Stachorutes cabagnerensis n. sp., Collembola (Neanuridae) from Central Spain, and a preliminary approach to phylogeny of genus

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Simón Benito, J. C., Espantaleón, D. & García–Barros, E., 2005. *Stachorutes cabagnerensis* n. sp., Collembola (Neanuridae) from Central Spain, and a preliminary approach to phylogeny of genus. *Animal Biodiversity and Conservation*, 28.2: 149–157.

Abstract

Stachorutes cabagnerensis *n. sp., Collembola (Neanuridae) from Central Spain, and a preliminary approach to phylogeny of genus*.— A new species of the genus *Stachorutes*, *Stachorutes cabagnerensis* n. sp., from central Spain is described. It is characterized by the presence of 6+6 eyes in the head, retinaculum 2+2 teeth, dentes with 5 hairs, and the absence of mucron. A phylogenetic analysis of this genus was attempted. Potential synapomorphies supporting the monophyly of *Stachorutes* are presented. One member of the genus (the Nearctic *S. navajellus*) appears as a basal form, phylogenetically distant from the remaining (Old World) species. There is evidence for a monophyletic infrageneric clade with the species *S. dematteisi, S. jizuensis and* S. *sphagnophilus*. However, more information is required for further phylogenetic resolution.

Key words: Collembola, *Stachorutes*, Spain, Phylogeny.

Resumen

Stachorutes cabagnerensis *sp. n., Collembola (Neanuridae) de la región central de España, y una aproximación preliminar a la filogenia del género*.— Se describe una nueva especie del genero *Stachorutes* de la region central de España. *Stachorutes cabagnerensis* nov. sp. se caracteriza por la presencia de 6+6 ojos en la cabeza, retinaculum con 2+2 dientes y 5 sedas en cada rama del dentes; la furca carece de mucrón. Se ha efectuado un análisis filogenético. Las sinapomorfias potenciales establecen la monofilia del género. Una especie del mismo, *S. navajellus,* aparece como forma basal, filogenéticamente distante del resto de especies (Viejo Mundo). Se podría establecer un clado infragenérico con las especies *S. dematteisi, S. jizuensis* y *S. sphagnophilus*. Sin embargo, se precisa de mayor información para poder confirmarlo.

Palabras clave: Colembolos, *Stachorutes*, España, Filogenia.

(Received: 13 VIII 04; Conditional acceptance: 18 XI 04; Final acceptance: 13 I 05)

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ISSN: 1578–665X

Introduction

The genus *Stachorutes* was established by Dallai (Dallai, 1973) from Italian specimens from the province of Canzo, according to the type species *Stachorutes dematteisi.* Dallai characterized it for its small Antenna IV with simple sensillae, jaw with two teeth, simple maxillae, 2+2 eyes disposed as in the genus *Micranurida*, postantennal organ present, claw without empodial appendage, tenent hairs absent, reticulum and furca present, and without anal spines. Deharveng & Lienhard (1983) established two new species taken from the Eastern French Pyrenees and the Swiss Alps, and re–defined the genus. A further re–definition was later proposed by Jordana et al. (1997) in their monograph on Iberian Collembola. Thibaud & Palacios–Vargas (2000) added new characters, which resulted in an even sharper definition of the genus. A summary of the morphological features of potential use for defining *Stachorutes* is given in table 1.

At present, *Stachorutes* Dallai consists of 16 species distributed all around the world. Eight species occur in Europe: S. *cabagnerensis* n. sp.; *S. dematteisi* Dallai, 1973*; S. longirostris* Deharveng & Lienhard, 1983; *S. ruseki* Kovac,1999; *S. scherae* Deharveng & Lienhard, 1983*, S. sphagnophilus* Slawaska, 1996*; S. tatricus* Smolis & Skarzynski 2001 (Smolis & Skarzynski, 2001)*, S. valdeaibarensis* Arbea & Jordana, 1991. One species is known from Africa (S. *dallai* Weiner and Najt, 1998), three from North America: S. *escobarae* (Palacios–Vargas, 1990)*, S. maya* Thibaud & Palacios–Vargas, 2000 and *S. navajellus* Fjellberg, 1994 and four in Asia: S. *ashrafi* (Yosii, 1966), *S. jizuensis* Tamura and Zhao, 1997; *S. tieni* Pomorski & Smolis, 1999 and *S. triocelatus* Pomorski & Smolis, 1999. The primary purpose of the present study was to describe a new taxon, S. *cabagnerensis* n. sp. However, since no attempt has currently been directed either at testing the monophyly of the genus, or at resolving its internal relationships, a preliminary approach to these questions was attempted. This task was complicated by the generally low degree of phylogenetic resolution of the group. However, given the small number of species, and the lack of information on the majority of them, any insight into the problem may help in facilitating taxa and character selection for further phylogenetic studies on pseudachorutine springtails.

Material and methods

The new species of *Stachorutes*

Soil samples were taken following the standard method designed for the research project "Bioasses". An area of 1 km^2 was chosen in each selected land unit and a sample was taken every 200 m. A total of 16 units was prospected, each consisting of six spots representing different stages in development of the vegetation. In Spain, the National Park of Cabañeros was chosen and divided into six different units. In each of them, samples were collected according to the method designed. Individuals belonging to the genus *Stachorutes* were obtained in wooded units only. These locations were: Unit 1. Natural wood with vegetation of holly oaks *Quercus ilex ilex* L., oaks *Quercus pyrenaica* Wild. and cork oaks *Quercus suber* L., with undergrowth of cistus *Cistus ladanifer* L., heather *Erica australis* L. and *Erica arborea* L., arbutus *Arbutus unedo* L., located in the province of Ciudad Real in Navas de Estenas, UTM: 30SVJ5754. Samples 106–H, fallen leaves from holly oak, with heather and moss, nine specimens. Unit 2. Reforestation pinewood, *Pinus pinaster* Aiton, also in the province of Ciudad Real, in Horcajo de los Montes, UTM: 30SVJ6973. Sample 204–H$_{2,}$ fallen pine leaves after second year, three specimens. Sample 207–H, fallen pine leaves, two specimens. All samples were taken during the months of April and May (2001), a period characterised by a seasonal maximum in the numbers of both individuals and species (Simón, unpubl. data).

Cladistic analysis

The data matrix was analysed using the program Henning 86 (Farris, 1988; options h*, mh* and bb*), treating all multistate characters as unordered. As an alternative exploratory option, the successive weighting approach (Farris, 1969, 1989) was attempted with the same programme. All other analyses, as well as character state optimisation, were completed through Winclada (Nixon, 2002) and Nona (Goloboff, 1993) (strict, majority consensuses, as well as bootstrap and jacknife tests with 100 replicates). Since the number of species currently included in *Stachorutes* is low, an effort was made to include all of them in the analyses. This resulted in two problems related to the character state coding (see character list below): First, only partial information from *S. ashrafi* was available, and as many as 5 of the 13 characters were coded as unknown. Second, character 12 was found to be variable among individuals of *S. longirostris* from Pyrenean samples. Given the inability of the cladistic packages used in this study to make a different treatment of unknown vs. non comparable character states, this species was entered as four different taxa (a,b,c,d). We believe that these decisions may be acceptable given the prospective nature of our approach.

Description

Stachorutes cabagnerensis n. sp.

Length of 0.66 mm in adult/s and 0.44 mm in young, dark blue in the adult/s, and light blue in the juveniles. Dorsal setae reduced, subequal, with sensillae longer and thicker than in normal hairs. Integument with thickly grained surface.

Reduced mouth parts, jaw with 4 teeth, maxilla

Table 1. Anatomical features of potential use in the definition of the genus *Stachorutes*, as stated by different authors (+ feature present; – feature absent): A. Dallai, 1973; B. Deharveng & Lienhard, 1983; C. Jordana et al., 1997; D. Thibaud & Palacios–Vargas, 2000. Note that some of these characters display no variation within *Stachorutes*, and were not coded for phylogenetic analyses.

Tabla 1. Carácteres anatómicos de uso potencial en la definición del género Stachorutes*, según distintos autores (+ caracter presente; – caracter ausente): A. Dallai, 1973; B. Deharveng & Lienhard, 1983; C. Jordana et al., 1997; D. Thibaud & Palacios–Vargas, 2000. Nótese que algunos de estos caracteres no presentan variación alguna dentro del género* Stachourutes*, y no fueron utilizados para los análisis filogenéticos.*

Anatomical features	A	B	C	D
Antenna IV with 5–6 sensilla cylindrical and one microsensilla		+	+	+
Antenna IV with sensilla in flame–shape and one microsensilla			+	
Antenna IV without hair–brush		+	+	
Antenna IV and III join		+	+	
Postantennal organ with vesicles simple never moruliform				+
Less than 8+8 eyes	+	+	+	+
Maxilla styliform	+	+	+	+
Empodial appendage	–	–	–	–
Tenent hairs	–	–	–	–
Furca reduced	+	+	+	+
Tenaculum	+	+	+	+
Mucron	–	+/–	+	+/–
Chaetotaxy dorsal reduced		+	–	+
Macrochaetae			–	–
Anal spines	–		–	–

styli form with two teeth,one ending in two apical teeth and the other in a hook with 5–6 teeth along the apical area. Labium without hair L, its relation with the length of the nail is 3 (fig. 2).

Ocular spot with 6 eyes, 3 anterior (A, B, C) and 3 posterior (E, F, G), the H and D are lacking (fig. 4).

Oval post antennal organ with 13 to 15 vesicles similar in size, disposed in one line, twice longer than the nearest corneola and with approximately the same diameter (fig. 4).

Antenna quite thick, the relation with the head diameter is 0.54 in adults and 0.58 in juveniles. Antenna I with 7 hairs, II with 12, III and IV are joined dorsally; segment III shows about 17 hairs and a sensorial organ formed by two microsensilla (si) as a war club and long thick lateral sensilla: (sgd) and (sgv) and an extra ventral microsensilla (sa). Antenna IV with normal hairs, straight, some small, without sensorial hair–brush in the ventral area. With 6 olfactory sensilla, 4 in the dorsal area (S1 to S4) forming a rhomb, and 2 in the ventro–apical area (S7, S8). Furthermore, there is a dorsal external microsensilla (m) and a very small distal organ. An apical tri–lobed vesicle is located at the apex of the antenna (fig. 5).

Reduced dorsal chaetotaxy (fig. 1), the position of the most internal sensilla S is: 3, 3/4, 4, 4, 4, 2 hairs, from thorax II to abdomen V. The formula of the dorsal inner hairs is 1, 3, 3/3, 3, 3, 2. Head without hair a_0, the hairs d_0 odd. Pronotum with 3+3 hairs. Mesonotum with a_2. Tibiotarsi I, II, III with 19, 19, 18 hairs disposed in two whorls, the apical with 11 hairs and the basal with 8 hairs, except in the third pair of legs which shows 7 hairs, without tenent hairs (fig. 3). Ventral tube with 4+4 hairs, 2+2 basal and 2+2 apical.

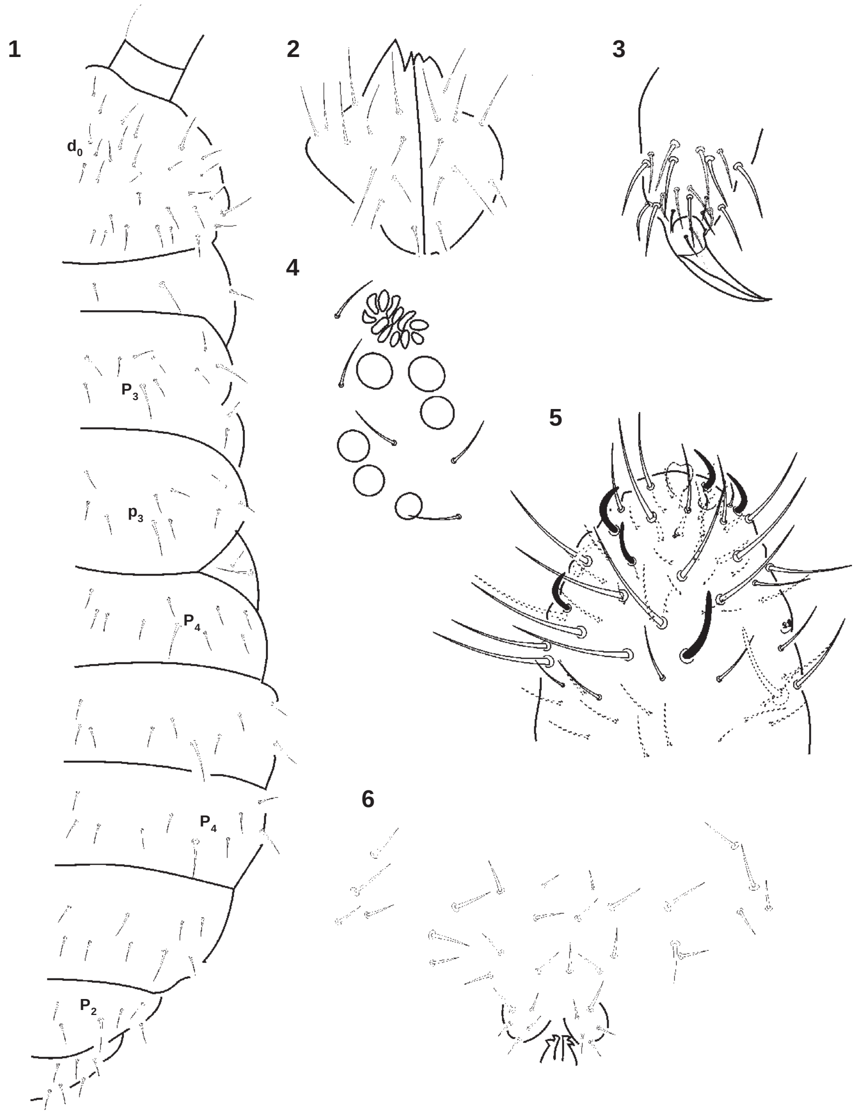
Claw without teeth and empodial appendage.

Tenaculum with 2+2 teeth. Dens without mucron, and five hairs, manubrium with 7–9+7–9 hairs (fig.6).

Genital orifice in the male with 18 hairs, in the female with 8 hairs in the anterior margin of the genital orifice, plus two central ones.

Discussion

The new species shows 6+6 eyes like two other species of this genus, *ruseki* Kovac, 1999 from Slovakia and *ashrafi* (Yosii, 1966) from Nepal. This latter species may however not belong to this genus because of the number of olfactory



Figs. 1–6. 1. Dorsal chaetotaxy; 2. Labium; 3.Tibiotarsus; 4. Eyes and postantennal organ; 5. IV and III antennal segment; 6. Furca.

Figs. 1–6. 1. Quetotaxia dorsal; 2. Labio; 3. Tibiotarso; 4. Ojos y órgano postantenal; 5. Segmento antenal III y IV; 6. Furca.

hairs. *Stachorutes cabagnerensis* differs from both in the number of teeth of the tenaculum (2 compared to 3), and in the structure of the dentes (5 hairs against 6), and in the lack of mucron.

Phylogenetic analysis

A matrix of 13 characters (8 binary and 5 multistate) was prepared (table 2). The state 0 corresponds to the plesiomorphic character state. Rooting was done with reference to *Pseudachorutes parvulus* Börner, 1901.

Results

Henning analysis produced 626 trees with a length of 50 steps (CI = 50, RI = 63). All characters except 2, 6 and 8 showed a certain degree of homoplasy, (table 3).

The strict consensus of these cladograms is shown in fig. 7 (tree length, 76; CI, 32; RI, 25). On the assumption that *Stachorutes* represents a monophyletic assemblage, its monophyly can be supported by the synapomorphies 0:1 and 4:2 (that is, state 1 of character 0, and state 2 of

Table 2. Matrix of species x character state. *Pseudachorutes parvulus* was used as outgroup: 0. Jaw (number of teeth: 0 = 4 teeth; 1 = 3 teeth; and 2 = 2 teeth); 1. Olfactory hairs of the Antenna IV (0 = tubular; 1 = in the shape of a sparkling flame); 2. PAO (shape of the postantenna organ: 0 = circular; 1 = elliptic); 3. Number of vesicles in the postantennal organ (0 = less than 10; 1 = 11 or more); 4. Number of eyes (0 = 8 eyes; 1 = 6 eyes; 2 = 5 eyes; 3 = 3 eyes; 4 = 2 eyes; 5 = 1 eye; 6 = 0 eyes); 5. Hair a_0 in the head (0 = with this hair; 1 = without it); 6. Hair d_0 in the head (0 = odd or without it; 1 = pair); 7. Number of hairs in the pronotum (0 = 3+3 hairs; 1 = 2+2 hairs; 2 = 4+4 hairs); 8. Hair a_2 in the mesonotum (0 = with hair; 1 = without hair); 9. Number of hairs in the tibiotarsum I, II, III (0 = 19, 19, 18; 1 = another condition); 10. Number of teeth in the retinaculum (0 = 3+3 teeth; 1 = 2+2 teeth); 11. Number of hairs in the dentes (0 = 6 hairs; 1 = 5 hairs; 2 = 4 hairs; 3 = 3 hairs; 4 = 2 hairs; 5 = 1 hairs); 12. Mucron (0 = mucron separated from the dentes; 1 = mucrodens; 2 = absent). ? Indicates that the character state is unknown.

Tabla 2. Matriz de especies x estados del carácter estudiado. Se utilizó a *Pseudachorutes parvulus como grupo externo: 0. Mandíbula (número de dientes: 0 = 4 dientes; 1 = 3 dientes; and 2 = 2 dientes); 1. Sedas olfactorias de la antena IV (0 = tubular; 1 = en forma de llama de bujía); 2. PAO (forma del órgano postantenal: 0 = circular; 1 = elíptica); 3. Numero de vesículas del órgano postantenal (0 = menos de 10; 1 = 11 o más); 4. Número de ojos (0 = 8 ojos; 1 = 6 ojos; 2 = 5 ojos; 3 = 3 ojos; 4 = 2 ojos; 5 = 1 ojo; 6 = 0 ojos); 5. Seda* a_0 *de la cabeza (0 = con esta seda; 1 = sin ella); 6. Seda* d_0 *de la cabeza (0 = impar o sin seda; 1 = par); 7. Número de sedas del pronoto (0 = 3+3 sedas; 1 = 2+2 sedas; 2 = 4+4 sedas); 8. Seda* a_2 *del mesonoto (0 = con seda; 1 = sin seda); 9. Número de sedas del tibiotarso I, II, III (0 = 19, 19, 18; 1 = otra condición); 10. Número de dientes del retináculo (0 = 3+3 dientes; 1 = 2+2 dientes); 11. Número de sedas del dentes (0 = 6 sedas; 1 = 5 sedas; 2 = 4 sedas; 3 = 3 sedas; 4 = 2 sedas; 5 = 1 sedas); 12. Mucrón (0 = mucrón separado del dentes; 1 = mucrodens; 2 = ausente). ? indican que se desconoce el estado del carácter citado.*

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	Distribution
Pseudachorutes parvulus	0	0	0	0	0	0	0	0	0	0	0	0	0	Cosmopolitan
Stachortes ashrafi	1	0	1	1	1	?	?	?	?	?	0	0	1	Nepal
S. cabagnerensis n. sp.	0	0	1	1	1	1	0	0	0	0	1	1	2	Spain
S. dallai	2	0	0	0	4	1	1	0	0	0	1	1	1	Tanzania
S. dematteisi	2	0	0	0	4	1	0	0	0	?	1	4	2	Italy
S. escobarae	2	0	1	0	6	1	0	0	0	0	1	3	1	Mexico
S. jizuensis	2	1	0	0	5	1	0	0	1	1	1	5	2	China
S. longirostris (a)	1	0	1	0	2	1	0	1	1	0	0	3	1	France (Pyrenees)
S. longirostris (b)	1	0	1	0	2	1	0	1	1	0	0	2	1	France (Pyrenees)
S. longirostris (c)	1	0	1	0	2	1	0	1	1	0	0	1	1	France (Pyrenees)
S. longirostris (d)	1	0	1	0	2	1	0	1	1	0	0	0	1	France (Pyrenees)
S. maya	0	0	1	1	4	1	1	2	0	1	0	2	1	Mexico
S. navajellus	1	0	0	0	2	0	0	0	0	?	1	0	0	USA and Canada
S. ruseki	1	0	1	0	1	1	0	0	1	0	0	0	0	Slovakia
S. scherae	1	0	1	0	2	1	0	0	0	0	0	0	1	Switzerland
S. sphagnophilus	0	1	0	0	4	1	0	0	1	1	0	4	2	Poland
S. tatricusa	2	0	1	0	4	1	0	0	1	0	0	0	1	Poland
S. tatricusb	2	0	1	1	5	1	0	0	1	0	0	0	1	Poland
S. tieni	2	0	0	0	2	1	1	1	1	1	0	2	1	Vietnam
S. triocellatus	1	0	0	0	3	1	1	1	1	1	1	3	1	Vietnam
S. valdeaibarensis	?	0	0	0	2	1	0	0	0	0	0	1	1	Spain

character 4). It is true, however, that the definition of the consensus tree was low, and that the monophyly of this and other pseudachorutine genera awaits further and more thorough reassessment based on a taxonomically wider sample. All the species except S. *navajellus* seem to belong to

Table 3. Performances of the characters 1–13 in the initial parsimony analysis (above; characters unordered, without weight), and in the strict consensus derived from these trees (below). The figures given are the number of steps in the tree, consistency index (CI) and retention index (RI).

Tabla 3. Comportamiento de los caracteres 1–13 en el análisis de parsimonia inicial (arriba; caracteres no ordenados, sin peso), y en el consenso estricto derivado de estos árboles (abajo). Las cifras son el número de escalones en el árbol, el índice de consistencia (CI) y el índice de retención (RI).

	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Best fits (all trees)													
Steps	6	11	3	2	8	1	2	2	2	2	4	8	3
CI	33	100	33	50	75	100	50	100	50	50	25	62	66
RI	55	100	75	66	71	100	66	100	87	75	50	62	80
Worst fits (all trees)													
Steps	8	1	4	4	9	1	3	2	4	3	5	9	4
CI	25	100	25	25	66	100	33	100	25	33	20	55	50
RI	33	100	62	0	57	100	33	100	62	50	33	50	60
Number of steps, CI and RI in the consensus tree													
Steps	10	1	5	4	12	1	3	6	8	3	7	12	4
CI	20	100	20	25	50	100	33	33	12	33	14	41	50
RI	11	100	50	0	14	100	33	20	12	50	0	12	60

one clade supported by the synapomorphies 2:1, 5:1, 8:1 y 12:1, while *navajellus* shows the plesiomorphic state for most of these characters. Two clades stand out from the main group: the one formed by (S. *dematteisi* + (S. *jizuensis* + S. *sphagnophilus*)), characterized by 11:4, and (S. *triocellatus* + *S. tieni),* which can only be defined through homoplasies.

Bootstrap and jacknife analyses rendered the same results (not presented in detail). Due to the low resolving power of the data, speculations may be ventured on the basis of three alternative procedures: setting all multistate characters as ordered (with analysis proceeding as beforehand), successive weighting (multistate characters unordered), and majority consensus based on the set of

Figs. 7–10. 7. Unordered multistate characters, strict consensus (L = 76, CI = 32, RI = 25, derived from 626 trees with L = 50, CI = 50, RI = 63). Each circle represents one change in one character (filled = homoplay–free apomorphies, empty = convergences or reversals). The number above each circle is the number of characters, the one below it is the state of that character at that node. 8. Strict consensus tree, multistate characters ordered; consensus (L = 88, CI = 28, RI = 33, derived from 235 trees with L = 60, CI = 41, RI = 63). 9. Strict consensus, based on rescaled consistency index (L = 72, CI = 34, RI = 30, derived from 11 trees with L = 177, CI = 63, RI = 74). 10. Majority rule consensus, based on more than 600 trees.

Figs. 7–10. 7. Caracteres multiestados no ordenados, consenso estricto (L = 76, CI = 32, RI = 25, derivados de 626 árboles con L = 50, CI = 50, RI = 63). Cada círculo representa un cambio en un carácter (lleno = apomorfias sin homoplasia, vacíos = convergencias o inversiones). El número que se halla sobre cada círculo es el número del carácter, y el de debajo el estado de dicho carácter en el nodo. 8. Árbol de consenso estricto, caracteres multiestados ordenados. Consenso (L = 88, CI = 28, RI = 33, derivados de 235 árboles con L = 60, CI = 41, RI = 63). 9. Consenso estricto, basado en un índice de consistencia re–escalado (L = 72, CI = 34, RI = 30, derivados de 11 árboles con L = 177, CI = 63, RI = 74). 10. Consenso de la mayoría, basado en más de 600 árboles.

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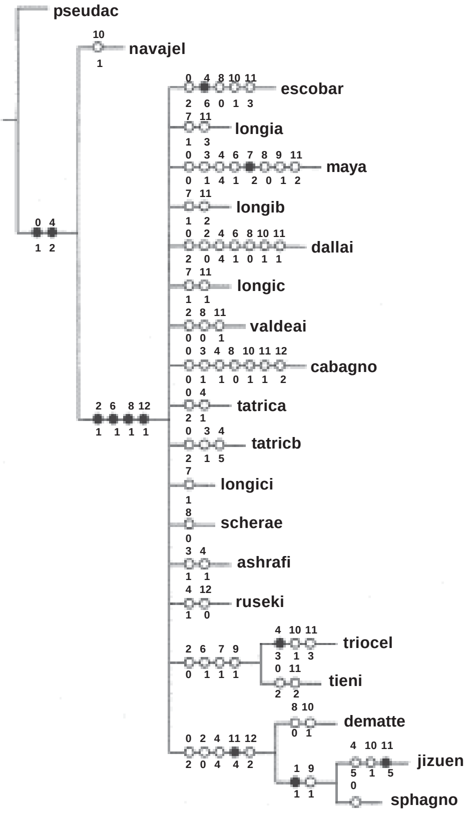
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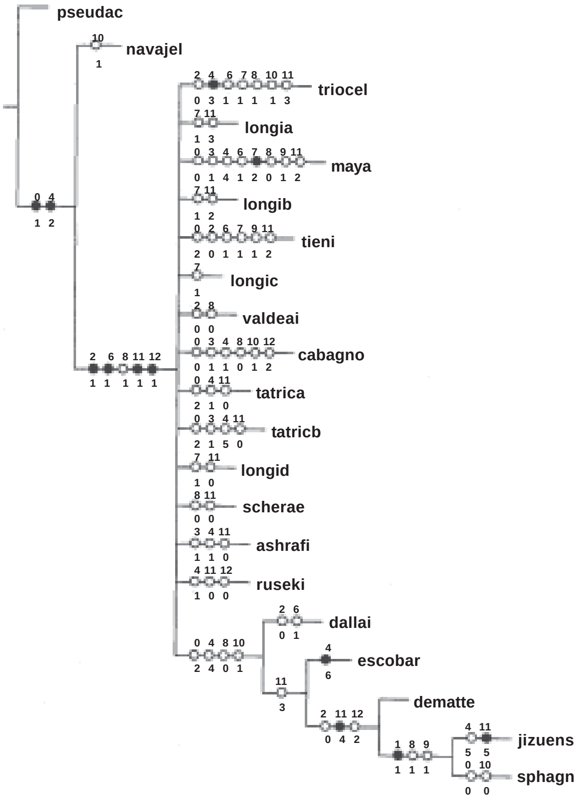
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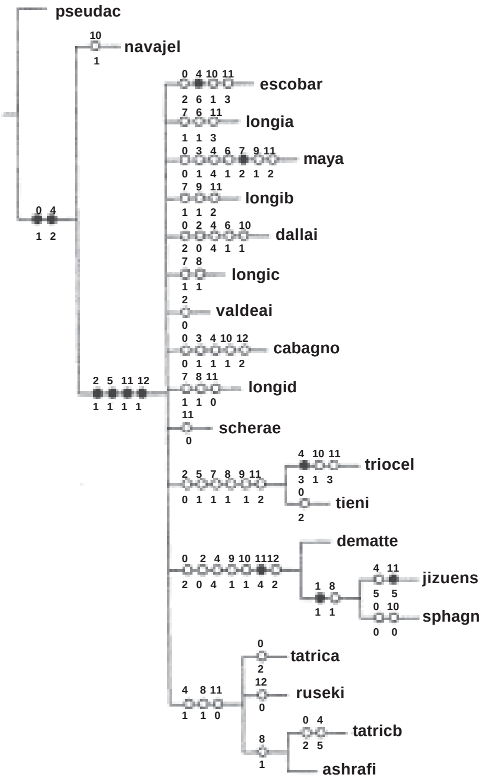
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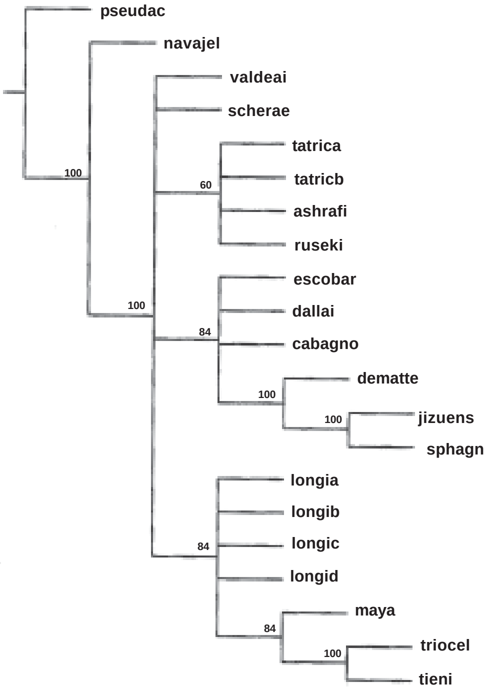
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cladograms obtained in the first trial. Treating the multistate characters as ordered resulted in 235 cladograms (L = 60, CI = 41, RI = 63); the consensus tree L = 88, CI = 28, RI = 33 is shown in fig. 8. In contrast with the former results, S. *dallai* and S. *escobarae* were associated to the clade formed by (*S. dematteis*i + (*S. jizuensis* + *S. sphagnophillus*)), although no synapomorphy free of homoplasy was found to define this group.

Further possible tree structures were suggested by the results of successive weighting (rescaled CI) and majority consensus. None of these trees represent a maximum parsimony solution. However, they are interesting to the extent that either the addition of new characters, or the recoding of characters where some states are non–applicable or unknown, might not support the present most parsimonious solution. These results suggested a potential link between *S. escobarae, S. dallai* and *S. cabagnensis*, and the clade formed by (*S. dematteisi* + (*S. jizuensis* + *S. sphagnophilus*)) (fig. 7), as well as a degree of relatedness between *S. longirostris* and *S. maya* with the clade (*S. triocellatus* + *S. tieni*) (fig. 9)**.** Finally, although not strongly supported and based on homoplastic features, some relationship between the species (*S. tatricus* + *S. ashrafi* + *S. ruseki*) could be determined (fig. 10).

Conclusions

Although the overall resolution of the cladograms is low, a few points can be highlighted: (1) from a parsimonious point of view, the anatomical information currently available does not permit a detailed, highly resolved, phylogenetic hypothesis. This could only be solved by adding new characters; (2) some partial conclusions may be of interest for further studies:

1. The monophyly of the group can be provisionally supported on the basis of two synapomorphies (fig. 7, characters 0 and 4: jaw with 3 teeth, and five ocelli present). This interpretation requires further assessment as there is no out–group taxon to polarise character state changes at the basal node (i.e., external to *Stachorutes* + *Pseudachorutes*). Characters 2, 5, 8 and 12 support the monophyly of an infrageneric clade including all the other members considered in this study except *navajellus*.

2. The position of *navajellus* is peculiar for it apparently belongs to an isolated basal group or,it may have lost some features of the rest of the group due to reversal in characters 2, 5 , 8 and 12.

3. Within the ingroup, the resolution of the consensus is low. Only one clade with three species (*dematteisi*, *jizuensis* y *sphagnophilus*) can be defined with some accuracy, and even so, on the basis of one single nonhomoplasic synapomorphy (character 11, state 4). There is some evidence for the existence of two or three additional clades, but this is supported by homoplastic features only.

The combination of the inferred phylogenetic information (e.g., fig. 10) and the known geographic distributions of the species dealt with here results in strikingly broad geographic ranges at the supra–specific clades, in contrast with rather local specific distributions. Thus, for instance, the clade comprising *S. tatricus, S. ashrafi* and *S. ruseki* could be classified as of wide Palaearctic distribution (or Eurasian, e.g. Cox, 2001; Morrone, 2002), ranging from Western Europe to the Himalayas (Yosii, 1966; Smolis & Skarzynski, 2001). The clade comprising S. *longirostris* and *S. tieni* includes species of the Western Palaearctic, Nearctic, and Oriental regions. The three species represented in the best supported clade (*S. dematteisi* + *S. jizuensis* + *S. sphagnophilus*) were described from Central Europe, Italy, and the Yunnan region in South–Western China. The closest relatives of these three taxa include one East African and one Nearctic member (Dallai, 1973; Palacios–Vargas, 1990), together with the new species *S. cabagnerensis* for Spain. A highly conservative interpretation of such patterns is recommended. Moreover, the authors' feeling is that either (a) very little insight on the phylogeny of the group has actually been gained, (b) the distributions of these springtail species are still very poorly known, or (c) an important number of related collembolan species in each of the main geographic areas mentioned have not yet been described. It is quite likely that all three hypotheses are equally pertinent.

Acknowledgements

This work was conducted with financial support from the European Union for the Research Project "Biodiversity assessment tools" (Grant Nº 0028, 2000).

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