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The first-instar larva of the genus *Arthropterus* (Coleoptera: Carabidae: Paussinae): implications for evolution of myrmecophily and phylogenetic relationships within the subfamily

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Abstract. The first-instar larva of the genus *Arthropterus* W.S. MacLeay, 1838 is described and illustrated. This is the first description of a newly hatched (first-instar) larva in the myrmecophilous tribe Paussini and the first known larva from a basal paussine lineage. A phylogenetic analysis of the subfamily based on larval characters confirms the placement of the genus *Arthropterus* as a sister-group of the remaining Paussini and supports the hypothesis that Metriini is the sister-group of Ozaenini+Paussini, with 'Ozaenini' as a paraphyletic group. Within this phylogenetic framework, we reassess which larval characters are diagnostic of the tribes Paussini and Ozaenini. Several larval features of *Arthropterus*, such as the riddled sensilla S-VIII and the fused terminal disk, are interpreted as adaptations to myrmecophily. This interpretation supports the hypothesis that larvae have played an important role in the evolution of myrmecophily within the subfamily Paussinae.

Introduction

The carabid subfamily Paussinae contains ~750 described species classified in 39 genera and four tribes: Paussini, Protopaussini, Ozaenini and Metriini. Adults and larvae of Paussinae exhibit varying degrees of association with ants. Although the natural history of most species is not well known, the external morphology of both larvae and adults can provide clues about their behaviour. Based on external morphology of adults and known larvae as well as some field observations, members of the tribes Paussini and Protopaussini, and the ozaenine genus *Physeia* Brullé, 1834, are thought to be myrmecophilous (obligate guests of ants) during at least one phase of their life history, whereas other ozaenines and metriines are thought to be free-living predators of other arthropods.

Larvae of Paussinae are known for only 21 species in 8 genera and 3 tribes (see Table 1). All known larvae share an unusual and unique trait, regardless of their degree of association with ants: the ninth abdominal segment is enlarged and fused with the tergum of the eighth segment. This fusion displaces the urogomphi and the tenth segment into a vertical plane, forming a rounded plate (the so-called anal plate, anal disk, terminal disk, or trichome disk). This feature is an undisputed apomorphy of the subfamily (Bousquet 1986). The terminal disk is used to trap prey in predaceous non-myrmecophilous larvae (Costa *et al.* 1988; Di Giulio and Vigna Taglianti 2001) and as a symphyllic

organ in myrmecophilous larvae (Oberprieler 1985; Bousquet 1986; Luna de Carvalho 1989).

Within the tribe Paussini, larvae from only two of the eight subtribes, Paussina and Platyrhopalina, are known with certainty (see Table 1). The generic and specific identifications of the larvae in the following larval descriptions are too speculative to be acknowledged: (1) the larva attributed to *Heteropaussus dohrni* (Ritsema, 1875), inadequately described by Wasmann (1918, sub *Pleuropterus*) (the location of this specimen is unknown); and (2) the larva attributed to *Heteropaussus* sp. described by Brauns (1914) and later considered a *Pentaplatarthrus* sp. by van Emden (1922). Therefore, we consider the larvae of the subtribes Pentaplatarthrina and Heteropaussina to be unknown.

In this paper, we describe the first-instar larva of a species in the genus *Arthropterus* W.S. MacLeay, 1838. *Arthropterus* comprises 66 species (Lorenz 1998) distributed in Australia, New Guinea and New Caledonia. This genus is classified in the subtribe Cerapterina, which is considered to be one of the most basal lineages of Paussini (Darlington 1950). *Arthropterus* adults show few adaptations to myrmecophily. Like most other Cerapterina, they lack trichomes and have typical predator-type mouthparts, rather than the reduced and highly modified mouthparts of the more derived paussines, which are known to be myrmecophilous as adults. In addition, *Arthropterus* adults rarely occur with ants (Darlington 1950) and can be collected under the bark

of eucalyptus trees (Luna de Carvalho 1973). For these reasons, Darlington (1950) hypothesised that species of *Arthropterus* might be myrmecophilous as larvae and that adults enter ant nests only to lay eggs.

The following description of the *Arthropterus* larva provides characters that allow us to refine the list of diagnostic features of Paussini and Ozaenini. In addition, this larva represents the first newly hatched (first-instar) larva known for the tribe Paussini, and therefore it allows us to directly compare first-instar larvae among the tribes Paussini, Ozaenini and Metriini (see Table 1).

Previous phylogenies of the subfamily based on larval characters differ with respect to tribal relationships (Beutel 1992, Vigna Taglianti *et al.* 1998, Di Giulio *et al.* 2003). Three hypotheses have been proposed: (1) Metriini as the sister-group of Ozaenini+Paussini, with Ozaenini as a paraphyletic group and the genus *Physeia* as the sister-group of Paussini (Beutel 1992); (2) Metriini as the sister-group only of the monophyletic Ozaenini, with the Paussini as the sister-group of Metriini+Ozaenini (Vigna Taglianti *et al.* 1998); and (3) Metriini as the sister-group of Ozaenini+Paussini, with Ozaenini as a paraphyletic group and the genus *Physeia* as the sister-group of Paussini, *Pachyteles* Perty, 1830 as sister-group to *Physeia*+Paussini and *Sphaerostylus* Chaudoir, 1848+ *Itamus* Schmidt-Goebel, 1846 forming a basal ozaenine clade (Di Giulio *et al.* 2003). The most recent phylogenetic analysis (Di Giulio *et al.* 2003) showed that most larval characters are morphoclines, resulting in an almost completely pectinate cladogram, where *Metrius* Eschscholtz, 1829 is the sister to all other Paussinae, and Paussini are a highly derived clade within an ozaenine grade. In the current study, we have added *Arthropterus* to this matrix and run a new cladistic analysis in order to infer the phylogenetic position of the genus and reassess larval character state evolution with the Paussinae.

Materials and methods

Specimens were mounted on slides with Canada balsam and were drawn using a Leitz Laborlux S microscope (Wetzlar, Germany) equipped with a drawing tube. Specimens were mounted on stubs, dried, sputtered with gold, and then photographed with a Philips XL30 scanning electron microscope (Eindhoven, The Netherlands) (L.I.M.E. laboratory, University 'Roma Tre', Rome, Italy). For general terminology of larval structures we refer to Lawrence (1991). Notation of primary setae and pores follows the system of Bousquet and Goulet (1984), modified for *Metrius contractus* Eschscholtz, 1829 (Bousquet 1986). Only setae additional to primary setae (as recognised by Bousquet and Goulet 1984) have been mentioned. As some of the sensilla of *Arthropterus* present on the abdomen and terminal disk are homologous to those recognised by Bousquet (1986) in *Metrius contractus* (sensilla S-I to S-V) and by Di Giulio *et al.* (2000) in *Pachyteles* spp. (sensilla S-I to S-VII), we adopted the same nomenclature used by these authors. Notations for microsculpture and urogomphal lobes follow those proposed by Bousquet (1986) for *Metrius contractus* and later modified by Vigna Taglianti *et al.* (1998) for the Ozaenini. An asterisk (*) following a coded seta or urogomphal lobe indicates that the homology between the structure on the *Arthropterus* larva and the corresponding code is questionable.

Larvae and species examined are indicated in Table 1 with the superscript letter E.

Definitions and terminology

Nasale. Attempts to identify and find homologies between characters of the 'nasale' among paussine larvae is problematic and has been the object of discussions for the past ten years (see Di Giulio *et al.* 2003 for a review). A four-toothed nasale homologous to that of other adepagan larvae is present only in *Metrius*, being variously modified or reduced in the other paussine taxa. Because a phylogenetic significance is commonly attributed to this structure, we have avoided using this term. Instead, we describe the anterior margin of frontoclypeolabrale.

Sensilla. Two unusual sensilla are present in the first-instar larva of *Arthropterus*: a peculiar form of sensilla S-I and a new type of sensilla, 'sensilla S-VIII.' These two types of sensilla are described below.

Sensilla S-I (Figs 23–24). Sensilla S-I are variously shaped in larvae of Paussinae (Bousquet 1986; Di Giulio *et al.* 2000; Di Giulio *et al.* 2003) and generally present exclusively on the surface of the terminal disk (in *Metrius* also on sternites). In *Arthropterus*, they are miniaturised (~10 µm), not 'rosette-like' as in *Metrius* or *Pachyteles* nor inflated as in *Physeia* and *Platyrhopalopsis* Desneux, 1905, and are composed of a short simple coniform base (1–3 µm) and a longer (~2 µm wide and 5–8 µm long), whitish, stick-like, blunt-tipped seta.

Sensilla S-VIII (Figs 26–27). Sensilla S-VIII are extremely long and thick setae, clavate to match-like, on dorsal and lateral surface of head and thorax, on sternum VIII and on the perimeter of the terminal disk (including urogomphi). Composed of a long cylindrical to slightly fusiform stem, straight or slightly curved, basally tapered and inserted in a hollow cuticular base; with a distally inflated apex, rounded and variously shaped. Entire surface longitudinally keeled (6–8 slightly protruding carinae) and riddled with holes, giving them a spongy appearance (Fig. 26). The sensilla S-VIII on the head and thorax are riddled with holes only on their dorsal surface, while their ventral surface is smooth (Fig. 27). The surface is always covered by a particulate whitish substance. Sensilla S-VIII are known only from *Arthropterus* and replace the sensilla chaetica S-II along the perimeter of the terminal disk or typical sensilla chaetica on head and thorax in other Paussinae.

Taxonomic treatment

Order **COLEOPTERA** Linnaeus

Family **CARABIDAE** Latreille

Subfamily **PAUSSINAE** Latreille

Tribe **PAUSSINI** Latreille

Subtribe **CERAPTERINA** Darlington

Genus *Arthropterus* W.S. MacLeay

Material examined

The description of the first-instar larva of *Arthropterus* sp. is based on nine specimens reared in the laboratory from eggs. Adults were

Table 1. Higher classification of the Paussinae and the taxonomic positions of described larvae

Higher classification	Species with described larvae	Specimens	Larval habitat	Locality	Reference
Metriini					
<i>Metrius</i>	<i>Metrius contractus</i> ^E	About 50 L ₁	Unknown: larvae reared from adults	USA, California, Lagunitas Creek nr. Tocaloma	Bousquet 1986
	<i>Metrius contractus</i> ^E	2 L ₃	Inside rotten logs	USA, California, Mill Valley	Beutel 1992
‘Ozaenini’					
Mystropomina	Unknown				
Ozaenina					
<i>Itamus</i>	<i>Itamus cavicola</i> ^E	2 L ₃	In cave, walking on bat guano	PAPUA NEW GUINEA, New Ireland, Kabase cave	Vigna Taglianti <i>et al.</i> 1998
<i>Sphaerostylus</i>	<i>Sphaerostylus luteus</i>	2 L ₂ or L ₃	Galleries in rotten wood	IVORY COAST, Costa do Marfim	Paulian 1947
<i>Pachyteles</i>	<i>Pachyteles</i> sp.	1 L ₂ or L ₃	Under bark of rotten wood	GUATEMALA, Primavera	van Emden 1942
	<i>Pachyteles</i> sp.	4 L ₂ or L ₃	In galleries dug in rotten wood and river banks	BRAZIL, S.Paulo: Peruipe e Saléspolis	Costa <i>et al.</i> 1988
	<i>Pachyteles mexicanus</i> ^E	1 L ₂ , 1 L ₃	In cave, walking on bat guano	MEXICO, Tamaulipas, Grutas de quintero	Vigna Taglianti <i>et al.</i> 1998
	<i>Pachyteles vignai</i> ^E	3 L ₁ , 2 L ₂ , 5 L ₃ and exuviae	Galleries in sand along stream bank	ECUADOR, Cotopaxi, S. Francisco de las Pampas	Di Giulio 1999
	<i>Pachyteles digiulioi</i> ^E	1 L ₂ and 13 L ₃	Galleries in sand along stream bank	ECUADOR, Cotopaxi, Otonga forest	Di Giulio 1999
	<i>Pachyteles</i> sp. ^E	1 L ₃	Inside rotten wood near a small river	ECUADOR, Sucumbios, El Higuérón	Undescribed
<i>Physeia</i>	<i>Physeia setosa</i> ^E	4 L ₃	In nests of <i>Atta sexdens</i> , in self-dug holes near the ‘mushroom chambers’	BRAZIL, Estado do Rio, Mendes	van Emden 1936; Di Giulio <i>et al.</i> 2003
Protopaussini	Unknown				
Paussini					
Cerapterina					
<i>Arthropterus</i>	<i>Arthropterus</i> sp. ^E	9	Unknown: larvae reared from adults	AUSTRALIA, Victoria, Robinvale	This study
Pentaplatarthrina	Unknown				
Homopterina	Unknown				
Heteropaussina	Unknown				
Platyrhopalina					
<i>Platyrhopalopsis</i>	<i>Platyrhopalopsis mellei</i> ^E	8	At 30 cm under ground inside an abandoned ant’s nest	INDIA, Kerala, Periyar Lake, 950 m	Luna de Carvalho 1977; Di Giulio <i>et al.</i> 2003
Ceratoderina	Unknown				
Paussina					
<i>Paussus</i>	<i>Paussus cultratus</i>	1	At the base of a nest of <i>Trinervitermes</i> sp., but together with <i>Pheidole</i> sp.	MOZAMBIQUE, Bengo (Gondola)	Luna de Carvalho 1992
	<i>Paussus cucullatus</i>	? (some)	At the base of a nest of termites, under stones, together with <i>Pheidole</i> sp.	ANGOLA, Dundo	Luna de Carvalho 1959
	<i>Paussus curtisi</i>	3	At the base of a nest of <i>Trinervitermes</i> sp., but together with <i>Pheidole</i> sp.	MOZAMBIQUE, Bengo (Gondola)	Luna de Carvalho 1951
	<i>Paussus horni</i>	1	With host ant: <i>Pheidole spathifera yerburi</i>	SRI LANKA, Bandarawella	Wasmann 1910
	<i>Paussus granulatus</i>	7	With host ant: <i>Pheidole punctulata</i>	SOUTH AFRICA, Pietermaritzburg	van Emden 1922
	<i>Paussus</i> aff. <i>distinguendus</i>	2 L ₂ , 12 L ₃	?	BURUNDI, Kayanza	Arndt and Beutel 1995
	<i>Paussus afzelii</i>	2 L ₃	?	BURUNDI, Kayanza	Arndt and Beutel 1995
	<i>Paussus kannegieteri</i> ^E	5 L ₃	With host ant: <i>Pheidole plagiaria</i> (?)	INDONESIA, Java, Pangerango	Böving 1907
	<i>Paussus cridaea</i>	? (some)	With host ant: <i>Pheidole megacephala</i>	ANGOLA, Dundo	Luna de Carvalho 1959
Larvae of uncertain identity					
	<i>Heteropaussus</i> sp. or <i>Pentaplatarthrus</i> sp.	1	In nests of <i>Myrmecaria eumenoides</i>	ZIMBABWE, Bulawayo	Brauns 1914; van Emden 1922
	<i>Heteropaussus dohrni</i>	1	In nests of <i>Myrmecaria eumenoides</i>	CAMEROON, Colónia Alemã dos Camarões, tra 730 e 800 m	Wasmann 1918

^ESamples directly examined by the authors.

collected in Australia (Robinvale, Victoria) by T. A. Weir, M. Hansen and J. F. Lawrence between 25 October and 3 November 1988. Larvae emerged 22 December 1988. Adults were collected in apparent association with a large ant, *Camponotus* Mayr, 1861 (J. F. Lawrence, personal communication). The larvae, preserved in 70% ethanol, are deposited in the Australian National Insect Collection (CSIRO) in Canberra, Australia.

Diagnosis

The first-instar larva of *Arthropterus* has some unique structural features that, as far as we know, can be considered autapomorphies of this genus: presence of a highly modified lacinia (Figs 7, 12a–12b) with a longitudinal row of hook-like setae; modified antennomere IV (Figs 5, 13a–13b) with an unusual stick-like sensory structure (Fig. 13b, arrow), very large and modified tarsal claws (Figs 19, 25); terminal disk biconvex (Fig. 1); sensilla S-I (Fig. 24) with extremely small base; and presence of extremely modified setae of a new type (sensilla S-VIII) around the terminal disk (Figs 2, 16–17, 20, 26) and on the head and thorax (Figs 10, 18, 27).

Description

Measurements

Body length ~2.2 mm (from tip of mandibles to the terminal disk); cephalic capsule maximum width (at the base of the antennae) 0.56 mm, medial length (from occipital foramen to anterior margin of frontoclypeolabrum) 0.34 mm; prothorax maximum width 0.76 mm, maximum length (along ecdysial suture) 0.32 mm; diameter of terminal disk 0.88 mm.

Habitus and coloration

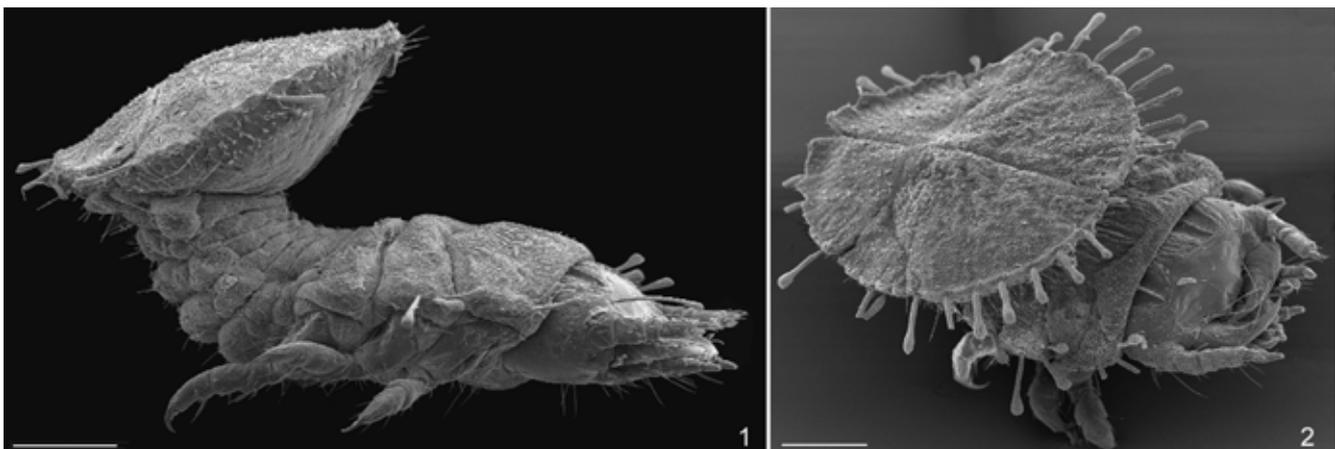
Body soft, weakly sclerotised, not physogastric. Terminal disk (Figs 1, 2, 16–17, 20) wide, rounded, biconvex, held in elevated position by short, flattened, bellows-like abdomen. Colour yellowish-white; distal half of mandibles, egg-bursters and claws thickly sclerotised and reddish brown.

Microsculpture

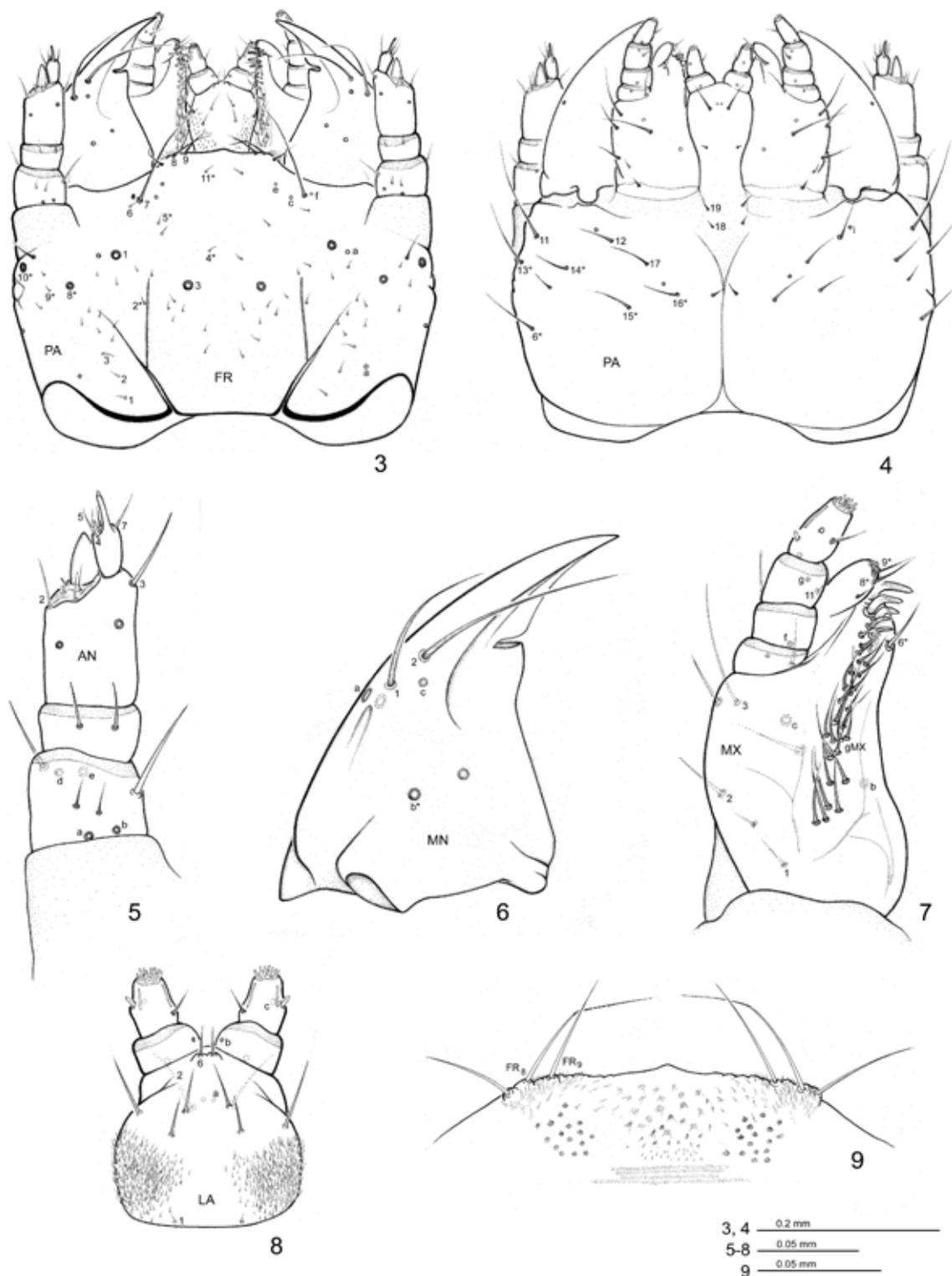
Sclerotised parts of body (e.g. apical part of cephalic capsule, mouthparts, thoracic and abdominal sclerites, pygidium) without or with only sparse, pointed microsculpture. Antennae, basal half of mandibles, basal part of cephalic capsule and legs with irregularly reticulate to scale-like (mostly on antennae) rugulose microsculpture (Figs 13, 15). Epipharynx (Fig. 9) and basal third of prementum (Fig. 8) dorsally with pointed or multi-pointed microsculpture, laterally with thin elongate sculpticells. Membranous areas of body rugulose to rugose, with pointed or papillate sculpticells (see on pronotum, Figs 10–11, 14). Distal half of claw with longitudinally corrugated microsculpture (Fig. 25). Surface of terminal disk with coarsely pustulate to granulate microsculpture (Figs 22–23), composed of blunt-tipped sculpticells (average diameter 1–5 μm , see Fig. 24). Pygidium smooth (Fig. 21).

Chaetotaxy

Frontale (Figs 3, 10–11) with ~14 small additional setae posterior to FR₃, between the egg-bursters; three pairs of small additional setae slightly posterior to FR₁; FR₁ and FR₃ of type S-VIII, anteriorly directed, about as long as the antenna; FR₂* small, slightly external and close to the egg-burster; FR₄* small, medial to frontal area; FR₅* small, internal and slightly posterior to FR₇; FR₆ small, slightly external and posterior to FR₇; FR₇ extremely long and thin, convergent anteriorly; FR₈ and FR₉ moderately long, inward directed, inserted at the anterior corners of the median prominence; one additional, moderately long seta close to FR₈, bent laterally; pores FR_b and FR_d absent; FR₁₁* small, medial to frontoclypeolabrum; FR₁₀ absent. Parietale (Figs 3–4) with group of six additional setae dorsally, between PA₈* and PA₃, possibly including setae PA₄, PA₅ and PA₇; 2 small additional setae dorsolaterally, slightly external to PA₈*; PA₆* ventrolateral; PA₉* small; PA₈* and PA₁₀* of



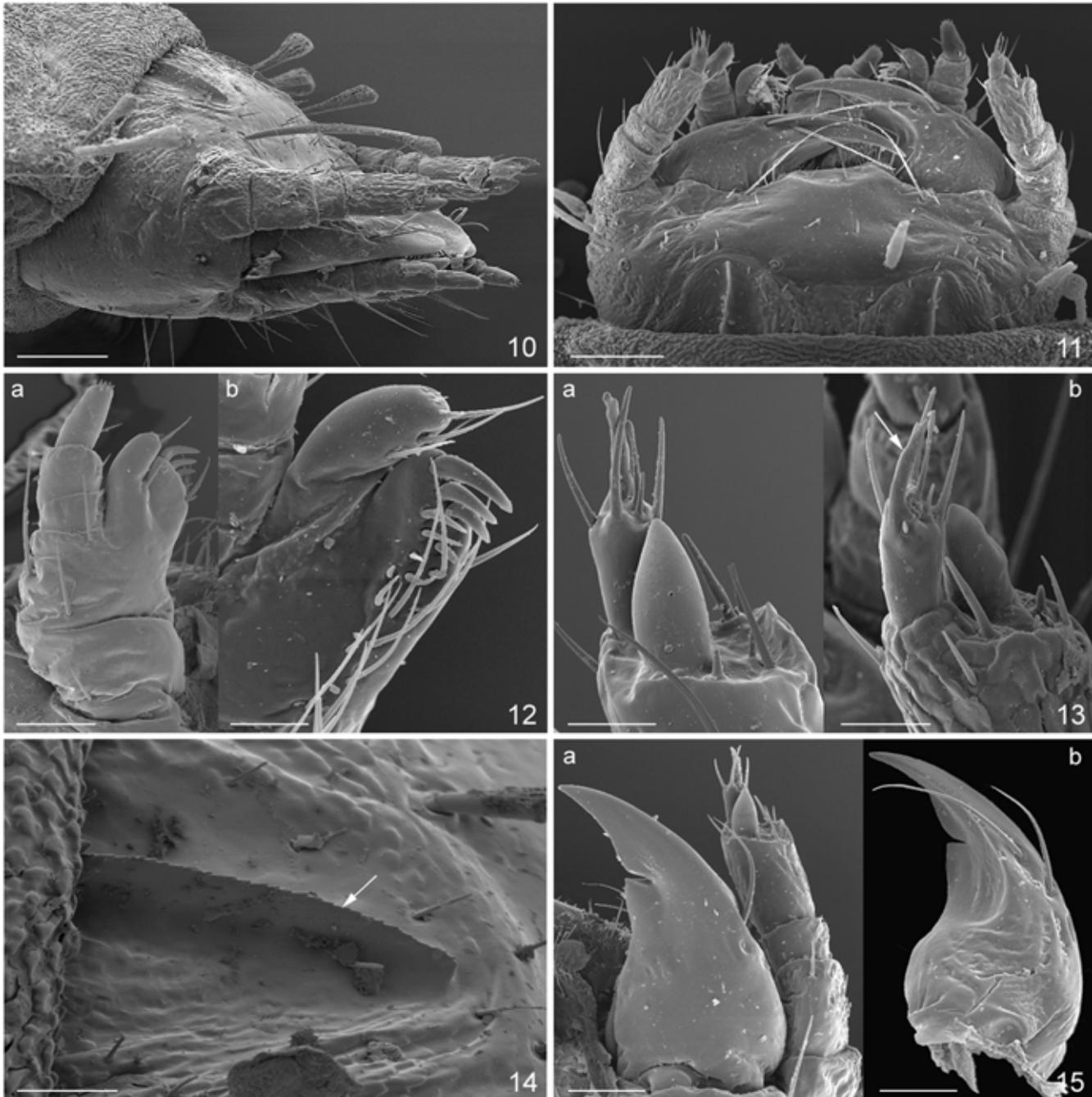
Figs 1, 2. Habitus of *Arthropterus* sp. first-instar larva: 1, lateral view (scale bar: 500 μm); 2, dorsolateral view (scale bar: 200 μm).



Figs 3–9. *Arthropterus* sp. first-instar larva: 3, head, dorsal view (only the bases of sensilla S–VIII are drawn); 4, head, ventral view; 5, left antenna, dorsal view; 6, left mandible, dorsal view; 7, left maxilla, dorsal view; 8, labium, dorsal view; 9, epipharynx.

type S-VIII. Antennomere I (Fig. 5) with four additional setae, two long (one medial and one ventrolateral) and two small (dorsolateral); II with two additional dorsal setae; III with four setae (two additional setae dorsolaterally), seta AN_1 absent; two small sensilla basiconica near sensorial appendage (Figs 13a–13b); IV with apex modified into an unusual

stick-like elongate protuberance (Fig. 13b, arrow) with possible sensory function, slightly shorter than article IV; four apical setae and one long basiconic sensillum on antennomere IV. Mandible (Figs 6, 15a–15b) without additional setae; MN_1 and MN_2 long, bent inward; MN_c^* between MN_1^* and MN_2^* , one additional pore ventrolater-



Figs 10–15. *Arthropterus* sp. first-instar larva: 10, head, right lateral view (scale bar: 100 μ m); 11, head, dorsal view (scale bar: 100 μ m); 12, (a) right maxilla, ventral view (scale bar: 50 μ m); (b) left galea and lacinia, dorsal view (scale bar: 20 μ m); 13, (a) apex of left antenna, ventral view (scale bar: 20 μ m); (b) apex of right antenna, dorsal view (scale bar: 20 μ m), the arrow indicates the stick-like sensorial protuberance; 14, right egg burster (arrow) (scale bar: 25 μ m); 15, (a) left mandible and antenna, ventral view (scale bar: 50 μ m); (b) right mandible, dorsal view (scale bar: 50 μ m).

ally. Setal group gMX (Figs 7, 12*b*) on stipes composed of 25 setae along occlusal margin; few additional setae (~6) on ventral side of stipes (Figs 7, 12*a*); maxillary palpomeres III–IV with one small seta along the occlusal margin; IV with one blunt-tipped basiconic sensillum on outer side and apical sensorial area composed of ~10 blunt tipped papillae (basiconic sensilla) and two longitudinal, dorsolateral, digitiform sensilla; galeomere I (Figs 7, 12*a*–12*b*) ventrally fused to the stipes, with one ventral seta (MX₇); three setae along occlusal margin of galeomere II; apical sensorial area on galeomere II, composed of 5–6 blunt tipped papillae (basiconic sensilla). Lacinia (Figs 7, 12*b*) with 7–8 stout, inwardly directed, hook-like setae along the occlusal edge, increasing in size from the basal to the apical seta; the three apical very large and pointed at tip, with longitudinally corrugated microsculpture; few other setae present at base, probably belonging to the gMX group. Prementum (Fig. 8) with six setae not inserted in protuberances, four dorsal and two lateral; LA₆ small; labial palpomere II (Fig. 8) with one additional seta on inner side, one blunt-tipped basiconic sensillum on outer side and two longitudinal digitiform sensilla, one dorsal and one lateral at the occlusal side; apical sensorial area of labial palpomere II composed of ~10 blunt-tipped papillae (basiconic sensilla). Pro-, meso- and metanotum (Figs 1, 2, 18) with many extremely small and truncate setae medially on discal area, on pronotum also along anterior margin; clusters of three long sensilla S-VIII present at each side of pro- and mesonotum, two on metanotum, bent outwards (Fig. 18). Trochanter (Fig. 19) with some spiniform and moderately long setae present distally on ventral side, including TR₄*; TR₈* about as long as TR₄* but thinner. Prosternum with 8–10 additional setae; pro-, meso- and metasternum with a lateral seta (MS₃*) much longer than the others. Abdominal tergites I–VII (Fig. 16) with 14–18 small setae. Tergal side of dorsal and lateral plates of terminal disk (Fig. 16) with many spinulate setae S-VII* (without protruded cylindrical base) of various sizes (distal setae very long), mostly concentrated on the posterior fourth; ventral plates (urogomphi) each with ~50 short spinulate setae S-III* and S-IV* on ventral side (Figs 21–22); perimeter of the disk (margin of dorsal, lateral and ventral plates) with 36–37 long sensilla S-VIII of various lengths (Figs 2, 16–17, 20), regularly spaced and radially projecting, in the same plane as the surface of terminal disk: 9–10 on each dorsal plate, four on each lateral plate and five on each ventral plate (urogomphus); surface of the terminal disk with many small sensilla S-I (Figs 23–24), regularly spaced: ~200 on dorsal plates, ~50 on lateral plates and ~150 on ventral plates (urogomphi). Epipleurites (Figs 16–17) and sternites (Fig. 17) with setae and spinulate sensilla S-II* of various lengths, those of epipleurites VII very long; epipleurites of abdominal segment I with one or two additional setae; epipleurites of abdominal segments II–VII with 2–5 additional setae. Outer sternites without additional setae; sternal area (including

anterior, inner and median sternites) with 18–20 setae on each abdominal segment (I–VIII); median sternite of segment VIII with two long sensilla S-VIII medially on posterior margin. Pygidium without setae (Fig. 21).

Head

Cephalic capsule (Figs 3–4, 10–11) strongly transverse (about two times as wide as long), prognathous, slightly rounded laterally, with maximum width at base of the antennae; base of cephalic capsule cylindrical, extremely convex dorsally, partially retracted into prothorax, without distinct neck region. Frontale widely extended to posterior margin of cephalic capsule; coronal suture absent; frontal sclerite convex posteriorly, steeply sloping anteriorly towards frontoclypeolabral prominence. Frontal sutures almost completely obliterated (vestigial basally); frontale fused with parietalia. Egg-bursters (Figs 3, 10–11, 14) blade-like, with serrate edge, consisting of two parallel, widely separated longitudinal keels. Anterior margin of frontoclypeolabrum (Figs 3, 9, 11) medially produced into a wide subrectangular prominence, poorly sclerotised, sloping anteriorly and partially covering prepharyngeal opening; transverse frontal keel absent. Parietale (Figs 3–4, 10) without distinct stemmata, but folded at the level of the stemmata; ventral walls of parietale medially fused into a complete single gular suture (Fig. 4). Antennae (Figs 5, 10–11, 13*a*–13*b*) 4-jointed, forwardly directed, inserted in voluminous membranous elevations; antennomeres I–III wide, slightly flattened laterally; I about twice as long as II; III about three times as long as II; II and IV subequal; IV very small compared to the others; sensorial appendage (Fig. 13*a*) ventrally positioned on antennomere III, conical, of about same length as IV; IV with apex (Fig. 13*b*) modified into a stick-like elongate protuberance (see above in ‘Chaetotaxy’ paragraph). Mandibles (Figs 6, 15*a*–15*b*) slightly falcate, subtriangular, 1.5 times as long as wide at base, with single, ventral cutting edge; dorsal surface (Fig. 15*b*) deeply excavate along occlusal margin, ventral surface (Fig. 15*a*) almost flat; apex and retinaculum sharp and pointed; retinaculum triangular, cuneiform, with apex forwardly directed; posterior edge of retinaculum slightly convex, forming together with expanded cutting edge a unique, sharp incisor area; anterior edge of retinaculum well separated from cutting edge by a deep sulcus; molar area ventrally furrowed; penicillus absent. Maxilla (Figs 7, 12*a*–12*b*) with undivided cardo, subrectangular stipes, 4-jointed palp, 2-jointed galea and 1-jointed lacinia. Dorsal surface of stipes slightly concave basally, without basal tooth; lateral margin of stipes distinctly curved, occlusal margin almost straight. Maxillary palpomeres gradually increase in length from I to IV; IV distinctly longer. Galeomere I ventrally fused with stipes and with II, the latter digitiform, inwardly directed, slightly longer than I. Lacinia (Fig. 7, 12*b*) basally fused with stipes and galeomere I,

represented by a subtriangular protuberance bearing 7–8 sharp, hook-like setae along occlusal edge (see above in 'Chaetotaxy' paragraph). Labium (Fig. 8) with membranous mentum, ventrally sclerotised prementum and distinctly diverging, 2-jointed palp. Basal half of prementum dorsally slightly convex and enlarged, with rounded sides; distal half subparallel-sided with small subapical ligula. Labial palpmere I wider and shorter than II; II subulate.

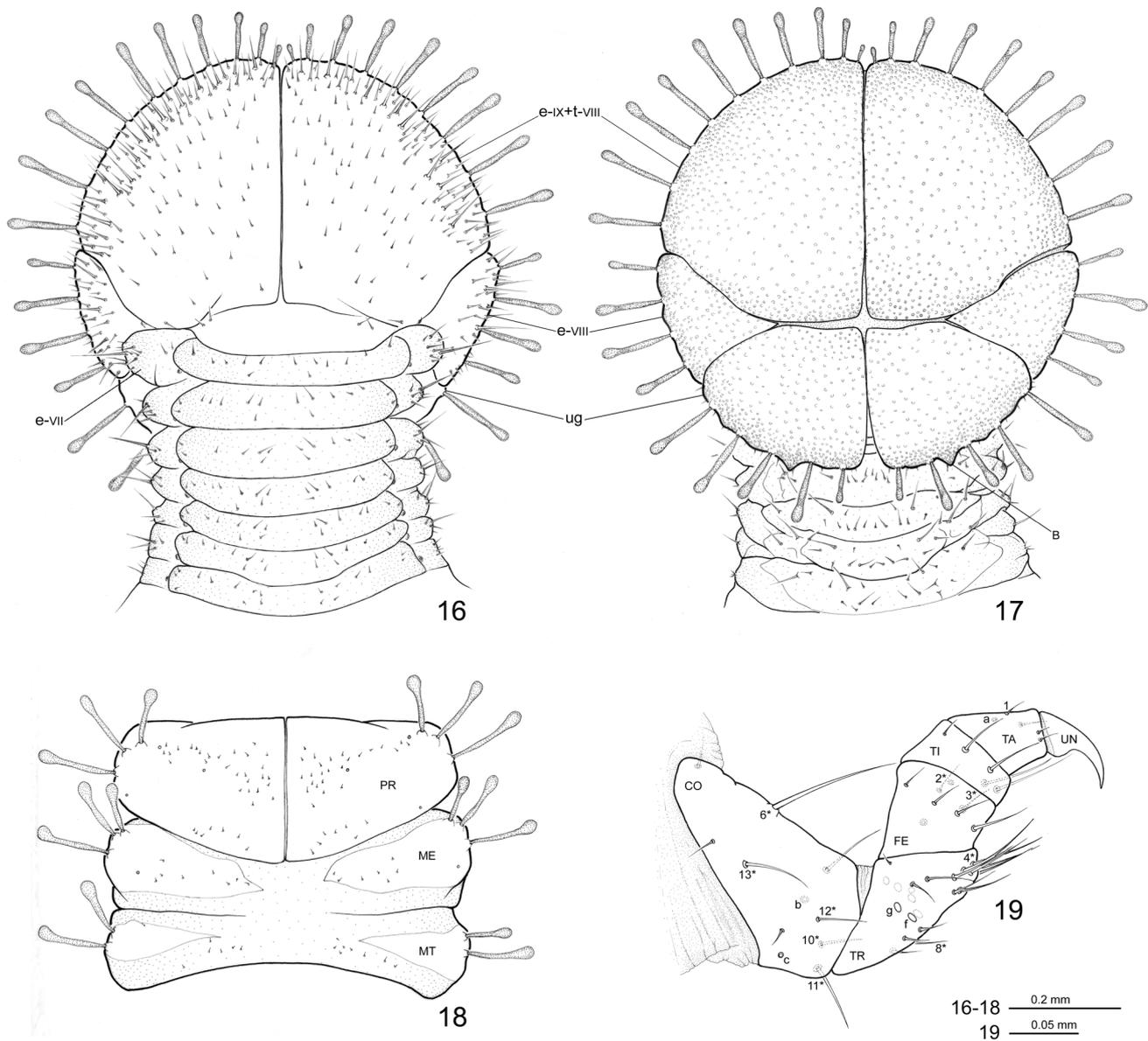
Thorax

Thoracic segments (Fig. 18) slightly sclerotised, except for prosternum; tergites convex, widely transverse, with

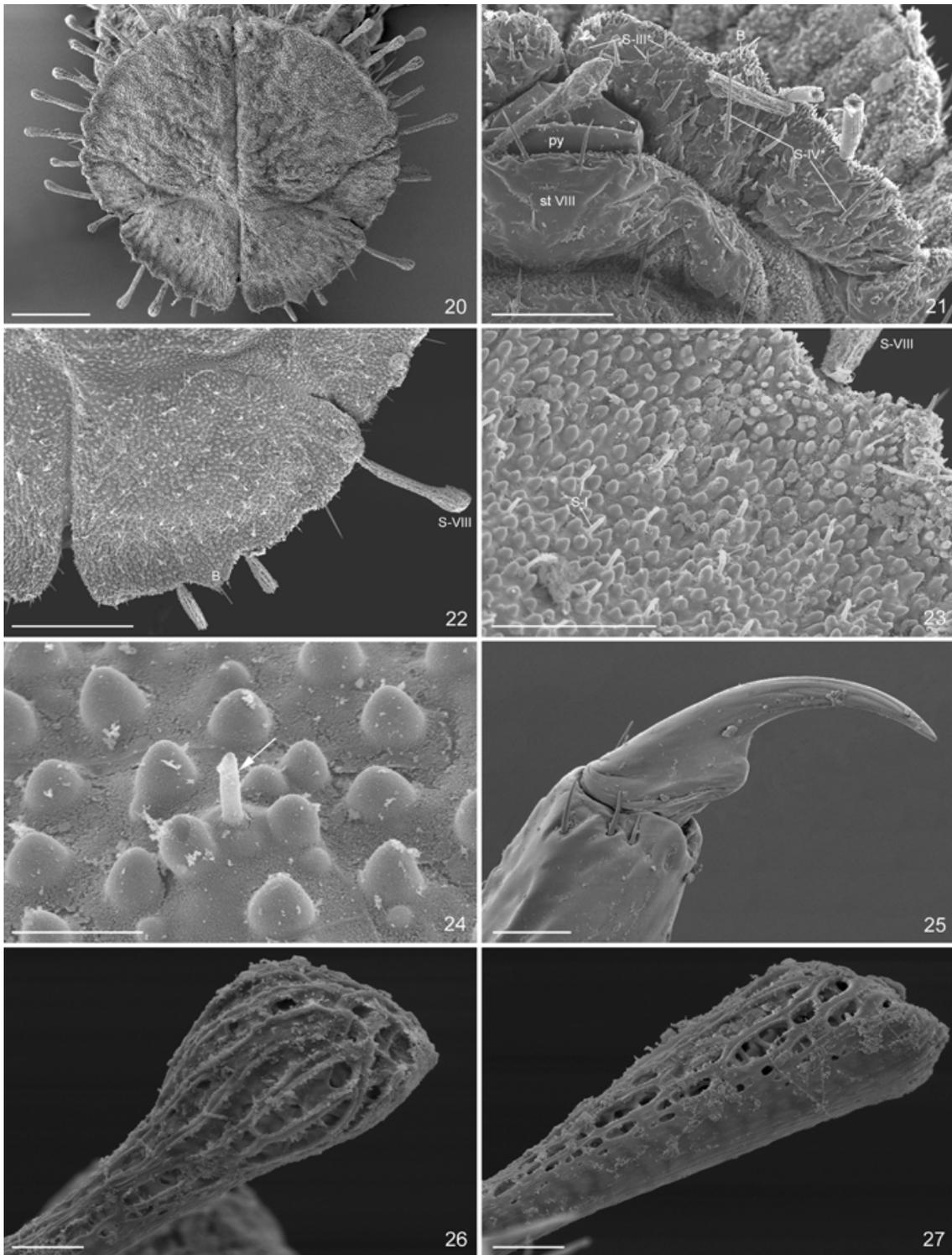
rounded lateral margins, decreasing in length from pro- to metanotum; longitudinal ecdysial line restricted to pronotum. Pronotum wide, straight anteriorly and rounded posteriorly, about three times as wide as long, partially dividing the mesonotum. Mesonotum narrow, concave anteriorly and straight posteriorly; small, annular spiracles on mesopleura. Metanotum extremely narrow and transverse, moderately enlarged and rounded laterally.

Legs

Legs well developed, 5-jointed (Fig. 19). Coxa stout, elongate and cylindrical; trochanter shorter than coxa, about



Figs 16–19. *Arthropterus* sp. first-instar larva: 16, abdomen, dorsal view; 17, terminal disk, apical view, with abdominal sternites I–IV visible; 18, thorax, dorsal view; 19, anterior leg, posterolateral view. *B*, lobe B of urogomphi; *CO*, coxa; *e*, epileurite; *FE*, femur; *ME*, mesonotum; *MT*, metanotum; *PR*, pronotum; *t*, tergum; *TA*, tarsus; *TI*, tibia; *TR*, trochanter; *ug*, urogomphus; *UN*, claw.



Figs 20–27. *Arthropterus* sp. first-instar larva: 20, terminal disk, apical view (scale bar: 200 μm); 21, pygidium and right urogomphus, ventral view (scale bar: 100 μm); 22, right urogomphus, dorsal view (scale bar: 100 μm); 23, sensilla S-I on dorsal surface of right urogomphus (scale bar: 50 μm); 24, sensillum S-I (arrow) and pustulate microsculpture on dorsal surface of urogomphus (scale bar: 10 μm); 25, left prothoracic claw, lateral view (scale bar: 20 μm); 26, apex of sensillum S-VIII on margin of terminal disk (scale bar: 10 μm); 27, apex of sensillum S-VIII on dorsal surface of head (scale bar: 10 μm). *B*, lobe B of urogomphi; *py*, pygidium; *S-I*, *S-III**, *S-IV**, *S-VIII*, abdominal sensilla; *st*, abdominal sternum.

as long as femur and tibia together; tarsus conical, about twice as long as tibia. Femur, tibia and tarsus flattened laterally (Fig. 1). Tarsus with one long, hook-like claw (Fig. 19, 25), about as long as the entire tarsus; base of claw smooth, wide, subtriangular, ventrally fitting to an apical tarsal emargination; distal half of claw thin, distinctly curved and acute at apex.

Abdomen

Abdominal segments I–VII not sclerotised, bellows-like (Figs 16–17), contracted dorsally to bring the large terminal disk into an elevated position (Fig. 1); segments progressively wider from III to VII; each segment dorsally flattened, with swollen pleural (especially segment VII) and sternal areas; sternal sclerite VIII moderately sclerotised. Spiracles extremely small, annular-uniform, dorsolaterally positioned above the epipleural areas on segments I–VIII (Fig. 16). Terminal disk (Figs 1, 2, 16–17, 20) extremely wide, biconvex, composed of 6 symmetrical subtriangular plates, joined by membranous areas along the entire length. Dorsal plates much wider than others, medially swollen; lateral plates small; size of ventral plates (urogomphi) intermediate between lateral and dorsal ones; dorsal and lateral plates without raised margins; ventral plates (Figs 17, 21–22) distally concave, with irregularly raised margin showing remnants of the fused component lobes both in dorsal and ventral views; lobe B recognisable as a pointed, triangular protrusion (Figs 17, 20–22); lobe D absent. Pygidium cylindrical, dorso-ventrally flattened, ventrally positioned to urogomphi.

Phylogeny

Material and methods

Taxa and characters

We included eight taxa representing the paussine genera for which larvae are known (Table 1). We used a total of 50 characters (see Table 2), corresponding to the whole character set used by Di Giulio *et al.* (2003), with the exception of six characters autapomorphic for the entire subfamily. For an extensive discussion of characters and character states, see Di Giulio *et al.* (2003). Character state assignments for all genera except *Sphaerostylus* were made by direct examination, using both optical and scanning electron microscopes, of several larval specimens (marked by a superscript E in Table 1). Since the location of the *Sphaerostylus luteus* (Hope, 1842) larva is unknown, we coded this species to the extent possible based on the original description (Paulian 1947). Unknown character states were coded as missing using the symbol '?' (see Table 3; data matrix also available as Accessory Material on the *Invertebrate Systematics* website). When multiple species of a genus (*e.g.* *Pachyteles* or *Paussus* Linnaeus, 1775) or different instars of the same species (*e.g.* *Metrius contractus* or *Pachyteles vignai* Deuve, 2000) were available both in our sample and in the literature, we checked for the congruency of the character states assigned to the single genus. First-instar larvae were not available for all of the selected taxa, and therefore we avoided using characters known to change between instars in carabid larvae (see Bousquet and Goulet 1984; *e.g.* chaetotaxic and morphometric characters).

Phylogenetic inference

We used the exhaustive search algorithm in the computer programme PAUP*4.0b10 (Swofford 2001) to search for the most parsimonious trees. All characters were unweighted and unordered. Trees were rooted by designating *Metrius* as the outgroup taxon, because this genus is widely recognised as the sister to all other Paussinae (Regenfuss 1975; Nagel 1979; Ball and McCleve 1990; Beutel 1992; Di Giulio *et al.* 2003).

Decay indices and bootstrap values were calculated for each internal node. Decay indices were determined by building constraint trees in MacClade (Maddison and Maddison 2003) and searching for the most parsimonious trees not compatible with each constraint tree by using the branch and bound algorithm in PAUP*. Bootstrap values were determined by using the branch and bound algorithm to search for most parsimonious trees for each of 500 bootstrap matrices.

Results

We found a single most parsimonious tree (tree length = 88 steps, rescaled consistency index (RC) = 0.8628) (see Fig. 28 and Table 4). *Arthropterus* attaches to the tree as the sister-group of all other Paussini, a position supported by adult morphology (Darlington 1950; Nagel 1979, 1987), 17 larval characters (16 of which have a consistency index (CI) of 1.00), and a high bootstrap value and decay index (Fig. 28). Adult characters that support this tribal affiliation include the loss of the elytral margin, the presence of a triangular median cell in the hindwings, absence of fixed setae, front coxae prominent and contiguous, abdominal sterna I–III fused, and the second antennomere reduced to a small ring-like structure located within the apex of the scape. The 17 larval characters that support this assignment (see Table 4) are: head prognathous (character 2), without neck constriction (character 1); lacking coronal suture (character 3); antennomere I broad (character 9) and inserted in a bulging membranous base (character 11); antennomere III with a large, bulbous sensorial appendage (character 12); mandibles short and subtriangular (character 14), with broad base and dorsal elongate setae (character 17); stipes without a basal tooth (character 20, also absent in *Metrius*, see Di Giulio *et al.* 2003) and with reduced gMX setal group (character 21); bulging prementum (character 27); labial palpomere I short (character 28); legs with one tarsal claw (character 31); terminal disk with fused and flat urogomphi (characters 37, 40, 41); pygidium ventral to urogomphi (character 50).

Some character states previously regarded as apomorphies of the tribe Paussini are not present in the *Arthropterus* larva. We now consider these character states as synapomorphies of the 'derivative Paussini' *sensu* Darlington (1950). They include: presence of an antero-median emargination of frontoclypeolabrum, presence of a 'prostheca' (see discussion in Di Giulio *et al.* 2003), absence of a lacinia, fusion of the femur, tibia and tarsus, completely rounded and distinctly raised distal margin of urogomphi, and absence of the long clavate sensilla, (sensilla S–VIII, see below).

Table 2. List of characters used for the larval *phylogenetic* analysis of PaussinaeFor a detailed discussion, see Di Giulio *et al.* 2003

-
- (1) *Neck*: 0, not constricted; 1, constricted.
- (2) *Head*: 0, hyperprognathous (bent upwards); 1, prognathous.
- (3) *Coronal suture*: 0, absent; 1, present.
- (4) *Frontal sutures*: 0, well marked, posteriorly convergent in an obtuse angle; 1, well marked, contiguous posteriorly without forming an obtuse angle; 2, partially obliterated anteriorly, subparallel or diverging posteriorly.
- (5) *Gular suture*: 0, ventral wall of head capsule medially divided by a complete gular suture; 1, reduced to a short medial line.
- (6) *Teeth on the anterior margin of the frontal sclerite*: 0, absent; 1, present.
- (7) *Transverse frontal keel*: 0, absent; 1, present, just behind the anterior margin; 2, present, much behind the anterior margin.
- (8) *Median prominence of anterior margin of frontoclypeolabrum*: 0, absent; 1, small; 2, wide.
- (9) *Antennomere I*: 0, slender; 1, broad.
- (10) *Antennomere I*: 0, without additional setae; 1, with additional setae.
- (11) *Antenna*: 0, inserted on a small membranous base; 1, membranous base voluminous, bulging, protruding laterally.
- (12) *Sensorial appendage*: 0, much shorter than half antennomere IV; 1, longer than half antennomere IV.
- (13) *Mandibular prosthema*: 0, absent; 1, present.
- (14) *Mandibles*: 0, curved, falcate, moderately enlarged at base; 1, short and pointed, subtriangular, with very broad base.
- (15) *Retinaculum*: 0, in medial or sub-basal position; 1, in subapical position.
- (16) *Retinaculum*: 0, securiform; 1, triangular.
- (17) *Mandibles*: 0, without elongate setae on dorsal surface; 1, with some elongate setae directed inwards.
- (18) *Lacinia*: 0, absent; 1, elongated and curved; 2, lobiform with strong, hook-like setae.
- (19) *Stipes*: 0, distinctly curved; 1, subrectangular.
- (20) *Ental surface of stipes*: 0, smooth; 1, with basal tooth.
- (21) *Stipes*: 0, with setal group gMX extremely reduced or absent; 1, with setal group gMX composed of many thin setae not inserted in protuberances; 2, with several setae inserted in sclerotised protuberances.
- (22) *Galea with galeomeres*: 0, articulated; 1, partially fused; 2, completely fused.
- (23) *Second galeomere*: 0, conical; 1, cylindrical; 2, enlarged from base to apex; 3, digitiform.
- (24) *Palpomere IV*: 0, distinctly longer than II; 1, about as long as II.
- (25) *Prementum*: 0, quadrate; 1, rectangular; 2, narrowed apically; 3, widened apically.
- (26) *Premental tubercles*: 0, absent; 1, small; 2, prominent.
- (27) *Prementum*: 0, flat or slightly convex; 1, bulging.
- (28) *Labial palpomere I*: 0, distinctly longer than broad; 1, about as long as broad.
- (29) *Ligula*: 0, dome-shaped; 1, elongate; 2, flat.
- (30) *Tarsus, tibia, femur*: 0, distinct and articulated; 1, fused.
- (31) *Number of tarsal claws*: 0, two; 1, one.
- (32) *Trochanter, femur, tibia and tarsus*: 0, with few and thick setae; 1, with numerous fine setae.
- (33) *Urogomphi with*: 0, distinct elongate branches; 1, branches partially reduced; 2, branches completely reduced and fused into a plate.
- (34) *Urogomphi with apices of lobes B, D, E*: 0, not protruding; 1, rounded; 2, pointed.
- (35) *Urogomphi with lobe A*: 0, indistinct; 1, short; 2, moderately long; 3, extremely long.
- (36) *Urogomphi with lobe B*: 0, indistinct; 1, simple; 2, with lobe B partially or totally divided into 2 sub-lobes (B1 and B2).
- (37) *Urogomphi with lobe D*: 0, reduced; 1, projecting dorsally from the base of lobes B-C; 2, projecting dorsally from the base of lobes E1-E2.
- (38) *Urogomphi with lobe D*: 0, reduced; 1, long and similar in diameter to the other lobes; 2, short or very short and distinctly smaller than the others; 3, bulbous and slightly larger than the others.
- (39) *Urogomphi with lobe E*: 0, fused to the others; 1, undivided; 2, divided into 2 sub-lobes (E1 and E2) with a distinct common base; 3, divided into 2 sub-lobes (E1 and E2) without a distinct common base.
- (40) *Urogomphi with lobe E*: 0, reduced; 1, longer than the others; 2, about as long as lobe B.
- (41) *Basal part of the urogomphi*: 0, cylindrical; 1, dorsally furrowed by a longitudinal sulcus; 2, completely flat.
- (42) *S-I sensilla*: 0, present on sterna; 1, absent on sterna.
- (43) *S-I sensilla*: 0, with elongate, simple, cylindrical bases; 1, with short, simple, conical bases; 2, with both simple and multilobed conical bases; 3, with multilobed conical bases only.
- (44) *S-I sensilla*: 0, with frayed or multilobed apex; 1, with simple, truncate apex; 2, inflated.
- (45) *Sensilla on margin of terminal disk*: 0, elongate and with prominent bases; 1, short and without prominent bases; 2, replaced by long fine setae; 3, elongate, clavate, without prominent bases.
- (46) *Dorsal plates of terminal disk*: 0, distinctly separated by a deep, V-shaped medial incision; 1, partially fused, with reduced medial incision; 2, completely fused, medial incision obliterated.
- (47) *Dorsal plates of terminal disk*: 0, with completely flat surface; 1, with flat surface except for the convex sensorial areas; 2, with completely convex surface.
- (48) *Dorsal and lateral plates of terminal disk*: 0, without distinctly raised margins; 1, with raised margins.
- (49) *Lateral plates of terminal disk*: 0, independent and widely separated from dorsal plates; 1, adjacent to dorsal plates; 2, fused with dorsal plates.
- (50) *Pygidium*: 0, between urogomphi, medial to the terminal disk; 1, ventral to urogomphi and terminal disk.
-

Table 3. Character state matrix

Taxa	Characters																																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50			
<i>Metrius</i>	1	0	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	2	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0		
<i>Pachyteles</i>	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	2	1	0	1	1	2	0	0	0	0	0	0	0	1	3	2	2	2	2	2	1	1	0	0	0	0	0	0	0	0	0		
<i>Itamus</i>	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	2	0	1	0	0	2	0	0	1	0	0	0	1	3	2	2	2	2	2	1	1	0	0	0	0	0	0	0	0	0			
<i>Sphaerostylus</i>	1	0	1	?	0	0	?	1	0	1	0	0	0	0	0	0	0	0	1	0	1	2	0	1	0	?	2	0	0	1	0	0	0	1	3	2	2	2	2	1	1	?	?	0	0	0	0	0	0	0			
<i>Physeia</i>	1	0	1	1	0	0	2	2	0	1	0	0	0	0	0	1	0	1	?	1	2	0	2	1	2	2	0	0	2	0	0	0	1	2	2	1	2	3	3	2	1	1	1	2	1	1	1	1	1	0			
<i>Arthropterus</i>	0	1	0	2	0	0	0	1	1	1	1	1	0	1	0	1	1	2	?	0	0	0	3	0	2	0	1	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	2	1	1	1	3	2	2	0	2	1	
<i>Platyrhopalopsis</i>	0	1	0	2	1	0	0	0	1	1	1	1	1	1	1	1	1	0	2	0	0	0	3	1	2	1	1	1	0	1	1	1	2	0	0	0	0	0	0	0	0	2	1	2	2	2	1	1	2	1	2	1	
<i>Paussus</i>	0	1	0	2	1	0	0	0	1	1	1	1	1	1	1	1	0	2	0	0	0	0	3	1	3	?	1	1	0	1	1	1	2	0	0	0	0	0	0	0	0	2	1	3	1	1	2	0	1	2	1	2	1

Arthropterus shares the following plesiomorphic characters with ozaenines: small median prominence ('labral spine' *sensu* Beutel 1992) on frontoclypeolabrum (character 8, Fig. 9), mandibles without a prostheca (character 13) and with the retinaculum in a medial position (character 15), basic number of maxillary palpomeres, long gular suture (character 5), legs with segments not fused (character 30) and with a moderate number of thick setae (character 32), absence of a 'metathoracic spiracle' (Di Giulio *et al.* 2003), terminal disk without distinctly raised margins (character 48).

Larvae of *Metriini* and *Ozaenini* differ from those of *Arthropterus* by the following character states, which are plesiomorphic to *Paussinae*: presence of a hyperprognathous head with distinct frontal sclerite and coronal suture; tarsi with two claws; presence of a simple hook-like lacinia; presence of slightly or deeply lobed urogomphi.

Discussion

The present phylogenetic analysis corroborates the hypotheses of Beutel (1992) and Di Giulio *et al.* (2003) of a sister-

group relationship between *Metriini* and *Ozaenini*+*Paussini*, with *Ozaenini* as a paraphyletic group. In our current analysis, the position of *Arthropterus* as a basal group of *Paussini* is supported by many larval characters.

Finding homologies among setae in carabid larvae is most easily done by comparing first instars. Finding setal homologies between first instars and latter instars, and among second and third instars, is rendered difficult owing to the greatly increased setation of later stages. The *Arthropterus* larva described here is the first newly hatched larva known for the tribe *Paussini* and it has allowed us to recognise several primary setae and pores on the head capsule, antennae, mouthparts and legs (see paragraph 'Chaetotaxy'). Thus, the description of a first-instar larva in *Arthropterus* is important in allowing us to compare homologous setae among the first-instar stages of three of the four paussine tribes for the first time.

Another character state of *Arthropterus*, unique to the first instar, is the blade-like serrate egg-burster, which is more robust than the multispinulate egg-burster, of *Metrius*

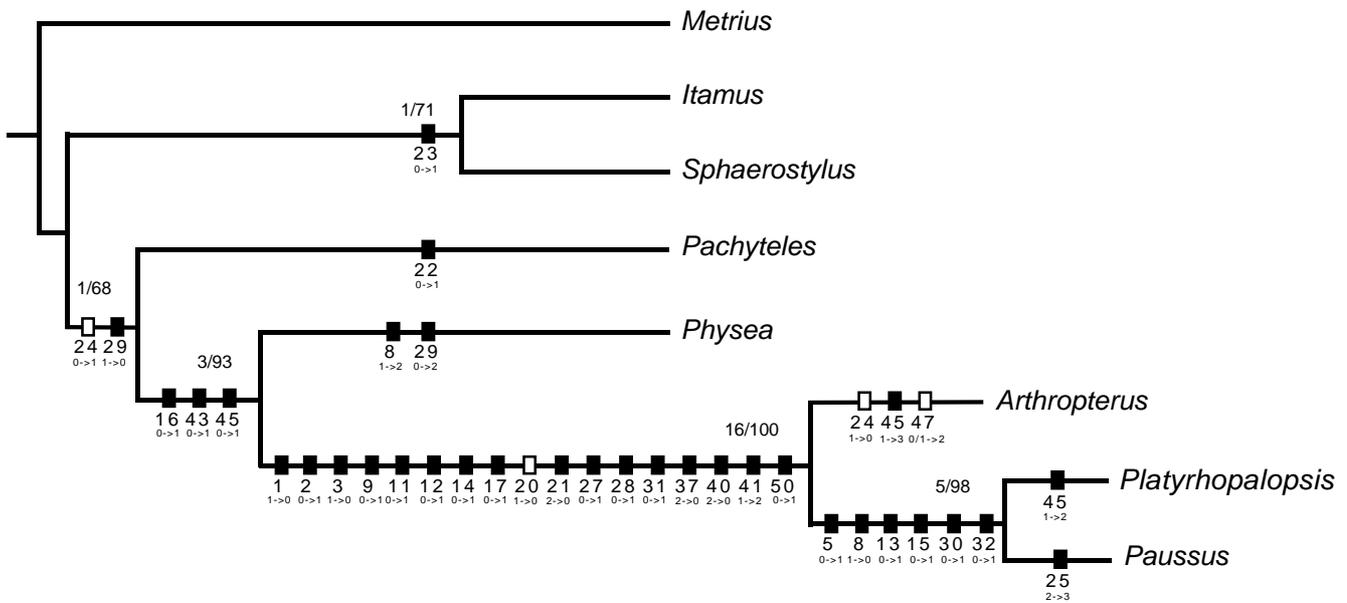


Fig. 28. Single most parsimonious tree (length = 88 steps, rescaled consistency index (RC) = 0.8628). Decay indices and bootstrap values are shown above internal branches. Characters with states unambiguously defining branches are shown, black bars indicate those characters with a consistency index (CI) of 1.00; character states are plotted under each character number.

and *Pachyteles* (see Bousquet 1986; Di Giulio 1999). The shape of the egg-bursters (Fig. 14) might be related to the thickness of the eggshell of *Arthropteris* (A. Kaupp, personal communication). The reduction of the air layer of the eggs in *Physeia*, *Arthropteris*, *Platyrhopalopsis* and *Paussus* either represents a synapomorphy for these taxa or is a result of convergent evolution correlated with a myrmecophilous lifestyle (Kaupp *et al.* 2000).

The anterior margin of frontoclypeolabrale of *Arthropteris* is medially produced into a wide subrectangular region between the base of the mandibles (Figs 3, 11). This structure is medially produced into a small anterior prominence (Fig. 9) that we consider homologous to the medial prominence ('labral spine' *sensu* Beutel 1992) of metriines and ozaenines. The structural characters of the mandible are intermediate between those of Ozaenini and Paussini: the triangular shape and the peculiar position and orientation of the retinaculum (Figs 6, 15a–15b), which is distally (rather than transversely) directed, support the hypothesis that this structure is homologous to the subapical tooth, rather than the prosthema of *Platyrhopalopsis* and *Paussus* (see discussion in Di Giulio *et al.* 2003).

The fused terminal disk of *Arthropteris* (Figs 16–17, 20) is definitely of the Paussini type. However, the distal margin of the urogomphi is not regularly rounded as it is in *Paussus* and *Platyrhopalopsis* larvae. Rather the margin has some protuberances that we interpret as remnants of the urogomphus lobes typical of Ozaenini larvae. In particular, lobe B is easily recognisable as a pointed triangular protuberance (Figs 17, 20–22), slightly flattened, and symmetrical in both urogomphi. It is worth noting that a similar relative position, upward orientation and pointed conical shape of lobe B is also present in *Physeia setosa* Chaudoir, 1868. The shape of the urogomphi of *Arthropteris* corroborates the hypothesis that this character is a morphocline (see Di Giulio *et al.* 2003), and we can reconstruct the following gradual transformation series, which is compatible with the hypothesis of van Emden (1936): (1) simple urogomphi of the carabid type; (2) 5-lobed urogomphi of the metriine type; (3) 6- or 7-branched urogomphi of the ozaenine type; (4) urogomphi with partially fused lobes as in *Physeia*; (5) urogomphi plate-like with completely fused lobes but with some remnants visible, as in *Arthropteris*; and (6) completely fused urogomphi without any trace of distinct lobes, as in the 'highly derived' Paussini.

Myrmecophily

Little is known about the life history of Paussinae. Some observations on the primitive predation strategy in non-myrmecophilous Ozaenini of the genus *Pachyteles* were studied by Di Giulio and Vigna Taglianti (2001). The *Pachyteles* larva attracts (by secreting unidentified substances) and captures prey insects, by clasping them with the sclerites of the terminal disk; at the same time the larva

brings its head towards the terminal disk, seizes the trapped insect with its mandibles, and brings the prey into the larval gallery to consume. The attraction of ants in the free living *Pachyteles* larvae, and the lack of aggressiveness of the ants observed in the laboratory, were interpreted as a possible pre-adaptation for the evolution of myrmecophily in Paussinae (Di Giulio 1999; Di Giulio and Vigna Taglianti 2001).

Only one ozaenine genus, *Physeia*, is known to be myrmecophilous. Larvae and adults of *Physeia setosa* have an obligate association with ants (see Di Giulio *et al.* 2003). *Physeia* larvae have been collected from galleries deep within the nests of the neotropical leaf cutter ant *Atta sexdens* Linnaeus, 1758 (van Emden 1936). Based on adult structural features, myrmecophily has been also hypothe-

Table 4. Complete list of synapomorphic character states for clades of interest

Characters with a consistency index of 1.00 are in bold face

<i>Sphaerostylus</i> + <i>Itamus</i>	
23: 0→1	Second galeomere cylindrical
<i>Pachyteles</i> + <i>Physeia</i> + <i>Arthropteris</i> + <i>Platyrhopalopsis</i> + <i>Paussus</i>	
24: 0→1	Palpomere IV about as long as II
29: 1→0	Ligula dome-shaped
<i>Physeia</i> + <i>Arthropteris</i> + <i>Platyrhopalopsis</i> + <i>Paussus</i>	
16: 0→1	Retinaculum triangular
43: 0→1	S-I sensilla with short, simple, conical bases
45: 0→1	Sensilla on margin of terminal disk elongate and with prominent bases
<i>Arthropteris</i> + <i>Platyrhopalopsis</i> + <i>Paussus</i>	
1: 1→0	Neck not constricted
2: 0→1	Head prognathous
3: 1→0	Coronal suture absent
9: 0→1	Antennomere I broad
11: 0→1	Antenna membranous base voluminous, bulging, protruding laterally
12: 0→1	Sensorial appendage longer than half antennomere IV
14: 0→1	Mandibles short and pointed, subtriangular, with very broad base
17: 0→1	Mandibles with some elongate setae directed inwards
20: 1→0	Ental surface of stipes smooth
21: 2→0	Stipes with setal group gMX extremely reduced or absent
27: 0→1	Prementum bulging
28: 0→1	Labial palpomere I about as long as broad
31: 0→1	Tarsi with one tarsal claw
37: 2→0	Urogomphi with lobe D reduced
40: 2→0	Urogomphi with lobe E reduced
41: 1→2	Basal part of the urogomphi completely flat
50: 0→1	Pygidium ventral to urogomphi and terminal disk
<i>Platyrhopalopsis</i> + <i>Paussus</i>	
5: 0→1	Gular suture reduced to a short medial line
8: 1→0	Median prominence of anterior margin of frontoclypeolabrum absent
13: 0→1	Mandibular prosthema present
15: 0→1	Retinaculum in subapical position
30: 0→1	Tarsus, tibia, and femur fused
32: 0→1	Trochanter, femur, tibia and tarsus with numerous fine setae

sised for the south-east Asian species *Dhanya mulu* Stork, 1985, and the south and central American genera *Ozaena* Olivier, 1812, and *Platycerozaena* Bänninger, 1927 (Stork 1985; Ball and McCleve 1990).

The morphological analysis of the first-instar larva of *Arthropterus* suggests that some larval characters can be interpreted as adaptations to myrmecophily, in particular (1) the presence of a wide, slightly sclerotised and bulged terminal disk, with completely fused plates and plate-like urogomphi, and (2) the transformation of some sensilla chaetica into long, thick clavate structures riddled with holes (sensilla S-VIII), which encircle the terminal disk (but are also present on head and thorax) and probably have a function associated with glands, as discussed below. The fusion of the urogomphal lobes and of the plates of the terminal disk observed in *Arthropterus*, and in all known Paussini larvae, renders the terminal disk immobile such that it cannot fold to capture insects. These larvae live in ant nests and are not burrow-trappers like ozaenines and metriines (Costa *et al.* 1988; Bousquet 1986; Di Giulio and Vigna Taglianti 2001). The terminal disk of Paussini is probably a glandular symphilous organ used to attract and appease ants. Oberprieler (1985) speculated that the terminal disk with raised margins of the Paussini is cup-shaped to hold the attractive secretions for the ants. It is worth noting that the myrmecophilous ozaenine *Physea setosa* has a partial fusion of the plates and a reduction of most urogomphal lobes. Both of these character states have been interpreted as an intermediate between 'Ozaenini' and Paussini, and possibly related to myrmecophily (Beutel 1992; Di Giulio *et al.* 2003).

An important larval adaptation of *Arthropterus* is the peculiar structure of sensilla S-VIII (Figs 26–27). Because of the position of these sensilla on the head, thorax and terminal disk and their longitudinally corrugated microsculpture, these appear to be extremely modified sensilla chaetica and we suspect that they function as mechanoreceptors. However, the surface of the sensilla is riddled with holes and covered by a particulate substance, indicating that they might also be glandular in function and related to the myrmecophilous lifestyle of the larvae. Alternatively, they could be chemoreceptors, their spongy surface possibly serving to collect odour particles from the ants.

The inferred larval myrmecophily of *Arthropterus* supports the hypothesis of Di Giulio and Vigna Taglianti (2001) that larval myrmecophily predates the evolution of adult myrmecophily in the Paussinae. Symphilic adaptations in adults are present in the derived paussines (Paussina) but not in the Cerapterina, to which *Arthropterus* belongs. The inferred myrmecophilic habit of the *Arthropterus* larva supports the hypothesis that larvae have played an important role in the evolution of myrmecophily within the subfamily. The likely myrmecophilous habits of *Arthropterus* also support the hypothesis that the myrmecophilous lifestyle of

the larvae arose before the appearance of the Paussini (as shown by its occurrence in their sister-taxon *Physeae*) and, as far as is known, it became established in all Paussini at least during their larval stage.

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