



The identity of figitid parasitoids (Hymenoptera: Cynipoidea: Figitidae) of anthomyiid flies in conifer cones

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Abstract. Larvae of *Strobilomyia* flies (Diptera: Anthomyiidae) are serious pests in conifer-seed orchards because they feed on the seed inside the cones. Figitid parasitoids (Hymenoptera: Cynipoidea) of *Strobilomyia* larvae in conifer cones are commonly reported but under various generic names. It is argued here that, across the entire Holarctic region, these figitids belong to *Amphitectus* and perhaps also to *Sarothrus* (Figitinae), but not to *Melanips* (Aspicerinae), contrary to some reports. We conclude that the identity of the commonly found figitid associated with conifer cones (*Larix* and *Picea*) in Europe and Asia is *Amphitectus austriacus* (Tavares, 1928) comb. n. This is most likely considering the original description and the host association, although the type specimen of *Seitneria austriaca* Tavares, 1928 is lost. This species name takes priority over the recently described *Amphitectus coriaceus* Paretas-Martinez & Pujade-Villar, 2013. *Seitneria* Tavares, 1928 becomes a new junior synonym of *Amphitectus* Hartig, 1840, and *Amphitectus coriaceus* Paretas-Martinez & Pujade-Villar, 2013 becomes a new synonym of *Amphitectus austriacus* (Tavares, 1928) comb. n.

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INTRODUCTION

Conifer cones host a diverse community of phytophagous insects and their natural enemies (Stadnitsky, 1969; Turgeon et al., 1994). Reduced seed production caused by insects is a particularly serious problem for forest regeneration that relies on seeds from genetically improved trees grown in seed orchards (Turgeon et al., 1994; Rosenberg et al., 2015). These seeds are primarily used in nurseries for the production of seedlings that are planted in regeneration areas after harvesting the previous forest stand (Nilsson et al., 2010). Parasitoids that affect the population dynamics of various pest insects are of great interest for integrated pest management in seed orchards (Brockerhoff & Kenis, 1996, 1997a). This study deals with the identity of certain parasitoids of anthomyiid flies of the genus *Strobilomyia*, which are among the more serious pest insects of conifer cones in temperate regions (Brockerhoff & Kenis, 1997b).

Species of Figitidae (Cynipoidea) are known to attack *Strobilomyia* fly larvae in cones of coniferous trees (“cone maggots”), both larches (*Larix*) and spruces (*Picea*), in Europe (Tavares, 1928; Stadnitskii et al., 1978; Annala, 1981; Pulkkinen, 1989; Roques & von Hirschheydt, 1990; Brockerhoff & Kenis, 1997b; Belova et al., 1998), North America (Fidgen et al., 1999; Sweeney et al., 2001) and

Asia (Stadnitsky & Grebenshchikova, 1977; Zhang et al., 1991; Belova et al., 1998; Roques et al., 2003). However, there has been considerable confusion as to naming of these figitids. They have been referred to as *Melanips*, *Sarothrus*, *Amphitectus* or *Seitneria*. None of these genera have been carefully revised in modern times, and most cone maggot figitids remain unidentified or only preliminarily identified to the genus level in collections and in papers on applied entomology. The aim of this study is to clarify the identity and generic placement of the figitid parasitoids attacking *Strobilomyia* larvae in conifer cones.

MATERIALS AND METHODS

This study is based on a morphological study of specimens in several museum collections, using various stereo microscopes at hand, as well as on literature records. Photographs were taken either with a Canon EOS D50 camera with a MP-E 65 mm lens, or a Canon EOS 7D camera with a bellows-mounted Mitutoyo microscope lens, both utilising Cognisys StackShot motorised rail, and pictures stacked using Zerene Stacker software.

Collection abbreviations

CNCI – Canadian National Collection of Insects, Ottawa, Canada; HNHN – Hungarian Natural History Museum, Budapest, Hungary; LZLP – Museu Nacional de História Natural e da

Ciência, Lisboa, Portugal; MHNG – Museum d'Histoire Naturelle, Genève, Switzerland; MZLS – Musée Zoologique, Lausanne, Switzerland; MZH – Luonnontieteellinen museo/Naturhistoriska Museet, Helsinki, Finland; MZLU – Zoologiska Museet, Lund, Sweden; NHMUK – Natural History Museum, London, UK; NHMW – Naturhistorisches Museum Wien, Austria; NHRS – Naturhistoriska Riksmuseet, Stockholm, Sweden; NMBE – Naturhistorische Museum, Bern, Switzerland; SLU – coll Göran Nordlander at Sveriges Lantbruksuniversitet (SLU), Uppsala, Sweden; USNM – US National Museum, Smithsonian Institution, Washington DC, USA; ZSM – Zoologische Staatssammlung München, Germany.

TAXONOMIC OVERVIEW

In order to clarify the identity and generic placement of the figitid parasitoids of *Strobilomyia* maggots in conifer cones, we start by presenting the generic names that have previously been used and draw conclusions about the extent to which they are applicable. Thereafter, figitids reared from cones in different geographic regions are reviewed, and finally, a comparative diagnoses of genera and species are presented.

Sarothrus and *Amphithecus*

Sarothrus and *Amphithecus* were both described by Hartig (1840). *Amphithecus* was monotypic but *Sarothrus* included three species, one of which was the male *Amphithecus*. Reinhard (1860) noted this overlap and synonymised the genera. This was followed by most subsequent authors. Later, *Amphithecus* was removed from synonymy by Ronquist (1999), without any explanation. Recently, *Amphithecus* was the subject of a review paper by Paretas-Martinez & Pujade-Villar (2013). Their study was based solely on 19th century specimens from only two classic authors' collections. They conclude that the difference between the females of the type species of the two genera is large enough to merit generic separation.

So far, we can rather easily ascribe available specimens, including unidentified specimens, that may correspond to poorly known species or represent undescribed species, to either morphological pole, and thus to either genus (at least the females). But there is some variation and they may eventually be found to merge in the middle. Furthermore, a phylogenetic analysis may perhaps show that *Amphithecus* is an apomorphic ingroup within *Sarothrus*. With the current state of knowledge, we are not confident about re-synonymising the two genera but choose to leave them as separate taxonomic units, recognising that a future phylogenetic analysis or a detailed morphological study considering the morphological variation may very well find it necessary to re-synonymise them.

Amphithecus

The genus *Amphithecus* was monotypic with *Amphithecus dahlbomi* Hartig, 1840 as the type species [a junior synonym of *A. areolatus* (Hartig, 1840), described in the same study in *Sarothrus*, with precedence established by Reinhard (1860) acting as the first reviser], until Paretas-Martinez & Pujade-Villar (2013) described a second species, *A. coriaceus*, based on a deviant specimen in Giraud's

series of *A. dahlbomi*. This species was thus only known from a single, old specimen from Germany in poor condition and without any biological data attached to it. *A. areolatus* is a rather well-known and easily identified species, but the new *A. coriaceus* could be expected to be still extant and should have been collected somewhere in Europe in modern times. We conclude that it is identical with the figitids reared from cone maggots (see under *Seitneria* below).

Sarothrus

Our concept of *Sarothrus* is based on the type species *Sarothrus canaliculatus* Hartig, 1840 [a junior synonym of *S. tibialis* (Zetterstedt, 1838)] and its close relative *S. brevicornis* Thomson, 1877. We cannot rule out the possibility that other species of nominal *Sarothrus* (and the supposedly closely related *Sarothrioides*), which have not been studied since their original description, are actually *Amphithecus*, either synonyms of species in the genus or additional species. There is one from Europe, *Sarothrus laevigatus* Hartig, 1840; three from North America, *S. californicus* Kieffer, 1907, *S. canadensis* Kieffer, 1907 and *S. nasoni* Ashmead, 1896; and three from Asia, *S. aterrimus* Belizin, 1954, *S. punctatus* Belizin, 1954, and *Sarothrioides frequens* Belizin, 1961 (from Mongolia, Kamchatka and Primorsk, respectively).

It has not been possible to locate any bibliographical references to original descriptions of *Sarothrus abietis* Belizin (quoted in Stadnitskiy et al., 1978) or *S. haemiscutellaris* P. Masner (quoted in Mikula, 1989) so these names must be considered unavailable nomina nuda and their identity becomes uninteresting from the taxonomic viewpoint.

Hosts for *Sarothrus* are still unknown, since literature records pertain to species of *Amphithecus*.

Seitneria

Seitneria and its single species *S. austriaca* were described from four specimens reared from *Larix* cones (Tavares, 1928), but the type material is lost. Tavares's own collection was destroyed by fire in Lisbon, and if the specimen was returned to its collector, Moritz Seitner, it should be in the NHMW. Repeated searches have proved unproductive (Pujade-Villar & Paretas-Martinez, 2013; Alexandra Marçal, Dominique Zimmerman and others, pers. comm.).

Seitneria was entered into synonymy with *Figites* by Weld (1952) and reinstated as a valid genus by Ronquist (1999). The reason for this was given in a paper the following year (Ros-Farré et al., 2000). In that paper, *Seitneria* is explicitly identified as the figitid commonly reared from *Larix* cones. However, Pujade-Villar & Paretas-Martinez (2013), reviewing the status of this genus, cite the discussion of *Seitneria* in Ros-Farré et al. (2000) as the opinion of only one of the three co-authors, namely Ronquist. Pujade-Villar & Paretas-Martinez (l.c.) emphasised that they had not seen any specimens, and chose not to follow Ronquist's concept. They claim that *Seitneria* "cannot be 'most similar' to *Melanips*, *Sarothrus* and *Amphithecus*" (as stated in Ros-Farré et al., 2000) since these genera are

characterized by having more or less dense lateral hair patches on the metasomal tergite, while *Seitneria*, according to the original description, has only “some setae”. In their conclusion, however, they admit the possibility that Ronquist’s *Seitneria* might have lateral hair patches, but nevertheless they finally refrain from any taxonomic conclusions and pronounce *Seitneria* a “genus dubidum, genus inquerendum” (sic).

The absence of type material is regrettable, but the major part of the original description of *Seitneria austriaca* in Tavares (1928) (Fig. 1A) corresponds well to modern specimens reared from cones. The drawing of the metasoma (Fig. 1B) (reproduced in Weld, 1952 and thereby made readily available to researchers, unlike the rare original publication) with a protruding large hypopygium shows a state characteristic of many females of *Amphitectus* [but not seen in other figitid taxa except the eucoiline *Trybliographa melanoptera* (Giraud, 1860) and some of its close relatives], and the emphasis on its coriaceous sculpture also corresponds to *Amphitectus*. The only thing in the original description contradicting the identification of *S. austriaca* with the cone maggot figitid that is usually collected is the description of the pubescence on the metasoma. The pubescence may however be somewhat understated in the description, or may be untypically sparse or worn off in the lost type specimen. A range of variation in this respect is present in modern specimens. The impression given by this pubescence may, in our experience, also vary rather significantly in suboptimal lighting conditions.

Without a type specimen, the possibility remains that *Seitneria austriaca* could refer to a very rare species that has never been seen again since 1928, but it is much more likely that the one figitid obtained by rearing from cone maggots in 1928 is the same as those reared in 1970s, 1980s, 1990s and the present.

Melanips

Melanips is a widespread and characteristic genus of figitids. This genus too is lacking revisions for most parts of the world but several European species are, nevertheless, recognisable. They were traditionally considered to belong to the Figitinae, but were moved to Aspicerinae in accordance with well-supported phylogenetic analyses (Buffington et al., 2007). Since they lack the traditional diagnostic characters of that subfamily, numerous papers from the research group in Barcelona (i.e. Ros-Farré & Pujade-Villar, 2009, 2013; Paretas-Martínez et al., 2012; Pujade-Villar et al., 2012; Paretas-Martínez & Pujade-Villar, 2013) argue against the inclusion of *Melanips* in Aspicerinae, but do not formally move it back into Figitinae. The placement in Aspicerinae is also supported by biological data. All rearing records of *Melanips* that have been corroborated are from aphidivorous flies of non-calyptrate families (Syrphidae and Chamaemyiidae), just like those of all other Aspicerinae, and there are no records confirmed by specialist identifications that link *Melanips* to any calyptrate flies (like Anthomyiidae), which are the principal hosts of Figitinae (and indeed the only corroborated hosts as far as current knowledge goes).

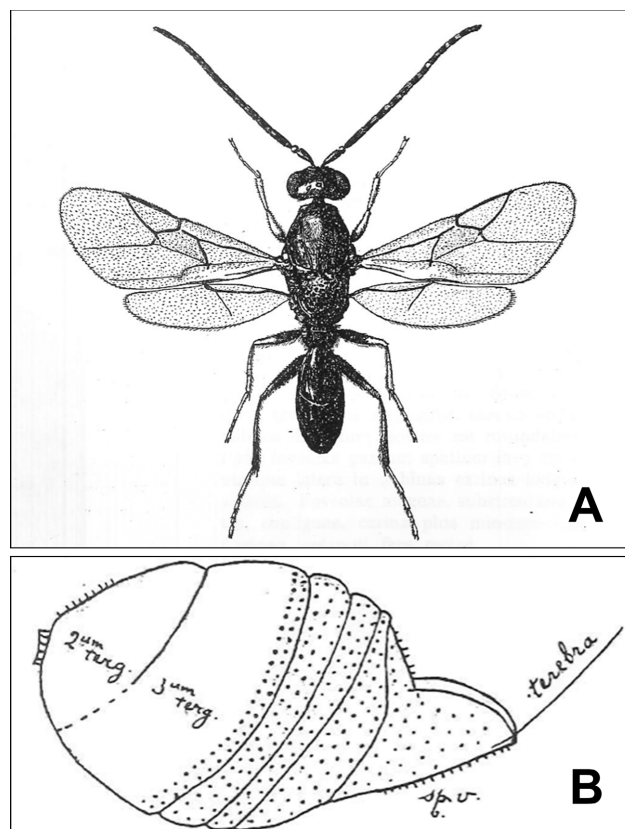


Fig. 1. Drawings from the original description of *Seitneria austriaca* in Tavares (1928). A – male, habitus; B – female, metasoma.

Taxonomic conclusion

In consequence of the considerations presented above, the figitids attacking cone maggots in Europe have two available names: *Seitneria austriaca* and the junior *Amphitectus coriaceus*. *Seitneria* Tavares, 1928 becomes a new synonym of *Amphitectus* Hartig, 1840, and *Amphitectus coriaceus* Paretas-Martínez & Pujade-Villar, 2013 becomes a new synonym of *Amphitectus austriacus* (Tavares, 1928) comb. n.

Specimens reared from cones in Europe

Figitid specimens reared from *Strobilomyia* in Europe have been referred to as *Seitneria austriaca* from larch (Tavares, 1928; Roques & Hirschheydt, 1990), *Melanips austriacus* from larch (Pulkkinen, 1989), *Sarothrus* sp. from spruce (Stadnitskii et al., 1978; Brockerhoff & Kenis, 1997), *Melanips* sp. from spruce (Annala, 1981) and *Sarothrus abietis* from spruce (Stadnitskii et al., 1978). We have studied Figitinae specimens reared from *Larix* and *Picea* cones from Switzerland, France, Finland and Sweden, representing material from several of the cited studies. All these specimens clearly belong to *Amphitectus*, and despite a range of variation they are, with the current state of knowledge, best considered to be a single species, *A. austriacus*.

Sarothrus abietis Belizin is mentioned in some papers as a species associated with “abies” (referring to either firs, *Abies* spp., or Norway spruce, *Picea abies*) and those records might refer to specimens of *A. austriacus*. However,

no original description of *S. abietis* has been found and it seems to be a nomen nudum, requiring no nomenclatural acts.

Specimens reared from cones in Asia

There are several literature records of Figitidae from cones of both *Larix* and *Picea obovata*, reported as *Seitneria austriaca*, *Sarothrus punctatus* and *Melanips opacus* (Stadnitsky & Grebenshchikova, 1977), *Sarothrus* sp. (Zhang et al., 1991) and “unidentified Figitidae” (Belova et al., 1998). The only Asian specimens that were readily available for examination were from Southern China (in MZLU). These specimens can readily be accommodated within the current limits of *A. austriacus*, though if more specimens become available and are subjected to careful study they might turn out to represent a distinct taxon.

Specimens reared from cones in North America

Specimens reared from *Picea* in North America are reported as “undescribed *Melanips* sp.” (Sweeney et al., 2001) and *Melanips* sp. (Fidgen et al., 1999). It has not been within the scope of the current investigation to revise North American specimens, but upon our request, curators at the CNCI and USNM (the former holds vouchers from the published studies) have confirmed that such specimens are more likely to belong to *Amphithecus* or *Sarothrus* than to *Melanips* (John Huber, Matt Buffington, pers. comm.). True *Melanips* are not uncommon in North America, but we find it unlikely that their biology would strongly differ from the rest of the genus and subfamily, and we strongly suspect all alleged *Melanips* from cones are misidentifications. *Sarothrus* are widespread too, and indeed species of *Sarothrus* are described from North America, but these species are unrevised and their identity presently unknown. *Amphithecus* is present in North America too, as yet undescribed species or among the nominal *Sarothrus* or *Melanips* species.

Comparative diagnosis of *Amphithecus*

Genus *Amphithecus* Hartig, 1840

Amphithecus Hartig, 1840

Sarothrus (pars) Hartig, 1840

Amphithecus Dahlbom, 1842 (misspelling)

Seitneria Tavares, 1928, syn. n.

Amphithecus can be confused with *Sarothrus* and *Melanips*.

Usually, *Melanips* are easily recognised by the heavy microsculpture on most of the mesosoma, rendering it obviously matt. *Amphithecus* and *Sarothrus* are usually shiny between the dense hair punctures, but sometimes they are coriaceous, and sometimes poor lighting conditions or dirty specimens will not allow a proper evaluation of this. *Melanips* usually have a far more elongate petiole, with the anterior part protruding dorsally ending in a smooth flange, that has been referred to as a “clam-shell petiolar lamina” (van Noort et al., 2015), whereas Figitinae, including *Amphithecus*, have a shorter petiole of more even width without a dorsal flange. Further, *Melanips* have stronger notauli (usually also very distinct lines outside the notauli), and a

more convex scutellum. Whenever one is uncertain about the degree of microsculpture, it can be useful to look at the mesopleura: in *Melanips* the lower (ventral) part of the mesopleuron is so covered in dense punctures and micro-punctures that striation is not obvious, in *Amphithecus* and *Sarothrus* the lower part of the mesopleuron is heavily striated.

Amphithecus females can usually be easily separated from *Sarothrus* by their very large and narrow metasoma, but this seems to be part of a continuum with an intermediate, probably undescribed American species and *Amphithecus areolatus* as the extreme case. All other characters exhibit a certain tendency to intergrade, and male specimens are indeed sometimes difficult to identify.

Sarothrus are, on average, smaller (males ca 3 mm, females usually 3–4 mm). The wings are diaphanous. The adpressed pubescence on most of the mesosoma is sparser than in *Amphithecus*. The mesonotum is usually convex, and there are deep and entire notauli present. The scutellum is notably uneven in sculpture, and sloping in lateral view, its posterior part clearly lower than “shoulder height” and usually with a notable weak upward-pointing tooth on posterodorsal edge. The central part of the pronotum dorsally (the “pronotal plate”) is often broadly smooth in the middle (glabrous and without punctuation), and the lateral parts of pronotum are only weakly convex, with a distinct but weak lateral carina. The female metasoma is not strikingly enlarged or flattened, in comparison with the mesosoma only slightly narrower and usually shorter. The head is round, approximately as high as wide, with longer genae and smaller eyes (gena length more than half eye length in anterior view), the face is shiny and in most areas sparsely punctate; a strongly microsculptured area below the eye in the malar space is narrow.

Amphithecus are, on average, larger (males up to 4 mm, females usually 4–5 mm). The wings are usually but not always infuscated. The adpressed pubescence on most of the mesosoma is strikingly dense. The mesonotum is remarkably straight, and notauli vary but are usually shallow and incomplete. The scutellum is relatively even in sculpture, only shallowly foveolate and not sloping in lateral view; its outline follows the line from the mesonotum, without a distinct tooth at the posterodorsal end. The entire dorsal part of the pronotum is densely punctate and pubescent (sometimes a small central spot glabrous), the lateral parts of the pronotum are strongly convex, almost forming a real “humeral carina” from the lateral carina to the tegula. The female metasoma is strikingly enlarged and flattened, much narrower and clearly longer than mesosoma. The head is broad, clearly wider than high, with shorter genae and larger eyes (length of gena less than half the length of eye in anterior view), the face is more or less coriaceous and densely punctate; a strongly microsculptured area below eye in malar space is broad.

Species diagnoses

Amphithecus areolatus (Hartig, 1840)

Sarothrus areolatus Hartig, 1840

Amphithecus Dahlbohmi Hartig, 1840

Amphitectus Dahlbomi Giraud, 1860 (emendation of species name, later considered to be in prevailing usage)
Figites piceus Dahlbom, 1842 (nomen nudum)
Melanips fumipennis Giraud, 1860

Diagnosis. Fig. 2A, B. In most cases, possible to separate from *A. austriacus* by shiny mesosoma; female metasoma longer, rather rectangular, narrower, usually red; wing usually more infusate; notauli less distinct; overall coloration paler, and pubescence denser, and more yellow.

Distinctly bicolored, partly brownish red; metasoma and legs usually red in their entirety, at least in females. Wing usually infusate more or less in its entirety. Mesosoma in in major parts without obvious microsculpture, more or less densely punctate (upper mesopleura entirely glabrous), usually shining between punctures, but occasionally more or less matt; punctures and pubescence quite dense, pubescence reddish yellow. Notauli in females moderately deep and usually but not always incomplete at anterior end, in males complete but very shallow; apart from notauli no obvious linear elements on mesoscutum. Scutellum without a median carina. Female metasoma dagger-shaped, more or less rectangular, very narrow; more than twice as long as high, dorsal and ventral outline almost parallel lines.

Distribution. Palearctic, known from Austria, Denmark, Finland, France, Germany, Italy, Kyrgyzstan, Netherlands, Norway, Poland, Russia, Slovenia, Sweden, Switzerland, United Kingdom (England), (Hellén, 1958, Fauna Europaea, Paretas-Martinez & Pujade-Villar, 2013) (specimens in NHMUK, MZLU, NHRS, SLU, ZSM, MZLS, NMBE, MHNG, HHNM, NHMW, MZH, ca 200 specimens seen).

Biology. A parasitoid of *Botanophila gnava* (Meigen, 1826) and *B. sonchi* (Hardy, 1872) (Anthomyiidae; in many publications cited as *Chorthophila*, *Phorbia* or *Pegohylomyia*) in *Lactuca* and *Sonchus* flowerheads (Harwood, 1919; Wille, 1930; Blair, 1946; Fergusson, 1986; Kählert, 1990). Harwood (1919) records emergence mainly in June and swarming also in July, but museum specimens were caught from June to November, the largest number in August. Apart from visiting the food plant of their host, they have also been observed among other parasitic wasps feeding on nectar on Apiaceae flowers (as early as by Reinhard in 1860). Occurs in meadows, parks, gardens, forest edges and beach edges (and probably in agricultural fields and ruderal areas too, considering its hosts). Most museum specimens for which the collection method is specified were collected by sweep netting.

Amphitectus austriacus (Tavares, 1928), comb. n.

Seitneria austriaca Tavares, 1928

Melanips austriacus sensu Pulkkinen, 1989

Sarothrus sp. sensu Bockerhoff & Kenis 1997

Amphitectus coriaceus Paretas-Martinez & Pujade-Vilar, 2013, syn. n.

?*Sarothrus abietis* Belizin, nomen nudum

Diagnosis. Fig. 3A–C. In most cases, possible to separate from *A. areolatus* by darker coloration; very often matt and coriaceous mesosoma; shorter female metasoma, of a rounded and somewhat drawn-out rhombic shape, broader,

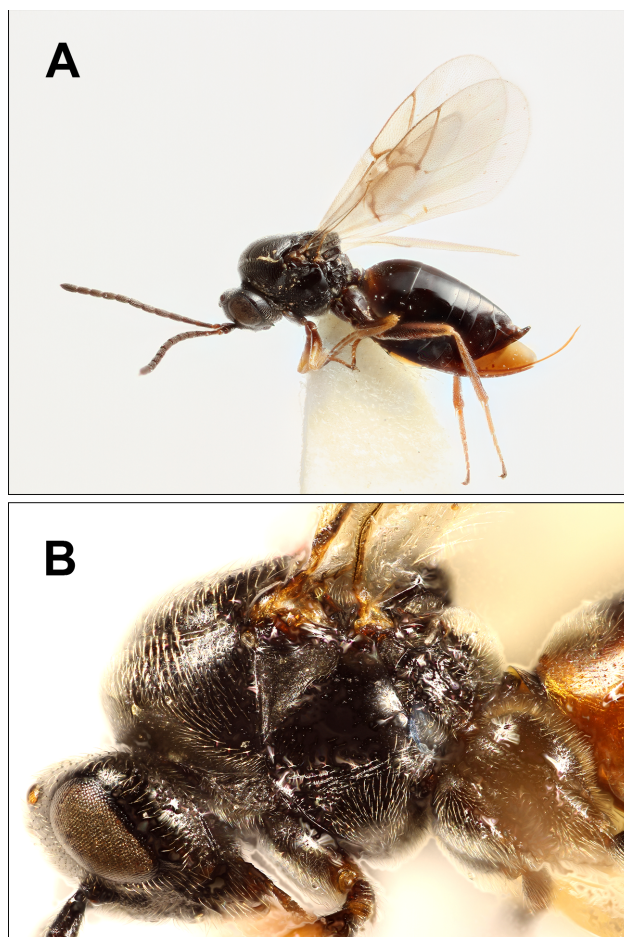


Fig. 2. *Amphitectus areolatus* (Hartig, 1840), female. A – habitus; B – mesosoma (light not diffused, so as to show the shiny habitus).

usually dark brown; wings less infusate; notauli more distinct, pubescence sparser, and paler.

Usually more or less all completely dark, but female metasoma typically paler in the anterior part, sometimes in its entirety, legs usually all dark but sometimes paler in apical parts or in their entirety. Wing infuscation variable, typically faintly infusate in its entirety with a slightly darker cubital cell, sometimes a much darker cubital cell, and sometimes also with some other regions of the wing clearly darker. Mesosoma very often quite matt with coriaceous microsculpture as well as notably sculptured with striate and rugose parts (Fig. 3B), but sculpture and microsculpture varies and mesosoma can be quite shiny with coriaceous pattern only indistinctly suggested in parts (as in Fig. 3C); punctures less dense than in *A. areolatus*, pubescence thus less dense, yellowish white. Notauli in females often complete and always at least traceable all the way, in males complete and rather deep; also glabrous lateral linear elements inside notauli in anterior half of mesoscutum and outside of notauli in posterior half. Scutellum often with a median carina in anterior half. Female metasoma extended posteriorly but not very long, never more than twice as long as high, and the dorsal and ventral outlines remain convex in their entirety; shape strongly resembles that of *Trybliographa melanoptera* (Hartig, 1843) (Eucoilinae)

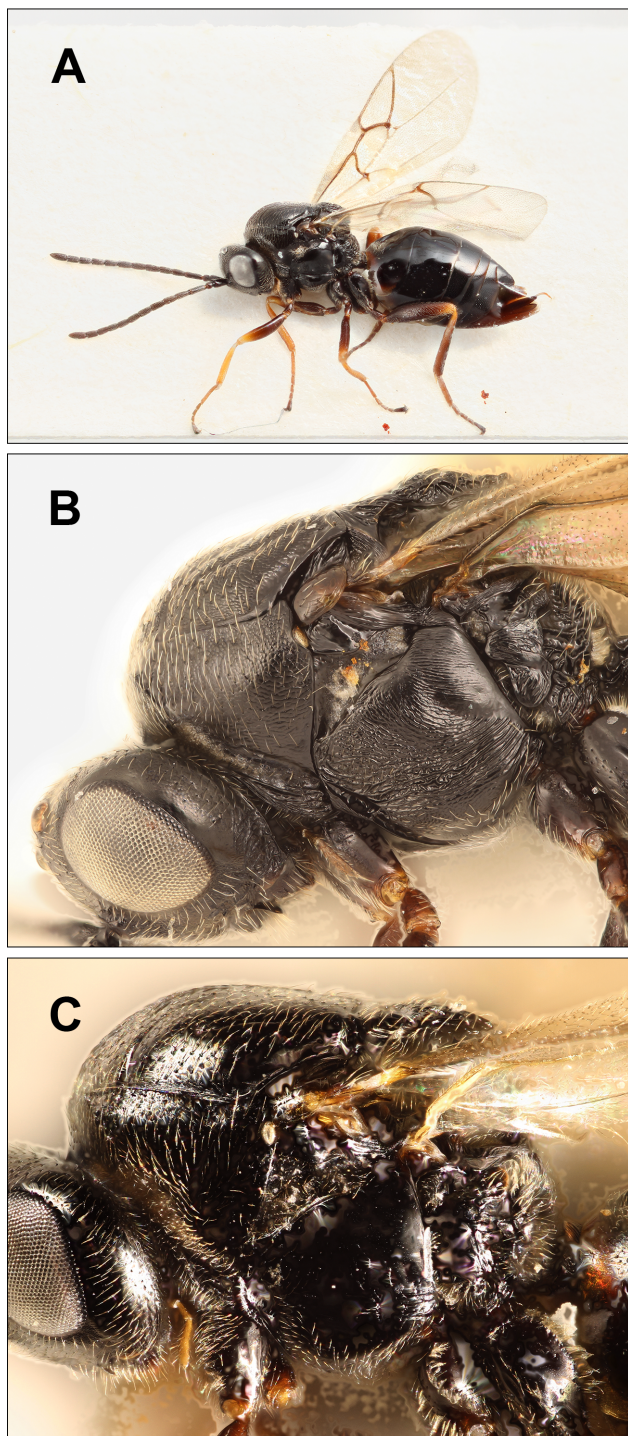


Fig. 3. *Amphithectus austriacus* (Tavares, 1928). A – female habitus; B – mesosoma from a specimen displaying dense, coriaceous microsculpture (male specimen, diffused light); C – mesosoma from a shiny specimen without dense microsculpture (female specimen reared together with the coriaceous male, light not diffused, in order to facilitate comparison with 2B).

and varies between somewhat compressed rhombic to drop-shaped (the cone-like drop shape of a normal Norway spruce cone). Thus, the three diagnostic characters emphasised in the original description of *A. coriaceus* based on a singleton (distinctly coriaceous microsculpture, very well-developed notauli, and distinct median carina in anterior half of scutellum; Paretas-Martinez et al., 2013) are com-



Fig. 4. *Amphithectus austriacus* ovipositing between the scales of an immature spruce cone (photograph: Olle Rosenberg).

mon but variable in this species when several specimens are taken into account.

Distribution. Palearctic, specimens have been examined from Austria, Switzerland, Finland, France, Germany, Sweden, plus southern China (Yunnan) (ca 60 specimens seen in MZLU, SLU and NHMUK). Also literature records from Siberia (Irkutsk, Priamurye) and Northern China (Heilongjiang) probably refer to this species. Apparently widespread in the Palearctic region. In Central Europe and southern China, all specimens come from high altitude areas (1200 m or more) with *Larix*, but North European specimens show a wider habitat range since *Picea abies* is more or less omnipresent, and there are Swedish specimens from the southernmost as well as northernmost provinces of that country (Skåne and Lapland).

Biology. A parasite of several species of *Strobilomyia* (Anthomyiidae; earlier referred to as *Lasiomma*). Females oviposit in developing *Larix* or *Picea* cones on trees in early summer (Fig. 4), and the parasitised larvae develop and fall to the ground to pupate in the ground litter layer late in the season. After hibernation, wasps hatch from the puparia (labels specify dates from March to June). Most museum specimens are reared, all come from coniferous forests or small patches thereof, including isolated seed orchards. No specimens have yet been obtained from Malaise traps or flight intercept traps, suggesting that vertical movement to tree-top level occurs soon after emergence, and horizontal movement of these wasps (including dispersal to the isolated stands mentioned) occurs at this height where little trapping occurs.

DISCUSSION

As noted, all specimens of Figitinae parasitising *Strobilomyia* maggots in cones in the Palearctic belong to a single species, *Amphithectus austriacus*. Until any evidence to the contrary is produced, all citations of *Melanips* as parasitoids of cone maggots are best considered as likely to be based on misidentifications or nomenclatural confusion.

A definite conclusion as to whether *Sarothrus* and *Amphithectus* should be synonymised or kept separate is not considered possible at this time. This would preferably be based on a phylogenetic analysis, which considers not just

the types of these genera but a broad sample of described and undescribed species from North America and also the eastern Palearctic. Vouchers from rearing from cones in North America need to be revised, and any biological data for *Sarothrus* sensu stricto would also be very interesting for this assessment.

The similar morphology of *Sarothrus* and *Amphithecus*, especially in terms of the metasomal hair patches and glabrous eyes, and their biology of attacking phytophagous flies, make them stand out as a distinct group within Figitinae, which we might call the “*Sarothrus* group” (which would tentatively also include the nominal genera *Sarothrioides* Belizin, *Paraschiza* Weld, *Ferpereira* Pujade-Villar and *Nebulovena* Pujade-Villar & Paretas-Martinez). These characteristics stand in contrast to the core Figitinae or “*Figites* group”, which share an overall morphology, including lack of metasomal hair patches but pubescent eyes, the habits of attacking calyptate hosts in ephemeral decomposing substrates (such as carrion and dung), and often but not always heavily striated sides of mesosoma, reduction of wing pubescence, and/or a scutellar spine. In terms of the phylogeny in Buffington et al. (2007), the “*Sarothrus* group” might perhaps be the sister of the “*Figites* group”, but as one *Amphithecus* was the sole representative of the former group included in the analysis, the results do not rule out the possibility of the “*Sarothrus* group” as a paraphyletic stem group to the latter.

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