

Molecular and morphological systematics of the Rastelloidina (Mygalomorphae)

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Abstract

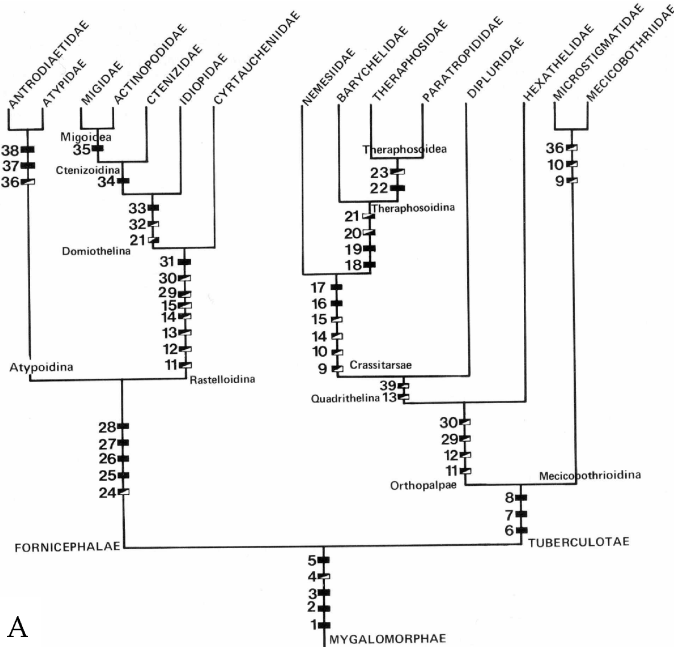
We tested monophyly in the higher taxonomic group Rastelloidina within Mygalomorphae, and in the families Actinopodidae, Migidae, Ctenizidae, Idiopidae and Cyrtauchenidae within Rastelloidina. We also tested the monophyly of the following taxa, covering the genus taxonomic level: *Cyrtauchenius*, *Latouchia*, *Ummidia*, *Cteniza*. For this purpose, 76 morphological characters sampled from 32 species were studied and 312 bp of the 16S rRNA gene were sequenced for 10 Rastelloidina species and three outgroup species, *Spiroctenus* sp., *Nemesia simoni* and *Atypoides riversi*. These sequences were unable to generate robust and accurate phylogenetic hypotheses. Highly homoplastic morphological characters such as the rastellum, the presence of tarsal scopula and the multilobar spermathecae could be identified. Several monophyletic taxa such as Actinopodidae, Migidae, Idiopinae, *Latouchia*, *Ummidia*, *Cteniza*, were recognized. On the other hand, Cyrtauchenidae, Idiopidae, Ctenizidae, Ctenizinae and *Cyrtauchenius* appeared to be polyphyletic. We can conclude that Rastelloidina monophyly is doubtful according to our combined molecular and morphological analysis.

Key words: Araneae, *Cyrtauchenius*, 16S rRNA, phylogeny, parsimony

INTRODUCTION

The Rastelloidina, established by Raven (1985), constitute a higher rank taxonomic group among mygalomorph spiders which includes five families: Actinopodidae, Migidae, Ctenizidae, Idiopidae and Cyrtauchenidae. Spiders in Rastelloidina are characterized by a generally broad, deep and procurved fovea. Cyrtauchenidae have two rows of teeth on broad paired tarsal claws. In Idiopidae male palpal bulbs are characterized by the second haematodocha extending below embolus. Ctenizidae female superior tarsal claws display only one strong tooth and

anterior legs show strong digging spines (Raven 1985). The phylogenetic relationships of these trapdoor spiders, however, appear to be problematic (Fig. 1). Cyrtauchenidae, elevated to family status and redefined by Raven (1985), is paraphyletic (Goloboff 1993). No synapomorphy is known to characterize Ctenizidae, and its monophyly has not been tested yet. Idiopidae monophyly is doubtful because it is considered to rely on plesiomorphic characters (Raven 1985). Furthermore, Goloboff (1993) obtained the monophyly of Idiopidae using only three taxa (*Idiops*, *Neocteniza* and *Misgolas*). On the other



A



B

Fig. 1. (A) Mygalomorphae phylogeny obtained by Raven (1985). (B) Mygalomorphae phylogeny obtained by Goloboff (1993).

hand, Actinopodidae and Migidae are strongly supported monophyletic taxa (Raven 1985; Goloboff 1993).

We performed an analysis based on both morphological characters (including newly defined ones) and molecular characters in order to shed light on phylogenetic

relationships within the Mygalomorphae. Our aim was to answer the following questions: Is Rastelloidina monophyletic? Are the families Ctenizidae and Idiopidae both monophyletic? Can monophyletic taxa be recognized within the doubtful group of Cyrtauchenidae?

MATERIAL AND METHODS

Taxonomic sampling

In the morphological study the monophyly of Rastelloidina and that of each of the five Rastelloidina families was tested using 37 terminals (from 4 Migoidea (including 2 Migidae and 2 Actinopodidae), 11 Ctenizidae (with Ctenizinae and Pachylomerinae), 8 Cyrtauchenidae, 9 Idiopidae, and 5 outgroup taxa) (Table 1). The monophyly of the genera *Cyrtauchenius* Thorell, 1869, *Latouchia* Pocock, 1901, *Ummidia* Thorell, 1875 and *Cteniza* Latreille, 1829 was tested using two species of each genus. Atypoidina (including Atypidae and Antrodiaetidae), the putative sister-group of Rastelloidina according to Raven (1985), and a clade formed by Nemesiidae and Theraphosidae, the putative sister-group of Rastelloidina according to Goloboff (1993), were used as outgroups. We chose *Nemesia simoni*, *Spiroctenus* sp., *Ischnocolus mogadorensis*, *Atypus affinis* and *Atypoides riversi* as outgroup representatives (Table 1). All specimens used in this study are collection materials. They belong to the MNHN of Paris collection and to the Musée de Beaulieu (Rennes 1) collection. Material studied is listed in Table 1.

In the molecular study 12 species from these were sequenced. One more species (*Misgolas gilliesi* (O.P.-Cambridge, 1878)) was added to test the monophyly of the genus *Misgolas*.

Morphological characters

We examined carapace, mouth parts, leg spines, abdomen and genitalia of our study organisms. All characters used to build our morphological matrix were based on characters used in the Raven (1985) and Goloboff (1993) studies. Only external somatic morphological characters were scored. We applied new coding to those characters and added new ones. Most characters were qualitative, but several were quantitative (Appendix 1). All the 76 characters were treated as unordered and were equally

weighted. Binary coding was preferred to multistate coding (10 multistate characters) when it did not add ambiguity or missing data.

Molecular characters

We sequenced a portion of the mitochondrial 16S rRNA, which has given good results within araneomorph phylogenetic relationships' studies (Huber 1993; Fang 2000). Specimens used were preserved in 75% ethanol. Genomic DNA was extracted from one or two legs using CTAB protocol (Winnepenninckx et al 1993). The approximately 530-bp region spanning the 5' end to the middle of the 16S rRNA gene was amplified using the primers LR-J-12887 5'-CCGGTCTGAACTCAGATCACGT-3' and the LR-J-13417 5'-ATGTTTTTGTAAACAGGCG-3' (reverse complement) (Simon et al 1994) and the primers "L1689" 5'-GTGCTAAGGTAGYATAAT-3' and "H16443" 5'-WTTAAAAGTCGAACAGA-3' designed for this study. PCR conditions applied are described in Palumbi (1996). Reactions begin with an additional step of 7 min at 94°C and are run for 30 cycles, each cycle consisting of denaturation for 40 s at 94°C, annealing for 40 s at 50°C and extension at 72°C for 40 s. Sequences were obtained using the CEQ2000 Beckman automatic sequencer.

Parsimony analysis

Tree searches were performed using PAUP* version 4.0 (Swofford 1998) with a heuristic search via a stepwise addition procedure (gaps were excluded in the molecular study). For the morphological analysis, we examined robustness with Bremer branch support indices (Bremer 1994) calculated with TreeRot (Sorenson 1999) and PAUP*. For the molecular analysis, robustness was assessed both by bootstrap values (Felsenstein 1985) and by Bremer branch support indices (Bremer 1994). We applied a priori molecular character weighting based on both consistency index and slopes of saturation curves (Hassanin et

Table 1. Specimens of each species used as terminals in morphological (all species) and molecular (species with *) analysis. References with AR, Buchli, and Lucas come from the MNHN collection. The others come from the Musée de Beaulieu collection. (CTE): Ctenizinae, (PAC): Pachylomerinae, (APO): Aptoroptychinae, (CYR): Cyrtaucheniinae, (EUC): Euctenizinae, (ARB): Arbanitinae, (IDI): Idiopinae, (GEN): Genysinae.

Families	Species	Collection references
Actinopodidae	<i>Actinopus scalops</i> (Simon, 1889)	23354 Simon
	<i>Missulena granulosa</i> (O.P.-Cambridge, 1869)	AR4119
Migidae	<i>Calathotarsus coronatus</i> Simon, 1903	AR4133
	<i>Migas nitens</i> Hickman, 1927 *	AR4131
Ctenizidae (CTE)	<i>Bothriocyrtum californicum</i> (O.P.-Cambridge, 1874)	AR4227
(PAC)	<i>Conothele malayana</i> (Doleschall, 1859)	AR4168
(CTE)	<i>Cteniza moggridgei</i> O.P.-Cambridge, 1874	538 Buchli
(CTE)	<i>Cteniza sauvagesi</i> (Rossi, 1788) *	MNHN
(CTE)	<i>Cyclocosmia ricketti</i> (Pocock, 1901)	AR4165
(CTE)	<i>Cyrtocarenum cunicularium</i> Olivier, 1811 *	89729 Beaulieu
(CTE)	<i>Latouchia davidi</i> (Simon, 1886)	zoothèque
(CTE)	<i>Latouchia japonica</i> Strand, 1910	AR4223
(CTE)	<i>Stasimopus</i> sp Simon, 1892	AR4117
(PAC)	<i>Ummidia aedificatoria</i> (Westwood, 1840)	Buchli
(PAC)	<i>Ummidia audouini</i> (Lucas, 1835)	847 et 848 Buchli
Cyrtaucheniidae	<i>Acontius africanus</i> Simon, 1889	AR4249
(APO)	<i>Ancylotrypa fasciata</i> Fage, 1936	AR4198
(APO)	<i>Bolostromus fauna</i> (Simon, 1889) *	AR4243
(CYR)	<i>Cyrtauchenius luridus</i> Simon, 1881 *	Beaulieu
(CYR)	<i>Cyrtauchenius walckenaeri</i> (Lucas, 1846)	AR 4267 et 9721 Lucas
(?)	<i>Entychides dugesi</i> Simon, 1888	AR7072
(APO)	<i>Fufius auricomus</i> (Simon, 1891)	AR8064
(EUC)	<i>Myrmekiaphila torreyi</i> Gertsch et Wallace, 1936 *	Buchli 827
Idiopidae (ARB)	<i>Arbanitis longipes</i> (L. Koch, 1873)	AR4501
(IDI)	<i>Galeosoma schreineri</i> Hewitt, 1913	AR4122
(GEN)	<i>Genysa bicalcarata</i> (Simon, 1902)	AR4500
(IDI)	<i>Gorgyrella</i> sp Purcell, 1902	AR4186
(IDI)	<i>Heligmomerus taprobanicus</i> Simon, 1892	AR4180
(GEN)	<i>Hiboka geayi</i> Fage, 1922	AR4509
(?)	<i>Misgolas crispus</i> (Karsch, 1878) *	AR4513
(?)	<i>Misgolas gilliesi</i> (O.P.-Cambridge, 1878) *	AR4514
(GEN)	<i>Scalidognathus oreophilus</i> Simon, 1892 *	AR4515
(IDI)	<i>Titanidiops maroccanus</i> Simon, 1909 *	Beaulieu
Nemesiidae	<i>Nemesia simoni</i> O.P.-Cambridge, 1874 *	82135 Beaulieu
	<i>Spiroctenus</i> sp *	AR4502
Theraphosidae	<i>Ischnocolus mogadorensis</i> Simon, 1909	89730 Beaulieu
Atypidae	<i>Atypus affinis</i> Eichwald, 1830	81976 Beaulieu
Antrodiaetidae	<i>Atypoides riversi</i> O.P.-Cambridge, 1883 *	2304 Buchli

al. 1998). The consistency index (CI) excluding uninformative sites, and the mutational saturation curves were obtained for each type of substitution using PAUP*, and were used to design step matrices in PAUP*. Incongruence between the data partitions was investigated using the ILD test (Farris et al. 1994, 1995) with PAUP* in order to fulfill a combined molecular and morphological analysis.

RESULTS

Morphological analysis

Seventy six characters form our morphological matrix (Appendix 2). Fifty eight of these characters have already been published (Goloboff 1993). Twenty-eight of these were

recoded. Eighteen new characters were added (Appendix 1). Two equally parsimonious trees were obtained (391 steps, CI=0.228, RI=0.493) (see the consensus strict of these in Fig. 2). More than fifty percent of the morphological characters used, had consistency and retention indices below 0.2. Nevertheless we identify some phylogenetically useful characters such as leg spination, ocular grouping and spinnerets (Table 2).

Molecular analysis

A total of 220 aligned sites (of which 109 were variable, and 74 informative for parsimony) were obtained from the 16 rRNA gene for 13 specimens. Two equally parsimonious trees

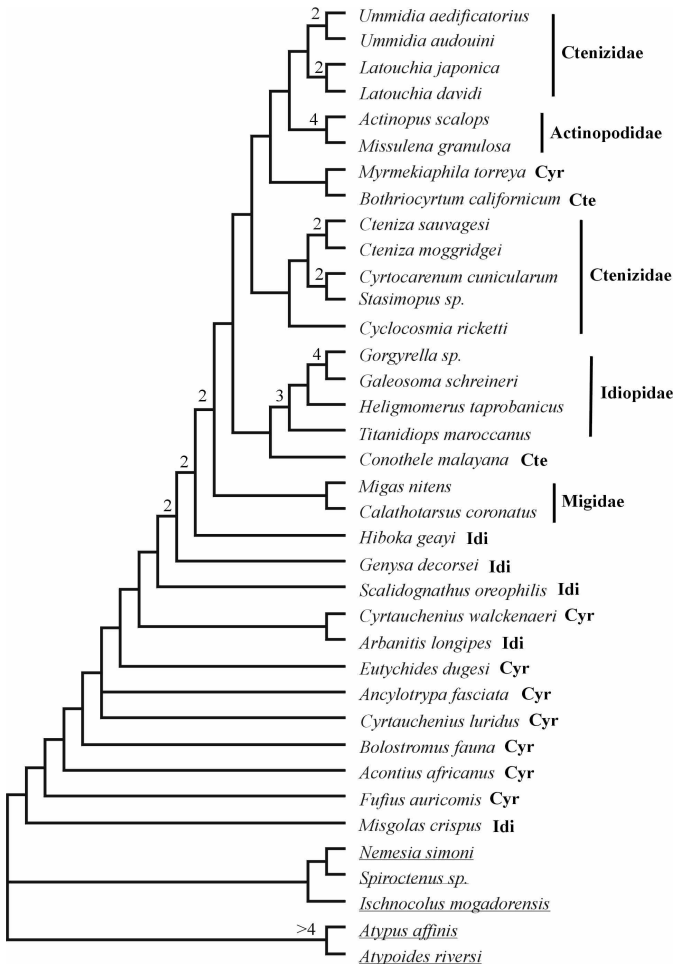


Fig. 2. Strict consensus MP tree obtained from the morphological analysis (76 characters, 37 terminals); two equally parsimonious trees are recovered (391 steps, CI=0.228, RI=0.493). Numbers above branches are Bremer indices above one. Outgroup taxa are underlined. Abbreviations are Cte for Ctenizidae, Idi for Idiopidae, Cyr for Cyrtacheniidae and Mig for Migidae.

Table 2. Higher level taxa apomorphies with characters and states numbers.

Taxa	Apomorphies
Rastelloidina	Unmodified maxillary lobe [29(1)]
	Spines of patella III in a unique row [47(1)]
	Anterior metatarsi scopulate [52(0)]
	Tarsi very desely scopulate apically [55(0)]
	Apical article of "PLS digitiform [58(0)]
Idiopinae	ALE isolated [4(2)]
	Four sternal sigilla [18(1)]
	Anterior eyes separated by AME larger [7(2)]
Actinopodidae	Eye group not scattered [4(1)]
	Eye tubercule absent [5(1)]
	ALE and PLE separated by more than ALE larger [10(1)]
	Post labial sigillum like a shallow suture [16(1)]
	Labium more long than large [11(2)]
	One row of chelicerae scopula [25(0)]
	Palpal coxae subquadrate [28(1)]
	Eye group occupies about half of the carapace width [70(0)]
Migidae	Chelicerae as long as the carapace [63(2)]
	Post labial spines absent [44(1)]
	Patella III spines absent [45(1)]
	Eye group occupies about half of the carapace width [70(0)]
	Cheliceral fang keeled [73(0)]

were obtained for the unweighted analysis (281 steps, CI=0.580, RI=0.359) (data not shown). Consistency and retention indices were low. Saturation for the A-G, C-T and A-T substitutions was very high, the slopes of saturation curves being 0.535, 0.479 and 0.487 respectively. The values used to design the step matrix were the following, A-C: 0.814, A-G: 0.282, A-T: 0.299, C-T: 0.324, C-G: 1 and G-T: 1. Portions of 16S rRNA sequences showed a typical A-T transversion bias (66%) (Clary & Wolstenholme 1985; Masta 2000). One most parsimonious tree was found for the weighted analysis (391 steps, CI=0.561, RI=0.348) (Fig. 3). Bootstrap values and Bremer indices remained low which implies that we can not make any indisputable statements. Nevertheless Rastelloidina, Idiopidae, Cyrtaucheniidae are not monophyletic while Ctenizidae and *Misgolas* are monophyletic.

Combined analysis

The α value of the ILD test of incongruence is 0.064. Therefore, there is no significant

incongruence between morphological and molecular data (0.05 level of significance). A combined analysis was carried out, but because of the relative low number of sequences obtained and because of the low α value of the ILD test obtained, we moderate our conclusions. Two equally parsimonious trees were obtained for the combined analysis (425 steps, CI=0.544, RI=0.349) (fig. 4). Rastelloidina is not monophyletic. Only one clade (*Cteniza sauvagesi*, *Cyrtocarenum cunicularium*) (Ctenizidae) was robust. This was the only clade that was obtained in all analyses. Idiopidae and Cyrtaucheniidae were shown to be paraphyletic.

DISCUSSION

Collection specimens and marker choice

Most of the specimens used in this study were old specimens preserved for a long time in 75% ethanol. These are not optimal conditions for amplification and sequencing of DNA fragments (Gurdebeke & Maelfait 2002). Nevertheless, 30% of specimens stored for

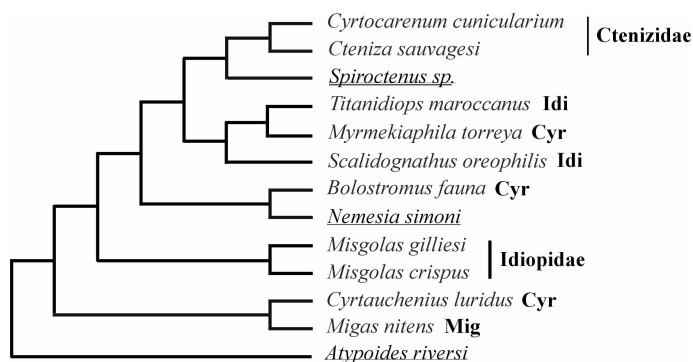


Fig. 3. Most parsimonious tree recovered from the weighted (no bootstrap values and Bremer indices calculated) molecular analysis (220 characters, 13 terminals); (391 steps, CI= 0.561, RI=0.348). Outgroup taxa are underlined. Abbreviations are Idi for Idiopidae, Cyr for Cyrtauchenidae and Mig for Migidae.

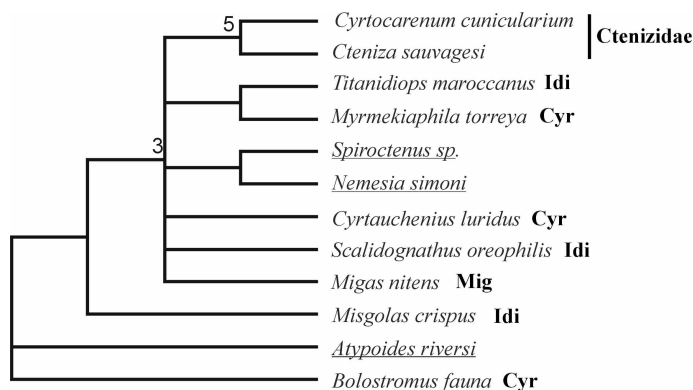


Fig. 4. Strict consensus MP tree obtained from the combined molecular and morphological analysis. Two equally parsimonious trees are recovered (425 steps, CI=0.544, RI=0.349). Numbers above branches are Bremer indices above one. Outgroup taxa are underlined. Abbreviations are Idi for Idiopidae, Cyr for Cyrtauchenidae and Mig for Migidae.

more than 50 years were sequenced (and 100% of the specimens stored for less than 10 years) (see Le Gleut 2001 for more details). The 16S gene fragment showed to be too variable for use at higher taxonomic levels (Rastelloidina) but is useful for studies at the generic level.

Phylogenetic implications

Only two major morphological studies have dealt with in the phylogenetic relationships Mygalomorphae. Raven's (1985) analysis was performed manually and his cladogram was obtained by the successive addition of arbitrarily defined sister-groups, while Goloboff applied a parsimony analysis with a character weighting method derived from the "successive weighting" approach (Goloboff 1993). Several characters defining groups such as Rastelloidina and Cyrtauchenidae were here shown to be highly homoplastic (rastellum, presence of tarsal scopula, multilobar spermathecae).

Rastelloidina

The monophyly of Rastelloidina is doubtful. On the morphological tree (Fig. 2) Rastelloidina is not very robust. Molecular and combined analyses resulted in the polyphyly of the Rastelloidina.

Actinopodidae and Migidae

The monophyly of Actinopodidae and of Migidae found by Goloboff (1993) was confirmed by the morphological part of our work (Actinopodidae was not tested in our molecular work because of the lack of adequate specimens). On the other hand, the classically recognized monophyly of the group Migoidea formed by Actinopodidae and Migidae (Migoidea) was not obtained here (Fig. 2).

Cyrtauchenidae

Cyrtauchenidae here was shown to be polyphyletic (Figs. 2-4), while it was

monophyletic in Ravens' study and paraphyletic in Goloboff's one. Although our taxonomic sampling includes several representatives of each Cyrtaucheniidae subfamily, we found no monophyletic group within Cyrtaucheniidae for any taxonomic level considered. The genus *Cyrtauchenius* was polyphyletic and a taxonomic revision of this genus is already in progress (Le Gleut et al. in prep).

Ctenizidae

The Ctenizidae are polyphyletic (Fig. 2). Two robust clades were formed by the genera *Ummidia* and *Latouchia* on one hand, and by the genera *Cteniza*, *Cyrtocarenum cunicularium*, *Stasimopus* sp. and *Cyclocosmia ricketti*, on the other hand. Ctenizinae and Pachylomerinae do not form monophyletic groups.

Idiopidae

Idiopidae was found to be polyphyletic (Figs. 2-4). Nevertheless, representatives of the subfamily Idiopinae (*Gorgyrella* sp., *Galeosoma schreineri*, *Heligmomerus taprobanicus* and *Titanidiops maroccanus*) form a well supported monophyletic group based on morphological dataset.

Taxonomic implications

In conclusion, we corroborate the doubts expressed by Goloboff concerning the monophyly of Cyrtaucheniidae (Goloboff 1993). On the other hand, we did not find Ctenizidae, Idiopidae and Migoidea to be monophyletic, which contradicts results obtained both by Raven (1985) and Goloboff (1993).

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Appendix 1. List of characters. Characters are here grouped by complexes of characters which are indicated in square brackets and character state numbers are in brackets. Abbreviations and symbols are AME: anterior median eye; PME: posterior median eye; ALE: anterior lateral eye; PLE: posterior lateral eye; ITC: inferior tarsal claws; STC: superior tarsal claws; AMS: anterior median spinneret; ALS: anterior lateral spinneret; PLS: posterior lateral spinneret. (*) Character and coding already used; (#) new coding; (!) new character; (⌘) character not observed.

[Carapace] 1. Shape of the carapace in lateral view (*): (0) caput low, (1) elevated; 2. Carapace ornamentation (#): (0) very slightly foveate, (1) remarkably foveate; 3. Shape of the fovea (#): (0) procurved, (1) recurved, (2) transverse, (3) longitudinal; 62. Clypeus (!): (0) broad, (1) narrow; Eye group 4. Eye group (#): (0) grouped, (1) not grouped, (2) ALE isolated; 5. Eye tubercle (*): (0) present, (1) absent; 6. Eye tubercle (#): (0) all eyes, (1) only AME; 70. Size of the ocular group (#): (0) occupies about half of the cephalothorax width, (1) about one third; 7. Distance between AME (#): (0) more than AME diameter, (1) smaller than AME diameter, (2) as long as AME diameter; 8. Relative size of AME/ALE (#): (0) AME < ALE, (1) AME > ALE; 9. Relative size of AME/PME (#): (0) AME < PME, (1) AME > PME; 10. Distance ALE/PLE (#): (0) separated by less than ALE larger, (1) separated by more than ALE larger (or the same larger);

[Labium] 11. Shape of the labium (#): (0) triangular, (1) squared, (2) rectangular (long), (3) rectangular (short and wide); 12. Shape of the labium border (!): (0) sinuous border, (1) straight border; 13. Cuspules (*): (0) present, (1) absent; 14. Cuspules number (#): (0) less than 5, (1) more than 10, (2) 10;

[Sternum] 15. Shape of the sternum border (*): (0) sternal sides parallel, (1) gradually narrowed in front; 16. Post labial sigillum (!): (0) present, (1) absent; 17. Post labial sigillum (*): (0) deeply excavate, (1) a shallow suture; 18. Number of sternal sigilla (!): (0) six, (1) four, (2) eight; 19. Posterior sternal sigilla (!): (0) lateral, (1) medial; 20. Shape of the posterior sigilla (!): (0) circular, (1) oval;

[Chelicerae] 63. Relative length of the chelicerae (!): (0) smaller than 0.5 of the carapace length, (1) longer than 0.5 of the carapace length, (2) as long as the carapace; 21. Rastellum (*): (0) present, (1) absent; 22. Rastellum apophyse (*): (0) present, (1) absent; 23. Shape of the rastellum apophyse (!): (0) anteriorly produced, (1) unmodified; 24. Chelicerae furrow (*): (0) one row of teeth, (1) two rows of teeth; 25. Number of row of chelicerae scopula (!): (0) one, (1) two; 26. Shape of the chelicerae fang (#): (0) parallel, (1) diagonal; 27. Chelicerae basal teeth (*): (0) present, (1) absent; 73. Chelicerall fang (*): (0) keeled, (1) normal;

[Legs: coxa] 28. Palpal coxae (*): (0) elongate, (1) subquadrate; 29. Maxillary lobe (*): (0) anteriorly produced, (1) unmodified; 30. Serrula (*): (0) present, (1) absent; 31. Spines (#): (0) present, (1) absent; 32. Maxillary cuspules (*): (0) present, (1) absent; 33. Maxillary cuspules (*): (0) confined on inner angle, (1) not confined;

[Legs: tarsal claws] 35. Number of teeth on tarsal claws (STC palp) (#): (0) one, (1) several, (2) absent; 36. Row of the tarsal claws teeth (STC all legs) (#): (0) present, (1) absent; 37. Number of row of the tarsal claws teeth (STC all legs) (#): (0) a single row, (1) two row of teeth; 38. Number of teeth (STC PI) (#): (0) one tooth, (1) several teeth; 39. ITC (*): (0) dentate, (1) edentate; 69. ITC (*): (0) normal, (1) reduced size;

[Legs: spines] 40. « claviformes » setae on palpal tarsi (!): (0) present, (1) absent; 34. Trochanter spines (!): (0) present, (1) absent; 41. Tarsal palpal spines (#): (0) present, (1) absent; 42. Tarsal palpal spines (!): (0) dense, (1) scattered; 43. Anterior tarsal spines (#): (0) present, (1) absent, (2) thornlike spines; 44. Posterior tarsal spines (!): (0) present, (1) absent; 45. Patella III spines (#): (0) present, (1) absent; 46. Number of patella III spines (#): (0) less than 5, (1) more than 10; 47. Distribution of patella III spines (!): (0) in a wide band, (1) in a row, (2) distal; 48. Patella III (*): (0) with apical comb of spines, (1) without apical comb of spines; 49. Posterior legs spines (*): (0) located dorsally, (1) distributed ventrally as well as dorsally; 72. Preening combs (*): (0) present, (1) absent; 50. Anterior tarsi (#): (0) scopulate, (1) without scopula; 51. Posterior tarsi (#): (0) scopulate, (1) without scopula; 52. Anterior metatarsi (!): (0) scopulate, (1) without scopula; 53. Posterior metatarsi (!): (0) scopulate, (1) without scopula; 54. Claw tufts (*): (0) present, (1) absent; 55. Apical tarsal scopula (!): (0) very densely scopulate, (1) without scopula; 65. Tarsal trichobothria (#): (0) present, (1) absent; 66. Tarsal trichobothria (#): (0) in a medial row, (1) forming a wide band; 67. Distribution des trichobothria (metatarses)(#): (0) in a straight row, (1) distal, (2) scattered;

[Pattes: shape] 56. Tibia III (*): (0) excavate, (1) not excavate; 64. Tibia III (!): (0) longer than patella III, (1) smaller or as long as patella III; 68. Shape of the tarse (*): (0) pseudosegmented, (1) integral;

[Spinnerets] 58. Apical article of PLS: (0) digitiform, (1) domed; 59. ALS (*): (0) present, (1) absent; 60. AMS (#): (0) close, (1) widely separated; 61. Spigots (#): (0) all the same, (1) two sorts;

[Genitalia] 71. Male palpal bulb (*): (0) without conductor, (1) with conductor; 74. Haematodocha (⌘): (0) small, (1) extending below embolus; 75. Cymbium (⌘): (0) palpal tarsus normal, (1) one cymbial lobe pointed; 76. Spermathecae (⌘): (0) unilobar, (1) multilobar; [Abdomen] 57. Dorsal abdominal scutum (*): (0) present, (1) absent.

Appendix 2. Morphological matrix. Missing data are coding with “?” and inapplicable data with “-”.

<i>Nemesia simoni</i>	1110001010	111-001001	0000101001	1001201111	011100-110	0001111111	0000010111	001000
<i>Spiroctenus</i> sp	1020001010	1101001001	11-0101001	1001-01011	1-11001110	0101111110	0100010111	001???
<i>Ischnocolus mogadorensis</i>	00201-1000	1000000000	11-0111101	100121--10	1-11000110	0101111111	?000000111	0-1001
<i>Atypus affinis</i>	1110000110	011-01-201	11-0100101	1011100101	1-11??01-1	1111111100	11201-0001	111000
<i>Atypoides riversi</i>	1030011010	001-000000	01-0011101	11-1100111	0111000111	1110111101	00201-0001	111000
<i>Ancylotrypa fasciata</i>	11001-2000	111-000001	0000111001	11-1101111	0100010110	1011111010	0011000101	011001
<i>Fufius auricomus</i>	1110011010	2000001000	11-0111110	0001-0111-	--01001110	1010111011	0010000101	011001
<i>Cyrttauchenius luridus</i>	1101010010	101-001011	0000111001	11-1101111	0100010110	1011111010	0101010101	011001
<i>Myrmekiaphila torreyi</i>	1020001010	011-101011	0000101011	1001-01011	--11010011	1111011011	1100000101	011001
<i>Acontius africanus</i>	1100001110	201-000001	11-?111111	1001-01111	--11011110	0001011110	0010000101	011001
<i>Cyrttauchenius walckenaeri</i>	11001-2011	3100000001	0010111011	1001100111	1-11001110	0001111110	000101-1?1	011???
<i>Bolostromus fauna</i>	1110001010	201-000001	01-0111100	1001101111	0100010110	1011011011	0110000101	011001
<i>Entychides dugesi</i>	1100011010	0101000011	0010101001	1011100111	0100010010	0001011-1-	-010010101	011000
<i>Bothriocyrtum californicum</i>	11001-1010	011-101011	0001101001	0011000011	0000002011	1111011010	1001002101	011000
<i>Ummidia aedificatoria</i>	1100001010	0102001011	0001101011	1010000110	0020001011	1111101010	0100011101	011000
<i>Ummidia audouini</i>	1100001010	0102001011	0011111001	1011-00010	1-00010010	1011101010	0000012101	011000
<i>Cyclocosmia ricketti</i>	1100001000	1100000011	0001101001	1011000011	0020010101	1111110010	1001011101	011000
<i>Cteniza sauvagesi</i>	1100012001	0000100011	0001111001	1001000011	0000001101	1111011011	1001010101	011000
<i>Cteniza moggridgei</i>	1100002001	1002101011	0001111001	1001000011	0000010101	1111011011	1001010101	011000
<i>Conothele malayana</i>	1100001110	110111-001	01-1101011	1011000010	0000010101	1111111110	1100011101	011000
<i>Cyrtocarenum cunicularium</i>	11001-2000	1100001010	000111101?	1001-0011-	--00001101	1111011110	1001012101	011000
<i>Latouchia japonica</i>	1100001010	001-101011	0011111001	1001000010	0020010011	1111011010	0101012101	011000
<i>Latouchia davidi</i>	1100002000	0000101011	0011111011	1001000010	0020010011	1110011010	1001012101	011000
<i>Stasimopus</i> sp	11011-2001	110011-011	000??11001	1001000111	0020010101	1111011110	1001010101	011000
<i>Gorgyrella</i> sp	1102002111	1102100001	0000101010	0011000011	0100010011	1111011111	0101010101	011110
<i>Hiboka geayi</i>	11101-1111	101-100010	0011111001	11-1-00111	--00010111	1110011010	?1000011?1	011110

Misgolas crispus	1020001110	0100000000	01-1111011	1001100111	0111001110	0011011011	1000001101	011110
Scalidognathus oreophilus	11101-2010	1100000011	0010111001	1001000010	0100010110	0111111111	0011010101	011110
Titanidiops maroccanus	1102001010	111-1011--	0001101001	1011000011	00000101-1	1111011011	1110010101	011110
Genysa bicalcarata	11111-1011	2100100011	001111100?	1011000011	1-11110100	1011011110	10110101?1	011110
Heligmomerus taprobanicus	1102001001	01021011--	1001101001	1011000011	0000010111	1111101111	11000101?1	011110
Galeosoma schreineri	1102001011	11000001--	0000111010	1011000011	0000010011	1111010110	11010101?1	011110
Arbanitis longipes	10201-1011	11020001--	0010101001	1001100011	1-00001110	0001011010	10010111?1	011110
Actinopus scalops	11011-1001	21?211-011	0001?11101	1011000011	0000002011	1111011010	0011010100	011000
Missulena granulosa	11011-0111	210101-001	01-0011101	1011000101	1-00110011	1111111010	?011000100	011000
Migas nitens	1110011010	1101101001	11-1011001	1011000011	01111--111	1111011110	1000011110	010000
Calathotarsus coronatus	11111-2000	210211-011	000?111001	1001200011	01011--111	1110011110	1000011100	010000