

Patterns of chaetome modifications in ground-beetle larvae (Coleoptera: Carabidae)

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Abstract. Important features of larval chaetome in Carabidae (Coleoptera), and principles of identification and homologisation of elements have been analyzed. Satisfactory homologisation of certain chaetome structures is possible only when additional markers, i.e. sigillae are used in analysis. Typology and topology of chaetome are described; new designations for a number of structures are suggested. Functional model of carabid larvae chaetome is discussed in its adaptive integrity based on correspondence of structure and functions of sensillae. Main chaetome functions are described, i.e. covering, sensory, locomotory, and feeding-related; different types of their realization are considered. Main ways of chaetome restructuring are distinguished and described. It is shown, that possibilities of chaetome modification in carabid larvae are restricted in general to three main types: oligochaetosis, heteropolychaetosis, and homopolychaetosis; they are specific within taxa of tribe rank. Chaetome modification type has to be taken into account in the studies of larvae taxonomy, and in elaboration of identification keys. „Primary“ set of sensillae as by Bousquet & Goulet (1984) is not plesiomorphic for carabids. It is suggested that primitive state of chaetome is characterized by irregular distribution of sensillae, and by slight differentiation of general structures. Key direction of chaetome evolution is optimization of sensory and covering functions; morphologically it is expressed in stabilization of chaetome and in formation of constant complexes of different sensillae. Ways of chaetome modifications are specific for certain taxa, and their analysis can be used for elaboration of relationship scheme in carabids.

Chaetotaxy, morphology, larva, Coleoptera, Carabidae

INTRODUCTION

Characters of chaetotaxy have been used in the systematics of ground-beetle larvae since the beginning of this century. However, their applicability has been hampered by the lack of a convenient system of designations. The attempts undertaken have mainly pursued but utility goals, that is, brevity of a description and/or compilation of keys to species of individual genera (e. g., Emden 1935 for Cicindelinae alacosternale sensu Horn 1926, Nichols 1986 for *Antilliscaris* Bänniger, 1937). Carabid larval chaetome being highly diverse and variable, this has not allowed to apply those schemes for other genera. It has long been quite clear, however, that a universal model of chaetotaxy can be developed concerning only a restricted set/number of setae. Designating only the biggest cephalic setae, Habu & Sadanaga (1961) have pioneered this work. This scheme has been applied to various ground-beetle groups (Habu 1973, 1981, Habu & Sadanaga 1961, 1965, 1970, Harris 1978, Zetto Brandmayr & Brandmayr 1978). A different practice of limiting the number of designated elements, which lies in using the chaetome of instar I, has been developed by Goulet (1983). In a modified way (Bousquet & Goulet 1984) that designation approach of the „primary setae and pores“ has gained the general acceptance. However, an over decade-long usage of that classification has revealed a number of defects which considerably restrict its applicability. First of all, this concerns the ambiguous term „pore“ (Makarov 1990, 1991; Maddison 1993) and highly formally criteria for delimiting „primary“

structures (Makarov 1991, 1993). This creates difficulties in designating the setae in larvae with strongly modified chaetome forcing some modern authors (e. g., Moore & Lawrence 1994) even to abandon approach of Bousquet & Goulet (1984) altogether.

According to Bousquet & Goulet (1984: 574) „setae and pores on the first instar larvae and their homologous structure on subsequent instars“ are just primary. Yet such a criterion of priority fails in very many cases.

First, among some ground-beetle larvae from the tribes Cicindelini, Elaphrini, Anthiini, Heluonini, etc., instar I displays more or less numerous accessory setae. Second, contrary trend is observed in a number of groups (Carabini – Makarov (1993), Bembidiini – Maddison (1993), Trechitae – Grebennikov (1995)), with instar I without some chaetome elements. A „primary“ set of pores is currently perceived as mainly plesiomorphic, though with neither proper embryological nor paleontological background, e. g., Arndt (1993). However, a study of well-preserved fossils (Makarov 1995) reveals that this requires confirmation.

It is thus reasonable to consider the scheme by Bousquet & Goulet (1984) as designating the most common set of cuticular sensory structures in carabid larvae. In this connection, below I shall avoid the notion „primary“, instead using „general“ as applied to the primary structures in the sense of Bousquet & Goulet (1984).

It is also noteworthy that technical difficulties in studying the carabid larval chaetotaxy force many authors to use traditional, largely macrostructural features as the leading diagnostic characters (Arndt 1993, Makarov 1994). Hence, chaetome characters serve rather for unravelling the relationships and for constructing phylogenetic trees or clades. In this way, chaetome structures require further investigations. Discarding phenetic schools, the basic characters underlying a phylogenetic reconstruction ought to meet a number of rather serious demands: (a) reliable homologization, (b) an exact revelation of the polarity/modality of a variation series, and (c) a low probability of a character's reversed condition (Ax 1987, Pesenko 1993). Though a phylogenetic importance of larval features has been repeatedly discussed (Goulet 1978, Arndt 1989, 1993, Makarov 1990), to the best of knowledge, no special evaluation of chaetome characters has hitherto been performed.

MATERIAL AND METHODS

Material serving the basis for this work is housed in the collection of Zoology and Ecology Department of the Moscow Teachers' Training University. This material comprises 453 species from 84 genera and 39 tribes, mostly fixed in 70% ethanol. Besides, larvae of beetles from other families have been studied (Dytiscidae – 4 species, Hydrophilidae – 4, Staphylinidae 5, Histeridae 2, Dryllidae – 1, Cantharidae – 2, Elateridae – 3, Tenebrionidae – 2) as well as larvae of allied Neuroptera (Osmylidae, Ascalaphidae and Myrmeleonidae - one species from each), for detailed list of material examined see Appendix. A proportion of samples is mounted either as constant micropreparations with the Faure-Berlese medium or as temporary micropreparations with glycerol, according to the conventional techniques. Altogether, 1780 specimens have been treated. Larvae were examined under MBS -1, MBI-2 and P-16 stereomicroscopes at magnitudes ranging from 6× to 900×.

Some fine structures of larvae were studied with a Cambridge Stereo-Scan 250MX and Hitachi S-450 scanning electron microscopes.

Statistics was performed for revealing the variation range of setal size groups. For this purpose, 8 model species (*Nebria kirgisica*, *Diacheila fausti*, *Blethisa multipunctata*, *Elaphrus lapponicus*, *Clivina fossor*, *Asaphidion flavipes*, *Agonum muelleri*, *Harpalus rufipes*, *Panagaeus cruxmajor*, *Cymindis lateralis*) were chosen for measuring the length of the setae on the frontal and parietal sclerites, on the pronotum, on abdominal tergite and sternite IV and on the urogomphi. From 6 to 25 setae have been measured on each of the sclerites, with their relative lengths considered as percentage of the longest (100%). Grouping was undertaken using K-means clustering with the program STATISTICA 4.3.

Suprageneric taxa accepted here are mainly according to the system proposed by Kryzhanovskij (1983) and Kryzhanovskij et al. (1995). Notation of setae and pores follows that of Bousquet & Goulet (1984).

Tab. 1. Representation of „general“ set setae and density of sensillae on body surface of some Carabidae larvae. (R – level of chaetome reduction, portion of seta in % from „general“ set; N – average number of all sensillae on 1 cm² of sclerite surface.)

Species	Sclerite							
	Frontale		Parietale		Sternum		Tergum	
	R	N	R	N	R	N	R	N
<i>Calosoma auropunctatum</i>	100	11.8	88	16.3	100	13.3	66	22.2
<i>Carabus glabratus</i>	94	23.7	70	22.2	100	11.8	60	32.6
<i>C. convallium</i>	82	22.2	65	20.7	100	13.3		26.6
<i>C. janthinus</i>	70	14.8	62	14.7	100	39.9	47	15.2
<i>C. cumanus</i>	82	20.7	70	23.7	83	8.9	60	23.7
<i>C. circassicus</i>	82	11.8	56	19.2	83	7.4	40	17.8
<i>C. protensus</i>	76	9.2	53	12.5	83	3.9	40	4.4
<i>Cychrus caraboides</i>	58	14.4	64	24.4	100	7.5	26	19.4

RESULTS

Phylogenetic evaluation of chaetome features

A study of the topography of larval sensillae in various beetle families (Hydrophilidae, Staphylinidae, Dytiscidae) shows that numerous, particularly soil-dwelling forms display a chaetotaxy often thoroughly similar to that typically occurring in ground-beetles. And several complexes of sensillae (e. g., PA_{1,2,3,a}; PA_{6,17,m,n}; FR_{1,a}) are traceable even among such taxa phylogenetically remote from ground-beetles as Tenebrionidae. For example, when comparing with the generalized carabid type, 16 out of 19 setae and 7 out of 15 „pores“ are reliably identifiable in the larvae of *Helophorus* (Hydrophilidae) (Fig. 2). A similar pattern is observed also among certain larvae of Staphylinidae (Figs 3, 4) and even in Elateridae (Fig. 12). The chaetome of tergites and sternites is often even more alike (Figs 5–11). For comparative purposes, it suffices to recall that, among the Carabini larvae, there are only 15 setae and 10 „pores“ on the parietal sclerites. Amongst lesser larvae of the supertribe Trechitae, a considerably reduced set of pores is marked (Grebennikov 1995), and soon.

Hence, as regard a similarity of larval chaetomes of various beetle families, only two hypotheses seem admissible: either the tipization is possible only at the order level (this being a fundamental feature of all beetle larvae), or the chaetome's adaptive modifications exceed significantly the extent of inadaptable restructurings within the family.

The larval chaetome of ground-beetles poorly resembling that of aquatic Adephaga (Dytiscidae, Gyrinidae), this is rather evidence favoring the second alternative. Thus, the resemblance between the generalized chaetome larval types of carabid and the typical diving beetle genus *Ilybius* (Adephaga: Dytiscidae) is significantly less than, for example, with the near-water genus *Helophorus* (Polyphaga: Hydrophilidae) (Figs 1, 2, 5, 6, 8, 11). More often these are sensillae which location is restricted to the sigilla both of the larger muscles (abductors and adductors of the mandibles, etc.) and endoskeleton.

Consequently one may speculate that, the structure of a chaetome is significantly determined by the way of larval life. The structural particularities are displayed only at the level of most strongly interrelated complexes of sensillae and sigilla. Thus, a generalized chaetome in the sense Bousquet & Goulet (1984) cannot be regarded ancestral to ground-beetles.

One more problem of a phylogenetic interpretation of chaetome characters is related to the difficulties in evaluating the plesiomorphies. The fact that a number of „primary“ sensillae are

lacking while „secondary“ setae are present in instar I larvae of certain tribes (Carabini, Cychnini, Brachinini, Dyschiriini, etc.) means that a generalized chaetome in the initial sense (Bousquet & Goulet 1984) is treated perhaps too formally and includes also „secondary“ structures. Besides that, in the cases when some chaetome elements are missing, it appears impossible to attribute that to convergences (homoplasy) or to symplesiomorphies, and this can result in wrong kinship evaluations. In addition, a possible instauration has been demonstrated for a number of insect structures, that is, repeated origins of a phenotypically lost feature due to conservation of genetic copies; setae thereby appear particularly strongly inclined to that process (Emelyanov 1987).

All this evidently questions the utility of the chaetome for studies on carabid phylogeny. In my opinion, the only way out lies in modifying the methodology of evolutionary reconstruction of larvae.

To a considerable extent, imaginal evolution is related to the development of reproductive isolation mechanisms, often without expressed adaptive roles. In contrast, the evolution of pre-imaginal stages is mainly adaptive. A natural way of reconstructing their phylogeny would lie in an analysis of their adaptive systems and functions.

As applied to arthropods, an evolutionary method of phylogenetic reconstructions based on an interpretation of adaptive traits of functional systems has been developed by Manton (1959, 1977). As regards ground-beetles, these problems have been analyzed mainly by Evans (Evans 1980, 1982, 1986, Evans & Forsythe 1984), the locomotor system of the imago taken as an example. It has been noted therewith that adaptive systems display polarity more readily and are not subjected to reversions (the law of progressive specialization). No study of larvae in this aspect has hitherto been conducted.

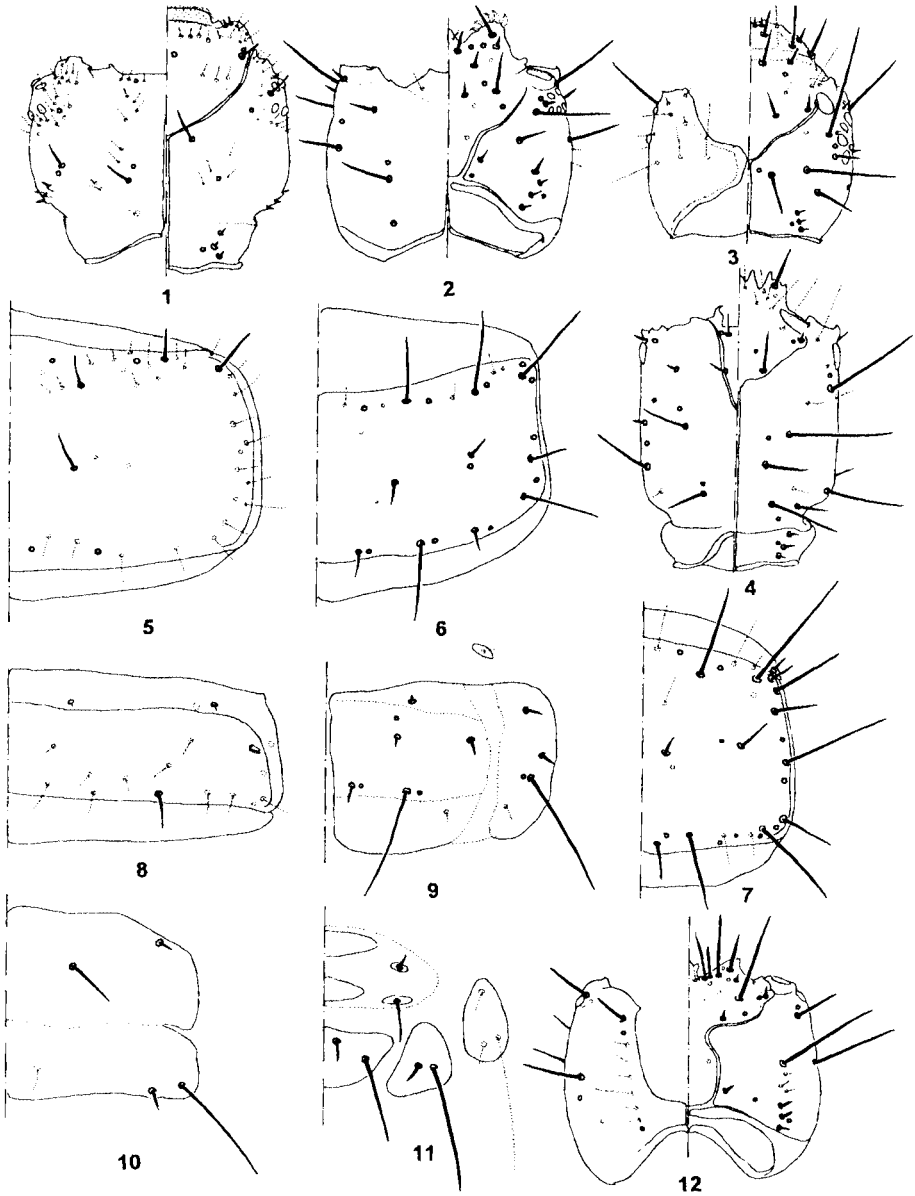
Hence, the objective of the present work can be defined both as a morphofunctional description of the chaetome and an analysis of its modifications.

Chaetome as a whole

The chaetome in a strict sense is understood here as all cuticular structures associated with primary external receptors, i.e. sensillae. Hence, the main function of a chaetome is sensory. In a broad sense, the chaetome also encompasses microtrichia (Fig. 44a) and spines (Fig. 29), i. e. a number of cuticular derivatives closely interacting with sensory elements. Multifunctionality of many sensillae and their interactions with non-sensory structures extend significantly the set of the functions carried out by a chaetome (see below).

In general, a ground-beetle larval chaetome can be characterized by the following particulars: (a) great diversity of sensillae, with numeral dominance of trichoid and basiconical mechanoreceptors; (b) low number of sensillae-distant receptors; (c) infrequent occurrence of complex setae of complex form; (d) absence of compound sensory organs (chordotonal and others al.), their functions taken up by individual sensillae.

From a standpoint of adaptive value, adaptive and largely inadaptive structures can be distinguished in a chaetome (Makarov 1990, 1991). A chaetome's functional integrity is evident, for such alterations as an increased number of setae, changes in their mean length, the formation of drusy setae, etc., take place coordinately in various sclerites. Often they are accompanied also by modifications of the sculpture, while changes in inadaptive structures are less evident. However, an analysis of the known patterns of reduction (Makarov 1991, 1993, Grebennikov 1995) shows that sensillae get lost in a regular way. Thus, Carabini display a reduced discal complex, where as among Trechitae the reductions concern the posterolateral groups of sensillae of the thoracic and abdominal tergites.



Figs 1-12. Chaetotaxy of the separate body parts of Coleoptera larvae in different families (schematic). 1-4, 12 - cephalic capsule (left - ventral view, right - dorsal view), 5-7 - right half of pronotum, dorsally, 8, 9 - abdominal tergite IV, dorsally, 10, 11 - abdominal ventrites IV, ventrally. 1, 5, 8, 10 - *Ilybius fuliginosus* (Fabricius), L3 (Dytiscidae), 2, 6, 9, 11 - *Helophorus aquaticus* (L.), L3 (Hydrophilidae), 3 - *Tachinus* sp., L3 (Staphylinidae), 4, 7 - *Philonthus* sp., L3 (Staphylinidae), 12 - *Athous* sp., L2 (Elateridae). Sensillae, corresponding to generalized type are shown as solid, other sensillae as dotted.

Hence, the larval chaetome of Carabidae can be considered as an integral system exhibiting its own patterns of change.

Below, the basics are briefly presented of a formal classification of chaetome elements.

The principles of identification and homologization of chaetome elements

In the framework of cladistics (Ax 1987) and considering the newest requirements of the hypothetical-deductive methodology (Pesenko 1993), the first condition of adequacy of a cladistic reconstruction is character analysis aimed at a revelation of homoplasies and of initial and derived states.

The specificity of larval stages (scarcity of fossil evidence, poorly developed biochemical and genetic approaches) greatly restrict the set of the methods admitted to establish the homologies. In fact only three Remane's criteria remain (Remane 1956, with consideration of additions by Pesenko 1993): resemblance of position, resemblance of special quality, and transitions through intermediate forms. Applicability of the latter criterion thereby faces additional difficulties, because even in well-studied carabid groups, larvae are known for less than 30% species.

At the same time, owing to both a well-expressed embryonization and a number of structures getting considerably modified in the course of carabid larval development, ontogenetic criteria appear partly useful as well in unravelling homologies by origin and polarities by antecedence.

Homologization of chaetome elements in ground-beetles is generally based on the fact of retention of sensillae innervation along with growth and development (Wigglesworth 1953). The known patterns of aberrations conserved for stage to stage (for example, duplicated setae PR₈ in *Carabus granulatus*) can be evidence of ontogenetic succession of chaetome elements as well.

Below, the main aspects of classification of chaetome elements and the methods of homologization are briefly considered.

Typology

The generally accepted classification of Bousquet & Goulet (1984) discriminated two classes of sensillae: setae and pores. Yet whereas a seta largely implied a trichoid-type sensilla, pores were understood as embracing all structures with a small agile portion: conical, campaniform, and placoid sensillae. A number of basiconical sensillae (PR₇, ME₁₀, TE₈) were therewith designated as setae, while a bit lesser sensillae (FR₇) as pores.

The typological classification of sensory structures of ground-beetles presented here roots in classics of insect morphology (Snodgrass 1935, Slifer 1970, McIver 1975, etc.), external receptor structures encountered in carabid larvae can be divided into functional groups with distinct morphological characters.

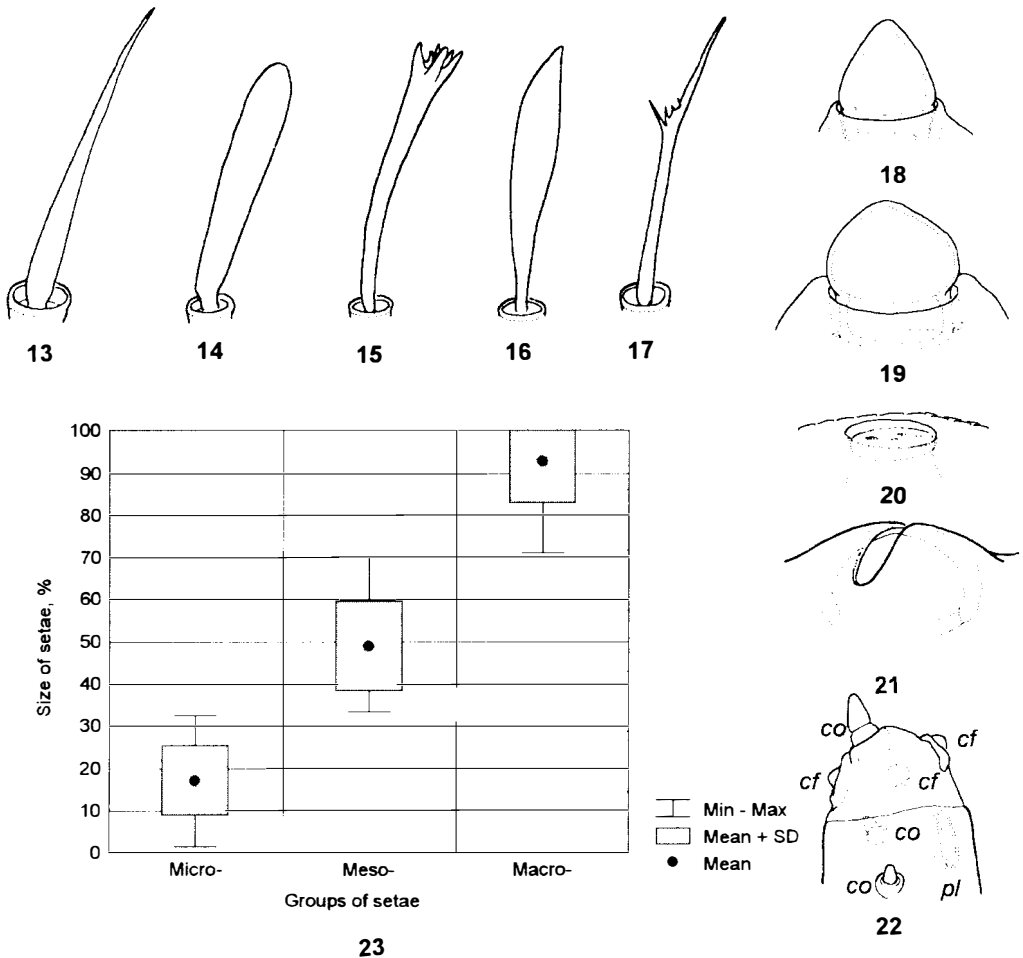
MECHANORECEPTORS. Formed on the basis of a bipolar neuron, associated with cuticular structures of three types:

(a) Trichoid sensillae or setae (hair sensilla, seta, sensilla chaetica, sensilla trichoidea), the biggest and the most thick-walled, often with an apical pore, they can also perform the function of a contact chemoreceptor (McIver 1975, Spence & Sutcliffe 1982). Receptor fields perceiving joints' articulation and typical in the imago are unknown in larvae. The only possible exception is gPS. These fields' function is carried out by individual sensillae located so that their contact to the environment is limited. Such are PY₁, TE₃, CO_{1 3}, CO_{14 17}, possible PA_{1 3}. Other proprioceptors are represented by campaniform sensillae (see below).

Accessory setae differ in shape: needlike, drusy, baccilliform and phylloid, boughform, spines etc. (Figs. 13–17).

Usually, larval setae differ in size quite considerably. A statistical analysis carried out has revealed that among them three groups can be reliably distinguished. I designate these groups as micro-, meso-, and macrosetae, respectively. The border between first two groups setae approach each other and, no differentiation into micro- or mesosetae being possible in some particular cases (Fig. 22).

The size restricts the morphological diversity of setae. Thus, only microsetae appear to display a bacilliform or phylloid appearance. In contrast, only meso- or macrosetae can be bacilliform or drusy.



Figs 13–23. Types of sensillae in carabid larvae. 13–17 – trichoid sensillae of different shape (13 – needleform (typical) seta, 14 – bacilliform, 15 – druseform, 16 – phylloid, 17 – boughform), 18 – conical sensilla, 19 – campaniform sensilla, 20 – placoid sensilla, 21 – „lyriform organs“ (deeped campaniform sensilla). Fig. 22 Scatter-diagram of the lengths of three dimensional setae group (explanation in text). Fig. 23. Unit of different sensillae on the top of last joint of labial palp in *Agonum muelleri*(Herbst), L3. Abbreviations: co – conical sensille. cf – campaniform sensille, pl – placoid sensille.

(b) Campaniform sensillae (Fig. 19), described already by Berlese (1910), are homologs of setae (Snodgrass 1935, Schmidt 1973). Their function is proprioceptive. Both special sensillae $TR_{a,r}$ (Fig. 21) and „lyriform organs“ on legs and tergites are referred here. Campaniform sensillae are widespread in beetle larvae (Zacharuk 1962), often being associated in functional units (McIver 1975).

(c) Digitiform sensillae are specialized derivatives of setae on mouthpart appendages. Despite an apical pore, they are only mechanoreceptive (Zacharuk et al. 1977). Apparently, they serve for orientation in soil tunnels, perceiving the vibration of walls emitted by the victim (op. cit.). Similar structures are known in the imago as well, although their function is olfactory (Honomilch 1980).

CHEMORECEPTORS. Chemoreceptors are less diverse in ground-beetle larvae. Morphologically, most can be attributed to a group of contact sensillae (Slifer 1970, Tyshchenko 1986) represented by microsetae, conical and, less frequently, placoid sensillae.

Microsetae are located at the apices of the antennae and urogomphi as well as on sides of tergites. Basi- and coeloconical sensillae (Fig. 18) are usually placed on the head capsule and both on thoracic and abdominal sclerites. They form most of „secondary pores“. Placoid sensillae (Fig. 20) seem to be the most highly specialized chemoreceptors (e. g., $AN_{a,d}$). Maddison (1993) believes that they represent chordotonal organs.

The large basiconical sensilla on antennomere 3, known as „sensorium“, is also referred to the group of chemoreceptors. Apparently, it performs a hygroreceptive function.

Regularly, chemo- and mechanoreceptors jointly form the functional groups. For example, frequently there is a medial chemoreceptor surrounded by campaniform mechanoreceptors at the apices of the antennae, maxillary and labial palps (Fig. 23).

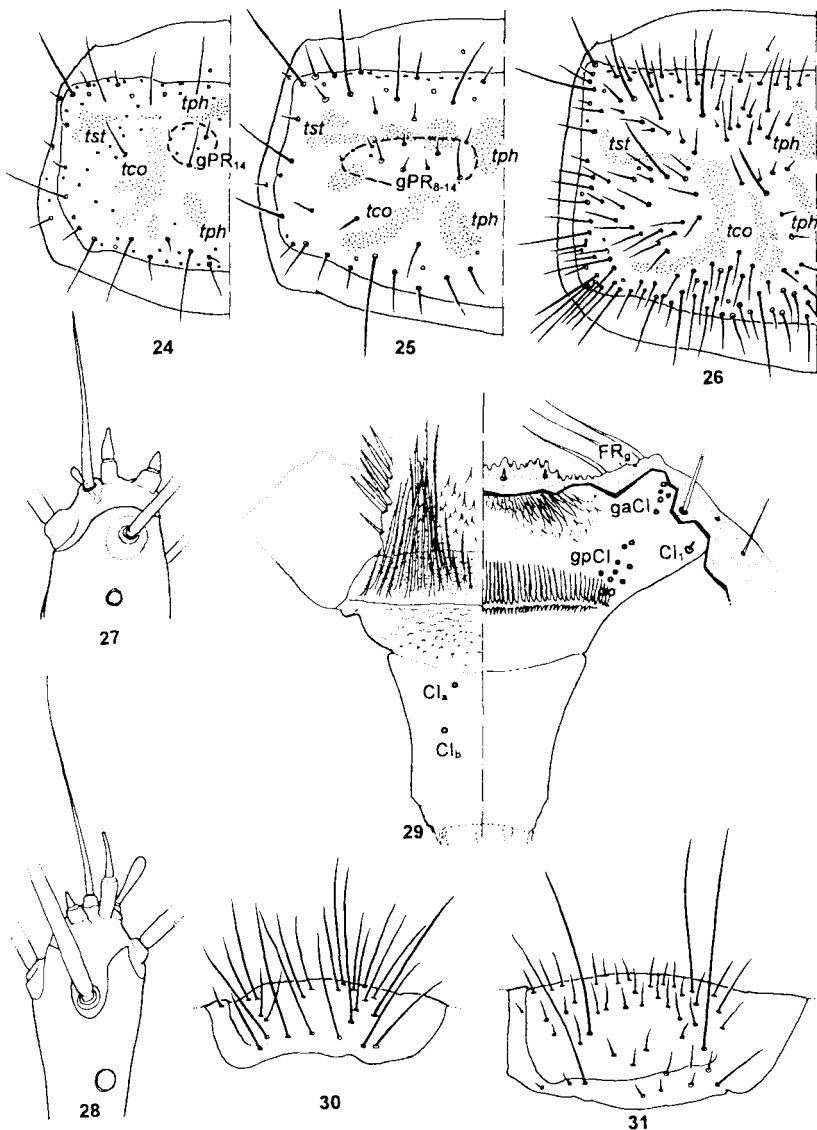
Intermediate sensillae forms are possible only amongst poorly specialized sensillae of trichoid or conical type.

Topology

The system of chaetome designations as developed by Bousquet & Goulet (1984) is based only upon the elements' dispositions. In so doing at least for two reasons, there are difficulties in an exact designation of sensillae: (a) a strong structural reorganization of larva body when the habitual system of topographic correlations is lost (e. g., Cicindelini), (b) substitution of one sensilla type by other one and (c) absence of individual chaetome elements (e. g. reduced tergal setae in Carabini), also deteriorating the system of designations. Subsequently, due to adoption of designations for some „secondary“ setae (like $AN_{a,d}$, the latter have been tended to be treated as homologous elements along with „primary“ setae (Arndt 1993). Recently, based on a statistic analysis of morphometric characters (Brinev 1995), the extent of correlation among setae has been shown to be independent from the distance between ones. Hence, identification of the setae based solely on their interpositions is insecure.

To overcome these difficulties, additional markers have been used for the determination of chaetome elements. The method of sigillotaxy (Makarov 1989, 1991, 1993) is based on the utilization of sigilla as markers for the sites of muscle attachment to the endoskeleton, all well distinguishable by a well-developed primary microsculpture. Another technique lies in using for diagnostic the rather stable functional complexes (usually, this is a trichoid sensilla in combination with a campaniform one). In both cases, a secure identification (and thus homologization) becomes possible of almost of structures of a chaetome.

As regards the larvae with a complex chaetome (e. g., Elaphrini, Callistini, Galeritini, Anthiini, numerous Harpalini and Lebiini, etc.), the problem of an exact homologization cannot be



Figs 24–31. Some details of chaetotaxy in carabid larvae. 24–26 – designations of pronotum seta groups show by the example of larvae in Elaphrini tribe (right half of pronotum, dorsally, muscles sigilles are dotted), 27–28 – structure variations of terminal sensory complex of fourth antenna joint, dorsal aspect, 29 – sensillae of cibarium, from the left – hypopharynx, from the right – epipharynx (explanation in text), 30, 31 – chaetome of abdominal tergite IV, lateral aspect (30 – homopolychaetosis, 31 – heteropolychaetosis). 24 – *Elaphrus riparius* (L.), L3, 25 – *E. cupreus* Duftschmid, L3, 26 – *Blethisa multipunctata* (L.), L2, 27 – *Pterostichus strenuus* (Panzer), L1, 28 – *Epaphius secalis* (Paykull), L3, 29 – *Agonum exaratum* (Mannerheim), L3, 30 – *Amara brunnea* (Gyllenhal), L3, 31 – *Cymindis vaporariorum* (L.), L3. Abbreviations: tph – tergo-phragmal, tst – tergo-sternal, tco – tergo-coxal muscle complexes. Designation of setae according to: Bousquet & Goulet 1984; muscle groups according to: Kiler 1964, with modifications.

solved at the level of individual elements. The notion of a group of sensillae has been introduced for such cases (Makarov 1993), meaning a unit of the chaetome structures delimited by demarcation zones (usually, by sigillae). In the norm, the groups are designated by the „primary“ seta, e. g. gPR_8 in *Elaphrus* (Fig. 24). More seldom, a group encompasses several setae (gPR_{8-14} – Fig. 25). Finally, in extreme cases of chaetome complication, one must speak only about the complexes of sensillae: anterolateral, anterodiscal, etc. (Fig. 26). Since it is sensillae innervation that is at the base of their homology, we consider the homology of an individual seta and a respective group as possible.

It is noteworthy that some sensillae retaining relative stability in structure and position remain undesigned (Maddison 1993). This mainly concerns complexes of sensillae of antennomeres 3 and 4 as well as of the buccal cavity.

The complex of sensillae of antennomere 3 comprises a big campaniform sensorium and a group of 1–3 sensillae placed more dorsally. The group usually encompasses two conical and/or bacilliform as well as one spherical or placoid sensilla. Modifications of this complex (besides the above variations in the sensorium) are reduced to a dwindling number of sensillae up to their complete decline.

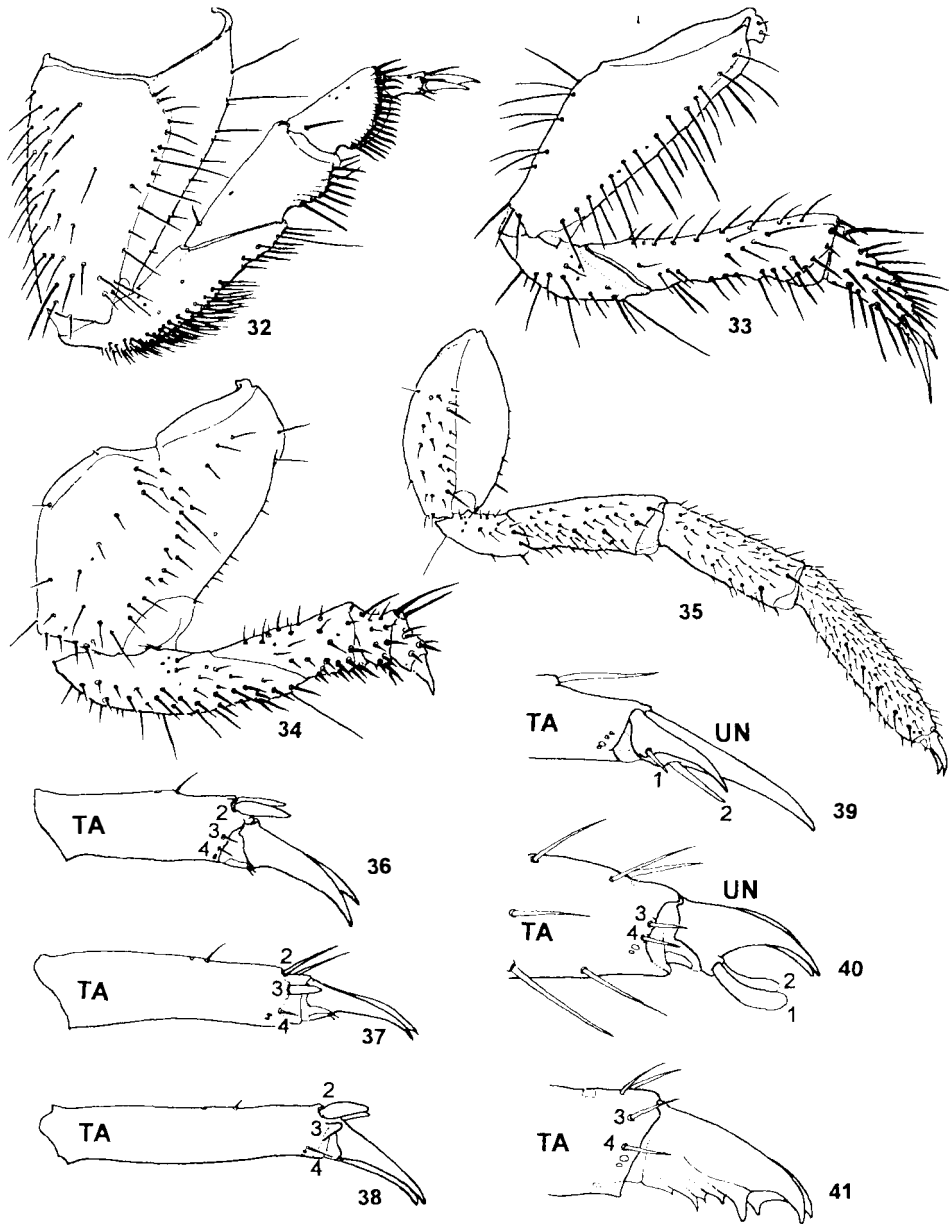
In a typical case, the terminal complex on the antenna includes one apical seta AN_6 , two dorsal conical and one ventral bacilliform sensilla. This set is relatively stable within the family. The modifications known to us lie in the bacilliform sensilla being substituted by campaniform ones, one of the conical sensillae reduced, and the length ratios changed in the chitinous derivatives of the tormogenous and trichogenous cells (Figs 27, 28).

The absence of additional markers in the apical part of antennomeres 3 and 4 makes it impossible to homologize the sensillae in case of any reduced or considerably modified elements. Hence, in contrast to the opinion of Maddison (1993) it appears hopeless to introduce designations for such structures. In their descriptions, it is advisable to use such toponymic notions as, e. g., a „medial conical sensilla“.

Finally, the buccal cavity supports its own complex of sensillae. Their main part (a group of conical and campaniform sensillae) are placed on the epipharynx, only two pairs of campaniform sensillae being located on the cibarium. The latter sensillae are highly stable throughout the family, while the epipharyngeal ones are highly variable. Among them, more or less constantly distinguishable is only a short lateral seta. In general, the remaining group forms a more or less distinct row of $FR_{8,9}$ setae to the fore angles of the cibarium, which is sometimes clearly divided by a medial impression of the epipharynx into an anterior and a posterior groups. Relative constancy of some mouthpart sensillae enables to give designations for them (Fig. 29). Analogously to Bousquet & Goulet (1984) lateral seta is called CI_1 (from cibarium), sensillae of cibarium itself are CI_a and CI_b , while epipharynx group of sensillae is gCI (and could be divided into subgroups $gaCI$ and $gpCI$).

One more sensillae, that has not yet been defined (Maddison 1993), lays on the front edge of paraclypeus in the area of $FR_{8,9}$ seta. It is rather constant, and in some cases could be considered as marker sensillae, dividing the groups of seta FR_8 from FR_9 (Fig. 29). It is suggested to define this sensillae as FR_g .

Topology of specialized sensillae (mostly distant chemo- and hygroreceptors) is more constant than the topology of little specialized trichoid and conical sensillae. Chaetome modification happens mainly due to contact chemo- and mechanoreceptors, which include typical seta and different conical and campaniform sensillae.



Figs 32–41. Structure and chaetotaxy of carabid larvae legs: 32–35 – middle leg, frontal view (32–34 – excavatory legs, 35 – running legs); 36–38 – tarsus of middle leg, frontal view; 39–41 – apex of tarsus, frontal view. 32 – *Scarites bucida* Pallas, L3, 33 – *Cicindela hybrida* L., L2, 34 – *Orthogonius ?acutangulus* Chaudoir, L3, 35 – *Callistus lunatus* (F.), L3, 36 – *Molops piceus* (Panzer), L1, 37 – *Tricholicinus setosus* J. Sahlberg, L3, 38 – *Masoreus wetterhali* (Gyllenhal), L3, 39 – *Loricera pilicornis* (F.), L2, 40 – *Drypta dentata* (Rossi), L3, 41 – *Paradromius linearis* (Olivier), L3. (35 after Makarova & Makarov (1996), other – orig.). Notation of „primary“ setae and pores follows that of Bousquet & Goulet (1984).

Functional model of chaetome

Functions of certain chaetome elements of carabid larvae are almost unknown, and special physiological experiments are needed to study them. However, more or less precise relationship between structure and function has been revealed for the majority of cuticle sensory structures of insects (Snodgrass 1935, Dethier 1963, Tystchenko 1986). Therefore already now it is possible to describe the general model of carabid larvae chaetome.

This model is based on the following statements:

- all cuticle structures including the number of derivative seta are sensory
- most thichoid sensillae judging by SEM data do not have apical pore, and thus are considered as mechanoreceptors
- distant receptors are lacking in typical cases

Chaetome as well as other derivatives of cuticle contributes to four functions, discussed below in order of their importance.

Covering structures

In this group we include trichoid sensillae of different size and microtrichia. Their presence in large numbers ensures isolation of larvae body from the environment, that is realized in three ways:

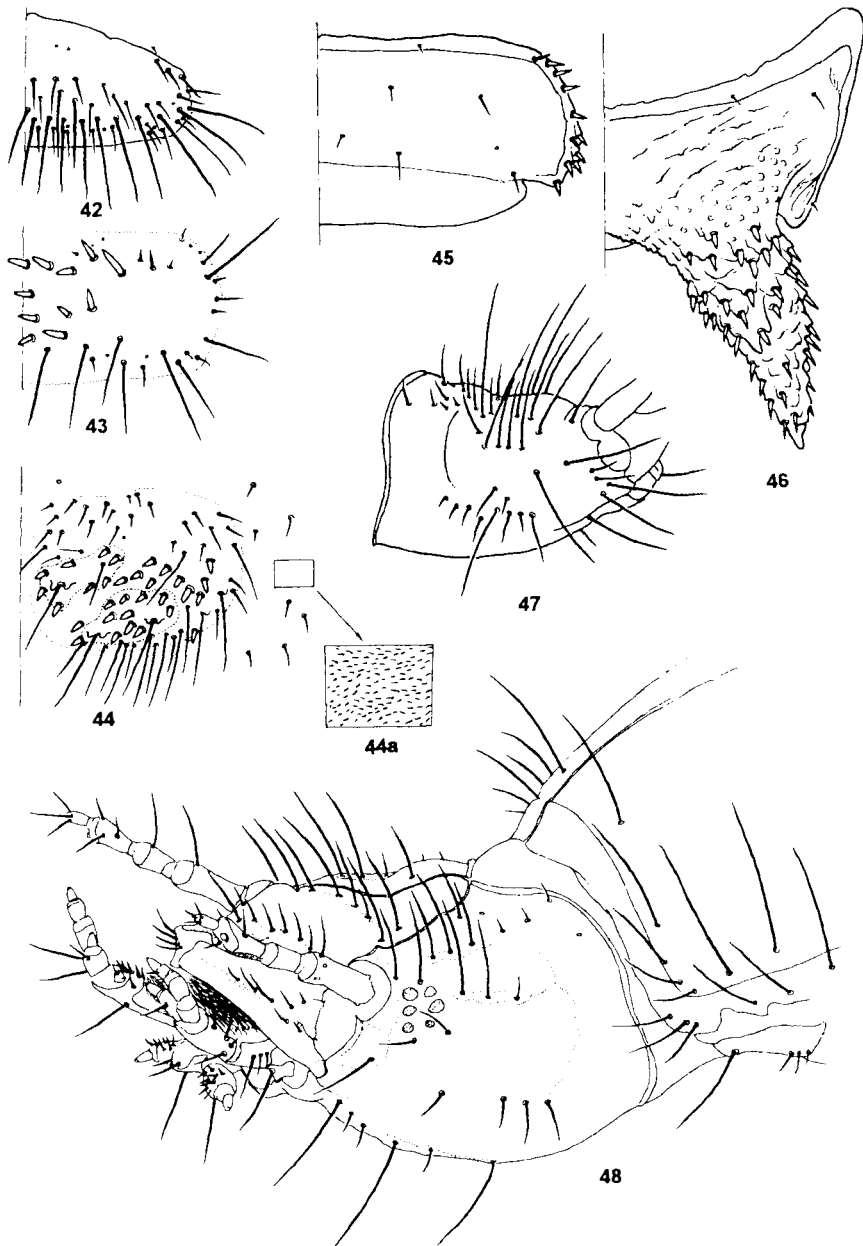
- a) The most hygrophilous forms which live in permanent contact with water (Callistini, Elaphrini) are characterized by noticeably different in size „general“ seta, numerous additional seta, and by development of isolating chaetome on the appendages (Callistini: *Callistus*).
- b) In xerophylic and psammophylic larvae (Anthiini, part of Zabryni and Harpalini) macrosetae prevail in secondary chaetome; sometimes their size is comparable to „general“ seta.
- c) In *Orthogonius* and *Cychnus* larvae very peculiar thin and dense protrusions are formed on sclerites on intersclerite membranes; the latter are microtrichia but not sensillae.

Locomotory and bulldozer structures

As locomotory we consider the structures of chaetome, which are helpful for larvae movements over or in the substrate. They are localized on appendages, and in excavating forms also on urogomphi and rarely on abdominal tergites. Excavatory structures which enable to move apart dense portions of substrate are treated as separate variant (Lyubarskiy 1992); they are located mainly on the head and anterior margin of pronotum.

Movements on solid dense substrates leads to elongation of distal parts of appendages and to development of more or less parallel rows of spines ($gTA_{5,6}$, $gFE_{3,4}$) mostly on the ventral side (Fig. 35). In specialized forms claws and $UN_{1,2}$ setae on pretarsus are modified as well (Figs 39–41).

On the contrary, in excavatory forms one can observe shortened distal parts of appendages (Figs 32–34), as well as formation of apical crowns of spines (gTA_{2-7} , gFE_{2-5}). Quite often non-allied forms have similar structure of appendages (for example *Omophron*, *Cicindela*, *Scarites*, *Orthogonius*). Unlike the surface-dwelling larvae, adaptations in excavatory ones cover a number of structures. Thus, besides appendages, urogomphi and abdominal tergites are adaptively modified as well (Figs 45, 46). Chaetome modifications are similar in all cases. Development of supporting structures such as spines and/or seta (Figs 42–44) on medium abdominal tergites (II–VI in *Omophron*, *Daptus* and *Orthogonius*; IV–V in *Brullea* (Harris 1978)) could be considered the most interesting. It is possible that specific structure of fifth abdominal segment in Cicindelini larvae represents the extreme variant of such specialization.



Figs 42–48. Supporting and bulldozer structures on dorsal surface in carabid larvae. 42–45 – abdominal tergite IV, right half, dorsally (44a – magnified part of Fig. 44), 46 – right half of abdominal tergite IX and right urogompha, dorsally, 47 – cephalic capsule, right aspect, 48 – head and anterior margin of prothorax, anterolateral aspect. 42 – *Omophron limbatum* (F.), L2, 43 – *Daptus vittatus* Fischer von Waldheim, L3, 44 – *Orthogonius ?acutangulus* Chaudoir, L3, 45, 46 – *Callisthenes semenovii* Motschulsky, L3, 47 – *Brullea antarctica* (F.), L3, 48 – *Zabrus spinipes* (F.), L2. (47 after Harris (1978), other – orig.).

Within one type of locomotory chaetome adaptations free combinations of different element functions can take place. Thus, in majority of ground-beetle larvae setae TA_{2,7} on the end of leg are modified into spines, while seta TA_{3,6} fulfil sensory function (Fig. 36). In *Tricholicinus* and *Masoreus* on the contrary TA_{2,7} fulfil sensory function, while TA_{3,6} is used in locomotion (Figs 37, 38). Similar alteration of functions is observed in appendages chaetome of *Thalassophilus* (Grebennikov 1996) and *Orthogonius* (Fig. 34).

It is necessary to mention, that the number of claws, although seeming to be adaptive feature, is not directly related with locomotion type.

Bulldozer structures are usually represented by rows of strong seta and spicules on the head, mandibles, and rarely on other appendages (Figs 47, 48). Sometimes modifications are found also in upper prothorax (for example thickened seta in front corners of prothorax found in *Epa-phius*).

Specialized sensory structures

This group includes only sensillae, specialized for analysis of certain signals. They are localized mostly on head, appendages, at the edges of tergites, and are represented by enlarged trichoid macrosetae (mechanoreceptors), as well as by basiconical, conical and placoid sensillae which act as chemoreceptors.

Comparison of chaetome in representatives of different tribes together with analysis of its' ontogenetic changes enables to outline the following main trends in development of sensory complex of carabid larvae:

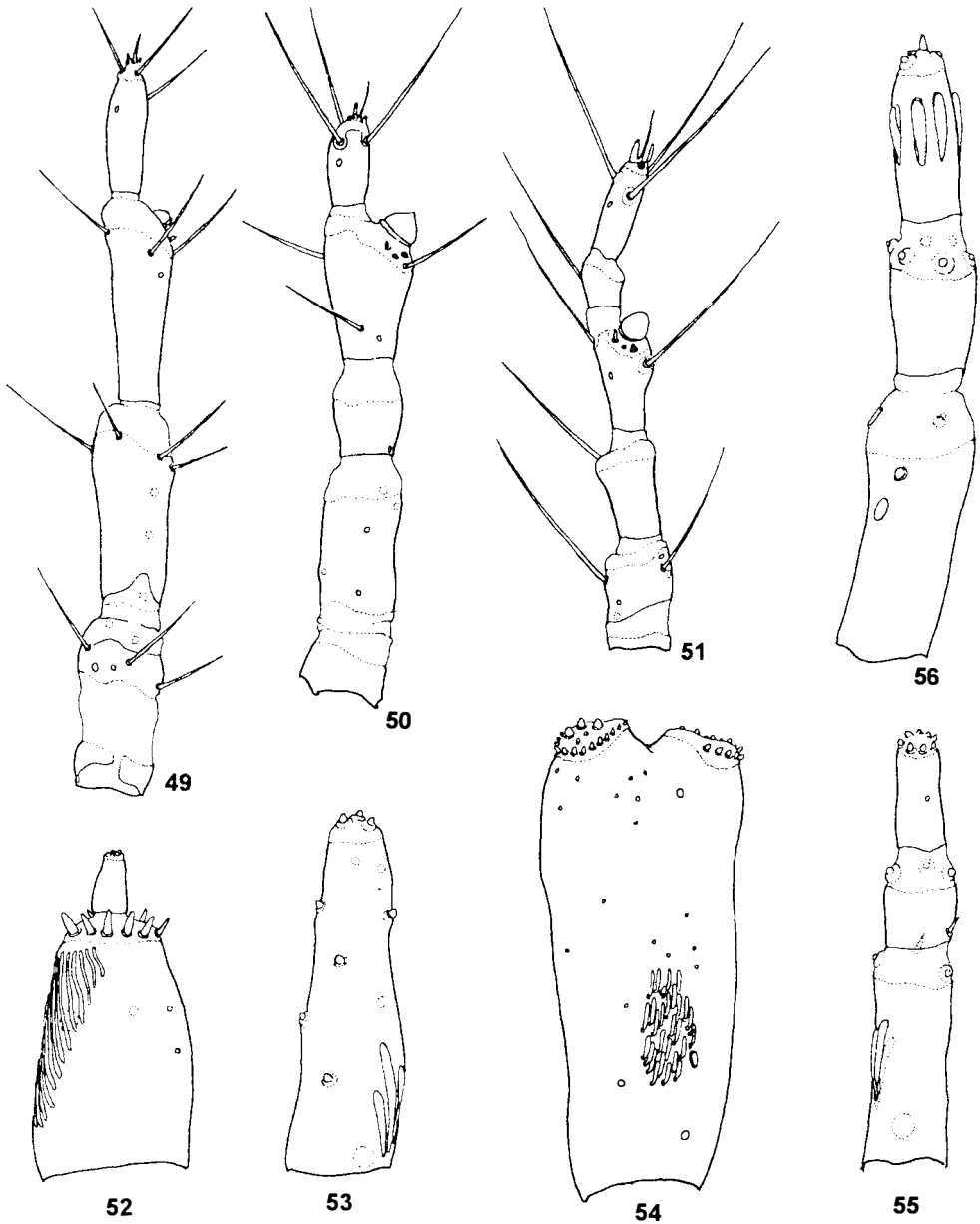
a) Increase in active zone of sensillae. Usually this is reached through prolongation of periphery trichoid sensillae mainly on head appendages and on urogomphi (for example in *Notiophilus*, *Leistus*, *Nebria*, *Loricera*, *Galerita*). In open-living forms with short seta (some Callistini and Carabini) compensatory elongation of seta-bearing appendages is observed.

b) Concentration of different sensillae into sensory fields, that sometimes coincide with increase in their size and number. The latter is most well expressed for groups of basiconical sensillae, located at apical segments of labiale and maxillary palps. In the most simple case two or three basiconical sensillae form diffused lateral group at the base of segment, other sensillae (conical and placoid) are located distally (Fig. 53). Complexity increases to enlarged number and/or size of basiconical I sensillae; they form more or less compact group which position shifts to distal (Fig. 54). Other types of sensillae are also included in this group. Such structure is characteristic mostly for open-living predatory larvae. Apical sensillae complexes on labiale and maxillary palps develop similarly.

On the periphery of tergites trends of sensillae concentration are less pronounced. The best example is found in Licinini tribe: dense concentrations of sensillae are formed on epypleuritis, and seta EP₁ and HY are noticeably prolonged.

Specific variant of increased complexity in antennae chaetome is found in Scaritini larvae, and also in some Harpalini and Pterostichini. In these cases different modifications of sensorium at the third antennae segment takes place, such as flattening, increase in size, or formation of a group of flat sensillae at the place of sensorium. These changes are characteristic mostly to the forms with slightly sclerotised covering which inhabit arid landscapes. It can be thus suggested that this trend is related to the need of precise orientation after humidity gradient.

c) Mobilization of sensory complexes. It is expressed in development of pseudosegment on head appendages. Four different variants of this trend have been found in carabid larvae: 1) separation of sensillae group in the apical part of labiale palp (Callistini – Fig. 52); 2) separation of antennal circle and formation of additional segment at the base of antennae (Pterostichini: *Mol-*



Figs 49–56. Structure and chactotaxy of head appendages in carabid larvae: 49–50, 52, 55, 56 – cases of pseudosegmentation; 53, 54 – location of sensillae on ultimate joint of labial palp, dorsolateral aspect, 56 – third and fourth maxillary joint, dorsal aspect). 49 – *Tricholicinus setosus* J. Sahlberg, L3, 50 – *Molops piceus* (Panzer), L1, 51 – *Badister bullatus* (Schrank), L3, 52 – *Callistus lunatus* (F.), L3, 53 – *Pterostichus strenuus* (Panzer), L1, 54 – *Carabus circassicus* (Gangelbauer), L2, 55, 56 – *Epaphius secalis* (Paykull), L3. (52 after Makarova & Makarov (1996), other – orig.).

ops, *Abax*; Licinini: *Tricholicimus* – Figs 49, 50); 3) separation of the upper part of the 3rd antennae segment (*Badister* – Fig. 51., probably also *Amblystogenium* – as from incomplete description by Womersley 1937); and 4) indistinct separation of distal segment of labiale and maxillary palps into 2–3 segments (Trechini – Figs 55, 56, some Clivinini). These variants are realized only in predatory forms, both open-living and typical geobionts.

Structures, used in the feeding process

Following Striganova (1966) mouthpart apparatus of Carabidae larvae is characterized as cutting or puncture-cutting. Morphological feeding-related adaptations are realized in carabid larvae mainly at the level of macrostructures, such as nasale and mouth appendages. Chaetome modifications only follow modifications of mouthparts, and happen in specific sensory apparatus for catching (but not for locating) the prey, and in mechanical structures for manipulating with food.

Analysis of mouthpart chaetome enables to distinguish in carabid larvae three main morphological types which can be considered as the extreme achievements in adaptive radiation of feeding-related structures.

a) Catching apparatus. Here protrusion of sensory structures which control quick closing of mandibles at the contact with prey are characteristic (Spence & Sutcliffe 1982): elongation of nasale teeth carrying $FR_{10,11}$ seta and of front corners of paraclypeus, enlarged MN_2 , gMX seta with small number of thick long setae located mostly in the distal part of stipes (Fig. 57). This type is typical for larvae of *Notiophilus*, *Loricera*, *Leistus*, *Galerita*. Usually it is accompanied by restructurisation of sensory sensillae complex for increase of sensory active zone. Interaction of sensory and feeding-related structures during hunting of these larvae has been described in details (Bauer 1979, Spence & Sutcliffe 1982, Bauer & Kredler 1988).

b) Cutting-filtering type of mouthpart structure is common for predatory larvae of ground-beetles. This type is characterized by moderate development of $FR_{10,11}$ seta, and by presence of Y-shaped setae functioning as food filters in gMX. In representatives of Lebiini tribe which have reduced gMX seta filtration function is carried by penicillus. The extreme development of this type is found in larvae of Licinini and Panagaeni tribes, which have rows of numerous teeth (Figs 58, 60–62) of different or igin almost on all mouthpart appendages.

c) Chewing-cracking type of mouthpart structure is developed in forms which feed on solid food. This type is characterized by smaller $FR_{10,11}$ setae (often they are completely hidden in the massive multirow nasale), and by differentiated apical group of thick setae in gMX (Fig. 59) or cone-like lobe on cardo. Almost all Zabrini and Harpalini, *Ortognius* are typical representatives of this type.

Quite important, that separate functional blocks of chaetome are not equal as related to their possibility for modification. Thus, subordinate character of feeding-related chaetome to relevant macro-morphological structures is obvious. At the same time covering complex is modified rather autonomously.

Presence of similar chaetome modifications in representatives of different carabid taxa proves its significant functional flexibility and large adaptive importance.

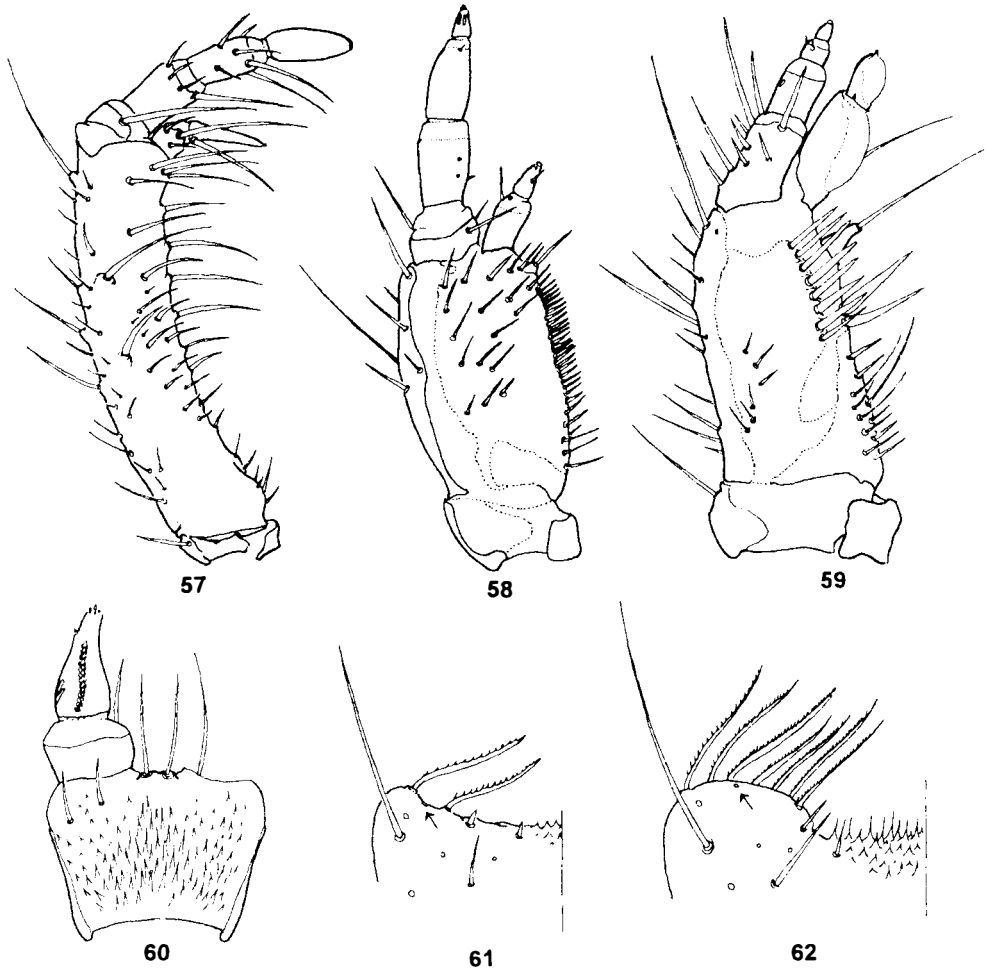
Morphological restructurisations of chaetome and their significance

Generalizing all the above it is possible to reveal two main processes of chaetome changes: changes in number of elements or qualitative transformations (uniformation and diversification of sensillae).

Changes in number of elements

Reduction is observed in carabid larvae rather rarely. Two kinds of this process can be distinguished:

1. Disappearance of certain chaetome elements. Usually it is observed within genera, or even in smaller taxonomic units. Although chaetome remains typical for the group in whole, some species can lack few elements of „general“ structure. These are the examples with absence of PR₁₃ seta in several *Amara* species, setae MX₁₁ and MX₁₂ in some Callistini. Reduction of one certain sensillae very rarely can act as diagnoses for higher taxa (for example Brachinini, Callistini).



Figs 57–58. Structure and chaetotaxy of carabid larvae mouthparts: 57–59 – different types of maxillae (57 – catch type, 58 – filtration type and 59 – crush type), dorsal aspect of left maxilla; 60–62 – filtering structures (60 – labium, dorsal view, left palp not shown, 61, 62 – left paraclypeus and adjacent part of nasale, dorsally). 57 – *Galerita feai* Bates, L3, 58 – *Panagaeus cruxmajor* (L.), L3, 59 – *Orthogonius? acutangulus* (Chaudoir), L3, 60, 61 – *Badister bullatus* (Schrank), L3, 62 – *Licinus depressus* (Paykull), L1. Arrow points to FR₆ conical sensille.

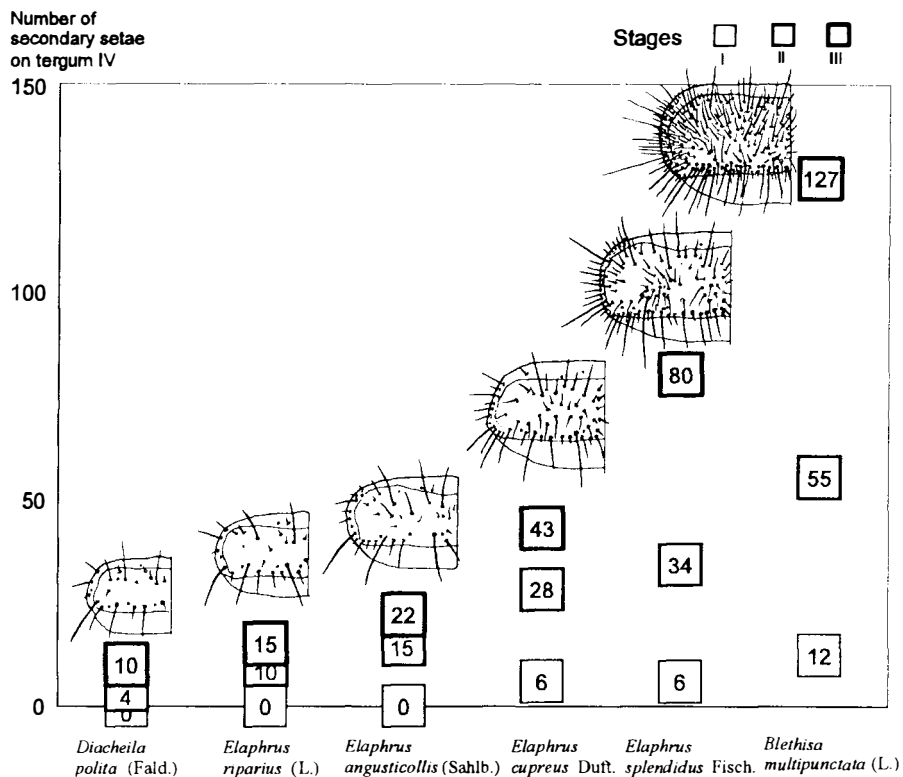


Fig. 63. Chaetome changes of abdominal tergite IV during ontogenesis of larvae in tribe Elaphrini.

2. Disappearance of smaller or larger complexes of seta and pores. Most often this kind of reduction is connected with overall enlargement and thickening of cuticle (tribes Carabini, Cychnini). As a rule oligomerisation involves chaetome of dorsal, more rarely of pleural and ventral sclerites. There reduction in number of „general“ seta coincides with appearance of numerous small conical sensillae, so that overall density of sensory elements on larval body does not decrease (Table 1).

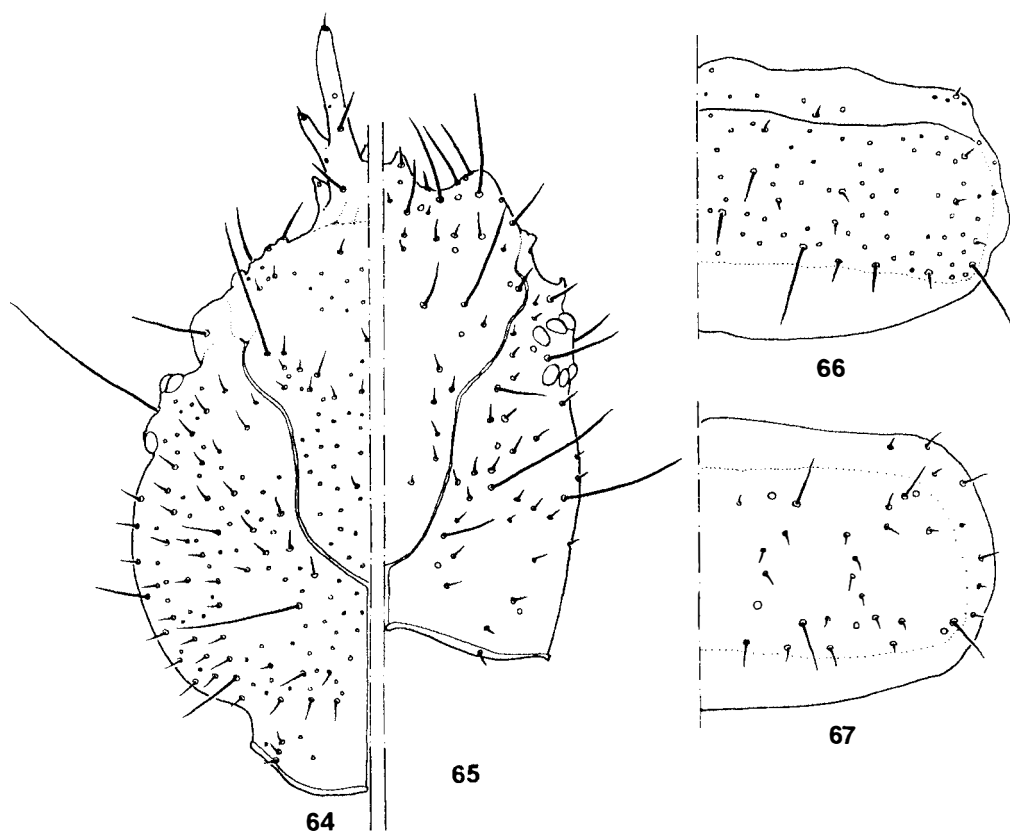
In some cases reduction of chaetome is natural. Thus, in larvae of Trechitae supertribe (Grebennikov 1995) lacking structures are those connected mostly with posterolateral corners of tergites.

Processes of reduction result in what could be called oligochaetosis, or in extreme cases achaetosis. The latter has recently only one described example, that is very simplified chaetome of larvae of *Cychrus*.

Now it is quite difficult to define the reasons for chaetome reduction. It seems obvious that minimization of body size does not lead directly to chaetome reduction. Anyway, in smallest carabid larvae (Trechitae, many Lebiini, I instar of Brachinini) all variants of chaetome deve-

lopment can be observed, i. e. from complete (*Microlestes*, *Synthomus*) to more or less reduced (*Brachinus*, Trechitae, especially Trechodini – Grebennikov 1996). Adaptive role of reduction is rather doubtful, and no correlations were found with larvae habits either. Absence of some elements can be in principle the result of mutation. Reduction of large setal complexes probably has different explanation. Two possible reasons could be suggested: (1) laconization of chaetome during phylogenesis, (2) general simplification of larvae organization due to disembryonization of development. The latter suggestion can be proved by noticeable reduction of chaetome in larvae with one claw (supertribe Trechitae, genus *Brachinus*), which indicates on emerging from eggs on earlier stages of development (Tikhomirova 1992). It could be possible to evaluate the reduction of sensillae numbers during evolution only after the ancestral state of chaetome (see below) is identified; thus recently it cannot yet be done.

Multiplication (polymerization) of sensillae is more or less characteristic to larvae of most carabids. This process is realized in ontogenesis almost always, when single sensillae of first instar larvae are altered in consequent instars with groups of homologous formations (Fig. 26). However quite often happens that already at the first stage of larvae development number of



Figs 64 - 67. Cases of primitive (64, 66) and advanced (65, 67) of chaetome patterns. 64, 65 – cephalic capsule, dorsally, 66, 67 – IV abdominal tergite, dorsally. 64, 66 – *Leistus terminatus* (Helwig in Panzer), L2, 65, 67 – *Paradromius linearis* (Olivier), L3.

sensillae is noticeably larger. This tendency is most expressed in representatives of Helluonini and Anthiini tribes, whose „primary“ chaetome consists only of groups of seta.

This result with increased number of sensillae we call polychaetosis (or hyperchaetosis).

Diversification or uniformation

Multiplication of chaetome elements can coincide with appearance of new kinds of sensillae compared to original ones. Therefore two variants of hyperchaetosis (Figs 30, 31) are distinguished: (1) homochaetosis, when new formations are analogous to original structures and do not differ in size from them, and (2) heterochaetosis, when new sensillae are either noticeably smaller in size than original ones, or belong to different sensillae type. In the latter case (for example additional phylloid seta on pleurites of *Carabus*, bacilliform seta of *Chlaenius*) it is worth to distinguish ordinary (basic) chaetome corresponding to „general“ type, and idiochaetome, which includes new formations. Homochaetosis of larvae usually appears due to absence of distinct morphological boundary between groups of macro- and mesoseta.

Homochaetosis is observed in carabid larvae rather rarely, and is connected with specialization to pawing of loose substrates (Anthiini, some Zabrinini).

Heterochaetosis is more common type of chaetome changes. It is realized differently in separate groups of carabid larvae. Thus, representatives of Callistini, Oodini, Panagaeini tribes, many Lebiini have firmly differentiated trichoid chaetome: large „general“ seta are well noticeable at the background of numerous evenly distributed small secondary seta. Formation of specialized spine-like seta on abdominal tergites (Carabini: *Callisthenes*, Harpalini: *Daptus*, Orthogonini: *Orthogonius*) belongs in principle also to this type of heterochaetosis. In Harpalini and several Zabrinini larvae secondary seta are distributed unevenly; they form more or less distinct groups sometimes located in depressions of cuticle. Usually these are transversal rows on forehead and tergites, and longitudinal rows on parietal sclerites; they are more expressed in pawing (excavating) forms. Together with development of secondary seta increase in number of basi- and coeloconical sensillae is usually observed.

Development of idiochaetome is obviously connected in most cases with advanced specialization of larvae. These are for example drusy setae of myrmeco- or termitophilous forms (*Metrius*, *Graphipterus*, *Pseudomorpha*), bacilliform setae in halophilous, digitiform of phylloid setae in some *Carabus*. Larvae of *Asaphidion* with numerous druseform setae, are probably the only exception from this rules, although almost nothing is known yet about their habits in nature.

Very peculiar chaetome has been found in representatives of Orthogonini and Cychrini tribes: numerous microtrichia which are not related to sensory function are developed on dorsal sclerites or on intersclerite membranes (Fig. 44). This similarity is even more interesting if one takes into account that larvae of *Cychrus* genus are specialized surface-dwelling mollusc predators with very simplified „general“ chaetome, while larvae of *Orthogonius* genus are termitophilous with well developed heterochaetosis. The presence of this feature in representatives of non-allied tribes indicates on its convergent origin, and thus proves relatively independent evolution of chaetome elements.

Described ways of chaetome restructuring form logically a natural row from simple forms of chaetome organization to complex ones. At the level of certain taxa this row is certainly determined both by ontogenetic development and simultaneously by phylogenetic trends. Thus, on the example of Elaphrini tribe larvae (Fig. 63) it can be observed, that very complicated chaetome of most specialized forms is connected with „general“ type by continuous row of ontogenetic anabolic modifications. Similar schemes could be produced for other taxa and for other features as well (for example IX–X segments in *Clivina*, heterochaetosis in Callistini and

Lebiini (*Cymindis*), some Calleidini (*Parena* – see Habu 1981), dorsal chaetome of Zabrinini etc.). However, even among evolutionary advanced groups of carabids (Pterostichini, Harpalini) chaetome structure which is close to general one often prevails; it is very similar to chaetome of upper Jura larvae of *Carabolarva* (which belongs probably to allied Eodromeinae group – Makarov 1995). Therefore it can be supposed that simplification or increased complexity of chaetome does not reflect general phylogenetic trends in the whole family.

Comparison of chaetome structure in larvae from tribes which are traditionally considered as most primitive among carabids (Nebriini, Carabini) has revealed one common peculiarity: very little difference in the structure of „primary“ and „secondary“ sensillae (especially of campaniform sensillae, which sometimes cannot be distinguished from each other – Figs 64, 66*), and relatively larger variability in their localization and distribution. On the contrary, in evolutionary progressive taxa these differences are pronounced, and characteristic groups of seta and sensillae of different types are more distinct (Figs 65, 66). This trend can be observed in the structures of three different functional blocks – covering, sensory, and locomotory.

Therefore it can be suggested that evolution of carabid larvae chaetome has in the background the principle of optimization of sensory functions, expressed morphologically in stabilization of chaetome and in formation of constant complexes of different sensillae (like trichoid FR₂ – campaniform FR₆). At the background of this main trend subordinate morphological peculiarities, such as oligomerisation of chaetome, homo- and heterochaetosis, are realized in different taxa. Ways of modifications depend on certain taxa, and their analysis can be used for elaboration of relationship scheme in carabids. Phylogenetic taxonomic aspects of this problem will be covered in a separate paper. Finally it is worth to add that all these trends can be revealed based on descriptions of elder instar larvae as well; this contradicts to the usual practice of recent decade to describe only 1st instar larvae.

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REFERENCES

- ARNDT E. 1989: Laufkäferlarven (Coleoptera, Carabidae) als Gegenstand phylogenetischer Untersuchungen. *Entomol. Nachr. Ber.* **33**: 255–260.
- ARNDT E. 1991: Familie Carabidae. Pp.: 45–141. In: KLAUSNITZER B. (ed.): *Die Larven der Käfer Mitteleuropas. 1. Band. Adepaga*. Krefeld: Goecke & Evers. 189 pp.
- ARNDT E. 1993: Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). *Stutt. Beitr. Naturk. Ser. A* **488**: 1–56.
- AX P. 1987: *Das phylogenetische System*. Stuttgart & New York: Fischer Verlag, 349 pp.
- BAUER T. 1979: The behavioural strategy used by imago and larva of *Notiophilus biguttatus* F. (Coleoptera, Carabidae) in hunting Collembola. *Misc. Pap. Landbouwhogesh. (Wageningen)* **18**: 133–144.
- BAUER T. & KREDLER M. 1988: Adhesive mouthparts in a ground beetle larva (Coleoptera, Carabidae, Loricera pilicornis F.) and their function during predation. *Zool. Anz.* **221**: 145–156.

* The larvae of two species invoked for comparison are similar in way of living (agile, living in surface, hibernate) and in body size; both species collected in one biotope

- BOUSQUET Y. 1987: Description of the larva of *Helluomorpha bicolor* Harris with comments on the relationships of the Helluonini (Coleoptera: Carabidae). *Can. Entomol.* **119**: 921–930.
- BOUSQUET Y. & GOULET H. 1984: Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Can. J. Zool.* **62**: 573–588.
- BILÝ S. 1975: Larvae of the genus *Amara* (subgenus *Celia* Zimm.) from Central Europe (Coleoptera, Carabidae). *Studie ČSAV* **13**: 1–74.
- BRINEV A. E. 1995: [The analysis of the variability of the topology of sensory structure larvae ground-beetles]. Moskva: Moscow Pedagogical State University, Department of zoology and ecology. Masters's Thesis, 124 pp. (in Russian) (unpubl.)
- DETHIER V. G. 1963: *The Physiology of Insect Senses*. New York: Wiley, 266 pp.
- EMEL'YANOV A. F. 1987: [Phylogeny of cicadas (Homoptera, Cicadina) according to comparative morphological data]. *Trans. USSR Entomol. Soc.* **69**: 19–109. (in Russian, Engl. abstr.)
- EMDEN F. I. van 1935: Die Larven der Cicindelinae I. Einleitendes und Alacosternala Phyle. *Tijdschr. Entomol.* **78**: 134–183.
- EMDEN F. I. van 1942: A key to the genera of larval Carabidae. *Trans. R. Entomol. Soc. Lond.* **92**: 1–99.
- EVANS M. E. G. 1980: The phylogenetic evidence of functional characters in ground beetles (Coleoptera: Carabidae). *Entomol. General.* **6**: 303–310.
- EVANS M. E. G. 1982: Early evolution of the Adephaga – some locomotor speculations. *Coleopt. Bull.* **36**: 596–606.
- EVANS M. E. G. 1986: Carabid locomotor: Habits and Adaptations. Pp. 59–77. In: DEN BOER P. J., LUFF M. L., MOSSAKOWSKI D. & WEBER F. (eds.): *Carabid Beetles: their adaptations and dynamics*. Stuttgart: Gustav Fischer Verlag, 551 p.
- EVANS M. E. G. & FORSYTHE T. G. 1984: A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera, especially Carabidae. *J. Zool. Lond.* **202**: 513–534
- EVANS M. E. G. & FORSYTHE T. G. 1985: Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Carabidae). *J. Zool. Lond.* **206**: 113–143
- GOULET H. 1977: Technique for the study of immature coleoptera in glycerine. *Coleopt. Bull.* **31**: 381–382.
- GOULET H. 1979: Contributions of characters of larvae to systematics of Carabidae. Pp. 205–208. In: ERWIN T. L., BALL G. E. & WHITEHEAD D. R. (eds.): *Carabid beetles: their evolution, natural history and classification*. Boston: W. Junk Publishers, 635 p.
- GOULET H. 1983: The genera of holarctic Elaphrini and species of *Elaphrus* Fabricius (Coleoptera: Carabidae): classification, phylogeny and zoogeography. *Quaest. Entomol.* **19**: 219–482.
- GREBENNIKOV V. V. 1995: Larvae of Bembidiini (Coleoptera: Carabidae): I. Diagnosis of tribe and genera. *Proceedings of 3rd International Symposium of Carabidology*, p. 24.
- GREBENNIKOV V. V. 1996: Description of the first instar larva of *Thalassophilus longicornis* (Coleoptera: Carabidae: Trechodini). *Acta Soc. Zool. Bohem.* **60**: 373–379.
- HABU A. 1973: *Carabidae, Harpalini (Insecta, Coleoptera)*. *Fauna Japonica*. Tokyo: Keigaki Publ. Co., 430 pp.
- HABU A. 1981: Larvae of two species of Lebiini (Coleoptera, Carabidae). *Entomol. Rev. Japan.* **36**: 63–73.
- HABU A. & SADANAGA K. 1961: Illustration for identification of larvae of Carabidae found in cultivated fields and paddy fields (I). *Bull. Natl. Inst. Agric. Sci. (Ser. C)* **13**: 212–222
- HABU A. & SADANAGA K. 1965: Illustration for identification of larvae of Carabidae found in cultivated fields and paddy fields (III). *Bull. Natl. Inst. Agric. Sci. (Ser. C)* **13**: 93–125, 200–215
- HABU A. & SADANAGA K. 1970: Descriptions of some larvae of the Carabidae found in cultivated fields and paddy fields. *Konty.* **38**: 9–23.
- HARRIS A. C. 1978: The larva of *Brullea antarctica* (Coleoptera: Carabidae: Broscinae). *N. Zeal. Entomol.* **6**: 401–405
- HONOMILCH K. 1980: Die digitiformen Sensillen auf dem Maxillarpalpus von Coleoptera. I. Vergleichend-topographische Untersuchung des Kutikularen Apparates. *Zool. Anz.* **204**: 1–12.
- KILER S. VON 1963: *Entomologisches Wörterbuch. 3. Aufl.* Berlin: Akademie-Verlag, 679 pp.
- KRYZHANOVSKIY O. L. 1983: *Žuki podotjrjada Adephaga: semejstva Rhysodidae, Trachypachyidae, semejstvo Carabidae (uvodnaja čast' i obzor fauny SSSR)*. *Fauna SSSR, Tom 1, vyp. 2* [The beetles of the suborder Adephaga: families Rhysodidae, Trachypachidae, Carabidae (Introduction and a review of the USSR fauna)]. *Fauna USSR, Vol. 1, Part 2*. Leningrad: Nauka, 341 pp. (In Russian).
- KRYZHANOVSKIY O. L., BELOUSOV I. A., KABAK I. I., KATAEV B. M., MAKAROV K. V. & SHILEMKOV V. G. 1995: *A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae)*. Moskva: Pensoft publishers, 271 pp.
- LYUBARSKIY G. Yu. 1992: [Functional morphology of bulldozer structures and diversity of vital forms in the family Cryptophagidae (Coleoptera Clavicornia)]. *Russ. Entomol. J.* **1**: 3–26 (in Russian, Engl. abstr.).
- MADDISON D. R. 1993: Systematics of the Holarctic beetle subgenus *Bracteon* and related Bembidion (Coleoptera: Carabidae). *Bull. Mus. Comp. Zool.* **153**: 143–299.
- MAKAROV K. V. 1990: [The role of the micromorphological signs of larvae in the systematic of ground-beetles of tribe Carabini (Coleoptera, Carabidae)]. *The successes of the entomology in the USSR: Coleoptera insects*. The materials of the IX congress VEO, 11–15 September 1989. Leningrad: ZIN AN USSR, pp. 84–87 (in Russian).

- MAKAROV K. V. 1991: Employment of the larval morphological features in the systematic of the genus *C.* (L.) Thoms. *Fortrage der XII SIEEC. (Kiew)*, pp. 295–299.
- MAKAROV K. V. 1993: Larvae of Ground Beetles of the genus *C. L.* (Coleoptera, Carabidae) of the fauna Russia and Neighboring Countries. I. Morphology of larvae. A key to the subgenera. *Entomol. Rev.* **72**: 94–117.
- MAKAROV K. V. 1994: A key to the genera of the ground-beetle larvae (Coleoptera, Carabidae) of the Palearctic region. *Boll. Mus. Regional. Sci. Natur. Torino* **12**: 221–254.
- MAKAROV K. V. 1995: New data on the larvae of the Jurassic Carabomorpha (Coleoptera, Adephaga). *Paleontol. J.* **1**: 122–125. (in Russian, Engl. abstr.)
- MAKAROV K. V., GURGUENIDZE L. N. & REKK N. G. 1991: [Description of the larva of *Zabrus (Pelor) trinii* F.-W. (Coleoptera, Carabidae), an endemic Caucasian species, and a diagnosis of the subgenus *Pelor* as based on its larval characters.] *Izv. Akad. Nauk Gruzii (ser. Biol)* **17**: 103–109. (in Russian, Engl. abstr.)
- MAKAROVA E. V. & MAKAROV K. V. 1996: Larval morphology and systematic position of the genus *Callistus* (Coleoptera, Carabidae). *Zool. Zh.* **75**: 57–63. (in Russian, Engl. abstr.)
- MANTON S. M. 1959: Functional morphology and taxonomic problems of Arthropoda. Pp.: 23–32. In: CAIN A. J. (ed.): *Function and Taxonomic importance*. London: Systematic Association, 486 pp.
- MANTON S. M. 1977: *The Arthropoda: habits, functional morphology and evolution*. Oxford: Oxford University Press, xx+527 pp.
- MCIVER S. B. 1975: Structure of cuticular mechanoreceptors of arthropods. *Annual. Rev. Entomol.* **20**: 281–397.
- MOORE B. P. & LAVRENCE J. F. 1994: The extraordinary larval characters of *Carenum Bonelli* and their bearing on the phylogeny of the Scaritidae (Coleoptera: Carabidae). *Can. Entomol.* **126**: 503–514.
- NICHOLS S. W. 1986: Description of larvae of Puerto Rican species of *Antilliscaris* Bänniger and notes about relationships and classification of *Antilliscaris* (Coleoptera: Carabidae: Scaritini: Scaritina). *Coleopt. Bull.* **40**: 301–311.
- PESENKO YU. A. 1993: [Methodological analysis of systematics. II. Phylogenetic reconstructions as scientific hypotheses]. *Proc. Zool. Inst. St. Petersburg* **234**: 61–155. (in Russian, Engl. abstr.)
- ROTH L. M. & SLIFER E. H. 1973: Spheroid sense organs on the cerci of polyphagid cockroaches. *Int. J. Insect Morphol. Embryol.* **2**: 13–24.
- SCHMIDT K. 1973: Vergleichende morphologische Untersuchungen an Mechanoreceptoren der Insecten. *Verh. D. Zool. Ges.* **66**: 15–25.
- SHAROVA I. Kh. 1981: *Žiznennyye formy žučelic [Life forms of Carabids (Coleoptera, Carabidae)]*. Moskva: Nauka, 360 pp. (in Russian, Engl. abstr.)
- SLIFER E. H. 1970: The structure of arthropod chemoreceptors. *Annual. Rev. Entomol.* **15**: 121–142.
- SNODGRASS R. E. 1935: *Principles of Insect Morphology*. New York: McGraw-Hill, 667 pp.
- SPENCE J. R. & SUTCLIFFE J. F. 1982: Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). *Can. J. Zool.* **60**: 2382–2394.
- STRIGANOVA B. R. 1966: [Regularities in structure of Coleoptera larvae mouthparts.] Moskva: Nauka, 125 pp.
- TIKHOMIROVA A. L. 1991: [Restructuring of ontogenesis as evolutionary mechanism in insects.] Moskva: Nauka, 168 pp.
- TYSHCHENKO V. P. 1986: [Physiology of insects.] Moskva: Vysšaja Škola, 303 pp. (in Russian).
- WIGGLESWORTH V. B. 1953: The origin of sensory neurones in an insects, *Rhodnius prolixus*. *Quart. J. Microsc. Sci.* **94**: 93–112.
- WOMERSLEY H. 1937: Coleoptera. Pp.: 25–26. In: JOHNSON H. (ed.): British, Australian and New Zealand Antarctic Research expedition 1929–1931. *Reports series B. Adelaide* **4**(1): 1–206.
- ZACHARUK R. Y. 1962: Sense organs of the head of larvae of some Elateridae (Coleoptera): their distribution, structure and innervation. *J. Morphol.* **111**: 1–34.
- ZACHARUK R. Y., ALBERT P. J. & BELLAMY F. W. 1977: Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). *Can. J. Zool.* **58**: 569–578.
- ZETTO BRANDMAYR T. & BRADMAYR P. 1978: Morfologia pre-imaginalc e note bionomiche su *Harpalus (Harpalophonus) circumpunctatus italicus* Schaum (Coleoptera, Carabidae). *Boll. Entomol. Bologna* **34**: 65–74.
- ZETTO BRANDMAYR T., MARANO I. & PIZZOLOTTO R. 1995: Larval morphology and bionomy of *Amara (Leirides) alpestris* Villa (Coleoptera, Carabidae). *Gortana, Atti Mus. Friul. Stor. Natur.* **16**(1994): 187–202.

APPENDIX

MATERIAL EXAMINED

COLEOPTERA

ADEPHAGA

HALIPLIDAE

Haliphus sp.

DYTISCIDAE

Hyphydrus ovatus (L., 1761), *Hydroporus* sp., *Ilybius fuliginosus* (Fabricius, 1762), *Acilius canaliculatus* (Nicolai, 1822).

CARABIDAE

Cicindelinae

Cicindelitae

Megacephalini: *Megacephala euphratica* Dejean, 1822.

Cicindelini: *Cicindela (Eumecus) germanica* L., 1758, *C. (Cephalota) deserticola* Faldermann, 1836, *C. (Cicindina) arenaria* Fuesslin, 1775, *C. (C.) sublacerata* Solsky, 1874, *C. (Lophyridia) fischeri* Adams, 1817, *C. (s. str.) hybrida* L. 1758, *C. (s. str.) albopilosa* Dokhturoff, 1885, *C. (s. str.) sylvatica* L. 1758, *C. (s. str.) soluta* Latreille et Dejean, 1822, *C. (s. str.) campestris* L. 1758, *C. (s. str.) turkestanica* Ballion, 1876, *C. (s. str.) clypeata* Fischer von Waldheim, 1821.

Omophroninae

Omophronini: *Omophron* (s. str.) *limbatus* (Fabricius, 1776).

Carabinae*

Nebriitae

Pelophilini: *Pelophila borealis* (Paykull, 1790).

Nebriini: *Leistus* (s. str.) *ferrugineus* (L., 1758), *L. (s. str.) terminatus* (Hellwig in Panzer, 1793), *L. (s. str.) fulvus* Chaudoir, 1846, *L. (s. str.) niger* Gebler, 1847, *Nebria (Eunebria) nigerrima* Chaudoir, 1846, *N. (E.) psammophila* Solsky, 1874, *N. (E.) kirgisica* Shilenkov, 1982, *N. (Paranebria) livida* (L., 1758), *N. (Boreonebria) frigida* R. Sahlberg, 1844, *N. (B.) rufescens* (Ström, 1768), *N. (B.) nivalis* (Paykull, 1798), *N. (B.) subdilata* Motschulsky, 1844, *N. (s. str.) brevicolis* (Fabricius, 1792), *N. (Alpaeus) bonelli* (Adams, 1817), *N. (A.) ?commixta* Chaudoir, 1850.

Notiophilitae

Notiophilini: *Notiophilus* (s. str.) *aquaticus* (L., 1758), *N. (s. str.) impressifrons* Morawitz, 1862, *N. (s. str.) palustris* Duftschmidt, 1812, *N. (s. str.) germinyi* Fauvel, 1863, *N. (Latviaphilus) biguttatus* Fabricius, 1779, *N. (L.) reitteri* Späth, 1899, *N. (Makarovius) rufipes* Curtis, 1829.

Carabitae

Carabini: *Calosoma* (s. str.) *sycophanta* (L., 1758), *C. (Acalosoma) inquisitor* (L., 1758), *C. (Campalita) auropunctatum* (Herbst, 1784), *C. (C.) chinense* Kirby, 1817, *C. (Caminara) denticolle* Gebler, 1833, *C. (C.) reitteri* Roeschke, 1897, *C. (Charmosta) investigator* (Illiger, 1798), *C. (C.) lugens* Chaudoir, 1869, *C. (s. str.) brevisculus* Mannerheim, 1830, *Callisthenes* (s. str.) *elegans* Kirsch, 1859, *C. (s. str.) semenovi* Motschulsky, 1859, *C. (s. str.) kuschakewitschi* Ballion, 1870, *C. (s. str.) pseudocarabus* Semenov, 1928, *C. (s. str.) regelianus* Morawitz, 1886, *C. (s. str.) usgentensis* Solsky, 1874, *Carabus (Acrocarabus) guerini* Fischer von Waldheim, 1842, *C. (A.) callisthenoides* Semenov, 1888, *C. (Eucarabus) arvensis* Herbst, 1784, *C. (E.) stscheglowi* Mannerheim, 1827, *C. (E.) billbergi* Mannerheim, 1827, *C. (E.) cumanus* Fischer von Waldheim, 1823, *C. (E.) ullrichi* Germar, 1824, *C. (Autocarabus) obsoletus* Sturm, 1815, *C. (A.) auratus* L., 1761, *C. (A.) cancellatus* Illiger, 1798, *C. (s. str.) granulatus* L., 1758, *C. (s. str.) sculpturatus* Ménétrics, 1832, *C. (s. str.) menetriesi* Faldermann, 1827, *C. (Morphocarabus) tarbagataicus* Kraatz, 1878, *C. (M.) aeruginosus* Fischer von Waldheim, 1822, *C. (M.) hummeli* Fischer von Waldheim, 1823, *C. (M.) henningi* Fischer von Waldheim, 1817, *C. (M.) odoratus* Motschulsky, 1844, *C. (M.) karpinskii* Khryzhanovskij et Matveev, 1993, *C. (M.) michailovi* Kabak, 1992, *C. (M.) mestscherjakovi*

* Larvae belong to tribes Opishiini, Collyrini, Ctenostomatini, Pamborini, Migadopini, Promecogthini, Siagonini, Enceladini, Pseudomorphini, Metriini, Psydrini, Peleciini, Ablystomini, Cnemacanthini, Odacanthini, Lachnophorini, Zuphiini, Tetragnoderini, Heliuodini, Mormolycini, subfamily Paussinae and family Trachypachidae are known to me only on publication

Lutshnik, 1924, *C. (M.) regalis* Fischer von Waldheim, 1822, *C. (M.) excellens* Fabricius, 1798, *C. (M.) hampei* Küster, 1846, *C. (Leptinocarabus) venustus* Morawitz, 1862, *C. (L.) wulffi* Morawitz, 1862, *C. (Trachycarabus) besseri* Fischer von Waldheim, 1822, *C. (T.) bosphoranus* Fischer von Waldheim, 1823, *C. (T.) haeres* Fischer von Waldheim, 1823, *C. (T.) campestris* Fischer von Waldheim, 1822, *C. (T.) scabriusculus* Olivier, 1795, *C. (T.) estreicherii* Fischer von Waldheim, 1822, *C. (T.) latreillei* Fischer von Waldheim, 1822, *C. (T.) mandibularis* Fischer von Waldheim, 1827, *C. (T.) sibiricus* Fischer von Waldheim, 1822, *C. (Ophiocarabus) aeneolus* Morawitz, 1886, *C. (Cryptocarabus) lindemanni* Ballion, 1878, *C. (C.) subparallelus* Ballion, 1878, *C. (Mimocarabus) maurus* Adams, 1817, *C. (M.) roseni* Reitter, 1897, *C. (Archicarabus) nemoralis* O. F. Müller, 1764, *C. (A.) victor* Fischer von Waldheim, 1836, *C. (Limnocarabus) clathratus* L., 1761, *C. (Homoeocarabus) maeander* Fischer von Waldheim, 1822, *C. (Hemicarabus) macleayi* Dejean, 1826, *C. (H.) nitens* L., 1758, *C. (H.) tuberculatus* Dejean, 1829, *C. (Aulonocarabus) canaliculatus* Adams, 1812, *C. (A.) careniger* Chaudoir, 1863, *C. (A.) kurilensis* Lapouge, 1913, *C. (A.) truncaticollis* Eschscholtz, 1833, *C. (Leptocarabus) arboreus* Lewis, 1882, *C. (Asthenocarabus) opaculus* Putzeys, 1875, *C. (Diocarabus) loschnikovi* Fischer von Waldheim, 1823, *C. (D.) slovtzovi* Mannerheim, 1849, *C. (D.) massagetus* Motschulsky, 1844, *C. (D.) beybienkoi* Kryzhanovskij, 1973, *C. (Pachycarabus) imitator* Reitter, 1883, *C. (P.) koenigi* Ganglbauer, 1886, *C. (P.) staehlini* Adams, 1817, *C. (Orinocarabus) linnei* Panzer, 1812, *C. (O.) silvestris* Panzer, 1793, *C. (Hadrocarabus) problematicus* Herbst, 1786, *C. (Oreocarabus) glabratus* Paykull, 1790, *C. (O.) hortensis* L., 1758, *C. (O.) cribratus* Quensel, 1806, *C. (Ulocarabus) stschurowskii* Solsky, 1874, *C. (U.) theanus* Reitter, 1895, *C. (Semnocarabus) erosus* Motschulsky, 1865, *C. (S.) carbonicolor* Morawitz, 1886, *C. (S.) regulus* Dohrn, 1882, *C. (S.) transiliensis* Semenov, 1896, *C. (Tomocarabus) convexus* Fabricius, 1775, *C. (T.) decolor* Fischer von Waldheim, 1823, *C. (T.) marginalis* Fabricius, 1794, *C. (T.) bessarabicus* Fischer von Waldheim, 1823, *C. (T.) scabripennis* Chaudoir, 1850, *C. (Scambocarabus) kruberi* Fischer von Waldheim, 1822, *C. (Pachystus) hungaricus* Fabricius, 1792, *C. (P.) cribellatus* Adams, 1812, *C. (Hygrocarabus) variolosus* Fabricius, 1787, *C. (Chaetocarabus) intricatus* L., 1761, *C. (Platycarabus) fabricii* Panzer, 1812, *C. (Panthophyrtus) turcomanorum* Thieme, 1881, *C. (P.) brachypedilus* Morawitz, 1886, *C. (Megodontus) vietinghoffi* Adams, 1812, *C. (M.) violaceus* L., 1758, *C. (M.) aurolimbatus* Dejean, 1929, *C. (M.) stroganowi* Zoubkoff, 1837, *C. (M.) gyllenhalii* Fischer von Waldheim, 1827, *C. (M.) exaratus* Quensel, 1806, *C. (M.) septemcarinatus* Motschulsky, 1840, *C. (Ainocarabus) kolbei* Roeschke, 1897, *C. (A.) avinovi* Semenov, 1932, *C. (Pachycranion) imperialis* Fischer von Waldheim, 1823, *C. (P.) schoenherri* Fischer von Waldheim, 1822, *C. (Carabulus) leachi* Fischer von Waldheim, 1823, *C. (C.) ermaki* Lutshnik, 1924, *C. (Chrysoacarabus) auronitens* Fabricius, 1792, *C. (Acopiolabus) constricticollis* Kraatz, 1886, *C. (A.) schrenckii* Motschulsky, 1860, *C. (A.) lopatini* Morawitz, 1886, *C. (Sphodristocarabus) armeniacus* Mannerheim, 1830, *C. (S.) adamsi* Adams, 1817, *C. (S.) bohemanii* Ménétriés, 1832, *C. (Cechenochilus) boeberi* Adams, 1817, *C. (C.) gusevi* Zamotajlov et Koval, 1989, *C. (C.) heydenianus* Starck, 1889, *C. (C.) kokujewi* Semenov, 1898, *C. (Eotribax) hieki* Kabak et Kryzhanovskij, 1990, *C. (E.) valikhonovi* Kabak, 1990, *C. (Leptoplesius) merzbacheri* Hausser, 1922, *C. (Cechenotribax) petri* Semenov et Znojko, 1932, *C. (Cratocechemus) akinini* Morawitz, 1886, *C. (C.) ovtshinnikovi* Gottwald, 1987, *C. (C.) corrugis* Dohrn, 1882, *C. (C.) cicatricosus* Fischer von Waldheim, 1842, *C. (C.) solskyi* Ballion, 1878, *C. (C.) balassogloi* Dohrn, 1882, *C. (Pseudotribax) validus* Kraatz, 1884, *C. (P.) ferghanicus* Breuning, 1933, *C. (Cratophyrtus) kaufmanni* Solsky, 1874, *C. (C.) medvedevi* Kryzhanovskij, 1968, *C. (C.) puer* Morawitz, 1886, *C. (C.) jacobsoni* Semenov, 1908, *C. (C.) redikortzevi* Semenov, 1933, *C. (Alipaster) pupulus* Morawitz, 1889, *C. (Tribax) circassicus* Ganglbauer, 1886, *C. (T.) agnatus* Ganglbauer, 1889, *C. (T.) titan* Zolotarev, 1913, *C. (T.) kasbekianus* Kraatz, 1877, *C. (T.) apschuanus* Rost, 1893, *C. (T.) biebersteini* Ménétriés, 1832, *C. (T.) constantinowi* Starck, 1894, *C. (T.) retezari* Gottwald, 1980, *C. (T.) fossiger* Chaudoir, 1877, *C. (T.) osseticus* Adams, 1817, *C. (T.) steveni* Ménétriés, 1832, *C. (Microplectes) argonautarum* Semenov, 1898, *C. (M.) convallium* Starck, 1889, *C. (M.) riedeli* Ménétriés, 1832, *C. (Microtribax) kasakorum* Semenov, 1896, *C. (Archiplectes) daphnis* Kurnakov, 1962, *C. (A.) protensus* Schaum, 1864, *C. (A.) plasoni* Ganglbauer, 1886, *C. (A.) faunus* Kurnakov, 1972, *C. (A.) lennoni* Gottwald, 1985, *C. (A.) apollo* Zolotarev, 1913, *C. (A.) satyrus* Kurnakov, 1962, *C. (A.) polychrous* Rost, 1892, *C. (A.) roussianus* Gottwald, 1985, *C. (A.) reitteri* Retowski, 1885, *C. (A.) juentheri* Reitter, 1899, *C. (A.) jason* Semenov, 1898, *C. (A.) starcki* Heyden, 1884, *C. (A.) edithae* Reitter, 1893, *C. (A.) kratkyi* Ganglbauer, 1890, *C. (A.) felicitanus* Reitter, 1893, *C. (A.) starckianus* Ganglbauer, 1886, *C. (A.) prometheus* Reitter, 1887, *C. (A.) basilianus* Starck, 1890, *C. (A.) miroshnikovii* Zamotajlov, 1990, *C. (Lamprostus) calleyi* Fischer von Waldheim, 1823, *C. (Procrustes) coriaceus* L., 1758, *C. (P.) clypeatus* Adams, 1817, *C. (P.) talyschensis* Ménétriés, 1832, *C. (Goniocarabus) gussakovskii* Kryzhanovskij, 1971, *C. (Deroplectes) coiffaitianus* Deuve, 1990, *C. (D.) sphinx* Reitter, 1895, *C. (Plesius) staudingeri* Ganglbauer, 1886, *C. (P.) dokhtouroffi* Ganglbauer, 1886, *C. (Axinocarabus) fedtschenkoi* Solsky, 1874, *C. (A.) miles* Semenov, 1887, *C. (Coptolabus) smaragdinus* Fischer von Waldheim, 1823, *C. (Damaster) rugipennis* Motschulsky, 1861, *C. (Procerus) scabrosus* Olivier, 1795, *C. (P.) caucasicus* Adams, 1817, *C. (Eupachys) glyptopterus* Fischer von Waldheim, 1827.

Cychnini: *Cychnus aeneus* Fischer von Waldheim, 1824, *C. caraboides* (L., 1758), *C. semigranosus* Palliard, 1825, *C. morawitzi* Géhin, 1863.

Elaphritac

Elaphrini: *Diacheila fausti* Heyden, 1887, *D. polita* (Faldermann, 1835), *Blethisa ?tuberculata* Motschulsky, 1844, *B. multipunctata* L., 1758, *Elaphrus (Arctelaphrus) lapponicus* Gyllenhal, 1810, *E. (Neolaphrus) splendidus* Fischer von Waldheim, 1828, *E. (N.) sibiricus* Motschulsky, 1844, *E. (N.) cupreus* Duftschmid, 1812, *E. (s. str.) riparius* (L., 1758), *E. (Elaphroterus) angusticollis* R. Sahlberg, 1844.

Loricritac

Loricrini: *Loricera* (s. str.) *pilicornis* (Fabricius, 1775).

Scarititac

Scaritini: *Scarites (Distichus) planus* Bonelli, 1813, *S. (s. str.) angustus* Chaudoir, 1855, *S. (s. str.) eurytus* Fischer von Waldheim, 1828, *S. (s. str.) laevigatus* Fabricius, 1792, *S. (s. str.) salinus* Dejean, 1859, *S. (s. str.) terricola* Bonelli, 1813, *S. (Scallophorites) bucida* Pallas, 1776.

Clivinini: *Clivina fossor* (L., 1758), *C. ypsilon* Dejean, 1829.

Dyschiriini: *Dyschirius arenosus* Stephens, 1827, *D. baicalensis* Motschulsky, 1844, *Dyschiriodes (Eudyschirius) globosus* (Herbst, 1783), *D. (s. str.) nitidus* (Dejean, 1825), *D. (s. str.) ?chalceus* (Erichson, 1837), *D. (s. str.) nigricornis* (Motschulsky, 1844), *D. (s. str.) tristis* (Stephens, 1827).

Broscitac

Broscini: *Broscus cephalotes* (L., 1758), *B. semistriatus* (Dejean, 1828), *B. asiaticus* Ballion, 1870, *B. punctatus* (Dejean, 1828), *Miscodera arctica* (Paykull, 1798).

Trechitac

Trechini: *Epaphius secalis* (Paykull, 1790), *Trechus quadristriatus* (Schrank, 1781), *T. rubens* (Fabricius, 1792), *T. go-liath* Belousov et Kabak, 1991, *T. ?almonius* Reitter, 1903.

Tachyini: *Tachys* sp., *Tachyta nana* (Gyllenhal, 1810).

Bembidiini: *Asaphidion flavipes* (L., 1761), *Bembidion (Bracteon) ?argenteolum* (Ahrens, 1812), *B. (Metallina) ?propersans* (Stephens, 1829), *B. (Notaphus) varium* (Olivier, 1795), *B. (Eupetedomus) dentellum* (Thunberg, 1787), *B. (Bembidion) quadrimaculatum* (L., 1761), *B. (Trichoplataphus) hasti* C. Sahlberg, 1827, *B. (Ocydromus) femoratum* Sturm, 1825, *B. (O.) tetracolum* Say, 1823.

Pogonini: *Pogonus (Pogonoidius) cumanus* Lutshnik, 1916, *P. (s. str.) luridipennis* (Germar, 1822).

Patrobitac

Patrobini: *Patrobus atrorufus* (Ström, 1768), *P. septentrionis* Dejean, 1828, *Diplous depressus* (Gebler, 1829).

Deltomerini: *Deltomerus elongatus* Dejean, 1831, *D. tibialis* Reitter, 1887.

Pterostichitac

Morionini: *Morion* sp.

Pterostichini: *Poecilus* (s. str.) *cupreus* (L., 1758), *P. (s. str.) versicolor* (Sturm, 1824), *P. (s. str.) fortipes* Chaudoir, 1850, *P. (s. str.) punctulatus* (Schaller, 1783), *Pterostichus (Platysma) niger* (Schaller, 1783), *P. (Myosodus) lacunosus* (Chaudoir, 1844), *P. (M.) variabilis* (Ménétriés, 1832), *P. (Argutor) vernalis* (Panzer, 1796), *P. (Melanias) anthracinus* (Illiger, 1798), *P. (M.) gracilis* (Dejean, 1828), *P. (M.) nigrita* (Paykull, 1790), *P. (Phonias) strenuus* (Panzer, 1797), *P. (Cryobius) brevicornis* (Kirby, 1837), *P. (C.) pinguedineus* Eschscholtz, 1823, *P. (Oreoplatysma) sp.*, *P. (Eurymelanius) caucasicus* Ménétriés, 1832, *P. (E.) chydaeus* (Tschitschérine, 1896), *P. (Steropus) aereipennis* Solsky, 1872, *P. (S.) aethiops* (Panzer, 1797), *P. (Steroperis) vermiculosus* Ménétriés, 1851, *P. (Bothriopterus) adstrictus* Eschscholtz, 1823, *P. (B.) quadrifoveolatus* Letzner, 1852, *P. (B.) oblongopunctatus* (Fabricius, 1787), *P. (B.) subovatus* Motschulsky, 1862, *P. (Morphnosoma) melanarius* (Illiger, 1798), *P. (Feronidius) melas* (Creutzer, 1799), *P. (Petrophilus) vladivostokensis* Lafer, 1980, *P. (Sterocerus) rubripes* Motschulsky, 1860, *P. (Calopterus) pilosus* (Host, 1789), *Abax parallelopedus* Piller et Mitterpacher, 1783, *A. parallelus* (Duftschmid, 1812), *A. schueppeli* Palliard, 1827, *Molops piceus* (Panzer, 1793).

Sphodrini: *Calathus* (s. str.) *distinguentus* Chaudoir, 1846, *C. (s. str.) fuscipes* (Goeze, 1777), *C. (s. str.) longicollis* Motschulsky, 1864, *C. (Neocalathus) ambiguus* (Paykull, 1790), *C. (Neocalathus) erratus* (C. Sahlberg, 1827), *C. (Neocalathus) melanocephalus* (L., 1758), *C. (Neocalathus) micropterus* (Duftschmid, 1812), *C. (Dolichus) halensis* (Schaller,

1783), *C. (Lindrothius) sp.*, *Pseudotaphoxenus sp.*, *Pseudotaphoxenus rufitarsis* (Fischer von Waldheim, 1823), *Taphoxenus* (s. str.) *gigas* (Fischer von Waldheim, 1823), *Eremosphodrus dvorshaki* Casale et Vereschagina, 1986, *Laemostenus (Antisphodroides) koenigi* (Reitter, 1887), *L. (Antisphodroides) tschitscherini* Semenov, 1908, *L. (A.) ljevushkini* Vereschagina, 1985, *L. (Pristonychus) mannerheimi* Kolnati, 1845, *L. (P.) tauricus* Dejean, 1828, *L. (P.) terricola* (Herbst, 1783).

Platynini: *Agonum* (s. str.) *rugicolle* Chaudoir, 1846, *A. (s. str.) mandli* Jedlička, 1933, *A. (s. str.) marginatum* (L., 1758), *A. (s. str.) muelleri* (Herbst, 1784), *A. (s. str.) sexpunctatum* (L., 1758), *A. (s. str.) viduum* (Panzer, 1797), *A. (Liebherrius) alpinum* Motschulsky, 1844, *A. (Europhilus) exaratum* (Mannerheim, 1853), *A. (E.) fuliginosum* (Panzer, 1809), *A. (E.) thoreyi* (Dejean, 1828), *Platynus* (s. str.) *assimile* (Paykull, 1790), *Oxypselaphus obscurum* (Herbst, 1784), *Anchomenus dorsalis* (Pontoppidan, 1763), *Olisthopus rotundatus* (Paykull, 1790), *Synuchus* (s. str.) *vivalis* (Illiger, 1798), *S. (Pristodactyla) agonus* (Tschitchérine, 1895).

Amarini: *Amara (Zezea) plebeja* (Gyllenhal, 1810), *A. (s. str.) aenea* (DeGeer, 1774), *A. (s. str.) communis* (Panzer, 1797), *A. (s. str.) eurynota* (Panzer, 1797), *A. (s. str.) similata* (Gyllenhal, 1810), *A. (Celia) bifrons* (Gyllenhal, 1810), *A. (C.) brunnea* (Gyllenhal, 1810), *A. (C.) ingenua* (Duftschmid, 1812), *A. (Paracelia) quenseli* (Schönherr, 1806), *A. (Oreoamara) cordicollis* Ménétrics, 1832, *A. (Bradytus) apricaria* (Paykull, 1790), *A. (B.) fulva* (O. F. Müller, 1776), *A. (B.) majuscula* (Chaudoir, 1850), *A. (Percosia) equestris* (Duftschmid, 1812), *Harpalodema lutescens* Reitter, 1888, *Curtonotus* (s. str.) *alpinus* (Paykull, 1790), *C. (s. str.) aulicus* (Panzer, 1797), *C. (s. str.) convexusculus* (Marsham, 1802), *C. (s. str.) gr. miser* Tschitschérine, 1899, *Zabrus* (s. str.) *morio* Ménétrics, 1832, *Z. (s. str.) tenebrioides* (Goeze, 1777), *Z. (Pelor) spinipes* (Fabricius, 1798), *Z. (P.) trinii* Fischer von Waldheim, 1817, *Z. (Eutroctes) aurichalceus* Adams, 1817.

Harpalitac

Harpalini: *Anisodactylus* (s. str.) *binotatus* (Fabricius, 1787), *A. (s. str.) signatus* (Panzer, 1797), *Bradycellus (Tachycellus) glabratus* (Reitter, 1894), *Dicheirotichus* (s. str.) *gustavii* Crotch, 1871, *Stenolophus* (s. str.) *mixtus* Herbst, 1784, *Acupalpus* (s. str.) *parvulus* (Sturm, 1885), *Daptus pictus* Fischer von Waldheim, 1824, *Harpalus rufipes* (DeGeer, 1774), *H. calceatus* (Duft. 1812), *H. rubripes* (Duftschmid, 1812), *H. quadripunctatus* Dejean, 1829, *H. ?pumilus* (Sturm, 1818), *H. zabroides* Dejean, 1829, *H. froelichi* Sturm, 1818, *H. latus* (L., 1758), *H. xanthopus* Gemminger et Harold, 1868, *H. affinis* (Schrank, 1781), *H. distinguendus* (Duftschmid, 1812), *Acinopus* (s. str.) *picipes* (Olivier, 1795), *A. (Osimum) ammophilus* Dejean, 1829, *Ophonus (Metophonus) nitidulus* Stephens, 1828, *O. (Metophonus) puncticollis* (Paykull, 1798), *O. (Hesperophonus) azureus* (Fabricius, 1775), *O. (s. str.) stictus* Stephens, 1828, *Liochirus cycloderus* (Solsky, 1874), *Machozethus lehmanni* (Ménétrics, 1849), *Chilotomus tschitscherini* Semenov, 1903.

Perigonitac

Perigonini: *Perigona ?nigrifrons* Motschulsky, 1861.

Panagacitac

Panagacini: *Panagaeus cruxmajor* (L., 1758), *Tefflus ?juvenilis muansanus* Kolbe, 1897.

Callistitac

Callistini: *Epomis dejeani* Dejean et Boisduval, 1830, *Dinodes decipiens* (Dufour, 1820), *Chlaenius (Stenochlaenius) coeruleus* (Steven, 1809), *C. (Chlaenites) spoliatus* (Rossi, 1790), *C. (s. str.) festivus* (Panzer, 1796), *C. (s. str.) flavicornis* Fischer von Waldheim, 1842, *C. (Chlaenius) pallipes* Gebler, 1823, *C. (Chlaeniellus) nitidulus* (Schrank, 1781), *C. (C.) tibialis* Dejean, 1826, *C. (C.) nigricornis* (Fabricius, 1787), *C. (C.) vestitus* (Paykull, 1790), *C. (C.) tristis* (Schaller, 1783), *C. (Agostenus) alutaceus* Gebler, 1829, *C. (Pelasmus) costulatus* Motschulsky, 1859.

Oodini: *Oodes (Oodes) helopioides* (Fabricius, 1792).

Licini: *Licinus* (s. str.) *depressus* (Paykull, 1790), *L. (s. str.) cassideus* (Fabricius, 1792), *Tricholicinus setosus* J. Sahlberg, 1880, *Badister* (s. str.) *bullatus* (Schrank, 1798), *B. (Baudia) ?dilatatus* (Chaudoir, 1837).

Masorecitac

Masorecini: *Masoreus wetterhalli* (Gyllenhal, 1813).

Corsyrini: *Corsyra fusula* (Steven in Dejean, 1825), *Discoptera komarovi* Semenov, 1889.

Lebiiatae

Lebiiini: *Demetrius* (s. str.) *monostigma* Samonelle, 1819, *Dromius* sp., *Paradromius* (*Manodromius*) *linearis* (Olivier, 1795), *Syntomus* ?*dilutipes* Reitter, 1887, *S. truncatellus* (L., 1761), *Charopterus paracentesis* (Motschulsky, 1889), *Microlestes minutulus* (Gocze, 1777), *Microlestes* sp., *Cymindis* (s.str.) *angularis* (Gyllenhal, 1810), *C.* (s.str.) *axillaris* (Fabricius, 1794), *C.* (s.str.) *humeralis* (Fourcroy, 1785), *C.* (s. str.) *lineata* (Quensel, 1806), *C.* (s. str.) *pecta* (Pallas, 1771), *C.* (*Paracymindis*) *mannerheimi* Gebler, 1843, *C.* (*Menas*) *impressa* Reitter, 1893, *C.* (*Tarsostinus*) *lateralis* Fischer von Waldheim, 1821, *C.* (*Tarulus*) *vaporariorum* (L., 1758).

Orthogoniini: *Orthogonius* ?*acutangulus* Chaudoir, 1852.

Anthiini: *Anthia mannerheimi* Chaudoir, 1842, *A.* ?*massilicata* Stygne Kolbe, 1906.

Helluodini: *Helluodes taprobanae* Westwood, 1834.

Galeritini: *Galerita feai* Bates, 1883, *Galerita* sp.

Dryptini: *Drypta dentata* (Rossi, 1790).

Brachininae

Brachinini: *Brachinus crepitans* (L., 1758), *B.* ?*explodens* Duftschmid, 1812.

POLYPHAGA

HYDROPHILIDAE

Helophorus aquaticus (L., 1758), *Helophorus* spp., *Berosus* ?*signaticollis* (Charpentier, 1825), *Hydrobius fuscipes* (L., 1758).

STAPHYLINIDAE

Oxytelus sp., *Lathrobium* sp., *Philonthus* sp., *Ontholestes* sp., *Tachynus* sp.

HISTERIDAE

Margarinotus sp., *Paromalus* sp.

DRYLIDAE

Drylus sp.

CANTHARIDAE

Cantharis sp., *Rhagonycha* sp.

ELATERIDAE

Athous sp., *Selatosomus* sp., *Agriotes obscurus* (L., 1758).

TENEBRIONIDAE

Pedinus sp., *Pisterotarsa* sp.

NEUROPTERA

OSMYLIDAE

Osmylus sp.

ASCALAPHIDAE

Ascalaphus sp.

MYRMELEONIDAE

Myrmelconidac gen. sp.