Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies

Matjaž Kuntner[1,2]*†, Jonathan A. Coddington[1] and Gustavo Hormiga[2]

[1]*Department of Entomology, National Museum of Natural History, Smithsonian Institution, NHB-105, PO Box 37012, Washington, DC 20013-7012, USA;* [2]*Department of Biological Sciences, The George Washington University, 2023 G St NW, Washington, DC 20052, USA*

The Pantropical spider clade Nephilidae is famous for its extreme sexual size dimorphism, for constructing the largest orb-webs known, and for unusual sexual behaviors, which include emasculation and extreme polygamy. We synthesize the available data for the genera *Nephila*, *Nephilengys*, *Herennia* and *Clitaetra* to produce the first species level phylogeny of the family. We score 231 characters (197 morphological, 34 behavioral) for 61 taxa: 32 of the 37 known nephilid species plus two *Phonognatha* and one *Deliochus* species, 10 tetragnathid outgroups, nine araneids, and one genus each of Nesticidae, Theridiidae, Theridiosomatidae, Linyphiidae, Pimoidae, Uloboridae and Deinopidae. Four most parsimonious trees resulted, among which successive weighting preferred one ingroup topology. Neither an analysis of an alternative data set based on different morphological interpretations, nor separate analyses of morphology and behavior are superior to the total evidence analysis, which we therefore propose as the working hypothesis of nephilid relationships, and the basis for classification. Ingroup generic relationships are (*Clitaetra* (*Herennia* (*Nephila*, *Nephilengys*))). *Deliochus* and *Phonognatha* group with Araneidae rather than Nephilidae. Nephilidae is sister to all other araneoids (*contra* most recent literature). Ethological data, although difficult to obtain and thus frequently missing for rare taxa, are phylogenetically informative. We explore the evolution of selected morphological and behavioral characters, discuss and redefine the homology of palpal sclerites, disprove *semientelegyny* in spiders, trace the newly interpreted evolution of the orb web, and show that nephilid genital morphologies coevolve with sexual behaviors and extreme sexual size dimorphism. Phylogenetic interpretations of behavior suggest new insights into spider biology and avenues for future research.
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Discovery of behavioral homologies has importance for biology and other human endeavors far beyond simply adding characters for phylogenetic analyses. Greene (1994)

Golden orb-weaving spiders (*Nephila*) and hermit spiders (*Nephilengys*) are among the most prominent and most researched tropical arachnids (reviewed in Kuntner, 2005, 2006, 2007a; Harvey et al., 2007). They are famous for extreme sexual size dimorphism in which males are many times smaller than the giant females (Fig. 1C,D) (Vollrath, 1980, 1998; Vollrath and Parker, 1992, 1997; Coddington, 1994; Coddington et al., 1997; Hormiga et al., 2000; Ramos et al., 2005), their unique webs of more than a meter diameter, and their unusual sexual behaviors (see Kuntner, 2007a,b), which may involve sexual cannibalism by the female and "opportunistic" mating by the male when the female is teneral or feeding. The closely related genera *Clitaetra* (Fig. 1H) and *Herennia* (Fig. 1F,G) both build rectangular ladder webs with parallel side frames, and *Herennia* exhibits male sexual mutilation and epigynal plugging, which remain poorly understood but have interesting evolutionary implications (Kuntner, 2005, 2006). The apparently Gondwanan nephilids are now treated as a family (see Kuntner, 2005, 2006, 2007a,b; Platnick, 2006), but

*Corresponding author:
E-mail address:* kuntner@gmail.com
†Present address: Institute of Biology, Scientific Research Center of the Slovenian Academy of Sciences and Arts, Novi trg 2, PO Box 306, SI-1001 Ljubljana, Slovenia
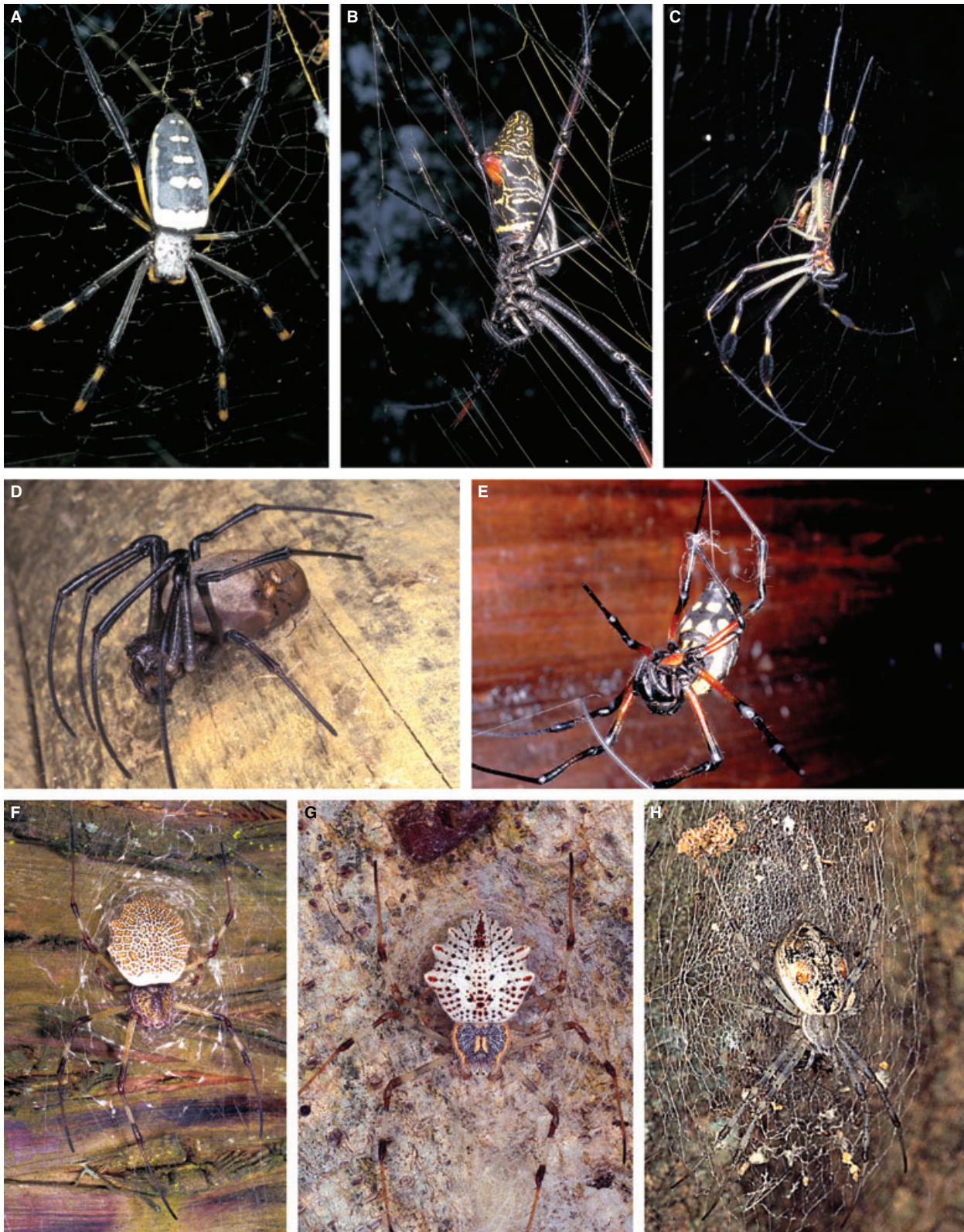
Fig. 1. Photographs of live nephilid spiders. (A–C) Pantropical genus *Nephila* (golden orb spider): (A) *N. senegalensis*, female from South Africa; (B) *N. inaurata*, female from South Africa; (C) *N. clavipes*, female (large) and male (small) from Costa Rica. (D, E) Pantropical genus *Nephilengys* (hermit spider): (D) *N. borbonica*, female (large) and male (small) from Madagascar; (E) *N. cruentata*, female from South Africa. (F, G) Australasian genus *Herennia* (coin spider): (F) *H. etruscilla*, female from Java; (G) *H. multipuncta*, female from Sri Lanka. (H) Afrotropical genus *Clitaetra*: *C. irenae*, female from South Africa.

were formerly and occasionally still are treated as a tetragnathid subfamily (Nephilinae Simon, 1894). The genera *Nephila* (especially the common New World *N. clavipes* (Linnaeus, 1767)) and *Nephilengys* have been the subject of over 2000 studies (Google Scholar) covering many aspects of their biology, and their popularity has resulted in many species synonymies (Kuntner, 2007a; Kuntner, in preparation). For example, in the upcoming *Nephila* revision, Kuntner (in preparation) will recognize only 15 valid species out of the over 150 available species-level names (Platnick, 2006).

Nephilids formerly contained eight genera placed as a subfamily in Tetragnathidae Menge, 1866 (Platnick, 1997). The first steps towards a species-level phylogeny were the removal of the African *Singafrotypa* and the Oriental *Perilla* from Nephilinae to Araneidae (Kuntner and Hormiga, 2002; Kuntner, 2002), and the revisions of *Herennia*, *Clitaetra* and *Nephilengys* (Kuntner, 2005, 2006, 2007a). These revisions included species-level phylogenetic analyses designed primarily to test the monophyly of nephilids and the genus being revised. The Australian *Deliochus* and *Phonognatha* have not been revised, and their phylogenetic position remains controversial (Kuntner, 2005, 2006). The prior analyses contained only a subset of *Nephila* species. Here we include all 15 known, valid *Nephila* species, based on two upcoming sources, the Australasian taxonomic treatment by Harvey et al. (2007), and the world revision of Kuntner (in preparation). Nephilidae now contains only *Nephila*, *Nephilengys*, *Herennia* and *Clitaetra* (Kuntner, 2006; Platnick, 2006).

Despite general interest in nephilid biology, the lack of any species-level phylogeny has made evolutionary interpretations of the available biological data difficult or impossible. The goals of this study were to test the monophyly and composition of Simon's Nephilinae in the broadest sense, to reassess the placement of the group within Araneoidea, to propose a species-level phylogeny for extant species and to examine the homology and evolution of selected morphological and behavioral traits.

Ethological homologies are of broad biological interest (Greene, 1994), although phylogenetic studies utilizing behavior are rare (Wenzel, 1992; Proctor, 1996; Danoff-Burg, 2002; see also Discussion). Behavior has been repeatedly shown to be phylogenetically informative (Coddington, 1986a,b,c; Prum, 1990; Wenzel, 1992; deQueiroz and Wimberger, 1993; Proctor, 1996; Price and Lanyon, 2002) and its analysis is no different from morphology (Wenzel, 1992). Phylogenies usually include direct observations of behavior (active behaviors *sensu* Proctor, 1996), i.e., those consisting of some sort of muscular activity, such as locomotion, courtship display and prey capture. However, a rich additional source of behavioral characters are observations of the products of behavior, such as nests of birds and wasps (Wenzel,

1993) and spider web architecture (Eberhard, 1982; Coddington, 1986a,b,c, 1989, 1990; Hormiga et al., 1995; Griswold et al., 1998; Agnarsson, 2004; Kuntner, 2005, 2006, 2007a). This study makes extensive use of both direct and indirect observations of behavior coded as discrete characters, combines them with the evidence from morphology, and explores the usefulness of ethology in araneoid spider phylogenetics. The results suggest that behavioral data, while difficult to obtain (and thus prone to the problem of missing entries), are phylogenetically informative, and, in the case of nephilids, less homoplasious than morphology.

Prior work

The encyclopedic treatise of world spiders by Eugène Simon (1892–1894) included a large family Argiopidae, approximately equivalent in composition to today's Araneoidea. Simon's argiopid subfamily Nephilinae (Simon, 1894, p. 744) consisted of:

1 Phonognatheae Simon (1894); with *Phonognatha* Simon (1894); *Singotypa* Simon (1894) and *Deliochus* Simon (1894);

2 Nephileae Simon (1894); with *Nephila* Leach (1815) (including *Nephilengys* L. Koch, 1872);

3 Clitaetreae Simon (1894); with *Clitaetra* Simon (1889);

4 Herennieae Simon (1894); with *Herennia* Thorell (1877).

Simon thought the phylogenetic position of nephilids was ambiguous. Based on the "external genital characters" Simon (1894, p. 744) hypothesized Nephilinae to be close to tetragnathines (equivalent to Tetragnathidae) through *Phonognatha* and to argiopines (equivalent to the Araneidae) through *Herennia*. Simon described male and female genitalia for representative species of *Phonognatha*, *Herennia* and *Nephila* (including in fig. 827 the palp of *Nephilengys* as *Nephila malabarensis*) but did not know the males of *Singotypa*, *Deliochus* or *Clitaetra*. Simon (1894, pp. 744–746) diagnosed Nephilinae by the male palp with a globular bulb (= tegulum), a semicircular basal piece (= subtegulum: fig. 827b), a denticulated basal part (= paracymbium: fig. 827c) and a complex distal part (= embolic conductor: fig. 827a). According to Simon, the simple epigynum of some species resembled that in *Meta* and the more complex epigyna of others (*Herennia* and *Nephilengys* as *Nephila malabarensis*) resembled that in *Argiope*. Simon's classification is translated into a dendrogram in Fig. 2A.

Dahl (1912) revised *Nephila* and *Nephilengys*, and placed them (without a formal classification) in "Radnetzspinnen" (Araneidae) based on a single character, the "Webestachel" or "Hamulus" (= sustentaculum; see characters 55–56 for homology). Dahl (1912, p. 26) diagnosed *Nephila* from other araneids by the long
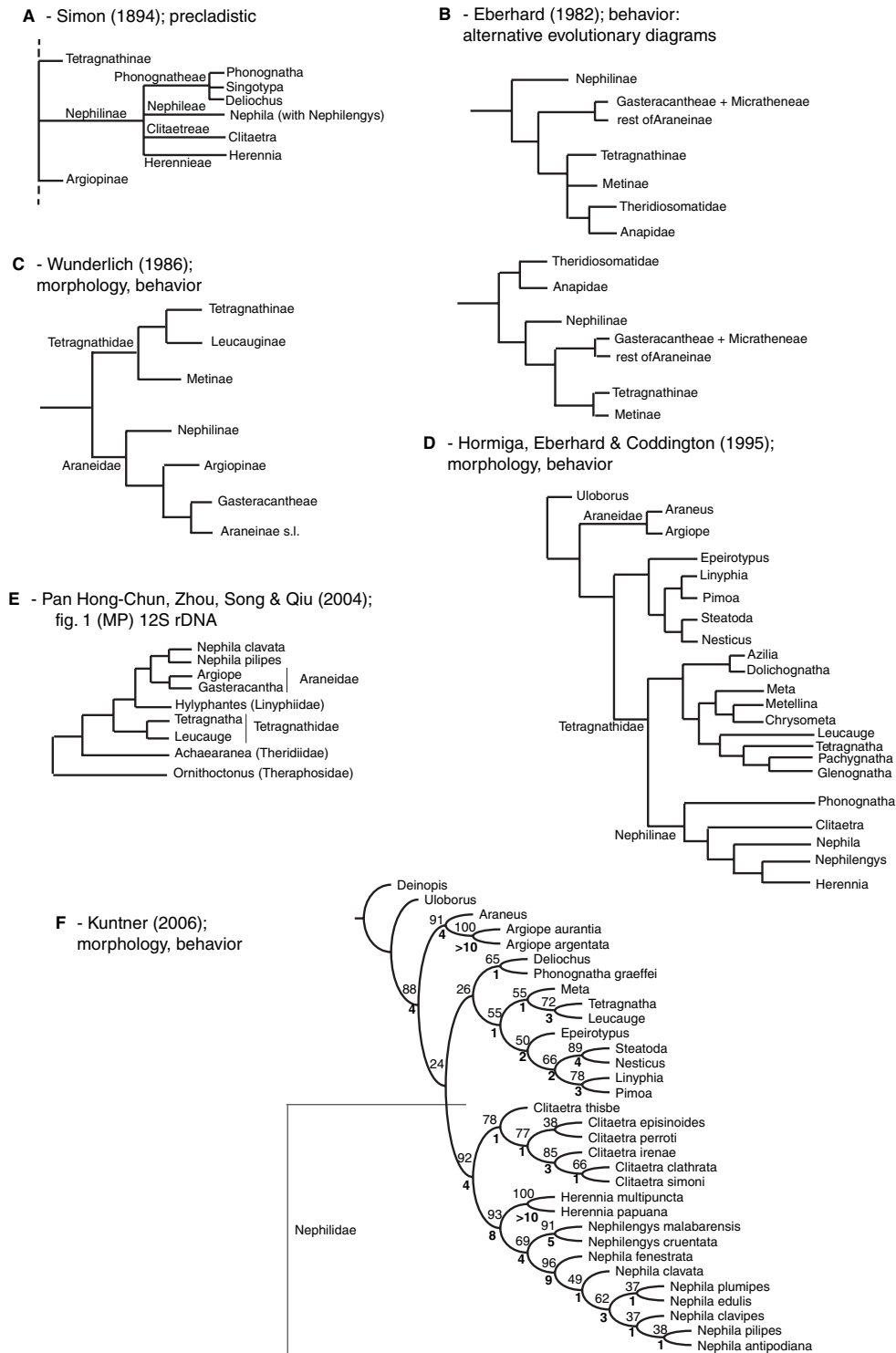
Fig. 2. Previous hypotheses of nephilid phylogeny and placement: (A) Simon's (1894) classification translated into a dendrogram; (B) two alternative hypotheses of araneoid relationships from Eberhard (1982) based on behavior, above, nephilids were basal araneoids, below, they were sister to the clade containing araneids and tetragnathids; (C) handmade cladogram of Wunderlich (1986) based on morphology and behavior, placing nephilids in Araneidae; (D) phylogeny of Hormiga et al. (1995), based on morphology and behavior, congruent in the tetragnathid placement of nephilids with other cladistic studies in the 1990s (Coddington, 1990; Scharff and Coddington, 1997; Griswold et al., 1998); (E) one of several gene trees of Pan et al. (2004), simplified, hypothesizing the araneid affiliation of *Nephila* (MP = maximum parsimony); (F) species-level phylogeny of Kuntner (2006) where Nephilidae did not group with Tetragnathidae or Araneidae, clade support given as bootstrap (above branch) and Bremer (below).

abdomen without humps, by a wide head region of the carapace and by the web's golden color.

Benoit (1962) described *Singafrotypa* for African *Singotypa*. Dondale (1966) placed the remaining *Singotypa* species in *Phonognatha*. Roewer (1942) catalog placed *Perilla* Thorell (1895) in Nephilinae. For most of the twentieth century Nephilinae was considered a subfamily of Araneidae (Roewer, 1942, 1954; Brignoli, 1983).

Levi placed *Nephila* in the "araneid" subfamily Metinae, but noted that it might belong in a separate subfamily (Levi, 1980, p. 9). Levi (1980, p. 8) diagnosed Metinae by the secondary eyes with canoe tapetum (**17, 18**) (references to characters in this study will be bold italic throughout), the lateral eyes close to the medians except in *Nephila* (**13**), the simple palp with embolus held by conductor (**165, 167, 168**), the spherical tegulum and subtegulum and other sclerites usually absent, the elaborate paracymbium attached to the cymbium, the simple epigynum often lacking fertilization ducts (**110**), the males mating with one palp at a time, the long endites, the webs with open hub (not in *Nephila*, **206–207**), and by the resting position with first and second femora extended forward (not in *Nephila*, **220**).

Eberhard (1982) presented behavioral evidence (mainly web construction) on araneoid relationships. His seminal study attempted to homologize stereotypic web-building behaviors across families and genera, and to identify constraints in web evolution. However, Eberhard's methods were only partially cladistic (for example he polarized characters based on hypotheses of adaptive value rather than outgroup comparison). Emphasizing characters that were uniform within major groups but different between, he presented two alternative phylogenetic hypotheses. Nephilids were either the most basal group within Araneoidea or sister to a clade containing araneines (equivalent to Araneidae today) + tetragnathines and metines (equivalent to Tetragnathidae today) (Fig. 2B). Almost all of Eberhard's character concepts have been used in subsequent cladistic treatments.

Wunderlich (1986) treated Nephilinae as a subfamily of Araneidae and proposed four alternative diagrams of araneoid relationships, but without published data matrices. Araneidae was always sister to Tetragnathidae and Nephilinae was sister to the remaining araneids (Fig. 2C). The hypothesized synapomorphies (pp. 103, 105) of Araneidae plus Tetragnathidae were a short clypeus (**19**) and a reduced tapetum in posterior eyes (**17**). Synapomorphies for Araneidae were the median eyes widely separated from laterals (**13**), sexual size dimorphism (see Discussion) and the presence of the median apophysis (**158**). Synapomorphies for Nephilinae were the loss of the median apophysis and "specialized web building." Wunderlich described five fossil *Nephila* species from Dominican amber.

Levi (1986, p. 99) considered *Nephila* and *Nephilengys* "probably" to belong in Tetragnathidae but expressed doubt about tetragnathid monophyly (Levi, 1986, p. 93). Levi included metine, nephiline and tetragnathine genera in Tetragnathidae. Levi and Eickstedt (1989) summarized Levi's views on differences between tetragnathids and araneids. Nephilinae shared five tetragnathid male palpal synapomorphies: a spherical tegulum with apical sclerites, lack of median apophysis and radix, embolus wrapped by the conductor, prominent tarsal organ, and paracymbium often a free sclerite. No phylogeny accompanied these proposed synapomorphies.

Coddington (1990) provided the first quantitative cladistic analysis including nephilids (*Nephila* and *Nephilengys*) based on morphological and behavioral evidence. He treated 32 orbicularian taxa scored for 87 characters, and recovered a monophyletic Nephilinae as sister to remaining tetragnathids represented by *Meta*, *Leucauge*, *Tetragnatha* and *Glenognatha*. Coddington (1990) proposed three nephilid synapomorphies, labium wider than long, nephilid radius construction (**210–211**), and sticky spiral localization with the outer fourth leg (**219**). He proposed four tetragnathid synapomorphies: metine palp conformation, hooked paracymbium, metine reservoir switchback, and the loss of the median apophysis. The latter character is used here, but the former are subdivided into more restrictive homology hypotheses.

Hormiga et al. (1995) studied tetragnathid phylogeny and added more characters, tetragnathid genera and the nephilid genera *Phonognatha*, *Clitaetra* and *Herennia*. They also recovered a monophyletic Nephilinae as sister to the remaining tetragnathids (Fig. 2D), and provided synapomorphies for many of the nodes relevant to this study. Kuntner and Alvarez-Padilla (2006) investigated the placement and monophyly of *Sancus* by adding it to the matrix of Hormiga et al. (1995).

Scharff and Coddington (1997) and Griswold et al. (1998) found the same topology in their studies of araneid and araneoid phylogeny, respectively. Because these successive studies basically extended the same character data to different taxa, the consistent phylogenetic result as regards nephilids is less independently corroborated than it initially appears. Likewise, Kuntner (2002), Kuntner and Hormiga (2002) and Smith (2005) used the Scharff and Coddington (1997) matrix to test the placement of various araneid taxa, and thus these studies also do not constitute independent tests of nephilid phylogeny.

Pan et al. (2004) presented molecular data (12S, 18S rRNA, and major ampullate spidroin-1) on *Nephila's* phylogenetic affinities. All three gene trees grouped *Nephila* with araneids rather than tetragnathids (e.g., Fig. 2E). The authors recommended transfer of *Nephila* to Araneidae or to elevate Nephilinae to family rank.

The main weakness of the study is its extremely broad but sparse taxonomic sample. Nephilinae was represented by only one, two or three species of *Nephila* depending on the gene (omitting other nephilid genera), araneids and tetragnathids by three to five species (*Araneus*, *Argiope*, *Gasteracantha*, *Tetragnatha*, *Leucauge*). The trees were rooted on a liphistiid (*Heptathela*), theraphosid (*Ornithoctonus*) or a pisaurid (*Dolomedes*), and no deinopoids (Deinopidae, Uloboridae) were studied. Such sampling ignores recent advances in spider phylogenetics (e.g., Griswold et al., 1998, 1999). Pan et al. (2004) did not analyze the combined data and did not justify partitioning the analysis.

In a monograph on fossil and extant spiders, Wunderlich (2004) placed Nephilinae in Araneidae and described the following new fossil nephilid genera from early Tertiary Baltic amber: *Paleonephila* (five species), *Eonephila* (three species) and *Luxurionephila* (monotypic), all in the new tribe Paleonephilini. Wunderlich's provisional placement of Paleonephilini in Nephilinae (including *Nephila*, *Nephilengys*, *Herennia* and "probably" *Clitaetra*, but not *Phonognatha*) was based on one male palpal character (apical conductor closely adjusting to the embolus). Wunderlich observed a median apophysis in Paleonephilini (figs 8–48), and, given the absence of the median apophysis in more recent Dominican amber *Nephila* (Wunderlich, 1986), proposed Paleonephilini as a "missing link" between Araneidae and Nephilinae (Wunderlich, 2004, pp. 265-266).

The first species-level nephilid phylogenies appeared in the revisions of *Clitaetra*, *Herennia* and *Nephilengys* (Kuntner, 2005, 2006, 2007a). None of these corroborated the composition of Nephilinae as circumscribed by Hormiga et al. (1995) nor its placement in tetragnathids. Nephilids did not group with araneids (*contra* Wunderlich, 1986, 2004; Pan et al., 2004). The four nephilid genera were consistently monophyletic but the placement of *Phonognatha* and *Deliochus* was unstable. Kuntner (2005) recovered the two as a grade basal to nephilids but the relationship collapsed in the strict consensus. In Kuntner (2006, 2007a) they were sister to tetragnathids plus distal araneoids, this clade then sister to nephilids (Fig. 2F). All of Kuntner's (2005, 2006, 2007a) data are presented and re-analyzed here. This analysis is the first to include all the species treated in earlier publications, adds the remaining eight species of *Nephila*, 13 additional outgroup taxa and 34 additional characters, and therefore constitutes the strongest test to date of nephilid monophyly, phylogenetic relationships, and behavioral and morphological evolution.

Materials and methods

Kuntner (2005, 2006, 2007a) provides the general methods for studying nephilid morphology and behav-ior. Ingroup taxa contain all nephilid species *sensu* Kuntner (2006) and Platnick (2006), except where data were sparse or unavailable. All *Clitaetra* (see Kuntner, 2006) and *Nephilengys* (see Kuntner, 2007a) species are included. All 15 valid *Nephila* species (Kuntner, in preparation) are included, including one not yet described, "*N. komaci*" (the latter name is disclaimed for purposes of zoological nomenclature). *Herennia oz*, *H. milleri*, *H. sonja* and *H. jernej*, which are known from a single sex (Kuntner, 2005) and too few specimens to be dissected, have been omitted to limit the number of unknown cells in the matrix.

The status of *Phonognatha* and *Deliochus* is ambiguous. Though currently not nephilids (Kuntner, 2005, 2006), they were previously considered to be "nephilines" (Simon, 1894; Hormiga et al., 1995), are still catalogued in Tetragnathidae (Platnick, 2006), and thus also represent the ingroup in a broad sense. *Phonognatha* has six described and approximately two undescribed species in Australasia (Kuntner, unpublished). The two most dissimilar species, the type *P. graeffei* and *P. melanopyga*, have been included. *Deliochus* has two described and approximately six undescribed species in Australasia (Kuntner, unpublished). As an exemplar, we include one undescribed species from Brisbane for which behavioral data are available, but also provide morphological illustrations for the two known species (Fig. 12).

While single exemplar species were consistently used for all scorings within the ingroup (see Prendini, 2001), outgroup taxon scoring had to be more opportunistic. Most morphological data on outgroup terminals came from one exemplar species, but behavioral data came from various sources and usually from various species. This approach assumes genus monophyly and that the features as coded will optimize to the root of the genus. However, the outgroup terminals in Table 1 are composite taxa.

Table 1 lists the outgroup taxa and the exemplar species used, with literature sources for observations that could not be checked from specimens. Deinopoidea is represented by *Deinopis* and *Uloborus*. Other distantly related outgroups include *Nesticus* (Nesticidae), *Steatoda* (Theridiidae), *Epeirotypus* (Theridiosomatidae), *Linyphia* (Linyphiidae) and *Pimoa* (Pimoidae). Argiopinae (Araneidae) is represented by two *Argiope* species with remarkably different somatic and genitalic morphology, Araneinae (Araneidae) is represented by *Araneus*, *Cyclosa* and *Araniella*. "Gasteracanthoids" are represented by *Caerostris*. The araneid *Acusilas* is added because it uses a rolled leaf as a retreat like *Phonognatha* and *Deliochus*, and *Singafrotypa* and *Perilla* to confirm their araneid identities. In addition to *Phonognatha graeffei*, *P. melanopyga* and *Deliochus* (see above) Tetragnathidae is represented by *Tetragnatha*, *Meta*, *Leucauge*, *Azilia*, *Dolichognatha*, *Chrysometa*, *Metellina*, *Glenognatha* and *Pachygnatha*, as

Table 1

Outgroup taxa, authors, current familial placements (Platnick, 2006), specimen data, and published sources of morphological and behavioral data for this study. *Phonognatha* and *Deliochus*, previously considered nephilines, are currently catalogued as tetragnathids (see text for details)

Terminal taxon	Morphology	Behavior
Deinopis MacLeay, 1839 (Deinopidae)	*D.* sp., Guyana (USNM), Coddington (1989), Scharff and Coddington (1997), Miller (unpubl. *D. spinosa*)	Coddington (1986c), this study (Guyana, Panama)
Uloborus Latreille, 1806 (Uloboridae)	*U. glomosus*, USA: MO, SC (USNM), Opell (1979), Hormiga et al. (1995), Miller (unpubl. *U. diversus*)	Eberhard (1982: various spp.), Hormiga et al. (1995), this study (Panama, Costa Rica)
Araneus Clerck, 1757 (Araneidae)	*A. diadematus*, Denmark (USNM), Grasshoff (1968); Hormiga et al. (1995), Scharff and Coddington (1997)	Eberhard (1982: various spp.), Hormiga et al. (1995), Scharff and Coddington (1997), this study (Slovenia)
Araniella Chamberlin & Ivie, 1942 (Araneidae)	*A. alpica*, Slovenia (USNM), Europe (USNM), Levi (1974), Scharff and Coddington (1997)	This study (Slovenia)
Cyclosa Menge, 1866 (Araneidae)	*C. conica*, Slovenia (USNM), USA, Massachusetts (USNM), Scharff and Coddington (1997), Levi (1999)	Marples and Marples (1937), Eberhard (1982), Levi (1999), this study (Costa Rica, Panama)
Perilla Thorell (1895) (Araneidae)	*P. teres*, Sumatra (NHMW), Kuntner (2002)	Kuntner (2002)
Singafrotypa Benoit (1962) (Araneidae)	*S. acanthopus*, Nigeria (BMNH), Kuntner and Hormiga (2002)	Kuntner and Hormiga (2002)
Argiope Audouin, 1826 (Araneidae)	*A. aurantia*, USA, Florida (USNM), Levi (1968), Scharff and Coddington (1997)	Eberhard (1982), Hormiga et al. (1995)
Argiope Audouin, 1826 (Araneidae)	*A. argentata*, Costa Rica (USNM), Levi (1968)	Eberhard (1982), this study (Costa Rica, Panama)
Acusilas Simon, 1895 (Araneidae)	*A. coccineus*, Sumatra (RMNH), Java (USNM)	Murphy and Murphy (2000): *A. gentingensis*, *A. malaccensis*
Caerostris Thorell, 1868 (Araneidae)	*C.* sp., Madagascar (USNM)	This study (Madagascar, South Africa)
Linyphia Latreille, 1804 (Linyphiidae)	*L. triangularis*, Denmark (USNM), van Helsdingen (1969, figs 21–28); Hormiga et al. (1995); Griswold et al. (1998); Hormiga (2000, plates 5–6), Agnarsson (2004, fig. 89B)	Hormiga et al. (1995)
Pimoa Chamberlin & Ivie, 1943 (Pimoidae)	*P. altioculata*, Oregon, Washington (USNM), Hormiga (1994a): 76–77, Hormiga et al. (1995), Agnarsson (2004, fig. 89A, *P. rupicola*)	Hormiga (1994a), Hormiga et al. (1995)
Steatoda Sundevall, 1833 (Theridiidae)	*S. americana*, WV, CA (USNM), Levi (1957); Hormiga et al. (1995), Agnarsson (2004, figs 71 and 72, *S. bipunctata*)	Hormiga et al. (1995), Agnarsson (2004)
Nesticus Thorell, 1869 (Nesticidae)	*N. paynei*, TN (USNM), Gertsch 1984: 28, f. 100–102, 159–160, Hormiga et al. (1995), Agnarsson (2004, figs 2 and 89, *N. reclusus*)	Hormiga et al. (1995), Agnarsson (2004)
Epeirotypus O. P.-Cambridge, 1894 (Theridiosomatidae)	*E. chavarria*, Costa Rica (USNM), Coddington (1986b), figs 56–65, Hormiga et al. (1995)	Coddington (1986b), Hormiga et al. (1995), this study (Costa Rica)
Tetragnatha Latreille, 1804 (Tetragnathidae)	*T. elongata* (USNM), *T. obtusa*, Slovenia (USNM), Wiehle (1963), Levi (1981), Hormiga et al. (1995)	Eberhard (1982: various spp.), Hormiga et al. (1995), this study (worldwide)
Glenognatha Simon, 1887 (Tetragnathidae)	*G. emertoni*, New Mexico (USNM), Levi (1980), Hormiga et al. (1995)	Eberhard (1982: *G.* sp.), Levi (1980: *G. foxi*), Hormiga et al. (1995)
Pachygnatha Sundevall, 1823 (Tetragnathidae)	*P. autumnalis* (USNM), Levi (1980), Hormiga et al. (1995)	Levi (1980: *P.* cf *degeeri*), Hormiga et al. (1995)
Azilia Keyserling, 1881 (Tetragnathidae)	*A. affinis*, Florida (USNM), Levi (1980), Hormiga et al. (1995)	Eberhard (1982: *A.* sp.), Levi (1980: *A. affinis*), Hormiga et al. (1995), this study (*A. guatemalensis*, Costa Rica)
Dolichognatha O. P.-Cambridge, 1869 (Tetragnathidae)	*D.* sp., Ecuador (USNM), *D. pentagona*, USA (USNM), Levi (1981), Hormiga et al. (1995)	Levi (1981), Hormiga et al. (1995), this study (*D.* sp., Panama)

Table 1
Continued

Terminal taxon	Morphology	Behavior
Meta C. L. Koch, 1836 (Tetragnathidae)	*M. ovalis* (Gertsch, 1933) (formerly *M. menardi* in America), WV (USNM), Levi (1980), Hormiga et al. (1995)	Eberhard (1982: *M. menardi = M. ovalis*), Hormiga et al. (1995), this study (*M. ovalis*, West Virginia, *M. menardi*, Slovenia)
Metellina Chamberlin & Ivie, 1941 (Tetragnathidae)	*M. segmentata*, Denmark (USNM), Levi (1980), Hormiga et al. (1995)	Hormiga et al. (1995), this study (Slovenia)
Chrysometa Simon (1894) (Tetragnathidae)	*C.* sp., Peru (USNM), Levi (1986), Hormiga et al. (1995), Alvarez-Padilla (2007), *C. alajuela*)	Eberhard (1982: *C.* sp.), Levi (1981), Hormiga et al. (1995)
Leucauge White, 1841 (Tetragnathidae)	*L. venusta*, USA (USNM), Levi (1980), Hormiga et al. (1995)	Eberhard (1982: *C.* spp.), Hormiga et al. (1995), Eberhard and Huber (1998: *L. mariana*), this study (worldwide)
Opadometa Archer, 1951 (Tetragnathidae)	*O.* nr. *grata*, Papua NG (CAS),	Murphy and Murphy (2000): *O. fastigata*, this study (Indonesia, Thailand)

Museum abbreviations: BMNH—The Natural History Museum, London, UK; CAS—California Academy of Sciences, San Francisco, USA; NHMW—Naturhistorisches Museum Wien, Vienna, Austria; RMNH—Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

well as *Opadometa* because, like *Nephila*, it has tufted fourth female tibiae, a more or less nephilid palp conformation and pronounced sexual size dimorphism. We add "nephilid-like" outgroups to test the homology of those similarities. However, adding only taxa that resemble nephilids, is a biased sample from the point of view of the outgroups, and runs considerable risk of producing biased character optimizations, especially if such taxa cluster at the roots of classical, relatively distinct clades such as Araneidae, Tetragnathidae, araneoid sheet-web weavers, deinopoids, etc.

Character analysis

This study scrutinized and used all morphological and behavioral data from Coddington (1990), Hormiga et al. (1995), Scharff and Coddington (1997) and Griswold et al. (1998) relevant to nephilid phylogeny, but interpreted some homologies differently as well as adding new data. The authors are not unanimous in their interpretations, but do agree that this analysis is justifiable, and, moreover, that alternative homology hypotheses do not significantly change these results (but, see Alvarez-Padilla, 2007, who uses old homology concepts and same nephilid subset of taxa as in Hormiga et al., 1995, and, not surprisingly, recovers that old nephilid topology). Some of these characters were used in Kuntner (2005, 2006, 2007a), but are all fully discussed here. The sources for the morphological and ethological evidence used previously in revisions are Kuntner (2005) for *Herennia*, Kuntner (2006) for *Clitaetra*, Kuntner (2007a) for *Nephilengys*, Kuntner (in preparation) for *Nephila*, Kuntner and Hormiga (2002) for *Singafrotypa* and Kuntner (2002) for *Perilla*.

We used reductive binary coding (Strong and Lipscomb, 1999) for nearly all characters (composite coding for **17, 18**, but results are unaffected). Eighteen characters are multistate. All characters were unordered (Fitch, 1971) to avoid assumptions of character state order. The phylogenetic matrix was maintained in the computer program NDE (Page, 2001).

The matrix (Appendix 1) had 61 taxa scored for 231 characters. Of these, 197 characters (85%) are morphological: 86 female and 12 male somatic; 27 female and 64 male genitalic; and eight spinneret. Thirty-four (15%) are behavioral (counting gross web architecture). Of the 14 091 cells in the matrix (Appendix 1) 1449 (10.3%) scores are missing (?) and 1440 (10.2%) are inapplicable (−). While missing entries occur sporadically throughout the matrix, blocks of unscored data are mostly in taxa with unknown males (*Clitaetra simoni*, *C. thisbe*, *Nephila komaci*, *Herennia tone*, *H. gagamba*, *H. agnarssoni*) and in the block of behavioral characters (**198–231**).

All other things being equal, we preferred character optimizations that maximize primary homology. If homoplasy-free, such hypotheses uncontroversially survive the congruence test of homology (Patterson, 1982; dePinna, 1991). If multiple origins are required, homology is refuted, but if all homoplasy is only secondary loss, it does not refute homology, as the initial derived state is everywhere homologous, only lost in distal clades. We therefore resolved ambiguous optimizations on a case by case basis (either ACCTRAN, DELTRAN, or a mix of both), to maximize primary homology and to avoid illogical optimizations. Character evolution was traced in MacClade (Maddison and Maddison, 2002).

Kuntner (2005, 2006, 2007a) rejected the homology of the nephilid and araneoid structures classically termed the "conductor." He regarded that feature in nephilids, *Phonognatha*, and *Deliochus* as part of the

embolic division and called it an "embolic conductor" (**165, 171**). Many workers (Levi, 1980; Schult and Sellenschlo, 1983; Schult, 1983; Wunderlich, 1986; Levi and Eickstedt, 1989; Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; as well as the two junior authors of this paper) regard the apical sclerite enveloping the embolus in *Nephila* and *Nephilengys* as a true araneoid conductor (and in *Clitaetra*, *Herennia* and *Phonognatha*, Hormiga et al., 1995).

The homology of the "conductor" as defined on the basis of function by Comstock (1910) across all spiders is certainly questionable. *Deliochus*, for example, has both a tegular and an embolic conductor (Fig. 12A). Saaristo (1978) labeled the sclerite in *Nephila* and *Nephilengys* as the "functional conductor", which accurately describes the sclerite's function but avoids a homology statement. The theridiid tegular apophysis (Agnarsson, 2004) and the median apophysis in *Perilla* (this study) are also functionally "conductors."

To test the effect of this controversy in homology on the results from this matrix, we modified Appendix 1 to produce an alternative matrix reflecting the classical point of view. This alternative matrix has the conductor scored as present in all nephilids (also in *Phonognatha* and *Deliochus*), the character "embolic conductor" deleted, and characters describing the "embolic conductor" were assumed to describe the classical conductor instead. This alternative matrix (Appendix 2) had all 61 taxa scored for 230 characters.

To evaluate the relative contributions of morphology and behavior to the results we also analyzed the morphological and behavioral data subsets separately.

Cladistic analysis

Parsimony analyses were performed using the computer programs NONA version 2.0 (Goloboff, 1993) and TNT (Tree Analysis Using New Technology) version 1.0 beta (Goloboff et al., 2004). Winclada 1.00.08 (Nixon, 2002) was used to display and manipulate trees and matrices for NONA. Mesquite 1.02 (Maddison and Maddison, 2006) was used to convert the nexus data files from NDE to Winclada. Exploratory searches were done in Winclada using the ratchet (implemented through NONA; under "amb-"), and then subjected to branch swapping (heuristic search in Winclada through NONA). The ratchet usually finds the shortest topology (Nixon, 1999), and branch swapping on the shortest trees under "amb-" finds many minimal length topologies. The final searches in NONA used the parameters "hold 1000", "mult*500", "max*", and "sswap" under both "amb-" and "amb=". In TNT both "traditional search" (Wagner trees with TBR) and the "New Technology search" (default settings) were used. Successive character weighting (Farris, 1969) analysis was performed in NONA with the command "run swt.run hold10000 hold/1000 mult*1000 jump50" (using the macro swt.run).

The calculations of Bremer support (BS) or decay index values (Bremer, 1988, 1994) use the commands in NONA as recommended by Goloboff (in litt. to G. Hormiga): h 500; mult*50; max*; h 1000; sub 1; find*; h 2000; sub 2; find*; h 4000; sub 3; find*; h 6000; sub 4; find*; h 8000; sub 5; find*; h 9000; sub 6; find*; h 10000; sub 7; find*; bs;. BS values higher than 7 were calculated in PAUP* (Swofford, 2002) by constraining nodes ("constrain") and searching for the shortest tree (heuristic search with 100 replicates of random taxon addition) that collapsed the node (Agnarsson, 2004; Miller and Hormiga, 2004). Bootstrap values (Felsenstein, 1985) were calculated in Winclada using default settings (100 replications, "mult*10").

Anatomical abbreviations

AC aciniform gland spigot(s)
AG aggregate gland spigot(s)
AL alveolus
ALE anterior lateral eyes
ALS anterior lateral spinneret
AME anterior median eyes
ATA apical tegular apophysis
B cheliceral boss
BH basal hematodocha
C conductor
CB cymbium
CBE cymbial transparent edge
CBP cymbial basal process
CD copulatory duct
CG conductor groove
CH chilum
ChD cheliceral denticles
CL conductor lobe
CO copulatory opening
CSA conductor secondary apophysis
CY cylindrical gland spigot(s)
DH distal hematodocha
E embolus
EA embolic apophysis
EAD epigynal anterior depression
EAR epigynal anterior rim
EB embolus base
EC embolic conductor
ECA embolic conductor arch
ECd embolic conductor distal sclerite
ECG embolic conductor groove
ECm embolic conductor medial sclerite
ECp embolic conductor proximal sclerite

EG epigynal groove
EH embolus hook
ELC epigynal lateral curve
EPC epigynal chamber
ES epigynal septum
ESA epigynal sclerotized arch
ESc epigynal scape
ETm embolus-tegulum membrane
F fundus
FD fertilization duct
FL flagelliform gland spigot(s)
M membrane(ous)
MA median apophysis
MAP major ampullate gland spigot(s)
mAP minor ampullate gland spigot(s)
MTA mesal tegular apophysis
N nubbin
P paracymbium
Pa patella
PCT promarginal cheliceral teeth
PI piriform gland spigot(s)
PLE posterior lateral eyes
PLS posterior lateral spinneret
PME posterior median eyes
PMS posterior median spinneret
PP pars pendula
PS paracymbial seta(e)
PPS palpal patellar seta(e)
PSL prosomal supracheliceral lobe
R radix
RCT retromarginal cheliceral teeth
S spermatheca
SD sperm duct
St stipes
ST subtegulum
STA subterminal apophysis
SU sustentaculum
T tegulum
TA terminal apophysis
TCp paired tarsal claw(s)
TCm median tarsal claw
Ti tibia
Tr trichobothrium(a)
VTA ventral tegular apophysis

Behavioral abbreviations

H hub
iL1 inner leg 1 tap (sticky spiral localization)
NSS non-sticky spiral (also termed auxiliary or temporary spiral)
oL1 outer leg 1 tap (sticky spiral localization)
oL4 outer leg 4 tap (sticky spiral localization)
RA radius (-i)
SS sticky spiral
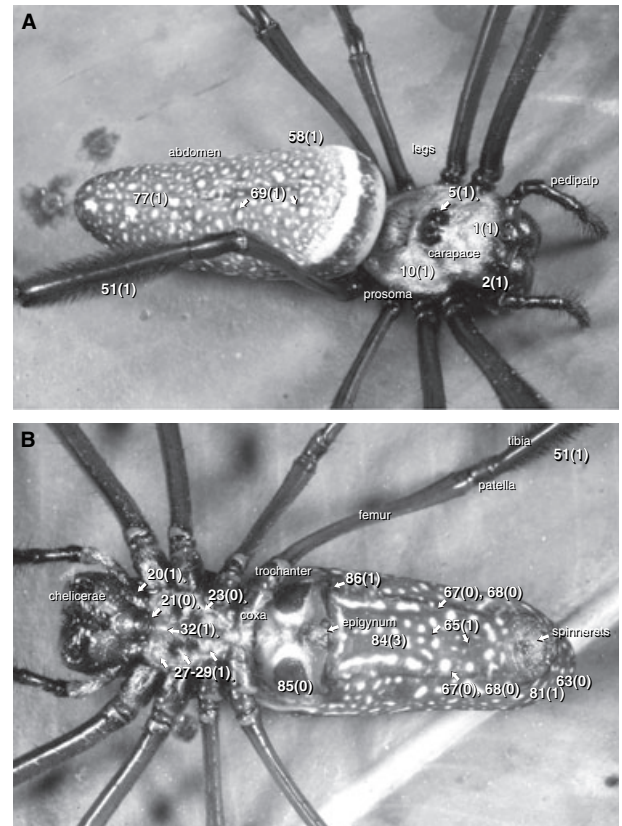
Fig. 3. *Nephila clavipes* female gross somatic morphology: (A) dorsal; (B) ventral. Numbers refer to characters (states), see text.

Character descriptions

Female somatic morphology

1 *Female cephalic region*: (**0**) low (Fig. 14A); (**1**) conspicuously high (Figs 3A and 4E). Female prosomal cephalic region is conspicuously higher than the thoracic region in *Nephilengys* (Fig. 4E) and most species of *Nephila* (Fig. 3A). The head region is low (not conspicuously higher than thorax) in *Clitaetra* (Kuntner, 2006, fig. 9A) and *Herennia* (Kuntner, 2005, fig. 1A,B).

2 *Female carapace*: (**0**) piriform (e.g., *Clitaetra*, Fig. 1H, Kuntner, 2006, fig. 1C; *Herennia*, Figs 1F,G and 4F, Kuntner, 2005, fig. 1C); (**1**) oval with wide head region (e.g., *Nephila*, Figs 1A and 3A, *Nephilengys*, Fig. 4E). Piriform refers to the wide thoracic and narrow eye region. Oval with wide head region is arbitrarily quantified as the head region of 70% or more carapace width.

3 *Female carapace edge (1)*: (**0**) smooth (Fig. 4E); (**1**) ridged (Fig. 4F). The carapace edge of all *Herennia* (Fig. 4F, Kuntner, 2005: figs 1C and 5B,D,E) and some *Nephila* species is ridged, while the carapace edge of
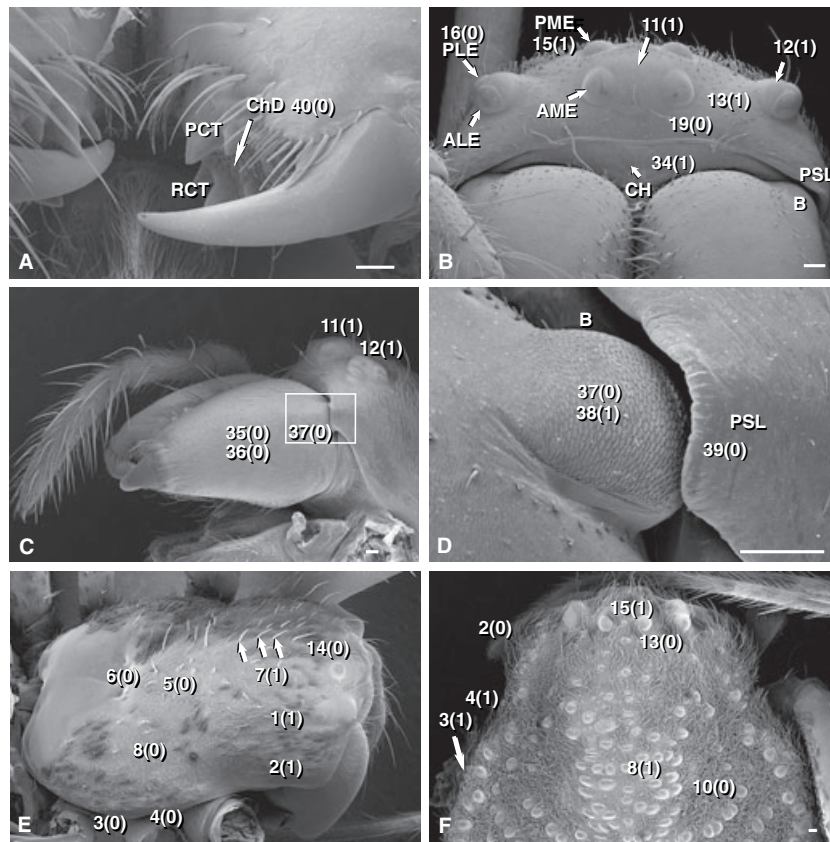
Fig. 4. Nephilid female prosomal morphology. (A–D) *Nephila constricta*: (A) chelicerae, apical, showing denticulated paturon furrow and fang; (B) head region, frontal, note eyes on tubercles, a divided chilum, and prosomal supracheliceral lobe over cheliceral boss; (C) head region and chelicerae, lateral, box defines area of image D; (D) striated cheliceral boss, partly hidden under prosomal supracheliceral lobe. (E) *Nephilengys papuana* female carapace with stout erect macrosetae (arrows). (F) *Herennia etruscilla* female carapace. Scale bars = 100 μm. Numbers refer to characters (states), see text.

other nephilids and outgroups is smooth. In *Nephila clavipes*, *N. constricta* and *N. plumipes*, the condition is polymorphic.

4 *Female carapace edge (2)*: (**0**) glabrous or with few hairs (Fig. 4E); (**1**) with an extensive row of hairs (Fig. 4F). The carapace edge of most nephilids is hairy, with a row of long white thin hairs especially conspicuous in *Clitaetra* (Kuntner, 2006, fig. 9A,B) and *Herennia* (Kuntner, 2005, fig. 5B,D,E). *Caerostris*, *Argiope* and *Uloborus* also possess hair-like setae.

5 *Female carapace surface*: (**0**) smooth (Fig. 4E); (**1**) with median pair of tubercles (Fig. 3A). Most *Nephila* species possess a pair of tubercles on mid carapace. These may be pointed (e.g., *N. sumptuosa*), round (e.g., *N. komaci*), inconspicuous (e.g., *N. inaurata*), polymorphic within populations (*N. constricta*) or among populations (*N. clavipes*, *N. pilipes*, *N. plumipes*). They are absent in *N. clavata*, *N. sexpunctata* and all other nephilid genera. A median pair of prosomal tubercles, in addition to a lateral pair, is found also in *Caerostris* (Scharff and Coddington, 1997, fig. 37).

6 *Fovea (female carapace)*: (**0**) inconspicuous (Fig. 4E); (**1**) pronounced. *Meta*, *Metellina* and some other tetragnathids have a pronounced fovea, a central depression on the carapace in the shape of a round hole. The fovea is less pronounced in other taxa.

7 *Female carapace macrosetae*: (**0**) normal (Fig. 3A); (**1**) stout and erect (Fig. 4E, arrows). While normal macrosetae are present on carapace in various ingroup and outgroup taxa, all *Nephilengys* species possess stout erect macrospines (Kuntner, 2007a).

8 *Female carapace setal bases*: (**0**) normal size (Figs 3A and 4E); (**1**) enlarged, wart-like (Fig. 4F). The carapace cuticle is warty (enlarged functional and non-functional setal bases) in all *Herennia* species (Kuntner, 2005), especially pronounced in *H. etruscilla* (Fig. 4F, Kuntner, 2005, fig. 19).

9 *Female carapace V-mark*: (**0**) absent (Fig. 1A,F,H); (**1**) present (Fig. 1G). A V-shaped yellow pigmented carapace mark is diagnostic (Kuntner, 2005) for *Herennia multipuncta* and certain other *Herennia* species (though dimorphic in *H. tone*).

10 *Female carapace vestiture*: (**0**) thin, white, hair-like (Figs 3A and 4F); (**1**) none. Apart from regular setae nephilids (and certain outgroups) have thin short white hair-like setae. In *Nephila* these are so numerous it gives the carapace a white or golden shine (Fig. 1A). *Deinopis* has short, star-shaped setae (not coded here because autapomorphic in this context). Scharff and Coddington (1997, character 41, hirsute versus glabrous) erred in coding *Nephila* as glabrous. The term hirsute is very broad (it may involve hairs, setae or spines) and is here avoided.

11 *Female median eye region*: (**0**) rounded; (**1**) median eyes on a tubercle (Fig. 4B,C). Most nephilids (with the exception of all *Clitaetra* species, see Kuntner, 2006) have median eyes on a slight tubercle, a condition also found in *Caerostris*. In *Deinopis*, PME are so enlarged that the condition cannot be established (coded inapplicable).

12 *Female lateral eye region*: (**0**) lateral eyes on separate tubercles; (**1**) lateral eyes on a single tubercle (Fig. 4B,C); (**2**) rounded. In most nephilids and some outgroups the lateral eyes are on a single tubercle, and in others the lateral eye region is smoothly rounded rather than tuberculate. In *Deinopis* the lateral eyes are each on separate tubercle.

13 *Female LE separation from ME*: (**0**) not widely separated (< 1) (Fig. 4F); (**1**) widely separated (> 1) (Fig. 4B). Modified from character 50 in Scharff and Coddington (1997), where the distance between the lateral eyes (LE) and the median eyes (ME) was given as the ratio of the distance between the LE and ME (at its widest point) divided by the width of the ME ocular area (at the widest point). If the ratio was less than 1, the separation was normal and if the ratio was more than 1, the separation was wide. Because the ratios can vary between the anterior and posterior eye groups, the character here is measured in the posterior eye row. Scharff and Coddington (1997) erred in coding *Nephila* as normal. The eyes are widely separated in *Nephila* and *Nephilengys*, as well as in *Phonognatha*, *Deliochus* and many other outgroups, and not widely separated in *Herennia* and *Clitaetra* among nephilids, or *Argiope*.

14 *Posterior eye row (dorsal view)*: (**0**) straight to recurved (Fig. 4E); (**1**) procurved. The posterior eye row is procurved in *Argiope*, *Caerostris*, *Nesticus* and *Epeirotypus*, and not so in other taxa (Scharff and Coddington, 1997, character 54).

15 *Female PME separation*: (**0**) less than one PME diameter; (**1**) one or more PME diameters (Fig. 4B,F). Posterior median eyes are well separated in all nephilids, and the condition varies among outgroups.

16 *Female PLE size*: (**0**) equal or less than PME (Fig. 4B); (**1**) larger than PME. Posterior lateral eyes are larger than the posterior medians in all *Clitaetra* (Kuntner, 2006, figs 1A and 3B) and certain *Nephila*

and *Herennia* species, as well as in *Argiope*. They are equal in *Opadometa* and *Perilla* and smaller in other taxa.

17 *PME canoe tapetum*: (**0**) absent; (**1**) full; (**2**) narrow. The tapetum is a reflecting crystalline layer in spider secondary (inverted) eyes (Homann, 1971; Foelix, 1996). The araneoid tapetum, if present, is canoe-shaped (Homann, 1971, figs 8 and 10A; Levi, 1983; Foelix, 1996, fig. 71c-CT). The presence of an eye tapetum is difficult to determine in old museum material, and some outgroup codings here may be contradicted in fresh material. In nephilids, PME and PLE tapeta are absent in *Clitaetra*, *Herennia* and *Nephilengys* (*contra* Scharff and Coddington (1997) for the *Nephilengys*), but seem to be universally present in *Nephila* (e.g., *N. clavipes*: Levi, 1980, fig. 38), though not observed in the old material of *N. komaci* and *N. ardentipes*. In nephilids both sexes always exhibit the same condition. Levi (1983, fig. 10) reported a narrow PME tapetum in Argiopinae, Cyrtophorinae, Mastophorinae, various araneines (including *Araneus*). Wunderlich (1986) hypothesized a reduced tapetum in "posterior eyes" as a synapomorphy for Araneidae plus Tetragnathidae. The feature, described later as character 4 of Hormiga et al. (1995), characters 51–52 of Scharff and Coddington (1997, fig. 38) and characters 28–29 of Griswold et al. (1998), served as an araneid synapomorphy. This study found the narrow PME tapetum only in *Argiope* and *Caerostris* among the examined araneids, and does not corroborate its presence in other araneid genera (e.g., *Araneus*).

18 *PLE canoe tapetum*: (**0**) absent; (**1**) full; (**2**) narrow. Most araneoids have a full canoe tapetum (Homann, 1971). A narrow PLE tapetum (see Levi, 1983, figs 9–11; Scharff and Coddington, 1997, fig. 38), also described as "reduced" (Scharff and Coddington, 1997) or "shrunk" (Levi, 1983, p. 252) is found in argiopines (*Argiope*, *Gea*, *Neogea*). Corresponds partly to character 4 in Hormiga et al. (1995) and character 53 in Scharff and Coddington (1997).

19 *Female clypeus height*: (**0**) low (< 3 AME diameters; Fig. 4B); (**1**) high (≥ 3 AME diameters). Both sexes of *Linyphia*, *Pimoa*, *Steatoda* and *Nesticus* and only *Epeirotypus* males have a high clypeus as defined here. Wunderlich (1986) regarded a low clypeus as synapomorphic for Araneidae + Tetragnathidae, but the feature seems to be symplesiomorphic for Orbiculariae and Araneoidea. Hormiga et al. (1995, character 6) used the character, but it is here redefined to apply only to females because it varies among sexes.

20 *Endites*: (**0**) very long (> 2 × width); (**1**) short (length < 2 × width; Fig. 3B). This character quantifies the observations of very long endites in tetragnathines (and *Deinopis*) and short endites in all nephilids and most outgroups. *Epeirotypus* has the shortest endites (wider than long).

21 *Labium and sternum*: (**0**) separate (Fig. 3B); (**1**) fused. Labium and sternum are almost fully fused in *Meta* and *Nesticus*, and laterally fused in *Leucauge* and *Linyphia* (also coded as fused). Corresponds to character 135 of Agnarsson (2004).

22 *Female sternum (1)*: (**0**) separate; (**1**) fused to pleura. In *Pachygnatha* and some *Tetragnatha* (*T. obtusa* and *Tetragnatha* sp. from Madagascar) the sternum is fused with the pleural sclerotization (Levi, 1980, fig. 152). Although the condition is polymorphic in *Tetragnatha*, the coding receives a 1 for the character to be informative.

23 *Female sternum (2)*: (**0**) longer than wide (Fig. 3B); (**1**) as wide as or wider than long. While the sternum of most nephilids is longer than wide (measured at maximum length and width), it is as wide as long or wider than long in most *Herennia* (Kuntner, 2005, fig. 1D).

24 *Sternal slit sensilla*: (**0**) prominent with light microscopy (Kuntner, 2006, fig. 3F); (**1**) inconspicuous or absent. Single slit sensilla are present on sternum of all the taxa treated, except, apparently, *Pimoa*, *Steatoda* and *Nesticus*. If present in these taxa, they are less conspicuous. In most nephilids the slit sensilla are found in groups adjacent to coxae 1–3 (e.g., *Clitaetra irenae*, Kuntner, 2006, fig. 9F).

25 *Female sternum color pattern*: (**0**) uniformly or dully colored; (**1**) uniformly orange/red; (**2**) medially dark, laterally pale; (**3**) medially light, laterally dark; (**4**) with yellow spots corresponding to tubercles (*Nephila sumptuosa*). The female sternum in *Herennia* and *Nephilengys* (live animals, but generally well preserved in alcohol) is bright orange or red (*Nephilengys*, Fig. 1E; *Herennia*, Kuntner, 2005, fig. 26B). In many *Nephila* species the bright yellow or orange spots correspond to sternal humps.

26 *Sternal white pigment*: (**0**) absent; (**1**) present (Kuntner, 2006, figs 12C and 19B). Subcutaneous, irregular patches of white pigment protrude through the sternum of some nephilid females (regardless of sternum color), notably *Clitaetra* and *Herennia*.

27 *Female sternal tubercle I*: (**0**) absent; (**1**) present (Fig. 3B). Paired elevations of the female sternum adjacent to coxae I–III are termed sternal tubercles I–III (also paired sternal humps). They are invariably present in *Nephila*, *Nephilengys*, *Herennia* (Kuntner, 2005, fig. 6E) and *Phonognatha* as well as *Meta*, many araneids and *Uloborus*. Other taxa may have some but not all tubercles (e.g., *Deliochus* has very slightly elevated tubercles I and III but not II, and *Opadometa* has only tubercle III but not I–II). Thus the features are coded as three characters. Whether an elevation amounts to a tubercle is sometimes ambiguous. See *31*. Agnarsson (2004, character 138) described similar sternocoxal tubercles in the theridiid subfamily Argyrodinae.

28 *Female sternal tubercle II*: (**0**) absent; (**1**) present (Fig. 3B). See *27*.

29 *Female sternal tubercle III*: (**0**) absent; (**1**) present (Fig. 3B). See *27*.

30 *Female sternal tubercle III size*: (**0**) small (e.g., *Nephilengys*, Kuntner, 2007a, fig. 5B); (**1**) large round projection (e.g., *N. ardentipes*). In some African *Nephila*, the third coxal tubercle is very pronounced.

31 *Female sternal tubercle IV*: (**0**) absent; (**1**) present. Elevation of the female sternum adjacent to coxae IV, if present, can be medial (e.g., *Nephila ardentipes*), or paired (e.g., *Opadometa*, *Herennia multipuncta*, Kuntner, 2005, fig. 6E, fourth arrow).

32 *Female frontal sternal tubercle*: (**0**) absent; (**1**) present (Fig. 3B). A frontal unpaired elevation of the female sternum is present in all species of *Nephila* except in *N. sexpunctata*. In some species this is a very large protuberance (e.g., *N. plumipes*), while in others it is small (*N. pilipes*, *N. edulis*, *N. constricta*); see *33*. A slight elevation of frontal sternum was also observed in *Meta* and *Araneus*, and coded as a tubercle.

33 *Frontal sternal tubercle*: (**0**) small; (**1**) large projection. In some *Nephila* species the frontal sternal tubercle is large and can be pointed (e.g., *N. plumipes*), while in others it is small and blunt (e.g., *N. constricta*).

34 *Female chilum*: (**0**) absent; (**1**) present (Fig. 4B). The chilum is a small sclerite at the base of chelicerae, just under the clypeus (e.g., Dippenaar and Jocqué, 1997). It is present in most nephilids (not in certain *Clitaetra* species) as a paired sclerite (Fig. 4B; Kuntner, 2005, fig. 1B; Kuntner, 2007a, fig. 1B); a paired chilum is also present in araneids with the exception of *Caerostris* (absent or perhaps hidden beneath the modified clypeus) and *Singafrotypa* (where the chilum is one sclerite). It is absent in tetragnathids.

35 *Female chelicerae*: (**0**) massive (width > ½ length; Fig. 4C); (**1**) slender (width < ½ length). Nephilids and most outgroups have massive chelicerae (width from profile more than ½ length). Relatively slender chelicerae appear sporadically in tetragnathids and derived araneoids.

36 *Cheliceral ectal margins*: (**0**) smooth (Fig. 4C); (**1**) with stridulatory striae. Most linyphiid and pimoid species have stridulatory striae on cheliceral margin (Hormiga 1994a,b; Hormiga et al., 1995, character 2; Griswold et al., 1998, character 37; Agnarsson, 2004, character 114, scored in males).

37 *Cheliceral boss*: (**0**) present (Fig. 4C, D); (**1**) absent. The cheliceral boss is present in all nephilids, tetragnathids (except *Metellina*) and araneids, as well as *Linyphia*, *Deinopis* (*D. spinosa*) and *Uloborus*. Hormiga et al. (1995, character 16, 17) and Griswold et al. (1998, character 39) described the features of the cheliceral boss and Griswold et al. (1998) note its absence in most derived araneoids, but did not code the presence of the boss itself. Agnarsson (2004, character 122) reports it absent in theridioids.

38 *Cheliceral boss surface*: (**0**) smooth; (**1**) striated (Fig. 4D). The boss is invariably striated in *Clitaetra* (Kuntner, 2006, figs 3E and 9C,D), *Nephilengys* (Kuntner, 2007a, figs 5D, 16B and 28D), *Nephila* (Fig. 4D) and *Herennia* (Kuntner, 2005, figs 6B and 20B). The feature is a nephilid synapomorphy (Hormiga et al., 1995).

39 *Prosomal supracheliceral lobe (PSL)*: (**0**) present (Fig. 4D); (**1**) absent. The carapace edge has a lobe over the cheliceral boss region in both sexes (e.g., female *Nephilengys*, Kuntner, 2007a, fig. 16B; male *Nephilengys*, Kuntner, 2007a, fig. 7 A,C,D) of all treated taxa except those of the "reduced piriform clade".

40 *Cheliceral furrow*: (**0**) denticulated (Fig. 4A); (**1**) smooth. The cheliceral furrow is denticulated in all nephilids, many araneids, *Uloborus* and *Deinopis* (here the denticles are in a row on caudal part of the furrow).

41 *Coxae III and IV*: (**0**) round; (**1**) with tubercle. The third and fourth coxae of some African *Nephila* species possess ventral humps.

42 *Female first femur*: (**0**) more/less straight; (**1**) sigmoidal (Fig. 14B, arrow). In dorsal view the first female femur is sigmoidal in *Phonognatha*, *Deliochus*, *Acusilas*, *Cyclosa*, *Singafrotypa* and *Perilla* (female, Fig. 14B, arrow; male, Fig. 14C, arrow). In *Araneus*, *Chrysometa* and *Pimoa* the femora are much less curved and so coded as "straight.

43 *Femoral macrosetae*: (**0**) present (Fig. 5A); (**1**) absent. Femoral spines or macrosetae are present in all nephilids and most araneoids. They are absent in theridioids among the taxa studied here (Griswold et al., 1998, character 59; Agnarsson, 2004, character 183).

44 *Femoral (I, II) macrosetae length*: (**0**) long (e.g., *Clitaetra*, Kuntner, 2006, fig. 9A); (**1**) short, stout (Fig. 5A). The femoral macrosetae of some species of *Nephila*, *Nephilengys* and *Herennia* are short and stout.

45 *Female femur I group of prolateral long spines*: (**0**) absent; (**1**) present (Kuntner, 2005, fig. 31B). Some species of *Herennia* and *Nephila* possess a group of long prolateral spines on the first femur (e.g., *H. tone*).

46 *Spine socket color*: (**0**) same as legs; (**1**) dark (Fig. 1H). African species of *Clitaetra* have a distinct spotted pattern on legs around spine sockets.

47 *Dorsal femoral trichobothria*: (**0**) absent; (**1**) present. All nephilids lack femoral trichobothria, present in *Uloborus*, tetragnathines, *Leucauge* and *Opadometa* (see below). Wunderlich (1986) hypothesized the presence of femoral trichobothria as a synapomorphy for "Tetragnathinae + Leucauginae" (see comments in Appendix 2, Clade 17).

48 *Femur IV trichobothria*: (**0**) scattered; (**1**) in rows. In *Leucauge* (see Levi, 1980, figs 50 and 51) and *Opadometa* as well as their possible close relatives (Kuntner and Alvarez-Padilla, 2006) the trichobothria are arranged in a paired row on prolateral fourth femur.

49 *Female tibia I tufts*: (**0**) absent; (**1**) present (Fig. 1A,C). All *Nephila* species at some stage possess dense tibial setae on legs I, II and IV, which may extend to distal femora and proximal metatarsi. These tufts or "gaiters" (Robinson and Robinson, 1973) may be absent in adults, notably in *N. turneri*. *Uloborus* species have tibial tufts on leg I, while *Opadometa* species have distinct brushes on fourth tibiae only. The presence of much weaker groups of
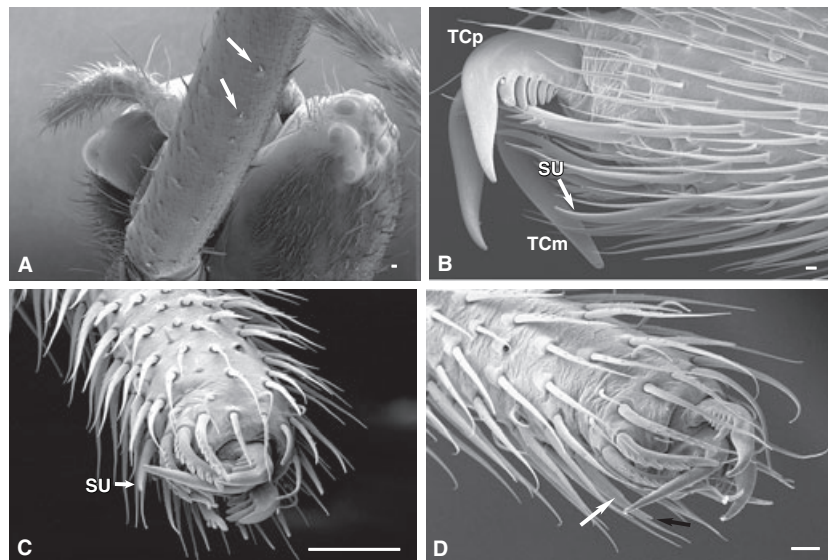
Fig. 5. Nephilid female appendages. (A) *Nephilengys papuana*, femur I with short macrosetae (arrow). (B–D) Tarsi IV, showing tarsal claws and sustentaculum: (B) *Nephilengys cruentata*; (C) *Herennia multipuncta*; (D) *Clitaetra episinoides* (both arrows). Scale bars: (A, C) 100 μm, (B, D) 20 μm.

tibial setae in *Nephilengys* (notably *N. cruentata* females from western Africa) and *Argiope* is not coded as tufts.

50 *Female tibia II tufts*: (**0**) absent; (**1**) present (Fig. 1A,C).

51 *Female tibia IV tufts*: (**0**) absent; (**1**) present (Figs 1A,C and 3A,B).

52 *Patella-tibia autospasy*: (**0**) absent; (**1**) present. Linyphiidae and Pimoidae uniquely possess the autospasy between the patella and the tibia (Roth and Roth, 1984; Wunderlich, 1986; Hormiga, 1994a, b; Hormiga et al., 1995; Griswold et al., 1998; Agnarsson, 2004), while other araneoids autotomize between the coxa and the trochanter.

53 *Ventral tarsus IV setae*: (**0**) irregular; (**1**) comblike. The theridiid tarsal comb is a synapomorphy of the spineless femur clade [Agnarsson (2004, character 193), see also Hormiga et al. (1995, character 10) and Griswold et al. (1998, character 62)]. The *Deinopis* setal "comb" does not resemble the theridiid condition (Griswold et al., 1998) but may be a homolog of the sustentaculum (see below).

54 *Tarsus IV median claw*: (**0**) long (as long as or longer than the paired claw; Fig. 5B,D); (**1**) short (shorter than the paired claw). The tarsus IV median claw is longer than the paired claw in all nephilids, extremely so in *Clitaetra perroti* (Kuntner, 2006, fig. 21F). Levi (1978, figs 1–8) provides images for *Leucauge*, *Nephila clavipes*, *Argiope argentata* and *Araneus*.

55 *Sustentaculum*: (**0**) present (Fig. 5B–D); (**1**) absent. The sustentaculum is a strong macroseta with a more or less bent tip, subterminally on tarsus IV. It is found in some but not all nephilids (see below for the difference with the typical araneid sustentaculum). The presence of the sustentaculum (termed "Webestachel" or "Hamulus") in *Nephila* and *Nephilengys* was documented by Dahl (1912, fig. 11), and served as the evidence that *Nephila* and *Nephilengys* were araneids ("Radnetzspinnen"). Scharff and Coddington (1997) and Griswold et al. (1998) attributed the term sustentaculum to Reimoser (1917), who actually used "Webestachel" for an unillustrated feature. A row of sustentaculum-like setae is found on *Deinopis* and *Uloborus* fourth tarsi (as it is in some araneids), suggesting possible homology of the araneid sustentaculum with the distal sustentaculum-like seta in *Deinopis* (coded as such). The only araneid (in this matrix) lacking the sustentaculum is *Perilla* (erroneously coded as present in Kuntner, 2002). Sustentaculum served as a synapomorphy of Araneidae in Hormiga et al. (1995, character 9), Scharff and Coddington (1997, character 40, fig. 40), and Griswold et al. (1998, character 64), but these authors overlooked the sustentaculum in nephilids.

56 *Sustentaculum angle*: (**0**) wide, diverging from other setae; (**1**) narrow, parallel to other setae (Fig. 5B–D). While in most araneids (also in *Deinopis*

and *Uloborus*, if homologous) the sustentaculum arises at a wide angle (Scharff and Coddington, 1997, fig. 40), the nephilid sustentaculum is less conspicuous, arising slightly laterally and at a narrow angle. A similar condition is found in *Caerostris* and *Micrathena* (Levi, 1985, plate 3, arrows).

57 *Female abdomen length*: (**0**) very long ($> 2 \times$ width); (**1**) long (longer than wide, but $< 2 \times$ width); (**2**) short (as wide as long or wider). This character somewhat arbitrarily quantifies the relative abdomen lengths. Some *Nephila* species, *Deinopis*, *Tetragnatha* and *Perilla* (Fig. 14A,B) have very long abdomens, some have long abdomens (e.g., *Nephilengys*, *Nephila clavipes*, Fig. 1C), while the abdomen of e.g., *Herennia* may be wider than long (Fig. 1F,G).

58 *Female abdomen width*: (**0**) elliptical; (**1**) widest anteriorly; (**2**) widest posteriorly; (**3**) pentagonal. Female abdomen (in dorsal view) may be elliptical (widest in the middle; e.g., *Herennia*, Fig. 1F,G), widest in the anterior part and gradually tapering posteriorly (e.g., *Nephila*, Figs 1A and 3A,B), widest posteriorly (*Opadometa*, also some *Phonognatha* spp.), or nearly pentagonal (*Clitaetra*, Fig. 1H).

59 *Female lateral abdominal margin*: (**0**) smooth; (**1**) with three to four pairs of lobes (Fig. 1F,G). Female abdomen is lobed in most *Herennia* species and in *Argiope argentata*.

60 *Female anterior abdominal humps*: (**0**) absent; (**1**) present. Nephilids lack abdominal dorsal humps. Some outgroup genera exhibit paired dorsal humps on the anterior abdomen (e.g., *Caerostris*, see Grasshoff, 1984, figs 1 and 6–10) and additional ones in mid-abdominal region (both present in e.g., *Dolichognatha pentagona*, see Levi, 1981, figs 1 and 2).

61 *Female mid-abdominal humps*: (**0**) present; (**1**) absent.

62 *Female abdomen tip*: (**0**) rounded; (**1**) truncated (Fig. 1G). In most species of *Herennia* the abdomen has a truncated end (Fig. 1F,G; Kuntner, 2005, figs 8a,B and 9B, arrow, and 10A,B,D), a similar condition to *Clitaetra irenae* (Fig. 1H; Kuntner, 2006, fig. 10A), *Argiope argentata* (Levi, 1968, figs 125, 126) and *Caerostris*.

63 *Female abdomen caudal part*: (**0**) protrudes somewhat beyond spinnerets (caudal/whole abdomen less than 0.2); (**1**) protrudes considerably beyond spinnerets (ratio caudal/whole abdomen > 0.2; Fig. 14A: ratio a/b). In some araneids the abdomen is extended considerably beyond the spinnerets. Kuntner (2002) diagnosed *Perilla* by the extreme abdomen elongation: the ratio caudal part of the abdomen to whole abdomen length was 0.53 compared with 0.29 in *Acusilas*, 0.23 in *Cyclosa* and 0.21 in *Singafrotypa* (see also Kuntner and Hormiga, 2002). The extreme abdomen elongation is here defined as the ratio a/b (Fig. 14A) exceeding 0.2. Most nephilid female abdomens, if slightly extended beyond spinnerets, have

shorter abdominal ends; however, some *Nephila* species come close to the arbitrary limit, notably *N. komaci* at 0.17.

64 *Tracheal spiracle*: (**0**) posterior; (**1**) advanced. The tracheal spiracle in nephilids is invariably close to the spinnerets (posterior), and the advanced condition is found only in *Glenognatha*. Hormiga et al. (1995), character 13) mistakenly coded *Pachygnatha* as advanced (see also Levi, 1980, p. 47), which makes the character uninformative for this taxon sample.

65 *Female abdominal ventro-median apodemes (1)*: (**0**) absent; (**1**) present (Fig. 3B; Kuntner, 2005, figs 8A–C and 9B–D). All nephilids possess a row of conspicuous sclerotized apodemes medially on the abdominal venter. These may be paired or fused in the middle (Kuntner, 2005, fig. 9B–D). While many non-araneoid groups also possess these, the *Deinopis* and *Uloborus* species examined here appear to lack them and the condition within araneoids varies (their visibility may correlate with abdominal sclerotization). In *Deliochus* the character was found to be polymorphic—only well sclerotized specimens possessed the apodemes. The apodemes are especially numerous in *Clitaetra* (see next character). In *Tetragnatha* (*elongata*) the presence of the ventral and dorsal (median) apodemes is restricted to the first third of the abdomen, unlike in *Nephila*, suggesting the extreme elongation of *Tetragnatha* and *Nephila* abdomen took different developmental/evolutionary pathways.

66 *Female abdominal ventro-median apodemes (2)*: (**0**) one to five pairs; (**1**) six to 11 pairs. *Clitaetra* species have between six and 11 paired ventral apodemes (Kuntner, 2006, figs 4A and 10A), while other nephilids have less than six (e.g., three to four pairs in *Herennia multipuncta*, Kuntner, 2005, figs 8A–C, 9B,C and 10A,C).

67 *Female ventro-lateral abdominal sclerotizations*: (**0**) present (Fig. 3B); (**1**) absent. One row (e.g., *Clitaetra*, Kuntner, 2006, fig. 4A—lower arrow, B, 10A—upper arrow, B) or several rows (*Herennia*, see next character) of lateral sclerotizations (smaller than the median apodemes) are typical for nephilids and are also found in certain outgroups, notably araneids.

68 *Ventro-lateral abdominal sclerotizations*: (**0**) one paired line of small dots; (**1**) sclerotizations in several lines (Kuntner, 2005, figs 8D–F and 10A–D). In *Herennia* and some *Nephila* species the lateral ventral sclerotizations are in several rows.

69 *Female dorso-median abdominal apodemes*: (**0**) absent; (**1**) 3–5 prominent pairs (Figs 1F,G and 3A; Kuntner, 2007a; Fig. 1C). All nephilids possess conspicuous paired median apodemes on dorsum, and the condition in outgroups varies. Agnarsson (2004, character 167) termed them sigillae (see below). Smaller sclerotizations appear medially and laterally

to the prominent apodemes (Kuntner, 2007a; Fig. 1C), termed here dorso-central and dorso-lateral sclerotizations (see **70, 71**).

70 *Female dorso-lateral abdominal sclerotizations*: (**0**) present (Kuntner, 2007a; Fig. 1C); (**1**) absent.

71 *Female dorso-central abdominal sclerotizations*: (**0**) absent; (**1**) present (Kuntner, 2007a; Fig. 1C).

72 *Female abdominal sigillae*: (**0**) absent; (**1**) present (Fig. 1F,G). Lateral sclerotizations on dorsum of *Herennia* and *Caerostris* take the form of sigillae (Kuntner, 2005, figs 1A,C and 9E,F; compare with character 56 of Scharff and Coddington, 1997). These are not sigillae *sensu* Agnarsson (2004, character 167)—see **69**.

73 *Female anterior abdomen*: (**0**) without; (**1**) with a broad light-pigmented band (Fig. 1E; Kuntner, 2007a, fig. 1A,D). A broad band of light pigment on anterior abdomen is diagnostic for females of *Nephilengys*.

74 *Female abdominal coloration*: (**0**) uniform; (**1**) patterned. Female abdominal color patterns in spiders are too diverse to score reliably across superfamilies, but within a small clade such as Nephilidae, there is clearly phylogenetic signal (e.g., *Clitaetra*, Fig. 1H, some *Nephila*, Fig. 1A). Color patterns can also disappear in older museum specimens (*Nephila sexpunctata* is scored as inapplicable). However, all *Nephilengys* (Fig. 1D; Kuntner, 2007a, fig. 1C), *Nephila ardentipes*, *plumipes* and *edulis*, and *H. deelemanae*, *gagamba*, *tone* and *agnarssoni* lack prominent dorsal abdominal color patterns, although the base color varies from whitish to black. They are therefore coded as inapplicable with regards to color patterns, as are all the outgroup taxa. The color patterns coded in characters 75–78 are each unique to a few taxa and non-overlapping, and, although might represent one multistate character, the coding technique in this case makes no practical difference. Characters 79–80 co-occur in some *Clitaetra* and therefore are not homologous. Abdomens show varied patterns of pigmented stripes, spots, or bands (see next characters).

75 *Female dorsum dark spots*: (**0**) absent; (**1**) present (Fig. 1F,G; Kuntner, 2005, figs 14 and 25). Some *Herennia* species possess numerous dark spots on dorsum, which appear to mimic the tree bark background.

76 *Female dorsum longitudinal light lines*: (**0**) absent; (**1**) present. Two *Nephila* species (*N. pilipes*, *N. constricta*) possess light pigmented thin longitudinal lines on dorsum. Very rarely in both species, some morphs lack the pattern.

77 *Female dorsum paired light spots*: (**0**) absent; (**1**) present (Fig. 1A). Some *Nephila* exhibit paired light pigmented dorsal spots (e.g., *N. sumptuosa*), which may be joined medially to form continuous patches (e.g., certain populations of *N. senegalensis*, Fig. 1A).

78 *Female dorsum wide notched band*: (**0**) absent; (**1**) present. Some *Nephila* species possess a wide light pigmented folium, which is notched at sides (e.g., *N. turneri, N. komaci*).

79 *Female dorsum ''butterfly'' pattern*: (**0**) absent; (**1**) present (Kuntner, 2006, figs 1A and 6A). The dorsum pattern in *Clitaetra clathrata* and *C. simoni* diagnostically consists of a frontal dark pigmented butterfly shaped patch. A less pronounced potentially homologous mark is found in other *Clitaetra* species with the exception of *C. thisbe*.

80 *Female dorsum ''grid'' pattern*: (**0**) absent; (**1**) present (Kuntner, 2006, figs 1A and 6A). The dorsum of *Clitaetra clathrata* and *C. simoni* diagnostically consists of a posterior dark pigmented grid-shaped pattern with two pairs of dark patches demarcated with white.

81 *Female abdomen tip color*: (**0**) like the subapical abdomen; (**1**) with paired white dots around spinnerets (Fig. 3B). Many araneoids possess a pair of white dots on posterior abdomen just lateral to the spinnerets (e.g., *Clitaetra episinoides*, Kuntner, 2006, fig. 12A,C; *C. perroti*, Kuntner, 2006, fig. 19B).

82 *Female abdomen silver pigment spots*: (**0**) absent; (**1**) present. Conspicuous abdominal silver pigment, typical for certain tetragnathids (e.g., *Leucauge*), is not present in nephilids.

83 *Female venter light pigmented pattern*: (**0**) absent; (**1**) present. The nephilid female venter always possesses some pattern of light pigment (see *84*).

84 *Female venter light pigmented pattern form*: (**0**) one central light area (e.g., Kuntner, 2006, fig. 19B); (**1**) transverse line(s) (e.g., *Nephila*, Fig. 1B); (**2**) four large spots (e.g., *Nephilengys*, Fig. 1E); (**3**) numerous spots (e.g., *Nephila clavipes*, Figs 1C and 3B); (**4**) longitudinal lines (e.g., *Argiope* sp., Fig. 26C).

85 *Booklung cover*: (**0**) grooved (Fig. 3B); (**1**) smooth. All species of *Nephila*, *Nephilengys* and *Herennia* but only some species of *Clitaetra* exhibit the grooved condition (Kuntner, 2005, 2006, 2007a).

86 *Area around female book lung spiracle*: (**0**) slightly sclerotized; (**1**) strongly sclerotized (Fig. 3B). The area around book lung covers is strongly sclerotized in nephilids (e.g., *Nephilengys*, Kuntner, 2007a, fig. 1D) except *Clitaetra* (Kuntner, 2006, figs 12C and 19B), as well as *Opadometa* and araneids.

Female genital morphology

87 *Epigynal plate*: (**0**) present (Fig. 3B); (**1**) absent. The epigynal plate is a sclerotization with copulatory openings leading to female genital system. It may be ventral and conspicuous (e.g., *Nephilengys*, Fig. 8K,N *Herennia*, Fig. 9I,J) or posterior and inconspicuous (e.g., *Clitaetra*, Fig. 10F,G,J,K; some *Nephila*, Fig. 7I,J,M,N). Tetragnathines (*Tetragnatha, Glenognatha*

and *Pachygnatha*) lack the epigynum (Wiehle, 1963, 1967a,b; Levi, 1980, 1981; Hormiga et al., 1995, character 40) but in other taxa the epigynal morphology varies substantially (see next characters). Such characters are inapplicable to tetragnathines.

88 *Posterior epigynal plate*: (**0**) round; (**1**) grooved (Fig. 8K). In some species of *Nephila* and *Nephilengys* the epigynal plate posterior edge is grooved and leads to lateral copulatory openings, hence termed the copulatory groove (see Kuntner, 2007a, figs 2A–D, 13A and 16C,D). The condition in *Phonognatha* and *Caerostris* is similar.

89 *Epigynal ventral area*: (**0**) low; (**1**) swollen (Fig. 7I). The epigynal area anterior to the epigynal plate is swollen (and often sclerotized) in most *Nephila* and some *Clitaetra* species (see Kuntner, 2006, figs 7B and 10C) and a similar condition is found in *Meta*.

90 *Epigynal posterior area*: (**0**) round; (**1**) tongue-shaped (Fig. 10J,K). The posterior epigynal area is tongue-shaped in *Clitaetra episinoides* (Fig. 10J,K; Kuntner, 2006, fig. 15B) and *C. perroti* (Kuntner, 2006, figs 19C–F and 22A,B) among nephilids. Among the outgroups an arguably similar morphology is found in *Pimoa* (Hormiga, 1994a), *Perilla* (Fig. 14D–F) and *Argiope aurantia* (Levi, 1968). However, in *Clitaetra* the tongue is weakly sclerotized and flat, while in other outgroups it is strongly sclerotized and three-dimensional (see also epigynal scape).

91 *Epigynal openings*: (**0**) superficial (e.g., Fig. 7J,N); (**1**) in chambers (Figs 8K and 9I,J). Copulatory openings are within larger chambers in *Nephilengys* (Fig. 8K; Kuntner, 2007a, fig. 29A,B), *Herennia* (Fig. 9I,J; Kuntner, 2005, fig. 11), as well as *Nephila constricta* and *N. fenestrata*. The condition is similar in *Deliochus*, *Phonognatha*, *Caerostris*, *Acusilas*, *Argiope argentata*, *Chrysometa* and *Linyphia*. The chambers present in the epigynum of some (but not all) specimens of *Nephila edulis* are different as they do not harbor the copulatory openings.

92 *Chamber opening position*: (**0**) medial; (**1**) lateral. Copulatory openings within chambers open medially (e.g., *Nephilengys papuana*, Fig. 8N) or laterally (e.g., *Herennia multipuncta*, Fig. 9I,J).

93 *Epigynal septum*: (**0**) absent; (**1**) present (Figs 8N and 9I,J). Epigynal chambers, if present, are usually divided by a medial septum (e.g., *Nephilengys*, Fig. 8N, Kuntner, 2007a, fig. 29A–C; *Herennia*, Fig. 9I,J; Kuntner, 2005, fig. 11), which can take various forms (see next characters).

94 *Epigynal septum shape*: (**0**) narrow border between chambers (Fig. 9I,J); (**1**) extensive, broader posteriorly (Fig. 8N); (**2**) extensive, broader anteriorly (Fig. 16E). The septum can be narrow (simple), broad posteriorly (e.g., *Nephilengys papuana*, Fig. 8N, Kuntner, 2007a, fig. 29A,B; *Deliochus*, Fig. 12C), or broad anteriorly (*Caerostris*, Fig. 16E; *Argiope argentata*, Levi, 1968, figs 121, 123 and 124).

95 *Epigynal paired sclerotized pocket*: (**0**) absent; (**1**) present (Fig. 8K). In *Nephilengys cruentata* and *N. borbonica* the copulatory openings are within a sclerotized round pocket (Fig. 8K; Kuntner, 2007a, figs 2A,B and 16C,D), and a similar pocket is found in *Nephila fenestrata*, *Araneus*, *Cyclosa* and *Caerostris* (Fig. 16E).

96 *Epigynal scape*: (**0**) absent; (**1**) present (Fig. 13C–E). A typical araneid scape, present in *Araneus* and *Singafrotypa* (Fig. 13C–E), originates on anterior epigynal rim, is annulate and ends with a distal pocket (see next character). A slightly different yet potentially homologous scape is found in *Perilla* (Fig. 14D–F; Kuntner, 2002 referred to it as tongue-shaped). *Nephila senegalensis* has a morphologically distinct feature also coded as scape because it also originates anteriorly. The *Linyphia* "scape" (coded here as absent) is different as it originates at the epigynal posterior rim. Corresponds to Scharff and Coddington (1997, character 28) but not to Agnarsson (2004, character 1) because the theridiid scape is not homologous.

97 *Paired epigynal flap*: (**0**) absent; (**1**) present (Fig. 12C). A paired lateral flap of the epigynal septum is diagnostic of *Deliochus* (Kuntner, unpublished). Though uninformative here it may be synapomorphic for *Deliochus*.

98 *Epigynum posterior*: (**0**) without a membrane; (**1**) with a membrane (Fig. 19G,H). In *Meta* and *Dolichognatha* the epigynum has an extensive posterior membrane.

99 *Anterior epigynal area*: (**0**) with a pair of apodemes (Fig. 7I,M); (**1**) round. In *Nephila* (Fig. 7I,M) and *Herennia* (Fig. 9I), the anterior epigynal area has a pair of apodemes, ventrally observed as a pair of depressions. A similar feature was observed in *Opadometa* and *Pachygnatha*.

100 *Cuticle anterior to the epigynal area*: (**0**) rounded; (**1**) depressed (Fig. 7I–M). Another larger unpaired depression is found anteriorly to the paired apodemes in *Nephila* (Fig. 7I–M), *Nephilengys* (Fig. 8K) and *Herennia* (Kuntner, 2005, fig. 10E) and in certain outgroups.

101 *Epigynal anterior area*: (**0**) round; (**1**) depressed (EAD in Fig. 10F). The epigynal plate of African *Clitaetra* species possesses a paired depression anterolaterally (Kuntner, 2006). A similar depression was observed in *Opadometa*.

102 *Epigynal lateral area*: (**0**) round; (**1**) curved (ELC in Fig. 10F). The epigynal plate of African *Clitaetra* species is laterally curved, as is that of *Opadometa*.

103 *Copulatory opening position*: (**0**) caudal (Figs 7I–N and 10F–K); (**1**) ventral (Figs 8K–P and 9I–L). In *Clitaetra* and most *Nephila* species the position of the copulatory openings is caudal (posterior). In *Nephilengys* and *Herennia* it is ventral. The outgroup condition varies.

104 *Caudal copulatory openings*: (**0**) on the posterior sclerotized epigynal margin (e.g., *Clitaetra episinoides*, Fig. 10K; see also Kuntner, 2006, figs 1C,E and 6C); (**1**) anterior to the posterior margin (e.g., *Clitaetra irenae*, Fig. 10G).

105 *Copulatory opening form*: (**0**) elongated slit openings (Fig. 7M,N); (**1**) rounded openings (Fig. 7J). Copulatory openings in many *Nephila* species are slit-shaped (e.g., *N. turneri*, *N. sumptuosa*), while in others they are round (e.g., *N. ardentipes*, Fig. 7J), or the feature is polymorphic (e.g., *N. senegalensis*, Kuntner, unpublished). *Epeirotypus* has a single caudal slit opening (Coddington, 1986b).

106 *Copulatory duct morphology*: (**0**) flattened duct (longer than wide, flat); (**1**) tube (longer than wide, cylindrical); (**2**) broad attachment to body wall (wider than long). Copulatory duct resembles a tube in most taxa (e.g., *Nephila ardentipes*, Fig. 7K,L), broadly attaches spermatheca to the body wall (e.g., *Nephilengys cruentata*, Fig. 8L,M), or is flattened as in *Nephila clavipes* (Kuntner, unpublished; see Higgins, 1989).

107 *Spermathecae*: (**0**) lobed (Fig. 11F,G,I); (**1**) spherical (Figs 7K,L and 8L,M,O,P); (**2**) oval (Fig. 9K,L). Nephilid genera have adjacent, well-sclerotized, unlobed spherical (oval in *Herennia*) spermathecae with gland pores over their entire surface (e.g., *Nephila*, Fig. 7K,L; *Nephilengys*, Fig. 8L,M,O,P; *Herennia*, Fig. 9K,L; *Clitaetra*, Fig. 10H,I). *Phonognatha* (Fig. 11F,G,I) and *Deliochus* (Fig. 12D) have adjacent lobed spermathecae. Two-lobed spermathecae (these well-separated) are also found in some tetragnathines (e.g., *Tetragnatha extensa*: Wiehle, 1963, fig. 18; *T. elongata*: Levi, 1981, figs 76–78). Spermathecae are strongly oval and narrow, and membranous (not sclerotized) in *Leucauge* and *Opadometa* (Fig. 18F), and a similar condition can be found in certain stages (polymorphic) of *Nephila constricta* (Kuntner, unpublished).

108 *Spermathecae separation*: (**0**) wide (separated more than two widths); (**1**) small or none (separated less than two widths).

109 *Spermathecal sclerotization*: (**0**) well sclerotized; (**1**) membranous.

110 *Fertilization ducts*: (**0**) present; (**1**) absent. Tetragnathines lack fertilization ducts (Wiehle, 1963, fig. 18; Levi, 1980, 1981, fig. 76).

111 *Epigynal sclerotized arch*: (**0**) absent; (**1**) present (ESA in Figs 8O,P and 9K). A sclerotized arch of the inner epigynum is present in *Nephilengys malabarensis* and *N. papuana* (Kuntner, 2007a), in some species of *Herennia* (Kuntner, 2005) and in *Nephila fenestrata*. An anterior sclerotization in the epigynum of *Caerostris* appears different (the form of an anterior denticulated edge, Fig. 16F).

112 *Female copulatory aperture*: (**0**) never plugged; (**1**) sometimes plugged with emboli and/or embolic conductors (Figs 7M,N, 9J and 12C,D). Males of many

nephilid species routinely break off sclerites of the embolic division during copulation, which apparently function to plug the female's copulatory openings. The behavior is common in *Herennia* (Fig. 9J; Kuntner, 2005, figs 10E,F and 11; see also Hormiga et al., 1995) and certain *Nephila* species (Fig. 7M,N), especially in *N. fenestrata* (Fromhage & Schneider, 2005a, 2006; Kuntner, unpublished). It has also been recorded in *Nephilengys cruentata* and *N. borbonica*, but not in other *Nephilengys* species (Kuntner, 2007a) and not in *Clitaetra* (judging from the examined material). Such plugs have also been observed in *Deliochus* (Fig. 12C,D), *Caerostris* and *Argiope* (this study), as well as in *Singafrotypa* (Kuntner and Hormiga, 2002), and some other araneoids (Wiehle, 1967b). Amorphous plugs covering the epigynal plate in, e.g., *Nephila pilipes* (as *N. maculata* in Robinson, 1982) are not considered here.

113 *Female copulatory plugs*: (**0**) emboli (Fig. 7M,N); (**1**) emboli plus (embolic) conductors (**171,** Fig. 9J; Kuntner, 2007a, fig. 2E). Most araneoid plugs are simple and consist of the broken-off embolus (Wiehle, 1967b), a relatively narrow sclerite. The plugs of *Herennia* (Kuntner, 2005, figs 10E,F and 11), *Neph-*

ilengys (Kuntner, 2007a, figs 2E and 16C,D), some *Nephila*, *Phonognatha* (Fig. 11H) and *Deliochus* (Fig. 12C,D) are more complex and consist of one or several distal sclerites of the embolic division. Fromhage and Schneider (2006) demonstrated that such a complex plug in *Nephila fenestrata* functions to protect the male's parental investment.

Female spinneret morphology

An almost uniform nephilid spinneret morphology (reviewed in Kuntner, 2005, 2006, 2007a) is as follows: ALS (Fig. 6A,B,E) with "normal PI field" where the PI spigot base is nearly as long or longer than the shaft (Griswold et al., 1998, character 69, fig. 48B), the major ampullate spigot and a nubbin, PMS (Fig. 6A,C,D) with a sparse aciniform field, and a nubbin, PLS (Fig. 6A,D,F) with the aggregate spigots embracing the flagelliform, and with the two cylindrical spigots of normal size, the mesal being peripheral. The apparent exception is *Clitaetra perroti*, where the ectal aggregate gland spigot was found apart from the flagelliform (Kuntner, 2006, fig. 22F). A similar condition was
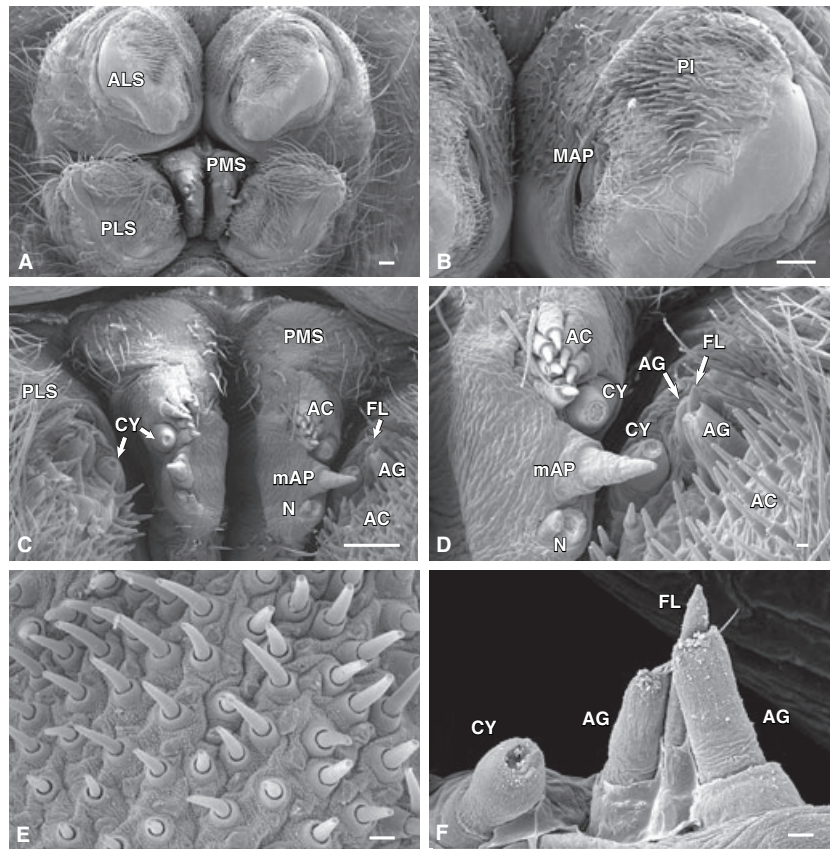
Fig. 6. Nephilid female spinneret morphology. (A–D) *Nephila senegalensis*: (A) all three spinneret pairs, ventro-apical; (B) anterior lateral spinneret; (C) posterior median spinnerets; (D) posterior median and lateral spinneret detail, note triad with aggregate spigot pair embracing flagelliform, and a double nubbin. (E,F) *Nephilengys papuana*: (E) piriform gland spigots on ALS; (F) triad (AG, FL) and cylindrical gland spigot on PLS. Scale bars: (A–C) 100 μm, (D–F) 10 μm.
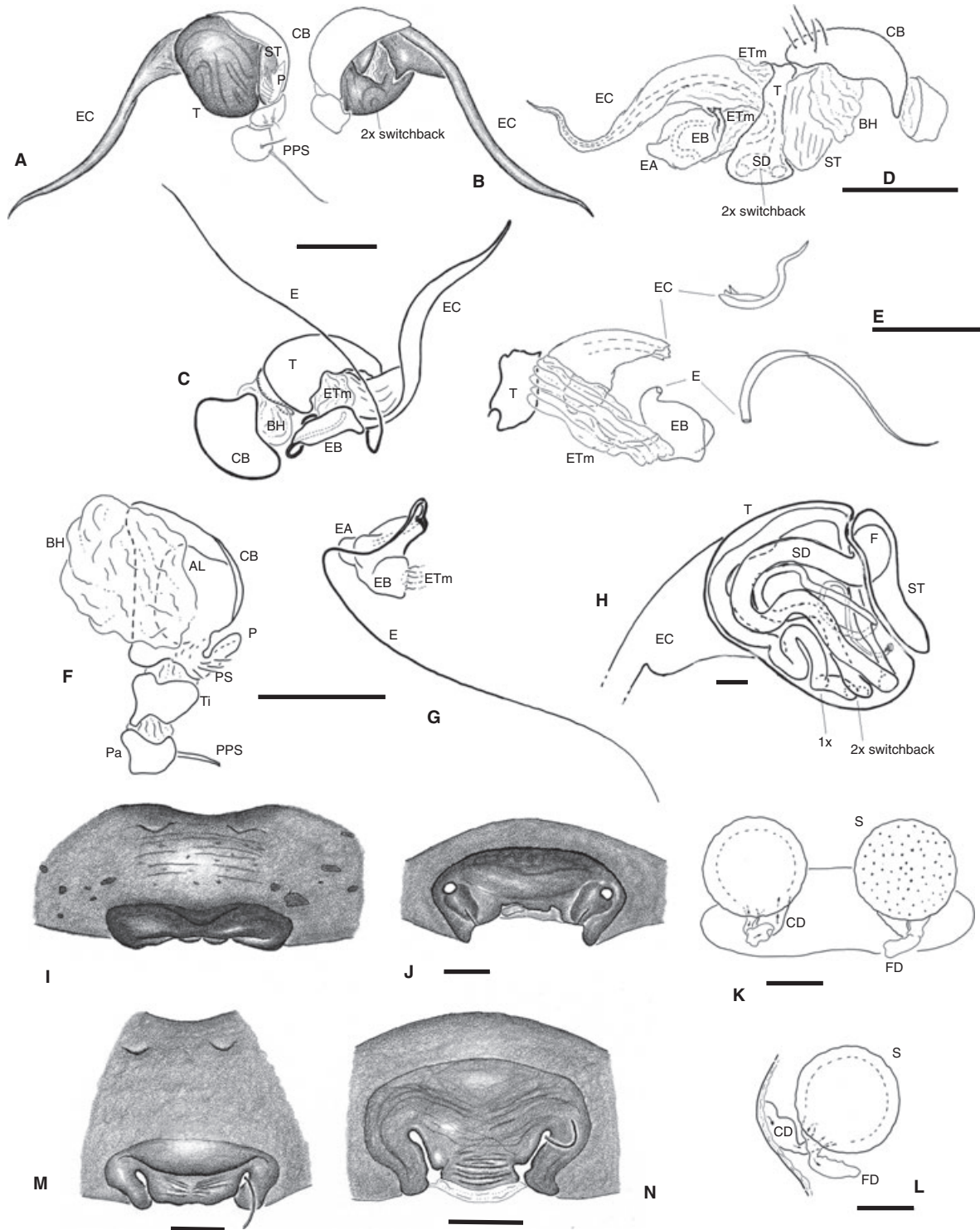
Fig. 7. *Nephila* genital morphology. (A–C) *Nephila turneri*, male palp: (A) ectal; (B) mesal; (C) expanded. (D,E) *Nephila constricta*, expanded and dissected right palp: (D) whole (embolus broken); (E) embolic division. (F–H) *Nephila senegalensis*: (F) left cymbium, bulb expanded and detached, ectoventral; (G) left embolus detached; (H) left bulb transparent, showing sperm duct. (I–L) *Nephila ardentipes* epigynum: (I) ventral; (J) posterior (note round copulatory openings); (K) cleared, dorsal; (L) cleared, left spermatheca, ectal. (M,N) *Nephila turneri* epigynum: (M) ventral; (N) posterior (note slit-shaped copulatory openings). Scale bars = 0.5 mm, except H = 0.1 mm.
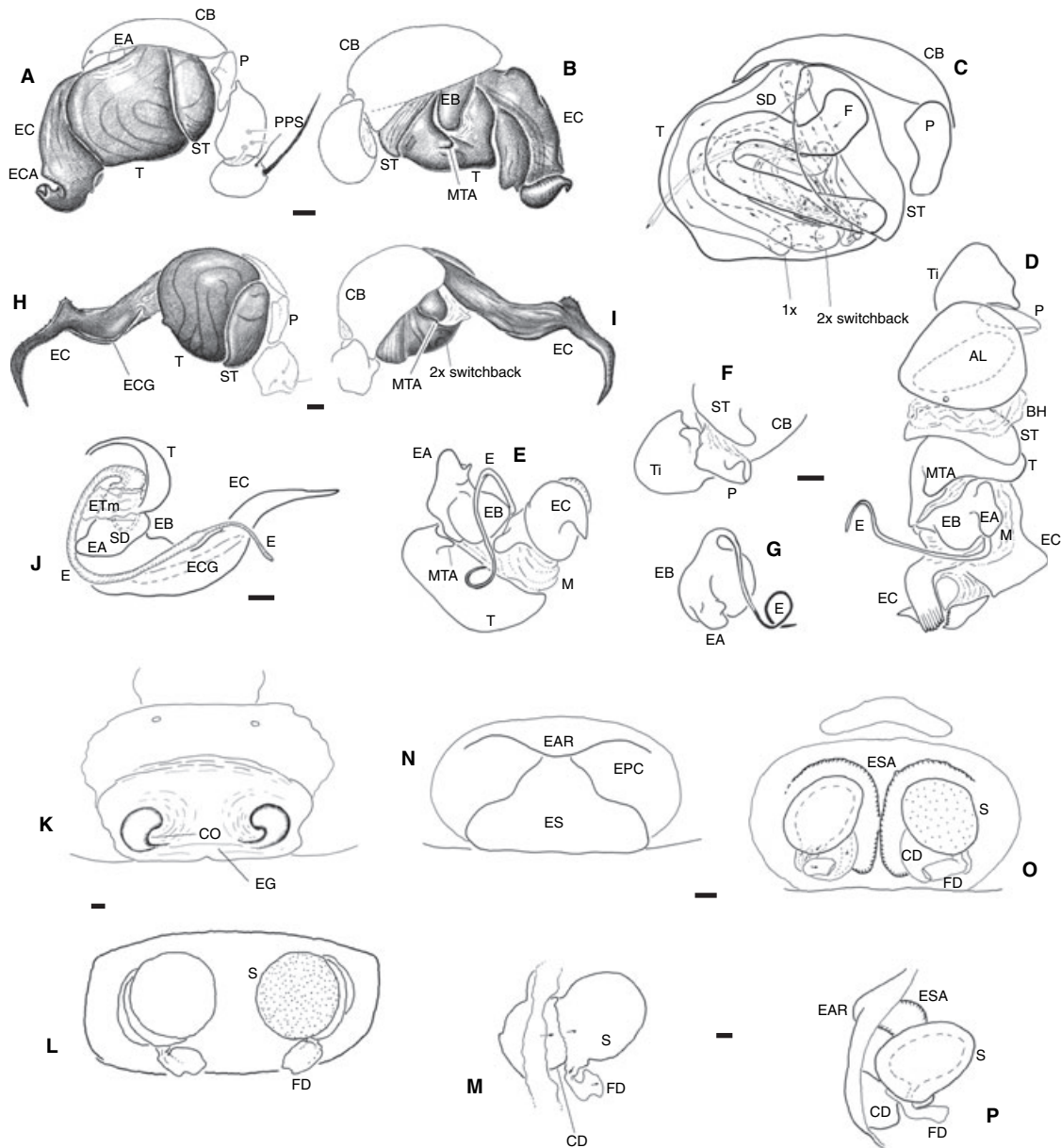
Fig. 8. *Nephilengys* genital morphology. (A–C) *Nephilengys cruentata*, male left palp: (A) ectal; (B) mesal; (C) left bulb transparent, showing sperm duct. (D–G) *Nephilengys borbonica*, palp expanded and dissected: (D,E) whole palp; (F) paracymbium; (G) embolus. (H,I) *Nephilengys malabarensis*, male left palp; (H) ectal; (I) mesal. (J) *Nephilengys papuana*, embolic division, dissected. (K–M) *Nephilengys cruentata* epigynum: (K) ventral; (L) cleared, dorsal; (M) cleared, left spermatheca, ectal. (N–P) *Nephilengys papuana* epigynum: (N) ventral; (O) cleared, dorsal; P, cleared, left spermatheca, ectal. Scale bars = 0.1 mm.

observed in small females of *Nephila constricta* (the large ones, however, showed the nephilid condition). Adult males lack the triad (Kuntner, 2006, fig. 17F). For *Phonognatha* and tetragnathid spigot morphology see Hormiga et al. (1995, figs 14–26).

114 *Cribellum*: (**0**) present; (**1**) absent. In Orbiculariae, the cribellum is present in *Deinopis* and *Uloborus*. Corresponds to the character 66 in Griswold et al. (1998).

The following spinneret spigot characters are unchanged from Hormiga et al. (1995, character 54–60), and follow the homology assessments of Coddington (1989).

115 *ALS piriform gland spigot bases*: (**0**) normal (Fig. 6A,B,E); (**1**) reduced.

116 *PMS nubbin*: (**0**) absent; (**1**) present (Fig. 6C,D).

117 *PMS aciniform field*: (**0**) extensive; (**1**) sparse (Fig. 6C,D).
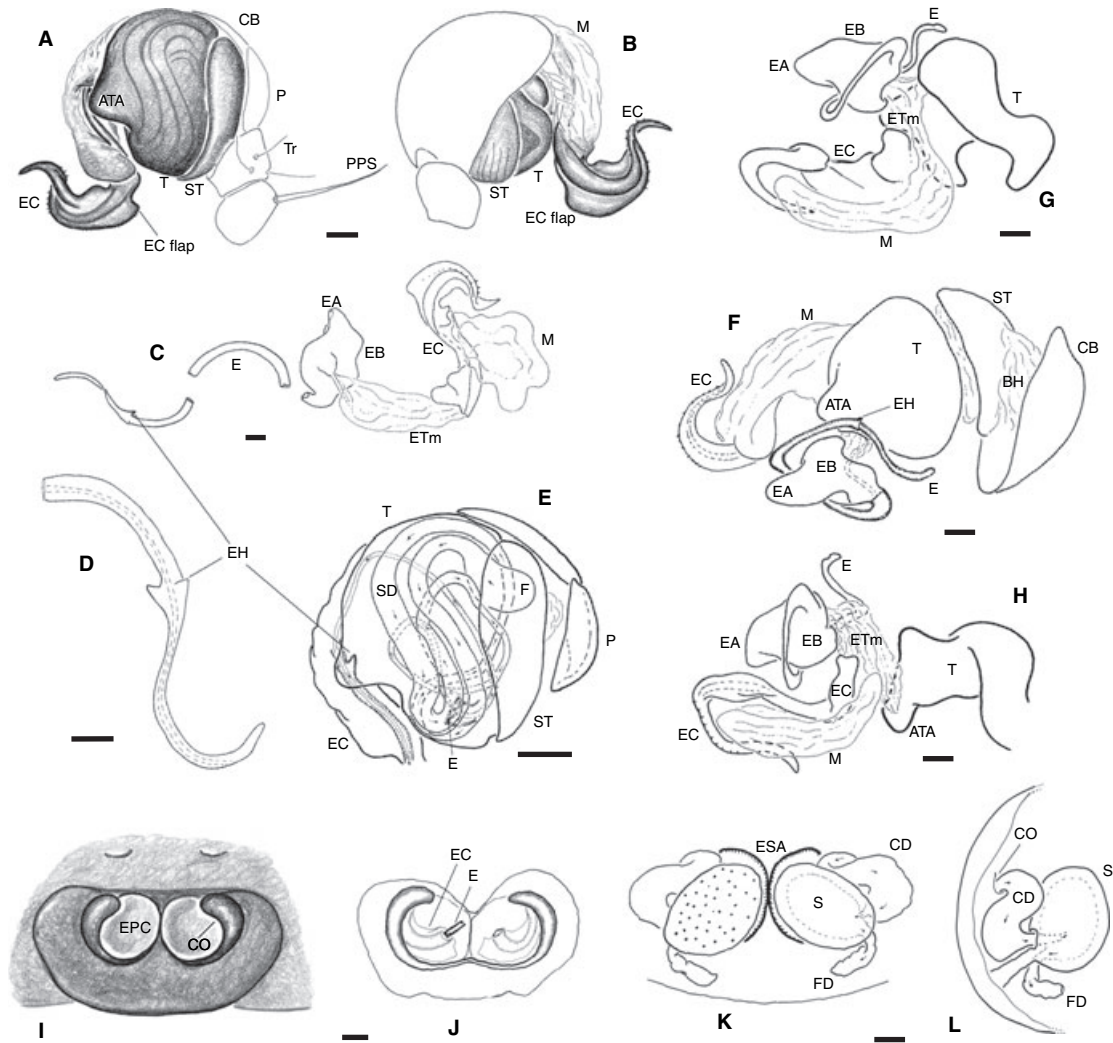
Fig. 9. *Herennia* genital morphology. (A–E) *Herennia multipuncta*, male left palp: (A) ectal; (B) mesal; (C) embolic division, expanded and dissected; (D) distal embolus, note embolus hook; (E) bulb transparent, showing sperm duct, ectal. (F–H) *Herennia papuana*, male left palp expanded and dissected: (F) whole palp; (G) distal sclerites, dissected; (H) further dissection of embolic division. (I–L) *Herennia multipuncta* epigynum: (I) ventral; (J) same (with embolic conductor plugs); (K) cleared, dorsal; (L) cleared, left spermatheca, ectal. Scale bars = 0.1 mm.

118 *PLS mesal cylindrical gland spigot base*: (**0**) subequal to other PLS cylindrical spigot; (**1**) larger.

119 *PLS mesal cylindrical gland spigot position*: (**0**) central; (**1**) peripheral.

120 *PLS aggregate-flagelliform relation*: (**0**) aggregates apart from flagelliform; (**1**) distal aggregate spigots embrace flagelliform (Fig. 6F).

121 *PLS aggregate gland spigot*: (**0**) normal; (**1**) large.

Male somatic morphology

122 *Male size*: (**0**) more than half the size of female (**1**) less than 0.4 female. The coding corresponds to Hormiga et al. (1995, character 14), arbitrarily quantifying the extreme sexual size dimorphism (SSD), within nephilids typical of *Nephila* (Fig. 1C), *Nephilengys*

(Fig. 1D; Kuntner, 2007a, fig. 1) and *Herennia* (Kuntner, 2005, fig. 1), and the araneids *Argiope*, *Caerostris* and *Acusilas*. Coding *Clitaetra* is problematic: *Clitaetra irenae* average male to female length ratio is 0.41 but the ratios of extreme values range from 0.28 to 0.63); similarly, in *C. clathrata* the ratio of averages is 0.5, and of extremes 0.37-0.72. These two species were scored as polymorphic. The range of extremes in *C. episinoides* is 0.45–1.0 (average ratio 0.65) and in *C. perroti* 0.41–0.77 (average ratio 0.55) and these were scored as not dimorphic. In *Deliochus* and *Phonognatha* the feature also varies within species. Relaxing the arbitrary definition of extreme sexual size dimorphism would alter codings for *Clitaetra*, *Phonognatha* and *Deliochus*. Hormiga et al. (2000) discussed the weakness of such character coding approach, and suggested that to study
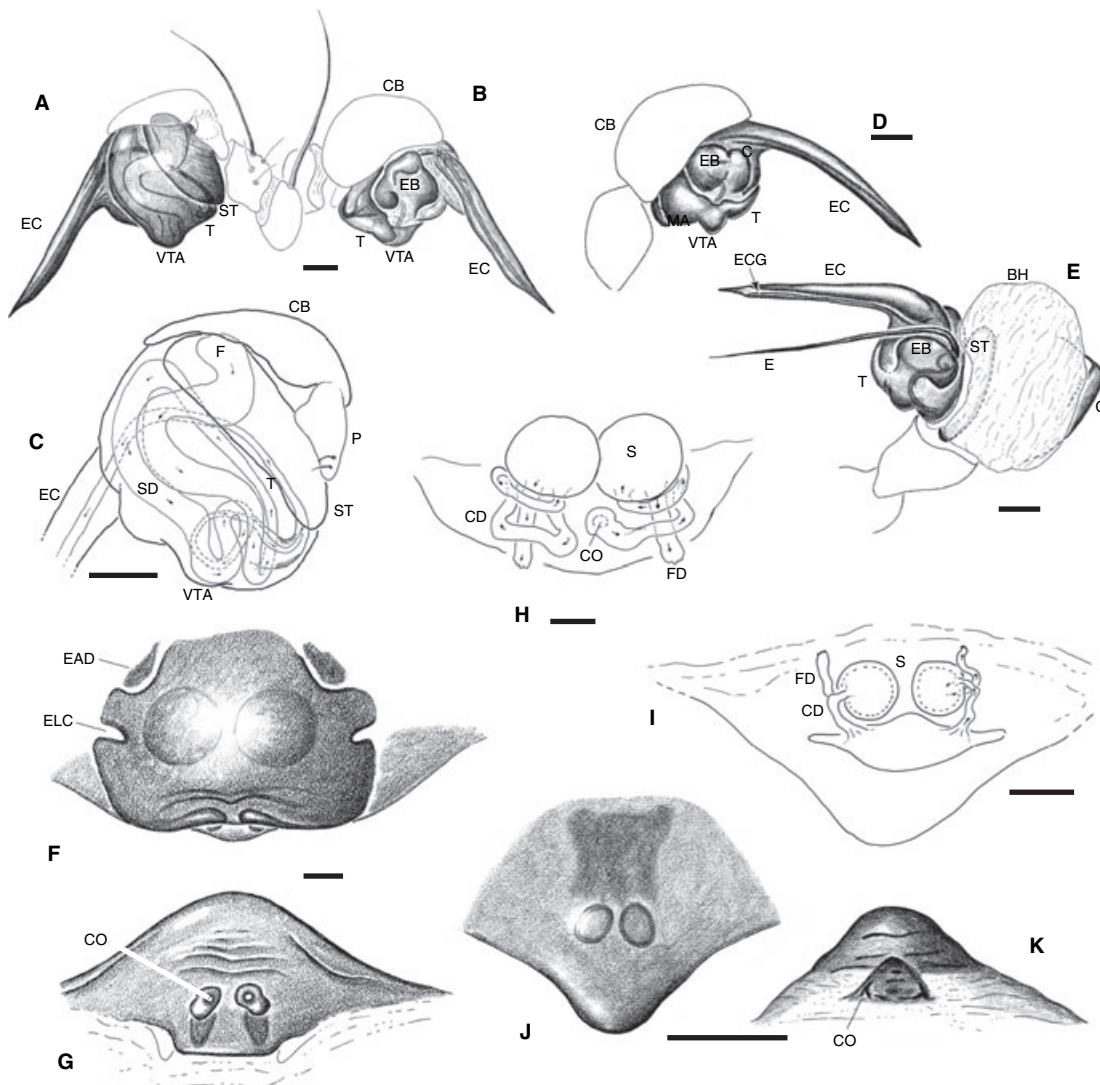
Fig. 10. *Clitaetra* genital morphology. (A–C) *Clitaetra irenae*, male left palp: (A) ectal; (B) mesal; (C) bulb transparent, showing sperm duct, ectal. (D, E) *Clitaetra episinoides*, male palp: (D) left palp, mesal; (E) right palp, expanded. (F–H) *Clitaetra irenae* epigynum: (F) ventral; (G) posterior; (H) cleared, dorsal. (I) *Clitaetra perroti*, dorsal epigynum (cleared). (J, K) *Clitaetra episinoides* epigynum: (J) ventral; (K) posterior. Scale bars = 0.1 mm, except J and K = 0.5 mm.

the evolution of SSD it is more appropriate to reconstruct male and female size as separate characters (see Discussion). Excluding the character from the analysis produces no changes in topology.

123 *Male dorsal abdomen*: (**0**) cuticle soft; (**1**) with scutum (Kuntner, 2005, fig. 24; Kuntner, 2006, fig. 17C–E). Male nephilids possess a scutum (Hormiga et al., 1995; Kuntner, 2005, 2006, 2007a). *Argiope argentata* and *Meta* males also exhibit hardened dorsum cuticle. Scutum is absent in male *Phonognatha* and *Deliochus*.

124 *Male lateral eyes*: (**0**) separate; (**1**) juxtaposed. See comments in Hormiga et al. (1995, character 3) and Agnarsson (2004, character 102).

125 *Male head region*: (**0**) narrower than in female (Fig. 14B,C); (**1**) head region at posterior eye row same proportion to cephalothorax as in female. In *Nephila*, *Nephilengys* and *Herennia* (but not *Clitaetra*) and various outgroups the prosoma is sexually dimorphic; the male head region is narrower (relative to prosoma width) than in the female (e.g., *Perilla*, Fig. 14B,C; see also Kuntner, 2005, fig. 1C,F; Kuntner, 2007a, fig. 1C,G).

126 *Male AME region*: (**0**) as in female; (**1**) advanced beyond clypeal margin (Kuntner, 2007a, fig. 1A,E). In *Nephila*, *Nephilengys* and *Herennia* (Kuntner, 2005, fig. 1A,E) (but not *Clitaetra*), and various outgroups the
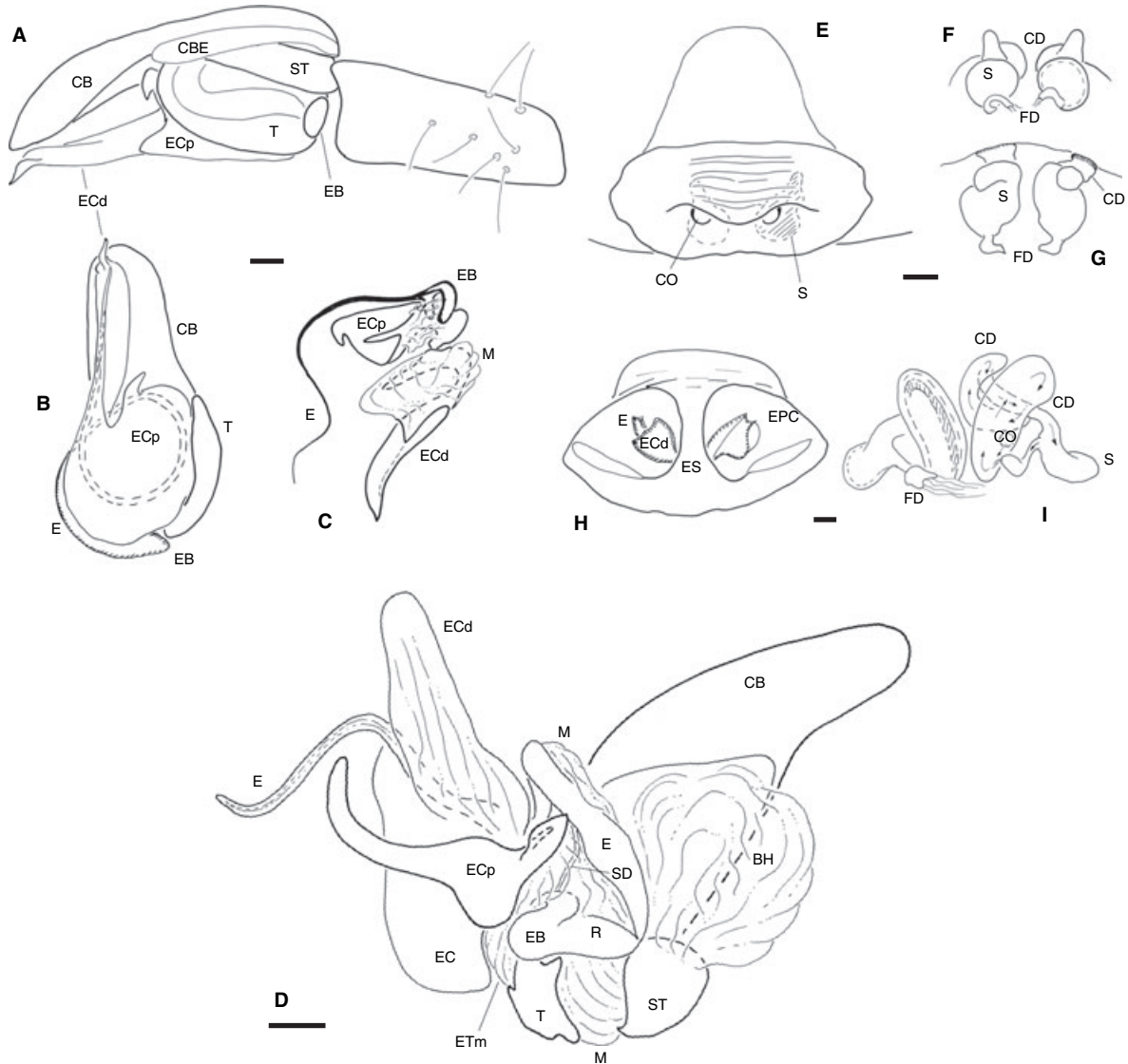
Fig. 11. *Phonognatha* genital morphology. (A–C) *Phonognatha graeffei*, male left palp: (A) ectal; (B) ventral; (C) embolic division separated from the tegulum. (D) *P. melanopyga*, male right palp, expanded, ventral. (E–G) *P. graeffei*, epigynum: (E) ventral; (F) cleared, dorsal; (G) cleared, frontal. (H, I) *P. melanopyga*, epigynum: (H) ventral; (I) cleared, dorsal. Scale bars = 0.1 mm.

male head region extends anteriorly further than in the female. The extreme condition is found in *Cyclosa*, where the angle of the clypeus is almost horizontal (Levi, 1999).

127 *Male* versus *female cheliceral size*: (**0**) same; (**1**) larger; (**2**) smaller. Corresponds to the Hormiga et al. (1995, character 15), but recoded in nephilids (not *Phonognatha*), where male chelicerae are relatively narrower (e.g., compare figs 1A with 1E in Kuntner, 2005, 2007a).

128 *Male cheliceral clasping spurs*: (**0**) absent; (**1**) present. Male chelicerae are equipped with clasping spurs in tetragnathines, e.g., *Tetragnatha* (Wiehle, 1963, figs 23 and 24A).

129 *Male paturon posterior surface*: (**0**) smooth; (**1**) with a tubercle. Diverse genera have a distinct tubercle on the male paturon posterior surface.

130 *Male coxa I hook*: (**0**) absent; (**1**) present. Scharff and Coddington (1997, character 33–34, fig. 27h) coded both the male coxal I hook and the part with which it interacts, the femur II groove. Because the two characters have the same distribution, only one is coded here.

131 *Male leg II tibial macrosetae*: (**0**) similar to those on tibia I; (**1**) stronger and more robust; (**2**) absent. No nephilid genera have modified setae.

132 *Male endite tooth*: (**0**) absent; (**1**) present (Scharff and Coddington, 1997, fig. 36). No nephilid genera
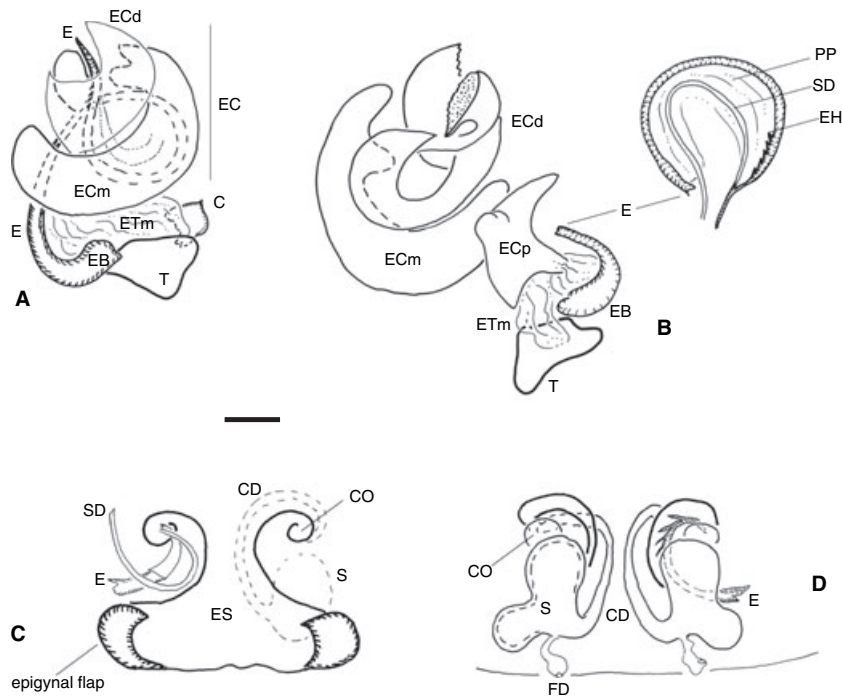
Fig. 12. *Deliochus* genital morphology. (A, B) *D. humilis* (L. Koch, 1867) (currently *Araneus humilis*) male palpal anatomy: (A) tegulum with distal sclerites dissected from subtegulum; (B) tegulum and embolic division dissected, embolus broken but both parts illustrated. (C, D) *D. zelivira*, epigynum: (C) ventral; (D) cleared, dorsal. Scale bar = 0.1 mm.

exhibit this typically araneine feature. *Opadometa* has a small round tubercle.

133 *Male endite depression*: (**0**) absent; (**1**) present. In *Acusilas* and *Phonognatha*, as well as in some "metines" the endites are medially depressed.

Male genital morphology

134 *Male palpal trochanter*: (**0**) short (twice the width or less); (**1**) long (more than twice the width). A long trochanter was described for *Leucauge mariana* by Eberhard and Huber (1998), who suggested the feature as a possible synapomorphy of *Leucauge* + tetragnathines. A long trochanter was also found in *Chrysometa*, *Azilia* and in undescribed Afrotropical *Meta* species (however, *Meta ovalis* exhibits the short condition).

135 *Male palpal femoral tubercle*: (**0**) absent; (**1**) present (Scharff and Coddington, 1997, fig. 4). No nephilid genera exhibit the feature, found in this analysis in the araneine genera except *Perilla*, and in uloborids (Opell, 1979, figs 6C–D and 7).

136 *Male palpal patella macrosetae*: (**0**) none; (**1**) one; (**2**) two. The character is variable within some *Nephila* species (e.g., *N. antipodiana*) and in *Araniella*, where a male can have two or three macrosetae.

137 *Male palpal tibia length*: (**0**) short (not exceeding 1.5 times its width; Fig. 7A,B); (**1**) long (exceeding 1.5 times its width; Fig. 11A). Nephilids (e.g., *Nephila*, Fig. 7A,B) and araneids (e.g., *Perilla*, Fig. 14G,H) have short palpal tibiae, but *Phonognatha* (Fig. 11A) and many tetragnathids have long tibiae.

138 *Cymbium*: (**0**) entire; (**1**) constricted. Corresponds to the character 20 in Hormiga et al. (1995), where the constricted cymbium served as a tetragnathine synapomorphy. In *Chrysometa* the cymbium is entire but its shape is peculiar (could be interpreted both ways).

139 *Cymbium length*: (**0**) short (less than 2 × width; Fig. 7A–C,F); (**1**) long (more than 2 × width; Fig. 11 A,B,D). All nephilids have a short cymbium (e.g., *Nephila*, Fig. 7A–C,F), while *Phonognatha* has it long (Fig. 11A,B,D).

140 *Cymbium orientation*: (**0**) dorsal; (**1**) mesal (Fig. 14C). In Hormiga et al. (1995, character 21, marked as 22), Scharff and Coddington (1997, character 5), and Griswold et al. (1998, character 2), the mesal cymbium orientation served as a synapomorphy of Araneidae (see also Levi, 1983, p. 251, fig. 8). However, the codings seem erroneous, as all araneoids plus *Uloborus* in this analysis exhibit that condition (e.g., *Clitaetra*, Kuntner, 2006, fig. 23A,B; *Nephilengys*,
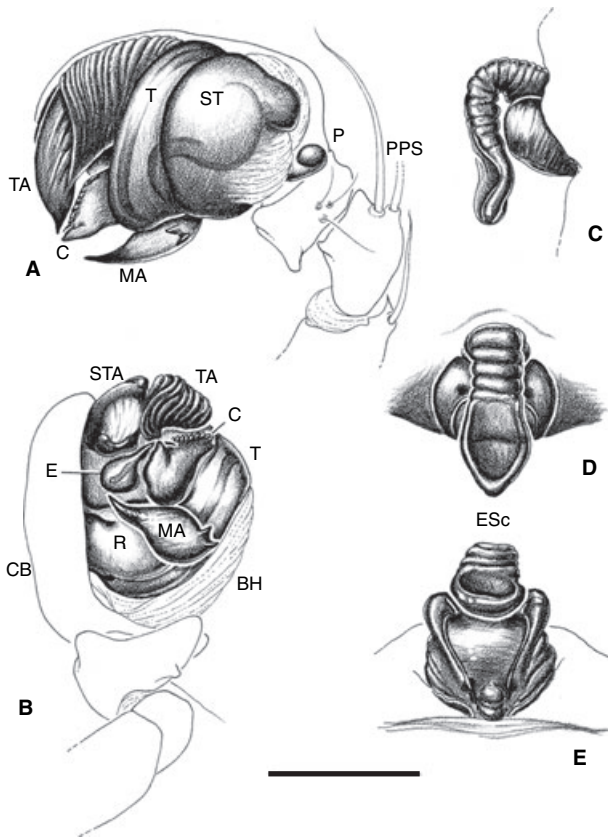
Fig. 13. *Singafrotypa* genital morphology. (A–E) *Singafrotypa acanthopus* (redrawn from Kuntner and Hormiga, 2002): (A) male left palp, ectal; (B) same, mesal; (C) epigynum, lateral; (D) same, ventral; (E) same, posterior. Scale bar = 0.5 mm.

Kuntner, 2007a, fig. 7A). "Metines" (*Meta*, *Metellina*, *Chrysometa*), though coded as dorsal in above studies, in fact exhibit an extreme mesal twist. In *Steatoda* the condition is even more extreme with the theridiid cymbium twist (Agnarsson, 2004). Only *Deinopis* was found to exhibit the dorsal condition.

141 *Cymbial ectal margin*: (**0**) sclerotized as cymbium; (**1**) transparent (Fig. 15E: CBE). The cymbial ectal margin is transparent in many nephilids, e.g., *Nephila ardentipes*, and outgroups (e.g., *Cyclosa*, Fig. 15E).

142 *Cymbial basal process (CBP)*: (**0**) absent; (**1**) present (Figs 18A–D and 19E). Kuntner and Alvarez-Padilla (2006) renamed the paracymbium secondary process from Hormiga et al. (1995, character 25) to better describe the topology of this apophysis. Levi (1986, p. 100) termed the feature an apophysis on the cymbium in *Chrysometa*. CBP is present in *Meta* (Fig. 19E), *Metellina*, *Opadometa* (Fig. 18A–D) and *Chrysometa*, but also in *Sancus* (Kuntner and Alvarez-Padilla, 2006) and a number of other tetragnathids. The feature termed paracymbium in *Perilla* (Kuntner, 2002, fig. 6P) was mislabeled and seems to be a CBP

(Fig. 14G) on topological considerations (in addition to the CBP, *Perilla* has a hook-shaped paracymbium). The pimoid cymbial sclerite (Hormiga, 1994a) differs in topology and morphology to the CBP (Kuntner and Alvarez-Padilla, 2006).

143 *CBP shape*: (**0**) simple projection (Fig. 18A–D); (**1**) complex, with further apophyses (Fig. 19E). In *Meta* and *Metellina*, the CBP is complex and possesses further apophyses (see also Hormiga et al., 1995, fig. 6A–E); these cannot be homologous to the apophyses on the paracymbium (see below). The CBP in *Chrysometa* examined here was simple, but other species may exhibit complex morphologies (see Hormiga et al., 1995, fig. 6G).

144 *Paracymbium (P)*: (**0**) absent (Fig. 16A); (**1**) present (Figs 7A, 8A, 9A and 10A). The paracymbium is present in most araneoids (a synapomorphy of the clade). *Nephila*, *Nephilengys*, *Clitaetra* and *Herennia* all possess a squat paracymbium (see below). *Caerostris* lacks the feature (Fig. 16A). In *Phonognatha*, Hormiga et al. (1995) described the paracymbium as the ectal cymbial edge (Fig. 8B,C,F). Although such coding is followed here (for *P. graeffei*), the feature is potentially susceptible to conjunction with the cymbial transparent edge (Fig. 11A: CBE), found also in some *Deliochus* species, which also possess a paracymbium. *Meta ovalis* also has a transparent cymbial edge as well as an elaborate paracymbium. *Phonognatha melanopyga* lacks a paracymbium. Only some *Deliochus* species have a paracymbium, so the terminal here is coded as polymorphic. The morphology of the *Deliochus* paracymbium, however, differs from any taxon in this analysis. Because *Deliochus* is a single terminal, its variant morphology provides no grouping information and is therefore scored as inapplicable for all dependent paracymbium characters. The nephilid paracymbium is uniformly a squat sclerite with a membranous base, a number of proximal setae, and with a folding of the distal margin (this invagination may extend into a prong): *Clitaetra*, Fig. 10(A,C), see also Kuntner (2006, figs 2, 5D,F, 8C, 11C,D, 13A,D and 18A,B); *Nephilengys*, Fig. 8(A,C,D,F,H), see also Kuntner (2007a, figs 9A,C, 14F and 23A,E); *Herennia*, Fig. 9(A,E), see also Kuntner (2005, figs 12A,F, 18A and 30A); *Nephila*, Fig. 7(A,F). The fold of the paracymbium margin hooks the embolic apophysis during palpal copulatory expansion, documented in *Nephilengys borbonica* (Kuntner, 2007a, fig. 14C). Hormiga et al. (1995, character 22) coded the absence of and morphological variation within the paracymbium as one multistate character, whereas here the presence or absence is coded separately to test for homology, as in Griswold et al. (1998, character 7) and Agnarsson (2004, character 29).

145 *Paracymbium attachment*: (**0**) integral; (**1**) intersegmental; (**2**) articulated.
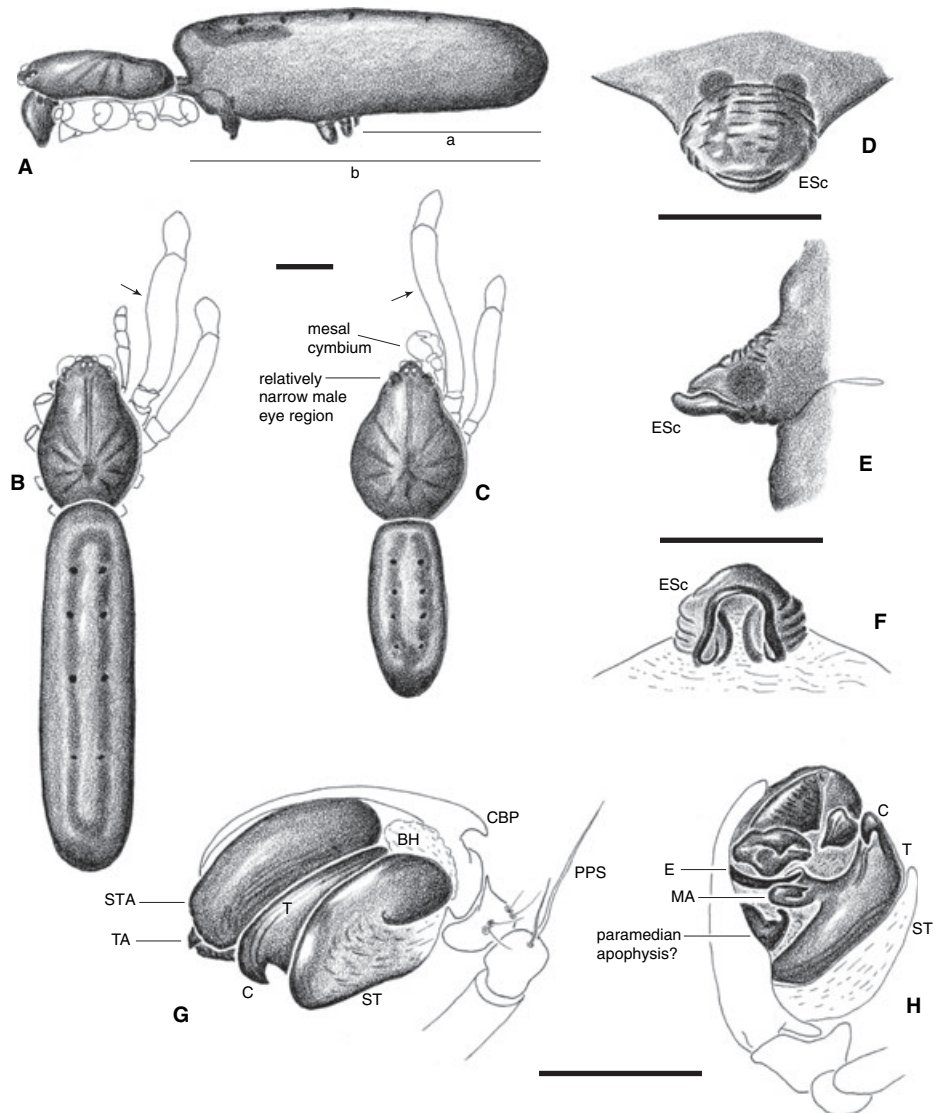
Fig. 14. *Perilla* somatic and genital morphology. (A–H) *Perilla teres*, redrawn from Kuntner (2002), with new homologies: (A) female, lateral; (B) female, dorsal; (C) male, dorsal; (D–F) epigynum; (D) frontal; (E) lateral; (F) caudal; (G, H) male left palp; (G) lateral; (H) mesal. Scale bars = 0.5 mm, except A–C = 1.0 mm.

146 *Paracymbial base sclerotization*: (**0**) like cymbium; (**1**) less sclerotized.

147 *Paracymbium morphology*: (**0**) short, hook-shaped (Fig. 13A); (**1**) longer than wide, finger-like (Fig. 19B); (**2**) flat, roughly rectangular (Figs 7A, 8A, 9A and 10A); (**3**) U-shaped; (**4**) flat, roughly triangular; (**5**) "*Phonognatha* condition" (Fig. 11A: CBE). Paracymbial shapes are frustratingly difficult to code (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998). Hormiga et al. (1995, character 24) coded the paracymbial diversity of their taxon sample into seven states, of which four were autapomorphies. They coded "metine" diversity uniformly as short and more or less hook-shaped (the same as araneids), which clearly does not accommodate known metine diversity. Given the greater diversity of tetragnathids in this matrix, it seems better to recognize that most tetragnathid paracymbia are indeed longer than wide, and thus are coded as "longer than wide and finger-like" (e.g., *Leucauge*, Fig. 19B), leaving the "hook-shaped" to apply more strictly to typical araneids (e.g., *Singafrotypa*, Fig. 13A; *Cyclosa*, Fig. 15E; *Acusilas*, Fig. 17C). The autapomorphic description of *Nesticus* (see Agnarsson, 2004, fig. 2A,B) in Hormiga et al. (1995) is discarded and it is recoded as "U-shaped", which is also applied to *Linyphia*, even though it bears apophyses. It could be coded as longer than wide. This approach eliminates
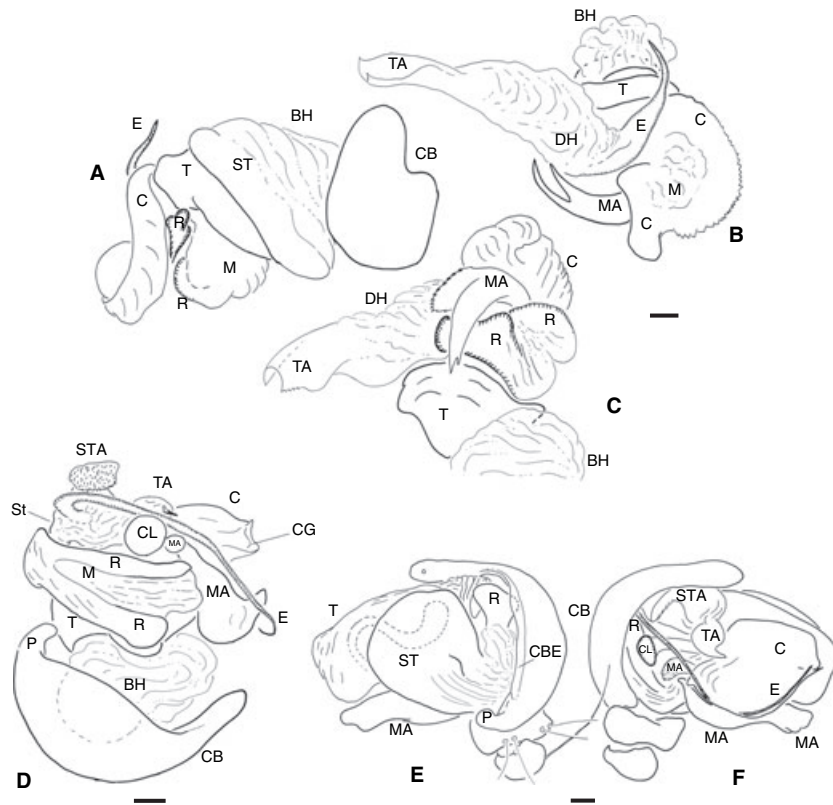
Fig. 15. Araneine genital morphology. (A–C) *Araniella alpica*, male left palp, expanded: (A) lateral, showing sclerite origin on tegulum; (B) apical; (C) caudal. (D, F) *Cyclosa conica*, male left palp: (D) expanded; (E) ectal; (F) mesal. Scale bars = 0.1 mm.

autapomorphic states, but may not, in the end, yield a clearer picture of paracymbial evolution. Agnarsson (2004, character 30) adopted an "exemplar approach" and named the different paracymbium morphologies after the taxa possessing them.

148 *Paracymbium edge*: (**0**) glabrous (Fig. 13A); (**1**) with setae (Fig. 7A,F). The paracymbium is glabrous in araneids (e.g., *Singafrotypa*, Fig. 13A; *Cyclosa*, Fig. 15E), but has setae in nephilids and tetragnathids (e.g., *Nephila*, Fig. 7A,F, *Nephilengys*, see Kuntner, 2007a, fig. 9A,C). If present, the paracymbium of *Deliochus* and *Phonognatha* is glabrous.

149 *Anterior paracymbial apophysis (APA)*: (**0**) absent; (**1**) present. Hormiga et al. (1995, character 26) coded the diversity of paracymbial apophyses as a multistate character. It is here broken in two characters. An anterior apophysis on paracymbium is found in certain tetragnathids (e.g., *Tetragnatha*, see Hormiga et al., 1995, fig. 7C), but not in *Meta* and *Metellina*, where the apophyses are on the anterior CBP margin. The condition in *Nesticus*, coded in Hormiga et al. (1995) as "several apophyses" is here considered putatively homologous to the single apophysis.

150 *Paracymbial margin fold*: (**0**) absent; (**1**) present (Fig. 8F). Contrary to Hormiga et al. (1995, character

26) who found a fold in *Phonognatha graeffei* (Fig. 8B,C,F) similar to the nephilid fold (see Kuntner, 2007a, fig. 9C), this analysis considers the fold absent in *P. graeffei*. If coded as present, the same trees result (one step longer), which argues that a *Phonognatha* PC "fold" is not homologous to the nephilid one.

151 *Paracymbium apically*: (**0**) rounded; (**1**) with a prong (Fig. 7A). An apical prong-like extension of the paracymbial distal fold is found in all nephilids but *Herennia* (see next character).

152 *Paracymbial apical prong*: (**0**) short (< one third PC length); (**1**) long (> one-third PC length). While in most nephilids the apical prong is short (e.g., *Clitaetra*, see Kuntner, 2006, figs 2A,C,D and 5F), a long prong (more than a third of paracymbium length) is found in *Nephila constricta* and *N. pilipes*.

153 *Tegulum in ectal view*: (**0**) same size as or larger than subtegulum (Fig. 7A); (**1**) smaller than subtegulum (Fig. 13A). In ectal view, the tegulum in all nephilids and most tetragnathids (not *Meta*; see Fig. 19E) is larger than the subtegulum (e.g., *Nephila*, Fig. 7A; *Phonognatha*, Fig. 11A; *Opadometa*, Fig. 18A). The opposite is true for araneids (not *Acusilas*) (e.g., *Singafrotypa*, Fig. 13A; *Perilla*, Fig. 14G; *Cyclosa*, Fig. 15E; *Caerostris*, Fig. 16A).
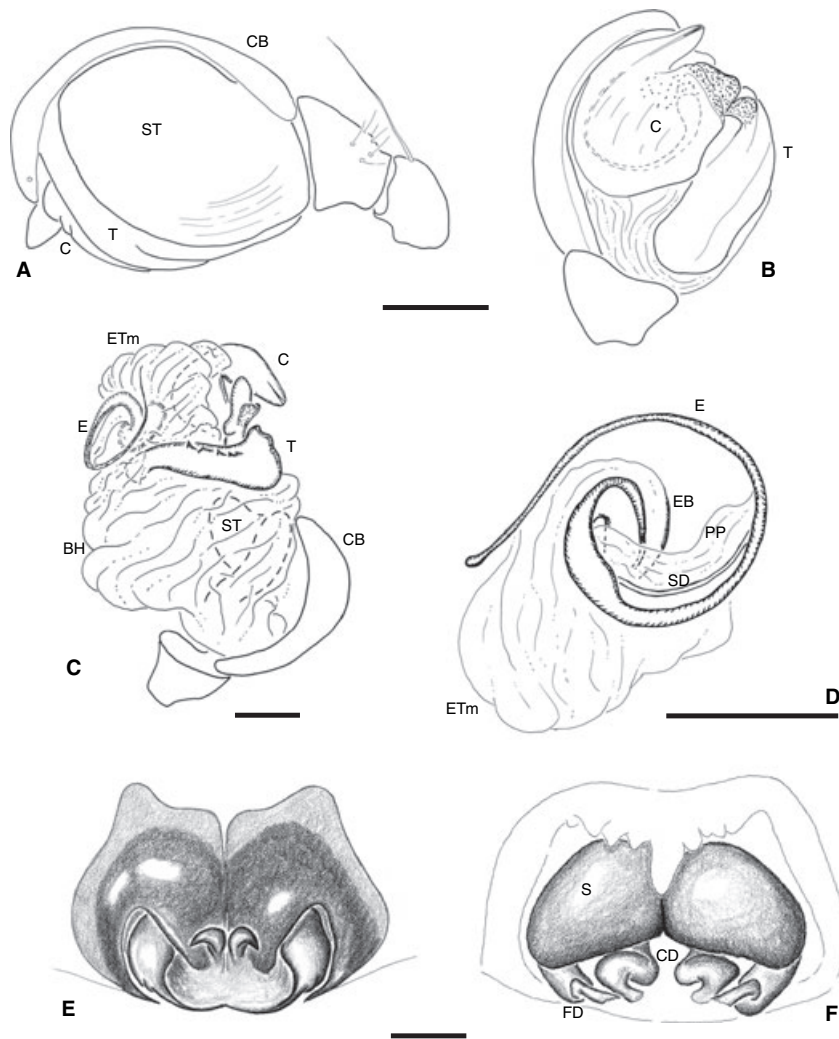
Fig. 16. *Caerostris* genital morphology (undescribed species from Madagascar). (A, B) Male left palp: (A) ectal (note paracymbium absence); (B) mesal. (C) Male right palp, expanded. (D) Embolic division, dissected, apical (note sperm duct within pars pendula, entering embolus mid-apically; note spatulate embolus tip). (E, F) Epigynum: (E) ventral; (F) cleared, dorsal. Scale bars = 0.5 mm.

154 *Sperm reservoir*: (**0**) normal; (**1**) enlarged. Corresponds to character 28 in Hormiga et al. (1995) with identical coding of the enlarged state. All nephilids have a normal sized reservoir (e.g., *Nephila*, Fig. 7H; *Nephilengys*, Fig. 8C; *Herennia*, Fig. 9E; *Clitaetra*, Fig. 10C).

155 *Reservoir course*: (**0**) spiraled; (**1**) with a switchback. Sperm reservoir (= sperm duct) takes taxon-specific turns and twists within the tegulum and these have a potential in phylogenetic homology assessments (Coddington, 1990; Hormiga et al., 1995). The nephilid sperm reservoir exhibits numerous switchbacks (e.g., *Nephila*, Fig. 7H; *Nephilengys*, Fig. 8C; *Herennia*, Fig. 9E; *Clitaetra*, Fig. 10C), but with the exception of the following character they are difficult to homologize.

156 *Ventral tegular switchback*: (**0**) single (Fig. 9E); (**1**) double (Fig. 7B,H and 8C). The ventral tegular switchback is either single (*Herennia*, *Clitaetra*) or double (one following the other), found in *Nephilengys* and *Nephila*. The double switchback can be easily observed in mesal palpal drawings of *Nephila* (Fig. 7B).

157 *Ejaculatory duct*: (**0**) entirely within the sclerotized portion of the embolus (Fig. 7C-E,G); (**1**) basally contained in the pars pendula (Fig. 12B,C). In all nephilids the ejaculatory duct is entirely within the sclerotized portion of the embolus (e.g., *Nephila*, Fig. 7C–E; *Nephilengys*, Fig. 8J; *Herennia*, Fig. 9C–F; *Clitaetra*, Fig. 10C). In diverse taxa the ejaculatory duct enters the sclerotized embolus only distally, and prior to
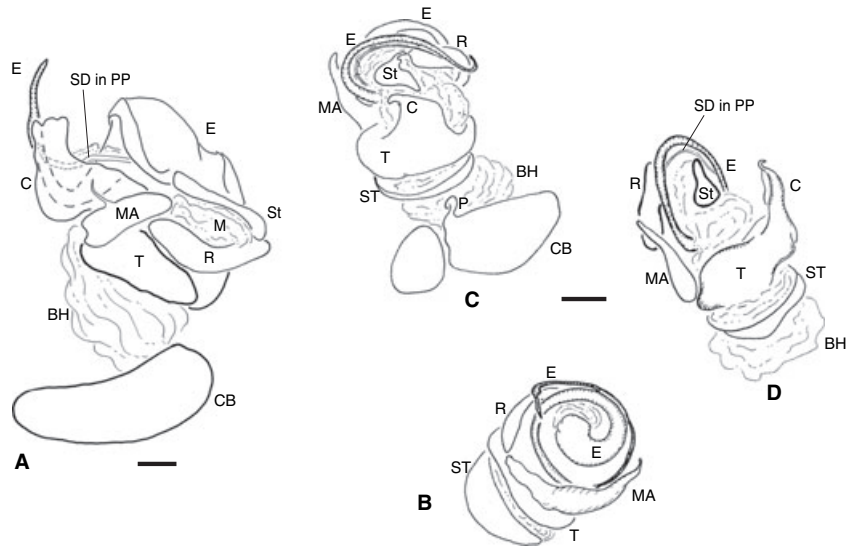
Fig. 17. Araneid genital morphology. (A) *Argiope argentata*, male right palp, expanded. (B–D) *Acusilas coccineus,* male left palp, expanded: (B) apical; (C) ectal; (D) mesal. Scale bars = 0.1 mm.
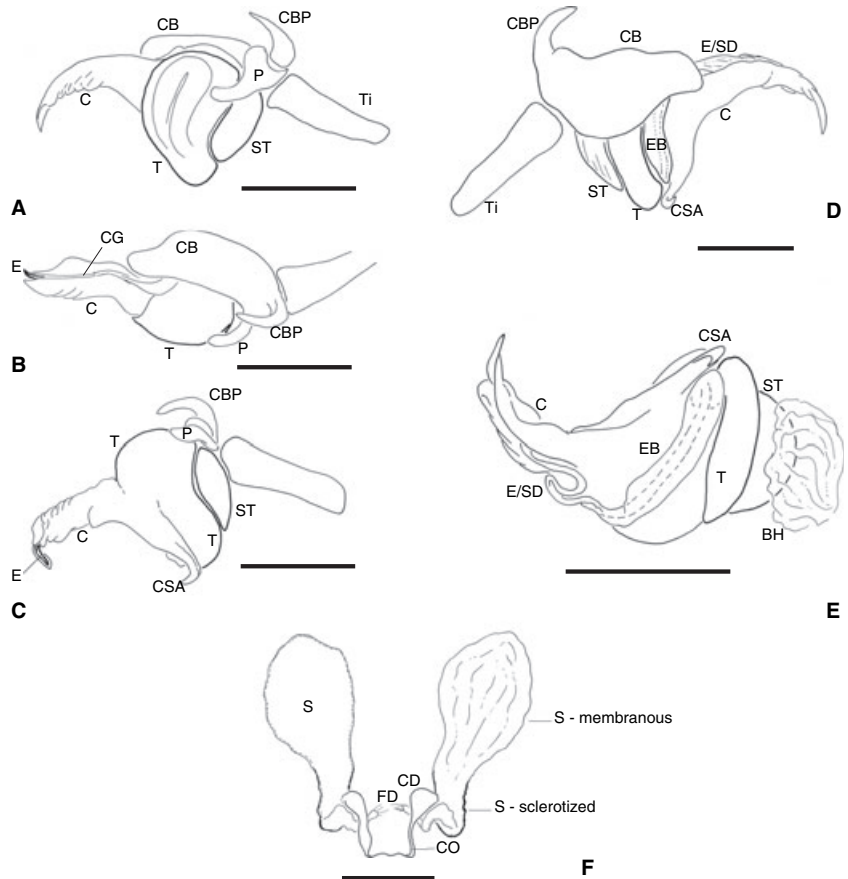
Fig. 18. *Opadometa* genital morphology (*O. nr. grata*, Papua NG). (A–F) male left palp: (A) ectal; (B) dorsal; (C) ecto-ventral; (D) mesal; (E) expanded, mesal; (F) epigynum, cleared, ventral. Scale bars = 0.5 mm.
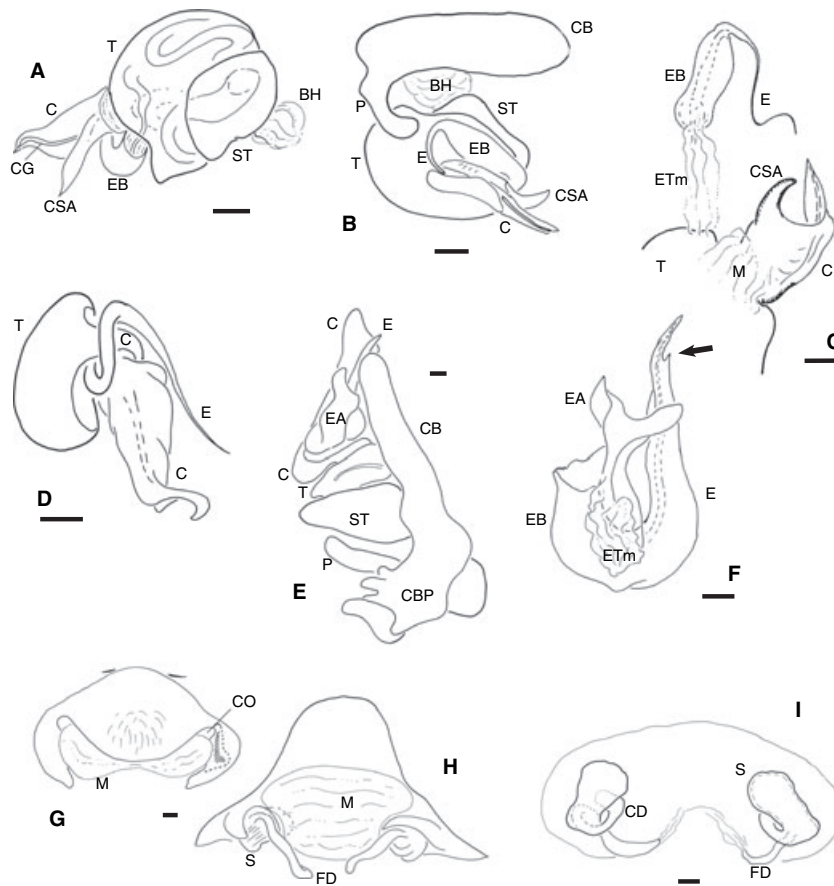
Fig. 19. Tetragnathid genital morphology. (A–C) *Leucauge venusta*, male palp dissection: (A) left palp, mesal; (B) right palp, ectal; (C) right tegulum with distal sclerites, embolus detached (note membranous connection of embolus and conductor with tegulum, but not with each other). (D) *Tetragnatha obtusa*, male left palp dissection, tegulum with distal sclerites. (E, F) *Meta ovalis*, male left palp: (E) partially expanded, ectal; (F) embolus dissected from tegulum (note subdistal embolic notch, arrow). (G–I) *Meta ovalis*, epigynum: (G) ventral; (H) posterior; (I) cleared, dorsal. Scale bars = 0.1 mm.

that runs through the more or less membranous pars pendula (e.g., *Deliochus*, Fig. 12B,C; *Caerostris*, Fig. 16D; *Argiope*, Fig. 17A; *Acusilas*, Fig. 17C,D; also *Tetragnatha*, *Singafrotypa*). A similar condition was found in *Phonognatha melanopyga* (Fig. 11D), but not *P. graeffei* (Fig. 11C). The condition also differs between the *Argiope* species.

158 *Median apophysis (MA)*: (**0**) absent; (**1**) present (Figs 13A,B, 15B–F and 17A–D). Coddington (1990, character 9), Hormiga et al. (1995, character 30), Scharff and Coddington (1997, character 10) and Griswold et al. (1998, p. 16) tended to regard single, non-embolic tegular apophyses as conductors, so that all resulting homoplasy was allocated to the median apophysis (Griswold et al., 1998). Agnarsson (2004, character 71) used topological similarity to homologize sclerites in theridiids, which approach is followed here. The MA is the sclerite arising from the mesal tegulum, to which it usually attaches via a membrane (Figs 13A,B, 15B–F and 17A–D). Scharff and

Coddington (1997) coded the single tegular sclerite in *Caerostris* (they examined *C. sexcuspidata* and *C. vinsoni*) as an MA, but in our exemplar (undescribed species from Madagascar, Fig. 16A–C) the structure is topologically more similar to a conductor. Kuntner (2002, fig. 5) labeled the MA in *Perilla* (Fig. 14H) as a conductor, but the sclerite labeled as an MA in that paper is probably homologous to the sclerite in *Chorizopes* that Scharff and Coddington (1997, character 18) labeled as a paramedian apophysis. The tegulum has a small apophysis in *Clitaetra* (Fig. 10A–D: VTA) and *Nephilengys* (Fig. 8B,D,E,I: MTA), which are not interpreted as the MA (see next characters) because topology differs. Thus, the MA is coded absent in all nephilids, *Phonognatha* and *Deliochus* as well as all tetragnathids and *Linyphia*. The deinopid tegular apophysis (Fig. 20A) could be interpreted as the MA (as in Davies, 1988, fig. 6), as it is separated from the tegulum by an extensive membrane. However, following the topology criterion, it is interpreted as the conductor
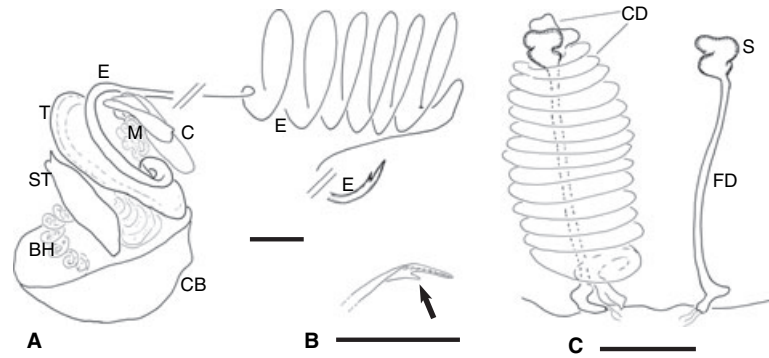
Fig. 20. *Deinopis* genital morphology (undescribed species from Guyana). (A–C) Male left palp, expanded and dissected: (A) mesal, embolus coiling, schematic; (B) embolus tip, ectal (note subdistal embolic notch, arrow); (C) epigynum, cleared, dorsal (right copulatory duct omitted). Scale bars = 0.5 mm.

(as in Coddington, 1990; Griswold et al., 1998) because it arises from the apical tegulum.

159 *Median apophysis*: (**0**) without sperm duct; (**1**) with a loop of the sperm duct. The MA only contains a loop of the sperm duct in Theridiidae and Nesticidae (Agnarsson, 2004, character 72).

160 *Median apophysis thread-like spur*: (**0**) absent; (**1**) present (Fig. 17A). Corresponds to the character 12 of Scharff and Coddington (1997, fig. 13, arrow). The median apophysis of *Argiope* has a thin spur (Fig. 17A; Levi, 1968, figs 56 and 135).

161 *Apical tegular apophysis (ATA)*: (**0**) absent; (**1**) present (Fig. 9A,H). *Herennia* species possess an apical tegular apophysis, which is partly membranous (Kuntner, 2005, fig. 13). See Discussion for the possible homology with the conductor.

162 *Ventral tegular apophysis (VTA)*: (**0**) absent; (**1**) present (Fig. 10A-D). *Clitaetra* species possess a ventral tegular bump (Kuntner, 2006, figs 5D,E, 11C–E, 18A–D and 24A,C,E,F). See MA (**158**) for alternative interpretation.

163 *Mesal tegular apophysis (MTA)*: (**0**) absent; (**1**) present (Fig. 8B,D,E,I). *Nephilengys* species possess a small apophysis on the mesal tegulum facing the embolus base (Kuntner, 2007a, fig. 9A). The feature is pronounced in *N. cruentata* and *N. borbonica*, and less so in *N. malabarensis* and *N. papuana*. See MA (**158**) for alternative interpretation.

164 *Theridiid tegular apophysis (TTA)*: (**0**) absent; (**1**) present. The TTA is present in Theridiidae and Nesticidae (Coddington, 1990; Hormiga et al., 1995, character 39; Agnarsson, 2004, character 80), and also Synotaxidae (Agnarsson, 2003, 2004).

165 *Conductor (C)*: (**0**) present (Fig. 19A-E); (**1**) absent. Structures coded as the conductor in Coddington (1990), Hormiga et al. (1995), Scharff and Coddington (1997) and Griswold et al. (1998) differ dramatically in their topology, shape and presumed function. Agnarsson (2004, character 62) considered the

conductor to be a sclerite that is an outgrowth of the tegulum. In theridiids it is completely fused to the tegulum, while the median apophysis is flexibly attached (Agnarsson, 2004). This study follows Agnarsson in treating the conductor as a tegular apophysis, but finds more diversity in "conductor" morphology among the taxa treated. The main conclusion (but see Results for alternative coding) is that the nephilid "conductor" (*sensu* Hormiga et al., 1995) in *Phonognatha*, *Clitaetra*, *Nephilengys*, *Herennia* and *Nephila* is actually part of the embolic division. Closely associated with both the tegulum and the embolus (and connected to both via the ETm) it wraps, protects and "conducts" the embolus, but is not a tegular apophysis. Rather, it remains connected to the embolus in dissections. It is thus termed the *embolic conductor* (see **171**). Ontogenies of the tegular conductor and the embolic division are different (Coddington, 1990). In tetragnathids the conductor is an outgrowth of the tegulum (e.g., *Meta*, Fig. 19E; *Leucauge*, Fig. 19A–C; *Opadometa*, Fig. 18A–E; *Tetragnatha*, Fig. 19D; see also *Azilia*, *Dolichognatha* in Hormiga et al., 1995, fig. 13). It may have a membranous base (e.g., *Leucauge*) or is a simple continuation of the tegulum (e.g., *Meta*). The araneids examined here also have a tegular conductor (*Acusilas*, Fig. 17B–D; *Caerostris*, Fig. 16A–C; *Argiope*, Fig. 17A), which also may have a membranous base (*Araneus*, see Scharff and Coddington, 1997, fig. 8). Agnarsson (2004) coded the nesticid conductor as present in *Nesticus* but absent in *Eidmanella*; the ancestral state for the family may be equivocal.

166 *Conductor size*: (**0**) small (less than half bulb volume); (**1**) large (more than half bulb volume).

167 *Conductor form*: (**0**) rounded; (**1**) grooved for embolus. In various taxa the conductor is grooved to accommodate the embolus: *Cyclosa*, Fig. 15(F); *Caerostris*, Fig. 16(B,C); *Opadometa*, Fig. 18(B–E); *Leucauge*, Fig. 19(A,B). Also described by Agnarsson (2004, character 64).

168 *Conductor and embolus association*: (**0**) separate (Figs 12A and 19E); (**1**) embolus enclosed in conductor (Fig. 18A–E); (**2**) embolus and conductor spiral.

169 *Conductor secondary apophysis*: (**0**) absent; (**1**) present (Fig. 18C–E). The conductor has a basal secondary apophysis (CSA) in *Opadometa* (Fig. 18C–E) and *Leucauge* (Fig. 19A–C).

170 *Conductor lobe (CL)*: (**0**) absent; (**1**) present. *Araniella* and *Cyclosa* possess a lobe on the conductor (Fig. 15D,F; Scharff and Coddington, 1997, character 8).

171 *Embolic conductor (EC)*: (**0**) absent; (**1**) present (Figs 7A–E, 8A,B,D,E,H–J, 11A–D and 12A,B). *Nephila*, *Nephilengys*, *Herennia*, *Clitaetra*, *Phonognatha* and *Deliochus* possess one or more sclerites of the embolic division, separated from the EB and T via the same membrane. The sclerite(s) function(s) as a conductor, enclosing the embolus. In *Nephila* (Fig. 7A–E) and *Clitaetra* (Fig. 10A,B,D,E, see also Kuntner, 2006, figs 2A,B, 5D,E, 11C,E,F, 18, 20E,F and 24A,C–F) the sclerite is simple, long and finger-like, with a groove in which the embolus sits fully wrapped. Though always slightly membranous proximally, it is a single sclerite. In *Nephilengys* (Fig. 8A,B,D,E,H–J, see also Kuntner, 2007a, figs 9A,B, 10, 23A–C, 27 and 32C,D) and *Herennia* (Fig. 9A–C,E–H, see also Kuntner, 2005, figs 12A–E, 13, 17B,C, 18A,B and 30) the sclerite is complex, wide and sigmoidal, with membranous and sclerotized parts (distally with ridged edges), though functioning as one large sclerite. In *Phonognatha* (Fig. 11A–D, see also Hormiga et al., 1995, fig. 8) there are two sclerites, one proximal to the embolus base and one distal, both divided by a membrane. In *Deliochus* (Fig. 12A,B) there are three sclerites. If divided (*Phonognatha*, *Deliochus*), the sclerites function as one large conductor; a dissection is necessary to establish the divisions.

172 *EC membrane*: (**0**) absent; (**1**) present (Fig. 8A,B,D,E,H–J). An additional distal EC membrane, distinct from the one separating EC from EB, is present in *Nephilengys* (Fig. 8A,B,D,E,H–J) and *Herennia* (Fig. 9A–C,F–H). Also coded as present in *Phonognatha* and *Deliochus*, where the EC is subdivided into sclerites via this membrane (see above; Figs 11A–D and 12A,B).

173 *EC shape*: (**0**) complex (Fig. 8A,B,D,E,H–J and 9A–C,E–H); (**1**) finger-like (Figs 7A,B and 10A,B,D,E).

174 *Finger-like EC*: (**0**) short; (**1**) long. Short is arbitrarily defined as a ratio of less than 0.7 between the EC distal to the notch and total EC length. Long, ratio greater than or equal to 0.7.

175 *EC (division)*: (**0**) entire; (**1**) subdivided into two or more sclerites (see above; Figs 11A–D and 12A,B).

176 *Distal EC flap*: (**0**) absent; (**1**) present (Fig. 9 A,B). In most *Herennia* species the EC has a distinct distal flap (Fig. 9A,B; Kuntner, 2005, figs 12 and 13).

177 *EC edge*: (**0**) smooth (Figs 7A,B and 10A,B,D,E); (**1**) ridged (Fig. 8A,B,D,E,H,I and 9A–C).

178 *EC curvature*: (**0**) more/less straight (Fig. 10A,B); (**1**) sigmoidal (Fig. 9A,B); (**2**) bent distally. Modified from character 32 in Hormiga et al., 1995), which described the conductor. The embolic conductor can be sigmoidal in some *Nephila* species and especially in *Herennia* (Fig. 9A,B), more or less straight (e.g., Fig. 10-A,B), or straight and distally bent (e.g., *Nephila clavipes*).

179 *EC tip*: (**0**) straight; (**1**) hooked (Fig. 11A,B). EC tip has a distal hook in *Nephila fenestrata* and *Phonognatha graeffei* (Fig. 11A,B).

180 *EC subdistal protuberance*: (**0**) absent; (**1**) present. The EC of *Nephila plumipes* has a triangular subdistal protuberance (Harvey et al., 2007; Kuntner, in preparation), and that of *N. fenestrata* has a rounded protuberance (shape varies).

181 *Embolus (E) length*: (**0**) long (> 2 × cymbium length); (**1**) medium (0.5-1.5 cymbium length); (**2**) short (< 1/2 cymbium length). The embolus is an extremely long sclerite in nephilids (e.g., *Nephila*, Fig. 7C,G) and certain outgroups, and very short in certain araneids (e.g., *Singafrotypa*, Fig. 13B).

182 *Embolus form*: (**0**) thin (Fig. 10E); (**1**) thick (Fig. 19F); (**2**) filiform (Fig. 7C,G). Embolus is thick in, e.g., *Meta* (Fig. 19F), *Araneus*, *Singafrotypa* (Fig. 13B), thin in, e.g., *Tetragnatha* (Fig. 19D), *Clitaetra* (Fig. 10E), *Herennia* (Fig. 9C,D,F–H) and *Nephilengys* (Fig. 8D,E,G,J) and some *Nephila* (Fig. 7E), and filiform (extremely thin) in most *Nephila* species (Fig. 7C,G). Quantification of this somewhat subjective observation seems impossible; the character was coded by comparing images.

183 *Embolus sclerotization*: (**0**) normal, sclerotized (Fig. 7C,G); (**1**) unsclerotized (Fig. 18E). While the embolus in nephilids and most outgroups is always fully sclerotized, in *Opadometa* it is not (Fig. 18E), and in *Leucauge* the sclerotization is slight (Fig. 19A–C).

184 *Embolus-tegulum orientation*: (**0**) parallel; (**1**) perpendicular (Fig. 7A,B). Corresponds to character 33 in Hormiga et al. (1995), there it is a synapomorphy of higher nephilids, and here a family synapomorphy. In nephilids the embolus (in its natural position within embolic conductor) is positioned roughly perpendicular to the bulb axis (e.g., Fig. 7A,B).

185 *Embolus-tegulum membrane (ETm)*: (**0**) absent; (**1**) present (Fig. 7C–E,G). All nephilids and some outgroups have an extensive membrane between the tegulum and the embolic division (consisting of the embolus and the embolic conductor): *Nephila*, Fig. 7(C–E,G); *Nephilengys*, Fig. 8(E,J); *Herennia*, Fig. 9(C,F–H); *Clitaetra*, Fig. 10(B); *Phonognatha*, Fig. 11(D); *Deliochus*, Fig. 12(A,B). Such a membrane was not observed in *Opadometa*. Corresponds to the character 38 in Hormiga et al. (1995), who coded the membrane between the radix and the tegulum in araneids as homologous to that between the E and T in nephilids (followed here). Hormiga et al. (1995) suggest that this

membrane could be considered homologous to the linyphiid column—thus, *Linyphia* score is present. (Coding it absent produces no change in topology but requires one more step on the cladogram.)

186 *Embolus base*: (**0**) thin; (**1**) enlarged (= radix). The embolus base is large in nephilids (e.g., *Nephila*, Fig. 7C–E,G; *Nephilengys*, Fig. 8D,E,G; *Herennia*, Fig. 9C,F–H; *Clitaetra*, Fig. 10B,D,E), tetragnathids (Figs 18D,E and 19B,C,E; see also Hormiga et al., 1995, fig. 13) and most araneids where it is termed the radix if separated from the embolus proper (Coddington, 1990, character 22; Hormiga et al., 1995, character 34; Scharff and Coddington, 1997, character 16; Griswold et al., 1998, character 20): *Singafrotypa*, Fig. 13(B); *Araniella*, Fig. 15(A,C); *Cyclosa*, Fig. 15(D-F); *Argiope*, Fig. 17(A); *Acusilas*, Fig. 17(B-D). This primary homology (embolus base = radix) is based on the similar topology (mid-mesal on the tegulum), similar morphology (round sclerite with membranous base = ET membrane), and function [see *Nephilengys borbonica*, in Kuntner, 2007a, fig. 14C, where the EB interacts with the paracymbium; similarly, the radix hooks to the paracymbium in the araneid *Mangora* (Grasshoff, 1973)]. Contrary to nephilids and tetragnathids, the araneid radix is separated from the embolus by a membrane (*189*).

187 *Embolus base distal part*: (**0**) smooth; (**1**) denticulated (Kuntner, 2006, fig. 24D,E, arrow). In some *Clitaetra* species the EB is distally denticulated.

188 *Embolic apophysis*: (**0**) absent; (**1**) present (Fig. 7C–E,G). Previous studies have homologized the ''metine embolic apophysis'' or MEA (Coddington, 1990; character 37 in Hormiga et al., 1995) found in various tetragnathid genera. However, most *Nephila*, *Nephilengys* and some *Herennia* (but no *Clitaetra*, *Phonognatha* or *Deliochus* species) also possess an apophysis on the embolus base (*Nephila*, Fig. 7C–E,G; *Nephilengys*, Fig. 8D,E,G,J; *Herennia*, Fig. 9C,F–H), which hooks with the paracymbium during the copulatory palpal twist (Kuntner, 2007a, fig. 14C). While the embolic apophysis in, e.g., *Meta* (Fig. 19F; see also Hormiga et al., 1995, fig. 13F,G) is more extensive, the one in, for example, *Metellina* (see Hormiga et al., 1995, fig. 13D,E) resembles the one in nephilids. Thus, metine and nephilid embolic apophyses are coded homologous (and the term ''metine'' to describe the feature is dropped).

189 *Radical membrane*: (**0**) absent (Fig. 7D,E,G); (**1**) present (Fig. 11D). In nephilids and most outgroups the junction between the radix (if present, see *186*) and the thin embolus (e.g., *Nephila*, Fig. 7D,E,G) is sclerotized. Typically, the connection between the araneid radix and the next distal sclerite of the embolic division (either stipes or embolus proper) is membranous: *Singafrotypa*, Fig. 13(B); *Araniella*, Fig. 15(A,C); *Cyclosa*, Fig. 15(D-F); *Argiope*, Fig. 17(A); *Acusilas*, Fig. 17(B–D). While *Deliochus* (Fig. 12A,B) and *Phonognatha graeffei*

(Fig. 11C) lack the radical membrane, *P. melanopyga* has it (Fig. 11D). Hormiga (2000) did not consider the radix in *Linyphia* homologous to the araneid one, so the radical membrane is coded as absent in *Linyphia*.

190 *Stipes (St)*: (**0**) absent; (**1**) present (Fig. 17A). The stipes, a sclerite between the EB (radix) and the embolus, is present in many araneids (e.g., *Cyclosa*, Fig. 15D; *Argiope*, Fig. 17A; *Acusilas*, Fig. 17C,D). In the current taxon sample the stipes is apparently absent in *Caerostris* and *Araniella* as well as in non-araneid taxa. Corresponds to character 35 in Hormiga et al. (1995) and character 19 in Scharff and Coddington (1997).

191 *Embolus constriction*: (**0**) absent; (**1**) present (Fig. 8J). The embolus has a subdistal constriction in *Nephilengys malabarensis* (see Kuntner, 2007a, fig. 23D) and *N. papuana* (Fig. 8J), and a similar condition is found in both *Argiope* species examined here (Fig. 17A).

192 *Embolus*: (**0**) smoothly curved; (**1**) sharply hooked (Figs 9C–F and 12B,D). Embolus has a single hook in *Argiope* and *Herennia* (Fig. 9C–F) and a row of hooks in *Deliochus* (Fig. 12B,D); the latter was also observed in *Phonognatha joannae*, not treated here.

193 *Embolic distal apophysis*: (**0**) present (Fig. 19F, arrow); (**1**) absent. A short distal apophysis is present on the embolus of *Uloborus* (Opell, 1979, fig. 7A), *Meta* (Fig. 19F, arrow), *Dolichognatha* and some species of *Deinopis* (Fig. 20A,B, arrow), but not in nephilids or other taxa treated here.

194 *Embolus tip*: (**0**) flat (Fig. 16D); (**1**) cylindrical (Fig. 7C,E,G). While the embolus tip in most taxa is cylindrical in cross-section (e.g., *Nephila*, Fig. 7C,E,G; *Herennia multipuncta*, Fig. 9C,D), it is more or less flat in various taxa (e.g., *Herennia papuana*, Fig. 9F–H; *Caerostris*, Fig. 16D; *Meta*, Fig. 19F; *Deinopis*, Fig. 20A,B).

195 *Distal hematodocha (DH)*: (**0**) absent; (**1**) present (Fig. 15B,C). Corresponds to the character 36 in Hormiga et al. (1995), where it was uninformative, and the character 17 in Scharff and Coddington (1997), who defined the feature as the membrane distal to the radix and connected to the stipes and/or the terminal apophysis (Fig. 8). Such a membrane is present in most araneids examined (e.g., *Araniella*, Fig. 15B,C), but not in *Argiope* and *Caerostris*.

196 *Subterminal apophysis (STA)*: (**0**) absent; (**1**) present (Fig. 13B). The subterminal apophysis (character 20 in Scharff and Coddington, 1997, fig. 8) is present in all araneines treated here except *Araniella*: e.g., *Singafrotypa*, Fig. 13(B); *Perilla*, Fig. 14(G); *Cyclosa*, Fig. 15(D,F).

197 *Terminal apophysis (TA)*: (**0**) absent; (**1**) present (Fig. 13A,B). The terminal apophysis (character 22 in Scharff and Coddington, 1997, fig. 18) is present in all araneines treated here (e.g., *Singafrotypa*, Fig. 13A,B; *Perilla*, Fig. 14G; *Araniella*, Fig. 15B,C; *Cyclosa*, Fig. 15D,F). Levi (1980, 1986, p. 100, figs 18–22)
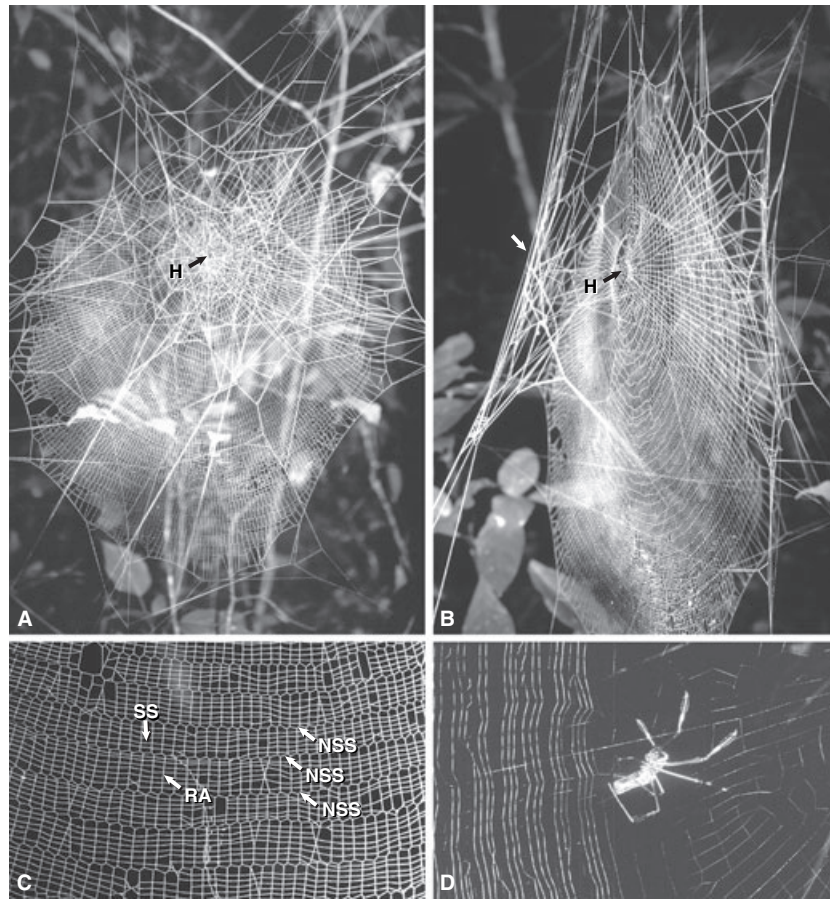
Fig. 21. *Nephila* web architecture: (A, B, D) *N. clavipes* penultimate female from Guatemala; (C) immature from Guatemala. (A) ventral view (orb height 30 cm, width 25 cm), note hub displaced up towards top frame; (B) lateral view, note barrier web (white arrow) ventral to spider at hub; (C) detail of lower part of orb, note zig-zag shaped NSS remaining in finished web; (D) sticky spiral construction (oL4). Specimen data and more images in Kuntner (in preparation).

hypothesized that some metines possess the terminal apophysis (although not separated by a distal hematodocha), although in *Chrysometa* the feature is clearly part of the conductor (own data; Alvarez-Padilla, pers. comm.). The TA in *Linyphia* is not homologous to the araneid one (Hormiga, 2000).

Behavior

198 *Web architecture*: (**0**) orb; (**1**) sheet; (**2**) gum foot. Theridioids spin gum foot, sheets, and sticky tangles webs (e.g., Agnarsson, 2004), linyphioids spin sheet webs (e.g., Hormiga, 2000, 2002, 2003) and all other taxa treated here (not observed in *Singafrotypa* or various *Clitaetra* and *Herennia* species) spin normal or modified orb webs (Figs 21–25). See Griswold et al. (1998, character 80) for comments. Nephilid web architectures are reviewed in Kuntner (2005, 2006, 2007a) and discussed in Kuntner et al. (submitted).

199 *Orb-web angle*: (**0**) horizontal (0–45°); (**1**) vertical (46–90°). The character contrasts the apparently intrin-

sic behavior of spinning more or less horizontal (e.g., *Leucauge*, *Tetragnatha*) versus more or less vertical (e.g., nephilids) orb webs. *Deinopis* web, at ≈45°, is coded polymorphic.

200 *Orb shape*: (**0**) round (Figs 21A,B, 22, 24 and 25); (**1**) rectangular (Fig. 23). While most orb webs are more or less round (e.g., *Nephila*, Fig. 21A,B), rectangular webs (elongate with parallel sides, in extreme cases termed ladder webs, see Robinson and Lubin, 1979) are typical for *Herennia* (Kuntner, 2005) and *Clitaetra* (Fig. 23; Kuntner, 2006; Kuntner et al., submitted).

201 *Silk color*: (**0**) white (Fig. 1H); (**1**) golden (Fig. 1A,B). Adult female *Nephila* orb webs contain sticky spirals of golden color (Holl and Henze, 1988). While golden webs have also been observed in araneids, e.g., some neotropical *Cyclosa* (Levi, 1999) and a *Neoscona* from Madagascar (Kuntner and Agnarsson, unpublished), the web color of all taxa (except *Nephila*) in this sample is white.

202 *Zig-zag stabilimentum*: (**0**) absent; (**1**) present (Fig. 26C,D, arrows). The typical zig-zag stabilimentum
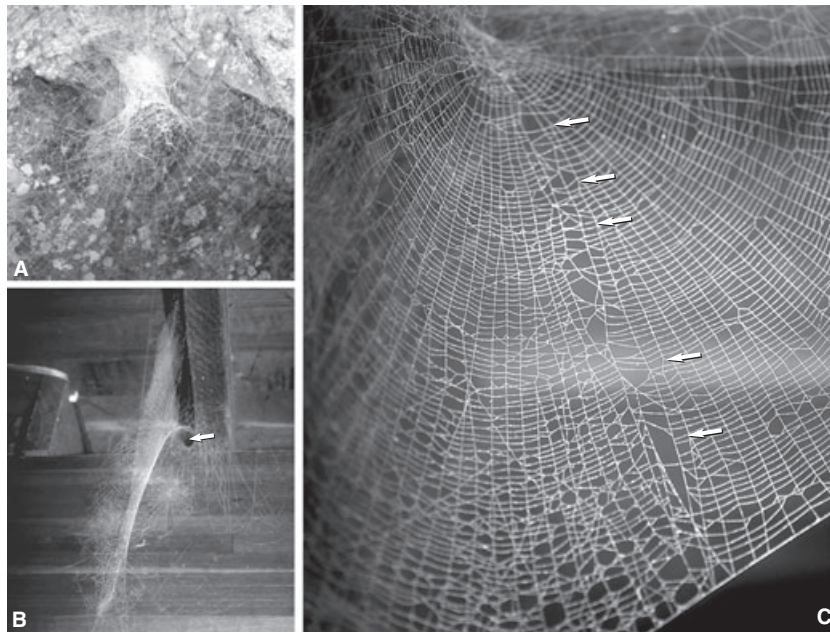
Fig. 22. *Nephilengys* web architecture. (A) *N. cruentata* female web with silken retreat built against rock outcrop (South Africa). (B, C) *Nephilengys papuana* female web (Queensland); (B) lateral, with tubular retreat (arrow); (C) front view, note hub displaced up towards top frame, left side of orb old, while right side recently rebuilt, note late radii split up to five times, arrows follow single radius. Specimen data and more images in Kuntner (2007a).
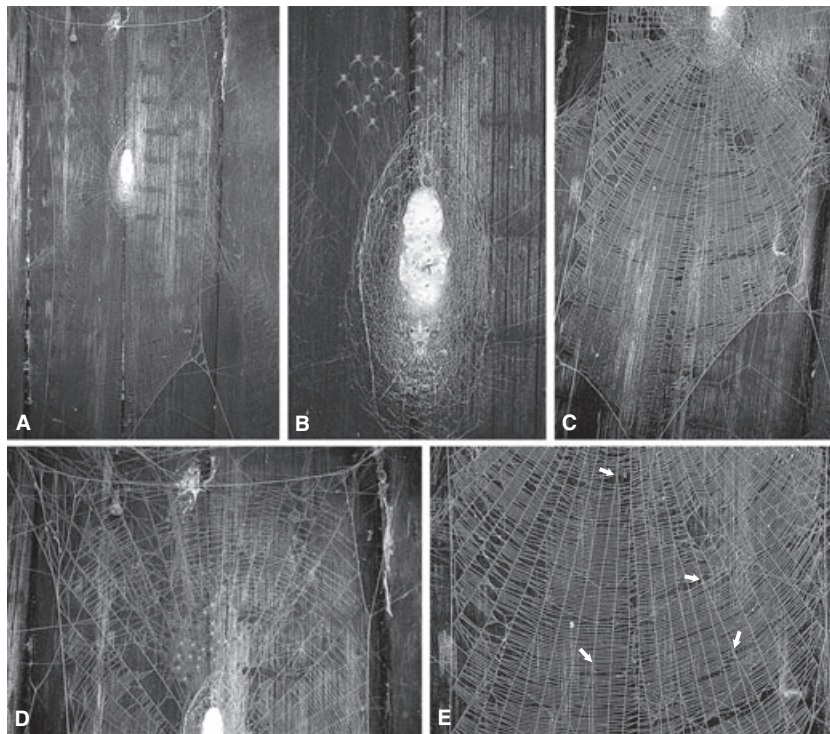
Fig. 23. *Clitaetra* web architecture. (A–E) *Clitaetra irenae* female, South Africa, ladder-web built tightly against wooden wall: (A) whole web (note rectangular shape); (B) close up of central web showing female in rest posture at hub on fine mesh of silk, egg-sac and offspring above hub; (C) lower web; (D) upper web; (E) web detail just below hub; note parallel side frames and split radii, two "tertiary radii" split at least twice (arrows). Specimen data in Kuntner (2006).
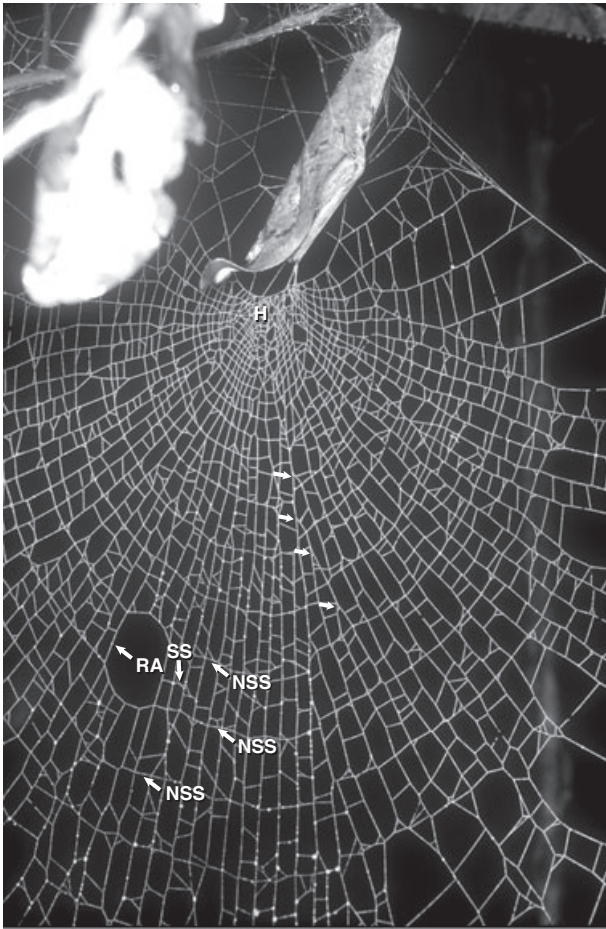
Fig. 24. *Phonognatha* web architecture: female web of undescribed species from Queensland, note hub displaced up towards top frame, rolled leaf-retreat connected to hub, linear NSS, late radii split up to four times, arrows follow single radius. Specimen data in Kuntner (in preparation).

of dense white silk is found in *Argiope* (Fig. 26C) and *Caerostris*. Among nephilids, a stabilimentum-like feature (of less dense silk than in *Argiope*, and sometimes golden in color) has been documented in juvenile *Nephila pilipes* (Robinson and Robinson, 1973, fig. 5; Kuntner, unpublished), *N. clavipes* (Kuntner, unpublished) and *N. inaurata* (Madagascar, Fig. 26D, Comoros: R. Jocqué, in litt.). While the definitions of stabilimentum vary (see Herberstein et al., 2001), it is here used in a broad sense to test the homology of the structure, and defined as a clearly recognizable zig-zag band of silk produced at a stage later than orb construction. Web decorations of debris are coded separately (*231*), as are silk hub reinforcements (see *208*).

203 *Barrier (three-dimensional) web*: (**0**) absent; (**1**) present (Fig. 21A,B). The barrier web is a three-dimensional mesh of silk above the orb, which may extend to surrounding the orb on its dorsal and/or ventral side

(Fig. 21B, arrow). It is typical of all *Nephila* juveniles, but is sometimes absent in adult webs. Immature *N. pilipes* and subadult *N. constricta* sometimes make an extensive elaborate barrier containing its own spirals (Kuntner, in preparation). Three-dimensional additions to the orb are also known in *Nephilengys* and *Phonognatha*, some *Leucauge* (scored as polymorphic), and juvenile *Argiope argentata*. The three-dimensional elements in linyphioid and theridioid webs are here coded similarly to test for potential homology. Certain araneid webs (e.g., *Zygiella*, *Metepeira*) also contain a three-dimensional element above the orb.

204 *Hub position*: (**0**) aerial (Figs 21A,B, 24 and 25A,B,E); (**1**) against substrate (Figs 1F–H, 22A,B and 23). The hub is built against the substrate (trees, walls, etc.) in *Clitaetra* (Figs 1H and 23), *Nephilengys* (Fig. 22A,B) and *Herennia* (Fig. 1F,G; Kuntner, 2005). Corresponds to character 44 in Hormiga et al. (1995). The condition in *Phonognatha* (Fig. 24) is aerial (coded differently than in Hormiga et al. (1995), who treated the retreat in the web as substrate).

205 *Hub relative position*: (**0**) central; (**1**) displaced up (Figs 21A,B, 22C, 23A and 24), (**2**) displaced down (Fig. 25A). The typical adult female nephilid hub is displaced upward and close to the upper frame of the orb (upper SS-hub distance to orb height ratio is less than 0.3). Most orb weavers spin more radially symmetric webs with more or less central hubs (ratio $0.3 < \times < 0.6$). Within this taxon sample *Deliochus* is unique because the hub is displaced downward (Fig. 25A, ratio > 0.6). More than one *Deliochus* species spin such webs, and the feature may be a synapomorphy of the genus.

206 *Hub bite-out*: (**0**) present; (**1**) absent. *Nephila*, *Nephilengys*, *Herennia*, *Clitaetra*, *Phonognatha* and *Uloborus* leave the hub intact after completing the orb, while araneids and tetragnathids remove it by biting it out. The evidence for the latter, if not directly observed, may come from a finished web with an open hub (Fig. 25B, see next character). Closed hubs may contain only lines built during radius and hub construction, or partially rebuilt after hub bite-out. The character corresponds to character 45 in Hormiga et al. (1995), which was modified from the states G1 (hub left intact), G2 (hub center removed) and G4 (entire hub removed) in Eberhard (1982).

207 *Hub*: (**0**) closed; (**1**) open (Fig. 25B). Identical to the character 46 in Hormiga et al. (1995); modified from the states G3 (hub center removed and replaced) in Eberhard (1982). This character is coded as inapplicable in all taxa lacking hub bite-out. Coded unknown in spiders with a known (closed) hub for which it is not known whether or not hub bite out occurs.

208 *Hub-cup*: (**0**) absent; (**1**) present (Fig. 1F,G). The hub of the *Herennia* species orbs is in the shape of a depression of dense silk, coming in touch with the
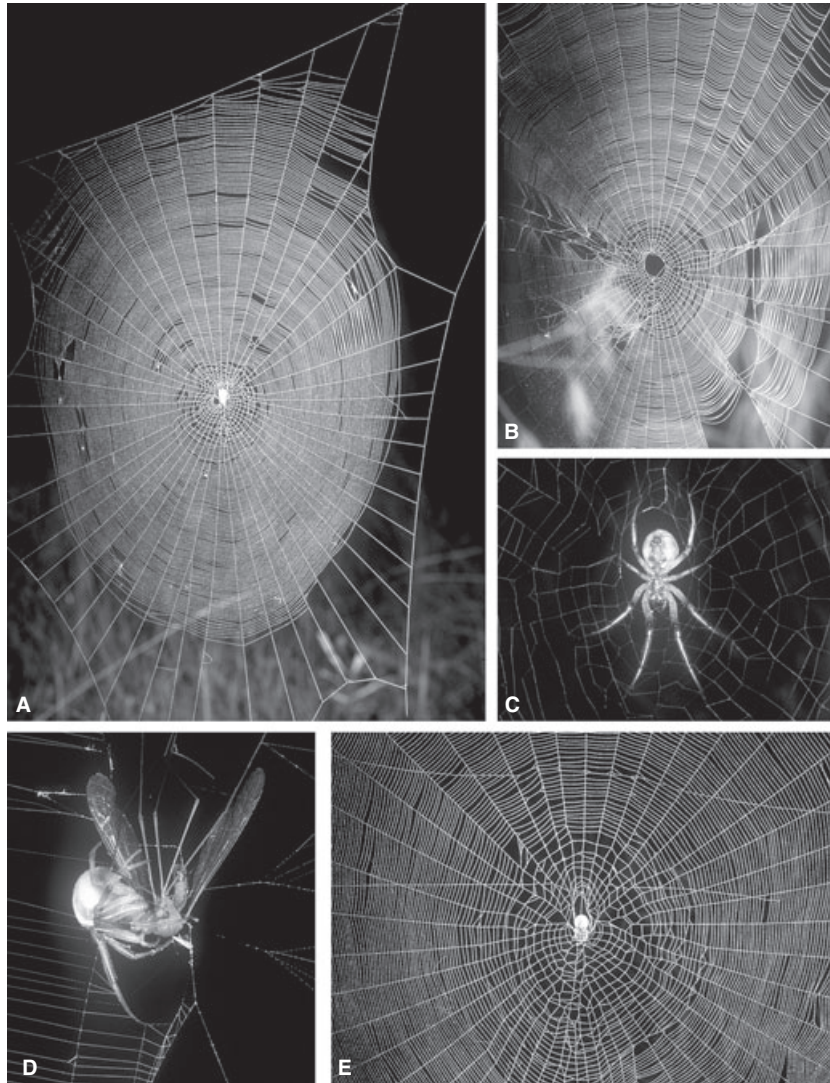
Fig. 25. *Deliochus* web architecture. (A–E) females of undescribed species from Queensland: (A, B, E) orb webs; with off-web silken-tube retreat in vegetation about 60 cm lateral to web (not shown); size of web in E = 23 cm width, 35 cm height, 19 cm top frame to hub; note fully vertical web, open hub, gradual hub loop–SS transition, absence of NSS, long primary radii without splits, and tight SS mesh; (C) female night prey-ready pose at hub; (D) bite attack. Specimen data in Kuntner (in preparation).

substrate (Fig. 1F,G; Kuntner, 2005, fig. 14A,B, arrows). This is the typical hub-cup (Robinson and Lubin, 1979). Similar hub structures, tested here for homology, are the terminal end of *Nephilengys* retreat (Fig. 22A,B) and the *Clitaetra* silk hub enforcement (Figs 1H and 23A,B). Such hub modifications are absent in *Nephila* and other araneoids (see also *230*).

209 *Hub loop—non-sticky spiral transition*: (**0**) gradual (Figs 21A,B, 22C, 23B–D, 24, 25A,B,E and 26C–E); (**1**) abrupt. Nephilid webs known show a gradual transition (Eberhard, 1982; Kuntner, 2005, 2006, 2007a). In contrast, typical tetragnathid webs show an abrupt transition (Hormiga et al., 1995; Kuntner and Alvarez-Padilla, 2006). Corresponds to the character 47

in Hormiga et al. (1995), misprinted in the publication as "hub loop—no sticky spiral shift."

210 *Radius construction*: (**0**) cut and reeled; (**1**) doubled. Corresponds to the character 49 in Hormiga et al. (1995) and in part to character 76 in Scharff and Coddington (1997), all modified from Eberhard's (1982) character F (states F1, F2, F4). In araneids and tetragnathids the trip from hub to frame via a pre-existing radius attaches a new "temporary radius", which is cut and then reeled in on the way back to the hub, laying a new one behind (see Eberhard, 1982, fig. 5A-D, character state F1). Uloborids and nephilids go out, attach, and return, thus spinning a "double" radius (Eberhard, 1982, figs 6 and 8). See *211*.
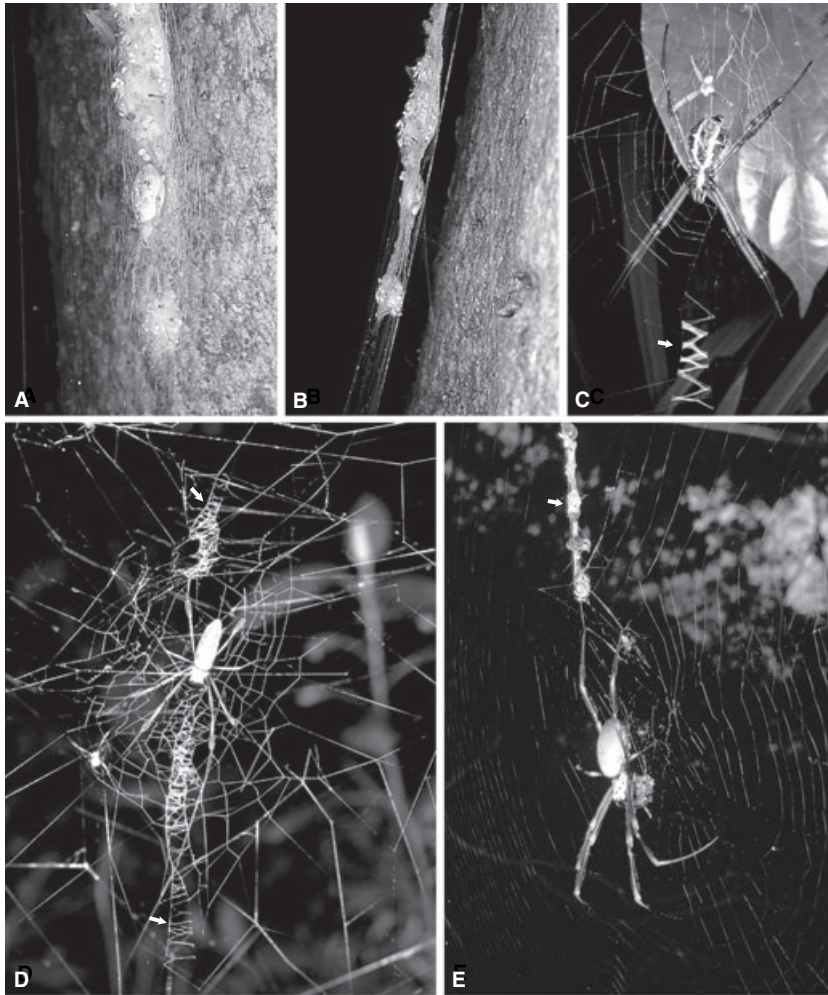
Fig. 26. Miscellaneous behaviors. (A,B) *Clitaetra irenae* from South Africa: (A) female in unalarmed resting posture at hub of web built against tree trunk (note egg-sac); (B) same female after threat response now on inner side of orb facing tree trunk. (C) *Argiope* sp. from Indonesia, small male (top) and large female (below) at hub of female web, in typical "leg-cross" rest pose, note stabilimentum (arrow). (D) Immature female *Nephila inaurata* from Madagascar in web with stabilimentum-like structure above and below hub (arrows). (E) *Nephila plumipes* small male (top) and large female feeding (below) at hub of female web from Queensland, note "debris web decoration" of prey remains (arrow) above hub.

211 *Radius attachment on frame*: (**0**) attached singly; (**1**) attached twice. While uloborids spin double radii (**210**; Eberhard, 1982, fig. 8, character state F4) their attachment to the frame and hub is single. Similarly, the frame attachment in the taxa that cut and reel is single (see **210**). In contrast, the typical nephilid attaches the radial line to two, closely juxtaposed points on the frame, thus resulting in two distinct radial lines, which, however, are attached at the same point at the hub (see Eberhard, 1982, fig. 6, character state F2). Two nephilid observations of a single attachment should be interpreted cautiously. In *Nephila pilipes*, for which published data (Eberhard, 1982 as *N. maculata*) suggest a double attachment, own observations of a juvenile (Queensland) revealed a single attachment. This should be confirmed in adult females. A web sample of *Nephilengys papuana* taken in Queensland also contained a single attachment (but see Eberhard, 1982).

212 *Secondary (split) radii*: (**0**) absent (Fig. 25-A,B,E); (**1**) present (Figs 21C, 22C, 23E and 24). A split radius is defined here as any radius that originates later than at the hub. While present sporadically in the outgroups, in typical nephilid webs late radii are common and originate at the junction of the non-sticky spiral and the previous radius (e.g., Fig. 22C). These are not "secondary" radii *sensu* Coddington (1986c).

213 *Tertiary or greater (split) radii*: (**0**) absent (Fig. 25A,B,E); (**1**) present (Figs 21C and 22C, arrows, 23E, arrows, 24, arrows). Defined as a split radius junction originating from a previously split radius. These are not "tertiary" radii *sensu* Coddington (1986c) but probably *sensu* Eberhard (1975, p. 103). Whereas outgroups occasionally show radii that split

once, nephilid radii typically split several times, e.g., up to nine times in *Nephila* (Kuntner, in preparation).

214 *Pseudoradii*: (**0**) absent; (**1**) present (Kuntner, 2005, figs 15 and 25). A unique feature in *Herennia* webs (where known) are "radii" (which do not run through the hub), perpendicular to each other, described and termed pseudoradii by Robinson and Lubin (1979, fig. 2 in *H. papuana*). The feature is a *Herennia* synapomorphy (Kuntner, 2005).

215 *Sticky spiral (SS)*: (**0**) spiraling (Figs 21,22C, 24 and 25); (**1**) parallel (Fig. 23; Kuntner, 2005, fig. 15). In most orb webs the sticky spiral, as the name implies, spirals around the hub. In ladder webs of *Herennia* and *Clitaetra* (where known), the sticky spiral runs more or less parallel (e.g., *Clitaetra irenae*, Fig. 23; for *Herennia papuana* see Robinson and Lubin, 1979, fig. 2), especially in the upper and lower parts of the orb.

216 *Non-sticky spiral (NSS)*: (**0**) removed (Fig. 25-A,B,E); (**1**) persists in web (Figs 21,22C, 23E and 24). Corresponds to the character 50 in Hormiga et al. (1995) where it served as a nephilid synapomorphy, and the character 77 in Scharff and Coddington (1997). The NSS, also termed the *temporary*, *provisional*, *structural* or *auxiliary* spiral (Eberhard, 1987; Zschokke, 1999), remains in finished webs of all nephilid genera (*Clitaetra*, *Herennia*, *Nephilengys* and *Nephila*) and *Phonognatha*, but is removed when laying the SS in most other orb-weaving spiders (Eberhard, 1982). Among the taxa not treated here, the araneid *Cyrtophora* and *Mecynogea* (Cyrtophorinae) webs also retain the NSS (Kullmann, 1958; Kullmann and Stern, 1975; Levi, 1980; Eberhard, 1982; Scharff and Coddington, 1997), as does the inverted ladder web of *Scoloderus tuberculifer* (Eberhard, 1975).

217 *NSS form*: (**0**) linear (Fig. 24); (**1**) zig-zag (*Nephila* form; Fig. 21C). In *Nephila* and *Nephilengys*, the NSS and the radius take a non-linear, zig-zag form (Fig. 21C; Zschokke, 2002, fig. 2; Kuntner, 2007a). The NSS is attached to the radius twice, and the tension of the NSS is higher than that of the radius and thus the NSS pulls the radius out of line. To our knowledge the only comparable NSS shape is known in *Cyrtophora* (Kullmann and Stern, 1975, fig. on p. 32).

218 *First SS spiral-NSS contact*: (**0**) NSS contacted; (**1**) no contact. Corresponds to the character 51 in Hormiga et al. (1995), modified from the character states D1 and D2 in Eberhard (1982), who noted that in some species the spider remains in contact with the outer loop of NSS while laying the first SS loop, while in others it moves farther out each radius, out of contact with the NSS.

219 *Sticky spiral localization*: (**0**) oL1; (**1**) iL1; (**2**) oL4 (Fig. 21D). Stereotypical behaviors used to locate the previously spun sticky spiral were described by Eberhard (1982, figs 1-4, character A) and have served as synapomorphies for major araneoid clades since (Codd-

ington, 1990; Hormiga et al., 1995: misprinted as "sticky spiral location"). Nephilids for which this behavior is known (*Herennia papuana*, *Nephilengys*: three spp., *Nephila*: three spp.) exhibit the oL4, outer fourth leg tap (Eberhard, 1982, fig. 4, character state A3). Typical araneid behavior is the oL1, outer first leg tap (Eberhard, 1982, figs 1 and 3, character state A2). Typical tetragnathid behavior is the iL1, inner first leg tap (Eberhard, 1982, fig. 2, character state A1). The behaviors of *Clitaetra* and *Deliochus* were unknown to Hormiga et al. (1995), and their observation for *Phonognatha* (oL4) seems erroneous. *Clitaetra irenae* uses oL4 (Kuntner, 2006). *Phonognatha graeffei* and *Deliochus* sp. in Queensland were here found to use the oL1 tap, although less consistently than in, e.g., araneids. In slow motion video *Deliochus* clearly uses oL1 most of the time, but also occasionally any other outer leg (opportunistically, if not randomly). Similarly, a *Leucauge* sp. in Queensland, while using iL1 for the most of the sticky spiral, used oL1 a few times close to the hub. Although SS localization behaviors in most taxa appears to be consistent, some taxa are notably variable, and this variation could be phylogenetically informative.

220 *Web posture*: (**0**) flexed legs I, II (Figs 1, 25C and 26); (**1**) extended legs I, II. Levi (1980) diagnosed the group Metinae by the resting position with first and second femora extended forward (plate 3: *Leucauge*; plate 6: *Metellina*). Coddington (1990) used the term "metine resting posture" referring to such extended leg pose of many metines (e.g., *Azilia*, *Leucauge*, *Dolichognatha*). This study found *Meta* species (*M. ovalis*, *M. menardi*) at hub in normal araneoid web pose with flexed legs. All nephilids rest with flexed legs (Kuntner, 2005, 2006, 2007a).

221 *Argiope posture*: (**0**) absent; (**1**) present (Fig. 26C). *Argiope* species typically rest with the first two and last two legs close together, thus forming a "leg-cross" (e.g., Levi, 1983, fig. 1). *Gea*, another argiopine, does the same.

222 *Attack behavior*: (**0**) wrap-bite; (**1**) bite-wrap (Fig. 25D). All nephilids (*Clitaetra*, *Herennia*, *Nephilengys*, *Nephila*) attack prey by biting first and then wrapping, regardless of prey size (Robinson and Robinson, 1973; Robinson, 1975; Robinson and Lubin, 1979; Eberhard, 1982, appendix 1; Kuntner, 2007a, fig. 20). Similar behavior was observed in *Deliochus* (Fig. 25D), *Phonognatha* and *Caerostris*. Many araneids and some tetragnathids attack by wrapping first, then biting (Eberhard, 1982: character states I2-I4).

223 *Wrap-bite silk*: (**0**) dry; (**1**) sticky. Some theridioids wrap-attack with sticky silk (Griswold et al., 1998, character 93; Agnarsson, 2004, character 229).

224 *Cheliceral clasp*: (**0**) absent; (**1**) present. Locking of male and female chelicerae during copulation is known in tetragnathines (see Bristowe, 1929, figs 11–13, for *Tetragnatha* and *Pachygnatha*; Levi, 1980, p. 68, for *Glenognatha foxi*), in *Leucauge mariana* and some other

tetragnathids (see Eberhard and Huber, 1998). The absence of the feature is coded only in the cases where mating behavior has been seen.

225 *Bulbus detachment (eunuchs)*: (**0**) absent; (**1**) present (Kuntner, 2005, fig. 23A–D; Kuntner, 2007a, fig. 24). Males of *Herennia* and *Nephilengys* often lack the palpal tarsi (reviewed in Kuntner, 2005, 2007a), the so-called "eunuch phenomenon" (Robinson and Robinson, 1980). *Phonognatha melanopyga*, *Deliochus* spp. and *Acusilas* males sometimes lack a palpal tarsus, and *Caerostris* males sometimes lack the bulb (but retain the cymbium). The emasculation in theridiid genera *Tidarren* and *Echinotheridion* is different, as those males autoamputate one entire palp before maturation (see Agnarsson, 2006).

226 *Body shake*: (**0**) absent; (**1**) present. *Clitaetra*, *Nephilengys*, some *Nephila* and *Argiope* shake their bodies vigorously at the hub in response to a threat such that the spider swings back and forth in a direction perpendicular to the plane of the orb.

227 *Side change*: (**0**) absent; (**1**) when in danger, slipping to other side of orb (Fig. 26A,B). *Clitaetra irenae* responses to threats by rapidly slipping through the web from one side to the other (Kuntner, 2006). *Argiope* (*A. argentata*, some African and SE Asian species, see Edmunds and Edmunds, 1986) do the same, and a very slow side change was observed in immature *Nephila pilipes*.

228 *Partial web renewal*: (**0**) absent; (**1**) present (Fig. 22C). Nephilids often repair only portions of their webs, parts of orbs being new and parts old (reviewed in Kuntner, 2005, 2006, 2007a), as do uloborids, linyphiids and pimoids. Araneids, tetragnathids, *Deliochus* sp. and *Phonognatha graeffei* take down and rebuild the entire web.

229 *Retreat*: (**0**) absent (Figs 21A,B and 23); (**1**) off-web (Fig. 22A,B); (**2**) in web (Fig. 24). Most orb-weaving taxa here do not construct retreats. *Nephilengys* makes its retreat off the web (tubular silk, above orb; Kuntner, 2007a) as does *Deliochus* (tubular silk with a leaf, to the side of web). *Phonognatha* and *Acusilas* build retreats from leaves inside the web (Fig. 24; Hormiga et al., 1995, figs 1–3; Murphy and Murphy, 2000). *Perilla* utilizes a rolled grass stem (Kuntner, 2002) at the hub. Present/absent coding of the retreat is here avoided as it would imply homology of all retreats. Retreats are found in many other araneids and theridiids, e.g., *Zygiella* (tubular, above orb), *Aculepeira* sp. (tubular), *Araneus* spp. (leaf), *Achaearanea lunata* (leaf), etc.

230 *Retreat form*: (**0**) silken tube (Fig. 22A,B); (**1**) utilization of a leaf (Fig. 24). See above.

231 *Debris web decoration*: (**0**) absent; (**1**) present (Fig. 26E, arrow). Some *Nephila* species decorate the web with a line of debris (prey remains, plant material, etc.) above the hub, e.g., *N. plumipes* (Fig. 26E, arrow).

Similar web decorations are found in *Cyclosa* (Levi, 1977) and *Dolichognatha* (Levi, 1977).

Results

Phylogeny

All equally weighted analyses of the complete data set (Appendix 1) in NONA and TNT (traditional and new technology search) resulted in the same four most parsimonious trees (L = 838, CI = 0.31, RI = 0.73). Two nodes collapse in the strict consensus (Fig. 27A). All trees support the monophyly of the classical nephilid genera (*Clitaetra* (*Herennia* (*Nephilengys*, *Nephila*))), which is sister to all remaining araneoids. The four trees differ only in ingroup relations: the position of two *Clitaetra* species relative to each other, *C. perroti* and *C. episinoides* as a grade or clade sister to the three African species, and the relations of the three *Herennia* species known from a single sex (*H. tone*, *H. gagamba*, *H. agnarssoni*; see polytomies in Fig. 27A). *Phonognatha* is monophyletic and sister to araneids (including *Acusilas*). *Deliochus* is sister to *Phonognatha* + araneids. All topologies corroborate the araneine position of *Singafrotypa* and *Perilla* (Kuntner, 2002; Kuntner and Hormiga, 2002). *Epeirotypus* (symphytognathoids) and araneoid "sheet web builders" (*Steatoda*, *Nesticus*, *Linyphia*, *Pimoa*) are monophyletic and sister to tetragnathids, corroborating Hormiga et al. (1995) and Griswold et al. (1998). Tetragnathid monophyly without nephilids is also confirmed, as well as the tetragnathine + *Leucauge* clade (including *Opadometa*) in agreement with Hormiga et al. (1995). The classical "metine" genera (*Meta*, *Metellina*, *Chrysometa*, *Azilia*, *Dolichognatha*, *Leucauge*, *Opadometa*) remain paraphyletic (Clades 16 and 17 in Fig. 28 and Appendix 3), also in agreement with Hormiga et al. (1995).

Successive weighting analysis of the complete data set in NONA stabilized after the second iteration and resulted in one tree (Fig. 27B; L = 841, CI = 0.31, RI = 0.73), three steps longer than the most parsimonious tree under equal weights. Used to choose among alternative topologies (Carpenter, 1988), the results prefer one of the four resolutions among nephilids, but rearranges two outgroup relationships (*Singafrotypa* and *Perilla* swap places and *Chrysometa* shifts). As this analysis focuses on nephilid relationships, we take the equally weighted most parsimonious cladogram with the ingroup topology favored by successive weighting as the preferred phylogenetic hypothesis (Fig. 28) (see Discussion for justification). Clade support (BS, bootstrap > 49%) is given on Fig. 28. Figure 30 shows character optimizations (only unambiguous changes as optimized by Winclada are shown) on the preferred phylogeny. Appendix 3 lists synapomorphies for major clades.
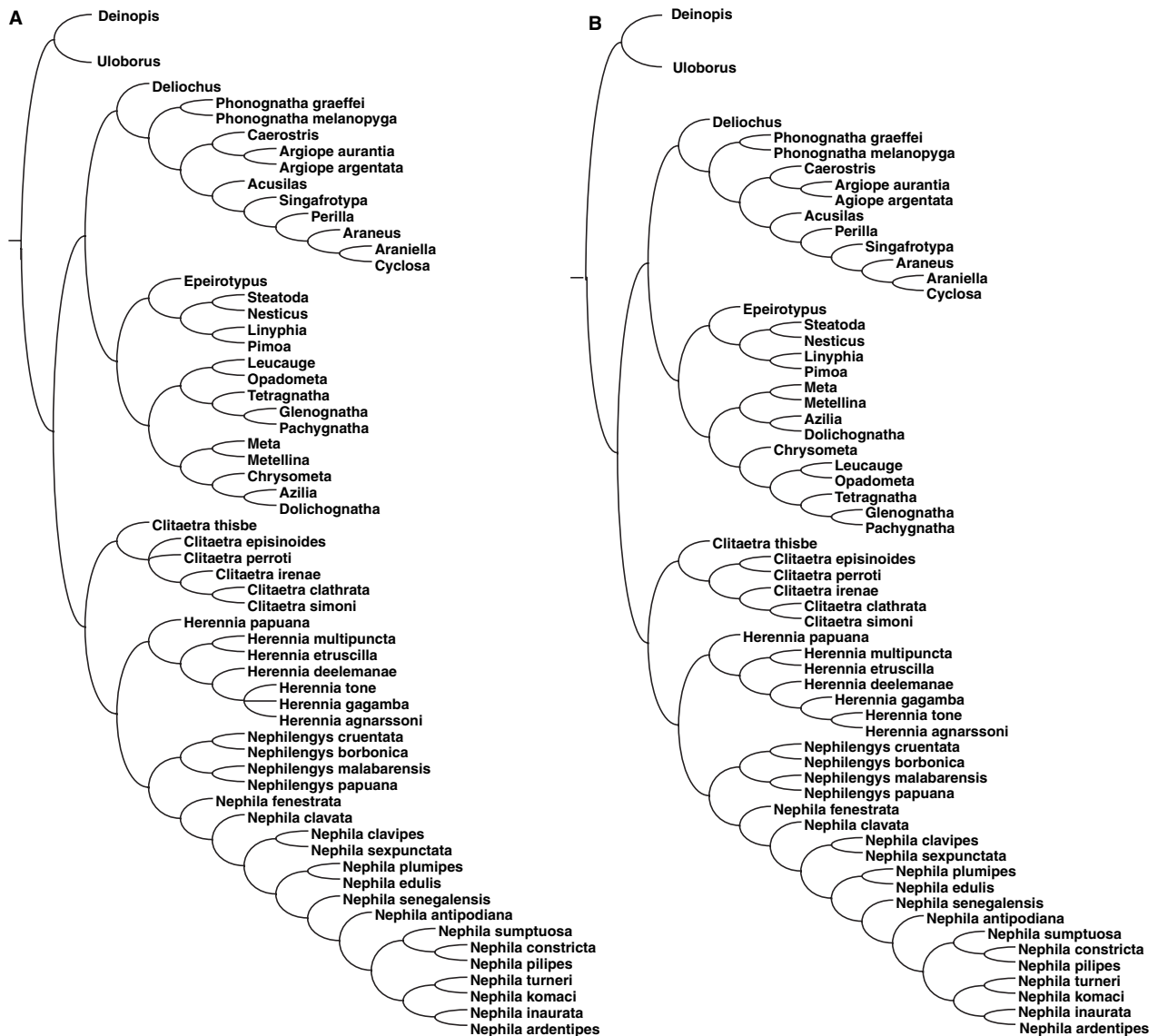
Fig. 27. Phylogenetic results. (A) Strict consensus of four most parsimonious cladograms (L = 838, CI = 0.31, RI = 0.73) under equally weighted parsimony. (B) Single cladogram (L = 841, CI = 0.31, RI = 0.73) resulting from successive weighting analysis in NONA.

Equally weighted analysis of the alternative data set in NONA and TNT (traditional search) also yielded four trees (L = 840, CI = 0.31, RI = 0.73) identical in topology to the complete data set but two steps longer.

The morphology matrix contained 197 characters and yielded 56 trees (L = 740, CI = 0.30, RI = 0.73), which markedly differ from the combined data (see strict consensus in Fig. 29). Nephilid relationships are merely less resolved (although the basalmost *Nephila* now is *N. clavata*), but the tetragnathid topologies and the grouping of distal araneoids with araneids (still including *Deliochus* and *Phonognatha*) are new. The behavioral data set contained 34 characters and yielded > 10 000 trees (L = 77, CI = 0.49, RI = 0.83) of which the consensus is a near bush with few resolved clades, none of which appear in the full analysis. Eliminating the taxa for which not a single behavioral observation exists (*Clitaetra thisbe*, *C. simoni*, *Nephila ardentipes*, *N. komaci*, *Herennia deelemanae*, *H. tone*, *H. gagamba*, *H. agnarssoni*) from the analysis also produces > 10 000 trees with only three resolved clades (*Pachygnatha* plus *Opadometa*, *Tetragnatha* plus *Glenognatha*, and *Clitaetra episinoides* plus *C. irenae*) in strict consensus.

Classification

Based on the preferred phylogeny, the familial classification outlined below is proposed (Fig. 28, see
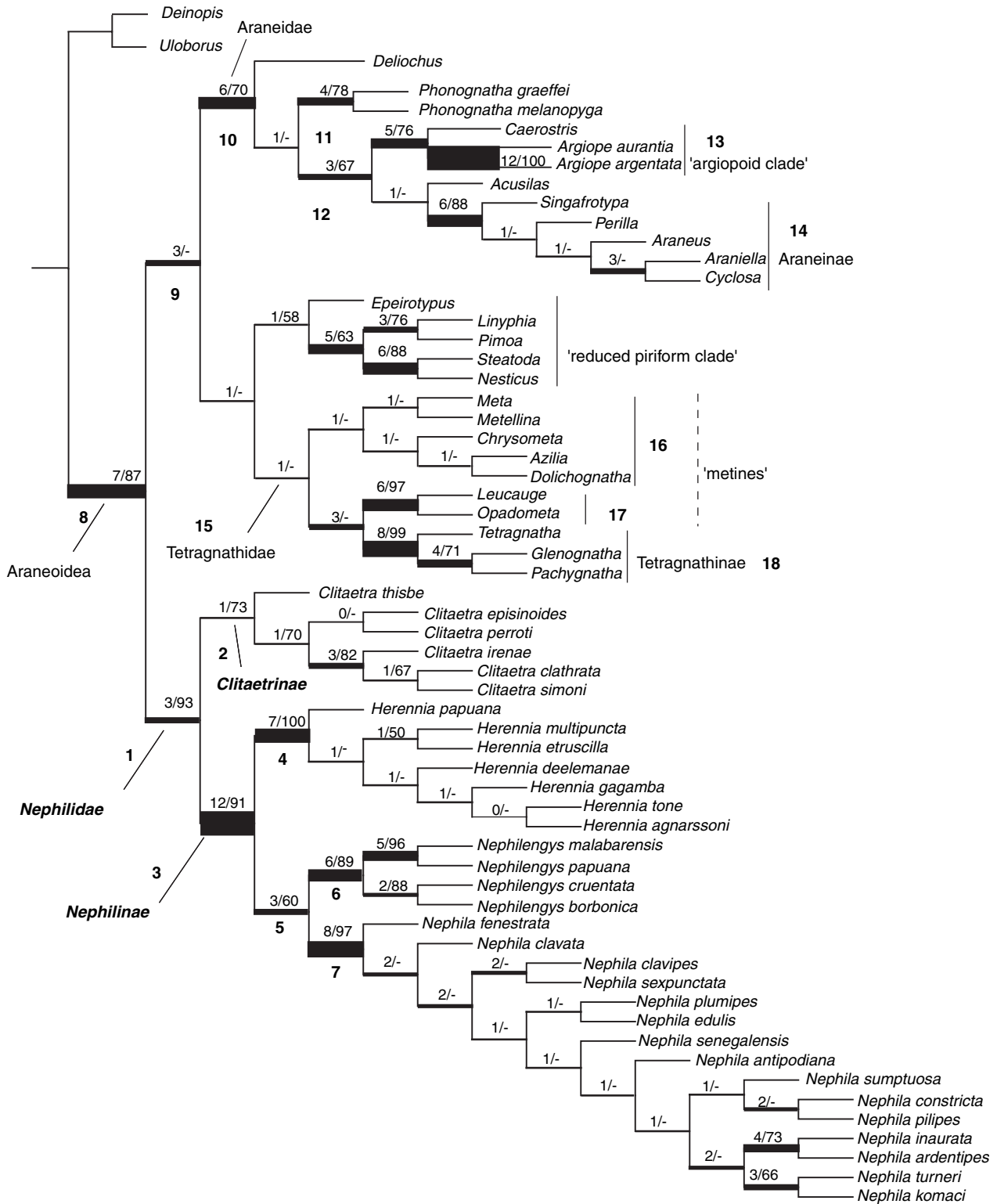
Fig. 28. The preferred phylogeny: one of the four fully resolved most parsimonious cladograms (L = 838, CI = 0.31, RI = 0.73) under equal weights, congruent with the successive weighting analysis in the ingroup relationships (see text for details). Clade support (Bremer/Bootstrap > 49%) and clade names are given. Horizontal branch thickness correlates with Bremer support values. Note that two clades, which collapse in the strict consensus, receive zero Bremer support. The phylogeny is the basis for classification (see clade diagnoses in Appendix 3): italicized names affect ingroup classification, other capitalized names are commonly accepted group names, names in quotes are informal clade names ("metines" are paraphyletic). Large numbers identify clades discussed in text.
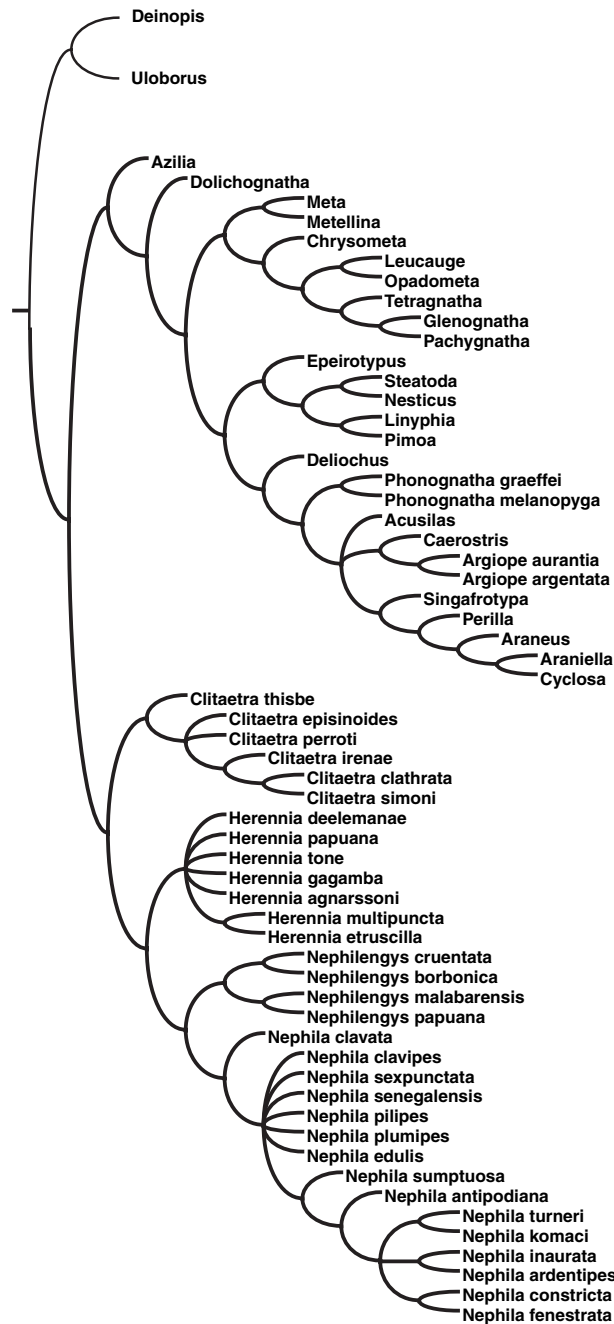
Fig. 29. Partitioned analyses, morphological character subset, strict consensus of 56 most parsimonious cladograms (L = 740, CI = 0.30, RI = 0.73) under equal weighted parsimony.

Appendix 3 for clade diagnoses), which follows the International Code for Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). *Deliochus* and *Phonognatha* are here newly transferred to Araneidae, and *Perilla* and *Singafrotypa* are confirmed as araneids. The classification within Nephilidae follows Kuntner (2006). Araneid and tetragnathid within family classifications are beyond the scope

of this paper, and the monophyly of the families Nesticidae, Theridiidae, Theridiosomatidae, Linyphiidae, Pimoidae, Uloboridae and Deinopidae was not tested.

Superfamily Araneoidea
 Family Nephilidae
  Subfamily Clitaetrinae
   Genus *Clitaetra*
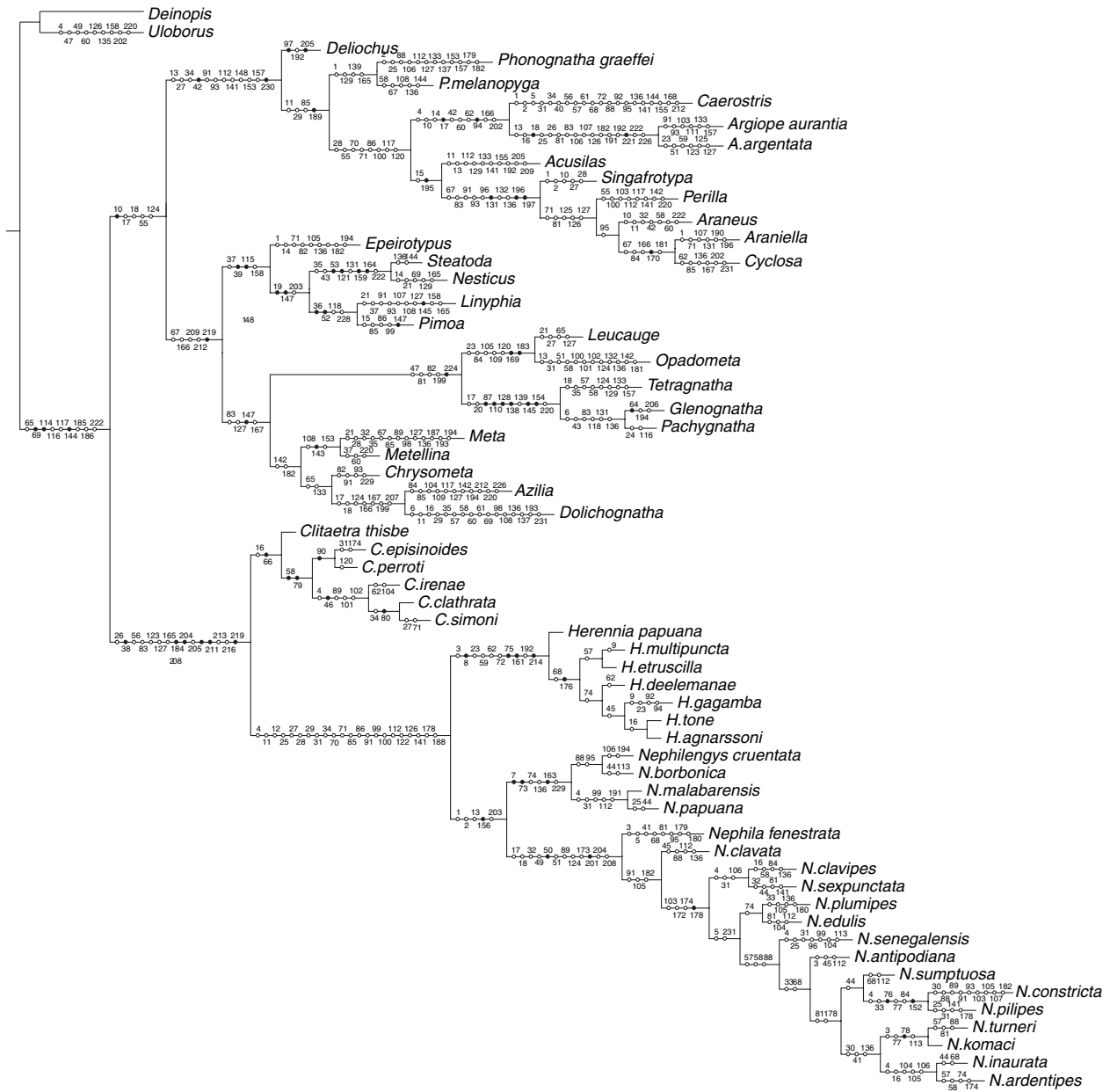
Fig. 30. Character state changes on the preferred phylogeny, unambiguous optimization from WinClada with character numbers; black circles mark non-homoplasious character state change, white circles mark homplasious character state changes.

Subfamily Nephilinae
  Genus *Herennia*
  Genus *Nephila*
  Genus *Nephilengys*
Family Araneidae
  Genus *Deliochus*, new placement
  Genus *Phonognatha*, new placement
  Genus *Caerostris*
  Genus *Argiope*
  Genus *Acusilas*

Genus *Singafrotypa*
Genus *Perilla*
Genus *Araneus*
Genus *Araniella*
Genus *Cyclosa*
Family Tetragnathidae
  Genus *Meta*
  Genus *Metellina*
  Genus *Chrysometa*
  Genus *Azilia*

Genus *Dolichognatha*
Genus *Leucauge*
Genus *Opadometa*
Genus *Tetragnatha*
Genus *Glenognatha*
Genus *Pachygnatha*

Discussion

The preferred phylogeny (Fig. 28) is one of the four shortest trees under equal weights, uses all available evidence from the complete data set, is fully resolved, and agrees with the successively weighted tree on ingroup relationships.

Although not specifically tested here, Araneoidea is well supported (BS 7/bootstrap 87) and agrees in composition with previous analyses (Coddington, 1990; Hormiga et al., 1995, 2000; Scharff and Coddington, 1997; Griswold et al., 1998). The monophyletic nephilids do not group with araneids *contra* Dahl (1912), Eberhard (1982) (Fig. 2B lower tree), Wunderlich (1986, 2004) (Fig. 2C), Kuntner (2003), and Pan et al. (2004) (Fig. 2E), nor are they "metids"/tetragnathids or sister to tetragnathids *contra* Levi (1980, 1986), Levi and Eickstedt (1989), Coddington (1990), Hormiga et al. (1995, 2000), Scharff and Coddington (1997) and Griswold et al. (1998). Instead, Nephilidae is sister to all other araneoids, while *Deliochus* and *Phonognatha* group with araneids (*contra* Hormiga et al., 1995; Wunderlich, 2004). The nephilid and *Phonognatha-Deliochus* results also contest previous nephilid species-level analyses (Kuntner, 2005, 2006, 2007a; Fig. 2F) based on fewer data. One of Eberhard's (1982) alternatives does agree with these results (Fig. 2B, above tree), although he considered "Nephilinae" as a whole rather than at the generic level.

Well supported ingroup clades (Appendix 3, Fig. 28) include Nephilidae (3/93), Nephilinae (12/91) and the clade *Nephilengys-Nephila*; (3/60), the latter disputing the doublet *Nephilengys—Herennia* to the exclusion of *Nephila* (Hormiga et al., 1995, 2000). The synapomorphies for "Nephilinae" hypothesized by Hormiga et al. (1995)—folded paracymbial apophysis, hub against substrate, absence of hub removal, persistence of non-sticky (temporary) spiral in finished orb, and the fourth leg sticky spiral localization—are among the now 15 unambiguous and 15 ambiguous synapomorphies of Nephilidae (without *Phonognatha*; Appendix 3). *Nephila* (8/97), *Nephilengys* (6/89) and *Herennia* (7/100) are well supported, but *Clitaetra* is poorly supported (1/73). Less inclusive, well supported ingroup clades include the subgenus *Afroetra* (*C. irenae, C. clathrata, C. simoni*; 3/82), the Australasian *Nephilengys* clade (*N. malabarensis, N. papuana*; 5/96), the African and Indian Ocean *Nephilengys* clade

(*N. cruentata, N. borbonica*; 2/88), and the two distal African sister clades of *Nephila* (*N. turneri, N. komaci*; 3/66; and *N. inaurata, N. ardentipes*; 4/73). Further research into species-level relationships, especially within *Nephila* and *Herennia* are needed in order to test the currently understood phylogeny and to test whether clades with low support are real.

Some basal nodes are also poorly supported (Fig. 28). Clade 9 (araneoids to the exclusion of nephilids) is supported by five unambiguous and eight ambiguous synapomorphies but is still weak (3/–). Griswold et al. (1998) recovered "derived araneoids" based on three synapomorphies: loss of the PMS aciniform brush, the peripheral position of the mesal PLS CY spigot, and the iL1 sticky spiral localization. Here, the PMS aciniform brush (**117**) and the mesal PLS CY spigot (*119*) are primitively present in *Deinopis* and *Uloborus*, originate independently in Araneidae, and are lost at the araneoid node.

Tetragnathid monophyly and interrelationships continue to be problematic. Hormiga et al. (1995) proposed two unambiguous synapomorphies for Tetragnathidae (including nephilids and *Phonognatha*): the loss of the median apophysis, and the conductor and embolus spiraling with each other. The apical position of the tegular sclerites was an ambiguous synapomorphy. This study hypothesizes multiple origins (non-homology) of the araneoid median apophysis, disputes the homology of the nephilid (also *Deliochus, Phonognatha*) conductor with the tetragnathid one, and regards the character homologizing the apical position of tegular sclerites as weak because it essentially repeats the observation that subapical sclerites (e.g., median apophysis) are absent. In effect, the tetragnathid clade recovered here (*sans* nephilids) is poorly supported (1/–), as is the "metine" clade (*Meta, Metellina, Chrysometa, Azilia, Dolichognatha*). Well supported tetragnathid clades are Tetragnathinae (*Tetragnatha, Pachygnatha, Glenognatha*: 8/99), and the doublet *Leucauge, Opadometa* (6/97). Clade supports were not presented in the phylogeny of Hormiga et al. (1995), but were for many nodes fairly low (Kuntner and Alvarez-Padilla, 2006). Further detailed investigations into the tetragnathid monophyly and its limits are needed. Multigene sequence data for all nephilid genera and for a broad sample of tetragnathids and araneids are currently being gathered, in conjunction with morphological and behavioral characters, to address this problem (Alvarez-Padilla et al., 2007).

Phonognatha monophyly is well corroborated (4/78), and probably will remain so in future studies as the two exemplars included here are morphologically quite dissimilar. Hormiga et al. (1995) used the type species, *P. graeffei* as their only exemplar and placed *Phonognatha* as sister to the remaining nephilines and Nephilinae as sister to the remaining tetragnathids. Kuntner (2005, 2006, 2007a) also included only *P. graeffei* in his

analyses, which grouped *Phonognatha* with nephilids (Kuntner, 2005) or with the derived araneoids (Kuntner, 2006, 2007a; Fig. 2F). Our examination of an additional species within a larger morphological and behavioral data set, results in this new placement of *Phonognatha*. The araneid placement of *Deliochus* and *Phonognatha* receives strong clade support (6/70), but the grouping of araneids to the exclusion of *Deliochus* is weak (1/−). Because this study includes so few araneids, and because much larger samples of Araneidae have been studied phylogenetically (Scharff and Coddington, 1997), the placement of *Deliochus-Phonognatha* relative to other araneid genera in Fig. 28 is provisional, at best.

Although araneid internal relationships were not a focus of this study, it recovers the two major araneid clades proposed by Scharff and Coddington (1997): the "argiopoid clade" (represented by *Caerostris* and *Argiope*; 5/76), including Argiopinae (here equivalent to *Argiope*; 12/100), and the Araneinae (*Araneus*, *Araniella*, *Cyclosa*, *Singafrotypa*, *Perilla*; 6/88). The basal araneid position of *Chorizopes* (recovered but questioned by Scharff and Coddington, 1997) has already been disputed (Kuntner, 2002). Scharff and Coddington (1997) proposed four synapomorphies for Araneidae: the mesal position of the cymbium, the presence of the radix, the wide separation of lateral eye group from the medians, and the narrow posterior median eye tapetum. This study found the mesal cymbium position, at least to some extent, occurring widely in Araneoidea and also in *Uloborus* (**140**). Within the taxa sampled, only *Deinopis* was found to exhibit a strict dorsal condition; this character distribution argues that first synapomorphy of Scharff and Coddington (1997) needs redefinition. This study homologizes the araneid radix with the embolus base (**186**, **189** for the radical membrane), unambiguously optimizing the broad shape of the sclerite to the base of Araneoidea (with a reversal to thin base in the reduced piriform clade under ACCTRAN). However, the presence of a radical membrane (**189**) is indeed an araneid feature, and optimizes at the base of the araneid clade to the exclusion of *Deliochus*. Finally, this study challenges the codings of the eye characters in Scharff and Coddington (1997) (**13, 17**). The wide separation of the lateral eyes from the medians (**13**) is corroborated as an araneid synapomorphy, in agreement with Scharff and Coddington (1997), although the character state also defines the clade *Nephila* + *Nephilengys*. However, the presence of a reduced tapetum defines the clade *Caerostris* + *Argiope*, and is not universal for Araneidae (**17**), although Kuntner and Levi (2006) urge caution with the araneid tapetum characters, as they are only reliable in freshly preserved specimens. Twelve unambiguous and nine ambiguous araneid synapomorphies are proposed here (Appendix 3), all but one is new at this node. Among new araneid synapomorphies, in addition to anatomical ones, are the presence of a rolled leaf as a retreat (**230**), the male emboli plugging the epigynum (**112**), apparently convergent in nephilids, and the male bulbus detachment (eunuch) behavior (**225**, ACCTRAN), also convergent to the condition in nephilids (optimizing at the base of Nephilinae with a reversal in *Nephila*).

According to Wunderlich (2004) Nephilidae (as Nephilinae) include an Eocene group Paleonephilini from Baltic amber (up to 40 million years old) and a Miocene group of fossil *Nephila* species from Dominican amber (up to 20 million years old). It was beyond the scope of the present study to test the nephilid placement and the monophyly of Paleonephilini, and so the deep nodes within Nephilidae cannot be dated with the currently available data, although Kuntner (2006) hypothesized them to be at least 160 million years old based on the *Clitaetra* distribution and Gondwanan vicariance. Some Dominican amber *Nephila* species appear to be correctly placed. Thus, some nodes (*Nephila* or *Nephila* + *Nephilengys*) could very crudely be estimated to be up to 20 million years old.

This study emphasized sampling tetragnathid and araneid outgroup genera, building on the background knowledge of araneoid relationships (e.g., Hormiga et al., 1995; Griswold et al., 1998). The somewhat surprising nephilid phylogenetic position should be further tested with a wider range of non-araneoid outgroups. To test the character polarities recovered here, further uloborid genera should be included in future analyses, as some of them exhibit interesting similarities in web architecture to the nephilids (e.g., late radii, partial web renewal, three-dimensional additions to the orb).

Although the topologies obtained through the analyses of the alternative data set are identical to the results of the complete set, the implied evolution of selected characters will differ. There is a logical problem with this alternative coding. While *Nephila*, *Nephilengys*, *Herennia*, *Clitaetra* and *Phonognatha* lack a tegular sclerite (apart from the functional conductor and the embolus), *Deliochus* possesses an additional apical tegular apophysis, which resembles the araneid conductor (Fig. 12A) and was scored as such in the original matrix. Conjunction refutes the homology of both features with the conductor. Thus, the alternative matrix codes the (embolic) conductor features as homologous to the tegular conductor, but ignores the presence of the tegular apophysis (which, if scored as a new feature, would then be autapomorphic in *Deliochus*).

Morphological versus behavioral data

This discussion concerns the usefulness of behavioral data in phylogeny reconstruction, not whether the phylogenetics has a role in the studies of behavior (Ryan, 1996). Some studies have utilized behavior

extensively in phylogenetic reconstruction, notably in ornithology (Prum, 1990; Price and Lanyon, 2002) and araneology (Eberhard, 1982) but such studies are exceptions (Wenzel, 1992; Proctor, 1996; Danoff-Burg, 2002). Danoff-Burg (2002) counted 69 zoological phylogenetic papers in recent Systematic Biology volumes, of which only five mentioned and only one used behavior or life history data in phylogeny reconstruction. In more exhaustive phylogenetic literature surveys of Sanderson et al. (1993) and Proctor (1996) less than 4% of 882, and 6% of 291 studies, respectively, relied on or treated behavioral data, although the survey of Sanderson et al. (1993) focused on molecular biology journals (Proctor, 1996). In recent lepidopteran literature, Kaila (2004) examined two of 193 (1%) behavioral to total characters and Pech et al. (2004) treated 11 of 90 (12%) ecological and life history to total characters. In recent studies of crickets (Robillard and Desutter-Grandcolas, 2004), beetles (Ahn and Ashe, 2004) and heteropterans (Guilbert, 2004) only morphological (193, 99 and 61 characters, respectively) and no behavioral characters were used. The numbers of behavioral to total characters in recent spider systematic studies are: 19 of 242 (8%) in Agnarsson (2004); 24 of 87 (28%; Coddington 1990); none of 101 (0%; Griswold 1990); 14 of 93 (15%; Griswold et al. 1998); none of 57 (0%; Harvey 1995); two of 73 (3%; Hormiga 2000); one of 56 (2%; Hormiga 2002); three of 75 (4%; Hormiga 2003); 12 of 60 (20%; Hormiga et al. 1995); six of 176 (3%; Miller and Hormiga 2004); none of 61 (0%; Huber 2000); 33 of 190 (17%; Kuntner 2005); 32 of 197 (16%; Kuntner 2006; 2007a); none of 34 (0%; Platnick 2002); one of 200 (0.5%; Ramírez 2003); nine of 82 (11%; Scharff and Coddington 1997); one of 80 (1.2%; Schuett 2003); and 34 of 231 (15%) in this study. In contrast, Eberhard's (1982) study of araneoid evolution was based exclusively on behavior with characters (e.g., sticky spiral localization), which still serve as synapomorphies of major araneoid clades.

The scarcity of behavioral data in phylogenies might be because most systematists are better trained as morphologists than as behaviorists, because behaviors are more difficult to define than morphologies, more costly or time consuming to obtain, and, possibly, are widely believed to be more homoplasious and thus of less use in phylogenetics (for reviews, see Wenzel, 1992; deQueiroz and Wimberger, 1993; Proctor, 1996; also Gittleman et al., 1996). The latter claim was challenged by deQueiroz and Wimberger (1993) who compared relative amounts of behavioral and morphological homoplasy in a variety of taxa and characters, found no significant differences in CI values among the data sources, and concluded that behavior is no more evolutionarily labile than morphology and thus just as useful. The same authors (Wimberger and de Queiroz, 1996) retested the above by measuring the amounts of

homoplasy (CI) and phylogenetic content (RI) of behavioral and morphological characters, and again concluded that behavior performs as well as morphology. The usefulness of behavior was also demonstrated in a phylogenetic analysis of display behavior in manakins (Prum, 1990). Another criticism of behavioral data, that their homology is difficult or impossible to determine (Atz, 1970; Ryan, 1996), has also been put to rest (for review see Wenzel, 1992; also deQueiroz and Wimberger, 1993). Wenzel (1992) convincingly argued that determining homology among behaviors is no different than among morphologies, that the classical a priori criteria, position, special quality, and connection by intermediates (Remane, 1952), apply also to behavior and that the strongest test is a posteriori congruence. Similarly, Price and Lanyon (2002) applied Remane's criteria in a phylogenetic analysis of bird songs. This study follows Wenzel in testing for homologies through congruence (Patterson, 1982; de Pinna, 1991).

We see no reason to exclude one kind of data from a cladistic analysis; hence, the incongruence-length difference test (ILD) (Mickevich and Farris, 1981; Farris et al., 1995) was not used here and we do not consider results from partitioned data sets as alternative topologies to that based on all data. Data partitions among morphology and behavior are, however, used to probe questions about those partitions. For example, Wenzel (1993) analyzed separate morphological and behavioral partitions in paper wasps in order to test the accuracy of polarity determination using behavioral ontogeny, Danoff-Burg (2002) analyzed separate behavioral and morphological partitions in ant-guest staphylinid beetles to test for evolutionary lability of discrete versus continuous behavioral data, and Prum (1990) partitioned his data to test for taxonomic congruence of behavioral and morphological subsets in the phylogeny of neotropical manakins. This study likewise compares the phylogenetic signal and the levels of homoplasy in morphological and behavioral partitions. Note that the ratio of cell entries to taxa (a measure of information density, unknowns and inapplicables included, as current algorithms cannot distinguish between them) differs greatly: 197 : 1 for morphology versus 33 : 1 for behavior. Sanderson and Donoghue (1989) investigated the levels of homoplasy in 60 cladistic studies and after correcting CI values for invariant and autapomorphic characters, found that the number of characters did not correlate with homoplasy level but that the number of taxa positively correlated. Here, taxon number was equal in both partitions (although six terminals are unscored for behavior).

The morphological partition (Fig. 29) retained most but not all of the structure of the combined analysis, but the behavioral partition retained almost none. The few relationships it resolved make no phylogenetic sense compared with the preferred tree. Superficially these

results imply that behavior is unnecessary, if not deleterious, in the reconstruction of araneoid relationships, and contradicts prior results from similar data partitioning (Prum, 1990; Wenzel, 1993). Ryan (1996), on the other hand, rejected the results from behavior (frog call evolution) in favor of morphology, DNA and allozymes.

The combined data results differ markedly in topology and resolution from those based on morphology alone. When combined with morphology, behavioral data do provide decisive phylogenetic signal. We interpret the poor behavior partition results as artifacts due to missing entries and low character: taxon ratios, *contra* Sanderson and Donoghue (1989). For one thing, 33 mostly binary characters cannot completely resolve 61 taxa. For morphology 26% of entries are missing (or inapplicable, as current algorithms cannot distinguish them); the same figure for behavior is 57%. Six terminals are completely unknown for behavior (eliminating these and rerunning the analysis still resulted in > 10 000 trees), and roughly 15 pairs of taxa are potentially identical to each other due to the pattern of missing entries and inapplicables. It is not therefore particularly surprising that behavior alone provides no resolution.

Nevertheless, although only 15% of the total characters are behavioral, they contribute seven of 15 (47%) unambiguous nephilid synapomorphies. Thus, behavioral data, while difficult to obtain or interpret, are useful. Furthermore, the potential of behavioral data in phylogenetic reconstruction appears justified by comparing the consistency and the retention indices between the data sets (behavior CI = 0.49, RI = 0.83; morphology CI = 0.30, RI = 0.73; complete data set CI = 0.31, RI = 0.73). These figures as well are skewed by differing amounts of missing data, as for the latter algorithms will "guess" so as to minimize homoplasy. Web-building behavior in spiders seems to evolve more slowly than morphology—particularly male genitalia (Scharff and Coddington, 1997)—and therefore even a few observations tend to be consistent among themselves and thus optimize without (much) homoplasy for missing entries.

Web-building behavior is far more difficult to observe than morphology, and even web architecture, which can be scored whenever an animal is encountered in the field, still requires targeted, contemporary fieldwork by specialists because classical collectors ignored it. Another problem is that animals in the field on the one hand may be capable of a behavior, but not perform it (e.g., derived attack behavior or split radii), or, on the other, features observed once (sample sizes for behavior are typically low) may be aberrant rather than typical of the lineage. No behavioral character is completely scored in this analysis. Missing data usually decrease resolution and increase the number of primary trees (Kearney, 2002; Kearney and Clark, 2003); this is true in the

behavioral matrix but not in the complete matrix, where the abundance of morphological characters structures the tree, yet is, in places, still indecisive.

In sum, behavior should be utilized in phylogenetics, although perhaps spider webs, wasp and bird nests provide more ample homology hypotheses than the behaviors and their products in other animal clades. Certainly, nephilid web architecture and web-building behaviors show high constancy within species and genera (Kuntner, 2005, 2006, 2007a; in preparation) and relatively low homoplasy as compared with theridiids (Eberhard et al., in press). However, the findings of some recent studies of araneoid spider web architecture found that this need not be the universal spider truth. Striking within species web architecture plasticity is known in theridiids (Agnarsson and Coddington, 2007a), some linyphiids (Hormiga, unpublished), and the araneid genus *Metazygia* (Kuntner, unpublished). More generally, Eberhard et al. in press) found high homoplasy levels in web evolution within Theridiidae.

Ethological homologies

The behavioral homologies highlighted by Eberhard (1982) have been used extensively in araneoid systematics ever since (Coddington, 1986a,b,c, 1989, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998; Agnarsson, 2004). All behavioral characters previously applied to nephilids (Hormiga et al., 1995; Kuntner, 2005, 2006, 2007a) have been used in this study. Many continue to serve as synapomorphies at the same nodes. The persistent non-sticky spiral (*216*) and outer leg 4 sticky spiral localization (*219*) remain unambiguous nephilid synapomorphies (Eberhard, 1982; Hormiga et al., 1995).

Typical uloborid, araneid and tetragnathid attack starts with wrapping the prey, followed by a bite (Eberhard, 1982). Nephilids, in contrast, bite their prey and then wrap (*222*). On this cladogram bite-wrapping defines Araneoidea, and is unreversed among nephilids (Fig. 34). However, because Deinopidae and Uloboridae are sister taxa and because likely non-orbicularian outgroups also bite-wrap, bite-wrapping may be plesiomorphic for a much larger clade. Wrap-bite, on the other hand, evolved six to seven times on this cladogram (present in Deinopoidea; independent origins in *Araneus*, *Argiope*, theridioids, and once or twice in tetragnathids).

Robinson and Robinson (1980) described the removal of the palpal tarsi in *Herennia* and *Nephilengys* males as the "eunuch" phenomenon. Kuntner (2005, 2007a) confirmed that the behavior is common in *Herennia* and *Nephilengys*, but here we report on a similar phenomenon in *Phonognatha*, *Deliochus* and *Acusilas*, apparently relatively basal araneids, and on a slightly different bulb loss in *Caerostris* (*225*). The optimization

in nephilids is ambiguous (basal in Nephilinae and secondarily lost in *Nephila*, or convergently gained in *Herennia* and *Nephilengys*, Fig. 35 is ACCTRAN). The same trait evolves convergently in araneids (four gains or a gain and three losses). Although it seems that bulb removal must be sexually selected, the phenomenon is complex and poorly understood (Kuntner, 2005, 2007a).

Body shake (**226**, Fig. 35), during which the spider rapidly and vigorously shakes itself and the web to become less conspicuous (Kuntner, 2006), is known thus far in one species of *Clitaetra*, *Nephilengys* and several *Nephila* and also in *Argiope* and *Azilia*. It may be homologous within nephilids and reversed in *Herennia* and *Nephila*, or convergently evolved in *Clitaetra* and *Nephilengys-Nephila*. Body-shaking in *Argiope* and *Azilia* evidently is convergent. Many of these animals are diurnal; the behavior probably confuses or repels predators.

Rectangular orb webs (**200**) probably evolved at the nephilid node and reversed to a more or less round orb in *Nephila* and *Nephilengys* (Fig. 32), although missing entries in *Clitaetra* make independent evolution possible within that genus. Web architecture tends to be consistent at generic levels in orb-weaving spiders, so the former is more likely. Kuntner et al. (submitted) studied web allometry in *Clitaetra irenae* during ontogeny, and hypothesized that the ladder web architecture (in adults) was an adaptation to arboricolous life history. An allometric growth of the web from an orb to a ladder allows the growing spider to remain on the same tree throughout its development because web width changes slower than web height. If such web architecture is homologous, the same may be true for *Herennia*.

Golden silk (**201**) is a *Nephila* synapomorphy (Fig. 32). It cannot be homologous to golden silk in some araneids. Particular *Cyclosa* and *Neoscona* species (although not in the current taxon sample) are known to produce golden webs (Levi, 1999; Kuntner and Agnarsson, unpublished), and some *Argiope* and *Cyclosa* egg cases are spun with golden silk (own data). Holl and Henze (1988) found yellow benzoquinones or napthoquinones in *Nephila clavipes* silk, and, based on reports by Bernays et al. (1984) and Estable et al. (1955), speculated that the substances may act against silk feeding animals, or have antibacterial properties. If the former, it seems unlikely to deter predacious insects as Holl and Henze suggested, but it might deter trapped prey from chewing their way free, or kleptoparasitic spiders, common in nephilids (not *Clitaetra*), from feeding on the host silk.

Three-dimensional barrier webs (**203**, Fig. 32) are not homologous among *Nephilengys-Nephila*, *Phonognatha*, araneoid sheet-web weavers, or *Leucauge* (scored as polymorphic). Blackledge et al. (2003) argue that wasp predation may have been one factor driving the evolu-tion of three-dimensional webs in araneoid sheetweb weavers. In nephilids it is synapomorphic for *Nephila* plus *Nephilengys*, which, as the largest araneoid spiders known, are probably subject to attack from various predators and parasitoids.

Hubs attached to substrate (**204**, Fig. 32) optimizes to the nephilid node but reverses at the *Nephila* node, as does the related feature "hub cup" (**208**, Fig. 33). Hub displacement evolves convergently in nephilids and araneids (**205**, Fig. 33). The feature probably increases attack efficiency on large webs because an animal starting from the top of the web has gravity on its side (Masters and Moffat, 1983; Kuntner et al. submitted). Double radius construction in *Uloborus* and nephilids (**210**, Fig. 33) and partial web renewal (**228**, Fig. 35) may be homologous (unknown due to the basal trichotomy not shown in figures). Double radius attachment has a single origin at the base of nephilids (**211**, Fig. 33, note comments re two reversals in *Nephila*). Secondary (split) radii here optimize as primitive for Orbiculariae, and their loss defines the tetragnathid plus reduced piriform clade (**212**, Fig. 34). Split radii are, however, quite rare in araneids, so again, the implication that they are primitively present in Araneidae may be incorrect. The persistent non-sticky spiral in the finished web evolves convergently in nephilids and *Phonognatha* (**216**, Fig. 34), *contra* Hormiga et al. (1995). Sticky spiral localization in orbicularians is primitively with the outer leg 1 (oL1), but independently changes to outer leg 4 (ol4) in nephilids and inner leg 1 (iL1) in the tetragnathid plus reduced piriform clade (**219**, Fig. 34). Leaf retreats optimize at the araneid node, but, again, the sample of araneids here is too poor to place much confidence in the implication that such is primitive for Araneidae and reversed in argiopoids and araneines. The off-web retreats of *Deliochus* and *Nephilengys* are not homologous (**229**, **230**, Figs 35 and 36). Web decoration with debris is not homologous in *Cyclosa*, *Dolichognatha* and *Nephila* (**231**, Fig. 36); all three *Nephila* species in which it was observed are Old World (possibly it is synapomorphic for that clade or a subset).

Evolution of sexual size dimorphism

This study followed Hormiga et al. (1995) in arbitrarily defining extreme sexual size dimorphism (SSD) as a male/female size ratio less than 0.4 (**122**; L = 3, CI = 0.33, RI = 0.91). SSD originates twice in Fig. 31: at the base of Nephilinae and convergently at the base of Araneidae (due to the reduced taxon sampling of Araneidae; see Hormiga et al., 2000). The araneid instance optimizes ambiguously. Fast optimization better preserves homology by reconstructing an origin at the base of araneids and loss in araneines (Fig. 31). If the (essentially arbitrary) definition of SSD is relaxed and *Clitaetra* scored as dimorphic, the
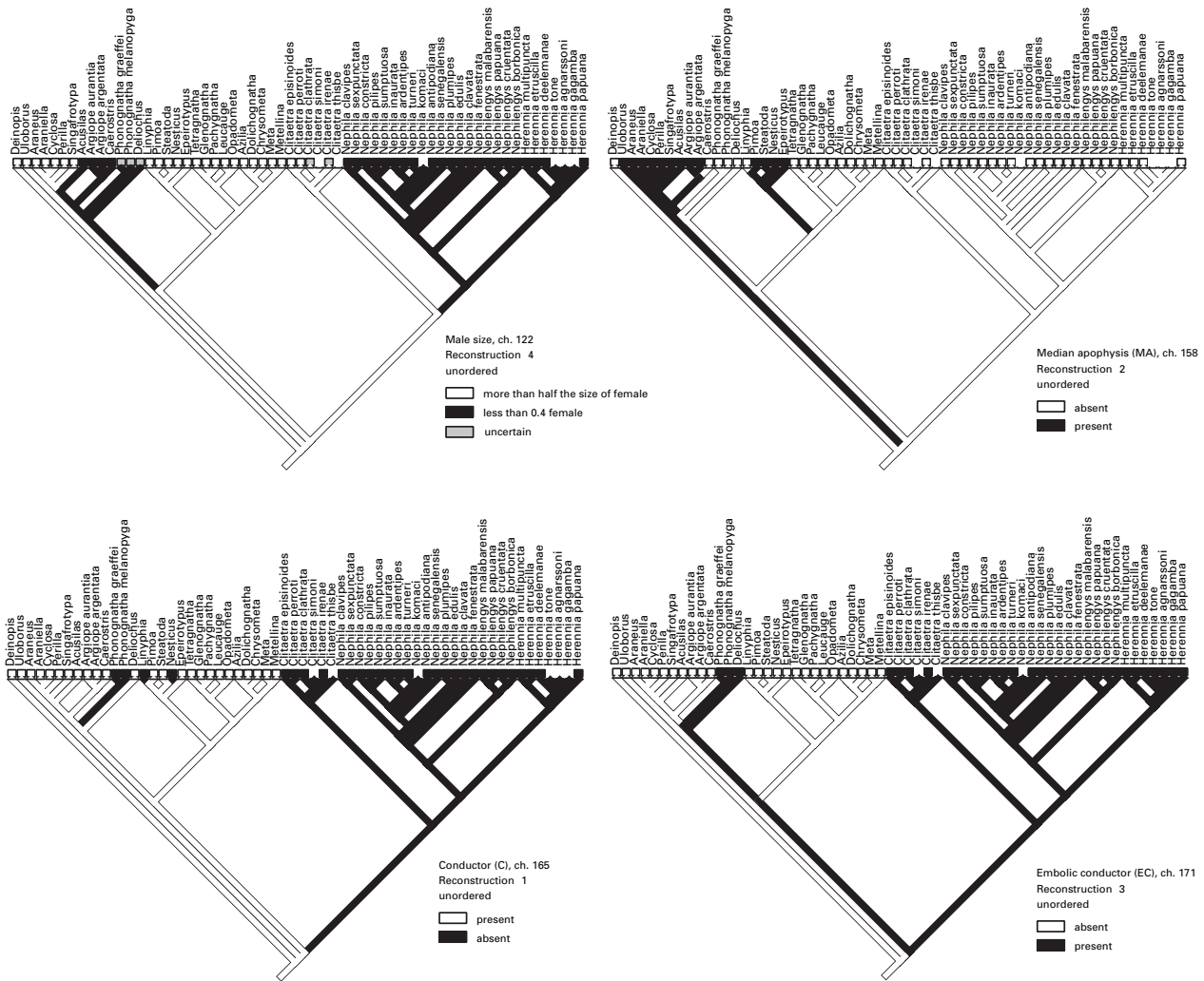
Fig. 31. Evolution of extreme sexual size dimorphism (character 122, L = 3, CI = 0.33, RI = 0.91), evolution of the median apophysis (character 158, L = 5, CI = 0.20, RI = 0.66), evolution of the conductor (character 165, L = 4, CI = 0.25, RI = 0.87) (unambiguous), evolution of the embolic conductor (character 171, L = 3, CI = 0.33, RI = 0.92) (ACCTRAN).

feature would be homologous on the cladogram, and lost twice distally.

Although SSD has been classically regarded as a nephilid autapomorphy, the possible placement of nephilids as sister to all remaining araneoids, and the relatively higher frequency of SSD in Araneidae means that SSD might have been arisen in the stem araneoid lineage, along with other intriguing innovations such as sticky silk.

However, regarding SSD as homologous is problematic. Sexual size dimorphism in spiders has been specifically discussed by Vollrath (1980, 1998), Vollrath and Parker (1992), Hormiga et al. (1995, 2000), Coddington et al. (1997), Moya-Laraño et al. (2002), and by Ramos et al. (2005). Coddington (1994) pointed out that "dimorphism" can arise via size change in either or both sexes, simultaneously or not, so that the apomorphy in a particular case cannot be inferred from the ratio alone.

Coddington et al. (1997) and Hormiga et al. (2000) made the same point.

Hormiga et al. (2000) optimized male and female body size independently on the cladogram and thereby inferred where SSD (arbitrarily defined) appeared, disappeared, and the relative contribution of each sex to the phenomenon. In the case of Nephilidae, SSD is clearly female gigantism rather than male dwarfism, as first suggested by Gerhardt (1924), because the trend was towards greater female size, not reduced male size (Coddington, 1994; Coddington et al., 1997; Hormiga et al., 2000; Higgins, 2002).

Male palpal homologies

Coddington (1990) broadly reviewed araneoid male palpal anatomy and discussed the problems in homology. His study was followed by more specialized

Fig. 32. Evolution of the orb web shape (character 200, L = 2, CI = 0.50, RI = 0.66) (ACCTRAN), evolution of silk color (character 201, L = 1, CI = 1.0, RI = 1.0) (unambiguous), evolution of the barrier/three-dimensional web (character 203, L = 3, CI = 0.33, RI = 0.88) (ACCTRAN), evolution of the hub position (character 204, L = 2, CI = 0.50, RI = 0.87) (unambiguous).

investigations into the palpal morphology of araneoid lineages: theridiids (Knoflach, 1994, 1996; Agnarsson, 2004; Knoflach and Pfaller, 2004; Agnarsson and Kuntner, 2005), pimoids (Hormiga, 1994a, 2003; Hormiga et al., 2005), linyphiids (Hormiga, 1994b, 2000; Miller and Hormiga, 2004), tetragnathids including nephilids (Hormiga et al., 1995; Kuntner, 2005, 2006, 2007a; Kuntner and Alvarez-Padilla, 2006; Alvarez-Padilla, 2007), araneids (Scharff and Coddington, 1997), cyatholipids (Griswold, 1997a,b, 2001), symphytognathids, anapids, micropholcommatids and anapids (Schuett, 2003), synotaxids (Agnarsson, 2003), and synaphrids (Lopardo et al., 2007; Miller, 2007; Lopardo and Hormiga, 2007). Most of these studies, including Griswold et al. (1998) but not Kuntner (2005, 2006, 2007a) applied similar character concepts to certain palpal sclerites such as the conductor and the median apoph-

ysis, although Coddington (1990; see **158, 165**) used fairly arbitrary rules to settle ambiguities in primary homology. Since then, new techniques are available (Agnarsson and Coddington, 2007b; Agnarsson et al., 2007). This study treats 64 palpal characters (**134–197**). Here we discuss the evolution of three selected palpal features, because their current interpretations differ and/ or this analysis suggests new homologies or character distributions.

Using topology as the principal criterion for primary homology, this study finds the presence of a median apophysis in *Uloborus*, most araneids and in the reduced piriform clade members, but not Linyphiidae (**158**, L = 5, CI = 0.20, RI = 0.66). The median apophysis is primitively absent in orbicularians, nephilids, tetragnathids, *Phonognatha* and *Deliochus*. The cladogram implies three to four independent

Fig. 33. Evolution of hub displacement (character 205, L = 4, CI = 0.50, RI = 0.86) (ACCTRAN), evolution of the hub-cup (character 208, L = 2, CI = 0.50, RI = 0.85) (unambiguous), evolution of radius construction (character 210, L = 2, CI = 0.50, RI = 0.85) (ACCTRAN), evolution of radius attachment on frame (character 211, L = 3, CI = 0.33, RI = 0.60) (unambiguous).

origins (Fig. 31), depending on optimizations within Araneidae. While the studies of Coddington (1990), Hormiga et al. (1995), Scharff and Coddington (1997), Griswold et al. (1998) and Agnarsson (2004) homologized the araneid median apophysis with the one in theridiosomatids, theridioids, pimoids and uloborids, the placement of *Deliochus* and *Phonognatha* at the base of Araneidae make convergent gain of the median apophysis more parsimonious.

Based on detailed dissections and new interpretations, the "conductor" (**165, 171**) in nephilids, *Phonognatha* and *Deliochus* is a part of the embolic division, not the tegulum (*contra* Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998). The phylogeny suggests that the conductor is primitively present in orbicularians and lost four times in Nephilidae, *Phonognatha*, Nesticidae and Linyphiidae (**165**, L = 4,

CI = 0.25, RI = 0.87, Fig. 31). However, in the alternative coding that homologizes the conductor of nephilids with that of the rest of Orbiculariae (Appendix 2), the conductor is universally present in araneoids and only absent in Nesticidae and Linyphiidae (in agreement with Coddington, 1990; Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998). Because both matrices produce identical topologies (see above), this study cannot refute either of the two alternative hypotheses of the homology of the conductor.

One of the two alternative matrices (Appendix 1) proposes a new homology within the Araneoidea: the embolic conductor in nephilids, *Deliochus* and *Phonognatha* (**171**). This sclerite attaches both to the embolus base and to the tegulum, unlike the conductor, which has no connection to the embolus base. Functionally but not topologically it is similar to most conductors (e.g.,
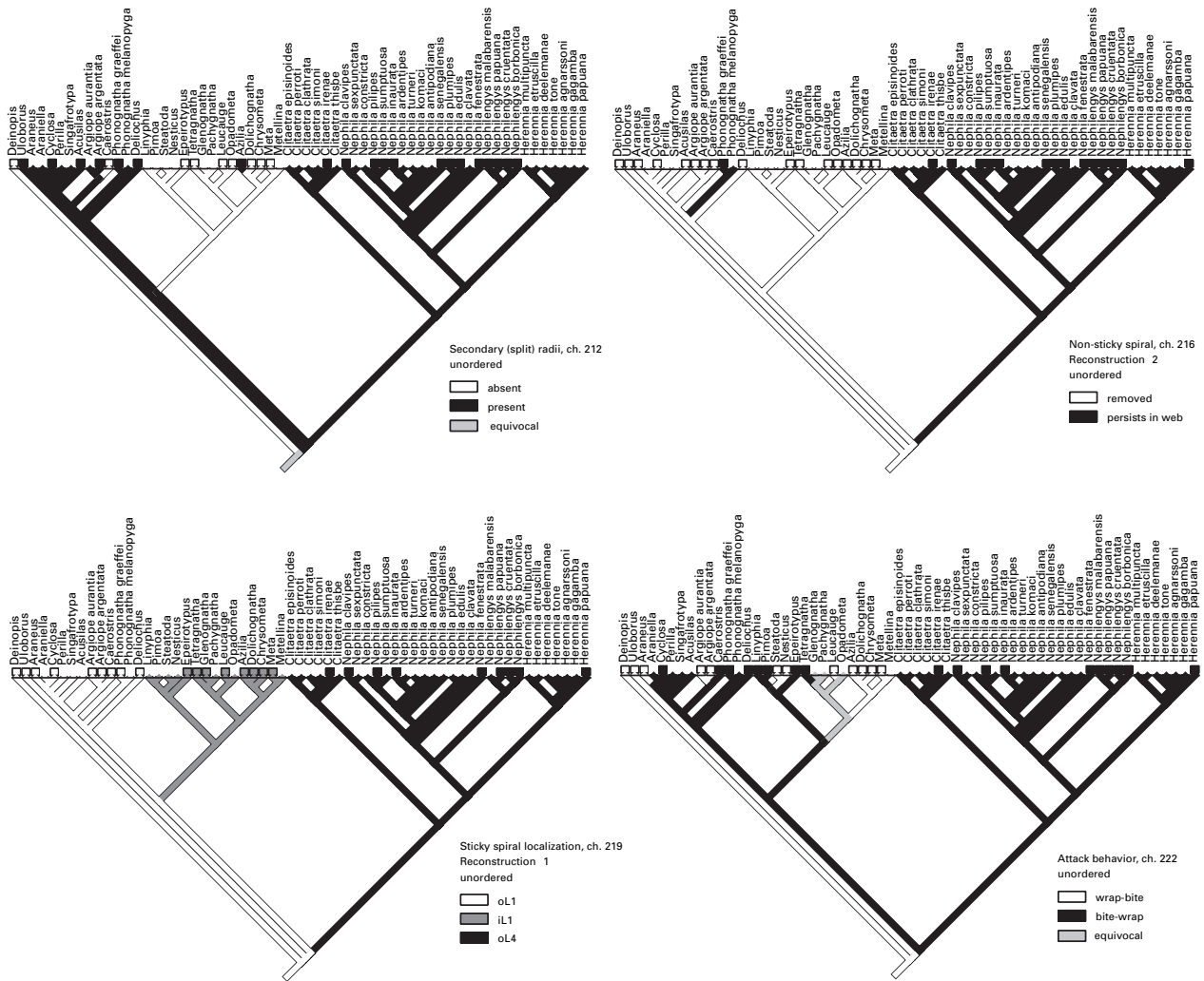
Fig. 34. Evolution of secondary (split) radii (character 212, L = 4, CI = 0.25, RI = 0.62) (unambiguous), evolution of non-sticky spiral removal/persistence (character 216, L = 2, CI = 0.50, RI = 0.92) (ACCTRAN), evolution of sticky spiral localization (character 219, L = 2, CI = 1.0, RI = 1.0) (unambiguous), evolution of attack behavior (character 222, L = 6, CI = 0.16, RI = 0.54) (unambiguous).

Tetragnatha, Leucauge): it protects the flexible embolus and facilitates entry into epignyal openings. Disjunct primary homology hypotheses normally preclude testing for potential homology of the nephilid embolic conductor with the araneoid (tegular) conductor through congruence. Therefore, we ran an alternative analysis (see above). The details in the embolic conductor differ between nephilids (one sclerite) and *Deliochus* and *Phonognatha*, where the embolic conductor is further subdivided, which brings into question the homology of the features. The outcome of the congruence test is ambiguous. While DELTRAN postulates three independent origins and thus refutes the homology of the nephilid sclerite with that of *Deliochus* and *Phonognatha*, the ACCTRAN alternative (Fig. 31) preserves the homology of the embolic conductor, optimizes its

presence as a synapomorphy for Araneoidea, and hypothesizes two losses, defining the classical araneids (argiopoid clade + Araneinae) *sensu* Scharff and Coddington (1997), and the "distal araneoids" *sensu* Griswold et al. (1998), but excluding the nephilids.

The ambiguity of the homology of the conductor and the embolic conductor is somewhat discouraging, but this study provides new homology hypotheses to be tested with new data sets. The distal palpal sclerites, which interact with the embolus (which contains the sperm duct) and with the female epigynum (itself varied) are extremely varied and are likely under severe selective pressure. As Scharff and Coddington (1997) demonstrated in the context of araneid morphology, the palpal characters are the most homoplasious, and thus it may not be surprising that
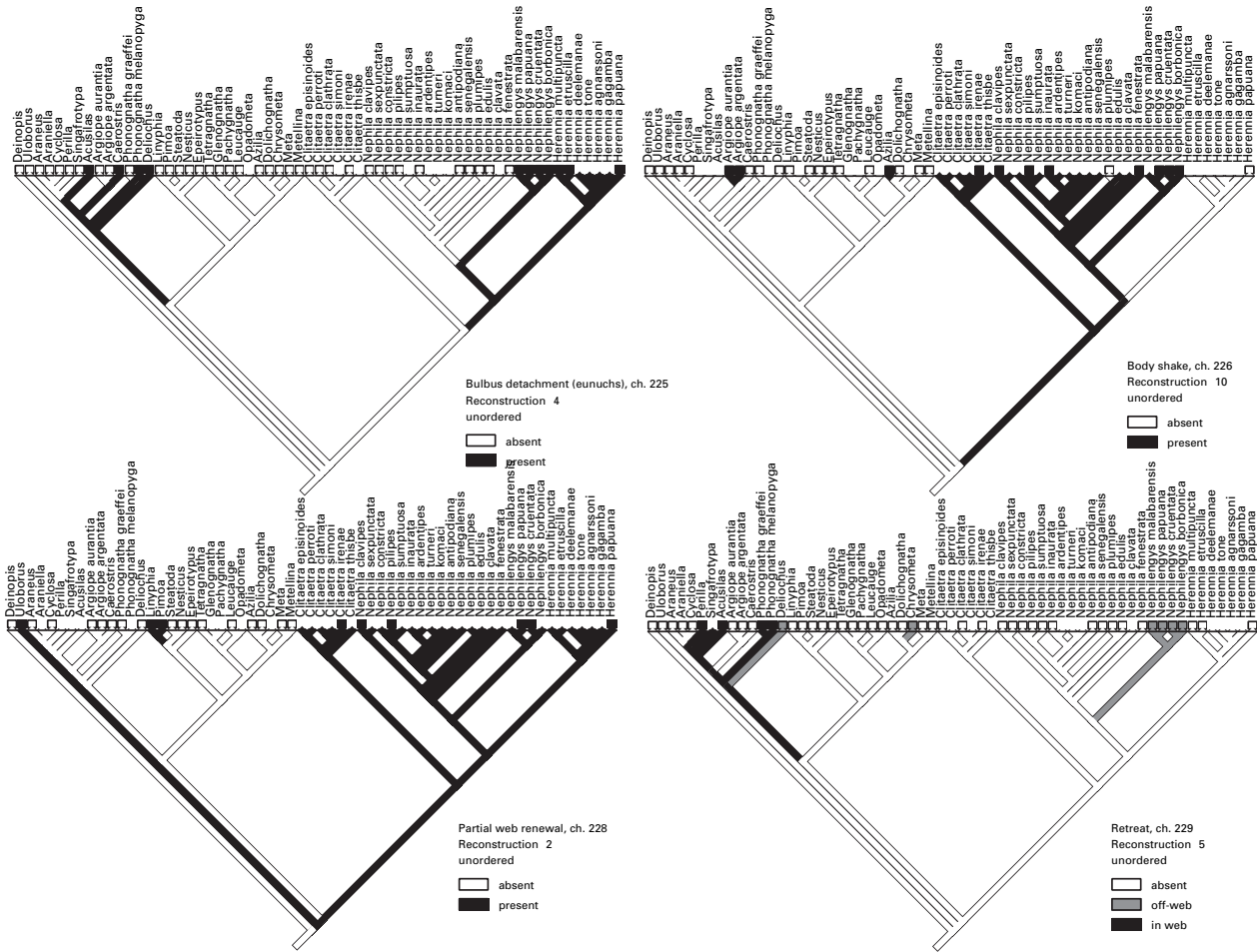
Fig. 35. Evolution of bulbus detachment (eunuch behavior, character 225, L = 6, CI = 0.16, RI = 0.50) (ACCTRAN), evolution of body shake (character 226, L = 5, CI = 0.20, RI = 0.60) (ACCTRAN), evolution of partial web renewal (character 228, L = 3, CI = 0.33, RI = 0.75) (ACCTRAN), evolution of retreat construction (character 229, L = 6, CI = 0.33, RI = 0.50) (ACCTRAN).

several non-homologous sclerites have taken the functional role of the conductor.

Nephilid genital evolution

Araneoid spiders are primitively entelegyne, possessing both the copulatory and fertilization ducts (**106, 110**). Only tetragnathines lack fertilization ducts (**110**) and thus exhibit a secondary haplogyne condition (not homologous to the condition found in Haplogynae). All nephilids are entelegyne, and so are *Meta* (Fig. 19H,I) and *Leucauge* (*contra* Wiehle, 1967a,b; who claimed *Meta* and *Nephila* are *semientelegyne*, and *Leucauge* is haplogyne).

The cladogram (Fig. 37) suggests that primitive nephilids had simple palps with a finger-like embolic conductor and unmodified embolus, and simple slit-like epigyna with small posterior copulatory openings. Ancestrally in nephilids (character evidence missing from *Clitaetra*), polygamy is not known. Figure 37

reveals that several genital and behavioral features coevolve: embolus breakage/plugging, extreme sexual size dimorphism, complex palps, bulb loss, and the chambered epigynum. While bulb loss reversal is a *Nephila* synapomorphy, simple long distal sclerites along with a simple slit epigynum and extreme female polyandry coevolve distally in *Nephila*. Extensive embolic conductors with distal hooks or curves in *Herennia* regularly block the epigyna, but derived *Nephila* (not *fenestrata*) have extremely thin, long, finger-like conductors that do not plug females as effectively (Schneider et al., 2001). Polyandry is not known to occur in *Nephilengys* and *Herennia*, which have the most complex palpal morphology.

Intersexual conflict is well documented in spiders but mostly in single species, and not in a phylogenetic context (Elgar, 1991; Schneider and Lubin, 1998; Schneider and Elgar, 2001, 2002; Herberstein et al., 2002; Fromhage and Schneider, 2005b; Schneider et al.,
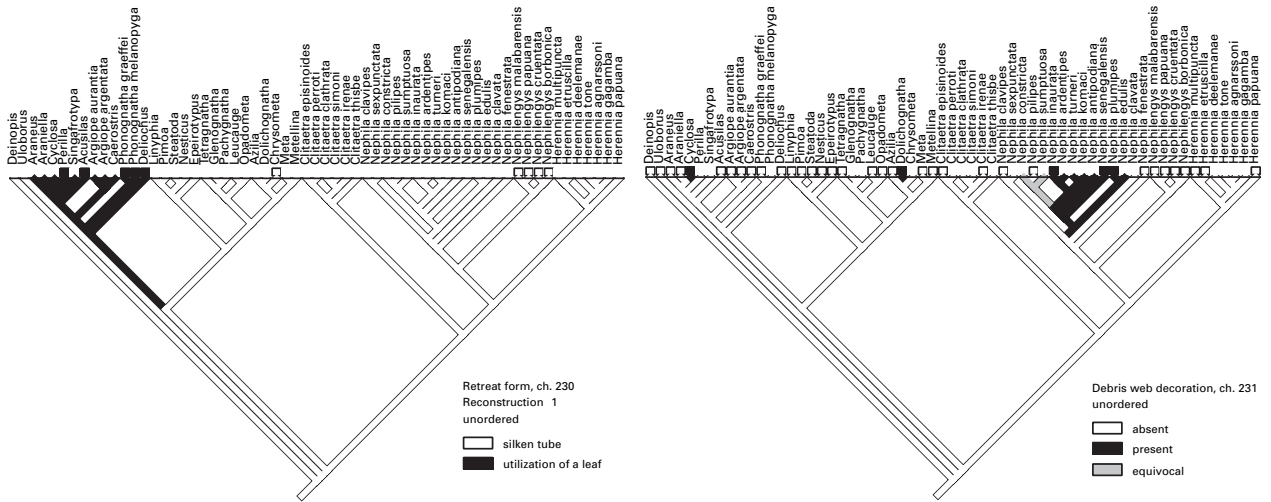
Fig. 36. Evolution of retreat form (character 230, L = 1, CI = 1.0, RI = 1.0) (ACCTRAN), evolution of debris web decoration (character 231, L = 4, CI = 0.25, RI = 0.25) (unambiguous).
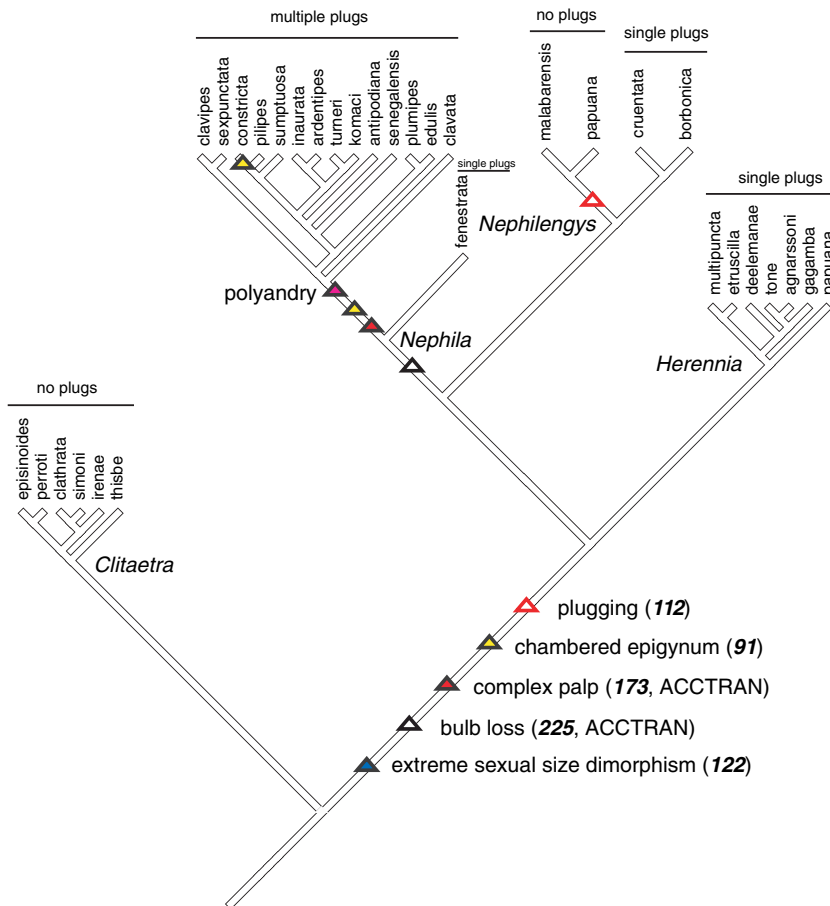
Fig. 37. Genital evolution with correlated behaviors and sexual size dimorphism.

2006). Recent literature (Huber, 1998; Eberhard, 2004) fails to confirm predictions of antagonistic coevolution in spiders and instead explains most genitalic diversity as driven by female choice (Eberhard, 1996). In the nephilid case, however, complex palpal morphology and male plugging behavior may be countermeasures to female polyandry. The plugging function of broken emboli in *Nephila fenestrata* is consistent with the latter and would provide support for the antagonistic coevolution scenario (Fromhage and Schneider, 2006).

Male genitalia apparently evolve rapidly and divergently (Eberhard, 1985). Araneid palps exhibit more homoplasy and thus more detectable evolutionary change than female genitalia (Scharff and Coddington, 1997). However, our results suggest that female epigyna in nephilids may coevolve just as rapidly as male palps, if subject to intersexual conflict and arms race. Nephilid genitalic evolution seems to contrast with better known animal models, and may be an example that challenges prevailing views of sexual selection and related evolutionary processes. As soon as the revision of *Nephila* is published (Kuntner, in preparation), Nephilidae will be completely revised and studied phylogenetically at the species level, and could become a model lineage for sexual evolution tests.

Conclusions

This new phylogeny of nephilid spiders poses new questions. Future studies should test the new nephilid placement at the base of the Araneoidea, and the placement of *Phonognatha* and *Deliochus* in or close to Araneidae with a denser taxonomic sample and different sources of data. Nephilid interrelationships are mostly weakly supported and also need further testing. The latter is especially important for testing evolutionary scenarios within nephilids. Has the evolution of male and female body size, as the results suggest, gradually changed towards the extreme sexual size dimorphism known in *N. constricta* and *N. pilipes*? Has web evolution indeed progressed from ladder webs on tree trunks towards large round aerial orb-webs? How does web architecture correlate with female gigantism? Hormiga et al. (1995) suggested that certain *Nephila* web features may have evolved in response to female size, but most nephilid web architectures pre-date giantism and are also found in small-bodied *Clitaetra*. Does golden silk, as faintly implied by Holl and Henze (1988) inhibit chewing by insects (or other spiders, e.g., kleptoparasites) and why does the feature persist within *Nephila*? Is the eunuch phenomenon adaptive, as more than a single origin on the phylogeny seems to suggest? Can the current evidence for antagonistic coevolution of male and female genital morphologies and sexual behaviors survive future tests? The present study serves as the basis for these further questions.

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Appendix 1

Data matrix.

Taxon/Character no. 1–63

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 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
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 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 0 0 2 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 0 0 0 0 0 0 0 0 - 0 ? 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0
Araneus	1 0 1 0 0 0 1 0 0 0 1 1 1 0 1 0 1 0 0 1 1 0 0 0 0 0 1 1 1 0 0 1 0 1 0 0 0 0 0 0 0 ? 0 0 0 - - - 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1
Araniella	0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 - 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Cyclosa	0 0 0 0 1 0 0 0 0 0 1 1 1 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 1 0 0 0 0 1 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 1
Perilla	0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0,3 1 1 1 1 0 0 1 - 1 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 1 1 - 0 0 0 0 1 1 1
Singafrotypa	1 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 2 0 0 0 0 0 0 0 3 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 - 1 1 1 1 1 1 0
Argiope_aurantia	0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 0 1 0 0 0 0 3 1 1 1 1 0 0 0 - 0 0 0 0 0 1 0 0 0 0 0 - - 0 - 0 0 0 0 0 0 0 - 1 0 0 0 1 1 0
Argiope_argentata	0 0 1 0 1 0 0 0 0 0 0 1 1 1 0 0 1 2 0 0 0 0 0 0 3 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 - - 0 - 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0
Acusilas	0 0 0 0 1 0 0 0 0 1 0 2 0 1 0 0 1 2 0 0 0 0 0 0 3 1 1 0 1 1 0 0 - 0 0 1 0 1 1 0 1 0 0 0 0 - - - 0 0 0 0 0 0 1 - 1 1 0 0 1 0 0
Caerostris	1 0 1 0 1 1 0 0 0 0 1 1 1 0 0 0 2 2 0 1 1 0 0 0 3 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 - 0 0 0 0 0 1 1 1 1 1 1 0 1 0 0
Linyphia	0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 1 - 1 0 0 0 1 1 0 0
Pimoa	0 0 0 0 0 0 0 0 0 0 0 2 2 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 1 0 1 1 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0
Steatoda	0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 1 0 0 0 0 0 1 1 - 1 0 0 1 0 0 0
Nesticus	0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 0 0 ? 0 0 1 1 1 - 0 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 1 1 - 2 1 0 1 0 0 0
Epeirotypus	1 0 0 0 0 0 0 0 0 1 1 2 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1 1 1 0 - 0 1 0 1 1 1 1 1 1 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 0 1 0 1 1 0
Tetragnatha	0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 1 1 0 1 0 0 0 0 0 1 0 1 - 1 0 1 0 0 0 - 0 1 0 1 0 0 0 0 1 1 - 0 2 0 0 0 0 0
Glenognatha	0 0 0 0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 1 0 1 0 0 0 3 1 1 1 0 - 1 0 0 1 1 1 0 1 0 1 0 0 1 0 0 - 1 0 1 0 0 0 0 1 1 1 0 2 0 1 0 0 0
Pachygnatha	0 0 0 0 1 0 0 0 0 1 1 2 2 0 0 0 1 0 1 0 1 0 0 0 3 1 1 1 0 - 0 0 0 0 1 1 1 1 0 1 0 0 0 0 - 0 0 0 0 0 0 0 0 1 1 - 1 2 0 0 0 0 0
Azilia	0 0 0 0 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 1 - 0 0 0 1 1 0 0 0 1 0 0 0 0 0 - - 1 - 1 1 0 0 1 1 1 - 0 0 0 0 0 0 0
Dolichognatha	0 0 0 0 0 0 0 0 0 0 1 2 2 0 0 0 0 0 0 0 0 0 0 ? 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 - 2 3 0 0 0 0 0
Meta	0 0 0 0 0 0 0 0 0 ? 0 2 0 0 0 0 1 0 0 0 1 0 0 0 3 0 1 1 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 - 1 1 1 0 0 1 1 1 1 0 0 1 0 0 0
Metellina	0 0 0 0 0 0 0 0 0 0 0 2 2 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0
Chrysometa	0 0 0 0 0 0 0 0 0 0 1 2 2 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0
Leucauge	1 0 0 0 0 0 0 0 0 0 1 2 2 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 - - 1 0 0 0 0 0 0 1 1 1 0 2 0 0 0 0 0
Opadometa	0 0 0 0 0 0 0 0 0 0 0 2 2 0 0 0 1 0 0 0 1 0 0 0 0 0 1 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 0 1 0,1 1 0 0,1 0 0 0 0 0
Deliochus	0 0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 0 1 0 2 0 0 0 0 0,1
Phonognatha_graeffei	1 0 0 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 0 1 0 0 1 0 0 1 1 1 0 - 0 1 1 1 0 0 0 0 0 1 1 0 1 0 0 - 1 0 0 0 1 0 0 0 0 1 0 0 0 0 1 1 1
Phonognatha_melanopyga	1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 0 1 0 3 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 0 0 1 1 2 3 0 0 0 0
Clitaetra_episinoides	0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 1 0 0 0 0 0 1 1 - 0 0 0 0 0 1 0
Clitaetra_perroti	0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 3 1 1 0 0 - 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 1 1 1 0 2 0 0 0 0 0
Clitaetra_clathrata	0 0 1 0 1 0 0 0 0 0 0 2 2 0 0 0 0 0 0 1 0 0 0 0 3 1 1 0 1 - 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 1 1 1 0 2 0 0 0 0 0
Clitaetra_irenae	0 0 0 0 1 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 1 0 0 0 3 1 1 0 1 - 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 1 1 1 0 3 0 0 0 0 0
Clitaetra_simoni	0 0 0 0 1 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 0 0 0 3 1 1 0 1 - 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 1 1 - 1 3 0 0 0 0 0
Clitaetra_thisbe	0 0 0 0 0 0 0 0 0 ? 0 2 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 - 0 0 0 1 1 1 1 0 0 1 1 0 1 0 0 - 0 - 0 1 1 1 1 1 1 1 1 3 0 0 0 0 0
Nephila_clavipes	1 1 0,1 0 0,1 0 0 0 0 0 1 1 1 0 0 0 1 0 1 1 0 0 0 0 2 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 1 1 0 1 1 1 1 1 1 1 0 1 1 1 0
Nephila_sexpunctata	1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 0 0 0 0 4 0 0 1 1 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0,1 - 0 0 0 1 1 0 0 1 0 0 1 0 0 0 1 0 1 0
Nephila_constricta	1 1 0,1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 2 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 1 1 0 1 1 0 1 0 0
Nephila_fenestrata	1 1 1 1 1 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 1 0 0 1 1 1 0
Nephila_senegalensis	1 1 0 0 1 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 2 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 1 0 0 1 0 0 0 1 1 1 0
Nephila_sumptuosa	1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 4 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 0 0 1 1 1 0
Nephila_inaurata	1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 1 0 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 1 1 0 0 1 1 1 0
Nephila_ardentipes	1 1 1 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0 0 4 0 0 1 1 0 0 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 0 0 1 1 1 0
Nephila_turneri	1 1 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 ? 1 0 0 0 0 0 4 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 0 0 1 1 1 0
Nephila_komaci	1 1 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 ? 1 0 0 0 0 ? 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 1 1 0 0 1 0 ? ? 1 0 0 1 1 1 0
Nephila_pilipes	1 1 0 0 0,1 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 0 0 0 0 0,1 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 0 0 0,1 0 1 1 1 0
Nephila_antipodiana	1 1 1 0 1 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 0 0 0 0 0,4 0 0 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 0 0 0 1 1 0
Nephila_clavata	1 1 0 0 1 0 0 0 0 0 0 1 1 0 0 0 1 0 1 0 0 0 0 0 3 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 0 0 1 1 0 0
Nephila_plumipes	1 1 1 0,1 0 0 0 0 0 0 1 1 1 0 0,1 0 1 0 0 0 0 0 0 0 4 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 0 0 1 1 1 0
Nephila_edulis	1 1 0,1 0 0 0 0 0 0 0 1 1 1 0 0,1 0,1 1 0 1 0 0 0 0 0 1 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 0 0 1 1 0 0
Herennia_multipuncta	0 0 1 1 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 1 0 0 1 1 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 1 1 0 1 1 0
Herennia_etruscilla	0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 ? 0 0 0 1 0 0 1 1 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 2 0 0 0 1 1 0
Herennia_deelemanae	0 0 1 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 2 0 0 0 1 0 0
Herennia_papuana	0 0 1 1 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 0 0 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 1 1 0 0 1 0 0 1 1 1 0 0 1 1 0
Herennia_tone	0 0 1 1 1 0 0 0 0,1 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 1 1 0 1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 1 0 0 2 0 0 0 1 0 0
Herennia_gagamba	0 0 1 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 2 1 0 1 1 0
Herennia_agnarssoni	0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 1 1 1 0 1 0 0
Nephilengys_malabarensis	1 1 0 0 0 0 0 1 0 0 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 1 1 1 1 1 - 1 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 2 1 0 1 1 0
Nephilengys_papuana	1 1 0 0 0 0 0 1 0 0 1 1 1 0 0 0 0 1 0 0 0 0 0 0 3 1 1 1 1 0 0 1 - 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0
Nephilengys_cruentata	1 1 0 0 1 0 0 1 0 0 0 1 1 0 0 0 0 1 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0
Nephilengys_borbonica	1 1 0 0 1 0 0 1 0,1 0 1 1 1 0 0 0 1 0 0 1 0 0 0 0 1 1 1 1 1 1 0 0 - 1 0 1 1 1 0 0 0 0 0 0 0 - 0 - 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0

Taxon/Character no.
- Deinopis
- Uloborus
- Araneus
- Araniella
- Cyclosa
- Perilla
- Singafrotypa
- Argiope_aurantia
- Argiope_argentata
- Acusilas
- Caerostris
- Linyphia
- Pimoa
- Steatoda
- Nesticus
- Epeirotypus
- Tetragnatha
- Glenognatha
- Pachygnatha
- Azilia
- Dolichognatha
- Meta
- Metellina
- Chrysometa
- Leucauge
- Opadometa
- Deliochus
- Phonognatha_graeffei
- Phonognatha_melanopyga
- Clitaetra_episinoides
- Clitaetra_perroti
- Clitaetra_clathrata
- Clitaetra_irenae
- Clitaetra_simoni
- Clitaetra_thisbe
- Nephila_clavipes
- Nephila_sexpunctata
- Nephila_constricta
- Nephila_fenestrata
- Nephila_senegalensis
- Nephila_sumptuosa
- Nephila_inaurata
- Nephila_ardentipes
- Nephila_turneri
- Nephila_komaci
- Nephila_pilipes
- Nephila_antipodiana
- Nephila_clavata
- Nephila_plumipes
- Nephila_edulis
- Herennia_multipuncta
- Herennia_etruscilla
- Herennia_deelemanae
- Herennia_papuana
- Herennia_tone
- Herennia_gagamba
- Herennia_agnarssoni
- Nephilengys_malabarensis
- Nephilengys_papuana
- Nephilengys_cruentata
- Nephilengys_borbonica

Character matrix (characters 126–180).

Taxon/Character no.	126	127	128	129	130	131	132	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	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	–	–	–	–	–	–	–	–	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	1	0	0	–	–
Araneus	1	2	0	0	1	1	1	0	0	1	1	0	0	0	1	1	0	–	1	0	0	0	0	0	0	0	0	1	0	0	–	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0
Araniella	1	2	0	0	0	0	1	0	0	1	2	0	0	0	1	1	0	–	1	0	0	0	0	0	0	0	0	1	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Cyclosa	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	1	0	0	?	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0
Perilla	1	2	0	0	1	1	1	0	0	0	2	0	0	0	1	1	0	–	1	0	0	0	0	0	0	0	0	?	0	0	?	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0
Singafrotypa	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	–	1	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Argiope_aurantia	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	?	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Argiope_argentata	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	–	1	0	0	0	1	1	0	0	0	?	0	1	?	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Acusilas	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	0	0	?	0	0	?	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0
Caerostris	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Linyphia	0	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	–	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pimoa	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0	0	0	0	–	1	1	–	1	1	1	1	0
Steatoda	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	–	1	1	3	3	3	0	0	0	0	0	0	0	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–	0	?	?	?	?	?	?	?	?
Nesticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	4	1	0	0	0	0	0	0	0	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–	0	?	?	?	?	?	?	?	?
Epeirotypus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	3	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0
Tetragnatha	0	0,1	1	1	0	2	0	1	1	0	0	1	0	0	0	0	0	–	0	2	3	3	1	1	0	0	0	0	0	0	–	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	2	2	0	0
Glenognatha	0	1	1	1	0	2	0	0	1	1	0	0	1	0	0	0	0	–	1	2	1	1	0	1	0	0	0	0	0	0	–	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	0	1	1	0	0
Pachygnatha	0	1	0	0	2	2	0	0	0	0	0	1	1	0	0	0	0	–	1	2	0	1	0	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	0	0	1	1	2	1	1	1	1	1	1	0	2	2	0	0
Azilia	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	–	1	0	1	1	1	1	0	0	0	0	0	0	–	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	0
Dolichognatha	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	–	1	1	0	1	0	1	0	0	0	0	0	0	–	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	1	1	0	0
Meta	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	3	3	1	0	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	0
Metellina	0	1	0	0	0	2	1	1	1	0	0	1	0	0	1	0	1	–	1	0	4	4	1	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0
Chrysometa	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	3	3	1	1	0	0	0	0	0	0	–	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	0
Leucauge	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	3	3	1	0	0	0	0	0	0	0	–	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
Opadometa	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	–	1	0	0	1	1	1	0	0	0	0	0	0	–	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1
Deliochus	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	0	–	0,1	0	0	5	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Phonognatha_graeffei	0	0	0	1	0	0	0	1	0	0	2	1	1	1	1	?	0	–	1	0	0	2	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Phonognatha_melanopyga	0	2	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	–	0	1	0	2	0	0	1	1	1	0	0	0	–	1	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Clitaetra_episinoides	0	2	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	–	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Clitaetra_perroti	0	2	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	–	1	0	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Clitaetra_clathrata	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	?	0	–	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Clitaetra_irenae	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	–	1	0	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Clitaetra_simoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Clitaetra_thisbe	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2	0
Nephila_clavipes	1	2	0	0	0	0	0	0	0	0	2	0	0	1	1	1	0	–	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	2	1	2	0	2	2	0	0
Nephila_sexpunctata	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	0	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_constricta	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_fenestrata	1	2	0	0	0	0	0	0	0	1	2	0	0	0	1	0	0	–	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_senegalensis	1	2	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	–	1	0	0	2	0	0	1	0	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_sumptuosa	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_inaurata	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_ardentipes	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_turneri	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_komaci	?	?	0	0	0	0	0	0	0	0	?	0	0	0	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	1	1	0	0
Nephila_pilipes	1	2	0	0	0	0	0	0	0	0,1	2	1	0	0	1	0	0	–	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_antipodiana	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_clavata	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	0	0
Nephila_plumipes	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Nephila_edulis	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0
Herennia_multipuncta	1	2	0	0	0	0	0	0	0	1	2	0	0	0	1	1	0	–	1	0	0	2	0	0	1	1	0	0	0	1	1	0	0	?	1	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0
Herennia_etruscilla	1	2	0	0	0	0	0	0	0	1	2	1	0	0	1	1	0	–	1	0	0	2	0	1	1	1	0	0	0	1	1	0	0	?	1	?	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1
Herennia_deelemanae	1	2	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	–	1	0	0	2	0	0	1	1	0	0	0	1	1	0	0	?	1	?	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1
Herennia_papuana	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	–	1	0	0	2	0	0	1	1	0	0	0	1	1	0	0	?	1	?	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1
Herennia_tone	?	?	0	0	0	0	0	0	0	0	2	0	0	0	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0	0	0	0	0	0	0	?	?	0	1	1	1	1	0	1
Herennia_gagamba	?	?	0	0	0	0	0	0	0	0	2	0	0	0	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0	0	0	0	0	0	0	?	?	0	1	1	1	1	0	1
Herennia_agnarssoni	?	?	0	0	0	0	0	0	0	0	2	0	0	0	?	?	0	–	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0	0	0	0	0	0	0	?	?	0	1	1	1	1	0	1
Nephilengys_malabarensis	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	1	1	2	1	0	1	1	0	0	0	1	0	0	0	–	0	0	0	0	1	0	0	0	0	–	1	1	1	0	1	0	1	1	0	0
Nephilengys_papuana	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	1	1	2	1	0	1	1	0	0	0	1	0	0	0	–	0	0	0	0	1	0	0	0	0	–	1	1	0	0	0	0	0	0	0	0
Nephilengys_cruentata	1	2	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	–	1	1	1	2	1	0	1	1	0	0	0	1	0	0	0	–	0	0	1	0	1	0	1	0	0	–	1	1	1	0	0	0	0	0	0	0
Nephilengys_bortonica	1	2	0	0	0	0	0	0	0	2	2	0	0	0	1	1	0	–	1	1	1	2	1	0	1	1	0	0	0	1	1	0	0	–	0	0	0	1	1	1	1	0	0	–	1	1	0	0	0	0	1	1	0	0

Taxon/Character no.	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231
Deinopis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	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	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	-	0	0	1	0	1	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	1	1	-	0
Araneus	2	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	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	0	0	0	0	0	-	0
Araniella	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	?	?	?	0	0	?	?	?	0	0	0	?	-	0	?	0	0	1	-	0	0	0	?	?	?	?	0
Cyclosa	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	?	?	0	0	0	?	?	?	0	0	0	0	0	0	?	0	0	1	-	?	0	1	1	0	?	-	1
Perilla	2	1	0	0	0	?	?	0	1	1	0	0	1	1	1	1	1	0	1	?	?	1	0	0	0	?	0	0	?	0	?	?	?	?	0	?	?	0	?	1	?	?	?	?	0	?	?	?	2	2	1
Singafrotypa	2	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	?	0	0	?	?	?	?	?	?	0	?	?	0	0	0	0	1	0	?	0	1	1	0	2	0	0
Argiope_aurantia	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	-	0
Argiope_argentata	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	?	0	0	0	1	0	0	0	0	1	0	2	2	0
Acusilas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Caerostris	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	-	0	1	0	0	0	-	-	0	0	1	0	0	1	0	0	0	1	1	0	-	0
Linyphia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	-	-	-	1	0	0	0	-	0	-	1	0	0	1	1	0	0	-	1	0	-	0
Pimoa	1	1	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	1	-	-	-	1	1	0	0	-	0	-	1	0	0	1	1	0	1	0	1	0	-	0
Steatoda	1	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	0	0	0	-	-	-	0	0	0	1	0	1	0	0	-	1	0	-	0
Nesticus	1	0	0	0	0	0	0	0	0	0	0	0	1	1	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	1	1	0	0	-	1	0	1	0
Epeirotypus	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	0	-	-	0	-	-	1	0	0	0	-	1	0	0	0	0	0	0	0
Tetragnatha	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	-	0	0	-	-	-	-	-	-	0	0	?	?	-	-	0	0	0	1	1	0	0	0	1	0	0	-	0	2	1	0
Glenognatha	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	-	-	0	0	-	-	-	-	-	-	0	0	0	?	-	-	-	-	-	1	1	0	0	0	1	0	0	-	0	1	1	0
Pachygnatha	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	-	-	-	1	1	0	0	0	1	0	0	0	0	1	1	0
Azilia	2	1	0	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	?	0	0	0	?	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Dolichognatha	2	1	0	0	1	0	?	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	0	0	0	1	0	0	0	0	0	0	0	0	0	2	2	0
Meta	2	1	0	0	?	?	?	1	0	?	0	0	0	1	?	?	0	1	1	0	0	0	0	?	1	0	0	0	0	0	0	1	0	0	0	?	0	1	2	0	0	0	0	0	0	0	0	0	0	?	0
Metellina	2	1	0	?	?	?	?	1	0	?	1	0	0	1	?	?	0	1	0	0	0	0	0	?	1	0	0	1	0	0	0	1	0	1	0	?	0	1	2	1	0	0	0	0	0	1	0	0	0	?	0
Chrysometa	2	1	0	0	?	?	?	1	0	0	0	0	?	1	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	?	2	2	1	0	0	0	0	0	1	0	0	1	?	0
Leucauge	1	0	1	0	?	?	?	1	0	1	0	0	?	1	?	?	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	-	-	-	1	1	0	0	0	-	0	1	0	1	1	0	1	0
Opadometa	0	0	0	1	0	0	?	0	0	0	0	0	0	1	?	?	0	0	0	-	-	0	0,1	-	0	0	0	0	-	-	-	0	0	1	-	-	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Deliochus	1	0	1	0	1	1	0	0	1	0	0	1	1	1	1	1	0	0	0,1	0	0	0	0,1	1	2	0	1	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Phonognatha_graeffei	1	2	0	0	1	1	1	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	1	1	1	?	0	0	1	0	0	0	?	0	0	0	0	0	1	0	1	1	1	1	2	2	1	1
Phonognatha_melanopyga	1	0	0	0	1	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	?	?	1	0	1	1	?	?	?	1	0	0	0	?	?	?	0	0	0	1	0	1	1	1	1	2	2	-	0
Clitaetra_episinoides	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	?	1	?	?	1	0	1	0	?	1	1	2	0	0	1	0	?	0	0	1	1	0	-	0
Clitaetra_perroti	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	?	?	1	1	1	?	?	?	1	0	1	0	?	0	?	?	0	0	1	0	?	0	0	1	0	0	-	0
Clitaetra_clathrata	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	?	0	?	1	1	1	1	?	?	?	1	1	1	0	?	0	?	?	0	0	1	0	?	0	0	1	0	0	-	0
Clitaetra_irenae	0	0	1	0	1	1	1	0	0	0	1	0	1	?	?	?	0	0	0	0	1	?	0	?	1	1	1	1	?	?	?	1	0	1	0	?	0	?	?	0	0	1	0	?	0	0	1	0	0	-	0
Clitaetra_simoni	?	?	?	?	?	?	?	0	0	0	1	0	1	?	?	?	0	0	0	0	1	?	0	?	1	1	1	1	?	?	?	1	0	1	0	?	0	?	?	0	0	1	0	?	0	0	1	0	0	-	0
Clitaetra_thisbe	0	2	0	0	1	1	1	0	0	0	1	0	?	?	?	?	0	0	0	0	1	?	0	?	1	1	1	1	?	?	?	1	0	1	0	?	0	?	?	0	0	1	0	?	0	0	1	0	0	-	0
Nephila_clavipes	0	2	0	1	1	1	1	1	0	0	0	0	1	1	1	1	0	1	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_sexpunctata	0	2	0	1	1	1	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	?	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_constricta	0	0	0	1	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_fenestrata	0	2	0	0	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_senegalensis	0	2	0	0	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_sumptuosa	0	2	0	0	1	1	1	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_inaurata	0	0	0	1	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_ardentipes	0	?	0	0	1	1	1	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_turneri	0	2	0	0	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_komaci	0	2	0	0	1	1	0	?	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_pilipes	0	2	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	1
Nephila_antipodiana	0	2	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_clavata	0	2	0	0	1	1	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_plumipes	0	2	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	0
Nephila_edulis	0	2	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	?	1	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	0	?	1
Herennia_multipuncta	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	0
Herennia_etruscilla	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	1
Herennia_deelemanae	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	1
Herennia_papuana	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	1
Herennia_tone	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	1
Herennia_gagamba	0	0	0	0	?	?	?	0	0	0	0	1	0	?	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	0
Herennia_agnarssoni	?	?	0	0	?	?	?	0	0	0	0	1	0	?	0	0	0	0	1	0	1	1	0	?	0	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	1	1	0	0	?	1
Nephilengys_malabarensis	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0	1	1	1	1	1	0	0
Nephilengys_papuana	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	1	1	1	2	0	0	0	1	0	1	1	0	1	1	0	0
Nephilengys_cruentata	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	-	1	1	1	1	1	1	1	0	1	1	1	2	0	0	1	-	1	1	1	0	1	1	0	0
Nephilengys_borbonica	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	?	1	1	?	1	0	1	1	1	1	0	0	1	1	?	2	0	0	1	-	?	1	1	0	1	1	0	0

Appendix 2

Alternative data matrix (see text for explanation).

Taxon/Character no.
Deinopis
Uloborus
Araneus
Araniella
Cyclosa
Perilla
Singafrotypa
Argiope_aurantia
Argiope_argentata
Acusilas
Caerostris
Linyphia
Pimoa
Steatoda
Nesticus
Epeirotypus
Tetragnatha
Glenognatha
Pachygnatha
Azilia
Dolichognatha
Meta
Metellina
Chrysometa
Leucauge
Opadometa
Deliochus
Phonognatha_graeffei
Phonognatha_melanopyga
Clitaetra_episinoides
Clitaetra_perroti
Clitaetra_clathrata
Clitaetra_irenae
Clitaetra_simoni
Clitaetra_thisbe
Nephila_clavipes
Nephila_sexpunctata
Nephila_constricta
Nephila_fenestrata
Nephila_senegalensis
Nephila_sumptuosa
Nephila_inaurata
Nephila_ardentipes
Nephila_turneri
Nephila_komaci
Nephila_pilipes
Nephila_antipodiana
Nephila_clavata
Nephila_plumipes
Nephila_edulis
Herennia_multipuncta
Herennia_etruscilla
Herennia_deelemanae
Herennia_papuana
Herennia_tone
Herennia_gagamba
Herennia_agnarssoni
Nephilengys_malabarensis1
Nephilengys_papuana
Nephilengys_cruentata
Nephilengys_borbonica

Taxon/Character no.

Character numbers: 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 99 100 101 102 103 104 105 106 107 108 109 110 111 112 113 114 115 116 117 118 119 120 121 122 123 124 125 126 127 128 129 130 131 132 133 134 135 136 137 138 139 140 141 142 143 144 145 146 147 148

Taxa:

- Deinopis
- Uloborus
- Araneus
- Araniella
- Cyclosa
- Perilla
- Singafrotypa
- Argiope_aurantia
- Argiope_argentata
- Acusilas
- Caerostris
- Linyphia
- Pimoa
- Steatoda
- Nesticus
- Epeirotypus
- Tetragnatha
- Glenognatha
- Pachygnatha
- Azilia
- Dolichognatha
- Meta
- Metellina
- Chrysometa
- Leucauge
- Opadometa
- Deliochus
- Phonognatha_graeffei
- Phonognatha_melanopyga
- Clitaetra_episinoides
- Clitaetra_perroti
- Clitaetra_clathrata
- Clitaetra_irenae
- Clitaetra_simoni
- Clitaetra_thisbe
- Nephila_clavipes
- Nephila_sexpunctata
- Nephila_constricta
- Nephila_fenestrata
- Nephila_senegalensis
- Nephila_sumptuosa
- Nephila_inaurata
- Nephila_ardentipes
- Nephila_turneri
- Nephila_komaci
- Nephila_pilipes
- Nephila_antipodiana
- Nephila_clavata
- Nephila_plumipes
- Nephila_edulis
- Herennia_multipuncta
- Herennia_etruscilla
- Herennia_deelemanae
- Herennia_papuana
- Herennia_tone
- Herennia_gagamba
- Herennia_agnarssoni
- Nephilengys_malabarensis1
- Nephilengys_papuana
- Nephilengys_cruentata
- Nephilengys_borbonica

Taxon/Character no.	149 150 151 152 153 154 155 156 157 158 159 160 161 162 163 164 165 166 167 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 183 184 185 186 187 188 189 190 191 192 193 194 195 196 197 198 199 200 201 202 203 204 205 206 207 208 209 210 211 212 213 214 215 216 217 218 219 220 221 222 223 224 225 226 227 228 229 230
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 1 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 0 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 - 0 0 0 0 - 0 0 0 - 0 0 - 0 0 0 0 0 0 - 0 - 0 0
Araneus	0 0 0 - 1 0 0 - 0 0 1 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 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 0 0 0 0 0 0 0 0 0

(character matrix continues — numeric/coded data for all listed taxa)

Taxa listed (rows): Deinopis, Uloborus, Araneus, Araniella, Cyclosa, Perilla, Singafrotypa, Argiope_aurantia, Argiope_argentata, Acusilas, Caerostris, Linyphia, Pimoa, Steatoda, Nesticus, Epeirotypus, Tetragnatha, Glenognatha, Pachygnatha, Azilia, Dolichognatha, Meta, Metellina, Chrysometa, Leucauge, Opadometa, Deliochus, Phonognatha_graeffei, Phonognatha_melanopyga, Clitaetra_episinoides, Clitaetra_perroti, Clitaetra_clathrata, Clitaetra_irenae, Clitaetra_simoni, Clitaetra_thisbe, Nephila_clavipes, Nephila_sexpunctata, Nephila_constricta, Nephila_fenestrata, Nephila_senegalensis, Nephila_sumptuosa, Nephila_inaurata, Nephila_ardentipes, Nephila_turneri, Nephila_komaci, Nephila_pilipes, Nephila_antipodiana, Nephila_clavata, Nephila_plumipes, Nephila_edulis, Herennia_multipuncta, Herennia_etruscilla, Herennia_deelemanae, Herennia_papuana, Herennia_tone, Herennia_gagamba, Herennia_agnarssoni, Nephilengys_malabarensis1, Nephilengys_papuana, Nephilengys_cruentata, Nephilengys_borbonica

Appendix 3

Clade diagnoses (clade numbers as in Fig. 28), and proposed classification: italicized names affect new classification (see text), other capitalized names are commonly accepted group names, names in quotes are informal clade names.

Clade 1—*Nephilidae*/Unambiguous synapomorphies: white sternal pigment (**character 26/state 1**), striated boss surface (**38/1**), narrow sustentaculum angle (**56/1**), female venter light pigmented pattern (**83/1**), male abdominal scutum (**123/1**), relatively smaller male chelicerae (**127/2**), absence of the conductor (**165/1**), embolus-tegulum orientation at 90° (**184/1**), hub position against substrate (**204/1**), hub displaced up (**205/1**), presence of hub-cup (**208/1**), double attachment of radius on frame (**211/1**), presence of tertiary split radii (**213/1**), NSS in finished web (**216/1**) and the outer leg 4 SS localization (**219/2**); ACCTRAN: white dots around spinnerets (**81/1**), lateral epigynal chamber openings (**92/1**), extensive embolic plugs (**113/1**), aggregate spigots embracing flagelliforms (**120/1**), membranous paracymbial base (**146/1**), rectangular paracymbium (**157/2**), paracymbial marginal fold (**150/1**), pronged apical paracymbium (**151/1**), very long embolus (**181/0**), rectangular orb web (**200/1**) with parallel sticky spirals (**215/1**), body shake (**226/1**); DELTRAN: reservoir with a switchback (**155/1**), hub bite-out absent (**206/1**), and partial web renewal (**228/1**).

Clade 2—*Clitaetrinae*/Unambiguous synapomorphies: PLE larger than PME (**16/1**) and large number of ventro-median sclerotizations (**66/1**); ACCTRAN: caudal copulatory openings (**103/0**), ventral tegular apophysis (**162/1**), absence of embolic conductor membrane (**172/0**), finger-like EC shape (**173/1**), denticulated embolus base (**187/1**), side change on web (**227/1**).

Clade 3—*Nephilinae*/Unambiguous synapomorphies: hairy carapace edge (**4/1**), ME and LE region tubercles (**11/1, 12/1**), orange/red sternum (**25/1**), sternal tubercles I, II, III, IV (**27/1, 28/1, 29/1, 31/1**), presence of a chilum (**34/1**), numerous dorso-lateral abdominal sclerotizations (**70/1**), dorso-central abdominal sclerotizations (**71/1**), grooved booklung cover (**85/0**), strongly sclerotized book lung spiracle area (**86/1**), epigynal openings in chambers (**91/1**), anterior epigynal area with apodemes and depression (**99/0, 100/1**), copulatory opening plugs (**112/1**), extreme sexual size dimorphism (**122/1**), horizontal male clypeus (**126/1**), transparent cymbium edge (**141/1**), sigmoidal EC (**178/1**), embolic apophysis (**188/1**); ACCTRAN: epigynal septum (**93/1**), epigynal sclerotized arch (**111/1**), ridged EC edge (**177/1**), zigzag NSS (**217/1**), eunuch behavior (**225/1**); DELTRAN: abdominal tip dots (**81/1**), ventral copulatory openings (**103/1**), extensive embolic plugs (**113/1**).

Clade 4—*Herennia*/Unambiguous synapomorphies: ridged carapace edge (**3/1**), carapace warts (**8/1**), wider than long sternum (**23/1**), lobed abdomen (**59/1**), truncated abdomen tip (**62/1**), abdominal sigillae (**72/1**), dark dorsum spots (**75/1**), apical tegular apophysis (**161/1**), hooked embolus (**192/1**), presence of pseudo-radii (**214/1**); ACCTRAN: short and stout femoral macrosetae (**44/1**), oval spermathecae (**107/2**), rounded apical paracymbium (**151/0**), flat embolus tip (**194/0**), body shake as threat response (**226/0**); DELTRAN: lateral epigynal chambers (**92/1**), epigynal septum (**93/1**), ridged EC edge (**177/1**), rectangular orb web (**200/1**) and bulbus detachment or eunuch behavior (**225/1**).

Clade 5—*Nephileae*/Unambiguous synapomorphies: high and wide female head region (**1/1, 2/1**), widely separated LE from ME (**13/1**), double ventral tegular switchback (**156/1**), presence of a barrier web (**203/1**); ACCTRAN: dorsum paired light dots (**77/1**), venter transverse lines (**84/1**), posteriorly broad epigynal septum (**94/1**), round orb shape (**200/0**), SS spiraling (**215/0**); DELTRAN: paracymbium apical prong (**151/1**), zigzag NSS (**217/1**) and body shake (**226/1**).

Clade 6—*Nephilengys*/Unambiguous synapomorphies: female carapace macrospines (**7/1**), light pigment abdominal band (**73/1**), inconspicuous dorsum pattern (**74/0**), two palpal patellar macrosetae (**136/2**), mesal tegular apophysis (**163/1**) and an off-web retreat (**229/1**); ACCTRAN: four spotted venter (**84/2**); DELTRAN: ridged EC edge (**177/1**), no NSS contact while laying first SS (**218/1**) and bulbus detachment or eunuch behavior (**225/1**).

Clade 7—*Nephila*/Unambiguous synapomorphies: presence of PME and PLE tapeta (**17/1, 18/1**), presence of the frontal sternal tubercle (**31/1**), tibial tufts (**49/1, 50/1, 51/1**), epigynal ventral swelling (**89/1**), juxtaposed male lateral eyes (**124/1**), finger-like EC shape (**173/1**), golden silk (**201/1**), aerial hub position (**204/0**), absence of the hub-cup (**208/0**); ACCTRAN: medially dark sternum (**25/2**), absence of the sternal white pigment (**26/0**), smooth EC edge (**177/0**), NSS contact while laying first SS (**218/0**), absence of eunuch behavior (**225/0**); DELTRAN: dorsum paired light dots (**77/1**), venter transverse lines (**84/1**).

Clade 8—*Araneoidea*/Unambiguous synapomorphies: female ventro-median sclerotizations (**65/1**), dorso-median abdominal apodemes (**69/1**), absence of cribellum (**114/1**), PMS nubbin (**116/1**), sparse PMS aciniform field (**117/1**), presence of the paracymbium (**141/1**), embolus-tegulum membrane (**185/1**), enlarged embolus base (**186/1**), bite-wrap attack (**222/1**); ACCTRAN: ventral copulatory opening position (**103/1**), peripheral PLS mesal cylindrical gland spigot position (**119/1**), male cephalic region normal (**125/1**), sperm reservoir switchback (**155/1**), presence of the embolic conductor (**171/1**), absence of the embolus distal apophysis (**193/1**), vertical orb-web (**199/1**), no NSS contact while laying first SS (**218/1**).

Clade 9—Araneidae + "derived araneoids"/Unambiguous synapomorphies: absence of carapace hairs (*10/1*), presence of PME and PLE tapeta (*17/1, 18/1*), absence of the sustentaculum (*55/1*), juxtaposed male LE (*124/1*); ACCTRAN: short tarsus 4 median claw (*54/1*), venter with longitudinal lines (*84/4*), subdivided EC (*175/1*), hub bite-out (*206/0*), cut and reeled radii (*210/1*), whole web replacement (*228/0*); DELTRAN: male cephalic region normal (*125/1*), embolus of medium length (*181/1*).

Clade 10—*Araneidae*/Unambiguous synapomorphies: wide LE separation from ME (*13/1*), sternal tubercle I (*27/1*), female chilum (*34/1*), sigmoidal first femur (*42/1*), epigynal chambers (*91/1*), epigynal septum (*93/1*), epigynal embolic plugs (*112/1*), transparent cymbial ectal margin (*141/1*), glabrous paracymbial edge (*148/0*), small tegulum (*153/1*), embolus only distally with ejaculatory duct (*157/1*), leaf retreat (*230/1*); ACCTRAN: advanced caudal copulatory openings (*104/1*), lobed spermathecae (*107/0*), extreme sexual size dimorphism (*122/1*), spiraled reservoir course (*155/0*), NSS contact while laying first SS (*218/0*), bulbus detachment (eunuch) behavior (*225/1*), off-web retreat (*229/1*). DELTRAN: ventral copulatory openings (*103/1*), subdivided EC (*175/1*).

Deliochus autapomorphies (potential synapomorphies though not tested) include (unambiguous): paired epigynal flap (*97/1*), hooked embolus (*192/1*), hub displaced down (*205/2*); ACCTRAN: posteriorly broad septum (*94/1*); DELTRAN: short tarsus 4 median claw (*54/1*), lobed spermathecae (*107/0*), EC presence (*171/1*), bulbus detachment (eunuch) behavior (*225/1*), off-web retreat (*229/1*).

Clade 11—*Phonognatha*/Unambiguous synapomorphies: high female head region (*1/1*), posterior male paturon tubercle (*129/1*), long cymbium (*139/1*), absence of conductor (*165/1*); ACCTRAN: extensive embolic plugs (*113/1*), "Phonognatha" type paracymbium (*147/5*), barrier web (*203/1*), hub displaced up (*205/1*), absence of hub bite-out (*206/1*), tertiary (split) radii (*213/1*), NSS in finished web (*216/1*); DELTRAN: short tarsus 4 median claw (*54/1*), lobed spermathecae (*107/0*), presence of EC (*171/1*), in-web retreat (*229/2*).

Clade 12— "Araneids excluding *Phonognatha, Deliochus*"/Unambiguous synapomorphies: sternal tubercle II (*28/1*), sustentaculum presence (*55/0*), dorso-lateral abdominal sclerotizations (*70/0*), dorso-central abdominal sclerotizations (*71/1*), strongly sclerotized booklung area (*86/1*), depression anterior to the epigynal area (*100/1*), extensive PMS aciniform field (*117/0*), distal aggregates embracing flagelliform spigots (*120/1*); ACCTRAN: LE tubercle (*12/1*), long tarsus 4 median claw (*54/0*), spherical spermathecae (*107/1*), central PLS mesal cylindrical gland spigot position (*119/0*), median apophysis (*158/1*), EC absent (*171/0*), presence of stipes (*190/1*); DELTRAN: closed hub (*207/0*).

Clade 13—"Argiopoid clade"/Unambiguous synapomorphies: hairy carapace and carapace edge (*4/1, 10/0*), procurved posterior eye row (*14/1*), narrow PME canoe tapetum (*17/2*), straight first femur (*42/0*), anterior abdominal humps (*60/1*), truncated abdomen tip (*62/1*), anteriorly broad epigynal septum (*94/2*), large conductor (*166/1*), stabilimentum (*202/1*); ACCTRAN: short caudal abdomen (*63/0*), median apophysis thread-like spur (*160/1*), conductor grooved for embolus (*167/1*), flat embolus tip (*194/0*), retreat absent (*229/0*); DELTRAN: lateral eyes on a tubercle (*12/1*), central PLS mesal cylindrical spigot (*119/0*), extreme sexual size dimorphism (*122/1*).

Clade 14—*Araneinae*/Unambiguous synapomorphies: ventro-lateral abdominal sclerotizations absent (*67/1*), venter light pigmented pattern (*83/1*), simple epigynal openings (no chambers) (*91/0*), epigynal septum absent (*93/0*), epigynal scape (*96/1*), strong male leg II tibial macrosetae (*131/1*), male endite tooth (*132/1*), two palpal patella macrosetae (*136/2*), subterminal apophysis (*196/1*), terminal apophysis (*197/1*); ACCTRAN: very long abdomen (*57/0*), no sexual size dimorphism (*122/0*), male coxa I hook (*130/1*), palpal femoral tubercle (*135/1*), short and thick embolus (*181/2, 182/1*), bulbus detachment behavior absent (*225/0*); DELTRAN: lateral eyes on a tubercle (*12/1*).

Clade 15—*Tetragnathidae*/Unambiguous synapomorphies: presence of venter light pigmented pattern (*83/1*), larger male versus female cheliceral size (*127/1*), finger-like paracymbium (*147/1*), conductor grooved for embolus (*167/1*); ACCTRAN: sternal tubercle III (*29/1*), posteriorly broad septum (*94/1*), oval spermathecae (*107/2*), long male palpal trochanter (*134/1*), wrap-bite attack (*222/0*); DELTRAN: pronounced fovea (*6/1*), smooth cheliceral furrow (*40/1*).

Clade 16—"Metines" (**In Part**)/The family group names Metinae and Metidae have been used in araneological literature. Brignoli (1983) ranked them in his catalog as a family (Metidae) and included 37 genera although he noted that a modern definition of the group was lacking. Hormiga et al. (1995) referred to this paraphyletic group as the "Metines" (in their sample the "Metines" included the genera *Azilia*, *Dolichognatha*, *Meta*, *Chrysometa*, *Metellina* and *Leucauge*, all of them in Brignoli's Metidae). As the results of the present analysis (Fig. 28) continue to suggest that the "metines" are a grade, we treat its two main lineages (Clades 16 and 17) as separate groups. Unambiguous synapomorphies of Clade 16 (*Azilia*, *Dolichognatha*, *Meta*, *Chrysometa*, *Metellina*): cymbial basal process (*142/1*), thick embolus (*182/1*); ACCTRAN: little separated PME (*15/0*), sternal tubercle I (*27/1*), short embolus (*181/2*), embolic apophysis (*188/1*); DELTRAN: sternal tubercle III (*29/1*), wrap-bite attack (*222/0*).

Clade 17—"Metines" (**In Part**) (*Leucauge* + *Opadometa*)/Wunderlich, 1986, p. 105) hypothesized three

synapomorphies for Leucauginae without specifying the group's taxonomic composition: feathery trichobothria (on femur IV), sclerotized epigynum and the cymbial apophysis. This study recovers the following unambiguous synapomorphies: wide sternum (*23/1*), femoral IV trichobothria in rows (*48/1*), central light pigmented spot on venter (*84/0*), slit-shaped copulatory openings (*105/0*), membranous spermathecae (*109/1*), aggregate spigots embracing flagelliforms (*120/1*), conductor secondary apophysis (*169/1*), unsclerotized embolus (*183/1*); ACCTRAN: embolic plugs (*112/1*); DELTRAN: sternal tubercle III (*29/1*), oval spermathecae (*107/2*), long palpal tibia (*137/1*), sperm reservoir switchback (*155/1*), embolus enclosed in conductor (*168/1*).

Clade 18—Tetragnathinae/Unambiguous synapomorphies: PME tapetum absent (*17/0*), long endites (*20/0*), epigynal plate absent (*87/1*), fertilization ducts absent (*110/1*), male cheliceral clasping spurs (*128/1*), constricted cymbium (*138/1*), long cymbium (*139/1*), articulated paracymbium attachment (*145/2*), enlarged sperm reservoir (*154/1*), embolus and conductor spiral (*168/2*), extended leg web posture (*220/1*); ACCTRAN: sternum fused to pleura (*22/1*), sternal tubercle III absent (*29/0*), lobed spermathecae (*107/0*), wide spermathecae separation (*108/0*), anterior paracymbial apophysis (*149/1*), spiraled reservoir course (*155/0*), bite-wrap attack (*222/1*); DELTRAN: anterior epigynal area apodemes (*99/0*).