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## Larvae of Ground Beetles of the Genus *Carabus* L. (Coleoptera, Carabidae) of the Fauna of Russia and Neighboring Countries\*

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**Abstract** Larvae of 162 species of the genus *Carabus* were studied using modern techniques. The general morphology and chaetotaxy are described in detail. Principles of homologization of the sensitive structures are worked out. A key to 53 subgenera is provided.

**Keywords** Coleoptera, Carabidae, *Carabus*, larval description

Larvae of the genus *Carabus* are the best studied among larvae of ground beetles. In the first half of the 19th century, works dedicated to their morphology were published (Brulle 1835, etc.). The next studies were concerned chiefly with the morphology and ecology of individual species and only in 1905 was the first summary on larvae of this genus published (Lapouge, 1905). Several regional summaries on larvae of Carabidae appeared later, including the genus *Carabus* (Bengtsson, 1927, Larsson 1941, Sharova, 1958, 1964, Sturani, 1962, Húrka 1971, Mikhaylov, 1978). The only attempt at using larval characters for developing system of the genus was in a paper by Lapouge (1929) based on study of larvae of 55 species. A recently published key to larvae of European species of *Carabus* (Arndt, 1985) includes 53 species.

Among 272 species of the genus living in the former Soviet Union (O. L. Kryzhanovskiy personal communication) data on larvae were available only for 24 species. My studies have revealed and identified larvae of 108 additional species.

In the process of accumulation of data on larvae of this genus identification by the use of a small number of traditional morphological characters became more difficult, making it necessary to use new characters for the identification and construction of a key to subgenera of larvae of the genus *Carabus*.

During the work material on larvae of *Carabus* in the following collections was used: Faculty of Zoology of the Lenin Moscow Pedagogical Institute; the Zoological Institute of the Russian Academy of Sciences; and the Severtsov Institute of Evolutionary Morphology and Ecology of Animals of the Russian Academy of Sciences, as well as collections of S. K. Alekseev, I. A. Belousov, V. G. Grachev, V. M. Dushenkov, A. S. Zamotaylov, T. K. Imekhenova, I. I. Kabak, V. E. Karpova, A. G. Koval, A. N. Kovtgin, V. A. Mikhaylov, V. G. Mordkovich, V. G. Shilenkov, and V. V. Yanushev.

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## MORPHOLOGY OF LARVAE OF THE GENUS *CARABUS*

In the systematics of larvae of the genus mainly macromorphological characters were used (Fig. 1). After works of Canadian entomologists (Goulet, 1977; Bousquet and Goulet, 1984) the techniques of investigation of detailed morphology of larvae of Carabidae (chaetotaxy and microsculpture) considerably increased the number of used characters. However, the chaetome of larvae of *Carabus* differs from the typical chaetome in this family in general so much that pure topological criteria used by the Canadian researchers do not result in reliable identification of setae. Study of the chaetome of larvae of *Carabus* became complex because of considerable sclerotization of their integument, reduction of several setae associated with this (= trichoid sensillae), and also because of the presence of numerous secondary sensillae and supporting structures, spines, and bristles on ventral sclerites and legs. For the study of delicate morphology of several larvae of *Carabus* I used a solution of glycerine according to standard technique (Goulet, 1977). Their study enabled me to work out criteria of distinctive primary and secondary sensilla and established topological regularities of position of various sensilla according to places of attachment to the cuticle of muscles and endoskeleton.

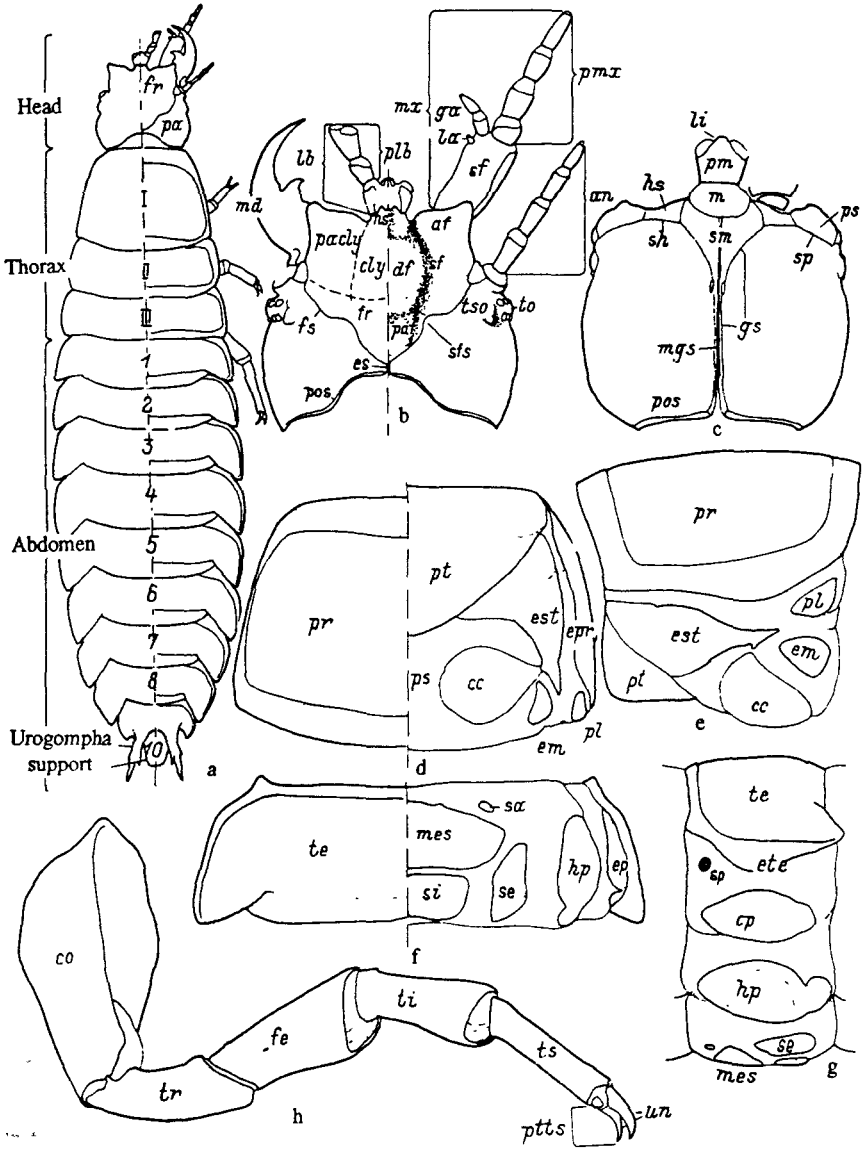
Primary sensilla, appearing ontogenetically earlier (Bousquet and Goulet, 1984), are probably a necessary minimum of sensitive structures of larva and are represented by trichoids with many neurons, basoconical, acetabulate, and placoid structures. Secondary sensilla usually appear at a later time in the process of ontogenesis and are predominantly specialized structures with 1 or 2 neurons. In association with these primary sensilla of any type that differ from secondary sensilla in shape and size of the cuticular canal (Fig. 2a, b). Even in those cases wherein secondary sensilla reach considerable size (for example, supporting spines), they retain specific shape of the pore canal (Fig. 2c). Secondary sensilla are also characterized by irregular, mostly asymmetrical position on the sclerite.

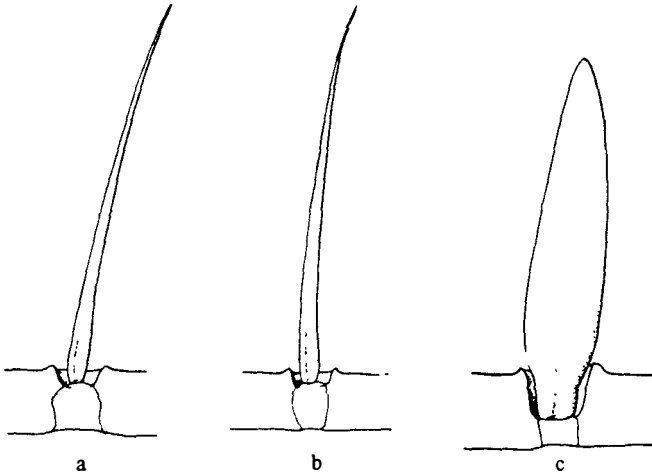
**Cephalic chaetome.** The head of larvae consists of 3 sclerites divided by 3 sutures: frontal, epicranial (= posterior coronal suture), and medigular, which are lines of separation of sclerites during molting (Du Porte, 1960; Hinton, 1963) and mostly do not coincide with true sutures appearing as a result of fusion of head segments. Short proximal branches of the frontal suture, anterior and posterior frontal sutures, remains of gular, occipital, hypostomal, and postgenal (pleurostomal) sutures (Fig. 1b, c) may be considered as true sutures. In all remaining cases borders between head segments may be determined only as accessory markers and often are very conditional (Fig. 3).

The chaetome of the head capsule in general reflects its segmentary composition when taking into account the specifics of the group (Fig. 3). Thus, increase of the area of attachment muscles causes reduction of sensilla  $PA_{4,5,6,b}$ , and shortening of the proximal part of  $gca$  leads to complete or partial reduction of  $PA_{10,c}$ . The chaetome of the frontal sclerite is relatively less changed, only sensillae  $FR_{1,a}$  (located in the area of the anterior tentorial pit, site of attachment of pretentorium forming here anterior [= dorsal] mandibular articulation) are very reduced. Among other primary sensilla  $FR_{c,f}$  are most often reduced.  $FR_{10,11}$  and 11 are represented by small spines entirely submerged into the cuticle. An increase in number of cephalic setae in larvae of species of *Carabus* is observed only as an exception.

The chaetome of cephalic appendages differs from the generalized type (Bousquet and Goulet, 1984) in the presence of accessory setae on the 2nd segment of antennae, 1st and 3rd segments of maxillary palpi, 1st segment of galea, and labial palpi; reduction of setae  $MX_{4,9,11,12}$ ; and modification of large apical sensilla of antennae, palpi, and galea (Fig. 4). The highly developed groups of setae  $gLA$  and  $gMX$  are very typical, the latter one with so-called split-branch shape (Fig. 4n).

**Chaetome of thoracal segments.** The chaetome of ventral sclerites in general fits the general-





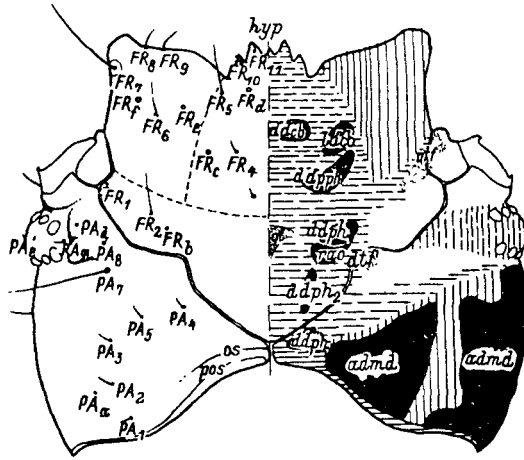
**Fig. 2.** *Carabus* L. Sensilla of larvae: a) primary trichoid sensillum, b) secondary trichoid sensillum, and c) supporting spine (modified secondary trichoid sensillum).

ized type; on the episternites, epimerites, and epipleurites secondary trichoid or clavate sensilla (setae, Fig. 5b) are often present. On the contrary, the primary setae of tergites are considerably reduced. Their minimal set is  $PT_{2,6,9,11,12,a}$ ,  $ME_{1,3,4,5,6,7,9,11,12,13,a}$ ; maximal  $PT_{1,2,3,6,8,9,11,12,13,14,a,b,l}$ ,  $ME_{1,3,4,5,6,7,8,9,11,12,13,14,a,b,q}$  (Fig. 5a). Numerous secondary sensilla are almost always developed.

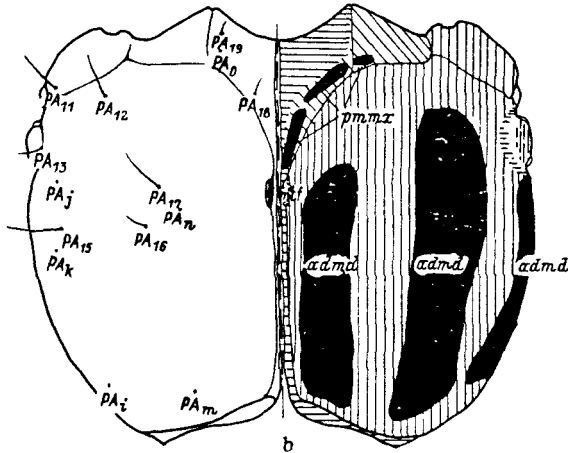
On the leg only sensillum  $Tla$  is reduced. The well-developed pretarsus consists of claws and an unpaired sclerite bearing setae  $TA_{1,2}$  is very typical of larvae of the genus *Carabus*. As a rule, the anterior surface of the coxa and the lower surface of the femur, tibia, and tarsus bear numerous accessory supporting spines (Fig. 6). The number of spines on the hindtarsi is always greater than on the fore and midtarsi.

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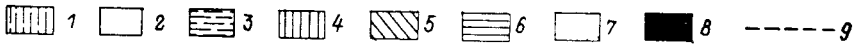
Fig. 1. *Carabus* L. Model of structure of larva: a) general dorsal view, b) head in dorsal view (left antenna and maxilla, right mandible, and left palpus not shown), c) head in ventral view (appendages, except prementum, not shown), d) prothorax (on left in dorsal view and on right in ventral view), e) prothorax in lateral view, f) abdominal segment (on left in dorsal view and on right in ventral view), g) abdominal segment in lateral view, h) leg; *af* - lobes of paraclypeus, *an* - antenna, *ca* - antennal cavity, *cc* - place of attachment of coxa, *cly* - clypeus, *co* - coxa, *df* - frontal disc, *em* - epimerite, *ep* - epipleuron, *epr* - epipleuron of pronotum, *es* - epicranial suture, *est* - episternite, *ete* - epipleuron of tergite, *fe* - femur, *fr* - frons, *fs* - frontal suture, *ga* - galea, *gs* - gular suture, *hs* - hypostome, *la* - lacinia, *lb* - ligula, *m* - mentum, *md* - mandible, *mes* - sternite, *mgs* - mediogular suture, *mx* - maxilla, *ns* - nasale, *pa* - parietal sclerite, *paf* - basal part of frons, *paly* - paraclypeus, *pl* - pleurite, *plb* - labial palpus, *pm* - prementum, *pmx* - maxillary palpus, *pas* - postoccipital suture, *pr* - pronotum, *ps* - sternite of prothorax, *prts* - pretarsus, *sa* - presternite, *se* - external poststernite, *sf* - frontal grooves, *sfs* - sinus of frontal suture, *sh* - hypostomal suture, *si* - inner poststernite, *sm* - submentum, *sp* - pleurostomal suture, *st* - stipes, *te* - tergite, *to* - ocellar tubercle, *tr* - trochanter, *ts* - tarsus, *tso* - superorbital tubercle, *un* - claws.



a



b



Differentiating characters of different instars of larvae of species of ground beetles of the genus *Carabus*

Characters	Instar of larva		
	I	II	III
Ratio of width of head to width of pronotum	≥1	<1	<1
Presence of pleural organ	+	±*	—
Presence of ovarian teeth	+	±	—
Presence of secondary setae on tarsus	—***	+	+
Presence of secondary setae on ventrites	—***	+	+

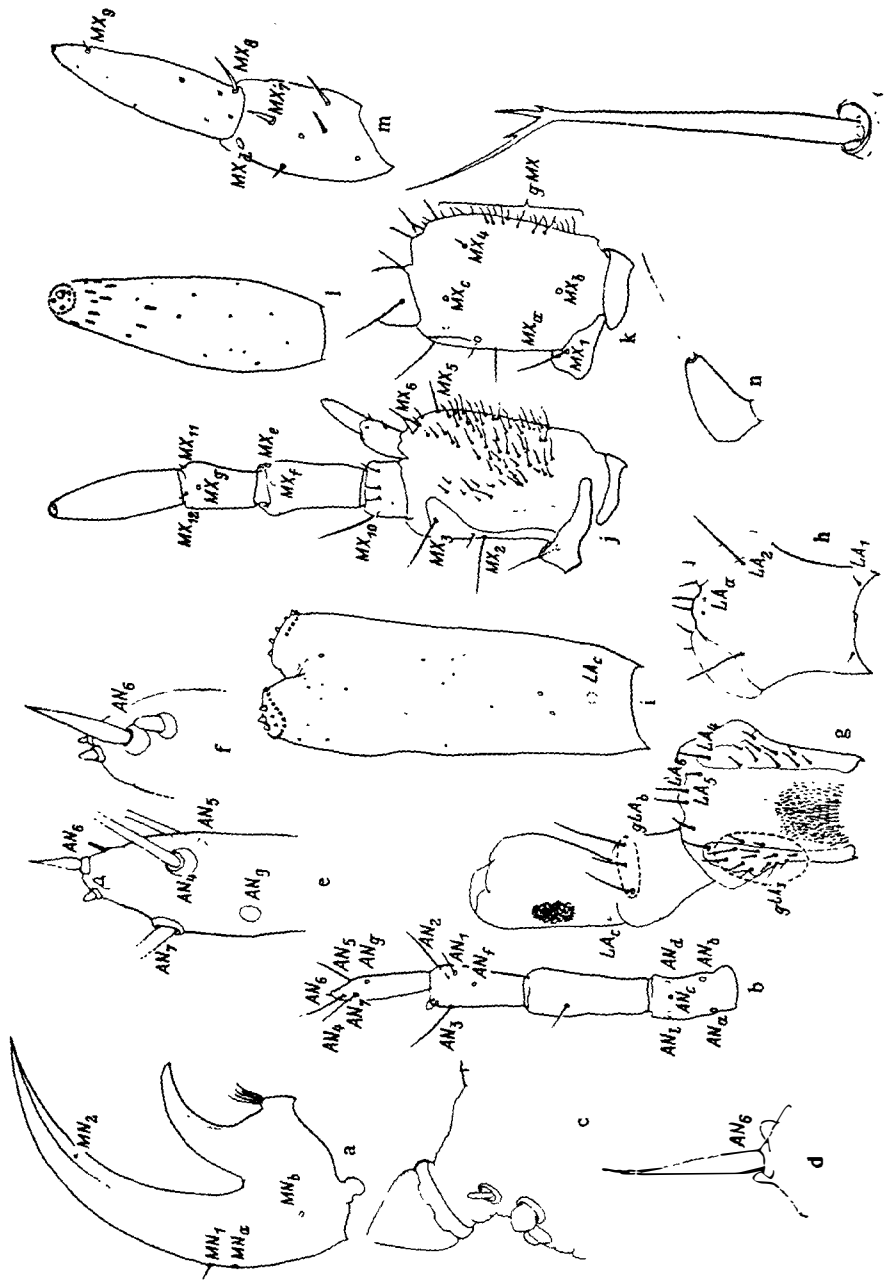
*Note* \*In larvae of instar I, in the center of the pleural organ a dark spot is always present, in some species of the group of *Neocarabus* sensu Bengtsson, 1927 the pleural organ is present in larvae of instar II, but it is pale in the middle, \*\*true only for larvae of the group of *Archeocarabus* sensu Bengtsson, 1927, \*\*\*in the group of *Neocarabus* sensu Bengtsson, 1927 only small secondary setae on sternites may be present

**Abdominal chaetome** differs from the generalized type considerably. Tergites possess a considerably smaller set of primary sensilla (minimal set of  $TE_{1,2,3,7,10,11}$ , and maximal set of  $TL_{1,2,3,4,5,6,7,9,10,11}$ ). Only primary sensilla of trichoid type (setae) are retained, all other setae are replaced by numerous secondary conical sensilla (Fig. 7a). All pleurites and ventrites of larvae are characterized by development of numerous accessory trichoid sensilla, individual numbering of which does not seem necessary. They are designated by additional group signs (Fig. 7b).

**Urogomphi** (Fig. 8c) of larvae of all instars have only the primary set of setae (only  $UR_3$  is reduced) and a slightly increased set of large sensilla. Urogomphi of *Carabus* are characterized by increase of the basal part and development of tubercles of setae  $UR_{4,5}$ , and shortening of the distal part.

**Supporting structure**, the pygidium, segment X, as well as all abdominal segments are characterized by decrease of number of primary sensilla of the tergite (the usual set is  $PY_{2,3,4,6,a,b}$  and devel-

Fig. 3 *Carabus* L. Model of structure of head of larvae: a) in dorsal view, b) in lateral view. On the left primary sensillar (nomenclature after Bousquet and Goulet, 1984), on the right segmentary zones, places of attachment of muscles, and tentorium (interpretation of segmentary zones and names of muscles are shown after Bitsch, 1966 and Das, 1937): *abmd* - abductor of mandible, *admd* - adductor of mandible, *atf* - anterior tentorial pit, *ddcb* - anterior dilator of cibarium, *ddph*<sub>1,2,3</sub> - 1st, 2nd, and 3rd upper dilators of pharynx, *ddpph* - upper dilator of prepharynx, *dtf* - upper tentorial pit, *gf* - projective frontal ganglion, *hyp* - hypodone, *mtf* - posterior tentorial pit, *os* - occipital suture, *pmmx* - muscles of maxilla, *pos* - occipital suture, *rao* - retractor of cibarium, 1) zone of protocephalon, 2) zone of deutocephalon, 3) zone of tritocephalon, 4) zone of mandibular segment, 5) zone of maxillary segment, 6) zone of labial segments, 7) sites of attachment of muscles, 8) sites of attachment of tentorium, 9) border of paraclypeus, clypeus, and frons.





opment of numerous accessory setae on the ventral surface (*gPY*<sub>7</sub>). Like the urogomphi, the basal part of the supporting structure is increased and the proximal part is shortened (Fig. 8a, b).

**Instars.** As in most ground beetles, during ontogenesis species of *Carabus* pass through 3 larval instars. Traditional morphological criteria for distinction of instars (indices of Emden, ovarian teeth) are not sufficiently reliable. If applied to larvae of this genus, values of indices *d* and *d* (Emden, 1942) in larvae with different habitus may overlap by 50-70%. Therefore, reliable determination of instar of larvae of *Carabus* is possible only by a complex of characters which take into account their taxonomical position (Table).

A key to 53 subgenera of the genus *Carabus* is offered below. This table was constructed basically on characters which are not very dependent on the instar of the larva. Exceptions are only numbers of setae in groups (*gST*<sub>1</sub>, *gPY*<sub>7</sub>, etc.); in larvae of instars I and II part of future setae may be represented by basicoeloconic and coeloconic sensilla. In cases wherein after the name of the subgenus in parentheses the species name is shown, diagnosis of the subgenus is based only on the study of larva of this species.

#### KEY TO SUBGENERA OF *CARABUS* BY LARVAE

See also table at end of key.

- 1(38). 2nd antennal segment on apex without setae (group of *Carabi brevimandibulare*).
- 2(15). Cutting edge of mandibles distal to retunaculum without sloped tooth (Fig. 9a); nasale never with 4 teeth; hypodon large, almost always well developed (Fig. 9d, e). Setae *FR*<sub>3,9</sub> single or reduced (group of subgenera of *Archeocarabus* sensu Bengtsson, 1927).
- 3(12). Pairs of setae *FR*<sub>3,3</sub> and *FR*<sub>4,4</sub> closer to each other (Fig. 9d). Accessory tooth of retunaculum present; if absent, then 2nd segment of labial palpi with only 1 sensory area. Setae *TE*<sub>8</sub> on lateral margins of tergites absent.
- 4(9). Hindcorners of abdominal sternites I-VIII without setae (Fig. 9c), *gRY*<sub>7</sub> with 1-2 pairs setae.
- 5(6). Setae *PA*<sub>9</sub> considerably shorter than *PA*<sub>7</sub>, approximately as long as diameter of ocellus. Cerci strongly granulose. Larvae black or dark brown. .... ***Morphocarabus*** Geh. + ***Trachycarabus*** Geh. (Larvae of these subgenera are very close morphologically and their division in agreement with the existing division of imago is impossible.)

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Fig. 4 *Carabus* L. Structure of appendages of head of larvae. a-d) *C. (Sphodristocarabus) janthinus* Ganglb., e, f, n, o) *C. (Megadontus) exaratus* Quens.; g, h) *C. (Plesius) staudingeri* Ganglb.; l, m) *C. (Tribax) schamyli* Hampe; a) mandible in dorsal views; b) antenna in dorsal view; c) sensory appendages of 3rd antennal segment; d, e) apex of 4th antennal segment; f) sensilla on apex of 4th antennal segment; g) labium in dorsal view, right palpus not shown; h) prementum in dorsal view; i) 2nd segment of palpus in lateral view; j) maxilla in dorsal view; k) stipes and cardo in ventral view; l) 4th segment of mandibular palpus in lateral view; m) galea; n) lacinia; n) seta of group *gMX*. Designations of sensilla after Bousquet and Goulet, 1984).

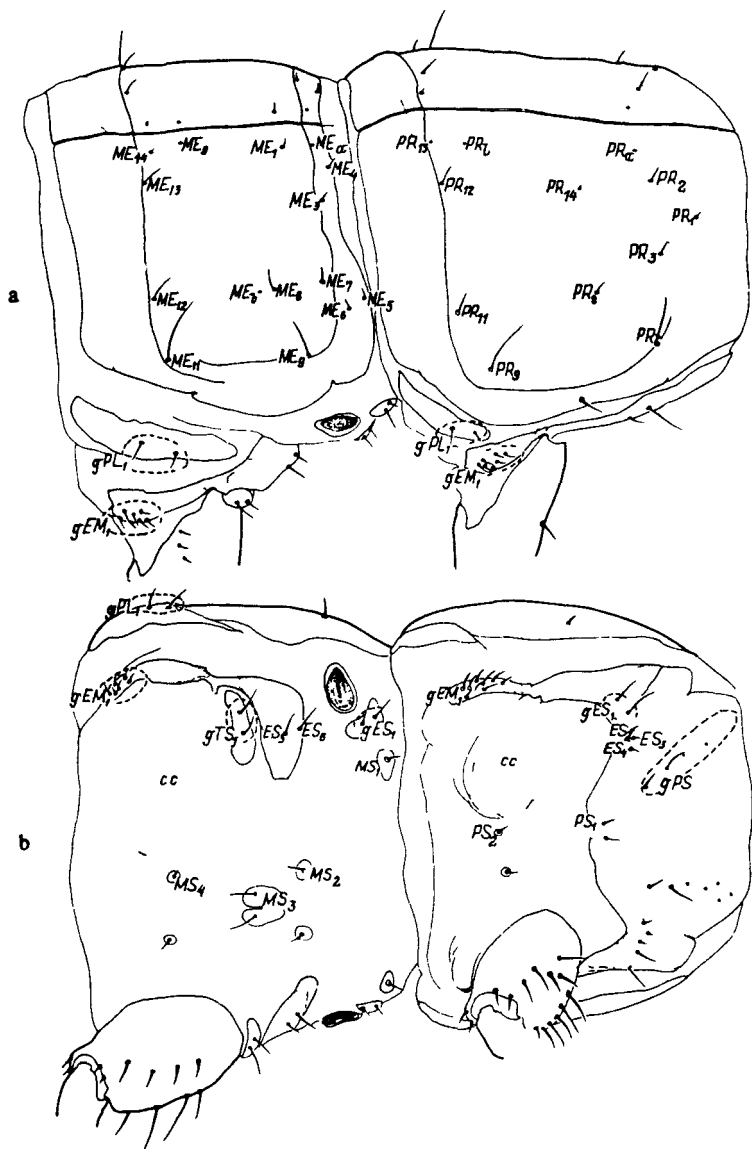


Fig 5 *Carabus* L. Prothorax and mesothorax of larva a) dorsolateral view, b) ventrolateral view  
 Nomenclature of sensilla after Bousquet and Goulet (1984) Other designations as in Fig 1

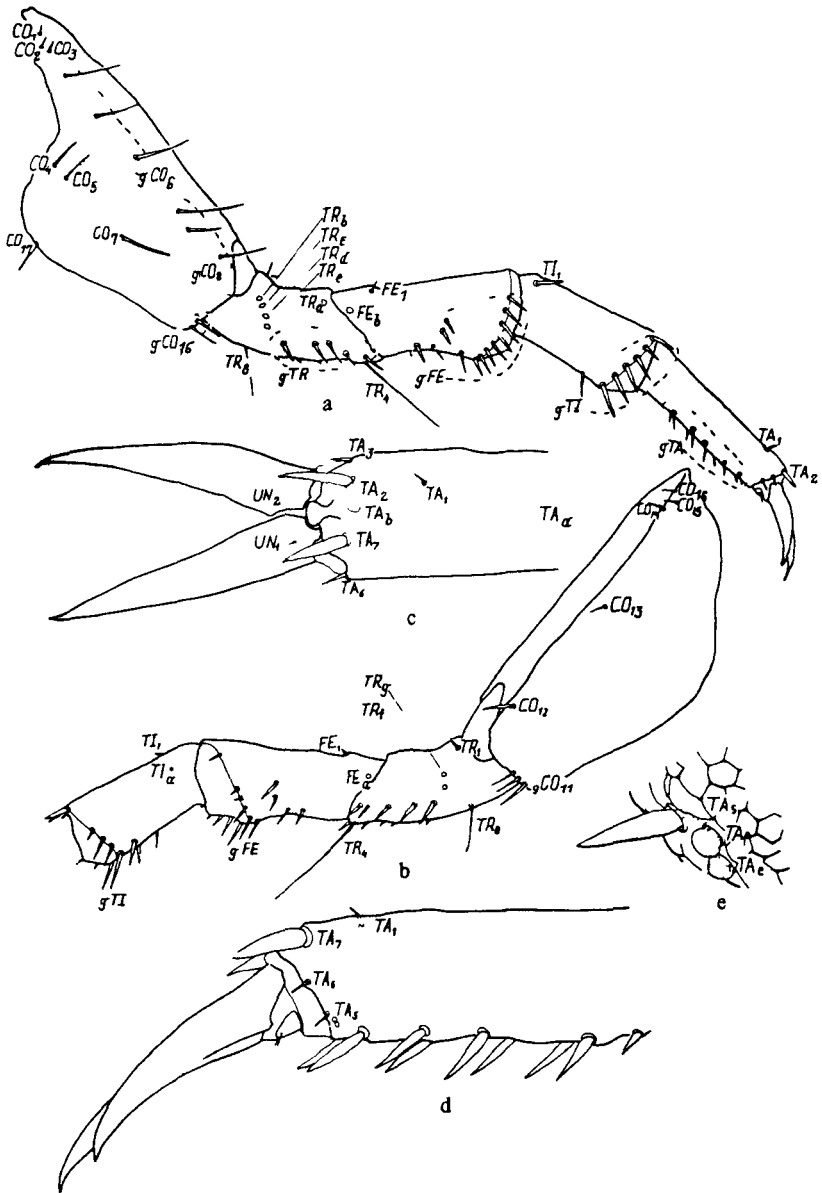
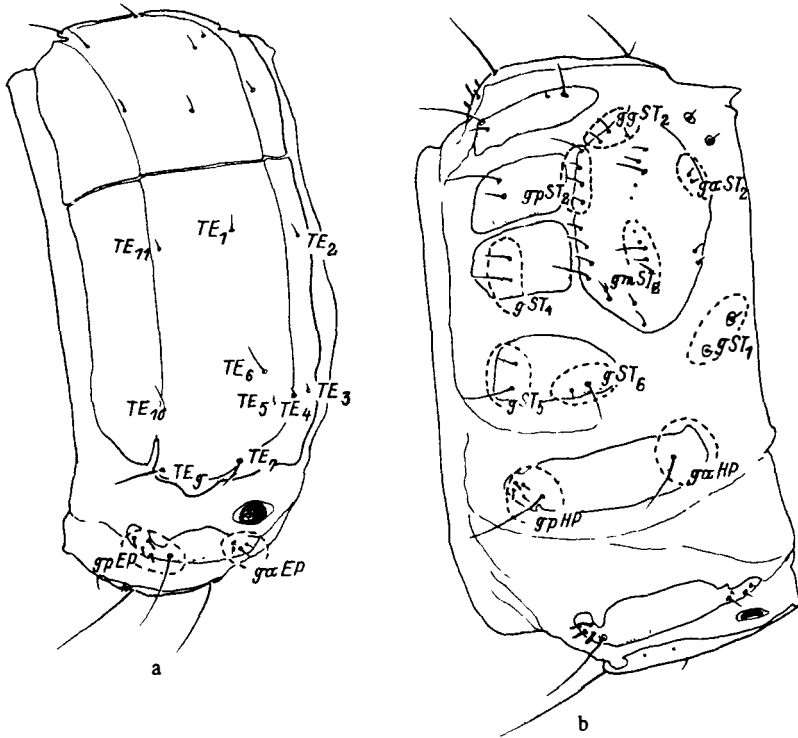


Fig 6 *Carabus* L. Leg of larva a) general anterior view, b) general posterior view, tarsus not shown, c) distal part of larva in dorsal view, d) same in lateral view, e) sensilla  $TA_5$ - $TA_7$  e) sensilla  $TA_5$ - $TA_7$  Nomenclature of sensilla after Bousquet and Goulet (1984)



**Fig. 7.** *Carabus* L. Abdominal segment of larva: a) dorsolateral view; b) ventrolateral view. Nomenclature of sensilla after Bousquet and Goulet (1984).

- 6(5). Setae  $PA_9$  only 1.5-2 times length of setae  $PA_7$ . Cerci smooth or slightly granulose. Larvae pale, yellow or yellow-brown
- 7(8). Setae  $PA_{2,3,11,12}$  almost as long as  $PA_{6,9}$ . Cerci smooth and short, their lateral tooth very small and blunt ..... *Cryptocarabus* Reitt.
- 8(7). Setae  $PA_{2,3,11,12}$  at least 3-4 times length of setae  $RT_{6,9}$ . Cerci long, slightly granulose, lateral tooth distinct and acute.
- 9(4). Hindcorners of sternite I-VIII with at least 1 seta (Fig. 9f),  $gPY_7$  with more than 2 pairs of setae.
- 10(11). Setae  $TE_{1,6}$  well developed and not or barely shorter than setae  $TE_{7,10,11}$ . ..... *Acrocarabus* Lap. (*C. callisternoides* Sem.).
- 11(10). Setae  $TE_{1,6}$  reduced ..... *Eucarabus* Geh. + *Carabus* s. str. L.

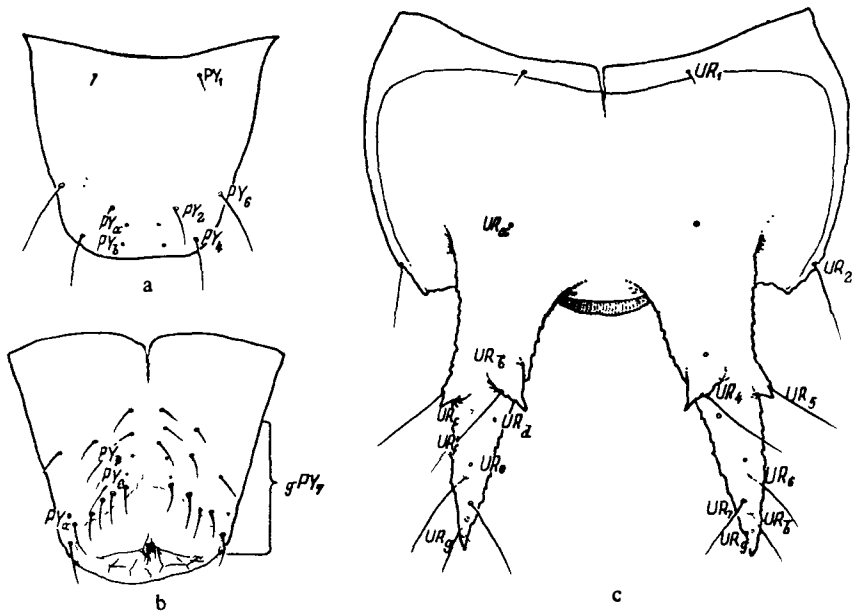


Fig. 8. *Carabus* L. Segments IX and X of abdomen of larva: a) segment X in dorsal view, b) segment X in ventral view, c) tergite of segment IX. Nomenclature of sensilla after Bousquet and Goulet (1984).

- 12(13). Pairs of setae  $FR_{3,3}$  and  $FR_{4,4}$  somewhat distant (Fig. 9e), accessory tooth of retinaculum often absent. Lateral margins of tergites with seta  $TE_8$  developed
- 13(14). Medial teeth of nasale and hypodon slightly extending (Fig. 9e), supraorbital tubercle smoothed out, 2nd segment of labial palpi with 2 sensory areas on doubled apex, cerci longer and thinner and with almost equally developed teeth..... *Archicarabus* Geh
- 14(13). Medial teeth of nasale and hypodon strongly extending (similar to those shown in Fig. 9d), supraorbital tubercle well developed, 2nd segment of labial palpi with 2 sensory areas on simple apex, cerci short and thick and dorsal tooth 1.8-2.5 times as long as lateral tooth. .... *Mimocarabus* Geh
- 15(2). Cutting edge of mandible distal to retinaculum with sloped tooth (Fig. 9b). Nasale with 4 distinct teeth, hypodon relatively smaller, sometimes not extending beyond apices of medial teeth (Fig. 10b, c). Setae  $FR_{8,9}$  always distinct and often at their place with group  $FR_{8,9}$  formed of 3-8 setae. (Group of subgenera of *Metacarabus* sensu Bengtsson, 1927)
- 16(17). Lateral margins of tergites with seta  $TE_9$  developed;  $gIST_1$  with 4-5 setae,  $gST_4$  with 3 setae,  $gST_5$  with 5 setae (Fig. 10e). Cerci longer than disc of segment IX, strongly granulose

<sup>1</sup>Diagnosis of the subgenus is constructed only from literature data (Lapouge, 1929).

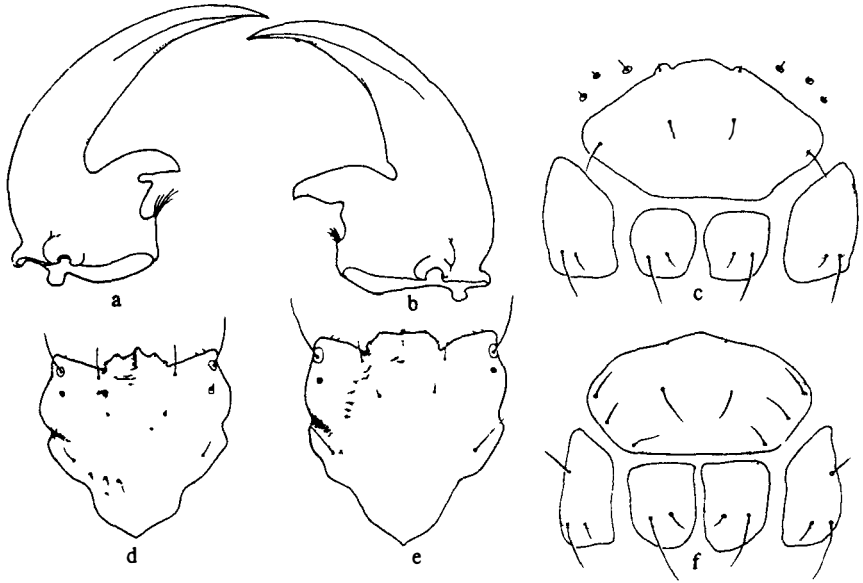


Fig 9 *Carabus* L. Details of structure of larvae a, c, d) *C. (Morphocarabus) hummeli* F - W , b) *C. (Pachycarabus) koenigi* Ganglb , f) *C. (S. Str) leandri* Kr , e) *C. (Archicarabus) memorialis* Müll a, b) Mandible in dorsal view, c, f) sternites of segment IV of abdomen, d, e) frontal sclerite

and with 2 large teeth (Fig 10d)

***Hemicarabus* Geh**

- 17(16).** Sides of tergites with seta  $TE_7$ ,  $gST_1$ , and  $gST_4$  with only 2 setae and  $gST_4$  with 3 setae Cerci of different shape
- 18(19) Outer corners of paraclypeus rounded Cerci long and thin, with 2 almost equal teeth (Fig 10a) ***Leptocarabus* (*C. procerulus* Chd)<sup>1</sup>**
- 19(18) Outer corners of paraclypeus somewhat acute and extended outside (Fig 10b, c, e) Cerci shorter and thicker and lateral tooth often reduced
- 20(27)  $gLA_b$  with only 1 seta, 4th segment of mandibular palpi always with 1 sensory area.

Fig 10 *Carabus* L. Details of structure of larvae a) *C. (Leptocarabus) procerulus* Chaud , b, g) *C. (Diocarabus) truncancolis* Esch , c, h) *C. (Pachycarabus) koenigi* Ganglb , d, e) *C. (Hemicarabus) macleayi* Dej , f) *C. (Tomacarabus) scabripennis* Schd , i) *(Hadrocarabus) problematicus* Herbst , j, k) *C. (Orinocarabus) silvestris* Pnaz , l) *C. (Aulonacarabus) canaliculatus* Ad , a) anterior margin of frontal sclerite and cerci, b, c, f) anterior margin of frontal sclerite, d) tergite IX in lateral view, g, h-j) tergite IX, right half in dorsal view, e) sternites of segment IV of abdomen, k, l) frontal sclerite, on left sculpture shown (a - after Lapouge, 1928, others original)



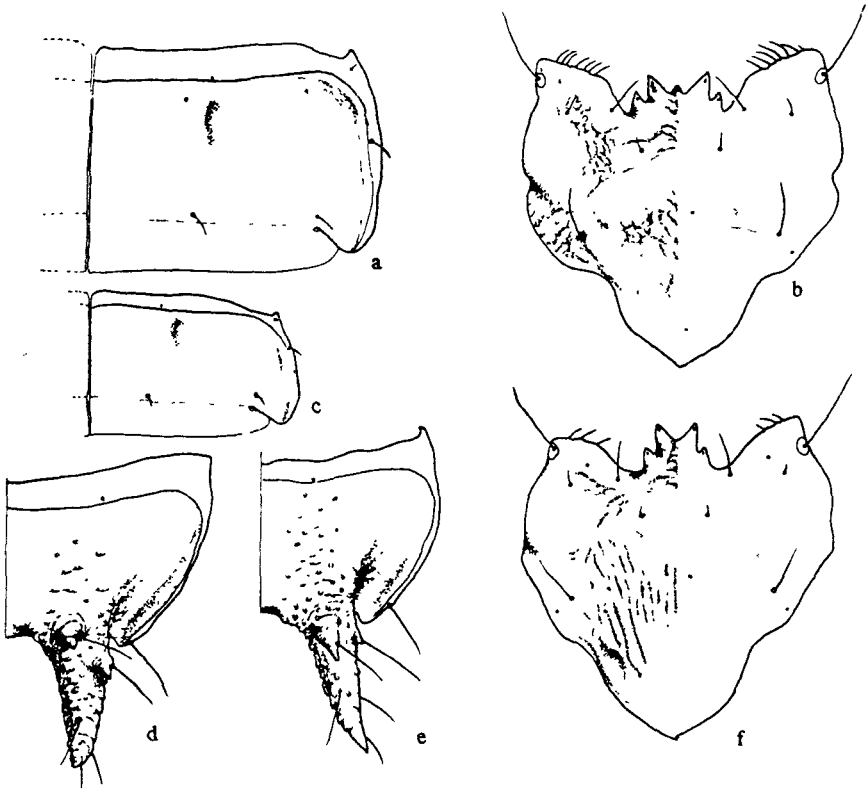


Fig. 11. *Carabus* L. Details of structure of larvae: a, d) *C. (Sennocarabus) erosus* Motsch.; c, e) *C. (Tomacarabus) krueberi* F. W.; b) *C. (Pachystus) cribellatus* Ad.; f) *C. (Sennocarabus) transiliensis* Sem.; a, c) right half of tergite of 4th segment of abdomen; b, f) frontal sclerite; d, e) tergite IV, right half.

- 21(24). Each outer notosternite with 2-3 setae; *gPY*<sub>7</sub> with not more than 7 setae.
- 22(23). Nasale extended and width of base less than length (Fig. 10b), *UR*<sub>2</sub> on apex of posterior lobes of tergite IX (Fig. 10g) 2nd segment of labial palpi shorter and wider, lobes of tergites less distinct, 4th antennal segment short, length twice its width. .... *Diocarabus* Reitt.
- 23(22). Nasale shorter and wider (Fig. 10c), *UR*<sub>2</sub> shifted to base of tergite IX (Fig. 10h), 2nd segment of labial palpi extended, 4th segment width. .... *Pachycarabus* Geh.
- 24(21). Outer poststernite with more than 3 setae, *gPY*<sub>7</sub> with not less than 8 setae.
- 25(26). Seta *UR*<sub>2</sub> in posterior third of lateral margin of tergite IX (Fig. 10j). ... *Orinocarabus* Kr.



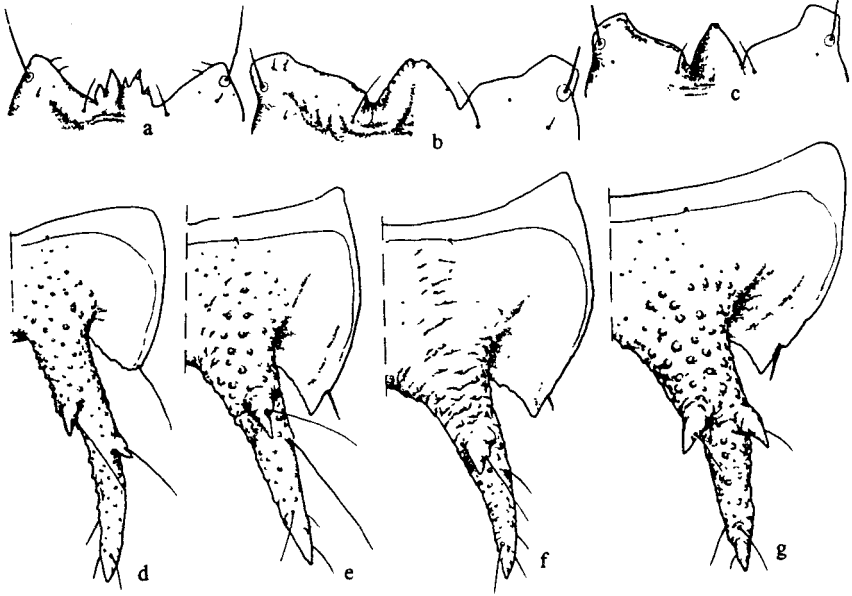


Fig. 12. *Carabus* L. Details of structure of larvae. a, d) *C. (Hygrocarabus) variolosus* F.; c) *C. (Sphodristocarabus) janthinus* Ganglb., b) *C. (Chrysocarabus) auronitens escheri* Pflrd.; e) *C. (Cechenochilus) boeberi* Ad., f) *C. (Megodontus) septemcarinatus* Motsch., g) *C. (Pachycranion) schoenherri* F. W.; a-c) anterior margin of frontal sclerite, on left sculpture shown; d-g) right half of tergite IX

- 27(20).  $gLA_b$  with 2-5 setae, 4th segment of mandibular palpi often with 2 sensory areas (in subgenus *Oreocarabus* with 1 sensory area) and sometimes with more approximated and poorly distinct sensory areas
- 28(31).  $gLA_b$  with 2 setae and  $gPY_7$  consisting of 2-4 setae
- 29(30). 4th segment of mandibular palpi with 2 approximated and fused sensory areas,  $gFR_{8,9}$  consisting of 4-7 setae, and outer metasternites with 3 setae. .... *Ulocarabus* Reitt.
- 30(29). 4th segment of mandibular palpi with 1 apical sensory area,  $gFR_{8,9}$  consisting of 3-4 setae, and outer metasternites with 1-2 setae. .... *Oreocarabus* Geh
- 31(28).  $gLA_b$  consisting of 3-5 setae and  $gPY_7$  of 4-7 setae.
- 32(33). Setae  $FR_8$  and  $FR_9$  single (Fig. 10) and 4th segment of mandibular palpi with 1 apical sensory area ..... *Aulonocarabus* Reitt. (*C. canaliculatus* Ad.).

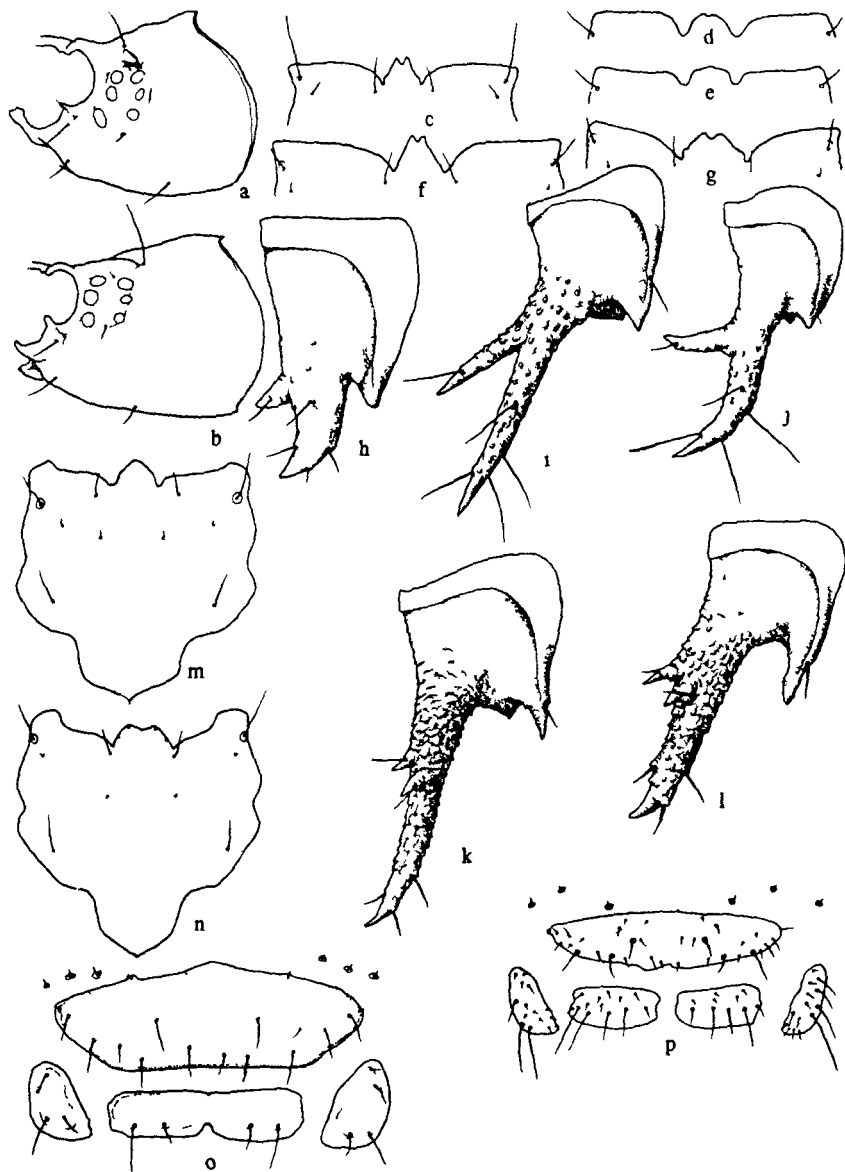


Fig 13 *Carabus* L. Details of structure of larvae a, m) *C. (Procrustes) coriaceus* L., b, i, n) *C. (Microplectes) convallium* Starck, c) *C. (Chaetocarabus) intricatus* L., d) *C. (Platycarabus) fabricii* Panz., e) *C. (Platycarabus) irregularis* F., f, k) *C. (Pantophyrtus) turcomanorum* Thieme, g, l, p) *C. (Cyclocarabus) vernus* Sem & Zn., h) *C. (Lamprostus) calleji* F-W., j) *C. (Tribax) schamyi* Hampe, o) *C. (Eotribax) cous* A. Mor., a, b) head capsule in lateral view, a-q) anterior margin of frontal sclerite, h-l) tergite IX in lateral view, m, n) frontal sclerite, o, p) sternites of abdominal segment IV (d and e - after Hurka (1971), others original)

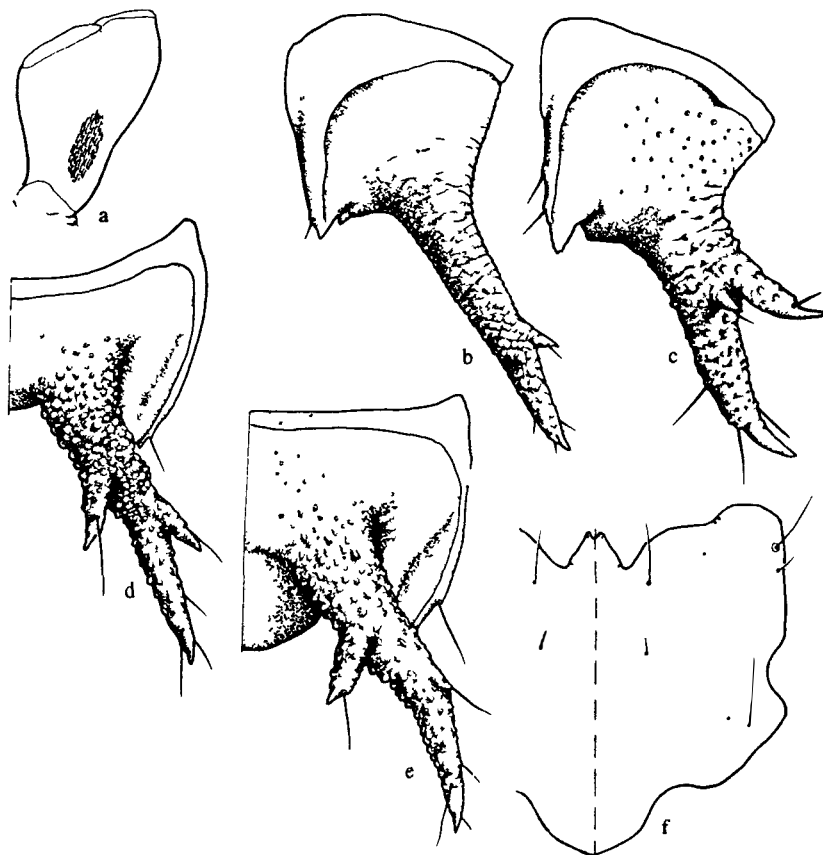


Fig 14 *Carabus* L. Details of structure of larvae a, g, i, j) *C (Eupachys) glyptopterus* F-W , b, f) *C (Axinocarabus, fedtschenko)* Sols , c) *C (Procerus) caucasicus* Ad , d, h, k) *C (Acoptolabrus) lopatin* A Mor , e) *C (Coptolabrus) smaragdinus* F-W , a) 2nd segment of labial palpus in lateral view, b, c) tergite of segment IX of abdomen in lateral view, d, e) tergite of abdominal segment IX, right half in dorsal view, f, g) frontal sclerite, right half, h, i) tergite IV of abdomen, right half, j, k) left half of head capsule and left maxilla

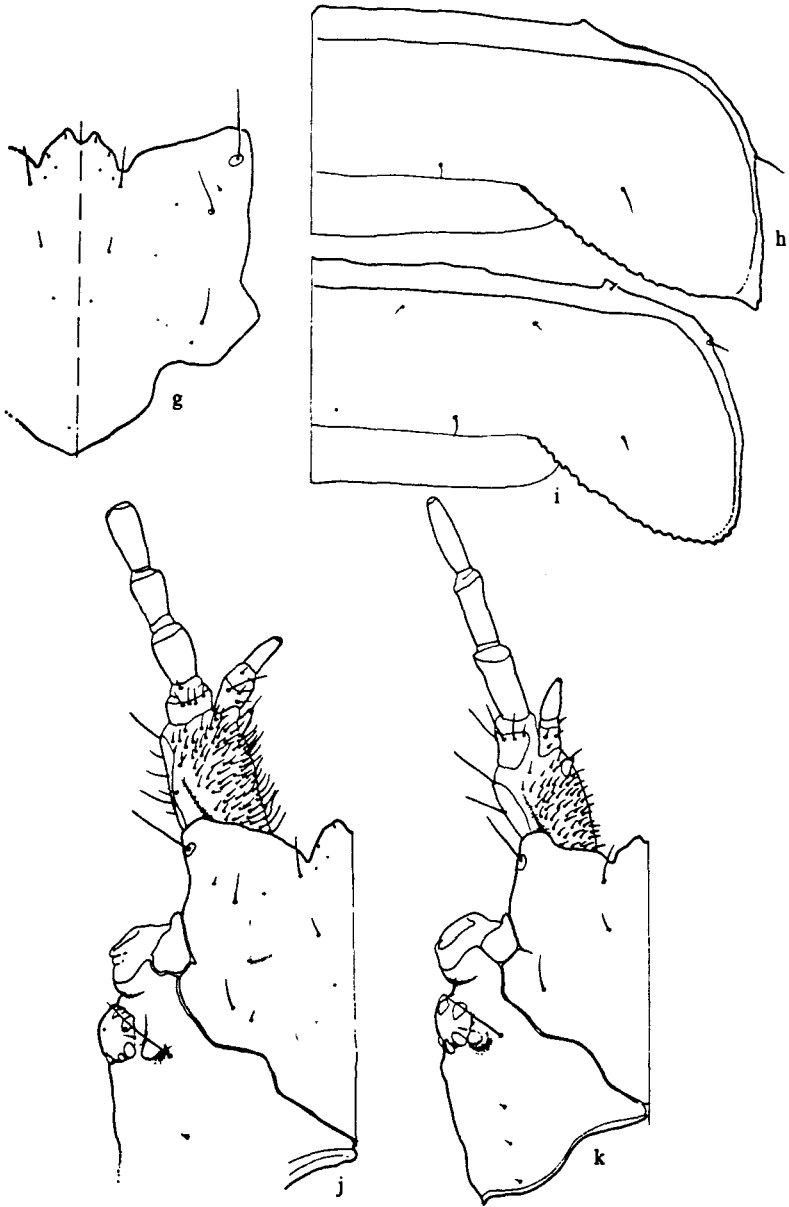


Fig. 14 (continued).

- 33(32).  $gFR_{8,9}$  with 3-6 setae (Figs. 10f, 11n, f), 4th segment of mandibular palpi usually with 2 apical sensory areas.
- 34(35). Lateral margins of abdominal tergites with rather long seta  $TE_8$  (Fig. 11a), seta  $UR_2$  often almost on apex of posterior lobes of tergite IX. Lateral tooth of cerci large and only 1.5 times length of dorsal tooth (Fig. 11d). ..... ***Semnocarabus*** Reitt.
- 35(34). Lateral margins of abdominal tergites with short seta  $TE_7$  (Fig. 11c);  $UR_2$  shifted to base of tergite IX; lateral tooth of cerci reduced (Fig. 11e).
- 36(37). Hypodon distinct, extending far beyond margin of medial emargination of nasale (Fig. 11b) and  $gLA_b$  with 4-7 setae. .... ***Pachystus*** Motsch.
- 37(36). Hypodon not apparent from above (Fig. 10f),  $gLA_b$  consisting of 3 setae and  $gFR_{8,9}$  of 4-6 setae. .... ***Tomocarabus*** Reitt.
- 38(1). 2nd segment of antenna with accessory setae (*Carabi longimandibulare* = group of subgenera *Neocarabus* sensu Bengtsson, 1927).
- 39(40). Setae  $gLA_b$ , and  $TE_{7,9}$  and setae on apex of 1st segment of mandibular palpi absent;  $UR_2$  on apex of posterior lobes of tergite IX (Fig. 12d). Nasale with 4 teeth, with large, distinct hypodon (Fig. 12a) . . . . . ***Hygrocarabus*** Thoms. (*C. variolosus* F.).
- 40(39). In  $gLA_b$  and on apex of 1st segment of mandibular palpi with at least one seta each;  $UR_2$  always shifted to base of tergite IX (Figs. 12e-g) and nasale never with 4 teeth (Figs. 12b, c).
- 41(66).  $gST_5$  and  $gST_4$  with at least 3 setae (Fig. 13n).
- 42(57).  $gST_5$  with 3 setae (in *Cechenotribax* with 3-5 setae), lateral tooth present, although small.
- 43(46). 2nd segment of antennae with only 1 seta,  $gST_4$  with 2 setae and nasale in form of triangular process, sometimes with small apical emargination (Figs. 12b, c).
- 44(45). Lateral tooth of cerci present,  $gST$  with 2 pairs of setae. Nasale as in Fig. 12b ..... ***Chrysocarabus*** Thoms.
- 45(44). Lateral tooth of cerci reduced,  $gST_1$  with 3 pairs of setae Nasale as in Fig. 12c. .... ***Sphodristocarabus*** Geh.
- 46(43). 2nd segment of antennae with 3-6 setae,  $gST_4$  usually with 3 setae, nasale never with true triangular shape.
- 47(56). Inner posternites always divided. Epicranial suture reduced, cerci more robust (Fig. 12e).
- 48(51).  $gLA_b$  consisting of somewhat similar setae;  $gST$  consisting of 4 setae; apex of 1st segment of mandibular palpi with 5-6 setae.
- 49(50). 1st segment of antennae with long seta  $AN_c$  not less than half length of sclerotized part of segment;  $gPY_7$  with more than 40 setae.

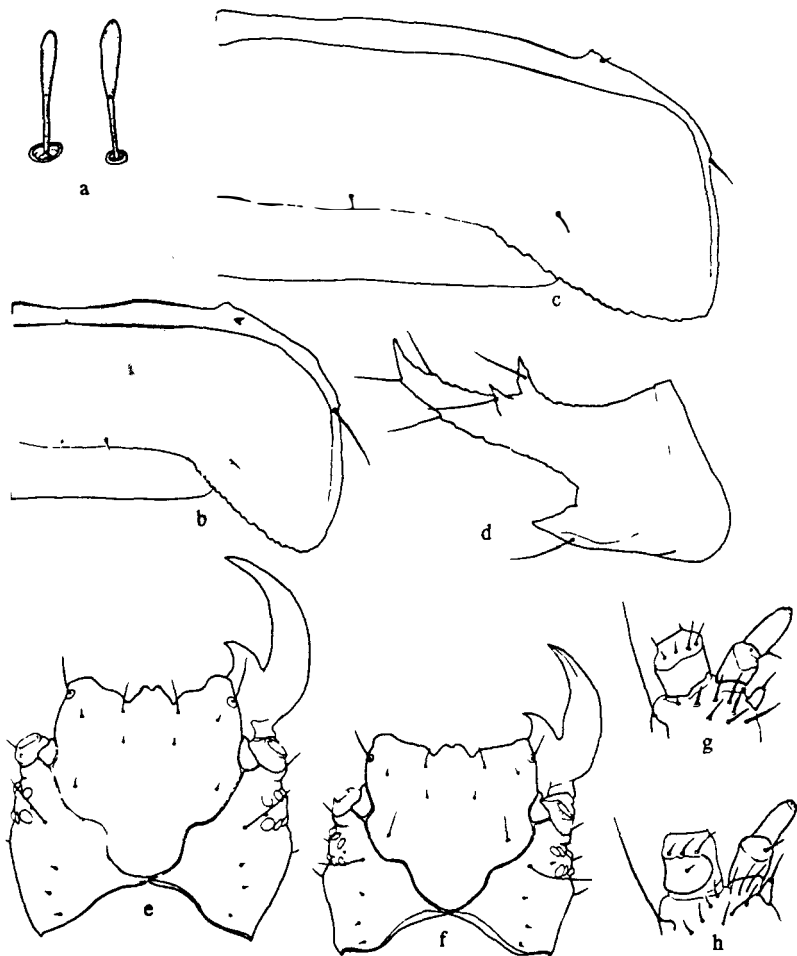


Fig 15. *Carabus* L. Details of structure of larvae a) *C. (Plesius) staudingeri* Ganglb., b) *C. (Gonicarabus) gussakovskii* Kryzh & Mich., c) *C. (Cratocephalus) cicatricosus* F-W, f, h) *C. (Alipaster) pupulus* A. Mor., g) *C. (Cratophyrtus) turcosimensis* Mandl., d, e) *C. (Pseudotrübax) validus* Kr.; a) setae  $FR_6$  (on left) and  $TE_7$  (on right), b, c) right half of abdominal tergite IV, e, f) head capsule with right mandible, g, h) apex of stipes, d) tergite IX in lateral view

- 50(49). 1st segment of antennae without setae, *gPY*<sub>7</sub> with less than 30 setae. ....  
 ..... *Eotribax* Sem. (C. ? *eous* Mor.).
- 51(48). *gLA*<sub>b</sub> consisting of 1 large and 2 small setae; *gST*<sub>1</sub> represented by 2 (rare by 3) setae; 1st segment of mandibular palpi usually with 3-4 setae.
- 52(53). *gST*<sub>4</sub> with 2 and *gST*<sub>5</sub> with 3-5 setae. Head barely narrower than pronotum; cerci almost straight and apical part distinctly shorter than basal part. ....  
 ..... *Cechenotribax* Sem. and Zn. (C. *petri* Sem. and Zn.).
- 53(52). *gST*<sub>4</sub> and *gST*<sub>5</sub> with 3 setae. Head considerably narrower than pronotum; cerci distinctly curved and basal part shorter than apical part.
- 54(55). *gPY*<sub>7</sub> with more than 25 setae; lateral tooth at cerci only slightly shorter than dorsal tooth.  
 ..... *Cratocarabus* Reitt.
- 55(54). *gPY*<sub>7</sub> with less than 20 setae; lateral tooth of cerci reduced (Fig. 12e). ....  
 ..... *Chechenochilus* Motsch.
- 56(47). Inner poststernites usually fused, epicranial suture on average not shorter than diameter of 4th antennal segment. Cerci slender (Fig. 12f, g) .....  
 ..... *Megodontus* Sol + *Pachycranion* Sol.
- 57(42). *gSI*<sub>5</sub> with only 2 setae; lateral tooth of cerci completely reduced.
- 58(59). Seta *FR*<sub>6</sub> almost in middle between *FR*<sub>4</sub> and *FR*<sub>7</sub>. Supraorbital tubercle large and strongly protruding (Fig. 13a, m). .... *Procrustes* Bon
- 59(58). Seta *FR*<sub>6</sub> closer to *FR* (Fig. 13n); supraorbital tubercle smoothed out or absent (Fig. 13b).
- 60(61). *gST*<sub>4</sub> and *gST*<sub>5</sub> with 1 seta each ..... *Archiplectes* Gottw.
- 61(60). *gST*<sub>4</sub> and *gST*<sub>5</sub> with at least 2 setae each.
- 62(63). 1st segment of mandibular palpi with only 1-2 small apical setae; 2nd antennal segment with seta; cerci short and thick and with robust dorsal tooth (Fig. 13h) .....  
 ..... *Lamprostus* Motsch.
- 63(62). Apex of 1st segment of mandibular palpi with 3-4 large setae; cerci longer and narrower (Fig. 13i; j).
- 64(65). Nasale with apical emargination and cerci almost straight (Fig. 13i). ... *Microplectes* Reitt.
- 65(64). Nasale without apical emargination and cerci always somewhat curved (Fig. 13j). ....  
 ..... *Tribax* Fisch. + *Microtribax* Gottw.
- 66(41). *gST*<sub>5</sub> and *gST*<sub>4</sub> with at least 4 setae each (Fig. 13p).
- 67(74). Anterior margin of paraclypeus not sinuate (Fig. 13c-g).

- 68(71). Lateral margins of abdominal tergites with setae  $LE_7$  and  $TE_9$ , 1st segment of labial palpi with only 1 seta  $LA_6$ , apex of 2nd segment of mandibular palpi with 1-2 setae and 1st segment without setae.
- 69(70). 4th segment of mandibular palpi with 2 sensory areas and anterior margin of nasale rather deeply emarginate (Fig. 13c). ..... *Chaetocarabus* Thoms. (*C. intricatus* L.)
- 70(69). 4th segment of mandibular palpi with single sensory area; anterior margin of nasale slightly or not at all emarginate (Fig. 13d, e). ..... *Platycarabus* Mor.
- 71(68). Lateral margins of tergites with only one seta  $TE_7$  (sometimes doubled); apex of 1st segment of labial palpi with 1 long and 2-3 short setae; 2nd segment of mandibular palpi with at least 3-4 setae and 1st antennal segment with at least 1 seta.
- 72(73). Nasale almost as long as wide (Fig. 13f) and cerci longer and thinner (Fig. 13k) ..... *Pantophyrus* Thieme.
- 73(72). Width of nasale almost twice length (Fig. 13g), urogomphi shorter and thicker (Fig. 13g). ..... *Cyclocarabus* Reitt.
- 74(67). Anterior margin of paraclypeus sinuate (approximately as in Fig. 13m, n).
- 75(85). 1st segment of galea with 2 well separated sensory areas (except in subgen. *Acoptolabrus* Mor.); 2nd segment of labial palpi very wide and with 2 large reniform sensory areas (Fig. 14a).
- 76(79). Seta  $FR_6$  close to lateral margin of paraclypeus (Fig. 14f); 1st segment of labial palpi with setae on sclerotized part.
- 77(78). Seta  $FR_3$  reduced. Cerci almost straight, lateral tooth barely indicated (Fig. 14b); tergites of abdomen bearing only lateral setae  $TE_7$  and ventrites covered with short spinose setae. Dorsum black and with weak metallic sheen. .... *Axinocarabus* Mor.
- 78(77). Setae  $FR_3$  developed, cerci rather curved and lateral tooth large (Fig. 14c). Tergites with 3-9 lateral setae, among which large setae  $TE_{7,8,9}$  may be conspicuously large; ventrites covered with long and thick setae. Dorsum with rather bright metallic blue sheen. .... *Procerus* Dej.
- 79(76). Seta  $FR_6$  only between setae  $FR_7$  and  $FR_4$  (Fig. 14g) and 1st segment of labial palpi bearing setae only on apex
- 80(81). Posterior angles of abdominal tergites rounded (Fig. 14i), mandibular palpi shorter and thicker and not longer than frontal sclerite (Fig. 14j); 1st segment of antennae without setae. .... *Eupachys* Chaud. (*C. glyptopterys* F.-W.).
- 81(80). Hindangles of abdominal tergites acute (Fig. 14h); mandibular palpi longer and thinner and not shorter than length of any sclerite (Fig. 14k), 1st antennal segment with 1-2 setae.
- 82(83). 4th segment of mandibular palpi with 1 sensory area; lateral tooth of cerci almost as long as dorsal tooth and cerci very coarsely granulose (Fig. 14d). .... *Acoptolabrus* Mor.



- 83(82). 4th segment of mandibular palpi with 2 sensory areas; lateral tooth of cerci a little shorter than dorsal tooth and granulose sculpture of cerci weaker (Fig. 14e).
- 84(85). Setae  $TE_7$  single; mandibular palpi and antennae relatively shorter; supraorbital tubercle strongly protruding upward ..... *Coptolabrus* Sol.
- 85(84).  $gTE_7$  present and consisting of 4-7 setae; mandibular palpi and antennae very long; supraorbital tubercle very small and barely protruding. .... *Damaster* Kol. (*C. blapoides* Kol.).
- 86(75). First segment of galea without accessory setae, if with 1-2 setae, then 4th segment of mandibular palpi with single sensory area.
- 87(90).  $gmST_1$  consisting of 3-5 setae,  $gPY_7$  with not fewer than 50 setae, setae  $FP_2$ ,  $PA_9$  and  $TE_{1,6,10,11}$  clavate (Fig. 15a)
- 88(89). Lower ocellus in posterior row considerably smaller than adjacent ocelli; labium shorter than  $gLA_3$ , consisting of 10-15 setae; secondary sculpture of head capsule weaker. .... *Deroplectes* Reitter.
- 89(88). Lower ocellus in posterior row only slightly smaller than adjacent ocelli; labium longer than  $gLA_3$ , consisting 20-22 setae and secondary sculpture of head capsule coarse. .... *Plesius* Sem.
- 90(87).  $gmST_1$  consisting of 1-2 setae,  $gPY_7$  with at least 40 setae, only seta  $PA_9$  may be clavate.
- 91(92). Lacinia with 2-3 setae on apex; 4th segment of labial palpi with 2 sensory areas, setae  $gLA_b$  not differentiated; setae  $PR_{12}$ ,  $ME_9$ ,  $TE_7$  long (Fig. 15b)..... *Goniocarabus* Geh.
- 92(91). Lacinia with only 1 seta on apex; 4th segment of labial palpi with 1 sensory area;  $gLA_b$  consisting of 1 large and 2-3 small setae,  $PR_{12}$ ,  $ME_9$ , and  $TE_7$  shorter (Fig. 15c)
- 93(94). 1st segment of antennae without setae (in *C. halassoglossus* with single spinose seta),  $gmST_1$  with 1 (rare with 2) setae ..... *Cratocephalus* Kirsch.
- 94(93). 1st segment of antennae with 1-5 setae;  $gmST_1$  with 2 setae.
- 94(96). Teeth of cerci relatively small, length considerably less than width of base of cerci (Fig. 15d); 1st segment of antennae with 3-5 setae on apex; genae in area of setae  $PA_{14}$  slightly convex (Fig. 15e)..... *Pseudotribax* Kr.
- 96(95). Teeth of cerci large, length of dorsal tooth not less than width of base of cerci; 1st antennal segment with 1-2 setae on apex; genae in area of setae  $PA_{14}$  swollen (Fig. 15f).
- 97(98). Seta  $MX_8$  on connecting membrane of 1st and 2nd segments of galea (Fig. 15g); setae on apex of 1st segment of antennae well developed, not shorter than diameter; lateral surface of head between setae with  $PA_{11}$  and  $PA_9$  thin, longitudinal carina extended; epipleura of mesonotum and metanotum with 1-2 setae. .... *Cratophyrtus* Reitt. (*C. turcosinensis* Mandl.).

- 98(97). Seta  $MX_8$  at base of 2nd segment of galea (Fig. 15h); setae on apex of 1st segment small and poorly distinguishable; carina on lateral surface of head absent; and epileura of mesonotum and metanotum without setae. .... *Alipaster* Reitt. (*C. pupulus* Mor.).

#### LITERATURE CITED

- ARNDT, E. 1985. Larvenbestimmungsschlüssel der *Carabus* Arten Europas (Col., Carabidae). Entomol. Nachr. Ber. 29(2): 49-62.
- BENGTSSON, S. 1927. Die Larven der nordischen Arten von *Carabus* Lin. Lunds Univ. Artskr., N. F. 2, 29(2): 49-62.
- BITSCH, J. 1966. L'Évolution des structures céphaliques chez les larves de Coléoptères. Ann. Soc. Entomol. Fr. (N. S.), 11(2): 255-328.
- BOUSQUET, Y., and H. GOULET. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). Canad. J. Zool. 62: 573-588.
- BREUNING, S. 1932. In: Monographie der Gattung *Carabus*. Bestimmung-Tab. d. Europ. Coleopteren. Troppau 104: 1-238; 105: 239-296; 106: 499-794; 1933, 107; 795-912; 1934, 108: 913-1112; 1935, 109: 1113-1360; 1937, 110: 1361-1610.
- BRULLE, A. 1835. Histoire Naturelle des Insects. Vol. V. Paris.
- DAS, G. 1937. The musculature and mouthparts of insect larvae. J. Microscop. Sci. 80: 39-80.
- DU PORTE, E. 1960. Evolution of cranial structure in adult Coleoptera. Canad. J. Zool. 38(3): 655-675.
- EMDEN, F. VAN. 1942. A key to the genera of larval Carabidae (Col.). Trans. Entomol. Soc. London 92: 1-99.
- GOULET, H. 1977. Technique for the study of immature Coleoptera in glycerine. Coleopt. Bull. 31: 381-382.
- HINTON, H. 1963. The ventral ecdysal lines of the head of endopterygote larvae. Trans. R. Entomol. Soc. London 115: 39-61.
- HURKA, K. 1971. Larvae der mitteleuropäischen *Carabus* und *Procerus*-Arten. Rozpr. Čechosl. Akad. Věd. Rada Mat. a Přírod. Věd. Ročn. 80, sčs 8: 1-135.
- ISHIKAWA, R. 1973. Notes on some basic problems in the taxonomy and phylogeny of the subtribe Carabina. Bull. Nat. Soc. Sci. Mus. Tokyo 16(2): 191-215.
- ISHIKAWA, R. A. 1979. A preliminary revision on the Carabogenici of the subtribe Carabina. Bull. Nat. Sci. Mus. Tokyo, ser. A (Zool.) 5(2).
- LAPOUGE, G. DE 1905. Tableaux de détermination des larves de *Carabus* et de Calosomes. L'Echange, Rev. Linn. de Moulins 21(248): 159-160; No. 249; 164-165, No. 250; 171-173.

- LAPOUGE, G DE 1929 Coleoptera Adepnaga subfam Carabinae Gen Ins fasc 192a. 1-129
- LARSSON, S 1941 Larven In Hansen, V (Ed ) Cicindelidae oy Carabidae Copenhagen 243-360
- MIKHAYLOV, V A 1978 Larvae of ground beetles of the genus *Carabus* from Central Asia. [In Russ ]  
Zool zh 57(6) 851-856
- SHAROVA, I KH 1958 Larvae of beneficial and agriculturally destructive ground beetles [In  
Russ ] Uchen Zap Mosk Gos Ord Lenin Inst 124(7) 4-164
- SHAROVA, I KH 1964 Family Carabidae [In Russ ] In Gilyarov, M S (Ed ) Oprelitel'  
obitayushchikh v pochve lichnok nasekomykh (Key to Larvae of Insects Living in the Soil)  
Moscow 112-195
- STURANI, M 1962 Osservazione e ricerche biologiche sul genere *Carabus* Linnaeus (sensu lato)  
(Coleoptera, Carabidae), Mem Soc Entomol Ital 41 85-202