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Larval juice anyone? The unusual behaviour and morphology of an ant nest beetle larva (Coleoptera: Carabidae: Paussini) from Thailand

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Abstract. The third instar larva of *Paussus siamensis* Maruyama, 2016 (Coleoptera, Carabidae, Paussini) from Thailand, belonging to the *Paussus hystrix* group (sensu Maruyama, 2016), is described and illustrated by using both light and scanning electron (SEM) microscopy. Unlike other *Paussus* larvae, this larva was found inside a self-dug hole, in a nest of *Pheidole plagiaria* ants. Behavioural observations, documented by pictures taken in the field, show a peculiar strategy of *P. siamensis* larva to exudate big drops of transparent liquid from the thorax, promptly sucked by worker host ants. Behaviour of *Paussus* larvae is still unknown, but, due to their structural homogeneity, we suspect that digging and supplying attractive substances can be widespread within this genus. The similarity between *P. siamensis* and *P. kannegieteri* larvae, both Indo-Malayan species and guests of the same ant, is in agreement with their recent placement in the subgenus *Scaphipaussus* Fowler (sensu Robertson & Moore, 2016).

Key words. *Paussus*, social parasites, Myrmecophily, Larvae, flanged bombardier beetles, SEM

INTRODUCTION

Larvae of the flanged bombardier beetles (Carabidae, Paussinae) are characterised by an up-curved abdomen and a peculiar sclerotised terminal disk (long acknowledged as the main apomorphy of the subfamily, see Bousquet, 1986), resulting from the modification of the last abdominal segments and urogomphi (Di Giulio, 1999; Di Giulio et al., 2000, 2003). Non-myrmecophilous larvae of Metriini (Bousquet, 1986), Mystropomini (Di Giulio & Moore, 2009) and Ozaenini tribes (Luna de Carvalho, 1992; Vigna Taglianti et al., 1998; Di Giulio, 1999; Moore & Di Giulio, 2006; Moore et al., 2011), use their terminal disk as a door to close galleries they construct in rotten wood, humid earth or sandy riverbanks, and use the moveable components of the terminal disk to trap their prey (small arthropods), seizing them with their sharp hyperprognathous mandibles through a backward spring-like movement (Costa et al., 1988; Di Giulio, 1999; Di Giulio & Vigna Taglianti, 2001). Due to their obligate myrmecophilous lifestyle spent in the concealed environment of the nests, almost no behavioural information is available on larvae of Paussini, except for the identity of the hosts and a few occasional observations in the field on damaged nests. In particular, larvae of the speciose genus *Paussus* Linnaeus are still scarcely known, being described at larval stage only 10 out of 342 species (Fattorini et al., 2013), listed in the following: *P. kannegieteri* Wasmann (see Bøving, 1907; Di Giulio, 2008), *P. horni* Wasmann (see Wasmann, 1910), *P. granulatus* Westwood (see van Emden, 1922), *P. curtisi* Westwood (see Luna de Carvalho, 1951), *P. cridae* Gestro (see Luna de Carvalho, 1959), *P. cucullatus* Westwood (see Luna de Carvalho, 1959), *P. cultratus* Westwood (see Luna de Carvalho, 1992), *P.* aff. *distinguendus* Reichensperger (see Arndt & Beutel, 1995), *P. afzelii* Westwood (see Arndt & Beutel, 1995), *P. favieri* Fairmaire (see Di Giulio et al., 2011).

A new highly derived *Paussus* species from Thailand, *P. siamensis* Maruyama, 2016, very close to *P. serraticornis* Nagel & Bednařík, 2013 from Laos and Vietnam, was recently described based on several adults (Fig. 1B), nine of which collected in an ant nest together with a mature larva of the same species (Fig. 1C, D)(Maruyama, 2016). The author unequivocally assigned *P. siamensis* to "*Paussus histrix*" group (sensu Maruyama, 2016), based on the head vertex ornamentation (frontal crest), but, in agreement with Nagel & Bednařík (2013) for *P. serraticornis*, refrained to assign the entire group to any known subgenus, though emphasised the similarities with both *Scaphipaussus* Fowler (sensu Luna de Carvalho, 1989) and some *Cochliopaussus* H. Kolbe species. However, based on combined molecular and morphological analyses, Robertson & Moore (2016) recently included *P. siamensis* (named "*Paussus* nr. *serraticornis*") in an Indo-Malayan *Scaphipaussus* (sensu n.) clade, inside *Paussus* II series. In this clade, several species of the polyphyletic *Cochliopaussus* are clustered together with acknowledged *Scaphipaussus* species, thus confirming that in *Paussus*, areas of endemism are better predictors of monophyly than the morphological characters traditionally used to define groups (Moore & Robertson, 2014).

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Fig. 1. A–D, *Paussus siamensis* Maruyama, 2016. A, environment where the third instar larva was found, together with 9 adults, inside a *Pheidole plagiaria* nest built inside an abandoned termite mound (*Macrotermes* sp.); B, adult, dorsal view; C, third instar larva, right lateral view; D, third instar larva interacting with a worker of *Pheidole plagiaria* (note the drops of clear liquid sucked by the host ant).

The finding of the above mentioned *P. siamensis* larva is particularly important, since it not only gives us the possibility to add new morphological and ecological data to this species, but also to increase the general knowledge on paussine larval taxonomy and biology. In particular, the behavioural observations and pictures taken of this larva in the field, though occasional and limited to a single specimen, add valuable information to the obscure life history of these beetles, and helped us to validate previous hypotheses mostly based on indirect speculations inferred from their external morphology (Di Giulio, 2008; Di Giulio et al., 2011).

Aims of this work are: (1) describe and illustrate by light and scanning electron (SEM) microscopy the fine morphology of the larva of *Paussus siamensis*, the first known for the Scaphipaussus subgenus, by using modern standards; (2) compare this larva with the other known larvae of the genus *Paussus* and of other Paussini, in order to infer about its subgeneric assignment; (3) describe the peculiar behaviour of this larva while interacting with the ants in the nest; (4) report new data on habitat preference and host ant identity.

MATERIALS & METHODS

Material examined. *Paussus siamensis* Maruyama, 2016: 9 adults and 1 mature larva in ant nest (Fig. 1): Thailand, Nakhon Ratchasima, Khao Yai National Park, KM33, 700m, 23 September 2007, Takashi Komatsu & Maruyama. Adult material is preserved in the M. Maruyama collection (Fukuoka, Japan), the larva is preserved in the A. Di Giulio collection (Rome, Italy).

The third instar larva was observed and photographed in the field prior to collecting (see Fig. 1C, D), then it was put in hot water for a few minutes and preserved in 80% EtOH. It was also photographed in the lab by a camera connected to a stereomicroscope (see Figs. 2, 3). For the SEM analysis, the larval specimen was dehydrated to EtOH 100%, critical point dried (by using a Bal-Tec CPD 030), mounted on stubs by using self-adhesive carbon disks, gold sputtered (by using a Emitech® K550) and analysed by FEI Dualbeam FIB/SEM Helios Nanolab (at L.I.M.E. laboratory, University “Roma Tre”, Rome, Italy), operating with the SEM column (HV set at 2 kV).

The general terminology of larval structures follows Lawrence (1991). Notation of primary setae and pores follows the system of Bousquet & Goulet (1984), modified for *Metrius contractus* (Bousquet, 1986). Notations for microsculpture, sensilla (S–I to S–V) and urogomphal lobes follow those proposed by Bousquet (1986) for *Metrius contractus* and later modified by subsequent authors (Vigna Taglianti et al.,

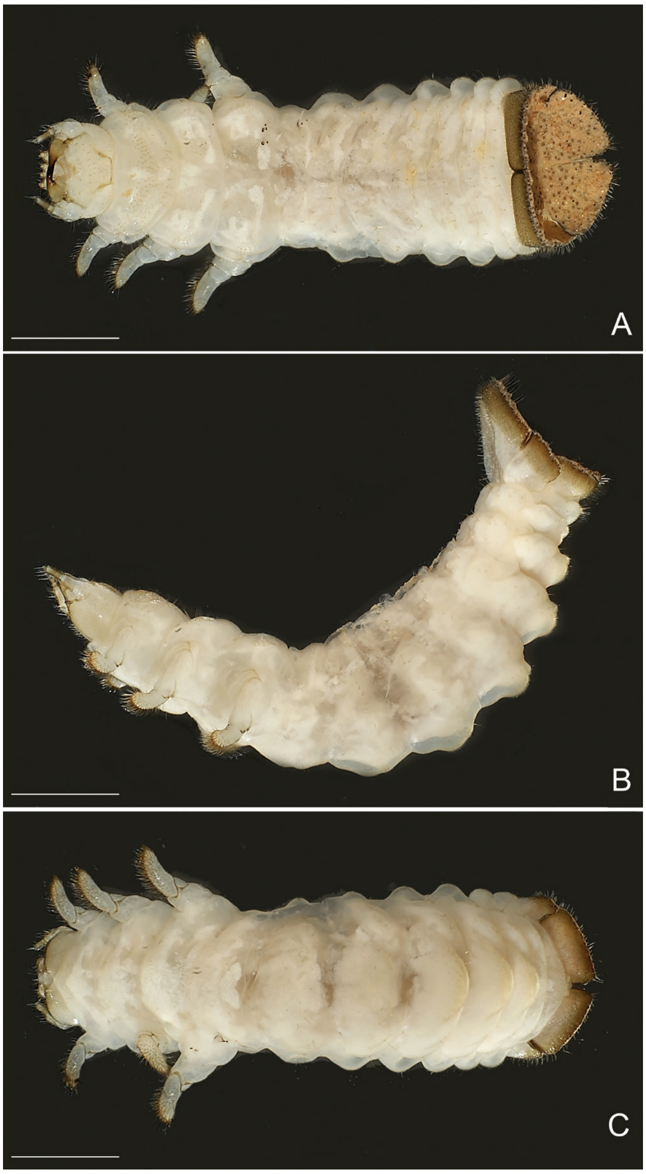

Fig. 2. A–C, *Paussus siamensis* Maruyama, 2016, third instar larva. A, habitus, dorsal view; B, habitus, left lateral view; C, habitus, ventral view. Scale bars = 1 mm.

1998; Di Giulio et al., 2000; Di Giulio & Moore, 2004). An asterisk (*) following a coded seta or pore indicates that the homology between the structure on the *P. siamensis* larva and the corresponding code is questionable.

RESULTS

***Paussus siamensis* third instar larva.** Body physogastric (Figs. 2A–C) with cup-shaped terminal disk (Figs. 3D, 6A), held in an elevated position by a thick, swollen abdomen (Figs. 1C, 2B); cephalic capsule, legs and thoracic tergites shiny and transparent, pale yellow, weakly sclerotised (Fig. 3A–C); thoracic and abdominal segments bulged, soft, opaque, whitish (Figs. 1C, D, 2A–C); frontoclypeolabrum more sclerotised and more yellowish than parietalia (Fig. 3A), with lateral and basal sides light brown; mouthparts, spiracles, claws and terminal disk distinctly sclerotised, light brown (Fig. 3A–E); apex of mandibles and margin of terminal disk thickly sclerotised, dark brown.

Measurements. Body length = 8 mm (from tip of mandibles to the terminal disk); cephalic capsule maximum width (at the base of the antennae) = 0.96 mm, medial length (from occipital foramen to anterior emargination of frontoclypeolabrum) = 0.44 mm, occipital foramen width = 0.6; antennal length = 0.41 mm; mandible length (measured along outer margin) = 0.43 mm, length of prostheca = 0.18 mm; pronotum maximum width = 1.25 mm, maximum length (along ecdysial suture) = 0.9 mm; diameter of terminal disk = 1.72 mm, dorsal plates length (measured along medial suture) = 0.92 mm, urogomphi (ventral plates) length (measured along medial suture) = 0.8 mm.

Microsculpture. Sclerotised parts of the body (e.g., cephalic capsule, mouthparts, thoracic and abdominal tergites, legs, pygidium) smooth or only slightly corrugated. Epipharynx and hypopharynx medially with pointed or multipointed microsculpture, arranged in many parallel, transverse rows; anterior margin of frontal emargination and sides of hypopharynx with tufts of thin elongate sculpticells. Membranous areas of the body completely covered by a carpet of thorn-like spiniform warts by thin, elongate, filiform apices, shortening towards sclerotised areas (Fig. 5C–E). Surface of the terminal disk with spinulate microsculpture (Fig. 6D–F), composed of conical, pointed sculpticells. Pygidium smooth.

Chaetotaxy. Head. Frontal area (laterally including part of parietale) with many (about 55) setae of different sizes, not all symmetrically disposed (Fig. 3A). Each half of parietal plate (Fig. 3A–C) with about 50 setae, subequally spaced except for a crown of about 10 setae around the antennal base (Fig. 3B). Antennae (Figs. 3A–C, 4A, C): antennomere I with about 13 additional setae, mainly dorsally and laterally, all primary pores present; antennomere II with a crown of 7 additional setae; antennomere III with about 10 additional setae mainly on dorsal side. Mandible (Fig. 4A, B, D, E) with 2 long additional setae directed mesad; seta MN_1 on lateral side, elongate; seta MN_2 absent. Setal group gMX on stipes with 7 setae lined along the ental edge of maxilla (Fig. 4F); about 10 additional setae present on lateral and ventral sides of stipes; setae MX_2 and MX_3 long; galea (Fig. 4D) with 2 setae at apex, one long, possibly MX_8* displaced apically, and MX_9* small; maxillary palpomere II (first visible) with lateral additional seta; palpomere III (second visible) with additional lateroventral seta; palpomere IV (third visible, Fig. 4D) with small additional seta on inner side and longer additional seta on outer side, 2 slender digitiform sensilla subapically and one apical sensorial area with 8 elongate (about 5 μm) subequal papillae (sensilla basiconica); cardo with 3 setae. Dorsal and lateral setae on prementum moderately long, ventral setae elongate and curved (Fig. 4B); seta LA_1 close to midline; LA_5 short; LA_6 subapical, about as long as palpomere I; 11 pairs of additional setae on prementum: 6 ventral, 1 ventrolateral and 4 dorsal; labial palpomere I with small additional seta ventrolaterally; II with 4 additional setae: 1 short on inner side, 2 on outer side (1 basal spiniform, about as long as internal, and 1 more distal very short), and 1 small ventral and subapical; 2 slender digitiform sensilla subapically

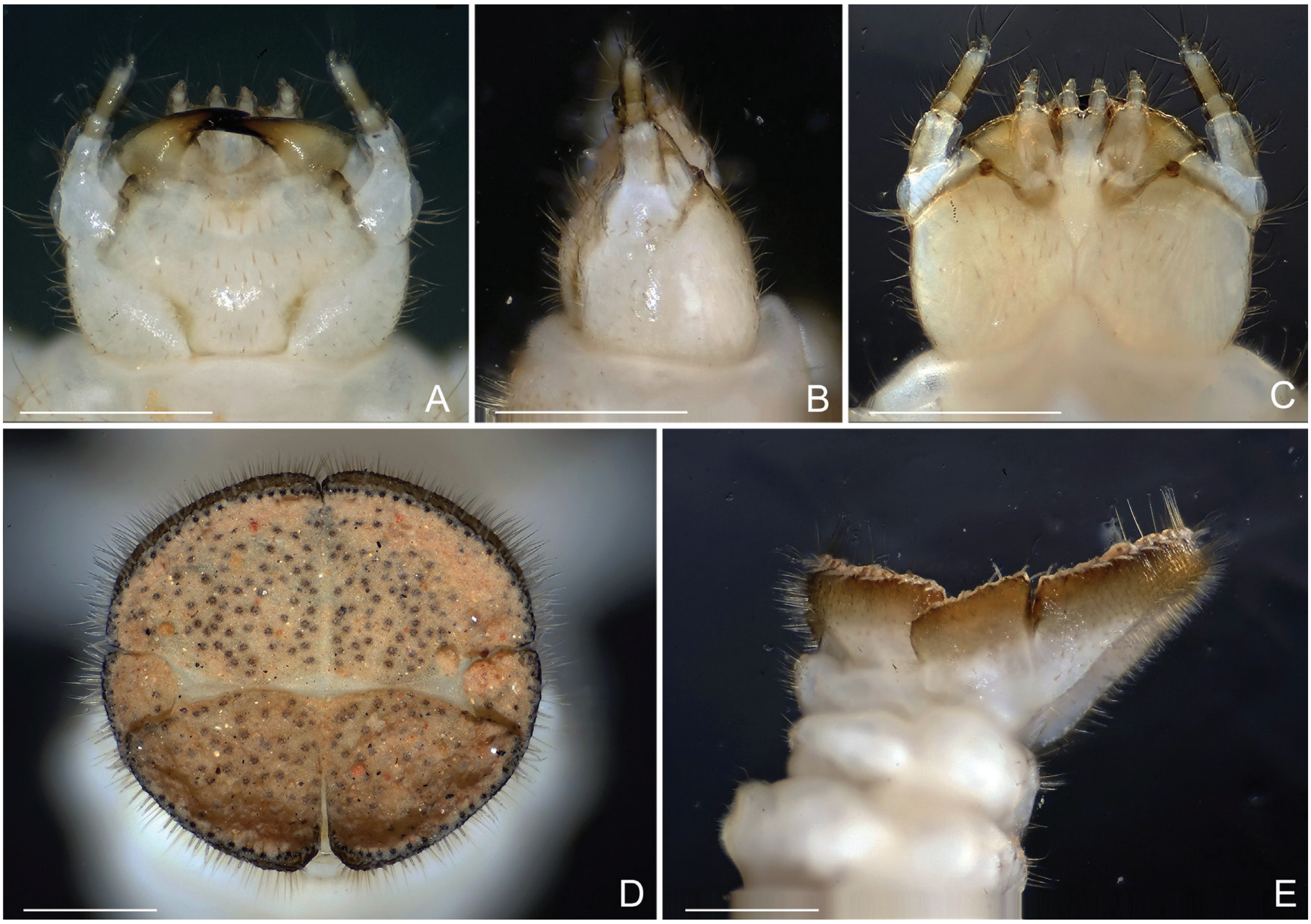

Fig. 3. A–E, *Paussus siamensis* Maruyama, 2016, third instar larva. A, head, dorsal view; B, head, right lateral view; C, head, ventral view; D, terminal disk, apical view; E, terminal disk, right lateral view. Scale bars = 500 µm.

and one apical sensorial area with about 8 elongate (about 5 µm) subequal papillae (sensilla basiconica), similar to those of maxillary palpomere IV. Thorax. Pronotum with about 40 additional setae on each side of ecdysial suture (primary setae impossible to identify), mainly on anterior and notopleural areas; notopleural setae very long and thin; mesonotum and metanotum with about 10 additional setae on each side of ecdysial line. Distal leg segment (corresponding to fused trochanter, femur, tibia and tarsus) ventrally and ventrolaterally with a tuft of about 70–80 long and lanceolate setae, with peculiar expanded and flattened apices (Fig. 5A, B). Abdomen. Terga of abdominal segments I–VII with about 20 pairs of setae each (identification not possible) and no pores. Dorsal and lateral plates of terminal disk dorsally (tergal side, Fig. 6B) with many short, spiniform, regularly spaced (every 30–50 µm) sensilla S–VII: about 100 on each dorsal, 20 on each lateral plate; ventral plates (urogomphi) each with about 20 setae on ventral side; perimeter of the disk (margin of dorsal, lateral and ventral plates), with a dense fringe of very long hairs (Fig. 6B); sensilla S–II stick-like abruptly tapered at apices (Fig. 6C), regularly spaced (every 50–70 µm) at margin of plates and urogomphi, radially oriented to the surface of terminal disk: about 15 on each dorsal plate, about 6 on each lateral plate and about 13 on each urogomphus; surface of the terminal disk (Figs. 3D, 6A, E) with many sensilla S–I (about 80 on each dorsal plate, 6 on each lateral plate, and 50 on each ventral plate, regularly spaced every 60–70 µm) of peculiar shape inserted perpendicularly to the surface of terminal disk (Fig. 6F), composed by an elongate basal stem (20–40 µm long and 10–15 µm wide) laterally and/or apically multilobed and multispinulate, and a short, stick-like smooth seta (8–15 µm), often clavate and apically truncate and fringed, medially emerging from a dome-like apex; row of sensilla S–I present along the raised margin terminal disk (about 20 along each dorsal, about 8 along each lateral, and about 15 along each ventral plate), characterised by a long, thin, straight seta perpendicularly directed to the disk surface (Fig. 6B, C). Epipleurites of abdominal segment I with 1 or 2 additional setae each; epipleurites of abdominal segments II–VII with 4–6 additional setae each; surface of terminal disk with many pores equally spaced every 10–40 µm from where thin structures come out (interpreted in the past as peculiar sensilla or glandular substances): about 150 on each dorsal plate, about 10 on each lateral plate and about 100 on each ventral plate. Hypopleurites of abdominal segments I–VII with 2–3 additional setae each. Sternal areas with 10–15 setae on each abdominal segment (homology assignment not possible). Pygidium without setae.

Head. Cephalic capsule (Fig. 3A–C) strongly transverse, more than two times as wide as long at middle, prognathous, with maximum width at base of antennae; base of cephalic capsule distinctly convex dorsally, partially retracted into

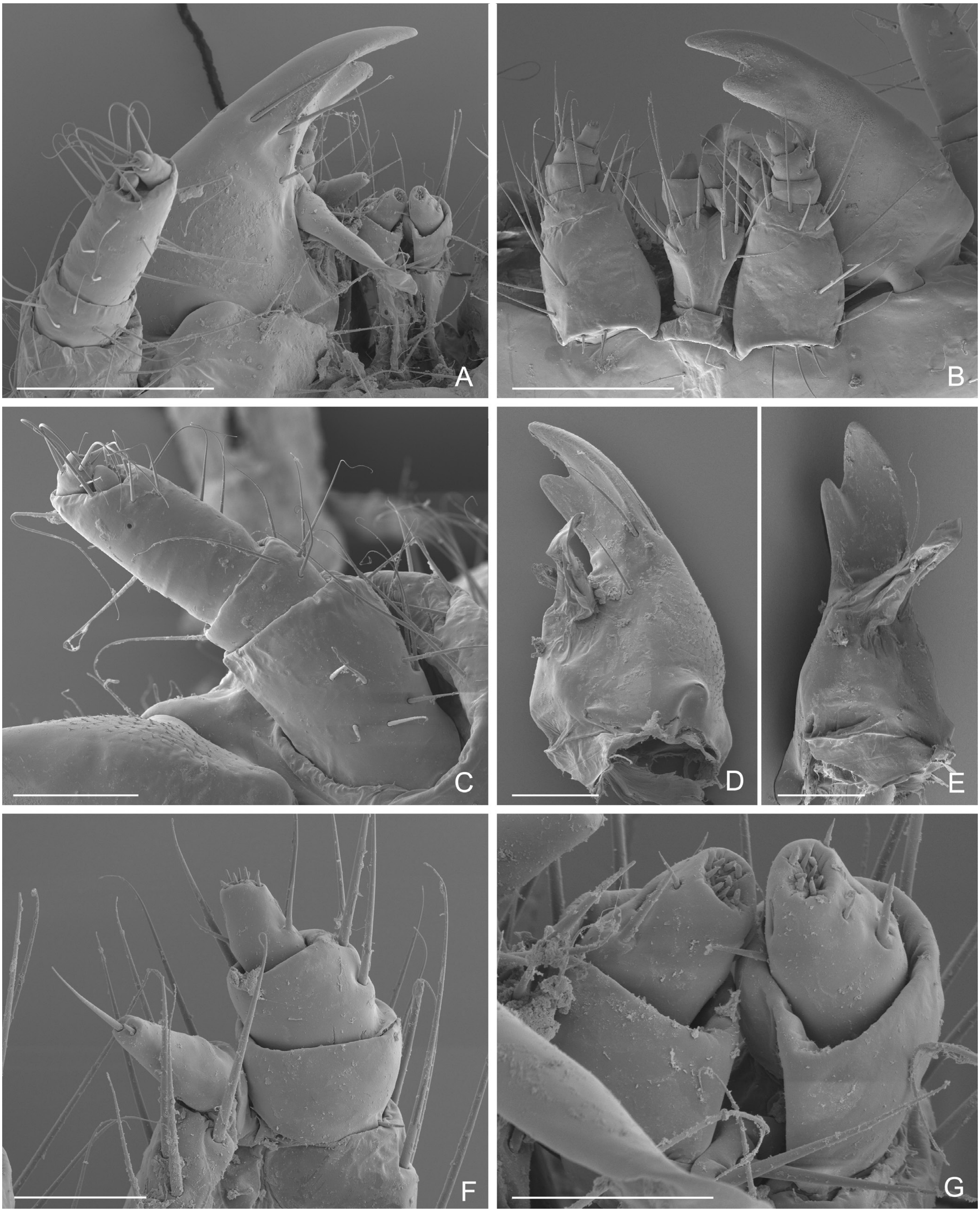

Fig. 4. A–G, *Paussus siamensis* Maruyama, 2016, third instar larva, details of head capsule imaged by SEM. A, left mandible, dorsal view; B, maxillae, prementum and left mandible, ventral view; C, left antenna, left lateral view; D, right mandible, mesodorsal view; E, right mandible ental surface; F, maxillary palp and galea of right maxilla, dorsal view; G, labial palps, dorsal view. Scale bars = 200 µm [A, B]; 100 µm [C, D, E]; 50 µm [F, G].

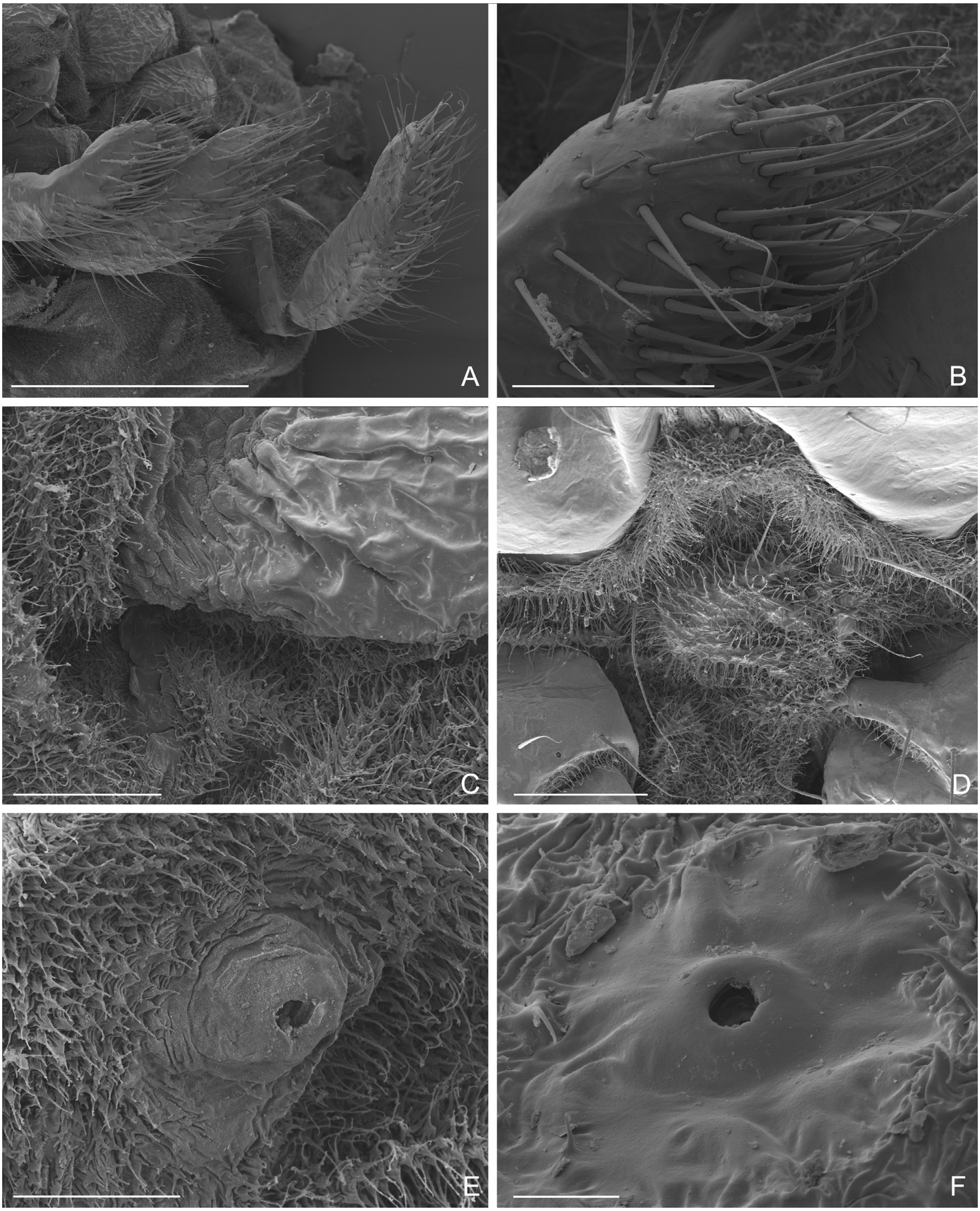

Fig. 5. A–F, *Paussus siamensis* Maruyama, 2016, third instar larva, details of thorax and abdomen imaged by SEM. A, left legs, ventrolateral view; B, apex of left prothoracic leg, anteroventral view; C, left lateral side of metanotum, showing different types of microsculpture, elongate and spiniform in membranous areas and smooth or slightly corrugated in more sclerotised areas; D, mesothoracic sternum; E, left abdominal spiracle II; F, setipherous socket on abdominal tergal side, showing a remnant of tergite III. Scale bars = 500 µm [A]; 100 µm [B, D]; 50 µm [C]; 40 µm [E]; 10 µm [F].

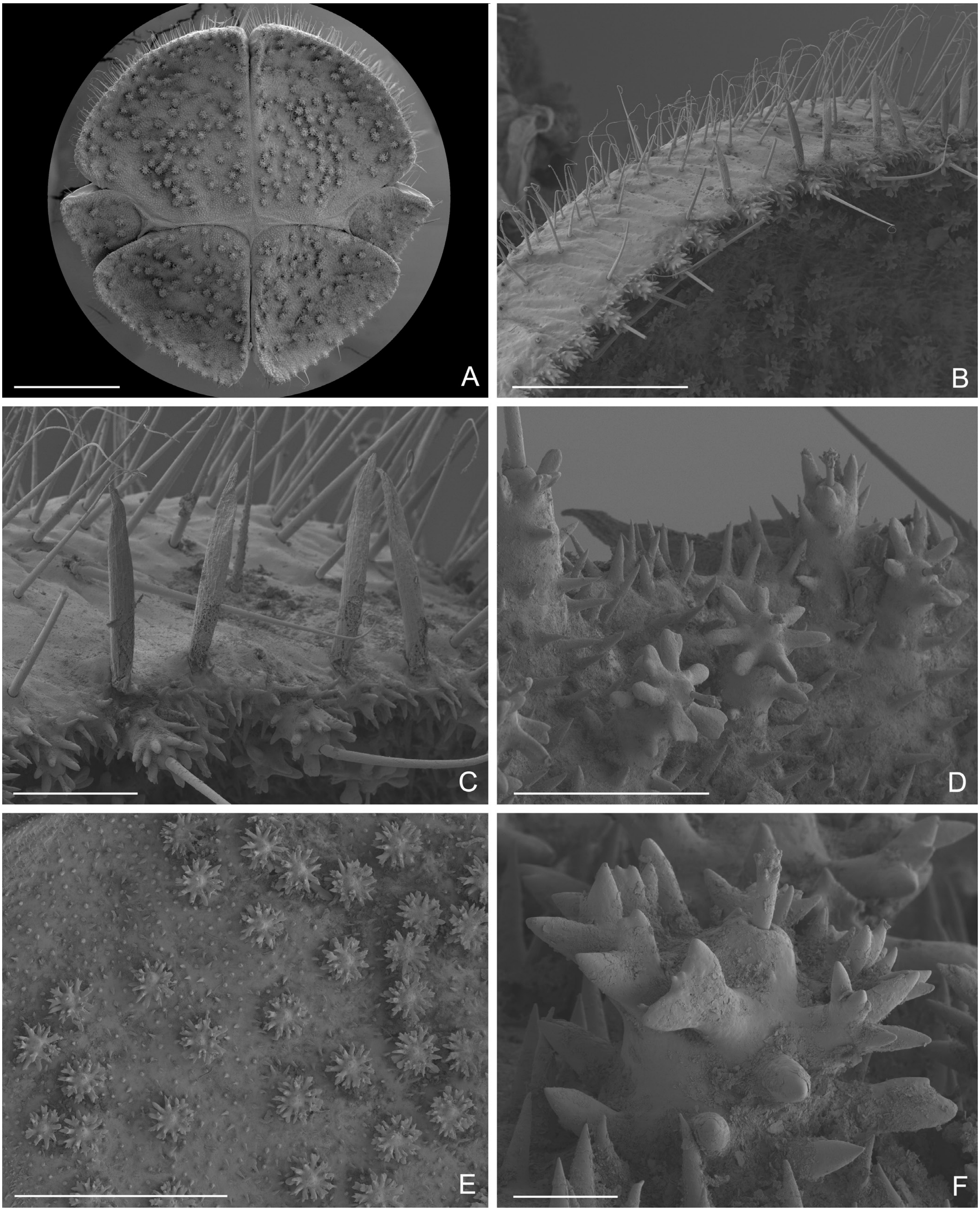

Fig. 6. A–F, *Paussus siamensis* Maruyama, 2016, third instar larva, abdominal terminal disk imaged by SEM. A, terminal disk, apical view; B, margin of left dorsal plate; C, sensilla S–II on margin of left dorsal plate; D, sensilla S–I on apex of left dorsal plate; E, sensilla S–I on medial part of left dorsal plate; F, lateral close-up of a sensillum S–I showing the multilobed crown of radial spines and spinulate surface of the plate. Scale bars = 500 µm [A]; 200 µm [B, E]; 50 µm [C, D]; 10 µm [F].

prothorax, without distinct neck region; posteroventral margin with a deep incision at the level of gular suture of parietalia (Fig. 3C). Frontoclypeolabrale (Fig. 3A) sub-hexagonal: anterior margin not sclerotised, widely emarginated medially; anterolateral margins anteriorly converging and strongly sclerotised, each as long as half anterior margin; posterolateral margins deeply concave, each slightly shorter than anterior margin; basal margin forming the mesodorsal part of the occipital margin, well-sclerotised and of about the same size as one of the anterolateral margins; surface distinctly convex posteriorly and anterolaterally, deeply concave anteromedially; transverse frontal keel absent; coronal suture absent; anterior arms of frontal suture partially obliterated (frontale fused with parietalia), basally sclerotised. Stemmata absent (Fig. 3A, B); ventral walls of parietale medially fused into a short gular suture (Fig. 3C). Antennae (Figs. 3A–C, 4C) four-jointed, forwardly directed and slightly convergent anteriorly, overreaching the apices of the mandibles, inserted in voluminous membranous, soft elevations; antennomeres I–III wide; I asymmetrical, shorter on inner side, about twice as long as II; II short, slightly wider than long; III about two times as long as II; IV shorter than II, ovoid, very small compared to the others; sensorial appendage ventrolaterally positioned on antennomere III, conical, more than half length as IV. Mandibles (Figs. 3A, 4A, B, D, E) slightly falcate, subtriangular, about 1.5 times as long as wide at base, with single, ventral cutting edge; dorsal surface deeply excavate along occlusal margin, ventral surface slightly convex; retinaculum triangular, cuneiform, sharp and pointed, anteriorly directed, displaced apically, forming, together with the pointed apex, a virtually bidentate mandible; posterior edge of retinaculum slightly convex; molar area produced into long, stiff, rather pointed, flat prostheca, with membranous margin on the occlusal side; prosthecae of mandibles crossing above the surface of prementum in resting position with closed mandibles; penicillus absent. Maxilla (Fig. 4B, F) with transversal, undivided cardo, subrectangular stipes slightly tapered to apex, three-jointed palp (first palpomere fused with stipes), one-jointed galea; lacinia absent; lateral margin of stipes distinctly curved and convex, occlusal margin straight without basal tooth; basal maxillary palpomere wider than long; medial palpomere subquadrate, slightly longer than basal; apical palpomere about as long as basal, but thinner and subulate (Fig. 4F). Galea (corresponding to galeomere II of Ozaenini, galeomere I being fused with stipes) digitiform, almost straight, distinctly tapered from base to apex. Labium (Fig. 4A, B, G) well-developed, anterior part free, posterior part lying between the cardines of the maxillae; mentum membranous, prementum ventrally sclerotised and palps two-jointed. Prementum (Fig. 4B) short, sclerotised and enlarged from base to apex in ventral view; basal half of prementum dorsally bulging and enlarged, slightly tapering apically; distal half at middle with small subapical ligula, slightly protruding. Labial palpomere I wider and longer than II (Fig. 4G); II subulate. Hypopharynx wide and bulged, tongue-like, thick, soft-skinned and densely covered by transverse parallel rows of papillae, closely fitting in the vault of the oral cavity.

Thorax. Thoracic segments slightly sclerotised; pronotum longer than other tergites (Fig. 2A, B); meso and metanotum similar in length, widely transverse with rounded lateral margins, distinctly increasing in width from pro- to metanotum (Fig. 2A); surface of tergites irregularly convex (Figs. 1C, 2A, B); longitudinal ecdysial line restricted to pronotum. Pronotum composed by a single distinct sclerite, about three times as wide as long. Mesonotum and metanotum, with tergites longitudinally subdivided into two rounded parts, separated by the bulged membranous areas. Sterna of thoracic segments unsclerotised (Fig. 2C).

Spiracles. Abdominal spiracles (Fig. 5E) extremely small, annular-uniforous, dorsolaterally positioned, partially embedded into the bulged membranous areas above the epipleurae on segments I–VIII; peritreme dome-shaped, convex and with a round hole at top; atrium poorly developed. Mesothoracic spiracles annular, similar but slightly larger than abdominal spiracles, with wider atrium. Small spiracle-like structure on metapleura (Fig. 2B) corresponding in position to mesothoracic spiracle, but without external peritreme.

Legs. Short and stout, all similar in type and length and directed upwards (Figs. 2A–C, 5A); legs two-jointed basal article representing the coxa, distally obliquely truncate; distal article cylindrical, digitiform, composed of completely fused trochanter, femur, tibia and tarsus; sutures between primary articles not visible. Procoxae slightly more slender than meso- and metacoxae. Tarsus with single, small claw (Fig. 5B), apically curved and pointed.

Abdomen. Swollen, scarcely or not sclerotised, distinctly curved in a strongly upturned position (Figs. 1C, 2B); largest width at segments IV–V, gradually narrowed anteriorly (Fig. 2A); larger thickness in lateral view at segment III, distinctly decreasing toward apex (Fig. 2B); terga flattened or slightly convex, pleura and sterna extremely thick and swollen, with multiple bulged areas in correspondence to primary sclerites. Terminal disk (Figs. 3D, 6A) regularly round, flat or slightly concave at middle, with perimeter strongly raised (Figs. 2A, 3D, E, 6B), corrugated and markedly sclerotised (Figs. 1C, 2A, 3D, E); with diameter slightly smaller than segment VII, composed of 6 symmetrical subtriangular plates (Figs. 3D, 6A), joined by thin membranous areas; dorsal plates slightly wider than others, lateral plates small; ventral plates corresponding to modified urogomphi. Pygidium ring-like, scarcely sclerotised, dorso-ventrally flattened, ventrally positioned to urogomphi (Fig. 3D).

Larval behavioural notes. *Paussus siamensis* larva (Fig. 1C) was collected together with nine adults (Fig. 1B) inside an ant nest of the myrmicine *Pheidole plagiaria* Smith, 1860. The ant nest was located inside an old, abandoned termite mound of *Macrotermes* sp., built at the bottom of a big tree (Fig. 1A). The larva was collected from a tunnel dug on soil mound, in a side wall of the ant nest.

In order to observe the host-parasite interactive behaviour, the larva was put among the alarmed ants. When the ants contacted the larva, this larva turned its body upside-down and secreted big drops of water-like transparent liquid just above the base of the hind legs (Fig. 1D). The ants showed an interest in the liquid and apparently fed on it for a few minutes (Fig. 1D). When the ants disappeared (they were busy with collecting their larvae in the destroyed nest), the liquid was absorbed back inside the larval body. The liquid was apparently not a wound exudate. The larva was not injured by the ants at all.

DISCUSSION

Compared to the amazing diversity of *Paussus* adults (Moore & Robertson, 2014), the general larval morphology, even among species belonging to very different subgenera and guests of unrelated ants, appears surprisingly stable (see discussion in Di Giulio, 2008). The *P. siamensis* larva described in this paper is not an exception, showing the general traits and habitus of the other known *Paussus* larvae. Such structural homogeneity of *Paussus* larvae, compared to the adult morphological diversity, can be attributed to different selective pressures acting on different semaphoronts of the same *Paussus* species. The peculiar characters at the level of mandibles, abdomen and terminal disk shown by the larva of *P. favieri* (Di Giulio et al., 2011), the single first instar larva described in *Paussus*, could be instar-related and widespread in all first instar larvae of *Paussus* (A. Di Giulio, pers. obs.), indicating the possibility of a larval polymorphism in this genus (i.e., first vs. later instars).

However, at a finer scale (especially by using SEM microscopy), differences in chaetotaxy, microsculpture, relative dimensions of head, mouthparts and terminal disk can be observed, even comparing larvae of the same instar. Interestingly, we found that *P. siamensis* larva closely mirrors the fine structural characters of *P.* (*Semipaussus*) *kannegieteri* larva from Java (recently redescribed and illustrated by using SEM by Di Giulio, 2008), another Indo-Malayan species guest of the same ant, *Pheidole plagiaria*. In particular, it is worth noting that the sensilla S–I of the terminal disk, usually very variable and used as diagnostic characters in Paussinae larvae (see Di Giulio, 1999), are almost identical in the two species. The close similarity of these larvae, despite their markedly different adult morphology (Moore & Robertson, 2014), represents an evidence of their close relationships, and it is in agreement with the recent placement of both species in the subgenus *Scaphipaussus* Fowler (Robertson & Moore, 2016), based on combined morphological and molecular data. The possibility of an Indo-Malayan morphological radiation of *Paussus*, similar to the Malagasy radiation (Robertson & Moore, 2014) seems likely.

In the past, it was questioned that the regressive, physogastric, short-legged larvae of Paussini were able to dig holes in the ground; additionally, their round terminal disk was considered more as a glandular symphilic organ than a phragmotic organ, possibly producing substances involved in the symbiotic interaction (Oberprieler, 1985; Bousquet, 1986; Luna de Carvalho, 1989, 1992; Di Giulio & Moore, 2004; Di Giulio, 2008; Di Giulio et al., 2011). For these reasons, it is of particular interest that the larva of *Paussus siamensis* was found in a self-dug tunnel inside the nest of its host ant *Pheidole plagiaria.* We can hypothesise that *Paussus* larvae spend their life in the brood chambers of the nest, attended by the ants, digging holes in the nest just before moulting or pupating. Though we cannot exclude a burrow-trapping strategy, it is likely that these larvae feed outside burrows, preying upon ant immatures, or being fed by the ants through trophallaxis (Di Giulio, 2008; Di Giulio et al., 2011).

Another behaviour performed by the larva of *P. siamensis* when it was extracted from its burrow and put among the ants is also remarkable: the larva secreted big drops of water-like transparent liquid from the base of the hind legs when touched by the ants; the ants were seen feeding on it for a few minutes. It is well known that adult Paussini, like most myrmecophilous beetles, show the presence of peculiar glandular organs on different parts of the body (especially on antennae, pronotum and pygidium), composed of trichomes (tufts of hairs) connected to exocrine glands for the release of chemicals secretions (Di Giulio et al., 2009). These secretions, of still unknown composition, have a strongly attractive (and possibly appeasing) effect on the ants, and seem to be the main strategy for the beetles to get into the nest and successfully parasitise the ants (Maurizi et al., 2012). However, a similar behaviour was never observed before in a paussine larva. The secretion of this big amount of liquid from inside the body of the *P. siamensis* larva, and the subsequent reabsorption, deserves some more in-depth analyses in the future. In fact, it is not clear (1) the nature of the liquid and its possible way of production and storage inside the body; (2) the opening from where it could be emitted (and likely reabsorbed); (3) the reason why it remains attached to the larval body instead of sliding away. Concerning the first issue, no anatomical study on these larvae is available at the level of the thorax and abdomen; however, no remnants of epidermal glands or cuticular reservoirs have ever been observed in slide-mounted larvae (A. Di Giulio, pers. obs.). One possibility is that the liquid observed represents just a drop of hemolymph, squeezed out from the body due to its contraction. In fact, in Fig. 1D, it is possible to observe the peculiar contracted position of the larva supplying the exudate to the *Pheidole plagiaria* worker. Concerning the pore of emission, it is worth to remember that larvae of the Paussini genera *Platyrhopalopsis* and *Paussus* (Di Giulio, 2008; Di Giulio et al., 2003, 2011), but not *Arthropterus* (Di Giulio & Moore, 2004), share the unique presence of a pleural spiracle-like unusual structure on metathorax, homologous in position to the mesothoracic spiracle, but without external peritreme. This opening is clearly connected to a duct with taenidial annulations. Functional metathoracic spiracles are primarily absent in larvae of Coleoptera and it is unclear if this duct, lacking an atrium, is connected to the tracheal system (Di Giulio, 2008). The ultrastructure and connections of this tubular structure need further investigations but could be a good candidate to perform the excretion of the liquid. Regarding the way the clear drop of substance remains attached to the larval body, the strongly multispinulate microsculpture characterised by extremely dense and elongate sculpticells (see Fig. 5C–E), atypical for a membranous larval microsculpture, could play an important role in this respect.

The present work, based on a single mature larval specimen, outlines the importance of any field observation and documentation to the knowledge of morphology and behaviour of incredibly rare and elusive species living in concealed environments like an ant nest.

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