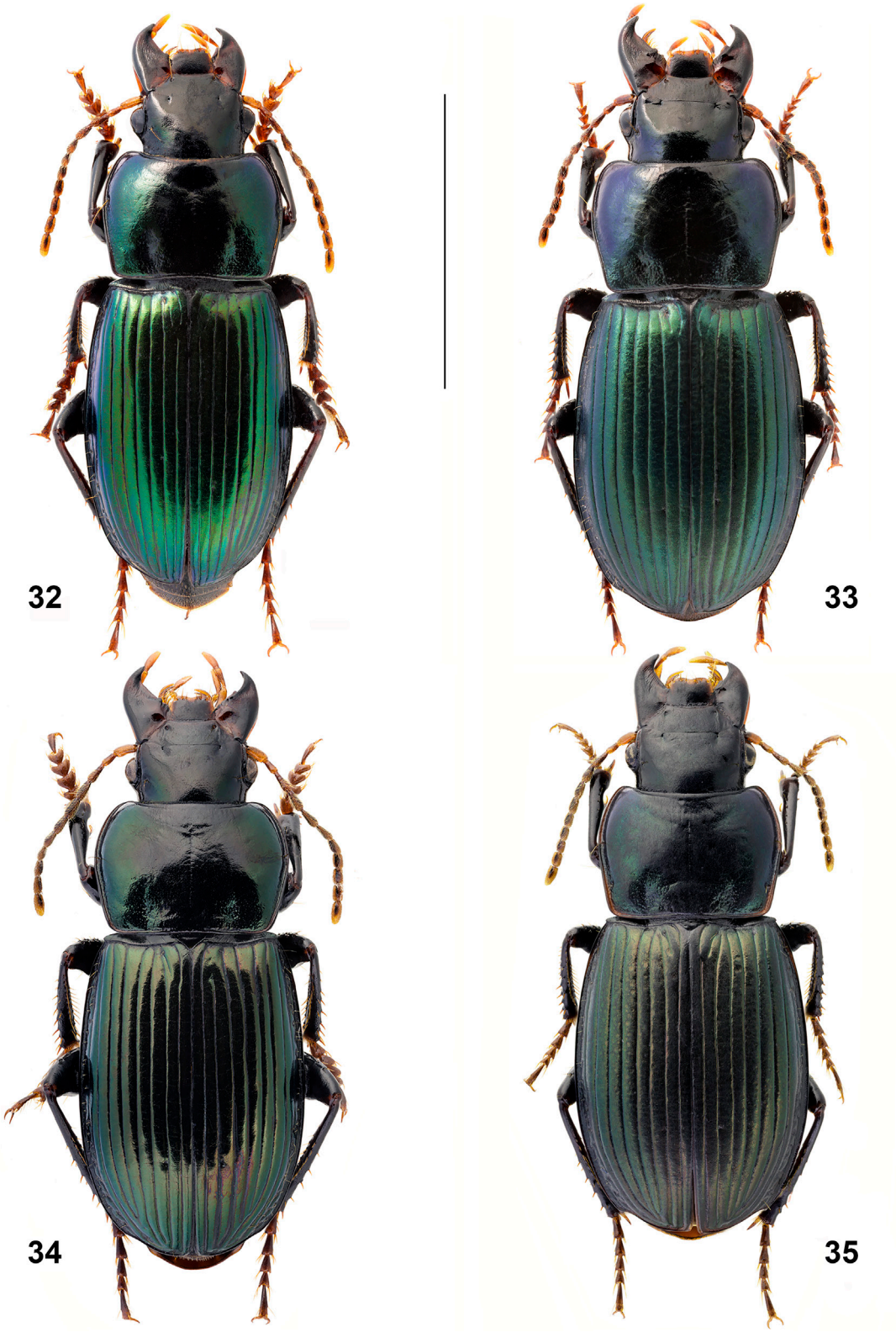
Type material. 1♂, lectotype, present designation (TMB), "*chrysopus* m., Circassien" (Reitter's handwriting), "Utsch Dere, leg. König", "coll. Reitter", "Holotypus, 1887, *Harpalus chrysopus* Reitter"; 1♀, paralectotype (TMB), "Circassien, Utsch Dere König", "coll. Reitter", "Paratypus, 1887, *Harpalus chrysopus* Reitter".

Material. 2♀ (ZIN), "Caucas. occ. от К. Праве [from K. Prave]"; 1♂, 1♀ (ZIN), "Cauc. Occ. König 1890"; 1♂ (ZIN), "Caucas. Occid. Starck", "676".

Russia. Krasnodar Region: 1♂, 1♀ (ZIN), "Caucas. occ. Circassien Leder Reitter", "460 Reitter [19]87 *H. chrysopus* Reitt"; Krasnoarmeysk Distr.: 1 ex. (ZMMU), Krasnodar, Krasny Les; Gelendzhik: 1 ex. (ZMMU), Aderbievka; 1 ex. (ZMMU), Kotsegur Mt. R., Mt. Ostraya; 2 ex. (MFNB), Anapa env., 06.1956 (L.N. Medvedev); 1♂ (ZIN), Krasnodar, second terrace of Kuban River, campus of Kuban Agricultural Institute, 30.04.1976 (A.S. Zamotajlov); Severskaya Distr.: 1 ex. (ZMMU), Mt. Sober-Oash; 1 ex. (ZMMU), Ubinskaya, 16.06.1953 (K.V. Arnoldi); 1♀ (ZIN), same data but 2.06.1974 (B.A. Korotyaev); 1♂ (ZIN), Ubinka River valley, S Ubinskaya, oak forest, 23.05.1990 (B.M. Kataev); Goryachiy Klyuch: 2♂ (ZIN), "Кубанская обл., Фанагорийское (70 в. Екатеринодара), VI.07, Н. Брянс." (Kuban Province, Fanagoriyskoe (about 75 km from Ekaterinodar (= Krasnodar)), VI.1907, N. Bryanskiy"); 1♀ (ZIN), "Перевал 25.V" (Pass 25.V), Goryachiy Klyuch, Khrebtovy Pass env., slopes of Chubataya and Shchetka mts., 550–650 m, 25.05.1985 (A.S. Zamotajlov); 1♂ (ZIN), Mt. Shchetka, 29.05.1985 (A.S. Zamotajlov); 1♀ (ZIN), Saratovskaya env., 5.05.1996 (A.Yu. Solodovnikov); 1♂ (cVK), Goryachiy Klyuch, 26.05.2000 (V.G. Knysh); 1♂ (MPSU), Goryachiy Klyuch Distr., 13 km WSW Fanagoriyskaya, Mt. Shchetka, 44°29.463′N / 38°58.797′E, 2–6.05.2005 (D.G. Kasatkin); 2♀ (MPSU), Goryachiy Klyuch Distr., N Khrebtovoe vill., Tkhamakhinskaya Shchel' Valley, 151 m, 44.55436°N / 38.95391°E, 29–30.05.2010 (I.V. Melnik); Tuapse Distr.: 1 ex. (cVSH), Tenginka; 1♀ (ZIN), Tuapse, 26.07.1909 (N. Bryanskiy); 2♂ (ZIN), "Георгиевская, Туапс. о., 30.V.1910" (Georgievskaya, Tuapse District); 1♀ (ZIN), "Иверско-Алек. слав. община, Туапс. о., 6.VI.10" (Iversko-Alek. Slavic community, Tuapse District, 6.06.1910); 2♂ (ZIN), Messazhay env., 4.05.1983 (A.S. Zamotajlov); 1♂, 1♀ (MPSU), ca 12 km N Tuapse, Kalikho mts, ca 300 m, 25.03.1994 (I.V. Melnik); 1♂ (MPSU), Tuapse env., 5–12.05.1995 (Kurkin); 1♂, 1♀ (ZIN), Saray-Gora, ca 400 m, 20.05.2017 (A. Gontarenko); Sochi: 1♂ (ZIN), "Сочинский округ Черноморской губернии" (Sochi District of Chernomorskaya (Black Sea) Province (now within Krasnodar Region)), "Paratypus", "*H. Chrysopus* Reitt. ab. *exspectatus* m. V. Lutshnik d." (this taxon was not described); 1♂ (ZIN), "Сочинский округ Черноморск. г." (Sochinskiy District Chernomorskaya (Black Sea) Province (now within Krasnodar Region)), "Monotypus", "*H. retowskianus* ab. *zolotarevi* m. V. Lutshnik d." (this taxon was not described); 7♂, 1♀ (ZIN), "Sochi distr. ст. Кичмай [Kichmay vill.]"; 1♀ (ZIN), "Achzu" (= Akhtsu); 1♀ (ZIN), E Dagomys, 9.08.1909; 1♂ (MPSU), W Dagomys River, "корыта" (troughs), 18.06.1999 (F.V. Melyakh); 3♂ (ZIN), "Чухукт, Туапс. окр., Брянский" (Chukhukt, Tuapse District, Bryanskiy); 2♂, 1♀ (ZIN), "Чухукт, Черномор.[ская] губ., 12.VI.10, Н. Брян" (Chukhukt, Chernomorskaya (Black Sea) Province (now within Krasnodar Region), 12.06.1910, N. Bryanskiy); 1♂ (ZIN), "Чухукт, Туапс. окр., 17.VI.10, Брянск" (Chukhukt, Tuapse District, 17.06.1910, Bryanskiy); 2♂, 3♀ (ZIN), "West-Caucas Utsch-Dere, E. König"; 3♂, 2♀ (ZIN), "Уч-Дере Черноморск. губ. 7.VI.10, Н. Брянский" (Uch-Dere Chernomorskay (Black Sea) Province (now within Krasnodar Region), 7.06.1910, N. Bryanskiy); 2♀ (ZIN), "Белореч. пер., Туапс. окр., 6.07.10" (Belorechenskiy Pass, Tuapse District), 6.07.1910); 1♂, 1♀ (ZIN), Mt. Fisht, Belorechenskiy Pass, 1768 m, 20.06.1983 (A.S. Zamotajlov); 1♂ (ZIN), "Сочи окр., р. Шахе, V–VI.1913" (Sochi District, Shakhe River); 5♂ (ZIN), "Sochi distr. p. Шахе [Shakhe River]"; 1♀ (cIAS), right bank of Shakhe River, W Babukaul; 1♂, (cIAS), 5 km from Verkhniy Babukaul, 1000 m, leaf forest; 1♂ (ZIN), Shakhe River, near Babukaul, 28.06.1957 (V.N. Kurnakov); 1♂ (cIMS), Solokh-aul, 800 m, leaf forest; 2♂, 3♀ (ZIN), system of Shakhe River, Solokh-Aul, 26.06.1957 (V.N. Kurnakov); 1♂ (cIAS), Solokh-aul, 600 m, beech-chestnut forest, 5–26.08.2007 (I.A. Solodovnikov); 3♂, 1♀ (ZIN), Ashe River, 30.06.1963 (V.N. Kurnakov); 1♂ (ZIN), same but 3.07.1963; 1♂ (MPSU), Lazarevskoe Distr., Krasnoaleksandrovskiy env., 14.04.1989 (I.A. Belousov); 2♂ (ZIN), Krasnoaleksandrovskiy vill., upper Ashe River, 24.07.1984 (V.N. Prasolov); 1♂, 1♀ (ZIN), Lazarevskoe, Psezuapse River, 18.07.1984 (V.N. Prasolov); 3♂ (ZIN), Lazarevskoe, upper Ashe River, 24.07.1984 (V.N. Prasolov); 1♀ (ZIN), Lazarevskoe, Soloniki, Mirny, 28.04.1989 (B.M. Kataev); 1♀ (ZIN), Kudepsta, 29.04.1989 (S. Khvylya); 1♂ (ZIN), Sochi, Soloniki, 27.05.1990 (I.A. Belousov); 4♂ (cAA), 6 km NE Soloniki, Sochi Nature Park, 28–30.05.2009 (A.V. Anichtchenko); Adler Distr.: 1♂ (MPSU), lower Chvizhepse River, right bank, 43°38′25″N / 40°04′33″E, 250 m, 28.04–4.05.2013 (K.V. Makarov, A.V. Matalin); 1♂ (MPSU), S slope of Mt. Iegosh, 1300–1400 m, 43°41′55″N / 39°58′29″E, 30.04.2013 (K.V. Makarov, A.V. Matalin); Apsheronsk Distr.: 5♂, 4♀ (ZIN), left bank of Serebryachka River, hornbeam-beech forest, on the road, 4.06.1981 (B.M. Kataev). Adygea: 1♂ (cIMS), Mt. Fisht, 1900 m, alpine zone; 1♂, 1♀ (ZIN), "Caucas Occid., Fischt, 14.X.1884, Starck"; 1♂ (TMB), "Caucas occid., Fischt, 14.X.[18]84 / Starck", "coll. Reitter", "Paratypus, 1887, *Harpalus* Retowskyi Reitt."; 1♀ (TMB), "Caucas occid., Fischt, 14.X.[18]84", "H. Retowskyi mih." (Reitter's handwriting), "coll. Reitter", "Holotypus, 1887, *Harpalus* Retowskyi Reitter"; 1♂ (ZIN), slope of Mt. Fisht, 7–8.08.1909; 2♂ (ZIN), "Сев. скл. Фишта Кубанской обл., 5.07.1910, с Брянский" (N slope of Fisht Kuban Province (now within Krasnodar Region), Bryanskiy); 2♂ (ZIN), Fisht – Guzeripl, 31.07.1955 (V.N. Kurnakov); 3♂ (ZIN), Fisht-Oshten Pass, 30.06.1957 (V.N. Kurnakov); 1♂, 1♀ (ZIN), Fisht, Dzhigursan Pass, 1851 m, 21.06.1983 (A.S. Zamotajlov); 2♂ (ZIN), Mt. Khuko, 6.07.1964 (V.N. Kurnakov); 3♂, 5♀ (ZIN), NW slope of Pshekhasu, 1700–2500 m, 5.06.1987 (B.M. Kataev); 1♂, 1♀ (ZIN), Mt. Oshten, 2300 m, 22.06.1959 (D.V. Panfilov); 2♂ (ZIN), Mt. Oshten, NW slope, 1800 m, 3–5.06.1999 (A.V. Putchkov).

Redescription. Habitus as in Figs 60–63. Pronotal sides more or less noticeably sinuate or almost straight basally; basal angles distinct, almost right or slightly obtuse, occasionally acute, somewhat sharp or at most slightly blunted at tip (Figs 64–67); disc medially in male generally without microsculpture, occasionally with almost indistinct meshes, in females generally with very fine, strongly obliterate meshes. Legs either reddish brown or black. Head relatively wide. Elytra with parascutellar (basal) pore; odd intervals generally without preapical setigerous pores or occasionally (mainly interval 7) with one or two (very rarely three) such pores, often only on one elytron (Figs 79, 80). Terminal lamella of aedeagus (Figs 85–93) not curved ventrally, straight or slightly curved dorsally, only slightly widened at apex in dorsal view; ventral margin of median lobe in lateral view generally without preapical sinuation; internal sac without small additional basal spiny patches on left side of median lobe.

Body size and proportions: see Table 2.

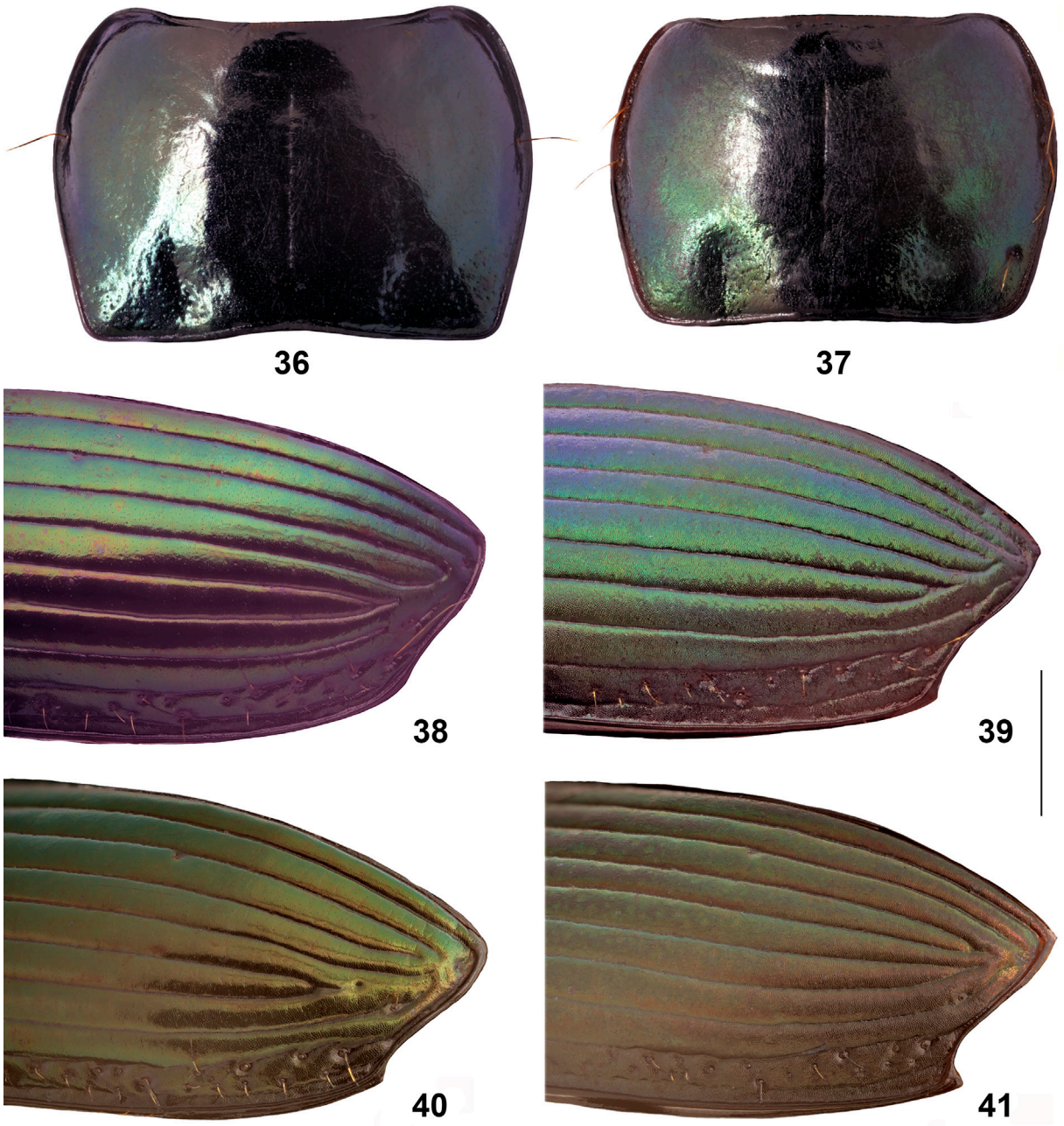


Figs 32–35. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, habitus, dorsal view.

32–33 – *H.* (*C.*) *b. belousovi* **subsp. n.** (Goldash): 32 – male, 33 – female; 34–35 – *H.* (*C.*) *b. conterminus* **subsp. n.** (Chiora): 34 – male, holotype, 35 – female, paratype. Scale bar 5 mm.

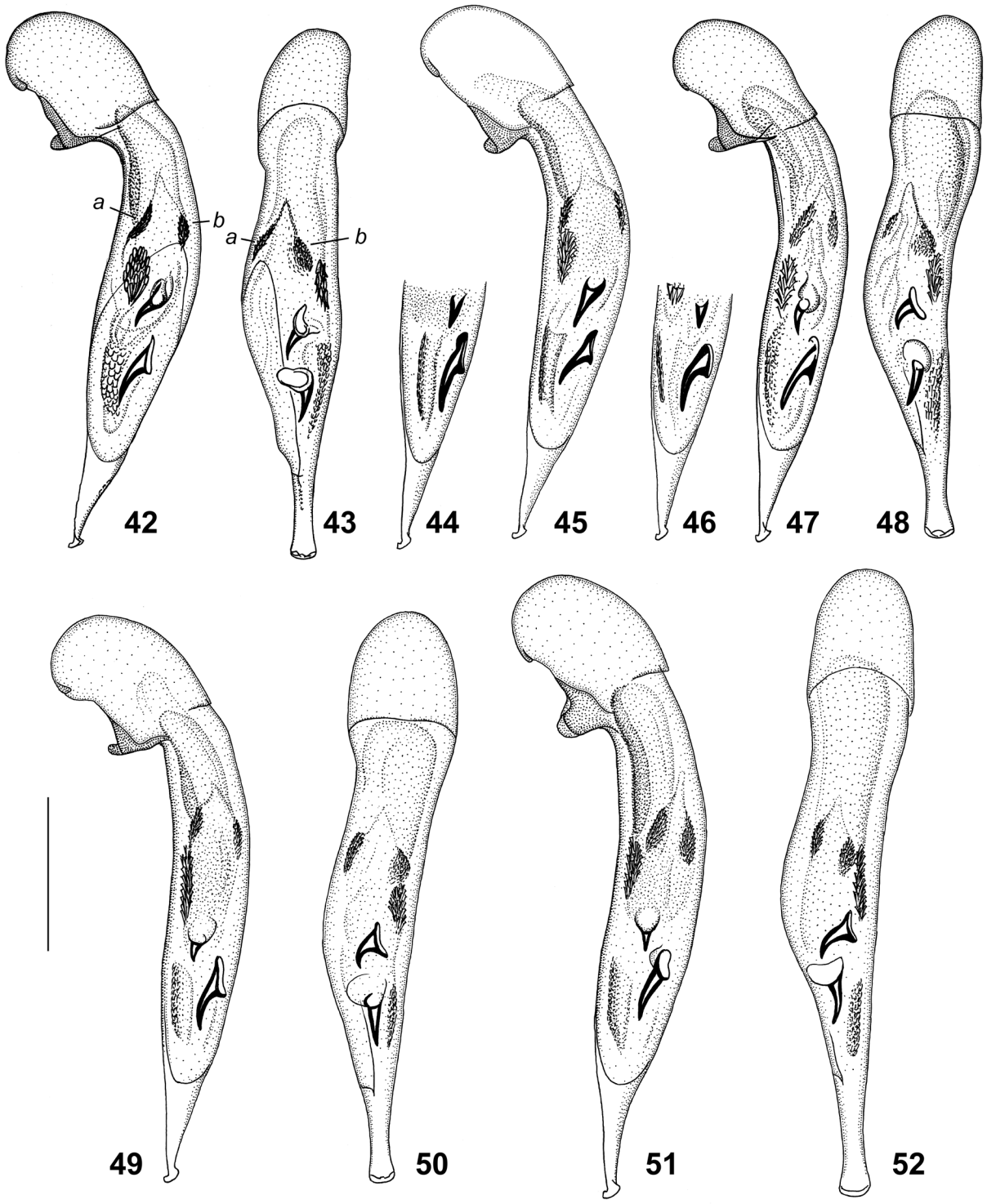
Рис. 32–35. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, габитус, вид сверху.

32–33 – *H.* (*C.*) *b. belousovi* **subsp. n.** (Гольдаш): 32 – самец, 33 – самка; 34–35 – *H.* (*C.*) *b. conterminus* **subsp. n.** (Чиора): 34 – самец, голотип, 35 – самка, паратип. Масштабная линейка 5 мм.



Figs 36–41. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, pronotum and apical part of left elytron.
36, 38–39 – *H.* (*C.*) *b. belousovi* **subsp. n.** (Goldash); 37, 40–41 – *H.* (*C.*) *b. conterminus* **subsp. n.** (37 – Mestia; 40–41 – Chiora, holotype and paratype). 38, 40 – males; 39, 41 – females. 36–37 – pronotum; 38–41 – apical part of left elytron. Scale bar 1 mm.
Рис. 36–41. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, переднеспинка и апикальная часть надкрылья.
36, 38–39 – *H.* (*C.*) *b. belousovi* **subsp. n.** (Гольдаш); 37, 40–41 – *H.* (*C.*) *b. conterminus* **subsp. n.** (37 – Местия; 40–41 – Чиора, голотип и паратип). 38, 40 – самцы; 39–41 – самки. 36–37 – переднеспинка; 38–41 – апикальная часть надкрылья. Масштабная линейка 1 мм.

Comparative diagnosis. The most important features of the nominotypical subspecies, distinguishing it from other subspecies, are the median lobe of the aedeagus in most specimens with terminal lamella not curved ventrally and without small additional basal spiny patches in the internal sac, and the relatively long elytra without preapical setigerous pores on the odd intervals. The head is, on average, relatively wider, the basal pronotal angles are usually sharper, and the dorsal tarsal setae are more developed than in most specimens of other subspecies. In the terminal lamella of the median lobe not curved ventrally, the nominotypical subspecies is similar only to the vicarious *H. ch. lutshniki*, which has, however, small additional basal spiny patches in the internal sac of the aedeagus, and elytra with preapical setigerous pores on the odd intervals. The latter two features, combined with the terminal lamella of the median lobe curved ventrally, also distinguish most specimens of the other vicarious subspecies, *H. ch. abasinus*, from the nominotypical subspecies.



Figs 42–52. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, median lobe of aedeagus and its apical part.

42–45 – *H.* (*C.*) *b. belousovi* **subsp. n.**; 46–52 – *H.* (*C.*) *b. conterminus* **subsp. n.** 42–43, 45, 47–52 – median lobe of aedeagus; 44, 46 – apical part. *a* – ventrolateral basal spiny patch; *b* – dorsal basal spiny patch. 42, 44–47, 49, 51 – lateral view; 43, 48, 50, 52 – dorsal view. Specimens: 42–43 – from right tributary of Kheledula; 44 – from Goldash; 45 – holotype, from Mananauri; 46–48 – from Latpari Pass; 49–50 – holotype, from Chiora; 51–52 – from Lechkhumi. Scale bar 1 mm.

Рис. 42–52. *Harpalus* (*Caucasoharpalus*) *belousovi* **sp. n.**, срединная доля эдеагуса и ее апикальная часть.

42–45 – *H.* (*C.*) *b. belousovi* **subsp. n.**; 46–52 – *H.* (*C.*) *b. conterminus* **subsp. n.** 42–43, 45, 47–52 – срединная доля эдеагуса; 44, 46 – апикальная часть. *a* – вентролатеральная базальная группа шипиков; *b* – дорсальная базальная группа шипиков. 42, 44–47, 49, 51 – вид сбоку; 43, 48, 50, 52 – вид сверху. Экземпляры: 42–43 – с правого притока Хеледулы; 44 – с Гольдаша; 45 – голотип, из Мананаури; 46–48 – с Латпарского перевала; 49–50 – голотип, из Чиоры; 51–52 – с Лечхумского хребта. Масштабная линейка 1 мм.

Notes. *Harpalus chrysopus* was originally described based on at least two specimens (body length range given) from Uch-Dere. According to the present interpretation, the nominotypical subspecies is represented by two forms, differing in the colour of their legs. The red-legged form (corresponding to the type specimens of the subspecies) occurs at lower altitudes, but up to about 2000 m, mainly in the forest belt, and occupies most of the range of the subspecies. The dark-legged form is found higher than the red-legged (in the range of about 700–2400 m on different ridges), from the middle forest belt to the alpine zone; it is found in the upper reaches of the Shakhe River, in the mountains of Khuko and Fisht-Oshten massif. As a rule, the dark-legged form is connected with the red-legged form at lower elevations on the same ridge by populations comprising the both these forms and specimens with intermediate characteristics (infuscate femora and red tibiae); in other characters, including the male genitalia, they are no different. Populations with both red-legged and dark-legged individuals are known at altitudes of 700–2000 m in the valleys of the Shakhe and Serebryachka rivers and on the slopes of the Fisht-Oshten Mountains. The highest locality of the red-legged form is the northwestern slopes of the Mount Pshekhasu (about 2000 m); the lowest known locality of the dark-legged form is the environs of Babuk-Aul in the Shakhe Valley (about 700 m). One of two examined specimens from Fanagoriyskoe (ca 100 m) not far from Goryachiy Klyuch also has black legs, but it cannot be ruled out that it was mislabelled. Although the shape of the pronotum is variable, dark-legged individuals have on average slightly more blunted basal angles, reflecting a general trend with increasing altitude.

Distribution (Fig. 146). The forest and alpine zones of the North-West Caucasus northwest of the Mzymta River, including the Fisht-Oshten Massif; in the north, at least to Anapa, Ubinskaya and Saratovskaya; also known from Krasnodar and its environs (Novaya Adygeya, Khomuty) [Zamotajlov, 1992; Zamotajlov, Makaov, 2010] and from Krasny Les to the east of Slavyansk-na-Kubani. In the north-east, it is replaced by *H. ch. retowskianus*.

Harpalus (*Caucasoharpalus*) *chrysopus retowskianus* Reitter, 1887, **stat. n.**
(Figs 68, 69, 94–98, 118, 146)

Harpalus Retowskii Reitter, 1887a: 246 (non Heyden, 1883) (type locality: "Circassien. ...Berg Atschischho", Krasnodar Region, Russia); Kryzhanovskij et al., 1995: 142 (as a junior synonym of *H. chrysopus chrysopus*).

Harpalus Retowskianus Reitter, 1887b: 500, nomen pro *H. retowskii* Reitter, 1897 (type locality: "Circassien. ...Berg Atschischho", Krasnodar Region, Russia); Csiki, 1932: 1151; Kryzhanovskij et al., 1995: 142 (as a junior synonym of *H. chrysopus chrysopus*).

Harpalus (*Harpaloxys*) *Retowskii*: Reitter, 1900: 95.

Harpalus (*Harpaloxys*) *Retowskianus*: Lutshnik, 1922: 61; Zamotajlov, 1992: 46.

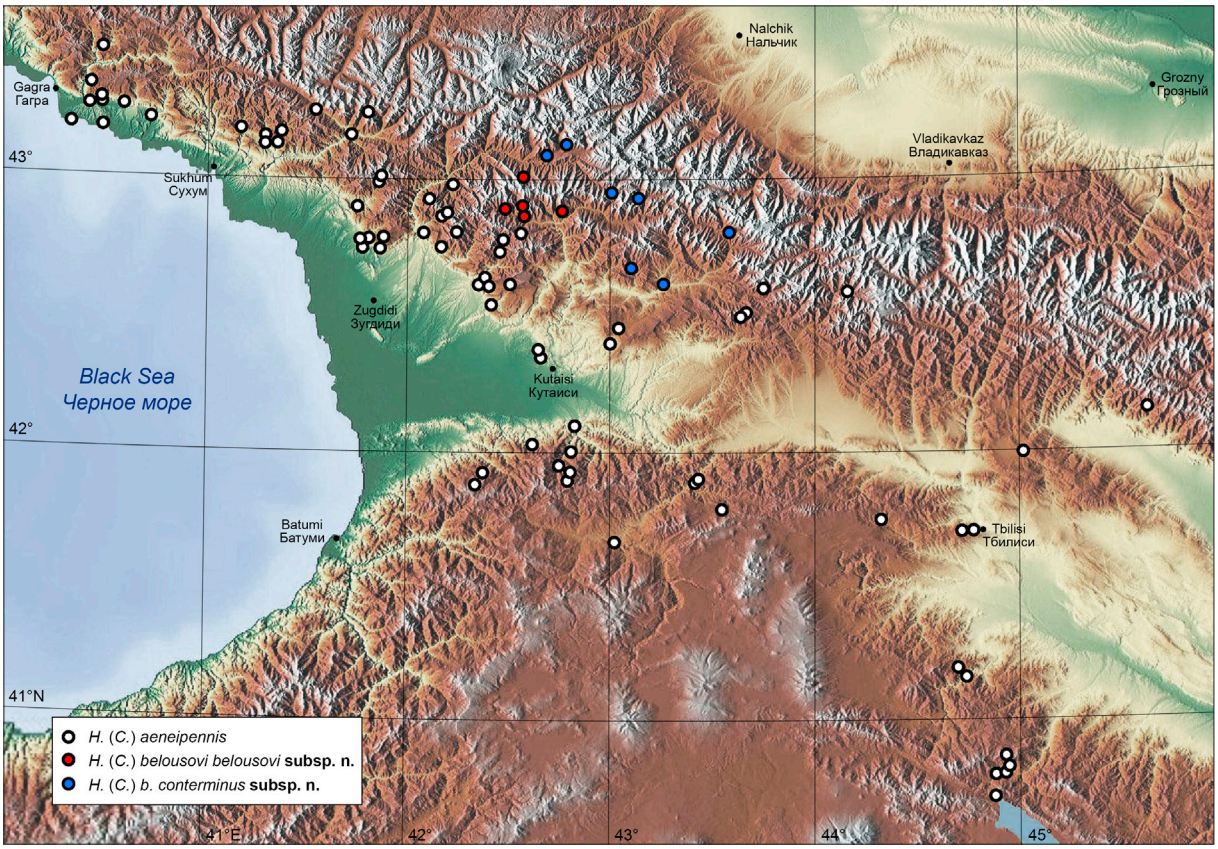
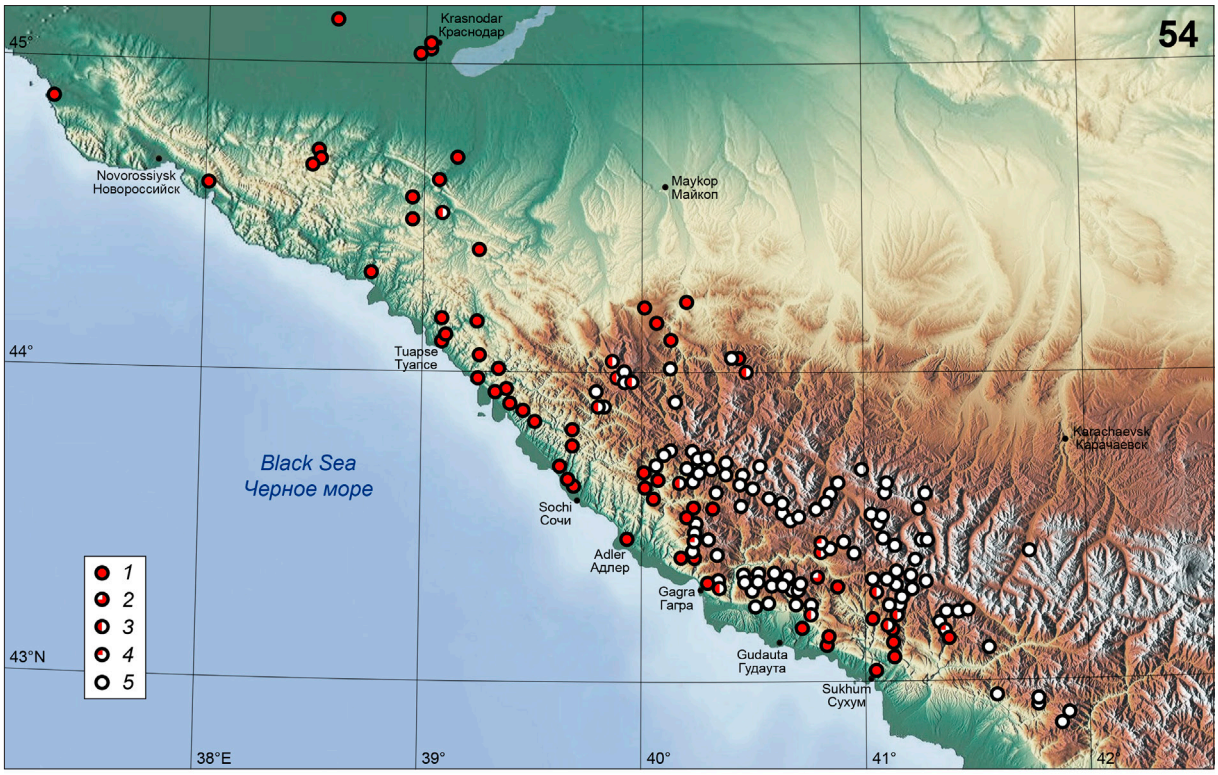
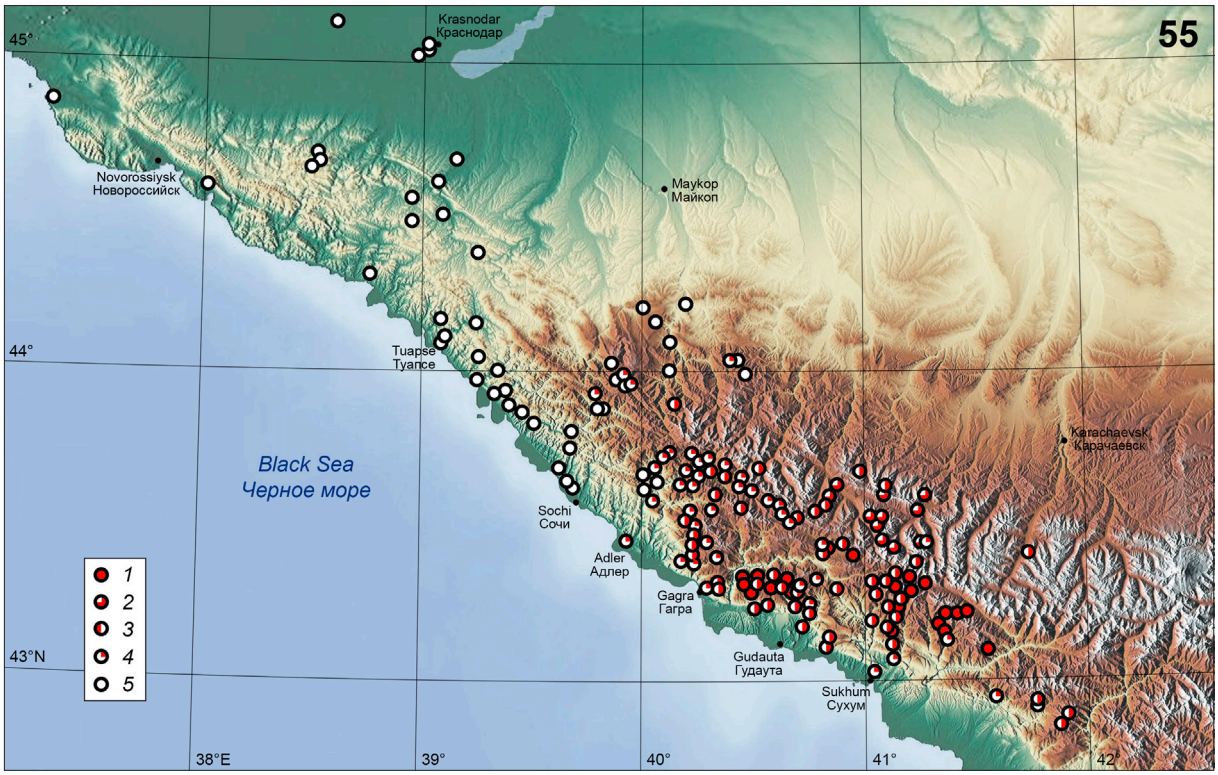


Fig. 53. *Harpalus* (*Caucasoharpalus*) spp., distribution.
Рис. 53. *Harpalus* (*Caucasoharpalus*) spp., распространение.



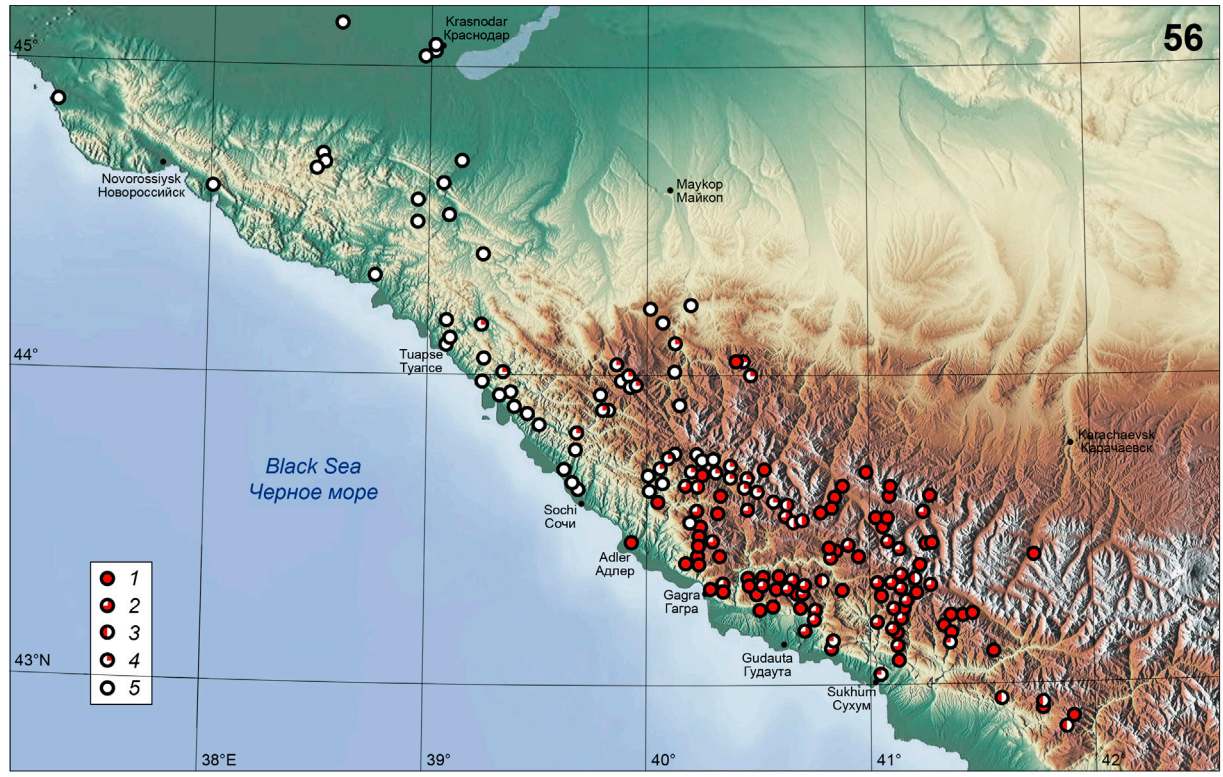


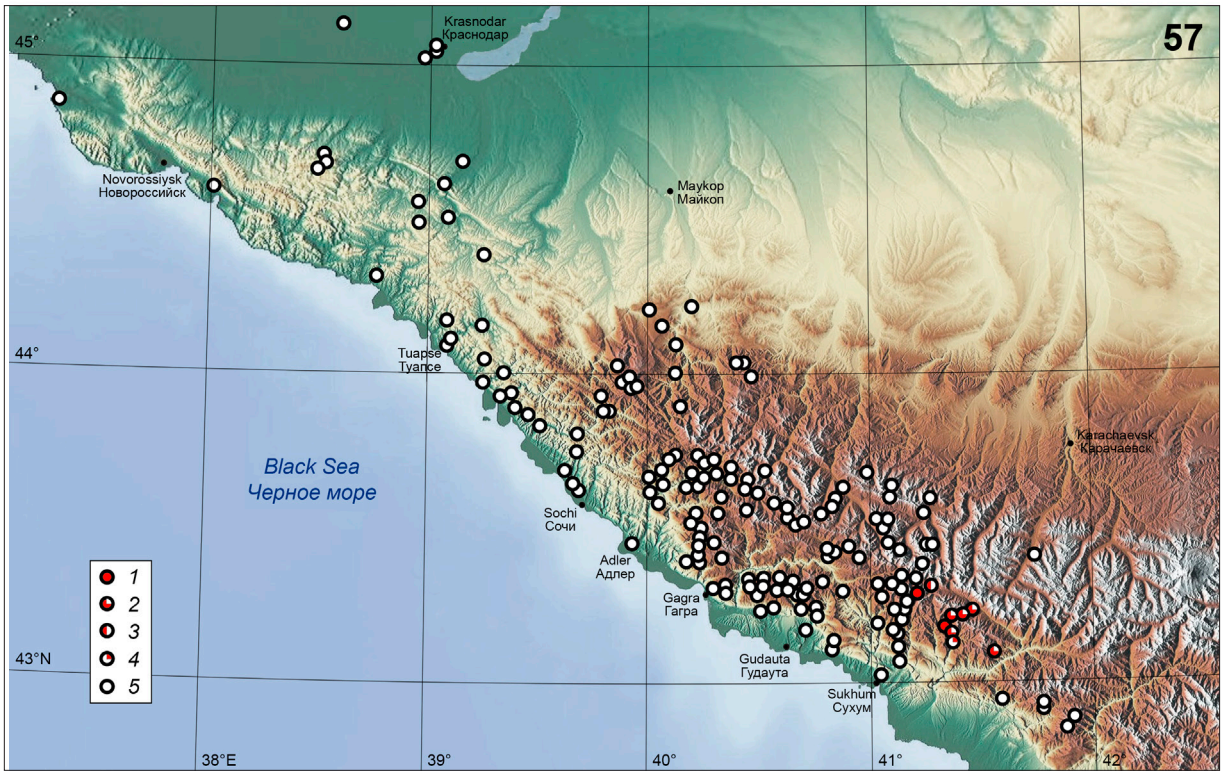
Figs 54–55. *Harpalus* (*Caucasoharpalus*) *chrysopus*, spatial distribution of specimens with certain distinctive features.

54 – leg colouration: *1* – reddish brown; *2* – mostly reddish brown; *3* – reddish brown and dark in approximately equal proportions; *4* – mostly dark; *5* – dark; 55 – basal angles of pronotum: *1* – rounded; *2* – mostly moderately rounded; *3* – moderately rounded or noticeably blunted at apex; *4* – noticeably blunted at apex; *5* – sharp or slightly blunted at apex).

Рис. 54–55. *Harpalus* (*Caucasoharpalus*) *chrysopus*, пространственное распределение особей с отдельными признаками.

54 – цвет ног: *1* – красно-коричневый; *2* – преимущественно красно-коричневый; *3* – красно-коричневый и темный примерно в равных пропорциях; *4* – преимущественно темный; *5* – темный; 55 – базальные углы переднеспинки: *1* – закругленные; *2* – преимущественно умеренно закругленные; *3* – умеренно закругленные или заметно притупленные на вершине; *4* – заметно притупленные на вершине; *5* – резкие или слегка притупленные на вершине.



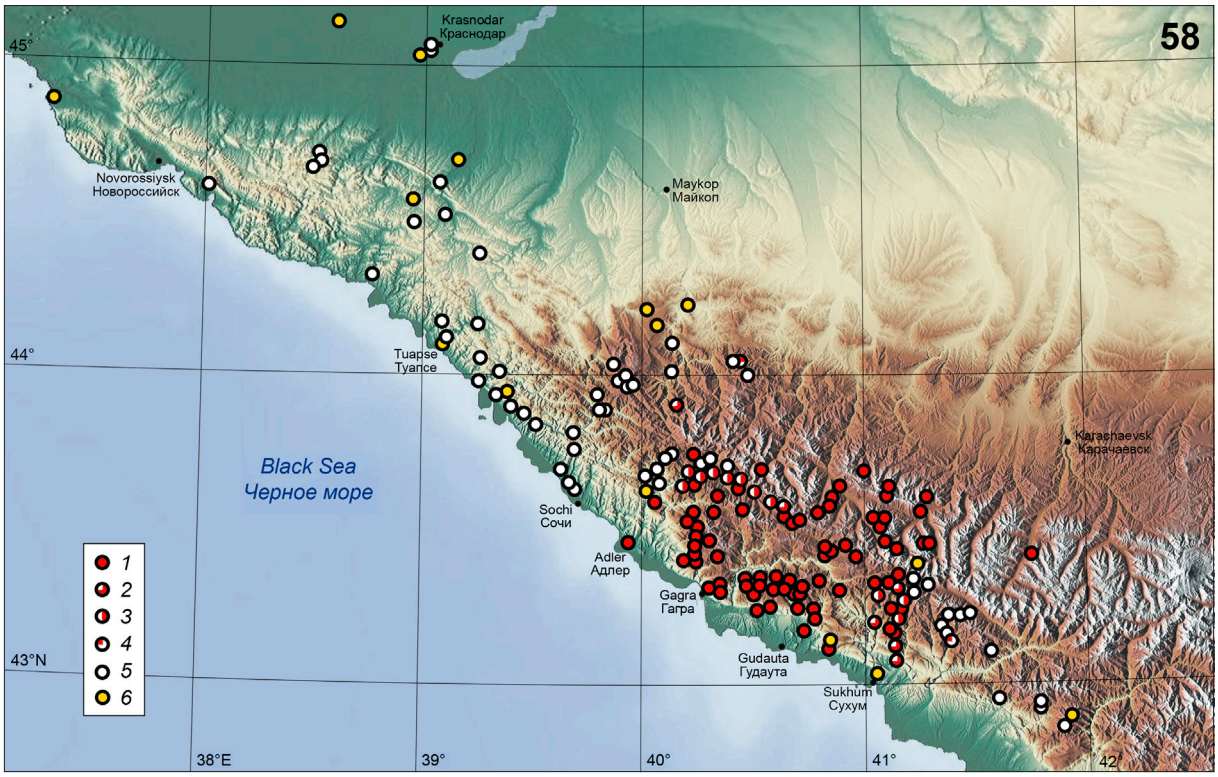


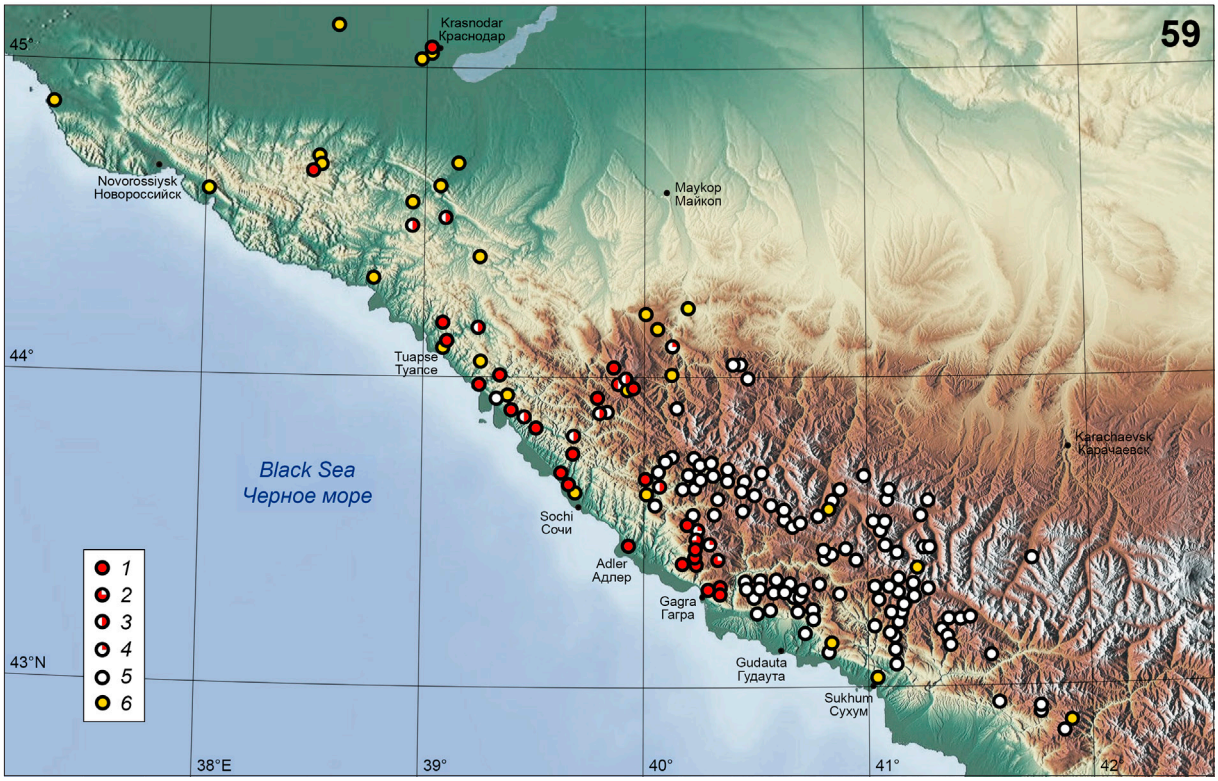
Figs 56–57. *Harpalus* (*Caucasoharpalus*) *chrysopus*, spatial distribution of specimens with certain distinctive features of elytra.

56 – preapical pores on odd intervals: *1* – present; *2* – mostly present; *3* – present or absent in approximately equal proportions; *4* – mostly absent; *5* – absent; 57 – parascutellar (basal) pores: *1* – present; *2* – mostly present; *3* – present or absent; *4* – mostly absent; *5* – absent.

Рис. 56–57. *Harpalus* (*Caucasoharpalus*) *chrysopus*, пространственное распределение особей с отдельными признаками надкрылий.

56 – предвершинные поры на нечетных промежутках: *1* – присутствуют; *2* – преимущественно присутствуют; *3* – присутствуют или отсутствуют примерно в равных пропорциях; *4* – преимущественно отсутствуют; *5* – отсутствуют; 57 – прищитковая (базальная) пора: *1* – присутствует; *2* – преимущественно присутствует; *3* – присутствует или отсутствует; *4* – преимущественно отсутствует; *5* – отсутствует.





Figs 58–59. *Harpalus* (*Caucasoharpalus*) *chrysopus*, spatial distribution of specimens with certain distinctive features of aedeagus.

58 – basal spiny patches (*a* and *b*) of internal sac: *1* – present; *2* – mostly present; *3* – present or absent in approximately equal proportions; *4* – mostly absent; *5* – absent; *6* – not examined; 59 – terminal lamella: *1* – clearly not curved ventrally or curved dorsally; *2* – mostly not curved ventrally; *3* – not curved or slightly curved ventrally; *4* – mostly sligtly curved ventrally or almost straight; *5* – clearly curved ventrally; *6* – not examined.

Рис. 58–59. *Harpalus* (*Caucasoharpalus*) *chrysopus*, пространственное распределение особей с отдельными признаками эдеагуса.

58 – базальные группы мелких шипиков (*a* и *b*) внутреннего мешка: *1* – присутствуют; *2* – преимущественно присутствуют; *3* – присутствуют или отсутствуют примерно в равных пропорциях; *4* – преимущественно отсутствуют; *5* – отсутствуют; *6* – не исследованы; 59 – концевая лопасть: *1* – явно не изогнута вентрально или изогнута дорсально; *2* – преимущественно не изогнута вентрально; *3* – не изогнута или слегка изогнута вентрально; *4* – преимущественно слегка изогнута вентрально или почти прямая; *5* – явно изогнута вентрально; *6* – не исследована.

Harpalus (*Harpaloxis*) *dinniki* Lutshnik, 1933: 131, **syn. n.** (type locality: "Temnolesskaja, distr. Maikopiensi", Krasnodar Region, Russia, here corrected to Khamyshki, Adygea, Russia based on the label data of the probable holotype); Kryzhanovskij et al., 1995: 142 (as a junior synonym of *H. chrysopus chrysopus*).

Type material. *H. dinniki*: 1♀, (?) holotype (ZIN), "Хамышки Майкопск. р., 24.07.933 К. Арнольди" (Khamyshki Maikop District, 24.07.1933, K. Arnoldi), "Monotypus", "*Harpalus dinniki* m., V. Lutshnik det." (Lutshnik's handwriting).

Material. 1♂ (ZIN), "Caucas Occid. Stark", "459 Reitter 87 *H. Retowskyi* Reitt." (Reitter's handwriting).

Russia. Krasnodar Region: Sochi: 1♂, 2♀ (ZIN), "Caucasus Occid. Medovej [= Medoveevka], Starck"; 1 ex. (cAK), Mt. Achishkho, near meteostation, 1900 m; 1♂ (ZIN), "Caucas Occid. Atchischo 1.IX.[18]82"; 1♀ (ZIN), "Ачишхо, Черном. о., Achishkho, 29.VI.909, А. Яковлев" (Chernomorskaya (Black Sea) Province (now within Krasnodar Region), 29.06.1909, A. Yakovlev); 1♂, 1♀ (ZIN), "Сочи окр., Черномор. г., г. Ачишхо (Кр. Поляна), 8000′ Н. Брянский" [(Sochi District, Chernomorskaya (Black Sea) Province (now within Krasnodar Region), Mt. Achishkho (Krasnaya Polyana), 8000′ (ca 2400 m) N. Bryanskiy); 1♀ (ZIN), "Красная Пол. (Ачишхо), Чер. г. 20.04.1912, Н.Л. Пастухов" (Krasnaya Polyana (Achishkho), Chernomorskaya (Black Sea) Province (now within Krasnodar Region), N.L. Pastukhov); 1♂ (ZIN), Achishkho Mt. R., 7.06.1954 (V.N. Kurnakov); 1♂ (ZIN), same data but 8.06.1954; 2♂, 1♀ (ZIN), same data but 28.07.1954 (V.N. Kurnakov); 1♂ (ZIN), same data but 28.06.1962 (V.N. Kurnakov); Apsheronsk Distr.: 1 ex. (ZMMU), "Камышановская, лес" (Kamyshanovskaya (? = Kamyshanova Polyana), forest); Mostovskiy Distr.: 1♂, 4♀ (ZIN), E slope of Mt. Bolshoy Tkhach, 1800–2000 m, 18.05.1990 (B.M. Kataev); 7♂, 4♀ (ZIN), watershed of Belaya and Malaya Laba rivers, SE of Mt. Bolshoy Tkhach, ca 2000 m, 19.05.1990 (B.M. Kataev); 1♂, 1♀ (cAK), Mt. Bolshoy Tkhach, ca 1800 m, 27.08.1993 (A.G. Koval). Adygea. 1 ex. (cVM), Guzeripl; 1♂ (ZIN), "Хамышки на р. Белой, Зап. Кавказ" (Khamyshki at Belaya River, West Caucasus), "*H. dinniki* m. Lutshnik det.", "vidi 1970 Dr. Z. Mlynář det."; 1♂ (ZIN (ex Coll. Lutshnik)), "Хамышки Майкопск. р., 24.07.933, К. Арнольди" (Khamyshki Maykop District, 24.07.1933, K. Arnoldi), "ab. n."; 1♂, 1♀ (ZIN), Khamyshki, 3.07.1957 (V.N. Kurnakov); 1♀ (ZIN), Dakhovskaya vill., 7.05.1983 (A.S. Zamotajlov).

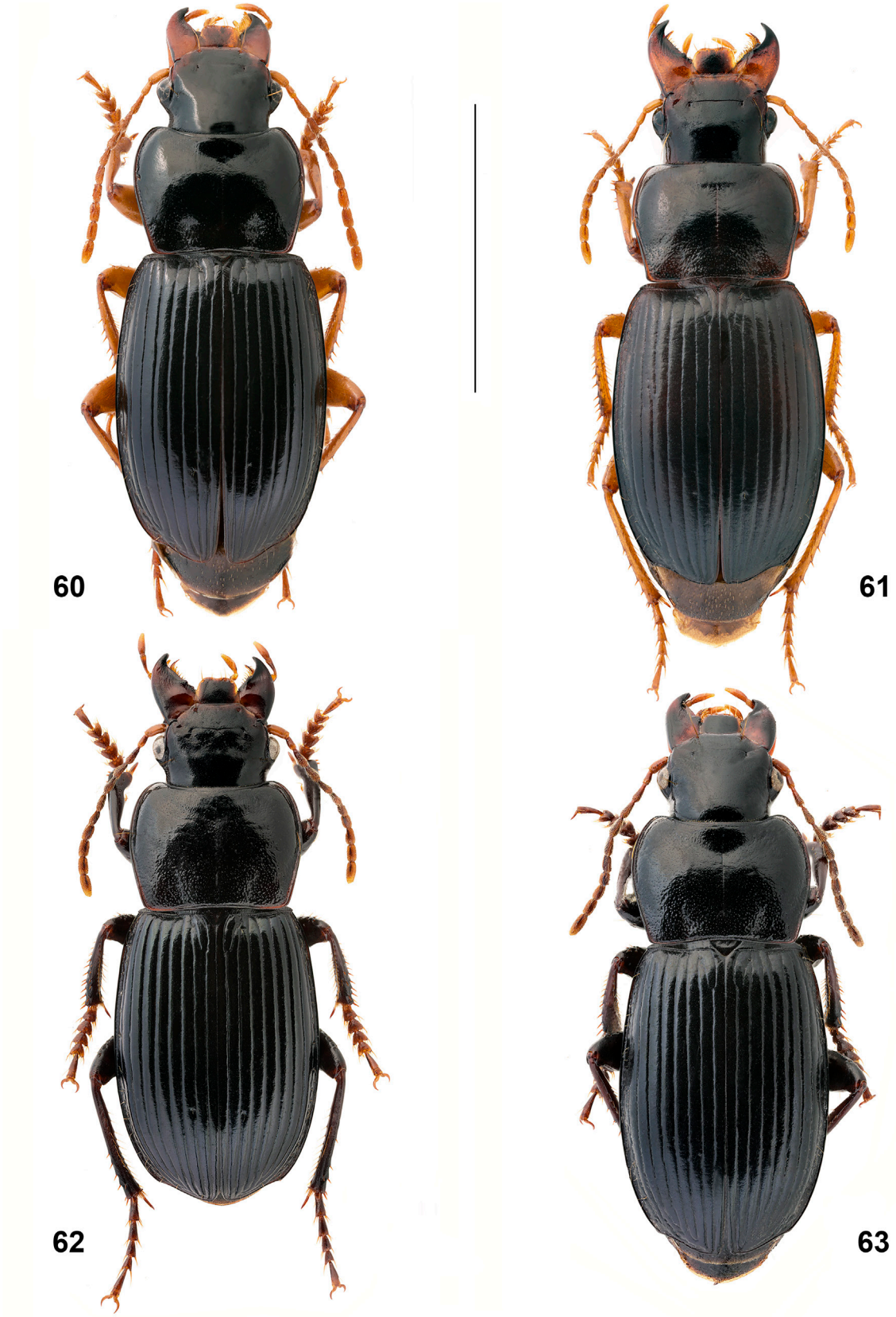
Redescription. Habitus as in Fig. 118. Pronotal sides straight or slightly sinuate basally; basal angles distinct, almost right or slightly obtuse, somewhat sharp or at most blunted at tip (Figs 68, 69); disc medially in males without microsculpture, in females generally with very fine, strongly obliterate meshes. Legs black or reddish brown. Head relatively wide. Elytra with parascutellar (basal) pore; odd intervals generally without preapical setigerous pores or occasionally (mainly interval 7) with one or two (rarely three) such pores. Median lobe of aedeagus (Figs 94–98) arcuate in lateral view, with terminal lamella more or less markedly curved ventrally, only slightly widened at apex in dorsal view; ventral margin of median lobe in lateral view with preapical sinuation; internal sac without small additional basal spiny patches on left side of median lobe.

Body size and proportions: see Table 2.

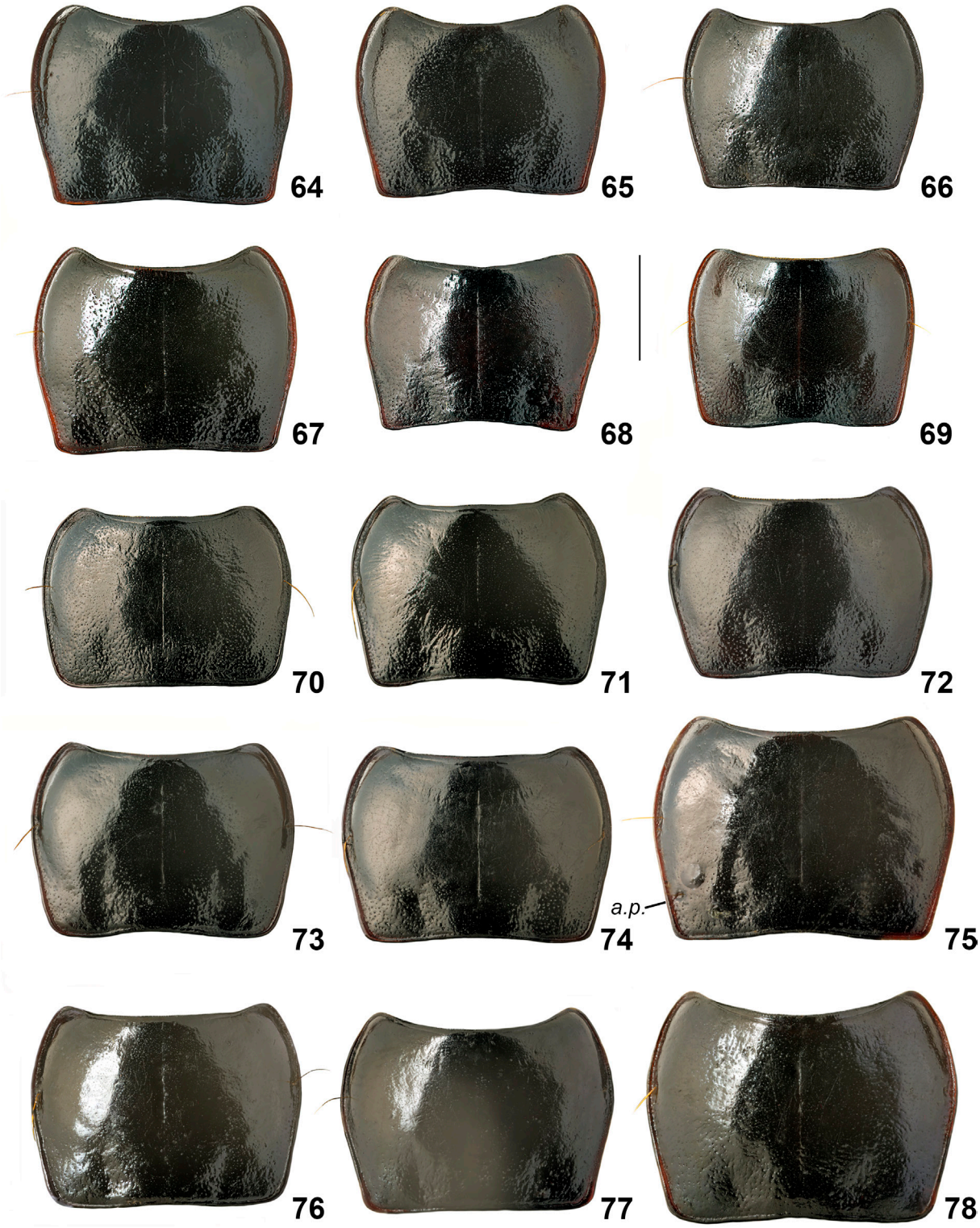
Comparative diagnosis. This subspecies is very similar in most characters to the nominotypical subspecies, but differs from it only in the shape of the median lobe of the aedeagus with terminal lamella curved ventrally. Like the nominotypical subspesies, it is characterized by relatively wide head. In the shape of the median lobe, *H. ch. retowskianus* is similar to the vicarious *H. ch. abasinus*, but differs from it, like the nominotypical subspecies, in the absence of small additional basal spiny patches in the internal sac of the aedeagus and the absence of preapical setigerous pores on the odd intervals of the relatively longer elytra; the basal pronotal angles are also generally sharper.

Notes. The status of this taxon, originally described as a separate species and then synonymized with the nominotypical subspecies [Kryzhanovskij et al., 1995], is questinable. Here it is treated as a subspecies of *H. chrysopus*, which in most characters is very similar to the nominotypical subspecies. Like the nominotypical subspesies, it is presented by red-legged and dark-legged forms. According to the original description [Reitter, 1887a], *H. retowskii* is based on a dark-legged series (males and females) collected in "Circassien" by Retowski and Starck; the author also specified the type locality as "Berg Atschischho [= Mt. Achishkho], Oktober 1884". The series of this taxon in Reitter's collection at TMB consists of three specimens collected by Starck, including a male and a female from "Fischt", dated 14.10.1884, and a male from "Abago" undated; no specimens were found from "Atschischho". Only one female from "Fischt" has original Reitter's determinational label "H. Retowskyi mih.". Although the holotype was not designated in the original description, this female was later erroneously labelled as the holotype by former museum curator Zoltán Kaszab, while the other two specimens were labelled by him as paratypes. However, these specimens are probably not syntypes, as neither Fisht nor Abago were mentioned in the original description. The ZIN collection also includes an additional pair from "Fischt", collected by Starck on 14.10.1884, as well as some other specimens collected by him in the Western Caucasus, all without Reitter's determinational labels. According to Reitter [1900], *H. retowskii* (= *H. retowskianus*) differs from *H. chrysopus* mainly in dark legs and in such interpretation corresponds to the dark-legged form of the latter. For this reason, both these names were considered synonyms [Kryzhanovskij et al., 1995], since in external characters, the dark-legged specimens from the Fisht-Oshten area are very similar to those from Achishkho; in addition, their aedeagi lack small basal spiny patches on the left side of the median lobes. However, all the examined specimens from Achishkho differ from those of the nominotypical subspecies, including the populations from the Fisht-Oshten area, in the shape of the median lobe of the aedeagus with a terminal lamella curved ventrally (Figs 94, 95). A similar structure of the aedeagus is also observed in specimens from the Bolshoy Tkhach area having reddish-brown and dark legs and in specimens from Khamyshki having reddish-brown legs, although in the latter locality this feature of the median lobe is expressed to a lesser degree (Figs 96–98). Based on this feature, *H. retowskianus* is treated here as a subspecies of *H. chrysopus*.

According to the original description [Lutshnik, 1933], *H. dinniki* is based on a single red-legged female from Temnolesskaya (Maykop District), a village located approximately 18 km northwest of Khamyshki. However, in Lutshnik's former collection (now in ZIN), the female designated by this author as a monotypus of *H. dinniki* was collected, judging by the label data, in Khamyshki, and not in Temnolesskaya. I do not know the reason for this discrepancy, but it is possible that this female is the holotype. Its morphological characteristics match the original description, although some doubts arise because the description of this species was published only two months after (25.09.1933) the female was collected (24.07.1933). In addition, Lutshnik's collection also includes a male collected together with this female, not mentioned in the original description, which has an additional label "ab. n.". Lutshnik [1933] compared *H. dinniki* only



Figs 60–63. *Harpalus* (*Caucasoharpalus*) *chrysopus chrysopus*, habitus, dorsal view.
60 – male (Soloniki); 61 – female (Mirny); 62 – male (Oshten); 63 – male (Khuko). Scale bar 5 mm.
Рис. 60–63. *Harpalus* (*Caucasoharpalus*) *chrysopus chrysopus*, габитус, вид сверху.
60 – самец (Салоники); 61 – самка (Мирный); 62 – самец (Оштен); 63 – самец (Хуко). Масштабная линейка 5 мм.



Figs 64–78. *Harpalus* (*Caucasoharpalus*) *chrysopus*, pronotum.

64–67 – *H.* (*C.*) *ch. chrysopus* (64 – Lazarevskoe; 65 – Uch-Dere; 66 – Chvizhepse; 67 – Fisht); 68–69 – *H.* (*C.*) *ch. retowskianus* (68 – holotype of *H. dinniki*, Khamyshki; 69 – Bolshoy Tkhach); 70–74 – *H.* (*C.*) *ch. abasinus* (70–71 – Tur'i Mountains, Aibga; 72 – Abishira-Akhuba; 73 – Reshivie; 74 – Chumkuzba); 75 – *H.* (*C.*) *ch. contumax*, holotype (Adler); 76–78 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (76 – Kuniashta; 77–78 – Apshara). *a.p.* – additional setigerous pore. Scale bar 1 mm.

Рис. 64–78. *Harpalus* (*Caucasoharpalus*) *chrysopus*, переднеспинка.

64–67 – *H.* (*C.*) *ch. chrysopus* (64 – Лазаревское; 65 – Уч-Дере; 66 – Чвижерсе; 67 – Фишт); 68–69 – *H.* (*C.*) *ch. retowskianus* (68 – голотип *H. dinniki*, Хамышки; 69 – Большой Тхач); 70–74 – *H.* (*C.*) *ch. abasinus* (70–71 – Турьи горы, Аибга; 72 – Абишира-Ахуба; 73 – Решивие; 74 – Чумкузба); 75 – *H.* (*C.*) *ch. contumax*, голотип (Адлер); 76–78 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (76 – Куниашта; 77–78 – Апшара). *a.p.* – дополнительная щетинконосная пора. Масштабная линейка 1 мм.

with *H. abasinus*, and based on the external characters, the former name, like *H. retowskianus*, was synonymized with *H. ch. chrysopus* [Kryzhanovskij et al., 1995]. Although I was unable to study the material from Temnolesskaya, based on the examined material from Khamyshki I now treat *H. dinniki* as a junior synonym of *H. ch. retowskianus*. This subspecies probably also includes specimens of *H. chrysopus* from Dakhovskaya and Lagonaki mentioned by Zamotajlov and Makaov [2010], as well as the specimens from Guzeripl and Kamyshanova Polyana, previously studied without examination of the male genitalia. The only specimen I examined from Dakhovskaya was a female. Males from this area should be examined in the future.

Harpalus ch. retowskianus forms a wide transition zone with *H. ch. abasinus* along the right bank of the middle and upper reaches of the Mzymta River, where intermediate populations occur both with and without small additional basal spiny patches in the internal sac on the left side of the medial lobe, as well as independently with or without preapical pores on the elytra. Their basal pronotal angles blunted or narrowly rounded at tip. Similar specimens are also found in Mount Abago and the westernmost part of the Aibga Range. In population from the Bolshoy Tkhach area, a slight transition to *H. ch. abasinus* is also observed: one red-legged male has a very indistinct additional spiny patch in the internal sac of the aedeagus ventrolaterally; in addition, compared to other populations, more individuals from there have preapical pores on the elytra. The intermediate populations distributed in the Abago and along the right bank of the Mzymta River upper Krasnaya Polyana (800–2400 m) include only dark-legged individuals.

Distribution (Fig. 146). North-West Caucasus between Achishkho, Lagonaki and Bolshoy Tkhach. In the east of the geographical range, in Mount Abago, the westernmost part of the Aibga Range and along the right bank of the middle and upper reaches of the Mzymta River, *H. ch. retowskianus* forms intermediate populations with *H. ch. abasinus*. In individuals from the Bolshoy Tkhach area, a slight transition to *H. ch. abasinus* is also observed.

Populations intermediate between *H. ch. retowskianus* and *H. ch. abasinus*. The following material refers to the transition zone, where the characteristics of two subspecies are mixed: legs black, pronotal basal angles blunted or narrowly rounded at tip, elytral intervals 7 and 5 with or without preapical pores, and median lobe of aedeagus with and without basal spiny patches; terminal lamella curved ventrally.

Material. Russia. Adygea: 1♂ (TMB), "Caucas occid., Abago Starck", "coll. Reitter", "Paratypus, *Harpalus Retowkyi* Reitter"; 1♂ (ZIN), "Caucas Occid. Abago Starck", "52", "*Harp. retowskii* Rttr. R. m. (Rttr. 88.)"; 1♀ (ZIN), "Caucas. Occid. Abago Starck", "676"; 1♂, 2♀, "Kuban., Abago, 27.07.1913". Krasnodar Region: Aibga Mt. Range: 1♂ (ZIN), "Aibga (Caucasus occidentalis)"; 1♂ (ZIN), "Аибга Кавказ" (Aibga Caucasus), "Monotypus", "*H. retowskianus* Reitt. ab. *sexpunctatus* V. Lutshnik d." (this taxon was not described); 1♂ (ZIN), "Аибга Кавказ" (Aibga Caucasus); 2♂ (ZIN), Aibga Mt. R., 28.06.1962 (V.N. Kurnakov); 1♂ (cAK), Aibga Mt. R, ca 2000 m, 7.09.1993 (P. Gorbachev); 1♀ (ZIN), 15 km E Adler, Mzymta River, 28.09.1993 (S. Ovtchinnikov); 6 ex. (cAK), Aibga Mt. R., ca 2000 m, 31.05.1995 (A.G. Koval); Main Caucasus Range: 5♂, 2♀ (ZIN), "Верх. М. Лабы, Куб. обл. 18.VIII.10 Н. Брянс" (upper of M. Laba, Kuban Province, 18.08.1910, N. Bryanskiy); 1♂ (ZIN), Puziko River, 18–25.07.1922 (B. Tkhachukov); 7♂ (ZIN), "Кр. Поляна Кавказ" (Krasnaya Polyana Caucasus); 1 ex. (MFNB), "Circassien, Krasnopol [Krasnaya Polyana], Carl Rost"; 5♂, 1♀ (ZIN), "Caucasus occ. Krasna. Polana Dr. Lgocki VIII"; 9♂, 2♀ (ZIN), "Caucasus occ. Krasnaja Polana [19]07... V", "Kiritschenko"; 1♀ (ZIN), same data but "[19]07.14.VII"; 1♀ (ZIN), same data but "[19]07.19.VII"; 1♂ (ZIN), same data but "[19]07.25.VII"; 1♂ (ZIN), Krasnaya Polyana, 800 m, 7.06.1954 (V.N. Kurnakov); 1♂, 2♀ (ZIN), Krasnaya Polyana, 7.07.1976 (V.G. Dolin); 6♂, 1♀ (ZIN), same data but 6.07.1978; 1♂ (ZIN), Krasnaya Polyana, 14.09.1978 (I.A. Belousov); 1♀ (ZIN), Krasnaya Polyana env., 7.08.1988 (A.I. Roubchenya); 2♂, 3♀ (cAT, ZIN), Krasnaya Polyana, 15.08.1988 (V.F. Shott); 1♂ (cAT), Krasnaya Polyana, 560 [m], 22.08.1988 (V.F. Shott); 7♂, 1♀ (cFM), Krasnaya Polyana env., Gorny shelter, 28.06.1999 (F.V. Melyakh); 1♀ (ZIN), "Pseaschcha [Pseashkho] 7000′ [ca 2130 m]"; 1♀ (ZIN), "Перев. Псеашхо 7000–8000′ 1900 Гриневецк." (Pseashkho Pass, 7000–8000′ (ca 2100–2400 m), 1900, Grinevetskiy); 1♂ (ZIN), Pseashkho Pass, Urushten River, 21.08.1909; 1♂ (ZIN), Pseashkho Pass, 29.06.1959 (V.N. Kurnakov); 1♀ (ZIN), Pseashkho Pass, 21.08.2009; 2♂, 2♀ (ZIN), "Верх. р. Пслух Черном. губ. 14.VIII.10, Н. Брянск" (upper Pslukh River, Chernomorskaya (Black Sea) Province (now within Krasnodar Region), 14.08.1910, N. Bryanskiy); 2♂, 1♀ (ZIN), Pslukh River, 21.08.1933 (K.V. Arnoldi); 3♂ (ZIN), valley of Pslukh River, 9.06.1954 (V.N. Kurnakov); 1♂ (cAZ), Krasnaya Polyana, Pslukh River, 1983 (A.S. Zamotajlov); 1♂ (cAP), Pslukh, 2000 m, 6.07.1999; 3♂, 2♀ (ZIN), "дор. на перевал Аишхо, Черном. г., 14–15.VIII.10. Н. Брянск" (road to Aishkho Pass, Chernomorskaya (Black Sea) Province (now within Krasnodar Region), 14–15.08.1910, N. Bryanskiy); 1♀ (ZIN), Aishkha, 24.07.1923 (K.V. Arnoldi); 1♂ (ZIN), same data but 22.08.1923; 2♂ (ZIN), Aishkho Pass, 2400 m, 16.05.1954 (V.N. Kurnakov); 2♂, 2♀ (ZIN), Aishkho Pass, 10.06.1954 (V.N. Kurnakov); 1♂ (ZIN), same data but 25.07.1954 (V.N. Kurnakov); 1♀ (MPSU), 25 km NE Estosadok, S slope of Mt. Aishkha, 43°38′10″N / 40°28′49″E, 1500 m, 7–13.08.2000 (D.G. Kasatkin); 2♂, 2♀ (ZIN), upper Pslushonok River near Aishkho Pass, 1500–2000 m, 31.08.2000 (A.G. Koval); 3♂ (ZIN), "дор. на оз. Кардывач, Черноморск. г., 22.VIII.909." (road to Lake Kardyvach, Chernomorskaya (Black Sea) Province (now within Krasnodar Region), 22.08.1909); 2♀ (ZIN), "Красн. пол. (Кардыв.) Черн. 12-VIII-912. Н.Л. Пастухов" (Krasnaya Polyana (Kardyvach) Chern. (Black Sea) 12.08.1912, N.L. Pastukhov); 4♂ (ZIN), Lake Kardyvach, 13.06.1954 (V.N. Kurnakov); 4♂ (cVZ, ZIN), Lake Kardyvach, 1600–1900 m, 25–26.06.1983 (B. Zvarič); 1♂ (ZIN), Lake Verkhniy Kardyvach, 2600 m, 24.08.1983 (A.S. Zamotajlov); 3♂ (ZIN), Bzych River, 1600 m, 23.08.1983 (A.S. Zamotajlov); 1♂ (ZIN), Caucasian Nature Reserve, Azmich [ca 43°34′N / 40°34′E], ca 1600 m, 12.06.1984 (V.P. Karasev); 1♂, 4♀ (ZIN), Mzymta River, Engelmanova Polyana, 1400–1600 m, subalpine, 9–13.06.2001 (V.G. Knysh); 2♂ (MPSU), basin of Mzymta River, mouth of Laura River, 600 m, alder (25 l. b.), 28.04–7.05.2004 (S. Alekseev, S. Tarasov); 2♂ (MPSU), basin of Mzymta River, Achipse River, 650–1500 m, 1.05–7.05.2004 (S. Alekseev, S. Tarasov); 1♂, 2♀ (MPSU), basin of Mzymta River, Achipse River, 650 m, beech-chestnut forest (25 l. b.), 6.05–22.07.2004 (S. Alekseev, S. Tarasov).

Harpalus (*Caucasoharpalus*) *chrysopus abasinus* Rost, 1892
(Figs 70–74, 81–84, 99–106, 107–117, 134, 146)

Harpalus abasinus Rost, 1892: 314 (type locality: "Abchasisches Hochgebirge", here restricted to Chipshira, Bzyb Mountain Range, Abkhazia based on the lectotype designation); Reitter, 1894: 117 (as a synonym of *H. retowskii*); Csiki, 1932: 1151.

Harpalus (*Harpaloxys*) *abasinus*: Reitter, 1900: 95; Lutshnik, 1922: 61; Zamotajlov, 1992: 46.

Harpalus chrysopus abasinus: Kryzhanovskij et al., 1995: 142.

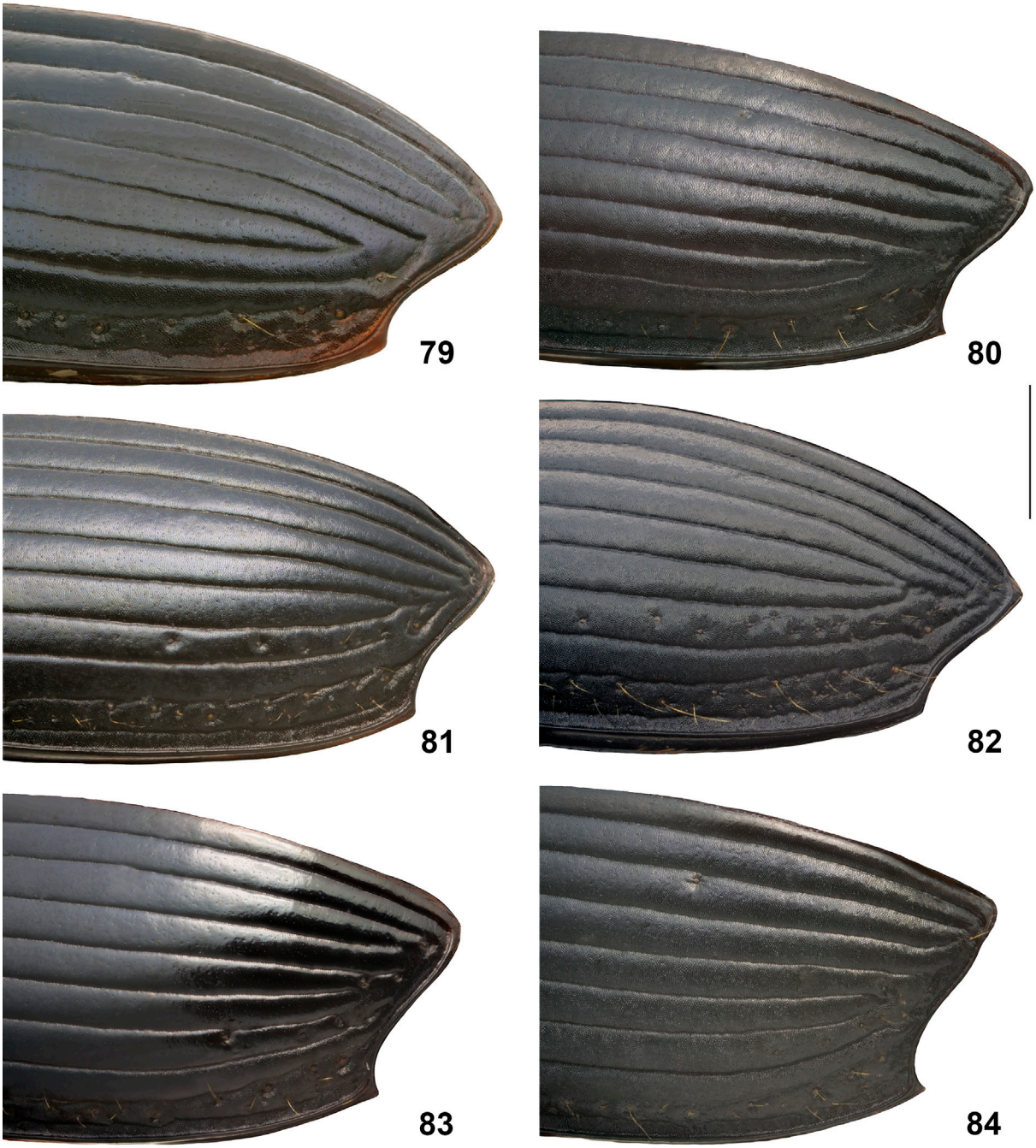
Harpalus (*Harpalus*) *chrysopus abasinus*: Lorenz, 1998: 345; Kataev et al., 2003: 374; Lorenz, 2005: 366; Kataev, Wrase, 2017: 525.

Harpalus (*Caucasoharpalus*) *chrysopus abasinus*: Kataev, 2023: 54.

Type material. 1♂, lectotype, present designation (SMTD), "Abchasia, Tschipchira, Rost", "*abasinus* m.", "ex. coll. Rost, Roenhke", "Type", "*Harpalus abasinus* Rost.", "ex coll. Rost", "Coll. Prof. Dr. Noesske, Ankauf, 1947", "Staatl. Museum für Tierkunde Dresden"; 1♂, paralectotype (TMB), "*H. abasinus* Rost, Type, Abchasien", "coll. Reitter", "Paratypus, *Harpalus abasinus* Rost"; 1♀, paralectotype (TMB), "Kaukasus, Abchasia, Rost", "coll. Reitter".

Material. Russia. Krasnodar Region: SW spur of Aibga Mt. Range: 1♀ (ZIN), 15 km E Adler, Mzymta River, 28.09.1993 (S.V. Ovchinnikov); 14♂, 4♀ (ZIN), Adler Distr., left bank of Mzymta River, 3–6 km E of Monastyr vill., forest [600–800 m], 14–16.06.2001 (B.M. Kataev); Aibga Mt. Range: 1♂, 1♀ (ZIN), "Аибга Зап. Кавказ К. Арнольди" (Aibga West Caucasus K. Arnoldi), "*Harpalus retowskianus* ab. *abasinus* Rost. Lutschnik d."; 1♂ (ZIN), "Аибга

Зап. Кавказ К. Арнольди" (Aibga West Caucasus K. Arnoldi), "Holotypus", "*H. chrysopus* Reitt. ab. *exspectatus* m. V. Lutshnik d." (this taxon was not described); 1♂ (ZIN), "Аибга 18.VIII.933 Зап. Кавказ К. Арнольди" (Aibga 18.08.1933 West Caucasus K. Arnoldi), "*Harpalus chrysopus* Reitt. Lutshnik d."; 1♂ (ZIN), "Аибга 18.VIII.933 Зап. Кавказ К. Арнольди" (Aibga 18.08.1933 West Caucasus K. Arnoldi), "*Harpalus retowskianus* Reitt. Lutshnik d."; 1♂, 2♀ (ZIN), "Аибга 18.VIII.933 Зап. Кавказ К. Арнольди" (Aibga 18.08.1933 West Caucasus K. Arnoldi); 1♀ (ZIN), "Аибга 18.VIII.933 Зап. Кавказ К. Арнольди" (Aibga 18.08.1933 West Caucasus K. Arnoldi), "Paratypus", "*H. chrysopus* Reitt. ab. *exspectatus* m. V. Lutshnik d." (this taxon was not described); 2♂, 3♀ (ZIN), Aibga, 13.07.1957 (V.N. Kurnakov); 2♂ (cIB), Aibga, Krasnaya Polyana, ca 2000 m, [43°38′38″N / 40°13′43″E], 15.09.1978 (I.A. Belousov); 1♂, 1♀ (cAK, ZIN), Aibga, subalpine zone, 1800–2000 m, ca 43°38′48″N / 40°13′42″E, 13.06.1987 (A.G. Koval); 1♂ (ZIN), Aibga, beech forest, 950 m, ca 43°38′54″N / 40°11′44″E, 23.08.1987 (A.G. Koval); 3♂, 2♀ (cIAS), Aibga Mt. R., S macroslope, subalpine-alpine zone, 2300 m, 23.06.1999 (I.A. Solodovnikov); 3♂, 3♀ (ZIN), Adler Distr., SW Aibga Mt. R., 4 km SE Krasnaya Polyana, upp. forest – subalpine zone,

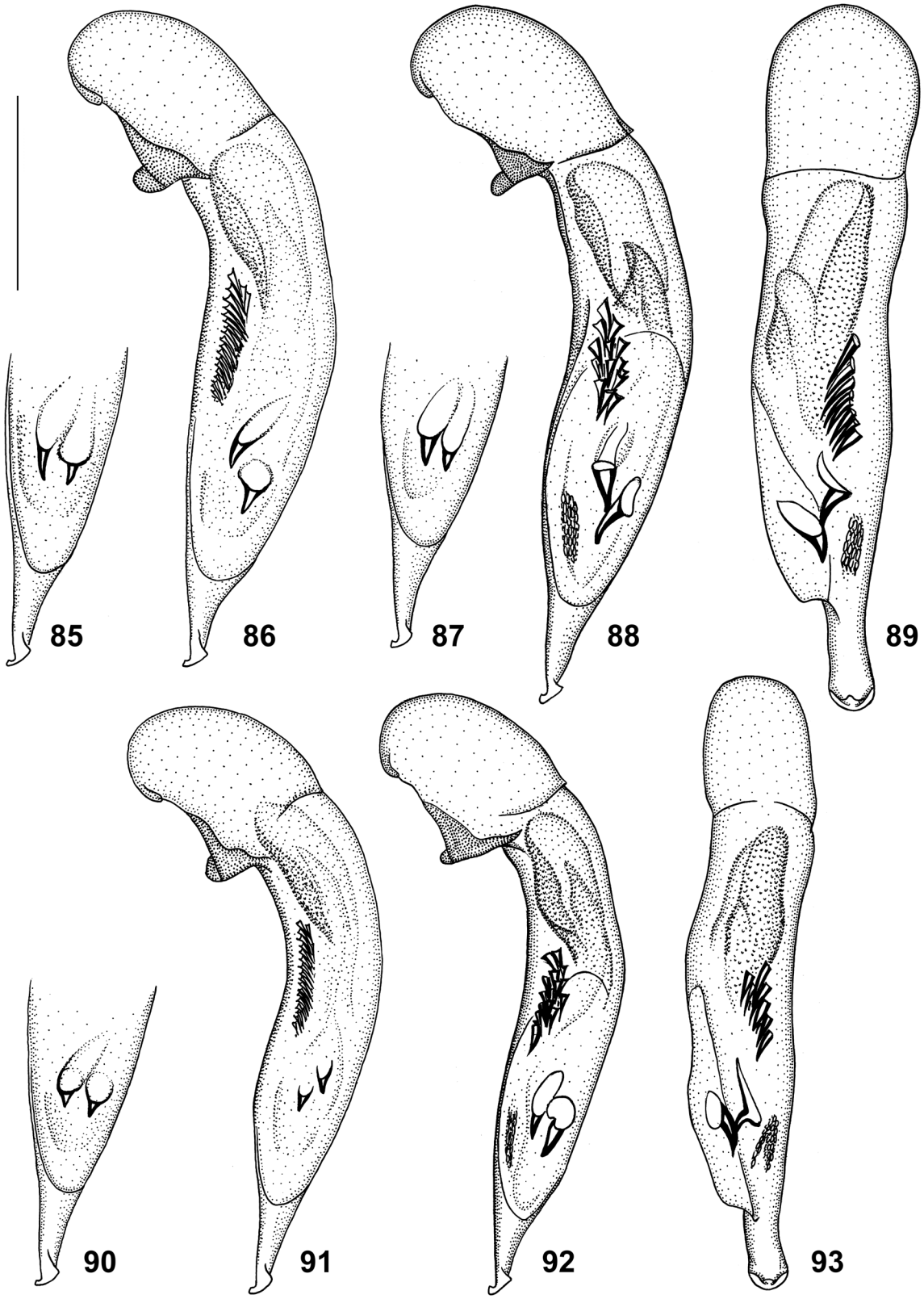


Figs 79–84. *Harpalus* (*Caucasoharpalus*) *chrysopus*, apical part of left elytron, dorsolateral view.

79–80 – *H.* (*C.*) *ch. chrysopus* (79 – Uch-Dere; 80 – Mirny); 81–84 – *H.* (*C.*) *ch. abasinus* (81 – Khimsul; 82 – Chipshira; 83–84 – to the east of Monastyr); 79, 81, 83 – males; 80, 82, 84 – females. Scale bar 1 mm.

Рис. 79–84. *Harpalus* (*Caucasoharpalus*) *chrysopus*, апикальная часть левого надкрылья, дорсолатеральный вид.

79–80 – *H.* (*C.*) *ch. chrysopus* (79 – Уч-Дере; 80 – Мирный); 81–84 – *H.* (*C.*) *ch. abasinus* (81 – Химсул; 82 – Чипшира; 83–84 – к востоку от Монастыря); 79, 81, 83 – самцы; 80, 82, 84 – самки. Масштабная линейка 1 мм.

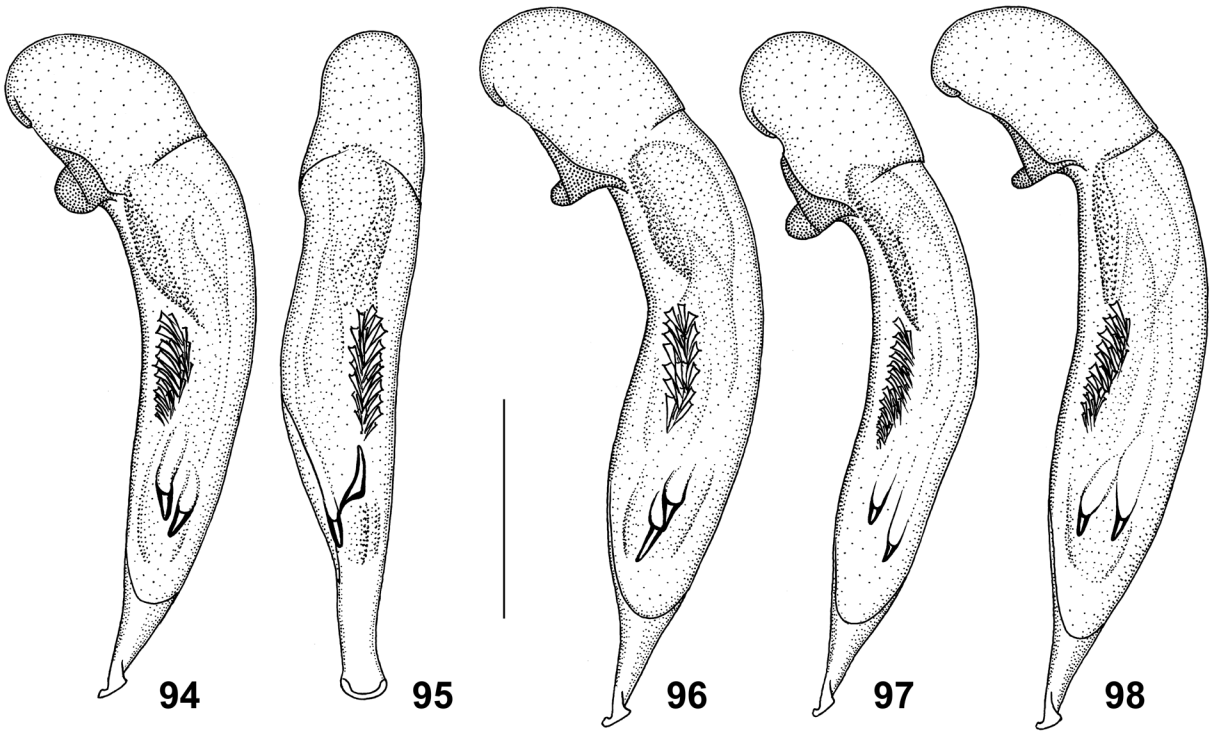


Figs 85–93. *Harpalus* (*Caucasoharpalus*) *chrysopus chrysopus*, median lobe of aedeagus and its apical part.

86, 88–89, 91–93 – median lobe of aedeagus; 85, 87, 90 – apical part of aedeagus. 85–88, 90–92 – lateral view; 89, 93 – dorsal view. Specimens: 85 – from Ubinskaya; 86 – from Kichmay; 87–89 – from Uch-Dere (88–89 – lectotype); 90 – from Iegosh; 91–93 – from Fisht. Scale bar 1 mm.

Рис. 85–93. *Harpalus* (*Caucasoharpalus*) *chrysopus chrysopus*, срединная доля эдеагуса и ее апикальная часть.

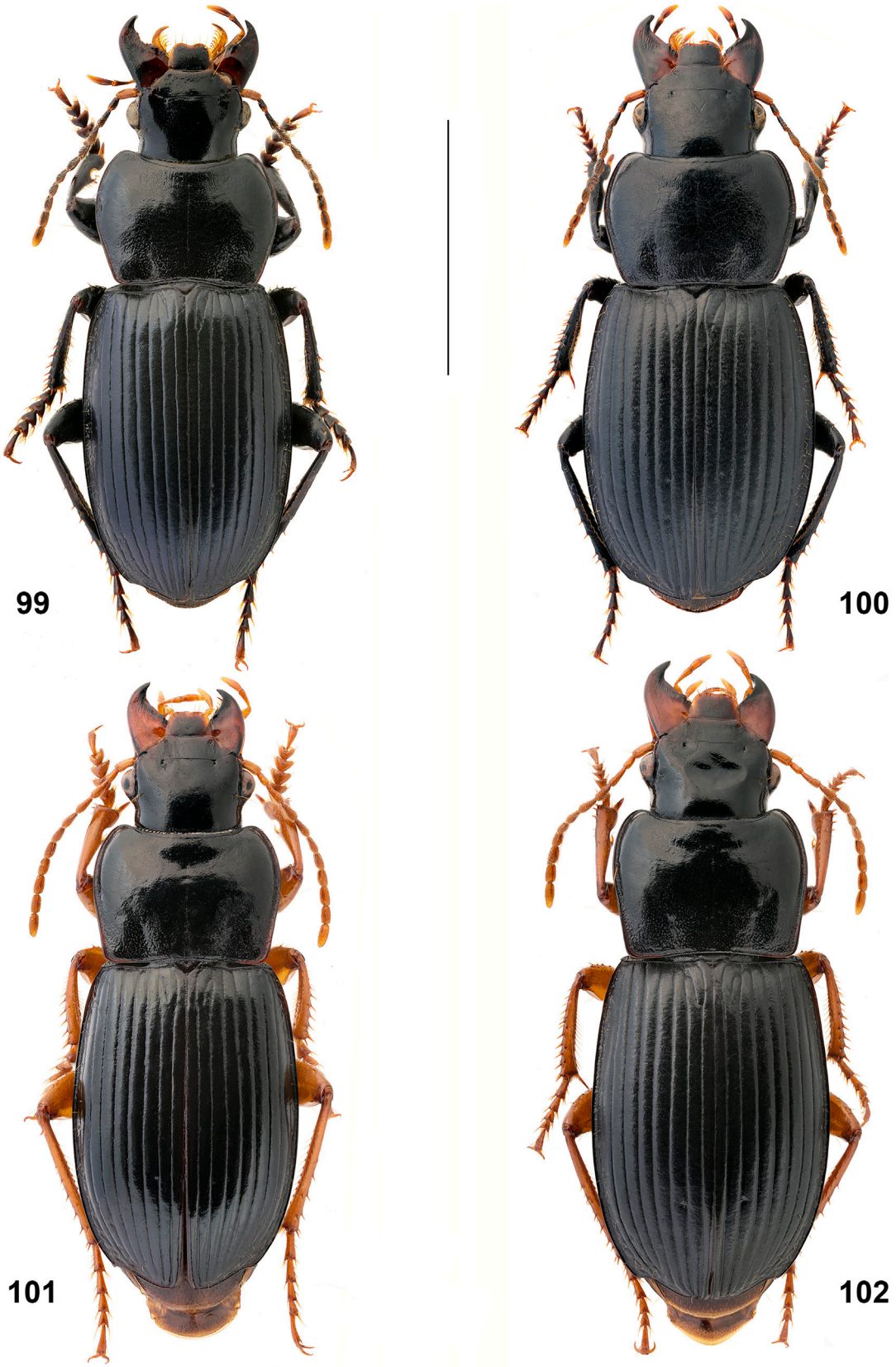
86, 88–89, 91–93 – срединная доля эдеагуса; 85, 87, 90 – апикальная часть. 85–88, 90–92 – вид сбоку; 89, 93 – вид сверху. Экземпляры: 85 – из Убинской; 86 – из Кичмая; 87–89 – из Уч-Дере (88–89 – лектотип); 90 – с Иегоша; 91–93 – с Фишта. Масштабная линейка 1 мм.



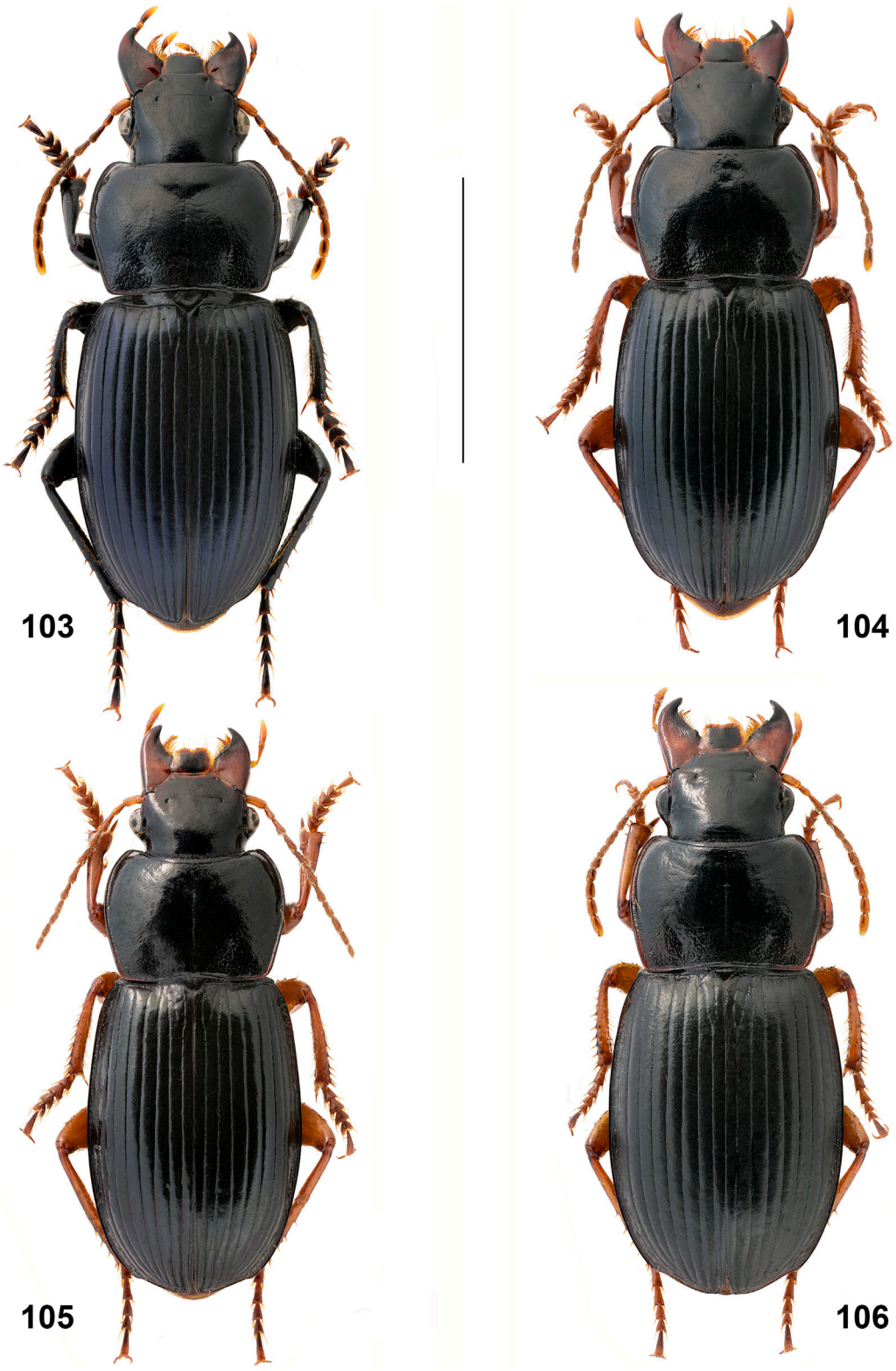
Figs 94–98. *Harpalus* (*Caucasoharpalus*) *chrysopus retowskianus*, median lobe of aedeagus.
94, 96–98 – lateral view; 95 – dorsal view. Specimens: 94–95 – from Achishkho; 96 – from Bolshoy Tkhach; 97–98 – from Khamyshki. Scale bar 1 mm.
Рис. 94–98. *Harpalus* (*Caucasoharpalus*) *chrysopus retowskianus*, срединная доля эдеагуса.
94, 96–98 – вид сбоку; 95 – вид сверху. Экземпляры: 94–95 – с Ачишхо; 96 – с Большого Тхача; 97–98 – из Хамышек. Масштабная линейка 1 мм.

17–18.06.2001 (B.M. Kataev); 2♂, 2♀ (ZIN), SW Aibga Mt. R., way to alpine zone [ca 2000 m], 19.06.2001 (B.M. Kataev); 2♂ (ZIN), Aibga Mt. R., S slope near Kamenny Stolb, forest – subalpine zone, 21.06.2001 (B.M. Kataev); 1♂ (ZIN), Aibga Mt. R., subalpine zone W of Tur'i Mts, 23.06.2001 (B.M. Kataev); 9♂, 2♀ (ZIN), S slope of Tur'i Mts, 21 km E Krasnaya Polyana, alpine-subalpine zone, 24.06.2001 (B.M. Kataev); 3♂, 2♀ (ZIN), watershed near Tur'i Mts, 25.06.2001 (B.M. Kataev); 1♂ (ZIN), waterfall Pdikarya, 43.851°N / 40.271°E, 1370 m, stream debris, 22.07.2016 (M. Salnitska). Karachay-Cherkessia: 1♂, 1♀ (ZIN), "Ур. Загдан, Куб. обл. хр. Аркасара, 30.VIII.10. Н. Брянский" (isolated terrain feature Zagedan, Kuban Province, Arkasara Mt. R., 30.08.1910, N. Bryanskiy); 2♂, 1♀ (ZIN), "8й пост ущелья Загдан Куб. о. 5.IX.11. Н. Брянский" (8th post in gorge of Zagedan, Kuban Province, 5.09.1911, N. Bryanskiy); 1♀ (MPSU), Mt. Zagedan upper Zagedan vill., lakes, ca 2000 m, 8.07.1994 (I.V. Melnik); 2♂, 2♀ (ZIN), Bolshaya Laba River system, source of Damkhurts River, 23.07.1957 (V.N. Kurnakov); 2♂ (ZIN), Arkasara Mt. R., upper Dukka River, 8.07.1987 (B.M. Kataev); 4♂, 3♀ (cIB), Arkasara Mt. R., SW slope of Mt. Dukka, 2200–2600 m, 10.07.1987 (I.A. Belousov); 4♂, 2♀ (ZIN), Arkasara Mt. R., Dukka Pass, 10.07.1987 (B.M. Kataev); 9♂, 10♀ (ZIN), upper Bolshaya Laba River lower mouth of Burnaya River, and right bank of Burnaya River, 10.07.1987 (B.M. Kataev); 2♂, 1♀ (MPSU), Urup Distr., Bolshaya Laba, Arkasara, 24–26.06.1997 (P.P. Ivliev, I.V. Shokhin); 1 ex. (cAP), Bolshaya Laba River; 1♂, 2♀ (ZIN), Mt. Sofia near Arkhyz, more than 2000 m, 17.07.1965 (V.N. Kurnakov); 1♂, 2♀ (MPSU), Abishira-Akhuba Mt. R., Lake Chilik env., ca 2000 m, 6.07.1987 (I.A. Belousov); 5♂, 1♀ (ZIN), S slope of Abishira-Akhuba, upper Rechepsta River, 7.07.1987 (B.M. Kataev); 7♂ (cIB), Arkhyz, Abishira-Akhuba Mt. R., Rechepsta River, 2200–2600 m, 7–8.07.1987 (I.A. Belousov); 1♀ (MPSU), same but 7.07.1987; 2♂ (cAP), Arkhyz, Abishira-Akhuba, 1700–2000 m, 3.07.1990 (A.V. Putchkov); 4♂ 1♀ (ZIN), N slopes of Abishira-Akhuba Mt. R., N slope of Mt. Dzhumarykly Tube, 43°36′15.99″N / 41°16′26.79″E, 2800–2900 m, 12–14.07.2009 (D.D. Fominykh); 1♂ (ZIN), upper Amanauz, tributary of Pshish River, 24.06.1990 (A.V. Putchkov); 1♀ (ZIN), upper Bolshoy Zelenchuk River, Amanauz, left tributary of Pshish River, 20.06.1992 (V.V. Grebennikov); 1♂ (MPSU), S slope of Mt. Urup to Atsgara River valley, 2500 m, 12–13.07.1994 (A.E. Brinev); 1♂ (MPSU), Arkhyz vill. env., upper Aykayra River, 43°26′08″N / 41°16′25″E, ca 2500–2600 m, 12.08.1998 (M.E. Chernyakhovskiy). Questionable localities: 1♂, 1♀ (MFNB), Teberda, 15.08.1974; 2♂, 1♀ (ZIN (ex Coll. S.V. Ovtchinnikov)), Teberda, Mashkhurts Mt. R., W Caucasus, 13.07.1994 (I.A. Belousov).

Abkhazia. Main Caucasus Range and its southern spurs: 1 ex. (cAR), Pskhu vill., Sanchar Pass env.; 5♂, 1♀ (ZIN), "ур. Псху, граница Черном. г. и Сух. о., 10.IX.10. Н. Брянск" (isolated terrain feature Pskhu, border of Chernomorskaya (Black Sea) Province (now within Krasnodar Region) and Sukhum Province (now Abkhazia), 10.09.1910, N. Bryanskiy); 2♂, 1♀ (ZIN), Sanchar Pass, 20.07.1954 (V.N. Kurnakov); 1♂ (ZIN), Pskhu vill., Chamashkha Pass, ca 2000 m, 20.04.1984 (V.P. Karasev); 1♂, 1♀ (ZIN, cISOL), Pskhu, Sancharo vill., 06.1991 (M.V. Maksimenkov); 2♂ (ZIN), 4 km N Pskhu vill., right bank of Aguripsta (Bavju) River, valley of Belaya River, 43°26′25.56″N / 40°48′53.77″E, 880 m, 11.05–30.06.2010 (D.D. Fominykh); 1♂ (ZIN), upper Bzyb River valley, 5.07.1954 (V.N. Kurnakov); 1♂, 1♀ (ZIN), Mt. Shemkhu, right bank of Bzyb River valley, 7.07.1954 (V.N. Kurnakov); 1♀ (ZIN), Chamagvara River (Bzyb River basin), 1–10.10.1984 (S. Kulik); 2 ex. (MFNB), Avadkhara, 2000–2800 m; 1♂ (cVZ), Audhara [Avadkhara], 1000–1600 m, 23–24.06.1983 (B. Zvarič); 1♂, 1♀ (ZIN), Avadkhara, 1800 m, 23.08.1983 (A.S. Zamotajlov); 1♂ (ZIN), Avadkhara, 18.09.1985 (Ushakov); 5♂, 1♀ (ZIN), N slopes of Mt. Anchkho, near Anchkho Pass, 43°2 8′49.97″N / 40°41′31.85″E, 2050 m, 26–28.06.2010 (D.D. Fominykh); 4♂, 2♀ (ZIN), S part of Main Caucasus Mt. R., near Anchkho Pass, Kamenistaya Polyana, 43°29′49.90″N / 40°44′17.52″E, 2100–2300 m, 9.07.2013 (D.D. Fominykh); 1♂ (cVS), Gudauta Distr., Pyv Pass [near Anchkho Pass], ca 2030 m, 21.08.2021 (V.A. Stolbov); Gagra Mt. Range: 6♂, 1♀ (cAK, ZIN), Psou River valley, W slope of Mt. Akh-Ag, ca 2000 m, 10.07.1989 (A.G. Koval); 1♀ (cVK), W slope of Gagra Mt. R., upper Krepostnaya River, 1125 m, forest zone, 10.06.2000 (V.G. Knysh); 3♂ (ZIN), sources of Krepostnaya River, 1125–1325 m, 27.07.2000 m (A.S. Zamotajlov). W Bzyb Mt. Range: 1♀ (ZIN), Novy Afon, 20.05.1896 (G.G. Sumakov), "*H. Retowskii* Reitt. var. Tschitscherin det."; 1♂, 2♀ (MFNB), Novy Afon, 3–8.07.1968 (F. Hieke); 1♀ (ZIN), Novy Afon env., near Anukhva vill., 700–800 m, 11.09.2015 (A.G. Koval); 2♂ (ZIN), Bzyb Mt. R. near Dou Pass, 15.07.1954 (V.N. Kurnakov); 4♂, 3♀ (ZIN), Gudauta Distr., subalpine meadows, 15.06.1955 (V.N. Kurnakov); 4♂, 1♀ (ZIN), Gudauta Distr., near Otkhara, subalpine zone, 7.06.1957 (V.N. Kurnakov); 2♀ (ZIN), N Achandara, 2000 m, 30.05.1961 (O. Kabakov); 1♀ (cAK), valley of Aapsta River, 300 m, 5.07.1985 (A.G. Koval); 2♂ (ZIN), Gudauta Distr., valley of Aapsta River, clearing in beech forest, ca 500 m, soil traps, 6.07–16.08.1985 (A.G. Koval); 1♂, 2♀ (MPSU), Gunarkhva [5–6 km N Khabyu on the trail; ca 700–800 m], 27.06.2003 (Yu.G. Arzanov); 2♂ (ZIN), Gudauta Distr., SE slope of Mt. Turetskaya Shapka, ca 1100 m, 13.06.1986



Figs 99–102. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, habitus, dorsal view.
99, 101 – males; 100, 102 – females. Specimens: 99 – from Khimsul; 100 – from Chipshira; 101–102 – to the east of Monastyr. Scale bar 5 mm.
Рис. 99–102. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, габитус, вид сверху.
99, 101 – самцы; 100, 102 – самки. Экземпляры: 99 – с Химсула; 100 – с Чипширы; 101–102 – к востоку от Монастыря. Масштабная линейка 5 мм.

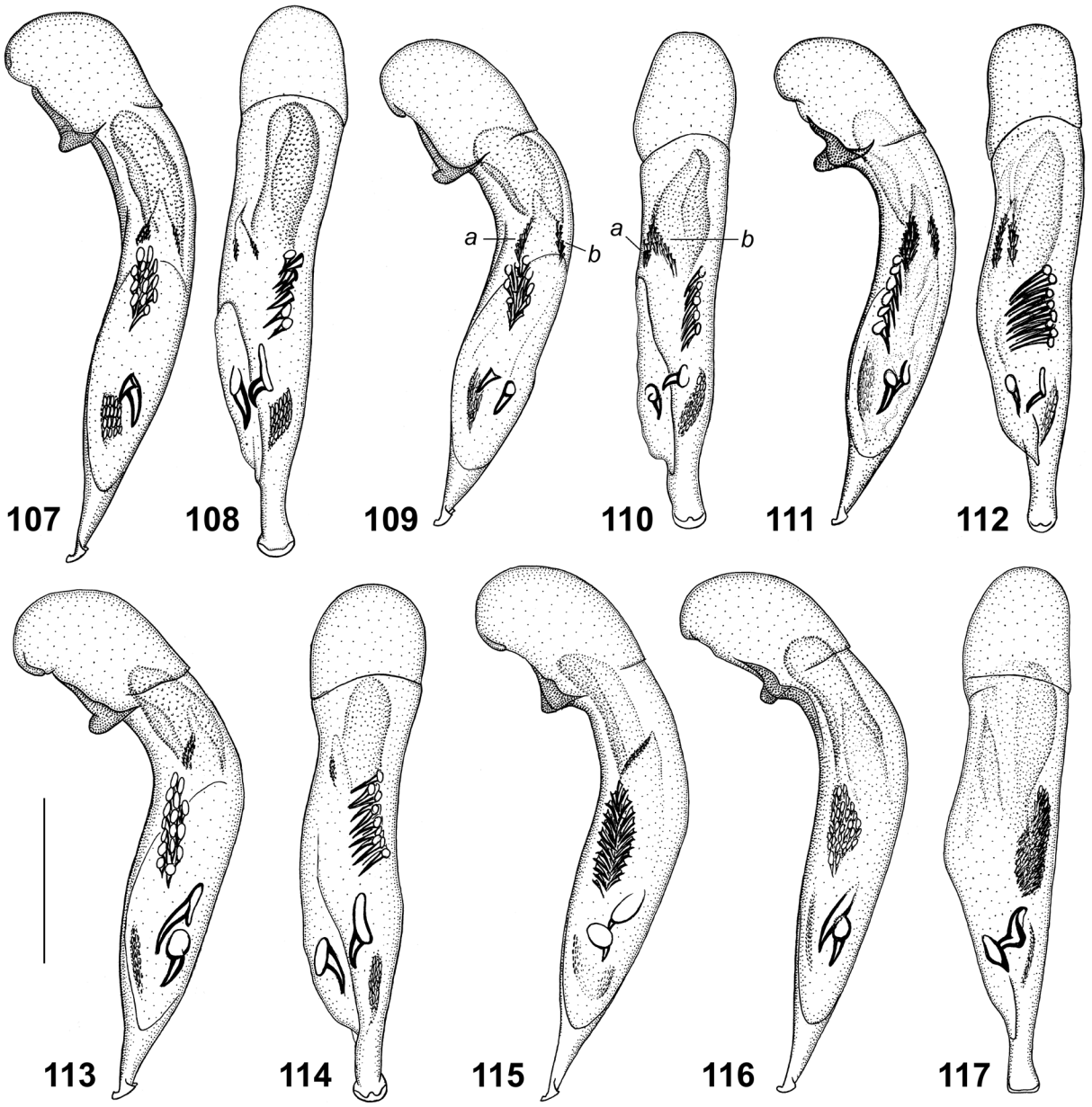


Figs 103–106. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, habitus, dorsal view.

103, 105 – males; 104, 106 – females. Specimens: 103 – from Khaka environs, Chedym; 104 – from Chumkuzba; 105–106 – from Chamagvara, Abkhazian Range. Scale bar 5 mm.

Рис. 103–106. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, габитус, вид сверху.

103, 105 – самцы; 104, 106 – самки. Экземпляры: 103 – из окрестностей Хаки, Чедым; 104 – с Чумкузбы; 105–106 – с Чамагвары, Абхазский хребет. Масштабная линейка 5 мм.



Figs 107–117. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, median lobe of aedeagus.

107, 109, 111, 113, 115–116 – lateral view; 108, 110, 112, 114, 117 – dorsal view. *a* – ventrolateral basal spiny patch; *b* – dorsolateral basal spiny patch. Specimens: 107–108 – intermediate between *H.* (*C.*) *ch. abasinus* and *H.* (*C.*) *ch. retowskianus*, from Abago; 109–110 – from Zagedan; 111–112 – lectotype, from Chipshira; 113–114 – from Novy Afon; 115–117 – from Chamagvara, Abkhazian Range. Scale bar 1 mm.

Рис. 107–117. *Harpalus* (*Caucasoharpalus*) *chrysopus abasinus*, срединная доля эдеагуса.

107, 109, 111, 113, 115–116 – вид сбоку; 108, 110, 112, 114, 117 – вид сверху. *a* – вентролатеральная базальная группа шипиков; *b* – дорсолатеральная базальная группа шипиков. Экземпляры: 107–108 – промежуточная форма между *H.* (*C.*) *ch. abasinus* и *H.* (*C.*) *ch. retowskianus*, с Абаго; 109–110 – из Загедана; 111–112 – лектотип, с Чипширы; 113–114 – из Нового Афона; 115–117 – с Чамагвары, Абхазский хребет. Масштабная линейка 1 мм.

(A.G. Koval); 2♂ (ZIN), same data but 700 m; 3♂, 1♀ (ZIN), E slope of Mt. Turetskaya Shapka, 1900 m, subalpine zone, 14.06.1986 (A.G. Koval); 1♀ (cAK), same data but 1700 m, soil traps, 14.06–9.08.1986 (A.G. Koval); 3♂ (MPSU), Mt. Turetskaya Shapka, 30.06.2001 (Yu.G. Arzanov); 1♀ (MPSU), same data but 1.07.2001; 3♂, 2♀ (MPSU), same data but 30.06–1.07.2001 (Yu.G. Arzanov, P.P. Ivliev); 1♀ (MPSU), same but 30–31.06.2003; 3♂, 9♀ (ZIN), N slopes of Mt. Turetskaya Shapka (Akibakhu), sources of Reshevie River, 43°17′47.43″N / 40°45′41.44″E, 1950 m, 3–5.07.2010 (D.D. Fominykh); 2♂, 4♀ (ZIN), camp near Mt. Turetskaya Shapka, 1840–1860 m, night, 3.07.2011 (A.S. Prosvirov); 5♂, 2♀ (ZIN), same data but day, 4.07.2011; 1♀ (ZIN), Khuap env., forest, 31.06–25.07.1986 (A.G. Koval); 1♂ (cIB), N Khuap vill., 1600–2000 m, 23–24.07.1987 (I.A. Belousov); 9♂, 8♀ (ZIN), Bzyb Karst Plateau, N Khuap, 1700–2100 m, 24.07.1987 (B.M. Kataev); 1♂ (cIB), N Khuap vill., Mt. Batakhu, 2200 m, 24–25.07.1987 (I.A. Belousov); 3♂, 2♀ (ZIN), same data but alpine zone, 2100–2400 m, 25.07.1987 (B.M. Kataev); 3♂, 3♀ (ZIN), N slope of Bzyb Karst Plateau, N Khuap, 25.07.1987 (B.M. Kataev); 1♀ (ZIN), Mt. Dzyshra, forest zone, 1400–1800 m, 14–15.07.1987 (B. Zvarič); 1♂ (cIB), way up along spur of Adzapshe, 12.06.1991 (I.A. Belousov); 2♂, 2♀ (ZIN, cIB), Mt. Napra and spur of Adzapsha, 12.06.1991 (I.A. Belousov); 4♂, 4♀ (ZMMU), 3.2 km NNW Mt. Napra, Abats, 43°20′00″N / 40°31′15″E, 2000 m, 15.06.2004 (A.A. Gusakov); 4♂, 1♀ (ZMMU, ZIN), 2.5 km NNE Mt. Napra, Abats, 43°19′35″N / 40°32′20″E, 2215 m, 16.06.2004 (A.A. Gusakov); 6♂, 6♀ (ZMMU, ZIN), 3.5 km NE Mt. Napra, foothills of Mt. Khimsul, 2100–2200 m,

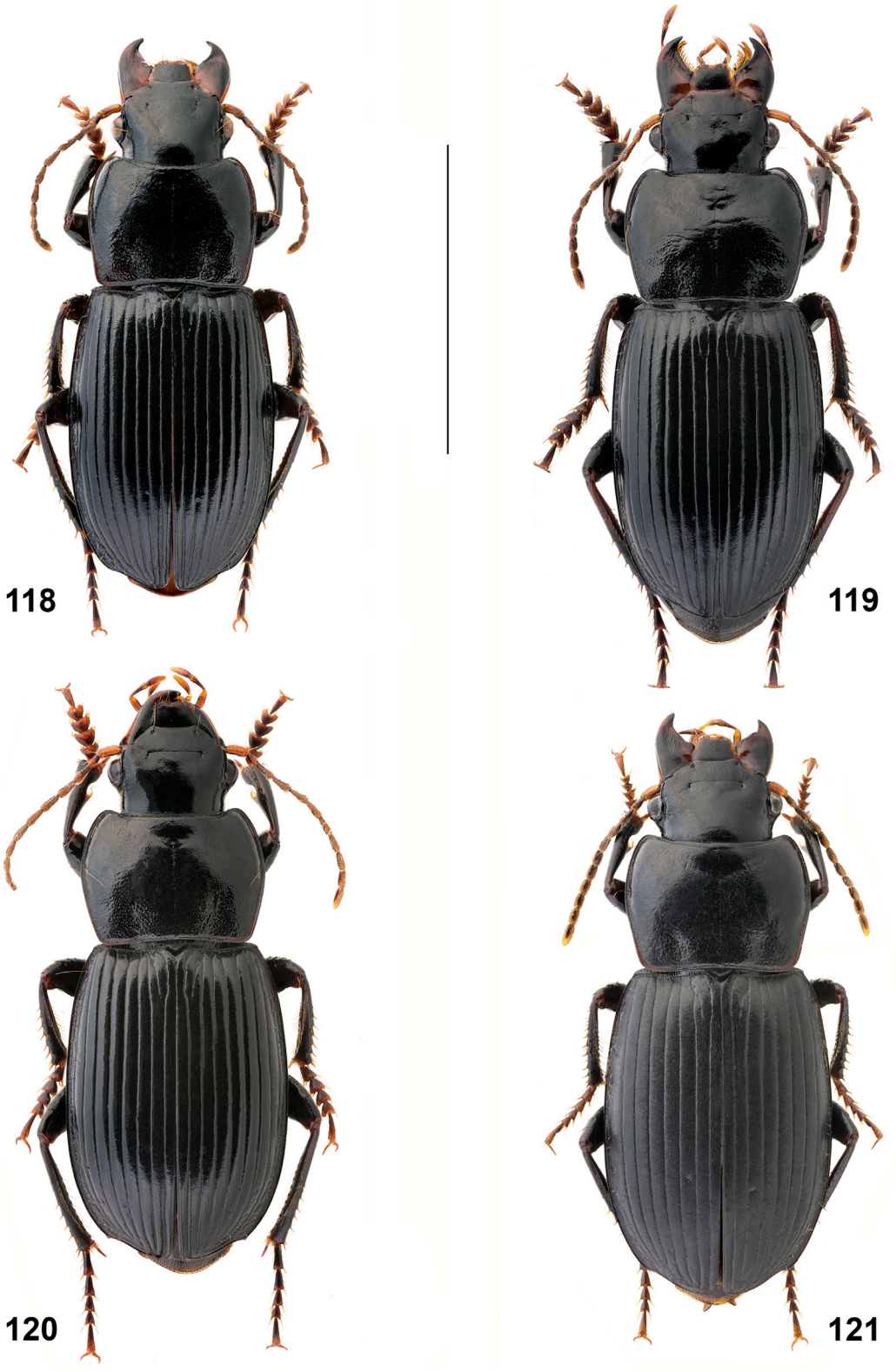
17.06.2004 (A.A. Gusakov); 4♂, 2♀ (ZMMU), 1.8 km NE Mt. Napra, 43°18′45″N / 40°32′55″E, 2240 m, 18.06.2004 (A.A. Gusakov); 3♂, 3♀ (ZMMU, ZIN), 1.6 km SEE Mt. Napra, S slope of Mt. Chipshira, 43°17′50″N / 40°32′55″E, 2210 m, 19.06.2004 (A.A. Gusakov); 3♂ (ZMMU), top of Mt. Napra, 43°20′00″N / 40°31′15″E, 2352 m, 19.06.2004 (A.A. Gusakov); 12♂, 1♀ (ZMMU, ZIN), 6 km E Mt. Napra, 2150 m, 43°18′30″N / 40°36′15″E, 20.06.2004 (A.A. Gusakov); 1♀ (cAK), NE slope of Mt. Chipshira, 2100 m, 15.08.2001 (L. Spiridonov); 1♀ (cAK), NE slope of Mt. Chipshira, 2200 m, 10–30.08.2010 (K.N. Gorbunova, V.A. Spodobin); 1♀ (cAK), same data but 2100–2200 m, 15–30.08.2010; 1♂ (cAK), Mt. Chipshira env., ca 2200 m, 25–28.08.2014 (K.N. Gorbunova); 1♀ (ZIN), Khipsta, 2050–2080 m, 24.06.2011 (A.S. Prosvirov); 6♂, 3♀ (ZIN), same data but 2050–2100 m, 25.06.2011; 2♀ (ZIN), camp near Mt. Khipsta, ca 2250 m, 27.06.2011 (A. Prosvirov); 5♂ (ZIN), camp W of Mt. Khipsta, 2240–2250 m, 28.06.2011 (A. Prosvirov); 2♂ (ZIN), Mt. Khipsta, pass, ca 2380 m, 29.06.2011 (A.S. Prosvirov); 1♂, 1♀ f (ZIN), Mt. Khipsta Massif, ca 2070–2080 m, 29.06.2011 (A.S. Prosvirov); 1♂ (ZIN), way up from forest to isolated terrain feature Khipsta, 1730–1780 m, 1.07.2011 (A.S. Prosvirov); 1♀ (ZIN), Bzyb Mt. R., way up along isolated terrain feature Khipsta, 2.07.2011 (A.S. Prosvirov); 1♂, 1♀ (ZIN), isolated terrain feature Khipsta, camp near pond, 1980–2000 m, 2.07.2011 (A.S. Prosvirov); 1♂ (cAK), near Mt. Khipsta, 1800–2000 m, 18.08.2015 (V.V. Rystsov); 3♂, 1♀ (cAK, ZIN), near Mt. Khipsta, 1850–1900 m, 43°15′54″N / 40°42′50″E, 21–25.08.2018 (A.G. Koval); 1♂, 1♀ (ZIN), way up to Mt. Akugra, 2110 m, 26.06.2011 (A.S. Prosvirov); 1♀ (cAPZ), N slopes of Bzyb Mt. R., Reshevie River, 700 m, 1–3.05.2012 (D.D. Fominykh); 5♂, 2♀ (ZIN), N slopes of Bzyb Mt. R., right bank of Reshevie River (left tributary of Bzyb River), 43°19′21.99″N / 40°49′17.60″E, 700–1000 m, 4.05–20.07.2012 (D.D. Fominykh). E Bzyb Mt. Range (Chedym and its southern spurs): 2♀ (ZIN), "Сухум Кутаиск. губ. 2.X.10. Н. Брянский" (Sukhum, Kutaisi Province, 2.10.1910, N. Bryanskiy); 1♀ (cIB), Gumista, 8.08.1976 (I.A. Belousov); 1♀ (ZIN), near foothills of Mt. Dzykhva, 13.08.1976 (I.A. Belousov); 1♂ (ZIN), Mt. Dzykhva, 2000 m, 7.06.1982 (V.I. Drabkin); 3♂, 1♀ (ZIN), same data but 2000–2400 m, 8.06.1982 (V.I. Drabkin); 4♀ (cVZ, ZIN), Mt. Dzykhva, region silvestris, 1400–1800 m, 14–15.07.1987 (B. Zvarič); 1♂, 1♀ (ZIN), spur of Mt. Dzykhva, clearning in forest, ca 1600 m, 23.07.1990 (V.I. Gusarov); 23♂, 12♀ (ZIN), S env. of Mt. Dzykhva, 43°11′19.3″N / 41°08′35.1″E – 43°13′02.9″N / 41°08′09.4″, 1600–2320 m, 24.06.2011 (B.M. Kataev); 9♂, 15♀ (ZIN), S slopes of Mt. Dzykhva, 43°13′02.9″N / 41°08′09.4″E, 2320 m, 24–25.06.2011 (B.M. Kataev); 1♂, 1♀ (ZIN), W slopes of Mt. Dzykhva, 43°13′02.9″N / 41°08′09.4″E – 43°14′21.5″N / 41°08′48.6″E, 2320–2150 m, 25.06.2011 (B.M. Kataev); 4♂ (ZIN), N of Mt. Dzykhva, N slope of Uim Pass, ca 2000 m, 26.06.2011 (B.M. Kataev); 5♂, 2♀ (ZIN), N of Mt. Dzykhva, S slope of Uim pass, ca 2000 m, 26.06.2011 (B.M. Kataev); 4♂, 2♀ (ZIN), NW slopes of Mt. Dzykhva, upper of Kot-Kot River, 43°13′20.29″N / 41°08′15.92″E, 2300 m, 29.04–2.07.2013 (D.D. Fominykh); 4♂, 2♀ (ZIN), Tsimur, 420 m, in leaf litter, 29–30.04.1980 (V.I. Drabkin); 2♀ (ZIN), Tsimur, 420 m, 3.06.1982 (V.I. Gusarov); 1♀ (ZIN), Tsimur, 450 m, 17–21.07.1990 (V.I. Gusarov); 4♂, 2♀ (cIB, ZIN), Chedym Mt. R., [above sources of Kuchkaya River, 43°17′56″N / 41°01′58″E], 2300–2700 m, 30.09–1.10.1987 (I.A. Belousov); 1♂ (ZIN), Mt. Chedym, 2400 m, 2.10.1987 (I.A. Belousov); 1♂ (ZIN), S slope of Chedym Mt. R., 2000 m, alpine zone, 4.09.1988 (A.G. Koval); 1♂, 1♀ (ZIN), Chedym Mt. R., Grecheskie summer camps, 2100 m, 4.09.1988 (A.I. Roubchenya); 1♂, 2♀ (ZIN), S slope of Chedym Mt. R., 1000 m, 5.09.1988 (A.G. Koval); 4♂ (ZIN), Chedym Mt. R., left trib. of East Gumista River, SW Khimsa Pass, 43°16′21.4″N / 41°08′46.5″E, 1875 m, upper forest zone, 26–27.06.2011 (B.M. Kataev); 16♂, 9♀ (ZIN), Chedym Mt. R., source of East Gumista River, E of Mt. Khaka, 43°17′51.3″N / 41°07′29.1″E, 2050 m, subalpine and alpine zones, 28–29.06.2011 (B.M. Kataev); 10♂, 2♀ (ZIN), Chedym Mt. R., way up from SE slope of Chedym to camp below Kervanka Pass, 1900–2100 m, 2.07.2012 (A.S. Prosvirov); 2♂, 1♀ (ZIN), Chedym Mt. R., camp below Kervanka Pass, 2000–2100 m, 3.07.2012 (A.S. Prosvirov); 1♂ (ZIN), same data but 2100 m, 4.07.2012 (A.S. Prosvirov); 1♀ (ZIN), Kelasur River valley, Pavlovka env., 800 m, forest, 17.09.1988 (A.G. Koval); 1♂ (ZIN), NE Sukhum, NE Odishi vill., 43°06′19.7″N / 41°07′39.3″E – 43°07′09.5″N / 41°07′32.5″E, 970–1140 m, 20.06.2011 (B.M. Kataev); 1♂, 2♀ (ZIN), same data but 43°07′44.4″N / 41°07′57.3″E, 1450 m, forest zone, 21.06.2011 (B.M. Kataev); 20♂, 7♀ (ZIN), SE of Mt. Chumkuzba, 43°08′19.8″N / 41°07′54.7″E – 43°08′50.7″N / 41°07′39.9″E, ca 1700 m, 22.06.2011 (B.M. Kataev); 3♂, 2♀ (ZIN), Mt. Chumkuzba, 43°08′50.7″N / 41°07′39.9″E, 2000 m, 23.06.2011 (B.M. Kataev). Abkhazian Mt. Range: 1♂ (ZIN), Chamagvara, 1000–1300 m, forest zone, 6.07.1989 (B.M. Kataev); 28♂, 16♀ (ZIN, cIB), Chamagvara, basin of Dzhampal River, meadow in upper forest zone, 1500–1600 m, 7.06.1989 (I.A. Belousov, B.M. Kataev).

Redescription. Habitus as in Figs 99–106. Pronotal sides from slightly rounded to slightly sinuate basally; basal angles almost right or obtuse, blunted or more or less rounded at tip (Figs 70–74); disc medially with or without fine microsculpture. Legs black or reddish brown. Elytra with parascutellar (basal) pore; intervals 7, often also 5 and rarely 3, with one or several (up to seven) preapical pores (intervals 5 and 3 with fewer pores than interval 7), occasionally without pores (Figs 81–84). Median lobe of aedeagus (Figs 107–117) markedly curved in lateral view, its terminal lamella more or less markedly curved ventrally and only slightly widened at apex in dorsal view; ventral margin of median lobe with preapical sinuation; internal sac generally with one or two small additional basal spiny patches (*a* and *b*) in internal sac on left side of median lobe (dorsolateral patch (*b*) or both patches in some specimens absent).

Body size and proportions: see Table 2.

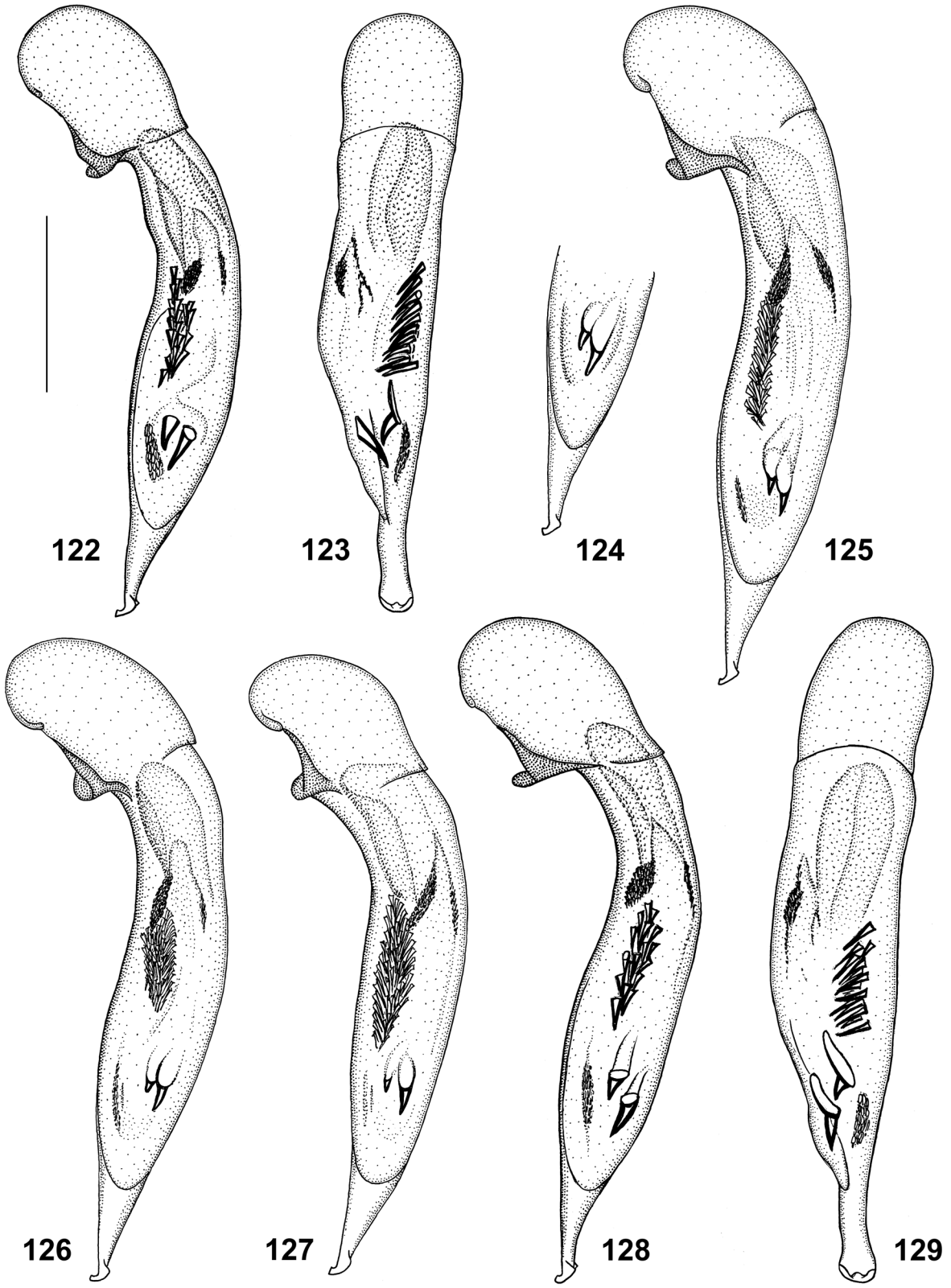
Comparative diagnosis. *Harpalus ch. abasinus* is recognized by having in most specimens the combination of three distinctive characters: 1) elytra with preapical pores on the odd intervals, 2) terminal lamella of aedeagus curved ventrally, 3) internal sac of the aedeagus with additional small basal spiny patches on the left side. This subspecies is most similar to *H. ch. contumax*, which also has additional basal spiny patches in the internal sac and preapical pores on the elytra, but differs from it in the terminal lamella of the aedeagus, which is curved ventrally; the terminal lamella of *H. ch. contumax* is straight or curved dorsally, as in the nominotypical subspecies. Other subspecies have no additional basal spiny patches in the internal sac of the aedeagus on the left side. *Harpalus ch. abasinus* also differs from the nominotypical subspecies and *H. ch. retowskianus* in having the elytra relatively shorter and in most specimens with preapical pores on the odd elytral intervals, the head relatively narrower and the pronotum with basal angles more rounded (accordingly, the base of the pronotum is narrower on average). It is also differs from the parapatric *H. ch. chkhaltensis* **subsp. n.** in the presence of parascutellar pores on the elytra.

Notes. *Harpalus ch. abasinus* is highly variable in habitus and, like the nominotypical subspecies, *H. ch. retowskianus* and *H. ch. contumax*, is represented by two forms, differing in leg colouration (black or dark brown and reddish brown). The dark-legged form corresponds to the type specimens of *H. abasinus*, described based on specimens from the Abkhazian Highlands (Bzyb Mountain Range). This form occurs at altitudes of about 500–2900 m in various mountains and occupies a larger part of the subspecies range. The red-legged form, like in other subspecies, is distributed in the lower altitudes than the dark-legged – from the Black Sea coast to 2300 m above sea level depending on the ridge; it occurs fragmentarily, but almost throughout the entire range of the subspecies from the Mzymta River to the Dzhampal Basin (Chamagvara) on the southern slopes of the Abkhazian Range. Without forming a continuous range, the red-legged form demonstrates gradual transitions to the dark-legged form at altitudes of about 500–2300 m on different ranges: in the western part of the Aibga Range, on the slopes of the Bzyb Range and on the southern slopes of the Main Caucasus in the Pskhu area. Although the red-legged form occurs on average lower than the dark-legged on each ridge, the elevation of the transition zone varies greatly depending on the mountain range and locality. The highest known localities of the red-legged individuals are the southern macroslopes of the Aibga and Dzykhva



Figs 118–121. *Harpalus* (*Caucasoharpalus*) *chrysopus*, habitus, dorsal view.
118 – *H.* (*C.*) *ch. retowskianus* (Achishkho); 119–121 – *H.* (*C.*) *ch. contumax* (119 – Zyrkhu; 120–121 – Mamdzyshkha). 118–120 – males; 121 – female. Scale bar 5 mm.

Рис. 118–121. *Harpalus* (*Caucasoharpalus*) *chrysopus*, габитус, вид сверху.
118 – *H.* (*C.*) *ch. retowskianus* (Ачишхо); 119–121 – *H.* (*C.*) *ch. contumax* (119 – Зырху; 120–121 – Мамдзышха). 118–120 – самцы; 121 – самка. Масштабная линейка 5 мм.

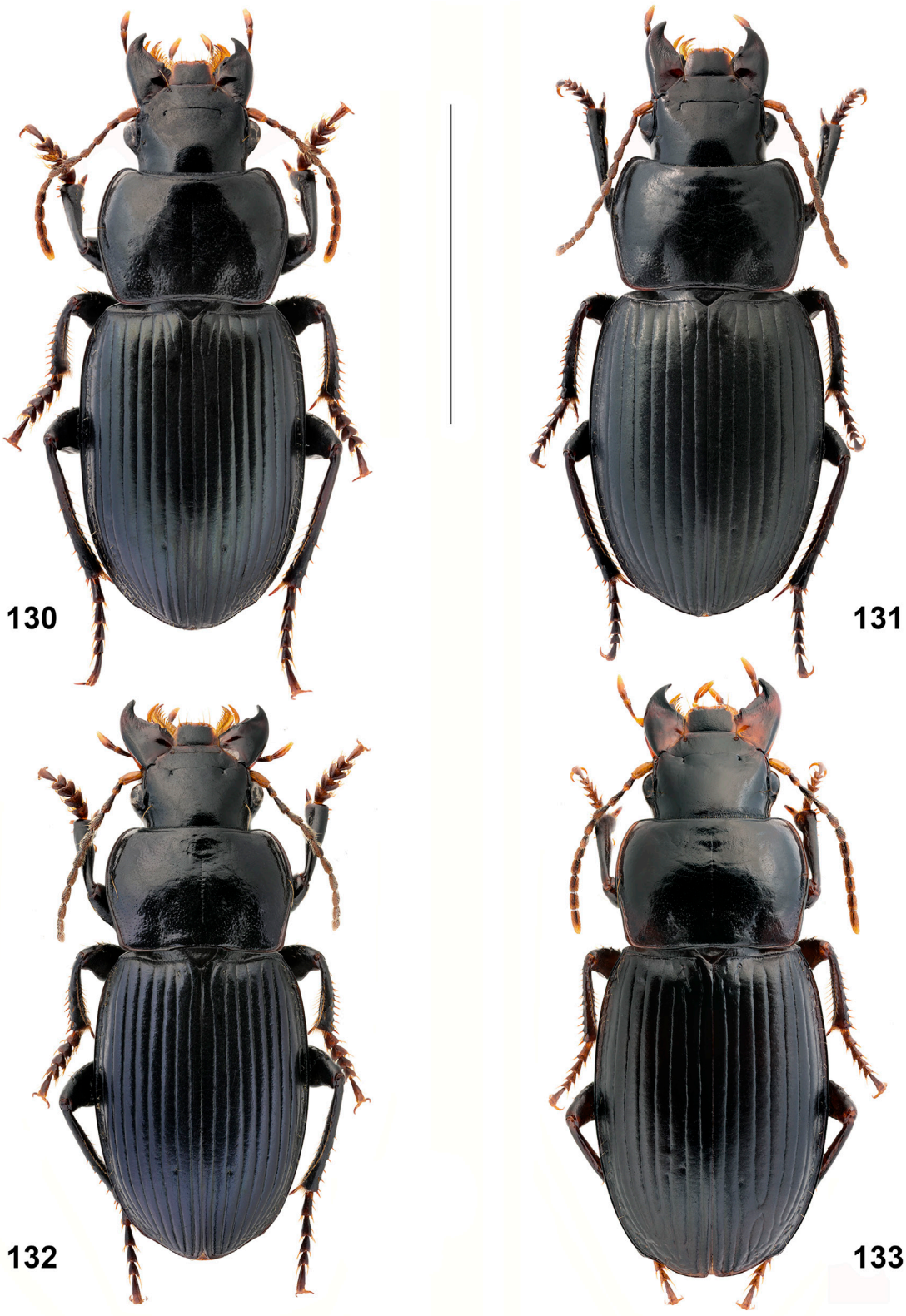


Figs 122–129. *Harpalus* (*Caucasoharpalus*) *chrysopus contumax*, median lobe of aedeagus and its apical part.

122–123, 125–129 – median lobe of aedeagus; 124 – apical part. 122, 124–128 – lateral view; 123, 129 – dorsal view. Specimens: 122–123 – holotype, from Adler; 124–125 – from Mamdzyshkha; 126 – from Gelgeluk; 127–129 – from Berchil. Scale bar 1 mm.

Рис. 122–129. *Harpalus* (*Caucasoharpalus*) *chrysopus contumax*, срединная доля эдеагуса и ее апикальная часть.

122–123, 125–129 – срединная доля эдеагуса; 124 – апикальная часть. 122, 124–128 – вид сбоку; 123, 129 – вид сверху. Экземпляры: 122–123 – голотип, из Адлера; 124–125 – с Мамдзышхи; 126 – из Гельгелука; 127–129 – с Берчиля. Масштабная линейка 1 мм.

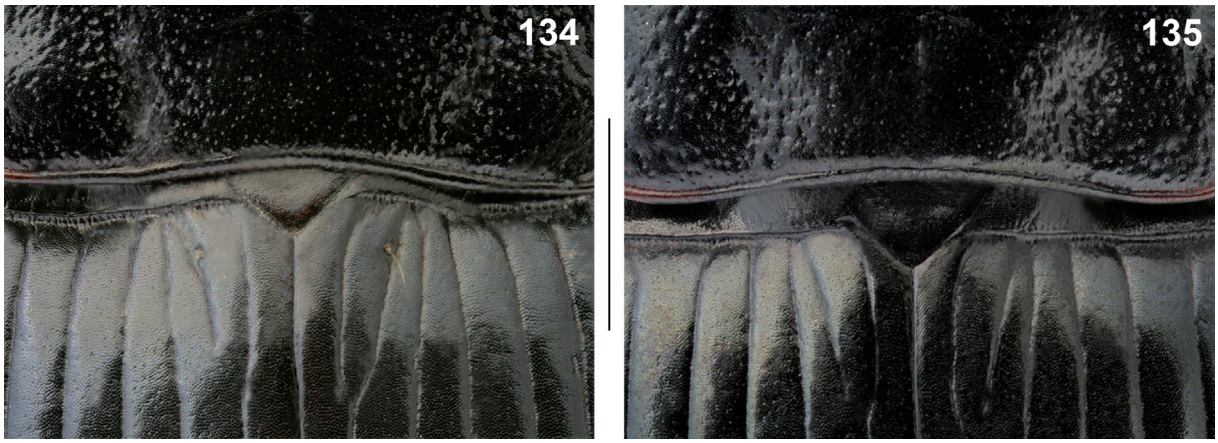


Figs 130–133. *Harpalus* (*Caucasoharpalus*) *chrysopus*, habitus, dorsal view.

130–131 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Shoudidi: 130 – holotype; 131 – paratype); 132–133 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (132 – Mokva; 133 – Kuniashta); 130, 132 – males; 131, 133 – females. Scale bar 5 mm.

Рис. 130–133. *Harpalus* (*Caucasoharpalus*) *chrysopus*, габитус, вид сверху.

130–131 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Шоудиди: 130 – голотип; 131 – паратип); 132–133 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (132 – Моква; 133 – Куниашта); 130, 132 – самцы; 131, 133 – самки. Масштабная линейка 5 мм.



Figs 134–135. *Harpalus* (*Caucasoharpalus*) *chrysopus*, scutellar area.
134 – *H.* (*C.*) *ch. abasinus* (Khimsul); 135 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Shoudidi). Scale bar 1 mm.
Рис. 134–135. *Harpalus* (*Caucasoharpalus*) *chrysopus*, прищитковая область.
134 – *H.* (*C.*) *ch. abasinus* (Химсул); 135 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Шоудиди). Масштабная линейка 1 мм.

Figs 136–139. *Harpalus* (*Caucasoharpalus*) *chrysopus*, apical part of left elytron, dorsolateral view.
136–137 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Shoudidi); 138–139 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (138 – Mokva; 139 – Kuniashta). 136, 138 – males; 137, 139 – females. Scale bar 1 mm.
Рис. 136–139. *Harpalus* (*Caucasoharpalus*) *chrysopus*, апикальная часть левого надкрылья, дорсолатеральный вид.
136–137 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (Шоудиди); 138–139 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (138 – Моква; 139 – Куниашта). 136, 138 – самцы; 137, 139 – самки. Масштабная линейка 1 мм.

mountains (about 2300 m); the lowest known findings of the dark-legged individuals are in the Aapsta River valley (about 500–700 m) on the southern macroslope of the Bzyb Mountain Range.

Both the dark-legged and red-legged forms generally possess all the main diagnostic features of the subspecies *H. ch. abasinus* listed above. Compared with the dark-legged form, the red-legged form has, on average, a relatively more elongate body and the pronotum with a relatively wider base and more distinct basal angles (PWmax/PWbas 1.15–1.24, *m* 1.2, *n* 22 versus 1.23–1.35, *m* 1.28, *n* 16). As in the case of the nominotypical subspecies, these characteristics reflect the general altitudinal pattern of variability. In addition, the microsculpture on the pronotum of the dark-legged form is more developed and present generally in males and females.

Geographic variation in some characters within subspecies is also observed. With minor individual characteristics of almost all local populations, the specimens of *H. ch. abasinus* from the eastern part of the subspecies range – the Chedym and, especially, the lower part of the Abkhazian Range – are characterized, on average, a smaller number (0–3) of preapical pores on the odd elytral intervals and less developed additional basal spiny patches in the internal sac of the aedeagus, of which only the ventrolateral one is often present (Figs 115–117). The red-legged population from the forest zone on the southern slopes of the Abkhazian Mountain Range (Chamagvara area, ca 1000–1600 m) is especially distinct in this regard, although it is quite similar to the red-legged populations from the southeastern spurs of the Chedym Range. In most individuals from Chamagvara, the elytral interval 7 is without preapical pores, occasionally with one or two pores (very rarely with greater number, up to five) and often only on one elytron; interval 5 is without preapical pores, rarely with one pore, usually also only on one elytron; in one examined male, the interval 3 has two preapical pores on each elytron; of 13 examined aedeagi, ten are without additional basal spiny patches in the internal sac, and three have only one very small spiny patch lateroventrally (as in Fig. 115). Interestingly, one male examined from Chamagvara has a parascutellar setigerous pore only on the right elytron. The absence of the parascutellar pores is characteristic of the dark-legged *H. ch. chkhaltensis* **subsp. n.**, which constantly lacks basal spiny patches in the internal sac of the aedeagus and is distributed mainly higher up the Abkhazian Range. Otherwise, the red-legged population of *H. ch. abasinus* from Chamagvara is quite separated from *H. ch. chkhaltensis* **subsp. n.** They probably do not form a transitional zone, although the absence of a parascutellar pore in one specimen from Chamagvara suggests that the genetic isolation between them is not absolute. The status of the red-legged population from the southern slopes of the Abkhazian Range needs further study.

Distribution (Fig. 146). This subspecies is distributed in the forest belt and highlands of the northern and southern slopes of the Main Caucasian Range and its spurs from the upper reaches of the Mzymta River to the upper reaches of the Bzyb River, also in the Abishira-Akhuba and Aibga ranges, in the western and northern parts of the Gagra Range, in the Bzyb Range, including the Chedym and Dzykhva, as well as in the southern slopes of the Abkhazian (Chkhalta) Range. It integrates with *H. ch. retowskianus*, forming a fairly wide transitional zone in the northwest of the subspecies range along the right bank of the middle and upper reaches of the Mzymta River and in Abago, and it is replaced by *H. ch. chkhaltensis* **subsp. n.** to the east of the Chedym Range and by *H. ch. contumax* in the southern part of the Gagra Range. The occurring of this subspecies in Teberda requires confirmation, as the above-mentioned specimens from there may have been mislabelled.

Harpalus (*Caucasoharpalus*) *chrysopus contumax* Lutshnik, 1933
(Figs 3, 75, 119–129, 146)

Harpalus (*Harpaloxis*) *contumax* Lutshnik, 1933: 131 (type locality: Adler, Krasnodar Region, Russia).

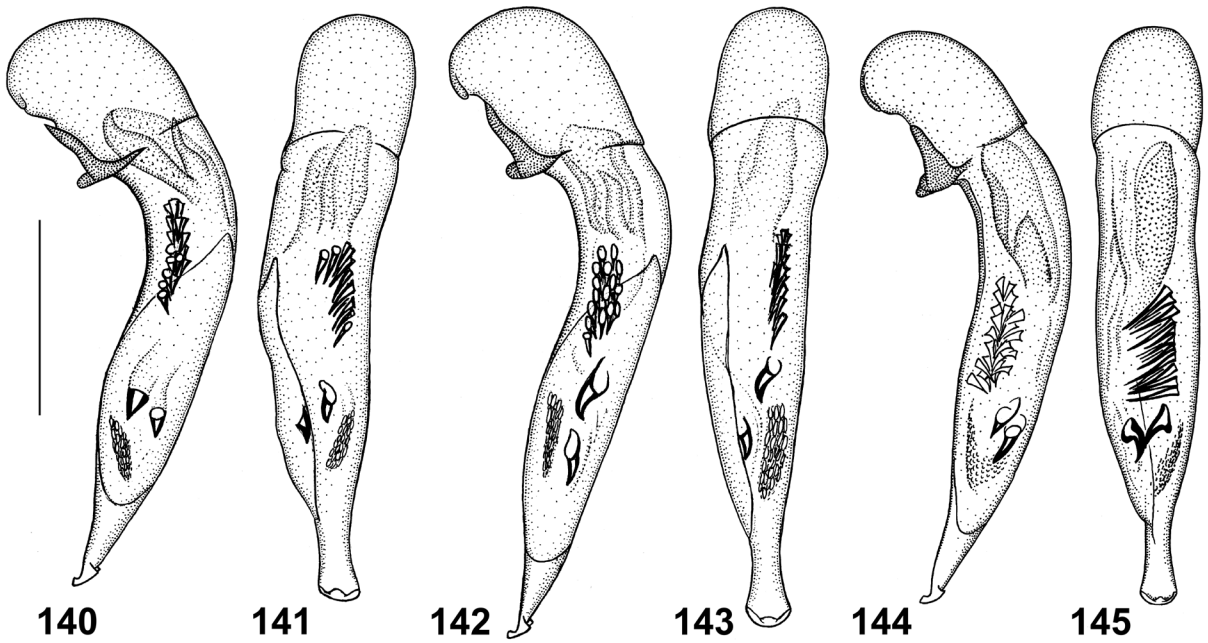
Harpalus chrysopus contumax: Kryzhanovskij et al., 1995: 142.

Harpalus (*Harpalus*) *chrysopus contumax*: Lorenz, 1998: 345; Kataev et al., 2003: 374; Lorenz, 2005: 366; Kataev, Wrase, 2017: 525.

Harpalus (*Caucasoharpalus*) *chrysopus contumax*: Kataev, 2023: 54.

Type material. 1♂, holotype (ZIN), "Адлер 8.08.931 Зап. Кавказ В. Лучник" (Adler, 8.08.1931 W Caucasus V. Lutshnik), "Monotypus", "*Harpalus contumax* m. V. Lutshnik det.", "vidi 1970 Dr. Z. Mlynář det.".

Material. Abkhazia. Gagra Mt. Range: 1♂ (ZMMU), Gagra; 1♀ (ZIN), "Gagry, alpes... under stones, 24.06.1909, A. Ya. and A. Zh."; 1♀ (ZIN), "Окр. Гагр Зап. Кавказ 19.VI.933 К. Арнольди" (Gagra env., West Caucasus, 19.06.1933, K. Arnoldi), "Ideotypus", "*Harpalus contumax* Lutshn., V. Lutshnik d."; 1♂ (cWR), Gagra env., 06.1976 (K. Denes); 1♂ (ZIN), Gagra Distr., 8 km NE Tsandrypsh vill. (Gantiadi), gorge of Khashupse River, forest, 6.09.2008 (A.V. Matveev); 4♂ (ZIN), Mamdzyshkha Mt. R., subalpine zone, 13.07.1955 (V.N. Kurnakov); 3♂ (cIB), Mt. Mamdzyshkha, 3.06.1984 (A.G. Koval); 1♂ (ZIN), same data but 15.06.1985; 1♂ (ZIN), Mt. Mamdzyshkha, 1300 m, 27.07.1984 (V.N. Prasolov); 1♂ (ZIN), same data but 1600 m, 27.07.1984; 16♂, 2♀ (ZIN), same data but 1700 m; 4♂ (ZIN), same data but 1500 m, 27–28.07.1984; 11♂, 1♀ (ZIN), same data but 1400 m, 28–29.07.1984; 1♂, 1♀ (ZIN), same data but 1000 m, 29.07.1984; 3♂, 2♀ (ZIN), "Mamdz 85" (= W slopes of Mt. Mamdzyshkha, Akhas summer camp env., 1600–1750 m, 1985 (A.S. Zamotajlov)); 2♂, 1♀ (ZIN), S spur of Arabika Massif [Mt. Mamdzyshkha], ca 2100 m, 5.07.1986 (A.G. Koval); 3♂, 1♀ (ZIN), Mt. Mamdzyshkha, 1600 m, 16.05.2012 (E.E. Khomitskiy); 1♂ (cVS), Mt. Mamdzyshkha, 27.08.2021 (V.A. Stolbov); 1♀ (ZIN), "Abchasien Arabica Geb. 7000', E. König"; 2♂ (ZIN), isolated terrain feature Gelgeluk (Arabika mts), 1750 m, subalpine zone, 1.09.1960 (V.N. Kurnakov); 13♂, 9♀ (cAK, ZIN), Mt. Arabika Massif, Gelgeluk valley, 1800–2100 m, 43°26′10″N / 40°18′33″E – 43°26′06″N / 40°19′29″E, 8–12.07.2018 (A.G. Koval); 1♂, 1♀ (cAK), Arabika Massif, Gelgeluk valley, 1800–1850 m, 43°26′03″N / 40°18′30″E, 13–15.09.2018 (A.G. Koval); 4♂, 2♀ (ZIN), Berchil Mt. R., near Mt. Arabika, 17.06.1962 (V.N. Kurnakov); 2♂, 2♀ (ZIN (ex Coll. A.S. Zamotajlov)), "Gizle 85" (= Gyuzlya, Arabika Massif, southern slopes of Berchil Mt. R., upper forest line and subalpine zone, ca 1600–1800 m, 1985); 3♂ (cAK), Gagra Mt. R., Arabika Massif, N slope of Berchil Mt. R., 2000–2300 m, 7.07.2016 (A.G. Koval); 8♂, 3♀ (ZIN), Berchil Mt. R., near Kushonskiy Pass, 2.5 km SW Mt. "Arbaika" (Arabika), 43°24′32.11″N / 40°19′31.01″E, 2270 m, 28.06–4.07.2021 (D.D. Fominykh); 1♂ (ZIN), Arabika Massif, SW slope of Mt. Zont, ca 2100 m, 16.07.1987 (A.G. Koval); 2♂ (ZIN), same data but 21, 28.08.1988 (A.I. Roubchenya); 1♀ (cAK), NW slope of Mt. Arabika, 1800–2300 m, 2–8.06.2012 (N.L. Ivanov, N.M. Fedorova, D.A. Gavryushkin); 1♀ (cAK), NW slope of Mt. Arabika, 2000–2300 m, 16–22.09.2013 (N.L. Ivanov); 1♂ (cAK), near (= NW of) Mt. Arabika, 2280 m, 43°25′39″N / 40°21′09″E, 12–22.08.2016 (N. Ivanov, A. Shikalova, L. Okulova); 4♂, 1♀ (cAK), near (= NW of) Mt. Arabika, 2260 m, 43°25′51″N / 40°20′23″E, 9.08.2019 (A.G. Koval); 1♂ (ZIN), Tepebashe Mt. R., near Achmarda vill., 2000 m, 20.08.1988 (A.I. Roubchenya); 4♂, 1♀ (ZIN, cIB), Zyrkhu Mt. R. before pass to basin of Kholodnaya Rechka, 800–1800 m, 7–8.06.1991 (I.A. Belousov); 5♂, 1♀ (ZIN, cIB), Zyrkhu Mt. R., basin of Kholodnaya Rechka, 800–1800 m, 7–8.06.1991 (I.A. Belousov); 4♂, 1♀ (ZIN, cIB), pass in Gechu from source of Kholodnaya Rechka, 10.06.1991 (I.A. Belousov).



Figs 140–145. *Harpalus* (*Caucasoharpalus*) *chrysopus*, median lobe of aedeagus.
140–143 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (140–141 – Adange; 142–143 – Kopshara); 144–145 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (Apshara). 140, 142, 144 – lateral view; 141, 143, 145 – dorsal view. Scale bar 1 mm.
Рис. 140–145. *Harpalus* (*Caucasoharpalus*) *chrysopus*, срединная доля эдеагуса.
140–143 – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.** (140–141 – Аданге; 142–143 – Копшара); 144–145 – *H.* (*C.*) *ch. kodorensis* **subsp. n.** (Апшара). 140, 142, 144 – вид сбоку; 141, 143, 145 – вид сверху. Масштабная линейка 1 мм.

Redescription. Habitus as in Figs 119–121. Body comparatively large. Pronotal sides straight or slightly sinuate basally; basal angles more or less obtuse, generally blunted or occasionally narrowly rounded at tip; disc medially in most males without microsculpture, occasionally with strongly obliterate meshes, in females generally with very fine, obliterate meshes. Legs reddish brown or black. Elytra with parascutellar (basal) setigerous pore; intervals 7, also often 5 and rarely 3, with one or several (up to five) preapical pores (intervals 5 and 3 with fewer pores than interval 7), occasionally without pores. Median lobe of aedeagus (Figs 122–129) moderately curved in lateral view, its terminal lamella not curved ventrally, straight or slightly curved dorsally, slightly widened at apex in dorsal view; ventral margin of median lobe generally without preapical sinuation; internal sac with additional one or two small basal spiny patches on left side of median lobe (dorsolateral patch occasionally absent).

Body size and proportions: see Table 2.

Comparative diagnosis. This subspecies is similar to *H. ch. abasinus* in proportions and in having additional basal spiny patches in the internal sac of the aedeagus and preapical pores on the odd intervals of the elytra, but differs mainly in the shape of the median lobe, which is on average less curved in the lateral view and with terminal lamella not curved ventrally, as is also observed only in the nominotypical subspecies. However, the latter subspecies lacks additional basal spiny patches in the internal sac of the aedeagus and preapical setigerous pores on the odd intervals of the elytra. The presence of additional basal spiny patches in the internal sac of the aedeagus, combined with a terminal lamella not curved ventrally, distinguishes *H. ch. contumax* from all other subspecies.

Notes. Originally described as a separate species based on a single male from Adler, it was later treated as a subspecies of *H. chrysopus* [Kryzhanovskij et al., 1995]. The shape of the apical portion of the median lobe of the aedeagus in *H. ch. contumax*, as in the nominotypical subspecies, varies even within a single population (Figs 127, 128), and some specimens, for example from the Arabica Massif, have median lobe, somewhat similar to that of specimens of *H. ch. abasinus*. On the other hand, all examined males of *H. ch. abasinus* from the environs of Monastyr Village to the east of the Mzymta River (about 17 km north of Adler) and the northwestern part of the Gagra Range (western slopes of Mount Akh-Ag and the valley of the Krepostnaya River), which are very similar in external features to the holotype of *H. contumax*, have a median lobe with a ventrally curved terminal lamella (4, 5 and 3 aedeagi from these localities were examined, respectively).

Like the nominotypical subspecies, *H. ch. retowskianus* and *H. ch. abasinus*, *H. ch. contumax* includes red-legged and dark-legged forms (the former corresponds to the holotype). The red-legged form is known from the vicinity of Adler and Gagra, the Zyrkhu, Tepebashe and Mamdzyshkha ranges at lower altitudes, but up to approximately 1400 m (Zyrkhu Range) and even 2000 m (southern slope of the Tepebashe Range). The dark-legged form is common in the Arabika Massif and the Zyrkhu and Mamdzyshkha ranges at altitudes of about 1000–2300 m. The transitional population with red-legged and dark-legged individuals is found on Mount Mamdzyshkha at an altitude of about 1000 m.

Distribution (Fig. 146). Foothills and southern part of the Gagra Mountain Range from the mouth of the Mzymta River to Bsyb River, including the Zyrkhu, Tepebashe and Mamdzyshkha ranges and the Arabica Massif.

Harpalus (*Caucasoharpalus*) *chrysopus chkhaltensis* **subsp. n.**
(Figs 12, 13, 130, 131, 135–137, 140–143, 146)

Material. Holotype, ♂ (ZIN): "ABKHAZIA: Abkhazian Mt. R., upper Shoudidi Riv., alpine zone [ca 2000–2100 m], 11.VI.1989, I. Belousov, B. Kataev leg.". Paratypes: 22♂, 15♀ (ZIN, cIB), same data as holotype; 2♂ (ZIN), "р. Шаудиди пр. прит. Чхалты Абхазия, Курнаков 16.7.56" (Shoudidi River, right tributary of Chkhalta, Abkhazia, Kurnakov 16.07.1956); 1♂, 2♀ (ZIN), "Абхазский хр. верх. Шоудиди 21.V.86, Замотайлов" (Abkhazian Mt. R., upper Shoudidi, 21.05.1986, Zamotajlov); 1♂, 1♀ (ZIN), "ABKHAZIA: Abkhazian Mt. R., Shoudidi, forest zone [ca 1300–1600 m], 12.VI.1989, I. Belousov, B. Kataev leg."; 2♂, 2♀ (ZIN), "пер. Аданге водораздел Бзыбь – Чхалта, Абхазия Курнаков 3.7.54" (Adange Pass watershed Bzyb – Chkhalta, Abkhazia, Kurnakov, 3.07.1954); 1♂ (ZIN), "Зап. Кавказ, пер. Аданге, Курнаков. 3.VII.954" (West Caucasus, Adange Pass, Kurnakov, 3.07.1954); 2♂, 3♀ (ZIN), "г. Лахта Абхазия 14.7.56 В. Курнаков" (Mt. Lakhta, Abkhazia, 14.07.1956, V. Kurnakov); 5♂, 1♀ (ZIN), "Абхазия верх. р. Копшара, 10.8.63, Курнаков" (Abkhazia, upper Kopshara River, 10.08.1963, Kurnakov); 4♂, 5♀ (ZIN), "Кавказ, Грузия, Абхазский хр. H ~ 2000, Вост. траверс, 31.VIII.1986, В. Прасолов" (Caucasus, Georgia, Abkhazian Mt. R., H ~ 2000, eastern traverses, 31.08.1986, V. Prasolov); 1♂ (ZIN), "USSR, Abkhasia, Cauc. SW upper Kelasur Valley, Chimsa peak env., ca 1900 m B. Březina ltg. 27.07.[19]87"; 3♂, 1♀ (ZIN), "ABKHAZIA: Abkhazian Mt. R., env. Chamagvara, Dzhampal basin, lower alpine zone, 7.VI.1989, I. Belousov, B. Kataev leg."; 15♂, 11♀ (ZIN, cIB), "ABKHAZIA: Abkhazian Mt. R., Chamagvara – Lakhta, 1800–2000 m, alpine zone, 9.VI.1989, I. Belousov, B. Kataev leg."; 7♂, 4♀ (ZIN), "ABKHAZIA: Abkhazian Mt. R., source of Lakhta Riv., ca 1500 m, forest zone, 9.VI.1989, I. Belousov, B. Kataev leg."; 10♂, 12♀ (ZIN, cIB), "ABKHAZIA: Abkhazian Mt. R., source of Kulamba R., alpine zone, ca 2000 m, 10.VI.1989, I. Belousov, B. Kataev leg."; 10♂, 8♀ (ZIN), "ABKHAZIA: Abkhazian Mt. R., Kulamba, way to Shoudidi Pass, alpine zone, 11.VI.1989, I. Belousov, B. Kataev leg.".

Description. Habitus as in Figs 130, 131. Body comparatively small, dorsum often with light greenish blue shine. Legs (at least femora and tibiae) black or dark brown. Pronotal sides more or less straight or slightly rounded basally; basal angles obtuse, more or less rounded at tip; disc medially with fine meshes in both sexes, but in females more distinct. Elytra generally without parascutellar (basal) setigerous pore (Fig. 135) (occasionally a pore present on one or both elytra); intervals 7 and 5 with preapical pores (up to eight and up to three, correspondingly) (Figs 136, 137); occasionally these pores absent. Median lobe of aedeagus (Figs 140–143) arcuate in lateral view, its terminal lamella curved ventrally, slightly widened at apex in dorsal view; ventral margin of median lobe generally with preapical sinuation; internal sac without additional small basal spiny patches on left side of median lobe.

Body size and proportions: see Table 2.

Comparative diagnosis. Differing from other subspecies in the elytra of most specimens lacking a parascutellar pore and the dorsum with light greenish blue shine. The new subspecies is very similar in general habitus to the dark-legged specimens of *H. ch. abasinus*, but additionally differs from them in the aedeagus constantly without basal spiny patches in the internal sac.

Notes. This subspecies is represented by the dark-legged form, although of 26 specimens collected along the route from Chamagvara (about 1500–1600 m) to Mount Lakhta (about 1800–2000 m), one female, lacking a parascutellar pore on one elyton, had dark reddish-brown legs. It is also worth noting that the two macrospines in the internal sac of the aedeagus at least in three examined males from the southeastern slopes of the Abkhazian Range (upper reaches of the Kopshara River) are located one after the other (Figs 142, 143), and not almost at the same level, as in males from other localities. Otherwise, they do not differ from other males of this subspecies. The significance of this feature and its possible constancy in some populations are still unclear.

Distribution (Fig. 146). Abkhazian (Chkhalta) Mountain Range from the middle forest belt to the highlands (about 1500–2200 m), also the easternmost part of the Bzyb Mountain Range (Mt. Khimsa, about 1900 m) and the Adange Pass (about 1300 m), where this subspecies replaces *H. ch. abasinus*.

Etymology. The subspecific name is derived from one of the names of the Abkhazian (Chkhalta) Mountain Range, where this subspecies is distributed.

Harpalus (*Caucasoharpalus*) *chrysopus kodorensis* **subsp. n.**
(Figs 14, 15, 76–78, 132, 133, 146)

Material. Holotype, ♂ (ZIN): "ABKHAZIA, Kodor Mt. R., N Tkvarchel, E slopes Kuniashta Mt., way to pass to Mokva basin, 42°55′46,7″N 41°46′28,9″E, 1950 m, 9.VII.2011, B. Kataev leg.". Paratypes: 1♂, 1♀ (ZIN), same data as holotype; 3♀ (cIB, ZIN), "Abkhazia, Kodor Mt. R., Akiba Ridge, Mt Apchiqva (= Avichikva) [42°53′52″N / 41°55′49″E], ca 2200 m, 17–19.VII.1986, I. Belousov leg."; 1♀ (cIB), "Abkhazia, Tkvarcheli, Mt. Akiba, 18.VII.1986, I. Belousov leg."; 10♂, 13♀ (ZIN, cIB), "ABKHAZIA: Akiba Mt. R., S slope of Mt. Apshara, alpine zone, ca 2000 m, 3.V.1989, I. Belousov, B. Kataev leg."; 2♂, 1♀ (ZIN), "ABKHAZIA: Kodor Mt. R., N Tkvarchel, 42°55′37.2″N 41°47′46.1″E, ca 1580 m, 7–8.VII.2011, B. Kataev leg."; 3♂ (ZIN), "ABKHAZIA: Kodor Mt. R., Mokva basin, way from Vovtske Mt. to Arasadzykh, 1000–2500 m, 15.VII.2011, B. Kataev leg.".

Description. Habitus as in Figs 132, 133. Body comparatively small. Pronotal sides straight or barely sinuate basally; basal angles obtuse, more or less rounded or blunted at tip; disc in both sexes generally with very fine, more or less obliterate, slightly transverse meshes, more distinct in females. Legs (at least femora and tibiae) black or dark brown. Elytra with parascutellar (basal) pore; intervals 7 and 5 with or without one to three preapical pores (Figs 138, 139). Median lobe of aedeagus (Figs 144, 145) arcuate in lateral view, its terminal lamella curved ventrally and markedly widened at apex in dorsal view; ventral margin of median lobe generally with preapical sinuation; internal sac without additional small basal spiny patches on left side of median lobe.

Body size and proportions: see Table 2.

Comparative diagnosis. This subspecies differs from the vicarious *H. ch. chkhaltensis* **subsp. n.**, distributed to the northwest of it, in having constantly a parascutellar setigerous pore on the elytra, and from the dark-legged *H. ch. abasinus* in the absence of additional basal spiny patches in the internal sac of the aedeagus. In combination of the characters, *H. ch. kodorensis* **subsp. n.** is formally very similar to the dark-legged specimens of *H. ch. retowskianus*, but given the significant distance between their ranges and the fact that they are separated by other subspecies, they are considered taxonomically different. Besides, compared to *H. ch. retowskianus*, this new subspecies has, on overage, relatively slightly wider elytra, less sharp basal angles of the pronotum, and a slightly more widened apically terminal lamella of the aedeagus in dorsal view; microsculpture on the pronotal disc, consisting of very fine, more or less obliterate, slightly transverse meshes, is present in both sexes. *Harpalus ch. chrysopus* and *H. ch. contumax* differ from *H. ch. kodorensis* **subsp. n.** in their aedeagi with terminal lamella not curved ventrally.

Notes. *Harpalus ch. kodorensis* **subsp. n.** is represented only by the dark-legged form.

The geographical variation of *H. ch. kodorensis* **subsp. n.** needs further study. Compared with the specimens from the Kodor Range, the specimens from the Akiba Range have relatively shorter elytra: EL/EW 1.37–1.41 (*m* 1.40, *n* 7) and 1.32–1.38 (*m* 1.35, *n* 10), respectively.

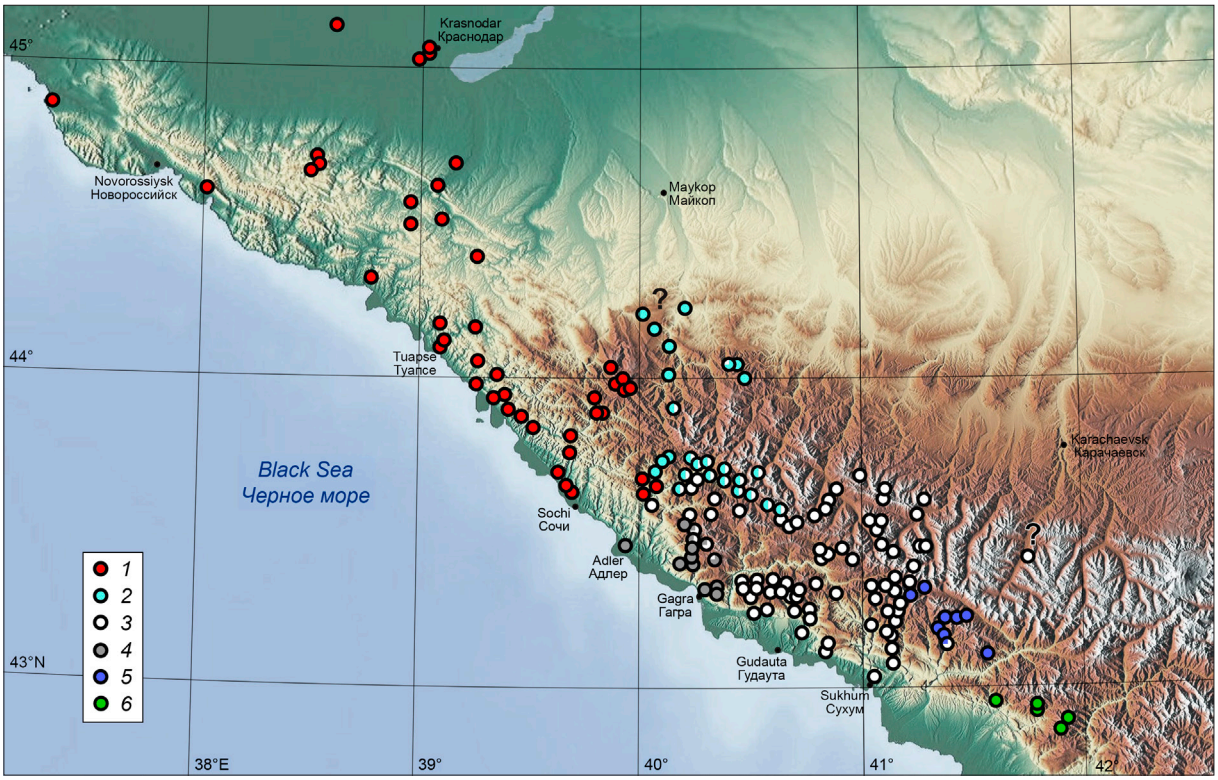


Fig. 146. *Harpalus* (*Caucasoharpalus*) *chrysopus*, distribution: *1* – *H.* (*C.*) *ch. chrysopus*; *2* – *H.* (*C.*) *ch. retowskianus*; *3* – *H.* (*C.*) *ch. abasinus*; *4* – *H.* (*C.*) *ch. contumax*; *5* – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.**; *6* – *H.* (*C.*) *ch. kodorensis* **subsp. n.** Circles highlighted in colour by sectors represent populations with intermediate characteristics to varying degrees.

Рис. 146. *Harpalus* (*Caucasoharpalus*) *chrysopus*, распространение: *1* – *H.* (*C.*) *ch. chrysopus*; *2* – *H.* (*C.*) *ch. retowskianus*; *3* – *H.* (*C.*) *ch. abasinus*; *4* – *H.* (*C.*) *ch. contumax*; *5* – *H.* (*C.*) *ch. chkhaltensis* **subsp. n.**; *6* – *H.* (*C.*) *ch. kodorensis* **subsp. n.** Кружки, выделенные цветом по секторам, представляют популяции с промежуточными в различной степени характеристиками.

Distribution (Fig. 146). This subspecies occupies the southeastern part of the species range: the Kodor Mountain Range, including its southeastern spur Akiba, at altitudes of about 1500–2200 m. The Akiba Range is probably not only the easternmost location of *H. ch. kodorensis* **subsp. n.**, but also of the species itself. It is interesting that during collection in the alpine zone of Mount Apshara in the south of the Akiba Range (about 2000 m) in 1989, about two dozen specimens of this subspecies were found, but not a single specimen of *H. aeneipennis*. At the same time, more than 30 specimens of the latter species were found in the upper forest and alpine belts of Mount Okhachkue (1800–2000 m), the southern spur of the Akiba Range, about six kilometers to the south, while *H. chrysopus* was not found there.

Etymology. The subspecific name refers to the Kodor Mountain Range, where this subspecies is distributed.

Discussion

The modern distribution, environmental preferences and obligate winglessness, combined with shortened metepisterna, indicate that the subgenus *Caucasoharpalus* arose and underwent further differentiation in mountainous conditions of the Caucasus. The exact time of the separation of the ancestral form of the subgenus is unknown, but it can be assumed that this occurred as a result of a relatively ancient invasion to the Great Caucasus, probably in the Miocene, during the period when the Caucasus was an island or had only short-term connections with neighboring territories (see, for example, Gvozdetskiy [1963], Popov, Patina [2023]). In any case, this occured significantly earlier than the penetration into the Caucasus of numerous xerophilic West Asian elements from the south, steppe elements from the north and widely distributed Mediterranean species, which constitutes the majority of the modern Caucasian fauna of *Harpalus*. Considering the position of the subgenus within the Palaearctic *Amblystus* subgroup sensu Kataev [2023], which includes several subgenera with both winged and wingless species, it can also be assumed that the ancestral form of *Caucasoharpalus* was one of the winged representatives of this subgroup, probably similar in life form to the modern *H.* (*Drymoharpalus*) *atratus* Latreille, 1804, living in forests. The *Amblystus* subgroup was obviously widespread at that time, mainly in the Western Palaearctic, since its modern obligatory flightless representatives are localized in various mountain systems from the Western Mediterranean to the Western Himalayas and Southwest China. In this early period, when the ancestor of *Caucasoharpalus* became isolated and, probably as a result, lost its wings, the Great Caucasus was still represented by low-mountain relief forms. The differentiation of this subgenus probably resulted from a combination of factors, primarily sea level

fluctuations, orographic processes, and climate change, with varying degrees of dominance of each in different periods. However, without knowing the exact timing of the separation of *Caucasoharpalus* and given the contradictory data on the geological history of the Caucasus (see, for example, Kuznetsov, Romanyuk [2025]), it is currently difficult to accurately link each stage of differentiation to a specific geological event or change in environmental structure. Here, the differentiation of the subgenus is presented as a relative sequence of possible events based solely on distinctive morphological characters and the distribution patterns of modern taxa, without specifying causes.

Comparative morphological analysis showed that for the recognition of species and subspecies within this subgenus, the most important distinctive features are the structural characteristics of the male genitalia, while many features of external morphology are too variable and are mostly adaptive in nature. The female genitalia also cannot be used since they are fairly uniform within the subgenus. Based on the characteristics of the aedeagi, it can be assumed that *H. belousovi* **sp. n.** is morphologically probably closest to the ancestral form of the subgenus, which was probably originally distributed on the territory of the modern Central Caucasus. Although this species is obviously most closely related to *H. aeneipenns*, the shape of its median lobe with an oblique apical capitulum and a rounded dorsal margin is very similar to that of *H. chrysopus* and most other *Harpalus* species of different subgenera. The median lobe of *H. aeneipennis* with a botton-like apical capitulum and sinuate dorsal margin is evidently an apomorphic feature compared with the median lobes of *H. belousovi* **sp. n.** and *H. chrysopus*, which should be treated as symplesiomorphy. The shape of the pronotum of *H. belousovi* **sp. n.**, particularly of its nominotypical subspecies, with more distinct basal angles than in *H. aeneipenns*, also reminds pronotum of many *H. chrysopus*. Most likely, *H. aeneipennis* should be considered as a derivative of *H. belousovi* **sp. n.**, and the arising of this species occurred after the separation of the ancestral form of the subgenus into the ancestor of the West Caucasian *H. chrysopus* and the ancestor of the Central Caucasian *H. belousovi* **sp. n.** and *H. aeneipenns.* Moreover, while *H. belousovi* **sp. n.** retained its original distribution in the Central Caucasus, *H. aeneipennis* subsequently spread widely throughout the Transcaucasus. Unlike *H. belousovi* **sp. n.**, having only two subspecies, and the monotypical *H. aeneipennis*, *H. chrysopus* underwent significant differentiation in the Western Caucasus, which, however, did not lead to the formation of separate species. The presence of small basal spiny patches in the internal sac of the aedeagus in *H. belousovi* **sp. n.**, *H. aeneipennis* and two subspecies of *H. chrysopus* (*H. ch. abasinus* and *H. ch. contumax*) suggests that such patches were probably present in the ancestor of *H. chrysopus*. The latter two subspecies, which occupy together the middle part of the species range, have retained ancestral condition of this character while the other subspecies have probably lost it independently: the northern *H. ch. chrysopus* and *H. ch. retowskianus* on the one hand and the southern *H. ch. chkhaltensis* **subsp. n.** and *H. ch. kodorensis* **subsp. n.** on the other hand. The independent development of small basal spiny patches in the internal sac in *H. belousovi* **sp. n.**, *H. aeneipennis* and *H. chrysopus* seems less likely. In contrast to this, a modification of the apical part of the median lobe of the aedeagus in *H. ch. chrysopus* and *H. ch. contumax* (with a terminal lamella straight or curved dorsally) probably occurred unidirectionally and independently due to some common, unfortunately unknown, reasons on the similar genetic basis. These subspecies are well separated from each other, but form transitions with *H. ch. retowskianus* and *H. ch. abasinus*, respectively, which lack such a modification. Similar modification of the terminal lamella, which should be treated as an apomorphy, is also observed in *H. belousovi conterminus* **subsp. n.** and *H. aeneipennis*. In the apomorphic state of the terminal lamella, which is not curved ventrally, these two taxa and *H. ch. chrysopus* and *H. ch. contumax* are somewhat similar to each other, but they do not, however, form together a single clade, since this similarity is obviously the result of parallel development. The complex pattern of independent geographical variation of some morphological features in *H. chrysopus* (Figs 54–59) is apparently explained both by their adaptive nature and by the fact that after the split and formation of subspecies in isolates, most of them came into secondary contacts, which led to a fairly extensive genetic exchange between them. The details of this process require further study.

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References

Chaudoir M. de. 1846. Carabiques. *In:* Chaudoir M. de, Hochhuth H. Énumération des carabiques et hydrocanthares, recueillis pendant un voyage au Caucase et dans les provinces transcaucasiennes par Baron M. de Chaudoir et le Baron A. de Gotsch. Kiew: J. Wallner: 47–209.

Csiki E. 1932. Carabidae: Harpalinae VI (Pars 121). *In:* Coleopterorum catalogus. Volumen III. Carabidae III. Berlin: W. Junk: 1023–1278.

Faldermann F. 1836. Coleoptera Persico-Armeniaca. I. Pentamera. *Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou.* 1835. 4: 1–310 + 10 pls.

Gvozdetskiy N.A. 1963. Kavkaz. Ocherk prirody [The Caucasus. Essay on nature]. Moscow: State Publishing House of Geographical Literature. 264 p. (in Russian).

Iablokoff-Khnzorian S.M. 1961. Opyt vosstanovleniya genezisa fauny zhestkokrylykh Armenii [An experiment to reconstruct the origin of the beetle fauna]. Yerevan: Academy of Sciences of Armenian SSR. 266 p. (in Russian).

Iablokoff-Khnzorian S.M. 1976. Fauna Armyanskoy SSR. Nasekomye zhestkokrylye. Zhuzhelitsy (Carabidae). Chast' I [Fauna of Armenian SSR. Beetle insects. Ground beetles (Carabidae). Part I]. Yerevan: Academy of Sciences of Armenian SSR. 297 p. (in Russian).

Kataev B.M. 1995a. Footnote 298. *In:* Kryzhanovskij O.L., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K.V., Shilenkov V.G. A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae). Sofia – Moscow: Pensoft Publishers: 142.

Kataev B.M. 1995b. Footnote 299. *In:* Kryzhanovskij O.L., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K.V., Shilenkov V.G. A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae). Sofia – Moscow: Pensoft Publishers: 142.

Kataev B.M. 2023. Classification of the genus *Harpalus* (Coleoptera, Carabidae) of the world based on imaginal morphology. *Diversity*. 15(971): 1–122. DOI: 10.3390/d15090971

Kataev B.M., Wrase D.W. 2017. Subtribe Harpalina Bonelli, 1810. *In:* Catalogue of Palaearctic Coleoptera. Volume 1. Archostemata – Myxophaga – Adephaga. Revised and Updated Edition. Leiden: Brill: 515–562.

Kataev B.M., Wrase D.W., Ito N. 2003. Harpalina. *In:* Catalogue of Palaearctic Coleoptera. Volume 1. Archostemata – Myxophaga – Adephaga. Stenstrup: Apollo Books: 367–397.

Kryzhanovskij O.L., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K.V., Shilenkov V.G. 1995. A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae). Sofia – Moscow: Pensoft Publishers. 271 p.

Kurnakov V.N. 1958. To knowledge of the fauna of ground beetles (Coleoptera, Carabidae) of the Caucasus I. On *Pterostichus ordinatus* Fisch.-W. and some related species. *Entomologicheskoe obozrenie.* 37(2): 414–431 (in Russian).

Kurnakov V.N. 1961. Beiträge zur Kenntnis der kaukasischen Laufkäferfauna (Coleoptera, Carabidae) III. Revision der Gattung *Lindrothius* nov. *Opuscula Entomologica.* 26: 209–227.

Kuznetsov N.B., Romanyuk T.V. 2025. On the onset time and mechanism of the Greater Caucasus uplift as well as genetic type and filling history of the Ciscaucasia troughs – traditional and modern interpretations. *Geodynamics & Tectonophysics.* 16(3): 0825. DOI: 10.5800/GT-2025-16-3-08-25

Lorenz W. 1998. Systematic list of extant ground beetles of the world (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). First edition. Tutzing: W. Lorenz. 502 p.

Lorenz W. 2005. A systematic list of extant ground beetles of the world (Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). Second edition. Tutzing: W. Lorenz. 530 p.

Lutshnik V.N. 1922. De Harpalinis novis vel parum cognitis. *Trudy Stavropol'skogo sel'skokhozyaystvennogo instituta.* 1921. 1(13): 51–66 (in Russian).

Lutshnik V.N. 1933. Dva nové druhy rodu *Harpalus* Latr. z Kavkazu. *Časopis Československů Společnosti Entomologické.* 30: 131–132.

Lutshnik V. 1939. To the fauna of Cicindelidae and Carabidae of Abkhasia. *In:* Materialy k faune Abkhazii [Materials to the fauna of Abkhazia]. Tbilisi: Academy of Sciences of the USSR, Georgian Branch – Zoological Sector: 193–196 (in Russian).

Marseul S.A. de. 1880. Nouveau répertoire contenant les descriptions des espèces de coléoptères de l'ancienmonde publiées isolément ou en langues étrangères, en dehors des monographies ou traités spéciaux et de l'Abeille. *L'Abeille, Journal d'Entomologie.* 19: 1–526.

Noonan G. 1976. Synopsis of the supra-specific taxa of the tribe Harpalini (Coleoptera: Carabidae). *Quaestiones Entomologicae.* 12: 3–87.

Noonan G.R. 1996. Classification, cladistics, and natural history of species of the subgenus *Anisodactylus* Dejean (Insecta: Coleoptera: Carabidae: Harpalini: *Anisodactylus*). *Milwaukee Public Museum Contributions in Biology and Geology.* 89: i–iii + 1–210.

Popov S.V., Patina I.S. 2023. History of Paratethys. *Priroda.* 6: 3–14 (in Russian). DOI: 10.7868/S0032874X23060017

Reck N., Chaladze G. 2004. Checklist of the ground beetles (Coleoptera, Carabidae) of Georgia. *In:* Proceedings of the Institute of Zoology. Vol. 22. Tbilisi: Universal: 127–157.

Reitter E. 1887a. Neue Coleopteren aus Europa, den angrenzenden Ländern und Sibirien, mit Bemerkungen über bekannte Arten. Dritter Theil. *Deutsche Entomologische Zeitschrift.* 31(1): 241–288.

Reitter E. 1887b. Neue Coleopteren aus Europa, den angrenzenden Ländern und Sibirien, mit Bemerkungen über bekannte Arten. Vierter Theil. *Deutsche Entomologische Zeitschrift.* 31(2): 497–528.

Reitter E. 1894. Coleopterologische Notizen. *Wiener Entomologische Zeitung.* 13: 115–117.

Reitter E. 1900. Bestimmungs-Tabellen der europäischen Coleopteren. XLI. Heft. Enthaltend Carabidae. Abtheilung: Harpalini und Licinini. *Verhandlungen des Naturforschenden Vereines in Brünn.* 1899. 38: 33–155.

Rost C. 1892. *Harpalus abasinus* Rost nov. sp. *Deutsche Entomologische Zeitschrift.* 1891. 35: 314.

Zamotajlov A.S. 1992. Fauna zhuzhelits (Coleoptera, Carabidae) Severo-Zapadnogo Kavkaza. Metodicheskoe posobie [Fauna of ground-beetles (Coleoptera, Carabidae) of the Northwest Caucasus. Methodological manual]. Krasnodar: Kuban State Agrarian University. 77 p. (in Russian).

Zamotajlov A.S., Makaov A.K. 2010. Family Carabidae – ground beetles. *In:* Zhestkokrylye nasekomye (Insecta, Coleoptera) respubliki Adygea (annotirovannyy catalog vidov). Seriya "Konspekty fauny Adygea", № 1 [Coleopterous insects (Insecta, Coleoptera) of Republic of Adygheya (annotated catalogue of species). Fauna conspecta of Adygheya, № 1]. Maykop: Adyghei State University: 19–58 (in Russian).

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