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## On new carabids of the genus Carabus L. (Coleoptera, Carabidae) from the Caucasus. 2nd contribution

by A. S. Zamotajlov

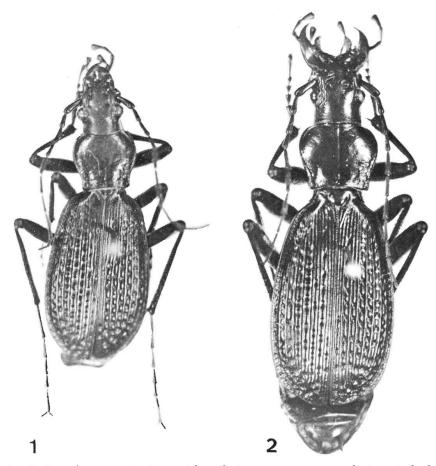
Abstract: One species and four subspecies of the genus Carabus L. from the Caucasus are described as new: C. (Tribax) constantinowi barakaicus n.ssp. (NW Caucasus), C. (Archiplectes) apollo lhychtensis n. ssp. (Abkhazia), C. (Archipletes) shachgireii n. sp. (NW Caucasus), C. (Archiplectes satyrus pseudopshuensis n. ssp. (Abkhazia), and C. (Archiplectes) juenthneri acheicus n. ssp. (Abkhazia). C. (Archiplectes) kaljuzhnyji Zamot. is considered to be a good species; the taxonomic status of C. (Archiplectes) ganglbaueri Reitt. is reduced to a subspecies. The hybrids between C. (Archiplectes) polychrous Rost and C. (Archiplectes) satyrus Kurn. and between C. (Archiplectes) kaljuzhnyji Zamot. and C. (Archiplectes) prometheus Reitt. are also described. Distributional notes on some other forms are given.

Key words: Coleoptera Carabidae - Caucasus - *Carabus* - new species and subspecies - taxonomy.

The present paper continues the author's studies on Caucasian *Carabus* L. (ZAMOTAJLOV, 1988, 1989). I wish to acknowledge the kind assistance of Dr. A. I. Miroshnikow and Dipl.—Agr. S. A. Kulik, who participated in the collecting trips to the Caucasus. I am also very indebted to Prof. I. K. Lopatin for forwarding to me the type specimen of *C. juenthneri acheicus* n. ssp., and to Dr. I. A. Belousow, Dr. A. G. Koval, Dr. A. S. Konstantinov, Dipl.-Ing. A. V. Shamaev, and Dipl.-Ing. V. V. Kosow for some interesting distributional information. The materials treated herein have been returned to or shared with the collections of the Zoological Institute of the USSR Academy of Sciences, Leningrad (ZIL), Natural History Museum, Basel (NHMB), and the author (AZ).

## **1. Carabus (Tribax) constantinowi barakaicus** n. ssp. Figs 1 – 5. Habitus (Figs 1, 2): Length 28.0 – 36.4 mm. Black, dorsum with a lacquer lustre.

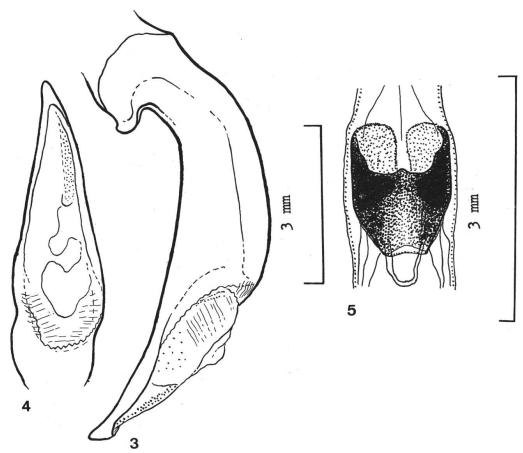
Body slender. Pronotum cordiform, 1.08 – 1.20 times as wide as long, its hind angles faintly extended laterad. Elytra oblongoval, 1.56 – 1.75 times as long as wide, interspaces 2 and 4, unlike others, rather sparsely interrupted by foveae, interspace 2 in the basal half not (or almost not) interrupted, bears 3 – 11 foveae, interspace 4 bears 8 – 11 foveae, other primary and secondary interspaces of the typical shape, with numerous foveae. Aedeagus (Figs 3, 4) and copulatory pieces (Fig. 5) resemble those of the nominative subspecies.



Figs 1 – 2: *Carabus constantinowi barakaicus* n.ssp., general view, 1, holotype. 2, paratype from environs of Sakharai.

Holotype:  $\mathcal{O}$  (AZ), NW Caucasus, Valley of river Malaya Laba, environs of Umpyr, 1200 m, 12. VII. 1985, A. Zamotajlov, Paratypes: 1  $\mathcal{O}$  (NHMB), same locality, 19. IX. 1961, Ivashkina, 1  $\mathcal{O}$  (AZ), NW Caucasus, Alous Mt. Range, vicinities of Lake Nasti, 2600 m, 14. VII. 1985, A. Zamotajlov, 1  $\mathcal{O}$  (NHMB); 1  $\mathcal{O}$  (AZ), NW Caucasus, environs of Sakhrai, 600 m, 5. V.  $\mathcal{O}$  21. VI. 1990, A. Zamotajlov & A. Miroshnikov.

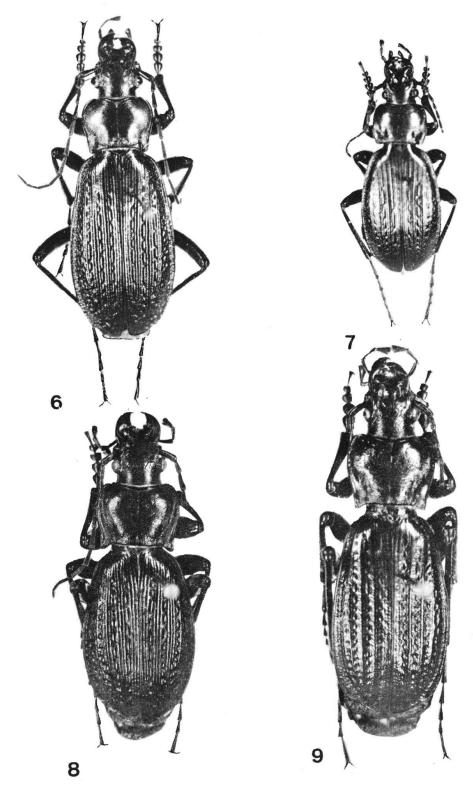
The new subspecies is somewhat more slender than the nominative one, copulatory pieces in the middle chitinized weaker; from all known forms of the *constantinowi*-group (after GOTTWALD, 1980) differs in the peculiarities of the elytral sculpture. This subspecies occupies the northwestern periphery of the range of *C. constantinowi* Starck and is apparently distributed in the North Caucasus between valleys of Malaya Laba and Belaya. Individuals, collected eastwards from the valley of Malaya Laba (in the valleys of Vengerka and Bolshaya Laba, in the environs of Arkhyz), possess normal elytral sculpture. In the district of Arkhyz *C. constantinowi* Starck occurs sympatric with *C. biebersteini* Mén.,



Figs 3 – 5: *Carabus cosntantinowi barakaicus* n.ssp., holotype. 3, aedeagus, left lateral view. 4, aedeagus, apex in dorsal view. 5, copulatory pieces.

the river Bolshoy Zelenchuk seems to be the eastern frontier of the range of *C. constantinowi* Starck in the North Caucasus. The nominative subspecies is distributed in the district of Sochi and West Abkhazia, it is also known from some localities of the Northwestern Caucasus (valley of river Tsytsa, Pass Fisht-Oshtenovskiy, Mt. Abago, Mt. Fisht). Specific status of another form of the *constantinowi*-group, *C. retezari* Gottw., seems to be rather obscure. I have collected specimens possessing the normal shape of copulatory pieces of *C. constantinowi* Starck at Kutekheku Mt. Range, just in the centre of the ascertained range of *C. retezari* Gottw. On the other hand, copulatory pieces of some specimens of *C. constantinowi otcharensis* Kurn. from the valley of Chkhalta are in complete accordance with the description of *C. retezari* Gottw., thus enabling us to treat this feature as an extreme case in the variation series.

Type specimens were collected in the different types of forest, Alpine and Subnival zones.



Figs 6 – 9: Carabus, general view, 6, C. apollo lhychtensis n. ssp., paratype. 7, C.shachgireii n.ssp., holotype. 8, C. satyrus pseudopshuensis n.ssp., holotype. 9, C. juenthneri acheicus n.ssp., holotype.

#### 2. Carabus (Archiplectes) apollo lhychtensis n. ssp.

Figs. 6, 12, 13, 17.

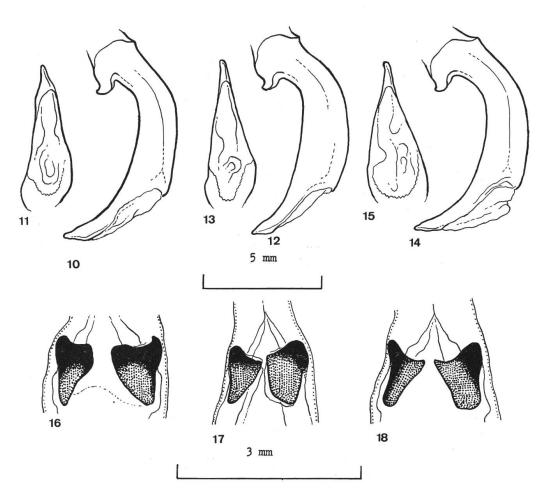
Carabus apollo apollo ZOLOTAREV, GOTTWALD, 1985, Acta entomol. bohemoslov. 82: 298 (partim).

Habitus (Fig. 6): Length 25.9 – 28.5 mm. Black, elytra, pronotum, and head greenish bronze.

Body slender, narrow. Pronotum slightly cordiform, 1.27 – 1.36 times as wide as long. Elytra elongate, 1.66 – 1.82 times as long as wide, the secondary interspaces elevated prominently stronger than the tertiary ones, sculpture rather coarse. Apical lamella of aedeagus (Figs 12, 13) narrow, regularly tapering towards apex; copulatory pieces (Fig. 17) contain two asymmetric sclerites, left one smaller, pointed at apex, right one at apex obtuse.

Holotype: & (AZ), Caucasus, Abkhazia, vicinities of Mt. Malyi Skhapach, 1700 m, 21.VI.1984, A. Zamotajlow, Paratype: 1 & (NHMB), same locality, together with holotype.

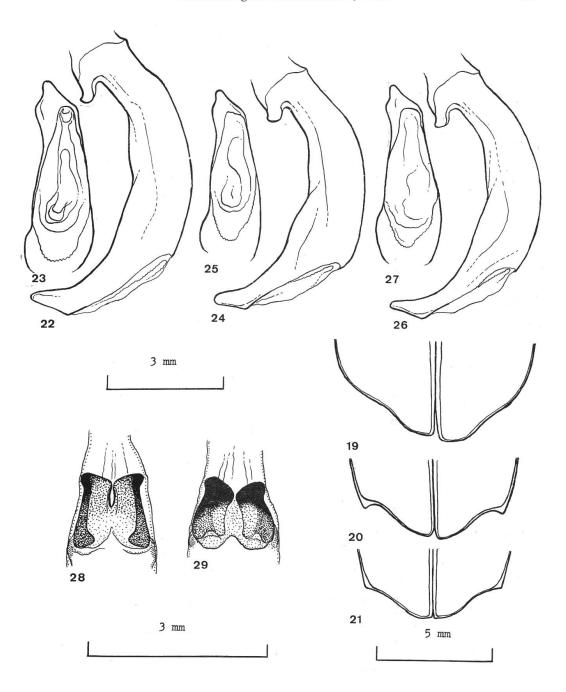
This subspecies resembles in body's shape C. apollo phoebus Kurn., although it is smaller, elytra more convex. From the nominative subspecies it differs in the smaller size, somewthat more slender body and more narrow pronotum, in the elytral sculpture, i. e. the secondary interspaces are elevated evidently stronger than the tertiary ones, and in the structure of male genitalia. Apical lamella of aedeagus more narrow (Figs 10 – 13), apex of the right sclerite of copulatory pieces obtuse (Figs 16, 17). According to both the habitual and genital (Figs 12 –15, 17, 18) characters, the new suspecies is the most closely related to C. apollo phoebus Kurn. The present form could evidently not be treated as an alticolate ecological race, because C. apollo apollo Zolot. occurs in different mountainous belts up to 2400 m. (KURNAKOV, 1962), though its size is rather constant. I have collected specimens measuring typically for the forest-dwelling individuals, at the source of river Shoudidi (Alpine zone) at about 2200 m. Apparently, the ranges of C. apollo lhychtensis n. ssp. and C. apollo phoebus Kurn. are not overlapping, the former one occupies the middle highlands of the southern slopes of the Bzybian Mt. Range between valleys of Kodori and Gumista. Westwards it is substituted by C. apollo tenebricosus Kurn. (which occurs in the environs of Novyi Aphon and Mtsara and in the valley of river Aapsta); valleys of the tributaries of Kodori, rivers Chkhalta and Kopshara, are populated by the nominative subspecies, Kopshara being pointed out



Figs 10 – 18: *Carabus*, male genitalia. 10, *C. apollo apollo* Zolot. from valley of Chkhalta, aedeagus in left lateral view. 11, idem, apex in dorsal view. 16, idem, copulatory pieces. 12, C. apollo lhychtensis n.ssp., paratype, aedeagus in left lateral view. 13, idem, apex in dorsal view. 17, idem, copulatory pieces. 14, *C. apollo phoebus* Kurn. from environs of Laty, aedeagus in left lateral view, 15, idem, apex in dorsal view. 18, idem, copulatory pieces.

by ZOLOTAREV (1913) and KURNAKOV (1962) as type locality for it. Besides, materials originating from the environs of Laty and considered by GOTTWALD (1985) as *C. apollo apollo* Zolot. belong actually to *C. apollo phoebus* Kurn.; this village was pointed out by KURNAKOV (1962) as type locality of this subspecies.

Type specimens were collected in the beech forest.



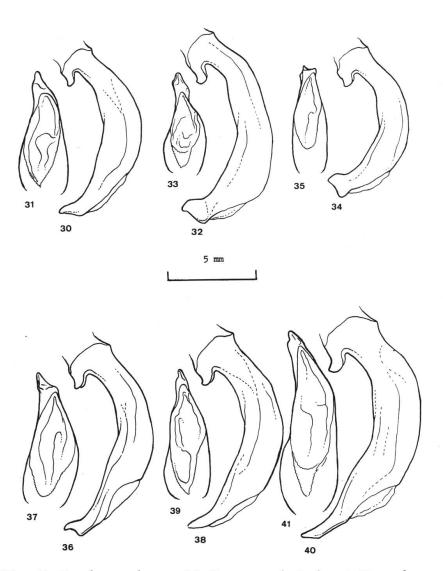
Figs 19 – 29: 19 – 21. Elytral apex of  $\[ Q \]$  of: 19, *Carabus kratkyi kratkyi* Ganglb. from Mt. Range Malyi Bambaki. 20, *C. shachgireii* n.sp., paratype. 21, *C. starcki* Heyd. from Mt. Pseashkho. 22 – 29. Male genitalia: 22, *Carabus kratkyi kratkyi* Ganglb. from Mt. Range Malyi Bambaki, aedeagus in left lateral view. 23, idem, apex in dorsal view. 28, idem, copulatory pieces. 24, *C. shachgireii* n. sp., holotype, aedeagus in left lateral view. 25, idem, apex in dorsal view. 29, idem, copulatory pieces. 26, *C. felicitanus* Reitt. from vicinities of Mt. Dzhuga, aedeagus in left lateral view. 27, idem, apex in dorsal view.

**3. Carabus (Archiplectes) shachgireii n. sp.** Figs 7, 20, 24, 25, 29. *Carabus kratkyi* GANGLBAUER, ZAMOTAJLOV, 1989, Ent. Bas. 13: 19 (partim). Habitus (Fig. 7): Length 19.9 – 21.1 mm. Black, elytra, pronotum, and head bronze to blackish bronze, dull, lateral margins of pronotum and elytra sometimes somewhat greenish. Habitually resembles *C. kratkyi* Ganglb. and *C. starcki* Heyd.

Head normal, frontal furrows short and rather shallow, eyes convex, prominent, anterior supraorbital pores located near anterior margin of eyes, posterior ones somewhat at the mid-eye level; upper surface slightly rugose; antennae rather long, reaching basal third of elytra, mentum tooth short, pointed. Pronotum rather narrow, subquadrate, slightly or not cordiform, widest a little before middle, 1.32 – 1.40 times as wide as long; lateral sides moderately arcuate, sometimes sinuated behind, hind angles rounded, weakly protrudent; reflexed lateral borders in apical half narrow, broadened backwards, basal foveae rather deep, median line prominent but weak; disk of pronotum rather smooth, slightly rugose, lateral sides and base with punctures and wrinkles; sides with 3 – 4 lateral setae. Elytra oblong-oval, 1.59 – 1.66 times as long as wide, weakly convex, with slightly prominent shoulders; sculpture triploid heterodynamous, surface in males with 13 prominent ridges, in females with 14; the primary interspaces interrupted by foveae (interspace 4 with 4 - 8, interspace 8 with 6 - 10, and interspace 12 with 7 – 10 foveae), the secondary interspaces protrudent not less than the primary ones, the tertiary interspaces very weakly elevated, almost flat, lateral sides of elytra coarsely punctate, with numerous granules and tubercles; elytral apex sharply emarginate in females (Fig. 20) and angulate in males, in both sexes each elytron at apex rounded, neither distinctly angulate nor confluent with each other. Ventral surface almost smooth, lateral sides gently rugose. Aedeagus (Figs 24, 25) of the same type as in C. felicitanus Reitt. and C. kratkyi kratkyi Ganglb., apical lamella rather narrow, nose-shaped in dorsal view, copulatory pieces (Fig. 29) consist of two massive and short, strongly chitinized sclerites.

Holotype:  $\Im$  (AZ), NW Caucasus, Alous Mt. Range, vicinities of Lake Nasti, 2600 m, 14.VII.1985, A. Zamotajlov, Paratypes: 1  $\Im$  (NHMB), same locality, together with holotype. 1  $\Im$  (AZ), NW Caucasus, Alous Mt. Range, 2100 m, 13.VII.1985, A. Zamotajlov.

The new species resembles in its habitus *C. kratkyi kratkyi* Ganglb., although differs in rather more narrow, not or hardly cordiform pronotum with less protrudent hind angles, less elongate elytra with more



Figs 30 – 41: Carabus, aedeagus. 30, C. satyrus duripshensis Kurn. from environs of Khuap, left lateral view. 31, idem, apex in dorsal view. 32, C. satyrus pseudopshuensis n.ssp., holotype, lef lateral view. 33, idem, apex in dorsal view. 34, C. juenthneri juenthneri Reitt. from valley of Bolshaya Laba, left lateral view. 35, idem, apex in dorsal view. 36, C. juenthneri acheicus n.ssp., holotype, left lateral view. 37, idem, apex in dorsal view. 38, hybrid between C. polychrous Rost & C. satyrus Kurn., left lateral view. 39, idem, apex in dorsal view. 40, C. polychrous Rost from environs of Khuap, left lateral view. 41, idem, apex in dorsal view.

narrow ridges, not so numerous foveave in the primary interspaces, and less elevated tertiary ones, in the sharply emarginate elytral apex in females (resembling apex of C. starcki Heyd., s. Figs 19-21). From C. starcki Heyd. females are distinguishable by more narrow, rounded, not so cordiform pronotum, weaker elevated lateral margins of elytra and more projected backwards apex of elytra with the rounded apex of each elytron (Figs 20, 21). In the structure of aedeagus the new species

resembles *C. felicitanus* Reitt. much more than *C. kratkyi kratkyi* Ganglb. (Figs 22 – 27). In the shape of copulatory pieces differs well from both *C. kratkyi* Ganglb. (Fig. 28) and *C. felicitanus* Reitt.

*C. shachgireii* n. sp. seems to be related to *C. felicitanus* Reitt., *C. kratkyi* Ganglb., and *C. edithae* Reitt., their ranges being conterminous with its range (their distribution s. Map 1). On the other hand, the new species occurs just near the confines of the range of *C. starcki* Heyd. The nearest findings of the former are: vicinities of Pass Chelipsi, 1600 m (coll. A. Zamotajlov); valley of river Urushten 1.5 km lower Camp Kholodnyi, 1700 m (coll. A. Zamotajlov); Mt. Pseashkho, 2500 m (coll. Ovcharenko).

Type specimens were collected in the Alpine and Subnival zones.

#### 4. Carabus (Archiplectes) satyrus pseudopshuensis n. ssp.

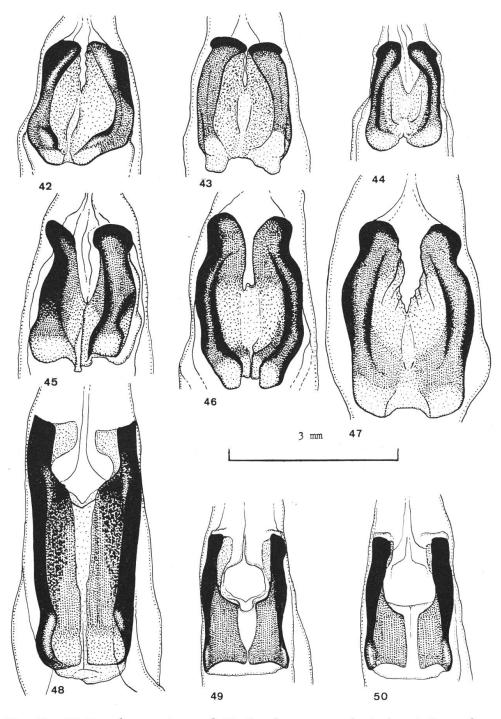
Figs. 8, 32, 33, 43.

Habitus (Fig. 8). Length 29.9 mm. Black, elytra, pronotum, and head violet. Habitually resembles *C. juenthneri* Reitt.

Body rather robust. Pronotum transverse, moderately cordiform, 1.24 times as long as wide. Elytra oblong-oval, 1.62 times as wide as long, elytral sculpture prominent, with clear margins of the ridges, the tertiary interspaces elevated only a little less than the secondary ones. Aedeagus (Figs 32, 33) very similar to *C. juenthneri* Reitt., apical lamella in lateral view broad, truncate; copulatory pieces (Fig. 43) of the same type as in other subspecies of *C. satyrus* Kurn.

Holotype: ♂ (AZ), Caucasus, Abkhazia, environs of Pskhu, VII. 1969, A. Kazadaev.

The new subpecies resembles most readily *C. satyrus duripshensis* Kurn., although it is smaller and more robust, pronotum more transverse, ridges of elytral sculpture with more distinct margins, less rugose, links of the primary interspaces somewhat broader, the tertiary interspaces more elevated and prominent, apical lamella of aedeagus of different shape (Figs 30 – 33). In the body's proportions and shape of aedeagus, it resembles also *C. juenthneri* Reitt. and *C. reitteri pshuensis* Gottw., however, copulatory pieces are normal for *C. satyrus* Kurn. (Figs 42, 43). The type locality of the new subspecies seems to be disjunct from the ranges of the other subspecies and presents the nothernmost outpost of the range of *C. satyrus* Kurn.



Figs 42 – 50: Copulatory pieces of: 42, *Carabus satyrus duripshensis* Kurn. from environs of Khuap. 43, *C. satyrus pseudopshuensis* n.ssp., holotype. 44, *C. juenthneri juenthneri* Reitt. from valley of Bolshaya Laba, 45, *C. juenthneri acheicus* n. ssp., holotype. 46, hybrid between *C. polychrous* Rost & *C. satyrus* Kurn. 47, *C. polychrous* Rost from environs of Khuap. 48, hybrid between *C. kaljuzhnyji* Zamot. & *C. prometheus* Reitt. 49, *C. kaljuzhnyji* Zamot. from Mt. Range Guam. 50, *C. obtusus ganglbaueri* Reitt. from valley of Kisha.

#### 5. Carabus (Archiplectes) juenthneri acheicus n. ssp.

Figs 9, 36, 37, 45.

Habitus (Fig. 9): Length 33.4 mm. Black, dorsum black with blue metallic lustre. Habitually resembles *C. reitteri* Retow.

Body slender. Pronotum cordiform, 1.20 times as wide as long. Elytra oblong-oval, 1.69 times as long as wide, links of the primary interspaces very short, at apex displayed as small tubercles, the tertiary interspaces flat, without distinct ridges, developed less than in *C. reitteri gagrinus* Starck. Aedeagus (Figs 36, 37) long, apical lamella rather narrow, its ventral process strongly protrudent; copulatory pieces (Fig. 45) large, of the same size as in *C. reitteri gagrinus* Starck, but more so of the typical *C. juenthneri* Reitt. shape.

Holotype: ♂ (AZ), Caucasus, Abkhazia, Gorge of river Bzyb, without precise locality, 17. VII., collector unknown.

Differs fron the other subspecies of *C. juenthneri* Reitt. in the elytral sculpture, i. e. links of the primary interspaces short, the tertiary interspaces flat. Aedeagus somewhat larger than in the nominative subspecies (Figs 34 – 37), its apical lamella with strongly produced ventral process, copulatory pieces larger (Figs 44, 45). Habitually resembles *C. reitteri* Retow., although it is distinguishable in the structure of copulatory pieces. This subspecies combines some characters of both *C. juenthneri* Reitt. and *C. reitteri* Retow. and seems to occupy a somewhat transitional position between these two species.

The type of *C. juenthneri acheicus* n. ssp. originates apparently from the district of Pskhu, some other subspecies of *C. juenthneri* Reitt. are also known from the environs of this village (s. Map 1). So we face a sympatric (or at least very near) occurence of the three closely related species in this region: *C. satyrus* Kurn. (ssp. *pseudopshuensis* Zamot), *C. reitteri* Retow. (ssp. *pshuensis* Gottw.), and *C. juenthneri* Reitt. Moreover, *C. juenthneri acheicus* n. ssp. and the above forms of the other species have somewhat transitional characters between each other, although their copulatory pieces retain normal structure. Judging from these facts, we ought to conclude Pskhu district to be an important centre of radiation of the *reitteri*-group (after GOTTWALD, 1985).

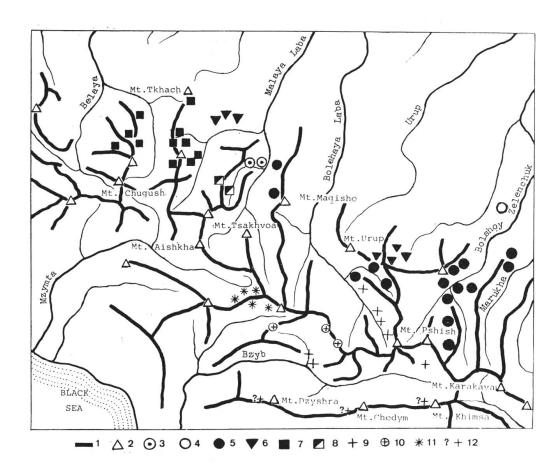


Plate 1: Distribution of *Carabus* species and subspecies in the NW Caucasus. 1, Main orographic lines. 2, Mt. summits. 3, *C. edithae edithae* Reitt. 4, *C. edithae exedithae* Gottw. 5, *C. edithae umpyrensis* Gottw. 6, *C. kratkyi kratkyi* Ganglb. 7, *C. felicitanus* Reitt. 8, *C. shachgireii* n.sp. 9, *C. juenthneri juenthneri* Reitt. 10, *C. juenthneri adsypschi* Gottw. 11, *C. juenthneri avadcharensis* Kurn. 12, forms of *C. juenthneri* Reitt. with unclear taxonomic status.

# **6. Carabus (Archiplectes) kaljuzhnyji** Zamotajlov, n. stat. Fig. 49. *Carabus starckianus kaljuzhnyji* Zamotajlov, 1988, Entomol, obozr. 67: 109. Examination of new materials revealed, that this form represents a well separated species of the *obtusus*-group, which is the most closely related to *C. obtusus* Ganglb. Habitually, it resembles smaller specimens of *C. prometheus* Reitt. and well differs from the other species of the group in somewhat more robust body and not or very weakly cordiform pronotum. Copulatory pieces somewhat broader, median membranous part is stronger contracted towards apex and not so narrow as

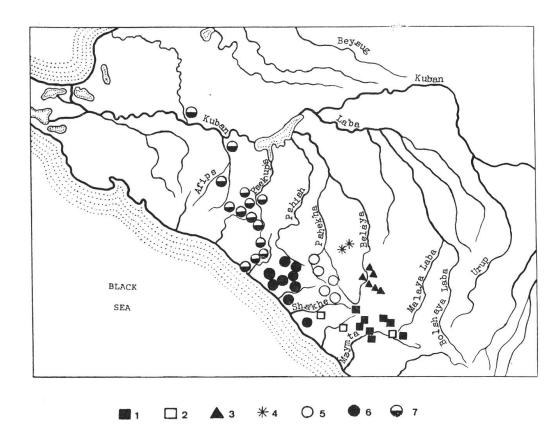


Plate 2: Distribution of *Carabus* species and subspecies in the NW Caucasus. 1, *C. obtusus obtusus* Ganglb. 2, *C. obtusus adelaidae* Starck. 3, *C. obtusus ganglbaueri* Reitt. 4, *C. kaljuzhnyji* Zamot. 5, *C. starckianus babukensis* Zamot. 6, *C. starckianus starckianus* Ganglb. 7, *C. starckianus theseus* Brian.

in *C. obtusus* Galnglb., both sclerites at apex approach each other veryu clsely (Figs 49, 50).

Material: Holotype, ♂ (ZIL), NW Caucasus, environs of Mezmay, 2.V.1975, A. Kaljuzhnyj, Paratype, 1 ♀ (ZIL), same locality, together with holotype. 8 ♂ & 18 ♀ (AZ); 1 ♂ & 1 ♀ (NHMB), NW Caucasus, environs of Mezmay, Mt. Range Guam, 900 m, 2.V. – 19.VI.1990, A. Zamotajlov & A. Miroshnikov.

This species is distributed rather far from both the ranges of related species *C. obtusus* Ganglb. and of *C. starckianus* Ganglb. (Map 2). At Mt. Range Guam *C. kaljuzhnyji* Zamot. occurs sometimes with *C. prometheus* Reitt., although usually they were found separately. Together

with the above species, was collected also a single specimen, male, of the intermediate size (length 33.4 mm) between two species. Both in habitual and genital (i. e. length of aedeagus, structure of copulatory pieces, s. Fig. 48) characters, this specimen occupies also a somewhat transitional position between *C. kaljuzhnyji* Zamot. and *C. prometheus* Reitt. (though judging from the structure of male genitalia it may be formally determined as *C. miroshnikovi* Zamot.). It seems to be apparently a hybrid between two mentioned species. However, precision of the real status of this form can be obtained only by means of experimental hybridization.

Examination of the extensive materials revealed also that the differences in the structure of copulatory pieces between *C. obtusus* Ganglb. and *C. ganglbaueri* Reitt., noted by GOTTWALD (1985), are false, and so the former has to be treated as a subspecies, in accordance with the opinion of BREUNING (1934), i. e. *C. obtusus ganglbaueri* Reitt., stat. rest.

### 7. On intraspecific hybridization between C. (Archiplectes) polychrous Rost and C. (Archiplectes) satyrus Kurn.

In 1990 in Abkhazia Dr. A. Miroshnikov and I collected a specimen of *Archiplectes* possessing somewhat intermediate characters between *C. polychrous* Rost and *C. satyrus* Kurn. It has been captured together with more than 300 ex. of *C. polychrous* Rost and about 30 ex. of *C. satyrus duripshensis* Kurn. As no more *Archiplectes* species occur in this region, the mentioned specimen could be interpreted as a hybrid between the above species. In body's size (length 35.5 mm) it resembles *C. satyrus duripshensis* Kurn., although somewhat more robust, head thick. From *C. polychrous* Rost this specimen differs in a smaller body and not so extended laterad hind angles of pronotum. Coloured violet. Male genitalia (Figs 38, 39, 46) also possess some transitional characters between both species (Figs 40, 41, 47).

Material: 1 ♂ (AZ), Caucasus, Abkhazia, Bzybian Mt. Range, environs of Khuap, 700 m, 14. V. – 8. VII. 1990, A. Zamotajlov & A. Miroshnikov.

Westwards from Khuap (in the environs of Otkhara) also occur rather small specimens of *C. polychrous* Rost, although they are closer to *C. rousianus* Gottw. The former species is distributed at the Black Sea Coast in the environs of Pitsunda and Mjussera (s. GOTTWALD, 1985) and at the western periphery of the Bzybian Mt. Range: W slopes of Mt. Adzapsh, 900 m (coll. A. Zamotajlov & A. Miroshnikov). An exact status of the above described transitional specimen can only be determined by means of experimental hybridization.

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