

Reorganization of the *Oreocarabus* Complex (Coleoptera, Carabidae) Based on Endophallic Morphology and Molecular Phylogeny

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Abstract Eighteen taxa of the genus *Carabus* (s. lat.) belonging to the subgenus *Oreocarabus* (*sensu* IMURA & MIZUSAWA, 1996) have been examined for endophallic morphology and mitochondrial ND5 gene sequences to analyse their phylogenetic relationships. This group, which has been integrated to a single subgenus *Oreocarabus*, is polyphyletic in a ND5 genealogical tree, and should be separated into at least 8 distinct lineages. One of them includes *Carabus* (“*Oreocarabus*”) *latro* that shares common ancestry with three species belonging to the subgenus *Rhigocarabus*. The other 7 lineages, *Orinocarabus*, *Cytilocarabus*, *Euporocarabus*, *Phricocarabus*, *Carpathophilus*, *Titanocarabus* and *Cavazzutiocarabus* are well isolated on the tree. As their branching points are ancient on the ND5 genealogical tree, it would be appropriate to regard each of them as an independent subgenus.

Introduction

Oreocarabus GÉHIN, 1876 (*sensu* IMURA & MIZUSAWA, 1996) is a fairly large subgenus in the genus *Carabus* (s. lat.), containing over 20 species distributed in the Eurasian Continent. It is characterized mainly by heptaploid elytral sculpture, and is otherwise rather poor in its own morphological peculiarity. All the *Oreocarabus* species bear such characters as bisetose penultimate segment of the labial palpus, hairy submentum, the presence of hairless ventral depressions (=thiridium) on the male antenna, well-developed hind angles of the pronotum and rather prominent elytral shoulders, etc., but none of them can be regarded as an autapomorphy for the subgenus. On the other hand, endophallic structure of the male genital organ reveals a considerable diversification, suggesting that *Oreocarabus* is not necessarily uniform, and may be classified into at least several species-groups (IMURA & MIZUSAWA, 1996).

In this paper, a revisional study has been made using totally 18 *Oreocarabus* taxa from Europe, Turkey, Caucasus and China, by examining detailed endophallic mor-

phology of the male genital organ and by constructing a genealogical tree based on the mitochondrial ND5 gene sequences.

Materials and Methods

The following specimens belonging to the subgenus *Oreocarabus* (*sensu* IMURA & MIZUSAWA, 1996) from Europe, Turkey, Caucasus and China were used. Localities and DDBJ/EMBL/GenBank accession numbers of the ND5 gene sequences are given in parentheses.

1. *Carabus putzeysianus putzeysianus* GÉHIN (NW. Italy, AB017451)
2. *C. p. raynaudianus* DEUVE et SIMARD (NW. Italy, AB017448)
3. *C. p. pedemontanus* GANGLBAUER (NW. Italy, AB017452)
4. *C. p. germanae* CASALE et CAVAZZUTI (NW. Italy, AB017453)
5. *C. p. omensis* BORN (NW. Italy, AB017454 & AB017456)
6. *C. fairmairei pelvicus* CAVAZZUTI (NW. Italy, AB017449 & AB017450)
7. *C. heteromorphus* DANIEL (NW. Italy, AB017455 & AB017457)
8. *C. concolor* DANIEL (C. Switzerland, AB017458)
9. *C. sylvestris* PANZER (E. Austria, AB017459)
10. *C. latreilleanus* CSIKI (NW. Italy, AB017478)
11. *C. linnei* PANZER (NE. Slovakia, AB017472; N. Slovakia, AB017473)
12. *C. hortensis* LINNÉ (W. Austria, AB017463; W. Slovakia, AB017464; NE. Slovakia, AB017465)
13. *C. cribratus* QUENSEL (NE. Turkey, AB017460)
14. *C. cribratus* QUENSEL (C. Caucasus, AB017461)
15. *C. porrectangulus* GÉHIN (NE. Turkey, AB017462)
16. *C. glabratus* PAYKULL (W. Austria, AB017466; N. & E. France, D86207; NE. Slovakia, AB017467)
17. *C. glabratus* PAYKULL (Mt. Casto, AB017468; Guardabosone, AB 017469; Andrate, AB017470; Canelli, AB017471; all from NW. Italy)
18. *C. latro minshanensis* DEUVE (Sichuan, China, AB017476)
19. *C. titanus* BREUNING (Sichuan, China, AB017474)
20. *C. sui* IMURA et ZHOU (Beijing, China, AB017475)

In addition to the above, the ND5 gene from one male example of *C. (Rhigo-carabus) pusio* SEMENOV from the Pass Gongga Ling of northern Sichuan, China (AB017477), was sequenced for comparison.

For each taxon except *C. cribratus* (C. Caucasus), endophallus of the male genitalia was fully everted, air-dried and figured. For the analytical methods of the ND5 gene sequences and construction of a genealogical tree by the neighbor-joining (NJ) method (SAITOU & NEI, 1987), see SU *et al.* (1996 a, b, '98), IMURA *et al.* (1997) and IMURA, KIM *et al.* (1998). To know the phylogenetic position of *Oreocarabus* species, the ND5 gene sequences of some other carabine species were used for constructing the tree.

Results and Discussion

Oreocarabus was first proposed by GÉHIN in 1876 (p. 12). He established this “vagabond” higher taxon for the following 20 species: *guadarramus*, *heydeni* (= *steuartii*), *errans* GORY, 1839 [nec FISCHER, 1823] (= *amplipennis* LAPOUGE, 1924), *deyrollei*, *ghillianii* (= *ghiliani*), *hortensis*, *linnei*, *carinthiacus*, *latreillei* DEJEAN, 1826 [nec FISCHER, 1822] (= *latreilleanus* CSIKI, 1927), *alpinus* (= *concolor*), *putzeysianus*, *lochnikowi* (= *loschnikovi*), *sylvestris*, *hoppei* (= *alpestris hoppii*), *fairmairei*, *lineolatus* (= *massagetus*), *boysi*, *marietti*, *storzowi* (= *loschnikovi*?) and *truncaticollis*. In view of the present criteria, they are nothing but an assemblage of various taxa by mere superficial resemblance, and some of them should be transferred to several other subgenera. GÉHIN did not designate the type species at that time.

In 1896, REITTER placed *Oreocarabus* as one of the 11 subgenera of the Carabi multistriati, and restricted it to several Iberian species such as *ghiliani*, *errans* (= *amplipennis*), *guadarramus* and *steuarti*.

LAPOUGE (1931) regarded *Oreocarabus* as a distinct genus belonging to the division Multistriés, and recognized in it four component subgenera, namely, *Oreocarabus* (s. str.), *Orinocarabus*, *Caucasocarabus* and *Neocarabus*. *Oreocarabus* (s. str.) in his sense comprises only a single species, *errans* (= *amplipennis*).

In his monograph, BREUNING (1932, '33) treated *Oreocarabus* as one of the subgenera in the division Multistriati, and divided it into the following 6 sections: *Oreocarabus* (s. str.), *Titanocarabus*, *Orinocarabus*, *Pachycarabus*, *Ulocarabus* and *Meganebrius*. The section *Oreocarabus* in his sense comprises the following 10 species: *amplipennis*, *pseudosteuarti*, *guadarramus*, *ghiliani*, *hortensis*, *wladimirskyi* (= *vladimirskyi*), *cribratus*, *gemellatus*, *taedatus* and *glabratus*. At the same time, he designated *Carabus amplipennis* as the type species of *Oreocarabus*.

According to DEUVE (1994), *Oreocarabus* is one of the 65 subgenera of the Lobifera, the largest division of the genus *Carabus* (s. lat.). He synonymized the following 8 higher taxa with the subgenus *Oreocarabus*: *Carpathophilus*, *Cytilocarabus*, *Euporocarabus*, *Hypsocarabus*, *Orinocarabus*, *Phricocarabus*, *Piocarabus* and *Titanocarabus*.

Recently, a new system was proposed by IMURA (1996), and was followed by IMURA and MIZUSAWA (1996). According to his classification, *Oreocarabus* is one of the 17 subgenera in the subdivision Latitarsi of the division Multistriati. It is composed of over 20 species distributed in the Eurasian Continent and may be classified into 5 species-groups.

Thus, there is no consensus of previous authors as to the taxonomy of *Oreocarabus* (s. lat.). Such a confusion seems to have been caused mainly by difficulty in determining autapomorphy for the species belonging to this higher taxon, except that they fundamentally have heptaploid elytral sculpture.

Figure 1 shows a genealogical tree constructed from the mitochondrial ND5 gene sequences including all the taxa analysed in this study together with some other carabine species. Eight well-defined lineages are recognized including “*Oreocarabus*” taxa,

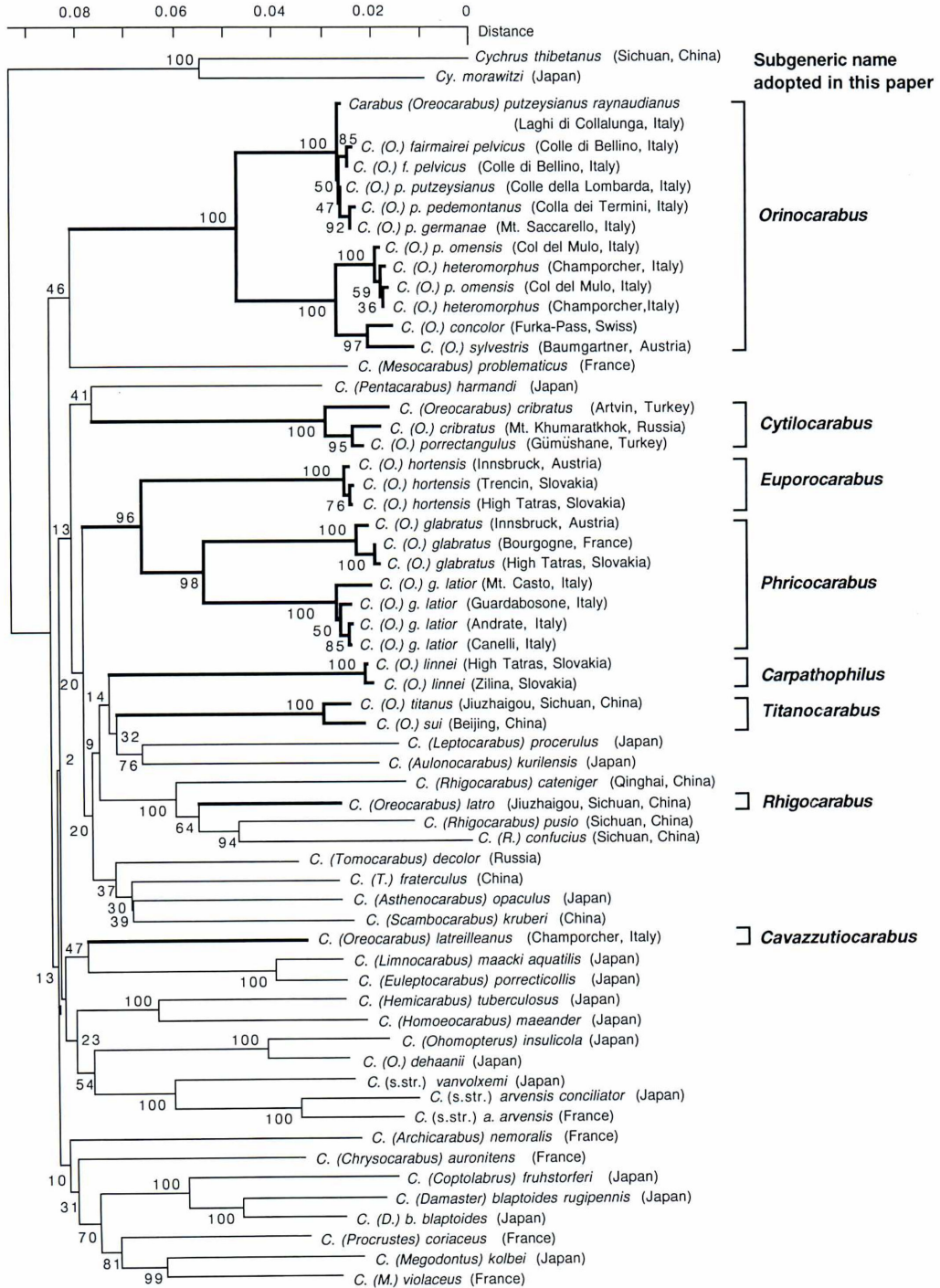
most of which emerged ca. 30 MYA (for dating, see KIM *et al.*, 1998), and were independent from all other carabine taxa, except that *Carabus* (“*Oreocarabus*”) *latro* was clustered with the *Rhigocarabus* species supported by a high bootstrap value. This would mean that the emergence of these lineages may be traced back to about the same time of the carabine radiation (SU, OKADA *et al.*, 1996; SU, KIM *et al.*, 1998).

The first cluster is composed of 5 species, *putzeysianus*, *fairmairei*, *heteromorphus*, *concolor* and *sylvestris*, and may be divided into two subclusters. The separation of the two subclusters is rather old and may be estimated to have taken place 12-16 MYA. Evolutionary distances between the taxa (species or subspecies) in each subcluster are small, especially in the first subcluster. The first subcluster contains 4 of 5 subspecies of *C. putzeysianus*, i.e., nominotypical *putzeysianus*, *pedemontanus*, *germanae* and *raynaudianus*, all having the “*putzeysianus*”-type male genitalia, together with *C. fairmairei pelvicus*, the male genitalia of which are of the “*fairmairei*”-type. The second one is composed of *C. putzeysianus omensis*+*C. heteromorphus* and *C. concolor*+*C. sylvestris*. *Omensis* is morphologically regarded beyond doubt as a subspecies of *C. putzeysianus*, as seen by the “*putzeysianus*”-type genitalic structure (see Fig. 15). From the ND5 gene sequences, however, it is most closely related to *C. heteromorphus* having the “*fairmairei*”-type genitalia. Since we have been unable to analyse the other races distributed in the intervening area between those of *p. omensis* and *heteromorphus*, i.e., another subspecies of *fairmairei* or *cenisius* (see Fig. 46), it is too premature to discuss the relation between phylogeny and morphological differentiation among these complicated alpine carabids.

As to the subgeneric name for this group, we adopt *Orinocarabus* KRAATZ (type species: *C. sylvestris*). Presumably the following species are included in this subgenus: *adamellicola*, *alpestris*, *bertolini*, *carinthiacus*, *castanopterus* and *cenisius*. Judging from the endophallic morphology, *Oreocarabus* (s. str.) (type species: *C. amplipennis* from the Iberian Peninsula, see Figs. 40 & 45) could be used, but the distributional areas of these two groups are completely separated from each other (Fig. 47). In our view, use of *Oreocarabus* (s. str.) should be restricted to several species distributed in the Iberian Peninsula (e.g., *ghiliani*, *guadarramus* and *pseudosteuarti*, etc.).

The second cluster is formed by *C. cribratus* and *C. porrectangulus*. *Carabus cribratus* from Caucasus and *C. porrectangulus* from northern Turkey are clustered together, and the evolutionary distance between them is very close. *Carabus cribratus* from northeastern Turkey is the outgroup of them. In other words, the two species are not divided from each other on the phylogenetic tree. As *cribratus* and *porrectangulus* are clearly distinguishable from one another mainly by the shape of aedeagal apex (see

Fig. 1. Genealogical tree of the mitochondrial ND5 gene of the *Oreocarabus* complex with some other carabine species. A NJ-tree was constructed by SINCA sequence analysis package using KIMURA's two-parameter evolutionary distance. The bootstrap confidence level (%) (based on 500 resamplings) is shown at each branching point. The ND5 gene sequences of two *Cychnus* species were used as an outgroup. The subgeneric names proposed in this paper for the *Oreocarabus* complex are indicated on the right column.



Figs. 29–31), morphological transformation should have taken place during evolution within relatively short time. Since they form a discrete cluster on the ND5 tree, the subgeneric name *Cytilocarabus* (REITTER, 1896) may be adopted for acceptance of this group. A unique Iranian species, *gemellatus* MÉNÉTRIÈS, belongs presumably to the same subgenus, though its range is omitted from the distribution map of *Cytilocarabus* shown in Fig. 47.

Carabus hortensis has been regarded as a typical member of *Oreocarabus* by most authors. However, it belongs to the unique (3rd) cluster in the ND5 tree, and we adopt *Euporocarabus* (REITTER, 1896) for it. This carabid seems to have an affinity with the next (4th) cluster composed solely of *C. glabratus*, though the branching point of these two clusters is considerably deep. These two groups are also similar with each other in morphology of the endophallus, especially of peculiarly shaped parapraeputial lobes (see Figs. 32–34).

The 4th cluster contains *C. glabratus*. Noteworthy is the relation between the population of northwestern Italy and those of the other regions (France, Austria and Slovakia). It is well-known that the geographical variation of *C. glabratus* is not remarkable despite its wide distributional range. Indeed, the Italian race is hardly distinguishable from those of France, Austria and Slovakia both in the external and genitalic structures, except that the former has a little wider pronotum (see Figs. 24–25, 33–34). In the ND5 tree, however, they are clearly divided into two clusters with a deep branching point, indicating that the morphological differentiation between the two races has been very slow in contrast to a long history after their separation. The similar situations may be recognized in certain groups of the Chinese *Apotomopterus* (SU *et al.*, 1998 b) or of the Japanese *Damaster* (s. str.) carabids (SU, TOMINAGA *et al.*, 1998), which also show very little morphological differences long after their diversification. Crossing experiments remain to be done to know whether these two *glabratus* races are regarded as sibling species or simply as subspecies retaining mating ability between them. We tentatively recognize the northwestern Italy population as a good subspecies under the name *latior*, which was described from Piemonte by BORN (1895) as a variety of *C. glabratus*. The two subspecies are apparently bordered by the European Alps (Fig. 48).

Carabus linnei has been placed in *Orinocarabus* by most authors, but it belongs to a discrete lineage far remote from that of *Orinocarabus*, and we adopt *Carpathophilus* (REITTER, 1896) for this species. This treatment is supported by characteristically shaped endophallus as shown in Fig. 35.

Carabus titanus and *C. sui*, the latter of which was described very recently from Beijing (IMURA & ZHOU, 1998), belong to a lineage independent from other “*Oreocarabus*” species. The tree suggests that the two species were separated rather recently. The applicable subgeneric name to this cluster would be *Titanocarabus*, which was established by BREUNING (1932) for *C. titanus*.

Carabus latro is endemic to northern Sichuan and has been one of the least known species of the Chinese Carabina until recent years. Its systematic position has been variable according to authors. Although SEMENOV (1898) established a monotypi-

cal higher taxon, *Hypsocarabus*, for this species, it was synonymized either with *Orinocarabus* (BREUNING, 1932, '33) or with *Oreocarabus* (DEUVE, 1994; IMURA & MIZUSAWA, 1996). From the ND5 genealogical tree, however, *C. latro* obviously belongs to the cluster containing such *Rhigocarabus* species as *cateniger*, *confucius* and *pusio*. In view of the external morphology, *C. latro* almost agrees in the fundamental structure with most species of *Rhigocarabus*. Also from the endophallic morphology, it seems to be consistent with the criteria established for all the other members of *Rhigocarabus*, though the membranous projections show considerable variation among the *Rhigocarabus* species. In Figs. 41–42 are shown the peculiarly shaped endophallus of *C. latro*, the details of which in full eversion are illustrated for the first time. Thus, *C. latro* should be regarded as a member of the subgenus *Rhigocarabus* (REITTER, 1896). This species comprises three subspecies (with the exception of *qinlingensis* IMURA of the Qinling Mountains, which should be regarded as an independent species). All of these are distributed in the easternmost periphery of the range of the subgenus as shown in Fig. 50.

Carabus latreilleanus is a small-sized species with a narrow distributional range, which is limited to the Pennine Alps and the Gran Paradiso Massif in the western part of the Alps (Fig. 47). Almost all the previous authors have regarded it as nothing but a regular member of *Orinocarabus* from its external morphology. However, the ND5 tree shows that this species belongs to an isolated lineage which is completely independent not only from that of *Orinocarabus* but also from the other 7 lineages mentioned above. The endophallic structure of *C. latreilleanus* is also very uniquely specialized in shape (see Figs. 43 & 44). On the basis of these findings, IMURA (1998) proposed a new subgenus under the name *Cavazzutiocarabus* for this unique alpine carabid. According to personal communication from Prof. P. CAVAZZUTI, who kindly collected for us a series of alcohol-treated carabid samples from northwestern Italy, *C. latreilleanus* is characterized also from the phenological viewpoint. In the spring, it starts into action much earlier than the other sympatrically occurring *Orinocarabus* species such as *C. heteromorphus* and *C. concolor*. As to the habitat, it prefers environment similar to that of *Platycarabus* rather than to the average biotope of *Orinocarabus*.

Reorganization of the Taxa Treated in this Study

I. Subgenus *Orinocarabus* KRAATZ, 1878

(Type species: *C. sylvestris* PANZER)

1. *C. (Orinocarabus) putzeysianus putzeysianus* GÉHIN, 1876
2. *C. (O.) p. raynaudianus* DEUVE et SIMARD, 1977
3. *C. (O.) p. pedemontanus* GANGLBAUER, 1892
4. *C. (O.) p. germanae* CASALE et CAVAZZUTI, 1977
5. *C. (O.) p. omensis* BORN, 1901
6. *C. (O.) fairmairei pelvicus* CAVAZZUTI, 1973

7. *C. (O.) heteromorphus* DANIEL, 1896
8. *C. (O.) concolor* DANIEL, 1896
9. *C. (O.) sylvestris* PANZER, 1793

II. Subgenus *Cytilocarabus* REITTER, 1896

(Type species: *C. cribratus* QUENSEL)

1. *C. (Cytilocarabus) cribratus* QUENSEL, 1806 (NE. Turkey)
2. *C. (Cy.) cribratus* QUENSEL, 1806 (C. Caucasus)
3. *C. (Cy.) porrectangulus* GÉHIN, 1885

III. Subgenus *Euporocarabus* REITTER, 1896

(Type species: *C. hortensis* LINNÉ)

1. *C. (Euporocarabus) hortensis* LINNÉ, 1758

IV Subgenus *Phricocarabus* REITTER, 1896

(Type species: *C. glabratus* PAYKULL)

1. *C. (Phricocarabus) glabratus glabratus* PAYKULL, 1790
2. *C. (P.) g. latior* BORN, 1895, bona subspecies

V. Subgenus *Carpathophilus* REITTER, 1896

(Type species: *C. linnei* PANZER)

1. *C. (Carpatophilus) linnei* PANZER, 1812

VI. Subgenus *Titanocarabus* BREUNING, 1932

(Type species: *C. titanus* BREUNING)

1. *C. (Titanocarabus) titanus* BREUNING, 1932
2. *C. (T.) sui* IMURA et ZHOU, 1998

VII. Subgenus *Rhigocarabus* REITTER, 1896

(Type species: *C. morawitzianus* SEMENOV)

1. *C. (Rhigocarabus) latro minshanensis* DEUVE, 1987

VIII. Subgenus *Cavazzutiocarabus* IMURA, 1998

(Type species: *C. latreilleanus* CSIKI)

1. *C. (Cavazzutiocarabus) latreilleanus* CSIKI, 1927

Appendix

Morphology of fully everted endophallus of each taxon used in this study is given below. Their distributional areas are shown in Figs. 46–50.

1) *Carabus (Orinocarabus) putzeysianus putzeysianus* GÉHIN, 1876

(Figs. 2, 11)

Male genitalia. Aedeagus peculiarly shaped, very long and slender, with the apical lobe short and dolabriform in lateral view; ostium lobe moderately sized, with the tip slightly bilobed; neither basal lateral lobes nor paraligula is visible, median lobe also not clearly recognized though the membranous wall for its position slightly inflated; prepraeputial lobes recognized as a small hairy area with faint inflation; para-praeputial lobes rather small and symmetrical; praeputial pad moderately developed and dome-like in shape; apical portion of endophallus rather short and simple, apical lobes small and podian lobes vestigial.

Specimens examined. 1 ♂ (for drawing of endophallus), Colle della Lombarda, Vinadio, Cuneo, Piemonte, NW. Italy, 7–VII–1968, P. CAVAZZUTI leg.; 1 ♂ (for DNA analysis), same locality (2,300 m), 15–VI–1997, P. CAVAZZUTI leg.

2) *Carabus (Orinocarabus) putzeysianus raynaudianus* DEUVE et SIMARD, 1977

(Figs. 3, 12)

Male genitalia. Aedeagus as in the nominotypical subspecies, but the dorsal tip of apical lobe a little less strongly protrudent; position for median lobe a little more strongly inflated than in the nominotypical subspecies; praeputial pad larger and more strongly projected dorsad.

Specimens examined. 1 ♂ (for drawing of endophallus), Laghi di Collalunga, 2,600 m, Vinadio, Cuneo, Piemonte, NW. Italy, 11–VII–1993, P. CAVAZZUTI leg.; 1 ♂ (for DNA analysis), same locality (2,700 m), 20–VII–1997, P. CAVAZZUTI leg.

3) *Carabus (Orinocarabus) putzeysianus pedemontanus* GANGLBAUER, 1892

(Figs. 4, 13)

Male genitalia. Aedeagus with the basal portion narrower and slenderer, and more acutely bent ventrad at basal third than in the nominotypical form; apical lobe of aedeagus more gently rounded as a whole; positions for basal lateral lobes and median lobe a little more strongly inflated than in the nominotypical form; podian lobes obviously protrudent ventrad, and apical lobes a little larger.

Specimens examined. 1 ♂ (for drawing of endophallus), Colla dei Termini, 2,000 m, Mt. Cinaiera, V. Corsaglia, Cuneo, Piemonte, NW. Italy, 23–VI–1997, P. CAVAZZUTI leg.; 1 ♂ (for DNA analysis), Val Casotto, 2,000 m, in the same mountain,

15–VI–1997, P. CAVAZZUTI leg.

4) *Carabus (Orinocarabus) putzeysianus germanae* CASALE et CAVAZZUTI, 1977

(Figs. 5, 14)

Male genitalia. Aedeagus similar to that of subsp. *pedemontanus*, but the basal portion not so strongly narrowed and a little less acutely bent ventrad, with the apical margin of apical lobe less roundly shaped; ostium lobe the largest and the most strongly projected dorsad, though its apex is not remarkably bilobed; prepraeputial lobes also the most remarkably recognized in all the subspecies of *putzeysianus*, though much smaller as compared with the other species of the same group; praeputial pad a little larger than that of *raynaudianus*; podian lobe a little smaller than in *pedemontanus*.

Specimens examined. 1 ♂ (for drawing of endophallus), Mt. Saccarello, 2,200 m, Viozene, V. Tanaro, Cuneo, Piemonte, NW. Italy, 24–VI–1994, L. & P. CAVAZZUTI leg.; 1 ♂ (for DNA analysis), same locality, 2–VI–1997, P. CAVAZZUTI leg.

5) *Carabus (Orinocarabus) putzeysianus omensis* BORN, 1901

(Figs. 6, 15)

Male genitalia. Aedeagus almost the same as in the nominotypical subspecies of *putzeysianus*, but more strongly bent ventrad at apical third; apical lobe of aedeagus less widely dilated in lateral view, with the apical ventral corner hardly protruded, apical dorsal one more sharply pointed; basal apical portion of endophallus moderately inflated and median lobe unclear; prepraeputial lobes vestigial but praeputial pad large and strongly projected dorsad as in *germanae*; apical lobes well-recognized but podian lobes vestigial.

Specimens examined. 1 ♂ (for drawing of endophallus), Col del Mulo, 2,300 m, Castelmagno, Cuneo, Piemonte, NW. Italy, 19–VI–1996, P. CAVAZZUTI leg.; 2 ♂♂ (for DNA analysis), same locality, 14–VI–1997, P. CAVAZZUTI leg.

6) *Carabus (Orinocarabus) fairmairei pelvicus* CAVAZZUTI, 1973

(Figs. 7, 16)

Male genitalia. Shape of aedeagus less specialized than in *putzeysianus*, with the apical lobe short and gradually narrowed towards apex; ostium lobe large and bilobed at tip; basal portion of endophallus simple, neither paralogula nor basal lateral lobes visible; prepraeputial lobes recognized as a pair of hairy weak membraneous inflation; parpraeputial lobes moderately developed and symmetrical; praeputial pad with a pair of hump-like inflation in frontal part; podian lobes wide and robust.

Specimens examined. 1 ♂ (for drawing of endophallus), Colle di Bellino, 2,800 m, Acceglio, Cuneo, Piemonte, NW. Italy, 14–IX–1997, P. CAVAZZUTI leg.; 2 ♀♀

(for DNA analysis), same locality (2,850 m), 16–VII–1997, P. CAVAZZUTI leg.

7) *Carabus (Orinocarabus) heteromorphus* DANIEL, 1896

(Figs. 8, 17)

Male genitalia. Much different from those of *C. fairmairei pelvicus* in the shape of aedeagal apex which is very short, robust and nearly oblong in shape in lateral view; ostium lobe smaller and hardly bilobed; endophallus almost as in subsp. *pelvicus*, though parapraeputal lobes a little larger.

Specimens examined. 1 ♂ (for drawing of endophallus), 2 ♂♂ (for DNA analysis), Champorcher, 2,400 m, V. d'Aosta, NW. Italy, 6–VII–1997, P. CAVAZZUTI leg.

Notes. The taxon *heteromorphus* was treated by BREUNING (1933, p. 747) as a "natio" of *C. cenisius* KRAATZ, while it was regarded by DEUVE (1994, p. 160) as one of the subspecies of *C. fairmairei* THOMSON. In fact, *heteromorphus* has a close affinity in the basic structure of endophallus with *C. fairmairei* as shown in Fig. 17, but it may be regarded as a distinct species based on the characteristic aedeagal features and the ND5 DNA sequences.

8) *Carabus (Orinocarabus) concolor* DANIEL, 1896

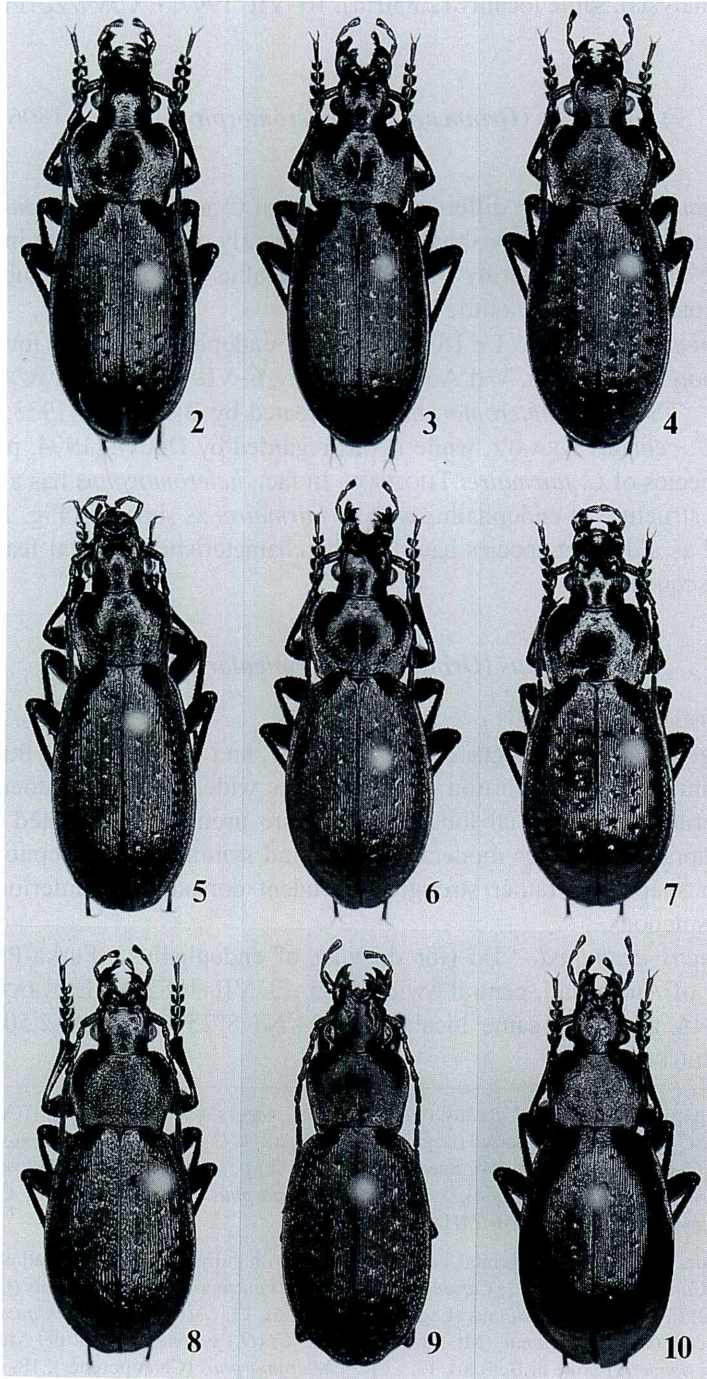
(Figs. 9, 18)

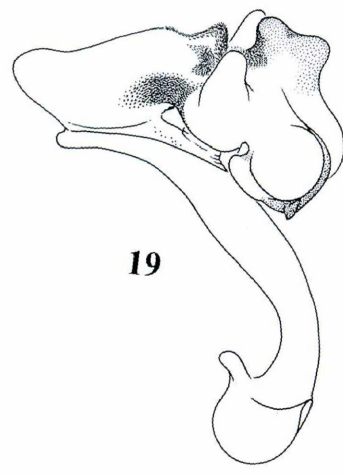
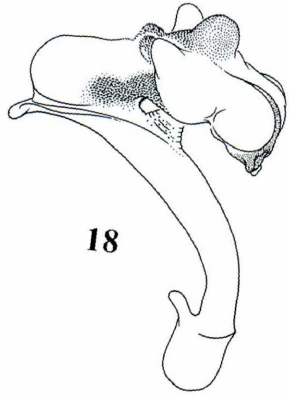
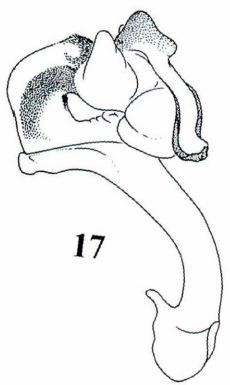
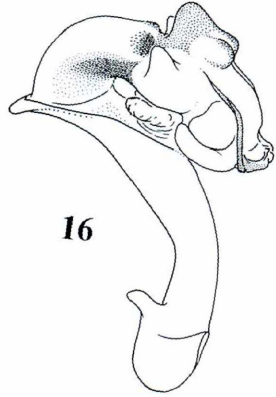
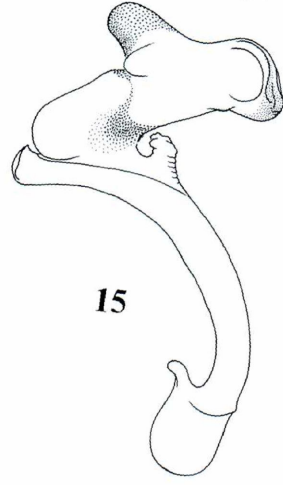
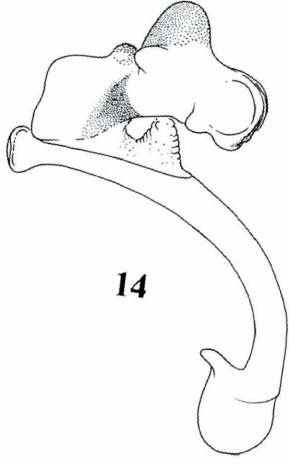
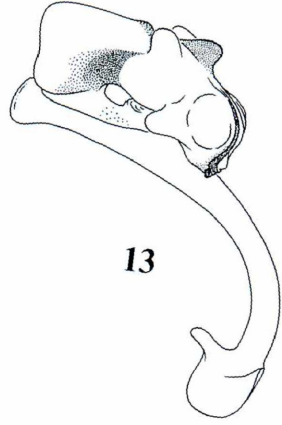
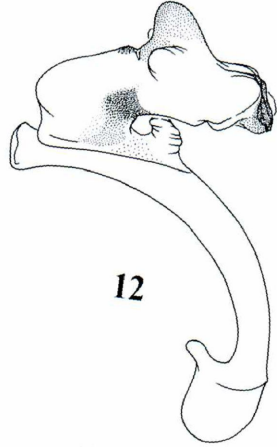
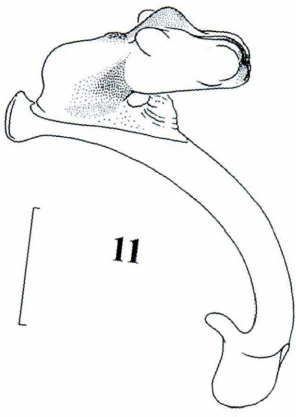
Male genitalia. Aedeagus long and slender, and gently arcuate throughout; ostium lobe unilobed; basal portion of endophallus wide, short and rather strongly inflated posteriad; prepraeputal lobes a little more prominently inflated than in *fairmairei*; parapraeputal lobes moderate in size and symmetrical; praeputal pad hemispherical in shape and rather strongly protrudent dorsad; both anterior and podian lobes inconspicuous.

Specimens examined. 1 ♂ (for drawing of endophallus), Furka-Pass, 2,431 m, Wallis, SW. of Andermatt, central Switzerland, 13–VII–1982, O. E. KRÄTSCHMER leg.; 1 ♂ (for DNA analysis), same locality (46°34'N/ 8°25'E), 2,300–2,500 m, 24–VI–1997, H. SCHÜTZE leg.

Figs. 2–10 (on p. 234). — 2, *Carabus (Orinocarabus) putzeysianus putzeysianus* (Colle della Lombarda); 3, *C. (O.) p. raynaudianus* (Laghi di Collalunga); 4, *C. (O.) p. pedemontanus* (Colla dei Termini); 5, *C. (O.) p. germanae* (Mt. Saccarello); 6, *C. (O.) p. omensis* (Col del Mulo); 7, *C. (O.) fairmairei pelvicus* (Colle di Bellino); 8, *C. (O.) heteromorphus* (Champorcher); 9, *C. (O.) concolor* (Furka-Pass); 10, *C. (O.) sylvestris* (Halz, Germany).

Figs. 11–19 (on p. 235). Male genital organ (aedeagus with fully everted endophallus in right lateral view) of *Carabus* spp. — 11, *Carabus (Orinocarabus) putzeysianus putzeysianus* (Colle della Lombarda); 12, *C. (O.) p. raynaudianus* (Laghi di Collalunga); 13, *C. (O.) p. pedemontanus* (Colla dei Termini); 14, *C. (O.) p. germanae* (Mt. Saccarello); 15, *C. (O.) p. omensis* (Col del Mulo); 16, *C. (O.) fairmairei pelvicus* (Colle di Bellino); 17, *C. (O.) heteromorphus* (Champorcher); 18, *C. (O.) concolor* (Furka-Pass); 19, *C. (O.) sylvestris* (Halz, Germany). Scale: 2 mm.





9) *Carabus (Orinocarabus) sylvestris* PANZER, 1793

(Figs. 10, 19)

Male genitalia. Aedeagus basically similar to that of *concolor*, though the median portion is weakly and widely bisinuate, apical lobe shorter and hardly bent ventrad; ostium lobe rather wide but much depressed, with the apex weakly bilobed; median lobe remarkably projected, with the apex obtuse; prepraeputial lobes rather prominently protruded dorsad and almost symmetrical; parapraeputial lobes also strongly projected dorsad; praeputial pad bi-tuberculate in lateral view; apical portion of endophallus rather short, with the podian lobes wide and robust.

Specimens examined. 1 ♂ (for drawing of endophallus), 1 ♂ (for DNA analysis), Baumgartner, Hoch Scheenberg, E. of Wiener Neustadt, E. Austria, 10~11-VIII-1997, N. & T. KASHIWAI leg.

10) *Carabus (Cytilocarabus) cribratus* QUENSEL, 1806 (from NE. Turkey)

(Figs. 20, 29)

Male genitalia. Aedeagus as shown in Fig. 32, with the apex finger- or tongue-shaped in lateral view; ostium lobe completely absent; basal portion of endophallus simple, neither paraligula nor basal lateral lobes developed, but rather strongly inflated posteriad with the lateral sides strongly pigmented; prepraeputial area unilobate and unusually developed to form a large asymmetrical balloon-like membraneous inflation; parapraeputial lobes moderately developed and almost symmetrical; praeputial pad triangular in shape in lateral view and strongly pigmented; apical portion of endophallus short and robust, with a large membraneous projection at the middle before gonopore.

Specimens examined. 1 ♂ (for drawing of endophallus), Artvin, Yusufeli, KILIÇKAYA, 1,700 m, NE. Turkey, 8~11-VII-1987, K. STAVEN leg.; 1 ♂ (for DNA analysis), same locality, summer in 1997, K. STAVEN leg.

11) *Carabus (Cytilocarabus) cribratus* QUENSEL, 1806 (from C. Caucasus)

(Figs. 21, 30)

Male genitalia. Aedeagus as in the Turkey form, though the apical lobe is a little shorter and more gently rounded in the dorsal side.

Specimen examined. 1 ♂ (for drawing of aedeagus and DNA analysis), Mt. Khumaratkchok, 2,300 m, on Skalystyi Mts., Osetia, C. Caucasus, G. E. DAVIDIAN leg.

Notes. Unfortunately a fully everted endophallus of the present race cannot be illustrated, since only a single specimen available for study was soaked in ethanol before extraction of the genital organ.

12) *Carabus (Cytilocarabus) porrectangulus* GÉHIN, 1885

(Figs. 22, 31)

Male genitalia. Much different from those of *cribratus* in the shape of aedeagal apex which is much shorter, more sharply pointed at the tip and much less strongly arcuate ventrad; endophallus with the basal portion more widely inflated and its lateral sides far more weakly pigmented; prepraeputial lobe much smaller, praeputial pad hemispherical and the apical portion smaller.

Specimens examined. 1 ♂ (for drawing endophallus), Anatolia sett., Ispir (Erzurum), 1,700 m, 14–VII–1987, P. CAVAZZUTI leg.; 1 ♀ (for drawing DNA analysis), Gümüşhane, s. Yagmurdere, s. Kostandag, n. Yayladere, 1,900 m, NE. Turkey, VIII–1996, K. STAVEN leg.

13) *Carabus (Euporocarabus) hortensis* LINNÉ, 1758

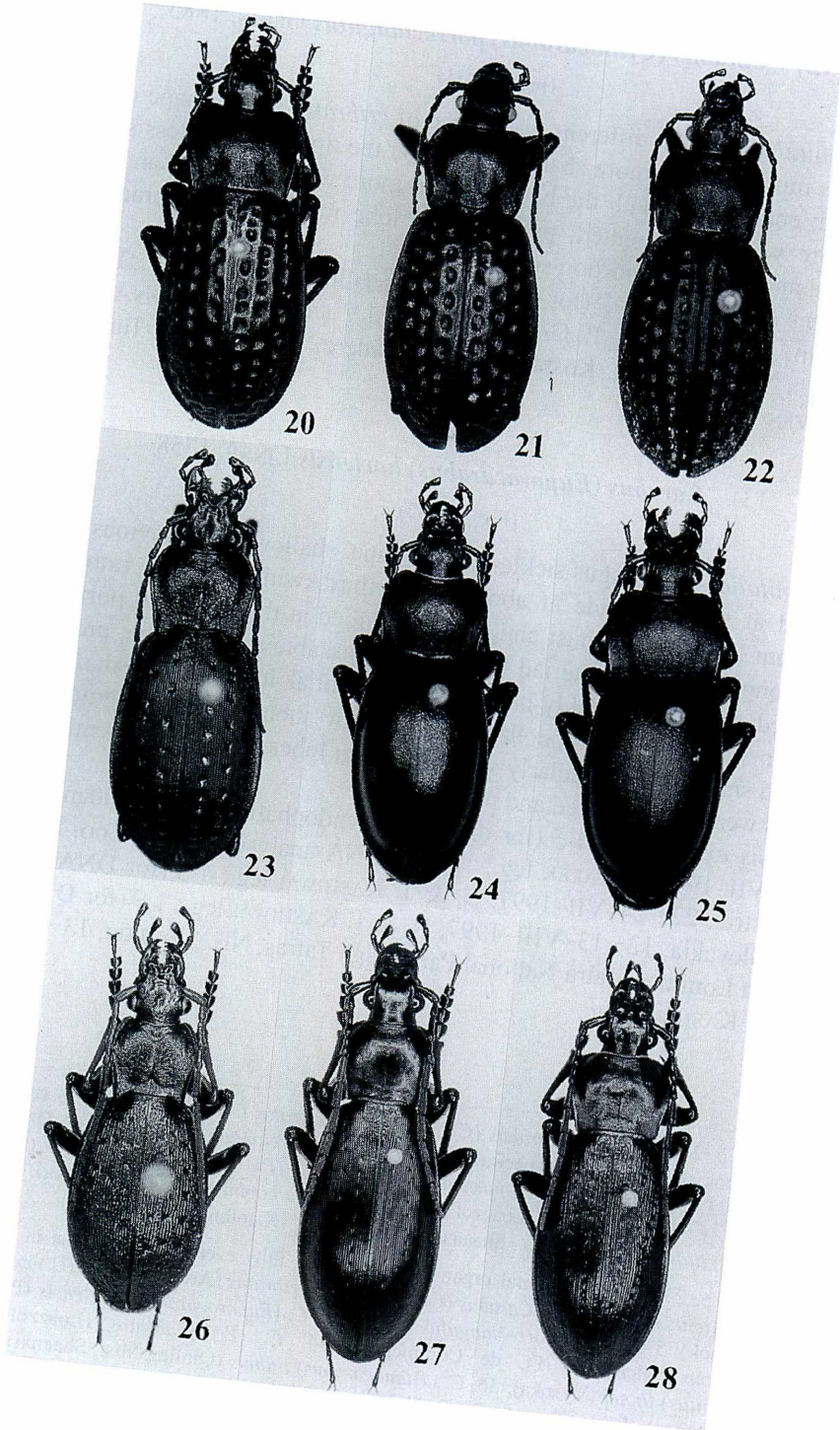
(Figs. 23, 32)

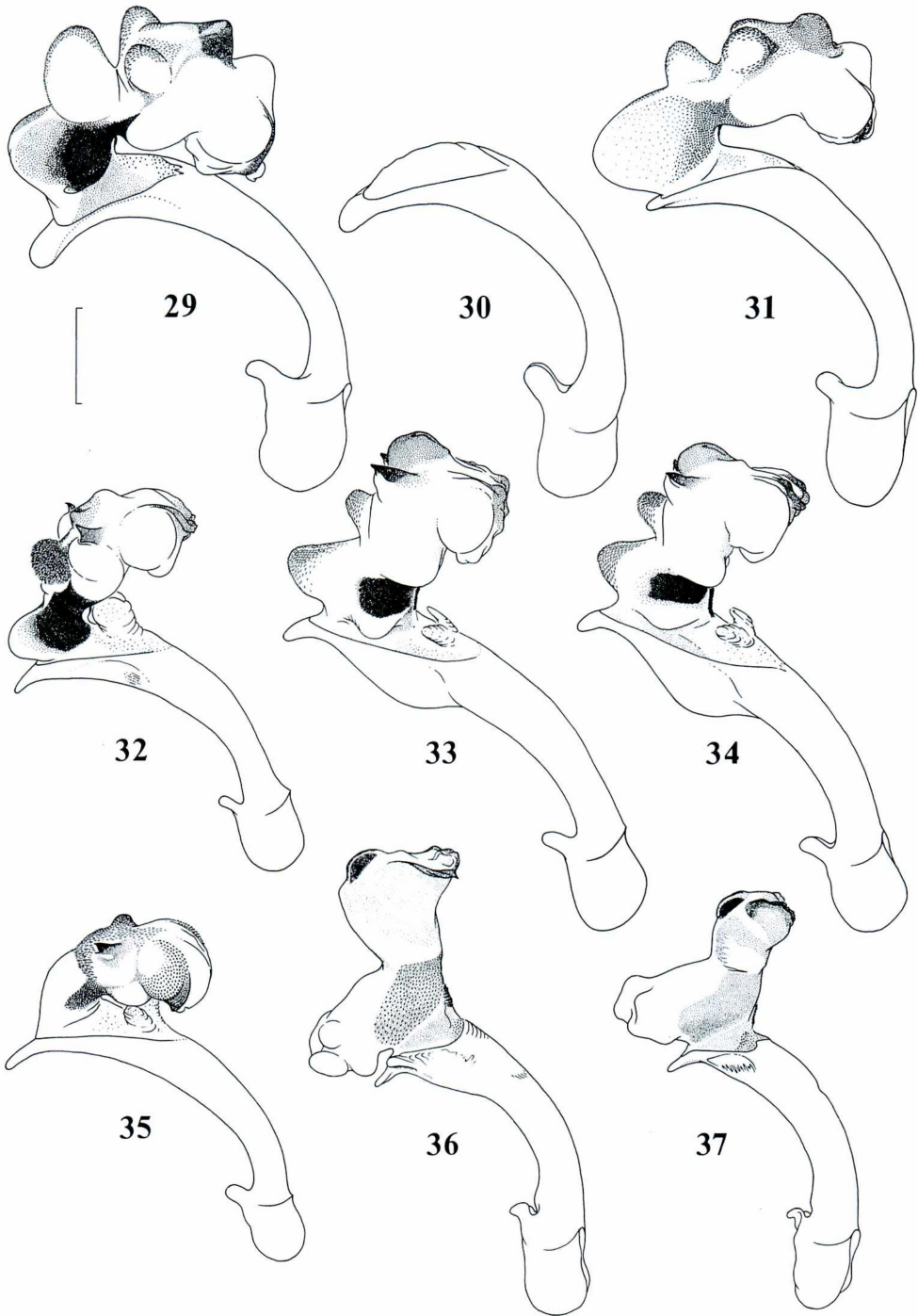
Male genitalia. Aedeagus sickle-like in shape, shallowly but obviously concave ventro-laterad at the right side at about apical third, with the apex rather sharply pointed; ostium lobe large, robust and slightly bilobed at the tip; basal portion of endophallus strongly inflated posteriad to form a remarkable median lobe; prepraeputial lobes unilobed, large and thickly-haired; parpraeputial lobes rather small with the dorso-anterior wall of each lobe flattened to form subtrapezoidal pigmented flap; praeputial pad small and triangularly shaped; podian lobes rather prominently inflated; aggonoporus weakly sclerotized and pigmented.

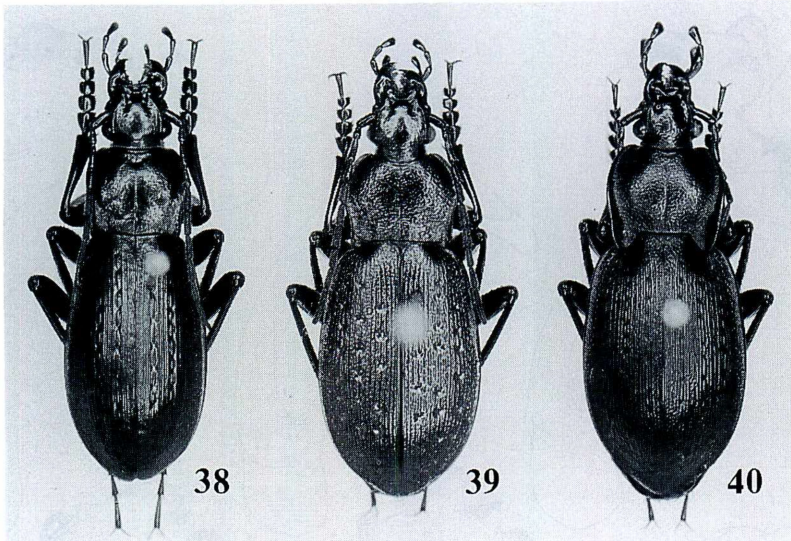
Specimens examined. 1 ♂ (for drawing of endophallus), Prad, 900 m, Südtirol, Italy, 3–20–VII–1977, SDRALEK leg.; 1 ♀ (for DNA analysis), Alpen Zoo, Innsbruck, Tirol, W. Austria, 22–24–VII–1997, N. & T. KASHIWAI leg.; 1 ♂ (for DNA analysis), Trenčín, W. Slovakia, 12–13–VIII–1997, N. & T. KASHIWAI leg.; 1 ♀ (for DNA analysis), Tatranska Lomnica, Tatra National Park, High Tatras, NE. Slovakia, 13–15–VIII–1997, N. & T. KASHIWAI leg.

Figs. 20–28 (on p. 238). — 20, *Carabus (Cytilocarabus) cribratus* (Artvin); 21, *C. (C.) cribratus* (Mt. Khumaratkhek; DNA-analyzed specimen); 22, *C. (C.) porrectangulus* (Gümüşhane; DNA-analyzed specimen); 23, *C. (Euporocarabus) hortensis* (Prad); 24, *C. (Phricocarabus) glabratus* (Ft. de Compiègne); 25, *C. (P.) glabratus* (Loazzolo); 26, *C. (Carpathophilus) linnei* (Vysoka); 27, *C. (Titanocarabus) titanus* (Qinling Mts., Shaanxi); 28, *C. (T.) sui* (Xiaolongmen, holotype).

Figs. 29–37 (on p. 239). Male genital organ (aedeagus with fully everted endophallus in right lateral view) of *Carabus* spp. — 29, *Carabus (Cytilocarabus) cribratus* (Artvin); 30, *C. (C.) cribratus* (Mt. Khumaratkhek); 31, *C. (C.) porrectangulus* (Ispir); 32, *C. (Euporocarabus) hortensis* (Prad); 33, *C. (Phricocarabus) glabratus* (Ft. de Compiègne); 34, *C. (P.) glabratus* (Loazzolo); 35, *C. (Carpathophilus) linnei* (Vysoka); 36, *C. (Titanocarabus) titanus* (Qinling Mts., Shaanxi); 37, *C. (T.) sui* (Xiaolongmen). Scale: 2 mm for 29–34; 1.3 mm for 35; 2.9 mm for 36 & 37.







Figs. 38–40. — 38, *Carabus (Rhigocarabus) latro minshanensis* (Jiuzhaigou); 39, *C. (Cavazzutiocarabus) latreilleanus* (Champorcher); 40, *C. (Oreocarabus) amplipennis* (Lugo).

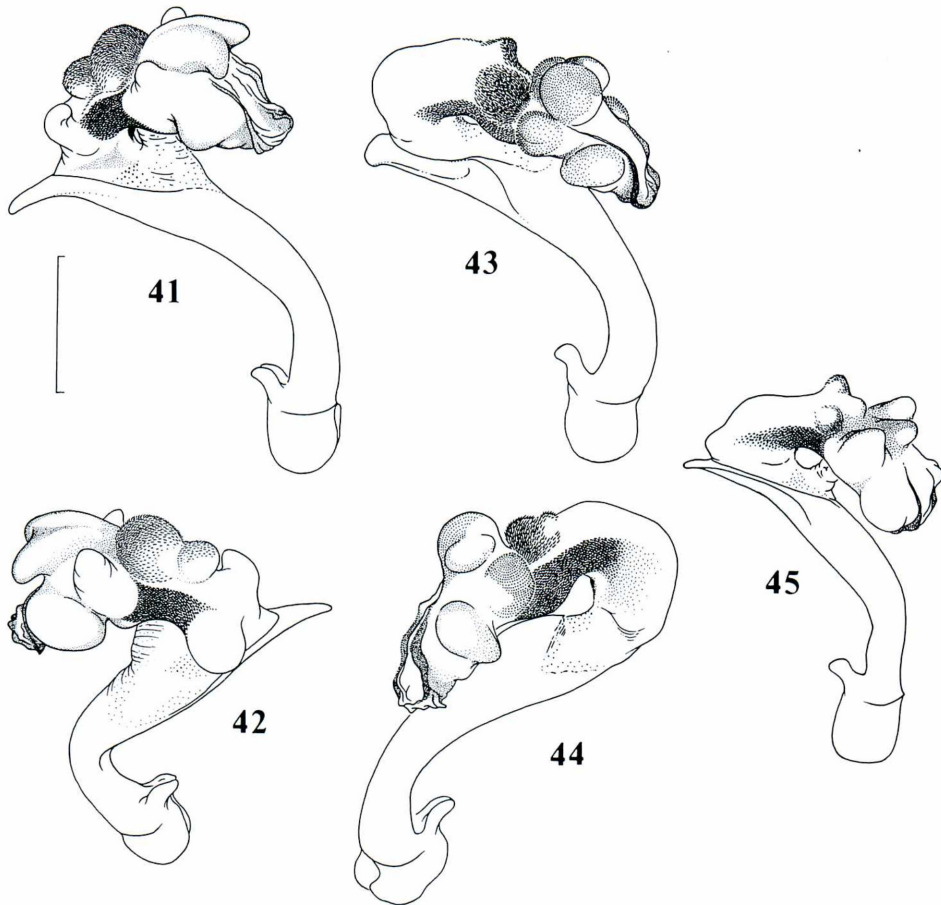
14) *Carabus (Phricocarabus) glabratus glabratus* PAYKULL, 1790

(from N. & E. France, NE. Slovakia and W. Austria)

(Figs. 24, 33)

Male genitalia. Aedeagus as shown in Fig. 35; ostium lobe completely bifurcate, with the dorsal portion of each lobe rather flattened; ligulum unusually developed to form a plate-like oblong sclerite with strong pigmentation; basal lateral lobes recognizable, with the right one much larger than the left; median lobe also well-developed, the surface of which is covered with minute hairs; prepraeputial area unilobate and markedly projected; dorso-anterior wall of parapraeputial lobe weakly sclerotized to form a flat and oblique plate with pigmentation; praeputial pad hemispherical in shape with marked pigmentation; anterior lobes inconspicuous but podian lobes well recognized; aggonoporus rather strongly sclerotized and pigmented.

Specimens examined. 1 ♂ (for drawing of endophallus), Ft. de Compiègne, Oise, N. France, VIII–1981; 3 ♂♂ (for DNA analysis), Bourgogne, E. France; 1 ♂ (for DNA analysis), Sary Smokovec, Tatra National Park, High Tatras, NE. Slovakia, 13~15–VIII–1997, N. & T. KASHIWA leg.; 1 ♀ (for DNA analysis), Volderau, Stubaital, Innsbruck, Tirol, W. Austria, 26~28–VII–1997, N. & T. KASHIWA leg.



Figs. 41–45. Male genital organ (aedeagus with fully everted endophallus) of *Carabus* spp. in right lateral view (41, 43, 45), left subdorsal view (42) and left subposterior view (45). — 41 & 42, *Carabus (Rhigocarabus) latro minshanensis* (Jiuzhaigou); 43 & 44, *C. (Cavazzutiocarabus) latreilleanus* (Champorcher); 45, *C. (Oreocarabus) amplipennis* (Lugo). Scale: 2 mm for 41 & 42; 1.6 mm for 43 & 44; 2.4 mm for 45.

15) *Carabus (Phricocarabus) glabratus latior* BORN, 1895, bona subspecies

(from NW. Italy)

(Figs. 25, 34)

Male genitalia. Almost the same in both aedeagal and endophallic structure as those of the nominotypical forms, and morphological difference between these two forms is hardly visible.

Specimens examined. 1 ♂ (for drawing of endophallus), Loazzolo, 400 m, Canelli, Cuneo, Piemonte, NW. Italy, 14–VI–1997, P. CAVAZZUTI leg.; 1 ♂ (for DNA

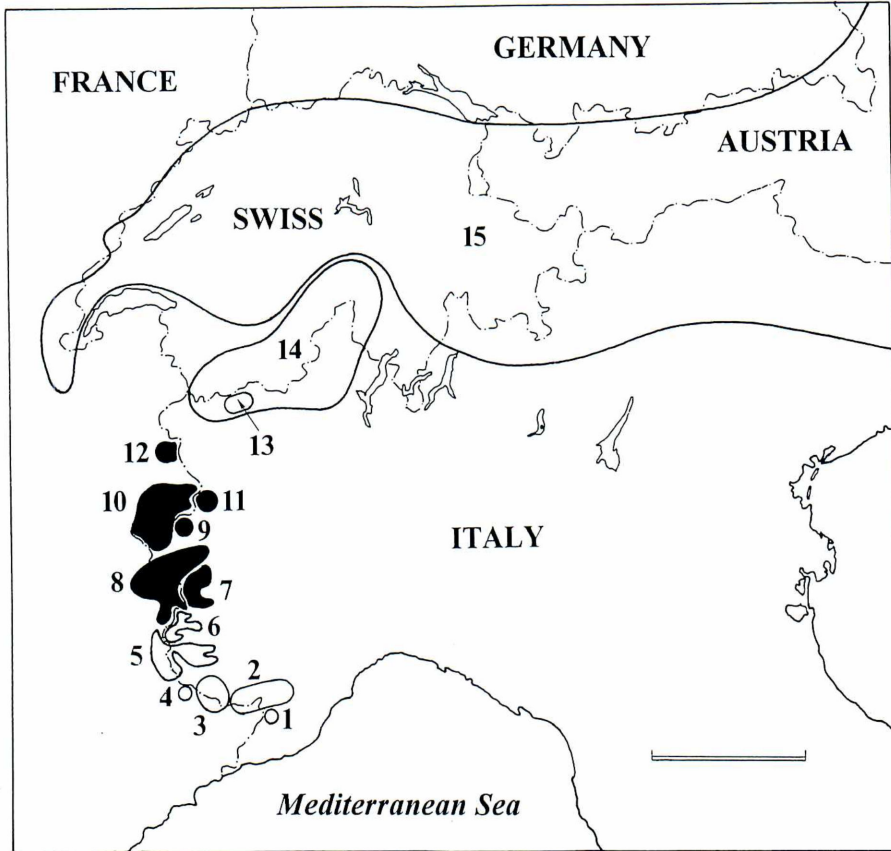


Fig. 46. Map showing the distributional ranges of the subgenus *Orinocarabus* in the Alps (black-shaded ranges indicate those of the taxa whose mitochondrial DNA sequences are unknown). — 1–5, *Carabus (Orinocarabus) putzeysianus*; 1, subsp. *germanae*, 2, subsp. *pedemontanus*, 3, subsp. *putzeysianus*, 4, subsp. *raynaudianus*, 5, subsp. *omensis*; 6–8, *C. (O.) fairmairei*; 6, subsp. *pelvicus*, 7, subsp. *fairmairei*, 8, subsp. *stecki*; 9–12, *C. (O.) cenisius*; 9, subsp. *fenestrellanus*, 10, subsp. *cenisius*, 11, subsp. *ceresiacus*, 12, subsp. *iseranicus*; 13, *C. (O.) heteromorphus*; 14, *C. (O.) concolor*; 15, *C. (O.) sylvestris*.

analysis), Mt. Casto, 1,000 m, Tavigliano, Biella, Piemonte, NW. Italy, VI–1997, brought by P. RATTI; 1 ♀ (for DNA analysis), near Guardabosone, 600 m, near Creva-cuore, Vercelli Pref., Piemonte, NW. Italy, VII–1997, LOCCA leg.; 1 ♂ (for DNA analysis), Andrate, Torino, NW. Italy, summer in 1997, brought by P. RATTI; 1 ♀ (for DNA analysis), Canelli, 450 m, Cuneo, Piemonte, NW. Italy, 10–VI–1997, P. CAVAZZUTI leg.

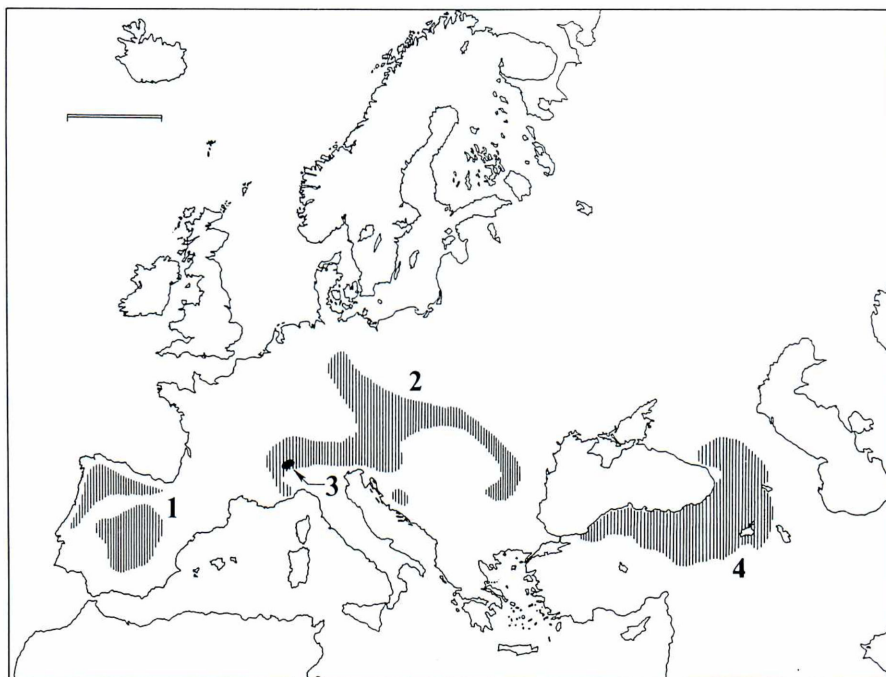


Fig. 47. Map showing the distributional ranges of the subgenera *Oreocarabus* (s. str.) (1), *Orinocarabus* (2), *Cavazzutiocarabus* (3) and *Cylilocarabus* (4). Scale: 600 km.

16) *Carabus (Carpathophilus) linnei* PANZER, 1812

(Figs. 26, 35)

Male genitalia. Aedeagus long and slender, less strongly bent ventrad at the basal part, with the apical lobe narrow and elongate; ostium lobe nearly completely bifurcate; basal portion of endophallus simple, neither paralingula nor basal lateral lobes recognizable; median portion wide and robust, with the prepraeputal lobes not projected at all; parapraeputal lobes small and low, forming a pair of strongly pigmented flaps with sharply pointed apices; praeputal pad small and hemispherical; apical portion of endophallus strongly inflated, though both the apical and podian lobes are inconspicuous.

Specimens examined. 1 ♂ (for drawing of endophallus), Tschechoslovakia, Mahren, Vseyinske, Vrchy, Vysoka, 1–VIII–1986; 1 ♀ (for DNA analysis), Start, Tatranska Lomnica Sakalnatepleso, Tatra National Park, High Tatras, NE. Slovakia, 14~15–VIII–1997, N. & T. KASHIWAI leg.; 1 ♀ (for DNA analysis), around the Hotel Boboty, Stefanova, Vratna dolina, Mala Fatra National Park, near Zilina, N. Slovakia, 15–VIII–1997, N. & T. KASHIWAI leg.

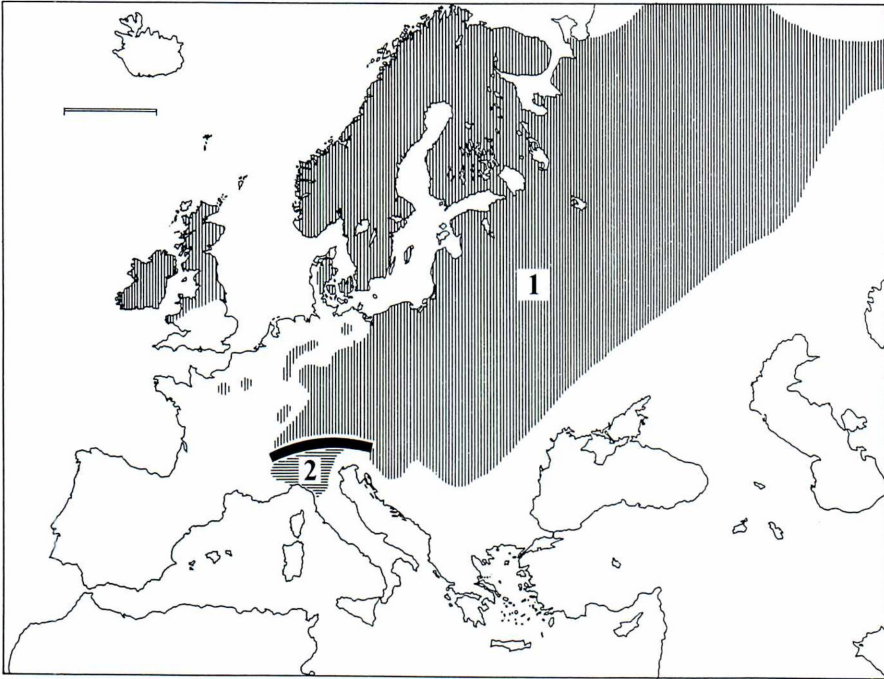


Fig. 48. Map showing the distributional range of *Carabus (Phricocarabus) glabratus* (black bar indicates the Alps) — 1, Subsp. *glabratus* (including the following lower taxa: *extensus*, *punctatocostatus*, *subglabratus*, *lapponicus*, *liebleri*, *gibbosus*, *carinthianus*, *ottofischeri*, etc.); 2, subsp. *latior*. Scale: 600 km

17) *Carabus (Titanocarabus) titanus* BREUNING, 1932

(Figs. 27, 36)

Male genitalia. As described and figured by IMURA (1993, p. 378). Supplementary descriptions on the endophallus:— Basal part of endophallus strongly inflated posteriorly and associated with 4 or 5 various-sized small humps; prepraeputal lobes completely absent; parpraeputal lobes only feebly inflated; praeputal pad weakly developed to form a hemispherical inflation with strong pigmentation; both apical and podian lobes vestigial; aggonoporus recognized as a pair of small sclerites with moderate pigmentation.

Specimen examined. 1 ♂ (for drawing of endophallus and DNA analysis), above Jiuzhai Zhen, 2,100–2,200 m, northern side of the Riv. Bai He, Jiuzhaigou Xian (= former Nanping Xian), N. Sichuan, China, 15–VI–1998, Y. IMURA & Z.-H. SU leg.

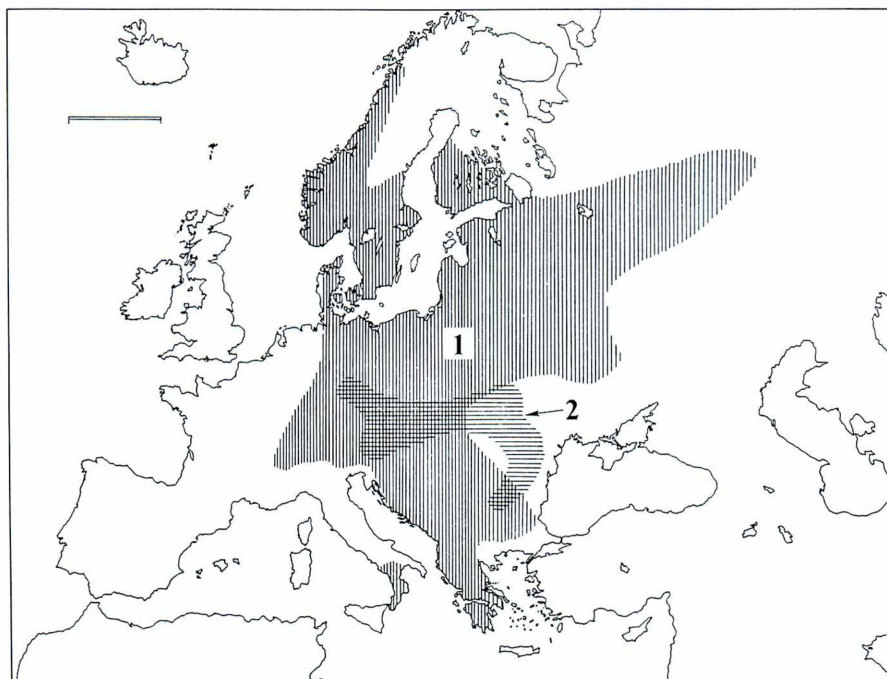


Fig. 49. Map showing the distributional ranges of the subgenera *Euporocarabus* (1, solely composed of *hortensis*, including two major subspecies, *preslii* and *neumeyeri*) and *Carpathophilus* (2, solely composed of *linnei*, including several minor subspecies). Scale: 600 km.

18) *Carabus (Titanocarabus) sui* IMURA et ZHOU, 1998

(Figs. 28, 37)

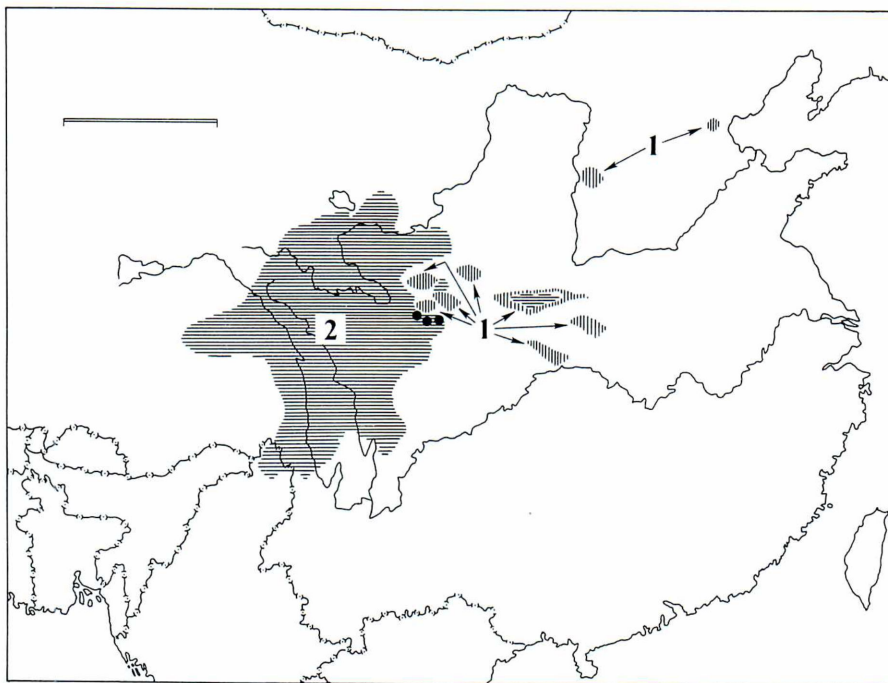
Male genitalia. As described and figured by IMURA and ZHOU (1998, p. 114). Supplementary descriptions on the endophallus:—Ligulum a little narrower and less prominently carinate, though more densely scattered with pigmented granules; general proportion of endophallus almost as in *titanus*, though the apical portion is much less strongly inflated and the humps on basal inflation smaller.

Specimens examined. 1 ♂ (for drawing of endophallus), Xiaolongmen in Mentougou, W. of Beijing, China, 25~30-VI-1998, H.-S. ZHOU leg.; 1 ♂ (for DNA analysis, paratype specimen), same locality, 19~22-VII-1997, H.-S. ZHOU leg.

19) *Carabus (Rhigocarabus) latro minshanensis* DEUVE, 1987

(Figs. 38, 41, 42)

Male genitalia. Ostium lobe large, robust, strongly inflated at base and unilobate at apex; basal lateral lobes recognized on both sides, with the left one larger than



Figs. 50. Map showing the distributional ranges of the subgenera *Titanocarabus* (1) and *Rhigocarabus* (2). Closed circles indicate the distribution of *Carabus* (*Rhigocarabus*) *latroi* (nominotypical subspecies, *minshanensis* and *huanglongensis*). Scale: 600 km.

the right; ligulum small though strongly protrudent, sclerotized and pigmented; prepraeputal lobes unified into a single lobe, with a smaller accessory hump near the base; parpraeputal lobes with the left one larger than the right; praeputal pad extraordinarily developed with bifurcate apex; both apical and podian lobes weakly inflated; aggonoporus vestigial, though barely recognized as a pair of small sclerites with faint pigmentation.

Specimens examined. 1 ♂ (for drawing of endophallus), 1 ♂ (for DNA analysis), ca. 5 km N. of the Pass Gongga Ling, 3,050–3,100 m (mixed forest), SW. of Jiuzhaigou Xian (= former Nanping Xian), N. Sichuan, China, 10~15-VI-1998, Y. IMURA & Z.-H. SU leg.

20) *Carabus* (*Cavazzutiocarabus*) *latreilleanus* CSIKI, 1927

(Figs. 39, 43, 44)

Male genitalia. As described by IMURA (1998). Here we give detailed illustrations in bilateral views.

Specimens examined. 1 ♂ (for drawing of endophallus), 2 ♂♂ (for DNA analy-

sis), Champorcher, 2,400 m, V. d'Aosta, NW. Italy, 6–VII–1997, P. CAVAZZUTI leg.

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We wish to express our deep gratitude to the following colleagues who kindly submitted invaluable specimens, either alcohol-treated or dried, to us for study: Dr. I. A. BELOUSOV (St. Petersburg, Russia), Prof. P. CAVAZZUTI (Pagno, Italy), Dr. B. DAVID (Bourgogne, France), Mr. & Mrs. N. KASHIWAI (Kawasaki, Japan), the late Mr. O. E. KRÄTSCHMER (Mainz, Germany), Mr. B. LASSALLE (Boissy les Perche, France), Mr. P. RATTI (Biella, Italy), Mr. H. SCHÜTZE (Gleichen, Germany), Mr. K. STAVEN (Broistedt, Germany) and Dr. H.-Z. ZHOU (Beijing, China).

要 約

井村有希・蘇 智慧・金 衝坤・大澤省三：雄交尾器内袋の形態と分子系統に基づくミヤマオサムシ類の分類再構築。—— ミヤマオサムシ *Oreocarabus* は、ユーラシア大陸産の20種強を含む比較的大きい亜属である。単一の亜属としてまとめられてはいるものの、形態学的にかなり変化に富む種が含まれていて、井村ら(1996)はこれを5種群に分類している。本論文では、このうち18の分類単位について、ミトコンドリアND5遺伝子の塩基配列(1,069 bp)に基づく分子系統樹を作成した。同時に、これまでほとんど検討されてこなかった♂交尾器内袋の構造をも図示、記載し、これら双方の知見から、ミヤマオサムシ類の系統関係の再構築を試みた。その結果、従来ミヤマオサムシ1亜属として扱われてきたものは単系統群としてまとまらず、少なくとも以下の独立した8クラスターからなる多系統群であることが判明した：アルプスオサムシ亜属 *Orinocarabus*、アナバネオサムシ亜属 *Cytilocarabus*、ニワオサムシ亜属 *Euporocarabus*、クロツヤオサムシ亜属 *Phricocarabus*、リンネオサムシ亜属 *Carpathophilus*、ティーターンオサムシ亜属 *Titanocarabus*、ドウガネオサムシ亜属 *Rhigocarabus*、ニセアルプスオサムシ亜属 *Cavazzutiocarabus*。クロツヤオサムシ亜属の基準種、クロツヤオサムシ *C. glabratus* は変異に乏しく、これまで単型種に近い扱いをうけてきたが、北西イタリア地方のものが、それ以外のヨーロッパ各地のものと非常に深い分岐をもって分かれていることが判明した。また、これまでアルプスオサムシ亜属の一員であろうと信じられてきた *C. latreilleanus* が、形態、分子系統の双方から、非常に独立性の高い、異なる系列に属する種であることが示唆された。これら各クラスターの分岐時期は古く、オサムシ亜族に属する各亜属が一斉に分岐、放散した頃にまで遡ることができる。

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