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A NEW *NALASSUS* MULSANT, 1854 (COLEOPTERA: TENEBRIONIDAE) FROM TRANSCAUCASIA WITH A KEY TO SPECIES FROM THE GREATER CAUCASUS AND NOTES ON THE TAXONOMY, DISTRIBUTION, BIONOMICS AND TROPHIC RELATIONS

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A brief well-illustrated review of the tenebrionid genus *Nalassus* Mulsant, 1854 from the Greater Caucasus is presented. A new species, *N.* (*Caucasonotus*) *negrobovi* Nabozhenko, **sp. n.** is described from the alpine zone of Abkhazia. This species is similar to *N. dombaicus* (Nabozhenko, 2000), *N. adriani* (Reitter, 1922) and *N. alanicus* (Nabozhenko, 2000), but differs in the structure of eyes, antennae, pronotum and elytral interstriae. The following new synonyms are proposed after examination of a series of beetles and type specimens: *Nalassus dissonus* Nabozhenko, 2001 = *Nalassus lutshniki* Nabozhenko, 2001, **syn. n.**; *Nalassus colchicus madlenae* Nabozhenko, 2013 = *Nalassus kartvelius* Nabozhenko, 2013, **syn. n.**; *Helops cambyses* Seidlitz, 1895 = *Cylindronotus ahngeri* Medvedev, 1998, **syn. n.** Keys to species from the Greater Caucasus on males and females are given. New data on bionomics, landscape and habitat distribution and trophic relations are given. Interesting patterns are observed at the level of ecological groups: forest species feed mainly on corticolous foliose lichens from the family Physciaceae Zahlbr., while alpine *Nalassus* use saxicolous foliose lichens from the family Parmeliaceae Zenker; steppe species feed on terricolous foliose lichens at least from the family Cladoniaceae Zenker.

Key words: new taxa, synonymy, darkling beetle, *Nalassus*, Coleoptera, Tenebrionidae, habitat, host lichen, Caucasus.

INTRODUCTION

Nalassus Mulsant, 1854 is a widespread genus in the North Hemisphere with 86 species and 6 subspecies in the Palaearctic (Nabozhenko 2020) and

three species in the Nearctic (Nabozhenko *et al.* 2016*a*). The Palaearctic range of the genus is disjunctive (Nabozhenko 2012) and includes two main hot spots of the diversity: the Western Palaearctic and the Eastern Palaearctic. The Central Asian exclave of the genus contains five species from deserts and subdeserts of Eastern Kazakhstan (Medvedev 1987), but this species-group probably does not belong to *Nalassus* and need a revision because it differs from congeners by the structure of the epipleura and the absence of ventral temple grooves of the head.

The first Palaearcic revision of the genus was published by Reitter (1922), who included this and many other taxa to the genus *Cylindrinotus* Faldermann, 1837 as subgenera. Later, Antoine (1949) interpreted one subgeneric name of *Nalassus* and the genus *Odocnemis* Allard, 1876 as subgenera of *Stenomax* Allard, 1876. Español (1956, 1961) presented a new conception of the tribe Helopini, where he separated *Nalassus* and *Cylindrinotus*. This conception was supported by Ardoin (1959) and much later by Nabozhenko (2001).

The Caucasian species of *Nalassus* were revised by Nabozhenko and co-author (Nabozhenko 2000, 2001, Abdurakhmanov & Nabozhenko 2011). Some new taxonomic changes and species were added to the Caucasian fauna later (Nabozhenko & Abdurakhmanov 2007, Nabozhenko 2008, 2013). One Caucasian species was transferred from *Nalassus* to the genus *Odocnemis* and is now interpreted as *O. aurichalcea* (Adams, 1817) (Nabozhenko 2020).

Here we describe an additional new alpine species from Abkhazia, establish a new synonymy and present a new key to species taking into account all taxonomic changes.

MATERIAL AND METHODS

The material on beetles from the following museums was used: DE MSU – Department of Entomology, Moscow State University (Moscow, Russia); HNHM – Hungarian Natural History Museum (Budapest, Hungary); ZIN – Zoological institute of the Russian Academy of Sciences (St Petersburg, Russia); PCEI – Private collection of Elena Il'ina (Makhachkala, Russia); PCMN – Private collection of Maxim Nabozhenko (Rostov-on-Don, Russia); UC – University of Cyprus (Nicosia, Cyprus).

Lichens and additional material on beetles were collected during expeditions on the North Caucasus in July 2020 and June 2021.

We used a light microscope Micromed MC-4-Zoom LED with the camera ToupCam 14.0 MP for the study of beetles. Photographs of beetles were made with Canon EOS 5D Mark IV Body, lens Canon MP-E65MM F2.8 Macro, flush bulb Canon Macro Twin Lite MT-26X-RT, stacking was made using Stack-shot 3X with enlarged macro rails s/n 3734; the photosystem is installed on a reproduction machine Kaiser Copy Stand RS 1. Images were stacked in Helicon Focus 7.7.4 Pro.

Cameral processing of the collected lichens was carried out by the traditional morphological and anatomical methods using light microscopes Carl Zeiss Primo Star, and Zeiss STEMI-2000 CS stereomicroscopes equipped with camera AxioCam ICc3. A standard

Table 1. Material on lichens (collected by M. V. Nabozhenko and partly I. A. Chigray, determined by L. V. Gagarina, deposited in LE).

Locality	Lichens
Russia, Karachay-Cherkessis, between Kurdzhinovo and Zagedan, N 43°50′44.6″ E 40°55′54.6″, 914 m, on *Fagus orientalis*, 2.07.2020	*Phaeophyscia hirsuta* (Mereschk.) Essl.
Russia: Karachay-Cherkessia, Verkhnyaya Teberda, 43°33'45.33"N, 41°48'52.90"E, 1150 m, 7–8.07.2021, on *Salix* sp.	*Phaeophyscia orbicularis* (Neck.) Moberg, *Physcia adscendens* (Fr.) H. Olivier, *Physcia stellaris* (L.) Nyl., *Physcia tenella* (Scop.) DC., *Physconia distorta* (With.) J. R. Launon, *Vulpicida juniperinus* (L.) J.-E. Mattsson & M. J. Lai
Russia, Karachay-Cherkessia, Teberdinsky Natural Reserve, Semenov-Bashi Mt., N 43°18′55.13″ E 41°33′52.35″, 2550 m, alpine meadows, on stones	*Arctoparmelia separata* (Th. Fr.) Hale, *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale
Russia, North Ossetia-Alania, Arkhon pass, piedmont of Dagov Mt., 42°50'48.05"N, 44°13'46.15"E, 2500 m, subalpine and alpine meadows, on stones, 15.07.2020	*Arctoparmelia separata* (Th. Fr.) Hale
Russia, Dagestan, N of Levashi, 42°27'55.21"N, 47°20'31.86"E, limestone mountain steppe, 1144 m, 14.06.2021	*Cladonia pyxidata* (L.) Hoffm.

set of reagents (KOH (K), 10% solution, J/KJ (J) – 1 mg J2 in 100 ml 10% solution KJ, P) was used to determine lichens (Smith *et al.* 2009, Andreev & Himelbrant 2014). The HPTLC method was used to identify chemically complex (in terms of the content of lichen substances) lichen species. The HPTLC was performed according to the standard procedure (Culberson & Ammann 1979, Orange *et al.* 2001, Kranner *et al.* 2002), using solvent systems A and B. In several cases, we used molecular methods to identify lichen samples. Extraction of DNA and PCR amplification were performed following the protocol of Cubero *et al.* (1999). ITS1F and ITS4 primers were used for nrITS rDNA sequences. Amplicons were sequenced at Eurogen. The lichen specimens are deposited in the lichenological herbarium (LE) of the Komarov Botanical Institute of the Russian Academy of Sciences (St Petersburg, Russia) (Table 1).

Acronyms of measurements: Y – Ratio of the head width at eyes to the distance between eyes; PH – Ratio of the maximal pronotal width to the maximal head width; PwPl – Ratio of the pronotal length at middle to the width at widest level; ElEw – Ratio of the elytral length (from apices to the base of scutellar shield) to the maximal width; EHw – Ratio of the elytral maximal width to the head maximal width; EPw – Ratio of the elytral maximal width to the pronotal maximal width; EPl – Ratio of the elytral length (from apices to the base of the scutellar shield) to the pronotal length at the middle.

Except for a new one, the material for each species was published in the previous revisions (Nabozhenko 2001, Nabozhenko & Abdurakhamanov 2007, Abdurakhmanov & Nabozhenko 2009, 2011). Below we present only new unpublished material from the Caucasus.

TAXONOMY

Subgenus *Nalassus* Mulsant, 1854

Species of the subgenus are distributed in North Africa, Europe, Anatolia, the Caucasus, Iran, south-western Turkmenistan, Kazakhstan, the Eastern Palaearctic, North America (USA, Canada). One invasive species is known from Israel (Nabozhenko & Kolov 2016). Species of the nominotypical subgenus occur mainly in foothills and low mountains in the Caucasus, sometimes reaching 1300 m along the river valleys or mountain steppes.

Nalassus (*Nalassus*) *brevicollis* (Krynicki, 1832) (Fig. 1)

Material. 10 specimens (UC): Russia: Karachay-Cherkessia, Verkhnyaya Teberda, 43°33'45.33"N, 41°48'52.90"E, 1150 m, 7–8.07.2021, on *Salix* sp. (leg. M. V. Nabozhenko, I. V. Shokhin, D. G. Kasatkin, E. N. Terskov). 5 ♂, 4 ♀ (PCMN): Abkhazia, the confluence of Bzyb and Gega rivers, 43°22'00.53"N, 40°27'21.26"E, 134 m, on *Carpinus betulus*, 26.05.2004 (collectors of Rostov State University).

Distribution in the Greater Caucasus. This species is widely distributed in low-mountain and foothill forests of the west and central parts of the North Caucasus, reaching 1150 m a.s.l. along the river valleys. Russia: Krasnodar and Stavropol regions, Adygea, Karachay-Cherkessia, Kabardino-Balkaria, North Ossetia–Alania. Abkhazia: the confluence of Bzyb and Gega rivers.

Nalassus (*Nalassus*) *dissonus* Nabozhenko, 2001 (Fig. 2)

= *Nalassus lutshniki* Nabozhenko, 2001, **syn. n.**

Material (DE MSU). 1 ♂: Russia, North Ossetia-Alania, Mozdok Distr., Oktyabrskoe, agrocenoses, 19.05.1988 (leg. S. K. Alexeev); 1 ♀: Russia, North Ossetia-Alania, Alagir Distr., Nizhniy Unal, 1200 m, opposite slopes, mountain steppe, 18.05.1985 (leg. S. K. Alexeev); 1 ♂: Russia, North Ossetia-Alania, Alagir Distr., Ardon River basin from Nizhniy Unal to Biz, 11.06.1985 (leg. S. K. Alexeev); 1 ♂: Russia, North Ossetia-Alania, Alagir Distr., Ardon River basin opposite slopes of Zintsar, 1000 m, Astragalus steppe, 9.06.1985 (leg. S. K. Alexeev); 1 ♂: the same label, but 9.07.1985 (leg. S. K. Alexeev).

Taxonomic notes. The species *Nalassus lutshniki* was described from Stavropol Region of Russia (Blagodarnoe). The first author (Nabozhenko 2001) erroneously interpreted differences between *N. dissonus* and *N. lutshniki*: presence or absence of the temple row on the ventral side of the epicranium and the structure of the apical piece of the aedeagus. In fact, both taxa are conspecific and have the same mentioned structures. Differences in the structure of aedeagus, illustrated by Nabozhenko (2001), belong to a variability. This re-

sults in the following synonymy: *Nalassus dissonus* Nabozhenko, 2001 = *Nalassus lutshniki* Nabozhenko, 2001, **syn. n.**

Distribution. Russia: Stavropol Region (probably extinct), North Ossetia-Alania, steppes.

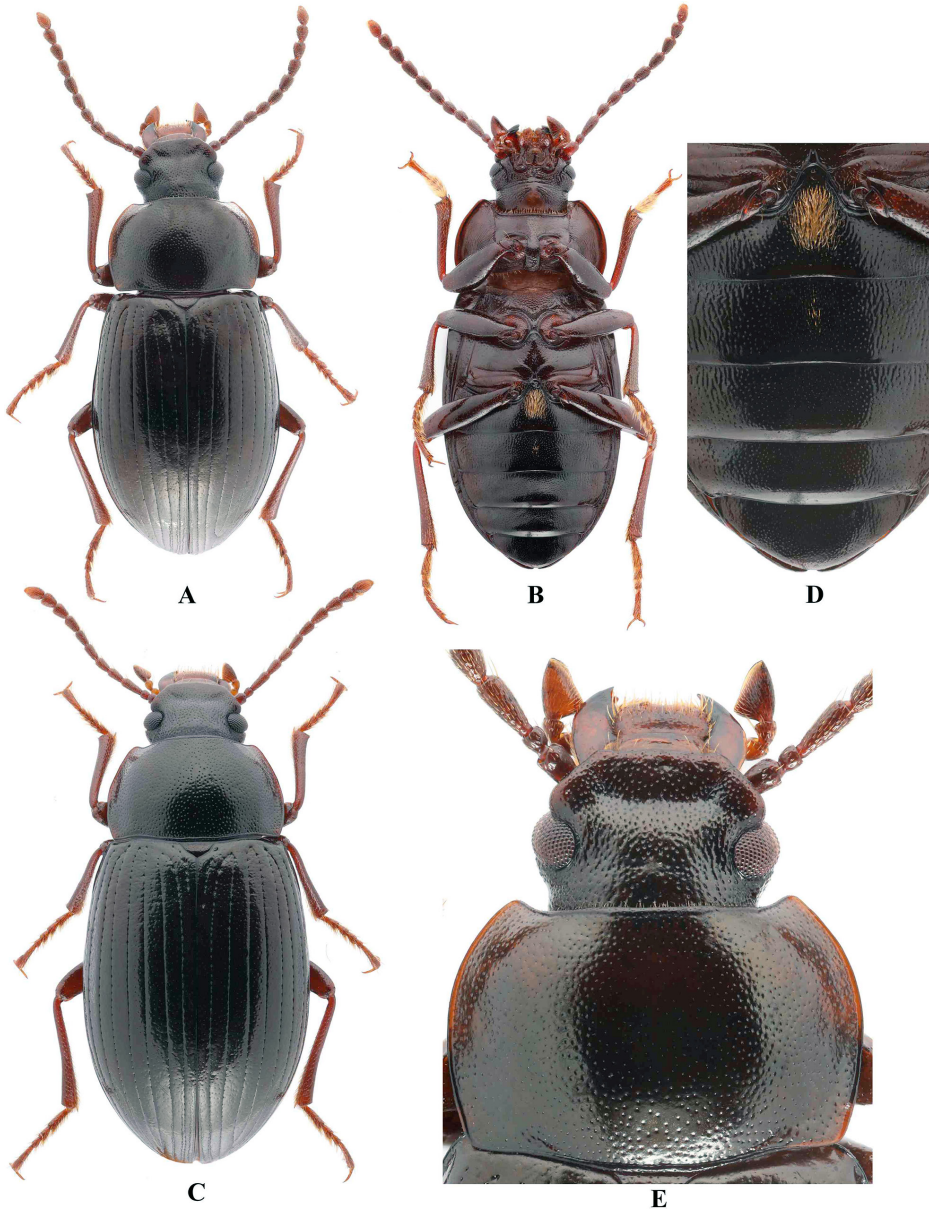

Fig. 1. *N. brevicollis*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

Nalassus (*Nalassus*) *faldermanni* (Faldermann, 1837) (Fig. 3)

Distribution in the Greater Caucasus. This species is widely distributed in the Ciscaucasia and semi-xerophytic foothills of the southern part of the Greater Caucasus: Russia (Krasnodar and Stavropol regions, North Ossetia-Alania, Ingushetia, Chechnya, Dagestan), Abkhazia (Sukhum), Georgia (North-Eastern regions), Azerbaijan (north provinces). Bionomics and differences between populations were published earlier (Nabozhenko *et al*. 2016*b*, Nabozhenko & Grimm 2019).

Nalassus (*Nalassus*) *kalashiani* Nabozhenko, 2001 (Fig. 4)

Material. 3 ♂, 3 ♀ (1 ♂, 2 ♀ in ZIN, 2 ♂, 1 ♀ in PCMN): Russia, Dagestan, N of Levashi, 42°27'55.21"N, 47°20'31.86"E, limestone mountain steppe, 1144 m, 14.06.2021 (leg. M. V. Nabozhenko, I. A. Chigray).

Distribution. The eastern part of the North Caucasus. Russia: Dagestan, Chechnya.

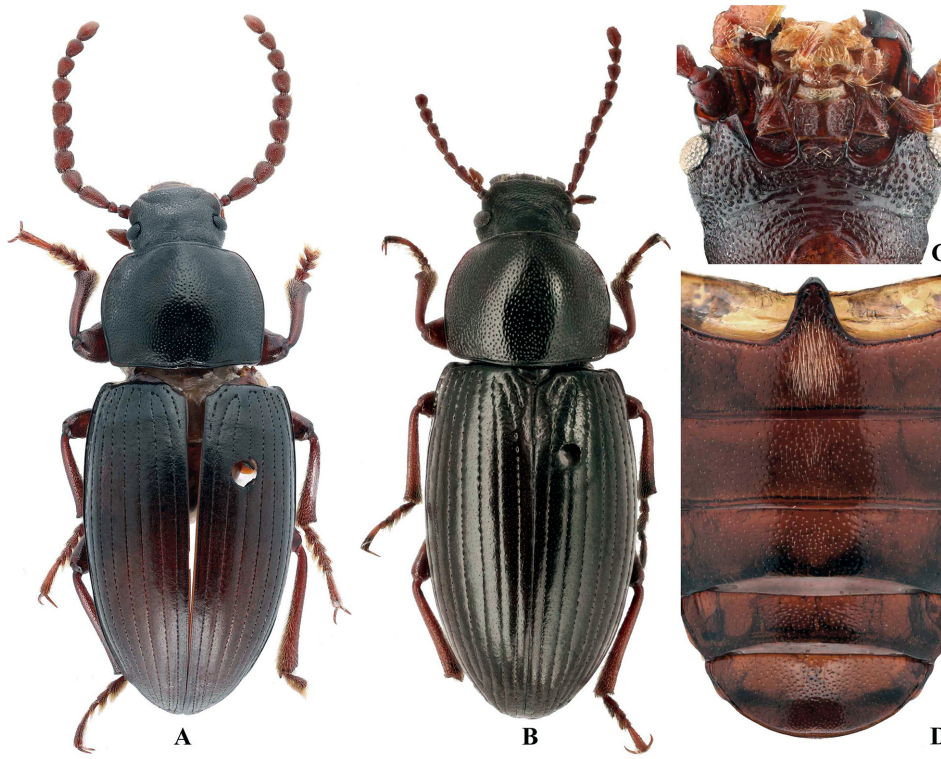

Fig. 2. *N. dissonus*, habitus, details of structure. A = ♂, holotype, dorsally; B = ♀, paratype, dorsally; C = head, ventrally; D = ♂, abdomen

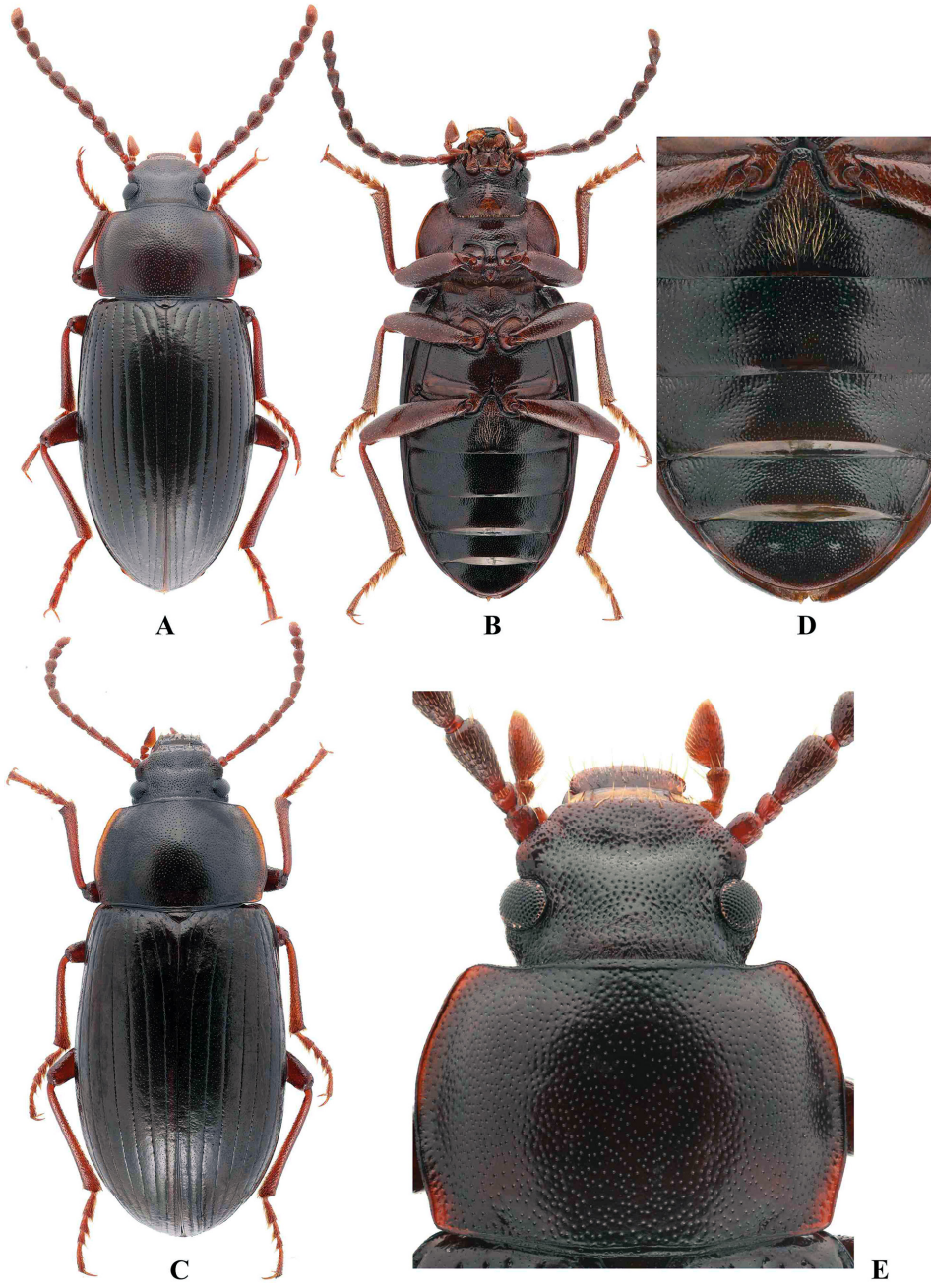

Fig. 3. *N. faldermanni*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

Subgenus *Caucasonotus* Nabozhenko, 2000

Species of the subgenus are widely distributed in forests and alpine meadows of the Greater Caucasus. Only some populations of *Nalassus diteras* and *N. colchicus* occur in the Lesser Caucasus.

Nalassus (*Caucasonotus*) *adriani* (Reitter, 1922) (Fig. 5)

Distribution. This species is known only from the southern part of the Klukhor pass in Abkhazia, where it inhabits stony alpine meadows.

Nalassus (*Caucasonotus*) *alanicus* (Nabozhenko, 2000) (Fig. 6)

Material. 1 ♂ (DE MSU): Russia, North Ossetia-Alania, Ardon River basin, slopes opposite of Zintsar, 1100 m, meadows, 4.10.1984 (leg. S. K. Alexeev); 1 ♀ (DE MSU): same, but 10.07.1984; 1 ♂ (DE MSU): same, but 18.05.1985; 3 ♂, 4 ♀ (DE MSU): Russia, North Ossetia-Alania, Ardon River basin, left slope of Alagir canyon, slopes opposite of Nizhniy Unal, 10.10.1984 (leg. S. K. Alexeev); 1 ♂ (DE MSU): Russia, North Ossetia-Alania, Ardon River basin, Skalisty Range, SW slopes above Zintsar, 950–1100 m, 3.04.1984 (leg. S. K. Alexeev); 1 ♂ (DE MSU): Russia, North Ossetia-Alania, Pastbishchny Range, N of Verkhnyaya Kartsa, Agom natural area, 2200 m, meadow, 12.05.1984 (leg. S. K. Alexeev); 1 ♂ (DE MSU): Russia,

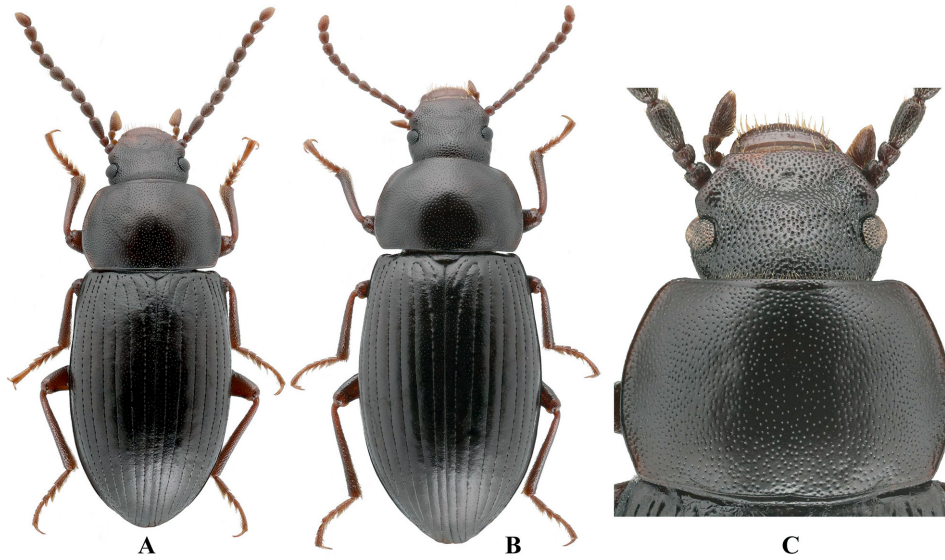

Fig. 4. *N. kalashiani*, habitus, details of structure. A = ♂, dorsally; B = ♀, dorsally; C = ♂, head and pronotum

North Ossetia-Alania, Ardon River basin, W slopes of Khumarat-Khokh Mt., Shubi natural area, meadow in the forest, 1.04.1984 (leg. S. K. Alexeev); 1 ♂, 1 ♀ (DE MSU): Russia, North Ossetia-Alania, near Nizhniy Unal, 2.09.1984 (leg. S. K. Alexeev). 1 ♂ (PCMN): Russia,

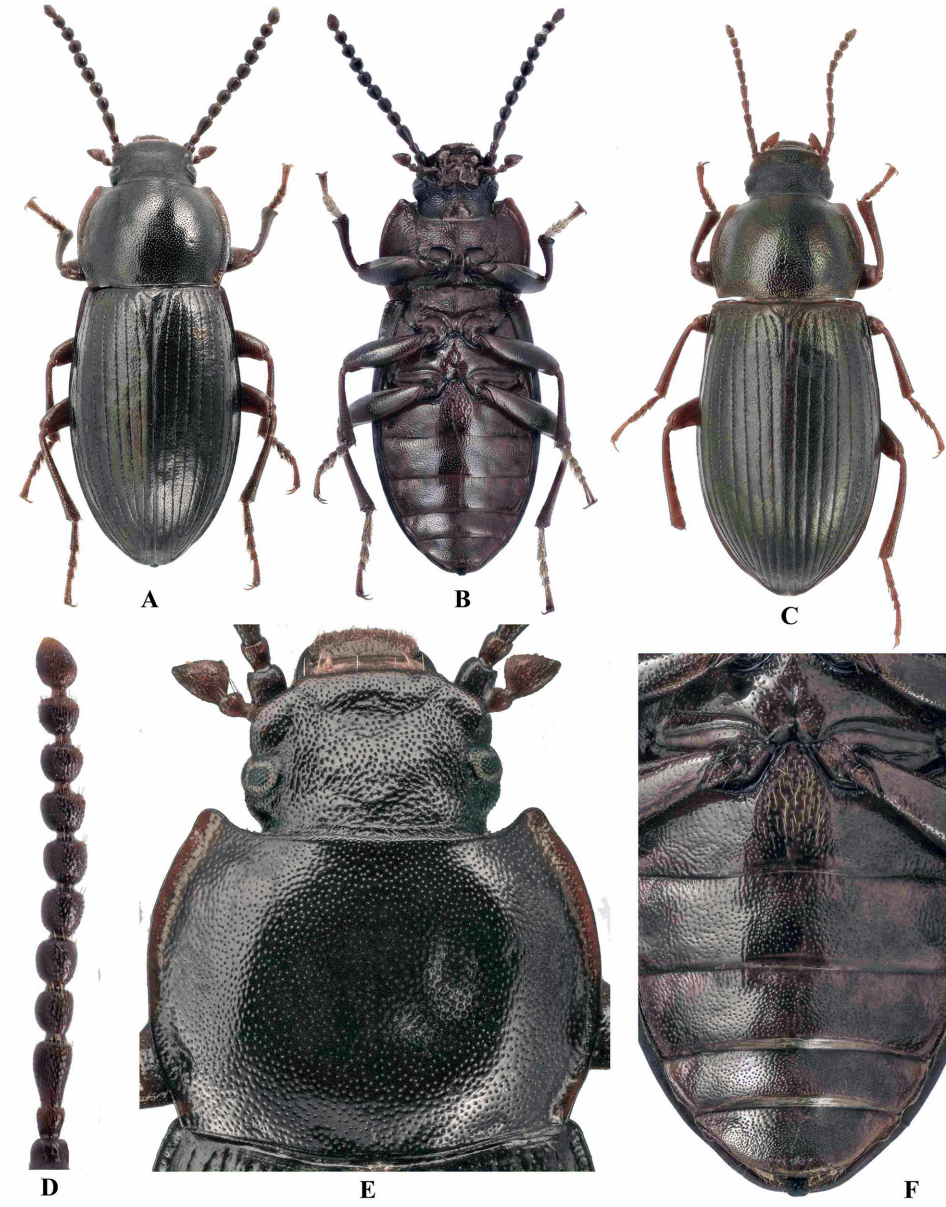

Fig. 5. *N. adriani*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, antenna; E = ♂, head and pronotum; F = ♂, abdomen

North Ossetia-Alania, Arkhon pass, piedmont of Dagov Mt., 42°50'48.05"N, 44°13'46.15"E, 2500 m, alpine meadows, 15.07.2020 (leg. M. V. Nabozhenko, D. G. Kasatkin, I. V. Shokhin, E. N. Terskov).

Distribution. Russia: Alpine and mid-mountain meadows in North Ossetia-Alania.

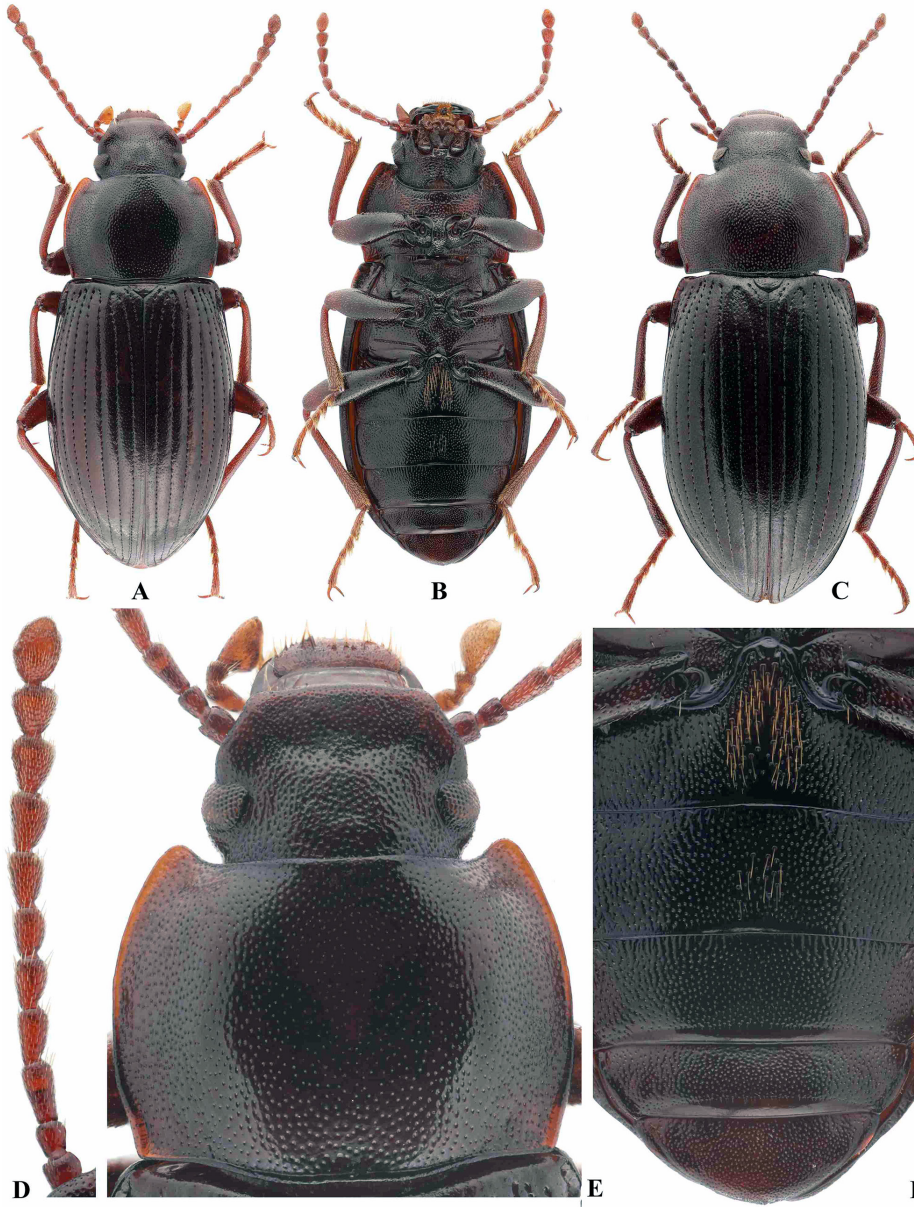

Fig. 6. *N. alanicus*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, antenna; E = ♂, head and pronotum; F = ♂, abdomen

Nalassus (*Caucasonotus*) *avaricus* Nabozhenko & Abdurakhmanov, 2007 (Fig. 7)

Material. 1 ♂, 1 ♀ (PCEI): Dagestan; 1 ♂ (PCEI): Dagestan, Bogos Range, Khvarshi canyon, 20.06.1985 (G.M. Abdurakhmanov).

Distribution. Russia: Dagestan (alpine meadows of the Avarskoe Koisu River basin in the upper reaches and Kurush in the south of the Republic).

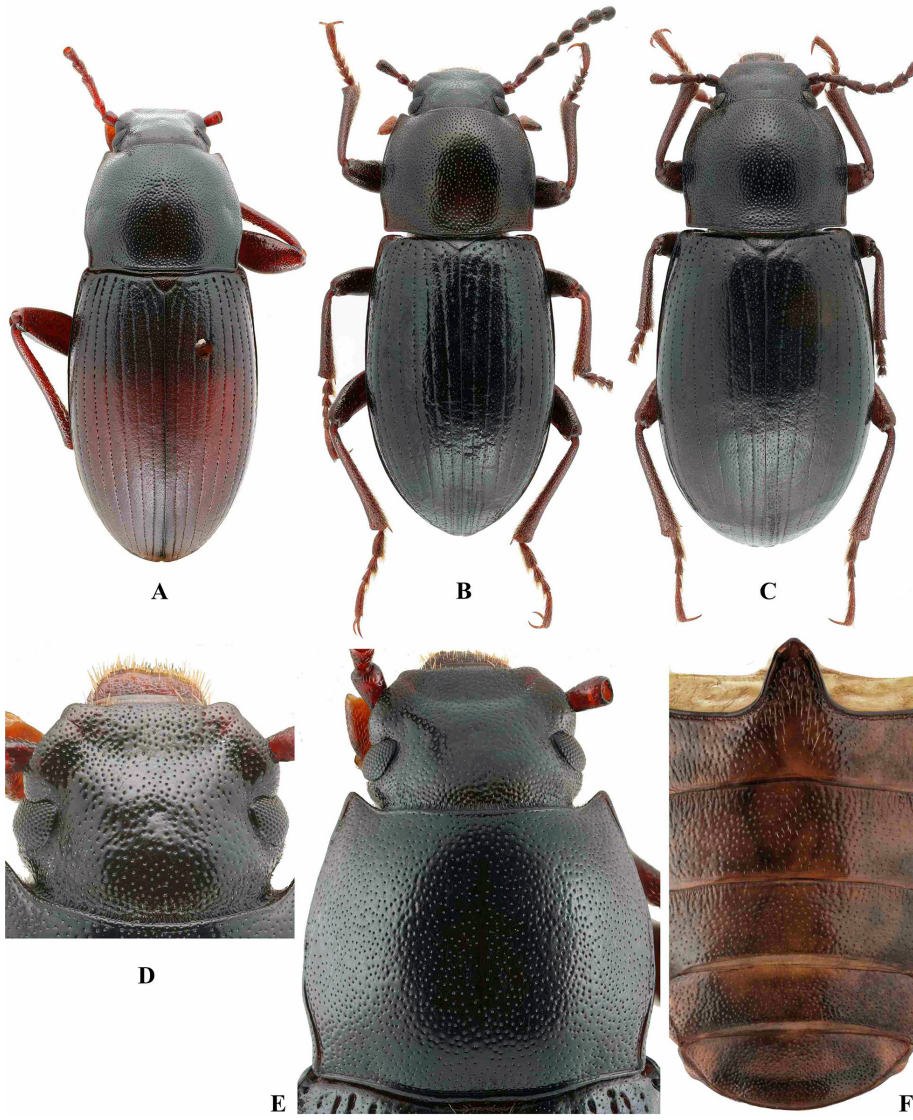

Fig. 7. *N. avaricus*, habitus, details of structure. A = ♂, holotype, dorsally; B = ♂, dorsally; C = ♀, dorsally; D = ♂, head; E = ♂, head and pronotum; F = ♂, abdomen

Nalassus (*Caucasonotus*) *colchicus madlenae* Nabozhenko, 2013 (Figs 8, 9)

= *Nalassus kartvelius* Nabozhenko, 2013, **syn. n.**

Material (PCMN). 2 ♂: Georgia, Samegrelo-Zemo Svaneti, Nenskra River valley, 14.04.2016 (leg. E. A. Khachikov); 1 ♂: Georgia, Shida Kartli, Kaspi, Lekhura River valley, 17.04.2016 (leg. E. A. Khachikov); 4 ♂, 3 ♀: Georgia, Samegrelo-Zemo Svaneti, between Kveda Vedi and Zeda Vedi, 14.04.2016 (leg. E. A. Khachikov); 1 ♂, 2 ♀: Georgia, Imereti, Khvamli Mt., 20.04.2016 (leg. E. A. Khachikov); 9 ♂, 4 ♀: Georgia, Racha Lechkhumi and Kvemo Svaneti, Nikortsminda, 25.04.2016 (leg. E. A. Khachikov); 2 ♂: Georgia, Racha Lechkhumi and Kvemo Svaneti, Grismintekhi, 25.04.2016 (leg. E. A. Khachikov).

Taxonomic notes. *Nalassus kartvelius* was described as a good species from the Racha historical region of Georgia, but later it was interpreted as a subspecies of *N. svaneticus* (Nabozhenko 2020). *Nalassus kartvelius* is indeed externally similar to *N. svaneticus*. However, the first co-author did not take into account a very important character in the structure of the eyes, which is very stable at the species level: *N. svaneticus* has small and weakly convex eyes, while *N. kartvelius* has large and moderately convex eyes. In addition, we found, after a more careful comparative morphological analysis, that *N. svaneticus* also differs in another set of characters from the population described as *N. kartvelius*: the pubescent head (males and females), setated elytral interstriae (only males) and triangular scutellar shield (males and females). As a result, *N. kartvelius* cannot be interpreted as a subspecies of *N. svaneticus*. The structure of the male genitalia has little differences in the Caucasian *Nalassus*, even from different subgenera, so these structures are difficult to use for diagnostics. We received a lot of material from Georgia from our colleague Eduard Khachikov, who collected a good series of *N. colchicus madlenae* from different regions of Northern Georgia. This allowed us to identify variability in colouration from bronze and bronze-green with a metallic sheen (as in typical specimens of *N. colchicus madlenae*) to brown with the reddish-brown pronotum in males (as in the population described as *N. kartvelius*). Colouration with a metallic sheen is typical for forest *Caucasonotus*, and without a metallic sheen for the alpine species of the subgenus. This pattern is very clearly revealed among all species of the subgenus, except for *N. colchicus madlenae*, where we found two different types of integument even in one population. Given the foregoing, the first author corrects his mistake and proposes the following synonymy: *Nalassus colchicus madlenae* Nabozhenko, 2013 = *Nalassus kartvelius* Nabozhenko, 2013, **syn. n.**

Distribution. This subspecies is widely distributed in dark coniferous, deciduous and mixed forests of the southern part of the Greater Caucasus in Georgia. The nominotypical species occur in the Lesser Caucasus in the Adzharia region of Georgia.

Nalassus (*Caucasonotus*) *diteras* (Allard, 1876)
(Fig. 10)

Material. 1 ♂ (DE MSU): Russia, North Ossetia-Alania, S slope of Tsey Range, *Pinus* with meadows, 24.10.1985 (leg. S. K. Alexeev); 2 ♂ (DE MSU): same, but 10.07.1985; 1 ♀ (DE

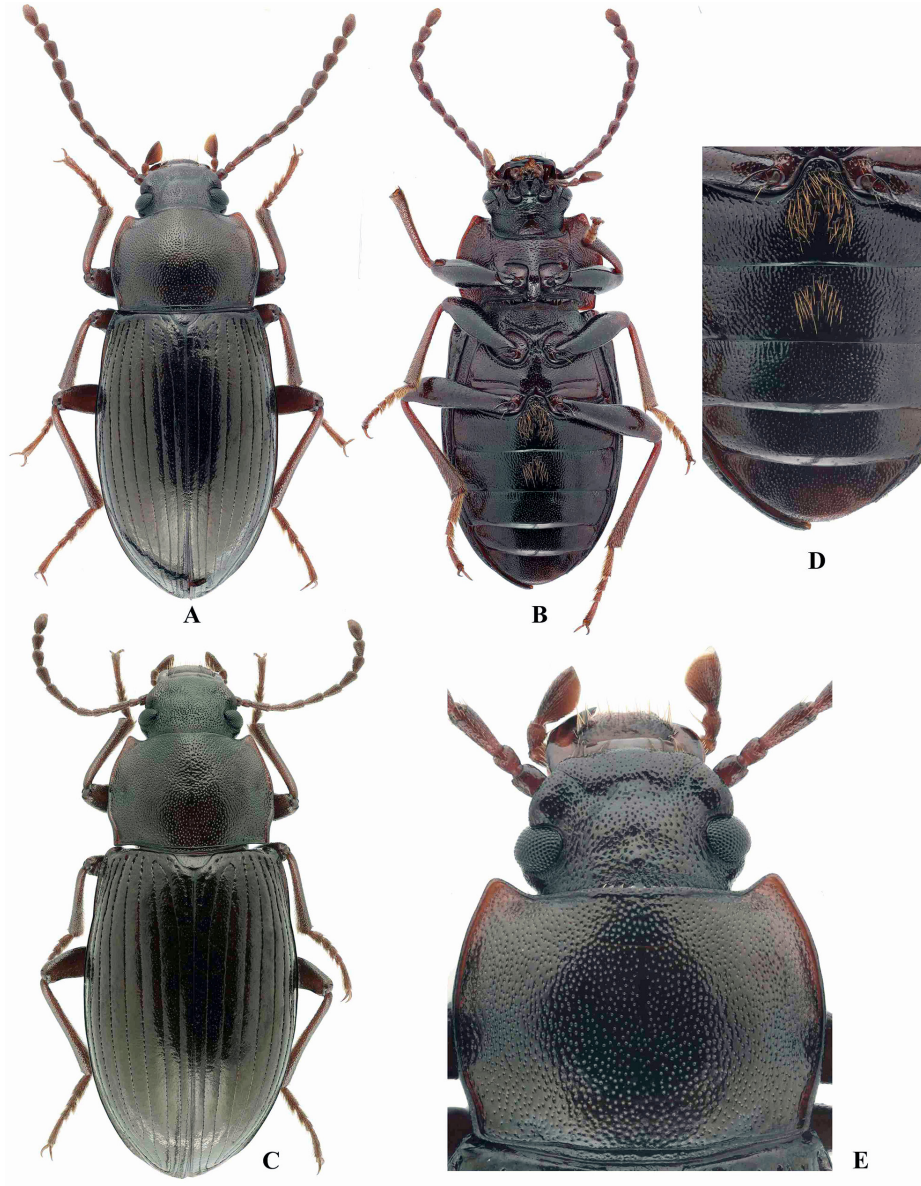

Fig. 8. *N. colchicus madlenae*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

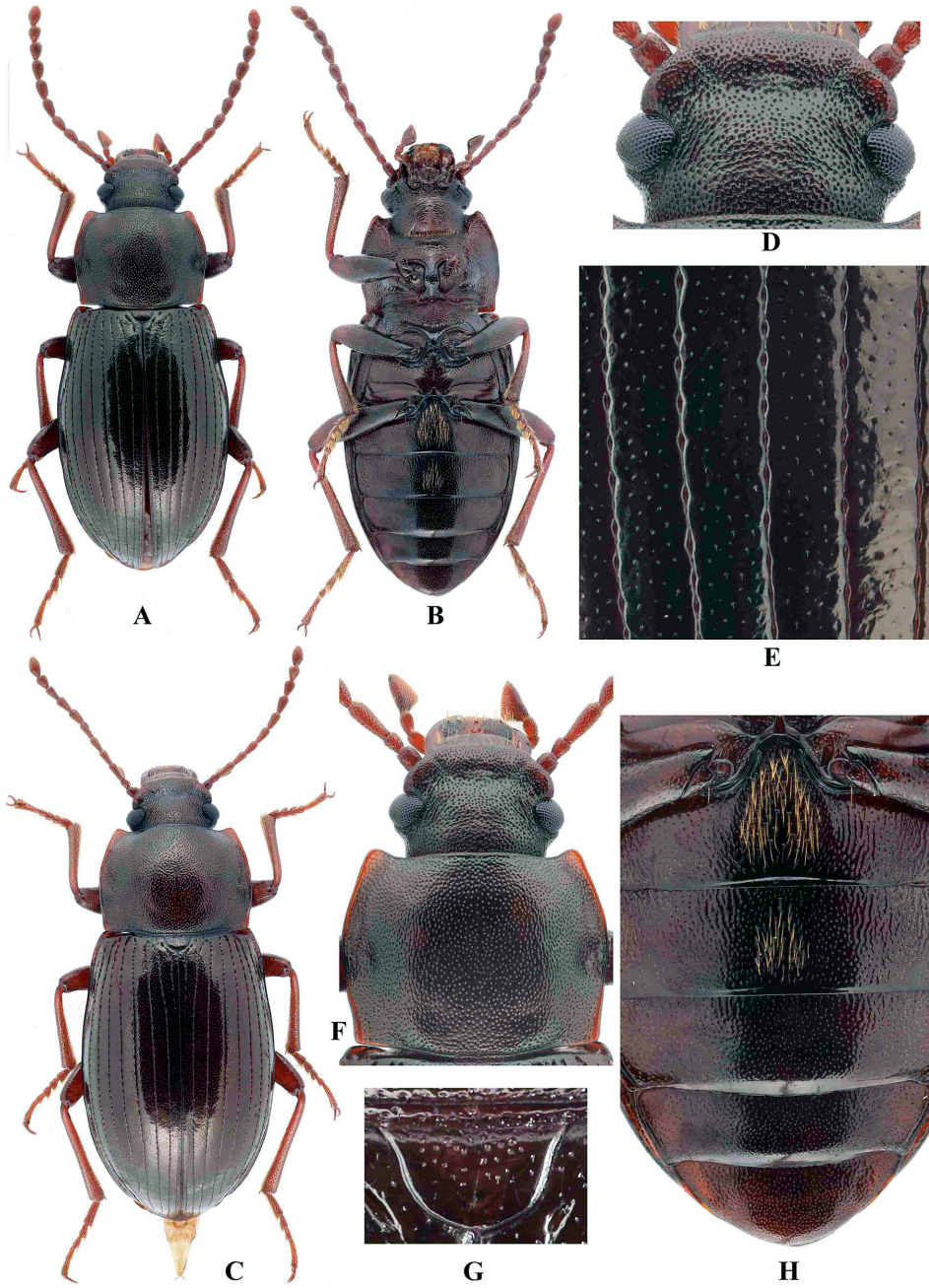

Fig. 9. *N. colchicus madlenae*, paratypes of *N. kartvelius*, **syn. n.** habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, head; E = ♂, elytral interstriae; F = ♂, head and pronotum; G = ♂, scutellar shield; H = ♂, abdomen

MSU): 1 ♀ (DE MSU): Russia, North Ossetia-Alania, Elkhotovo, near Bekan Lake, 3.06.1986 (leg. S. K. Alexeev); 1 ♂ (DE MSU): Russia, North Ossetia-Alania, Skalisty Range, Kariukhokh Mts., Kallon Mt., 2300 m, subalpine meadow, 12.07.1985 (leg. S. K. Alexeev); 2 ♂ (DE MSU): Russia, North Ossetia-Alania, Kasarsky canyon, Uiltsa natural area, 1500 m, mead-

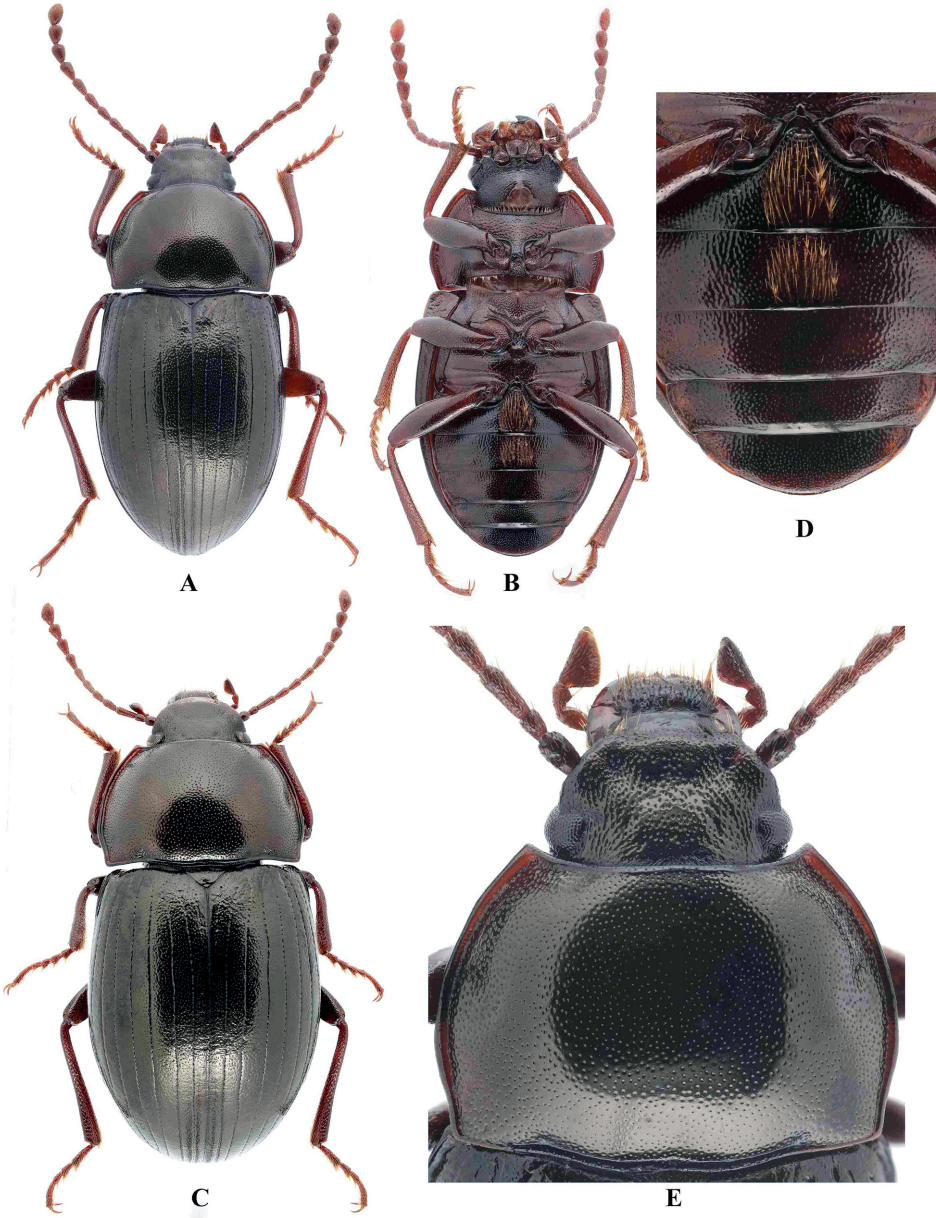

Fig. 10. *N. diteras*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

ow, 31.05.1985 (leg. S. K. Alexeev); 1 ♀ (DE MSU): same, but, 14.09.1988; 1 ♀ (DE MSU): Russia, North Ossetia-Alania, Ardon River basin, 2 km S of Alagir, Duraftuan Mt., 800 m, *Fagus* forest, 25.07.1984 (leg. S. K. Alexeev); 1 ♂, 1 ♀ (DE MSU): Russia, North Ossetia-Alania, Ardon River basin, southern outskirts of Alagir, left terrace of Ardon River, meadow, 650 m, 22.06.1984; 1 ♀ (PCMN): Russia, North Ossetia-Alania, 1 ♂ (PCMN): Russia, North

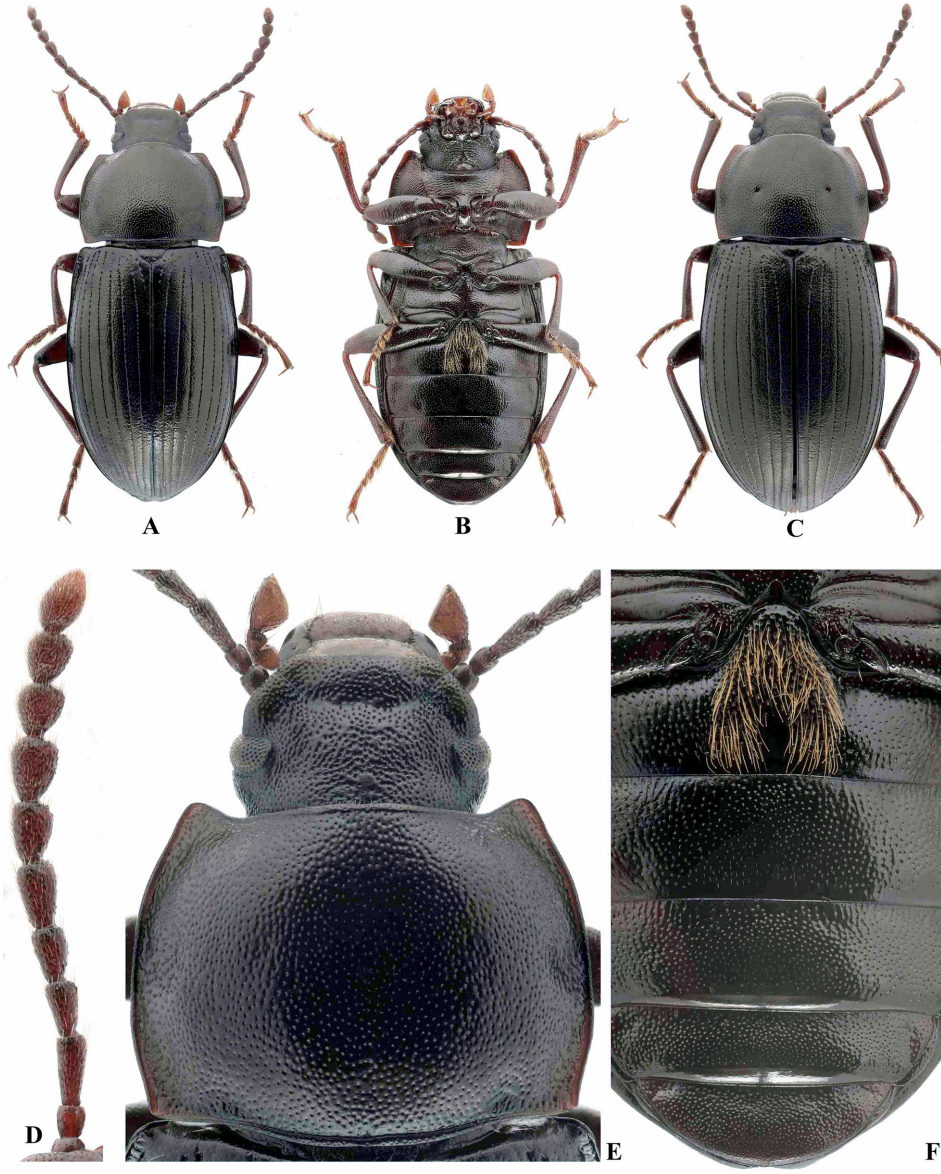

Fig. 11. *N. dombaicus*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, antenna; E = ♂, head and pronotum; F = ♂, abdomen

Ossetia-Alania, Arkhon pass, piedmont of Dagov Mt., 42°50'48.22"N, 44°13'27.55"E, 2400 m, subalpine meadow with *Betula* and *Pinus*, 15.07.2020 (leg. M. V. Nabozhenko, D. G. Kasatkin, I. V. Shokhin, E. N. Terskov); 1 ♂, 1 ♀ (PCMN): Russia, Dagestan, Tabasaran Distr., W of Gurkhun, 42°00'33.97"N, 47°53'41.35"E, 1170 m, 11.05.2008 (leg. M. V. & S. V. Nabozhenko, A. K. Teymurov); 1 ♀ (PCMN): Russia, Dagestan, Levashi Distr., near Tsudakhar, above high mountain botanical garden of the Russian Academy of Sciences, 42°27'55.21"N, 47°20'31.86"E, 1295 m, meadows, rocks, 13.07.2021 (M. V. Nabozhenko, I. A. Chigray). 1 ♀ (HNHM): Georgia, Kazbegi, 1700 m, 13–18.07.1990 (leg. D. Szalóki).

Distribution in the Greater Caucasus. Widely distributed in all regions of the Greater Caucasus, usually on subalpine meadows (but can be found in *Fagus* forests), except for the Stavropol Region of Russia.

Nalassus (*Caucasonotus*) *dombaicus* (Nabozhenko, 2000) (Fig. 11)

Material. 1 ♀ (PCMN): Russia, Karachay-Cherkessia, Teberdinsky Natural Reserve, Semenov-Bashi Mt., 43°18'55.13"N, 41°33'52.35"E, 2550 m, alpine meadows, rocks, 9.07.2020 (M. V. Nabozhenko, I. V. Shokhin).

Distribution. Russia (Karachay-Cherkessia), Abkhazia (Lakhta Range). Alpine meadows from 2400 to 3200 m.

Nalassus (*Caucasonotus*) *ludmilae* Nabozhenko, 2001 (Fig. 12)

Material. 1 ♂ (HNHM): Abkhazia, Bzyb fl., 26.05.1975 (leg. K. Székely); 4 ♂ (ZIN, PCMN): Abkhazia, Lashipse River valley above Ritsa Lake, 43°29'10.93"N, 40°37'21.05"E, on *Abies nordmanniana*, 24.05.2004 (leg. local collectors).

Distribution. Abkhazia, dark coniferous and mixed forests (Bzyb River valley and tributaries).

Nalassus (Caucasonotus) negrobovi Nabozhenko, sp. n. (Fig. 13)

Type material (ZIN). Holotype (♂) and paratype (♀) with labels: "N Caucasus, Abkhazia, Atshibakh Mt. R. 43°17'08"N, 41°29'07"E, 1930 m – 43°25'17"N, 40°35'37"E, 2215 m", "20–24.VII.2016. D. S. Vakhromov, V. A. Gulymanova, O. A. Minnikov, D. Yu. Skokov leg."

Description. Male. Body robust, bare, black, dull. Measurements: Y – 1.5; PH – 1.66; PwPl – 1.36; ElEw – 1.5; EHw – 2.05; EPw – 1.24; EPl – 2.54.

Head. Head widest at eye level. Eyes moderately large, convex. Anterior margin of epistoma straight, with eight marginal and two discal chaetae. Lateral margin of head sinuate between epistoma and gena. Lateral margin of genae strongly rounded in basal third and straight in apical two thirds. Punctation of head dorsally moderately coarse and dense, uneven: punctures coarser and denser at middle of frons (puncture diameter subequal to distance between punctures) and finer and sparser in basal part, on epistoma and genae. Ventral temple grooves (extending from eyes) well expressed. Ventral side of epicranium

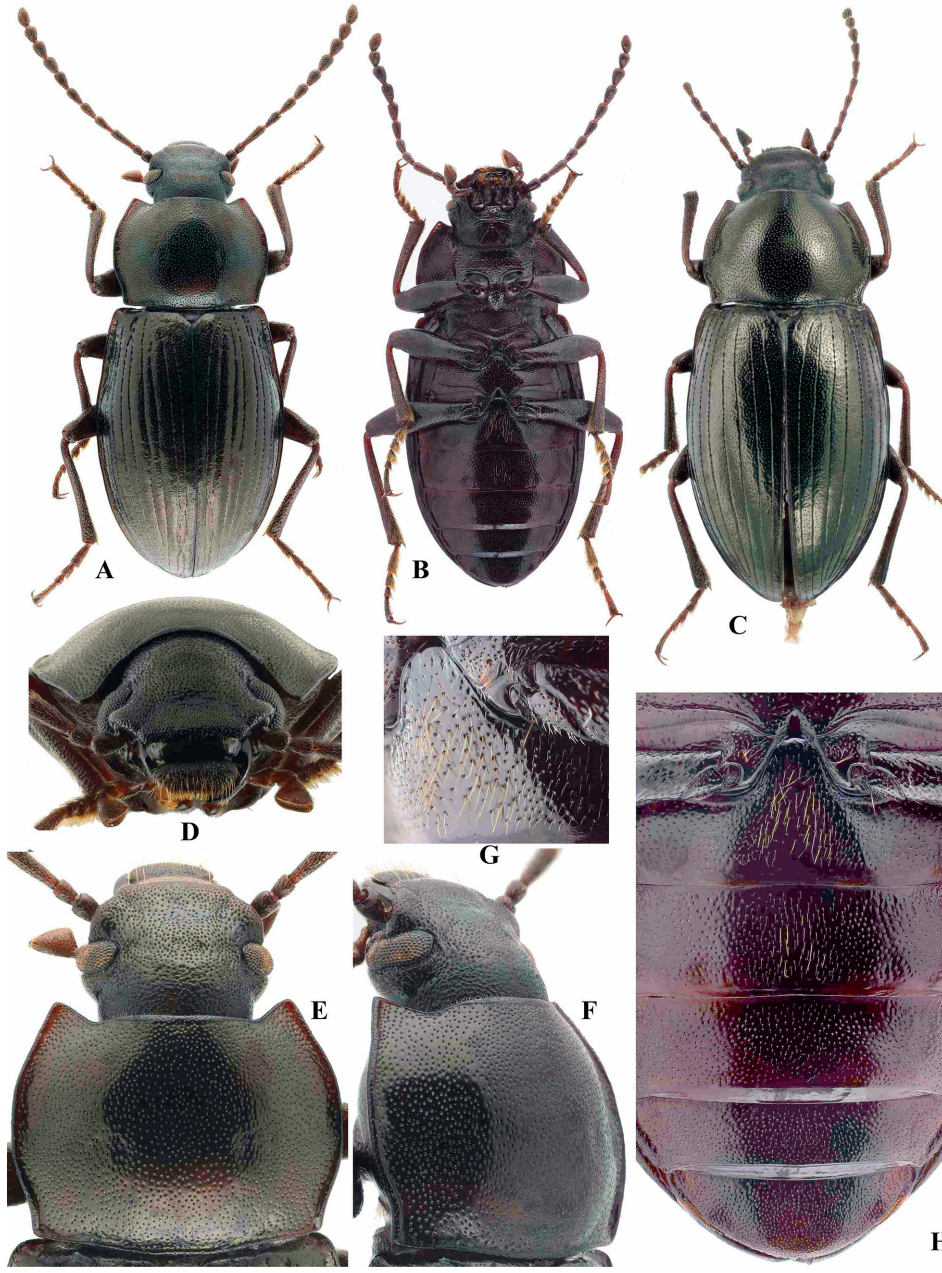

Fig. 12. *N. ludmilae*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, holotype, dorsally; D = ♂, head and pronotum, frontal view; E = ♂, the same, dorsal view; F = ♂, the same, dorso-lateral view; G = ♂, abdominal ventrite 1 in middle, dorso-lateral view; H = ♂, abdomen

with coarse and dense punctation and wrinkles around mouthparts and fine sparse punctation on other surface. Antennae moderately long, with two distal antennomeres extending beyond base of pronotum. Antennae thickened. Widest antennomeres are 8 and 9. Antennomeres 4–7 subcylindrical. Ratio of length / width of antennomeres 2–11: 1.9/1.6, 4/1.6, 3/1.8, 2.8/2, 3.1/2.2, 3/2.2, 3/2.5, 2.6/2.5, 2.5/2.4, 3/2.1.

Prothorax. Pronotum transverse, widest little behind middle. Lateral margins of pronotum regularly rounded, slightly undulate. Anterior margin weakly rounded, base bisinuate, moderately rounded at middle. Antero-lateral corners strongly projected, acute with rounded apex; postero-lateral corners obtuse, pointed at apex. Lateral margins and

Fig. 13. *N. negrobovi*, sp. n., habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, antenna; E = ♂, head and pronotum; F = ♂, abdomen; G = ♂, aedeagus, ventrally; H = the same, laterally; I = spiculum gastrale

base beaded (bead at middle of base and in basal third of lateral margins thicker); anterior margin with interrupted bead at middle. Disc of pronotum moderately convex, weakly and narrowly flattened only near corners; punctation of disc moderately sparse and fine (puncture diameter much shorter, than interpuncture distance). Prothoracic hypomera with irregular coarse wrinkles, lateral margins flattened only near corners. Prosternum with fine and sparse punctation and transverse fine wrinkles. Prosternal process bare, shine, smooth, not beaded, weakly convex.

Pterothorax. Elytra widest at middle, lateral margins slightly emarginate in basal 1/5. Punctures in striae connected by furrows. Interstriae slightly convex, with very sparse and very fine punctation and smoothed transverse wrinkles only in basal quarter. Mesoventrite with coarse and dense punctation in anterior part and sparse and fine punctation between mesocoxae. Mesepisterna, mesepimera, metepisterna and metaventrite with fine and sparse punctation. Metaventrite bare.

Legs. Trochanters bare, only with one long sensillum. Femora covered with sparse short setae. Tibiae straight, denser pubescent, especially on distal inner side. Protarsi not wider than in female, but more slender.

Abdomen. Abdominal ventrites finely and sparsely punctate; ventrite 1 with much coarser punctation at middle and ^-shaped hair brush (setae come from these coarse punctures); ventrite 5 completely beaded at apex and denser punctate. Aedeagus typical for *Nalassus*, weakly sclerotized, with laterally compressed keel at apex of parameres; median lobe baculi wide, connected in middle. Spiculum gastrale with thin rods and common stem.

Body length 8.5 mm, width 3.7 mm.

Female. Body more robust. Measurements: PH – 1.66; PwPl – 1.46; ElEw – 1.45; EHw – 2; EPw – 1.2; EPl – 2.58. Antennae shorter; middle antennomeres not widened, antennae regularly widened from proximal to distal part, widest antennomeres 9–11. Disc of pronotum narrowly and completely flattened along lateral margins, with two foveae at middle. Legs stronger, all parts shorter, than in male. Body length 9.3 mm, width 4 mm.

Etymology. This new species is named in honour of Oleg Pavlovich Negrobov (1941–2021), a famous entomologist and teacher of many dipterologists (Nartshuk *et al.* 2021).

Comparative diagnosis. The new species belongs to the alpine subgroup of the subgenus *Caucasonotus* Nabozhenko, 2000 having rounded apex of anterolateral corners of pronotum (*N. dombaicus*, *N. alanicus*, *N. adriani*), but differs from three mentioned species by larger and more convex eyes (Y = 1.5 in the new species and 1.34–1.43 in other three species). *Nalassus negrobovi* **sp. n.** is externally very similar to *N. dombaicus* by the black body and connected strial punctures on elytra, but differs from the latter by the following additional characters: lateral sides of pronotal disc and prothoracic hypomera are narrowly weakly flattened only near corners (entirely flattened in *N. dombaicus*), punctation of interstriae very fine and sparse, weakly visible (coarser and well expressed in *N. dombaicus*); male antennomeres 4–8 are thickened, the widest ones are the 8th and 9th (not thickened in *N. dombaicus*, widest are antennomeres 9–11); female tarsomeres thicker and shorter, protarsomer 5 1.33 times as long as protarsomeres 1–4 together (*N. dombaicus*: tarsomeres thinner and longer, protarsomer 5 subequal to the length of 1–4 ones together). The new species differs from *N. alanicus* by a black body, male antennomeres 4–8 are

thickened, only one hair brush on the male abdominal ventrite 1 and strial punctures connected by furrow (*N. alanicus*: body brown, male middle antennomeres simple, not thickened, abdominal ventrites 1 and 2 with hair brush at the middle, strial punctures not connected by furrow). *Nalassus adriani* differs from the new species by brown, more elongated body, much shorter and thicker antennomeres 3–8 and widely flattened lateral sides of the pronotal disc.

Nalassus (*Caucasonotus*) *pharnaces* Allard, 1876
(Fig. 14)

Material. 1 ♂, 1 ♀ (DE MSU): Russia, Krasnodar Region, above Estosadok, Caucasian Natural Reserve, Achipse River valley, 1200 m, 8.05–22.07.2004 (leg. V. Perov); 14 ♂, 7 ♀ (PCMN): Russia, Krasnodar Region, E of Matsesta, Agurchik River valley, 43°32'49.38"N, 39°48'49.86"E, 10.04.2007 (leg. M. V. Nabozhenko); 4 ♂, 2 ♀ (PCMN): Russia, Krasnodar Region, above Goryachy Klyuch, Shchyotka Mt., 2–4.05.2011 (leg. D. G. Kasatkin); 2 ♂, 1 ♀ (PCMN): Russia, Adygea, Maykop, forest, southern environs of the town, left bank of Belaya River, 9.05.2011 (D. G. Kasatkin); 5 specimens (UC): Russia, Karachay-Cherkessis, between Kurdzhinovo and Zagedan, N 43°50’44.6” E 40°55’54.6”, 914 m, on Fagus, 2.07.2020 (leg. M. V. Nabozhenko, I. V. Shokhin, E. N. Terskov, D. G. Kasatkin); 1 ♂ (HNHM): Abkhazia, Hypsa fl., 27.05.1976 (leg. K. Székely); 1 ♂ (HNHM): Abkhazia, Gvandra, 900 m, 14.07.1979 (leg. K. Székely); 2 ♂, 3 ♀ (HNHM): Abkhazia, Gvandra, Klich River valley, 900 m, 29.06.–1.07.1983 (leg. I. Retezár); 1 ♀ (PCMN): Abkhazia, Dzykhva Mt., 43°11'25.14"N, 41°07'15.60"E, 1450 m, on Fagus, 17–18.08.2005 (collectors from Rostov State University).

Distribution. Western Caucasus. Russia (Krasnodar Region, Adygea, Karachay-Cherkessia), Abkhazia (south to Kodor River Bassin). Beech forests.

Nalassus (*Caucasonotus*) *svaneticus* Nabozhenko & Dzhambazishvili, 2001
(Fig. 15)

Distribution. Georgia: Racha-Lechkhumi and Kvemo Svaneti. It is known only from Tskhenitskali River Bassin. Subalpine zone.

Nalassus (*Caucasonotus*) *zakatalensis* Nabozhenko, 2001
(Fig. 16)

Distribution. Southern slopes of the east part of the Greater Caucasus. Azerbaijan: Zaqatala and Belokana districts, alpine meadows.

Subgenus *Horistelops* Gozis, 1910

The synonymy *Horistelops* = *Helopondrus* Reitter, 1922 was established recently (Bouchard *et al.* 2021). Representatives of the subgenus are distributed in Europe, Anatolia, Western Kazakhstan (Uralsk), North Iran and South-West Turkmenistan.

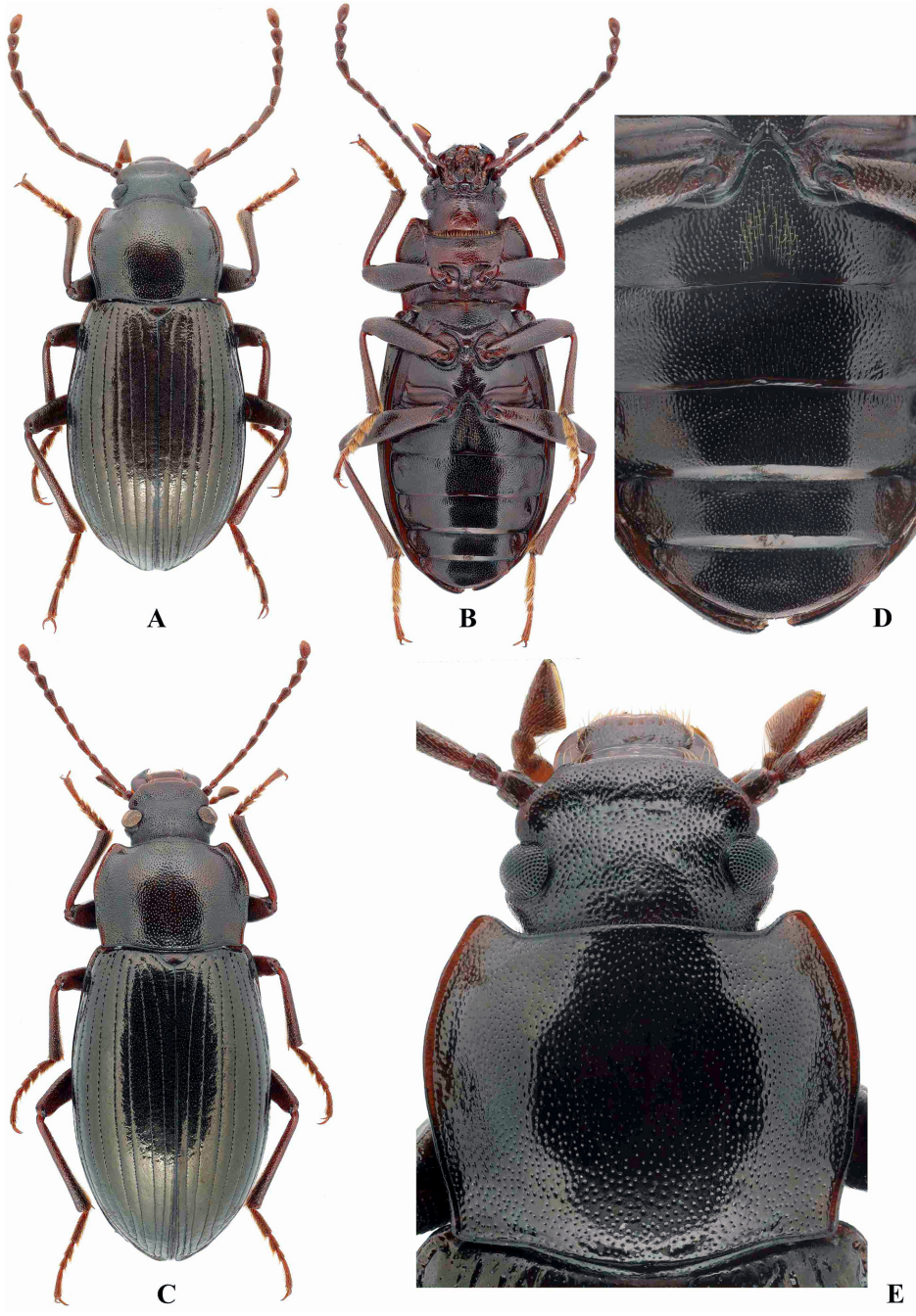

Fig. 14. *N. pharnaces*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

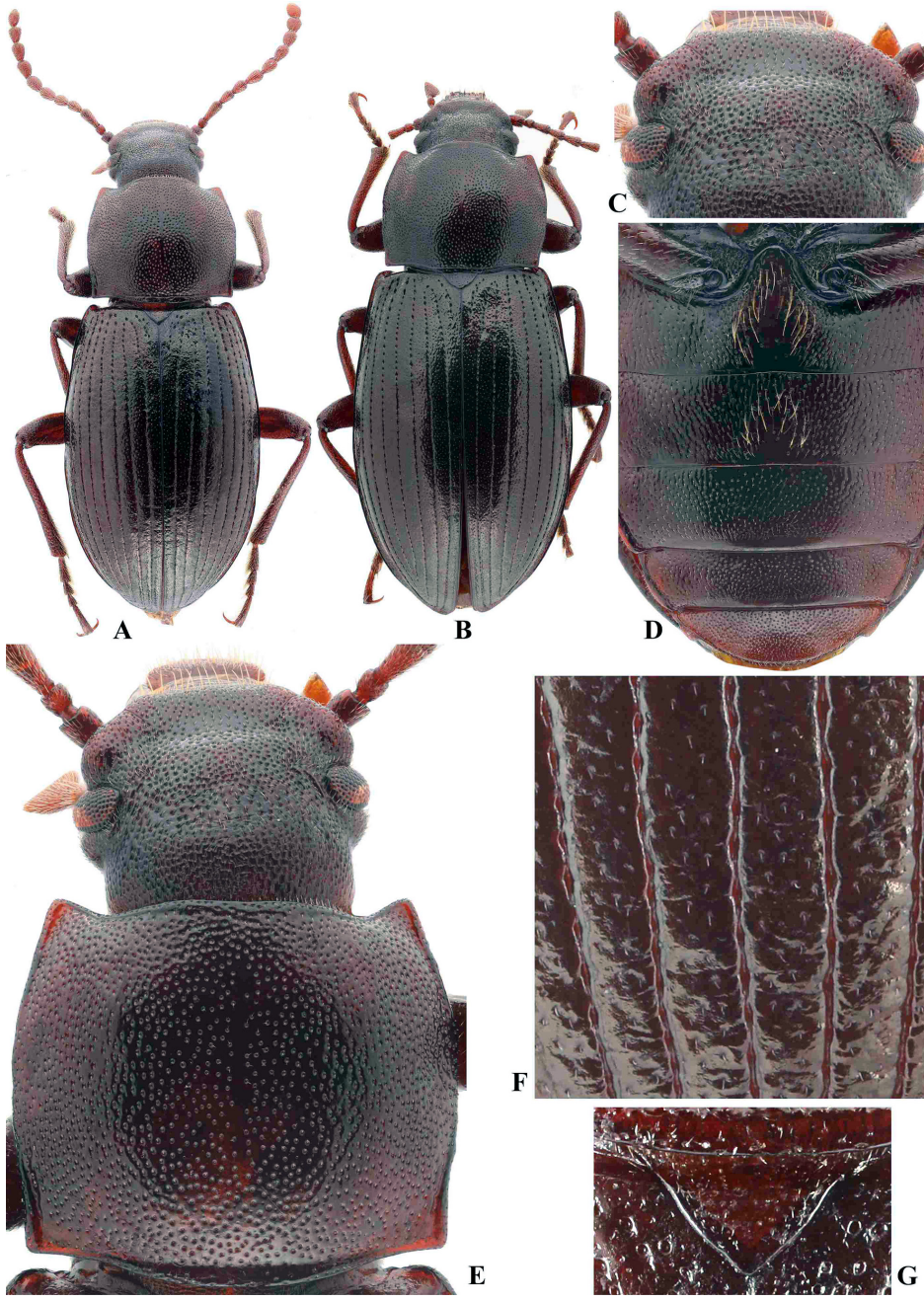

Fig. 15. *N. svaneticus*, paratypes, habitus, details of structure. A = ♂, dorsally; B = ♀, dorsally; C = ♂, head; D = ♂, abdomen E = ♂, head and pronotum; F = ♂, elytral interstriae; G = ♂, scutellar shield

Notes. In a previous paper (Nabozhenko 2010) we listed data on the holotypes of two species from Iran and Turkmenistan, *N. cambyses* (Seidlitz, 1895) and *N. ahngeri* (Medvedev, 1998) and suggested that these names could be synonymous. The original descriptions and figures for *N. ahngeri* are presented in the original descriptions (Seidlitz 1895, Medvedev 1998) and figures for *N. cambyses* are illustrated in Nabozhenko (2010). Both taxa are conspecific, and studied specimens from Kopetdag described as *N. ahngeri* (Nabozhenko 2010), differ only by smaller body size from populations from Elburs. As a result, the following synonymy is proposed: *Helops cambyses* Seidlitz, 1895 = *Cylindronotus ahngeri* Medvedev, 1998, **syn. n.**

Nalassus (*Horistelops*) *abkhasicus* Nabozhenko, 2001
(Fig. 17)

Material. 1 ♂, 3 ♀ (ZIN): Abkhazia, Bzybsky Range, left bank of Bzyb River, 3 km above the confluence of Gega and Bzyb rivers (leg. Yu. G. Arzanov, D. G. Kasatkin, V. Murashov).

Distribution. Abkhazia (Bzyb and Gega canyons), on rocks.

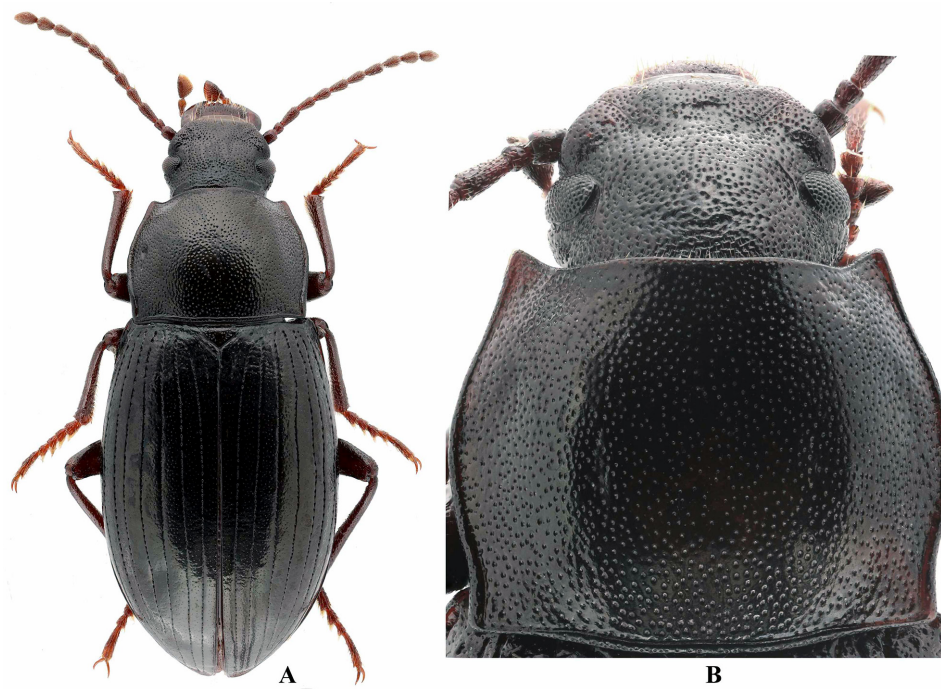

Fig. 16. *N. zakatalensis*, ♀, habitus, details of structure. A = habitus, dorsally; B = head and pronotum

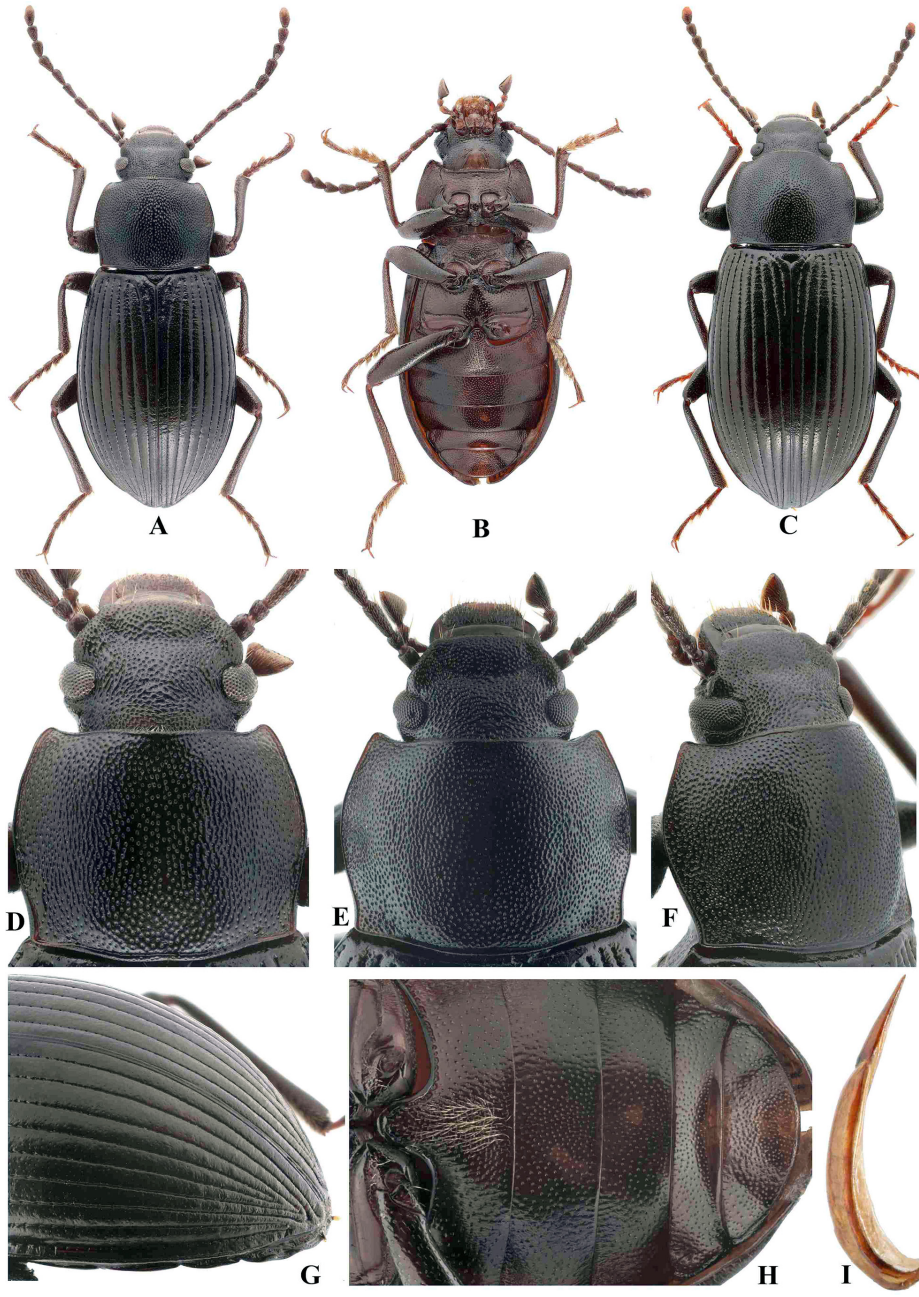

Fig. 17. *N. abkhasicus*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, head and pronotum, dorsally; E = ♀, head and pronotum, dorsal view; F = the same, dorso-lateral view; G = ♀, apical part of elytra, dorso-laterally; H = ♂, abdomen; I = ♂, aedeagus, laterally

Nalassus (*Horistelops*) *lineatus* (Allard, 1877) (Fig. 18)

Material. 1 ♀ (ED MSU): Russia, Krasnodar Region, Vityazevo near Anapa, 17–21.04.2004 (leg. S. K. Alexeev); 7 specimens (PCMN): Krasnodar Region, Sochi, near Slava Metreveli stadium, 14–15.05.2009; 1 ♀ (HNHM): Abkhazia, Klich River valley, Yuzhny Priyut, 11–14.07.1979 (leg. K. Székely).

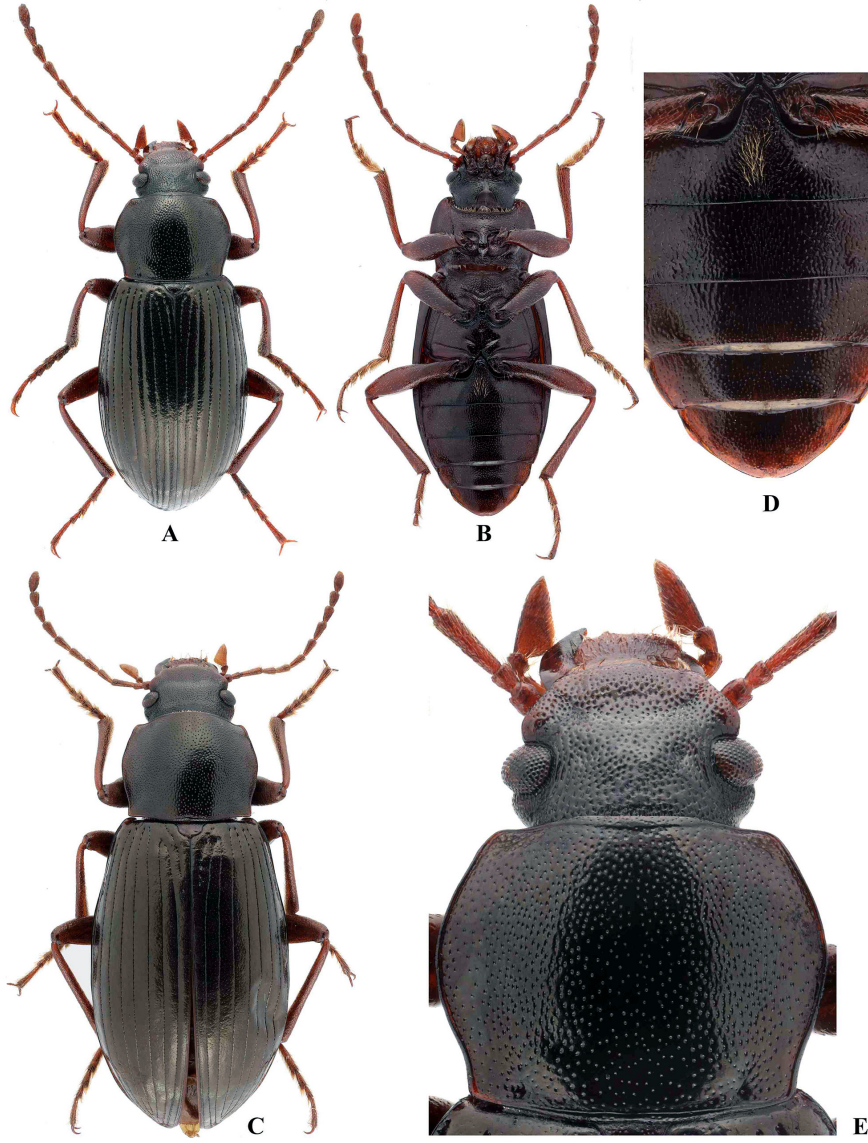

Fig. 18. *N. lineatus*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum

Distribution in the Greater Caucasus. This species has a disjunctive range (Nabozhenko 2001). The western exclave: the Western Caucasus from Anapa (Russia) in the north to Adzharia (Georgia) in the south and Kaspi (Georgia) in the east. *Nalassus lineatus* occurs on plains and foothills, but sometimes it reaches low mountains through canyons.

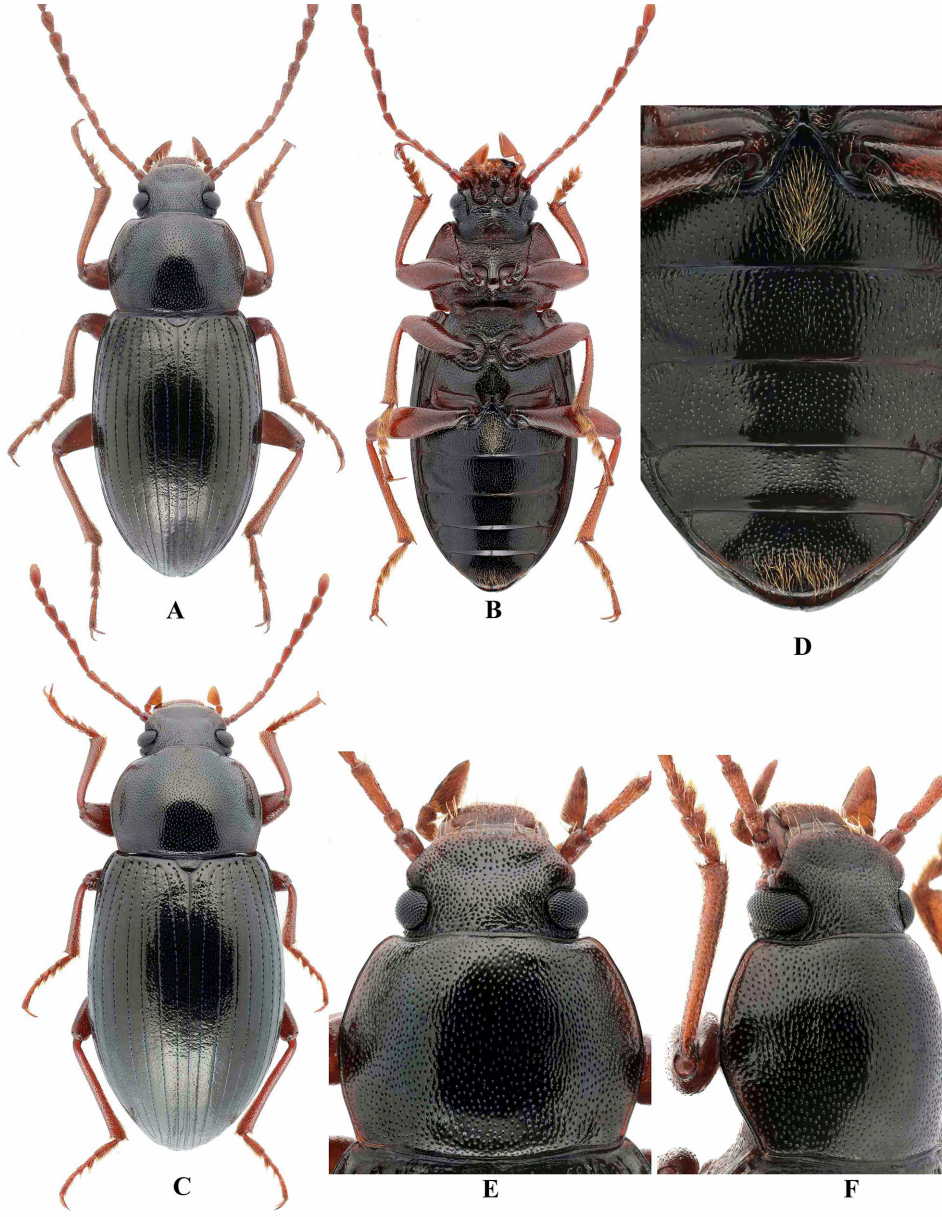

Fig. 19. *N. sareptanus*, habitus, details of structure. A = ♂, dorsally; B = ♂, ventrally; C = ♀, dorsally; D = ♂, abdomen; E = ♂, head and pronotum, dorsally; F = the same, dorso-laterally

Nalassus (*Horistelops*) *sareptanus* (Allard, 1876)
(Fig. 19)

Distribution in the Greater Caucasus. This widely distributed species (Nabozhenko 2020) occurs on foothills and low mountains within the belt of oak forests and in plain steppes in the Ciscaucasia. Russia (Krasnodar and Stavropol regions, Adygea), Abkhazia.

KEY TO *NALASSUS* SPECIES FROM THE GREATER CAUCASUS ON MALES

(external sexual dimorphism is the presence of the hair brush on the abdominal ventrite 1)

1 Hair brush ^-shaped on abdominal ventrite 1 and sometimes 2; punctation on surface under this brush coarse and sparse, punctures much larger and sparser than on another surface of ventrites (Figs 5F, 6F, 7F, 8D, 9H, 10D, 11F, 12H, 13F, 14D, 15D) 2

– Hair brush oval on abdominal ventrite 1; punctation on surface under this brush fine and dense, punctures the same on size and denser than on another surface of ventrites (Figs 17H, 18D, 19D) 12

2 Body robust, very wide and strongly convex (Figs 10A, B, C). Pronotum with deep groove along lateral margin on each side (Figs 10C, E). Epipleura in base very wide, much wider than width of mesofemora, and wider than metepisterna on level of posterior portion of metaventrite (Fig. 10B) *N. diteras*

– Body slender or moderately slender, weakly or moderately convex (Figs 5A,B, 6A,B, 7A,B, 8A,B, 9A,B, 11A,B, 12A,B, 13A,B, 14A,B, 15A). Pronotum without deep groove along lateral margin on each side (Figs 5E, 6E, 7E, 8E, 9F, 11E, 12D–F, 13E, 14E, 15E, 16B). Epipleura in base not strongly widened, the same or narrower than width of mesofemora; epipleura and metepisterna on the level of posterior portion of metaventrite with subequal width (Figs 5B, 6B, 8B, 9B, 11B, 12B, 13B, 14B) 3

3 Antero-lateral corners of pronotum strongly projected, acute, pointed or very narrowly rounded at apex (Figs 7E, 8C,E, 9C,E, 9C,F, 12C,E,F, 15E, 16B) 4

– Antero-lateral corners of pronotum strongly projected, acute, but widely rounded at apex (Figs 5, B, E, 6E, 11E, 13E, 14E) 8

4 Eyes large, convex (Y = 1.57–1.62) (Figs 8E, 9E) 5

– Eyes small, weakly convex (Y = 1.42–1.45) (Figs 7D, 15C, 16B) 6

5 Lateral sides of pronotal disc not flattened and not elevated (Figs 8C, E) *N. colchicus madlenae*

– Lateral sides of pronotal disc widely flattened and slightly elevated (Figs 12C–F) *N. ludmilae*

6 Head pubescent with recumbent setae (Fig 15C). Body red-brown (Figs 15A,B) *N. svaneticus*

– Head bare (Figs 7B, 16B). Body black (Figs 7A–C, 16A) 7

7 Lateral margins of pronotum widely emarginate in anterior third (Fig. 16B) *N. zakatalensis*

– Lateral margins of pronotum almost straight or weakly rounded in anterior third (Figs 7B,C,E) *N. avaricus*

8 Eyes large, convex (Y = 1.7) (Fig. 14E). Body with metallic bronze-greenish shine dorsally (Figs 14A,C) *N. pharnaces*

– Eyes small or moderate in size, usually weakly convex (Y = 1.34–1.5) (Figs 5E, 6E, 11E, 13E). Body brown or black, without metallic shine dorsally (Figs 5A,C, 6A,C, 11A,C, 13A,C) 9

9 Antennomeres 4–8 strongly thickened, bead-like, each of antennomeres 4–7 not broadened from proximal to distal part (Figs 5D, 13D) 10

– Antennomeres 4–8 not thickened, antennae gradually widened to apex, each of antennomeres 4–7 broadened from proximal to distal part (Figs 6D, 11D) 11

10 Lateral sides of pronotal disc and prothoracic hypomera narrowly flattened only near corners (Figs 13B,D). Body black. Elytra lesser elongate, ElEw = 1.48 (Fig. 13A). Antennomeres 7 and 8 are the widest (Fig. 13D). Eyes more large and closer (Y = 1.5) (Fig. 13E) *N. negrobovi* sp. n.

– Lateral sides of pronotal disc widely flattened along the entire length (Figs 5B,E). Body brown. Elytra more elongate, ElEw = 1.6 (Fig. 5A). Antennomeres 3–8 are widest (Fig. 5D). Eyes small and widely separated (Y = 1.35) (Fig. 5E) *N. adriani*

11 Body black. Lateral sides of pronotal disc widely flattened along entire length, lateral margins not emarginated in base (Fig. 11E). Elytra with deep entire strial furrows (Fig. 11A). Only abdominal ventrite 1 with ^-shaped hair brush (Fig. 11F) *N. dombaicus*

– Body brown. Lateral sides of pronotal disc narrowly flattened only near corners, lateral margins shortly emarginated in base (Fig. 6E). Strial

punctures not connected by furrow (Fig. 6A). Abdominal ventrite 1 with ^-shaped hair brush, ventrite 2 with smaller oval brush (Fig. 6F) *N. alanicus*

12 Ventral side of epicranium without temple groove (Fig. 2C). Antennomeres 3–8 strongly thickened, much thicker than other antennomeres (Fig. 2A) *N. dissonus*

– Ventral side of epicranium with temple groove, coming from the ventral margin of eye (Figs 1B, 3B). Antennomeres 3–8 thickened, but subequal in width with other ones (Figs 3A, 4A), or antennae not thickened and gradually widened from to apex (Fig. 1A) 13

13 Pronotum with longitudinally elongate punctation on sides of middle (Figs 17D–F, 19E,F). Apical piece of aedeagus flattened dorso-ventrally, laminate at apex (Fig. 17I) 14

– Pronotum with simple round punctation on the entire disc. Apical piece of aedeagus with laterally compressed keel at apex (Figs 13G, H) 16

14 Antero-lateral corners strongly projected, acute, very narrowly rounded at apex (Figs 17D,E) *N. abkhasicus*

– Antero-lateral corners not projected, obtuse, widely rounded at apex (Figs 18E, 19E,F) 15

15 Pronotum not cordiform, widest at middle, lateral margins usually not emarginate near base (steppe populations) (Fig. 19E) or slightly emarginate (most of specimens from the Caucasian forest populations). Abdominal ventrites 1 and 5 and sometimes 2 with hair brush (Fig. 19D) *N. sareptanus*

– Pronotum cordiform, widest before middle or rarely at middle, lateral margins widely emarginate in base (Fig. 18E). Only abdominal ventrite 1 with hair brush (Fig. 18D) *N. lineatus*

16 Body shiny, integument smooth. Antennae gradually widened to apex, antennomeres 8–10 are widest (Fig. 1A) *N. brevicollis*

– Body dull due to hexagonal micro sculpture of integument. Antennomeres 3–8 thickened, antennomeres 3–11 with subequal width (Figs 3A, 4A) 17

17 Eyes small, weakly convex (Y = 1.37) (Fig. 4C). Lateral sides of pronotal disc not flattened or very weakly narrowly flattened (Fig. 4C) *N. kalashiani*

– Eyes large, strongly convex (Y = 1.52) (Fig. 3E). Lateral sides of pronotal disc flattened, translucent (Fig. 3E) *N. faldermanni*

KEY TO *NALASSUS* FROM THE GREATER CAUCASUS ON FEMALES

(external sexual dimorphism is the lack
of the hair brush on the abdominal ventrite 1)

1 Ventral side of epicranium without temple groove (Fig. 2C) *N. dissonus*

– Ventral side of epicranium with temple groove, coming from ventral margin of eye (Figs 1B, 3B, 5B, 6B, 8B, etc.) 2

2 Pronotum with deep groove along lateral margin on each side (Fig. 10C). Epipleura in base very wide, much wider than width of mesofemora, and wider that metepisterna on the level of posterior portion of metaventrite (Fig. 10B) *N. diteras*

– Pronotum without deep groove along lateral margin on each side (Figs 1C, 3C, 4B, 5C, 6C, 7C, 8C, 9C, 11C, 12C, 13C, 14C, 15B, 16B, 17E, 18C, 19C). Epipleura in base not strongly widened, narrower than width of mesofemora; epipleura and metepisterna on the level of posterior portion of metaventrite with subequal width (Figs 5B, 6B, 8B, 9B, 11B, 12B, 13B, 14B) 3

3 Antero-lateral corners of pronotum acute, strongly projected, pointed (Figs 7C, 8C, 9C, 12C, 15B, 16B) or rounded (Fig. 14C) at apex 4

– Antero-lateral corners of pronotum obtuse, not projected, with widely or narrowly rounded apex (Figs 1C, 3C, 4B) 14

4 Lateral elytral carina (dorsal side of epipleura) near apex wider than 8 and 9 interstriae together; interstriae 3–9 with small tubercles with coeloconic sensilla (Fig. 17G) *N. abkhasicus*

– Lateral elytral carina (dorsal side of epipleura) near apex narrower, than 8 and 9 interstriae together. Interstriae without tubercles 5

5 Apex of anterolateral corners pointed or very narrowly rounded (Figs 7C, 8C, 9C, 12C, 15B, 16B) 6

– Apex of anterolateral corners widely rounded (Figs 5C, 6C, 11C, 13C, 14C) 10

6 Eyes large, convex (Y = 1.57–1.62) (Figs 8C, 9C) 7

– Eyes small, weakly convex (Y = 1.34–1.45) (Figs 7D , 15B,C, 16B) 8

7 Lateral sides of pronotal disc not flattened and not elevated (Figs 8C, 9C) *N. colchicus madlenae*

– Lateral sides of pronotal disc widely flattened and elevated (Fig. 12C) *N. ludmilae*

8 Head pubescent with recumbent hairs (Fig. 15C). Body red-brown (Fig. 15B) *N. svaneticus*

– Head bare (Figs 7D, 16B). Body black (Figs 7C, 16A) 9

9 Lateral margins of pronotum widely emarginated in anterior third (Fig. 16A) *N. zakatalensis*

– Lateral margins of pronotum weakly rounded, almost straight in anterior third (Fig. 7C) *N. avaricus*

10 Eyes large, convex (Y = 1.7) (Figs 14C,E). Body with metallic bronze-greenish shine (Fig. 14C) *N. pharnaces*

– Eyes small or moderate in size, weakly convex. (Y = 1.42–1.5) (Figs 5C,E, 6C,E, 11C,E, 13C). Body brown or black, without metallic shine (Figs 5C, 6C, 11C, 13C) 11

11 Elytral strial punctures not connected by furrow (Fig. 6C). Abdominal ventrite 1 with several sparse long setae at middle. Body brown *N. alanicus*

– Elytral strial punctures connected by entire deep furrow (Figs 5C, 11C, 13C). Abdominal ventrite 1 without long setae at middle. Body black or brown 12

12 Lateral sides of pronotal disc widely flattened along the entire length (Figs 5C, 11C). Eyes smaller and lesser convex (Y = 1.34–1.42) 13

– Lateral sides of pronotal disc weakly narrowly rounded only near corners (Fig. 13C). Eyes larger and more convex (Y = 1.5) *N. negrobovi* **sp. n.**

13 Body brown. Elytra more elongate, ElEw = 1.58–1.6. Elytral interstriae smooth (Fig. 5C) *N. adriani*

– Body black. Elytra lesser elongate, ElEw = 1.5. Elytral interstriae with fine clear transverse wrinkles (Fig. 11C) *N. dombaicus*

14 Pronotum with simple round punctation on entire disc 15

– Pronotum with longitudinally elongate punctation on sides of middle 17

15 Body shine, integument smooth *N. brevicollis*

– Body dull due to hexagonal micro sculpture of integument 16

16 Eyes small, weakly convex (Y = 1.37). Lateral sides of pronotal disc not flattened (Fig. 4B) *N. kalashiani*

– Eyes large, strongly convex (Y = 1.52). Lateral sides of pronotal disc flattened, translucent (Fig. 3C) *N. faldermanni*

17 Pronotum not cordiform, widest at middle, lateral margins usually not emarginate near base (steppe populations) (Fig. 19C) or slightly emarginate (most of specimens from the Caucasian forest populations) *N. sareptanus*

– Pronotum cordiform (Fig. 18C), widest before middle or rarely at middle, lateral margins widely emarginated in base. Only abdominal ventrite 1 with hair brush *N. lineatus*

BIONOMICS AND TROPHIC RELATIONS OF *NALASSUS* IN THE GREATER CAUCASUS

Landscape and habitat distribution – All species of *Nalassus* from the Greater Caucasus can be divided into three ecological groups: forest, alpine and steppe species. Some widespread species occur in several landscapes.

The forest *Nalassus* occur mainly in the west part of the North Caucasus and the southern slopes of the Greater Caucasus. The majority of them inhabits deciduous forests and occurs at night on trunks of trees. Only two species from the southern part of the Greater Caucasus are associated with dark coniferous forests: *Nalassus ludmilae* occurs on fir and *N. colchicus madlenae* on spruce. *Nalassus pharnaces* inhabits only beech trees throughout the entire range. Therefore, forest species of the subgenus *Caucasonotus* are associated with certain forests and even tree species. Two of these species, *N. ludmilae* and *N. pharnaces* are sympatric and occur together in mixed forests, but the first species is only on *Abies nordmanniana* (Steven) Spach, and the second one is only on *Fagus orientalis* Lipsky. The latter species is also sympatric with *N.* (*Horistelops*) *sareptanus* in several localities of the North-Western Caucasus (for example, on Shchetka Mt., Krasnodar Region of Russia), but in this case, *N. pharnaces* also inhabits only *Fagus orientalis*, while *N. sareptanus* never occurs on beech. Taxa from the subgenera *Nalassus* and *Horistelops* are widespread in multi-species deciduous forests (within the belt of oak forests), as well as in orchards and feed of corticolous lichens. *Nalassus abkhasicus* inhabits sympatrically with *N. brevicollis* in Abkhazia, but it has an unusual habitat and occurs on rocks inside deciduous forests. The same highly specialized ecological niche is known for *N.* (*Horistelops*) *clavicornis* Allard, 1876 in the Hatila River valley in north-eastern Anatolia (Keskin *et al.* 2017). *Nalassus brevicollis* sympatrically inhabits also with *N. sareptanus*, but we have not yet been able to understand how they are divided by ecological niches. The taxocene of lichenophagous beetles *N. brevicollis*, *N. alanicus* and *N. dissonus* is registered in Sadon-Unal sub-arid mountain basin, but these taxa occur in different habitats: pine forest, meadows and phryganoid steppes, respectively.

The only eight representatives of *Caucasonotus* are known among alpine and subalpine species of *Nalassus* in the Greater Caucasus. All these species

Table 2. Ecological distribution and trophic relations of *Nalassus* from the Greater Caucasus.

Species	Landscape	Habitat	Host lichens
		Subgenus *Nalassus*	
N. brevicollis	Foothill and low mountain forest	Deciduous trees, a wide range (except for *Fagus*), on trunks, *Pinus silvestris*	Corticolous foliose lichens: *Phaeophyscia orbicularis* (Neck.) Moberg, *Physcia adscendens* (Fr.) H. Olivier, *Physcia stellaris* (L.) Nyl., *Physcia tenella* (Scop.) DC., *Physconia distorta* (With.) J. R. Launon, (Physciaceae) *Vulpicida juniperinus* (L.) J.-E. Mattsson & M. J. Lai (Parmeliaceae), scales of male pine cones on *Pinus*
N. dissonus	Foothill and mountain steppes (phryganoid vegetation)	Under prickly *Astragalus*, in soil	Terricolous foliose lichens
N. faldermanni	Sparse forests and woodlands in xerophytic landscapes, sands (Taman Peninsula)	On trunks of deciduous trees, a wide range sandy population among feather grassroots	Corticolous foliose lichens: *Physcia adscendens* (Fr.) H. Olivier (Physciaceae), *Xanthoria parietina* (L.) Th. Fr. (Teloschistaceae),
N. kalashiani	Phryganoid steppes on limestones	Under prickly *Astragalus* sp. and the roots of *Stipa* sp., in soil	Terricolous foliose lichens (Cladoniaceae): *Cladonia pyxidata* (L.) Hoffm.

		Subgenus *Caucasonotus*	
N. adriani	Alpine meadows	On stones	? Saxicolous foliose lichens (Parmeliaceae)
N. alanicus	Alpine meadows, mid-mountain meadows	On stones	Saxicolous foliose lichens (Parmeliaceae): *Arctoparmelia separata* (Th. Fr.) Hale
N. avaricus	Alpine meadows	On stones	Saxicolous foliose lichens (Parmeliaceae)
N. colchicus madlenae	Mountain dark coniferous and mixed forests	On trunks of *Picea orientalis*, very rarely on *Fagus orientalis*	Corticolous foliose lichens (Physciaceae)
N. diteras	Subalpine meadows with *Betula* or *Pinus*, mountain forests	Subalpine zone: on stones. Forests: on trunks of *Fagus orientalis*	Saxicolous foliose lichens (Parmeliaceae): *Arctoparmelia separata* (Th. Fr.) Hale, Corticolous foliose lichens (Physciaceae)
N. dombaicus	Alpine meadows	On stones	Saxicolous foliose lichens (Parmeliaceae): *Arctoparmelia separata* (Th. Fr.) Hale, *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale,
N. ludmilae	Mountain dark coniferous and mixed forests	On trunks of *Abies nordmanniana*	Corticolous foliose lichens (Physciaceae)
N. negrobovi	Alpine meadows	On stones	? Saxicolous foliose parmelioid lichens
N. pharnaces	Mountain deciduous and mixed forests	On trunks of *Fagus orientalis*	Corticolous foliose lichens (Physciaceae): *Phaeophyscia hirsuta* (Mereschk.) Essl.
N. svaneticus	Subalpine meadows	On stones	Saxicolous foliose lichens (Parmeliaceae)
N. zakatalensis	Alpine meadows	On stones	Saxicolous foliose lichens (Parmeliaceae)
		Subgenus *Horistelops*	
N. abkhasicus	Mountain forests	On rocks	Saxicolous foliose lichens
N. lineatus	Foothill and low mountain forests	On trunks of deciduous trees, a wide range	Corticolous foliose lichens (Physciaceae)
N. sareptanus	Foothill steppes and low mountain forests	Steppes: on soil. Forests: mainly on *Quercus robur*	Corticolous foliose lichens (Physciaceae): *Physcia adscendens* (Fr.) H. Olivier

are widespread from 2000 to 3200 m and occur in stony habitats, where beetles feed on saxicolous lichens on stones and rocks at night. All these species are allopatric. One *N. diteras* is widespread in the subalpine zone of all Greater Caucasus and is registered as probably a sympatric species with *N. alanicus* in Kariukokh Mts. in North Ossetia-Alania (Russia). At least these two species were collected nearby, but in different microhabitats: *N. diteras* on stones with subalpine bushy *Betula* sp., while *N. alanicus* was collected a little above, in the alpine meadow. Forest populations of *N. diteras* are known in the central (North Ossetia, Kabardino-Balkaria) and eastern (Dagestan: Tabasaran District) parts of the North Caucasus. All these populations inhabit *Fagus* forests and beetles feed on foliose corticolous lichens on trunks.

Two xerophytic steppe species, *N.* (s. str.) *dissonus* and *N.* (s. str.) *kalashiani* are distributed in arid mountain basins of the central and eastern parts of the North Caucasus: the first taxon in Sadon-Unal basin (North Ossetia), the second one in Itum-Kale (Chechnya) and Levashi basin (Dagestan). The historical formation of the endemic tenebrionid fauna in these basins has already been considered earlier (Abdurakhmanov & Nabozhenko 2009). Both species occur in phryganoid steppes and inhabit soil under *Astragalus* spp. and *Stipa* spp. At night these species feed on epigean lichens. *Nalassus sareptanus* is also spread in steppes but only in foothills and plains. We know two types of populations of *N. sareptanus*, forest populations occur only in the low mountains of the Western Caucasus, steppe populations are widespread from East Europe to North-Western Kazakhstan. However, beetles of steppe populations feeding on epigean lichens usually change their habitats and feed on corticolous lichens in forest belts when ploughing the steppes (Nabozhenko *et al.* 2016*b*).

Trophic relations – Trophic relations of darkling beetles of the tribe Helopini are poorly studied. At best, we have information about the life form of the lichen and its high taxonomic position (Nabozhenko *et al.* 2017). Recently, data on trophic associations of nine species from Turkey and two species from Cyprus were published (Nabozhenko *et al.* 2021*a*, *b*). In Table 2, we demonstrate only several collected and determined host lichens for eight species of beetles (first time for five species). In other cases, we present only a life form and a family. Usually, beetles of this tribe choose widespread common species of host lichens because such competition as in herbivorous insects is absent. Only some sympatric species probably have some trophic specialization, at least, this is observed in habitat and tree associations for *N. pharnaces* and *N. ludmilae*. Interesting patterns are observed at the level of ecological groups. Forest species feed mainly on corticolous foliose lichens from the family Physciaceae (Fig. 20A), while alpine *Nalassus* use saxicolous foliose lichens from the family Parmeliaceae (Figs 20B,C). Unfortunately, we have little data on mountain-steppe species. Therefore we cannot discuss the patterns, but it is

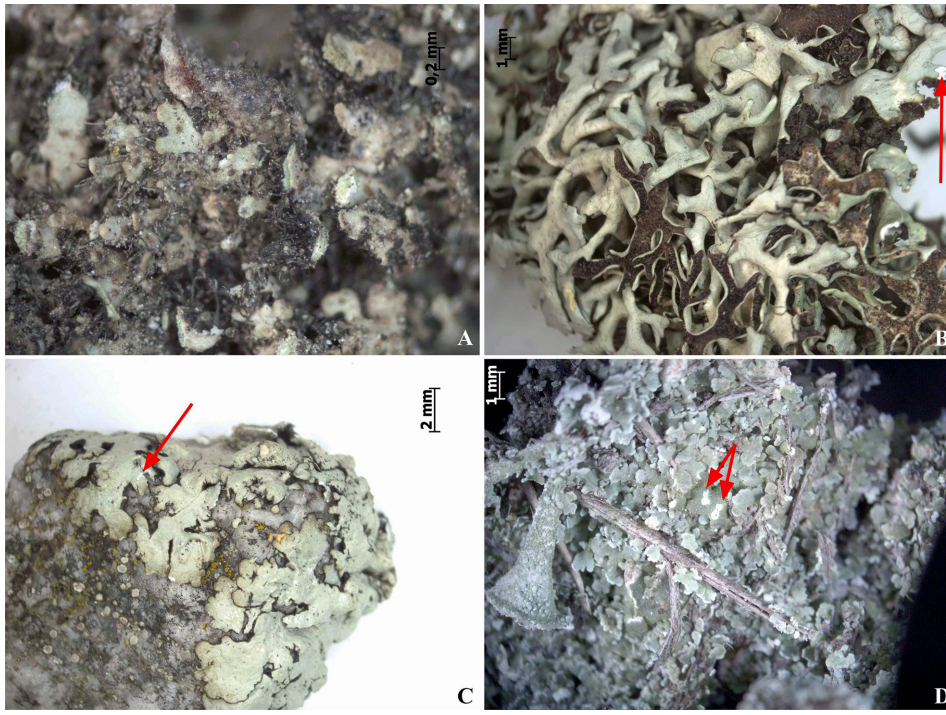

Fig. 20. Host lichens of *Nalassus*. A = *Phaeophyscia hirsuta*, host lichen of *N. pharnaces*; B = *Arctoparmelia separata*, host lichen of *N. diteras*, *N. dombaicus* and *N. alanicus*; C = *Xanthoparmelia conspersa*, additional host lichen of *N. dombaicus*; D = *Cladonia pyxidata*, host lichen of *N. kalashiani*. Arrows show areas of the thallus damaged by beetles

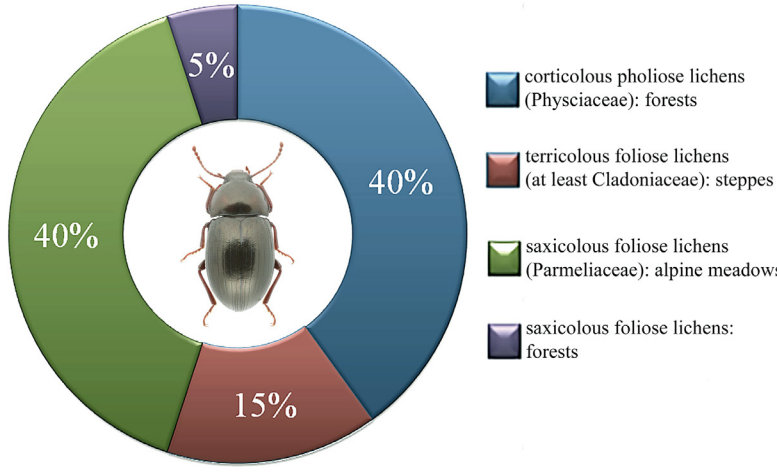

Fig. 21. Proportions of trophic and ecological groups of *Nalassus* in the Greater Caucasus

obvious that the steppe *Nalassus* feed on terricolous lichens and at least *N. kalashiani* on *Cladonia* species (Fig. 20D).

In total, the majority of *Nalassus* species are distributed in forests and alpine zone and feed on lichens from the families Physciaceae and Parmeliaceae, respectively; 15% of species are adapted to the xerophytic steppe landscapes with phryganoid vegetation and feed on terricolous lichens, at least Cladoniaceae; only one species feed on saxicolous lichens but inhabit deciduous forests (Fig. 21).

*

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