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# Phylogeny of the millipede genus *Sphaeriodesmus* Peters, 1864 (Polydesmida: Sphaeriodesmidae) based on morphological characters

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## Abstract

In order to understand the evolutionary relationships among the species encompassed within the genus *Sphaeriodesmus* Peters, 1864, a cladistic analysis including 63 species was conducted. Ninety-five morphological characters were used for the phylogenetic reconstruction. The results suggested that the current composition of the genus *Sphaeriodesmus* does not circumscribe a monophyletic group; instead, the genera *Eusphaeriodesmus*, *Colobodesmus*, and *Proeilodesmus* are here synonymized under *Sphaeriodesmus*. Although raw morphological data had suggested the genus *Lophocyclus* as the sister taxon of *Sphaeriodesmus*, the phylogenetic analysis under implied weight identified the genus *Cyphodesmus* as the taxon most closely related to *Sphaeriodesmus*. *Sphaeriodesmus isolatus* Chamberlin, 1940 is a subjective synonym of *Sphaeriodesmus conformans* Chamberlin, 1925. The putative subdivisions previously proposed within *Sphaeriodesmus* do not hold as monophyletic either. Low stability was observed concerning the higher-level phylogenetic relationships of *Sphaeriodesmus*. *Sphaeriodesmus crucis* (Loomis, 1974), *S. mecistonyx* (Hoffman, 1990), and *S. triramus* (Kraus, 1954) are new combinations.

***Keywords:*** Diplopoda; Polydesmida; Sphaeriodesmidae; *Sphaeriodesmus*; Phylogeny

## Introduction

Millipedes are a diverse group of over 12,000 described species of terrestrial arthropods distributed on all continents except Antarctica. The group is particularly species-rich in tropical and temperate forest ecosystems, but certain species are also adapted to desert ecosystems (Crawford et al. 1987; Crawford 1989).

Millipedes are one of the major components of soil fauna and have considerable ecological importance for litter breakdown within the decomposition cycle (Schäfer 1990; Crawford 1992; Curry 1994; Wolters and Ekschmitt 1997). They have been categorized as predominantly saprophagous (Curry 1994). Millipedes, therefore, contribute to improving the humic part of the soil and help to increase the microflora through their fecal pellets (Bano 1996).

The 145 currently recognized families of millipedes are classified in 16 orders (Shelley 2003). The highest diversity is found in the order Polydesmida, which has a widespread distribution with members found practically

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all around the world. Polydesmida encompasses over 5000 species (P. Sierwald unpublished data) that are assigned to 30 families (Shelley 2003). One of them is the family Sphaeriodesmidae, with 86 nominal species in 13 genera traditionally segregated into three subfamilies: Sphaeriodesminae, Desmoninae, and Bonetesminae.

The millipede genus *Sphaeriodesmus* Peters, 1864 comprises 34 Neotropical nominal species, ranging from northern Mexico to Panama, and is also found in the Greater Antilles, except in Puerto Rico and Haiti (Hoffman 1999). The highest diversity within this genus is encountered in southern Mexico, where 58% of the described species can be found (Bueno-Villegas et al. 2004). Mexico hosts 21 endemics, which represent 87.5% of the species inhabiting the country. Although several species have been collected in caves (Shear 1973, 1986), most species live in leaf litter and under or inside decaying logs (Bueno-Villegas and Rojas 1999).

Peters (1864) recognized the genus *Sphaeriodesmus* based on the size of the fourth and fifth trunk tergites being larger than the others, thus making this feature the diagnostic character of the genus. As with all diplopods, especially in the large clade Helminthomorpha (Filka and Shelley 1989; Fontanetti 2002), species discrimination in *Sphaeriodesmus* is based largely on features of the male gonopods, modified appendages at the seventh body ring in adult males used for sperm transfer. Shear (1973) suggested dividing the genus *Sphaeriodesmus* into two subgroups, and elevating the species group with simpler gonopods, large gonopod sterna and unmodified first pair of legs in males to genus level. Later, considering exclusively the anatomy of the gonopods, Shear (1986) proposed four species groups within *Sphaeriodesmus* (Table 1) defined entirely on the basis of male gonopod anatomy: the *mexicanus* group (9 species), *longitubus* group (11), *cobanus* group (9), and *stilifer* group (4 species), including *Eusphaeriodesmus* and *Colobodesmus* species among them.

Several authors (e.g. DeSaussure 1859; Peters 1864; Shear 1973) suggested *Sphaeriodesmus* as a natural group because of the presence of enlarged paranota on trunk segments 4 and 5 (Fig. 1). This traditional diagnostic character, however, has been found in the genus *Colobodesmus* as well. Furthermore, when some species originally assigned to *Sphaeriodesmus* were transferred to new genera (*Eusphaeriodesmus* Brölemann, 1916; *Ischnosphaeriodesmus* Brölemann, 1916) inside the family Sphaeriodesmidae, that traditional genus-level character became an assumed symplesiomorphy for *Sphaeriodesmus*, no longer supporting the monophyly of the genus.

The main goal of the present study was to undertake a comprehensive cladistic approach to the systematics of *Sphaeriodesmus* and closely related species. This should allow us to test the monophyly of the genus and identify its sister group, and lead to better understanding of character evolution.

**Table 1.** List of morphological characters used to distinguish species groups within *Sphaeriodesmus* (sensu Shear 1986)

| Species group | Diagnostic characters | Species in the group |
|---|---|---|
| *mexicanus* | Simplest gonopods. Prefemoral and tibiotarsal regions nearly equal in length, evenly curved; tibiotarsus may be nearly rod-like or flattened; often with definite shoulder on mesal side where the two gonopod divisions meet. Termination of tibiotarsus may be bifid, presenting solenomerite and parasolenomerite, or may be a cingulum near tip. | *mexicanus*, *medius*, *saussurei*, *coriaceus*, *nortoni*, *salto*, *griseus*(?), *cotzalostoc*, *robertsoni* |
| *longitubus* | Base of tibiotarsus bears flat, squarish, plate-like process. Tips of gonopods may be bifid, and there may be a dorsomesad contortion. | *longitubus*, *hondurasanus*, *bukowinus*, *oniscus*, *digitatus*, *prehensor*(?), *neglectus*(?), *angustus*(?), *griseus*(?), *sanjose*, *rabonus* |
| *cobanus* | Complex gonopods often resembling a hand with palm and fingers formed by tibiotarsus, and thumb by a prefemoral process. Solenomerite much smaller than very large parasolenomerite, the latter always present. Tibiotarsal process large, often divided to add additional "fingers" to the "hand". Gonopod has undergone about 60° of torsion mesally. | *cobanus*, *trullatus*, *redondo*, *golondrinensis*, *zontehuitz*, *cruzbelem*, *prehensor*(?), *neglectus*(?), *iglesia* |
| *stilifer* | Very elongate prefemur, solenomerite, parasolenomerite, and tibiotarsal process all clustered near gonopod apex; prefemoral process absent. | *stilifer*, *longiramus*, *nodulosus*, *digitatus*(?) |

? = dubious assignment.

## Material and methods

Specimens were loaned from the following institutions: American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Essig Museum, University of California, Berkeley (EMEC); Field Museum of Natural History, Chicago (FMNH); Florida State Collection of Arthropods, Gainesville (FSCA); Instituto de Ecología, A. C., Xalapa (IEXA); Museum of Comparative Zoology, Cambridge (MCZ); North Carolina State Museum, Raleigh (NCSM); Naturhistorisches Museum Wien, Vienna (NMW); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF); National Museum of Natural History, Washington, DC (USNM); Virginia Museum of Natural History, Martinsville (VMNH); and Zoological Museum, Copenhagen (ZMC).

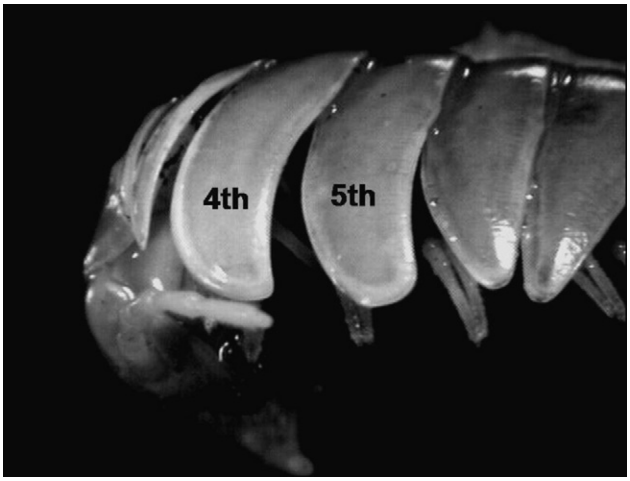

**Fig. 1.** Lateral view of fourth and fifth tergites of *Sphaeriodesmus mexicanus*, showing the enlarged paranota on the trunk. This character is one of the synapomorphies of the genus *Sphaeriodesmus*; for the other two synapomorphies, see Figs. 3 and 4.

## Taxon sampling

The selection of taxa used in the present analysis was designed to test the monophyly of the genus *Sphaeriodesmus*. In total, 63 species were scored (Table 2). For the ingroup all 34 named species currently assigned to *Sphaeriodesmus* (Shear 1986) plus eight unknown morphs (Bueno-Villegas & Sierwald in preparation) were considered. The outgroup was composed of 21 species from the three subfamilies traditionally included in the family Sphaeriodesmidae. From the subfamily Sphaeriodesminae we chose species from the genera *Haplocyclodesmus* (2 species), *Colobodesmus* (3), *Eusphaeriodesmus* (5), *Ischnosphaeriodesmus* (1), *Proeilodesmus* (1), and *Lophocyclus* (2 species). Two species each from *Desmonus* and *Hybocestus*, and one species from *Cyphodesmus* represented the subfamily Desmoninae. Two species from *Bonetesmus* were used as representatives for the subfamily Bonetesminae.

**Table 2.** Taxonomic references and type localities of the taxa studied

| Species | Original description; additional references | Type locality |
|---|---|---|
| *Bonetesmus ojo* | Shear, 1973 | Ojo de Agua Tlilapan, Orizaba, Veracruz, ME |
| *Bonetesmus soileauae* | Shear, 1982 | Cueva de las Maravillas, Oaxaca, ME |
| *Cyphodesmus trifidus* | (Silvestri, 1910) | Cuernavaca, Morelos, ME |
| *Colobodesmus crucis* | Loomis, 1974 | Finca Las Cruces, Puntarenas, CR |
| *Colobodesmus cobanus* | (Chamberlin, 1952) | Coban, Alta Verapaz, GU |
| *Colobodesmus triramus* | Kraus, 1954 | Finca La Yoya, Sonsonete, SA |
| *Desmonus pudicus* | (Bollman, 1888); also Cook (1898) | Little Rock, Pulaski Co., Arkansas, US |
| *Desmonus earli* | Cook, 1898 | Auburn, Lee Co., Alabama, US |
| *Hybocestus plagiodon* | Hoffman, 1959 | Finca Trece Aguas, Alta Verapaz, GU |
| *Eusphaeriodesmus angustus* | (Pocock, 1909) | Senahu, Alta Verapaz, GU |
| *Eusphaeriodesmus bilobatus* | Loomis, 1972 | Cairo, Limón, CR |
| *Eusphaeriodesmus prehensor* | (Pocock, 1909) | Omilteme, Guerrero, ME |
| *Eusphaeriodesmus robustus* | (Pocock, 1909) | San Andrés Tuxtla, Veracruz, ME |
| *Eusphaeriodesmus stylifer* | (Pocock, 1909) | Volcán Iraza, Cartago, CR |
| *Haplocyclodesmus crassartus* | (Loomis, 1936) | Fond des Negre, HA |
| *Haplocyclodesmus montanus* | (Loomis, 1936) | Morne Pilboreau, HA |
| *Ischnosphaeriodesmus digitatus* | (Pocock, 1909) | Volcán de Agua, Sacatepequez, GU |
| *Hybocestus octonodus* | Hoffman, 1959 | Coban, Alta Verapaz, GU |
| *Lophocyclus munitus* | Loomis, 1936 | Roche Croix, HA |
| *Lophocyclus pumilus* | Loomis, 1936 | Morne La Hotte, HA |
| *Proeilodesmus mecistonyx* | Hoffman, 1990 | Cerro Rabón, Huautla de Jiménez, Oaxaca, ME |

**Table 2.** (*continued*)

| Species | Original description; additional references | Type locality |
|---|---|---|
| *Sphaeriodesmus bruesi* | (Chamberlin, 1918); also Loomis (1937) | Liguanea Plain, St. Andrew Par, JA |
| *Sphaeriodesmus bukowinus* | Chamberlin, 1952; also Shear (1986) | Bukowina, BE |
| *Sphaeriodesmus conformans* | (Chamberlin, 1925); also Loomis (1961) | Barro Colorado Island, PA |
| *Sphaeriodesmus coriaceus* | Pocock, 1909 | San Juan, Alta Verapaz, GU |
| *Sphaeriodesmus cotzalostoc* | Shear, 1986 | Sumidero Cotzalostoc Totolacatla, Veracruz, ME |
| *Sphaeriodesmus cruzbelem* | Shear, 1973 | Cueva Cruzbelem Comitán, Chiapas, ME |
| *Sphaeriodesmus filamentosus* | Loomis, 1973 | Finca Las Cruces, Puntarenas, CR |
| *Sphaeriodesmus golondrinensis* | Shear, 1973 | Cueva de la Golondrina Bochil, Chiapas, ME |
| *Sphaeriodesmus griseus* | Chamberlin, 1943 | Volcán Orizaba, Veracruz, ME |
| *Sphaeriodesmus grubbsi* | Shear, 1986 | Sótano Río Iglesia, Huautla de Jiménez, Oaxaca, ME |
| *Sphaeriodesmus hondurasanus* | Chamberlin, 1922 | San Juan Pueblo, Yoro, HO |
| *Sphaeriodesmus iglesia* | Shear, 1986 | Sótano de Río Iglesia, Huautla de Jiménez, Oaxaca, ME |
| *Sphaeriodesmus isolatus* | Chamberlin, 1940 | Barro Colorado, PA |
| *Sphaeriodesmus longiramus* | Kraus, 1954 | San Jorge, Santa Ana, SA |
| *Sphaeriodesmus longitubus* | Loomis, 1963 | Mesa Chipinque Monterrey, Nuevo León, ME |
| *Sphaeriodesmus medius* | Carl, 1902 | Guatemala |
| *Sphaeriodesmus mexicanus* | (DeSaussure, 1859); also DeSaussure (1860), Peters (1864), Carl (1902) | Córdoba, Veracruz, ME |
| *Sphaeriodesmus michoacanus* | Chamberlin, 1942 | Cerro San Miguel Tancitaro, Michoacán, ME |
| *Sphaeriodesmus neglectus* | Carl, 1902 | Huautla de Jiménez, Oaxaca, ME |
| *Sphaeriodesmus nodulosus* | Kraus, 1954 | Hacienda Los Planes, Santa Ana, SA |
| *Sphaeriodesmus nortoni* | Shear, 1973 | Cueva Chica de la Perra Gómez Farías, Tamaulipas, ME |
| *Sphaeriodesmus oniscus* | Pocock, 1909 | San Andrés Tuxtla, Veracruz, ME |
| *Sphaeriodesmus pinetorum* | (Chamberlin, 1922); also Loomis (1937) | Isla de la Juventud, CU; Soledad, Cienfuegos, CU |
| *Sphaeriodesmus rabonus* | Shear, 1986 | Cerro Rabón Huautla de Jiménez, Oaxaca, ME |
| *Sphaeriodesmus redondo* | Shear, 1977 | Cueva de Puente Redondo Yitotol, Chiapas, ME |
| *Sphaeriodesmus robertsoni* | Shear, 1986 | Sumidero de Cotzalostoc, Veracruz, ME |
| *Sphaeriodesmus salto* | Shear, 1973 | El Salto, San Luis Potosí, ME |
| *Sphaeriodesmus sanjose* | Shear, 1986 | Cueva de San José, Hidalgo, ME |
| *Sphaeriodesmus saussurei* | Attems, 1899; also DeSaussure and Humbert (1872), Carl (1902) | Cerro Escamela Orizaba, Veracruz, ME |
| *Sphaeriodesmus secundus* | Loomis, 1977 | Windsor Great Cave, Trelawney Par, JA |
| *Sphaeriodesmus sprousei* | Shear, 1986 | Cueva de Galindo, Tamaulipas, ME |
| *Sphaeriodesmus tortus* | Shear, 1986 | Actun Loltum Oxkutzcab, Yucatán, ME |
| *Sphaeriodesmus trullatus* | Shear, 1977 | Grutas de Llano Grande Huixtla, Chiapas, ME |
| *Sphaeriodesmus zontehuitz* | Shear, 1973 | Cuava Arcotete San Cristóbal de las Casas, Chiapas, ME |
| *Sphaeriodesmus* sp. n. "tuxtlas" | Bueno-Villegas & Sierwald (in preparation) | Estación Los Tuxtlas San Andrés Tuxtla, Veracruz, ME |
| *Sphaeriodesmus* sp. n. "mapastepec" | Bueno-Villegas & Sierwald (in preparation) | Mapastepec, Chiapas, ME |
| *Sphaeriodesmus* sp. n. "ixtlan" | Bueno-Villegas & Sierwald (in preparation) | Ixtlan, Chiapas, ME |
| *Sphaeriodesmus* sp. n. "talquian" | Bueno-Villegas & Sierwald (in preparation) | Talquian, Chiapas, ME |

**Table 2.** (*continued*)

| Species | Original description; additional references | Type locality |
|---|---|---|
| *Sphaeriodesmus* sp. n. "teapa" | Bueno-Villegas & Sierwald (in preparation) | Teapa, Tabasco, ME |
| *Sphaeriodesmus* sp. n. "palenque" | Bueno-Villegas & Sierwald (in preparation) | Ruinas de Palenque, Chiapas, ME |
| *Sphaeriodesmus* sp. n. "soledad" | Bueno-Villegas & Sierwald (in preparation) | Soledad, Oaxaca, ME |
| *Sphaeriodesmus* sp. n. "lasflores" | Bueno-Villegas & Sierwald (in preparation) | Las Flores, Chiapas, ME |

Country codes: BE = Belize, CR = Costa Rica, CU = Cuba, GU = Guatemala, HA = Haiti, HO = Honduras, JA = Jamaica, ME = Mexico, PA = Panama, SA = El Salvador, US = U.S.A.

## Character assessment

Wherever possible for any given taxon, all characters were assessed by examining several specimens from different localities. Studying specimens from different locations allowed us to screen for intraspecific morphological variation. All available holotypes were examined. In addition, all relevant species descriptions in the literature were scrutinized; features cited there were compared with specimens and type material. Because species discrimination in most millipedes is traditionally based on adult male gonopod characters, monotypic genera based on female holotypes only were not included in the analysis (i.e. *Tetraporosoma* Loomis, 1966; *Cyclodesmus* Humbert & DeSaussure, 1869). Since holotypes or other specimens of *Sphaeriodesmus medius* Carl, 1902 and *Sphaeriodesmus zontehuitz* Shear, 1973 were not available, the corresponding character states were determined from the original descriptions. Morphological characters used in these analyses were taken from adult specimens only (both males and females) and examined using dissecting microscopes. Scanning electronic microscopy was carried out with a Carl Zeiss EVO 60 microscope after specimens had been critical-point dried and sputter-coated.

## Character selection

A total of 95 characters (30 binary and 65 multistate) were coded, which represent the structural variation observed in the different taxa. Most of the character variation was found in the tergites (33 characters), antennae (3), legs (11), male gonopods (43), and female genitalia (4 characters). Also, we were able to identify one behavioral character (Appendix A: character 53). Most of these characters have been understudied throughout millipedes, in particular the characters referring to female reproductive structures. Shear (1973) described the shape of the cyphopod valves for a few species of *Sphaeriodesmus*. In our study we analyzed the shape of the female genitalia for the majority of the species.

## Phylogenetic analysis

All characters were treated as unordered (i.e. non-additive). Where specimens were not available or it was not possible to observe certain structures due to deteriorated specimens, the states were coded as missing data (?); inapplicability of a character was coded as a dash (–). Three characters (44, 59 and 60) were coded as polymorphic and were treated as such throughout all analyses (Appendix B).

Parsimony analysis using equal weighting (EW) and implied weighting (IW) was performed. The EW analyses were conducted with NONA (Goloboff 1999) running under the WinClada interface (Nixon 2002). Tree space was surveyed via heuristic searches with 1000 replicates of random addition, retaining 50 trees per replicate, and full tree-bisection-reconnection (TBR) branch swapping was implemented. Internal branches were considered as unsupported and collapsed during searches when minimum length was zero. To emulate the sensitivity analysis frequently used in molecular data analysis (Wheeler 1995), and to test the stability of the nodes, implied character weighting (Goloboff 1993) was conducted as implemented in TNT (Goloboff et al. 2003), using values of concavity ($k$) from 4 to 12. The resultant topologies were compared with those of the EW analysis to test which nodes were stable to parameter variation. Sensitivity analysis provides an assessment of the relative robustness of clades under different analytical parameters, testing the stability of the results with respect to parameter variation (Prendini 2003). If a group appears to be monophyletic under a very specific combination of parameters only, less confidence may be placed in the supposition that the data robustly support monophyly than in the case of a group appearing to be monophyletic under a wider range and combination of parameters (Prendini 2003).

Clade support for most parsimonious trees was estimated by Bremer support (Bremer 1988, 1994) and parsimony jackknifing (Farris et al. 1996), as implemented in the program TNT (Goloboff et al. 2003). Relative

Bremer support values (Goloboff and Farris 2001) were estimated calculating the suboptimal trees by one additional step; when the search had finished we checked the support values in the Bremer option. Jackknife analysis was conducted with 1000 replicates, using a traditional search option and outputting results as absolute frequencies. Next, a simple sequential character removal analysis (Davis et al. 1993) was conducted as implemented in WinClada (Nixon 2002). The following parameters were used: TBR set to 100 replications holding 20 trees, followed by more extensive TBR holding 5000 trees for each of the matrices resulting from the sequential elimination of one character. Each of the resulting 95 trees was compared visually to assess the relevance of each character in the topology. Finally, the unambiguous characters present in all most parsimonious trees where mapped onto the consensus tree for equal weights (EW), and for each of the trees resultant from the implied weights (IW) analyses, using the function "apo[" from Nona (Goloboff 1999).

## Results

The parsimony analysis of the data matrix under EW resulted in 18 shortest trees (MPT) of 863 steps, with a consistency index of 0.25 and retention index of 0.51. Individual trees differed from each other in the interrelationships among the major subclades within *Sphaeriodesmus.*

The strict consensus of all the shortest trees (Fig. 2) revealed that the genus *Sphaeriodesmus* as previously delineated is obviously not monophyletic, as its components in the tree are intermingled with representatives of the genera *Colobodesmus*, *Eusphaeriodesmus*, *Proeilodesmus* and *Ischnosphaeriodesmus*. From here on we will refer to this clade as *Sphaeriodesmus* sensu lato (Fig. 2, node A). According to this phylogenetic hypothesis, the synapomorphies that define *Sphaeriodesmus* sensu lato (s.l.) are: Largest tergites at fourth and fifth positions (Fig. 1, char. 2); shapes of largest tergites in lateral view, as in *Sphaeriodesmus mexicanus* (Fig. 1, char. 3); horseshoe-shaped body form in transverse section, as in *S. mexicanus* (Fig. 3, char. 18); and undivided posterior projection at sternite of gonopod aperture (Fig. 4, char. 48). The topology within *Sphaeriodesmus* s.l. encompassed several clades, of which we discuss four (Fig. 2, nodes B–E). The amount of terminal taxa included within these four major clades ranged from 5 to 21 species. None of these clades were formed exclusively by *Sphaeriodesmus* species; each clade contained species assigned to at least one other genus. Postulated outgroup genera were recovered within every one of the major subclades of the ingroup. Furthermore, putative outgroup genera recovered within *Sphaeriodesmus* appeared to be non-monophyletic (Fig. 2).

In general, the support values obtained for the different sections of the phylogeny were relatively low. For most nodes, Bremer support values ranged from 1 to 3. Level-1 and level-2 suboptimal trees were used to estimate the relative Bremer support. We obtained a total of 730 level-1 suboptimal trees (863–864 steps), and 39,279 level-2 suboptimal trees (863–865 steps), giving relative Bremer support values that ranged from 5% to 100%. Jackknife frequencies were generally low. Most nodes showed support levels below 50%, and only six ingroup nodes received more than 50% jackknife frequency. The clade encompassing the sister species *S. bruesi* and *S. secundus* received 72% jackknife support. The linage joining *S. grubbsi*, *S. robertsoni* and *Proeilodesmus mecistonyx* was also recovered in 72% of the jackknife trees. The node linking *S. golondrinensis*, *S.* sp. n. "palenque", *S. cruzbelem*, *S. redondo* and *S. zontehuitz* was recovered in 75% of the jackknifed trees. Only three terminal nodes within *Sphaeriodesmus* were supported with a jackknife value of 100%. Finally, the family Sphaeriodesmidae had a jackknife value of 100% (Fig. 2).

The IW analyses under concavity values from 4 to 12 found just one tree for each concavity, except for $k = 8$ under which two trees were obtained. The principal difference between those phylogenetic hypotheses was the sister group. *Cyphodesmus trifidus* occupied that place in all trees obtained. As in EW, *Sphaeriodesmus* s.l. was not recovered as monophyletic, and the species groups proposed by Shear (1986) were not recovered as natural groups. In all trees, however, six nodes were monophyletic as in the EW analysis: the three nodes with jackknife values of 100%; the clade encompassing the sister species *S. bruesi* and *S. secundus*; the lineage joining *S. grubbsi*, *S. robertsoni* and *Proeilodesmus mecistonyx*; and the node linking *S. golondrinensis*, *S.* sp. n. "palenque", *S. cruzbelem*, *S. redondo*, and *S. zontehuitz* (though for the last clade with different arrangement inside the node on trees under $k$ values from 9 to 12) (Fig. 5).

The phylogenetic hypothesis obtained in the EW analysis was extremely sensitive to character manipulation. Eighty-three characters showed conflict at decisive tree sections. In general, when we removed any of those characters the phylogenetic structure within *Sphaeriodesmus* s.l. collapsed (Fig. 6a). Another seven characters had the opposite effect. After removing any of them the topology obtained was nearly or completely resolved (Fig. 6b). The most-resolved tree resulted by deleting the following characters: 19 (form of internal body cavity in frontal view), 33 (gonopod coxal length/telopodite ratio), 38 (setae at coxal process), 48 (sternite of gonopod aperture, posterior projection), 55 (robustness of legs), 66 (position of valvae aperture in female gonopore or cyphopode), and character 73 (form of cyphopodes). Only five characters had a relatively minor effect on the internal structure of the topology: the form of the anterior margin of the largest tergite (char. 4), the form of the internal body

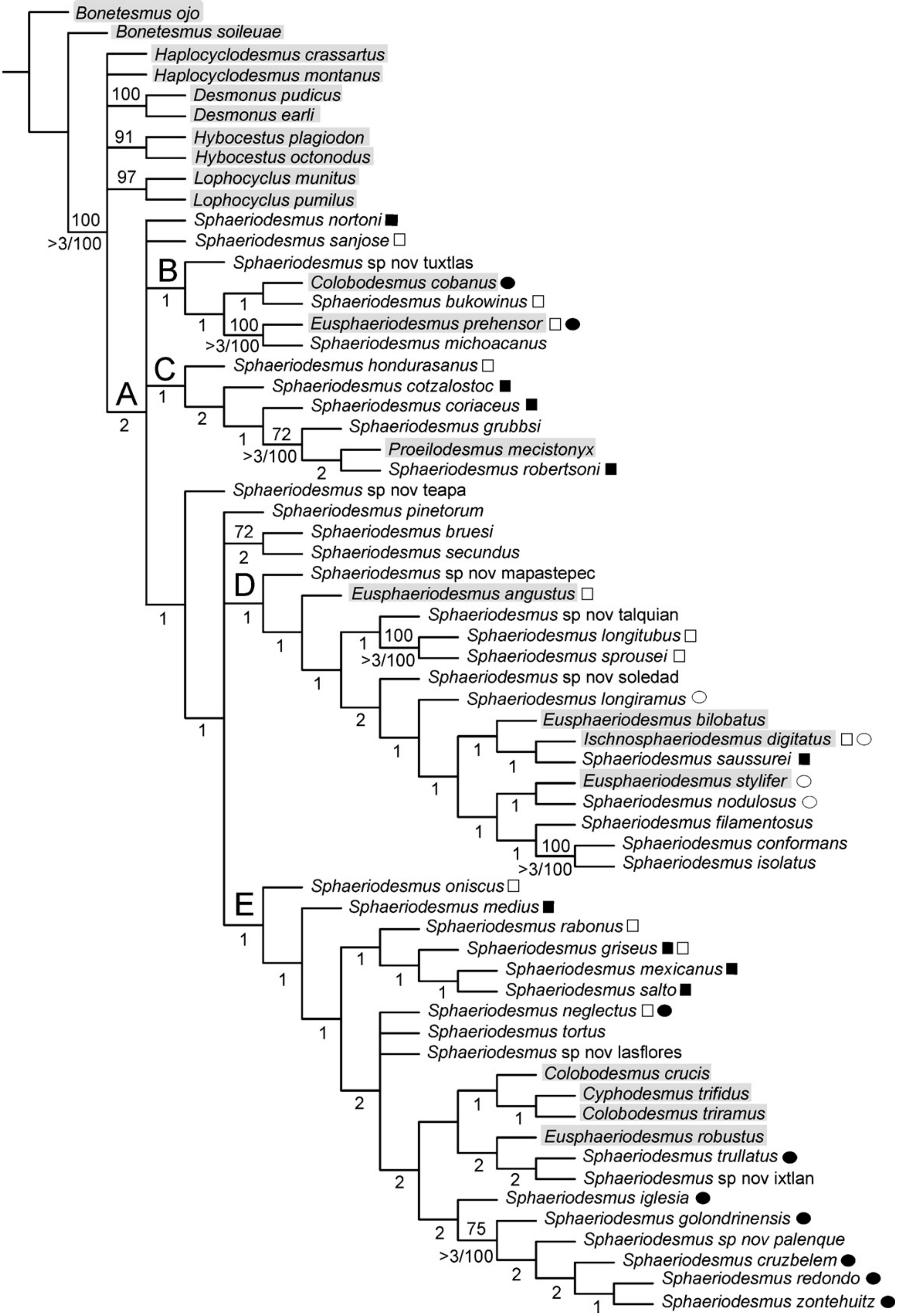

**Fig. 2.** Consensus of the 18 equally most parsimonious trees ($L = 863$; CI = 0.25, RI = 0.51). Jackknife support higher than 50% is shown above the respective branch. Numbers below branches indicate Absolute/Relative Bremer support. Letters indicate major nodes recovered for the ingroup (see text). Highlighted names refer to putative outgroup taxa. Species group assignments (Shear 1986): (■) *mexicanus* group; (●) *cobanus* group; (○) *stilifer* group; (□) *longitubus* group.

**Fig. 3.** Body form in a transverse plane, showing the typical horseshoe shape as in *Sphaeriodesmus mexicanus*. Scale bar = 100 μm.

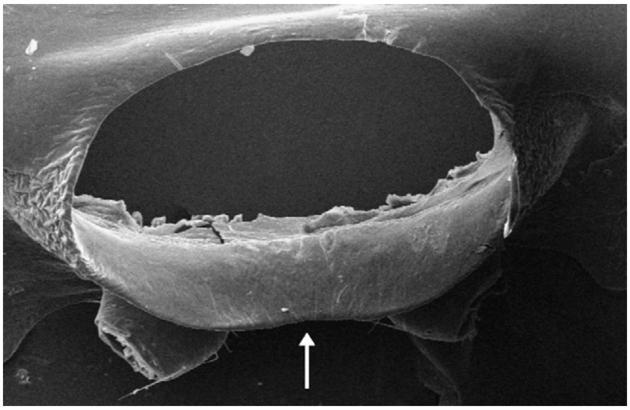

**Fig. 4.** Posterior projection at sternite of gonopod aperture in *Sphaeriodesmus bruesi*.

cavity in posterior view (char. 20), the defensive volvation shape (char. 53), the shape of the tip of the gonopod tibiotarsus (char. 87), and the longitudinal shape of the gonopod prefemur (char. 88). With all five characters included the interrelationships among *S. neglectus*, *S. tortus* and *S.* sp. n. "lasflores" were obscured, but when any of them was removed the polytomy among these taxa (Fig. 7) could be resolved in one way or another.

## Discussion

### Taxonomic considerations

The systematic knowledge of small-size organisms such as the millipedes in the genus *Sphaeriodesmus* has been based on a limited number of external morphological characters. We are certain that many morphological characters have been omitted, thus thorough anatomical exploration using traditional transmission light microscopy could retrieve complementary characters. A better understanding of the evolutionary interrelationships of such groups will only be reached after traditional characters have been explored in more detail (Sierwald et al. 2003). Using more efficient observational tools will allow us to explore additional character sources for groups with a relatively uniform external morphology. The scanning electron microscope, for example, has provided access to a wide variety of morphological characters suitable for cladistic analyses. In the present study, SEM was used to code 14 of the 95 characters that are difficult to observe under the dissection microscope.

The phylogenetic reconstruction obtained from the morphological data set under EW and IW neither corroborated the putative monophyly of the genus *Sphaeriodesmus* nor the monophyly of the genera *Eusphaeriodesmus* and *Colobodesmus* that were used as outgroups (Figs. 2 and 5). Based on the results obtained in the present study it is necessary to introduce modifications to the taxonomy of *Sphaeriodesmus* (see Appendix C for a list of proposed synonymies and new combinations).

In addition to the large size of the fourth and fifth tergites that has been used as the traditional diagnostic character for this genus (Peters 1864), *Sphaeriodesmus* s.l. shares three additional synapomorphies (Fig. 5). The form of the largest tergite in lateral view (Fig. 1, char. 3), the typical horseshoe-shaped body in cross-section (Fig. 3, char. 18), and the undivided posterior projection at the sternite of the gonopod aperture (Fig. 4, char. 48). The results obtained in our analyses suggest that at least three genus names, *Eusphaeriodesmus*, *Ischnosphaeriodesmus* and *Proeilodesmus*, must be synonymized with *Sphaeriodesmus*. This, however, is not a completely novel result. Pocock (1903–1910) originally included the type species of these genera (except *Proeilodesmus mecistonyx*) within *Sphaeriodesmus* (Appendix C). Silvestri (1910) proposed the new genus *Peridysodesmus*, taking into consideration that the third and fourth tergites were subequal in size. He also commented that there was enough variation in the shape of the first pair of legs, and some specific distinctiveness in the male gonopods, for adopting this new genus. Several decades later, nonetheless, *Peridysodesmus* was synonymized with *Cyphodesmus* Peters, 1864 by Hoffman (1979). Then Shelley (2000), based on a revision of all *Cyphodesmus* species, proposed the genus to be part of the subfamily Desmoninae. *Eusphaeriodesmus* was proposed by Brölemann (1916) arguing that its species had a robust telopodite with two sub-equal branches that showed enough differences in the male genitalia to be considered a new genus. *Ischnosphaeriodesmus digitatus* (Pocock, 1909) was considered a new subgenus within *Eusphaeriodesmus* by Brölemann (1916) due to the presence of a longer telopodite and distinctly more slender branches than in the species currently recognized within *Sphaeriodesmus*. *Proeilodesmus* Hoffman, 1990

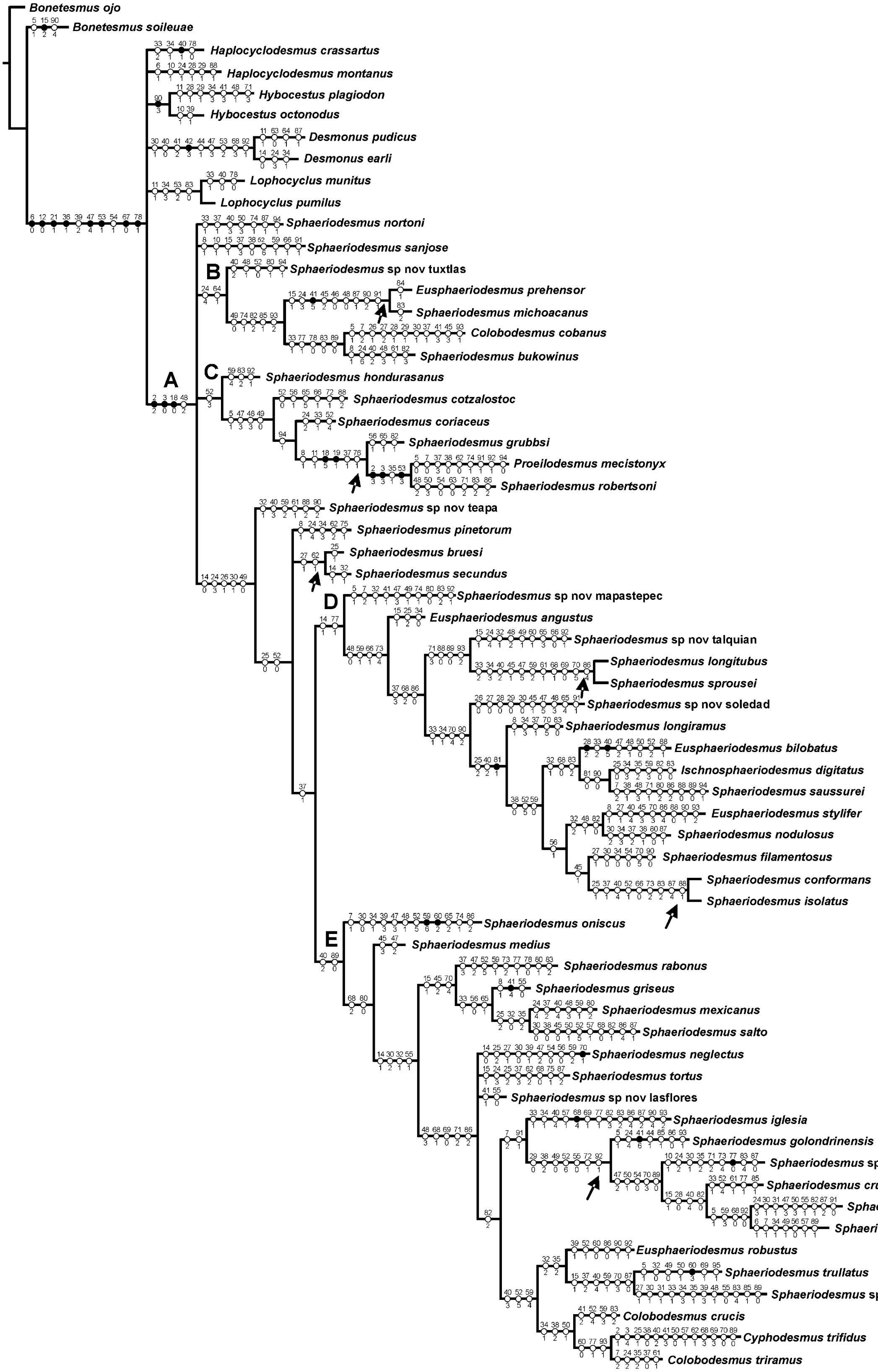

**Fig. 5.** Unambiguously optimized characters in the original consensus tree for 18 equally MPT. Numbers above dots indicate characters; numbers below dots indicate character states. Black dots indicate non-homoplastic apomorphic states; white dots indicate homoplastic apomorphies. Arrows indicate nodes recovered in EW and IW analyses under *k* values from 4 to 12.

**Fig. 6.** Character removal effect: (a) consensus tree when character 93 was removed; (b) consensus tree when character 19 was removed.

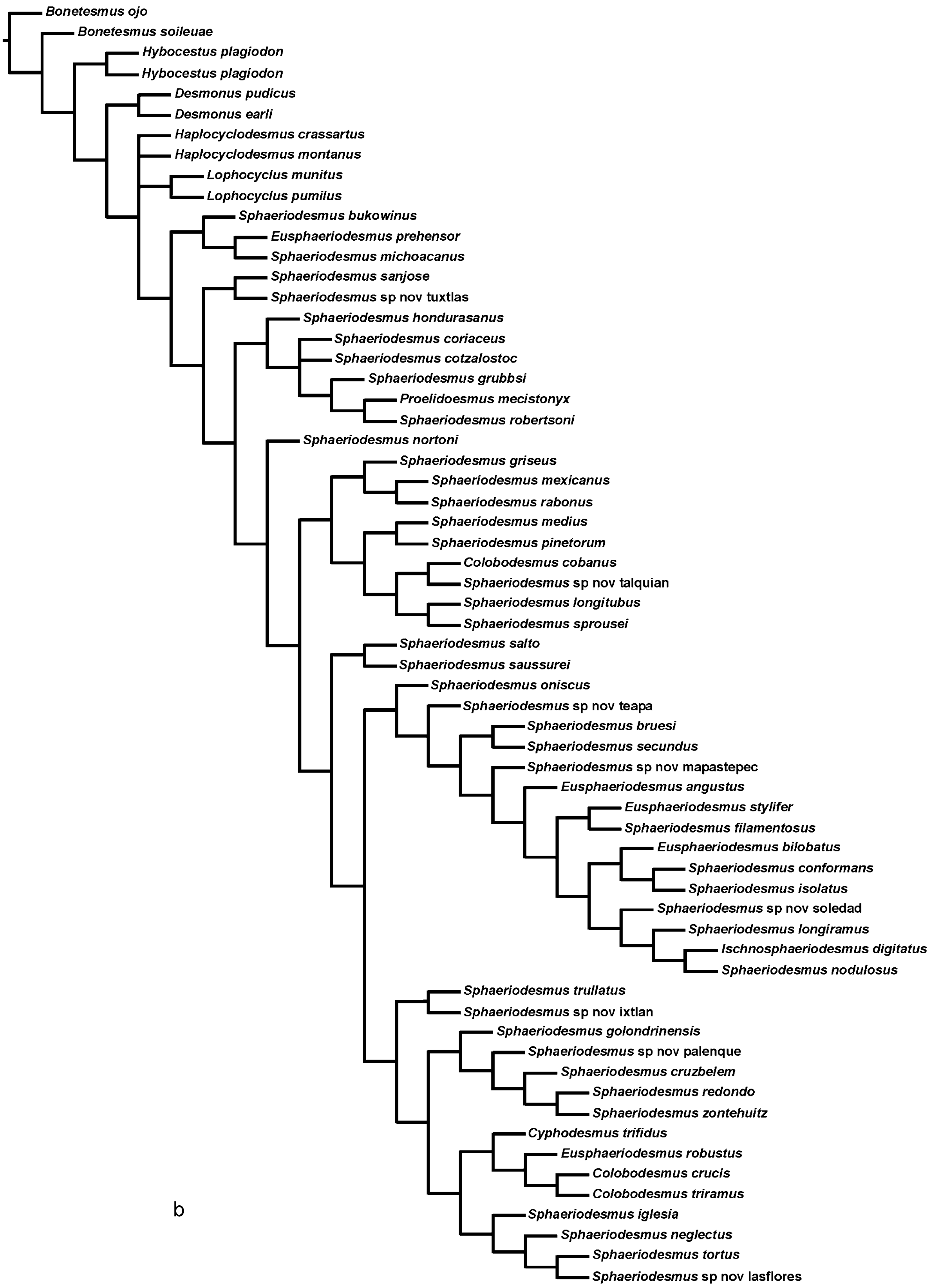

**Fig. 6.** (*Continued*)

**Fig. 7.** Effect of selective character removal: (a) consensus tree when characters 20, 53 or 88 were removed; (b) consensus tree after removing characters 4 and 87. ▌ indicate sections of the topology affected by the respective character removal.

**Fig. 7.** (*Continued*)

was established as a new genus based on the fourth paranota being slightly larger than the others, and on the ventrally deflected paranota at the mid-body segments that were also remarkably wide.

Three species currently assigned to *Colobodesmus* must be transferred to *Sphaeriodesmus*. The genus *Colobodesmus* Brölemann, 1905 was recognized considering that the torsion of the telopodite could be identified as a diagnostic character for this level. The type species, *C. biolleyi*, was not included in the current analysis, but the other three species of the genus are nested within the ingroup. The discussion above demonstrates that in the past genus delineations were based on morphological divergence alone, not on shared-derived characters.

Detailed character analysis suggests that the current status of some species within *Sphaeriodesmus* must be reconsidered as well. The absence of autapomorphies for *S. sprousei* Shear, 1986 indicates that this species is not different from its sister taxon, *S. longitubus* Loomis, 1963. Shear (1986) separated *S. sprousei* from *S. longibutus* based on slightly larger body size in the former. To corroborate Shear's statement it would be necessary to undertake further morphometric analyses of several specimens from different populations. A second species for which we were unable to detect autapomorphic characters was *S. isolatus* Chamberlin, 1940. Based on that fact, and after analyzing a series of specimens (including the holotypes of both species) from several localities in Panama and Costa Rica, we synonymize *S. isolatus* with *S. conformans* Chamberlin, 1925 (Appendix C). Finally, analysis of the type specimen of *S. michoacanus* Chamberlin, 1942 indicates that this species may not be different from its sister taxon, *S.* (*Eusphaeriodesmus*) *prehensor* Pocock, 1909. The tibiotarsus of the type specimen of *S. michoacanus* is flattened compared to the condition observed in *S. prehensor*. However, since we only observed the holotype of *S. michoacanus*, the possible intraspecific variation of this character could not be assessed.

Shear (1986) proposed that the genus *Sphaeriodesmus* could be subdivided in at least four species groups. The latter were named the "*cobanus*", "*longitubus*", "*mexicanus*", and "*stylifer*" groups. Although Shear defined a set of characters for recognizing each species group he was unable to assign several species unambiguously to a definitive group. Due to such problems he did not propose formal taxonomic categories for his species groups (Shear 1986). The phylogenetic interrelationships recovered here did not support the existence of any of these species groups (Fig. 2).

In spite of the relative low support for the nodes and the apparent sensitivity of the cladogram to character manipulation, the basic results presented here were supported by the data. Even so, our conclusions must be seen as a guideline for further systematic research in this group. We must emphasize, nonetheless, that the taxonomic arrangements proposed here were mainly derived from the phylogenetic hypothesis recovered from the cladistic analysis of a limited number of specimens and morphological characters. It is possible that the inclusion of further data (i.e. new taxa or characters) might result in alternative hypotheses for taxa interrelationships, and the recovery of alternative monophyletic groups.

## Higher-level relationships of *Sphaeriodesmus*

The taxon sampling included in the present analysis does not allow establishing robust conclusions about any putative subdivisions within Sphaeriodesmidae. The character analysis, nonetheless, identified 10 synapomorphies for the family node (Fig. 5), which was also supported by a jackknife value of 100% (Fig. 2). This does not contradict Hoffman's (1990) suggestion that Bonetesmidae should be accepted as a valid family closely related to Sphaeriodesmidae, nor his alternative consideration of Bonetesminae as a subfamily of Sphaeriodesmidae (Hoffman 1980).

Systematic ambiguity is a constant problem at all levels within the class Diplopoda. Only a few attempts have been made at applying a phylogenetic approach to understanding the evolutionary history within this group (e.g. Enghoff 1984; Enghoff et al. 1993; Vohland 1998; Regier and Shultz 2001; Sierwald et al. 2003; Regier et al. 2005). These efforts, however, stopped far short of resolving even the most basic taxonomic questions. Most of our knowledge is based exclusively on traditional classifications. For instance, Hoffman (1990) proposed that the subfamily Sphaeriodesminae should encompass nine genera (*Colobodesmus*, *Cyclodesmus*, *Cylionus*, *Eusphaeriodesmus*, *Haplocyclodesmus*, *Ischnosphaeriodesmus*, *Lophocyclus*, *Proeilodesmus*, and *Sphaeriodesmus*). Almost every one of these genera was used in the present study. *Cyclodesmus* and *Cylionus* were not included as their members are rarely found; unfortunately, no male specimens were available for character coding. Further studies, therefore, must be performed in order to understand their taxonomic status within the subfamily. Our results imply that *Eusphaeriodesmus*, *Colobodesmus*, *Ischnosphaeriodesmus*, and *Proeilodesmus* must be synonymized with *Sphaeriodesmus* in order to make the latter genus a monophyletic group. Finally, although the strict consensus tree did not provide resolution of the basal nodes, 12 of the 18 equally parsimonious trees under EW identified *Lophocyclus* as a potential sister group of *Sphaeriodesmus*. Four trees indicated that the clade including *Lophocyclus* and *Haplocyclodesmus* species could be the potential sister group; the remaining two trees showed a monophyletic clade including *Lophocyclus*, *Haplocyclodesmus*, *Hybocestus* and *Desmonus* as sister group to *Sphaeriodesmus*. However, the IW analyses in all the trees from all concavity values used here identified *Cyphodesmus trifidus* as the sister group, which supports the traditional taxonomic assessment that *C. trifidus* is not a *Sphaeriodesmus* species.

Perhaps the most striking conclusion was that millipede systematics is more complex than we had supposed. The discovery of eight putative new species and the absence of autapomorphies for some terminal groups call for a detailed review at population level. The inclusion of alleged alien genera within *Sphaeriodesmus* advocates a careful analysis to determine diagnostic characters to establish real natural groups. The exploration of alternative character sources (e.g. morphometrics, internal anatomy, female genitalia, molecular partitions, etc.) is imperative in order to develop a complete phylogenetic history for this group.

## Acknowledgments

We would like to thank Jason E. Bond for discussions of character coding during the early stages of this study, and Gonzalo Giribet for comments that helped improve earlier versions of our manuscript. This study was supported by grants from the Partnership-for-Enhancing-Expertise-in-Taxonomy (PEET) program of the National Science Foundation (NSF grant DEB 97-12438) to P. Sierwald and W.A. Shear. The Consejo Nacional de Ciencias y Tecnología sponsored J. Bueno-Villegas through a graduate student grant (CONACyT 15940).

## Appendix A

Character list, character states and coding

1. Number of tergites: (0) 19; (1) 20.
2. Position of the largest tergite: (0) second ring; (1) third ring; (2) fourth and fifth ring; (3) fourth ring.
3. Form of largest tergite in lateral view as in: (0) *Sphaeriodesmus mexicanus* (Fig. 1); (1) *Bonetesmus* (see Shear 1973, fig. 22); (2) *Haplocyclodesmus* (see Loomis 1936, fig. 40a); (3) *Proeilodesmus* (see Hoffman 1990, fig. 2); (4) *Lophocyclus* (see Loomis 1936, fig. 48).
4. Anterior margin of largest tergite: (0) simple; (1) with a kind of channel.
5. Posterior margin of largest tergite: (0) smooth; (1) with a series of small teeth.
6. Anterior margins of tergites posterior to largest tergite: (0) smooth; (1) with a series of small teeth.
7. Posterior margins of tergites posterior to largest tergite: (0) smooth; (1) with small teeth widely separated from each other; (2) with small teeth close together; (3) with larger-size teeth.
8. Angle of posterior border on penultimate tergite: (0) round; (1) acute.
9. Pits at frontal base of paranota: (0) absent; (1) present.
10. Simple setae on collum and second tergite: (0) absent; (1) present.
11. Simple setae on all other tergites: (0) absent; (1) present.
12. Branched setae: (0) absent; (1) present.
13. Granules on tergites: (0) absent; (1) conical in random distribution; (2) conical forming one transverse line; (3) conical forming several transverse lines on tergites 17–20 only.
14. Striations under posterior margin of each body ring: (0) absent; (1) present.
15. Ornamentation on pleurite surfaces: (0) absent; (1) striation; (2) scales.
16. Conical protuberances on sternites: (0) absent; (1) present.
17. Caudal lines of tergites in lateral view: (0) straight; (1) with deep notch at base of paranota; (2) with hump at base of paranota.
18. Body form in cross-section: (0) horseshoe-shaped as in *Sphaeriodesmus mexicanus* (Fig. 3); (1) horseshoe-shaped as in *Desmonus* (see Shelley 2000, fig. 7); (2) horseshoe-shaped as in *Lophocyclus*; (3) horseshoe-shaped as in *Haplocyclodesmus* (see Cook 1898, fig. 2f); (4) horseshoe-shaped as in *Bonetesmus* (see Shear 1973, fig. 20); (5) horseshoe-shaped as in *Proeilodesmus* (see Hoffman 1990, fig. 4).
19. Form of internal body cavity in frontal view: (0) round; (1) oval.
20. Form of internal body cavity in posterior view: (0) round; (1) trapezoidal; (2) arched.
21. Anterior apodeme of each body ring calcified and extended to internal cavity: (0) absent; (1) present.
22. Landmark delimiting prozona and metazona: (0) line; (1) plain wider line; (2) wider line with transverse lines.
23. Metazona/prozona length ratio: (0) at least 2.0; (1) around 1.0.
24. Prolongations at posterior corners of paranota: (0) absent; (1) ring 19 only; (2) rings 18–19; (3) rings 17–19; (4) rings 16–19; (5) rings 15–19; (6) rings 14–19.
25. Hypoproct, shape of posterior margin: (0) rounded; (1) acute; (2) truncated; (3) with three acute teeth.
26. First leg pair in males, femur dorsal surface (Fig. 8): (0) as in other walking legs; (1) with hump.
27. First leg pair in males, femur ventral surface (Fig. 8): (0) as in other walking legs; (1) straight; (2) concave.
28. First leg pair in males, prefemur ventral surface (Fig. 8): (0) as in other walking legs; (1) straight; (2) concave.
29. First leg pair in males, prefemur dorsal surface (Fig. 8): (0) as in other walking legs; (1) with hump.

30. First leg pair in males, ventral projection on femur (Fig. 8): (0) absent; (1) small as in *Sphaeriodesmus bruesi*; (2) very large as in *Cyphodesmus trifidus*.
31. First leg pair in males, position of ventral projection at femur: (0) on proximal end; (1) at middle of ventral surface.
32. First leg pair in males, setal pads (Fig. 8): (0) absent; (1) on postfemur and tibia; (2) on postfemur, tibia and tarsus.
33. Gonopod coxa/telopodite length ratio: (0) coxa robust and shorter than telopodite; (1) coxa as long as telopodite; (2) coxa robust and longer than telopodite.
34. Apophysis of gonopod coxa: (0) longer than coxa; (1) longer than half of coxa; (2) shorter than half of coxa; (3) as long as coxa.
35. Form of coxal aperture in gonopods: (0) circular; (1) oval and short; (2) squared; (3) oval and long; (4) triangular.
36. Setae on gonopod coxa: (0) absent; (1) present.
37. Process on gonopod coxa (Fig. 9): (0) absent; (1) rounded; (2) large and truncated; (3) short, spear-head-shaped as in *S. bruesi*.
38. Setae at coxal process: (0) absent; (1) in random arrangement; (2) in a row.
39. Cannula: (0) absent; (1) robust; (2) thin; (3) plate-like.
40. Setae position on gonopod prefemur: (0) absent; (1) lateral; (2) dorsolateral; (3) covering entire surface; (4) dorsal; (5) mesal.
41. Prefemoral process: (0) absent; (1) axe-shaped; (2) subcylindrical; (3) conical; (4) spine-shaped; (5) hook-shaped; (6) spatulate.
42. Prefemoral process tip: (0) rounded; (1) straight; (2) acute; (3) bifurcate.
43. Prefemoral process position: (0) close to base of telopodite; (1) on middle of telopodite.
44. Prefemoral process surface ornamentation: (0) absent; (1) setae; (2) scales.
45. Parasolenomerite: (0) absent; (1) shorter than solenomerite; (2) as long as solenomerite; (2) longer than solenomerite.
46. Parasolenomerite shape: (0) straight; (1) curved.
47. Prostatic groove position: (0) absent; (1) wraps around telopodite in loose corkscrew fashion; (2) mesoventral; (3) ventral; (4) mesal; (5) mesal but goes external to prefemoral or tibiotarsal process as in *S. sprousei* (Shear 1986, fig. 38).
48. Sternite of gonopod aperture, posterior projection: (0) absent or very small; (1) divided in two sections; (2) undivided; (3) semi-divided.
49. Antennae: (0) thin; (1) robust.
50. Relative lengths of second to sixth antennomeres: (0) third and sixth longest; (1) sixth longest; (2) third longest; (3) second to sixth approximately same length; (4) third and fifth longest.

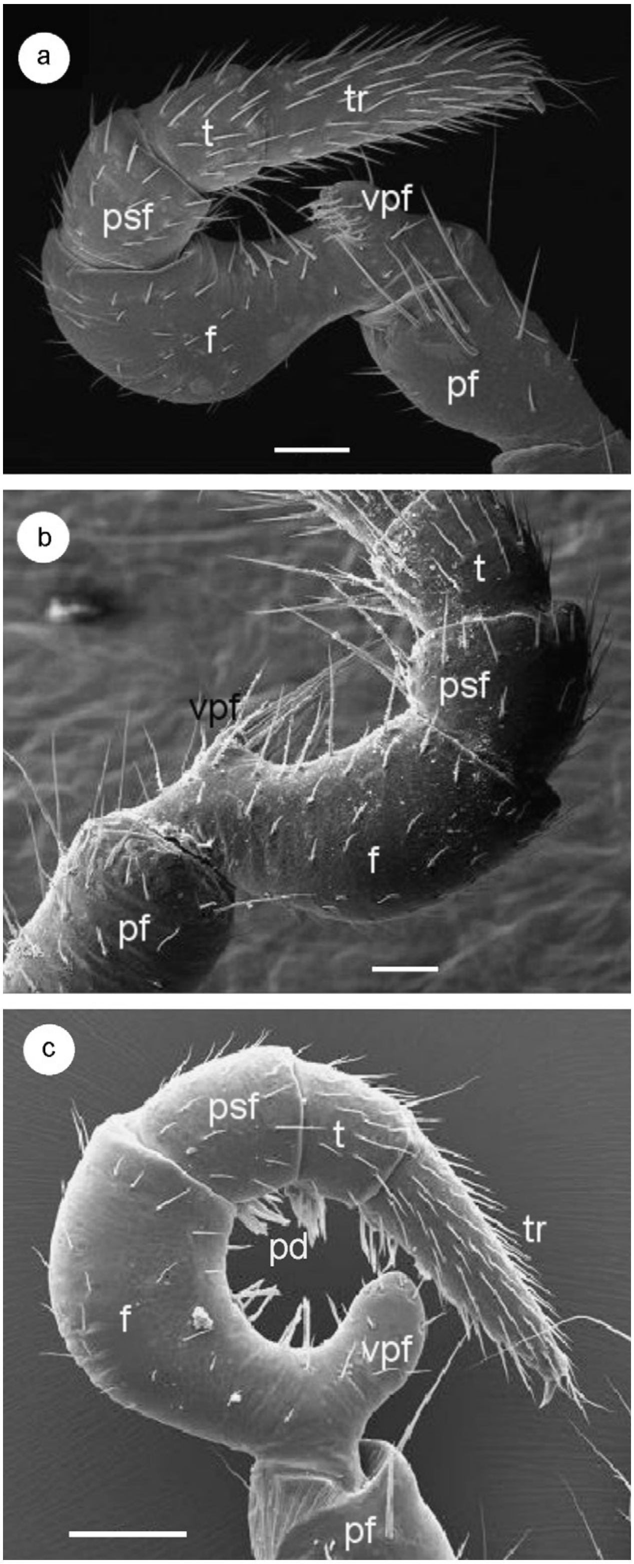

**Fig. 8.** Male first pairs of legs, showing dorsal and ventral surfaces of prefemur, femur, postfemur, tibia, and tarsus: (a) *Sphaeriodesmus saussurei*; (b) *S. bruesi*; (c) *Cyphodesmus trifidus*. f = femur, pd = setal pads on postfemur and tibia, pf = prefemur, psf = postfemur, t = tibia, tr = tarsus, vpf = ventral projection on femur. Scale bars = 100 μm.

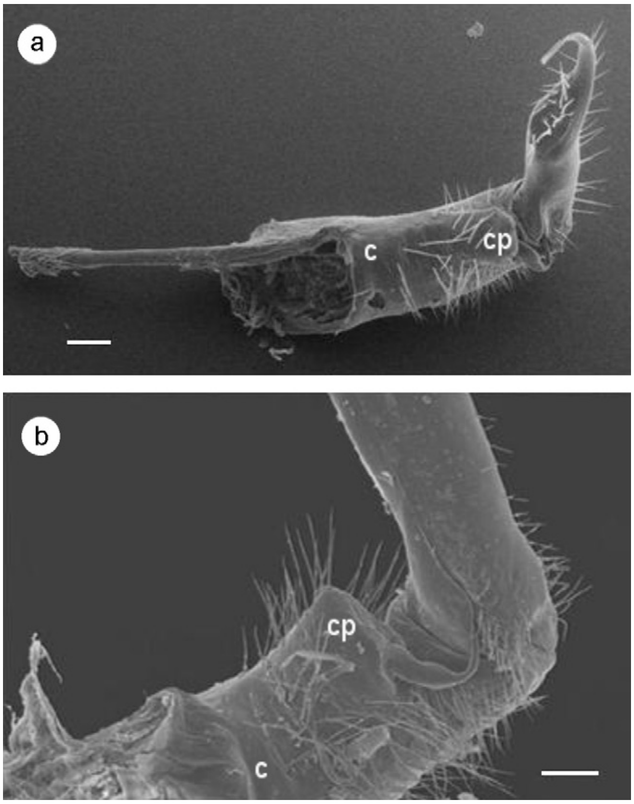

**Fig. 9.** Gonopods, showing coxal processes: (a) *Sphaeriodesmus saussurei*, with large and truncated coxal process; (b) *S. bruesi*, with coxal process short spearhead-shaped. c = coxa, cp = coxal process. Scale bars = 100 μm.

51. Additional sensorial organs on antennomeres: (0) on sixth; (1) on fifth and sixth; (2) on fifth to seventh.
52. Sternal plate between gonopod coxae (Fig. 10): (0) trapezoidal as in *S. bruesi*; (1) boomerang-shaped with anterior angles projecting anteriorly; (2) T-shaped; (3) drop-shaped; (4) cross-shaped; (5) long rectangle as in *C. trifidus*; (6) shaped like a long, slender wedge.
53. Defensive volvation shape of specimens: (0) spiral; (1) perfect sphere; (2) sphere flattened at poles; (3) rhomb-like.
54. Penis: (0) short; (1) long.
55. Robustness of legs: (0) femora 10 times as long as thick; (1) femora 4 times as long as thick.
56. Size of legs of pairs 2–7 (anterior to gonopods): (0) not enlarged; (1) enlarged.
57. Sensorial areas on coxae of legs anterior to gonopods (leg pairs 2–7): (0) absent; (1) present.
58. Shape of dorsal surface of specimen in lateral view: (0) arch; (1) wide, shallow notch; (2) arch with hump on metazona.
59. Gonopod tibiotarsal process: (0) absent; (1) triangular; (2) spoon-shaped; (3) hook-like; (4) spatulate; (5) like a straight spine; (6) like a square plate.
60. Gonopod tibiotarsal process tip: (0) rounded; (1) acute; (2) straight; (3) with small teeth, (4) bifurcate.
61. Surface of gonopod tibiotarsal process: (0) flat; (1) concave.
62. Cingulum in telopodite between prefemur and tibiotarsus: (0) absent; (1) with slight torsion; (2) torsion of 180° (close to border between prefemur and tibiotarsus; see Shear 1986, figs. 46 and 47).
63. Sternite projection at posterior margin of cyphopodal aperture: (0) absent or reduced; (1) present and straight.
64. Cyphopod caps: (0) absent; (1) present, in anterior position; (2) present, in inner-lateral position.
65. Margins of valves: (0) smooth; (1) one hump; (2) two humps; (3) three spatulate humps; (4) irregular waves; (5) with concave wave; (6) with small teeth.
66. Valvae opening: (0) ventral direction; (1) external-lateral direction.
67. Line of sternite in transversal view: (0) straight; (1) wavy; (2) circular.
68. Solenomerite: (0) fused to telopodite on entire length; (1) branches off from middle of telopodite; (2) branches off at tip of telopodite; (3) branches off externally at base of telopodite; (4) branches off internally at base of telopodite.

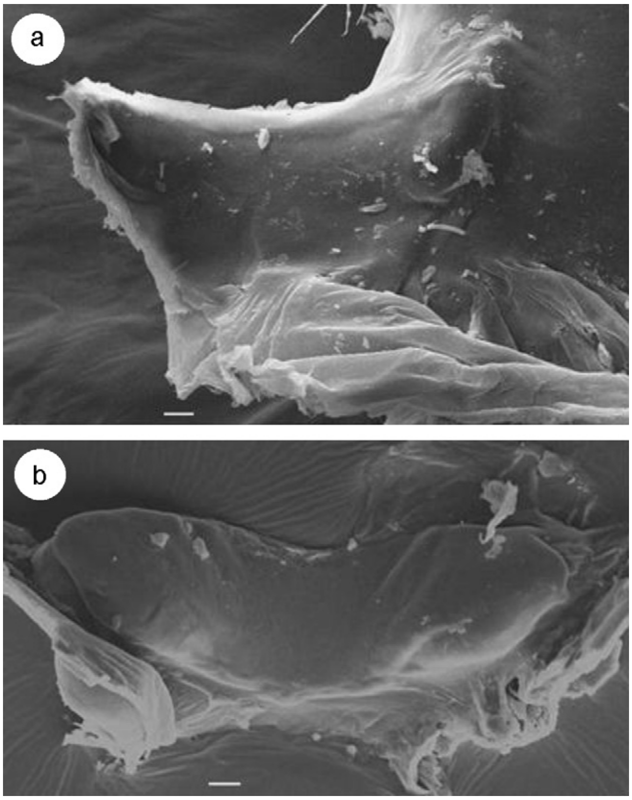

**Fig. 10.** Sternal plates between gonopod coxae: (a) trapezoidal shape in *Sphaeriodesmus bruesi*; (b) long rectangle shape in *Cyphodesmus trifidus*. Scale bars = 20 μm.

69. Relative length of solenomerite: (0) as long as half of telopodite; (1) nearly 1/3 of telopodite; (2) nearly 1/4 of telopodite; (3) as long as telopodite.
70. Solenomerite shape: (0) long flagellum; (1) small leaf-like; (2) small cone; (3) hook-like; (4) small, flat triangle or horsehead-like; (5) stick-like.
71. Direction of solenomerite with respect to telopodite: (0) parallel; (1) to base; (2) distal; (3) internal-lateral.
72. Small holes on dorsal surface of tergite: (0) absent; (1) present.
73. Form of cyphopodes: (0) long and flat; (1) globular; (2) rhomboidal; (3) long and subcylindrical; (4) triangular.
74. Sternite between coxae of female second pair of legs: (0) narrow or acute; (1) as wide as base of coxa; (2) wide or divided and not calcified.
75. Lateral margins of tergites 11–16: (0) straight; (1) with central invagination.
76. Claws: (0) shorter than 1/3 length of tarsus; (1) longer than 1/3 of tarsus.
77. Gonopod coxa shape: (0) globular; (1) cylindrical; (2) pear-like.
78. Diameter of gonopod coxa: (0) not dorsoventrally flattened; (1) dorsoventrally flattened.
79. Prozonite in ventral view: (0) present; (1) virtually obliterated.
80. Long setae at base of gonopod tibiotarsus: (0) absent; (1) randomly distributed; (2) concentrated in triangular patch; (3) on globular mount.
81. Long, flagellum-like setae at distal margin of gonopod prefemur: (0) absent; (1) present.
82. Gonopod telopodite diameter: (0) slightly decreasing from prefemur to tibiotarsus; (1) strongly reduced at base of tibiotarsus; (2) identical at base and tip; (3) gradually increasing from prefemur to tibiotarsus.
83. Shape of gonopod tibiotarsus or principal branch of tibiotarsus: (0) cylindrical; (1) dorsoventrally flattened; (2) sagitally flattened; (3) bowl-like; (4) concave.
84. Concavity on gonopod tibiotarsus: (0) absent; (1) present.
85. Gonopod tibiotarsus: (0) simple; (1) deeply bifurcate; (2) trifurcate.
86. Gonopod tibiotarsus direction: (0) straight; (1) ventrally curved and with tip directed to base of telopodite; (2) ventrally curved but not directed to telopodite base; (3) curved in external-lateral direction; (4) curved in internal-lateral direction.
87. Tip of gonopod tibiotarsus (Fig. 11): (0) acute; (1) round; (2) truncate; (3) bifurcate as in *S. mexicanus*; (4) bifurcate as in *S. medius*; (5) with three teeth.
88. Longitudinal shape of gonopod prefemur: (0) straight; (1) curved distally; (2) curved proximally.
89. Relative length of gonopod prefemur: (0) short, as long as half of telopodite; (1) long, longer than half of telopodite; (2) at most about 1/3 of telopodite.
90. Diameter of gonopod prefemur: (0) nearly cylindrical; (1) dorsoventrally flattened; (2) sagitally flattened; (3) conical; (4) nearly spherical or cubical.
91. Gonopod coxal apophysis shape: (0) cylindrical; (1) dorsoventrally flattened.
92. Gonopod coxal apophysis direction (relative to body axis): (0) mesal; (1) posterior.
93. Gonopod tibiotarsal surface: (0) smooth, without scales or setae; (1) scales; (2) setae.
94. Shoulder on gonopod prefemur: (0) absent; (1) present.
95. Gonopod prefemur/femur length ratio: (0) $\leqslant 1$; (1) $> 1$.

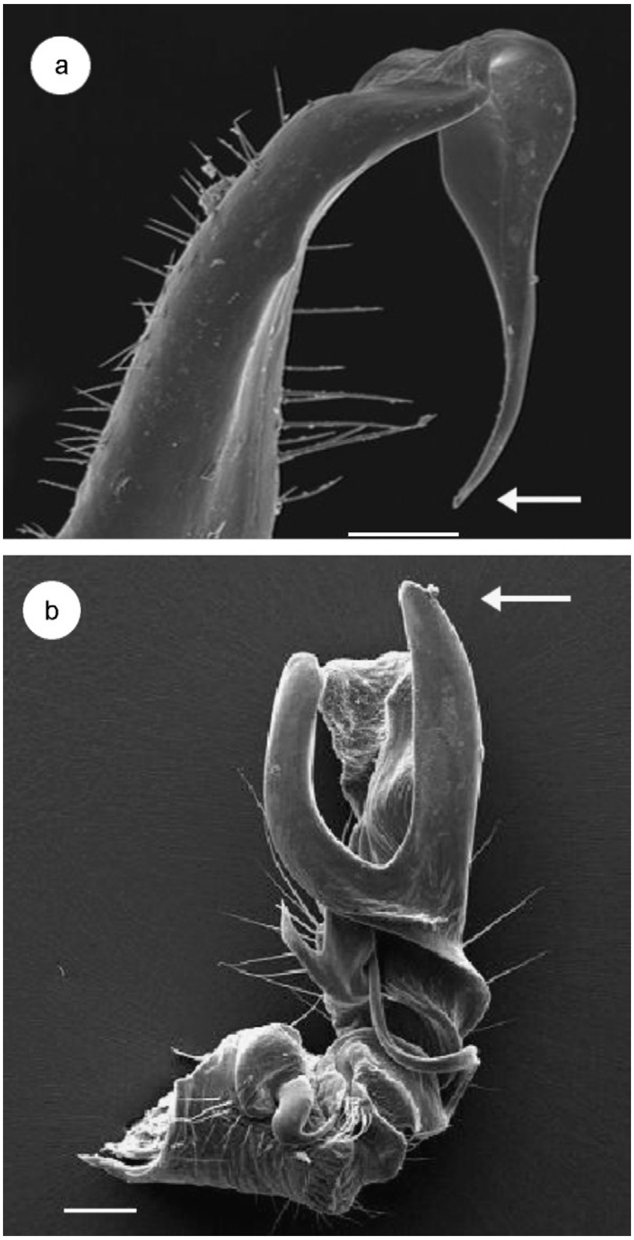

**Fig. 11.** Tips of gonopod tibiotarsi: (a) *Sphaeriodesmus bruesi*, with acute tip; (b) *Cyphodesmus trifidus*, with rounded tip. Arrows point to tips of tibiotarsi. Scale bars = 100 μm.

# Appendix B

## Data matrix

| Species | Character no. | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 000000000 | 1111111111 | 2222222222 | 3333333333 | 4444444444 | 5555555555 | 6666666666 | 7777777777 | 8888888888 | 999999 |
| | 123456789 | 0123456789 | 0123456789 | 0123456789 | 0123456789 | 0123456789 | 0123456789 | 0123456789 | 0123456789 | 012345 |
| *Bonetesmus ojo* | 001001211 | 0010100140 | 0011000000 | 0-022100-0 | 40- - -0-001 | 4150000013 | 100????20- | -00??01100 | 0012004500 | 000000 |
| *Bonetesmus soileauae* | 001011201 | 0010120010 | 0011000000 | 0-012100-0 | 40- - -0-000 | 2150000010 | - -0100120- | -004000100 | 0012001002 | 400000 |
| *Cyphodesmus trifidus* | 114000000 | 0000101000 | 1100611211 | 2010101102 | 232000-301 | 0251111104 | 0010000133 | 0000000111 | 0021022100 | 000100 |
| *Colobodesmus crucis* | 120000000 | 0000101000 | 1100601211 | 2010101122 | 321000-121 | 1241011003 | 1001040110 | 2000000211 | 0022012102 | 000000 |
| *Colobodesmus cobanus* | 120010200 | 0000101000 | 1100401211 | 1001211111 | 4321031120 | 1221100004 | 000????121 | 320??00101 | 0020012000 | 001100 |
| *Colobodesmus triramus* | 120000200 | 0000101000 | 1100201211 | 2010?21022 | 30- - -0-131 | 12?1011004 | 010????110 | 200??00111 | 0021122102 | 0??100 |
| *Desmonus pudicus* | 114100301 | 0103101110 | 1100001200 | 1000211202 | 023010-301 | 1012100120 | - -00101033 | 0004000210 | 0001000102 | 001000 |
| *Desmonus earli* | 114000311 | 0002001110 | 1100321200 | 1000111102 | 023010-301 | 1012110120 | - -01001033 | 0004000210 | 0001000002 | 001000 |
| *Hybocestus plagiodon* | 112000311 | 0102100110 | 2121011111 | 0-013110-2 | 232000-410 | 1151111120 | - -0126100- | -304000111 | 1000004001 | 300000 |
| *Eusphaeriodesmus angustus* | 120000000 | 0000111000 | 1100321211 | 1000011112 | 40- - -0-400 | 3201101001 | 000100110- | -004000101 | 1001001021 | 000000 |
| *Eusphaeriodesmus bilobatus* | 120000000 | 0000101000 | 1100621221 | 2012111302 | 50- - -0-210 | 0221100000 | - -0100110- | -004000101 | 1112000011 | 200000 |
| *Eusphaeriodesmus prehensor* | 120000000 | 0000111000 | 1100320000 | 0-00111211 | 4521020400 | 1251100000 | - -01100122 | 3003100211 | 0021112101 | 210200 |
| *Eusphaeriodesmus robustus* | 120000000 | 0000101000 | 1100431211 | 2020221111 | 30- - -0-321 | 3211111004 | 0001040110 | 2203200211 | 0021100102 | 101000 |
| *Eusphaeriodesmus stylifer* | 120000010 | 0000101000 | 1100421111 | 1021111302 | 40- - -31410 | 1251101003 | 0001051122 | 3004000101 | 1101004001 | 100200 |
| *Haplocyclodesmus crassartus* | 112100000 | 0000110230 | 1100000200 | 0-02131112 | 10- - -0-401 | 1211111100 | - -0????00- | -00??00101 | 0002000001 | 000000 |
| *Haplocyclodesmus montanus* | 112101100 | 1000100230 | 1100120211 | 0-002310-2 | 20- - -0-401 | 1251101000 | - -0000000- | -004000111 | 1011003011 | 000000 |
| *Ischnosphaeriodesmus digitatus* | 120000000 | 0000101000 | 1100201211 | 2011321302 | 20- - -0-400 | 3251100003 | 100????10- | -00??00101 | 1000000021 | 000000 |
| *Hybocestus octonodus* | 012000311 | 1001100110 | 2121010000 | 0-012110-1 | 20- - -0-400 | 1111111120 | - -0????00- | -00??00111 | 1000004001 | 300000 |
| *Lophocyclus munitus* | 114100100 | 0100111020 | 1100020000 | 0-013210-2 | 00- - -0-401 | 1252100010 | - -0????10- | -10??00101 | 3000001001 | 000000 |
| *Lophocyclus pumilus* | 114100100 | 0100111020 | 1100020000 | 0-003210-2 | 20- - -0-401 | 1252100010 | - -0????10- | -00??00111 | 1000000001 | 000000 |
| *Proeilodesmus mecistonyx* | 133000010 | 0100111051 | 1100000000 | 0-00211302 | 40- - -0-330 | 1233100000 | - -0110010- | -101101211 | 0001001201 | 011000 |
| *Sphaeriodesmus bruesi* | 120000000 | 0000001000 | 1100311111 | 1000211312 | 40- - -0-420 | 1201101000 | - -1100010- | -201000211 | 1001001001 | 000000 |
| *Sphaeriodesmus bukowinus* | 120000010 | 0000101000 | 1100630000 | 0-01211212 | 20- - -0-530 | 1231100002 | 010110110- | -201100101 | 0030012000 | 001200 |
| *Sphaeriodesmus conformans* | 120000000 | 0000101000 | 1100611211 | 1001111102 | 40- - -10401 | 1211101000 | - -01000122 | 4002000101 | 1112000411 | 200000 |
| *Sphaeriodesmus coriaceus* | 120010200 | 0000111000 | 1100200000 | 0-01201212 | 40- - -0-330 | 1241100000 | - -1100010- | -101000211 | 0001001000 | 000010 |
| *Sphaeriodesmus cotzalostoc* | 120010200 | 0000111000 | 1100000000 | 0-00231212 | 40- - -0-330 | 1201101000 | - -0105110- | -114000211 | 0001001020 | 000000 |
| *Sphaeriodesmus cruzbelem* | 120000200 | 0100111000 | 1100001200 | 2001201123 | 4201A0-230 | 124100100B | C101021110 | 3010000101 | 0001112100 | 111001 |
| *Sphaeriodesmus filamentosus* | 120000000 | 0000101000 | 1100521111 | 0-01011302 | 20- - -10401 | 1251001000 | - -01001122 | 5004000101 | 1111000021 | 000000 |
| *Sphaeriodesmus golondrinensis* | 120010200 | 0100101000 | 1100401210 | 2000201222 | 260010-430 | 3261101000 | - -01031110 | 2010?00211 | 0021110102 | 011101 |
| *Sphaeriodesmus griseus* | 120000010 | 0000111000 | 1100001211 | 2011211112 | 2421021420 | 3201100000 | - -11110122 | 4101000211 | 0001001300 | 000000 |
| *Sphaeriodesmus grubbsi* | 120010210 | 0100101051 | 1100000000 | 0-00?01112 | 40- - -0-230 | 12?1101000 | - -1111010- | -101001??1 | 0011001001 | 0??010 |
| *Sphaeriodesmus hondurasanus* | 120000200 | 0000101000 | 1100020000 | 0-00201212 | 40- - -0-421 | 1231100004 | 001100010- | -104000211 | 0002001000 | 001000 |
| *Sphaeriodesmus iglesia* | 120000200 | 0000101000 | 1100001211 | 2011101212 | 40- - -0-431 | 3201111100 | - -0????141 | 200??00111 | 0032104202 | 410200 |
| *Sphaeriodesmus isolatus* | 120000000 | 0000101000 | 1100611211 | 1001111102 | 40- - -10401 | 1211101000 | - -01000122 | 4002000101 | 1112000411 | 200000 |
| *Sphaeriodesmus longiramus* | 120000010 | 0000101000 | 1100221211 | 1001311112 | 20- - -0-400 | 3201100001 | 000????122 | 500??00101 | 1110000021 | 200000 |

**Appendix B.** (*continued*)

| Species | Character no. | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 000000000<br>123456789 | 1111111111<br>0123456789 | 2222222222<br>0123456789 | 3333333333<br>0123456789 | 4444444444<br>0123456789 | 5555555555<br>0123456789 | 6666666666<br>0123456789 | 7777777777<br>0123456789 | 8888888888<br>0123456789 | 999999<br>012345 |
| *Sphaeriodesmus longitubus* | 120000000 | 0000101000 | 1100301211 | 1002321312 | 20- - -11500 | 3201101002 | 010????110 | 530??00101 | 2032014000 | 000200 |
| *Sphaeriodesmus medius* | 120000000 | 0000001000 | 11004?1211 | 1000??1112 | 20- - -312?? | ?2?1?0??00 | - -0????122 | 21???00211 | 0001001400 | 0??000 |
| *Sphaeriodesmus mexicanus* | 120000000 | 0000111000 | 1100421211 | 2001321212 | 40- - -21430 | 3201110001 | 0011110122 | 4101000211 | 2001001300 | 000010 |
| *Sphaeriodesmus michoacanus* | 120000000 | 0000111000 | 1100320000 | 0-00111211 | 4521020400 | 1251100000 | - -0????122 | 300??00211 | 0022012101 | 210200 |
| *Sphaeriodesmus neglectus* | 120000000 | 0000001000 | 1100021111 | 0-11211111 | 20- - -0-231 | 3201010002 | 1101000110 | 1202000211 | 0002002100 | 000200 |
| *Sphaeriodesmus nodulosus* | 120000000 | 0000101000 | 1100421211 | 2021311212 | 20- - -0-411 | 32?1101005 | 100????122 | 400??00101 | 0101000121 | 200000 |
| *Sphaeriodesmus nortoni* | 120000200 | 0000101000 | 1100000000 | 0-01241112 | 30- - -0-421 | 3251100000 | - -0100010- | -101100211 | 0011001100 | 000010 |
| *Sphaeriodesmus oniscus* | 120000100 | 0000001000 | 1100301211 | 0-00111113 | 20- - -0-310 | 3251101006 | 200112010- | -001100211 | 1001002000 | 000000 |
| *Sphaeriodesmus pinetorum* | 120000010 | 0000001000 | 1100401211 | 1000311212 | 40- - -0-420 | 3201100000 | - -2100010- | -103010211 | 1001001001 | 000000 |
| *Sphaeriodesmus rabonus* | 120000000 | 0000111000 | 1100001211 | 2010211312 | 20- - -21221 | 3251111001 | 0021100122 | 4102000101 | 1002001300 | 000010 |
| *Sphaeriodesmus redondo* | 120010200 | 0100111000 | 1100301200 | 1110201121 | 40- - -0-310 | 3261011003 | 100???10- | -01??00211 | 0011102200 | 000000 |
| *Sphaeriodesmus robertsoni* | 133010210 | 0100101051 | 1100000000 | 0-00211112 | 40- - -0-220 | 3233000000 | - -1000010- | -201001211 | 0002002100 | 000010 |
| *Sphaeriodesmus salto* | 120000000 | 0000111000 | 1100021211 | 0-01121102 | 20- - -0-420 | 1251110100 | - -0???10- | -10??00211 | 0011004100 | 000010 |
| *Sphaeriodesmus sanjose* | 120000010 | 1000111000 | 1100020011 | 0-00211302 | 40- - -0-521 | 1261001001 | 000100110- | -201000211 | 0012002001 | 010000 |
| *Sphaeriodesmus saussurei* | 120000200 | 0000101000 | 1100121211 | 1011111312 | 20- - -0-430 | 3251100000 | - -0110110- | -101000101 | 2012002000 | 000010 |
| *Sphaeriodesmus secundus* | 120000000 | 0000101000 | 1100301111 | 1010211312 | 40- - -0-420 | 1201101000 | - -1100010- | -201000211 | 1001001001 | 000000 |
| *Sphaeriodesmus sprousei* | 120000000 | 0000101000 | 1100301211 | 1002321312 | 20- - -11500 | 3201101002 | 0101001110 | 5300000101 | 2032014000 | 000200 |
| *Sphaeriodesmus tortus* | 120000000 | 0000111000 | 1100321211 | 2010301312 | 20- - -0-431 | 3201111000 | - -2114010- | -201010211 | 0001002201 | 000000 |
| *Sphaeriodesmus trullatus* | 120010200 | 0000111000 | 1100421211 | 2000221212 | 432000-520 | 1251111001 | 300???111 | 300??00211 | 0021102002 | 000001 |
| *Sphaeriodesmus zontehuitz* | 120011100 | 0100111000 | 1100001200 | 2000101121 | 420100-2?1 | 12?1?00103 | 100101110- | -010-00211 | 0001102101 | 410001 |
| *Sphaeriodesmus* sp. n. “tuxtlas” | 120000000 | 0000101000 | 1100420000 | 0-00111212 | 20- - -0-511 | 1201000000 | - -0110010- | -201000211 | 1011002001 | 001010 |
| *Sphaeriodesmus* sp. n. “mapastepec” | 120010200 | 0000101000 | 1100301211 | 1010211112 | 411000-321 | 1201101000 | - -0110010- | -001100101 | 0002001021 | 001000 |
| *Sphaeriodesmus* sp. n. “ixtlan” | 120000100 | 0000111000 | 1100421111 | 1121311213 | 411000-511 | 3251101001 | 100???110 | 320??00211 | 0024112000 | 000000 |
| *Sphaeriodesmus* sp. n. “talquian” | 120000000 | 0000111000 | 1100401211 | 1010201312 | 40- - -0-421 | 3201100001 | 1001030122 | 0303000101 | 0033020000 | 001200 |
| *Sphaeriodesmus* sp. n. “teapa” | 120000200 | 0000001000 | 1100321211 | 1010211212 | 30- - -0-520 | 1251100002 | 010100010- | -004000211 | 1012002021 | 200000 |
| *Sphaeriodesmus* sp. n. “palenque” | 120000200 | 1000101000 | 1100201210 | 1010221122 | 20- - -0-230 | 1261001000 | - -01001110 | 3214000001 | 0024102000 | 111000 |
| *Sphaeriodesmus* sp. n. “soledad” | 120000000 | 0000101000 | 1100300000 | 0-01111312 | 40- - -10530 | 3201100001 | 0001041122 | 4004000101 | 1011000021 | 210000 |
| *Sphaeriodesmus* sp. n. “lasflores” | 120000000 | 0000101000 | 1100001211 | 2011311112 | 211010-431 | 3201101000 | - -01100110 | 3201000211 | 0002002101 | 000100 |

Character state symbols: A = [0, 2]; B = [0, 4]; C = [1, 4]; ? = unknown character state.

# Appendix C

## List of synonymies and new combinations

***Sphaeriodesmus* Peters**

*Sphaeriodesmus* Peters, 1864: 529. Type species (by monotypy): *Glomeridesmus mexicanus* Humbert & DeSaussure, 1869; not examined.

*Ischnosphaeriodesmus* Brölemann, 1916: 561; new synonym – Hoffman (1980: 162, 1999: 391). Type species (by original designation): *Sphaeriodesmus digitatus* Pocock, 1909; not examined.

*Eusphaeriodesmus* Brölemann, 1916: 561, 605; new synonym – Loomis (1968: 43), Hoffman (1980: 162, 1999: 388). Type species (by original designation): *Sphaeriodesmus angustus* Pocock, 1909; not examined.

*Proeilodesmus* Hoffman, 1990: 672; new synonym – Hoffman (1999: 392). Type species (by original designation): *P. mecistonyx* Hoffman, 1990; examined.

***Sphaeriodesmus conformans* Chamberlin**

*Sphaeriodesmus conformans* Chamberlin, 1925 (Proc. Biol. Soc. Wash. 38): 44. Type locality: Barro Colorado Isld., Panama. Holotype (MCZ) examined.

*Sphaeriodesmus isolatus* Chamberlin, 1940 (Bull. Univ. Utah 30): 13; new synonym. Type locality: Barro Colorado Isld., Panama. Holotype (USNM) examined.

***Sphaeriodesmus crucis* (Loomis)**

*Colobodesmus crucis* Loomis, 1974 (Fla. Entomol. 57): 180, figs. 16–18; new combination. – Hoffman (1999: 387).

***Sphaeriodesmus mecistonyx* (Hoffman)**

*Proeilodesmus mecistonyx* Hoffman, 1990 (Rev. Suisse Zool. 97): 674, figs. 1–5; new combination.

***Sphaeriodesmus triramus* (Kraus)**

*Colobodesmus triramus* Kraus, 1954 (Senckenb. Biol. 35): 320, figs. 47–49; new combination. – Hoffman (1999: 387).

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