PENSOFT

SENCKENBERG
world of biodiversity

Leibniz Association

Revision of the genus *Attaphila* (Blattodea: Blaberoidea), myrmecophiles living in the mushroom gardens of leaf-cutting ants

Horst Bohn[1], Volker Nehring[2], Jonathan G. Rodríguez[3], Klaus-Dieter Klass[4]

1 *Zoologische Staatssammlung München, Münchhausenstrasse 21, 81247 München, Germany*

2 *Universität Freiburg, Biologie I, Hauptstraße 1, 79104 Freiburg, Germany*

3 *Universidad del Valle, Grupo de Ecología en Agroecosistemas y Hábitats Naturales, Calle 13 No. 100-00, Ciudad Universitaria Meléndez, Cali, Colombia*

4 *Senckenberg Natural History Collections Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden, Germany*

http://zoobank.org/5BE5330D-71CA-4F12-BB2E-C7B29A5C33B2

Corresponding authors: Horst Bohn (bohn@zi.biologie.uni-muenchen.de); Klaus-Dieter Klass (klaus.klass@senckenberg.de)

Received 9 October 2020
Accepted 9 April 2021
Published 5 July 2021

Academic Editor Monika J.B. Eberhard

Citation: Bohn H, Nehring V, Rodríguez JG, Klass K-D (2021) Revision of the genus *Attaphila* (Blattodea: Blaberoidea), myrmecophiles living in the mushroom gardens of leaf-cutting ants. Arthropod Systematics & Phylogeny 79: 205–280. https://doi.org/10.3897/asp.79.67569

Abstract

The genus *Attaphila*, comprising minute myrmecophilous cockroaches, is revised, including now six previously known (*A. aptera*, *A. bergi*, *A. flava*, *A. fungicola*, *A. schuppi*, *A. sexdentis*) and three new species (*A. multisetosa* **sp. nov.** Bohn and Klass, *A. paucisetosa* **sp. nov.** Bohn and Klass, *A. sinuosocarinata* **sp. nov.** Bohn and Klass). All species are described or redescribed and depicted with their main characteristics; determination keys allow the identification of males and females. Especially the male characters allow a distribution to two species-groups with differing host specificity: *bergi*-group associated with *Acromyrmex* (and possibly *Amoimyrmex*) ants, *fungicola*-group associated with *Atta* ants; the former appears paraphyletic, the latter monophyletic. The genus *Attaphila* is characterised emphasising its unique features: (1) insertion of antennae at the bottom of a wide funnel-shaped deepening; (2) antenna with the possibility of a rectangular bending between scapus and pedicellus (associated with a distal excavation of the scapus) and (3) with an unusual shape and low number of antennomeres; (4) femora of legs with a ventral groove allowing a close spacing of femur and tibia during a strong flexion; (5) a complex and unusual shape of the laterosternal shelf area of the female genitalia (lack of shelf, presence of a pair of complicated tubular invaginations); and (6) lateral parts of abdominal tergite T9 of male ending in a pair of ventromesally directed arms, which contact the lateral margins of the subgenital plate. Functional aspects and the possible biological roles of these features are discussed. Older biological data are summarised and new observations are presented. The position of *Attaphila* within Blattodea is discussed. Like a recent molecular study, the morphology of the male genitalia places the genus in the Blaberoidea. The molecular result of *Attaphila* being closest to three particular blattellid genera, however, is conflictual from the morphological perspective.

Key words

New species, determination keys, myrmecophiles, leaf-cutting ants, genitalia, morphology, biology

Copyright *Horst Bohn* et al.: This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

1. Introduction

The species of the cockroach genus *Attaphila* are myrmecophiles living in the mushroom gardens of leaf-cutting ants of the genera *Atta*, *Acromyrmex*, and *Amoimyrmex* (all Formicidae: Myrmicinae: Attini and forming a monophyletic group: Cristiano et al. 2020). With their body length of 2.5–3.5 mm, *Attaphila* specimens are among the smallest cockroaches. The first species, *Attaphila fungicola*, was formally described from Texas (Wheeler 1900). Within the following five years four further species from various countries in South America were described by Bolívar (1901, 1905): *A. aptera* from Colombia, *A. bergi* from Argentina and Uruguay, as well as *A. sexdentis* and *A. schuppi* from Brazil. It took more than 30 years till the sixth and hitherto last species was described: *A. flava* from Honduras by Gurney (1937).

Due to their hidden life in ant nests *Attaphila* species are rarely collected and recorded, although they are apparently quite often seen by researchers working on the ant hosts. There are only few further reports apart from the descriptions listed above and these only concern part of the species. *A. aptera* was, according to Bruijning (1959), also found in Surinam. Bruch (1916, 1929) added some new localities for *A. bergi* in Argentina and described a new variety (var. *minor*) of it. *A. fungicola* was reported from Texas (Hebard 1916), Panama and Guyana (as British Guiana) (Wheeler 1928), and Trinidad (Brossut 1976).

Recent excavations of nests of leaf-cutting ants in Panama (near Gamboa) by one of us (V.N.) revealed that a large number of the nests were inhabited by *Attaphila* specimens. This allowed investigations of the chemical factors involved in the communication between ants and their cockroach "guests" (Nehring et al. 2016). Unfortunately, a determination of these *Attaphila* specimens to species-level was not possible, since none of the hitherto existing descriptions contains characterisations allowing a distinction of the various species.

In order to get the desired information for the determination it was necessary to study the type specimens of the described species, most of which were deposited in the Maastricht Museum (NHME). Having all available types at disposal offered the possibility for an urgently needed revision of the genus including a study of male and female genitalia. For this purpose, numerous museums of North, Central and South America and research groups working on leaf-cutting ants were asked for additional material. The result was disappointing and did not significantly improve the highly unsatisfying situation concerning the material available for the revision. Regarding the previously described species, the types of *A. bergi* and of its variety var. *minor* are lost; and the sole type specimen of *A. aptera* turned out to be a juvenile lacking almost all species-specific characters necessary for an unequivocal identification. Under inclusion of the species newly described herein, for three of the species only a single adult specimen was available, and less than half of the species were represented by both sexes. Despite this situation, we consider a taxonomic revision of *Attaphila* at the present as appropriate, since the status of its systematics is highly confused, the genus is of great interest for ecological work, and our sample most likely includes most (if not all) of the specimens currently available worldwide.

Princis (1963: pp. 76, 110) placed *Attaphila* in a separate family (Attaphilidae) in the "subordo" Polyphagoidea (now considered as a family, Corydiidae: Beccaloni 2014). This, however, was based neither on reasoning in accord with phylogenetic systematics nor on consideration of the morphology of the male genitalia, which are the key character system for morphology-based phylogenetic studies in Blattodea (see Grandcolas 1996; Klass 1997, 2001; Klass and Meier 2006; Djernæs et al. 2015). Roth (1968, 2003) assigned *Attaphila* to the family Blattellidae (= Ectobiidae if both names are used in their wider sense; see Beccaloni 2014), classifying it as a monogeneric subfamily (Attaphilinae) of this taxon. Roth's considerations were based on his own observations concerning the structure of ovarioles and on still unpublished drawings of male and female genitalia of *A. fungicola* and *A. bergi* made by F. A. McKittrick, which were available to L. Roth. *Attaphila* has not been included in any of the major published morphology-based contributions on the phylogeny of Blattodea (McKittrick 1964; Klass 1997, 1998; Klass and Meier 2006), and morphological data on the genus (see Brossut 1976) are overall very limited. However, the genus has recently been included in Djernæs et al.'s (2020) molecular-based study of cockroach phylogeny (focused on the well-established cockroach clade Blaberoidea), where it was placed deeply subordinate in Ectobiidae-Blattellinae[1], as the sister-taxon of a *Xestoblatta* species (this genus appearing as polyphyletic). In the present revision, we thus also discuss whether or not previously published and newly acquired morphological data agree with this hypothesis on the phylogenetic position of *Attaphila*. The evidence from this will be fragmentary due to the very limited morphological treatment of the Blaberoidea.

2. Materials, methods, terminologies, and abbreviations

2.1. Systematics

Blattodea. We follow Djernæs et al. (2020) and Evangelista et al. (2021) regarding the outline of Blaberoidea (i.e. excluding Anaplectidae), and regarding the division

1 "Blattellidae" therein. In Djernæs et al. (2020) the groupings addressed by "Blattellidae" = "Ectobiidae" in their wider sense (see Beccaloni 2014 for synonymy in this sense) are not accepted as taxa due to lacking monophyly. Instead, the former subfamilies Blattellinae, Ectobiinae, Pseudophyllodromiinae, and Nyctiborinae are ranked as families Blattellidae, Ectobiidae, Pseudophyllodromiidae, and Nyctiboridae, thereby having the same rank as Blaberidae. These five families together form the Blaberoidea; see 2.1. herein

of Blaberoidea into the five families Pseudophyllodromiidae, Blattellidae, Ectobiidae, Nyctiboridae, and Blaberidae (i.e. we treat the four former subfamilies that together formed the family Ectobiidae in its older, wider sense as families); and we follow Djernæs et al. (2020) regarding the formal assignment of *Attaphila* to Blattellidae. This classification agrees with the results of recent molecular-based phylogenetic studies; but we note that for only few of the numerous genera currently assigned to one of the formerly "ectobiid" families this assignment is supported in a phylogenetic sense (taxa in Djernæs et al. 2020: table 4 plus taxa additionally sampled in Evangelista et al. 2021). Regarding the assignment of genera not included in recent phylogenetic studies to the five main classificatory units of Blaberoidea, we follow Beccaloni (2014; exceptions to this are specified below). To address the former "Ectobiidae", which is occasionally needed for the sake of their shared plesiomorphies and for comparison with older literature, we use the term "non-blaberid Blaberoidea".

Hymenoptera-Formicidae. Regarding genus- and species-level taxonomy of the reported host ants of *Attaphila* we follow the catalogue of Bolton (2021). Phylogenetic and evolutionary hypotheses are taken from Schultz and Brady (2008), Branstetter et al. (2017), and Cristiano et al. (2020), who used successively increasing taxon samples. Cristiano et al. (2020) find the leaf-cutting ants and its three genera monophyletic, with the relationships *Amoimyrmex* + (*Acromyrmex* + *Atta*), the genus *Amoimyrmex* having been newly defined therein (its species were formerly assigned to *Acromyrmex*).

2.2. Preparation of cuticular structures

Soft tissues were removed by treatment with 10% KOH at 40°C for 12 hours. For examination the cleared cuticular parts were either put in a petri dish (direct examination for drawings) or slide-mounted in Euparal using tiny glass rods as spacers between slide and cover slip (for photography). Slide(s) and the remnants of the corresponding specimens got an identification code (Xy or XY numbered) specified in the 'Material studied' paragraphs of the species descriptions and in the figure captions; the letter combination **Bo** is used for material not belonging to the collection of H.B., all other combinations indicate the country of origin: **Al** Algeria, **Cb** Colombia, **CR** Costa Rica, **Ma** Morocco, **Sp** Spain.

2.3. Illustrations and orientation

Regarding photography, the phase contrast images were made with a Sony Nex-5N camera on a Zeiss Photomikroskop II, all other photos were made with a Jenoptic camera (ProgRes SpeedXTcore5) on a Leica microscope (DM 5000B) using software ProgRes CapturePro v.2.8.0 and Helicon Focus 5.3. For drawings, the preparations were examined under a Leica M125 stereo microscope and gradually dissected; initial handmade drawings were scanned and then completed using the computer programs CorelPhotoPaint and CorelDraw. In the figures the orientation of the structures is – unless otherwise stated – with the anterior end on top, or with the base on top (antennae, legs, tegmina); tergites shown in dorsal, sternites in ventral view. For legs and tegmina morphological orientations are given as if they were stretched at right angle from the longitudinal axis of the body towards the side.

2.4. Morphological terminologies and concepts of abbreviation

Armament of tibiae. The distribution of spines on fore-, mid-, and hindtibia is – as hitherto (see e.g. Bohn et al. 2010) – specified by the following formula: [d·a·v][d·a·v][d·a·v]. Compared to the numbering system for tibial spines introduced by Klass et al. (2009), the explanation of the letters is now read as follows: **d** number of spines on the dorsal surface outside the apical armament (spines **Td** excluding **Td1m**), **a** number of spines of the apical armament (terminal tibial spines **Tt1–5** plus distidorsal spine **Td1m**), **v** number of spines on the ventral surface outside the apical armament (spines **Tv** in Klass et al. 2009).

Borders of tergites. In the preparations of successive abdominal tergites (e.g. Fig. 6) there are many transversal lines of different kind and distinctness; as some are important in the descriptions, the pattern is briefly explained and illustrated in Supplement 2 (Fig. S1 and associated text). The taxonomic descriptions consider mainly the following lines (***n*** representing the sequential number): The posterior borders of tergites (posterotergal bending lines **T*n*-p**, fixed and discrete); the anterior borders of tergites (anterior margins of tergites **T*n*-a**, fixed but rarely discrete); the lateral borders of tergites (lateral bending lines of tergites, fixed and discrete); and the tergal transversal ridges (**tr*n***, fixed and usually discrete). Note that the anteroposterior succession of the transversal lines is not always regular due to a longitudinal shift of part of the series of tergites (as evident from Fig. S1D).

Bristles on tergites. Bristles can be present along the transversal ridge (**tr*n***), along the lateral and posterior borders, and on the surface area in between. Those in between are called 'surface bristles'. The center of a surface area is its middle part both in the longitudinal and the transversal direction.

Male and female genitalia. Selecting a terminology and associated abbreviations is problematic for both sexes. There are, on the one hand, simple terminologies that have been used in recent taxonomic contributions on Blaberoidea, e.g. that of H. Bohn (various papers mainly on Ectobiidae; both sexes: e.g. Bohn 2004; Bohn et al. 2010; Bohn and Chládek 2011; Bohn et al. 2013; Bohn 2019). Their abbreviations are quite arbitrarily designed,

as their goal is just cross reference between text and illustrations. However, only the few structures evaluated for taxonomic purposes are named. On the other hand, there is the more elaborate terminology of K.-D. Klass (males: mainly Klass 1997; females: various papers on non-dictyopterans, e.g. Klass and Matushkina 2018; both sexes: Brannoch et al. 2017 for Mantodea). It has the additional goal to express homology hypotheses through-

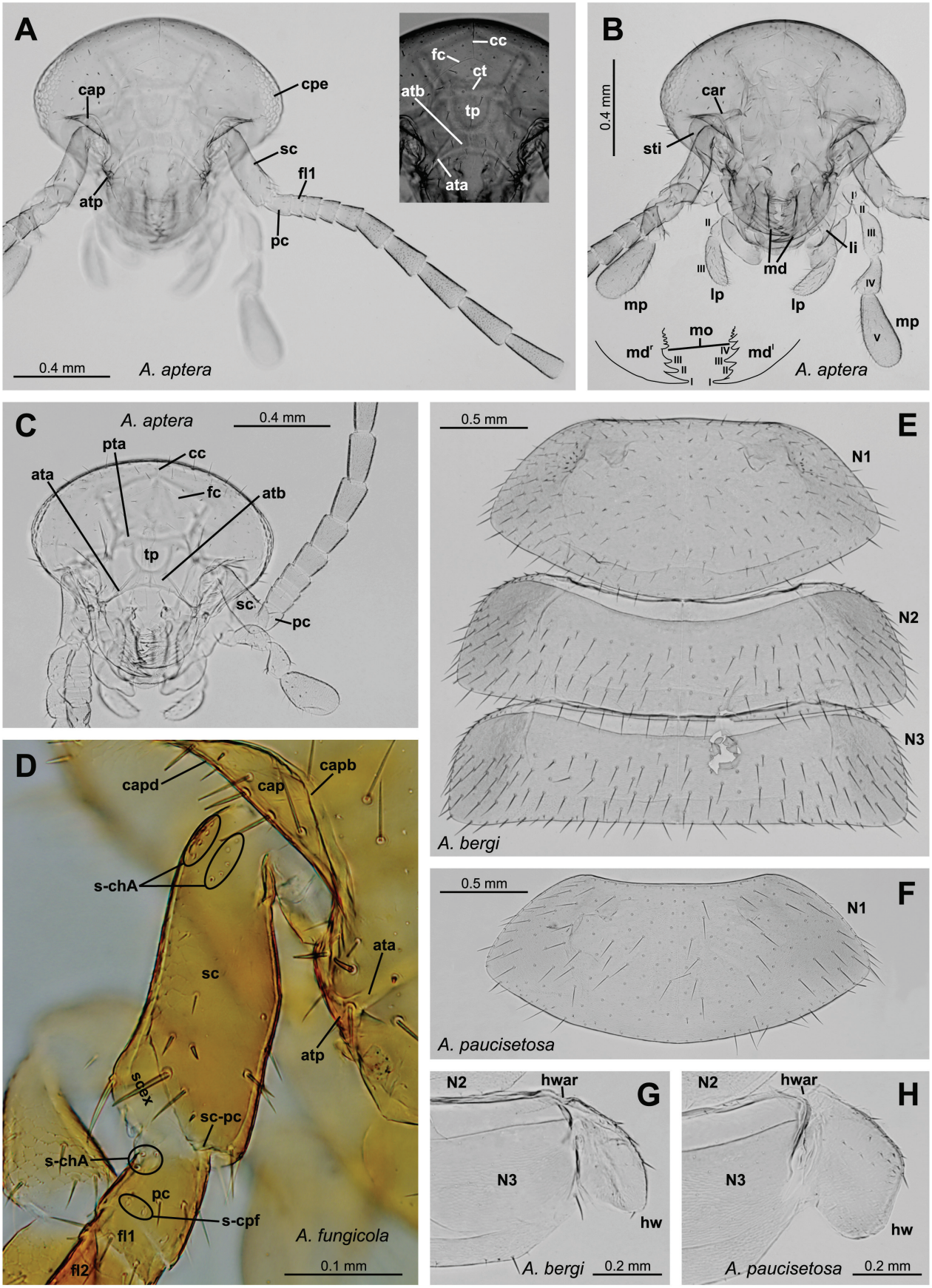


Figure 1. A–D: Head structures of *Attaphila* species, head made transparent by treatment with KOH. **A**: Entire head with focus on antennae and circumantennal pit (inset: median part, darkened). **B**: Entire head with focus on mouthparts (cardo and stipes seen behind circumantennal pit; inset: scheme of mandibular dentition in anterior view, md^l = left, md^r = right, elements above transversal line belonging to mola). **C**: Entire head with left antenna rectangularly bent between scapus and pedicellus. In A–C different levels of tentorium visible internally. **D**: Base of right antenna and surrounding parts of head capsule at higher magnification, also showing dorsal excavation at distal end of scapus allowing the strong bend shown in C. **E–H:** Thoracic nota of *Attaphila* species. **E**: All thoracic nota of a female, stretched. **F**: Pronotum of a male. **G**, **H**: Right part of metanotum of males with the strongly reduced hindwing. — ***Species***: **A–C**: *A. aptera*, male (A, B: Bo 1224), larval female (C: Bo 1243); **D**: *A. fungicola*, male (Bo 1229); **E**, **G**: *A. bergi*, female (Bo 1239), male (Bo 1283); **F**, **H**: *A. paucisetosa*, male (Bo 1240). — ***Abbreviations***: **ata** anterior tentorial arm; **atb** anterior tentorial bridge; **atp** anterior tentorial pit; **car** cardo of maxilla; **cap** circumantennal pit (with sharp dorsal edge **capd** visible and bottom **capb** of the pit shining through); **cc** coronal cleavage line; **cpe** compound eye; **ct** corpotentorium; **fc** frontal cleavage line; **fl** fagellum (all antennomeres following pedicellus, numbered from base as **fl1** etc.); **hw** hindwing; **hwar** level of (reduced) hindwing articulation; **li** lacinia; **lp** labial palpus (I–III: palpomeres); **md** mandible (left $\mathbf{md^l}$, right $\mathbf{md^r}$; I–IV: tip and incisivi); **mo** mola of mandible; **mp** maxillary palpus (I–V: palpomeres); **N** thoracic notum (**N1** pro-, **N2** meso-, **N3** metanotum); **pc** pedicellus; **pta** posterior tentorial arm; **sc** scapus; **sc-pc** scapus-pedicellus articulation; **scex** dorsal excavation at distal end of scapus; **s-chA** field of sensilla chaetica A; **s-cpf** row of sensilla campaniformia; **sti** stipes of maxilla; **tp** tentorial perforation.

out Dictyoptera or Insecta, and homonomies among segments. Its abbreviations are designed according to a coherent system (e.g. by using different kinds of terms for sclerotisations and elements of shape, such as processes), and the abbreviations actually constitute the terminology. This complex terminology provides names for most elements of the genitalia. However, it has not yet been applied to a broader sample of Blaberoidea, where some homology problems need to be resolved prior to its broad application to this taxon. To cope with this conflict, we apply herein a mixture of the terminologies used by Bohn and Klass. The synonymy between the two is given in the text at first mention and is surveyed in Supplement 3 Fig. S2 (female; synonymy with abbreviations in McKittrick 1964 additionally indicated) and Supplement 4 Fig. S3 (male). The terminologies of Klass are explained, with a focus on Mantodea, in Brannoch et al. (2017: pp. 28–30, figs 14, 15, supplement 9).

2.5. Sources for comparison

For comparing **any body parts** between *Attaphila* and other cockroaches (especially Blaberoidea), we used a variety of taxonomic papers, focally those of H. Bohn, to the extent these include relevant information; and we used several morphological treatments (such as Wipfler et al. 2016 on the head of *Periplaneta americana*). For the **antennae** we provide illustrations based on own studies on some Blattellidae species (Fig. 2).

For the genitalia, which are only superficially described in most of the taxonomic literature, we additionally used morphological contributions. The main data source for **female genitalia** is McKittrick (1964, abbreviated MK64 in the following), where a fairly rich selection of Blaberoidea is covered; in her drawings, however, many spatial relationships between structural elements are unclear, which makes comparison difficult. In addition, the very limited information in Klass (1998: *Supella* being the only sampled blaberoid) was used; and Brannoch et al. (2017) was taken for interpretation at the Dictyoptera level. The main data sources for **male genitalia** are MK64 (with the same problems as for female genitalia) and Klass (1997), where cockroach phallomeres are described in great detail, but only for very few blaberoid species. In addition, for some crucial points we provide illustrations from own preliminary studies on genitalia of selected Blattellidae and Ectobiidae (Figs 30–33).

Our own examinations in taxa apart from *Attaphila* refer to: the Blattellidae *Blattella germanica* (Linnaeus, 1767) (ex cult.), *Blattella lobiventris* (Saussure, 1895) (Gabon), *Loboptera decipiens* (Germar, 1817) (Spain), *Symploce pallens* (Stephens, 1835) (ex cult.), *Xestoblatta cantralli* Fisk and Gurney, 1968 (Costa Rica), *Xestoblatta hamata* (Giglio-Tos, 1898) (Costa Rica), *Pseudomops* Serville, 1831 sp. indet. (Mexico), *Ischnoptera* Burmeister, 1838 sp. indet. (Costa Rica), *Lobopterella dimidiatipes* (Bolívar, 1890) (ex cult.), and *Parcoblatta lata* (Brunner v. W., 1865) (USA); and the Ectobiidae *Ectobius lapponicus* (Linnaeus, 1758) (Germany), *Dziriblatta haffidi* (Bolívar, 1908) [taxonomic status according to Bohn 2019: p. 18] (Morocco), and *Dziriblatta kroumiriensis* (Adelung, 1914) [taxonomic status according to Bohn 2019: p. 11] (Algeria).

2.6. List of abbreviations

Morphological terms. All abbreviations are listed in Supplement 1; those used in the figures are additionally listed in the associated legends. The abbreviations **T** + number (abdominal tergite) and **S** + number (abdominal sternite; **S7** = subgenital plate of female; **S9** = subgenital plate of male) are frequently used in the text; terms like **T6,7** and **S1–5** refer to two or several, respectively, tergites or sternites, as indicated by the numbers. Lower-case ***n*** in italics is inserted in morphological terms to address all numbered elements in question.

Type specimens. HT – Holotype; **LT** – Lectotype; **PT(s)** – Paratype(s); **ST(s)** – Syntype(s).

Larval stages. L – Larva, larval (**L-** early larval stage, **L+** late larval stage).

Museums and collections. Below we use abbreviations including the full name of the city (usually following M. = Museum), but here we additionally list the acronyms suggested by Evenhuis (2016). AMNH, M. New York – American Museum of Natural History, New York (USA); MACN, M. Buenos Aires – Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (Argentina); MTD, M. Dresden – Museum of Zoology, Sencken-

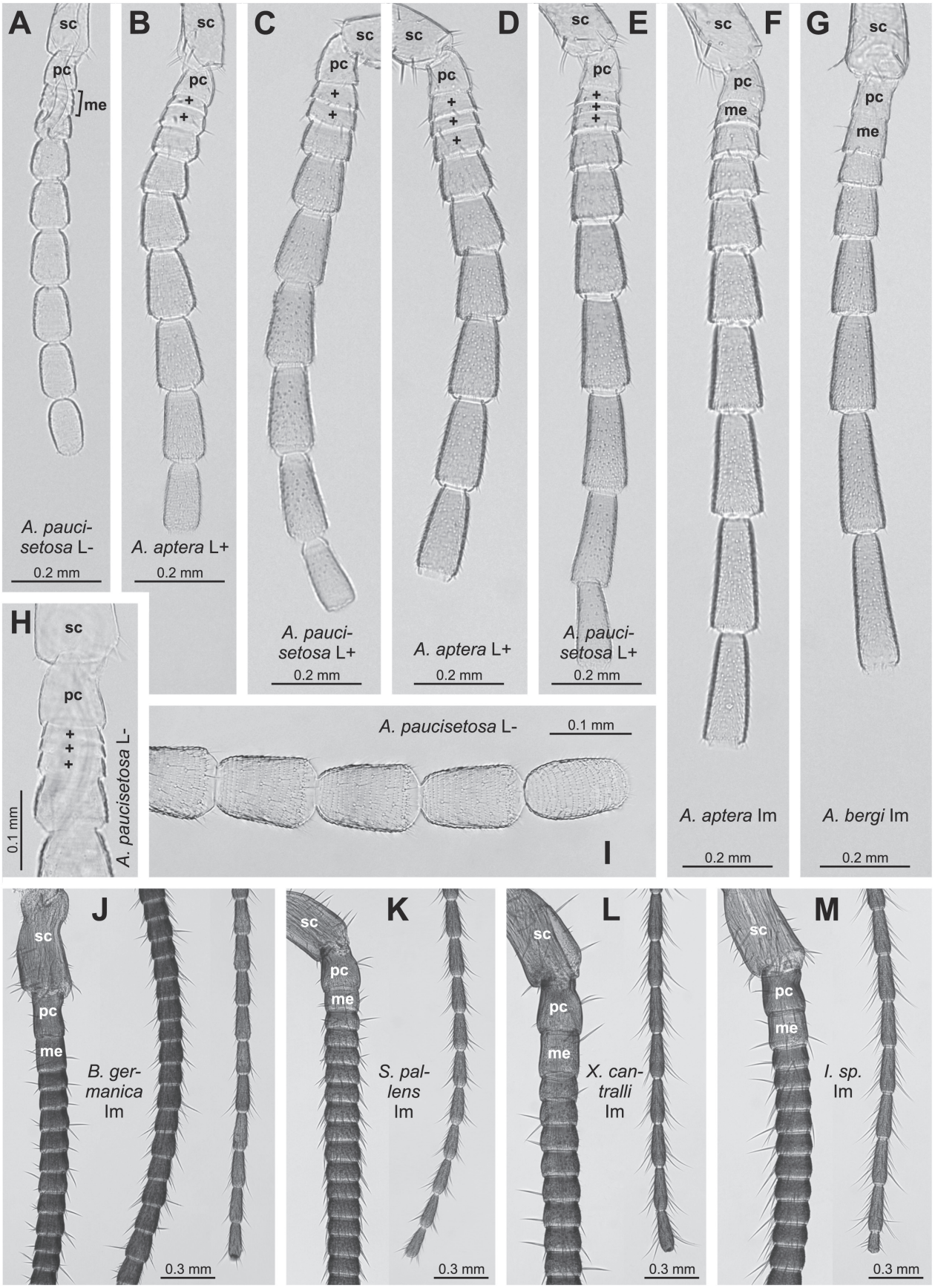


Figure 2. A–I: Antennae of *Attaphila* species of various age. **A**, **H**, **I**: Presumably second stage larva (head width 0.52 mm), with enlarged details of the proximal (H) and distal regions (I, distal end to the right), both from (A); **B**–**E**: intermediate and late larval stages, head width 0.66 (B), 0.61 (C), 0.76 (D), 0.73 mm (E); **F**, **G**: imagines. **J–M:** Imaginal antennae of Blattellidae species, in (J) showing parts of the proximal, intermediate and distal region, in (K–M) only of the proximal and distal region. **— *Species***: **A**, **C**, **E**, **H**, **I**: *Attaphila paucisetosa* (A, H, I: Colombia, Cb 4/3; C: Bo 1458; E: Bo 1433); **B**, **D**, **F**: *A. aptera* (B: Bo 1457; D: Bo 1292; F: Bo 1225); **G**: *A. bergi* (Bo 1274); **J**: *Blattella germanica* (ex cult.); **K**: *Symploce pallens* (ex cult.); **L**: *Xestoblatta cantralli* (Costa Rica, CR 15); **M**: *Ischnoptera* sp. (Costa Rica, CR 13/1). **— *Abbreviations and symbols***: **sc** scapus; **pc** pedicellus; **me** meriston (first flagellomere of current stage); **+** new proximal flagellomeres generated by a division of the meriston into two or three flagellomeres during the preceding intermoult period in B, E, H, in C, D the division had presumably already occurred one moult earlier; **L-** early larval stage; **L+** intermediate or late larval stage; **Im** imago.

berg Natural History Collections Dresden, Dresden (Germany); MZSP, M. São Paulo – Museo de Zoologia, Universidade de São Paulo, São Paulo (Brazil); NHME, M. Maastricht – Natuurhistorisch Museum, Maastricht (Netherlands); RMNH, M. Leiden – Naturalis Biodiversity Centre, Leiden (Netherlands); TAMU – Department of Entomology, Texas A&M University, College Station, Texas (USA); USNM, M. Washington – National Museum of Natural History (Smithsonian Institution), Washington (USA); ZSM, ZS Munich – Zoologische Staatssammlung München, München (Germany).

3. Characterisation of the genus *Attaphila*

3.1. Overall features of body

Figs 21D, 28

Size very small, 2.5–3.5 mm long. Body rather stout, in dorsal view wide-oval, with strongly vaulted thoracic dorsum. Surface of pronotum, tegmina, and abdominal tergites up to **T5** loosely covered with rather long and thin bristles. Colouration almost uniform, in larvae yellowish, in imagines slightly darker, orange-brown; legs always darker than the remaining parts of the body.

3.2. Head

Figs 1A–D, 2

Head capsule in frontal view rounded-triangular (Fig. 1A–C), relatively short, in lateral view not compressed, with well-rounded occiput and frons. The lateral part of the head capsule between the anteroventral margin of the compound eye and the lateral margin of the clypeus forms a rather wide and deep funnel-shaped pit (Fig. 1A, D: **cap**; Bolívar 1901: p. 334, pl. 6); dorsal margin of the pit forming a fairly sharp edge (**capd**), walls of the trough otherwise gradually passing over to the surface of the head capsule. Ventromesal half of the pit bearing the antenna insertion, with the base of the scape being surrounded by a fairly wide articulatory membrane and approached by a tongue-shaped antennifer from ventrally. Epistomal ridge absent except for lateralmost parts. Coronal (**cc**) and frontal (**fc**) cleavage lines distinct.

Compound eyes (Fig. 1A, D: **cpe**) placed laterally, very small, not prominent from overall outline of head, with not more than about 70 ommatidia (see also Wheeler 1900). **Ocelli** missing.

Antennae (Figs 1A, C, D, 2): Scapus (**sc**) relatively long, with a distinct bend of ca. 70° at its very base (in anterior view: Fig. 1D); pedicellus (**pc**) and few basal flagellomeres (**fl1** and following) rather short; the distally following flagellomeres rapidly increasing in length, reaching their maximal length about at the level of the 7th flagellomere (ca. 3.4 × as long as wide; Figs 1A, 2F, G); diameter of flagellomeres slightly increasing up to the 6th or 7th, then slightly decreasing again; shape of flagellomeres conical, widening towards their apical end. Number of flagellomeres unknown: in imagines in most cases 7–10 (only one specimen found with 11) were present, but all antennae appear as being incomplete (Wheeler 1900; Bolívar 1901, 1905; Brossut 1976), since an intact terminal flagellomere with apically closed cuticle has never been observed (but see larval development in 3.13.). Retained distal flagellomeres according to Brossut (1976: figs 4, 5) provided with a relatively low number of sensory bristles. Hebard (1916) reports that "the joints beyond the first [scapus] are carried normally at a decided angle to it". Among the specimens available to the authors several showed an almost rectangular upward deflection of the pedicellus versus the scapus (Fig. 1C); the strong deflection is enabled by the scapus having distally a distinct rounded dorsal excavation (Fig. 1D: **scex**, which is flanked by the two usual scapo-pedicellar articulations, one visible in Fig. 1D: **sc-pc**). Two fields of sensilla basally on the scapus and one basally on the pedicellus are likely comprised of sensilla chaetica A (Fig. 1D: **s-chA**), and a few sensilla distally on the pedicellus are likely representatives of a circumferential row of sensilla campaniformia (Fig. 1D: **s-cpf**; compare Drilling and Klass 2010: S-VL, S-DL, P-D, and oval symbols in fig. 5).

Mouthparts (not studied in detail) with mandibles (**md**) and laciniae (**li**; Fig. 1B) shaped as typical for cockroaches (see Wipfler et al. 2016); mandibular dentition asymmetrical as usual in cockroaches: left mandible with 4 teeth, right one with 3 teeth (Fig. 1B inset: **I–IV**, including tip and incisivi; compare Wipfler et al. 2016: fig. 9E,

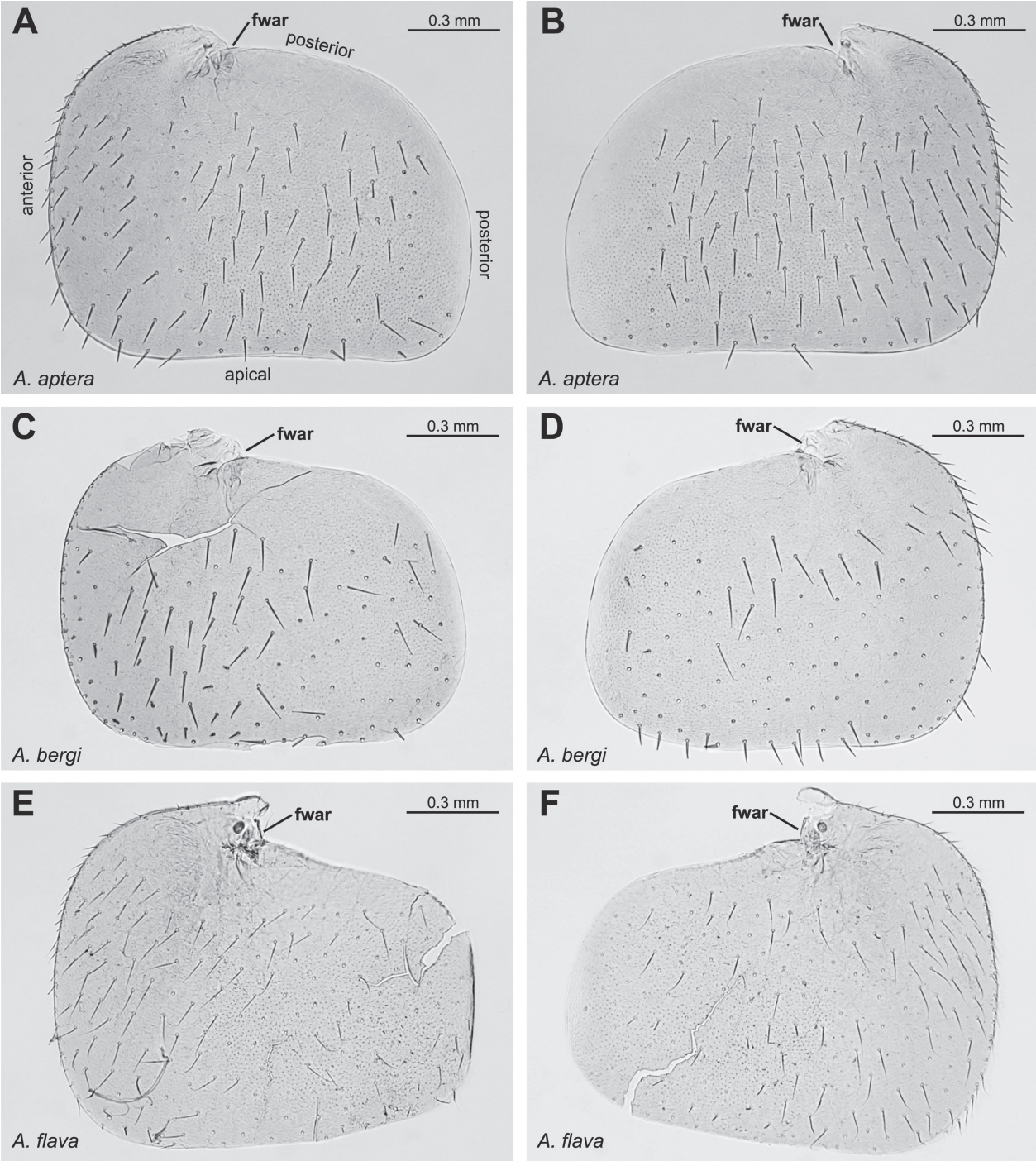


Figure 3 (A–F). Tegmina (forewings) of males of *Attaphila* species, dorsal views, left tegmen at the left. – Species: **A**, **B**: *A. aptera* (Bo 1252); **C**, **D**: *A. bergi* (Bo 1443); **E**, **F**: *A. flava* (HT Bo 1280).— ***Abbreviation***: **fwar** forewing articulation area. In A borders specified as addressed in the text.

F). Maxillary palps with 5, labial palps with 3 palpomeres (**I–V** of **mp**, **lp** in Fig. 1B), the apical one in both cases the longest and widest, and, according to Brossut (1976: figs 6–9), on the ventral surface densely covered with sensory bristles; **mpIV** with a distinct basal bend.

Tentorium (Fig. 1A, C, D) of typical blattodean structure (compare Klass and Eulitz 2007: figs 2–8), with anterior transversal bridge (**atb**) and perforation (**tp**) behind it; origin of anterior arms (**ata**) from head capsule in typical position but very narrow (Fig. 1C, D).

3.3. Thoracic nota

Fig. 1E, F

Pronotum (**N1**) almost completely concealing the head, in dorsal view rounded-trapezoidal, narrowing towards the anterior, with almost straight anterior border. Meso- (**N2**) and metanotum (**N3**) in females (in dorsal view) with fairly straight anterior and posterior borders and widely rounded anterolateral corners; in males more or less trapezoidal, narrowing towards the posterior (Fig. 1G, H).

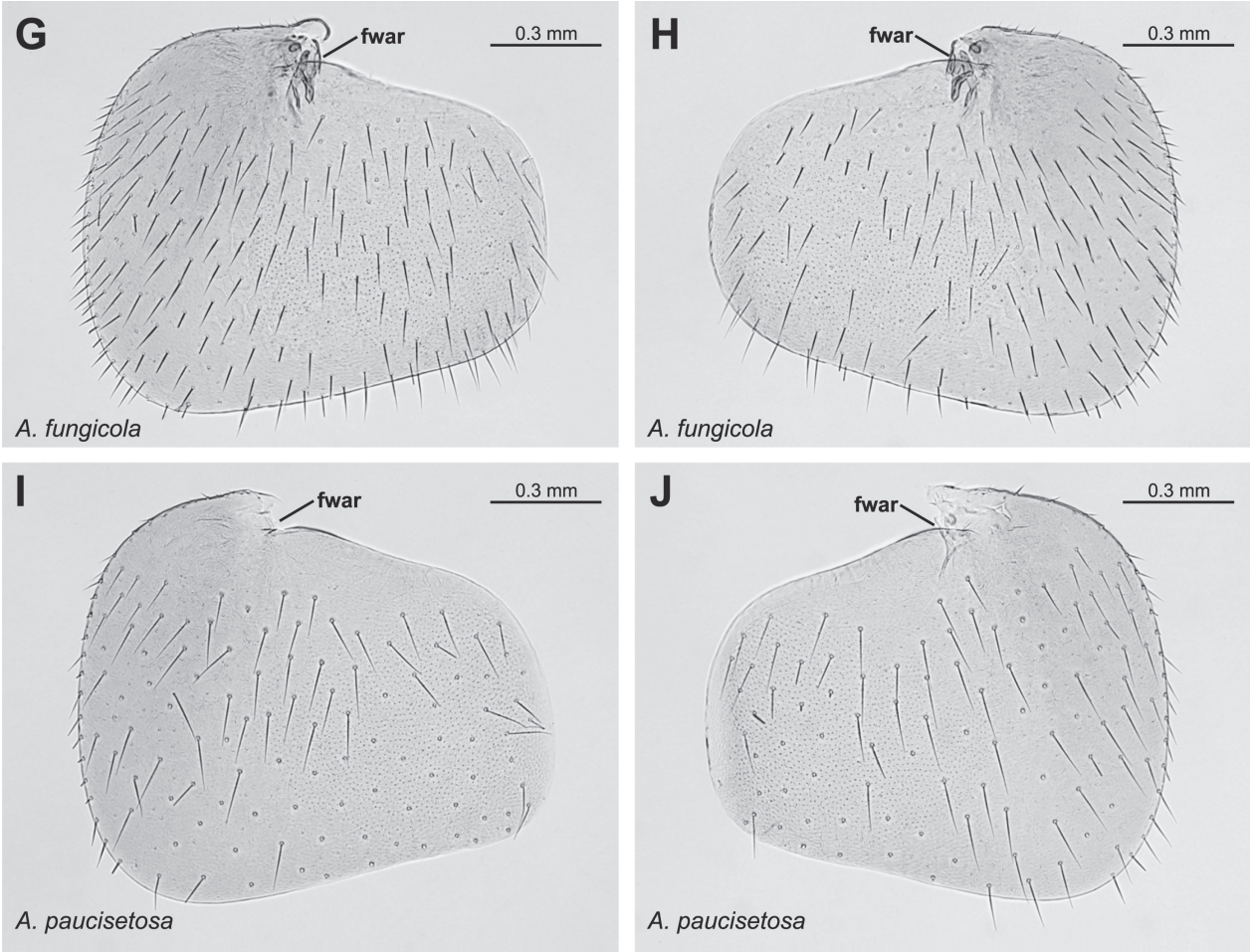


Figure 3 (G–J). Tegmina (forewings) of males of *Attaphila* species, dorsal views, left tegmen at the left. – Species: **G**, **H**: *A. fungicola* (Bo 1229); **I**, **J**: *A. paucisetosa* (Bo 1441). — ***Abbreviation***: **fwar** forewing articulation area. In A borders specified as addressed in the text.

3.4. Wings

Figs 1G, H, 3

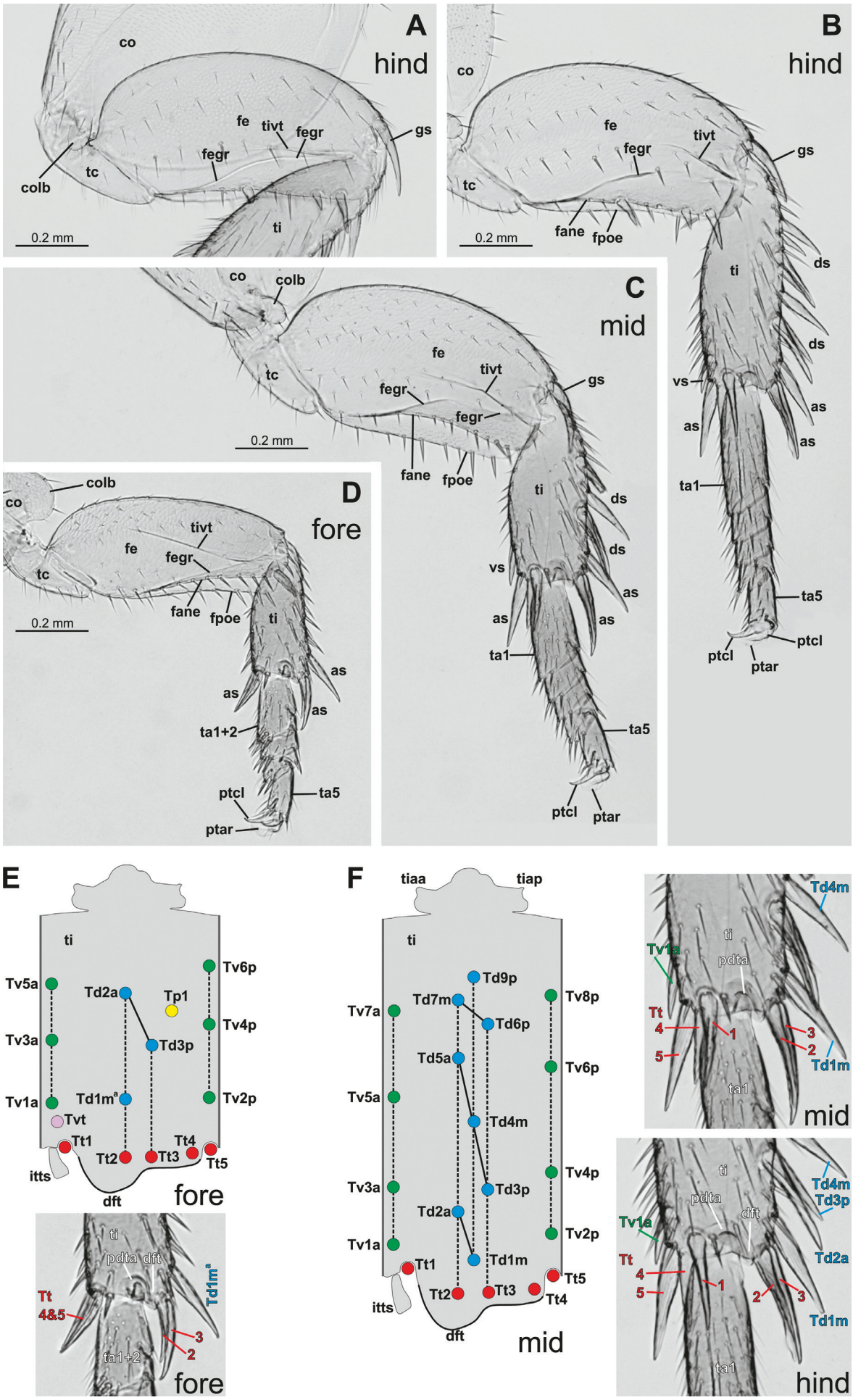
Males with tegmina (Figs 3, 28A–E) short, apically either transversally or obliquely cut (i.e. either at right angle or from anterodistally to posteroproximally, relative to longitudinal axis of wing), posteriorly scarcely surpassing the metanotum, mesally reaching the thoracic midline, without any venation, loosely covered with long and thin bristles; hindwings (Fig. 1G, H) only consisting of tiny lobes of about half the length of the metanotum. Females without wings (Figs 1E, 21D).

3.5. Legs

Fig. 4

Rather short and stout. Each coxa with a distinct coxal lobelet (**colb**) on its distal border (as in most or perhaps all Dictyoptera). Femora (**fe**) and tibiae (**ti**) anteroposteriorly compressed. Femora at the base with steeply increasing height (dorsoventral extension). Anterior and posterior walls considerably protruded beyond the narrow ventral surface (edges **fane** and **fpoe**), thus forming a proximally flattening groove (femoral groove **fegr**) which can take up part of the tibia during a strong flexion (Fig. 4A). Apical dorsal fold of tibia (**dft**; at bases of spines **Tt2**, **Tt3** in Fig. 4E, F) virtually absent (compare **dft** in Klass et al. 2009: figs 1, 2). Tarsi (**ta**) rather stout, with five tarsomeres (Fig. 4H of right tarsus; four tarsomeres with vestigial dorsal separation of tarsomeres 1 and 2 in left foreleg, Fig. 4D, G, likely result from regeneration after loss), tarsomeres 1–4 fairly cylindrical, without basal constriction, tightly closed together, borders between them oblique, without euplantulae, ventroapically supplied with small spines in a transversal row. Pretarsus consisting of two symmetrical unspecialised claws (**ptcl**) and a large arolium (**ptar**) in between.

Spine armament of femora. Forefemur (Fig. 4D) with only one apical spine, positioned at the anteroventral edge (**fane**) and proximally followed by a row of more or less strong setae (Type D1, Roth 2003). Midfemur (Fig. 4C) also with only one spine, but apically at the dorsal surface (**gs** = genicular spine). Hindfemur (Fig. 4A, B) also with one genicular spine and 2–4 spines at the anteroventral edge (**fane**); one of the latter always near midlength of femur, the others at some distance near apex.


A
hind
co
fe
tivt
fegr
gs
fegr
tc
colb
ti
0.2 mm
B
hind
co
fe
tivt
fegr
gs
tc
fane
fpoe
ti
ds
ds
vs
as
as
as
ta1
ta5
ptcl
ptcl
ptar
0.2 mm
C
mid
co
colb
fe
tivt
tc
fegr
gs
fegr
fane
fpoe
ti
ds
ds
vs
as
as
as
ta1
ta5
ptcl
ptar
0.2 mm
D
fore
colb
co
tivt
fe
fegr
tc
fane
fpoe
ti
as
as
as
ta1+2
ptcl
ta5
ptar
0.2 mm
E
ti
Tv5a
Td2a
Tp1
Tv6p
Tv4p
Tv3a
Td3p
Tv1a
Td1m^a
Tv2p
Tvt
Tt1
Tt4
Tt2
Tt3
Tt5
itts
dft
fore
ti
pdta
dft
Tt
4&5
Td1m^a
3
2
ta1+2
fore
F
tiaa
tiap
ti
Td9p
Td7m
Tv8p
Tv7a
Td6p
Td5a
Tv6p
Tv5a
Td4m
Tv4p
Tv3a
Td3p
Td2a
Tv2p
Tv1a
Td1m
Tt1
Tt5
Tt2
Tt3
Tt4
itts
dft
mid
Td4m
ti
Tv1a
pdta
Tt
4
1
3
2
5
Td1m
ta1
mid
ti
Td4m
Td3p
pdta
dft
Tv1a
Td2a
Tt
4
1
2
3
5
Td1m
ta1
hind

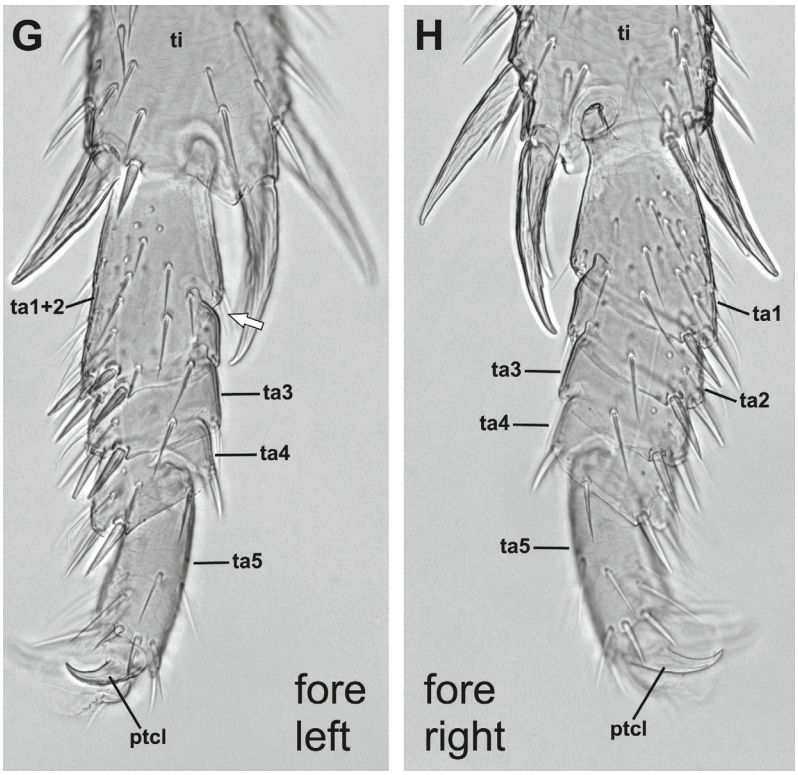


Figure 4. Legs of left side (A–G) or right side (H) of female *Attaphila paucisetosa* (A: Bo 1235, B–D, H, G: PT Bo 1226), anterior view, made transparent by treatment with KOH. Hindleg (**A**, **B**), midleg (**C**), and foreleg (**D**, **G** [left leg regenerated, with only four tarsomeres], **H** [right leg with five tarsomeres]), with conventional terminology of tibial spines. **E** and **F** show a general scheme of cockroach tibia spination of the foreleg (**E**) and midleg (**F**; similar on hindleg) (tibia base on top, tibia cut along ventral midline and spread, spine bases represented by circles filled with different colours according to groups of spines) and distal part of tibia of fore- (**E**), mid-, and hindleg (**F**) of *Attaphila* (from B, C, D, 1.5× enlarged), with spine terminology according to Klass et al. (2009) and unpublished work by K.-D. Klass and coworkers. **G** and **H** show tarsus of left (**G**) and right (**H**) foreleg enlarged (compare D); white arrow in G pointing to dorsal vestige of subdivision between tarsomeres 1 and 2. — ***Abbreviations***: **co** coxa; **colb** coxal lobelet; **tc** trochanter; **fe** femur; **fegr** ventral groove of femur which can take up part of tibia during strong flexion as shown in (A) (bottom of groove indicated); **fane** and **fpoe** antero- resp. posteroventral edge flanking femoral groove; **ti** tibia; **tiaa** and **tiap** anterior resp. posterior articulation of tibia with femur; **tivt** ventral basal tendon of tibia; **dft** dorsal fold on apical margin of tibia; **itts** intertibiotarsal sclerite; **pdta** posterodorsal tibiotarsal articulation (on opposite side of leg); **ta1–5** tarsomeres 1–5; **ptcl** claws of pretarsus; **ptar** arolium of pretarsus; **gs** genicular spine of femur. Spines of tibia (see Supplement 1 for complete abbreviations): **as** apical spines (= terminal spines **Tt1–5** plus distal mediodorsal spine **Td1m** [mid- and hindleg] or distal anterodorsal spine **Td1m**[a] [foreleg]); **ds** dorsal spines (= dorsal spines **Td** excluding **Td1m** [mid- and hindleg] and **Td1m**[a] [foreleg]); **vs** ventral spines (= ventral spines **Tv**).

Table 1. Spine armament of *Attaphila* legs: Number of spines on femur and tibia. ***Femur***: 1st column = genicular spine, 2nd column = spines along anteroventral edge. ***Tibia***: 5.6.1 etc. = 5 spines on **d**orsal suface outside apical armament, 6 spines in **a**pical armament, 1 spine on **v**entral surface outside apical armament; corresponds with information [d a v] given in formula (see 2.4.). Numbers in brackets: rare events. * Only one leg from one specimen available; the occurrence of only 5 apical spines in the hindtibia of *A. multisetosa* is doubtful; whether this number is the rule in *A. sexdentis* is also uncertain since, as in the former species, only one leg was available for counting.

***Attaphila* species**	**Foreleg**			**Midleg**			**Hindleg**		
	Femur		Tibia	Femur		Tibia	Femur		Tibia
A. aptera	0	1	0.5.0	1	0	(4)5.6.1	1	2–3(4)	7–8(9).6.1
A. bergi	0	1	0.5.0	1	0	(4)5.6.1	1	(3)2	7.6.1
A. flava	0	1	0.5.0	1	0	4.6.1	1	3	6.6.1
A. fungicola	0	1	0.5.0	1	0	4.6.1	1	3	(7)6.6.1
A. multisetosa	0	1	0.5.0	1	0	5.6.1	1	3	7.5?.1*
A. paucisetosa	0	1	0.5.0	1	0	4.6.1	1	3	6–7.6.1(0)
A. schuppi	0	1	0.5.0	1	0	5.6.1	1	2	7.6.1
A. sexdentis	0	1	0.?.0	1	0	4.6.1	1	4	7.5.1*
A. sinuosocarinata	0	1	0.5.0	1	0	4–5.6.1	1	3	7.6.1
Attaphila, range	0	1	0.5.0	1	0	4–5.6.1	1	2–4	6–9.5–6.0–1

Spine armament of tibiae. Spine formula (for explanation see section 2 and Table 1) [0·5·0][4–5·6·1][6–9·5–6·0–1]. Apical armament (**as**) of mid- and hindtibiae (Fig. 4B, C, F) as typical for cockroaches with 5 terminal spines (**Tt1–5**), all in typical positions (compare in Klass et al. 2009: figs 1, 2 for *Blaberus*), and a far distally placed middorsal spine (**Td1m**); in foretibia (Fig. 4D, E) with 4 terminal spines (**Tt2–5**; spine **Tt1** missing)

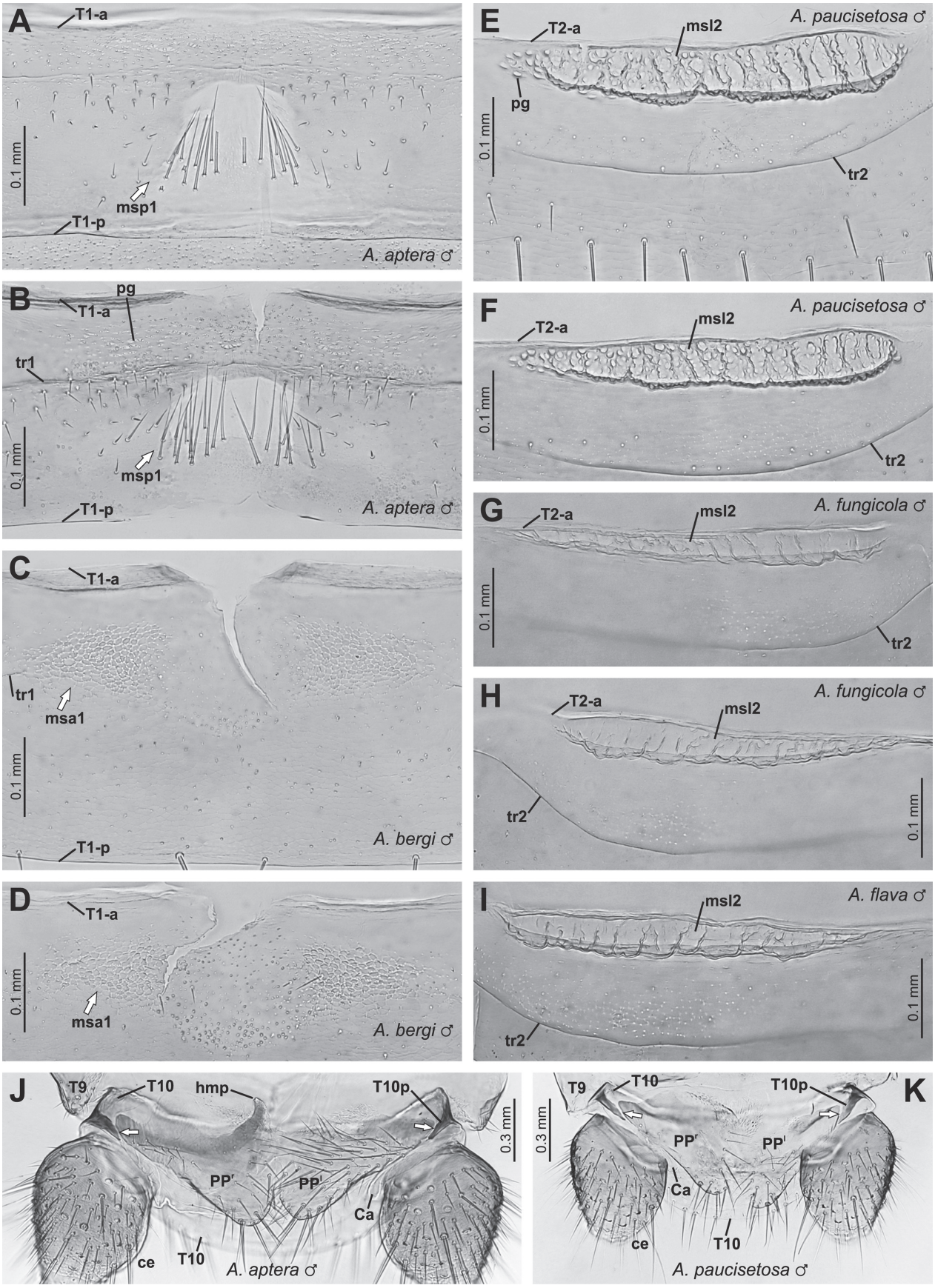


Figure 5. A–I: Tergite specialisations of the males of *Attaphila* species, medially on T1 (**A**–**D**), or laterally at the anterior border of T2 (**E**–**I**), in E–G from right side of tergite, in H and I from left side. — ***Species***: **A**, **B**: *A. aptera* (Bo 1227, HT Bo 1258); **C**, **D**: *A. bergi* (Bo 1283, Bo 1274); **E**, **F**: *A. paucisetosa* (PT Bo 1254, Bo 1256); **G**, **H**: *A. fungicola* (LT Bo 1265); **I**: *A. flava* (HT Bo 1280). — ***Abbreviations***: **T1-a**, **T2-a** anterior borders of tergites T1,2; **T1-p** posterior border of T1; **tr1**, **tr2** transversal ridges of T1,2; **msa1** anterior median specialisation of tergite T1; **msl2** lateral specialisation of tergite T2; **msp1** posterior median specialisation of tergite T1; **pg** pores of glands, tiny in A, B, between T1-a and tr1, larger in E as part of msl2 specialisations. — **J**, **K:** Paraprocts, tergite 10 and cerci in ventral view, of **J**: *A. aptera* (Bo 1224) and **K**: *A. paucisetosa* (HT Bo 1258). — ***Abbreviations and arrows***: **Ca** sclerite at mesal base of cercus; **ce** cercus; **hmp** hook-like mesal projection of paraproct; **PP^{l}**, **PP^{r}** left and right paraproct; **T9** tergite 9; **T10** tergite 10 with its ventrally bent lateral (paratergal) parts **T10p** (larger median parts of T10 out of focus); white arrows: articulation between mesal end of T10p and lateral end of paraproct.

and a distal anterodorsal spine (**Td1m^{a}**). Foretibia with no dorsal (besides **Td1m^{a}**) and no ventral spine; midtibia with 4–5 dorsal (in addition to **Td1m**) and 1 ventral spine; hindtibia with 6–9 dorsal (in addition to **Td1m**) and 1 ventral spine. The numbers of spines on femora and tibiae show fairly wide ranges of variation within the species combined with much overlap among the species; spine armament is therefore unsuitable for species identification.

3.6. Abdominal tergites

Figs 5–13

Shape. T1,2 with weakly convex, **T3–6** with fairly straight posterior border (**T*n*-p**). **T7** of females (e.g. Fig. 6E) in the median half with a short, wide lobe-like posterior expansion, whose posterior border is medially slightly convex or concave, or straight; posterior border **T7-p** laterally of the lobe concave; transversal ridge **tr7** always distinct and in parallel with the posterior tergal border **T7-p**. **T7** of males (Fig. 6A) with median lobe less prominent, transversal ridge **tr7** usually distinct, but in some species weakly developed (Fig. 13D) or completely missing (Fig. 13E, F). **T8,9** (Figs 6B, 7C) in both sexes rather short, weakly sclerotized, concealed below the preceding tergite **T7**. **T10** (Figs 6B, 19A) rather short, with widely rounded posterior border **T10-p**; the lateral parts **T10p** bending to the ventral side (to meet the paraprocts, **PP**) are very narrow (Fig. 5J, K, arrows point to contact between **T10p** and **PP**).

Distribution of bristles. T1–5 usually loosely covered with long and thin bristles; the males of *A. aptera* and *A. bergi* on **T1** without such long bristles. They are in all species arranged in one line along the lateral and posterior borders. The distribution of the remaining bristles on the surface, between the transversal ridge **tr*n*** and the posterior border **T*n*-p**, is species-specifically different: either in only one distinct transversal line (Fig. 9B, E), in two very irregular transversal lines (Fig. 7A), or more or less irregularly dispersed (Fig. 8C). The bristles along the lateral borders are usually slightly shorter, but stronger than those along the posterior border and on the surface; the bristles along the posterior border of **T5** are often more densely arranged than on the preceding tergites (Fig. 7A, D). **T6,7** in both sexes along the lateral borders with similar bristles as on the preceding tergites. Size and arrangement of bristles at other places of **T6,7** different in the two sexes: ***Females*** (Figs 12A–F, 13A, B) always without bristles along the posterior border of both **T6** and **T7**. Transversal ridge **tr6** usually with several bristles of small or medium size, **tr7** with only two rather small bristles at a distance of about ¼ of tergite width. Surface behind the ridge provided with bristles species-specifically varying in size and number; the bristles are usually arranged in a wide median transversal stripe of varying lateral extension (ranging from slightly less than ½ to about ⅔ of tergite width), on **T7** usually in lower density and extension. ***Males*** (Fig. 13C–F) with much smaller bristles along the transversal ridge, bristles on the surface or along the posterior border present or absent.

Male tergite glands. Glandular pores occur on **T1–5** in the area anteriorly of the transversal ridge, mostly rather dispersed, but in *A. aptera* in extremely high density (Fig. 5A, B); they are usually tiny, larger ones are found in and near the specialisations on **T2** (**msl2**).

Male tergite specialisations. The males of *A. flava*, *A. fungicola*, and *A. paucisetosa* have a pair of specialisations laterally at the anterior border of tergite **T2**, each consisting of a shallow transversal trough with a mesolateral extension of about ¼ of tergite width (Figs 9B, 5E–I: **msl2**). The bottom of each trough shows a more or less complicated relief generated by rather low, rounded ridges crossing the trough. The males of *A. aptera* and *A. bergi* have a specialisation medially on tergite **T1**. In *A. aptera* (Figs 6A, 5A, B: **msp1**) this is a small, fairly rounded, weakly sclerotized area with two groups of relatively long bristles pointing anteriorly, located immediately posterior to ridge **tr1**. In *A. bergi* (Fig. 5C, D: **msa1**) the specialisation consists of a pair of small areas in the anterior part of **T1** showing a net-like pattern produced by delicate furrows (for the identification as furrows rather than ridges see explanation in Supplement 6 Fig. S4), along which tiny glandular pores are sporadically arranged; specialised areas occasionally with few small bristles (Fig. 5D). The net-like pattern of the specialisation is strongly emphasised microreticulation, which is continuous with much less emphasised microreticulation further posteriorly on **T1**. **T1** in the former three species and **T2** in the latter two species without specialisations. **T1** in the latter two species ad-

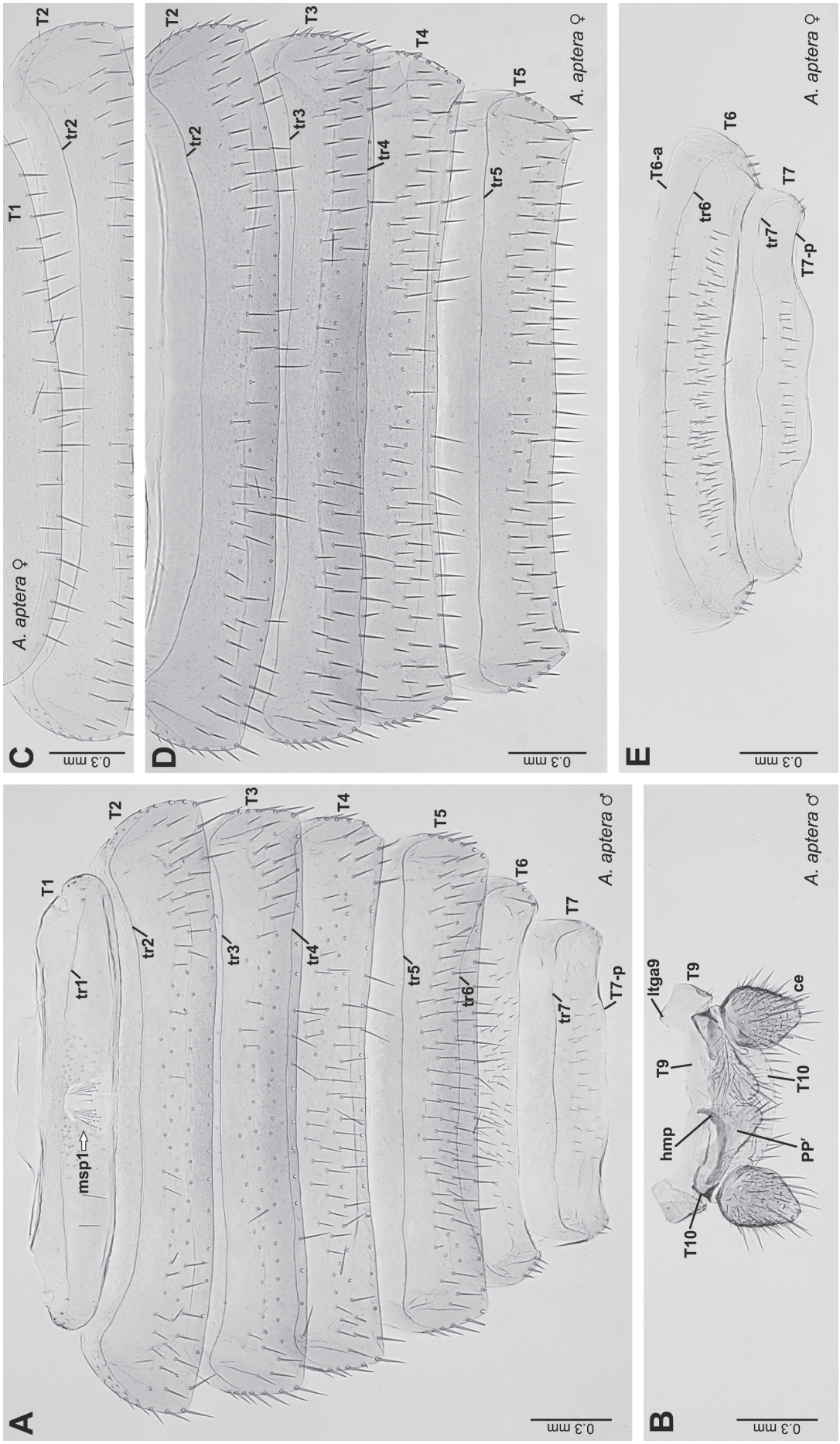


Figure 6. Abdominal tergites and terminalia of *Attaphila aptera*. **A**, **B:** Male. **A**: T1–7 (Bo 1227; see also Fig. S1A), T1 with median specialisation including its bristles, otherwise without long bristles (the two long bristles on the left have no base and are certainly contaminations from other tergites); **B**: Terminalia (Bo 1256), ventral view, with T9 and T10, cerci, and paraprocts. **C**–**E:** Female. **C**: Parts of T1,2 (Bo 1257); **D**: T2–5 (Bo 1253; see also Fig. S1B); **E**: T6,7 (Bo 1253). — ***Abbreviations***: **ce** cercus; **hmp** hook-like mesal projection on right paraproct; **ltga9** lateral tergal apodeme of tergite T9; **msp1** posterior median specialisation of T1; **PP'** right paraproct; **T*n*** tergite (numbered); **T*n*-a** anterior border of tergite (numbered); **T*n*-p** posterior border of tergite (numbered); **tr*n*** transversal ridge of tergite (numbered).

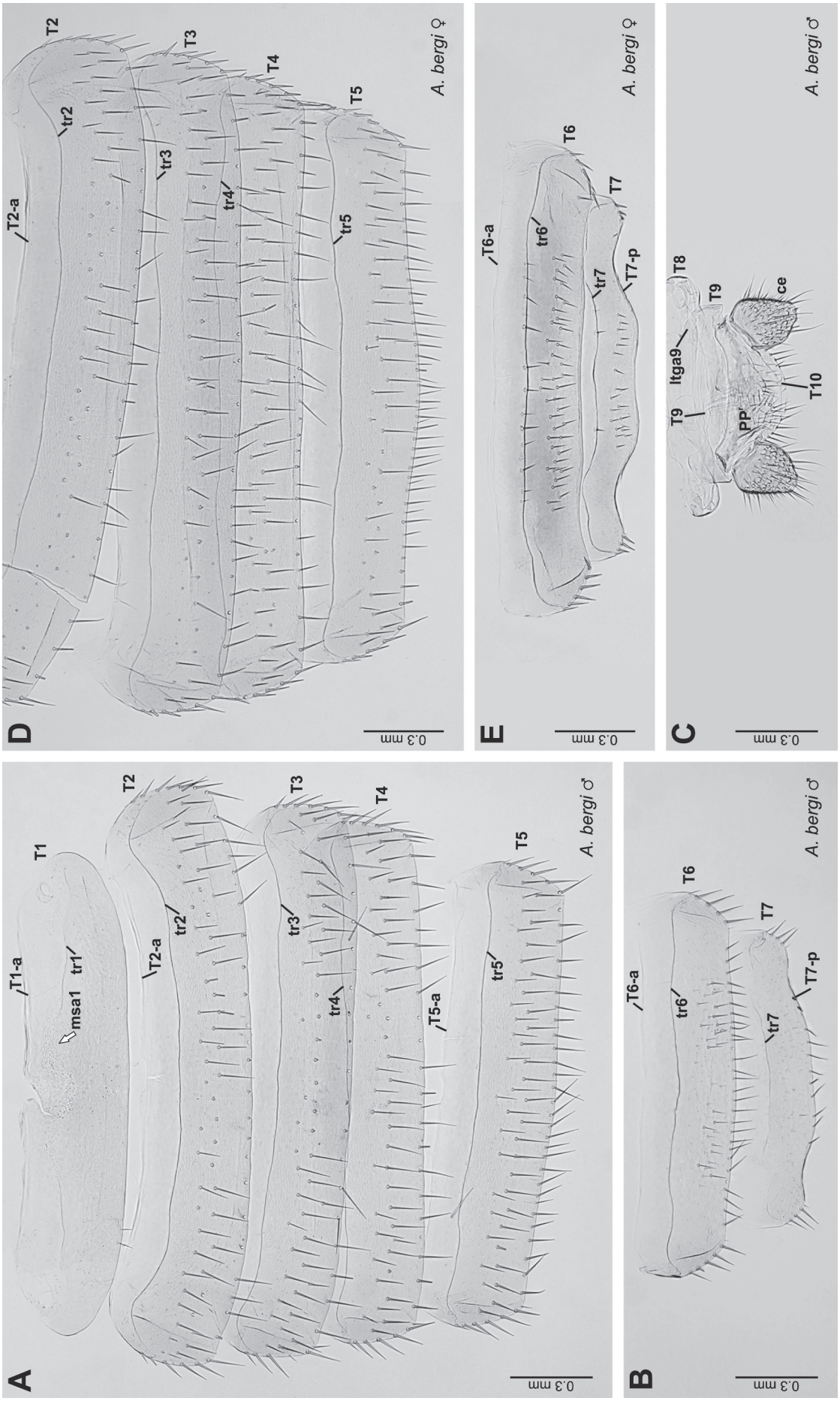


Figure 7. Abdominal tergites and terminalia of *Attaphila bergi*. **A–C:** Male (Bo 1274). **A**: T1–5 (see also Fig. S1C), T1 without long bristles, the median specialisation, around the median scratch, is hardly visible (see Fig. 5D); **B**: T6,7; **C**: Terminalia, ventral view, with T8–10, cerci, and paraprocts. **D, E:** Female (Bo 1282). **D**: T2–5; **E**: T6,7. — ***Abbreviations***: **ce** cercus; **ltga9** lateral tergal apodeme of tergite T9; **msa1** anterior median specialisation of T1; **PP'** right paraproct; **T*n*** tergite (numbered); **T*n*-a** anterior border of tergite (numbered); **T*n*-p** posterior border of tergite (numbered); **tr*n*** transversal ridge of tergite (numbered).

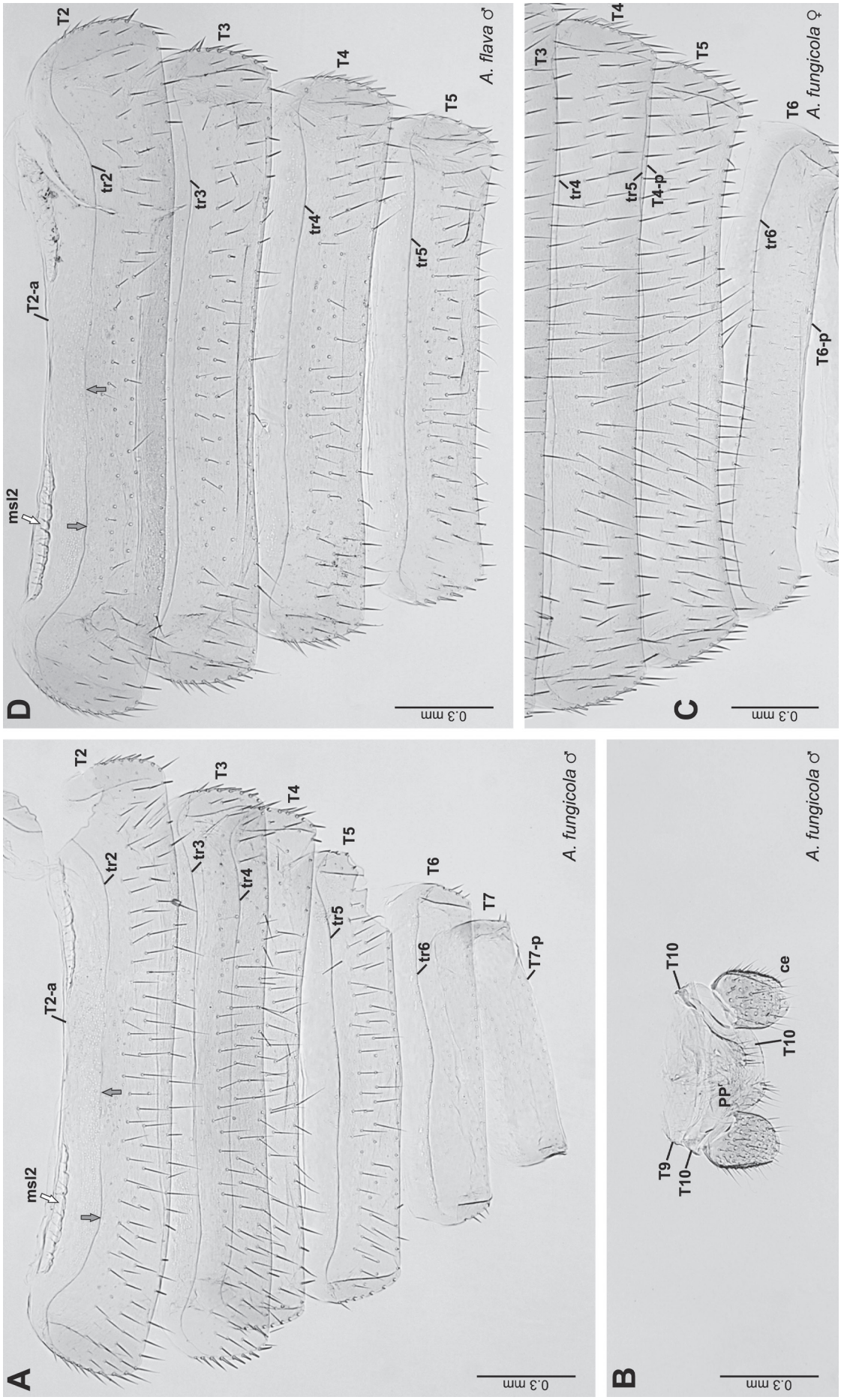


Figure 8. Abdominal tergites and terminalia of *Attaphila* species. **A–C:** *A. fungicola*. **A, B**: Male (Bo 1229). **A**: T2–7, T2 with lateral specialisations; **B**: Terminalia, ventral view, with T9 (damaged: only right half) and T10, cerci, and paraprocts. **C**: Female (Bo 1264), T4–6. **D**: *A. flava*, male (HT Bo 1280), T2–5, T2 with lateral specialisations. — ***Abbreviations***: **ce** cercus; **ltga9** lateral tergal apodeme of tergite T9; **msl2** lateral specialisation of T2; **PP**r right paraproct; **T*n*** tergite (numbered); **T*n*-a** anterior border of tergite (numbered); **T*n*-p** posterior border of tergite (numbered); **tr*n*** transversal ridge of tergite (numbered). **Grey arrows** pointing to excurvations of male **tr2**.

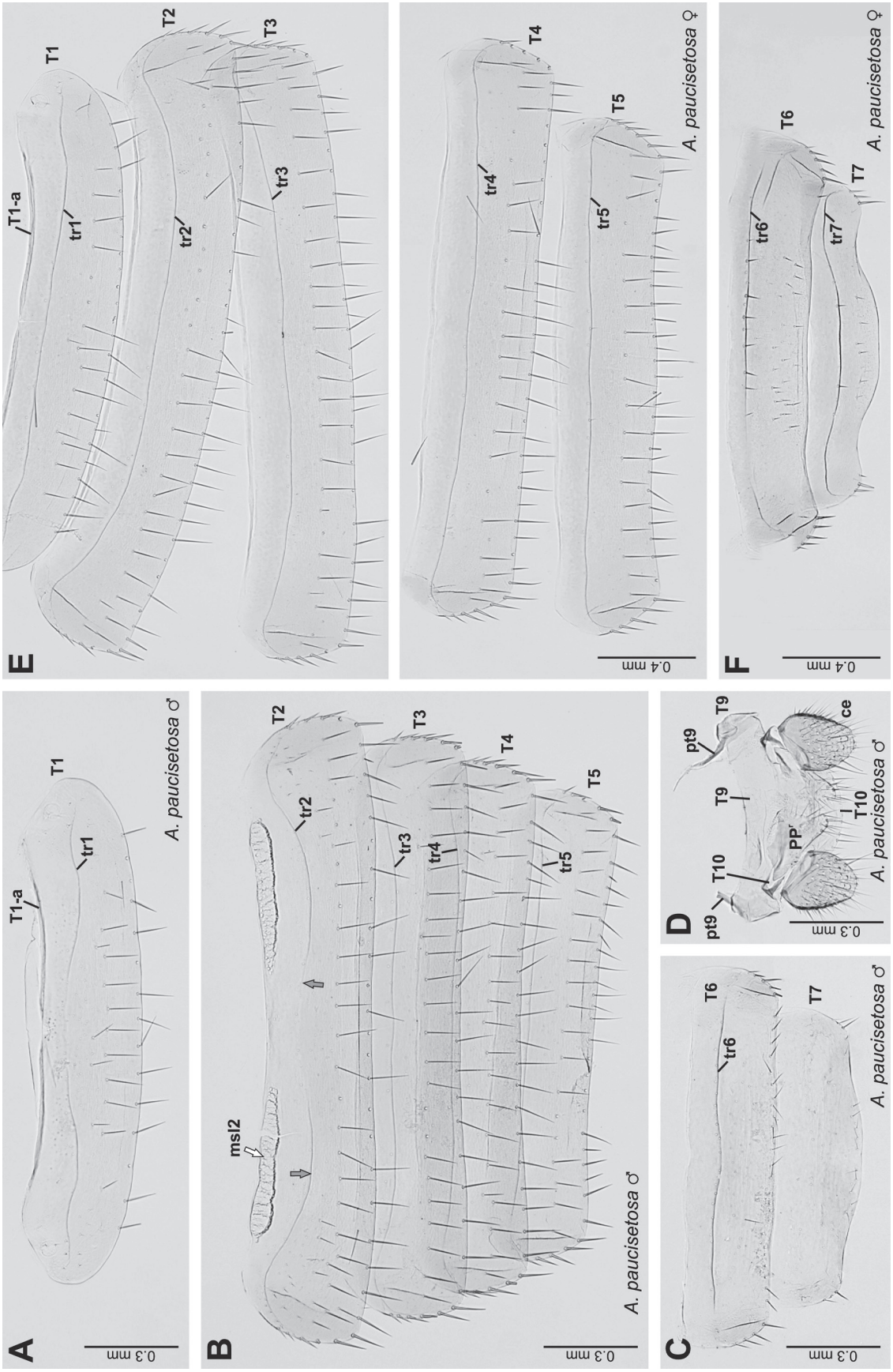


Figure 9. Abdominal tergites and terminalia of *Attaphila paucisetosa*. **A–D:** Male (HT Bo 1258). **A**: T1; **B**: T2–5, T2 with lateral specialisations; **C**: T6,7. **D**: Terminalia, ventral view, with T9 (with lateral extension) and T10, cerci, and paraprocts. **E, F:** Female (PT Bo 1255). **E**: T1–5; **F**: T6,7. — ***Abbreviations***: **ce** cercus; **msl2** lateral specialisation of T2; **PP'** right paraproct; **T*n*** tergite (numbered); **pt9** extension of paratergite of T9; **T*n*-a** anterior border of tergite (numbered); **tr*n*** transversal ridge of tergite (numbered). **Grey arrows** pointing to excurvations of male **tr2**.

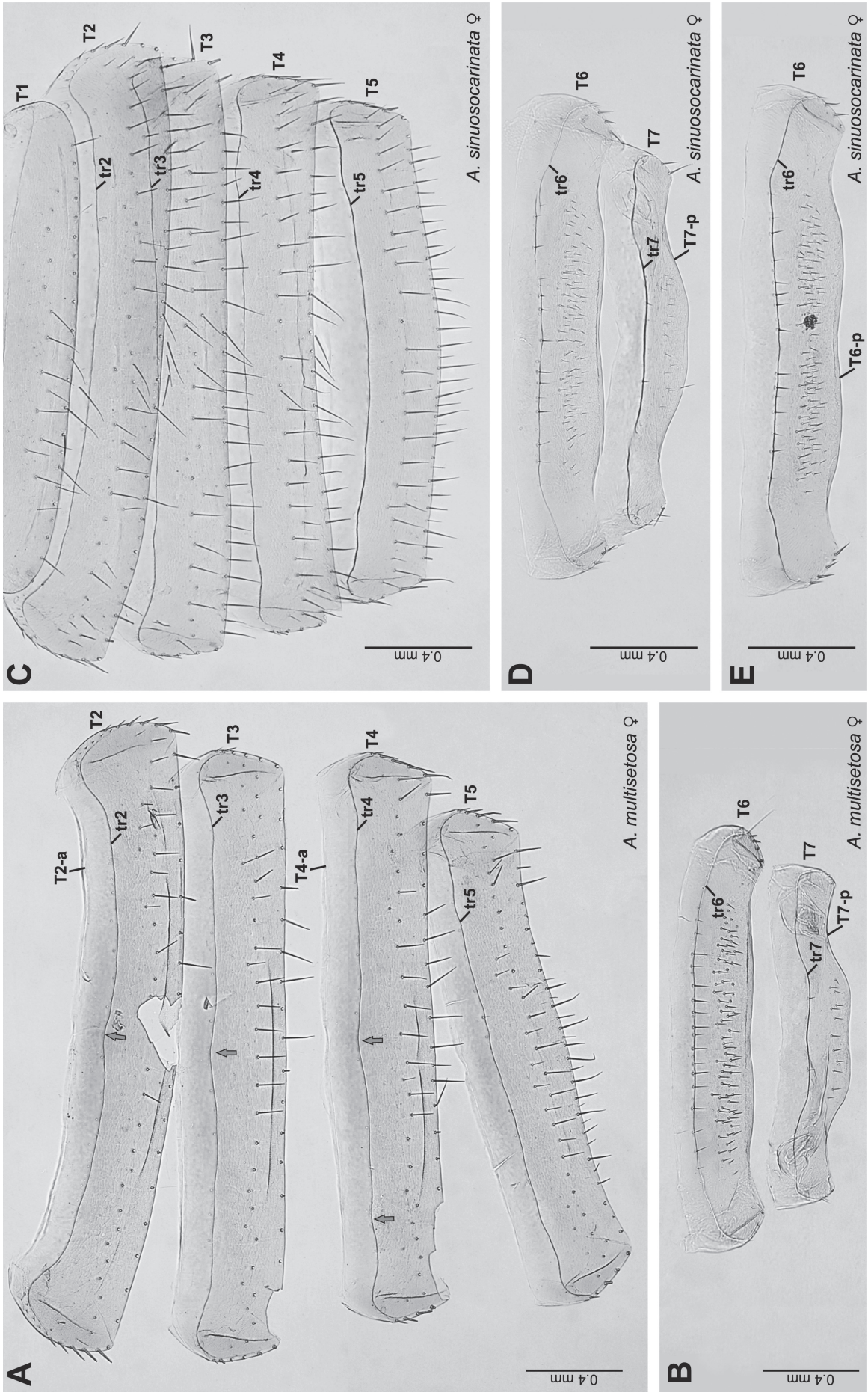


Figure 10. Abdominal tergites of *Attaphila* species only known from the female sex. **A**, **B**: *A. multisetosa* (HT Bo 1270). **A**: T2–5; **B**: T6,7. **C**–**E**: *A. sinuosocarinata*. **C**: T1–5 (HT Bo 1273); **D**: T6,7 (HT Bo 1273); **E**: T6 (PT Bo 1288). — ***Abbreviations***: **T*n*** tergite (numbered); **T*n*-a** anterior border of tergite (numbered); **T*n*-p** posterior border of tergite (numbered); **tr*n*** transversal ridge of tergite (numbered). **Grey arrows** pointing to weak median and lateral excurvations of transversal ridges to the anterior.

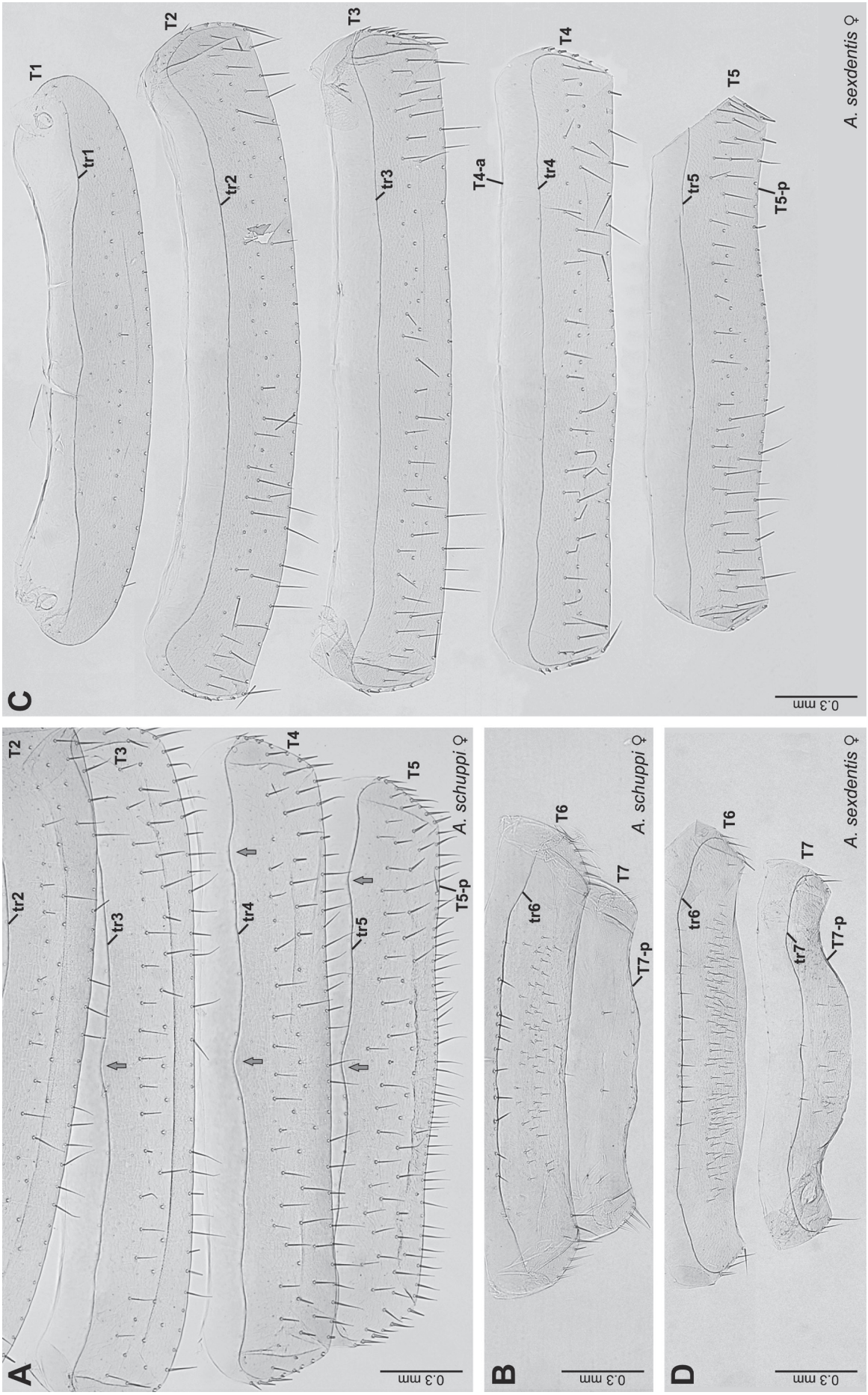


Figure 11. Abdominal tergites of *Attaphila* species only known from the female sex. **A, B:** *A. schuppi* (ST Bo 1237). **A**: T2–5; **B**: T6,7. **C, D:** *A. sexdentis* (HT Bo 1233). **C**: T1–5; **D**: T6,7. — ***Abbreviations***: **T*n*** tergite (numbered); **T*n*-a** anterior border of tergite (numbered); **T*n*-p** posterior border of tergite (numbered); **tr*nn*** transversal ridge of tergite (numbered). **Grey arrows** pointing to median and lateral excurvations of transversal ridges to the anterior.

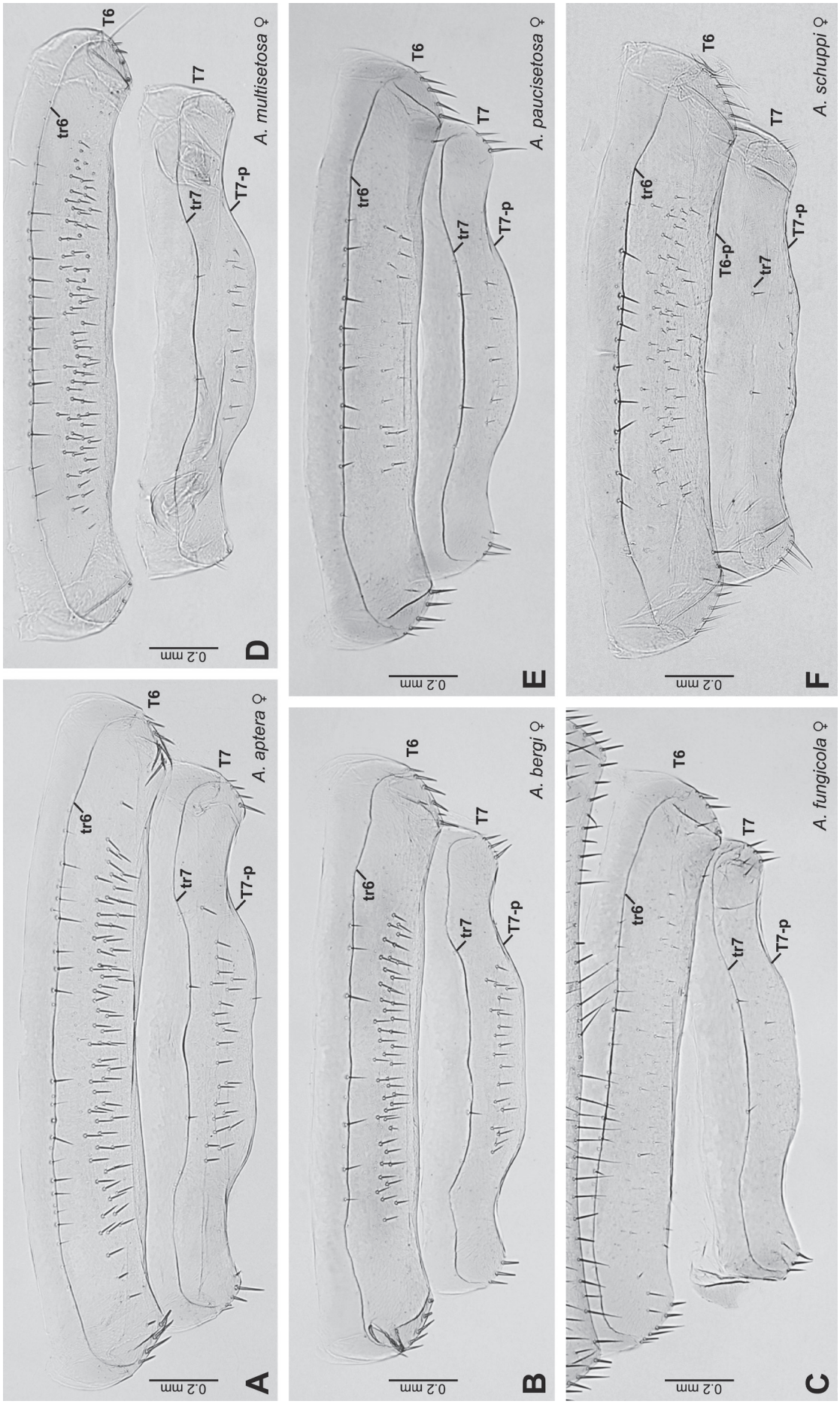


Figure 12. Abdominal tergites T6,7 of females of *Attaphila* species. **A**: *A. aptera* (Bo 1257). **B**: *A. bergi* (Bo 1282). **C**: *A. fungicola* (Bo 1264). **D**: *A. multisetosa* (HT Bo 1270). **E**: *A. paucisetosa* (PT Bo 1255). **F**: *A. schuppi* (ST Bo 1237), transversal ridge tr7 almost completely missing, only tiny remnants present near the associated bristles (see Fig. 14F). — ***Abbreviations***: **T6**, **T7** tergites T6, T7; **T6-p**, **T7-p** posterior borders of tergites T6, T7; **tr6**, **tr7** transversal ridges of tergites T6, T7.

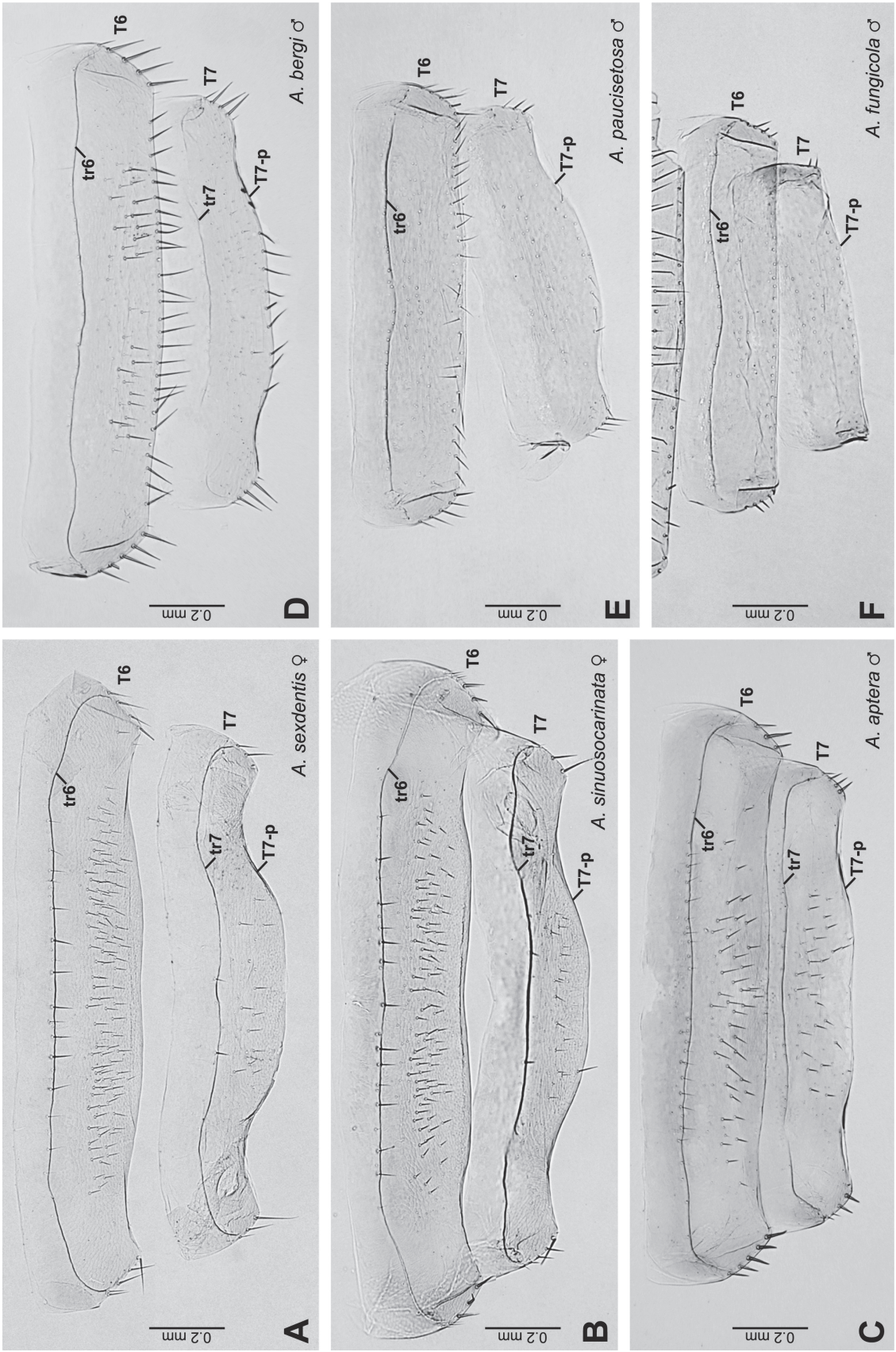


Figure 13. Abdominal tergites T6,7 of females (**A**, **B**) and males (**C**–**F**) of *Attaphila* species. **A**: *A. sexdentis*, female (Bo 1233). **B**: *A. sinuosocarinata*, female (HT Bo 1273). **C**: *A. aptera*, male (Bo 1256). **D**: *A. bergi*, male (Bo 1274), transversal ridge tr7 weakly developed, sublaterally with a large gap. **E**: *A. paucisetosa*, male (Bo 1240), transversal ridge tr7 missing. **F**: *A. fungicola*, male (Bo 1229), transversal ridge tr7 missing. — ***Abbreviations***: **T6**, **T7** tergites T6, T7; **T6-p**, **T7-p** posterior borders of tergites T6, T7; **tr6**, **tr7** transversal ridges of tergites T6, T7.

ditionally characterised by the abovementioned absence of long bristles on surface and lateral and posterior borders.

Tergite T9. In both sexes **T9** and **T8** are very short and entirely hidden as they are overfolded by the hind part of **T7**. Dorsolaterally the anterior border of **T9** of both sexes forms on each side a distinct semicircular apodeme (**ltga9**, for males in Figs 6B, 7C; schematic view in Fig. 28G). The ventrally bent lateralmost part of **T9** (paratergal part **T9p**) is narrowed towards the anterior, its terminal part forming an anteromesally directed, slightly mesally curved sclerite arm running along the anterior border of segment 9 (paratergal extension **pt9** of male, **pt8,9** of female). The tip of this arm closely approaches the lateral margin of **S9** in the male, forming a loose articulation (**A1**) with it (Figs 24A, 25A–D, 29C, H); in the female it approaches the lateral gonangulum sclerite (**gg-l**) if this is present, forming a close articulation (**A1**) with it (Fig. 19A; for further contacts of the female **pt8,9** see 3.9.). In both sexes the paratergal extension is strengthened by an internal ridge, which is part of the antecosta of segment 9 (**ac9**, for male see inserted section in Fig. 29G). We call the arm of the female **pt8,9**, as generally in Dictyoptera the posterior part of **T8** contributes to this structure (although with varied clarity in different taxa, and not resolved for *Attaphila*; Klass 1998: figs 11–18; Brannoch et al. 2017: TG8+9ε in fig. 14C). In the male we call the arm **pt9**, as there is no indication of a contribution from **T8**.

3.7. Cerci

Very short, without any annular divisions; dorsal surface almost plane, smooth, lateral and mesal flanks of cerci not visibly depressed to form a keel (compare *Lobopterella* in Fig. 29D); bristles and sensilla mostly restricted to the vaulted ventral surface. Outline in ventral or dorsal view egg-shaped (males of all species, Fig. 6B, and female of *A. schuppi*, Fig. 20C, D); or asymmetrically widened (more strongly laterally) and wider than long (remaining females, Fig. 19A).

3.8. Abdominal sternites

Female subgenital plate S7 (Figs 16–18)**.** Anterior part without apodemes. Posterior part located in ventral wall of subgenital lobe (expanded ventral fold **vf7**; with no delimitation of the lobe in the ventral segmental wall on **S7**; see **vf7** in Fig. 16A and compare MK64: fig. 40A). Subgenital lobe in all species with three short rounded apical lobes, a very wide median one and two much narrower and slightly shorter lateral ones. **S7** either semicircular (*A. sexdentis*, Fig. 17F) or rounded-rectangular (remaining species, Fig. 17B). In semicircular type anterior border strongly curved and lateral borders anteriorly converging, thus all together forming an arch. In rounded-rectangular type anterior border less strongly curved and lateral borders parallel, thus all together being quite rectangular. Subgenital plate towards its anterior border with rather weak, gradually fading sclerotisation; anterior outline in the figures, therefore, not always well visible. The transversal sternal ridge (**sr7** in Figs 16, 17), starting latero-posteriorly at the lateral base of each lateral lobe, forms a wide anterior curvature; lateral parts (**sr7-l**) very steep and reaching far to the anterior (yet converging), either fairly straight (Fig. 16A) or more or less strongly curved mesad around their midlength (Fig. 17A–D), near the anterior border of **S7** continuing into the transversal median part of the ridge (**sr7-m** in Fig. 16A). Median part either continuous across middle (only *A. bergi*, Figs 16A, B, 18C, D), or with some traces of discontinuities (arrows in Fig. 18E, G), or with a distinct gap of varied width (between bars in e.g. Fig. 18A, I, J). The median part **sr7-m** of the ridge is best examined at high contrast, because with low contrast parts of it can be difficult to recognise (compare Figs 17E and 18G, which were made from the same object). The different course of the anterior border of **S7** in the two types correlates with a different extension of sclerite **S7** beyond the lateral parts of the transversal ridge in anterolateral direction: it is very wide in the rounded-rectangular type, but rather limited in the semicircular type with anterior border and transversal ridge running almost in parallel at short distance. Surface of **S7** in the posterior 2/3 covered with dispersed rather long and strong bristles, especially densely arranged along the posterior border.

Male subgenital plate S9. Anterior part with a pair of rather long, slender, and strong apodemes (**sta9**) of about equal length (Figs 24A–D, 25B, C). Posterior part located in ventral wall of subgenital lobe (expanded ventral fold **vf9**). Subgenital lobe in all five species with males known (Figs 24–26) with a deep excavation along the left side, the conical left stylus (**sl^{l}**) inserted at the base of the excavation, not reaching tip of lobe; the more strongly projecting right part of the subgenital lobe tongue-shaped. In *A. aptera* and *A. bergi* right part of lobe widely tongue-shaped, without excavation on right side; a small knob-like right stylus (**sl^{r}**) present, situated subterminally on right flank of tip (Fig. 24A–D). In *A. flava*, *A. fungicola*, and *A. paucisetosa* right part of lobe narrowly tongue-shaped (and slightly curved towards the left) due to an excavation on right side, which is of similar depth as the excavation on the left side; right stylus absent (Fig. 25A–D). Due to the presence of an excavation on only one side the subgenital lobe appears very asymmetrical in the two former species, whereas due to the presence of an excavation on each side the lobe appears quite symmetrical in the three latter species. On each side the lateral margin of the subgenital plate articulates with the ventral extension of tergite 9 (**pt9**, e.g. Fig. 24A; see 3.6.).

Male paraprocts. Right paraproct (**PP^{r}**) of *A. aptera* (Figs 5J, 6B) mesally with a sclerotised hook-like projection (**hmp**), other species with known male without such a differentiation (Figs 5K, 7C, 8B).

3.9. Female genitalia

Overall structuring largely as typical for Blattodea: There are two cavities in anteroposterior succession, i.e. a large posterior vestibulum (space above subgenital lobe **vf7**), which continues anteriorly into a narrower genital chamber. The elements of the female genitalia are distributed over the upper and lower walls of these cavities. Problematic interpretations are discussed in Supplement 5.

The ***genital chamber*** (**gc**) is divided in a dorsal and a ventral subchamber by a flat transversal fold arising from the anterior and lateral walls of the genital chamber (genital chamber fold **gcf** in Fig. 23A, B, its posterior edge labelled **gcf** in Figs 19A, B, 21A; fold in same position as the one bearing 'sp.pl.' in MK64: fig. 40A of *Supella*, but much deeper); fold **gcf** is asymmetrical, projecting further posteriorly on the left side. The ***gonopore*** (opening of common oviduct **oc**) lies in the anterior wall of the ventral subchamber (Fig. 23A, B); there is no genital papilla, but the oviduct widens quite gradually and continues into the lumen of the chamber. The ***spermathecal plate*** (**sp**; SP in Supplement 3 Fig. S2B) lies in the dorsal wall of the fold **gcf** (Fig. 23A); like the fold it usually exhibits a distinct asymmetry (with a left-side focus in Figs 23A, S2B); a division was not observed. We did not find any paired or unpaired cuticular structures that could reasonably be considered ***spermathecae***, neither on plate **sp**, nor in any other position. The anterior wall of the dorsal subchamber forms a folded, anteriorly directed pouch (genital chamber pouch **gcp** in Figs 19–21, 23A) on the side opposite to where the spermathecal plate has its focus.

The left and right ***valvifers*** (**vlf** = part of 8th-segmental coxal sclerites CX8; Figs 19–21, 23A) in the roof of the genital chamber (**gc^{d}**) strongly converge anteriorly, where they are connected across the midline, forming together a single arch-shaped sclerite. The posterior ends show a discrete contact (articulation **A5**) with the paratergal extension (**pt8,9**), and the adjacent part of **vlf** is curved laterally (often showing some asymmetry). The anterior part traversing the midline appears as a discrete ribbon-like continuation of the posterolateral parts in some species (Figs 19A, B, 21B), but is indistinctly delimited, weaker and wider, and perhaps incomplete in others (mesad of arrow in Fig. 20B, D; a distinction between valvifer arch and spermathecal plate, which are placed one above the other in a preparation, is then partly difficult). Note that the area where the valvifer arch crosses the midline is placed morphologically posteriad of the spermathecal plate. Individualised basivalvulae (part of 8th-segmental coxal sclerites CX8) were not found; these sclerotisations could be included laterally in the sclerite here called **vlf**, or in the sclerite **ls** (see below), or be absent (discussion in Supplement 5). In some species the central dorsal wall of the genital chamber (**gc^{d}**) bears a microsculpture of small knobs (Figs 19A, 21A, B, shown enlarged in inserts), possibly associated with very weak sclerotisation that appears medially divided (putative mesal border shown by arrow in Figs 19A, 21A, B and their inserts).

The ***1st valves*** (**v1** = 8th-segmental gonapophyses gp8) show the usual configuration, with their bases (including the basal sclerotisation GP8) reaching far laterally to join articulation **A5** (e.g. Fig. 19A).

Of the ***gonangulum*** (**gg** = 9th-segmental laterocoxal sclerites LC9) the mesal part (**gg-m** in Figs 19A, B, D, 20B, D, 21A, B) is distinct; it forms the typical articulations **A2** (with the posterior lobe **pl**, see below; Fig. 19A, B) and **A3** (with the gonapophyseal sclerotisation GP8 at the dorsal base of the 1st valve; Fig. 19A). The lateral part (**gg-l**) forming a hinge-like contact **A1** with the paratergal extension **pt8,9** (see 3.6.) is present in *A. aptera* (Fig. 19A; lateral part of LC9 in Fig. S2A, B), where it is completely separated from the mesal part, but appears to be absent in the other species (Figs 19B, D, 20B, D, 21A, B).

The ***anterior arch*** (**aa** = anterior part CX9μ of medially fused 9th-segmental coxae CX9, compare Fig. 19A and Supplement 3 Fig. S2C for its outline) usually has a darker anterior margin, possibly due to a transversal internal ridge. The shape of the anterior border of **aa** appears to vary among species, being straight, biconcave, or convex to a varied extent (compare Figs 19A, B, D, 20B, D); however, its shape could be influenced by the angle of view upon the preparation. The ***posterior lobes*** (**pl** = posterolateral parts CX9β of 9th-segmental coxae CX9, see Supplement 3 Fig. S2A, B) are well developed.

The ***2nd valves*** (**v2** = 9th-segmental gonapophyses gp9) and the ***3rd valves*** (**v3** = 9th-segmental gonoplacs gl9) overall show the usual configuration, but their structural details, especially those near the base, are not seen in the preparations due to the overlapping of several elements in the area.

Intercalary sclerites (**IC** in Fig. 19A, B) are very weak, often indistinctly delimited, limited to the median area, likely medially fused, and close to the paraproct anterior border.

The floor of the vestibulum (= dorsal wall of subgenital lobe **vf7**; **vfl** in Fig. 22A, B, 23A) appears to be entirely membranous. It bears ***membranous folds*** (which are part of **vfl**): a pair of longitudinal intersternal folds (**isf** in Figs 22D, H, 23A) and a transversal ventral vestibular fold (**vtf** in Fig. 23A) between them. When the membranous floor of the vestibulum is cut off from the sclerotised, stabilising ventral wall of the subgenital lobe, sternite **S7**, the folds tend to get distorted or to collapse (as in most pictures of Fig. 22).

The laterosternal-shelf area represents the posterior floor of the genital chamber adjoining the floor of the vestibulum. A large W-shaped ***laterosternal-shelf sclerite*** (**ls** in Fig. 23A, halves of W open posteriorly; LG7 + LC8? in Fig. S2E) extends over this area, anteriorly and laterally of the **isf** folds. The middle part of sclerite **ls** is U-shaped (U open anteriorly, i.e. the middle peak of the W is rounded or truncate), consisting of a central arch (**ls-c**) and lateral arms (**ls-a** in Figs 22A, 23C). The elongated, oblique lateral parts, the wings (**ls-w** in Fig. 22A), have a plate-like anterior portion, but extend far posterolaterally, where they become much narrower; the apical parts (**ls-p**, possibly the "posterior extensions" sensu MK64, then part of laterocoxa LC8) are twisted relative to the wing part **ls-w** (black arrows in Fig. 22A, D, I). Where the middle and lateral parts of sclerite **ls** approach

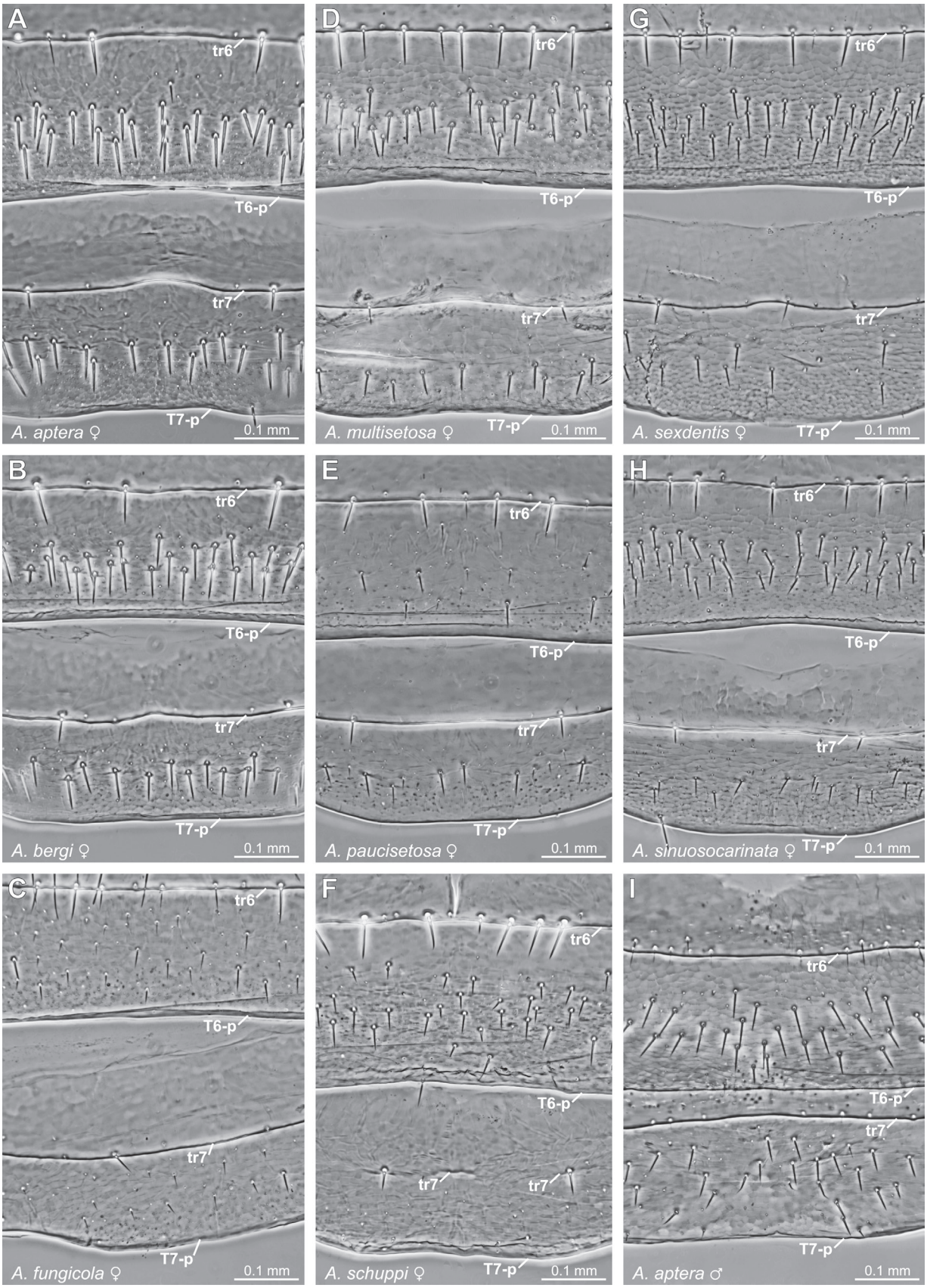


Figure 14. Size and distribution of bristles in the median part of tergites T6,7 in females (**A–H**) and males (**I**) of *Attaphila* species, phase contrast images. **A**: *A. aptera*, female (Bo 1257). **B**: *A. bergi*, female (Bo 1282). **C**: *A. fungicola*, female (Bo 1264). **D**: *A. multisetosa*, female (Bo 1270). **E**: *A. paucisetosa*, female (PT Bo 1255). **F**: *A. schuppi*, female (ST Bo 1237), with only short remnants of transversal ridge tr7. **G**: *A. sexdentis*, female (Bo 1233). **H**: *A. sinuosocarinata*, female (HT Bo 1273). **I**: *A. aptera*, male (Bo 1256). — ***Abbreviations***: **T6-p**, **T7-p** posterior borders of tergites T6, T7; **tr6**, **tr7** transversal ridges of tergites T6, T7.

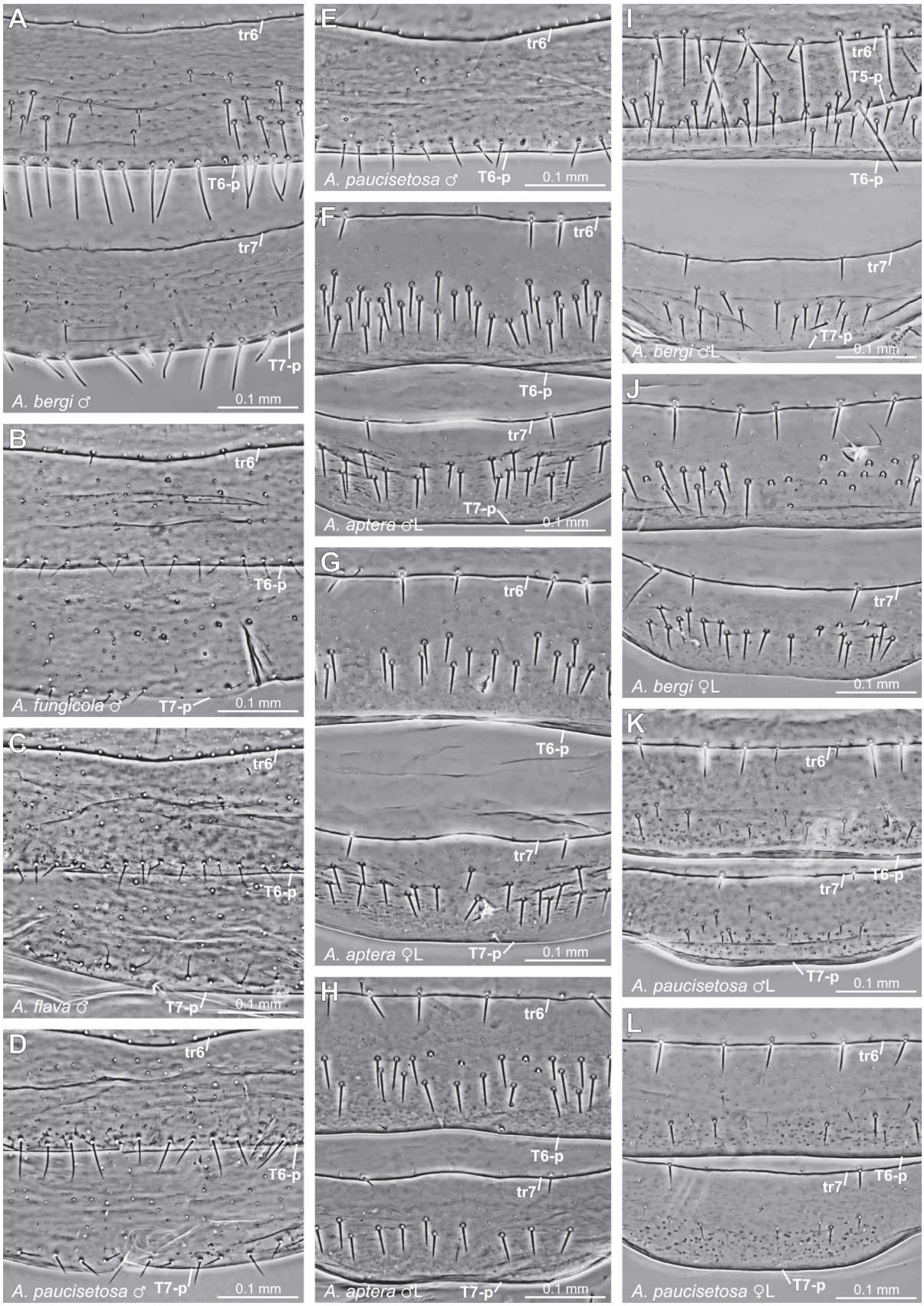


Figure 15. Size and distribution of bristles in the median part of tergites T6,7 in males (**A**–**E**) and in larval males and females (**F**–**L**) of *Attaphila* species, phase contrast images. **A**: *A. bergi*, male (Bo 1274). **B**: *A. fungicola*, male (LT Bo 1265). **C**: *A. flava*, male (HT Bo 1280). **D**: *A. paucisetosa*, male (Cb 2/1). **E**: *A. paucisetosa*, male, with slightly shorter bristles than in preceding specimen (Bo 1445). **F**: *A. aptera*, larval male (Bo 1291). **G**: *A. aptera*, larval female (Bo 1289). **H**: *A. aptera*, larval male (HT Bo 1232). **I**: *A. bergi*, larval male (Bo 1230); medium sized bristles belong to T6, the very long ones are from T5 covering most of T6. **J**: *A. bergi*, larval female (Bo 1285). **K**: *A. paucisetosa*, larval male (Bo 1433). **L**: *A. paucisetosa*, larval female (Bo 1293). — ***Abbreviations***: **T5-p**, **T6-p**, **T7-p** posterior borders of tergites T5, T6, T7; **tr6**, **tr7** transversal ridges of tergites T6, T7.

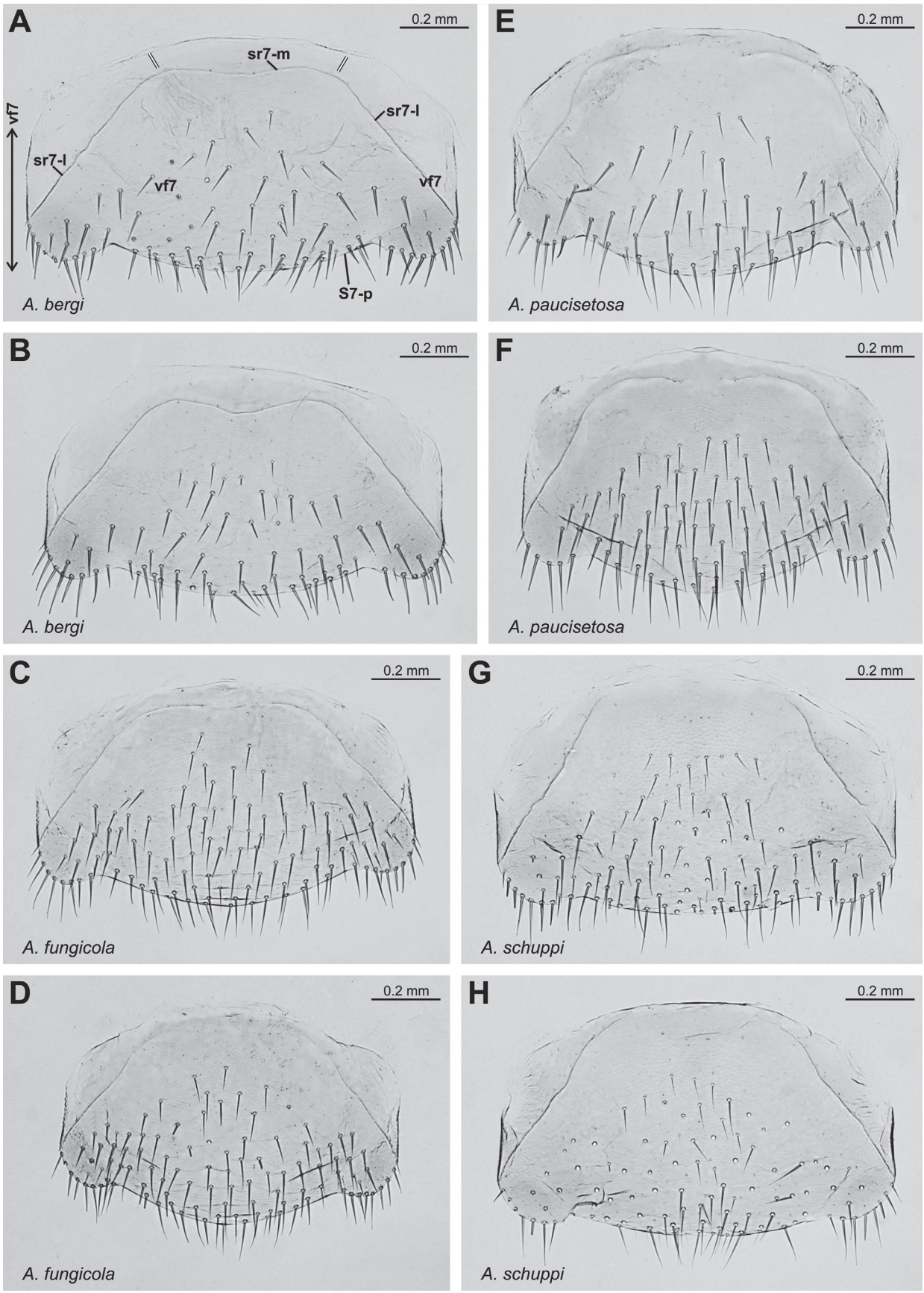


Figure 16. Subgenital plate (sternite S7) of females of *Attaphila* species. **A**, **B**: *A. bergi* (Bo 1275, Bo 1282). **C**, **D**: *A. fungicola* (Bo 1264, Bo 1228). **E**, **F**: *A. paucisetosa* (Cb 2/2, PT Bo 1255). **G**, **H**: *A. schuppi* (ST Bo 1237, ST Bo 1234). — ***Abbreviations***: **S7-p** posterior border of subgenital plate S7; **sr7-l**, **sr7-m** lateral, median part of transversal ridge of subgenital plate S7 (borders indicated by double bars); **vf7** ventral fold of segment 7 = subgenital lobe (across entire width of S7; approximate longitudinal extension given by double-headed arrow).

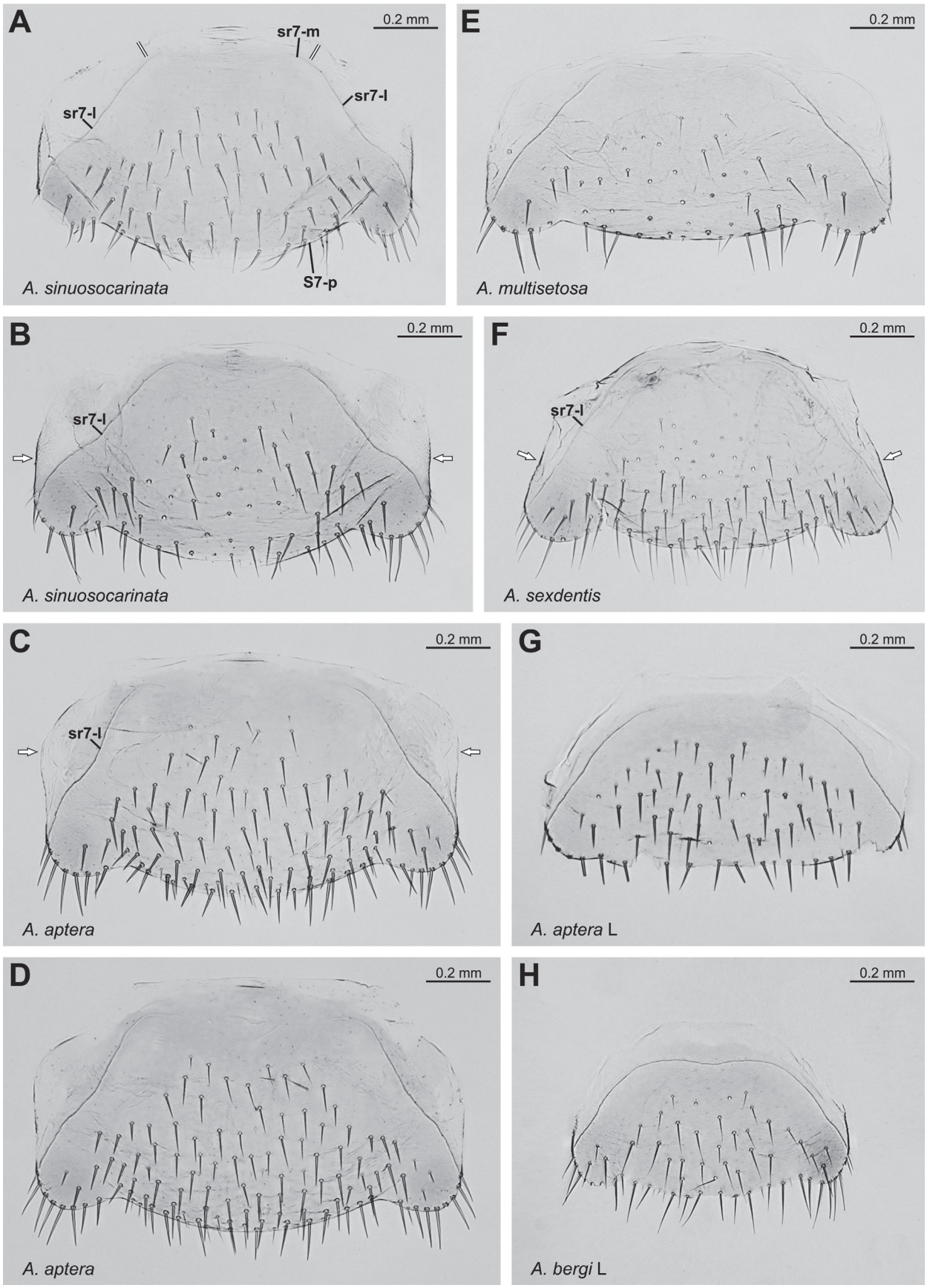


Figure 17. Subgenital plate (sternite S7) of females (**A**–**F**) and larval females (**G**, **H**) of *Attaphila* species. **A**, **B**: *A. sinuosocarinata* (PT Bo 1287, HT Bo 1273). **C**, **D**: *A. aptera* (Bo 1225, Bo 1253). **E**: *A. multisetosa* (HT Bo 1270). **F**: *A. sexdentis* (HT Bo 1233). **G**: *A. aptera*, larval female (Bo 1289). **H**: *A. bergi*, larval female (Bo 1231). — ***Abbreviations and arrows***: **S7-p** posterior border of subgenital plate S7; **sr7-l**, **sr7-m** lateral, median part of transversal ridge of subgenital plate S7 (borders indicated by double bars). Arrows in B,C,F pointing to lateral borders of S7, which are parallel or slightly divergent (to the anterior) in A–E, but convergent in F.

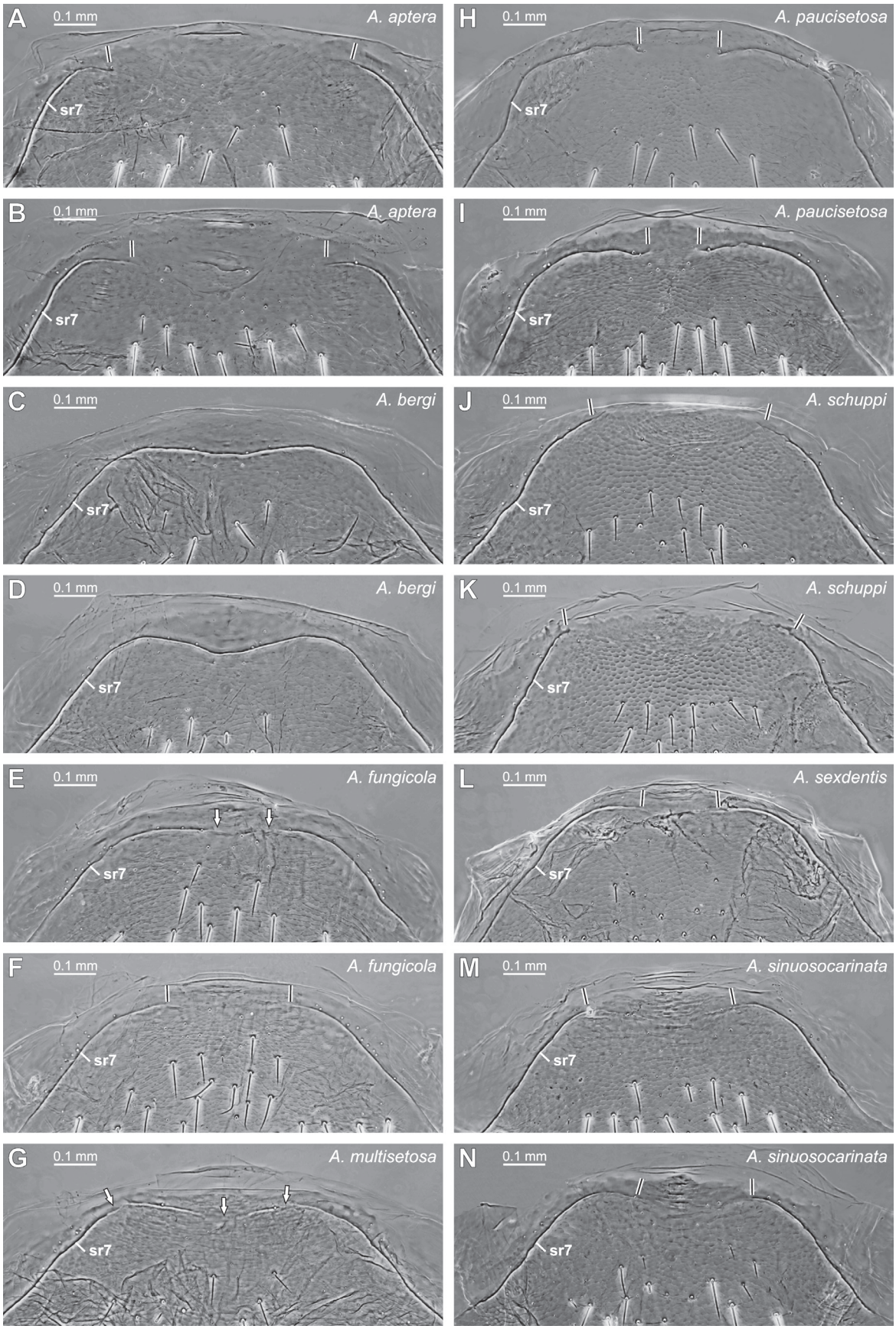


Figure 18. Anterior half of subgenital plate (sternite S7) of females of *Attaphila* species, shape of sternal transversal ridge, phase contrast images (same objects as shown in Figs. 16, 17, except for Bo 1236 in F). **A**, **B**: *A. aptera* (Bo 1225, Bo 1253). **C**, **D**: *A. bergi* (Bo 1275, Bo 1282). **E**, **F**: *A. fungicola* (Bo 1264, Bo 1236). **G**: *A. multisetosa* (HT Bo 1270). **H**, **I**: *A. paucisetosa* (Cb 2/2, PT Bo 1255). **J**, **K**: *A. schuppi* (ST Bo 1234, ST Bo 1237). **L**: *A. sexdentis* (HT Bo 1233). **M**, **N**: *A. sinuosocarinata* (PT Bo 1287, HT Bo 1273). — ***Abbreviations and symbols***: **sr7** transversal ridge of subgenital plate S7; short interruptions of this ridge indicated by arrows, larger gaps delimited by double bars.

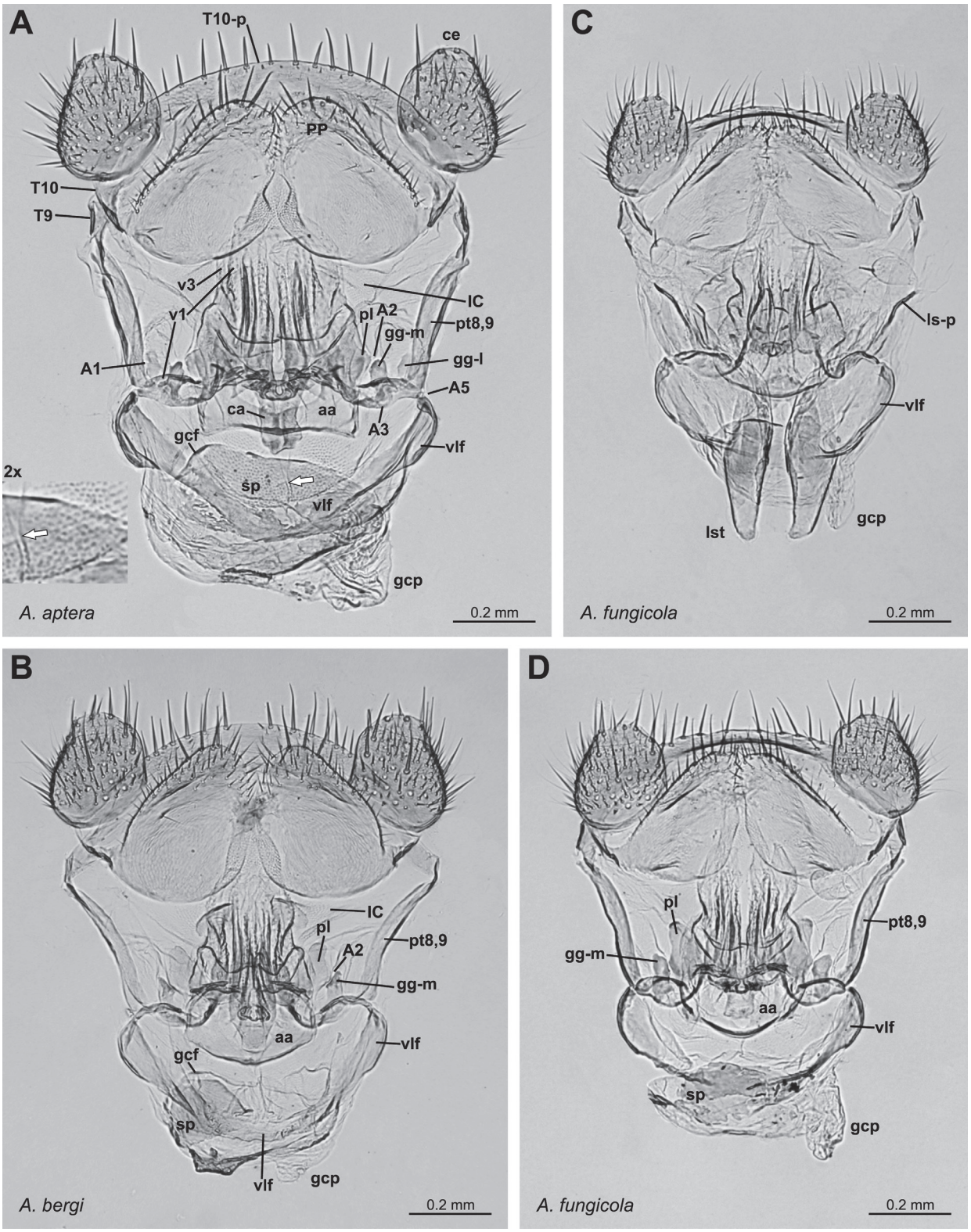


Figure 19. Terminalia with genitalia of females of *Attaphila* species, ventral view, posterior end on top. **A**: *A. aptera* (Bo 1253), without laterosternal shelf area; inset showing median part of genital chamber dorsal wall. **B**: *A. bergi* (Bo 1239), without laterosternal shelf area. **C**, **D**: *A. fungicola* (Bo 1236, Bo 1264), C with, D without laterosternal shelf area. — ***Abbreviations***: **aa** anterior arch; **ca** central apodeme; **ce** cercus; **gcf** fold dividing genital chamber (posterior edge labeled); **gcp** pouch of genital chamber (one-sided); **gg-m**, **gg-l** mesal and lateral gonangulum sclerites, the latter present only in *A. aptera*; **IC** intercalary sclerite; **ls-p** posterolateral extremity of laterosternal-shelf sclerite; **lst** laterosternal-shelf tube; **pl** posterior lobe; **PP** paraproct; **pt8,9** extension of paratergite 9; **sp** spermathecal plate; **T9**, **T10** abdominal tergites 9 and 10; **T10-p** posterior border of tergite 10; **v1**, **v3** 1st and 3rd valves of ovipositor; **vlf** valvifer of segment 8; **A** articulations, **A1** between gg-l and pt8,9, **A2** between gg-m and pl, **A3** between gg-m and basal sclerotisation of v1, **A5** between pt8,9 and vlf. **Arrow** in A showing mesal border of putative weak sclerotisation in dorsal wall of genital chamber. (See Supplement 1 and Supplement 3 Fig. S2A, B, C for additional explanations and more complete labeling using different terminologies.)

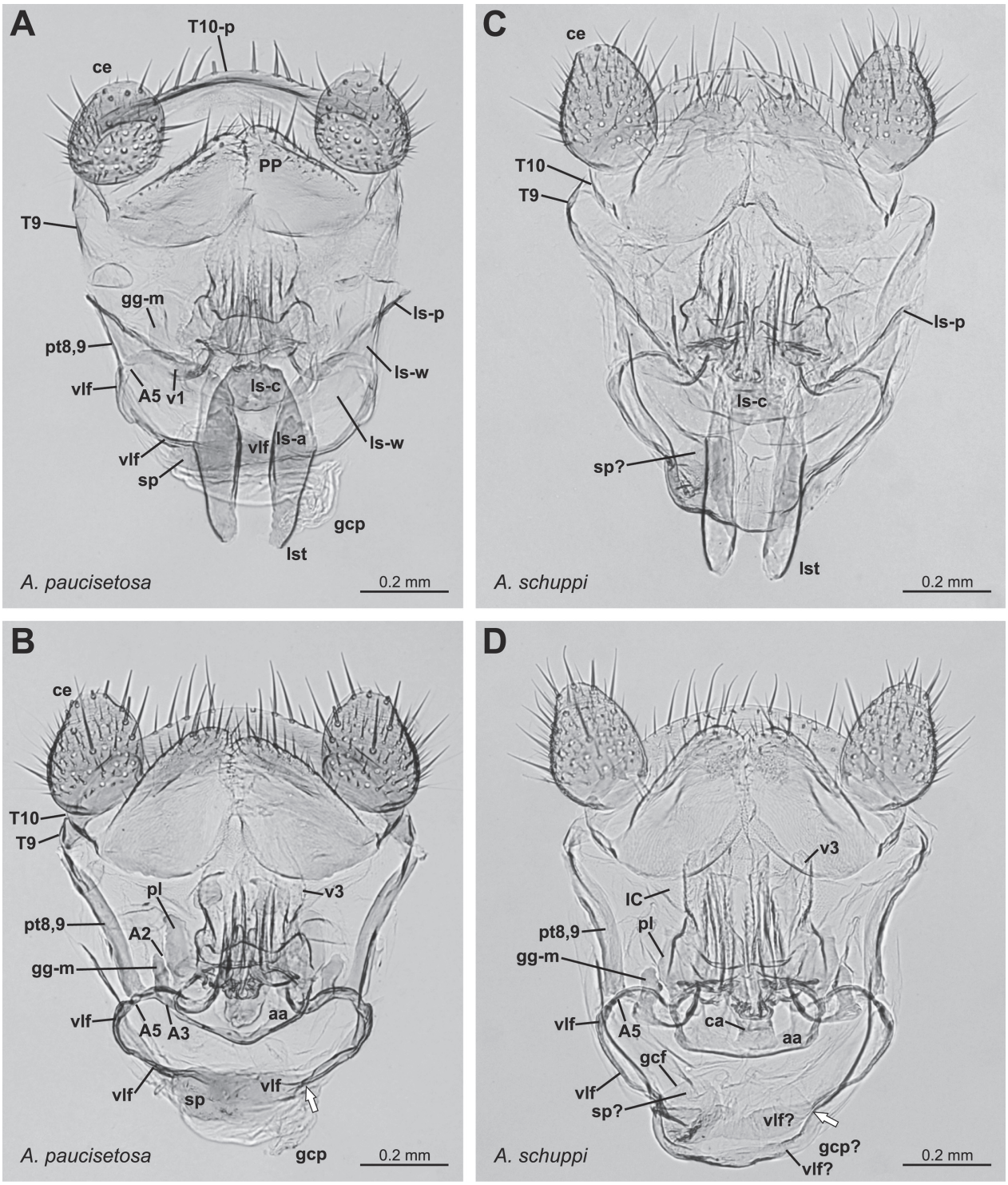


Figure 20. Terminalia with genitalia of females of *Attaphila* species, ventral view, posterior end on top. **A**, **B**: *A. paucisetosa* (PT Bo 1226, PT Bo 1255), A with, B without laterosternal shelf area. **C**, **D**: A. *schuppi* (ST Bo 1234, ST Bo 1237), C with, D without laterosternal shelf area. — ***Abbreviations***: **aa** anterior arch; **ca** central apodeme; **ce** cercus; **gcf** fold dividing genital chamber (posterior edge labeled); **gcp** pouch of genital chamber (one-sided); **gg-m** mesal gonangulum sclerite; **IC** intercalary sclerite; **ls** laterosternal-shelf sclerite (with central part **c**, arm part **a**, wing part **w**, posterolateral extremity **p**); **lst** laterosternal-shelf tube; **pl** posterior lobe; **PP** paraproct; **pt8,9** extension of paratergite 9; **sp** spermathecal plate; **T9**, **T10** abdominal tergites 9 and 10; **T10-p** posterior border of tergite 10; **v1**, **v3** 1st and 3rd valves of ovipositor; **vlf** valvifer of segment 8 (**arrow** pointing to zone where median widening starts). **A** articulations, **A2** between gg-m and pl, **A3** between gg-m and basal sclerotisation of v1, **A5** between pt8,9 and vlf. (See Supplement 1 and Supplement 3 Fig. S2A, B, C for additional explanations and more complete labeling using different terminologies.)

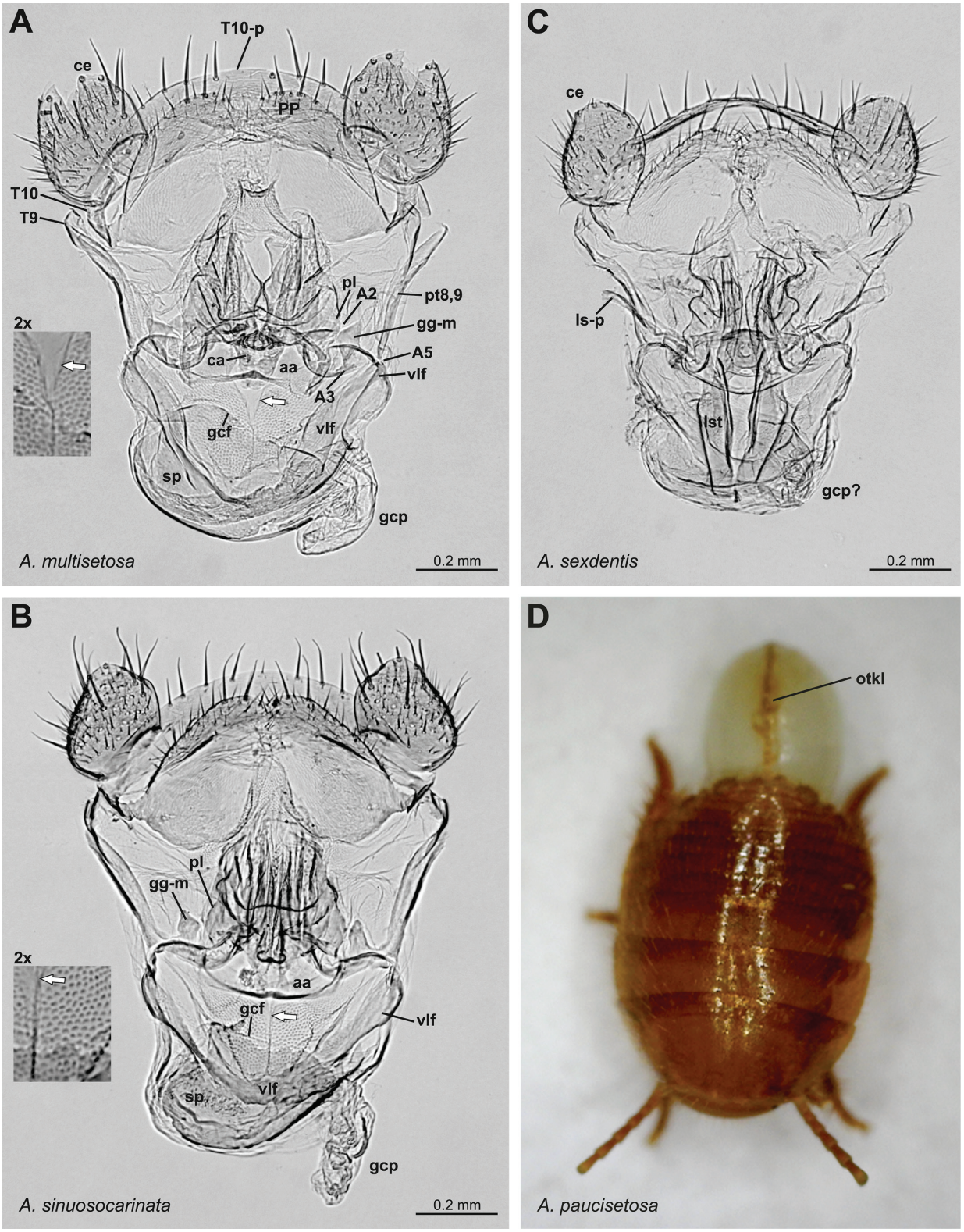


Figure 21. A–C: Terminalia with genitalia of females of *Attaphila* species, ventral view, posterior end on top. **A**: *A. multisetosa* (HT Bo 1270), without laterosternal shelf area, cerci damaged; inset showing median part of genital chamber dorsal wall. **B**: *A. sinuosocarinata* (HT Bo 1273), without laterosternal shelf area; inset showing median part of genital chamber dorsal wall. **C**: *A. sexdentis* (HT Bo 1233), with laterosternal shelf area. — **D**: Female of *A. paucisetosa* carrying an ootheca; length of animal ca. 3 mm. — ***Abbreviations***: **aa** anterior arch; **ca** central apodeme; **ce** cercus; **gcf** fold dividing genital chamber (posterior edge labeled); **gcp** pouch of genital chamber (one-sided); **gg-m** mesal gonangulum sclerite; **IC** intercalary sclerite; **ls** laterosternal-shelf sclerite (with posterolateral extremity **p**); **lst** laterosternal-shelf tube; **otkl** ootheca keel; **pl** posterior lobe; **PP** paraproct; **pt8,9** extension of paratergite 9; **sp** spermathecal plate; **T9**, **T10** abdominal tergites 9 and 10; **T10-p** posterior border of tergite 10; **vlf** valvifer of segment 8; **A** articulations, **A2** between gg-m and pl, **A3** between gg-m and basal sclerotisation of v1, **A5** between pt8,9 and vlf. **Arrow** in A, B showing mesal border of putative weak sclerotisation in dorsal wall of genital chamber. (See Supplement 1 and Supplement 3 Fig. S2A, B, C for additional explanations and more complete labeling using different terminologies.)

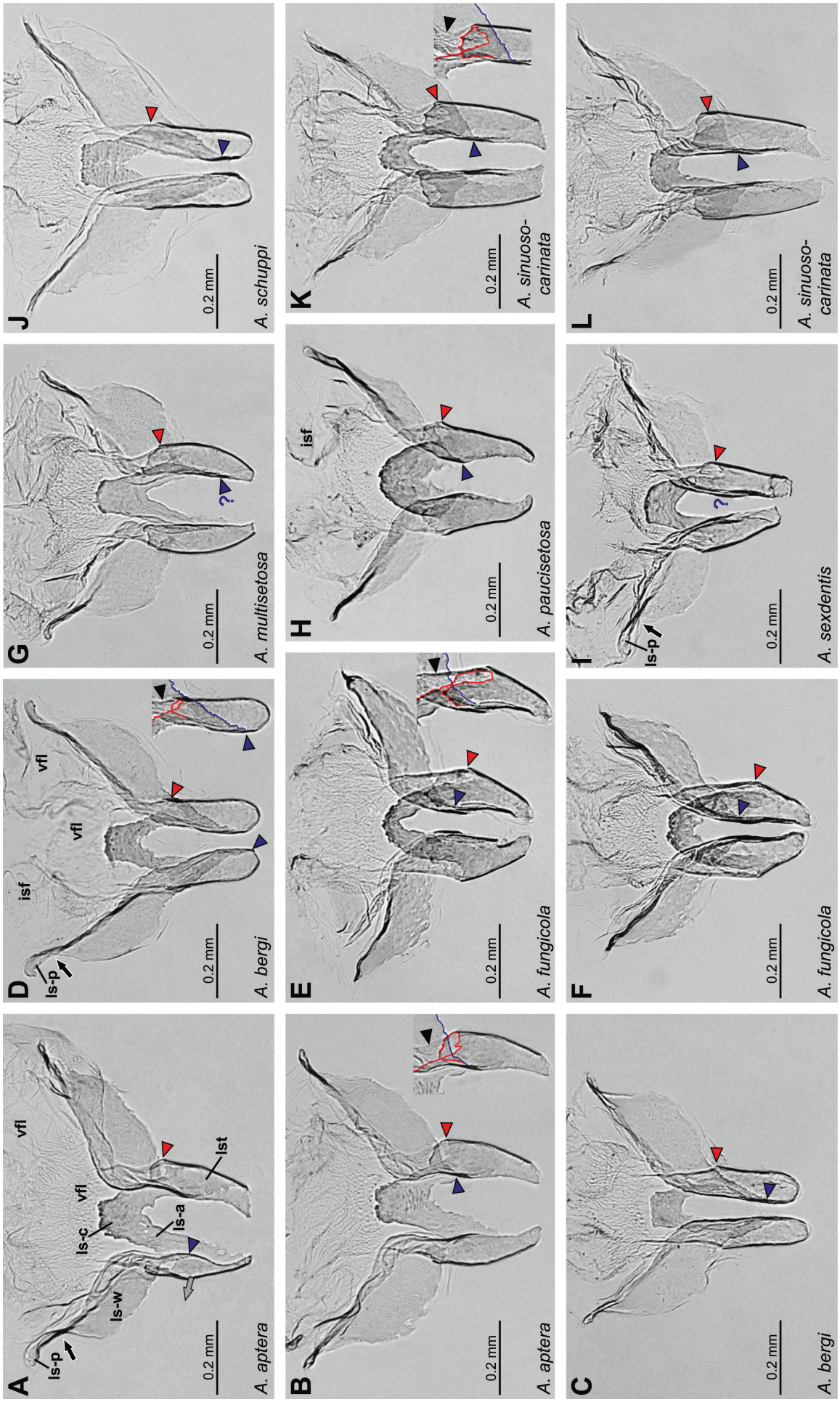

A
ls-p
ls-w
ls-c
vfl
vfl
ls-a
lst
0.2 mm
A. aptera
D
ls-p
isf
vfl
vfl
0.2 mm
A. bergi
G
?
0.2 mm
A. multisetosa
J
0.2 mm
A. schuppi
B
0.2 mm
A. aptera
E
0.2 mm
A. fungicola
H
isf
0.2 mm
A. paucisetosa
K
0.2 mm
A. sinuoso-carinata
C
0.2 mm
A. bergi
F
0.2 mm
A. fungicola
I
ls-p
?
0.2 mm
A. sexdentis
L
0.2 mm
A. sinuoso-carinata

Figure 22. Laterosternal shelf area of females of *Attaphila* species, ventral view, posteriorly on top. **A**, **B**: *A. aptera* (Bo 1225, Bo 1257), in A left tube distorted (ventral part of tube squeezed laterally, as indicated by grey arrow). **C**, **D**: *A. bergi* (Bo 1282, Bo 1239). **E**, **F**: *A. fungicola* (Bo 1264, Bo 1447). **G**: *A. multisetosa* (HT Bo 1270). **H**: *A. paucisetosa* (PT Bo 1255). **I**: *A. sexdentis* (HT Bo 1233). **J**: *A. schuppi* (ST Bo 1237). **K**, **L**: *A. sinuosocarinata* (HT Bo 1273, PT Bo 1288). — ***Abbreviations***: **isf** intersternal folds (of floor of vestibulum); **ls** laterosternal-shelf sclerite (with central part **c**, arm part **a**, wing part **w**, posterolateral extremity **p**); **lst** laterosternal-shelf tube; **vfl** floor of vestibulum. (See Supplement 3 Fig. S2D, E for more complete labeling using different terminologies.) — ***Arrows***: Black arrows in A, D, I: twisting of sclerite at transition between **ls-w** and **ls-p**. Grey arrow in A indicates direction of squeezing of tube **lst**. Blue arrowheads: anterior extremity of wing part **ls-w** on mesal border of tube **lst**, **ls-w** either restricted to posterior half of tubes **lst** (e.g. K) or reaching far into anterior half (e.g. D). Red arrowheads: area where the posterior margin of **ls-a** bends dorsally, and where a bend or kink is often present in (inner) lateral border of tube **lst** (compare white arrowheads in Fig. 23C, D, H, I, J). Black arrowheads: membranous inner lateral border of tube **lst** posterior to the bend or kink (compare Fig. 23C, D, H, I and black arrowheads in sections beside D). — ***Inserts*** in B, D, E, K showing right (of picture and animal) tube **lst** with posterior margin of **ls-a** (red line; compare Fig. 23C–E) and anterior margin of **ls-w** (blue line; compare Fig. 23F, G).

each other, a deep, anteriorly directed tube-shaped pouch is present on each side, the ***laterosternal-shelf tube*** (**lst** in Figs 22A, 23). The pouch is rolled up and thus has a C-shaped cross section in its anterior part (lowest cross section left of Fig. 23D: the black margins of the C represent the cuticle, the body of the C is external world, the areas surrounding the C – including the area embraced by it – represent the interior of the animal). Both the arm and wing parts of sclerite **ls** extend into the tube walls and bend along them (shown in Fig. 23C–F and G–J), whereby much of the **lst** walls are sclerotised; **ls-a** and **ls-w** are likely synsclerotic inside the tube (at edge indicated by grey arrows in Fig. 23E–H; but a clear observation was not possible). A ***laterosternal shelf***, i.e. a physical step upward between the floors of vestibulum and genital chamber (see MK 1964: figs 2, 10, 40b, representing the 7th-segmental genital lobe) is absent.

The laterosternal shelf area shows considerable interspecific variation and can, therefore, serve as an important means for species distinction in the female sex. This concerns the shape of the central sclerotisation **ls-c** and of the tubes **lst** (Fig. 22), the anterior extension of the wing part **ls-w** on tubes **lst** (blue arrowheads in Fig. 22), and the anteroposterior position of the area where the anterior margin of the arm part **ls-a** bends from the ventral inner wall of the tube into the dorsal one (red arrowheads in Fig. 22; often associated with a laterally directed angular bend or kink). The shape characteristics of the tubes **lst** (as seen in preparations: Fig. 22) appear variously reliable due to the composition of the tube walls of sclerotised and membranous parts. For instance, the (inner) lateral border of **lst** is sclerotised and thus stable anterior to the red arrowheads (reliable), but membranous and thus flexible posterior to them (not reliable; area indicated by black arrowheads in inserts of Fig. 22B, D, E, K); the distinctness of the angular bend depends partly on the mesal bending of the posterior part (compare left and right sides in Fig. 22I, L) and is thus not a very reliable character.

In situ, the lateral wing parts (**ls-w**) of sclerite **ls** are positioned beneath the area embraced by the lateral parts of the valvifer arch (**vlf**), but extend further posterolaterally beneath the paratergal extensions (**pt8,9**; Fig. 20A, compare labelling on left and right sides). The central part (**ls-c**) is then placed beneath the anterior arch (**aa**; compare positions of **ls-c** in Fig. 20A and **aa** in Fig. 20B), and the arms **ls-a** and tubes **lst** reach anteriorly well beyond the anterior bottom of the dorsal genital subchamber. The intersternal folds (**isf** in Fig. 22D), which follow behind the **ls-c** part (upward in Fig. 20A), are in the right place to embrace the group of valves located above them in the roof of the vestibulum, and to form a mould for a new ootheca built in the vestibulum. The case where the central part (**ls-c**) is placed further posteriorly beneath the central apodeme, and where the arms (**ls-a**) and tubes (**lst**) do not exceed the dorsal genital subchamber (Fig. 21C) could be due to artificial shifts during dissection.

3.10. Female gonads

The ovarioles of *Attaphila fungicola* are described by Roth (1968: fig. 17) as being similar to other non-blaberid Blaberoidea ("Blattellidae" therein), with only one oocyte showing incorporation of yolk material.

3.11. Ootheca

A female carrying an ootheca was only once observed, among the specimens of *A. paucisetosa* collected by one of the authors (R.R.G.) in a nest of *Atta cephalotes* in Colombia (Fig. 21D). The ootheca appeared scarcely sclerotised, with a very low brownish keel (**otkl**), and contained five eggs; their upright orientation and the dorsal position of the keel signalise that the ootheca was not rotated. Since the female was fixed shortly after its capture, the question of a possible rotation of the ootheca before its deposition could not be resolved. With the very soft sheath and the low keel the ootheca resembles that of ovoviviparous species. These features can be seen as an adaptation to the certainly moist atmosphere in the mushroom chambers of the ants, which makes a strong hardening of the sheath unnecessary. A weakly developed keel was also described by Roth (1971: fig. 81) for the ootheca of *A. fungicola.* Waller and Moser (1990) placed alates of *Atta texana* with attached *A. fungicola* females in jars. Within few days the females produced oothecae, which they deposited at the bottom the jars. Unfortunately, it is not noted whether the oothecae were rotated prior to their deposition.

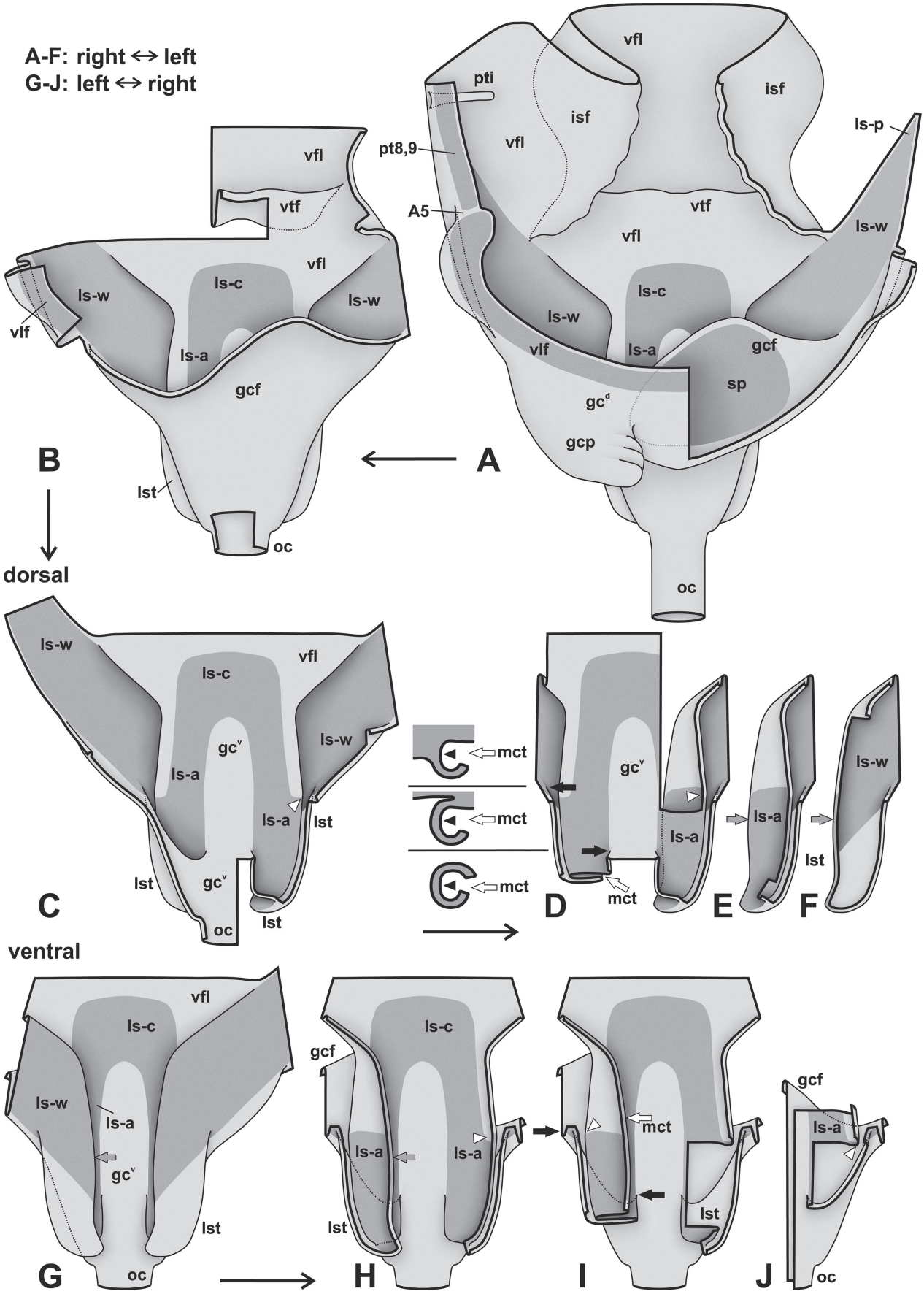

A-F: right ↔ left
G-J: left ↔ right
vfl
pti
isf
isf
ls-p
pt8,9
vfl
A5
vtf
vfl
ls-w
ls-c
ls-w
vlf
ls-a
gcf
sp
gc^d
gcp
oc
A
vfl
vtf
vfl
ls-w
ls-c
ls-w
vlf
ls-a
gcf
lst
oc
B
dorsal
ls-w
vfl
ls-c
gc^v
ls-w
ls-a
ls-a
lst
lst
gc^v
oc
lst
C
ventral
mct
mct
mct
gc^v
ls-a
mct
D
ls-a
E
ls-w
lst
F
vfl
ls-c
ls-w
ls-a
gc^v
lst
oc
G
ls-c
gcf
ls-a
ls-a
lst
H
mct
lst
I
gcf
ls-a
oc
J

Figure 23. Genital chamber and laterosternal shelf area of *Attaphila* female, semi-schematic representation showing exoskeletal morphology, posteriorly on top. **A**, **B**: Dorsal view; selected parts removed from A to B. **C**–**F**: Dorsal view of median part of laterosternal shelf area; series of pictures with selected parts removed stepwise from C to F (only parts of one tube lst retained in E, F); lefthand of D cross sections (dorsal side up) at three anteroposterior levels shown (posterior to, in between, and anterior to the levels indicated by two black arrows in D), including mesal cleft mct of tube. **G**–**J**: Ventral view of median part of laterosternal shelf area; series of pictures with selected parts removed stepwise from G to J. — ***Explanations***: Thick black lines are (virtual) cutting lines. Continuous thin black lines are freely visible edges (= lines along which the cuticle bends away from the observer's view). Dashed thin black lines are edges hidden beneath other cuticle (only some shown). Membranous cuticle in very light grey, sclerotised cuticle in darker grey; cuticle shaded darker where it dives beneath other cuticle. Dashed grey lines in A show hidden part of margin of spermathecal sclerite. — ***Abbreviations***: **A5** articulation between pt8,9 and vlf; **gc** genital chamber (with ventral wall **gc^{v}** and dorsal wall **gc^{d}**); **gcf** fold dividing genital chamber horizontally; **gcp** pouch of genital chamber; **isf** intersternal folds; **ls** laterosternal-shelf sclerite (with central part **c**, arm part **a**, wing part **w**, posterolateral extremity **p**); **lst** laterosternal-shelf tube (mostly sclerotised by sclerite ls: part ls-w in ventral wall; part ls-a in two further dorsal layers forming inner walls of tube); **mct** mesal cleft of laterosternal-shelf tube; **oc** common oviduct; **pt8,9** extension of paratergite 9; **pti** paratergal invagination; **sp** spermathecal plate; **vfl** floor of vestibulum; **vlf** valvifer; **vtf** vestibular transversal fold. — ***Arrows***: in D and I, black arrows showing anteroposterior levels of transition between cross sections lefthand of D (corresponding to posterior end of the edge pointed to); in E, F, G, H, grey arrows indicating edge around which ls-sclerotisations **ls-a** and **ls-w** are likely continuous; in C, D, H, I, J, white arrowheads pointing to kink area of lateral border of inner tube (**lst**) wall where sclerotisation **ls-a** bends from dorsal to ventral inner wall; in sections lefthand of D, black arrowheads pointing to membranous inner lateral border of tube **lst**.

3.12. Male genitalia

All interpretations of structural components are unproblematic (i.e. there are no major homology problems relative to other Blaberoidea).

Left phallomere. Hook (**h** in Fig. 24A, E; process hla bearing L3 sclerite in Supplement 4 Fig. S3A, B) fully retractable due to a long membranous proximal part, which is inverted in the retracted condition (part **p**, inverted in Fig. 24E, everted but only a short part included in Fig. 25E); sclerotised distal half with a wide basal part (**b**), a much more slender, variously widely curved intermediate part (**n** neck), and a claw-shaped apical part (**cl**) bearing an anterior groove (**hge**) with a cleft (**hcl**). Endophallic apodeme (**ea** in Fig. 24A, F; apodeme lve bearing L2D sclerite in Supplement 4 Fig. S3A, C) long rod-shaped, anteriorly widened. Base of apodeme associated with two posteriorly directed sclerotised processes (Fig. 32F–I), sclerotisation (**L2**) forked to cover both of them. The left branch of **L2** is essentially limited to the virga process (**vi** in Fig. 32F–I; process via bearing the compound sclerite L2E+L4N), which arises at the **L2** fork, is narrowed to a more or less acute apex, and is variously curved; in most preparations one or two longitudinal grooves are apparent (**vge** in Figs 24A, B, 25A, D; **vge1**, **vge2** in Fig. 32F–I; compare Klass 1997: vge in fig. 273), but their extension, structure, and occurrence in the various species remained quite unclear. The tongue-shaped right branch of **L2** extends posteriorly, its right-posterior parts being located in the dorsal wall of the angular or rounded, rightward-directed process **psa**. The sclerotisation of the virga (L2E) is probably not separated from that of the apodeme (L2D) by an articulation (A10; the apparent separation only in *A. aptera* seems to be due to a brighter area placed beneath, marked as A10? in Fig. 32F and Supplement 4 Fig. S3A). Opening of ejaculatory duct not unambiguously detected.

Right phallomere. **R3** sclerite slender, elongate (Fig. 24A, G), the anterior (**a**), ventroposterior (**v**), and dorsoposterior (**d**) portions are narrowed to arm-like extensions. The short ventroposterior arm is associated with the cleft sclerite (**cs**; compound sclerite R2+R1S in Supplement 4 Fig. S3A, D), but the articulation was not clearly observed (compare Klass 1997: A7 in figs 282–284). The longer dorsoposterior arm is distinctly articulated (**A3** in Fig. 24G) with the curved dorsal sclerite (**R1P**) extending along the posterodorsal lobe of the phallomere. The dorsal part **R1S** of the cleft sclerite has a free end, i.e. is separated from sclerite **R1P**.

3.13. Larval development of some characters

Antennae. These could be studied in 25 larval specimens of various stages, which were roughly determined by measuring the width of the head; the incompleteness and heterogeneity of the material (larvae of several species had to be used) did not allow a clear distribution to specific larval stages. The antennae of the youngest available larva (*A. paucisetosa*, head width 0.52 mm, Fig. 2A, H, I; head width in adults 0.76–0.89 mm) has a flagellum with 8 flagellomeres, well separated by interflagellomeral constrictions increasing in strength towards the apex. The constrictions cause an unusual shape of the flagellomeres, being rounded at both ends. The last flagellomere in this specimen appears to have a closed cuticle at its terminal end, but histological sections are necessary for a final decision. Diameter of flagellomeres slightly increasing up to the third, reaching there about that of the scapus and remaining constant up to the antennal apex; length of flagellomeres slightly increasing up to the fourth. First flagellomere (called meriston by Campbell and Priestley 1970) incompletely partitioned into three annuli, interflagellomeral membranes already visible,

but without corresponding constrictions; the completion of the flagellomere division would be expected to take place at the following moult. The specimen certainly represents a very early, presumably the second larval stage (the presence of a dividing meriston is not expected to be present in a freshly hatched larva). The remaining larvae belong to intermediate and late larval stages (head width 0.61–0.75 mm, Fig. 2C–E) and show with increasing size

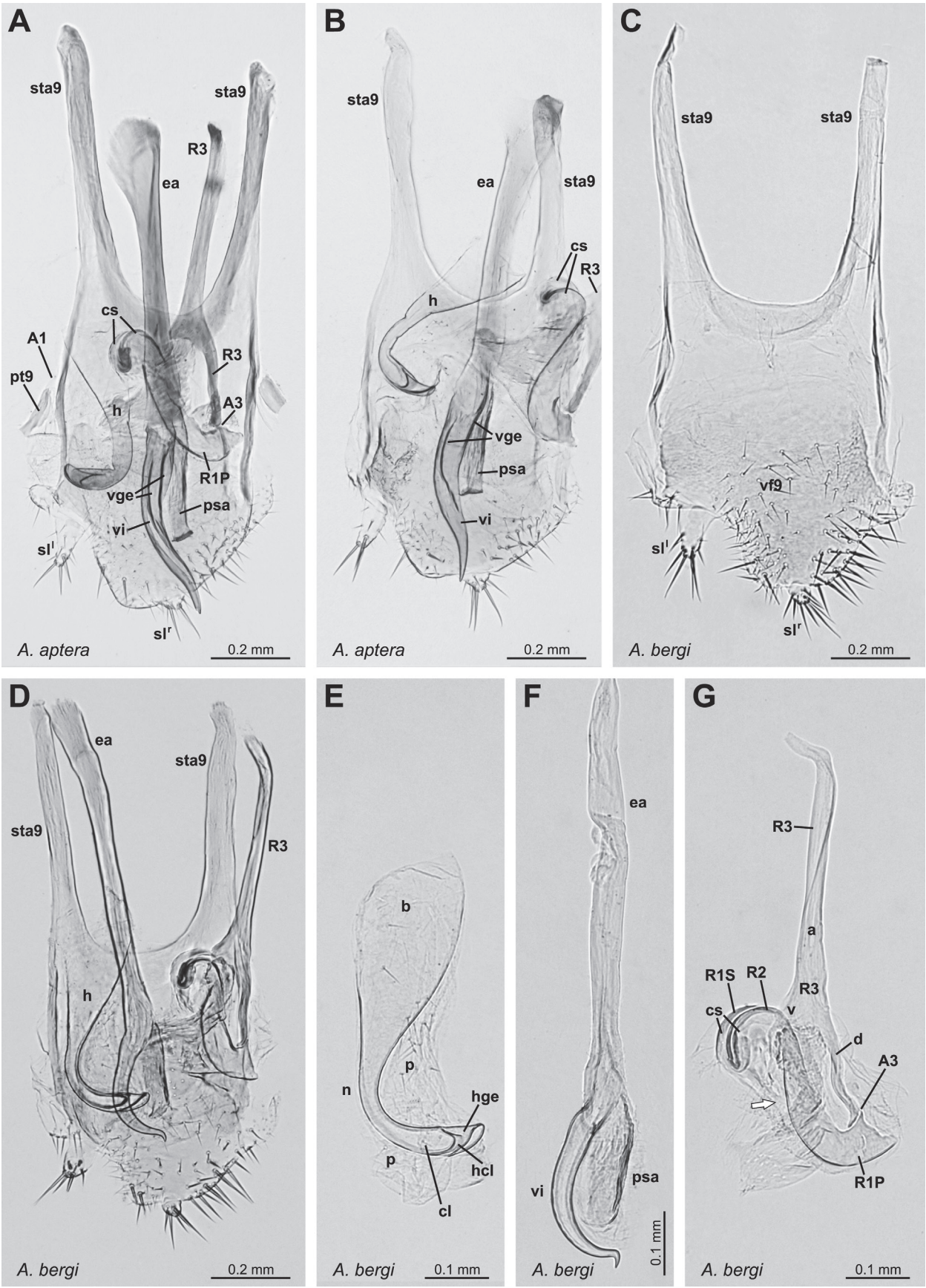


Figure 24. Subgenital plate (sternite S9) and phallomeres of males of *Attaphila* species, dorsal view, anteriorly on top. **A**, **B**: *A. aptera*, subgenital plate with phallomeres (Bo 1256, Bo 1224), anterior part of R3 sclerite out of frame in B. **C–G**: *A. bergi*. **C**: Subgenital plate without phallomeres (Bo 1274); **D**: Subgenital plate with phallomeres (Bo 1283); **E**: Isolated hook of left phallomere (Bo 1274); **F**: Isolated endophallic apodeme (damaged near midlength), virga, and psa-process of left phallomere (Bo 1274); **G**: Isolated right phallomere (Bo 1274). — ***Abbreviations***: **A** articulations, **A1** between S9 and pt9, **A3** between sclerites R3 and R1P; **cs** cleft sclerite, composed of the dorsally fused R1S and R2, R2-part in contact with arm v of R3 sclerite (not visible, contact area indicated by **white arrow** in G); **ea** endophallic apodeme; **h** hook (with long membranous base **p**, wide base **b** of sclerotised part, neck **n**, and claw **cl**); **hcl** cleft in wall of groove hge; **hge** groove upon claw part of hook; **psa** process; **pt9** extension of paratergite 9 contacting sternite 9; **R1** (divided in **R1S** and **R1P**), **R2**, **R3** (with anterior arm **a**, dorsoposterior arm **d**, ventroposterior arm **v**) are the principal sclerotisations of the right phallomere; **sl**^{l}, **sl**^{r} left and right stylus; **sta9** anterior apodeme of subgenital plate S9; **vf9** subgenital lobe; **vge** grooves along virga (see vge1, vge2 in Fig. 32I); **vi** virga.

an increasing approximation to the imaginal structure of the antenna: interflagellomeral constrictions diminished, but flagellomeres still well set off by their conical shape, their length strongly increasing towards the antennal apex (Figs 1A, 2F, G). In two thirds of the larvae signs of a division of the meriston could be found, sometimes restricted to only one of the two antennae. The meriston can be divided into two flagellomeres of different size, the proximal one being much smaller than the distal one (Fig. 2B, observed in seven specimens), or into three flagellomeres of fairly equal size (Fig. 2C, nine specimens). The divisions appear to be incomplete as in the young larva described above and obviously need at least one additional moult for completion. Even then signs of a previous division of the meriston may still be visible as is assumed for the antennae depicted in Fig. 2C, D: size and shape of the proximal flagellomeres are interpreted as showing a weak reminiscence of an earlier division of the meriston into two (Fig. 2C) or three (Fig. 2D) flagellomeres (compare with Fig. 2B, E). There was no evidence for a subdivision of flagellomeres distad of the meriston (no meristonal annuli).

Sex-specific characters. Species determination in larvae is difficult since the larvae are missing most species-specific characters. Larval stages of four species with available larval material (*A. aptera*, *A. bergi*, *A. fungicola*, *A. paucisetosa*) were studied for species-specific characters. As a result, three character sets were found which, under favourable conditions, may allow an identification at least in late larval stages: the bristle patterns on abdominal **T2–5** and on **T6,7**, and, in the female sex only, the structure of the subgenital plate. The bristle patterns of **T2–5** – surface bristles either in one transversal line or dispersed – are the same in imagines (of both sexes) and late larval stages; in earlier larval stages of all species the bristles are arranged approximately in one transversal line. The bristle patterns of **T6,7**, in the imagines showing strong differences between males and females, are the same in the larvae of the two sexes and correspond to the pattern of the imaginal female; the typical male pattern only appears after the imaginal moult (Fig. 15F–L). On the female subgenital plate **S7**, the transversal ridge (**sr7**) has in several species a very specific shape, which is already visible in late larval instars (Fig. 17G, H). For instance, an *A. aptera* larva (Fig. 17G) already showed the wide median gap of ridge **sr7** as present in the adult *A. aptera* female (Fig. 17C, D), whereas an *A. bergi* larva (Fig. 17H) had a medially continuous and bisinuate **sr7** as the adult *A. bergi* female (Fig. 16A, B).

4. Species descriptions

4.1. *Attaphila aptera* Bolívar, 1905

Figs 1A–C, 2B, E, F, 3A, B, 5A, B, J, 6A–E, 12A, 13C, 14A, I, 15F–H, 17C, D, G, 18A, B, 19A, 22A, B, 24A, B, 28H, S1A, B, S2A–C, S3A

Attaphila aptera Bolívar, 1905: 137; Princis 1963: 111.

Material studied. ***Type material.*** Holotype, 1L♂, Columbien, Esperanza, Dibulla, b. *Atta 8-spinosa* Reiche (Forel!) (completely on two slides: Bo 1232) (M. Maastricht). — ***Other material.*** Panama, Gamboa, IV–VI.2009, leg. V. Nehring, in nest of *Acromyrmex octospinosus*: 1♂ (completely on one slide: Bo 1224), 1♀ (completely on one slide: Bo 1225) (M. Maastricht, NHMM 2021 001, 002); 1♂ (completely on one slide: Bo 1227), 1♂ (abdomen on slide: Bo 1256, remains for DNA), 1♀ (abdomen on one slide: Bo 1257, remains for DNA), 1L♂ (head on one slide: Bo 1457), 2L♂ (each completely on one slide: Bo 1242, Bo 1291), 1L♂ (head and abdomen on two slides: Bo 1292), 3L♀ (each completely on one slide: Bo 1243, Bo 1289, Bo 1290) (M. Dresden). – Panama, Gamboa, IV–VI.2009, leg. V. Nehring, in nest of *Acromyrmex echinatior*: 1♂ (abdomen, tegmina, and head on three slides: Bo 1252), 1♀ (abdomen and head on two slides: Bo 1253) (ZS Munich).

Diagnosis. ***Male***: Well characterised by several features unique in *Attaphila*: the specialisation on **T1** involving moderately long bristles (**msp1**), the bristle distribution on **T6,7** with numerous bristles on the surface but none along the posterior border, and the specially shaped virga (with a moderate sinusoidal curvature). ***Female***: Surface bristles of **T2–5** dispersed, of **T6** numerous, relatively long and strong. Unique among *Attaphila* species by presence of a lateral gonangulum sclerite (unknown for *A. sexdentis*). From *A. bergi* distinguished by **S7** having a median gap in the transversal ridge. *A. sexdentis* also has numerous, but smaller bristles on **T6** and a differently shaped **S7**.

Description. ***Size***: Length of body (in alcohol): male 2.81–3.31 mm, female 3.16–3.36 mm. ***Surface bristles***

of tergites 2–5 (definition in 2.4.) dispersed, not arranged in transversal rows (Fig. 6A, C, D). ***Transversal ridges*** **tr2–5** without distinct excurvations (Fig. 6A, D, compare grey arrows in Fig. 11A, and in Fig. 9B for male **tr2**).

Male**. Tegmina** (Fig. 3A, B) widest at about 2/3 of length; overall shape roughly triangular; posterior border convex from tegmen base (**fwar**) onward, its wide curvature very uniform throughout, joining the apical border

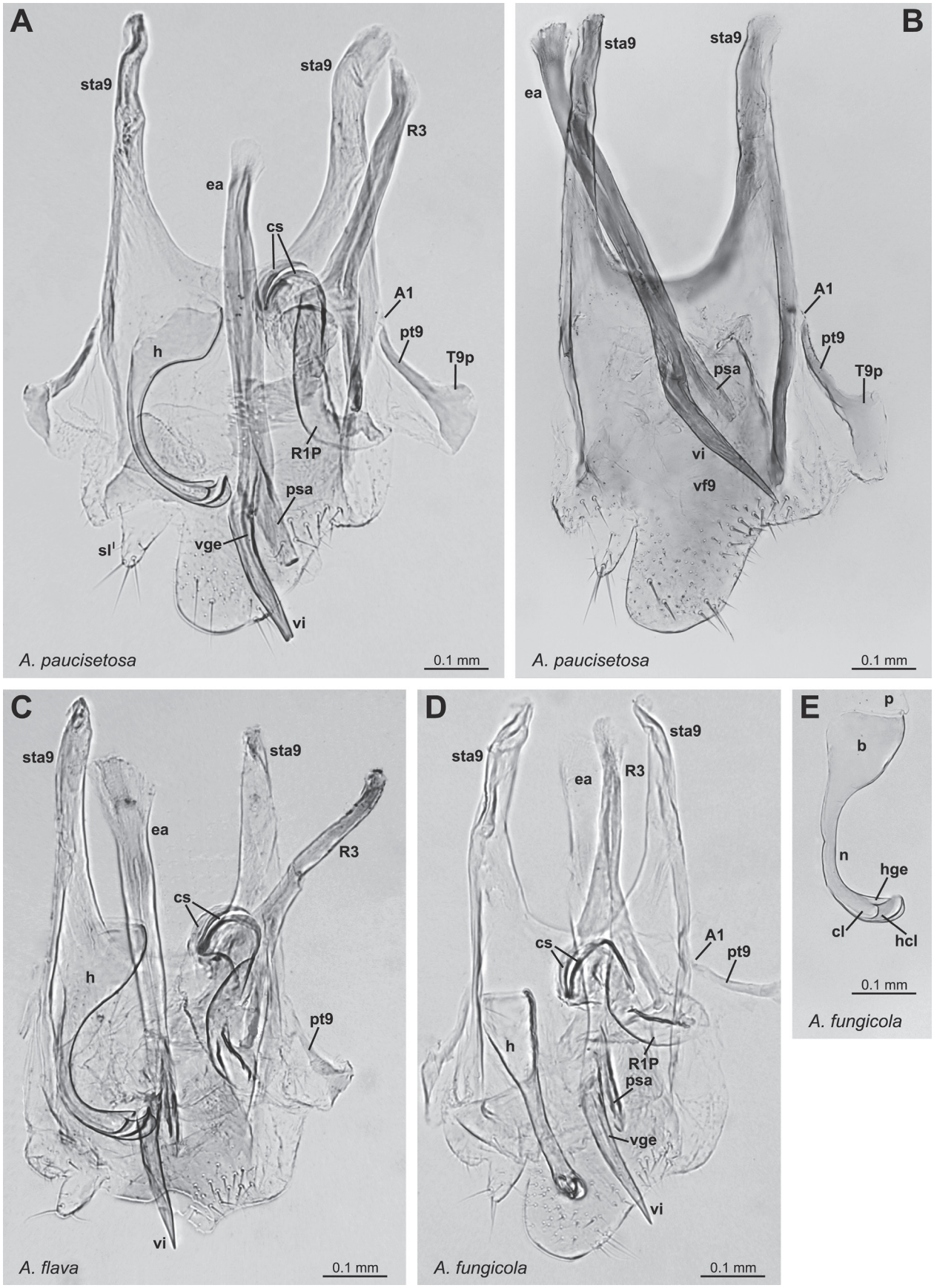


Figure 25. Subgenital plate (sternite S9) and phallomeres of males of *Attaphila* species, dorsal view, anteriorly on top. **A**, **B**: *A. paucisetosa*, subgenital plate with phallomeres (PT Bo 1254, Bo 1444), hook and right phallomere removed in B. **C**: *A. flava*, subgenital plate with phallomeres (HT Bo 1280). **D**, **E**: *A. fungicola*. D showing subgenital plate with phallomeres (LT Bo 1265), hook not seen in profile; E showing isolated hook seen in profile (Bo 1229). — ***Abbreviations***: **T9p** ventrally bent lateral (paratergal) part of tergite 9; otherwise as for Fig. 24.

far apically in a much tighter curvature (also tighter than in *A. bergi*); apical border transversal, fairly straight; surface bristles moderately strong. **Hindwings** fairly rhombic, with obtuse apex (similar to Fig. 1H). **Glandular pores** on **T1–5** in the area between the transversal ridge and the anterior border, numerous and tiny, especially densely arranged in median third of tergite (Fig. 5A, B). **Tergite 1** without long bristles on surface and borders (in contrast to long bristles on **T2–5**); medially, immediately posteriorly of the transversal ridge **tr**, with a specialisation (**msp1**) consisting of a more or less rounded, weakly sclerotised area with two groups of medium-sized bristles pointing anteriorly; on both sides of this area with some much smaller bristles of varying orientation (Figs 5A, B, 6A). Ridge **tr1** almost continuous across midline, but more or less weakened and fragmented. **Tergite 2** without specialisations. **Tergites 6,7**: (Figs 13C, 14I, 15F, H(larval)) Median lobe of **T7** (definition in 3.6.) very short, but distinct; transversal ridges **tr6** and **tr7** well developed; posterior borders of **T6** and **T7** without bristles, surfaces with dispersed bristles of moderate to small size, on **T6** larger than on **T7**, in radiating orientation. **Subgenital lobe**: (Fig. 24A, B) distal part with a deep excavation only along left side; lobe posterior to level of excavation widely tongue-shaped; with two styli, the larger left one (**sl**^{l}) conical, inserted at base of excavation, not reaching tip of lobe, the much smaller right one (**sl**^{r}) knob-like, situated subterminally on right flank of tip; stylus and borders of distal lobe with numerous bristles, most of them of moderate size, some rather long and strong. **Phallomeres**: (Fig. 24A, B) Sclerotised part of hook (**h**) from the long, wide base (**b**) very gradually narrowing into a slender, fairly short neck (**n**; shorter than in *A. fungicola*) which is hardly curved and bends almost rectangularly into the slightly wider claw part (**cl**). Endophallic apodeme (**ea**) not narrowed at base (forking site of sclerite). Relative to the axis of the endophallic apodeme (**ea**), the virga (**vi**) shows a distinct but quite shallow sinusoidal excurvation to the left, its apical part being moderately curved (back into the **ea**-axis) and gradually narrowed to a rather stout tip; virga longitudinally grooved. **Paraprocts**: Right paraproct with a sclerotised hook-like projection (**hmp** in Figs 5J, 6B), left one without a projection.

Female. **Tergites 6,7**: (Figs 6E, 12A, 14A, 15G(larval)) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally at most with a very weak bend; surface bristles (definition in 2.4.) numerous and rather long and strong; focused to central (= longitudinal and transversal middle) part of surface area (between transversal ridge and posterior border). **Subgenital plate** (Figs 17C, D, 18A, B) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) in the middle with a shallow, but distinct mesally directed curvation, lateral terminal parts fairly straight; ridge mesally ending shortly after having reached a transversal orientation, with a very wide median gap, partly recurved **sr7-m** ends indicating the ridge to be at least slightly bisinuate. **Genitalia**: Spermathecal plate **sp** large (reaching far to the left), pouch **gcp** moderately sized (Fig. 19A). In laterosternal shelf sclerite (**ls** in Fig. 22A, B) central part (**c**) moderately long and posteriorly more or less transversally cut, arms (**a**) moderately wide, wing parts (**w**) moderately to very wide, their base restricted to posterior half of tubes (blue arrowhead); tubes (**lst**) slightly curved mesad and slightly narrowed towards the anterior. Lateral and mesal gonangulum sclerites distinct (**gg-l**, **gg-m** in Fig. 19A).

Host species. *Acromyrmex octospinosus* (Reich, 1793) (Bolívar 1905), *Acr. echinatior* (Forel, 1899).

Distribution. Panama (Gamboa); Colombia (Dibulla).

Remarks. *Attaphila aptera* was described on the basis of a single specimen, a last-stage larval male which Bolívar (1905) interpreted as an adult; the corresponding adult stages were hitherto not known and their identification is problematic due to the scarcity of species-specific characters in larvae. A study of larval characters in four species (see 3.13.) has shown that the bristle patterns of tergites may contribute to an identification of the corresponding imagines: the bristle pattern of male (and female) larvae is very similar to that of the imaginal female.

The type specimen of *Attaphila aptera* has dispersed bristles on **T2–5**, thus ruling out the specimens herein classified as *A. multisetosa*, *A. paucisetosa*, and *A. sinuosocarinata* as its conspecifics. The bristles on the surface of **T6,7** are numerous and relatively long and strong (Fig. 15H), comparable to those observed in larvae and females of *A. bergi* (Figs 14B, 15I, J) and of the specimens from Gamboa (Panama) found in the nests of *Acromyrmex octospinosus* and *Acr. echinatior* (Figs 14A, 15F, G). There is no similarity with the bristle pattern of the remaining four species, which, therefore, can also be eliminated from the list of candidates for conspecifity with the *A. aptera* type: *A. sexdentis* has considerably smaller bristles in much higher numbers and density, *A. fungicola* and *A. schuppi* have fewer and/or smaller bristles on **T6,7**. *A. flava* is only known from the male sex, but the high similarity with the male of *A. fungicola* justifies the assumption of a corresponding similarity between the females of the two species.

The long distance between the localities of the larval *A. aptera* type (Colombia) and the localities where *A. bergi* (Argentina, Uruguay) was found, and the different host species, *Acr. octospinosus* versus *Acr. lundii* (which are

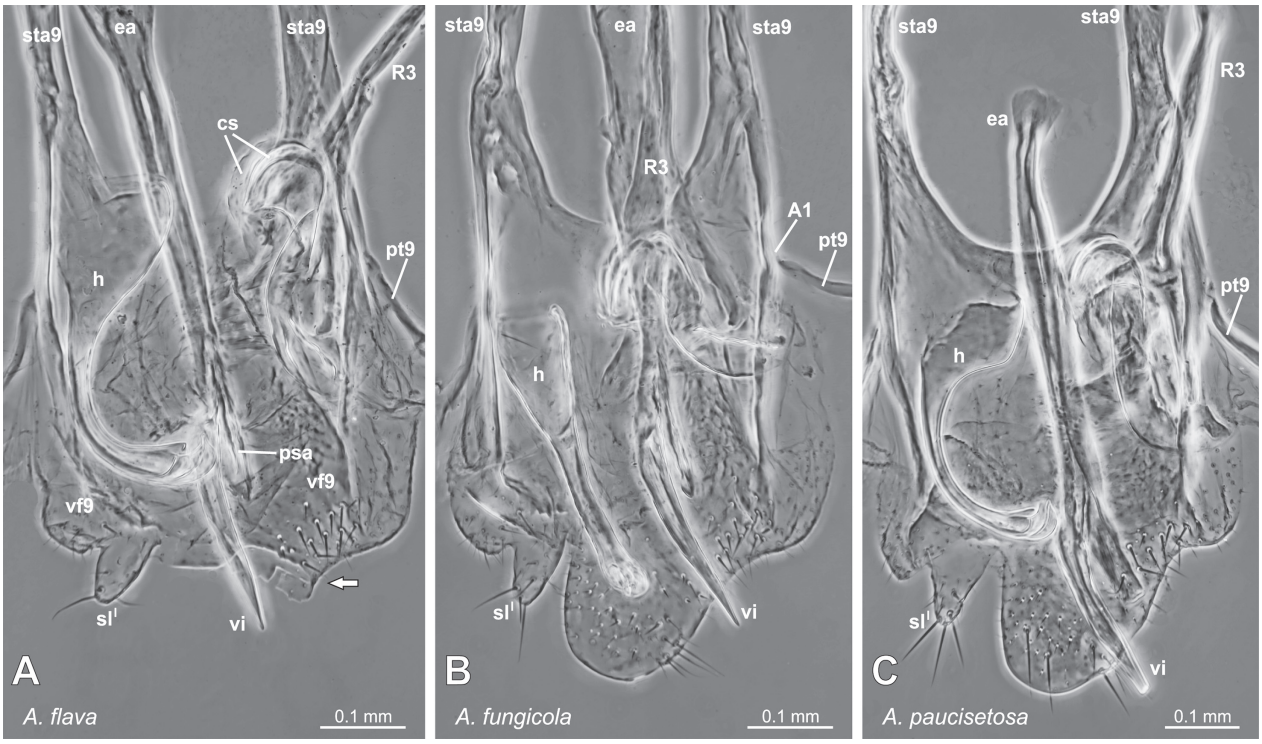


Figure 26. Subgenital plate (sternite S9) and phallomeres of males of *Attaphila* species, phase contrast images of the same objects as shown in Fig. 25A, C, D, anteriorly on top. **A**: *A. flava* (HT Bo 1280). **B**: *A. fungicola* (LT Bo 1265). **C**: *A. paucisetosa* (PT Bo 1254). — ***Abbreviations***: **A1** articulation between S9 and pt9; **cs** cleft sclerite of right phallomere; **ea** endophallic apodeme; **h** hook; **psa** process; **pt9** extension of paratergite 9 contacting sternite 9; **R3** anterior principal sclerite of right phallomere; **sl'** left stylus; **sta9** anterior apodeme of subgenital plate S9; **vf9** subgenital lobe; **vi** virga. ***Arrow***: in A indicating that the distal part of the subgenital lobe is broken off.

phylogenetically disjunct: Cristiano et al. 2020; Fig. 27), argue against the assumption that both could belong to the same species. The *A. aptera* type is much more likely conspecific with (or, at least, most closely related to) the species from Panama: their localities are much closer together and the host species reported for the *A. aptera* type is among the two host species known for the species from Panama. We did not find a character contradicting the assumption of conspecifity.

Because of the still existing uncertainties it may be seen as premature to assign the specimens from Gamboa to *A. aptera*. But the possible alternative, to describe them as a new species, appears to be less appropriate. If some day it turns out that the assignment to *A. aptera* is wrong, the species from Gamboa has to get a new name; if the alternative fails, the system is enriched by a new synonym.

4.2. *Attaphila bergi* Bolívar, 1901

Figs 1E, G, 2G, 3C, D, 5C, D, 7A–E, 12B, 13D, 14B, 15A, I, J, 16A, B, 17H, 18C, D, 19B, 22C, D, 24C–G, S1C, S3B–D

Attaphila bergi Bolívar, 1901: 335, pl. 6; Princis 1963: 111.
Attaphila bergi var. *minor* Bruch, 1916: 329, fig. 17A–F.

Material. ***Type material*** (presumably lost)**.** Syntypes, 2♂, 6♀, Argentina (Buenos Aires?), Uruguay. — ***Material studied.*** 2♀, [Argentina], B[ueno]s. A[ire]s (abdomen of each on one slide: Bo 1284, Bo 1440); 4L♀, Argentina, [Prov.] B[ueno]s Aires, Castelar, M.Viana and R.Maniglia, # 41175 (together with a worker of *Acromyrmex lundii* on one pin); 4L♀, same data as preceding (together with a worker of *Acromyrmex lundii* on one pin) (abdomen of 1L♀ on one slide: Bo 1285); 3♂, 1♀, [Argentina], [Prov.] Entre Ríos, Paranacito, [1931, acc. to loan form], Daguerre, # 28 994 (together with a worker of *Acromyrmex lundii* on one pin) (1♂ completely on two slides: Bo 1286; abdomen and tegmina of 1♂ on two slides: Bo 1443; abdomen of ♀ on one slide: Bo 1275) (M. Buenos Aires). – 1♂, 1♀, [Argentina, Prov. Buenos Aires], Moreno BA, 30.XI.[19]38, M.D.Jurado, # MACN-En 7781/7780 (♂ completely on two slides: Bo 1283; abdomen and part of legs of the ♀ on one slide: Bo 1282) (M. Maastricht, NHMM 007, 008); 10L, Argentina, [Prov. Buenos Aires], La Plata, VII.1918, C.Bruch (on 4 pins, each with a worker of *Acromyrmex lundii*) (1L♂ completely on two slides: Bo 1230; 1L♀ completely on two slides: Bo 1231) (M. Maastricht). – 1♂ [Argentina], [Prov.] Entre Ríos, Paranacito, [1931, acc. to loan form], Daguerre, # 28 944 (from a pin with a worker of *Acromyrmex lundii*) (completely on two slides: Bo 1274); 1♀, [Argentina, Prov. Santa Fé], Rosario, Coll. Hubrich, # 15 A 16 (completely on two slides: Bo 1239); 6L♀, [Argentina], Rosario (?), Coll. Hubrich, # R.66, B.p.77 (together with a worker of *Acromyrmex lundii* on one cardboard) (1L♀ completely on one slide: Bo 1238) (ZS Munich).

Diagnosis. ***Male***: Well characterised by several features unique in *Attaphila*: the rather inconspicuous specialisation anteromedially on **T1** with a pair of areas showing strongly developed microreticulation (**msa1**), the bristle distribution on **T6,7** with some bristles on the surface

of **T6** and long bristles along the posterior borders, and the specially shaped virga (with a very strong sinusoidal curvature). With *A. aptera* it shares the absence of long bristles on surface and borders of **T1**. ***Female***: Distinguished from all other species by **S7** having a continuous, uninterrupted transversal ridge.

Description. ***Size***: Length of body (dried, type specimens after Bolívar 1901): male 2.8 mm, female 2.8 mm. ***Surface bristles of tergites 2–5*** arranged in about two irregular transversal rows (Fig. 7A, D). ***Transversal ridges*** **tr2–5** without distinct excurvations (Fig. 7A, D, compare grey arrows in Fig. 11A, and in Fig. 9B for male **tr2**).

Male: **Tegmina** (Fig. 3C, D) widest at about 2/3 of length; overall shape more rectangular than triangular; posterior border straight or slightly concave near tegmen base (**fwar**), slightly converging with the apical border, soon bending into a rather tight curvation (as compared to *A. aptera*), finally joining the apical border in a still tighter curvation (though less tight than in *A.aptera*); apical border transversal, fairly straight; surface bristles strong (stronger than in *A. aptera*). **Hindwings** lanceolate, with narrowly rounded apex (Fig. 1G). **Glandular pores** only on **T1**, in the area of the specialisation and some more around (Fig. 5C, D). **Tergite 1** without long bristles on surface and borders (in contrast to long bristles on **T2–5**); medially, about at the level of the medially obsolete ridge **tr1** (far anteriorly on **T1-a**), with an inconspicuous specialisation (**msa1**) consisting of a pair of small areas showing a net-like pattern produced by delicate furrows or ridges along which tiny glandular pores are sporadically arranged; area in between either unstructured or with dispersed small pores, occasionally also with few small bristles (Fig. 5C, D). Ridge **tr1** interrupted by the specialisation. **Tergite 2** without specialisations. **Tergites 6,7**: (Figs 7B, 13D, 15A, I(larval)) Median lobe of **T7** very short, but distinct; transversal ridge **tr6** well developed, **tr7** rather weakly developed, perhaps with gaps in lateral parts; posterior border of **T6** and **T7** with a row of rather long and strong bristles, almost reaching the size of those of the lateral borders; surface of **T6** in the posterior half with dispersed bristles of slightly smaller size, sometimes distributed in two groups, of **T7** only with few isolated and usually much smaller bristles. **Subgenital lobe**: (Fig. 24C, D) distal part with a deep excavation only along left side; lobe posterior to level of excavation widely tongue-shaped; with two styli, the larger left one (**sl**^{l}) conical, inserted at base of excavation, not reaching tip of lobe, the much smaller right one (**sl**^{r}, relatively larger than in *A. aptera*) knob-like, situated subterminally on right flank of tip; stylus and borders of distal lobe with numerous bristles, most of them large (on average longer and stronger than in *A. aptera*), some rather long and strong. **Phallomeres**: (Fig. 24D–G) Sclerotised part of hook (**h**) from the long, wide base (**b**) very gradually narrowing into a slender, very short neck (**n**; shorter than in *A. aptera*) which is evenly curved into the slightly wider claw part (**cl**; neck thus hardly set off from both the base and the claw part). Endophallic apodeme (**ea**) not narrowed at base (forking site of sclerite). Relative to the axis of the endophallic apodeme (**ea**), the virga (**vi**) shows a distinct, deep sinusoidal curvature to the left, the apical part being very strongly and tightly curved (back into the **ea**-axis), and gradually narrowed to a rather acute tip ending shortly after the termination of the recurvation, hence hook-like (presence of a groove on the virga unclear). **Paraprocts**: Both lacking a sclerotised projection (Fig. 7C).

Female: **Tergites 6,7**: (Figs 7E, 12B, 14B, 15J(larval)) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally with a distinct bend; surface bristles numerous and rather long and strong (in length comparable to those of *A. aptera*, but less strong), strongly focused to central part of surface area. **Subgenital plate** (Figs 16A, B, 18C, D) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) almost straight; median part (**sr7-m**) complete, slightly (Fig. 16A) to strongly (Fig. 16B) bisinuate. **Genitalia**: Spermathecal plate **sp** rather small, pouch **gcp** rather small (Fig. 19B). In laterosternal shelf sclerite (Fig. 22C, D) central part (**c**) moderately long and posteriorly transversally cut, arms (**a**) very narrow (narrower than in *A. aptera*), wing parts (**w**) moderately wide, their base reaching far into anterior half of tubes (blue arrowhead); tubes (**lst**) straight, of fairly uniform width throughout, anterior end widely rounded. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 19B).

Host species. *Acromyrmex lundii* (Guérin-Méneville, 1838); host species of var. *minor* according to Bruch (1916) *Acr. lobicornis* (Emery, 1888), and *Amoimyrmex silvestrii* (Emery, 1905).

Distribution. Argentina: Prov. Buenos Aires (Castelar, La Plata, Moreno), Prov. Entre Rios (Paranacito), Prov. Santa Fé (Rosario). The var. *minor* is reported from the Provinces San Luis and Catamarca; the report of *A. bergi* from Córdoba (Bruch 1929) most likely is a mistake and refers to the occurrence of var. *minor* in San Luis, not mentioned in this paper; Uruguay.

Remarks. The loss of the type specimens of *A. bergi* and the insufficient original description of the species prevent an unequivocal identification. But for several reasons the determination of the available Argentine specimens as *A. bergi* is most probably correct: They have the same host ant species, *Acromyrmex lundii*; no other species of *Attaphila* has so far been found in nests of this ant. The specimens studied are from at least 5 different localities in rather close distance, not very far from the localities of the type specimens (Argentina: Buenos Aires?, Uruguay), without showing remarkable differences among each other.

Bruch (1916) described a var. *minor* occurring in nests of *Amoimyrmex silvestrii* (Prov. San Luis) and *Acromyrmex lobicornis* (Prov. Catamarca; belonging to *Amoimyrmex* or *Acromyrmex* clade not yet phylogenetically tested), of smaller size and paler colour than the nominate form. This characterisation and the missing of males raise the suspicion that the type specimens were larvae, possi-

bly of normal *A. bergi*. On the other hand, the complete or partial association with *Amoimyrmex* hosts, which form the sister taxon of *Acromyrmex* + *Atta* and are thus phylogenetically far remote from *Acromyrmex lundii* (Cristiano et al. 2020) raises doubt on var. *minor* being conspecific with *A. bergi*. The type specimens of var. *minor*, formerly deposited in the Museo de La Plata, are no longer present there and presumably lost.

4.3. *Attaphila flava* Gurney, 1937

Figs 3E, F, 5I, 8D, 15C, 25C, 26A

Attaphila flava Gurney, 1937: 106, fig. 9; Princis 1963: 111.

Material studied. Holotype, 1♂, British Honduras, Belize, Botanic Gardens, 11.VII.1904, P.G.Goll Type No. 52014 U.S.N.M. (abdomen and legs on two slides: Bo 1280) (M. Washington).

Diagnosis. ***Male***: The type specimen of *A. flava* is very similar to the male of *A. fungicola* and only shows slight differences in few characters: tegmina with apical border slightly convex, less oblique, surface bristles less strong; hook of left phallomere from the wide sclerotised base more gradually narrowing into a shorter neck, endophallic apodeme near its posterior base less strongly narrowed; and it has a different, though unknown host species.

Description. ***Size***: Length of body (dried): male 2.83 mm. ***Surface bristles of tergites 2–5*** dispersed, not arranged in transversal rows (Fig. 8D). ***Transversal ridges*** **tr2–5** without distinct small excurvations to the anterior (Fig. 8D; compare grey arrows in Fig. 11A), but male **tr2** posteriorly of the specialisations with a wide excurvation to the posterior, mesally followed by a wide, very shallow excurvation to the anterior (grey arrows in Fig. 8D).

Male: **Tegmina** (Fig. 3E, F) widest at about 1/2 of length; slightly obtusely wedge-shaped due to the converging course of the basalmost part of the posterior border and the apical border, both connected in a rather wide curvature; posterior border with a slight concavity near the tegmen base, oblique apical border throughout slightly convex; surface bristles fine. **Hindwings** fairly rhombic, with obtuse apex. **Glandular pores** on **T2–5** (and perhaps **T1**) in the area between the transversal ridge and the anterior border, dispersed, in moderately high density (Fig. 5I). **Tergite 1** without specialisations (occurrence of long bristles could not be studied for T1; they are present on T2–5). **Tergite 2** along anterior border with a pair of specialisations (**msl2**) consisting of a shallow, narrow transversal trough the bottom of which is patterned by low crossing ridges (Figs 5I, 8D; very similar to those of *A. fungicola*). **Tergites 6,7**: (Fig. 15C) Median lobe of **T7** very short, but distinct; transversal ridge **tr6** well developed, **tr7** absent; posterior border of **T6** and **T7** with a relatively dense row of very short and thin bristles much smaller than those of the respective lateral borders; surface of **T6** and **T7** only with few isolated and very small bristles, still smaller than those of the posterior borders. **Subgenital lobe**: (Figs 25C, 26A) distal part with a deep excavation each along left side and right side; lobe posterior to level of excavations narrowly tongue-shaped and presumably inclined leftward (tip of lobe not retained in specimen); only left stylus present (**sl^{l}**), which is quite conical, inserted at base of left excavation; at the base of the right excavation with a group of short and strong bristles; stylus with few rather long and thin bristles. **Phallomeres**: (Figs 25C, 26A) Sclerotised part of hook (**h**) from the short, wide base (**b**) gradually narrowing into a slender neck (**n**; shorter than in *A. fungicola*) with a hardly curved proximal part, terminating in a slightly wider claw part (**cl**). Endophallic apodeme (**ea**) slightly narrowed at base (forking site of sclerite). Relative to the axis of the endophallic apodeme (**ea**), the virga (**vi**) shows a weak, very shallow sinusoidal curvature to the left, its apical part being hardly curved (back into the **ea**-axis) and gradually narrowed to a rather acute tip, distinctly more acute than in *A. paucisetosa*; virga likely longitudinally grooved. **Paraprocts**: Both lacking a sclerotised projection.

Female: Unknown.

Distribution. Only known from the type locality Belize, Belize City.

Host species. Unknown, certainly not *Atta texana* as in *A. fungicola* since the distribution of this ant species does not reach further south than northeast Mexico. In view of the great similarity of *A. flava* with *A. fungicola*, its host is likely an *Atta* species. It could be *Atta cephalotes*, the only species of *Atta*, *Acromyrmex*, and *Amoimyrmex* so far reported for Belize (according to https://antwiki.org and https://www.antweb.org, both accessed on 19.i.2021), although *Acromyrmex echinatior* is known from all neighbouring countries (https://www.antweb.org).

Remarks. In the description of *A. flava* Gurney (1937) only noted one difference to *A. fungicola*, the very short subgenital plate (his fig. 9). But the subgenital plate of the type specimen is damaged and missing its apical part (Figs 25C, arrow in 26A); it might have been of the same length and shape as in *A. fungicola* (Fig. 26B). In view of the weak differences between the males of *A. flava* and *A. fungicola* one might have doubts whether the type specimen of *A. flava* really represents a separate species. But as long as neither the corresponding female nor the full shape of the subgenital plate is known, synonymisation with *A. fungicola* appears unjustified.

4.4. *Attaphila fungicola* Wheeler, 1900

Figs 1D, 3G, H, 5G, H, 8A–C, 12C, 13F, 14C, 15B, 16C, D, 18E, F, 19C, D, 22E, F, 25D, E, 26B

Attaphila fungicola Wheeler, 1900: 860, figs 3–6; Hebard 1916: 214, pl. X, figs 5–6; ?Wheeler 1928: 255 (reports from British Guiana and Panama); Princis 1963: 110; ?Brossut 1976: 167, figs 1–9; Roth 1968: 135, fig. 17; Roth 1971: 130, fig. 21.

Material studied. ***Type material.*** Lectotype, 1♂, Texas, Austin, XI.00, *Atta fervens* with *Attaphila fungicola*, Nov. 20.1900, W.M.Wheeler Coll. (left tegmen and abdomen on two slides: Bo 1265) (M. New York). – Paralectotypes: 7L, same data as Lectotype (M. New York); 2L, Texas, Austin, 4/1900, Wheeler!, b. *Atta fervens* (M. Maastricht). — ***Other material.*** 1♂, 1♀, Texas, Milam Co., Sugarloaf Mt., 300', 4 mi. N Gause, 19.IX.1992, Godwin, Quinn, Riley et al. (each completely on two slides: Bo 1229, Bo 1228) (M. Maastricht, NHMM 2021 004, 005). – 4♀, Texas, Freestone Co., Old Spring Seat Church, nr. Donie, pit-fall in *Atta* nest, 26.–31.V.[19]95, Wm.Godwin and E.Riley; 1♀, 9L, Texas, Milam Co., Sugarloaf Mt., 300', 4 mi. N Gause, 19.IX.1992, Godwin, Quinn, Riley et al. (3L♀, each completely on one slide: Bo 1435, Bo 1436, Bo 1437); 4L, LA [Louisiana], Natchitoches Par. Red Dirt Wdlf. Mn. Ar., nr. Red Buff Campgr., 26.IX.1992, E.G. and T.J.Riley et al. (1L♀ completely on slide: Bo 1438); 1♀, USA, Texas, Guadalupe Co., 14.5 km SE Seguin, 29.48282°N 97.85017°W, ±5 m, 4.XII.2014, A.Graf, B.Hays, B.Lyons, J.Oswald, E.Riley and W.Ryan, ex nest of *Atta texana* from depth of 2–8 ft. (Coll. TAMU). – 1♀, Texas, Freestone Co., Old Spring Seat Church, nr. Donie, pit-fall in *Atta* nest, 26.–31.V.[19]95, Wm.Godwin and E.Riley (completely on two slides: Bo 1236); 1♀, USA, Texas, Travis Co., Austin, University of Texas, Brackenridge Field Lab., *Atta texana* nest, 30.28444 N 97.78194 W, 1.VII.2010, leg. U.Mueller (abdomen on one slide: Bo 1264) (ZS Munich).

Diagnosis. ***Male***: As in *A. paucisetosa* with specialisations on **T2** (**msl2**, but these are narrower, with simpler ridges), distinguished by having dispersed surface bristles on **T2–5**. For differences to *A. flava*, see 4.3. ***Female***: Well characterized by the combined occurrence of two characters: **T2–5** with dispersed surface bristles, **T6,7** with only few and small surface bristles. The latter feature is also shared by *A. paucisetosa*, in which, however, the surface bristles of **T2–5** are arranged in one line.

Description. ***Size***: Length of body (dried): male 2.65–3.5 mm, female 2.45–3.5 mm (after Hebard 1916). ***Surface bristles of tergites 2–5*** dispersed, not arranged in transversal rows (Fig. 8A, C). ***Transversal ridges*** **tr2–5** without distinct small excurvations to the anterior (Fig. 8A, C; compare grey arrows in Fig. 11A), but male **tr2** posteriorly of the specialisations with a wide excurvation to the posterior, mesally followed by a wide, very shallow excurvation to the anterior (grey arrows in Fig. 8A).

Male: **Tegmina** (Fig. 3G, H) widest at about 1/2 of length; obtusely wedge-shaped due to the converging course of the basalmost part of the posterior border and the apical border, connecting curvature shorter than in *A. flava* thanks to the slightly more oblique course of the borders; likewise, posterior border near the tegmen base less concave, oblique apical border fairly straight; surface bristles rather fine (stronger than in *A. flava*). **Hindwings** fairly rhombic, with obtuse apex. **Glandular pores** on **T2–5** in the area between the transversal ridge and the anterior border, dispersed, in moderately high density (Fig. 5G, H). **Tergite 1** with long bristles on surface and borders (like **T2–5**); without specialisations. **Tergite 2** along the anterior border with a pair of specialisations (**msl2**) consisting of a shallow, narrow transversal trough the bottom of which is patterned by low crossing ridges (Fig. 5G, H). **Tergites 6,7**: (Figs 8A, 13F, 15B) Median lobe of **T7** scarcely visible; transversal ridge **tr6** well developed, **tr7** absent; posterior border of **T6** and **T7** with a relatively dense row of very short and thin bristles, much smaller than those of the respective lateral borders; surface of **T6** and **T7** only with few isolated and very small bristles, still smaller than those of the posterior borders. **Subgenital lobe**: (Figs 25D, 26B) distal part with a deep excavation each along left side and right side; lobe posterior to level of excavations narrowly tongue-shaped and inclined leftward; only left stylus present (**sl**^{l}), which is conical, inserted at base of left excavation, not reaching tip of lobe; at the base of the right excavation with a group of short and strong bristles; distal lobe and stylus with few rather long and thin bristles. **Phallomeres**: (Fig. 25D, E, 26B) Sclerotised part of hook (**h**) from the short, wide base (**b**) almost gradually narrowing (not as gradually as in *A. flava*, but with a weak, yet distinct shoulder, Fig. 25C) into a slender neck (**n**) with a hardly curved proximal part, terminating in a slightly wider claw part (**cl**). Endophallic apodeme (**ea**) strongly narrowed at base (forking site of sclerite). Relative to the axis of the endophallic apodeme (**ea**), the virga (**vi**) shows a weak, very shallow sinusoidal curvature to the left, its apical part being hardly curved (not fully back into the **ea**-axis) and gradually narrowed to a rather acute tip, distinctly more acute than in *A. paucisetosa*; virga likely longitudinally grooved. **Paraprocts**: Both lacking a sclerotised projection (Fig. 8B).

Female: **Tergites 6,7**: (Figs 12C, 14C) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally at most with a very weak bend; surface bristles numerous, very few of medium size, most between very small and tiny; dispersed all over the surface between transversal ridge and posterior border. **Subgenital plate** (Figs 16C, D, 18E, F) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) fairly straight; median part (**sr7-m**) with gap(s) of various size and number: two cases with one rather wide gap, and one case with two quite narrow gaps, then indicated to be slightly bisinuate. **Genitalia**: Spermathecal plate (**sp**) moderately large, pouch **gcp** present (size not determinable; Fig. 19C, D). In laterosternal shelf sclerite (Figs 19C, 22E, F) central part (**c**) fairly short and posteriorly rounded, posterior and lateral margins of central part and arms together forming a quite evenly curved horseshoe arch, arms (**a**) fairly narrow, wing parts (**w**) moderately wide, their base restricted to posterior half of tubes (blue arrowhead); tubes (**lst**) with angular bend exceptionally far anteriorly (at red arrowhead: near midlength of lateral border), from there towards the anterior rather strongly narrowed and curved mesad. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 19D).

Host species. *Atta texana* (Buckley, 1860). [The current taxonomic status (according to Bolton 2021) is that (1) *Atta fervens* (Drury, 1782), the name to which the sampling of *Attaphila fungicola* type specimens in "Material studied" above most likely refers, is a synonym of *Atta cephalotes* (Linnaeus, 1758), but that (2) the "*Atta fervens*" populations from Texas, the area of this sampling,

were described as a separate species *Atta texana* (Buckley, 1860), which is a currently valid name.]

Distribution. USA: Texas (Austin, Donie, Gause, Seguin), Louisiana (Natchitoches). The reports of Wheeler (1928) from British Guiana and Panama and of Brossut (1976) from Trinidad most likely concern other species.

Remarks. In his description of the species Wheeler (1900) reported that he had collected four males, two females, and about seventy immature specimens from a nest of "*Atta fervens*" (i.e. *Atta texana*) (excavated on the 10th of April). It is not indicated which of the specimens he considered as type specimens.

Specimens labelled as types of *A. fungicola* are present in the Collection Wheeler, which is preserved in the American Museum of Natural History (New York). It comprises one male and seven larvae, each labelled with "Austin, Texas, W.M.Wheeler, Coll."; additionally, there is a common handwritten label: "Atta fervens with Attaphila fungicola, Austin, Nov. 20. 1900".

A second sample of pretended type specimens is deposited in the Wasman Collection in the Natuurhistorisch Museum in Maastricht, consisting of two immatures. They are labelled – in Wasmann's handwriting – with "Attaphila fungicola Wheel. (Typen), b. Atta fervens, 4/1900 Wheeler!, Austin (Tex.)".

The agreement in the date shows that the specimens from Maastricht undoubtedly belong to the series which Wheeler described in his paper, while the New York series was collected later in the year. But the only specimen among the two series which could serve as an informative type is the sole adult specimen, the male from the New York series. Since both series were collected by Wheeler, in the same year, at the same locality, in nests of the same ant species, it appears legitimate to consider the two series together as a Syntype series, from which the male specimen is here selected as the Lectotype, while all other specimens are designated as Paralectotypes.

4.5. *Attaphila multisetosa* sp. nov. Bohn and Klass

Figs 10A, B, 12D, 14D, 17E, 18G, 21A, 22G

http://zoobank.org/A17A1082-D1D3-45D1-AD22-3EA136614D6E

A. aptera Bolívar, 1905 in Bruijning 1959: 23, figs 7, 8 (misidentification).

Material studied. Holotype, 1♀, Suriname, [Distr. Wanica], Lelydorp, in *Atta*-nest, 20.V.1938, Geijskes (completely on two slides: Bo 1270) (M. Leiden). – Paratype, 1L♀, same data as holotype (terminalia on one slide Bo 1449) (M. Leiden).

Diagnosis. ***Female***: Arrangement of bristles on **T2–5** similar to *A. paucisetosa* and *A. sinuosocarinata*, but much more irregular, only partly in one line; from the former distinguished by having numerous and rather long and strong bristles on **T6** and a larger spermathecal plate, from the latter by the course of the **T6** transversal ridge sublaterally not having an angular bend, and from both by the unique structure of the middle part of the laterosternal shelf sclerite (**ls**).

Etymology. The species name refers to the numerous (Latin: *multi*) bristles (Latin: *setae*) present on **T6,7**.

Description. ***Size***: Length of body (dried): female 2.8 mm. ***Surface bristles of tergites 2–5*** at least in median third of tergites arranged in one fairly regular transversal row (though almost two-rowed on **T5**), towards laterally distribution less regular, appearing two-rowed (Fig. 10A). ***Transversal ridges*** **tr2–5** medially and in part sublaterally with a very weak small excurvation to the anterior (grey arrows in Fig. 10A; weaker than in *A. schuppi*, Fig. 11A).

Male: Unknown.

Female: **Tergites 6,7**: (Figs 10B, 12D, 14D) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally without angular bend; surface bristles numerous on **T6**, rather few on **T7**, of medium size (slightly smaller than in *A. bergi*), strongly focused to central part of surface area. **Subgenital plate** (Figs 17E, 18G) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) fairly straight; median part (**sr7-m**) with three small gaps, weakly bisinuate. **Genitalia**: Spermathecal plate (**sp**) large, pouch **gcp** large (Fig. 21A). In laterosternal shelf sclerite (Fig. 22G) central part (**c**) very long and posteriorly widely rounded, arms (**a**) moderately wide, wing parts (**w**) very wide, their base reaching far into anterior half of tubes (blue arrowhead; but interpretation not entirely clear); tubes (**lst**) with an evenly convex lateral border and a straight mesal border, narrowed towards the anterior. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 21A).

Host species. *Atta*, species unknown. (Three *Atta* species known from Suriname: *A. cephalotes*, *A. laevigata*, and *A. sexdens*; Bolton 2021)

Distribution. So far only known from the type locality Lelydorp, Distr. Wanica, Suriname.

4.6. *Attaphila paucisetosa* sp. nov. Bohn and Klass

Figs 1F, H, 2A, C, D, H, I, 3I, J, 4A–D, 5E, F, K, 9A–F, 12E, 13E, 14E, 15D, E, K, L, 16E, F, 18H, I, 20A, B, 21D, 22H, 25A, B, 26C, S2D, E

http://zoobank.org/867238EB-C302-4D4C-A7BF-ADB2D3B-4F3B4

Material studied. ***Type material.*** Holotype, 1♂, Panama, Gamboa, in nest of *Atta colombica*, IV.–VI.2009, leg. V. Nehring (abdomen on slide:

Bo 1258) (M. Maastricht, NHMM 2021 006). – 5 Paratypes, same data as holotype: 1♀ (completely on two slides: Bo 1226) (M. Maastricht, NHMM 2021 003), 1♂ (abdomen, tegmina, and head on three slides: Bo 1441), 1♀ (abdomen on two slides: Bo 1241) (ZS Munich), 1♂ (abdomen on one slide: Bo 1254; remains for DNA), 1♀ (abdomen on one slide: Bo 1255; remains for DNA) (M. Dresden). — ***Other material.*** Same data as holotype: 1♂ (completely on two slides: Bo 1240), 1♂ (abdomen and head on two slides: Bo 1442), 2♂ (each with abdomen on one slide: Bo 1444, Bo 1445), 1L♂ (abdomen and head on two slides: Bo 1433), 1L♂ (abdomen on one slide: Bo 1434), 1L♂ (head on one slide: Bo 1458), 1L♀ (abdomen on one slide: Bo 1293; remains for DNA), 2L♀ (each with abdomen on one slide: Bo 1295, Bo 1446), 2L♀ (each with abdomen and head on two slides: Bo 1294, Bo 1296) (M. Dresden). – 1♀, Panama, Panamá Par. Nac. Soberiana, Pipeline Rd., km 2, at entrance to *Atta* [*colombica*] nest at night, 16.V.1993, E.Riley (completely on two slides: Bo 1235) (Coll. TAMU). – 1♀, Panama, Gamboa, 14.VI.2010, attached to a queen of *Atta cephalotes*, leg. R.Adams (abdomen on one slide: Bo 1268) (ZS Munich). – 1♂, 4♀, 3L, Colombia, Valle del Cauca, Cali, Vereda los Andes, El Cabuyal, 3°24′50.37″N 76°35′38.34″W, 1360 m, Nido de *Atta cephalotes*, colecta manual, 25.XI.2012, leg. Jonathan Rodríguez G. (abdomen and head of ♂ on two slides: Cb 4/1, legs of a female on slide Cb 4/2, head of a L on slide Cb 4/3); 1♂, 1♀, 3L, Colombia, Valle del Cauca, Cali, Vereda el Peón, Loma larga, 3°20′23.69″N 76°35′13.17″W, 1399 m, Nido de *Atta cephalotes*, colecta manual, 24.X.2013, leg. Jonathan Rodríguez G. (abdomen and head of ♂ and ♀ each on two slides: Cb 2/1, Cb 2/2); 1♀, Colombia, Valle del Cauca, Buenaventura, Vereda el Salto, La Vibora, 3°50′29.5″N 76°47′32.0″W, 600 m, Nido de *Atta cephalotes*, colecta manual, 7.V.2014, leg. Jonathan Rodríguez G. (Cb 3) (ZS Munich).

Diagnosis. ***Male***: As in *A. fungicola* and *A. flava* with specialisations on **T2** (but these are wider, with more complicated ridges), distinguished by the arrangement of the surface bristles of **T2–5** in one transversal line. ***Female***: Well characterized by the combined occurrence of two features: bristles of **T2–5** arranged in one strict transversal line, and **T6,7** with only few and rather small bristles. The latter feature is also shared by *A. fungicola*, which, however, has dispersed surface bristles on **T2–5**. The species *A. sinuosocarinata* and *A. multisetosa* resemble *A. paucisetosa* in the first feature, but are distinguished by having numerous surface bristles on **T6,7** and by differences in the laterosternal shelf area.

Etymology. The species name refers to the few (Latin: *pauci*) bristles (Latin: *setae*) being present on **T6,7**.

Description. ***Size***: Length of body (in alcohol): male 2.7–3.43 mm, female 2.61–3.49 mm. ***Surface bristles of tergites 2–5*** strictly arranged in one straight transversal row, only on **T2** near the lateral borders bristles often less regularly distributed (Fig. 9A, B, E). ***Transversal ridges*** **tr2–5** without distinct small excurvations to the anterior (Fig. 9B, E; compare grey arrows in Fig. 11A), but male **tr2** posteriorly of the specialisations with a wide excurvation to the posterior, mesally followed by a wide, very shallow excurvation to the anterior (grey arrows in Fig. 9B).

Male: **Tegmina** (Fig. 3I, J) widest at about 1/2 of length; obtusely wedge-shaped due to the roughly converging course of the basalmost part of the posterior border and the apical border, connecting curvature similarly short as in *A. fungicola*; basalmost part of posterior border and the oblique apical border slightly concave; surface bristles rather fine (as in *A. flava* but longer and at a lower density). **Hindwings** fairly rhombic, with obtuse apex (Fig. 1H). **Glandular pores** on **T1–5** in the area between the transversal ridge and the anterior border, dispersed, in moderately high density (Fig. 5E, F). **Tergite 1** with long bristles on surface and borders (like **T2–5**); without specialisations. **Tergite 2** along the anterior border with a pair of specialisations (**msl2**) consisting of a shallow, fairly wide transversal trough the bottom of which is patterned by low crossing ridges that are more complicated than in *A. flava* and *A. fungicola*, forming a net-like relief (Figs 5E, F, 9B). **Tergites 6,7**: (Figs 9C, 13E, 15D, E, K(larval)) Median lobe of **T7** very short, but distinct; transversal ridge **tr6** well developed, **tr7** absent; posterior border of **T6** and **T7** with a row of relatively long and thin bristles, distinctly shorter and thinner than those at the respective lateral borders; surface of **T6** and **T7** only with few isolated and small bristles, still smaller than those at the posterior borders. **Subgenital lobe**: (Figs 25A, B, 26C) distal part with a deep excavation each along left side and right side; lobe posterior to level of excavations narrowly tongue-shaped and inclined leftward; only left stylus present (**sl^{l}**), which is conical, inserted at base of excavation, not reaching tip of lobe; at the base of the right excavation with a group of short and strong bristles; distal lobe and stylus with few rather long and thin bristles. **Phallomeres**: (Figs 25A, B, 26C) Sclerotised part of hook (**h**) from the short, wide base (**b**) suddenly narrowing into a slender neck (**n**) widely and uniformly curved from the beginning, terminating in a slightly wider claw part (**cl**). Endophallic apodeme (**ea**) not narrowed at base (forking site of sclerite). Relative to the axis of the endophallic apodeme (**ea**), the virga (**vi**) shows a weak, angular proximal bend to the left, its apical part being hardly curved (not fully back into the **ea**-axis) and gradually narrowed to a fairly stout tip; virga likely longitudinally grooved. **Paraprocts**: Both lacking a sclerotised projection (Figs 5K, 9D).

Female: **Tergites 6,7**: (Figs 9F, 12E, 14E, 15L(larval)) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally with a weak, but distinct bend; surface bristles very few, of medium size or smaller; focused to central part of surface area. **Subgenital plate** (Figs 16E, F, 18H, I) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) with a weak mesally directed curvation, lateral terminal parts with a weak laterally directed curvation; ridge mesally ending well after having reached a transversal orientation, close to a bristle-bearing point upon it, with a moderately wide median gap, recurved **sr7-m** ends indicating the ridge to be bisinuate. **Genitalia**: (Figs 20A, B, 22H) Spermathecal plate **sp** small, pouch **gcp** fairly small (Fig. 20A, B). In laterosternal shelf sclerite (Figs 20A, 22H) central part (**c**) fairly long and posteriorly rounded, posterior and lateral margins of central part and arms together forming a quite evenly curved horseshoe arch,

arms (**a**) fairly wide, wing parts (**w**) fairly narrow, their base restricted to posterior half of tubes (blue arrowhead); tubes (**lst**) narrowed towards the anterior and curved mesad. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 20B).

Host species. *Atta colombica* Guérin-Méneville, 1844, *Atta cephalotes* (Linnaeaus, 1758).

Distribution. Panama (Gamboa); Colombia: Depart. Valle del Cauca (Cali, Buenaventura).

4.7. *Attaphila schuppi* Bolívar, 1905

Figs 11A, B, 12F, 14F, 16G, H, 18J, K, 20C, D, 22J

Attaphila schuppi Bolívar, 1905: 138; Princis 1963: 111.

Material studied. ***Type material.*** Syntypes, 2♀, [Brazil, Estado Rio Grande do Sul], Porto Alegre, acc. by *Atta nigra* Schupp (each on two slides: Bo 1234 [labelled "Lectoholotype, det. A.B.Gurney, 1971"] and Bo 1237) (M. Maastricht).

Diagnosis. ***Female***: Characterised by a series of unique features: Transversal ridge of **T2–5** mesally and laterally with a small but distinct anterior excurvation (much weaker present also in *A. multisetosa*), transversal ridge absent on **T7**, cerci longer than wide.

Description. ***Size***: Length of body (dried): female 3.5 mm. ***Surface bristles of tergites 2–5*** approximately arranged in two transversal rows (Fig. 11A). ***Transversal ridges*** **tr2–5** medially and sublaterally with a small but distinct excurvation to the anterior (grey arrows in Fig. 11A; much stronger than in *A. multisetosa*, Fig. 10A).

Male: Unknown.

Female: **Tergites 6,7**: (Figs 11B, 12F, 14F) Median lobe of **T7** short, but distinct; transversal ridge **tr6** well developed, **tr7** missing except for few short remnants including also the two **tr7**-associated bristles, **tr6** sublaterally with a weak, but distinct angular bend; surface bristles numerous on **T6**, small to very small, focused to wider central part of surface area; absent on **T7**. **Subgenital plate** (Figs 16G, H, 18J, K) rounded-rectangular, with parallel lateral borders; posterior border rather weakly trilobed; lateral parts of transversal ridge (**sr7-l**) fairly straight, ridge mesally ending before having reached a transversal orientation (near anterior border of **S7**, and hardly curved mesad), with a very wide median gap. **Genitalia**: (Figs 20C, D, 22J) Spermathecal plate **sp** likely small (not clearly identifiable), pouch **gcp** likely absent (Fig. 20C, D). In laterosternal shelf sclerite (Fig. 22J) central part (**c**) moderately long and posteriorly transversally cut, arms (**a**) fairly wide, wing parts (**w**) fairly wide, their base reaching far into anterior half of tubes; tubes (**lst**) straight, of fairly uniform width throughout, anterior end widely rounded. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 20D).

Host species. *Acromyrmex niger* (F. Smith, 1858) (as "*Atta nigra* Schupp" in Bolívar 1905; originally placed in *Atta*, since 1913 attributed to *Acromyrmex*, and placed deeply in *Acromyrmex* according to Cristiano et al. 2020).

Distribution. Brazil: Est. Rio Grande do Sul, only known from the type locality Porto Allegre.

Remarks. The Wasmann Collection in Maastricht keeps two female specimens (on one pin) labelled by Wasmann as follows: "Attaphila schuppi (m) Boliv., Typen"; there are no labels concerning locality and species of the ant host. Bolívar's description contains, after a short morphological characterisation, the following data: "♂ Long. 3,5 mill. *Hab.* Porto Alegre. Elle se trouve en compagnie de *Atta nigra* Schupp. ...". The discrepancy between the two data sets raises the question whether the females from Maastricht had really been the subjects of Bolívar's description.

The absence of a number ahead of the sex symbol does not necessarily mean that Bolívar had only one specimen for study; in the descriptions of some other new species in the same paper Bolívar never noted the number of treated specimens. The strongest doubts in considering the Maastricht specimens as type specimens of *A. schuppi* concern the sex determination. It is extremely unlikely that Bolívar should have confused the two sexes. In the description of *A. aptera* in the same paper Bolívar emphasises the exceptional case of that species having wingless males (a wrong assumption, as a larval male is concerned, see 4.1.). On the other hand, it appears unlikely that Bolívar had males in his hands when he described the species *A. schuppi.* The description does not contain any remarks concerning wings, and the posterior border of the last sternite is described as being "transverso trisinuato", as is typical for the subgenital plate of *Attaphila* females. The simplest solution for the conflicting pieces of information would be to assume an error in the printing of the sex symbol.

The last remaining issue is the incomplete labelling of the type specimens. Wasmann had got the specimens from R.P. Schupp, possibly already without a label and only with a verbal information about the collecting data, which he might have passed on to Bolívar. After getting back the specimens he might have forgotten to label them accordingly. In spite of the dubious circumstances, the authors are convinced that the Maastricht specimens represent the type specimens of *A. schuppi*.

A.B. Gurney had labelled one of the specimens as lectotype: "Top specimen (mature ♀) designated lectoholotype *schuppi.* det. A.B.Gurney 1971". In fact, both specimens are mature females, and since the designation was not published, it is ignored.

4.8. *Attaphila sexdentis* Bolívar, 1905

Figs 11C, D, 13A, 14G, 17F, 18L, 21C, 22I

Attaphila sexdentis Bolívar, 1905: 137; Princis 1963: 111.

Material studied. ***Type material.*** Holotype, 1♀, [Brazil], Rio Grande do Sul, San Leopoldo, b. *Atta sexdens*, (Dr. Dutra!) (completely on three slides: Bo 1233) (M. Maastricht).

Diagnosis. ***Female***: Characterised by the unique shape of **S7**: posterior parts of the lateral borders anteriorly converging, in all other species (more or less) parallel.

Description. ***Size***: Length of body (dried): female 3 mm. ***Surface bristles of tergites 2–5*** approximately arranged in two transversal rows (Fig. 11C). ***Transversal ridges*** **tr2–5** without distinct excurvations (Fig. 11C, compare grey arrows in Fig. 11A).

Male: Unknown.

Female: **Tergites 6,7**: (Figs 11D, 13A, 14G) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally with a weak, but distinct bend; surface bristles very numerous on **T6**, only few on **T7**, small (slightly smaller than the larger ones in *A. paucisetosa*), focused to central part of surface area. **Subgenital plate** (Figs 17F, 18L) semicircular, lateral borders distinctly converging to the anterior; lateral parts of transversal ridge (**sr7-l**) fairly straight, ridge mesally ending well after having reached a transversal orientation, with a fairly narrow median gap (end parts of ridge only slightly more developed than in *A. aptera*, but lateral parts more strongly inclined mesally, thus leaving a narrower gap), hardly recurved **sr7-m** ends indicating the ridge to be at most weakly bisinuate. **Genitalia**: (Figs 21C, 22I) Spermathecal plate **sp** and pouch **gcp** not clearly identifiable. In laterosternal shelf sclerite (Fig. 22I) central part (**c**) moderately long and posteriorly widely truncate (slightly rounded), arms (**a**) moderately wide, wing parts (**w**) moderately wide, their base restricted to posterior half of tubes; tubes (**lst**) with a straight mesal border and slightly narrowed towards the anterior, anteriorly more or less transversally cut. Mesal gonangulum (**gg-m**) sclerites distinct (presence of lateral ones questionable; Fig. 21C).

Host species. *Atta sexdens* (Linnaeus, 1758).

Distribution. Brazil: Est. Rio Grande do Sul, only known from the type locality San Leopoldo.

4.9. *Attaphila sinuosocarinata* sp. nov. Bohn and Klass

Figs 10C–E, 13B, 14H, 17A, B, 18M, N, 21B, 22K, L

http://zoobank.org/52429161-53F1-4228-8730-66F6B95D3F09

Material studied. ***Type material.*** Holotype, 1♀, [Brazil], São Paulo, Baxnery, XI.20., A.Hempel leg., #20 242 (head missing, otherwise completely on one slide: Bo 1273) (M. São Paulo). – Paratypes, 9♀: 1♀, same data as holotype (completely on two slides: Bo 1439) (ZS Munich). 1♀, same data as holotype (abdomen on one slide: Bo 1288) (M. Maastricht, NHMM 2021 009). 2♀, same data as holotype (M. São Paulo). 5♀, [Brazil], São Paulo, Hinanga, # 6287 A (abdomen and legs of 1♀ on one slide: Bo 1272; abdomen of 1♀ on one slide: Bo 1287) (M. São Paulo).

Diagnosis. ***Female***: Surface bristles of **T2–5** similar as in *A. paucisetosa* and *A. multisetosa* fairly in one line, distinguished from the former by the more numerous bristles on **T6**, and from both by the more strongly bent transversal ridge of **S7** and the unique shape of tubes **lst** (see key).

Etymology. The species name refers to the sine-shaped (Latin: *sinuosus*) transversal ridge (Latin: *carina*) of **S7**.

Description. ***Size***: Length of body (dried): female 2.75–3.2 mm. ***Surface bristles of tergites 2–5*** arranged in one transversal row (less regular than in *A. paucisetosa*; Fig. 10C). ***Transversal ridges*** **tr2–5** without distinct excurvations (Fig. 10C, compare grey arrows in Fig. 11A).

Male: Unknown.

Female: **Tergites 6,7**: (Figs 10D, E, 13B, 14H) Median lobe of **T7** rather long; transversal ridges **tr6** and **tr7** complete, **tr6** sublaterally with a weak, but distinct bend; surface bristles very numerous on **T6**, only few on **T7**, very small, focused to central part of surface area. **Subgenital plate** (Figs 17A, B, 18M, N) rounded-rectangular, with parallel lateral borders; lateral parts of transversal ridge (**sr7-l**) with a strong mesally directed curvation, lateral terminal parts with a distinct laterally directed curvation; at least in part of the cases ridge mesally ending after having reached a transversal orientation, with a fairly wide median gap, partly recurved **sr7-m** ends indicating the ridge to be bisinuate (course of the transveral ridge very similar as in *A. aptera*, but lateral parts more strongly inclined mesally, thus leaving a narrower gap). **Genitalia**: (Figs 21B, 22K, L) Spermathecal plate **sp** large, pouch **gcp** quite large (Fig. 21B). In laterosternal shelf sclerite (Fig. 22K, L) central part (**c**) moderately long and posteriorly widely rounded-truncate, arms (**a**) moderately wide, wing parts (**w**) moderately wide, their base restricted to posterior half of tubes; tubes (**lst**) with a straight mesal border, slightly narrowed towards the anterior, anteriorly more or less transversally cut. Mesal gonangulum sclerites (**gg-m**) distinct, lateral ones absent (Fig. 21B).

Host species. Unknown.

Distribution. Brazil: Est. São Paulo (the possible localities “Baxnery” and “Hinanga” indicated on the labels could not be identified).

5. Determination keys

5.1. Key for females via various characters

1 Surface bristles (= bristles between transversal ridge and posterior border of tergite, excluding bristles along these two lines) of T2–5 dispersed (Fig. 8C) or in two very irregular lines (Fig. 7D) **4**

1' Surface bristles of T2–5 at least partly in one transversal line (Figs 9E, 10C) **2**

2 Surface bristles of T6 very few (Fig. 12E), of T2–5 in a strict line (Fig. 9E) ..... ***A. paucisetosa* sp. nov. Bohn and Klass**

2' Surface bristles of T6 numerous (Figs 12D, 13B), of T2–5 less regularly lined up (Fig. 10A, C) **3**

3 Transversal ridge of T6 laterally angularly bent, surface bristles of T6 small (Fig. 13B); transversal ridge of S7 in median part with one wide gap (Fig. 18M, N), lateral parts with a distinct concavity (Fig. 17A, B) ..... ***A. sinuosocarinata* sp. nov. Bohn and Klass**

3' Transversal ridge of T6 laterally regularly curved, surface bristles of T6 medium-sized (Fig. 12D); transversal ridge of S7 in median part with three small gaps or discontinuities (Fig. 18G), lateral parts without a distinct concavity (Fig. 17E) ..... ***A. multisetosa* sp. nov. Bohn and Klass**

4 T7 without transversal ridge (except for a few short remnants: Figs 12F, 14F); cerci with weak intrinsic asymmetry, fairly conical, longer than wide (Fig. 20C, D) ..... ***A. schuppi***

4' T7 with transversal ridge (e.g. Fig. 7E); cerci with strong intrinsic asymmetry, wider than long (Fig. 19A) **5**

5 Surface bristles of T6 of heterogeneous size, mostly between very small and tiny (Fig. 14C), sparsely distributed all over the surface between transversal ridge and posterior border (Fig. 12C) ..... ***A. fungicola***

5' Surface bristles of T6 of fairly homogeneous size between small and large (e.g. Fig. 14B), densely arranged in a wide median band extending variously far laterally, well remote from both the transversal ridge and the posterior tergal border (Figs 12A, B, 13A) **6**

6 S7 in outline semicircular, lateral borders converge towards the anterior (Fig. 17F); surface bristles of T6 very small and very numerous (Fig. 13A) ..... ***A. sexdentis***

6' S7 in outline rounded-rectangular, lateral borders quite parallel (Fig. 16A, B); surface bristles of T6 larger and less numerous **7**

7 S7 with transversal ridge uninterrupted (Figs 16A, B, 18C, D); surface bristles of T6 medium-sized (Figs 12B, 14B) ..... ***A. bergi***

7' S7 with transversal ridge interrupted by a very wide median gap (Figs 17C, D, 18A, B); surface bristles of T6 longer and stronger than in *A. bergi* (Figs 12A, 14A) ..... ***A. aptera***

5.2. Key for females via structure of laterosternal shelf

1 Wing-part (ls-w) base not reaching beyond posterior (proximal) half of tubes (lst) (Fig. 22B, E, H, L: blue arrowhead), central part (ls-c) posteriorly rounded or transversally cut **4**

1' Wing-part base reaching far into anterior (distal) half of tubes (Fig. 22C, D, G, J: blue arrowhead), almost up to their anterior end, central part posteriorly transversally cut **2**

2 Tubes with convex lateral borders, strongly narrowing towards the anterior, anterior end appearing more or less transversally cut (Fig. 22G) ..... ***A. multisetosa* sp. nov. Bohn and Klass**

2' Tubes with straight lateral borders, parallel-sided or slightly widening towards the anterior, anterior end appearing rounded (Fig. 22D) **3**

3 Arm parts (ls-a) immediately following central part (ls-c) about as wide as widest part of tube near apex (Fig. 22J) ..... ***A. schuppi***

3' Arm parts (ls-a) immediately following central part (ls-c) much narrower than widest part of tube near apex (Fig. 22C, D) ..... ***A. bergi***

[*A. schuppi* and *A. bergi* have a very similar laterosternal shelf area, but are otherwise easily distinguished by characters of S7, T6,7, and cerci.]

4 Tubes rather strongly narrowing towards the anterior and distinctly curved mesad **6**

4' Tubes not or only weakly narrowing towards the anterior and, if at all, only slightly curved mesad **5**

5 Tubes with lateral outline slightly but distinctly curved, anterior end obliquely cut (Fig. 22K, L) ..... ***A. sinuosocarinata* sp. nov. Bohn and Klass**

5' Tubes with lateral outline not curved, fairly straight, anterior end transversally cut (Fig. 22I) ..... ***A. sexdentis***

[*A. sinuosocarinata* and *A. sexdentis* have a very similar laterosternal shelf area, but are otherwise easily distinguished by the very different shape of S7.]

6 Central part (ls-c) posteriorly transversally cut (Fig. 22A, B) ..... ***A. aptera***

6' Central part posteriorly rounded, together with the two arms (ls-a) forming a horseshoe arch **7**

7 Width of horseshoe arch measured along longitudinal midline as large as or larger than maximal width of tube (Fig. 22H); angular bend of lateral border of tube quite far posteriorly (at red arrowhead)..... ***A. paucisetosa* sp. nov. Bohn and Klass**

7' Width of horseshoe arch measured along longitudinal midline less than maximal width of tube (Fig. 22E, F); angular bend of lateral border of tube far anteriorly (at red arrowhead) ..... ***A. fungicola***

[*A. paucisetosa* and *A. fungicola* have a very similar laterosternal shelf area, but are otherwise easily distinguished by the very different distribution of bristles on T2–5.]

5.3. Key for females mainly via structure of S7

Attaphila fungicola shows an unusual high variability in the structure of the median part of the sternal transversal ridge (**sr7** in Fig. 18E, F) and is, therefore, not included in the key. Applying the key to its specimens would lead to several places following slot 2'. The females of *A. fungicola* are otherwise well characterised by the mostly tiny bristles distributed all over the surface of **T6**. — Note that features of the anteromedian part of the transversal ridge (**sr7**) should be examined at high contrast (as, e.g., in Fig. 18G compared to Fig. 17E).

1 S7 semicircular, lateral borders converge towards the anterior (Fig. 17F: white arrows); transversal ridge interrupted by a fairly narrow median gap (Fig. 18L)..... ***A. sexdentis***

1' S7 rounded-rectangular, lateral borders quite parallel (Fig. 17B: white arrows); transversal ridge interrupted or not **2**

2 Anteromedian part of transversal ridge uninterrupted, bisinuate by median excurvation to the posterior (Fig. 18C, D) ..... ***A. bergi***

2' Anteromedian part of transversal ridge medially interrupted by one variously wide gap or several discontinuities **3**

3 Gap very wide, almost completely comprising the transversal anteromedian part of the ridge **5**

3' Gap narrower, comprising less than half of the transversal anteromedian part of the ridge, or with several very narrow discontinuities **4**

4 With one medium sized gap, mesal ends of the ridge with a short curvation towards the posterior prior to their termination close to a bristle-bearing point upon it, the incomplete median part of the ridge thereby appearing bisinuate (Fig. 18H, I); lateral parts with a weak mesally directed curvation (Fig. 16E, F)..... ***A. paucisetosa* sp. nov. Bohn and Klass**

4' With three narrow discontinuities, median part of the ridge slightly bisinuate (Fig. 18G); lateral parts fairly straight (Fig. 17E) ..... ***A. multisetosa* sp. nov. Bohn and Klass**

5 Lateral parts of transversal ridge fairly straight (Fig. 16G, H), ridge ending close to the anterior border of S7 after having just started to bend mesad (Fig. 18J, K)..... ***A. schuppi***

5' Lateral parts of transversal ridge with a distinct mesally directed curvation (Fig. 17A–D), ridge ending less close to the anterior border of the plate, mostly after having already reached a transversal direction **6**

6 Lateral parts of transversal ridge rather steeply ascending (Fig. 17C, D), gap between their endings, therfore, very wide (Fig. 18A, B), lateral parts posteriorly of the mesal curvation only with a weak lateral curvation (i.e. with a fairly straight terminal part; Fig. 17C, D) ..... ***A. aptera***

6' Lateral parts of transversal ridge less steeply ascending (Fig. 17A, B), gap between their endings narrower (Fig. 18M, N), lateral parts posteriorly of the mesal curvation with a distinct and uniform lateral curvation (Fig. 17A, B)..... ***A. sinuosocarinata* sp. nov. Bohn and Klass**

5.4. Key for males

The key has to be used with care since adult males are only known from 5 of the 9 species described: *Attaphila paucisetosa*, *A. fungicola*, *A. flava*, *A. aptera*, and *A. bergi*.

1 Subgenital lobe excavated only on left side, with two styli, a well-developed left one and a very small right one (Fig. 24A, C); T1 without long bristles on surface and borders, but with a median specialisation (Fig. 5A–D) having in one species two tufts of medium-sized bristles (Fig. 5A, B); T2 without specialisations; T6,7 along posterior border with or without bristles; tegmina with transversal apical border (Fig. 3A–D)..... **4**

1' Subgenital lobe excavated both on left and right side, with only one stylus, the well-developed left one (Fig. 25A, B); T1 with long bristles on surface and borders (character not known for *A. flava*), without specialisation; T2 anterolaterally with glandular specialisations (Fig. 5E–I); T6,7 along posterior border with bristles, sometimes very fine ones; tegmina with oblique apical border (Fig. 3E–J) **2**

2 Surface bristles of T2–5 arranged strictly in one transversal line; bristles along posterior border of T6,7 relatively strong, almost of the strength of those on the lateral borders (Fig. 13E, 15D, E) ..... ***A. paucisetosa* sp. nov. Bohn and Klass**

2' Surface bristles of T2–5 dispersed; bristles along posterior border of T6,7 very fine (Fig. 15B, C).....**3**

3 Tegmina with straight apical border (Fig. 3G, H); endophallic apodeme near the forking site of the sclerite rather strongly narrowed, narrower than the virga at its widest part (Fig. 25D).....***A. fungicola***

3' Tegmina with weakly convex apical border (Fig. 3E, F); endophallic apodeme near the forking site of the sclerite scarcely narrowed, about as wide as the virga at its widest part (Fig. 25C).....***A. flava***

4 Median specialisation of T1 consisting of a pair of tufts of medium-sized bristles upon weakened sclerotisation immediately posterior to ridge tr1, no microreticulation involved (Fig. 5A, B); T6,7 along posterior border without bristles (Figs 13C, 14I); virga of left phallomere with a weak sinusoidal excurvation terminating in a long, weakly curved apical part with a relatively stout tip (Fig. 24A, B)..... ***A. aptera***

4' Median specialisation of T1 consisting of a pair of fields of emphasised microreticulation, far anteriorly, about at the level of the medially obsolete tr1, no tufts of bristles involved (Fig. 5C, D); T6,7 along posterior border with rather long bristles (Figs 13D, 15A); virga of left phallomere with a strong sinusoidal excurvation terminating in a short, almost rectangularly bent (and thus hook-like) apical part with a relatively fine tip (Fig. 24D, F).....***A. bergi***

6. Biology of *Attaphila*

Attaphila cockroaches live in colonies of leaf-cutting ants of all three genera: *Atta*, *Acromyrmex*, and *Amoimyrmex* (see 4.1.–4.9.; Table 2), which are – as far as species have been sampled – all monophyletic and show the relationships (*Atta* + *Acromyrmex*) + *Amoimyrmex* (Cristiano et al. 2020; Fig. 27A). The ants are directly or indirectly involved in most aspects of the life history of *Attaphila*. Leaf-cutting ants collect leaves to farm an obligately mutualistic fungus, the polyploid *Leucoagaricus gongylophorus* (Möller) Singer, 1986 (Agaricaceae; alternatively assigned to genus *Leucocoprinus*; www.indexfungorum.org), which is their main source of nutrition (Schultz and Brady 2008; Branstetter et al. 2017). The fungus garden is an overall sponge-like formation with numerous tunnels and crevices. Leaf-cutting ants are distributed across the Americas, from the southern USA down to Uruguay and Argentina (with a concentration in the southern subtropics: Mueller et al. 2017); the same geographical range is true for *Attaphila* (Fig. 27B, Table 2), although with much more sporadic records. While some of the leaf-cutting ant species are well-studied (such as *Atta texana*, *Atta cephalotes*, and *Atta sexdens* as well as *Acromyrmex echinatior*, *Acromyrmex octospinosus*, and *Acromyrmex lundii*), the knowledge on others is variously extensive.

6.1. Fragmentary data and resulting problems

Data on the biology of *Attaphila* cockroaches and on the symbiosis with their host ants are quite fragmentary, although with very few aspects studied quite intensely in selected species (see below). In the attempt to combine the available data into a more coherent picture, there are three major problems:

(1) Due to the hidden life within the ant nests, in situ studies on *Attaphila* biology inside the nests are difficult and therefore quite rare. Observations on *Attaphila* cockroaches outside the ant nests may partly concern typical behaviours (related to, for instance, dispersal), but may also concern untypical cases of emergency (for instance, after a destruction of the home colony). And results from studies in the laboratory may include to an unknown extent artifacts in some aspects of biology.

(2) In view of the species diversity of both *Attaphila* cockroaches and their host ants, of the biological diversity of the host ants (e.g. regarding nest size and plants used for fungus cultures, see below), and of the wide distribution spanning different climate zones, some life history traits could well be quite different among the species of *Attaphila*. The observations on individual species reported below can thus not be generalized to all *Attaphila* species.

(3) The 9 species of *Attaphila* recognised herein have been found in colonies of only 10 species of host ants (Table 2; mainly the abovementioned well-studied species) out of ca. 78 extant species of leaf-cutting ants (according to https://antwiki.org). The absence of *Attaphila* records from the vast majority of leaf-cutting ant species may suggest highly incomplete sampling.

These issues should be kept in mind in the following.

6.2. Association with ants and host specificity

Attaphila are only known from nests of leaf-cutting ants (*Atta*, *Acromyrmex*, *Amoimyrmex*), with one questionable exception, an undetermined *Attaphila* individual briefly spotted in the nest of an undetermined *Trachymyrmex* species[2] (VN personal observation). It is noteworthy that *Attaphila* individuals were also observed to follow trails of *Trachymyrmex* (see 6.5.). While leaf-cutting ants farm

2 *Trachymyrmex* in the older sense as in e.g. Branstetter et al. 2017; this paraphyletic (with respect to leaf-cutting ants) genus has recently been split into several genera according to phylogenetic relationships, see Cristiano et al. 2020

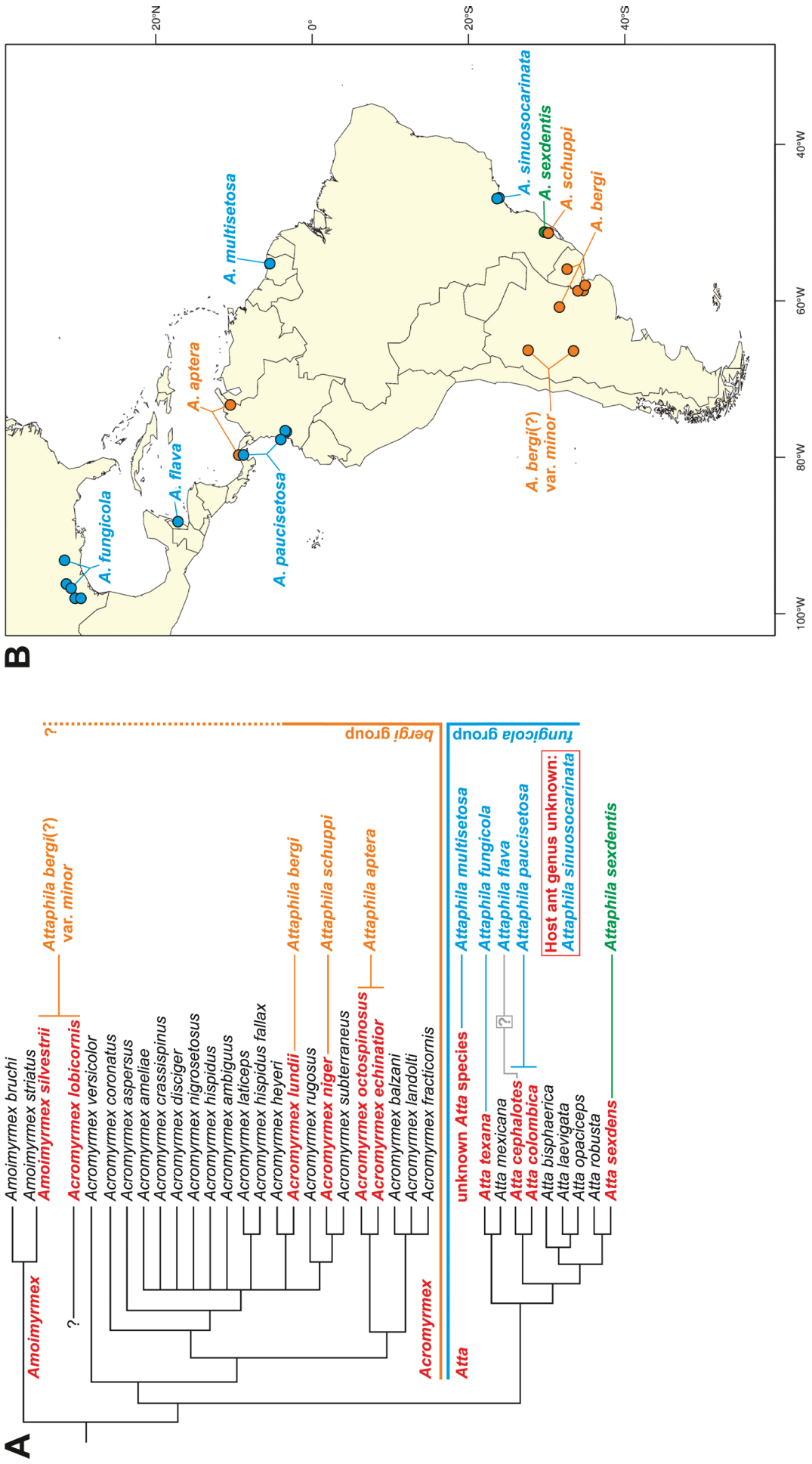


Figure 27. **A**: Phylogenetic tree of leaf-cutting ants (according to Cristiano et al. 2020; *Acromyrmex lobicornis* added, relationships unknown; terminals with several conspecific exemplars simplified). Ant species reported as *Attaphila* hosts in red and boldface, their association with *Attaphila* species indicated by coloured lines (based on specimen labels and partly associated reports in literature, or on own results) or grey line with "?" (based on reported occurrence of only this leaf-cutting ant species in region where *Attaphila* species was collected). *Attaphila* divided in *bergi* group (orange, with *Acromyrmex*; possibly paraphyletic), *fungicola* group (blue, with *Atta*, but unknown for *A. sinuosocarinata*; likely monophyletic), and the isolated *A. sexdentis* (green, with *Atta*). Status of *Attaphila bergi*(?) var. *minor* unclear (see text 4.2.). **B**: Geographic distribution of *Attaphila* species in Neotropical and southern Nearctic regions (based on specimen labels and partly associated reports in literature, or on own results). *Attaphila* divided in *bergi* group (orange), *fungicola* group (blue), and *A. sexdentis* (green).

Table 2. Geographical distribution of *Attaphila* species and their host ants (from north to south). Different ant genera in different colours. 2nd column gives the number of collecting occasions from which a species was recorded, separately for different ant species (compare "material" and "host species" paragraphs in species descriptions chapter 4., data from literature added). — ***Abbreviations***: *A.* = *Attaphila*; *Acr.* = *Acromyrmex*; *Amoi.* = *Amoimyrmex*.

***Attaphila* species**	**No. localities**	**Distribution of *Attaphila* species**	**Species of host ants**	**Distribution of host ants**
A. fungicola	many	USA: Texas, Louisiana	*Atta texana*	USA: Texas, Louisiana
A. flava	1	Belize	*Atta cephalotes*?	Mexico to northern half of South America
A. paucisetosa	4	Panama, Colombia	*Atta cephalotes*	Mexico to northern half of South America
	2	Panama	*Atta colombica*	Costa Rica to Colombia and Peru
A. aptera	1	Panama	*Acr. echinatior*	Mexico to Panama
	2	Panama, Colombia	*Acr. octospinosus*	Mexico to northern South America
A. multisetosa	1	Suriname	*Atta*, species unkown	--
A. sinuosocarinata	2	Brazil: Est. São Paulo	unknown	--
A. sexdentis	1	Brazil: Est. Rio Grande do Sul	*Atta sexdens*	Costa Rica to Uruguay and Argentina
A. schuppi	1	Brazil: Est. Rio Grande do Sul	*Acr. niger*	Brazil
A. bergi	5	Uruguay, Argentina	*Acr. lundii*	Brazil to Uruguay and Argentina
A. bergi(?) var. *minor*	1?	Argentina (Catamarca)	*Acr. lobicornis*	Brazil to Uruguay and Argentina
	1?	Argentina (San Luis)	*Amoi. silvestrii*	Uruguay, Argentina

an obligately symbiotic fungus that is not able to live without the ants, and provide the fungus almost exclusively with fresh plant material, *Trachymyrmex* and all other non-leaf-cutting Attini ("lower attines") primarily use detritus (de Fine Licht and Boomsma 2010) to farm an array of different fungi that can also live without their host ants (Schultz and Brady 2008; Branstetter et al. 2017). Leaf-cutting ants typically also have larger bodies and live in larger colonies than the lower attines. Either of these three factors might be responsible for *Attaphila* being rare or absent in the lower attines.

For *Attaphila* we found records of co-occurrence with only 10 of the 78 valid species of leaf-cutting ants (*Atta* 20, *Acromyrmex* 55, and *Amoimyrmex* 3 according to https://antwiki.org). Most leaf-cutting ant species for which no association with *Attaphila* has been reported had already been formally described (nearly all before 1910) at the time when the labels indicating host ants were produced for collected *Attaphila* specimens examined herein. This means that the set of reported *Attaphila* host ants is unlikely to be artificially small because relevant species had not yet been described when the *Attaphila* were labelled. In addition, many relevant determinations of the ants were conducted (in case of *Attaphila* and their ants collected by VN or JRG) or tested (in case of determined ants pinned together with formerly collected *Attaphila*) by ourselves based on literature altogether reflecting up-to-date species-level taxonomy (Santschi 1925; Gonçalves 1961; Borgmeier 1951; Schultz et al. 1998).

The few host records of *Attaphila* are distributed over the entire leaf-cutting ant phylogeny (Fig. 27A; Cristiano et al. 2020; Bacci Jr. et al. 2009): *Atta sexdens* (host ant of *Attaphila sexdentis*), *Atta texana* (host ant of *Attaphila fungicola*), and the species pair *Atta cephalotes* and *Atta colombica* (host ants of *Attaphila paucisetosa*) are representatives of the three principal lineages within *Atta*, i.e. they are phylogenetically as disjunct as possible within the genus. Within the genus *Acromyrmex*, *Acr. octospinosus* and *Acr. echinatior* (host ants of *Attaphila aptera*) are in a different main clade than *Acr. lundii* (host ant of *Attaphila bergi*) and *Acr. niger* (host ant of *Attaphila schuppi*), and *Acr. lundii* and *Acr. niger* are also not very closely related. This pattern may suggest that *Attaphila* cockroaches inhabit the nests of far more leaf-cutting ant species than we know of so far. If a targeted search of *Attaphila* in the nests of a variety of leaf-cutting ant species is successful, it would either reveal additional *Attaphila* species or wider host ranges (see below) of the species already known. If, in contrast, no *Attaphila* specimens are found in association with the many further leaf-cutting ant species, the limitation of *Attaphila* to few disjunct subclades in the leaf-cutting ant clade will pose an interesting biological question. One case in view of this question may be the strictly grass-cutting ants – some species of *Atta* (within the Epiatta clade) and *Acromyrmex* that forage grass instead of dicot leaves and flowers, in particular in the grasslands of southern South America (Bacci Jr. et al. 2009; De Fine Licht and Boomsma 2010; Mueller et al. 2017). For these, *Attaphila* has not yet been recorded. *Acromyrmex lobicornis* and likely *Amoimyrmex silvestrii*, the hosts of *Attaphila bergi*(?) var. *minor*, forage both grass and dicots (Mueller et al. 2017; no data for *Amoimyrmex silvestrii*, but the most closely related *Amoimyrmex striatus*, Fig. 27A, does forage grass and dicots). Whether the absence of *Attaphila* records from strictly grass-cutting species has biological reasons or is due to limitations in the sampling of these ant species remains open.

Regarding the degree of host specificity, the data available for associations between species of *Attaphila* and their host ants (Table 2; Fig. 27A) only allow for very limited conclusions. For three of the nine *Attaphila* species, no specific host ant species have been recorded so far (*A. multisetosa*, *A. sinuosocarinata*, *A. flava*). Two further species have only been recorded once (*A. sexdentis*, *A. schuppi*), so that it is not surprising that also only one host species is known. One species, *A. fungicola*, has been recorded many times and consistently in association with a single ant species, *Atta texana*; however, there is

no other species from the three relevant ant genera that occurs in the distribution area of *A. fungicola* in Texas and Louisiana (USA). The six foregoing species can therefore not contribute to assessing host specificity of *Attaphila* species.

Three further species of *Attaphila* have been recorded on several occasions and in association with more than one species of Attini: (1) *A. paucisetosa* with *Atta cephalotes* and *Atta colombica*; (2) *A. aptera* with *Acromyrmex octospinosus* and *Acromyrmex echinatior*; (3) *A. bergi* with *Acromyrmex lundii* and, if the hosts reported for its "var. *minor*" are considered, also with *Acromyrmex lobicornis* and *Amoimyrmex silvestrii*, i.e. across a wide phylogenetic range (Fig. 27A). Case (3), however, is obscure because specimens classified as "var. *minor*" (all probably larvae) could not be examined in our study, whereby both the conspecifity of the various var. *minor* specimens (those found with *Acromyrmex lobicornis* and those found with *Amoimyrmex silvestrii*) and their assignment to *A. bergi* remain questionable (see 4.2.). Cases (1) of *A. paucisetosa* and (2) of *A. aptera* are thus the only ones demonstrating that host specificity of *Attaphila* is not necessarily limited to a single ant species. Notably, in both cases the host ants are closely related: *Atta cephalotes* with *Atta colombica*, and *Acromyrmex echinatior* with *Acromyrmex octospinosus* (Fig. 27A; Sumner et al. 2004; Bacci et al. 2009; Cristiano et al. 2020).

This leads to the current picture that *Attaphila* species are likely limited to single ant species or to groups of closely related ant species (far below the level of the respective ant genera). With the sparse sampling that is currently available, however, other possibilities cannot be excluded: The closely related species might also share relevant ecological traits, and other, phylogenetically disjunct leaf-cutting ant species with a similar ecological profile might be as useful as hosts for the same *Attaphila* species. Or, the closely related species might just be the only ones of a larger ant clade (e.g. of a clade classified as a genus) that are available in the distribution area of the *Attaphila* species concerned, while in other regions the same *Attaphila* species might (or would) have a wider host range (e.g. at genus-level). Furthermore, the degree of host specificity may vary strongly among the various *Attaphila* species. We also note that there appears to be some cryptic genetic variation in leaf-cutting ants (Kooji et al. 2018) that in the future might lead to the splitting of species and to an increased species number in leaf-cutting ants. This could also influence our view on the degree of species-specificity of the *Attaphila*-ant associations.

Host specificity at least at the level of ant genera is, with regard to the mentioned species pairs of *Atta* and *Acromyrmex*, especially convincing in the case of the locality Gamboa (Panama). There, all four ant species live in sympatry, and the nests of *Atta colombica* and two species of *Acromyrmex* (*Acr. octospinosus*, *Acr. echinatior*) occur only few meters from each other (VN personal observations). Despite the close proximity of the nests of all three ant species, *A. aptera* was never found in the nests of the *Atta* species, and *A. paucisetosa* never in those of the *Acromyrmex* species. On a larger scale, *fungicola*-group cockroaches have only been found in colonies of *Atta* ants, and *bergi*-group cockroaches seem to be restricted to *Acromyrmex* and *Amoimyrmex* (Fig. 27A). This may reflect the striking ecological differences between the two ant groups: *Atta* colonies can reach a size of a house and dominate their ecosystems with their long foraging trails and by defoliating the immediate surroundings of their nests, while *Acromyrmex* and *Amoimyrmex* nests are rarely larger than a basketball and rather inconspicuous. On the other hand, experiments under laboratory conditions showed that the cockroaches can survive at least for a short time in colonies of non-host leaf-cutting ants (Moser 1964; Nehring et al. 2016). So far, no specific life-history differences (in e.g. diet, life cycle, or dispersal) among *Attaphila* species or potential specific adaptations to host ants of a specific clade (or species), or a specific ecological profile have been described.

6.3. Diet

Wheeler (1900) initially believed *Attaphila* cockroaches feed on the fungus garden just like their host ants. He concluded this from gut dissections, which yielded a whitish substance that he interpreted as masticated remains of the mycelium (remains of the chitinous hyphal walls are not reported). *Attaphila* individuals were also observed to manipulate fungus fragments with their mouthparts (Nehring et al. 2016), suggesting the fungus to be at least part of their diet. However, later Wheeler (1910) proposed that cockroaches may lick lipids off the ant cuticle when riding on them (see 6.4.). We submit that this source alone could hardly explain the abovementioned gut contents, and it might appear as too meagre to sufficiently nourish the cockroaches – both regarding the amount and the biochemical diversity of what could be licked from an ant's surface.

6.4. Interaction with host ants in the nest

Attaphila cockroaches have frequently been reported to be found deeply inside the nests of their host ants, mainly in the fungal chambers (e.g. Wheeler 1900; Brossut 1976; Waller and Moser 1990; Nehring et al. 2016). Their small compound eyes (relative to those of other cockroaches) may suggest that the cockroaches spend most of their life in the darkness inside the nest (Wheeler 1900) and that they rarely leave this well-protected habitat – although it is hard to estimate the amount of life-time they spend outside the nest (see 6.5.), and the number of leaving events.

Attaphila cockroaches are known to ride on workers within the ant nest (*A. fungicola*: Wheeler 1900, Phillips et al 2017; *A. paucisetosa* and *A. aptera*: Nehring et al. 2016; Fig. 28E; observations mostly made in cultures). This behaviour, enabled by presumably strong attachment abilities via well-developed pretarsal arolia (Brossut 1976), triggered the idea that cockroaches feed on the ants' cuticular lipids (see 6.3.), and it also serves the in-

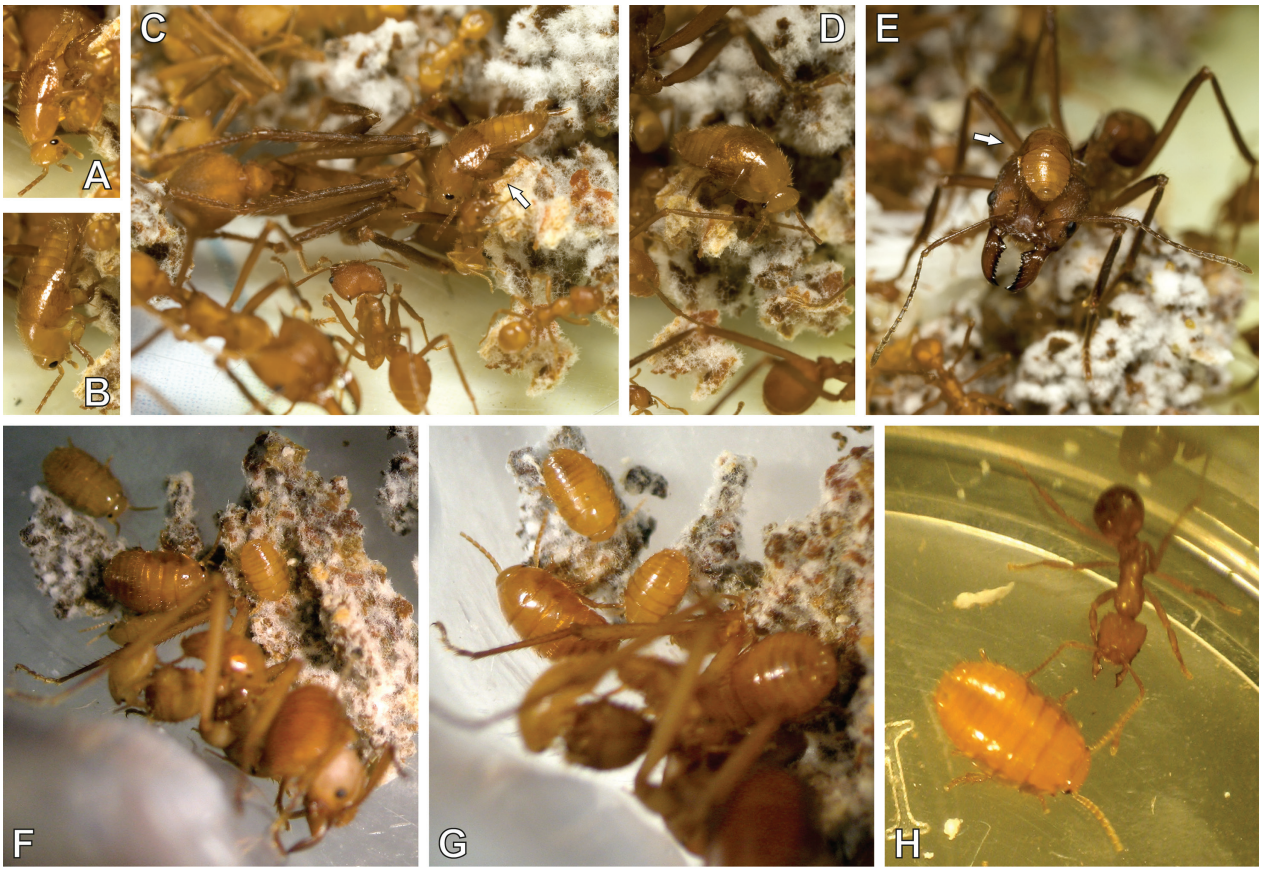


Figure 28. Pictures of live *Attaphila* and their host ants in lab culture, all taken from ant nests in Gamboa, Panama. **A**–**E**: A male *Attaphila paucisetosa* together with *Atta colombica* ants (white arrow in C, E pointing to cockroach). **F**, **G**: Females and larvae of *Attaphila aptera* together with *Acromyrmex octospinosus* ants. **H**: *Attaphila aptera* female or larva together with *Acromyrmex octospinosus* worker.

trinsic dispersal, i.e. between fungus chambers within the same nest (Phillips 2021). An ant worker's back or head may also be a rather safe spot for a cockroach that is always under threat to be killed by its hosts. The cockroaches generally smell like their host colony, probably because they acquire host-specific substances from the ants and/or fungus garden (Nehring et al. 2016), but a genetic disposition to the odour of a specific host species may also be one aspect of the host specialization of the cockroaches. In any case, the cockroaches are still sometimes attacked by their own host colony's workers, at least when isolated in laboratory set-ups, which may cause stress to the ant workers (Nehring et al. 2016). Tightly clamping onto an ant might allow the cockroach to better blend in with its surroundings and be less of a suspicious particle.

When not actively attached to them, the cockroaches appear to avoid contact with ant workers as much as possible. The cockroaches flee when touched by ants and otherwise hide in the fungus garden with its multiply folded surface providing many crevices (Nehring et al. 2016).

6.5. Extrinsic dispersal

Attaphila cockroaches have to leave the ant nest at least for their extrinsic dispersal to other ant colonies, which could either be already existing ones or newly founded ones. There are basically two ways to reach another colony: the cockroach could either join the ants in their dispersal activities (vertical transmission; e.g. by phoresis during mating flights); or it could conduct its own activities independent of the ants (horizontal transmission; e.g. by leaving its natal nest and searching for another).

Females and – less commonly – larvae (and in a single reported case a male: Phillips et al. 2017) of *Attaphila fungicola* (Moser 1967) as well as females of *Attaphila paucisetosa* (see 4.6. "Material") have been seen attached to swarming virgin ant queens that were about to found new colonies. Attachment to alates has additionally been reported for *Attaphila bergi* (Bolivar 1901). Female *A. fungicola* that had experimentally been separated from the virgin ant queens prior to their mating flight produced oothecae within a few days (Waller and Moser 1990), indicating that they were mature and presumably also inseminated, so that they would have been able to populate the newly founded host colony. *Attaphila fungicola* females have indeed been found in newly established colonies (Moser 1967). This all is in line with a vertical transmission system where inseminated cockroach females disperse with host ant alate females to establish new populations in newly founded ant colonies. If vertical transmission were the major or only dispersal mechanism, all cockroaches in an *Atta* colony would be expected to be

the offspring of one or few cockroach females that were transported by the colony's queen.

In contrast, in studies on *Attaphila paucisetosa* and its host *Atta cephalotes* in Colombia (Rodríguez et al. 2013; JRG unpublished observations), *Attaphila* specimens were only found in nests older than two years and larger than 30 m^2. Their absence from newly founded ant nests indicates vertical transmission to be either uncommon or not very effective. Observations by Phillips et al. (2017) that *Attaphila fungicola* females indeed do not survive well in newly founded *Atta* nests corroborate this.

The latter cases suggest that horizontal transmission is also (or even more) important. One prerequisite for this seems to be present since *Attaphila fungicola* can follow ant pheromone traces in the laboratory (Moser 1964) and generally track ants (Sánchez-Peña 2005), and *Attaphila schuppi* has been found on ant foraging trails in the field (Bolívar 1905). There seems to be little specificity of trail following behaviour since *Attaphila fungicola* cannot only follow the trails of its host *Atta texana*, but also those of *Trachymyrmex* ants (Moser 1964). However, trail following alone would not be sufficient for dispersal because the trails of different *Atta* nests are unlikely to be connected.

Phillips (2021) suggests a combination of extrinsic dispersal via swarming queens and via ant trails: He observed *Attaphila fungicola* females to dismount the *Atta texana* queens after the mating flight and to search for ant trails instead of remaining with the queen. Once on a trail – most likely one of a foreign colony – the cockroaches would not walk to the nest themselves, but mount foraging ant workers, or even leaf fragments carried by the ants, as vehicles. Such a two-step dispersal makes use of long-range dispersal via swarming queens but avoids the problem that a high rate of foundress nests will fail, and is in line with all observations above. Riding into a new colony on the back of a worker may be a way for the cockroaches to avoid their hosts' nestmate recognition system (see 6.4.). Ants recognize intruders by their smell, and in laboratory experiments leaf-cutting ant workers indeed attacked and killed *Attaphila paucisetosa* and *A. aptera* originating from other colonies than their own (Nehring et al. 2016). However, being carried by a nestmate worker that is carrying food to the nest might allow the cockroaches to "fly" under the radar and avoid detection.

6.6. Life cycle

Few details of the *Attaphila* life cycles are known, mostly from *Attaphila fungicola* in Louisiana, where observations indicate that the *Attaphila* life cycle is linked to that of the host ant: Waller and Moser (1990) report that the ratio of mature females to larvae in an ant nest is much lower after the mating flight than before, indicating that many mature females have left the nest. It thus appears plausible that there is a gradual maturation of the *Attaphila* population in a nest throughout the year; during the swarming of the ants, inseminated mature *Attaphila* females can disperse with virgin ant queens (see 6.5.); in their new host colonies, *Attaphila* females then produce oothecae, and larvae hatch, which develop into adults before the next ant mating flight in the following year. Then, another cycle begins with the appearance of small larvae. Females can be collected from the colonies throughout the year and can live for longer than one year in laboratory colonies (Waller and Moser 1990), suggesting that they can go through more than one reproductive cycle.

While both males and females have been collected from *Atta texana* colonies in Texas, only females have been reported from Louisiana (Waller and Moser 1990). It is unclear whether the lack of males is due to incomplete sampling or due to a potential local evolution of parthenogenesis.

7. Discussion

7.1. Characters usable for species identification

The species of *Attaphila* are in both sexes provided with a series of interspecifically variable characters allowing in most cases a clear identification (summarised in Table 3). In addition to the sex-specific characters listed below there is one which is identically expressed in both sexes: the arrangement of the surface bristles on abdominal tergites **T2–5**.

Important **male** characters are shape characteristics of the tegmina including the orientation of the apical border; the shape of the hindwings; the presence of long bristles on **T1**, the structure and position of tergite specialisations; the size and arrangement of bristles along the posterior border and on the surface of **T6,7**; the development of the transversal ridge of **T7**; the presence of a hook on the right paraproct; and the structure of the subgenital lobe (with one or two styli, with a lateral excavation on one or on both sides) and the phallomeres (curvation of virga, shape of hook). The variability in the latter two body parts is, at least within the two species groups (see below), astonishingly low; *A. flava*, *A. fungicola*, and *A. paucisetosa* are according to their male genital characters almost indistinguishable (Figs 25A, C, D, 26A–C).

In the **females** distinguishing features can be found in the size and arrangement of the surface bristles of **T6,7**; in the development of the transversal ridge of **T7**; and in the features of the subgenital plate (**S7** shape and (dis) continuity of transversal ridge) and of the genitalia (shape characteristics of laterosternal shelf area, gonangulum sclerites, spermathecal plate). In the latter, the laterosternal shelf area is most important, showing the highest variability; the females of the eight species with known females are all well characterised by specific details of this area (Fig. 22A–L). This is a rather unusual situation for Blattodea, which contain many genera (like the ectobiids *Ectobius* and *Phyllodromica*) in which species determination of females via morphology is extremely difficult or even impossible. Nevertheless, a similar case as in

Table 3. Characters of *Attaphila* species and grouping of species. — ***Abbreviations and colours***: ♂, ♀ in 1st column indicating whether a character is relevant to male or female sex or both. S + number = sternite, T + number = tergite, ?? = unknown. Entries "type 1" and "type 2" for laterosternal shelf area mark species pairs with great similarity in this area (for details see species descriptions). Colours mark putative species groups: orange = *bergi* group, blue = *fungicola* group, both pale if assignment poorly supported, green = not assigned to a group. num. = numerous, med. = medium.

	A. aptera	***A. bergi***	***A. schuppi***	***A. flava***	***A. fungicola***	***A. paucisetosa***	***A. multisetosa***	***A. sinuosocar-inata***	***A. sexdentis***
Sexes with adults known	♂♀	♂♀	-♀	♂-	♂♀	♂♀	-♀	-♀	-♀
Host ant genus	*Acromyrmex*	*Acromyrmex*	*Acromyrmex*	*Atta*?	*Atta*	*Atta*	*Atta*?	??	*Atta*
♂: apical border of tegmen	strictly transversal	strictly transversal	??	oblique	oblique	oblique	??	??	??
♂: shape of hindwing	rhombic	lanceolate	??	rhombic	rhombic	rhombic	??	??	??
♂: tergal specialisations	T1 median posterior	T1 median anterior	??	T2 lateral	T2 lateral	T2 lateral	??	??	??
♂: T7 ridge tr	well developed	weakly developed	??	absent	absent	absent	??	??	??
♂: subgenital lobe right stylus	present	present	??	absent	absent	absent	??	??	??
♂: subgenital lobe right excavation	absent	absent	??	present	present	present	??	??	??
♂: curvation of virga	sinusoidal	sinusoidal	??	weakly curved	weakly curved	weakly curved	??	??	??
♂: hook on right paraproct	present	absent	??	absent	absent	absent	??	??	??
♂: long bristles on surface and borders of T1	absent	absent	??	present?	present	present	??	??	??
♂: bristles on posterior border of T6,7	absent	present, large	??	present, very small	present, very small	present, small	??	??	??
♂: surface bristles on T6,7	num., med.-sized to small	T6 num., med.-sized to small T7 few very small ones	??	if any, very tiny	if any, very tiny	if any, very tiny	??	??	??
♂,♀: surface bristles on T2–5	dispersed	two irregular lines	dispersed	dispersed	dispersed	strictly in one line	in one line in middle	mostly in one line	two irregular lines
♀: surface bristles on T6,7	many, large	many, large	T6 many, small T7 if any, very tiny	??	very few small ones, others tiny	few, med.-sized	T6 many, med.-sized T7 few, med.-sized	T6 many, small T7 few, small	T6 many, small T7 few, small
♀: T7 ridge tr	present	present	absent	??	present	present	present	present	present
♀: S7 shape	rectangular	rectangular	rectangular	??	rectangular	rectangular	rectangular	rectangular	semicircular
♀: S7 ridge sr in middle	discontinuous	fully continuous	discontinuous	??	discontinuous	discontinuous	discontinuous	discontinuous	discontinuous
♀: laterosternal shelf area	(different)	type 1	type 1	??	type 2	type 2	(different)	(different)	(different)
♀: lateral gonangular sclerite	present	absent	absent	??	absent	absent	absent	absent	??

Attaphila is also found in the blattellid genus *Loboptera* (Bohn 1991), where the variable structures of the female genitalia, including also the laterosternal shelf area, allow an unequivocal determination of almost all species.

7.2. Interspecific relationships in *Attaphila*

For most of the characters that distinguish *Attaphila* species (see 7.1.), outgroup comparison with other blaberoid taxa is problematic for a variety of reasons (often in combination): either the elements concerned are likely unique to *Attaphila* (e.g. tubes of laterosternal shelf); or they show a unique condition (middle part of laterosternal shelf sclerite); or data on other blaberoids are insufficient (concerning structural detail or the number of taxa studied). In other cases outgroup comparison is conceivable, but conflicting (e.g. gonangulum sclerites); homoplasy can occur to a considerable extent. Relationships in *Attaphila* can thus to a large extent only be discussed without indications on character polarity, or based on polarity hypotheses derived from the specific kind of structural differences (e.g. conditions with stronger reduction, asymmetry, or segmental differences as putative apomorphies).

According to male characters (see Table 3), *A. aptera*, *A. bergi*, *A. flava*, *A. fungicola*, and *A. paucisetosa* (the species with males known) can be sorted into two species groups: the *bergi*-group, as we may call it, containing *A. aptera* and *A. bergi*, and the *fungicola*-group with *A. flava*, *A. fungicola*, and *A. paucisetosa* (matching colours in Table 3). The *bergi*-group is characterised by the transversal apical border of the tegmina, the absence of long bristles on **T1**, the presence of a median specialisation on abdominal **T1** (though this is represented by different cuticular structures in the two species), the presence of transversal ridge **tr7**, a subgenital lobe with an excavation only on the left side and two styli, and the distinct sinusoidal excurvation of the phallomere virga. The *fungicola*-group is characterised by the oblique apical border of the tegmina, the presence of long bristles on **T1** (unknown for *A. flava*), the presence of lateral specialisations on abdominal **T2** (with corresponding cuticular structures in the species), the absence of transversal ridge **tr7**, a subgenital lobe with an excavation on both sides and only one stylus, and the only weakly curved or bent virga. The differing sets of features are accompanied by a different host specificity: the species of the *bergi*-group live in nests of *Acromyrmex* species, those of the *fungicola*-group in nests of *Atta* species. The genus specificity in the host selection seems to be very strong, while a comparable species specificity does not seem to exist (see 6.2.).

The idea of a division into two species groups does not get much support by characters of the females. At first glance, the size and arrangement of the surface bristles of **T6,7** appear to be in agreement with this grouping. The bristles are numerous and large in the *bergi*-group, even the largest in the *fungicola*-group are smaller and they are much less numerous. These differences, however, become obsolete when the remaining species – *A. multisetosa*, *A. schuppi*, *A. sexdentis*, and *A. sinuosocarinata*, i.e. those with only females known – are included in the considerations. The size of the bristles in these females varies strongly from slightly smaller than in the *bergi*-group to much smaller than the largest in the *fungicola*-group; a separation into two well defined groups by this character, therefore, is not possible.

Other female characters usable for the elucidation of interspecific relationships concern the laterosternal shelf area with its high interspecific variability. The great similarity in the shape characteristics of the laterosternal shelf area between *A. fungicola* and *A. paucisetosa* (Fig. 22E, F, H; represented as "type 2" in Table 3), for example, may well be interpreted as an indication of a close relationship between the two species, confirming their assignment to the same species group. The species *A. bergi* and *A. schuppi* represent another pair with very similar laterosternal shelf areas (Fig. 22C, D, J; "type 1" in Table 3) also suggesting a close relationship. The deviating shape characteristics of the laterosternal shelf area in *A. aptera* (Fig. 22A, B) do not necessarily contradict the suggestion to place the three species together in a *bergi* species group. The high variability in the shape characteristics of the laterosternal shelf area can be seen as a sign for rapid evolutionary changes in these structures, in contrast to male genital structures (subgenital lobe, phallomeres) showing only small differences within each of the two species groups. Thus, while the male genital structures thanks to their slower evolution might still indicate a close relationship between *A. aptera* and *A. bergi*, these indications may no longer be present in the structure of the laterosternal shelf. The suggested assignment of *A. schuppi* to the *bergi*-group is also supported by its ant host belonging to *Acromyrmex* (*Acr. niger*; Table 2).

Female characters cannot contribute to the clarification of the position of the other three species with unknown males: *A. multisetosa*, *A. sinuosocarinata*, and *A. sexdentis*; neither the laterosternal shelf area nor the subgenital plate allow conclusions on their relationships with other species. However, two of the species, *A. multisetosa* (with an *Atta* host ant) and *A. sinuosocarinata* (with host ants unknown), show similarities in the arrangement of the surface bristles on abdominal **T2–5** with *A. paucisetosa.* The bristles are arranged in a strict line in *A. paucisetosa*, less strictly in *A. sinuosocarinata*, with singular bristles being slightly apart; in *A. multisetosa* bristles arranged in one line are only found in the median third of **T2–4**. The similarities might be interpreted as signs of close relationships suggesting the assignment of the two species to the *fungicola*-group. The suggestion would in case of *A. multisetosa* also get support from its host, a species of the genus *Atta*. But the proposed assignment remains doubtful for two reasons: first, the respective character, the arrangement of bristles in one line, is not very complex and thus potentially prone to homoplasy; second, since the larvae of species having dispersed bristles in later stages also have bristles in a single line in early stages, it could be a plesiomorphy (though alternatively a paedomorphic apomorphy).

For some of the male characters separating the two species groups, tentative conclusions on their polarity can be made. **(1)** The presence of a stylus on each side of the male subgenital lobe in the *bergi*-group would appear plesiomorphic, and the lack of a stylus on the right side as an apomorphy of the *fungicola*-group, as a pair of styli is part of the basic body-plan of Blattodea. A lack of the right stylus only sporadically occurs in other Blaberoidea (e.g. Roth 1999: fig. 7G). **(2)** In both groups the male subgenital plate has an excavation on the left side bearing the left stylus; the formation of an additional excavation on the right side in the *fungicola*-group may be considered as apomorphic in comparison with the *bergi*-group, as such an excavation only sporadically occurs in other, likely phylogenetically remote blaberoid taxa (e.g. Bohn 2019: fig. 19K). However, polarity within *Attaphila* is a bit doubtful, because it is unknown from which position the right stylus was lost in the *fungicola*-group: either from a proximal position comparable to the left stylus of the *bergi*-group (the distal shift of the right stylus then being an apomorphy of the *bergi*-group, and the presence of an excavation on both sides possibly representing a plesiomorphic symmetrical condition); or from a distally shifted position as the right stylus of the *bergi*-group (the distal shift of the right stylus then being a groundplan feature of *Attaphila*, and excavations of the two sides not representing a symmetrical condition, the right one being an independent apomorphy). **(3)** The absence of male **tr7** might be an apomorphy of the *fungicola*-group, as it constitutes a difference between segments (male **tr2–6** are in all species well developed). **(4)** The transversally cut tegmina of the *bergi*-group may be considered as more plesiomorphic than the obliquely cut tegmina of the *fungicola*-group – if the latter can reasonably be considered as including a further advanced reduction of the posterior part of the tegmen. **(5)** The lack of long bristles on male **T1** might be an apomorphy of the *bergi*-group, as it constitutes a difference between segments (all *Attaphila* males have long bristles on **T2–5**). Characters (1)–(4) tentatively support the *Atta*-associated *fungicola*-group as monophyletic. This may then additionally be supported by the shared specialisations on male tergite **T2** (for which outgroup comparison is not conclusive, see 7.3.3.). On the other hand, only one character (5) suggests the monophyly of the *Acromyrmex*-associated *bergi*-group.

Paraphyly of the *bergi*-group is more strongly supported than its monophyly by the retention of three putative plesiomorphies only in *A. aptera* but not in *A. bergi* (and other *Attaphila* species): the presence of the lateral part of the gonangulum (**gg-l** in Fig. 19A, clearly a plesiomorphy by outgroup comparison, see 7.4.2. – although with some instances of homoplasy); the well-developed male **tr7** (see character (3) above; only weakly developed in *A. bergi*); and the presence of a hook on the right paraproct. Paraproctal hooks are ubiquitous in Blaberoidea (except for Pseudophyllodromiidae) and most likely an autapomorphy (under exclusion of Pseudophyllodromiidae if this is the sister group of the remaining Blaberoidea); its presence in *A. aptera* may represent a unique plesiomorphy within *Attaphila* (though only with regard to species with known male sex). In this case the aberrant laterosternal shelf of *A. aptera* (see above in 7.2.) could rather be seen as a further indication of this species being an early offshoot. On the other hand, the fully continuous condition of the transversal ridge on the female subgenital plate only in *A. bergi* (**sr7** in Fig. 16A, B) is possibly a plesiomorphic condition suggesting this species to be the earlier offshoot; yet, both continuous and interrupted **sr7** ridges occur in various other blaberoid genera, indicating a high degree of homoplasy for this character. As a third alternative, *A. schuppi* is supported as the basalmost offshoot within *Attaphila* by the probable lack of the genital chamber pouch (**gcp**). This structure has not been reported from other Blaberoidea (but may have been overlooked) and may thus appear as an autapomorphy of *Attaphila* excluding *A. schuppi*.

The last remaining species, *A. sexdentis* (only known from the female holotype), differs from all other species by the semicircular female subgenital plate **S7** (Figs 17F, 18L, Table 3), which is based on the throughout rounded-converging course of the lateral plus anterior borders in short distance to the transversal ridge **sr7**. This is another character for which outgroup comparison is difficult. The first reason is conflicting outgroup comparison, as in other blaberoids the lateral borders of **S7** variously diverge to the anterior, are parallel, or converge to the anterior (red lines in Fig. 30A–F, compare Fig. 30G, H showing the two conditions occurring in *Attaphila*). The anterolateral extension of **S7** sclerotisation beyond **tr7**, which in *A. sexdentis* is much shorter than in other *Attaphila* species (compare green lines in Fig. 30G and H), also varies strongly in other blaberoids (green lines in Fig. 30A–F) and is often unclear in addition due to gradual fading (indicated by dashed parts of green lines in Fig. 30). These and other shape characteristics of the female **S7** are generally difficult to compare between *Attaphila* and the blaberoids shown in Fig. 30 due to the aberrant course of ridge **sr7** in *Attaphila*, with very steep lateral parts. The evidence from **S7** of *A. sexdentis* on the grouping of *Attaphila* species thus remains unclear. The observed association of *A. sexdentis* with a species of *Atta* supports the assignment to the *fungicola*-group, and its host ant *Atta sexdens* (Table 2) is, in addition, more closely related to those of *A. paucisetosa* (*Atta colombica* and *Atta cephalotes*) than the latter ants with the host ant of *A. fungicola* (*Atta texana*) (Fig. 27; Cristiano et al. 2020: fig. 2).

In conclusion, **(i)** *A. flava*, *A. fungicola*, and *A. paucisetosa* likely form a clade (supported by four potential apomorphies in males), to which *A. sinuosocarinata* and *A. multisetosa* may also belong (based on similarities among the females); this is the *Atta*-associated (unknown or doubtful, respectively, for the two latter species; Table 2) *fungicola*-group. **(ii)** *A. aptera*, *A. bergi*, and *A. schuppi*, the members of the *Acromyrmex*-associated *bergi*-group, are poorly supported as a clade, while plesiomorphies support each of these species to be the sister taxon of the remaining *Attaphila*; this position is most strongly supported for *A. aptera*. **(iii)** There is no evidence on the position of *A. sexdentis* in this grouping

of species, except that its association with *Atta* favours its assignment to the *fungicola*-group. This picture is very preliminary and partly contradictory. It mainly suffers from the lacking knowledge of the male sex in several species and from the limited availability and/or ambiguity of outgroup comparison with other Blaberoidea, especially Blattellidae.

It is thus too early for conclusions on a possible co-evolution between *Attaphila* and its host ant genera. Branstetter et al. (2017: p. 4, fig. 1) date all splits from that between *Atta* + *Acromyrmex* + *Amoimyrmex* (*Acromyrmex striatus* therein) and its *Trachymyrmex* sister clade down to that between *Acromyrmex* and *Atta* to a fairly short time span of ca. 20–17 Ma ago; this places the origin of leaf cutting in ants to about 20–18 Ma ago. This was then possibly also the time when, in close succession, the life habits of *Attaphila* originated and the early dichotomies within *Attaphila* have occurred together with the dichotomies in the ants. Alternatively, these events in *Attaphila* evolution could have occurred later if one or several host shifts from one ant genus to the other are involved despite the apparent present-day stability in host choice. Due to the above finding of *Acromyrmex*-associated *Attaphila* possibly being paraphyletic and *Atta*-associated *Attaphila* more likely being monophyletic, a host shift from *Acromyrmex* to *Atta* is more likely than one in the opposite direction.

7.3. Special features of *Attaphila*

7.3.1. Antennae

The antennae of *Attaphila* show several special characteristics not known from any other Blattodea (see 3.2.): **(1)** their shortness, scarcely reaching half of the length of the body (also typical for termites), in combination with a low number of flagellomeres not surpassing 11; (**2)** their insertion at the bottom of a rather deep funnel-shaped pit; **(3)** the dorsal membranous excavation at the apical end of the scapus, which allows a rectangular bend between scapus and pedicellus; **(4)** the unusual size relations of the flagellomeres along the longitudinal axis.

The biological significance of the deepening of the antennal insertion is not clear. The shortness of the antennae might be seen as an adaptation to living in the narrow chambers and galleries of the ant nest, possibly in connection with another selective pressure: to approximate the shape of the antennae to that of the host ant (with 10 flagellomeres), to which the development of the sharp bend between scapus and pedicellus may also contribute (bend in the ant also between scapus and pedicellus, but because of a longer scapus further distally). Though chemical signals are certainly of greater importance than visual and tactile ones in the communication between ant guest and host, the latter may also play a role. The strong dorsal bending between pedicellus and scapus may, in addition, provide some replacement for the dorsal bending of the antenna at its origin from the head capsule, which in *Attaphila* is likely limited by its deepened insertion.

The peculiarities of *Attaphila* in the shape of the flagellum will be pointed out by a comparison with related genera, to be expected among the numerous genera united in Blattellidae (see 7.4.). Accordingly, the antennae of adult representatives of several genera were studied (*Blattella*, *Ischnoptera*, *Loboptera*, *Parcoblatta*, *Pseudomops*, *Symploce*, *Xestoblatta*; and *Ectobius* from Ectobiidae; see 2.5. for details on taxa), of which some examples are shown in Fig. 2J–M. They all agree in the longitudinal pattern of the flagellomeres showing two antidromic gradients: **(A)** The **relative length** (length/width) of the flagellomeres, beginning with the second (the first flagellomere, the meriston, has a variable length; in most cases it is longer than the one following), steadily increases towards the tip; at the base of the flagellum they are much wider than long, at about 1/3 or 1/4 of flagellum length as long as wide, and towards the tip much longer than wide. **(B)** The **diameter** of the flagellomeres steadily decreases towards the antenna tip. In the flagellum of *Attaphila* gradient **A** is well visible, even more conspicuous than in the other genera, since it is with a comparable amplitude distributed over a much lower number of flagellomeres. But gradient **B** is very weakly expressed; the flagellum has about the same diameter along the entire length, the most distal flagellomeres are only slightly narrower and, therefore, unusually long and wide.

To get an idea of the biological basis of the deviating structure in *Attaphila*, the growth processes during larval life have to be considered that mainly determine the imaginal structure of the antenna. The postembryonic development of the antenna of *Blattella* was thoroughly analysed by Campbell and Priestley (1970; see their fig. 1): The hatched larva starts with about 24 flagellomeres, comprising the 'meriston' at the base of the flagellum, followed by about 7 'meristonal annuli' and 17–18 'singletons'. Despite the much lower number of flagellomeres, the flagellum already shows the proportions of the imaginal antenna: flagellomeres towards the tip with steadily increasing length and decreasing diameter. At each of the following moults the number of flagellomeres is increased by divisions of the old meriston producing 4–12 new meristonal annuli (and leaving a basalmost flagellomere as the new meriston), and by a division of each of the old meristonal annuli to a 'doublet group'. The singletons do never divide, and the same is true for the flagellomeres of the doublet groups. The expected number of up to 115 flagellomeres after 6 larval stages is not reached because of losses of terminal annuli, by which all singletons and some flagellomeres of the most distal doublet groups disappear. The new formation of flagellomeres by divisions of meriston and meristonal annuli has also been observed in other genera of Blattodea (*Leucophaea*: Schafer 1973; *Periplaneta*: Schafer and Sanchez 1973; *Eucorydia*: Fujita and Machida 2014), but in *Blatta* (Qadri 1938) and termites (Fuller 1920) the divisions are restricted to the meriston.

The antennal flagellum of the first larval stage of *Attaphila*, as deduced from the assumed second larval stage depicted in Fig. 2A, should – in contrast to *Blattella* (see above) – not have more than 8 flagellomeres having about

the same diameter throughout the flagellum. A similarly structured flagellum is also found in first stage larvae of *Eucorydia* (Fujita and Machida 2014: fig. 6b), likewise consisting of rather few (11) flagellomeres. But while the number of flagellomeres in *Eucorydia* during larval life increases to up to 40 by divisions of meriston and meristonal annuli, the number in *Attaphila* does not exceed 11. The reason for this is the obviously low rate of proliferation of new flagellomeres, which seems to be restricted to the meriston producing at one time only one or two flagellomeres (and leaving a new meriston basally); divisions of more distal flagellomeres were not observed. The small size of the meriston after a division (Fig. 2B, C) suggests that a new division could only occur during the intermoult period after the next moult, what is also supported by the observation that one third of the larvae studied do not show any signs of a division. Thus, the number of new flagellomeres generated during larval life is very restricted and possibly counterbalanced by the loss of distal flagellomeres as observed in other Blattodea (*Blattella*: Campbell and Priestley 1970; *Leucophaea*: Schafer 1973; *Periplaneta*: Schafer and Sanchez 1973).

The characteristic shape of the flagellum in early larval stages of *Attaphila*, with all flagellomeres having about the same diameter, is maintained up to the imago, resulting – in connection with increasing flagellomere length towards the apex – in unusually large distal flagellomeres. The small size of the distal flagellomeres in other Blattodea is presumably caused by a switch in the growth processes of the flagellomeres leaving the proximal division zone; they further on elongate to some extent, possibly at the expense of the diameter, till they finally stop their growth. Meanwhile, at the flagellum base the next generation of flagellomeres with a larger diameter is generated, and so on. The presence of the aberrant feature already at a very early larval stage in *Attaphila* cannot be the only reason for its presence also in later stages, since in *Eucorydia*, having a similar flagellum as *Attaphila* in the early larval stages (see above), the flagellomeres of the imaginal antenna are distinctly decreasing in diameter towards the apex. It seems that the flagellomeres in *Attaphila* have lost the ability to stop growth in diameter, or that this ability is not activated in the distal flagellomeres. The aberrant shape of the flagellum can be seen as a consequence of its shortness. A short antenna cannot have the same proportions as a long one, the few flagellomeres have to be enlarged and strengthened to get the necessary stability and enough surface for sensory organs. In other insects with relatively short but overall unmodified antennae (termites, Hymenoptera, Coleoptera) the flagellum, similarly as in *Attaphila*, is not or only very weakly narrowed towards the apex.

Wheeler (1900) suggested that the low and variable number of flagellomeres and the terminal incompleteness of the flagellum are due to mutilation by the host ants rather than to the genetic disposition of the cockroaches. A weak point in Wheeler's argumentation, however, is his own observation that flagellomere number, though varying among specimens, is in most cases the same on the two sides of a specimen. This can hardly be explained by mutilation, as Wheeler himself admits. Our own studies do not support Wheeler's idea of a substantial influence of the host ants on antennal length of *Attaphila* and suggest that, if mutilation by the host ant occurs, it should only concern few distal flagellomeres. Loss of distal flagellomeres seems to be a quite common event during the larval development of Blattodea (Campbell and Priestley 1970; Schafer 1973; Schafer and Sanchez 1973) and may have different causes: Programmed degeneration followed by passive detachment or pruning by the cockroach itself, difficulties during moulting, and mutilation by a foreign species, by conspecific specimens or by the bearer itself. There are sporadic reports in the literature of cockroach larvae eating their own apical flagellomeres (Campbell and Ross 1979 for *Blattella*; Nalepa 1990 for *Cryptocercus*). Many termites show a behaviour of antennal cropping (Nalepa et al. 2011); rare direct observations suggest this to result from terminal antennomeres being bitten off by the animal bearing them or by its mate (Heath 1903). A further clarification of this issue in *Attaphila* was not possible with the material at hand, since the occurrence of an artificial loss of flagellomeres during handling could not be excluded. For a final solution a directed analysis, including possibly also the attempt to breed *Attaphila* without their hosts, would be necessary to clarify how the antenna looks in a freshly hatched larva and how it develops further on.

7.3.2. Legs

The legs of *Attaphila* (Fig. 4) are rather strong and stout and certainly not appropriate for fast running, especially since the tightly joined tarsomeres would scarcely allow expansive movements. The high femora, especially of hind- and midlegs, are, on the one hand, reminiscent of legs of certain jumping insects (e.g. psyllids), where the thickening of the femur is due to enlarged tibia extensors. On the other hand, they also resemble the thickened femora of Embioptera; these harbour enlarged tibia depressors (Davis 1936; Ross 2000: p. 24, fig. 21), which according to Ross (2000) facilitate backward movements in narrow galleries. While *Attaphila* cockroaches may hardly need the ability to jump (and were never reported to do so), they may well benefit from a strong depression of the tibiae: **(1)** Improved backward movement into a crevice may be advantageous to them. **(2)** Strong tibia depression may also support the clinging of *Attaphila* females to ant queens when these start their nuptial flight, or to some fixed object when aggressive ants try to remove them. **(3)** It may also maximise a tight and firm adduction of the tibia to the femur (and of the entire legs to the body); when all legs are flexed in this way, possible attacks of ants or other insects may be overcome without severe wounding since the mandibles of the aggressor cannot find working points. The efficiency of this posture could be further increased by the especially deep ventral femoral groove, into which the tibia can tightly fit (as also noted by Brossut 1976), and by the anteroposteriorly compressed shape of the legs, which likely allows their close clinging to the ventral body surface. Whether the species of *Attaphila* re-

ally show the behaviours associated with points (1)–(3) remains to be examined. In contrast to the above point (2), Brossut (1976) suggests that the fixation to the ant queen is mainly supported by the adhesive forces of the well-developed pretarsal arolia.

The tight closing up of femur and tibia can only work when there are no spines along that part of the ventral side of the tibia, which during flexion becomes positioned in the femoral groove. In other Blattodea, the ventral side of the tibia is usually provided with several spines, at least in the mid- and hindleg. *Attaphila* exhibits only one ventral spine on the mid- and hindtibiae, which is situated far distally (Fig. 4B, C); the foretibia has no ventral spine (Fig. 4D). There is an interesting parallel in the jumping cockroach *Saltoblattella montistabularis* Bohn et al., 2010, which also has ventral femoral grooves, but only on the hindleg, the saltatory leg (Bohn et al. 2010). In this case, the narrow closing up of femur and tibia takes place immediately prior to the jumping movement and serves to get a maximal stretching of the leg. As in *Attaphila*, the corresponding tibia has only one ventral spine far distally.

In contrast to that, the dorsal and apical spines of the tibiae are well developed in *Attaphila*. They may, as in other cockroaches, serve for a strong forward pushing of the cockroach using the coarseness of the surrounding substrate (into which the spine tips can grip); based on the same mechanism, these spines would also make it difficult to drag the cockroach out of a crevice backwardly. The mechanism of these spines, however, is in conflict with a good ability of moving backward within crevices, which, therefore, is unlikely to be the reason for the thickened femora (see point (1) above).

7.3.3. Male tergite specialisations

Glandular pores are ubiquitous structures on the tergites of male Blattodea, sometimes occurring in rather large size and such a density that the cuticle appears perforated like a sieve (Bohn 1993). The glandular pores occurring in *Attaphila* species are usually very small and sparsely distributed in the preridge areas of **T1–5** (e.g. Fig. 5E–I, posteriorly of **msl2**). Only in *A. aptera* these areas are very densely covered with pores (Fig. 5A, B). Slightly larger glandular pores are only present in the species with specialisations on **T2** (**msl2**), namely within and around the specialisations (Fig. 5E, F).

Tergal specialisations (i.e. differentiations beyond the glandular pores) are found in nearly every family of Blattodea, especially frequently in the blaberoid families apart from Blaberidae. They often consist of groups of specifically arranged bristles serving as retainers for glandular secretions produced elsewhere in their neighbourhood, not seldom combined with variously deep and extended pits or troughs for the storage of the secretions. The specialisations can occur on any of the abdominal tergites from **T1** to **T10**, often on several of them (Roth 1969).

The specialisation on **T1** of *A. aptera* (Fig. 5A, B, **msp1**) represents a relatively simple form of this type of a specialisation bearing bristles. It only consists of a pair of sparse tufts of bristles within a field of weaker sclerotisation situated in the middle of **T1**, immediately posteriorly of the ridge **tr1**. The question is where the secretions are produced which should be retained by the bristles. Possible sources are the field with weaker sclerotisation, or the glandular pores present in high numbers and density in the anteriorly adjacent area up to the anterior border of **T1**. Most likely, the bristles additionally (or alternatively) serve as sensory organs when the female, after mounting the male, feeds or palpates the dorsum of the male. Specialisations on **T1** are widely distributed among Blattodea: they are frequently found in Blattidae, but also occur in Blattellidae, e.g. in some species of *Xestoblatta*. The specialisations of Blattidae are similarly simple as in *A. aptera*, but they are basically located around the level of **tr1**, and the number of bristles is usually much higher (Roth 1969). In *Xestoblatta* the specialisations of **T1** are rather variable in size and composition, and essentially placed posterior to **tr1** (illustrations in Silva-da-Silva and Lopes 2015). Some species have a huge transversal deepening extending over the full width of the tergite (Silva-da-Silva and Lopes 2015: figs 4, 15); in others the specialisation is much smaller and restricted to the middle of the tergite; it can, as in *Attaphila aptera*, only consist of a more or less extended assemblage of bristles (Gurney 1939), or the bristles are combined with a pair of small pit-like deepenings (Gurney 1939: fig. 42; Grandcolas 1992).

The specialisation on **T1** of *A. bergi* (Fig. 5C, D, **msa1**) is very different from the aforementioned specialisations; it has no bristles and only consists of a pair of areas with emphasised microreticulation and associated glandular pores on the anterior part of **T1** (Fig. 5C, D). A similar structure has not yet been reported from another cockroach – maybe because it is inconspicuous and easily overlooked, more likely, however, because it does not occur in the larger Blattodea since such constructions, developed for a very small animal, might not be able to function satisfyingly in much larger animals.

The specialisations of the *fungicola*-group consist of a trough situated laterally at the anterior border of **T2** (Fig. 5E–I, **msl2**); bristle structures are not involved. The troughs presumably are reservoirs of glandular secretions released through relatively large pores lining the wall of the trough; in Fig. 5E some isolated pores (of glands? **pg**) can be seen outside the trough. Most surprisingly, a very similar structure at the same position (laterally, near the anterior border of **T2**) is also found in species of the subgenus *Paucisclerobla*tta of the genus *Dziriblatta* (Ectobiidae; Bohn 2019, see therein for taxonomic status, which differs from Beccaloni 2014). In all species of this subgenus (Bohn 2020: e.g. fig. 2A, H) the corresponding area is densely covered with very large glandular pores; in two of the altogether six species part of the porous area is deepened to a similar trough as in the species of the *fungicola*-group, from which it, however, differs by the absence of crossing ridges. So far, comparable structures have not been found in any other species of Blattodea. The isolated occurrence of the **T2** trough in only some members each of the likely only distantly related blaberoid genera *Attaphila* and *Dziriblatta* argue against homology of the troughs in these taxa.

7.3.4. Male tergite 9

The narrow anteromesally directed arm of male tergite **T9** (**pt9** in Figs 9D, 24A, 25A–D, 29A, B, C, G, H) is a structure not yet known from male dictyopterans, where usually the ventrally bent lateral parts of tergite **T9** are roundedly truncate and in full length either shortly overlap the lateralmost parts of sternite **S9** (e.g. Klass 1997:

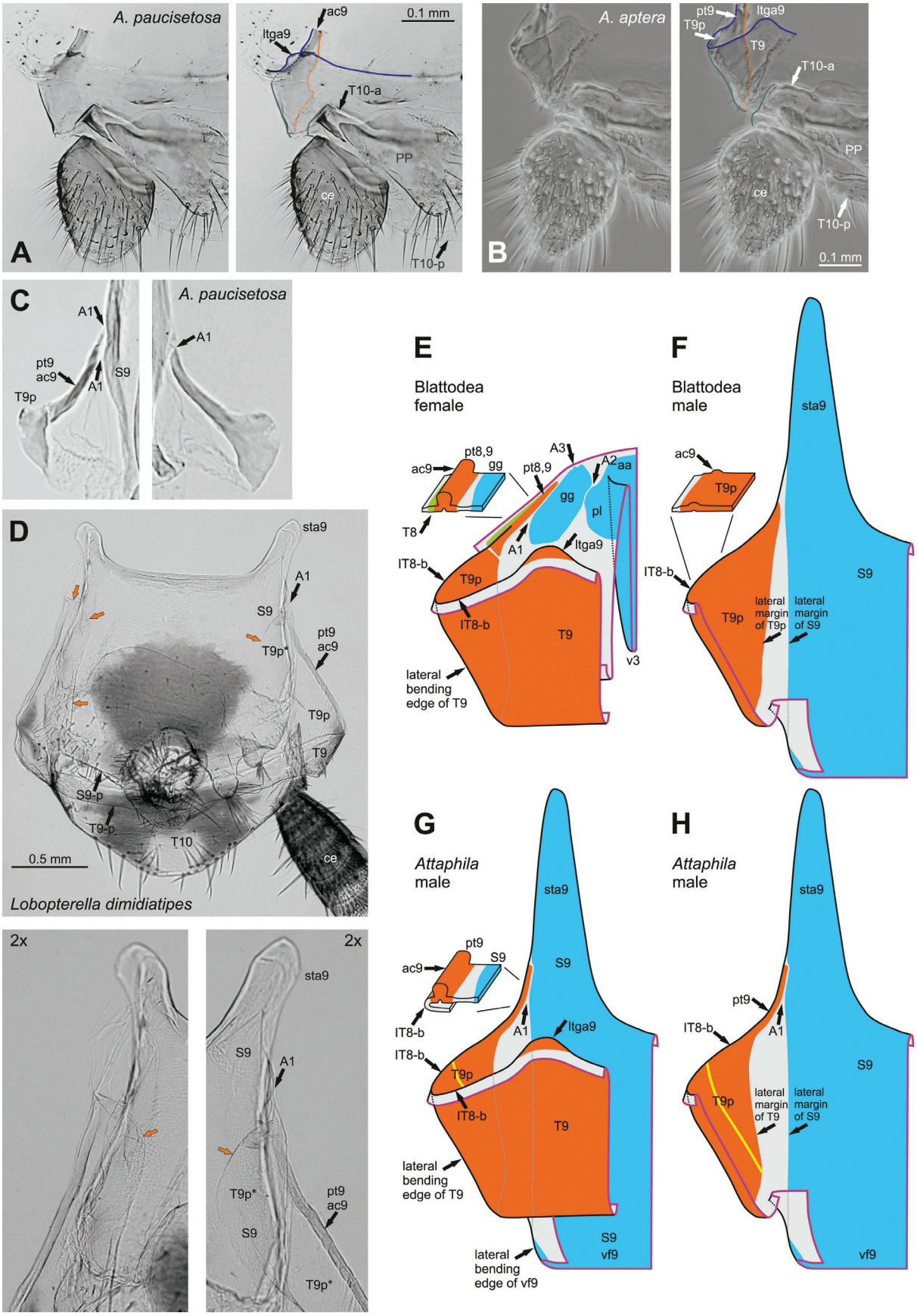


Figure 29. Lateral parts of tergite T9 and their relation to lateral parts of 9th-segmental (latero)coxal sclerites in males (A–D, F–H) and females (E). **A**: *Attaphila paucisetosa* (HT Bo 1258), left half of terminal abdomen, digital photograph, right picture with interpretations. **B**: *Attaphila aptera* (Bo 1256), left half of terminal abdomen, phase contrast image, right picture with interpretations. **C**: *Attaphila paucisetosa* (PT Bo 1254), parts of T9 (T9p including pt9) and S9 near their contact, for both sides of body (from Fig. 25A). **D**: *Lobopterella dimidiatipes* (ex culture), terminal abdomen (phallomeres removed), digital photograph, lower pictures showing parts of T9 (T9p including pt9; T9p* = part of T9p located underneath S9) and S9 near their contact 2× enlarged, for both sides of body; orange arrows point to ventromesal margins of T9p. **E**–**H**: Schematic drawings of left-lateral parts of segment 9 in dorsal view, with included tergal (T9, T8) and (latero)coxal (male S9; female gg, aa, pl) sclerotisations; showing generalised conditions for female (E) and male (F) blattodeans and condition in male *Attaphila* (G, H; dorsal parts of T9 mostly removed in H); small pictures on left top in E, F, G showing a block diagram of the lowest anterior portion of T9 (selected as shown by indicator lines). — ***Abbreviations***: See Supplement 1. — ***Colour of lines in A, B***: orange – ventrally located lateral margin of T9 (compare F, H), dashed where hidden beneath T9; blue – bending line of cuticle to the posterior (IT8-b) immediately in front of anterior margin of T9 (T9-a) (compare Fig. S1D left part); green – lateral borders of T9 and T10 (lateral bending edges where they turn to the ventral side). — ***Colours and lines in E–H***: Thick lines in magenta are (virtual) cutting lines through the cuticle. Continuous black lines are freely visible edges (= lines along which the cuticle bends away from the observer's view). Dashed black lines are edges hidden beneath other cuticle (only some shown). Dashed gray lines show hidden part of lateral margins of T9p or S9. Sclerites shaded in blue (coxal and laterocoxal sclerotisations of segment 9, which together form most of "sternite" S9 in F–H), orange (tergal sclerotisations of segment 9), or green (tergal sclerotisations of segment 8); membrane shaded in light grey. Thick lines in yellow represent a potential weak zone within T9 (on part T9p).

T9p in figs 202, 236a, 264; fold stretched in Fig. 29F) or, more rarely, bend inward above sternite **S9** (Klass 1997: **T9p** in fig. 295a). However, the male **pt9** reminds of the (para)tergal extension of the female (**pt8,9** in e.g. Fig. 19A, 29E), which is present in all Dictyoptera. The female **pt8,9** is predominantly formed by tergite **T9** (along the antecosta of segment 9, **ac9**), but at least to its proximal portion tergite **T8** also contributes – less distinctly in most Blattodea than in Mantodea (Fig. 29E; **te** in Klass 1998: figs 2–4, 11–18; **TG8+9ε** in Brannoch et al. 2017: fig. 14C). The arm **pt9** of the male also originates from the anterior part of **T9** (Figs 25A, 29G, H), but a contribution of **T8** is not evident. The arms of female dictyopterans serve for the abutment of the entire ovipositor; their ventral ends are in contact with several 8th-segmental sclerites, and with the 9th-segmental gonangulum (**gg** = laterocoxa LC9; Klass 1998: figs 11–18). In the males the 9th-segmental ventral sclerites (laterocoxal and coxal ones of both sides) are all combined in the subgenital plate **S9** (compare blue sclerites in Fig. 29E–H), and it is possible (though difficult to demonstrate) that the male tergal arm **pt9** contacts the laterocoxal portion of **S9**. The tergal arm of male *Attaphila* is thus possibly a feature that has been taken over from the morphology of the female. Similarly, the shortness of tergites **T8** and **T9** to the extent seen in male *Attaphila*, and their overfolding by tergite **T7**, is also unusual among male Dictyoptera but normal in females.

The function of the rigid tergal arms of the male might be as follows: When the subgenital plate is pushed backward (by muscles connecting the anterior ends of apodemes **sta9** of **S9** with sternite **S8**), the arms **pt9** may act as a lever lifting tergite **T9** and the terminal part of the abdomen posterior to it a bit upward. Such a movement would plausibly open the space above the subgenital plate, where the phallomeres are located, to the back, e.g. during mating. A tighter at-rest closure of this genitalic space compared to many other Dictyoptera might be another element of preventing the host ants' mandibles from gripping a body part of the cockroach, in this case the subgenital lobe (see 7.3.2. for legs).

A male tergal arm **pt9** has so far not been reported for a dictyopteran; the same is true for very short male **T8** and **T9** covered by **T7** – with the exception of Cryptocercidae, which have a huge **T7** expanded to the posterior tip of the abdomen. However, we found a similar situation in *Lobopterella dimidiatipes* (Bolívar, 1890), a member of Blattellidae (Djernæs et al. 2020: table 4 based on results of Wang et al. 2017, Bourguignon et al. 2018, and Evangelista et al. 2019; Evangelista et al. 2021). In this species the ventrally bent part of **T9** (**T9p**) overlaps **S9** ventrally as in most Dictyoptera (Fig. 29D, ventromesal border of **T9p** indicated by orange arrows). The anterior marginal part of **T9p** is evidently much stronger and thicker (**ac9**) than further posterior parts of **T9p**, thus corresponding with arm **pt9** of *Attaphila*; and the **pt9** of *Lobopterella* approaches the lateral border of **S9** as in *Attaphila* (**A1** in Fig. 29C, D) – though perhaps less tightly, as indicated by the fairly wide membrane separating **pt9** and **S9** on the left side of Fig. 29D. **T9** morphology in *Lobopterella* could thus be plausibly interpreted as an early evolutionary stage of **T9** morphology in *Attaphila*. It shows how an arm like **pt9** of *Attaphila* likely has originated, and that it is not a sclerite element newly formed. In the Blattodea that have **T9p** overlapping **S9** (including *Lobopterella*), the anteromesal corner of **T9p** is quite usually also close to the lateral margin of **S9** (as in Fig. 29F; Klass 1997: figs 262–265). The specialities of *Lobopterella* and *Attaphila* are then the strengthening of the antecosta (**ac9**) along the anterior margin of **T9p** and the far anterior extension of **T9p**; a ventromesal part of **T9p** posterior to arm **pt9** seems to be weakened in *Lobopterella*, and desclerotised in *Attaphila*, which rendered the anterior part arm-like. *Lobopterella* additionally shows, like *Attaphila*, unusually short male **T8** and **T9**.

7.3.5. Female genitalia

The laterosternal shelf area is a highly variable part of the dictyopteran female genitalia (exemplified in Klass 1998: figs 5–10). This concerns the shape of the shelf, which can be simply step-like, or with the upper part of the step projecting posteriorly as a lobe or a pair of lobes; and it concerns the features of its main sclerite (**ls**).

The absence of a shelf (i.e. of a physical step upward) between the laterosternal shelf area (with sclerite **ls**) and

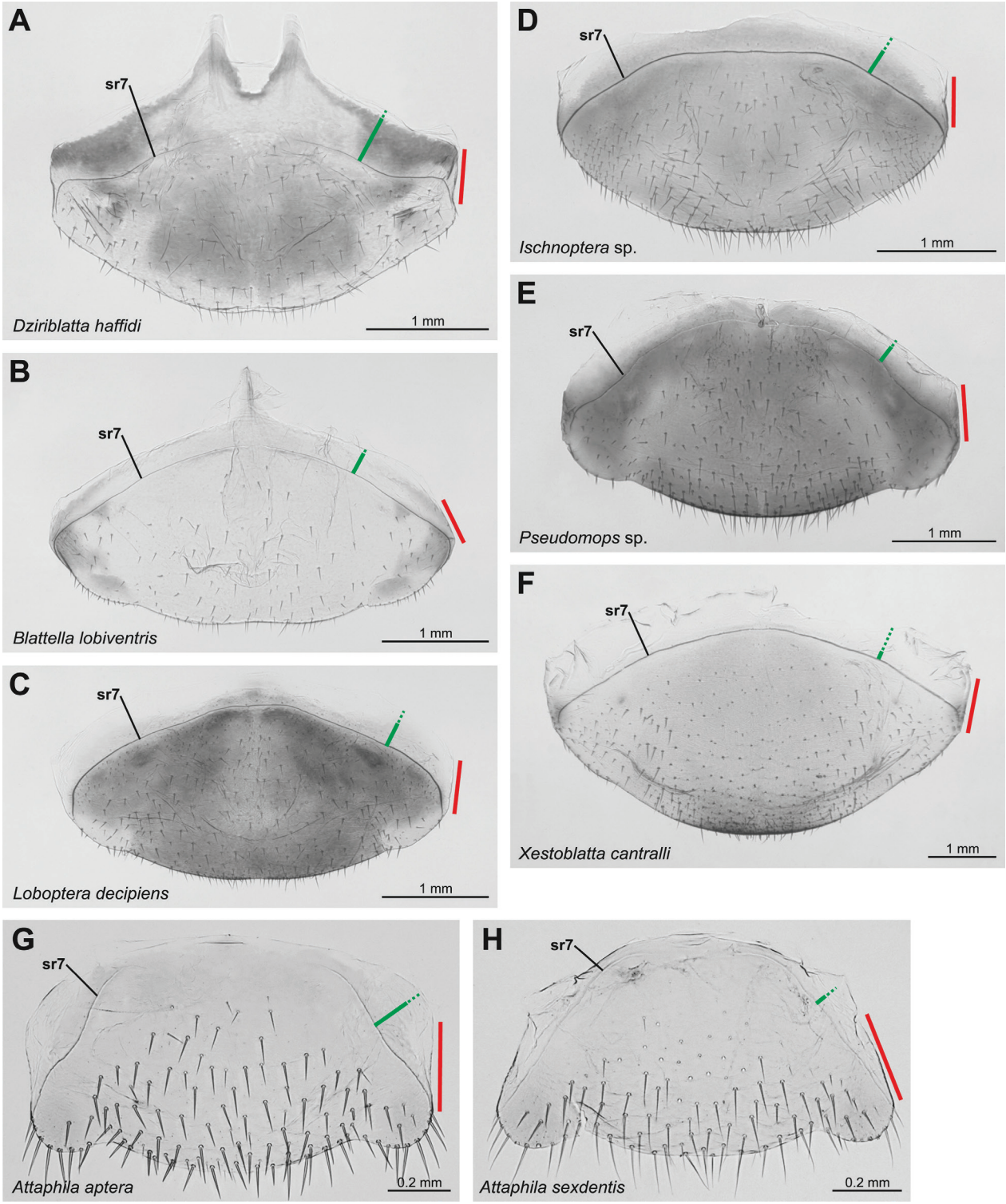


Figure 30. Subgenital plate (sternite S7) of females of various Ectobiidae (A) and Blattellidae species (B–H). **A**: *Dziriblatta haffidi* (Ma 87b/4). **B**: *Blattella lobiventris* (Gabon, Bo 1080). **C**: *Loboptera decipiens* (Sp 38/5). **D**: *Ischnoptera* sp. (CR 13, ex cult.). **E**: *Pseudomops* sp. (Mexico, Bo 1455). **F**: *Xestoblatta cantralli* (CR 15/2). **G**: *Attaphila aptera* (from Fig. 17C). **G**: *Attaphila sexdentis* (from Fig. 17F). — ***Abbreviations and line colours***: **sr7** transversal ridge of subgenital plate S7. **Red line** showing inclination of lateral border of subgenital lobe. **Green line** showing anterolateral extension of S7 sclerotisation beyond transversal ridge (continuous: unambiguous sclerotisation; dashed: gradually fading weak sclerotisation; border between the two also partly gradual).

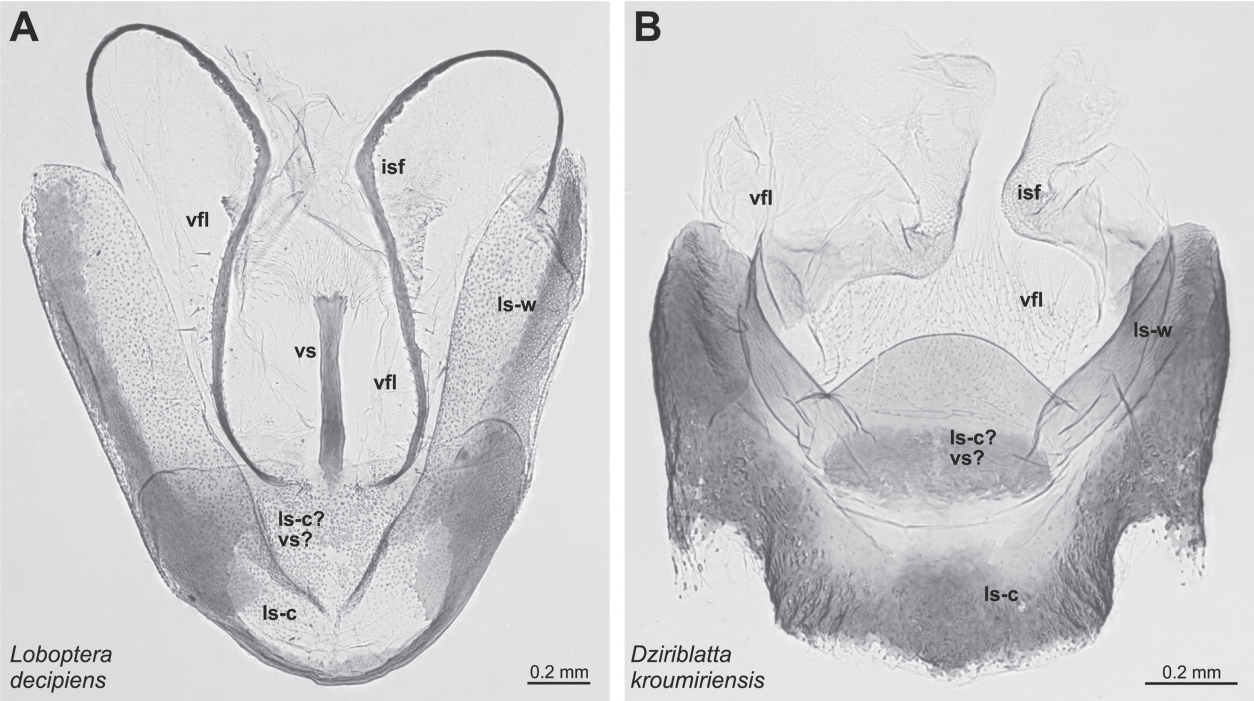


Figure 31. Laterosternal shelf area of females of Blattellidae (A) and Ectobiidae (B) species, ventral view, posteriorly on top. **A**: *Loboptera decipiens* (Sp 7/4). **B**: *Dziriblatta kroumiriensis* (Al 4/11). — ***Abbreviations***: **isf** intersternal folds (of floor of vestibulum); **ls** laterosternal-shelf sclerite (with central part **c**, wing part **w**); **vfl** floor of vestibulum; **vs** vestibular sclerite. **?** added if interpretation is ambiguous.

the vestibular floor (with sclerite **vs** if present) could be a speciality of *Attaphila*. Most Dictyoptera have a shelf with an anteriorly bulged wall (as in MK64: fig. 2, see also 'se' in Klass 1998: figs 5–10). This is also true for many Blaberoidea (MK64: fig. 40B of *Supella*), and in Blaberidae the deepening of the wall of the shelf to the anterior leads to the formation of a brood sac (compare MK64: figs 40B and 79B). However, it is unclear from the illustrations in MK64 to what extent a shelf is present in many of the remaining Blaberoidea she studied, so this character is difficult to judge.

In many Blaberoidea sclerite **ls** is continuous across the midline (e.g. Fig. 31A, B); and a strongly convex posterior margin of the middle part occurs in many Ectobiidae (*Dziriblatta* in Fig. 31B; *Ectobius*, *Capraiellus*, *Planuncus* in Bohn et al. 2013: fig. 4I–M). However, the middle part (**ls-c** and **ls-a**) being shaped as a U open to the anterior (Fig. 22) seems to be known only from *Attaphila*. We also note that in many Blaberoidea the identification of **ls** versus **vs** sclerotisations is not entirely clear – including those in Fig. 31 (as expressed by "?" in the labelling).

The tubes **lst** (Figs 22, 23) associated with sclerite **ls** are striking structures of *Attaphila*. Yet, some Blaberoidea show potentially homologous structures (character not clear in many illustrations in the literature including MK64): In *Saltoblattella*, likely a member of Pseudophyllodromiidae (Evangelista et al. 2021), the same parts of the **ls** sclerite are anteriorly expanded, the expansions plausibly being part of the walls of a pair of pouches (Bohn et al. 2010: fig. 5I); however, details of these structures are not known, and they do not appear to be rolled up as in *Attaphila* (cross sections in Fig. 23D). The only evidence of similarly placed (but simpler) pouches in MK64 concerns the pseudophyllodromiids *Neoblattella* and *Lophoblatta* (MK64: figs 47 [lowermost structures apart from spermathecae], 59 [thin extensions immediately laterad of spermathecae]). The biological significance of the tubes **lst** remains obscure. They might serve for muscle attachment (for bundles 'B' and 'Bd' in Klass 1998: fig. 20 resp. 21), though this does not seem to be the case at least for the elements of *Lophoblatta* (MK64: figs 58, 59), and the rolled-up condition of **lst** in *Attaphila* would be untypical for such a function. The **lst** of *Attaphila* have a position similar to the spermathecae in other Blaberoidea, and in *Attaphila* we could not find any other structures more clearly representing spermathecae; yet, due to their shape and extensive sclerotisation it is unlikely that tubes **lst** of *Attaphila* represent the typical blaberoid pair of spermathecae.

One more speciality of *Attaphila* is the wide, sparsely folded opening of the common oviduct (**oc** in Fig. 23A–C), which is in contrast to the narrow but strongly folded (for expansion during egg-laying) opening of the common oviduct upon a genital papilla or plateau in most Dictyoptera (as in Klass 1998: 'go' in figs 20, 21; MK64: g.p. in figs 52, 73A).

Furthermore, the right-sided pouch **gcp** upon the genital chamber (Figs 19A, B, D, 21A–C, 23A) might be special for *Attaphila*; at least, we are not aware of such a distinct pouch having been reported previously for a blaberoid. Pouch **gcp** creates one of the rare regular asymmetries found in the female genitalia of Dictyoptera. We note that if arranged symmetrically over the entire

width of the genital chamber, such a membranous pouch would be much less conspicuous and perhaps often overlooked. Only the distinct asymmetry of this element may thus be special to *Attaphila*, and this may be correlated with the distinct asymmetry of the neighbouring spermathecal plate (**sp** in Fig. 23A).

7.3.6. Cerci

The undivided cerci may also be mentioned as a speciality of *Attaphila*, though this feature is not surprising in view of the small size of the animals and the relative shortness of these appendages. Undivided cerci are also present in similarly small Blattodea like *Atticola* Bolívar, 1905 (Bolívar 1905) and *Myrmeblattina* Chopard, 1926 (Chopard 1924, under the genus name *Phileciton*), both also myrmecophiles but presumably not closely related with *Attaphila*. However, they also occur in the much larger Cryptocercidae (Deitz et al. 2003).

7.4. Position of *Attaphila* within Blattodea

7.4.1. Assignment of *Attaphila* to Blaberoidea

Recent molecular-based studies of the phylogeny of Blattodea have almost consistently yielded seven principal blattodean lineages: Blaberoidea, Corydioidea (= Corydiidae + Nocticolidae), Blattidae, Tryonicidae, Lamproblattidae, Anaplectidae, and Cryptocercidae + Isoptera (Murienne 2009; Djernæs et al. 2012, 2015, 2020; Legendre et al. 2015; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2019, 2021). In the most recent of these studies, the five latter groups form a clade Blattoidea, and for the basal relationships Blaberoidea + (Corydioidea + Blattoidea) appears to consolidate (Evangelista et al. 2019, 2021), although Corydioidea + (Blaberoidea + Blattoidea) is still an alternative (Djernæs et al. 2020).

Blaberoidea is the second-most speciose of the seven principal lineages (after the Cryptocercidae + Isoptera lineage). According to Djernæs et al. (2020) and Evangelista et al. (2021) (and Grandcolas 1996 before), Blaberoidea is classified in five families: Pseudophyllodromiidae, Ectobiidae, Blattellidae (including *Attaphila*), Nyctiboridae (four of the former subfamilies of an "Ectobiidae s.l."), and Blaberidae. The monophyly of Blaberoidea with this content was first hypothesised by MK64 (text-fig. 3, as sister taxon to Anaplectinae/-idae) and has remained undisputed since. The monophyly of Blaberidae is also undoubted (papers mentioned above). For each of the four up-ranked "ectobiid s.l." families monophyly can be concluded from a conspectus of the abovementioned molecular studies (Djernæs et al. 2020: table 4) and from a phylogenomic study (Evangelista et al. 2021). However, this concerns only a small set of genera that form a monophyletic core of each family, while for the vast majority of the genera and species the taxonomic assignment to one of the four "ectobiid s.l." families has remained unsupported from a phylogenetic perspective (see Klass 2001 for apparent support presented in Grandcolas 1996). The relationships among the five blaberoid families have been highly controversial (situation summarised in Djernæs et al. 2020); the probably most robust hypothesis (Evangelista et al. 2021) is Ectobiidae + (Pseudophyllodromiidae + (Blaberidae + (Blattellidae + Nyctoboridae))).

Attaphila was rarely considered explicitly in cockroach classification due to the limited knowledge of this genus. Djernæs et al. (2020; focused on Blaberoidea), the first molecular study including *Attaphila*, found it to be deeply subordinate in Blattellidae. Considering the taxa included in Djernæs et al. (2020), they found a blattellid subclade *Ischnoptera* + (*Pseudomops* + (*Xestoblatta* sp. + *Attaphila*)) with moderate support values (*Xestoblatta* being non-monophyletic in that study, and even grossly so according to work of A. Vélez-Bravo, pers. comm.). Like *Attaphila*, the other three genera are Neotropical plus southern Nearctic (with few exceptions; Beccaloni 2014), but their members are normally sized, usually fully winged, and live in leaf litter; and no myrmecophilous habits are known from them. Not much reminds of the minute, brachypterous, and myrmecophilous *Attaphila*. To what extent do morphological features confirm or contradict this placement of *Attaphila* in Blaberoidea, in Blattellidae (sensu Djernæs et al. 2020), and in a blattellid subclade together with *Pseudomops* and some *Xestoblatta*, and perhaps *Ischnoptera*? (This would correspond with an assignment to Pseudomopini as defined in Evangelista et al. 2021: fig. 2.)

The male genitalia are the most instructive morphological character system with regard to phylogenetic relationships in Blattodea (under exclusion of the Isoptera, whose male genitalia are strongly reduced: Klass 2000; Klass et al. 2000). They were a major character system in MK64's breakthrough reclassification of Blattodea; and all the principal lineages of Blattodea that were hypothesised by Klass (1997) and Klass and Meier (2006) based mainly on phallomere morphology were later confirmed by molecular studies (yet, the proposed relationships among the principal lineages and the hypothesised lineage Anaplectidae + Blaberoidea = Blaberoidea s.l. did not stand molecular analyses: Djernæs et al. 2015; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2019, 2021; Djernæs et al. 2020). Accordingly, if *Attaphila* belonged to Blaberoidea, this should be evident from the male genital characters. However, a closer association of *Attaphila* to a particular blaberoid family or group of genera is not expected based on such characters, mainly because the comparative morphology of male genitalia in Blaberoidea has remained grossly understudied, but also because homoplasies occur (e.g. morphology of posterior part of L2 sclerite, with or without articulation A10, in Klass 1997: fig. 328). There are no sound morphological arguments in favour of the monophyly of any of the blaberoid families, except for Blaberidae (see Klass 2001 for arguments proposed in Grandcolas 1996; characters listed in Evangelista et al. 2021: supplement pp. 8–11 require a more coherent and taxonomically

broader testing). Female genitalia were also essential for MK64's classification and are another character system with a great phylogenetic potential, but the degree of study is even lower than for the male genitalia.

The assignment of *Attaphila* to Blaberoidea is suggested by several features of the male genitalia that can be considered autapomorphies of Blaberoidea, but there are problems in the details. In the following, character state numbers are from Klass and Meier (2006: fig. 4 and Appendix), and evolutionary character evaluation is based on the character state distribution over taxa and the phylogenetic relationships found therein. The relationships are: *Anaplecta* = ***A*** + (*Nahublattella* = ***N*** + (*Supella* = ***S*** + remaining Blaberoidea including *Euphyllodromia* = ***RB***)); *Nahublattella*, *Supella*, and *Euphyllodromia* are the sampled representatives classified as Pseudophyllodromiinae/-idae. For phallomere elements see Supplement 4 Fig. S3 and compare illustrations in Klass (1997: figs 200–319, 324 and 328 [L2], 330 [R1, R2]).

In *Attaphila* we observed the following relevant states of characters: **(45-1)** ***A*** + ***N*** + ***S*** + ***RB***: On left phallomere, the distinctly rod-like condition of the endophallic apodeme (**ea** = **lve**). **(52-2)** ***A*** + ***N*** + ***S*** + ***RB***: On left phallomere, the location of the base of the hook (**h** = **hla**) at the posterior edge of the left phallomere. **(53-2)** ***A*** + ***N*** + ***S*** + ***RB***: On left phallomere, the long membranous basal part of the hook (**h** = **hla**), which allows its complete retraction. **(54-1)** ***S*** + ***RB***: On left phallomere, the presence of a distinct groove (**hge**) along the basad-directed surface of the claw part of the hook. **(55-1)** ***S*** + ***RB***: On left phallomere, the presence of a distinct notch or cleft (**hcl**, '**45**') in one wall of the groove **hge**. **(34-1)** ***RB***: On right phallomere, sclerite region **R1t** fused to sclerite **R2** in the former articulation **A6** (**R1t** in this configuration often isolated from other **R1** sclerotisations, forming sclerite **R1S**, the compound sclerite then being **R1S+R2** = cleft sclerite **cs**). **(37-1)** ***RB***: On right phallomere, sclerite **R3** longer than wide, side margins at least slightly concave, and anterior tip a bit widened. On the other hand: **(8-1)** ***N*** + ***S*** + ***RB***: On left phallomere, the presence of a division between the **L2** sclerotisation on process **paa** and the remaining **L2** sclerotisations (articulation **A10**) is likely not true for *Attaphila* (and many other Blaberoidea, likely due to secondary loss).

The apomorphies 45-1, 52-2, and 53-2 agree with a placement of *Attaphila* in Blaberoidea. However, they also occur in Anaplectidae, which in light of recent molecular analyses (Anaplectidae phylogenetically remote from Blaberoidea) leads to the assumption that homoplasy has occurred regarding these apomorphies, which are then not very convincing. Apomorphies 54-1, 55-1, 34-1, and 37-1 support the assignment of *Attaphila* to blaberoid subclades that include *Euphyllodromia* but exclude *Nahublattella* or both *Nahublattella* and *Supella*. It is unclear, however, whether the four latter features can be used for arguing subgroups within Blaberoidea (and the assignment of *Attaphila* to them), since according to the conspectus of recent molecular analyses in Djernæs et al. (2020) and to the results of Evangelista et al. (2021) and A. Vélez-Bravo (pers. comm.) *Euphyllodromia*, *Supella*, and *Nahublattella* are all deeply subordinate in the Pseudophyllodromiidae clade. This requires either homoplasy or reversals in these four apomorphies. While male genital morphology thus altogether supports the assignment of *Attaphila* to Blaberoidea – though with numerous ambiguities – *Attaphila* does not show any genital character that is in conflict with this assignment, and its male genitalia are overall typically blaberoid. We additionally note that the very long sclerite **R3** of the right phallomere (Fig. 24G; a shape characteristic of **R3** going beyond that specified in apomorphy 37-1 above) is suggestive of a position of *Attaphila* in Blattellidae; such a condition is typical for members of this family (e.g. Fig. 33), but is not found in the other blaberoid families.

Some further relevant characters could not be observed in our study of *Attaphila*: **(57-1)** ***A*** + ***N*** + ***S*** + ***RB***: On left phallomere, the presence of a discrete inward-directed fold (**fpe**) between hook (**h** = **hla**) and endophallic apodeme (**ea** = **lve**). **(61-2)** ***N***? + ***S*** + ***RB***: On left phallomere, the presence of a slender tendon (**ate**) arising from the anterior ventral wall of the left phallomere. **(68-1)** ***RB***: On right phallomere, the presence of an internal cuticular swelling (**cwe**) in the contact area of sclerite region **R1t** and sclerite **R2**. **(27-1)** ***RB*** (but not in Blaberidae, with primary or secondary connection?): On right phallomere, the division between regions **R1t** and **R1c** of the **R1** sclerotisations (**R1t** region called sclerite **R1S** if isolated from the remaining **R1** sclerotisations, the latter forming sclerite **R1P**; compare 34-1 above). Apomorphies 61-2, 68-1, and 27-1 could be, like 34-1 and 37-1 above, autapomorphies of a clade Blaberoidea under exclusion of *Nahublattella* and partly *Supella*. However, molecular studies do not support such a clade.

The presence of a hook on the right paraproct (**hmp** in Figs 5J, 6B) in *Attaphila aptera* (though not in the other *Attaphila* species with males known; see 7.2.) may point to an assignment of *Attaphila* to Blaberoidea excluding all Pseudophyllodromiidae. From Pseudophyllodromiidae such hooks are unknown (including *Euphyllodromia*), while they are widespread in the remaining families of Blaberoidea (see e.g. Bohn 2004: fig. 11, 2019: fig. 25 for Ectobiidae, considering mirrored morphology of male postabdomen), also in presumably all species of *Ischnoptera*, *Pseudomops* and *Xestoblatta*. Yet, the absence of the **hmp** hook in e.g. part of *Attaphila* leaves the possibility of its lack in Pseudophyllodromiidae also being secondary (which appears quite likely in view of the relationships among blaberoid families in Evangelista et al. 2021, see above).

7.4.2. Possible relationships of *Attaphila* to other genera of Blaberoidea

According to Djernæs et al.'s (2020) finding of a clade *Ischnoptera* + (*Pseudomops* + (*Xestoblatta* sp. + *Attaphila*)), we focused our attention on these three blattellid genera; close relationships of these were also hypothesised in Grandcolas (1992) and supported in Evangelista et al. (2021: Blattellidae, tribe Pseudomopini), but with *Attaphila* not being considered in both contributions.

Based on own observations and data from the literature (MK64; Gurney 1939; Rocha e Silva Abuquerque and Fraga 1975; Silva-da-Silva and Lopes 2015), we looked for potentially apomorphic features that members of these genera share with *Attaphila*. However, we did not find any striking features of this category. In none of the

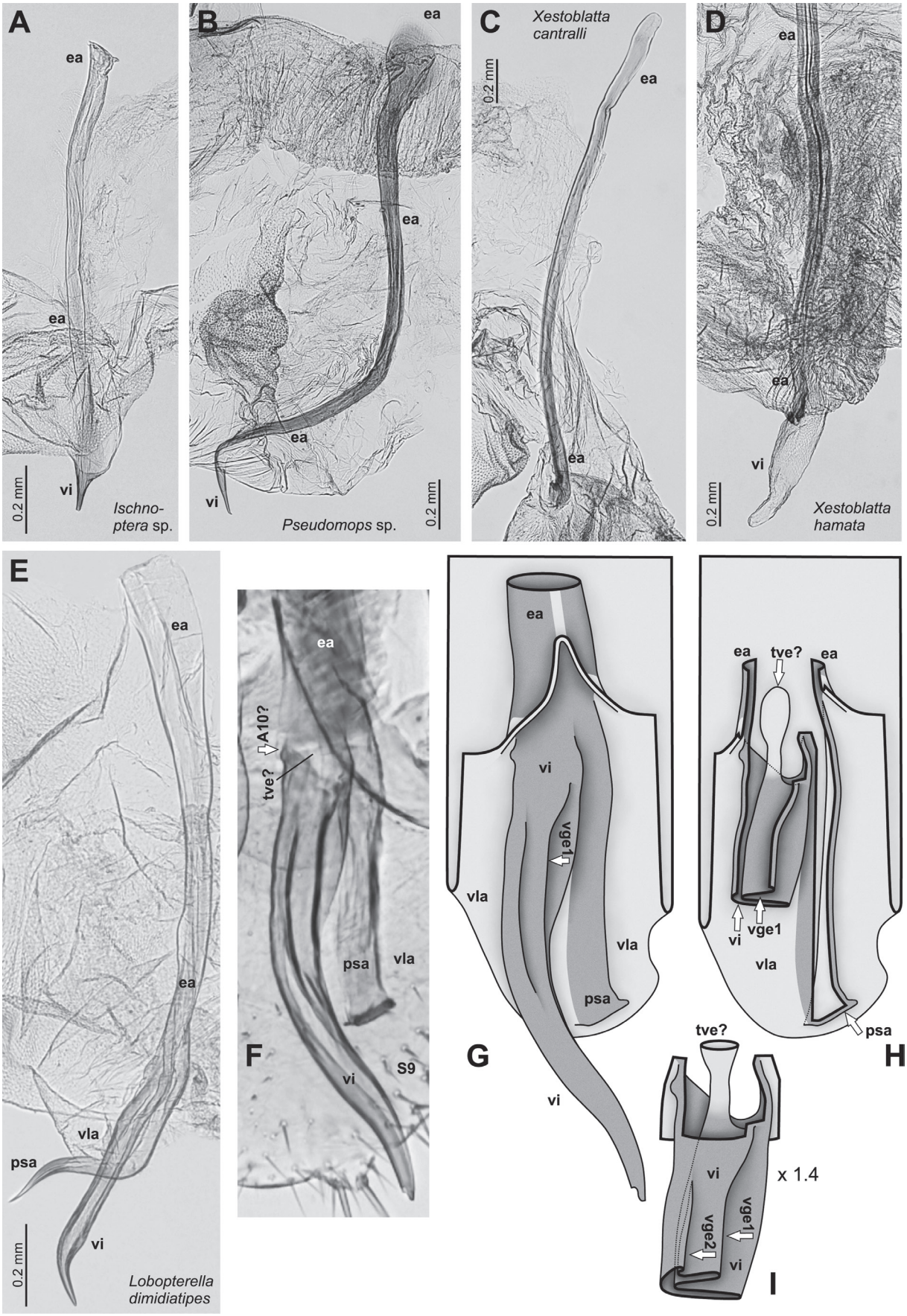


Figure 32. Endophallic apodeme and associated processes of *Attaphila* and several other Blattellidae species. **A**: *Ischnoptera* sp. (CR 13, ex cult.). **B**: *Pseudomops* sp. (Mexico, Bo 1454). **C**: *Xestoblatta cantralli* (CR 15/1). **D**: *Xestoblatta hamata* (CR 9/1). **E**: *Lobopterella dimidiatipes* (ex cult.). **F–I**: *Attaphila aptera*, photograph (**F**, taken from Fig. 24A) and tentative reconstruction drawings (**G** complete; **H** with dorsal parts cut off; **I**: proximal part of virga cut out); all included sclerotisations belong to main sclerite L2; identification of element tve tentative; F–H at same scale, I 1.4× — ***Abbreviations***: **A10?** possible articulation at base of virga (presence unlikely); **ea** endophallic apodeme; **psa** process; **tve** virga tendon; **vge1**, **vge2** virga grooves; **vi** virga; **vla** ventral lobe of left phallomere (= "ventral phallomere"). — ***Explanations*** for G–I: Thick black lines are (virtual) cutting lines through the cuticle. Continuous thin black lines are freely visible edges (= lines along which the cuticle bends away from the observer's view). Dashed thin black lines are edges hidden beneath other cuticle (only some shown). Membranous cuticle in very light grey, sclerotised cuticle in darker grey; cuticle shaded darker where it dives beneath other cuticle.

said blattellid genera the antennae and legs show any indication of the special features seen in *Attaphila* (Figs 2, 4). Specialisations on male tergite **T1** occur in some *Xestoblatta* (see 7.3.3.; Hebard 1916; Gurney 1939: fig. 13; Silva-da-Silva and Lopes 2015: figs 4, 15; Grandcolas 1992), but also in many other Blaberoidea (Roth 1969), and they are absent in the majority of the *Xestoblatta* species and in all species of *Ischnoptera* and *Pseudomops*.

On the contrary, some male genital features found in *Xestoblatta*, *Pseudomops*, and *Ischnoptera* are not well in accord with a close relationship to *Attaphila*. The area around the posterior portion of sclerite **L2** is among the parts of the male genitalia that show the richest variation within Blaberoidea (see Klass 1997: fig. 328 for main points of variation). **L2** extends over most parts of the walls of the endophallic apodeme (**ea** = **lve**), but usually its posterior portion additionally extends beyond the apodeme walls; then this exposed part of **L2** is either **(1)** forked distally and each branch is associated with a process (virga **vi** = **via** and process **psa**; each of them can be branched further; fig. 328b); or it is **(2)** unforked and only one process is present (**via**; fig. 328c–e, h–k). Alternatively, **(3) L2** can be limited to the walls of the apodeme and there is no process following posteriorly (fig. 328f, g). Further distinctions concern the presence of the phallomere gland, which opens in this area; the presence of a tendon **tve** (bearing one attachment of muscle **l10** to apodeme **lve**); the way how the ejaculatory duct joins the area; the presence of an articulation (**A10**) separating the sclerotisation on the virga **via** from the rest of **L2** (division into **L2D** and **L2E**); and the presence of muscle **l10** moving the virga **via** relative to apodeme **lve**, which according to the sparse current knowledge is correlated with the presence of articulation **A10**. In cases where only one process is present ((2) above), the positioning of articulation **A10**, of the phallomere gland, of tendon **tve**, and of the attachment of muscle **l10** usually allow the identification of the process as **via** or **psa** (likely **via** in all sufficiently studied cases). The full set of the mentioned elements is likely plesiomorphic for Blaberoidea (**via**, **psa**, **tve**, **A10**, **l10**, phallomere gland), but there are clearly many homoplasious losses of some or all of them (e.g. lack of **A10**, **l10**, and **psa** in the pseudophyllodromiid *Euphyllodromia* and the blaberid *Blaberus*, fig. 328d, k). In the *Xestoblatta*, *Pseudomops*, and *Ischnoptera* species with male genitalia sufficiently known, either the posterior portion of **L2** is unforked and only one process is present ((2) above, Fig. 32A, B, D), or **L2** is limited to the **lve** apodeme and there is no process ((3) above, Fig. 32C). Finding *Attaphila* with its putatively plesiomorphic features of a forked **L2** and two associated processes (**vi** and **psa** in Fig. 32F–H) subordinate in this group of blattellid genera leads into conflict. In the construction of this part of the genitalia *Attaphila* shows more similarity with e.g. *Saltoblattella montistabularis* (possibly Ectobiidae, see Djernæs et al. 2020, but more likely Pseudophyllodromiidae, see Evangelista et al. 2021; Bohn et al. 2010: figs 5B, 6: process 'lo' plus sclerotised bulge upward to it) and *Lobopterella dimidiatipes* (Blattellidae, tribe Hemithyrsocerini according to Evangelista et al. 2021; Fig. 32E). Furthermore, at least some *Attaphila* species have one or two grooves along the virga (**vge1**, **vge2** in Fig. 32F–I, with structural details not being entirely clear), which is not known from *Xestoblatta*, *Pseudomops*, and *Ischnoptera* species and most other Blaberoidea. However, the presence of one such groove is known from *Parcoblatta lata* (Klass 1997: figs 272–275; belonging to Blattellidae, tribe Parcoblattini according to Evangelista et al. 2021) and is a potential synapomorphy suggesting a closer relationship between *Attaphila* and this genus. On the other hand, *Parcoblatta* lacks a **psa** process. The evidence from this character system is thus quite conflictual.

The second part of the male genitalia that is highly variable within Blaberoidea is the posterior part of the right phallomere. The distinctions mainly concern various subdivisions and fusions of the **R1** sclerotisations and their relations to **R2** (such as the fusion leading to a cleft sclerite **cs**, see apomorphy 34-1 above), the pattern of teeth and ridges on these sclerites, and the presence of additional putatively apomorphic sclerites **R4** (most dorsally) and **R5** (most ventromesally). Details of this part of the genitalia are poorly studied (for basics see Klass 1997: fig. 280–287, 308–319, 330n–s). In various species of *Ischnoptera*, *Pseudomops*, and *Xestoblatta* we found a large ventromesal sclerite, which likely represents **R5** ('Ri' in Grandcolas 1992), and which in some (but not all) species forms a spined process (Fig. 33A–C). The lack of such a sclerite in *Attaphila* requires the assumption of its secondary loss. However, as sclerite **R5** is present in some but not all taxa of both Blaberidae (absent in e.g. *Nauphoeta*) and Blattellidae (absent in e.g. *Parcoblatta*) (Klass and Meier 2006: char. 39), while both families appear monophyletic in molecular analyses (including

the genera here considered, see Djernæs et al. 2020 and Evangelista et al. 2021), a secondary loss of **R5** has most likely occurred several times, which is then also plausible for *Attaphila*. In *Lobopterella* sclerite **R5** is possibly present, but fused with the cleft sclerite (Fig. 33D). A sclerite

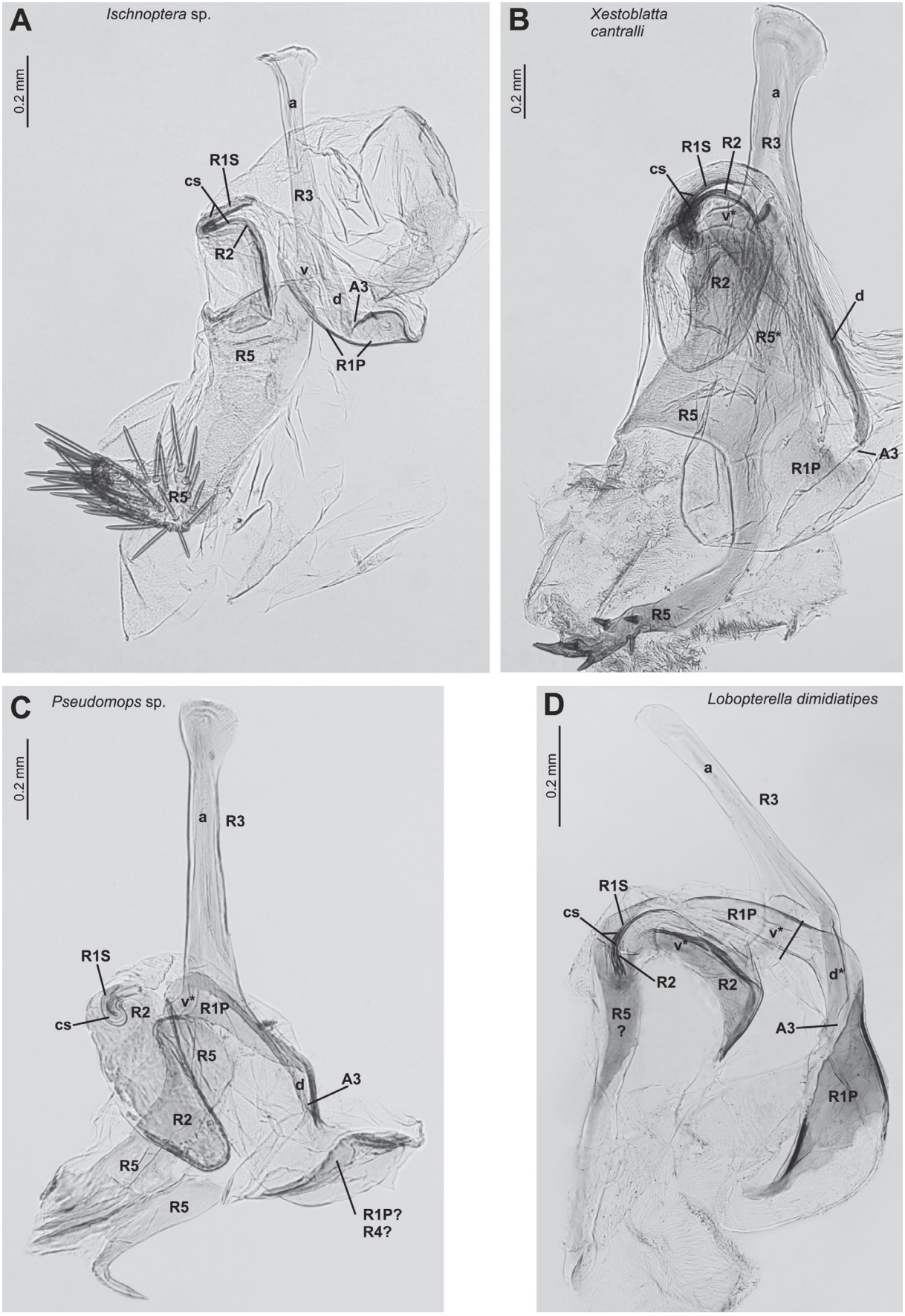


Figure 33. Right phallomere of several Blattellidae species. **A**: *Ischnoptera* sp. (CR 13, ex cult.). **B**: *Xestoblatta cantralli* (CR 15/1). **C**: *Pseudomops* sp. (Mexico, Bo 1454). **D**: *Lobopterella dimidiatipes* (ex cult.). — ***Abbreviations***: **R1** (divided in **R1S** and **R1P**), **R2**, **R3** (with anterior arm **a**, dorsoposterior arm **d**, ventroposterior arm **v**), **R4**, **R5** are the principal sclerotisations of the right phallomere; **cs** cleft sclerite, composed of the dorsally fused R1S and R2, R2-part in contact with arm v of R3 sclerite; **A3** articulation between arm d of R3 and R1 (R1P). **?** added if interpretation is ambiguous. * added for elements located underneath others.

R4 is probably absent in *Attaphila* as well as *Ischnoptera*, *Pseudomops*, *Xestoblatta*, and *Lobopterella* (Fig. 33).

The unusual shortness of male tergites **T8** and **T9** and the special condition of the ventrally bent lateral parts of **T9** – with a strengthened anterior antecostal rim (forming **pt9**) extending far to the anterior and a poorly sclerotised posterior part (see 7.3.4.) – are noteworthy apomorphies shared between *Attaphila* and *Lobopterella dimidiatipes*; both appear to reflect conditions of dictyopteran females. There are no molecular analyses including both *Lobopterella* and *Attaphila*. In analyses including *Lobopterella* it falls in Blattellidae; within this taxon it is variously far remote from the included members of the *Xestoblatta* + *Pseudomops* + *Ischnoptera* group: placed in the sister taxon of this group (Evangelista et al. 2021: see sister tribes Pseudomopini and Hemithyrsocerini), in a different inclusive main branch (Wang et al. 2017), or sister to remaining Blattellidae in Bourguignon et al. (2018). This data does not allow to estimate possible *Lobopterella-Attaphila* relationships and the extent of associated phylogenetic conflict.

In the female genitalia, the subdivision of the gonangulum (or the loss of its lateral portion) could be of interest. In all *Attaphila* the gonangulum (**gg** = laterocoxa 9 **LC9**) is represented by the mesal part (**gg-m**) bearing articulations **A2** and **A3** (Fig. 19A). The lateral part (**gg-l**) having a hinge-like contact **A1** with the paratergal extension **pt8,9** is either also present but separated from the mesal part (plesiomorphy of *A. aptera*? Fig. 19A, see 7.2.) or absent (other species, Fig. 20B; as the outline of the mesal part corresponds with that in *A. aptera*, this could be derived from the divided condition). Many Blaberoidea from several families show a plesiomorphic undivided gonangulum comprising both parts (as in Klass 1998: figs 11–18): e.g. *Neoblattella* from Pseudophyllodromiidae, *Parcoblatta* from Blattellidae, *Ectobius* from Ectobiidae, and *Epilampra* from Blaberidae (MK64: figs 46, 64, 73, 91). A division as characterised above is reported for various Pseudophyllodromiidae (*Riatia*, *Supella*) and Blattellidae (*Blattella*, *Symploce*) (MK64: figs 48, 52, 66, 67). A (near-)absence of the lateral part seems to apply to e.g. *Allacta* from Pseudophyllodromiidae, *Pseudomops*, *Loboptera*, and *Xestoblatta festae* from Blattellidae, and *Blaberus* from Blaberidae (MK64: figs 56, 62, 68, 70, 87). (The gonangulum is represented by the lateral parts = ltst. IX and the mesal parts = pt.m. + c.p. in MK64's figures according to her "crosspiece" hypothesis, which has been rejected by Klass 1998.) As a conclusion, the apomorphy of a divided to laterally reduced gonangulum is found in *Attaphila* and at least the studied species of *Pseudomops* and *Xestoblatta*, but this feature shows a high degree of homoplasy and is thus not convincing.

The laterosternal-shelf sclerotisations (**ls**) are highly variable across Dictyoptera, including the presence or absence of a division along the midline (Klass 1998: fig. 5–10). Although the medially undivided condition appears to be plesiomorphic for insects (undivided sclerotisation of the genital lobe = languette in zygentomans: Rousset 1973), the polarity within Dictyoptera is ambiguous. *Pseudomops* (MK64: figs 61, 62) has, like *Attaphila* (Figs 22, 23A), a medially continuous sclerite **ls** that also has wing parts (**w**) extending far posterolaterally. While this seems to be exceptional for Blaberoidea according to the illustrations in MK64, it also occurs in members of several families, e.g. *Riatia* (MK64: fig. 48), *Dziriblatta*, and *Loboptera* (Fig. 31A, B; independently of the problems in the distinction between **ls** and vestibular sclerite **vs**), and can thus hardly support a close relationship between *Attaphila* and *Pseudomops*. We note that in *Riatia*, *Pseudomops*, and *Loboptera* unambiguous vestibular sclerites are additionally present posterior to the middle part of sclerite **ls** (MK64: vst.s. in figs 48, 62; **vs** in Fig. 31A); this may be seen as support for our interpretation of the entire sclerite **ls** in Fig. 23 of *Attaphila* as laterosternal-shelf sclerite, a vestibular sclerite being absent. Yet, the identification of sclerites as **ls** versus **vs** (each of which might be subdivided) is partly ambiguous (also in Fig. 31, expressed by question marks), which puts some doubt on arguments based thereon.

The elements in the dorsal and anterior walls of the genital chamber may in the future also provide indications on the relationships of *Attaphila*, but this requires extensive comparative studies (see Supplement 5). The posteriorly folded orientation of the spermathecal plate of *Attaphila*, combined with the presence of a fold dividing the genital chamber (**sp** and **gcf** in Fig. 23), could be a character of interest; yet, this is apparently also found in the Pseudophyllodromiidae *Supella* (MK64: fig. 40A, with a shallow fold at sp.pl.), *Euthlastoblatta*, and *Allacta* (MK64: figs 55, 57, with an apparently deeper fold evident from the position of sp.pl.), and in *Symploce* from Blattellidae (MK64: fig. 67B, also with a deep fold). Other features of *Attaphila*, such as the lack of separate basivalvulae and the anteromedian junction of the valvifers, also occur in a variety of other Blaberoidea from several families. Species of *Xestoblatta*, *Pseudomops*, and *Ischnoptera* differ from *Attaphila* by showing a fairly complicated structuring of the dorsal and lateral walls of the genital chamber, e.g. with basivalvulae. These parts neither provide support for a relationship between *Attaphila* and these blattellid genera.

Attaphila shows a distinctly trilobate shape of the hind margin of the female subgenital lobe (Figs 16, 17). While this is quite unique in Blaberoidea, a weak trilobation as viewed in slide mounts is wide-spread in the group (Fig. 30B, C), and in *Pseudomops* (Fig. 30E; not in *Xestoblatta cantralli*, Fig. 30F) it is almost as pronounced as in *Attaphila*. Yet, this similarity is partly due to an artifact: the appearance of trilobation is in *Pseudomops* increased by the flattening of the strongly vaulted **S7** for slide mount-

ing; in situ, trilobation is hardly visible in *Pseudomops*, but distinct in *Attaphila*. The significance of this similarity is thus limited.

7.4.3. Conclusions on *Attaphila*

Molecular and morphological data agree regarding the assignment of *Attaphila* to Blaberoidea. The molecular-based placement of *Attaphila* in Blattellidae is neither significantly supported nor contradicted by the morphological data at hand; this has been expected, since except for Blaberidae no apomorphies are known to clearly support any of the blaberoid families. The close relationship of *Attaphila* with the blattellid genera *Xestoblatta*, *Pseudomops*, and *Ischnoptera* as seen in the molecular study (Djernæs et al. 2020) is not supported by morphological features, and is even contradicted by the posteriorly forked **L2** sclerite of *Attaphila*. From the morphological perspective, the blattellid *Lobopterella dimidiatipes* would appear as a better candidate in view of its tergal arm **pt9** (and perhaps the similar forking of **L2**). This species occurs across the Ethiopian and Oceanic faunal regions, not in the Neotropics, where *Attaphila*, *Xestoblatta*, *Pseudomops*, and *Ischnoptera* have their focal distribution ranges. The molecular evidence on this possibility is so far not conclusive. A clearer picture of the cladogenetic and anagenetic evolution of *Attaphila* and its blaberoid relatives requires a much broader sampling for molecular studies (as currently done by A. Vélez-Bravo for Neotropical taxa) combined with a detailed and taxon-rich comparative study of genital structures in Blaberoidea (especially the former "ectobiid" families).

8. Authors' contributions

H.B. made the concept of the manuscript. H.B. gathered cockroach specimens from collections worldwide, V.N. contributed specimens from Gamboa (Panama), and J.R.G. from Colombia. H.B. produced all photographs except Fig. 21D produced by J.R.G. and Fig. 28 produced by V.N.; K.D.K. produced all drawings. H.B. and K.D.K. wrote the manuscript, except that V.N. was the lead author of chapter 6 on the biology of *Attaphila*.

9. Acknowledgements

H.B. is much obliged to the following persons for their kindness to provide us with important material from their museum or collection: Rachelle Adams (The Ohio State University, Columbus, USA), Arturo Roig Alsina (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires), Paul Beuk (Natuurhistorisch Museum, Maastricht), Eliane Marques Cancello (Museo de Zoologia, Universidade de São Paulo), Ulrich Mueller (University of Texas, Austin), David A. Nickle (Smithsonian Institution, National Mueum of Natural History, Washington), Y.D. van Nierop (National Museum of Natural History, Leiden), E.G. Riley (Texas A&M University), Stephan Schmidt (Zoologische Staatssammlung München), R.T. Schuh (American Museum of Natural History, New York). H.B. also has to thank his colleagues Martin Spies, Roland Melzer and Bernhard Ruthensteiner from the Zoologische Staatssammlung München, the first for his valuable nomenclatoric advice, the latter two for allowing the use of their microscopic and photographic equipment. We also greatly appreciate the very dedicated reviews and helpful comments of Marie Djernæs, an anonymous referee, and the associate editor Monika Eberhard.

10. References

AntWeb. Version 8.48.2. California Academy of Science. Available at: https://www.antweb.org [Accessed on 20.i.2021]

Beccaloni GW (2014) Cockroach Species File Online. Version 5.0/5.0. Available at: http://Cockroach.SpeciesFile.org [Accessed on 08.i.2021]

Bohn H (1991) Revision of the *Loboptera* species of Morocco (Blattaria: Blattellidae: Blattellinae). Entomologica Scandinavica 22: 251–295. https://doi.org/10.1163/187631291X00129

Bohn H (1993) Revision of the *panteli*-group of *Phyllodromica* in Spain and Morocco (Blattaria: Blattellidae: Ectobiinae). Entomologica Scandinavica 24: 49–72. https://doi.org/10.1163/187631293X00064

Bohn H (2004) The Blattoptera fauna of Switzerland and the adjacent regions of France, Italy and Austria. I. The species of the *sylvestris*-group of *Ectobius* (Blattellidae, Ectobiinae). Spixiana 27: 253–285.

Bohn H (2019) Revision of the genus *Dziriblatta* Chopard, 1936 (Blattodea, Ectobiidae, Ectobiinae) from North Africa, Spain, and the Macaronesian islands. I. The nine subgenera of the genus. Zootaxa 4610: 1–73. https://doi.org/10.11646/zootaxa.4610.1.1

Bohn H (2020) Revision of the genus *Dziriblatta* Chopard, 1936 (Blattodea, Ectobiidae, Ectobiinae). II. The species of the subgenera *Paucisclerobblatta* and *Monoscleroblatta*. Zootaxa 4728(3): 301–333. https://doi.org/10.11646/zootaxa.4728.3.1

Bohn H, Beccaloni G, Dorow WHO, Pfeifer MA (2013) Another species of European Ectobiinae travelling north – the new genus *Planuncus* and its relatives (Insecta: Blattodea: Ectobiinae). Arthropod Systematics and Phylogeny 71: 139–168.

Bohn H, Chládek F (2011) Revision of the *maculata*-group of *Phyllodromica*: species from Central Europe (Insecta: Blattodea: Blattellidae: Ectobiinae). Arthropod Systematics and Phylogeny 69: 3–54.

Bohn H, Picker MD, Klass KD, Colville J (2010) A jumping cockroach from South Africa, *Saltoblattella montistabularis*, gen. nov., spec. nov. (Blattodea, Blattellidae, Blattellinae). Arthropod Systematics and Phylogeny 68: 53–69.

Bolívar I (1901) Un nuevo ortóptero mirmecófilo *Attaphila Bergi*. Comunicaciones del Museo Nacional de Buenos Aires 1(10): 331–336.

Bolívar I (1905) Les blattes myrmécophiles. Mitteilungen der Schweizer Entomologischen Gesellschaft 11 (1903–1905): 134–141.

Bolton B (2021) An online catalog of the ants of the world. Available at: https://www.antcat.org [Accessed on 11.i.2021]

Borgmeier T (1959) Revision der Gattung *Atta* Fabricius (Hymenoptera, Formicidae). Studia Entomologica 2(1–4): 321–390.

Bourguignon T, Tang Q, Ho SYW, Juna F, Wang ZQ, Arab DA, Cameron S.L, Walker J, Rentz D, Evans TA, Lo N (2018) Transoceanic dispersal and plate tectonics shaped global cockroach distributions: evidence from mitochondrial phylogenomics. Molecular Biology and Evolution 35(4): 970–983. https://doi.org/10.1093/molbev/msy013

Brannoch SK, Wieland F, Rivera J, Klass KD, Béthoux O, Svenson GJ (2017) Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). Zookeys 696: 1–100. https://doi.org/10.3897/zookeys.696.1254

Branstetter MG, Ješovnik A, Sosa-Calvo J, Lloyd MW, Faircloth BC, Brady SG, Schultz TR (2017) Dry habitats were crucibles of domestication in the evolution of agriculture in ants. Proceedings of the Royal Society B: Biological Sciences 284: 20170095. https://doi.org/10.1098/rspb.2017.0095

Brossut R (1976) Étude morphologique de la blatte myrmécophile *Attaphila fungicola* Wheeler. Insectes Sociaux 23(2): 167–174. https://doi.org/10.1007/BF02223849

Bruch C (1916) Contribución de las Hormigas de la Provincia de San Luis. Revista del Museo de La Plata 2. Ser., Tomo 10, 23: 291–357.

Bruch C (1929) Neue myrmekophile Histeriden und Verzeichnis der aus Argentinien bekannten Ameisengäste. Zoologischer Anzeiger 82: 421–437.

Bruijning CFA (1959) The Blattidae of Surinam. Studies on the Fauna of Suriname and other Guyanas 2: 1–103.

Campbell FL, Priestley JD (1970) Fagellar annuli of *Blattella germanica* (Dictyoptera: Blattellidae). Changes in their numbers and dimensions during postembryonic development. Annals of the Entomological Society of America 63(1): 81–88. https://doi.org/10.1093/aesa/63.1.81

Campbell FL, Ross MH (1979) On the pruning of its flagella by the German cockroach during postembryonic development. Annals of the Entomological Society of America 72: 580–582. https://doi.org/10.1093/aesa/72.5.580

Chopard L (1924) Description d'un Blattide myrmécophile nouveau [Orth.]. Bulletin de la Société Entomologique de France 1924: 131–132.

Cristiano MP, Cardoso DC, Sandoval-Gómez VE (2020) *Amoimyrmex* gen. nov. and relevant taxonomic changes attributed to Cristiano, M. P.; Cardoso, D. C.; Sandoval-Gómez, V. E. Pp. 647–674 in: Cristiano MP, Cardoso DC, Sandoval-Gómez VE, Simões-Gomes F (2020) *Amoimyrmex* Cristiano, Cardoso & Sandoval, gen. nov. (Hymenoptera: Formicidae): a new genus of leaf-cutting ants revealed by multilocus molecular phylogenetic and morphological analyses. Austral Entomology 59: 643–676. https://doi.org/10.1111/aen.12493

Davis C (1936) Studies in Australian Embioptera part 1 – Systematics part II. Further notes on systematics. Proceedings of the Linnean Society of New South Wales 61: 229–258.

De Fine Licht HH, Boomsma JJ (2010) Forage collection, substrate preparation, and diet composition in fungus-growing ants. Ecological Entomology 35(3): 259–269. https://doi.org/10.1111/j.1365-2311.2010.01193.x

Deitz LL, Nalepa CA, Klass KD (2003) Phylogeny of Dictyoptera re-examined. Entomologische Abhandlungen 61: 69–91.

Djernæs M, Klass KD, Eggleton P (2015) Identifying possible sister groups of Cryptocercidae + Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. Molecular Phylogenetics and Evolution 84: 284–303. https://doi.org/10.1016/j.ympev.2014.08.019

Djernæs M, Klass KD, Picker MD, Damgaard J (2012) Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. Systematic Entomology 37: 65–83. https://doi.org/10.1111/j.1365-3113.2011.00598.x

Djernæs M, Kotyková Varadínová Z, Kotyk M, Eulitz U, Klass KD (2020) Phylogeny and life history evolution of Blaberoidea (Blattodea). Arthropod Systematics and Phylogeny 78: 29–69.

Drilling K, Klass KD (2010) Surface structures of the antenna in Mantophasmatodea (Insecta). Zoologischer Anzeiger 249: 121–137. https://doi.org/10.1016/j.jcz.2010.07.001

Evangelista DA, Wipfler B, Béthoux O, Donath A, Fujita M, Kohli MK, Legendre F, Liu S, Machida R, Misof B, Peters RS, Podsiadlowski L, Rust J, Schuette K, Tollenaar W, Ware JL, Wappler T, Zhou X, Meusemann K, Simon S (2019) An integrative phylogenomic approach illuminates the evolutionary history of cockroaches and termites (Blattodea). Proceedings of the Royal Society B: Biological Sciences 286: 9 pp. https://doi.org/10.1098/rspb.2018.2076

Evangelista DA, Simon S, Wilson MM, Kawahara AY, Kohli MK, Ware JL, Wipfler B, Béthoux O, Grandcolas P, Legendre F (2021) Assessing support for Blaberoidea phylogeny suggests optimal locus quality. Systematic Entomology 46: 157–171. https://doi.org/10.1111/syen.12454

Evenhuis NL (2016) The insect and spider collections of the world website. Previously available at: http://hbs.bishopmuseum.org/codens [Accessed on 25.vii.2016].

Fujita M, Machida R (2014) Reproductive biology and postembryonic development of a polyphagid cockroach *Eucorydia yasumatsui* Asahina (Blattodea: Polyphagidae). Arthropod Systematics and Phylogeny 72: 193–211.

Fuller C (1920) Studies of post-embryonic development of the antennae of termites. Annals of the Natal Museum 4: 235–295.

Gonçalves CR (1961) O gênero *Acromyrmex* no Brasil (Hym. Formicidae). Studia Entomologica 4(1–4): 113–180.

Grandcolas P (1992) Evolution du mode de vie, répartition et nouveaux taxons dans le genre *Xestoblatta* Hebard, 1916 (Dictyoptera, Blattellidae, Blattellinae). Revue Francaise d'Entomologie 14(4): 155–168.

Grandcolas P (1996) The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. Canadian Journal of Zoology 74: 508–527. https://doi.org/10.1139/z96-059

Gurney AB (1937) Studies in certain genera of American Blattidae (Orthoptera). Proceedings of the Entomological Society of Washington 39(5): 101–112.

Gurney AB (1939) A revision of the neotropical genus *Xestoblatta* Hebard (Orthoptera; Blattidae; Pseudomopinae). Proceedings of the Entomological Society of Washington 41(4): 97–128.

Heath H (1903) The habits of California termites. Biological Bulletin 4: 47–63. https://doi.org/10.2307/1535553

Hebard M (1916) Studies in the group Ischnopterites (Orthoptera, Blattidae, Pseudomopinae). Transactions of the American Entomological Society 42: 337–383.

Index Fungorum. Royal Botanic Gardens Kew, Landcare Research NZ, and Chinese Academy of Science. Available at: www.indexfungorum.org [Accessed on 10.ii.2021]

Klass KD (1997) The external male genitalia and the phylogeny of Blattaria and Mantodea. Bonner Zoologische Monographien 42: 1–341.

Klass KD (1998) The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. Zoologischer Anzeiger 236: 69–101.

Klass KD (2000) The male abdomen of the relic termite *Mastotermes darwiniensis* (Insecta: Isoptera: Mastotermitidae). Zoologischer Anzeiger 239: 231–262.

Klass KD (2001) Morphological evidence on blattarian phylogeny: "phylogenetic histories and stories" (Insecta, Dictyoptera). Deutsche Entomologische Zeitschrift 48: 223–265. https://doi.org/10.1002/mmnd.4800480203

Klass KD, Eulitz U (2007) The tentorium and anterior head sulci in Dictyoptera and Mantophasmatodea (Insecta). Zoologischer Anzeiger 246: 205–234. https://doi.org/10.1016/j.jcz.2007.06.001

Klass KD, Eulitz U, Schmidt C, Barton A (2009) The tibiotarsal articulation and intertibiotarsal leg sclerite in Dictyoptera (Insecta). Insect Systematics and Evolution 40: 361–387. https://doi.org/10.1163/139956009X12506607684878

Klass KD, Matushkina NA (2018) The exoskeleton of the male genitalic region in Archaeognatha, with hypotheses on the early evolution and the morphological interpretation of genitalia in insects. Arthropod Systematics and Phylogeny 76: 235–294.

Klass KD, Meier R (2006) A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. Entomologische Abhandlungen 63: 3–50.

Klass KD, Thorne BL, Lenz M (2000) The male postabdomen of *Stolotermes*: termites with unusually well-developed external genitalia (Dictyoptera: Isoptera: Stolotermitinae). Acta Zoologica (Stockholm) 81: 121–130. https://doi.org/10.1046/j.1463-6395.2000.00045.x

Kooij PW, Dentinger BM, Donoso DA, Shik JZ, Gaya E (2018) Cryptic diversity in Colombian edible leaf-cutting ants (Hymenoptera: Formicidae). Insects 9(4): 191. https://doi.org/10.3390/insects9040191

Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R, Grandcolas P (2015) Phylogeny of Dictyoptera: dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence. Plos one 10(7): p.e0130127. https://doi.org/10.1371/journal.pone.0130127

McKittrick FA (1964) Evolutionary studies of cockroaches. Cornell University Agricultural Experiment Station Memoirs 389: 1–197.

Moser JC (1964) Inquiline roach responds to trail-marking substance of leaf-cutting ants. – Science N.S. 143 Nr. 3610: 1048–1049. https://doi.org/10.1126/science.143.3610.1048

Moser JC (1967) Mating activities of *Atta texana* (Hymenoptera, Formicidae). Insectes Sociaux 14: 295–312. https://doi.org/10.1007/BF02252831

Mueller UG, Ishak HD, Bruschi SM, Smith CC, Herman JJ, Solomon SE, Mikheyev AS, Rabeling C, Scott JJ, Cooper M, Rodrigues A, Ortiz A, Brandão CRF, Lattke JE, Pagnocca FC, Rehner SA, Schultz TR, Vasconcelos HL, Adams RMM, Bollazzi M, Clark RM, Himler AG, LaPolla JS, Leal IR, Johnson RA, Roces F, Sosa-Calvo J, Wirth R, Bacci M Jr (2017) Biogeography of mutualistic fungi cultivated by leafcutter ants. Molecular Ecology 26(24): 6921–6937. https://doi.org/10.1111/mec.14431

Murienne J (2009) Molecular data confirm family status for the *Tryonicus-Lauraesilpha* group (Insecta: Blattodea: Tryonicidae). Organisms Diversity and Evolution 9: 44–51. https://doi.org/10.1016/j.ode.2008.10.005

Nalepa CA (1990) Early development of nymphs and establishment of hindgut symbiosis in *Cryptocercus punctulatus* (Dictyoptera: Cryptocercidae). Annals of the Entomological Society of America 83: 786–789. https://doi.org/10.1093/aesa/83.4.786

Nalepa CA, Evans TA, Lenz M (2011) Antennal cropping during colony foundation in termites. Zookeys 148: 185–196. https://doi.org/10.3897/zookeys.148.1854

Nehring V, Dani FR, Calamai L, Turillazzi S, Bohn H, Klass KD, d'Ettorre P (2016) Chemical disguise of myrmecophilous cockroaches and its implications for understanding nestmate recognition mechanisms in leaf-cutting ants. BMC Ecology 16: 35. https://doi.org/10.1186/s12898-016-0089-5

Phillips ZI (2021) Emigrating together but not establishing together: a cockroach rides ants and leaves. The American Naturalist 197(1). https://doi.org/10.1086/711876

Phillips ZI, Zhang MM, Mueller UG (2017) Dispersal of *Attaphila fungicola*, a symbiotic cockroach of leaf-cutter ants. Insectes Sociaux 64: 277–284. https://doi.org/10.1007/s00040-016-0535-6

Princis K (1963) Blattariae: Subordo Polyphagoidea: Fam.: Homoeogamiidae, Euthyrrhaphidae, Latindiidae, Anacompsidae, Atticolidae, Attaphilidae. Subordo Blaberoidea: Fam. Blaberidae. In: Beier M (Ed.), Orthopterorum Catalogus Pars 4: 75–172. Junk, s'Gravenhage.

Qadri MAH (1938) The life-history and growth of the cockroach *Blatta orientalis*, Linn. Bulletin of Entomological Research 29: 263–276. https://doi.org/10.1017/S0007485300035616

Rocha e Silva Abuquerque I, Fraga CRC (1975) Estudo sobre o gênero *Xestoblatta* Hebard, 1916 (Blattariae): descrição de três espécies novas da Amazônia. Boletim do Museu Paraense Emílio Goeldi 79: 1–15.

Rodríguez GJ, Montoya-Lerma J, Calle DZ (2013) Primer registro de *Attaphila fungicola* (Blattaria: Polyphagidae) en nidos de *Atta cephalotes* (Hymenoptera: Myrmicinae). Boletín Científico, Centro de Museos, Museo de Historia Natural 17(1): 219–225.

Ross ES (2000) EMBIA: contributions to the biosystematics of the insect order Embiidina, part 1. Occasional Papers of the California Academy of Sciences 149: 1–53.

Roth LM (1968) Ovarioles of the Blattaria. Annals of the Entomological Society of America 61: 132–140. https://doi.org/10.1093/aesa/61.1.132

Roth LM (1969) The evolution of the male tergal glands in the Blattaria. Annals of the Entomological Society of America 62: 176–208. https://doi.org/10.1093/aesa/62.1.176

Roth LM (1971) Additions to the oöthecae, uricose glands, ovarioles, and tergal glands of Blattaria. Annals of the Entomological Society of America 64: 127–141. https://doi.org/10.1093/aesa/64.1.127

Roth LM (1999) New cockroach species, redescriptions, and records, mostly from Australia, and a description of *Metanocticola christmasensis* gen. nov., sp. nov., from Christmas Island (Blattaria). Records of the Western Australian Museum 19: 327–364.

Roth LM (2003) Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). Oriental Insects 37(1): 1–186. https://doi.org/10.1080/00305316.2003.10417344

Rousset A (1973) Squelette et musculature des regions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la region génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida). International Journal of Insect Morphology and Embryology 2: 55–80. https://doi.org/10.1016/0020-7322(73)90006-8

Sánchez-Peña SR (2005) Essays on Organismal Aspects of the Fungus-Growing Ant Symbiosis: Ecology, Experimental Symbiont Switches and Fitness of *Atta*, and a New Theory on the Origin of Ant Fungiculture. Unpublished PhD thesis, The University of Texas at Austin.

Santschi F (1925) Revision du genre *Acromyrmex* Mayr. Revue Suisse de Zoologie 31(10): 355–398. https://doi.org/10.5962/bhl.part.117790

Schafer R (1973) Postembryonic development in the antenna of the cockroach, *Leucophaea maderae*: growth, regeneration, and the development of the adult pattern of sense organs. Journal of Experimental Zoology 183: 353–364. https://doi.org/10.1002/jez.1401830309

Schafer R, Sanchez TV (1973) Antennal sensory system of the cockroach, *Periplaneta americana*: postembryonic development and morphology of the sense organs. Journal of Comparative Neurology 149: 335–354. https://doi.org/10.1002/cne.901490304

Schultz TR, Bekkevold D, Boomsma JJ (1998) *Acromyrmex insinuator* new species: an incipient social parasite of fungus-growing ants. Insectes Sociaux 45: 457–471. https://link.springer.com/article/10.1007/s000400050101

Schultz TR, Brady SG (2008) Major evlolutionary transitions in ant agriculture. Proceedings of the National Academy of Sciences U.S.A. 105: 5435–5440.

Silva-da-Silva LR, Lopes SM (2015) Two new species of *Xestoblatta* Hebard, 1916 from Brazil, a redescription of *Xestoblatta roppai* Rocha e Silva Albuquerque & Fraga, 1975 and a key for the species of the buscki group (Blattodea, Ectobiidae, Blattellinae). ZooKeys 526: 117–129. https://doi.org/10.3897/zookeys.526.6077

Solomon SE, Rabeling C, Sosa-Calvo J, Lopes CT, Rodrigues A, Vasconcelos HL, Bacci M Jr, Mueller UG, Schultz TR (2019) The molecular phylogenetics of *Trachymyrmex* Forel ants and their fungal cultivars provide insights into the origin and coevolutionary history of 'higher-attine' ant agriculture. Systematic Entomology 44: 939–956. https://doi.org/10.1111/syen.12370

Sumner S, Aanen DK, Delabie J, Boomsma JJ (2004) The evolution of social parasitism in *Acromyrmex* leaf-cutting ants: a test of Emery's rule. Insectes Sociaux 51: 37–42. https://doi.org/10.1007/s00040-003-0723-z

Waller DA, Moser JC (1990) Invertebrate enemies and nest associates of the leaf-cutting ant *Atta texana* (Buckley) (Formicudae, Attini). In: Cedeno C (Ed.) Applied Myrmecology, a World Perspective. Westview Press, Boulder (Colorado) and Oxford, 256–273.

Wang Z, Shi Y, Qiu Z, Che Y, Lo N (2017) Reconstructing the phylogeny of Blattodea: robust support for interfamilial relationships and major clades. Scientific Reports 7: 3903. https://doi.org/10.1038/s41598-017-04243-1

Wheeler WM (1900) A new myrmecophile from the mushroom gardens of the Texan leaf-cutting ant. American Naturalist 34: 851–862. https://doi.org/10.1086/277806

Wheeler WM (1910) Ants – their Structure, Development and Behavior. Columbia University Biological Series IX. New York, The Colombia University Press, 663 pp. https://doi.org/10.5962/bhl.title.1937

Wheeler WM (1928) The social insects. Their origin and evolution. London, Kegan Paul & Co., 254–255. https://doi.org/10.5962/bhl.title.140774

Wipfler B, Weißing K, Klass KD, Weihmann T (2016) The cephalic morphology of the American roach *Periplaneta americana* (Blattodea). Arthropod Systematics and Phylogeny 74(3): 267–297.

Supplementary material

File 1

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: List of abbreviations used in text and illustrations (with some explanations).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl1

File 2

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: Explanation of transversal lines on abdominal dorsum.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl2

File 3

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: Terminologies and abbreviations used for female genitalia.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl3

File 4

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: Terminologies for male genitalia and subgenital plate.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl4

File 5

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: Problems in the interpretation of the female genitalia in *Attaphila* and other Blaberoidea.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl5

File 6

Authors: Bohn et al. (2021)
Data type: .pdf
Explanation note: Orientation of surface sculpture (microreticulation) in the male specialisation on tergite T1 of *Attaphila bergi*.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/asp.79.e67569.suppl6

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2021

Band/Volume: 79

Autor(en)/Author(s): Bohn Horst, Nehring Volker, Rodriguez Jonathan G., Klass Klaus-Dieter

Artikel/Article: Revision of the genus Attaphila (Blattodea: Blaberoidea), myrmecophiles living in the mushroom gardens of leafcutting ants 205-280