

## A Revision of the Higher Taxa of the Subtribe Carabina (Coleoptera, Carabidae)

By

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A remarkable differentiation at the species and subspecies level in the subtribe Carabina is considered to be owing largely to the degeneration of hind wings that restricted their possibilities of dispersal and thereby intensified the effect of geographical segregation among them. Notwithstanding their superficial diversity in form and color, there are actually few morphological features which should be used for grouping species into supraspecific taxa of the subtribe; most of the characters so far used are in reality features of simple structure which may vary adaptationally even at the species level. Naturally, therefore, the estimation of these features as taxonomic characters is different according to authors, as shown by the fact that the principal systems proposed by THOMSON (1875), REITTER (1896), LAPOUGE (1931–1932), BREUNING (1932–1937), etc. differ from one another so remarkably; nevertheless they were established practically upon the same sorts of characters. It is required, accordingly, to found a system on more reliable, if possible, characters of complex structure than those of simple one on which existing systems are exclusively based.

The present study on the subtribe Carabina was intended primarily to revise some genera and subgenera of seemingly mere assemblage of heterogeneous species on the basis of the genitalic characters rather than the extragenitalic ones of traditional use. The first provisional part was already published (ISHIKAWA, 1973) and this is an extension of it. Since that time, I have been able to examine a large number of additional species representing the great majority of genera, subgenera and sectiones so far established, and came to be convinced that the taxa of suprageneric level should also be revised. In the present paper, discussions on the taxonomic significance of the genitalic and extragenitalic characters are given, and, as a conclusion, a new system for the subdivisions of the subtribe is proposed. The revisional studies of the genus and species level upon which this conclusion is based are too lengthy to be included here, but will be published separately in succession.

Before going further, I must express my gratitude to entomologists who supported me in the course of the present study. I am most greatly indebted to Mr. Carl L. BLUMENTHAL, Troisdorf, Germany, because this study would have never been attempted but for his friendly support in many ways for nearly twenty years. Mr. Walter HEINZ, Wald-Michelbach, Germany, offered to me so generously valuable specimens

of great taxonomic importance which were not otherwise possible to get, and also took trouble of copying literature for me. Dr. Stephan BREUNING, Paris, and Dr. Karl MANDL, Wien, both authorities who have founded the basis of the modern carabology, kindly sent me a number of specimens and publications which were indispensable to this study. As to the material of the USSR, I am obliged to Dr. O. L. KRYZHANOVSKIJ, Leningrad, who gave me opportunities to examine a series of Asiatic species of taxonomic importance which were not accessible in other ways. Mr. Toku WATANABE, Sendai, kindly kept for my study a drowned pair of *Carabus insulicola* in copula which evidenced my presumption of the function of the copulatory organs as mentioned in the text.

Finally, I have to thank Dr. Yoshihiko KUROSAWA and Dr. Shun-Ichi UÉNO of the National Science Museum, Tokyo, for their friendly help in various ways ever since I began taxonomic studies of the Carabina.

### **Taxonomic Significance of Endophallic Characters**

The use of the endophallic characters as taxonomic bases was attempted in my studies primarily for the simple reason that the basic structure of the endophallus is remarkably similar among related species particularly those which range close together within certain geographically defined areas. Although sclerotized parts of the male genitalia, such as the aedeagus, the copulatory piece and others have been used as taxonomic characters for discriminating among species or subspecies, they are not more than components of the organ and too simple structurally to characterize higher taxa because of a resemblance in their features alone. On the other hand, the male copulatory organ as a whole, the endophallus in particular, has so elaborate an external structure including the sclerotized parts that a resemblance in it between taxa, if any, cannot be regarded simply as the result of convergence or coincidence, but is considered more properly to evidence their phylogenetic relationship provided that the homology of the component parts is established. This judgement is based, however, primarily upon a hypothesis that the more complex a structure the taxa have in common, the higher its reliability is as a character to evidence the affinity between them. It does not mean, therefore, that the extragenital characters are less significant taxonomically than the genitalic, but, in reality, most of them are features of simple structure, and difference in them for taxonomic use is not more than the difference in the degree of specialization in certain parts of body, so only a share of them in common is not always sufficient to evidence an affinity between taxa unless presence of any correlation with other, more reliable character is established. In this respect, the endophallus is the most compact unit of characters that constitute an intromittent apparatus and work together in one body. It is my opinion that the likeness in the basic structure of endophallus between taxa, if any, is one of the most reliable morphological bases that suggest their relationship, whereas simple extragenital characters are apparently more circumstantial, and only supplementary to the

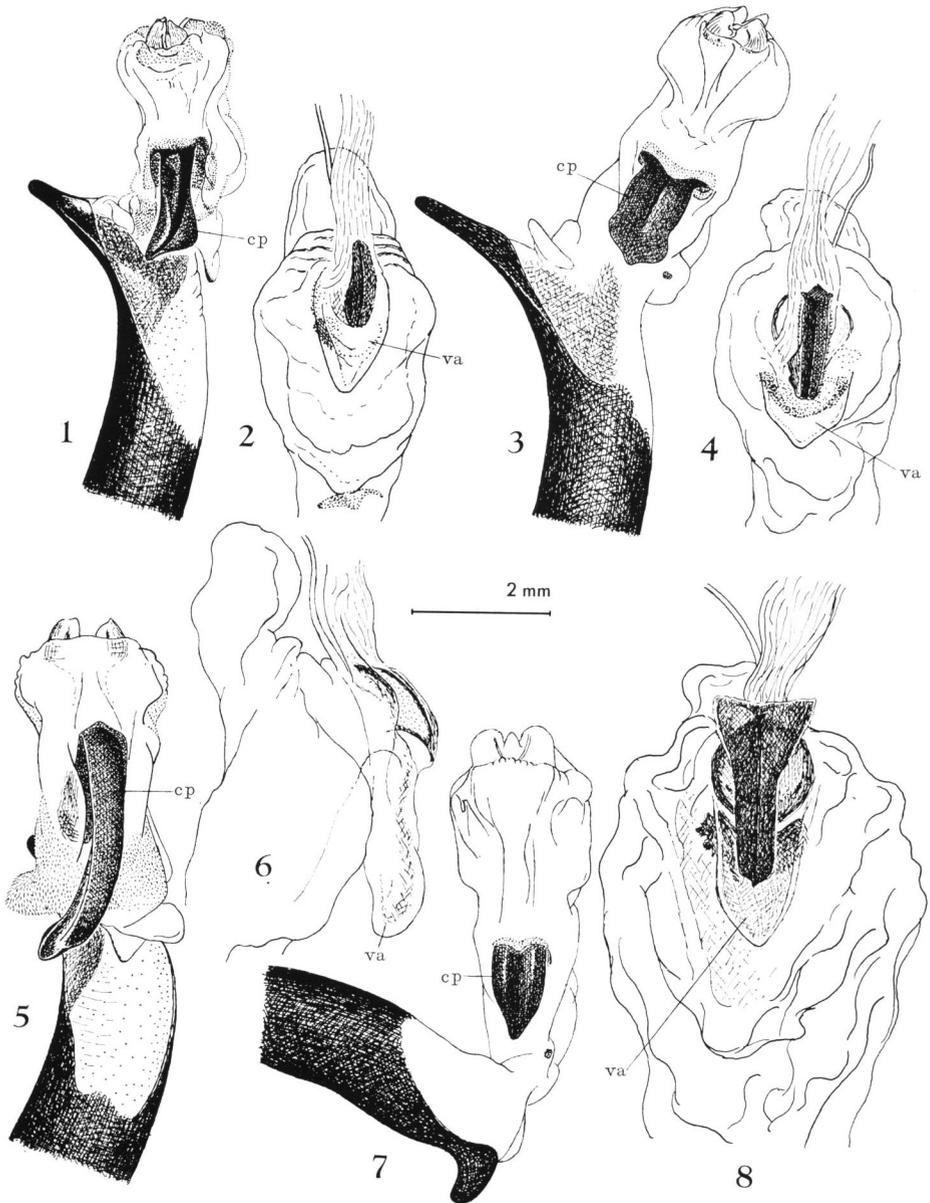
genitalic ones, at least as characters for grouping species into higher taxa.

It should not be overlooked that their structures are greatly concerned with their function. In the Carabina, the endophallus is the real copulatory organ of male that works as an intromittent apparatus. Its size and the peculiar shape, if any, are presumed to take part in fitting itself with the female copulatory receptacle of the same species or subspecies during copulation. Possibly, the characteristic features of the endophallus have the same relationship to those of the vagina as the serration of a key does to its lock. I was able to confirm the lock and key relationship in *Carabus (Ohomopterus) insulicola insulicola* CHAUDOIR by dissecting a pair in copula which died by drowning in a baited trap. In this case, both the copulatory organs were combined in exactly the same condition as I illustrated (ISHIKAWA, 1973, p. 209). In the subgenus *Ohomopterus*, the female copulatory receptacle, the vagina, bears a membranous pocket termed the vaginal appendix which is correlated in size and shape with the copulatory piece of the male of the same species or subspecies (Figs. 1–8). These parts of the copulatory organs exhibit the utmost development in *C. (O.) uenoi* ISHIKAWA (see ISHIKAWA, 1973, p. 210). Thus, there is little doubt in that these structures of the copulatory organs would work for segregation of lower taxa in this group of species. Similar morphological correlation both in size and shape between the male and female copulatory organs exists in some other genera or subgenera. Notable examples are found in the species belonging to *Sphodristocarabus* (Figs. 9–18), *Tribax* (Figs. 19–28) and *Neoplectes*. In these groups of species, at least, the copulatory organs are supposed to play an important part in the reproductive isolation which is considered to work eventually for differentiation in diverging populations. Naturally, therefore, their features seem to have considerable taxonomic significance also as characters at the species level. Another important nature of these characters to be noted is that the endophallus does not possibly change itself without structural correlation to the female copulatory receptacle as its counterpart. In this respect, the copulatory organs differ from other functional structures in that their morphological modifications cannot be considered to be an adaptation to other environmental factors, but more possibly be a result of reciprocal correlation of the organs between the opposite sexes of the same species or subspecies.

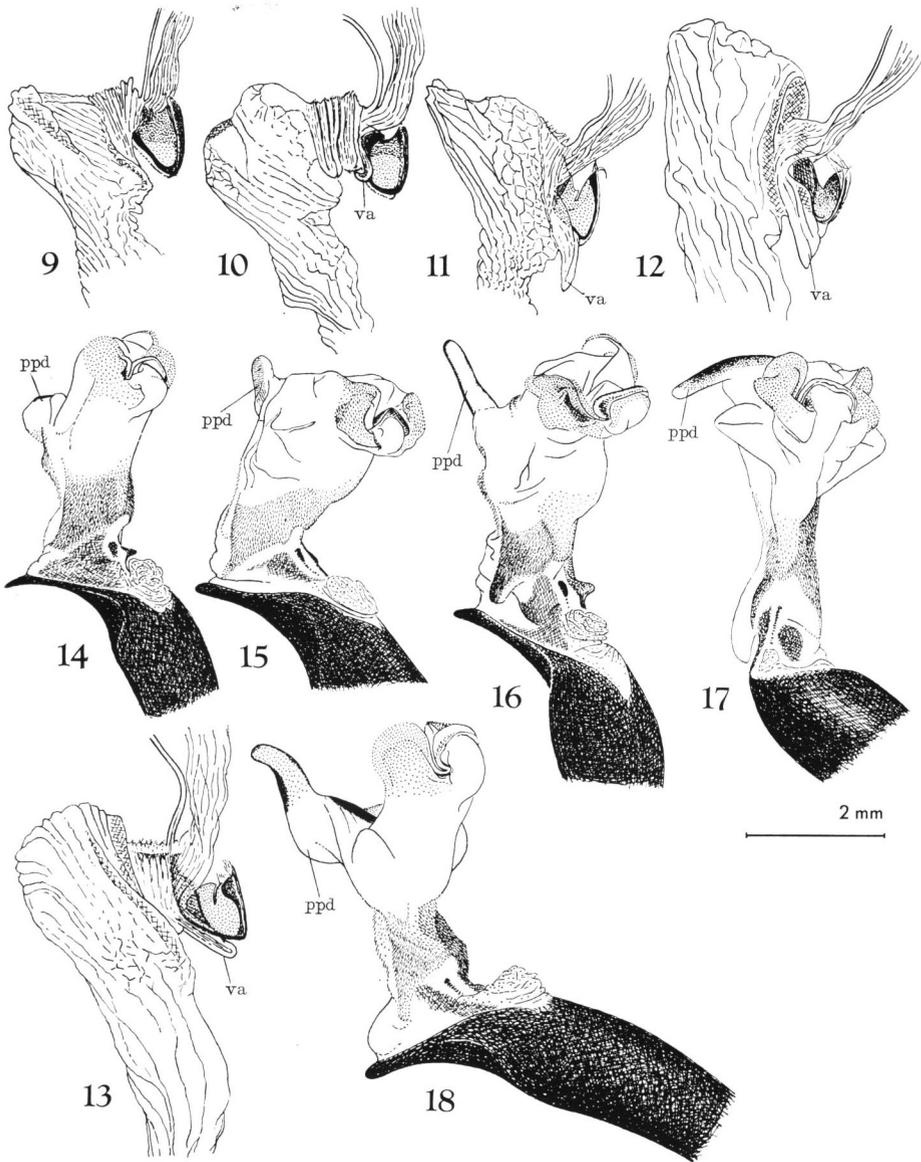
It is my conclusion that the genitalia as a whole, not their component parts, bear useful and significant taxonomic characters not only for separating between superficially resembling taxa of species or subspecies level by different features of their component parts but also for grouping them into higher taxa, at least those just above the species level, such as subgenera or genera, by the resemblance in their basic structure.

### Genitalic Characters for Subdivisions of the Carabina

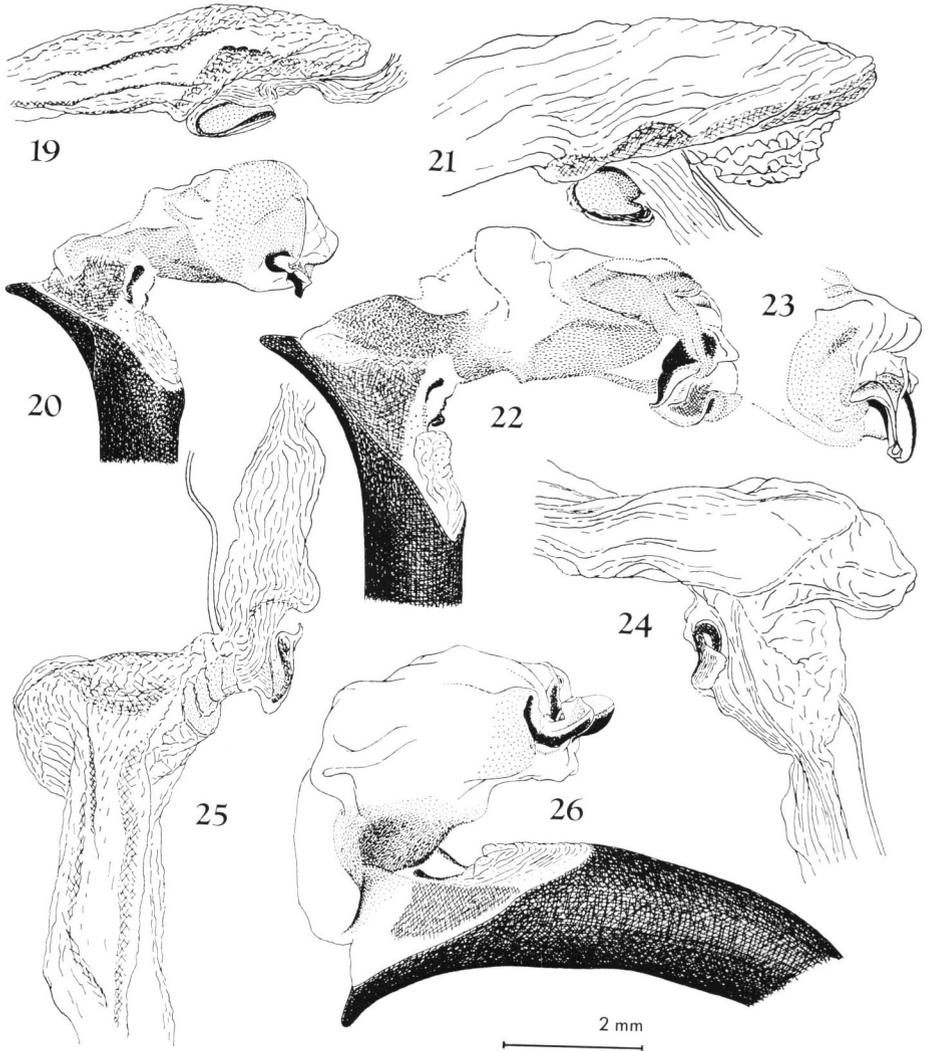
No attempt has been made to classify suprageneric taxa of the Carabina on the basis of the genitalic characters doubtless because the membranous parts of them



Figs. 1-8. Copulatory organs of *Carabus* (subgenus *Ohomopterus*) in which the copulatory piece (cp) corresponds in size and shape with the vaginal appendix (va) of the same species or subspecies; 1, 3, 5 & 7, aedeagi with the endophalli everted; 2, 4, 6 & 8, vaginæ. — 1 & 2, *C. (O.) esakii* CSIKI; 3 & 4, *C. (O.) yaconinus* BATES; 5 & 6, *C. (O.) insulicola* CHAUDOIR; 7 & 8, *C. (O.) dehaanii tosanus* NAKANE *et al.*



Figs. 9-18. Copulatory organs of *Sphodristocarabus* in which the praeputial pad (ppd) of the endophallus shows a tendency to become digitate, and it corresponds in length with the vaginal appendix (va) of the same species or subspecies; 9-13, vaginae; 14-18, aedeagi with the endophalli everted. — 9 & 14, *S. esperanzae esfandarii* HEINZ; 10 & 15, *S. macrogonus schweigerinae* SCHWEIGER; 11 & 16, *S. separatus persa* LAPOUGE; 12 & 17, *S. sovitzi gilnicki* DEYROLLE; 13 & 18, *S. tokatensis* ROESCHKE.



were overlooked or neglected. NAKANE (1960) suggested the polyphyletic origin of the Carabina because of diversified features of male genitalia in this group, but did not propose any concrete system for them on these characters. As a matter of fact, there are few single features of the male genitalia which seem to be absolutely diagnostic all alone for subdivisions of the Carabina just below the subtribe level, yet, examinations of the genitalia of the great majority of species made it evident that the features of the ligula and of the preostium, whether there is an ostium lobe or not, are a useful diagnostic character for grouping genera into three major subdivisions, with but few exceptions at the species or subspecies level.

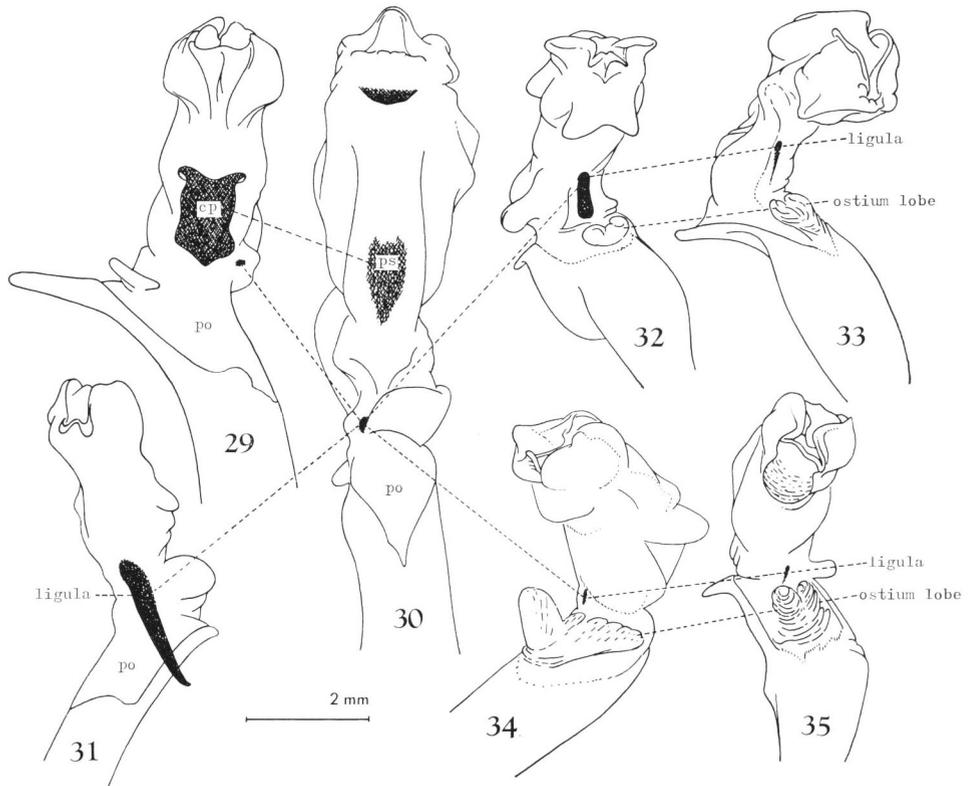


Figs. 19–28 (on pp. 50–51). Copulatory organs of *Tribax* in which the endophallus corresponds in size with the vagina of the same species; 19, 21, 24, 25 & 27, vaginae; 20, 22, 26 & 28, aedeagi with the endophalli everted; 23, apical part of the endophallus. — 19 & 20, *T. puschkini* ADAMS; 21 & 22, *T. platessa platessa* MOTSCHULSKY; 23 & 24, *T. circassicus justinae* REITTER; 25 & 26, *T. biebersteini ishikawaianus* BREUNING et RUSPOLI; 27 & 28, *T. agnatus* GANGLBAUER.

The species that do not bear an ostium lobe in the preostium (Figs. 29–31) constitute a group which corresponds approximately to the Carabi carabogenici (*sensu* BREUNING=Carabogéniens LAPOUGE, 1931); whereas the species that bear an ostium lobe (Figs. 32–35) constitute another well defined group which comprises the Carabi multistriati (*sensu* BREUNING=Multistriés LAPOUGE, 1931>Carabi multistriati REIT-

TER, 1896) and the Carabi longimandibulares (*sensu* BREUNING=Psilogoniens+Pliochètes+Tribacogeniens LAPOUGE, 1931).

The Carabi carabogenici are, however, not a homogeneous group and should be subdivided further into two groups by the feature of the ligula of the male genitalia.



Figs. 29–35. Homology of the component parts of the male genitalia; cp, copulatory piece; ps, pigmented spot; po, preostium. — 29, *Carabus (Ohomopterus) yaconinus* BATES; 30, *Lipaster (Morphocarabus) monilis consitus* PANZER; 31, *Apotomopterus (Limnocarabus) clathratus* LINNÉ; 32, *Oreocarabus glabratus* PAYKULL; 33, *Pachystus cavernosus variolatus* COSTA; 34, *Procrustes (Procrustes) chevrolati persimilis* CSIKI; 35, *Macrothorax rugosus baeticus* DEYROLLE.

The species with a prominent spine-like ligula (Fig. 31) differ in many respects from those of which the ligula is greatly reduced (Figs. 29–30). I propose a name *Spinulati* m. (=genus *Apotomopterus* HOPE, 1838, *sensu* ISHIKAWA, 1973) for the former group of species because of their peculiar shape of the ligula and the latter group of species remains as the Carabogenici of the present sense.

As thus defined, the Carabi brevimandibulares that consist of the Carabi carabogenici and the Carabi multistriati do not seem to be a natural group so far as the

genitalic characters are concerned. On the other hand, the Carabi multistriati are doubtlessly more closely related to the Carabi longimandibulares than to the Carabi carabogenici, not only in having the ostium lobes in common but also in other morphological characteristics as discussed in the following chapters.

### Cephalic Characters for the Higher Taxa of the Carabina

Different classification of the Carabina have been attempted by former workers, but the most commonly accepted system is the one by BREUNING (1932) who subdivided the genus *Carabus* (s. l.) into two groups by the characters as given below:

“Mandibeln kurz, meist breit, am Innenrande ziemlich gerade, erst am ende jäh nach innen gebogen und zugespitzt. . . . Bei den Larven der Clypeus am Voderrand mit 4–5 mehr oder weniger gleichmässigen Zähnen oder dieselben zuweilen mehr oder weniger verschmolzen, die beiden äusseren jedoch vorher nicht reduziert.

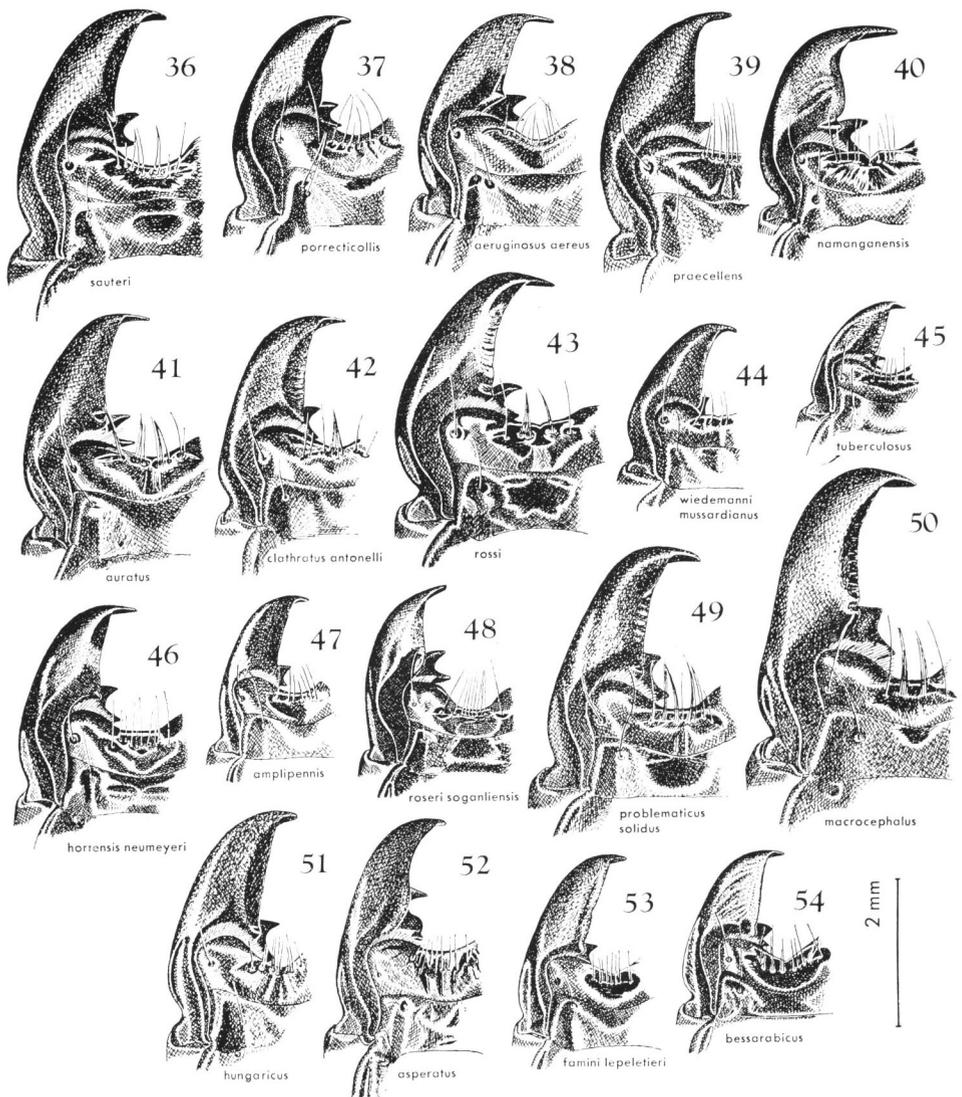
*Carabi brevimandibulares*”

“Mandibeln lang, schmal, am Innenrande bis zur Spitze gleichmässig stark gebogen oder überhaupt—auch am Ende—wenig gebogen und dann nicht zugespitzt, sondern stumpf. . . . Bei den Larven der Clypeus mit parallelen Seiten und 2 mehr oder weniger verschmolzenen Zähnen oder bloss mit einem Zahn am Voderrand, die beiden äusseren reduziert.

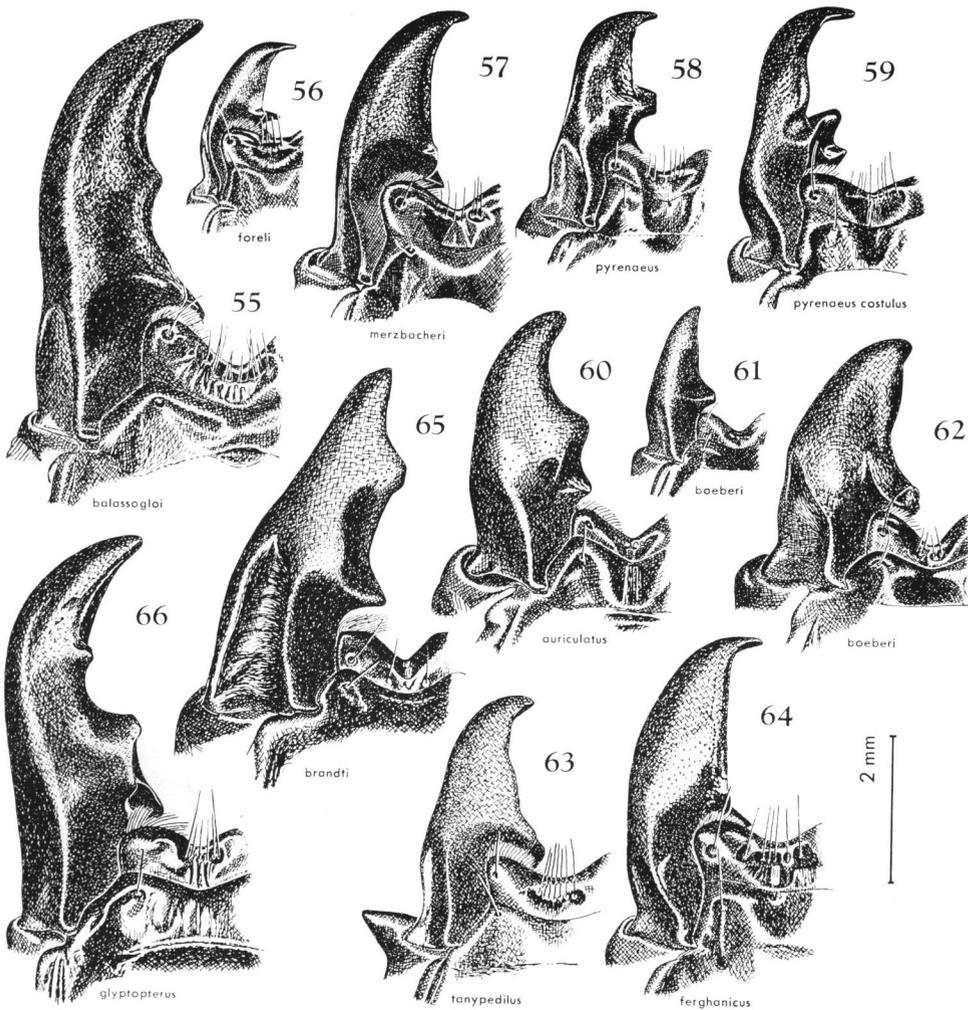
*Carabi longimandibulares*”

Many authors including JEANNEL (1941) adopted these subdivisions, but such characteristics of the mandibles are recognizable only as tendencies in each group as thus defined, and a careful observation of mandibles of representative species will make it clear that there is no definite difference by which they should be subdivided into two distinct groups. Especially, the mandibles of the Carabi longimandibulares (Figs. 55–92) are so remarkably varied that it is not possible to treat them as a well defined group on the basis of this character alone. It does not mean, however, that the features of the mandibles have no taxonomic value at all, because they are usually similar between related species and useful to presume their affinity. Particularly, in such genera as *Cyclocarabus* (Fig. 40), *Ischnocarabus* (Fig. 75), *Axinocarabus* (Fig. 79) and *Goniocarabus* (Fig. 80), their peculiar shape is characteristic of each genus. But, there are so many unrelated species with similar mandibles. In such case, the resemblance is considered to be coincidental, owing to convergence or parallelism, if not because of the lack of specialization by which primitive features have been preserved, and therefore does not prove the phylogenetic relationship between them. Since the mandibles of the Carabina are feeding organs, their shape is supposed to have been modified adaptively to the food habit of each species.

Many species of the Carabina are known to feed on earthworms, terrestrial arthropods including insects, slugs etc., while others are particularly malacophagous, living essentially or exclusively upon various species of land snails. The species of the former group are comparatively less specialized in external features and have in common the characteristics of the Carabi brevimandibulares. The malacophagous species show a

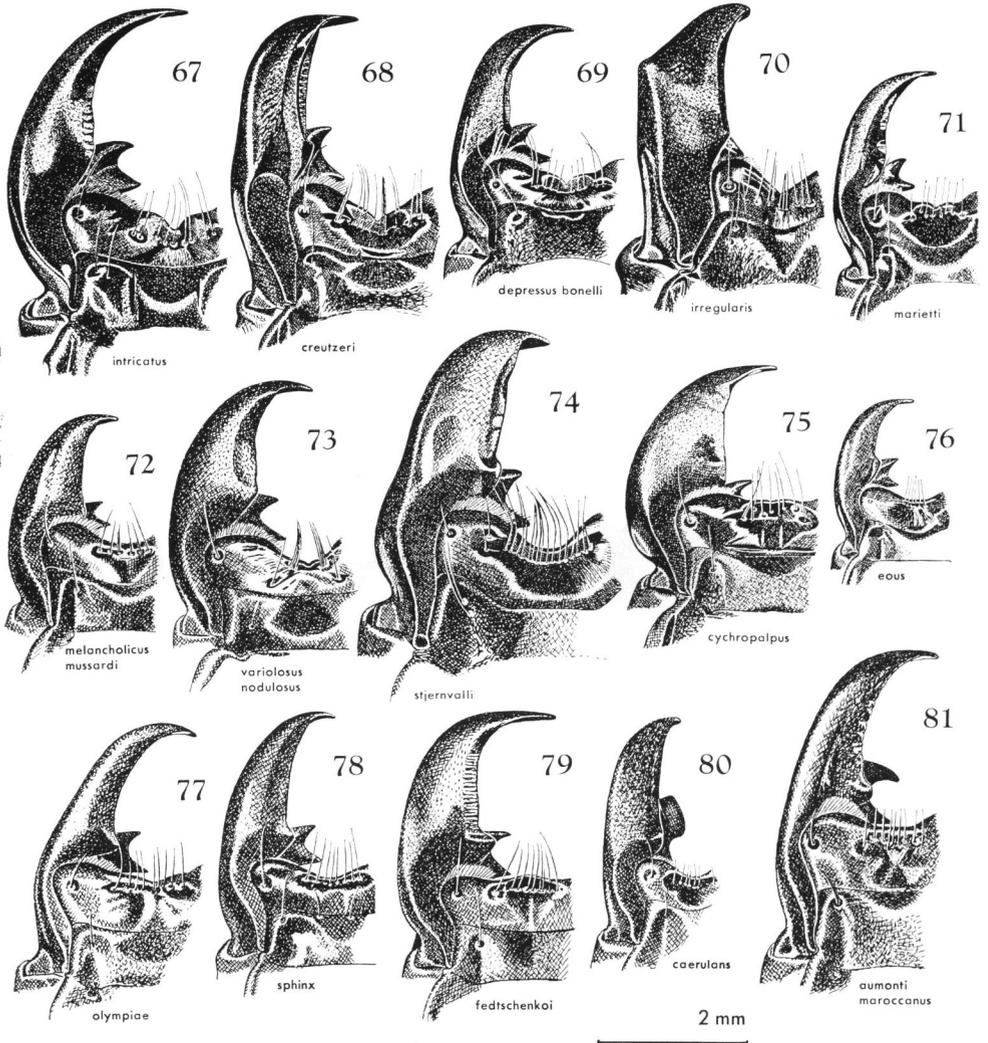


Figs. 36–54. Left mandibles, labra and clypei of the Carabi brevimandibulares. — 36, *Apotomopterus sauteri* ROESCHKE; 37, *Apotomopterus (Euleptocarabus) porrecticollis* BATES; 38, *Morphocarabus aëuginosus aëreus* FISCHER; 39, *M. praecellens* PALLAS; 40, *Cyclocarabus namanganensis* HEYDEN; 41, *Autocarabus auratus* LINNÉ; 42, *Apotomopterus (Limnocarabus) clathratus antonelli* LUIGIONI; 43, *Archicarabus rossi* DEJEAN; 44, *Archicarabus wiedemanni mussardianus* BREUNING; 45, *Hemicarabus tuberculatus* DEJEAN et BOISDUVAL; 46, *Oreocarabus hortensis neumeyeri* SCHAU; 47, *O. amplipennis* LAPOUGE; 48, *Pachycarabus roseri soganliensis* HEINZ et KORGE; 49, *Mesocarabus problematicus solidus* LAPOUGE; 50, *M. macrocephalus* DEJEAN; 51, *Pachystus hungaricus hungaricus* FABRICIUS; 52, *Cathoplius asperatus* DEJEAN; 53, *Eurycarabus famini lepeletieri* BEDEL; 54, *Tomocarabus bessarabicus bessarabicus* FISCHER.

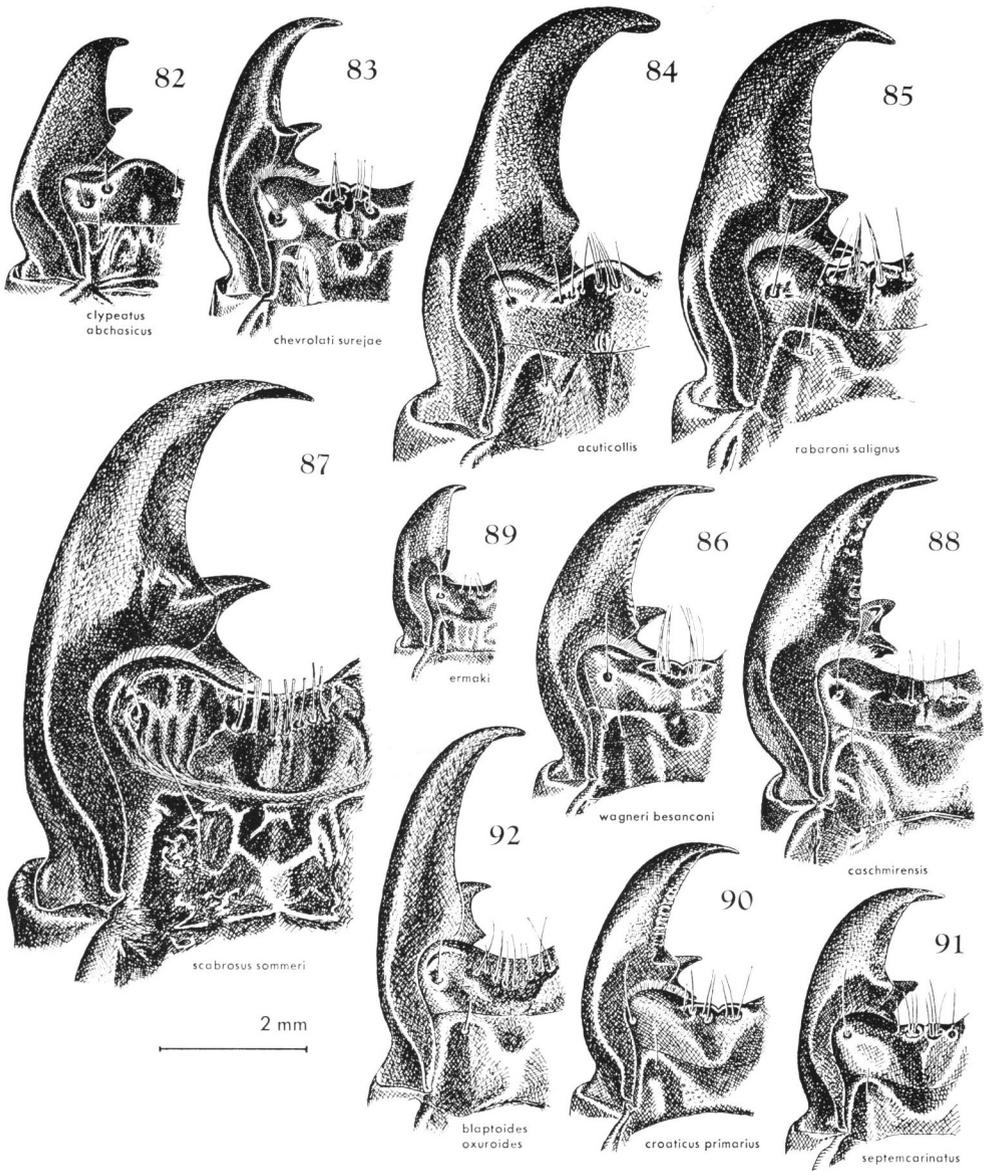


Figs. 55–66. Left mandibles, labra and clypei of the Carabi longimandibulares (Subgenus *Cechenus*, sensu BREUNING); all females, unless otherwise marked. — 55, *Cratocephalus balassogloi* DOHRN; 56, *Leptoplesius foreli* HAUSER; 57, *L. merzbacheri* HAUSER; 58, *Iniopachus pyrenaeus pyrenaeus* SERVILLE; 59, *I. pyrenaeus costulus* GÉHIN; 60, *I. auriculatus* PUTZEYS; 61, *Cechenus boeberi* ADAMS ♂; 62, *C. boeberi* ADAMS; 63, *Pantophyrtus tanypedilus* MORAWITZ; 64, *Pseudotribax ferghanicus* BREUNING ♂; 65, *Cathaicus brandti* FALDERMANN; 66, *Eupachys glyptopterus* FISCHER.

tendency of morphological specialization towards opposite extremes presumably as adaptations to their feeding habits, known as stenocephalism or macrocephalism. The stenocephalism is best represented by *Damaster blaptoides* and *Macrothorax aumonti*, in which the forebody, particularly the head, has become narrowly elongated,



Figs. 67–81. Left mandibles, labra and clypei of the Carabi longimandibulares. — 67, *Chaetocarabus intricatus intricatus* LINNÉ; 68, *Platycarabus creutzeri creutzeri* FABRICIUS; 69, *P. depressus bonelli* DEJEAN; 70, *Pseudocechenus irregularis irregularis* FABRICIUS; 71, *Heterocarabus marietti marietti* CRISTOFORIS et JAN; 72, *Rhabdotocarabus melancholicus mussardi* ANTOINE; 73, *Hygrocarabus variolosus nodulosus* CREUTZER; 74, *Lipaster stjervalli* MANNERHEIM; 75, *Ischnocarabus cychropalpus* PEYRON; 76, *Eotribax eous* MORAWITZ; 77, *Chrysocarabus olympiae* SELLA; 78, *Deroplectes sphinx* REITTER; 79, *Axinocarabus fedtschenkoi* SOLSKY; 80, *Gontiocarabus caerulans* MORAWITZ; 81, *Macrothorax aumonti aumonti* LUCAS.



Figs. 82–92. Left mandibles, labra and clypei of the Carabi longimandibulares. — 82, *Procrustes clypeatus abchasicus* MOTSCHULSKY; 83, *P. chevrolati surejae* CSIKI; 84, *P. acuticollis* MOTSCHULSKY; 85, *Lamprostus rabaroni salignus* SCHWEIGER; 86, *Oxycarabus wagneri besanconi* BREUNING et RUSPOLI; 87, *Procerus scabrosus sommeri* MANNERHEIM; 88, *Imaiibus caschmirensis* REDTENBACHER; 89, *Megodontus ermaki* LUTSHNIK; 90, *M. croaticus primarius* LAPOUGE; 91, *M. septemcarinatus* MOTSCHULSKY; 92, *Damaster blaptoides oxuroides* SCHAUM.

as called "cychriziert" in German. The macrocephalism is most conspicuously developed in many species of the subgenus *Cechenus* (*sensu* BREUNING); heads of them show a tendency towards enlargement, often to an enormous size disproportionate to the other parts of the body. STURANI (1962) named the species with narrow, elongate heads the Prostenocarabi, and those with massive heads the Promacrocarabi.

The stenocephalic species are supposed to have been adapted to feed on snails by inserting the narrow head into the shell, whereas the macrocephalic species would feed on them by breaking their shells with powerful stout mandibles. This habit appears to cause a considerable wear of mandibles (Figs. 60, 62, 63, 65) in Promacrocarabi, as exhibited by the fact that the specimens with immaculate mandibles are actually very rare.

Such specialization of the forebody as macrocephalism or stenocephalism has developed independently in unrelated taxa of the Carabina as STURANI stated. Of course, there are grades among them, and the majority of species have the head of moderate size. Naturally, therefore, the taxonomic value of the features which are simply due to the enlargement or elongation of the head requires a critical estimation particularly as characters for higher taxa. For example, the labrum is disproportionately small in macrocephalic species. This feature was noticed by authors and employed as a key character for higher taxa. BREUNING discriminated the subgenus *Cechenus* from all other subgenera of the Carabi longimandibulares by this character. It is, however, not always so constant a feature even if it is in reality a significant characteristic of the subgenus, because it is applicable for only macrocephalic species or even only macrocephalic individuals in the case of species which are variable in the comparative size of the head. In small headed individuals of *foreli* (sect. *Leptoplesius*) (Fig. 56), for example, the labrum is scarcely narrower than clypeus; on the other hand, there are many species with equally small labra in the extralimital groups, such as *Mesocarabus macrocephalus* (Fig. 50), *Pseudocechenus irregularis* (Fig. 70), *Lipaster stjernvalli* (Fig. 74), etc. On the contrary, the labrum is always larger in the stenocephalic or microcephalic species (Figs. 52, 81, 82, 92, etc.). Thus, the comparative size of the labrum of the Carabina is of allometric nature, showing more or less inverse proportion to the width of the head; consequently, its taxonomic value is absolutely circumstantial, at least as a diagnostic character for any of the higher taxa.

It should be noted that all the species with specialized heads, either stenocephalic or macrocephalic, have mandibles with features which BREUNING recognized to characterize the Carabi longimandibulares. He cited *Mesocarabus riffensis* as an exceptional species for the Carabi brevimandibulares because of its elongate mandibles, but all other macrocephalic species or subspecies of *Mesocarabus*, such as *lusitanicus*, *macrocephalus* and some forms of *problematicus*, have similarly elongated mandibles (Figs. 49, 50).

On the other hand, *asperatus* and *stenocephalus*, the representatives of *Cathoplius*, which are characterized by remarkably narrowed heads, also share similar features in their mandibles (Fig. 52). Mention must also be made of *Lipaster stjernvalli* (Fig. 74)

and *L. osellai* (comb. nov.) which have been regarded as belonging to the Carabi longimandibulares by the shape of mandibles and also by enlarged heads which give them an appearance suggesting their relationship to *Cechenus*. In reality, however, they are related to *Morphocarabus* and its allies, which are typical groups of the Carabi brevimandibulares, according to the genitalic characters as discussed in a paper to be published.

Species of the Carabina are known to ingest by means of preoral or extraintestinal digestion: they excrete from the mouth a fluid that acts chemically to reduce the flesh to a liquid to be ingested. This digestive fluid is squirted into the body of the prey through the punctures of the body walls perforated by mandibles. The mandibles of the brevimandibulate species are hooked with sharp apical points which seem to be adapted for piercing hard exoskeleton of the prey; whereas those of the malacophagous species are diversified in shape and size to fit probably particular modes of feeding. Accordingly, there are unrelated species with similar mandibles doubtless due to convergence, and related species with different mandibles as well. The macrocephalic species have strong mandibles with their retinacula showing a tendency to be fused with the posterior angles of the incisor lobes (Figs. 55, 57–66, 70, 84). Obviously, they are adapted for breaking the shells of snails to be fed on. The mandibles of other longimandibulate species are comparatively more slender, arcuate and gradually narrowed to the apical points. They seem to be fitted rather for gripping slimy body of snails than to tear it, because the digestive fluid will act directly on the naked skin of the prey.

Thus, the diagnostic features in the mandibles of the Carabi longimandibulares are most likely to be features due to specialization towards malacophagy, so it is not as reasonable to acknowledge them to be a natural group by only a share of them as to do with the Carabi brevimandibulares simply because of unmodified or less specialized mandibles. In fact, as shown in Figs. 55–92, the mandibles of the Carabi longimandibulares are so varied in shape and size that it is difficult in reality to distinguish them as a well defined group because of a share of the characters alone as stated by BREUNING. Moreover, I could not find any additional character, either genitalic or extragenitalic, that evidences this grouping sufficiently.

Another cephalic character of taxonomic importance is the setosity of the penultimate segment of the labial palpus. In the majority of species, there are usually but two bristles as called bisetose, while in the others there are usually several bristles on that segment. The latter condition, which is called multisetose, develops in limited groups, so it is practically one of useful diagnostic characters for them. But, the bristles are very variable not only in number but also in distribution even within species, and individuals with more than two bristles are not seldom in the species of bisetose groups; moreover, there are species, such as those of *Apotomopterus* and of *Eurycarabus*, in which there are two or more bristles as to be described “bi- or multisetose”. Since the multisetose groups are not otherwise similar to one another, this feature does not seem to have more significance than as a character suggesting

the level of specialization of the group concerned. The labial palpus with many bristles seems to be less specialized than that with but two bristles, and the latter state is considered to be at the level of the utmost specialization on condition that the bristles have any particular function.

### Larval Characters for the Higher Taxa of the Carabina

As cited already, BREUNING's diagnostics for the Carabi brevimandibulares and the Carabi longimandibulares are supplemented with larval characters. Certain features of the larval stages afford doubtlessly reliable characters that manifest the relationships among the higher taxa, although our knowledge of the larvae of the Carabina is as yet much poorer than that of the imagines, and many problematical supraspecific taxa are known only in the adult stage. Moreover, the analysis of the available characters of the larvae does not seem to have been made properly; apparently too much importance was attached to the shape of the epistoma alone, although it is a very simple structure and changes its shape not only by the instar but also with age. Yet, they have indeed a considerable taxonomic importance even more than adult characters if used with sufficient analysis. In fact, the classification of imagines on the basis of the genitalic characters corresponds in many respects with that by the larval characters according to my interpretation of them.

It was LAPOUGE (1929, 1931) who introduced larval characters into the classification of the Carabina. He subdivided them into three groups, viz. Carabes rostrilabres, *C. quadricuspides* and *C. serrilabres* (or Rostrilabres, Quadricuspides and Serrilabres, respectively), principally by the shape of the epistoma of the larvae. LAPOUGE, however, confronted difficulties in defining these three groups by the characters of the imagines correspondingly, and pointed out that the only "presque propre et presque constant" adult character that he found to be useful for distinguishing the Rostrilabres from the two others is the features of mandibles which are "plus grandes en general et plus droites" than in the others. In the classification of the imagines, therefore, he did not propose a definite grouping which corresponds with the Rostrilabres, and subdivided them further into three subgroups, viz. Psilogoniens, Pliochètes and Tribacogéniens. Independently of LAPOUGE, BENGSSON (1927) concluded his studies on the larvae of Nordic *Carabus* (s. l.) with the grouping of species, subdividing it into three groups by larval characters, viz. Archeocarabus (*nec Archaeocarabus* SEMENOW, 1898), Metacarabus and Neocarabus (*nec* HATCH, 1949). They correspond respectively to the Serrilabres, the Quadricuspides and the Rostrilabres of LAPOUGE.

Although BREUNING combined the Carabi multistriati (=Multistriés =Quadricuspides =Metacarabus) with the Carabi carabogenici (=Carabogéniens =Serrilabres =Archeocarabus) to form the Carabi brevimandibulares, this treatment is apparently conventional, because the larvae of these two groups are quite different from each other as STURANI (1962) stated. The only character that they have in common is that the apical margin of the epistoma is not "rostriform" but serrated or quadridentate.

The larvae of the Serrilabres appear to be the least specialized of these three groups morphologically but have characteristics of their own; whereas the larvae of the Quadricuspides appear to share obviously more features in common with those of the Rostrilabres than they do with the Serrilabres.

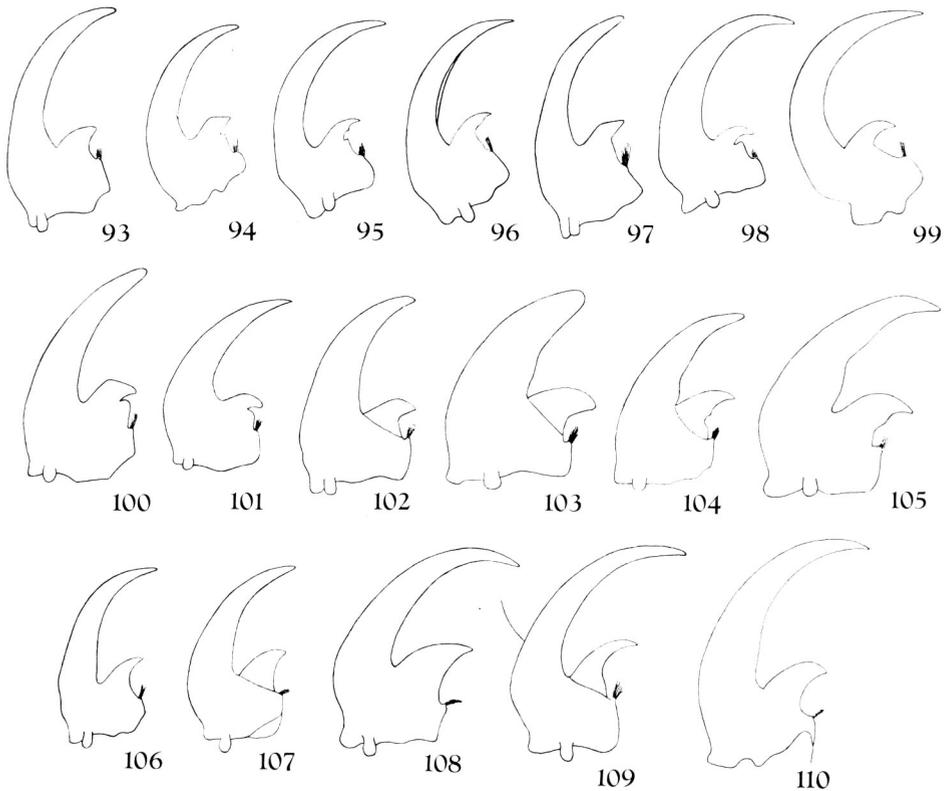
The shape of the epistoma that characterizes the Rostrilabres is the simplest of all the three groups; however, it is not necessarily considered to be a character which evidences an affinity among them by a share of it, but may be, more possibly, not more than a feature derived regressively from the quadridentate epistoma. Actually, there are longimandibulate species of which epistoma is more or less quadridentate, showing intermediate characteristics towards the Quadricuspides.

In relation to the epistomal characters, features of mandibles in the larval stage should not be overlooked though they have never been used as characters for higher taxa by former workers.

Differing so conspicuously from the imagines, the larvae of the Carabi brevimandibulares are clearly divided into two groups by the shape of the mandibles (Figs. 93–110). The first group (Figs. 93–99) is characterized by long, narrow and strongly but rather evenly arcuate apical part, with a smaller retinaculum. The second group (Figs. 100–110) is distinguished from the first by shorter, broader or less arcuate, and more abruptly tapering apical part usually with a larger retinaculum.

The first group corresponds to the Carabi carabogenici of BREUNING, if some heterogeneous species, such as *cancellatus* (Fig. 100), *auratus* (Fig. 101), *clathratus* (Fig. 102), etc. are not included in them. Authors who studied the larvae of the Carabina appear to have adhered too much to the existing classifications which are based exclusively upon the imagines to attempt a revision of them by the larval characters only; that is doubtless the reason why they have ignored, if not overlooked, the distinct features of the larvae of these species which were traditionally combined to the representative genera of this group. These species have somewhat ambiguous features in the epistoma, but the shape of the apical part of the mandibles suggests that they are not more closely related to the Carabi carabogenici than to the Carabi multistriati (Figs. 103–105). It should be noted that both *cancellatus* and *auratus* have well developed ostium lobes in the male genitalia and are related in this respect also to the Carabi multistriati.

The species belonging to the Carabi carabogenici and the Carabi multistriati are known or supposed to feed mainly on terrestrial small animals including insects, earthworms, slugs, etc., but not exclusively malacophagous. At least, no partiality for particular animal group as their food is known as it is exclusively to snails in the Carabi longimandibulares. It is noteworthy, therefore, that the mandibles of the larvae are so conspicuously different between them. Together with the characters of the mandibles, the shape of the epistoma, whether serrated with a median tooth or quadridentate without a distinct median tooth, though not always sufficiently diagnostic, distinguishes between these groups fairly definitely. It is presumable that the toothed epistoma work effectively for clutching a prey that struggles to escape when a larva bites it with



Figs. 93–110. Mandibles of the larvae; the numerals in parentheses indicate the instar. — 93, *Archicarabus nemoralis* MÜLLER (3); 94, *Carabus conciliator hokkaidensis* LAPOUGE (3); 95, *C. arvensis* HERBST (2); 96, *C. granulatus* LINNÉ (1); 97, *C. granulatus* LINNÉ (3); 98, *Morphocarabus monilis* FABRICIUS (2); 99, *Carabus insulicola pseudinsulicola* ISHIKAWA (3); 100, *Cancellocarabus cancellatus* ILLIGER (3); 101, *Autocarabus auratus* LINNÉ (1); 102, *Limnocarabus clathratus* LINNÉ (2); 103, *Oreocarabus glabratus* PAYKULL (2); 104, *O. hortensis* LINNÉ (2); 105, *Mesocarabus problematicus* HERBST (3); 106, *Chrysocarabus auronitens* FABRICIUS (1); 107, *Megodontus violaceus* LINNÉ (3); 108, *Procrustes coriaceus* LINNÉ (2); 109, *Chaetocarabus intricatus* LINNÉ (1); 110, *Damaster blaptoides rugipennis* MOTSCHULSKY (2). [Adopted from BENGTTSSON, 1927, except 94, 99, and 110.]

mandibles through which the venomous digestive secretion is injected into its body. In the Carabi carabogenici, the epistomal teeth are smaller but their mandibles are longer and strongly arcuate; whereas in the Carabi multistriati, the teeth are larger and more prominent, though the mandibles are shorter with larger retinacula. Thus, the mouth parts differ so much between these two groups in important characteristics as to be able to distinguish from each other sufficiently, but so far as their function is concerned, they seem to be at the similar level of specialization. The differences may presumably show their phylogenetic discreteness but not likely to be adaptational to

their feeding habits or selection of food.

The known larvae of the Carabi longimandibulares are characterized by a conspicuous feature of epistomae as termed "rostrilabre" by LAPOUGE. This feature is, I believe, adaptational to their specialized food selection, as suggested by the fact that a similar feature is known in the larvae of exclusively snail eating *Cychnus*. Functionally, a toothed epistoma does not appear to be of use for slippery body of snails which excrete a large amount of slime when attacked by enemies. It is obvious that narrow and elongate mandibles as they have are more effective for this purpose.

Like their imagines, the mandibles of the larvae of the Carabi longimandibulares (Figs. 106–110) appear to be diversified in shape, but, in reality, they are different from one another only in the length of their apical parts; moreover, it should be noted that they are not different from those of the Carabi multistriati (Figs. 103–105) in the characteristic shape of the basal parts including the retinacula. Thus, there is little doubt that the modification in their mandibles is adaptational to malacophagy, and it is my conclusion that the shape of the mandibles of the larvae also suggests that the Carabi longimandibulares are merely specialized forms of the Carabi multistriati.

### Subdivisions of the Carabina

In conclusion, I propose here to recognize three phyletic series as subdivisions of the Carabina as follows:

1. Carabogenici
2. Spinulati, nov.
3. Multistriati

The Carabogenici as here defined are equal to the Carabogeniens LAPOUGE, 1931 and the Carabi carabogenici BREUNING, 1932 in outline, but differ essentially from them in that they do not include the genus *Apotomopterus* HOPE, 1838 (*sensu* ISHIKAWA, 1973) for which the Spinulati are proposed as a distinct subdivision of the Carabina. The Multistriati in the present sense include the Carabi longimandibulares BREUNING, 1932 (=Psilogoniens+Pliochètes+Tribacogeniens LAPOUGE, 1931) in addition to the Carabi multistriati BREUNING, 1932 (=Multistriés LAPOUGE, 1931).

This new system involves a number of new combinations of taxa included. Many species are transferred to the Multistriati from the traditional combinations with the Carabi carabogenici; on the other hand, no species of the Carabi multistriati and only a few species of the Carabi longimandibulares have to be moved to the Carabogenici. This fact will suggest that the morphological specialization towards malacophagy is, if any, much less conspicuous in the Carabogenici than in the Multistriati, and that the brevimandibulate species with less specialized external features were grouped conventionally under the Carabi carabogenici.

#### CARABOGENICI

Diagnostic characters: Male genitalia (Figs. 29, 30) without an ostium lobe in the

membraneous preostium; chitinized part of the ligula greatly reduced or absent altogether. Larva: Mandible (Figs. 93–99) with the apical part long, narrow and evenly arcuate, not so conspicuously tapering from the base, with a smaller retinaculum; epistoma usually with 2 smaller lateral teeth on each side or may be serrate, and with a distinct median tooth.

This subdivision comprises species with seemingly the least specialized external features both in the larvae and in the imagines. There are, however, some exceptionally specialized forms in this group, such as *stjernvalli* and *osellai* which have erroneously been assigned to the Carabi longimandibulares. The male genitalia are very greatly diversified though the membraneous preostium does not bear even a trace of an ostium lobe. The majority of species have a membraneous expansion, which STURANI (1967) confused with the ligula, at the dorsal base of the endophallus. This membraneous lobe varies in size and shape but constant within species and is considered to be homologous to the membraneous ligula of the Calosomes lobés. The sclerotized part of the ligula is usually rudimentary or absent. In a number of species, the dorsal wall of the endophallus has a pigmented spot or a sclerotized projection called the copulatory piece. The peripheral rim of gonopore is diversified and characteristically developed in many species. The apical segments of palpi not or barely dilated except in a peculiar genus, *Ischnocarabus* which seems to belong here. Elytron without a humeral crenulation. Many species are known to have large membraneous hind wings though said to be only exceptionally functional.

The genera *Carabus* LINNÉ, 1758 (*sensu* ISHIKAWA, 1973), *Lipaster* MOTSCHULSKY, 1865 (including *Morphocarabus* GÉHIN, 1885, *Trachycarabus* GÉHIN, 1885, etc.), *Archicarabus* SEIDLITZ, 1887 and others are principal representatives of this group.

#### SPINULATI, nov.

Diagnostic characters: Male genitalia (Fig. 31) without an ostium lobe in the membraneous preostium; ligula strongly developed, spine-like and heavily chitinized; peripheral rim of gonopore not conspicuously developed. Larva: Mandible (Fig. 102) broader and shorter with a larger retinaculum, the apical part broad at base and strongly tapering to apex, the basal part broader in proportion to the whole length.

The species belonging to this group are readily distinguished by the spine-like ligula of the endophallus and the lack of the ostium lobe in the preostium. The external features are less specialized; the forebody is not adapted particularly for malacophagy. The apical segments of palpi slender, not or barely dilated. The penultimate segment of the labial palpus bi- or multisetose, occasionally variable in number even within species. Elytron with a distinct or conspicuous preapical emargination, and not rarely with humeral crenulations. The hind wing is only exceptionally membraneous. The larvae are not sufficiently known to me, but, according to STURANI (1962), that of *clathratus* appears to have characteristics of both “quadri-cuspides” and “rostrilabres”.

This subdivision comprises *Apotomopterus* HOPE, 1838, *Limnocarabus* GÉHIN,

1885, and *Euleptocarabus* NAKANE, 1955, which I combined to *Apotomopterus* as subgenera (ISHIKAWA, 1973).

#### MULTISTRIATI

Diagnostic characters: Male genitalia (Figs. 32–35) with an ostium lobe in the membraneous preostium, very rarely rudimentary or absent; ligula in many species reduced to a patch of granules or altogether absent, but not rarely well developed to a small sclerite of which distal end may be free from the membraneous wall and pointed, though never so strongly projected spine-like as in the Spinulati. Larva: Mandible (Figs. 100, 101, 103–110) with the apical part either short, broad at base and strongly tapering to apex, or may be longer and narrower, but not so conspicuously nor evenly arcuate as in the Carabogenici; the basal part usually broader in proportion to its whole length, with a larger retinaculum. Epistoma as a rule quadridentate or rostriform.

The rest of the Carabina fall within the Multistriati by reason that the genera treated as belonging to the Carabi longimandibulares are not separable from the Carabi multistriati in both larval and adult characteristics on condition that the diagnostic characters that distinguish the Carabi longimandibulares are admitted to be features modified adaptationally for malacophagy which has developed independently in unrelated taxa. Naturally, this subdivision comprises remarkably diversified supra-specific taxa, but they have essentially an ostium lobe which has been reduced or absent only in a few species. The endophallus has, usually, a recognizable ligula though very diversified in structure. The apical segments of palpi are distinctly or conspicuously dilated in many species, and sexual differentiation in this part is not unusual. No species is known to have membraneous hind wings. Elytron has humeral crenulations in some species and not rarely with a conspicuous preapical emargination. The larvae are quadridentate or “rostriform” in the shape of the epistoma, and the lateral margins of the urotergites are usually lobate and distinctly produced, most conspicuously so in the species with a rostriformed epistoma.

In addition to the species which have been assigned to the Carabi multistriati and the Carabi longimandibulares, a number of species which have traditionally been combined to the Carabi carabogenici belong to this subdivision. *Autocarabus* SEIDLITZ, 1887, *Cancellocarabus* LUTSHNIK, 1924 and *Tmesicarabus* REITTER, 1896 of Europe, and *Semnocarabus* REITTER, 1896 and *Anthracocarabus* LAPOUGE, 1931 of Central Asia are the Multistriati. Of the Japanese representatives, *Leptocarabus* GÉHIN, 1885, *Adelocarabus* LAPOUGE, 1931, *Asthenocarabus* LAPOUGE, 1931, *Aulonocarabus* REITTER, 1896 and *Pentacarabus* ISHIKAWA, 1972 belong here. Their larvae are “Quadricuspides” and their genitalia have distinct ostium lobes though reduced in some species or subspecies.

### Relationships between the Carabina and the Calosomina

In the classification of the higher taxa of the Carabina, a comparison with the Calosomina is indispensable, because they are so closely related groups, and as I stated already (ISHIKAWA, 1973), the Carabina are discriminated from the Calosomina simply because certain extragenital structures have not become specialized as they are in the Calosomina. It means that the taxa belonging to the Carabina share few definite characters that evidence their homogeneity. This state suggests that the Carabina have not necessarily been derived monophyletically from the common ancestor which also gave rise to the Calosomina. In this respect, the genitalic characters have naturally to be taken into consideration.

The Calosomina differ from the Carabina most conspicuously in that they have well developed and differentiated ligulae, but their endophalli are much less developed than in the latter. This is probably the reason why the aedeagi of the Calosomina are disproportionately smaller in size than those of the Carabina, since the aedeagus of the Carabini is nothing but a container of the endophallus functionally. It is presumable, therefore, that the copulatory organs of the Calosomina do not work for reproductive segregation so positively as are supposed to be in the Carabina.

The ligula (=“Zahn” of FRANZ, 1929; “ligule” of JEANNEL, 1940) of the Calosomina is a prominent structure which projects from the preostium over the slit of the ostium when inactive, or raises vertically when the endophallus is everted. It is a membraneous lobe with a median sclerotized stripe which extends longitudinally to form an apical point in most species, or does not reach apex in the others. JEANNEL (1940) subdivided the Calosomina into two groups, namely, “Calosomes ongulés” and “Calosomes lobés” by this character. The median sclerotized stripe which supports the lobe of the ligula is considered to have been modified from a vestige of sclerotized walls of the aedeagus, because it is noticeably extended as a fine streak across center of the membraneous preostium (Fig. 111).

The male genitalia of the Carabina are not so uniform as in the Calosomina owing largely to the development of the endophallus. In the species belonging to the Carabina, the lobe-like ligula is not present, but at the dorsal base of the endo-

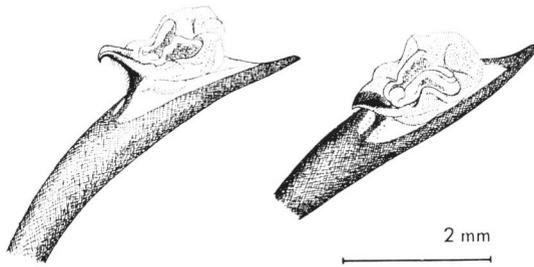


Fig. 111. Male genitalia of the Calosomes ongulés, *Campalita chinense* KIRBY. Aedeagus with the endophallus everted.

phallus there is a vestigial sclerite, a patch of granules, a spine-like projection or a membranous expansion, which I believe to be homologous with the ligula of the Calosomina and used to call it the ligula in the Carabina, because this sclerite looks very like a small ligula in many species of the Carabina for its position as well as its appearance. Particularly, the species belonging to the Spinulati are distinguished in having a spine-like ligula which is so closely similar to that of the Calosomes ongulés and suggests their relationship to the latter. STURANI (1967) stated that the membranous lobe at the preostium of the Carabina, which I named the ostium lobe, is homologous with the ligula, but this opinion cannot be accepted unless the basal sclerite of the Carabina is proved to have been originated otherwise. It seems to be more difficult to establish the homology of the ligula with the ostium lobe than to do with the basal sclerite, because the ostium lobe is developed only in the species belonging to the Multistriati, possibly the most evolved group of the Carabina. In my opinion, the membranous lobe at the dorsal base of the endophallus of the species belonging to *Lipaster* (in the present sense) is homologous with the membranous part of the ligula of the Calosomes lobés, but differs absolutely from the ostium lobe of more specialized Carabina.

The Carabogenici seem to have more features in common with the Calosomes lobés than to do with the Calosomes ongulés. In many species of this group, particularly in *Lipaster*, as mentioned already, the endophallus has, at its dorsal base, a conspicuous membranous swelling which I think to be homologous with ligula of the Calosomes lobés. In the Carabogenici, the sclerotized part of the ligula is strongly reduced or absent, and, I believe, the membranous part of the ligula has remained as a lobe. As to the extragenital characters, the humeral crenulations of elytra are not developed in any species belonging to the Carabogenici and the Calosomes lobés, although it is not rare in other subdivisions of the Carabina and of the Calosomes ongulés.

The Spinulati may be related to the Calosomes ongulés in having a spine-like ligula which is wholly visible even in the condition that the endophallus is completely withdrawn. Also, the humeral crenulations, which are conspicuous in many species of the Calosomes ongulés, develop not rarely in the species of this group.

The Multistriati are highly diversified with their external features being most evidently specialized in many species. Yet, there are species, such as those of *Hemicarabus*, which reserve some of peculiar features that suggest their affinity to the Calosomes ongulés. The humeral crenulations are found in comparatively less specialized species. The male genitalia differ from those of the Calosomina in having an ostium lobe in addition to the ligula which is well reserved in many species as a small sclerite. The apical segments of palpi are dilated triangularly in many species, though not all, belonging to this group, and this is a feature also recognizable in the Calosomes ongulés though much less conspicuous than in the Carabina.

Thus, it is not difficult to presume the affinity between the suprageneric taxa of the Carabina with those of the Calosomina by the similarity of the male genitalia and

by the share of some extragenital characters. It is probable that the Carabogenici are more closely related to the Calosomes lobés than to the Spinulati and the Multistriati, as the latter two are to the Calosomes ongulés. If this be evidenced, the classification of the higher taxa of the tribe Carabini should also be revised fundamentally.

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