

A Preliminary Revision of the Carabogenici of the Subtribe Carabina (Coleoptera, Carabidae)

By

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In my previous paper (1978), I recognized three subdivisions for the subtribe Carabina of the subfamily Carabinae. This conclusion was based upon comparative studies of the genitalia of the lower taxa included, which are yet to be published. The present paper deals with one of the subdivisions, the Carabogenici, with a synoptic revision of the component genera and subgenera. Although the characterization of the subdivisions was based exclusively upon the morphological characters, much importance was attached to their distribution in the classification of the taxa of the lower level. The classification of subgenera of the genus *Lipaster* proposed in this paper is tentative, because I was able to study only a part of so many, mostly Asiatic species that constitute this genus. I was confronted with other, exclusively nomenclatural problems yet unsolved, concerning the availability of genus-group names published by G. Vacher DE LAPOUGE who established a number of genera and subgenera in *Genera Insectorum* (1929–1932). The keys to subtribes, groups, genera and subgenera, and “catalogue raisonné”, in which statements for new taxa are given, were published in 1931–1932. According to the Article 12 (2) of the International Code of Zoological Nomenclature, most of these names are unavailable, since he did not designate type-species at all. These names appeared, however, in the genealogical discussions, published in 1930, which barely satisfy the provisions of the Article 12 of the Code, so I have regarded them as available and designated the type-species for them.

I must thank entomologists who kindly offered me invaluable materials on which the present study is based. Mr. Carl L. BLUMENTHAL, Troisdorf, Mr. Walter HEINZ, Wald-Michelbach, and Prof. Dr. Karl MANDL, Wien, generously sent me a number of taxonomically important species including rarities which I particularly needed. I also owe a great debt of gratitude to Dr. Oleg L. KRYZHANOVSKIY, Leningrad, for the gift and loan of many Asiatic specimens which were indispensable for the present study.

Distribution as Taxonomic Characters

In the systematic studies of animals, the ranges and patterns of distribution have

considerable importance. It is particularly true in such insects as the Carabina which have no other way of dispersal than by means of crawling on the ground due to the loss of functional hind wings; their distribution seems to show their phases of evolution more simply than those with functional wings do. I have noticed some peculiar patterns of distribution exhibited by the Carabina and have introduced here new concepts and terms which will give useful bases for presumption of the relationship between the taxa concerned as supplementary to the morphological characters.

In the species belonging to the Carabina, differentiation into subspecies seems to have taken place allopatrically, usually as a result of simple geographical segregation among populations. The area where the subspeciation has occurred is the centre of differentiation, but I propose to call it the primary range of the species by the reason as discussed below. The delimitation of the primary range of each species, on the basis of analyses of distribution patterns, is very important because the phylogenetic relationship among related species may be presumed from the disposition of their primary ranges. Two related species of which primary ranges are wholly overlapped are not possibly more closely related to each other than those of which primary ranges are not overlapped, because they must have been distinct from each other reproductively before their ranges came into contact. Although the allopatry of the primary ranges is not always an evidence of affinity between species, it is highly probable that they are derivatives from a common ancestor or at least one of them, if they constitute a homogeneous group within a definite area, or are not proved to be more heterogeneous morphologically than others of the same region.

I have proposed the term "primary range" meaning the centre of differentiation, because a number of species, most noticeably in Europe, have ranges apparently different from the ranges where subspeciation would have taken place, which seem to be more appropriate to call the secondary ranges of the species (cf. vicarious area). For example, *Autocarabus auratus* (LINNÉ) is widespread over Europe from northern Spain so far northeast to Germany and Poland (BŁAZEJEWSKI, 1956), but the greater part of its range is represented by only one subspecies, the nominate *auratus*. A great diversity of this species is recognized only within a restricted area in south France where a number of subspecies have been described. Although there may be a difference of opinions as to the taxonomic validity of these subspecies, it is certain that this species is much more varied in this region than elsewhere in the north within its whole range. A similar pattern is exhibited by *Ischnocarabus nemoralis* (MÜLLER) as discussed in this paper (Fig. 40). *Oreocarabus hortensis* (LINNÉ) ranges more extensively, extending from Balkan so far north to Skandinavia and European Russia, but the most part of its range is occupied also by the nominate subspecies alone, and all other subspecies are confined to the southwestern part of the Balkan Peninsula and a restricted area in the peninsular part of Italy. It should be noted that the areas where these species show a remarkable diversity at the subspecies level are mostly mountainous or hilly regions belonging to the Tertiary folding where animals are known to have taken refuge in and differentiated into subtaxa during the last glacial period when the

North European Plain was largely covered with ice-sheets. The wide ranging, less variable subspecies in the northern parts of their ranges must have had superior adaptability which made them possible to establish themselves the present localities rapidly, after the retreat of the glaciers. Naturally, therefore, the ranges as thus acquired should be discriminated from the areas where these subspecies would have been differentiated. The subspecies that represent the secondary ranges are called accordingly the secondary subspecies in contrast with the primary subspecies that represent the primary ranges.

In the Japanese fauna, there are also good examples, such as *Carabus (Ohomopterus) insulicola* (CHAUDOIR), *C. (O.) dehaanii* (CHAUDOIR), etc., which have similar northerly secondary ranges though the influence of cold climate during the glacier period is uncertain.

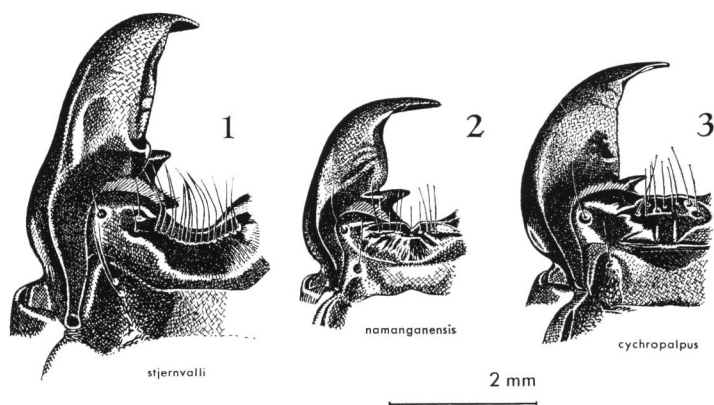
The concept of the primary and the secondary ranges may be applied to the taxa of the supraspecific level. At least, it is useful for the definition of certain genera and subgenera of which one or a few component species (in reality, their secondary subspecies) have ranges even wider than the whole of the "primary range" of the genus. Overlaps of and the distance among the primary ranges of supraspecific taxa are also suggestive of their phylogenetic relationship as they are at the species level.

Subdivision **Carabogenici**, *sensu* ISHIKAWA, 1978

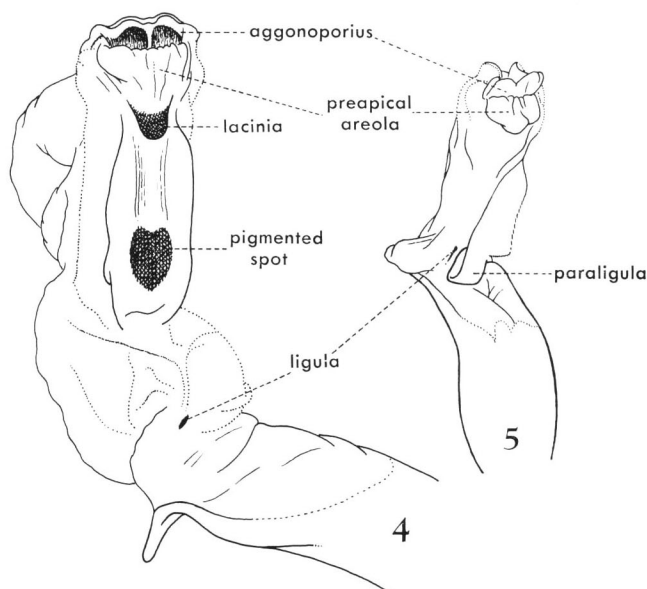
Because of the least specialized external features, species of this subdivision do not seem to have been classified properly. Apparently too much importance was attached to subtle peculiarities in the extragenitalic features. This resulted in admitting unreasonably large, wide ranging taxa such as *Eucarabus*, *Trachycarabus*, etc., only because of the presence of seemingly "intermediate species" in contrast with small, localized taxa such as *Lipaster* (Fig. 1), *Cyclocarabus* (Fig. 2), *Ischnocarabus* (Fig. 3), etc., which were ranked as equivalent to the larger ones simply because of superficially distinct, specialized facies. The peculiar features that characterize the latter groups are, however, largely adaptational, as I discussed already (ISHIKAWA, 1978), and the taxonomic value of such characters is highly circumstantial.

The structure of the endophallus elucidates the relationships between them more convincingly, and the grouping of species on the basis of the genitalic characters are evidenced sufficiently by the share of the extragenitalic characters as well as the pattern of geographical distribution.

I have recognized three genera, namely, *Carabus*, *Lipaster* and *Ischnocarabus* in this subdivision. The genus *Carabus* is distinguished in having a conspicuous copulatory piece on the endophallus. There is no exceptional species as to this character. The genus *Lipaster* (Figs. 4, 6–29) is characterized in having a membranous inflation at the base of the endophallus around the ligula. The endophallus shows a different degree of specialization which is indicated by the development of the pigmented spot, of the lacinia and of the aggonoporus. The former two may be



Figs. 1-3. The Carabogenici, with specialized mandibles, labra and clypei. — 1. *Lipaster (Lipaster) stjernvalli humboldti* (FALDERMANN); Caucasus. — 2. *Lipaster (Cyclocarabus) namanganensis* (HEYDEN); Turkestan, Central Asia. — 3. *Ischnocarabus (Ischnocarabus) cychropalpus* (PEYRON); Anatolia (from ISHIKAWA, 1978).



Figs. 4-5. Terminology of the endophallus of the Carabina employed in the present paper. — 4. *Lipaster (Morphocarabus) gebleri* (FISCHER). — 5. *Ischnocarabus (Deuterocarabus) congruus akkusanus* (BREUNING).

rudimentary or absolutely lost in some species. The preapical areola is never well outlined. The genus *Ischnocarabus* (Figs. 5, 31-39) seems to be the most diversified of all three genera in the endophallic structure. They are similar in general, but few

of noticeable characters are shared by all three subgenera. Aggonoporiis is well developed and characteristic of species. Preapical areola is well outlined and lobate except the subgenus *Aptocarabus*. A conspicuously lobate paraligula (Figs. 5, 31–34, 37–39) covers the ostium when the endophallus is withdrawn (Fig. 39), except in the subgenus *Archicarabus*.

There is little doubt that the genus *Ischnocarabus* is a group of the most recent origin of the Carabogenici, as suggested by the fact that its primary range is confined to the Mediterranean coast of Eurasia so far east to the Caspian Sea through Asia Minor; moreover, even the component subgenera are nearly allopatric in distribution within this area; sympatry seems to occur only at the species level (Fig. 40).

The genus *Lipaster* is apparently older in its time of differentiation than the genus *Ischnocarabus*. Many subgenera comprising homogeneous species are sporadically scattered around Central Asia, while others are more widely distributed over Europe, Siberia and Central Asia where they show different degree of differentiation either specific or subspecific. The latter groups may be largely overlapped in distribution though it is uncertain if they are actually sympatric. Some species, such as *L. hummeli*, *L. henningi*, *L. regalis* and *L. aeruginosus*, seem to have very wide ranges in Siberia where, except *L. hummeli*, they are largely overlapped. In Europe, "Artenkreis" of "*Carabus monilis* FABRICIUS" shows a remarkable divergence at the species level; its primary range seems to be a region in and around Rumania according to MANDL (1965). Such patterns of distribution as they show suggest that the present distribution of *Lipaster* has been established as a result of repeated subspecific/specific differentiation and dispersal. The primary range of this genus is no longer presumable.

The genus *Carabus* has still wider range than the genus *Lipaster*. It has a purely Nearctic subgenus *Lichnocarabus* besides the Palaearctic ones and is thus distributed over the whole of the Holarctic region. Moreover, there are species, such as *C. granulatus* and *C. arvensis-conciliator* complex which range transcontinentally over Europe so far east to Japan through Asia. The only comparable species is *Apotomopterus* (*Limnocarabus*) *clathratus* (LINNÉ) of the Spinulati, though it is far more sporadically distributed.

Genus *Carabus* LINNÉ, 1758

Carabus: ISHIKAWA, 1973. Bull. Natn. Sci. Mus. Tokyo, 16: 205.

In my previous paper (loc. cit.), I defined the genus *Carabus* for the inclusion of the species with a distinct copulatory piece on the endophallus of the male genitalia. They have apparently other characteristic features in common, and appear to be a natural group. Although they show a different degree of specialization in the structure that they share, differences between species do not appear to be so great as to justify the further splitting of the genus as thus characterized. So far as I know, there seems to be no questionable species that connects the genus *Carabus* in the present sense with other related genera by the possession of the intermediate characters in the male

copulatory organ.

In many respects, however, the species belonging to *Morphocarabus* (*sensu* ISHIKAWA, 1973) are presumed to be related to *Carabus*. Notably, the presence of a pigmented spot at the dorsal wall of the endophallus in the species of *Morphocarabus* will suggest their affinity to the species of *Carabus* on condition that the pigmented spot is proved to be homologous to the copulatory piece of the genus *Carabus* as I assumed it to be. In reality, they are similar to each other also in other external features, and most authors treated them as belonging to the same or closely related groups. BREUNING (1932), for example, lumped many species of *Carabus* together with other superficially least specialized species under the sectio *Eucarabus* in the subgenus *Carabus*, and *Morphocarabus* was included therein as a synonym.

The endophallus of *Morphocarabus* is highly specialized, with elaborate structures which characterize the group very distinctly. But, it should be noted that exactly the same basic structure is developed in the species which are distributed among traditionally separated groups such as *Trachycarabus* and its allies and also *Cyclocarabus*. The problem is discussed below under the genus *Lipaster*.

As thus defined, the genus *Carabus* has a very wide range of distribution almost over the whole of the Holarctic Region. Few of other genera of the subtribe Carabina is competed with it in this respect and these facts will suggest the older origin of the genus.

This genus consists of a large number of species and was subdivided into subgenera. The grouping of species into subgenera has to be revised on the basis of the genitalic characters and of analyses of the distributional pattern.

Genus *Lipaster* MOTSCHULSKY, 1865

Lipaster is the oldest available name for this superficially diversified group which is, however, well defined by the share of conspicuous characters in the male genitalia.

Nobody has attempted to combine seemingly highly specialized *Lipaster* with comparatively featureless *Morphocarabus*, but, apart from certain peculiar features apparently due to macrocephalism, there is actually no particular difference that distinguishes between them, and I propose here to regard them as congeneric on the basis of the similarity in the endophallic characteristics. Of the extragenitalic characters what may suggest the affinity between *Lipaster* and *Morphocarabus* are the multisetosity of pronotum, the lack of sternal sutures with but few exceptions, the features of palpi without sexual differentiation and trisetose metacoxa.

The characteristic features of endophallus which are peculiar to this group are best expressed in the species belonging to the subgenera *Morphocarabus* in the strict sense, *Trachycarabus* in the present sense, *Cyclocarabus* and others. The unique diagnostic character that all the congeneric species share is the presence of a conspicuous inflation of the membraneous walls at the dorsal base of the endophallus. This structure is presumed to be homologous to the membraneous part of the ligula

of the Calosomina, and suggests the relationship between the Calosomes lobés and the present genus.

There are a considerable number of species which I think belong to this genus, though strictly Palaearctic in distribution. At least twenty supraspecific names were proposed for them, but, as mentioned already, nobody has treated these seemingly heterogeneous groups of species as a taxon as in the present sense. In the system proposed by BREUNING (1932), for example, they are distributed among the following subgenera and sectiones:

Subgenus *Carabus* LINNÉ, 1758

Sectio *Eucarabus* GÉHIN, 1885 (part).

Sectio *Trachycarabus* GÉHIN, 1885 (part).

Subgenus *Cyclocarabus* REITTER, 1896

Subgenus *Lipaster* MOTSCHULSKY, 1865

The genus *Lipaster*, as thus defined, is widespread transcontinentally over the temperate and boreal regions of Eurasia, but the component subgenera in the present sense are mostly localized.

Subgenus *Lipaster* MOTSCHULSKY, 1865

Lipaster MOTSCHULSKY, 1865. Bull. Soc. imp. Nat. Moscou, **38**: 296. Type-species: *Carabus stjernwalli* (!) MANNERHEIM, 1830. Desig. by GÉHIN, 1885.

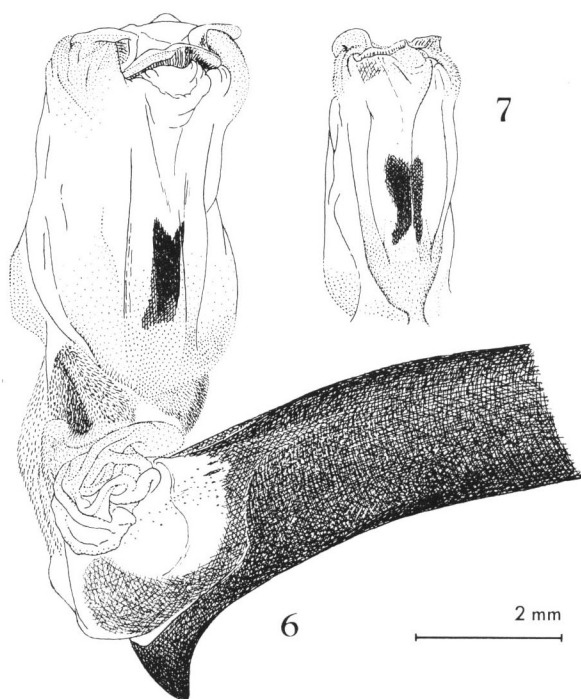
Lamprocarabus C. G. THOMSON, 1875. Opusc. ent., **7**: 639, 673. Type-species: *Carabus humboldti* FALDERMANN, 1835 (= *C. stjernwalli humboldti* FALDERMANN, 1835). Original designation.

Titanocechenus BREUNING et RUSPOLI, 1970. Entomops, **19**: 86. Type-species: *Carabus osellai* BREUNING et RUSPOLI, 1970. Original designation.

BREUNING and RUSPOLI (loc. cit.) established the sectio *Titanocechenus* for the reception of *C. osellai* which was described simultaneously. It is a remarkable carabid with an enlarged head that gives it an appearance resembling *Eupachys* and *Cathaicus*, and the authors combined it with the subgenus *Cechenus*, *sensu* BREUNING.

In reality, however, the characteristic features of the endophallus (Figs. 6, 7) prove its relationships to *L. stjernwalli*, and I was unable to find any reliable morphological difference that distinguishes *Titanocechenus* from *Lipaster* as a discrete supra-specific taxon. Thus, *Titanocechenus* is treated here as a junior synonym of *Lipaster* (see ISHIKAWA, 1978, p. 59). These two species share the following characters:

Head large, scarcely punctate. Labrum not wider than clypeus at base (Fig. 1), its apical margin deeply emarginate. Frons between eyes wrinkled. Eye less convex, distinctly broader than long. Mandible elongate, its outer margin convexly produced before a deep emargination near base; the retinaculum normally bidentate, not fused with the posterior angle of the incisor lobe. Mentum with the median tooth sharply pointed, short, not elevated nor carinated; lateral lobes rounded. Submentum with gular setae. Apical segments of palpi not conspicuously enlarged and no distinct sexual differentiation. Antenna short, the second and the third segments depressed



Figs. 6-7. Male genitalia of the genus *Lipaster* (subgenus *Lipaster*). — 6. *Lipaster* (*Lipaster*) *osellai* (BREUNING et RUSPOLI); Armenia. — 7. *L. (L.) stjernvalli humboldti* (FALDERMANN); Caucasus.

at base where the posterior margins are edged; the hairy segments unmodified in both sexes. Pronotum much broader than long, broadest before middle and conspicuously narrowed behind; lateral rims broad and elevated, higher posteriorly, and set off from the median disc by broad sublateral depressions which become broader and deeper posteriorly to form basal depressions connected by a transverse groove; the anterior margin deeply and subangularly emarginated; 4-5 marginal setae on either side; median line complete, fine but sharply impressed. Elytra elongate oval, without preapical emarginations; sculpture triploid, with intervals rudimentary and with three rows of deep small punctures on each elytron; marginal areas broadly granulate. Hind coxa with three setae. Femora transversely striated in all legs. Sternites without distinctly impressed suture.

Aedeagus subcylindrical, with an end piece broad and rounded at apex. Endophallus (Figs. 6, 7) with an ample inflation of membraneous walls at its dorsal base; dorsal aspect broadly flattened and smooth with a large, oblong pigmented spot; preapical lacinia absent; peripheral rim of gonopore short, but well developed at the dorsal margin.

Lipaster osellai (BREUNING et RUSPOLI, 1970) differs from *L. stjernvalli* (MANNERHEIM, 1830) in larger size, usually multisetose penultimate segment of the labial palpus, more strongly cordate pronotum, less convex elytra with recognizably elevated intervals and with more convex shoulders, and in coloration of the elytra which is more extensively bluish.

Distribution. Caucasus and Armenia.

Subgenus *Morphocarabus* GÉHIN, 1876

- Morphocarabus* GÉHIN, 1876. Cat. Carab., p. 22. Type-species: *Carabus monilis* FABRICIUS, 1792. Desig. by JEANNEL, 1941.
- Promorphocarabus* REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 161. Type-species: *Carabus gebleri* FISCHER, 1817. Present designation.
- Pancarabus* REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 172. Type-species: *Carabus aeruginosus* FISCHER, 1822. Monotypy.
- Apostocarabus* REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 173. Type-species: *Carabus odoratus* MOTSCHULSKY, 1844. Present designation.
- Ancylocarabus* REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 173. Type-species: *Carabus tarbagataicus* KRAATZ, 1878. Monotypy.
- Leptinocarabus* REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 191. Type-species: *Carabus acute-sculptus* CHAUDOIR, 1877 (= *C. venustus* MORAWITZ, 1862). Present designation.
- Gigantocarabus* SEMENOW, 1898. Horae Soc. ent. ross., **31**: 536. Type-species: *Carabus gebleri* FISCHER, 1817. Monotypy.
- Basilicocarabus* LAPOUGE, 1930. Gen. Ins., (192): 269. Type-species: *Carabus regalis* FISCHER, 1822. Present designation.

At least eight names, as enumerated above, were proposed for discriminating superficially least specialized species that constitute the subgenus *Morphocarabus* in the present sense. In the structure of the endophallus, however, they exhibit nothing but different degree of specialization as shown in the Figs. 8–19, and are not separable definitely from one another in this respect. *Leptinocarabus* (Fig. 8) seems to be the least specialized in the endophallic structure, not having even a trace of the lacinia and of the pigmented spot. In *Pancarabus* (Figs. 9–10), the lacinia is indicated by a weak pigmentation, but the pigmented spot is absent. In *L. regalis* (Fig. 11), both the pigmented spot and a trace of the lacinia are constantly developed and this condition seems to be intermediate between *Pancarabus* and *L. gebleri* (Fig. 15) or *L. hummeli* (Fig. 13). The latter two species are considered to belong properly to *Morphocarabus* in the strict sense which is characterized by possession of a well developed pigmented spot and a distinctly lobate lacinia. *Ancylocarabus*, which was established for *Carabus tarbagataicus* KRAATZ (Fig. 19), seems to be absolutely a synonym of *Morphocarabus* as suggested by KRYZHANOVSKIJ (1953, p. 69, and also in personal correspondence) although it was synonymized under *Trachycarabus* by BREUNING. On the other hand, the lacinia is well lobate but the pigmented spot is absent in *L. odoratus* (Fig. 12), for which and for *L. massagetus* (MOTSCHULSKY) the subgenus *Apostocarabus* was proposed.

Although I was able to study only a part of so many species that belong possibly to the subgenus *Morphocarabus* in the present sense, there is little doubt that they are derivatives of a common ancestor; however, there are other complex groups which BREUNING lumped under the sectio *Trachycarabus*. They must be taken into consideration in the classification of this group, because the most of them have quite similar endophallic structures and are doubtlessly congeneric with *Lipaster* as thus defined. By exactly the same reason, *Cyclocarabus* should not be treated separately.

Trachycarabus GÉHIN, 1876, *sensu* BREUNING, 1932

Trachycarabus GÉHIN, 1876 was proposed for the reception of several species including *Carabus scabriusculus* OLIVIER, 1795. BREUNING (1932) included in it a number of superficially diversified species for which at least eleven more names had been proposed as subgenera or sectiones by GÉHIN (1876), REITTER (1896), SEMENOW (1898) and LAPOUGE (1930). This treatment has been accepted by many authors, but the discussions given by him for not recognizing further subdivisions are by no means convincing. He attached too much importance to the existence of seemingly intermediate forms among them. On the other hand, the system proposed by LAPOUGE (1931) is largely artificial so far as these groups are concerned.

In the course of the present study, I have examined the male genitalia of a series of species including the type-species of ten out of twelve supraspecific taxa, which were synonymized by BREUNING under *Trachycarabus*, as follows (the type-species in brackets):

Trachycarabus GÉHIN, 1876 [*Carabus scabriusculus* OLIVIER, 1795. Desig. by BREUNING, 1932]

Mimocarabus GÉHIN, 1876 [*Carabus maurus* ADAMS, 1817. Desig. by GÉHIN, 1885]

Ancylocarabus REITTER, 1896 [*Carabus tarbagataicus* KRAATZ, 1878. Monotypy]

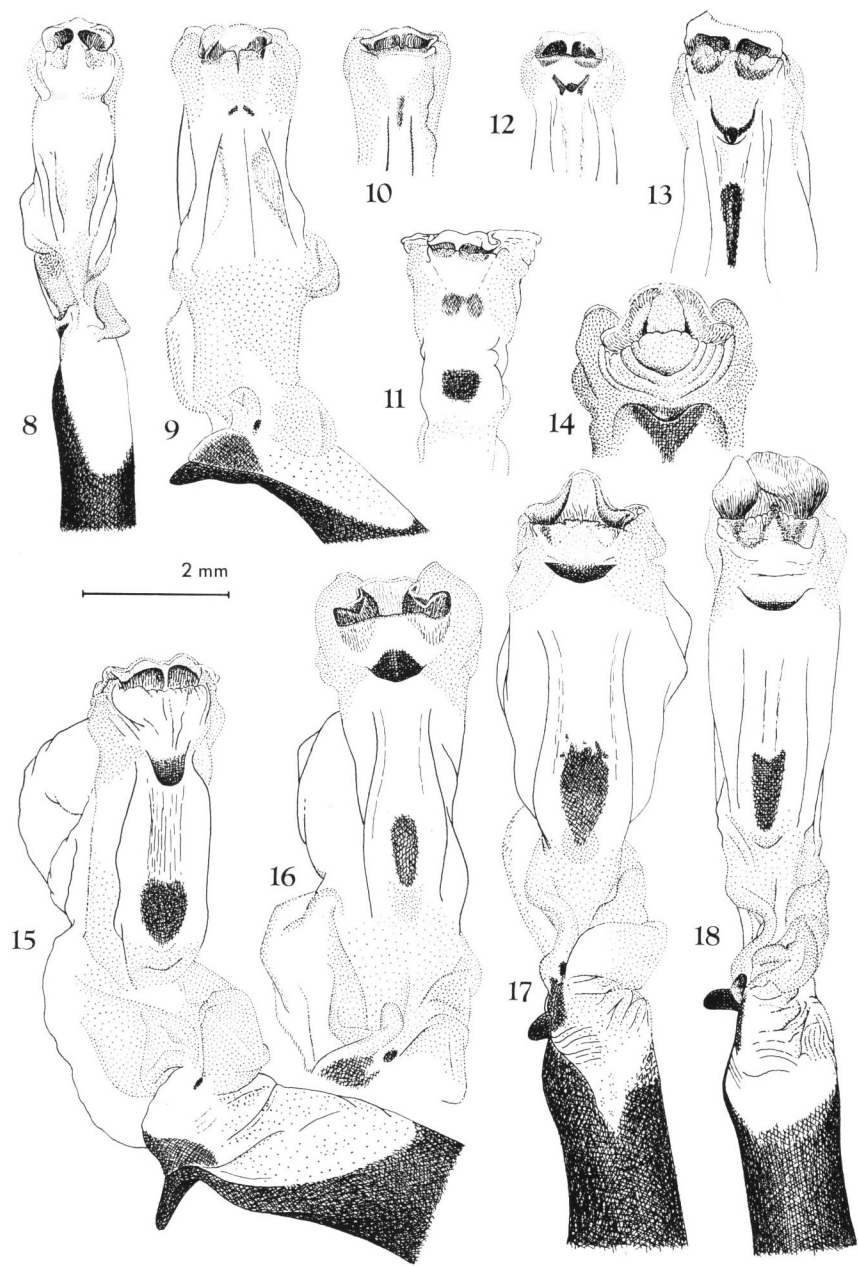
Ophiocarabus REITTER, 1896 [*Carabus striatulus* GÉHIN, 1885. Monotypy]

Cryptocarabus REITTER, 1896 [*Carabus lindemanni* BALLION, 1878. Monotypy]

Semnocarabus REITTER, 1896 [*Carabus regulus* DOHRN, 1882. Monotypy]

Haplocarabus SEMENOW, 1898 [*Carabus confinis* SEMENOW, 1888 (= *C. variabilis*)]

Figs. 8–18. Male genitalia of the genus *Lipaster* (subgenus *Morphocarabus*); the subgeneric names referred in the text are given in the brackets. — 8. *L. (M.) wulffi* (MORAWITZ) [*Leptinocarabus*]; Siberia. — 9. *L. (M.) herrmanni* (MANNERHEIM) [*Pancarabus*]; Russia. — 10. *L. (M.) aeruginosus aerus* (DEJEAN) [*Pancarabus*]; Russia. — 11. *L. (M.) regalis* (FISCHER) [*Basilicocarabus*]; Siberia. — 12. *L. (M.) odoratus septentrionalis* (BREUNING) [*Apostocarabus*]; Siberia. — 13. *L. (M.) hummeli hummeli* (FISCHER) [*Morphocarabus*]; Siberia. — 14. *L. (M.) zawadskii* (KRAATZ) [*Morphocarabus*]; Czechoslovakia. — 15. *L. (M.) gebleri* (FISCHER) [*Promorphocarabus*, *Gigantocarabus*]; Siberia. — 16. *L. (M.) hampei* (KÜSTER) [*Morphocarabus*]; Rumania. — 17. *L. (M.) monilis consitus* (PANZER) [*Morphocarabus*]; Switzerland. — 18. *L. (M.) scheidleri floriani* (PENECKE) [*Morphocarabus*]; Austria.





Figs. 19–29. Male genitalia of the genus *Lipaster*; the subgeneric names referred in the text are given in the brackets. — 19. *L. (M.) tarbagataicus* (KRAATZ) [*Ancylocarabus*]; Siberia. — 20. *L. (Trachycarabus) sibiricus bosphoranus* (FISCHER); Caucasus. — 21. *L. (T.) scabriusculus bulgarus* (LAPOUGE); Rumania. — 22. *L. (Haplocarabus) variabilis* (BALLION) [*Ophiocarabus*]; Tien-shan, Central Asia. — 23. *L. (Mimocarabus) maurus maurus* (ADAMS); Transcaucasus. — 24. *L. (Acrocarabus) guerini* (FISCHER); Alatau, Central Asia. — 25. *L. (Cryptocarabus) lindemanni* (BALLION); Wernyi, Central Asia. — 26. *L. (Microcarabus) subparallelus* (BALLION) [*Cryptocarabus*]; Alatau, Central Asia. — 27. *L. (Lyperocarabus) estreicheri* (FISCHER); European Russia. — 28. *L. (Ophiocarabus) striatulus* (GÉHIN); Tien-shan, Central Asia. — 29. *L. (Cyclocarabus) martynovi* (SEMENOV et ZNOJKO); Turkestan.

BALLION, 1878). Monotypy]

Acrocarabus LAPOUGE, 1930 [*Carabus guerini* FISCHER, 1842. Monotypy]

Lyperocarabus LAPOUGE, 1930 [*Carabus estreicheri* FISCHER, 1822. Present designation]

Anthracocarabus LAPOUGE, 1930 [*Carabus erosus* MOTSCHULSKY, 1865. Desig. by KRYZHANOVSKI, 1953]

Semnocarabus and *Anthracocarabus* must be excluded from here. They are different from others under consideration in having a well developed, bilobate ostium lobe, characteristic features of the peripheral rim of gonopore (Fig. 30), and in not having a basal inflation of the membranous walls at the dorsal base of the endophallus. They belong properly to the Multistriati as I stated already (ISHIKAWA, 1978).

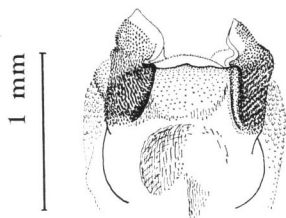


Fig. 30. Apical part of the endophallus of "*Anthracocarabus*" *erosus erosus* (MOTSCHULSKY), in which the dorsal margin of the peripheral rim of gonopore is not produced to form an aggonoporiis. This is a feature characteristic of major groups of the Multistriati.

All the others have in common a characteristic membranous inflation at the dorsal base of the endophallus, a unique structure that suggests their relationship to *Lipaster* in the present sense. Of these, *Ancylocarabus* is considered a synonym of *Morphocarabus* as discussed already, but *Trachycarabus*, *Mimocarabus* and *Haplocarabus* are also closely similar to it in the endophallic structure in having a well developed lacinia and a conspicuous pigmented spot as shown in Figs. 19–23. Notwithstanding their diversity in the extragenitalic features which seems to make it difficult to distinguish them into clearly defined supraspecific taxa as BREUNING stated, the structure of genitalia, of endophallus in particular, is not so diversified, and the species assigned to the sectio *Trachycarabus* by him seem to fall into well defined groups by the genitalic characters. These groups, which I have treated here provisionally as subgenera may be distinguished synoptically as follows:

- 1 (4) Lacinia not lobate nor outlined.
- 2 (3) No pigmented spot nor streaks on dorsal aspect of endophallus
.....Subgenera *Microcarabus* ISHIKAWA, nov. (Fig. 26),
and *Acrocarabus* LAPOUGE (Fig. 24).
- 3 (2) A pair of pigmented streaks present near apex of the dorsal aspect of the
endophallus where it is not outlined to form a lacinia
.....Subgenus *Lyperocarabus* LAPOUGE (Fig. 27).
- 4 (1) Lacinia lobate or at least distinctly outlined.
- 5 (8) Pigmented spot absent.
- 6 (7) Peripheral rim of gonopore normally developed dorsally to form an ag-
gonoporiisSubgenus *Ophiocarabus* REITTER (Fig. 28).

- 7 (6) Peripheral rim of gonopore very short at the dorsal margin and barely forming an aggonoporiis.....
Subgenus *Cryptocarabus* REITTER (Fig. 25).
- 8 (5) Pigmented spot well developed.....
Subgenera *Mimocarabus* GÉHIN (Fig. 23),
Haplocarabus SEMENOW (Fig. 22),
 and *Trachycarabus* GÉHIN (Figs. 20, 21).

Haplocarabus, which comprises only one representative species *variabilis* BALLION, is distinct from *Ophiocarabus* with which KRYZHANOVSKIJ (1953) combined it. Its endophallus (Fig. 22) is similar to that of *Trachycarabus*, but shorter and robuster with a larger aggonoporiis; the lacinia is well outlined and marked with a marginal pigmentation but not lobate; the pigmented spot large and broadly contiguous to the pigmentation of the area of the lacinia.

Ophiocarabus is similar to *Haplocarabus* in the endophallic structure, but in *striatulus* GÉHIN (Fig. 28), the only species I have seen, the lacinia is more elongate and lobate apically, without a pigmented spot, and the basal inflation of the membrane is not so distinctly lobate as in *variabilis*.

Mimocarabus (Fig. 23) seems to be a well defined group, with a broad peripheral rim of gonopore that forms an aggonoporiis, a broad, triangularly lobate lacinia and an elongate pigmented spot.

Cryptocarabus (auctt.) comprises two distinct groups of species and they should be discriminated. The type-species, *lindemanni* BALLION (Fig. 25), has the endophallus of peculiar structure not found in any other species of the related groups. The peripheral rim of gonopore of this species is so inconspicuous at the dorsal margin that the aggonoporiis is not differentiated as a pleated collar, but there is a pair of longitudinal broad pigmented depressions near apex; a lobate lacinia is developed, but no pigmented spot. I have examined, besides *lindemanni*, *subparallelus* BALLION and *kirghisorum* KRYZHANOVSKIJ. In the latter two species (Fig. 26), the endophallus has a normal aggonoporiis as in *Mimocarabus*, but lacks a trace of the lacinia and of the pigmented spot, with a small shoulder-like membranous angulation on either side of the dorsal aspect. I propose for them the subgenus *Microcarabus* nov. (type-species: *Carabus subparallelus* BALLION, 1878 by present designation).

Lyperocarabus LAPOUGE, 1930 is used here for a unique *Carabus estreicheri* FISCHER (Fig. 27) as the type-species which is distinct in having a pair of pigmented stripes near apex on the dorsal aspect of the endophallus and there is a minute membranous projection between the stripes instead of a lobate lacinia to which it may be homologous. Pigmented spot is also absent. Apparently, *Lyperocarabus* is a discrete taxon so far as the endophallic structure is concerned.

Acrocarabus seems to be the most peculiar and distinct of all the related groups, if the species belonging to this group share the same endophallic characters with the type-species, the sole representative species I was able to study. It has a shorter

endophallus (Fig. 24) with an aggonoporiis similar to that of *Trachycarabus*, *Mimocarabus*, etc., without even a trace of the lacinia and of the pigmented spot, with a well developed, differentiated basal lobe on the left side of the ligula resembling the paraligula of *Deuterocarabus*; moreover, the dorsal margin of the endophallus is longitudinally elevated towards the base where it is terminating in a projection before the ligula.

Thus, the supraspecific names proposed for a variety of species seem to represent mostly well defined species-groups, but the species that I have been able to study are not yet quite sufficient in number to prove their discreteness, so that they are treated here as subgenera of the genus *Lipaster* provisionally as enumerated below, with the species examined being given in the brackets.

Subgenus *Trachycarabus* GÉHIN, 1876 [*besseri* FISCHER, 1822; *bosphoranus* FISCHER, 1824; *haeres fossulatus* DEJEAN, 1826; *mandibularis* FISCHER, 1828; *sibiricus* FISCHER, 1822; *scabriusculus scabriusculus* OLIVIER, 1795; *scabriusculus bulgarus* LAPOUGE, 1908]

Subgenus *Haplocarabus* SEMENOW, 1898 [*variabilis* BALLION, 1878]

Subgenus *Mimocarabus* GÉHIN, 1876 [*maurus maurus* ADAMS, 1817; *maurus hochhuthi* CHAUDOIR, 1846; *pumilio* KÜSTER, 1846; *elbursensis* BREUNING, 1947]

Subgenus *Ophiocarabus* REITTER, 1896 [*striatulus* GÉHIN, 1885]

Subgenus *Lyperocarabus* LAPOUGE, 1930 [*estreicheri* FISCHER, 1822]

Subgenus *Cryptocarabus* REITTER, 1896 [*lindemanni* BALLION, 1878]

Subgenus *Microcarabus* ISHIKAWA, nov. [*subparallelus* BALLION, 1878; *kirghisorum* KRYZHANOVSKIJ, 1953]

Subgenus *Acrocarabus* LAPOUGE, 1930 [*guerini* FISCHER, 1842]

Further studies in the genitalic characters of a larger number of species are desirable for a more sound classification of these groups including the species belonging to the subgenus *Cyclocarabus* which is discussed below.

Subgenus *Cyclocarabus* REITTER, 1896

Cyclocarabus REITTER, 1896. Verh. naturf. Ver. Brünn, **34**: 169. Type-species: *Carabus mnischechi* REITTER, 1896 (nec CHAUDOIR, 1852) (= *C. namanganensis* HEYDEN, 1886). Monotypy.

Cyclocarabus has been regarded as a discrete group because of its specialized external features. The endophallus (Fig. 29) is, however, exactly the same as that of *Morphocarabus*-*Trachycarabus* group, and there is no fundamental difference between them in its highly specialized structure.

Cyclocarabus is a small group of homogeneous species restricted to the steppe region of Turkestan in Central Asia. The principal characteristic features are the shape of mandibles, of labrum as shown in Fig. 2 and degenerated elytral sculpture, but they are considered to be adaptational to peculiar ecological condition and possibly to specialized food habits. At least, there is no inevitable morphological difference

that may evidence its phylogenetic discreteness from *Trachycarabus* despite their identity in the endophallic structure. It will be a mere isolated branch of specialized forms derived from the common ancestor with *Trachycarabus* or its related groups, and I regard *Cyclocarabus* as a subgenus of *Lipaster*. KRYZHANOVSKIJ (1953) included it in the Carabi longimandibulares, but this combination does not seem to have been made properly.

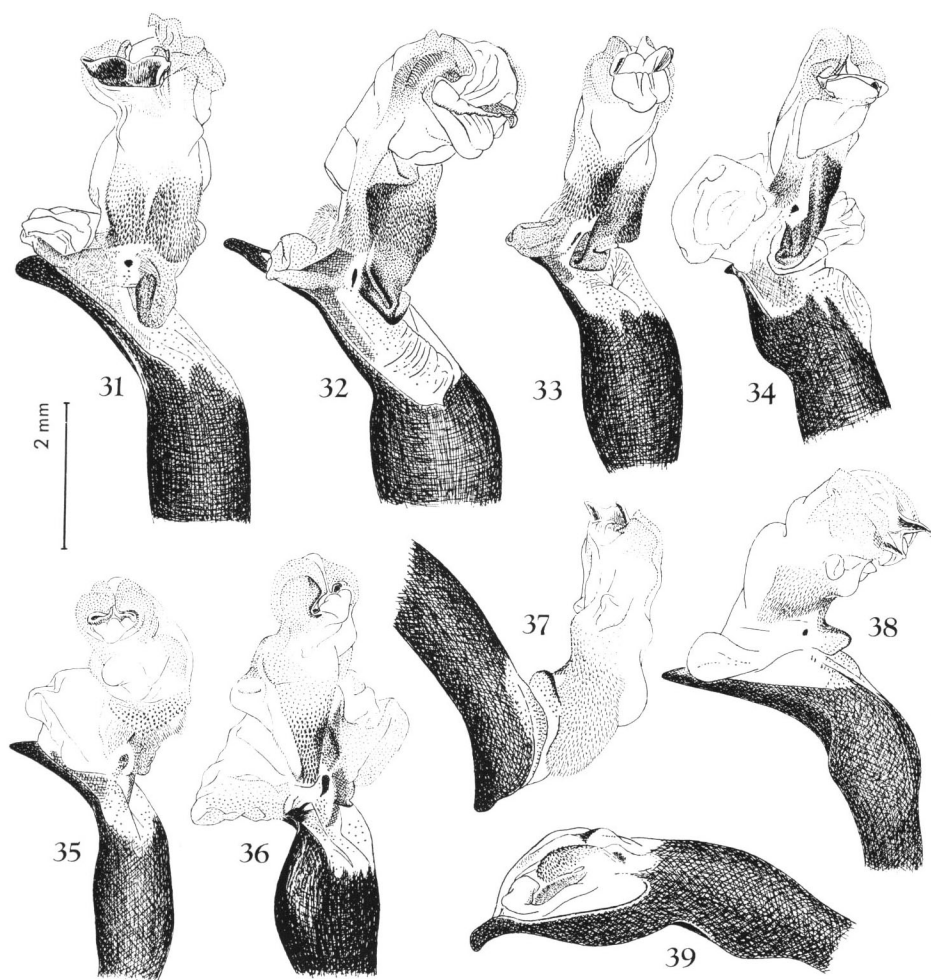
Genus *Ischnocarabus* KRAATZ, 1877

- Ischnocarabus* KRAATZ, 1877. Dtsch. ent. Z., 21: 78–80. Type-species: *Ischnocarabus tenuitarsis* KRAATZ, 1877. Original designation.
Archicarabus SEIDLITZ, 1887. Fauna baltica, ed. 2, Arten p. 6. Type-species: *Carabus nemoralis* MÜLLER, 1764. Monotypy.
Deutero-carabus REITTER, 1896. Best.-Tab. eur. Coleopt., Carab., pp. 141, 179. Type-species: *Carabus montivagus* PALLIARD, 1825. Present designation.
Aptocarabus REITTER, 1896. Best.-Tab. eur. Coleopt., Carab., p. 94. Type-species: *Carabus rossii* DEJEAN, 1826. Monotypy.

The genus *Ischnocarabus* in the present sense comprises the species which have been distributed among above mentioned subgenera by authors. The latter three have usually been regarded as related groups, but nobody has combined them with seemingly highly specialized *Ischnocarabus*. The systematic position of *Ischnocarabus* in the strict sense differs according to authors: KRAATZ (1877) and LAPOUGE (1930) compared it with *Lamprostus* and *Lipaster*, but BREUNING (1935) presumed its affinity with *Procrustes*. Either of these presumptions may have reasonable bases on the extragenital characters, but so far as the genitalic characters are concerned, it belongs evidently to the Carabogenici and appears to be most closely related to *Deutero-carabus*. Except for some peculiar cephalic features that characterize *Ischnocarabus*, however, there seem to be few extragenital characters that distinguish this group decidedly from *Archicarabus*, *Deutero-carabus* and *Aptocarabus*.

BREUNING (1932) treated *Archicarabus* as a sectio of the genus *Carabus* and included therein *Aptocarabus*, *Deutero-carabus* and *Rhipocarabus* as synonyms. JEANNEL (1941), however, combined *Archicarabus* with the genus *Orinocarabus* as a subgenus of the latter, and synonymized *Tomocarabus*, *Euporocarabus* and *Phricocarabus* under *Archicarabus*, but transferred *Aptocarabus* to *Hadrocarabus* (= *Mesocarabus*) as a synonym. As regards the endophallic structure, *Tomocarabus*, *Euporocarabus*, *Phricocarabus* and *Orinocarabus* belong doubtlessly to the Multistriati, and *Rhipocarabus* with the unique type-species *Carabus alysidotus* ILLIGER, also has characteristics of the Multistriati, although its endophallus is unusually modified. JEANNEL's treatment of *Aptocarabus* involves a double mistake owing to his wrong presumption that *rossii* DEJEAN is congeneric with *genei* GENÉ which he thought to belong to *Hadrocarabus*. In reality, however, *genei* is not a *Hadrocarabus* at all but an *Eurycarabus* as stated properly by CASALE and STURANI (1977).

All the species belonging to this genus (Figs. 5, 31–39) have in common a narrower



Figs. 31–39. Male genitalia of the genus *Ischnocarabus*. — 31. *I. (Aptocarabus) rossii* (DEJEAN); Italy. — 32. *I. (Deutero-carabus) wiedemanni wiedemanni* (MÉNÉTRIÉS); Anatolia. — 33. *I. (D.) congruus akkusanus* (BREUNING); Anatolia. — 34. *I. (D.) montivagus blandus* (FRIVALDSKY); Hungary. — 35. *I. (Archicarabus) monticola monticola* (DEJEAN); France. — 36. *I. (A.) nemoralis pseudomonticola* (LAPOUGE); France. — 37 & 38. *I. (Ischnocarabus) tenuitarsis* (KRAATZ); Anatolia. — 39. *I. (I.) cycchropalpus* (PEYRON); Anatolia.

preostium. In the species belonging to *Ischnocarabus* s. str. (Figs. 37–39), *Deutero-carabus* (Figs. 32–34) and *Aptocarabus* (Fig. 31), endophallus has a conspicuous paraligula which covers ostium as an elongate flap when the endophallus is withdrawn (Fig. 39), but this structure is inconspicuous in *Archicarabus* (Figs. 35–36). The ventral base of the endophallus has a membraneous inflation of which size and

structure are highly characteristic of species. The peripheral rim of gonopore forms an aggonoporiis whose feature is peculiar to each species. Preapical areola is well outlined and occasionally lobate though not at all differentiated in *Aptocarabus* (Fig. 31), of which peripheral rim of gonopore is very asymmetrical laterally, but forms a conspicuous aggonoporiis on the dorsal margin. These endophallic characters and their combinations distinguish these groups from one another fairly definitely, and their contiguous, though mostly allopatric, distribution as they show also suggest their distinctness as well as their affinity. It seems to be reasonable to regard them as subgenera of *Ischnocarabus* on the basis of these genitalic characters as summarized in the following key:

- 1 (4) Preapical areola distinctly outlined, convex or tongue-like; peripheral rim of gonopore symmetrical.
- 2 (3) Paraligula at most rudimentary; aggonoporiis short, barely projecting . .

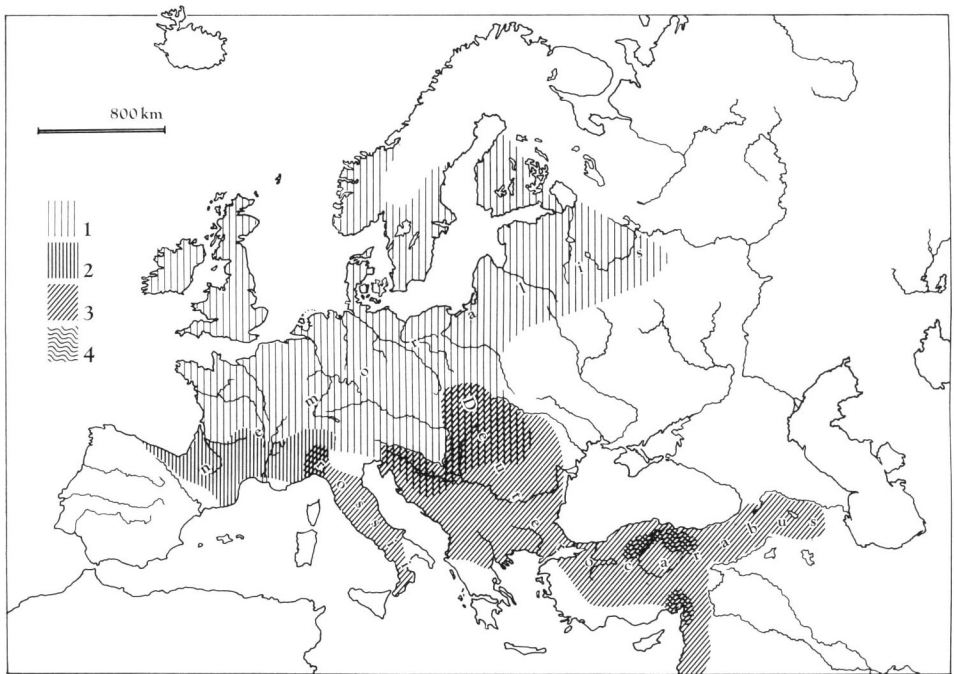


Fig. 40. Distribution of the genus *Ischnocarabus*. — 1. The secondary range of the genus established by *I. nemoralis nemoralis*; 2, 3 & 4, the primary range of the genus; 2, the range of the subgenus *Archicarabus* exclusive of *I. nemoralis nemoralis* and *I. (?) steuarti* which I have not seen; 3, the ranges of the subgenus *Deuterocarabus* and of the subgenus *Aptocarabus* which is represented by only one species *I. rossii*; 4, the range of the subgenus *Ischnocarabus*. (Data from: BLUMENTHAL, 1976; BREUNING, 1932–1937; HEINZ, 1977; JEANNE, 1970; JEANNEL, 1941; LAPOUGE, 1929–1932; MACHARD, 1974; TURIN, HAECK & HENGEVELD, 1977, etc.)

-Subgenus *Archicarabus* SEIDLITZ (Figs. 35, 36).
- 3 (2) Paraligula conspicuously lobate; aggonoporus well differentiated and projectingSubgenera *Ischnocarabus* KRAATZ (Figs. 37–39) and *Deutero-carabus* REITTER (Figs. 32–34).
- 4 (1) Preapical areola not at all differentiated; peripheral rim of gonopore asymmetrical with the aggonoporus strongly developed; paraligula conspicuously lobateSubgenus *Aptocarabus* REITTER (Fig. 31).

The genus *Ischnocarabus* is distributed over the greater part of Europe and Asia Minor (Fig. 40), but its primary range should be delimited to the region along the Mediterranean coast, the Balkan Peninsula so far north to the Carpathians, and Asia Minor so far east nearly to the Caspian Sea, because the rest of its range is occupied by only one, nominate subspecies of *I. nemoralis* which shows little geographical variation and is considered to have become established there rather recently. *I. nemoralis* is varied in south France where a number of subspecies have been described.

The subgenera as here recognized are distributed nearly allopatrically within the range of the genus if the secondary range is ignored, and there is little doubt that they became distinct as a result of simple allopatric differentiation. The largest subgenus *Deutero-carabus* seems to have had major differentiation at the species level in Asia Minor possibly after the separation from the subgenus *Ischnocarabus*. The subgenera *Aptocarabus* of Italy and *Archicarabus* of southern France must have established themselves the present ranges quite independently.

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