

Phylogeny of the genus *Palmanura* (Collembola: Neanuridae)

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Abstract

In order to assess the phylogenetic structure of the springtail genus *Palmanura*, as well as to test the monophyly of the tribe Sensillanurini (Neanuridae: Neanurinae), a data matrix of morphological (chaetotactic and other) characters of members of this group was assembled and analysed in the light of Wagner parsimony. The data matrix included all the known members of the Neotropical genus *Palmanura*, plus representatives of *Sensillanura* and *Americanura*. Although not all the clades obtained were highly supported by bootstrap resampling, some structures were relatively constant under different approaches. Alternative analyses (unordered and ordered character states, rescaled weighting procedure) were applied. While alternative solutions were obtained, a number of structures were shared by the results irrespective of the method used. On this basis, the results suggest that some further reassessment is required to confirm formally the monophyly of the tribe Sensillanurini. The genera *Palmanura* and *Americanura* are mutually poly/paraphyletic; we thus suggest that *Palmanura* should be considered as a synonym of *Americanura*, although some character reassessment and more varied outgroup species may be necessary before a formal generic redefinition can be proposed. Finally, a comparison of the performance of the characters under Wagner parsimony analysis indicated that differences in the characters' retention indexes are due not to the topological (tagmal) position of the traits involved, but to character coding: the characters describing quantitative features (generally numbers of setae) generally performed worse than other types of characters under parsimony. An updated list of the known members of the Sensillanurini (Collembola: Neanuridae: Neanurinae) is presented.

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The springtails (Hexapoda: Collembola) are interesting from several points of view: they might have been among the first arthropods to have colonized inland habitats, and their phylogenetic relationships with other arthropod taxa are still under debate (Wheeler et al., 2001; Giribet et al., 2004; Willmann, 2004; Grimaldi and Engel, 2005; Najt et al., 2005; Machida, 2006). Despite this, their internal phylogenetic relationships are poorly known. The present taxonomy of the Collembola has a predominantly intuitive basis (Cassagnau, 1974), and the relatively small amount of work done on this group might be due to the difficulties of studying them, including their small size (often within the range 0.1–1 mm). Thus phylogenetic approaches in this group are

recent. They include studies based on either morphological evidence (Lee, 1985; Deharveng, 1989; Deharveng and Bedos, 1991; D'Haese and Weiner, 1998; Simón Benito et al., 2005); molecular data (Fрати et al., 1997, 2000a,b, 2001; Frati and Carapelli, 1999; Frati and Dell'Ampio, 2000; D'Haese, 2002; Dell'Ampio et al., 2002); or total evidence (Lee et al., 1995, 1996; Lee and Thibaud, 1998). These approaches have often covered limited numbers of sample species within selected genera, such as *Friesea* (Deharveng and Bedos, 1991) or *Willemia* (D'Haese and Weiner, 1998), rarely including a majority of the known species from a given genus (D'Haese, 2000), or at highest taxonomic levels (D'Haese, 2003a,b).

Among the Collembola, the family Neanuridae (sensu Deharveng, 2004) is of special interest because of its cosmopolitan distribution and its high diversity (more

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than 1370 species in 155 genera). The family consists of six subfamilies, of which Neanurinae is the largest (727 species, 97 genera) and most thoroughly studied. Within the Neanurinae, Cassagnau (1982, 1983a,b, 1989) proposed the lineage ‘Sensillanurina’ on the basis of the hypertrophied sensilla S7 in the fourth antennal segment (Cassagnau, 1982), in contrast to the eight subequal sensillae found in other members of the group (putatively the primitive condition). This was the basis for Deharveng (1981) to erect the genus *Sensillanura*. Later, Cassagnau and Palacios-Vargas (1983) described several Mexican species with ‘Sensillanurina’ features, which they ascribed to the genera *Americanura* and *Palmanura* (both formerly created by Cassagnau, 1983a).

The Sensillanurini are interesting as a subject for the study of the evolution of setal morphology in springtails. They present setae of varied sizes, with setal shapes including long, narrow, wide or even flat (palmate), which may bear ciliations or barbulations and other ornamentations that give them the appearance of tree leaves. There is also a clear reduction of the number of dorsal setae in some species. At present, this tribe includes three genera: *Sensillanura* Deharveng, 1981; with six species of Holarctic distribution (Europe, USA, and Canada, and one undescribed species from the north of Mexico); *Americanura* Cassagnau, 1983, with 20 species (Nearctic and Neotropical ranging from Canada to Venezuela and the Galapagos Islands); and *Palmanura* Cassagnau, 1983, with 17 species of Neotropical distribution (central Mexico to Colombia). A detailed list of the known species and distributions is given in Appendix 1.

Materials and methods

Species and outgroups

This study covered all known species of the genus *Palmanura* Cassagnau (Appendix 1), including three species not yet described (Palacios-Vargas and Simón Benito, in press), plus representatives of the other two ‘Sensillanurina’ genera: two species of *Americanura* (*Americanura mexicana* Cassagnau, 1983 and *Americanura setaefoliacea* Cassagnau and Palacios-Vargas, 1983), and one of *Sensillanura*, *S. austriaca* (da Gama, 1963). Two non-‘Sensillanurina’ Neanuridae were used as outgroups: *Neanura muscorum* (Templeton, 1836) and *Paranura ieti* (Yosii, 1966). This selection was reinforced by the fact that these species apparently retain the presumed plesiomorphic state of most characters of potential interest for the study of the ingroup (Cassagnau, 1983a,b). The character states of the outgroup species were not coded as 0, thus facilitating an interpretation of the subjective a priori interpretation of the available information (Appendix 3).

Characters

Character selection and coding for the ‘Sensillanurina’ species relied on the original descriptions of the species, as well as on reassessment of the type specimens unless these were not available. Whenever possible, all features were assessed in one to five specimens of each species. Further details can be found in Cassagnau (1983a,b); Cassagnau and Palacios-Vargas (1983); Palacios-Vargas (1984, 1986, 1996); Vázquez and Palacios-Vargas (2005).

The character list and the matrix of species \times character states are presented in Appendices 2 and 3. A detailed character database for Sensillanurini was previously developed by the authors (Palacios-Vargas and Simón, unpublished data); this preliminary character list (with more than 140 binary or quantitative features) was compacted and recoded for the present study, resulting in a list of 153 characters, 24 of which are binary and 129 multistate. In terms of percentage, about one-third (51) of the final characters refer to setal numbers and might be treated as numerical; the remaining 102 describe setal types or shapes, or the presence/absence of setae or of other structures.

While more information on the morphology of Neanurinae is available, we discarded features without variation within the ingroup as well as characters that have frequently been overlooked in species descriptions, such as the setae of antennal segments I to III, those of the tibiotarsus, labrum, and labium, and the ventral chaetotaxy or that of the anal valves (D’Haese, 2003a,b). For similar reasons, the arrangement of ‘s’ setae was discarded for this study as it is similar to that of other springtail families such as Hypogastruridae, Odontelliidae (D’Haese, 2003a).

Cladistic and phenetic routines

The analysis based on Wagner parsimony was carried out using the programs Winclada (Nixon, 1999) and NONA (Goloboff, 1993), using the heuristic search routine and the settings hold = 500, mult* n = 100 and hold/= 100, and the procedure Multiple TBR + TBR as search strategy. When pertinent, bootstrap values (Felsenstein, 1985) were obtained using NONA (500 replications, mult* n = 100 and hold/= 100). This search was done with all the characters set as nonadditive (unordered character states), as usually recommended to avoid biased results due to the authors’ intuitive criteria (Wiley et al., 1991; Forey et al., 1992). Character polarities at the basal node were established by the authors based on the available background taxonomic knowledge (of the two initial outgroup species, *N. muscorum* remained in the most basal position in all trials).

The results displayed poor bootstrap support (< 50) for about one-half of the tree branches. To seek

alternative topologies, we reanalysed the data matrix as described above, but allowing the character state transformations to be additive (ordered) for those characters where this might be logical: for characters 26, 29, 31, 33, 35, 36, 38, 42, 47, 49, 51, 55, 57, 59, 61, 63, 65, 67, 69, 71, 75, 77, 81, 83, 87, 89, 91, 94, 100, 108, 111, 116, 120, 122, 124, 128, 131, 132, 136, 139, 141, 143, 145, 146, 148, 150, and 152 from Appendix 2. Lastly, we applied the procedure of successive weighting using the rescaled consistency index (RCI; Farris, 1989) to the same matrix (with all characters set as unordered, using the program Hennig86; Farris, 1988). This is an iterative method that starts from a previously determined most parsimonious tree, then gives highest weights to those characters that displayed lowest homoplasy scores in that tree, and repeats the procedure until the character weights stabilize.

For a further test on the performance of the different characters under parsimony analysis, we divided them according to their information, both topological (head, thorax, and abdomen) and according to their nature (shape, setal counts, and presence/absence binary data). These features were coded as factors for each variable, and the characters' retention indexes (RI) from the first cladogram (parsimony analysis of nonadditively coded characters, described below) were compared by analysis of variance.

Finally, to measure overall similarity among the species in the absence of phylogenetic information—as an alternative way to discuss or explain the present position of conflicting species—we assembled a phenogram based in a square matrix (species \times species) of

Gower's distances. This measure (Gower, 1971) is suitable for use with a combination of numerical and categorical variables. Before any calculations, the non-recorded values for the numerical characters stated above were retrieved from the original database. The unweighted pair-group method with arithmetic mean (UPGMA; Sneath and Sokal, 1973) was applied as the linkage rule.

Results

The heuristic search based on unordered character states resulted in 13 most parsimonious trees with 445 steps (CI = 0.60, RI = 0.61). The strict consensus tree was moderately well resolved (67%), as shown in Fig. 1 (character statistics and character state changes are detailed in Appendices 4 and 5). Only six of the 13 clades found bootstrap support higher than 0.5, suggesting a poor performance of most characters (only 26 characters displayed retention indexes of 1.00; Appendix 4). One of the ingroup species, *Palmanura wilsoni*, clustered together with one of the outgroup species, *Paranura ieti*, suggesting a paraphyletic status of the Sensillanurini.

The search with one subset or multistate characters set as ordered led to another 16 trees that, as expected, were less parsimonious than those based on unordered character states: 504 steps, CI = 0.53, RI = 0.62. The strict consensus ($L = 520$, CI = 0.51, RI = 0.60; Fig. 2, detailed statistics not presented) departed from the topology shown in Fig. 1 in a number of details, remarkably in the position of *P. wilsoni*, which was

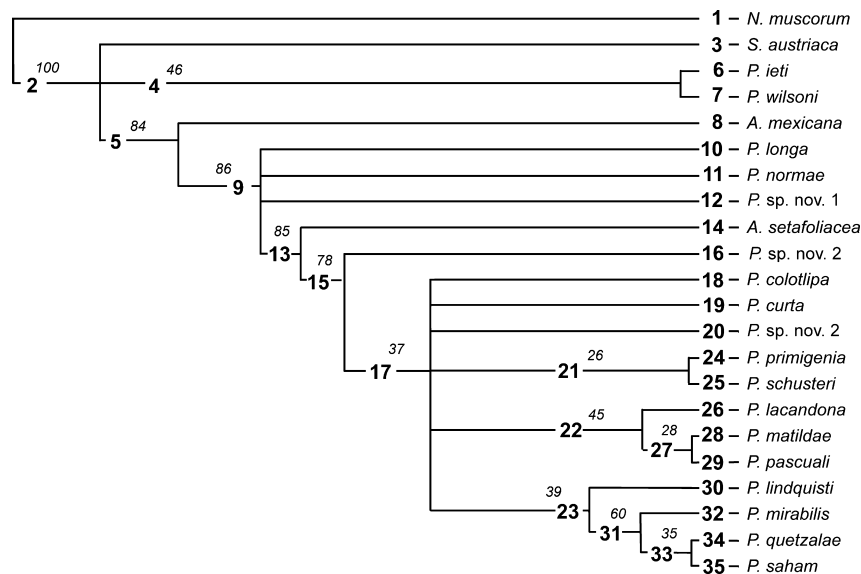


Fig. 1. Strict consensus tree of the 13 cladograms derived from analyses of the data matrix with all characters set as nonadditive (length of the consensus = 445 steps; consistency index, CI = 0.60; retention index, RI = 0.61). For further details see text and Appendices 4 and 5.

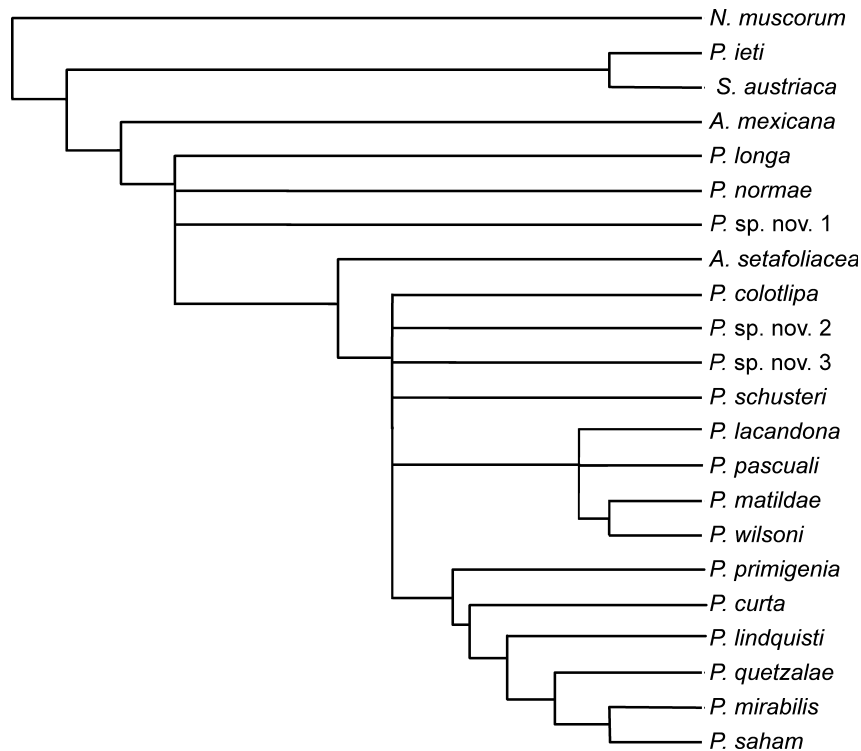


Fig. 2. Strict consensus of the 16 most parsimonious trees found setting one part of the multistate characters as ordered (additive). Length of the consensus = 520 steps; consistency index, CI = 0.51; retention index, RI = 0.60.

placed in a relatively distal clade within *Palmanura* instead of as the sister species of *Paramura ieti*. As in the former analysis, the *Americanura* species were either placed in relatively basal positions among the *Palmanura* species, or as the sister species of the remaining palmanuroid clade (*A. setafoleacea*).

The results of successive weighting by rescaled consistency indexes on nonadditive character states consisted of a final tree with a length of 1561 steps (CI = 0.84, RI = 0.90; Fig. 3). This cladogram supported the monophyly of the Sensillanurini except for the position of *P. wilsoni*, similar to that in Fig. 1, but again no evidence in favour of a monophyletic genus *Americanura* appeared. The weights applied to the characters in this analysis are shown in Appendix 4.

Although some structures revealed high consistency across the different approaches (e.g. an apical clade with *P. lindquisti*, *P. mirabilis*, *P. quetzalae*, and *P. saham*), a strict consensus of all the former results was poorly resolved due to the different positions of several species in the three sets of cladograms. An Adams consensus tree (Adams, 1986) was calculated to retrieve the relevant information on potential monophyletic groups while discarding the effects of species with incongruent positions across the three analyses (Fig. 4).

The phenogram based on quantitative and qualitative information differed from the former approaches,

and suggested a cohesive clade equivalent to *Palmanura*, with the two species of *Americanura* either basally associated to *Palmanura*, or clustering with the outgroup species (Fig. 5). However, the internal structure of *Palmanura* had little in common with the results of the cladistic approaches, with the exception of a couple of associations between species, e.g. (*P. mirabilis* + *P. saham*) and (*P. pascuali* + *P. matilda*).

Finally, the ANOVA of character RI values (from Appendix 4) using topology and type of character as independent variables was significant overall (whole model $F_{4,148} = 5.86$, $P = 0.0002$). There was no significant effect of the tagmal position of the characters ($F = 0.89$, $P = 0.41$), but the type of character had a significant weight on the RI scores ($F = 11.38$, $P = 0.00003$). A *post hoc* comparison of the means revealed no significant differences between the mean character RI values of the 'size or shape' characters and the binary ones, while the 'size or shape' characters displayed significantly higher retention indexes than those implying setal counts ($P < 0.00001$, Fisher's *post hoc* test). The mean RI scores (and standard errors) for the three character types were 17.76 ± 4.27 (setal counts), 31.21 ± 5.56 (binary characters), and 48.69 ± 4.90 (characters involving descriptions of shape, size, or setal type).

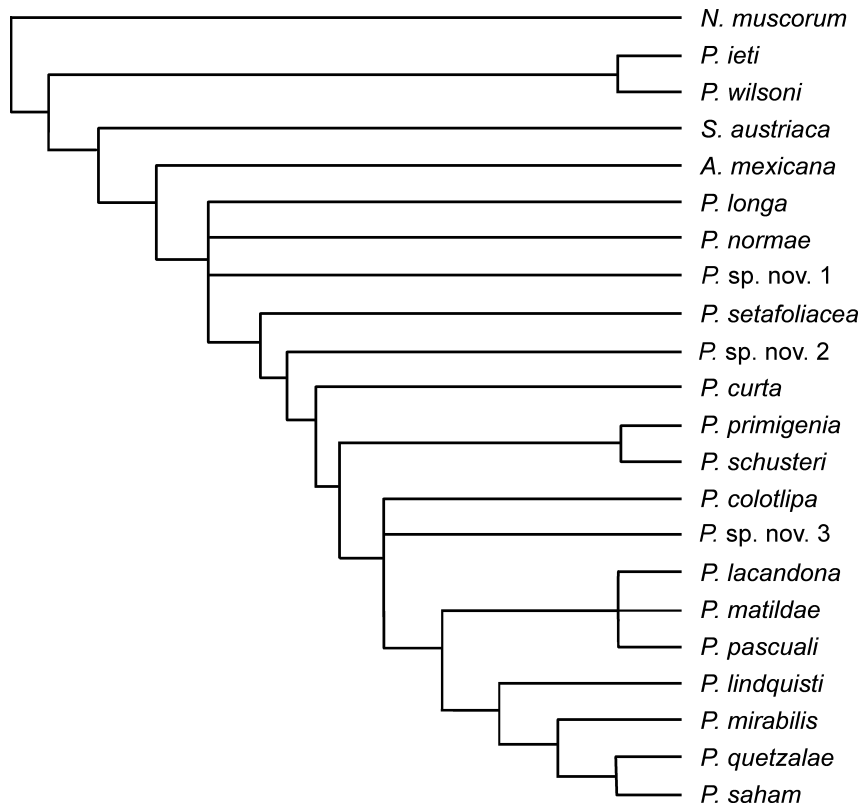


Fig. 3. Tree obtained from successive reweighting of the data matrix with all character transformations set to unordered (length of the consensus = 1561, consistency index, CI = 0.84, retention index, RI = 0.90).

Discussion

The phylogenetic reconstructions obtained under the different parsimony-based approaches were not fully conclusive, and support for most of the branches in the cladograms was low. Within these limits, however, it is remarkable that the general cladogram topologies largely did not vary, except in the positions of some of the species. This caused a complete lack of resolution of a strict consensus of the three methods. However, there was ample congruence between the two analyses done without character weights (character states unordered and ordered). This general structure (not presented graphically in the results) shares many features with the Adams consensus presented. Most cladistic practitioners would argue against the use of additive-coded characters and/or the method of successive character weighting. The former imposes a subjective weight on character polarities, based on the author's experience; the latter discards one part of the information; while both may lead to less parsimonious trees (Farris, 1989; Forey et al., 1992). Thus the following discussion relies primarily on the first of the cladistic analyses (Fig. 1). However, due to the prospective nature of this study, and to the overall congruence among methods, we also summarize the results by means of an Adams consensus

(Fig. 4) which may be of help for identifying the conflictive species and characters. This will help to identify species and characters that are in conflict with other evidences. It is important to note that the interpretation of an Adams consensus is different from that of a strict consensus tree. In this type of consensus, the conflicting terminals are moved to the most basal position found in the series of trees, while the structures that include members of a monophyletic clade in all trees are maintained. Thus the unresolved nodes include those species that might appear within more terminal positions in some of the trees found, while the dichotomies do not imply that no other species might occur within that level.

Interestingly, the monophyly of the taxon Sensillanurini is not fully supported. The diagnostic character, a hypertrophied sensilla S7 on antennal segment IV (Fig. 6), was interpreted as homoplastic due to reversal in the basally positioned *S. austriaca* and *P. wilsoni*, and in fact outweighed by a combination of several homoplastic characters. Only treating the character states as additive (ordered) resulted in support for the monophyly of the taxon (as proposed by Cassagnau (1982, 1983a,b, 1989). This, combined with the results of the phenetic analysis, suggests that the current classification of this group may partly express an intuitive appreciation of

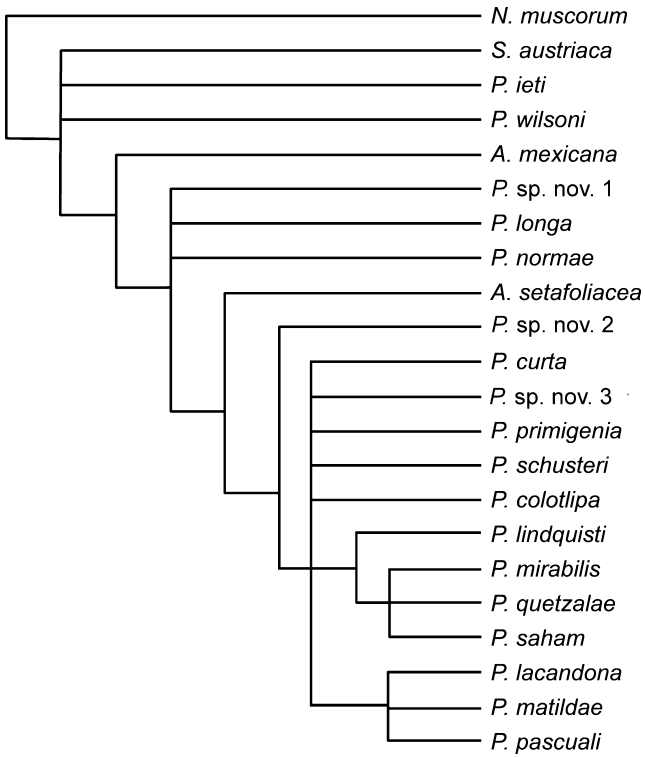


Fig. 4. Adams consensus summarizing the nesting patterns shared by trees in Figs 1–3.

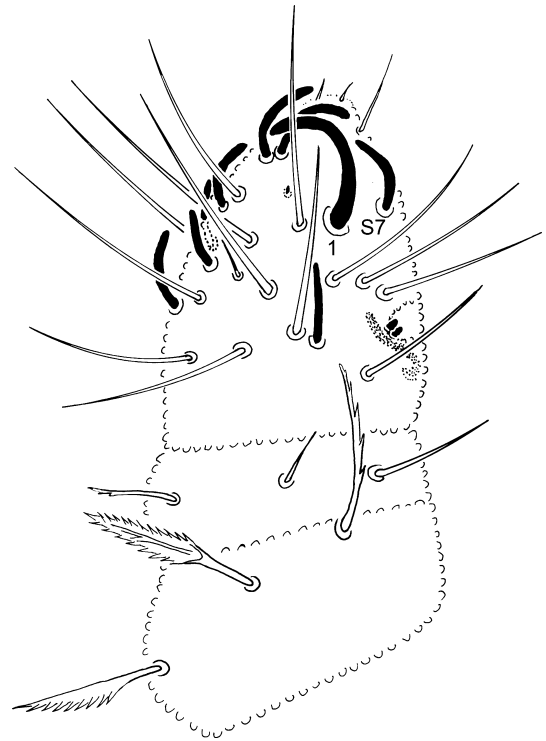


Fig. 6. Dorsal chaetotaxy of the antenna of the genus *Palmanura*, showing the eight sensilla of the fourth antennal segment and the hypertrophied sensilla S7.

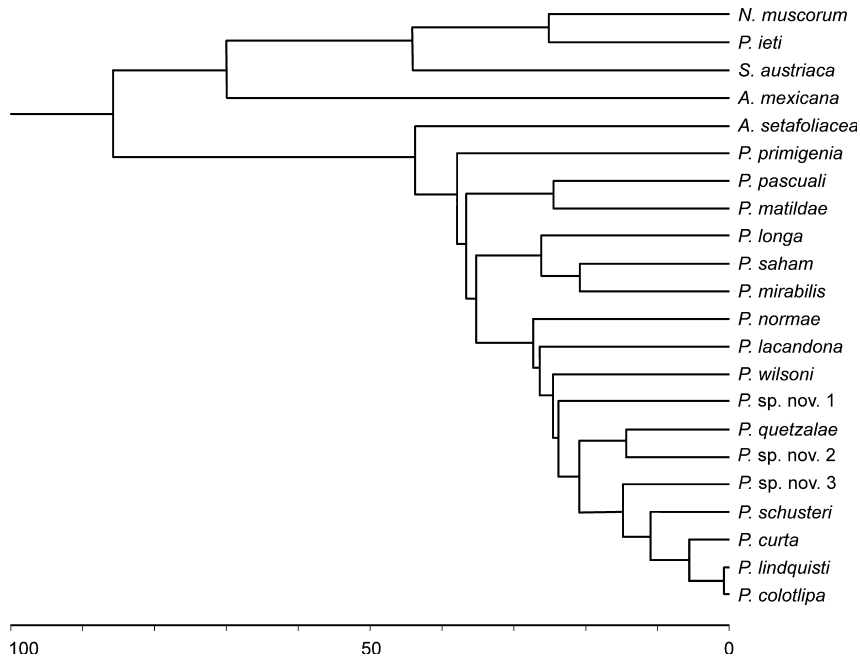


Fig. 5. Phenogram showing the apparent relationships among the set of species analysed (unweighted pair-group method with arithmetic mean (UPGMA) procedure, applied to a matrix of Gower distances, *G*).

gradients in ‘quantitative (or measurable) characters’, namely setal counts. However, we have shown that these characters behave less consistently than categoric

features under a parsimony analysis for this data set. Further, there is the risk that the number of setae at different body positions is correlated to some extent.

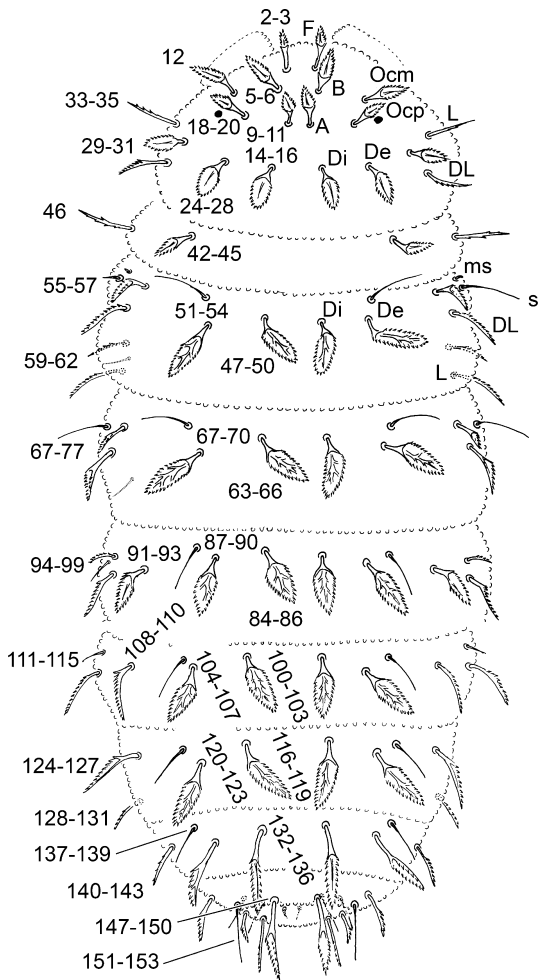


Fig. 7. Dorsal chaetotaxy of the body of *Palmanura*. The formal setal designation is shown on the right; the corresponding character numbers, as used in this work, on the left.

Further analyses including a higher number of potential outgroup species are needed to reassess this point. If the positions of *S. austriaca* and *P. wilsoni* are not taken into account, the monophyly of the remaining members of the taxon (Fig. 1, node 5) is supported by several features (Appendix 5), including the presence of the cephalic setae D, E, and O (Fig. 7), and by the loss of setae in the dorso-internal tubercle of the first thoracic segment.

Based on the present results, the genera *Americanura* and *Palmanura* do not represent monophyletic assemblages. *Americanura mexicana* has a consistently basal position, while *A. setafoleacea* occupies an internal node within *Palmanura* (in a clade with support from nonhomoplastic synapomorphic states of characters 25, 30, 43, 48, 52, 56, 64, 68, 73, 74, 84, 88, 92, 101, 105, and 109; Appendix 5). Within this clade, the internal node giving rise to 13 *Palmanura* species is supported by six nonhomoplastic changes in characters 117, 121, 125, 133, 137, and 147. As shown in Fig. 4, this clade was

nearly constant across analyses, and excluded *P. wilsoni* unless the successive weighting method was applied. This may be interpreted in terms of frequent character reversal in that species, or as evidence for a rather plesiomorphic position of *P. wilsoni*. Alternatively, however (and more consistent with our results), the position of *P. wilsoni* within *Palmanura* can be challenged.

In addition to the comparatively well supported wide clade of *Palmanura* species (node 15 in Fig. 1), two further clades deserve mention. One is the group of *P. lindquisti*, *P. mirabilis*, *P. quetzalae*, and *P. saham*, which is robust to the type of treatment under parsimony. The other is formed by the three species characterized by the head with subocular (SO) macrosetae of two types, smooth and palmate: *P. lacandona*, *P. matildae*, and *P. pasquali* (these associate to *P. wilsoni* if the characters are given weights).

Thus, in conclusion, Sensillanurini might prove monophyletic, but this statement requires reassessment with a larger data matrix including information from more non-‘sensillanurina’ neanurids. The genera *Palmanura* and *Americanura* are mutually polyphyletic, hence a revision of the morphology of the species presently classified under *Americanura* proves necessary. However, and as far as the chaetotaxy of the two *Americanura* spp. tested here was assessed by the senior author, we suggest that *Palmanura* should be treated as a synonym of *Americanura*. The phenetic approach (Fig. 5), and the parsimony analysis of the data matrix with character states treated as additive, suggest that quantitative evidence (namely the number of setae that, as stated in Materials and methods, accounts for an important proportion of the morphological evidence available) might have driven the present taxonomy.

Overall, setal shape proved to be more robust than setal numbers in terms of retention index values under a parsimony approach. This may be worth noting for further studies, as it suggests that setal numbers may be correlated across different body parts, thus increasing the risk of giving an excessive weight to some homoplastic features. Alternatively, it may also reflect the difficulties of coding quantitative characters for parsimony analyses in general (Rae, 1995; Forey and Kitching, 2000; Wiens, 2000; Ried and Sidwell, 2002), and specifically in cladistic work on the Collembola (Deharveng, 1989).

The classification of the Collembola is heavily based on chaetotactic features. Alternative sources of information include DNA sequencing (Fрати and Carapelli, 1999; Frати and Dell’Ampio, 2000; Shao et al., 2000; D’Haese, 2002; Dell’Ampio et al., 2002) as well as nonmorphological information (e.g. ecological specialization: D’Haese, 2003b). From this point of view, it is worth noting that the traditional techniques for studying these arthropods prevent the preservation of soft tissues (e.g. digestion in lactic acid and mounting on micro-

scope slides for morphologic study), and that this process usually precedes identification. This will not facilitate the reassessment of type specimens except on morphological grounds, thus more thorough analysis of the available morphological evidence would be useful in order to build wide databases of chaetotactic and other characters. Further, the erection of genera in this group has followed heterogeneous criteria, thus making necessary not only a reassessment of the adscription of species to genera, but also a test for the cladistic support for the genera themselves.

Due to the large number of known collembolan species (presently nearly 8000—less than one-fifth of the estimated number of species: Hopkin, 1998; Janssens, 2009), the work to be done on the taxonomy of this group is still very large. Phylogenetic reconstruction involves a self-feedback process where partial solutions provide the materials for analyses with a wider taxonomic scope, which, in turn, set the bases for new lower-scale (in a taxonomic context) work. The present results provide potential sample species for further analyses (e.g. a well supported distal clade of *Palmanura* species) together with evidence for the necessity of redefining the genera *Palmanura* and *Americanura* and, to some extent, of the Sensillanurini. Also, for phylogenetic reconstruction, they suggest that characters based on setal counts may not be as reliable as other types of morphological information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Palmanura.nex Data matrix (Nexus format)

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Appendix 1

Checklist of the known genera and species of Collembola, family Neanuridae Börner, 1901 (sensu Deharveng, 2004): subfamily Neanurinae Börner, 1901 (sensu Cassagnau, 1989): Tribe Sensillanurini Cassagnau, 1983a,b.

Sensillanura Deharveng, 1981

1. *S. austriaca* (da Gama, 1963). Austria, France.
 2. *S. barberi* (Handschin, 1928). Canada and USA.
 3. *S. bullsa* (Wray, 1953). USA.
 4. *S. caeca* (Folsom, 1916). Canada and USA.
 5. *S. illina* (Christiansen and Bellinger, 1980). USA.
 6. *S. millsii* (Christiansen and Bellinger, 1980). Canada and USA.
 7. *Sensillanura* sp. Palacios-Vargas, 1990. Mexico: Chihuahua.
- ### *Americanura* Cassagnau, 1983a,b
1. *A. banksi* (Denis, 1933). Costa Rica.
 2. *A. bara* (Christiansen and Bellinger, 1980). Canada and USA.
 3. *A. castillorum* Palacios-Vargas and Najt, 1986. Mexico: Tamaulipas.
 4. *A. guatemalteca* Cassagnau and Palacios-Vargas, 1983. Guatemala and Lesser Antilles.
 5. *A. imitator* Cassagnau and Palacios-Vargas, 1983. Mexico: Mexico.
 6. *A. interrogator* Cassagnau and Palacios-Vargas, 1983. Venezuela and Galapagos Islands (Ecuador).
 7. *A. izabalana* Palacios-Vargas and Ríos, 1996. Guatemala.
 8. *A. macgregori* Cassagnau and Palacios-Vargas, 1983. Mexico: Morelos, Veracruz; Guatemala.
 9. *A. medellini* Palacios-Vargas and Ríos, 1996. Mexico: Chiapas.
 10. *A. mexicana* Cassagnau, 1983a,b. Mexico: Morelos.
 11. *A. nova* (Christiansen and Reddell, 1986). Mexico: Tamaulipas.
 12. *A. prima* Cassagnau and Palacios-Vargas, 1983. Mexico: Hidalgo.
 13. *A. setafoleacea* Cassagnau and Palacios-Vargas, 1983. Mexico: Veracruz.
 14. *A. sotanophila* Cassagnau and Palacios-Vargas, 1983. Mexico: Querétaro.
 15. *A. unguimiti* Palacios-Vargas and Najt, 1986. Mexico: Tamaulipas.

Palmanura Cassagnau, 1983a,b

1. *P. colotlipa* Palacios-Vargas, 1996. Mexico: Guerrero: Colotlipa, 700 m.
2. *P. curta* Palacios-Vargas, 1996. Guatemala: Izabal, Las escobas, 150 m.
3. *P. lacandona* Palacios-Vargas, 1996. Mexico: Chiapas, Chapul, 100 m.
4. *P. lindquisti* Palacios-Vargas, 1996. Guatemala: Zacapa, San Lorenzo, 1700 m
5. *P. longa* Palacios-Vargas, 1996. Mexico: Guerrero, near Grieta de la Hoya.
6. *P. matildae* Palacios-Vargas, 1996. Mexico: Oaxaca, Mantas, Vista Hermosa-Cerro Pelón, 1350 m.
7. *P. mirabilis* Cassagnau, 1983a,b. Mexico: Veracruz, Palma Sola.
8. *P. normae* Palacios-Vargas, 1996. Mexico: Morelos, Villa de Ayala.
9. *P. pascuali* Palacios-Vargas, 1996. Mexico: Oaxaca, Tuxtepec.
10. *P. primigenia* Palacios-Vargas, 1986. Mexico: San Luis Potosí, El Sabinito, 430 m.
11. *P. quetzalae* Palacios-Vargas, 1984. Mexico: Puebla, La Unión.
12. *P. saham* Vázquez and Palacios-Vargas, 2005. Mexico: Chiapas, Palenque.
13. *P. schusteri* Palacios-Vargas, 1996. Guatemala: Zacapa, San Lorenzo, 2100 m.
14. *P. wilsoni* Palacios-Vargas, 1996. Mexico: Chiapas, Lagunas de Monte Bello, 1400 m.
15. sp. nov. 1 ('sernaius') (Palacios-Vargas and Simón Benito, in press). Colombia.
16. sp. nov. 2 ('goyai') (Palacios-Vargas and Simón Benito, in press). Mexico: Oaxaca.
17. sp. nov. 3 ('hieronimus') (Palacios-Vargas and Simón Benito, in press). Mexico: Oaxaca.

Appendix 2

Characters and character state definitions. The character state codes are 0–6. In the character state matrix (Appendix 3), unknown character states (due to the lack of reliable information) were coded as '?', and not applicable states as '-'. For simplicity, the following abbreviations for the tagmata, the tagmal segments and the topological identity of the tubercles were used: H = head (cephalic), TI–TIII = thoracic segments I to III, AI–AV = abdominal segments I to V, DET = dorsal-external tubercle, DLT = dorsal-lateral tubercle, DIT = dorsal-internal tubercle, LT = lateral tubercle, SO = subocular tubercle. Thus combinations of tagmal, segment, and tubercle abbreviations read as e.g. H-DIT, TII-DIT, AIV-LT.

Head (characters 1–39)

1. Sensilla S7 on antennal segment IV of normal size (0), hypertrophied (1) (Fig. 6).
2. Type of cephalic seta F: microseta (0), macroseta (1) (Fig. 7).
3. Shape of cephalic seta F: smooth (0), barbulate macroseta (1), palmate (2).
4. Seta G: present (0), absent (1).
5. Development of seta B: microseta (0), macroseta (1).
6. Shape of seta B: smooth (0), barbulate (1), palmate (2).
7. Seta D: present (0), absent (1).
8. Seta E: present (0), absent (1).
9. Cephalic seta A: present (0), absent (1).
10. Type of cephalic seta A: microseta (0), macroseta (1).
11. Shape of seta A: smooth (0), barbulate (1), palmate (2).
12. Cephalic seta O: present (0), absent (1).
13. Seta C: present (0), absent (1).
14. Anterior ocular seta (OC a): present (0), absent (1).
15. Medial ocular setae (OC m): present (0), absent (1).
16. Medial ocular setae (OC m), type: microseta (0), macroseta (1).

17. Medial ocular setae (OC m), shape: smooth (0), barbulate (1), palmate (2).
 18. Posterior ocular seta (OC p): present (0), absent (1).
 19. Posterior ocular seta (OC p), type: microseta (0), macroseta (1).
 20. Posterior ocular seta (OC p), shape: smooth (0), barbulate (1), palmate (2).
 21. H-DIT, macroseta: absent (0), present (1).
 22. H-DIT, shape of macroseta: smooth (0), barbulate (1), palmate (2).
 23. H-DIT, number of microsetae: none (0), one (1).
 24. H-DET, macroseta: absent (0), present (1).
 25. H-DET, macrosetal shape: smooth (0), barbulate (1), palmate (2).
 26. H-DET, number of microsetae: absent (0), one microseta (1), two microsetae (2).
 27. H-DET, microsetal shape: smooth (0), with palmate or barbulate setae (1).
 28. H-DET, microsetae, shape when not smooth: barbulate (0), palmate (1).
 29. H-DLT, number of macrosetae: absent (0), one (1), two (2), six (3).
 30. H-DLT, shape of macrosetae, smooth (0), barbulate (1), palmate (2).
 31. H-DLT, number of microsetae: absent (0), one (1), two (2), four (3).
 32. H-DLT, shape of the microsetae: smooth (0), palmate (1).
 33. H-LT, macrosetae: absent (0), one seta (1), two setae (2), three setae (3).
 34. H-LT, shape of macrosetae: smooth (0), barbulate (1), palmate (2), smooth and palmate (3), barbulate and palmate (4).
 35. H-LT, number of microsetae: absent (0), one (1), three (2).
 36. H-SO, number of macrosetae: absent (0), one (1), two (2), three (3), four setae (4).
 37. H-SO, shape of the macrosetae: smooth (0), barbulate (1), palmate (2), smooth and barbulate (3), smooth and palmate (4).
 38. H-SO, number of microsetae: (0) to (6) = one to seven setae.
 39. H-SO, shape of the microsetae: smooth (0), smooth and barbulate (1).
- Thorax** (characters 40–82)
40. TI-DIT seta: present (0), absent (1).
 41. TI-DIT, type of seta: microseta (0), macroseta (1).
 42. TI-DET Number of macrosetae of DET: absent (0), one (1), two (2).
 43. TI-DET Shape of macroseta on DET: smooth (0), barbulate (1), palmate (2).
 44. TI-DET microsetae: absent (0), one microseta present (1).
 45. TI-DET, microsetal shape: smooth (0), palmate (1).
 46. TI-DLT, macrosetal shape: smooth (0), barbulate (1), palmate (2).
 47. TII-DIT, macrosetae: absent (0), one seta (1), three setae (2).
 48. TII-DIT, macrosetae: smooth (0), barbulate (1), palmate (2).
 49. TII-DIT, microsetae: absent (0), one seta (1), two setae (2).
 50. TII-DIT, shape of the microsetae: smooth (0), palmate (1).
 51. TII-DET, number of macrosetae: absent (0), one seta (1), two setae (2).
 52. TII-DET, macrosetal shape: smooth (0), barbulate (1), palmate (2).
 53. TII-DET, microsetae: absent (0), present (1).
 54. TII-DET, shape of the microsetae: smooth (0), barbulate (1), palmate (2).
 55. TII-DLT, number of macrosetae: no setae (0), one (1), two (2), three (3).
 56. TII-DLT, macrosetal shape: smooth (0), barbulate (1), palmate (2), barbulate and palmate (3).
 57. TII-DLT, number of microsetae: none (0), one (1), two (2).
 58. TII-DLT, shape of the microsetae: smooth (0), palmate (1).

59. TII-LT, macrosetae: absent (0), one seta (1), two setae (2), three setae (3).
60. TII-LT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2), barbulate and palmate (3).
61. TII-LT, number of microsetae: absent (0), one (1), two (2).
62. TII-LT, type of microsetae: smooth (0), one smooth and one barbulate (1).
63. TIII-DIT, number of macrosetae: absent (0), a single seta (1), three (2).
64. TIII-DIT, shape of macrosetae: smooth (0), barbulate (1), palmate (2).
65. TIII-DIT, number of microsetae: absent (0), one (1), two microsetae (2).
66. TIII-DIT, shape of the microsetae: when present, smooth (0), at least one seta of palmate shape (1).
67. TIII-DET, number of the macrosetae: none (0), one (1), two (2).
68. TIII-DET, macrosetal shape: smooth (0), barbulate (1), palmate (2).
69. TIII-DET, number of microsetae: absent (0), one (1), two (2).
70. TIII-DET microsetae, shape: smooth (0), barbulate or palmate (1).
71. TIII-DLT, macrosetae: absent (0), one to three setae (respectively states 1, 2, 3).
72. TIII-DLT, shape of the macrosetae: smooth (0), complex, either barbulate or palmate (1).
73. TIII-DLT, shape of the complex macrosetae: barbulate setae (1), other (0).
74. TIII-DLT, shape of the complex macrosetae: palmate setae (1), other (0).
75. TIII-DLT, number of microsetae: absent (0), one (1), two (2).
76. TIII-DLT, shape of the microsetae: smooth (0), palmate (1).
77. TIII-DLT, number of macrosetae: absent (0), one (1), two (2), three (3).
78. TIII-LT, macrosetal shape: smooth (0), complex (barbulate or palmate) (1).
79. TIII-LT, shape of the 'complex' macrosetae: barbulate (1), other (0).
80. TIII-LT, shape of the 'complex' macrosetae: palmate (1), other (0).
81. TIII-LT, microsetae: absent (0), one (1), two (2).
82. TIII-LT, microsetae: all of the smooth type (0), at least one barbulate (1).
- Abdomen** (characters 83–153)
83. AI-DIT, number of macrosetae: none (0), one (1), two (2).
84. AI-DIT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
85. AI-DIT, number and shape of the microrosetae: absent (0), one seta present (1).
86. AI-DIT, shape of the microseta: smooth seta (0), barbulate (1), palmate (2).
87. AI-DET, number of macrosetae: absent (0), one (1), two (2).
88. AI-DET, macroseta type: smooth (0), barbulate (1), palmate (2).
89. AI-DET, number of microsetae: absent (0), one (1), two setae (2).
90. AI-DET, shape of the microsetae: smooth seta (0), barbulate (1).
91. AI-DLT, number of macrosetae: absent (0), one (1), two (2).
92. AI-DLT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
93. AI-DLT, microsetae: absent (0), one (either smooth or barbulated) (1).
94. AI-LT, number of macrosetae: absent (0), one (1), two (2), three (3).
95. AI-LT, macrosetal shape: smooth (0), complex, barbulate or palmate (1).
96. AI-LT, shape of the 'complex' macrosetal setae: barbulate (1), other (0).
97. AI-LT, shape of the 'complex' macrosetal setae: palmate (1), other (0).
98. AI-LT, number of smooth microsetae: none (0), one or more (1).
99. AI-LT, presence of barbulate setae: none (0), one or two (1).
100. AII-DIT, number of macrosetae: absent (0), one (1), two (2).
101. AII-DIT, macrosetal shape: smooth (0), barbulate (1), palmate (2).
102. AII-DIT, microsetae: absent (0), present (1).
103. AII-DIT, shape of the microsetae: smooth (0), barbulate (1), palmate (2).
104. AII-DET, number of macrosetae: absent (0), one (1), two (2).
105. AII-DET, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
106. AII-DET, microsetae absent (0), one or more setae present (1).
107. AII-DET, microsetae smooth (0), palmate (1).
108. AII-DLT, number of macrosetae: absent (0), one (1), two (2).
109. AII-DLT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
110. AII-DLT, microseta: absent (0), present (1).
111. AII-LT, number of macrosetae: none (0), one (1), two (2), three setae (3).
112. AII-LT, shape of the macrosetae: smooth (0), not smooth (palmate or barbulate) (1).
113. AII-LT, shape of the non-smooth macrosetae: barbulate (0), palmate (1).
114. AII-LT, microsetae: absent (0), with one or two setae (1).
115. AII-LT, microsetae, shape: all smooth (0), at least one barbulate microseta (1).
116. AIII-DIT, number of macrosetae: absent (0), one (1), two setae (2).
117. AIII-DIT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
118. AIII-DIT, microsetae: absent (0), present (1).
119. AIII-DIT, shape of the microsetae: smooth (0), barbulate (1), palmate (2).
120. AIII-DET, number of macrosetae: absent (0), one (1), two (2).
121. AIII-DET, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
122. AIII-DET, microsetal number: no microsetae (0), one (1), two (2).
123. AIII-DET, microsetal shape: smooth (0), palmate (1).
124. AIII-DLT, number of macrosetae: absent (0), one (1), two (2).
125. AIII-DLT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
126. AIII-DLT, microsetae: absent (0), present (one seta) (1).
127. AIII-DLT, microsetae, shape: smooth (0), barbulate (1).
128. AIII-LT, number of macrosetae: absent (0), one (1), two (2), three (3).
129. AIII-LT, shape of the macrosetae: smooth (0), other than smooth (1).
130. AIII-LT, shape of the non-smooth macrosetae: barbulate (0), palmate (1).
131. AIII-LT, number of microsetae: no setae (0), one seta (1), two setae (2).
132. AIV-DIT, number of macrosetae: absent (0), one (1), two (2).
133. AIV-DIT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
134. AIV-DIT, microsetae: absent (0), one seta (1).
135. AIV-DIT, microseta, when present: smooth (0), palmate (1).
136. AIV-DET, number of macrosetae: absent (0), one (1), two (2).
137. AIV-DET, macrosetal type: smooth (0), barbulate (1), palmate (2).
138. AIV-DET, microseta: absent (0), present (1).
139. AIV-DLT, number of macrosetae: absent (0), one (1), three macrosetae (2).
140. AIV-DLT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2).
141. AIV-DLT, number of setae: absent (0), one (1), two (2).

142. AIV-DLT, all setae (when present) smooth (0), with one barbulate seta (1).

143. AIV-LT, number of macrosetae: absent (0), one (1), two (2), three (3), five (4).

144. AIV-LT, shape of the macrosetae: smooth (0), barbulate (1), palmate (2), smooth and barbulate (3).

145. AIV-LT, number of microsetae: absent (0), one (1), two (2), three (3), four (4).

146. AIV-DIT, number of macrosetae: absent (0), one (1), two (2).

147. AIV-DIT, macrosetal shape: smooth (0), barbulate (1), palmate (2).

148. AV-DIT, number of microsetae: none (0), one (1), two (2).

149. AV-DIT, shape of the microsetae: smooth (0), barbulate (1).

150. AV, number of macrosetae in DET + DLT + LT: none (0), one (1), two (2), three (3), more than four setae (4) (five or six setae are found in *N. muscorum* and *P. ieti*).

151. AV, shape of the DET + DLT + LT macrosetae: smooth (0), barbulate (1), smooth and barbulate (2), barbulate and palmate (3).

152. AV, number of microsetae in DET + DLT + LT: absent (0), one (1), two (2).

153. AV, shape of the dorsal and lateral microsetae: smooth (0), barbulate (1).

Appendix 3

Matrix of characters and character states ('?' = unknown; '-' = not applicable). Note that the character states of operative outgroup species *N. muscorum* were not necessarily coded as '0'. See Appendix 1 for details on the species names and distribution.

Species	Characters 1–60					
<i>N. muscorum</i>	0100100001	0000010010	1001010-30	300-040300	1200-0200-	2010300-20
<i>P. ieti</i>	010010001-	-000010010	1001020-10	1010210200	0101001020	2010201010
<i>S. austriaca</i>	1000000000	0000000000	0-11020-10	1030040400	010100200-	200-300-20
<i>A. Mexicana</i>	1110111101	1100011012	1101120011	1021043401	-111011120	1111310-31
<i>A. setafoleacea</i>	111111111-	-111011011	120120--22	0-21010001	-120-1120-	120-120-21
<i>P. colotlipa</i>	1120121101	2111012012	120120--11	0-120?????1	-120-?120-	120-210-21
<i>P. curta</i>	1120121101	2111012012	120120--12	0-11043201	-120-2120-	120-220-21
<i>P. lacandona</i>	1120121101	21111--012	120120--12	0-23010301	-120-1120-	120-120-12
<i>P. lindquisti</i>	1120121101	2111012012	120120--22	0-21023411	-120-2120-	120-220-21
<i>P. matildae</i>	1121121101	2111012012	120120--12	0-21011401	-120-1120-	120-120-11
<i>P. mirabilis</i>	1120121101	2111012012	120120--22	0-22024401	-120-2120-	120-220-23
<i>P. longa</i>	1110111101	1111011011	110110--21	0-21022401	-110-1110-	110-210-21
<i>P. normae</i>	1110111101	1111011011	110110--21	0-21010301	-110-0110-	110-110-11
<i>P. pascuali</i>	1121121101	21110111--	120110--21	0-22010001	-120-1120-	120-120-11
<i>P. primigenia</i>	1121121101	2111012012	120120--12	0-11011211	-120-11221	120-220-11
<i>P. quetzalae</i>	1121121101	2111012012	120120--22	0-24024001	-120-2120-	120-120-21
<i>P. saham</i>	1120121101	2111012012	120120--12	1022034301	-120-2120-	120-120-23
<i>P. schusteri</i>	1120121101	2111010012	120120--12	0-12011201	-120-0120-	120-210-21
<i>P. wilsoni</i>	1020021100	2111002002	1200-1110-	210-120601	-0-1200-11	0-120-210-
sp. nov. 1	1110111101	1111011011	110110--11	0-11040301	-110-1110-	110-210-21
sp. nov. 2	1121121101	2111012012	120120--22	0-2100-301	-120-1120-	120-230-21
sp. nov. 3	1120121101	2111012012	120120--12	0-11010501	-120-1120-	120-230-21
Species	Characters 61–120					
<i>N. muscorum</i>	10200-2010	30--0-20--	10200-2010	2003---002	00-2010200	30-0-200-2
<i>P. ieti</i>	2010202020	20--1010--	2010101020	10110--201	0101010101	10-1010101
<i>S. austriaca</i>	10200-200-	30--0-20--	101010100-	20020--101	010100-200	20-1010101
<i>A. mexicana</i>	0-11201101	31110-3110	0-11101110	2102110001	1101110210	2100-11101
<i>A. setafoleacea</i>	10120-120-	11010-2110	10120-120-	1202110001	20-120-120	2100-110-1
<i>P. colotlipa</i>	10120-120-	21100-2110	10120-120-	1201110101	20-120-120	11010120-1
<i>P. curta</i>	10120-120-	21010-2110	10120-120-	1202110101	20-120-120	21010120-1
<i>P. lacandona</i>	10120-120-	11010-1101	10120-120-	1201110001	20-120-120	1100-120-1
<i>P. lindquisti</i>	10120-120-	21010-2110	10120-120-	1201110101	20-120-120	11010120-1
<i>P. matildae</i>	21120-120-	11010-1110	21120-120-	1201110101	20-120-120	11010120-1
<i>P. mirabilis</i>	10120-120-	21010-2111	10120-120-	1202101101	20-120-120	20110120-1
<i>P. longa</i>	10110-110-	21100-2110	10110-110-	1102110101	10-110-110	21010110-1
<i>P. normae</i>	0-110-110-	11100-1110	10110-110-	1101110001	10-110-110	1100-110-1
<i>P. pascuali</i>	0-120-120-	11010-1110	0-120-120-	1201110101	20-120-120	11010120-1
<i>P. primigenia</i>	201221120-	21010-1110	201211120-	1202110101	211120-120	2101012111
<i>P. quetzalae</i>	10120-120-	11010-2110	10110-120-	1201101001	10-120-120	1110-110-1
<i>P. saham</i>	10120-120-	11010-2111	10120-120-	1201101001	20-120-120	11110120-1
<i>P. schusteri</i>	10120-120-	21100-2110	10120-120-	1202110101	20-120-120	21010120-1
<i>P. wilsoni</i>	200-100-10	0---210---	2000120-21	0-10---110	-120-110-1	0--110-120
sp. nov. 1	0-110-110-	21100-2110	0-110-110-	1102110101	10-110-110	21010110-1
sp. nov. 2	10120-120-	21110-2110	10120-120-	1202110101	20-120-120	21010120-1
sp. nov. 3	10120-120-	21110-2110	10120-120-	1201110111	20-120-120	11010120-1

(Continued)

Species	Characters 121–153			
<i>N. muscorum</i>	010200–30–	1200–20020	0–40120104	010
<i>P. ieti</i>	020101010–	2101010120	2030210204	020
<i>S. austriaca</i>	00–200–20–	2101010110	1020410103	00–
<i>A. mexicana</i>	110210–210	0111021011	10301210–3	00–
<i>A. setafoleacea</i>	10–110–110	1110–11011	0–231110–3	20–
<i>P. colotipa</i>	20–120–110	1120–12011	0–112120–2	10–
<i>P. curta</i>	20–120–110	1120–12012	0–231120–2	30–
<i>P. lacandona</i>	20–120–110	1120–12010	0–102120–1	111
<i>P. lindquisti</i>	20–120–110	1120–12011	0–113120–2	30–
<i>P. matildae</i>	20–120–110	2120–12011	0–112120–1	111
<i>P. mirabilis</i>	20–120–201	1120–12011	0–112120–2	30–
<i>P. longa</i>	10–110–210	1110–11011	0–110110–2	10–
<i>P. normae</i>	10–110–110	1110–11011	0–???110–1	111
<i>P. pascuali</i>	20–120–110	0120–12011	0–???120–1	110
<i>P. primigenia</i>	20–120–110	2120–12012	0–113120–2	30–
<i>P. quetzalae</i>	20–120–110	2120–12012	0–113120–2	10–
<i>P. saham</i>	20–120–111	1120–12012	10121120–2	30–
<i>P. schusteri</i>	20–120–110	2120–12012	0–11?120–2	10–
<i>P. wilsoni</i>	–110–110–	10–110–10–	110–10–110	–20
sp. nov. 1	10–110–210	1110–11011	0–232110–0	–0–
sp. nov. 2	20–120–210	1120–12012	0–232120–3	10–
sp. nov. 3	20–120–200	2120–12011	0–???120–2	10–

Appendix 4

Character statistics from the parsimony analysis based on unordered (nonadditive) character states: character number, number of steps on the tree, consistency index and retention index (CI and RI, respectively; RI values of 0.00 denote characters that were noninformative in this context). *w*, final weights given under a subsequent successive weighting analysis of the same data (details in main text).

No.	Steps	CI	RI	<i>w</i>	No.	Steps	CI	RI	<i>w</i>
1	2.0	0.5	0.0	0.0	27	1.0	1.0	0.0	1.0
2	2.0	0.5	0.0	0.0	28	1.0	1.0	0.0	1.0
3	3.0	0.7	0.8	0.5	29	8.0	0.4	0.3	0.1
4	5.0	0.2	0.2	0.0	30	4.0	0.5	0.7	0.3
5	2.0	0.5	0.0	0.0	31	4.0	0.8	0.7	0.5
6	3.0	0.7	0.8	0.5	32	1.0	1.0	0.0	1.0
7	2.0	0.5	0.5	0.2	33	7.0	0.4	0.4	0.2
8	2.0	0.5	0.5	0.2	34	7.0	0.6	0.4	0.2
9	2.0	0.5	0.0	0.0	35	2.0	0.5	0.0	1.0
10	2.0	0.5	0.0	0.0	36	9.0	0.4	0.4	0.2
11	3.0	0.7	0.8	0.5	37	7.0	0.6	0.5	0.2
12	2.0	0.5	0.5	0.2	38	14.0	0.4	0.1	0.1
13	2.0	0.5	0.7	0.3	39	2.0	0.5	0.0	0.0
14	2.0	0.5	0.7	0.3	40	2.0	0.5	0.5	0.2
15	1.0	1.0	0.0	1.0	41	1.0	1.0	0.0	1.0
16	2.0	0.5	0.0	0.0	42	2.0	0.5	0.0	1.0
17	5.0	0.4	0.6	0.2	43	2.0	1.0	1.0	1.0
18	1.0	1.0	0.0	1.0	44	2.0	0.5	0.7	0.3
19	2.0	0.5	0.0	0.0	45	2.0	1.0	0.0	1.0
20	4.0	0.5	0.6	0.3	46	5.0	0.4	0.7	0.2
21	1.0	1.0	0.0	1.0	47	3.0	0.7	0.0	0.0
22	3.0	0.7	0.8	0.5	48	2.0	1.0	1.0	1.0
23	1.0	1.0	0.0	1.0	49	4.0	0.5	0.0	0.0
24	1.0	1.0	0.0	1.0	50	2.0	0.5	0.0	0.0
25	3.0	0.7	0.8	0.5	51	2.0	1.0	1.0	1.0
26	3.0	0.7	0.7	0.4	52	2.0	1.0	1.0	1.0

No.	Steps	CI	RI	w	No.	Steps	CI	RI	w
53	2.0	0.5	0.7	0.3	104	2.0	0.5	0.0	1.0
54	2.0	0.5	0.0	1.0	105	2.0	1.0	1.0	1.0
55	7.0	0.4	0.5	0.2	106	2.0	0.5	0.5	0.3
56	6.0	0.5	0.6	0.3	107	2.0	0.5	0.0	1.0
57	2.0	1.0	0.0	1.0	108	3.0	0.7	0.0	0.3
58	1.0	1.0	0.0	1.0	109	2.0	1.0	1.0	1.0
59	6.0	0.5	0.4	0.2	110	3.0	0.7	0.0	1.0
60	4.0	0.8	0.7	0.5	111	11.0	0.3	0.0	0.3
61	8.0	0.3	0.0	0.1	112	2.0	0.5	0.8	0.3
62	1.0	1.0	0.0	1.0	113	1.0	1.0	1.0	1.0
63	3.0	0.7	0.0	0.0	114	5.0	0.2	0.0	0.0
64	2.0	1.0	1.0	1.0	115	2.0	0.5	0.0	1.0
65	4.0	0.5	0.0	0.0	116	2.0	0.5	0.0	1.0
66	1.0	1.0	0.0	1.0	117	3.0	0.7	0.9	0.5
67	2.0	1.0	1.0	1.0	118	3.0	0.3	0.3	0.1
68	2.0	1.0	1.0	1.0	119	2.0	1.0	1.0	1.0
69	3.0	0.7	0.0	1.0	120	2.0	0.5	0.0	1.0
70	1.0	1.0	0.0	1.0	121	2.0	1.0	1.0	1.0
71	8.0	0.4	0.4	0.2	122	3.0	0.7	0.0	0.3
72	1.0	1.0	1.0	1.0	123	2.0	0.5	0.0	1.0
73	5.0	0.2	0.4	0.1	124	3.0	0.7	0.0	0.3
74	3.0	0.3	0.6	0.2	125	2.0	1.0	1.0	1.0
75	2.0	0.5	0.0	0.0	126	2.0	0.5	0.0	1.0
76	2.0	0.5	0.0	1.0	127	2.0	0.5	0.0	1.0
77	6.0	0.3	0.3	0.2	128	8.0	0.4	0.0	0.1
78	1.0	1.0	1.0	1.0	129	3.0	0.3	0.6	0.1
79	2.0	0.5	0.0	1.0	130	2.0	0.5	0.0	0.0
80	3.0	0.3	0.0	0.0	131	8.0	0.3	0.0	0.0
81	6.0	0.3	0.0	0.0	132	2.0	0.5	0.0	1.0
82	2.0	0.5	0.0	1.0	133	2.0	1.0	1.0	1.0
83	2.0	0.5	0.0	1.0	134	2.0	0.5	0.5	0.3
84	3.0	0.7	0.9	0.5	135	2.0	0.5	1.0	1.0
85	3.0	0.3	0.3	0.1	136	2.0	0.5	1.0	0.0
86	2.0	1.0	1.0	1.0	137	2.0	1.0	1.0	1.0
87	2.0	0.5	0.0	1.0	138	2.0	0.5	0.7	0.2
88	2.0	1.0	1.0	1.0	139	3.0	0.7	0.0	1.0
89	3.0	0.7	0.0	0.3	140	8.0	0.3	0.3	0.2
90	2.0	0.5	0.0	1.0	141	4.0	0.5	0.0	0.1
91	3.0	0.7	0.0	0.3	142	2.0	0.5	0.0	1.0
92	2.0	1.0	1.0	1.0	143	8.0	0.5	0.2	0.4
93	3.0	0.7	0.0	1.0	144	7.0	0.4	0.3	0.4
94	11.0	0.3	0.0	0.3	145	10.0	0.4	0.0	0.0
95	1.0	1.0	0.0	1.0	146	2.0	0.5	0.0	0.0
96	2.0	0.5	0.7	1.0	147	2.0	1.0	1.0	1.0
97	1.0	1.0	1.0	1.0	148	2.0	1.0	1.0	1.0
98	8.0	0.3	0.0	0.0	149	2.0	0.5	0.0	1.0
99	3.0	0.3	0.0	0.0	150	9.0	0.4	0.4	0.3
100	2.0	0.5	0.0	1.0	151	7.0	0.4	0.4	0.2
101	3.0	0.7	0.8	0.5	152	5.0	0.4	0.4	0.3
102	3.0	0.3	0.3	0.1	153	2.0	0.5	0.7	0.2
103	2.0	1.0	1.0	1.0					

Appendix 5

Character state changes along the cladogram based in parsimony analysis of unordered character states. Branch labels (bold) correspond to those in Fig. 1. The syntax is used is 'character number: plesiomorphic > apomorphic'. The nonhomoplastic changes are given first for each branch; state changes in brackets denote homoplastic state changes (see Appendix 3 for details on character performance on that tree). Polarity of changes along branches 1 and 2 was set intuitively based on the available evidence.

1. 29:1 > 3, 31:1 > 3, 41:0 > 1, 42:1 > 2, 94:2 > 3, 111:2 > 3, 128:2 > 3, 143:2 > 4; (10:0 > 1, 89:0 > 1, 150:3 > 4, 152:0 > 1). **2.** 1:0 > 1, 26:1 > 2, 44:0 > 1, 83:2 > 1, 87:2 > 1, 98:0 > 1, 100:2 > 1, 104:2 > 1, 114:0 > 1, 116:2 > 1, 120:2 > 1, 132:2 > 1, 134:0 > 1, 138:0 > 1; (38:3 > 4, 47:2 > 1, 63:2 > 1, 69:1 > 0, 85:0 > 1, 102:0 > 1, 118:0 > 1, 136:2 > 1, 139:2 > 1, 141:0 > 1, 146:2 > 1). **3.** 21:1 > 0, 23:0 > 1, 33:0 > 3, 145:1 > 4; (2:1 > 0, 5:1 > 0, 16:1 > 0, 19:1 > 0, 47:1 > 2, 53:1 > 0, 63:1 > 2, 106:1 > 0, 122:1 > 0, 131:1 > 2). **4.** 28:0 > 1, 35:0 > 1, 49:0 > 1, 55:3 > 0, 57:0 > 1, 59:2 > 0, 65:0 > 1, 71:3 > 0; 77:2 > 0, 89:0 > 2, 91:2 > 0, 94:2 > 0, 108:2 > 0, 110:0 > 1, 111:2 > 0, 124:2 > 0, 126:0 > 1, 128:2 > 0, 139:1 > 0, 143:2 > 0, 152:0 > 2; (11:0 > 2, 36:4 > 1, 38:4 > 2, 61:1 > 2,

69:0 > 1, 75:0 > 1, 81:1 > 2, 150:3 > 0). **5.** 3:0 > 1, 6:0 > 1, 11:0 > 1, 20:0 > 1, 22:0 > 1, 34:0 > 1, 43:0 > 1, 46:0 > 1, 48:0 > 1, 51:2 > 1, 52:0 > 1, 54:0 > 1, 64:0 > 1, 67:2 > 1, 68:0 > 1, 70:0 > 1, 72:0 > 1, 78:0 > 1, 88:0 > 1, 92:0 > 1, 105:0 > 1, 109:0 > 1, 112:0 > 1, 121:0 > 1, 125:0 > 1, 129:0 > 1, 133:0 > 1, 137:0 > 1, 140:0 > 1, 147:0 > 1, 148:0 > 1, 153:0 > 1; (7:0 > 1, 8:0 > 1, 10:0 > 1, 12:0 > 1, 17:0 > 1, 25:0 > 1, 30:0 > 1, 33:0 > 2, 40:0 > 1, 50:0 > 1, 60:0 > 1, 61:1 > 0, 84:0 > 1, 101:0 > 1, 117:0 > 1, 138:1 > 0). **6.** 35:1 > 2, 69:1 > 2, 98:1 > 2, 122:1 > 2, 141:1 > 2, 148:1 > 2; (1:1 > 0, 9:0 > 1, 33:0 > 1, 49:1 > 2, 55:0 > 2, 59:0 > 1, 65:1 > 2, 71:0 > 2, 77:0 > 1, 91:0 > 1, 94:0 > 1, 108:0 > 1, 111:0 > 1, 124:0 > 1, 128:0 > 1, 131:1 > 2, 139:0 > 2, 143:0 > 3, 145:1 > 2, 150:0 > 4). **7.** 24:1 > 0, 27:0 > 1, 29:1 > 0, 31:1 > 2, 32:0 > 1, 38:2 > 6, 42:1 > 0, 45:0 > 2, 47:1 > 0, 51:2 > 0, 54:0 > 2, 47:1 > 0, 51:2 > 0, 54:0 > 2, 57:1 > 2, 58:0 > 1, 63:1 > 0, 67:2 > 0, 75:1 > 2, 76:0 > 1, 83:1 > 0, 86:0 > 2, 87:1 > 0, 90:0 > 1, 100:1 > 0, 103:0 > 2, 104:1 > 0, 107:0 > 1, 115:0 > 1, 116:1 > 0, 119:0 > 2, 120:1 > 0, 123:0 > 1, 127:0 > 1, 132:0 > 1, 135:0 > 1, 136:1 > 0, 142:0 > 1, 146:1 > 0, 149:0 > 1; (2:1 > 0, 3:0 > 2, 5:1 > 0, 6:0 > 2, 7:0 > 1, 8:0 > 1, 12:0 > 1, 13:0 > 1, 14:0 > 1, 16:0 > 1, 17:0 > 2, 19:1 > 0, 20:0 > 2, 22:0 > 2, 26:2 > 1, 36:1 > 2, 40:0 > 1, 50:0 > 1, 99:0 > 1). **8.** 59:2 > 3, 77:2 > 3; (20:1 > 2, 37:0 > 3, 49:0 > 2, 66:0 > 2, 75:0 > 1, 81:1 > 0, 89:0 > 1, 98:1 > 0; 114:1 > 0, 131:1 > 0, 136:1 > 2, 143:2 > 3, 146:1 > 2). **9.** 26:2 > 0, 31:1 > 0, 66:0 > 1, 88:0 > 1, 103:0 > 1, 119:0 > 1; (13:0 > 1, 14:0 > 1, 29:1 > 2, 36:4 > 1, 38:4 > 3, 44:1 > 0, 50:0 > 1, 53:1 > 0, 55:3 > 2, 71:3 > 2, 85:1 > 0, 91:2 > 1, 102:1 > 0, 106:1 > 0, 108:2 > 1, 118:1 > 0, 122:1 > 0, 124:2 > 1, 134:1 > 0, 141:1 > 0, 144:0 > 3, 145:1 > 2, 151:0 > 1). **10.** 37:0 > 2, 145:2 > 0; (36:1 > 2, 38:3 > 4, 61:0 > 1, 143:2 > 1, 144:3 > 1, 150:3 > 2). **11.** (45:1 > 0, 55:2 > 1, 59:2 > 1, 71:2 > 1, 77:2 > 1, 94:2 > 1, 98:1 > 0, 111:2 > 1, 114:1 > 0, 128:2 > 1, 150:3 > 1, 152:0 > 1). **12.** (29:2 > 1, 33:2 > 1, 36:1 > 4, 81:1 > 0, 150:3 > 0). **13.** 25:1 > 2, 30:1 > 2, 43:1 > 2, 48:1 > 2, 52:1 > 2, 56:1 > 2, 64:1 > 2, 68:1 > 2, 73:1 > 0, 74:0 > 1, 84:1 > 2, 88:1 > 2, 92:1 > 2, 101:1 > 2, 105:1 > 2, 109:1 > 2; (4:0 > 1, 11:1 > 2, 128:2 > 1). **14.** 151:1 > 2; (9:0 > 1, 38:3 > 0, 55:2 > 1, 71:2 > 1, 98:1 > 0, 114:1 > 0, 145:2 > 1). **15.** 117:1 > 2, 121:1 > 2, 125:1 > 2, 133:1 > 2, 137:1 > 2, 147:1 > 2; (3:1 > 2, 6:1 > 2, 17:1 > 2, 20:1 > 2). **16.** 36:1 > 0; (56:2 > 3, 73:0 > 1, 128:1 > 2, 140:1 > 2). **17.** (4:1 > 0, 29:2 > 1, 33:2 > 1, 38:3 > 2, 94:2 > 1, 111:2 > 1, 143:2 > 1, 144:3 > 1, 150:3 > 2). **18.** (30:2 > 1, 34:1 > 2, 56:2 > 1, 73:0 > 1, 74:1 > 0). **19.** (36:1 > 4, 37:0 > 3, 46:1 > 2, 94:1 > 2, 111:1 > 2, 140:1 > 2, 143:1 > 2, 144:1 > 3, 145:2 > 1, 151:1 > 3). **20.** 38:2 > 5; (56:2 > 3, 73:0 > 1, 99:0 > 1, 128:1 > 2, 129:1 > 0, 131:1 > 2). **21.** (37:0 > 1, 94:1 > 2, 111:1 > 2, 131:1 > 2, 140:1 > 2, 145:2 > 3). **22.** (33:1 > 2, 38:2 > 0, 55:2 > 1, 59:2 > 1, 71:2 > 1, 77:2 > 1, 150:2 > 1, 152:0 > 1). **23.** (29:1 > 2, 33:1 > 2, 36:1 > 2, 37:0 > 3, 38:2 > 4, 46:1 > 2, 145:2 > 3, 151:1 > 3). **24.** (4:0 > 1, 39:0 > 1, 49:0 > 2, 59:2 > 1, 61:1 > 2, 65:0 > 2, 77:2 > 1, 81:1 > 2, 85:0 > 1, 102:0 > 1, 118:0 > 1, 151:1 > 3). **25.** (17:2 > 0, 34:1 > 2, 46:1 > 0, 56:2 > 1, 73:0 > 1, 74:1 > 0). **26.** 150:0 > 1, 34:1 > 3, 60:1 > 2, 79:1 > 0; (38:0 > 3, 80:0 > 1, 98:1 > 0, 114:1 > 0, 140:1 > 0, 144:1 > 0). **27.** 62:0 > 1; (40:0 > 1, 61:1 > 0, 81:1 > 0, 131:1 > 0). **28.** (37:0 > 1, 38:0 > 4, 61:0 > 2, 81:0 > 2, 131:0 > 2). **29.** (17:2 > 1, 25:2 > 1, 29:1 > 2, 30:2 > 1, 34:1 > 2, 133:1 > 0). **30.** (39:0 > 1). **31.** 37:3 > 4, 60:1 > 3, 96:1 > 0, 97:0 > 1, 113:0 > 1, 130:0 > 1; (34:1 > 2). **32.** (94:1 > 2, 111:1 > 2, 112:1 > 0, 128:1 > 2, 129:1 > 0, 145:3 > 2). **33.** (38:4 > 0, 55:2 > 1, 71:2 > 1, 98:1 > 0, 140:1 > 2). **34.** 34:2 > 3; (4:0 > 1, 60:3 > 1, 80:1 > 0, 84:2 > 1, 101:2 > 1, 114:1 > 0, 117:2 > 1, 130:1 > 0, 131:1 > 2, 151:3 > 1). **35.** 38:2 > 3, 144:1 > 2; (29:2 > 1, 31:0 > 1, 38:0 > 3, 141:0 > 1, 145:3 > 1).