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Progress in erigonine spider phylogeny—the *Savignia*-group is not monophyletic (Araneae: Linyphiidae)

Holger Frick · Wolfgang Nentwig · Christian Kropf

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Abstract We present the most inclusive study on the higher-level phylogeny of erigonine spiders, including about 30% of all erigonine genera. By expanding the previously most comprehensive analysis (Miller and Hormiga Cladistics 20:385–442, 2004) we tested the robustness of its results to the addition of closely related taxa, and also the monophyly of the *Savignia*-group defined by Millidge (Bulletin of the British Arachnological Society 4:1–60, 1977). The character matrix was expanded by adding 18 newly scored species in 15 genera, and also includes all species scored by other authors. This adds up to 98 species in 91 erigonine genera plus 13 outgroup taxa. The parsimony analysis led to eight fully resolved most parsimonious trees (L=1084). The topology concerning the taxa basal to the 'distal erigonines' remained unchanged, and the latter clade still shares 67% of all nodes with the original analysis. The *Savignia*-group is not monophyletic at genus level with respect to *Saloca diceros* and *Alioranus pastoralis*, and the same applies at species level in *Diplocephalus* and *Erigonella*. From the *Savignia*-group, *Glyphesis servulus*, *Diplocephalus cristatus*, *Savignia frontata*, and two representatives each of *Erigonella*, *Dicymbium* and *Araeoncus* combine to form a monophyletic clade.

Keywords Phylogeny · Morphology · Complex genital organs · Dwarf spiders · Erigoninae

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H. Frick (✉) · C. Kropf
Department of Invertebrates, Natural History Museum Bern,
Bernastrasse 15,
3005 Bern, Switzerland
e-mail: holger.frick@gmx.li

H. Frick · W. Nentwig
Community Ecology, Institute of Ecology and Evolution,
University of Bern,
Baltzerstrasse 6,
3012 Bern, Switzerland

Introduction

Linyphiidae are the second most diverse spider family in the world and the most diverse in the northern hemisphere, including 4359 species in 576 genera (Platnick 2010). The systematics of Linyphiidae struggles with a tremendous amount of genera with ambiguous genus delimitations. A morphological phylogeny at genus level is therefore required for better, synapomorphy-based genus definitions as well as for understanding the evolution of the somatic and especially complex genital morphology.

The earliest cladistic analyses of Linyphiidae mainly addressed subfamily relations (Hormiga 1993, 1994). The first major contribution at the genus level focused on the largest subfamily, the Erigoninae or dwarf spiders (Hormiga 2000). It tested the genus groups formed by Merrett (1963) and especially by Millidge (1977), who had defined them based on the conformations of the male genital organs. Only three genus groups emerged as monophyletic clades in Hormiga (2000), while the *Entelecara*-group clustered within the *Savignia*-group in Miller and Hormiga (2004). The latter work, the most comprehensive study of erigonine phylogeny prior to the present study, became influential as a reference scheme for subsequent work at the genus level. Consequently, it will be referred to hereafter as the 'original data'. Miller and Hormiga (2004) used 176 morphological characters to investigate 70 ingroup taxa in 65 genera,

including many from the Neotropics. The topology of their resultant tree has proven more or less resistant to the addition of 1–4 more taxa (e.g. Dupérré and Paquin 2007; Miller 2005a, b).

The present analysis tests the stability of the known erigonine phylogeny as well as the monophyly of the *Savignia*-group. We discuss the stability of certain clades and identify wildcard taxa. This is done by adding all taxa that have been coded according to Miller and Hormiga's (2004) characters in several subsequent studies (see below). We increased the sampling density of the *Savignia*-group and its potentially close relatives by scoring another 18 species from 15 genera. Thus, we include representatives of about one third of all erigonine genera (based on the presence of a tibial apophysis, a roughly estimated 300 generic type species belong to the subfamily Erigoninae). This is a further step towards a sound phylogeny of erigonine spiders, which will hopefully motivate researchers to add many more taxa for a full genus-level phylogeny.

Methods and material

Taxa

We used the data from the 82 taxa coded by Miller and Hormiga (2004), and the data on representatives of the genera *Anthrobia*, *Porrhomma* (from Miller 2005a, b), *Scirites* (from Dupérré and Paquin 2007), *Frederickus* (from Paquin et al. 2008), *Caracladus* (from Frick and Muff 2009), and *Venia* (from Seyfulina and Jocqué 2009), all of which were coded accordingly. In addition, another 18 species (see list in Appendix 1) were scored for the first time.

The *Savignia*-group sensu stricto includes three subgroups (Millidge 1977): the *Savignia* genus group (*Alioranus*, *Araeoncus*, *Diastanillus*, *Dicymbium*, *Diplocephalus*, *Erigonella*, *Glyphesis*, *Saloca* and *Savignia*) and two other subgroups (one containing *Dactylopisthes*, the other *Microctenonyx*, *Janetschekia*, and *Thaumatoncus*). We have restricted the present analysis to the *Savignia* genus group. *Diastanillus* and other taxa later assigned to this group (e.g. Eskov 1991; Marusik et al. 2001; Tanasevitch 1987) could not be included, due to lack of suitable material.

The following species of the *Savignia*-group were scored: *Alioranus pastoralis*, *Araeoncus humilis, Dicymbium nigrum*, *Dicymbium tibiale, Diplocephalus latifrons, Diplocephalus picinus*, *Erigonella hiemalis, Erigonella ignobilis*, *Glyphesis servulus*, and *Saloca diceros*. From the closely related *Erigonoplus*- and *Entelecara*-groups we included *Erigonoplus globipes* and *Entelecara erythropus*, respectively.

Additionally, we enlarged the dataset with taxa that had been hypothesized to be close relatives of these genus group, i.e. with *Dismodicus bifrons* (as found by Miller and Hormiga 2004) and also *Abacoproeces saltuum*, *Hypomma bituberculatum* and *Monocephalus fuscipes*, which Millidge (1977) suggested as being close to *Dismodicus*. Since Merrett (1963) considered *Panamomops tauricornis* and *Silometopus elegans* as close to *Saloca diceros*, we added them as well.

Characters

Taxon scoring followed the morphological characters as defined and numbered in Miller and Hormiga (2004). The character matrix for the newly coded taxa, including the indices of consistency, retention, and rescaled consistency for all characters, is available as "Electronic Supplementary Material" 1 in the online edition of this paper. The entire character matrix with character numbers corresponding to Miller and Hormiga (2004), along with the strict consensus tree from the equal-weighted analysis, is also available from TreeBASE (matrix: M5022; study: S2624).

We adopted the following coding alterations: The inadvertently reversed coding of characters 35, 68 and 77 in the matrix of Miller and Hormiga (2004) was corrected by Dupérré and Paquin (2007). This was also done for the species added in Miller (2005a, b). Character 35 was presented incorrectly in the coding of Dupérré and Paquin (2007), thus has been reversed here. Moreover, character 36 was also inverted in the matrix of Miller and Hormiga (2004), therefore was corrected by us for all taxa coded subsequently (Dupérré and Paquin 2007; Frick and Muff 2009; Miller 2005a, b; Miller and Hormiga 2004; Paquin et al. 2008; Seyfulina and Jocqué 2009). These adjustments only switch the two states of a given binary character for all taxa. This has no influence on the calculation of trees, as the character-state distribution remains the same. However, correcting these inversed/reversed codings will be essential in future additions of taxa, in order to avoid erroneous coding due to the inconsistency between the description and the matrix on which tree calculations are based.

We have found a minor miscoding in Miller and Hormiga's character matrix available online (http://www.gwu.edu/~spiders/cladograms.htm). Character 55, "anterior radical process", is coded as "0" (absent) in *Intecymbium antarcticum*, *Dolabritor spineus* and *Gonatoraphis lysistrata*; therefore, character 56, "anterior radical process type", cannot be coded as "robust" and is recoded as inapplicable ("–") instead of as absent ("0") in all three genera. The coding is correct, however, in Appendix B in Miller and Hormiga (2004).

Character 2, "cymbial retromedian process dentation", was coded as "0" for *Porrhomma cavernicola* in Miller (2005a). We have recoded it as inapplicable ("–"), because there is no cymbial retromedian process in *P. cavernicola* (see character 1). Either character 69 or 70 is missing in

Miller (2005a). Both characters are coded as "0" here (as seen in Miller 2005a: figs. 5, 6).

Tapinocyba praecox and *Caracladus avicula* were recoded from Frick and Muff (2009) as lacking a marginal suprategular apophysis (character 34, state 0 instead of 1), following the original coding for *Tapinocyba praecox* in Miller and Hormiga (2004). The following characters were recoded from Miller and Hormiga (2004): character 123 (number of cheliceral teeth on the retrolateral margin of the fang furrow) was recoded for *Entelecara acuminata* (state 4 instead of 3; specimen from NMBE Ar3990), for *Parapelecopsis nemoralis* (state 3 instead of 2; specimen from NMBE Ar565), for *Bolyphantes luteolus* and *Tenuiphantes tenuis* (both state 3 instead of 4; specimens from NMBE Ar4630 and Ar6654, respectively). Character 17 (protegular papillae) was recoded as present in *Entelecara acuminata* (see Hormiga 2000: figs. 9A, E). The sac-like structure on the tegulum of *Araeoncus crassiceps* is considered as a tegular sac rather than a protegulum, due to its highly elongated form as seen in other species (e.g. *Gonatium rubens*; fig. 10E in Hormiga 2000). Characters 16–19 have been adjusted accordingly. The palpal patella in *Diplocephalus cristatus* was measured as 2.3 times longer than broad (specimen from NMBE Ar1187); the distal macroseta is considered to be moderate rather than very strong (character 78). The cephalic lobe in *Savignia frontata* is an AME-lobe not a PME-lobe (characters 102 and 106; e.g. fig. 39f in Roberts 1993).

Scoring

Alcohol-preserved specimens (80%) were scored using a Leica MZ16 stereomicroscope. For more detailed observations under the light microscope we removed the genital organs. The epigynes were examined in Hoyer's solvent (Kraus 1984), the male palps in glycerin 85% or glycerol gelatine ($C_3H_8O_3$). To investigate the tracheal system, the abdomen was opened dorsally and cleared overnight with eye-lens cleaner (half a tablet of AMO Ultrazyme with Subtilisin A diluted in 1 ml of distilled water). Afterwards, it was stained in toluidine blue for one minute and observed in distilled water. Ultrastructural characters were coded based on pictures taken with a JEOL JSM 840 scanning electron microscope (SEM). A selection of photographs is provided for every newly scored taxon (18 plates in total) in "Electronic Supplementary Material" 2. Frick and Muff (2009) provide more detailed descriptions on the preparation techniques for the SEM.

Institutional abbreviations

MHNG = Natural History Museum of Geneva, Switzerland; NHMB = Natural History Museum Basel, Switzerland; NMBE = Natural History Museum Bern, Switzerland; ZMUC = Zoological Museum, Copenhagen, Denmark.

Analysis

Heuristic tree searches

The parsimony analyses were conducted with TNT Version 1.1 (Goloboff et al. 2008), using a traditional search with tree bisection reconnection based on one random seed of Wagner trees (string of commands: *mult=tbr replic 10 hold 10000;*). The number of replicates (10–10000) and the number of trees kept per replication (10000–10) was varied to increase the probability of finding the optimal tree (many hits). Ambiguously supported branches were collapsed ("rule 3", min. length=0) during the tree search and condensed after it (commands: *collapse 1; collapse [;*). This analysis was repeated with a TBR ratchet (commands: *ratchet: iter 200; mult=ratchet replic 10 tbr hold 10000;*) with different combinations of replications and holds as above.

Weighting schemes

We reran the analysis with the TBR parameters that led to the highest number of hits for the implied weights analysis (commands: *piwe=1; mult=tbr replic 300 hold 300;*). The constant of concavity K was varied from relatively high to relatively low costs (1–6, 10, 15) set to homoplasies (Goloboff 1993).

Support values and synapomorphies

Bremer support values (Bremer 1994) were calculated based on the trees generated by increasing the tree buffer and the suboptimal threshold by steps in TNT (Goloboff et al. 2008; command: *bsupport;*). Starting with the eight most parsimonious trees, a traditional search with 20 replicates was performed keeping 2000 trees with one step suboptimal (commands: *mult 20; sub 1; hold 2000;*). Another 15 cycles followed, increasing the suboptimal bound by one and the tree buffer by 2000 in each run (commands: *sub 2; hold 4000; sub 3; hold 6000;…; sub 16; hold 32000;*).

Tree and matrix editing

Mesquite version 2.5 (Maddison and Maddison 2009) was used to build and edit the character matrix, to reconstruct character evolution, and to calculate tree length including uninformative characters. WinClada (Nixon 1999) was utilised to generate and edit the character optimisation tree, which was corrected according to the unambiguous synapomorphies common to all shortest topologies calcu-

lated by TNT (Goloboff et al. 2008; command: *apo[;*). The consensus tree was exported from TNT including Bremer support values. To summarise the implied weighting as a network, we used SplitsTree 4 (Huson and Bryant 2006).

Results

Heuristic tree searches and support values

The same eight fully resolved most parsimonious trees were found under all different tree search regimes using equally weighted characters (L=1084; CI=0.20; RI=0.59; excluding the phylogenetically uninformative characters 104 and 155: L=1082; CI=0.20; RI=0.59) (Figs. 1, 2, 3, 4, 5 and 6; TreeBASE S2624). The number of hits was very low using TBR alone, i.e. ranged from 2 to 30%. The number of hits represents the frequency of finding the most parsimonious topology. The higher the value the more confident one can be that the most parsimonious topology has been found. Therefore, the analysis was repeated using 200 iterations of a ratchet together with TBR hitting the optimal trees in 50 to 72% of the replications. The optimal combination of tree search parameters was 300 replications holding 300 trees each, resulting in 217 hits (72%) with the TBR ratchet. In the analysis using TBR alone this combination resulted in 66 hits (22%).

The strict consensus tree (L=1088; CI=0.20; RI=0.59) of the eight most parsimonious trees is shown in Figs. 1 and 2, including Bremer support values. The character optimisations are shown for the 'distal erigonines' only (Figs. 3 and 4), plotted on the strict consensus tree. Unambiguous character optimisations are shown, accounting for character changes that are present in all eight most parsimonious topologies. See "Electronic Supplementary Material" 1 for the ci, ri and rc values of the corresponding characters.

The average Bremer support for the Erigoninae is 2.06 in our results (1.27 in Hormiga 2000; 1.71 in Miller and Hormiga 2004). For the 'distal erigonines' only, the average Bremer support is 2.31 (1.25 in Hormiga 2000; 1.81 in Miller and Hormiga 2004). The median is independent of outliers, i.e. of the few nodes with extremely high Bremer

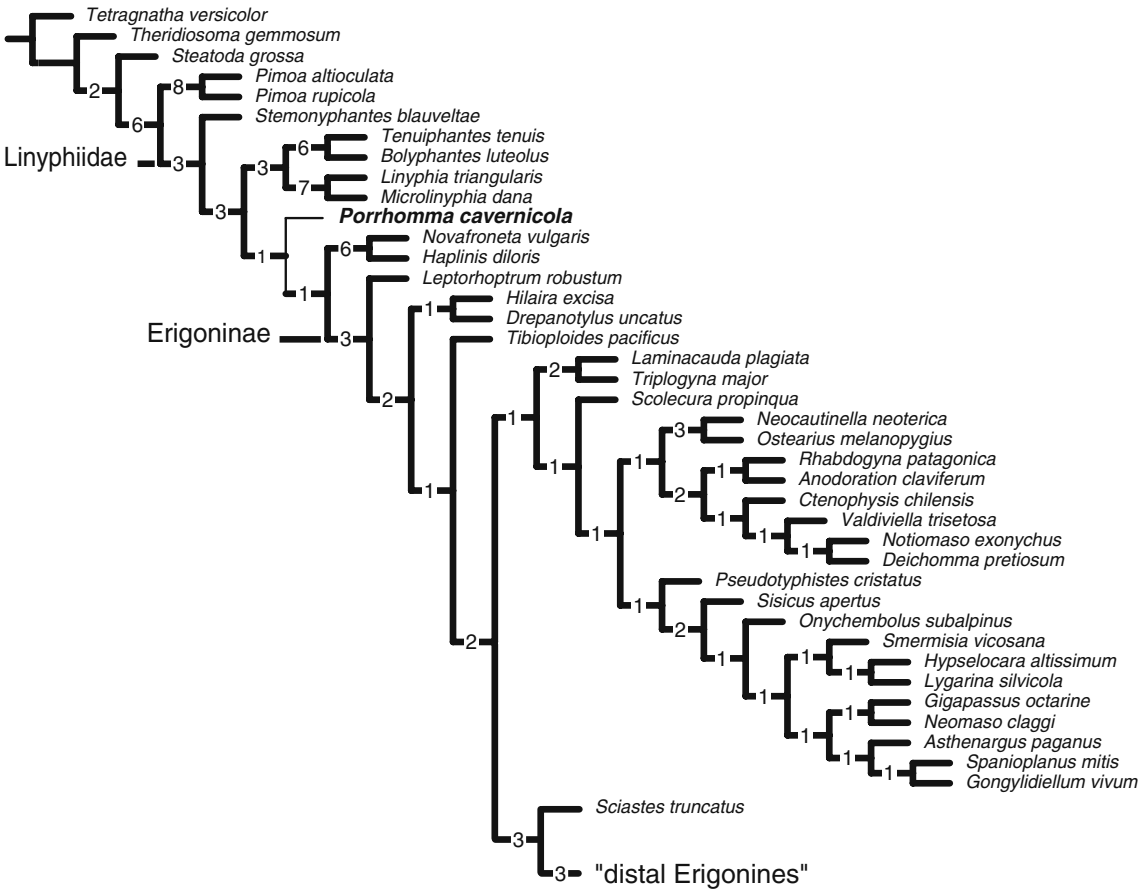

Fig. 1 Strict consensus tree of all eight most parsimonious trees, with Bremer support values (TreeBASE S2624) shown besides nodes; for tree section with 'distal erigonines', see Fig. 2. Topology congruent with results in Miller and Hormiga (2004) indicated by heavy branch lines; names of added species given in boldface

Fig. 2 Continuation of Fig. 1, showing the 'distal erigonines'. *Savignia*-group according to Millidge (1977) indicated by grey field with black right margin

support values. It is 1 in the original analyses for the erigonines and the 'distal erigonines' (Hormiga 2000; Miller and Hormiga 2004) and 2 for both groups in the present analysis. The total support index (ti) as a measure of tree stability (Bremer 1994) is 0.22 (0.25 in Hormiga 2000; 0.17 in Miller and Hormiga 2004).

Sensitivity to weighting schemes

Using implied weighting, the analysis found between 27 and 540 trees, depending on the K values (tree length is based on the equally weighted characters calculated in TNT). The results are listed in detail in Table 1. Only 171 of the total of 1161 trees were not fully resolved, and we found a general pattern similar to the one in the equal-weighted analysis. The strict consensus of all these trees is more or less unresolved for all erigonines. Illustrating them using a phylogenetic network, however, indicates trends and shows one well-structured clade among the 'distal erigonines', i.e. node 37, which includes all but two *Savignia*-group taxa (*Araeoncus*, *Dicymbium*, *Diplocephalus, Erigonella* and *Savignia*). The nodes in clade 37 that unite two sister taxa are supported under both weighting schemes (Fig. 2). However, *Erigonella ignobilis* plus *Glyphesis*

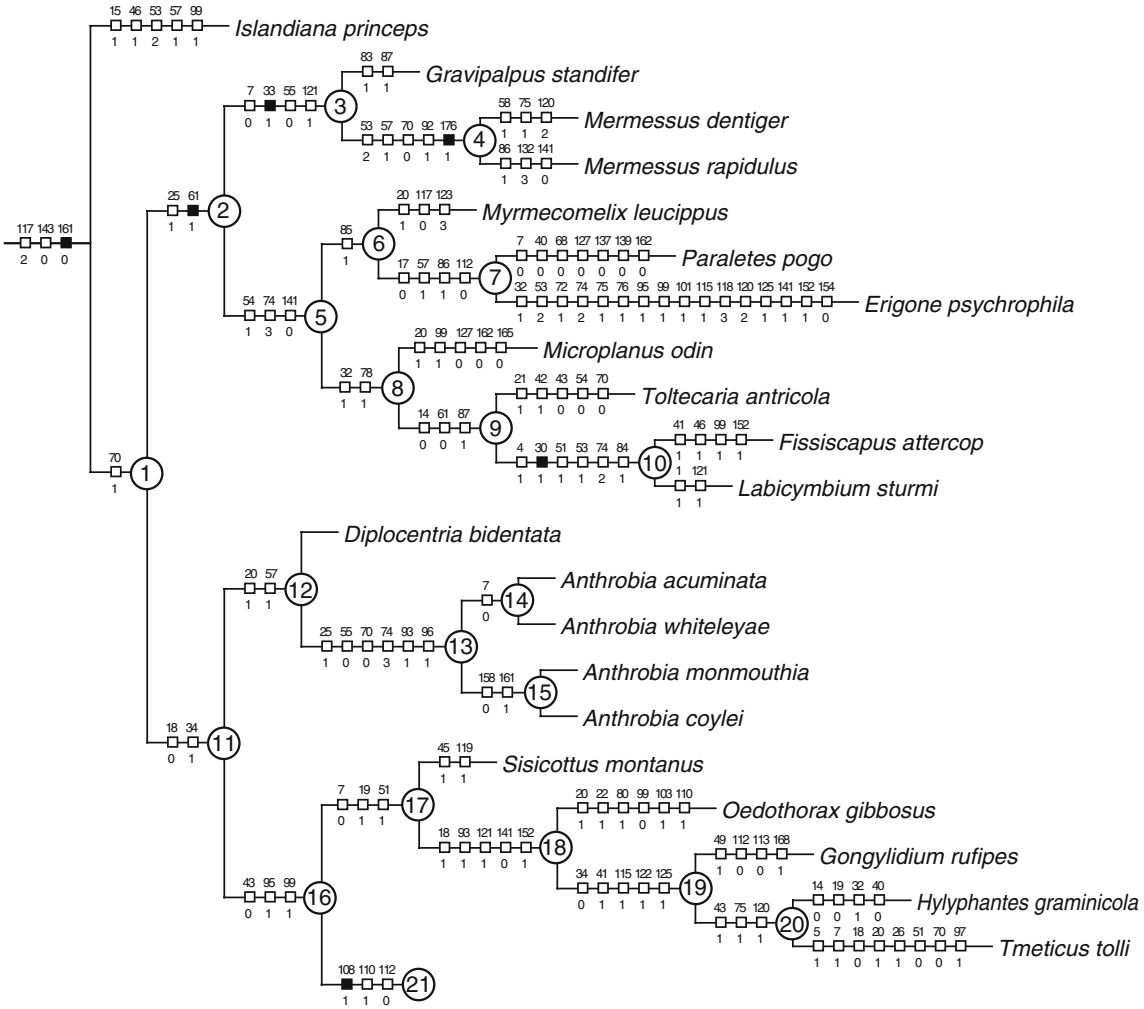

Fig. 3 Strict consensus tree of the 'distal erigonines', with unambiguous character optimisation (squares) and clade numbers (in circles); see also Figs. 4, 5 and 6. Squares mark homoplasious (white) and non-homoplasious (black) character-state changes; character and character-state numbers given above and below squares, respectively

servulus are sister taxa only in the analysis based on implied weights (Fig. 7).

Stability of clades

All clades basal to node 22, i.e. to *Typhocrestus digitatus*, are congruent with those in the single most parsimonious tree found by Miller and Hormiga (2004). These are all clades basal to the 'distal Erigonines' and another 17 basal taxa within them (clades identified by heavy lines in Fig. 1). Altogether, the equivalent taxon subset shares 28 nodes (67%) in the 'distal erigonines' (Fig. 2) with the original analysis of Miller and Hormiga (2004). A larger clade (node 62) including six South American species is also congruent with the original analysis. Clade 62 is well supported by five characters and a Bremer support of 4. Additionally, only the sister relationships between *Hybocoptus* plus *Dismodicus*, *Gonatium* plus *Asemostera*, *Gonatoraphis* plus *Dolabritor* and node 57 are in accordance with Miller and Hormiga (2004).

As regards the pruned, equal taxon sample, only the clades with new taxa added to those from previous analyses differ from what was found by Miller and Hormiga (2004). This concerns nodes 22–60 with the exception of nodes 33, 44 and 57 in the current analysis.

Discussion

The tree topologies and character evolution have been discussed at length for most taxa in Miller and Hormiga (2004) and in the subsequent studies based on the original matrix (Dupérré and Paquin 2007; Frick and Muff 2009; Miller 2005a, b; Paquin et al. 2008; Seyfulina and Jocqué 2009). Here, we focus on differences from those topologies caused mainly by taxon additions.

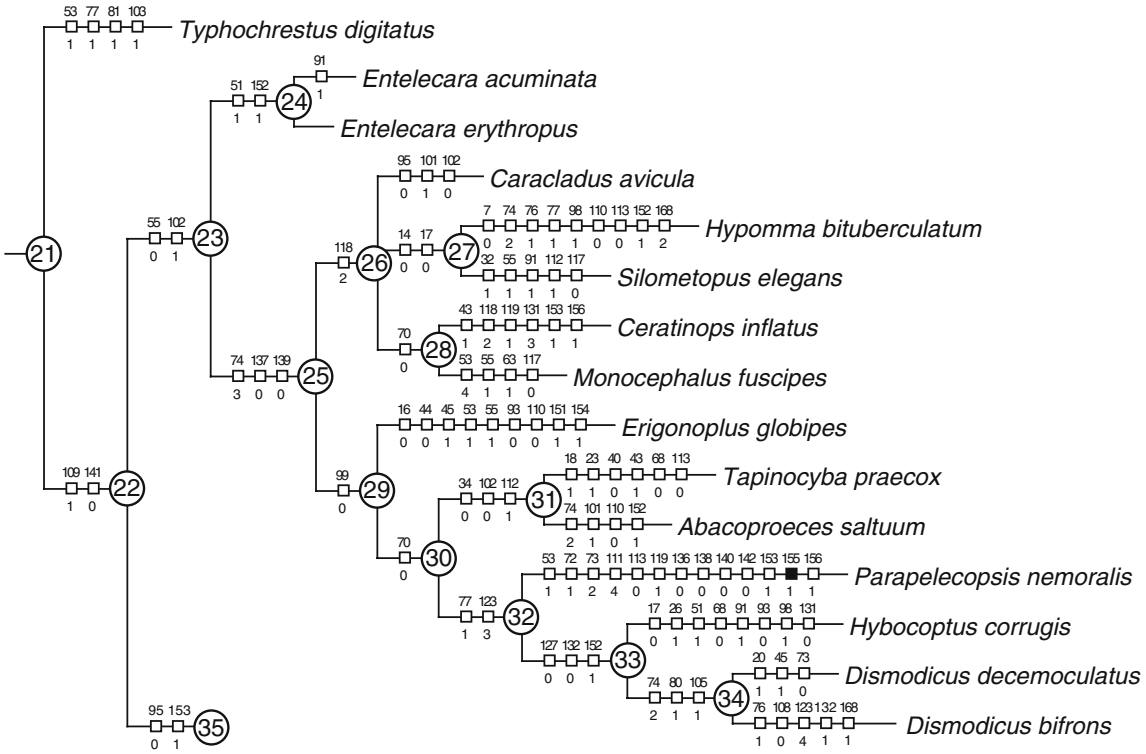

Fig. 4 Continuation of Fig. 3, showing clade 21

Robust clades

The topology concerning the taxa basal to the 'distal erigonines' is very robust. It has not changed in any study (Dupérré and Paquin 2007; Frick and Muff 2009; Miller 2005a, b; Paquin et al. 2008; Seyfulina and Jocqué 2009) that added taxa to the matrix of Miller and Hormiga (2004). Among the 'distal erigonines', to which a total of 28 taxa have been added, our consensus tree still shares 67% of the nodes with the original analysis. However, the shared nodes are mainly among those clades to which no taxa were added, i.e. the most basal and the most distal clades of the 'distal erigonines' (Fig. 2). The 'distal erigonines' were also stable against the addition of several single taxa (*Porrhomma* by Miller 2005a; *Anthrobia* by Miller 2005b; *Scirites* by Dupérré and Paquin 2007). This supports Miller and Hormiga's (2004: 400) prediction that "future addition of a moderate number of taxa will imply only minor revisions to the topology."

Ambiguous clades and wildcard taxa

Changes were minor when single taxa were added, but considerable among those clades to which many taxa were added (e.g. clades 22–57 in the 'distal erigonines'). These clades correspond to nodes with a Bremer support of 1 in the original analysis (e.g. the backbone between nodes 56 and 68 in figures 3, 6 and 7 in Miller and Hormiga 2004). The support values of this backbone are slightly higher in the current analysis than in the original one, but still very low (nodes 22–57; Figs. 2, 4, 5 and 6).

Lophomma apparently is a wildcard taxon, i.e. one that emerges at different places in the topology. It is sister to *Typhocrestus* and usually basal to *Araeoncus* and its relatives (Frick and Muff 2009; Hormiga 2000; Paquin et al. 2008; Seyfulina and Jocqué 2009). The only exceptions to the latter placement occurred in Miller and Hormiga (2004) and the present analysis, where *Lophomma* appears among members of the following genus groups: the *Savignia*- (clade 37), *Entelecara*-, *Tapinocyba*-, and *Pelecopsis*-groups, and two other genera (clade 23). To resolve this clade, it will be very important to add taxa especially from these genus groups (for their definitions see Millidge 1977).

The Afrotropical *Venia* considerably changed its position from the base of the 'distal erigonines' (in Seyfulina and Jocqué 2009) to the clade's distal part in the present analysis (clade 54; Fig. 6). Future topological changes concerning *Venia* are possible, since the African erigonine fauna is not well known and underrepresented in this analysis. In the present dataset, *Venia* is the only taxon endemic to Africa (Seyfulina and Jocqué 2009), while only a few of the considered genera also have representatives in Africa (*Araeoncus*, *Asthenargus*, *Gonatium*, *Oedothorax*, *Walckenaeria*, and others; in Scharff 1990).

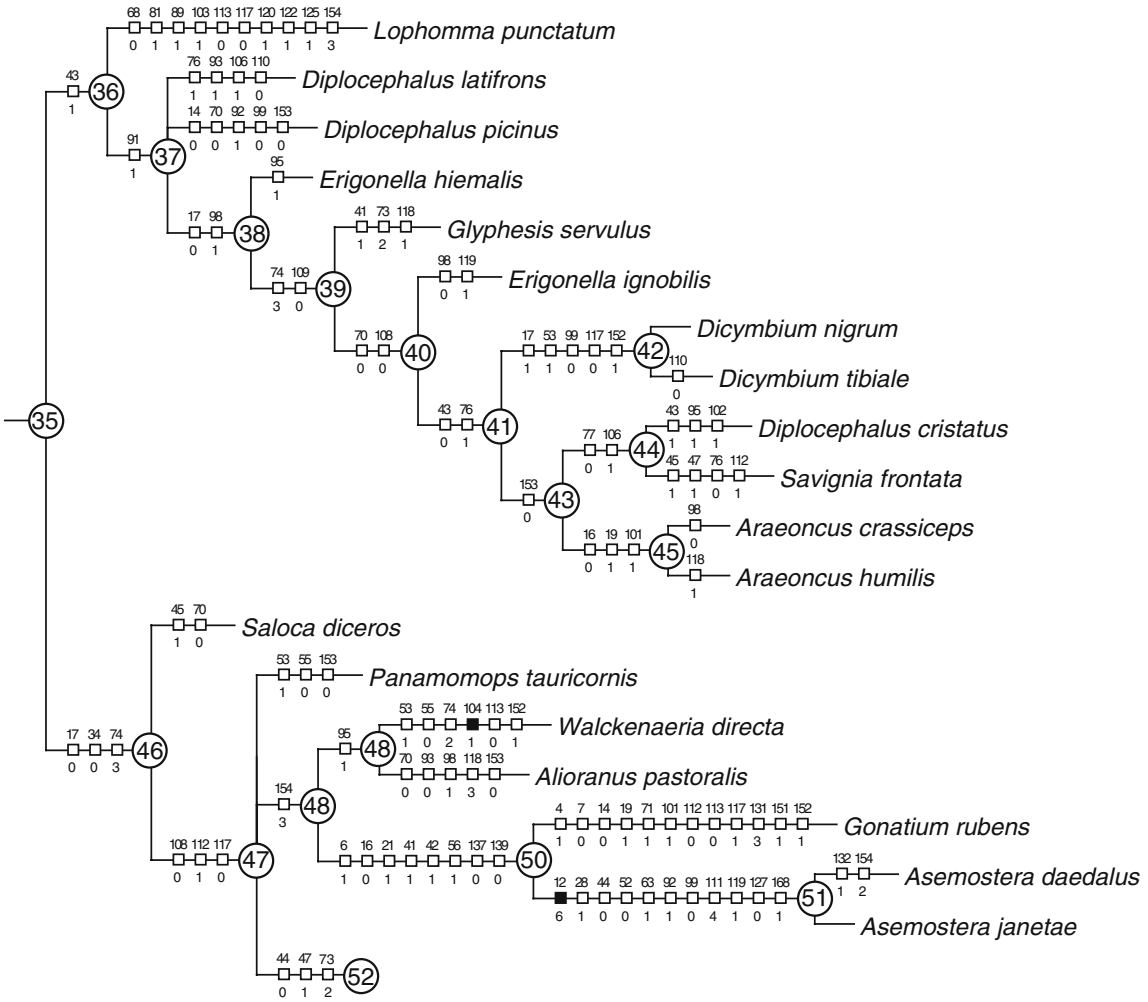

Fig. 5 Continuation of Fig. 4, showing clade 35

The position of these taxa changes dependent on the taxon sampling. Still, they add phylogenetic information and help to resolve the weakly supported backbone mentioned above. Pruning the taxon sampling for *Lophomma* and *Venia* leads to many more most parsimonious trees, and to an unresolved strict consensus tree among the newly added taxa in the 'distal erigonines'.

Sensitivity to weighting schemes

The implied weighting analysis led to over 1000 trees. Since the strict consensus tree was mainly unresolved, we relied on a phylogenetic network based on all these trees. This network showed the same general pattern as the equal-weighting analysis, but was ambiguous in most clades (e.g. fuzzy parts in Fig. 7). Exceptional are the clades among the *Savignia*-group: interestingly, most sister-group relations are found in both equal and implied weighting analyses, with the exception of *Erigonella ignobilis* and *Glyphesis servulus* (compare Figs. 5 and 7).

Implied weighting weights down homoplastic characters. Mainly highly homoplastic characters supported the backbone of clade 37 in the equal-weighting analysis (see below). Therefore, it is not surprising that down-weighting these characters led to ambiguous relationships within the *Savignia*-group (see unresolved phylogenetic network in Fig. 7). Still there are clades that emerge in both weighting schemes, which means that these clades are supported by characters with valuable phylogenetic information. This is exemplified by the respective monophyly of *Dicymbium* and *Araeoncus* (Figs. 5 and 7). These are well-supported by relatively high Bremer values in the equal-weighting analysis (Fig. 2), and are also monophyletic in the implied weighting analysis, independent of the K-value (Fig. 7). The same is true for the sister relationship between *Savignia frontata* and *Diplocephalus cristatus* with low Bremer support in the equal-weighted analysis (Fig. 2). Instead, this relationship (node 44) is supported by the presence of the rarely found AME-lobe (character 106).

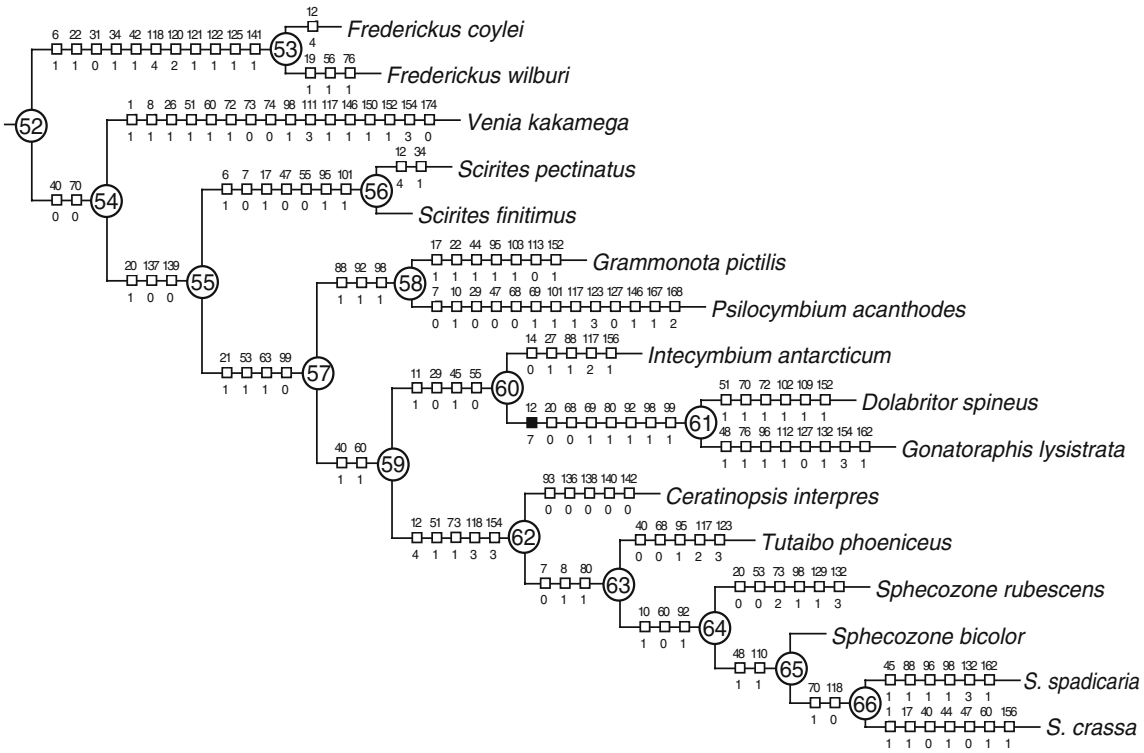

Fig. 6 Continuation of Fig. 5, showing clade 52

The latter is found in only one more taxon at the base of the *Savignia*-group, *Diplocephalus latifrons*.

The *Savignia*-group: clades and characters

The delimitation of the *Savignia*-group has been under debate since Merrett (1963) and Millidge (1977); only the three most species-rich genera (*Araeoncus*, *Diplocephalus*, and *Savignia*) were included in the cladistic approaches of Hormiga (2000) and Miller and Hormiga (2004).

Savignia-group in general

The *Savignia*-group as defined by Millidge (1977) finds no cladistic support. It is non-monophyletic, due to the position of *Saloca* and *Alioranus*. However, hereafter the term '*Savignia*-group' will be restricted to those 11 of the 13 taxa included by Millidge (1977) that form clade 37 (Fig. 5): *Araeoncus crassiceps*, *Araeoncus humilis*, *Diplocephalus cristatus*, *Diplocephalus latifrons*, *Diplocephalus picinus*, *Dicymbium nigrum*, *Dicymbium tibiale*, *Erigonella hiemalis*, *Erigonella ignoblis*, *Glyphesis servulus*, and *Savignia frontata*. Clade 37 is well supported by a bisected epigyne (character 91, ci=0.25; plates 3M, 6M, 10M in "Electronic Supplementary Material" 2; e.g. pl. 21D in Hormiga 2000), a character earlier suggested as typical for the *Savignia*-group (e.g. Bosmans 1996; Millidge 1984). It is formed by wing-like branches protruding from the ventral plate forming a central longitudinal bisection (Millidge 1984). It is likely that not everything that was coded as a bisected epigyne in the past is homologous. Theoretically, the bisected epigyne could represent two lobes protruding from the ventral plate, or else two folds that are directed towards the inside. However, it is also expressed in a few other dwarf spiders, such as in *Silometopus elegans* (pl. 18M in "Electronic Supplementary Material" 2; fig. 26a in Roberts 1993), and in two species of the *Entelecara*-group that are considered in the present analysis: *E. acuminata* and *Hybocoptus corrugis*. If these structures are indeed homologous, this would indicate a close relation to the *Entelecara*-group as suggested by Millidge (1977). Originally, the *Savignia*-group was defined (Millidge 1977) based on another character: the

Table 1 Summarised results of the implied weighting analyses using different K-values

K-value	Best score	No. of trees	No. of hits	Tree length
1	105.98214	81	3	1195–1158
2	89.92339	540	7	1174
3	79.16901	243	124	1163
4	71.15779	27	28	1143
5	64.80699	135	29	1137
6	59.61331	27	40	1120
10	45.63208	81	3	1114
15	35.68423	27	3	1105

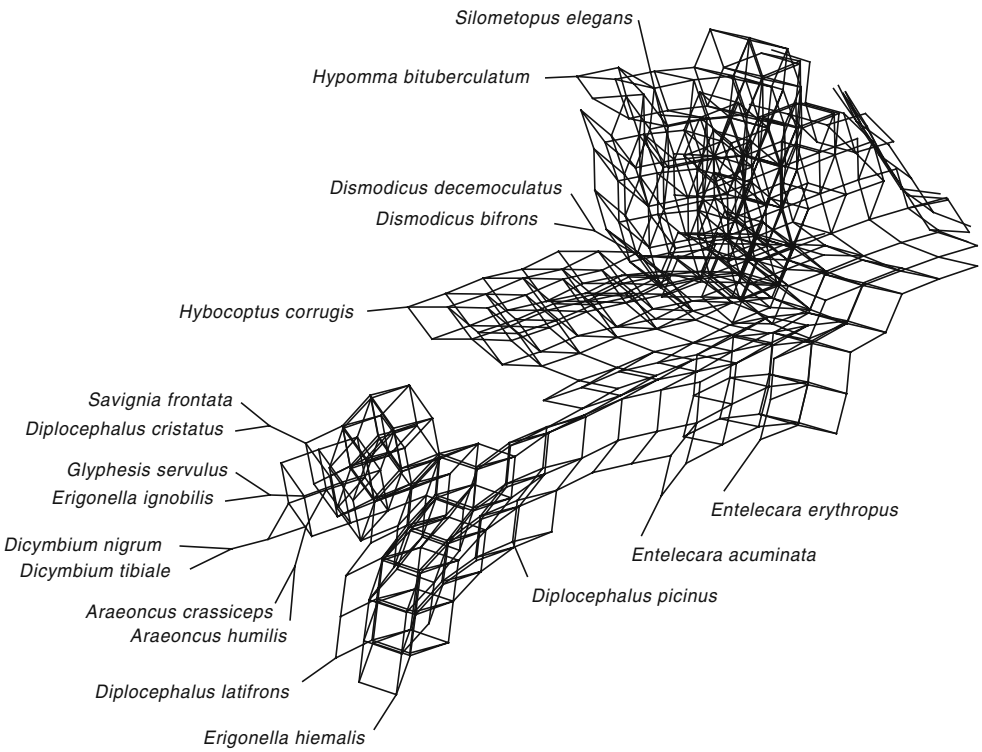

Fig. 7 Detail of phylogenetic network of the *Savignia*-group based on all trees, using implied weights (K1–15)

round suprategular apophysis of the male copulatory organ keeping the radix in place (e.g. pls. 4E, 7E, 9E in "Electronic Supplementary Material" 2; figs. 65C, 66B, 67C, 68D in Merrett 1963). This character is not included in Miller and Hormiga (2004) but is obviously present in all taxa originally assigned to the *Savignia*-group; therefore it occurs in all taxa of clade 37. Both *Saloca diceros* and *Alioranus pastoralis* lack a bisected epigyne (pls. 17M, N and 2M, N in "Electronic Supplementary Material" 2; fig. 33f in Roberts 1993; fig. 116 in Tanasevitch 1989), but have the typical round suprategular apophysis (pls. 17E, 2E in "Electronic Supplementary Material" 2). This character might link these two taxa to the *Savignia*-group if it is included in future analyses.

Diplocephalus and Erigonella

The genera *Diplocephalus* and *Erigonella* are not monophyletic (Fig. 2). The male palp of *Erigonella hiemalis* is very similar to that of *Diplocephalus latifrons* (e.g. compare pl. 10A–E, G with pl. 6A–E, G in "Electronic Supplementary Material" 2, or fig. 64A–C in Merrett 1963 with figs. 947–949 in Wiehle 1960). *Erigonella ignobilis* (e.g. pl. 11B, C, E in "Electronic Supplementary Material" 2; figs. 1035–1037 in Wiehle 1960) has a relatively simple palpal conformation compared to other *Savignia*-group members (e.g. pls. 3–7, 10 in "Electronic Supplementary Material" 2; figs. 63–68 in Merrett 1963). *Glyphesis servulus* (e.g. pl. 13A–C, E, F in "Electronic Supplementary Material" 2; fig. 62A–C in Merrett 1963) also has a simple palpal conformation, and emerged as a close relative or even sister taxon of *Erigonella ignobilis* in the implied-weighting analysis (Fig. 7). *Diplocephalus latifrons* and *D. picinus*, with ambiguous relationships (and rather different palpal conformations; compare pl. 6A–E, G with pl. 7A–E, G in "Electronic Supplementary Material" 2) are the most basal taxa of the *Savignia*-group, whereas *Diplocephalus cristatus* is most derived as sister to *Savignia* (Fig. 5).

Backbone of the Savignia-group

Clades 38–41 and 43, which form the backbone of the *Savignia*-group, are likely to change with future additions of taxa. They are supported by low Bremer values (1 in all nodes) and highly homoplastic characters. They range from 11–15 steps (ci 0.06–0.12), with the exception of two characters (108 and 109; ci=0.25 and 0.20) that support clades 39 and 40, respectively. These characters, the lateral sulci and the pit that is lying within it (e.g. pls. 1F; 9F, H; 14F, H; 18G–I in "Electronic Supplementary Material" 2), are particularly interesting with respect to the phylogeny of erigonine spiders. The lateral sulci defined only two clades in Hormiga (2000: fig. 47) and only clade 21 in the present analysis with three reductions, one of which occurs in node 40 among the *Savignia*-group. These two characters are often interdependent, but in rare cases, as in *Glyphesis servulus,* only one of them is present (sulci without pit; pl. 13H in "Electronic Supplementary Material" 2; fig. 39c in

Roberts 1993). The pits and sulci serve functions related to mating (e.g. Bristowe 1931; Uhl and Maelfait 2008).

However, there are no changes in these weakly supported nodes (38–41, 43) compared to the original analysis, i.e. only *Araeoncus crassiceps*, *Diplocephalus cristatus* and *Savignia frontata* were considered in the current and the original analyses. In most analyses, either *Araeoncus humilis* and/or *A. crassiceps* emerge as sister species to *Diplocephalus cristatus* plus *Savignia frontata* (Frick and Muff 2009; Hormiga 2000; Paquin et al. 2008; Seyfulina and Jocqué 2009), or *Araeoncus* appears basally to the others (e.g. Dupérré and Paquin 2007; Miller 2005a, b; Miller and Hormiga 2004: fig. 7). However, their respective closest relative varies from *Entelecara* in the original to *Lophomma* in the present analysis. These relations are each supported by a Bremer value of 1 and might also change in future analyses.

Savignia-group with complex morphology

Clade 41 includes those species from the *Savignia*-group with the most complex male genital morphology (e.g. compare Merrett 1963: figs. 63, 65, 66, 68 to figs. 62, 64, 67). Within this clade, two genera from the *Savignia*-group for which more than one species each was considered emerge as monophyletic genera, i.e. *Araeoncus* and *Dicymbium* (clades 45 and 42, respectively). They are well supported by relatively high Bremer values (3 and 5) and by several respective synapomorphies. *Araeoncus* is supported by the shared absence of the protegulum (character 16, ci=0.10) and by the presence of a similar structure named tegular sac (character 19, ci=0.20; pl. 3B in "Electronic Supplementary Material" 2) on the male copulatory organ ("PT" in fig. 1A in Hormiga 2000). *Araeoncus* also has a cephalic lobe that bears all eyes (character 101, ci=0.11), situated either above the thoracic furrow (fig. 41c in Roberts 1993) or shifted frontally to the clypeus (fig. 440 in Wiehle 1960) or even missing in rare cases (fig. 41b in Roberts 1993; pl. 3H, I in "Electronic Supplementary Material" 2). These characters are not unique, but especially the tegular sac is rarely found in dwarf spiders. In the current analysis it is synapomorphic only for clade 17 (reduced in *Hylyphantes graminicola*) and for clade 45 (*Araeoncus*) but also occurs in two single species, *Gonatium rubens* (pl. 27B, C in Hormiga 2000) and *Frederickus wilburi*.

Dicymbium is highly supported by Bremer values and the number of character state changes. However, four out of five characters are extremely homoplastic, supporting another 16–21 clades and have consistency indices between 0.05 and 0.14. Still, *Dicymbium* is also supported by a spiral radical tailpiece (character 53, ci=0.24; pls. 4C, 5C in "Electronic Supplementary Material" 2) that supports three clades (including the large clade 59) and another five single species. Even though this may not be striking evidence, the genus is well-defined and supported by a couple of characters that are not considered in this analysis (e.g. a peculiar long palpal patella and the form of the embolus; pls. 4A–C, E and 5A–C, E in "Electronic Supplementary Material" 2; fig. 10c–f in Roberts 1993).

Savignia and Diplocephalus

Clade 44 unites *Savignia* and *Diplocephalus*, the two most diverse genera in the *Savignia*-group. This clade is not well supported, as it relies on a Bremer value of 1 only. Still, out of the two characters that support this node, the AME-lobe (character 106, ci=0.50) is very rarely found. This is a cephalic lobe that only bears the anterior median eyes and can vary from relatively small (in *Diplocephalus cristatus*; fig. 39g in Roberts 1993) to very large (in *Savignia frontata*; fig. 39f in Roberts 1993). The second occurrence of this character in the current dataset is at the base of the "*Savignia*-group" in *D. latifrons*, which has a very tiny, yet visible AME-lobe (fig. 39i in Roberts 1993; pl. 6H, I in "Electronic Supplementary Material" 2). This lobe is not found very often in erigonine spiders compared to the much more common PME-lobe (e.g. pls. 7H, 9H, 10H, 15H, 18H in "Electronic Supplementary Material" 2; figs. 32–35 in Hormiga 2000). In the current analysis it is only present in two *Diplocephalus* species and in *Savignia*. Based on our results it is not possible to judge whether it has a convergent origin or has been reduced and regained in clade 44. The AME-lobe is also found in species that were assigned to other genera (e.g. in *Araeoncus galeriformis*; Tanasevitch 1987: fig. 123) but were not included in the present analysis. Its origin should be discussed based on a denser taxon sampling of the *Savignia*-group, since *Diplocephalus* was used as a 'waste' container for taxa with clear assignment to the *Savignia*-group but of uncertain placement. *Diplocephalus picinus* and *D. latifrons* show all synapomorphies of the *Savignia*-group but differ from *D. cristatus* in several characters of the embolic division.

Taxa outside the Savignia-group

Saloca diceros appears distal to all other *Savignia*-group members (Fig. 5). Merrett (1963) considered *Saloca* to be more closely related to *Panamomops* than to the taxa later defined as the *Savignia*-group. However, he underlined that the palpal structures of these two species are not very similar (compare pl. 17A–G with pl. 16A–F in "Electronic Supplementary Material" 2). In the present analysis *Saloca* appears between *Lophomma* plus the *Savignia*-group and clade 47, which includes *Panamomops tauricornis*, *Walckenaeria directa* plus *Alioranus pastoralis* (Fig. 5) at its

base, thus does not belong to the *Savignia*-group. However, we did not consider taxa from the other, presumably more basal subgroups of the *Savignia*-group. The addition of these taxa might change especially the basal topology of the *Savignia*-group, and influence the position of *Saloca*.

Alioranus pastoralis does not belong to Millidge's (1977) *Savignia*-group. It is sister to *Walckenaeria directa* in all most parsimonious trees. *Alioranus pastoralis* (e.g. pl. 2E in "Electronic Supplementary Material" 2; fig. 116 in Tanasevitch 1989) and *A. pauper* (e.g. fig. 3 in Denis 1949) show the round suprategular apophysis and the overall conformation of the male unique to the *Savignia*-group (e.g. fig. 128 in Millidge 1977), but they do not have a bisected epigyne (character 91; pl. 2M, N in "Electronic Supplementary Material" 2), which is also present in most members of the *Savignia*-group (e.g. Bosmans 1996; Millidge 1984).

Forcing *Saloca* and *Alioranus* into the *Savignia*-group, i.e. setting a constraint for the *Savignia*-group sensu Millidge (1977), elongates the tree by 4 steps to a total of 1088 steps and results in over 1800 most parsimonious topologies. This speaks for non-monophyly of the *Savignia*-group with respect to *Alioranus* and *Saloca*.

Savignia-group relatives and ancestors

Based on the conformation of the male palp, Millidge (1977: fig. 200) regarded *Erigonoplus* as the sister taxon of the *Entelecara*-group plus the *Savignia*-group, with both having evolved from a *Lophomma*-like ancestor. The close relationship between those groups is supported by the present analysis, but their relationships differ from what Millidge (1977) predicted. *Lophomma* is sister to most members of the *Savignia*-group but not to *Erigonoplus* and *Entelecara*. The relation between the *Entelecara*-group (*Entelecara*, *Hybocoptus*) and the *Savignia*-group differs in details between most phylogenetic analyses: the *Entelecara*-group emerged either as a distant relative of the *Savignia*-group (Hormiga 2000: fig. 40), as a clade among the non-monophyletic *Savignia*-group (Miller and Hormiga 2004: fig. 7) or among a clade basal or distal to the *Savignia*-group (present study: Fig. 5; Frick and Muff 2009: fig. 67; Paquin et al. 2008: fig. 20; Seyfulina and Jocqué 2009: fig. 4). Therefore, the relationships between these groups remain unclear. Clade 23 includes members of the *Pelecopsis*-group (*Parapelecopsis*, *Silometopus*, *Hypomma*, *Abacoproeces*, *Dismodicus*), the *Tapinocyba*-group (*Tapinocyba*, *Ceratinops*), the *Entelecara*-group, the *Erigonoplus*-group (*Erigonoplus*), as well as taxa that were not assigned to any group (*Caracladus*, *Monocephalus*). Consequently, the relationships among these groups are close but far from clear, and likely to change with the addition of more taxa. Especially the delimitation of the *Pelecopsis*-group is very ambiguous, with some more taxa emerging also distal to the *Savignia*-group (*Panamomops*, *Gonatium*, *Grammonota*).

Conclusions and outlook

To a large extent the genus-level phylogeny of erigonines is still unknown. However, earlier studies and especially the present one have proven that the matrix of Miller and Hormiga (2004) withstands the addition of many, even closely related, taxa. Furthermore, we now have a general picture of the (character) evolution of about a third of all described erigonine genera. In the present analysis, major changes due to taxon addition occurred among genera belonging to Millidge's *Pelecopsis* and *Tapinocyba* groups and also concerning the position of *Venia*, the only Afrotropical genus considered so far. Focusing on the addition of taxa from these genus groups and African genera would expand our knowledge of erigonine evolution considerably.

Our analysis provides yet another example of how the addition of closely related taxa can change the topology of the ingroup. But the addition of outgroup taxa is also likely to change the topology of the erigonine tree. Previously, Mynogleninae looked like the sister group of erigonines (e.g. Hormiga 2000 in part; Miller and Hormiga 2004). However, in the recent work by Arnedo et al. (2009), which for the first time also included molecular data on linyphiid spiders, Micronetinae emerged as sister to Erigoninae.

The next important step in reconstructing the phylogeny of erigonine spiders will be to separate plesiomorphic from apomorphic character states by advancing research on the genus-level phylogenies of the potential sister subfamilies.

Among the erigonines we should focus on adding representatives of the remaining 40% of non-monotypic genera. This will give us a general idea of the phylogeny of erigonine spiders and potentially serve as a tool to better understand the character evolution and biogeography of about 70% of their genera and approximately 90% of the corresponding species.

The matrix of Miller and Hormiga (2004) will have its limits as to how many more taxa can be added without consideration of further characters. The present analysis shows that we might be approaching a certain limit already. The topology concerning the newly added taxa is not well supported, as it relies mainly on highly homoplastic characters. If we intend to reconstruct the entire phylogeny of erigonine spiders we should also focus on the addition of more hypotheses of homology. The very complex genital morphology of linyphiid spiders still offers many more characters to be scored, especially if already included discrete characters are refined to account for their various forms.

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Appendix 1: Specimens

Abacoproeces saltuum (L. Koch, 1872): Germany, Brandenburg, Stolzenhagen, 19.vi.–20.vii.1995, leg. M. Sommer, det. B. von Broen; NMBE (Ar421); 1♂1♀ (6♂1♀) for SEM.

Alioranus pastoralis (O. P. Cambridge, 1872): Israel, Sede Teiman, 11.–18.ii.2007, leg. and det. T. Plüss, coll. M. Schmidt (3232); 1♀ (1♀) for SEM.—Israel, Eshkol, 12.–19.ii.2007, leg. and det. T. Plüss, coll. M. Schmidt (3695–3702); 2♂ for SEM and 1♂ for tracheae (3♂).

Araeoncus humilis (Blackwall, 1841): Austria, Salzburg, Gastein, Kötschachtal, 19.iv.–10.v.1994, leg. and det. V. Relys. NMBE (Ar3186); 1♂1♀ for SEM and 1♂ for tracheae (26♂4♀).

Dicymbium nigrum (Blackwall, 1834): Denmark, Jægersborg Dyrehave, 09.iv.2003, leg. J. Pedersen, det. O. Gudik-Sørensen; ZMUC (9996); 1♀ for SEM.—Germany, Berlin, Berlin-Friedrichsfelde, Tierpark, 28.iv.1985, leg. and det. B. von Broen; NMBE (Ar637); 1♀ (3♂) for SEM.—Germany, Brandenburg, Kern mountains, 07.–20.xi.1996, leg. Deutsches Entomologisches Institut, det. B. von Broen; NMBE (Ar1309); 1♂ for tracheae (4♂1♀).

Dicymbium tibiale (Blackwall, 1836): Denmark, Rise Skov, 22.iv.2003, leg. H. Liljehult and J. Pedersen, det. J.-B. Schmidt; ZMUC (11430); 1♂ for SEM (1♂1♀).—Denmark, Hestehaven, Rønde, 01.x.1994, leg. P. de P. Bjørn et al., det. P. de P. Bjørn; ZMUC (11213); 1♀ for SEM (2♀).—Switzerland, Basle, leg. and det. E. Schenkel; NMB (1507a); 1♂ for tracheae (22♂27♀).

Diplocephalus latifrons (O. P. Cambridge, 1863): Austria, Styria, Oppenberg, Gulling bank, SW Rottenmann, 12.vii.1995, leg. and det. Kropf; NMBE (Ar1262); 1♂ for SEM (11♂).—Austria, as above except 17.vii.1995; NMBE (Ar1261); 1♀ for SEM (9♀).—Austria, Salzburg, Gastein, 26.vii.–15.viii.1993, leg. and det. V. Relys; NMBE (Ar3301); 1♂ for tracheae (7♂5♀).

Diplocephalus picinus (Blackwall, 1841): Austria, Styria, Laufnitzdorf, vi.1995, leg. W. Paill and O. Winder, det. C. Kropf; NMBE (Ar6694); 1♀ for SEM (1♀).—Austria, Styria Graz, 03.vi.1995, leg. W. Paill and O. Winder, det. C. Kropf; NMBE (Ar6645); 1♂ for SEM (2♂).—Germany, Brandenburg, Staffelde, 04.–25.v.1995, leg. M. Sommer, det. B. von Broen; NMBE (Ar546); 1♂ for tracheae (10♂).

Dismodicus bifrons (Blackwall, 1841): Germany, Thuringia, Südharz, Brandesbachtal, 12.–27.v.1996, leg. Taeger, det. B. von Broen; NMBE (Ar1192); 1♂1♀ for SEM and 1♂ for tracheae (2♂3♀).

Entelecara erythropus (Westring, 1851): Austria, Styria, Rothleiten, 04.vi.1995, leg. and det. C. Kropf; NMBE (Ar172); 1♂ for SEM (3♂).—Austria, as above except NMBE (Ar173); 1♀ for SEM and 1♂ for tracheae (10♀).

Erigonella hiemalis (Blackwall, 1841): Denmark, Zealand, Enemaerket, v. Naesbyholm, 19.ii.1997, leg. J. Pedersen, det. N. Scharff; ZMUC; 1♂1♀ for SEM.—Germany, Lower Saxony, Göttingen, 17.v.2001, leg., det. and coll. M. Schmidt; 1♂ for tracheae (1♂1♀).

Erigonella ignobilis (O. P. Cambridge, 1871): Germany, Brandenburg, Uckermark, Lychen, 18.v.1998, leg. and det. B. von Broen; NMBE (Ar2880); 1♂ for SEM (3♂).—Germany, as above except NMBE (Ar2881); 1♂ for tracheae (4♂).—Switzerland, Aargau, Siggenthal, 1974, leg. and det. R. Maurer; NHMB (792f) (ex. *Glyphesis servulus*); 1♀ for SEM (21♂8♀).

Erigonoplus globipes (L. Koch, 1872): Switzerland, Bern, Ligerz, 04.v.2005. leg., det. and coll. M. Schmidt (2CIIIL); 1♂1♀ for SEM and 1♂ for tracheae (25♂19♀).—Switzerland, as above except (3BIIIL); 1♂ for SEM (8♂).

Glyphesis servulus (Simon, 1881): Switzerland, Aargau, Siggenthal, 1974, leg. and det. R. Maurer; NHMB (792f); 2♂1♀ for SEM and 1♂ for tracheae (21♂8♀).

Hypomma bituberculatum (Wider, 1834): Germany, Brandenburg, Criewen, Uckermark, lower Oder valley, 05.–25.v.1995, leg. M. Sommer, det. B. von Broen; NMBE (Ar553); 1♂1♀ for SEM and 1♂ for tracheae (3♂3♀).

Monocephalus fuscipes (Blackwall, 1836): Switzerland, Bern, Bremgarten forest and Wohlen, iv., v., ix.1925, leg. M. Bartels, det. E. Schenkel; NMBE (Ar2626); 1♂1♀ for SEM and 1♂ for tracheae (10♂18♀).

Panamomops tauricornis (Simon, 1881): Switzerland, Grisons, Sur, Alp Flix, Salategnas, 27.v.–24.vi.2005, leg. P. Muff, det. H. Frick; NMBE (UN11.06); 1♂1♀ for SEM and 1♂ for tracheae (2♂1♀).

Saloca diceros (O. P. Cambridge, 1871): Austria, Gastein, Kötschachtal, Salzburg, Prossau, 25.v.–17.vi.1993, leg. and det. V. Relys; NMBE (Ar3289); 1♂ for SEM and 1♂ for tracheae (5♂).—Denmark, Tofte Skov, Bøgebakken, 01.vi.2003, leg. J. Pedersen, det. J. B. Schmidt; ZMUC (11364); 1♀ for SEM (9♀).

Silometopus elegans (O. P. Cambridge, 1872): Germany, Brandenburg, Uckermark, Lychen, 18.v.1998, leg. and det. B. von Broen; NMBE (Ar2886); 1♂1♀ for SEM and 1♂ for tracheae (17♂3♀).

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