

A monograph of *Nephilengys*, the pantropical ‘hermit spiders’ (Araneae, Nephilidae, Nephilinae)

MATJAŽ KUNTNER

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. and Department of Biological Sciences, George Washington University, Washington DC, U.S.A.

Abstract. The nephilid genus *Nephilengys*, known for its synanthropic habits, large webs with a retreat and the extreme sexual size dimorphism, is revised. Of the twenty-three available names, only four species with a globally allopatric distribution are recognized, illustrated and described from both sexes: *N. cruentata* (Fabricius, 1775) inhabits tropical Africa and South America, where it has probably been introduced; *N. borbonica* (Vinson, 1863) is found on Madagascar, Comoros, Seychelles and the Mascarene Islands; *N. malabarensis* (Walckenaer, 1842) ranges from India and Sri Lanka to China, Japan and eastern Indonesia; *N. papuana* Thorell, 1881 **stat.n.** is known from New Guinea and tropical Australia. *Nephila instigans* Butler, 1876 is the proposed **syn.n.** of *N. borbonica*; *N. borbonica livida* Vinson, 1863 is **syn.n.** of *N. borbonica*; *N. niahensis* Deeleman-Reinhold, 1989 is **syn.n.** of *N. malabarensis*; *N. rainbowi* Hogg, 1899 is **syn.n.** of *N. papuana*. *N. kenmorei* Barrion & Litsinger, 1995, here proposed as a *nomen dubium*, is an araneid. *Nephilengys* biology is reviewed and its anatomy summarized for use in a phylogenetic analysis of 197 characters scored for all *Nephilengys*, selected nephilid species and non-nephilid outgroups. Two new clades are circumscribed, the ‘*cruentata* species group’ (with *N. cruentata* and *N. borbonica*) and the ‘*malabarensis* species group’ (with *N. malabarensis* and *N. papuana*).

Introduction

Species of *Nephilengys* L. Koch, 1872 are familiar to most tropical biologists. They construct large aerial orb webs more than a metre high with a tubular retreat connected to the hub. Their webs lack the golden colour typical of *Nephila*, and are always built against substrates such as tree trunks (Figs 12B; 21; 34A) or rock outcrops (Fig. 12C), but are noted mostly against house walls (Figs 18C, D; 19) or roofs (Figs 12A; 20; 34B). *Nephilengys* species are the most synanthropic of all nephilids and even have vernacular names, e.g. hermit spiders in South Africa (Filmer, 1991; Leroy & Leroy, 2000). Their extreme sexual size dimorphism with giant females (Figs 1; 11; 19; 25D) and vivid coloration (Figs 11; 18; 25; 33) make them popular subjects of biological studies (see ‘Biology’ for a review). With an understanding of the systematics of the group, *Nephilengys*

may challenge the better known sister genus *Nephila* in becoming a model organism in many biological studies.

Nephilengys appears regularly in popular natural history literature on the spiders of Africa (Leroy & Leroy, 2000: 28, 65; Filmer, 1991: 51) and Asia (Koh, 1989: 26; Vijayalakshmi & Ahimaz, 1993: 72; Murphy & Murphy, 2000: 383), although, curiously, not in Australian and American popular literature. Despite much biological interest, the genus remains unrevised and impossible to identify reliably in certain regions, notably in Australasia and Madagascar with adjacent islands. The most recent taxonomic revision (with compiled taxonomic history) of *Nephilengys* is Dahl’s (1912) worldwide treatment of *Nephila* and *Nephilengys*. Dahl (1912: 46–49) recognized only two *Nephilengys* species, *N. cruentata* (Fabricius, 1775) with three subspecies and *N. malabarensis* (Walckenaer, 1842). The latest spider catalogue prior to this revision (Platnick, 2005) lists six species and an additional subspecies of *Nephilengys* worldwide.

According to Kuntner (2005a, 2006), the orb-weaving spider family Nephilidae Simon contains the (sub)tropical genera *Nephila* Leach, 1815, *Herennia* Thorell, 1877 and *Clitaetra* Simon, 1889 in addition to *Nephilengys*. In this study, four

Correspondence: Matjaž Kuntner, Institute of Biology, Scientific Research Centre of the Slovenian Academy of Sciences and Arts, Novi trg 2, PO Box 306, SI-1001 Ljubljana, Slovenia. E-mail: kuntner@gmail.com

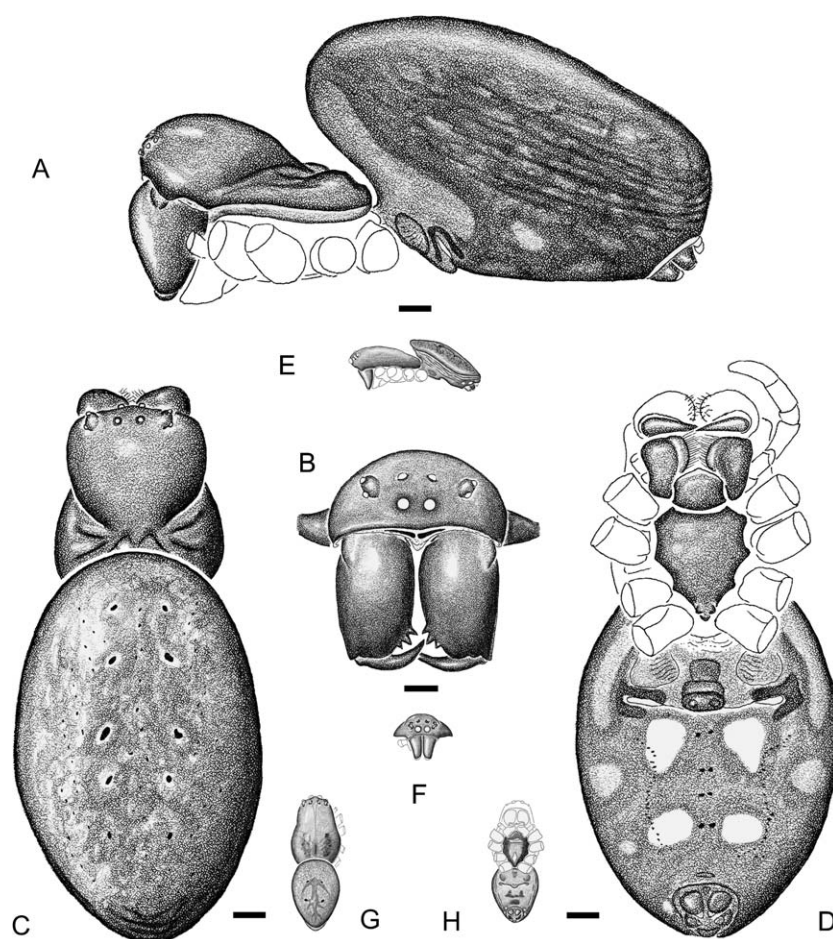


Fig. 1. *Nephilengys cruentata* somatic morphology and sexual dimorphism. A–D, female from South Africa (ng12/fl1): A, lateral; B, frontal; C, dorsal; D, ventral. E–H, male from Mozambique (ng8/m1): E, lateral; F, frontal; G, dorsal; H, ventral. Note that corresponding female and male views are on the same scale. Scale bars = 1.0 mm.

species of *Nephilengys* are recognized, diagnosed, described and illustrated. *Nephilengys* biology, based on observations of all four species, and anatomy are >reviewed for use in a species-level nephilid phylogenetic analysis; this is based on the matrix of Kuntner (2006) but with the inclusion of all *Nephilengys* species. New clades, the ‘*cruentata* species group’ (with *N. cruentata* and *N. borbonica*) and the ‘*malabarensis* species group’ (with *N. malabarensis* and *N. papuana*), match Dahl’s delimitation of *N. cruentata* and *N. malabarensis*.

Materials and methods

Nephilid specimen database

Two thousand, two hundred and sixty-one *Nephilengys* specimens were examined representing 757 species records. Here, only the type material is listed, but the complete specimen examined lists are provided as Supplementary material and online (www.nephilidae.com) as an extraction from BIOTA (Colwell, 1999). Nephilid

specimen databasing is described in Kuntner (2005a, 2006). At least one specimen from each examined sample received a unique specimen code; these are listed throughout the paper in descriptions, behavioural observations and figure captions to facilitate museum voucher comparisons.

The following museum abbreviations are used:

AM Australian Museum, Sydney, Australia (Mike Gray, Graham Milledge).

AMNH American Museum of Natural History, New York, U.S.A. (Norman I. Platnick, Lou Sorkin).

BMNH The Natural History Museum, London, U.K. (Janet Beccaloni).

CAS California Academy of Sciences, San Francisco, California, U.S.A. (Charles Griswold, Darrel Ubick).

DNSM Durban Natural Science Museum, Durban, South Africa (Tanza Crouch).

FM Field Museum, Chicago, Illinois, U.S.A. (Petra Sierwald, Philip Parillo).

MCSNG Museo Civico di Storia Naturale, Genova, Italy (Giuliano Doria).

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (Gonzalo Giribet, Laura Leibesperger).

MHNG Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland (Peter Schwendinger).

MNHN Muséum National d'Histoire Naturelle, Paris, France (Christine Rollard).

NHMW Naturhistorisches Museum Wien, Vienna, Austria (Jürgen Gruber).

NMB Naturhistorisches Museum Basel, Switzerland (Ambros Haengggi, Edi Stöckli).

NMP Natal Museum, Pietermaritzburg, South Africa (Guy Redman).

OUMNH Oxford University Museum of Natural History, Oxford, U.K. (James E. Hogan).

PPRI Plant Protection Research Institute, Pretoria, South Africa (Ansie Dippenaar-Schoeman).

QM Queensland Museum, Brisbane, Australia (Robert Raven).

RMCA Musée Royal de l'Afrique Centrale, Tervuren, Belgium (Rudy Jocqué).

RMNH Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands (Erik J. van Nieukerken, Kees van den Berg).

SAM South African Museum, Cape Town, South Africa (Margie Cochrane, Dawn Larsen).

SMF Senckenberg Naturmuseum, Frankfurt, Germany (Peter Jaeger).

SMN State Museum of Namibia, Windhoek, Namibia (E. Griffin).

SMNH Swedish Museum of Natural History, Stockholm, Sweden (Torbjörn Kronstedt).

USNM National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. (Jonathan A. Coddington, Scott Larcher, Dana M. De Roche).

WAM Western Australian Museum, Perth, Australia (Mark Harvey).

ZMB Museum fuer Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany (Jason A. Dunlop).

ZMH Zoologisches Institut und Zoologisches Museum Universität Hamburg, Hamburg, Germany (Hieronymus Dastych).

ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark (Nikolaj Scharff).

copy (SEM) photographs were taken on a Leo 1430VP scanning electron microscope (Carl Zeiss NTS, Oberkochen, Germany) at the Department of Biological Sciences of George Washington University, Washington DC, U.S.A. For SEM preparation, specimens were cleaned ultrasonically for 1 min, transferred to 100% ethanol overnight, dissected, submitted to critical point drying, mounted on rivets using glue and copper wire, and then sputter coated. Female genitalia and male palps were dissected with scalpels and needles. Male palpal anatomy and internal female genital structure were examined by clearing the organs in methyl salicylate (Holm, 1979), mounting them on a temporary slide (Coddington, 1983) and illustrated under a compound microscope. The dissected epigyna were further exposed to concentrated KOH to completely digest any soft tissues. Male palps were expanded by exposing them to concentrated KOH for up to 1 h, followed by immersion in distilled water.

The following anatomical abbreviations are used in the text and figures: AC, aciniform gland spigot(s); AG, aggregate gland spigot(s); AL, alveolus; ALE, anterior lateral eyes; ALS, anterior lateral spinneret; AME, anterior median eyes; AT, anal tubercle; B, cheliceral boss; BH, basal haematodocha; CB, cymbium; CD, copulatory duct; ChD, cheliceral denticles; CO, copulatory opening; CY, cylindrical gland spigot(s); E, embolus; EA, embolic apophysis; EAR, epigynal anterior rim; EB, embolus base; EC, embolic conductor; ECA, embolic conductor arch; ECG, embolic conductor groove; EG, epigynal groove; EP, epigynum; EPC, epigynal chamber; ES, epigynal septum; ESA, epigynal sclerotized arch; Etm, embolus-tegulum membrane; F, fundus; FD, fertilization duct; Fe, femur; FL, flagelliform gland spigot(s); M, membrane(ous); MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); Me, metatarsus; 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; PS, paracymbial seta(e); PPS, palpal patellar seta(e); PS�, prosomal supracheliceral lobe; RCT, retromarginal cheliceral teeth; S, spermatheca; Sc, scutum; SD, sperm duct; ST, subtegulum; SU, sustentaculum; T, tegulum; Ta, tarsus; TC, tarsal claw(s); TCp, paired tarsal claw(s); TCm, median tarsal claw; Ti, tibia; TO, tarsal organ; Tr, trichobothrium(a).

Morphological examination

Detailed methods are described in Kuntner (2005a, 2006). All measurements in millimetres were made using a micrometer eyepiece. Morphological observations and illustrations of external structures were made using a Leica MZ APO dissecting microscope with a camera lucida (Leica Microsystems, Wetzlar, Germany). For internal palpal and epigynal anatomy, a Leica DMRM compound microscope with a camera lucida was used. Microscope images were taken using a Nikon DXM 1200 digital camera (Nikon, Tokyo, Japan), and assembled with Syncroscopy Automontage software. Digital scanning electron micros-

Behavioural observations

Behavioural observations were made in the field, aided by a red-filtered headlamp at night. Behaviours and web architecture were photographed after the webs had been dusted with cornstarch (Eberhard, 1976; Carico, 1977). In addition, web samples of crucial parts of orb webs were taken using microscope slides coated on the edges with thick tape with glue on both sides. Such web samples were later examined under the microscope to establish exact thread junctions and their nature. Voucher specimens were deposited at USNM. Some behaviours described here are novel,

but most derive from the literature (Eberhard, 1982; Coddington, 1986a, b, c, 1990; Hormiga *et al.*, 1995; Scharff & Coddington, 1997; Griswold *et al.*, 1998; Agnarsson, 2003, 2004, 2005; Agnarsson & Kuntner, 2005; Kuntner, 2005a, 2006).

The following behavioural abbreviations are used: NSS, non-sticky spiral (also termed auxiliary or temporary spiral); SS, sticky spiral.

Phylogenetic analysis

Kuntner (2006) provides the first nephilid species-level phylogeny emphasizing *Clitaetra* species. This matrix forms the basis for this analysis. To test for *Nephilengys* monophyly and species relationships, two species untreated previously, *N. papuana* and *N. borbonica*, were scored for the 197 morphological and behavioural characters of Kuntner (2006) with the following new data (unknown entries, ?; inapplicable data, –). *N. papuana*: 110000100111010000-10003111100–100010000100000000001100001000101010–1012010001011011001–111110–101101101100120000-020011112101101100–00101–110–011000011101001011-010001111–10?011011?2001–?110110. *N. borbonica*: 11010010011101000010001111110–1000100001000000-00001100001000101010–101201100110–101001–11110101-01101101100120000020011112101101100–00101–110–01100-001110100001101000111?01111011?2001–?110?10.

This full phylogenetic matrix of 197 characters scored for thirty-four taxa in NONA format (ss) is available as Supplementary material and online (www.nephilidae.com). Multi-state characters were treated unordered (Fitch, 1971) to avoid unnecessary assumptions of character state adjacency. NONA version 2.0 (Goloboff, 1993) was used with parameters 'hold 1000', 'mult*500', 'max*' and 'sswap' under both 'amb –' and 'amb =' for the cladistic analysis and WINCLADA 1.00.08 (Nixon, 2002) to display and manipulate trees and matrices for NONA. Successive character weighting (Farris, 1969) analysis was performed in NONA with the command 'run swt.run hold10000 hold/100 mult*100' (using the macro swt.run). The bootstrap values (Felsenstein, 1985) were calculated in WINCLADA using default settings (100 replications, 'mult*10'). Bremer support or decay index values (Bremer, 1988, 1994) were calculated in NONA using the commands 'hold 10000' and 'bs10'. All trees are output from WINCLADA and their format does not imply non-monophyly of the group Deinopoidea, represented here by the two primary outgroups, *Deinopsis* + *Uloborus*.

Classification

A combination (Kuntner, 2006) of the (classical) zoological nomenclature (International Commission on Zoological Nomenclature, 1999) and phylogenetic nomenclature (Cantino & de Queiroz, 2004) was used. Clade names in this study are consistent with zoological ranks up to the family level, but are precisely circumscribed following the

PhyloCode (PC) Articles 7, 9–11 (Cantino & de Queiroz, 2004). Thus, all names are consistent with the zoological nomenclature (International Commission on Zoological Nomenclature, 1999). Phylogenetic definitions (PC Article 9, Note 9.4.1) are node-based such that 'clade (A and B)' means the least inclusive clade containing A and B.

Biology

This review is based on published accounts as well as personal observations of all four *Nephilengys* species. I observed *N. cruentata* in South Africa in 2001 (Figs 11A–D; 12), *N. borbonica* in Madagascar in 2001 (Figs 18A–D; 19–21), *N. malabarensis* in Sri Lanka in 1995 and Indonesia in 1996 (Fig. 25) and *N. papuana* in Australia in 2002 (Figs 33; 34). The behaviour and natural history of all four species seem to be uniform and are thus summarized together.

The *Nephilengys* literature includes papers on webs (Edmunds & Edmunds, 1986; Edmunds, 1993; Japyassu & Ades, 1998), behaviour (Robinson, 1975; Robinson & Robinson, 1978, 1980; Eberhard, 1982; Jackson, 1986; Schuck-Paim, 2000; Schuck-Paim & Alonso, 2001; Japyassu & Viera, 2002), anatomy (Roth & Roth, 1984), venom (Itagaki *et al.*, 1997a, b; Palma *et al.*, 1997, 1998), development (Roth & Roth, 1984; Japyassu & Ades, 1998; Santos Filho, 1998), morphological phylogenetics (Coddington, 1990; Hormiga *et al.*, 1995; Scharff & Coddington, 1997; Griswold *et al.*, 1998) and evolution of sexual size dimorphism (Coddington *et al.*, 1997; Hormiga *et al.*, 2000). Robinson & Robinson (1980) provide especially thorough descriptions of mating behaviours in *N. cruentata* and *N. papuana* (as *malabarensis*).

Nephilengys species are highly synanthropic, commonly found in and around human dwellings (Figs 12A; 18C, D; 19; 20; 25D; 34B, C) on all continents (Robinson & Robinson, 1980). Another preferred web site is against the trunks of medium to large trees, such that the orb is aerial, but the tubular retreat is against the bark (Figs 12B; 21; 34A). As such, the spiders exploit walls, eaves under roofs, verandas and porches (Robinson & Lubin, 1979). Another natural habitat found in Africa is rocky walls and outcrops (Fig. 12C). Invariably, the retreat, which is juxtaposed to the orb hub, is built against a hard surface. *N. cruentata* females select web sites where other conspecifics are present (Schuck-Paim & Alonso, 2001).

Although the orbs of immature spiders are more or less symmetric (Fig. 34A), those of adult females typically are highly (vertically) eccentric, meaning that the hub is disproportionately close to the top frame (Fig. 34B, C). Japyassu & Ades (1998) described such developmental shift from orb webs to 'semiorb webs' in *N. cruentata*. A rare form of horizontal eccentricity (Fig. 21) was observed in an individual *N. borbonica* in Madagascar.

Like other nephilids, *Nephilengys* engages in partial web renewal (Figs 21; 34C). Most orb weavers renew damaged webs completely.

Nephilengys spiders are nocturnal, spending most of the day inside the retreat (Figs 11D; 12A; 18D, E) and nights at the hub (Fig. 25D), although sometimes they are observed in the web during the day.

In addition to the unique retreat (Figs 12C; 18D, E; 20D), which may be homologous to the 'hub cup' of *Herennia* (see Kuntner, 2005a) and the hub silk reinforcement of *Clitaetra* (see Kuntner, 2006), *Nephilengys* webs include typical nephilid features (mostly described in *Nephila*, listed below). Web architecture and building behaviour are summarized as: SS localization with the outer fourth leg; hub loop–SS transition gradual; hub bite-out absent; hub closed; radii attached twice on frame (except late radii, attached singly), and once on hub; radii not cut-and-reeled; NSS persists in finished web; NSS forms zig-zag (as in *Nephila*); late radii numerous, reaching as many as five late origins (Fig. 34C) and originating on NSS. *Nephilengys* differs from *Nephila* by the absence of a barrier web and golden silk, and building the web against a substrate. The latter is shared with *Clitaetra* and *Herennia* (Hormiga *et al.*, 1995; Kuntner, 2005a, 2006). Apart from web architecture adapting to the available space, little web building plasticity (e.g. in web construction behaviour) has been noted.

As in other nephilids (Kuntner, 2005a, 2006), *Nephilengys* attacks prey with a stereotyped bite-attack, and never wraps first as typical for araneids (Eberhard, 1982). Although behaviours show a level of plasticity depending on the prey (Japyassu & Viera, 2002), a typical sequence is recorded in *N. borbonica* (Fig. 20). The female rushed to the hymenopter prey entangled in the orb, delivered a bite and held on to the prey in the chelicerae for more than a minute. She then started wrapping the prey (not holding in the chelicerae), followed by cutting it out of the web, attaching it to her spinnerets and carrying it to the hub. There, she suspended the wrapped prey, assumed the resting pose, and then took the prey and fed on it.

Adult *Nephilengys* males abandon web building and accordingly lack the PLS triad (two aggregate and one flagelliform silk gland spigot, Fig. 17A) associated with sticky silk production. The males are often found in adult or immature female webs, where they may live communally for several weeks. Cohabitation of males with immature females is documented in *N. cruentata* (figures available), *N. malabarensis* (Jackson, 1986; unverified identification) and *N. papuana* (Robinson & Robinson, 1980: as *N. malabarensis*). Cohabiting males often mate with a freshly moulted female, which is soft and cannot prevent copulations (Fig. 11E), a so-called 'opportunistic mating' (Robinson & Robinson, 1980). Cohabitation of (several) males with adult females is common in all species (e.g. Figs 18E; 19; 25D).

Mating attempts involve no preparatory behaviours. A sequence recorded in *N. borbonica* is presented (Fig. 19). The male approached the female resting at the hub, walked on her dorsum and crossed to her venter, where he attempted copulation. Apparently, mating is not necessarily confined to the female retreat as documented by Robinson & Robinson (1980). Furthermore, the observed *N. borbonica*

female offered no access posture as recorded by Robinson & Robinson (1980) in *N. papuana*.

Predators of *N. malabarensis* may include the salticid spider *Portia*. Label information on ng273 (two females) and ng274 (a male and two juveniles), both from Sri Lanka, reads 'Portia associate orb webs'.

Nephilengys typically responds to threat by rushing into the retreat. I have also observed *N. cruentata*, *N. borbonica* and *N. papuana* to shake their bodies vigorously when manually disturbed.

Theridiid kleptoparasites of the genus *Argyrodes* (*sensu lato*) are common in webs of all *Nephilengys* species. The maximum I have observed was twenty-four in a single female *N. borbonica* web in deep rainforest with no conspecific webs nearby.

Male emboli were found stuck in female *N. cruentata* and *N. borbonica* copulatory openings. The distal part of the embolic conductor with distal embolus thus forms a plug stuck in the epigynal copulatory opening (Figs 2E; 13B; 16C, D). Kuntner (2005a) provides a discussion of male plugging.

An intriguing behaviour known in *Nephilengys* (also in *Herennia* and *Deliochus*) is the 'eunuch phenomenon' (Robinson & Robinson, 1978; Roth & Roth, 1984; Kuntner, 2005a), where the males lose (or remove) a part of their pedipalp during or after copulation but live on in a sterile state, remaining in the female web. Eunuch males, lacking one or both palpal bulbs broken between the palpal tibia and tarsus (Fig. 24), were found commonly in all species. Bulb severance appears to be deliberate (Robinson & Robinson, 1980), but the significance is unknown.

Phylogeny

Equally weighted analyses resulted in eight most parsimonious trees [$L = 536$, consistency index (CI) = 42, retention index (RI) = 85]. In the strict consensus, three nodes collapse (Fig. 36A). *Nephilengys* monophyly is confirmed, always containing two species groups: *N. cruentata* + *N. borbonica* and *N. malabarensis* + *N. papuana*. Otherwise, these eight trees are identical to those of Kuntner (2006). All trees support the monophyly of Nephilidae (*Clitaetra* (*Herennia* (*Nephilengys*, *Nephila*))), but the sister group to nephilids remains ambiguous. Nephilids are not tetragnathids (contra Hormiga *et al.*, 1995; Kuntner, 2002; Kuntner & Hormiga, 2002), nor are they araneids (contra Wunderlich, 1986, 2004; Kuntner, 2003; Pan *et al.*, 2004). The monophyly of *Clitaetra*, *Herennia* and *Nephila* is corroborated, and the sister group to *Nephilengys* is *Nephila*.

Successive weighting analysis, which stabilized after the second iteration, gave a single tree identical to one of the fundamental cladograms (Fig. 36B). Not surprisingly, this tree is identical to the successively weighted tree of Kuntner (2006), but with the *Nephilengys* species groups, *N. cruentata* + *N. borbonica* and *N. malabarensis* +

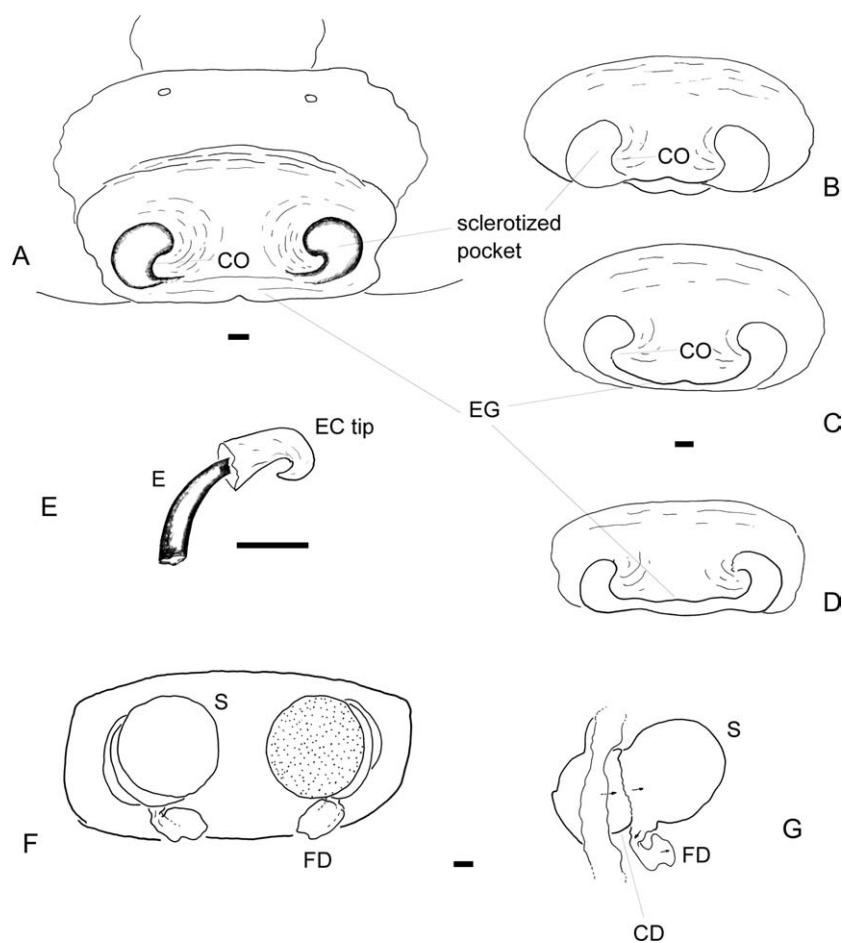


Fig. 2. *Nephilengys cruentata*, female genital morphology and variation, from South Africa (except E). A–D, epigynum, ventral: A, from Sodwana Bay (ng12/fl); B–D, from a single sample from Durban (ng110/fl–3); note variation. E, epigynal plug (broken EC and embolus) as extracted from copulatory opening of a female from DR Congo (108/fl). F, epigynum, cleared (from Sodwana Bay, ng12/fl), dorsal. G, same, ectal. Scale bars = 0.1 mm.

N. papuana. Figure 37 shows the character optimizations for the *Nephilengys* part of the preferred phylogeny (successively weighted), which forms the basis for the newly proposed classification and taxonomy (below).

Taxonomy

Nephilengys L. Koch, 1872

(Figs 1–34)

Aranea: Fabricius, 1775: 439, description of *Aranea cruentata* (= *Nephilengys cruentata*).

Epeira: Walckenaer, 1842: 103, description of *Epeira malabarensis* (= *Nephilengys malabarensis*).

Nephila: O. P.-Cambridge, 1871: 618, description of *Nephila rivulata* (= *Nephilengys malabarensis*); Simon, 1894: 745, f. 827; Bonnet, 1958: 3064.

Nephilengys L. Koch, 1872: 144 [Type species, by subsequent designation (Bonnet, 1958), *N. schmeltzii* L. Koch (= *N. malabarensis*)].

Nephilengys: Roewer, 1942: 933; Brignoli, 1983: 241; Dippenaar-Schoeman & Jocqué, 1997: 338; Murphy & Murphy, 2000: 383; Platnick, 2005.

Metepeira: Tikader, 1977: 181, f. 12A–C, description of *Metepeira andamanensis* (= *Nephilengys malabarensis*).

Etymology. Unknown. The name is feminine in gender (Bonnet, 1958: 3086). The vernacular name, adopted here from the use in southern Africa, refers to the spider's habit of staying in the seclusion of its retreat during the day (see 'Biology').

Monophyly. Many authors (Simon, 1894; Pocock, 1900; Bösenberg & Strand, 1906; Bonnet, 1958; Chrysanthus, 1959, 1971; Wiehle, 1967; Tikader, 1982; Millidge, 1988; Yin *et al.*, 1990) have considered *Nephilengys* as a junior synonym of *Nephila* Leach. Koch (1872: 143) diagnosed the newly described genus *Nephilengys* from *Nephila* by the different eye arrangement, shorter legs and shorter metatarsus I. This separation was supported by Dahl (1912: 47),

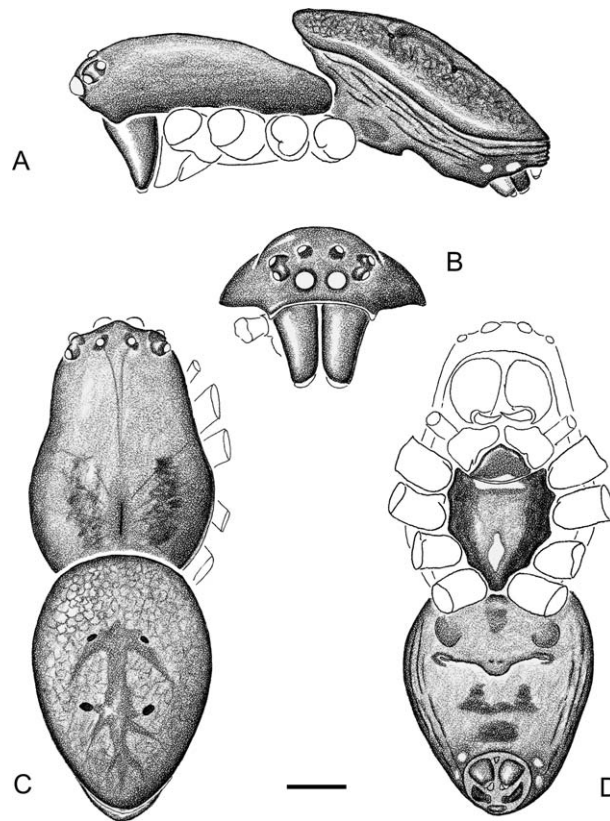


Fig. 3. *Nephilengys cruentata*, male from Mozambique (ng8/m1): A, lateral; B, frontal; C, dorsal; D, ventral. Scale bar = 0.5 mm.

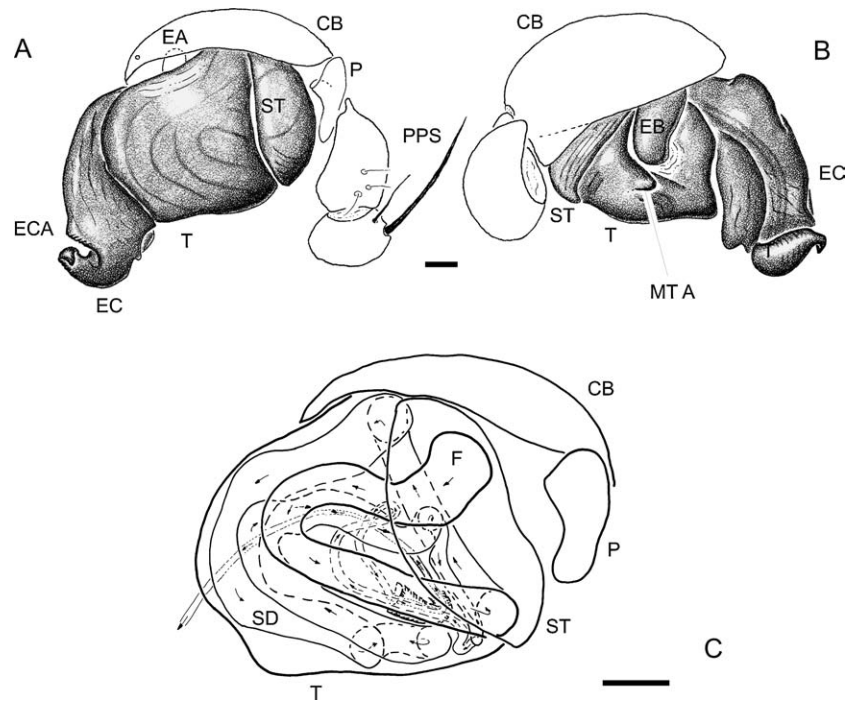


Fig. 4. *Nephilengys cruentata*, male pedipalp, from Mozambique (ng8/m1): A, ectal; B, mesal; C, bulb transparent, showing sperm duct, ectal. Scale bars = 0.1 mm.

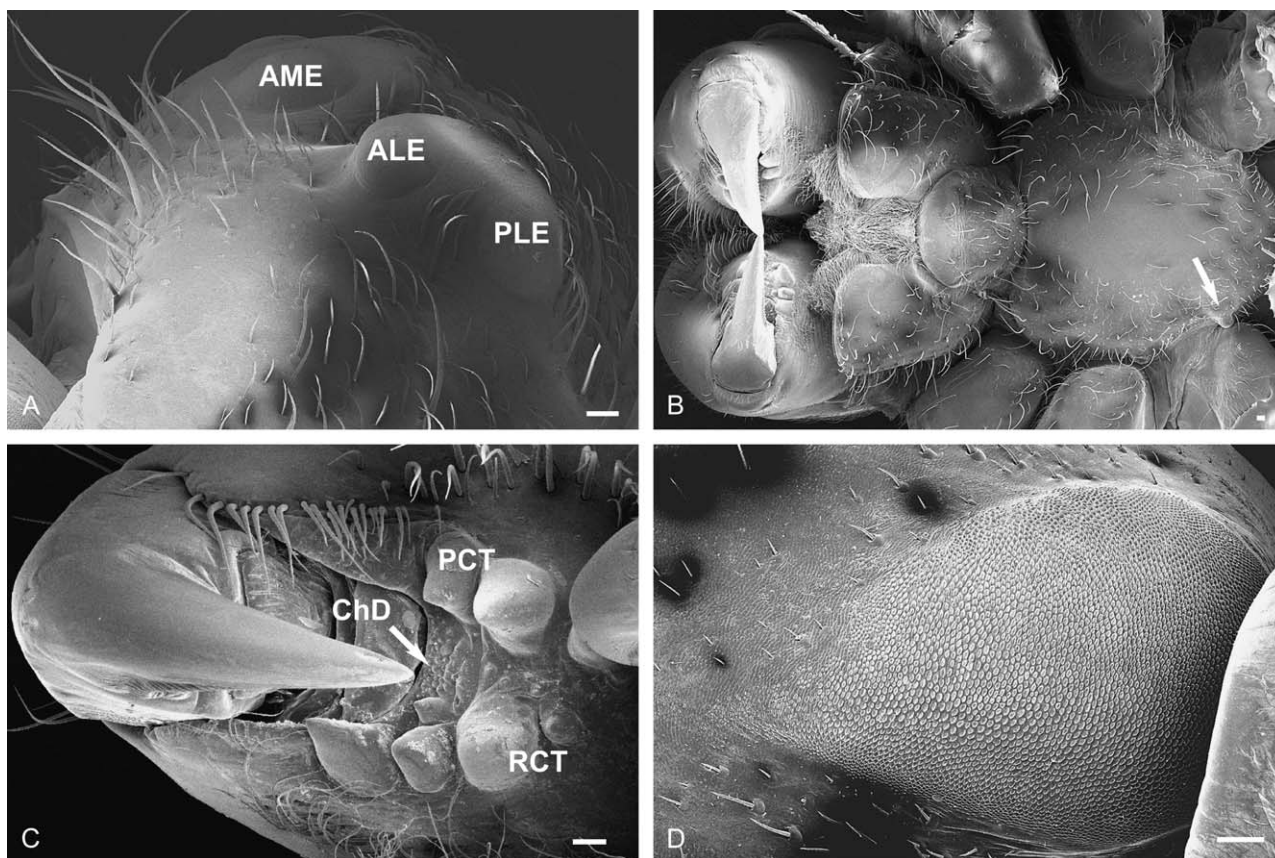


Fig. 5. *Nephilengys cruentata*, female prosoma, from Liberia (ng54): A, head region, ectal; B, prosoma, ventral, showing paired tubercle (arrow) adjacent to third coxa; C, chelicerae, apical; D, chelical boss, ectal. Scale bars = 100 µm.

who provided additional diagnostic features (stouter habitus and distinct biology of *Nephilengys* compared with *Nephila*).

Nephilengys monophyly is supported here by the following unambiguous synapomorphies (Fig. 37): female carapace macrospines (character 7/state 1; Figs 15; 28C), light

pigment anterior abdominal band (65/1; Figs 1A; 11A, C; 19C; 25C), inconspicuous dorsum pattern (66/0; Fig. 1C), mesal tegular apophysis (138/1; Figs 4B; 9A; 23B, C) and an off-web retreat (196/1; Figs 12C; 18D, E; 20D; 34B). Further ambiguous synapomorphies include (ACCTAN, Fig. 37) four-spotted venter (74/2; Figs 1D; 11B; 18B, C;

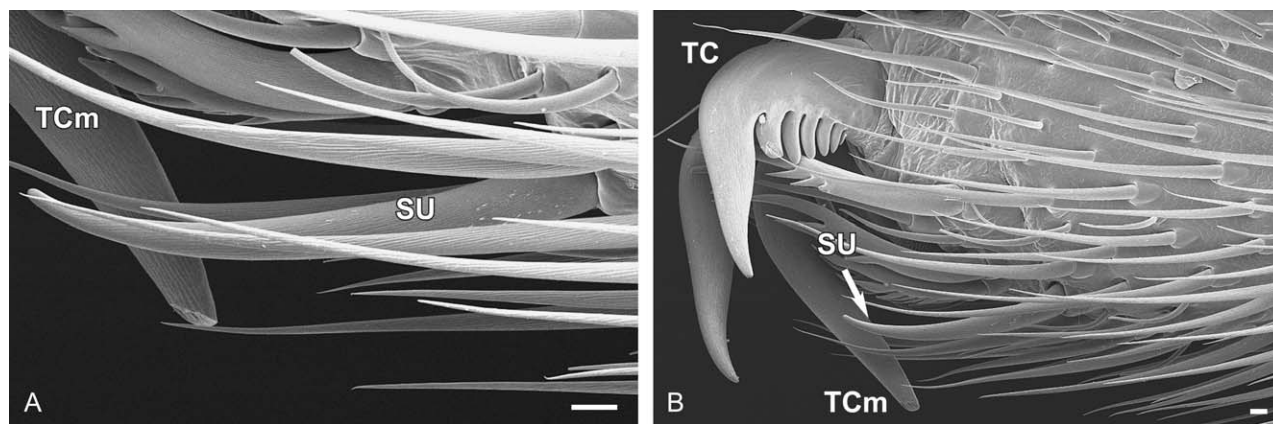


Fig. 6. *Nephilengys cruentata*, female fourth tarsus, from Liberia (ng54), showing tarsal claws and sustentaculum. A, lateral; B, ventro-lateral. Scale bars = 20 µm.

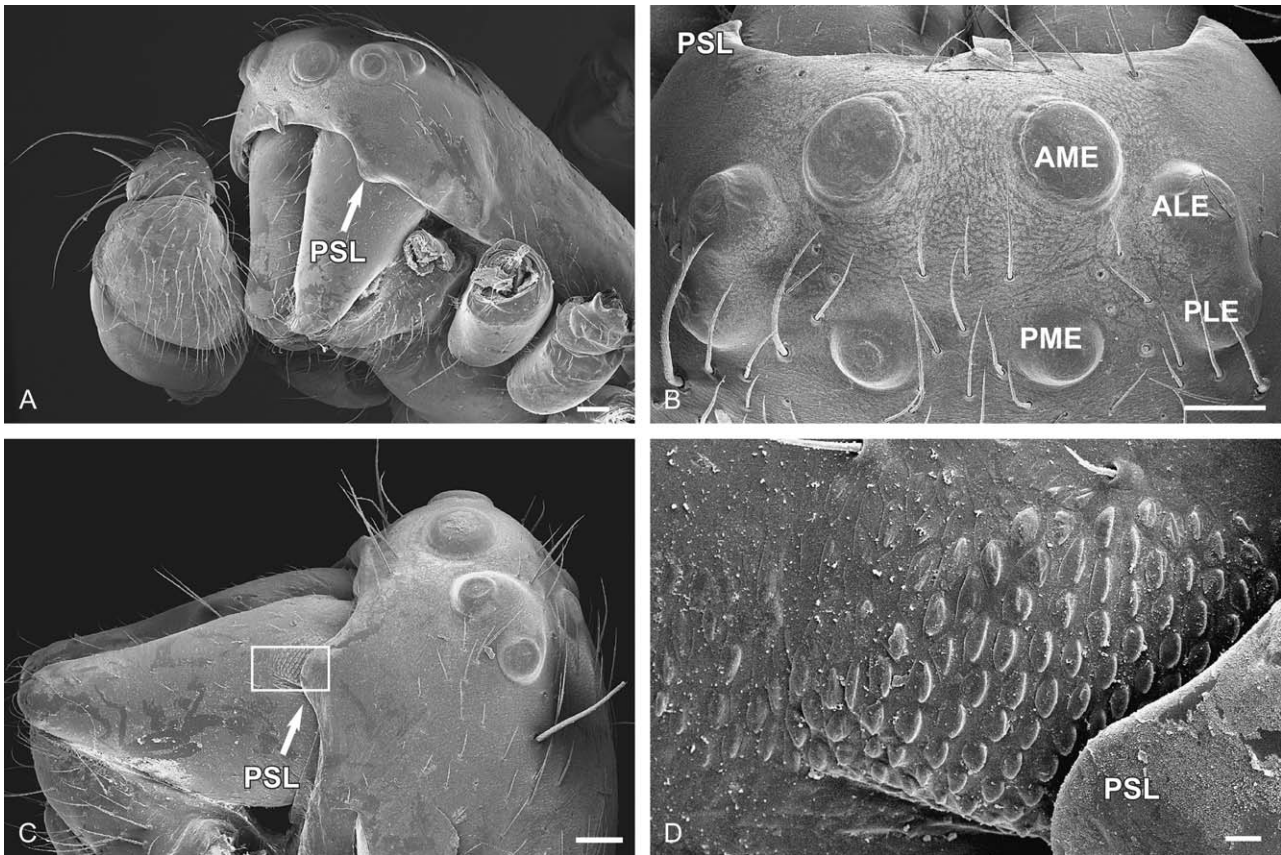


Fig. 7. *Nephilengys cruentata*, male prosoma, from South Africa (ng9/ml-2): A, antero-ectal; B, eye region, dorsal; C, head region, lateral, box delimits area of image D; D, cheliceral boss. Scale bars: A–C = 100 μ m; D = 10 μ m.

19A; 25B, D; 33B, D) and (DELTRAN, Fig. 37) two palpal patellar macrosetae (117/2; Figs 4A; 14A; 27A), ridged embolic conductor edge (149/1; Figs 10; 14A–D; 23A–C; 27A, B; 32D) and bulbus detachment or eunuch behaviour (192/1; Fig. 24).

Phylogenetic definition. The genus *Nephilengys* is defined as the least inclusive clade containing the species *N. cruentata*, *N. borbonica*, *N. malabarensis* and *N. papuana*.

Diagnosis. *Nephilengys* differs from all non-nephilid spiders by the striated cheliceral boss in both sexes (Figs 5D; 7C, D; 28D). *Nephilengys* females differ from all other nephilids by the presence of strong carapace spines (Figs 15; 28C), and further from species of *Nephila* by the absence of carapace humps and of tapetum in secondary eyes. *Nephilengys* males differ from other nephilids except *Herennia* by the strongly sigmoid and ridged embolic conductor (Figs 4A, B; 9A, B; 10; 14A–D; 23A–C; 27A, B; 32D). The embolus of *Nephilengys* males is smooth (Fig. 14C–G) or with a small distal enlargement (Figs 23D; 27C), whereas, in *Herennia*, it has a pronounced distal hook. *Nephilengys* males have a wider eye region than *Herennia* males (eye region to carapace width ratio 0.57–0.58 in *Nephilengys* and 0.43 in

Herennia), and an oval abdominal scutum (Figs 1E, G, H; 8A; 17B; 32B) (rounded in *Herennia*). *Nephilengys* webs differ from those of *Herennia*, *Nephila* and *Clitaetra* by the presence of a silken retreat above the orb (Figs 12C; 18D, E; 20D; 34B). *Nephilengys* webs are built against tree trunks (Figs 12B; 21; 34A), rock outcrops (Fig. 12C), walls (Figs 18C, D; 19) or building roofs (Figs 12A; 20; 25D; 34B, C) and windows, but always with a clearance of at least a few centimetres between the orb plane and the substrate, such that the orb is in a single plane. In contrast, the webs of *Herennia* are built tightly against tree trunks, rocks or walls, such that the orb plane follows the substrate shape (Kuntner, 2005a).

Description. Female: The general somatic morphology is illustrated in *N. cruentata* (Fig. 1). Body size 10–28 mm. **Prosoma** with wide and high head region (Figs 1A–C; 15; 28B, C). Carapace with erect spines and short hairs (Figs 15; 28C). Carapace edge with row of long white hairs. Sternum with three paired groups of slit sensilla. Three or four pairs of sternal humps present, often inconspicuous. Sternum with medially protruding irregular white pigment patches. Labium slightly wider than long (Figs 1D; 5B). Both eye rows slightly recurved. Lateral eyes on tubercle, not

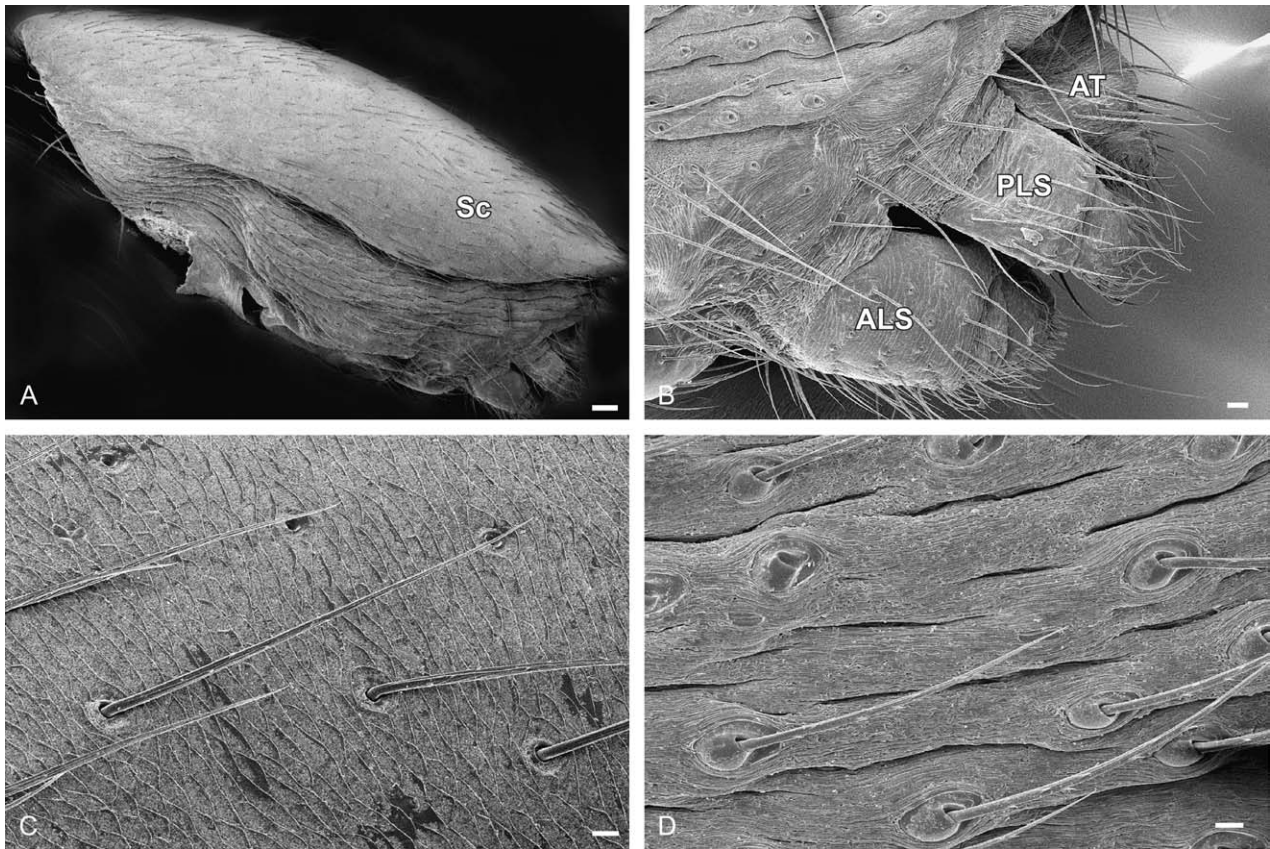


Fig. 8. *Nephilengys cruentata*, male opisthosoma, from South Africa (ng9/ml-2): A, lateral; B, spinneret area, lateral; C, detail of scutum; D, detail of lateral opisthosoma. Scale bars: A = 100 μ m; B = 20 μ m; C, D = 10 μ m.

juxtaposed, widely separated from the medians. Tapeta absent from secondary eyes. Chelicerae massive (Figs 1A, B; 15C; 16A, B), with three prolateral and four (three large, fourth small) retrolateral teeth, cheliceral furrow (inconspicuously) denticulated (Figs 5C; 28A). Paturons medially with macrosetae (Fig. 16A). Cheliceral boss with hundreds of striae (Figs 5D; 16B; 28D). *Appendages.* Legs long, tibiae distally with weak tuft of dark hairs. Leg formula 1-2-4-3. Sustentaculum present (Fig. 6). *Opisthosoma* (Fig. 1A, C, D) oval, cylindrical, high, widest in middle; dorsum with five apodeme pairs, rows of small central and lateral sclerotizations (Fig. 1C). Abdomen entirely covered with short hairs. Venter with four pairs of median sclerotizations, paired line of lateral sclerotizations (Fig. 1D). Book lung covers grooved (Figs 1D; 29C). Light pigment band on anterior abdomen. Spinnerets (Fig. 30) of typical nephiline condition (see Hormiga *et al.*, 1995): ALS with 'normal PI field' where PI spigot base is nearly as long or longer than the shaft (Griswold *et al.*, 1998: ch. 69, fig. 48B), major ampullate spigot and nubbin, PMS with sparse aciniform field, nubbin, PLS with aggregate spigots embracing flagelliform, with two cylindrical spigots of normal size, mesal being peripheral. *Epigynum* ventral, conspicuous. Spermathecae round, with gland pores all over their surface (Figs 2F; 13C; 22B; 26D). Copulatory and fertilization ducts well sclerotized.

Male: The general somatic morphology is illustrated in *N. cruentata* (Fig. 3). Body size 3.1–5.9 mm. *Prosoma* pear-shaped, highest in middle, cephalic region low. Carapace with macrosetae anteriorly, weak setae posteriorly. Sternum transparent, medially protruding irregular white pigment patches (Fig. 3D). Labium broader than long (Fig. 3D). Both eye rows slightly recurved, eyes roughly equidistant. Large AME extending anteriorly over clypeus (Figs 3; 7A–C). Lateral eyes on tubercle (Figs 3; 7A–C), not juxtaposed, not widely separated from medians. Tapeta absent. Chelicerae with three prolateral, three retrolateral teeth, approximately 12 cheliceral denticles. Cheliceral boss with roughly 70 striae (Fig. 7C, D). Legs long, slender, with long spines on femora and tibiae (Fig. 31B). Leg formula 1-2-4-3. *Pedipalp* (Figs 4; 9; 10; 14; 23; 27; 32C, D) with short globular cymbium, rectangular paracymbium with invagination, large flat or globular tegulum containing sperm duct, prominent and separate subtegulum, massive sigmoidal embolic conductor enveloping the embolus. A short, sometimes obscure apophysis present on the mesal part of the tegulum, labelled as mesal tegular apophysis (Figs 4B; 9A; 23B, C) (This apophysis could be argued to correspond in topology but not in shape to the araneoid median apophysis). Two macrosetae (prominent and weak one; Figs 4A; 14A; 24A; 27A) present on distal part of palpal

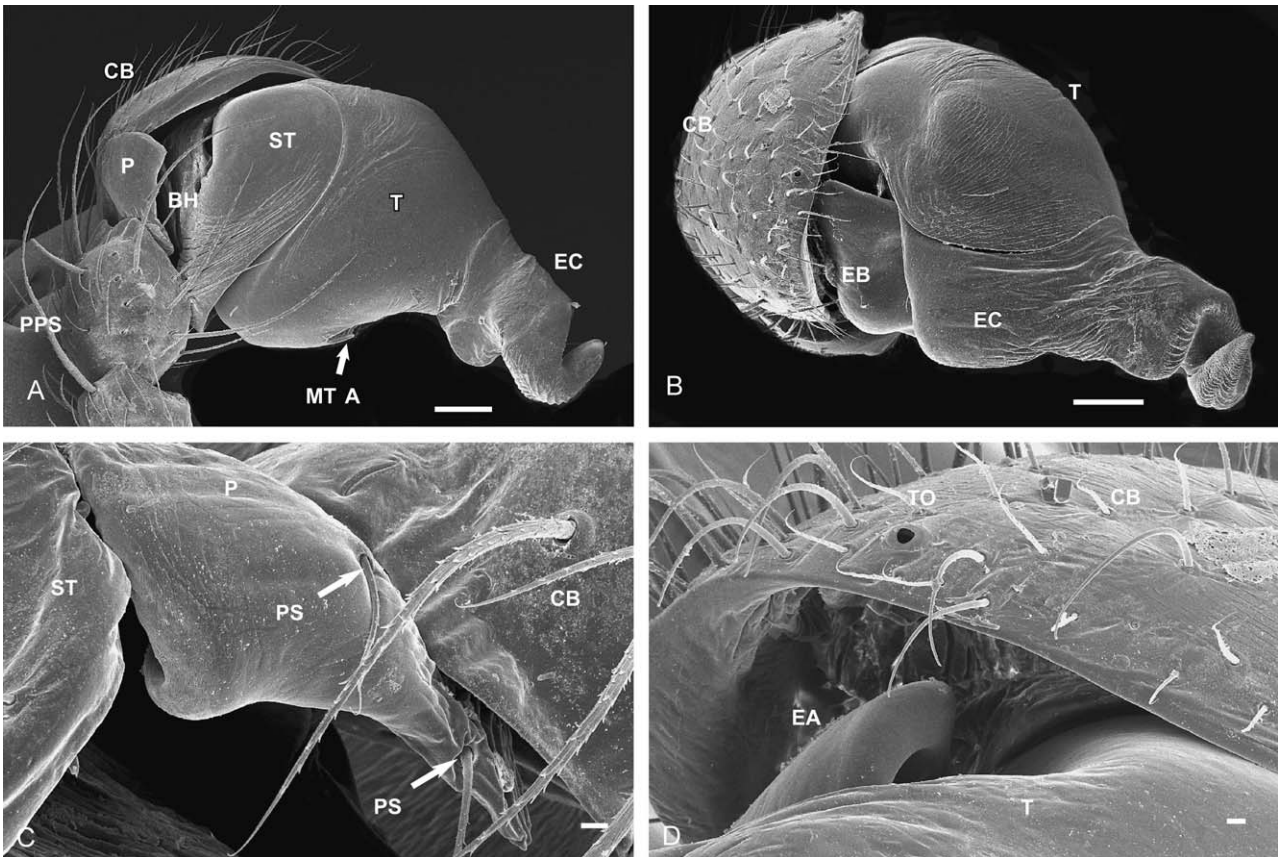


Fig. 9. *Nephilengys cruentata*, male pedipalp, from South Africa (ng9/m1): A, ectal; B, apical; C, paracymbium, ectal; D, dorsal palp detail. Scale bars: A, B = 100 μ m; C, D = 10 μ m.

patella. Embolus base with apophysis (Figs 9B, D; 14C–E, G; 27C), which locks with paracymbium fold during copulation (*N. borbonica* in Fig. 14C). Embolus long, thin (but, not filiform, see *Nephila*), smooth (Figs 14C–E, G; 23C, D; 27C), without distal hooks or modifications, other

than distal constriction in *N. malabarensis* and *N. papuana* (Figs 23D; 27C). *Opisthosoma* (Figs 3; 8A; 32B) oval, dorso-ventrally flattened, with dorsal scutum. Dorsum with two apodeme pairs, may be inconspicuous. Venter with inconspicuous rows of median and lateral sclerotizations

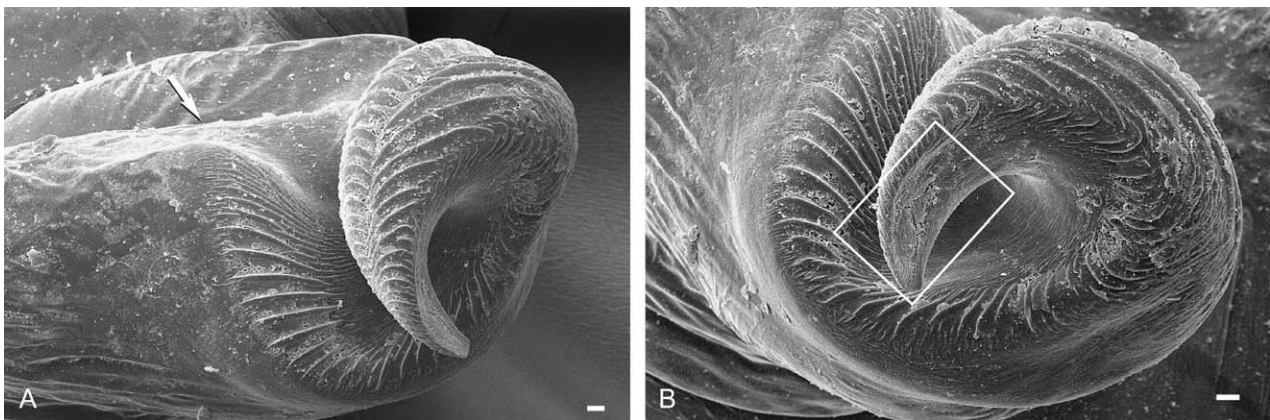


Fig. 10. *Nephilengys cruentata*, male right embolic conductor, from South Africa (ng9/m1), showing the distal hook, ridges, EC groove (A, arrow) and the tip opening for embolus (B, box). Scale bars = 10 μ m.

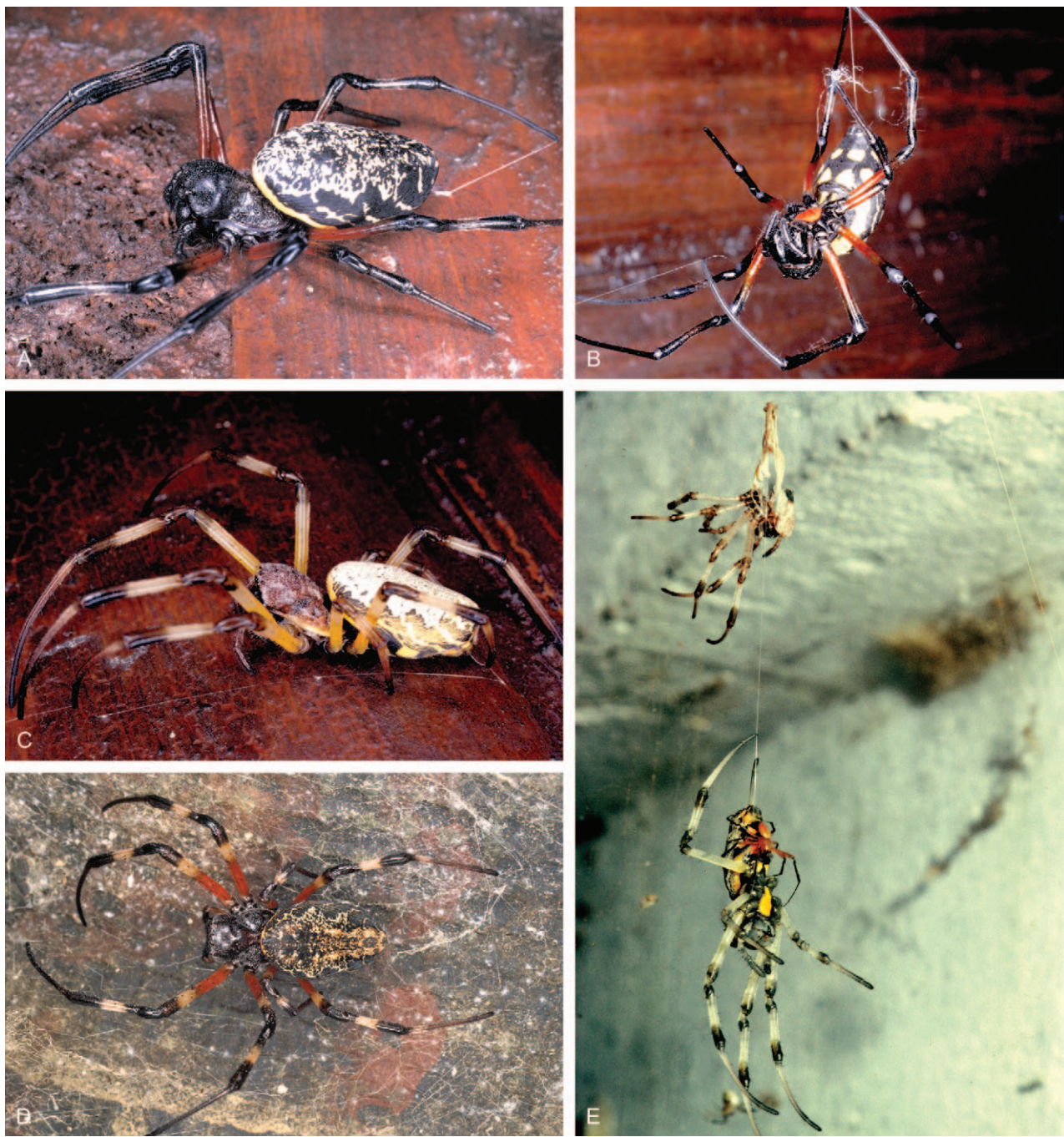


Fig. 11. *Nephilengys cruentata*, photographs of live spiders: A, B, female 1 from Sodwana Bay, South Africa, taken from web; note blood-red sternum and femora, and yellow spots and bands on almost black opisthosoma; C, female 2 from Sodwana Bay, South Africa, taken from web; note less intense coloration and an almost white opisthosoma; D, female 3 from Sodwana Bay, South Africa, in rest posture in retreat built into a roof of a wooden house; E, male copulating with a freshly moulted female, from Adiépo Doumé, Ivory Coast (photograph by R. Jocqué).

(Fig. 17B). Book lung covers not grooved, but with sculptured cuticle (Fig. 32A). PLS black, other spinnerets pale. One or two pairs of white spots lateral to spinnerets. PLS triad absent in adults (Fig. 17A), represented by nubbins. Epiandrous gland spigots as in Figs 17(D) and 32(A).

Composition. The genus contains four species: *N. cruentata*, *N. borbonica*, *N. malabarensis* and *N. papuana*.

Distribution (Fig. 35). Tropical South America, tropical and subtropical Africa, Indian Ocean Islands, Asia, Australia.

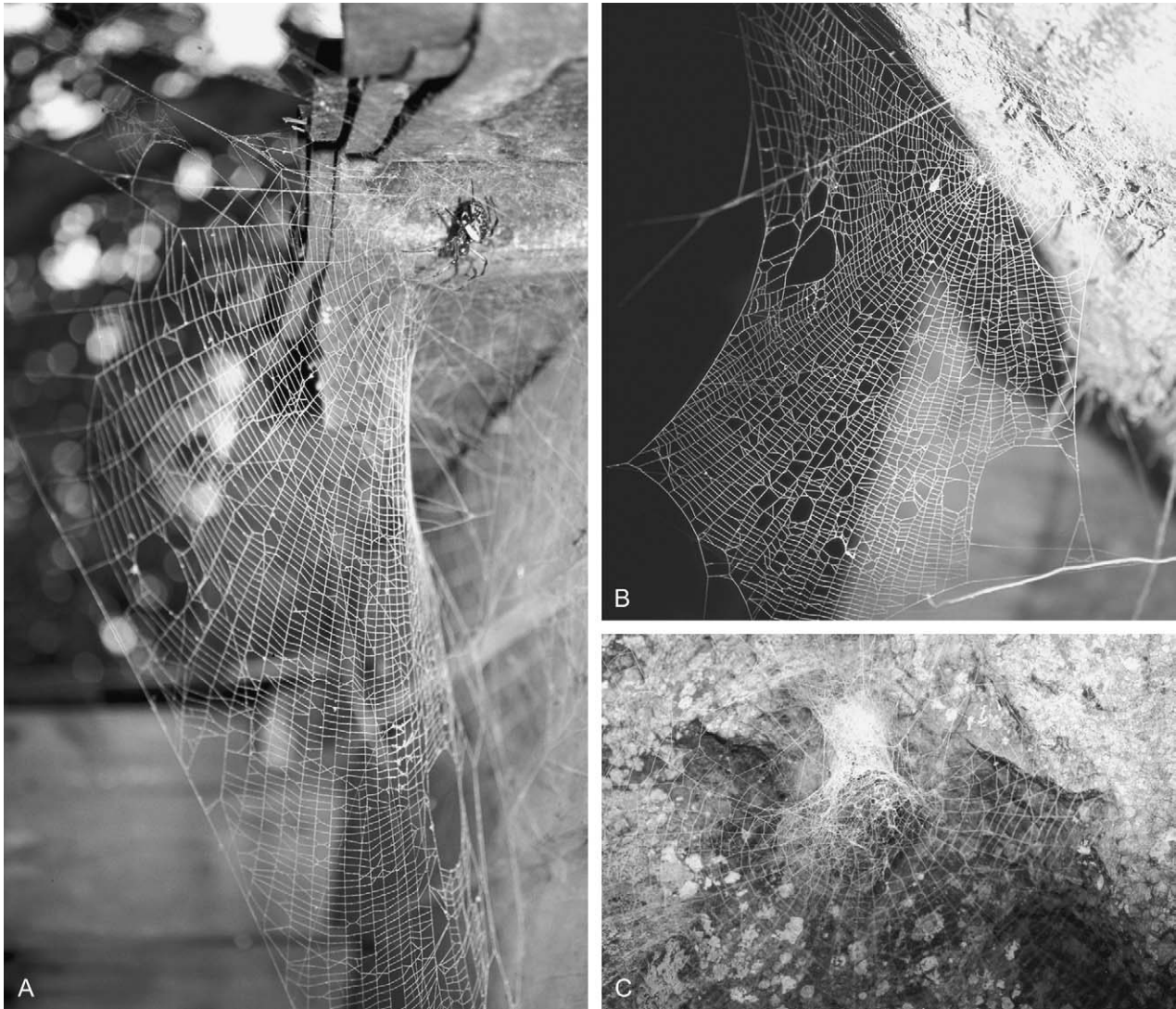


Fig. 12. *Nephilengys cruentata*, photographs of live spiders from South Africa's KwaZulu-Natal: A, female and her web built against a house, retreat leading below the roof, Sodwana Bay; B, female web built against a large tree branch at Fanies Island, St. Lucia; C, female hub and retreat built against a rock at Phinda.

Taxonomic history. Koch (1872: 143) included four species in the new genus *Nephilengys*: *Epeira malabarensis* Walckenaer, 1842, *Nephila rivulata* O. P.-Cambridge, 1871, *Nephilengys schmeltzii* L. Koch, 1872 and *Nephilengys hofmanni* L. Koch, 1872, all synonymized with *N. malabarensis* by Dahl (1912). Koch (1872) did not designate a type species, and evidently did not know the African *Epeira cruentata* Fabricius, 1775, which fits the diagnosis of *Nephilengys* (Simon, 1887, 1894: 750). Bonnet (1958: 3086) subsequently designated *N. schmeltzii* L. Koch (= *N. malabarensis*) as the type species of the genus.

Many twentieth century authors (Pocock, 1900; Bösenberg & Strand, 1906; Bonnet, 1958; Wiehle, 1967; Tikader, 1982; Millidge, 1988; Yin *et al.*, 1990) followed Simon (1894) in using '*Nephila malabarensis*' for *Nephilengys malabarensis*,

as in Thorell (1878), Dahl (1912), Roewer (1942), Deeleman-Reinhold (1989), Barrion & Litsinger (1995), Song *et al.* (1999) and Platnick (2005).

Key to the species of *Nephilengys*

1. Epigynum (Figs 22A, C; 26A–C, E; 29A–C) roughly as long as wide, with (inverted T-shaped) epigynal septum, medial copulatory openings and anterior rim; inner epigynum with sclerotized arch (Figs 22B, C; 26D, E). Females medium sized (10–18 mm). Males orange, palp with long and slender EC (Figs 23A, B; 27A, B); embolus with distal bulge (Figs 23D; 27C) 2
- Epigynum (Figs 2A–D; 13A, B; 16C, D) wider than long, with posterior groove and lateral copulatory

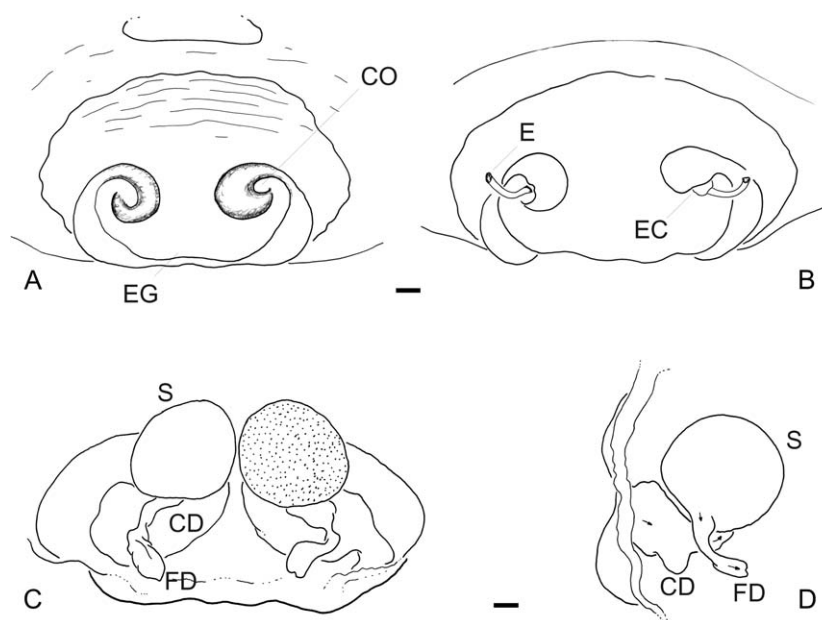


Fig. 13. *Nephilengys borbonica*, female epigynum: A, ventral, from Madagascar (103/f1); B, ventral, from Mauritius (ng92/f1), note a complex of EC and embolus in each copulatory opening; C, cleared (from Madagascar, ng69), dorsal; D, same, ectal. Scale bars = 0.1 mm.

- openings, without septum and anterior rim; inner epigynum without sclerotized arch (Figs 2F, G; 13C, D). Females large (16–28 mm). Males yellow, grey or brown, palp with short and wide EC (Figs 4A, B; 9A, B; 10; 14A–D); embolus distally smooth (Fig. 14C–G) 3
2. Female sternum (Fig. 25B) orange (white in alcohol) with thin brown lateral edges, first femur with sparse and long prolateral spines, venter (Fig. 25B, D) with two large and up to two pairs of small orange dots (white in alcohol), epigynum generally with a narrow septum, and long copulatory and fertilization ducts (Fig. 22). EC (Fig. 23A, B) proximally straight and sclerotized, distally with a long tip, viewed from ectal and mesal sides appears hooked. South, South-East Asia *N. malabarensis* (Walckenaer)
- Female sternum (Fig. 33B, D) black with two medial white patches (sometimes fused to form a continuous white median area), first femur with numerous short spines (Fig. 28B), venter (Fig. 33B, D) brown, with two irregularly shaped pairs of white or orange patches, may be connected to form continuous white or orange area, epigynum generally with broad septum, short copulatory and fertilization ducts (Figs 26; 29A–C). EC (Fig. 27A, B) proximally undulating and membranous, distally with shorter tip, viewed from ectal and mesal sides is rounded, dorso-ventrally flattened and two-dimensional. Australia, New Guinea *N. papuana* Thorell
3. Female sternum (Fig. 11B) blood-red (pale in preserved material), femoral macrosetae long, epigynum (Fig. 2) wide with lateral-posterior copulatory openings, short copulatory ducts, which broadly attach spermathecae

to epigynal wall, short fertilization ducts. EC (Figs 4A, B; 9A, B; 10) with slender tip and subdistal arch (Fig. 4A). Mainland Africa, South America *N. cruentata* (Fabricius)

– Female sternum (Fig. 18B, C) coloration varies (red to orange, white, creamy or dark brown with narrow median light band), femoral macrosetae short, epigynum (Figs 13; 16C, D) longer with lateral-anterior position of copulatory openings, long copulatory ducts, which do not broadly attach spermathecae to the epigynal wall, longer fertilization ducts. EC (Fig. 14A–E) with broad tip and extensive distal arch (Fig. 14A). Madagascar, Indian Ocean Islands *N. borbonica* (Vinson)

The ‘*cruentata* species group’

Monophyly. The clade is supported by the following unambiguous synapomorphies (Fig. 37): posterior epigynal plate grooved (character 77/state 1; Figs 2A–D; 13A; 16C, D), lateral epigynal chamber openings (81/1; Figs 2A–D; 13A, B; 16C, D) and epigynal paired sclerotized pocket (84/1; Fig. 2A, B). Ambiguous synapomorphies include (ACCTRAN) the absence of the epigynal septum (82/0) and the absence of the epigynal sclerotized arch (95/0).

Diagnosis. Epigynum (Figs 2A–D; 13A, B; 16C, D) wider than long, with posterior groove and lateral copulatory openings, lacks septum and anterior rim; inner epigynum lacks sclerotized arch (Figs 2F, G; 13C, D); females large (16–28 mm); males yellow, grey or brown, palp with short and wide embolic conductor (Figs 4A, B; 9A, B; 10; 14A–D), embolus without distal modifications (Fig. 14C–G).

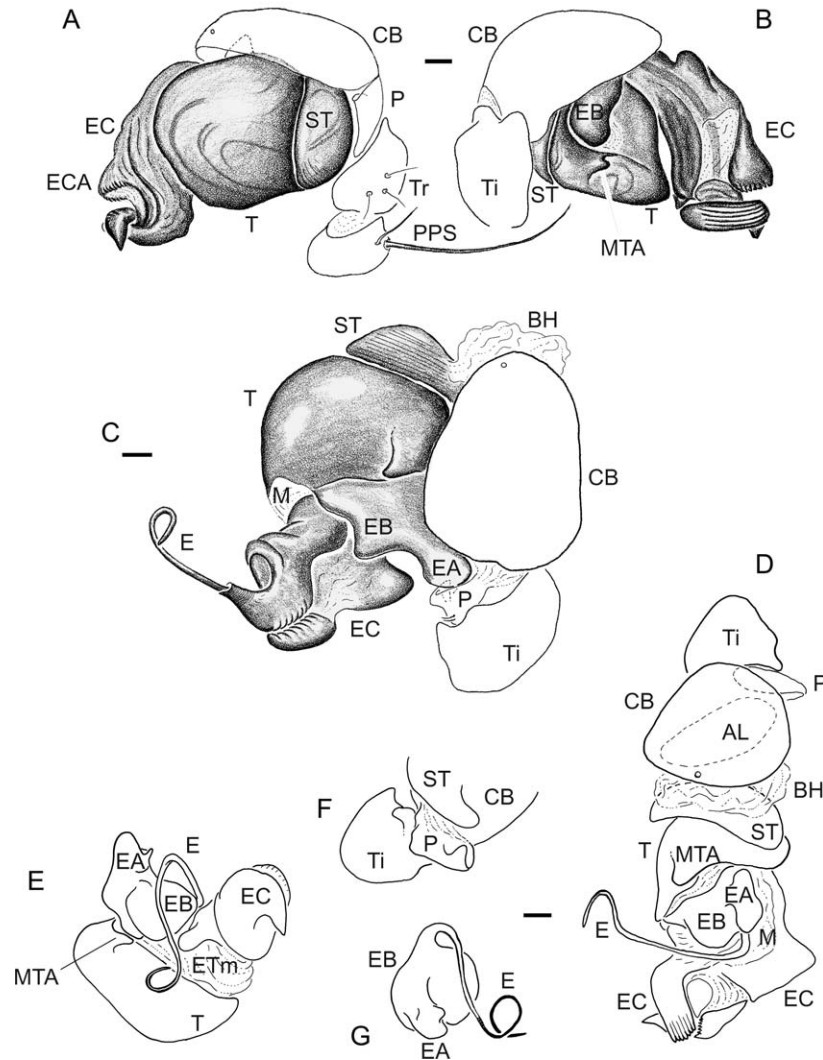


Fig. 14. *Nephilengys borbonica*, male palpal morphology and functional anatomy, from Madagascar (A, B, ng69/ml; C, ng74/ml; D–G, ng68/ml). A, left palp intact, ectal; B, same, mesal; C, left palp in copulatory expansion, ectal (note hooking of embolic apophysis with paracymbium fold, interaction of EC ridged edges and penetration of embolus from EC tip); D, left palp, expanded (embolus pulled out of EC groove), ventral; E, same, distal sclerites; F, same, proximal sclerites, ventral (note paracymbial fold); G, embolic division, dissected. Scale bars = 0.1 mm.

Composition. *Nephilengys cruentata*, *N. borbonica*.

Distribution (Fig. 35). Neotropics (Brazil, Colombia, Paraguay), Africa, Madagascar, Mascarene Islands, Comoros, Seychelle Islands, Aldabra Atoll.

***Nephilengys cruentata* (Fabricius, 1775)**
(Figs 1–12)

Aranea cruentata Fabricius, 1775: 439, description of female (from Brazil); type(s) not found in BMNH, presumed lost (Zimsen, 1964).

Epeira diadela Walckenaer, 1842: 54, description of female (from Brazil); type(s) not found in MNHN (depository cited by Simon, 1887: 271).

Epeira brasiliensis Walckenaer, 1842: 101, description of female (from Brazil); type(s) not found in MNHN (depository cited by Simon, 1887: 271).

Epeira azzara Walckenaer, 1842: 102, description of female (from Brazil); type(s) not found in MNHN (depository cited by Simon, 1887: 271).

Nephila genualis Gerstaecker, 1873: 502, description of female (from Kenya); holotype female in ZMB, from 'Mombas [Mombasa, Kenya], v d Decken, 1873', examined.

Epeira rhodosternon: van Hasselt, 1875 (see Dahl, 1912; who insufficiently cites this unknown work), record from Liberia, misidentification.

Nephilengys borbonica mossambicensis Karsch, 1878: 318, pl. 1, f. 3, description of female (from Mozambique); five

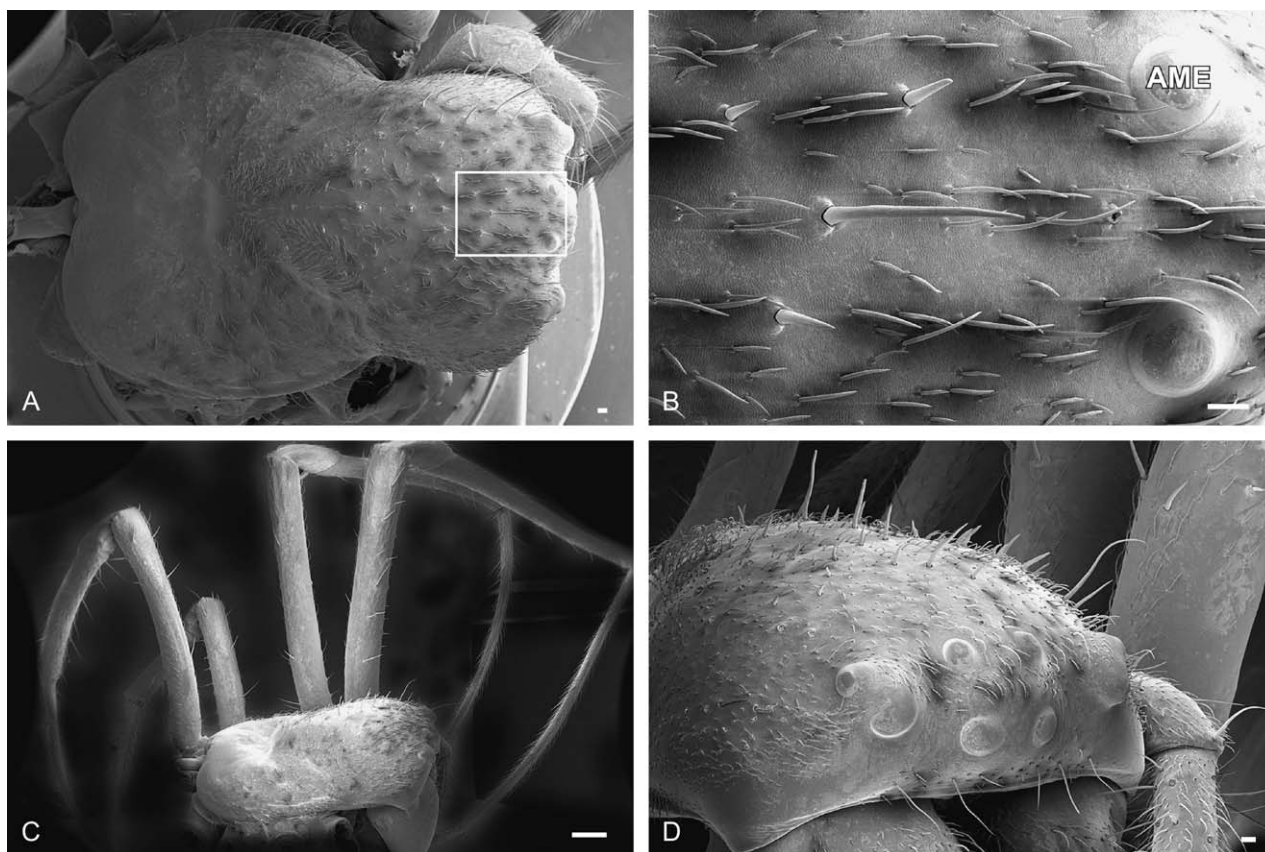


Fig. 15. *Nephilengys borbonica*, female prosoma, from Madagascar (ng66/fl): A, dorsal, box delimits area of image B; B, same, detail; C, dorso-ectal; D, frontal-ectal. Scale bars = 100 µm, except C = 1.0 mm.

syntype females (not female holotype, contra Levi & von Eickstedt, 1989) in ZMB, unreadable label, examined.

Nephila brasiliensis: Bertkau, 1880: 83, pl. 2, f. 29.

Nephilengys cruentata: Simon, 1887: 271; de Lessert, 1936: 244, f. 39, description of male; Roewer, 1942: 933; Schmidt & Jocqué, 1986: 209, f. 10–11; Levi & von Eickstedt, 1989: 48, f. 16–25; Hormiga *et al.*, 1995: 323, f. 5E–F, 12A–E; Platnick, 2005.

Nephila cruentata: Simon, 1894: 750; Bonnet, 1958: 3071.

Araneus diadelus: Petrunkevitch, 1911: 289.

Nephilengys cruentata cruentata: Dahl, 1912: 48.

Nephila cruentata chiloangensis Strand, 1920: 109, description of female (from Chiloango, Angola); holotype female not found in RMCA, presumed lost (Levi & von Eickstedt, 1989).

Nephilengys cruentata chiloangensis: Roewer, 1942: 933.

Etymology. *Cruentus* (Latin) = bloody (Brown, 1956), probably referring to the female red sternum.

Diagnosis. *Nephilengys cruentata* females differ from those of *N. malabarensis* and *N. papuana* by the epigynum with lateral copulatory openings (Fig. 2A), the presence of the epigynal copulatory groove (cf. Fig. 16C, D in

N. borbonica) and the absence of the epigynal septum and anterior rim. *N. cruentata* females differ from those of *N. borbonica* by the more lateral-posterior position of the copulatory openings (Fig. 2A–D), short copulatory ducts (Fig. 2F, G), which broadly attach spermathecae to the epigynal wall, and by shorter fertilization ducts (Fig. 2F, G). A further diagnostic character of *N. cruentata* females is the (normally) long femoral macrosetae. The embolic conductor of *N. cruentata* males is short and wide (Figs 4A, B; 9A, B; 10), not long and slender as in *N. malabarensis* and *N. papuana*. The distal embolic conductor of *N. cruentata* has a slender tip and a subdistal arch (Fig. 4A), whereas that of *N. borbonica* has a broad tip and an extensive distal arch (Fig. 14A).

Note. The strikingly red sternum (Fig. 11B) generally distinguishes *N. cruentata* females from those of the other *Nephilengys* species. To my knowledge, all live adult *N. cruentata* females possess the red sternum coloration. However, although the sternum of most *N. borbonica* females is not red, in some females from Madagascar and in all examined females from the Comoros it was red, and thus the character is not diagnostic. In addition, the red colour readily disappears in preserved material and, as such, is of little taxonomic use.

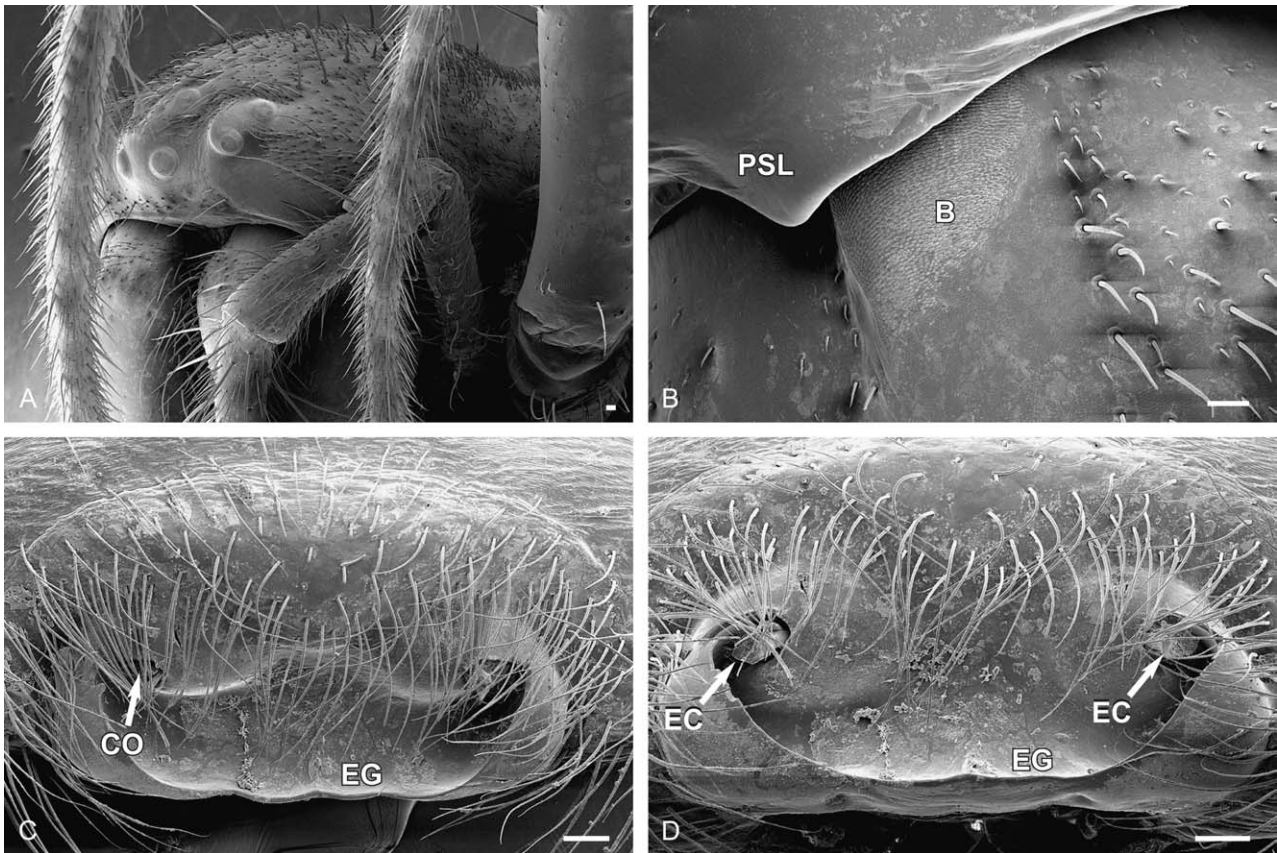


Fig. 16. *Nephilengys borbonica*, female from Madagascar (ng66/f1): A, prosoma, prolateral; B, cheliceral boss; C, epigynum, ventral; D, same, posterior, note an EC in each copulatory opening. Scale bars = 100 µm.

Description. *Female* (ng76/f1 from Sodwana Bay, South Africa; Figs 1; 2; 5; 6; 11A–D): Total length 23.9. *Prosoma* 9.9 long, 7.1 wide, 6.2 high; dark red-brown. Chelicerae black. Sternum 4.3 long, 3.9 wide; strikingly red, with dark brown edge. Labium, maxillae dark brown, with distal white edge. AME diameter 0.38, ALE 0.25, PME 0.25, PLE 0.23. AME separation 0.50, PME separation 0.78, PME–PLE separation 1.25, AME–ALE separation 1.1, AME–PME separation 0.70, ALE–PLE separation 0.4. Clypeus height 0.6. *Appendages.* Legs, palp annulated: coxae, trochanters, distal femora, patellae, distal tibiae, metatarsi, tarsi dark brown, proximal femora, tibiae light red-brown. Leg I length 41.0 (Fe 11.5, Pa 3.2, Ti 10.2, Me 13.0, Ta 3.1). *Opisthosoma* 17.4 long, 10.0 wide, 9.3 high. Dorsum yellowish, with dark brown pattern (Fig. 1C). Venter dark brown, with two central pairs of white patches, several lateral yellow patches (Fig. 1D). *Epigynum* as diagnosed (Fig. 2), spermathecae separated.

The prosoma length ranges from 7.8 to 11.3; total length from 17.4 to 28.0 ($n = 15$). Coloration varies greatly (cf. Fig. 11) and does not seem to be geographically distinct (except where indicated). Carapace colour ranges from grey through red, red-brown (most common, Fig. 11C) to black (Fig. 11A, B, D). In females from Bioko and Liberia,

sternum black edge is wider than described, such that the red area is confined to the median part of the sternum. Legs may be uniformly dark red or brown, or annulated as described, ranging in colour intensity from yellow and brown (Fig. 11C) to intensive red and black (Fig. 11A, B, D). Dorsum colour ranges from almost black (Fig. 11A, D), dark brown, light brown to whitish (Fig. 11C), with irregular light patches. Venter in some western African populations (Gabon) has two transverse yellow bands (in alcohol) as opposed to two pairs of spots. These females also have relatively widely separated copulatory openings. Most females' frontal abdomen with light band (Fig. 11A). Book lung covers in some females are iridescent. Sternal humps more pronounced in western African females (Liberia). Cheliceral teeth generally as described for the genus, but may vary. A female from Bioko had only two promarginal teeth on one side, three on the other, and had four teeth in two rows on the retromargin. The fourth retromarginal cheliceral tooth is small and can be overlooked, cheliceral furrow may have 10–20 inconspicuous denticles. Epigynum variation (Fig. 2A–D) not geographically defined. Some females have a weak septum in the middle epigynum, whereas most lack it altogether (as described). Inner epigynal morphology varies in the separation of spermathecae

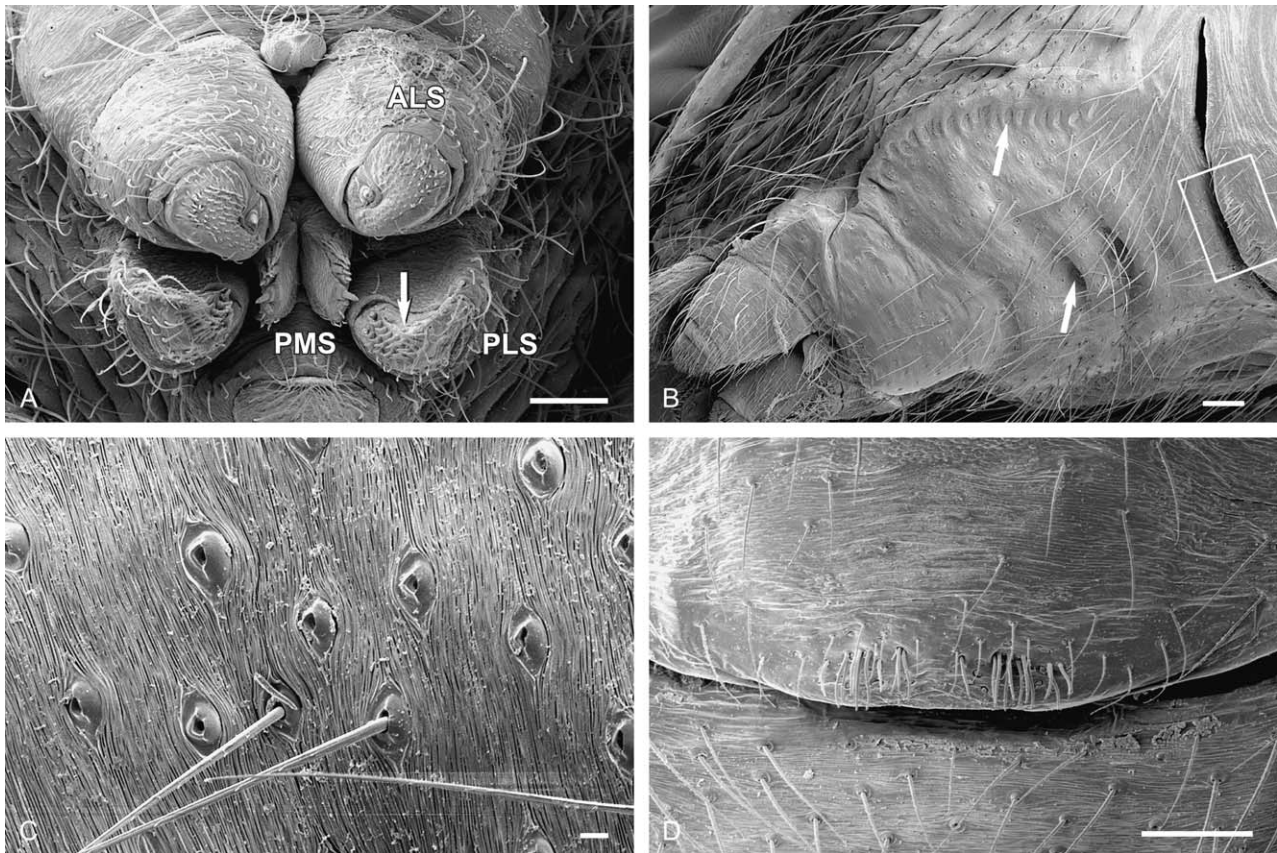


Fig. 17. *Nephilengys borbonica*, male from Madagascar (ng66/m1): A, spinnerets (note absence of triad, arrow); B, opisthosoma, ventro-lateral, showing ventral apodemes and lateral sclerotizations (arrows), box delimiting area of image D; C, detail of venter; D, epigastric region with epandrous gland spigots. Scale bars = 100 μ m, except C = 10 μ m.

but not in the diagnostics ($n = 5$, from Brazil, Liberia, Uganda, South Africa). Separation of spermathecae varies from widely separated (Fig. 2F) to almost touching. Immature females show all female somatic features, except less overall coloration.

Male (ng77/m1 from Makakatana Bay, South Africa; Fig. 3): Total length 3.9. *Prosoma* 2.0 long, 1.6 wide, 1.2 high; yellow-brown. Sternum 1.0 long, 0.8 wide; yellow-brown, darker laterally. AME diameter 0.18, ALE 0.09, PME 0.08, PLE 0.08. AME separation 0.13, PME separation 0.18, PME–PLE separation 0.22, AME–ALE separation 0.09, AME–PME separation 0.16, ALE–PLE separation 0.09. Clypeus height 0.13. *Appendages*. Legs proximally yellow–light brown (coxae, trochantera, femora); tibiae, metatarsi, tarsi, distal femur IV dark brown. Leg I length 10.0 (Fe 2.5, Pa 0.8, Ti 2.3, Me 3.1, Ta 1.3). *Opisthosoma* 2.4 long, 1.6 wide, 1.0 high. Dorsum (scutum) grey, with white pigment dots and dark brown midband (Fig. 3A, C), venter grey, laterally with black longitudinal stripes on lateral integument folds (Fig. 3A, D). *Pedipalp* as diagnosed (Figs 4; 9; 10).

Prosoma length ranges from 1.8 to 2.0; total length from 3.1 to 3.9 ($n = 10$). Prosomal coloration dull grey to brown

and bright red (Fig. 11E), chelicerae reddish-brown to light grey. Examined males from Brazil lacked paracymbial setae (Fig. 9C) but did not differ in diagnostic characters from the African populations.

Distribution (Fig. 35). Tropical and subtropical Africa and limited areas of South America: Brazil, Colombia, new record [immature ng249/j1 from COLOMBIA: Cartagena, 1905 (*Gagzo*) (ZMH)], Paraguay, new record [two females ng247/f1 from PARAGUAY: no locality data, 19.v.1899 (*Ahlborn*) (ZMH)]. I examined a sample of seven males from Moroni, Comoros (ng622). I found no other material of *N. cruentata* from Comoros, where populations of *N. borbonica* naturally occur. Although sample ng622 implies that, on Njazidja Island, the two species are sympatric, such interpretation merits caution. Namely, the label data state ‘... reared in KBIN ...’. If reared, the spiders may not have originated in Comoros. Additionally, the RMCA database reports different, probably erroneous coordinates for Moroni (S12°15' E43°45'). Thus, the locality data for ng622 are probably erroneous and that locality is omitted from the distribution map (Fig. 35) of *N. cruentata*.



Fig. 18. *Nephilengys borbonica*, photographs of live spiders. A–D, from Madagascar; A, B, female from Périnet Special Reserve taken from its web; A, placed on tree trunk, dorsal (note blue dorsum); B, hand-held, ventral (note blood-red patches on black sternum); C, D, female from Ranomafana in its web built against a wooden house; C, at hub, ventral (note almost uniformly dark sternum); D, in retreat, dorsal (note creamy-brown dorsum); E, female (left, note white dorsum) and male (right) in retreat, from Mauritius, photograph by H. C. Kiesbüy; F, female (note red dorsum) from Réunion (Piton des Neiges path, Cirque de Cilaos – at 1400 m altitude; photograph by H. C. Kiesbüy, information by D. Hansen).

Natural history. During a recent survey (2001) in South Africa, the species was common synanthropically (Figs 11 A–D; 12). See ‘Biology’.

Taxonomic history. The first species of the genus was described by Fabricius in 1775 (not in 1793 as cited by Dahl,

1912: 46) as *Aranea cruentata* from Brazil. Walckenaer (1842) apparently was not aware of Fabricius’ description when adding three new species from Brazil to the synonymy (see Simon, 1887: 271) of *A. cruentata*: *Epeira diadela* Walckenaer, 1842, *Epeira brasiliensis* Walckenaer, 1842

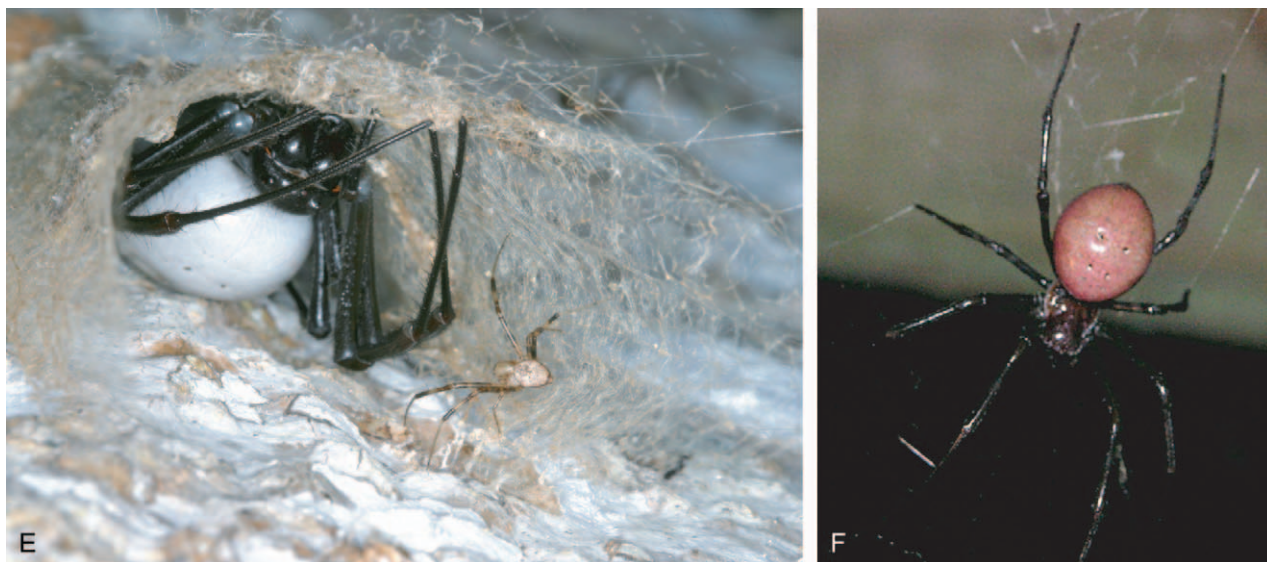


Fig. 18. Continued.

and *Epeira azzara* Walckenaer, 1842. Walckenaer's (1842) descriptions of *E. diadela* and *E. azzara* are sufficient to confirm the synonymy with *Aranea cruentata*, but the description of *E. brasiliensis* is not (cf. Dahl, 1912: 46). However, Simon's (1887) synonymy was based on a re-examination of Walckenaer's type material (Simon, 1887: 272), including that of *E. brasiliensis*. Furthermore, Bertkau's (1880) redescription of *Nephila brasiliensis* (Walck.) clearly deals with *Nephilengys cruentata*. Today, Walckenaer's type material of *E. diadela*, *E. brasiliensis* and *E. azzara* is lost (Levi & von Eickstedt, 1989). These names continue in synonymy of *Nephilengys cruentata* as proposed by Simon (1887), Dahl (1912) and Levi & von Eickstedt (1989). Gerstäcker (1873) first treated African *Nephilengys* by describing *Nephila genualis* from Kenya. The description of the female clearly deals with *N. cruentata*, as recognized by Simon (1887) and Dahl (1912). In an unknown reference, van Hasselt (1875) [cited in Dahl (1912)] recorded *Epeira rhodosternon* Dolesch. (= *N. malabarensis*) from Liberia, which was a misidentification of *N. cruentata* (see Dahl, 1912). Karsch (1878) described a female *Nephilengys borbonica mossambicensis* from Mozambique, correctly synonymized with *Nephilengys cruentata* by Dahl (1912). Simon (1887) first recognized that *Epeira cruentata* belonged to the genus *Nephilengys*. Later, Simon (1894) apparently changed his mind by treating *Nephilengys* as a synonym of *Nephila*. Most twentieth century authors (Dahl, 1912; Lessert, 1936; Benoit, 1963; Schmidt & Jocqué, 1986; Levi & von Eickstedt, 1989; Hormiga *et al.*, 1995), however, continued to apply the name *Nephilengys cruentata*, although the circumscription of their species varied. For example, Dahl (1912) revised *Nephilengys* and recognized three subspecies of *N. cruentata*. Here, I demonstrate that *N. cruentata* is found in mainland Africa and in Brazil, and not on the Indian Ocean Islands off Africa's east coast (contra Dahl, 1912).

My circumscription of *Nephilengys cruentata* thus corresponds to *N. c. cruentata* (*sensu* Dahl, 1912); I treat the remaining two subspecies (*sensu* Dahl, 1912), *N. c. borbonica* and *N. c. livida*, as *N. borbonica*. Strand (1920) (not 1918 contra Platnick, 2005) described *Nephila cruentata chiloangensis* from Angola, based on variation in female abdominal coloration. The holotype is lost (Levi & von Eickstedt, 1989), and the name continues as a synonym of *N. cruentata* (Levi & von Eickstedt, 1989). Lessert (1936: 244, fig. 39) redescribed a male *N. cruentata* from east Africa, and provided the first illustration of a male palp (although of little use for general identification). Schmidt & Jocqué (1986: 209, f. 10–11) diagnosed the species from *N. borbonica*, and Levi & von Eickstedt (1989: 48, f. 16–25) redescribed *N. cruentata* with the emphasis on the Neotropical material. Hormiga *et al.* (1995) provided palpal anatomical illustrations (figs 5E–F; 12) and female spinneret images (fig. 18) in a phylogenetic context.

Nephilengys borbonica (Vinson, 1863) (Figs 13–21)

Epeira borbonica Vinson, 1863: 170, 309, pl. 4, f. 1, description of female (from Réunion); type(s) not found, presumed lost.

Epeira livida Vinson, 1863: 175, 310, pl. 14, f. 1, description of female (from Madagascar); type(s) not found, presumed lost.

Nephila instigans Butler, 1876: 442, description of female (from Rodriguez); **syn.n.** A female and a juvenile syntype (ng269) in BMNH, labelled '76.13, *Nephila cruentata* Fabr., Rodriguez, G. Guliver (c). Transit of Venus Exped. 1874–1875. [*Nephila instigans* Butler Cotypes]. Hirst revised 1876', examined; removed from syn. of *N. cruentata* (contra Levi & von Eickstedt, 1989: 48).

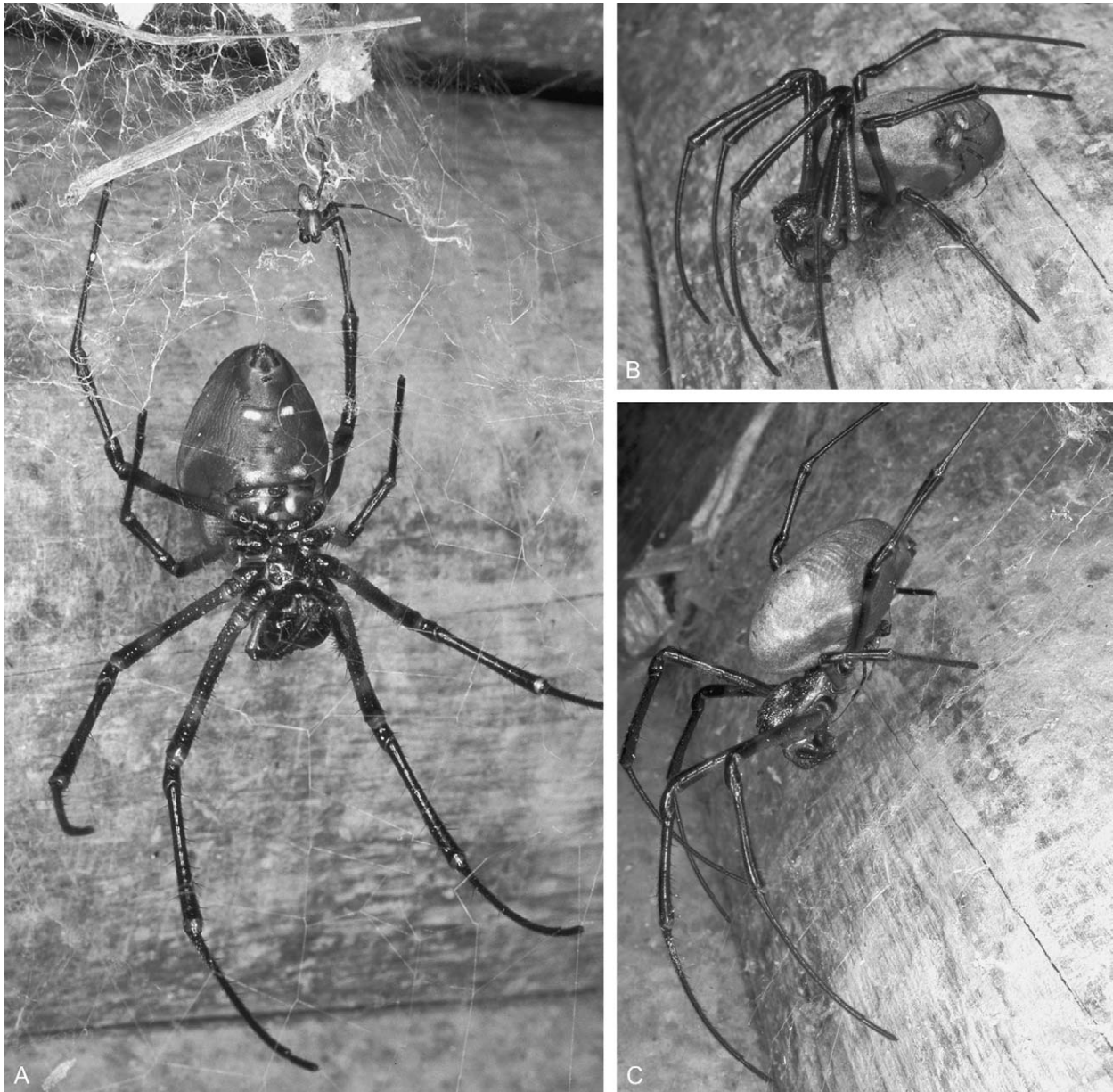


Fig. 19. *Nephilengys borbonica*, courtship behaviour documented in Ranomafana, Madagascar (ng65): A, male (above) approaches female in her web; B, male climbs on female abdomen while she moves around, male approaches female venter; C, male on female venter attempts copulation.

Nephila instigans: Butler, 1878: 504, pl. 52, f. 10, redescription of female.

Nephila cruentata: Lenz, 1891: 180, pl. 2, f. 19, description of male, misidentification.

Nephilengys cruentata borbonica: Dahl, 1912: 48; Roewer, 1942: 933.

Nephilengys cruentata livida: Dahl, 1912: 48; Roewer, 1942: 933.

Nephila borbonica: Bonnet, 1958: 3067.

Nephilengys borbonica: Benoit, 1963: 369; Platnick, 2005.

Nephilengys borbonica livida, **syn.n.** Benoit, 1963: 368;

Benoit, 1964: 312; Schmidt & Jocqué, 1986: 209, f. 7–9, description of male and female; Platnick, 2005.

Nephilengys borbonica borbonica: Benoit, 1964: 312.

Nephilengys cruentata: Saaristo, 1978: 120, f. 211–223, description of male and female, misidentification; Roberts, 1983: 284, 285, f. 222–224, misidentification.

Etymology. *Borbonica* (Latin) = ‘of the Bourbon’ [Island, today’s Réunion].

Diagnosis. *Nephilengys borbonica* females differ from those of *N. malabarensis* and *N. papuana* by the epigynum

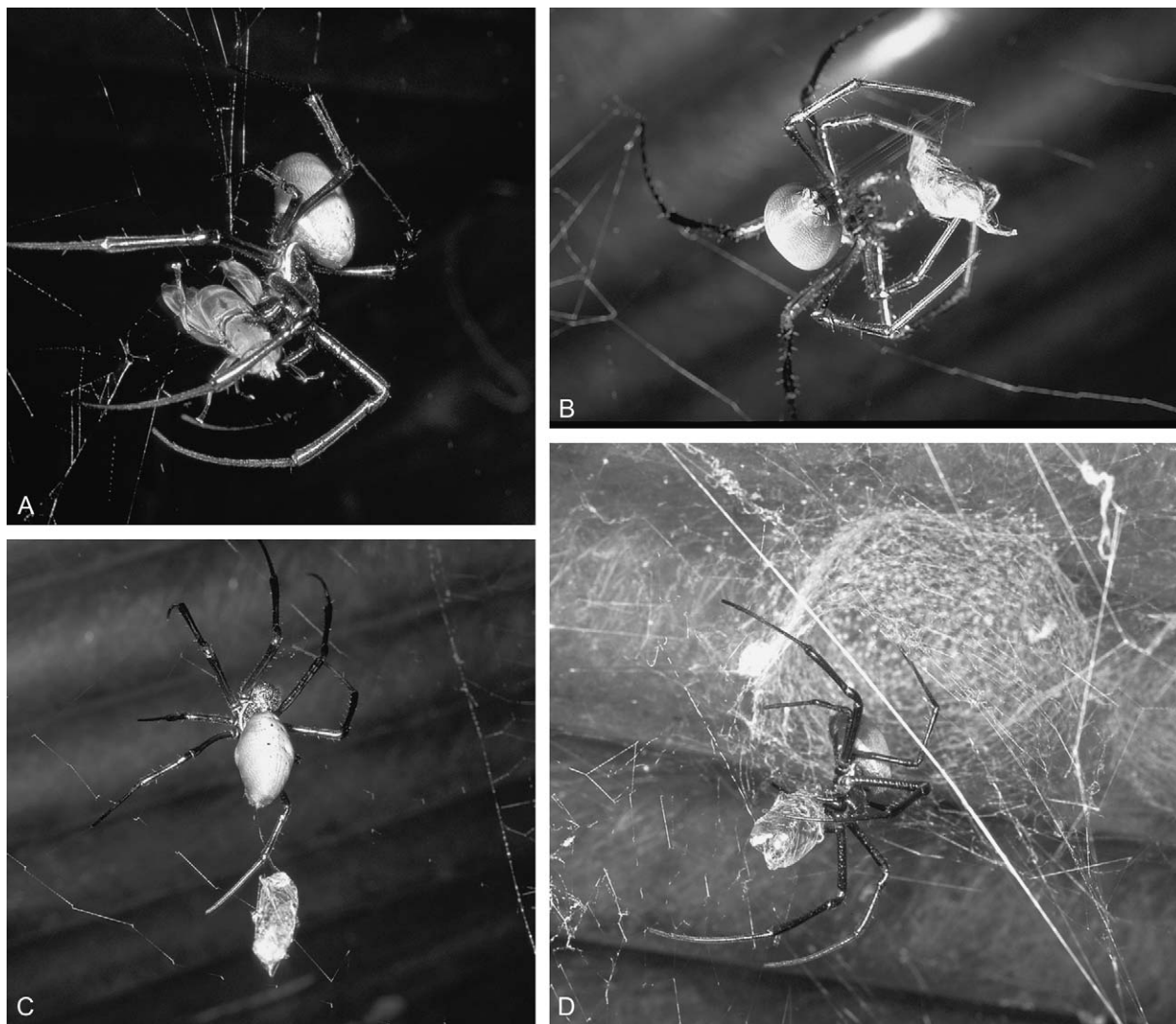


Fig. 20. *Nephilengys borbonica*, female attack behaviour documented in Ranomafana, Madagascar. Flying hymenopteran prey gets trapped in the orb, female rushes to it, delivers a bite and holds the prey in its jaws for more than a minute (A), then wraps it (B). Female then cuts the prey out of the web, attaches it to her spinnerets (C) and carries it to the hub, where she suspends the wrapped prey, assumes the head-down resting pose, then re-takes the prey and starts feeding (D). Note proximity of hub and retreat (D).

with antero-lateral copulatory openings (Fig. 13A, B), the presence of the epigynal copulatory groove (Figs 13A; 16C, D) and the absence of the epigynal septum and anterior rim. *N. borbonica* females differ from those of *N. cruentata* by the more anterior position of the copulatory openings (Fig. 13A, B), long copulatory ducts (Fig. 13C, D), which do not broadly attach spermathecae to the epigynal wall, and by longer fertilization ducts (Fig. 13C, D). A further character distinguishing *N. borbonica* females from those of *N. cruentata* is the presence of short stout macrosetae on femora 1 and 2. The EC of *N. borbonica* males (Fig. 14A–E) is short and wide, not long and slender as in *N. malabarensis* and *N. papuana*. Distal EC of *N. borbonica* has a broad tip and an extensive distal arch (Fig. 14A), whereas that of *N. cruentata* has a slender tip and a subdistal arch.

Note on diagnosis. The sternum of most *N. borbonica* females is not red (as in *N. cruentata*), but in females from the Comoros and in some females from Madagascar it is so (see variation). This and other coloration characteristics with considerable intraspecific variation (such as abdomen colour) should be observed with caution.

Description. *Female* (ng93 from Ranomafana, Madagascar; Figs 13; 15; 16; 18C, D): Total length 23.6. *Prosoma* 9.3 long, 6.3 wide, 5.6 high at head region; red–brown. Chelicerae dark red–brown. Sternum 4.0 long, 3.3 wide; light red, with dark brown edge. Labium, maxillae dark brown, with distal white edge. AME diameter 0.37, ALE 0.22, PME 0.22, PLE 0.22. AME separation 0.47, PME separation 0.63, PME–PLE separation 1.2, AME–ALE separation 0.95,



Fig. 21. *Nephilengys borbonica*, female web built vertically between two trees such that the orb is eccentric horizontally, central Madagascar (ng99). Note that upper portion of orb had been recently rebuilt, whereas parts of the lower orb are old.

AME–PME separation 0.5, ALE–PLE separation 0.25. Clypeus height 0.6. *Appendages.* Ventral, frontal femora 1 and 2 with numerous short stout spines. Legs, palp annulated as in *N. cruentata* (but, see variation). Leg I length 44.9 (Fe 12.4, Pa 3.5, Ti 10.2, Me 15.2, Ta 3.6). *Opisthosoma* 16.7 long, 11.7 wide, 9.9 high. Dorsum creamy brown (but, see variation), venter dark brown, with smaller central pairs of white patches than illustrated in *N. cruentata* (see variation). *Epigynum* as diagnosed (Figs 13; 16C, D); prominent lateral sclerotized chambers with copulatory openings opening anteriorly. Tubular copulatory ducts connect to spermathecae in their posterior part. Spermathecae juxtaposed.

In females from Madagascar, prosoma length ranges from 7.4 to 10.2; total length from 15.5 to 23.6 ($n = 10$). The number of cheliceral teeth may depart from the typical condition (see genus description): one female from Périnet had a single large promarginal tooth on one and the typical 3 + 1 on another chelicera. Sternal humps more or less conspicuous. Sternum colour varies from dark red (Fig. 18B) to orange and white, or can be centrally dark (Fig. 18C). Abdomen colour in live animals varies from dark grey to brown (Fig. 18C, D) to purple (Fig. 18A, B). Examined

females from Mauritius and Réunion were smaller than most females from Madagascar: prosoma length ranges from 7.4 to 8.7; total length from 14.6 to 17.7 (ng92: $n = 9$). The female sternum in these females was dark brown with a narrow median light band [Dahl (1912: 75) used this character to separate *Nephilengys cruentata borbonica* from *N. c. livida*], which can be discontinuous in the mid-sternum. Cheliceral denticles absent or inconspicuous. Abdomen colour in live spiders is white (Fig. 18E), observed in females from Mauritius (D. Hansen, pers. comm., Institute of Environmental Sciences, University of Zurich, Switzerland), or red (Fig. 18F), observed in females from Réunion (D. Hansen, pers. comm.). Genital morphology of Mascarene Island females is indistinguishable from that of females from Madagascar.

Male (ng93/ml from Ranomafana, Madagascar; Figs 14; 17): Total length 3.5. *Prosoma* 1.9 long, 1.4 wide, 1.0 high; yellow–brown. Sternum 0.74 long, 0.70 wide; yellow–brown, darker laterally. AME diameter 0.13, ALE 0.10, PME 0.10, PLE 0.10. AME separation 0.13, PME separation 0.16, PME–PLE separation 0.19, AME–ALE separation 0.06, AME–PME separation 0.16, ALE–PLE separation 0.06. Clypeus height 0.13. *Appendages.* Legs annulated yellow, dark grey. Leg I length 8.9 (Fe 2.3, Pa 0.6, Ti 2.0, Me 2.8, Ta 1.2). *Opisthosoma* 2.1 long, 1.4 wide, 1.0 high. Dorsum grey, with white pigment dots and dark brown central area, venter dark grey with two pairs of white dots, laterally with black longitudinal stripes on lateral integument folds. *Pedipalp* as diagnosed (Fig. 14).

Prosoma length ranges from 1.9 to 2.5; total length from 3.1 to 4.9 ($n = 10$).

Distribution (Fig. 35). Madagascar, Mascarene Islands, Comoros, Seychelle Islands, Aldabra Atoll.

Natural history. During a Madagascar survey (2001), the species was common in synanthropic environments (Figs 18A–D; 19–21, see ‘Biology’). In Réunion, females were observed in cloud forests at 1400–1500 m elevation (D. Hansen, pers. comm.).

Taxonomic history. Vinson (1863) described *Epeira borbonica* from Bourbon Island (today Réunion, France), and *E. livida* from Madagascar. Vinson’s species diagnoses were based exclusively on female coloration (pl. 4: fig. 1; pl. 14: fig. 1). Vinson noted (p. 177) that males of both species were alike and that the females differed only in the abdomen colour, which was red in *E. borbonica* and variable in *E. livida* from pale purple, livid (hence the species name) to shades of black. Indeed, I found the abdomen colour of females from Madagascar to vary from white through creamy brown (Fig. 18C, D) to purple (Fig. 18A, B); female abdomens from Mauritius were white (Fig. 18E) and those from Réunion were red (Fig. 18F). However, based on the somatic and genitalic morphology, these populations are conspecific. In 1876, Butler described and, in 1878, re-described *Nephila instigans* from Rodriguez. Dahl (1912) synonymized the species with *Nephilengys cruentata borbonica*, and Levi & von Eickstedt (1989: 48) listed the name

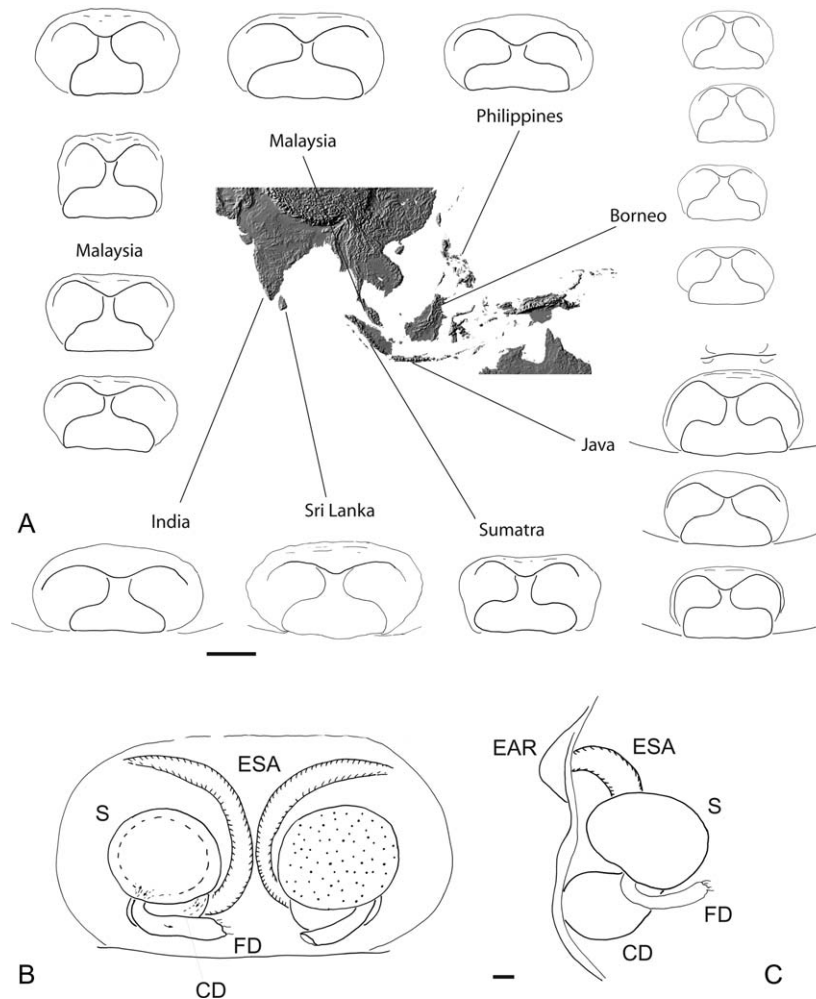


Fig. 22. *Nephilengys malabarensis*, epigynal morphology and variation: A, size and shape variation, ventral (note same scale; all epigyna illustrated from one region are from same sample; sample from Niah, Borneo represents types of *N. niahensis*, and resembles females from elsewhere in Borneo, see text); B, cleared epigynum (from Kalimantan, ng124/fl, representing anatomy throughout species range), dorsal; C, same, ectal. Scale bars: A = 0.5 mm; B, C = 0.1 mm.

under synonymy of *N. cruentata*. Here, I remove it from the synonymy of *N. cruentata* and treat it as a synonym of *N. borbonica*. Lenz (1891: 180) treated *E. borbonica* and *E. livida* as synonyms of *N. cruentata* and, in the same publication, described the male of the form '*livida*' for the first time. Dahl (1912: 48) treated these two names as subspecies of *N. cruentata* and provided a key to separate them (Dahl, 1912: 75). Benoit (1963) recognized that *N. borbonica* and *N. livida* were distinct from *N. cruentata*. He elevated *N. borbonica* from a subspecies of *N. cruentata* and treated the Madagascar (*livida*) form as a subspecies (*N. borbonica livida*), both subspecies differing only by the sternum coloration. Recent treatments of the Indian Ocean *Nephilengys* as *N. cruentata* from the Seychelle Islands (Saaristo, 1978) and Aldabra atoll (Roberts, 1983) are mis-identifications, and clearly depict *N. borbonica*. Schmidt & Jocqué (1986) supported Benoit's distinction between *N. cruentata* and *N. borbonica livida* (from Comoros) as

distinct species, and provided detailed illustrations of male and female genital characters diagnostic for each species.

I have been unable to locate Vinson's types of *E. borbonica* and *E. livida*. However, from the examined material from Madagascar and other Indian Ocean islands, I conclude that only one species can be diagnosed from the region, and that all somatic variation (mainly coloration) between the Madagascar and the Mascarene Islands populations can be attributed to intraspecific variation. The specific names *N. livida* (Vinson, 1863) and *N. borbonica* (Vinson, 1863) were published simultaneously. Benoit (1963: 2, 3), as first reviser, selected *N. borbonica* as the valid species name.

The '*malabarensis* species group'

Monophyly. The clade is supported by the following unambiguous synapomorphies (Fig. 37): glabrous female

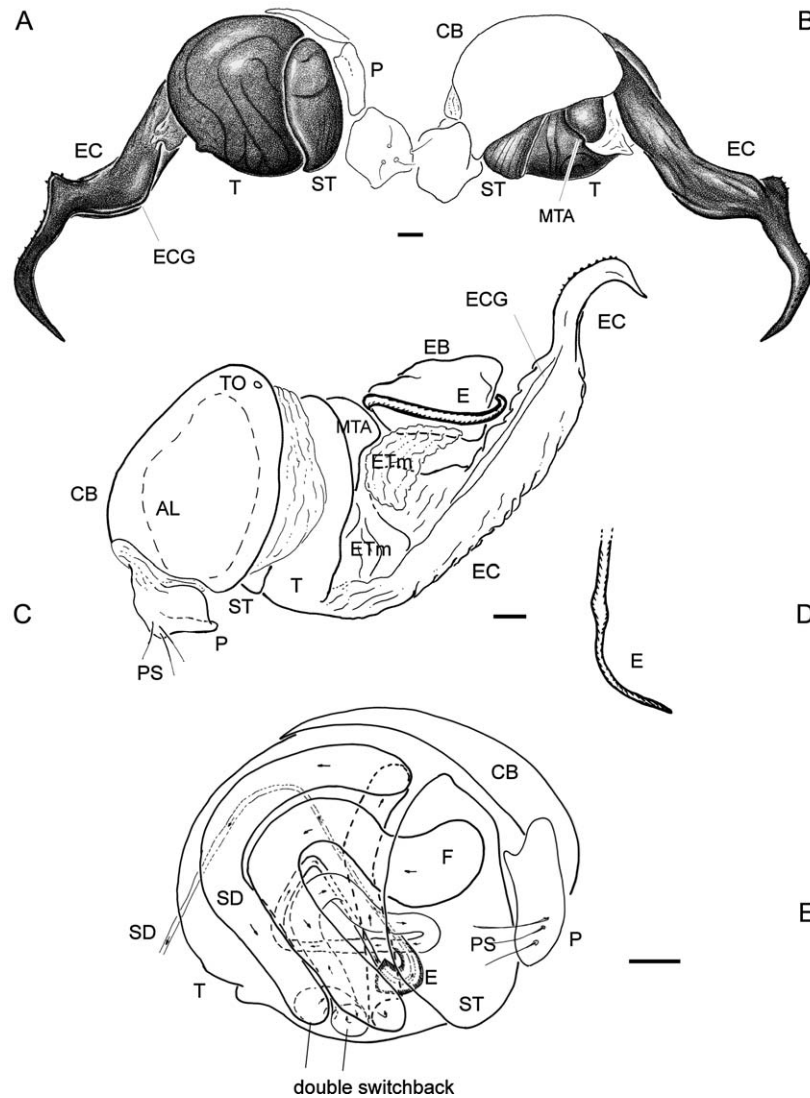


Fig. 23. *Nephilengys malabarensis*, male pedipalp, from Sri Lanka (ng4/m1): A, left palp, ectal; B, same, mesal; C, right palp, expanded (embolus broken, distal end shown in image D); D, embolus distal end (broken); E, bulb transparent, showing sperm duct, ectal. Scale bars = 0.1 mm.

carapace edge (character 4/state 0; Fig. 28C), absence of female sternal tubercle IV (28/0), round anterior epigynal area (85/1; Fig. 29A), unplugged female copulatory openings (96/0; Fig. 29A, B) and the embolus constriction (162/1; Figs 23D; 27C). Ambiguous synapomorphies include (ACCTRAN, Fig. 37) single radius attachment on frame (179/0) and (DELTRAN, Fig. 37) epigynal septum (82/1, Fig. 39 A–C) and epigynal sclerotized arch (95/1; Figs 22B, C; 26D, E).

Diagnosis. Epigynum (Figs 22A, C; 26A–C, E; 29A–C) roughly as long as wide, with (inverted T-shaped) epigynal septum, medial copulatory openings and anterior rim; inner epigynum with sclerotized arch (Figs 22B, C; 26D, E); females medium sized (10–18 mm); males orange, palp with

long and slender embolic conductor (Figs 23A, B; 27A, B), embolus with distal bulge (Figs 23D; 27C).

Composition. *Nephilengys malabarensis*, *N. papuana*.

Distribution (Fig. 35). South and South-East Asia, New Guinea, Australia.

***Nephilengys malabarensis* (Walckenaer, 1842)**
(Figs 22–25)

Epeira malabarensis Walckenaer, 1842: 103, description of female (from Malabar Coast, India); female holotype in MNHN (ng206), jar 1192 BIS labelled 'Museum Paris Cote de Malabar Dussumier *Nephilengys malabarensis* Walck. Type!', examined.

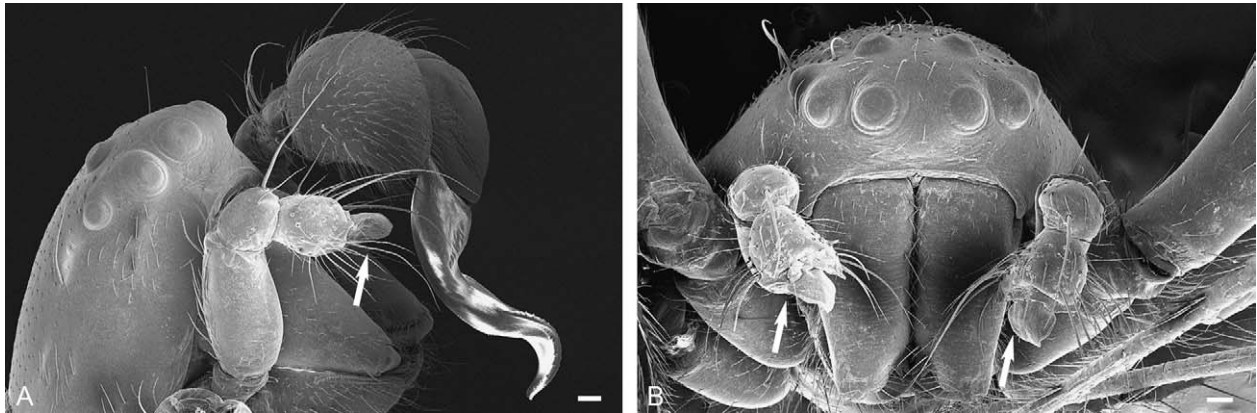


Fig. 24. *Nephilengys malabarensis*, male 'eunuchs' (individuals with severed palps, arrows) from Sri Lanka: A, male lacking right palpal tarsus (ng4); B, male lacking both palpal tarsi (ng5/m1). Scale bars = 100 μ m.

Epeira anama Walckenaer, 1842: 102, description of female (from Anam or Cochinchina, today's Vietnam); type(s) not found.

Epeira malabarica Doleschall, 1857: 420 [lapsus calami].

Epeira rhodosternon Doleschall, 1859: 40, pl. 12, f. 6,

description of female (from Java); syntype female in RMNH, examined (see below).

Nephila rivulata O. P.-Cambridge, 1871: 618, pl. 49, f. 1–2, description of male and female (from Labuan, China Sea); syntypes in OUMNH, examined (see below).

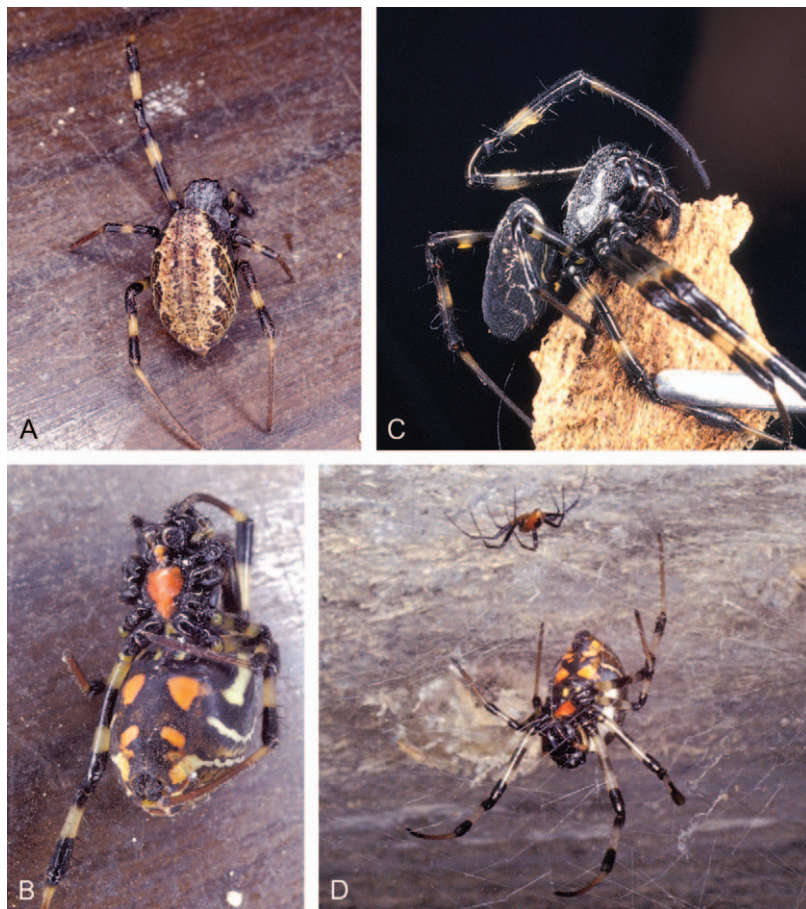


Fig. 25. *Nephilengys malabarensis*, photographs of live spiders (all but C from Sri Lanka): A, B, female taken from web, placed on ground; A, dorsal (note brown and grey dorsum); B, ventral (note bright orange sternum and patches on venter); C, female from Java taken from web (note almost black prosoma and opisthosoma); D, male (above) cohabiting in female's (below) web.

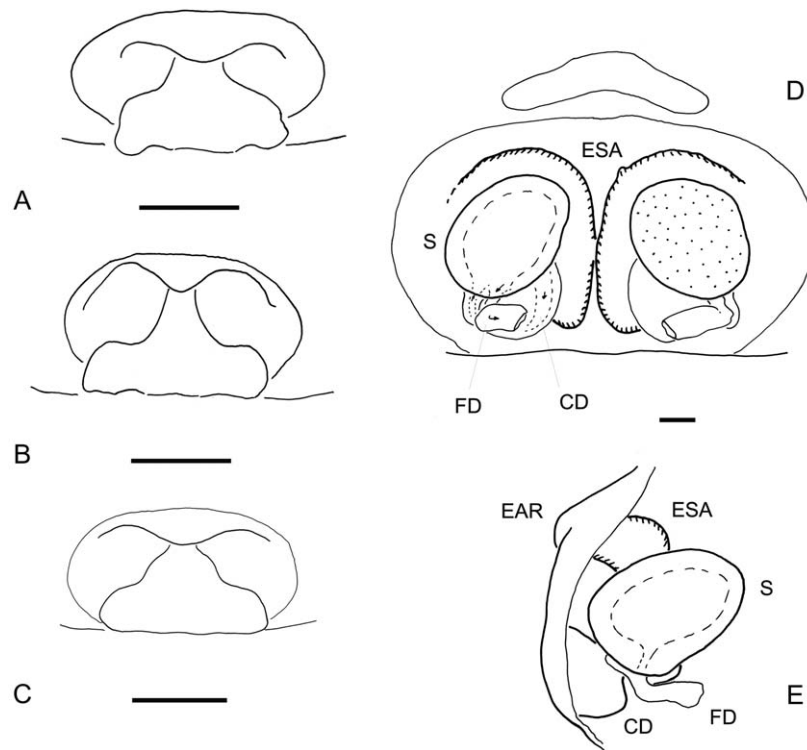


Fig. 26. *Nephilengys papuana*, epigynal morphology and variation: A–C, ventral views showing variation (note same scale); A, from Queensland; B, from northern Papua New Guinea (ng2); C, from south-east Papua New Guinea (ng129); D, dorsal; E, ectal. Scale bars A–C = 0.5 mm; D, E = 0.1 mm.

Nephilengys schmeltzii L. Koch, 1872: 144, pl. 11, f. 7, description of female (from the Philippines); type information below.

Nephilengys hofmanni L. Koch, 1872: 145, pl. 11, f. 8, description of female (from Borneo); type information below.

Nephilengys malabarensis: Thorell, 1878: 123; Dahl, 1912: 49; Roewer, 1942: 933; Deeleman-Reinhold, 1989: 624, f. 11–14; Barrion & Litsinger, 1995: 565, f. 350a–c; Song *et al.*, 1999: 217, f. 125F–I; Platnick, 2005.

Nephila urna van Hasselt, 1882: 28, pl. 4, f. 12–14, description of male (from Sumatra); type(s) not found.

Nephilengys malabarensis var. *γ*, *annulipes* Thorell, 1890: 188, description of male and immature female (from Sumatra); type information below.

Nephila malabarensis: Simon, 1894: 745, f. 827; Pocock, 1900: 217, 219; Bösenberg & Strand, 1906: 192, pl. 11, f. 216; Bonnet, 1958: 3079; Wiehle, 1967: 195, f. 48; Tikader, 1982: 95, f. 183–186; Millidge, 1988: 258, f. 24; Yin *et al.*, 1990: 3, 141, f. 6–9.

Metepeira andamanensis Tikader, 1977: 181, f. 12A–C, description of female.

Nephilengys niahensis Deeleman-Reinhold, 1989: 626, f. 15–16, description of female (from Borneo); **syn.n.** Female holotype, three female and an immature paratype from Niah Cave, Sarawak, East Malaysia, in MHNG, examined.

Comments on types. Likely syntype female of *Epeira rhodosternon* examined in RMNH (ng230). Doleschall based his description on illustration ('N.K.', see Doleschall, 1859: 2). However, the specimen in RMNH might be the one on which N.K. illustration was based, which would make it type (ICZN: Art. 72.5.6). Female parts are scattered around the vial, in extremely bad shape, but examination of the epigynum was possible.

Syntypes of *Nephila rivulata* examined in OUMNH. The jar labelled '*Nephilengys malabarensis* W, *Nephila rivulata* Cb Types, Ceylon, 1. Amboina Thorell' contains three vials, one with a male and two with a female each of *N. malabarensis*. The type localities, interpreted as Sri Lanka and Ambon, Indonesia, do not match the description (see also 'Taxonomic history').

Type(s) of *Nephilengys schmeltzii* and the holotype female of *Nephilengys hofmanni* may have been housed in Stuttgart. If so, they are no longer available, as the collection was destroyed in fire during World War II (W. Schawaller, pers. comm., Staatliches Museum für Naturkunde, Stuttgart, Germany).

Type(s) of *Nephilengys malabarensis annulipes* may be in MCSNG, requested, but not received.

Holotype female and four paratype females of *Metepeira andamanensis* from Diglipur, North Andaman, India (Tikader, 1977: 183) in ZSI, requested, but not received.

The type material of *N. niahensis* seems to represent a population conspecific with *Nephilengys malabarensis*,

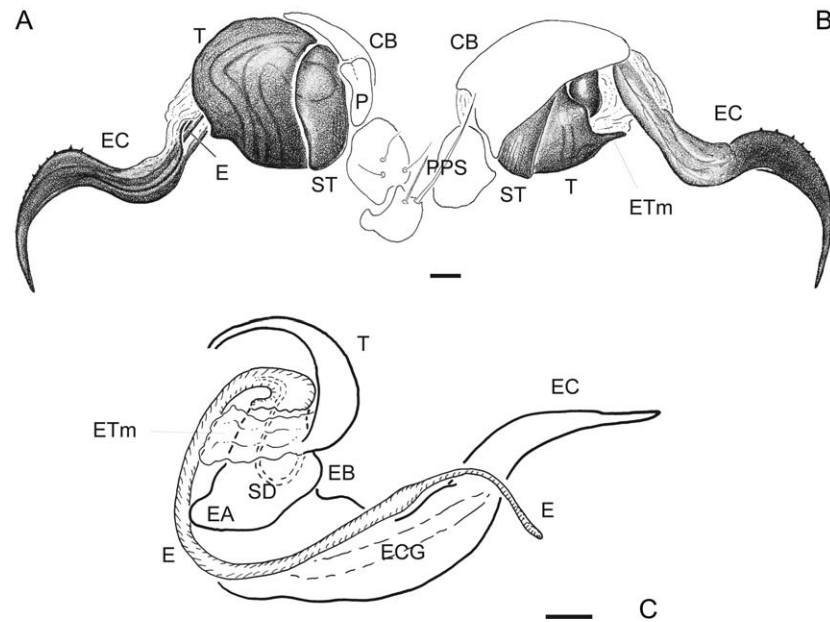


Fig. 27. *Nephilengys papuana*, male pedipalp, from Queensland (ng64): A, left palp, ectal; B, same, mesal; C, right palpal distal sclerites, expanded and dissected. Scale bars = 0.1 mm.

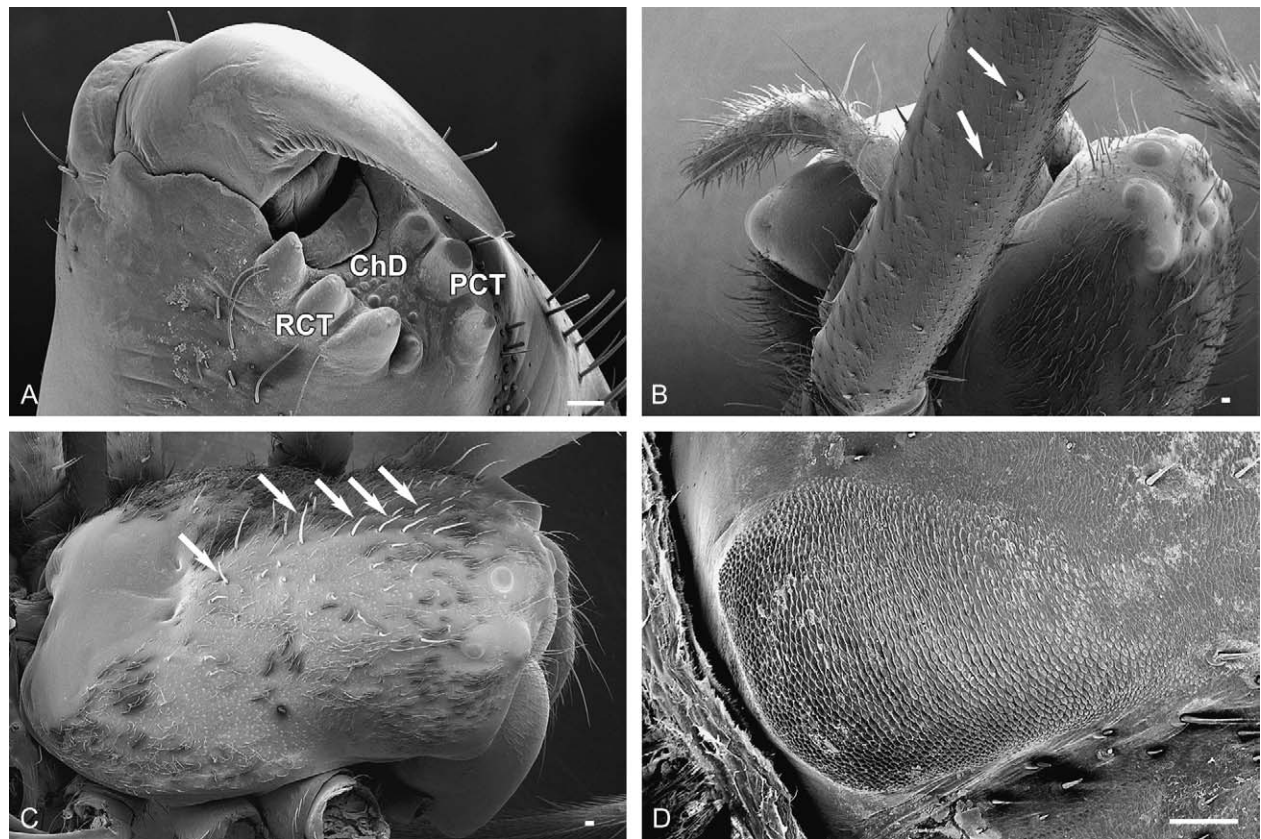


Fig. 28. *Nephilengys papuana*, female prosoma, from Queensland (ng64): A, right chelicera, apical; B, prosoma and femur I with short macrosetae (arrow); C, carapace with stout erect macrosetae (arrows); D, cheliceral boss. Scale bars = 100 μ m.

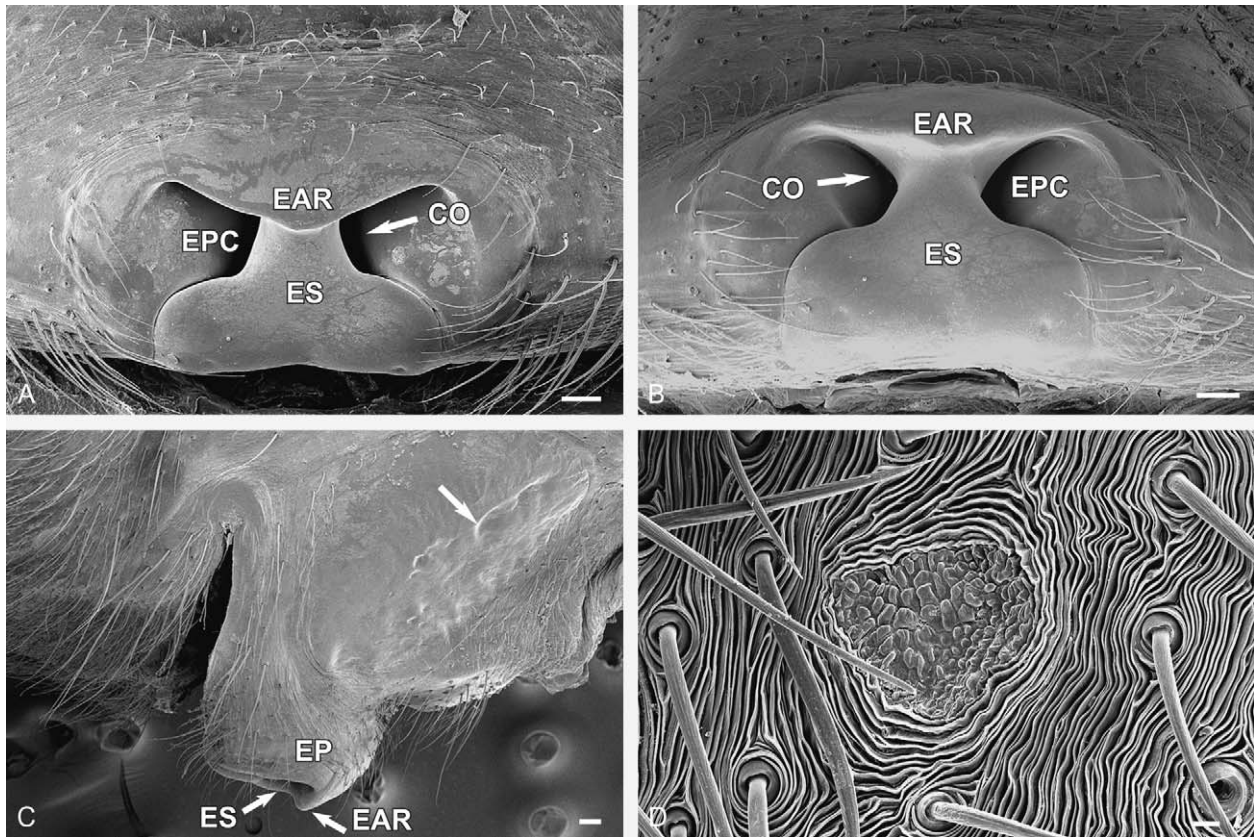


Fig. 29. *Nephilengys papuana*, female opisthosoma, from Queensland (ng64): A, epigynum, ventral; B, same, posterior; C, epigastral area, lateral, with epigynum, and slightly grooved (arrow) book lung cover; D, dorsal abdominal cuticle with posterior dorsal sclerotization. Scale bars = 100 μ m, except D = 10 μ m.

with admittedly small individuals, but quite typical epigynal shape and variation for this species (epigyna labelled Borneo in Fig. 22A illustrated from the type series). Additional female material examined from other parts of Borneo has shown similar epigynal and size features, and has been matched with males of *N. malabarensis* [NB: although not examined, the types of *Nephilengys hofmanni* L. Koch, 1872 may also be from the Bornean population with similar features, conspecific with *N. malabarensis*]. Thus, *N. niahensis* is proposed as a junior synonym of *N. malabarensis*, as the types possess all diagnostic features of this species, and none unique to the population. No males of *N. niahensis* have been described. The first male *Nephilengys* from Niah cave (ng208) available to my examination is *N. malabarensis*, and thus supports the proposed synonymy.

Etymology. *Malabarensis* (Latin) = of the Malabar [Coast, India].

Diagnosis. *Nephilengys malabarensis* females differ from those of *N. cruentata* and *N. borbonica* by the presence of a well-defined anterior rim and the epigynal septum (Fig. 22A), which separates two chambers with medially orientated copulatory openings, by the presence of a sclerotized arch

in the inner epigynum (Fig. 22B, C) and by the absence of the epigynal copulatory groove. Unlike males, the separation of *N. malabarensis* females from *N. papuana* is not straightforward. They differ from *N. papuana* by the combination of the following: sternum orange (Fig. 25B, D), rarely with a thin dark brown lateral edge, venter with two conspicuous pairs of orange dots (Fig. 25B, D), first femur with sparse prolateral spines of normal length, epigynum with a narrow septum (Fig. 22A, but see variation in *N. papuana*) and both copulatory and fertilization ducts longer than the spermatheca radius (Fig. 22B, C). *N. malabarensis* males differ from those of *N. cruentata* and *N. borbonica* by the long and slender EC (Fig. 23A, B) and by the distal modification of the embolus in the form of a bulge (Fig. 23D). They differ from *N. papuana* by the size (prosoma length 2.5–3.1; total length 5.0–5.9) as well as the embolic conductor shape and sclerotization (Fig. 23A, B): distal EC, viewed from ectal and mesal sides, appears hooked, due to its spiralling, and has a longer tip; proximal embolic conductor is long, straight and sclerotized.

Description. *Female* (ng5/f1 from Kandy, Sri Lanka, Fig. 25A, B): Total length 15.4. *Prosoma* 7.1 long, 4.7

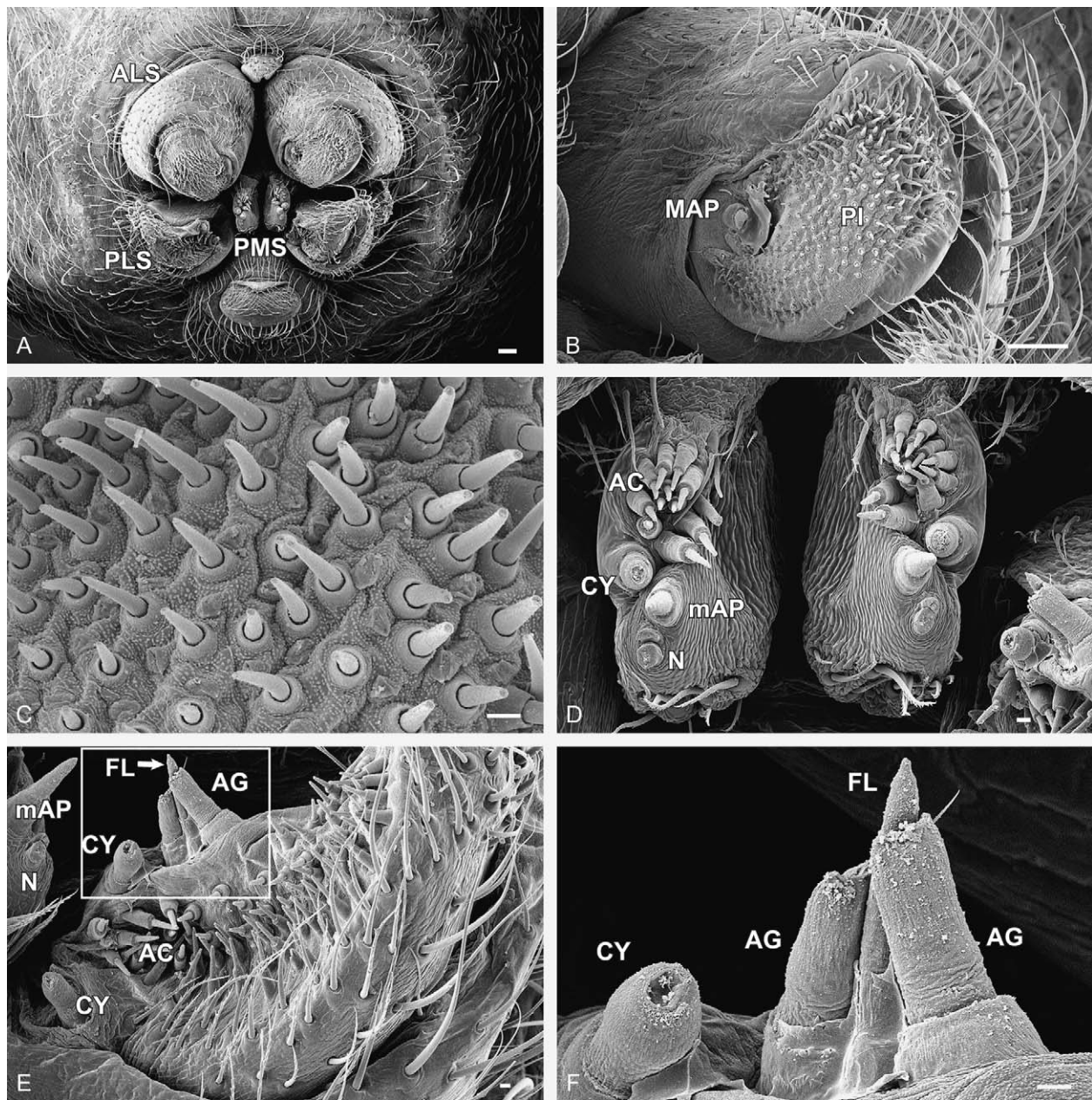


Fig. 30. *Nephilengys papuana*, from Queensland (ng64), female spinneret morphology: A, spinnerets, apical; B, ALS; C, detail of ALS with piriform gland spigots; D, PMS; E, PLS, box delimits area of image F; F, PLS detail with triad (AG, FL) and cylindrical gland spigot. Scale bars: A, B = 100 μ m; C–F = 10 μ m.

wide, 5.0 high at head region; dark red–brown. Chelicerae black. Sternum 3.1 long, 2.6 wide; orange in live animal (white in alcohol) with broad lateral brown bands. Sternal humps I to III present, hump IV absent. Maxillae dark brown, labium laterally brown, medially white. AME diameter 0.35, ALE 0.25, PME 0.28, PLE 0.25. AME separation 0.41, PME separation 0.54, PME–PLE separation 0.74, AME–ALE separation 0.57, AME–PME separation 0.54, ALE–PLE separation 0.44. Clypeus height 0.6. *Appendages.* Legs, palp annulated yellow and black (brown

in alcohol): coxae, trochanters, distal femora, patellae, distal tibiae, metatarsi, tarsi black (dark brown), proximal femora, tibiae yellow. Femur I with strong long spines, notably prolaterally. Leg I length 28.0 (Fe 7.4, Pa 2.5, Ti 6.8, Me 8.7, Ta 2.6). Tibiae I, II, IV distally weakly tufted. *Opisthosoma* 9.9 long, 6.8 wide, 6.7 high. Dorsum white with brown dots. Lateral opisthosoma with dorso-ventral-longitudinal brown bands. Venter brown, with two large irregularly shaped pairs and one small pair of orange patches (live specimen, see Fig. 25B, D; patches white in

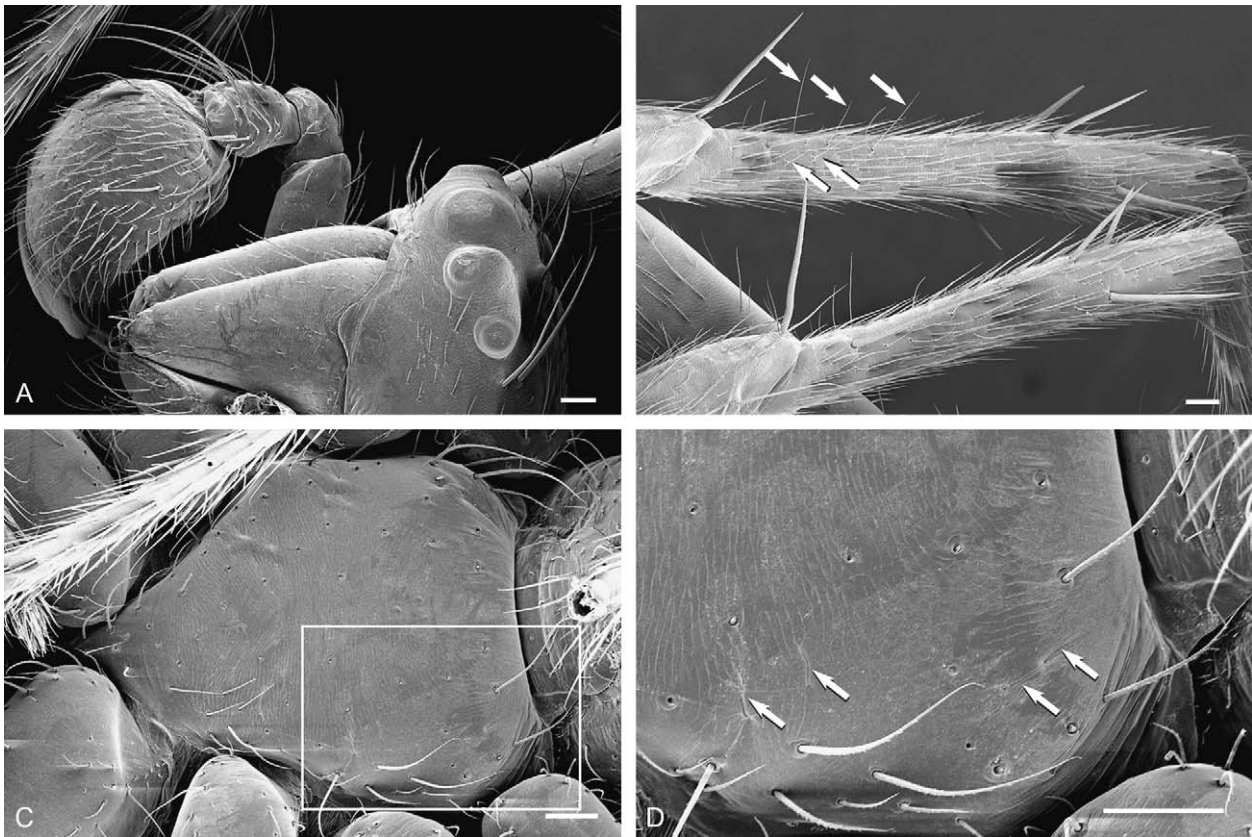


Fig. 31. *Nephilengys papuana*, male prosoma, from Queensland (ng64/m1): A, anterior prosoma, ectal; B, right tibiae I–II, ectal, with setae, macrosetae and trichobothria (arrows); C, sternum, ventral, box delimiting area of image D; D, sternum detail, with slit sensilla (arrows). Scale bars = 100 μ m.

alcohol), first medially continuous. Another pair of small orange dots anteriorly on venter between epigynum and pedicel. Two pairs of white dots posteriorly around spinnerets. *Epigynum* as diagnosed (Fig. 22A, ng4f1 from Sinharaja, Sri Lanka). Septum narrow anteriorly, broad posteriorly. Inner epigynum as in Fig. 22(B) and (C), but round spermathecae juxtaposed medially (see variation). Copulatory ducts round and heavily sclerotized, fertilization ducts long.

Prosoma length ranges from 4.9 to 8.1; total length from 10.4 to 18.6 ($n = 30$). Sternum colour variable, but generally bright orange in live specimens and yellow or white in preserved ones, with dark brown lateral edge of variable width. Abdominal colour varies from white through all shades of grey to black (Fig. 25). Two or three pairs of orange (live specimens) to white patches (preserved material) on venter vary in size, shape and colour intensity, can be medially connected. Somatic coloration variation does not seem to be geographically fixed. Epigynal shape, likewise, varies considerably even within populations (Fig. 22A). General geographical trend seems to be relatively wider septa in eastern populations. Prolateral spines on femur I can be conspicuous, but generally less numerous and longer than in *N. papuana* (see 'Diagnosis').

Male (ng4/m1 from Sinharaja, Sri Lanka, Figs 23; 24; 25D): Total length 4.4. *Prosoma* 2.5 long, 1.8 wide, 1.4 high; orange. Sternum 1.0 long, 0.9 wide; orange, laterally dark grey, medially white. AME diameter 0.19, ALE 0.12, PME 0.16, PLE 0.11. AME separation 0.13, PME separation 0.19, PME–PLE separation 0.22, AME–ALE separation 0.06, AME–PME separation 0.22, ALE–PLE separation 0.13. Clypeus height 0.16. *Appendages*. Legs grey–black, except yellow coxae, trochanters, proximal femora. Leg I length 10.5 (Fe 2.8, Pa 0.9, Ti 2.3, Me 3.1, Ta 1.4). *Opisthosoma* 2.5 long, 1.6 wide, 1.3 high. Scutum orange, medially black in live specimens (grey in alcohol), venter light brown–grey with two pairs of lighter spots, lateral opisthosoma black and grey. *Pedipalp* as diagnosed (Fig. 23).

Prosoma length ranges from 2.5 to 3.1; total length from 5.0 to 5.9 ($n = 10$). Male palpal morphology uniform, with exception of males from China: EC illustrated in Yin *et al.* (1990: figs 8; 9) appears less hooked than material examined.

Distribution (Fig. 35). South, South-East and East Asia: from India and Sri Lanka to the Philippines, north to China (Yunnan: Yin *et al.*, 1990), north-east to Japan (Saga, Kompira: Bösenberg & Strand, 1906: 192), east to Ambon (Thorell, 1878: 123; 1881: 157).

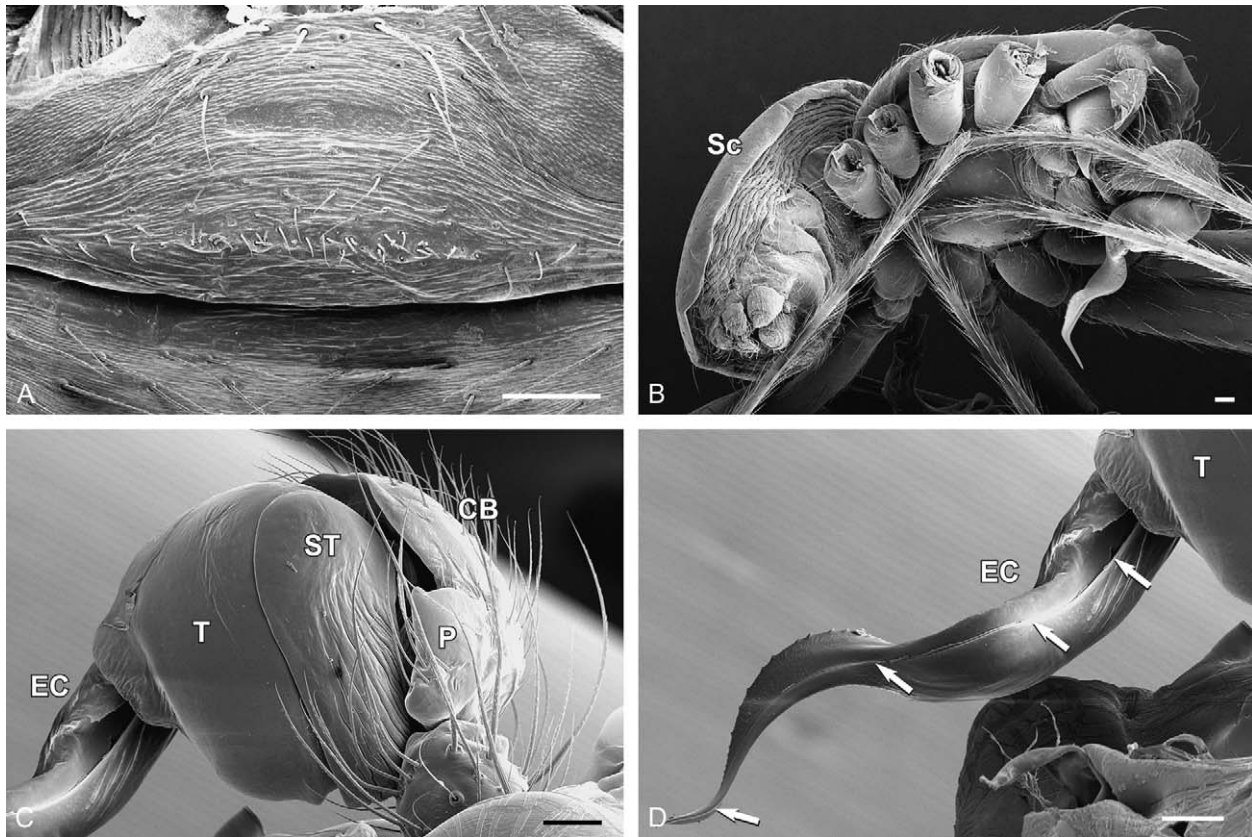


Fig. 32. *Nephilengys papuana*, male morphology, from Queensland (ng64/ml-2): A, epigastric area with epiandrous gland spigots; B, whole body, ventral; C, D, left palp, ecto-ventral; C, bulb detail; D, EC detail, arrows following EC groove. Scale bars = 100 μ m.

Natural history. In South and South-East Asia, the species is common synanthropically (Fig. 25) and less common in rainforest (Murphy & Murphy, 2000). At least the Niah (Borneo) population inhabits cave entrances (Deeleman-Reinhold, 1989).

Taxonomic history. Walckenaer (1842) described *Epeira anama* from Vietnam and *E. malabarensis* from India's Malabar Coast. Dahl (1912: 46) pointed out their synonymy and chose to keep the name *Nephilengys malabarensis*. Walckenaer's type series in MNHN is scattered and partly lost, enabling me to examine the holotype of *E. malabarensis* but not the type(s) of *E. anama*, but the material at hand, coupled with Walckenaer's description, support the synonymy. The first record of *N. malabarensis* in Java was by Doleschall (1857), who, perhaps unintentionally (cf. Dahl, 1912: 46), used the incorrect name *Epeira malabarica* (Walck.). He later described another species from Java, *Epeira rhodosternon* Doleschall, 1859. This was synonymized with *N. malabarensis* by Thorell (1881), and confirmed as such by Dahl (1912), also in this study. In 1871, O. P.-Cambridge described *Nephila rivulata* from Labuan, in the China Sea. Koch (1872: 143) and Dahl (1912: 47) cited the type locality of this species as Ceylon (Sri Lanka). The

exact type locality(ies) of *N. rivulata* remain(s) dubious; see type label data, where Ceylon [Sri Lanka] and Amboina [Ambon] are cited as the type localities. 'Labuan' could be in the Philippines, Malaysia or Indonesia (hence, the broad geographical term China Sea). As O. P.-Cambridge noted (p. 619), his *N. rivulata* is 'nearly allied to *Epeira malabarensis*'. In fact, it is synonymous, as pointed out by Dahl (1912: 47). O. P.-Cambridge's description of both sexes is detailed enough and sufficiently illustrated to confirm that *N. rivulata* is a synonym of *N. malabarensis*. My examination of syntypes supports the synonymy. However, O. P.-Cambridge has to be given credit for recognizing the importance of male genitalic characters in spider taxonomy. His vivid description of the male palpal 'corkscrew-spine' is in fact the first detailed description of the male (embolic) conductor of this species. Koch (1872: 143) described two new species, *Nephilengys schmelzii* L. Koch, 1872 and *Nephilengys hofmanni* L. Koch, 1872, from the Philippines and Borneo, respectively. Dahl (1912) synonymized both with *N. malabarensis* and declared that the epigynum figure of *N. schmelzii* in Koch (1872: pl. 11, f. 7) depicts an immature animal. Koch's illustrations of the epigyna are not detailed enough for a reliable identification, but both do show adult epigyna. My examination of *Nephilengys* material from the Philippines and Borneo and the study of epigynal



Fig. 33. *Nephilengys papuana*, photographs of live spiders, from Queensland: A, B, female taken from web on house in Daintree NP (Cow Bay); A, dorsal (note light grey and brown dorsum and reddish brown prosoma); B, ventral (note white and brown sternum and venter); C, D, female taken from web on tree in Daintree NP (Emmagem); C, dorsal (note almost black coloration); D, ventral (note white and black sternum, orange and black venter).

variation support the synonymy with *N. malabarensis*. Thorell (1878: 123) recorded *N. malabarensis* from Amboina (Ambon, Maluku, Indonesia), possibly the species' easternmost locality. From Sumatra two new names were introduced. van Hasselt, 1882: 28) described a male of *Nephila urna*, and Thorell (1890: 188) described a new subspecies, *N. malabarensis annulipes*. Dahl (1912: 49) synonymized both with *N. malabarensis* and redescribed the species (without illustrations). In 1977, Tikader described the female of a new species, *Metepeira andamanensis*, from Andaman Islands, which he later (Tikader, 1982) correctly synonymized with *Nephila malabarensis* (= *Nephilengys m*). Deeleman-Reinhold (1989: 626) described a new species, *Nephilengys niahensis*, from Borneo. Having examined the holotype and paratype females, as well as additional male and female material from Borneo, including a male from the type

locality, I propose that *N. niahensis* is a junior synonym of *N. malabarensis* (see above).

Most authors (Chrysanthus, 1959, 1971; Davies, 1988) have treated all Australasian *Nephilengys* as *N. malabarensis*. This is incorrect, as the populations from New Guinea and Australia can be diagnosed as a distinct species, *N. papuana*. Hence, I delimit the geographical distribution of *N. malabarensis* to include South and South-East Asia, but not New Guinea and Australia.

***Nephilengys papuana* (Thorell, 1881)**
(Figs 26–34)

Nephilengys malabarensis var. β , *Papuana* Thorell, 1881: 156, description of female (from New Guinea); **stat.n.** (removed from the syn. of *N. malabarensis*). Syntype female

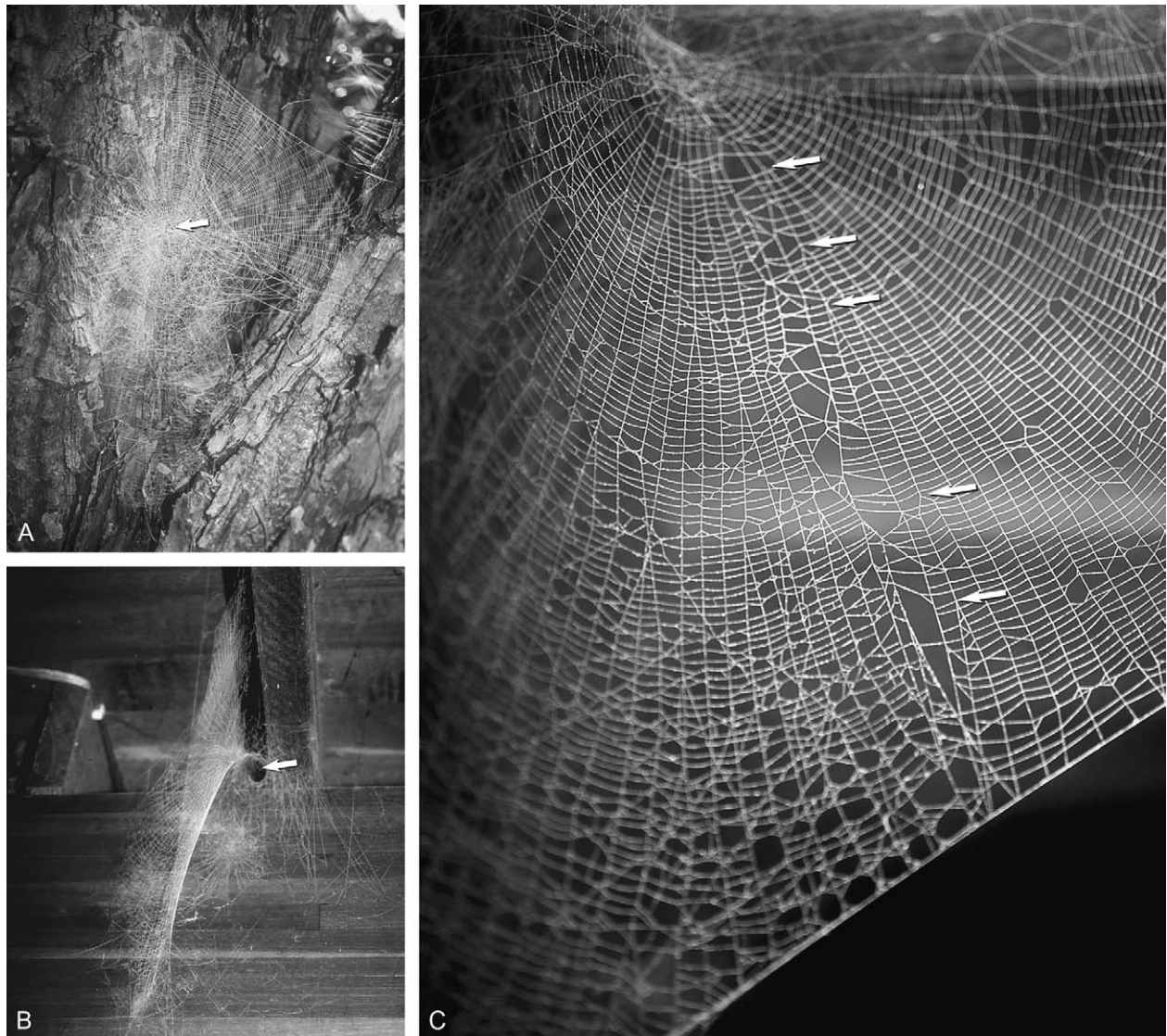


Fig. 34. *Nephilengys papuana*, photographs of female webs, from Queensland: A, web of immature female built against tree trunk in Daintree NP, Emmagem coastal forest (note non-eccentric orb, hub marked with arrow); B, C, female web built against wooden roof at Mission Beach; B, side view (note tubular retreat attached to hub, arrow); C, front view (note hub eccentricity, note left side of orb old, whereas right side recently rebuilt, note late radii split up to five times, arrows follow single radius).

labelled '*Nephilengys Malabarensis* (Walck.) var. *Papuana* Thor., Nova Guinea: Yule (...), Doria ...' and 'Collectio T. Thorell, *Nephila malabarensis* Walck. var. *papuana* Thor., N. Guinea: Yule (Doria ...), No. 730 K.', in SMNH, examined (ng276).

Nephilengys rainbowsi Hogg, 1899: 141, pl. 13, f. 1, description of female (from Queensland); **syn.n.** (removed from the syn. of *N. malabarensis*). Holotype female in BMNH, labelled '1924.III.I.260 DIIA, *Nephilengys rainbowsi* Hogg Type, Upper Endeavour River, Queensland, Hogg. Coll.', examined (ng270).

Nephilengys malabarensis: Roewer, 1942: 933; Davies, 1988: 296, f. 20; Platnick, 2005.

Nephila malabarensis papuana: Bonnet, 1958: 3080.

Nephila malabarensis: Chrysanthus, 1959: 199, f. 4, 8, 28; Chrysanthus, 1971: 42, f. 92–93; misidentification.

Comments on types. In addition to the examined *Nephilengys malabarensis papuana* type (above), another syntype from Fly River, New Guinea and possibly another from Cape York may exist (Thorell, 1881: 157), possibly in MCSNG.

Etymology. *Papuana* (Latin) = of Papua.

Note on nomenclature. Thorell's (1881) original name *Nephilengys malabarensis* var. β , *Papuana* is subspecific in

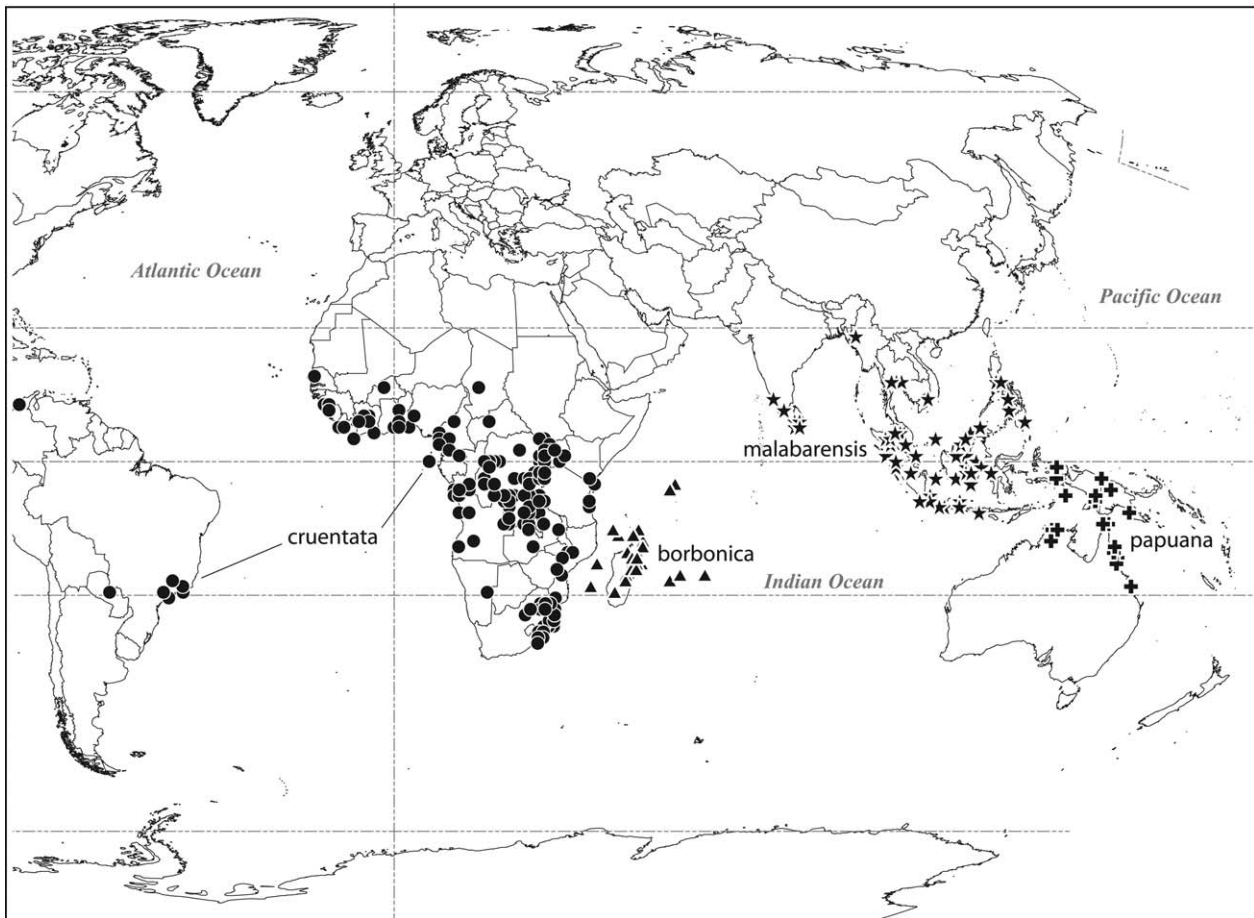


Fig. 35. *Nephilengys* species distributions appear globally allopatric. Omitted is questionable record of *N. cruentata* from Comoros (see text).

rank and is available as a species-group name (International Commission on Zoological Nomenclature, 1999: Article 45.6.4).

Note on diagnosis. Thorell (1881) based his subspecies description on female sternum and venter coloration. Dahl (1912: 48) pointed out that the sternum in many populations of *N. malabarensis* can be partly dark, and synonymized *Nephilengys malabarensis papuana* Thorell with *N. malabarensis*. Although the sternum coloration in both *N. malabarensis* and *N. papuana* indeed varies, *N. papuana* can be diagnosed by other characters, notably the male palp.

Diagnosis. *Nephilengys papuana* females differ from those of *N. cruentata* and *N. borbonica* by the presence of a well-defined anterior rim and the epigynal septum (Fig. 29A–C), which separates two chambers with medially orientated copulatory openings, by the presence of a sclerotized arch in the inner epigynum (Fig. 26D, E) and by the absence of the epigynal copulatory groove. They differ from *N. malabarensis* females by the combination of the following: sternum (Fig. 33B, D) black with two medial

white patches (sometimes fused to form a continuous white median area), venter with two pairs of poorly defined white or orange patches (Australia, Fig. 33B, D) or completely white/orange (New Guinea), first femur with short spines (Fig. 28B; not conspicuous in New Guinea material), the epigynum with a broad septum (Figs 26A; 29A, B; but see variation, Fig. 26B) and both copulatory and fertilization ducts shorter than the spermatheca radius (Fig. 26D, E). *N. papuana* males differ from those of *N. cruentata* and *N. borbonica* by the long and slender embolic conductor (Figs 27; 32D) and by the distal modification of the embolus in the form of a bulge (Fig. 27C). They differ from *N. malabarensis* males by the size (prosoma length 1.9–2.4; total length 3.5–4.7) and embolic conductor shape and sclerotizations (Fig. 27A, B); distal EC, viewed from ectal and mesal sides, is rounded (vs. hooked), dorso-ventrally flattened and more or less two-dimensional (vs. spiralling), and has a shorter tip; proximal embolic conductor is short, undulating and membranous.

Description. *Female* (ng64 from Mission Beach, Queensland; Figs 26; 28–30; 33): Total length 17.4. *Prosoma* 7.8 long, 5.6 wide, 4.4 high at head region; dark red–brown.

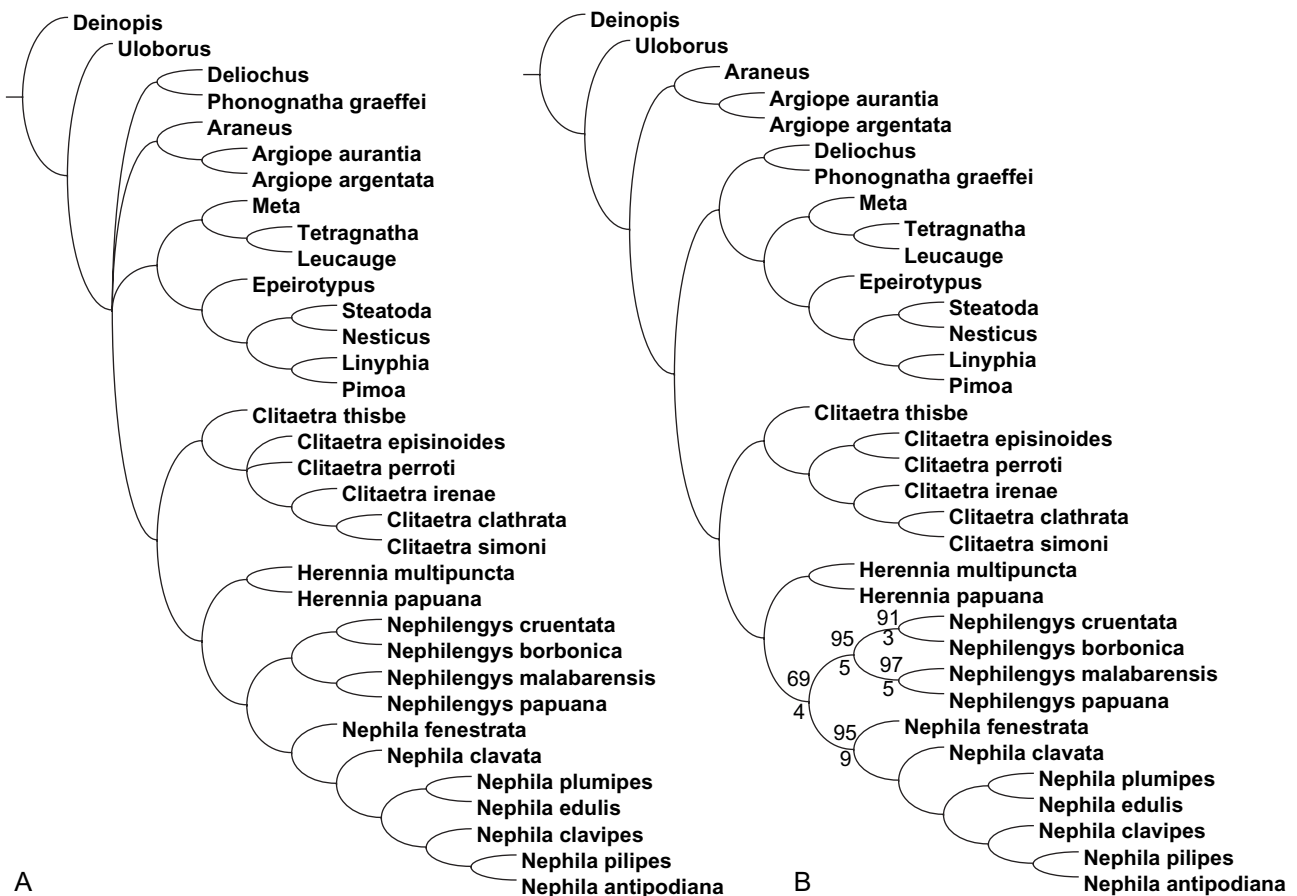


Fig. 36. Phylogenetic results: A, strict consensus of eight shortest cladograms ($L = 536$, $CI = 42$, $RI = 85$) collapsing three nodes; B, successively weighted tree identical to one of fundamental cladograms. Clade support given for *Nephilengys* part of tree (bootstrap above, Bremer below).

Chelicerae black. Sternum 3.4 long, 2.9 wide; brown, with anterior T-shaped and posterior I-shaped white patch. Sternal humps I to III present, but weak, hump IV absent. Labium, maxillae dark brown, with distal white edge. Eyes, clypeus as in *N. malabarensis*. *Appendages*. Legs, palp annulated (Fig. 33): coxae, trochanters, distal femora, patellae, distal tibiae, metatarsi, tarsi dark brown, proximal femora, tibiae yellow. Femur I with strong semishort spines, especially prolaterally. Leg I length 30.3 (Fe 8.5, Pa 2.8, Ti 7.3, Me 9.1, Ta 2.6). *Opisthosoma* 12.4 long, 7.3 wide, 6.9 high. Dorsum (Fig. 33A, C) brown, darker along middle and sides. Venter (Fig. 33B, D) brown, with two irregularly shaped pairs of white patches. *Epigynum* as in Figs 26(A) and 29(A)–(C), with broad septum anteriorly, inner epigynum as in Fig. 26(D) and (E).

Prosoma length ranges from 5.9 to 7.8; total length from 13.3 to 17.4 ($n = 10$). Sternum coloration varies (Fig. 33B, D), but is always medially white. Venter coloration varies (Fig. 33B, D), with a continuous median white area in New Guinea females.

Male (ng64 from Mission Beach, Queensland; Figs 27; 31, 32): Total length 4.7. *Prosoma* 2.4 long, 1.8 wide, 1.5 high; orange. Sternum 1.0 long, 0.78 wide; orange. Eyes, clypeus

as in *N. malabarensis*. *Appendages*. Legs grey–black, except yellow coxae, trochanters. Leg I length 10.5 (Fe 2.9, Pa 0.85, Ti 2.4, Me 3.1, Ta 1.2). *Opisthosoma* 2.7 long, 1.9 wide, 1.9 high. Scutum orange, medially grey, venter light brown–grey, lateral opisthosoma yellow, grey. *Pedipalp*: Figs 27 and 32(C), (D).

Prosoma length ranges from 1.9 to 2.4; total length from 3.5 to 4.7 ($n = 4$). Opisthosoma shape from round (as described) to dorso-ventrally flattened. EC shape varies between New Guinea and Australian populations and has to be viewed for diagnostic features in the exact same angle as illustrated (Fig. 27A, B).

Distribution (Fig. 35). New Guinea, tropical Australia (Queensland).

Taxonomic history. Thorell (1881) described *Nephilengys malabarensis* var. *papuana* from females from New Guinea. Thorell diagnosed the species by its sternum and venter coloration which, in his words, departed from the typical form from Siam (Thailand) and Ambon. Dahl (1912: 48, 49) synonymized Thorell's subspecies with *N. malabarensis* by noting that the sternum coloration exhibits all possible

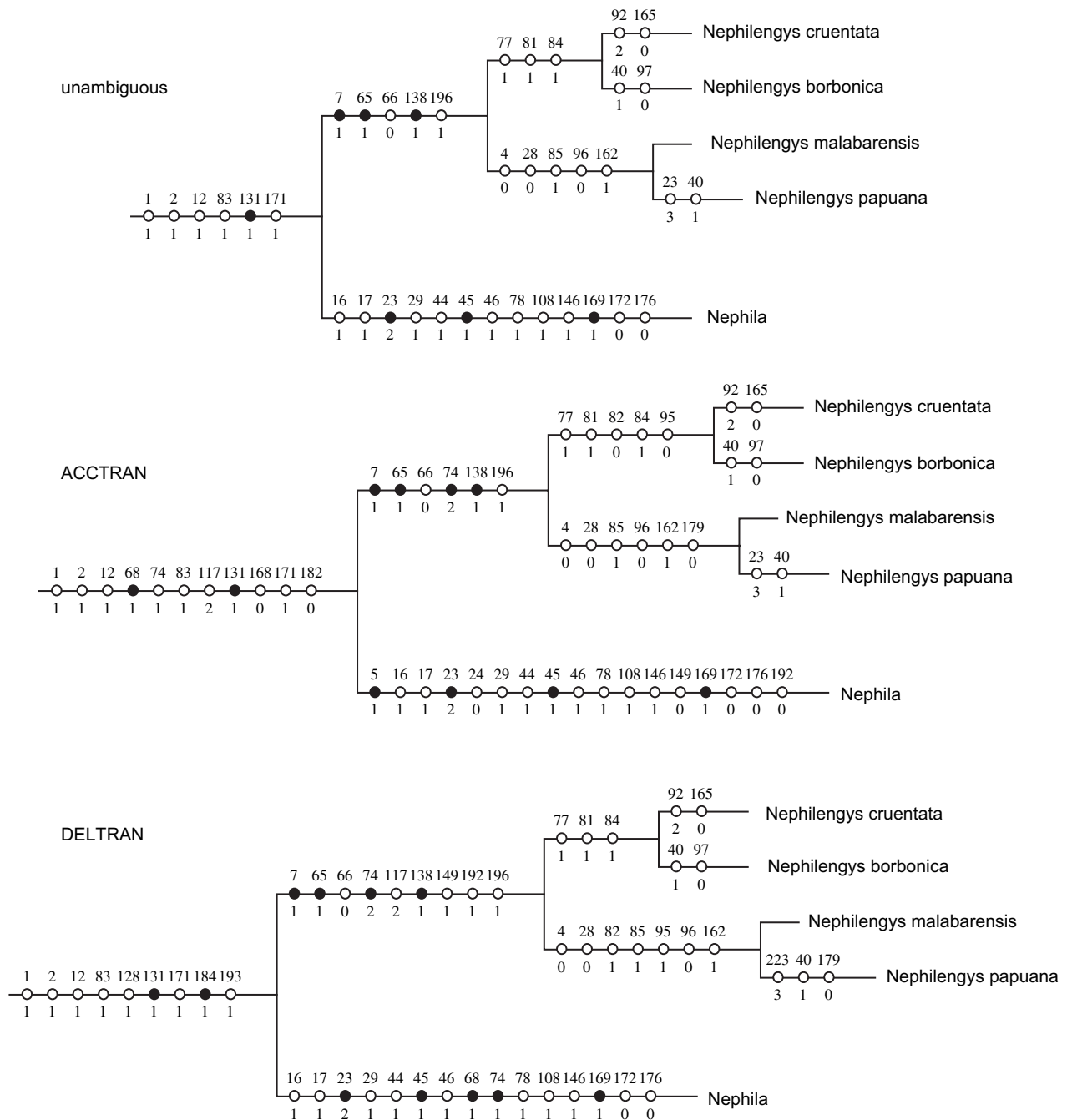


Fig. 37. *Nephilengys* character support on preferred tree, alternative optimizations. Character numbers (from Kuntner, 2006) above, character state numbers below; filled circles mark non-homoplasious character state changes, open circles mark homoplasious character state changes.

transitions between the form described in *N. malabarensis papuana* and the typical subspecies. Dahl concluded with a somewhat sarcastic remark that, if Thorell's practice is to be adopted, every single specimen should be called by a different name. As hypothesized here, the New Guinea *Nephilengys* populations actually do belong to a species occurring in Australia and New Guinea, distinct from *N. malabarensis*. It can be diagnosed most easily by the male

genital characters, and less by the female epigynum, sternum and venter colour. The oldest available species-level name for this species is Thorell's subspecies *N. m. papuana*. Hogg (1899: 141) described a female of a new species, *Nephilengys rainbowi*, from Queensland. He correctly recognized it as being distinct from *N. schmeltzii* and *N. hofmanni* (both synonyms of the Asian *N. malabarensis*), but was evidently not aware of the older name. Chrysanthus

(1959) recorded and illustrated a female of *Nephila* (*Nephilengys*) *malabarensis* from New Guinea and noted that it corresponded to Thorell's variety *papuana*. Later, Chrysanthus (1971) illustrated a male palp of *Nephila* (*Nephilengys*) *malabarensis* from west New Guinea, which is the first treatment of *N. papuana* male. The only recent illustration from Australia is that of Davies (1988: as *N. malabarensis*).

Kulczyn'ski (1911) hypothesized the tetragnathid *Metimorpha tullia* Bösenberg & Strand, 1906 as a likely synonym of *Nephilengys malabarensis papuana*. However, Kuntner (2005b) transfers *Metimorpha* Strand, 1906 to Araneidae and proposes it as a *nomen dubium*, as the genus diagnosis was based on juvenile features.

Misplaced species

Eustala fuscovittata (Keyserling, 1864) belongs to Araneidae Simon, 1895

Epeira fusco-vittata Keyserling, 1864: 129, pl. 6, figs 7–8.

Nephila? hirta Taczanowski, 1873: 149 (description of male and female from French Guiana). Synonymy by Kuntner & Levi, 2006).

Nephilengys hirta: Roewer, 1942: 934; Platnick, 2005.

Eustala fuscovittata: Kuntner & Levi (2006) [for transfer and justification of synonymy].

Nephilengys kenmorei Barrion & Litsinger, 1995, *nomen dubium*

Nephilengys kenmorei Barrion & Litsinger, 1995: 565, f. 349a–j, description of female (from Philippines).

Nephilengys kenmorei: Platnick, 2005.

Types. Female holotype, deposited at International Rice Research Institute in Manila, is presumed lost (T. Wai, pers. comm., International Rice Research Institute, Los Banos, Laguna, Philippines). No other specimens of this species are known.

Comments and justification. The species description of Barrion & Litsinger (1995) is sufficient to establish that *N. kenmorei* does not belong in *Nephilengys*. In fact, the species lacks any nephilid features, and should be transferred to Araneidae. However, such transfer seems unreliable before the male becomes known. No generic match could be made based on the description of the single female. Characters contesting the *Nephilengys* placement (contrasted with *Nephilengys* states) include:

- 1 small size (6.88 mm)/at least 10 mm in *Nephilengys*;
- 2 LE touching/apart in *Nephilengys*;
- 3 clypeus height equals one-quarter AME diameter/more than one AME diameter in *Nephilengys*;
- 4 apparent lack of carapace spines/present in *Nephilengys*;
- 5 four promarginal and three retromarginal cheliceral teeth/vice versa in *Nephilengys*;

- 6 lack of cheliceral denticles (Barrion & Litsinger 1995: fig. 349f)/present in *Nephilengys*;
- 7 epigynum without a septum and chambers/both present in *Nephilengys*;
- 8 habitat (specimen collected in pitfall trap).

Supplementary material

Specimen examined lists and the phylogenetic matrix are available online at www.blackwell-synergy.com under DOI reference doi: 10.1111/j.1365-3113.2006.00348.x and at the author's website (www.nephilidae.com).

Acknowledgements

The views, opinions, interpretations and potential errors in this paper are my own. I thank Jonathan Coddington and Gustavo Hormiga for advice, Ingi Agnarsson and Jeremy Miller for their help and comments, and Marc Allard, Jim Clark, Diana Lipscomb and Chris Thompson for their comments on an early draft. Helpful comments by Frank Krell, Hilton Japyassú and two anonymous reviewers further improved the paper. Fernando Alvarez-Padilla, Lara Lopardo, Dana deRoche and Scott Larcher offered assistance and help, Scott Whittaker and Patrick Herendeen provided SEM help, and Karie Darrow kindly helped with digital image manipulation. Numerous curators, collection managers and other biologists have assisted with loans (see 'Materials and methods') and with collecting the specimens. I especially thank those enabling my visits to collections: Janet Beccaloni, Margie Cochrane, Tanza Crouch, Hieronymus Dastych, Christa Deeleman-Reinhold, Jason Dunlop, Mike Gray, Juergen Gruber, James E. Hogan, Rudy Jocqué, Jean-Pierre Michiels, Erik van Nieukerken, Norman Platnick, Robert Raven, Guy Redman, Christine Rollard and Lou Sorkin. Rudy Jocqué, Heine C. Kiesbüy and Dennis Hansen kindly provided their unpublished photographs together with relevant natural history. I thank Jonathan Coddington and Ingi Agnarsson for their help in live spider manipulation and web building observation in the field. The fieldwork in South Africa, with I. Agnarsson, M. Arnedo, J. Coddington, G. Hormiga and M. Ramirez, was made possible by the help of Michelle Hamer, Tanza Crouch, Cheryl Whitmore, Lorenzo Prendini, Ansie Dippenaar-Schoeman, Norman Larsen, Astri and John Leroy, and Alastair Kilpin. Phinda Resource Reserve is kindly acknowledged for their hospitality. The fieldwork in Madagascar, with I. Agnarsson, was made possible by the help of Forbes Maner, James Clark, Leonard Hirsch, Patricia Wright, Fredrica van Berkum, Charles Griswold, Benjamin Andriamihaja and the ANGAP/MICET crew. The fieldwork in Australia, with F. Alvarez-Padilla, G. Hormiga, S. Larsen and N. Scharff, was made possible by the help of Robert Raven and Tracey Churchill. I especially thank Michael Rix for his valuable help in the field. The fieldwork in tropical Asia was performed jointly with Irena Kuntner, Matjaž Bedjanič and Gregor Antauer. This project was

supported by the U.S. National Science Foundation (PEET grant DEB-9712353 to Hormiga and Coddington), by the Sallee Charitable Trust (grant to Agnarsson and Kuntner) and by the OTS-STRI-Mellon Research Exploration Award (to Kuntner and Šereg). I further acknowledge material and financial support from the George Washington University, Smithsonian Institution, the Ministry of Science of the Republic of Slovenia and the Biological Institute of the Slovenian Academy of Sciences and Arts. At the latter institution, the support (1999–2001) was coordinated by Rajko Slapnik, and the final stages were kindly endorsed by Branko Vreš and Oto Luthar. I dedicate this work to my wife Irena and my parents Sonja and Tone.

References

- Agnarsson, I. (2003) The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae), a new species from Guyana, and notes on theridioid phylogeny. *Invertebrate Systematics*, **17**, 719–734.
- Agnarsson, I. (2004) Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society*, **141**, 447–626.
- Agnarsson, I. (2005) A revision and phylogenetic analysis of the American *ethicus* and *rupununi* groups of *Anelosimus* (Araneae, Theridiidae). *Zoologica Scripta*, **34**, 389–413.
- Agnarsson, I. & Kuntner, M. (2005) Madagascar: An unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae). *Systematic Entomology*, **30**, 575–592.
- Barrion, A.T. & Litsinger, J.A. (1995) *Riceland Spiders of South and Southeast Asia*. CAB, Wallingford, Oxfordshire.
- Benoit, P.L.G. (1963) Araneidae-Nephilinae africains du Zoologisches Staatsinstitut und Zoologisches Museum Hamburg (Araneae). *Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum Hamburg*, **2**, 367–372.
- Benoit, P.L.G. (1964) La distribution géographique des Araneidae-Nephilinae africaino-malgaches des genres *Nephila* et *Nephilengys*. *Revue de Zoologie et de Botanique Africaines*, **69**, 311–326.
- Bertkau, P. (1880) Verzeichnis der von Beneden in Brasilien gesammelten Arachniden. *Mémoires Couronnés et Mémoires des Savants Étrangers (Bruxelles)*, **43**, 1–120.
- Bonnet, P. (1958) *Bibliographia Araneorum*, 2. Part 4, (N-S). Les Frères Douladoure, Toulouse.
- Bösenberg, W. & Strand, E. (1906) Japanische Spinnen. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **30**, 93–422.
- Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795–803.
- Bremer, K. (1994) Branch support and tree stability. *Cladistics*, **10**, 295–304.
- Brignoli, P.M. (1983) *A Catalogue of the Araneae Described Between 1940 and 1981*. Manchester University Press, Manchester.
- Brown, R.W. (1956) *Composition of Scientific Words*. Smithsonian Institution Press, Washington.
- Butler, A.G. (1876) Preliminary notice of new species of Arachnida and Myriopoda from Rodriguez, collected by Messrs George Gulliver and H.H. Slater. *Annals and Magazine of Natural History*, **17**, 439–446.
- Butler, A.G. (1878) Myriapoda and Arachnida in Zoology of Rodriguez. *Philosophical Transactions of the Royal Society of London*, **168**, 497–509.
- Cambridge, O.P. (1871) Notes on some Arachnida collected by Cuthbert Collingwood, Esq., M.D., during rambles in the China Sea. *Proceedings of the Zoological Society of London*, **1871**, 617–622.
- Cantino, P.D. & de Queiroz, K. (2004) Phylocode: a Phylogenetic Code of Biology Nomenclature, Version 2b. URL <http://www.ohiou.edu/phylocode> [accessed 23 January 2005].
- Carico, J.E. (1977) A simple dusting device for coating orb webs for field photography. *Bulletin of the British Arachnological Society*, **4**, 100.
- Chrysanthus, F. (1959) Spiders from South New Guinea II. *Nova Guinea*, **10**, 197–206.
- Chrysanthus, F. (1971) Further notes on the spiders of New Guinea I (Argyropidae). *Zoologische Verhandlungen*, **113**, 1–52.
- Coddington, J.A. (1983) A temporary slide-mount allowing precise manipulation of small structures. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, New Series*, **26**, 291–292.
- Coddington, J.A. (1986a) The monophyletic origin of the orb web. *Spiders. Webs, Behavior, and Evolution* (ed. by W.A. Shear), pp. 319–363. Stanford University Press, Stanford.
- Coddington, J.A. (1986b) The genera of the spider family Theridiommatidae. *Smithsonian Contributions to Zoology*, **422**, 1–96.
- Coddington, J.A. (1986c) Orb webs in non-orb-weaving ocre-faced spiders (Araneae: Dinopidae): a question of genealogy. *Cladistics*, **2**, 53–67.
- Coddington, J.A. (1990) Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneocladia: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology*, **496**, 1–52.
- Coddington, J.A., Hormiga, G. & Scharff, N. (1997) Giant female or dwarf male spiders? *Nature*, **385**, 687–688.
- Colwell, R.K. (1999) *BIOTA: the Biodiversity Database Manager*, Version 1.6.0. Sinauer Associates, Sunderland, Massachusetts.
- Dahl, F. (1912) Seidenspinne und Spinnenseide. *Mitteilungen aus dem Zoologischen Museum in Berlin*, **6**, 1–90.
- Davies, V.T. (1988) An illustrated guide to the genera of orb-weaving spiders in Australia. *Memoirs of the Queensland Museum*, **25**, 273–332.
- Deeleman-Reinhold, C.L. (1989) Spiders from Niah Cave, Sarawak, East Malaysia, collected by P. Strinati. *Revue Suisse de Zoologie*, **96**, 619–627.
- Dippenaar-Schoeman, A.S. & Jocqué, R. (1997) *African Spiders – an Identification Manual*. ARC – Plant Protection Research Institute, Pretoria.
- Doleschall, C.L. (1857) Bijdrage tot de Kennis der Arachniden van den Indischen Archipel. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **13**, 399–434.
- Doleschall, C.L. (1859) Tweede Bijdrage tot de Kennis der Arachniden van den Indischen Archipel. *Verhandelingen der Natuurkundige Vereeniging in Nederlandsch Indië*, **5**, 1–60.
- Eberhard, W.G. (1976) Photography of orb webs in the field. *Bulletin of the British Arachnological Society*, **3**, 200–204.
- Eberhard, W.G. (1982) Behavioral characters for the higher classification of orb-weaving spiders. *Evolution*, **36**, 1067–1095.
- Edmunds, J. (1993) The development of the asymmetrical web of *Nephilengys cruentata* (Fabricius). *Memoirs of the Queensland Museum*, **33**, 503–506.
- Edmunds, J. & Edmunds, M. (1986) The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa. *Proceedings of the Ninth International Congress of Arachnology, Panama, 1983* (ed. by W.G. Eberhard, Y.D. Lubin and B.C. Robinson), pp. 73–89. Smithsonian Institution Press, Balboa, Panama.
- Fabricius, J.C. (1775) *Systema Entomologiae, Sistens Insectorum Classes, Ordines, Genera, Species, Adiectis, Synonymis, Locis Descriptionibus Observationibus*. Kortii, Flensburgi et Lipsiae.

- Farris, J.S. (1969) A successive approximations approach to character weighting. *Systematic Zoology*, **18**, 374–385.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.
- Filmer, M. (1991) *Southern African Spiders. An Identification Guide*. Struik, Cape Town.
- Fitch, W.M. (1971) Towards defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology*, **20**, 406–416.
- Gerstäcker, A. (1873) Arachnoidea. *Reisen in Ostafrika* (ed. by C. von der Decken), pp. 463–503. Leipzig.
- Goloboff, P.A. (1993) *NONA*, Version 2.0. URL <http://www.cladistics.com> [accessed 18 September 2001].
- Griswold, C.E., Coddington, J.A., Hormiga, G. & Scharff, N. (1998) Phylogeny of the orb-weaving spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society*, **123**, 1–99.
- van Hasselt, A.W.M., (1882) Araneae. *Midden Sumatra* (ed. by P.J. Veth), pp. 1–56. Leiden.
- Hogg, H.R. (1899) Notes on some spiders from the Upper Endeavour River, Queensland, with description of two new species. *Proceedings of the Royal Society of Victoria*, **11**, 137–147.
- Holm, Å. (1979) A taxonomic study of European and East African species of the genera *Pelecopsis* and *Trichopterna* (Araneae, Linyphiidae) with descriptions of a new genus and two new species of *Pelecopsis* from Kenya. *Zoologica Scripta*, **8**, 255–278.
- Hormiga, G., Eberhard, W.G. & Coddington, J.A. (1995) Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). *Australian Journal of Zoology*, **43**, 313–364.
- Hormiga, G., Scharff, N. & Coddington, J.A. (2000) The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology*, **49**, 435–462.
- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*, 4th edn. International Trust for Zoological Nomenclature, London.
- Itagaki, Y., Naoki, H., Fujita, T., Hisada, M. & Nakajima, T. (1997a) Characterization of spider venom by mass spectrometry, construction of analytical system. *Yakugaku Zasshi*, **117**, 715–728.
- Itagaki, Y., Fujita, T., Naoki, H., Yasuhara, T., Andriantsiferana, M. & Nakajima, T. (1997b) Detection of new spider toxins from a *Nephilengys borbonica* venom gland using on-line [mu]-column HPLC continuous flow (FRIT) FAB LC/MS and MS/MS. *Natural Toxins*, **5**, 1–13.
- Jackson, R.R. (1986) Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. *Journal of Natural History*, **20**, 1193–1210.
- Japyassu, H.F. & Ades, C. (1998) From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour*, **135**, 931–956.
- Japyassu, H.F. & Viera, C. (2002) Predatory plasticity in *Nephilengys cruentata* (Araneae: Tetragnathidae): relevance for phylogeny reconstruction. *Behaviour*, **139**, 529–544.
- Karsch, F. (1878) Übersicht der von ihm in Mossambique gesammelten Arachniden. *Monatsberichte der Königlich Preussischen Akademie des Wissenschaften zu Berlin*, **1878**, 314–338.
- Keyserling, E. (1864) Beschreibungen neuer und wenig bekannter Arten aus der Familie Orbitelae Latr. oder Epeiridae Sund. *Sitzungsberichte der Isis zu Dresden*, **1863**, 63–98, 119–154.
- Koch, L. (1872) *Die Arachniden Australiens*. Nürnberg.
- Koh, J.K.H. (1989) *A Guide to Common Singapore Spiders*. Singapore Science Centre, Singapore.
- Kulczynski, W. (1911) *Spinnen aus Nord-Neu-Guinea. Résultats de l'Expedition Scientifique Néerlandaise a la Nouvelle Guinée en 1903 sous les Auspices d'Arthur Wichmann*, pp. 423–518. Leiden.
- Kuntner, M. (2002) The placement of *Perilla* (Araneae, Araneidae) with comments on araneid phylogeny. *Journal of Arachnology*, **30**, 281–287.
- Kuntner, M. (2003) The systematics of nephiline spiders (Araneae, Tetragnathidae). *American Arachnology*, **66**, 9.
- Kuntner, M. (2005a) A revision of *Heremnia* (Araneae, Nephilidae, Nephilinae), the Australasian 'coin spiders'. *Invertebrate Systematics*, **19**, 391–436.
- Kuntner, M. (2005b) On the validity of the Japanese spider genus *Metimorpha* (Araneae, Araneidae). *Zoological Science*, **22**, 1277–1278.
- Kuntner, M. (2006) Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). *Zoologica Scripta*, **35**, 19–62.
- Kuntner, M. & Hormiga, G. (2002) The African spider genus *Singafrotypa* (Araneae, Araneidae). *Journal of Arachnology*, **30**, 129–139.
- Kuntner, M. & Levi, H.W. (2006) *Nephila hirta*, a new synonym of *Eustala fuscovittata* (Araneae, Araneidae). *Journal of Arachnology*, in press.
- Lenz, H. (1891) Spinnen von Madagascar und Nossi-Bé. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten*, **9**, 153–181.
- Leroy, A. & Leroy, J. (2000) *Spiderwatch in Southern Africa*. Struik, Cape Town.
- de Lessert, R. (1936) Araignées de l'Afrique orientale portugaise, recueillies par MM.P. Lesne et B.-B. Cott. *Revue Suisse de Zoologie*, **43**, 207–306.
- Levi, H.W. & von Eickstedt, V.R.D. (1989) The Nephilinae spiders of the Neotropics (Araneae: Tetragnathidae). *Memorias do Instituto Butantan*, **51**, 43–56.
- Millidge, A.F. (1988) The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). *Bulletin of the British Arachnological Society*, **7**, 253–268.
- Murphy, F. & Murphy, J. (2000) *An Introduction to the Spiders of South East Asia*. Malaysian Nature Society, Kuala Lumpur.
- Nixon, K. (2002) *Winclada*, Version 1.00.08. URL <http://www.cladistics.com> [accessed 27 May 2002].
- Palma, M.S., Itagaki, Y., Fujita, T., Hisada, M., Naoki, H. & Nakajima, T. (1997) Mass spectrometric structure determination of spider toxins: Arginine-containing acylpolyamines from venoms of Brazilian garden spider *Nephilengys cruentata*. *Natural Toxins*, **5**, 47–57.
- Palma, M.S., Itagaki, Y., Fujita, T., Naoki, H. & Nakajima, T. (1998) Structural characterization of a new acylpolyaminotoxin from the venom of Brazilian garden spider *Nephilengys cruentata*. *Toxicon*, **36**, 485–493.
- Pan, H.C., Zhou, K.Y., Song, D.X. & Qiu, Y. (2004) Phylogenetic placement of the spider genus *Nephila* (Araneae: Araneoidea) inferred from rRNA and MaSp1 gene sequences. *Zoological Science*, **21**, 343–351.
- Petrunkovitch, A. (1911) A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Tierra del Fuego, Galapagos, etc. *Bulletin of the American Museum of Natural History*, **29**, 1–791.
- Platnick, N.I. (2005) *The World Spider Catalog*, Version 6.0. URL <http://research.amnh.org/entomology/spiders/catalog/> [accessed 17 May 2005].

- Pocock, R.I. (1900) Arachnida. *The Fauna of British India, Including Ceylon and Burma*. Taylor & Francis, London.
- Roberts, M.J. (1983) Spiders of the families Theridiidae, Tetragnathidae and Araneidae (Arachnida: Araneae) from Aldabra Atoll. *Zoological Journal of the Linnean Society*, **77**, 217–291.
- Robinson, M.H. (1975) The evolution of predatory behaviour in araneid spiders. *Function and Evolution in Behavior* (ed. by G. Baerends, C. Beer & A. Manning), pp. 292–312. Clarendon Press, Oxford.
- Robinson, M.H. & Lubin, Y.D. (1979) Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea, 1. *Herennia ornata*, *Argiope ocyaloides* and *Arachnura melanura* (Araneae: Araneidae). *Pacific Insects*, **21**, 97–132.
- Robinson, M.H. & Robinson, B. (1978) The evolution of courtship systems in tropical araneid spiders. *Symposia of the Zoological Society of London*, **42**, 17–29.
- Robinson, M.H. & Robinson, B. (1980) Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects Monograph*, **36**, 35–218.
- Roewer, C.F. (1942) *Katalog der Araneae von 1758 bis 1940, bzw 1954*, Vol. 1. P. Budy, Bremen.
- Roth, V.D. & Roth, B.M. (1984) A review of appendotomy in spiders and other arachnids. *Bulletin of the British Arachnological Society*, **6**, 137–146.
- Saaristo, M.I. (1978) Spiders (Arachnida, Araneae) from Seychelles Islands, with notes on taxonomy. *Annales Zoologici Fennici*, **15**, 99–126.
- Santos Filho, P. (1998) Development and survivorship of male *Nephilengys cruentata* (Araneae: Tetragnathidae) in the laboratory. *Bulletin of the British Arachnological Society*, **11**, 62–66.
- Scharff, N. & Coddington, J.A. (1997) A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society*, **120**, 355–434.
- Schmidt, G.E.W. & Jocqué, R. (1986) Die Nephilinae der Comoren (Araneae, Araneidae). *Revue de Zoologie Africaine*, **100**, 205–212.
- Schuck-Paim, C. (2000) Orb-webs as extended-phenotypes: web design and size assessment in contests between *Nephilengys cruentata* females (Araneae, Tetragnathidae). *Behaviour*, **137**, 1331–1347.
- Schuck-Paim, C. & Alonso, W.J. (2001) Deciding where to settle: conspecific attraction and web site selection in the orb-web spider *Nephilengys cruentata*. *Animal Behaviour*, **62**, 1007–1012.
- Simon, E. (1887) Etudes arachnologiques. 19e Mémoire, XXVII. Arachnides recueillis à Assinie (Afrique occidentale) par MM. Chaper et Alluaud. *Annales de la Société Entomologique de France*, **7**, 261–276.
- Simon, E. (1894) *Histoire Naturelle des Araignées*, **1**, pp. 489–760. Paris.
- Song, D., Zhu, M. & Chen, J. (1999) *The Spiders of China*. Hebei Science and Technology Publishing House, Shijiazhuang.
- Strand, E. (1920) Arachniden aus Belgisch Kongo. I. *Archiv für Naturgeschichte*, **85**(A12), 98–113.
- Taczanowski, L. (1873) Les Aranéides de la Guyane française. *Horae Societatis Entomologicae Rossicae*, **9**, 113–150, 261–286.
- Thorell, T. (1878) Studi sui ragni Malesi e Papuani. II. Ragni di Amboina raccolti Prof. O. Beccari. *Annali del Museo Civico di Storia Naturale di Genova*, **13**, 1–317.
- Thorell, T. (1881) Studi sui ragni Malesi e Papuani. III. Ragni dell'Austro Malesia e del Capo York, conservati nel Museo civico di storia naturale di Genova. *Annali del Museo Civico di Storia Naturale di Genova*, **17**, 7–27.
- Thorell, T. (1890) Studi sui ragni Malesi e Papuani. IV, 1. *Annali del Museo Civico di Storia Naturale di Genova*, **28**, 1–419.
- Tikader, B.K. (1977) Studies on spider fauna of Andaman and Nicobar islands, Indian Ocean. *Records of the Zoological Survey of India*, **72**, 153–212.
- Tikader, B.K. (1982) Spiders: Araneae, Vol. II. Part 1: Family Araneidae (= Argiopidae), typical orbweavers. *The Fauna of India*, pp. 1–293. Zoological Survey of India, Calcutta.
- Vijayalakshmi, K. & Ahimaz, P. (1993) *Spiders: an Introduction*. Cre-A Publications, Madras.
- Vinson, A. (1863) *Aranéides des Îles de la Réunion, Maurice et Madagascar*. Roret, Paris.
- Walckenaer, C.A. (1842) Aptères. *Histoire Naturelle des Insects*, Vol. 2, pp. 1–549. Roret, Paris.
- Wiehle, H. (1967) *Meta* – eine semientelegyne Gattung der Araneae. *Senckenbergiana Biologica*, **48**, 183–196.
- Wunderlich, J. (1986) *Spinnenfauna Gestern und Heute. Fossile Spinnen in Bernstein und ihre Heute Lebenden Verwandten*. Erich Bauer, Quelle & Meyer, Wiesbaden.
- Wunderlich, J. (2004) Fossil spiders in amber and copal. Conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. *Beiträge zur Araneologie*, **3A-B**, 1–1908.
- Yin, C.M., Wang, J.F., Xie, L.P. & Peng, X.J. (1990) New and newly recorded species of the spiders of family Araneidae from China (Arachnida, Araneae). *Spiders of China: One Hundred New and Newly Recorded Species of the Families Araneidae and Agelenidae*, pp. 1–171. Normal University Press, Hunan.
- Zimsen, E. (1964) *The Type Material of I.C. Fabricius*. Munksgaard, Copenhagen.

Accepted 28 February 2006

First published online 17 October 2006