A REVISED PHYLOGENETIC ANALYSIS FOR THE SPIDER GENUS *CLITAETRA* SIMON, 1889 (ARANEAE, ARANEOIDEA, NEPHILIDAE) WITH THE FIRST DESCRIPTION OF THE MALE OF THE SRI LANKAN SPECIES *CLITAETRA THISBE* SIMON, 1903

DIMITAR DIMITROV,[1,4] SURESH P. BENJAMIN,[2] AND GUSTAVO HORMIGA[3]

ABSTRACT.   In this study, we describe the previously unknown male of the spider *Clitaetra thisbe* Simon, 1903, from Sri Lanka and provide some data on its natural history. In light of this new information, we present results from the first cladistic analyses of *Clitaetra* species that include male morphological characters of *C. thisbe* and DNA sequence data for representatives of all nephilid genera and a broad sample of outgroups. The monophyly of *Clitaetra* and the basal position of *C. thisbe* within the genus are corroborated. Our results also support the hypothesis that *Nephila* is a sister group to the clade *Herennia + Nephilengys*, which challenges the current hypothesis for nephilid relationships that has been used extensively for the study of genitalic and web evolution in Nephilidae. We also discuss some of the previously proposed interpretations and primary homology statements for several male genitalic characters in nephilids.

INTRODUCTION

Nephilids are orb-weaving spiders that inhabit the tropical and subtropical regions of the world. *Nephila* Leach, 1815, species are probably among the most conspicuous spiders in these geographical areas in that females can reach up to about 4 cm body length and their webs often exceed 1 m in diameter (Harvey et al., 2007; Jocqué and Dippenaar-Schoeman, 2006; Robinson and Robinson, 1973). The first cladistic studies that included *Nephila* and its relatives placed this araneoid lineage as sister to a clade comprising all other tetragnathids and treated it as a subfamily within Tetragnathidae (Coddington 1990; Griswold et al., 1998; Hormiga et al., 1995). A recent revisionary study elevated the group containing the genera *Nephila; Herennia* Thorell, 1877; *Nephilengys* L. Koch, 1872; and *Clitaetra* to family rank and refuted the placement of nephilids as a tetragnathid lineage (Kuntner, 2006; see also Kuntner et al., 2008). More recently, in a study that featured a multilocus molecular dataset combined with morphological evidence, Álvarez-Padilla et al. (2009) also found that nephilids do not represent a tetragnathid lineage. Kuntner (2006) also revised and phylogenetically tested the monophyly and the relationships of *Clitaetra* and demonstrated that the genera *Deliochus* Simon, 1894, and *Phonognatha* Simon, 1894, do not belong within Nephilidae. The latter two genera were formally transferred to the family Araneidae by Kuntner et al. (2008).

Kuntner's (2006) revision of *Clitaetra* represents the most comprehensive study of this genus to date. One of the findings of his revision is the basal phylogenetic position of the Sri Lankan species *Clitaetra thisbe* as sister to a clade that includes the remaining species in the genus. This hypothesis makes *C. thisbe* (Fig. 1A, B) particularly important for the polarization

[1] Department of Biological Sciences, The George Washington University, Washington D.C. (e-mail: dimitard@gwu.edu).
[2] Senior Research Fellow, Institute of Fundamental Studies, Hantana Road, Kandy, Sri Lanka (e-mail: suresh.benjamin@gmail.com).
[3] Department of Biological Sciences, The George Washington University, Washington, D.C. Research Associate, Department of Invertebrates, Museum of Comparative Zoology (e-mail: hormiga@gwu.edu).
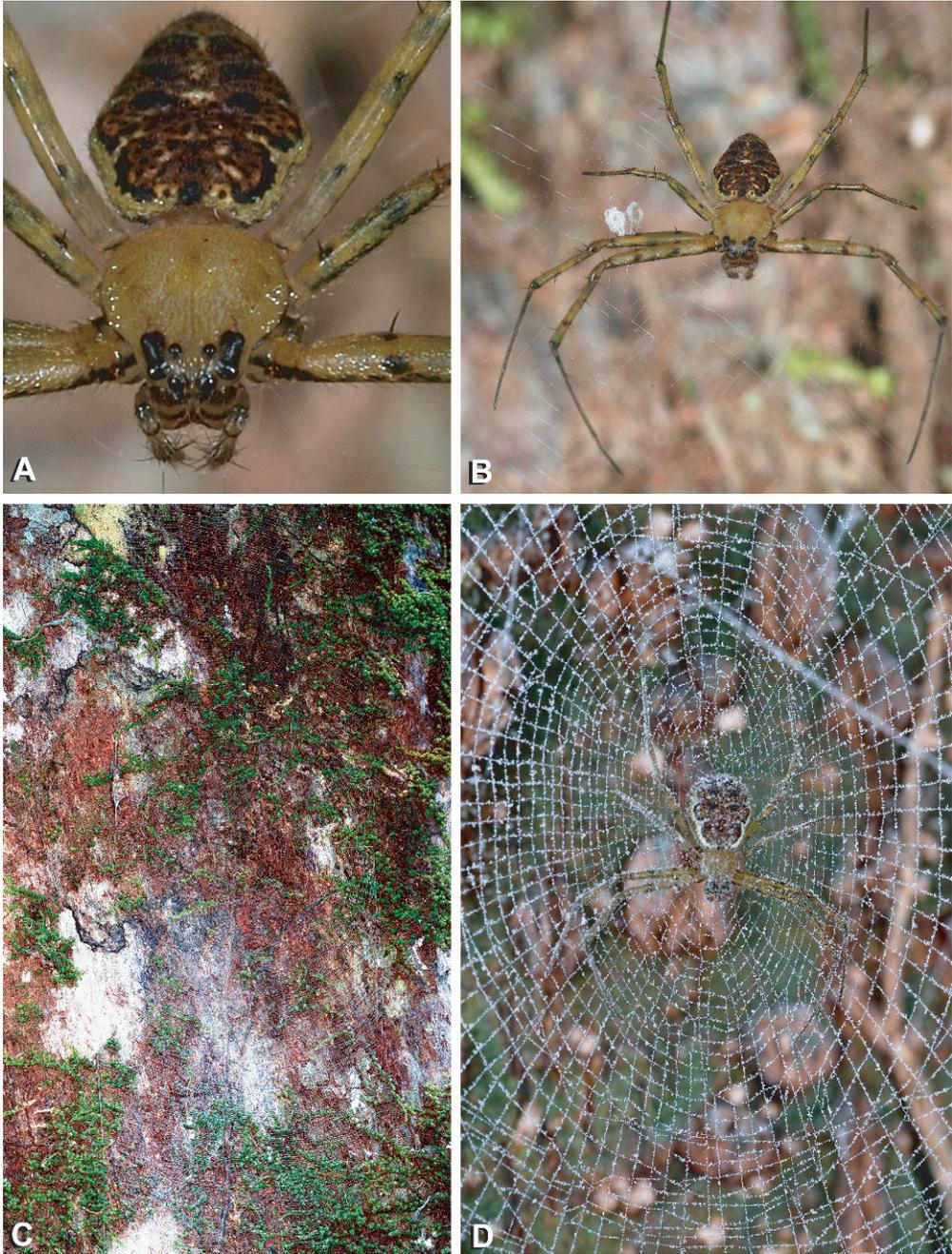[4] Corresponding author.

Figure 1.   *Clitaetra thisbe* female from Gilimale Forest Reserve: dorsal/frontal view A/B; web C; hub detail D. Photos by SPB.

of nephilid characters. In this study, we describe the previously unknown male of *C. thisbe*, correct some errors of interpretation of the female genitalic structures and revise the phylogeny of *Clitaetra* by including the new and revised information. Part of the material of *C. thisbe* (Bodinagala Forest Reserve) was collected not far from its type locality in Sri Lanka, the city of Galle. The forests of Galle, although degraded, were not "disastrously affected by the 2004 tsunami" as claimed by Kuntner (2006). We also analyze multilocus sequence data for many of the studied species. The molecular data resulted from our own ongoing work on araneoid phylogeny (e.g., Álvarez-Padilla et al., 2009; these sequences are readily available in GenBank). The included nucleotide data provide additional lines of evidence and allow a more rigorous test of phylogenetic hypotheses.

Kuntner's (2006) classification recognized two subfamilies within Nephilidae: Clitaetrinae, containing the genus *Clitaetra*, and Nephilinae, containing the remaining three nephilid genera. Clitaetrinae was further split into three subgenra: *Indoetra*, *Clitaetra*, and *Afroetra*. Kuntner's (2006) classification of *Clitaetra* has been used recently as a case example of a new approach to classification (Kuntner and Agnarsson, 2006). It is thus relevant to provide some comments on the merits of this approach, and we do so in the Discussion section of this paper.

MATERIALS AND METHODS

Specimens were examined with a Leica MZ16A stereoscopic microscope with a camera lucida and Leica DMRM compound microscope with a drawing tube. Drawings were done with graphite pencils on acid-free cotton paper. Hairs and macrosetae are not depicted in the final drawings. The right male palp was illustrated (the only intact palp available), and scanned images were digitally transposed. The epigynum was treated with SIGMA Pancreatin LP 1750 enzyme complex (Álvarez-Padilla and Hor-

miga, 2008) to digest remaining tissues and transferred to methyl salicylate solution for examination and drawing.

All pencil drawings were scanned and further improved with the help of GIMP 2.4 and Adobe Photoshop CS2 programs. Digital images of the specimens were taken in alcohol media with a Nikon DXM1200F digital camera mounted on a Leica MZ16A stereoscopic microscope. The final plate's layout and editing was done with Adobe Illustrator CS2. Webs were dusted with cornstarch for observation and photo documentation.

Phylogenetics

Characters. The character matrix of this study is taken from Kuntner's revision of *Clitaetra* (Kuntner, 2006). After submission of this paper for publication, Kuntner and Agnarsson (2009) published a study on Indian Ocean *Clitaetra*, in which they revised some of the scorings of four web-building characters for three *Clitaetra* species. Their analysis of a matrix with the revised character scores did not change the *Clitaetra* cladistic topology reported in Kuntner (2006) and Kuntner et al. (2008). For most of the characters, we have scored the male morphology of *C. thisbe* in accordance with the original character definitions of Kuntner (2006). These characters are discussed elsewhere (Kuntner, 2006, and references therein). One discrepancy between our analyses and Kuntner's work comes from differences in the interpretation and coding of some male pedipalpal sclerites. Arguably the most controversial point in this respect is Kuntner's treatment of the sclerite in the male palp functioning as a conductor. He states that in nephilids this sclerite, for which he uses the term "embolic conductor," is a novel structure that is part of the embolic division and thus non-homologous to the araneoid conductor (Kuntner, 2005, 2006; Kuntner et al., 2008; Kuntner and Agnarsson, 2009). We disagree with this interpretation and our rationale has been discussed elsewhere

(Dimitrov and Hormiga, 2009; see also Álvarez-Padilla, 2007; Álvarez-Padilla et al., 2009). In the present analyses, the conductor of nephilids is treated as homologous to the araneoid conductor, and character definitions and scorings in the matrix for the conductor and the "embolic conductor" are revised accordingly: character 144 coding the presence or absence of "embolic conductor" is removed from the matrix and characters 145–151 refer now to the conductor instead of the "embolic conductor." One additional state has been added to character 148 (conductor curvature) to describe the spirally curved conductor in some tetragnathids—circularly curved, following the tegular margin. In addition, several errors in the original matrix were corrected. Kuntner (2006) coded *Nesticus* as lacking a conductor; however, a conductor is present in this genus (e.g., Agnarsson, 2004; Griswold et al., 1998; Huber, 1993), and accordingly, we have corrected the scoring for *Nesticus* to reflect it. Careful examination of the epigynum of *C. thisbe* suggests that the copulatory ducts open ventrally (Fig. 2E G) and not caudally as suggested by Kuntner (2006). Our interpretation is also supported by SEM observations (Fig. 5D). As a result, the structures in *C. thisbe* referred to as "copulatory ducts" by Kuntner (2006: fig. 25B, C) are actually the fertilization ducts and vice versa. The complete morphological matrix used in the analyses is given in Appendix 1.

In addition to the morphological characters, molecular data available in GenBank for many of the taxa were downloaded and used in the analyses. We have used sequences from three nuclear (28S, 18S, and H3) and three mitochondrial genes (12S, 16S, and COI). The accession numbers of the sequences used in the analyses are given in Appendix 2. Several terminals are "composed" of two species: *Argiope argentata* (Fabricius, 1775) is represented by *A. argentata* and *Argiope savignyi* Levi, 1968 (as in Álvarez-Padilla et al., 2009); *Clitaetra episinoides* Simon, 1889, by *C. episinoides* and *Clitaetra* sp. from South Africa (as in Álvarez-Padilla et al., 2009). Although such "chimaeras" are not desirable, the monophyly of neither *Argiope* nor *Clitaetra* has been questioned; therefore, any potential errors in phylogenetic inference caused by these composed terminals should be minimal.

Analyses. All data, morphological and molecular, were analyzed simultaneously under the parsimony criterion. Because positional homology in ribosomal genes is not a trivial problem due to the presence of insertion and deletions, we have investigated two different approaches to this problem. In the first case, we used the traditional "static homology approximation" where, before the phylogenetic analysis, the homologous gene fragments are aligned with a multiple sequence alignment algorithm. To generate the alignments, we have used the program MAFFT v6 and the L-INS-I method (Katoh et al., 2002, 2005). Aligned gene fragments were combined with the morphological data and were analyzed with TNT v1.1 (Goloboff et al., 2003). Data were analyzed under both equal and implied weights (Goloboff, 1993), either with 1,000 replications, keeping 10 trees per replication, or 500 replications, keeping 200 trees per replication. In both cases, gaps were treated as missing data. Trees were swapped by the TBR algorithm, and minimum length = 0 (the default in TNT) was used as a collapsing rule in all searches. Jackknife with 36% probability of character removal and bootstrap support values with 1,000 pseudoreplications were calculated in TNT for the static alignments. For the analyses under implied weights, we have sampled different *k* values within a wide range of variation allowed by TNT 1.1. Values from 1 to 100 were sampled; with denser sampling in the lower range (1–20) until topology converged to the one from equal weights (see also Dimitrov and Hormiga, 2009).

One alternative approach to the problem of positional homology is direct optimization (Wheeler, 1996). Parsimony analyses
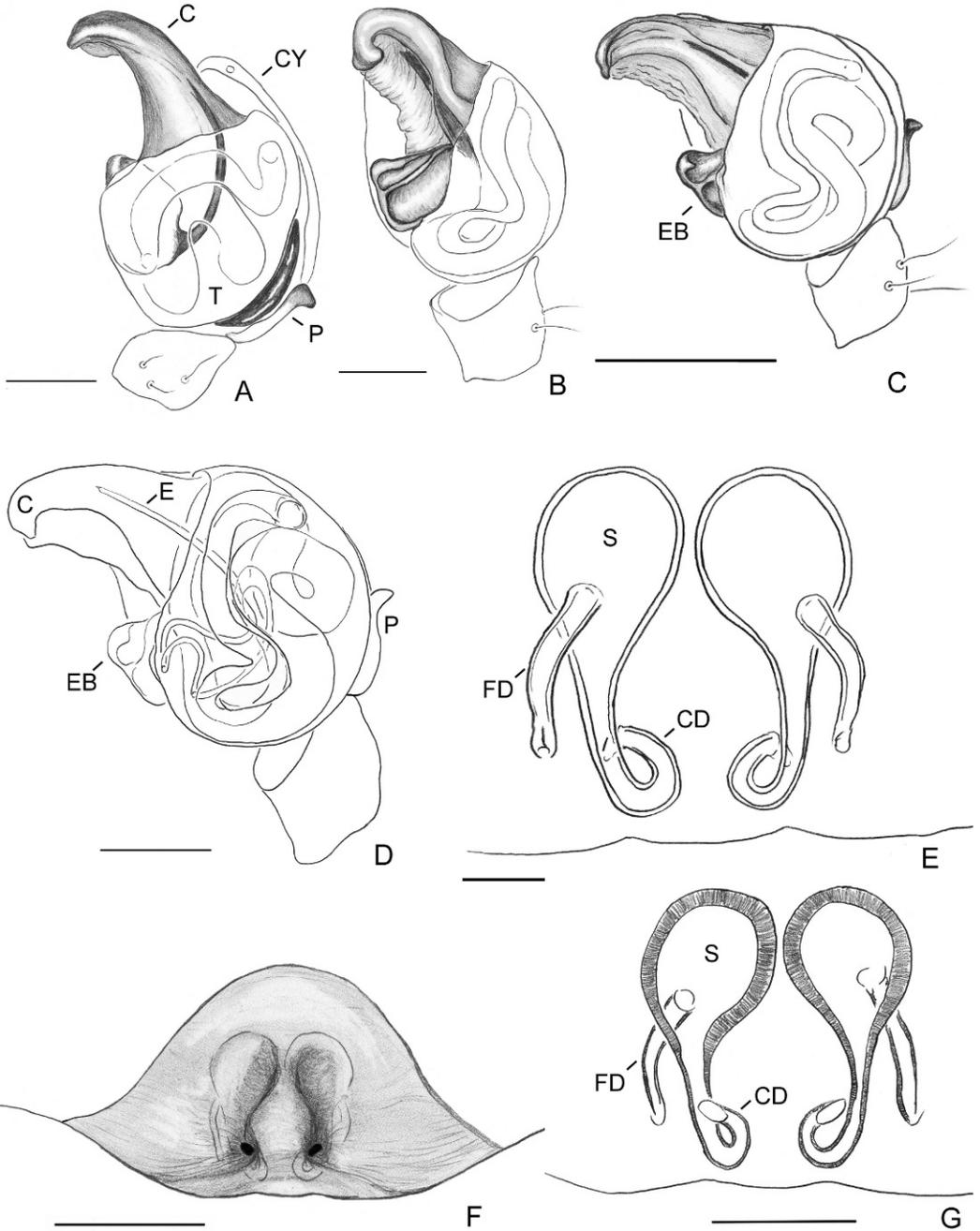
Figure 2. *Clitaetra thisbe* male: A, palp retrolateral; B, palp prolateral; C, palp ventral; D, palp schematic. *Clitaetra thisbe* female: E, vulva dorsal; F, epigynum ventral; G, schematic drawing of the female genitalia. Note the broken embolus. *Scale lines:* A, B, D, E, G 0.1 mm; C, F 0.2 mm.

under direct optimization were performed with the computer program POY 4 (Varón et al., 2008). POY allows different weighting schemes to be set for nucleotide substitutions and insertion/deletions. To test the sensitivity of the results to different weighting schemes, several different weighting combinations were investigated.

For the direct optimization analysis, jackknife values were calculated in POY 4. Analyses under direct optimization were run on the Biocluster at the University of Copenhagen (Copenhagen, Denmark).

More thorough phylogenetic analyses, including Bayesian inference and sensitivity analyses, on the basis of a very similar data set but with larger taxon sampling, have been recently published elsewhere (Álvarez-Padilla et al., 2009). Comparable analyses for the present data are beyond the scope of this paper.

ABBREVIATIONS USED IN TEXT AND FIGURES

ALE	anterior lateral eyes
AME	anterior median eyes
C	conductor
CD	copulatory ducts
CO	copulatory openings
CY	cymbium
E	embolus
EB	embolus base
FD	fertilization ducts
MNHN	Muséum national d'histoire naturelle, Paris, France
MPT	most parsimonious tree/s
P	paracymbium
PLE	posterior lateral eyes
PME	posterior median eyes
S	spermathecae
ST	subtegulum

RESULTS FROM CLADISTIC ANALYSES

We only present the trees from the analyses with TNT under equal weights because they are practically identical to the results from POY and to most of the results under implied weights. Differences in

results between different analytical criteria are discussed in the text. Tree search under equal weights in TNT resulted in four MPT (L = 6,600, RI = 0.588, CI = 0.438). The strict consensus of these four trees (L = 6,658, RI = 0.583, CI = 0.426) is shown in Figure 6. Nephilids are found to be monophyletic, and, as in previous analyses, *Clitaetra* is the most basal member of Nephilidae (sister to a clade with the remaining nephilid genera). *Nephilengys* is the sister group of *Herennia*, and the clade composed by these two genera is the sister lineage of *Nephila*. *Epeirotypus* (Theridiosomatidae) appears as sister group to Nephilidae but this placement does not receive bootstrap or jackknife support. Relationships of families within Araneoidea are mainly unresolved, resulting in a large polytomy. Within *Clitaetra*, *C. thisbe* is the most basal species (sister to a clade with the remaining species in the genus), whereas relationships between the rest of the species mirror the results of Kuntner (2006), with *C. episinoides* being either the sister species of *Clitaetra perroti* or sister to a clade that includes *Clitaetra irenae*, *Clitaetra clathrata* and *Clitaetra simoni*.

Low values of *k* weight against homoplasious characters very strongly, and its use is discouraged (Goloboff, 1993, 1995), especially when analyzing molecular characters in which homoplasy is rampant. Results from analyses of the static alignment, together with the morphological data under implied weighting, recover the exact same topology for the relationships of nephilids, except for the arrangement of species within *Nephila* even with very low *k* values (1–3). None of the alternative topologies of *Nephila* interspecific relationships receives robust support. Independently of the value of *k*, relationships within *Clitaetra* were found to be the same as in the preferred tree of Kuntner (Kuntner, 2006: fig. 27B), where *C. perroti* is sister to *C. episinoides*.

Analyses under direct optimization in POY converge to the same topology for nephilid relationships as the results from TNT with statically aligned sequences. The only difference is that under some cost

combinations (1, 1 gap opening 1; and 2, 1 gap opening 1), *Nephila* was not recovered as monophyletic. This is most likely an artifact from the high proportion of missing data in the molecular partition for this genus. The relationships of araneoid families change with different cost combinations, and in some cases, tetragnathids are again the closest relatives to nephilids (when costs are set to 1, 2 and gap opening 1); however, none of these topologies receives jackknife support over 50.

DISCUSSION

Our results corroborate the monophyly of Nephilidae and their placement outside Tetragnathidae. However, the closest relatives of nephilids within Araneoidea and relationships of araneoid families remain to be satisfactorily resolved, but this is a problem that is beyond the scope of this paper. One possible explanation might be the limited taxonomic sampling of nonnephilid araneoid families in our study, which is certainly not designed to answer this question. Our results also confirm that *Deliochus* and *Phonognatha* belong to Araneidae, as already suggested by other authors (Álvarez et al., 2009; Kuntner et al., 2008), thus leaving in Nephilidae the genera *Clitaetra*, *Nephila*, *Herennia*, and *Nephilengys*. The monophyly of *Clitaetra* is well supported, and this genus is the sister group to a lineage with the remaining nephilid taxa, as first suggested by Hormiga et al. (1995). Relationships within *Clitaetra* are the same as in the results of Kuntner (2006), with *C. thisbe* being the most basal species in this lineage. Analyses under implied weighting corroborated the monophyly of *C. episinoides* + *C. perroti,* as suggested by Kuntner (2006), and this topology was selected as our preferred hypothesis for *Clitaetra* relationships (Fig. 7). The main difference between our results and the results of Kuntner (2006) and Kuntner et al. (2008) resides in the placement of *Nephila*. Here the closest relative of *Nephila* is not *Nephilengys* but the clade *Nephi-lengys* + *Herennia* as proposed by other studies (Álvarez-Padilla et al., 2009; Dimitrov and Hormiga, 2009; Hormiga et al., 1995). The analyses here add molecular data to the nephilid taxon sample of Kuntner (2006) to investigate the internal nephilid relationships. All analyses that we performed recover ((*Nephilengys* + *Herennia*) *Nephila*), and the clade *Nephilengys* + *Herennia* was always well supported. This topology is particularly relevant for character optimizations because numerous ethological and evolutionary studies use *Nephila* species as model organisms (e.g., Higgins, 2002; Robinson and Robinson 1973; Schneider and Elgar, 2002; and many more). For example, the widely discussed behavior of bulbus detachment (eunuch behavior) was previously thought to be secondarily lost in *Nephila* (Kuntner et al., 2008, 2009). Our results show that under parsimony, bulbus detachment is actually a synapomorphy of the clade *Herennia* + *Nephilengys*, with a single appearance in this group and thus primitively absent (not lost) in the *Nephila* clade (see Fig. 7, character 190; see also Álvarez-Padilla et al., 2009).

As we have mentioned above, Kuntner (2006) recognized two subfamilies within Nephilidae: Clitaetrinae (containing *Clitaetra*) and Nephilinae (containing the remaining three nephilid genera). However, Kuntner's (2006) proposal to subdivide the family Nephilidae into two subfamilies seems not only poorly justified but also contrary to the "advice" that he dispenses when he urges systematists to abandon the use of the subfamilies and subgenera, among other ranks (Kuntner and Agnarsson, 2006). "Clitaetrinae" and "Nephilinae" are indeed monophyletic groups, but what is to be gained from formally establishing subfamilial ranks, particularly when the content of "Clitaetrinae" is identical to that of *Clitaetra*? Furthermore, Kuntner (2006) also subdivided the genus *Clitaetra* into three subgenera on the basis of the monophyletic groups of his preferred phylogenetic hypothesis (as he notes, the subgenus *Indoetra* is actually composed of a single

species). While acknowledging that the Linnaean system does not require assigning formal ranks to all clades, Kuntner (2006: 52) nevertheless justifies "formal lineage names" for species groups in *Clitaetra* for the purpose of biogeographical discussions. How the use of a formal label, such as "subgenus *Afroetra*," as opposed to the informal name "clade Afroetra," improves communication or facilitates discussion is a mystery to us. Kuntner (2006) based his classification on a purported "compromise approach" between traditional Linnaean nomenclature (ICZN, 1999) and the so-called "phylogenetic nomenclature" (Cantino and de Queiroz, 2007). Such a "nomenclatural system" was discussed in more detail in a separate contribution (Kuntner and Agnarsson, 2006), in which the classification of *Clitaetra* is used as a showcase example of the authors' "recommendations for the future of biological classification." Interestingly, their paper starts with a significant factual error: Contrary to their claims, binomial nomenclature did not start with Clerck's *Aranei Svecici* and the 10th edition of Linnaeus' *Systema Naturae*. Some readers of Kuntner and Agnarsson (2006), ourselves included, might very well have expected that a scholarly work that essentially aims to review and advise on how to produce biological classifications from cladograms would have extensively cited the large body of previous research that addressed this issue. Such works span no less than two decades after the publication of *Phylogenetic Systematics* (Hennig, 1966), and, incidentally, many of them appeared in the pages of the same journal in which Kuntner and Agnarsson (2006) discussed their singular method (in those days, published under the name *Systematic Zoology*). We find the omission of so many relevant works (e.g., Eldredge and Cracraft, 1980; Farris, 1976; Hennig, 1975; Nelson, 1972, 1974; Wiley, 1979, 1981) simply appalling. In fact, given how their paper is written and what relevant works they decided to cite, we would be hardly surprised if a naïve reader

concluded that explicitly phylogenetic classifications did not start until the proponents of "phylogenetic taxonomy" began to publish their views. Of course, such a conclusion would be simply preposterous. As Farris (1976) had succinctly summarized, a phylogenetic classification "requires only that each monophyletic group be a taxon, each taxon be a monophyletic group, and the natural inclusion relations of monophyletic groups be retained by the taxa." This statement, more than three decades old, is anything but a novel proposition nowadays. We do not aim to discuss in depth Kuntner and Agnarsson's (2006) approach; however, we fail to see how it is superior to the explicitly phylogenetic Linnaean classifications currently used by many practicing taxonomists. Except for the dismissal of some of what they call "intermediate ranks" and of type taxa, Kuntner and Agnarsson's proposal is anything but new, as taxonomists have been building Linnaean phylogenetic classifications with explicitly monophyletic and empirically supported higher taxa for more than three decades. Their own example (Kuntner and Agnarsson, 2006: 778, fig. 1) does illustrate that, in practice, their "combination approach" does not differ significantly from a cladistic Linnean classification, except for the use of the label "clade" instead of "subgenus." We do have to agree with Kuntner and Agnarsson's (2006: 781) assessment that "their" own requirement that "superspecific names represent monophyletic groups" is, more than half a century after the publication of Hennig's *Grundzüge einer Theorie der Phylogenetischen Systematik*, trivial. That the codes (e.g., the ICZN) do not include the word "monophyly" and "synapomorphy" (Kuntner and Agnarsson, 2006: 781) is simply a moot point to those who understand the underlying principles upon which the codes are based, because nomenclature does not aim to determine the inclusiveness or exclusiveness of any taxon. Kuntner's (2006) implementation of Kuntner and Agnarsson's (2006) nomenclatural approach is probably the most signif-
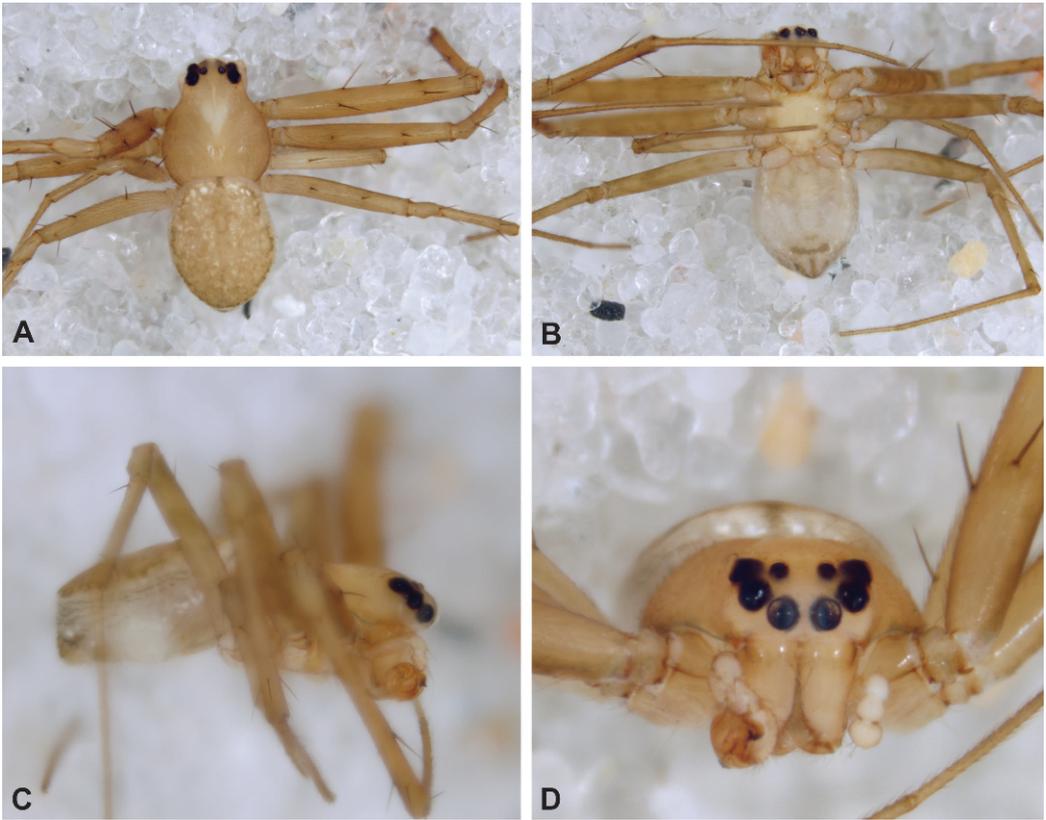
Figure 3. *Clitaetra thisbe* male: A, dorsal; B, ventral; C, lateral; D, frontal.

icant confirmation that it does not offer any substantial changes, other than terminological, to the existing cladistic implementations of the Linnaean system. After a lengthy discussion about the advantages of a rankless system, as proposed by the "Phylocode," Kuntner adopts a system for the classification of *Clitaetra* that has three subgenera and two subfamilies for Nephilidae! Furthermore, the proposed subgenus *Indoetra* contains just one species—thus, it might not be monophyletic (Platnick, 1976, 1977)—contradicting the requirement for monophyly of higher taxa.

TAXONOMY

Family Nephilidae Simon, 1894
Genus *Clitaetra* Simon, 1889

Clitaetra thisbe Simon, 1903
Figures 1–5

Type: Female holotype from Sri Lanka in MNHN, not examined.
C. thisbe Simon, 1903: 24.
C. thisbe Kuntner, 2006: 51, figs. 25A–C.

Diagnosis. As noted by Kuntner (2006), *C. thisbe* is much smaller than other congeners and has spermathecae, fertilization, and copulatory ducts that are easily observed through the abdominal cuticle. In Kuntner's (2006) diagnosis, the female genital morphology is misinterpreted and the copulatory openings are described as being posteriorly oriented (they are actually ventrally oriented; see Figs. 2E–G, 5D). The size and shape of the conductor is
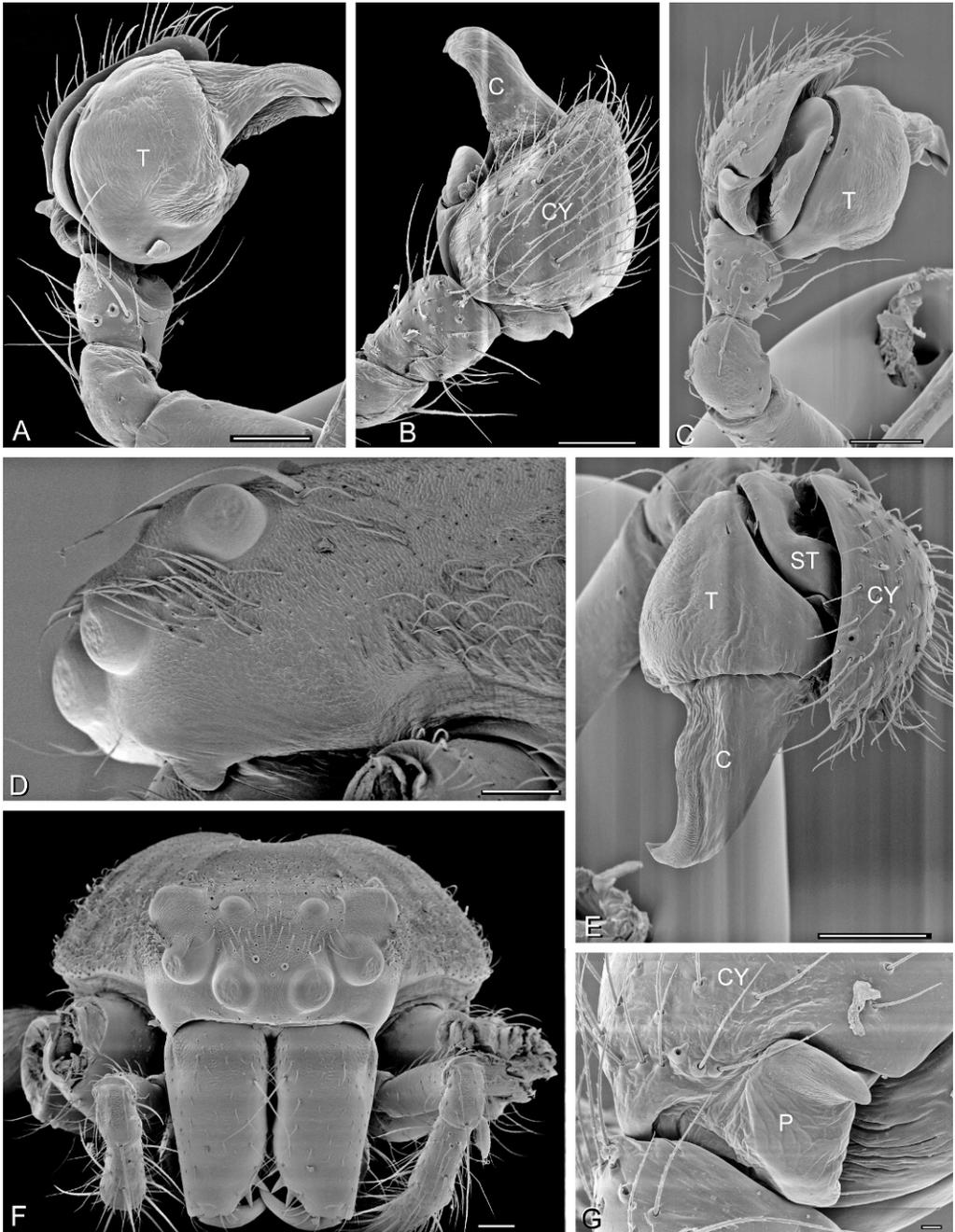
Figure 4.   *Clitaetra thisbe* male: A, palp ventral; B, dorsal; C, dorso-retrolateral; E, palp retrolateral; G, paracymbium. *Clitaetra thisbe* female: D, prosoma lateral; F, prosoma frontal. *Scale lines:* A–F 100 µm; G 10 µm.
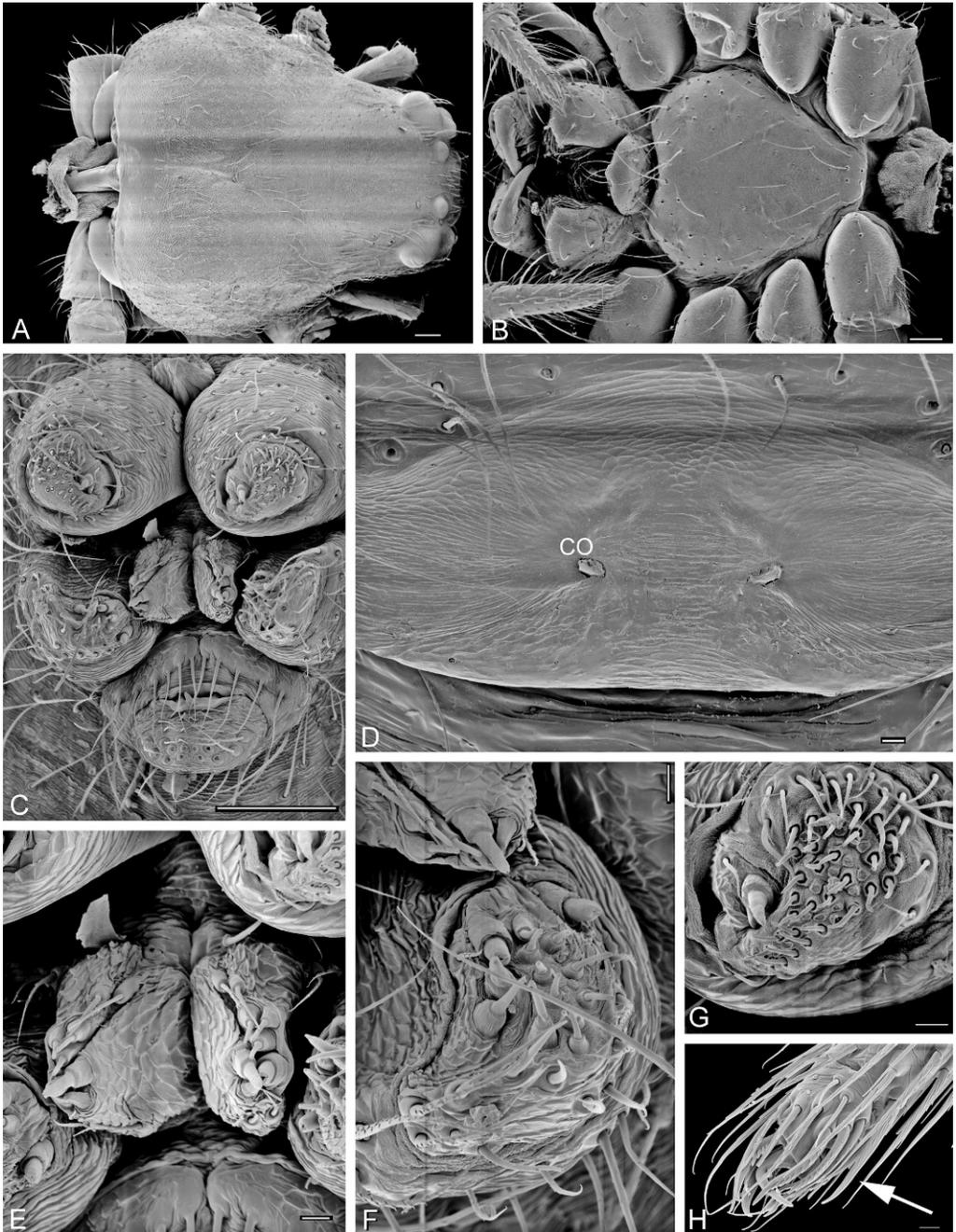
Figure 5.   *Clitaetra thisbe* female: A, prosoma dorsal; B, prosoma ventral; C, spinnerets; D, epigynum; E, PMS; F, PLS; G, ALS; H, tarsus leg IV, arrow points to sustentaculum. *Scale lines:* A–C 100 μm; D–H 10 μm.
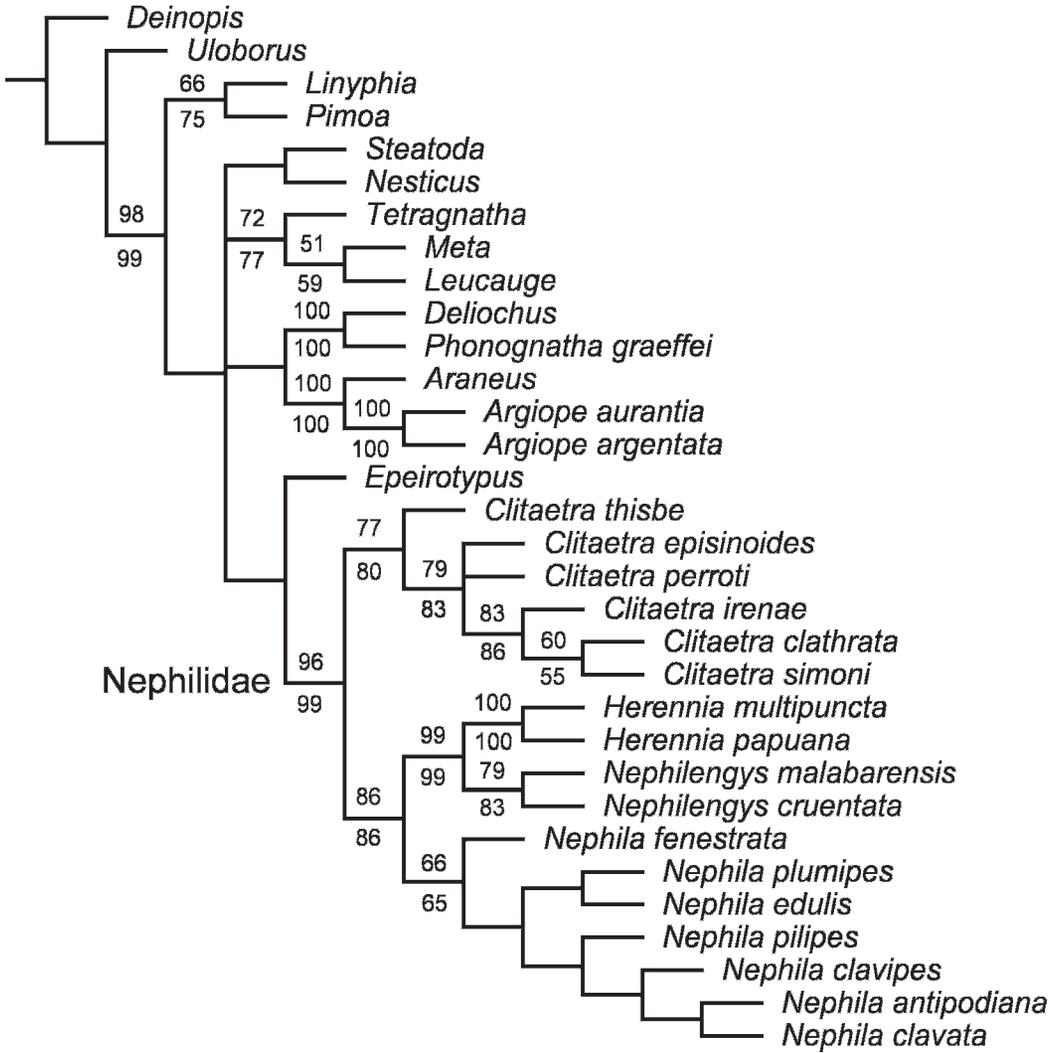
Figure 6.   Consensus of four MPT found under equal weights analyzing statically aligned sequences and morphological data. Values above branches represent bootstrap support; values below branches represent jackknife support (bootstrap and jackknife values <50 are not indicated in the figure).

unique to the males of this species, being much wider and straighter than in the other species of *Clitaetra* (Figs. 2A–C, 4A, B, E).

Description (male). Small spiders with fairly long legs relative to body size. Total body length 2.57, prosoma 1.24 long, 1.06 wide, 0.69 high; abdomen 1.33 long, 1.05 wide, 0.75 high. Prosoma light brown–yellowish with darker pigmentation surrounding eyes (Fig. 3A, D). Sternum yel-

lowish, 0.59 wide, 0.65 long. Labium triangular, distally with wide rectangular base. Eyes in two recurved rows, PME smaller than other eyes; all other eyes of similar size relatively close together, separated by less than 1 AME/PLE diameter, except for distance between PME, which is more than 1 PME diameter. Clypeus low; clypeus height 0.1, 0.3 times 1 AME diameter. Chelicerae yellowish. Abdomen
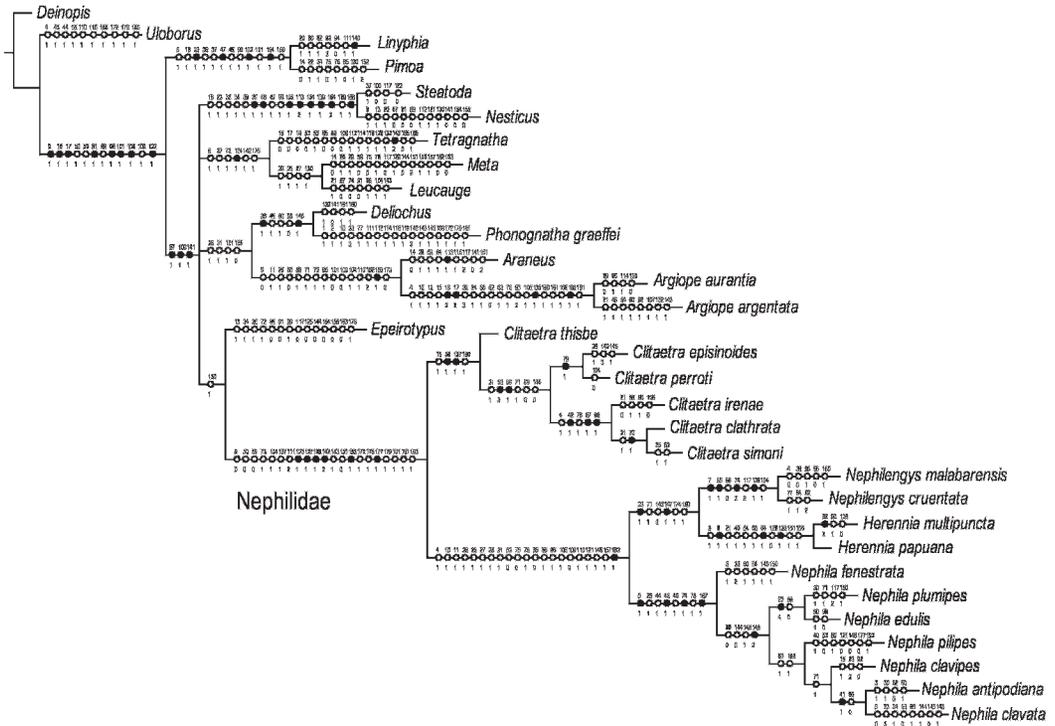
Figure 7. Character optimization on one of the four MPT under equal weights analyzing statically aligned sequences and morphological data representing the working hypothesis of *Clitaetra* relationships. Black circles represent unique gains; white circles represent homoplasic gains or reversals. Numbers above and below the circles indicate the character number and its state, respectively. Only the unambiguous character changes are mapped.

with slightly darker dorsal scutum and numerous white dots (Fig. 3A); ventral color light with white dots around spinnerets (despite high degree of discoloration of specimens, darker transverse band just anterior to spinnerets is observable). Legs darker than prosoma, brownish, with darker spines. Palp (Figs. 2A–D, 4A–C, E, G) with rounded tegulum and relatively short but very robust fingerlike conductor.

Description (female). A very detailed description of the female holotype was provided by Kuntner (2006). Here, we simply correct his interpretation of the epignal morphology on the basis of our observations, including SEM images. The ducts labeled fertilization ducts by Kuntner (2006) are in fact the copulatory ducts, and they open ventrally on the epignum (Figs. 2E–G, 5D). The other pair of ducts,

copulatory ducts *sensu* Kuntner, are in fact the fertilization ducts.

Distribution. Endemic to Sri Lanka. *Clitaetra thisbe* is also the only species of the genus found outside Africa and adjacent Islands.

Natural History. These spiders build their dual-ladder webs on tree trunks. All observed webs were nearly vertical, around three times longer than wide, and with nearly parallel vertical sides (Fig. 1C). Webs were never built during the day. The central one-third of the web is a perfect orb (Fig. 1C, D); the dual ladders (the remaining two-thirds of the web) extend upward and downward, respectively. The hub of the orb was not visibly reinforced or modified with silk. All radii at their origination points are equally spaced (Fig. 1C, D); the web includes many secondary and tertiary split

radii. Spiders rest at the hub during the day (Fig. 1A, B). It appears that these spiders do not digest used silk and instead roll it up and attach it to radii. A detailed account of the behavior will be published separately.

Material Examined. SRI LANKA: Sabaragamuwa Province: Ratnapura district: Gilimale Forest Reserve, 11-II-2007, hand collecting, Suresh Benjamin & Ziyard Jaleel, 1 male, 1 female, and 2 juveniles. Kegalle district: Kitulgala, degraded lowland rainforest, 14-II-2007, hand collecting, Ziyard Jaleel, 1 male and 2 females. Western Province: Kalutara District: Ingiriya, Bodinagala Forest Reserve, 10-II-2007, hand collecting, Suresh Benjamin & Ziyard Jaleel, 1 male, 1 female, and 1 juvenile. All the specimens are deposited in the Muséum d'histoire naturelle (Genève, Switzerland).

ACKNOWLEDGMENTS

APPENDIX 1.
MORPHOLOGICAL MATRIX.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Deinopis	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0
Uloborus	0	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Araneus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0
Argiope aurantia	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	2	2	1	1	0	0	0	3	1	1	1	1	1	1	0	0	0	0
Argiope argentata	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	2	2	0	1	0	0	0	3	1	1	1	1	1	0	—	1	0	1
Linyphia	0	0	0	0	0	1	0	0	1	0	2	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	—	1	0	1
Pimoa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	—	0	0	0
Steatoda	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	—	1	1	1
Nesticus	0	1	0	0	0	0	0	0	1	0	2	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	—	0	0	0
Epeirotypus	1	0	0	0	0	1	0	0	1	0	2	0	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	—	0	1	0
Tetragnatha	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	—	1	1	0
Meta	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	1	0
Leucauge	0	0	0	0	0	0	0	0	1	1	2	1	1	0	0	1	0	1	1	1	1	0	0	0	1	1	1	0	1	—	0	0	0
Deliochus	1	1	0	0	0	0	0	0	1	1	2	0	0	1	1	1	0	1	1	1	1	0	3	0	1	1	0	0	0	—	1	0	0
Phonognatha graeffei	1	1	0	0	0	0	0	0	1	1	2	1	0	1	1	1	0	1	1	1	1	0	3	0	1	1	1	1	0	—	1	0	0
Clitaetra episinoides	0	0	0	0	0	0	0	0	0	1	2	0	0	1	1	1	1	0	0	1	1	0	3	1	0	0	0	1	0	—	0	0	0
Clitaetra perroti	0	0	0	0	0	0	0	0	0	1	2	0	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	—	1	0	0
Clitaetra clathrata	0	0	0	1	0	0	0	0	0	1	2	0	0	1	1	1	0	0	0	1	1	0	3	1	0	0	0	0	0	—	0	0	0
Clitaetra irenae	0	0	0	1	0	0	0	0	0	1	2	0	0	1	1	1	0	0	0	1	0	0	3	1	1	0	0	0	0	—	1	0	0
Clitaetra simoni	0	0	0	1	0	0	0	0	?	0	2	0	0	1	1	1	0	0	0	1	1	0	3	1	1	0	0	0	0	—	0	0	0
Clitaetra thisbe	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	—	0	0	0
Nephila clavipes	1	1	0/1	0	0/1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	1	0	2	0	1	1	1	0	1	1	0	0	0
Nephila fenestrata	1	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	2	0	1	1	0	0	0	0	1	0	0
Nephila pilipes	1	1	0	0	0/1	0	0	0	0	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	1	0	0
Nephila antipodiana	1	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0/4	0	1	1	1	1	0	1	1	0	0
Nephila clavata	1	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	3	1	1	1	0	1	1	0	1	0	0
Nephila plumipes	1	1	0/1	1	0/1	0	0	0	0	0	1	1	0	1	0/1	1	1	0	1	0	0	0	4	0	1	1	0	1	0	—	1	0	0
Nephila edulis	1	1	0	1	1	0	0	1	0	0	1	1	0	1	0/1	1	1	0	1	0	1	0	4	0	1	1	0	1	1	0	1	0	0
Herennia multipuncta	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	0
Herennia papuana	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	—	1	0	0
Nephilengys malabarensis	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	—	1	0	0
Nephilengys cruentata	1	1	0	1	0	0	1	0	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	—	1	0	0

APPENDIX 1. CONTINUED.

Taxon	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Deinopis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	—	0	0	0	0	0	0	—
Uloborus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	—	0	0	0	1	0	0	0	—
Araneus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	—
Argiope aurantia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0/1	0	0	1	1	1	0	0	—	1	0	0	0	0	—
Argiope argentata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	1	1	1	0	0	—
Linyphia	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	—	1	0	0	1	0	0	—	—	—	—	1	0	0	0	—
Pimoa	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	—	1	0	0	0	0	1	0	1	—	1	1	0	0	0	—
Steatoda	1	—	1	1	0	1	—	—	—	0	0	0	0	0	1	1	1	—	1	0	0	0	0	0	1	—	—	—	1	0	0	0	—
Nesticus	1	—	1	0	0	1	—	—	—	0	0	0	0	0	1	1	1	—	1	0	0	0	0	0	0	1	—	1	1	0	0	0	—
Epeirotypus	1	—	1	0	1	1	—	—	—	0	0	0	0	0	1	1	1	—	1	1	0	0	0	0	0	—	0	0	1	1	0	0	—
Tetragnatha	0	0	0	1	1	0	—	—	—	1	0	0	0	1	1	0	1	—	1	0	0	0	0	1	0	1	0	1	1	0	0	0	—
Meta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	—	0	1	0	0	0	1	0	—	0	1	0	1	0	0	—
Leucauge	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	—	1	0	0	0	1	0/1	—	1	—	1	1	1	0	0	1
Deliochus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	—	0	0	0	0	0	0/1	1	0/1	—	1	0	0	0	0	1
Phonognatha graeffei	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	—	1	0	0	0	0	1	0	0	0	1	1	1	0	0	1
Clitaetra episinoides	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	3	0	0	0	1	1	0	0	1	0	0	0	0	1
Clitaetra perroti	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	3	0	0	0	1	1	0	0	1	1	1	0	0	1
Clitaetra clathrata	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	—	1	3	0	0	0	1	1	0	0	1	1	0	0	0	1
Clitaetra irenae	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1
Clitaetra simoni	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	?	1	1	3	0	0	0	1	1	0	0	1	0	0	0	0	1
Clitaetra thisbe	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	?	1	3	0	0	0	1	1	0	0	1	1	1	0	0	1
Nephila clavipes	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	1
Nephila fenestrata	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0/1	0/1	0	0	1	1	0	1	1	1	1	1	0	0	1
Nephila pilipes	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1
Nephila antipodiana	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	1
Nephila clavata	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1
Nephila plumipes	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0/1	0	0	0	0	0	0
Nephila edulis	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0
Herennia multipuncta	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	1	1	1	0	1	1	0	1	1	0	0	1
Herennia papuana	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	1	1
Nephilengys malabarensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0
Nephilengys cruentata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	0	1	0

Appendix 1. Continued.

Taxon	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Deinopis	—	—	—	—	0	0	0	—	0	0	0	0	0	0	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0
Uloborus	—	—	—	—	0	0	0	—	1	0	0	0	0	0	—	0	—	0	1	0	0	0	0	0	1	1	1	1	0	0	—	0	0
Araneus	—	—	—	—	1	0	1	4	0	0	0	0	0	0	—	0	—	1	1	1	0	0	0	—	1	?	1	1	?	1	—	1	1
Argiope aurantia	—	—	—	—	1	1	1	4	0	1	0	0	0	0	0	0	—	0	1	1	0	0	1	—	1	2	2	1	0	1	0	1	0
Argiope argentata	—	—	—	—	1	0	1	4	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	—	1	2	2	1	0	1	0	1	0
Linyphia	—	—	—	—	0	0	0	—	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	—	1	1	2	0	0	0	—	1	1
Pimoa	—	—	—	—	0	0	0	—	0	1	0	0	0	0	—	0	0	0	1	0	0	0	1	—	1	1	1	1	0	0	—	1	1
Steatoda	—	—	—	—	0	0	0	—	0	1	0	0	0	0	—	0	—	0	1	0	0	0	0	0	1	1	1	1	0	0	—	1	1
Nesticus	—	—	—	—	0	0	0	—	1	0	0	0	0	1	—	0	—	0	1	0	0	0	1	0	1	1	1	1	0	0	—	1	1
Epeirotypus	—	—	—	—	1	1	0	—	1	0	0	0	0	0	—	0	—	0	0	0	0	0	0	0	1	1	1	0	0	0	—	1	1
Tetragnatha	—	—	—	—	1	1	1	4	1	0	—	0	0	—	—	—	—	0	1	1	—	—	1	—	1	—	0	0	0	0	—	1	0
Meta	—	—	—	—	0	0	1	0	0	0	0	1	0	0	—	0	—	0	0	0	0	0	0	?	0	2	2	1	0	0	0	1	0
Leucauge	—	—	—	—	1	1	1	1	1	0	0	0	0	1	0	1	—	1	1	0	0	1	1	—	1	0	1	1	0	1	2	1	0
Deliochus	—	—	—	—	0	0	0	—	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	—	0	2	0	1	0	0	0	1	0
Phonognatha graeffei	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0/1	0	0	1	0	0	0	1	0	0	2	0	1	0	0	—	1	0
Clitaetra episinoides	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	—	0	1	0	0	—	1	0
Clitaetra perroti	0	0	1	1	1	0	1	0	1	0	0	0	0	0	—	0	—	0	1	0	0	0	0	0	1	1	1	1	0	0	—	1	0
Clitaetra clathrata	0	0	1	0	1	0	1	0	0	0	0	1	0	0	—	0	—	0	1	0	0	0	1	0	1	1	1	1	0	0	—	1	0
Clitaetra irenae	0	0	1	1	1	0	1	0	1	0	1	0	0	0	—	0	—	0	0	0	1	1	0	1	1	1	1	1	0	0	—	1	0
Clitaetra simoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	—	0	1	0	1	1	0	0	1	?	?	?	?	0	—	1	0
Clitaetra thisbe	0	0	0	0	0	1	1	0	1	0	0	0	0	0	—	0	—	0	1	0	1	1	0	—	1	1	1	1	?	0	—	1	0
Nephila clavipes	0	1	0	0	1	0	3	0	0	1	1	0	0	0	0	0	—	0	1	0	0	1	1	0	0	0	1	1	0	1	0	1	0
Nephila fenestrata	0	1	0	0	0	0	1	1	0	1	0	1	0	1	1	1	1	1	0	1	0	0	0	—	1	0	1	1	0	1	0	1	0
Nephila pilipes	0	1	0	0	0	0	1	3	0	1	1	1	1	0	0	—	—	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0
Nephila antipodiana	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	—	0	0	1	1	1	0	0	0	0	1	1	0	0	—	1	0
Nephila clavata	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	—	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Nephila plumipes	—	—	—	—	1	0	0	0/1	0	0	0/1	0	0	0	—	0	—	0	0	0	1	0	0	1	0	—	1	1	0	1	1	1	0
Nephila edulis	—	—	—	—	0	1	1	1	0	1	0	1	0	1	—	0/1	—	0	0	0	0	0	1	1	1	0	1	1	0	0	—	1	0
Herennia multipuncta	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	1	0	1	—	1	—	2	1	0	0	1	1	1
Herennia papuana	1	1	0	0	1	1	1	2	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	—	1	?	?	?	?	1	1	1	0
Nephilengys malabarensis	—	—	—	—	1	0	0	2	2	0	1	0	1	0	1	—	1	0	1	0	0	0	0	—	1	?	1	1	0	1	—	1	0
Nephilengys cruentata	—	—	—	—	1	1	1	2	0	1	1	0	0	1	1	0	—	1	1	1	0	0	1	—	1	2	1	1	0	1	1	1	0

APPENDIX 1. CONTINUED.

Taxon	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132
Deinopis	0	0	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0	0	—	0
Uloborus	0	0	0	—	0	0	0	0	0	0	1	2	0	0	0	1	0	2	0	0	1	0	0	0	—	—	—	—	—	0	0	—	0
Araneus	1	0	0	0	1	0	0	1	1	0	1	2	1	0	0	0	1	2	0	1	1	1	0	0	0	0	0	0	0	1	0	—	0
Argiope aurantia	1	0	0	1	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	1	0	3	0	0	0	0	0	0	1	—	0
Argiope argentata	1	0	1	1	0	1	1	1	1	1	1	2	0	0	0	0	0	1	0	1	1	1	0	3	0	0	0	0	1	0	0	—	1
Linyphia	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	3	1	0	0	0	0	0	0	—	0
Pimoa	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	4	1	0	0	0	0	1	1	0	0
Steatoda	0	1	0	1	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Nesticus	1	1	0	1	1	1	0	0	1	1	0	1	2	0	0	0	0	1	0	1	0	1	0	3	1	1	1	0	0	1	0	?	0
Epeirotypus	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	?	0
Tetragnatha	1	1	1	0	0	0	0	0	0	1	0	0/1	0	1	1	0	0	1	1	0	0	1	—	1	1	1	1	0	1	0	1	—	1
Meta	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0
Leucauge	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0
Deliochus	1	1	1	0	0	0/1	0/1	1	1	1	0	1	0	1	0	1	0	1	1	1	1	0/1	0	0	1	0	1	1	1	1	0	0	1
Phonognatha graeffei	1	1	1	0	0	0/1	0/1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	0	5	0	1	1	1	1	0	0	0
Clitaetra episinoides	1	1	1	0	0	0	1	1	0	1	0	2	0	0	?	0	0	1	0	?	1	1	1	1	2	0	0	1	0	0	1	0	0
Clitaetra perroti	1	0	1	1	0	0	1	0	1	0	0	2	0	0	?	0	0	1	0	1	0	1	1	1	2	1	0	1	1	1	1	0	1
Clitaetra clathrata	1	1	1	1	0	0/1	0/1	1	1	0	0	2	0	0	?	0	0	0/1	0	?	1	1	1	1	2	1	0	1	1	1	1	0/1	0
Clitaetra irenae	1	1	1	1	0	0/1	1	0	1	1	1	2	0	0	?	0	0	2	0	?	1	1	1	1	2	1	1	1	1	1	1	0	0
Clitaetra simoni	1	1	1	1	0	?	?	1	?	0	?	2	?	?	?	0	?	2	?	?	?	1	1	1	2	1	?	?	1	?	?	?	0
Clitaetra thisbe	1	1	1	1	0	0	0	1	1	1	0	2	0	0	?	0	0	0	0	1	1	1	1	1	2	1	0	0	0	0	1	0	0
Nephila clavipes	1	1	1	1	0	1	1	1	0	1	1	2	0	0	0	0	0	2	0	1	1	1	1	1	2	0	0	0	0	0	1	0	0
Nephila fenestrata	1	1	1	1	0	1	1	1	1	0	0	2	0	0	0	0	0	2	0	1	1	1	1	1	2	0	0	0	0	0	1	0	0
Nephila pilipes	1	1	1	1	0	1	1	1	0	1	1	2	0	0	0	0	0	1	0	0	1	0	1	1	2	0	0	0	0	0	1	0	0
Nephila antipodiana	1	1	1	1	0	1	1	1	1	0	1	2	0	0	0	0	0	0/1	0	1	1	1	1	1	2	0	0	1	1	1	1	0	0
Nephila clavata	1	1	1	1	0	1	1	1	1	1	1	2	0	0	0	0	0	2	0	1	1	1	1	1	2	1	0	0	1	1	1	0	0
Nephila plumipes	1	1	1	1	0	1	1	1	1	0	0	2	0	0	0	0	0	2	0	1	1	1	1	1	2	1	0	0	1	1	1	0	0
Nephila edulis	1	1	1	1	0	1	1	1	0	0	1	2	0	0	0	0	0	1	0	1	1	1	1	1	2	1	0	0	1	1	1	?	0
Herennia multipuncta	1	1	1	1	0	1	1	1	0	1	1	2	0	0	0	0	0	1	1	1	1	1	1	1	2	0	0	0	0	1	1	0	1
Herennia papuana	1	1	0	1	0	1	1	0	0	1	1	2	0	0	0	0	0	0	0	1	1	1	1	1	2	0	1	1	0	0	1	0	0
Nephilengys malabarensis	1	1	1	1	0	1	1	1	1	0	1	2	0	0	0	0	0	2	0	1	1	1	1	1	2	1	1	1	1	1	1	1	0
Nephilengys cruentata	1	1	1	1	0	1	1	0	1	0	1	2	0	0	0	0	0	2	0	1	1	1	1	1	2	1	0	1	1	1	1	0	0

APPENDIX 1. CONTINUED.

Taxon																		Character														
	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
Deinopis	0	1	—	0	0	0	0	0	0	0	0	0	—	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0/1
Uloborus	1	0	0	0	0	0	0	0	0	0	1	1	—	0	0	?	0	0	2	2	0	0	0	0	0	1	0	1	0	1	1	0	0
Araneus	1	0	0	0	0	0	0	0	0	0	1	0	—	0	0	?	0	0	2	2	0	0	1	0	0	1	0	1	0	0	0	0	1
Argiope aurantia	1	0	1	0	0	0	0	0	1	0	1	1	—	0	0	?	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	0	1
Argiope argentata	1	0	1	0	0	0	0	1	1	0	1	?	—	0	0	?	0	0	1	2	0	1	1	0	1	1	1	1	0	0	1	0	1
Linyphia	0	—	—	0	0	1	1	0	1	—	0	1	—	—	—	—	—	—	1	0	0	0	0	0	0	0	0	1	1	1	1	1	—
Pimoa	1	0	0	0	0	0	0	1	0	0	0	0	—	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	0	1	1	1	—
Steatoda	1	1	0	0	0	0	1	0	0	?	0	1	—	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	2	—
Nesticus	1	0	0	0	1	0	1	0	1	?	0	1	—	—	—	—	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	2	—
Epeirotypus	1	0	0	0	0	0	1	0	0	0	0	0	—	—	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	—
Tetragnatha	0	0	0	0	0	0	0	0	1	0	2	1	—	0	0	3	0	0	2	2	0	0	0	1	0	0	0	0	0	1	0	0	0
Meta	0	—	—	0	0	0	0	0	1	1	0	0	—	0	0	3	0	0	2	1	0	0	1	0	1	0	0	0	0	1	1	0	1
Leucauge	0	—	—	0	0	0	0	0	0	1	1	0	—	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0/1
Deliochus	0	—	—	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1
Phonognatha graeffei	0	—	—	0	0	0	0	0	0	3	1	1	1	0	0	?	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	?	1
Clitaetra episinoides	0	—	—	1	0	0	0	0	1	3	1	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	0	1	1	?	1
Clitaetra perroti	0	—	—	0	1	0	0	0	0	2	1	0	0	0	0	?	0	0	1	1	0	0	1	1	0	0	1	0	0	1	?	?	?
Clitaetra clathrata	0	—	—	0	1	0	0	0	0	2	1	0	0	0	0	3	0	0	1	1	0	0	1	1	0	0	1	0	0	1	?	?	?
Clitaetra irenae	0	—	—	0	0	0	0	?	0	2	1	0	0	0	0	3	0	0	1	1	0	1	?	?	0	0	1	0	0	1	?	0	?
Clitaetra simoni	?	?	?	1	?	?	?	0	?	2	?	?	?	0	0	?	?	?	1	?	1	?	?	?	?	0	1	0	0	1	?	?	?
Clitaetra thisbe	0	—	—	0	1	0	0	0	0	2	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1
Nephila clavipes	0	—	—	0	0	0	0	0	0	2	1	1	1	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Nephila fenestrata	0	—	—	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Nephila pilipes	0	—	—	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Nephila antipodiana	0	—	—	0	0	0	0	0	0	2	1	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	?
Nephila clavata	0	—	—	0	0	0	0	0	0	2	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Nephila plumipes	0	—	—	0	0	0	0	0	0	2	1	0	1	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Nephila edulis	0	—	—	0	0	0	0	0	0	2	1	1	1	0	0	2	0	1	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1
Herennia multipuncta	0	—	1	0	1	0	0	0	0	3	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1
Herennia papuana	0	—	1	0	0	0	0	0	0	3	1	1	1	0	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1
Nephilengys malabarensis	0	—	0	1	0	0	0	1	0	3	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1
Nephilengys cruentata	0	—	0	0	0	0	1	0	1	3	1	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	1

APPENDIX 1. CONTINUED.

Taxon															Character															
	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
Deinopis	0	0	0	0	0	0	0	—	—	0	0	0	0	0	0	0	—	—	0	0	0	0	—	—	0	0	0	0	0	—
Uloborus	0	0	1	1	0	0	1	—	0	0	0	0	1	0	0	0	—	—	0	1	0	0	—	0	0	1	0	1	0	—
Araneus	0	0	0	0	0	0	0	—	0	0	0	0	?	0	0	0	—	0	0	0	0	0	0	0	0	?	1	0	0	—
Argiope aurantia	0	1	0	0	1	0	0	0	0	0	0	0	?	0	0	0	—	0	0	0	1	0	0	0	1	?	0	1	0	—
Argiope argentata	0	1	0/1	1	0	0	0	0	0	0	0	0	?	0	0	0	—	?	0	0	1	0	0	?	0	1	1	0	0	—
Linyphia	—	0	1	1	—	—	—	—	—	—	0	0	1	—	—	—	—	—	—	0	1	1	—	0	0	—	1	1	0	—
Pimoa	—	0	0	1	—	—	—	—	—	—	0	0	0	—	—	—	—	—	—	0	0	—	—	?	?	—	0	1	0	—
Steatoda	—	0	0	1	—	—	—	—	—	—	0	0	0	—	—	—	—	—	—	0	1	1	0	?	0	—	0	0	0	—
Nesticus	—	0	0	1	—	—	—	—	—	—	0	0	0	—	—	—	—	—	—	0	0	—	0	0	0	—	0	0	0	—
Epeirotypus	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	—	1	1	0	0	1	—	0	0	0	0	0	0	—
Tetragnatha	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	—	1	1	1	0	1	1	1	0	0	0	0	0	—
Meta	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	—	1	1	0	?	1	0	0	1	0	0	0	0	—
Leucauge	0	0	0/1	0	2	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	2	0
Deliochus	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	?	?	0	0	?	1	0	1	1	0	2	2	0	1
Phonognatha graeffei	?	0	0	0	1	?	?	?	0	?	?	?	?	1	1	0	?	0	?	?	?	1	?	?	0	?	0	?	0	?
Clitaetra episinoides	?	1	?	1	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	1	?	?	?	?	?	?	2	?
Clitaetra perroti	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	1	?	?	?	?	?	?	0	?
Clitaetra clathrata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	1	?	?	?	?	?	?	0	?
Clitaetra irenae	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	2	0	0	1	?	1	0	1	1	1	0	?
Clitaetra simoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	?	?	?	?	?	?	0	?
Clitaetra thisbe	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0/1	0	1	0	0	0	1	1	1	1	1	0	0	0	0	?
Nephila clavipes	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	1	1	2	0	0	1	?	1	0	1	0	0	0	?
Nephila fenestrata	0	1	0	0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	2	0	0	1	?	?	0	1	1	0	0	?
Nephila pilipes	0	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	2	0	0	1	?	?	0	1	1	0	0	?
Nephila antipodiana	0	?	?	0	?	1	?	?	?	?	?	?	1	1	0	0	1	1	2	0	?	1	?	?	0	1	?	0	0	?
Nephila clavata	?	1	?	0	1	1	?	?	?	0	?	?	1	0	1	1	?	0	?	0	?	1	?	?	0	1	?	0	0	?
Nephila plumipes	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	?	0	0	1	?	?	0	1	0	0	0	?
Nephila edulis	0	1	0	1	0	1	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0	1	?	0	1	1	0	0	1	?
Herennia multipuncta	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	?	0	1	1	0	0	0	—
Herennia papuana	1	0	0	1	?	?	1	?	?	?	1	1	1	0	1	1	?	?	2	0	0	1	?	0	1	1	?	0	1	—
Nephilengys malabarensis	0	0	0	1	1	1	1	1	1	1	?	?	1	1	0	1	1	1	?	0	0	1	?	0	1	?	?	1	1	0
Nephilengys cruentata	0	0	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	2	0	1	1	—	0	1	0	1	1	1	0

APPENDIX 2.
GENE FRAGMENTS AND GENBANK SEQUENCE ACCESSION NUMBERS.

Species	12S	16S	COI	H3	18S	28S
Araneus marmoreus	EU003230	NA	EU003278	EU003312	EU003341, EU003341, EU003341	EU153158, EU003397, EU003397
Argiope aurantia	NA	DQ146832.1	DQ146862.1	NA	NA	DQ018858.1
Argiope savignyi	EU003231	NA	EU003279	NA	EU003388, EU003388	EU153159, EU003398, EU003398
Clitaetra sp.	NA	NA	EU003281	EU003315	NA	NA
Deinopis sp.	NA	EU003249	NA	NA	EU003382, EU003383, EU003383	EU153163, EU003403, EU003403
Deliochus sp.	EU003234	EU003259	EU003284	NA	EU003345, EU003345, EU003345	EU153164, EU003404, EU003404
Epeirotypus brevipes	NA	EU003273	EU003286	EU003318	EU003347, EU003347, EU003347	EU153166, EU003406
Herennia multipuncta	EU003236	EU003260	EU003288	EU003320	EU003384, EU003385, EU003386	EU003432, EU003433
Leucauge venusta	EU003238	EU003263	EU003290	EU003322	EU003350, EU003350, EU003350	EU153169, EU003409, EU003409
Linyphia triangularis	EU003239	AY078664.1	EU003292	AY078702.1	EU003390, EU003390	EU153170, EU003410, EU003410
Meta menardi	NA	EU003268	EU003295	EU003325	EU003353, EU003353, EU003353	EU153173, EU003413, EU003413
Nephila clavata	AY164671.1	NA	AY052586.1	NA	AY425721.1	
Nephila clavipes	NA	NA	EU003302	EU003333	EU003377, EU003378	EU003422, EU003422
Nephila pilipes	NA	EU003276	DQ779283.1	NA	NA	NA
Nephila antipodiana	NA	NA	AY052587.1	NA	NA	NA
Nesticus cellulanus	NA	NA	NA	NA	AF005447, AF005447, AF005447	NA
Nephilengys malabarensis	EU003244	NA	EU003303	EU003334	EU003392	EU003434, EU003434
Phonognatha graeffei	EU003245	EU003275	NA	NA	EU003379, EU003380, EU003381	EU153183, EU003426, EU003426
Pimoa sp. X131	NA	AY230940.1	AY231025.1	AY230985.1	AY230893.1	AY231072.1
Steatoda borealis	NA	NA	EU003307	NA	EU003393, EU003393	EU153184, EU003428, EU003428
Tetragnatha versicolor	EU003246	NA	EU003308	NA	EU003394	EU153185, EU003429, EU003429
Uloborus glomosus	EU003247	NA	EU003310	EU003340	EU003366, EU003366, EU003366	EU003437, EU003438, EU003439

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