

Larval chaetotaxy in the genus *Rhysodes* Dalman, 1823 and the position of Rhysodidae within Adephaga (Coleoptera)

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SUMMARY

A thorough study of larval morphology in *Rhysodes sulcatus* (Fabricius, 1787) and *Rh. comes* (Lewis, 1888) (Rhysodidae) revealed a unique arrangement of the mouthparts and allowed for homologies of their elements to be elucidated. A special microporous structure was found in the labiomaxillar complex. An analysis of the larval characters resulted in rejection of all the hypotheses treating the Rhysodidae as a taxon subordinate to the Carabidae. The similarity of Rhysodidae larvae to those of the remaining Geadephaga was found to be insignificant. Instead they share some essential larval features with the suborder Archostemata. The hypothesis was put forth that Rhysodidae and Paussinae could have originated from the common ancestor within Archostemata.

Keywords: larvae, morphology, chaetotaxy, mouthparts, Coleoptera, Rhysodidae, Carabidae, relationship

INTRODUCTION

The beetle family Rhysodidae, encompassing about 350 species, is widespread in the tropical and temperate belts (Bell & Bell, 1978). Trophically, rhysodiids are suggested to be intimately associated with Myxomycetes in their ameoboid stage of development (Bell, 1998). The larvae live inside dead wood (Burakowski, 1975; Mamaev & Pototskaya, 1979) and regularly occur together with adults. Their life history and feeding remain poorly-known.

In the 19th century, this family was regarded as being close to Cucujidae and Colydiidae (Reitter, 1882), but later its placement within Adephaga was justified (Ganglbauer, 1892; Peyerimhoff, 1903; Böving, 1929). Inside this suborder, Rhysodidae were considered as an independent, rather primitive family (Jeannel, 1941; Crowson, 1955; Ponomarenko, 1995), as the sister-group to (Beutel, 1990, 1992a), or a specialized derivative of, Carabidae (Beutel, 1992b, 1993, 1995), sometimes also as a member of Carabidae in the rank of a subfamily, tribe or even subtribe (Bell & Bell, 1962; Erwin & Sims, 1984; Erwin, 1985; Bell, 1998).

For the first time, larvae of Rhysodidae were briefly described in the early 20th century, without precise species identification (Peyerimhoff, 1903). Later, some larval characters of *Clinidium sculptile* were used by Böving (1929) in discussing the taxonomic position of the family Rhysodidae. However, most of larval morphological evidence was published rather recently (Grandi, 1956, 1972; Burakowski, 1975; Vanin & Costa, 1978; Mamaev & Pototskaya, 1979; Costa et al., 1988). These papers included rather detailed accounts of the external morphology of larvae and, partly, of their anatomy (Beutel, 1992b). However, no special studies on larval chaetotaxy in rhysodids have hitherto been conducted. My research on *Rhysodes sulcatus* (Fabricius, 1787) and *Rh. comes* (Lewis, 1888) larvae allows for a detailed description of larval chaetotaxy in the genus to be made, also suggesting a new view of Rhysodidae relationships.

MATERIAL AND METHODS

A total of 58 larvae of all stages belonging to 2 species of *Rhysodes* were studied.

Rhysodes sulcatus (Fabricius, 1787: 165)

Poland, Białowieża Primeval Forest (National Park), in yellowish-rotting, damp sapwood of *Populus tremula* L., 2.VII.1968, leg. B. Burakowski (MIZ 80475-MIZ 80478) – 3 L3, 1 pupa (*Al*); Northern Caucasus, Krasnodar Territory, Guzeripl, 17.VI.1988, leg. N. Nikitsky – 1 L3 (*Eu*); Northwestern Caucasus, Adygeya, 4 km E of Filimonov's Mt., in *Abies* wood, 25.VI.2007, leg. A. Zaitsev – 3 L1 (2 – *Al*, 1 – *Eu*), 8 L2 (7 – *Al*, 1 – *Eu*).

Rhysodes comes (Lewis, 1888: 79)

Primorye, Southern Sikhote-Alin Mts, Lazovsky Nature Reserve, cordon Korpad', floodplane of Kedrovaya River, in rotten wood of *Betula* sp., 9.VIII.2007, leg. A. Zaitsev & K. Makarov – 1L1, 7L3, 1 pupa (*Al*); same location, in *Ulmus* sp. wood, 10.VIII.2007, leg. A. Zaitsev & K. Makarov – 2L1 (1 – *Al*, 1 – *Eu*), 12L2 (11 – *Al*, 1 – *Eu*), 9L3 (8 – *Al*, 1 – *Eu*); same district, cordon Prosyolochnaya, in rotten wood of *Alnus* sp., 17.VIII.2007, leg. A. Zaitsev & K. Makarov – 6L3, 2 pupa (*Al*); same location, in *Alnus* wood, 20.VIII.2007, leg. A. Zaitsev & K. Makarov – 5L3, (4 – *Al*, 1 – *Eu*), 1L2 (*Al*).

Most specimens are preserved in 70% alcohol (*Al*), and deposited in the collection of the Department of Zoology and Ecology of the Moscow Pedagogical University and in the Museum and Institute of Zoology of the Polish Academy of Sciences. Some specimens were mounted in Euparal microscopic slides (*Eu*) for chaetome investigations.

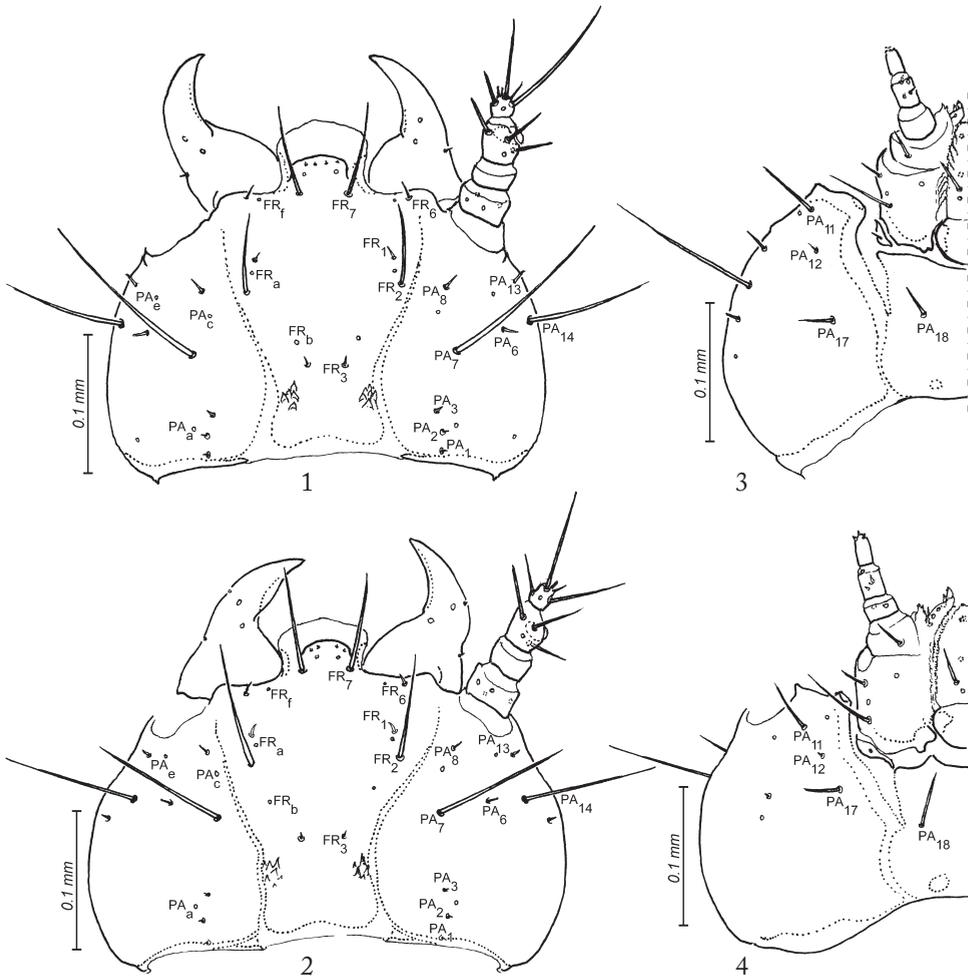
The external larval morphology of Rhysodidae, including that of both studied species of *Rhysodes*, have been described many times (Grandi, 1972; Burakowski, 1975; Vanin & Costa,

1978; Mamaev & Pototskaya, 1979; Costa et al., 1988). This is why below I mainly give chaetotaxy characteristics followed by the necessary comments. The sensillar nomenclature developed by Bousquet & Goulet (1984) was used, with minor modifications (Makarov, 1996).

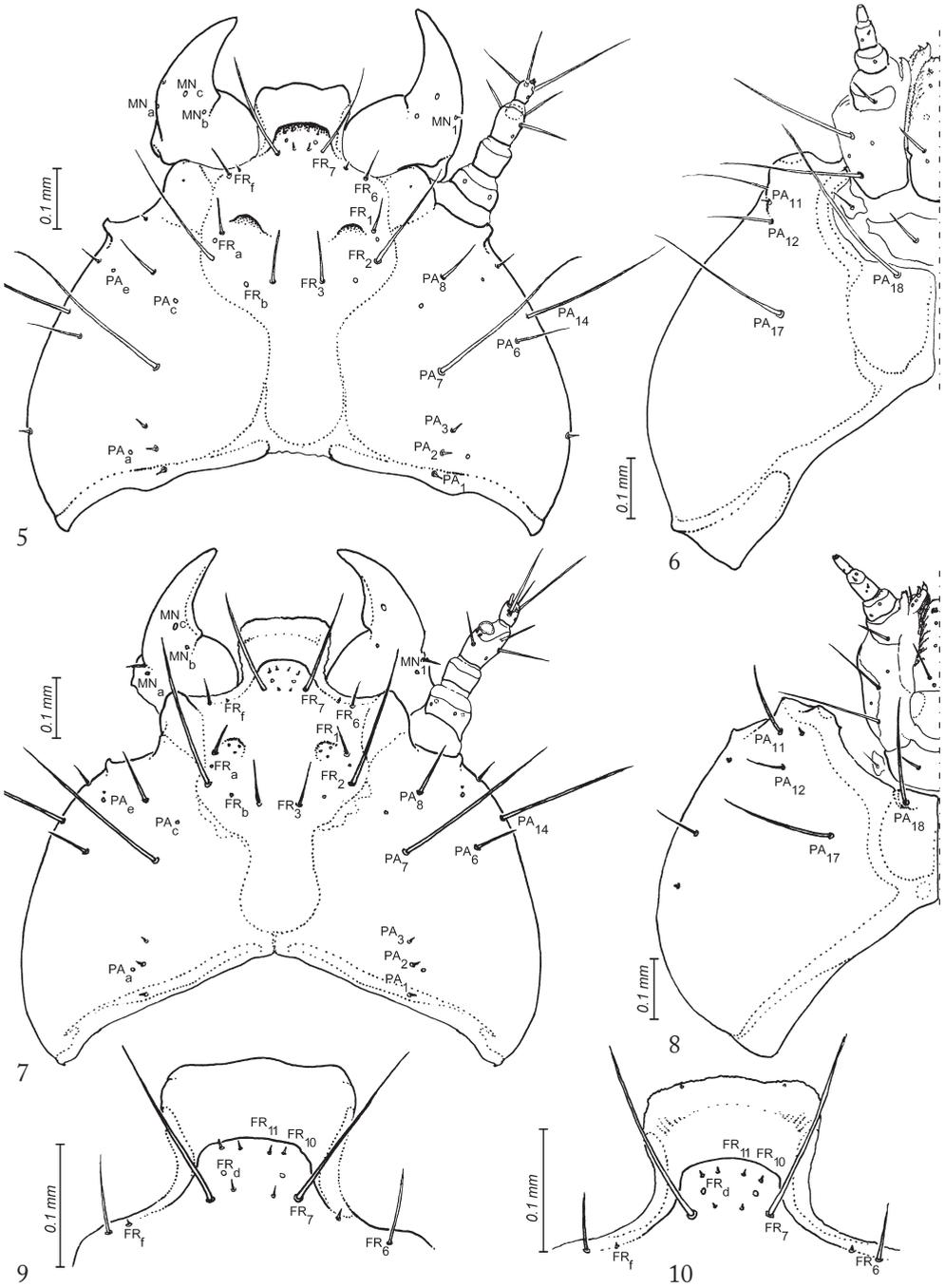
RESULTS

Genus *Rhysodes* Dalman, 1823: 93

LARVAL CHAETOTAXY. Head capsule (Figs 1-10) with a reduced set of sensilla. Frontale with neither an antediscal sensillar complex (FR₄, FR₅ and FR_{c,e}) nor sensilla of anterior margin of paraclypeus FR₈₋₉, FR_g. Sensilla FR₁ and FR_a, commonly associated



Figs 1-4. *Rhysodes* spp., first instar larvae: 1, 3 – *Rb. sulcatus*; 2, 4 – *Rb. comes*; 1-2 – head, dorsal view, left antenna and labiomaxillar complex not show; 3-4 – right half of head, ventral view.



Figs 5-10. *Rhyssodes* spp., third instar larvae: 5-6, 9 – *Rb. sulcatus*; 7-8, 10 – *Rb. comes*; 5, 7, – head, dorsal view, left antenna and labiomaxillar complex not show; 6, 8 – right half of head, ventral view; 9-10 – nasale, dorsal view.

with lateral sclerite corners, displaced mediad and positioned anterior to macrosetae FR_2 . Location of setae FR_7 also unusual, they being close together so that the distance between their insertions is equal to nasale width. Both FR_3 and FR_b thereby in usual positions, posterior to line FR_2 - FR_2 . Macrosetae FR_2 and FR_7 2-7 times longer than other setae (Figs 1, 3, 5, 7). Nasale setae FR_{10} - FR_{11} tiny, visible only in cleared specimens (Figs 9-10). Some setae of parietale fully reduced, i.e. dorsal PA_4 , PA_5 , PA_9 and PA_{10} , and ventral PA_{15} and PA_{16} . Gular area with one pair of setae in anterior part (versus two pairs of setae, PA_{18} and PA_{19} , typical of carabids), their identification as PA_{18} being tentative because of lack of additional markers in this area (Figs 2, 4, 6, 8). Many sensilla absent, including PA_b , PA_d and most of ventrolateral non-trichoid sensilla.

Antenna of typical structure, its chaetotaxy without essential distinctions from basal carabid pattern (Figs 11-13). It is significant that antennomere 3 is with a flattened sensorium in ventral position; apical and subapical sensillar complexes rather poor, latter including only 1-2 basiconical sensilla.

Mandible without penicillus, seta MN_2 absent, seta MN_1 short, in ventrolateral position; sensilla MN_a and MN_b present (Figs 1, 3, 5, 7).

Maxilla considerably membranous, forming together with labium a functionally entire labiomaxillar complex (Figs 14-15). Its chaetotaxy original: internal stipes margin without gMX so very typical of carabids, serving as a filtration organ. It is replaced by a system of oblique folds covered with rows of cuticular spinules. Coupled with complementary folds of labium, they make a microporous structure. Besides this, galea and lacinia fused with top of stipes and internal margin of palpifer forming a distal extension of microporous structure. Though galea and lacinia cannot be distinguished, sensilla MX_6 , $MX_{7,9}$, and MX_d easily recognizable, as well as apical conical sensilla of galeomere 2 (Fig. 16). In spite of such essential transformations, sensillar set of external surface of stipes and maxillar palp almost the same as in carabids, except for reduction of MX_4 , MX_5 and total absence of digitiform sensilla in subapical sensorial complex.

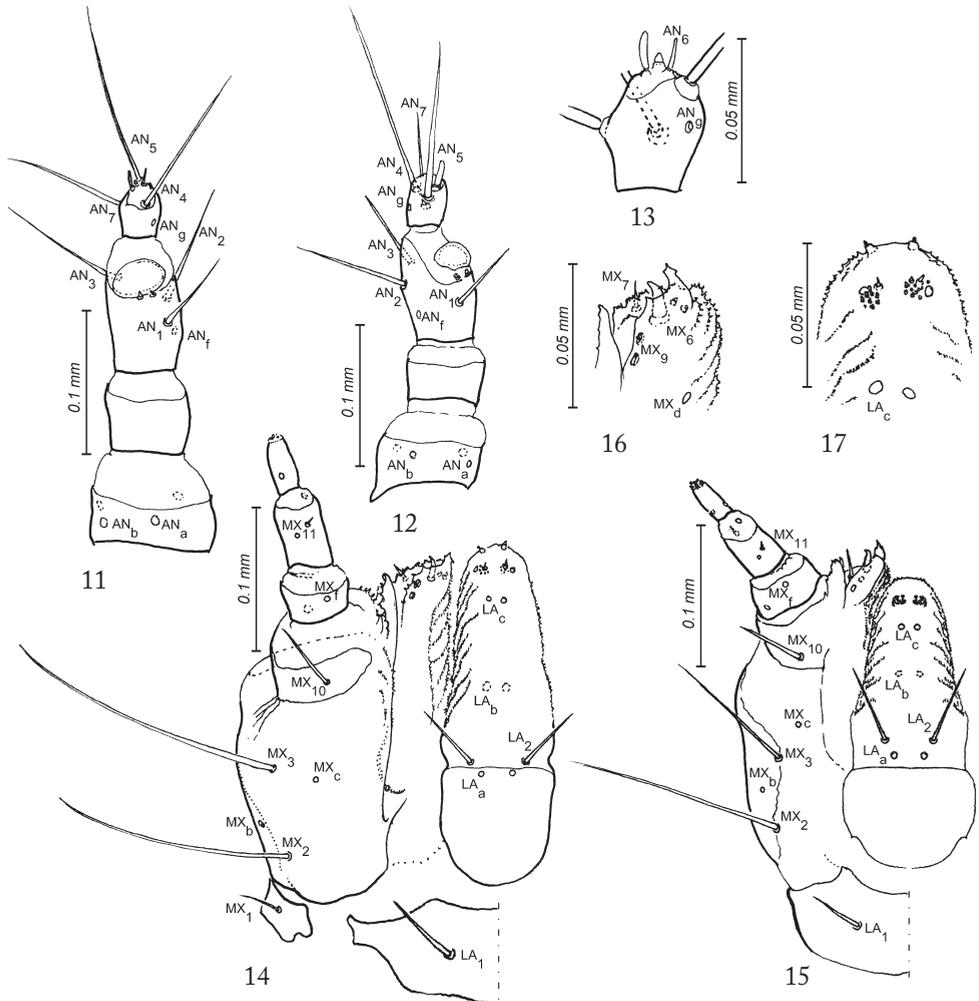
Labium of *Rhysodes* larvae representing a merged subcylindrical structure with lateral surfaces tightly adjacent to maxillar stipites and covered with cuticular spinules (Figs 14-15). Labial chaetome reduced strongly enough, but all of its elements corresponding to generalized pattern. Like on maxilla, a number of lateral and apical setae ($LA_{3,4,5,6,7}$) replaced by a microporous formation. Digitiform sensilla totally absent, basal seta of mentum LA_1 misplaced. Sensillar composition of labial palps thereby without modifications, i.e. LA_a , as well as LA_b , LA_c and a ring-shaped complex of conical sensilla usually located on palpomeres, all clearly recognizable (Fig. 17); latter complex forming a distal sensory area.

Thoracal segments with a reduced generalized sensillar set (Figs 18, 26), the number of setae only on tergites of older instar larvae being increased (Figs 20, 28). Pronotum with distinct setal complexes situated medially near anterior and posterior sclerite margins. Some stable combination of different types of sensilla characteristic of basal chaetotaxic pattern recognizable: PR_2 - PR_a , PR_3 - PR_b near anterior margin, PR_{13} - PR_l , PR_{12} - PR_j , PR_{11} - PR_k near posterior one. In contrast, chaetome of lateral sclerite part, especially in

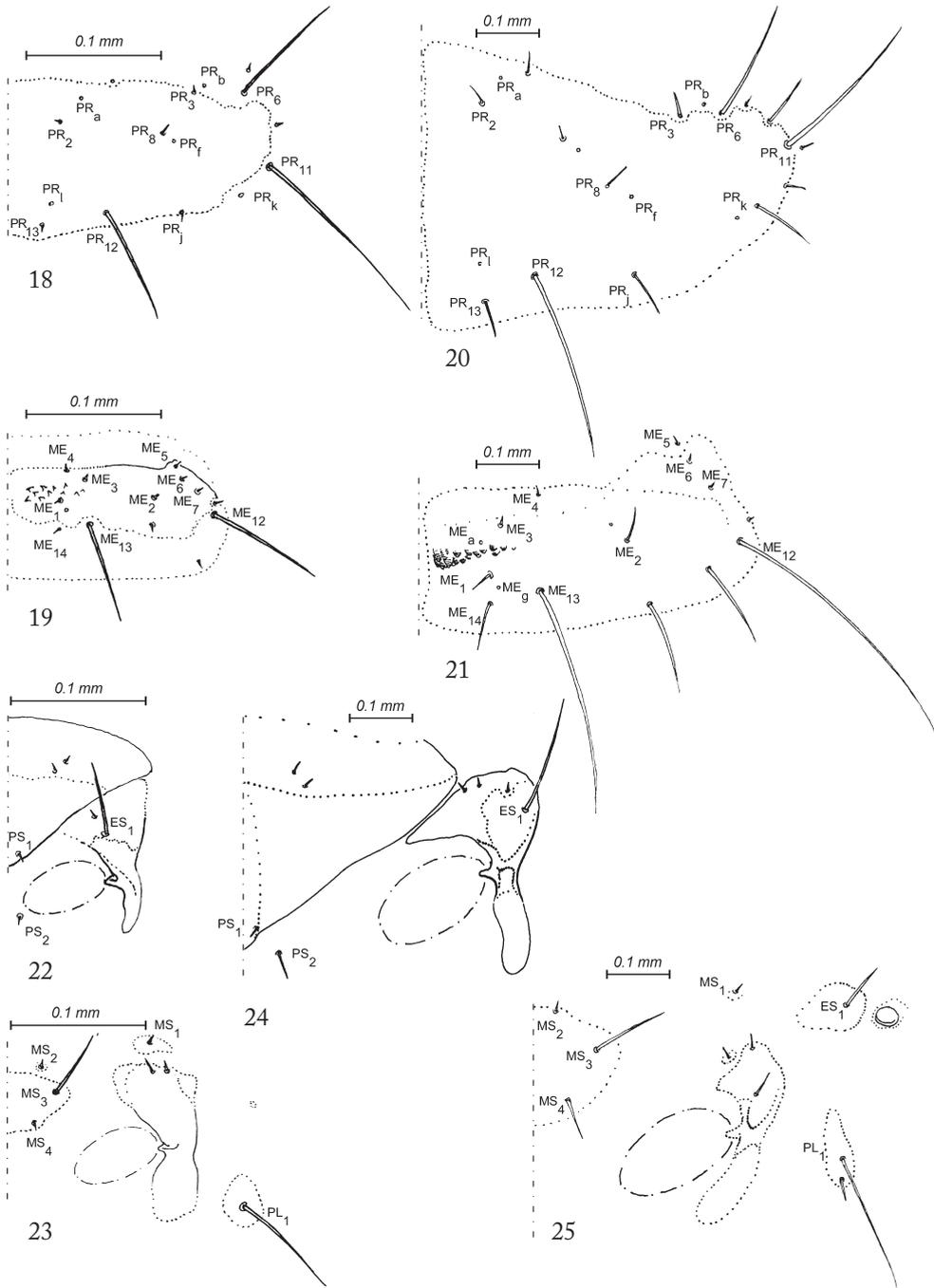
anterior corner area, remarkably modified, with questioned homologies of sensilla. Obviously, generalized chaetotaxic set represented only by macroseta PR_6 and microsetae PR_5, PR_7 . Pronotal disc without medial seta PR_{14} , but with a lateral complex PR_8-PR_7 . Pronotal macrosetae (PR_6, PR_{11}, PR_{12}) 7-10 times longer than microsetae.

Prosternite with an ordinary setal set of PS_1 and PS_2 , epimeron without seta EM_1 , episternum without distal setae ES_3, ES_4 , most of episternal setae short, only ES_1 large (Figs 22, 24, 30, 32).

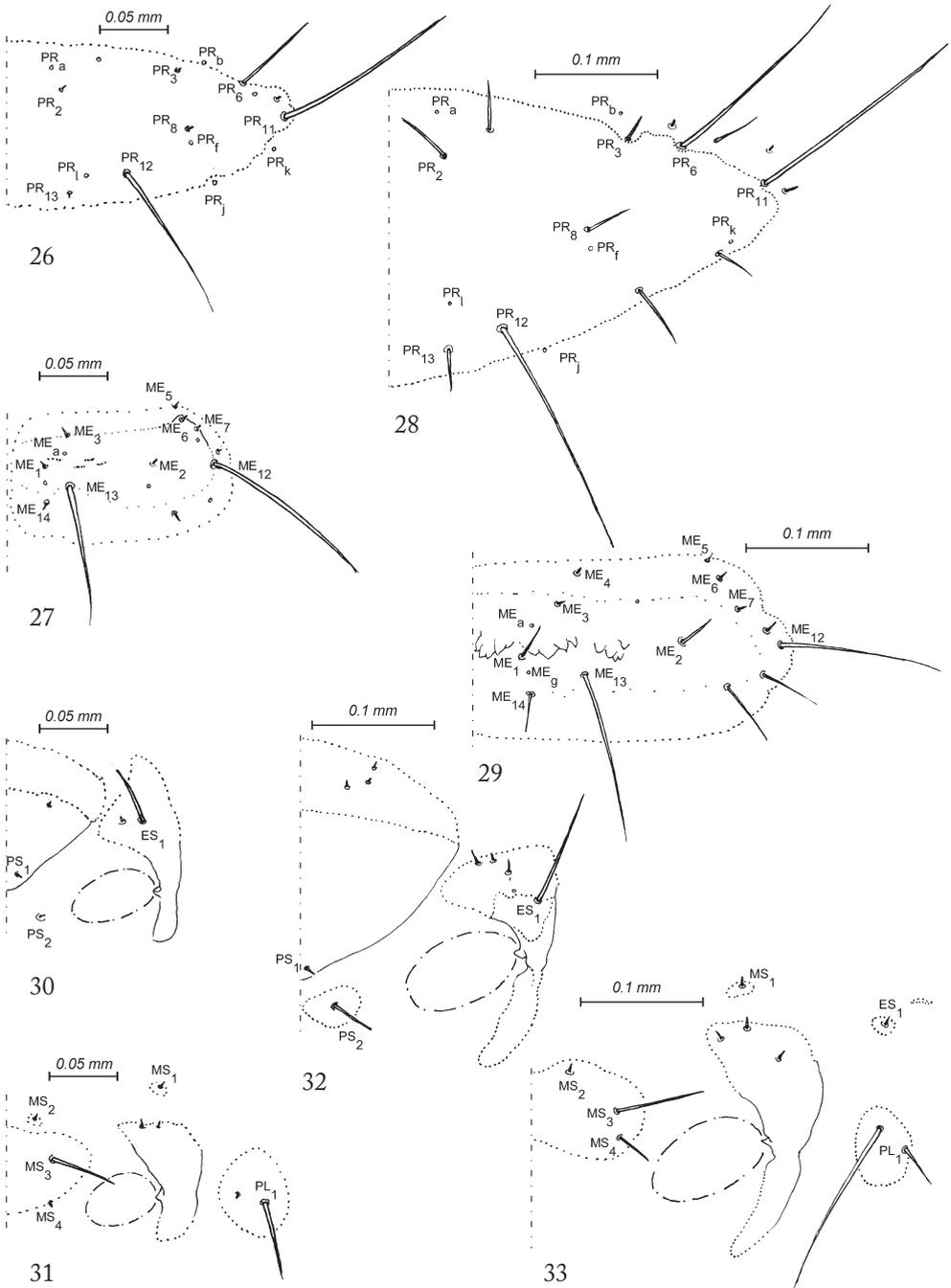
Chaetome of meso- and metathorax modified in a similar way (Figs 19, 21, 27, 29). Microsetal groups of pretergite ($ME_3, ME_4, ME_5, ME_6, ME_7$), sensilla associated both with anterior tergal keel (ME_1-ME_a, ME_2) and posterior sclerite margin ($ME_{14}-$



Figs 11-17. *Rhyssodes* spp., third instar larvae: 11, 13, 14, 16-17 – *Rh. sulcatus*; 12, 15 – *Rh. comes*; 11-12 – left antenna, dorsal view; 13 – antennomere 4, dorsal view; 14-15 – labiomaxillar complex, ventral view; 16 – apical part of stipes, ventral view; 17 – apical part of labium, ventral view.



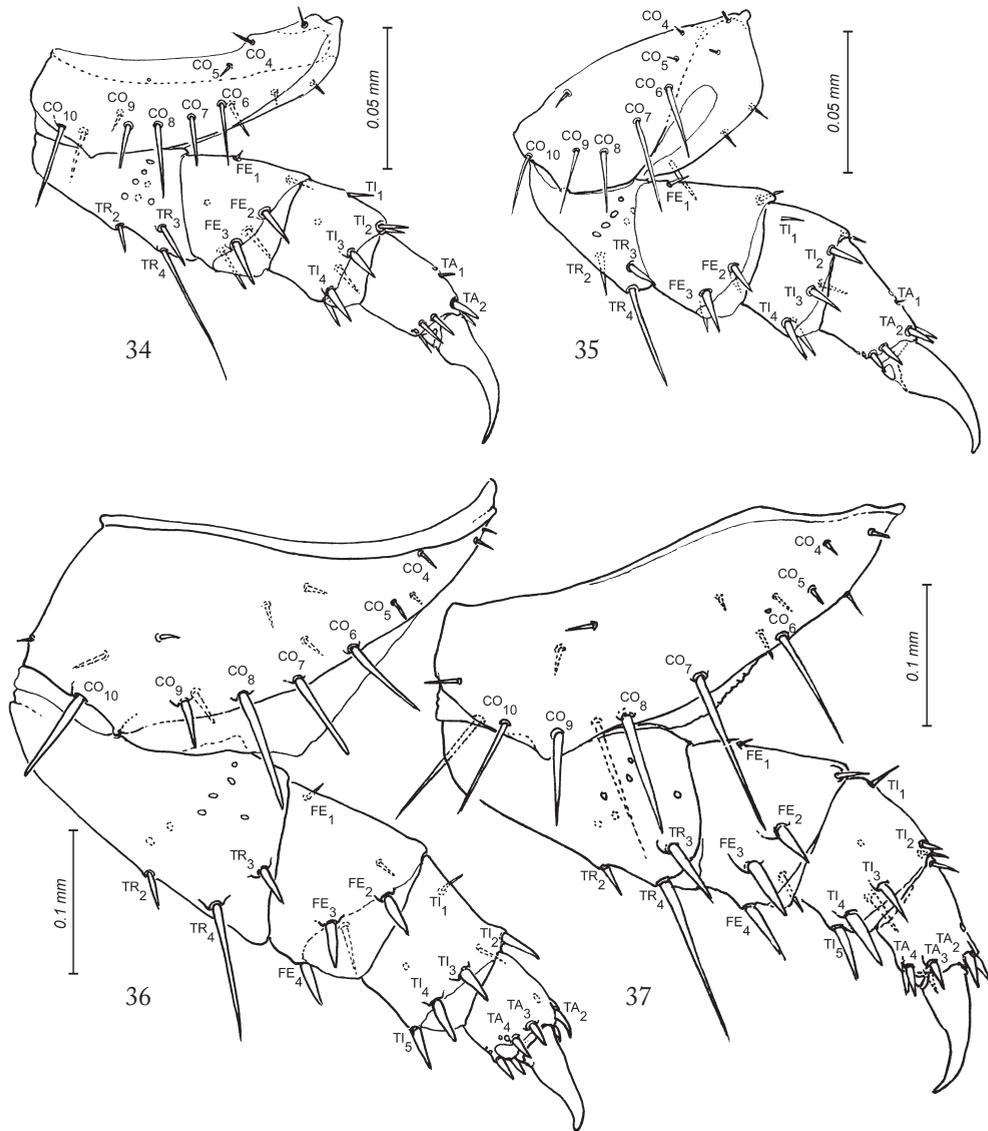
Figs 18-25. *Rhysodes sulcatus*: 18-19, 22-23 – first instar larvae; 20-21, 24-25 – third instar larvae; 18, 20 – left half of pronotum, dorsal view; 19, 21 – left half of mesonotum, dorsal view; 22, 24 – left half of prosternum, ventral view; 23, 25 – left half of mesosternum, ventral view.



Figs 26-33. *Rhyssodes comes*: 26-27, 30-31 – first instar larvae; 28-29, 32-33 – third instar larvae; 26, 28 – left half of pronotum, dorsal view; 27, 29 – left half of mesonotum, dorsal view; 30, 32 – left half of prosternum, ventral view; 31, 33 – left half of mesosternum, ventral view.

ME₈, ME₁₃, ME₁₂) retained from generalized set. Apparently, only ME₈ retained from lateral group. In contrast, chaetome of sternites and pleurites (Figs 23, 25, 31, 33) close to generalized pattern and differing by a few setae reduced, namely EM₁ and MS₄; most of setae tiny, only PL₁ developed as a macroseta.

Leg of structure typical of Adephaga, set of chaetotaxic elements similar to generalized one (Figs 34-37); remarkable differences lying only in trochanter chaetome: trichoid



Figs 34-37. *Rhysodes* spp., left middle leg: 34, 36 – *Rh. sulcatus*; 35, 37 – *Rh. comes*; 34-35 – first instar larvae; 36-37 – third instar larvae; anterior view.

sensilla TR_1 , TR_8 and spiniform seta TR_6 lacking. Besides this, location of macrosetae on anterior surface of coxa (CO_6 , CO_7 , CO_8 and CO_9) original, they being clustered and forming a row near external margin; CO_{17} missing. Pretarsus simplified: a single claw present, setae UN_1 , UN_2 lacking.

Structure and chaetotaxy of sclerites of different abdominal segments notably distinct. Tergites 1-7 with groups of cuticular tubercles and spines, forming rather spacious fields in first instar larvae (Figs 38-39) and building compact transverse ridges in older instar larvae. Chaetotaxy of these tergites, unlike generalized pattern, possessing some peculiarities: (i) anterior and posterior rows of setae close together while lateral seta TE_6 sometimes placed almost at posterior margin of tergal disc; (ii) setae of anterior row (TE_1 , TE_6) generally much shorter than those of posterior row, including macrosetae TE_{10} and TE_9 ; (iii) like on thoracic segments, sensilla of lateral complex, except TE_9 , visibly reduced or absent. Older instar larvae often with 1-2 additional setae in TE_{10} - TE_9 area; the number and position of additional setae varied (Figs 42-43, 46-49). Thus, segment 7 usually with one additional seta, whereas segment 8 sometimes without additional setae.

Tergite 8 with a few cuticular spinules not arranged in transverse rows, tergite 9 without spinules. Setal composition of tergite 8 similar to generalized pattern (Fig. 49), differing mainly in diminished setae TE_6 and TE_7 .

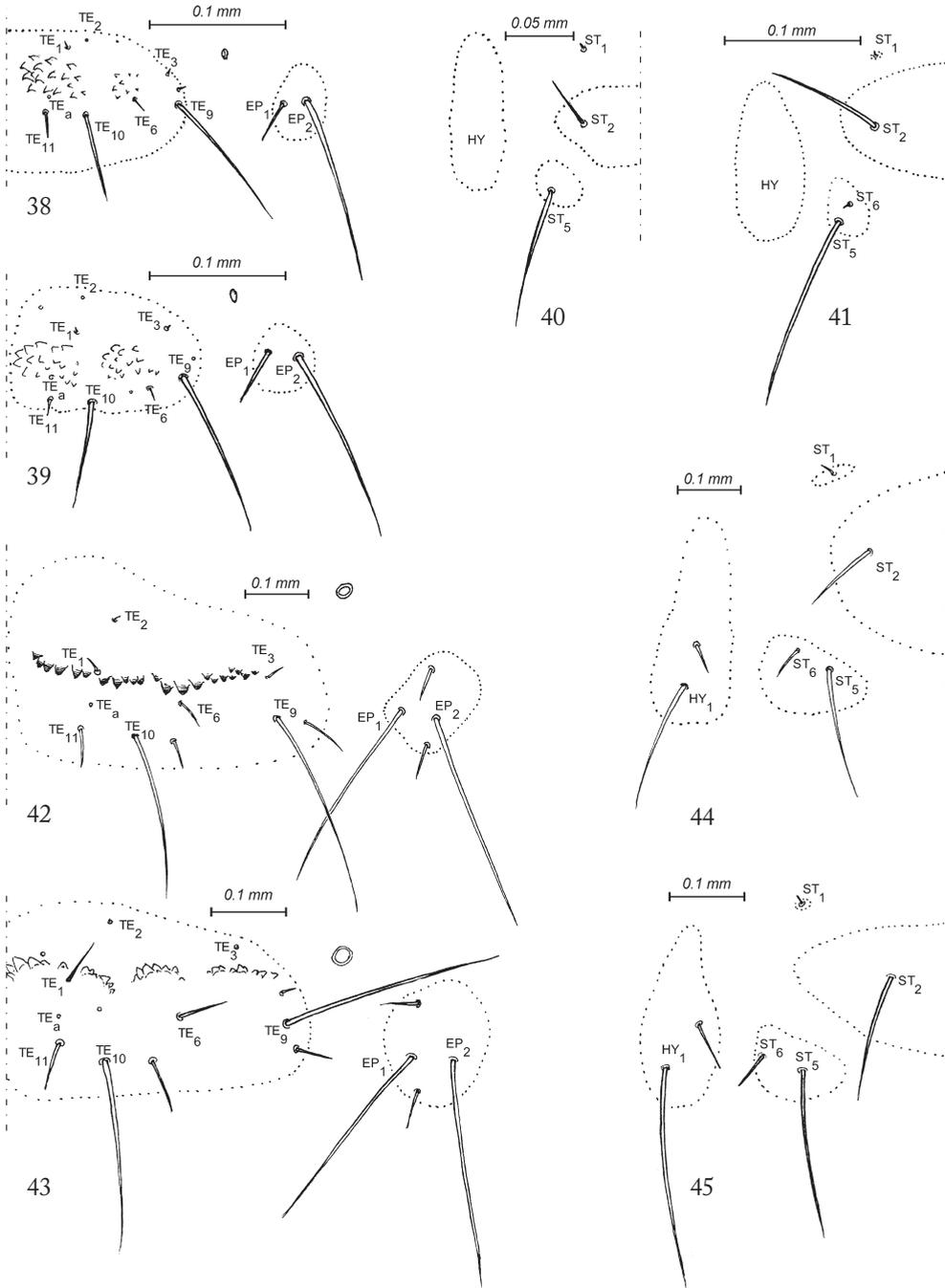
Tergite of penultimate segment lacking urogomphi, its chaetome particular and distinct from that of preceding segments (Figs 50-53). Posterior margin of penultimate tergite with 2-4 macrosetae, disc with 1-2 macrosetae. The absence here of urogomphi leads us to the use of the same sensillar nomenclature as that developed for other abdominal tergites. Thus, TE_1 , TE_2 and TE_a can be identified near anterior margin of segment, TE_{10} and TE_{11} near its posterior margin. Lateral group, by analogy with other segments, considered as including TE_7 (? TE_8) and TE_9 .

Sternites and pleurites 1-9 similar in structure and chaetotaxy. Larvae of both examined species of *Rhysodes* without sternella interior; as a result, setae ST_3 and ST_4 lacking (Figs 40-41, 44-45). In all other respects, the set of sensilla and setae not differing from generalized pattern. Older instar larvae bearing additional setae on hypopleurite, usually one microseta in anterior half and 1-2 macrosetae in posterior half (Figs 44-45).

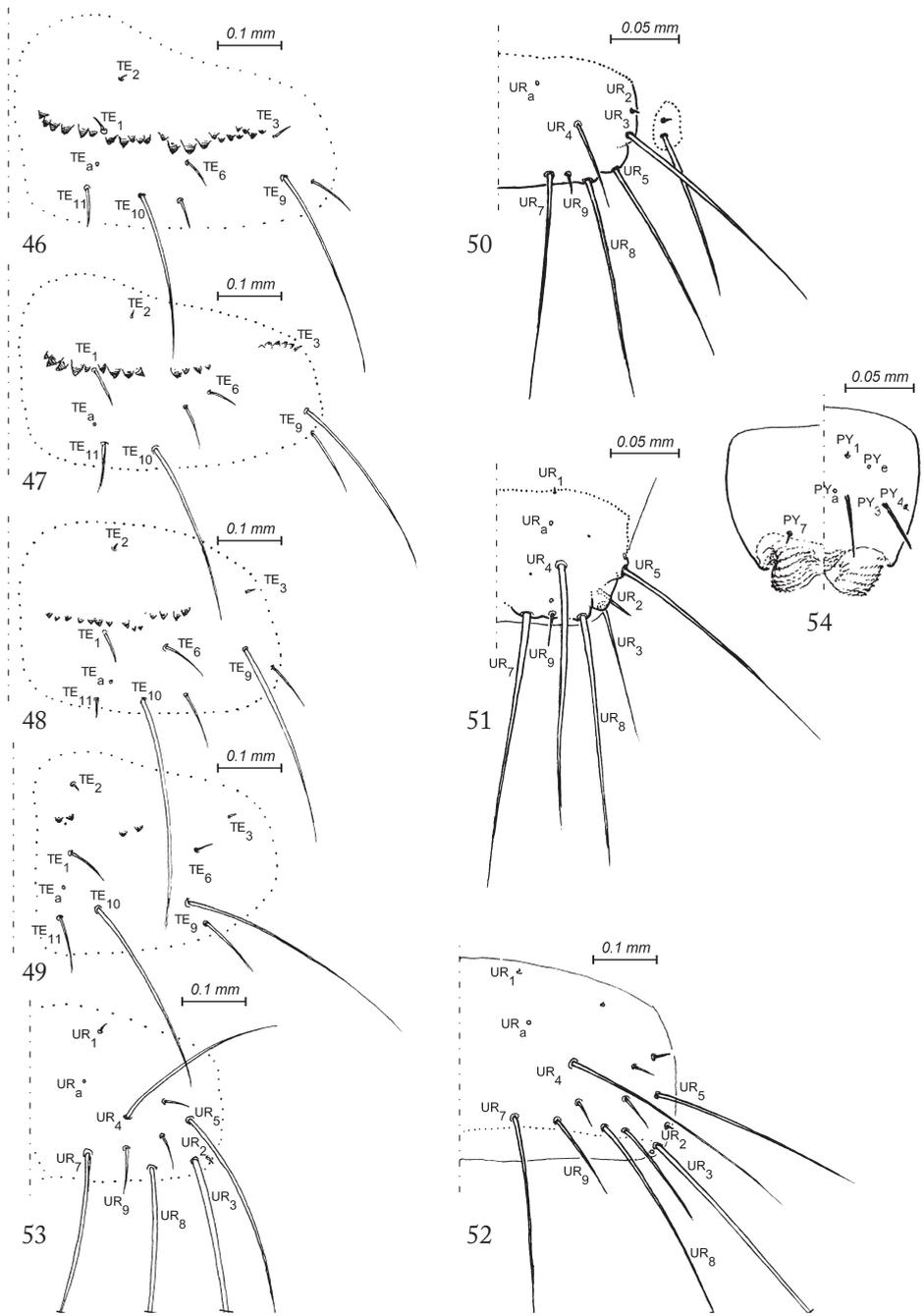
Segment 10 (pygidium) short (Fig. 54), with a simplified chaetome: besides basal PY_1 , very stable in Adephaga, only 3 pairs of setae forming an apical crown (PY_7 , PY_3 , PY_4) present, as well as dorsolateral placoid sensilla PY_a , PY_c and PY_d .

It is noteworthy that the larval chaetomes of both examined species appear to be strongly variable. In most cases, the topology, infrequently also the composition, of the sensilla on the left and right sides of sclerites are different, this greatly complicating the elucidation of a chaetotaxy pattern.

BETWEEN-INSTAR DIFFERENCES. The first instar larvae differ in the presence of egg busters represented by groups of cuticular spinules (Figs 1, 3), by altered arrangements of spines on the abdominal tergites (not forming distinct ridges, but covering almost the entire sclerite disc) and in chaetotaxic details. Length differences of micro- and macrosetae are more pronounced; setae FR_3 are small, shifted into the



Figs 38-45. *Rhysodes* spp., right half of 4th abdominal segment: 38, 40, 42, 44 – *Rh. sulcatus*; 39, 41, 43, 44 – *Rh. comes*; 38-41 – first instar larvae; 42-45 – third instar larvae; 38-39; 42-43 – tergite and epipleurite, dorsal view; 40-41, 44-45 – sternite and hypopleurite, ventral view.



Figs 46-54. *Rhysodes* spp., right half of abdominal segments: 46-49, 50, 53-54 – *Rb. sulcatus*; 51-52 – *Rb. comes*; 46-49, 52-53 – third instar larvae; 50-51, 54 – first instar larvae; 46-49 – tergite of 5th-8th segments respectively, dorsal view; 50-51, 52-53 – tergite of 9th segment, dorsal view; 54 – 10th segment, left – dorsal view, right – ventral view.

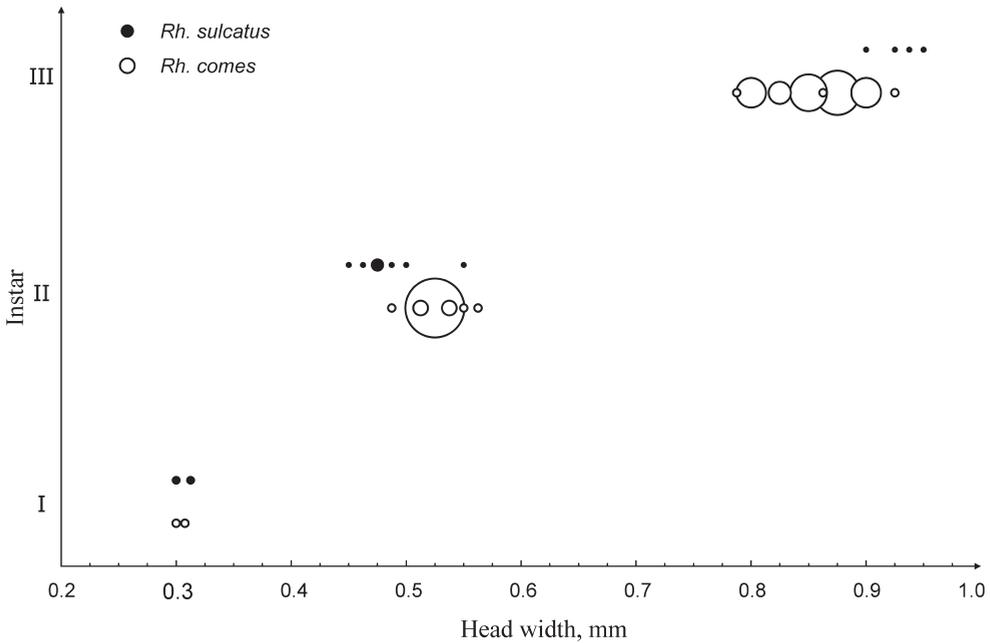


Fig. 55. Head width in different instars of *Rhysodes* spp. larvae. Circle size corresponds to the number of specimens.

basal part of the frontal sclerites (Figs 1, 3); additional setae at the posterior margin of tergites and on the hypopleurites are absent (Figs 38-41); seta TR_4 (Figs 34-35) is thin and long (spiniform in older instar larvae).

Older instar larvae are hardly different, variation concerning the number of additional setae in groups PR_{12} - PR_{11} (Figs 20, 28) and TE_{10} - TE_9 (Figs 42-43). To securely distinguish the older instars, head capsule measurements are suitable (Fig. 55). In both species, head width of first instar larvae is 0.30-0.312 mm ($M=0.305$, $SD=0.006$, $SE=0.003$; $n=4$), second instar larvae – 0.45-0.56 mm ($M=0.514$, $SD=0.029$, $SE=0.006$, $n=22$), third instar larvae – 0.79-0.95 mm ($M=0.864$, $SD=0.044$, $SE=0.008$, $n=29$).

BETWEEN-SPECIES DIFFERENCES. The first instar larvae of *Rh. sulcatus* and *Rh. comes* are very similar, differing only in some chaetotaxic details: in *Rh. sulcatus*, the poststernites are usually with a retained microseta ST_6 , the disc of abdominal tergite 9 without macroseta UR_1 , as a rule.

Old instar larvae are distinguishable by the size of tubercles on the frontal sclerite (in *Rh. sulcatus*, they are much larger than in *Rh. comes*), in structure of the cuticular ridges on abdominal tergites (usually entire in *Rh. sulcatus*, but subdivided into 2-3 tubercles in *Rh. comes*) and in the position of seta PA_7 (equidistant from PA_3 and PA_8 in *Rh. sulcatus*, close to PA_8 in *Rh. comes*).

DISCUSSION

It is important to notice that larval morphology of other genera of Rhysodidae, such as *Omoglymmius* Ganglbauer, 1892 and *Rhysodiastes* Fairmaire, 1895, known from literature (Grandi, 1972; Vanin & Costa, 1978; Costa et al., 1988), often in details coincides with the data on *Rhysodes* larvae. It makes it possible to extrapolate further deductions on an entire family.

Special features of larval morphology and chaetotaxy in Rhysodidae

Their chaetome is distinctly of carabid type and the considerable part of setae can be surely homologized with basic elements of Carabidae' chaetome (Bousquet & Goulet, 1984).

Generally, the chaetotaxy of *Rhysodes* larvae is characterized by moderate oligochaetosis. Some chaetotaxic peculiarities are obviously associated with exoskeleton transformations. Thus, the partly reduced frontal sensilla and the unusual location of FR_{γ} , FR_1 and FR_a are probably accounted for by the diminished area of the anterior part of the frontale and by the vanished paraclypeus lobes (Figs 1, 3, 5, 7, 9-10). The absence of eyes and the enlarged sigilla of the mandibular adductor (m. craniomandibularis internus) result in disproportions of the parietal sclerites, this being reflected by the reduction of some setae and sensilla (PA_{4-5} , PA_{9-10} , PA_{15} - PA_{16} ; PA_b , PA_d and others). Therefore, the basal part of the head capsule became almost bare, with the exception of the complex $PA_{1,2,3,a}$ which is highly stable not only in carabid larvae, but also in larvae of other coleopteran families. In general, no such head chaetome modifications have hitherto been known among ground-beetle larvae.

The microporous structure formed in the place of contact of the stipes and labium probably serves not as a filter, but a capillary sponge facilitating liquid food consumption. Its functional analogue is known in mycetophagous larvae of the genus *Sepedophilus* Gistel, 1856, Staphylinidae (Leschen & Beutel, 2001).

In previous publications concerning the larval morphology of Rhysodidae (Grandi, 1972; Burakowski, 1975; Vanin & Costa, 1978; Mamaev & Pototskaya, 1979; Costa et al., 1988), the structure of the maxilla and labium was repeatedly discussed. It was always suggested thereby that the lacinia, galea, ligula and labial palp in rhysodid larvae were absent, with the exception of small rudiments in *Omoglymmius* (Grandi, 1972). The chaetotaxy, in particular the topology of placoid and conical sensilla (Figs 16-17), allows to conclude that, in this case, I deal not with simple reductions but with fusion of all these structures, resulting in the formation of a sucking labiomaxillar complex; the degree of this fusion varies in different genera. The labium of the *Omoglymmius* larva seems to be the least modified: the distal segments of the labial palp remain separate while proximal ones fused, but their articulation with the mentum is mobile. Earlier, these fused proximal segments were mistakenly interpreted as a prementum (Mamayev & Pototskaya, 1979).

The peculiar structure and chaetotaxy of the leg seem to mainly be accounted for by the beetles' xylobiotic life-style. Among these features, there are the shortening of

distal parts, the retention of one claw, the reduction of sensilla (TR_1, UN_1, UN_2), and the unification of macrosetae. Most of the macrosetae become enlarged, spiniform except for the typically trichoid TR_4 in the first instar larva.

The investigation of the chaetotaxy of abdominal tergites brings two interesting conclusions. Firstly, the groups or rows of cuticular spinules on tergites highly characteristic of the family are almost always located between sensilla TE_1-TE_a in the medial area and between sensilla TE_3-TE_6 in the lateral area (Figs 42-48). This proves their homology to the transverse keel separating the pretergite from the tergite in carabid larvae. Secondly, the missing urogomphi allow to ascertain the serial homology of the setae of abdominal tergite 9 to the setae on the tergites of preceding segments and to suggest correspondence between the setae of tergite 9 and those on the urogomphi (Figs 42-49 *vs* 50-53). Thus, sensilla UR_a corresponds to TE_a , seta TE_2 corresponds to $UR_1, TE_1 - UR_4, TE_3 - UR_2, TE_9 - UR_3, TE_6 - UR_5, TE_{10} - UR_8$, and $TE_{11} - UR_7$.

The composition and location of the sternites and pleurites in *Rhysodes* larvae have not been discussed yet, apparently due to their very weak sclerotization. The study of their chaetotaxy reveals full reduction of the internal poststernites, including their setae. Larvae of older instars are also without setae in this area, despite the development of some additional setae in the sternopleural region.

Thus, I can homologize most of the chaetome elements of *Rhysodes* larvae typical of Adephaga. A number of features of rhysodid macromorphology (the formation of a labiomaxillar complex accompanied by fusion of the labial palps, the modification of the tergal keel into supporting structures), as well as chaetotaxic traits (the unusual chaetome of the anterior margin of the frontale, the reduction of numerous parietal setae; the incomplete set of trochanteral setae) are unique in this family within the suborder.

Taxonomic position of Rhysodidae

At present, the placement of the Rhysodidae within the group Geadephaga of the suborder Adephaga is proved by numerous morphological data drawn from both the adults (Forbes, 1926; Baehr, 1979; Beutel, 1995) and larvae (Böving, Craighead, 1930; Beutel, 1992b, 1993), being currently regarded as doubtless. However, the understood taxonomic rank varies greatly, ranging from an independent family down to a subtribe within Carabidae (Böving, 1929; Crowson, 1955; Ponomarenko, 1995; Jeannel, 1941; Beutel, 1990, 1992a, b, 1993, 1995; Erwin & Sims, 1984; Erwin, 1985; Bell & Bell, 1962; Bell, 1998). Different aspects of this problem are discussed below, based on new information on larval chaetotaxy.

Subtribe Rhysodina within the tribe Scaritini?

Integration of Rhysodidae and Carabidae was first suggested by Bell & Bell (1962), based mainly on adult external morphological features (structure of meso- and metacoxae, metendosternite, and fore tibia) and related to locomotion in a dense substrate. In this case, the

Rhysodini and the Scaritini were regarded as sister-groups, whose formation was accounted for by specializations to different environments. Later, this viewpoint was supported by the knowledge of the structure of the repugnatorial glands (Forsyth, 1972). Recently, further development of this approach (Bell, 1998) resulted in a still greater decrease in rhysodine rank, namely, the Rhysodina was accepted as a specialized subtribe of Scaritini. This was due to more data accumulated (Adis, 1981; Dostal, 1993) as regards the morphology of some rare and highly specialized tropical Salcediina (now regarded as a subtribe of Clivinini; see Balkenohl, 2001) which show some features determining their habitual similarity to Rhysodidae.

In such a situation, it is important to evaluate the features shared by larvae of Rhysodidae and Scaritini s.l. (including Clivinini and Dyschiriini). The caraboid larvae of Scaritini show not a single characteristic of Rhysodidae in structure of the mouthparts, as well as in the chaetotaxy of the head and body tergites. The single feature in common is the presence of one claw on the pretarsus in some scaritins (Clivinini and Dyschiriini). But this cannot be interpreted as the proof of a relationship since a reduced number of claws is known in many not so closely related carabid groups (Broscini, Trechini, Bem-bidiini and Pogonini, Orthogoniini, Brachinini). It is noteworthy that, among carabid larvae, there are numerous cases of specialization to moving through thick substrates, including wood (Morionini). All of them are developed on the basis of rather insufficient transformations of the chaetome and exoskeleton. Undoubtedly, both the known and newly revealed differences in the traditional morphology and chaetotaxy of Rhysodidae and Scaritini larvae fail to correspond to the level of distinctions between tribes and, especially, subtribes.

Subfamily Rhysodinae within the family Carabidae?

Since the grounds for the incorporation of the Rhysodidae into the Carabidae mainly lay in similarities shown by adaptive features (e.g. Bell, 1970; Hlavac, 1975), the position of Rhysodidae within this family was repeatedly revised. In particular, the presence of shared characters was revealed, such as disjunct middle coxal cavities both in Rhysodidae and a number of basal carabid groups (Paussini, Cicindelini, Loricerini, Elaphrini, Scaritini and so on). The viewpoint of Erwin & Sims (1984) and Erwin (1985) was particularly meaningful in suggesting similarities between Rhysodidae and some basal representatives of Pterostichini, Morionini and, especially, Psydrini. Erwin considered this group as a disjunct supertribe which, together with Psydrinae and Trechitae, form the subfamily Psydrinae of a separate division, Psydriformes. Any further discussion of the rank and position of Rhysodidae in this context is only possible if the following question is answered positively: Do Rhysodidae really belong in the family Carabidae?

In general, the larval structure in Rhysodidae, including chaetotaxy, is indeed similar in many ways to that of Carabidae. This is reflected in the same groundplan of the chaetome (setae and sensilla as homologized above being the proof), antennae (4-segmented with a developed sensorium on antennomere 3) and legs (moveably articulated tibia and tarsus, a developed pretarsus with a claw). However, none of these

characters can be treated as synapomorphies of Rhysodidae and Carabidae. Thus, the structure of the antennae and legs is shared by most of the Adephaga, whereas among the securely homologized setae there are many (e.g. PA₁-PA₂-PA₃-PA_a and EP₁-EP₂ complexes, etc.) that are also known in a wide range of beetle families, both Adephaga and Polyphaga.

At the same time, some of the larval features of *Rhysodes* can securely be regarded as high-level autapomorphies, since none of them shows any analogs amongst Carabidae while some are even unique to the Coleoptera as a whole.

This primarily concerns the structure of the labiomaxillar complex (Figs 14-15) characterized by general consolidation. Thus, in the maxilla, the fused galea and lacinia are merged both with the stipes apex and palpifer, whereas all the appendages of the labium are fused to the mentum. The labiomaxillar complex is enlarged, fully covering both the oral opening and the ventral surface of the mandibles, with a particular porose structure formed in the narrow fissures between the labium and the maxillae. This structure can be suggested to provide fluid food, possibly myxomycetes, to be sucked in due to capillary powers. Carabidae do show some cases of feeding on fluid or fungal food (Mormolycini), but no such structures appear (Lieftinck & Wiebes, 1968). Furthermore, liquid food consumption in Carabidae is always accompanied by the formation of pharyngeal pump musculature, whereas in *Omoglymmius* larvae these muscles are relatively poorly developed (Beutel, 1990b). Larval mandibles in Rhysodidae probably do not take part in feeding, because, when closed, they stay isolated from the antebuccal cavity through a long lobe of the epipharynx. So the mouthparts of Rhysodidae, certainly being homologs of those in Carabidae, show nonetheless no functional similarities to any of the mouthpart types occurring in Carabidae. Obviously, some analogs can only be traced to the larval mouthparts of the some mycetophagous Staphylinidae (Leschen & Beutel, 2001).

The next highly specific feature of Rhysodidae larvae is the total absence of digitiform sensilla in the sensory complex of mouthpart appendages (Figs 14-17). This type sensilla are known in all studied Carabidae larvae, including such disjunct specialists as Paussini, Cicindelini, Mormolycini (Lieftinck & Wiebes, 1968), Peleciini (Liebherr & Ball, 1990), Brachinini, Pseudomorphini (Erwin, 1981), etc. At the same time, they are lacking in most of the Hydradephaga (Noteridae, Dytiscidae, Gyrinidae, Haliplidae), but occur in Trachypachidae. As far as possible to judge, the presence or absence of digitiform sensilla is not related to a xylobiotic way of life. In any case, sensilla of similar types are met with in wood-dwelling larvae of Archostemata (Grebennikov, 2004) and numerous Polyphaga families.

Finally, there are some more special peculiarities to differ the larvae of Rhysodidae and Carabidae. These concern the retention in Rhysodidae of only a single pair of setae in the gular area, the original chaetotaxy of the frontale (see above), the total reduction of internal poststernites of the abdomen.

Therefore, a whole complex of larval traits emphasizes a sufficiently high degree of singularity of Rhysodidae to prevent them from being incorporated within Carabidae. It is noteworthy that most of the students who based their results on adult characters

(Bell & Bell, 1962; Hlavac, 1975; Bils, 1976; Bell, 1978; Baehr, 1979; Beutel, 1990, 1992a, 1995, 1998; Liebherr & Will, 1998) considered the rhyssodines as only a taxon subordinate to Carabidae, whereas those who investigated the larvae (Böving, 1929; Böving & Craighead, 1930; Burakowski, 1975; Beutel, 1992b; Arndt, 1998) invariably arrived at the opposite conclusions.

Family Rhyssodidae within the suborder Adephaga?

Recognition of the independence of Rhyssodidae as a family of their own allows for a discussion of their relationships within the suborder Adephaga.

As noted above, opinions about the taxonomic position of Rhyssodidae differ greatly. Thus, Crowson (1960) suggested that Rhyssodidae are one of the most primitive groups within Adephaga and therefore can be considered as the sister-group to the other families of the suborder. At present, the attribution of Rhyssodidae to the Geadephaga remains unchallenged (Böving, 1929; Kryzhanovsky, 1983; Baehr, 1979; Beutel, 1990), but the extent of their interrelations with Carabidae is seen differently. In some cases, they are treated as primitive Geadephaga (Böving & Craighead, 1930; Jeannel, 1941; Kryzhanovsky, 1983; Ponomarenko, 1995), in other cases as the sister-group to (Beutel, 1990, 1992a) or a specialized derivative of Carabidae (Beutel, 1992b, 1993, 1995).

The larvae of Rhyssodidae show a large set of highly specialized characters missing in carabids and partly unique among the beetles as a whole. The above larval features about equally well distinguish Rhyssodidae from the remaining Recent families of Geadephaga, namely, Trachypachidae and Carabidae. The lack in Rhyssodidae of digitiform sensilla and the presence of a labiomaxillar complex appear to be especially important distinctions. The labiomaxillar complex in Rhyssodidae is associated with paired glands (Beutel, 1990b) which have no analogs amongst the larvae of Adephaga.

Along with these apomorphies, the features uniting the Rhyssodidae with Trachypachidae or Carabidae are rather insignificant. The poorly delineated palpifer fused with the galea and, partly, lacinia is known in the Trachypachidae as well as some basal groups of Carabidae, such as Cicindelini, Paussini, Ozaenini, Metriini (Bousquet, 1986; Arndt & Beutel, 1995; Di Giulio & Moore, 2004, Moore & Di Giulio, 2006). In some Paussinae (Ozaenini), the nasale with setae FR₁₀, FR₁₁ can be shifted proximally, so that a plate devoid of setae is formed before it (Di Giulio et al., 2003). These carabids possess a strongly enlarged labium, although no labiomaxillar complex is developed. The full absence of urogomphi being characteristic of Rhyssodidae is probably not so important, because this feature is found in different, often not closely related carabid groups, namely, Cicindelini, Cychrini, Peleciini, Orthogoniini, Brachinini and some Harpalini. Thus, the Rhyssodidae reveals the greatest similarity to the highly specialized, partly myrmecophilous and relatively primitive carabids, viz. Paussini and Ozaenini. The resemblance of these taxa was mentioned as early as in the end of 19th century, when Wasmann (1896) suggested even the family Rhyssopaussidae. Later the viewpoint was rightly criticized (Escherich, 1898) and was left without further development.

At the same time, a number of features are shared by the larvae of Rhysodidae and several families of the suborder Archostemata (Grebennikov, 2004) which show a strongly enlarged labium forming, together with the maxillae, a functionally integrated structure; the labial palps are located ventrally and partly merged with the prementum, the shortened gular area, the galea and lacinia partly fused with the prementum. Some more special characters can be mentioned. Thus, the leg chaetotaxy, the structure of the basal part of the frontale and, partly, its chaetotaxy in *Priacma* LeConte, 1874, Cupedidae in general resemble the respective conditions observed in Rhysodidae; the chaetotaxy of the thoracic tergites in *Distocupes* Neboiss, 1984, Cupedidae and *Rhysodes* also show some common traits. The remaining larval features quite evidently separate these taxa, but none of the other Recent groups among Adephaga displays such a variety of features common with Archostemata. It is noteworthy that all known larvae of Archostemata, except for Micromaltidae, are highly specialized saproxylic forms adapted to feeding on hard xylem. This alone prevents from any possible adaptive similarity in mouthparts structure of these groups to Rhysodidae.

The similarity of the larvae of the Rhysodidae and Archostemata, on the one hand, and the cardinal differences between Rhysodidae and Geadephaga, on the other, suggest at least two hypotheses of rhysodine origin: (i) from an ancestor common with Geadephaga (meaning a revived viewpoint of Crowson), and (ii) from some group within Archostemata which was poorly specialized to a xylobiotic life-style.

One must remember that all known fossil larvae of Geadephaga are Mesozoic in age (Ponomarenko, 1985; Makarov, 1995) and they already possessed a typical caraboid structure down to the details of chaetotaxy. Unfortunately, the fossil records of Rhysodidae are represented only by an adult beetle from the Eocene and Miocene amber (Grimaldi & Engel, 2005; Kirejtshuk & Ponomarenko, 2007). Therefore, a relatively late appearance of this highly specialized group can be suggested, apparently in the times when the Geadephaga had contained already several fully developed subtaxa, infrequently Recent ones. Thus, the formation of the highly disjunct larvae of Rhysodidae based on any of the then existing typical, specialized prototypes of Geadephaga larvae seems to be improbable, being supported by no morphological evidence.

Our knowledge of the larval stages of Archostemata is restricted to recent organisms only, but their structural details and life-style do not contradict a hypothesized "archostematan" ancestor of Rhysodidae. At the same time, the larvae of modern Archostemata show such a substantial number of apomorphies (endocarina presence, labral structure etc.) that this group could hardly be considered as direct ancestors of Rhysodidae. Despite this, based on morphological larval similarities, the hypothesis of Rhysodidae ancestry shared with Archostemata is certainly preferable.

In this connection, Wasmann's (1896) assumption concerning the close relationship between the Rhysodidae and the Paussinae acquires a new dimension. One cannot exclude that the latter taxon could be derived from the same archostematan group which gave rise to Rhysodidae. In this case, Carabidae are to be considered as a paraphyletic group. Any further discussion of this still poorly-grounded hypothesis requires new evidence to

be brought in, but its development seems to be fruitful in the polemics concerning the placement of Paussini and related groups within the Carabidae. At present this debate comprises highly contradictory and questionable assumptions. In particular, within the framework of this hypothesis both the highly specialized and plesiomorphic features occurring in combination in such a relatively young (Nagel, 1997) group as Paussinae can be accounted for.

The ideas on the young phylogenetic age of Paussinae are based only upon the obvious myrmecophily in certain groups within this subfamily that force to suggest their relatively late appearance after the true ants (Nagel, 1997). However the recent study of morphology and life style of the Ozaenini larvae (Di Giulio & Vigna Taglianti, 2001; Di Giulio et al, 2003) clearly show that the majority of specialized “myrmecophilous” features are related to the specific hunting way, namely from the shelter. Thus, in general Paussinae might appear to be significantly more ancient group (due to the great number of imago plesiomorphies) that makes my “archostemat” hypothesis even more probable.

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