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

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**Abstract**

The genus *Attaphila*, comprising minute myrmecophilous cockroaches, is revised, including now six previously known (*A. aptera*, *A. bergi*, *A. flavá*, *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. sinusosocarinata* 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 *Amoymyr- mex*) 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
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 *Amoioymex* (all Formicidae: Myrmicinae: Attini) 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 Bolivar (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 ants or 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 *A. bergi* 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, Corydiiidae: 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 monogenic 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 Blatodea (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 Blaberoidae), where it was placed deeply subordinate in Ectobiidae-Blattellinae, as the sister-taxon of a *Xesto blatta* 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 Blaberoidae.

2. Materials, methods, terminologies, and abbreviations

2.1. Systematics

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

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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, Ectobininae, Pseudophyllodromiinae, and Nycitobininae are ranked as families Blattellidae, Ectobiidae, Pseudophyllodromiidae, and Nycitoboridae, thereby having the same rank as Blaberidae. These five families together form the Blaberoidae; see 2.1. herein.
of Blaberoidea into the five families Pseudophyllodromi-dae, Blattellidae, Ectobiidae, Nyctiboridae, and Blaberi-dae (i.e. we treat the four former subfamilies that together formed the family Ectobiidae in its older, wider sense as families); and we follow Djiænes 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 Djiænes 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 sam-
ple sizes, which, in the case of the last named authors, comprised all species of Blaberoidea. Following the catalogue of Bolton (2021), we follow the recent subdivision of the Blaberoidea into the five families Pseudophyllodromidae, Blattellidae, Ectobiidae, Nyctiboridae, and Blaberiidae (i.e. we treat the four former subfamilies that together formed the family Ectobiidae in its older, wider sense as families); and we follow Djiænes 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 Djiænes 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”.

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). Slides 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, Ch 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 Jenoptik camera (ProgRes SpeedXCore5) 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 distadorsal 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 Tn–p, fixed and discrete); the anterior borders of tergites (anterior margins of tergites Tn–a, fixed but rarely discrete); the lateral borders of tergites (lateral bending lines of tergites, fixed and discrete); and the tergal transversal ridges (trn, 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 (trn), 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-
out Dictyoptera or Insecta, and homonymes 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 terminological complex. This terminology provides names for most elements of the genitalia. However, it has not yet been applied to a broader sample of Blaberoida, where some homology problems need to be resolved prior to its broad application to this taxonomy. To cope with this conflict, we apply herein a mixture of the terminologies used by Bohn and Klass. The synonomy between the two is given in the text at first mention and is surveyed in Supplement 3 Fig. 2.

2.5. Sources for comparison

For comparing any body parts between Attaphila and other cockroaches (especially Blaberoida), 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 Blattelidae 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 Blaberoida 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 Branco 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 phallopores 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), Sympleco pallens (Stephens, 1835) (ex cult.), Xestoblatta centralis Fisk and Gurney, 1968 (Costa Rica), Xestoblatta hamata (Giglio-Tos, 1898) (Costa Rica), Pseudomops Serriveille, 1831 sp. indet. (Mexico), Ischnoptera Burmeister, 1838 sp. indet. (Costa Rica), Lobopierella dimidiatipes (Bolivar, 1890) (ex cult.), and Parcoblatta lata (Brunner v. W., 1865) (USA); and the Ectobiidae Ectobius lapponicus (Linnaeus, 1758) (Germany), Dziri blatta haffidi (Bolivar, 1908) [taxonomic status according to Bohn 2019: p. 18] (Morocco), and Dzirblatta kromir-Kiensis (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-
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 anterocentral margin of the compound eye and the lateral margin of theclypeus forms a rather wide and deep funnel-shaped pit (Fig. 1A, D: cap; Bolivar 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. Ventromesial 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.

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 (pe) and few basal flagellomeres (H1 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; Bolivar 1901, 1905; Brossaut 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 Brossaut (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-pe). 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,
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).
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 lobele (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 (ptel) 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.
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. posteroverentral edge flanking femoral groove; ti tibia; tiaa and tiap anterior resp. posterior articulation of tibia with femur; tivt ventral basal tendon of tibia; dfi dorsal fold on apical margin of tibia; itts intertibiotarsal sclerite; pdta posteroventral 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 mediiodorsal spine Td1m [mid- and hindleg] or distal anterodorsal spine Td1m [foreleg]); ds dorsal spines (= dorsal spinesTd excluding Td1m [mid- and hindleg] and Td1m [foreleg]); vs ventral spines (= ventral spines Tv).

Table 1. Spine armament of *Attaphila* legs: Number of spines on femur and tibia. **Femur**: 1° column = genicular spine, 2° column = spines along anteroverentral edge. **Tibia**: 5.6.1 etc. = 5 spines on dorsal suface outside apical armament, 6 spines in apical armament, 1 spine on ventral 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.

<table>
<thead>
<tr>
<th>Attaphila species</th>
<th>Foreleg</th>
<th>Midleg</th>
<th>Hindleg</th>
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<td>Tibia</td>
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<td>1.5</td>
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<tr>
<td>A. sinuosocarinata</td>
<td>0</td>
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<td>Attaphila, range</td>
<td>0</td>
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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).
and a distal anterodorsal spine (Td1m). Foretibia with no dorsal (besides Td1m) 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

Figures 5–13

Shape. T1,2 with weakly convex, T3–6 with fairly straight posterior border (Tr-n). 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 trn and the posterior border Tr-n, 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: msl1) 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: msl1) 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 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; Tn tergite (numbered); Tn-a anterior border of tergite (numbered); Tn-p posterior border of tergite (numbered); trn 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; Tn tergite (numbered); Tn-a anterior border of tergite (numbered); Tn-p posterior border of tergite (numbered); trn transversal ridge of tergite (numbered).
Figure 8. Abdominal tergites and terminalia of Attaphila species. A–C: *A. fungicola*. A: Male (Bo 1229), 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 right paraproct; Tn tergite (numbered); Tn-a anterior border of tergite (numbered); Tn-p posterior border of tergite (numbered); trn transversal ridge of tergite (numbered). Grey arrows pointing to excrévations 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; Tn tergite (numbered); pt9 extension of paratergite of T9; Tn-a anterior border of tergite (numbered); trn transversal ridge of tergite (numbered). Grey arrows pointing to excursions of male tr2.
Figure 10. Abdominal tergites of *Attaphila* species only known from the female sex. A, B: *A. multiseta* (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:* **Tn** tergite (numbered); **Tn-a** anterior border of tergite (numbered); **Tn-p** posterior border of tergite (numbered); **trn** transversal ridge of tergite (numbered). Grey arrows pointing to weak median and lateral excursions 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:* Tn tergite (numbered); Tn-a anterior border of tergite (numbered); Tn-p posterior border of tergite (numbered); trn transversal ridge of tergite (numbered). Grey arrows pointing to median and lateral excursions 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, 7 tergites T6, T7, T6-p, T7-p posterior borders of tergites T6, T7. tr6, tr7 transversal ridges of tergites T6, T7.

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 overlaid by the hind part of T7. Dorso-laterally the anterior border of T9 of both sexes forms on each side a distinct semicircular apodeme (f9ga, 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 p9 of male, p8,9 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 p8,9 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 p8,9, 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: T8G+9ε in fig. 14C). In the male we call the arm p9, 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. schuppii, 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. berghi, 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 stylius (sf) 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. berghi right part of lobe widely tongue-shaped, without excavation on right side; a small knob-like right stylius (sf) 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 stylius 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 (p9, e.g. Fig. 24A; see 3.6.).

**Male paraprocts.** Right paraproct (PP) 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 \textit{vl7}), 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 \textit{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 (\textit{genital chamber fold gcf} in Fig. 23A, B, its posterior edge labelled \textit{gef} in Figs 19A, B, 21A; fold in same position as the one bearing 'sp.pl.' in MK-64: fig. 40A of \textit{Supella}, but much deeper); \textit{fold gef} is asymmetrical, projecting further posteriorly on the left side. The \textit{gonopore} (opening of common oviduct \textit{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 \textit{spermathecal plate (sp; SP in Supplement 3 Fig. S2B)} lies in the dorsal wall of the fold \textit{gef} (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 \textit{spermathecae}, neither on plate \textit{sp}, nor in any other position. The anterior wall of the dorsal subchamber forms a folded, anteriorly directed pouch (genital chamber pouch \textit{gcp} in Figs 19–21, 23A) on the side opposite to where the spermathecal plate has its focus.

The left and right \textit{valvifers (vlf \textit{=} part of 8\textsuperscript{th}-segmental coxal sclerites CX8}; Figs 19–21, 23A) in the roof of the genital chamber \textit{(ge6)} 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 \textit{A5}) with the pararteral extension \textit{(pt8,9)}, and the adjacent part of \textit{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 posteriorial of the spermathecal plate. Individualised basivalvulae (part of 8\textsuperscript{th}-segmental coxal sclerites CX8) were not found; these sclerotisations could be included laterally in the sclerite here called \textit{vlf}, or in the sclerite \textit{ls} (see below), or be absent (discussion in Supplement 5). In some species the central dorsal wall of the genital chamber \textit{(ge6)} 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 \textit{1\textsuperscript{st} valves (vl \textit{=} 8\textsuperscript{th}-segmental gonapophyses gp8)} show the usual configuration, with their bases (including the basal sclerotisation GP8) reaching far laterally to join articulation \textit{A5} (e.g. Fig. 19A).

Of the \textit{gonangulum (gg \textit{=} 9\textsuperscript{th}-segmental laterocoxal sclerites LC9)} the mesal part \textit{(gg-m)} in Figs 19A, B, D, 20B, D, 21A, B) is distinct; it forms the typical articulations \textit{A2} (with the posterior lobe \textit{pl}, see below; Fig. 19A, B) and \textit{A3} (with the gonophsyle sclerotisation GP8 at the dorsal base of the \textit{1\textsuperscript{st} valve}; Fig. 19A). The lateral part \textit{(gg-4)} forming a hinge-like contact \textit{A1} with the pararteral extension \textit{pt8,9} (see 3.6.) is present in \textit{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 \textit{anterior arch (aa \textit{=} anterior part CX9\textmu} of mediually fused 9\textsuperscript{th}-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 \textit{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 \textit{posterior lobes (pl \textit{=} posterolateral parts CX9\textbeta} of 9\textsuperscript{th}-segmental coxae CX9, see Supplement 3 Fig. S2A, B) are well developed.

The \textit{2\textsuperscript{nd} valves (v2 \textit{=} 9\textsuperscript{th}-segmental gonapophyses gp9)} and the \textit{3\textsuperscript{rd} valves (v3 \textit{=} 9\textsuperscript{th}-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.

\textit{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 paraprost anterior border.

The floor of the vestibulum (= dorsal wall of subgenital lobe \textit{vl7}; \textit{vll} in Fig. 22A, B, 23A) appears to be entirely membranous. It bears \textit{membranous folds} (which are part of \textit{vll}): a pair of longitudinal intersternal folds \textit{(isf in Figs 22D, H, 23A)} and a transversal ventral vestibular fold \textit{(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 \textit{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 \textit{W}-shaped \textit{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 \textit{isf} folds. The middle part of sclerite \textit{ls} is U-shaped (U open anteriorly, i.e. the middle peak of the \textit{W} is rounded or truncate), consisting of a central arch \textit{(ls-c)} and lateral arms \textit{(ls-a} in Figs 22A, 23C). The elongated, oblique lateral parts, the wings \textit{(ls-w in Fig. 22A)}, have a plate-like anterior portion, but extend far posterolaterally, where they become much narrower; the apical parts \textit{(ls-p}, possibly the “posterior extensions” sensu MK64, then part of laterocoxa LC8) are twisted relative to the wing part \textit{ls-w} (black arrows in Fig. 22A, D, 1). Where the middle and lateral parts of sclerite \textit{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 paraprost; 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; cgef fold dividing genital chamber (posterior edge labeled); cgp pouch of genital chamber (one-sided); cgg-m mesal gonangulum sclerite; cIC intercalary sclerite; cIs laterosternal-shelf sclerite (with central part c, arm part a, wing part w, posterolateral extremity p); cIst laterosternal-shelf tube; cpl posterior lobe; cPP paraproct; cpt8,9 extension of paratergite 9; cs spermathecal plate; cT9, cT10 abdominal tergites 9 and 10; cT10-p posterior border of tergite 10; cv1, cv3 1st and 3rd valves of ovipositor; cvlf valvifer of segment 8 (arrow pointing to zone where median widening starts). A articulations, A2 between cgg-m and pl, A3 between cgg-m and basal sclerotisation of cv1, A5 between cpt8,9 and cvlf. (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.)
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 membranous posterior of the 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 paratgal 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 (lsf in Fig. 22D), which follow behind the lst-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 *Attaghila fungicola* are described by Roth (1968: fig. 17) as being similar to other non-blaberid Blaberoidae (“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.
3.12. Male genitalia

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

Left phallomere. Hook (h in Fig. 24A, E; process hla bearing L3 scerite 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); scerotised 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 (el) bearing an anterior groove (hge) with a cleft (hcl). Endophallic apodeme (ea in Fig. 24A, F; apodeme lve bearing L2D scerite in Supplement 4 Fig. S3A, C) long rod-shaped, anteriorly widened. Base of apodeme associated with two posteriorly directed scerotised processes (Fig. 32F–I); scerotisation (L2) forked to cover both of them. The left branch of L2 is essentially limited to the virga process (v1 in Fig. 32F–I; process via bearing the compound scerite 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 scerotisation 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 scerite 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 scerite (es; compound scerite 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 scerite (R1P) extending along the posterodorsal lobe of the phallomere. The dorsal part R1S of the cleft scerite has a free end, i.e. is separated from scerite 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 antenna of the youngest available larva (A. paucisetosa, head width 0.52 mm, Fig. 2A, H; 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 meristome 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 phallemeres of males of *Attaphila* species, dorsal view, anteriorly on top. A, B: *A. aptera*, subgenital plate with phallemeres (Bo 1256, Bo 1224), anterior part of R3 sclerite out of frame in B. C–G: *A. bergi*. C: Subgenital plate without phallemeres (Bo 1274); D: Subgenital plate with phallemeres (Bo 1283); E: Isolated hook of left phallemer (Bo 1274); F: Isolated endophallic apodeme (damaged near midlength), virga, and psa-process of left phallemer (Bo 1274); G: Isolated right phallemer (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 c); hel cleft in wall of groove hge; hge groove upon claw part of hook; psa process; pt9 extension of paratergit 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 phallemer; sl' left and right stylus; sta9 anterior apodeme of subgenital plate S9; vi9 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 distal 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* Bolivar, 1905


*Attaphila aptera* Bolivar, 1905: 137; Princis 1963: 111.

Material studied. **Type material.** Holotype, 1L♂, Columbien, Espenanza, 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), 1♂ (head on one slide: Bo 1457), 2♀ (completely on one slide: Bo 1242, Bo 1291), 1♀ (head and abdomen on two slides: Bo 1292), 3♀ (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 excursions (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
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 (sf) conical, inserted at base of excavation, not reaching tip of lobe, the much smaller right one (sf') 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. Phallogomeres: (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 clav 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. 

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.

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 (= transversal and middle part) 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 (e) 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) (Bolivar 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 Bolivar (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. simosocarinata* 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 conspecificity with the *A. aptera* type: *A. sexdens* 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
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 like—ly 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


*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. A[ire]s (abdomen of each on one slide: Bo 1284, Bo 1440); 4L♂, 4L♀, Argentina, [Prov.] B[ueno]s A[ire]s, Castelar, M. Viana and R. M. [Manigla], # 41175 (together with a worker of Acromyrmex lundii on one pin); 4L♂, 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); 10♀, Argentina, [Prov. Buenos Aires], La Plata, VII.1918, C. Bruch (on 4 pins, each with a worker of *Acromyrmex lundii*) (1♂ 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.

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**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 p9; 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; vlf subgenital lobe; vi virga. **Arrow:** in A indicating that the distal part of the subgenital lobe is broken off.

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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 Bolivar 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 excursions (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). Glanular 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 and 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, occasionaly 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, l(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 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 (slf) conical, inserted at base of excavation, not reaching tip of lobe, the much smaller right one (slf, 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. PhalIomeres: (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). Paraaprocts: 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 gep rather small (Fig. 19B). In laterosternal shelf sclerite (Fig. 22C, D) central part (e) 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 Ríos (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 excursions to the anterior (Fig. 8D; compare grey arrows in Fig. 11A), but male tr2 posteriorly of the specialisations with a wide excetration to the posterior, mesally followed by a wide, very shallow excetration 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 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′), 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. *Phalomes*: (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 19.1.2021), 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


**Diagnosis. Male.** As in *A. paucisetosa* with specialisations on T2 (ms2, but these are narrower, with simpler ridges), distinguished by having dispersed surface bristles on T2–5. For differences to *A. flavia*, 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 excavations to the anterior (Fig. 8A, C; compare grey arrows in Fig. 11A), but male tr2 posteriorly of the specialisations with a wide excavation to the posterior, mesally followed by a wide, very shallow excavation 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. flavia* 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. flavia*). **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 (ms2) 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 (st), 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. **Phallosomes:** (Fig. 25D, E, 26B) Sclerotised part of hook (h) from the short, wide base (b) almost gradually narrowing (not as gradually as in *A. flavia*, 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). Endophaclic apodeme (ea) strongly narrowed at base (forking site of sclerite). Relative to the axis of the endophaclic 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. **Para-procts:** 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 gep present (size not determinable; Fig. 19C, D). In laterosternal shelf sclerite (Figs 19C, 22E, F) central part (c) fairly short and posteri- orly rounded, posterior and lateral margins of central part and arms together forming a quite evenly curved horse-shoe 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 fervers* (Drury, 1782), the name to which the sampling of *Attaghila fungicola* type specimens in “Material studied” above most likely refers, is a synonym of *Atta cephalotes* (Linnaeus, 1758), but that (2) the “*Atta fervers*” 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 *Atthaphila 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 “*Atthaphila 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. *Atthaphila multisetosa* sp. nov. Bohn and Klass

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

http://zoobank.org/A17A1082-D1D3-45D1-AD22-3E136614D6E

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

**Material studied.** Holotype, 1♀, Suriname, [Distr. Wanica], Lelydorp, in *Atta*-nest, 20.VI.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. simuosocarinata*, 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 excrescence 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. berti*), 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-I) 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 (bst) 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. *Atthaphila paucisetosa* sp. nov. Bohn and Klass


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 one slide: Bo 1442), 2♀ (each with abdomen on one slide: Bo 1444, Bo 1445), 1♀ (abdomen and head on two sides: Bo 1433), 1♂ (abdomen on one slide: Bo 1434), 1♀ (head on one slide: Bo 1458), 1♀ (abdomen on one slide: Bo 1293; remains for DNA), 2♀ (each with abdomen on one slide: Bo 1295, Bo 1446), 2L♀ (each with abdomen and head on two sides: 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. Jonathan Rodríguez G. (Cb 3) (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.XII.2013, leg. Jonathan Rodríguez G. (abdomen and head of ♂ on two sides: 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 sides: 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, 660 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 lateralosternal 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 excursions to the anterior (Fig. 9B, E; compare grey arrows in Fig. 11A), but male *tr2* posteriorly of the specialisations with a wide excursion to the posterior, mesally followed by a wide, very shallow excursion to the anterior (grey arrows in Fig. 9B).

**Male:** Tegmina (Fig. 31, 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 (msl1) 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, 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 lateralward; only left stylus present (*sl*), 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 26A, 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 (*sr7–1*) with a weak mesally directed curvature, lateral terminal parts with a weak laterally directed curvature; 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 (*e*) 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 medially. Mesal gonangulum sclerites (gg-m) distinct, lateral ones absent (Fig. 20B).


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

4.7. *Attaphila schuppi* Bolivar, 1905

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

*Attaphila schuppi* Bolivar, 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 excrucitation (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 excrucitation 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 (sr7-1) 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 Bolivar 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: “*Atta schuppi* (m) Boliv., Typen”; there are no labels concerning locality and species of the ant host. Bolivar’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 Bolivar’s description.

The absence of a number ahead of the sex symbol does not necessarily mean that Bolivar had only one specimen for study; in the descriptions of some other new species in the same paper Bolivar 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 Bolivar should have confused the two sexes. In the description of *A. aptera* in the same paper Bolivar 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 Bolivar 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 sinuato”, 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 Bolivar. 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 lectotype *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* Bolivar, 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. Mastraich)

**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 excursions (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. Mastraich, 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. multisitosa* 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: *simusus*) 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 excursions (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 transversal 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. pauciseta 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. multiseta 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. aperita
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) ................................................. A. sexdentis
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. aperita
6’ S7 in outline rounded-rectangular, lateral borders quite parallel (Fig. 16A, B); surface bristles of T6 larger and less numerous ................................................................. A. sexdentis
7 S7 with transversal ridge uninterrupted (Figs 16A, B, 18C, D); surface bristles of T6 medium-sized (Figs 12B, 14B) ................................................................. A. fungicola
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. aperita (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. multiseta 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) ................................................................. ................................. A. aperita
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. aperita
[A. schuppi and A. aperita 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) ..................... 7
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. aperita
6’ Central part posteriorly rounded, together with the two arms (ls-a) forming a horseshoe arch .......................... 7
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 excavation to the posterior (Fig. 18C, D) .......................................................................................................................................................... *A. bergi*

2’ Anteromedian part of transversal ridge medially interrupted by one variably 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 curvature 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 mesal 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 medially (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, therefore, 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 styli, 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. pauciseta 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 excuration 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; 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 excuration 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 (Müller) Singer, 1986 (Agaricaceae; alternatively assigned to genus Leucocprinus; 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 atypical 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 species2 (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 lobicorns* 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. sinoosocarinata*; 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.

<table>
<thead>
<tr>
<th>Attaphila species</th>
<th>No. localities</th>
<th>Distribution of Attaphila species</th>
<th>Species of host ants</th>
<th>Distribution of host ants</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. fungicola</td>
<td>many</td>
<td>USA: Texas, Louisiana</td>
<td>Atta texana</td>
<td>USA: Texas, Louisiana</td>
</tr>
<tr>
<td>A. flava</td>
<td>1</td>
<td>Belize</td>
<td>Acr. cephalotes (?)</td>
<td>Mexico to northern half of South America</td>
</tr>
<tr>
<td>A. paucisetosa</td>
<td>4</td>
<td>Panama, Colombia</td>
<td>Atta cephalotes</td>
<td>Mexico to northern half of South America</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Panama</td>
<td>Atta colombica</td>
<td>Costa Rica to Colombia and Peru</td>
</tr>
<tr>
<td>A. aptera</td>
<td>1</td>
<td>Panama</td>
<td>Acr. echinatior</td>
<td>Mexico to Panama</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Panama, Colombia</td>
<td>Acr. octospinosus</td>
<td>Mexico to northern South America</td>
</tr>
<tr>
<td>A. multisetosa</td>
<td>1</td>
<td>Suriname</td>
<td>Attaphila, species unkown</td>
<td>--</td>
</tr>
<tr>
<td>A. sinuosocarinata</td>
<td>2</td>
<td>Brazil: Est. São Paulo</td>
<td>unknown</td>
<td>--</td>
</tr>
<tr>
<td>A. sexdens</td>
<td>1</td>
<td>Brazil: Est. Rio Grande do Sul</td>
<td>Atta sexdens</td>
<td>Costa Rica to Uruguay and Argentina</td>
</tr>
<tr>
<td>A. schuppi</td>
<td>1</td>
<td>Brazil: Est. Rio Grande do Sul</td>
<td>Acr. niger</td>
<td>Brazil</td>
</tr>
<tr>
<td>A. bergi</td>
<td>5</td>
<td>Uruguay, Argentina</td>
<td>Acr. lundii</td>
<td>Brazil to Uruguay and Argentina</td>
</tr>
<tr>
<td>A. bergi(?) var. minor</td>
<td>12</td>
<td>Argentina (Catamarca)</td>
<td>Acr. lobicornis</td>
<td>Brazil to Uruguay and Argentina</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Argentina (San Luis)</td>
<td>Amoi. silvestrii</td>
<td>Uruguay, Argentina</td>
</tr>
</tbody>
</table>

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 Atti (“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 lobicornsis* 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 conspecificity of the various var. minor specimens (those found with *Acromyrmex lobicornsis* 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 sympathy, 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 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-
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* males 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 (Rodriguez et al. 2013; JRG unpublished observations), *Attaphila* specimens were only found in nests older than two years and larger than 30 m². 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 phalomeres (curvature 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.

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

For most of the characters that distinguish Ataphila 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 Ataphila (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); homoplasys can occur to a considerable extent. Relationships in Ataphila 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 sinuoidal excuvuation 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 come 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 (Ac. 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 homoplasys; 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 Blaberoidae (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-I 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 Blaberoidae (except for Pseudophyllodromiidae) and most likely an autapomorphy (under exclusion of Pseudophyllodromiidae if this is the sister group of the remaining Blaberoidae); 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 Blaberoidae (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. flavà, 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* + *Ammoimyrmex* (*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 flagellome, 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 mouls 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 meristern and meristonal annuli has also been observed in other genera of Blattodea (*Lencophaea*: Schäfer 1973; *Periplaneta*: Schäfer and Sanchez 1973; *Eucorypha*: Fujita and Machida 2014), but in *Blatta* (Qadri 1938) and termites (Fuller 1920) the divisions are restricted to the meristern.

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 meristomal 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 meristem 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*: Schäfer 1973; *Periplaneta*: Schäfer 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 ant 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; Schäfer 1973; Schäfer 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 its 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 extendors. 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 tibia: (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 Brosset 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 *Saltoblabella 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 ms1). 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 (ms1), 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 palpatates 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, ms1) 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, ms1); 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 *Pauciscleroblatta* of the genus *Dzierblatta* (Ecrobidae; 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 *Dzierblatta* 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: A).
**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 1259), 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 2x 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+9; in Brannoeh 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 genital 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* (Bolivar, 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

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**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). **H:** 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).
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. 41–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 Blaberoida 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 Blaberoida 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. 51); 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 Blaberoida, 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 (oce 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 gep 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 gep creates one of the rare regular asymmetries found in the female genitalia of Dictyoptera. We note that if arranged symmetrically over the entire

**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* (AI 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.
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* Bolivar, 1905 (Bolivar 1905) and *Myrmeblattina* Chopard, 1926 (Chopard 1924, under the genus name *Philection*), 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, Corydioidae (= Corydiidae + Nocticolidae), Blattidae, Tryonicidae, Lamproblattidae, Anaplectidae, and Cryptocercidae + Isoptera (Murielle 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 + (Corydioidae + Blattoidea) appears to consolidate (Evangelista et al. 2019, 2021), although Corydioidae + (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 + Nyctiboridae))).

*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, brachyterous, 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 phallic 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 *Euphyllostromia* = RB)), *Nahublattella, Supella, and Euphyllostromia* are the sampled representatives classified as Pseudophyllostromiidae-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 endophalic apodeme (ea = lve). (52-2) A + N + S + RB: On left phallomere, the location of the base of the hook (h = hlav) 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 = hlav), 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 R1f 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 *Euphyllostromia* 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.) *Euphyllostromia, Su-
pella, and Nahublattella are all deeply subordinate in the Pseudophyllostromiidae clade. This requires either homoplasies 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 (ipe) between hook (h = hlav) and endophalic 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 5I, 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 Pseudophyllostromiidae. From Pseudophyllostromiidae such hooks are unknown (including *Euphyllostromia*), 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 Pseudophyllostromiidae 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 Albuquerque 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 apotera, 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; vl ventral lobe of left phallomere (= “ventral phallemore”). — 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 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 n10 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 n10 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, n10, phallomere gland), but there are clearly many homoplasy losses of some or all of them (e.g. lack of A10, n10, and psa in the pseudophyllodromid Euphyllodromia and the blaberid Blaberus, fig. 328d, k). In the Xestoblatta, Pseudomops, and Ischnoptera species with male genitalia sufficiently known, either the posterior or 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 Djemaa 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 Hemithyriscerini 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 (“R” 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 Blaberoidea (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
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 Pseudomopsini and Hemithyriscerini), 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. aperta? Fig. 19A, see 7.2.) or absent (other species, Fig. 20B; as the outline of the mesal part corresponds with that in A. aperta, this could be derived from the divided condition). Many Blaberoidae from several families show a plesiomorphic undivided gonangulum comprising both parts (as in Klass 1998: figs 11–18): e.g. Neoblatellla 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, Sympleco) (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 = Ist. IX and the mesal parts = pt.m. + c.p. in MK64’s figures according to her “crospiece” 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: Rousson 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 Blaberoidae 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: vs.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 Sympleco from Blattellidae (MK64: fig. 67B, also with a deep fold). Other features of Attaphila, such as the lack of separate basivulvae and the antero-median junction of the valvifers, also occur in a variety of other Blaberoidae 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 basivulvae. 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 Blaberoidae, 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 Blaberoidae. 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 $L_2$ sclerite of Attaphila. From the morphological perspective, the blattellid Lobopterella dimidiatipes would appear as a better candidate in view of its tergal arm $pt_9$ (and perhaps the similar forking of $L_2$). This species occurs across the Ethiopian and Oceanic faunal regions, not in the Neotropics, where Attaphila, Xestoblatta, Pseudomops, and Ischnoptera have their fossil 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-Bra-vo for Neotropical taxa) combined with a detailed and taxon-rich comparative study of genital structures in Blaberoidae (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.

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10. References


Waller DA, Moser JC (1990) Invertebrate enemies and nest associates of the leaf-cutting ant Atta texana (Buckley) (Formicudae, Attini).


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).
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File 2

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Data type: .pdf
Explanation note: Explanation of transversal lines on abdominal dorsum.
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File 3

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Data type: .pdf
Explanation note: Terminologies and abbreviations used for female genitalia.
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File 4

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Data type: .pdf
Explanation note: Terminologies for male genitalia and subgenital plate.
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File 5

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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*.
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