

Pupal morphology in the subfamily Paussinae (Coleoptera: Carabidae)

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Pupal morphology in the subfamily Paussinae (Coleoptera: Carabidae).

- Pupae of the Ozaenini lineage (*Pachyteles vignai* Deuve, 2000, *P. digiulioi* Deuve, 2000 and *Physeia setosa* Chaudoir, 1868) and the Paussini lineage (*Platyrhopalopsis melleii* (Westwood, 1833) and *Paussus kannegieteri* Wasmann, 1896), are described and shown in figures, and compared with other adaphagan taxa. In contrast to the customary assumption that pupal characters are uninformative with regard to systematics, this analysis shows the importance of pupal characters for phylogenetic reconstruction at different levels. Differences between basal and derived Paussinae occur in the arrangement of setae and in the folding of gonothecae, while some characters, like the microsculpture, the inversion of the last abdominal segments and perhaps the reduction of the 7th abdominal spiracle, support Paussinae monophyly. The extent of pubescence is a morphocline among Adephaga, with reduction in several unrelated taxa. Finally, the possibility of recognising distinct abdominal segments and antennal articles at the pupal stage, in taxa where they appear fused at the adult stage, may provide an ontogenetic basis for elucidating phylogenetic relationships.

Keywords: Coleoptera - Carabidae - Paussinae - pupae - morphology - phylogeny.

INTRODUCTION

Coleoptera have exarate pupae with free body appendages. The body is slightly bent, with the head sharply turned downwards. The legs (podothecae) lay in a backward position appressed to the ventral side of the body, the pterothecae (covers of the wings) are turned downwards and partially cover the hind legs. As stated by Jeannel (1941, 1949), and Sturani (1962), both pairs of metapterothecae are generally fully developed in Adephaga, even in the pupae of non-alate species. The antennothecae are turned backwards and lay between the mid legs and the mesopterothecae. The only residual larval characters are the sometimes remnant urogomphi and the pigment of the

stemmata, which is only present in young pupae, disappearing later during the pupal stage.

While knowledge about larval morphology of Carabidae has grown very quickly in the last decades, the pupal morphology has rarely been investigated. Also, most of the research on the morphology of aedepteran pupae has dealt with the description of the habitus, and no structure has been characterised in terms of its taxonomic importance.

The scarce interest in pupal biology may be a consequence of the difficulties encountered in obtaining and identifying pupae, as well as the perception that pupal morphology is of minor systematic importance, generally reflecting characters of the adult stage. Although pupae exhibit a number of characters shared with adults and larvae (such as those mentioned above), they also possess some unique characters.

The pupae of Coleoptera are immobile and they do not feed. Therefore the main function of the pupal integument is to protect the body as it undergoes metamorphosis. All carabid pupae have specialised setae on the dorsal surface, which are unique to this life stage (von Lengerken, 1924; Jeannel, 1949). However, the distribution of these setae differs considerably among lineages within the Carabidae (see Fig. 1). Dorsal setae may be found on the head, on one of the three tergites of the thorax, on the abdominal tergites 1 to 8, on the abdominal pleurites 2 to 7, and, if everted, also on the 9th and 10th abdominal segments. During the pupal stage, which lasts about 14 to 28 days in Carabidae (Sturani, 1962), the pupa rests in a prostrate position in the pupal chamber. These setae most likely function to isolate the body from the surface of the pupal chamber. In contrast, the ventral surface and the legs are completely glabrous, presumably because they are not in contact with the ground. Therefore the distribution of the pupal setae generally allows one to infer the resting position of the pupae within the pupal chamber. However, pupae of Amphizoidae, Hygrobiidae and Dytiscidae, are exceptions to this general rule. Although dorsal setae are fully developed in these groups (Bertrand, 1972), the pupae rest in labile equilibrium on their prolonged urogomphi and on the setae on the head and the anterior region of the pronotum, with their dorsal surface directed upwards and not in contact with the ground. As far as we know this resting position is unique to these taxa and represents a derived condition (Ruhnau, 1986).

Very few aedepteran pupae have been described. The resulting lack of knowledge impedes detailed phylogenetic analyses based solely on pupal characters. However, some hypotheses about the phylogenetic utility of these characters can be inferred based on our present knowledge of Aedepteran phylogeny.

Complete dorsal pubescence is present in *Dyscolus* (Carabidae, Platyninae) and *Dromius* (Carabidae, Lebiini), and in most Hydradephaga, where it occurs on the head, as well as all segments of the thorax and abdomen (Bertrand, 1972). This pattern indicates that the full set of setae covering head, pro-, meso-, metanotum, abdominal tergites 1-8 (and the following tergites if everted), and pleurites 2-8, represents an ancestral (plesiomorphic) condition. Consequently, the lack of pubescence on one of these body parts represents a derived (apomorphic) condition. For example, the pupae of *Clinidium* have dorsal pubescence on all segments except for the head. In other groups of carabids the dorsal pubescence is lacking from additional segments. For

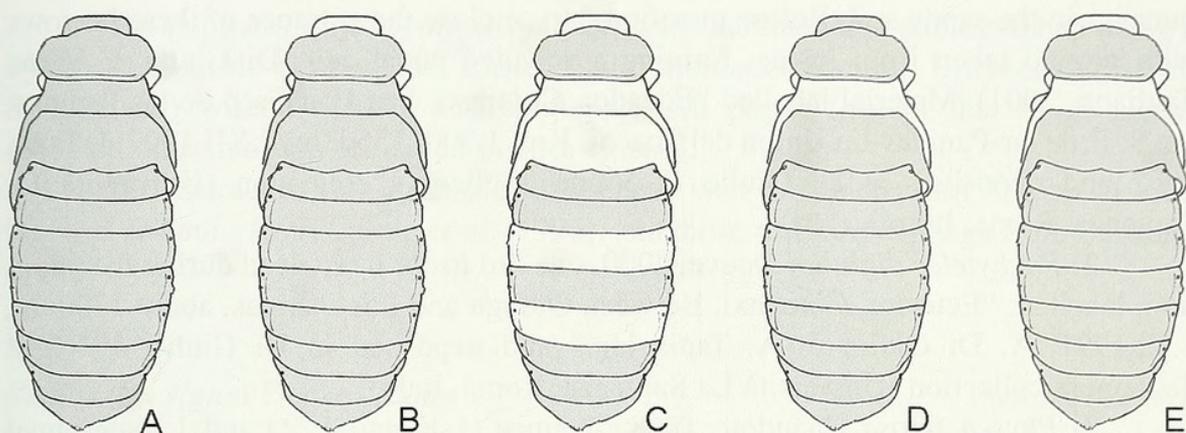


FIG. 1

Cartoons of Adephagan pupae, showing the distribution of dorsal setae in various lineages. The presence of dorsal setae in various segments is indicated by the gray color. Note that the head is drawn in unnatural position for illustrative purposes. (A) Hydradephaga, *Dyscolus* and *Dromius*. (B) *Clinidium*. (C) *Carabus*. (D) Ozaenini. (E) Paussini.

example, the pupae of *Carabus* and *Cychrus* lack setae on the head, mesonotum and metanotum, in addition some species in these groups lack setae on some of the abdominal segments (Sturani, 1962).

Another important pupal character is the number and shape of the spiracles. According to Jeannel (1949), the pupae of Adephaga possess a pair of spiracles on the mesothorax, and 6 or 7 spiracles on the abdominal segments, with the spiracles 6th and 7th closed. The 8th abdominal spiracle is always missing in both pupae and adults. The mesothoracic spiracles are closed in the pupae of Hydraenidae, Amphizoidae, Hygrobiidae and Dytiscidae (Ruhnau, 1986), open in Carabidae (Sturani, 1962), including Paussinae.

Within the subfamily Paussinae, pupae have been described from only 5 species, all belonging to the tribe Paussini: *Paussus kannegieteri* Wasmann, 1896 (Böving, 1907), *P. curtisi* (Westwood, 1864) (Luna de Carvalho, 1951), *P. cridae* (Gestro, 1916) and *P. cucullatus* (Westwood, 1850) (Luna de Carvalho, 1959) and *Platyrhopalopsis melleii* (Westwood, 1833) (Luna de Carvalho, 1977). Most of these descriptions are too superficial for well-founded morphological comparison.

In this paper, we provide the first comparative study of the pupal morphology of Paussinae. In particular, pupae of the tribe Ozaenini are described and illustrated for the first time. Detailed redescriptions and figures of Paussini pupae are also provided for comparative purposes. The pupae of Paussinae are compared with those of other Carabidae and some other adephagan groups, and the morphological characters with potential phylogenetic significance are discussed.

MATERIAL EXAMINED

CARABIDAE, PAUSSINAE, OZAENINI

1) *Pachyteles vignai* Deuve, 2000: 3 pupae (1 ♂ and 2 ♀♀) and 2 pupal exuviae (1 ♂ and 1 ♀). Pupae were obtained from 1st and 2nd instar larvae reared in the laboratory. The larvae were collected along a riverbank, where they had constructed

burrows in the sandy soil. Before pupation, larvae close the entrance of these burrows with ground taken from inside, forming a rounded pupal cell (Di Giulio & Vigna Taglianti, 2001). Material labelled "Ecuador, Cotopaxi. San Francisco de las Pampas, str. S. F. de las Pampas-La Union del Toachi, Km 1.300, 1550 m, 7.XII.1997, I. Tapia leg." and deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

2) *Pachyteles digiulioi* Deuve, 2000, one 3rd instar larva dead during the pupation, labelled: "Ecuador, Cotopaxi. Between Otonga and Las Pampas, about 1700 m, 1.VI.1997, A. Di Giulio & A. Tapia leg." and deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

3) *Physea setosa* Chaudoir, 1868, 2 pupae (1 ♂ and 1 ♀) and 1 male pupal exuvia collected together with larvae and adults in small holes near the "mushroom chambers" within a nest of leafcutter ants *Atta sexdens* (Linnaeus, 1758) (van Emden, 1936). Material labelled "Mendes, 25.9.1933, Ausgrabungsbau, in Erdhöhlen zwischen den Panellas, H. Eidmann" and deposited at the Naturhistorisches Museum, Basel (Switzerland).

CARABIDAE, PAUSSINAE, PAUSSINI

4) *Platyrhopalopsis melleii* (Westwood, 1833), 1 male pupa, labelled "India, Kerala Periyar – Lake, près de l'Hotel Aranya Nivas, 4.XI.1972, 950 m", preserved at the Natural History Museum of Geneva (Switzerland). The pupa is one of seven ones, collected by Besuchet in the ground at the foot of an old trunk, together with 8 larvae and 80 adults; no ants were observed nearby (Luna de Carvalho, 1977), even though *Platyrhopalopsis* species are considered to be myrmecophilous.

5) *Paussus kannegieteri* Wasmann, 1896, 3 male and 2 female pupae labelled "Java, Buitenzorg, Pangerango, 15-21.III.1904, Hjalmar Jensen" and deposited in the Zoological Museum of Copenhagen (Denmark). The pupae were collected together with some larvae and many adults inside an ant nest (Böving, 1907).

CARABIDAE, PLATYNINAE

6) *Dyscolus megacephalus* (Bates, 1891): 2 female pupae labelled "Ecuador, Cayambe, 4300 m, 01.IX.85 P. Moret", deposited in Moret's collection (Toulouse, France).

RHYSODIDAE

7) *Clinidium canaliculatum* (Costa, 1839), 1 female pupa labelled "Italia, Calabria, Pollino, Colle Gaudolino, 10.VII.71, V. Vomero", deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

METHODS

All pupae were studied and drawn by using a stereomicroscope equipped with drawing tube. The description of chaetotaxy refers to only one half of the pupal body, since the positioning of the setae are nearly symmetrical on both sides of the body. One female pupa of *Pachyteles vignai*, was mounted on stub after critical point dehydration and gold sputtering, and examined and photographed (Figs 5-11) using a scanning electron microscope (S.E.M.) Philips XL 30 (Interdepartmental Laboratory of Electron Microscopy, L.I.M.E., University 'Roma Tre', Rome, Italy).

The pupa of *Platyrrhopalopsis melleii* was examined and photographed using a Philips E.S.E.M. (Labor für Raster-Elektronenmikroskopie, Universität Basel, Switzerland) without drying and sputtering. All pupae (except that of *P. vignai* mounted on a stub) are preserved in 70% ethanol.

The characters of *Carabus* and *Cychnus* were obtained from Sturani (1962), those of *Dromius* from Casale *et al.* (1996), and those of Hydradephaga from Bertrand (1972).

RESULTS

Pachyteles vignai Deuve, 2000

Figs 2-11, 22-23

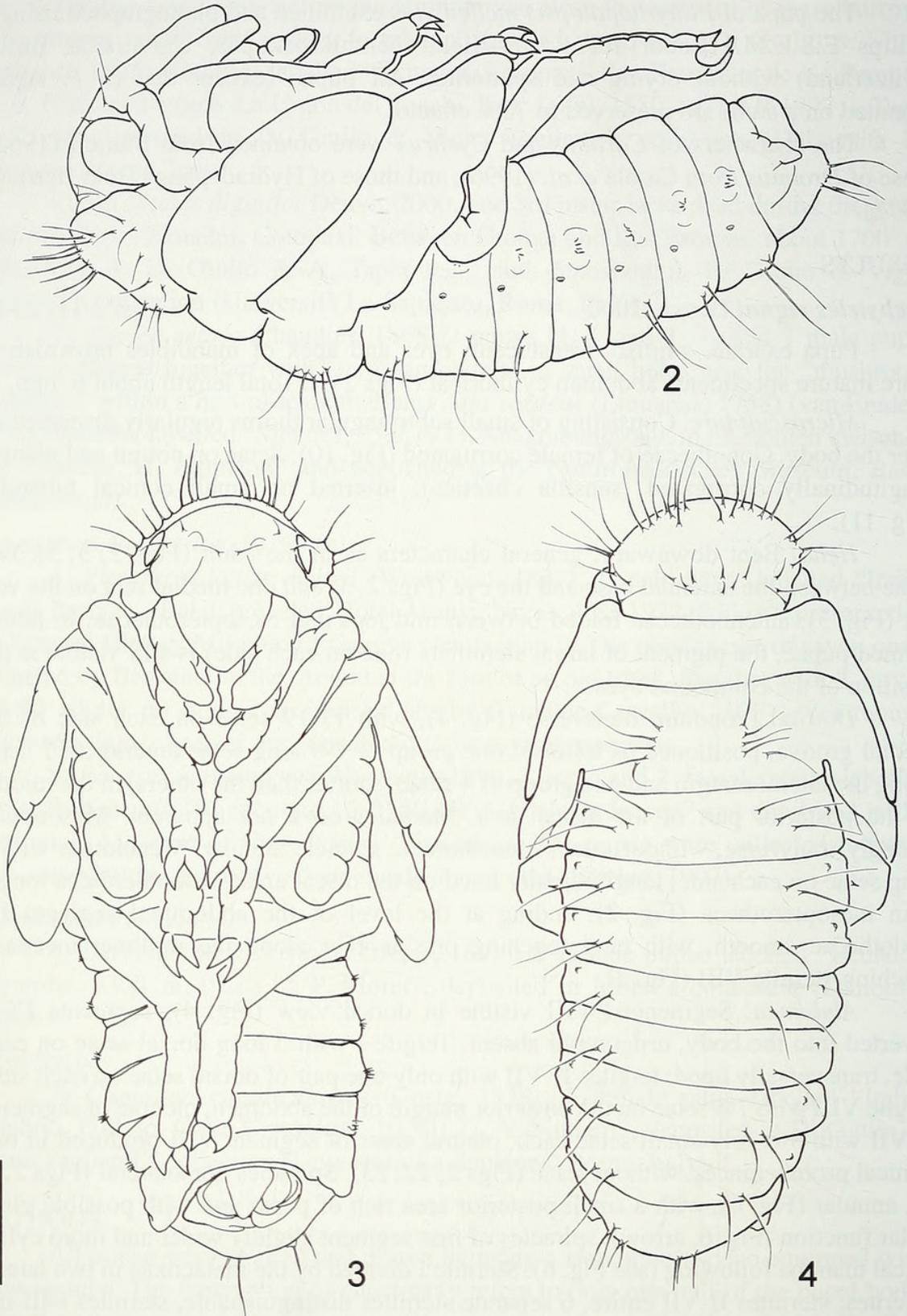
Pupa exarate, whitish, translucent; eyes and apex of mandibles brownish in more mature specimens; abdomen cylindrical (Figs 2-5). Total length about 6 mm.

Microsculpture. Consisting of small subtriangular thorns regularly dispersed all over the body. Gonothecae of female corrugated (Fig. 10). Setae on notum and pleurae longitudinally corrugated (sensilla chaetica), inserted on small conical tubercles (Fig. 11).

Head. Bent downward; general characters as in the adult (Figs 2, 3, 5); two setae between the antennal base and the eye (Figs 2, 3) and one medial seta on the vertex (Fig. 3); antennothecae folded between mid legs and mesopterothecae. In newly formed pupae, the pigment of larval stemmata (one on each side) is still visible at the position of the compound eyes.

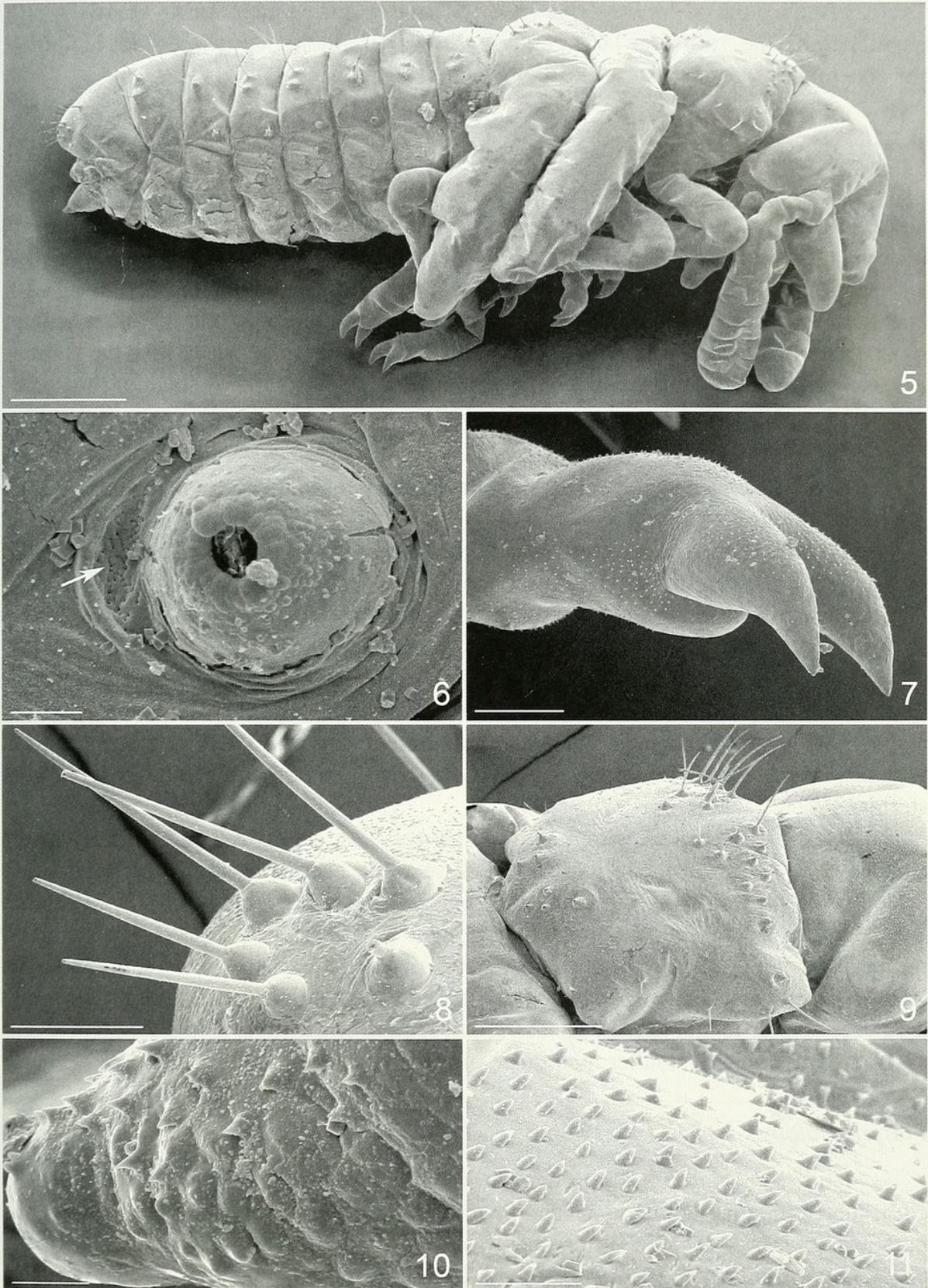
Thorax. Pronotum transverse (Fig. 4), with 17-19 setae on each side of the medial groove, positioned as follows: one group of 7-8 long setae anterior, 6-7 setae along the lateral margin and one group of 4 setae, shorter than the others, in the middle of the posterior part of the discal area. Medial groove not apparent. Mesonotum strongly transverse, without setae. Mesothoracic spiracle annular. Metanotum with 5 long setae on each side, longitudinally lined on the discal area; metapheroteca longer than mesopterotheca (Fig. 2), ending at the level of the abdominal segment IV. Podothecae smooth, with tarsi touching one another along the midline; metatarsi reaching sternite VIII (Fig. 3).

Abdomen. Segments I-VIII visible in dorsal view (Fig. 4); segments IX-X inverted into the body, urogomphi absent. Tergite I with 3 long dorsal setae on each side, transversally lined; tergites II-VII with only one pair of dorsal setae on each side; tergite VIII with 7-8 setae on the posterior margin of the abdomen; pleurae of segments II-VII with 3-6 very small setae each; pleural areas of segment VIII produced in two conical protuberances, without setae (Figs 2, 22, 23). Spiracles dorsolateral (Figs 2, 4, 5), annular (Fig. 6), with a small posterior area rich of pores and with possible glandular function (Fig. 6, arrow); spiracles of first segment slightly wider and more cylindrical than the following (see Fig. 6). Sternite I divided by the metacoxae in two lateral sclerites; sternites II-VII entire, 6 separate sternites distinguishable, sternites I-III not fused. Male gonotheca (Fig. 22) asymmetrical, well visible, composed of a medial swollen and multilobed area, aedeagus not clearly turned toward the left side, as in the majority of carabid pupae (Jeannel, 1941; Sturani, 1962); female gonothecae (covering the two gonapophyses) conical and symmetrical (Figs 5, 10, 23), pointed at the tip, touching one another along the midline.



FIGS 2-4

Pachyteles vignai, male pupa: (2) habitus from left lateral, (3) ventral and (4) dorsal view. Scale bar = 1 mm.



FIGS 5-11. *Pachyteles vignai*, female pupa: (5) habitus, right lateral view; (6) right abdominal spiracle II with posterior glandular area (arrow); (7) claw of right metathoracic leg; (8) group of setae on abdominal tergum VIII; (9) pronotum, right lateral view; (10) microsculpture at apex of right gonoteca; (11) microsculpture on head. Scale bars: Fig. 5 = 1 mm; Figs 6, 11 = 20 μm ; Figs 7, 8 = 100 μm ; Fig. 9 = 500 μm ; Fig. 10 = 10 μm .

A male pupa of *Pachyteles digiulioi*, deceased during pupation and partially still enveloped by the 3rd instar larval exuvia, shows morphological characters, including the chaetotaxy, very similar to those of *Pachyteles vignai*.

Physea setosa Chaudoir, 1868

Figs 12-14, 24-25

The general pupal morphology and chaetotaxy of *Physea setosa* (Figs 12-14) and *Pachyteles vignai* are similar. Differences in the habitus, mostly of the prothorax, abdomen, legs and gonothecae (Figs 24, 25), reflect those of the adults. *Physea setosa* is one of the few myrmecophilous species of Ozaenini with adaptations for living with ants during both the adult stage (e.g. flattening of legs and body) and larval stage (e.g. physogastry of the body, cf. van Emden, 1936, Di Giulio *et al.*, 2003). In the following, we concentrate on the differences between the two taxa. Most setae of the specimens examined are broken, but their position is marked by small conical tubercles. Total length about 14 mm.

Head. One seta on the vertex near the antennal base; frons with 2 small swollen areas.

Thorax. Pronotum strongly transverse, flattened, with 20-25 setae on each side of the medial groove, disposed as in the following: one group of 8-10 anterior setae, 7-10 setae irregularly dispersed from the anterior corner to the lateral side and one group of 4-6 setae, medially on the posterior part. Mesonotum transverse and slender, without setae. Metanotum with 5 setae on each side, transversally lined on discal area; stigma of mesothorax well developed; metapteroteca smaller than in *Pachyteles vignai* in respect to body size, ending at the level of abdominal segment III. Podothecae smooth, with pro- and mesotarsi touching one another along the midline; metatarsi reaching the sternite IV.

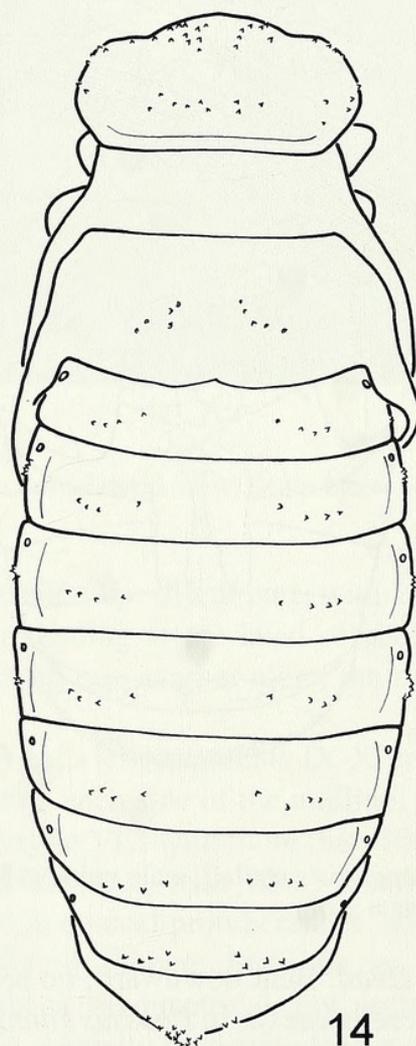
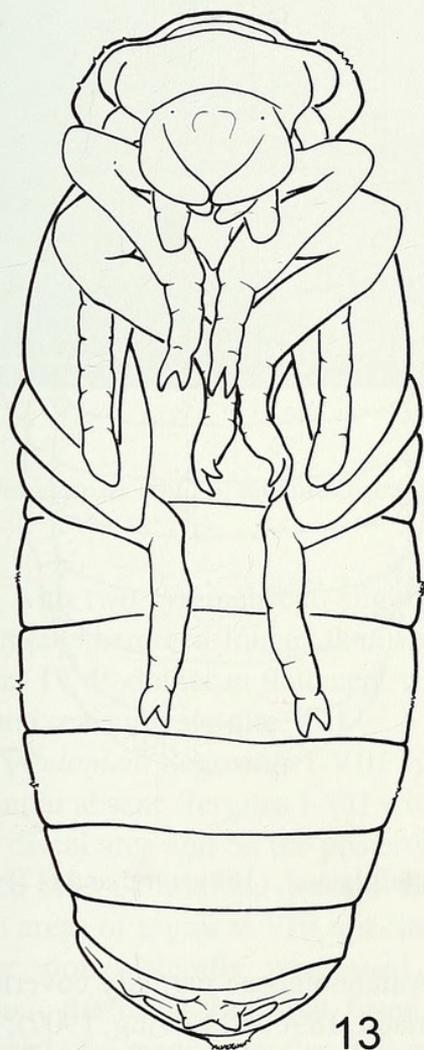
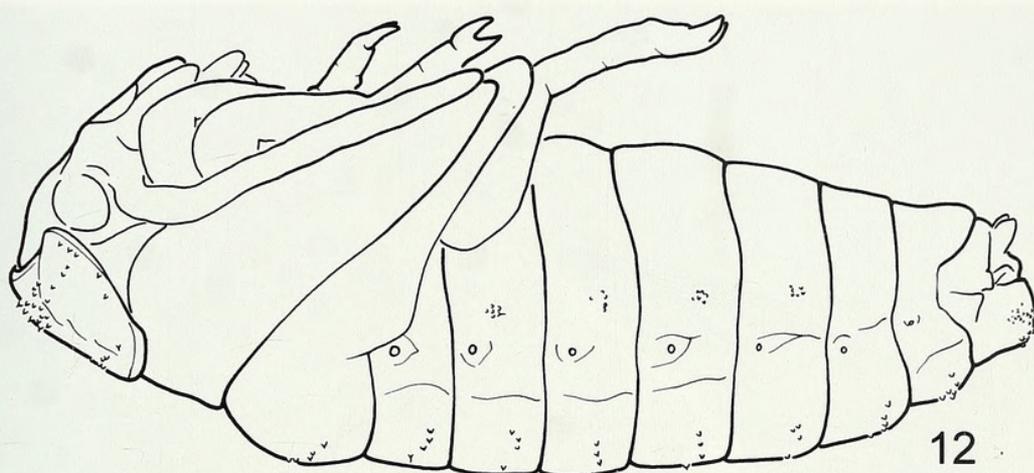
Abdomen. Tergite I with 3 long dorsal setae on each side, transversally lined; tergites II-VII with only one pair of dorsal setae on each side; tergite VIII with 7-8 setae on the posterior margin of the abdomen; pleurae of segments I-VII each with 2-6 very small setae; pleural areas of segment VIII produced in two small conical protuberances, without setae; sternites like in *Pachyteles vignai*. Male gonotheca (Fig. 24) asymmetrical, well visible, composed of a medial, swollen and multilobed area very similar to that of *Pachyteles vignai*; female gonothecae (Fig. 25) conical and symmetrical, pointed, smaller than those of *Pachyteles vignai*.

Platyrophalopsis melleii (Westwood, 1833)

Figs 15-18

Highly specialised adult characters (e.g. flattened legs, lens-shaped antennal club, subrectangular and flattened abdomen, small prothorax) are also visible in the pupa (Figs 15-17). The main differences from the pupae of Ozaenini include a richer chaetotaxy of notum and pleurae, and a different position of the gonothecae, partially hidden in the large sternite VII. The number of the visible tergites and sternites is the same as in the Ozaenini.

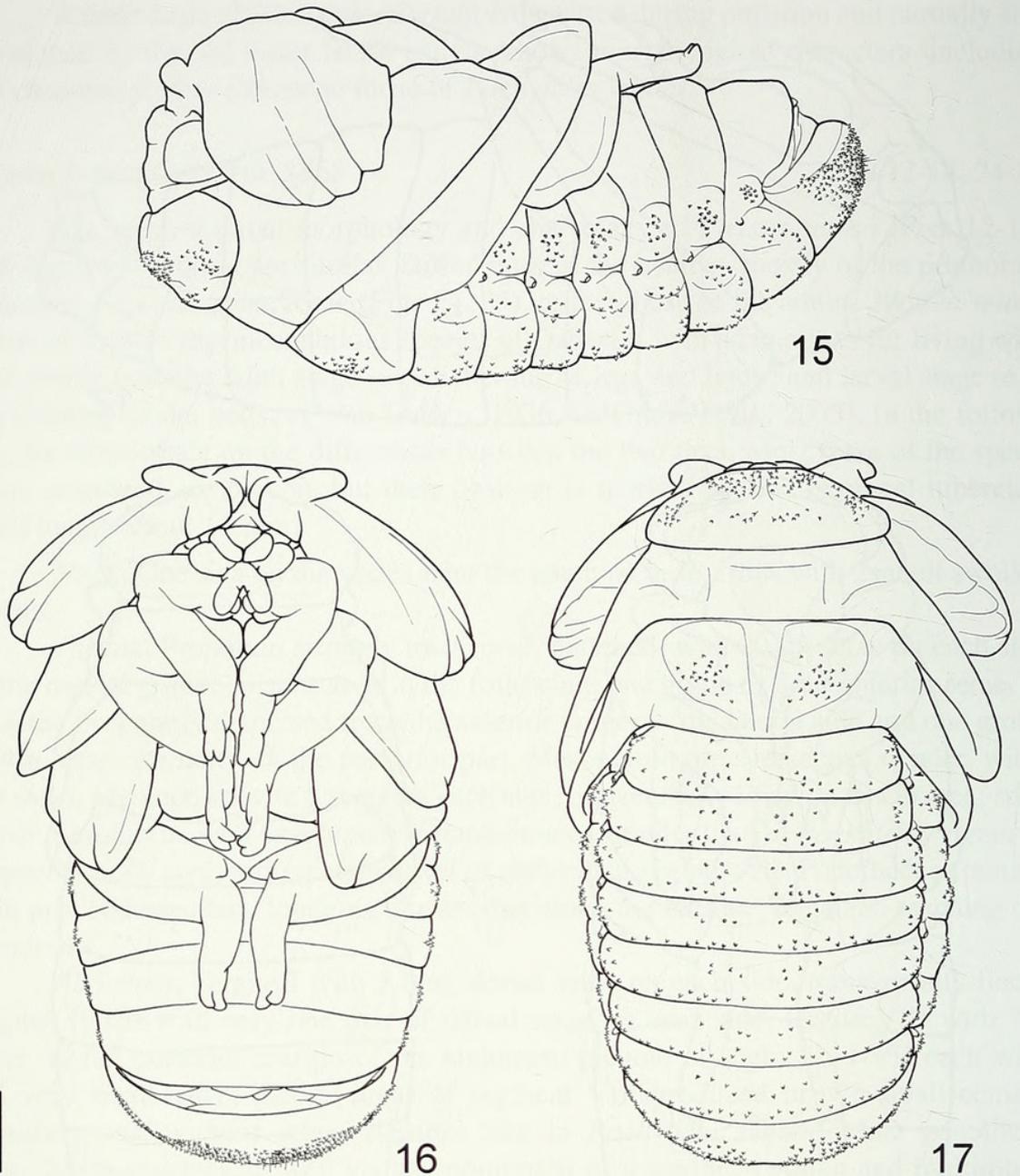
Almost all setae are broken but marked by small conical tubercles. Total length about 9 mm.



FIGS 12-14

Physea setosa, female pupa: (12) habitus from left lateral, (13) ventral and (14) dorsal view. Scale bar = 2 mm.

Microsculpture. Similar to that of *Pachyteles vignai*, with small triangular thorns (length about $3\ \mu\text{m}$, distance between thorns about $15\ \mu\text{m}$).



FIGS 15-17

Platyrhopalopsis melleii, male pupa: (15) habitus from left lateral, (16) ventral and (17) dorsal. Scale bar = 2 mm.

Head. Bent downward; no setae present. Antennothecae partially covering the fore-pterothecae (as in *Paussus kannegieteri* Wasmann, 1896, cf. Böving, 1907); 3 sub-apical denticulations present at the posterior margin of the antennal club of the antennotheca; in contrast to the adult, 6 or 7 antennomeres can be identified by transverse grooves, one small protuberance at the apex (Fig. 18).

Thorax. Pronotum transverse, subtriangular, with more than 50 setae on each side of the medial groove on the discal area, disposed as in the following: 26-30 anterior setae, 17-18 lateral setae and 6-8 posterior setae. Medial groove not apparent. Mesonotum highly transverse, without setae; mesothoracic spiracle annular. Meta-

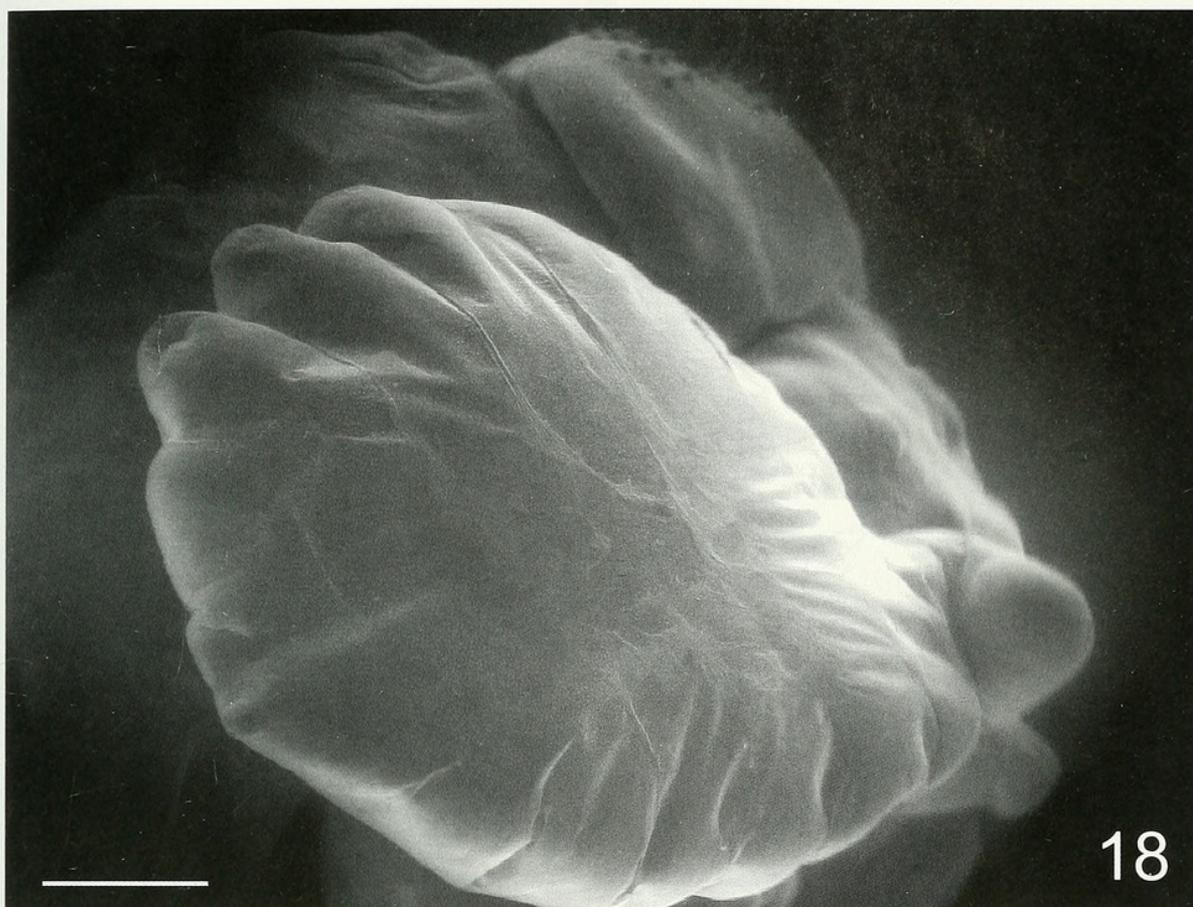


FIG. 18

Platyrhopalopsis melleii: antennotheca of male pupa in dorsolateral view. Scale bar = 500 μ m.

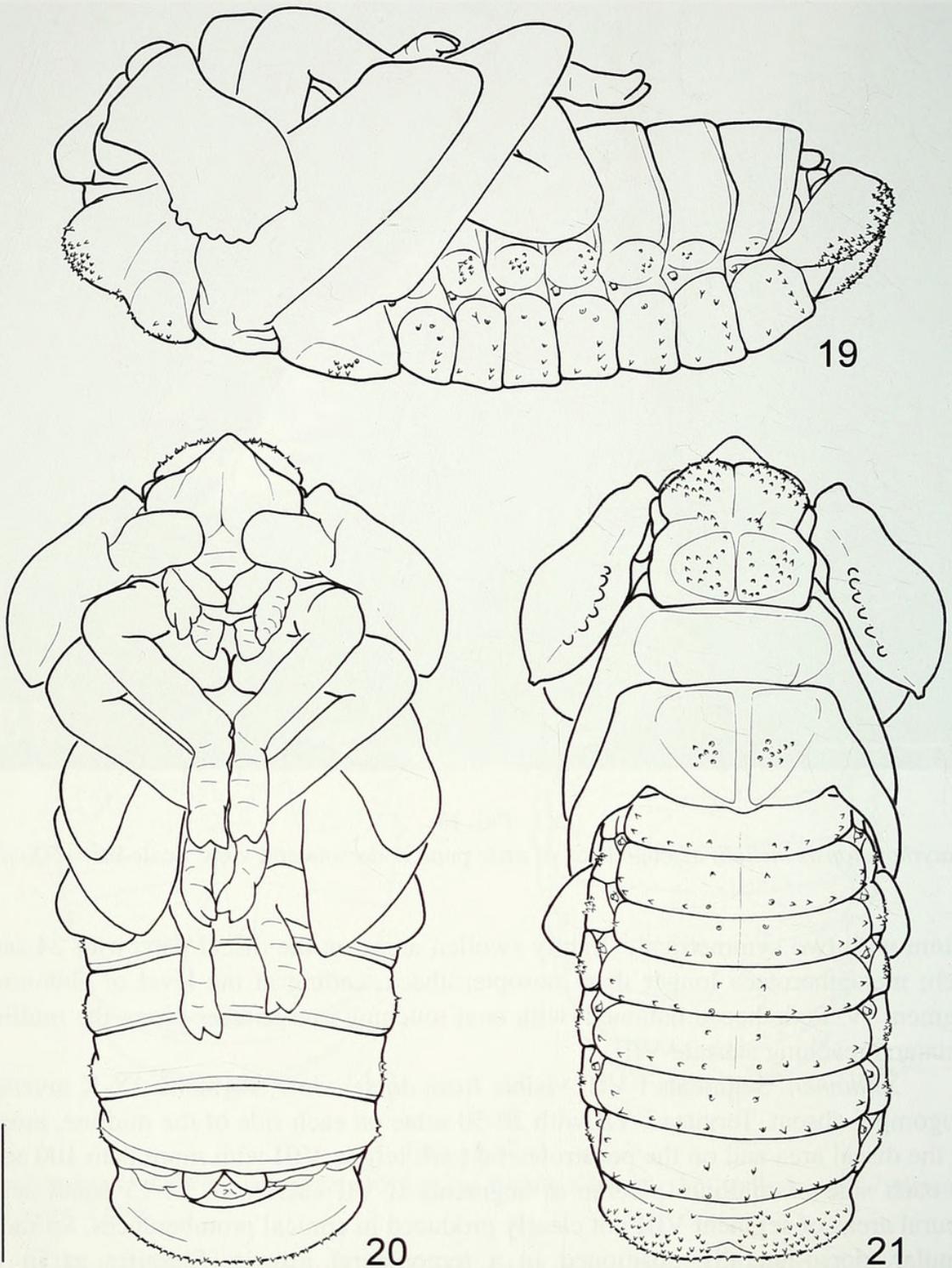
notum with two symmetrical, slightly swollen areas on the discal part, with 24 setae each; metapterotheca longer than mesopterotheca, ending at the level of abdominal segment IV. Podothecae flattened, with tarsi touching one another along the midline; metatarsi reaching sternite VIII.

Abdomen. Segments I-VIII visible from dorsal view; segments IX-X inverted, urogomphi absent. Tergites I-VII with 20-30 setae on each side of the midline, mostly on the discal area and on the posterolateral part; tergite VIII with more than 100 setae on each side of midline; pleurae of segments II-VII each with 10-15 small setae; pleural areas of segment VIII not clearly produced in conical protuberances. Spiracles annular, dorso-laterally positioned in a tergopleural groove. Sternites as in the Ozaenini, the basal three not fused. Male gonotheca asymmetrical, not protruding, composed of a medial swollen and multilobed area, partially hidden under the sternite VII.

Paussus kannegieteri Wasmann, 1896

Figs 19-21, 26-27

Body elongate, subcylindrical, with chaetotaxy similar to that of *Platyrhopalopsis melleii*, but less rich. The setae of the available pupae are almost all broken. Total length about 6 mm.

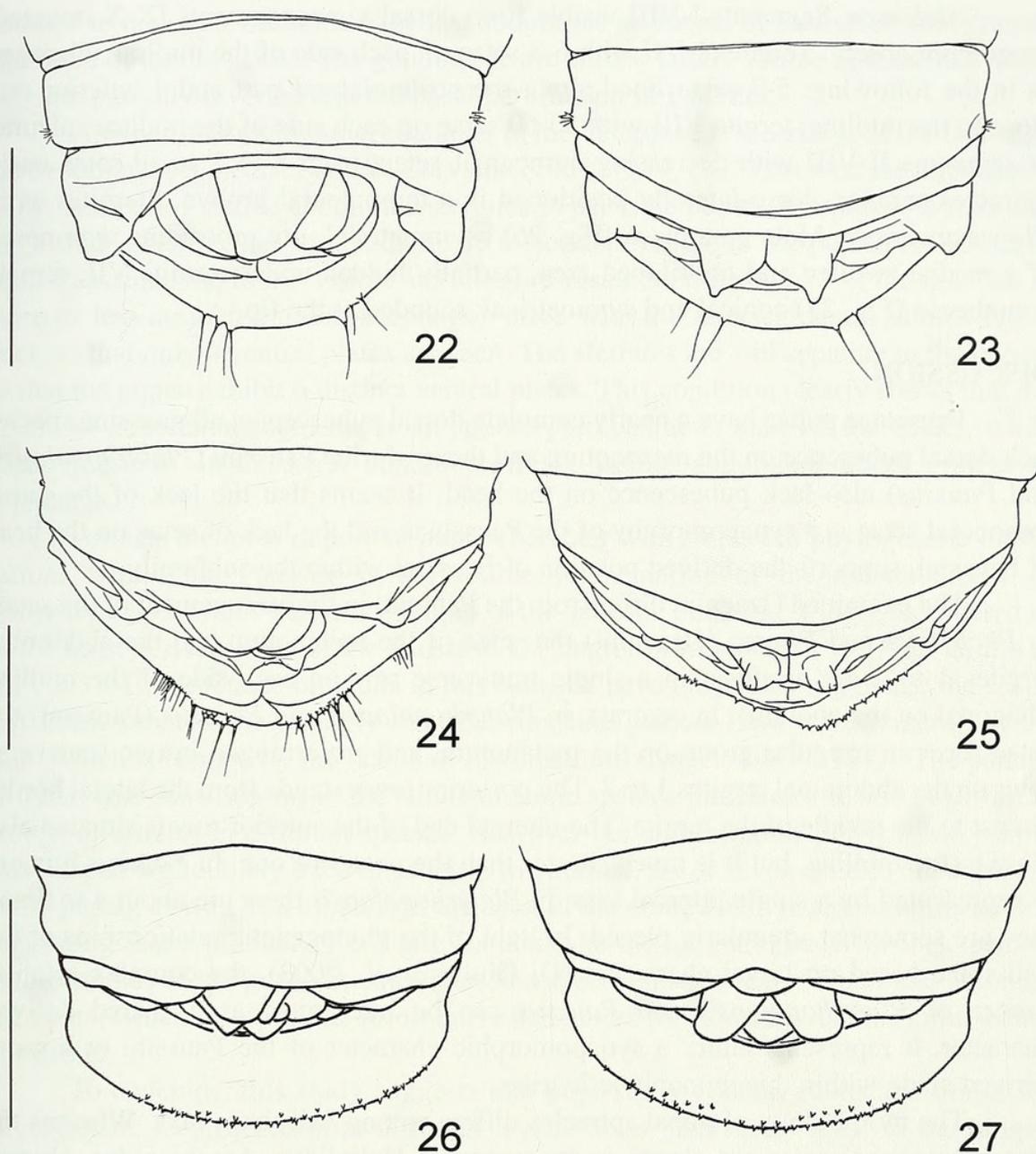


FIGS 19-21

Paussus kannegieteri, female pupa: (19) habitus from left lateral, (20) ventral and (21) dorsal view. Scale bar = 1 mm.

Microsculpture. As in *Platyrhopalopsis melleii*.

Head. Bent downward; no setae present. Antennothecae partially covering the anterior pterothecae; the 6 teeth on the posterior margin of the antennal club clearly visible; transversal sutures on the antennotheca absent; small protuberance present at apex.



FIGS 22-27

Last abdominal segments of the pupae in ventral view: (22) *Pachyteles vignai* male. (23) *P. vignai* female. (24) *Physea setosa* male. (25) *P. setosa* female. (26) *Paussus kannegieteri* male. (27) *Paussus kannegieteri* female.

Thorax. Pronotum subquadrate, divided in four parts by a distinct transverse constriction and a slight longitudinal medial groove; posterior half longer and slightly wider than the anterior; about 50 setae on each side of the medial groove, positioned as follows: about 25 anterior setae, 4-5 medial setae and 14-16 posterior setae. Mesonotum shorter than metanotum, highly transverse, without setae; mesothoracal stigma present. Metanotum with two symmetrical, slightly swollen areas on the discal part, with 7-9 setae each; metapterotheca longer than mesopterotheca, ending at the level of abdominal segment IV. Podothecae cylindrical, slightly flattened, with tarsi touching one another along the midline; metatarsi reaching the sternite VII.

Abdomen. Segments I-VIII visible from dorsal view; segments IX-X inverted, urogomphi absent. Tergites I-VII with 6-8 setae on each side of the midline, disposed as in the following: 5-7 setae lined along the posterolateral part and 1 anterior seta close to the midline; tergite VIII with 50-60 setae on each side of the midline; pleurae of segments II-VIII with decreasing number of setae, from 8 to 2 small setae each. Spiracles annular, dorso-laterally positioned in a tergopleural groove. Sternites as in *Platyrhopalopsis*. Male gonotheca (Fig. 26) asymmetrical, not protruding, composed of a medial swollen and multilobed area, partially hidden under sternite VII; female gonothecae (Fig. 27) conical and symmetrical, rounded at the tip.

DISCUSSION

Paussinae pupae have a nearly complete dorsal pubescence: all paussine species lack dorsal pubescence on the mesonotum and those of tribe Paussini (*Platyrhopalopsis* and *Paussus*) also lack pubescence on the head. It seems that the lack of the pupal mesonotal setae is a synapomorphy of the Paussinae and the lack of setae on the head of Paussini, supports the derived position of Paussini within the subfamily.

The examined Ozaenini differ from the Paussini in the arrangement of the setae. In *Pachyteles* and *Physeia* (Ozaenini) the setae of the metanotum and the abdominal tergites 1 to 7 are arranged in a single transverse row on each side of the midline (diagonal on metanotum). In contrast, in *Platyrhopalopsis* and *Paussus* (Paussini) the setae form an irregular group on the metanotum, and are arranged in two transverse rows on the abdominal tergites 1 to 7. The posterior row extends from the lateral border almost to the middle of the tergite. The internal end of the anterior row is situated also close to the midline, but it is much shorter than the posterior one. In *Paussus* it is only represented by a single internal seta; in *Platyrhopalopsis* there are about 4 to 5 and they are somewhat irregularly placed. In light of the phylogenetic relationships of the Paussinae based on larval characters (Di Giulio *et al.*, 2003), the complex setation pattern of *Platyrhopalopsis* and *Paussus* can be interpreted as a shared derived character. It represents either a synapomorphic character of the Paussini or a more derived clade within this monophyletic tribe.

The morphology of pupal spiracles differs among Adephaga taxa. Whereas the mesothoracic spiracles are closed in the pupae of Haliplidae, Amphizoidae, Hygrobiidae and Dytiscidae (Ruhnau, 1986), they are well developed in Carabidae. Seven (presumably functional) abdominal spiracles of similar sizes and shapes are present in the pupae of *Carabus* and most Hydradephaga according to the illustrations (Sturani, 1962; Bertrand, 1972). However the 1st abdominal spiracle is larger than the following six in *Clinidium canaliculatum* and *Dyscolus megacephalus*, and the 7th abdominal spiracle is smaller and more weakly sclerotised than the other spiracles in the Paussinae.

The pupal integument of all Paussinae examined have a unique microsculpture. The entire body is covered by a uniform pattern of more or less regularly spaced, small triangular thorn-like sculpticells.

In Carabidae, the last abdominal segments are visible and the 9th tergite often contains remnants of the larval urogomphi, as in *Carabus* and *Dyscolus*. The shape of pupal urogomphi, as well as their setae, seem to be true remaining larval characters. In

contrast to the other Carabidae, the last abdominal segments of Paussinae are inverted and more or less invisible. The gonothecae are almost totally visible in Ozaenini while they are partially inverted and the basal part hidden in Paussini.

Another important pupal character in the Paussinae is the extent of the fusion of the abdominal segments. Luna de Carvalho (1951, 1959, 1977) stressed the importance of the number of visible abdominal sternites in paussine pupae. In contrast to four distinguishable sternites in adults, there are 6 sternites visible in the pupae. However, in adult Paussinae the first 3 visible sternites are fused (sternites 2 to 4 – the first one is more or less atrophied in all Adephaga), often with the intersegmental sutures indistinct, so that only 4 ventral plates are seen. The sternites are still separate in the pupae, so that the pupae exhibit 6 distinct ventral plates. This condition clearly shows that the fusion of abdominal segments is an apomorphic character state of the adults, while pupae preserve an ancestral condition of six visible abdominal plates typical of Adephaga.

Perhaps the most important pupal character with respect to phylogenetic implications within the Paussini is the visible segmentation of the antennothecae of *Platyrhopalopsis*. This genus is member of the subtribe Paussina, widely considered to be the most derived clade of the Paussini (Darlington, 1950; Nagel, 1997; Di Giulio *et al.*, 2003). The antennae of adults in this subtribe have only three segments: the scape (1st antennomere), the strongly reduced, ring-like pedicel (2nd antennomere), and a club, which is formed by the fusion of the flagellum (Nagel, 1987, 1997). The pattern of transverse constrictions in the adults of some species indicates a fusion of different groups of articles in different species. However the club of adult *Platyrhopalopsis* is lens-shaped without any trace of articles. In contrast, six or seven articles are apparent in the pupae, as well as a tubercle at the apex of the club, which is absent in the adults, suggesting that a number of 6-7 articles could be the ancestral state for this species. Future studies of the pupae in other Paussina species may reveal more or less antennal segments, which may provide informative characters for inferring relationships within this group.

To conclude, this study suggests that pupae may contain characters useful for phylogenetic reconstruction at different levels. Some characters, such as the unique microsculpture, the inversion of the last abdominal segments and perhaps the reduction in the size of the 7th abdominal spiracle, probably represent apomorphies of the Paussinae. The extent of pubescence is interpreted as a morphocline among Adephaga, with an increased reduction in pubescence in derived taxa. The arrangement of setae and the folding of gonothecae differ between basal and derived Paussinae. Finally, the possibility of recognising distinctly separate abdominal segments and traces of originally separate antennal articles at the pupal stage in taxa with fused metameric parts in the adult stage provides a potential ontogenetic basis for elucidating phylogenetic relationships in this group.

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