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Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses

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Abstract

This study aimed to resolve the differences in the two currently used classifications of Mutillidae, which differ in many respects. Cladistic analyses of 101 genera and subgenera of Mutillidae (represented by females of 253 species and males of 260 species) and four outgroups (pepsine Pompilidae, anthoboscine Tiphiidae and both fedtschenkiine and sapygine Sapygidae) based on 230 morphological characters treated in various ways, produced most-parsimonious trees which were in broad agreement but differed in many details. Evaluation of these results led to the proposal of a compromise tree which reflected each proposed taxon as monophyletic, while trying to keep disruptions to the current classifications to a minimum. The result differs from both previous classifications, and proposes the recognition of eight subfamilies: Myrmosinae (with the tribes Kudakrumiini and Myrmosini), Pseudophotopsidinae, Rhopalomutillinae, Ticoplinae (with the tribes Smicromyrmillini and Ticoplini), Sphaeropthalminae (with the tribes Sphaeropthalmini, Dasymutillini **trib. n.**, and Pseudomethocini with the subtribes Euspinoliina **subtrib. n.** and Pseudomethocina), Myrmillinae, Dasylabrinae (with the tribes Apteromutillini **trib. n.** and Dasylabrini) and Mutillinae (with the tribes Ctenotillini **trib. n.**, Smicromyrmini, Mutillini with the subtribes Ephutina and Mutillina, and Trogaspidiini). Notably, Myrmosinae were consistently strongly supported as monophyletic with the remaining Mutillidae (disagreeing with a recent molecular analysis), and thus retained as a mutillid subfamily. The placements of all currently valid genera and subgenera in the proposed classification are provided.

Keywords

Biogeography, cladistics, new tribe, new subtribe, parsimony, polymorphism, Sapygidae

Introduction

The family Mutillidae (velvet-ants) includes approximately 4300 described species in 216 valid genera and 30 valid subgenera (Lelej 2007; Lelej and Brothers 2008; Aguiar et al. 2013, updated; Appendix 4 below), with many more species and genera yet to be described. Mutillids are parasitoids on hosts which are enclosed in some sort of container, such as hidden cells of burrowing or stem-nesting Hymenoptera, exposed mud or resin cells of other Hymenoptera, buried or exposed oothecae or hard cocoons of cockroaches, flies, moths, or even beetles in ants' nests (Brothers 1989; Brothers et al. 2000). Extreme sexual dimorphism is the rule; the females are invariably completely apterous with the mesosoma forming a fused box-like structure (although a few species have the pronotum articulated), and the males are almost all fully winged (but several genera demonstrate various degrees of wing reduction and mesosomal modification, from wings which are membranous but too small for flight, to wing stubs scarcely discernible under the tegulae but the mesosomal sutures retaining articulation, to complete absence of any trace of wings and varying degrees of reduction and fusion of mesosomal sutures to a situation where the mesosoma of males is essentially identical in form to that of females).

The higher classification of Mutillidae has changed considerably over time, but the first cladistic analysis of the aculeate Hymenoptera as a whole, by Brothers (1975), in which he proposed recognition of only three superfamilies (Chrysidoidea, Vespoidea and Apoidea), resulted from a focus on elucidating the relationships of the groups then considered to belong to Mutillidae and their relatives. The classification of Mutillidae presented there, based on 43 selected characters (from an initial 96) derived from examination of specimens from about 90% of the described genera, and groundplans for the putative subtaxa, included seven subfamilies: Myrmosinae (transferred there from Tiphiidae), Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Sphaeropthalminae (including the tribes Dasylabrini and Sphaeropthalmini with subtribes Sphaeropthalmina and Pseudomethocina), Myrmillinae, and Mutillinae (including the tribes Ephutini and Mutillini with subtribes Mutillina and Smicromyrmina) (Brothers 1975). Three groups which had been considered as mutillids were transferred to an expanded family Bradynobaenidae, as the subfamilies Typhoctinae, Chyphotinae and Apterogyninae. Gratifyingly, the classifications proposed in that paper were largely adopted, with minor adjustments as required by later discoveries. Subsequently, Lelej and Nemkov (1997) undertook an analysis of 15 taxa of mutillids (putative subfamilies and tribes), based on the 71 "best" of 89 characters, many different from those previously used at this level, and, instead of using groundplans, characters showing polymorphisms within taxa were coded as non-applicable; they proposed a classification recognizing 10 subfamilies: Myrmosinae, Kudakrumiinae, Pseudophotopsidinae, Ticoplinae (with the tribes Ticoplini and Smicromyrmillini), Rhopalomutillinae, Ephutinae (with the tribes Ephutini and Odontomutillini), Dasylabrinae, Sphaeropthalminae (with the tribes Sphaeropthalmini and Pseudomethocini), Myrmillinae and Mutillinae (with the tribes Mutillini, Trogaspidiini, Petersenidiini and Smicromyrmini). As part of a re-evaluation and expan-

sion of his 1975 paper, Brothers (1999) re-analyzed the data for Mutillidae, and concluded that Myrmosini and Kudakrumiini should be considered as tribes within the subfamily Myrmosinae. He also re-evaluated the characters used by Lelej and Nemkov (1997), correcting apparent coding errors and eliminating redundant characters, and upon analysis of the modified data found (unpublished) results more similar to his own, thus casting doubt on Lelej and Nemkov's (1997) scheme. Soon thereafter Mitchell and Brothers (2002) also validated two tribes (Ticoplini and Smicromyrmillini) in the Ticoplinae. Unfortunately, Brothers's intention to pursue further analyses were not realized. Much more recently, Pilgrim et al. (2008) undertook a molecular analysis based on four nuclear genes of 64 taxa across the entire Vespoidea, in which they concluded that the superfamily and some families were paraphyletic, and proposed recognition of six "vespoid" superfamilies (Formicoidea, Pompiloidea, Scolioidea, Tiphioidea, Thynnoidea and Vespoidea) and transfer of Myrmosinae from Mutillidae to its own family (Myrmosidae), both within Pompiloidea (with Pompilidae and Sapygidae), but they lacked specimens of most of the mutillid subfamilies and had only one of Myrmosinae, so the basis for their results was limited. Two broad analyses of the Hymenoptera as a whole, based on molecular data, have recently been published (Branstetter et al. 2017; Peters et al. 2017), but of necessity were limited in their representation of mutillids (one species of each of nine genera, and one species of each of two genera, respectively) and therefore of little relevance to the classification of the family as such.

Currently, there are thus two somewhat different classifications of Mutillidae being used (Fig. 1), discounting the suggestions by Pilgrim et al. (2008). Although the arrangement and taxonomic levels of the taxa near the bases of the trees is very similar (excepting the consideration of Myrmosinae to include Kudakrumiinae or not), the major differences between the schemes are as follows (DB = Brothers, LN = Lelej & Nemkov): DB considers Dasylabrini as a tribe within Sphaeropthalminae and sister to the remaining Sphaeropthalminae, but LN has Dasylabrinae as a subfamily sister to Ephutinae, and both sister to Sphaeropthalminae; DB considers Ephutini as a tribe within Mutillinae, and not closely related to *Odontomutilla* and relatives (which DB places in Mutillina), which are placed as a tribe within Ephutinae by LN; apart from the exclusion of Ephutinae from Mutillinae by LN, DB's subtribe Smicromyrmina is divided into three tribes (Trogaspidiini, Petersenidiini and Smicromyrmini) by LN, although retained in Mutillinae. These differences are obviously potentially confusing, specially when they occur in major manuals and catalogues; for example, DB's classification was used in a manual of world Hymenoptera (Brothers 1993), manuals of Neotropical Hymenoptera (Brothers 2006a, 2006b), a catalogue of Neotropical mutillids (but considering Myrmosidae as distinct) (Nonveiller 1990), and LN's classification was used in catalogues of Palaearctic and Oriental Mutillidae (Lelej 2002, 2005) and a catalogue of Malagasy Mutillidae (Brothers et al. 2011). Consequently, in 2008 Brothers contacted Lelej and suggested that they collaborate on a new, more comprehensive, analysis of mutillid diversity with the aim of deriving a revised single and mutually agreed classification. This paper reports the results of that collaboration. It is based entirely on morphological characters since genetic data are currently available only for

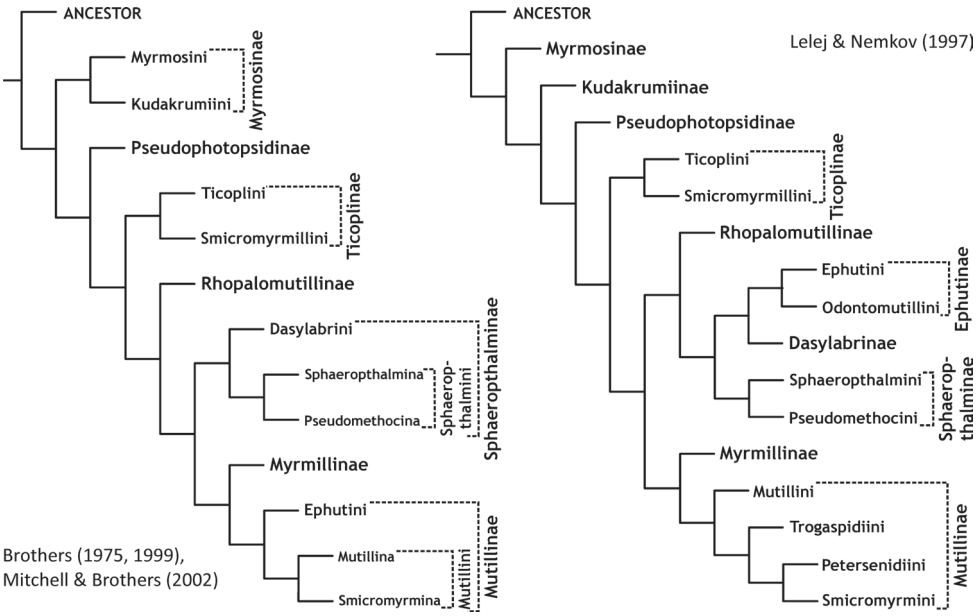


Figure 1. Competing current phylogenies and classifications of Mutillidae.

relatively few species of Mutillidae from a fairly limited spectrum of genera; collection of fresh specimens and their processing for genetic data across the sort of representation of genera available for morphological studies would also have been extremely difficult and expensive. It is hoped that the results obtained here will facilitate the choice of suitable exemplars for genetic analysis in future.

Materials and methods

Because of their extreme sexual dimorphism, we considered it essential to ensure that all terminals included in the study were known from both sexes, and preferably with at least one species represented by both sexes. We thus accumulated specimens of 101 sub/genera, including females of 253 species and males of 260 species of Mutillidae, and, as outgroups, we also included specimens of the three families which had previously been found to be those most closely related to Mutillidae in morphological analyses (Brothers 1975, 1999; Brothers and Carpenter 1993), Pompilidae (Pepsinae), Tiphiidae (Anthoboscinae) and Sapygidae (Fedtschenkiinae and Sapyginae) (Appendix 1). Most specimens are in Brothers's collection (DJBC, to be deposited in the Iziko South African Museum, Cape Town, SAMC, in due course) but several are in the Federal Scientific Center of East Asian Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia (IBSS) and a few are elsewhere. Species identifications were done by both authors or were checked when they had been done by others, using the most recent revisions and catalogues available. Appendix 1

also shows the placement of each sub/genus according to both current classifications. In the text, below, for brevity we do not provide the names of the authors of those taxa which are included in Appendix 1, but only for those which do not appear there, nor do we provide the original references for those names (they may be obtained from Lelej and Brothers 2008 and an update thereof which is in preparation). The sole exceptions are the names of the type genera for the new taxa proposed herein, for which authors, dates (Ashmead 1899, 1903; Bischoff 1920) and citations are provided, in accordance with the provisions and recommendations of the Code (International Commission on Zoological Nomenclature 1999).

We scored all specimens individually for 230 characters derived from those previously considered by Brothers (1975, 1999) and Lelej and Nemkov (1997) supplemented by others which had been used at the generic level in Mutillidae and a few newly discovered ones, comprising 783 different states; 7 characters applied to both sexes, 90 to females only, and 133 to males only (Appendix 2). Where apparently identical characters were duplicated as applicable to the different sexes separately (e.g. characters 65 and 160, 72 and 166), this was because the state distribution in the two sexes differed. We used genera (or subgenera) as the terminals, and scored any observed variation in character states within these as polymorphisms, since our interest was in estimating the relationships of the terminals at that level rather than individual species (which would also have produced an excessively large matrix with much missing data for species known from one sex only). The final data matrix is presented in Appendix 3.

Estimated phylogenies were derived under maximum parsimony using the Willi Hennig Society edition of TNT version 1.5 (Goloboff et al. 2003, 2016), using the default settings except allowing memory for 99 999 trees and 10 000 replicates under traditional searches. Relative group support, using GC (**G**roup present/**C**ontradicted) values, which are frequency differences (Goloboff et al. 2003), was estimated by symmetric resampling using the default settings and traditional searches, but 10 000 replicates; when evaluating numbers of groups with or without resampling support, the trivial always-supported sister-group relationship of the first outgroup terminal with the remainder was ignored. Although positive GC values indicate that the relevant group was found in over half of the resampled trees, and therefore had majority support, the degree of such support is indicated by the GC values obtained. Somewhat arbitrarily, we have described the level of support as follows: 1–15 = very low; 16–30 = low; 31–50 = moderate; 51–70 = good; 71–85 = high; 86–100 = very high.

Several versions of the data were analysed, investigating the effects of additivity of character states, the influence of polymorphisms, and sexual differences: a) all terminals, considering all characters as non-additive/unordered; b) all terminals, considering many characters (those for which reasonable evolutionary sequences could be specified) as additive/ordered (as in Appendix 2); c) all terminals, considering many characters as additive/ordered, but with all terminals duplicated and recoded by allocating the lowest-numbered states to the first terminal and the highest-numbered states to the second terminal (distinguished by adding "1" and "2" to the taxon name, respectively) for all characters showing polymorphisms within the original terminals; d)

all terminals, considering many characters as additive/ordered, but all characters which showed polymorphisms in at least 10% of the terminals (see Appendix 2) deleted; e) females only, considering all characters as non-additive/unordered; f) females only, considering many characters as additive/ordered; g) males only, considering all characters as non-additive/unordered; h) males only, considering many characters as additive/ordered. All data sets were analysed under equal weights and also using implied weighting (Goloboff et al. 2003) which reduces the effects of the more-homoplasious characters, applying several values of the concavity index (*k*) set using a modification of the unpublished *setK* script derived by J. Salvador Arias. Only those results found when assigning the least homoplasious characters 5 times the weight of the most-homoplasious ones ($N = 5$) are reported, however, since those results generally identified single trees which were one of the most-parsimonious ones found under equal weighting or a single tree at most one step longer; heavier weighting also generally had little effect on the identification of the major groups, mainly affecting arrangements within them. WinClada version 1.00.08 (Nixon 2002) was used for generation of tree plots and optimizations of character-state changes (as "fast"/"accelerated", except for characters considered unlikely to show reversals (Dollo's Law) which were optimized individually as "slow"/"delayed") (see Appendix 2). For all analyses, testing the influence of choice of outgroup showed that choosing *Hemipepsis* (Pompilidae) or *Anthobosca* (Tiphiidae) had no influence on the results, and both taxa are thus shown in a trichotomy with Sapygidae + Mutillidae at the base of each tree. Figures of trees were produced using CorelDRAW Graphics Suite X8.

Since the results obtained for the various analyses differed in several respects, although generally reflecting a similar basic pattern, and it was not possible to determine which method was most likely to produce the "best" result, it was necessary to develop a compromise tree upon which the proposed classification could be based. Two basic principles were used in its construction. First, arrangements which would result in major disruptions to the currently used classifications were minimised, so as to promote nomenclatural stability as far as possible; this required a marked change in topology in only one instance. Second, paraphyletic groups for which the component terminals were separated by branches with only few and/or weak (homoplasious) apomorphies were rearranged so as to be reflected as monophyletic, also taking into account whether such groupings had been found to be supported by resampling in any of the analyses. Given the extent of homoplasy and polymorphism found for many of the characters, it was considered reasonable for the final compromise tree to be less than 1% longer than the comparable most parsimonious trees. Further details about the actual rearrangements proposed, and justifications for them, are provided below.

Results

The initial analysis of all terminals based on both sexes was done employing minimal assumptions (all characters non-additive and equally weighted). The number of most-

parsimonious trees (MPTs) found was 618 (length = 2633, ci = 0.20, ri = 0.59), and the strict consensus of these trees is shown in Fig. 2. It is evident that, although several groups are clearly shown, the relationships of many terminals within those groups are unresolved, and various of the major groups are not supported by resampling (only 62 groups (79.5%) had positive GC values, as compared to 78 in the resampling analysis). There is nevertheless reasonable structure towards the base of the tree, with five monophyletic groups arising in turn and in agreement with the results of previous studies (Sapygidae as sister to Mutillidae, Myrmosinae, Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae), and all supported by moderate to high GC values. The remainder of the Mutillidae also form a moderately well supported monophyletic group, but the first three genera (*Liotilla–Brachymutilla*, all of which have apterous males) form a paraphyletic group, and the subsequent terminals form a monophyletic group with very low support. The next three genera (*Euspinolia–Hoplocrates*) form a monophyletic group with very high support, apparently as sister to the remainder of the mutillids, but this with no support. Apicad, there are four supported monophyletic groups: the first (*Cystomutilla–Hoplomutilla*) has very low support but corresponds to a grouping recognized in both existing classifications (Spheropthalmini/ae, but here excluding *Euspinolia–Hoplocrates*), and shows some internal structure (monophyletic groups comprising *Cystomutilla–Scaptodactyla*, and *Ancistrotilla–Hoplomutilla* within which two further monophyletic groups occur, viz. *Cephalomutilla–Tobantilla* and *Dimorphomutilla–Hoplomutilla*); the second monophylum (*Chrestomutilla–Seyrigilla*) and the third (*Dasylabroides–Tricholabiodes*) each have very low support, and these groups together comprising the previously recognized Dasylabrini/ae; the fourth monophyletic group has low support and comprises the remainder of the Mutillidae (*Viereckia–Wallacidia*), and comprises two monophyla in turn (*Viereckia–Platymyrmilla*, the previously recognized Myrmillinae with low support, and *Pristomutilla–Wallacidia*, the Mutillinae with very low support, within which, discounting *Pristomutilla*, there are two supported monophyla (*Mimecomutilla s.s.–Ctenotilla* with high support, and *Promecilla–Wallacidia* with very low support, neither previously recognized as taxa). The separation of *Mutilla–Tropidotilla* and *Ephuta–Yamanetilla* as two distinct monophyletic groups, with very low to high support, accords more closely with LN's arrangement than DB's. The monophyletic *Ancanthomutilla–Wallacidia* group includes a further monophyletic group (*Amblotropidia–Wallacidia*), both with low support.

Still considering all characters non-additive, the effect of implied weighting was then tested, and using $N = 5$ ($k = 60$), a single fully resolved tree was found which was only one step longer than the MPTs produced by the equal-weights analysis (raw length = 2634, ci = 0.20, ri = 0.59) (Fig. 3). Here too some major groups were found, but again several were not supported by resampling, although the proportion of groups so supported was greater than for the analysis using equal weights (64 supported groups (84.2%) compared with 76 for resampling). The basic pattern was similar to that for the equally weighted analysis, except, of course, that the tree was fully resolved; the support values were generally slightly higher than previously. The Sphaeropthalmini/ae group was better supported (although still at a very low level), Dasylabrini/ae remained

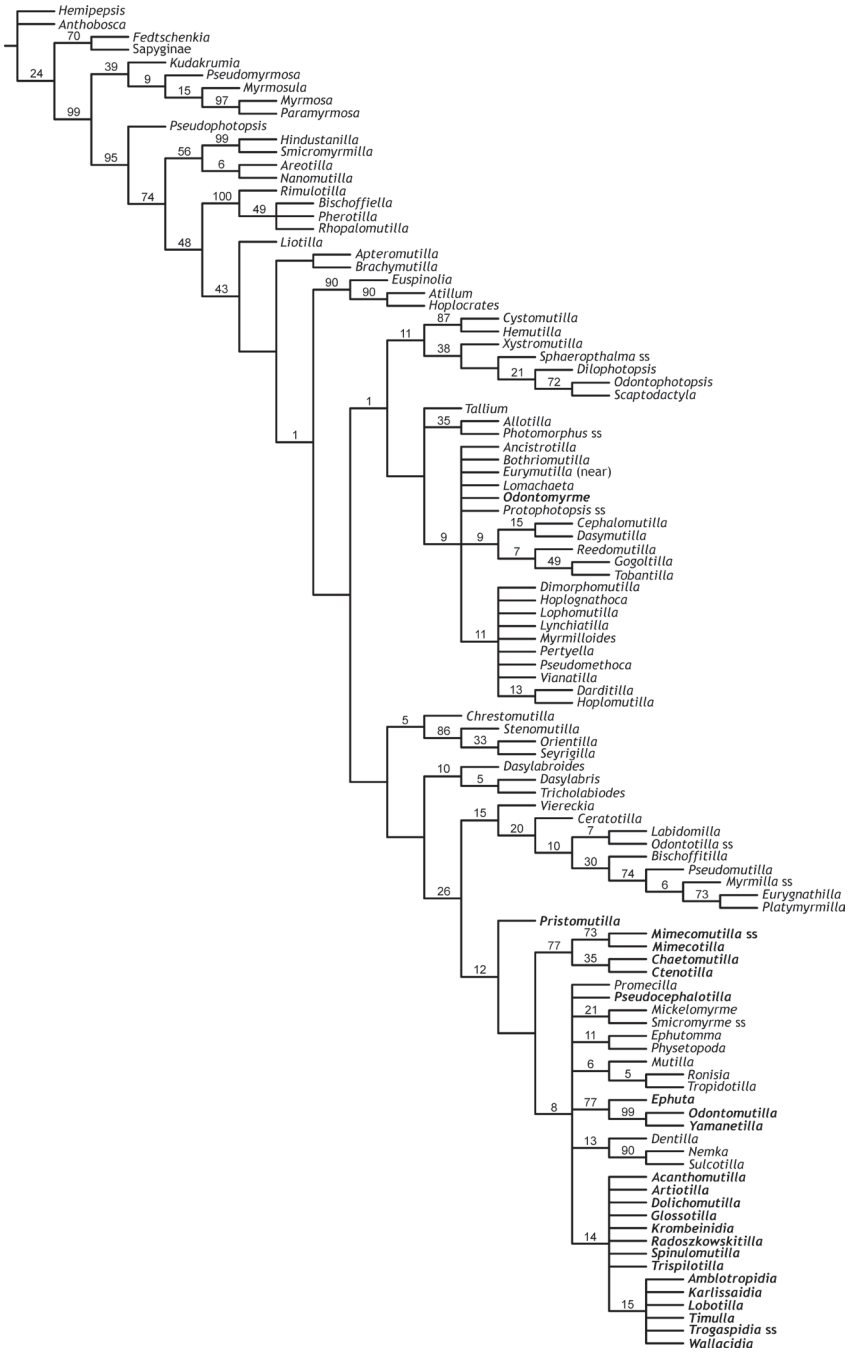


Figure 2. Strict consensus of 618 most-parsimonious trees (length = 2633, ci = 0.20, ri = 0.59), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters all non-additive and equally weighted. Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

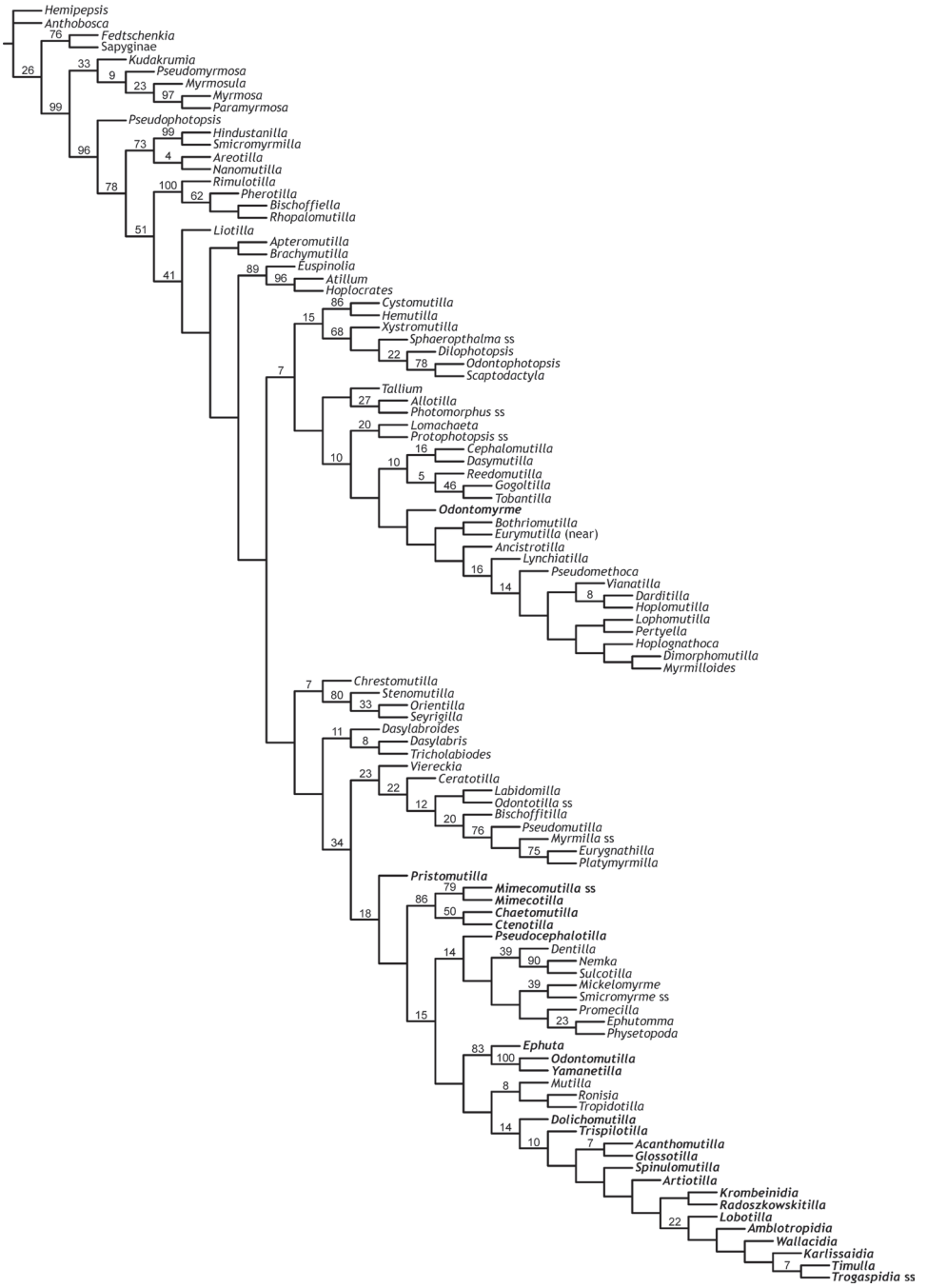


Figure 3. Single most-parsimonious tree (raw length = 2634, ci = 0.20, ri = 0.59), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters all non-additive and with implied weighting (N = 5, k = 60). Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

paraphyletic, and, in addition to the *Mimecomutilla s.s.–Ctenotilla* group, additional structure in the Mutillinae showed a monophyletic group (*Pseudocephalotilla–Physetopoda*, with very low support) that corresponds to the restricted sense of Smicromyrmini of LN. Furthermore, the *Mutilla–Tropidotilla* group is shown here as sister to the major *Dolichomutilla–Trogaspidia s.s.* group (although with no support), and the *Ephuta–Yamanetilla* group as sister to these groups together. The same two apical monophyletic groups (here *Dolichomutilla–Trogaspidia s.s.* and *Lobotilla–Trogaspidia s.s.*) were found as in the equally weighted analysis.

Analysis of all terminals for both sexes but considering all characters additive (except for those where a logical evolutionary sequence could not be postulated, see Appendix 2) was then undertaken. Considering all characters of equal weight resulted in 38 MPTs (length = 2828, ci = 0.19, ri = 0.61), of which the strict consensus is shown in Fig. 4. As for the non-additive analysis, several groups were identified, but many were unresolved or not supported by resampling (only 55 groups (71.4%) had positive GC values, as compared to 77 in the resampling analysis). The same "basal" groups were found, in the same sequence, as in the non-additive analysis, but the Sphaeropthalmini/ae was fragmented into several unrelated components (but with the *Cystomutilla–Scaptodactyla* and the *Dimorphomutilla–Hoplomutilla* groups each with moderate to low support), the Dasylabrini/ae (*Dasylabris–Seyrigilla*) was now apparently monophyletic (but without support), and the Myrmillinae was fragmented, but the Mutillinae (*Pristomutilla–Trogaspidia s.s.*) was monophyletic with low support, with the *Mimecomutilla s.s.–Ctenotilla* group with high support, *Ronisia–Yamanetilla* forming a monophyletic group with very low support (instead of two distinct groups), and the *Amblotropidia–Trogaspidia s.s.* group with very low support.

When implied weighting was applied ($N = 5$, $k = 81$), a single tree was found, one of the original MPTs (raw length = 2828, ci = 0.19, ri = 0.61) (Fig. 5). Again, several major groups were found but sometimes with no resampling support (69 supported groups (84.1%) compared with 82 for resampling), although many more were supported than in the equal-weights analysis. Again, the "basal" groupings were the same as for the other analyses, and the general arrangement of terminals and groups was similar to that for the weighted non-additive analysis, except that Dasylabrini/ae (*Dasylabroides–Seyrigilla*) was shown as monophyletic (although without resampling support), the restricted-sense Smicromyrmini now excluded *Pseudocephalotilla* and *Promecilla* (making it paraphyletic), and *Dolichomutilla* plus the monophyletic *Ronisia–Yamanetilla* together formed a monophyletic group (although with no support). This tree was preferred for further comparisons because it was one of the MPTs found in the equal-weights analysis, and showed more of the major subtaxa as monophyletic than the non-additive analyses (a tree of identical topology but with all characters non-additive had length = 2646, ci = 0.20, ri = 0.59). Nevertheless, if one considers that groupings without positive resampling support are unreliable, redrawing the tree with such unsupported internodes as collapsed (Fig. 6), demonstrates that many of the groups contain unresolved components.

Analysis of the double-sized matrix (with duplicated and recoded terminals to explore polymorphisms, see above) under equal weights produced 98 MPTs (length = 3822, ci

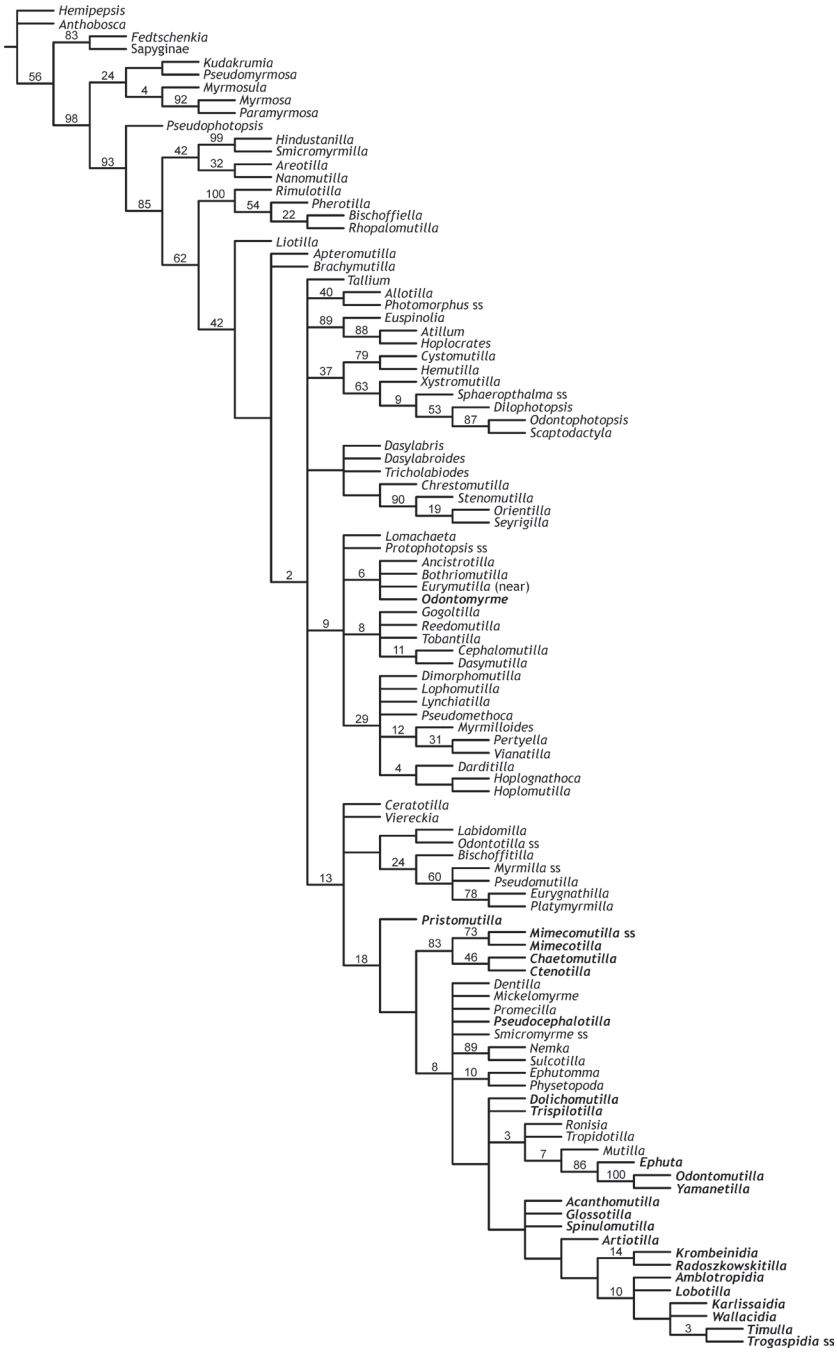


Figure 4. Strict consensus of 38 most-parsimonious trees (length = 2828, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters many additive and all equally weighted. Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

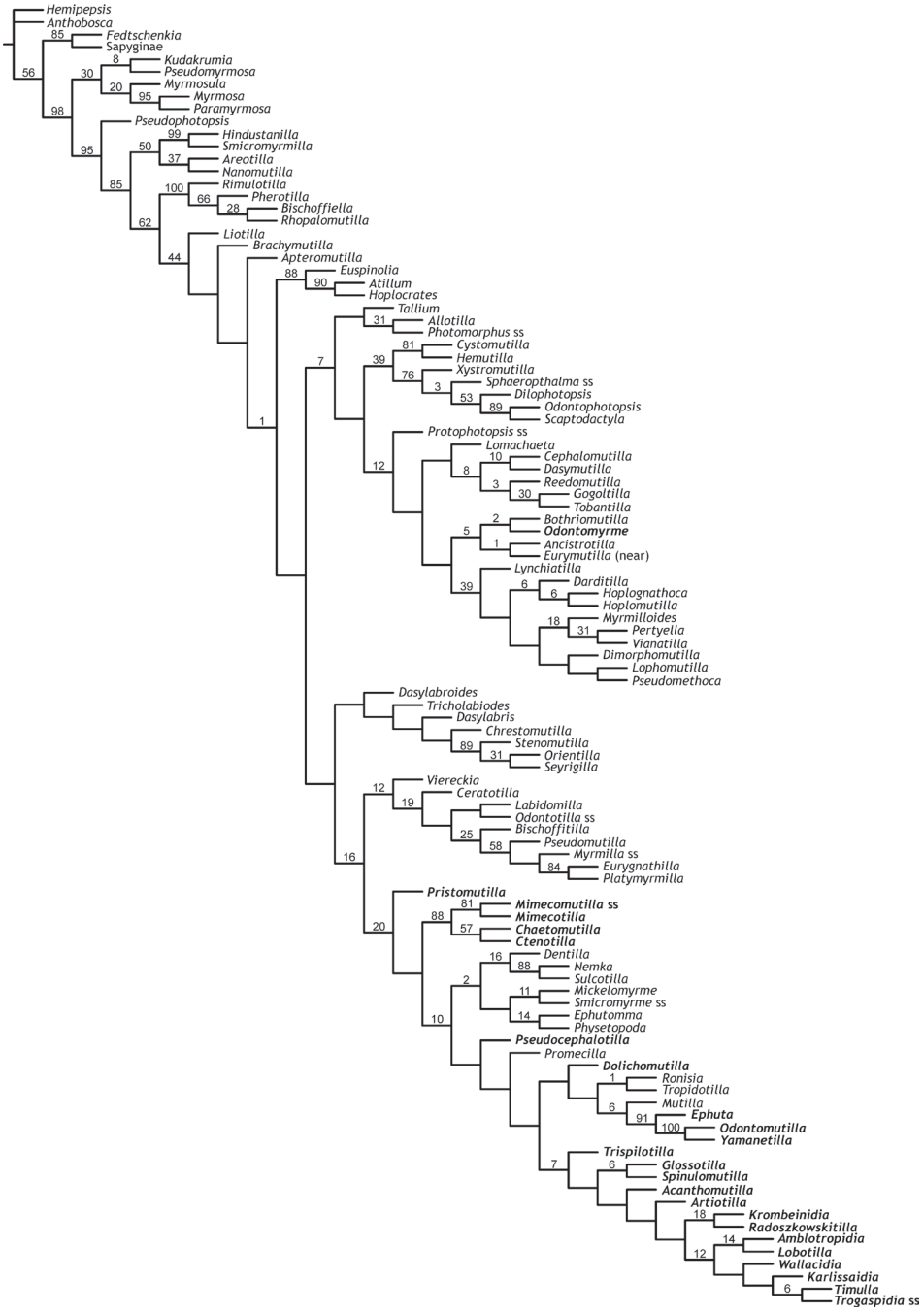


Figure 5. Single most-parsimonious tree (raw length = 2828, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters many additive and all with implied weighting (N = 5, k = 81). Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

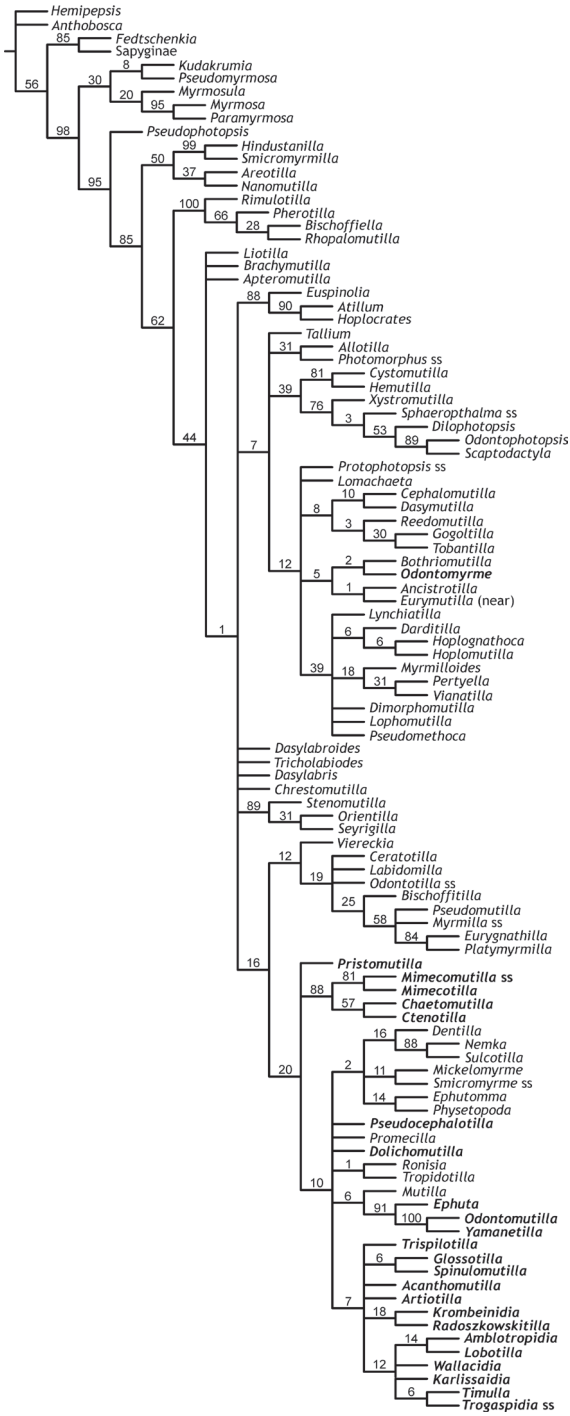
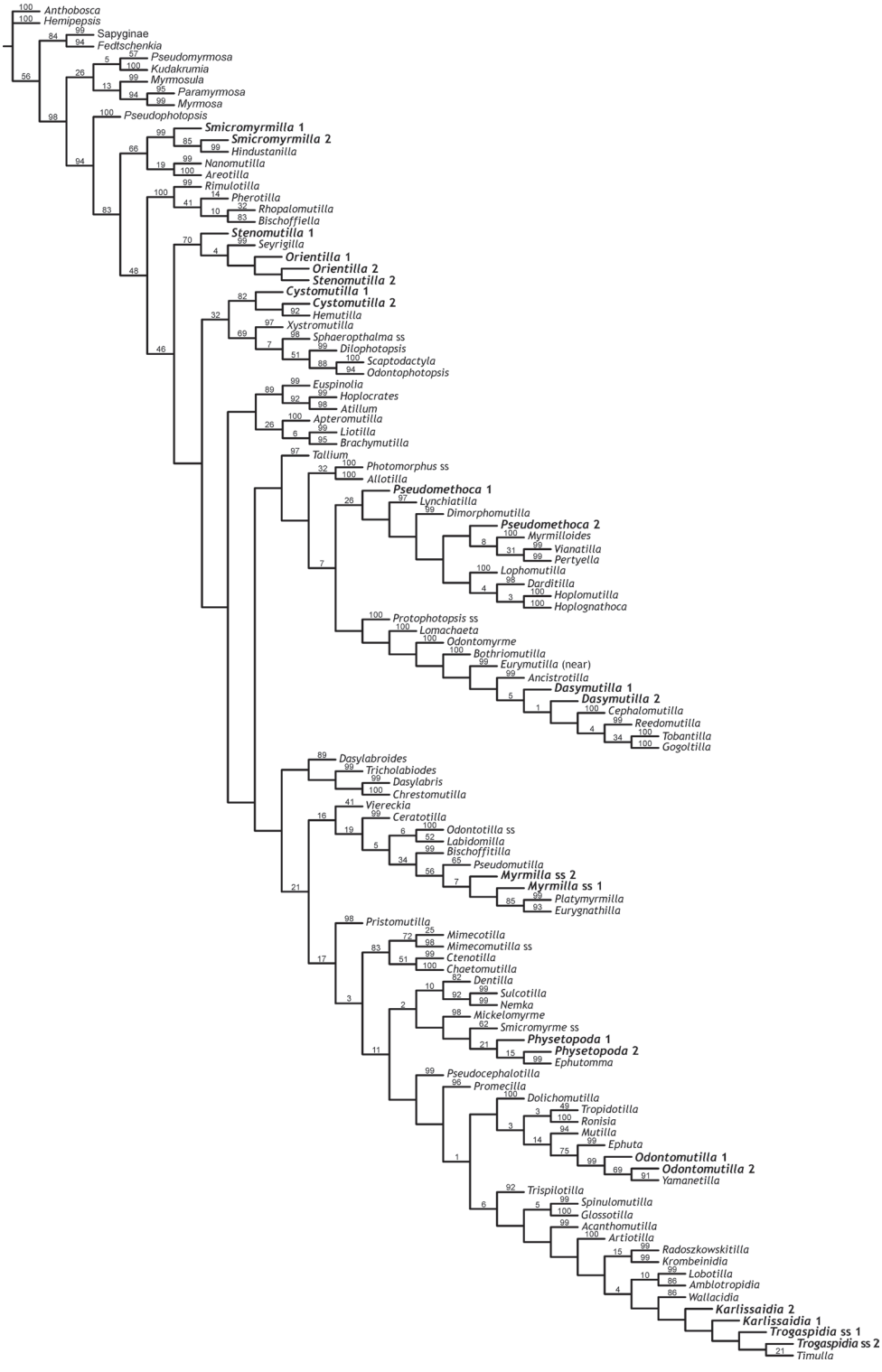


Figure 6. Most-parsimonious tree (see Fig. 5) with branches not supported by resampling (i.e., without positive GC values) collapsed. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).


Anthobosca
Hemipepsis
Sapyginae
Fedtschenkia
Pseudomyrmosa
Kudakrumia
Myrmosula
Paramyrmosa
Myrmosa
Pseudophotopsis
Smicromyrmilla 1
Smicromyrmilla 2
Hindustanilla
Nanomutilla
Areotilla
Rimulotilla
Pherotilla
Rhopalomutilla
Bischoffiella
Stenomutilla 1
Seyrigilla
Orientilla 1
Orientilla 2
Stenomutilla 2
Cystomutilla 1
Cystomutilla 2
Hemutilla
Xystromutilla
Sphaeropthalma ss
Dilophotopsis
Scaptodactyla
Odontophotopsis
Euspinolia
Hoplocrates
Atillum
Apteromutilla
Liotilla
Brachymutilla
Tallium
Photomorphus ss
Allotilla
Pseudomethoca 1
Lynchiatilla
Dimorphomutilla
Pseudomethoca 2
Myrmilloides
Vianatilla
Pertyella
Lophomutilla
Darditilla
Hoplomutilla
Hoplognathoca
Protophotopsis ss
Lomachaeta
Odontomyrme
Bothriomutilla
Eurymutilla (near)
Ancistrotilla
Dasymutilla 1
Dasymutilla 2
Cephalomutilla
Reedomutilla
Tobantilla
Gogoltilla
Dasylabroides
Tricholabiodes
Dasylabris
Chrestomutilla
Viereckia
Ceratotilla
Odontotilla ss
Labidomilla
Bischoffitilla
Pseudomutilla
Myrmilla ss 2
Myrmilla ss 1
Platymyrmilla
Eurygnathilla
Pristomutilla
Mimecotilla
Mimecomutilla ss
Ctenotilla
Chaetomutilla
Dentilla
Sulcotilla
Nemka
Mickelomyrme
Smicromyrme ss
Physetopoda 1
Physetopoda 2
Ephutomma
Pseudocephalotilla
Promecilla
Dolichomutilla
Tropidotilla
Ronisia
Mutilla
Ephuta
Odontomutilla 1
Odontomutilla 2
Yamanetilla
Trispilotilla
Spinulomutilla
Glossotilla
Acanthomutilla
Artiotilla
Radoszkowskitilla
Krombeinidia
Labotilla
Amblotropidia
Wallacidia
Karlissaidia 2
Karlissaidia 1
Trogaspidia ss 1
Trogaspidia ss 2
Timulla

= 0.14, ri = 0.75), and implied weighting (N = 5, *k* = 169) found one of these trees. Fig. 7 shows that tree, but with those pairs of terminals which were monophyletic collapsed into a single terminal each (the degree to which such collapsed terminals are polymorphic can be estimated from their GC values), and only those pairs of terminals which came out as not monophyletic having both components shown. Discounting the GC values for the monophyletic combined terminals, this tree shows 73 groups supported by resampling, 84.9% of those with positive GC values (86) in the resampling analysis. The arrangements and delimitations of the basal groups were again the same as for the other analyses. However, when compared with the tree in Fig. 5, the two components of the Dasylabrini/ae (*Stenomutilla* 1–*Stenomutilla* 2 and *Dasylabroides*–*Chrestomutilla*) were dissociated and apparently far apart on the tree (although it should be noted that none of the intervening internodes had any resampling support), the Sphaeropthalmini/ae was fragmented (although again without support), and the *Euspinolia*–*Atillum* and *Apteromutilla*–*Brachymutilla* groups together formed an unsupported monophyletic group (with each of those groups themselves being monophyletic with high to low support). The relationships of the Myrmillinae and Mutillinae were essentially unchanged. The terminals found not to be monophyletic are discussed under their relevant groups in the final proposed classification below.

When the reduced matrix (198 instead of 230 characters, those showing polymorphisms in at least 10% of the terminals having been deleted) was analysed under equal weights, 1330 MPTs (length = 2023, ci = 0.21, ri = 0.63) were found; using implied weighting (*N* = 5, *k* = 81), a single tree was found (length = 2024, ci = 0.21, ri = 0.63), only one step longer than the equal-weight MPTs (Fig. 8); it included 77.6% of the groups supported by resampling (59 versus 76). When compared with Fig. 5, it was evident that most groupings were essentially the same, but the delimitation of subgroups within the Mutillinae had been destroyed (except for the *Ctenotilla*–*Mimecotilla* group which had very high support).

In order to explore the degree to which the two sexes produced similar results (the tree/s found for each sex separately should at least be compatible and not contradictory if they actually are reflections of the evolutionary histories of the terminals) the characters of females and of males were analysed separately (seven characters applied to both sexes and so were included in both matrices). Analysis of the females (97 characters) considering all characters non-additive and of equal weight produced 358 MPTs (length = 1052, ci = 0.21, ri = 0.59), and under implied weighting (*N* = 5, *k* = 53) a single tree was found (raw length = 1057, ci = 0.20, ri = 0.59), five steps longer than the MPTs. When most characters were considered additive and all of equal weight 68 MPTs were found (length = 1131, ci = 0.19, ri = 0.61). Under implied weighting (*N* = 5, *k* = 81)

Figure 7. Single most-parsimonious tree (raw length = 3822, ci = 0.14, ri = 0.75), of 101 sub/genera of Mutillidae and 4 outgroups (but each duplicated and recoded so as to reflect maximal character-state differences for polymorphisms, and taxa retained as monophyletic collapsed in the figure, see text), both sexes, 230 characters many additive and all with implied weighting (N = 5, k = 169). Group support (GC) values shown for all groups supported by resampling. Names in bold are of "terminals" shown not to be monophyletic.

Figure 8. Single most-parsimonious tree (raw length = 2024, ci = 0.21, ri = 0.63), of 101 sub/genera of Mutillidae and 4 outgroups both sexes, 198 characters (32 of the original 230 deleted, those found to be polymorphic in at least 10% of terminals) many additive and all with implied weighting (N = 5, k = 81). Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

a single tree was found (length = 1134, ci = 0.19, ri = 0.61), only three steps longer than the MPTs (Fig. 9); it included 79.0% of the groups supported by resampling (49 versus 62). Analysis of the males (140 characters) considering all characters non-additive and of equal weight produced 60 MPTs (length = 1508, ci = 0.21, ri = 0.62), and under implied weighting ($N = 5$, $k = 60$) two trees were found (raw length = 1510, ci = 0.21, ri = 0.62), each two steps longer than the MPTs. When most characters were considered additive and all of equal weight 1714 MPTs were found (length = 1621, ci = 0.20, ri = 0.63). Under implied weighting ($N = 5$, $k = 71$) a single tree was found (length = 1622, ci = 0.20, ri = 0.63), only one step longer than the MPTs (Fig. 10); it included 80.3% of the groups supported by resampling (53 versus 66), slightly more than the analysis of females. Comparison of the results for females (Fig. 9) with those for males (Fig. 10) showed many discrepancies, although the broad patterns found in the full analyses were generally evident. Both showed Mutillinae as monophyletic (although *Pristomutilla* females were excluded from it) but the internal groupings differed considerably; in particular, males showed a monophyletic group (*Ephuta–Yamanetilla* plus *Mutilla–Tropidotilla*, the latter including *Dolichomutilla*) but females had *Ronisia*, *Tropidotilla* and *Mutilla* (here monophyletic with *Ctenotilla*) scattered and well separated from the *Ephuta–Yamanetilla* group and from *Dolichomutilla*. Males showed Myrmillinae as monophyletic, but females excluded *Ceratotilla–Viereckia* from it and instead showed a monophyletic group comprising the remainder of the Myrmillinae (*Labidomilla–Platymyrmilla*) plus the *Euspinolia–Hoplocrates* group, but with very low support. Females of *Liotilla*, *Brachymutilla* and *Apteromutilla* were scattered into other groups, but their males formed a monophyletic group with good support, and apparently sister to the *Euspinolia–Hoplocrates* group. Females of Dasylabrini/ae formed three neighbouring groups (*Brachymutilla–Stenomutilla*, *Dasylabroides–Tricholabiodes* and *Apteromutilla*), but males were scattered into separate parts of the tree (monophyletic *Stenomutilla–Seyrigilla* and *Apteromutilla–Liotilla*, and a paraphyletic placement of *Dasylabroides* + *Tricholabiodes*, *Chrestomutilla* and *Dasylabris*). The many discrepancies between the results for females and males demonstrated that their character evolution was likely driven by different selection pressures and adaptations. This was also influenced by the consolidation of the mesosomal components into a single rigid box-like structure in most females which limited the variation observed and the potential number of informative characters. Males, by contrast, generally had many complex characters of the mesosoma, including the wings, providing a rich source of information, but this was limited in those terminals where the wings had been much reduced or lost, or the mesosoma had become fused as in the females.

Discussion

The results outlined above, as well as additional permutations which were tested, indicate that the structure near the base of the phylogeny is generally supported by a variety of analyses, and indicates a monophyletic Mutillidae, with the generally

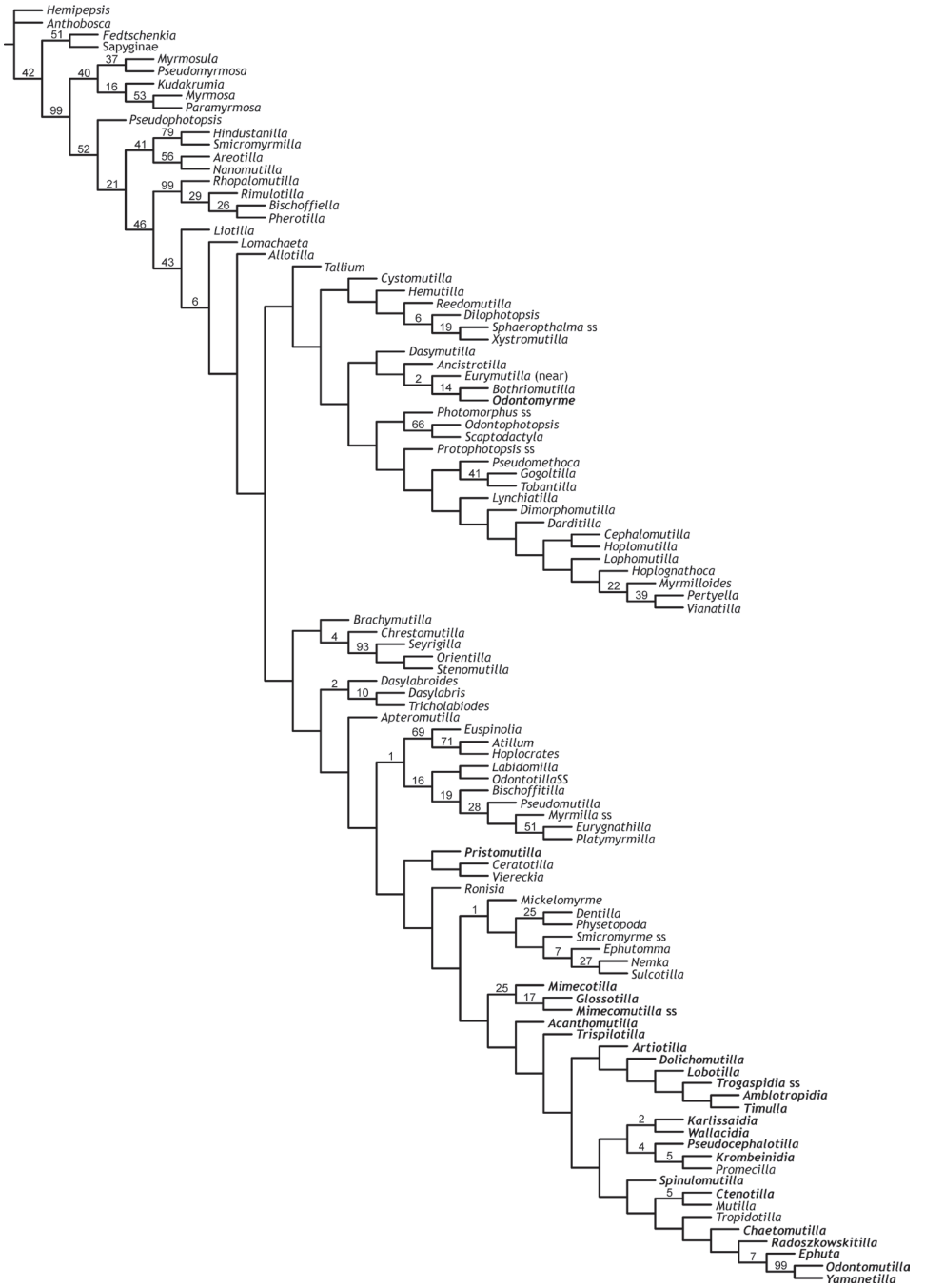


Figure 9. Single most-parsimonious tree (raw length = 1134, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, females only, 97 characters many additive and all with implied weighting (N = 5, k = 81). Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

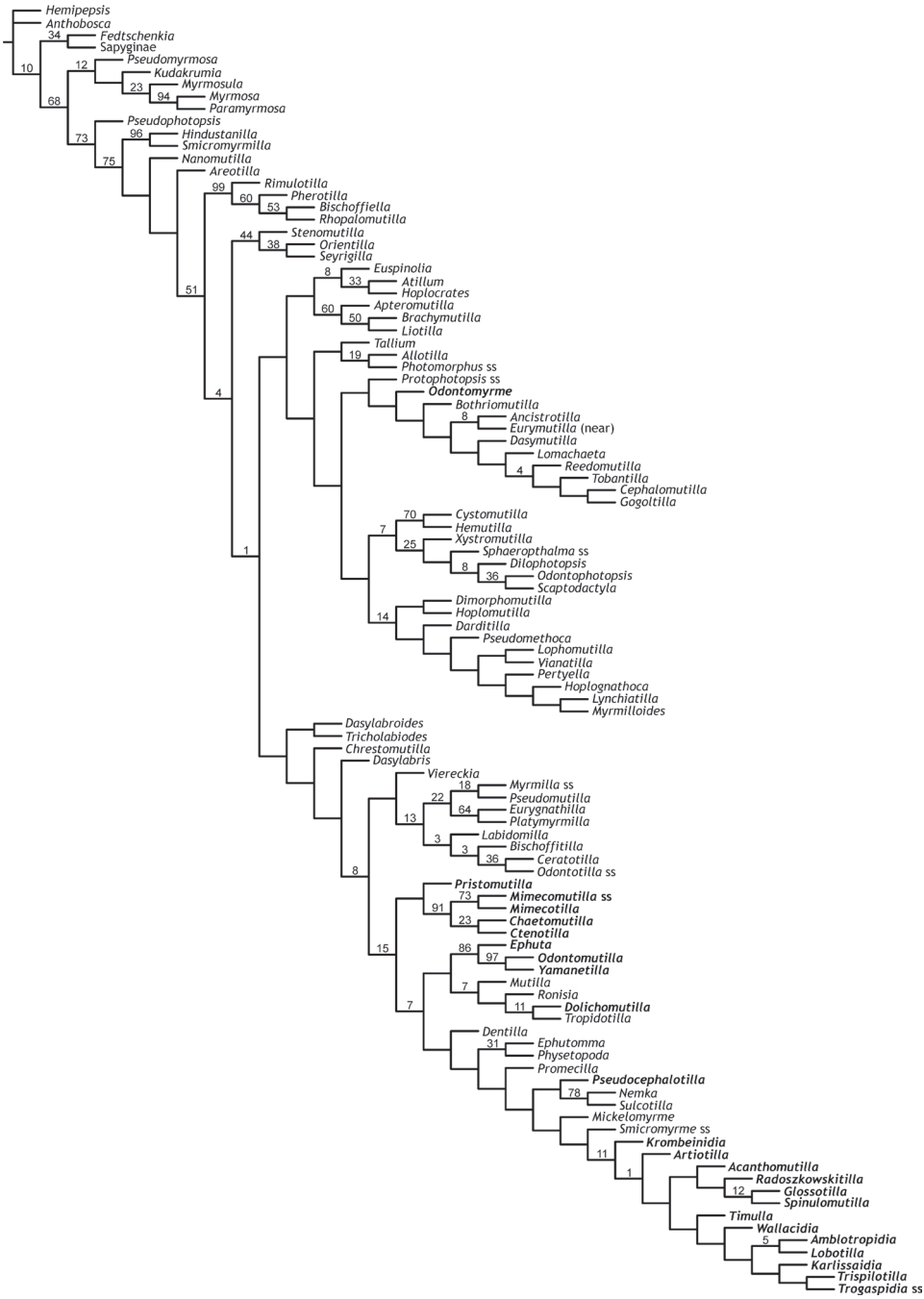


Figure 10. Single most-parsimonious tree (raw length = 1622, ci = 0.20, ri = 0.63), of 101 sub/genera of Mutillidae and 4 outgroups, males only, 140 characters many additive and all with implied weighting (N = 5, k = 71). Group support (GC) values shown for all groups supported by resampling. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

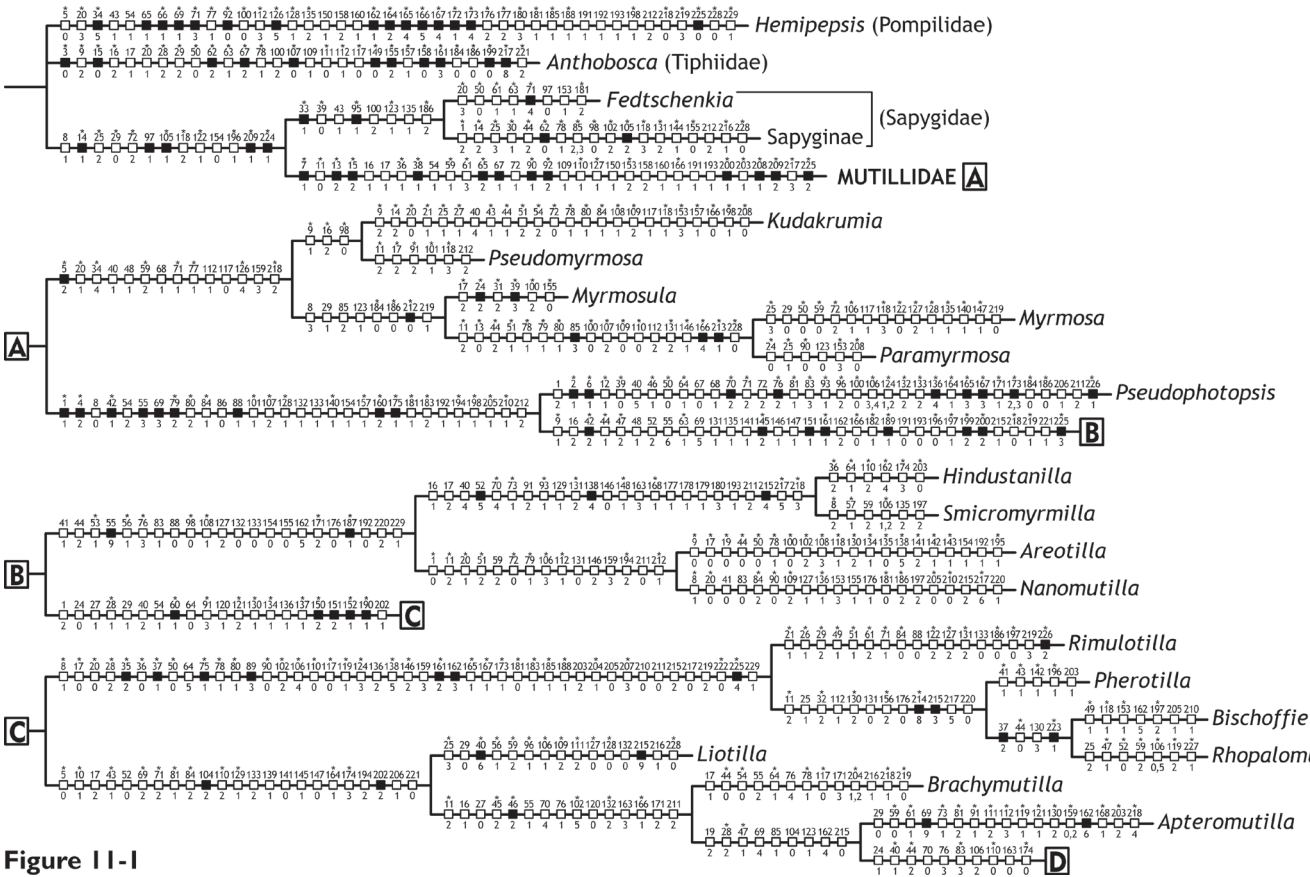


Figure 11-1

Figures 11-1 to 11-5. Preferred most-parsimonious tree (see Fig. 5) showing distribution of characters (upper numbers) and states (lower numbers) optimized as in Appendix 2. Asterisks (*) indicate character states unambiguously placed (position not changing under any optimization). Solid hashmarks indicate unique state changes, and open hashmarks are homoplasies. Letters within boxes indicate breaks in branches to enable effective layout. [continued over 5 pages]

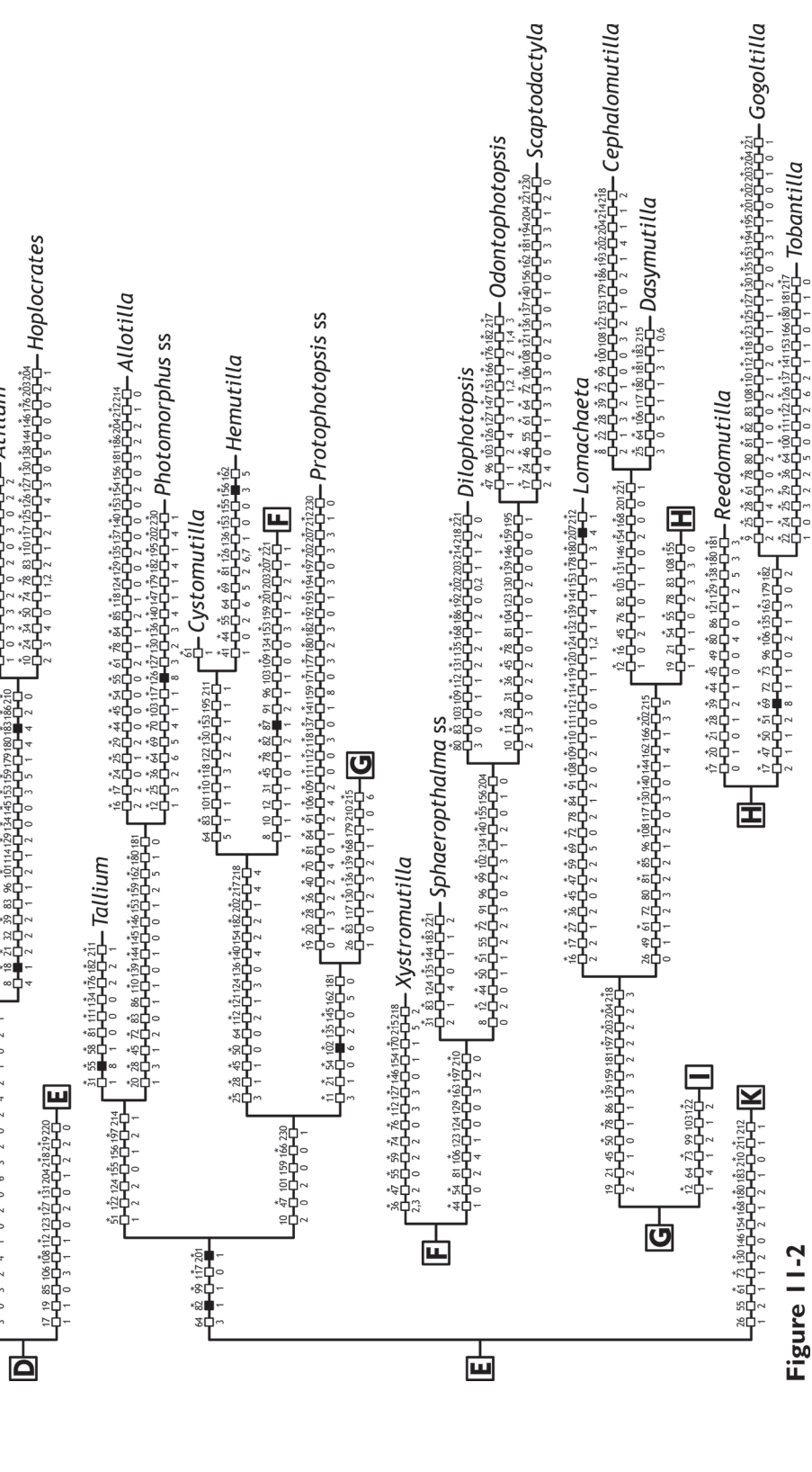

Euspinolia
Atillum
Hoplocrates
Tallium
Allotilla
Photomorphus ss
Cystomutilla
Hemutilla
Protophotopsis ss
Xystromutilla
Sphaeropthalma ss
Dilophotopsis
Odontophotopsis
Scaptodactyla
Lomachaeta
Cephalomutilla
Dasymutilla
Reedomutilla
Gogoltilla
Tobantilla
D
E
F
G
H
I
K

Figure 11-2

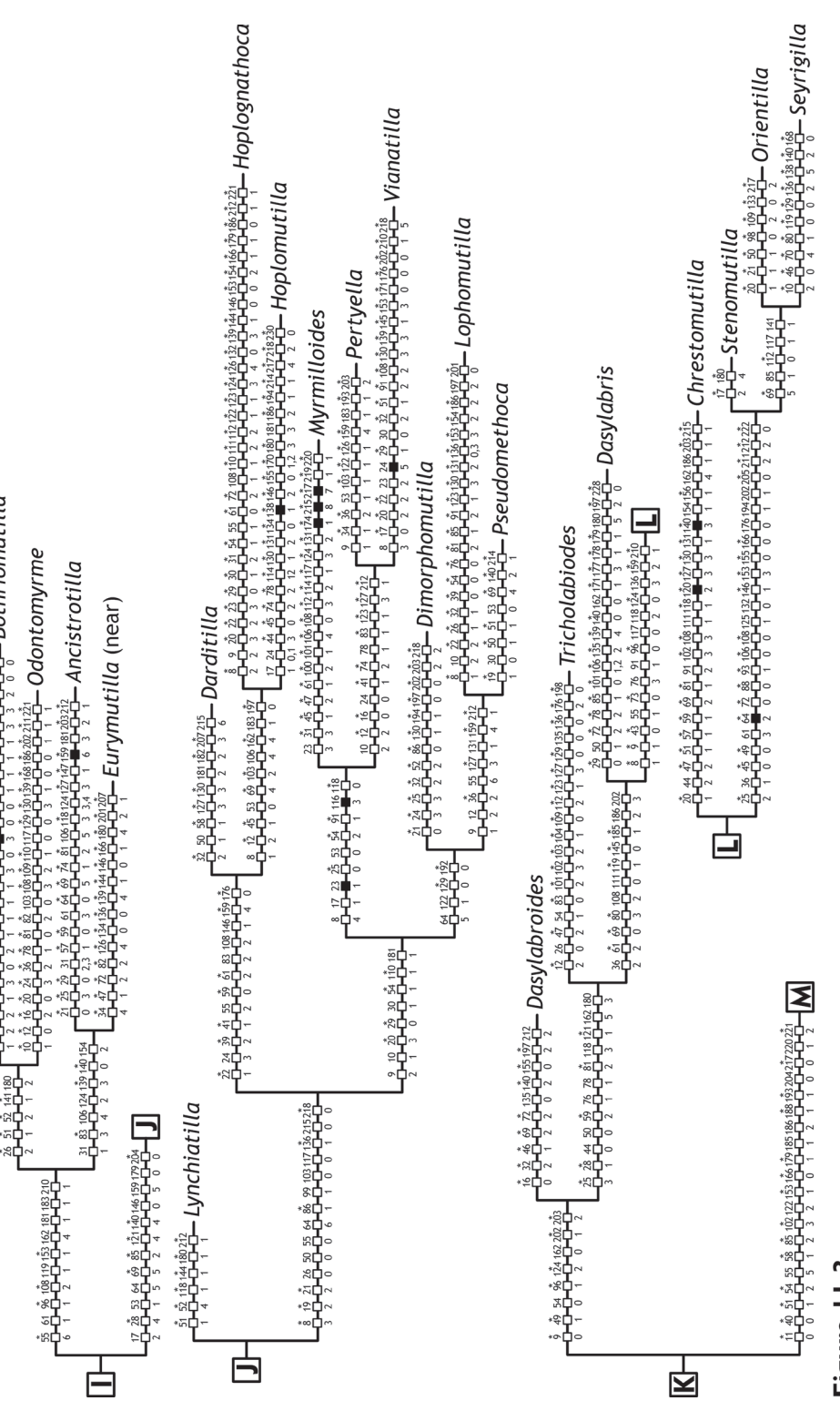

Bothriomutilla
Odontomyrme
Ancistrotilla
Eurymutilla (near)
Lynchiatilla
Darditilla
Hoplognathoca
Hoplomutilla
Myrmilloides
Pertyella
Vianatilla
Dimorphomutilla
Lophomutilla
Pseudomethoca
Dasylabroides
Tricholabiodes
Dasylabris
Chrestomutilla
Stenomutilla
Orientilla
Seyrigilla
I
J
K
L
M

Figure 11-3

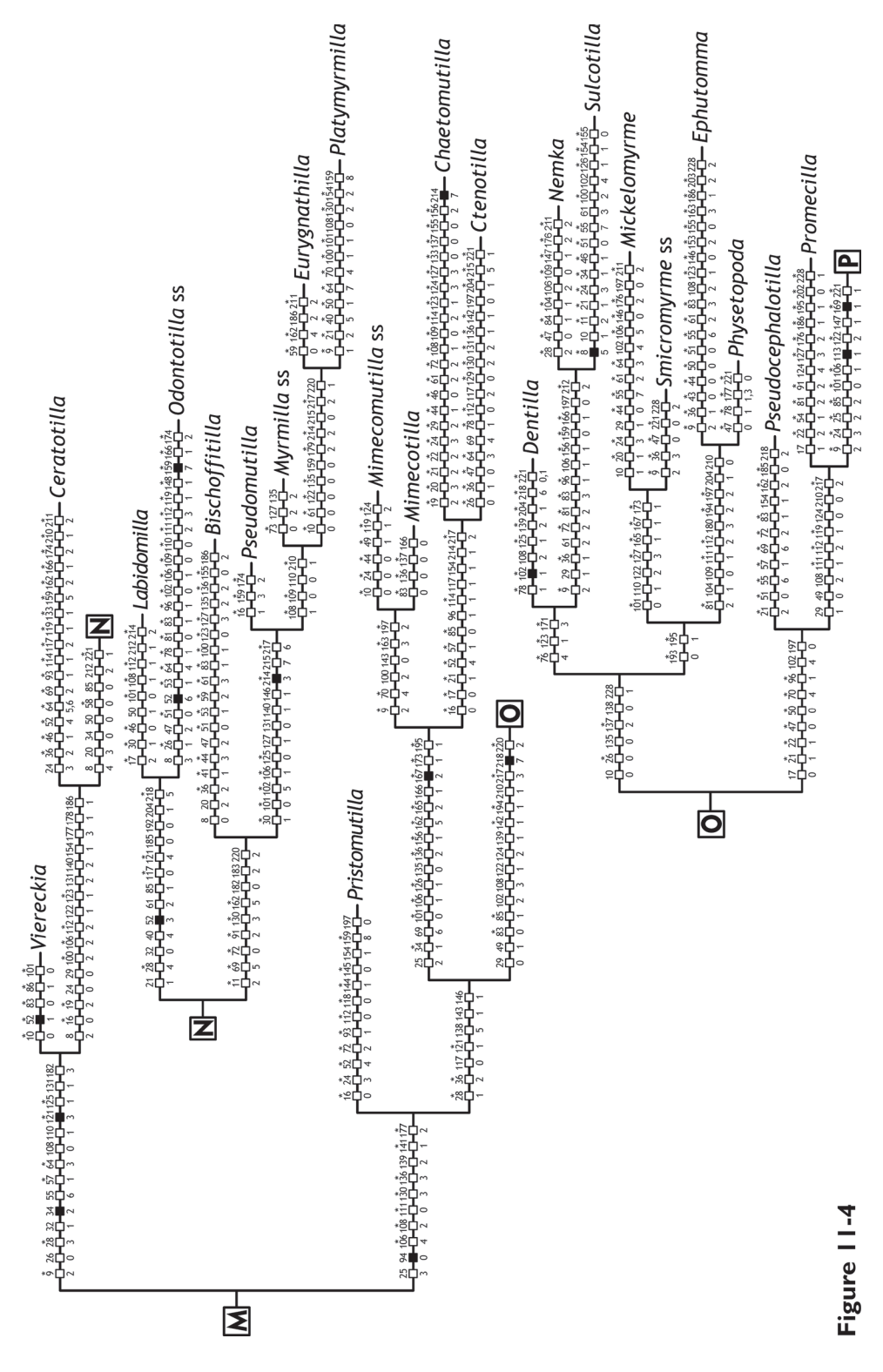

Viereckia
Ceratotilla
Labidomilla
Odontotilla ss
Bischoffitilla
Pseudomutilla
Myrmilla ss
Eurygnathilla
Platymyrmilla
Pristomutilla
Mimecomutilla ss
Mimecotilla
Chaetomutilla
Ctenotilla
Dentilla
Nemka
Sulcotilla
Mickelomyrme
Smicromyrme ss
Ephutomma
Physetopoda
Pseudocephalotilla
Promecilla
M
N
O
P

Figure 11-4

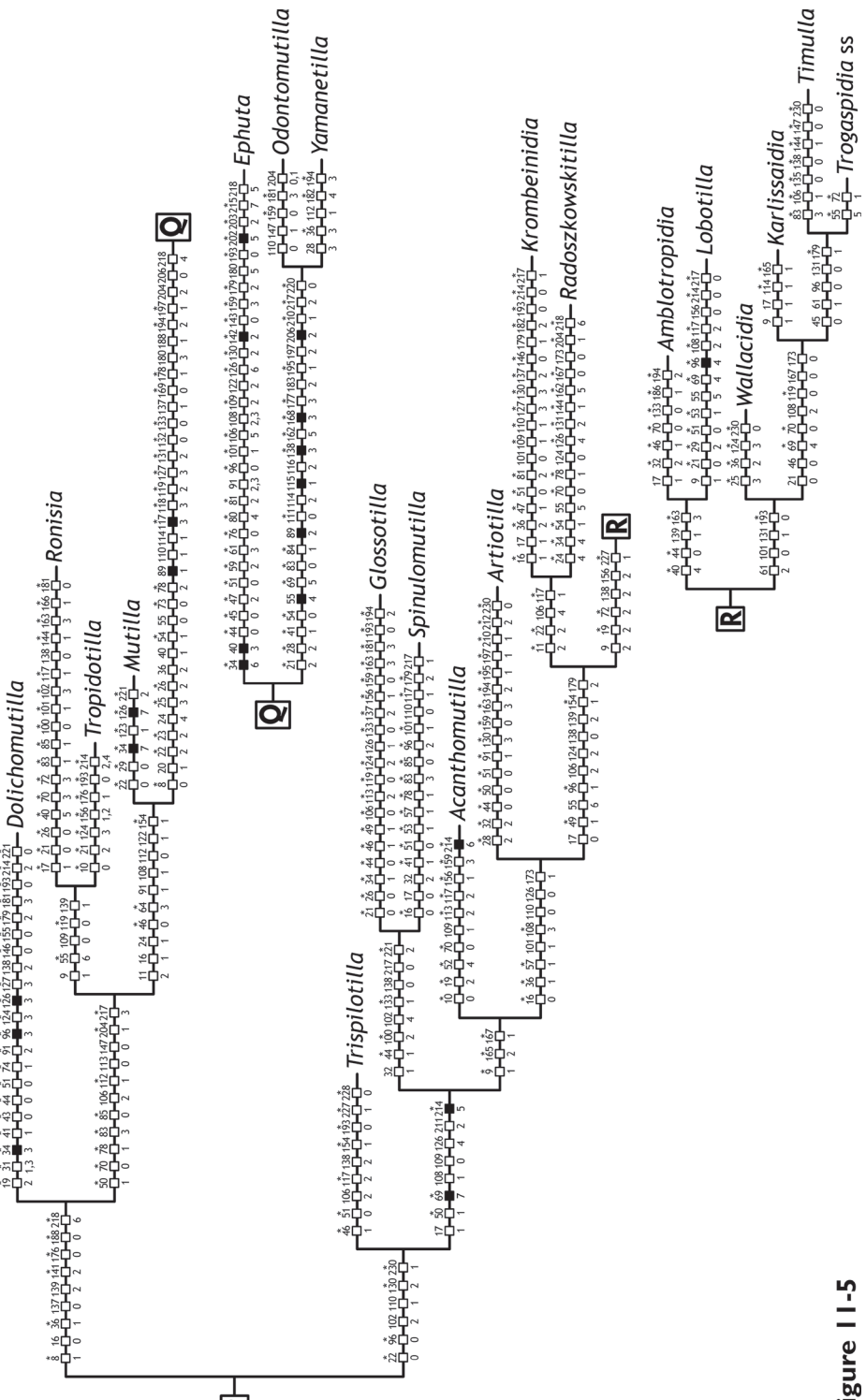

P
Dolichomutilla
Ronisia
Tropidotilla
Mutilla
Q
Ephuta
Odontomutilla
Yamanetilla
Glossotilla
Spinulomutilla
Trispilotilla
Acanthomutilla
Artiotilla
Krombeinidia
Radoszkowskitilla
R
Amblotropidia
Lobotilla
Wallacidia
Karlissaidia
Timulla
Trogaspidia ss

Figure 11-5

monophyletic subfamilies Myrmosinae, Pseudophotopsidinae, Ticoplinae and Rhopalomutillinae, but there is considerable variation in the groupings found above these taxa. Using the analysis of all terminals with additive characters of both sexes and implied weighting (identifying one of the MPTs as preferred) as the basis (see Figs 5 and 6, and 11 which shows the characters and states plotted using the mixed optimizations outlined above and specified in Appendix 2), we discuss each group identified there in turn and suggest putative limits to the taxa which are indicated, relating these to the DB and LN classifications (see Fig. 1, Appendix 1). The outcome, which attempts to harmonize the taxa identified previously as informed by the present analyses, is illustrated in Fig. 12.

The arrangement of taxa in Fig. 12 shows most of the major groups of Mutillidae (recognized at the subfamily level) to be monophyletic: Myrmosinae, Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Myrmillinae and Mutillinae, as also shown in Fig. 6 (the tree of Figs 5 and 12 redrawn to collapse those internodes without resampling support). Two putative subfamilies (Sphaeropthalminae and Dasylabrinae) are not monophyletic, however, and their components require further analysis at this level. Three of the monophyletic subfamilies (Pseudophotopsidinae, Rhopalomutillinae and Myrmillinae) have no recognized subtaxa and need little further discussion here. However, comments are needed on the other three.

The Myrmosinae has either included (DB) or excluded the Kudakrumiini/ae (LN). Either way, these two taxa have seemed clear-cut. The current analysis has shown, however, that the *Kudakrumia–Myrmosula* group is paraphyletic, with *Myrmosula* more closely related to *Myrmosa–Paramyrmosa* than to the other genera. Nevertheless, the arrangement shown necessitates that functional ocelli in the females were regained in *Myrmosa–Paramyrmosa* after having been lost in the ancestral mutillid (character 13, Fig. 11-1), an evolutionarily unlikely scenario (and see below).

The Pseudophotopsidinae includes only the genus *Pseudophotopsis*, but its species complicate the analysis because the females vary in having functional ocelli, reduced ocelli, or no ocelli whatsoever (character 13, Appendix 3), potentially influencing the relationships shown within the Myrmosinae (see above).

The Ticoplinae is clearly divided into the two accepted tribes, each comprising two terminals in this analysis and thus agrees with previous concepts.

The Sphaeropthalminae is clearly paraphyletic, with the *Euspinolia–Hoplocrates* group (considered as members of the pseudomethocine grouping by both DB and LN) arising as sister to the remainder of the Mutillidae. However, examination of Fig. 6 shows that these relationships are uncertain, with the *Euspinolia–Hoplocrates* group, the remainder of the Sphaeropthalminae (*Tallium–Pseudomethoca*), five lineages in the Dasylabrinae (*Dasylabroides–Seyrigilla*), and the internode subtending Myrmillinae + Mutillinae potentially unresolved. The placement of the *Euspinolia–Hoplocrates* group within Sphaeropthalminae is thus not unreasonable, although the group probably warrants formal recognition even if placed amongst the pseudomethocines. The other pseudomethocines (*Lynchiatilla–Pseudomethoca*) comprise a moderately supported monophyletic group (Figs 5, 6), but the terminals comprising the Sphaeropthalmina/i form

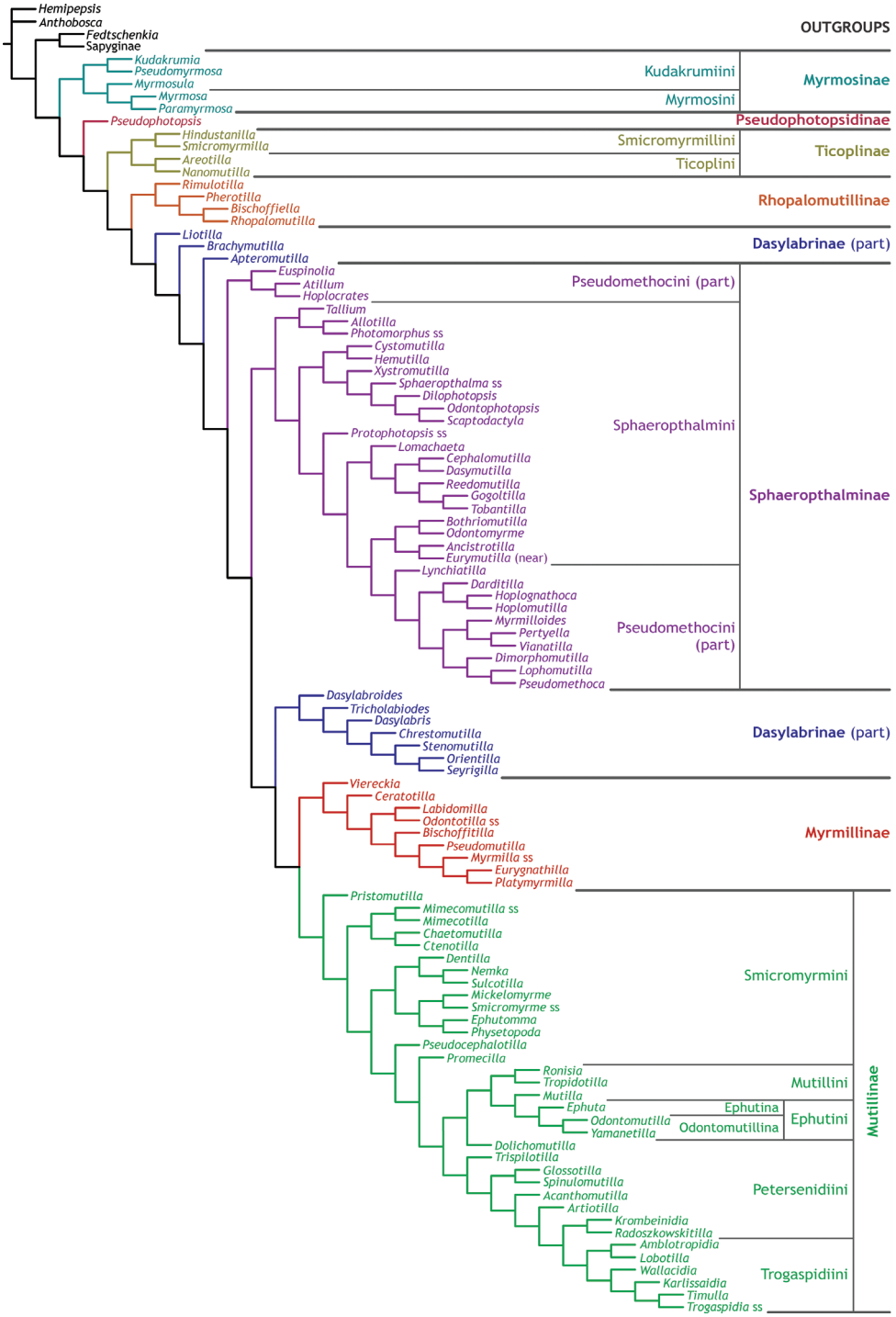


Figure 12. Preferred most-parsimonious tree (see Fig. 5) with potential groups incorporating ideas from both previous classifications indicated.

a paraphyletic group of five sequentially arising lineages (*Tallium–Photomorphus s.s.*, *Cystomutilla–Scaptodactyla*, *Protophotopsis s.s.*, *Lomachaeta–Tobantilla* and *Bothriomutilla–*"*Eurymutilla*"), the last being sister to the *Lynchiatilla–Pseudomethoca* group. It is notable that *Odontomyrme* (placed by LN in their Ephutinae based on females only) is instead clearly part of the *Bothriomutilla–*"*Eurymutilla*" group of Australian genera.

Liotilla, *Brachymutilla* and *Apteromutilla* appear as separate terminals sequentially diverging from the spine of the tree basal to the sphaeropthalmines; all three have completely apterous males with the mesosomal sutures entirely or substantially obliterated and both sexes very similar morphologically. They are restricted to southern Africa. *Brachymutilla* and *Apteromutilla* have previously been placed in the Dasylabrinae, but *Liotilla* (until now known only from the female holotype of its type species, *L. laevis* Bischoff) was placed in the Myrmillinae by Bischoff (1920). We have, however, recently been able to examine several species and both sexes of *Liotilla*, all collected in pitfall traps, which has enabled clarification of their relationships. When females only were analysed, these three genera appeared well separated on the tree (Fig. 9), although both *Brachymutilla* and *Apteromutilla* were placed with or close to components of the Dasylabrinae. In contrast, the analysis of males only showed *Apteromutilla–Liotilla* to form a well supported monophyletic group, but sister to the *Euspinolia–Hoplocrates* group (Fig. 10), an arrangement also found in the full analysis where the terminals were duplicated to account for polymorphisms (Fig. 7), although in both cases not supported by resampling. Given the apterous nature of the males, and the reduced nature of their male genitalia, we suspected that these characteristics may have distorted their relationships. The effects of the deletion of characters associated with winglessness (those of the wings themselves and the mesosomal structures affected) as well as those of the genitalia, were investigated in various combinations. None of these manipulations had any significant effect on the structure of the trees found (not shown here), however, specially with reference to these terminals. The placement of these three genera in Fig. 6 (the preferred tree with unsupported internodes collapsed) shows that the resampling support for a monophyletic group of all mutillids above their position is extremely low and questionable. Recognition of these three genera as a valid group, associated with the Dasylabrinae, is thus not unreasonable, given the uncertainties and contradictions about their placement in our different analyses. Furthermore, the relationships of the other dasylabrine terminals are also somewhat uncertain; although the *Dasylabroides–Seyrigilla* group is shown as monophyletic in the preferred tree (Fig. 5), various components are dissociated in various ways in several of the other analyses, and the group as a whole has no resampling support (Fig. 6), and may thus actually be paraphyletic (as was indicated in the DB and LN trees, which had no apomorphies for the group, although the current preferred tree shows six unambiguously placed but homoplasious synapomorphies for it, see Fig. 11-3).

The Myrmillinae (*Viereckia–Platymyrmilla*) formed a monophyletic group with low support in almost all of the analyses including both sexes (Figs 2, 3, 5–8), only the strict consensus tree derived from the analysis using equal weights and additive characters (Fig. 4) showing ambiguity on this. The analyses based on one sex only produced

different results, that for the males (Fig. 10) being similar to the full analyses, but that for the females (Fig. 9) splitting the terminals (see results, above). It is notable that *Pristomutilla*, placed in Myrmillinae by LN, is associated with two other myrmilline genera (*Ceratotilla* and *Viereckia*) in the analysis of females, but is reasonably well supported as a mutilline in all of the other analyses. Using the preferred tree (Fig. 5) as the basis, moving *Pristomutilla* to be sister to the Myrmillinae adds seven steps, but making it sister to the *Mimecomutilla s.s.–Ctenotilla* group instead (the arrangement found in the analysis of males only) adds only one step; that assignment thus seems preferable.

The Mutillinae (*Pristomutilla–Trogaspidia s.s.*) formed a monophyletic group with low support in all of the analyses except for that of females only, which excluded *Pristomutilla* (Fig. 9, and see above). This is the taxon containing most of the discrepancies between the DB and LN classifications (Fig. 1), notably the inclusion of *Ephuta* (as Ephutini) and *Odontomutilla* (within Mutillina) by DB but their exclusion by LN, the recognition of a single subtribe (Smicromyrmina, within Mutillini) for most of the genera, but these split into three tribes (Smicromyrmini, Petersenidiini and Trogaspidiini) and some (*Ctenotilla* and relatives) included in Mutillini by LN. Examination of Fig. 6 shows that there are three supported "basal" lineages, *Pristomutilla*, *Mimecomutilla s.s.–Ctenotilla* and *Dentilla–Trogaspidia s.s.*, and the same groupings were found for the non-additive analyses (Figs 2, 3). It is clear that the *Ctenotilla* group is not closely related to the Mutillina/i, and *Pristomutilla* may be associated with the *Ctenotilla* group (see above). The third grouping has seven "basal" lineages, four of which associate various sets of terminals with some support. The relationships of three terminals (*Pseudocephalotilla*, *Promecilla* and *Dolichomutilla*) are unresolved, although the weighted analysis using non-additive characters (Fig. 3) showed the first two as part of a monophyletic group (*Pseudocephalotilla–Physetopoda*, with low support) which includes *Smicromyrme s.s.*, and *Dolichomutilla* at the base of another monophyletic group (*Dolichomutilla–Trogaspidia s.s.*, also with low support). [*Pseudocephalotilla* was placed in the *Ctenotilla* group by LN, in accordance with indications by Bischoff (1920) and Nonveiller (1979), based on the male only, but subsequent unpublished investigations by DJB have shown that the females are very different from those in the *Ctenotilla* group and were placed in *Smicromyrme* by Bischoff (1921).] Fig. 6 also shows *Ronisia* and *Tropidotilla* grouped, but with very low support, and *Mutilla–Yamanetilla* forming a monophyletic group, also with very low support. These relationships were not confirmed by the non-additive analyses (Figs 2, 3) where *Mutilla*, *Ronisia* and *Tropidotilla* formed a monophyletic group with very low support (agreeing with both the DB and LN classifications), and *Ephuta*, *Odontomutilla* and *Yamanetilla* together formed a separate monophyletic group with high support (agreeing with the LN classification, although that placed the group well outside the Mutillinae). The last grouping in Fig. 6 (*Trispilotilla–Trogaspidia s.s.*) had very low support, and comprised six lineages, only one of which (*Amblotropidia–Trogaspidia s.s.*) showed significant further grouping of terminals with very low support; this group corresponded to the Trogaspidiini of LN, and the other unresolved lineages collectively to LN's Petersenidiini (although LN had placed *Dolichomutilla* in the Trogaspidiini).

Although Fig. 12 reflects the best estimate of the groupings of higher taxa taking the previous classifications into account and attempting to harmonize them using the tree produced by the weighted analysis of additive characters of both sexes as its base, this has clearly resulted in many paraphyletic groupings. It must be recognized, however, that that tree, although the preferred one, is questionable as an accurate reflection of the evolutionary histories of the terminals involved. The discussion above has highlighted many of the significant discrepancies between the results obtained from the different analyses performed, and suggested alternative placements for many of the terminals. In light of this, the tree (Fig. 12) was restructured so as to make all of the proposed taxa monophyletic (Fig. 13), the length of which is only about 1% longer than the preferred tree (raw length = 2858 (versus 2828), ci = 0.19, ri = 0.60 when considering characters additive; length = 2671 (versus 2646), ci = 20, ri = 59 when considering characters non-additive). Fig. 13 additionally shows the highest resampling-support values obtained when analysing the data considering many characters additive or all non-additive, and under equal weights or implied weighting (N = 5). Most of the supported groups were found in all analyses, but some were recovered in only one or two analyses. It is perhaps significant that 81 (out of a potential total of 102) of the groups shown in Fig. 13 had positive GC values, indicating resampling support, compared with 55, 62, 64 and 69 of the groups found in the parsimony analyses (Figs 2–5, and see above), the highest number of those being in the preferred tree. At least one additional group with low resampling support in all four of these analyses (*Karlissidia* sister to *Wallacidia*, a group not found in any of the parsimony analyses, however) could have been derived by a further minimal change to the tree, involving only one additional step, but this would have made no effective difference to the relationships seen.

The most contentious parts of the suggested rearrangements involve the *Liotilla–Apteromutilla* and *Euspinolia–Hoplocrates* groups, these together accounting for much of the increase in length of the tree. Their suggested placements, with Dasylabrinae and Pseudomethocini respectively, are not supported by resampling, however. Based on Fig. 5, making *Liotilla–Apteromutilla* monophyletic adds four steps, and then moving it to be sister to the *Dasylabroides–Seyrigilla* group adds a further six steps, for a total increase in length of 10 steps. Moving the *Euspinolia–Hoplocrates* group to be sister to the remaining Sphaeropthalminae adds six steps, and then moving it to be sister to the *Lynchiatilla–Pseudomethoca* group adds another 12 steps, for a total increase of 18 steps. Both moves together add 25 steps. Conversely, using the proposed arrangement (Fig. 13) as the base, moving the *Euspinolia–Hoplocrates* group to be sister to the remaining Sphaeropthalminae–Mutillinae (its original position) shortens the tree by only five steps (not 18), and restoring the original positions and relationships of *Liotilla–Apteromutilla* subtracts seven steps (not 10); both moves together shorten the tree by only 13 steps (not 25). The marked differences in these step changes, depending on the starting tree, result from the cumulative effects of the several other small moves reflected in Fig. 13 when compared with Fig. 5.

Despite Fig. 13 not representing a most-parsimonious tree, but recognizing that the sample analysed, although substantial in terms of the number of sub/genera included,

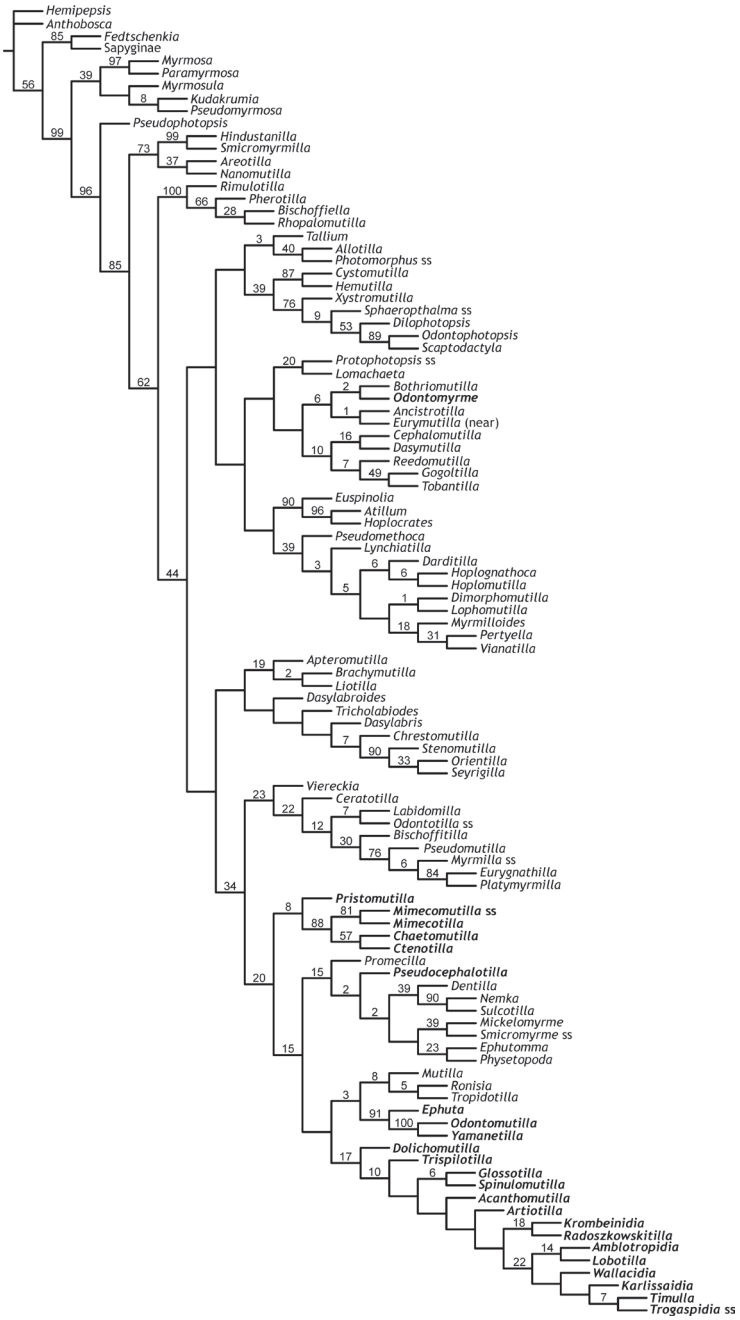


Figure 13. Tree based on preferred tree (see Fig. 5) but with branches re-arranged to make the potential recognizable groups (see Fig. 12) monophyletic (length = 2858, ci = 0.19, ri = 0.60). Group support (GC) values shown for all groups supported by resampling; the highest values obtained when resampling all non-additive or mostly additive characters, using equal weights and implied weights (N = 5), are shown. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).

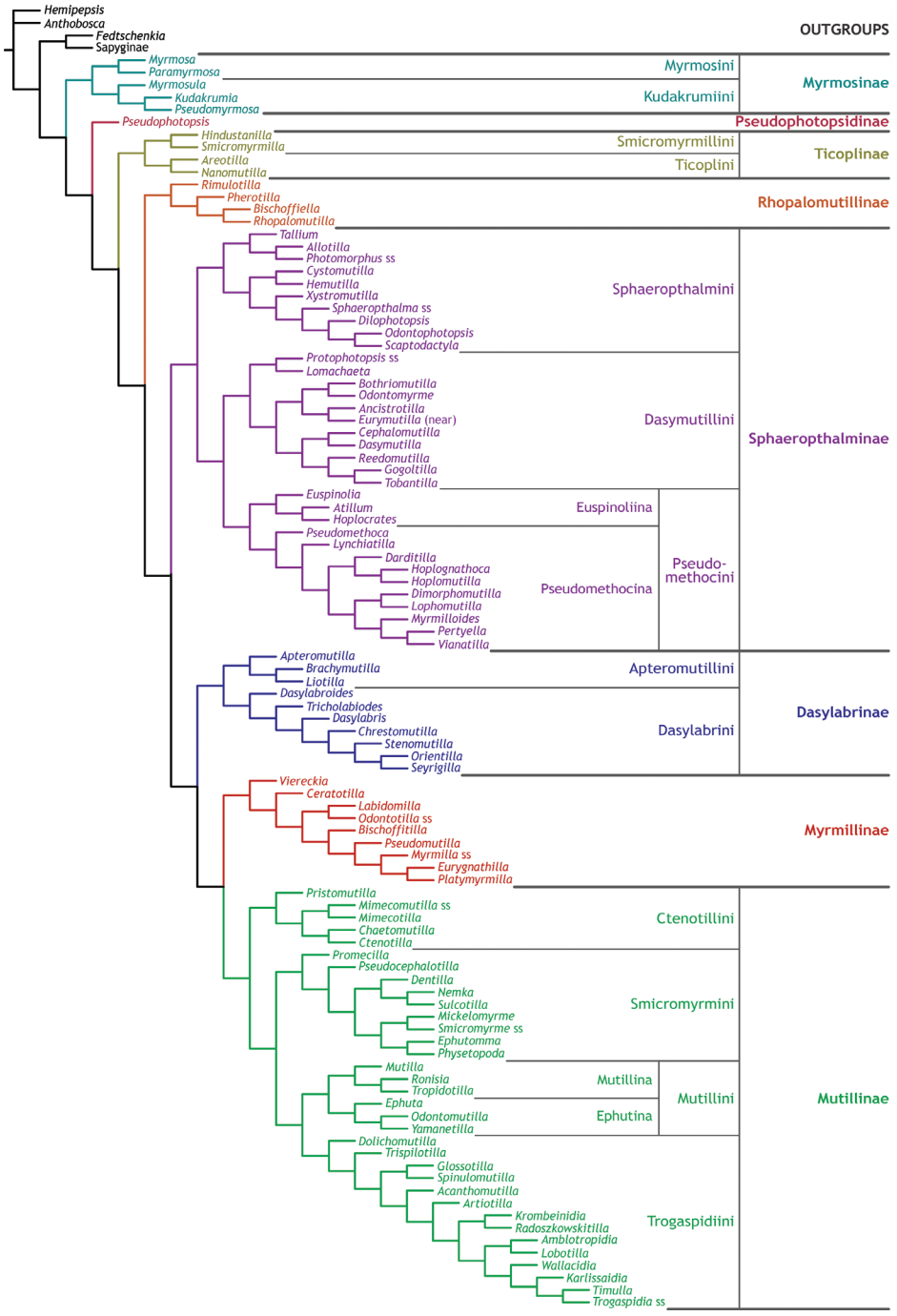


Figure 14. Proposed higher classification of Mutillidae as reflected by the rearranged tree (Fig. 13) of length about 1% greater than the previously preferred tree (Fig. 5) (lengths = 2858 *vs* 2828 for additive characters, 2671 *vs* 2646 for non-additive characters). (See Appendix 4 for classification including all currently valid genera and subgenera.)

could not completely encompass the mutillid variation actually present, and that the various analyses produced differing results, we consider that it is a reasonable estimate of relationships and results in a scheme which requires few changes from the existing classifications, thus promoting stability. The classification we propose here, based on the terminals analysed, is shown in Fig. 14. Although it agrees to a large extent with that in Fig. 12, there are a few differences. We discuss and justify the proposed taxa below, referring to the resampling-support values reflected in Fig. 13 where relevant, and to their defining character states as shown on the subtending internodes of the tree reflecting the proposed classification (Fig. 15), and with reference to their distribution as shown in the preferred tree where relevant (Fig. 11). It should be noted that character states may be subsequently changed within the taxa for which they appear as subtending states, and this is not shown in Fig. 15, nor are the states for the outgroups. Where justifications for group rearrangements are provided above, they are not repeated below. A summary diagram of the proposed classification appears in Fig. 16, and the taxa are dealt with below in the sequence shown there, derived from the presumed phylogenetic sequence but with terminal sister groups arranged alphabetically. Comments on geographical distributions (regions ranked in descending order of number of taxa found in each) and degree to which both sexes are known for the taxa are based on our knowledge of all valid genera and subgenera, as shown in Appendix 4.

Sapygidae + Mutillidae: As expected, the family Mutillidae is sister to Sapygidae, that association having good resampling support (here GC = 56), and supported by three unique and unambiguously placed synapomorphies for both additive and non-additive characters: 14.1 and 105.1, antennal "tubercle" in females and males (although further modified in male Sapyginae); 224.1, non-fusion of penis valves. An additional two unique and unambiguously placed synapomorphies were shown for the additive characters only: 118.2, short pleurostomal carina (although modified in Sapyginae); 209.1, posterior differentiation of sternum I in males (although further modified in Mutillidae).

Mutillidae Latreille, 1802: Monophyly of the Mutillidae (including Myrmosinae) has very high resampling support (GC = 99) and is supported by 10 unique and unambiguously placed synapomorphies for both additive and non-additive characters: 7.1, articulation of tergum II and sternum I in both sexes; 15.2, form of base of scape in females; 38.1, loss of wings in females; 65.2, closed metacoxal cavities in females; 90.1 and 208.1 stridulitrum on Tergum III in females and males (although apparently secondarily lost in some male myrmosines, and females of Rhopalomutillinae); 92.2 and 209.2, form of sternum I posteriorly in females and males; 200.1, reduction in

Figure 15. Subtending states for tree reflecting proposed taxa as monophyletic. Blue indicates states found only when most characters were considered additive, red only when all states were considered non-additive, and black under both conditions. Solid hashmarks indicate unique state changes, and open hashmarks are homoplasies. Letters within boxes indicate breaks in branches to enable effective layout.

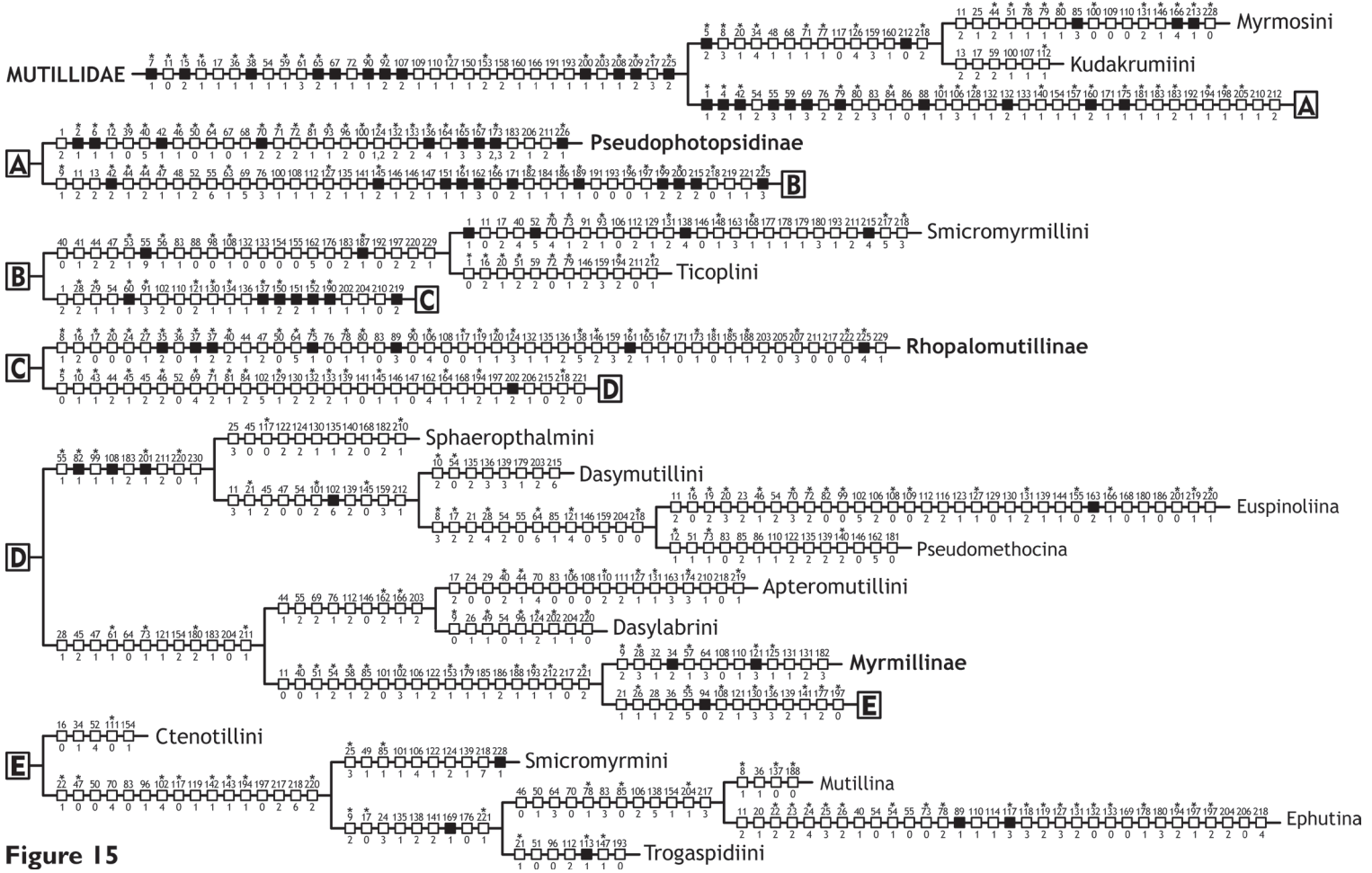

MUTILLIDAE
Myrmosini
Kudakrumiini
A
Pseudophotopsidinae
B
Smicromyrmillini
Ticoplini
C
Rhopalomutillinae
D
Sphaeropthalmini
Dasymutillini
Euspinoliina
Pseudomethocina
Apteromutillini
Dasylabrini
Myrmillinae
E
Ctenotillini
Smicromyrmini
Mutillina
Ephutina
Trogaspidiini

Figure 15

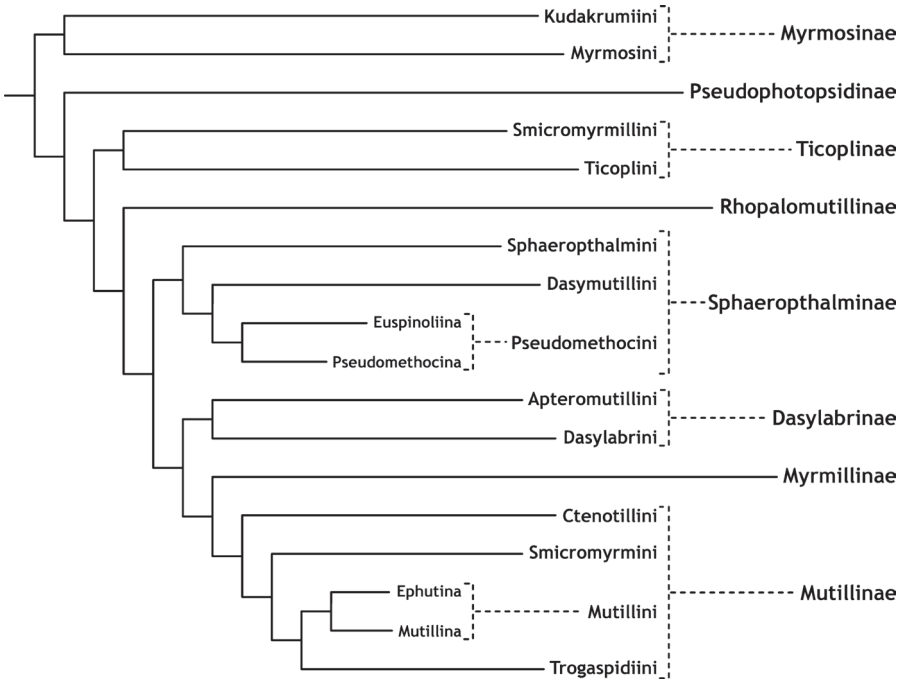


Figure 16. Final proposed higher classification of Mutillidae, as related to the rearranged tree (cf. Fig. 1).

jugal lobe of hind wing in males (although entirely lost subsequently); 225.2, form of penis valve (although subsequently modified in most terminals). There are also seven unambiguously placed but homoplasious states, the most significant being: 36.1, maxillary palp longer than fore tibia in females (but shorter in rhopalomutillines and *Euspinolia*, and even longer in scattered terminals); 61.3, metapleural-propodeal suture entirely obliterated on surface in females (but distinct in a few scattered terminals, and partially distinct in many; these apparently widespread reversals cast doubt on the accuracy of this placement); 127.1, maxillary palp longer than fore tibia in males (but shorter in *Liotilla*, and even longer in scattered terminals); 153.2, metapleural-propodeal suture obliterated dorsally and vague ventrally in males (but entirely distinct in a few scattered terminals, and partially distinct in many; these apparently widespread reversals cast doubt on the accuracy of this placement); 203.1, tergum I >0.5 <0.75 × width of tergum II in males (but broader in *Hindustanilla* and some *Pseudophotopsis*, even narrower in several scattered terminals). An additional unique and unambiguously placed state appears in the initially preferred tree (Fig. 11): 13.2, loss of ocelli in females, but then ocelli would have to be regained in some Myrmosinae and some *Pseudophotopsis*, so that placement is unlikely in evolutionary terms. (That character state shows separate derivations in Myrmosini, some *Pseudophotopsis* and the entire group sister to Pseudophotopsidinae in the proposed tree, Fig. 13.) The family as a whole is cosmopolitan, with 246 sub/genera; females are known for 84% and males for 89% of those taxa.

Myrmosinae Fox, 1894: This is a taxon whose estimated affinities have fluctuated in the past, and has recently been recognized again as a distinct family by Pilgrim et al. (2008), based on a molecular analysis using a single species of *Myrmosula* to represent it, and found to be sister to Sapygidae (represented by two species of *Sapyga* Latreille). Brandstetter et al. (2017) also recognized Myrmosidae (represented by a single species of *Myrmosa*) as distinct from Mutillidae, although it was found to be sister to the remaining Mutillidae. Our analysis included several genera and species as exemplars of Myrmosinae and found strong evidence linking them as the sister taxon to the other Mutillidae; we thus recognize the group as a subfamily of Mutillidae, as in Brothers's earlier classifications (Fig. 1). Monophyly of the Myrmosinae has moderate resampling support (GC = 39) and is supported by one unique and unambiguously placed synapomorphy for both additive and non-additive characters: 5.2, lamellate process of metacoxa in both sexes. There are an additional seven unambiguously placed but homoplasious states supporting this, the most significant being: 34.4 and 126.4, flattened prementum in females and males (also found sporadically in a few other terminals elsewhere in the tree); 71.1, narrow pectinate fore calcar blade in females (also found in *Rimulotilla*); 77.1, inner metatibial spur modified as a cleaner in females (found elsewhere only in the pompilid outgroup). The subfamily is Palaearctic, Oriental and Nearctic in distribution, with 13 sub/genera; females are known for 85% and males for 85% of those taxa.

Kudakrumiini Krombein, 1979: In the originally preferred tree (Figs 5, 6, 11) the kudakrumiines are paraphyletic, with *Myrmosula* sister to *Myrmosa* and *Paramyrmosa*. However, shifting the *Myrmosula* branch to make Kudakrumiini monophyletic (Figs 13, 14) adds only two steps to the tree, and is thus not unreasonable. Monophyly of the Kudakrumiini in this configuration has no positive resampling support, though, and is supported by only one weak unambiguously placed but homoplasious state for both additive and non-additive characters: 112.1, flagellomere I shape in males (also found in many other scattered terminals). There are five other homoplasious states supporting this grouping, however, the most significant being: 13.2, absence of ocelli in females (also found in some Pseudophotopsidinae and all mutillids distal to Pseudophotopsidinae); 107.1, simple angled scape–radicle junction in males (found in some outgroups but no other mutillids). The tribe is Oriental, Palaearctic and Nearctic in distribution, with six genera (including a fossil one); females are known for 100% and males for 67% of those taxa.

Myrmosini Fox, 1894: This group was found to be monophyletic with very high resampling support in all analyses (here GC = 97), and is supported by two unique and unambiguously placed synapomorphies for both additive and non-additive characters: 166.4, many meso- and metatibial articulated spines in males; 213.1, hypopygium concealed and modified in males. There are an additional nine unambiguously placed but homoplasious states supporting this, the most significant being: 79.1, tergum I with paired vertical ridges basally in females (found elsewhere only in some Ticoplinae); 228.0, basal

lobe of volsella forming inner projection (found elsewhere only in some outgroups and a few scattered terminals). The tribe is Palaearctic, Nearctic and Oriental in distribution, with seven sub/genera; females are known for 71% and males for 100% of those taxa.

The remaining Mutillidae (apart from Myrmosinae) form a monophyletic group with very high resampling support in all analyses (here GC = 96), supported by four unique and unambiguously placed synapomorphies for both additive and non-additive characters: 4.2, metasternum with posterior median process(es) in both sexes; 79.2, tergum I with expanded "auricles" basally in females (although apparently reversed in a few Ticoplinae); 160.2, metacoxal cavities closed in males; 175.1, fore wing venation ending before distal margin of wing. There are an additional two unambiguously placed synapomorphies for additive characters only: 1.1, eye pubescence absent but pores present in both sexes (but subsequently modified in some groups); 42.1, pro-mesonotal suture distinct but fused in females (but subsequently modified in almost all). There are an additional 11 unambiguously placed but homoplasious states supporting the monophyly, the most significant being: 84.1, increased length of tergum II in females (subsequently modified in most terminals, reversed in *Rimulotilla*, and independently developed in *Kudakrumia*); 128.1, labial palp with mid segments expanded in males (although subsequently reversed in *Liotilla*, and independently developed in *Myrmosa* and one outgroup); 157.1, mid coxae slightly separated in males (but also in *Kudakrumia* and one outgroup); 194.1, hind wing crossvein r-m proximal (although subsequently modified in some); 205.1, felt line on tergum II present in males (although subsequently reversed in a few terminals; the female equivalent, 88.1, is not unambiguously placed here, but has a similar pattern).

Pseudophotopsidinae Bischoff, 1920: This group, comprising the single variable genus *Pseudophotopsis*, is confirmed as sister to the rest of the Mutillidae (except for Myrmosinae), in agreement with all previous analyses. Despite the small size of the group, it warrants recognition at the subfamily level, being morphologically very distinct, with a mixture of plesiomorphic (e.g., 13.0, presence of functional ocelli in females of some species; 42.1, distinct but fused pro-mesonotal suture in females; 189.0, 200.1, presence of a jugal lobe on both wings) and apomorphic states. It is supported by eight unique and unambiguously placed synapomorphies for both additive and non-additive characters: 2.1, pubescent pit on pronotum in both sexes; 6.1, pubescent depressions on sternum I in both sexes; 70.2, outer vertically elongate groove/pore on fore tibia in females; 136.4, interrupted faint parapsidal groove in winged males; 165.3, 167.3 and 173.2,3, pulvillus on 2nd–4th tarsomeres of all legs in males (absent on 2nd in some); 226.1, articulated spines on penis valve. It is also supported by several other unambiguously placed but homoplasious states (Fig. 15). The subfamily is Palaearctic, Afrotropical and Oriental in distribution, with one genus; females and males are known.

The remaining Mutillidae (apart from Myrmosinae and Pseudophotopsidinae) also form a monophyletic group with very high resampling support in all analyses (here GC

= 85), supported by seven unique and unambiguously placed synapomorphies for both additive and non-additive characters: 42.2, pro-mesonotal suture very indistinct or obliterated in females (although somewhat distinct in some *Euspinolia* species); 145.2, propodeal disc with three large fields in winged males (although apparently subsequently modified in most terminals since this state present only in Rhopalomutillinae and many Ticoplinae); 161.1, tarsal claws simple in males (subsequently modified in Rhopalomutillinae); 189.1 and 200.2, both wings without jugal lobe; 199.2, anal lobe not indicated on hind wing; 225.3, penis valve with simple apex and ventral tooth on apical half (but modified in Rhopalomutillinae). There are also several unambiguously placed but homoplasious states supporting this grouping (Fig. 15).

Ticoplinae Nagy, 1970: This group was found to be monophyletic with high resampling support (here GC = 73) in all analyses (except that for males only where it appeared as paraphyletic, Fig. 10); it is supported by one unique and unambiguously placed synapomorphy for both additive and non-additive characters: 187.1, fore wing with cell 1S petiolate anteriorly (although also present in some *Myrmosa* species). It is also supported by one unique ambiguously placed synapomorphy: 55.9, fine mesopleural ridge approaching prothoracic spiracle in females (although modified in some *Smicromyrmilla*). There are an additional three unambiguously placed but homoplasious states supporting it: 53.1, dentate or spinose posterolateral margin of propodeum in females (but also in several scattered subsequent terminals); 56.1, mesopleural ridge dorsal to mid coxa in females (but also in *Liotilla* and reversed in some *Smicromyrmilla*); 98.0, head narrow across mandibular bases in males (but also in some Kudakrumiini, some Pseudophotopsidinae, *Orientilla* and within an outgroup). The subfamily is Oriental, Afrotropical and Palaearctic in distribution, with six genera; females are known for 83% and males for 62% of those taxa.

Smicromyrmillini Argaman, 1988: This group was found to be monophyletic with very high resampling support in all analyses (here GC = 99), and is supported by three unique but ambiguously placed synapomorphies for both additive and non-additive characters: 52.5, posterodorsal margin of propodeum with two median teeth and two lateral spines or teeth in females (but this present in only some species of *Smicromyrmilla*, so probably unreliable); 138.4, mesoscutellum posteriorly produced over metanotum in winged males; 215.4, hypopygium with complex narrow apical emargination (although plotted as ambiguous by Winclada, this state is unique to this group so is effectively unambiguously placed here). There are an additional eight unambiguously placed but homoplasious states supporting the group, the most significant being: 93.1, sternum II with felt line in females (although sporadically present in a few other terminals); 148.1, posterolateral margin of propodeum dentate or spinose in males (but also in *Odontotilla s.s.* and some members of Ephutina); 217.5, cercus short, flattened basally and clavate apically in males (but also in most Rhopalomutillinae). In the analysis of duplicated terminals (Fig. 7), *Smicromyrmilla* was found not to be monophyletic, but rather paraphyletic with respect to *Hindustanilla*. This is not surprising since the main

diversity of smicromyrmillines (Afrotropical) has not been revised, and it is probable that the species examined may yet be found to represent different genera; we were unfortunately not able to include specimens of the rarely collected Palaearctic type species, *Mutilla ariasi* André. The tribe is Oriental, Afrotropical and Palaearctic in distribution, with four genera; females are known for 50% and males for 50% of those taxa.

Ticoplini Nagy, 1970: This group was found to be monophyletic with moderate resampling support (here GC = 37) in all analyses except for that of males only (there paraphyletic, Fig. 10). It is not supported by any unique synapomorphies, but is supported by six unambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 51.2, posterodorsal margin of propodeum ridgelike in females (but also in *Kudakrumia* and some Dasymutillini); 79.1, tergum I with paired vertical ridges basally in females (but also found in Myrmosini and some *Smicromyrmilla*, and tergum I simple in some *Nanomutilla*). The tribe is Afrotropical in distribution, with two genera; females and males are known for both.

The remaining Mutillidae (distal to Ticoplinae) also form a monophyletic group with good resampling support in all analyses (here GC = 62) , supported by five unique and unambiguously placed synapomorphies for both additive and non-additive characters: 60.1 and 152.1, meso-metapleural "bridge" present in females and males; 137.1, posterolateral margin of mesoscutum lobed in winged males (but sporadically subsequently modified or reversed in many terminals); 150.2, meso-metapleural suture fused in winged males; 190.1, basal hamuli on hind wing absent. The group is also supported by six unambiguously placed homoplasious synapomorphies, the most significant being: 28.2 and 121.2, oral and mandibular fossae separated by cuticular bridge in females and males (but reduced or elaborated in many subsequent terminals); 91.3, bounded pygidial plate present in females (but sporadically reduced or absent in many terminals); 134.1, mesoscutum extended far anterior to tegula in winged males (but sporadically shortened in several subsequent terminals).

Rhopalomutillinae Schuster, 1949: This group was found to be monophyletic with extraordinarily high resampling support in all analyses (here GC = 100), and is supported by four unique and unambiguously placed synapomorphies for both additive and non-additive characters: 35.2, maxillary palp unsegmented in females (although two-segmented in some species of *Pherotilla* and *Rhopalomutilla*): 75.1, metatibia broadened and smooth on inner surface in females; 161.2, tarsal claws lamellate basally and acute apically in males; 225.4, penis valve with rounded apex and ventral prominence at about half length. There are an additional 27 unambiguously placed but homoplasious states supporting the group, the most significant being: 20.0, flagellomere I wider than long in females (but also in *Kudakrumia*, *Nanomutilla* and *Odontomyrme*); 27.1 and 120.1, postmandibular carina present as blunt ridge in females and males (but also in *Kudakrumia* females, *Lomachaeta* and *Liotilla*); 36.0, maxillary palp shorter than protibia in females (but also in outgroups and *Euspinolia*); 40.2, mesosomal form in females (but similar in *Protophotopsis s.s.* and some Apteromutillina); 64.5,

metasternal process long, unidentate and acute in females (but also in a few scattered Sphaeropthalminae); 80.1, tergum I posteriorly parallel-sided and discontinuous with tergum II in females (but similar in some Myrmosinae and *Seyrigilla*); 90.0, no stridulitrum on tergum III in females (but also in *Paramyrmosa* and *Nanomutilla*); 165.1, 167.1 and 173.1, pulvillus on 4th tarsomere of all legs in males (but also in various Mutillinae); 207.3, apical setae on tergum II strong and curved in males (but also in *Protophotopsis s.s.* and *Darditilla*, and straight with split apices in some *Rimulotilla*); 222.0, gonostylus without parapenial lobe (but also in some Dasylabrinae). The subfamily is Afrotropical and Oriental in distribution, with four genera; females and males are known for all genera. The genera were recently reviewed by Brothers (2015).

The remaining Mutillidae (distal to Rhopalomutillinae) form a poorly to moderately supported monophyletic group in all analyses (here GC = 44), but not supported by any unique and unambiguously placed synapomorphies for both additive and non-additive characters. There is a single unique but ambiguously placed synapomorphy: 202.2, tergum I gradually broadened, short and sessile posteriorly (but subsequently modified in various ways in many subsequent terminals). There are an additional 15 unambiguously placed but homoplasious states supporting the group, however, the most significant being: 5.0, metacoxa posterodorsally simple in both sexes (otherwise found only in some Sapyginae, so unique here in Mutillidae); 43.1, pronotum lateral length shorter than distance between prothoracic and propodeal spiracles in females (but also in *Kudakrumia* and *Pherotilla*, and reversed in a few Dasylabrinae and Mutillinae); 71.2 and 164.1, fore calcar blade expanded and longish in females and males (also only in Pseudophotopsidinae); 84.2, tergum II much longer than terga III–VI in females (but also in *Nanomutilla*, and about the same length in a few scattered subsequent terminals); 139.1, posterolateral surface of axilla concave in winged males (although subsequently modified in many terminals). The *Liotilla–Apteromutilla* and the *Euspinolia–Hoplocrates* groups appear in different positions in the proposed arrangement, as discussed above.

Sphaeropthalminae Schuster, 1949 (1903): This group was paraphyletic in most of the analyses, with the *Euspinolia–Hoplocrates* group appearing as sister to the group containing the rest of the Sphaeropthalminae and the remaining Mutillidae, but this with negligible or no resampling support (Figs 2, 3, 5, 8). The remaining Sphaeropthalminae were found to be monophyletic in almost all analyses, but with very low or seldom no resampling support. Using the tree containing all proposed rearrangements (Fig. 13) as the basis, moving the *Euspinolia–Hoplocrates* group to be sister to all other Sphaeropthalminae shortened the tree by only four steps, and to its position as in the preferred tree (Fig. 5) made it only one further step shorter. Thus, placing the *Euspinolia–Hoplocrates* group within the Pseudomethocini (rather than sister to all other Sphaeropthalminae) required only four extra steps, a negligible difference in the context of attempting to minimize disruptions to the higher classification, given the uncertainties found in the analyses. In the final rearrangement, the Sphaeropthalminae has no resampling support, but is supported by two unique and unambiguously placed synapomorphies for both additive and non-additive characters:

82.1 and 201.1, tergum I and/or propodeum with plumose pubescence in females and males (although simple in a few scattered subsequent terminals); this is the classic characteristic of the group. There are an additional three unambiguously placed but homoplasious states supporting the group, however, the most significant being: 55.1, mesopleural ridge strong and joined to mesonotal tubercle (but also in some Dasylabrinae, and subsequently reduced or otherwise modified in several terminals); 99.1, head with plumose pubescence in males (although simple in *Cephalomutilla* and the *Euspinolia–Hoplocrates* group); 220.0, gonostylus (paramere) apically upcurved (but also in many Dasylabrinae and a few scattered terminals elsewhere, and straight in the *Euspinolia–Hoplocrates* group and *Myrmilloides*). Within the subfamily, the traditional split into sphaeropthalmines *s.s.* and pseudomethocines was not entirely supported, the sphaeropthalmines being clearly paraphyletic with about half the terminals most closely related to the pseudomethocines *s.s.* (excluding the *Euspinolia–Hoplocrates* group) with some resampling support, and the remainder appearing more basally (Figs 5, 6); the pseudomethocines *s.s.* were clearly monophyletic with good support. Consequently, we propose to recognize three tribes of Sphaeropthalminae, grouping the terminals as efficiently as possible to reflect these groupings. The subfamily is Neotropical, Nearctic, Australian, Oriental and Palaearctic in distribution, with 69 sub/genera; females are known for 88% and males for 91% of those taxa.

Sphaeropthalmini Schuster, 1949 (1903): This group comprises those sphaeropthalmines which are more basal than those more closely related to the pseudomethocines (see above). The *Cystomutilla–Scaptodactyla* group is moderately well supported (here GC = 39) in all of the analyses (except that of females only), but the positions of *Tallium*, *Allotilla* and *Photomorphus s.s.* vary somewhat. Using Fig. 13 as the basis, shifting the components to agree with the arrangement in the preferred tree (Fig. 5) has no effect on tree length, however, effectively implying that the proposed rearrangement is equally likely, the group thus formed being monophyletic although not being supported by resampling. The group is not supported by any unique synapomorphies, but is supported by two unambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 117.0, hypostomal carina simple in males (but also in many pseudomethocines and some dasymutillines, and flangelike in a few); 210.1, sternum II with lateral felt line in males (but also in some dasymutillines and a few pseudomethocines, and absent in a few). There are also some ambiguously placed homoplasious synapomorphies, the most significant being: 168.0, metacoxa simple mesad in males (but also in a few dasymutillines and pseudomethocines and most more-basal mutillids, carinate in *Dilophotopsis*, and dentate in some *Hemutilla*). It is surprising that *Cystomutilla* turned out to be paraphyletic with respect to *Hemutilla* (although without resampling support) in the analysis of duplicated terminals (Fig. 7), but this may have overestimated the spectrum of diversity within the genus, since the duplicated terminals reflected the potential maximum divergences rather than the actual states in the two species since they were not individually scored. The

tribe is Neotropical, Nearctic, Oriental and Palaearctic in distribution, with 24 sub/genera; females are known for 71% and males for 96% of those taxa.

The remaining Sphaeropthalminae (distal to Sphaeropthalmini, and disregarding the *Euspinolia–Hoplocrates* group) form a poorly supported monophyletic group in most analyses, but the proposed combined group is not supported by resampling or by any unique and unambiguously placed synapomorphies. There is, however, a single unique but ambiguously placed synapomorphy for both additive and non-additive characters: 102.6, eye subcircular with convex inner margin and long axis horizontal in males (but long axis vertical in the *Euspinolia–Hoplocrates* group and some *Dimorphomutilla*). It is also supported by three unambiguously placed homoplasious synapomorphies: 21.1, head with genal carina in females (but also in several other terminals, and absent in a few); 101.2, eye strongly convex in males (but also in some Sphaeropthalmini and *Tricholabiodes*, and only moderately convex in *Euspinolia* and *Myrmilloides*); 145.0, propodeal disc evenly sculptured in winged males (but also in a few Sphaeropthalmini, some Dasylabrinae, a few Mutillinae and many basal-most mutillids, and different in *Bothriomutilla*, *Euspinolia* and *Vianatilla*).

Dasymutillini Brothers & Lelej, trib. n.
http://zoobank.org/5F3C2042-451E-4B27-8058-711F055D6834
Type genus. *Dasymutilla* Ashmead, 1899. This group is paraphyletic in most analyses, although, interestingly, monophyletic in the tree derived from males only (Fig. 10) and that from the matrix with duplicated terminals reflecting maximum polymorphisms (Fig. 7), and almost so in the tree derived from the reduced matrix in which the most polymorphic characters had been deleted (Fig. 8). Using Fig. 13 as the base, moving the terminals to reflect the arrangement in the preferred tree (Fig. 5) (except in retaining the *Euspinolia–Hoplocrates* group as sister to the remaining pseudomethocines) actually added four steps, making the proposed final arrangement preferable in this regard. The group is not supported by resampling nor by any unique and unambiguously placed synapomorphies, but there is a single unique but ambiguously placed synapomorphy for both additive and non-additive characters: 10.2, eye strongly convex in females (but also in several other sphaeropthalmines and *Seyrigilla*, and less convex in *Odontomyrme*). There are also some ambiguously placed homoplasious synapomorphies, the most significant being: 135.2, mesoscutal notaulus absent in winged males (but also in most pseudomethocines, a few sphaeropthalmines *s.s.* and scattered terminals elsewhere, and present in *Gogoltilla* and *Tobantilla*). It is not surprising that *Dasymutilla* was shown to be paraphyletic in the analysis of duplicated terminals (Fig. 7), since it is generally recognized that the genus is highly variable (and even very difficult to separate from *Traumatomutilla* André), although recent reviews have not suggested the recognition of further genera or even subgenera; we tried to capture some of that variability in the selection of exemplars. The tribe is Neotropical, Australian and Nearctic in distribution, with 24 sub/genera; females are known for 100% and males for 95% of those taxa.

Pseudomethocini Brothers, 1975: The two components of this grouping are not closely associated in any of the analyses, but they are placed together here on the basis of their consistent positions in the current classifications, and the fact that this arrangement adds only five steps when compared with that in the preferred tree (Fig. 5; and see above). Because the two components are consistently shown as monophyletic in almost all of the analyses, and acknowledging the uncertainties about their true relationships to each other, however, we propose that they be recognized as distinct subtribes. The whole group is not supported by resampling nor by any unique and unambiguously placed synapomorphies, but there are six unambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 8.3, head broad, long and rounded posterolaterally in females (but also in a few scattered terminals, and further modified in several pseudomethocines); 17.2, pedicel longer than wide in females (but also in a few other scattered terminals, and not so long in some pseudomethocines); 28.4 and 121.4, oral and mandibular fossae separated by fused superficial cuticular bridge in females and males (elsewhere only in *Gogoltilla* females and two Myrmillinae); 64.6, metasternal process long and apically obtuse in females (but also in *Hemutilla* and *Photomorphus s.s.*, acute in a few pseudomethocines, and reduced in *Euspinolia*). The tribe is Neotropical and Nearctic in distribution, with 24 genera; females are known for 96% and males for 83% of those taxa.

Euspinoliina Brothers & Lelej, subtrib. n.

http://zoobank.org/7C3A602B-EA0F-46D5-8CEE-15BAA2875D00

Type genus. *Euspinolia* Ashmead, 1903. This group was found to be monophyletic in all analyses with very high resampling support (here GC = 90), but somewhat inconsistent in its placement; our justification for including it in the Pseudomethocini appears above. The close association of *Atillum* and *Hoplocrates* has long been recognized, but the inclusion of *Euspinolia* with them and separate from the other pseudomethocines is unexpected. The group is not supported by any unique and unambiguously placed synapomorphies, but there is one unique but ambiguously placed synapomorphy for both additive and non-additive characters: 163.2, fore tibia with obliquely elongate outer secretory pore in males (but absent in some *Euspinolia*). There are 13 unambiguously placed homoplasious synapomorphies, the most significant being: 70.3, fore tibia with obliquely elongate outer secretory pore in females (also only in *Ronisia*); 82.0 and 201.0, tergum I and/or propodeum with simple pubescence in females and males (within Sphaeropthalminae also only in *Cephalomutilla*, *Gogoltilla*, some *Dasymutilla*, some *Bothriomutilla* females, and *Lophomutilla* males); 99.0, head with simple pubescence in males (within Sphaeropthalminae also only in *Cephalomutilla*); 219.1 and 220.1, gonostylus (paramere) short, tapered and apically straight (within Sphaeropthalminae also only in *Myrmilloides*). The subtribe is Neotropical, with three genera; females and males are known for all genera.

Pseudomethocina Brothers, 1975: This group was found to be monophyletic in all analyses (except for that of females only) with low to moderate resampling support (here GC = 39). The group is not supported by any unique synapomorphies, but there are three ambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 12.1, ommatidia faintly distinguishable in females (but also in several terminals elsewhere and further modified in some here); 73.1, metacoxa carinate mesad in females (but also in several other groups); 140.2, axilla anterolaterally with broad vertical flange in winged males (but also in several Sphaeropthalmini *s.s.*). Within the group, the position of *Pseudomethoca* differs from that in the preferred tree (Fig. 5); in the context of the final proposed arrangement (Fig. 13) its position at the base of the group shortens the tree by two steps and is thus preferred; that position was found in one of the analyses (Fig. 8) and approximated in some others. In the analysis of duplicated terminals (Fig. 7), *Pseudomethoca* appeared in two positions, the components being separated by *Lynchiatilla* and *Dimorphomutilla*, but none of the subtending branches had any resampling support. As for *Dasymutilla* (see above), *Pseudomethoca* is generally regarded as a very variable genus (sometimes regarded as distinct from *Sphinctopsis* Mickel, although currently not so), but there has been no comprehensive review of its species, specially recognizing that very many Neotropical taxa are undescribed; we thus tried to capture a fair spectrum of its diversity, mainly for the Nearctic species. The genus obviously needs critical evaluation. The subtribe is Neotropical and Nearctic in distribution, with 21 genera; females are known for 95% and males for 81% of those taxa.

The remaining Mutillidae (distal to Sphaeropthalminae, and disregarding the proposed inclusion of the *Liotilla–Apteromutilla* group) form a monophyletic group in the preferred tree (Fig. 5) and most of the other analyses, but without any resampling support. It is thus not surprising that the group is not supported by any unique synapomorphies, although there are three ambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 61.1, metapleural-propodeal suture obliterated dorsally only in females (but also in several other groups, and apparently a reversal here, so unreliable); 73.1, metacoxa carinate mesad in females (but also in several sphaeropthalmines and a few other terminals, and not in some scattered terminals here); 180.2, pterostigma short and broader than base (but also in *Protophotopsis s.s.* and *Odontomyrme*, and further modified in some terminals).

Dasylabrinae Invrea, 1964: This group (disregarding the *Liotilla–Apteromutilla* group which is now placed here as a distinct tribe) was found to be monophyletic in some of the analyses, including the preferred tree (Figs 4, 5, 8), although generally without resampling support (well illustrated in Fig. 6). In several analyses, however, the *Chrestomutilla*/*Stenomutilla–Seyrigilla*/*Orientilla* and *Dasylabroides–Dasylabris*/*Chrestomutilla* groups were paraphyletic (e.g., Figs 2, 3, 9), and sometimes these components were even more distantly separated (e.g., Figs 7, 10). The analysis of females only produced a paraphyletic grouping which could also be interpreted as including *Brachymutilla* and *Apteromutilla* (Fig. 9), whereas the analysis of males only dissociated these components

markedly, with the *Apteromutilla–Liotilla* group associated with the *Euspinolia–Hoplocrates* group (Fig. 10). The proposed composition of the Dasylabrinae is also discussed above, and seems reasonable. Given the uncertainties, however, it is not surprising that the group is not supported by resampling nor by any unique synapomorphies, and there are only two unambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 162.2, fore tibia with perforated secretory depression in males (also in *Ceratotilla* and *Pseudocephalotilla*, and modified in several terminals here); 166.1, 5–9 articulated meso- and metatibial spines in males (also in several scattered terminals elsewhere, and fewer in some terminals here). In addition, there are six ambiguously placed homoplasious synapomorphies, the most significant being: 55.2, mesopleural ridge strong and joined to mesonotal tubercle in females (also in several sphaeropthalmines, and weaker in some terminals here); 76.1, metatibia with setose secretory patch in females (also in *Cephalomutilla*, some *Dasymutilla* and some *Odontomutilla*, and modified in some terminals here); 203.2, tergum I <0.5 × width of tergum II in males (also in several rhopalomutillines and sphaeropthalmines and a few other terminals, and slightly wider in a few terminals here). The subfamily is Afrotropical, Palaearctic, Oriental and Australian in distribution, with 14 sub/genera; females are known for 93% and males for 100% of those taxa.

Apteromutillini Brothers & Lelej, trib. n.
http://zoobank.org/8CE3B67F-59AC-43DE-B8E4-7111B7E83428

Type genus. *Apteromutilla* Ashmead, 1903. Although the terminals in this group were closely associated in most analyses (see above), and it has low resampling support here (GC = 19), it is not supported by any unique synapomorphies, but there are six unambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 40.2, mesosomal form in females (also in rhopalomutillines and *Protophotopsis s.s.*, and modified in *Liotilla*); 110.2, pedicel distinctly longer than wide in males (also in *Hindustanilla* only); 131.1, humeral angle blunt in males (also in some scattered terminals, and carinate in some *Liotilla*); 174.3, apterous without any trace of wings or tegula in males (also only in *Hindustanilla* and some *Viereckia*); 219.1, gonostylus (paramere) short and narrow (also in ticoplines, some myrmosines and sphaeropthalmines, *Dasylabroides* and *Dasylabris*, and lamellate in *Brachymutilla*). Of interest is that *Brachymutilla* and *Liotilla* are apparently the only Mutillidae to lack cerci in the males (Fig. 11, 216.1), a state found in our analyses also only in Sapyginae, and which is a unique and unambiguous synapomorphy in Mutillidae for those two genera here. The tribe is Afrotropical, with three genera; females and males are known for all genera.

Dasylabrini Invrea, 1964: Although a *Stenomutilla* group was separated from a *Dasylabris* group in several analyses (see above), the position of *Chrestomutilla* varied, being associated with either group. There is thus no good reason to recognize these subgroups formally. The group is not supported by resampling nor by any unique synapomor-

phies, but there are six unambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 49.1, mesosoma with scutellar scale in females (also in most smicromyrmines, many trogaspidiines and several other scattered terminals, and absent in some here); 202.1, tergum I >0.5 × length of tergum II and apically constricted in males (also in most rhopalomutillines and sphaeropthalmines *s.s.* and a few scattered terminals, tergum I shorter in *Dasylabris* and *Chrestomutilla*); 220.0, gonostylus (paramere) apically upcurved (also in most sphaeropthalmines and a few other scattered terminals). In the analysis of duplicated terminals (Fig. 7), both *Stenomutilla* and *Orientilla* emerged as non-monophyletic, the two versions of *Stenomutilla* in particular being separated by *Seyrigilla* and the two paraphyletic *Orientilla* terminals. This suggests that these genera may actually be composite and in need of subdivision, or else that all three "genera" should be combined into a single highly variable *Stenomutilla*. The tribe is Palaearctic, Afrotropical, Oriental and Australian in distribution, with 11 sub/genera; females are known for 91% and males for 100% of those taxa.

The remaining Mutillidae (distal to Dasylabrinae) form a monophyletic group with low to moderate resampling support (here GC = 34) in all of the analyses (except for that of females only, which associated the *Euspinolia–Hoplocrates* group here, and in which most groupings had no resampling support). The group is not supported by any unique synapomorphies, but there are 10 ambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 40.0, mesosoma parallel-sided in females (also in *Areotilla* only, but subsequently modified in a few scattered terminals); 58.1, meso-metapleural suture strongly angled in females (also only in *Tallium*, *Darditilla* and some *Lophomutilla*, and weakly curved in several myrmillines); 179.1, fore wing with constriction in Sc+R only at pterostigmal base (also in several scattered terminals and many dasymutillines, and subsequently modified in some terminals here); 188.1, fore wing crossvein 3r-m without bulla (also in rhopalomutillines, and with bulla in mutillines *s.s.* and *Dolichomutilla*). There are also two ambiguously placed homoplasious synapomorphies for the analysis using additive characters: 54.2, mesopleuron with dorsal region depressed in females (also in ticoplines, some pseudomethocines, *Kudakrumia* and *Pseudophotopsis*, subsequently modified in a few scattered terminals here); 153.1, metapleural-propodeal pleural suture obliterated dorsally but distinct ventrally in winged males (also in many dasymutillines and a few other terminals, and modified in a few terminals here).

Myrmillinae Bischoff, 1920: This group was found to be monophyletic with slight to low resampling support (here GC = 23) in most analyses (excepting only the unweighted analysis using additive characters, consensus tree in Fig. 4, and that of females only, Fig. 9, where *Ceratotilla* and *Viereckia* were associated with *Pristomutilla*, but with no support). It is supported by one unique synapomorphy for both additive and non-additive characters, unambiguously placed for additive characters: 121.3, oral and mandibular fossae separated by fused and depressed cuticular bridge in males (but bridge superficial in *Labidomilla*

and *Odontotilla s.s.*) (28.3, the equivalent state for females, has the same distribution, but is also found in a few sphaeropthalmines and mutillines). There is also one unique but ambiguously placed synapomorphy: 34.2, prementum with sharp posterior median elevation in females (but only in the two "basal" terminals, and thus either reversed in most myrmillines or convergently developed). There are three unambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 9.2, occipital carina undeveloped in females (also in several scattered terminals elsewhere, and distinct dorsally in *Platymyrmilla*); 57.1, mesopleural ridge ventrally sharply carinate in females (also in a few scattered terminals elsewhere and several trogaspidiines); 125.1, mandible with inner basal tooth in males (also in a few scattered terminals elsewhere, and tooth absent in some myrmillines). In the analysis of duplicated terminals (Fig. 7), *Myrmilla s.s.* was non-monophyletic, the two components appearing between *Pseudomutilla* and *Platymyrmilla–Eurygnathilla*. *Platymyrmilla* is currently regarded as a distinct genus, and the other three as subgenera of *Myrmilla*, but all analyses (even those for one sex only) showed *Platymyrmilla* as sister to *Eurygnathilla*, suggesting that *Myrmilla s.l.* is paraphyletic. The analyses did not include other similar genera, such as *Blakeius* Ashmead, however, so their status needs further investigation. The subfamily is Afrotropical, Palaearctic and Oriental in distribution, with 29 sub/genera; females are known for 86% and males for 83% of those taxa.

Mutillinae Latreille, 1802: This group was found to be monophyletic with low resampling support (here GC = 20) in most analyses (excepting that of females only (Fig. 9) where *Pristomutilla* was associated with *Ceratotilla* and *Viereckia*, but with no support). It is supported by one unique but ambiguously placed synapomorphy for both additive and non-additive characters: 94.0, sternum II felt line as dispersed traces in females (but found only in *Odontomutilla* and some *Pristomutilla*; all other mutillines and almost all mutillids have no sternal felt lines in females, so this placement of a putative synapomorphy is highly misleading, it is almost certainly convergent in those two terminals). There are seven unambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 55.5, mesopleural ridge present ventrally only with narrow dorsal ridge to pronotal spiracle in females (also in *Ceratotilla*, and subsequently modified in several terminals here, and varied throughout the mutillids); 136.3, mesoscutal parapsidal furrow much reduced in winged males (also in *Chrestomutilla* and several sphaeropthalmines, and obvious in most ctenomutillines); 141.1, tegula elongated to about trans-scutal articulation (also in ticoplines, rhopalomutillines, some dasymutillines and dasylabrines, and even longer in several terminals here); 177.2, pterostigma unsclerotized (but slight sclerotization in a few terminals). The subfamily is Afrotropical, Oriental, Palaearctic, Neotropical, Nearctic and Australian in distribution, with 110 sub/genera; females are known for 78% and males for 87% of those taxa.

Ctenotillini Brothers & Lelej, trib. n.

http://zoobank.org/98A799DE-7235-4C2B-9009-F12FC85D7525

Type genus. *Ctenotilla* Bischoff, 1920. A group including four terminals (*Mimecomutilla s.s.–Ctenotilla*) was found to be monophyletic in all analyses with high resampling

support and almost always with *Pristomutilla* just basal to it, although generally without support; *Pristomutilla* was more distant in the analysis in which the most-polymorphic characters had been deleted (Fig. 8), but the five terminals formed a monophyletic group in the analysis of males only (Fig. 10), and they were greatly disrupted in the analysis of females only (Fig. 9). As discussed above, inclusion of *Pristomutilla* here seems justified. Given the uncertainties surrounding *Pristomutilla*, it is notable that the Ctenotillini has resampling support (although very low, here GC = 8), but it is not supported by any unique synapomorphies; there is a single unambiguously placed homoplasious synapomorphy for both additive and non-additive characters: 111.0, flagellomere I <0.6 × length of flagellomere II in males (also in most smicromyrmines, some ephutines and some scattered terminals elsewhere). There are also four ambiguously placed homoplasious synapomorphies, the most significant being: 34.1, prementum with posterior dome-like tubercle in females (also in a very few scattered terminals elsewhere, and absent in some *Pristomutilla*); 52.4, posterodorsal margin of propodeum with >3 spines in females (also in *Lynchiatilla*, *Ceratotilla* and *Acanthomutilla*, and no spines in *Mimecomutilla s.s.* and *Mimecotilla*). Despite the fairly poor support for this group as reflected in the trees, we propose that it be formally recognized, specially since it appears as sister to the remaining Mutillinae, with some resampling support, in the proposed final arrangement (Fig. 13). The tribe is Afrotropical, Oriental and Palaearctic in distribution, with 13 sub/genera; females are known for 77% and males for 92% of those taxa.

The remaining Mutillinae (distal to Ctenotillini) formed a monophyletic group with low resampling support in all of the analyses (here GC = 15), except for that where the most-polymorphic characters were deleted (Fig. 8), and that of females only (Fig. 9). The group is not supported by any unique synapomorphies, but there are seven ambiguously placed homoplasious synapomorphies for both additive and non-additive characters, the most significant being: 47.0, posteroventral margin of pronotum distinct and complete in females (also in myrmosines, *Pseudophotopsis*, most sphaeropthalmines, some *Viereckia* and *Ctenotilla*, and modified in some smicromyrmines, *Ephuta* and *Krombeinidia*); 102.4, eye subcircular with inner margin deeply emarginate in males (but eye oval in several terminals and only weakly emarginate in a few); 142.1, tegula posteriorly recurved (also in *Areotilla*, *Pherotilla*, some *Rhopalomutilla*, *Bothriomutilla* and *Ctenotilla*, but posteriorly flattened in some *Mickelomyrme* and longitudinally angulate in *Ephuta*); 143.1, free posterior inner margin of tegula distinctly concave (also in *Areotilla*, some *Smicromyrmilla*, *Bothriomutilla*, *Chaetomutilla* and *Ctenotilla*, and straight in *Ephuta*); 220.2, gonostylus (paramere) apically downcurved (also in most ticoplines, a few myrmillines and some *Chaetomutilla*, and weakly upcurved in *Odontomutilla* and *Yamanetilla*).

Smicromyrmini Bischoff, 1920: This group was found to be monophyletic with some resampling support only in the weighted analysis of non-additive characters (Fig. 3), but was otherwise dissociated in various ways. Many of its component terminals were usually grouped, however, the exceptions being *Promecilla* and *Pseudocephalotilla* which were often shown branching off sequentially distal to the other members (e.g.,

in the preferred tree, Fig. 5). The proposed arrangement (Fig. 13) with *Promecilla* sister to the remaining smicromyrmines and *Pseudocephalotilla* the next to diverge is based on their relative positions in Fig. 5 (*Pseudocephalotilla* there being closer to the other smicromyrmines than *Promecilla*). However, using Fig. 13 as the basis, moving *Promecilla* to be sister to *Ephutomma–Physetopoda* (as in Fig. 3) made no difference to the length of the proposed tree, nor did moving both to reflect the relationships in the preferred tree (Fig. 5). The proposed arrangement thus seems the most reasonable, and additionally has resampling support, although low (GC = 15). The group is supported by one ambiguously placed unique synapomorphy for both additive and non-additive characters: 228.1, volsella with basal ventral lamellate expansion (but no basal lobe in *Pseudocephalotilla*, *Ephutomma* and *Smicromyrme s.s.*). There are two ambiguously placed homoplasious synapomorphies, the more significant being: 85.1, tergum II with unpaired (odd-numbered) discal markings in females (also in various scattered terminals elsewhere, and no markings in some *Promecilla*). In the analysis of duplicated terminals (Fig. 7), *Physetopoda* appeared as paraphyletic to *Ephutomma*. The relationships of these and other taxa closely related to *Smicromyrme* need extensive revision; we recognized that *Smicromyrme* is currently a diverse portmanteau grouping and deliberately restricted our choice of exemplars to include only the type species and a few very similar species, so its appearance as monophyletic in this analysis was expected. The tribe is Afrotropical, Palaearctic and Oriental in distribution, with 30 sub/genera; females are known for 77% and males for 90% of those taxa.

The remaining Mutillinae (distal to Smicromyrmini) formed a monophyletic group, although with no or negligible resampling support, in most of the analyses, except for the equal-weights analysis of non-additive characters (Fig. 2), that of females only (Fig. 9) and that of males only (Fig. 10); resampling support (although very low and thus questionable, GC = 1) was found only in the analysis of duplicated terminals with maximal polymorphy (Fig. 7). The group is supported by one ambiguously placed unique synapomorphy for both additive and non-additive characters: 169.1, metatibia with longitudinal glabrous ridge posteriorly in males (but absent in the *Ephuta–Yamanetilla* group). There are two ambiguously placed homoplasious synapomorphies, the more significant being: 17.0, pedicel shorter than wide in females (also in rhopalomutillines and some scattered terminals elsewhere, and pedicel relatively longer in various terminals here).

Mutillini Latreille, 1802: This group was found to be monophyletic, although with weak to no resampling support, in both analyses of additive characters (Figs 4, 5) and the analyses investigating polymorphisms (Figs 7, 8). All other analyses either showed the two component subgroups as paraphyletic or the components dissociated in various ways. Using the proposed arrangement as the basis (Fig. 13), moving the *Ephuta* group to be sister to the remaining mutillines (as in the weighted analysis of non-additive characters, Fig. 3), an arrangement which would accord better with the LN classification where *Ephuta* and *Odontomutilla* are associated, adds two steps; conversely, making the *Mutilla* group sister to the rest adds three steps. Although the

number of steps involved is small, we prefer to recognize a single tribe including all of these terminals rather than two small tribes; because the components form two distinct groups in most analyses, however, we recognize them at subtribal level. The Mutillini has some resampling support (although very low, here GC = 3), but is supported by no unique synapomorphies; there is, however, one unambiguously placed homoplasious synapomorphy for both additive and non-additive characters: 85.0, tergum II without discal markings in females (also in many scattered terminals elsewhere, and with markings in *Ronisia*, and some *Ephuta* and *Odontomutilla*). There are two additional homoplasious synapomorphies which are also unambiguously placed but for additive characters only: 78.1 and 204.1, tergum I with anterior and dorsal faces distinct but merging in females and males (also in several scattered terminals elsewhere, and faces bounded in *Ephuta*, *Yamanetilla*, and some *Odontomutilla* and *Tropidotilla*). The tribe is Neotropical, Oriental, Afrotropical, Palaearctic, Nearctic and Australian in distribution, with 22 sub/genera; females are known for 73% and males for 73% of those taxa.

Ephutina Ashmead, 1903: This group corresponds to the Ephutinae of the LN classification. The association of *Ephuta* and *Odontomutilla*/*Yamanetilla* is intuitively surprising, since they appear very different morphologically, but it is strongly supported in all analyses (here resampling support is very high, GC = 91). The group is supported by one unique and unambiguously placed synapomorphy for both additive and non-additive characters: 117.3, hypostomal carina strong anterolaterally but obsolete posteriorly in males (not found elsewhere); there is also one unique but ambiguously placed synapomorphy: 89.1, tergum II with felt line a broad patch in females (not found elsewhere, but subsequently uniquely modified in *Odontomutilla* and *Yamanetilla*, so questionably a synapomorphy here). In addition there are 15 unambiguously placed homoplasious synapomorphies, the most significant being: 23.2, gena with strong tooth anteroventrally in females (also in *Atillum* and *Pertyella*, and absent in some *Odontomutilla*); 24.4, hypostomal carina strong anterolaterally but obsolete posteriorly in females (also in *Scaptodactyla* and *Radoszkowskitilla*); 26.2 and 119.2, postgenal ridge distinct and merging with hypostomal carina in females and males (also in females of *Bothriomutilla*, *Odontomyrme* and some *Mimecotilla*, and in males of *Rhopalomutilla*); 73.0, metacoxa smoothly rounded mesad (also in many "more-basal" terminals but in no other mutillines); 118.3, pleurostomal carina long and straight with hypostomal carina to outer mandibular articulation (also in some scattered terminals elsewhere but in no other mutillines); 178.1, fore wing with vein SC lost or much reduced and pterostigma not delimited basally (also in most myrmillines and a few scattered terminals elsewhere but in no other mutillines). In the analysis of duplicated terminals (Fig. 7), *Odontomutilla* appeared as paraphyletic with respect to *Yamanetilla*. The latter essentially comprises a group of species of smaller body size but otherwise very similar to various Oriental *Odontomutilla*, so this result is not surprising, specially when considering that the appearance of the Afrotropical species differs from that of most of the Oriental ones; this is another group which requires extensive revision. The subtribe is Neotropical, Oriental, Nearctic, Afrotropical, Palaearctic and Australian in distribu-

tion, with 12 sub/genera (but *Ephuta* and relatives are New World, and *Odontomutilla* and relatives are Old World, the two components of the subtribe thus not only being morphologically but also biogeographically distinct); females are known for 50% and males for 83% of the taxa. It should be noted that *Cockerellidia* Lelej & Krombein and *Karlidia* Lelej, originally described as pseudomethocines based on females only (see Lelej, 2005), are actually close to *Odontomutilla* and thus fall here (Appendix 4).

Mutillina Latreille, 1802: This group was monophyletic (with low resampling support) only in the analyses using non-additive characters (Figs 2, 3). Otherwise, including in the preferred tree (Fig. 5), *Mutilla* was shown as sister to the ephutines, rendering the remaining Mutillini paraphyletic, or else the components of this group were scattered (the analysis of females only, Fig. 9), or the group included *Dolichomutilla* (the analysis of males only, Fig. 10). Using the proposed arrangement (Fig. 13) as the base, restoring *Mutilla* as sister to the *Ephuta* group shortened the tree by only two steps. The proposed arrangement is thus only insignificantly longer, it accords more closely with the previous classifications, was also shown in some of the analyses, and is thus preferred. The group has some, although very low, resampling support (here GC = 8) and is supported by no unique synapomorphies, but by three ambiguously placed homoplasious synapomorphies for both additive and non-additive characters: 8.1, head not much broadened but long and rounded posteriorly in females (also in *Dolichomutilla*, rhopalomutillines and scattered terminals elsewhere, but not in any other mutillines, and head not long in some *Tropidotilla*); 137.0, mesoscutum posterolaterally evenly rounded in winged males (also in several scattered terminals and the "most-basal" groups, but not in any other mutillines except for *Chaetomutilla*, *Mimecotilla* and some *Dolichomutilla*); 188.0, fore wing crossvein 3r-m with bulla (also in most groups "basal" to Myrmillinae, except rhopalomutillines, and in *Dolichomutilla* but no other mutillines). The subtribe is Afrotropical, Oriental and Palaearctic in distribution, with 10 genera; females are known for 100% and males for 60% of the taxa. It should be noted that *Standfussidia* Lelej, originally described as a pseudomethocine based on the female only (see Lelej, 2005), is similar in appearance to a small *Ronisia*, and falls here (Appendix 4).

Trogaspidiini Bischoff, 1920: Disregarding *Dolichomutilla* (sometimes associated with Mutillini), this group was found to be monophyletic in most analyses: those of non-additive characters (Figs 2, 3), the weighted analysis with additive characters (Figs 5, 6), that with duplicated terminals investigating polymorphisms (Fig. 7) and that of males only (Fig. 10). The other analyses produced varied results, although most components generally grouped together. Within the group, the preferred tree (Fig. 5), and several of the other analyses, showed a moderately supported monophyletic group of six terminals (*Amblotropidia–Trogaspidia s.s.*) which corresponds to LN's Trogaspidiini; the remaining terminals (which would have been placed in LN's Petersenidiini) were generally serially paraphyletic, however, not forming any defined group themselves. Consequently, and because some "petersenidiines" show states approaching those of the "trogaspidiines" and are thus difficult to distinguish from them, we prefer not to recognize LN's "petersenidi-

ine" group, placing its members in Trogaspidiini. *Dolichomutilla* is somewhat aberrant, but it has never previously been associated with the *Mutilla* or *Ephuta* groupings; even in our analyses, although it appeared as sister to the Mutillini in the preferred tree (Fig. 5), this arrangement had no resampling support. In the analyses using non-additive characters (Figs 2, 3) it was sister to the remaining mutillines distal to the *Mutilla* grouping, with some resampling support. That position is therefore proposed here; although placing *Dolichomutilla* sister to *Trispilotilla* shortened the tree by one step, such a position was not found in any of the analyses and so is not proposed for the final arrangement. Using the proposed arrangement as the base (Fig. 13), moving *Dolichomutilla* back to be sister to the Mutillini shortened the tree by only two steps. The group has resampling support (although low, GC = 17), and is supported by one unique and unambiguously placed synapomorphy for both additive and non-additive characters: 113.1, flagellomere I weakly flattened ventrally in males (but strongly flattened in a few). There is also one unambiguously placed homoplasious synapomorphy: 147.1, propodeum with dorsolateral margin carinate in winged males (also in several scattered terminals elsewhere, and rounded in *Timulla* and some species of a few other terminals). In addition, there are four ambiguously placed homoplasious synapomorphies, the most significant being: 112.2, flagellomere I much longer than wide in males (also in several scattered terminals elsewhere). In the analysis of duplicated terminals (Fig. 7), both *Karlissaidia* and *Trogaspidia* were non-monophyletic. In the case of *Karlissaidia*, this is not surprising since our allocation of *K. sexmaculata* to this genus was based on a putative but highly likely association of male and female specimens collected at the same time and place, and differed from its position in Lelej's (2005) catalogue of Oriental species (there placed in *Radoszkowskius* Ashmead, actually *Wallacidia*, the currently valid name for the genus, see Lelej and Brothers 2008). *Trogaspidia* is recognized as needing revision; several genera or subgenera were proposed by Nonveiller (1995) as a first attempt at subdividing it, and we therefore limited our choice of exemplars to a few Afrotropical species expressly included in *Trogaspidia s.s.*, so it is surprising that its two versions emerged as paraphyletic. In the case of both taxa, however, there are very few sex associations for particular species, and much more work is needed to provide greater clarity. The tribe is Afrotropical, Oriental, Palaearctic, Neotropical, Nearctic and Australian in distribution, with 45 sub/genera; females are known for 82% and males for 91% of the taxa.

Conclusions

The variations seen in the results of the different analyses of this most-representative sample of Mutillidae examined to date, including both sexes, many more characters than previous efforts, and aspects of polymorphism, cast doubt on the accuracy of any one of the approaches to be a best estimate of the actual phylogeny/evolutionary history of the components of the family. It is also evident that including many more exemplars and characters, and not using groundplans, has greatly complicated the results, but probably made them more realistic. Consequently, we have proposed a compromise higher classification which takes the results of our various analyses into account

and amalgamates them, and also deviates from the current classifications as little as possible, but thereby provides an informed framework for future studies (Fig. 16). It is obvious from our results, however, that many of the proposed taxa are very difficult to characterize on the basis of unique synapomorphies, generally requiring the presence of a balance of several conditions, none of which is characteristic of the entire taxon. We have thus not attempted the production of a new key to the higher taxa of the Mutillidae of the world [that included in Brothers (1993) did not attempt to take all of the variation within the taxa into account and thus does not successfully place all of the genera]. Regional keys will be more feasible. Appendix 4 places all of the currently valid genera and subgenera into the taxa proposed here, however, and may be used in lieu of a key (individual genera are likely to be more easily recognized than the higher taxa in any case). Despite the extensive nature of our analyses, it is evident that they are not conclusive, being limited to less than 5% of the species, although about 40% of the genera and subgenera. Various of the genera require revision and redelimitation, however, since several are excessively polymorphic. A major limitation has been the lack of genetic molecular data for such a broad representation of exemplars; it will be of considerable interest to see the results of such molecular analyses, and we offer this revised classification as a framework against which those results can be evaluated and compared with the morphological information. Ideally, a combined analysis may then also be done.

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Appendix 1

Specimens examined for phylogenetic analysis of sub/genera of Mutillidae and four outgroup taxa. * = type species of relevant genus/subgenus; "Spp. ♀♀" and "Spp. ♂♂" = number of species represented by female and male specimens respectively; "% poly." = proportion of characters showing polymorphisms in taxon, values above 9% in bold; "Current classification" = placement as in specified papers, or as appropriate for taxa described later (see Fig. 1 for context, differences beyond those of mere taxonomic level in bold); "DB" = lowest taxon in classification of Brothers (1975, 1999) and Mitchell and Brothers (2002); "LN" = lowest taxon in classification of Lelej and Nemkov (1997).

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
Pompilidae, Pepsinae: *Hemipepsis* Dahlbom, 1843: *H. capensis* (Linnaeus, 1764) ♀, ♂, South Africa; **H. errabunda* (de Dalla Torre, 1897) ♀, ♂, South Africa; *H.* ?*hilaris* (Smith, 1879) ♀, ♂, South Africa	3	3	1%	-	-
Tiphiidae, Anthoboscinae: *Anthobosca* Guérin de Méneville, 1838: *A.* spp. ♀♀, ♂♂, South Africa	2	2	1%	-	-
Sapygidae, Fedtschenkiinae: *Fedtschenkia* de Saussure, 1880: *F. grossa* de Saussure, 1880 ♀, ♂, Turkmenistan; *F. anthracina* (Ashmead, 1898) ♀, ♂, USA	2	2	1%	-	-
Sapygidae, Sapyginae: *Krombeinopyga pumila* (Cresson, 1880) ♀, ♂, USA; *Polochrum* sp. ♀, USA; *Sapygina* sp. ♂, South Africa	2	2	7%	-	-
***Acanthomutilla* Nonveiller, 1995:** **A. comparanda* (Bischoff, 1920) ♀, ♂, Zambia, Zimbabwe	1	1	0%	**Smicromyrmina**	**Myrmillinae**
***Allotilla* Schuster, 1949:** **A. gibbosa* Schuster, 1949 ♀, ♂, Paraguay	1	1	0%	Pseudomethocina	Pseudomethocini
***Amblotropidia* Nonveiller, 1995:** **A. aurea* (Bischoff, 1920) ♂, Cameroon; *A. niveomaculata* (André, 1898) ♀, ♂, Eritrea	1	2	5%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Ancistrotilla* Brothers, 2012:** *A. aenigmatica* Brothers, 2012 ♂, New Caledonia; **A. azurea* Brothers, 2012 ♂, Vanuatu; *A. caledonica* (André, 1896) ♀, New Caledonia; *A.* ?*depressa* (Smith, 1879) ♀, ♂, Australia; *A. fabricii* (André, 1898) ♀, ♂, Australia	3	4	2%	Sphaeropthalmina	Sphaeropthalmini
***Apteromutilla* Ashmead, 1903:** **A. aede* (Péringuey, 1899) ♂, South Africa; *A. aethra* (Péringuey, 1899) ♀, South Africa; *A.* spp. ♀♀, ♂♂, South Africa	3	3	1%	Dasylabrini	Dasylabrinae
***Areotilla* Bischoff, 1920:** **A. areolata* Bischoff, 1920 ♂, Lesotho; *A. marshalli* (André, 1903) ♂, Malawi; *A. perplexa* Mitchell & Brothers, 1998 ♀, South Africa; *A. vulgaris* Mitchell & Brothers, 1998 ♂, South Africa	1	3	1%	Ticoplini	Ticoplini
***Artiotilla* Invrea, 1950:** **A. biguttata* (Costa, 1858) ♀, ♂, Cyprus, Montenegro	1	1	0%	**Smicromyrmina**[1]	**Petersenidiini**[1]
***Atillum* André, 1902:** *A. albicomum* Mickel, 1943 ♀, Argentina; *A. allophylum* Mickel, 1943 ♀, Argentina; *A. jucundum* Mickel, 1943 ♀, Argentina; *A. picturatum* Mickel, 1943 ♂, Argentina; *A.* spp. nr. *optabile* Mickel, 1943 ♂♂, Argentina; *A.* sp. nr. *picturatum* Mickel, 1943 ♂, Argentina	3	4	4%	Pseudomethocina	Pseudomethocini
***Bischoffiella* Brothers, 2015:** **B. cristata* (Bingham, 1912) ♀, ♂, Zimbabwe; *B.* sp. ♀, ♂, South Africa	2	2	1%	Rhopalomutillinae	Rhopalomutillinae
***Bischoffitilla* Lelej, 2002:** *B. byblis* (Mickel, 1934) ♀, Philippines; *B. clypealis* (Mickel, 1935) ♂, Malaysia; *B.* spp. ♀, ♂♂, India, Malaysia, Vietnam	2	3	5%	Myrmillinae	Myrmillinae

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Bothriomutilla* Ashmead, 1899:** **B. rugicollis* (Westwood, 1843) ♀, ♂, Australia	1	1	0%	Sphaeropthalmina	Sphaeropthalmini
***Brachymutilla* André, 1901:** **B. androgyna* (André, 1901) ♂, South Africa; *B. gynandromorpha* (André, 1901) ♂, South Africa; *B. namana* Bischoff, 1920 ♀, Namibia; *B. peringueyi* Bischoff, 1920 ♀, South Africa; *B. scabrosa* Bischoff, 1920 ♀, ♂, South Africa; *B.* spp. ♀, ♂, Namibia	4	4	6%	Dasylabrini	Dasylabrinae
***Cephalomutilla* André, 1908:** *C.* ?*confluenta* Mickel, 1960 ♀, Argentina; **C. graviceps* (André, 1903) ♀, Argentina; *C.* ?*vulnerifera* (André, 1908) **comb. n.** ♂, Argentina; *C.* sp. nr. *vulnerifera* (André, 1908) ♂, Argentina	2	2	1%	Sphaeropthalmina	Sphaeropthalmini
***Ceratotilla* Bischoff, 1920:** **C. dolosa* (Smith, 1879) ♀, ♂, South Africa; *C.* spp. ♀♀, South Africa	3	1	4%	Myrmillinae	Myrmillinae
***Chaetomutilla* Nonveiller, 1979:** **C. fornasinii* (Gribodo, 1894) ♀, ♂, South Africa; *C. lobognatha* (André, 1902) ♂, South Africa	1	2	2%	**Smicromyrmina**	**Mutillini**
***Chrestomutilla* Brothers, 1971:** *C.* ?*maja* (Péringuey, 1898) ♀, ♂, South Africa	1	1	0%	Dasylabrini	Dasylabrinae
***Ctenotilla* Bischoff, 1920:** **C. caeca* (Radoszkowski, 1879) ♀, ♂, Armenia, Crimea; *C. guangdongensis* Lelej, 1992 ♀, ♂, China, Laos	2	2	1%	**Smicromyrmina**	**Mutillini**
***Cystomutilla* André, 1896:** **C. ruficeps* (Smith, 1855) ♀, ♂, Croatia, France; *C. teranishii* Mickel, 1935 ♀, ♂, Japan	2	2	0%	Sphaeropthalmina	Sphaeropthalmini
***Darditilla* Casal, 1965:** *D. araxa* (Cresson, 1902) ♀, Paraguay; *D. garciai* Casal, 1968 ♀, Argentina; *D.* spp. ♂♂, Brazil, Costa Rica	2	2	3%	Pseudomethocina	Pseudomethocini
***Dasylabris* Radoszkowski, 1885:** *D. m. maura* (Linnaeus, 1758) ♀, ♂, France; *D. maura sungora* (Pallas, 1773) ♂, Kazakhstan; *D. mephitis* (Smith, 1855) ♀, ♂, South Africa; *D. siberica* (Christ, 1791) ♂, Russia; *D. stimulatrix* (Smith, 1879) ♀, ♂, South Africa	3	5	5%	Dasylabrini	Dasylabrinae
***Dasylabroides* André, 1901:** *D. bechuana* Péringuey, 1914 ♂, Namibia; *D. caffra* (Kohl, 1882) ♂, South Africa; *D. canace* (Péringuey, 1899) ♀, South Africa; **D. capensis* (Saussure, 1867) ♀, South Africa; *D.* ?*neavei* André, 1909 ♀, Zambia; *D. phylira* (Péringuey, 1898) ♂, South Africa; *D.* sp. nr. *idia* (Péringuey, 1899) ♀, ♂, South Africa	4	4	**11%**	Dasylabrini	Dasylabrinae
***Dasymutilla* Ashmead, 1899:** *D. dilucida* Mickel, 1928 ♀, USA; **D. gorgon* (Blake, 1871) ♀, USA; *D. melancholica* (Smith, 1879) ♀, ♂, Dominican Republic; *D. occidentalis* (Linnaeus, 1758) ♀, ♂, USA; *D. quadriguttata* (Say, 1823) ♀, ♂, USA; *D. vestita* (Lepeletier, 1845) ♂, USA	5	4	**18%**	Sphaeropthalmina	Sphaeropthalmini
***Dentilla* Lelej, 1980:** *D. dichroa* (Sichel & Radoszkowski, 1869) ♂, Afghanistan; **D. curtiventris* (André, 1901) ♀, ♂, Armenia; *D. persica* (Sichel & Radoszkowski, 1869) ♀, ♂, Armenia, Greece; *D. saharica* (Giner Mari, 1945) ♀, ♂ Algeria, Morocco, Tunisia	3	4	4%	Smicromyrmina	Smicromyrmini
***Dilophotopsis* Schuster, 1958:** **D. concolor* (Cresson, 1865) ♂, Mexico, USA; *D. stenognatha* Schuster, 1958 ♀, ♂, USA	1	2	3%	Sphaeropthalmina	Sphaeropthalmini
***Dimorphomutilla* Ashmead, 1903:** *D. formosa* Mickel, 1938 ♀, Chile; *D. herbsti* (André, 1904) ♂, Chile; *D.* ?*punctifera* Mickel, 1938 ♂, Chile; *D. reedi* Mickel, 1938 ♀, Chile; *D. suavissima* (Gerstaecker, 1874) ♀, ♂, Chile	3	3	5%	Pseudomethocina	Pseudomethocini

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Dolichomutilla* Ashmead, 1899:** *D. conigera* (André, 1896) ♂, Cameroon; *D. livingstonis* (Kohl, 1882) ♀, South Africa; *D. minor minor* Bischoff, 1920 ♀, ♂, South Africa; *D. scutellifera* (André, 1894) ♀, Cameroon; *D. sycorax* (Smith, 1855) ♀, ♂, South Africa	4	3	4%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Ephuta* Say, 1836:** *E.* ?*arpala* Casal, 1968 ♂, Brazil; *E.* ?*huavunca* Casal, 1968 ♀, Argentina; *E. s. sabaliana* Schuster, 1951 ♂, USA; *E.* sp. nr. *aillanca* Casal, 1968 ♀, Argentina; *E.* sp. nr. *melina* Casal, 1968 or *sauca* Casal, 1968 ♀, Argentina; *E.* ?*spinifera* Schuster, 1951 ♀, USA; *E.* spp. ♀♀, ♂, Mexico, Panama; *E.* ?*tapiola* Casal, 1968 ♂, Argentina	6	4	**12%**	**Ephutini**[2]	**Ephutini**[2]
***Ephutomma* Ashmead, 1899:** *E. angustata* (Skorikov, 1935) ♀, ♂, Kazakhstan, Turkmenistan; **E. turcestanica* (de Dalla Torre, 1897) ♀, ♂, Kazakhstan, Turkmenistan	2	2	0%	Smicromyrmina	Smicromyrmini
***Eurygnathilla* Skorikov, 1927:** **Myrmilla* (*E.*) *ephutommatina* Skorikov, 1927 ♀, ♂, Turkmenistan, Uzbekistan	1	1	0%	Myrmillinae	Myrmillinae
***Eurymutilla* Ashmead, 1899 (near):** nr. *E.* spp. ♀♀♀, ♂♂, Australia	3	2	1%	Sphaeropthalmina	Sphaeropthalmini
***Euspinolia* Ashmead, 1903:** *E.* ?*albicoma* Mickel, 1938 ♂, Chile; *E. canescens* Mickel, 1938 ♂, Chile; *E. clypeata* Mickel, 1938 ♀, Chile; *E. insignita* Mickel, 1938 ♀, Chile; *E. irregularis* (Smith, 1879) ♂, Chile; *E. militaris* Mickel, 1938 ♀, Chile	3	3	6%	Pseudomethocina	Pseudomethocini
***Glossotilla* Bischoff, 1920:** *G. adelpha fuelleborni* Bischoff, 1920 ♀, ♂, South Africa; *G. suavis speculatrix* (Smith, 1879) ♀, ♂, South Africa	2	2	1%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Gogoltilla* Williams, Brothers & Pitts, 2011:** **G. chichikovi* Williams, Brothers & Pitts, 2011 ♀, ♂	1	1	0%	Pseudomethocina	Pseudomethocini
***Hemutilla* Lelej, Tu & Chen in Tu** et al., **2014:** *H. bifurcata* (Chen, 1957) ♀, China; *H. cheni* Tu & Lelej in Tu, Lelej & Chen, 2014 ♀, China; *H. ferrugineipes* Tu, Lelej & Chen, 2014 ♂, China; **H. granulata* Tu, Lelej & Chen, 2014 ♂, China; *H. hoozana* (Zavattari, 1913) ♂, China; *H. tuberculata* Tu, Lelej & Chen, 2014 ♂, China	2	4	6%	Sphaeropthalmina	Sphaeropthalmini
***Hindustanilla* Lelej in Lelej & Krombein, 2001:** **H. indica* Lelej in Lelej & Krombein, 2001 ♂, India; *H. nathani* Lelej in Lelej & Krombein, 2001 ♀, India; *H.* sp. ♂, India	1	2	1%	Smicromyrmillini	Smicromyrmillini
***Hoplocrates* Mickel, 1937:** **H. cephalotes* (Swederus, 1787) ♀, Brazil; *H.* ?*mystica* (Gerstaecker, 1874) ♂, Brazil; *H. pompalis* Mickel, 1941 ♀, Trinidad; *H. speculatrix* (Gerstaecker, 1874) ♀, ♂, Brazil; *H. tartarina* Mickel, 1941 ♀, Ecuador	4	2	7%	Pseudomethocina	Pseudomethocini
***Hoplognathoca* Suárez, 1962:** *H. costarricensis* Suárez, 1962 ♀, ♂, Costa Rica	1	1	0%	Pseudomethocina	Pseudomethocini
***Hoplomutilla* Ashmead, 1899:** *H. acutangula* (Gerstaecker, 1847) ♂, Venezuela; *H. caerulea* Mickel, 1939 ♂, Venezuela; *H. gigantea* (Perty, 1833) ♀, Brazil; *H. opima* Mickel, 1939 ♀, ♂, Trinidad; *H. panamensis* Mickel, 1939 ♀, Panama; *H. rapax* Mickel, 1939 ♀, Ecuador	4	3	5%	Pseudomethocina	Pseudomethocini
***Karlissaidia* Lelej, 2005:** **K. medvedevi* Lelej, 2005 ♀, ♂, Sri Lanka; *K. turneri* Lelej, 2005 ♀, Sri Lanka; *K. sexmaculata* (Swederus, 1787) **comb. n.** ♀, ♂, India	3	2	**12%**	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Krombeinidia* Lelej, 1996:** *K. lilliputiana* (André, 1894) ♂, India; **K. peterseni* Lelej, 1996 ♀, ♂, Sri Lanka; *K.* sp. ♀, Sri Lanka	2	2	2%	**Smicromyrmina**[1]	**Petersenidiini**[1]

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Kudakrumia* Krombein, 1979:** **K. mirabilis* Krombein, 1979 ♀, ♂, Sri Lanka	1	1	0%	Kudakrumiini	Kudakrumiinae
***Labidomilla* André, 1902:** *L. subinermis* André, 1903 ♀, South Africa; **L. tauriceps* (Kohl, 1882) ♀, ♂, South Africa; *L.* spp. ♀♀, ♂♂♂, Malawi, South Africa	4	4	**10%**	Myrmillinae	Myrmillinae
***Liotilla* Bischoff, 1920:** *L.* spp. ♀♀♀♀, ♂♂♂♂♂, Botswana, Namibia, South Africa	4	5	3%	Myrmillinae	Myrmillinae
***Lobotilla* Bischoff, 1920:** **L. leucopyga* (Klug, 1829) ♀, ♂, Cameroon; *L. leucospila* (Cameron, 1910) ♀, ♂, South Africa	2	2	1%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Lomachaeta* Mickel, 1936:** **L. hicksi* Mickel, 1936 ♀, ♂, USA	1	1	0%	Sphaeropthalmina	Sphaeropthalmini
***Lophomutilla* Mickel, 1952:** *L. prionophora* (Burmeister, 1866) ♀, Brazil; *L. seabrai* Casal, 1968 ♀, Brazil; *L.* spp. ♂♂, Brazil, Costa Rica	2	2	4%	Sphaeropthalmina	Sphaeropthalmini
***Lynchiatilla* Casal, 1963:** *L. hoplites* (Gerstaecker, 1874) ♀, Argentina; *L. leguera* Casal, 1963 ♀, ♂, Argentina; *L.* sp. ?*chayera* Casal, 1963 ♂, Argentina; *L. tacana* Casal, 1963 ♀, Argentina	3	2	2%	Pseudomethocina	Pseudomethocini
***Mickelomyrme* Lelej, 1995:** *M.* ?*exacta* (Smith, 1879) ♂, Laos; **M. hageni* (Zavattari, 1913) ♀, ♂, Japan; *M.* ?*kuznetsovi* Lelej, 1996 ♀, Laos; *M. yunnanensis* Lelej, 1996 ♂, Laos	2	3	6%	Smicromyrmina	Smicromyrmini
***Mimecomutilla* Ashmead, 1903:** *M.* (*M.*) *renominanda* Bischoff, 1920 ♀, ♂, South Africa; *M.* (*M.*) *umtata* (Péringuey, 1909) ♀, ♂, South Africa	2	2	2%	**Smicromyrmina**	**Mutillini**
***Mimecotilla* Nonveiller, 1998:** *Mimecomutilla* (*M.*) *bitaeniata* Bischoff, 1920 ♀, ♂, South Africa; **Mimecomutilla* (*M.*) *nyassicola* Bischoff, 1920 ♀, ♂, Cameroon	2	2	4%	**Smicromyrmina**	**Mutillini**
***Mutilla* Linnaeus, 1758:** *M. coerulea* Bischoff, 1920 ♂, Cameroon; **M. europaea* Linnaeus, 1758 ♀, ♂, Austria, Bosnia, Switzerland; *M. quinquemaculata* Cyrillo, 1797 ♀, ♂, Cyprus, Malta; *M. scabrofoveolata penicillata* André, 1895 ♀, South Africa	3	3	7%	Mutillina	Mutillini
***Myrmilla* Wesmael, 1851:** **M. calva* (Villers, 1789) ♀, ♂, Greece, Serbia, Spain; *M. erythrocephala* (Latreille, 1792) ♀, ♂, Cyprus, Greece	2	2	3%	Myrmillinae	Myrmillinae
***Myrmilloides* André, 1902:** **M. grandiceps* (Blake, 1872) ♀, ♂, USA	1	1	0%	Pseudomethocina	Pseudomethocini
***Myrmosa* Latreille, 1797:** **M. atra* Panzer, 1801 ♀, ♂, Denmark, Italy; *M. unicolor* Say, 1824 ♀, ♂, USA	2	2	2%	Myrmosini	Myrmosinae
***Myrmosula* Bradley, 1917:** **M. parvula* (Fox, 1893) ♀, ♂, USA; *M. rutilans* (Blake, 1879) ♀, USA; *M.* sp. nr. *rufiventris* (Blake, 1879) ♂, USA	2	2	0%	Kudakrumiini	Kudakrumiinae
***Nanomutilla* André, 1900:** **N. vaucheri* (Tournier, 1895) ♀, Gibraltar; *N.* spp. ♀♀, ♂♂♂, South Africa, Zimbabwe	3	3	3%	Ticoplini	Ticoplini
***Nemka* Lelej, 1985:** *N. viduata bartholomaei* (Radoszkowski, 1865) ♀, ♂, Kazakhstan; *N. viduata insulae* (Invrea, 1940) ♀, ♂, Cyprus; **N. v. viduata* (Pallas, 1773) ♀, ♂, Czech Republic, Greece, Italy, Slovakia	3	3	1%	Smicromyrmina	Smicromyrmini

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
Odontomutilla **Ashmead, 1899:** *O.* ?*aegrota* (Cameron, 1898) ♀, Zimbabwe; *O.* ?*chione* (Péringuey, 1898) ♀, Lesotho, South Africa; *O.* ?*chionella* Bischoff, 1920 ♂, Lesotho; *O.* ?*cleopatra* (Péringuey, 1899) ♂, South Africa; *O.* ?*fracta* (Saussure, 1891) ♀, Kenya; *O.* ?*inanis* Mickel, 1935 ♀, Papua New Guinea; *O. pulchrina* (Smith, 1855) ♀, ♂, India; *O.* sp. nr. *calida* André, 1908 ♀, Zambia; *O.* sp. nr. *tamensis* (Cameron, 1906) ♀, Australia; *O. tisiphonella* Bischoff, 1920 ♂, South Africa; *O.* ?*tomyris* (Péringuey, 1899) ♀, South Africa	8	4	**11%**	**Mutillina**	**Odonto-mutillini**
Odontomyrme **Lelej, 1983:** *O.* spp. ♀♀♀♀♀, ♂♂♂, Australia, Papua New Guinea	5	3	2%	**Sphaerop-thalmina**	**Odonto-mutillini**
Odontophotopsis **Viereck, 1903:** *O. inconspicua* (Blake, 1886) ♀, ♂, USA; *O. villosa* Mickel in Mickel & Clausen, 1983 ♀, ♂, USA	2	2	9%	Sphaerop-thalmina	Sphaerop-thalmini
Odontotilla **Bischoff, 1920:** **O. bidentata* (André, 1905) ♀, ♂, South Africa	1	1	0%	Myrmil-linae	Myrmil-linae
Orientilla **Lelej, 1979:** *O. aureorubra* (Sichel et Radoszkowski, 1870) ♀, ♂, Sri Lanka; *O. desponsa* (Smith, 1855) ♀, ♂, Vietnam; *O. kallata* (Nurse, 1902) ♀, ♂, Sri Lanka; *O. krombeini* Lelej, 1998 ♀, ♂, Vietnam; *O.* sp. ♂, Vietnam; *O. tausignata* (Chen, 1957) ♀, China	5	5	8%	Dasylab-rini	Dasylab-rinae
Paramyrmosa **de Saussure, 1880:** *P. brunnipes* (Lepeletier, 1845) ♀, ♂, Austria, Serbia; *P. pulla* (Nylander, 1847) ♀, Russia	2	1	1%	Myrmo-sini	Myrmo-sinae
Pertyella **Mickel, 1952:** *P.* ?*beata* (Cameron, 1894) ♀, ♂, Panama; *P. holmbergii* (E.Lynch Arribálzaga, 1878) ♀, Argentina; *P.* ?*salutatrix* (Smith, 1879) ♀, ♂, Costa Rica; *P.* sp. nr. *lenti* Casal, 1964 ♀, Argentina; *P.* sp. ♂, Peru	4	3	2%	Pseudo-methocina	Pseudo-methocini
Pherotilla **Brothers, 2015:** **P. mlanjeana* (Bischoff, 1920) ♀, ♂, Malawi; *P. oceanica* (Mickel, 1935) ♀, ♂, Brunei; *P. rufitincta* (Hammer, 1957) ♀, ♂, Kenya	3	3	**10%**	Rhopalo-mutillinae	Rhopalo-mutillinae
Photomorphus **Viereck, 1903:** *P.* (*P.*) *alogus* Viereck, 1903 ♀, ♂, USA; *P.* (*P.*) *myrmicoides* (Cockerell, 1895) ♀, USA; *P.* (*P.*) *quintilis* (Viereck, 1906) ♂, USA	2	2	0%	Sphaerop-thalmina	Sphaerop-thalmini
Physetopoda **Schuster, 1949:** *P. halensis* (Fabricius, 1787) ♀, ♂, Kazakhstan; *P. pierrei* (Suárez, 1958) ♂, Mauritania, Chad; *P. punctata* (Latreille, 1792) ♀, ♂, Spain; *P. portschinskii* (Radoszkowski, 1888) ♂, Kazakhstan; *P. scutellaris* (Latreille, 1792) ♂, Kazakhstan; *P. daghestanica* (Radoszkowski, 1885) ♂, Kazakhstan, Ukraine	2	6	7%	Smicro-myrmina	Smicro-myrmini
Platymyrmilla **André, 1900:** **P. quinquefasciata* (Olivier, 1811) ♀, ♂, Armenia, Ukraine	1	1	0%	Myrmil-linae	Myrmil-linae
Pristomutilla **Ashmead, 1903:** *P. dentidorsis* (André, 1908) ♀, Malawi; *P. meigangana* Nonveiller, 1995 ♂, Cameroon; *P.* sp. nr. *ctenophora* Bischoff, 1921 ♂, South Africa; *P.* spp. ♀♀, ♂, South Africa, Tanzania	3	3	7%	**Smicro-myrmina**	**Myrmil-linae**
Promecilla **André, 1902:** *P. decora* (Smith, 1879), **comb. n.** ♀, ♂, Malaysia; **P. regia* (Smith, 1855) ♀, ♂, India; *P.* spp. ♀♀, India	4	2	8%	Smicro-myrmina	Smicro-myrmini
Protophotopsis **Schuster, 1947:** **P.* (*P.*) *veneraria* (Melander, 1903) ♀, ♂, USA	1	1	0%	Sphaerop-thalmina	Sphaerop-thalmini
Pseudocephalotilla **Bischoff, 1920:** *P. atropos kalahariensis* (Bischoff, 1921), **comb. n.** ♂, South Africa; *P. beira* (Péringuey, 1914), **comb. n.** ♀, ♂, South Africa; **P. beirana* Bischoff, 1921, Mozambique; *P. tettensis brunni* (Bischoff, 1921), **comb. n.** ♀, South Africa	2	3	7%	**Smicro-myrmina**	**Mutillini**

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Pseudomethoca* Ashmead, 1896:** **P. frigida* (Smith, 1855) ♀, ♂, USA; *P. harpalyce* (Fox, 1899) ♀, USA; *P. oceola* (Blake, 1871) ♂, USA; *P. oculata* (Banks, 1921) ♀, USA; *P. propinqua* (Cresson, 1865) ♀, ♂, USA; *P. ravula* (Cameron, 1894) ♀, Mexico; *P. sanbornii* (Blake, 1871) ♂, USA	5	4	**18%**	Pseudomethocina	Pseudomethocini
***Pseudomutilla* Costa, 1885:** **Myrmilla* (*P.*) *capitata* (Lucas, 1849) ♀, ♂, Italy, Spain; *Myrmilla* (*P.*) *mavromoustakisi* Hammer, 1950 ♀, ♂, Cyprus	2	2	3%	Myrmillinae	Myrmillinae
***Pseudomyrmosa* Suárez, 1980:** *P. gobicola* Lelej, 1981, ♀, ♂, Russia; **P. minuta* (Morawitz, 1894) ♀, ♂, Russia; *P. schlettereri* (Morawitz, 1890) ♀, ♂, Turkmenistan	3	3	3%	Kudakrumiini	Kudakrumiinae
***Pseudophotopsis* Andre, 1896:** *P. binghami* Bischoff, 1920 ♂, United Arab Emirates; *P. continua* (Fabricius, 1804) ♀, ♂, Cameroon; **P. komarovii* (Radoszkowski, 1885) ♀, ♂, Turkmenistan; *P. schachruda* (Skorikov, 1935) ♀, ♂, Cyprus; *P. irana* (Skorikov, 1935) ♂, Iran	3	5	5%	Pseudophotopsidinae	Pseudophotopsidinae
***Radoszkowskitilla* Lelej, 2005:** **R. ceylonica* (Lelej, 1993) ♀, India, Sri Lanka; *R. karnataka* Lelej, 2005 ♂, India; *R. sinhala* Lelej, 2005 ♂, Sri Lanka; *R. tamila* Lelej, 2005 ♂, Sri Lanka	1	3	1%	**Smicromyrmina**[1]	**Petersenidiini**[1]
***Reedomutilla* Mickel, 1964:** *R. dureti* Casal, 1968 ♀, Argentina; *R. fritzi* Casal, 1968 ♂, Argentina; **R. gayi* (Spinola) ♀, ♂, Chile; *R. heraldica* (Smith, 1855) ♀, Argentina; *R. pubescens* (Smith, 1875) ♂, Argentina	3	3	6%	Sphaeropthalmina	Sphaeropthalmini
***Rhopalomutilla* André, 1901:** *R. anguliceps* (André, 1909) ♀, ♂, South Africa; *R. carinaticeps* Bischoff, 1920 ♀, ♂, Kenya, South Africa, Togo; **R. clavicornis* (André, 1901) ♂, Zimbabwe	2	3	7%	Rhopalomutillinae	Rhopalomutillinae
***Rimulotilla* Brothers, 2015:** *R. conifera* (Bischoff, 1920) ♀, ♂, Kenya; **R. tongaana* (Péringuey, 1909) ♀, ♂, South Africa	2	2	2%	Rhopalomutillinae	Rhopalomutillinae
***Ronisia* Costa, 1858:** **R. b. brutia* (Petagna, 1787) ♀, ♂, Austria, Malta	1	1	0%	Mutillina	Mutillini
***Scaptodactyla* Burmeister, 1875:** **S. ?heterogama* Burmeister, 1875 ♀, ♂, Argentina	1	1	0%	Sphaeropthalmina	Sphaeropthalmini
***Seyrigilla* Krombein, 1972:** **Stenomutilla* (*S.*) *nigroaurea* (Sichel & Radoszkowski, 1869) ♂, Madagascar; *Stenomutilla* (*S.*) *splendida* Olsoufieff, 1938 ♀, Madagascar	1	1	0%	Dasylabrini	Dasylabrinae
***Smicromyrme* Thomson, 1870:** *S. bidenticulata* Chen, 1957 ♂, Russia; *S. lewisi* Mickel, 1935 ♀, ♂, Russia, Japan; **S. rufipes* (Fabricius, 1787) ♀, ♂, Austria, England	2	3	3%	Smicromyrmina	Smicromyrmini
***Smicromyrmilla* Suárez, 1965:** *S. ?alata* (Bischoff, 1920) ♂, South Africa; *S. tessmanni* (Bischoff, 1920) ♂, Cameroon; *S.* spp. ♀♀♀♀, ♂, Lesotho, South Africa, Tanzania	4	3	9%	Smicromyrmillini	Smicromyrmillini
***Sphaeropthalma* Blake, 1871:** *Sphaeropthalma* (*S.*) *a. auripilis* (Blake, 1871) ♀, ♂, USA; *Sphaeropthalma* (*S.*) *pensylvanica floridensis* Schuster, 1945 ♀, USA; *Sphaeropthalma* (*S.*) *p. pensylvanica* (Lepeletier, 1845) ♂, USA; **Sphaeropthalma* (*S.*) *pensylvanica scaeva* (Blake,) ♂, USA	2	3	2%	Sphaeropthalmina	Sphaeropthalmini
***Spinulomutilla* Nonveiller, 1994:** *S. aureocincta* (Magretti, 1884) ♀, ♂, Cameroon; *S. braunsi* (Bischoff, 1920) ♀, South Africa; **S. inaequalis* Nonveiller, 1994 ♂, Cameroon; *S. zoe* (Péringuey, 1901) ♂, South Africa	2	3	2%	**Smicromyrmina**[1]	**Trogaspidiini**[1]

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Stenomutilla* André, 1896:** **S. argentata* (Villers, 1789) ♀, ♂, Italy, Spain; *S.* ?*colligera* (André, 1899) ♂, South Africa; *S. eurydice* (Péringuey, 1898) ♀, ♂, Namibia; *S. hottentota* (Fabricius, 1804) ♂, Malta; *S. mlanjiana* Bischoff, 1921 ♂, Zambia; *S.* sp. nr. *togoana* Bischoff, 1921 ♀, Zambia; *S.* sp. ♂, Lesotho; *S. tetrazonia* Skorikov, 1935 ♀, ♂, Kazakhstan, Uzbekistan	4	7	**14%**	Dasylabrini	Dasylabrinae
***Sulcotilla* Bischoff, 1920:** **S. sulcata* (Magretti, 1884) ♀, ♂, Cameroon, Mali, Niger, Senegal	1	1	0%	Smicromyrmina	Smicromyrmini
***Tallium* André, 1902:** *T. catulus* (Burmeister, 1875) ♀, ♂, Argentina; *T. proseni* Casal, 1965 ♀, Argentina; *T.* sp. nr. *precarium* Suárez, 1960 ♂, Argentina; *T. suarezi* Casal, 1968 ♀, Argentina; *T. tenebrosum* (Gerstaecker, 1874) ♀, ♂, Argentina	4	3	5%	Pseudomethocina	Pseudomethocini
***Timulla* Ashmead, 1899:** **T. dubitata* (Smith, 1855) ♀, ♂, USA; *T. ferrugata* (Fabricius, 1804) ♀, ♂, USA; *T. vagans* (Fabricius, 1798) ♀, ♂, USA	3	3	5%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Tobantilla* Casal, 1965:** *T. aleatrix* Williams, Brothers& Pitts, 2011 ♀, Argentina; *T. charrasca* Casal, 1969 ♀, Argentina; *T. drosa* Williams, Brothers& Pitts, 2011 ♂, Argentina; *T. ephemera* Williams, Brothers& Pitts, 2011 ♂, Argentina; **T. montonera* Casal, 1965 ♀, Argentina	3	2	0%	Sphaeropthalmina	Sphaeropthalmini
***Tricholabiodes* Radoszkowski, 1885:** *T. arabicus* Suárez, 1967 ♂, United Arab Emirates; *T. carinifer* Bischoff, 1920 ♀, ♂, Namibia; *T.* ?*lividus* André, 1909 ♀, Namibia; *T. semistriatus* (Klug, 1829) ♀, Israel; *T.* sp. nr. *signatipennis* (André, 1901) ♂, South Africa; *T.* sp. ♂, United Arab Emirates	3	4	7%	Dasylabrini	Dasylabrinae
***Trispilotilla* Bischoff, 1920:** *T. dewitziana* (de Saussure, 1891) ♀, Mozambique; *T. liopyga* (Bischoff, 1920) ♀, South Africa; *T. melanocephala* Bischoff, 1920 ♂, Malawi; *T. monteiroae* Bischoff, 1920 ♂, South Africa; *T. rugifera* Nonveiller, 1973 ♀, Zimbabwe	3	2	3%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Trogaspidia* Ashmead, 1899:** *T. fedtschenkoi* (Radoszkowski, 1877) ♀, ♂, Turkmenistan, Uzbekistan; *T. major* Nonveiller & Petersen, 1995 ♀, ♂, South Africa; *T.* sp. nr. *caffrariae* Bischoff, 1920 ♀, South Africa; *T. themis* (Péringuey, 1898) ♀, ♂, South Africa	4	3	4%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Tropidotilla* Bischoff, 1920:** *T. cruenticeps* (André, 1901) ♀, Cyprus; *T. cypriadis* Invrea, 1940 ♂, Cyprus; *T. fimbriata* (Klug, 1829) ♀, Eritrea; **T. litoralis* (Petagna, 1787) ♀, ♂, Croatia, Greece, Spain; *T. milmili* (Magretti, 1898) ♂, Cameroon	3	3	9%	Mutillina	Mutillini
***Vianatilla* Casal, 1962:** **V. nummularis* (Gerstaecker, 1874) ♀, Argentina; *V.* spp., ♂♂, Costa Rica	1	2	3%	Pseudomethocina	Pseudomethocini
***Viereckia* Ashmead, 1903:** *V.* ?*acrisione* (Péringuey, 1898) ♀, South Africa; *V.* ?*nigra* (Arnold, 1960) ♀, ♂, South Africa; *V.* spp. ♀♀♀, ♂♂♂, Lesotho, South Africa	5	4	**10%**	Myrmillinae	Myrmillinae
***Wallacidia* Lelej & Brothers, 2008:** *W. melmora* (Cameron, 1905) ♂, Indonesia; *W. philippinensis* (Smith, 1855) ♀, ♂, Philippines; *W. singapora* (Mickel, 1935) ♂, Malaysia	1	3	2%	**Smicromyrmina**[1]	**Trogaspidiini**[1]
***Xystromutilla* André, 1905:** **X. asperiventris* André, 1905 ♀, ♂, Brazil; *X. turrialba* Casal, 1969 ♀, ♂, Panama	2	2	**11%**	Sphaeropthalmina	Sphaeropthalmini

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
***Yamanetilla* Lelej, 1996:** *Y. cassiope* (Smith, 1879) ♂, Malaysia; *Y.* ?*cassiope* (Smith, 1879) ♀, Malaysia; **Y. nipponica* (Tsuneki, 1972) ♀, ♂, Japan; *Y. pedaria* (Mickel, 1934) ♀, ♂, Philippines, Vietnam; *Y.* spp. ♀, ♂, Laos, Malaysia	4	4	2%	**Mutillina**	**Odonto-mutillini**
	262	269			

[1]Although the taxon recognized by LN is a component of that recognised by DB, this is considered a sufficient difference to note.

[2]Ephutini is placed in different subfamilies by DB and LN, hence it differs in relationship although not in level.

New combinations specified above are proposed for: *Cephalomutilla* ?*vulnerifera* (André, 1908), **comb. n.** (from *Traumatomutilla* André, 1901, based on sex associations made from molecular-genetic data by Kevin Williams, pers. com.); *Karlissaidia sexmaculata* (Swederus, 1787), **comb. n.** (from *Wallacidia* Lelej & Brothers, 2008, based on putative sex association from specimens collected at same time and place); *Promecilla decora* (Smith, 1879), **comb. n.** (from *Sinotilla* Lelej, 1995, in agreement with assignation by the late Børge Petersen); *Pseudocephalotilla atropos kalahariensis* (Bischoff, 1921), **comb. n.** (from *Smicromyrme* Thomson, 1870, based on as-yet-unpublished comparisons by DJB with the type species of *Pseudocephalotilla*); *Pseudocephalotilla beira* (Péringuey, 1914), **comb. n.** (from *Mutilla* Linnaeus, 1758, as per previous justification); *Pseudocephalotilla tettensis brunni* (Bischoff, 1921), **comb. n.** (from *Smicromyrme* Thomson, 1870, as per previous justification).

Appendix 2

Characters and states for phylogenetic analysis of sub/genera of Mutillidae and four outgroup taxa

All characters are additive/ordered, unless otherwise stated; characters optimized as "fast"/"accelerated" (favouring reversals), except for those considered unlikely to show reversals, and therefore optimized as "slow"/"delayed" (favouring convergences) in Figs 11 and 15: 1, 13, 35, 37, 42, 47, 48, 59, 60, 65, 68, 135, 149, 150, 152, 153, 160, 174, 183, 184, 189, 190, 195–200, 216, 229. Values between square brackets "[…]" are: the percentages of taxa showing polymorphisms for the relevant characters, values above 9% in bold; length (number of steps for state changes, considering additivity), consistency (ci) and retention (ri) indices, as reflected in the most-parsimonious trees found by an unweighted analysis including additive characters.

1. Both sexes — Eye, pubescence and pores: 0 = Both present; 1 = Pubescence absent, pores present; 2 = Both absent. [0%; length = 6, ci = 0.33, ri = 0.80]
2. Both sexes — Pronotum, latero-ventral pubescent pit: 0 = Absent; 1 = Present. [0%; length = 1, uninformative]
3. Both sexes — Metasternum, level: 0 = Not depressed; 1 = Depressed. [0%; length = 1, uninformative]
4. Both sexes — Metasternum, form: 0 = Simple and flattened; 1 = With Y- to V-shaped carina or ridge, posterior arms leading to metacoxae bounding posterior median depression; 2 = With posterior median process(es) only. (NONADDITIVE) [1%; length = 1, ci = 1.00, ri = 1.00]
5. Both sexes — Metacoxa, postero-dorsally: 0 = Simple; 1 = With carinate tubercle; 2 = With lamellate process. [2%; length = 3, ci = 0.66, ri = 0.94]
6. Both sexes — Sternum I, posterolateral rounded densely pubescent depression: 0 = Absent; 1 = Present. [0%; length = 1, uninformative]
7. Both sexes — Tergum II and sternum I: 0 = Not articulated; 1 = Articulated, tergum II overlying lateral extremities of sternum I. [0%; length = 1, ci = 1.00, ri = 1.00]
8. Female — Head, shape: 0 = Normal, transverse, rounded posterolaterally; 1 = Normal, long, rounded posterolaterally; 2 = Broad, transverse, rounded posterolaterally; 3 = Broad, long, rounded posterolaterally; 4 = Broad, long, rectangular posterolaterally; 5 = Broad, transverse, protuberant/angular posterolaterally. (NONADDITIVE) [7%; length = 26, ci = 0.19, ri = 0.46]
9. Female — Occipital carina: 0 = Distinct and reflexed, complete; 1 = Distinct and reflexed, dorsal only; 2 = Absent, or not reflexed and scarcely discernible. [4%; length = 25, ci = 0.08, ri = 0.45]
10. Female — Eye, form: 0 = Weakly convex, following head contour; 1 = Moderately convex, distinct from head contour; 2 = Strongly convex, disjunct from head contour. [4%; length = 18, ci = 0.11, ri = 0.66]

11. Female — Eye, shape: 0 = Oval, inner margin more-or-less convex, long axis vertical; 1 = Oval, inner margin obviously sinuate or emarginate; 2 = Subcircular, inner margin convex, long axis vertical; 3 = Subcircular, inner margin convex, long axis horizontal. (NONADDITIVE) [**10%**; length = 13, ci = 0.23, ri = 0.82]
12. Female — Eye, surface: 0 = Ommatidia distinct; 1 = Ommatidia faintly distinguishable; 2 = Smooth, ommatidia not distinguishable. [3%; length = 13, ci = 0.15, ri = 0.63]
13. Female — Ocelli: 0 = Present, functional; 1 = Present but rudimentary; 2 = Absent. [1%; length = 4, ci = 0.50, ri = 0.80]
14. Female — Antennal socket, rim: 0 = Simple; 1 = Dorsally expanded as lamellate "tubercle" overhanging antennal base; 2 = Frons expanded as a ledge overhanging antennal socket. (NONADDITIVE) [0%; length = 3, ci = 0.66, ri = 0.50]
15. Female — Scape, radicle: 0 = Simple annular differentiation, not angled; 1 = Simple annular differentiation, angled; 2 = Flangelike expansion above radicle, angled. [0%; length = 2, ci = 1.00, ri = 1.00]
16. Female — Pedicel, length: 0 = Very short, <0.4 × length of flagellomere I; 1 = Short, >0.4 <0.7 × length of flagellomere I; 2 = About as long as flagellomere I. [4%; length = 23, ci = 0.08, ri = 0.51]
17. Female — Pedicel, shape: 0 = Shorter than wide; 1 = As long as wide; 2 = Longer than wide. [6%; length = 32, ci = 0.06, ri = 0.26]
18. Female — Flagellomere number: 0 = 10; 1 = 11. [0%; length = 1, ci = 1.00, ri = 1.00]
19. Female — Flagellomere I, length: 0 = Shorter than flagellomere II; 1 = 1–1.5 × length of flagellomere II; 2 = >1.8 × length of flagellomere II. [4%; length = 13, ci = 0.15, ri = 0.63]
20. Female — Flagellomere I, shape: 0 = Shorter than wide; 1 = About as long as wide; 2 = >1.3 <2.0 × as long as wide; 3 = >2 × as long as wide. [7%; length = 25, ci = 0.12, ri = 0.48]
21. Female — Genal carina: 0 = Absent; 1 = Present but weak; 2 = Present and strong. [**11%**; length = 28, ci = 0.07, ri = 0.54]
22. Female — Genal carina, extent (carina absent = -): 0 = Ending distant from hypostomal carina; 1 = Ending adjacent to hypostomal carina; 2 = Continuous with hypostomal carina. [3%; length = 17, ci = 0.11, ri = 0.37]
23. Female — Genal carina, armature (carina absent = -): 0 = Carina simple, unarmed; 1 = With small lamellate tooth anteroventrally; 2 = With strong conical or pyramidal tooth anteroventrally; 3 = With teeth posterodorsally and anteroventrally. (NONADDITIVE) [3%; length = 6, ci = 0.50, ri = 0.40]
24. Female — Hypostomal carina: 0 = Complete, simple; 1 = Complete, flange-like; 2 = Complete, with distinct tooth laterally; 3 = Complete, with tooth/tubercle/elevation at about midlength; 4 = Strong anterolaterally but obsolete posteriorly; 5 = Strong posteriorly but absent anterolaterally. (NONADDITIVE) [7%; length = 25, ci = 0.20, ri = 0.53]

25. Female — Pleurostomal carina: 0 = Absent; 1 = Slight, ending at inner mandibular edge; 2 = Distinct, together with hypostomal carina forming curved to angulate ridge ending at outer mandibular articulation; 3 = Distinct, together with hypostomal carina forming straight ridge ending at outer mandibular articulation. [4%; length = 28, ci = 0.10, ri = 0.46]
26. Female — Postgenal carina/ridge: 0 = Absent; 1 = Distinct, separate from hypostomal carina; 2 = Distinct, merging with hypostomal carina. [4%; length = 15, ci = 0.13, ri = 0.66]
27. Female — Postmandibular carina (posteroventral to mandible base): 0 = Absent; 1 = Present, simple blunt ridge. [0%; length = 4, ci = 0.25, ri = 0.50]
28. Female — Oral and mandibular fossae: 0 = Continuous, junction about half mandible width or more; 1 = Continuous, junction much narrowed; 2 = Separated by anteriorly unfused depressed cuticular bridge; 3 = Separated by anteriorly fused much-depressed cuticular bridge; 4 = Separated by anteriorly fused superficial cuticular bridge. [3%; length = 26, ci = 0.15, ri = 0.78]
29. Female — Mandible, apical teeth: 0 = Three; 1 = Two; 2 = One. [7%; length = 23, ci = 0.08, ri = 0.40]
30. Female — Mandible, shape: 0 = Apically not expanded; 1 = Apically expanded. [3%; length = 7, ci = 0.14, ri = 0.33]
31. Female — Mandible, posteroventral basal expansion: 0 = Absent; 1 = Present, toothlike; 2 = Present, flangelike, apically abrupt; 3 = Present, flangelike, apically oblique. (NONADDITIVE) [5%; length = 11, ci = 0.27, ri = 0.00]
32. Female — Mandible, inner basal tooth: 0 = Absent; 1 = Present, acute; 2 = Present, mediobasal obtuse flange. (NONADDITIVE) [2%; length = 13, ci = 0.15, ri = 0.35]
33. Female — Labio-maxillary complex: 0 = Short; 1 = Elongated prementum and stipes. [0%; length = 1, ci = 1.00, ri = 1.00]
34. Female — Prementum: 0 = Evenly convex to weakly medio-longitudinally carinate; 1 = With posteromedian domelike tubercle or elevation; 2 = With sharp posteromedian elevation; 3 = With anteriorly indented posteromedian domelike elevation; 4 = Flattened, depressed to weakly concave; 5 = Longitudinally convex with deep narrow anteromedian groove; 6 = With strong long narrow median carina; 7 = With paired medial longitudinal carinae. (NONADDITIVE) [3%; length = 14, ci = 0.50, ri = 0.50]
35. Female — Maxillary palp, segments: 0 = Six-segmented; 1 = Two-segmented; 2 = Unsegmented. [2%; length = 2, ci = 1.00, ri = 1.00]
36. Female — Maxillary palp, length: 0 = Shorter than fore tibia; 1 = 1–1.5 × length fore tibia; 2 = >1.5 <2 × length fore tibia; 3 = >2 × length fore tibia. [**10%**; length = 28, ci = 0.10, ri = 0.37]
37. Female — Labial palp, segments: 0 = Four-segmented; 1 = Two-segmented; 2 = Unsegmented. [2%; length = 2, ci = 1.00, ri = 1.00]
38. Female — Wings: 0 = Present; 1 = Absent. [0%; length = 1, ci = 1.00, ri = 1.00]

39. Female — Mesosomal dorsum, flattened decumbent setae: 0 = Absent; 1 = Present, laterally flattened, slender, arcuate; 2 = Present, laterally flattened, broad, lanceolate; 3 = Present, dorsoventrally flattened, slender, arcuate. (NONADDITIVE) [0%; length = 8, ci = 0.37, ri = 0.44]
40. Female — Mesosoma, form (dorsal view; winged = -): 0 = More or less parallel-sided; 1 = Mesothorax protuberant well anterior to metathoracic spiracle, propodeum narrower than prothorax; 2 = Mesothorax protuberant just anterior to metathoracic spiracle, propodeum narrower than prothorax; 3 = Ovate, propodeum about as broad as prothorax; 4 = Mesothorax margin straightish, propodeum much broader than prothorax; 5 = Mesothorax margin dorsally concave, pronotum broadest; 6 = Pronotum broadest, mesothoracic margin straightish, mesosoma evenly narrowed posteriorly. (NONADDITIVE) [6%; length = 15, ci = 0.40, ri = 0.81]
41. Female — Mesosoma, dorsolateral margin: 0 = Smooth, sinuate or weakly tuberculate; 1 = With distinct teeth. [5%; length = 11, ci = 0.09, ri = 0.33]
42. Female — Pro-mesonotal suture: 0 = Distinct and freely articulating; 1 = Distinct but fused, not articulating; 2 = Obliterated or very indistinct and fused, not articulating. [1%; length = 2, ci = 1.00, ri = 1.00]
43. Female — Pronotum, lateral length: 0 = About as long as distance between pronotal and propodeal spiracles; 1 = <0.8 × distance between pronotal and propodeal spiracles. [2%; length = 8, ci = 0.12, ri = 0.61]
44. Female — Pronotum, humeral angle: 0 = Rounded; 1 = Abrupt; 2 = Vertically carinate to weakly dentate; 3 = With prominent tooth or spine. [8%; length = 43, ci = 0.06, ri = 0.33]
45. Female — Pronotum, dorsolateral setose area/epaulet: 0 = Absent; 1 = Present, dispersed patch; 2 = Present, clearly delimited tubercle/tuft. [3%; length = 21, ci = 0.09, ri = 0.71]
46. Female — Pronotum, anterodorsal setose area/epaulet: 0 = Absent; 1 = Present, dispersed patch; 2 = Present, clearly delimited tubercle/tuft. [5%; length = 22, ci = 0.09, ri = 0.67]
47. Female — Pronotum, posteroventral margin: 0 = Distinct and complete; 1 = Indistinct or interrupted; 2 = Obliterated. [4%; length = 27, ci = 0.07, ri = 0.59]
48. Female — Meso-metanotal suture: 0 = Distinct; 1 = Obliterated or very indistinct. [0%; length = 2, ci = 0.50, ri = 0.75]
49. Female — Mesosoma, scutellar scale (winged = -): 0 = Absent; 1 = Present. [2%; length = 11, ci = 0.09, ri = 0.61]
50. Female — Propodeum, shape: 0 = >0.6 × as long as wide; 1 = <0.6 × as long as wide. [4%; length = 26, ci = 0.03, ri = 0.35]
51. Female — Propodeum, posterodorsal margin, form: 0 = Smoothly rounded; 1 = Abrupt but not ridgelike; 2 = Carinate or ridgelike. [3%; length = 28, ci = 0.07, ri = 0.51]
52. Female — Propodeum, posterodorsal margin, dentition: 0 = Smooth or tuberculate; 1 = With one weak median spine or vertical tubercle; 2 = With two

lateral spines or teeth only; 3 = With three spines; 4 = With more than three spines; 5 = With two median teeth and two lateral spines or teeth; 6 = With two large sublateral cylindrical spines. (NONADDITIVE) [2%; length = 14, ci = 0.42, ri = 0.38]

53. Female — Propodeum, posterolateral margin: 0 = Smooth or tuberculate; 1 = Dentate or spinose. [0%; length = 10, ci = 0.10, ri = 0.25]
54. Female — Mesopleuron, dorsal region: 0 = Strongly protuberant; 1 = Weakly convex; 2 = Depressed. [4%; length = 22, ci = 0.09, ri = 0.73]
55. Female — Mesopleural ridge (usually setose): 0 = Absent; 1 = Indistinct and joined to mesonotal tubercle; 2 = Strong and joined to mesonotal tubercle; 3 = Joined to pronotal spiracle; 4 = Present only ventrally, with a narrow dorsal ridge to mesonotal tubercle; 5 = Present only ventrally, with a narrow dorsal ridge to pronotal spiracle; 6 = Present only ventrally; 7 = Ventrally evanescent, a dorsal ridge to pronotal spiracle; 8 = Entirely indistinct, joined to pronotal spiracle; 9 = A fine ridge approaching pronotal spiracle. (NONADDITIVE) [**10%**; length = 34, ci = 0.26, ri = 0.62]
56. Female — Mesopleural ridge, ventral section, position (absent = -): 0 = Anterior to midpoint of mesocoxa; 1 = Dorsal to midpoint of mesocoxa. [1%; length = 2, ci = 0.50, ri = 0.66]
57. Female — Mesopleural ridge, ventral section, form (absent = -): 0 = Blunt; 1 = Sharply carinate. [4%; length = 9, ci = 0.11, ri = 0.68]
58. Female — Meso-metapleural suture, direction (indistinguishable = -): 0 = Weakly curved (separate from mesopleural ridge); 1 = Strongly angled (joining mesopleural ridge). [2%; length = 4, ci = 0.25, ri = 0.91]
59. Female — Meso-metapleural suture, development: 0 = Distinct; 1 = Distinct ventrally only; 2 = Obliterated on surface. [4%; length = 18, ci = 0.11, ri = 0.38]
60. Female — Meso-metapleural "bridge": 0 = Absent; 1 = Present. [0%; length = 1, ci = 1.00, ri = 1.00]
61. Female — Metapleural-propodeal suture, development: 0 = Entirely distinct; 1 = Obliterated dorsally, distinct ventral to endophragmal pit; 2 = Obliterated dorsally, vague ventral to endophragmal pit; 3 = Entirely obliterated on surface; 4 = Distinct dorsally, obliterated ventral to endophragmal pit. (NONADDITIVE) [**11%**; length = 29, ci = 0.13, ri = 0.55]
62. Female — Mesosternum just anterior to mesocoxae: 0 = Smoothly rounded; 1 = With paired transverse/oblique carinae (may be toothed mesally); 2 = With paired lamellate projections mesally. (NONADDITIVE) [1%; length = 2, uninformative]
63. Female — Mesocoxae, contiguity: 0 = Contiguous mesally; 1 = Slightly separated mesally. [1%; length = 3, ci = 0.33, ri = 0.71]
64. Female — Metasternum, posterior median process (absent = -): 0 = Shorter than coxal height, tridentate; 1 = Shorter than coxal height, shallowly bidentate; 2 = Shorter than coxal height, deeply bidentate; 3 = Shorter than coxal height, unidentate; 4 = Longer than coxal height, tridentate; 5 = Longer than coxal

height, acutely unidentate; 6 = Longer than coxal height, obtusely unidentate; 7 = Shorter than coxal height, a transverse crenulate ridge. (NONADDITIVE) [5%; length = 28, ci = 0.25, ri = 0.58]

65. Female — Metacoxal cavities: 0 = Open; 1 = Partially closed; 2 = Closed. [0%; length = 3, ci = 0.66, ri = 0.80]
66. Female — Tarsomeres, apicoventral median ovoid pulvillus: 0 = Absent; 1 = On tarsomeres I–IV. [0%; length = 1, uninformative]
67. Female — Tarsal claws: 0 = Midventrally toothed; 1 = Simple; 2 = Apically deeply bifid. (NONADDITIVE) [0%; length = 3, ci = 0.66, ri = 0.66]
68. Female — Arolia: 0 = Present; 1 = Absent. [0%; length = 2, ci = 0.50, ri = 0.80]
69. Female — Fore tibia, inner (anterior) secretory structure: 0 = None; 1 = Broad coarsely setose delimited patch; 2 = Linear to oval finely perforated depression; 3 = Vertically elongate groove/pore; 4 = Obliquely elongate groove/pore; 5 = Obliquely oval to circular pore; 6 = Obliquely elongate groove/pore and linear finely perforated depression; 7 = Two apical separated obliquely oval pores; 8 = Linear to oval finely perforated convexity; 9 = Basal elongate/oval and separated apical round pores. (NONADDITIVE) [6%; length = 27, ci = 0.33, ri = 0.64]
70. Female — Fore tibia, outer (posterior) secretory structure: 0 = None; 1 = Linear to oval finely perforated depression; 2 = Vertically elongate groove/pore; 3 = Obliquely elongate groove/pore; 4 = Obliquely oval to circular pore. (NONADDITIVE) [3%; length = 17, ci = 0.17, ri = 0.36]
71. Female — Fore calcar blade: 0 = Linearly narrow, margin entire; 1 = Linearly narrow, margin finely pectinate; 2 = Expanded, longish >0.4 × length of calcar; 3 = Expanded, almost square, <0.4 × length of calcar; 4 = Concave, narrow, apically expanded. (NONADDITIVE) [0%; length = 6, ci = 0.66, ri = 0.84]
72. Female — Meso- and metatibial articulated spines, mean number: 0 = 0–4; 1 = 5–9; 2 = 10–14; 3 = >14. [**12%**; length = 28, ci = 0.10, ri = 0.40]
73. Female — Metacoxa, mesally: 0 = Smoothly rounded; 1 = Longitudinally carinate. [5%; length = 9, ci = 0.11, ri = 0.80]
74. Female — Metatibia, apex dorsally: 0 = Evenly rounded; 1 = With elevated tubercle bearing spine(s); 2 = With cylindrical process bearing spine. [3%; length = 9, ci = 0.22, ri = 0.22]
75. Female — Metatibia, posterior (inner) surface: 0 = Convex, setose, punctate; 1 = Flattened and broadened, with smooth delimited area. [0%; length = 1, ci = 1.00, ri = 1.00]
76. Female — Metatibia, posteroapical secretory structure: 0 = Absent; 1 = Present, delimited patch of dense setae; 2 = Present, linear setose felt-line-like; 3 = Present, a small pore; 4 = Present, a deep narrow longitudinal groove. (NONADDITIVE) [3%; length = 12, ci = 0.33, ri = 0.63]
77. Female — Metatibia, apical spurs: 0 = Both similar, unmodified; 1 = Inner modified as cleaner. [0%; length = 2, ci = 0.50, ri = 0.80]

78. Female — Tergum I, profile: 0 = Broadly convex; 1 = Anterior and dorsal faces merging; 2 = Anterior and dorsal faces distinct, bounded. [**10%**; length = 30, ci = 0.06, ri = 0.37]
79. Female — Tergum I, base: 0 = Simple; 1 = With paired vertical ridges; 2 = With paired expanded "auricles". (NONADDITIVE) [2%; length = 3, ci = 0.66, ri = 0.88]
80. Female — Tergum I, shape: 0 = ≥0.5 × length of tergum II, gradually broadened posteriorly, sessile on tergum II; 1 = ≥0.4 × length of tergum II, strongly broadened, parallel-sided posteriorly, discontinuous with tergum II; 2 = <0.5 × length of tergum II, gradually broadened posteriorly, sessile on tergum II; 3 = <0.5 × length of tergum II, gradually broadened posteriorly, constricted apically, disjunct from tergum II; 4 = <0.25 × length of tergum II, entirely parallel-sided, discontinuous with tergum II. (NONADDITIVE) [4%; length = 11, ci = 0.36, ri = 0.63]
81. Female — Tergum I, apical width: 0 = >0.75 × width of tergum II; 1 = <0.75 >0.5 × width of tergum II; 2 = <0.5 × width of tergum II. [5%; length = 21, ci = 0.09, ri = 0.51]
82. Female — Tergum I and propodeum, pubescence: 0 = All simple; 1 = Some brachyplumose; 2 = Some fully plumose. [2%; length = 6, ci = 0.33, ri = 0.87]
83. Female — Tergum I apex, pale pubescent markings: 0 = None; 1 = Median pale spot; 2 = Paired pale spots; 3 = Pale band. (NONADDITIVE) [**15%**; length = 31, ci = 0.09, ri = 0.39]
84. Female — Tergum II, length: 0 = <0.75 × length of terga III–VI; 1 = 0.75–1.25 × length of terga III–VI; 2 = >1.25 × length of terga III–VI. [1%; length = 10, ci = 0.20, ri = 0.73]
85. Female — Tergum II, pale markings, number: 0 = None; 1 = Odd number (unpaired); 2 = Even number (paired); 3 = Broad band. (NONADDITIVE) [**13%**; length = 21, ci = 0.14, ri = 0.63]
86. Female — Tergum II, pale markings, composition (absent = -): 0 = Pubescence only; 1 = Integumental. [6%; length = 7, ci = 0.14, ri = 0.50]
87. Female — Tergum II, apical fringe setae: 0 = Entirely simple; 1 = Some densely plumose. [0%; length = 1, ci = 1.00, ri = 1.00]
88. Female — Tergum II, felt line, presence: 0 = Absent; 1 = Present = 1. [1%; length = 4, ci = 0.25, ri = 0.81]
89. Female — Tergum II, felt line, form (absent = -): 0 = Linear and superficial; 1 = Broad lateral patch; 2 = Invaginated (elongate or pitlike); 3 = Small indefinite anterior patch. (NONADDITIVE) [0%; length = 3, ci = 1.00, ri = 1.00]
90. Female — Tergum III, stridulitrum: 0 = Absent; 1 = Present. [0%; length = 4, ci = 0.25, ri = 0.66]
91. Female — Tergum VI, form: 0 = Entirely evenly sculptured; 1 = Evenly sculptured except apical area much finer/smoother; 2 = With smooth(ish) unbounded longitudinal median area, laterally sculptured; 3 = With distinct bounded pygidial plate. (NONADDITIVE) [6%; length = 19, ci = 0.15, ri = 0.52]

92. Female — Sternum I, differentiation: 0 = Smoothly overlapping sternum II; 1 = Briefly declivous and abutting sternum II; 2 = Depressed posteriorly, constricted and abutting sternum II. [1%; length = 2, ci = 1.00, ri = 1.00]
93. Female — Sternum II, felt line, presence: 0 = Absent; 1 = Present. [3%; length = 5, ci = 0.20, ri = 0.42]
94. Female — Sternum II, felt line, form (absent = -): 0 = Dispersed traces only; 1 = Distinctly compact and linear. [1%; length = 1, uninformative]
95. Female — Sternum VI, sting aperture: 0 = Lateral areas differentiated, sting aperture slit-like; 1 = Lateral areas dorsomesally produced, sting aperture circular. [0%; length = 1, ci = 1.00, ri = 1.00]
96. Female — Sternum VI, armature: 0 = Without processes; 1 = With pair of apical processes (apex notched); 2 = With pair of acute lateral teeth basally; 3 = With two pairs of lateroventral tubercles; 4 = With two pairs of apical processes/teeth (apex 4-lobed). (NONADDITIVE) [8%; length = 22, ci = 0.18, ri = 0.41]
97. Female — Gonapophysis IX, sting curvature: 0 = Weakly convexly arcuate dorsally; 1 = Strongly convexly arcuate dorsally, apex directed downwards. [0%; length = 2, ci = 0.50, ri = 0.50]
98. Male — Head, width across mandibular bases: 0 = <0.6 × maximum head width; 1 = >0.6 × maximum head width. [1%; length = 4, ci = 0.25, ri = 0.57]
99. Male — Head, pubescence: 0 = Entirely simple; 1 = Some brachyplumose; 2 = Some fully plumose. [2%; length = 6, ci = 0.33, ri = 0.88]
100. Male — Occipital carina: 0 = Distinct and reflexed, complete; 1 = Distinct and reflexed, dorsal only; 2 = Absent, or not reflexed and scarcely discernible. [5%; length = 17, ci = 0.11, ri = 0.28]
101. Male — Eye, form: 0 = Weakly convex, following head contour; 1 = Moderately convex, distinct from head contour; 2 = Strongly convex, disjunct from head contour. [5%; length = 21, ci = 0.09, ri = 0.66]
102. Male — Eye, shape: 0 = Broadly oval, inner margin convex to weakly sinuate; 1 = Broadly oval, inner margin acutely but shallowly emarginate; 2 = Broadly oval, inner margin acutely and deeply emarginate; 3 = Subcircular, inner margin sinuate to weakly emarginate; 4 = Subcircular, inner margin acutely and deeply emarginate; 5 = Subcircular, inner margin roughly convex, long axis vertical; 6 = Subcircular, inner margin roughly convex, long axis horizontal. (NONADDITIVE) [6%; length = 19, ci = 0.31, ri = 0.82]
103. Male — Eye, surface: 0 = Ommatidia distinct; 1 = Ommatidia faintly distinguishable; 2 = Smooth, ommatidia not distinguishable. [2%; length = 13, ci = 0.15, ri = 0.31]
104. Male — Ocelli: 0 = Present, normal; 1 = Present, much enlarged; 2 = Absent. (NONADDITIVE) [3%; length = 6, ci = 0.33, ri = 0.20]
105. Male — Antennal socket, rim: 0 = Simple; 1 = Dorsally expanded as lamellate "tubercle" overhanging antennal base; 2 = Frons expanded as a ledge overhanging antennal socket. (NONADDITIVE) [0%; length = 2, ci = 1.00, ri = 1.00]

106. Male — Antennal scrobe, dorsal secretory tubercle and carina: 0 = No tubercle, no carina; 1 = Weak transverse carina only; 2 = Strong transverse carina only; 3 = Secretory tubercle only; 4 = Secretory tubercle and weak transverse carina; 5 = Secretory tubercle and strong transverse carina. (NONADDITIVE) [**19%**; length = 37, ci = 0.13, ri = 0.54]
107. Male — Scape, radicle: 0 = Simple annular differentiation, not angled; 1 = Simple annular differentiation, angled; 2 = Flangelike expansion above radicle, angled. [0%; length = 3, ci = 0.66, ri = 0.83]
108. Male — Scape, ventral ridges: 0 = None; 1 = One only; 2 = Two, one less developed; 3 = Two, equally well developed. [**11%**; length = 38, ci = 0.07, ri = 0.58]
109. Male — Pedicel, length: 0 = Very short, <0.4 × length of flagellomere I; 1 = Short, >0.4 <0.8 × length of flagellomere I; 2 = About as long as flagellomere I. [**10%**; length = 24, ci = 0.08, ri = 0.35]
110. Male — Pedicel, shape: 0 = Distinctly shorter than wide; 1 = About as long as wide; 2 = Distinctly longer than wide. [**12%**; length = 25, ci = 0.08, ri = 0.37]
111. Male — Flagellomere I, length: 0 = <0.6 × length of flagellomere II; 1 = Subequal to flagellomere II; 2 = >1.3 × length of flagellomere II. [6%; length = 15, ci = 0.13, ri = 0.43]
112. Male — Flagellomere I, shape: 0 = Wider than long; 1 = About as long as wide; 2 = >1.3 <2.0 × as long as wide; 3 = >2 × as long as wide. [**12%**; length = 30, ci = 0.10, ri = 0.54]
113. Male — Flagellomere I, form: 0 = Cylindrical; 1 = Weakly flattened ventrally only; 2 = Strongly flattened and broadened. [1%; length = 4, ci = 0.50, ri = 0.85]
114. Male — Head, genal carina: 0 = Absent; 1 = Present but weak; 2 = Present and strong. [**10%**; length = 12, ci = 0.16, ri = 0.16]
115. Male — Head, genal carina, extent (carina absent = -): 0 = Ending distant from hypostomal carina; 1 = Ending adjacent to or continuous with hypostomal carina. [1%; length = 1, uninformative]
116. Male — Head, genal carina, armature (carina absent = -): 0 = Carina simple, unarmed; 1 = With small lamellate tooth anteroventrally; 2 = With strong conical tooth anteroventrally; 3 = With teeth posterodorsally and anteroventrally; 4 = With strong short lamellate tooth posterodorsally. (NONADDITIVE) [3%; length = 3, ci = 0.66, ri = 0.50]
117. Male — Hypostomal carina: 0 = Complete, simple; 1 = Complete, flangelike; 2 = Complete, with tooth/tubercle/elevation at about midlength; 3 = Strong anterolaterally but obsolete posteriorly. (NONADDITIVE) [**10%**; length = 29, ci = 0.10, ri = 0.39]
118. Male — Pleurostomal carina: 0 = Absent; 1 = Slight, ending at inner mandibular edge; 2 = Distinct, together with hypostomal carina forming curved to angulate ridge ending at outer mandibular articulation; 3 = Distinct, together with hypostomal carina forming straight ridge ending at outer mandibular articulation. [4%; length = 26, ci = 0.11, ri = 0.28]

119. Male — Postgenal carina/ridge: 0 = Absent; 1 = Distinct, separate from hypostomal carina; 2 = Distinct, merging with hypostomal carina. [2%; length = 17, ci = 0.11, ri = 0.54]
120. Male — Postmandibular carina (posteroventral to mandible base): 0 = Absent; 1 = Present, simple blunt ridge; 2 = Present, broad smooth tubercle. (NONADDITIVE) [0%; length = 4, ci = 0.50, ri = 0.60]
121. Male — Oral and mandibular fossae: 0 = Continuous, junction about half mandible width or more; 1 = Continuous, junction much narrowed; 2 = Separated by anteriorly unfused depressed cuticular bridge; 3 = Separated by anteriorly fused much-depressed cuticular bridge; 4 = Separated by anteriorly fused superficial cuticular bridge. [1%; length = 14, ci = 0.28, ri = 0.88]
122. Male — Mandible, apical teeth: 0 = Four; 1 = Three; 2 = Two. [9%; length = 20, ci = 0.10, ri = 0.58]
123. Male — Mandible, shape: 0 = Apically not expanded; 1 = Apically expanded. [8%; length = 19, ci = 0.05, ri = 0.33]
124. Male — Mandible, posteroventral basal tooth: 0 = Absent; 1 = Present, small, toothlike; 2 = Present, enlarged, toothlike; 3 = Present, lamellate, apically oblique; 4 = Present, lamellate, apically abrupt. (NONADDITIVE) [**10%**; length = 26, ci = 0.11, ri = 0.39]
125. Male — Mandible, inner basal tooth: 0 = Absent; 1 = Present. [5%; length = 6, ci = 0.16, ri = 0.37]
126. Male — Prementum: 0 = Evenly convex or weakly medio-longitudinally carinate; 1 = With posteromedian domelike tubercle or elevation; 2 = With sharp posterior median elevation; 3 = With anteriorly indented posterior domelike elevation; 4 = Flattened, depressed to weakly concave; 5 = Longitudinally convex with deep narrow anteromedian groove; 6 = With strong long narrow median carina; 7 = With paired longitudinal carinae; 8 = Flattened with posterior median transversely lamellate projection. (NONADDITIVE) [5%; length = 19, ci = 0.36, ri = 0.36]
127. Male — Maxillary palp, length: 0 = Shorter than fore tibia; 1 = >1 <1.5 × length of fore tibia; 2 = >1.5 <2 × length of fore tibia; 3 = >2 × length of fore tibia. [5%; length = 28, ci = 0.10, ri = 0.43]
128. Male — Labial palp, mid segments: 0 = More or less cylindrical; 1 = Flattened and expanded, asymmetrical. [0%; length = 4, ci = 0.25, ri = 0.57]
129. Male — Mesosomal dorsum, decumbent setae: 0 = Cylindrical, slender, straight to weakly arcuate; 1 = Laterally flattened, slender, arcuate; 2 = Laterally flattened, broad, lanceolate. [**10%**; length = 12, ci = 0.16, ri = 0.61]
130. Male — Pro-mesonotal suture (indistinguishable = -): 0 = Weakly concave; 1 = Strongly but evenly concave; 2 = Broadly V-shaped (laterally straight, mesal third curved); 3 = Abruptly V-shaped (laterally straight, mesally angled). [**10%**; length = 29, ci = 0.10, ri = 0.61]
131. Male — Pronotum, humeral angle: 0 = Smoothly rounded; 1 = Blunt; 2 = Vertically carinate or dentate; 3 = Prominent tooth or spine. [**10%**; length = 36, ci = 0.08, ri = 0.34]

132. Male — Pronotum, dorsolateral setose area/epaulet: 0 = Absent; 1 = Present, dispersed patch; 2 = Present, clearly delimited tubercle/tuft. [6%; length = 12, ci = 0.16, ri = 0.75]
133. Male — Pronotum, anterodorsal setose area/epaulet: 0 = Absent; 1 = Present, dispersed patch; 2 = Present, clearly delimited tubercle/tuft. [9%; length = 16, ci = 0.12, ri = 0.67]
134. Male — Mesoscutum, length (apterous/brachypterous = -): 0 = Short anterior to tegulae; 1 = Extended far anterior to tegulae. [0%; length = 9, ci = 0.11, ri = 0.57]
135. Male — Mesoscutum, notaulus (apterous/brachypterous = -): 0 = Present and complete; 1 = Present but incomplete; 2 = Absent. [**11%**; length = 24, ci = 0.08, ri = 0.55]
136. Male — Mesoscutum, parapsidal furrow (apterous/brachypterous = -): 0 = Obvious, complete; 1 = Obvious posteriorly only, absent or a mere scar anteriorly; 2 = An obvious groove anteriorly only, absent posteriorly; 3 = Much reduced, at most a superficial scar anteriorly; 4 = Interrupted, a faint groove posteriorly, a superficial scar anteriorly. (NONADDITIVE) [8%; length = 21, ci = 0.19, ri = 0.62]
137. Male — Mesoscutum, posterolateral margin (apterous/brachypterous = -): 0 = Rounded; 1 = Lobed but flattish; 2 = Dentate and protruding upwards. [8%; length = 13, ci = 0.15, ri = 0.62]
138. Male — Mesoscutellum (apterous/brachypterous = -): 0 = Simple, even with metanotum; 1 = Pulvinate with smooth median ridge; 2 = Posteromesally produced (conical) with smooth median ridge; 3 = Laterally produced as curved posteriorly dentate flange; 4 = Posteriorly produced and overhanging metanotum; 5 = Swollen, discontinuous with metanotum. (NONADDITIVE) [5%; length = 17, ci = 0.29, ri = 0.47]
139. Male — Axilla, posterolateral dorsal margin (apterous/brachypterous = -): 0 = Rounded, posterolateral surface convex or flat; 1 = Narrowly rounded, posterolateral surface concave; 2 = Carinate, posterolateral surface concave; 3 = Flangelike, apex broadly obtuse; 4 = Flangelike, apex strongly dentate. [**13%**; length = 21, ci = 0.19, ri = 0.72]
140. Male — Axilla, anterolateral dorsal extremity (apterous/brachypterous = -): 0 = Evenly rounded (vertical ridge may be present ventrally); 1 = With slight vertical ridge broadening ventrally; 2 = With strong evenly developed vertical ridge or flange; 3 = With blunt tubercle or tooth dorsally; 4 = With abrupt broad vertical flange dorsally. [4%; length = 27, ci = 0.14, ri = 0.62]
141. Male — Tegula, length (apterous/brachypterous = -): 0 = Short, round, posteriorly distant from trans-scutal articulation; 1 = Slightly elongate, posteriorly reaching trans-scutal articulation or slightly beyond; 2 = Elongate, posteriorly extending well beyond trans-scutal articulation. [2%; length = 10, ci = 0.20, ri = 0.84]
142. Male — Tegula, form (apterous/brachypterous = -): 0 = Evenly convex to flattish posteriorly; 1 = Posteriorly recurved; 2 = Longitudinally angulate basally. (NONADDITIVE) [2%; length = 6, ci = 0.33, ri = 0.86]

143. Male — Tegula, free posterior inner margin (apterous/brachypterous = -): 0 = More or less straight or weakly convex; 1 = Distinctly concave. [1%; length = 5, ci = 0.20, ri = 0.87]
144. Male — Propodeum, length (apterous/brachypterous = -): 0 = About as long as high; 1 = Much shorter than high. [2%; length = 14, ci = 0.07, ri = 0.23]
145. Male — Propodeum, disc sculpture (apterous/brachypterous = -): 0 = Evenly sculptured; 1 = Larger basal fields and smaller distal fields; 2 = Three large fields bordered by strong longitudinal carinae. (NONADDITIVE) [5%; length = 9, ci = 0.22, ri = 0.83]
146. Male — Propodeum, disc and declivity (apterous/brachypterous = -): 0 = Broadly rounded; 1 = Distinct but merging; 2 = Abruptly differentiated. [**10%**; length = 24, ci = 0.08, ri = 0.38]
147. Male — Propodeum, dorsolateral margin (apterous/brachypterous = -): 0 = Rounded; 1 = Carinate or distinctly angled. [7%; length = 11, ci = 0.09, ri = 0.54]
148. Male — Propodeum, posterolateral margin: 0 = Smooth or tuberculate; 1 = Dentate or spinose. [2%; length = 2, ci = 0.50, ri = 0.50]
149. Male — Prepectus: 0 = Articulating with mesepisternum; 1 = Fused to mesepisternum. [0%; length = 1, uninformative]
150. Male — Meso-metapleural suture, fusion (apterous/brachypterous = -): 0 = Articulating; 1 = Immovable although not fused; 2 = Partially or entirely fused. [0%; length = 3, ci = 0.66, ri = 0.92]
151. Male — Meso-metapleural suture, shape (apterous/brachypterous = -): 0 = Entirely almost straight; 1 = Posteriorly convex; 2 = Sinuate, ventral section scarcely to strongly concave. (NONADDITIVE) [0%; length = 2, ci = 1.00, ri = 1.00]
152. Male — Meso-metapleural "bridge": 0 = Absent; 1 = Present. [0%; length = 1, ci = 1.00, ri = 1.00]
153. Male — Metapleural-propodeal suture (apterous/brachypterous = -): 0 = Entirely distinct; 1 = Obliterated dorsal to endophragmal pit, distinct ventrally; 2 = Obliterated dorsal to endophragmal pit, vague ventrally; 3 = Entirely obliterated on surface. [**20%**; length = 26, ci = 0.11, ri = 0.54]
154. Male — Oblique metapleural suture (apterous/brachypterous/obliterated = -): 0 = Running anteroventrally from endophragmal pit; 1 = Running horizontally from endophragmal pit; 2 = Running anterodorsally from endophragmal pit. [**11%**; length = 22, ci = 0.09, ri = 0.41]
155. Male — Mesosternum, just anterior to mesocoxae: 0 = Smoothly rounded; 1 = With paired transverse/oblique carinae (may be toothed mesally); 2 = With paired lamellate projections mesally. (NONADDITIVE) [6%; length = 18, ci = 0.11, ri = 0.33]
156. Male — Mesosternum, midway to anterior margin: 0 = Evenly convex; 1 = With distinct paired teeth or tubercles; 2 = With distinct paired (separated) transverse carinae or ridges; 3 = With paired longitudinal high lamellae acuminate apically. (NONADDITIVE) [6%; length = 15, ci = 0.20, ri = 0.36]

157. Male — Mesocoxae, contiguity: 0 = Contiguous mesally; 1 = Slightly separated mesally. [0%; length = 3, ci = 0.33, ri = 0.66]
158. Male — Mesocoxa, insertion: 0 = Large basicoxite, coxal cavities large and approximated; 1 = Large basicoxite, coxal cavities large and widely separated; 2 = Reduced basicoxite, coxal cavities small and widely separated. [0%; length = 3, ci = 0.66, ri = 0.50]
159. Male — Metasternum, posterior median process (absent = -): 0 = Shorter than coxal height, tridentate; 1 = Shorter than coxal height, shallowly bidentate; 2 = Shorter than coxal height, deeply bidentate; 3 = Shorter than coxal height, unidentate; 4 = Longer than coxal height, acutely unidentate; 5 = Longer than coxal height, obtusely unidentate; 6 = Shorter than coxal height, tridentate with median tooth incised; 7 = Longer than coxal height, tridentate with median tooth acute; 8 = Shorter than coxal height, forming a transverse crenulate ridge. (NONADDITIVE) [**16%**; length = 29, ci = 0.27, ri = 0.54]
160. Male — Metacoxal cavities: 0 = Open; 1 = Partially closed; 2 = Closed. [0%; length = 3, ci = 0.66, ri = 0.90]
161. Male — Tarsal claws: 0 = Midventrally toothed; 1 = Simple; 2 = Ventrally basally lamellate, distinct apex acute; 3 = Apically deeply bifid. (NONADDITIVE) [0%; length = 3, ci = 1.00, ri = 1.00]
162. Male — Fore tibia, inner (anterior) secretory structure: 0 = None; 1 = Broad coarsely setose delimited patch; 2 = Linear to oval finely perforated depression; 3 = Vertically elongate groove/pore; 4 = Obliquely elongate groove/pore; 5 = Obliquely oval to circular pore; 6 = Basal elongate/oval and separated apical round pores. (NONADDITIVE) [**12%**; length = 26, ci = 0.23, ri = 0.54]
163. Male — Fore tibia, outer (posterior) secretory structure: 0 = None; 1 = Linear to oval finely perforated depression; 2 = Obliquely elongate groove/pore; 3 = Obliquely oval to circular pore. (NONADDITIVE) [7%; length = 12, ci = 0.16, ri = 0.37]
164. Male — Fore calcar blade: 0 = Linearly narrow; 1 = Expanded, longish >0.5 × length of calcar; 2 = Expanded, almost square, <0.4 length of calcar. (NONADDITIVE) [0%; length = 3, ci = 0.66, ri = 0.93]
165. Male — Fore tarsomeres, apicoventral median ovoid pulvillus: 0 = Absent; 1 = On 4th tarsomere only; 2 = On 3rd & 4th tarsomeres; 3 = On 2nd–4th tarsomeres; 4 = On 1st–4th tarsomeres. [5%; length = 14, ci = 0.28, ri = 0.68]
166. Male — Meso- and metatibial articulated spines, mean number: 0 = 0–4; 1 = 5–9; 2 = 10–14; 3 = 15–19; 4 = 20–24; 5 = >24. [7%; length = 25, ci = 0.20, ri = 0.52]
167. Male — Mesotarsomeres, apicoventral median ovoid pulvillus: 0 = Absent; 1 = On 4th tarsomere only; 2 = On 3rd & 4th tarsomeres; 3 = On 2nd–4th tarsomeres; 4 = On 1st–4th tarsomeres. [6%; length = 14, ci = 0.28, ri = 0.54]
168. Male — Metacoxa, mesally: 0 = Simple; 1 = Longitudinally carinate; 2 = Dentate; 3 = With setaceous pit. (NONADDITIVE) [8%; length = 9, ci = 0.22, ri = 0.79]

169. Male — Metatibia, posterior longitudinal smooth glabrous ridge/carina: 0 = Absent; 1 = Present. [0%; length = 2, ci = 0.50, ri = 0.93]
170. Male — Metatibia, apex dorsally: 0 = Evenly rounded; 1 = With elevated tubercle bearing spine(s); 2 = With distinct cylindrical process bearing spine. [4%; length = 2, ci = 0.50, ri = 0.00]
171. Male — Metatibia, posteroapical secretory structure: 0 = Absent; 1 = Present, delimited patch of dense setae; 2 = Present, a small pore; 3 = Present, a deep narrow longitudinal groove. (NONADDITIVE) [2%; length = 8, ci = 0.37, ri = 0.73]
172. Male — Metatibia, apical spurs: 0 = Both unmodified; 1 = Inner modified as cleaner. [0%; length = 1, uninformative]
173. Male — Metatarsomeres, apicoventral median ovoid pulvillus: 0 = Absent; 1 = On 4th tarsomere only; 2 = On 3rd & 4th tarsomeres; 3 = On 2nd–4th tarsomeres; 4 = On 1st–4th tarsomeres. [7%; length = 12, ci = 0.41, ri = 0.50]
174. Male — Wings and tegula: 0 = Fully developed; 1 = Brachypterous, wing exceeding propodeum apex, tegula present; 2 = Micropterous, wing shorter than propodeum base, tegula present; 3 = Apterous, tegula absent. [2%; length = 16, ci = 0.18, ri = 0.18]
175. Male — Fore wing, extent of venation (apterous/brachypterous = -): 0 = Reaching distal margin; 1 = Ending before distal margin. [0%; length = 1, ci = 1.00, ri = 1.00]
176. Male — Fore wing, vein Sc+R (apterous/brachypterous = -): 0 = <0.5 × length of 1st abscissa of RS; 1 = Subequal to 1st abscissa of RS; 2 = >1.5 × length of 1st abscissa of RS. [6%; length = 16, ci = 0.12, ri = 0.30]
177. Male — Fore wing, pterostigma, sclerotization (apterous/brachypterous = -): 0 = Entirely well sclerotized; 1 = Sclerotization reduced anteriorly; 2 = Unsclerotized; 3 = Entirely faintly sclerotized. (NONADDITIVE) [2%; length = 8, ci = 0.37, ri = 0.87]
178. Male — Fore wing, pterostigma, delimitation (apterous/brachypterous = -): 0 = Completely delimited by distinct veins or completely sclerotized; 1 = Vein SC lost or much reduced, pterostigma not delimited basally. [0%; length = 5, ci = 0.20, ri = 0.60]
179. Male — Fore wing, pterostigma, base (apterous/brachypterous = -): 0 = With interruption/constriction in C and Sc+R; 1 = With interruption/constriction in Sc+R only; 2 = Without interruptions/constrictions. [2%; length = 17, ci = 0.11, ri = 0.71]
180. Male — Fore wing, pterostigma, shape (apterous/brachypterous = -): 0 = Elongate, broader than base; 1 = Elongate, as narrow as base; 2 = Short, broader than base; 3 = Short, as narrow as base; 4 = Very short, narrowed from base; 5 = Minuscule or absent. (NONADDITIVE) [5%; length = 22, ci = 0.22, ri = 0.66]
181. Male — Fore wing, radial (marginal) cell apex (apterous/brachypterous = -): 0 = Acute; 1 = Blunt; 2 = Rounded; 3 = Obtuse with posterior spur. (NONADDITIVE) [**10%**; length = 24, ci = 0.12, ri = 0.27]

182. Male — Fore wing, vein RS2 (apterous/brachypterous = -): 0 = Absent; 1 = Present and complete, basally tubular or solid nebulous; 2 = Present and complete, entirely pigmented spectral; 3 = Apically present but basally absent, pigmented nebulous or spectral; 4 = Present as short stub only. (NONADDITIVE) [**14%**; length = 12, ci = 0.33, ri = 0.66]
183. Male — Fore wing, closed submarginal cells (apterous/brachypterous = -): 0 = Three, all veins tubular; 1 = Three, vein 3r-m nebulous; 2 = Two, all veins tubular; 3 = Two, vein 2r-m nebulous; 4 = One. [**15%**; length = 13, ci = 0.30, ri = 0.74]
184. Male — Fore wing, cell 1R1 (first submarginal) (apterous/brachypterous = -): 0 = Rudiment of crossvein 1r-rs present, at least with third abscissa of vein RS slightly thickened near base; 1 = Rudiment of crossvein 1r-rs absent, third abscissa of vein RS of even width throughout. [2%; length = 3, ci = 0.33, ri = 0.50]
185. Male — Fore wing, vein RS third abscissa, bulla (apterous/brachypterous = -): 0 = Present, even if indistinct; 1 = Absent. [2%; length = 6, ci = 0.16, ri = 0.88]
186. Male — Fore wing, vein RS third abscissa, course (apterous/brachypterous = -): 0 = With distinct angle; 1 = With weak angle; 2 = Straight or very weakly and evenly curved. [**10%**; length = 24, ci = 0.08, ri = 0.56]
187. Male — Fore wing, cell 1S (second submarginal) (apterous/brachypterous = -): 0 = Sessile anteriorly; 1 = Petiolate anteriorly. [1%; length = 1, ci = 1.00, ri = 1.00]
188. Male — Fore wing, crossvein 3r-m (absent/apterous/brachypterous = -): 0 = With bulla; 1 = Without bulla. [4%; length = 5, ci = 0.20, ri = 0.87]
189. Male — Fore wing, jugal lobe (apterous/brachypterous = -): 0 = Present; 1 = Absent. [0%; length = 1, ci = 1.00, ri = 1.00]
190. Male — Hind wing, basal hamuli, occurrence (apterous/brachypterous = -): 0 = Present; 1 = Absent. [0%; length = 1, ci = 1.00, ri = 1.00]
191. Male — Hind wing, basal hamuli, position (none/apterous/brachypterous = -): 0 = Dispersed; 1 = Basal cluster. [0%; length = 3, ci = 0.33, ri = 0.60]
192. Male — Hind wing, apical hamuli (apterous/brachypterous = -): 0 = <11; 1 = >10. [4%; length = 8, ci = 0.12, ri = 0.41]
193. Male — Hind wing, vein RS junction with vein SC (apterous/brachypterous = -): 0 = At acute angle; 1 = At right angle. [9%; length = 16, ci = 0.06, ri = 0.53]
194. Male — Hind wing, crossvein r-m (apterous/brachypterous = -): 0 = Distal; 1 = Proximal, complete; 2 = Proximal, incomplete; 3 = Absent. [**11%**; length = 16, ci = 0.18, ri = 0.69]
195. Male — Hind wing, vein M free apical section (apterous/brachypterous = -): 0 = Present; 1 = Absent. [8%; length = 11, ci = 0.09, ri = 0.47]
196. Male — Hind wing, vein Cu free apex (apterous/brachypterous = -): 0 = Present, even if only a small stub or nebulous trace; 1 = Absent. [1%; length = 3, ci = 0.33, ri = 0.75]
197. Male — Hind wing, crossvein cu-a (apterous/brachypterous = -): 0 = Present, tubular or solid; 1 = Present, nebulous; 2 = Absent. [9%; length = 24, ci = 0.08, ri = 0.63]

198. Male — Hind wing, vein A free apical section (apterous/brachypterous = -): 0 = Present; 1 = Absent. [1%; length = 4, ci = 0.25, ri = 0.57]
199. Male — Hind wing, anal lobe (apterous/brachypterous = -): 0 = Moderate incision on margin; 1 = Shallow definite notch on margin; 2 = Not indicated on margin (at most very shallowly sinuate). [0%; length = 2, ci = 1.00, ri = 1.00]
200. Male — Hind wing, jugal lobe (apterous/brachypterous = -): 0 = Present, large with incision about half length; 1 = Present, small with incision nearly to base; 2 = Absent. [0%; length = 2, ci = 1.00, ri = 1.00]
201. Male — Tergum I and propodeum pubescence: 0 = Entirely simple; 1 = Some brachyplumose; 2 = Some fully plumose. [3%; length = 6, ci = 0.33, ri = 0.87]
202. Male — Tergum I, shape: 0 = Gradually broadened posteriorly, ≥0.5 × length tergum II, apically sessile on tergum II; 1 = Gradually broadened posteriorly, ≥0.5 × length tergum II, apically constricted from tergum II; 2 = Gradually broadened posteriorly, <0.5 × length tergum II, apically sessile on tergum II; 3 = Gradually broadened posteriorly, <0.5 × length tergum II, apically constricted from tergum II; 4 = Parallel-sided posteriorly, ≥0.4 × length tergum II, discontinuous with tergum II; 5 = Entirely parallel-sided, <0.5 × length tergum II, discontinuous with tergum II. (NONADDITIVE) [9%; length = 17, ci = 0.29, ri = 0.68]
203. Male — Tergum I, apical width: 0 = >0.75 × width tergum II; 1 = >0.5 <0.75 × width tergum II; 2 = <0.5 × width tergum II. [3%; length = 18, ci = 0.11, ri = 0.40]
204. Male — Tergum 1, anterodorsal profile: 0 = Broadly convex; 1 = Anterior and dorsal faces merging; 2 = Anterior and dorsal faces distinct. [9%; length = 22, ci = 0.09, ri = 0.53]
205. Male — Tergum II, felt line, presence: 0 = Absent; 1 = Present. [2%; length = 5, ci = 0.20, ri = 0.71]
206. Male — Tergum II, felt line, form (absent = -): 0 = Dispersed traces; 1 = Linear, superficial; 2 = Linear, abruptly invaginated. (NONADDITIVE) [0%; length = 4, ci = 0.50, ri = 0.66]
207. Male — Tergum II, apical fringe: 0 = Setae many, slender arcuate, simple to slightly flattened; 1 = Setae many, some densely plumose; 2 = Setae many, apically split; 3 = Setae many, strong and curved; 4 = Setae few, strong, long, convergent. (NONADDITIVE) [1%; length = 6, ci = 0.50, ri = 0.70]
208. Male — Tergum III, stridulitrum: 0 = Absent; 1 = Present. [0%; length = 3, ci = 0.33, ri = 0.60]
209. Male — Sternum I, differentiation: 0 = Smoothly overlapping sternum II; 1 = Briefly declivous and abutting sternum II; 2 = Depressed posteriorly, constricted and abutting sternum II. [1%; length = 2, ci = 1.00, ri = 1.00]
210. Male — Sternum II, lateral felt line, presence: 0 = Absent; 1 = Present. [7%; length = 18, ci = 0.05, ri = 0.50]
211. Male — Sternum II, lateral felt line, form (absent = -): 0 = Dispersed traces only; 1 = Distinct but minute; 2 = Well developed. [5%; length = 15, ci = 0.13, ri = 0.27]

212. Male — Sternum VII: 0 = Entirely exposed, about as long as sternum VI; 1 = Partly exposed, much shorter than sternum VI; 2 = Concealed. [4%; length = 22, ci = 0.09, ri = 0.58]
213. Male — Hypopygium, visibility: 0 = Almost entirely exposed, lateral margin entire or only shallowly notched; 1 = Almost entirely concealed, lateral margin very deeply incised, hypopygium tri- or pentalobate. [0%; length = 1, ci = 1.00, ri = 1.00]
214. Male — Hypopygium, exposed surface (hidden = -): 0 = Convex to flat, more or less evenly sculptured, punctate to smooth; 1 = Concave, more or less evenly punctured to smooth with lateral longitudinal carina; 2 = Evenly convex, with median tubercle on basal half; 3 = Convex mediolongitudinally, with abrupt lateral depression; 4 = Convex, with median smooth ridge; 5 = Convex to flat, with sublateral paired longitudinal oblique ridges; 6 = Convex, with median Y-shaped ridge; 7 = With longitudinal smooth median depression, dense punctures laterally; 8 = With median excavation, lateral peg-like projection. (NONADDITIVE) [5%; length = 18, ci = 0.38, ri = 0.47]
215. Male — Hypopygium, apex: 0 = Simple, rounded or obtuse; 1 = With shallow broad median emargination; 2 = With simple deep narrow median emargination; 3 = With broad lobed median emargination; 4 = With deep narrow median emargination with internal sclerites; 5 = With median tooth or peg; 6 = With two small approximated teeth or slight notch; 7 = Broadly bilobed; 8 = With two small lateral teeth; 9 = With two separated moderate teeth. (NONADDITIVE) [4%; length = 20, ci = 0.45, ri = 0.38]
216. Male — Cercus: 0 = Present; 1 = Absent. [0%; length = 3, ci = 0.33, ri = 0.00]
217. Male — Cercus, form (absent = -): 0 = Elongate, cylindrical or weakly evenly broadened apically; 1 = Elongate, strongly clavate (with narrow basal stalk); 2 = Elongate, narrow, flattened; 3 = Short, base narrow, distinctly flattened; 4 = Short, base widened, apex narrowed, distinctly flattened; 5 = Short, flattened basally, clavate apically; 6 = Short, evenly clavate; 7 = Vestigial; 8 = Broad-based diskiform, flattened. (NONADDITIVE) [0%; length = 24, ci = 0.33, ri = 0.62]
218. Male — Gonobase, form: 0 = Complete, dorsal and ventral lengths similar, as long as paramere base; 1 = Complete, dorsal and ventral lengths similar, very short and annular; 2 = Complete, dorsal length shorter than ventral, ventrally as long as paramere base; 3 = Complete, dorsal and ventral lengths similar, longer than paramere base; 4 = Complete, dorsal length shorter than ventral, ventrally longer than paramere base; 5 = Complete, dorsal length shorter than ventral, much shorter than paramere base; 6 = Dorsally incomplete, dorsal length shorter than ventral, ventrally as long as paramere base; 7 = Dorsally absent, very short. (NONADDITIVE) [2%; length = 25, ci = 0.28, ri = 0.68]
219. Male — Gonostylus, form, lateral view: 0 = Short, lamellate with rounded apex; 1 = Short, tapered with narrow to acute apex; 2 = Elongate, tapered with acute apex; 3 = Elongate, lamellate with rounded apex. (NONADDITIVE) [2%; length = 9, ci = 0.33, ri = 0.68]

220. Male — Gonostylus, apical curvature, lateral view: 0 = Upcurved; 1 = Straight; 2 = Downcurved. [4%; length = 11, ci = 0.18, ri = 0.87]
221. Male — Gonostylus, dorsal transverse suture (distant from gonobase): 0 = Well developed, extending at least halfway to lateral margin; 1 = Absent or short, longitudinal suture ending distant from gonobase; 2 = Absent, longitudinal suture reaching gonobase. [3%; length = 25, ci = 0.08, ri = 0.63]
222. Male — Gonostylus, parapenial lobe: 0 = Absent; 1 = Present. [1%; length = 2, ci = 0.50, ri = 0.83]
223. Male — Gonostylus, dorsal oblique stout setae: 0 = None; 1 = Present, arising under dorsal flange. [0%; length = 1, ci = 1.00, ri = 1.00]
224. Male — Gonapophysis IX (penis valve), fusion: 0 = Fused dorsally for most of length; 1 = Free for most of length. [0%; length = 1, ci = 1.00, ri = 1.00]
225. Male — Gonapophysis IX (penis valve), shape: 0 = Apex elongate, rounded, no ventral tooth; 1 = Apex rounded, ventral tooth about midway; 2 = Apex dorsally produced, ventral tooth about midway; 3 = Apex dorsally simple, ventral tooth on apical half; 4 = Apex rounded, produced, ventral prominence about midway. (NONADDITIVE) [0%; length = 4, ci = 1.00, ri = 1.00]
226. Male – Gonapophysis IX (penis valve), articulated spines or long setae: 0 = Absent; 1 = Present, strong short spines; 2 = Present, thick long setae. (NONADDITIVE) [0%; length = 2, uninformative]
227. Male — Gonapophysis IX (penis valve), right: 0 = Same shape and length as left gonapophysis IX; 1 = Longer and more elaborate than left gonapophysis IX. [1%; length = 3, ci = 0.33, ri = 0.71]
228. Male — Volsella, basal lobe: 0 = Present, as distinct prominent inner projection; 1 = Present, as rounded ventral long-setose expansion well differentiated from slender apicodorsal section; 2 = Absent, even though slight inner swelling may be evident or base may be somewhat broader than apex. (NONADDITIVE) [0%; length = 10, ci = 0.20, ri = 0.27]
229. Male — Volsella, digitus: 0 = Present, distinct; 1 = Absent or scarcely discernible. [0%; length = 3, ci = 0.33, ri = 0.75]
230. Male — Volsella, paracuspis: 0 = Absent; 1 = Present, as tubercle/swelling/projection at base of cuspis and lateral to digitus. [0%; length = 10, ci = 0.10, ri = 0.75]

Appendix 3

Data matrix for phylogenetic analysis of sub/genera of Mutillidae and four outgroup taxa

Polymorphisms are indicated between square brackets, inapplicable characters are indicated by hyphens, and missing data are indicated by question marks. (An operational version in Nona format is supplied as Suppl. material 1.)

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Hemipepsis	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	3	0	-	-	1	0	0	0	0	1	0	0	0	0	5	0	0	0	0	1	-
Anthobosca	0	0	0	[01]	1	0	0	0	2	0	1	0	0	0	0	2	1	0	1	1	0	-	-	1	0	0	0	2	2	0	0	0	0	0	0	0	0	0	1	-
Fedtschenkia	0	0	1	1	[12]	0	0	1	0	0	1	0	0	1	1	0	0	0	1	3	0	-	-	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-
Sapyginae	2	0	1	1	[01]	0	0	1	[02]	0	1	0	0	2	1	[01]	[01]	0	1	2	0	-	-	1	3	0	0	0	0	1	0	0	0	1	0	0	0	0	0	-
Acanthomutilla	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	1	0	2	2	1	0	0	3	2	1	0	1	1	0	0	0	0	0	0	2	0	1	1	0
Allotilla	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	2	2	0	1	1	0	-	-	0	1	0	0	3	2	0	0	0	0	0	0	0	1	1	1	1
Amblotropidia	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	0	1	0	2	2	1	0	0	3	2	1	0	1	1	0	0	2	0	0	0	1	0	1	1	4
Ancistrotilla	2	0	1	2	0	0	1	0	1	2	3	1	2	1	2	1	1	0	1	2	0	-	-	1	3	1	0	2	0	0	[23]	0	0	0	0	1	0	1	1	1
Apteromutilla	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	1	2	0	2	2	0	-	-	0	2	0	0	2	0	0	0	0	0	0	0	1	0	1	1	2
Areotilla	0	0	1	2	1	0	1	0	0	0	2	0	2	1	2	2	0	0	0	1	0	-	-	1	2	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Artiotilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	1	0	1	2	1	0	0	3	2	1	0	2	1	0	0	2	0	0	0	1	0	1	1	0
Atillum	2	0	1	2	0	0	1	4	1	1	2	0	2	1	2	0	1	1	2	3	2	[01]	2	1	0	0	0	4	[12]	0	3	[02]	0	0	0	1	0	1	2	1
Bischoffiella	2	0	1	2	1	0	1	1	1	0	2	0	2	1	2	2	0	0	1	0	0	-	-	0	1	0	1	2	1	0	0	2	0	0	2	0	2	1	1	2
Bischoffitilla	2	0	1	2	0	0	1	0	2	1	2	0	2	1	2	0	1	0	2	2	[01]	0	0	[01]	2	0	0	3	0	0	0	1	0	0	0	2	0	1	1	0
Bothriomutilla	2	0	1	2	0	0	1	1	1	2	3	2	2	1	2	1	1	0	1	2	2	0	0	1	2	2	0	2	1	0	0	0	0	0	0	1	0	1	1	1
Brachymutilla	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	1	1	0	1	2	0	-	-	[013]	2	0	0	1	1	0	0	0	0	0	0	1	0	1	1	2
Cephalomutilla	2	0	1	2	0	0	1	2	1	2	3	1	2	1	2	0	1	0	2	2	2	1	0	1	2	0	0	3	1	0	0	0	0	0	0	1	0	1	2	1
Ceratotilla	2	0	1	2	0	0	1	2	2	1	0	0	2	1	2	0	1	0	2	2	[01]	0	0	3	2	0	0	[23]	[012]	[01]	0	[01]	0	2	0	2	0	1	1	0
Chaetomutilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	0	0	2	3	2	2	0	3	2	1	0	1	2	0	0	0	0	1	0	2	0	1	1	0
Chrestomutilla	2	0	1	2	0	0	1	1	1	1	2	0	2	1	2	1	1	0	1	1	0	-	-	1	3	1	0	1	1	0	0	0	0	0	0	2	0	1	1	1
Ctenotilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	0	0	1	2	1	0	0	1	2	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0
Cystomutilla	2	0	1	2	0	0	1	0	1	2	2	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Darditilla	2	0	1	2	0	0	1	[34]	1	2	3	1	2	1	2	1	[12]	0	2	2	2	1	0	3	2	0	0	4	1	0	0	2	0	0	0	1	0	1	2	1
Dasylabris	2	0	1	2	0	0	1	0	0	1	2	0	2	1	2	1	1	0	1	2	[01]	0	0	1	3	1	0	1	0	0	0	0	0	0	0	2	0	1	1	1
Dasylabroides	2	0	1	2	0	0	1	[01]	0	1	2	0	2	1	2	0	1	0	[12]	2	0	-	-	1	2	1	0	2	1	0	0	2	0	0	0	[12]	0	1	1	1
Dasymutilla	2	0	1	2	0	0	1	[014]	1	2	3	[12]	2	1	2	0	[01]	0	[12]	[23]	[02]	0	0	1	3	0	0	2	1	0	0	0	0	0	0	[12]	0	1	1	1
Dentilla	2	0	1	2	0	0	1	0	1	[01]	0	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	0	0	0	0	0	0	2	0	1	1	1	0
Dilophotopsis	2	0	1	2	0	0	1	0	1	1	2	2	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	1	0	1	0	0	0	0	1	0	1	1	1
Dimorphomutilla	2	0	1	2	0	0	1	3	2	1	3	1	2	1	2	1	2	0	2	3	0	-	-	3	3	0	0	4	[01]	[01]	0	2	0	0	0	1	0	1	1	1
Dolichomutilla	2	0	1	2	0	0	1	1	2	1	[02]	0	2	1	2	0	0	0	2	2	1	[12]	0	3	2	1	0	1	1	0	[13]	0	0	3	0	1	0	1	1	0
Ephuta	2	0	1	2	0	0	1	0	[12]	1	[02]	0	2	1	2	1	[01]	0	1	[12]	[01]	2	2	4	3	2	0	1	1	0	0	0	0	6	0	[12]	0	1	1	3
Ephutomma	2	0	1	2	0	0	1	0	2	0	0	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0
Eurygnathilla	2	0	1	2	0	0	1	4	2	0	2	0	2	1	2	0	1	0	2	3	0	-	-	0	2	0	0	3	0	1	0	1	0	0	0	1	0	1	1	0
***Eurymutilla* (Near)**	2	0	1	2	0	0	1	0	1	2	3	1	2	1	2	1	1	0	1	2	1	0	0	1	2	1	0	2	1	0	1	0	0	4	0	1	0	1	1	1
Euspinolia	2	0	1	2	0	0	1	3	1	1	2	0	2	1	2	0	2	0	2	3	0	-	-	1	2	0	0	4	1	0	0	0	0	0	0	0	0	1	1	1
Glossotilla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	1	1	0	1	2	0	-	-	3	2	0	0	1	1	0	0	1	0	1	0	2	0	1	1	0
Gogoltilla	2	0	1	2	0	0	1	0	2	2	3	0	2	1	2	1	2	0	1	2	1	0	0	1	1	0	0	4	1	0	0	0	0	0	0	1	0	1	1	1
Hemutilla	2	0	1	2	0	0	1	0	1	2	2	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Hindustanilla	1	0	1	2	1	0	1	0	1	0	0	0	2	1	2	1	2	0	1	2	0	-	-	1	2	0	0	0	0	0	0	0	0	0	2	0	1	1	1	4
Hoplocrates	2	0	1	2	0	0	1	4	[12]	2	2	0	2	1	2	0	2	1	2	3	2	0	[23]	3	2	0	0	4	[01]	0	0	2	0	4	0	1	0	1	2	1
Hoplognathoca	2	0	1	2	0	0	1	2	2	2	3	2	2	1	2	1	2	0	2	3	2	2	3	3	2	0	0	4	0	1	2	0	0	0	0	1	0	1	2	1
Hoplomutilla	2	0	1	2	0	0	1	1	1	2	3	2	2	1	2	1	1	0	2	2	2	1	0	[01]	2	0	0	4	1	0	0	0	0	[06]	0	1	0	1	2	1
Karlissaidia	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	1	0	[12]	2	[01]	0	0	3	[23]	[01]	0	1	1	0	0	0	0	0	0	[12]	0	1	1	[04]
Krombeinidia	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	1	1	0	1	2	1	2	0	3	[23]	1	0	1	1	0	0	0	0	0	0	2	0	1	1	0
Kudakrumia	0	0	1	1	2	0	1	1	2	0	0	0	2	2	2	2	1	0	1	0	1	0	0	1	1	0	1	?	0	0	0	0	0	4	0	1	0	1	1	4
Labidomilla	2	0	1	2	0	0	1	4	2	1	0	0	2	1	2	0	2	0	2	3	[01]	0	0	0	2	0	0	4	0	1	0	0	0	0	0	1	0	1	1	[04]
Liotilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	2	2	0	1	2	0	-	-	[01]	3	0	1	1	0	0	0	0	0	0	0	1	0	1	1	6
Lobotilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	0	0	2	2	0	-	-	3	2	1	0	1	2	0	0	0	0	0	0	1	0	1	1	4
Lomachaeta	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	2	2	0	2	2	2	0	0	1	2	1	1	2	1	0	0	0	0	0	0	2	0	1	1	1
Lophomutilla	2	0	1	2	0	0	1	1	1	2	3	2	2	1	2	1	2	0	2	3	2	2	0	1	2	1	0	4	0	1	0	1	0	0	0	2	0	1	0	1
Lynchiatilla	2	0	1	2	0	0	1	0	1	2	3	1	2	1	2	1	2	0	1	2	1	0	0	1	2	1	0	4	1	0	0	0	0	0	0	1	0	1	1	1
Mickelomyrme	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	1	1	0	1	1	0	-	-	3	3	0	0	1	1	0	0	0	0	0	0	2	0	1	1	0
Mimecomutilla ss	2	0	1	2	0	0	1	0	2	0	0	0	2	1	2	1	1	0	1	2	0	-	-	0	2	1	0	1	1	0	0	0	0	1	0	2	0	1	1	0

Appendix 3 (cont.)

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Mimecotilla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	1	1	0	1	2	0	-	-	1	2	[012]	0	1	1	0	0	0	0	1	0	2	0	1	1	0
Mutilla	2	0	1	2	0	0	1	1	2	[01]	[02]	0	2	1	2	1	0	0	1	2	[01]	0	0	1	2	1	0	1	0	[01]	0	0	0	7	0	1	0	1	1	0
Myrmilla ss	2	0	1	2	0	0	1	4	2	1	[02]	0	2	1	2	0	1	0	2	3	0	-	-	0	2	0	0	3	0	1	0	1	0	0	0	0	1	0	1	1	0
Myrmilloides	2	0	1	2	0	0	1	4	2	1	3	1	2	1	2	1	1	0	2	3	2	0	3	1	0	0	0	4	0	1	3	0	0	0	0	1	0	1	1	1
Myrmosa	0	0	1	1	2	0	1	[13]	0	0	2	0	0	1	2	1	1	0	1	1	0	-	-	1	3	0	0	0	0	0	0	0	0	4	0	[12]	0	1	1	1
Myrmosula	0	0	1	1	2	0	1	3	0	0	0	0	2	1	2	1	2	0	1	1	0	-	-	2	2	0	0	0	1	0	2	0	0	4	0	1	0	1	3	1
Nanomutilla	0	0	1	2	1	0	1	1	1	0	2	0	2	1	2	2	1	0	1	0	0	-	-	1	2	0	0	0	0	0	0	0	0	0	0	1	0	1	1	[04]
Nemka	2	0	1	2	0	0	1	0	2	0	0	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	2	1	0	0	0	0	0	0	1	0	1	1	0
Odontomutilla	2	0	1	2	0	0	1	0	2	1	[02]	0	2	1	2	1	0	0	1	1	2	[12]	[02]	4	3	2	0	[23]	1	0	0	0	0	0	0	2	0	1	1	1
Odontomyrme	2	0	1	2	0	0	1	0	1	1	3	0	2	1	2	2	1	0	1	0	1	0	0	3	2	2	0	2	1	0	0	0	0	0	0	2	0	1	1	1
Odontophotopsis	2	0	1	2	0	0	1	0	1	2	3	2	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	3	1	0	0	0	0	0	0	2	0	1	1	1
Odontotilla ss	2	0	1	2	0	0	1	3	2	1	0	0	2	1	2	0	1	0	2	3	1	0	0	0	2	1	0	4	0	0	0	0	0	0	0	1	0	1	1	4
Orientilla	2	0	1	2	0	0	1	1	1	1	2	0	2	1	2	1	1	0	1	1	1	0	0	1	2	1	0	1	[12]	0	0	0	0	0	0	1	0	1	1	1
Paramyrmosa	0	0	1	1	2	0	1	3	0	0	2	0	0	1	2	1	1	0	1	1	0	-	-	0	1	0	0	0	1	0	0	0	0	4	0	1	0	1	1	1
Pertyella	2	0	1	2	0	0	1	4	1	2	3	2	2	1	2	0	1	0	2	3	2	0	1	0	0	0	0	4	0	1	[03]	0	0	1	0	2	0	1	1	1
Pherotilla	2	0	1	2	1	0	1	1	1	0	2	0	2	1	2	2	0	0	1	0	[01]	0	0	0	1	0	1	2	1	0	0	2	0	0	[12]	0	[12]	1	1	2
Photomorphus ss	2	0	1	2	0	0	1	0	1	1	2	1	2	1	2	1	1	0	1	1	0	-	-	1	3	0	0	3	1	0	0	0	0	0	0	2	0	1	1	1
Physetopoda	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	[01]	[01]	0	1	2	0	-	-	1	3	0	0	1	0	0	0	0	0	0	0	2	0	1	1	0
Platymyrmilla	2	0	1	2	0	0	1	4	1	0	2	0	2	1	2	0	1	0	2	3	2	0	0	0	2	0	0	3	0	1	0	1	0	0	0	1	0	1	1	5
Pristomutilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	0	1	0	1	2	[01]	0	0	3	3	1	0	[23]	[01]	0	0	0	0	[01]	0	1	0	1	1	0
Promecilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	1	1	0	1	2	1	2	0	[01]	3	1	0	1	1	0	0	0	0	0	0	2	0	1	1	0
Protophotopsis ss	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	1	0	0	1	1	0	0	1	2	0	0	3	1	0	0	0	0	0	0	2	0	1	1	2
Pseudocephalotilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	1	0	0	1	2	2	1	0	1	3	1	0	1	0	0	0	0	0	0	0	2	0	1	1	0
Pseudomethoca	2	0	1	2	0	0	1	[234]	1	1	3	[12]	2	1	2	1	2	0	1	[23]	[12]	0	[01]	[13]	[0123]	0	0	4	[01]	0	0	0	0	[01]	0	2	0	1	1	1
Pseudomutilla	2	0	1	2	0	0	1	4	2	1	2	0	2	1	2	1	1	0	2	3	0	-	-	0	2	0	0	3	0	1	0	1	0	0	0	1	0	1	1	[04]
Pseudomyrmosa	0	0	1	1	2	0	1	1	1	[01]	2	0	2	1	2	2	2	0	1	1	0	-	-	1	2	[01]	0	0	0	0	0	0	0	4	0	1	0	1	1	1
Pseudophotopsis	2	1	1	2	1	1	1	0	0	0	0	1	[012]	1	2	1	1	0	1	2	0	-	-	1	2	0	0	0	0	0	[01]	0	0	0	0	[01]	0	1	0	5
Radoszkowskitilla	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	0	0	0	1	2	1	2	0	4	2	[01]	0	1	1	0	0	0	0	4	0	1	0	1	1	0
Reedomutilla	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	0	0	1	1	0	-	-	1	[23]	0	0	1	1	0	0	0	0	0	0	1	0	1	2	1
Rhopalomutilla	2	0	1	2	1	0	1	1	1	0	[02]	0	2	1	2	2	0	0	1	0	0	-	-	0	2	0	1	2	1	0	0	2	0	0	[12]	0	2	1	1	2
Rimulotilla	2	0	1	2	1	0	1	1	1	0	0	0	2	1	2	2	0	0	1	0	1	0	0	0	2	1	1	2	2	0	0	0	0	0	2	0	[12]	1	1	2
Ronisia	2	0	1	2	0	0	1	1	[02]	1	0	0	2	1	2	0	1	0	1	2	0	-	-	3	2	0	0	1	1	0	0	0	0	0	0	1	0	1	1	5
Scaptodactyla	2	0	1	2	0	0	1	0	1	2	3	2	2	1	2	1	2	0	1	2	0	-	-	4	3	0	0	3	1	0	0	0	0	0	0	2	0	1	1	1
Seyrigilla	2	0	1	2	0	0	1	1	1	2	2	0	2	1	2	1	1	0	1	2	0	-	-	1	2	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Smicromyrme	2	0	1	2	0	0	1	0	2	0	[02]	0	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	0	0	0	0	0	0	0	3	0	1	1	0
Smicromyrmilla	1	0	1	2	1	0	1	2	1	0	0	0	2	1	2	1	[12]	0	1	[12]	0	-	-	1	2	0	0	0	0	0	0	0	0	0	0	1	0	1	1	[04]
Sphaeropthalma ss	2	0	1	2	0	0	1	1	1	1	2	1	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	1	0	2	0	0	0	0	1	0	1	1	1
Spinulomutilla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	0	0	0	1	2	1	0	0	3	2	1	0	1	1	0	0	2	0	0	0	2	0	1	1	0
Stenomutilla	2	0	1	2	0	0	1	1	1	1	2	0	2	1	2	[01]	2	0	[12]	[23]	[012]	0	0	[01]	2	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Sulcotilla	2	0	1	2	0	0	1	5	2	1	2	0	2	1	2	1	1	0	1	2	1	0	0	3	3	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0
Tallium	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	1	1	0	1	2	0	-	-	1	2	0	0	2	1	0	1	0	0	0	0	1	0	1	1	1
Timulla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	0	0	0	2	2	0	-	-	3	2	1	0	1	1	0	0	0	0	0	0	[12]	0	1	1	0
Tobantilla	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	2	0	1	2	1	1	0	0	3	0	0	2	2	0	0	0	0	0	0	2	0	1	1	1
Tricholabiodes	2	0	1	2	0	0	1	0	0	1	[02]	2	2	1	2	[12]	1	0	1	[12]	0	-	-	1	3	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Trispilotilla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	1	0	0	1	2	1	0	0	3	2	1	0	1	1	0	0	0	0	0	0	[12]	0	1	1	0
Trogaspidia	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	0	0	0	2	2	0	-	-	3	2	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0
Tropidotilla	2	0	1	2	0	0	1	[01]	1	0	[02]	0	2	1	2	0	0	0	1	[23]	2	1	0	3	2	1	0	1	1	0	0	0	0	0	0	[12]	0	1	1	0
Vianatilla	2	0	1	2	0	0	1	3	2	2	3	2	2	1	2	0	0	0	2	2	2	2	2	5	0	0	0	4	1	0	0	2	0	0	0	1	0	1	1	1
Viereckia	2	0	1	2	0	0	1	[013]	2	0	0	0	2	1	2	1	1	0	1	2	0	-	-	1	2	0	0	3	1	0	0	1	0	2	0	1	0	1	1	[05]
Wallacidia	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	0	0	0	2	2	1	0	0	3	3	1	0	1	1	0	0	0	0	0	0	2	0	1	1	0
Xystromutilla	2	0	1	2	0	0	1	1	1	[12]	[23]	[01]	2	1	2	1	1	0	1	2	0	-	-	1	3	0	0	1	1	0	[13]	0	0	0	0	[23]	0	1	1	1
Yamanetilla	2	0	1	2	0	0	1	0	2	1	2	0	2	1	2	1	0	0	1	1	2	2	2	4	3	2	0	3	1	0	0	0	0	0	0	3	0	1	1	1

Appendix 3 (cont.)

Taxon \ Character	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Hemipepsis	0	0	1	0	0	0	0	0	-	1	[02]	0	0	1	0	-	-	0	0	0	0	1	0	-	1	1	0	0	1	0	3	3	0	0	0	0	1	0	0	0
Anthobosca	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	-	-	0	0	0	0	2	1	-	0	0	2	0	0	0	0	3	0	0	0	0	0	0	1	0	0
Fedtschenkia	0	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	-	0	0	0	1	1	1	-	0	0	0	0	0	0	4	2	0	0	0	0	0	0	0	0
Sapyginae	0	0	[01]	2	0	0	0	0	-	1	0	0	0	0	0	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	[13]	0	0	0	0	0	1	0	0
Acanthomutilla	0	2	1	2	2	2	0	1	0	1	1	4	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	7	0	2	1	1	0	0	3	0	0	2	2
Allotilla	0	2	1	0	0	2	1	1	0	1	1	0	0	0	0	-	-	0	1	1	2	1	1	3	2	0	1	0	4	0	2	2	0	0	0	3	0	1	2	2
Amblotropidia	0	2	1	0	2	1	0	1	1	1	1	0	0	2	6	0	1	1	1	1	1	1	1	0	2	0	1	0	7	0	2	2	1	0	0	3	0	0	2	2
Ancistrotilla	0	2	1	2	2	2	0	1	0	1	0	0	0	0	6	0	1	0	0	1	3	1	1	0	2	0	1	0	5	0	2	1	1	1	0	3	0	0	2	2
Apteromutilla	0	2	1	1	2	2	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0	2	0	1	0	9	4	2	1	1	0	0	1	0	0	2	2
Areotilla	1	2	0	0	0	0	2	1	0	0	2	2	1	2	9	1	0	0	2	0	3	1	1	3	2	0	1	0	5	0	0	0	0	0	0	3	0	1	1	2
Artiotilla	0	2	1	0	2	2	0	1	0	0	0	0	0	2	5	0	1	1	1	1	1	1	1	0	2	0	1	0	7	4	2	1	1	0	0	3	0	0	2	2
Atillum	0	2	1	2	2	1	0	1	0	1	0	0	0	2	0	-	-	0	1	1	3	1	1	6	2	0	1	0	4	3	2	2	0	0	0	3	0	0	2	2
Bischoffiella	0	2	0	0	0	0	2	1	1	0	0	2	0	1	6	0	0	0	1	1	3	1	1	5	2	0	1	0	5	0	0	1	0	0	1	0	0	1	2	1
Bischoffitilla	1	2	1	3	2	2	2	1	0	0	0	0	1	2	6	0	1	0	2	1	3	1	1	3	2	0	1	0	5	0	2	0	[01]	0	0	3	0	[01]	2	2
Bothriomutilla	1	2	1	3	2	2	0	1	0	0	1	2	0	0	2	0	1	0	1	1	1	1	1	4	2	0	1	0	4	0	2	1	1	0	0	3	0	0	2	2
Brachymutilla	0	2	1	0	2	2	2	1	0	1	0	0	0	0	2	0	0	0	[012]	1	3	1	1	1	2	0	1	0	2	4	2	[12]	0	0	0	4	0	1	2	2
Cephalomutilla	0	2	1	2	2	2	0	1	1	0	0	0	0	0	1	-	-	0	1	1	1	1	1	3	2	0	1	0	4	0	2	2	1	0	0	0	0	1	2	3
Ceratotilla	0	2	1	2	2	1	1	1	0	1	1	4	0	2	[56]	0	1	1	1	1	1	1	1	[56]	2	0	1	0	2	0	2	1	1	0	0	3	0	[01]	2	2
Chaetomutilla	0	2	1	1	2	0	1	1	0	1	1	4	0	2	5	0	1	1	1	1	2	1	1	0	2	0	1	0	6	0	2	2	1	0	0	3	0	0	2	2
Chrestomutilla	0	2	0	2	2	2	2	1	1	0	1	0	0	0	1	0	1	0	1	1	2	1	1	0	2	0	1	0	2	0	2	1	0	0	0	3	0	1	2	3
Ctenotilla	0	2	1	2	2	2	0	1	0	1	1	4	0	2	5	0	1	1	1	1	1	1	1	3	2	0	1	0	4	0	2	1	1	0	0	3	0	1	2	2
Cystomutilla	0	2	1	2	1	2	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	5	2	0	1	0	4	0	2	1	0	0	0	3	0	0	2	2
Darditilla	1	2	1	2	2	2	0	1	0	1	[01]	0	1	0	2	0	[01]	1	0	1	2	1	1	6	2	0	1	0	5	0	2	1	1	0	0	3	0	0	2	2
Dasylabris	0	2	1	0	2	2	1	1	1	1	0	0	0	0	2	0	0	0	2	1	[23]	1	1	[02]	2	0	1	0	0	0	2	2	1	0	0	1	0	2	2	3
Dasylabroides	0	2	1	2	2	1	1	1	1	1	0	0	0	0	2	0	0	0	1	1	1	1	1	0	2	0	1	0	2	[01]	2	2	1	0	0	[23]	0	0	2	2
Dasymutilla	[01]	2	1	2	2	2	0	1	[01]	[01]	0	0	0	0	[012]	0	0	0	[01]	1	1	1	1	0	2	0	1	0	[045]	[04]	2	[12]	0	[01]	0	[13]	0	[01]	2	[23]
Dentilla	0	2	1	2	2	2	[12]	1	1	1	1	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	4	0	2	1	1	0	0	4	0	1	2	2
Dilophotopsis	0	2	1	0	0	2	0	1	0	1	1	0	0	0	2	0	0	0	1	1	3	1	1	0	2	0	1	0	4	0	2	2	0	0	0	3	0	1	2	3
Dimorphomutilla	0	2	1	2	[012]	2	0	1	0	0	0	2	1	1	0	-	-	0	1	1	3	1	1	5	2	0	1	0	5	0	2	1	1	0	0	3	0	[01]	2	2
Dolichomutilla	1	2	0	0	2	2	0	1	0	0	0	0	0	2	5	0	[01]	1	1	1	1	1	1	0	2	0	1	0	4	4	2	[01]	1	1	0	3	0	0	2	2
Ephuta	0	2	[01]	0	0	0	2	1	0	[01]	0	0	0	1	0	-	-	-	2	1	3	1	1	3	2	0	1	0	4	0	2	[01]	0	0	0	0	2	2	4
Ephutomma	0	2	0	0	2	2	1	1	1	0	0	0	0	2	6	0	0	1	1	1	2	1	1	0	2	0	1	0	4	0	2	1	1	0	0	3	0	0	2	2
Eurygnathilla	0	2	1	2	2	2	1	1	0	0	1	0	0	2	6	0	1	0	0	1	0	1	1	3	2	0	1	0	5	0	2	0	1	0	0	3	0	0	2	2
Eurymutilla (Near)	0	2	1	2	2	2	1	1	0	1	0	0	0	0	6	0	0	0	1	1	1	1	1	4	2	0	1	0	4	0	2	2	1	0	0	3	0	0	2	2
Euspinolia	[01]	[12]	1	2	2	[01]	0	1	0	1	[01]	0	0	[012]	[02]	0	0	0	1	1	4	1	1	7	2	0	1	0	4	3	2	3	0	0	0	3	0	0	2	2
Glossotilla	0	2	1	0	2	1	0	1	1	1	1	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	7	4	2	1	1	0	0	3	0	0	2	2
Gogoltilla	0	2	1	2	1	2	1	1	1	1	2	0	0	1	0	-	-	0	1	1	3	1	1	3	2	0	1	0	8	0	2	1	1	0	0	3	0	0	2	2
Hemutilla	1	2	1	0	1	2	0	1	0	0	0	0	0	[01]	2	0	0	0	1	1	3	1	1	6	2	?	1	0	5	?	?	[01]	0	0	0	3	0	0	2	2
Hindustanilla	1	2	0	2	0	0	2	1	0	1	0	5	1	2	9	1	0	0	1	0	3	1	1	1	2	0	1	0	5	4	0	1	1	0	0	3	0	0	2	2
Hoplocrates	0	2	1	2	2	[12]	0	1	0	0	0	0	0	2	[07]	0	0	0	[12]	1	3	1	1	6	2	0	1	0	4	3	2	2	0	1	0	3	0	[12]	2	[12]
Hoplognathoca	1	2	1	2	1	2	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	6	2	0	1	0	4	0	2	2	1	0	0	3	0	0	2	2
Hoplomutilla	1	2	1	3	0	2	0	1	0	0	0	0	0	0	2	0	0	0	[01]	1	2	1	1	[56]	2	0	1	0	4	0	2	1	1	2	0	3	0	2	2	2
Karlissaidia	0	2	1	2	2	[02]	0	1	1	1	1	0	0	2	6	0	1	1	1	1	[02]	1	1	0	2	0	1	0	4	0	2	[12]	1	0	0	3	0	[01]	2	2
Krombeinidia	0	2	1	2	2	2	1	1	1	1	0	0	0	2	6	0	1	1	1	1	1	1	1	0	2	0	1	0	7	4	2	1	1	0	0	3	0	0	2	2
Kudakrumia	0	0	1	1	0	0	0	1	0	1	2	0	0	2	0	-	-	-	2	0	3	1	0	-	2	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1
Labidomilla	[01]	2	1	[02]	2	0	[12]	1	0	1	1	3	0	2	[06]	0	1	[01]	1	1	[123]	1	1	3	2	0	1	0	[45]	0	2	1	1	0	0	3	0	0	2	2
Liotilla	0	2	1	1	0	0	2	1	0	1	0	0	0	1	6	1	0	-	2	1	3	1	1	0	2	0	1	0	2	0	2	1	0	0	0	0	0	0	2	2
Lobotilla	0	2	1	0	2	2	0	1	1	1	0	0	1	2	5	0	1	1	1	1	1	1	1	0	2	0	1	0	4	4	2	2	1	0	0	3	0	0	2	2
Lomachaeta	0	2	1	2	0	2	2	1	0	0	0	0	0	0	1	0	0	0	2	1	3	1	1	3	2	0	1	0	5	0	2	0	0	0	0	3	0	2	2	2
Lophomutilla	[01]	2	1	2	2	2	0	1	0	0	0	0	1	0	6	0	0	[01]	1	1	3	1	1	5	2	0	1	0	5	0	2	1	1	0	0	0	0	0	2	2
Lynchiatilla	0	2	1	2	2	2	0	1	0	1	1	4	1	0	1	0	0	0	1	1	[23]	1	1	5	2	0	1	0	5	0	2	1	1	0	0	3	0	0	2	2
Mickelomyrme	0	2	1	0	2	2	1	1	1	1	1	0	0	2	7	-	-	1	1	1	2	1	1	3	2	0	1	0	4	0	2	[12]	1	0	0	3	0	0	2	2
Mimecomutilla ss	0	2	1	0	2	2	1	1	1	1	1	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	6	4	2	1	1	0	0	3	0	0	2	2

Appendix 3 (cont.)

Taxon \ Character	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Mimecotilla	0	2	1	2	2	2	1	1	0	1	1	0	0	2	5	0	0	1	1	1	[01]	1	1	[03]	2	0	1	0	6	[34]	2	1	1	0	0	3	0	0	2	2
Mutilla	0	2	1	2	2	0	0	1	0	1	1	0	0	2	5	0	[01]	1	1	1	1	1	1	3	2	0	1	0	4	0	2	[12]	1	0	0	3	0	1	2	2
Myrmilla ss	0	2	1	2	2	2	1	1	0	0	1	0	0	2	6	0	1	0	1	1	1	1	1	3	2	0	1	0	5	0	2	0	0	0	0	3	0	0	2	2
Myrmilloides	0	2	1	2	1	2	2	1	0	0	0	0	0	2	0	-	-	0	1	1	1	1	1	6	2	0	1	0	5	0	2	1	1	0	0	3	0	0	2	2
Myrmosa	0	0	0	2	0	0	0	1	0	0	1	0	0	1	0	-	-	0	0	0	3	1	0	-	2	0	1	1	0	0	1	2	0	0	0	0	1	1	1	1
Myrmosula	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	-	-	0	2	0	3	1	0	-	2	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0
Nanomutilla	0	2	0	2	0	0	2	1	0	1	2	2	1	2	9	1	0	-	2	0	3	1	1	3	2	0	1	0	5	0	0	0	0	0	0	3	0	0	[01]	2
Nemka	0	2	1	2	2	2	0	1	1	1	1	0	0	2	5	0	0	1	1	1	2	1	1	0	2	0	1	0	4	0	2	2	1	0	0	4	0	0	2	2
Odontomutilla	1	2	1	2	2	0	0	1	0	1	1	[02]	0	0	4	0	0	1	1	1	1	1	1	3	2	0	1	0	5	0	2	[01]	0	0	0	[13]	0	[12]	2	2
Odontomyrme	0	2	1	2	2	2	0	1	0	1	1	2	0	0	6	0	0	0	1	1	1	1	1	4	2	0	1	0	4	0	2	[12]	[01]	0	0	3	0	1	2	2
Odontophotopsis	0	2	1	[02]	2	2	1	1	0	1	1	0	0	0	2	0	0	0	1	1	[23]	1	1	0	2	0	1	0	4	0	2	2	0	0	0	3	0	0	2	[23]
Odontotila ss	0	2	1	2	2	2	2	1	0	0	0	6	1	2	6	0	1	0	1	1	2	1	1	4	2	0	1	0	4	0	2	1	1	0	0	3	0	1	2	2
Orientilla	0	2	0	[02]	0	2	1	1	0	1	0	0	0	0	1	0	0	0	2	1	3	1	1	2	2	0	1	0	5	0	2	0	0	[01]	0	3	0	1	2	3
Paramyrmosa	0	0	0	2	0	0	0	1	0	1	1	0	0	1	0	-	-	0	2	0	3	1	0	-	2	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1
Pertyella	1	2	1	2	2	2	0	1	0	0	0	0	1	2	0	-	-	0	1	1	[23]	1	1	6	2	0	1	0	5	0	2	1	1	2	0	3	0	[01]	2	2
Pherotilla	1	2	1	[12]	0	0	2	1	0	0	0	2	0	[01]	6	0	0	0	1	1	3	1	1	5	2	0	1	0	5	0	0	1	0	0	1	0	0	1	2	1
Photomorphus ss	0	2	1	2	1	2	1	1	0	1	1	0	0	1	1	0	0	0	1	1	3	1	1	6	2	0	1	0	5	4	2	2	0	0	0	3	0	0	2	2
Physetopoda	0	2	1	2	2	2	0	1	1	1	1	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	4	0	2	1	1	0	0	3	0	1	2	2
Platymyrmilla	0	2	1	2	2	2	1	1	0	1	1	0	0	2	6	0	1	0	1	1	0	1	1	7	2	0	1	0	5	4	2	0	1	0	0	3	0	0	2	2
Pristomutilla	0	2	1	2	2	2	1	1	0	1	1	4	0	2	5	0	0	1	1	1	[01]	1	1	0	2	0	1	0	[47]	0	2	2	1	0	0	3	0	0	2	2
Promecilla	0	2	1	2	2	2	0	1	[01]	0	1	0	0	1	[05]	0	[01]	1	1	1	[123]	1	1	0	2	0	1	0	4	4	2	1	1	0	0	3	0	0	2	2
Protophotopsis ss	0	2	1	2	2	2	0	1	0	1	0	0	0	0	1	0	0	0	1	1	3	1	1	3	2	0	1	0	4	4	2	1	0	0	0	3	0	0	2	2
Pseudocephalotilla	0	2	1	2	2	[02]	0	1	1	0	0	0	0	2	6	0	1	1	1	1	1	1	1	0	2	0	1	0	6	4	2	2	1	0	0	3	0	0	2	2
Pseudomethoca	[01]	2	1	2	[02]	2	0	1	0	1	1	0	0	[12]	[016]	0	0	0	1	1	[23]	1	1	[56]	2	0	1	0	4	0	2	[12]	1	0	0	3	0	0	2	2
Pseudomutilla	0	2	1	2	2	2	[12]	1	0	0	1	0	0	2	6	0	1	0	1	1	1	1	1	3	2	0	1	0	5	0	2	[01]	1	0	0	3	0	0	2	2
Pseudomyrmosa	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	-	-	0	2	0	3	1	0	3	2	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0
Pseudophotopsis	0	1	0	0	0	1	0	0	0	0	0	0	0	2	3	0	0	0	1	0	3	1	0	1	2	0	0	1	3	2	2	2	[01]	[01]	0	2	0	0	2	2
Radoszkowskitilla	0	2	1	2	2	2	0	1	1	1	1	0	0	1	5	0	1	1	1	1	1	1	1	0	2	0	1	0	7	0	2	1	1	0	0	3	0	1	2	2
Reedomutilla	0	2	1	1	0	2	0	1	0	0	0	0	0	1	0	-	-	0	1	1	1	[01]	1	3	2	0	1	0	[45]	0	2	2	0	0	0	3	0	2	2	4
Rhopalomutilla	0	2	0	0	0	0	1	1	0	0	0	0	0	1	6	0	0	0	2	1	3	1	1	5	2	0	1	0	5	0	0	1	0	0	1	0	0	1	2	1
Rimulotilla	0	2	0	1	0	0	2	1	1	0	1	2	0	1	[06]	0	0	0	1	1	2	1	1	5	2	0	1	0	5	0	1	1	0	0	1	0	0	1	2	1
Ronisia	0	2	1	2	2	2	0	1	0	1	1	0	0	2	6	0	0	1	1	1	1	1	1	0	2	0	1	0	4	3	2	3	1	0	0	3	0	1	2	2
Scaptodactyla	0	2	1	0	2	0	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	1	3	2	0	1	0	4	0	2	3	0	0	0	3	0	0	2	2
Seyrigilla	0	2	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1	3	1	1	2	2	0	1	0	5	4	2	0	0	0	0	3	0	1	2	1
Smicromyrme	0	2	1	2	2	2	0	1	1	1	1	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	4	0	2	1	1	0	0	3	0	0	2	2
Smicromyrmilla	1	2	0	2	0	0	2	1	0	[01]	0	[125]	1	2	[69]	[01]	1	0	2	0	3	1	[01]	3	2	0	1	0	5	4	0	1	1	0	0	3	0	0	[12]	2
Sphaeropthalma ss	0	2	1	1	0	2	0	1	0	0	0	0	0	0	1	0	0	0	1	1	3	1	1	0	2	0	1	0	4	0	2	1	0	0	0	3	0	1	2	2
Spinulomutilla	1	2	1	1	2	2	0	1	0	1	0	0	1	2	5	0	1	1	1	1	[01]	1	1	0	2	0	1	0	7	4	2	1	1	0	0	3	0	1	2	2
Stenomutilla	0	2	0	0	0	2	1	1	0	0	0	0	0	0	1	0	0	0	2	1	3	1	1	2	2	0	1	0	0	0	2	0	[01]	0	0	3	0	1	2	3
Sulcotilla	0	2	1	2	2	1	1	1	1	1	0	0	0	2	7	-	-	1	1	1	3	1	1	0	2	0	1	0	4	0	2	2	1	0	0	4	0	0	2	2
Tallium	0	2	1	2	2	2	1	1	0	1	1	0	0	1	8	0	0	1	1	1	[23]	1	1	3	2	0	1	0	4	0	2	1	0	0	0	3	0	0	2	2
Timulla	0	2	1	[012]	[02]	[02]	0	1	1	[01]	1	0	0	2	6	0	1	1	1	1	1	1	1	0	2	0	1	0	[47]	0	2	2	1	0	0	3	0	0	2	2
Tobantilla	0	2	1	[12]	1	2	1	1	1	1	2	0	0	1	0	-	-	0	1	1	1	1	1	5	2	0	1	0	8	0	2	1	1	0	0	3	0	2	2	3
Tricholabiodes	0	2	1	[02]	2	2	2	1	1	0	0	0	0	1	[12]	0	0	0	2	1	1	1	1	0	2	0	1	0	4	0	2	1	[01]	0	0	1	0	[01]	2	2
Trispilotilla	0	2	1	2	2	1	0	1	0	0	0	0	0	2	5	0	0	1	1	1	1	1	1	0	2	0	1	0	4	4	2	1	1	0	0	3	0	0	2	2
Trogaspidia	0	2	1	[12]	0	0	0	1	1	1	1	0	0	2	5	0	1	1	1	1	1	1	1	0	2	0	1	0	4	0	2	1	1	0	0	3	0	0	2	2
Tropidotilla	0	2	1	2	2	2	0	1	0	1	1	0	0	2	6	0	0	1	1	1	1	1	1	0	2	0	1	0	4	0	2	1	1	0	0	3	0	[12]	2	2
Vianatilla	1	2	1	2	2	2	0	1	0	0	1	0	0	2	0	-	-	0	1	1	3	1	1	6	2	0	1	0	5	0	2	1	1	2	0	3	0	1	2	2
Viereckia	0	2	1	2	2	2	[012]	1	0	1	1	1	0	2	6	0	1	1	1	1	1	1	1	3	2	0	1	0	4	0	2	1	1	0	0	3	0	0	2	2
Wallacidia	0	2	1	2	2	2	0	1	1	1	1	0	0	2	6	0	1	1	1	1	2	1	1	0	2	0	1	0	7	4	2	2	1	0	0	3	0	0	2	2
Xystromutilla	0	2	1	2	0	2	2	1	0	0	0	0	0	1	0	-	-	-	2	1	3	1	1	0	2	0	1	0	[45]	0	2	1	0	2	0	0	0	1	2	[23]
Yamanetilla	1	2	1	2	2	0	0	1	0	1	1	0	0	0	4	0	0	1	1	1	1	1	1	3	2	0	1	0	5	0	2	[01]	0	0	0	3	0	2	2	2

Appendix 3 (cont.)

Taxon \ Character	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Hemipepsis	0	0	0	0	0	-	0	0	-	0	0	0	0	-	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	3	0	0	-	-	1	0	0	0
Anthobosca	0	0	0	0	0	-	0	0	-	0	0	1	0	-	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-	-	0	0	0	0
Fedtschenkia	0	0	0	0	0	-	0	0	-	0	0	1	0	-	1	0	0	1	0	2	0	0	0	0	1	0	1	0	0	0	1	2	0	0	-	-	1	2	0	0
Sapyginae	0	0	0	0	[23]	1	0	0	-	0	0	[01]	0	-	1	0	1	0	0	[02]	0	2	0	0	2	0	1	0	[01]	[01]	[12]	2	0	0	-	-	1	3	0	0
Acanthomutilla	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	0	2	0	0	1	1	2	1	1	1	1	2	2	0	-	-	2	2	1	0
Allotilla	1	1	0	1	2	1	0	1	0	1	3	2	0	-	0	0	1	1	1	1	1	5	0	0	1	3	2	1	1	1	1	1	0	0	-	-	0	1	0	0
Amblotropidia	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	1	2	0	0	1	[12]	2	3	[01]	[01]	1	2	1	[01]	0	0	[01]	2	1	0
Ancistrotilla	2	1	3	2	0	-	0	1	0	1	[23]	2	0	-	0	1	1	1	2	1	2	6	1	0	1	5	2	2	1	[01]	1	1	0	0	-	-	1	3	1	0
Apteromutilla	2	0	0	2	[12]	0	0	1	0	1	1	2	0	-	0	0	1	1	0	1	1	5	0	0	1	0	2	0	1	2	2	3	0	0	-	-	1	2	1	0
Areotilla	0	0	1	1	0	-	0	0	-	1	0	2	0	-	0	0	1	0	0	0	1	2	0	0	1	3	2	3	1	[01]	1	1	0	0	-	-	1	1	0	0
Artiotilla	1	0	0	2	2	0	0	1	0	1	1	2	0	-	0	0	1	1	0	1	1	2	0	0	1	1	2	3	0	0	1	2	1	0	-	-	0	2	1	0
Atillum	1	0	1	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	2	5	0	0	1	2	2	0	0	0	1	3	0	2	0	2	1	0	0	0
Bischoffiella	0	0	0	1	0	-	0	1	3	0	3	2	0	-	0	0	1	1	0	1	1	2	0	0	1	4	2	0	1	0	1	1	0	[02]	0	0	0	1	1	1
Bischoffitilla	1	0	1	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	0	1	1	3	0	0	1	2	2	0	1	1	1	2	0	0	-	-	[01]	2	0	0
Bothriomutilla	1	[01]	1	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	1	1	2	6	1	0	1	3	2	2	1	0	1	1	0	0	-	-	1	3	0	0
Brachymutilla	1	0	[01]	2	0	-	0	1	0	1	3	2	[01]	1	0	0	1	1	0	1	1	5	0	2	1	0	2	0	1	2	1	[23]	0	0	-	-	0	2	0	0
Cephalomutilla	2	0	[02]	2	2	1	0	1	0	1	3	2	0	-	0	1	1	1	0	0	2	6	1	0	1	3	2	3	1	0	1	1	0	0	-	-	0	2	0	0
Ceratotilla	1	0	[03]	2	2	0	0	1	0	1	3	2	1	1	0	0	1	1	0	2	1	3	0	0	1	2	2	0	1	1	1	2	0	1	0	0	2	2	1	0
Chaetomutilla	1	0	3	2	0	-	0	1	0	1	3	2	0	-	0	1	1	1	0	[01]	0	3	0	0	1	[12]	2	1	0	0	0	1	0	2	0	[04]	1	2	0	0
Chrestomutilla	1	0	3	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	0	1	1	3	0	0	1	3	2	3	1	0	1	1	0	0	-	-	0	1	1	2
Ctenotilla	1	0	3	2	0	-	0	1	0	1	3	2	0	-	0	[01]	1	1	0	1	0	3	0	0	1	1	2	2	1	0	0	0	0	1	0	0	2	2	0	0
Cystomutilla	1	1	1	2	0	-	0	1	0	1	3	2	0	-	0	0	1	1	1	1	1	5	0	0	1	3	2	1	1	1	1	2	0	0	-	-	0	3	0	0
Darditilla	1	1	[02]	2	2	[01]	0	1	0	1	3	2	0	-	0	0	1	1	1	1	2	6	0	0	1	3	2	2	1	0	1	1	0	0	-	-	0	2	0	0
Dasylabris	2	0	3	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	0	5	0	0	1	[12]	2	2	1	0	0	1	0	0	-	-	1	3	1	0
Dasylabroides	1	0	[23]	[12]	0	-	0	1	0	1	3	2	0	-	0	1	1	1	0	1	1	5	0	0	1	3	2	[01]	1	0	[01]	[12]	0	0	-	-	[01]	2	0	0
Dasymutilla	2	[01]	[013]	2	[12]	[01]	0	1	0	1	3	2	0	-	0	1	1	1	1	1	2	6	1	0	1	5	2	2	[01]	0	1	[12]	0	0	-	-	1	2	0	0
Dentilla	1	0	0	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	[01]	1	0	0	1	[45]	2	2	[01]	0	0	[12]	0	0	-	-	0	2	0	0
Dilophotopsis	2	2	0	2	0	-	1	1	0	1	3	2	0	-	0	0	1	1	2	1	2	3	0	0	1	4	2	1	1	[01]	1	1	0	0	-	-	0	2	0	0
Dimorphomutilla	1	1	0	2	2	0	0	1	0	1	[23]	2	0	-	0	0	1	1	1	1	2	[56]	0	0	1	3	2	1	1	1	1	1	0	0	-	-	0	2	0	0
Dolichomutilla	1	0	0	2	2	0	0	1	0	1	2	2	0	-	0	3	1	1	0	1	0	[34]	0	0	1	1	2	2	1	0	1	2	1	0	-	-	0	2	1	0
Ephuta	2	0	3	2	[02]	0	0	1	1	1	[23]	2	0	-	0	0	1	1	0	1	1	4	0	0	1	5	2	[23]	2	1	1	[01]	0	[01]	0	0	3	3	2	0
Ephutomma	2	0	3	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	1	2	0	1	1	[24]	2	2	0	0	1	2	0	0	-	-	0	2	0	0
Eurygnathilla	1	0	3	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	0	2	0	5	0	0	1	1	2	1	0	0	1	2	0	0	-	-	1	2	0	0
Eurymutilla (Near)	1	2	3	2	0	-	0	1	0	1	3	2	0	-	0	1	1	1	2	1	2	6	1	0	1	4	2	2	1	0	1	1	0	0	-	-	1	2	1	0
Euspinolia	1	0	3	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	1	5	0	0	1	4	2	0	0	0	1	2	0	0	-	-	1	2	1	0
Glossotilla	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	[01]	1	1	0	2	0	4	0	0	1	0	2	1	0	1	1	2	2	0	-	-	0	2	0	0
Gogoltilla	1	0	0	2	2	1	0	1	0	1	3	2	0	-	0	0	1	1	1	1	2	6	0	0	1	2	2	2	1	1	1	2	0	0	-	-	0	0	0	0
Hemutilla	2	1	[01]	2	0	-	0	1	0	1	3	2	0	-	0	0	1	1	1	1	1	5	0	0	1	3	2	1	1	1	1	2	0	0	-	-	0	3	0	0
Hindustanilla	0	0	1	1	0	-	0	0	-	1	2	2	1	1	0	0	1	0	0	1	1	0	0	0	1	0	2	[01]	1	2	1	2	0	0	-	-	1	2	0	0
Hoplocrates	1	0	2	2	1	[01]	0	1	0	1	3	2	0	-	0	[01]	1	1	0	1	2	5	0	0	1	2	2	0	0	1	1	2	0	[01]	0	[12]	2	2	0	0
Hoplognathoca	1	1	2	2	2	1	0	1	0	1	3	2	0	-	0	0	1	1	1	1	2	6	2	0	1	4	2	1	1	1	2	2	0	0	-	-	0	2	0	0
Hoplomutilla	1	1	2	2	2	[01]	0	1	0	1	[23]	2	0	-	0	[01]	1	1	1	1	2	6	2	0	1	[34]	2	2	1	0	1	1	0	[12]	0	0	[01]	2	0	0
Karlissaidia	[12]	0	0	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	0	2	0	0	1	[25]	2	[13]	0	0	1	2	1	1	0	0	0	2	0	0
Krombeinidia	2	0	0	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	0	2	0	0	1	4	2	3	1	1	1	2	[12]	0	-	-	1	2	1	0
Kudakrumia	0	0	0	1	0	-	0	0	-	1	0	2	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	1	2	1	1	1	0	0	-	-	1	1	0	0
Labidomilla	1	0	3	2	[01]	0	0	1	0	1	[23]	2	0	-	0	0	1	1	0	2	0	3	0	0	1	2	2	1	1	1	1	1	0	0	-	-	0	2	0	0
Liotilla	1	0	0	2	0	-	0	1	0	1	3	2	[01]	1	0	1	1	1	0	1	1	0	0	2	1	1	2	0	2	2	2	2	0	0	-	-	1	2	0	1
Lobotilla	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	4	1	1	0	1	1	2	0	0	1	2	2	2	0	0	1	2	1	0	-	-	2	2	1	0
Lomachaeta	1	1	0	1	0	-	0	1	0	1	2	2	0	-	0	0	1	1	1	1	2	6	0	0	1	3	2	0	2	1	0	0	0	1	0	0	1	2	1	1
Lophomutilla	2	1	[03]	2	1	1	0	1	0	1	2	2	0	-	0	0	1	1	1	1	2	6	0	0	1	3	2	1	1	1	1	1	0	0	-	-	0	2	0	0
Lynchiatilla	1	1	0	2	2	0	0	1	0	1	3	2	0	-	0	0	1	1	2	1	2	6	1	0	1	3	2	1	1	[01]	1	1	0	0	-	-	1	1	0	0
Mickelomyrme	1	0	0	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	[01]	0	4	0	0	1	5	2	[23]	1	[01]	0	[01]	0	0	-	-	[01]	2	0	0
Mimecomutilla ss	1	0	3	2	[02]	0	0	1	0	1	3	2	0	-	0	0	1	1	0	2	0	[34]	0	0	1	1	2	2	1	0	0	1	0	0	-	-	0	2	1	0

Appendix 3 (cont.)

Taxon \ Character	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Mimecotilla	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	[01]	1	1	0	[12]	0	3	0	0	1	1	2	[12]	1	0	0	1	0	0	-	-	[01]	2	0	0
Mutilla	[01]	0	3	2	0	-	0	1	0	1	1	2	0	-	0	1	1	1	0	1	0	[34]	0	0	1	[12]	2	[01]	1	0	1	0	0	0	-	-	0	2	1	0
Myrmilla ss	1	0	3	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	1	2	0	5	0	0	1	[13]	2	1	0	0	1	2	0	0	-	-	1	2	0	0
Myrmilloides	1	1	0	2	2	1	0	1	0	1	1	2	0	-	0	0	1	1	1	2	1	6	0	0	1	4	2	0	1	1	1	3	0	2	0	3	1	0	0	0
Myrmosa	0	0	0	0	3	1	0	0	-	1	0	2	0	-	0	0	1	1	0	0	0	0	0	0	1	1	2	0	0	0	1	2	0	0	-	-	1	3	0	0
Myrmosula	0	0	0	0	2	1	0	0	-	1	0	2	0	-	0	0	1	1	0	2	0	0	0	0	1	0	1	0	1	1	1	1	0	0	-	-	0	2	0	0
Nanomutilla	0	0	0	2	0	-	0	0	-	0	0	2	0	-	0	0	1	0	0	1	1	0	0	0	1	3	2	1	2	1	[01]	1	0	0	-	-	1	2	0	0
Nemka	2	0	3	1	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	1	2	0	1	1	2	2	3	0	0	0	1	0	0	-	-	0	2	0	0
Odontomutilla	1	0	[012]	1	[01]	0	0	1	2	1	1	2	[01]	0	0	1	1	1	0	1	[01]	4	0	0	1	2	2	1	1	0	0	0	0	[12]	[01]	[02]	3	3	2	0
Odontomyrme	0	2	0	2	0	-	0	1	0	1	3	2	0	-	0	1	1	1	2	1	2	6	0	0	1	3	2	3	2	1	1	1	0	0	-	-	0	2	1	0
Odontophotopsis	[12]	2	3	2	0	-	1	1	0	1	3	2	0	-	0	1	1	1	2	1	2	3	2	1	1	4	2	1	0	0	1	[23]	0	0	-	-	[01]	2	0	0
Odontotilla ss	0	0	1	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	2	1	0	0	0	1	1	2	0	0	0	2	3	0	0	-	-	0	2	1	0
Orientilla	2	0	[23]	2	[01]	0	0	0	-	1	1	2	1	1	0	[01]	1	0	0	1	1	5	0	0	1	[03]	2	0	2	0	0	0	0	0	-	-	1	2	1	0
Paramyrmosa	0	0	0	0	[03]	[01]	0	0	-	0	0	2	0	-	0	0	1	1	0	0	0	0	0	0	1	0	2	0	0	0	1	2	0	0	-	-	0	2	0	0
Pertyella	1	1	1	2	[12]	[01]	0	1	0	1	1	2	0	-	0	0	1	1	1	1	2	6	1	0	1	3	2	1	1	1	1	1	0	0	-	-	0	0	0	0
Pherotilla	0	0	0	1	0	-	0	[01]	3	0	3	2	0	-	0	0	1	1	0	1	1	2	0	0	1	4	2	0	[12]	[01]	1	[12]	0	0	-	-	0	[13]	[01]	1
Photomorphus ss	1	1	0	2	0	-	0	1	0	1	3	2	0	-	0	0	1	1	1	1	1	5	1	0	1	3	2	1	1	1	1	1	0	0	-	-	1	2	0	0
Physetopoda	2	0	0	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	[01]	2	0	[01]	1	[45]	2	3	[01]	[01]	1	2	0	0	-	-	0	2	0	0
Platymyrmilla	1	0	3	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	0	1	1	5	0	0	1	1	2	0	0	0	1	2	0	0	-	-	1	2	0	0
Pristomutilla	1	0	[03]	2	2	0	0	1	0	1	3	2	1	[01]	0	0	1	1	0	1	[01]	3	0	0	1	4	2	2	1	0	0	0	0	0	-	-	1	0	0	0
Promecilla	2	0	0	2	[01]	0	0	1	0	1	2	2	0	-	0	1	1	1	0	1	1	4	0	[01]	1	4	2	2	[01]	0	1	2	0	0	-	-	0	2	1	0
Protophotopsis ss	0	1	3	1	0	-	0	1	0	1	2	2	0	-	0	0	1	1	1	1	2	6	0	0	1	4	2	1	2	0	0	0	0	0	-	-	0	3	0	0
Pseudocephalotilla	1	0	1	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	1	4	0	0	1	[45]	2	3	1	0	0	1	0	[01]	0	0	0	2	0	0
Pseudomethoca	1	1	0	2	[02]	1	0	1	0	1	3	2	0	-	0	0	1	1	1	1	2	6	[01]	0	1	[03]	2	[01]	1	1	1	1	0	[01]	0	0	[01]	[02]	0	0
Pseudomutilla	1	0	3	2	0	-	0	1	0	1	2	2	0	-	0	0	1	1	0	2	0	5	0	0	1	1	2	0	1	[12]	1	2	0	0	-	-	1	2	0	0
Pseudomyrmosa	0	0	0	0	0	-	0	0	-	1	2	2	0	-	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	-	-	0	3	0	0
Pseudophotopsis	1	0	3	1	0	-	0	1	0	1	0	2	1	1	0	2	1	[01]	0	0	1	0	0	0	1	[34]	2	0	1	1	1	2	0	0	-	-	1	2	0	0
Radoszkowskitilla	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	1	2	0	0	1	4	2	3	0	0	1	2	1	0	-	-	1	2	1	0
Reedomutilla	2	1	[13]	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	1	1	2	6	0	0	1	[35]	2	3	1	0	1	1	0	0	-	-	0	[23]	0	0
Rhopalomutilla	[01]	0	0	1	0	-	0	1	3	0	3	2	0	-	0	0	1	1	0	1	1	2	0	0	1	[05]	2	0	1	0	1	1	0	[012]	0	0	0	2	2	1
Rimulotilla	0	0	0	0	0	-	0	0	-	0	3	2	0	-	0	0	1	1	0	1	1	2	0	0	1	4	2	0	1	0	1	2	0	0	-	-	0	2	1	1
Ronisia	1	0	1	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	0	1	3	0	0	1	2	2	2	0	0	1	1	0	0	-	-	1	2	0	0
Scaptodactyla	1	2	3	2	0	-	1	1	0	1	3	2	0	-	0	0	1	1	2	1	2	3	1	1	1	3	2	0	0	0	1	2	0	0	-	-	0	2	0	0
Seyrigilla	2	0	3	2	1	0	0	0	-	1	1	2	1	1	0	0	1	1	0	1	1	5	0	0	1	0	2	0	1	0	0	0	0	0	-	-	1	2	0	0
Smicromyrme	1	0	0	2	1	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	0	2	0	0	1	4	2	3	1	1	0	1	0	0	-	-	0	2	0	0
Smicromyrmilla	0	0	[13]	1	0	-	0	0	-	1	[023]	2	1	1	0	0	1	0	0	1	1	0	0	0	1	[12]	2	[12]	1	1	1	[12]	0	0	-	-	1	2	0	0
Sphaeropthalma ss	2	2	1	2	0	-	1	1	0	1	2	2	0	-	0	1	1	1	1	1	2	5	1	0	1	4	2	1	0	0	1	2	0	0	-	-	0	2	0	0
Spinulomutilla	1	0	3	2	0	-	0	1	0	1	3	2	0	-	0	2	1	1	0	2	1	4	0	0	1	1	2	[12]	0	0	1	2	1	0	-	-	1	2	1	0
Stenomutilla	[12]	0	[13]	2	0	-	0	0	-	1	1	2	1	1	0	[01]	1	1	0	1	1	5	0	0	1	0	2	0	[12]	[01]	[01]	[123]	0	[01]	0	0	0	2	1	0
Sulcotilla	2	0	3	2	1	0	0	1	0	1	3	2	0	-	0	1	1	1	0	2	1	4	0	0	1	1	2	3	1	0	0	1	0	0	-	-	0	2	0	0
Tallium	0	1	[123]	2	[01]	0	0	1	0	1	3	2	0	-	0	0	1	1	[12]	1	1	5	0	0	1	3	2	1	1	0	0	1	0	0	-	-	0	2	0	0
Timulla	1	0	3	2	2	0	0	1	0	1	3	2	0	-	0	0	1	1	0	1	0	2	0	0	1	1	2	2	0	0	1	2	1	0	-	-	0	2	0	0
Tobantilla	2	1	3	2	2	1	0	1	0	1	3	2	0	-	0	0	1	1	1	0	2	6	0	0	1	2	2	3	1	0	0	1	0	0	-	-	0	2	0	0
Tricholabiodes	2	0	0	2	0	-	0	1	0	1	3	2	0	-	0	1	1	1	0	1	2	3	2	1	1	[34]	2	1	0	0	1	2	0	0	-	-	1	3	0	0
Trispilotilla	1	0	[01]	2	2	0	0	1	0	1	3	2	0	-	0	0	1	1	0	[12]	0	2	0	0	1	2	2	2	1	1	1	2	1	0	-	-	2	2	1	0
Trogaspidia	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	[01]	1	1	0	1	0	2	0	0	1	2	2	2	0	0	1	2	1	0	-	-	0	2	[01]	0
Tropidotilla	1	0	3	2	0	-	0	1	0	1	3	2	0	-	0	1	1	1	0	1	0	4	0	0	1	[12]	2	2	[01]	0	[01]	[12]	0	0	-	-	0	2	0	0
Vianatilla	1	1	1	2	2	1	0	1	0	1	2	2	0	-	0	0	1	1	1	1	2	6	0	0	1	3	2	2	1	[01]	1	[12]	0	0	-	-	[02]	[03]	0	0
Viereckia	1	0	0	2	2	1	0	1	0	1	3	2	0	-	0	0	1	1	0	1	0	[35]	0	0	1	[13]	2	[02]	[12]	[01]	[01]	[01]	0	0	-	-	1	2	0	0
Wallacidia	1	0	0	2	2	0	0	1	0	1	3	2	0	-	0	1	1	1	0	1	0	2	0	0	1	2	2	3	[01]	0	1	2	1	0	-	-	0	2	1	0
Xystromutilla	1	2	3	2	[01]	0	1	1	0	1	2	2	0	-	0	1	1	1	[12]	1	[12]	[35]	[01]	[01]	1	3	2	1	0	0	1	3	0	0	-	-	[01]	2	0	0
Yamanetilla	1	0	0	1	0	-	0	1	2	1	1	2	0	-	0	1	1	1	0	1	0	4	0	0	1	2	2	[01]	1	1	0	1	0	2	1	2	3	3	2	0

Appendix 3 (cont.)

Taxon \ Character	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Hemipepsis	0	2	0	0	0	5	0	1	[01]	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	2	-	1
Anthobosca	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	-	0
Fedtschenkia	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	-	0
Sapyginae	0	1	1	0	0	0	0	0	0	0	2	0	0	0	[12]	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	-	0
Acanthomutilla	1	2	0	0	0	4	2	1	1	2	0	2	2	1	1	3	1	5	[12]	1	1	1	1	0	1	1	1	0	1	2	2	1	1	2	1	1	1	2	3	2
Allotilla	2	2	0	0	0	0	2	1	0	1	0	2	2	1	2	1	0	0	0	0	0	0	0	1	0	0	0	0	1	2	2	1	0	2	0	0	1	2	2	2
Amblotropidia	1	2	0	2	0	0	2	1	1	2	0	[02]	0	1	1	3	1	2	[12]	1	1	1	1	0	1	[12]	1	0	1	2	2	1	1	1	1	2	1	2	[18]	2
Ancistrotilla	2	2	0	[34]	0	0	3	1	1	2	0	2	2	1	2	3	1	0	3	0	0	0	0	0	0	1	1	0	1	2	2	1	[12]	2	1	0	1	2	6	2
Apteromutilla	1	1	1	0	0	0	1	1	1	2	1	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	[02]	2
Areotilla	0	1	0	0	0	0	2	1	0	2	0	0	0	1	0	0	0	5	0	1	2	1	1	0	2	2	1	0	1	1	1	0	[23]	1	0	0	1	2	3	2
Artiotilla	1	2	0	0	0	0	2	1	1	3	0	2	2	1	1	3	1	5	1	1	1	1	1	0	1	1	1	0	1	2	2	1	1	2	1	0	1	2	0	2
Atillum	4	2	0	3	0	0	1	1	2	1	2	2	[02]	0	0	1	[01]	0	1	2	0	0	0	1	0	1	0	0	1	2	2	1	3	1	0	0	1	2	5	2
Bischoffiella	2	1	0	3	0	0	1	1	0	3	[01]	1	1	1	1	2	1	5	0	1	1	0	0	0	2	2	1	0	1	2	2	1	1	1	1	2	1	2	3	2
Bischoffitilla	3	1	0	0	1	0	3	1	1	3	2	2	2	1	2	2	1	0	1	2	0	0	0	0	[01]	0	0	0	1	2	2	1	[12]	1	0	0	1	2	1	2
Bothriomutilla	2	2	0	0	0	0	2	1	1	2	3	2	2	0	2	0	1	0	2	1	1	1	1	1	1	1	0	0	1	2	2	1	1	-	1	0	1	2	0	2
Brachymutilla	[12]	1	0	0	[01]	0	1	1	1	[01]	1	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	1	2
Cephalomutilla	2	2	0	0	0	0	2	1	1	3	1	2	2	1	2	3	1	0	3	0	0	0	0	1	0	0	0	0	1	2	2	1	1	2	1	0	1	2	3	2
Ceratotilla	3	1	1	0	1	0	2	1	1	2	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	5	2
Chaetomutilla	1	2	1	3	0	1	3	1	1	3	0	2	0	1	0	2	0	5	2	1	1	0	1	0	1	1	1	0	0	1	2	1	1	1	0	2	1	2	1	2
Chrestomutilla	1	1	0	0	0	0	3	1	1	3	1	2	2	1	1	3	1	0	1	3	0	0	0	0	0	0	0	0	0	1	2	1	2	1	1	1	1	2	2	2
Ctenotilla	1	2	0	[01]	0	1	2	1	0	2	2	2	2	1	0	1	1	5	2	1	1	1	1	0	1	1	0	0	1	2	2	1	1	1	1	1	1	2	1	2
Cystomutilla	1	2	0	3	0	0	2	1	1	2	0	2	2	1	1	0	1	0	1	4	0	0	0	0	1	1	0	0	1	2	2	1	1	[12]	1	0	1	2	0	2
Darditilla	4	2	0	0	0	0	3	1	1	3	0	2	2	1	2	1	1	0	2	4	0	0	0	0	0	1	0	0	1	2	2	1	2	-	1	0	1	2	4	2
Dasylabris	1	[01]	[01]	[24]	0	0	2	1	1	[23]	0	2	2	1	2	1	1	0	4	0	0	0	0	0	0	0	0	0	1	2	2	1	[23]	[12]	1	0	1	2	1	2
Dasylabroides	2	[01]	[01]	[12]	[01]	0	2	1	1	2	0	2	2	1	0	1	[12]	0	1	2	0	0	0	0	1	[01]	0	0	1	2	2	1	[13]	[12]	0	[01]	1	2	1	2
Dasymutilla	2	1	0	0	0	0	2	1	1	[23]	1	2	2	1	2	[03]	1	0	[34]	0	0	0	[01]	0	[01]	0	0	1	2	2	2	1	[13]	2	1	0	1	2	[034]	2
Dentilla	1	1	1	2	1	0	[23]	1	1	3	0	2	2	1	0	3	2	0	2	1	1	1	1	0	1	1	0	0	1	2	2	1	1	2	1	0	1	2	[16]	2
Dilophotopsis	1	1	1	0	0	0	2	1	0	1	2	2	2	1	2	0	1	0	1	[12]	0	0	0	0	1	1	0	0	1	2	2	1	3	2	0	1	1	2	1	2
Dimorphomutilla	4	[12]	[01]	0	[01]	0	2	1	0	1	0	2	2	1	2	1	1	0	[12]	4	0	0	0	0	0	0	0	0	1	2	2	1	2	1	0	1	1	2	5	2
Dolichomutilla	1	2	0	3	0	3	3	1	1	3	0	2	2	1	1	3	[01]	2	2	[01]	2	1	1	0	1	0	1	0	1	2	2	1	1	2	0	0	1	2	1	2
Ephuta	1	2	0	0	0	6	3	1	1	2	2	[01]	[01]	1	[12]	3	1	5	2	1	2	2	0	0	1	[12]	[01]	[01]	1	2	2	1	[123]	[12]	[01]	0	1	2	3	2
Ephutomma	1	1	1	2	0	0	2	1	1	3	0	2	2	1	0	3	2	0	1	1	1	1	1	0	1	0	0	0	1	2	2	1	2	2	0	0	1	2	1	2
Eurygnathilla	3	0	1	0	0	0	1	1	1	3	0	2	2	1	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1	2	2	1	1	1	1	0	1	2	0	2
Eurymutilla (Near)	2	2	0	2	0	4	2	1	1	2	0	2	2	0	2	0	1	0	4	0	0	0	0	1	0	0	0	0	1	2	2	1	1	[12]	1	0	1	2	0	2
Euspinolia	4	1	1	0	0	0	1	1	0	1	2	2	[02]	1	0	[013]	0	0	1	1	0	0	0	1	1	2	[01]	0	1	2	2	1	[12]	1	0	0	1	2	1	2
Glossotilla	1	2	0	2	0	1	2	1	1	2	0	2	0	1	1	3	2	0	1	1	1	1	1	0	1	1	1	0	1	2	2	1	1	2	1	1	1	2	0	2
Gogoltilla	2	1	1	0	1	0	1	1	1	2	0	2	2	1	0	3	1	0	3	0	0	0	0	1	0	1	0	0	1	2	2	1	3	1	0	0	1	2	3	2
Hemutilla	1	[12]	[01]	[134]	0	[67]	2	1	1	2	0	2	2	1	1	1	1	0	1	4	0	0	0	0	1	1	0	0	1	2	2	1	0	2	0	3	1	2	0	2
Hindustanilla	0	1	0	0	0	0	2	1	1	-	2	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	0	-	-	0	0	1	2	[01]	2
Hoplocrates	4	1	1	0	1	4	3	1	2	0	2	2	[12]	0	1	1	1	5	[12]	1	0	0	0	0	0	0	0	0	1	2	2	1	3	1	0	0	1	2	5	2
Hoplognathoca	4	1	1	3	0	4	2	1	1	2	0	0	2	1	2	1	1	0	3	4	0	0	0	1	0	0	0	0	1	2	2	1	0	2	1	0	1	2	4	2
Hoplomutilla	4	2	0	0	0	[06]	2	1	1	1	2	2	2	0	2	1	1	1	2	4	0	0	0	0	0	2	0	0	1	2	2	1	2	1	0	1	1	2	4	2
Karlissaidia	1	2	[01]	[12]	0	0	2	1	1	2	[12]	2	2	1	1	3	[12]	2	[12]	1	1	1	1	0	1	1	[01]	0	1	2	2	1	1	[12]	1	[02]	1	2	[01]	2
Krombeinidia	1	2	0	2	0	0	3	1	1	3	0	2	2	1	1	3	2	0	2	1	1	1	1	0	1	0	[01]	0	1	2	2	1	1	1	1	0	1	2	1	2
Kudakrumia	?	1	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	3	0	1	0	1	2	-	1
Labidomilla	4	1	1	0	[01]	0	2	1	1	2	[02]	2	2	1	[01]	1	1	0	[01]	2	0	0	0	0	1	[01]	0	0	1	2	2	1	1	1	1	0	1	2	[01]	2
Liotilla	2	1	0	0	0	0	0	0	1	-	[12]	0	[02]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	[01]	2
Lobotilla	1	2	0	2	0	0	2	1	1	2	0	2	2	1	1	3	1	2	1	1	1	1	1	0	1	1	1	0	1	2	2	1	1	1	1	0	1	2	1	2
Lomachaeta	2	1	0	[12]	0	0	2	1	1	2	0	1	2	1	2	3	1	0	4	1	1	0	0	0	0	1	0	0	1	2	2	1	3	-	1	0	1	2	3	2
Lophomutilla	4	1	1	0	0	0	3	1	0	3	2	2	2	1	2	[03]	1	0	2	4	0	0	0	0	0	0	0	0	1	2	2	1	3	2	1	0	1	2	4	2
Lynchiatilla	4	2	0	0	0	0	2	1	1	2	0	2	2	1	2	3	1	0	2	4	0	0	0	1	0	0	0	0	1	2	2	1	[12]	1	1	0	1	2	5	2
Mickelomyrme	1	2	0	2	0	0	3	1	[01]	3	0	2	2	1	[01]	3	2	0	[12]	1	[12]	[01]	1	0	1	0	0	0	1	2	2	1	1	[12]	1	0	1	2	[01]	2
Mimecomutilla ss	1	[12]	[01]	2	0	1	2	1	1	3	0	2	2	1	0	2	1	5	2	1	1	0	0	0	1	1	0	0	1	2	2	1	1	2	1	1	1	2	1	2

Appendix 3 (cont.)

Taxon \ Character	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Mimecotilla	1	2	0	0	0	1	2	1	1	3	0	2	2	1	0	0	0	5	2	1	1	0	0	0	1	1	0	0	1	2	2	1	[01]	2	1	1	1	2	1	2
Mutilla	1	1	1	0	0	7	2	1	[01]	3	0	2	2	1	1	3	0	5	2	1	2	1	1	[01]	1	1	[01]	0	1	2	2	1	1	1	1	0	1	2	[01]	2
Myrmilla ss	3	1	1	0	0	[02]	2	1	1	3	[02]	2	2	1	2	1	1	0	1	1	0	0	0	0	1	1	0	0	1	2	2	1	1	1	1	0	1	2	1	2
Myrmilloides	4	2	0	3	0	0	2	1	1	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	5	2
Myrmosa	0	0	1	0	0	4	2	1	0	0	2	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	2	0	1	0	0	2	-	1
Myrmosula	0	1	1	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	2	-	1
Nanomutilla	0	1	0	0	0	0	1	1	0	0	0	0	0	0	[12]	1	0	0	0	1	1	0	0	0	2	[12]	1	0	1	1	1	0	3	0	1	0	1	2	3	2
Nemka	1	1	1	2	0	0	2	1	1	3	0	2	2	1	0	3	2	0	1	1	1	1	1	0	1	1	1	0	1	2	2	1	1	2	1	1	1	2	0	2
Odontomutilla	1	1	0	0	0	0	[23]	1	1	3	2	[02]	[01]	1	[12]	3	1	3	2	1	2	1	1	0	1	1	1	[01]	1	2	2	1	1	1	1	[02]	1	2	0	2
Odontomyrme	2	2	0	0	0	0	2	1	0	3	0	2	2	1	2	3	1	0	1	1	1	0	0	0	0	1	1	0	1	2	2	1	1	1	1	0	1	2	0	2
Odontophotopsis	1	1	[01]	[01]	0	4	3	1	0	[12]	0	2	2	1	[01]	0	1	0	0	2	0	0	0	0	[01]	0	1	0	1	2	2	1	[12]	2	[01]	1	1	2	[02]	2
Odontotilla ss	4	1	1	0	1	0	2	1	1	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	1	0	1	2	7	2
Orientilla	1	1	0	0	1	0	2	1	1	2	0	0	0	1	1	[13]	1	[03]	1	1	[01]	0	0	0	0	1	0	0	1	2	2	1	[23]	[12]	[01]	0	1	2	2	2
Paramyrmosa	0	1	0	0	0	4	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	3	0	1	0	0	2	-	1
Pertyella	4	1	1	0	0	1	3	1	1	2	0	2	2	1	2	1	1	0	2	4	0	0	0	0	0	0	0	0	1	2	2	1	2	1	1	0	1	2	4	2
Pherotilla	2	1	0	3	0	0	[12]	1	0	[23]	0	1	1	1	1	2	1	5	0	1	1	1	0	0	2	[12]	1	0	1	2	2	1	[012]	1	1	2	1	2	3	2
Photomorphus ss	2	2	0	2	0	8	3	1	1	2	0	2	2	1	1	3	1	0	0	4	0	0	0	1	0	0	1	0	1	2	2	1	1	1	0	1	1	2	2	2
Physetopoda	1	[12]	0	2	0	0	[23]	1	1	3	[02]	2	2	1	0	3	[12]	0	1	1	1	1	1	0	1	1	0	0	1	2	2	1	1	[12]	1	0	1	2	[12]	2
Platymyrmilla	3	0	1	0	0	0	1	1	1	2	0	2	2	1	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1	2	2	1	1	2	1	0	1	2	8	2
Pristomutilla	2	2	0	0	0	0	2	1	[01]	3	0	2	2	1	1	3	1	0	2	1	1	0	0	1	0	0	0	0	1	2	2	1	[01]	1	1	0	1	2	8	2
Promecilla	1	1	0	4	0	0	3	1	1	3	0	2	[12]	1	[01]	3	1	[05]	[12]	[01]	1	1	1	0	1	1	0	0	1	2	2	1	1	2	1	0	1	2	1	2
Protophotopsis ss	2	1	0	0	0	0	2	1	1	1	0	2	2	1	2	1	0	0	1	1	1	0	0	0	0	1	0	0	1	2	2	1	2	1	1	0	1	2	8	2
Pseudocephalotilla	1	1	0	2	0	0	[23]	1	1	3	0	2	2	1	[01]	3	[12]	[05]	1	1	1	1	1	0	[01]	1	[01]	0	1	2	2	1	[01]	1	1	0	1	2	[12]	2
Pseudomethoca	4	[12]	0	0	0	0	3	1	[01]	[12]	[01]	[02]	2	1	2	1	[12]	0	[1234]	2	0	0	0	0	0	[01]	0	0	1	2	2	1	[12]	1	[01]	0	1	2	4	2
Pseudomutilla	3	[12]	1	0	0	0	1	1	1	3	[02]	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	1	-	-	1	0	1	2	3	2
Pseudomyrmosa	0	1	0	0	0	4	1	0	[01]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	[01]	0	0	2	3	1
Pseudophotopsis	0	1	0	[12]	0	0	1	1	0	0	0	2	2	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	2	1	1	0	1	2	1	2
Radoszkowskitilla	1	2	0	0	0	4	2	1	1	2	2	2	2	1	1	3	1	0	2	1	1	1	1	1	1	0	1	0	1	2	2	1	1	1	1	0	1	2	[16]	2
Reedomutilla	1	1	0	0	0	0	2	1	2	3	0	2	2	1	2	3	1	5	3	0	0	0	0	1	0	0	1	0	1	2	2	1	[12]	-	0	[02]	1	2	[03]	2
Rhopalomutilla	2	1	0	3	0	0	1	1	0	[123]	[01]	[01]	[01]	1	1	2	1	5	0	1	1	[01]	0	0	2	2	1	0	1	2	2	1	2	1	1	2	1	2	3	2
Rimulotilla	2	2	0	3	0	0	2	1	0	1	2	1	0	1	1	[02]	1	5	0	1	1	0	0	0	2	2	1	0	1	2	2	1	2	1	1	0	1	2	3	2
Ronisia	1	2	0	0	0	0	2	1	1	3	0	2	2	1	1	3	0	0	1	1	2	1	1	1	1	1	0	0	1	2	2	1	1	2	1	0	1	2	1	2
Scaptodactyla	2	1	0	0	0	0	2	1	0	2	0	2	2	1	1	3	0	0	0	1	0	0	0	0	1	0	0	0	1	2	2	1	3	2	0	0	1	2	0	2
Seyrigilla	1	1	0	0	1	0	2	1	0	2	0	0	2	1	1	2	1	5	1	2	1	0	0	0	0	1	0	0	1	2	2	1	3	2	0	0	1	2	2	2
Smicromyrme	1	[12]	0	2	0	0	3	1	1	3	0	2	2	1	0	3	2	0	[12]	1	1	1	1	0	1	1	0	0	1	2	2	1	1	2	1	0	1	2	[01]	2
Smicromyrmilla	0	1	0	0	0	0	2	1	[01]	0	2	0	0	0	2	0	0	4	0	1	1	0	[01]	0	[12]	0	1	1	1	1	1	0	[23]	0	[01]	0	1	2	1	2
Sphaeropthalma ss	1	1	1	4	0	0	2	1	[01]	1	0	2	2	0	0	0	1	0	1	4	0	0	0	1	1	1	0	0	1	2	2	1	[23]	2	1	0	1	2	1	2
Spinulomutilla	1	2	0	0	0	4	2	1	1	2	0	2	1	1	1	3	1	[05]	1	1	1	1	1	0	1	1	[01]	0	1	2	2	1	1	[12]	1	0	1	2	1	2
Stenomutilla	1	1	[01]	0	[01]	0	2	1	[01]	[12]	0	[02]	[02]	1	[12]	[123]	1	[05]	1	1	0	0	0	0	0	1	0	0	1	2	2	1	3	[12]	0	0	1	2	2	2
Sulcotilla	1	1	1	2	0	1	2	1	1	3	0	2	2	1	0	3	2	0	1	1	1	1	1	0	1	1	0	0	1	2	2	1	1	1	0	1	1	2	0	2
Tallium	2	2	0	2	0	0	2	1	1	1	0	2	2	0	1	[13]	1	0	1	[12]	0	0	0	0	1	1	0	0	1	2	2	1	[23]	1	0	1	1	2	1	2
Timulla	1	2	0	[23]	0	0	2	1	1	2	0	2	2	1	0	3	1	0	2	1	1	1	1	1	1	0	0	0	1	2	2	1	1	1	1	2	1	2	1	2
Tobantilla	2	2	0	0	0	6	2	1	1	3	0	2	2	1	1	3	2	0	3	0	1	0	0	1	0	1	0	0	1	2	2	1	1	1	0	0	1	2	3	2
Tricholabiodes	1	1	1	2	0	0	3	1	0	[12]	0	2	2	1	0	0	[12]	0	1	1	0	0	0	0	1	1	0	0	1	2	2	1	[23]	2	1	0	1	2	1	2
Trispilotilla	1	2	0	0	0	0	2	1	1	2	0	2	2	1	1	3	1	2	1	1	1	1	0	0	1	[12]	1	0	1	2	2	1	1	1	1	[02]	1	2	[01]	2
Trogaspidia	1	2	0	2	0	[04]	2	1	1	2	0	2	2	1	1	3	1	2	[12]	1	1	1	1	0	1	1	1	0	1	2	2	1	1	1	1	2	1	2	1	2
Tropidotilla	1	2	0	3	0	0	2	1	[01]	3	0	2	2	1	1	3	0	5	[12]	1	2	1	1	0	1	1	0	0	1	2	2	1	1	[12]	1	[12]	1	2	1	2
Vianatilla	4	2	1	0	0	0	3	1	1	3	0	2	2	1	2	1	1	0	3	4	0	0	0	0	1	0	0	0	1	2	2	1	3	-	1	0	1	2	5	2
Viereckia	3	2	0	0	1	[02]	[12]	1	[01]	2	[02]	2	2	1	[01]	1	1	0	1	1	0	0	0	0	1	[01]	0	0	1	2	2	1	1	2	1	0	1	2	[13]	2
Wallacidia	1	2	0	3	0	0	2	1	1	2	1	2	2	1	1	3	1	2	[12]	1	1	1	1	0	1	1	0	0	1	2	2	1	1	1	1	2	1	2	1	2
Xystromutilla	1	1	0	[23]	0	0	3	1	1	[12]	[02]	2	2	0	1	[03]	1	0	1	4	0	0	0	0	[01]	0	0	0	1	2	2	1	3	1	1	0	1	2	1	2
Yamanetilla	1	1	0	0	0	0	3	1	1	3	2	0	0	1	[12]	3	1	3	2	1	2	1	1	0	1	1	0	0	1	2	2	1	1	1	1	0	1	2	1	2

Appendix 3 (cont.)

Taxon \ Character	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Hemipepsis	0	1	0	2	4	5	4	0	0	0	0	1	4	0	0	2	2	0	0	3	1	0	0	1	1	[12]	0	1	0	0	1	1	1	0	0	0	0	1	1	0
Anthobosca	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	[01]	0	0	0	0	0	0	0	0
Fedtschenkia	0	0	0	0	0	[23]	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	0	2	0	0	0	0	0	[01]	0	0	0	1	0	0	1	0
Sapyginae	0	0	0	0	0	[14]	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	[01]	0	0	1	0	0	1	0
Acanthomutilla	1	4	0	1	2	0	1	1	1	0	2	0	0	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	1	0	0	0	2	2	2
Allotilla	1	5	0	1	0	1	0	0	0	0	2	0	0	0	1	1	0	0	0	1	3	1	2	1	0	2	0	-	1	1	-	1	0	2	0	0	2	1	2	2
Amblotropidia	1	4	3	1	[02]	0	[01]	1	1	0	2	0	[01]	0	1	1	2	0	2	2	1	1	1	1	1	1	0	1	1	1	-	1	1	2	0	0	0	1	2	2
Ancistrotilla	1	4	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	1	0	3	1	1	1	0	1	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Apteromutilla	1	6	3	1	0	1	0	1	0	0	[12]	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Areotilla	1	5	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	1	1	2	1	0	1	1	-	1	0	0	1	0	2	1	0	1	1	2	2
Artiotilla	1	4	3	1	2	0	1	1	1	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	2	1	0	1	1	2	2
Atillum	1	4	2	1	0	1	0	0	0	0	2	0	0	0	1	1	0	0	[01]	4	2	[12]	4	1	0	2	0	-	1	1	-	1	0	2	0	0	[12]	1	2	2
Bischoffiella	2	5	0	0	1	0	1	0	0	0	0	0	1	0	1	[01]	0	0	0	0	0	1	1	1	1	1	0	1	1	1	-	1	0	1	0	0	2	1	2	2
Bischoffitilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	3	1	1	2	1	0	2	1	1	2	0	-	1	1	-	1	1	[23]	[01]	0	1	1	2	2
Bothriomutilla	1	4	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	1	3	3	1	1	1	0	1	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Brachymutilla	1	2	3	1	0	1	0	0	0	0	3	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalomutilla	1	4	0	1	0	1	0	0	0	0	2	0	0	0	1	1	0	0	0	0	[12]	[12]	2	1	0	2	0	-	1	1	-	1	1	2	0	0	2	1	2	2
Ceratotilla	1	2	0	1	0	1	0	1	0	0	2	0	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetomutilla	1	5	0	1	2	1	2	1	0	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	2	1	0	1	1	2	2
Chrestomutilla	1	4	0	1	0	1	0	1	0	0	2	0	0	0	1	1	0	0	0	3	1	1	1	1	1	1	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Ctenotilla	1	5	0	1	2	1	2	1	0	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	2	1	0	0	1	2	2
Cystomutilla	1	4	0	1	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	1	2	2	1	0	1	0	-	1	1	-	1	0	2	1	0	1	1	2	2
Darditilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	2	2	2	1	0	1	0	-	1	1	-	1	0	2	0	0	1	1	2	2
Dasylabris	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	3	1	1	5	1	1	[12]	1	1	2	0	0	1	1	-	1	0	2	0	0	2	1	2	2
Dasylabroides	1	[02]	[01]	1	0	1	0	1	0	0	[12]	0	0	[02]	1	1	0	0	0	2	1	1	1	1	0	1	0	0	1	1	-	1	0	2	0	0	2	1	2	2
Dasymutilla	1	[45]	0	1	0	[01]	0	0	0	0	2	0	0	0	1	1	0	0	1	1	3	[12]	1	1	0	[01]	0	[01]	1	1	-	1	0	2	0	0	[12]	1	2	2
Dentilla	1	4	0	1	0	0	0	1	0	0	3	0	0	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	[12]	0	0	1	1	2	2
Dilophotopsis	1	4	3	1	0	0	0	1	0	[01]	2	0	0	0	1	1	0	0	0	0	1	2	[12]	1	0	2	0	0	1	1	-	0	0	2	[01]	0	2	1	2	2
Dimorphomutilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	1	1	2	1	0	1	0	-	1	1	-	0	0	1	0	0	0	1	2	2
Dolichomutilla	1	4	0	1	0	0	0	1	1	0	2	0	0	0	1	0	2	0	2	2	3	1	1	1	1	2	0	0	1	1	-	1	0	[12]	0	0	0	1	2	2
Ephuta	1	4	0	1	0	0	0	[01]	0	0	2	0	0	0	1	0	2	1	2	5	1	[12]	[12]	1	1	2	0	1	1	1	-	1	0	2	0	0	[12]	1	2	2
Ephutomma	1	4	3	1	0	0	0	1	0	0	2	0	0	0	1	1	2	0	1	3	1	1	1	1	1	1	0	1	1	1	-	1	0	2	1	0	2	1	2	2
Eurygnathilla	1	4	0	1	0	0	0	1	0	0	2	0	0	0	1	1	3	1	2	2	1	0	2	1	1	2	0	-	1	1	-	1	1	2	0	0	1	1	2	2
Eurymutilla (near)	1	4	0	1	0	1	0	1	0	0	2	0	0	0	1	1	0	0	1	4	1	1	1	1	0	1	0	[01]	1	1	-	1	0	2	0	0	1	1	2	2
Euspinolia	1	4	[02]	1	0	2	0	0	0	0	2	0	0	0	1	1	0	0	0	1	[12]	1	[12]	[01]	0	0	0	0	1	1	-	1	0	2	1	0	1	1	2	2
Glossotilla	1	4	3	1	0	0	0	1	1	0	2	0	0	0	1	1	2	0	1	2	3	1	1	1	1	2	0	1	1	1	-	1	0	2	[01]	0	0	1	2	2
Gogoltilla	1	4	3	1	0	1	0	1	0	0	2	0	0	0	1	1	0	0	0	0	2	2	2	1	0	1	0	-	1	1	-	1	0	3	1	0	2	1	2	2
Hemutilla	1	5	?	?	?	[01]	?	[02]	0	0	2	0	?	0	1	1	0	0	0	0	1	[12]	2	1	0	1	0	-	1	1	-	1	0	2	1	0	1	1	2	2
Hindustanilla	1	4	3	0	0	0	0	1	0	0	2	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hoplocrates	1	[45]	2	1	0	1	0	0	0	[01]	2	0	0	0	1	0	0	0	1	4	1	[12]	4	1	0	2	0	-	1	1	-	1	0	2	0	0	1	1	2	2
Hoplognathoca	1	4	0	1	0	1	0	1	0	0	2	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	-	1	0	2	0	0	0	1	2	2
Hoplomutilla	1	4	0	1	0	0	0	1	0	[12]	2	0	0	0	1	1	0	0	0	3	3	1	1	1	0	2	0	0	1	1	-	1	0	1	0	0	0	1	2	2
Karlissaidia	1	4	0	1	1	0	0	1	1	0	2	0	0	0	1	1	2	0	2	2	[13]	1	1	1	1	2	0	1	1	1	-	1	[01]	1	0	0	[01]	1	2	2
Krombeinidia	1	4	0	1	2	0	1	1	1	0	2	0	1	0	1	1	2	0	1	2	1	2	1	1	1	2	0	1	1	1	-	1	0	[12]	[01]	0	0	1	2	2
Kudakrumia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1
Labidomilla	1	[45]	0	1	0	0	0	[01]	0	0	2	0	0	0	1	1	3	1	1	2	1	3	[12]	1	0	1	0	1	1	1	-	0	[01]	2	0	0	1	1	2	2
Liotilla	1	2	0	1	0	0	0	0	0	0	0	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lobotilla	1	4	3	1	[12]	0	1	1	1	0	2	0	[01]	0	1	1	2	0	2	2	1	1	1	1	1	2	0	1	1	1	-	1	1	1	0	0	0	1	2	2
Lomachaeta	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	1	1	3	2	1	2	1	0	1	0	-	1	1	-	1	0	2	0	0	2	1	2	2
Lophomutilla	1	5	0	1	0	0	0	1	0	[01]	2	0	0	0	1	1	0	0	0	0	1	[12]	[12]	1	0	2	0	0	1	1	-	0	0	2	[01]	0	2	1	2	2
Lynchiatilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	1	0	1	[12]	1	0	1	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Mickelomyrme	1	4	0	1	1	0	1	1	0	0	2	0	1	0	1	2	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	[01]	1	1	0	0	1	2	2
Mimecomutilla ss	1	5	3	1	2	1	2	1	0	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	[01]	2	1	0	2	1	2	2

Appendix 3 (cont.)

Taxon \ Character	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200
Mimecotilla	1	[45]	3	1	2	0	2	1	0	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	2	1	0	2	1	2	2
Mutilla	1	[45]	0	1	0	0	0	1	1	0	2	0	0	0	1	[01]	2	0	1	2	1	1	1	1	1	2	0	0	1	1	-	1	1	1	0	0	0	1	2	2
Myrmilla ss	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	3	1	1	[24]	[13]	0	2	1	1	1	0	-	1	1	-	1	1	2	0	0	1	1	2	2
Myrmilloides	1	5	0	1	0	0	0	1	0	0	2	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrmosa	0	0	0	0	0	4	0	[01]	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	[01]	0	0	1	0	1	0	0	1	0	0	1	1
Myrmosula	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1
Nanomutilla	1	5	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	[02]	0	[12]	[24]	1	0	2	1	-	1	0	0	0	0	2	0	0	2	1	2	2
Nemka	1	4	0	1	0	1	[01]	1	0	0	3	0	[01]	0	1	2	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	1	1	0	0	0	1	2	2
Odontomutilla	1	5	0	1	0	0	0	3	0	0	2	0	0	0	1	0	3	1	1	3	3	[12]	2	1	1	2	0	-	1	1	-	1	1	2	1	0	2	1	2	2
Odontomyrme	1	4	0	1	0	[01]	0	0	0	0	2	0	0	0	1	1	0	0	1	2	1	1	1	1	0	0	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Odontophotopsis	1	4	[03]	1	0	1	0	0	0	0	2	0	0	0	1	2	0	0	0	0	1	[14]	[12]	1	0	1	0	0	1	1	-	1	0	2	1	0	2	1	2	2
Odontotilla ss	1	4	0	1	0	1	0	1	0	0	2	0	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orientilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	[34]	1	1	1	1	1	[12]	0	[01]	1	1	-	1	0	[12]	0	0	[12]	1	2	2
Paramyrmosa	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1
Pertyella	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	1	-	1	1	2	0	0	1	1	2	2
Pherotilla	2	[03]	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	[12]	[12]	1	1	1	0	1	1	1	-	1	0	1	0	1	[01]	1	2	2
Photomorphus ss	1	5	0	1	0	1	0	0	0	0	2	0	0	0	1	1	0	0	1	1	0	4	2	1	0	1	0	-	1	1	-	1	0	2	1	0	2	1	2	2
Physetopoda	1	4	0	1	0	0	0	1	0	0	2	0	0	0	1	1	[13]	0	[12]	[23]	1	1	1	1	1	2	0	1	1	1	-	1	0	2	1	0	2	1	2	2
Platymyrmilla	1	5	0	1	0	0	0	1	0	0	2	0	0	0	1	1	3	1	2	2	1	0	2	1	1	1	0	-	1	1	-	1	1	2	0	0	1	1	2	2
Pristomutilla	1	[24]	0	1	0	0	0	1	0	0	2	0	0	0	1	1	2	0	1	2	1	[01]	[12]	1	1	2	0	1	1	1	-	1	[01]	[12]	0	0	0	1	2	2
Promecilla	1	[45]	[03]	1	[01]	0	[01]	1	0	0	2	0	[01]	0	1	2	2	0	1	2	[01]	1	1	1	1	1	0	1	1	1	-	1	1	1	1	0	0	1	2	2
Protophotopsis ss	1	5	0	1	0	0	0	0	0	0	0	0	0	0	1	1	3	0	0	2	0	3	2	1	0	1	0	-	1	1	-	0	1	3	0	0	0	1	2	2
Pseudocephalotilla	1	2	[03]	1	0	[01]	0	1	0	0	2	0	0	0	1	[12]	2	0	1	2	1	1	1	1	0	2	0	1	1	1	-	1	1	1	0	0	0	1	2	2
Pseudomethoca	1	[45]	0	1	0	0	0	[01]	0	0	2	0	0	0	1	[01]	0	0	0	0	[01]	[012]	[12]	1	0	1	0	0	1	1	-	[01]	0	2	0	0	[12]	1	2	2
Pseudomutilla	1	5	0	1	0	0	0	1	0	0	2	0	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudomyrmosa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	[01]	0	[01]	0	0	0	0	1	0	1	0	0	1	0	1	1	1
Pseudophotopsis	0	0	0	1	3	1	3	0	0	0	1	0	[23]	0	1	1	0	0	0	0	1	0	2	0	0	0	0	-	0	0	1	1	1	1	0	1	0	1	1	1
Radoszkowskitilla	1	5	0	1	2	0	0	1	1	0	2	0	0	0	1	1	2	0	2	2	1	1	1	1	1	2	0	1	1	1	-	1	1	1	[01]	0	0	1	2	2
Reedomutilla	1	4	0	1	0	[01]	0	[01]	0	0	2	0	0	0	1	1	0	0	1	3	3	1	[12]	1	0	[01]	0	0	1	1	-	1	0	2	0	0	2	[01]	2	2
Rhopalomutilla	2	3	0	0	1	0	1	0	0	0	0	0	1	0	1	[01]	0	0	0	0	0	1	[12]	1	1	1	0	1	1	1	-	[01]	0	1	0	[01]	1	1	2	2
Rimulotilla	2	[03]	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	-	1	0	1	0	0	0	1	2	2
Ronisia	1	4	3	1	0	1	0	1	1	0	2	0	0	0	1	0	2	0	1	2	0	1	1	1	1	2	0	0	1	1	-	1	1	1	0	0	0	1	2	2
Scaptodactyla	1	5	3	1	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	3	2	2	1	0	1	0	-	1	1	-	1	0	3	1	0	2	1	2	2
Seyrigilla	1	5	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	3	1	1	1	1	1	2	0	0	1	1	-	1	0	1	0	0	1	1	2	2
Smicromyrme	1	4	0	1	1	0	1	1	0	0	2	0	1	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	0	[12]	1	0	[012]	1	2	2
Smicromyrmilla	1	5	[03]	0	0	0	0	1	0	0	2	0	0	0	1	0	1	1	1	3	1	1	2	1	0	1	1	-	1	0	0	0	1	1	0	0	2	1	2	2
Sphaeropthalma ss	1	4	3	1	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	1	2	1	1	0	[01]	0	0	1	1	-	1	[01]	2	0	0	2	1	2	2
Spinulomutilla	1	4	0	1	0	0	0	1	1	0	2	0	0	0	1	1	2	0	2	2	1	1	1	1	1	2	0	1	1	1	-	1	1	1	0	0	0	1	2	2
Stenomutilla	1	[05]	0	1	0	0	0	[01]	0	0	2	0	0	0	1	[01]	0	0	0	4	1	1	1	1	[01]	[12]	0	[01]	1	1	-	1	0	[12]	0	0	[02]	1	2	2
Sulcotilla	1	4	0	1	0	1	0	1	0	0	3	0	0	0	1	1	2	0	1	2	[01]	1	1	1	1	2	0	1	1	1	-	1	1	1	0	0	0	1	2	2
Tallium	1	4	0	1	0	1	0	0	0	0	2	0	0	0	1	2	0	0	0	0	1	2	2	1	0	1	0	-	1	1	-	1	0	2	[01]	0	2	1	2	2
Timulla	1	4	0	1	2	0	[01]	1	1	0	2	0	[01]	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	[01]	[12]	0	0	0	1	2	2
Tobantilla	1	4	3	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	1	1	2	2	1	0	1	0	-	1	1	-	1	0	2	0	0	2	1	2	2
Tricholabiodes	1	5	0	1	0	1	0	[012]	0	0	2	0	0	0	1	2	0	0	0	[023]	1	1	[12]	1	0	1	0	0	1	1	-	1	0	2	0	0	1	0	2	2
Trispilotilla	1	4	[03]	1	0	0	0	1	1	0	2	0	0	0	1	1	2	0	1	2	1	1	1	1	1	2	0	1	1	1	-	1	0	1	0	0	0	1	2	2
Trogaspidia	1	4	0	1	[12]	0	[01]	1	1	0	2	0	0	0	1	1	2	0	1	2	[13]	1	1	1	1	2	0	1	1	1	-	1	0	[12]	0	0	0	1	2	2
Tropidotilla	1	4	0	1	[012]	0	[01]	1	1	0	2	0	[01]	0	1	1	[23]	0	1	2	1	1	1	1	1	[12]	0	0	1	1	-	1	0	[12]	0	0	0	1	2	2
Vianatilla	1	[45]	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	[01]	[12]	[12]	1	0	1	0	0	1	1	-	1	0	2	0	0	1	1	2	2
Viereckia	1	4	0	1	0	0	0	1	0	0	2	0	0	[03]	1	1	0	0	1	2	1	[13]	1	1	[01]	2	0	1	1	1	-	1	[01]	2	0	0	1	1	2	2
Wallacidia	1	4	0	1	2	0	1	1	1	0	2	0	1	0	1	1	2	0	2	2	[13]	1	1	1	1	[12]	0	1	1	1	-	1	0	1	0	0	0	1	2	2
Xystromutilla	1	4	0	1	0	0	0	0	0	1	2	0	0	0	1	1	0	0	0	0	[01]	2	2	1	0	[01]	0	-	1	1	-	1	0	[12]	[01]	0	1	1	2	2
Yamanetilla	1	5	0	1	0	0	0	3	0	0	2	0	0	0	1	0	3	1	1	3	1	4	2	1	1	2	0	-	1	1	-	1	1	3	1	0	2	1	2	2

Appendix 3 (cont.)

Taxon \ Character	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230
Hemipepsis	0	0	0	0	0	-	0	0	0	0	-	2	0	0	0	0	0	0	3	1	0	1	0	0	0	0	0	0	1	0
Anthobosca	0	0	0	0	0	-	0	0	0	0	-	1	0	0	0	0	0	8	1	0	2	1	0	0	1	0	0	0	0	0
Fedtschenkia	0	0	0	0	0	-	0	0	1	0	-	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	2	0	0
Sapyginae	0	0	0	1	0	0	-	0	0	[01]	0	-	2	0	0	1	-	1	0	1	0	1	0	0	1	1	0	0	0	0
Acanthomutilla	0	2	1	0	1	1	0	1	2	0	-	1	0	6	0	0	2	7	2	2	1	0	1	0	1	3	0	0	2	0
Allotilla	1	2	1	2	1	1	0	1	2	1	2	1	0	0	0	0	3	2	2	0	1	1	0	1	3	0	0	2	0	0
Amblotropidia	1	2	2	1	1	1	0	1	2	1	2	2	0	0	6	0	3	2	2	0	1	1	0	1	3	0	0	2	0	1
Ancistrotilla	1	2	2	1	1	1	0	1	2	1	2	2	0	0	0	0	3	2	2	0	1	1	0	1	3	0	0	2	0	1
Apteromutilla	0	0	2	2	0	1	0	1	2	1	0	1	0	0	0	0	3	4	1	2	1	1	0	1	3	0	0	2	0	0
Areotilla	0	0	2	1	0	1	0	1	2	1	2	2	0	0	1	0	3	0	1	2	1	1	0	1	3	0	0	2	1	0
Artiotilla	0	0	2	1	0	1	0	1	2	1	2	2	0	0	5	0	2	7	2	2	1	1	0	1	3	0	0	2	0	0
Atilium	0	0	2	1	0	1	0	1	2	0	-	2	0	0	0	[07]	0	3	0	1	0	1	0	1	4	0	0	2	0	0
Bischoffiella	0	0	1	2	1	1	0	1	2	0	1	2	0	0	3	0	0	5	0	2	2	[12]	0	1	3	0	0	2	1	0
Bischoffiilla	0	0	2	1	0	1	0	1	2	0	-	2	0	[02]	0	0	0	2	2	[12]	1	1	0	1	3	0	0	2	0	0
Bothriomutilla	1	0	2	2	0	1	0	1	2	1	2	2	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	1
Brachymutilla	0	0	2	1	[12]	1	1	0	1	2	[01]	[12]	[12]	0	1	1	-	1	0	1	0	1	0	1	3	0	0	2	0	0
Cephalomutilla	0	0	4	2	1	1	0	1	2	1	0	-	2	0	1	5	0	3	2	2	0	1	0	1	3	0	0	2	0	1
Ceratotilla	0	0	2	1	0	1	0	1	2	1	2	1	0	0	0	0	0	2	2	1	2	1	0	1	3	0	0	2	0	0
Chaetomutilla	0	0	2	1	0	1	0	1	2	0	-	1	0	7	0	0	0	2	2	[12]	2	1	0	1	3	0	0	2	0	0
Chrestomutilla	0	0	3	1	1	1	0	1	2	0	1	1	0	0	[07]	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0
Ctenotilla	0	0	2	1	1	1	0	1	2	0	1	1	0	[13]	5	0	2	2	2	1	0	1	0	1	3	0	0	2	0	0
Cystomutilla	1	1	1	1	1	1	0	1	2	1	1	2	0	0	6	0	4	4	2	0	0	1	0	1	3	0	0	2	0	1
Darditilla	1	2	1	0	1	1	0	1	2	0	-	2	0	0	0	0	3	0	2	0	0	1	0	1	3	0	0	2	0	1
Dasylabris	0	3	2	1	0	1	0	1	2	0	-	1	0	0	0	0	3	2	[12]	0	0	1	0	1	3	0	0	0	0	0
Dasylabroides	0	1	2	1	1	1	0	1	2	0	-	2	0	0	0	0	3	2	[12]	0	0	1	0	1	3	0	0	2	0	0
Dasymutilla	[01]	[13]	2	2	1	1	0	1	2	0	-	2	0	0	[06]	0	3	3	2	0	1	1	0	1	3	0	0	2	0	1
Dentilla	0	2	1	1	1	1	0	1	2	0	1	1	0	0	0	0	3	6	2	0	[01]	0	0	1	3	0	0	1	0	0
Dilophotopsis	2	[02]	1	0	1	1	0	1	2	0	1	2	0	1	0	0	4	2	2	0	0	1	0	1	3	0	0	2	0	1
Dimorphomutilla	1	0	2	[01]	1	1	0	1	2	0	-	2	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	1
Dolichomutilla	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	2	6	2	0	0	1	0	1	3	0	0	2	0	0
Ephuta	0	5	2	2	[01]	0	0	1	2	0	0	[12]	0	0	0	0	3	5	2	2	1	1	0	1	3	0	0	2	0	0
Ephutomma	0	0	2	1	1	1	0	1	2	0	-	1	0	0	0	0	3	7	2	2	2	1	0	1	3	0	0	2	0	0
Eurygnathella	2	2	1	1	1	1	0	1	2	1	2	2	0	0	0	0	3	2	2	1	0	1	0	1	3	0	0	2	0	0
Eurymutilla (Near)	0	2	1	1	1	1	0	1	2	1	2	1	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	1
Euspinolia	0	2	1	0	1	1	0	1	2	0	-	1	0	5	0	0	0	3	5	1	1	0	1	0	1	3	0	0	2	0
Glossotilla	0	2	1	0	0	1	0	1	2	0	-	1	0	5	0	0	0	3	7	2	2	1	0	1	3	0	0	2	0	1
Gogotilla	0	0	1	1	1	1	0	1	2	0	-	2	0	0	5	0	0	3	?	2	0	1	0	1	3	0	0	2	0	1
Hemutilla	1	1	1	1	1	1	0	1	2	0	[01]	[12]	2	0	[01]	0	0	4	4	2	0	1	0	1	3	0	0	2	0	1
Hindustanilla	0	0	0	0	1	0	1	0	1	2	1	2	2	0	4	0	0	5	3	1	2	1	0	1	3	0	0	2	1	0
Hoplocrates	0	2	2	1	1	1	0	1	2	0	-	2	0	0	0	0	3	0	1	1	0	1	0	1	3	0	0	2	0	0
Hoplognathoca	1	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	0	2	0	0	1	0	1	3	0	0	2	0	1
Hoplomutilla	1	2	1	1	0	1	0	1	2	0	-	2	0	1	0	0	0	4	2	0	0	1	0	1	3	0	0	2	0	1
Karlissaidia	0	[02]	1	0	1	1	0	1	2	0	-	[01]	0	5	0	0	0	2	7	2	2	[01]	1	0	1	3	0	1	2	0
Krombeinidia	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	1	7	2	2	1	1	0	1	3	0	0	2	0
Kudakrumia	0	0	1	0	0	-	0	0	1	0	-	1	0	0	0	0	0	3	2	0	1	0	1	0	1	2	0	0	2	0
Labidomilla	0	2	1	[01]	1	1	0	1	2	0	-	1	0	0	0	0	0	5	2	1	1	1	0	1	3	0	0	2	0	0
Liotila	0	2	1	0	1	1	0	1	2	[01]	1	2	0	0	9	1	0	-	0	1	1	0	1	0	1	3	0	0	0	0
Lobotilla	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	7	2	2	1	1	0	1	3	0	0	1	0	1
Lomachaeta	1	2	2	2	1	1	4	1	2	0	-	1	0	0	6	0	0	3	3	2	0	1	0	1	3	0	0	1	0	1
Lophomutilla	0	[02]	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	0	2	0	0	1	0	1	3	0	0	2	0	1
Lynchiatilla	1	2	1	0	1	1	0	1	2	0	-	1	0	0	6	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0
Mickelomyrme	0	[02]	1	0	1	1	0	1	2	1	2	1	0	0	0	0	0	3	7	2	2	1	0	1	3	0	0	1	0	0
Mimecomutilla ss	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	2	2	1	2	1	0	1	3	0	0	2	0	0

Appendix 3 (cont.)

Taxon \ Character	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230
Mimecotilla	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	2	2	1	2	1	0	1	3	0	0	2	0	0
Mutilla	0	2	1	1	1	1	0	1	2	1	-	1	0	0	0	0	3	6	2	2	1	1	0	1	3	0	0	2	0	0
Myrmilla ss	0	2	1	0	1	1	0	1	2	1	1	2	0	3	7	0	6	2	2	2	1	1	0	1	3	0	0	2	0	0
Myrmilloides	1	2	1	0	1	1	0	1	2	0	-	2	0	0	8	0	7	0	1	1	0	1	0	1	3	0	0	2	0	1
Myrmosa	0	0	1	0	0	-	0	1	2	0	-	0	1	0	-	0	0	3	2	0	1	1	0	1	2	0	0	0	0	0	0
Myrmosula	0	0	1	0	0	-	0	1	2	0	-	0	1	0	0	0	0	3	2	1	1	0	1	0	1	2	0	0	0	0	0
Nanomutilla	0	0	1	0	0	-	0	1	2	0	-	1	0	0	0	0	0	3	2	1	1	1	0	1	3	0	0	2	1	0
Nemka	0	2	1	0	1	1	0	1	2	1	2	2	0	0	0	0	0	3	7	2	2	1	1	0	1	3	0	0	1	0	0
Odontomutilla	0	2	1	[01]	1	2	0	1	2	1	[01]	1	0	0	0	0	0	2	[24]	2	0	1	1	0	1	3	0	0	2	0	0
Odontomyrme	[12]	1	1	1	1	1	1	1	2	1	1	2	0	0	0	6	0	3	2	2	1	1	1	0	1	3	0	0	2	0	0
Odontophotopsis	2	[01]	[12]	0	1	1	1	1	2	[01]	2	2	0	0	0	0	3	4	2	0	1	1	1	0	1	3	0	0	2	0	1
Odontotilla ss	0	2	1	1	1	0	1	1	2	0	-	2	0	0	0	0	0	5	2	1	0	1	1	0	1	3	0	0	2	0	0
Orientilla	0	1	2	1	0	-	0	1	2	0	-	2	0	0	0	0	0	2	2	0	0	1	1	0	1	3	0	0	2	0	0
Paramyrmosa	0	0	1	0	0	-	0	0	2	0	-	0	1	-	0	0	3	2	1	1	0	1	0	1	2	0	0	0	0	0	0
Pertyella	1	2	2	0	1	-	0	1	2	0	-	1	0	0	0	0	3	0	2	[01]	0	1	0	1	4	0	[01]	2	1	0
Pherotilla	0	1	1	1	[01]	0	3	1	2	[01]	0	2	0	8	3	0	5	0	2	0	1	0	0	1	3	0	0	2	0	1
Photomorphus ss	1	4	1	1	1	1	0	1	2	1	2	2	0	1	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	1
Physetopoda	0	2	1	[01]	1	1	0	1	2	0	-	1	0	0	0	0	3	[67]	2	2	0	1	0	1	3	0	0	1	0	0
Platymyrmilla	0	2	1	0	1	1	0	1	2	0	1	2	0	0	0	0	2	2	2	1	1	1	0	1	3	0	0	2	0	0
Pristomutilla	0	0	1	0	1	1	0	1	2	0	-	1	0	[02]	0	0	0	2	2	2	2	1	0	1	3	0	0	2	0	0
Promecilla	0	0	1	0	1	1	0	1	2	0	-	1	0	0	0	0	2	7	2	2	2	1	0	1	3	0	0	1	0	0
Protophotopsis ss	1	3	1	1	1	1	3	1	2	1	2	1	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0
Pseudocephalotilla	0	2	1	1	1	1	0	1	2	1	[12]	1	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0
Pseudomethoca	1	2	1	1	0	1	1	1	2	0	-	1	0	1	0	0	3	0	2	0	0	1	0	1	3	0	0	2	0	1
Pseudomutilla	0	2	1	1	0	1	1	1	2	0	-	2	0	3	7	0	6	2	2	2	1	1	0	1	2	0	0	2	0	0
Pseudomyrmosa	0	0	1	0	0	-	0	1	2	0	-	2	0	0	0	0	3	2	0	1	0	1	0	1	2	0	0	2	0	0
Pseudophotopsis	0	[01]	[01]	0	1	1	0	1	2	1	2	2	0	0	[05]	0	3	1	0	1	0	1	0	1	2	1	0	2	0	0
Radoszkowskitilla	0	2	1	1	1	1	1	1	2	1	[12]	1	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0
Reedomutilla	1	3	2	2	1	1	0	1	2	0	-	2	0	0	5	0	3	3	2	0	0	1	0	1	3	0	0	2	0	1
Rhopalomutilla	0	[13]	2	1	0	-	3	1	2	0	-	2	0	0	8	3	0	5	0	3	2	[01]	1	0	1	1	4	0	1	0
Rimulotilla	0	1	2	1	1	1	[23]	1	2	0	-	2	0	0	0	0	0	0	3	1	0	1	0	1	1	4	0	2	0	0
Ronisia	0	2	1	1	1	1	0	1	2	0	-	1	0	0	0	0	3	6	2	2	1	1	0	1	3	0	0	2	0	0
Scaptodactyla	2	1	2	1	1	1	1	1	2	0	-	2	0	0	0	0	4	4	2	0	2	1	0	1	3	0	0	2	0	0
Seyrigilla	0	1	2	1	0	-	0	1	2	1	2	2	0	0	0	0	3	2	2	0	0	0	0	1	3	0	0	2	0	0
Smicromyrme	0	2	1	[01]	1	1	0	1	2	1	1	1	0	0	0	0	3	7	2	2	0	1	0	1	3	0	0	2	0	0
Smicromyrmila	0	0	1	0	1	1	0	1	2	1	2	2	0	0	4	0	5	3	1	2	0	1	0	1	3	0	0	2	1	0
Sphaeropthalma ss	2	1	2	1	1	1	1	1	2	0	-	2	0	0	0	0	4	4	2	0	2	1	0	1	3	0	0	2	0	1
Spinulomutilla	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	1	7	2	2	2	1	0	1	3	0	0	2	0	1
Stenomutilla	0	1	2	1	0	-	0	1	2	1	2	2	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0
Sulcotilla	0	2	1	0	1	1	0	1	2	1	1	2	0	0	0	0	3	7	2	2	2	1	0	1	3	0	0	1	0	0
Talium	[12]	2	1	[12]	1	1	0	1	2	1	1	[12]	1	1	[06]	0	3	2	2	0	2	1	0	1	3	0	0	2	0	0
Timulla	0	2	1	0	1	1	0	1	2	0	-	1	0	5	0	0	2	7	2	2	1	1	0	1	3	0	0	2	0	0
Tobantilla	1	3	2	2	1	1	0	1	2	[01]	1	1	0	0	5	0	0	3	2	0	0	[01]	0	1	3	0	0	2	0	1
Tricholabiodes	0	1	2	1	1	1	0	1	2	[01]	1	1	0	0	0	0	3	2	2	0	1	1	0	1	3	0	0	2	0	1
Trispilotilla	0	2	1	0	1	1	0	1	2	[01]	1	1	0	0	0	0	2	7	2	2	1	1	0	1	3	0	1	0	0	1
Trogaspidia	0	2	1	0	1	1	0	1	2	0	-	1	0	5	0	0	2	7	2	2	2	1	0	1	3	0	0	2	0	0
Tropidotilla	0	2	1	[01]	1	1	0	1	2	0	-	1	0	[24]	0	0	3	6	2	2	[01]	1	0	1	3	0	0	2	0	0
Vianatilla	1	0	1	0	1	1	0	1	2	1	2	1	0	0	0	0	3	5	2	0	0	1	0	1	3	0	0	2	0	1
Viereckia	0	[02]	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	2	2	0	2	1	0	1	3	0	0	2	0	0
Wallacidia	0	2	1	0	1	1	0	1	2	0	-	1	0	5	0	0	2	7	2	2	1	1	0	1	3	0	0	1	0	0
Xystromutilla	2	1	[12]	[02]	1	1	1	1	2	1	2	2	0	0	5	0	0	4	2	0	1	1	0	1	3	0	0	2	0	1
Yamanetilla	0	2	1	2	1	2	0	1	2	1	[01]	1	0	0	0	0	2	4	2	0	1	1	0	1	3	0	0	2	0	0

Appendix 4

Proposed higher classification of genera and subgenera of Mutillidae

All currently valid genera (216) and subgenera (30) are listed (for convenience simply under the heading of "Genera"), indicating the sexes known for each (whether described or not), and those included in the current analysis are in **boldface**. Details for each name appear in Lelej and Brothers (2008), except for those more recently published; they will be dealt with in a separate paper updating the 2008 listing. († = fossil taxon)

Family: Mutillidae Latreille, 1802
Subfamily: Myrmosinae Fox, 1894
Tribe: Kudakrumiini Krombein, 1979
Genera: ***Kudakrumia*** Krombein, 1979 (♂, ♀); *Leiomyrmosa* Wasbauer, 1973 (♀); ***Myrmosula*** Bradley, 1917 (♂, ♀); *Nothomyrmosa* Krombein, 1979 (♀); *Protomutilla*† Bischoff, 1916 (♂, ♀); ***Pseudomyrmosa*** Suárez, 1980 (♂, ♀)
Tribe: Myrmosini Fox, 1894
Genera: *Carinomyrmosa* Lelej, 1981 (♂, ♀); *Erimyrmosa* Lelej, 1984b (♂); *Krombeinella* Pate, 1947 (♂, ♀); ***Myrmosa*** Latreille, 1797 (♂, ♀); *Myrmosina* Krombein, 1940 (♂); ***Paramyrmosa*** Saussure, 1880 (♂, ♀); *Taimyrmosa* Lelej, 2005 (♂, ♀)

Subfamily: Pseudophotopsidinae Bischoff, 1920
Genus: ***Pseudophotopsis*** André, 1896 (♂, ♀)

Subfamily: Ticoplinae Nagy, 1970
Tribe: Smicromyrmillini Argaman, 1988
Genera: *Cameronilla* Lelej in Lelej & Krombein, 2001 (♂); *Eosmicromyrmilla* Lelej & Krombein, 2001 (♂, ♀); ***Hindustanilla*** Lelej in Lelej & Krombein, 2001 (♂, ♀); ***Smicromyrmilla*** Suárez, 1965 (♂, ♀)
Tribe: Ticoplini Nagy, 1970
Genera: ***Areotilla*** Bischoff, 1920 (♂, ♀); ***Nanomutilla*** André, 1900 (♂, ♀)

Subfamily: Rhopalomutillinae Schuster, 1949
Genera: ***Bischoffiella*** Brothers & Nonveiller in Brothers, 2015 (♂, ♀); ***Pherotilla*** Brothers, 2015 (♂, ♀); ***Rhopalomutilla*** André, 1901 (♂, ♀); ***Rimulotilla*** Brothers, 2015 (♂, ♀)

Subfamily: Sphaeropthalminae Schuster, 1949 (1903)
Tribe: Sphaeropthalmini Schuster, 1949 (1903)
Genera: *Acanthophotopsis* Schuster, 1958 (♂); *Acrophotopsis* Schuster, 1958 (♂); ***Allotilla*** Schuster, 1949 (♂, ♀); *Ceratophotopsis* Schuster, 1949 (♂); *Chilemutilla* Cambra & Quintero, 2007 (♂, ♀); *Chilephotopsis* Cambra

& Quintero, 2006 (♂); ***Cystomutilla*** André, 1896 (♂, ♀); ***Dilophotopsis*** Schuster, 1958 (♂, ♀); ***Hemutilla*** Lelej, Tu & Chen in Tu et al., 2014 (♂, ♀); *Laminatilla* Pitts, 2007 (♂); *Limaytilla* Casal, 1964 (♂, ♀); *Morsyma* Fox, 1899 (♂, ♀); *Nanotopsis* Schuster, 1949 (♂, ♀); ***Odontophotopsis*** Viereck, 1903 (♂, ♀); *Photomorphina* Schuster, 1952 (♂, ♀); ***Photomorphus*** Viereck, 1903 (♂, ♀); *Ptilomutilla* André, 1905 (♀); ***Scaptodactyla*** Burmeister, 1875 (♂, ♀); *Schusterphotopsis* Pitts, 2003 (♂); ***Sphaeropthalma*** Blake, 1871 (♂, ♀); *Stethophotopsis* Pitts in Pitts & McHugh, 2000 (♂, ♀); ***Tallium*** André, 1902 (♂, ♀); *Xenomorphus* Schuster, 1958 (♂); ***Xystromutilla*** André, 1905 (♂, ♀)

Tribe: Dasymutillini Brothers & Lelej, trib. n.

Genera: ***Ancistrotilla*** Brothers, 2012 (♂, ♀); *Ascetotilla* Brothers, 1971 (♂, ♀); *Australotilla* Lelej, 1983 (♂, ♀); ***Bothriomutilla*** Ashmead, 1899 (♂, ♀); ***Cephalomutilla*** André, 1908 (♂, ♀); ***Dasymutilla*** Ashmead, 1899 (♂, ♀); *Ephutomorpha* André, 1902 (♂, ♀); *Eurymutilla* Ashmead, 1899 (♀); [***Eurymutilla*** (genus near this) (♂, ♀);] *Frigitilla* Williams in Bartholomay et al., 2015 (♂, ♀); ***Gogoltilla*** Williams, Brothers & Pitts, 2011 (♂, ♀); *Leucospilomutilla* Ashmead, 1903 (♂, ♀); ***Lomachaeta*** Mickel, 1936 (♂, ♀); *Neomutilla* Reed, 1898 (♂, ♀); ***Odontomyrme*** Lelej, 1983 (♂, ♀); *Ponerotilla* Brothers, 1994 (♀); *Protophotopsiella* Schuster, 1949 (♂, ♀); ***Protophotopsis*** Schuster, 1947 (♂, ♀); ***Reedomutilla*** Mickel, 1964 (♂, ♀); *Suareztilla* Casal, 1968 (♂, ♀); ***Tobantilla*** Casal, 1965 (♂, ♀); *Traumatomutilla* André, 1901 (♂, ♀);

Tribe: Pseudomethocini Brothers, 1975

Subtribe: Euspinoliina Brothers & Lelej, subtrib. n.

Genera: ***Atillum*** André, 1902 (♂, ♀); ***Euspinolia*** Ashmead, 1903 (♂, ♀); ***Hoplocrates*** Mickel, 1937 (♂, ♀)

Subtribe: Pseudomethocina Brothers, 1975

Genera: *Anomophotopsis* Schuster, 1949 (♂, ♀); *Calomutilla* Mickel, 1952 (♂, ♀); *Chaetotilla* Schuster, 1949 (♂); ***Darditilla*** Casal, 1965 (♂, ♀); ***Dimorphomutilla*** Ashmead, 1903 (♂, ♀); *Gurisita* Casal, 1970 (♀); ***Hoplognathoca*** Suárez, 1962 (♂, ♀); ***Hoplomutilla*** Ashmead, 1899 (♂, ♀); *Horcomutilla* Casal, 1962 (♂, ♀); *Invreiella* Suárez, 1966 (♀); ***Lophomutilla*** Mickel, 1952 (♂, ♀); *Lophostigma* Mickel, 1952 (♂, ♀); ***Lynchiatilla*** Casal, 1963 (♂, ♀); *Mickelia* Suárez, 1966 (♀); ***Myrmilloides*** André, 1902 (♂, ♀); *Pappognatha* Mickel, 1939 (♂, ♀); *Patquiatilla* Casal, 1962 (♂, ♀); ***Pertyella*** Mickel, 1952 (♂, ♀); ***Pseudomethoca*** Ashmead, 1896 (♂, ♀); *Seabratilla* Casal, 1963 (♀); ***Vianatilla*** Casal, 1962 (♂, ♀)

Subfamily: Dasylabrinae Invrea, 1964

Tribe: Apteromutillini Brothers & Lelej, trib. n.

Genera: ***Apteromutilla*** Ashmead, 1903 (♂, ♀); ***Brachymutilla*** André, 1901 (♂, ♀); ***Liotilla*** Bischoff, 1920 (♂, ♀)

Tribe: Dasylabrini Invrea, 1964

Genera: *Baltilla* Lelej, 1976 (♂, ♀); ***Chrestomutilla*** Brothers, 1971 (♂, ♀); *Craspedopyga* Lelej, 1976 (♂, ♀); ***Dasylabris*** Radoszkowski, 1885 (♂, ♀); ***Dasylabroides*** André, 1901 (♂, ♀); *Inbaltilla* Lelej, 1976 (♂, ♀); *Jaxartilla* Lelej, 1984 (♂); ***Orientilla*** Lelej, 1979 (♂, ♀); ***Seyrigilla*** Krombein, 1972 (♂, ♀); ***Stenomutilla*** André, 1896 (♂, ♀); ***Tricholabiodes*** Radoszkowski, 1885 (♂, ♀)

Subfamily: Myrmillinae Bischoff, 1920

Genera: *Arnoldtilla* Nonveiller, 1996 (♂, ♀); *Bethsmyrmilla* Krombein & Lelej, 1999 (♀); *Bidecoloratilla* Turrisi & Matteini Palmerini in Turrisi et al., 2015 (♂, ♀); *Bimaculatilla* Turrisi & Matteini Palmerini in Turrisi et al., 2015 (♂, ♀); ***Bischoffitilla*** Lelej, 2002 (♂, ♀); *Bisulcotilla* Bischoff, 1920 (♂); *Blakeius* Ashmead, 1903 (♂, ♀); *Botswanotilla* Nonveiller, 1996 (♂); *Brahmatilla* Lelej, 2005 (♀); *Cataractaetilla* Nonveiller, 1996 (♂, ♀); ***Ceratotilla*** Bischoff, 1920 (♂, ♀); *Clinotilla* Arnold, 1956 (?♂, ♀); ***Eurygnathilla*** Skorikov, 1927 (♂, ♀); ***Labidomilla*** André, 1902 (♂, ♀); *Liomutilla* André, 1907 (♂, ♀); ***Myrmilla*** Wesmael, 1851 (♂, ♀); *Myrmotilla* Bischoff, 1920 (♀); ***Odontotilla*** Bischoff, 1920 (♂, ♀); *Odontotilloides* Nonveiller, 1996 (♂, ♀); *Omotilla* Invrea, 1943 (♂, ♀); ***Platymyrmilla*** André, 1900 (♂, ♀); ***Pseudomutilla*** Costa, 1885 (♂, ♀); *Pygomilla* Hammer, 1955 (♀); *Saganotilla* Invrea, 1943 (♂, ♀); *Sigilla* Skorikov, 1927 (♂, ♀); *Somaliatilla* Nonveiller, 1996 (♀); *Spilomutilla* Ashmead, 1903 (♂, ♀); *Squamulotilla* Bischoff, 1920 (♂); ***Viereckia*** Ashmead, 1903 (♂, ♀)

Subfamily: Mutillinae Latreille, 1802

Tribe: Ctenotillini Brothers & Lelej, trib. n.

Genera: *Arcuatotilla* Nonveiller, 1998 (♂, ♀); *Bidentotilla* Nonveiller, 1979 (♂); *Cephalotilla* Bischoff, 1920 (♂, ♀); ***Chaetomutilla*** Nonveiller, 1979 (♂, ♀); ***Ctenotilla*** Bischoff, 1920 (♂, ♀); *Lehritilla* Lelej, 2005 (♂); ***Mimecomutilla*** Ashmead, 1903 (♂, ♀); ***Mimecotilla*** Nonveiller, 1998 (♂, ♀); *Montanomutilla* Nonveiller, 1979 (♀); ***Pristomutilla*** Ashmead, 1903 (♂, ♀); *Strangulotilla* Nonveiller, 1979 (♂, ♀); *Taeniotilla* Nonveiller, 1979 (♂); *Zeugomutilla* Chen, 1957 (♂, ♀)

Tribe: Smicromyrmini Bischoff, 1920

Genera: *Andreimyrme* Lelej, 1995 (♂, ♀); *Antennotilla* Bischoff, 1920 (♂); *Astomyrme* Schwartz, 1984 (♂, ♀); *Corytilla* Arnold, 1956 (♂, ♀); *Ctenoceraea* Nonveiller, 1993 (♂); ***Dentilla*** Lelej in Lelej & Kabakov, 1980 (♂, ♀); *Ephucilla* Lelej 1995 (♂, ♀); ***Ephutomma*** Ashmead, 1899 (♂, ♀); *Eremotilla* Lelej, 1985 (♂, ♀); *Erimyrme* Lelej, 1985 (♂, ♀); *Guineomutilla* Suárez, 1977 (♀); *Gynandrotilla* Arnold, 1946 (♂); *Indratilla* Lelej, 1993 (♂, ♀); *Karunaratnea* Lelej, 2005 (♂, ♀); ***Mickelomyrme*** Lelej, 1995 (♂, ♀); ***Nemka*** Lelej, 1985 (♂, ♀); *Nordeniella* Lelej, 2005 (♂, ♀); *Nuristan-*

illa Lelej in Lelej & Kabakov, 1980 (♀); *Paglianotilla* Lelej in Lelej & van Harten, 2006 (♂); ***Physetopoda*** Schuster, 1949 (♂, ♀); ***Promecilla*** André, 1902 (♂, ♀); *Psammotherma* Latreille, 1825 (♂); ***Pseudocephalotilla*** Bischoff, 1920 (♂, ♀); *Rasnitsynitilla* Lelej in Lelej & van Harten, 2006 (♂); *Rhombotilla* Nagy, 1966 (♀); *Sinotilla* Lelej, 1995 (♂, ♀); *Skorikovia* Ovtchinnikov, 2002 (♂, ♀); ***Smicromyrme*** Thomson, 1870 (♂, ♀); ***Sulcotilla*** Bischoff, 1920 (♂, ♀); *Tsunekimyrme* Lelej, 1995 (♂)

Tribe: Mutillini Latreille, 1802

Subtribe: Ephutina Ashmead, 1903 (= Odontomutillini Lelej, 1983, **syn. n.**)

Genera: *Cockerellidia* Lelej & Krombein, 1999 (♀); *Ephuamelia* Casal, 1968 (♂); *Ephuchaya* Casal, 1968 (♂); *Ephuseabra* Casal, 1968 (♂); *Ephusuarezia* Casal, 1968 (♂); ***Ephuta*** Say, 1836 (♂, ♀); *Ephutopsis* Ashmead, 1904 (♂, ♀); *Karlidia* Lelej in Lelej & Krombein, 1999 (♀); ***Odontomutilla*** Ashmead, 1899 (♂, ♀); *Onoretilla* Pagliano in Pagliano, Cambra & Quintero, 2017 (♂); *Xenochile* Schuster, 1957 (♂); ***Yamanetilla*** Lelej, 1996 (♂, ♀)

Subtribe: Mutillina Latreille, 1802

Genera: *Barymutilla* André, 1901 (♂, ♀); *Hadrotilla* Bischoff, 1920 (♂, ♀); *Kurzenkotilla* Lelej, 2005 (♀); *Macromyrme* Lelej, 1984 (♀); ***Mutilla*** Linnaeus, 1758 (♂, ♀); *Nanomyrme* Lelej, 1977 (♀); ***Ronisia*** Costa, 1858 (♂, ♀); *Standfussidia* Lelej, 2005 (♀); *Storozhenkotilla* Lelej, 2005 (♂, ♀); ***Tropidotilla*** Bischoff, 1920 (♂, ♀)

Tribe: Trogaspidiini Bischoff, 1920 (= Petersenidiina Lelej, 1996, **syn. n.**)

Genera: ***Acanthomutilla*** Nonveiller, 1995 (♂, ♀); *Acutitropidia* Nonveiller, 1995 (♂, ♀); *Allotropidia* Nonveiller, 1996 (♂); ***Amblotropidia*** Nonveiller, 1995 (♂, ♀); *Arcuatotropidia* Nonveiller, 1995 (♂); ***Artiotilla*** Invrea, 1950 (♂, ♀); *Aureotilla* Bischoff, 1920 (♂, ♀); *Carinotilla* Nonveiller, 1973 (♂, ♀); *Chilotropidia* Nonveiller, 1995 (♂, ♀); *Chrysotilla* Bischoff, 1920 (♂, ♀); *Curvitropidia* Nonveiller, 1995 (♂, ♀); *Dentotilla* Nonveiller, 1977 (♂, ♀); *Diacanthotilla* Nonveiller, 1995 (♀); ***Dolichomutilla*** Ashmead, 1899 (♂, ♀); *Eotrogaspidia* Lelej, 1996 (♂, ♀); ***Glossotilla*** Bischoff, 1920 (♂, ♀); *Hildbrandetia* Özdikmen, 2005 (♀); *Inflatispidia* Nonveiller, 1995 (♂, ♀); ***Karlissaidia*** Lelej, 2005 (♂, ♀); ***Krombeinidia*** Lelej, 1996 (♂, ♀); ***Lobotilla*** Bischoff, 1920 (♂, ♀); *Lobotropidia* Nonveiller, 1995 (♂, ♀); *Lophotilla* Bischoff, 1920 (♂); *Neotrogaspidia* Lelej, 1996 (♂, ♀); *Nonveilleridia* Lelej, 1996 (♂); *Orientidia* Lelej, 1996 (♂, ♀); *Pagdenidia* Lelej, 1996 (♂, ♀); *Petersenidia* Lelej in Lelej & Yamane, 1992 (♂, ♀); *Promecidia* Lelej, 1996 (♂, ♀); *Protrogaspidia* Lelej, 1996 (♂); *Pseudolophotilla* Nonveiller & Ćetković, 1995 (♂, ♀); ***Radoszkowskitilla*** Lelej, 2005 (♂, ♀); *Serendibiella* Lelej, 2005 (♂); *Seriatospidia* Nonveiller & Ćetković, 1996 (♀); ***Spinulomutilla*** Nonveiller, 1994 (♂, ♀); *Spinulotilla* Bischoff, 1920 (♂, ♀); *Sylvotilla* Viette, 1978 (♀); *Taiwanomyrme* Tsuneki, 1993 (♂, ♀); ***Timulla*** Ashmead, 1899 (♂, ♀); ***Trispilotilla*** Bischoff, 1920 (♂, ♀); ***Trogaspidia***

Ashmead, 1899 (♂, ♀); *Tuberocoxotilla* Nonveiller, 1980 (♂); *Vanhartenidia* Lelej in Lelej & van Harten, 2006 (♂, ♀); ***Wallacidia*** Lelej & Brothers, 2008 (♂, ♀); *Zavatilla* Tsuneki, 1993 (♂)

Family Mutillidae *incertae sedis*

Genus: *Cretavus*† Sharov, 1957 (♂)

Supplementary material 1

Data matrix for phylogenetic analysis of sub/genera of Mutillidae and four outgroup taxa

Authors: Denis J. Brothers, Arkady S. Lelej

Data type: Taxon versus character-state matrix

Explanation note: This is an operational version of the data matrix in Nona format.

Link: https://doi.org/10.3897/jhr.60.20091.suppl1

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Unique nest architecture in the North African osmiine bee *Hoplitis* (*Hoplitis*) *mucida* (Hymenoptera, Megachilidae)

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Abstract

The osmiine bee species *Hoplitis mucida* is considered to consist of two subspecies with *H. mucida mucida* (Dours, 1873) ranging from northwestern Africa to Israel and Jordan and *H. mucida stecki* (Frey-Gessner, 1908) occurring in southwestern Europe and Sicily. The discovery of nests of *H. mucida* in Morocco and Tunisia revealed striking differences in the nesting biology of the two subspecies. In North Africa, females construct fully exposed, cake-like nests of mud on the flat surface of rocks and stones containing 8–12 vertically oriented brood cells, rendering these nests unique among osmiine bees regarding both nesting site and nest architecture. In contrast, in Europe females build their few-celled mud nests inside small rock cavities. This discrepancy in the nesting biology is paralleled by considerable morphological differences between the two subspecies suggestive of a long geographical isolation. Due to these biological and morphological differences, we propose to elevate the European subspecies *H. mucida stecki* to species rank.

Keywords

Apiformes, *Echium*, heat tolerance, *Hoplitis adunca* species group, labial glands

Introduction

The osmiine bee species *Hoplitis mucida* (Dours, 1873) is a member of the large subgenus *Hoplitis* Klug, which comprises about 90 described and 50 undescribed species restricted to the Palaearctic region (Müller 2017). Within this subgenus, *H. mucida* belongs to the *Hoplitis adunca* species group representing the most basal member of that clade (Sedivy et al. 2013a). It is morphologically well characterized by its large size, lack of distinct hair bands along the tergal margins and two unique characters in the male sex, i.e. the hooked last antennal segment and the four-toothed tergum 6 (Amiet et al. 2010, Müller 2016). The distribution area of *H. mucida* encompasses southwestern Europe, Sicily, the Maghreb (Morocco, Algeria, Tunisia) and the Levant (Israel and Palestine, Jordan) (Müller 2017). Based on morphologically deviating specimens from Switzerland, Frey-Gessner (1908) established the subspecies *H. mucida stecki* (Frey-Gessner, 1908), which was later found by Warncke (1992) to be distributed throughout southwestern Europe. The division of *H. mucida* into a European and a non-European subspecies was followed by later authors (Ungricht et al. 2008, Müller 2017).

Hoplitis mucida is narrowly oligolectic, it exclusively collects pollen on flowers of *Echium* L. (Boraginaceae) throughout the entire species' range (Sedivy et al. 2013b). The discovery of a nest in southern Spain consisting of a single brood cell hidden in a small rock cavity and constructed from mud (Le Goff 2005) revealed that the nesting biology of *H. mucida* closely corresponds to that of many other members of the *Hoplitis adunca* species group, which also build nests in depressions, fissures or holes of stones and rocks, and use mud as main nest building material (Sedivy et al. 2013a).

In spring 2017, two nests of *Hoplitis mucida* were found in southern Morocco, which strongly differed from the nest discovered in Spain with respect to both nesting site and nest architecture. These two Moroccan nests were very similar to a nest of *H. mucida* found in northern Tunisia in spring 2012 indicating striking differences in the nesting biology between North African and European populations. This discrepancy in nesting behaviour is paralleled by morphological differences between populations of North Africa and the Levant on the one hand and European populations on the other hand (Pérez 1902, Frey-Gessner 1908, Mavromoustakis 1947, Zanden 1990, Warncke 1992).

In the present contribution, we describe the peculiar North African nests of *Hoplitis mucida*, reevaluate the morphological differences between non-European and European populations and - based on both nesting biology and morphology - propose to elevate the European subspecies *H. mucida stecki* to species rank.

Methods

Two nests of *Hoplitis mucida* were found in southern Morocco near Tlata Uonass about 4 km east of Ait Baha (30°03'42"N; 9°06'55"W) at an elevation of 610 m a.s.l. on 16 April 2017. One nest was already finalized, whereas the female of the second nest applied the last portions of mud onto its nest before she finally left the nesting

site shortly after. As both nests adhered to large stones or rocks, which could not be transported back to the lab to let the bees emerge, the nests were opened with a knife to ascertain the number and arrangement of the brood cells. An additional nest of *H. mucida* was discovered in northern Tunisia near Sidi Mtir about 17 km southwest of El Kef (36°03'16"N; 8°36'26"E) at an elevation of 510 m a.s.l. on 28 April 2012. This nest was initially attributed to an unknown species of *Megachile* (*Chalicodoma*) but later turned out to belong to *H. mucida* based on the bees that emerged in the lab.

To exclude the possibility that the discrepancy in the nesting behaviour between North African and European populations of *Hoplitis mucida* is simply due to a misidentification, the correct determination of the female that had constructed the nest discovered in southern Spain (Le Goff 2005) was confirmed by examining the voucher specimen kindly provided by G. Le Goff.

To find new and reevaluate already published morphological differences (Pérez 1902, Frey-Gessner 1908, Mavromoustakis 1947, Zanden 1990, Warncke 1992) between non-European and European populations of *Hoplitis mucida*, 21 females and 10 males of *H. m. mucida* (originating from Morocco, Tunisia, Israel and Jordan) and 16 females and 8 males of *H. m. stecki* (originating from Portugal, Spain, southern France, northern Italy and Sicily) were investigated under a stereomicroscope. Morphological terminology follows Michener (2007) with the following specifications: i) the distance between lateral ocellus and preoccipital ridge was measured in top view rather than in lateral view; ii) the diameter of the lateral ocellus was measured under inclusion of the ocellar border, which is of the same colour as the surrounding cuticle thereby differing from the light colour of the central part of the ocellus; iii) the numbering of the antennal segments starts from the scape, which is antennal segment 1.

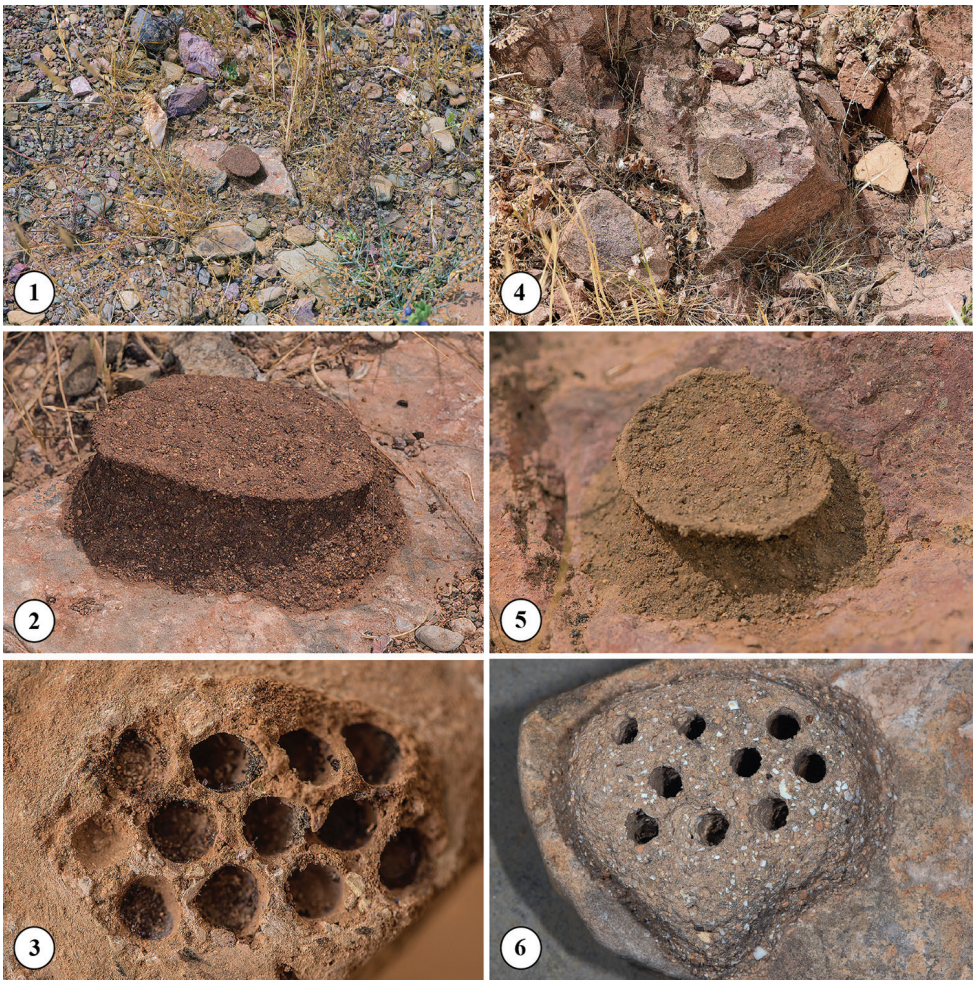
Results

Nesting site and nest architecture

The three nests of *Hoplitis mucida* found in Morocco and Tunisia had been constructed freely on horizontal to slightly sloping and almost flat surfaces of stones and rocks (Table 1, Figs 1–6). The stones serving as substrate for nests 1 and 3 were immovable as they were partly buried in the ground. All three nests were completely built from mud including small sand grains but without addition of larger pebbles. They were extremely hard and adhered strongly to the substrate making it impossible to remove them from the stony surface without damaging them.

The three nests were all of roundish to oval shape measuring 4.5–6.2 cm in maximal length, 4.0–5.1 cm in maximal width and 1.7–2.0 cm in maximal height (Table 1). The flat upper surface of the two Moroccan nests slightly projected beyond the concave sides (Figs 2, 5), whereas the Tunisian nest lacked a projecting rim and had convexe sides (Fig. 6).

The nests contained 8–12 brood cells, which had been built side by side (Table 1, Figs 3, 6). From nest 3, which contained 11 cells, four females and five males emerged



Figures 1–6. Nests of *Hoplitis mucida* (see Table 1): **1–2** Nest 1 near Ait Baha in southern Morocco glued to the flat surface of a middle-sized stone **3** Nest 1 opened shortly after its finalization with cell contents removed **4–5** Nest 2 near Ait Baha in southern Morocco glued to the flat surface of a rock **6** Nest 3 originating from near El Kef in northern Tunisia glued to the flat surface of a small stone and photographed after bee emergence.

(Fig. 6), whereas the bees in the remaining two cells had died during their development. As the careful examination of the contact zones between adjacent brood cells revealed double walls (Fig. 3), the wall of each new cell had been mortared directly onto the wall of the neigbouring cell. The longitudinal axes of the brood cells in all three nests were oriented almost perpendicular to the stony surface (Figs 3, 6), indicating that the first cell had been built freely upright without lateral support by the substrate. As the more central cells of nest 1 contained larvae that already had spun a cocoon whereas the outer cells still contained large amounts of pollen, the construction of the brood cells had proceeded from the inside to the outside. The examination of opened nests

Table 1. Characteristics of three nests of *Hoplitis mucida* (Dours 1873) discovered in North Africa.

	Nest 1 (Figs 1–3)	**Nest 2 (Figs 4–5)**	**Nest 3 (Fig. 6)**
Locality	near Ait Baha in southern Morocco	near Ait Baha in southern Morocco	near El Kef in northern Tunisia
Nest substrate	middle-sized stone (28 cm × 18 cm) partly buried in the ground	rock	small stone (16 cm × 7 cm) partly buried in the ground
Maximal length × maximal width of nest	6.2 cm × 5.1 cm	4.5 cm × 4 cm	5.4 cm × 4.8 cm
Maximal height of nest	2.0 cm	1.9 cm	1.7 cm
Sides of nest	concave	concave	convex
Number of brood cells	12	8	11

revealed substantial amounts of mud added to both the top and the lateral sides of the nest (Fig. 3). Thus, the females had smoothed out irregularities and hollow spaces between the apical ends of the brood cells as well as between the walls of the outermost cells with mud, which resulted in a contiguous and uniform top and lateral layer giving the nest a cake-like form completely concealing the shape of the brood cells (Figs 2, 5). The question whether this extra addition of mud had started after all brood cells had been finalized or already earlier remains open. However, based on the observation that the female of nest 1 applied mud onto the flat upper nest surface before she finally left the nesting site, we hypothesize that the construction of the top layer is the last part of the nest building activity probably preceded by the building of the side layer.

Morphology

The examination of specimens of *Hoplitis mucida* collected throughout the species' distribution area revealed distinct morphological differences in both sexes between individuals from North Africa and the Levant on the one hand and individuals from southwestern Europe and Sicily on the other hand (Table 2, Figs 7–18), supporting the findings of earlier authors (see Introduction). In contrast, no clear morphological differences were found among individuals originating from Morocco, Tunisia, Israel and Jordan and among individuals collected in Portugal, France, northern Italy and Sicily, respectively.

Discussion

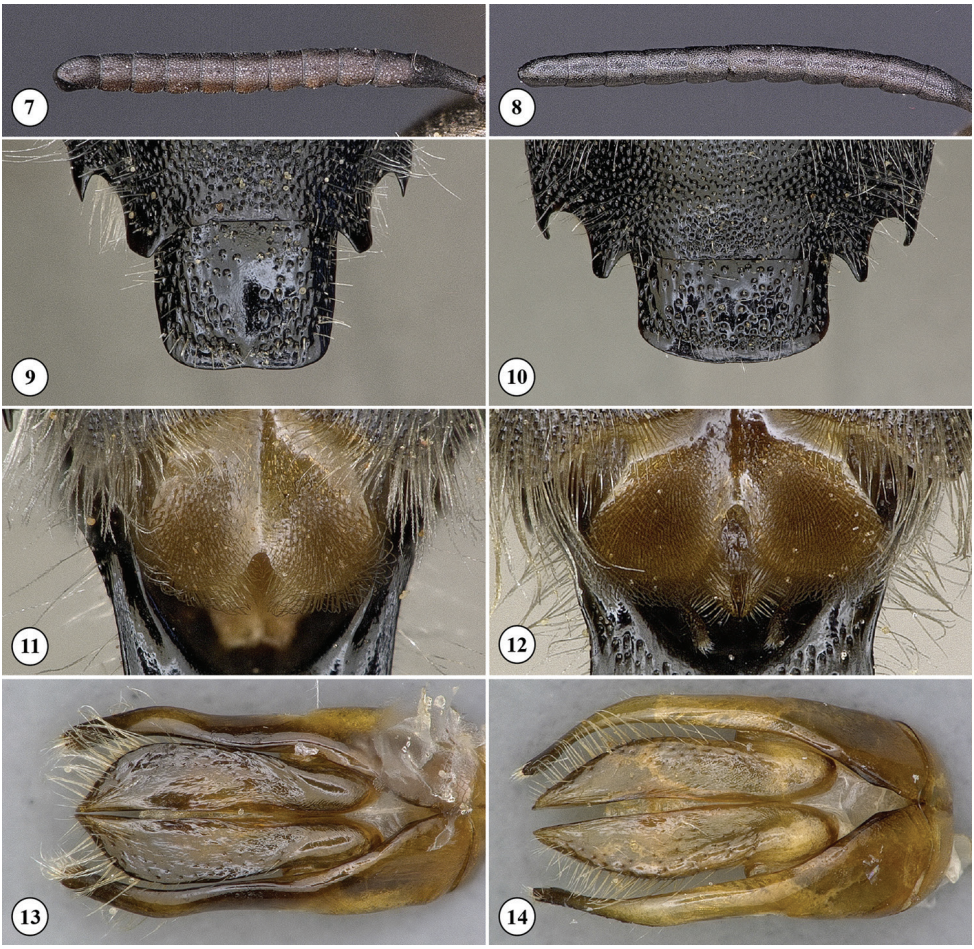
Nesting site and nest architecture

Among bees, exposed nests constructed from mud and glued to the surface of stones and rocks are known only from a few taxa of megachiline and osmiine bees. Free-standing mud nests occur in numerous *Megachile* species of the subgenus *Chalicodoma*

Table 2. Biological and morphological differences between *Hoplitis mucida* (Dours, 1873) and *H. stecki* (Frey-Gessner, 1908).

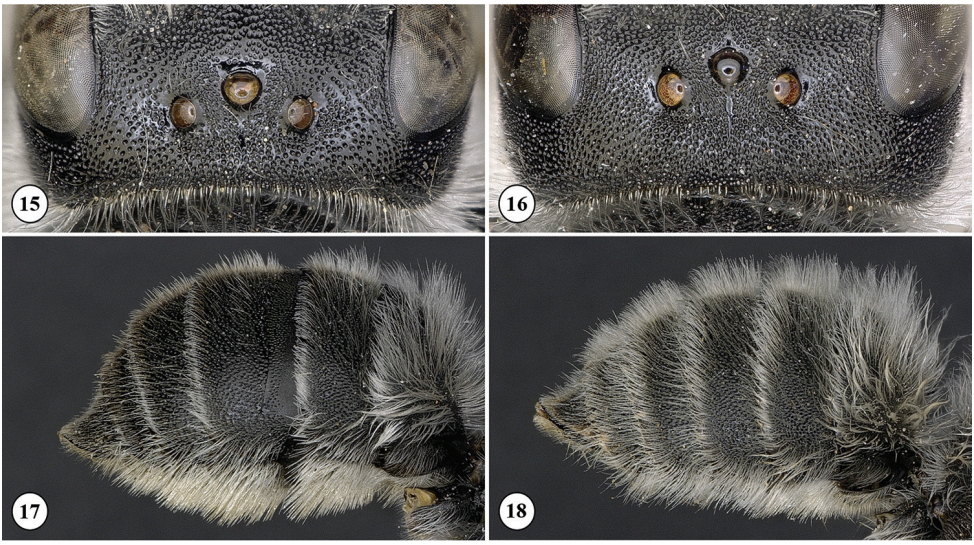
	Hoplitis mucida	***Hoplitis stecki***
Distribution	Maghreb (Morocco, Algeria, Tunisia) and Levant (Israel and Palestine, Jordan)	southwestern Europe (Iberian Peninsula, southern France, northern Italy, southern Switzerland) and Sicily
Nesting biology	free-standing, cake-like nests constructed from mud on horizontal and flat surfaces of stones and rocks containing 8-12 brood cells	hidden nests built in small cavities of rocks containing one to possibly few brood cells constructed from mud (Le Goff 2005)
Male characters	antennal segments 6–12 slightly shorter than wide (Fig. 7)	antennal segments 6–12 slightly longer than wide (Fig. 8)
	distance between lateral ocellus and preoccipital ridge 1.5–1.65× as long as ocellar diameter	distance between lateral ocellus and preoccipital ridge 1.8–2× as long as ocellar diameter
	pilosity of tergal discs less strongly developed, on apical half of discs 3–5 distinctly shorter than on basal half	pilosity of tergal discs more strongly developed, on apical half of discs 3–5 about as long as on basal half
	apical rectangular plate of tergum 7 almost as long as wide (Fig. 9)	apical rectangular plate of tergum 7 distinctly wider than long (Fig. 10)
	transversal subapical swellings of sterna 2–4 more strongly developed	transversal subapical swellings of sterna 2–4 less strongly developed
	lateral lobes of membraneous appendage of sternum 6 narrower and less diverging, separated from each other by a shorter incision and densely covered with yellowish-white pilosity (Fig. 11)	lateral lobes of membraneous appendage of sternum 6 wider and more diverging, separated from each other by a deeper incision and densely covered with yellowish-brown pilosity (Fig. 12)
	apex of gonostylus and outer margin of penis valve with distinctly longer hairs (Fig. 13)	apex of gonostylus and outer margin of penis valve with distinctly shorter hairs (Fig. 14)
	penis valve more or less parallel-sided except for its apicalmost part and apically more rounded (Fig. 13)	penis valve tapering towards its apex and apically more acute (Fig. 14)
Female characters	distance between lateral ocellus and preoccipital ridge 1.5–1.6× as long as ocellar diameter (Fig. 15)	distance between lateral ocellus and preoccipital ridge 1.8–1.9x as long as ocellar diameter (Fig. 16)
	pilosity of tergal discs shorter, on discs 3–4 less than 1.5× as long as maximal width of antennal flagellum (Fig. 17)	pilosity of tergal discs longer, on discs 3–4 about 2× as long as maximal width of antennal flagellum (Fig. 18)

(Praz 2017, and references therein) and in several *Hoplitis* species of the *Hoplitis adunca* species group (Sedivy et al. 2013a, and references therein). To the present knowledge, these species all prefer strongly inclined to vertical areas of stones and rocks for nesting, they usually build their nests in depressions or irregularities of the stony surface and the longitudinal axes of their brood cells are more or less parallel to the underground with the cells being often constructed in lateral contact to the substrate. In contrast, North African females of *Hoplitis mucida* select horizontal to slightly inclined areas for nesting, they build their nests on flat portions of the stony surface and the longitudinal axes of their brood cells are perpendicular to the underground with the cells being constructed upright without lateral contact to the substrate. These differences make the cake-like nests of North African populations of *H. mucida* unique among both megachilid bees and members of the *Hoplitis adunca* species group.



Figures 7–14. Morphological differences in the male sex between *Hoplitis mucida* (left) and *H. stecki* (right) (see Table 2): **7–8** Antenna **9–10** Tergum 7 **11–12** Membraneous appendage of sternum 6 **13–14** Genitalia.

The nests of *Hoplitis mucida* were found to be extremely hard and it proved to be impossible to perforate their walls even with a strong knife. They are thus similary hard as the exposed mud nests of *Megachile* (*Chalicodoma*) species. The hardness of *Megachile* (*Chalicodoma*) nests is most probably due to the mixing of mud with secretions of the labial glands, which harden the mud and render the nests hydrophobic protecting them against the erosive effects of rain (Kronenberg and Hefetz 1984). It seems probable that the females of *H. mucida* also add glandular secretions to the collected mud to make the nests hard and weatherproof, suggesting the convergent evolution of a mud binding agent in these two only distantly related bee taxa. In fact, females of *Hoplitis anthocopoides*, a species that is closely related to *H. mucida* and also constructs free-standing mud nests, were observed to mix a fluid probably originating from the enlarged salivary glands with mud as the latter was collected on the ground (Eickwort 1973, 1975).



Figures 15–18. Morphological differences in the female sex between *Hoplitis mucida* (left) and *H. stecki* (right) (see Table 2): **15–16** Vertex **17–18** Pilosity of tergal discs.

The two nesting sites of *Hoplitis mucida* in southern Morocco and northern Tunisia are exposed to average maximum daily air temperatures during July and August of more than 30°C and 40°C, respectively (https://de.climate-data.org), resulting in ground temperatures that may regularly reach far beyond 50°C during the day (Kerr et al. 1984). Thus, the larvae of *H. mucida* must have an amazing ability to withstand extreme temperatures given the fully sun-exposed position of the nests, the stony nest substrate and - at least in the two moroccan nests - the non-reflective dark colour of the nest building material. As all nests were found to have been finished mid to end April coincident with the end of the flowering period of *Echium*, the species' exclusive host plant, all larvae likely entered the prepupal stage till end of May latest before the environmental temperatures reached close-to-lethal levels. Thus, the ability to resist such extreme summer temperatures pertains to the diapausing prepupae of *H. mucida*.

Some members of the *Hoplitis adunca* species group known to build exposed mud nests at the surface of rocks and stones, such as *Hoplitis anthocopoides, H. benoisti, H. loti* or *H. ravouxi*, occasionally also nest in small holes and fissures, where their brood cells are more or less hidden (Sedivy et al. 2013a, and references therein). Obviously, these species have the flexibility to colonize rock cavities of variable shape and size, ranging from small holes often containing only one or two hidden brood cells to surface depressions or irregularities serving as substrate for free-standing nests with numerous cells. Given the highly elaborated and unique architecture of Moroccan and Tunisian nests of *Hoplitis mucida*, we consider it highly improbable that North African populations of *H. mucida* use small holes or fissures in rocks and stones as

alternative nesting sites as the species mentioned above. Similarly, it appears highly unlikely that European *H. mucida* also build fully exposed, cake-like nests like their North African relatives since such conspicuous nests would certainly have been found in the well explored southwestern European region, where studies on the nesting biology of bees have a long tradition, particularly in France (e.g. Fabre 1879-1907, Ferton 1923). Instead, we strongly assume that the nesting biology of North African and European populations of *H. mucida* strongly differ with respect to both nesting site and nest architecture.

Morphology

The morphological analysis revealed a distinct morphological gap between non-European and European populations of *Hoplitis mucida*, but morphological uniformity among specimens distributed in the Maghreb and the Levant. This finding indicates that North African and southwestern European populations were geographically and genetically isolated for a long time and suggests that the separation of the populations of the Maghreb from those of the Levant is a rather recent event, possibly taking place at the end of the greening period of the Sahara about 6000 years before present (Claussen and Gayler 1997). Based on the lack of clear morphological differences between North African and Levantinian populations and their probably recent geographical separation, we expect the still unknown nesting biology of the latter to closely correspond to that described in the present contribution.

Conclusion

European populations of *Hoplitis mucida* substantially differ from North African populations in nesting site, nest architecture and morphology. These differences justify the recognition of the European populations as a biological species of its own. Thus, we propose to elevate the European subspecies *H. mucida stecki* to species rank, i.e. *H. stecki* (Frey-Gessner, 1908), stat. n.

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C. Praz and C. Sedivy participated in an excursion to Tunisia in 2012. C. Praz bred the nest of *H. mucida* discovered in Tunisia in the lab. G. Le Goff provided the voucher female of the nest he found in Spain. H. Baur (Naturhistorisches Museum Bern) provided access to a digital imaging system for taking photomicrographs. Comments by V. Gonzalez, C. Praz, C. Rasmussen and J. Neff substantially improved the manuscript.

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An alternative host of *Hymenoepimecis japi* (Hymenoptera, Ichneumonidae) on a novel family (Araneae, Araneidae), with notes on behavioral manipulations

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Abstract

Polysphinctine wasps of the genus *Hymenoepimecis* act as koinobiont ectoparasitoids of orb-weaver spiders. *Hymenoepimecis japi* is already known to parasitize the tetragnathid spider *Leucauge roseosignata.* Here, we record the dome-weaver spider *Mecynogea biggiba* as a second host for *H. japi*, as well as the behavioral manipulations induced by the parasitoid. We found that *H. japi* alters the web construction behavior of *M. biggiba*, resulting in a complex three-dimensional cocoon web. This modified web differs from that of *L. roseosignata,* which is a simpler structure composed of a few support threads. Our finds add to the literature the first case of a *Hymenoepimecis* species parasitizing spiders of two distinct families.

Keywords

Cocoon web, parasitoid wasp, *Polysphincta* genus-group, polysphinctine, Serra do Japi

Introduction

Spider-wasp interactions are considered a hot topic in the understanding of behavioral manipulation, since some parasitoid wasps can improve their own survival by inducing the host spiders to construct a modified web or "cocoon web" (Eberhard 2000a, b).

Several studies have described behavioral manipulations of spiders by the clade of koinobiont ectoparasitoid wasps of the *Polysphincta* genus-group (hereafter polysphinctine wasps) (Ichneumonidae: Pimplinae) (Gonzaga and Sobczak 2007, 2011, Matsumoto 2009, Korenko and Pekár 2011, Eberhard 2013, Sobczak et al. 2014, Kloss et al. 2016). Eberhard (2010) proposed that psychotropic substances released by wasp larva are the driving force behind behavioral manipulations of host spiders, but no additional studies have confirmed this hypothesis. Thus, every new record focused on spider-polysphinctine interactions is of value to comprehend the mechanism of behavioral manipulation induced by wasps.

Within polysphinctine wasps, the Neotropical genus *Hymenoepimecis* Viereck, 1912 is probably the most studied with respect to interactions with host spiders (Pádua et al. 2016). These parasitoid wasps are known to attack spiders of five genera, namely: *Nephila* (Araneidae; Finke et al. 1990, Gauld 1991, 2000, Gonzaga et al. 2010), *Leucauge* (Tetragnathidae; Gauld 1991, Eberhard 2000a, 2001, Sobczak et al. 2009, Eberhard 2013, Pádua et al. 2016), *Cyrtophora* (Araneidae; Gauld 2000), *Araneus* (Araneidae; Gonzaga and Sobczak 2007, Sobczak et al. 2011, Sobczak et al. 2012, 2014) and *Manogea* (Araneidae; Sobczak et al. 2009). Until now, 12 of the 20 valid-species of *Hymenoepimecis* are confirmed to be capable of parasitizing subadult and adult orb-weaving spiders (summarized in Pádua et al. 2016) and inducing their hosts to construct a variety of cocoon web designs, from simple two-dimensional to complex three-dimensional tangles of non-sticky threads.

On current understanding, *Hymenoepimecis*-spider interactions are frequently species-specific, with an exception in *H. veranii* Loffredo & Penteado-Dias, 2009 that parasitizes two congeneric and sympatric araneid spiders *Araneus omnicolor* (Keyserling, 1893) and *A. orgaos* Levi, 1991 (Gonzaga and Sobczak 2007, Sobczak et al. 2014). Our study species, *Hymenoepimecis japi* Loffredo & Penteado-Dias, 2009 (male described by Sobczak 2012), is known to parasitize the orb-weaver spider *Leucauge roseosignata* Mello-Leitão, 1943 (Tetragnathidae) (Sobczak et al. 2009). Through this parasitism, the spiders experience behavioral manipulation that results in the host constructing a cocoon web with a simple structure composed of a few strong radial lines and the absence of the sticky spirals that are characteristic of orb-weavers. Here we report a novel spider family parasitized by *H. japi* and describe the behavioral manipulations on *Mecynogea biggiba* Simon, 1903 (Araneidae) by the parasitoid wasp.

Material and methods

Study species

The genus *Mecynogea* comprises 10 valid species distributed in the Americas (World Spider Catalog 2017) and belongs to Cyrtophorinae, a peculiar subfamily of Araneidae with three-dimensional dome webs. *Mecynogea biggiba* (Fig. 1A), our study species, is a small spider (total length of adult individuals ranging from 3 to 5.5 mm) which

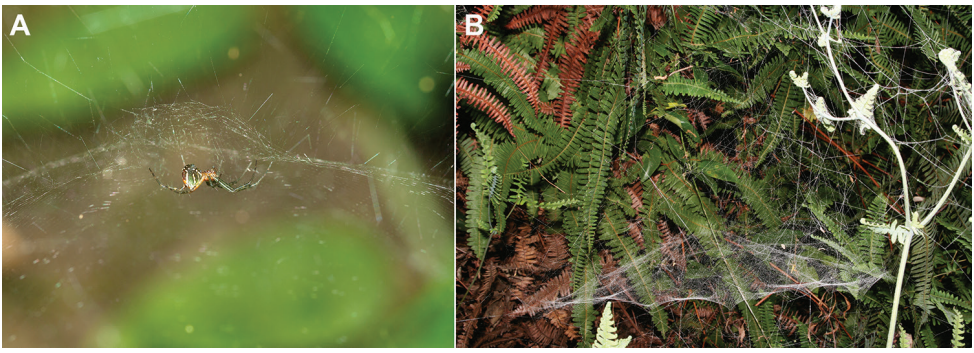

Figure 1. A *Mecynogea biggiba* resting on its web hub **B** Typical dome-shaped web of *M. biggiba*.

attaches its webs to shrubs and herbaceous vegetation. This species constructs a dome web of small mesh that lacks viscid threads. The web consists of a lower and horizontally dome-shaped part connected to the vegetation through support threads, with the addition of several interception threads to guide flying insects towards the dome (Fig. 1B). In southeastern Brazil, *M. biggiba* is sympatric with the spider *L. roseosignata*, another host of *H. japi* which builds horizontal orb-webs.

Study area

We conducted our research in Serra do Japi, a semi-deciduous rainforest located in Jundiaí, São Paulo, Brazil (23°15'S, 46°57'W). The climate is seasonal, with average monthly temperature from 13.5°C in July to 20.3°C in January (Pinto 1992). The altitude of Serra do Japi ranges from 740 m to 1294 m above the sea level, resulting in different floristic zones along its altitudinal gradient (Leitão-Filho 1992). We conducted this study in lower to mid altitudes (740–1000 m) of the mountain, where the abundance of our study species is highest.

Larval behavior and field observations

In February 2010, we performed visual searches for parasitized individuals of *M. biggiba* along forest edges and ecological trails of the study area. We marked the web location of one parasitized spider to observe wasp-induced behavioral modification *in situ*. We collected two other spider specimens (one adult male and one adult female) having a larvae of *H. japi* attached to its abdomen and we transported the individuals to the laboratory to study the wasp's larval development. To obtain adult wasps, we maintained the parasitized spiders in plastic tubes containing a cotton ball with water and fed the individuals daily with *Drosophila melanogaster* (Meigen, 1830) (Drosophilidae). We observed and photographed all developmental stages of *H. japi,* from the first instar larvae to the adult stage. We deposited voucher specimens of adult wasps in the collection of Universidade

Federal de São Carlos, São Carlos (DCBU, A.M. Penteado-Dias, curator) and adult spiders in the collection of Instituto Butantan, São Paulo (IBSP, A.D. Brescovit, curator).

We performed a second field expedition in December 2010 in lower altitudes of Serra do Japi (800–850 m above sea level). We conducted visual searches for both parasitized and non-parasitized *M. biggiba* individuals to determine the parasitism frequency. We collected all spiders found on the trail (n = 71), measured the total length (abdomen + cephalothorax), and determined the sex of each individual to study the sex ratio and host size selection for specific spiders.

Results

In total, we found four parasitized spiders, one adult male (body length = 5.2 mm) and two adult females (5 and 5.3 mm) in February plus one adult female (5.4 mm) in December 2010 (Fig. 2A–B). *Hymenoepimecis japi* completed its immature growth through three larval stages (Fig. 2A–C). The larvae remained attached dorsolaterally or anterodorsally on the host's abdomen, feeding on the spider's hemolymph through a small hole in its cuticle. The third (final) instar larvae presented eight dorsal tubercles with minute hooks, which will serve to hold the larva on the cocoon web (Fig. 2C–E).

Before reaching the third instar, the penultimate instar larva modified the host's behavior, inducing the spider to construct a modified web composed of several threads interconnected with the vegetation and converging radially to the center of the web (Fig. 3). All cocoon webs were built in the same site of the normal webs as a modification of the previous one. The dome-shaped part was absent, except for its hub, and we noted a dense tangle of threads surrounding the central portion. The larva constructs its cocoon attached to the lower surface of the hub, and the cocoon remains suspended between the hub and a dense tangle of barrier threads. Following web construction by the spider, the parasitoid larva performed its last ecdysis, killed the host and sucked its hemolymph, and then discarded the host's drained carcass. To build its cocoon, the parasitoid larva moved towards the hub of the modified web, turned downwards, and wove several threads repeatedly on the lower surface of the center of the web. The larvae (N = 4) built their cocoons over approximately 9 h. The cocoon is initially white, acquiring an orange coloration in approximately three days (Fig. 2F), and it was not possible to observe the larva through the dense cocoon threads (Fig. 2G). The larva released the meconium three days after cocoon construction and, in one case, a female adult wasp emerged after ten days. The wasp remained on the external surface of the cocoon for approximately 10 minutes before flying away.

During the second expedition, we found a low frequency of parasitism (N = 1 female; 0.014%). We analyzed 71 adult individuals of *M. biggiba*, of which 32 were males and 39 females. The tertiary sex ratio of the species was not biased, presenting similar number of male and female individuals (1 male:1.2 females). The average body length of female (3.78 mm ± 0.79) and male (3.78 mm ± 0.68) spiders did not differ ($t = 0.04$, $df = 69$, $p = 0.4841$).

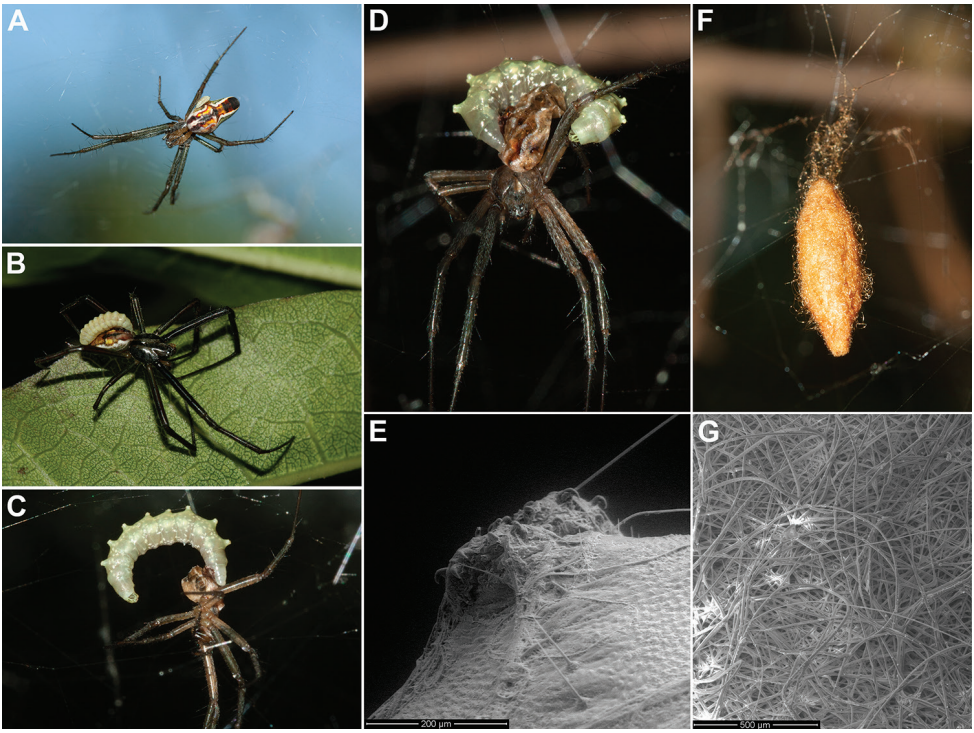

Figure 2. *Mecynogea biggiba* parasitized by *Hymenoepimecis japi*. **A** Adult female spider and first instar larvae **B** Adult female spider with second instar larvae on its abdomen **C** Third instar larvae of *H. japi* after killing its host spider **D** Third instar larvae consuming the hemolymph of *M. biggiba* **E** Detail of dorsal tubercles bearing several hooks **F** Cocoon of *H. japi* **G** Dense weave of cocoon threads in detail.

Discussion

The cocoon web constructed by *M. biggiba* resembles those induced by other *Hymenoepimecis* (Gonzaga et al. 2010) and *Acrotaphus* wasp parasitism (Gonzaga and Sobczak 2011) by the presence of a dense and irregular tangle of non-sticky threads with several points of contact with the surrounding vegetation. The absence of the normal dome shaped portion and the high number of condensed support threads consists of a physical barrier that probably protects the cocoon and enhances the stability of the web. Unlike the cocoon web of *M. biggiba*, the modified web of *L. roseosignata* (another host of *H. japi*) consists of three axes made of several radial threads and a closed hub, where the parasitoid constructs its cocoon (see Sobczak et al. 2009). Thus, we believe that the modified web's architecture is defined not only by the wasp, but by both the host spider and the wasp.

We observed a low rate of parasitism by *H. japi* on *M. biggiba.* In fact, many spider–polysphinctine interactions typically occur at low relative frequency, with little impact on their host spider's populations. In contrast, Gonzaga and Sobczak (2007) reported a high mortality rate (~40%) of *Araneus omnicolor* (Keyserling, 1893) (Araneidae) caused by the polysphinctine wasp *H. veranii* Loffredo & Penteado-Dias,

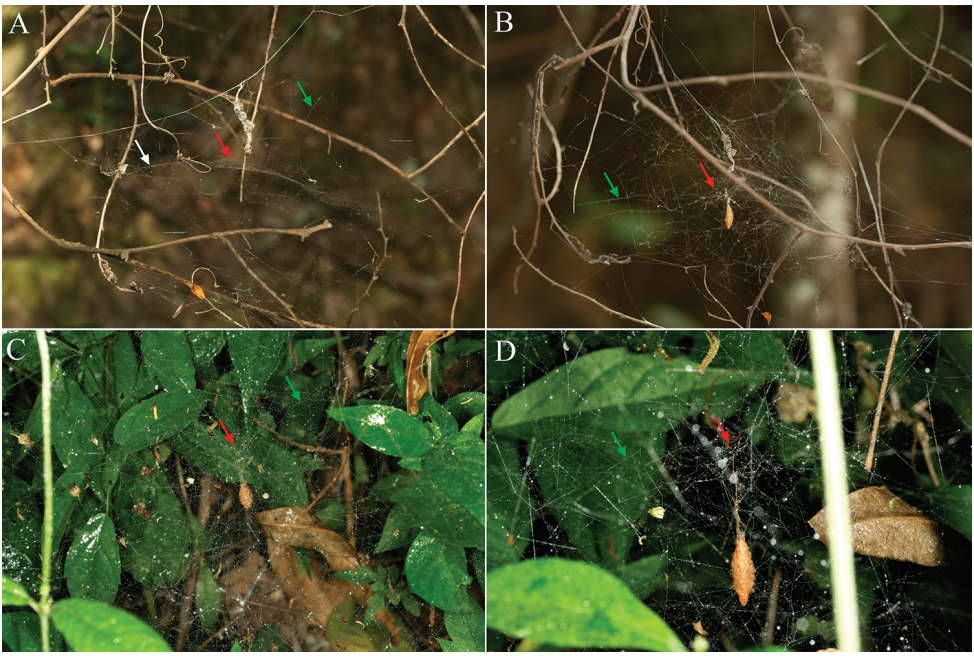

Figure 3. Web modification in *Mecynogea biggiba* induced by the parasitoid wasp *Hymenoepimecis japi*. **A** Normal web of *M. biggiba* **B–C** Cocoon webs in lateral view, and **D** close of the center of the cocoon web. Arrows indicate the dome-shaped part of the web (white), hub of the dome (red) and support threads (green).

2009. Although we have found few spiders parasitized, they were all large adult individuals. Previously, Gonzaga and Sobczak (2011) have argued that some wasp species attack intermediate-sized spiders more frequently as this size class provides sufficient biomass for parasitoid larval development while minimizing the risk to the wasp during its attack on the spider (Gonzaga and Sobczak 2011). For the interaction we studied, we believe that even the larger adult spiders of *M. biggiba* (~ 5 mm) are significantly smaller than adult *H. japi* (~ 9 mm; Sobczak et al. 2009), and are easily managed by the wasps during the attack. Thus, we encourage future studies that investigate host selection by the wasps for specific host sizes.

Although most interactions between spiders and polysphinctine wasps are species-specific, in some cases the wasps may have a broader host range. To the best of our knowledge, our finds add to the literature the first *Hymenoepimecis* species that parasite spiders belonging to different families. Even though building quite different webs, both *L. roseosignata* (orb-weaver) and *M. biggiba* (dome-weaver) present similarities in their natural histories and foraging strategies. These species are visually similar (at least under the human visual system), inhabiting shrub vegetation at forest edges, and construct horizontal webs, positioning themselves facing the ground. Therefore, it is possible that *H. japi* selects its hosts according to these traits and it would be interesting to know whether the use of host from more than one spider family is seen in populations from different environments, but additional studies are necessary to test these hypotheses.

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RESEARCH ARTICLE

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Differentiating between gynes and workers in the invasive hornet *Vespa velutina* (Hymenoptera, Vespidae) in Europe

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Abstract

In theVespinae, morphological differences of castes are generally well-marked, except for some *Vespa* species, where it is difficult to distinguish between future queens and workers in autumn-winter colonies. Individual weights have widely been used as a distinguishing factor but recently cuticular hydrocarbon profiles seems to be the definitive tool, although much more expensive and time-consuming. Parameters such as size (mesoscutum width), wet and dry weight were analysed, throughout several colonies, to differentiate female castes (workers and gynes) in the hornet *Vespa velutina* in Europe. These parameters were compared to cuticular hydrocarbon profiles. The results showed that in late autumn, but not earlier, populations are divided into two size groups, which, based on their CHC profiles, can be hypothesized to correspond to workers and gynes. This differentiation mirrored a good separation by size that proves to be more accurate than weight (wet and dry). The size limit between workers and gynes is established at a mesoscutum width of 4.5 mm.

Keywords

caste differentiation, CHCs, chemical signature, size, weight, yellow-legged hornet

Introduction

The Vespidae includes both solitary and eusocial groups with extensive variation among the social wasps (Cowan 1991). Caste polymorphism is one of the most widely studied point (Noll et al. 2004). Traditionally, it has been considered that Vespinae wasps (*Vespa, Provespa*, *Dolichovespula* and *Vespula*) present morphological differences between female castes, with queens being larger than workers (Felippotti et al. 2009, Jeanne and Suryanarayanan 2011). However, not all species present the same degree of caste differentiation. *Dolichovespula* shows the weakest caste differentiation (Greene 1991) and *Vespula*, the highest (Spradbery 1973). In the case of *Vespa* there are species, such as *Vespa mandarinia*, *V. affinis*, *V. crabro* or *V. simillima,* in which castes present clear size separation. By contrast, hornets like *V. tropica* and *V. analis*, show an overlap of caste sizes (Matsuura and Yamane 1990). So, in most vespine wasps, size variation among females is discontinuous, although without any clear external physical distinction between gynes and workers aside from size. It seems that *Vespa velutina* conforms to this pattern. Moreover, there are few studies of *V. velutina* on morphological differences between female castes and those use a complex wing morphometric procedure (Perrard et al. 2012).

The size difference between castes can be expressed in various ways. For example, mesoscutum width (MW) from tegula to tegula is one of the most-used parameters to distinguish castes in some Vespidae species (Noll et al. 1997, Felippotti et al. 2009; Felippotti et al. 2010). In contrast, in some other species it is hard to find morphological features to distinguish castes; for this reason, some authors have looked into other kinds of parameters. Strassmann et al. (1984) reported differences linked to the capability of gynes to overwinter. This explained why foundresses develop multistratified fat bodies whereas workers do not (Eickwort 1969, Toth et al. 2009). For that reason, many authors have used weight to distinguish between workers and gynes (Monceau et al. 2013, Rome et al. 2015).

Apart from size and weight, cuticular hydrocarbon profiles (CHCs) can be used to differentiate between castes in a colony (Liebig 2010, Darrouzet et al. 2014). CHCs are complex mixtures of long-chain aliphatic and methyl-branched alkanes and/or alkenes present on the epicuticle of these insects (Blomquist and Bagnères 2010). This layer of CHCs not only protects insects against desiccation (Gibbs and Rajpurohit 2010), but is also part of inter- and intraspecific communication (Howard and Blomquist 2005, Blomquist and Bagnères 2010). The pattern of cuticular chemical compounds is linked to several biological aspects such as, dominance, fertility (reproductives and non-reproductives) (Liebig 2010), workers' activity (Rahman et al. 2016), nesting sites (Steinmetz et al. 2003) or recognition between species, castes, nest mates (Howard and Blomquist 2005) and sexual mates (Spiewok et al. 2006).

In European populations of the yellow-legged hornet, *Vespa velutina*, CHC profiles differ between individuals, depending on caste and sex (Gévar et al. 2017), as they are in several other social insects (Liebig 2010), even though there is genetic homogeneity (Arca et al. 2015) and inbreeding (Darrouzet et al. 2015). These differences are based mainly on the relative quantities of the various compounds that make up the chemical signature.

The natural distribution of *Vespa velutina* ranges from Afghanistan to eastern China, Indo-China and Indonesia (Villemant et al. 2011). Nowadays, the *nigrithorax* form of this species is an invader in Europe, since about 2004 (Rortais et al. 2010) and in South Korea since 2003 (Kim et al. 2006). New colonies of *V. velutina* are established in the spring by mated queens, after the overwintering period. Colonies go through a period in which an increasingly large number of workers are produced in order to ensure colony growth, and then produce sexual individuals (males and gynes) in autumn (Monceau et al. 2013, Rome et al. 2015).

The aim of this study was (1) to study the dynamics of colony population and individual morphometric variations throughout the annual nesting cycle of *Vespa velutina* in Europe, measuring mesoscutum width, as an index of linear body size. As an alternative discriminator, (2) we tested the cuticular hydrocarbon (CHC) profiles of known autumn females. Finally (3), we compared the CHC profiles with size, wet weight, and dry weight with the goal of discovering rapid, simple and useful parameters for determining castes or groups.

Methods

Sample collection

In this study, 11 nests at different developmental stages were used. These nests were collected from June to December between 2011 and 2015 at different locations in the Basque Country (Spain) and Indre-et-Loire (France) (Table 1). In both countries the species was well established (Goldarazena et al. 2015; Rome et al. 2013). The collected nests were frozen, dissected and the individuals separated by sex. Only the females were used for this study. All of the individuals were kept frozen at -20°C until they were studied. Three types of data were analysed: size, weight, and CHC profile of individuals.

Table 1. Dates and locations of collected colonies.

Colony	Date	Location
1	02/12/2011	Civray de Touraine (Tours, France)
2	22/11/2013	Tours (Tours, France)
3	02/06/2014	Ibarrangelu (Biscay, Spain)
4	22/06/2014	Loiu (Biscay, Spain)
5	23/07/2014	Mungia (Biscay, Spain)
6	26/07/2014	Gatika (Biscay, Spain)
7	28/08/2014	Lasarte (Gipuzcoa, Spain)
8	30/08/2014	Astigarraga (Gipuzcoa, Spain)
9	01/10/2014	Mungia (Biscay, Spain)
10	26/10/2014	Maruri (Biscay, Spain)
11	13/11/2015	Civray de Touraine (Tours, France)

Size and weight analyses

Size of individuals: the mesoscutum width (MW) from tegula to tegula was measured in a stereomicroscope coupled to a camera system. The MW was used as an index of overall linear size (Noll and Zucchi 2002, Ohl and Thiele 2007). Size measurements are given in mm.

Weight of individuals: wet (WW) and dry weight (DW) were taken using a high precision balance (0.01mg). The wet weight was obtained after two hours of defrosting specimens to avoid moisture on the body surface. For dry weight, hornets were dried in an oven at 70°C for 24h (modified from Monceau et al. 2012). Weight measurements are given in g.

Chemical analyses

CHC profiles were analysed to determine the castes of individuals. CHCs were extracted by placing hornets in 1 ml of pentane and shaken for 2 minutes in a Wheaton™ V Vial™ glass. 500 µl of the extract was placed in another vial and stored at -20°C until the samples were analysed. Ten µl of standard n-eicosane (C20) (10^{-3} g/ml) was added to each sample and, immediately afterwards, 2 µl of sample was injected into a gas chromatograph (Agilent 7820A) coupled with a flame ionisation detector (FID). The analysis was carried out with a 413HP5 (30m × 320µm × 0.25µm) capillary column. The oven temperature programmed was from 50°C to 200°C (8°C/min), from 200°C to 315 (5°C/min) and 315°C for 5 min. The injection was in splitless mode and helium was used as a carrier gas (1.7 ml/min). All data were processed with ChemStation B.04.03 software. The relative proportions of each peak were calculated as described in Bagnères et al. (1990).

Statistical analysis

MW histograms were used to see how the sizes of individuals change throughout the season. All of the females in the eight Spanish colonies, including the queens, were used.

The XLSTAT 2014 add-on for Microsoft Excel® was used to perform the Gaussian mixture model (GMM), fitted using an EM algorithm, with the MW data of 350 individuals from the four late autumn colonies pooled together to detect potential size classes between reproductive and sterile castes. Using the same individuals, identical procedure was follow to verify whether potential weight (wet and dry) classes existed.

A Principal Components Analysis (PCA) of the individual CHC signatures of four autumn colonies was performed. The independent variables were the relative area of the most important peaks (≥ 0.1%) in the chromatogram. A Cluster Analysis (Pearson correlation index and k-nearest neighbour algorithm) was performed to define the chemical groups. After that, a Discriminate Analysis with cross-validation, over those

groups to test the fitness of categories separation, was performed. In order to test how the size or weight classes, got from GMMs, fit to PCA CHC profiles, distinct representations of the PCA plots were made. The analyses were carried out using IBM SPSS Statistics 23.

Results

The distribution of the morphometric MW variable in the different colonies from June to October is represented in Figure 1. The frequency distribution of mesoscutum width was unimodal throughout most of the colony cycle (from early June to mid October), with a single large individual (the queen) lying outside the mode. The distribution became bimodal late in the colony cycle with the appearance of new gynes.

Apart from the modality, individual numbers and body size also changed (Fig. 1). As the season went by, the number of individuals in each colony increased from N=20 in Colony 3 to N=249 in Colony 10. The same occurred with the sizes of individuals. In unimodal colonies, the MW of none of the hornets reached 4.5 mm, with the exception of the large individual which is outside the group. However, in late-season Colony 10, which was bimodal, the size of the MW varied from 3.79 mm to 4.49 mm for the population on the left, and from 4.61 mm to 4.87 mm for the one on the right. In most of the colonies represented in Fig. 1, the individual that is outside the unimodal distribution had a MW greater than 4.5 mm, except for Colony 6 where this was 4.48 mm. The MW of 4.5 mm was the threshold used to separate the two groups in the bimodal colony.

Figure 2 shows the Gaussian mixture model (GMM) of autumn colony data, performed to establish the threshold between the two populations according to size (MW) and weight (WW and DW).

The GMM analysis for MW split the distribution into two size classes, separated by a threshold or mid-point value of 4.5 mm (Fig. 2A). The 5% uncertainty level was set at 4.4 mm for workers and 4.58 mm for gynes. The same GMM analysis was performed for wet weight (WW) and dry weight (DW). In the case of WW (Fig. 2B) the model did not have the same bimodal distribution as MW. Even so, the threshold calculated was 0.618 g, with the 5% uncertainty level at 0.445 g for workers and 0.797 g for gynes. Unlike WW, the DW GMM did show a bimodal distribution (Fig. 2C), with a threshold value of 0.225 g separating the two groups. The 5% uncertainty value was 0.202 g for workers and 0.247 g for gynes.

For each of the three GMMs, the mid-point or threshold was compared to the highest values for the 5% uncertainty interval, in percentage terms, to check which of the three presented the smallest uncertainty interval. A higher percentage showed a lower uncertainty interval, resulting in a clearer separation between groups. These values were 98.25% for MW, 77.54% for WW, and 91.09% for DW.

The Cluster Analysis of the CHC profiles of the four late-season colony hornets, showed three clearly well-separated chemical groups, named as 1, 2 and 3. They are

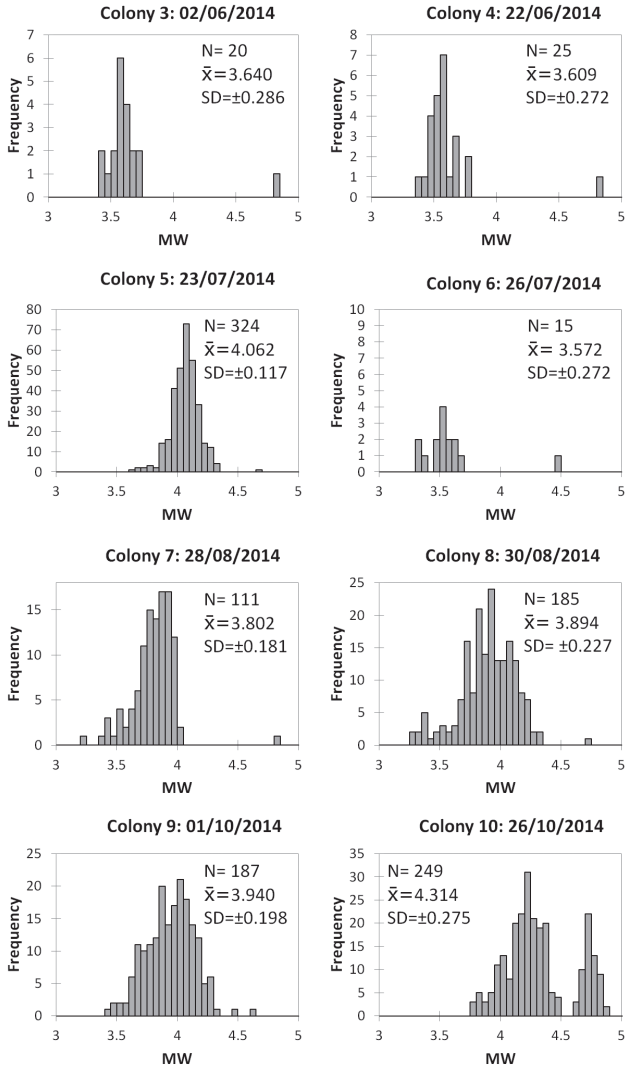

Figure 1. MW histograms. Histograms showing MW (mesoscutum width) from eight different colonies, sorted by collection date.

represented in the axes I and II of the ACP (Fig. 3). The Discriminant Analysis showed all the hornets were chemically well classified. The group 1 hornets showed to be chemically more similar to each other, since the dots cloud was more compact. The group 2 was more scattered, showing they were chemically more heterogeneous. The group 3 had very few individuals.

In the PCA of the figure 3, ordination plots were displayed according to the size or weight class of each hornet. In the size (MW) column (Figure 3), all individuals classified as "small" belonged to the same chemical group (group 1) and the "large" to the

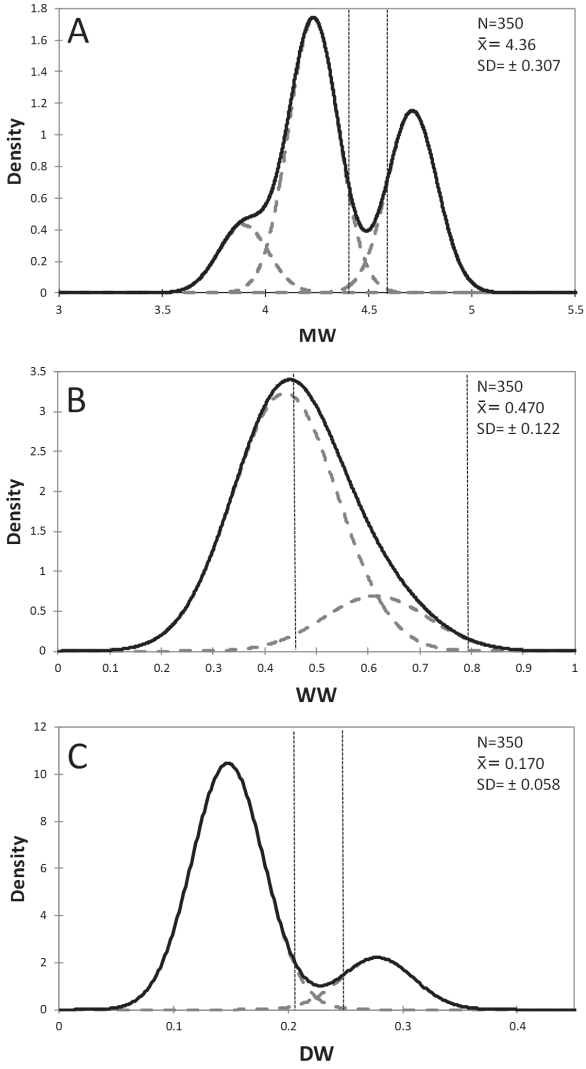

Figure 2. GMMs of hornet size, WW and DW. *Vespa velutina* size (**A**), wet weight (**B**), and dry weight (**C**) distribution using a Gaussian Mixture Model. Two-dimensional distribution is represented by continuous line **A** workers < 4.5 mm, gynes ≥4.5mm **B** workers < 0.618 g, gynes ≥ 0.618 g and **C** workers < 0.225 g, gynes ≥ 0.225 g. The dashed lines represent group densities. The 5% level of uncertainty is shown by dotted lines **A** 4.4 mm–4.58 mm **B** 0.445 g–0.797 g and **C** 0.202 g–0.247 g. 4 colonies: Colony 1, N= 30; Colony 2, N= 30; Colony 10, N= 240; Colony 11, N=50.

other two (groups 2 and 3). This showed a good agreement between both PCA chemical groups and size ones. There was an exception in Colony 1, where three individuals classified as "small" appeared in the group 2.

In the column showing the PCA for wet weight (Fig. 3), it can be observed that the three CHC groups did not match well to the two WW defined groups. In Colony

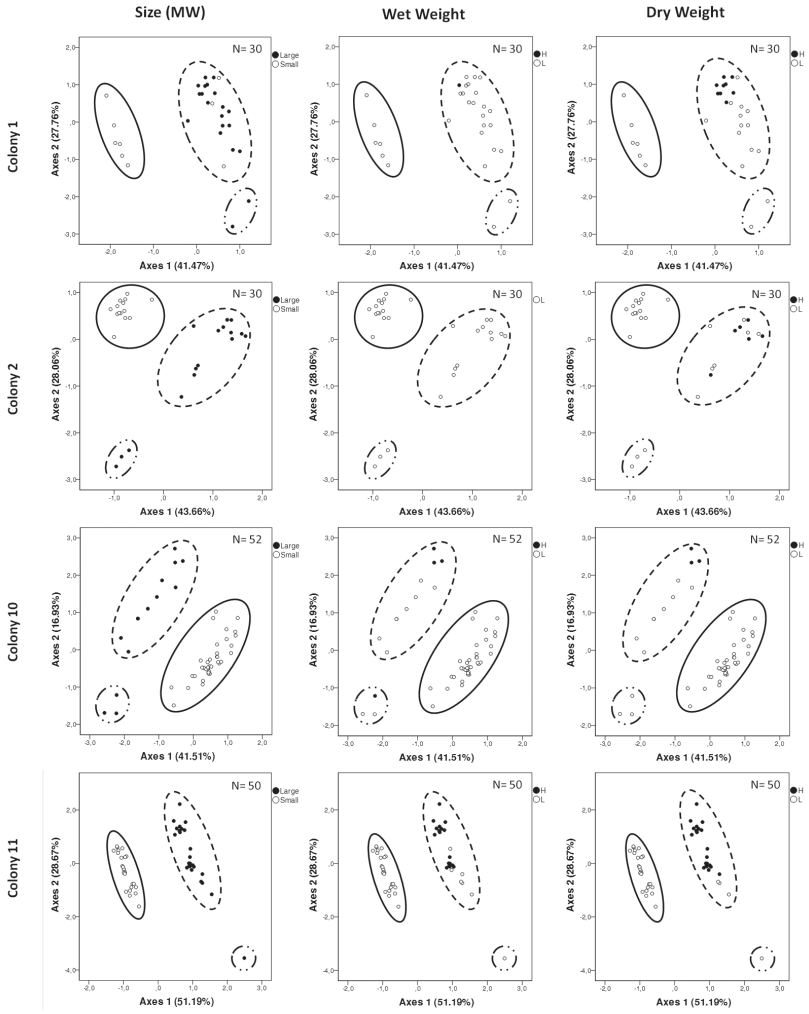

Figure 3. PCA of the three CHC profiles labelled by hornet size, WW and DW. Principal Component Analysis of CHC profiles in each of the four autumn colonies. Chemical groups are defined by continuous line: Group 1; dash line: Group 2 and dot-dash line: Group 3. PCA dots show representations according to GMMs size, wet weight and dry weight thresholds of hornets. Size, Black dots: Large females (MW ≥ 4.5 mm); White dots: Small females (MW < 4.5 mm). Wet weight, Black dots: Heavy fresh females (≥ 0.618 g); White dots: Light fresh females (< 0.618 g). Dry weight, Black dots: Heavy dry females (≥ 0.225 g); White dots: Light dry females (< 0.225 g).

1, all individuals, except one, were "light". In Colony 2 there were no hornets classified as "heavy". In Colony 10 there are four "heavy" individuals spread in the second and third CHC groups. In the case of Colony 11 all the "heavy" hornets were in the second chemical group, most of them in the top of the group.

Lastly, in the column showing the PCA for dry weight (Fig. 3), all colonies contained "heavy" individuals, which are located in the top part of the CHC group 2.

Discussion

Mesoscutun width (MW) seems to be one of the most common parameters used in morphometry, as it is relatively large and constant, thus minimising errors in measurement, and can be taken easily (Noll and Zucchi 2002, Ohl and Thiele 2007). As a result, this size parameter was chosen, among all the used measures, to study the dynamics of the *Vespa velutina* population as well as individual morphometric changes from June to October. The latter, had not been studied until now.

Early in the season, the number of individuals per colony was low and they were also smaller in size. However, close to the end of the colony life cycle, both individual numbers and sizes are larger and the individual size distribution changes from unimodal to bimodal. From June to early October, we observed that all of the unimodal colonies studied contained only one individual that was notably larger in size than the other females, being the queen of those colonies. Moreover, these females matched the size of individuals in the second population (MW > 4.5mm) in the autumn nests. In the other hand, females captured in early spring, which are overwintering survivor gynes, also presented MW > 4.5mm (Pérez-de-Heredia, personal observation). Therefore, it can be said that these larger autumn females will become the queens of the following year's colonies. This population dynamic is typical in aculeate colonies which are founded by a single queen. The first cohort is raised by the queen alone and comprises the smallest workers; the following cohorts increase in size until the largest workers appear. This happens together with, or is followed by, the production of gynes and males (Wilson 1971, Miyano 1981). At the same time as gynes are being produced, female size distribution starts turning from unimodal to bimodal. This bimodality corresponds to the differentiation between castes, workers and gynes (Spradbery 1973). This size increase in females, during the annual colony cycle, is associated with the trophic advantages of having more workers in the nest to feed larvae. Another explanation for this increase in individual size is the sizes of the cells where larvae are raised, which gradually increase as the nest grows larger (Spradbery 1972). Edwards (1980) showed that, in *Vespa crabro*, the size of individuals is conditioned by the size of the cells in which they are raised. There were two size classes among males, some of which were raised in worker cells and others in gyne cells.

The bimodality of the size parameter in late autumn colonies led us to consider size as a good caste differentiator. Nevertheless, hitherto, only the weight of individuals has been used to differentiate castes in *Vespa velutina*. For that reason, we also analysed WW and DW using the GMM procedure to establish the threshold for each of them and compare the results to MW, to determine the best caste predictor.

According to the three GMMs, the MW size presents less overlap bimodality between groups, making it more accurate and reliable than either of the weights. This can be explained because once an insect emerges as an adult; its body is enclosed in a solid, non-regenerative cuticle, making body plates invariable. Unless it is damaged, no morphological changes occur in any hardened (sclerotized) body part (O´Donnell 1998) regardless of insect age or physiological state.

The GMM for WW presents a greater overlap between groups, resulting in a unimodal distribution. This can be explained because there is great variability in the WW for individuals of the same size, influenced by differences in metabolic status, age of individuals (Hilligsøe and Holmstrup 2003) or by physiological variations, as occurs in collembolans (Verhoef 1981). By contrast, the GMM of DW presents a bimodal pattern, which means that the parameter is more constant for a given group of hornets and in consequence is more reliable.

Our study shows that the thresholds for separating the two classes or groups were 0.618 g for WW and 0.225 g for DW. These data differ a little from those observed by Rome et al. (2015), which considered that individuals with WW exceeding 0.593 g and DW exceeding 0.250 g were considered to be gynes, while those with lower weights were workers. These discrepancies in the DW may be due to differences in methodology, such as the temperature and drying time for the individuals. Even so, the variation in the DW rank linked to 5% uncertainty was very similar: 91.09% in our study and 87.72% in the data of Rome et al. (2015).

The three chemically-differentiated groups observed in the four autumn colonies, are explained as follows. Hornets of groups 2 and 3 presented sizes equal or bigger than 4.5 mm (except for three individuals in Colony 1). In addition, only hornets of the group 2 (classified as "large" hornets) presented high weights. So, following to Rome et al. 2015, it can be hypothesized that this group belongs to the gynes. The cuticular profiles discriminate by castes, workers being in chemical group 1 and gynes in group 2. Group 3, located apart from the other two, is an undefined chemical group, different from the other two.

The aforementioned three mismatched individuals in Colony 1 have the size of workers but they have the chemical signature of gynes. It is possible that, in some nests, this type of gyne could be raised in workers' cells, resulting in small gynes. This was also observed in *Vespula germanica* (Spradbery 1993), but further studies are needed to confirm that. In all cases large hornets always had gyne CHC profiles. This can be explained because, when gynes start emerging, the production of workers is interrupted (Matsuura and Yamane 1990, Monceau et al. 2013).

Group 2, consist of both high and low weights gynes. The gynes are the only members of the colony that will survive the winter (Monceau et al. 2014). Recently-emerged gynes spend some days inside the nest before leaving it to hibernate, as long as 13–14 days in the case of *Vespa affinis* (Martin 1993). During those days, they are fed by trophallaxis with substances regurgitated by workers and larvae. Most of this food is converted into fat reserves to last the winter (Matsuura and Yamane 1990). The workers, however, have no such energy reserve, and this makes them lighter than gynes (Martin 1993). For that reason we can assume that hornets with a large MW but low weights are young gynes which have had no time to feed enough to reach high weight. All these hornets have a similar chemical profile so, it can be concluded that PCA axis II discriminated the groups by age. Thus, the workers (group 1) are more homogeneous, because all of them have similar ages contrary to what hap-

pens in gynes (group 2) which have hornets with different ages. Finally, group 3 is comprised presumably by just emerged hornets, which have not had enough time to develop and get a defined chemical profile (Lorenzi et al. 2004). Thus, it can be hypothesized that they belong to the caste of the just emerged gynes. This is supported by the fact that there are no individuals of the chemical group 1 with a MW equal or bigger than 4.5mm.

According to the DW threshold of 0.250 g given by Rome et al. (2015), recently-emerged gynes which have no time to feed are classified in the group of light individuals, i.e. workers. The same happens with colonies collected at the end of autumn, when feeding conditions may not be ideal due to the lack of food or because there are not enough workers to feed larvae (Matsuura and Yamane 1990). Both workers and final instar larvae are feeders of recently-emerged hornets (Matsuura and Yamane 1990). So, the two castes tend to be lighter from November to December (Rome et al. 2015). The heaviest females in the chemical gynes group, which appeared close together, are probably the oldest ones. They have remained feeding in the nest for a longer time accounting for their greater amounts of reserves.

Since *Vespa velutina* was introduced into Europe, a number of scientific questions have been analysed regarding this invasive species. For some of them, it is crucial to discriminate between female castes to better understand some of the biological aspects, such as when the first gynes emerge and how many gynes are produced per nest. So, considering the data set out here, *V. velutina* seems to present distinctive morphological female castes depending on their MW. Moreover, the variable rank corresponding to the 5% uncertainty level in the GMM is lower in the MW than in the weight data, with less potential for error. This is confirmed by the results from the CHC profiles. Hornets with a MW of 4.5 mm or more are considered to be gynes, while those with a MW of less than 4.5 mm are considered to be workers. This MW size parameter is easier, faster and cheaper to measure than analysing CHC profiles. DW worked better than WW but neither of them is as accurate as MW at least with young or not well fed gynes.

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RESEARCH ARTICLE

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Translucent cuticle and setiferous patches in Megaspilidae (Hymenoptera, Ceraphronoidea)

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Abstract

All Ceraphronoidea have metasomal patches of translucent cuticle and setae that have never been investigated before, despite their potential behavioral and phylogenetic relevance. To understand the internal and external morphology of these structures, specimens were examined using a broad array of histology-based methods, including transmission electron microscopy (TEM), scanning electron microscopy (SEM), confocal laser scanning microscopy (CLSM) and serial block-face scanning electron microscopy (SBFSEM). For the first time, the setiferous patches are shown to be associated with exocrine glands in Ceraphronoidea. The proposed glandular function is the secretion of pheromones, with the setae above the pore openings serving as a surface for evaporation. The translucent cuticle is morphologically distinct from the setiferous patches; structures resembling lamellar bodies were found underneath the translucent cuticle, and may be associated with photoreceptors or endocrine glands. The locations of translucent cuticle on the metasoma are unique to different families and genera within Ceraphronoidea, and could be useful for inferring phylogenetic relationships. The character distribution suggests that the genera *Trassedia* and *Masner* are more closely related to Ceraphronidae than Megaspilidae. We found similar structures containing translucent cuticle in Orussidae and Ichneumonoidea, indicating that these structures are potentially a rich character system for future phylogenetic analysis in Hymenoptera.

Keywords

Megaspilus, *Conostigmus*, *Dendrocerus*, Lagynodinae, felt field, felt line, setal patch, translucent patch, thyridium, gastrocoelus

Introduction

Ceraphronoidea is a small but widespread superfamily of parasitoid wasps that contains approximately 600 species and is comprised of two families, Megaspilidae and Ceraphronidae (Johnson and Musetti 2004). Although ceraphronoids are commonly collected (Martinez de Murgia et al. 2001; Mikó et al. 2013; Schmitt 2004) and include species that are agriculturally important (Boenisch et al. 1997; Chow and Mackauer 1999; Ferrière 1933; Kamarudin et al. 1996; Ortiz-Martínez and Lavandero 2017; Polaszek et al. 1994) the taxon is full of phylogenetic uncertainties. Even the relationship of Ceraphronoidea to other Hymenoptera remains unclear, although the superfamily is robustly monophyletic (Mikó et al. 2013). Different molecular analyses have grouped Ceraphronoidea with Stephanoidea, Ichneumonoidea, Megalyroidea, or with Ichneumonoidea and Proctotrupomorpha (Klopfstein et al. 2013; Mao et al. 2014; Peters et al. 2017; Sharkey 2007; Sharkey et al. 2012). Contrary to the belief that ceraphronoids are too small for morphological characters to be of phylogenetic use (Klopfstein et al. 2013), the group contains taxa with morphological structures that may serve as characters to corroborate both the phylogenetic relationships among members within the superfamily.

On the metasoma of all ceraphronoid wasps, there are pairs of translucent patches of cuticle on the syntergite and synsternite, referred to as the syntergal and synsternal translucent patches (stp) (Mikó and Deans 2009) (Fig. 1). These translucent patches may be similar to the smooth patches of cuticle found on the metasoma of in Orussidae and Xiphydriidae (Vilhelmsen 2003), the gastrocoelus and thyridium of Ichneumonidae and Proctotrupidae, and the pseudothyridium which occurs widely across Hymenoptera (Liu et al. 2006; Townes 1969). In addition to these translucent patches, all Ceraphronoidea possess patches of setae on the synsternite near the synsternal translucent patches, known as the synsternal setiferous patches (smp) (Mikó and Deans 2009) (Fig. 1). These setiferous patches are only found on the ventral surface of the metasoma and appear similar to the felt lines and felt fields on the metasoma of other Hymenoptera, including Mutillidae (Debolt 1973) and Platygastroidea (Masner and Huggert 1989).

Even though translucent and setiferous patches have been observed in several hymenopteran taxa, little work has been done to investigate their morphology and potential functions. The translucent cuticle in the gastrocoelus, thyridium and pseudothyridium has never been studied before, even though differences in the thyridium have been used to distinguish between proctotrupid species (Liu et al. 2006). Translucent cuticle is found in many different insects and is associated with different functions, from light dispersal in fireflies (Coleoptera: Lampyridae) (Kim et al. 2012) to glandular activity in giant silk moths (Lepidoptera: Saturniidae).

More research has been done to investigate the structure and function of setiferous patches found in other Hymenoptera. In Mutillidae, there is a “felt line organ” underneath the felt lines that appears to function as an exocrine gland (Debolt 1973).

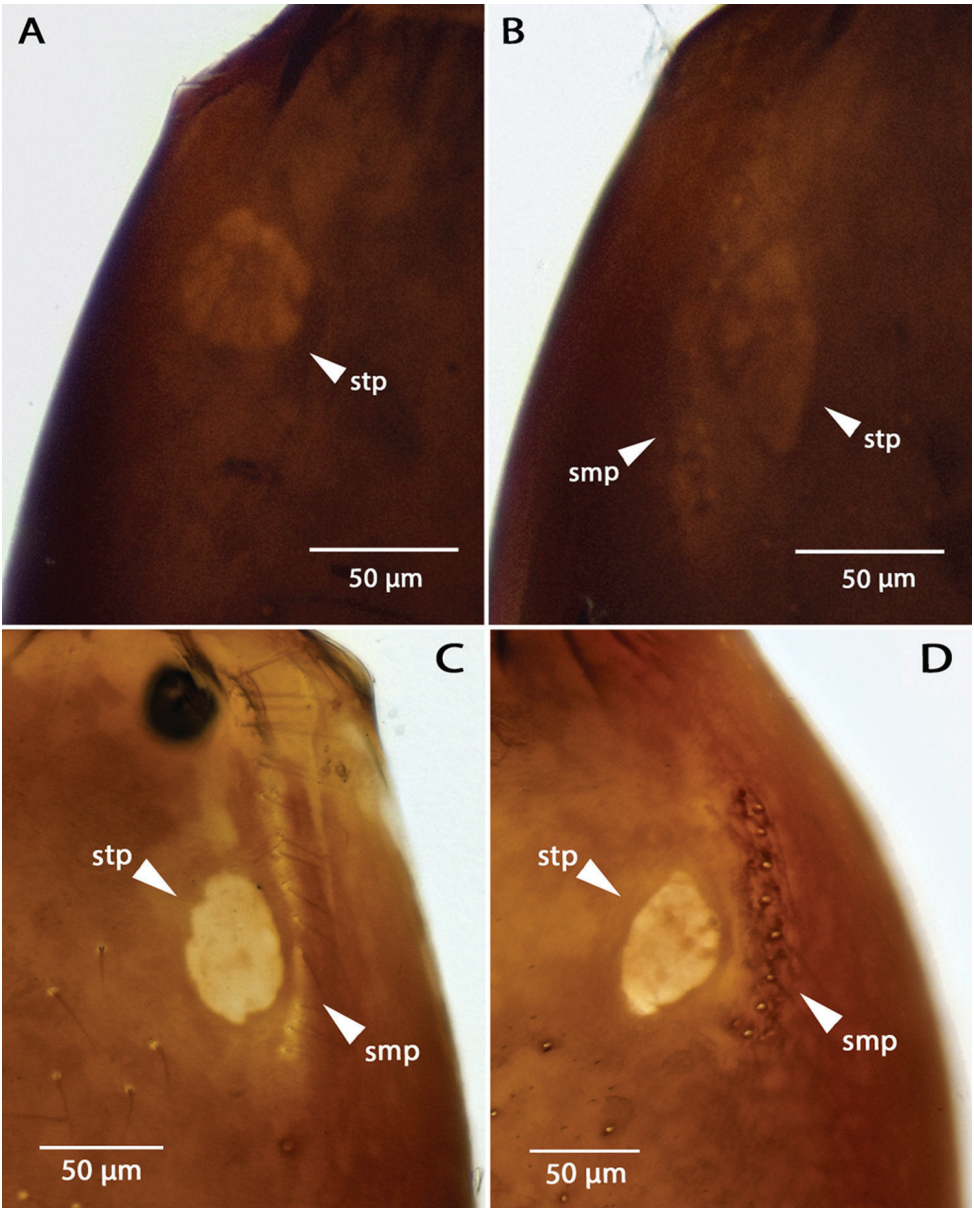

Figure 1. Brightfield images of syntergal and synsternal translucent patches and synsternal setiferous patches in different species of *Conostigmus* (Hymenoptera: Megaspilidae), viewed externally. **A** Dorsal surface (syntergite) within a *C. bipunctatus* Kieffer, 1907 (Hymenoptera: Megaspilidae) specimen (identifier: IM 1751) **B** Ventral surface (synsternite) within the same *C. bipunctatus* specimen **C** Ventral surface of *Conostigmus* sp. C7A (identifier: CLEV 22741) **D** Ventral surface of *Conostigmus* sp. C7B (identifier: PSUC_FEM 83781) Abbreviations: smp = synsternal setiferous patch; stp = syntergal/synsternal translucent patch. The species notations given are not issued for purposes of zoological nomenclature, and are not published within the meaning of the International Code of Zoological Nomenclature.

Debolt (1973) described ducts passing from gland cells in the felt line organ to cuticular pores located directly underneath the felt fields. Glandular pores and openings have also been observed underneath patches of setae in Megachilidae (Noirot and Quennedey 1974), Braconidae (Buckingham and Sharkey 1988) and Platygastroidea (Mikó et al. 2010). It has been proposed that setae might increase the surface area for the diffusion of glandular products secreted from these pores, such as pheromones (Buckingham and Sharkey 1988; Debolt 1973; Mikó et al. 2007, 2010; Noirot and Quennedey 1974; Quicke and Falco 1998). Given that pheromones play a wide variety of important ecological, behavioral and physiological functions within insects, understanding these structures could have important implications for species recognition, sexual selection, and other forms of chemically-mediated communication and behavior within Hymenoptera (Howard and Blomquist 2005).

To understand the morphology of the translucent and setiferous patches in Ceraphronoidea, we dissected and imaged specimens with brightfield microscopy, scanning electron microscopy (SEM) and confocal laser scanning microscopy (CLSM). Orussid and ichneumonid specimens were also dissected and imaged with brightfield microscopy for comparison. We also utilized histological methods; we used transmission electron microscopy (TEM) to investigate the cuticle and underlying structures, and serial block-face scanning electron microscopy (SBFSEM) to build three-dimensional representations of these structures. SBFSEM is a novel technology that has only recently been applied to studying arthropod physiology, but it is a promising approach for studying external and internal morphology (Büsse et al. 2016; Friedrich et al. 2014; Lipke et al. 2014). This study comprises the first in-depth investigation of the translucent patches, setiferous patches and underlying structures within Ceraphronoidea.

Methods

Pinned and point-mounted Orussidae, Ceraphronoidea and Ichneumonoidea specimens were obtained from the Frost Entomological Museum (PSUC), the C. A. Triplehorn Insect Collection (OSUC), the American Museum of Natural History (AMNH), the North Carolina State University Insect Museum (NCSU), and the Wisconsin Insect Research Collection (WIRC). Live specimens for histology were collected with sweep nets and aspirators from local field sites around State College, Pennsylvania, USA. A list of the specimens used in this study and associated data is available in Suppl. material 1.

All specimen observations and dissections were done under an Olympus SZX16 stereomicroscope with an Olympus SDF PL APO 1X PF objective (115X) and an Olympus SDF PL APO 2X PFC objective (230X magnification). Point-mounted specimens were prepared for dissection by incubating them at room temperature in 20–25% KOH for 24 hours, acetic acid for 24 hours, and then distilled water for one hour. Afterwards, specimens were placed on individual concave slides in glycerin for dissection and storage. Dissections were done in glycerin with #2 insect pins and

#5 forceps. Brightfield images were taken using an Olympus DP71 digital camera attached to an Olympus ZX41 compound microscope. Images were then aligned and stacked using Zerene Stacker Version 1.04 Build T201404082055 (see protocol in Trietsch et al. 2015). Adobe Photoshop elements Version 3.1 was used to add scale bars to images and create figures.

For CLSM, metasomata were removed from point-mounted megaspilid specimens and either put directly into glycerin, or incubated at room temperature in 35% hydrogen peroxide for 48 hours before being put in glycerin. The purpose of this incubation was to bleach melanin-rich structures, which can interfere with autofluorescence. All metasomata were dissected in glycerin, mounted between 1.5 mm thick, 24×50 mm cover glasses and then imaged using an Olympus FV10i confocal laser scanning microscope. Auto-fluorescence of the structures was collected between 470 and 670 nm with three channels assigned contrasting pseudocolors (420–520nm, blue; 490–520nm, green; and 570–670nm, red). Images were processed in ImageJ (Version 2.0.0-rc-54/1.51g, Build 26f53fffab) (Schindelin et al. 2015) using FIJI (Schindelin et al. 2012).

For TEM, live megaspilid specimens were dissected in cacodylate buffer, fixed with glutaraldehyde, stained with osmium tetroxide and uranyl acetate, dehydrated through an ethanol series, and embedded in eponite (protocol available at https://doi.org/10.6084/m9.figshare.4993793). Blocks were trimmed and sectioned using a Leica UCT ultramicrotome. Sections were collected on slot and mesh grids and then double-stained with lead citrate and uranyl acetate. Sections were imaged with a JEOL 1200 TEM.

Live specimens for SBFSEM were also dissected in cacodylate buffer, fixed in glutaraldehyde, and then stained with osmium tetroxide, potassium ferrocyanide, thiocarbohydrazide (TCH) solution, uranyl acetate, and lead aspartate. Specimens were then dehydrated through an ethanol series and embedded in eponite (Protocol available at https://doi.org/10.6084/m9.figshare.4993796.v1), modified from Deerinck et al. (2010). Blocks were trimmed and sectioned using a Leica UCT ultramicrotome, then mounted into a Zeiss SIGMA VP-FESEM with a Gatan 3View2 accessory for sectioning and imaging. Data was processed in Avizo (Version 9.1.1). The images were aligned and cropped in ImageJ (Version 2.0.0) then imported into Avizo (Version 9.1.1). The images were stacked and volume rendered, then each unique morphological component was marked as an individual label field and modeled through manual outlining and interpolation. The generated surface model was smoothed and the polygon points were simplified to make the file more manageable. The images were then converted into a gif and respective jpeg images that allowed cross-sectional viewing of the models (Mikó et al. in prep). For SEM, metasomata were mounted on carbon tape on top of an aluminum stud. Half of the specimens used were coated in iridium, while half remained uncoated as a control. SEM images were taken on an FEI Quanta 200 Environmental SEM and processed in Aztec (version 3.1 SP1, Oxford Instruments).

Anatomical terms follow the Hymenoptera Anatomy Ontology (Yoder et al. 2010). All specimen data and images of specimens were compiled in the MX database

(http://purl.oclc.org/NET/mx-database). All figures, tables, media files, three dimensional models, protocols and supplementary files are available on figshare at https://figshare.com/projects/Translucent_cuticle_and_setiferous_patches_in_Megaspilidae_Hymenoptera_Ceraphronoidea_/21395. The specimen data included in Supplementary file 1 was published using the Integrated Publishing Toolkit (https://www.gbif.org/news/82852/new-darwin-core-spreadsheet-templates-simplify-data-preparation-and-publishing) and made available on GBIF and figshare (https://doi.org/10.6084/m9.figshare.5325574.v1).

Results

Specimen observations, brightfield imaging and SEM Imaging

Translucent and setiferous patches were found in all Ceraphronoidea observed, including both males and females. SEM revealed that the syntergal and synsternal translucent patches lack setae and bear the impression of units that resemble epidermal cells, also known as scutes (Mikó et al. 2016) (Fig. 2A, B). No gland openings were found in the translucent cuticle. The syntergal and synsternal translucent patches occur in pairs on the metasoma. The translucent patches in each pair have roughly the same size and shape in all of the studied specimens, and appear to be bilaterally symmetrical. However, this is not the case for the syntergal and synsternal translucent patches, which additionally differ in size and shape between species (Fig. 1).

The synsternal setiferous patches also occur in pairs on the synsternite and are bilaterally symmetrical. Comparisons between different species of *Conostigmus* revealed species-specific differences in the length and shape of the setiferous patches (Fig. 1). SEM imaging also revealed the presence of scutes in the cuticle between the setae (Fig. 2B and C), as well as openings in the cuticle that could be related to gland function (Fig. 2C).

The location of the synsternal setiferous patches in relation to the synsternal translucent patches differs between the families and subfamilies of Ceraphronoidea (Figs 3–4; Mikó and Deans 2009; Mikó et al. 2013, 2016). In the family Ceraphronidae, the synsternal setiferous patches are located posterior to the synsternal translucent patches (Fig. 3A). This is also seen in the genus *Masner* (Fig. 3B). Within the family Megaspilidae, the locations of the synsternal patches differed between subfamilies (Figs 3–4; Mikó et al. 2013, 2016). In Megaspilinae, the synsternal setiferous patches occur laterally to the synsternal translucent patches (Fig. 3C), while in Lagynodinae, the synsternal setiferous patches are located anterior to the synsternal translucent patches (Fig. 4). The genus *Trassedia* has the synsternal setiferous patches located posterior to the synsternal translucent patches, similar to Ceraphronidae (Fig. 3D).

Observations of Orussidae revealed smooth patches of cuticle occurring on the anterior portion of both the second abdominal sternite and tergite. The patches were translucent in some specimens observed (Fig. 5A, B), while in others the patches were

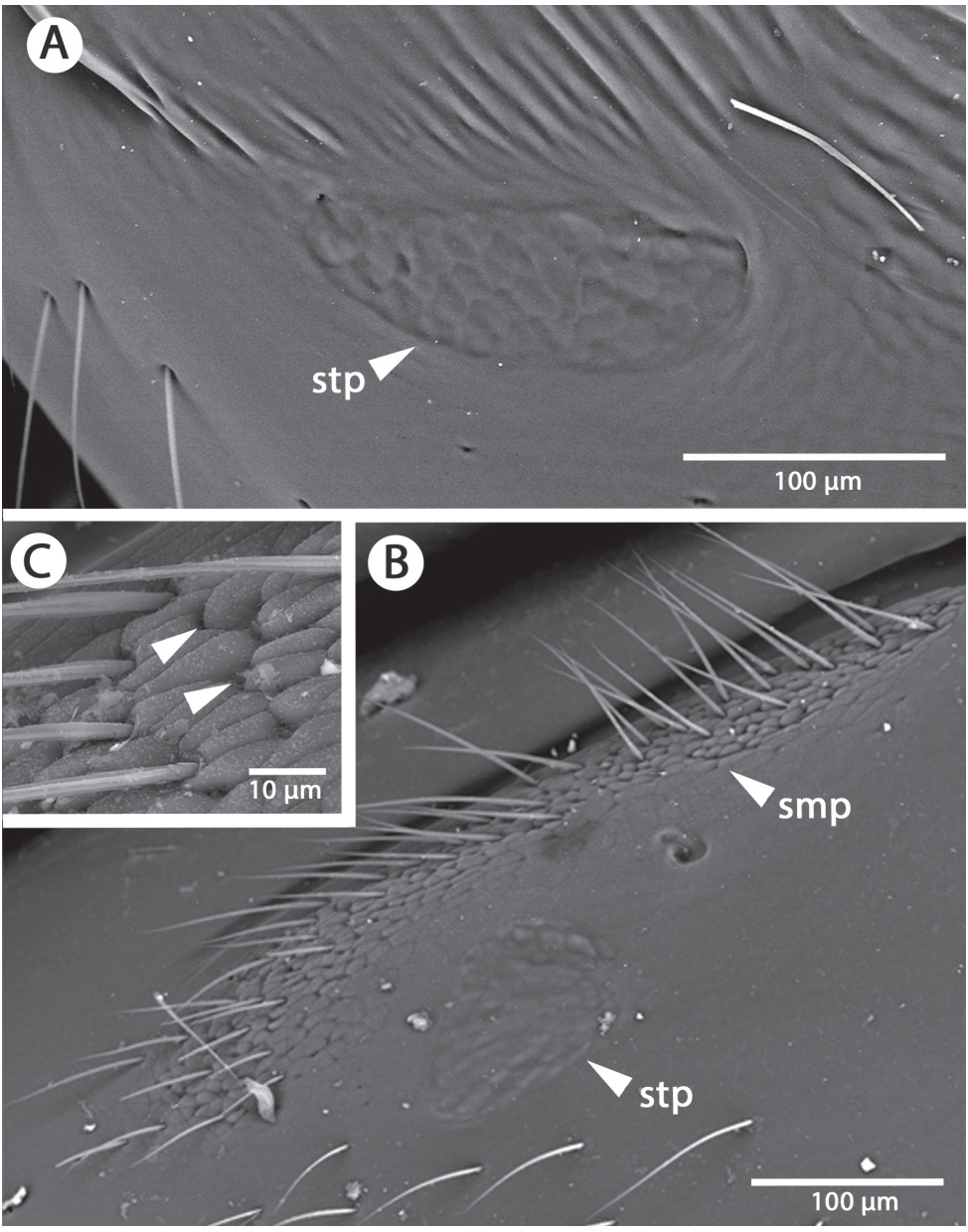

Figure 2. SEM images of the syntergal and synsternal translucent patches and synsternal setiferous patches in male *Megaspilus armatus* Say, 1836 (Hymenoptera: Megaspilidae) specimens. **A** Dorsal surface of the metasoma, showing the scutes (identifier PSUC_FEM 68527) **B** Ventral surface of the metasoma (identifier: PSUC_FEM 50127) **C** Closer view of the synsternal setiferous patch and scutes, with arrows pointing to pore openings in the cuticle (identifier: PSUC_FEM 50127) Abbreviations: smp = synsternal setiferous patch; stp = synsternal translucent patch.

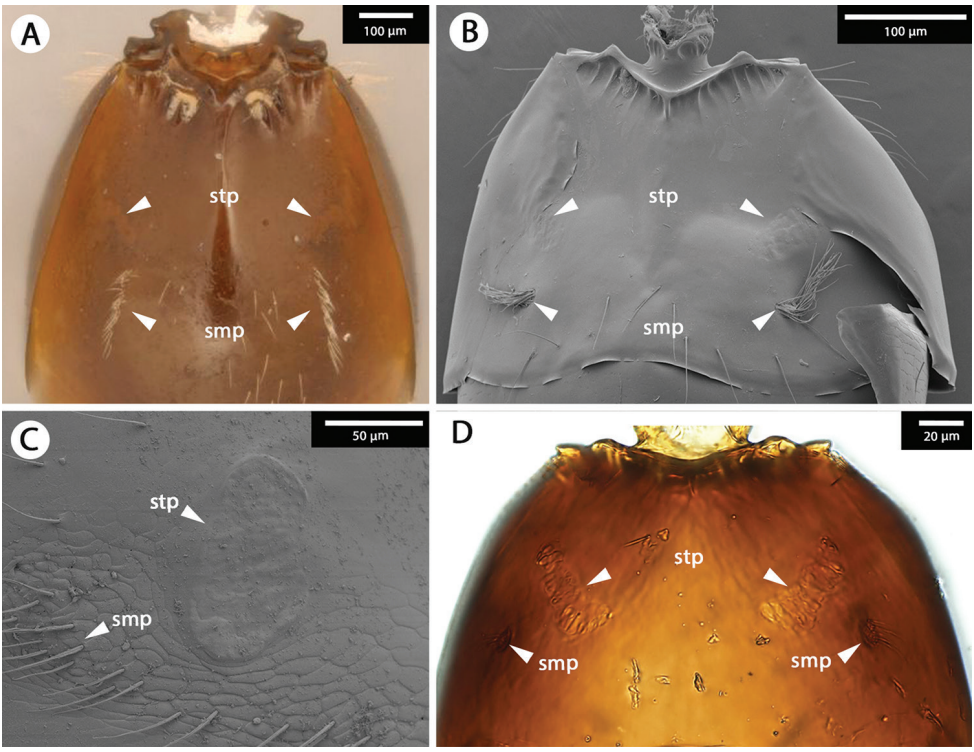

Figure 3. Images of the synsternal translucent and setiferous patches in the metasoma of different Ceraphronoidea. **A** Brightfield image of a *Ceraphron* sp. (Hymenoptera: Ceraphronidae) (identifier: PSUC_FEM 27234) **B** SEM image of *Masner lubomirus* Deans & Mikó, 2015 (Hymenoptera: Ceraphronidae) (identifier: PSUC_FEM 470955) **C** SEM image of *Trichosteresis glabra* Boheman, 1832 (Hymenoptera: Megaspilidae) (identifier: IM 1512) **D** Brightfield image of a *Trassedia* sp. (Hymenoptera: Ceraphronidae) (identifier: IM 1109/ NCSU 71196) Abbreviations: smp = synsternal setiferous patch; stp = synsternal translucent patch.

the same color as the surrounding cuticle, and differed only in their surface sculpturing (Fig. 5C, D). The ventral patches of translucent cuticle were obscured by the hind coxa and only visible through dissection of the specimen (Fig. 5B). No patches of setae were observed near the patches of smooth or translucent cuticle on the tergite or sternite.

Patches of translucent cuticle were also observed in Ichneumonidae on the second metasomal tergite and sternite (Fig. 6). On the tergite, the appearance of these structures varied from patches to deep depressions. As in Orussidae, no patches of setae were found to be associated with the patches of translucent cuticle present on the tergite or sternite.

Confocal Laser Scanning Microscopy (CLSM)

CLSM was used to check for the presence of resilin in the synsternal and syntergal translucent patches in male (Fig. 7A; animated version available on figshare at

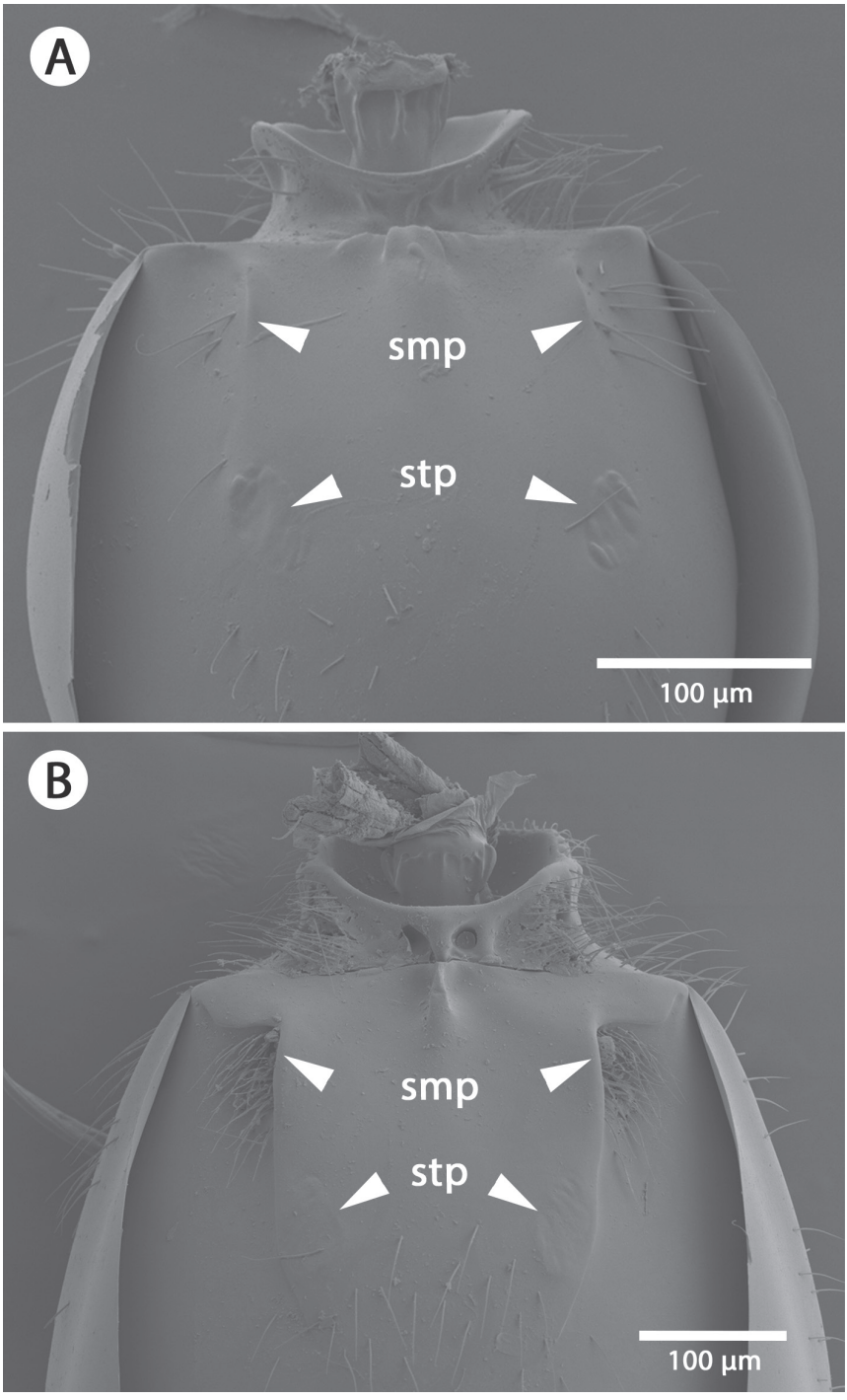

Figure 4. SEM image of the synsternal translucent patch and synsternal setiferous patch in a male (**A**) and female (**B**) *Lagynodes* sp. (Hymenoptera: Megaspilidae) Specimens from lot IM 930. Abbreviations: smp = synsternal setiferous patch; stp = synsternal translucent patch.

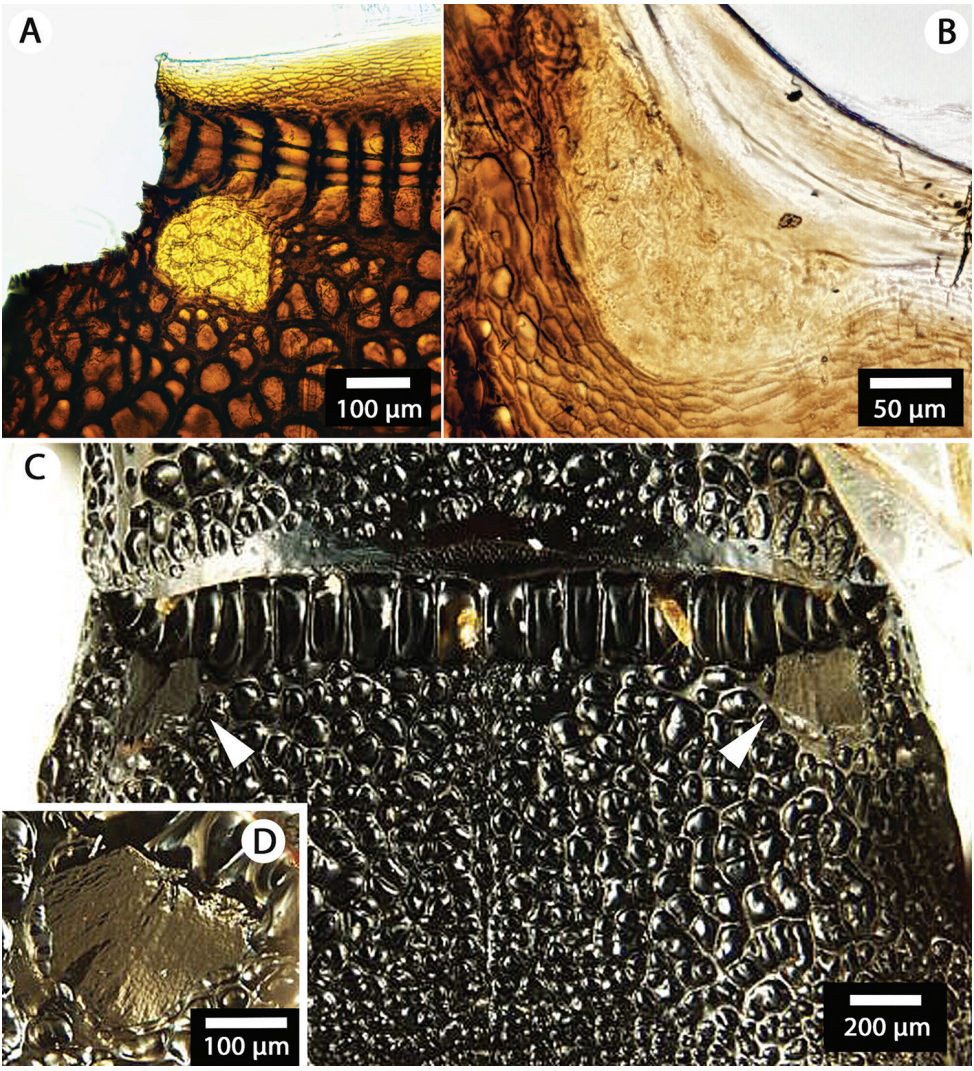

Figure 5. Brightfield images showing the dorsal and ventral patches of translucent cuticle in Orussidae, viewed externally. **A** Dorsal view of an *Orussus* sp. (Hymenoptera: Orussidae), viewed externally (identifier: IM 1445/ NCSU 53625) **B** Ventral view of the same specimen **C** Arrows pointing to dorsal patches of translucent cuticle in *Orussus abietinus* Scopoli, 1763 (Hymenoptera: Orussidae) (identifier: PSUC_FEM 86200) **D** A closer view of one of the translucent patches from the same specimen.

https://doi.org/10.6084/m9.figshare.4993820) and female (Fig. 7B; animated version available on figshare at https://doi.org/10.6084/m9.figshare.4993826.v1) *Megaspilus armatus* Say, 1836 specimens. Though resilin was not detected, the translucent patches of cuticle fluoresced differently than the surrounding cuticle in

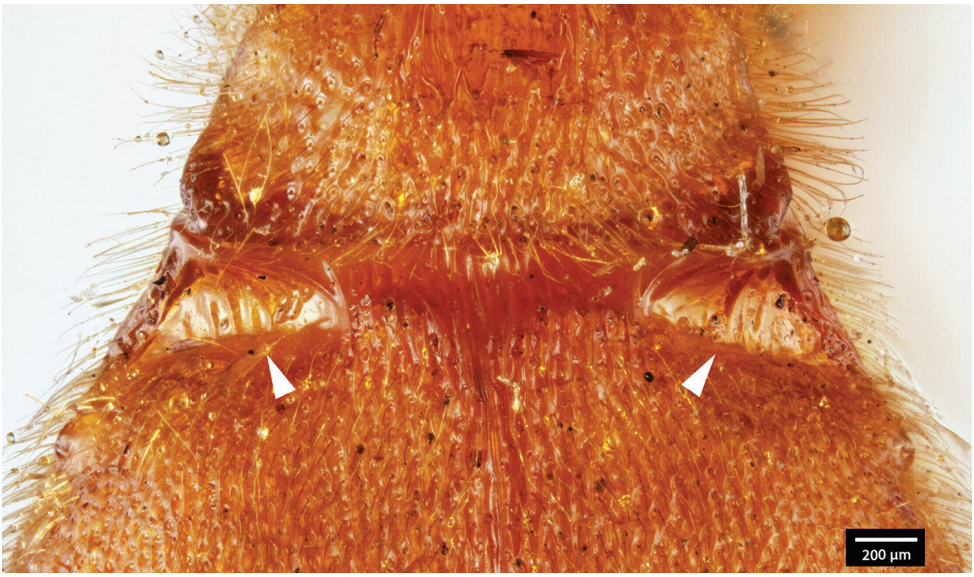

Figure 6. Brightfield images with arrows pointing to the patches of translucent cuticle in a *Trogus* sp. (Hymenoptera: Ichneumonidae) (identifier: PSUC_FEM 86178).

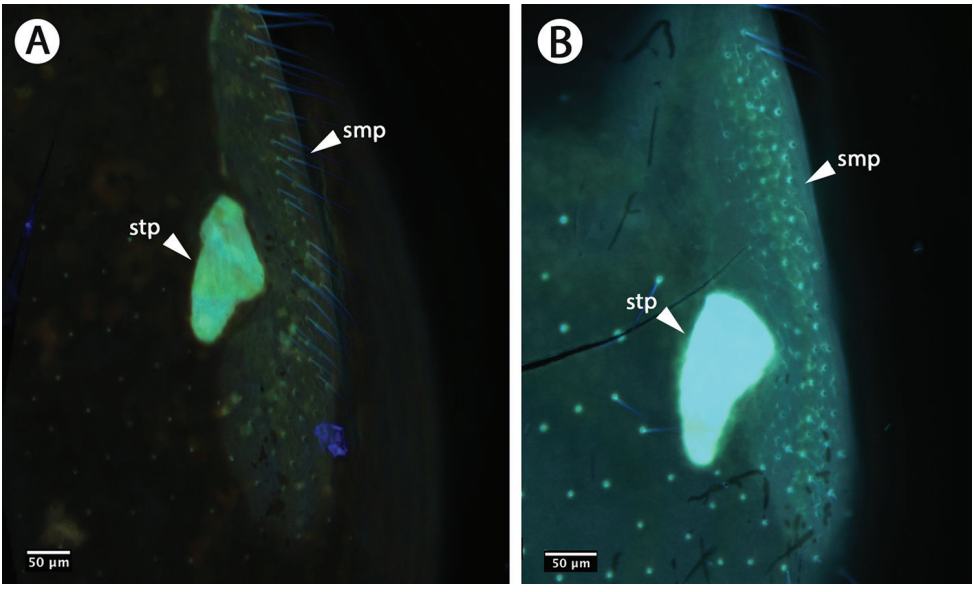

Figure 7. CLSM image of the synsternal translucent patch and setiferous patch in a male (**A** identifier: PSUC_FEM 86236) and female (**B** identifier PSUC_FEM 86240) *Megaspilus armatus* Say, 1836 specimen (Hymenoptera: Megaspilidae), viewed externally. Abbreviations: smp = synsternal setiferous patch; stp = synsternal translucent patch.

both male and female specimens (Fig. 7). CLSM also revealed fluorescence of tissue underneath the cuticle of the setiferous patch that occurred in the same shape as the patch. The setae of the synsternal setiferous patch appeared to be rich in resilin, a feature that is shared among other setae present on the sternite. No differences were found between male and female specimens.

Histology

Histological cross sections of the metasoma of *Dendrocerus* sp. and *Conostigmus* sp. (Hymenoptera: Megaspilidae) specimens revealed the presence of pore canals directly underneath the setae of the synsternal setiferous patches (Fig. 9). SBFSEM was used to build a three-dimensional model tracing a duct from a gland cell to an opening in the cuticle (Fig. 8A; animated version available at https://doi.org/10.6084/m9.figshare.4004157.v1). Closer inspection of the cuticle with TEM revealed smaller pores fringed with cells containing smooth endoplasmic reticulum (Fig. 9).

The internal structures associated with the synsternal translucent patches were different than those of the synsternal setiferous patches. Histological cross sections did not show any pore canals in the translucent cuticle. However, TEM and SBFSEM revealed membrane-bound structures with excess membrane folds present underneath the translucent patches (Fig. 10). SBFSEM was used to build a three dimensional model of one of these structures, revealing it to have a rounded shape (Fig. 8B; animation available at https://doi.org/10.6084/m9.figshare.4993832.v1).

Discussion

Overview of the setiferous patches

Histological cross sections of the metasoma of *Dendrocerus* sp. and *Conostigmus* sp. (Hymenoptera: Megaspilidae) specimens revealed pore canals directly underneath the setae of the synsternal setiferous patches (Fig. 9). These appear to be class 3 gland cells, each consisting of a gland cell and a secretory duct that connects it to the cuticle (Noirot and Quennedey 1974; Quennedey 1998). Using SBFSEM, a three-dimensional model was built tracing a duct from a gland cell to an opening in the cuticle (Fig. 8A; animated version available at https://doi.org/10.6084/m9.figshare.4004157.v1). This confirms the presence of gland cells underneath the synsternal setiferous patches within Ceraphronoidea.

Closer inspection of the cuticle with TEM revealed smaller pores fringed with cells containing smooth endoplasmic reticulum (Fig. 9B), often found in gland cells producing pheromones or lipids (Quennedey 1998). These appear to be class one gland cells, which adjoin the cuticle and secrete products either directly through the cuticle

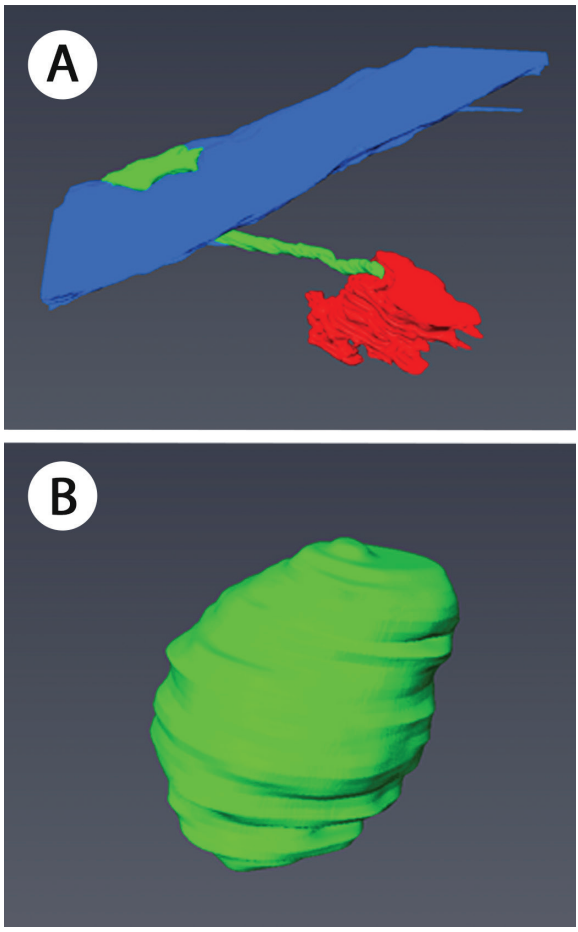

Figure 8. A A three-dimensional model of a class 3 gland cell found underneath the cuticle. The model shows the cuticle in blue, the gland cell in red, and then secretory duct connecting them in green **B** A three-dimensional model of a lamellar body.

or through epicuticular canals (Noirot and Quennedey 1974; Quennedey 1998). Since both class one and class three gland cells are present, the gland underneath the synsternal setiferous patch appears to be a composite gland comprised of multiple gland cell types (Noirot and Quennedey 1974). CLSM imaging may even show the outline of this gland, fluorescing underneath the cuticle in the same shape as the synsternal setiferous patch (Fig. 7A). Patches of setae have long been known to be associated with glandular activity in Hymenoptera (Buckingham and Sharkey 1988; Debolt 1973; Mikó et al. 2010; Noirot and Quennedey 1974), but this is the first time that this has been confirmed in Ceraphronoidea.

Glands underneath patches of setae in Hymenoptera are thought to secrete pheromones, with the setae acting to increase the surface area for diffusion of these secretions

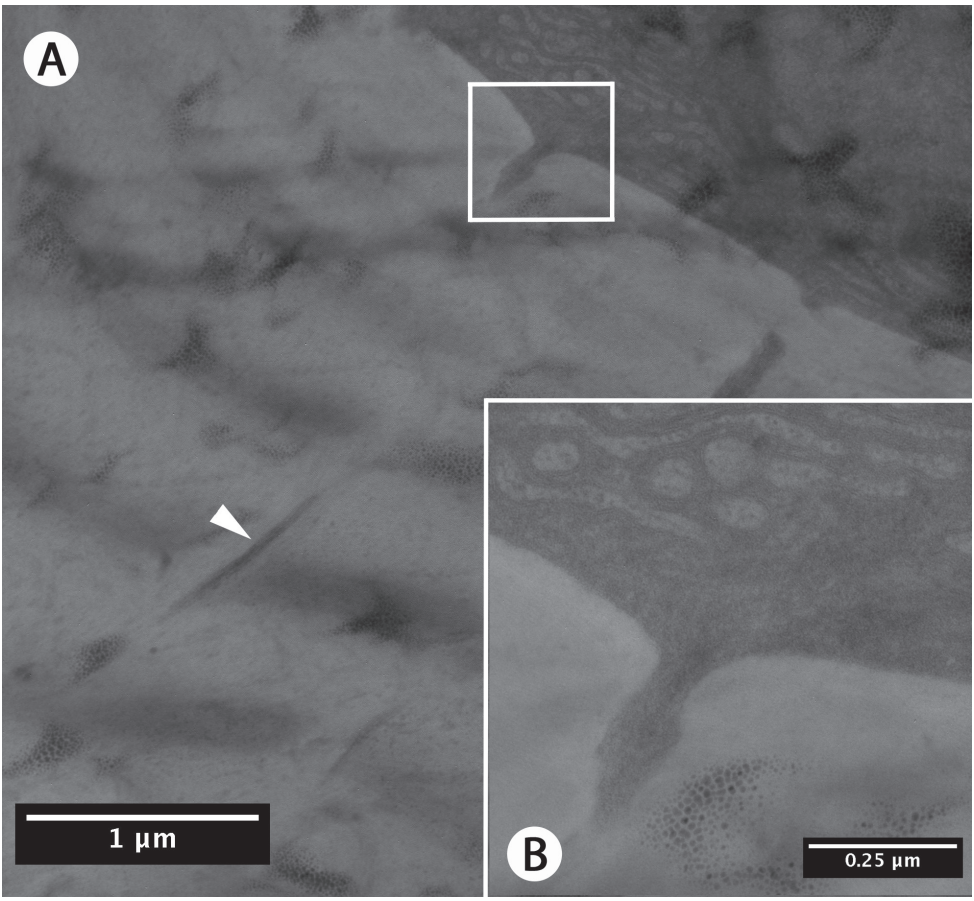

Figure 9. A TEM image of the class one gland cells found underneath the synsternal translucent patch in a *Dendrocerus* sp. (Hymenoptera: Megaspilidae) The arrow points to the secretory duct in the cuticle, while the square outlines the gland cells at the base of these ducts **B** A closer look at the class one gland cells at the base of one of these ducts. Specimen identifier: IM 5442.

(Debolt 1973; Mikó et al. 2007; Noirot and Quennedey 1974). Pheromones have a wide variety of important ecological, behavioral, and physiological functions in insects (Howard and Blomquist 2005). One possible function of these glands could be the production of defensive pheromones, which has been proposed for abdominal glands in Ichneumonoidea (Buckingham and Sharkey 1988; Townes 1939). It is also possible that these abdominal glands could produce pheromones that play roles in courtship, mate recognition or sexual selection, which has been found in other parasitoid wasps (Niehuis et al. 2013; Ruther et al. 2007, 2009). There may be behaviors associated with these patches as well. Very little is known about the behavior of Ceraphronoidea, but the pumping motion of the abdomen in Braconidae has been proposed to be associated with abdominal glands (Buckingham 1968; Buckingham and Sharkey 1988) and could help to disperse pheromones.

Overview of translucent cuticle in Ceraphronoidea

Translucent cuticle over the compound eyes and ocelli in insects often contains resilin, a structural protein that autofluoresces between 320 nm and 415 nm (Andersen 1963; Michels and Gorb 2012), allowing for detection and visualization using CLSM (Deans et al. 2012). CLSM of the translucent patches did not indicate resilin; however, the patches fluoresced differently than the surrounding cuticle, indicating that the patch has a different structural composition. Though the patches do not appear to contain resilin, they may contain a resilin-derivative or other protein involved in the structure of translucent and transparent cuticle, such as crystallin (Janssens and Gehring 1999). The identity of what makes the patch fluoresce differently remains to be determined.

The internal structures associated with the synsternal translucent patches were different that those of the synsternal setiferous patches. Histological cross sections did not show any pore canals in the translucent cuticle. However, TEM and SBFSEM revealed membrane-bound structures with excess membrane folds present underneath the translucent patches (Fig. 10). These structures were identified as lamellar bodies, which are membrane-bound structures with excess membrane folds that are produced when fat bodies or vacuoles are broken down(McDermid and Locke 1983; Quennedey 1998; Vigneron et al. 2014). A three-dimensional model of one of these lamellar bodies was built using SBFSEM, revealing that these structures have a rounded shape (Fig. 8B; animation available at https://doi.org/10.6084/m9.figshare.4993832.v1).

Lamellar bodies are involved in organelle recycling, and can have glandular functions such as storage and secretion (McDermid and Locke 1983; Quennedey 1998; Vigneron et al. 2014). Lamellar bodies can also be associated with photoreceptors (White 1968). Extraocular photoreceptors, which are photoreceptors found outside of the eyes and ocelli, have been found underneath translucent cuticle in other insects (Williams and Adkisson 1964). It is possible that there may be extraocular photoreceptors underneath these patches of cuticle, and that the cuticle is transparent to allow light into the metasoma. Such a system could be important for the regulation of circadian rhythms or for sensing seasonal changes in photoperiod (Mizoguchi and Ishizaki 1982; Renninger et al. 1997). This system has never been described before in Ceraphronoidea; any further work investigating the translucent cuticle offers a high potential for new discovery.

Phylogenetic relevance of the syntergal and synsternal translucent patches

Both patches of setae (Masner and Huggert 1989; Mikó et al. 2010) and patches of translucent cuticle (Liu et al. 2006) have been used to distinguish between species and even genera in other Hymenoptera (Vilhelmsen 2003). The same is true within Ceraphronoidea. Work done on the genera *Conostigmus* and *Dendrocerus* (Hymenoptera: Megaspilidae) revealed differences in the shape and size of translucent and setiferous patches of cuticle between species (Dessart 1997, 1999, 2001), making differences in

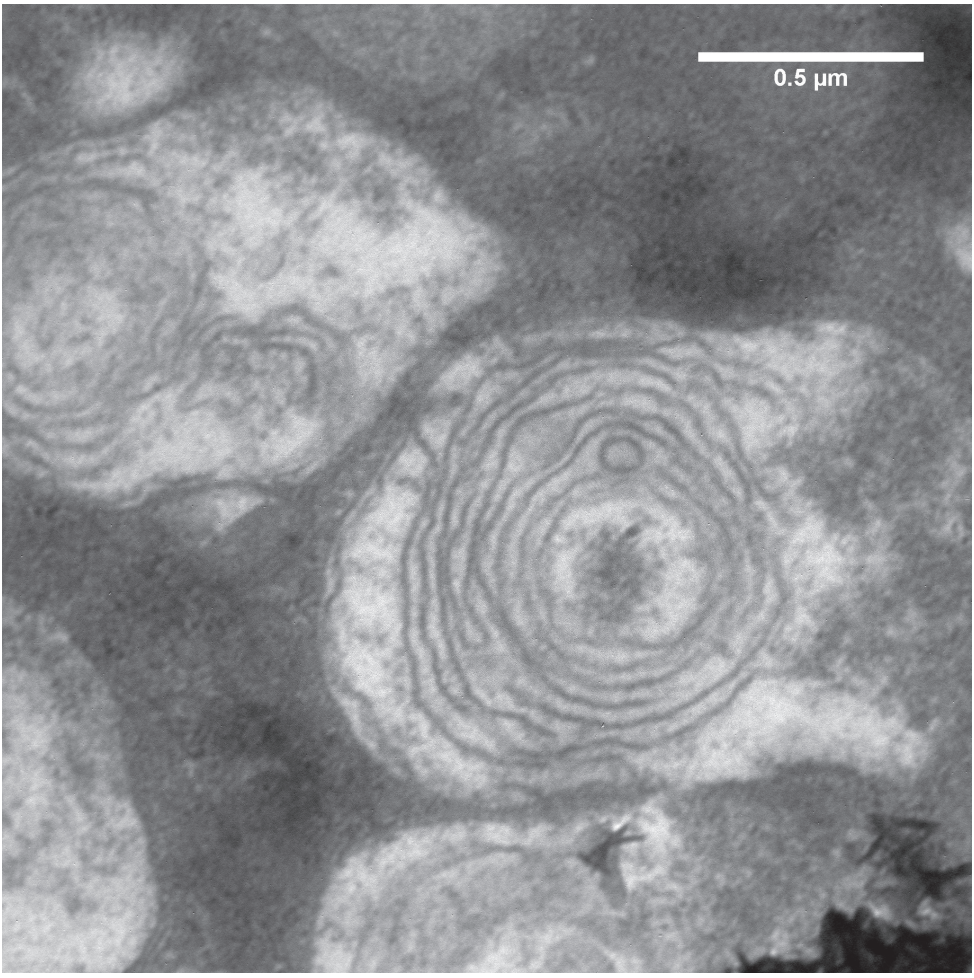

Figure 10. TEM image of the lamellar bodies found underneath the synsternal translucent patch in a *Dendrocerus* sp. (Hymenoptera: Megaspilidae) Specimen identifier: IM 5442.

their structure a potent diagnostic feature to distinguish between species. To date, there are no indications of sexual dimorphism concerning these characters, making it possible to match males and females in situations where only one sex has been described.

There are also differences in the locations of the setiferous and translucent patches between different members of Ceraphronoidea. The synsternal setiferous patches are located posteriorly to the synsternal translucent patches in the family Ceraphronidae, laterally to them in the Megaspilinae, and anteriorly to them in Lagynodinae. It is unclear why these structures occur in different locations across different groups. If the setiferous patches secrete substances that play a role in courtship or defense, the locations of the setiferous patches could indicate different courtship or defensive behaviors in different groups. It is also possible that these structures could have evolved

independently. The phylogenetic relationships between the families and subfamilies in Ceraphronoidea are unresolved (Mikó et al. 2013). The variation in the locations of the translucent and setiferous patches are consistent in each subfamily and could represent a putative synapomorphy for each lineage, thought further analysis is needed to verify the phylogenetic relevance of these structures.

The locations of the translucent and setiferous patches in relation to each other could also provide relevant information concerning the placement of difficult genera within Ceraphronoidea. The genus *Masner* is perplexing in that it shares characters with both Megaspilidae and Ceraphronidae. It is thought to be sister to Ceraphronidae (Mikó and Deans 2009; Mikó et al. 2013), a hypothesis which is supported by our findings in the relative location of the synsternal setiferous and translucent patches. Another perplexing genus with uncertain placement within Ceraphronoidea is *Trassedia*, which was formerly grouped with Megaspilidae based on the presence of a pterostigma and nine flagellomeres in females (Cancemi 1996). However, based on other morphological characters, such as the presence of Waterston's evaporatorium, a single mesotibial spur, and axillular setae, and absence of an occipital depression and a narrow sclerite anterior to the synsternum, the genus is now thought to be part of Ceraphronidae (Mikó et al. 2013). In *Trassedia,* the synsternal setiferous patches occur posteriorly to the synsternal translucent patches as in Ceraphronidae supporting placement in that family (Mikó et al. 2013).

Whereas patches of setae have long been known to be associated with glandular openings in Hymenoptera (Buckingham and Sharkey 1988; Debolt 1973; Mikó et al. 2010; Noirot and Quennedey 1974), and are found in several distantly related groups ranging from Megachilidae (Noirot and Quennedey 1974) and Mutillidae (Debolt 1973) to Platygastroidea (Mikó et al. 2010), the presence of translucent patches of cuticle in the metasoma is much less common. As the putative sister to Apocrita, Orussidae represent an important step in the evolution of Hymenoptera and the parasitoid lifestyle (Mao et al. 2014; Peters et al. 2017; Sharkey 2007). Orussidae also have patches of smooth cuticle similar to the syntergal and synsternal translucent patches found in Ceraphronoidea. Just as in Ceraphronoidea, the patches in Orussidae occur in pairs and are found both dorsally and ventrally. Their location in Orussidae (second abdominal tergite and sternite) is comparable to their location in Ceraphronoidea (first metasomal tergite and second metasomal sternite). Based on these similarities, the structures in Orussidae and Ceraphronoidea may have similar functions or evolutionary origins.

Similar structures are also present in Ichneumonidae on both the dorsal and ventral surfaces of the metasoma. The structures present on the tergite are known by different names. According to Townes (1969), these structures are known collectively as the thyridia, described as patches of cuticle with different surface sculpturing occurring in pairs anterior to the spiracle on the second tergite. However, Goulet and Huber (1993) identifies these structures as the gastrocoeli, and considers the thyridia to be the unique cuticular structure specific to the gastrocoeli. Whether these translucent patches are called the gastrocoeli or the thyridia, both authors note that they differ between ich-

neumonoids and are not always present (Goulet and Huber 1993; Townes 1969). In Ichneumonidae, the thyridia or gastrocoeli are located on the second tergite, not on the first as in Ceraphronoidea or Orussidae. However, in Ceraphronoidea, the first tergite is longer than the successive tergites, and may have been formed by the fusion of multiple tergites; thus, the structures may be comparable between Ceraphronoidea and Ichneumonidae, and may also have similar functions or evolutionary origins.

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Supplementary material 1

Specimen locality information

Authors: Carolyn Trietsch, István Mikó, Jonah M. Ulmer, Andrew R. Deans

Data type: specimens data

Explanation note: A table listing all of the specimens used in this study, and their associated locality and repository information.

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RESEARCH ARTICLE

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Morphological characterization of immature stages of *Habrobracon hebetor* (Hymenoptera, Braconidae) ectoparasitoid of *Ephestia kuehniella* (Lepidoptera, Pyralidae)

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Abstract

Habrobracon hebetor (Say) is a cosmopolitan idiobiont braconid which parasitizes Pyralidae larvae, a pest of stored products, such as *Ephestia kuehniella* (Zeller). The objective was to describe the morphology of immature forms of *H. hebetor* and morphological changes throughout its development. Mated females of *H. hebetor* were individualized in Petri dishes containing larvae of *E. kuehniella* for parasitism for six hours. Then, the females were removed, leaving only the eggs placed on the host. The development was evaluated every 12 hours, recording all stages and changes until the emergence of adults. Using stereoscopic optical and scanning electron microscopy, photographs of immature individuals were taken. The results showed that this parasitoid completes its development between 10–12 days. There were stages overlaps during egg to adult development. Eggs are hymenopteriform, with a smooth surface. According to cephalic capsule and larval length measurements of *H. hebetor*, it was possible to determine four instars. In general, the instars are similar to each other, differing mainly in the size and shape of segments. Larvae present a gradual loss of transparency, becoming opaquer at each successive instar. Last instar larvae distanced from the host to form the cocoon and to pupate. This study was relevant for a better understanding of the physiological interactions between *E. kuehniella* and *H. hebetor*.

Keywords
Bionomy, Pre-imaginal period, Parasitoid, Electro micrographs

Introduction

In Hymenoptera 15 superfamilies and 62 families of parasitoid are recognized (Melo et al. 2012). Braconidae is the second in number of described species (18,000) with 34 subfamilies (Quicke 2015). Braconinae, is one of the largest subfamilies, containing 2,800 valid described species distributed into more than 185 genera (Yu et al. 2012). Several species of Braconinae are potential biological control agents of Lepidoptera and Coleoptera larvae (Quicke 1997).

Habrobracon hebetor (Say) (Hymenoptera: Braconidae) is an idiobiont ectoparasitoid with a cosmopolitan distribution (Eliopoulos and Stathas 2008). It parasites mainly Pyralidae larvae, among them *Ephestia kuehniella* (Zeller) (Magro and Parra 2001, Athié and Paula 2002), considered a secondary pest of stored products because it feeds on residues left by other insects as well as processed products (Lorini et al. 2015).

The number of instars, development time and feed consumption of *H. hebetor* was evaluated by Magro et al. (2006) for the improvement of an artificial diet, however without morphological details. According to Forouzan et al. (2008) and Chen et al. (2012), the time of development of immature stages of the parasitoid *H. hebetor* decreases as the temperature increases.

The morphological characteristics of immature stages play an important role in the recognition, taxonomy and classification of parasitoid wasps (Zhao et al. 2014). For the understanding of host-parasitoid relations, the recognition of immature stages at different stages of development is relevant.

In taxonomic studies, most morphological descriptions of Braconidae are concentrated in the adult stage, while the biology and morphology of immature stages still lack information (Quicke 2015). Even though there are descriptions of the immature external morphology of some braconid species (Yu et al. 2008, Carabajal-Paladino et al. 2010, Pinheiro et al. 2010, Qureshi et al. 2016). The study by Sudheendrakumar et al. (1982) describes the biology and morphology of the immature stages of *Bracon brevicornis* (Wesmael) (Hymenoptera: Braconidae), species denominated junior synonym of *H. hebetor* (Yu et al. 2012). But there are gaps in the morphological descriptions.

Although some aspects of biology at immature stages of *H. hebetor* have been studied, researches are mainly focused on the interactions between parasitoid, host and environmental factors (Eliopoulos and Stathas 2008, Chen et al. 2012, Farag et al. 2015). The morphological characterizations of immature stages aiding in taxonomy (Gumovsky 2007). However, for this species does not well elucidated. The objective of this study was to describe the development of the immature forms of *H. hebetor* based on a detailed description of external morphology in order to provide knowledge on the recognition of the immature stages of this species.

Material and methods

Laboratory creations

Rearings of *H. hebetor* and its host *E. kuehniella* were kept in the Laboratory of Entomology of the University of Santa Cruz do Sul (UNISC), Brazil. Laboratory conditions were maintained at 28 ± 2 °C, 50 ± 20% RH and 12:12 L:D. *Ephestia kuehniella* was kept on an artificial diet consisting of wheat flour (97%) and brewer yeast (3%), following the methodology proposed by Parra et al. (2014).

Morphological characterization of immature stages and development time

Twenty mated females of *H. hebetor* were individualized in Petri dishes containing one larva of *E. kuehniella* for parasitism for six hours. Then, the females were removed and leaving just one egg placed on the host, the others removed. The development time was evaluated every 12 hours by recording all stages and changes until the emergence of adults.

For the determination of the number of larval instars, a segmented regression model was used according to Ambrosano et al. (1997), with an r^2 = 99%. Twenty individuals at each stage (egg, larva, prepupa and pupa) were evaluated. We measured the largest width and length in dorsal view and the width of the cephalic capsule using micrometric lens with a stereoscopic microscope (Motic Quimis Q764ZT). The largest width was measured from the larger portion of the eggs and from the body segments of larvae, prepupa and pupa. All stages were photographed in the same stereomicroscope previously mentioned using a digital camera (Canon EOS Rebel T3).

A sample of each stage was fixed in 25% glutaraldehyde solution in a 0.2 M phosphate buffer and distilled water for 14 days. The samples were then washed three times (30 min/wash) in 0.2 M phosphate and distilled water (1:1 ratio) dehydrated in a graduated series of acetone (30, 50, 70, 90 and 100%). They were dried (Balzers CPD030) and metallized (Balzers SCD050), after which a scanning electron microscope (Jeol JSM 6060) was performed. Electro micrographs of all immature stages were made.

To the description of each stage, one individual at every stage with an average age was used. Comments on morphological changes that may occur during each stage were added after the diagnoses. For cephalic capsule chaetotaxy, last instar larvae were used as model since the distribution of setae is the same for all larval instars and prepupa (Short, 1952).

Morphological terminologies (Fig. 1).

Abbreviations:

A abdominal segment
AS anal segment
T thorax segment

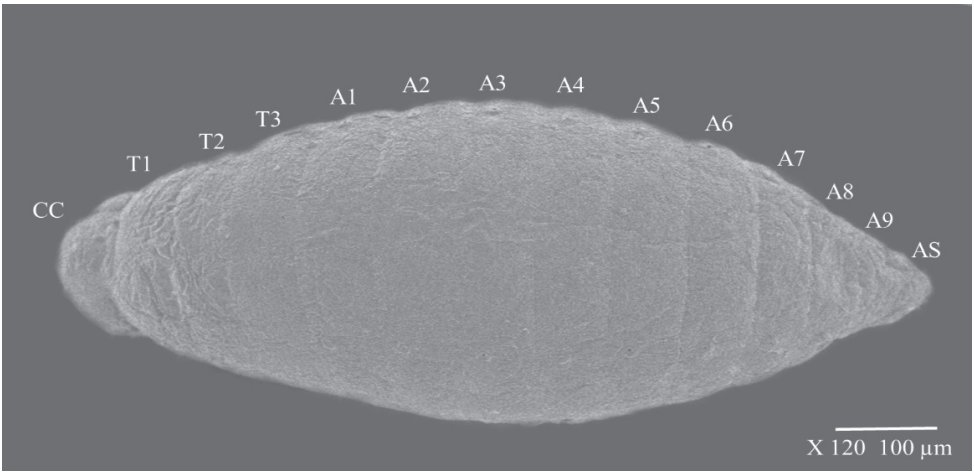

Figure 1. Second instar larva of *Habrobracon hebetor* (dorsal view) illustrating the terminology used in the text (A1-A9 abdominal segments, AS anal segment, CC cephalic capsule, T1-T3 thoracic segments).

The examined material was registered at the Entomological Collection of Santa Cruz do Sul (CESC), under lots no. 79,495 (Egg), 79,496 (Larva, 1st instar), 79,497 (Larva, 2nd instar), 79,498 (Larva, 3rd instar), 79,499 (Larva, 4th instar), 79,500 (Prepupa), 79,501 (female pupa) and 79,502 (male pupa).

Results

There was stage overlap (between replicates) during the egg to adult development of *H. hebetor*, indicating variations in development time. The amplitude of each immature stage was small, especially in the first instars. Thus, four days after oviposition, the larvae were already at the fourth and last instar, initiating the formation of the cocoon to pupate. The pupal phase was the longest of all development stages, lasting more than four days (Table 1).

The diagnosis of the entire development of *H. hebetor* is presented below with photographs and electro micrographs presenting some details of each stage, distribution and nomenclature of setae on the cephalic capsule, and comments on the morphological changes at each stage.

Egg

Diagnosis: opaque white, with a smooth surface (Fig. 5A), typically hymenopteriform, elongated, more or less elliptical, approximately four times longer than wide, anterior extremity (where the cephalic capsule of the embryo forms) rounded and opposite tip slightly pointed (Fig. 3A and B).

Table 1. Development time and sizes of immature stages of *Habrobracon hebetor* in *Ephestia kuehniella* larvae (12 h photophase, 28 ± 2°C and 50 ± 20% RH).

Stage/instar	Duration (Days ± SD)	Body length (mm ± SD)	Maximum body width (mm ± SD)	Cephalic capsule width (mm ± SD)
Egg	1.35 ± 0.343	0.52 ± 0.056	0.12 ± 0.011	-
Larva 1	0.73 ± 0.089	0.44 ± 0.073	0.10 ± 0.019	0.10 ± 0.014
Larva 2	0.41 ± 0.050	0.89 ± 0.142	0.36 ± 0.022	0.18 ± 0.019
Larva 3	0.90 ± 0.110	1.87 ± 0.283	0.60 ± 0.086	0.24 ± 0.019
Larva 4	1.22 ± 0.150	2.67 ± 0.139	0.90 ± 0.079	0.30 ± 0.026
Prepupa	1.97 ± 0.374	2.90 ± 0.182	0.84 ± 0.035	0.38 ± 0.022
Female pupa	4.47 ± 0.413	2.46 ± 0.113	0.91 ± 0.037	0.56 ± 0.011
Male pupa		2.50 ± 0.164	0.78 ± 0.027	0.56 ± 0.013

Measurements: overall length: 0.52 mm; maximum width: 0.12 mm.

Comments: approximately 12 hours after oviposition, it is possible to observe the embryo in formation and its development (Fig. 3B), and later the hatching.

Larva

It was possible to determine four larval instars of *H. hebetor* based on cephalic capsule length and larval body length, (Table 1) using the segmented regression model (r^2 = 99%).

In general, the four larval instars are similar to each other, differing mainly in the size and shape of segments. Larvae present a gradual loss of transparency, becoming opaquer at each successive instar with the enlargement of the intestine. Each instar had a different development time (Table 1).

First instar

Diagnosis: spherical cephalic capsule, width equal to the length of three thorax segments together, visible short antennae below the vertex region, sparse setae in the frontal region of the cephalic capsule (Fig. 2), body with 13 post-cephalic segments: three thoracic segments (T1-T3) and ten abdominal, including one anal segment (A1-A9, AS). A1-A5 had an almost equal length and width, A6-A9 width gradually decreasing up to the AS (Fig. 3C), a pair of spiracles per segment T and A (Fig. 5C), AS width equal to one third of the cephalic capsule width, smooth body surface, no setae (Fig. 5C).

Measurements: overall length: 0.42 mm; cephalic capsule: 0.10 mm; maximum width: 0.10 mm.

Comments: at the initial phase of the first instar, the larva is translucent and the cephalic capsule is as wide as the following segments. As the larva develops, its body grows rapidly and the segmentation becomes more noticeable. During the first instar, the thoracic segments exceeded the width of the cephalic capsule.

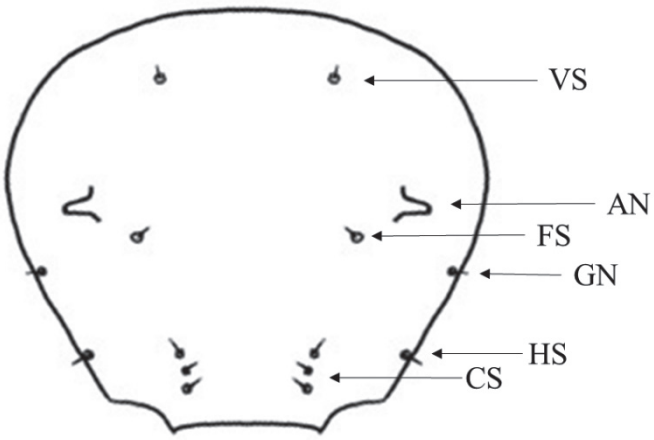

Figure 2. Cephalic capsule (frontal view) of fourth instar larva of *Habrobracon hebetor* illustrating chaetotaxy (AN antenna, CS clypeal setae, FS frons setae on the antennal region, GN genal setae, HS hypostomal setae, VS vertex setae).

Second instar

Diagnosis: spherical cephalic capsule, almost twice as wide as that of the first instar, short visible antennae with sparse setae in the frontal region of the cephalic capsule (Fig. 2), T2 and T3 twice as wide as the cephalic capsule, segments A1-A5 almost with the same length and width of T2-T3, A6-A9 with width gradually decreasing up to the AS (Fig. 3D), a pair of spiracles per segment T and A (Fig. 5C), AS with half of cephalic capsule width, smooth body surface, no setae (Fig. 5C).

Measurements: overall length: 0.92 mm; cephalic capsule: 0.18 mm; maximum width: 0.36 mm.

Comments: the width of the cephalic capsule increases, but less than the width of the body segments. With the increase in larval body size, the intestine occupies an increasing volume, reaching up to a third of the body's space at this phase of development.

Third instar

Diagnosis: spherical cephalic capsule 2.5 times larger than that of the first instar, visible short antennas with sparse setae in the frontal region of the cephalic capsule (Fig. 2), posterior part of the cephalic capsule covered by T1, T2 and T3 twice as large as the cephalic capsule, A1-A6 segments 1.5 times wider than T2-T3, A7-A9 with width gradually decreasing up to the AS (Fig. 3E), a pair of spiracles per segment T and A, width of the AS equal to two-thirds the cephalic capsule width, thoracic and abdomen dorsal with short and dense setae on all surfaces (Fig. 5B) along with sparse trichoid sensilla three times longer than setae (Fig. 5D), smooth ventral side without setae.

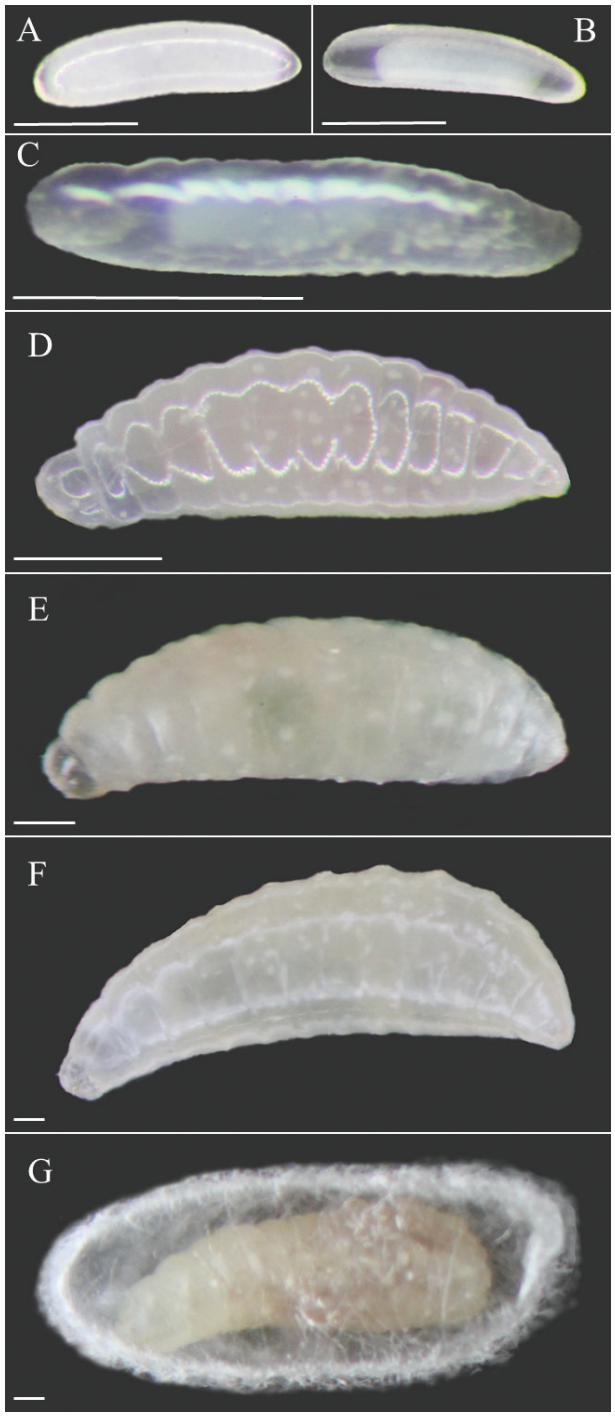

Figure 3. Immature stages of *Habrobracon hebetor* (side view): **A** egg after oviposition **B** embryo in development **C** first larval instar **D** second larval instar **E** third larval instar **F** fourth larval instar **G** cocoon in formation. Scale: (**A–C**) 0.25 mm (**D–G**) 0.5 mm.

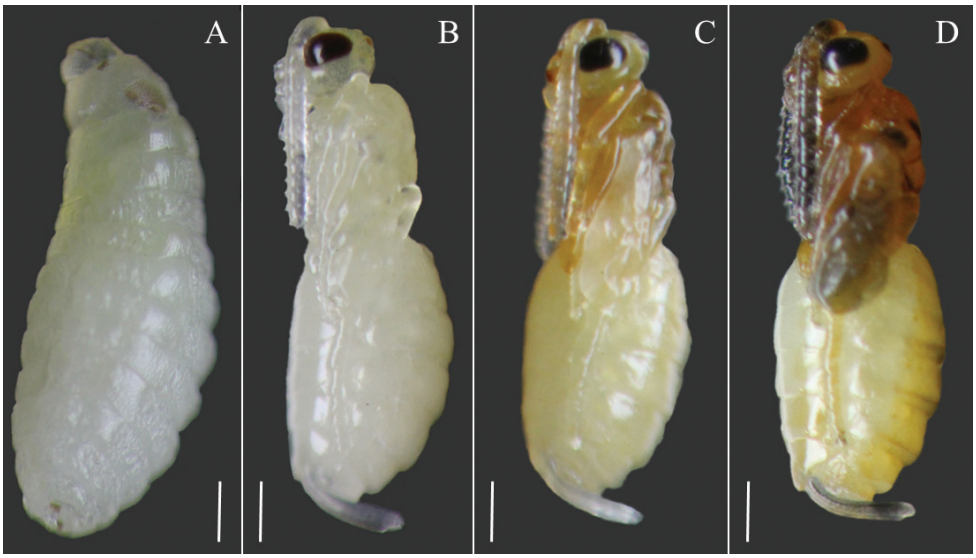

Figure 4. Immature stages of *Habrobracon hebetor* female (side view): **A** Prepupa **B** first pupal phase **C** second pupal phase **D** third pupal phase before adult emergence. Scale: 0.5 mm.

Measurements: overall length: 1.52 mm; cephalic capsule: 0.24 mm; maximum width: 0.62 mm.

Comments: as the body segments increase in size, the cephalic capsule begins to be covered in the back by the T1, reaching up to a third of the cephalic capsule. Unlike the first and second instar, the surface has short, dense setae, easily visible, scattered across the thorax and abdomen. Trichoid sensilla are developed, with a base and cone shape, reaching twice the size of setae. The larva becomes opaquer and the intestine occupies two-thirds of the body at this instar.

Fourth instar

Diagnosis: spherical cephalic capsule 3 times larger than that of the first instar, visible short antennas with sparse setae in the frontal region of the cephalic capsule (Fig. 2), cephalic capsule covered dorsally by T1, approximately with the same width, T2 twice as large as T1, T2 and T3 twice as long as the cephalic capsule, A1-A8 segments with the same length and almost four times wider than the cephalic capsule (Fig. 3F), a pair of spiracles per segment T and A, AS with the same width as the cephalic capsule, thoracic and abdomen dorsal with short and dense setae on all surfaces (Fig. 5B) along with sparse trichoid sensilla three times longer than setae (Fig. 5D), smooth ventral side without setae.

Measurements: overall length: 2.64 mm; cephalic capsule: 0.29 mm; maximum width: 0.95 mm.

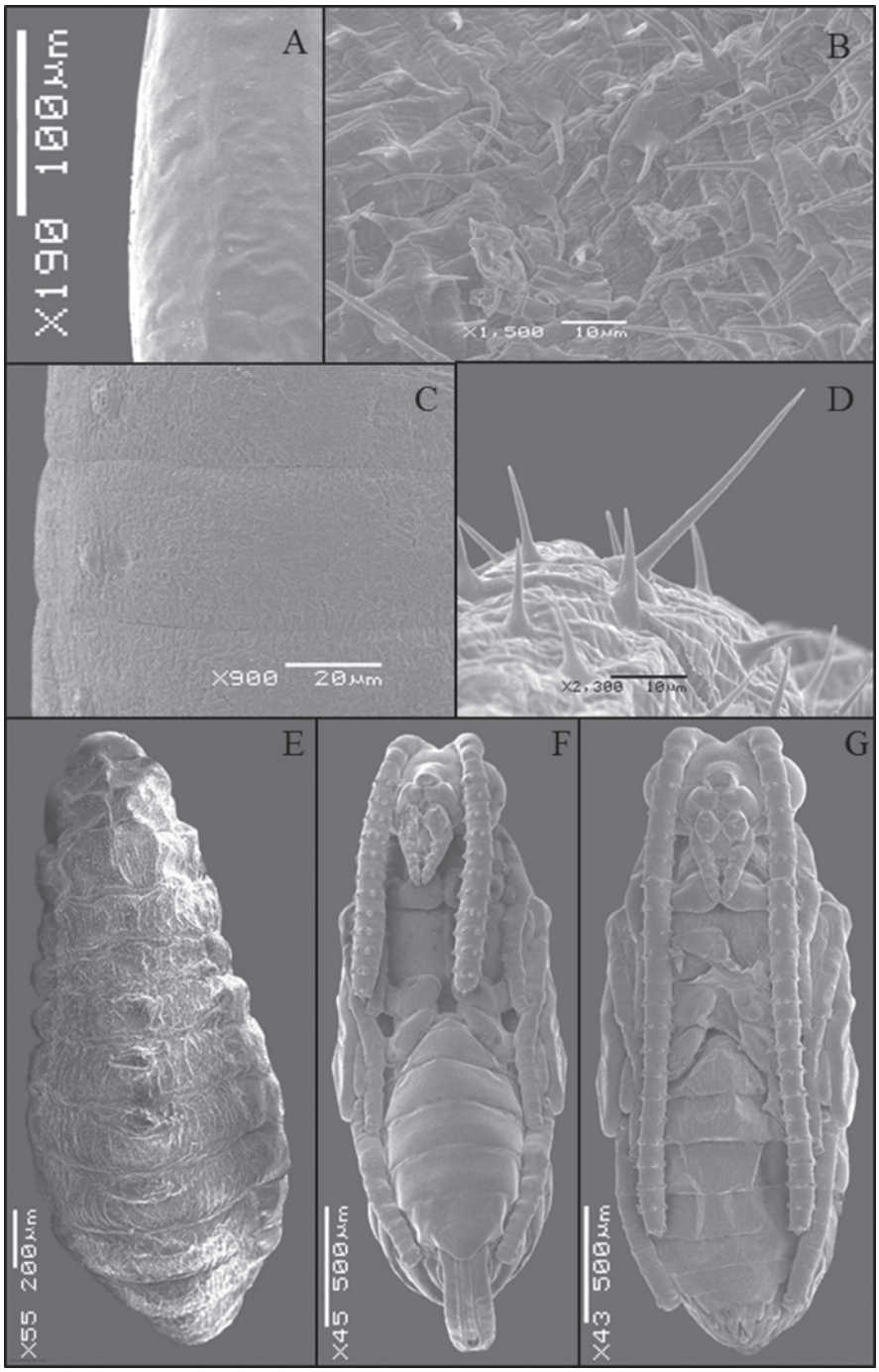

Figure 5. Scanning electron micrographs of immature stages of *Habrobracon hebetor*: **A** detail of the smooth surface of the egg **B** detail of the setae on the dorsal surface of the thorax and abdomen of third and fourth larval instars and prepupa **C** detail of the smooth dorsal surface of first and second larval instars with spiracles **D** detail of a trichoid sensillum **E** prepupa **F** female pupa **G** male pupa.

Comments: as they grow, body segments increase in size, making the cephalic capsule proportionally the smallest part of the larva in addition to being almost totally involved dorsally by the first thoracic segment. Many granules appear as small white patches scattered under the cuticle of the abdominal segments. Approximately 84 h after parasitism, larvae of the fourth instar had already consumed almost all the tissues of the host and distanced themselves from it to initiate the formation of the cocoon, which is woven with silk produced by the labial glands, forming a thick layer of threads over its body (Fig. 3G).

Prepupa

Diagnosis: cephalic capsule distinctly separated from the rest of the body, with an enlargement of the posterior lobe (Fig. 4A), visible short antennas with sparse setae in the frontal region of the cephalic capsule (Fig. 2), T1 almost as long as T2 and T3 together, T2 and T3 four times wider than long, thoracic segments separated from abdominal segments by a slight constriction, A1-A6 with length and width almost equal to T3, A7-A9 with width gradually decreasing up to the AS (Fig. 5E), a pair of spiracles per segment T and A, AS width equal to one third of the cephalic capsule width, thoracic and abdomen dorsal with short and dense setae on all surfaces (Fig. 5B), sparse trichoid sensilla three times longer than setae (Fig. 5D), and smooth ventral side without setae.

Measurements: overall length: 2.90 mm; cephalic capsule: 0.38 mm; maximum width: 0.84 mm.

Comments: at the end of the fourth instar, the prepupal transformation occurs with the fully formed, oval-shaped and white-shaped cocoon, a lighter color and absence of movement. With the connection of the midgut to the posterior intestine, there is the elimination of the meconium, which is adhered to the cocoon, making the intestine translucent. There is a differentiation in the cephalic capsule with the expansion of the posterior lobe, where, at the end of this stage, the composite eyes and the three dorsal ocelli become visible, presenting a reddish-brown coloration.

Pupa

Female diagnosis: characteristics of the head as in adults, pigmented eyes and ocelli fully formed, antennas curved down to the thorax, ending in the insertion of the last pair of legs, 13 flagellomeres of equal size, 1.5 times wider than long, containing a ring of eight spines in each segment, spines at the base as large as long with approximately half the length of each flagellomere, buccal apparatus with sclerotized mandibles, thorax as in adults but with wing structures folded laterally to the thorax, reaching A2, legs developed close to the body, abdomen with nine segments, ovipositor curved upward at the back of the abdomen (Fig. 5F).

Measurements: overall length: 2.46 mm; cephalic capsule: 0.56 mm; maximum width (abdomen): 0.94 mm.

Male diagnosis: pupa similar to that of female, differing in the longest antennas reaching ventrally A5, containing 20 equal-sized flagellomeres, as large as long, with a ring of eight spines in each segment, spines at the base as large as long with approximately one-third of the length of each flagellomere, absent ovipositor (Fig. 5G).

Measurements: overall length: 2.50 mm; cephalic capsule: 0.56 mm; maximum width (abdomen): 0.76 mm.

Comments: exarate pupa is protected by the cocoon produced by the last instar larva. Initially, only eyes and ocelli are pigmented (Fig. 4B). The mandibles and mesoscale become sclerotized, followed by the remaining parts of the thorax, acquiring an orange coloration (Fig. 4C). The abdomen, the ovipositor and the antennae are the last parts of the body to become pigmented, making the abdomen brownish yellow and the other parts brown (Fig. 4D). On average, five days after turn into pupa, the adult breaks the cocoon with its jaws and emerges, leaving the cocoon.

Discussion

The time of development from egg to adult emergence was similar to that reported for *H. hebetor* by Serra (1992), Magro et al. (2006) and Alam et al. (2014). Between 26-28°C, the immature stage occurs after 10-12 days in *E. kuehniella* larvae or other hosts. The same authors concluded that the time of development of this parasitoid is directly dependent on temperature. It can be faster at high temperatures. The development time of *B. brevicornis* evaluated by Sudheendrakumar et al. (1982) for each stage of development can not be compared with the present study. The authors do not mention the temperature at which the parasitoid was reared, since this factor is determinant to development time.

This work evaluates in more depth information about the development stages of *H. hebetor* reported in the article by Sudheendrakumar et al. (1982) by descriptions and colored photographs of all immature stages. Also scanning electromyography was used to detail structures difficult to observe under optical microscopy.

The detailed diagnoses of all immature stages are a complement to the study conducted by Alam et al. (2014), who made brief comments regarding the development time and the basic morphological characteristics of the stages of *H. hebetor* parasitizing *Galleria mellonella* L. (Lepidoptera: Pyralidae), however without associating images and a detailed diagnosis of each period. The confirmation of the morphological characteristics before emergence is important to recognize the species also at the immature stage while it is over its host.

Eggs with an elongated hymenopteriform shape were expected because, as Ide et al. (2006) reported, most Hymenoptera eggs have such a format. However, according to the same author, the corium may be smooth or rough and may present hooks. In *H. hebetor*, the egg's corium is smooth, without other structures.

The existence of four larval instars of *H. hebetor* was found by adjusting the total length and width of the cephalic capsule measurements data by a segmented regression model (Ambrosano et al. 1997) differing from the previous assessment by Magro et al. (2006), who, based on the size of jaws, recorded the existence of only three larval instars for this parasitoid using the same host. This was also opposite to the result observed by Sudheendrakumar et al. (1982), in which the authors reported the occurrence of five larval instars according to length of mandible and diameter of prothoracic spiracle. However, comparing measurements of body length, maximum body width and cephalic capsule width, it is possible to verify that the fourth and fifth instars correspond to the fourth instar described in the present study.

According to Costa and Ide (2006), the definition of the number of instars may be variable according to the methodology used for its determination, and may even be different among individuals of the same species. Thus, we reinforce the relevance of our results, considering that the morphological differences are sufficient to define the four larval instars.

Larvae with low structural complexity and successive pigmentation changes in body color had been reported for other species of parasitoids. Thomazini et al. (2000), Bittencourt and Berti Filho (2004), Yu et al. (2008) and Zhao et al. (2014) reported that the body of parasitoids becomes opaquer and less translucent throughout their development.

In the third and fourth larval instars were observed short and dense setae on all dorsal surface of the thorax and abdomen. In the description of *B. brevicornis* made by Sudheendrakumar et al. (1982) the authors reported the occurrence of these setae only in the last instar, but it was possible to observe in electronic microscopy that the setae come from the third instar.

The appearance of white granules along the abdomen at the last larval instar has also been reported for a parasitoid of the same superfamily, *Diadromus collaris* (Gravenhorst) (Hymenoptera: Ichneumonidae) (Zhao et al. 2014). According to Parra (2009), such globules are fat bodies that store lipids and supply long-term energy reserves for adults. These lipids accumulated during the larval stage provide the adults with energy for approximately 10 days (Istvan et al. 2011).

Four days after oviposition, the parasitoid is already at the last larval instar and moves away from the host. This behavior is justified because, as reported by Quicke (1997) for ectoparasitoid, there is a potential risk of putrefaction of non-consumed host tissues. As a consequence, the parasite tends to develop rapidly at the larval stage. This reduces the effects of any decline in host quality which occurs naturally or as a result of infections by microorganisms (Quicke 2015).

After leaving the host, the parasitoid begins the construction of the cocoon to pupate. The formation of the cocoon with a thick layer of silk, according to Tagawa and Kitano (1981), indicate its importance for the survival of ectoparasitoid, as it is a protection against physical damage, predators, hyperparasitoids and desiccation. An exarate pupa is formed, with appendices separated from the body, as in most Hymenoptera (Ide et al. 2006). In addition, the morphological description made by Sud-

heendrakumar et al. (1982) of the pupa stage for female and male was performed, detailing the morphological differences existing for each sex.

The development of *H. hebetor* is similar in many ways to other braconids. However, in this study, we documented the whole development of *H. hebetor*, including morphological changes, thus providing a detailed basis for the morphological characterization of the immature stages and the development of *H. hebetor*.

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Rediscovery of *Cladiucha insolita* Konow (Hymenoptera, Tenthredinidae), description of the male and intraspecific variation

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Abstract

Cladiucha insolita Konow was described in 1902 from a single female from Vietnam, and this has remained the only recorded specimen. A series from Laos associates the sexes and shows some variation in wing venation, size, and number of antennomeres. The female is redescribed, the male is described for the first time, and intraspecific variation is noted.

Keywords

sawflies, Allantinae, southeastern Asia

Introduction

Cladiucha Konow is an unusual tenthredinid genus in that the antennae are multi-antennomered, serrate in the female and biramose in the male, more similar to Diprionidae and some Pergidae rather than the usual filiform, nine-antennomered antennae of Tenthredinidae. Benson (1938) placed the genus in the subfamily Allantinae because of similar wing venation and other structural characters (Benson 1938) but created a new tribe, Cladiuchini, for the genus. Taeger et al. (2010) continued with placement

in the Allantinae but did not recognize tribes. Wei (1997) recognized the Cladiuchini but placed it in a new subfamily, Megabelesesinae, along with *Megabeleses* Takeuchi, *Tripidobeleses* Wei, and *Conobeleses* Wei.

Four species of *Cladiucha* are known: *C. insolita* Konow, 1902, *C. manglietiae* Xiao, 1994, *C. magnoliae* Xiao, 1994, and *C. megatheca* Wei, 2010. Xiao (1994) and Wei (2010) each gave a key to species. The latter three species are known from China, and the host plants are members of the Magnoliaceae: *C. manglietiae* is on *Manglietia hainanensis* Dandy and *C. magnoliae* and *C. megatheca* are on *Magnolia officcinalis* Rehd. et Wils. (Xiao 1994, Wei 2010). *Cladiucha insolita* was described from a single female from Indo-China, „Tonkin (Mauson-Gebirge)" (Konow 1902), in northern Vietnam. To this date, this has been the only recorded specimen, and the male was not known. A long series of both sexes of this species was recently collected in Laos, and here I describe the male and note some intraspecific variation.

Materials and methods

Specimens are from the collection of the Oberösterreichische Landesmuseen, Linz, Austria (OLML). A few are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM).

The holotype of *Cladiucha insolita* (Fig. 1) is in the Senckenberg Deutsche Entomologische Institut, Müncheberg, Germany (SDEI), and was studied during my visit in 2006. It is broken, with the abdomen and parts of the legs, antennae, and wings glued onto a piece of cardboard beneath the specimen. Paratypes of *C. magnoliae* and *C. manglietiae* in the USNM were also examined.

Images were acquired through an EntoVision micro-imaging system. This system included a Leica M16 with a JVC KY-75U 3-CCD digital video camera or a GT-Vision Lw11057C-SCI digital camera attached that fed image data to a notebook or desktop computer. The program Cartograph 6.6.0 was then used to merge an image series into a single in-focus image.

Results

Cladiucha insolita Konow

Figs 1–10

Cladiucha insolita Konow, 1902: 389.—Xiao 1994: 20 (in key).—Wei 2010: 639 (in key).

Description. Female: Length 15–17 mm (holotype, 17 mm). Black, with light purple metallic lustre, with following white: labrum brown to white; apical 3 or 4 antennomeres ventrally; narrow stripe on upper surface of hind coxa; outer surface of apical half of fore femur; inner surfaces of basal two-thirds of mid and hind femora; fore and

Figure 1. Holotype of *Cladiucha insolita*. Lateral and dorsal views, labels attached, and broken parts glued onto cardboard beneath specimen (from Taeger and Kutzcher 2017).

mid tibiae except for black apex; basal third of hind tibia; fore and midtarsi; small lateral spot on first tergite; small transverse stripe at center of apical tergite; apical margin of apical tergite; cercus brown to white. Wings darkly uniformly infuscated; veins and stigma black. *Head*: With short, white hairs; rugose to punctate on frons, interantennal area, and clypeus, shiny with scattered punctures on vertex and gena. Antenna (Fig. 5) with 21–23 antennomeres (holotype 23), first and second about as long as broad, third about 2 × longer than broad, fourth to 19th or 20th antennomeres with apex broader than long and with short apically projecting rami; length of rami about equal to basal width of antennomere; apical 3 antennomeres without rami; apical 5 or 6 antennomeres with pale ventral sensory areas; length 1.8 × head width. Malar space very short, less than half diameter of front ocellus; lower interocular distance 1.3 × eye height; distances between eye and hind ocellus, between hind ocelli, and between hind ocellus and posterior margin of head as 1.0:0.8:1.3; postocellar area slightly convex, about 1.2 × broader than long. *Thorax*: Shiny with short, white hairs; almost impunctate, with very few small widely-spaced punctures on mesonotum and somewhat larger punctures on posterior half of mesoscutellum and posttergite. Forewing with vein 2A+3A basal to the anal cross vein complete, faint, or partially atrophied (partially atrophied in holotype). Hindwing without cell M, but partially present or present in about half of specimens examined (absent in holotype); anal cell with short petiole. Tarsal claw with long inner tooth, longer and stouter than outer tooth. Hind basitarsus about 5.0 × longer than broad. Pulvilli on hind tarsomeres 1–4, those on 3 and 4 larger than those

on 1 and 2. *Abdomen*: Shiny. Sheath (Fig. 8) uniformly slender in dorsal view; straight above and rounded at apex and below in lateral view. Cercus about 3.0 × longer than broad, half length of sawsheath. Lancet (Fig. 7) with about 30 serrulae; serrulae flat with 4 or 5 anterior subbasal teeth, serrulae indistinct at apex.

Male: Length 10–13 mm. Color as female except hind coxa entirely black; abdomen black; harpe whitish on apical third to half. Similar to female except for antenna and sexual characters. *Head*: Antenna (Fig. 6) with 27–29 antennomeres, bipectinate except apical antennomere; apical antennomere rounded, blunt at apex; rami long, those of central rami equal to length of 6 or 7 antennomeres; third antennomere with inner ramus about half length of outer ramus; length 1.5 × head width. *Abdomen*: Hypandrium rounded at apex. Genitalia in Figs 9, 10; harpe slightly expanded toward apex, apex broadly rounded; penis valve sharply bent, valviceps oval.

Specimens examined. LAOS: NE Laos, Hua Phan Pr., Mt. Phu Pane, ~1500 m, 20°12'N, 103°59'E, S-Jak1, 1-20.VI.2011 (3 ♀), same except 10-22.V.2011 (2 ♀); Prov. Hua Phan, Phou Pan, Umg. Ort Ban Saleui, 20°13'30"N, 103°59'26"E, 1350-1900 m MSL, 11.V.2011, leg. C. Holzschuh & locals (2 ♀), same except 21.V.2011 (1 ♀), 16.V.2011 (2 ♂), 18.IV.2012 (1 ♀, 1 ♂), 23.IV.2012 (1 ♀); Hua Phan Prov., Ban Salleui; Phou Pan. Mt., 20°13'30"N, 103°59'26"E, 1350-1900 m, 16.V.2011, leg. C. Holzschuh + locals (2 ♂), same except 18.IV.2010 (1 ♀, 1), 19.IV.2010 (1 ♂), 01.V.2010 (2 ♀, 1 ♂), 13.V.2010 (1 ♂), 08.V.2011 (3 ♀, 1 ♂), 21.V.2011 (1 ♀, 2 ♂), 13.V.2011 (1 ♀, 1 ♂), 07.V.2011 (1 ♀), 15.V.2011 (2 ♂), 19.V.2011 (1 ♂), 24.IV.2010 (1 ♂), 01.V.2011 (1 ♀), 05.V.2011 (1 ♂), 06.V.2011 (1 ♀), 29.IV.2012 (1 ♀). VIETNAM: Holotype female: "Tonkin (Mauson-Gebirge)" (Konow 1902), „Tonkin, Montes Mauson" on label (Fig. 1).

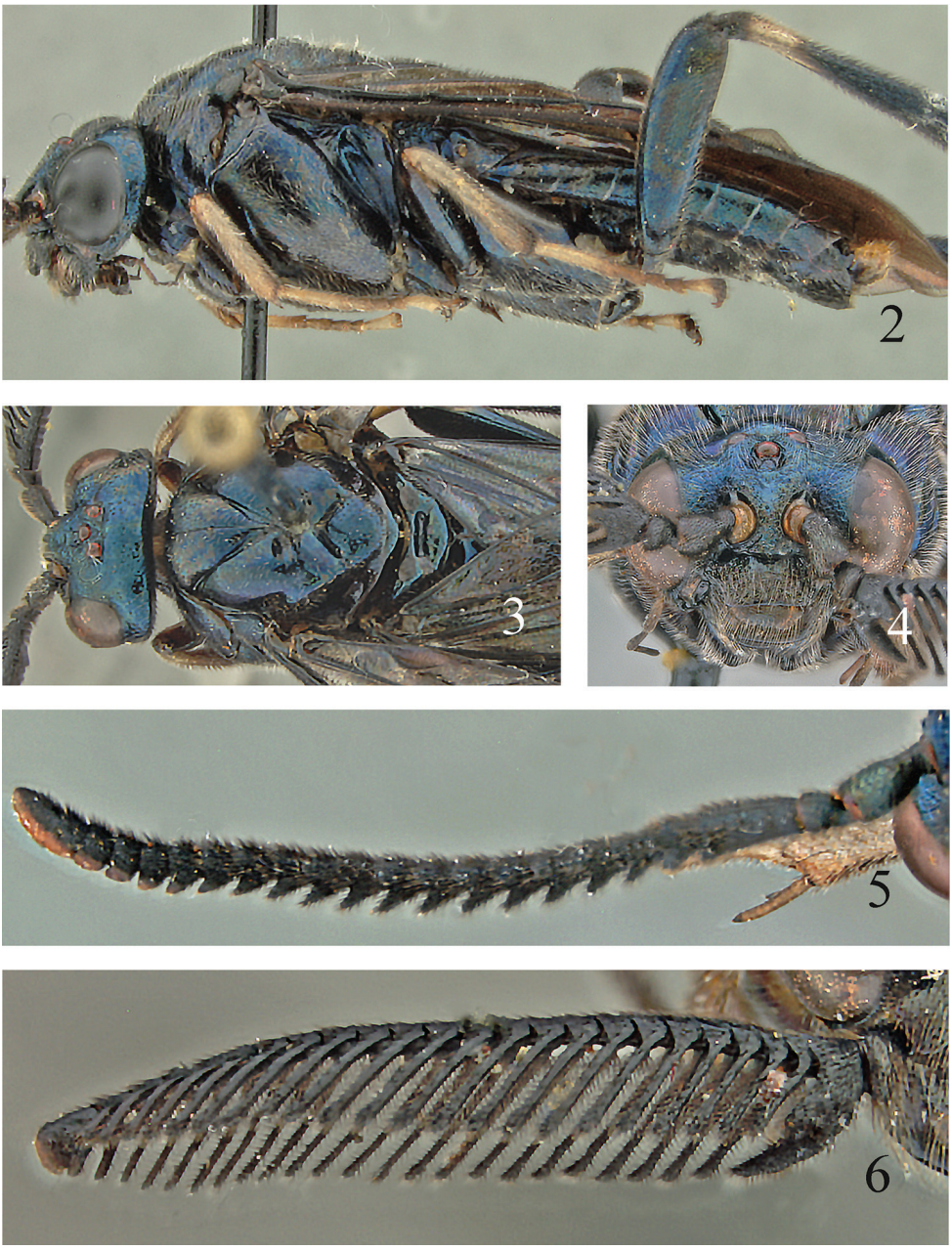
Distributon. Laos, Vietnam.

Variation. The length of specimens of each sex varies by 2 or 3 mm, the female from 15–17 mm and the male from 10–13 mm. The number of antennomeres in the female varies from 21–23 and in the male 27–29. In the forewing, the portion of vein 2A+3A basal to the anal crossvein is partially atrophied in most specimens (17), but faint to present in several (4). In the hind wing in specimens where visible, cell M is absent in most specimens (14), but present or partially present in others (11), or present in one wing and absent in the other (3).

Discussion. The holotype was collected in „April, Mai", consistent with the April and May collection dates of specimens examined.

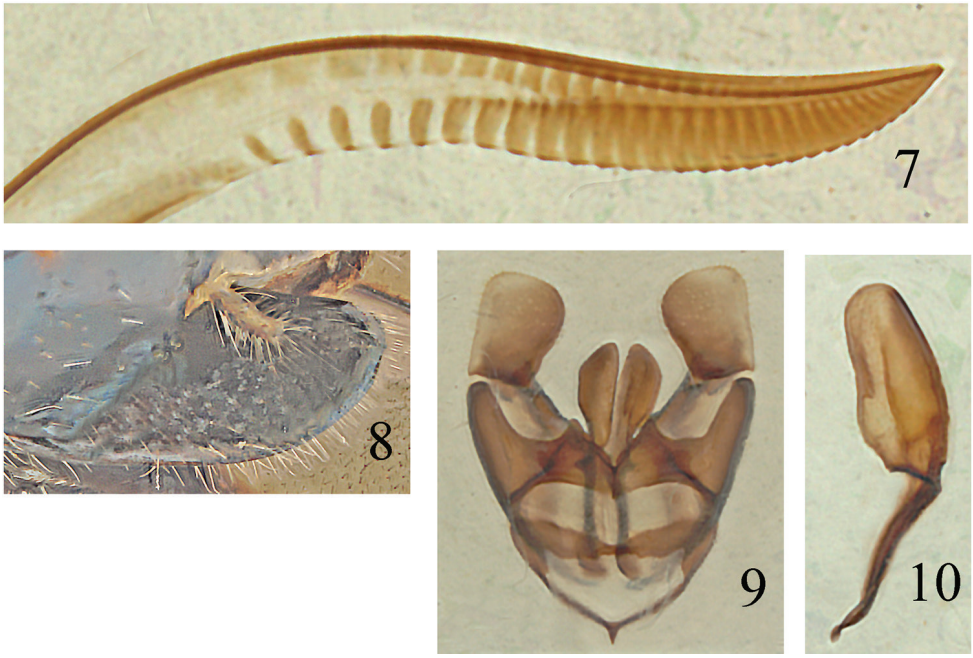
In existing keys to species of *Cladiucha* (Xiao 1994, Wei 2010), the black color, absence of cell M in the hind wing, length of the female, and number of antennomeres were used to separate *C. insolita*. Both sexes of *C. insolita* will key correctly, though use of these characters needs some discretion because of the variation noted. The black clypeus and pronotum seem to be the most stable characters to use.

Comparison with the figures in Xiao, the male appears closest to *C. manglietiae* (Xiao 1994, fig. 11). Both have the penis valve of similar shape and strongly curved. In *C. magnoliae*, the penis valve is straight (Wei 2010, fig. 15) and the harpe more oval and broadly rounded apically (Wei 2010, fig. 13) than the longer and more parallel-sided harpe of *C. insolita* (Fig. 9).



Figures 2–6. *Cladiucha insolita*. **2** Male, lateral **3** Male, dorsum of head and thorax **4** Male, head front **5** Female antenna **6** Male antenna.

The serrate serrulae of the female with about 6 subbasal teeth, is more similar to *C. magnoliae* (Wei 1997, fig. 15; Wei 2010, fig. 12) than the more widely separated serrulae with only about three subbasal teeth of *C. manglietiae* (Xiao 1994, fig. 7).



Figures 7–10. *Cladiucha insolita*. **7** Lancet **8** Sheath, lateral **9** Genital capsule ventral **10** Penis valve, lateral.

Wei (1997) described a new subgenus, *Acladiucha*, for *C. magnoliae*, separated from the typical subgenus by the closed cell M in the hindwing, presence of 19 or 20 antennomeres in the female and 23 in the male, linear malar space, and serrulae of the lancet widely separated. Taeger et al. (2010) did not recognize subgenera and synonymized *Acladiucha* under *Cladiucha*. Considering the variation noted in *C. insolita* and only the slightly broader malar space and shape of the serrulae, recognition of subgenera does not seem warranted.

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SHORT COMMUNICATION

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First record of *Megaphragma* (Hymenoptera, Trichogrammatidae) in Columbia, and third animal species known to have anucleate neurons

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Abstract

Megaphragma is recorded for the first time in Columbia where it is represented by *M. caribea* that emerged from leaves of *Terminalia catappa* infested by the thrips (*Heliothrips haemorrhoidalis* and *Selenothrips rubrocinctus*). *M. caribea* has anucleate neurons, the third species of *Megaphragma* shown to have this feature.

Keywords

Megaphragma caribea, anucleate neurons, Columbia

Introduction

Megaphragma includes some of the smallest insects. The genus contains 15 described species, distributed mainly in tropical and subtropical regions; only five of them have been recorded in the Western Hemisphere (Pinto 2006, Viggiani et al. 2009). A unique feature has been described in two of the species: the cell bodies and nuclei undergo lysis during a later pupal stage in over 95% of the neurons. As a result, the central nervous system of the adult is represented mostly by anucleate neurons (Polilov 2012). *M. caribea* Delvare, 1993, known only from the type series collected in Guadeloupe, is the smallest species of *Megaphragma* with a body length reported as 0.17 mm (Delvare 1993) and one of the smallest flying insects (Huber and Noyes 2013). Further information on the biology and distribution of *M. caribea* is reported here.

Methods

Adults of *M. caribea* (27 specimens) were collected as they emerged from leaves of *Terminalia catappa* Linneaus, 1767 colonized by the thrips *Heliothrips haemorrhoidalis* (Bouché, 1833) and *Selenothrips rubrocinctus* (Giard, 1901). The leaves were gathered in Cartagena, Columbia, on 22 January 2015 (coordinates 10.422, -75.553).

Specimens were fixed in FAE (formaldehyde—acetic acid—ethanol), preserved in 70% ethanol, critical point dried (Hitachi HCP-2), sputter coated with gold (Giko IB-3) and examined under a Jeol JSM-6380 scanning electron microscope (SEM) where body length was measured. For studying internal morphology, fixed material was dehydrated and embedded in Araldite M. The resulting blocks were cut into complete series of cross sections or longitudinal sections 0.5 μm thick using a Leica RM2255 microtome. The sections were stained with DAPI and studied under an Olympus BX43 microscope with a fluorescent module and a Tucsen TCC-6.1ICE camera.

Results and discussion

The record of *M. caribea* in Columbia considerably expands the known range of this species known previously only from 11 specimens collected from leaves of *Psidium guajava*

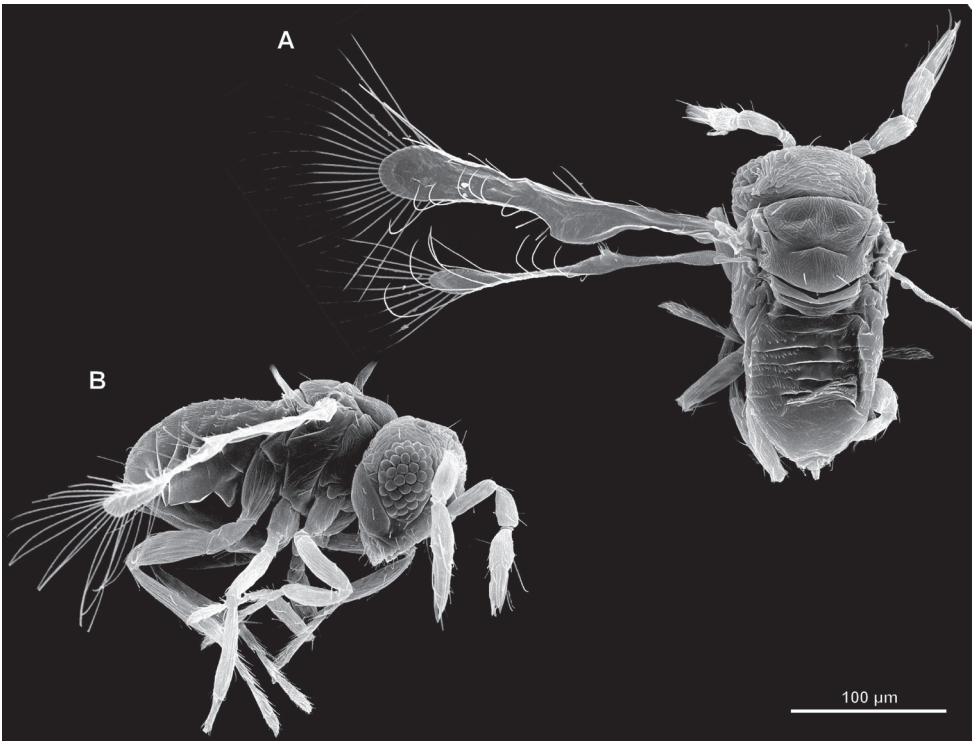

Figure 1. Habitus of *Megaphragma caribea*, SEM: **A** dorsal view **B** lateral view.

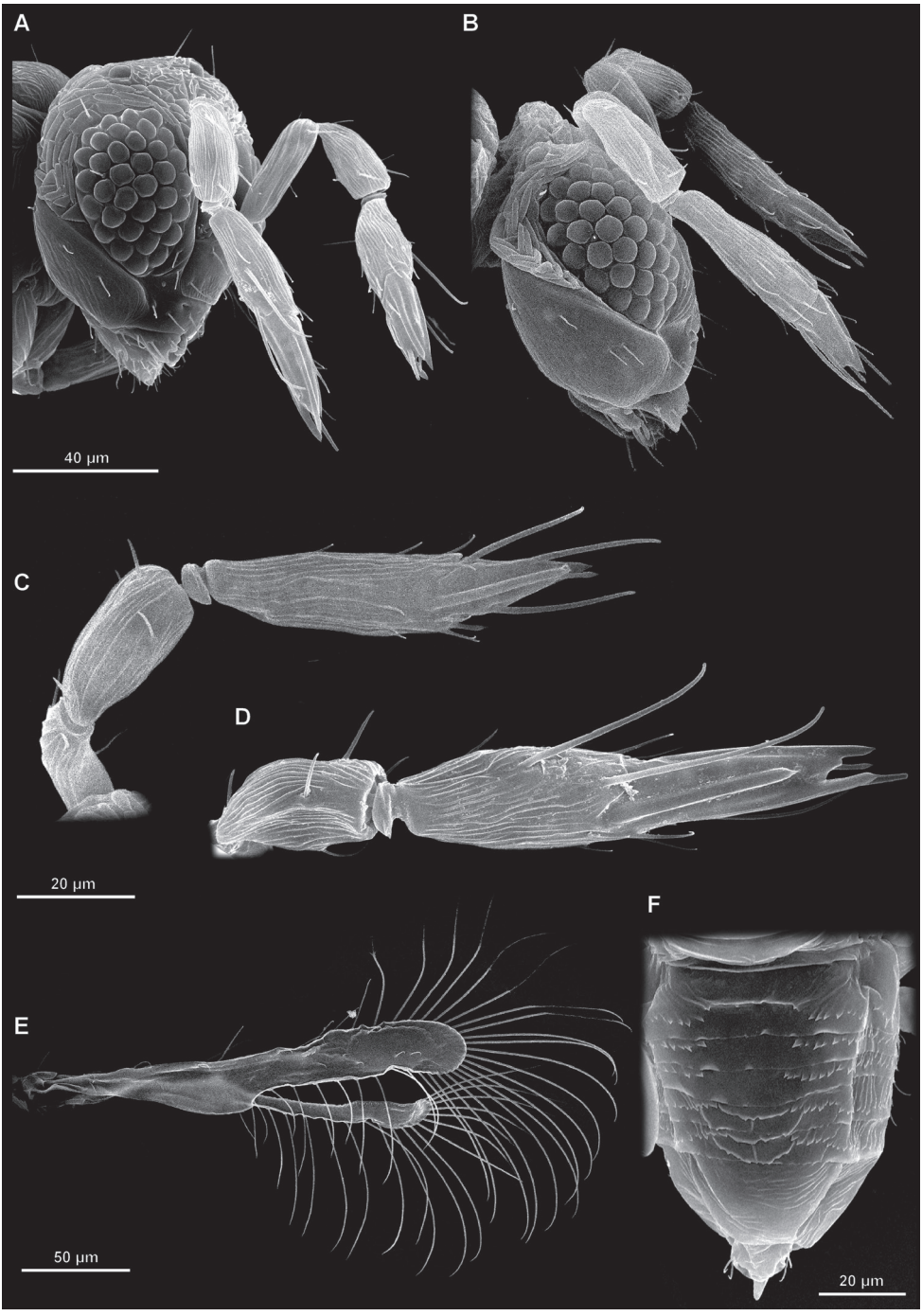

Figure 2. Diagnostic characters of *Megaphragma caribea*, SEM: **A** head of female **B** head of male **C** antennal club, male **D** antennal club, female **E** wings **F** terga of metasoma.

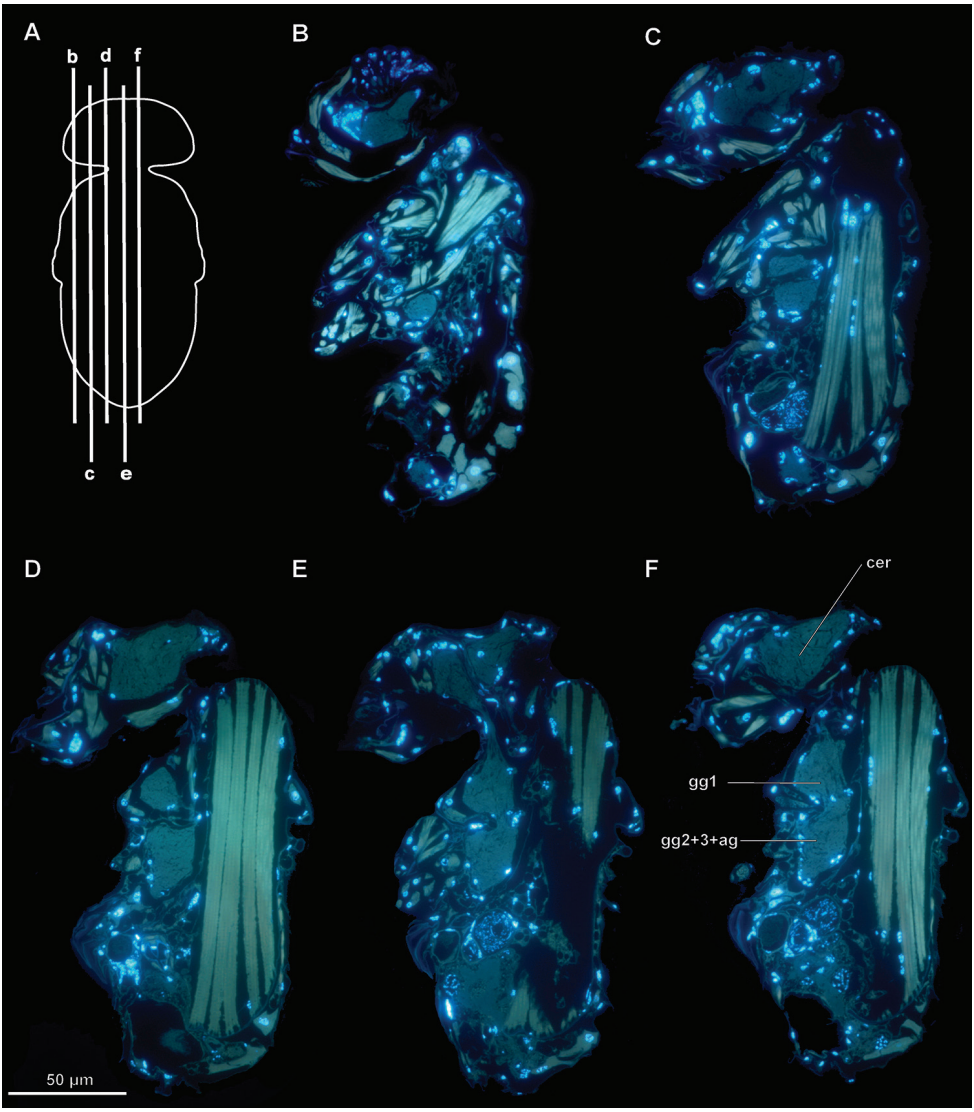

Figure 3. Internal morphology of *Megaphragma caribea*: **A** scheme of sections, dorsal view **B–F** sagittal sections, DAPI and autofluorescence; ag – abdominal ganglion, cer – cerebrum, gg1,2,3 – pro-, meso-, and metathoracic ganglion.

infested by *Selenothrips rubrocinctus* in Vieux Habitans (Guadeloupe) by J. Etienne on 17 November 1988 (Delvare 1993). The host plant and host insect(s) recorded here increase the range of plants and possibly host Thysanoptera in which *M. caribea* can develop.

M. caribea differs from the other species of the genus in its smaller body size, antenna without funicle, two-segmented antennal club, and wing chaetotaxy (Figs 1, 2). The body length of *M. caribea* measures was 181–224 µm (M = 199, n = 12), which is slightly greater than the measurement (170 µm) provided by Delvare (1993). Similar

imprecision of measurements was recently shown also for the smallest known free-living insect, the beetle (Polilov 2015).

Analysis of the anatomy of *M. caribea* has shown that the central nervous system of this species has only a few nuclei (Fig. 3) instead of the cortical layer typical of other insects. The central nervous system of *M. caribea* contains about 600 nuclei, 390 of them in the cerebrum. Organization of the neuropil is otherwise no different from that of other hymenopterans. Taking into account the relative volume and structure of the neuropil and the number of nuclei, which is similar to other species of *Megaphragma* examined earlier but fundamentally different from that of other minute insects. I suggest that *M. caribea* also displays the unique phenomenon of lysis of cell bodies and nuclei in neurons prior to the emergence of the adult from the pupa, as described earlier in *M. mymaripenne* (Polilov 2012) and *M. amalphitanum* (Polilov 2017). Thus, all species of *Megaphragma* whose anatomy has been studied have unique anucleate neurons. Interestingly, the nervous system of *M. caribea* contains almost twice as many nuclei as in the larger representatives of the genus.

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