

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 Tiphidae 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, Rholomutillinae, Ticoplineae (with the tribes Smicromyrmillini and Ticoplini), Sphaerophthalminae (with the tribes Sphaerophthalmini, Dasymutillini **trib. n.**, and Pseudomethocini with the subtribes Euspinoliina **subtrib. n.** and Pseudomethocina), Myrmillinae, Dasylabrinae (with the tribes Apteromutillini **trib. n.** and Dasylabrinini) 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 (Chrysoidea, 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 Tiphidae), Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Sphaerophthalminae (including the tribes Dasylabrini and Sphaerophthalmini with subtribes Sphaerophthalmina 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 Ticopline and Smicromyrmillini), Rhopalomutillinae, Ephutinae (with the tribes Ephutini and Odontomutillini), Dasylabrinae, Sphaerophthalminae (with the tribes Sphaerophthalmini and Pseudomethocini), Myrmillinae and Mutillinae (with the tribes Mutillini, Trogspidiini, Peterseniidiini 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 Sphaerophthalminae and sister to the remaining Sphaerophthalminae, but LN has Dasylabrinae as a subfamily sister to Ephutinae, and both sister to Sphaerophthalminae; 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 Smicromyrmmini) 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

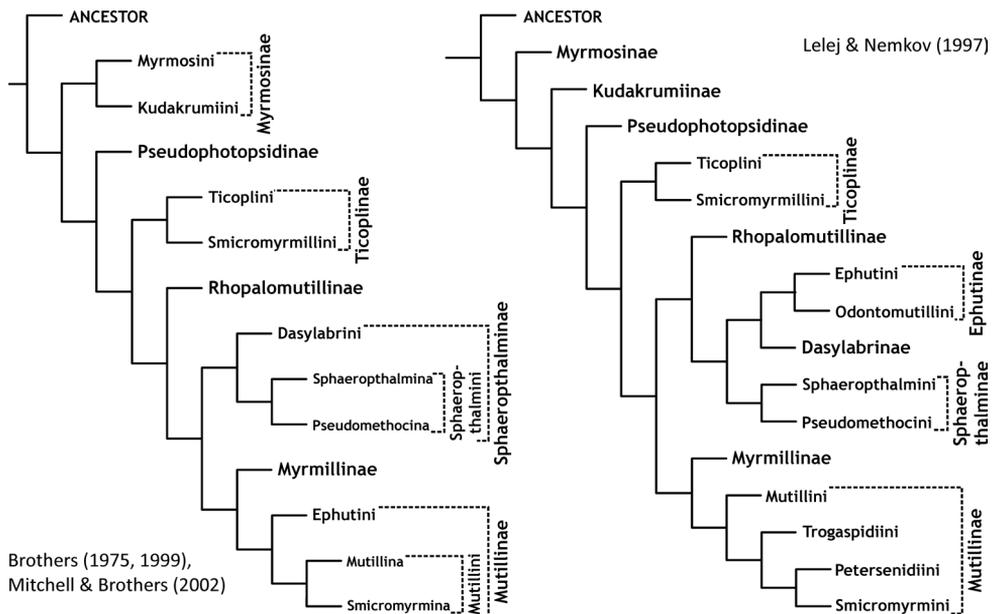


Figure 1. Competing current phylogenies and classifications of Mutillidae.

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 (Group present/Contradicted) 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* (Tiphidae) 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, Ticoptinae, 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 (Sphaerophthalmini/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 *Acanthomutilla*–*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 Sphaerophthalmini/ae group was better supported (although still at a very low level), Dasylabrini/ae remained

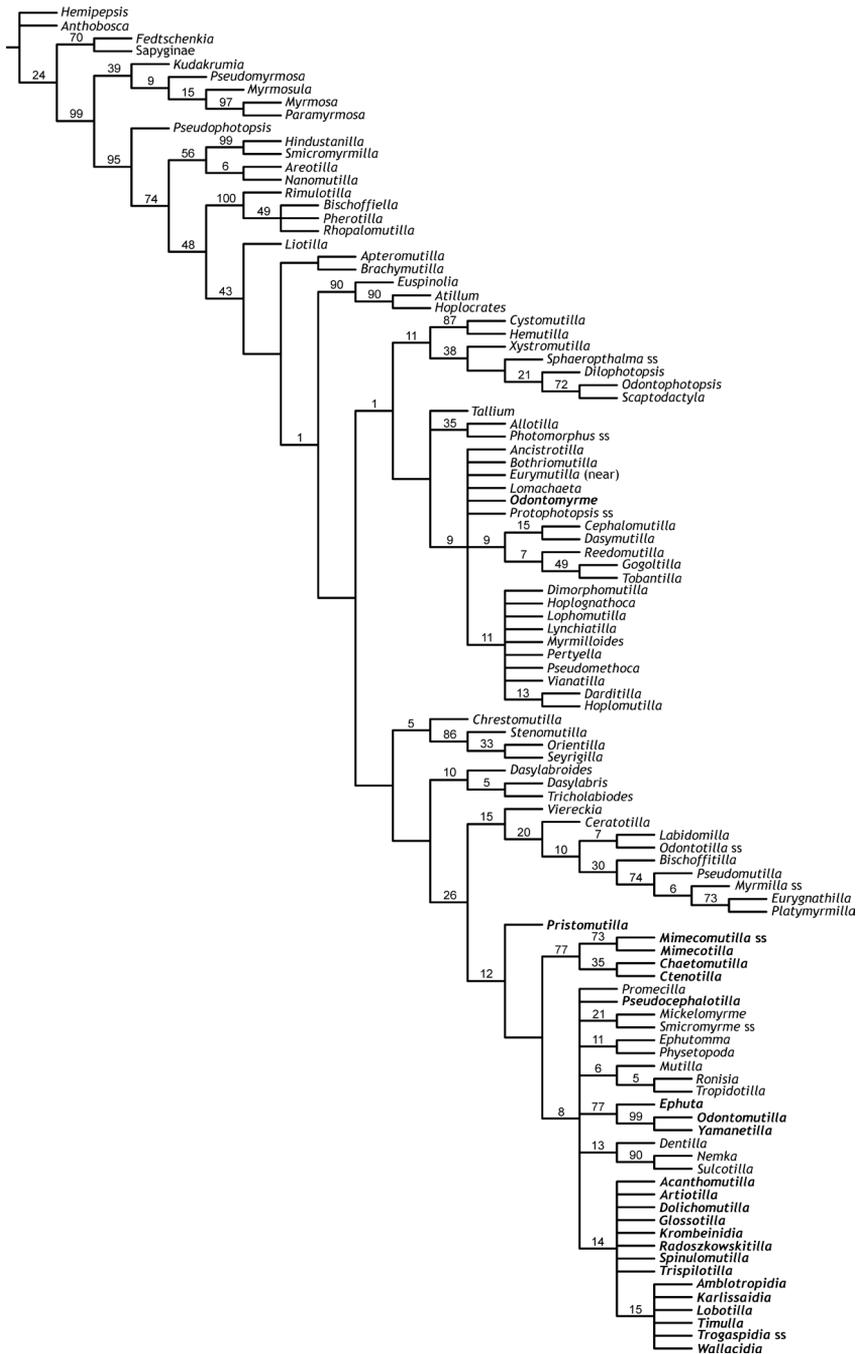


Figure 2. Strict consensus of 618 most-parsimonious trees (length = 2633, ci = 0.20, ri = 0.59), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters all non-additive and equally weighted. Group support (GC) values shown for all groups supported by resampling. Terminals in bold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

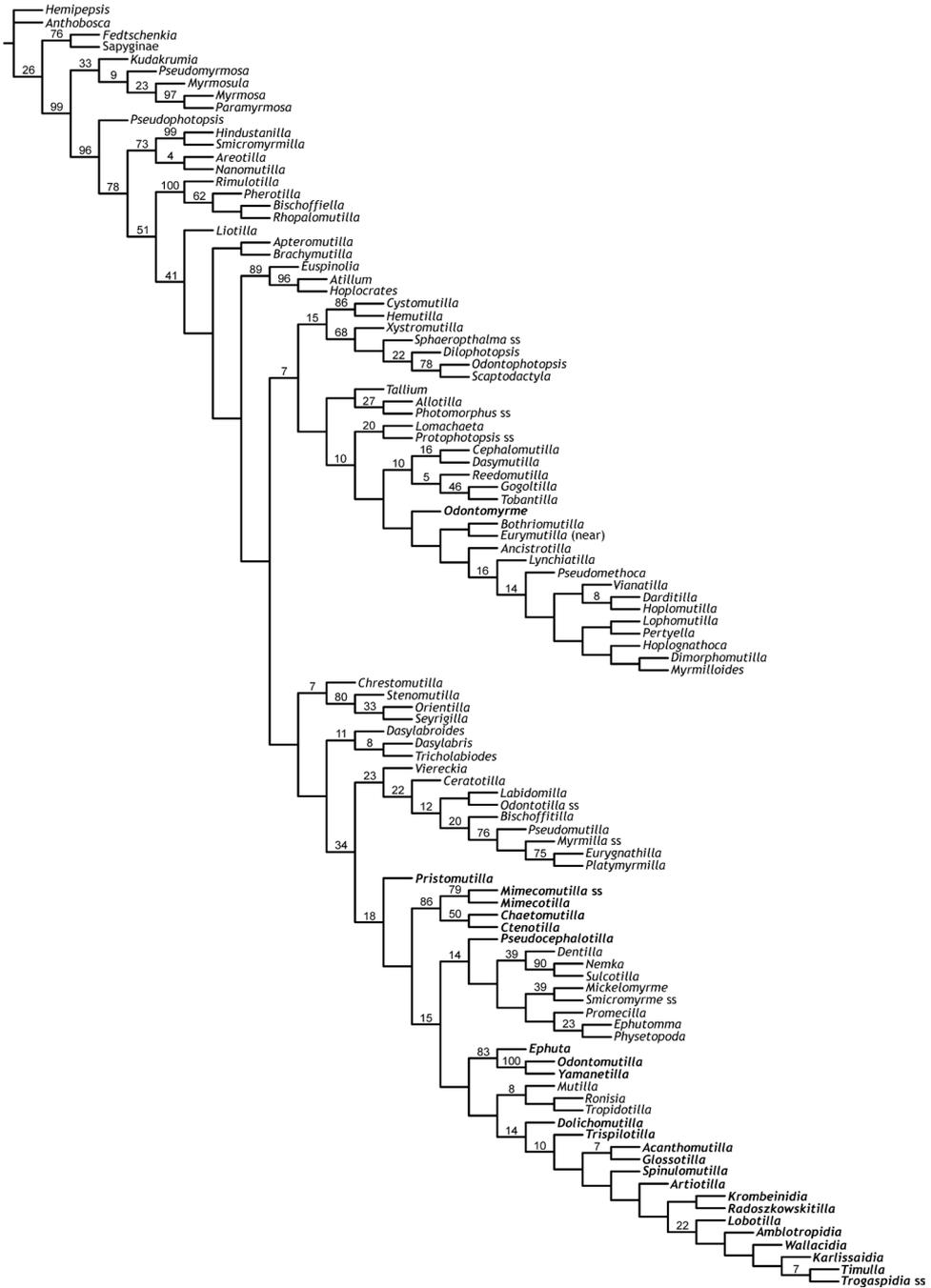


Figure 3. Single most-parsimonious tree (raw length = 2634, ci = 0.20, ri = 0.59), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters all non-additive and with implied weighting (N = 5, k = 60). Group support (GC) values shown for all groups supported by resampling. Terminals 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 Sphaerophthalmini/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

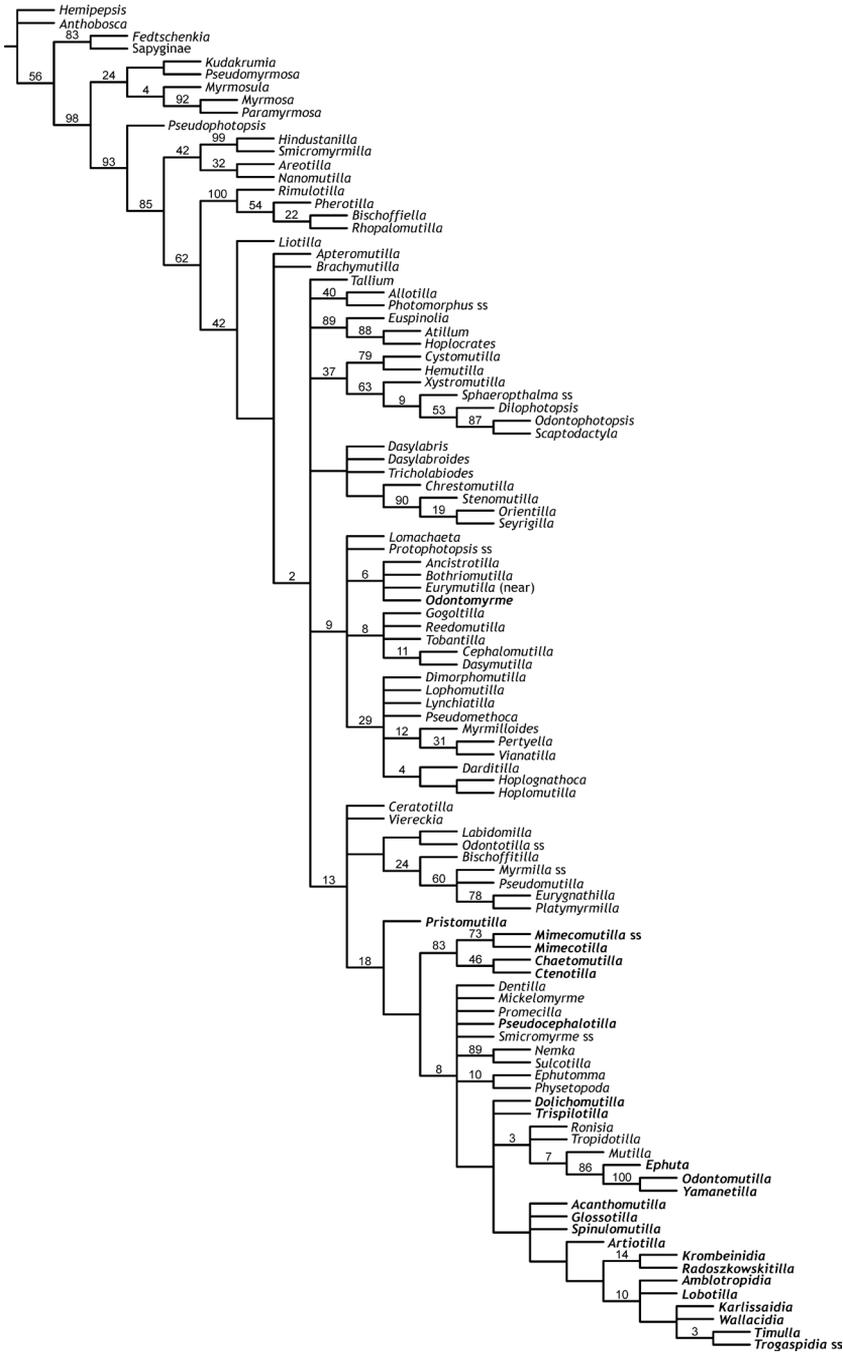


Figure 4. Strict consensus of 38 most-parsimonious trees (length = 2828, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters many additive and all equally weighted. Group support (GC) values shown for all groups supported by resampling. Terminals in bold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

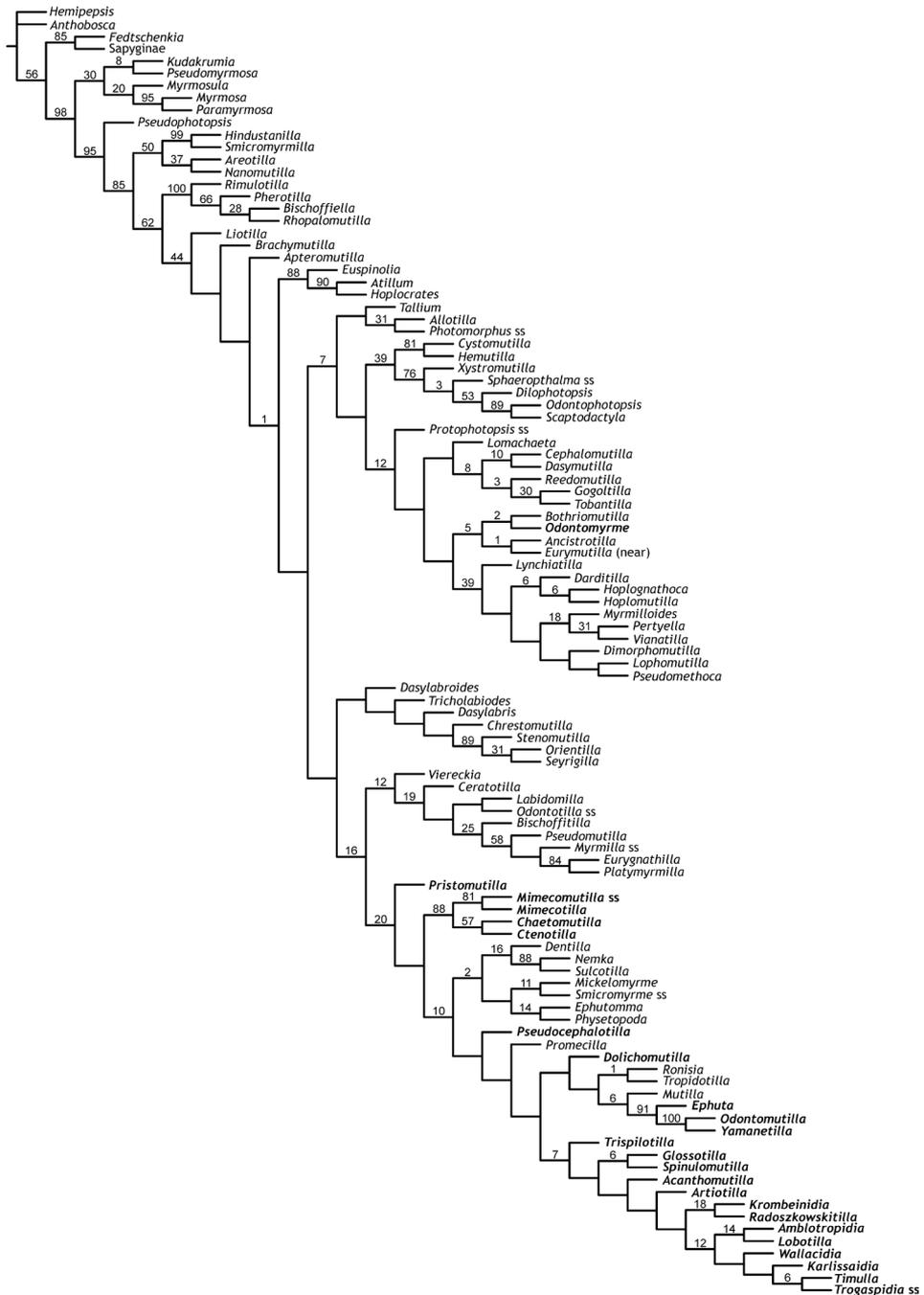


Figure 5. Single most-parsimonious tree (raw length = 2828, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, both sexes, 230 characters many additive and all with implied weighting (N = 5, k = 81). Group support (GC) values shown for all groups supported by resampling. Terminals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

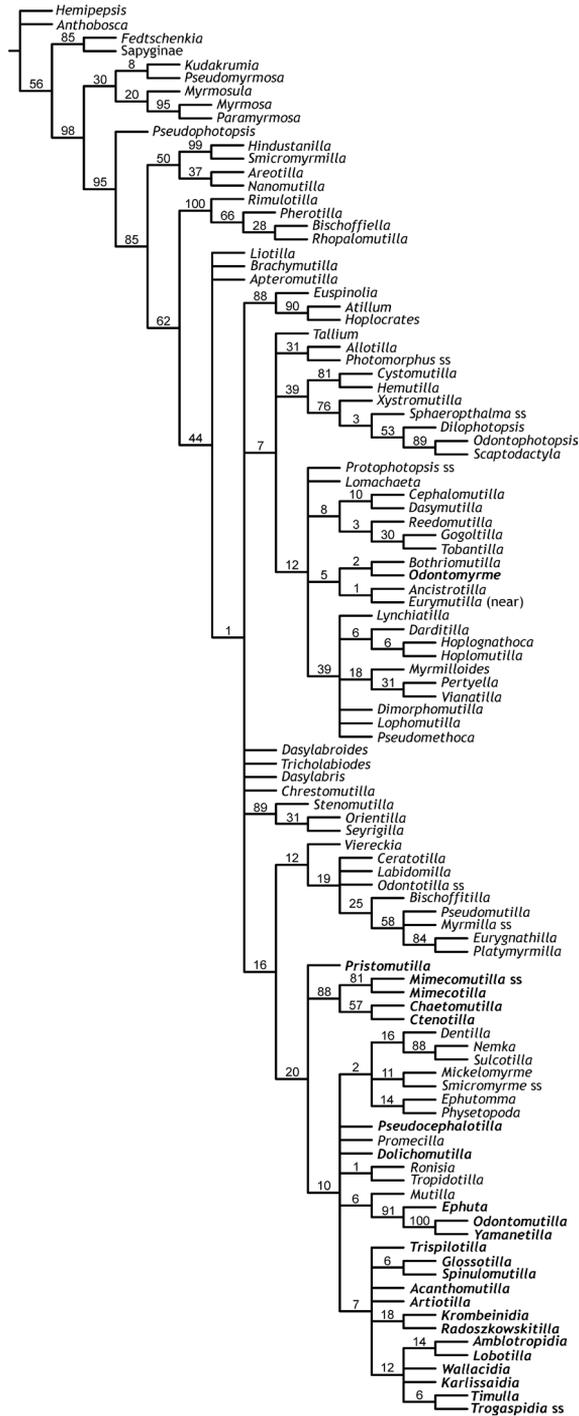
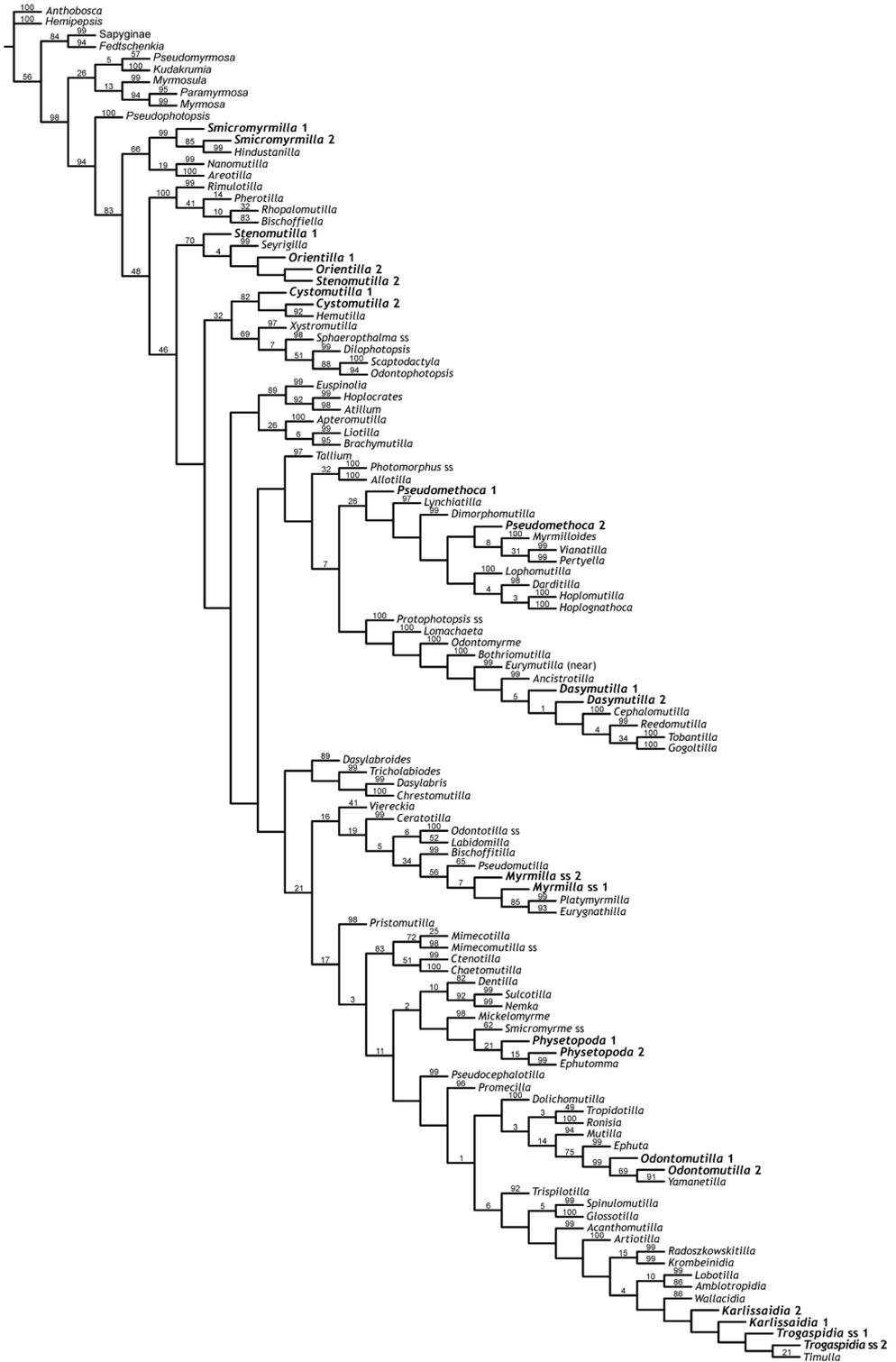


Figure 6. Most-parsimonious tree (see Fig. 5) with branches not supported by resampling (i.e., without positive GC values) collapsed. Terminals in bold are those whose placements differ by more than mere taxonomic level in the classifications of DB and LN (see Appendix 1).



= 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 Dasyabrini/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 Sphaerophthalmini/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

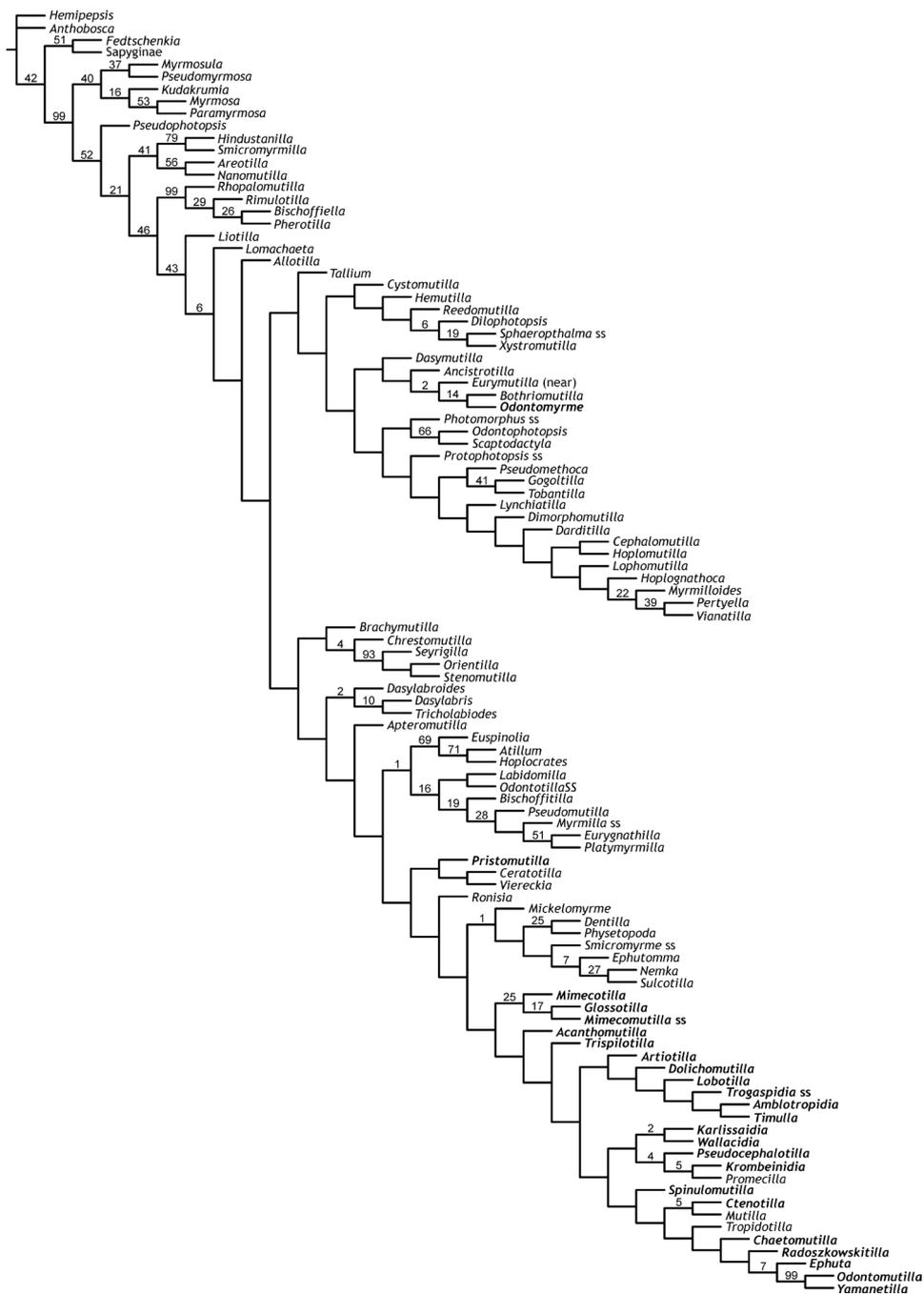


Figure 9. Single most-parsimonious tree (raw length = 1134, ci = 0.19, ri = 0.61), of 101 sub/genera of Mutillidae and 4 outgroups, females only, 97 characters many additive and all with implied weighting (N = 5, k = 81). Group support (GC) values shown for all groups supported by resampling. Terminal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

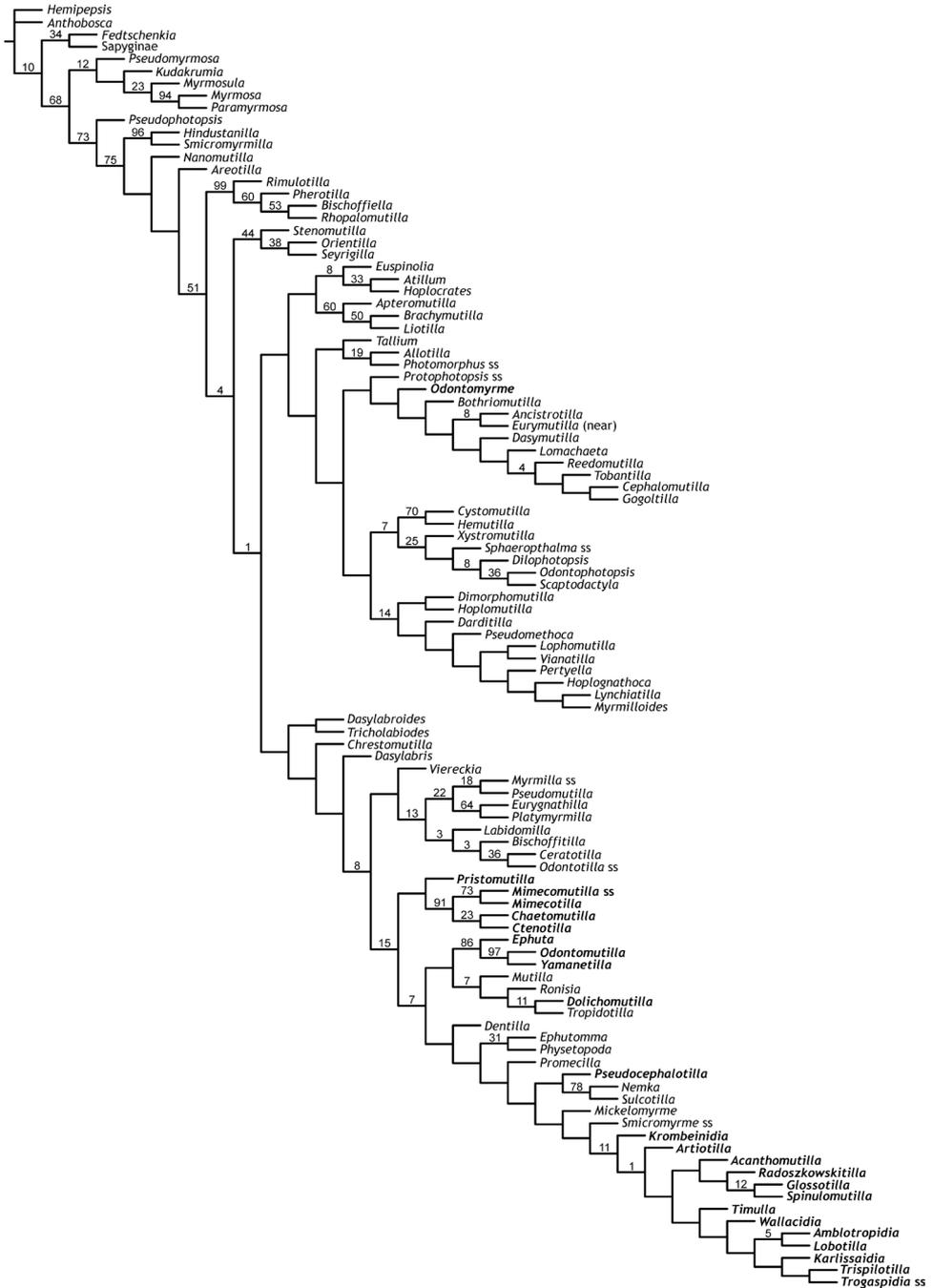


Figure 10. Single most-parsimonious tree (raw length = 1622, ci = 0.20, ri = 0.63), of 101 sub/genera of Mutillidae and 4 outgroups, males only, 140 characters many additive and all with implied weighting (N = 5, k = 71). Group support (GC) values shown for all groups supported by resampling. Terminal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

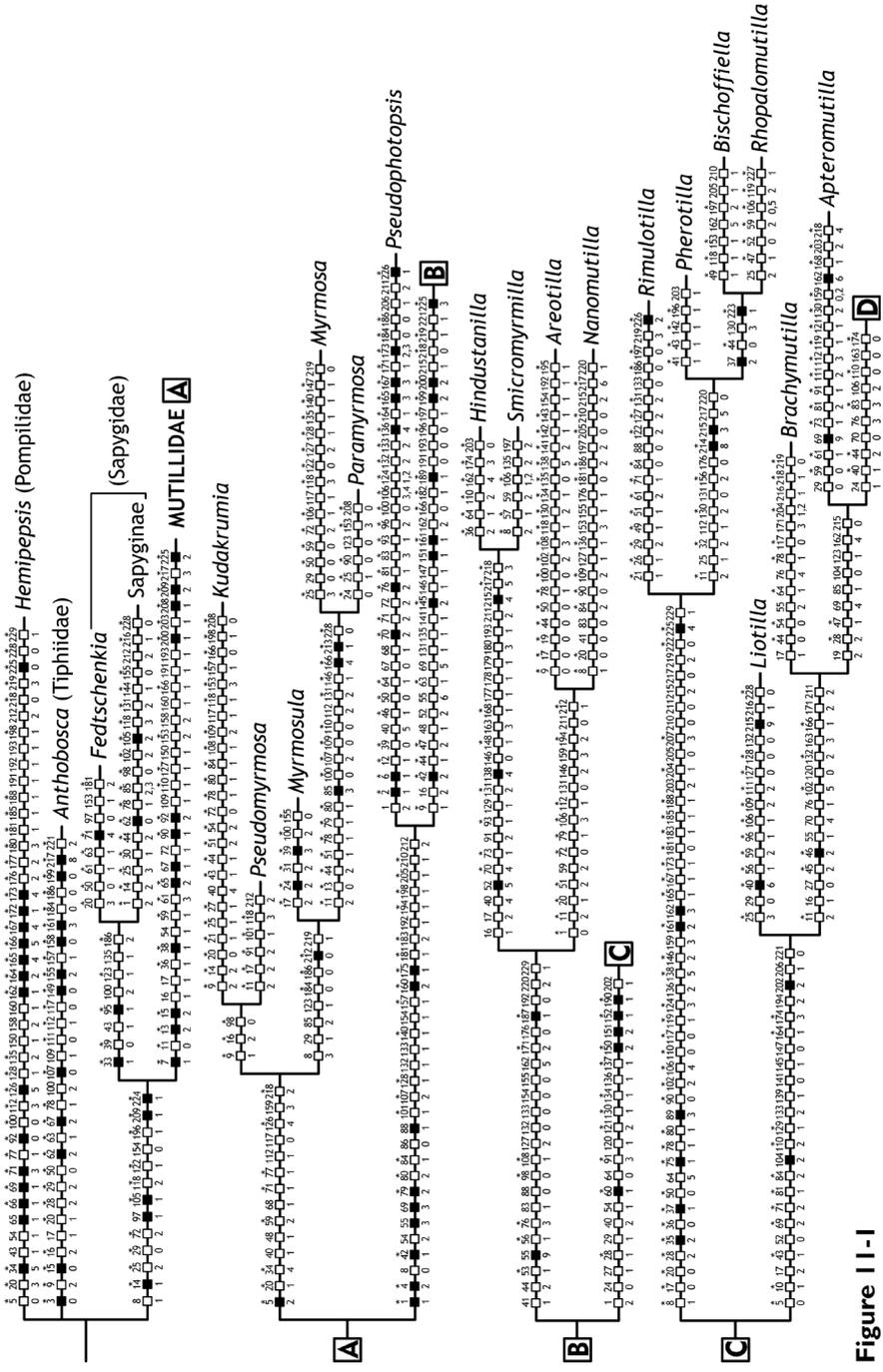


Figure 11-1

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]

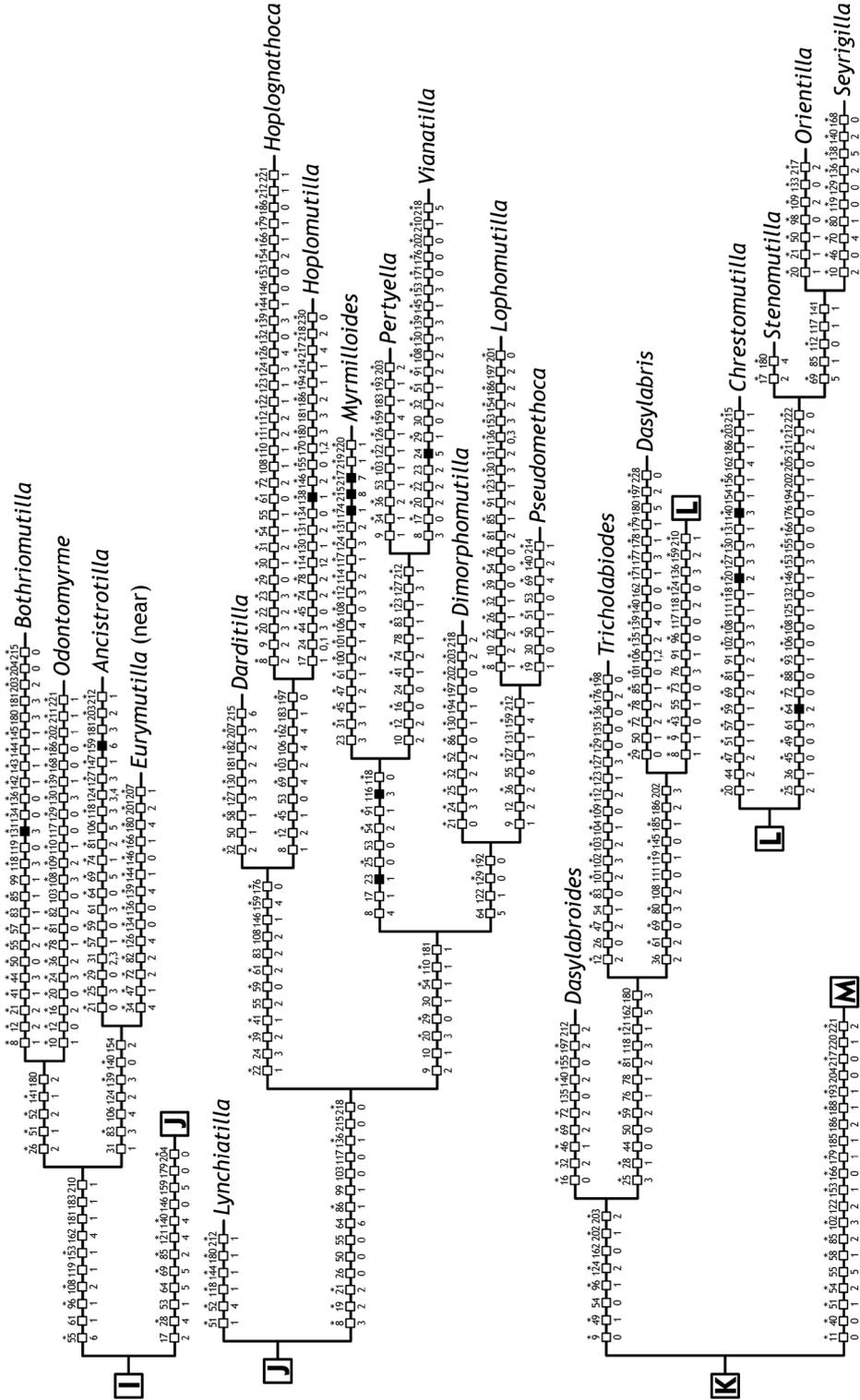


Figure 11-3

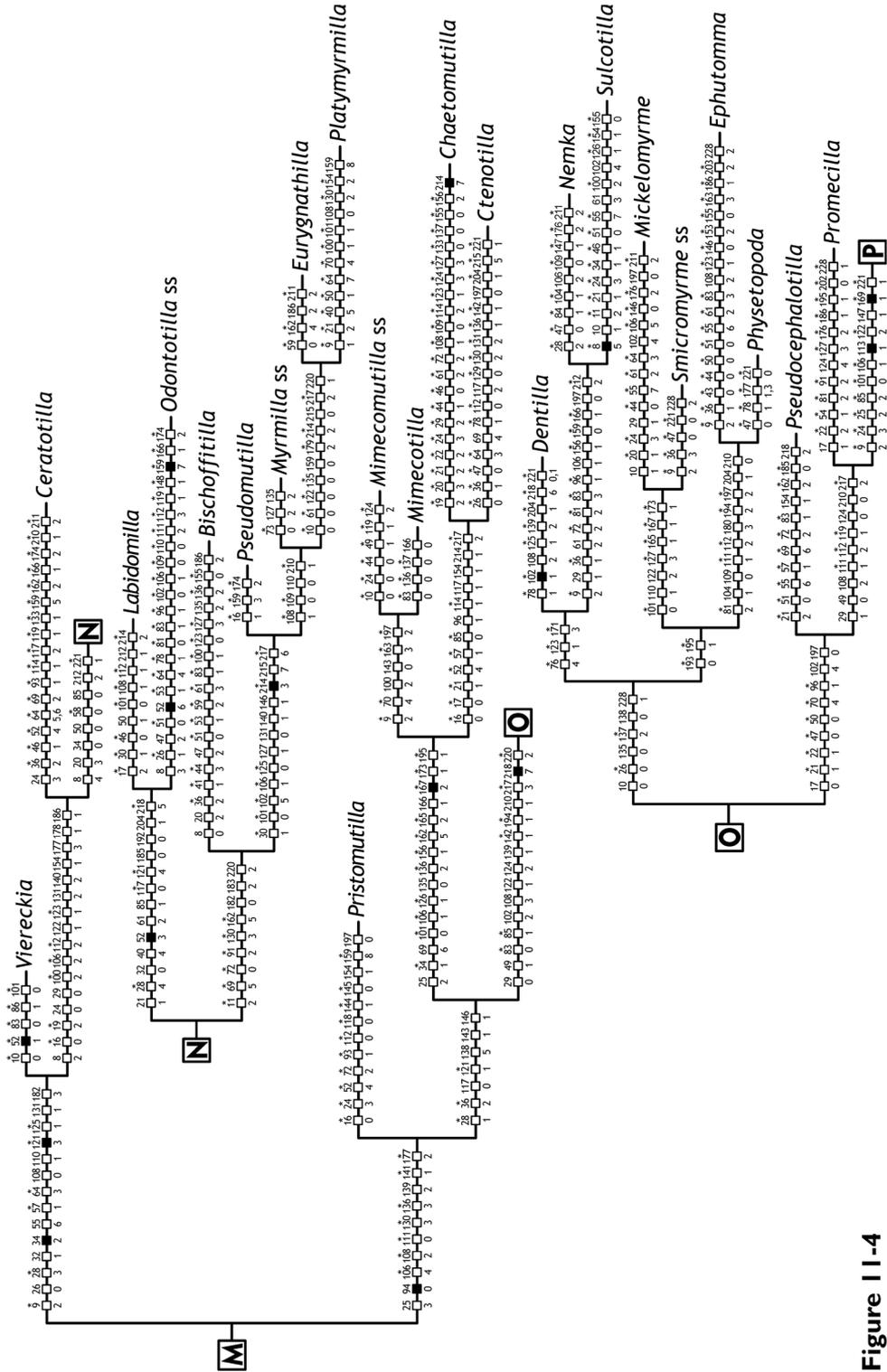


Figure 11-4

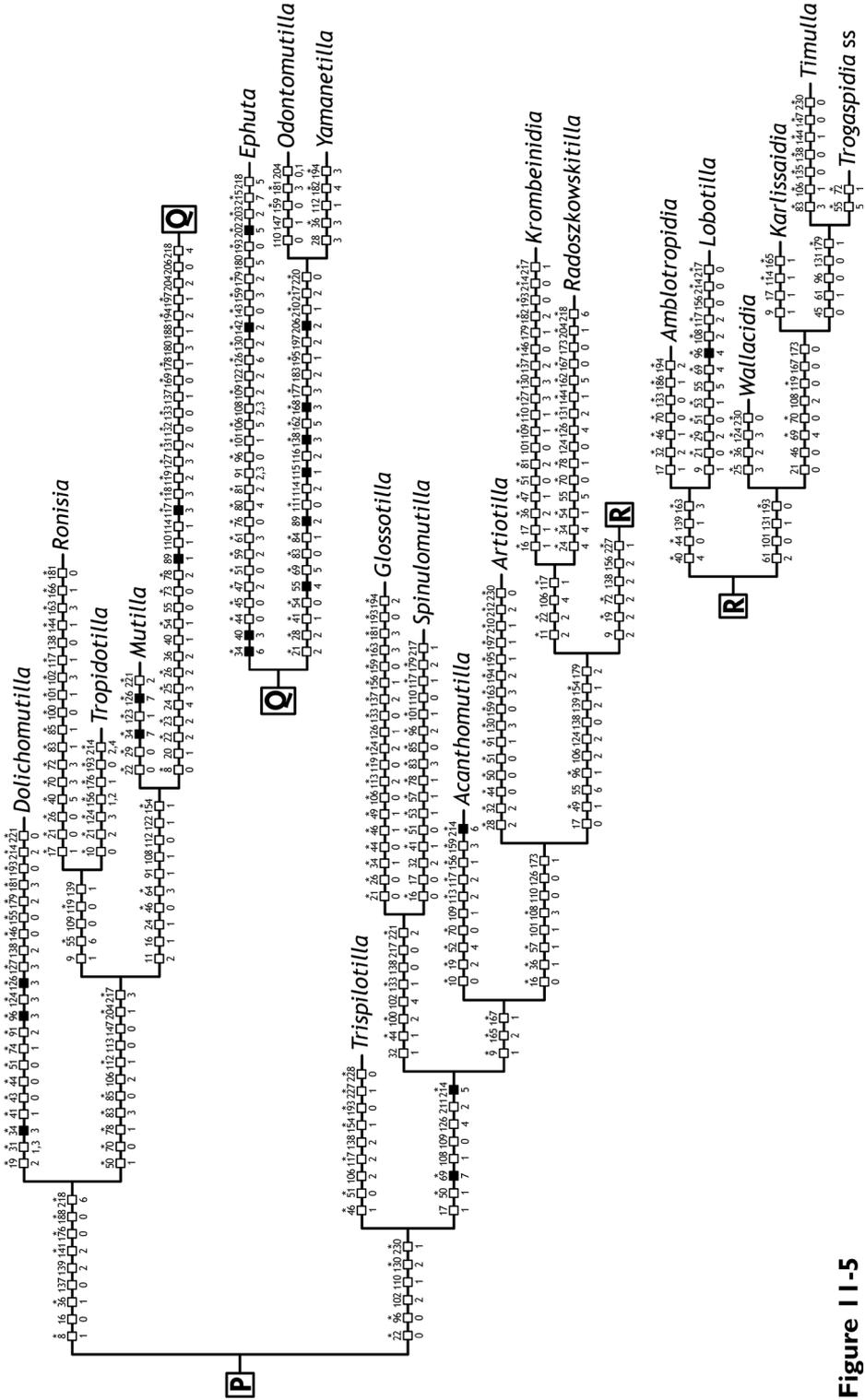


Figure 11-5

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 (Sphaerophthalminae 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 Sphaerophthalminae 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 Sphaerophthalminae (*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 Sphaerophthalminae 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 Sphaerophthalmina/i form

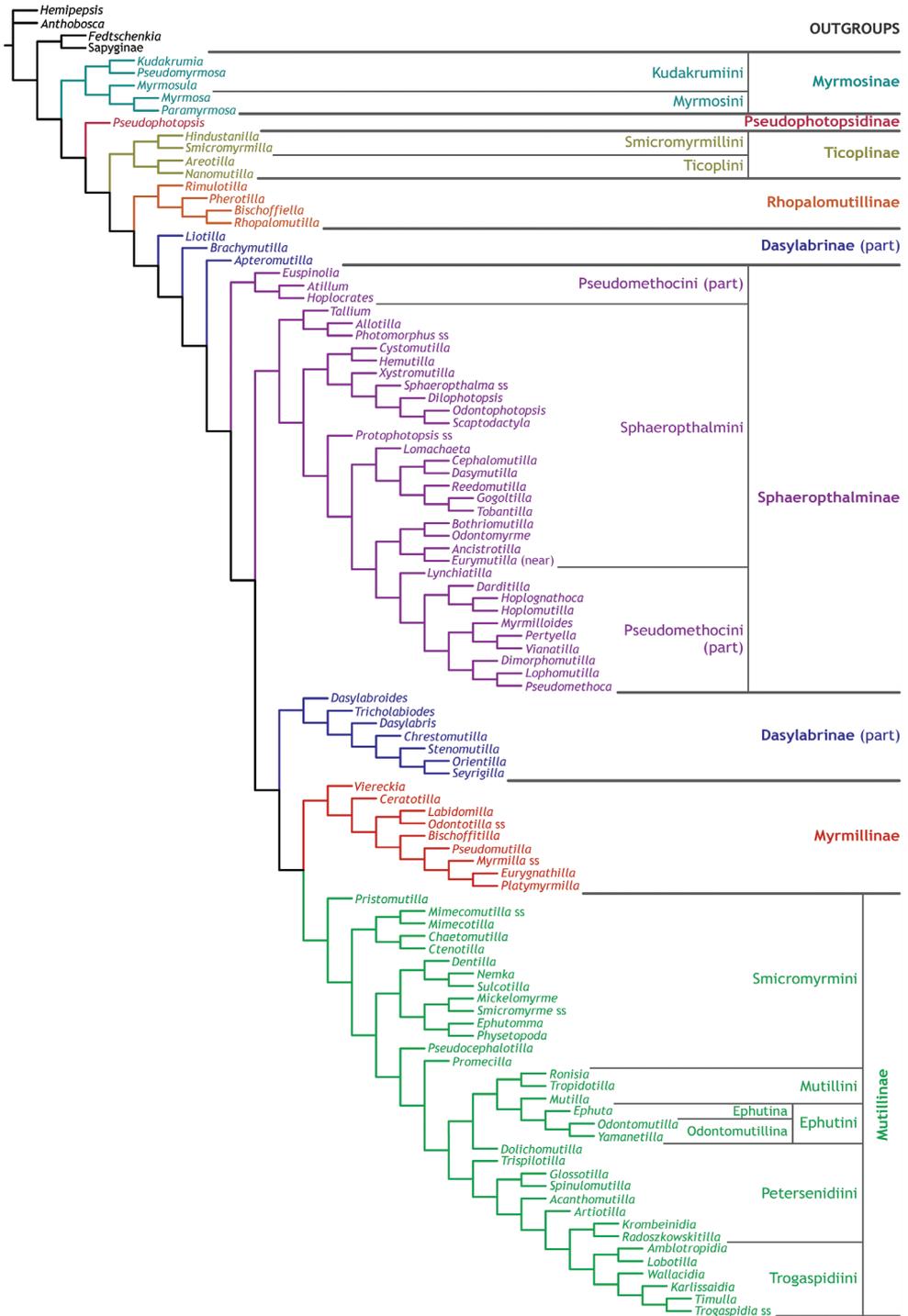


Figure 12. Preferred most-parsimonious tree (see Fig. 5) with potential groups incorporating ideas from both previous classifications indicated.

a paraphyletic group of five sequentially arising lineages (*Tallium*–*Photomorphus* s.s., *Cystomutilla*–*Scaptodactyla*, *Protophopsis* 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 sphaerophthalmines; 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 Sphaerophthalminae 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 Sphaerophthalminae–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,

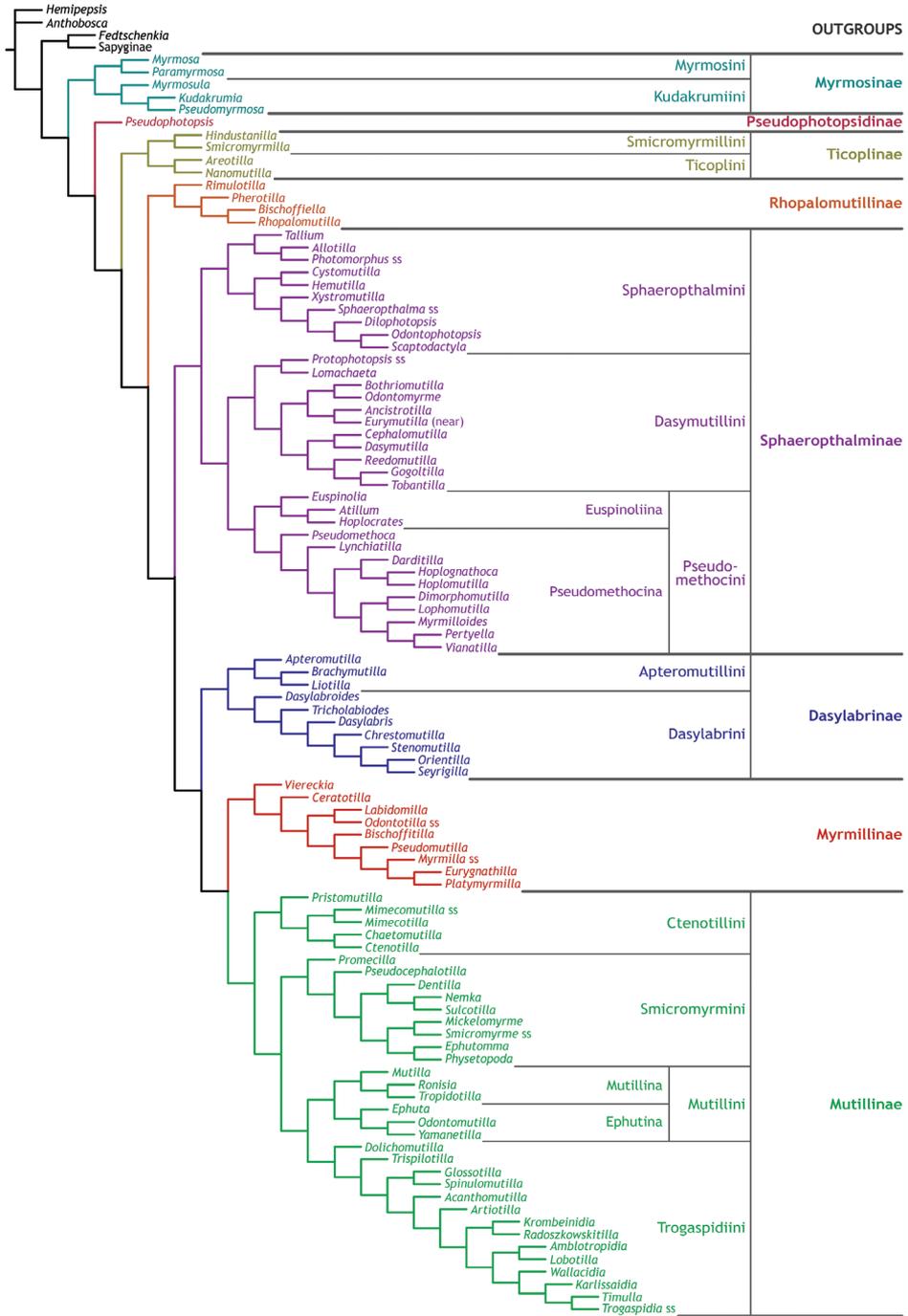


Figure 14. Proposed higher classification of Mutillidae as reflected by the rearranged tree (Fig. 13) of length about 1% greater than the previously preferred tree (Fig. 5) (lengths = 2858 vs 2828 for additive characters, 2671 vs 2646 for non-additive characters). (See Appendix 4 for classification including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

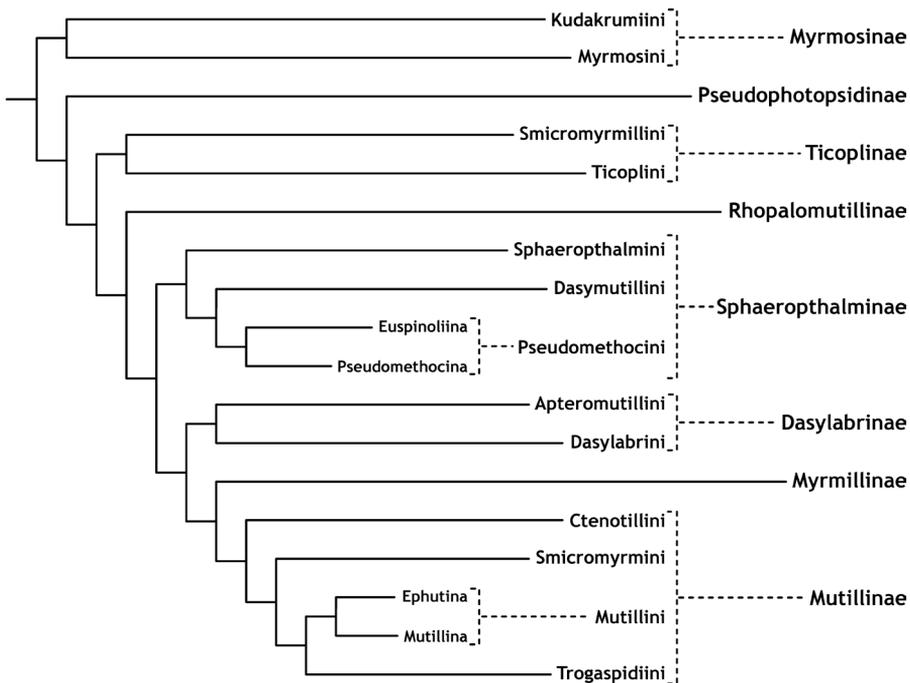


Figure 16. Final proposed higher classification of Mutillidae, as related to the rearranged tree (cf. Fig. 1).

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 $>0.5 <0.75 \times$ 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 Palearctic, 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 Ticopliinae); 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 Palearctic, 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 Ticoptinae); 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).

Ticoptinae 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 Palearctic 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 *Odonatomyrme*); 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 Sphaerophthalminae); 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.

Sphaerophthalminae 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 Sphaerophthalminae and the remaining Mutillidae, but this with negligible or no resampling support (Figs 2, 3, 5, 8). The remaining Sphaerophthalminae 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 Sphaerophthalminae 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 Sphaerophthalminae) 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 Sphaerophthalminae 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 sphaerophthalmines *s.s.* and pseudomethocines was not entirely supported, the sphaerophthalmines 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 Sphaerophthalminae, 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.

Sphaerophthalmini Schuster, 1949 (1903): This group comprises those sphaerophthalmines 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 subgenera; females are known for 71% and males for 96% of those taxa.

The remaining Sphaerophthalminae (distal to Sphaerophthalmini, 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 sub-circular 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 Sphaerophthalmini and *Tricholabiodes*, and only moderately convex in *Euspinolia* and *Myrmilloides*); 145.0, propodeal disc evenly sculptured in winged males (but also in a few Sphaerophthalmini, some Dasytabrinae, 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 sphaerophthalmines 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 sphaerophthalmines *s.s.* and scattered terminals elsewhere, and present in *Gogolilla* 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 subgenera; 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 Sphaerophthalminae also only in *Cephalomutilla*, *Gogoltilla*, some *Dasymutilla*, some *Bothriomutilla* females, and *Lophomutilla* males); 99.0, head with simple pubescence in males (within Sphaerophthalminae also only in *Cephalomutilla*); 219.1 and 220.1, gonostylus (paramere) short, tapered and apically straight (within Sphaerophthalminae 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 Sphaerophthalmini *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 Sphaerophthalminae, 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 sphaerophthalmines 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 sphaerophthalmines, 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 sphaerophthalmines 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 *Protophopsis* 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 ticoplinae, some myrmosines and sphaerophthalmines, *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 $>0.5 \times$ length of tergum II and apically constricted in males (also in most rhopalomutillines and sphaerophthalmines *s.s.* and a few scattered terminals, tergum I shorter in *Dasylabris* and *Chrestomutilla*); 220.0, gonostylus (paramere) apically upcurved (also in most sphaerophthalmines 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 ticoplinae, 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 *Ceratilla* 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 sphaerophthalmines 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 subgenera; 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 sphaerophthalmines, and obvious in most ctenomutillines); 141.1, tegula elongated to about trans-scutal articulation (also in ticoplinae, rhopalomutillines, some dasymutillines and dasylabrine, 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 subgenera; 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 $<0.6 \times$ 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 Palearctic 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 sphaerophthalmines, 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*, *Bothriomotilla* 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*, *Bothriomotilla*, *Chaetomotilla* and *Ctenotilla*, and straight in *Ephuta*); 220.2, gonostylus (paramere) apically downcurved (also in most ticoiplines, a few myrmillines and some *Chaetomotilla*, and weakly upcurved in *Odontomotilla* 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 polymorphism (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 subgenera; 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 Peterseniidiini) were generally serially paraphyletic, however, not forming any defined group themselves. Consequently, and because some “peterseniidiines” show states approaching those of the “trogaspidiines” and are thus difficult to distinguish from them, we prefer not to recognize LN’s “peterseniidi-

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 dorso-lateral 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 *Radoszkowskiius* 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, Palearctic, 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 I

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

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

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

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

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
Odontomutilla Ashmead, 1899: <i>O. ?aegrota</i> (Cameron, 1898) ♀, Zimbabwe; <i>O. ?chione</i> (Péringuey, 1898) ♀, Lesotho, South Africa; <i>O. ?chionella</i> Bischoff, 1920 ♂, Lesotho; <i>O. ?cleopatra</i> (Péringuey, 1899) ♂, South Africa; <i>O. ?fiacta</i> (Saussure, 1891) ♀, Kenya; <i>O. ?inanis</i> Mickel, 1935 ♀, Papua New Guinea; <i>O. pulchrina</i> (Smith, 1855) ♀, ♂, India; <i>O. sp. nr. calida</i> André, 1908 ♀, Zambia; <i>O. sp. nr. tamensis</i> (Cameron, 1906) ♀, Australia; <i>O. tsiphonella</i> Bischoff, 1920 ♂, South Africa; <i>O. ?tomyrus</i> (Péringuey, 1899) ♀, South Africa	8	4	11%	Mutillina	Odontomutillini
Odontomyrme Lelej, 1983: <i>O. spp.</i> ♀♀♀♀♀♀, ♂♂♂♂, Australia, Papua New Guinea	5	3	2%	Sphaeropthalmina	Odontomyrmini
Odontophotopsis Viereck, 1903: <i>O. inconspicua</i> (Blake, 1886) ♀, ♂, USA; <i>O. villosa</i> Mickel in Mickel & Clausen, 1983 ♀, ♂, USA	2	2	9%	Sphaeropthalmina	Sphaerophthalmini
Odontotilla Bischoff, 1920: * <i>O. bidentata</i> (André, 1905) ♀, ♂, South Africa	1	1	0%	Myrmilinae	Myrmilinae
Orientilla Lelej, 1979: <i>O. aureorubra</i> (Sichel et Radoszkowski, 1870) ♀, ♂, Sri Lanka; <i>O. desponsa</i> (Smith, 1855) ♀, ♂, Vietnam; <i>O. kallata</i> (Nurse, 1902) ♀, ♂, Sri Lanka; <i>O. krombeini</i> Lelej, 1998 ♀, ♂, Vietnam; <i>O. sp.</i> ♂, Vietnam; <i>O. tausignata</i> (Chen, 1957) ♀, China	5	5	8%	Dasylabrini	Dasylabrini
Paramyrmosa de Saussure, 1880: <i>P. brunnipes</i> (Lepelletier, 1845) ♀, ♂, Austria, Serbia; <i>P. pulla</i> (Nylander, 1847) ♀, Russia	2	1	1%	Myrmosini	Myrmosinae
Pertyella Mickel, 1952: <i>P. ?beata</i> (Cameron, 1894) ♀, ♂, Panama; <i>P. holmbergii</i> (E.Lynch Arribáizaga, 1878) ♀, Argentina; <i>P. ?salutatatrix</i> (Smith, 1879) ♀, ♂, Costa Rica; <i>P. sp. nr. lenti</i> Casal, 1964 ♀, Argentina; <i>P. sp.</i> ♂, Peru	4	3	2%	Pseudomethocina	Pseudomethocini
Pherotilla Brothers, 2015: * <i>P. mlanjeana</i> (Bischoff, 1920) ♀, ♂, Malawi; <i>P. oceanica</i> (Mickel, 1935) ♀, ♂, Brunei; <i>P. rufitincta</i> (Hammer, 1957) ♀, ♂, Kenya	3	3	10%	Rhopalomutillinae	Rhopalomutillinae
Photomorphus Viereck, 1903: <i>P. (P.) alogus</i> Viereck, 1903 ♀, ♂, USA; <i>P. (P.) myrmicooides</i> (Cockerell, 1895) ♀, USA; <i>P. (P.) quintilis</i> (Viereck, 1906) ♂, USA	2	2	0%	Sphaeropthalmina	Sphaerophthalmini
Physetopoda Schuster, 1949: <i>P. halensis</i> (Fabricius, 1787) ♀, ♂, Kazakhstan; <i>P. pierrei</i> (Suárez, 1958) ♂, Mauritania, Chad; <i>P. punctata</i> (Latreille, 1792) ♀, ♂, Spain; <i>P. portschinskii</i> (Radoszkowski, 1888) ♂, Kazakhstan; <i>P. scutellaris</i> (Latreille, 1792) ♂, Kazakhstan; <i>P. daghestanica</i> (Radoszkowski, 1885) ♂, Kazakhstan, Ukraine	2	6	7%	Smicromyrmina	Smicromyrmini
Platymyrmylla André, 1900: * <i>P. quinquefasciata</i> (Olivier, 1811) ♀, ♂, Armenia, Ukraine	1	1	0%	Myrmilinae	Myrmilinae
Pristomutilla Ashmead, 1903: <i>P. dentidorsis</i> (André, 1908) ♀, Malawi; <i>P. meigangana</i> Nonveiller, 1995 ♂, Cameroon; <i>P. sp. nr. ctenophora</i> Bischoff, 1921 ♂, South Africa; <i>P. spp.</i> ♀♀, ♂, South Africa, Tanzania	3	3	7%	Smicromyrmina	Myrmilinae
Promecilla André, 1902: <i>P. decora</i> (Smith, 1879), comb. n. ♀, ♂, Malaysia; * <i>P. regia</i> (Smith, 1855) ♀, ♂, India; <i>P. spp.</i> ♀♀, India	4	2	8%	Smicromyrmina	Smicromyrmini
Protophotopsis Schuster, 1947: * <i>P. (P.) veneraria</i> (Melander, 1903) ♀, ♂, USA	1	1	0%	Sphaeropthalmina	Sphaerophthalmini
Pseudocephalotilla Bischoff, 1920: <i>P. atropos kalabariensis</i> (Bischoff, 1921), comb. n. ♂, South Africa; <i>P. beira</i> (Péringuey, 1914), comb. n. ♀, ♂, South Africa; * <i>P. beirana</i> Bischoff, 1921, Mozambique; <i>P. tettensis brunni</i> (Bischoff, 1921), comb. n. ♀, South Africa	2	3	7%	Smicromyrmina	Mutillini

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

Taxon	Spp. ♀♀	Spp. ♂♂	% poly.	Current classification	
				DB	LN
Stenomutilla André, 1896: * <i>S. argentata</i> (Villers, 1789) ♀, ♂, Italy, Spain; <i>S. ?colligera</i> (André, 1899) ♂, South Africa; <i>S. eurydice</i> (Péringuey, 1898) ♀, ♂, Namibia; <i>S. hottentota</i> (Fabricius, 1804) ♂, Malta; <i>S. mlanjiana</i> Bischoff, 1921 ♂, Zambia; <i>S. sp. nr. togoana</i> Bischoff, 1921 ♀, Zambia; <i>S. sp.</i> ♂, Lesotho; <i>S. tetrazonia</i> Skorikov, 1935 ♀, ♂, Kazakhstan, Uzbekistan	4	7	14%	Dasylab-rini	Dasylab-rinae
Sulcotilla Bischoff, 1920: * <i>S. sulcata</i> (Magretti, 1884) ♀, ♂, Cameroon, Mali, Niger, Senegal	1	1	0%	Smicro-myrmina	Smicro-myrmini
Tallium André, 1902: <i>T. catulus</i> (Burmeister, 1875) ♀, ♂, Argentina; <i>T. proseni</i> Casal, 1965 ♀, Argentina; <i>T. sp. nr. precarium</i> Suárez, 1960 ♂, Argentina; <i>T. suarezi</i> Casal, 1968 ♀, Argentina; <i>T. tenebrosus</i> (Gerstaecker, 1874) ♀, ♂, Argentina	4	3	5%	Pseudo-methocina	Pseudo-methocini
Timulla Ashmead, 1899: * <i>T. dubitata</i> (Smith, 1855) ♀, ♂, USA; <i>T. ferrugata</i> (Fabricius, 1804) ♀, ♂, USA; <i>T. vagans</i> (Fabricius, 1798) ♀, ♂, USA	3	3	5%	Smicro-myrmina¹	Trogas-pidiini¹
Tobantilla Casal, 1965: <i>T. aleatrix</i> Williams, Brothers& Pitts, 2011 ♀, Argentina; <i>T. charrasca</i> Casal, 1969 ♀, Argentina; <i>T. drosa</i> Williams, Brothers& Pitts, 2011 ♂, Argentina; <i>T. ephemera</i> Williams, Brothers& Pitts, 2011 ♂, Argentina; * <i>T. montonera</i> Casal, 1965 ♀, Argentina	3	2	0%	Sphaerop-thalmina	Sphaerop-thalmini
Tricholabiodes Radoszkowski, 1885: <i>T. arabicus</i> Suárez, 1967 ♂, United Arab Emirates; <i>T. carinifer</i> Bischoff, 1920 ♀, ♂, Namibia; <i>T. ?lividus</i> André, 1909 ♀, Namibia; <i>T. semistriatus</i> (Klug, 1829) ♀, Israel; <i>T. sp. nr. signatipennis</i> (André, 1901) ♂, South Africa; <i>T. sp.</i> ♂, United Arab Emirates	3	4	7%	Dasylab-rini	Dasylab-rinae
Trispilotilla Bischoff, 1920: <i>T. dewitziana</i> (de Saussure, 1891) ♀, Mozambique; <i>T. liopyga</i> (Bischoff, 1920) ♀, South Africa; <i>T. melanocephala</i> Bischoff, 1920 ♂, Malawi; <i>T. monteiroae</i> Bischoff, 1920 ♂, South Africa; <i>T. rugifera</i> Nonveiller, 1973 ♀, Zimbabwe	3	2	3%	Smicro-myrmina¹	Trogas-pidiini¹
Trogaspidia Ashmead, 1899: <i>T. fedtschenkoi</i> (Radoszkowski, 1877) ♀, ♂, Turkmenistan, Uzbekistan; <i>T. major</i> Nonveiller & Petersen, 1995 ♀, ♂, South Africa; <i>T. sp. nr. caffrariae</i> Bischoff, 1920 ♀, South Africa; <i>T. themis</i> (Péringuey, 1898) ♀, ♂, South Africa	4	3	4%	Smicro-myrmina¹	Trogas-pidiini¹
Tropidotilla Bischoff, 1920: <i>T. cruenticeps</i> (André, 1901) ♀, Cyprus; <i>T. cypriadis</i> Invrea, 1940 ♂, Cyprus; <i>T. fimbriata</i> (Klug, 1829) ♀, Eritrea; * <i>T. litoralis</i> (Petagna, 1787) ♀, ♂, Croatia, Greece, Spain; <i>T. milmili</i> (Magretti, 1898) ♂, Cameroon	3	3	9%	Mutillina	Mutillini
Vianatilla Casal, 1962: * <i>V. nummularis</i> (Gerstaecker, 1874) ♀, Argentina; <i>V. spp.</i> , ♂♂, Costa Rica	1	2	3%	Pseudo-methocina	Pseudo-methocini
Viereckia Ashmead, 1903: <i>V. ?acrisione</i> (Péringuey, 1898) ♀, South Africa; <i>V. ?nigra</i> (Arnold, 1960) ♀, ♂, South Africa; <i>V. spp.</i> ♀♀♀, ♂♂♂, Lesotho, South Africa	5	4	10%	Myrmil-linae	Myrmil-linae
Wallacidia Lelej & Brothers, 2008: <i>W. melmora</i> (Cameron, 1905) ♂, Indonesia; <i>W. philippinensis</i> (Smith, 1855) ♀, ♂, Philippines; <i>W. singapora</i> (Mickel, 1935) ♂, Malaysia	1	3	2%	Smicro-myrmina¹	Trogas-pidiini¹
Xystromutilla André, 1905: * <i>X. asperiventris</i> André, 1905 ♀, ♂, Brazil; <i>X. turrialba</i> Casal, 1969 ♀, ♂, Panama	2	2	11%	Sphaerop-thalmina	Sphaerop-thalmini

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

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

²Ephutini 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, $<0.4 \times$ length of flagellomere I; 1 = Short, $>0.4 <0.7 \times$ 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 = $1-1.5 \times$ length of flagellomere II; 2 = $>1.8 \times$ 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 = $>1.3 <2.0 \times$ as long as wide; 3 = $>2 \times$ 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 dome-like 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 = $<0.8 \times$ 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 = $>0.6 \times$ as long as wide; 1 = $<0.6 \times$ 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 $>0.4 \times$ length of calcar; 3 = Expanded, almost square, $<0.4 \times$ 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 = $\geq 0.5 \times$ length of tergum II, gradually broadened posteriorly, sessile on tergum II; 1 = $\geq 0.4 \times$ length of tergum II, strongly broadened, parallel-sided posteriorly, discontinuous with tergum II; 2 = $< 0.5 \times$ length of tergum II, gradually broadened posteriorly, sessile on tergum II; 3 = $< 0.5 \times$ length of tergum II, gradually broadened posteriorly, constricted apically, disjunct from tergum II; 4 = $< 0.25 \times$ 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 = $> 0.75 \times$ width of tergum II; 1 = $< 0.75 > 0.5 \times$ width of tergum II; 2 = $< 0.5 \times$ 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 = $< 0.75 \times$ length of terga III–VI; 1 = $0.75\text{--}1.25 \times$ length of terga III–VI; 2 = $> 1.25 \times$ 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 = $<0.6 \times$ maximum head width; 1 = $>0.6 \times$ 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, $<0.4 \times$ length of flagellomere I; 1 = Short, $>0.4 <0.8 \times$ 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 = $<0.6 \times$ length of flagellomere II; 1 = Subequal to flagellomere II; 2 = $>1.3 \times$ 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 = $>1.3 <2.0 \times$ as long as wide; 3 = $>2 \times$ 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 = $>1 < 1.5 \times$ length of fore tibia; 2 = $>1.5 < 2 \times$ length of fore tibia; 3 = $>2 \times$ 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 = Flange-like, 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 $>0.5 \times$ 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 = $<0.5 \times$ length of 1st abscissa of RS; 1 = Subequal to 1st abscissa of RS; 2 = $>1.5 \times$ 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, $\geq 0.5 \times$ length tergum II, apically sessile on tergum II; 1 = Gradually broadened posteriorly, $\geq 0.5 \times$ length tergum II, apically constricted from tergum II; 2 = Gradually broadened posteriorly, $< 0.5 \times$ length tergum II, apically sessile on tergum II; 3 = Gradually broadened posteriorly, $< 0.5 \times$ length tergum II, apically constricted from tergum II; 4 = Parallel-sided posteriorly, $\geq 0.4 \times$ length tergum II, discontinuous with tergum II; 5 = Entirely parallel-sided, $< 0.5 \times$ length tergum II, discontinuous with tergum II. (NONADDITIVE) [9%; length = 17, ci = 0.29, ri = 0.68]
203. Male — Tergum I, apical width: 0 = $> 0.75 \times$ width tergum II; 1 = $> 0.5 < 0.75 \times$ width tergum II; 2 = $< 0.5 \times$ 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. (NON-ADDITIVE) [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. (NON-ADDITIVE) [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 out-group 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	0	0	0	0	1	3	0	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1				
Anthobosca	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
Fedtschenkia	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	3	0	0	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Sapyginae	2	0	1	1	[02]	0	0	1	[02]	0	0	0	0	2	1	[01]	[01]	0	1	3	0	0	-	-	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Acanthomutilla	2	0	1	2	0	0	1	0	1	0	2	0	0	2	1	2	1	0	2	2	1	0	0	-	0	3	2	1	0	0	3	2	0	0	0	2	0	1	0	1	1	0		
Allotilla	2	0	1	2	0	0	1	0	1	0	2	0	0	2	1	2	0	1	0	1	0	0	-	0	3	2	1	0	0	1	0	0	0	0	0	0	1	0	1	1	4			
Ambtropidia	2	0	1	2	0	0	1	0	2	1	3	0	0	2	1	2	0	1	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	1	0	1	1	4			
Ancistrofilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	1	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	1	0	1	1	2			
Aperomutilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	1	0	1	2			
Areotilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0			
Artitilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0			
Atitlum	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0		
Bischoffella	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0		
Bischoffitilla	2	0	1	2	0	0	1	0	2	1	0	0	0	2	1	2	0	0	0	2	0	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2		
Bothromutilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	1	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0		
Brachymutilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	1	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2		
Cephalomutilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	1	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2		
Ceratotilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	0	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0		
Chaetomutilla	2	0	1	2	0	0	1	1	0	2	0	0	0	2	1	2	0	0	0	2	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
Chrestomutilla	2	0	1	2	0	0	1	1	1	2	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
Ctenotilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
Cystomutilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Darditilla	2	0	1	2	0	0	1	0	1	2	3	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Dasylabroides	2	0	1	2	0	0	1	0	0	1	2	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Dasytomutilla	2	0	1	2	0	0	1	0	1	[014]	0	1	2	0	1	2	0	0	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Dentilla	2	0	1	2	0	0	1	0	1	[01]	0	1	2	0	0	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Dilophotopsis	2	0	1	2	0	0	1	0	1	1	2	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Dimorphomutilla	2	0	1	2	0	0	1	3	2	1	[02]	0	2	0	2	0	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Dolichomutilla	2	0	1	2	0	0	1	0	2	[02]	0	0	0	2	1	2	0	1	0	0	2	1	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ephuta	2	0	1	2	0	0	1	0	0	0	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ephutomma	2	0	1	2	0	0	1	0	2	[12]	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Eurygnathilla	2	0	1	2	0	0	1	0	4	2	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Eurygnathilla (Near)	2	0	1	2	0	0	1	0	4	2	0	0	0	2	1	2	0	1	0	0	2	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euspinoria	2	0	1	2	0	0	1	0	3	1	2	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Glossotilla	2	0	1	2	0	0	1	0	2	1	2	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gogotilla	2	0	1	2	0	0	1	0	2	3	0	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemutilla	2	0	1	2	0	0	1	0	1	2	0	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hindustanilla	2	0	1	2	0	0	1	0	1	0	2	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hoplocrates	2	0	1	2	0	0	1	4	[12]	0	2	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hoplognathoca	2	0	1	2	0	0	1	2	2	2	3	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hoplomutilla	2	0	1	2	0	0	1	1	2	3	0	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karlissaidia	2	0	1	2	0	0	1	1	1	0	2	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krombeinidia	2	0	1	2	0	0	1	1	1	2	0	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kuakarrumia	2	0	1	2	0	0	1	1	2	0	0	0	0	2	1	2	0	0	0	2	3	0	-	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebidomilla	2	0	1	2	0	0	1	4	2	1	0	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	0	0	0	2	1	2	1	0	1	0	1	2	0	0	0	1	2	0	1	0	1	0	0	0	1	7	0	2	0	1	1	0					
Mutilla	2	0	1	2	0	0	1	1	2	0	[01]	0	2	1	2	0	1	0	1	0	1	0	[01]	0	1	2	0	1	0	1	0	0	0	1	0	1	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	0	2	3	0	0	0	2	1	0	1	0	1	0	0	0	1	0	1	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	0	0	3	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1				
Myrmosa	0	0	1	1	2	0	1	[13]	0	0	0	0	2	1	2	1	1	0	0	1	1	0	-	1	3	0	0	0	0	0	0	0	0	4	0	0	0	0	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	0	-	2	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1	3	1				
Nanomutilla	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	2	1	0	1	0	0	-	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	[04]	0			
Nemka	2	0	1	2	0	0	1	0	2	0	0	0	2	1	2	1	2	1	0	1	2	0	[12]	[02]	4	3	2	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0			
Odonomutilla	2	0	1	2	0	0	1	0	2	0	[02]	0	2	1	2	1	2	1	0	1	0	2	1	0	3	2	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0			
Odonomyrme	2	0	1	2	0	0	1	0	1	1	3	0	2	1	2	1	2	1	0	1	0	1	0	0	3	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1			
Odonotopoptosis	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	2	1	0	1	0	1	0	0	3	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1			
Odonotilla ss	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	2	1	0	2	3	1	0	0	3	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1			
Orientilla	2	0	1	2	0	0	1	1	1	1	2	0	2	1	2	1	2	1	0	1	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4		
Paramyrmosa	0	0	1	1	2	0	1	3	0	0	0	0	2	1	2	1	1	0	1	1	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1			
Peryella	2	0	1	2	0	1	1	4	1	1	2	0	2	1	2	1	2	1	0	0	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		
Pherotilla	2	0	1	2	0	1	1	1	1	0	[01]	0	2	1	2	1	2	1	0	1	0	[01]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2		
Photomorphus ss	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	2	1	0	1	0	0	-	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
Physetopoda	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
Platymyrmilla	2	0	1	2	0	0	1	0	1	0	0	0	2	1	2	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5		
Pristomutilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Promecilla	2	0	1	2	0	0	1	0	1	1	0	0	2	1	2	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Prototopopsis ss	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	2	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Pseudocephalotilla	2	0	1	2	0	0	1	0	1	2	0	0	2	1	2	1	2	1	0	1	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	0
Pseudomethoca	2	0	1	2	0	0	1	4	1	1	3	[12]	2	1	2	1	2	1	0	2	3	[12]	0	0	[13]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	[04]	
Pseudomutilla	2	0	1	2	0	0	1	1	2	0	0	0	2	1	2	1	2	1	0	1	0	0	-	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pseudomyrmosa	0	0	1	1	2	0	1	1	0	1	[01]	0	2	1	2	1	2	1	0	1	0	0	-	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Pseudophotopsis	2	0	1	2	0	1	1	0	0	0	0	0	2	1	2	1	2	1	0	1	0	0	-	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Radoszkowskitilla	2	0	1	2	0	0	1	0	1	2	0	0	2	1	2	1	2	1	0	1	2	1	2	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Reedomutilla	2	0	1	2	0	0	1	0	1	2	3	0	2	1	2	1	2	1	0	1	0	0	-	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalomutilla	2	0	1	2	0	1	1	1	0	0	[02]	0	0	2	1	2	2	0	0	1	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
Ronisia	2	0	1	2	0	0	1	1	0	0	0	0	0	2	1	2	2	0	0	1	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
Scaptolactyla	2	0	1	2	0	0	1	0	[02]	1	0	0	2	1	2	1	2	0	1	0	1	0	-	4	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Seyrigilla	2	0	1	2	0	0	1	1	2	0	2	0	2	1	2	1	2	1	0	1	2	0	-	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smicromyrme	2	0	1	2	0	0	1	0	2	0	[02]	0	2	1	2	1	2	1	0	1	2	0	-	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinicromyrmilla	2	0	1	2	0	0	1	2	0	0	0	0	2	1	2	1	2	1	0	1	0	0	-	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerophthalma ss	2	0	1	2	0	0	1	0	1	1	2	0	2	1	2	1	2	1	0	1	0	0	-	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinulomutilla	2	0	1	2	0	0	1	0	1	2	0	0	2	1	2	1	2	1	0	1	2	1	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenomutilla	2	0	1	2	0	0	1	1	1	2	0	0	2	1	2	1	2	1	0	1	0	[012]	[012]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sulcotilla	2	0	1	2	0	0	1	5	2	1	2	0	2	1	2	1	2	1	0	1	2	1	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tallium	2	0	1	2	0	0	1	0	1	2	0	0	2	1	2	1	2	1	0	1	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Timulla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	1	2	1	0	1	0	0	-	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tobantilla	2	0	1	2	0	0	1	0	2	1	0	0	2	1	2	1	2	1	0	1	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tricholabiodes	2	0	1	2	0	0	1	0	0	1	3	0	2	1																																

Appendix 3 (cont.)

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		
<i>Mixocotilla</i>	0	2	1	2	2	2	0	1	1	0	1	1	0	0	0	0	0	0	1	1	[01]	1	1	[03]	2	2	0	0	2	1	1	0	0	3	0	0	0	0	2	2		
<i>Mutilla</i>	0	2	1	2	2	2	0	1	1	0	1	1	0	0	5	0	0	1	1	1	1	1	1	3	2	0	0	1	0	2	1	1	0	0	3	0	0	0	0	2	2	
<i>Myrmilla</i> ss	0	0	2	1	2	1	2	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	6	2	0	1	0	2	1	1	0	0	3	0	0	0	0	1	1	1	
<i>Myrmilloides</i>	0	0	0	2	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	3	1	0	0	-	2	0	1	1	0	2	0	0	0	0	0	1	0	1	0	1	1	
<i>Myrmosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	3	1	0	-	2	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Myrmosula</i>	0	2	1	2	2	2	0	1	1	1	2	1	0	2	9	1	0	0	0	2	1	1	3	3	2	0	1	0	0	2	1	0	0	0	4	0	0	0	0	0	0	
<i>Nanomutilla</i>	0	2	1	2	2	2	0	1	1	1	0	0	0	0	0	0	0	0	1	2	1	1	1	3	2	0	1	0	0	2	1	0	0	0	3	0	0	0	0	0	0	
<i>Odontomutilla</i>	1	2	1	2	2	2	0	1	1	1	1	2	0	0	0	0	0	0	1	1	1	1	1	4	2	0	1	0	0	1	0	0	0	0	3	0	0	0	0	0	2	
<i>Odontomyrme</i>	0	2	1	[02]	2	2	0	1	1	1	1	1	0	0	6	0	0	0	1	[23]	1	1	1	3	2	0	1	0	4	0	2	0	0	3	0	0	0	0	0	0	2	
<i>Odontophotopsis</i>	0	2	1	[02]	2	2	2	1	1	0	0	6	1	2	6	0	1	0	1	1	2	1	1	4	2	0	1	0	4	0	2	1	0	0	3	0	0	0	0	0	0	[23]
<i>Odontotilla</i> ss	0	2	0	[02]	2	2	2	1	1	0	1	0	0	0	0	0	0	0	2	3	1	1	2	2	0	2	0	1	0	0	0	0	0	3	0	1	1	1	1	1		
<i>Orientilla</i>	0	0	0	[02]	2	0	0	1	1	0	1	0	0	0	0	0	0	0	2	3	1	1	0	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	
<i>Paramyrmosa</i>	1	2	1	[12]	2	2	0	1	1	0	1	0	0	1	0	0	0	0	0	[23]	1	1	6	2	0	1	0	1	0	0	1	0	0	0	3	0	0	[01]	1	1	2	
<i>Pertyella</i>	0	2	1	[12]	2	2	0	2	1	0	0	2	0	0	6	0	0	0	1	[23]	1	1	5	2	0	1	0	5	0	2	1	1	0	1	0	0	0	0	0	0	0	
<i>Photomoropus</i> ss	0	2	1	2	1	2	2	0	1	1	1	0	0	0	1	0	0	0	1	3	1	1	6	2	0	1	0	5	0	2	1	1	0	1	0	0	0	0	0	0	0	
<i>Physotopoda</i>	0	2	1	2	2	2	2	0	1	1	1	0	0	2	5	0	0	0	1	3	1	1	6	2	0	1	0	5	4	2	1	0	0	3	0	0	0	0	0	0	0	
<i>Platymyrmilla</i>	0	2	1	2	2	2	2	1	1	0	1	0	0	2	5	0	0	0	1	0	1	1	7	2	0	1	0	5	4	2	0	1	0	0	3	0	0	0	0	0	0	
<i>Pristonutilla</i>	0	2	1	2	2	2	2	1	1	0	1	4	0	0	2	6	0	0	1	0	[01]	1	0	7	2	0	1	0	5	4	2	0	1	0	0	3	0	0	0	0	0	0
<i>Promecilla</i>	0	2	1	2	2	2	2	0	1	0	1	4	0	0	0	0	0	0	1	[01]	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Protophotopsis</i> ss	0	2	1	2	2	2	2	0	1	0	0	0	0	0	0	0	0	0	1	[123]	1	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pseudocephalotilla</i>	0	2	1	2	2	2	[02]	2	0	1	0	0	0	0	0	0	0	0	1	3	1	1	3	2	0	1	0	4	4	2	1	0	0	3	0	0	0	0	0	0	0	
<i>Pseudomethoca</i>	[01]	2	1	2	[02]	2	2	1	0	1	0	0	0	0	6	0	0	0	1	1	1	1	0	3	2	0	1	0	6	4	2	1	0	0	3	0	0	0	0	0	0	
<i>Pseudomutilla</i>	0	2	1	2	2	2	[12]	2	0	1	0	0	0	0	2	6	0	0	1	[23]	1	1	[56]	3	2	0	1	0	4	0	2	[01]	1	0	0	3	0	0	0	0	0	
<i>Pseudomyrmosa</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0	3	2	0	1	0	5	0	2	0	0	0	0	0	0	0	0	0	0		
<i>Pseudophotopsis</i>	0	2	1	2	2	2	0	1	1	1	1	0	0	0	3	0	0	0	1	0	3	1	0	3	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Radoszkowskilla</i>	0	2	1	2	2	2	0	1	1	1	1	0	0	0	1	5	0	0	1	1	1	1	0	1	2	0	1	0	7	0	2	0	0	3	0	0	0	0	0	0	0	
<i>Reedmutilla</i>	0	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	3	2	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhopalotilla</i>	0	2	0	1	0	0	0	1	1	0	0	0	0	0	1	6	0	0	2	3	1	1	5	2	0	1	0	5	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Rhinotilla</i>	0	2	0	1	0	0	0	2	1	0	0	1	2	0	0	0	0	0	0	3	1	1	5	2	0	1	0	5	0	1	0	0	1	0	0	0	0	0	0	0	0	
<i>Rovisia</i>	0	2	1	2	2	2	0	1	1	0	0	0	0	0	6	0	0	0	1	1	1	1	5	2	0	1	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Scapiooctetyla</i>	0	2	1	2	2	2	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	5	2	0	1	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Seyrigilla</i>	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	3	2	0	1	0	4	3	2	3	1	0	0	3	0	0	0	0	0		
<i>Smicromyrmica</i>	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	1	1	3	2	0	1	0	4	3	2	3	0	0	0	0	0	0	0	0	0		
<i>Smicromyrmilla</i>	1	2	0	2	2	2	0	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	3	2	0	1	0	4	3	2	3	0	0	0	0	0	0	0	0	0		
<i>Sphaerophthalma</i> ss	1	2	1	1	0	2	0	1	0	0	0	[125]	1	0	[69]	[01]	0	0	1	1	1	[01]	3	2	0	1	0	4	0	2	1	0	0	3	0	0	0	0	0	0	[12]	
<i>Spinulomutilla</i>	0	2	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	3	1	1	0	3	2	0	1	0	7	4	2	1	0	0	3	0	0	0	0			
<i>Stenomutilla</i>	0	2	1	2	2	2	1	1	1	0	0	0	0	0	0	0	0	0	2	[01]	1	1	2	0	2	0	1	0	4	2	1	0	0	0	0	0	0	0	0	0		
<i>Sulcotilla</i>	0	2	1	2	2	2	1	1	1	0	1	0	0	0	7	0	0	0	1	3	1	1	3	2	0	1	0	4	0	2	2	1	0	0	0	0	0	0	0	0		
<i>Tallium</i>	0	2	1	[012]	[02]	2	0	1	1	0	1	0	0	0	8	0	0	0	1	[23]																						

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	
Hemipepis	0	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	0	1	0	1	0	0	1	0	0	0	0	0	
Fedtschenkia	0	0	0	0	0	-	0	0	0	0	-	2	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	
Sapyginae	0	0	2	1	0	0	0	0	[01]	0	-	2	0	6	0	1	2	7	2	2	2	1	1	0	1	3	0	0	0	0	
Acanthomutilla	1	2	1	2	1	1	1	0	1	2	0	1	0	5	0	0	3	2	2	2	2	0	1	1	3	0	0	2	0	0	
Alloilla	0	2	1	2	1	1	0	1	2	0	2	1	0	0	6	0	3	2	2	2	1	0	1	1	3	0	0	2	0	1	
Ambtropidia	1	2	2	1	1	1	0	1	2	0	1	2	0	0	0	0	3	4	2	1	0	1	0	1	3	0	0	2	0	0	
Ancistroilla	0	2	2	0	1	1	0	1	2	1	2	2	0	0	1	0	3	4	1	0	1	0	1	1	3	0	0	2	0	1	
Aperomutilla	0	2	1	0	1	0	0	1	2	1	0	2	0	5	0	1	0	3	2	1	0	1	0	1	3	0	0	2	0	0	
Areolla	0	2	1	0	1	1	0	1	2	1	2	2	0	5	0	0	3	7	2	2	1	1	0	1	3	0	0	2	0	0	
Artrolla	0	2	1	0	1	1	0	1	2	0	-	2	0	0	[07]	0	3	0	2	0	1	0	1	1	3	0	0	2	0	0	
Atillum	0	2	1	0	1	1	0	1	2	0	0	2	8	3	0	0	5	0	2	0	1	0	1	1	4	0	0	2	0	0	
Bischoffella	0	1	2	1	1	0	3	1	2	0	0	2	0	0	[02]	0	0	2	2	0	1	1	0	1	3	0	0	2	0	1	
Bischoffilla	0	2	2	0	1	1	0	1	2	0	-	2	0	0	0	0	2	2	0	2	0	0	1	0	1	3	0	0	2	0	0
Bothromutilla	1	2	2	0	1	1	0	1	2	1	[12]	2	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	1	
Brachymutilla	0	2	1	0	1	1	0	1	2	0	[01]	2	0	0	1	1	-	1	0	1	0	1	0	1	3	0	0	2	0	0	
Cephalomutilla	0	4	2	1	1	1	0	1	2	0	-	2	0	1	5	0	3	2	2	0	1	1	0	1	3	0	0	2	0	1	
Ceratotilla	0	2	1	0	1	1	0	1	2	0	2	1	0	0	0	0	0	2	2	1	2	1	0	1	3	0	0	2	0	0	
Chaetomutilla	0	2	1	0	1	1	0	1	2	0	1	1	0	7	0	0	0	2	2	1	2	1	0	1	3	0	0	2	0	0	
Chrestomutilla	0	3	1	1	1	1	0	1	2	0	1	1	0	0	1	0	3	2	2	0	1	1	0	1	3	0	0	2	0	0	
Ctenotilla	0	2	1	1	1	1	0	1	2	0	1	1	[13]	5	0	0	4	2	2	0	1	1	0	1	3	0	0	2	0	1	
Cystomutilla	1	2	1	1	1	1	0	1	2	0	1	2	0	0	0	0	4	4	2	0	0	1	0	1	3	0	0	2	0	1	
Darditilla	0	3	2	1	1	1	0	1	2	0	-	2	0	0	0	0	3	0	2	0	0	1	0	1	3	0	0	2	0	0	
Dasyfabris	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	
Dasytroides	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	
Dasytutilla	[01]	[13]	2	2	1	1	0	1	2	0	-	2	0	0	[06]	0	3	3	2	0	1	0	1	1	3	0	0	2	0	1	
Denitilla	0	2	1	0	1	1	0	1	2	1	1	1	0	1	0	0	3	6	2	0	[01]	1	0	1	3	0	0	2	0	0	
Dilophotopsis	2	[02]	2	1	0	1	1	1	2	0	-	2	0	1	0	0	4	2	2	0	0	1	0	1	3	0	0	2	0	1	
Dimorphomutilla	1	0	2	0	1	1	0	1	2	0	-	2	0	0	0	0	3	2	2	0	0	1	0	1	3	0	0	2	0	0	
Dolichomutilla	0	5	2	1	0	1	0	1	2	0	-	1	0	2	0	7	0	5	2	2	0	1	0	1	3	0	0	2	0	0	
Ephuta	0	2	2	1	0	0	1	1	2	0	-	1	0	0	0	0	3	6	2	2	0	1	0	1	3	0	0	2	0	0	
Ephutomma	0	2	2	1	1	1	0	1	2	0	-	1	0	0	0	0	3	7	2	2	1	0	1	3	0	0	2	0	0	0	
Eurygnathilla	0	2	1	0	1	1	0	1	2	0	2	2	0	2	0	0	2	2	2	1	1	1	0	1	3	0	0	2	0	0	
Eurymutilla (Near)	2	2	1	0	1	1	1	1	2	1	2	2	0	0	6	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	2	1	0	0	0	3	5	1	0	1	0	1	0	1	3	0	0	2	0	0
Glossotilla	0	2	1	0	1	1	0	1	2	0	-	2	0	5	0	0	3	7	2	2	2	1	0	1	3	0	0	2	0	1	
Gogotilla	1	1	1	0	1	1	0	1	2	0	[12]	2	0	0	[01]	0	4	3	2	0	0	1	0	1	3	0	0	2	0	1	
Hemutilla	1	1	1	1	1	1	0	1	2	0	[01]	2	0	4	0	0	5	4	2	0	0	1	0	1	3	0	0	2	0	1	
Hindustanilla	0	0	0	0	1	1	0	1	2	0	-	2	0	0	0	0	3	1	2	1	0	1	0	1	3	0	0	2	0	1	
Hoplocrates	1	2	1	0	1	1	0	1	2	0	-	2	0	0	0	0	4	3	1	2	1	0	1	0	1	3	0	0	2	0	1
Hoploomutilla	1	2	1	0	1	1	0	1	2	0	-	2	0	0	0	0	3	0	2	0	1	0	1	0	1	3	0	0	2	0	0
Hoploomutilla	1	2	1	0	1	1	0	1	2	0	-	2	0	0	0	0	4	2	0	1	0	1	0	1	3	0	0	2	0	0	0
Kardissaidia	0	[02]	1	0	1	1	0	1	2	0	-	2	0	5	0	0	2	7	2	2	0	[01]	1	0	1	3	0	1	2	0	0
Krombeinidia	0	2	1	0	1	0	0	1	2	0	-	1	0	0	0	0	3	2	2	1	0	1	0	1	3	0	0	2	0	0	1
Kudakrumia	0	2	1	0	0	0	0	0	2	0	-	1	0	0	0	0	3	2	0	1	0	1	0	1	3	0	0	2	0	0	0
Labidomutilla	0	2	1	0	1	1	0	1	2	0	-	1	0	2	0	0	0	5	2	1	0	1	0	1	3	0	0	2	0	0	0
Liobilla	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	0	0	1	0	1	0	1	3	0	0	2	0	0	0
Lobotilla	0	2	1	0	1	1	0	1	2	0	[01]	1	0	0	0	0	0	0	0	1	0	1	0	1	3	0	0	2	0	0	1
Lomachaeta	1	2	2	1	0	1	1	0	1	2	-	1	0	0	0	0	0	0	7	2	1	0	1	0	1	3	0	0	2	0	1
Lophomutilla	0	[02]	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	3	2	0	0	1	0	1	3	0	0	2	0	1	0
Lynchiatilla	1	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	2	0	0	0	1	0	1	3	0	0	2	0	1	0
Micelomyrme	0	[02]	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	7	2	2	1	0	1	0	1	3	0	0	2	0	1
Mimemutilla ss	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	0	2	0	2	1	0	1	3	0	0	2	0	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
Mimecrotilla	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	0	1	2	0	0	0	0	3	6	2	2	1	2	1	0	1	3	0	0	2	0
Myrmilla ss	0	2	1	0	1	1	0	1	2	0	-	2	0	3	7	0	6	2	2	2	1	1	1	0	1	3	0	0	2	0
Myrmilloides	1	0	2	1	0	1	0	1	2	0	-	0	1	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	0	0	0	0	3	2	0	1	0	1	0	1	3	0	0	2	0	0
Myrmosula	0	0	1	0	0	-	0	1	2	0	-	0	0	0	2	0	6	0	1	1	0	1	0	1	2	0	0	2	1	0
Nanomutilla	0	0	1	0	0	-	0	1	2	0	-	0	0	0	0	0	6	0	1	1	0	1	0	1	3	0	0	2	1	0
Nemta	0	0	2	1	0	1	0	1	2	1	2	2	0	0	0	0	3	7	2	2	0	1	1	0	1	3	0	0	1	0
Odonomutilla	[12]	0	2	1	1	2	0	1	2	1	[01]	1	0	0	0	2	2	[24]	2	0	1	1	0	1	3	0	0	2	0	1
Odonomyrme	1	1	1	1	1	1	0	1	2	1	1	2	0	0	6	0	3	2	2	0	1	1	0	1	3	0	0	2	0	1
Odonotopopsis	2	[01]	[12]	0	1	1	1	0	2	[01]	2	2	0	0	0	3	4	5	2	0	1	1	0	1	3	0	0	2	0	1
Odonotilla ss	0	2	1	1	1	1	0	1	2	0	-	2	0	0	0	0	2	2	1	1	1	0	1	3	0	0	2	0	0	0
Orientilla	0	0	1	2	1	0	-	0	2	0	-	0	1	0	0	0	2	2	1	0	0	0	0	1	3	0	0	2	0	0
Paramyrmosa	0	0	0	1	0	0	-	0	2	0	-	0	1	0	0	0	3	2	1	0	1	0	1	2	0	0	0	2	0	0
Pertyella	1	2	2	0	1	1	0	3	1	[01]	0	2	0	8	3	0	5	0	2	0	0	1	0	1	3	0	0	2	1	0
Pherotilla	0	4	1	1	1	1	0	1	2	1	2	2	0	1	0	0	3	2	2	0	0	1	0	1	4	0	0	2	1	0
Photomorphus ss	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	0	3	[67]	2	0	1	1	0	1	3	0	0	2	0	1
Physatopoda	0	2	1	0	1	1	0	1	2	1	1	2	0	2	0	0	2	2	2	1	1	1	0	1	3	0	0	2	1	0
Platymyrmilla	0	2	1	0	1	1	0	1	2	1	-	1	0	0	0	0	2	2	1	2	1	1	0	1	3	0	0	2	1	0
Pristomyrmilla	0	0	1	0	1	1	0	1	2	0	-	1	0	0	0	0	2	2	1	2	1	1	0	1	3	0	0	2	1	0
Pronocilla	0	0	1	0	1	1	0	1	2	0	-	1	0	0	0	0	2	2	1	2	1	1	0	1	3	0	0	2	1	0
Prototopopsis ss	1	3	1	1	1	1	1	0	2	0	-	1	0	0	0	0	2	2	2	2	1	1	0	1	3	0	0	2	1	0
Pseudocephalotilla	1	2	1	0	1	1	0	1	2	1	[12]	1	0	0	0	0	3	2	2	0	2	1	0	1	3	0	0	2	0	0
Pseudomethoca	1	2	1	0	1	1	0	1	2	0	-	2	0	3	7	0	6	2	2	0	1	1	0	1	3	0	0	2	0	1
Pseudomyrmilla	0	2	1	0	1	1	0	1	2	0	-	2	0	0	0	0	3	2	0	1	0	1	0	1	2	0	0	2	0	0
Pseudotopopsis	0	[01]	[01]	0	1	0	-	0	2	0	-	2	0	0	[05]	0	0	0	3	1	0	1	0	1	2	1	0	2	0	0
Radoszkowskitilla	0	2	1	1	1	1	0	1	2	0	-	2	0	5	0	0	3	2	0	1	0	1	0	1	3	0	0	2	0	1
Reedomutilla	0	3	2	2	1	1	0	1	2	0	-	2	0	0	5	0	3	2	0	0	0	1	0	1	3	0	0	2	0	1
Rhopalomutilla	0	[13]	2	1	0	-	3	1	2	0	-	2	0	8	3	0	5	0	2	0	1	0	1	1	4	0	0	2	1	0
Rimulotilla	0	1	2	1	0	-	[23]	1	2	0	-	2	0	0	2	0	0	0	3	-	1	1	0	1	4	0	0	2	1	0
Ronisia	0	2	1	1	1	1	1	0	2	0	-	2	0	0	0	0	4	2	2	1	1	0	1	1	3	0	0	2	1	0
Scaptodactyla	2	1	2	1	1	1	1	1	2	0	-	2	0	0	0	0	3	6	2	2	0	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
Smicromyrmilla	0	2	1	0	1	1	0	1	2	1	2	1	0	0	0	0	3	2	0	2	0	0	0	1	3	0	0	2	0	0
Spinicrophthalma ss	0	2	1	0	1	1	0	1	2	1	1	2	0	0	4	0	5	3	2	1	2	1	0	1	3	0	0	2	1	0
Spinulomutilla	2	1	2	1	1	1	1	1	2	0	-	2	0	0	0	0	4	7	2	2	0	2	1	0	1	3	0	0	2	0
Stenomutilla	0	2	1	0	1	0	-	0	2	0	-	2	0	0	0	0	3	2	2	0	0	0	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	0	2	1	0	1	3	0	0	2	0
Tallium	[12]	2	1	0	1	1	0	1	2	1	[12]	1	0	1	[06]	0	0	2	2	0	1	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	3	2	2	0	1	1	0	1	3	0	0	2	0	1
Tobantilla	1	3	2	2	1	1	0	1	2	0	-	2	0	0	5	0	0	3	2	0	0	0	1	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	0	[01]	0	1	3	0	0	2	0	0
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	0	1	0	1
Trogaspidia	0	0	2	1	0	1	1	0	1	2	0	-	1	0	0	0	2	2	1	0	0	1	1	0	1	3	0	0	1	0
Tropidotilla	0	2	1	0	1	1	0	1	2	0	-	1	0	5	0	0	2	7	2	2	[01]	1	1	0	1	3	0	0	1	0
Vianatilla	1	0	2	1	0	1	1	0	1	2	1	2	0	0	0	0	3	6	2	2	1	0	1	1	3	0	0	2	0	1
Viereckia	0	[02]	1	0	1	1	0	1	2	0	-	1	0	0	0	0	0	5	2	0	1	0	1	1	3	0	0	2	0	0
Wallacida	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	1
Xystromutilla	2	1	[12]	[02]	1	1	1	1	2	0	-	2	0	0	5	0	4	2	2	1	1	1	0	1	3	0	0	2	0	0
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 (♂, ♀); *Tai-myrrmosa* 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: Sphaerophthalminae Schuster, 1949 (1903)

Tribe: Sphaerophthalmini 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 (♂); **Sphaerophthalma** 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 (♂, ♀); **Suarezitilla** 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 (♂, ♀); **Patquiattilla** 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 (♂, ♀); *Liomotilla* André, 1907 (♂, ♀); *Myrmilla* Wesmael, 1851 (♂, ♀); *Myrriotilla* Bischoff, 1920 (♀); *Odontotilla* Bischoff, 1920 (♂, ♀); *Odontotilloides* Nonveiller, 1996 (♂, ♀); *Omotilla* Invrea, 1943 (♂, ♀); *Platymyrmilla* André, 1900 (♂, ♀); *Pseudomotilla* Costa, 1885 (♂, ♀); *Pygomilla* Hammer, 1955 (♀); *Saganotilla* Invrea, 1943 (♂, ♀); *Sigilla* Skorikov, 1927 (♂, ♀); *Somaliatilla* Nonveiller, 1996 (♀); *Spilomotilla* 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 (♂, ♀); *Chaetomotilla* Nonveiller, 1979 (♂, ♀); *Ctenotilla* Bischoff, 1920 (♂, ♀); *Lebritilla* Lelej, 2005 (♂); *Mimecomutilla* Ashmead, 1903 (♂, ♀); *Mimecotilla* Nonveiller, 1998 (♂, ♀); *Montanomutilla* Nonveiller, 1979 (♀); *Pristomotilla* Ashmead, 1903 (♂, ♀); *Strangulotilla* Nonveiller, 1979 (♂, ♀); *Taeniotilla* Nonveiller, 1979 (♂); *Zeugomotilla* Chen, 1957 (♂, ♀)

Tribe: Smicromyrmini Bischoff, 1920

Genera: *Andreimyrmex* Lelej, 1995 (♂, ♀); *Antennotilla* Bischoff, 1920 (♂); *Astomyrmex* Schwartz, 1984 (♂, ♀); *Corytilla* Arnold, 1956 (♂, ♀); *Ctenoceraea* Nonveiller, 1993 (♂); *Dentilla* Lelej in Lelej & Kabakov, 1980 (♂, ♀); *Ephucilla* Lelej 1995 (♂, ♀); *Ephutomma* Ashmead, 1899 (♂, ♀); *Eremotilla* Lelej, 1985 (♂, ♀); *Erimyrmex* Lelej, 1985 (♂, ♀); *Guineomotilla* Suárez, 1977 (♀); *Gynandrotilla* Arnold, 1946 (♂); *Indratilla* Lelej, 1993 (♂, ♀); *Karunaratnea* Lelej, 2005 (♂, ♀); *Mickelomyrmex* 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 (♂, ♀); *Psammotherna* 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 (♂); *Ephusarezia* 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 (= Peterseniidiina 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 (♂, ♀); *Peterseniidia* Lelej in Lelej & Yamane, 1992 (♂, ♀); *Promecidia* Lelej, 1996 (♂, ♀); *Protrogaspidia* Lelej, 1996 (♂); *Pseudolophotilla* Nonveiller & Četković, 1995 (♂, ♀); *Radoszkowskitilla* Lelej, 2005 (♂, ♀); *Serendibiella* Lelej, 2005 (♂); *Seriatospidia* Nonveiller & Četković, 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 (♂); *Vanharteni-*
dia 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 out-group 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.

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