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# The systematics and biology of the spider genus *Nephila* (Araneae : Nephilidae) in the Australasian region

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**Abstract.** Five species of the nephilid genus *Nephila* Leach are found in the Australasian region, which for the purposes of this study was defined as Australia and its dependencies (including Lord Howe I., Norfolk I., Christmas I., Cocos (Keeling) Is), New Guinea (including Papua New Guinea and the Indonesian province of West Papua), Solomon Is, Vanuatu, New Caledonia, Fiji, Tonga, Niue, New Zealand and other parts of the south-west Pacific region. All species are redescribed and illustrated. *Nephila pilipes* (Fabricius) occurs in the closed forests of eastern and northern Australia, New Guinea, Solomon Is and Vanuatu (through to South-East Asia); *N. plumipes* (Latreille) is found in Australia (including Lord Howe I. and Norfolk I.), New Guinea, Vanuatu, Solomon Is and New Caledonia; *N. tetragnathoides* (Walckenaer) inhabits Fiji, Tonga and Niue; *N. antipodiana* (Walckenaer) occurs in northern Australia (as well as Christmas I.), New Guinea and Solomon Is (through to South-East Asia); and *N. edulis* (Labillardière) is found in Australia (including Cocos (Keeling) Is), New Guinea, New Zealand and New Caledonia. *Epeira* (*Nephila*) *walckenaeri* Doleschall, *E.* (*N.*) *hasseltii* Doleschall, *N. maculata* var. *annulipes* Thorell, *N. maculata jalorensis* Simon, *N. maculata* var. *novae-guineae* Strand, *N. pictithorax* Kulczyński, *N. maculata* var. *flavornata* Merian, *N. pictithorax* Kulczyński, *N. maculata* var. *flavornata* Merian, *N. maculata piscatorum* de Vis, and *N.* (*N.*) *maculata* var. *lauterbachi* Dahl are proposed as new synonyms of *N. pilipes. Nephila imperialis* var. *novaemecklenburgiae* Strand, *N. ambigua* Kulczyński, *N. sarasinorum* Merian and *N. celebesiana* Strand are proposed as new synonyms of *N. antipodiana. Meta aerea* Hogg, *N. meridionalis* Hogg, *N. adelaidensis* Hogg and *N. meridionalis hermitis* Hogg are proposed as new synonyms of *N. edulis. Nephila picta* Rainbow is removed from the synonymy of *N. plumipes* and treated as a synonym of *N. edulis*, and *N. nigritarsis insulicola* Pocock is removed from the synonymy of *N. plumipes* and treated as a synonym of *N. antipodiana*. Allozyme data demonstrate that *N. pilipes* is distinct at the 80% FD level from *N. edulis*, *N. plumipes* and *N. tetragnathoides. Nephila plumipes* and *N. tetragnathoides*, deemed to represent sister-taxa owing to the shared presence of a triangular protrusion of the male pedipalpal conductor, were found to differ at 15% FD in the genetic study. No genetic differentiation was found between 10 populations of *N. edulis* sampled across mainland Australia. Species of the genus *Nephila* have been extensively used in ecological and behavioural studies, and the biology of *Nephila* species in the Australasian region is extensively reviewed and compared with studies on *Nephila* species from other regions of the world.

## Introduction

Spiders of the genus *Nephila* Leach are abundant and conspicuous in many parts of the world, particularly in the tropics where they rank as some of the most spectacular denizens of closed forests. The large size of females and their diurnal habits have rendered various species of *Nephila* as some of the best studied spiders (e.g. Robinson and Robinson 1973, 1976; Austin and Anderson 1978; Christenson *et al.*1985; Miyashita 1986, 1992; Schneider *et al*. 2000; Elgar *et al*. 2003*a*; Su *et al*. 2007). Indeed, the American species, *N. clavipes* (Linnaeus), has been closely studied, and aspects of its reproductive biology and behaviour are becoming very well known (e.g. Christenson and Goist 1979; Christenson *et al*. 1979, 1985; Hill and Christenson 1981; Brown and Christenson 1983). All species construct large, asymmetrical orb-webs that include extensive yellow silk elements (e.g. Robinson and Robinson 1973; Austin and Anderson 1978) leading to the common name 'golden orb-weaving spiders'. Mating behaviour of *Nephila* spp. is well documented and has been used to examine more fundamental aspects of mating systems in spiders, particularly the evolution of sexual size dimorphism, male competition and sexual cannibalism (e.g. Vollrath and Parker 1992; Elgar and Fahey 1996; Coddington *et al*. 1997; Schneider *et al*. 2000; Schneider and Elgar 2002). Male *Nephila* are much smaller than females, generating debate on whether the dimorphism has evolved through giant females or dwarf males (Vollrath and Parker 1992, 1997; Hormiga *et al*. 1995, 2000; Coddington *et al*. 1997; Elgar 1998; Elgar and Schneider 2004). In many respects *Nephila* spp. have been at the forefront of spider research, during the past 30 years,

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including studies on the biochemistry and molecular biology of web silk (Craig 2003).

Three main regions of the world are populated by species of *Nephila* (Dahl 1911). The first is the neotropical zone ranging from the southern USA to southern Brazil and northern Argentina. Dahl (1911, 1912) and Levi (1980) recognised only *N. clavipes* from this region, although Archer (1958) considered *N. cornuta* (Pallas), originally described from Guyana, as specifically distinct. Levi (1980: p. 22) appeared to relegate *N. cornuta* to the synonymy of *N. clavipes*, although the former does not appear amongst the list of synonyms (pp. 17–18) or in the table of contents. Levi and von Eickstedt (1989) subsequently recognised *N. sexpunctata* Giebel from Brazil, Paraguay and Argentina as distinct from *N. clavipes*.

The second region is Africa, south of the Sahara, including Madagascar and the southern tip of the Arabian peninsula. Eight species were recognised by Dahl (1911), but he later (1912) recorded only six species: *N. senegalensis* (Walckenaer), *N. sumptuosa* Gerstäcker, *N. constricta* Karsch, *N. inaurata* (Walckenaer), *N. fenestrata* Thorell and *N. turneri* Blackwall. Two additional species were subsequently described from this region, *N. comorana* Strand from the Comores and *N. thomensis* Benoit from São Tomé, but the latter was synonymised with the American species *N. clavipes* by Levi (1980). *Nephila inaurata madagascariensis* (Vinson, 1863) has occasionally been treated as a valid species (e.g. Schneider *et al.* 2005) but currently is regarded at subspecies level (Platnick 2006).

The third area is the Indo-Australasian region, ranging from India through eastern Asia, Indonesia, New Guinea and Australia as far east as Samoa and Tonga. Dahl (1911, 1912) recorded eight species: *N. clavata* L. Koch, *N. edulis* (Labillardière), *N. pilipes* (Fabricius) (as *N. maculata* (Fabricius)), *N. antipodiana* (Walckenaer), *N. vitiana* (Walckenaer), *N. laurinae* Thorell (as *N. imperialis* (Doleschall)), *N. plumipes* (Latreille) and *N. tetragnathoides* (Walckenaer). Since then, several additional taxa have been described: *N. meridionalis* Hogg, *N. adelaidensis* Hogg and *N. meridionalis hermitis* Hogg from Australia, *N. clavatoides* Schenkel from China, *N. robusta* Tikader from India, *N. ambigua* Kulczyński and *N. pictithorax* Kulczyński from Irian Jaya, and *N. sarasinorum* Merian and *N. celebesiana* Strand from Sulawesi. *Nephila kuhlii* Doleschall was removed from the synonymy of *N. pilipes* by Tikader (1962).

Despite Dahl's (1911, 1912) revisions, the Australasian species of *Nephila* have often proved difficult to identify, and distributional limits have not been firmly established despite some species being subjected to detailed behavioural studies. Therefore, a major aim of the current study was to elucidate the systematics of the genus *Nephila* from the Australian region based upon detailed examination of all available material. To enhance the comprehensiveness of this revision, we have included allozyme data from the four species for which frozen material could be obtained, both as an independent test of the integrity of species boundaries in Australiasan *Nephila*, and as an initial examination of broad population structure in the two widespread species, *N. edulis and N. plumipes*.

This study complements current research revising the systematics of the Nephilidae on a worldwide basis (Kuntner 2005, 2006, 2007). As such, the present study is specifically restricted to the Australasian region, presenting for the first time a consistent treatment of species, and illustrating and diagnosing males of some species for the first time. In addition, we summarise the available biological data on the Australasian species.

## Materials and methods

### Morphological analysis

An examination of all State and National museum collections in Australia was made by the senior author, in addition to some important overseas collections. These institutions are listed below:

| | |
|---|---|
| AM | Australian Museum, Sydney, NSW, Australia |
| AMNH | American Museum of Natural History, New York, USA |
| AMNZ | Auckland Museum, Auckland, New Zealand |
| ANIC | Australian National Insect Collection, CSIRO, Canberra, ACT, Australia |
| BMNH | Museum of Natural History, London, England |
| BPBM | Bishop Museum, Honolulu, Hawaii, USA |
| CAS | California Academy of Sciences, San Francisco, CA, USA |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA |
| MMS | MacLeay Museum, University of Sydney, Sydney, NSW, Australia |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France |
| MNZ | Museum of New Zealand, Wellington, New Zealand |
| MV | Museum of Victoria, Melbourne, Vic., Australia |
| MWNH | Museum Wiesbaden, Wiesbaden, Germany |
| MZPW | Muzeum i Instytut Zoologii, Warsaw, Poland |
| NMB | Naturhistorisches Museum, Basel, Switzerland |
| NTMAG | Museum and Art Gallery of the Northern Territory, Darwin, NT, Australia |
| NZAC | New Zealand Arthropod Collection, Auckland, New Zealand |
| OUM | Oxford University Museum, Oxford, England |
| QM | Queensland Museum, Brisbane, Qld, Australia |
| RMNH | National Museum of Natural History, Leiden |
| SAM | South Australian Museum, Adelaide, SA, Australia |
| SMF | Naturmuseum Senckenburg,Frankfurt, Germany |
| SMNH | Swedish Museum of Natural History, Stockholm, Sweden |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart, Germany |
| TMAG | Tasmanian Museum and Art Gallery, Hobart, Tas., Australia |
| USNM | United States National Museum, Smithsonian Institution, Washington DC, USA |
| WAM | Western Australian Museum, Perth, WA, Australia |
| WINC | Waite Insect and Nematode Collection, Adelaide University, Adelaide, SA, Australia |
| ZMB | Zoologischen Museum, Berlin, Germany |
| ZMH | Zoologisches Institut und Zoologisches Museum, Hamburg, Germany |

The geographic regions covered by this revision (Fig. 10) include Australia, along with the four Australian Dependencies known to possess species of *Nephila* (Lord Howe I., Norfolk I., Christmas I. and Cocos (Keeling) Is), New Guinea (including both Papua New Guinea and the Indonesia province of West Papua), Solomon Is, Vanuatu, New Zealand, New Caledonia, Fiji, Tonga and neighbouring areas in the south-west Pacific region.

Of the five species treated in this revision, two also occur outside of the study area, but we have not included lists of specimens examined from these outlying localities, as we have not undertaken a comprehensive review of this material. We have only included full locality data for type specimens. Those data that are not available on the locality labels are included within square brackets in the lists provided below. These are principally locality coordinates, but we have been able to occasionally add other information, such as full spellings when abbreviated on the label. For the remainder of the specimens examined, we have provided only abbreviated lists of *Material examined*, along with detailed distribution maps showing those localities that could be traced or localised. A more comprehensive list is available from the senior author or from the editorial office of the journal.

The species are treated in the following order: the type species *N. pilipes*, followed by three morphologically similar taxa, *N. plumipes*, *N. tetragnathoides* and *N. antipodiana*, followed by *N. edulis*.

Specimens were examined, measured and illustrated with a Wild M7A stereomicroscope (Heerbrugg, Switzerland) fitted with a graticule for measurements and a grid for illustrations. Measurements were taken at the highest possible magnification. The longest measurements were taken with a pair of dial calipers. Female genitalia were excised using micro-scissors and sharpened needles, macerated in 10% potassium hydroxide at room temperature for several hours before examination under the stereomicroscope. Illustrations were obtained by tracing structures onto graph paper after comparison with the structure through a grid graticule fitted in the eyepiece of the stereomicroscope. Most setae were omitted from illustrations for clarity.

The scanning electron micrographs were obtained in a Philips XL30 scanning electron microscope (Eindhoven, The Netherlands) after the specimens were prepared by dehydration in 1,1,1,3,3,3-Hexamethyldisilazane (HMDS), air-drying and mounting on SEM stubs with carbon tape.

### Common names

Although common or vernacular names are sparingly used for individual species of Australasian spiders, we here propose common names for each species treated in this monograph because they are highly visible spiders and are often used as models in behavioural and ecological studies (see *Biology* section below), and commonly encountered by natural historians and the general public. In particular we propose a change from 'giant wood spider' initiated and promulgated by Hingston (1922*a*, 1922*b*, 1922*c*, 1923) and Robinson and Robinson (1973), because Australasian forests are not locally referred to as 'woods'. Species of *Nephila* are generally referred to as 'golden orb-weaving spiders' (e.g. Clyne 1969; Mascord 1970; Main 1976, 1980; Brunet 1994), owing to the inclusion of yellow colouration of the silk used to produced their webs. We adopt this name, with each species prefixed with a descriptive term such as 'Australian' or 'Giant'.

### Allozyme analysis

Given that allozyme electrophoresis requires access to fresh or freshly frozen tissues, not all species or geographic regions were accessible for analysis. Nevertheless, four of the five species ultimately recognised were able to be included in the allozyme study, with two of these species being represented by a sufficiently broad geographic coverage to permit a rudimentary assessment of population structure.

Leg muscle was chosen as the most convenient and suitable material for allozyme analysis. Spiders were transported alive to the laboratory where they were anaesthetised using carbon dioxide and the legs on one side of the body removed for snap freezing at –80°C. Each specimen was then immediately preserved in 70% ethanol for subsequent morphological analysis. Table 1 presents the details of the 60 animals surveyed electrophoretically, and Fig. 10 maps their geographic distribution.

Allozyme characterisation was undertaken according to the principles and procedures outlined in Richardson *et al*. (1986). Two or three legs from each animal were pooled together and homogenised by hand in an equal volume of cold homogenising solution (Richardson *et al*. 1986), using the microtip of a sonicator as the pestle. Homogenates were then centrifuged at 10 000*g* for 5 min, and either loaded directly on to gels (for about one-third of the enzymes screened) or frozen at –20°C as separate 10–20 μL aliquots until required for subsequent runs.

The following enzymes or non-enzymatic proteins produced interpretable banding patterns: aconitate hydratase (ACON, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), adenylate kinase (AK, EC 2.7.4.3), fructose- bisphosphate aldolase (ALD, EC 4.1.2.13), arginine kinase (ARGK, EC 2.7.3.3), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPD, EC 1.2.1.12), aspartate aminotransferase (GOT, EC 2.6.1.1), general proteins (GP), glucose-6-phosphate dehydrogenase (G6PD, EC 1.1.1.49), glycerol-3-phosphate dehyrogenase (GPD, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), hexokinase (HK, EC 2.7.1.1), isocitrate dehydrogenase (IDH, EC 1.1.1.42), L-lactate dehydrogenase (LDH, EC 1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), 'malic' enzyme (ME, EC 1.1.1.40), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEPA, EC 3.4.13), tripeptide aminopeptidase (PEPB, EC 3.4.11), proline dipeptidase (PEPD, EC 3.4.13), dipeptidase (PEPS, EC 3.4.13), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), and triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature for referring to loci and allozymes follows Adams *et al*. (1987).

The genetic affinities among populations were assessed using both phenetic and phylogenetic analyses of the pairwise genetic distance estimates. The former assumes a constant rate of molecular evolution and thus requires no outgroup, whereas the latter allows unequal rates but requires the inclusion of an outgroup to root trees. No suitable outgroup could be found for

**Table 1. Specimens used in allozyme study**
See Fig. 1 for map depicting localities.

| Species | Country | State | Locality | Code | Registration no., sex and stage | No. of specimens utilised |
|---|---|---|---|---|---|---|
| *Nephila pilipes* | Australia | Qld | Rockhampton | M | WAM 95/1271–1272 (2 ♀) | 2 |
| *Nephila plumipes* | Australia | | Lord Howe I. | H | WAM T52210–52215 (6 juv. ♀) | 4 |
| | Australia | NSW | Pearl Beach | P2 | WAM T52203–T52209 (7 ♀) | 3 |
| | Australia | NSW | Woolooware Bay, Sydney | P1 | WAM T52217–T52228 (12 ♀) | 3 |
| | Australia | Qld | Paddington, Brisbane | P3 | WAM 92/541–546 (6 ♀) | 4 |
| *Nephila tetragnathoides* | Fiji | | Nasese, Suva | F | WAM 97/6–7 (1 ♀, 4 juv. ♀) | 5 |
| *Nephila edulis* | Australia | NT | Yulara Resort, Uluru Natl Park | E6 | WAM 94/1948–1956 (4 ♀, 4 juv. ♀) | 4 |
| | Australia | SA | Chambers Gorge | E8 | WAM T41897–T41906 (7 ♀, 3 juv. ♀) | 3 |
| | Australia | SA | Wilpena Pound | E7 | WAM T41907–T41915 (8 ♀, 1 juv. ♀) | 3 |
| | Australia | Vic. | Violet Town | E9 | WAM T41880–T41895 (2 ♀, 5 juv. ♀) | 4 |
| | Australia | WA | Barrow I. | E5 | WAM (4 ♀) | 4 |
| | Australia | WA | Exmouth | E4 | WAM 92/559–566 (8 ♀) | 4 |
| | Australia | WA | Greenough R. | E1 | WAM 95/460–472 (13 ♀) | 6 |
| | Australia | WA | Hampton Tower | E3 | WAM 95/1261–1270 (10 ♀) | 3 |
| | Australia | WA | Lake Kununurra | E10 | WAM T41986–41995 (10 ♀) | 4 |
| | Australia | WA | Mt Claremont, Perth | E2 | WAM T42016–42027 (12 ♀) | 4 |

this study, and the finding that members of the ingroup displayed levels of genetic divergence beyond the saturation point for allozyme data (Richardson *et al.* 1986) demonstrated that outgroup analysis was inappropriate in any case. Approaches that employed genetic distances were used because the occurrence of within-population polymorphism at most informative loci in our dataset presents an unresolvable difficulty for character-based methods of analysis (Swofford *et al.* 1996).

Genetic divergence between populations was calculated as both percentage fixed differences (% FD: Richardson *et al.* 1986) and corrected Nei distances (Nei D: Nei 1978). As discussed by Richardson *et al.* (1986), the former is particularly appropriate for the delineation of species boundaries whereas the latter has more general applicability in population genetics and systematics. One phenetic (UPGMA) and two phylogenetic (neighbour-joining and Fitch–Margoliash) methodologies were applied to both sets of pairwise genetic distance estimates, resulting in a total of six trees. These analyses were undertaken using the NEIGHBOUR and FITCH programs included in the computer package PHYLIP 3.5c (Felsenstein 1993).

Assessments of population substructuring within species were undertaken by the pairwise comparison of allele frequencies for different sites (alleles pooled into two classes where necessary), either by calculating the Fisher's exact probability for each 2 × 2 contingency table or by calculating the Yates-corrected $\chi^2$ where sample sizes were sufficiently large (Zarr 1984).

### *Abbreviations*

The following abbreviations are used in the descriptions: ALE, anterior lateral eye; AME, anterior median eye; MOQ, median ocular quadrangle; PLE, posterior lateral eye; PME, posterior median eye.

## Biology of *Nephila*

Compared with most spiders, the biology of *Nephila* has been well studied, albeit mostly for one species, *N. clavipes* from the New World, which has become a favoured model for research on the reproductive biology and behaviour of orb-weaving spiders. Biological information on *Nephila* spp. for the Australasian region has been gradually accumulating since the early work on *N. pilipes* (= *N. maculata*) from New Guinea (Robinson and Robinson 1973, 1976, 1980) and *N. plumipes* from the Sydney region (Austin and Anderson 1978) (misidentified as *N. edulis*). More recently, numerous authors (e.g. Herberstein and Elgar 1994; Elgar and Fahey 1996; Uhl and Vollrath 1998*a*, 1998*b*; Schneider *et al.* 2000; Uhl and Vollrath 2000; Schneider *et al.* 2001; Schneider and Elgar 2002; Elgar *et al.* 2003*a*, 2003*b*; Griffiths *et al.* 2003) have undertaken several studies on evolutionary aspects of mating and feeding strategies in *N. plumipes* and *N. edulis* that also document various aspects of the natural history and ecology of these species.

Here we present a summary of what is known about the biology of *Nephila* spp. from Australasia, and briefly compare these findings with the major works published on *N. clavipes* and other species from outside Australasia in an attempt to highlight similarities and differences among taxa and regions. It should be noted that this section does not represent a comprehensive review of *Nephila* biology, which was beyond the scope of the current study, but rather serves to provide complementary biological information to support the taxonomic revision undertaken here.

### *Web structure*

*Nephila* spp. construct large orb-webs that are asymmetric in shape and include extensive yellow silk elements (hence the common name 'golden orb-weavers'). The orb of most adult *Nephila*, including the three species from mainland Australia, is 0.5–1.0 m in diameter, but the extensive anchor lines, frame and barrier web substantially extend the dimensions of the structure. These are enhanced further when females aggregate (Rypstra 1985) and the webs become connected and therefore continuous over many square meters, for example in *N. plumipes* (Austin and Anderson 1978; Elgar 1989 (misidentified as *N. edulis* in both references)) but to a lesser degree in *N. edulis* (Schneider *et al*. 2000). The orb is asymmetric in that the hub is centred in the upper part of the web, so that the sticky elements of the prey catching area are concentrated disproportionally in the lower half of the web (Robinson and Robinson 1973; Austin and Anderson 1978).

*Nephila* spp., for example *N. plumipes* (Elgar 1989; Herberstein and Elgar 1994), remain permanently in their webs, which are themselves permanent structures that function as a prey-catching device during both the day and night. As a consequence both juveniles and adult females are possibly more exposed to diurnal hunting predators over relatively long periods of time, and their webs are exposed to damage from birds, grazing mammals and large insects. Several physical and behavioural adaptations have resulted to minimise these effects. The extensive 'barrier' web either side of the orb of large juveniles and adults has been postulated by Higgins (1992*a*) to protect or warn the resident spider of large aerial predators. Aggregating behaviour, where the webs of multiple females are interconnected, further reduces predation (see below under *Natural enemies*), but the results of studies to examine the function of this behaviour are contradictory. For *N. clavipes*, studies by Rypstra (1985) and Hodge and Uetz (1992) indicate that aggregating behaviour has positive benefits for prey capture efficiency and reduced predation, while Farr (1976) proposed that 'web clumping' is a random process influenced by population density and results in decreased predation success. Elgar (1989) has demonstrated that orb-web aggregations of *N. plumipes* in Australia experience higher kleptoparasite (i.e. *Argyrodes*) intensity and may therefore suffer reduced food availability. The permanent occupation of the web by *Nephila* spp. contrasts with members of the sister genus, *Nephilengys* L. Koch, where the spiders are positioned in their web at night and in a retreat during the day (Kuntner 2007).

Juveniles sometimes construct a 'stabilimentum' above and below the hub (Robinson and Robinson 1973, 1974*a*, 1978*a*; Austin and Anderson 1978; see Fig. 7), a structure that is more common in other orb-weavers such as *Argiope* Audouin (Herberstein *et al*. 2000). In *N. plumipes* and *N. pilipes* stabilimenta have only been observed in ~5% or less of juvenile webs. This structure has been examined experimentally in a range of orb-weaving spiders (but not *Nephila*) and may act to reduce damage by birds (Eisner and Nowicki 1983), although this may not be the only function of stabilimenta (see Robinson and Robinson 1973, 1974*a*; Herberstein *et al*. 2000; Bruce 2006). *Nephila* also characteristically places wrapped prey in a line above or below the hub (referred to as a 'food cache' (e.g. Bjorkman-Chiswell *et al*. 2004). Apart from acting as a food reserve, this structure also serves other functions (see below).

If partly damaged, the webs of *N. plumipes* and *N. pilipes* are repaired by the resident spider within 10–60 min after disturbance, but if the damage is severe, the spider will usually consume the remaining web, rest in the vegetation and then construct a new web at the same or a nearby locality. Repeated disturbance of the web or lack of prey inevitably results in relocation of the web to a nearby site, usually within 2–10 m. Gravid females do not repair their webs for the few days before oviposition and they can appear somewhat tattered if damaged during this time (Robinson and Robinson 1973).

### Prey and feeding

*Nephila* spp., like most diurnal orb-weavers, are opportunistic though sometimes selective predators, feeding on any suitable prey that adheres to their web (Robinson and Mirick 1971; Robinson and Robinson 1973; Austin and Anderson 1978; Higgins 1987; Herberstein and Elgar 1994). Various studies have documented a large number of prey groups, including various species of Orthoptera, Diptera, Coleoptera, Lepidoptera and, generally to a lesser degree, Hymenoptera and Odonata. However, ~90% of the prey of *N. plumipes* in mangroves in coastal New South Wales, Australia, comprised just three species of fulgoroid leafhoppers (Austin and Anderson 1978), whereas for a nearby but more inland site, prey of the same species comprised mostly Diptera and Hymenoptera (Herberstein and Elgar 1994). Most well studied *Nephila* spp. have also been observed to avoid or remove particular insects from their webs without feeding on them. These include vespid wasps (Austin and Anderson 1978), alate ants (Higgins 1987), 'unpalatable' butterflies (Vasconcellos-Neto and Lewinsohn 1984), and numerous 'obnoxious' groups including lycid beetles, Hemiptera and Neuroptera that produce distasteful secretions (Robinson and Robinson 1973).

*Nephila* is clearly able to deal with a large size range of prey, from ~2 mm in length up to insects larger and heavier than themselves. In several studies in various parts of the world *Nephila* prey are numerically dominated by small insects but prey biomass is dominated by a few large items (Robinson and Robinson 1973; Higgins 1987; Miyashita 1992). There are a large number of studies that have examined the predatory behaviour of *Nephila*. In brief, these show that the stimulus for orientation and approach is mediated through web vibrations (e.g. Klärner and Barth 1982), and that the attack behaviour varies for prey of different sizes. Essentially, small prey are simply 'seized and removed' from the web, while large prey are bitten by the resident spider that then waits for the venom to subdue the prey before it is cut out of the web and wrapped in silk (e.g. Robinson and Mirick 1971; Robinson and Robinson 1973). Predatory behaviour also changes dramatically from the early free-living (pre-dispersal) spiderling stage, when they live in a communal web and apparently feed opportunitistically, to second and third instars that capture live prey in individual webs (Hill and Christenson 1981; Brown and Christenson 1983). Adult females of *N. clavipes* respond to decreased food availability by moving their webs (e.g. Vollrath 1985), and this phenomenon may be common for several species. However, the frequency of occurrence and selective advantage of the behaviour is unclear given that *N. clavipes* also shifts its webs randomly, independent of prey availability (Vollrath and Houston 1986).

*Nephila* spp. are also known to construct food caches, usually above the hub of the web, which are utilised when there is a shortage of food (Champion de Crespigny *et al*. 2001). Caches vary in size and composition and are influenced by prey density, encounter rates and prey type (Griffiths *et al*. 2003). Large caches may contain as many as 12–15 prey items and may be 10–12 cm in length (Fig. 7). When prey is added to the cache it is usually densely wrapped in silk and placed at either the top or bottom of the cache so the connected prey forms a near vertical line. The dense silk covering probably helps to reduce dehydration of the prey, but it and the cache may also have other functions. Recently, studies on the food caches of *N. edulis* and *N. plumipes* (Champion de Crespigny *et al.* 2001; Griffiths *et al.* 2003) show that they are constructed and expanded during periods of high prey availability, and that access to a cache reduces weight loss, particularly for large females, at times of prey scarcity. Also, there are differences among species in the composition of the cache in that, compared with other species, *N. edulis* also includes plant material in its cache and this may serve to attract other prey to the web (Griffiths *et al.* 2003; Bjorkman-Chiswell *et al.* 2004).

Apparently unique among *Nephila* spp. and possibly other orb-weavers is that the normal and melanic colour morphs of *N. pilipes* on Taiwan are differentially attractive to prey, and that this is mediated by variation in the amount of ultraviolet reflected by the spider's body (Tso *et al.* 2002).

### Mating

Mating behaviour of *Nephila* has been well documented for several species including those in Australasia. In addition, it has been used to examine more fundamental aspects of mating systems in spiders, particularly the evolution of sexual size dimorphism, sperm competition and sexual cannibalism (e.g. Vollrath and Parker 1992; Elgar and Fahey 1996; Coddington *et al.* 1997; Hormiga *et al.* 1995, 2000; Schneider *et al.* 2000; Schneider and Elgar 2002; Elgar and Schneider 2004). *Nephila* is typified by extreme sexual size dimorphism where males can be 4–10 times smaller than females (e.g. Robinson and Robinson 1973; Austin and Anderson 1978; Coddington *et al.* 1997; Schneider *et al.* 2000; Elgar *et al.* 2003*a*). Once males reach adulthood in early summer they leave their own web and search for those of mature or subadult females, possibly using web characteristics and/or web-based chemical cues to locate and recognise conspecific webs (Christenson *et al.* 1985; Hill and Christenson 1988). Although short-distance pheromonal stimulation of males is postulated for *Nephila*, there is no evidence of long distance pheromone-based attraction to female webs. It is common for multiple males to occupy the web of a single female, who normally mates with more than one male (Elgar *et al.* 2003*a*). For some species, including *N. plumipes*, *N. clavata* and *N. clavipes*, larger males are capable of displacing smaller males from the hub region of the web where mating takes place, but they are also more likely to suffer sexual cannibalism than smaller males (Christenson and Goist 1979; Elgar and Fahey 1996). Compared with other species of approximately the same size, male *N. edulis* vary far more in size (by an order of magnitude), and it has been suggested that this variation is maintained by the different size-dependent startegies for winning or preventing sperm competition (Schneider *et al.* 2000; Elgar *et al.* 2003b). Further, males will alter the frequency and duration of copulation depending on the number and size of competing males in the same web, and the mating history of the female (Elgar *et al.* 2003*a*, 2003*b*). Recent work has also revealed several mating differences between the two common Australian species *N. edulis* and *N. plumipes*. For example, *N. edulis* mate more frequently and for longer with virgin females compared with previously mated females that are more aggressive; they have a lower rate of sexual cannibalism, and use both pedipalps during copulation compared with a single pedipalp by *N. plumipes* (Schneider *et al.* 2000; Herberstein *et al.* 2002; Elgar *et al.* 2003*a*, 2003*b*). Larger *N. edulis* males often mate from the other side of the web to the female and require several attempts to attain successful mating (Schneider *et al.* 2000). Also, for males of *N. plumipes* (unlike *N. edulis*) the palpal conductor breaks off and remains inside the female genital tract, although the function of this process is so far unclear (Schneider *et al.* 2001).

For these and other species, although there are intra- and interspecific differences in mating behaviour, generally it involves a series of common elements (see for example Robinson and Robinson 1973, 1976, 1980; Austin and Anderson 1978; Christenson *et al.* 1985; Herberstein *et al.* 2002; Elgar *et al.* 2003*a*, 2003*b*): male cautiously approaching the female, sometimes plucking a radial line. If the female is receptive the male will move to a position on the female's ventral abdomen, facing forwards, and begin mating. Sometimes copulation is preceded by the male touching the hind legs of the female or tapping the pedipalps against the epigynum. Copulation varies in duration from just a few seconds to over a minute, but matings of very short duration are generally considered not to be successful (i.e. sperm transfer does not occur), but this has not been demonstrated in all cases. If the female reacts aggressively to the presence of an approaching male, he will first become motionless, often for 10–15 min, and if she continues to be aggressive when the male resumes an approach, he retreats from the hub.

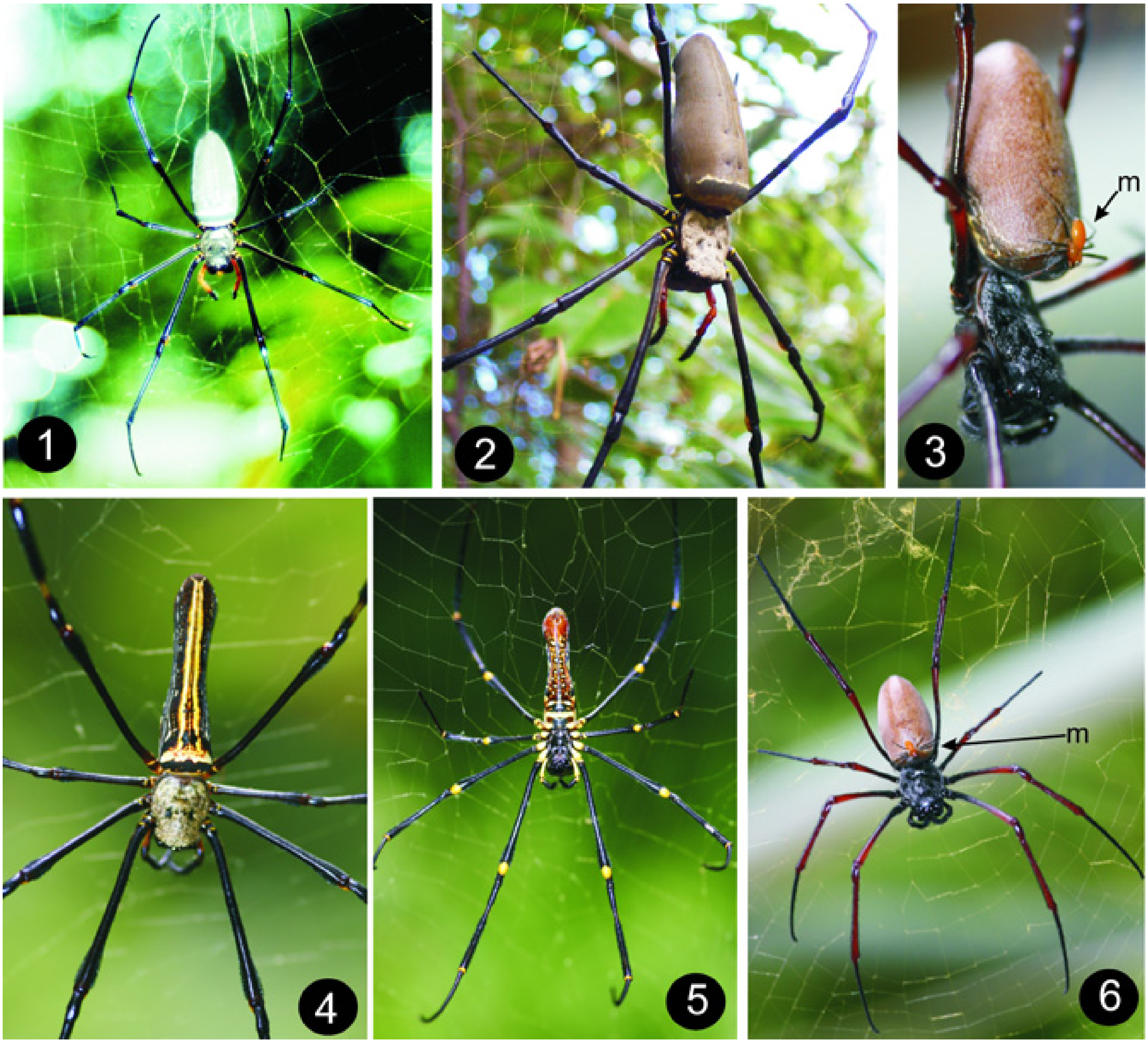
Sexual cannibalism is generally uncommon in orb-weaving spiders, but in *Nephila* spp. its frequency differs among species (e.g. Robinson and Robinson 1980; Schneider *et al.* 2000; Schneider and Elgar 2002; Elgar *et al.* 2003*b*) owing to likely selective differences (Elgar and Fahey 1996; Schneider and Elgar 2002), but also possibly a result of environmental, behavioural and physiological factors such as time of the year, nutritional and reproductive state of the female, age of the female, and number and size of males on the web (see also Schneider *et al.* 2000; Elgar and Schneider 2004). Several behavioural adaptations in males have been identified that act to reduce sexual cannibalism. In particular this includes mating with newly moulted adult females that are largely inactive, and mating when the female is feeding, but also, to a lesser degree, approaching the female on the opposite side of the orb web (e.g. Austin and Anderson 1978; Christenson *et al.* 1985; Fromhage and Schneider 2004).

Mating behaviour in *N. pilipes* (and possibly *N. antipodiana*, Fig. 3) departs significantly from that described for the above species. *Nephila pilipes* has a more complex premating behaviour that includes the male laying down a fine mat of silk on the dorsal side of the abdomen and pedicel of the female; matings are of much longer duration (often in excess of 30 min), are far less aggressive and sexual cannibalism appears to be very rare (Robinson and Robinson 1973, 1976).

### Fecundity and oviposition

Ovipositional behaviour among *Nephila* spp. is similar in that females construct a dense flocculent egg-sac in vegetation adjacent to the orb web. A non-viscid dense silk platform is first produced, eggs are oviposited onto this platform, and then a thick layer of bright yellow, loose, flocculent (looped) silk is placed over the eggmass. Several short silk lines are used to firmly attach the egg-sac to surrounding leaves and twigs. The egg-sac is almost always at least partly hidden underneath green leaves or shaded beneath them. This behaviour has been documented for several temperate and subtropical species including *N. plumipes* (Austin and Anderson 1978), *N. edulis* (A. Austin, personal observation) and *N. clavipes* (Christenson and Wenzl 1980). Within a few days, egg-sacs turn yellow-green, are more cryptic and sometimes difficult to find. In at least one species (*N. plumipes*) oviposition occurs at night. At least for *N. clavipes*, a significant proportion of eggs within an egg-sac can sometimes be inviable and this appears to vary regionally and with time (Moore 1977; Christenson *et al*. 1979). Egg inviability has been measured from 4% to 100% and is probably related to mating frequency, with the proportion of inviable eggs increasing later in the breeding season (Moore 1977; Austin and Anderson 1978; Christenson *et al*. 1979; Christenson and Wenzl 1980).

Again, *N. pilipes* is the only species studied that departs substantially from this pattern of oviposition in that females construct an egg-sac in a shallow depression excavated on the forest floor. This behaviour is postulated to have evolved in response to the otherwise high levels of predation and parasitism that are



**Figs 1–6.** *1*, *Nephila pilipes* (Fabricius), adult female from Litchfield Natl Park, NT, Australia (photographed by M. S. Harvey); *2*, *N. pilipes* (Fabricius), adult female from Coffs Harbour, NSW, Australia (photographed by M. Rix); *3*, *N. antipodiana* (Walckenaer), adult female and adult male (m) from Christmas I., Australia (photographed by V. Framenau); *4–5*, *N. pilipes* (Fabricius), adult female from Christmas I., Australia (photographed by V. Framenau), *4*, dorsal, *5*, ventral; *6*, *N. antipodiana* (Walckenaer), adult female and adult male (m) from Christmas I., Australia (photographed by V. Framenau). Figs 3 and 6 display the striking size dimorphism characteristic of all species of the genus.

recorded for other tropical orb weavers, and possibly protection from ultraviolet light (Robinson *et al*. 1986). Although such evolutionary hypotheses are difficult to test, it does raise interesting questions regarding the function of different types of spider egg-sacs (see Austin 1985). Christenson and Wenzl (1980) have experimentally examined several egg-sac characteristics for *N. clavipes* and shown that egg-sacs placed on the ground were highly susceptible to fungal growth and predation.

Fecundity varies substantially among species. For example, female *N. plumipes* in Australia generally produce several egg-sacs in a season (Schneider and Elgar 2002) each containing on average 380 eggs (Austin and Anderson 1978); *N. edulis* probably has a similar egg-laying pattern to *N. plumipes*, but differs across its geographic range with arid zone populations sometimes producing only a single egg-sac (ADA personal observation); *N. clavipes* from the southern USA and central Americas produces 1–3 egg-sacs contain 'several hundred' to over 1000 eggs (Christenson and Wenzl 1980; Higgins 1992b), while the tropical rainforest species, *N. pilipes*, produces up to nine egg-sacs over a prolonged period of time averaging 2470 eggs per egg-mass (Robinson and Robinson 1973, 1976).

### Thermoregulatory behaviour

Like other orb-weaving spiders, *Nephila* spp. adopt specific body postures to reduce radiant heat load from the sun (Krakauer 1972; Robinson and Robinson 1974*b*, 1978*b*). This behaviour has been observed in all species examined and occurs in both tropical and more temperate regions. An initial response occurs at temperatures above ~32°C, and involves orientation of the posterior abdomen towards the sun but with the cephalothorax staying parallel to the plane of the web. As the temperature increases, the whole body aligns with the position of the sun, further reducing the area exposed to direct sunlight. A further increase in temperature (>~40°C) will result in the spider abandoning its web, often after a series of agitated movements, and moving into shade beside the web (Humphreys 1993). Increased temperature can also result in the spider adopting a drooping posture where it hangs by its hind legs, limp in the web. This occurs mostly in newly moulted females and may result from reduced hydrostatic pressure (Humphreys 1993). Although other possible functions for body posturing have been suggested, Humphreys (1993) has developed several criteria and methods to distinguish thermoregulatory behaviour from that of other behavioural adaptations.

### Habitat preferences and seasonality

Of the three species of *Nephila* that are found on mainland Australia, *N. pilipes* is strongly associated with rainforest habitats in northern and eastern Australia (Fig. 28; Robinson and Robinson 1973). When it is found in other sites, they are inevitably moist and well shaded, such as domestic gardens in coastal Northern Territory and Queensland. *Nephila plumipes* is often found in coastal habitats, and is particularly associated with mangroves (Austin and Anderson 1978). However, it also occurs in dry sclerophyll and low shrublands, up to several hundred kilometres from the coast (Fig. 46), although at such locations the occurrence of populations is sporadic and population densities are often low. This species is also common on islands (e.g. Great Barrier Reef, Lord Howe I. (Fig. 9)) where females often build webs near to or against buildings and other human structures. The widespread and ubiquitous *N. edulis* is found in a great range of climatic zones including the arid interior, tropical savannah, subtropical, Mediterranean and temperate coastal habitats, and subalpine locations (Fig. 87). The webs of this species are often found between bushes and trees in open situations, sometimes near small water-courses, but they also occur in dense vegetation with a closed canopy. Like *N. plumipes*, this species sometimes constructs webs against buildings and other structures.

Given the large number of studies that have focused on the behaviour and evolutionary biology of *Nephila* spp., it is somewhat surprising that little work has been undertaken on their population biology. In the Sydney region, adult female *N. plumipes* are univoltine, appearing in late December to February (depending on the year), and reproduce from late summer to autumn (February–May) (Austin and Anderson 1978; Elgar *et al*. 2003*a*). From June to September (winter–early spring) the population comprises a range of immature size classes, and a declining number of adult females that have all disappeared by August–September. This pattern becomes more complex in the northern, tropical part of the distribution of *N. plumipes*, where the breeding season is more prolonged, and populations may be bivoltine (A. Austin, personal observation).

Far less is known about the population biology of *N. edulis*, which occurs throughout the arid interior of the continent (Fig. 87). In arid regions this species appears to have more transient populations, where dense aggregations of adult females will occur at a particular site in one autumn and then disappear, often for many years (A. Austin, personal observation). Although populations of *N. plumipes* can also be transient at some locations, this species usually has semi-permanent or permanent populations in coastal areas, particularly in mangroves (Austin and Anderson 1978; Elgar *et al*. 2003*a*) and on off-shore islands.

The phenology and breeding pattern of *N. pilipes* in New Guinea differs markedly from *N. edulis* and *N. plumipes*, as well as from the other well studied species *N. clavipes* (southern USA) and *N. clavata* (Japan) (e.g. Moore 1977; Christenson and Wenzl 1980; Miyashita 1986, 1992; Higgins 1992*a*). Unlike these species, adult female *N. pilipes* are present throughout the year and they produce multiple egg-sacs (up to nine per individual), which, along with juveniles, are present in the field continuously. Also, adult males are present in the population for much longer, approximately six months spanning the wet season (Robinson and Robinson 1973). It is not known how this pattern differs for *N. pilipes* populations in Australia that extend down the east coast to the south of Brisbane.

### Other spiders and insects associated with Nephila

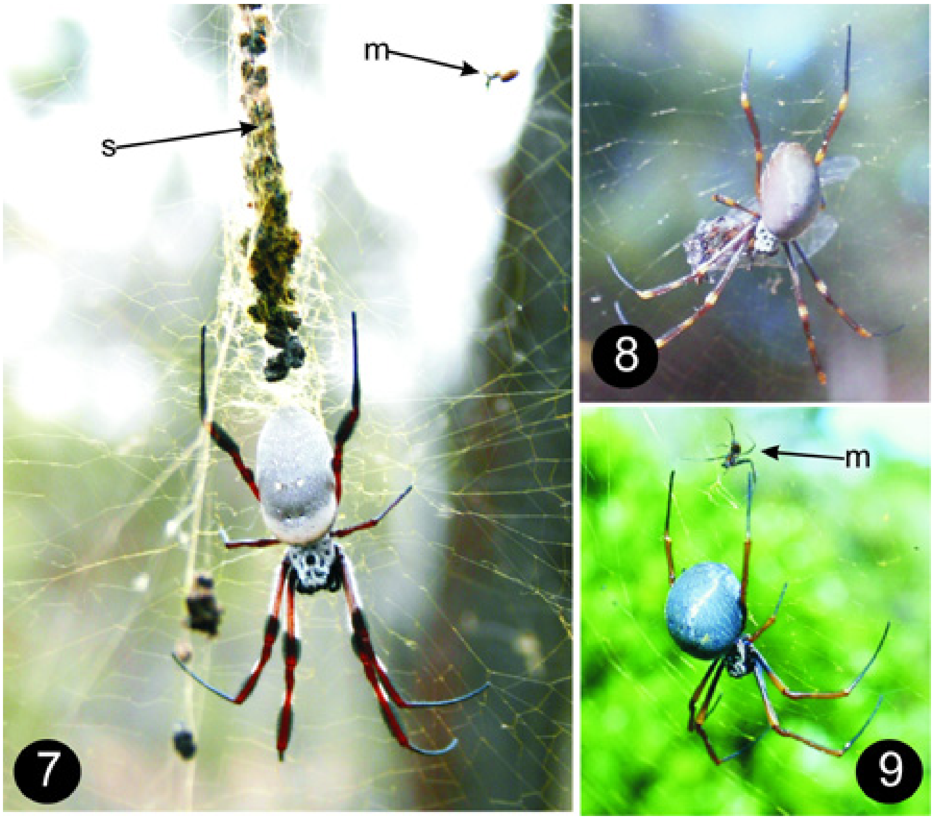
The webs of *Nephila* spp. provide a habitat for several other small species of spider and insects. The most commonly encountered spiders on *Nephila* webs are *Argyrodes* spp. (Theridiidae) that feed on insects caught in the 'host' web. They are known to occur on the webs of virtually all *Nephila* spp. worldwide, including the three common species in Australasia, *N. edulis*, *N. pilipes* and *N. plumipes* (Robinson and Robinson 1973; Elgar 1989; Grostal and Walter 1997). Such species have been referred to as ‘kleptoparasites’ to indicate that they may have a negative effect on the resident *Nephila* female. This hypothesis has largely remained untested although several specific adaptations have been identified in *Argyrodes* to living in *Nephila* webs (see Elgar 1993 for review). Elgar (1989) has shown that webs in *N. plumipes* aggregations have a higher colonisation rate of *Argyrodes* than solitary webs. Recently, Grostal and Walter (1997) have shown experimentally that *A. antipodianus* Cambridge causes decreased weight gain in female *N. plumipes* and causes them to relocate their webs more often. These effects have been attributable to *A. antipodianus* removing prey and/or damaging the web of the ‘host’ spider.

Many flying insects are also found on the webs of *Nephila*. They use the silk lines particularly in the upper part of the web as a resting site. In many cases this behaviour is apparently opportunistic, but it is also possible that insects are resting in webs to avoid predation by large insects or birds, which in turn avoid *Nephila* webs so as not to get tangled in them (Robinson and Robinson 1976).

### Natural enemies

Information on the natural enemies of *Nephila* spp. and the levels of mortality they cause are restricted to anecdotal observations and there are no detailed studies available. Unlike other spiders, *Nephila* spp. are apparently rarely attacked in their webs by predatory or parasitic Hymenoptera. The only reported case is for *N. clavipes* in Panama, which is parasitised by the ichneumonid *Hymenoepimecis* sp. (Fincke *et al*. 1990). The major predators of adults and subadults appear to be birds, although this assessment is largely based on the assumption that females missing from webs have been taken by birds (see Higgins 1992*a*; Hodge and Uetz 1992). Robinson and Robinson (1976) have observed several bird species to feed on orb-weavers including *N. pilipes*, which learn to avoid being tangled in webs after flying through them only once (see above under *Web structure*). Predation may be greatest on immature *Nephila* as documented in Panama for *N. clavipes*, where damsel flies, predatory wasps and hummingbirds were observed to remove spiders from their webs (Vollrath 1985). Female *Nephila* often aggregate with each other and with other colonial orb-weavers so that their webs become interconnected. This behaviour has been shown to reduce the rate of aerial predation in *N. clavipes* compared with females that construct solitary webs (Hodge and Uetz 1992).

In South-East Asia and the Pacific humans have used *Nephila* as a food source and may, in the past, have reduced the size of populations around villages and settlements. Robinson and Robinson (1976) reported native tribes in the New Guinea highlands cooking and eating *N. pilipes*; Bristowe (1932)



**Figs 7–9.** *7*, *Nephila edulis* (Labillardière), adult female and adult male (m) (WAM T57878) from Albany Highway, just south of Arthur R. Crossing, WA, Australia, with food cache (fc) (photographed by M. S. Harvey); *8*, *N. plumipes* (Latreille), adult female from Pearl Beach, NSW, Australia, feeding (photographed by A. D. Austin); *9*, *N. plumipes*, adult female and adult male (m) from Lord Howe I., Australia (photographed by A. D. Austin). Fig. 9 displays the striking size dimorphism characteristic of all species of the genus.

referred to people in Thailand eating *Nephila* both raw and cooked; and Labillardière (1799) applied the name 'edulis' (meaning 'edible') to *N. edulis* after he observed native people in New Caledonia eating this spider.

Predators and parasitoids of *Nephila* eggs are not common. Egg parasitoids from the wasp family Scelionidae that are obligate endoparasitoids of insect and spider eggs are not known from *Nephila* eggs, nor are the dipteran families Chloropidae and Sarcophagidae that contain several genera associated with preying on the eggs of other orb-weavers (Austin 1985). However, Robinson and Robinson (1976) have recorded larvae of an unknown dipteran from the egg-sacs of *N. pilipes*, as well as predation on egg-sacs by rats in experimental field cages. The only well documented natural enemy is the larva of the moth *Anatrachyntis terminella* (Walker), which preys on the eggs of *N. plumipes* on the central coast of New South Wales (Austin 1977). This species has been recorded from 80% of egg-sacs and causes on average 60% egg mortality. Moore (1977) recorded a mantispid (Neuroptera) preying on the egg-sacs of *N. clavipes* in Texas, with the unidentified species being responsible for ~18% egg mortality.

## Allozyme analysis of Australasian *Nephila*

The 31 enzymes or non-enzymatic proteins surveyed were encoded by 37 putative allozyme loci. Allozyme profiles at these 37 loci are presented in Table 2 for each of the 60 spiders screened. No site displayed any evidence of deviation from the general expectations for a single population in Hardy-Weinberg equilibrium, and thus each site can be used to represent a single population of a single species.

As each of the six phenetic or phylogenetic analyses undertaken (i.e. UPGMA, neighbour-joining, and Fitch-Margoliash on both % FDs and Nei Ds) produced networks with the same basic topological relationships among populations, any one analysis is suitable for summarising the genetic relationships amongst the 16 population examined. We have therefore chosen to present the UPGMA tree (owing to the lack of an outgroup) based on % FD values (being particularly suited to an examination of species boundaries, see Richardson *et al*. 1986). This analysis is displayed in Figure 11.

Four major genetic groupings are present, each diagnosable by the presence of numerous fixed differences. *Nephila pilipes* was quite distinct from all other taxa, exhibiting diagnostic differences at over 80% of the loci sampled. The remaining sites fell tightly into groups referable to *N. edulis*, *N. plumipes* or *N. tetragnathoides*. Within this lineage, the primary dichotomy occurs between *N. edulis* and the two other species that differ at an average of ~33% FD (equal to 12 diagnostic differences). *Nephila tetragnathoides* and *N. plumipes* differ on average at 15% of the loci examined (i.e. 5–6 fixed differences). This level of divergence contrasts markedly with the maximum level encountered for any within-species comparison. With one exception, no fixed differences were present between sites in either *N. plumipes* or *N. edulis*. The single exception was the Lord Howe I. population of *N. plumipes*, which displayed a single fixed difference from each of the three mainland Australian sites at *Pgm* (Table 3).

The small sample sizes per site used in this study preclude any detailed analysis of population substructuring within individual species. Nevertheless, pairwise comparisons of individual sites within both *N. plumipes* and *N. edulis* do reveal some general trends worthy of note. Table 3 lists those loci that display statistically significant heterogeneity between sites. Within *N. plumipes*, the Lord Howe I. population differed significantly from each mainland site at two loci. None of the mainland sites were significantly different from one another, and indeed, none of the 'common' allozymes (i.e. with an overall frequency of >20%) were confined to only one site. Within *N. edulis*, comparisons of individual sites reveal marginally significant heterogeneity between some sites at the locus *PepA* (Table 2). This heterogeneity results from the presence or absence of the $PepA^c$, an allele detected only at the Western Australian sites. Further comparison between the pooled Western Australian sites *v.* the remaining sites pooled indicates the two groups displayed a highly significantly difference at this locus ($\chi^2 = 8.74$, $P < 0.001$). This subdivision between a Western Australian group and the rest was not supported by statistical comparisons at any of the other 24 polymorphic loci.

### Discussion

The allozyme data presented here strongly support the recognition of the four species of *Nephila* studied electrophoretically. *Nephila pilipes* is extremely distinct from the remaining species (80% FD), and brings into question the generic position of the remaining species. Other animal groups with an FD level of 80% are often treated in separate genera. However, we refrain from dividing *Nephila* into two or more genera until further revisionary work has been undertaken on other members of the genus and a detailed phylogeny has been derived.

The remaining species treated in the allozyme analysis, *N. plumipes*, *N. tetragnathoides* and *N. edulis*, appear to be more similar, which is reflected in their morphology (see below).

*Nephila tetragnathoides* differs from *N. plumipes* at 15% FD. It could of course be argued that the two taxa represent divergent populations of the same species, as such levels of genetic distance are sometimes found within a species (Richardson *et al*. 1986). Two factors mitigate against such a conclusion. The first is theoretical: the dispersal ability of *Nephila* (e.g. its current distribution) suggests that gene flow should be possible between the two populations over time. The second is observational: populations of both *N. plumipes* and *N. edulis* that are widely separated (up to or greater than 2000 km apart) show little or no genetic divergence (Fig. 11). The key to fully resolving the taxonomic status of *N. tetragnathoides* lies in an allozyme examination of *Nephila* on the other Pacific islands from which the two species have been recorded (Fig. 46), or a thorough molecular phylogeny of the group.

Allozyme data also suggest that little population substructuring occurs within either *N. plumipes* or *N. edulis*. The Lord Howe I. population of *N. plumipes* was significantly different from those on the mainland at two of the seven polymorphic loci in this species. No evidence was found that genetic divergence existed amongst the three mainland populations of *N. plumipes*, and only one locus of the 25 found to be polymorphic in *N. edulis* supported a subdivision into 'western' and 'central/eastern' subpopulations. Thus, the genetic data support the notion that immature *Nephila* are capable of rapid and long-

**Table 2. Allozyme profiles for the 60 specimens of *Nephila* examined in this study**

A dash indicates that the locus was either not expressed in this species or was not scorable in this animal owing to poor isozyme activity. Code for loci: 1, *Acon-1*; 2, *Acon-2*; 3, *Acp-1*; 4, *Acp-2*; 5, *Ak*; 6, *Ald*; 7, *Argk*; 8, *Enol*; 9, *Est*; 10, *Fdp-1*; 11, *Fdp-2*; 12, *Fum*; 13, *Gapd*; 14, *Got-1*; 15, *Got-2*; 16, *Gp-1*; 17, *Gp-2*; 18, *G6pd*; 19, *Gpd*; 20, *Gpi*; 21, *Hk*; 22, *Idh*; 23, *Ldh*; 24, *Mdh-1*; 25, *Mdh-2*; 26, *Me*; 27, *Mpi*; 28, *Ndpk*; 29, *PepA*; 30, *PepB*; 31, *PepD*; 32, *PepS*; 33, *Pgam*; 34, *Pgk*; 35, *Pgm*; 36, *Pk*; 37, *Tpi*.

| Taxon | Population | Locus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 |
| *Nephila pilipes* | M | b | e | ac | a | b | b | c | d | c | a | b | c | a | c | b | – | a | d | d | a | a | b | cd | c | a | b | f | a | a | b | d | a | c | b | e | c | a |
| | M | b | e | c | a | b | b | c | d | c | a | b | c | a | c | b | – | a | d | d | a | a | b | cd | c | a | b | f | a | a | b | d | a | c | b | e | c | a |
| *Nephila tetragnathoides* | F | c | d | c | b | a | a | b | a | b | a | a | b | a | b | c | a | b | b | b | b | b | a | b | b | a | a | b | b | d | a | cd | b | c | b | f | b | d |
| | F | cd | de | c | b | a | a | b | a | b | a | a | b | a | b | c | a | b | b | b | b | b | a | b | b | a | a | b | b | d | a | cd | b | c | b | f | b | d |
| | F | cd | d | c | b | a | a | b | a | b | a | a | b | a | b | c | a | b | b | b | b | b | a | b | b | a | a | b | b | d | a | d | b | c | b | f | b | d |
| | F | c | d | c | b | a | a | b | a | b | a | a | b | a | b | c | a | b | b | b | b | b | a | b | b | a | a | b | b | d | a | d | b | c | b | f | b | d |
| | F | c | d | c | b | a | a | b | a | b | a | a | b | a | b | c | a | b | b | b | b | b | a | b | b | a | a | b | b | d | a | d | b | c | b | f | b | d |
| *Nephila plumipes* | H | c | de | d | b | a | a | b | a | ab | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | a | b | b | a | d | b | bc | b | cf | b | b |
| | H | c | d | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | a | b | b | a | d | b | b | b | cf | b | b |
| | H | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | bc | b | cf | b | b |
| | H | c | ce | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | a | b | b | a | d | b | b | b | f | b | b |
| *Nephila plumipes* | P1 | c | de | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | bd | bd | b | b |
| | P1 | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | bd | b | b |
| | P1 | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | bd | b | b |
| *Nephila plumipes* | P2 | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | cd | b | b | a | b | b | a | a | a | b | b | a | d | b | c | b | b | b | b |
| | P2 | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | b | b | b |
| | P2 | c | e | d | b | a | a | b | a | bd | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | bd | b | b |
| *Nephila plumipes* | P3 | c | de | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | b | b | b |
| | P3 | c | de | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | b | c | b | b | b | be |
| | P3 | c | e | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | b | b | b | a | d | b | c | b | b | b | b |
| | P3 | c | de | d | b | a | a | b | a | b | a | a | b | a | b | c | a | b | c | d | b | b | a | b | b | a | a | ab | b | b | a | d | bc | c | b | bd | b | b |
| *Nephila edulis* | E1 | a | cd | d | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | cd | a | b | b | b | b | b | b | c |
| | E1 | a | ac | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E1 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | a | a | a | ae | b | d | a | b | b | b | b | b | b | c |
| | E1 | a | c | d | b | a | a | a | c | b | a | a | b | a | ab | b | b | b | a | b | c | b | a | ab | b | a | a | c | b | cd | a | b | b | b | b | b | b | c |
| | E1 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | a | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | bc | b | b | c |
| | E1 | a | c | d | b | a | a | a | c | b | a | a | ab | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E2 | a | c | d | b | a | a | a | c | ab | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | bc | b | d | a | b | b | ab | b | b | b | c |
| | E2 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | c | a | b | b | b | b | b | b | c |
| | E2 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | bc | a | a | c | b | cd | a | b | b | b | b | b | b | c |
| | E2 | a | c | d | b | a | a | a | ac | a | a | a | b | a | b | b | ab | b | a | b | c | b | a | b | b | a | a | ac | b | cd | a | b | b | bc | b | b | b | c |
| | E3 | a | bc | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E3 | a | c | d | b | a | a | a | c | b | ab | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | cd | a | b | b | b | b | b | b | c |
| | E3 | a | c | d | b | a | a | a | c | b | a | a | b | a | ab | b | b | b | a | b | c | b | a | ab | b | a | a | c | b | cd | a | b | bc | ab | b | b | b | c |
| | E4 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E4 | a | c | d | b | a | a | a | c | b | ab | a | b | a | b | a | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E4 | a | cd | d | b | a | a | a | bc | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | bc | b | b | b | b | c |
| | E4 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E5 | a | c | d | b | a | a | a | c | b | a | a | b | a | ab | b | b | b | a | b | c | b | a | ab | b | a | a | ac | b | cd | a | b | b | b | b | b | b | c |
| | E5 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | cd | a | b | bc | b | b | b | b | c |

(*continued next page*)

**Table 2.** (continued)

| Taxon | Population | Locus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 |
| | E5 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | ce | b | cd | a | b | bc | b | b | ab | b | c |
| | E5 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | cd | b | a | b | b | a | a | ce | b | c | a | b | bc | b | b | b | b | c |
| | E6 | a | c | bd | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | ab | b | b | b | b | b | c |
| | E6 | a | cd | d | b | a | a | a | c | b | a | a | b | a | b | a | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | ab | b | b | b | b | b | c |
| | E6 | a | c | d | b | a | a | a | c | b | a | a | bc | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | cd | a | b | b | b | b | b | b | c |
| | E6 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | ae | b | d | a | b | b | b | b | b | b | c |
| | E7 | a | c | d | b | a | a | a | c | ab | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | bc | b | d | a | b | b | b | b | b | ab | c |
| | E7 | a | c | d | b | a | a | a | c | bd | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | ab | b | c |
| | E7 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | bc | a | b | b | a | a | cd | b | d | a | b | b | b | b | b | b | c |
| | E8 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | ab | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E8 | a | c | d | b | ab | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | ac | b | d | a | b | b | bd | ab | b | b | c |
| | E8 | a | cd | d | b | a | a | a | c | b | a | a | b | ab | ab | b | b | b | a | b | c | b | a | ab | b | ab | a | c | b | d | a | b | b | b | b | b | b | c |
| | E9 | a | d | d | b | a | a | a | c | bd | a | a | b | ab | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E9 | a | cd | d | b | a | a | a | c | b | a | a | b | a | b | ab | b | b | a | b | c | b | a | b | b | a | a | ce | b | d | a | b | b | b | b | b | b | c |
| | E9 | a | cd | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | bc | b | d | a | b | bc | b | b | b | b | c |
| | E9 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | ce | b | d | a | b | b | ab | b | b | b | c |
| | E10 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | ae | b | d | a | b | b | b | b | b | b | c |
| | E10 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E10 | a | c | d | b | a | a | a | c | b | a | a | b | a | b | b | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |
| | E10 | a | c | d | b | a | a | a | c | bd | ab | a | b | – | b | ad | b | b | a | b | c | b | a | b | b | a | a | c | b | d | a | b | b | b | b | b | b | c |

**Table 3. Summary of loci displaying significant heterogeneity following pairwise comparisons of sites for allele frequencies**

In each case, Fisher's exact probabilities were calculated from 2 × 2 contingency tables derived from Table 2. Probability values less than 0.05 are shown, although it is recognised that the number of pairwise comparisons made for *N. edulis* would require $P < 0.01$ for a strict statistical analysis of this species

| Species | Sites compared | No. of variable loci | Significant loci |
|---|---|---|---|
| *N. plumipes* | H *v*. P3 | 7 | *Pgam* ($P = 0.007$); *Pgm* ($P = 0.001$) |
| | H *v*. P1 | 6 | *Pgam* ($P = 0.010$); *Pgm* ($P = 0.000$) |
| | H *v*. P2 | 6 | *Pgam* ($P = 0.010$); *Pgm* ($P = 0.000$) |
| | All others | 6–7 | None |
| *N. edulis* | E4 *v*. E5 | 11 | *PepA* ($P = 0.026$) |
| | E5 *v*. E7 | 10 | *PepA* ($P = 0.031$) |
| | E5 *v*. E8 | 15 | *PepA* ($P = 0.031$) |
| | E5 *v*. E9 | 12 | *PepA* ($P = 0.026$) |
| | E5 *v*. E10 | 10 | *PepA* ($P = 0.026$) |
| | All others | 6–16 | None |

range dispersal. Nevertheless, the allozyme data demonstrate that both *N. edulis* and *N. plumipes* are not panmictic throughout their entire range, indicating that whatever gene flow occurs over the medium to long-term is not always able to fully counter the short-term effects of genetic divergence and/or genetic drift.

Interestingly, a recent phylogeographic study of *N. pilipes* using sequence data from the COI gene (Su *et al*. 2007) showed little genetic structure among populations from Okinawa to Bali, but that more recognisable clades were evident for populations on the periphery of the species' distribution including from north-east Australia and India.

## Taxonomy and distribution

### Family **NEPHILIDAE** Simon

#### *Remarks*

As discussed by Hormiga *et al*. (1995), Kuntner (2002), Kuntner and Hormiga (2002) and Kuntner *et al*. (in review), the Nephilidae was first recognised by Simon (1894: p. 749, as Nephileae) who included the genera *Phonognatha* Simon, *Singotypa* Simon, *Deliochus* Simon, *Nephila* (along with *Nephilengys* L. Koch), *Clitaetra* Simon and *Herennia* Thorell. The genera *Perilla* Thorell and *Singafrotypa* Benoit were later added to the Nephilinae by Roewer (1942) and Benoit (1962),

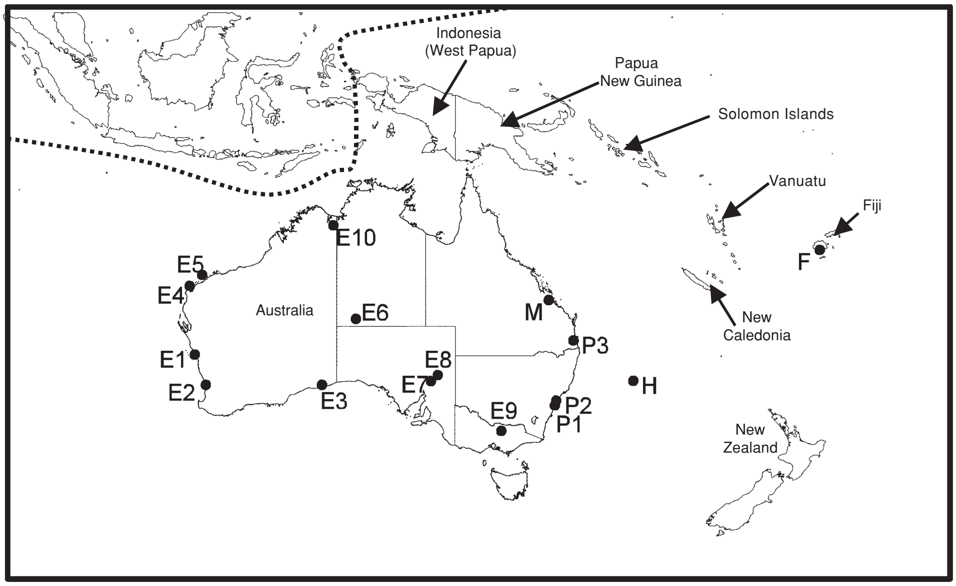


**Fig. 10.** Map showing extent of study region, and depicting the 16 populations of *Nephila* utilised in the genetic study.

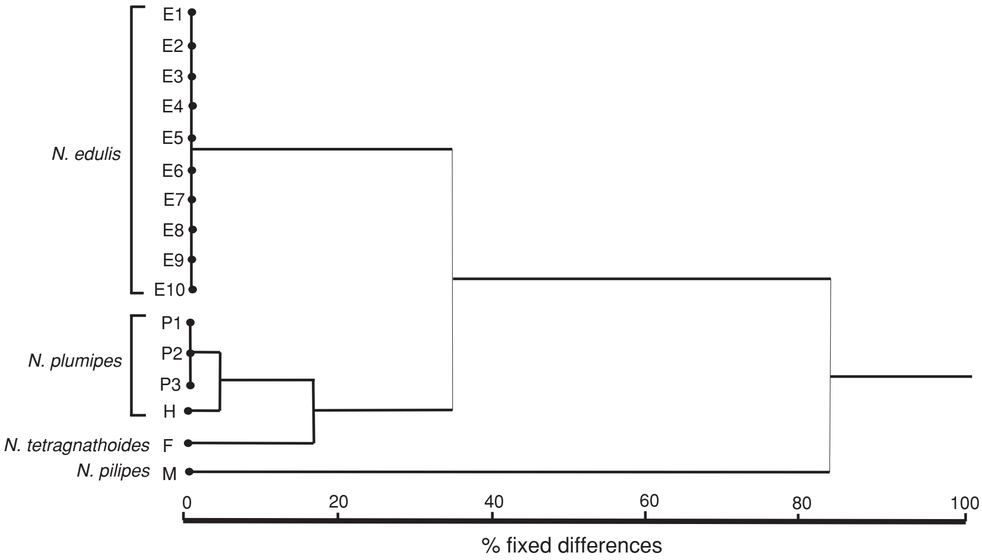


**Fig. 11.** Phenogram depicting the genetic relationships amongst the 16 populations of *Nephila* sampled.

respectively, but both have been recently transferred to the Araneidae by Kuntner (2002) and Kuntner and Hormiga (2002). The genus *Singotypa* was rendered a synonym of *Phonognatha* by Dondale (1966).

The systematic position of these spiders has wavered. They have been traditionally regarded as members of the family Araneidae or the synonymous Argiopidae (Simon 1894), but were specifically included in the Tetragnathidae by Levi and von Eickstedt (1989). Recent analyses (e.g. Hormiga *et al.* 1995; Griswold *et al.* 1998) have also placed them as members of the Tetragnathidae where they lie as the sister-group to the remaining tetragnathids. Pan *et al.* (2004) once again refer *Nephila* and their relatives to the Araneidae, but detailed morphological research has found *Nephila* and its relatives to lie outside of the Tetragnathidae (Alvarez-Padilla 2007), and Kuntner (2005, 2006, 2007) and Kuntner *et al.* (in press) have recognised the family Nephilidae. We follow this decision and herein refer *Nephila* to the Nephilidae.

The systematic position of the Australian genera *Deliochus* and *Phonognatha* appear to lie with the Araneidae, and in a forthcoming review (Kuntner *et al.* in press), will be removed from the Nephilidae.

## Genus ***Nephila*** Leach

*Nephila* Leach, 1815: 133. Type species: *Aranea maculata* Fabricius, 1793 (junior homonym of *Aranea maculata* Olivier, 1789, replaced by the next available name *Aranea pilipes* Fabricius, 1793), by monotypy.

*Nephila* (*Chondronephila*) Dahl, 1911: 275. Type species: none designated (species included: *Nephila fenestrata* Thorell, 1859 and *Nephila turneri* Blackwall, 1833).

*Nephila* (*Poecilonephila*) Dahl, 1911: 275. Type species: *Nephila constricta* Karsch, 1879, by monotypy.

*Nephila* (*Cyphonephila*) Dahl, 1911: 275. Type species: none designated (species included: *Aranea plumipes* Latreille, 1804, *Epeira tetragnathoides* Walckenaer, 1842, *Epeira* (*Nephila*) *imperialis* Doleschall, 1857, *Nephila wallacei* Thorell, 1877 and *Epeira antipodiana* Walckenaer, 1842).

*Nephila* (*Zeugonephila*) Dahl, 1911: 276. Type species: none designated (species included: *Epeira madagascariensis* Vinson, 1863 and *Epeira inaurata* Walckenaer, 1842).

*Nephila* (*Lionephila*) Dahl, 1911: 276. Type species: none designated (species included: *Nephila sumptuosa* Gerstäcker, 1873, *Epeira senegalensis* Walckenaer, 1842, *Nephila bragantina* Brito Capello, 1867 (as subspecies of *N. senegalensis*), *Nephila keyserlingii* Blackwall, 1865 (as subspecies of *N. senegalensis*), *Nephila annulata* Thorell, 1859 (as subspecies of *N. senegalensis*) and *Aranea edulis* Labillardière, 1799).

*Nephila* (*Trichonephila*) Dahl, 1911: 72–73. Type species: none designated (species included: *Nephila clavata* L. Koch, 1878 and *Aranea clavipes* Linnaeus, 1767).

*Nephila* (*Dasynephila*) Dahl, 1912: 63–65. Type species: *Nephila fenestrata* Thorell, 1859, by monotypy.

*Nephila* (*Nothonephila*) Archer, 1958: 3. Type species: *Aranea cornuta* Pallas, 1772, by monotypy.

### Diagnosis

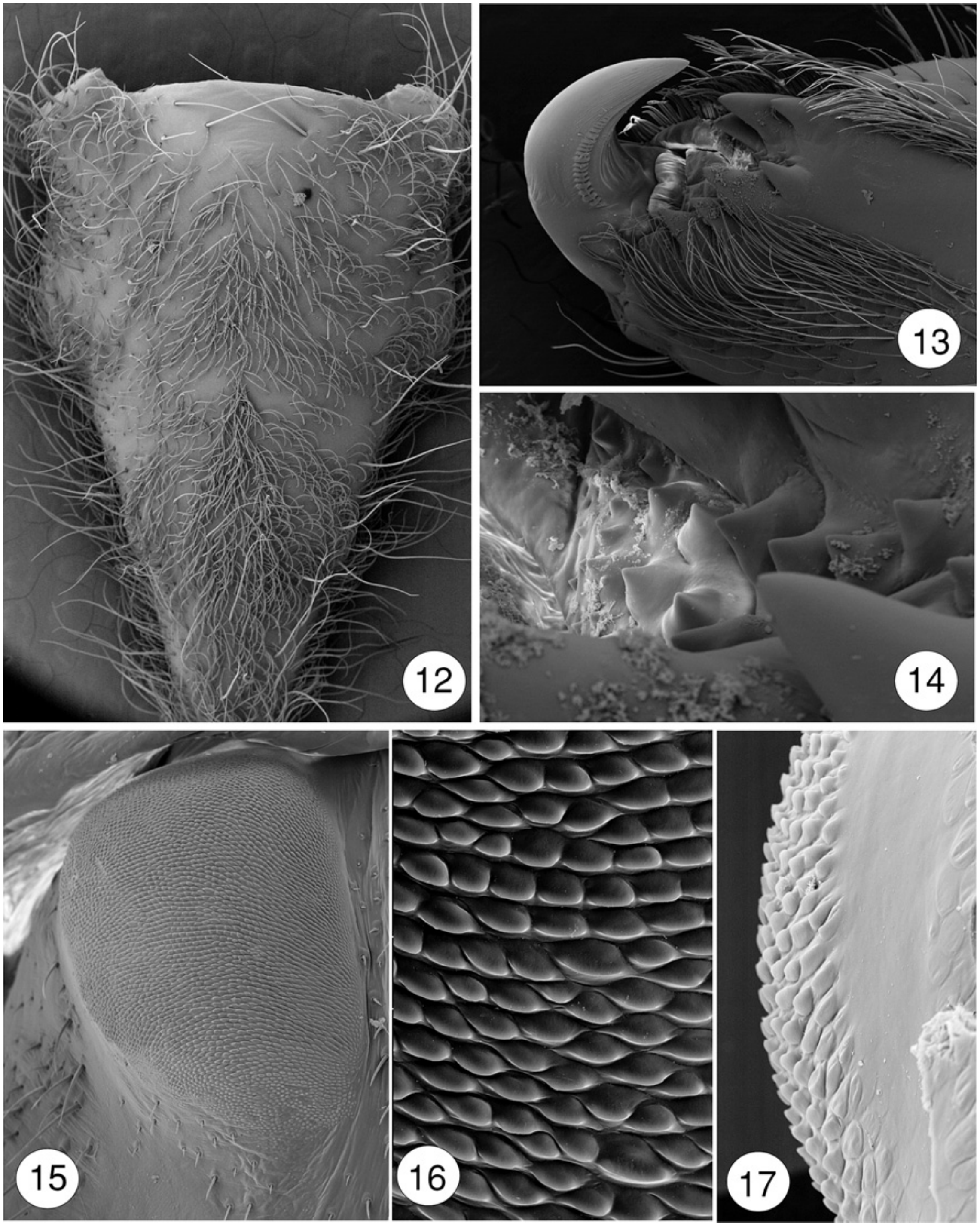
Adult *Nephila* differ from other nephilids by the following combination of characters: lateral eyes nearly contiguous, and situated on a small tubercle (at least in females) (e.g. Fig. 21); sexual dimorphism pronounced, with males considerably smaller than females (Figs 3, 6, 7, 9); males with an extremely long conductor that encloses an equally long embolus (Figs 18, 25, 26, 39, 40, 53, 54, 66, 67, 80, 81); male abdomen with dorsal scute; secondary eyes with tapetum. Females and juveniles of all Australasian species except *N. pilipes* possess tibial setal tufts, thus presenting a plumose appearance (Fig. 7); abdomen without lobes or a flattened abdomen (Figs 1–9, 22–24, 36–38, 50–52, 63–65, 77–79).

### Description

A full description of all members of the genus was beyond the scope of this study, as we have only examined five *Nephila* species.

### *Remarks*

The genus *Nephila* has been well defined and segregated from similar genera by several authors (e.g. Dahl 1912; Coddington 1990; Hormiga *et al*. 1995; Kuntner 2005, 2006; Kuntner *et al*. in review) and belongs to the family Nephilidae along with *Clitaetra* Simon, *Deliochus* Simon, *Herennia* Thorell, *Nephilengys* L. Koch and *Phonognatha* Simon (Simon 1894; Hormiga *et al*. 1995). Hormiga *et al*. (1995) have shown that *Nephila* forms the sister-group to *Herennia* + *Nephilengys*; all three then form the sister-group to *Clitaetra*, which is turn



**Figs 12–17.** *Nephila edulis* (Labillardière), female (unless stated otherwise) from Barrow I., WA, Australia, scanning electron micrographs: *12*, sternum, ventral; *13*, cheliceral fang and furrow; *14*, detail of cheliceral furrow; *15*, cheliceral boss, lateral; *16*, detail of cheliceral boss; *17*, cheliceral boss, male.

forms the sister-group to *Phonognatha*. *Nephila* spp. differ from all other nephilids, except *Clitaetra* (see *Diagnosis*), by the morphology of the male pedipalp in which the conductor is long and slender and completely encloses the similarly long and slender embolus (Figs 18, 25, 26, 39, 40, 53, 54, 66, 67, 80, 81).

### The Australasian fauna

A bewildering array of species-group names have been applied to the genus *Nephila*, and the synonymies of some species are probably the longest of any spider taxa. Five species are here recognised within the Australasian fauna, *N. pilipes*, *N. plumipes*, *N. tetragnathoides*, *N. antipodiana* and *N. edulis*, of which *N. pilipes*, *N. plumipes* and *N. antipodiana* have also been recorded outside of the study area. *Nephila vitiana* (Walckenaer) has been reported from within the study area, but we here present evidence that they represent material based upon mislabelled specimens.

*Nephila vitiana* (*Walckenaer*). Walckenaer (1847) described *Epeira vitiana* from a single female collected from 'l'île Viti' in the 'Iles Salomon', which was later recognised as the senior synonym of *N. wallacei* Thorell, 1877 and *N. piepersii* Thorell, 1877 by Dahl (1912), presumably on the basis of Walckenaer's description of the sternum as 'brune', rather than 'noire' as described for other species of *Nephila*. Dahl (1912) reduced the known range to Sulawesi (Celebes) and Timor. The senior author could not locate any specimens in MNHN that could be reasonably suspected as type material of *E. vitiana*, and there are no specimens present in the collections listed above from the region currently under study. It is therefore excluded from this revision. The extensive collections of *Nephila* spp. from the Solomon Is that are available to us have failed to produce a single specimen of *N. vitiana*, and it seems likely that Walckenaer's material was mislabelled. Nevertheless, the presence of a red-brown sternum easily distinguishes *N. vitiana* from other members of the *N. antipodiana* species-group (Dahl 1912), and we have examined specimens from near Benoa Harbour, Bali, Indonesia (WAM 90/605–606, 92/537–538, 92/539, 88/844–846), from Sulawesi (ZMB 25294, ZMB 198) and from Timor (ZMB 25295) that are clearly referrable to this species.

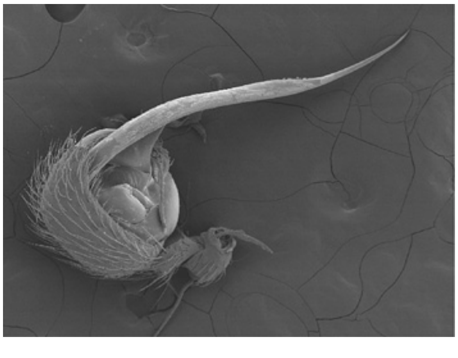


**Fig. 18.** *Nephila edulis* (Labillardière), male from Barrow I., WA, Australia, scanning electron micrograph, pedipalp, mesal view.

## Key to species of *Nephila* from the Australasian region

*Females*

1. Sternum with conspicuous conical tubercle near anterior margin, and with five other smaller tubercles on lateral margins . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
   Sternum without tubercles, or with very small tubercles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

2(1). Abdomen at least twice as long as wide (Figs 63, 64); sternum black or dark brown, with small red or yellow spots on antero-lateral corners, and on tubercles II and III . . . . . . . . . . . . . *Nephila antipodiana* (Walckenaer)
   Abdomen less than twice as long as wide (Figs 36, 37, 50, 51); sternum with distinct yellow pattern . . . . . . . . . 3

3(2). Carapaceal tubercles usually large (Fig. 35); ventral surface of abdomen usually without distinctive white patch (Fig. 37) . . . . . . . . *Nephila plumipes* (Latreille)
   Carapaceal tubercles very small, sometimes absent (Fig. 49); ventral surface of abdomen with distinctive white patch (Fig. 51) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Nephila tetragnathoides* (Walckenaer)

4(1). Sternum entirely black (Fig. 20), or occasionally with yellow spots; carapaceal tubercles absent (Fig. 21); basal segments of pedipalps bright red (in life, Figs 1, 2, 4) or yellow (in ethanol); carapace much shorter than tibia IV (Fig. 1). . . . . *Nephila pilipes* (Fabricius)
   Sternum with large areas of yellow (Fig. 75); carapaceal tubercles large (Fig. 76); basal segments of pedipalps dark-brown; carapace same length as or longer than tibia IV (Fig. 7) . . . . . . *Nephila edulis* (Labillardière)

*Males*

1. Conductor with subdistal triangular protuberance (Figs 39–40, 53–55). . . . *Nephila plumipes* (Latreille) . . . . . . . . . and *Nephila tetragnathoides* (Walckenaer) . . . . . . (males are morphologically indistinguishable)
   Conductor without subdistal triangular protuberance (Figs 25–27, 66–68, 80–82) . . . . . . . . . . . . . . . . . . . 2

2(1). Conductor straight and long, about twice as long as bulb (Figs 25, 26) . . . . . . . . . . . *Nephila pilipes* (Fabricius)
   Conductor slightly curved and only slightly longer than bulb (Figs 66, 67, 80, 81). . . . . . . . . . . *Nephila edulis* . . . . . . . . . . (Labillardière) and *Nephila antipodiana* . . . . . . . . . (Walckenaer) (males are morphologically . . . . . . . . . . . . . . . . . . . . . . . . . . indistinguishable)

## ***Nephila pilipes*** (Fabricius)
### Giant golden orb-weaving spider

(Figs 1, 2, 4, 5, 19–32)

*Aranea longipes* Fabricius, 1781: 545–546 (junior primary homonym of *Aranea longipes* Fuesslin, 1775).

*Aranea maculata* Fabricius, 1793: 425 (junior primary homonym of *Aranea maculata* Olivier, 1789).

*Aranea pilipes* Fabricius, 1793: 425.

*Epeira chrysogaster* Walckenaer, 1805: 53–54.

*Epeira sebae* Walckenaer, 1805: 55.

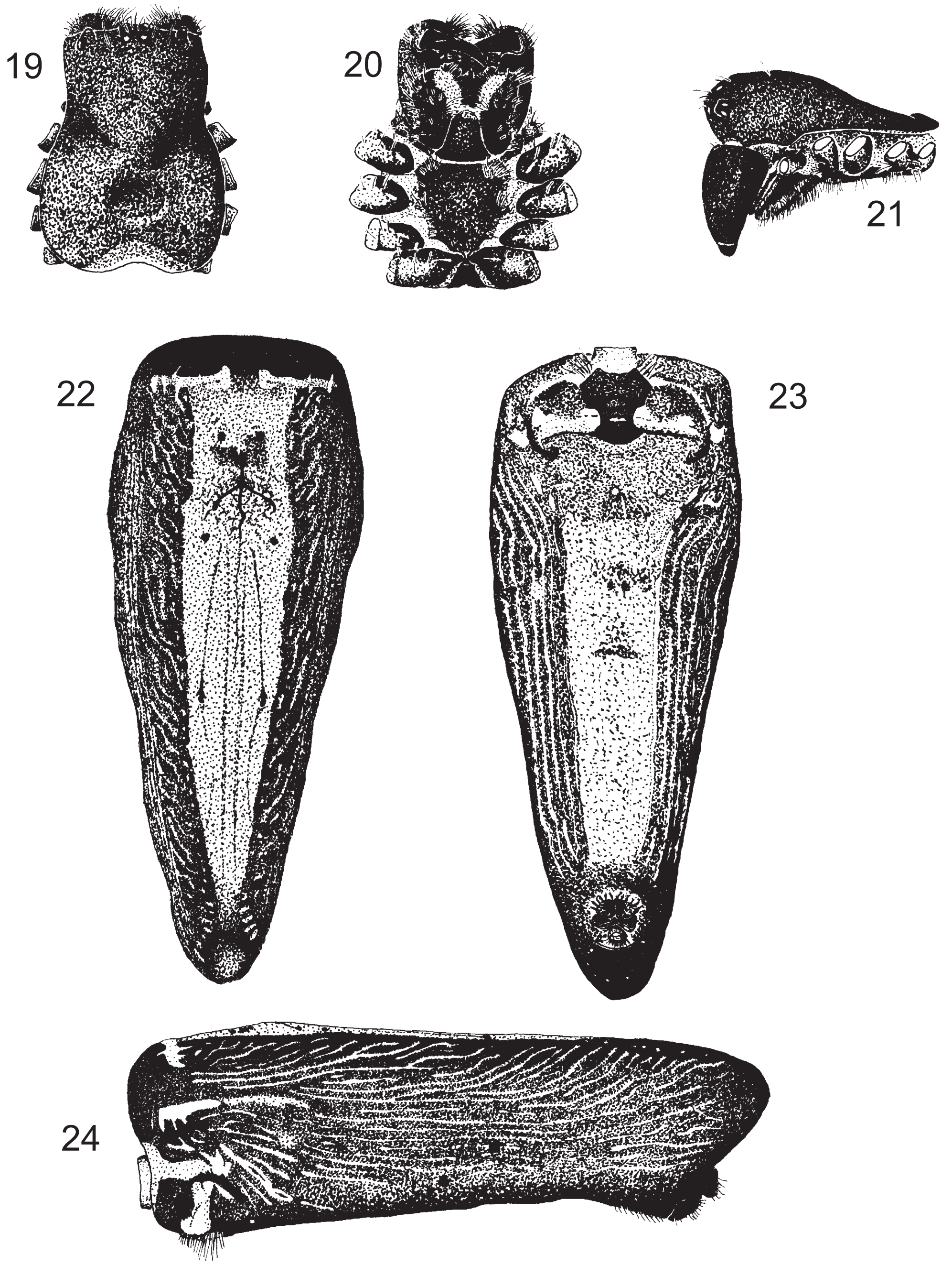
*Nephila fuscipes* C. L. Koch, 1839: 136–138, fig. 528.

*Epeira caliginosa* Walckenaer, 1842: 100.

*Epeira doreyana* Walckenaer, 1842: 100.

*Nephila ornata* Adams, 1847: 291.

*Epeira* (*Nephila*) *walckenaeri* Doleschall, 1857: 412. **New synonymy**.
*Epeira* (*Nephila*) *penicillum* Doleschall, 1857: 413.
*Epeira* (*Nephila*) *hasseltii* Doleschall, 1859: 27–28, plate 13, fig. 5. **New synonymy**.
*Epeira* (*Nephila*) *harpyia* Doleschall, 1859: 28, plate 14, fig. 1.
*Meta ornata* L. Koch, 1872: 134, plate 11, fig. 6.
*Nephila pecuniosa* L. Koch, 1872: 157–159, plate 13, fig. 2.
*Nephila aurosa* L. Koch, 1872: 160–162, plate 13, fig. 4.
*Nephila procera* L. Koch, 1872: 162–163, plate 14, fig. 1.
*Nephila sulphurosa* L. Koch, 1872: 163–165, plate 14, fig. 2.
*Nephila tenuipes* L. Koch, 1872: 165–166, plate 13, figs 5, 5*a*.
*Nephila maculata* var. *annulipes* Thorell, 1881: 146. **New synonymy**.
*Nephila maculata jalorensis* Simon, 1901: 58. **New synonymy**.
*Nephila maculata* var. *novae-guineae* Strand, 1906*a*: 261–262. **New synonymy**.
*Nephila pictithorax* Kulczyński, 1911: 469–470, fig. 40. **New synonymy**.
*Nephila maculata* var. *flavornata* Merian, 1911: 195–196. **New synonymy**.
*Nephila maculata piscatorum* de Vis, 1911: 167–168. **New synonymy**.



**Figs 19–24.** *Nephila pilipes* (Fabricius), female from Cahills Crossing, Kakadu Natl Park, NT, Australia (WAM 97/2946): *19*, cephalothorax, dorsal; *20*, cephalothorax, ventral; *21*, cephalothorax, lateral; *22*, abdomen, dorsal; *23*, abdomen, ventral; *24*, abdomen, lateral.

*Nephila* (*Nephila*) *maculata* var. *lauterbachi* Dahl, 1912: 53. **New synonymy**.

### Type material

*Type*(*s*) *of Aranea longipes*. Australasia ('Dom. Banks', depository unknown, not examined).

*Type*(*s*) *of Aranea maculata*. China (depository unknown, not examined).

*Type*(*s*) *of Aranea pilipes*. East Indies ('Dom. Lund.', depository unknown, not examined).

*Type*(*s*) *of Epeira chrysogaster*. East Indies (not found in MNHN, not examined).

*Type*(*s*) *of Epeira sebae*. East Indies (not found in MNHN, not examined).

*Type*(*s*) *of Nephila fuscipes*. No locality (depository unknown, not examined).

*Type*(*s*) *of Epeira caliginosa*. Guam (13°27′N, 144°45′E) (not found in MNHN, not examined).

*Type*(*s*) *of Epeira doreyana*. Port de Dorey (= Teluk Doreh, 0°55′S, 134°04′E), West Papua, Indonesia (not found in MNHN, not examined).

*Type*(*s*) *of Nephila ornata*. Singapore (1°17′N, 103°51′E) (probably lost, not examined).

*Syntypes of Epeira* (*Nephila*) *walckenaerii*. Numerous ♀, Ambon (as Amboina), Maluku, Indonesia (3°35′S, 128°20′E) (RMNH and NHMW, not examined).

*Syntype of Epeira* (*Nephila*) *penicillum*. 1 juvenile ♀, Ambon (as Amboina), Maluku, Indonesia (3°35′S, 128°20′E) (NHMW, not examined).

*Probable syntypes of Epeira* (*Nephila*) *hasseltii*. 2 ♀, Bogor (as Buitenzorg), Java, Indonesia (6°36′S, 106°48′E) (RMNH, not examined).

*Syntype of Epeira* (*Nephila*) *harpyia*. 1 juvenile ♀, Bogor (as Buitenzorg), Java, Indonesia (6°36′S, 106°48′E) (RMNH, not examined).

*Holotype of Meta ornata*. Juvenile ♀, Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (ZMH).

*Syntypes of Nephila pecuniosa*. Several ♀, Polillo (as 'Pallilo'), Philippines (14°50′N, 121°55′E) (not in ZMH, see Rack (1961); ZMB, BMNH, not examined).

*Type*(*s*) *of Nephila aurosa*. Unknown number of specimens, Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (not found, not examined).

*Syntypes of Nephila procera*. 2 juv. ♀, Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (ZMH, Mus. Godeffroy No. 6500); 1 specimen, Buru, Maluku, Indonesia (3°30′S, 126°30′E) (SMNS, not examined).

*Syntypes of Nephila sulphurosa*. 4 juv. ♀, Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (ZMH, Mus. Godeffroy No. 7207).

*Holotype of Nephila tenuipes*. ♀, Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (ZMH, Mus. Godeffroy No. 6087).

*Holotype of Nephila maculata* var. *annulipes*. ♀, 'Korido ins. Midori' (Korido, West Papua = 0°50′S, 135°35′E), Beccari (probably in MCG, not examined).

*Holotype of Nephila maculata jalorensis*. Subadult ♀, Bukit Besar, Jalor, Malaysia (5°57′N, 100°25′E) (possibly lodged in OUM, but not found by M. Kuntner (in litt.), not examined).

*Holotype of Nephila submaculata*. ♀, Cameroon, Schötz (MWNH, destroyed during World War II, Dr M. Geisthardt, in litt., 5.xi.1996).

*Holotype of Nephila maculata* var. *novaeguineae*. ♀, Bogadjim, Madang Province, Papua New Guinea (5°26′S, 145°44′E), W. Diehl (MWNH, destroyed during World War II, Dr M. Geisthardt, in litt., 5.xi.1996).

*Holotype of Nephila maculata malagassa*. ♀, Madagascar (SMNS, not examined).

*Syntypes of Nephila pictithorax*. 1 ♀, 'Sinum Humboldtii' (= Teluk Humboldt), West Papua, Indonesia (2°30′S, 140°50′E) (not in MZPW, not examined); 1 ♀, 5 juveniles, Moaif, West Papua, Indonesia (2°21′S, 140°03′E), 26.vi.–4.vii.1903 (MZPW).

*Holotype of Nephila maculata* var. *flavornata*. ♀, Macassar (= Ujung Pandang), Sulawesi, Indonesia (5°07′S, 119°24′E), Dec. (18)94 (NMB 600.I).

*Holotype of Nephila maculata piscatorum*. ♀, Dunk Island, Queensland, Australia (17°57′S, 146°09′E), E. J. Banfield (QM W2120).

*Syntypes of Nephila* (*Nephila*) *maculata* var. *lauterbachi*. 1 ♀, 1 juv., Erima, Madang Province, Papua New Guinea (5°24′S, 145°44′E), 7.v.1896, Lauterbach (ZMB 25148, not examined); 1 ♀, 'Holl. New Guinea' (= West Papua, Indonesia), 1911, Moskowski (ZMB 25149, not examined) (data taken from Moritz and Fischer 1986).

### Other material examined

**Australia: Christmas Island:** (WAM 65624, T65624). **New South Wales:** Bellingen (AM KS33591); Coffs Harbour (AM KS2078); Glenreagh (AM KS33500); Murwillumbah district (QM S28998); Repton, Bellingen R. (AM KS33590); Viewmont, Bowraville (AM KS33778). **Northern Territory:** 25 km NE of Mt Cahill (ANIC); 8 miles S of Finis R. on Wangi Station (NTMAG); Adelaide R. (SAM); Angurugu (NTMAG); Baroalba Springs, Kakadu Natl Park (WAM T51502–51505); Berry Springs (NTMAG; WAM T51506–51507); Cahills Crossing, Manngarre Rainforest, Kakadu Natl Park (WAM 97/2945–2946); Darwin (MV K-3333, 3339); Darwin (MV K-3343); Holmes Jungle (NTMAG); Katherine and district (MV K-3334); Melville I. (NTMAG); Mt Gilruth, gorge NE of (QM S28971, S28973); no precise locality (SAM); Palm Jungle, W Dennelli (NTMAG); Radon Ck (QM S28955); Tracumbi Falls, Melville I. (NTMAG); Uptons Gorge, via Koongarra (AM KS44993); West Alligator mouth (QM S28957). **Queensland:** Amos Bay, near Cooktown (QM S28948); Atherton (AM KS33491; SAM); Babinda (QM W1537); Badu I. (QM S33038); Bald Head, Landsborough (QM W1600); Banks (Moa) I. (MV K-3336); Bellenden Ker (SMNH); Bellenden Ker Range, Cableway Base Station (QM S31076); Blue Lagoon, Moreton I. (QM S28951); Bluewater Range (QM S33078); Boonjee (QM S28983); Border Range (QM S28944); Brandy Ck (QM S33096); Broadwater Park, 35 km NW of Ingham (QM S28945); Buderim (QM S28943, S23024); Bulburin State Forest (QM S33091); Burleigh Heads (MV K-3347); Cairns (AM KS33451, KS33498, KS33639; MV K-3337; QM S28889, S42947, S46670); Cairns, Caravan Park (AM KS4672); Cape Hillsborough Natl Park (QM S28975, S28984); Cape Tribulation (QM S28891, S28907); Cape York (QM W1605); Cardwell Range, Mt Macalister (QM S33045); Carlisle I. (QM S28953); Cathu State Forest, Muirs Rd (QM S21649); Clifton Beach (QM S28958); Conway Natl Park (QM S28949, S28993; WAM T41757, 98/1278); Cooktown (MNHN 18827; MV K-3346); Cooloola (QM S33053); Crystal Cascades (QM S28892); Currumbin (ANIC); Dagun Gap, via Imbil (QM S42933); Danbulla State Forest, Danbulla Forest Drive, 3 km by Rd E of Mobo Ck Crater (AM KS52398); Darnley I. (QM S28999, S33036; MCZ); Dunk I. (QM S28893; MCZ); Enoggera, Army Lands (QM S22421); Esk (QM S28981); Eumundi (QM W218); Eurimbula (AM KS250); Finch Hatton (QM S33057); Finch Hatton Gorge, track above Doolamai Falls (QM S40705); Finch Hatton Natl Park (QM S9944); Fitzroy I. (AM KS5081); Freshwater, Cairns (AM KS44465; WAM T51501); Fritz Ck (AM KS445); Gladstone (QM W1966); Goomeri (QM W56); Gordon Ck, Iron Range (QM S28994, S28997); 6 miles (= 10 km) W of Gordonvale (CAS); Green I., Great Barrier Reef (AM KS33569, KS33570); Hayman I. (AM KS33671); Home Rule (QM S33100); Home Rule Falls, Mt Hartley (QM S33093); Ingham (QM S31080); Iron Range (QM S28905, S28956, S28992, S33112); Iron Range, camp at East Claudie R. (AMNH); Junction Ck, Russell R. (AMNH); Kennedy (QM S28895); Kuranda (SAM); Landsborough (QM S28888); Lankelly Ck, Coen (QM S33099, S33103); Lindeman I. (AM KS33804); Lockerbie (QM S28952); Lomond Hill, summit (QM S33111); Mackay (AM KS34062); Maer (as 'Mer'), Murray I. (MCZ); Maroochydore (AM KS17640); McLeod R. crossing near Hwy (AM KS45538, KS45609); Moa I. (QM S33034, S33040); Mossman R. Gorge (AMNH); Mt Abbott (QM S41085); Mt Cleveland (QM S40743); Mt Cook (QM S28985); Mt Dryander (lower slopes) (AM KS311);

Mt Elliot, Mt Woodstock (QM S28990); Mt Finlay (QM S28987); Mt French (QM S42950); Mt Larcom (QM W91, S28894); Mt Molloy (QM S28950, S28995, S28976); Mt Tamborine (CAS); Murray I. (QM S33035, S33037; AM KS33700); Nambour (QM S3627); near 'Trench', Moreton I. (QM S28967); near Kuranda (NTMAG); Newcastle Bay, 2.5 miles S of Somerset (AMNH); Normanby Station (QM S33063); Olsens Caves, near Rockhampton (AM KS33492); Palm I. (QM W110); Paluma (WAM T51517); Percy Isles (QM S42939, S42940); Port Mackay (ZMH 6087, 6500, 7207); Port Stewart, old slab hut (QM S31073); Prince of Wales I. (QM S33039); Rockhampton (QM S28942, S33043; MNHN 44; WAM 95/1271–1272); Russell R. at Bellenden Ker Landing (QM S31077); Searys Scrub, Cooloola Natl Park (QM S28941); Shiptons Flat (QM S28969, S28988); Somerset (SMNH 728; ZMB 25045; QM S28954); Speewah Camp, Clohesy R. (AMNH); Stephens I. (QM S12455); Stone Ck (QM S41624); The Hummock, Mt Hedley (QM S33090); The Hummock, Mt Hedley, Intake Falls (QM S33092); Thunderbird Park, Mt Tamborine (QM S28996); Thursday I. (QM S33042; WAM T41756); Tinaroo Falls (MCZ); Tolga (MV K-3332); Tower Mtn Rd, Nambour (QM S23018); Tozar Gap, Cape York (QM S28947); 'Trench', Moreton I. (QM S28991); Trinity Park (AM KS45505); Tully (QM S28887); 'Tully & Cooktown' (AM KS33494); Twelve Mile Scrub, Gap Ck (QM S28989); Weier I. (QM S33033); Wenlock Crossing, Archer R. (AMNH); Yarrabah (SMNH); Yeppoon (QM S33032; WAM T51516). **Victoria:** Bacchus Marsh, Baker's property (probably mislabelled) (WAM T51637). **Western Australia:** Charnley R., East Walcott Inlet (WAM T51511); Kalumburu (WAM T51508–51509); 4 km W of King Cascade (WAM 97/10); Lone Dingo vine thicket, Mitchell Plateau (WAM T51510); Mt Trafalgar (WAM 97/11–12, T51515); Walcott Inlet (WAM T51512–51514). **Indonesia: West Papua (West Papua):** Ambraideru (RMNH 7608); Betabib (RMNH 7148, 7150); Pulau Biak (RMNH 7144, 7163, 7166); Bokondini, 40 km N of Balim Valley (BPBM); Cyclops Mts (AMNH); Dorey (= Teluk Doreh) (MNHN); Demboke near Kigonmedib (RMNH 7152); Doromena, near Jayapura (as Hollandia) (AMNH); Elles (RMNH 7167); Etna Baai [= Teluk Etna) (RMNH 7141); Grime R., Tussen Borowai en Oranjebrug (RMNH 7168); 'Hollandia and L. Sentani' (AMNH); Ifaar (BPBM); Jayapura (as Hollandia) (AMNH); Katem (RMNH 7161); Kotabaru (RMNH 7615); Legare, Cenderawasih, Teluk (as Geelvinkbaai) (AMNH); Maffin Bay, now Teluk Maffin (CAS); Merauke (RMNH 4942, 8255); Middelburg I. (= Pulau Middelburg) (RMNH 7159); Mindiptana (RMNH 7616, 7157); Moaif (MZPW); Nenei (WAM T51631); Obone, Ifaar (BPBM); Ok Sibil (RMNH 7133, 7138, 7153); Pionier-bivak Aande, Hamberama-rivier (AMNH); Sedorfojo (RMNH 7137); Sentani Danau (as W Sentani), Cyclops Mts (BPBM); Seroei [now Serui), Japen I. (RMNH 7142); Swart Val., W side (now Ilim) (BPBM); Takum, Kamp Hifob (RMNH 7154); Tomerbivak-1 (AMNH); Waris (BPBM). **Papua New Guinea: Central Province:** Agenehambo, 15 miles (= 24 km) E of Popondetta (SAM); Bora Bada (= Porebada) (MV K-3341); Daradai Plantation, near Port Moresby (BPBM); Oidobu, near Mamai Est. (BPBM); Bora Bada (= Porebada) (MV K-3345); Tapini (BPBM); Tapini (BPBM); Vailala R. (AMNH). **Chimbu Province:** Dirima, via Omkdai (MNHN); Kondiu (AMNH); Wimba, Kubor Range (RMNH 7130). **East New Britain Province:** Gaulim (BPBM); Ilugi (Ck), Upper Warangoi, Gazelle Peninsula (BPBM); Keravat (BPBM); Rabaul (MV K-3335); Warangoi V., Gazelle P(eninsula) (BPBM). **East Sepik Province:** Jimmie R., 33 miles NE of Hagen air-strip (AM KS33746); Kairiru I. (AM KS8036, KS7940, AM KS7960). **Eastern Highlands Province:** Arau (AMNH); Goroka town site (WAM T51623–51624); Karimui, S of Goroka (BPBM); Karimui, S of Goroka (BPBM); Wahgi region (AMNH). **Gulf Province:** near Kariava (SAM); **Madang Province:** Aiome, Ramu Valley (AM KS33780); Baiteta (CAS, WAM T51627); Bogadjim (as Stephansort), Astrolabe Bay (AM KS33587, KS33589); Buso R. (QM S31075); NW. Kamba-Veneg village (WAM T51629–51630); Kevasop, Karkar I. (CAS); Madang (BPBM); 25 km N of Madang (MCZ); Maritambu, Adelbert Mts (AMNH); S of Naru (WAM T51628); Nobanob-Mt Hansman (WAM T51622, T51625–51626); Nobonob Hill, 7 km NW of Madang (CAS); Wanuma, Adelbert Mts (BPBM). **Manus Province:** Rossun (BPBM). **Milne Bay Province:** Abaleti, SSW of Mt Rossel, Rossel I. (AMNH); Bolubolu, Goodenough I. (AMNH); Dawadawa (AMNH); Engineers Group, E coast (AM KS33603); Goodenough I. (AMNH); Kiriwina I., now Trobriand I. (AM KS4657, AMNH); Kulumadau, Woodlark I. (AMNH); Menapi, Cape Vogel Peninsula (AMNH); Milne Bay (AMNH); Misima I. (MV K-3340); Modewa, Modewa Bay (AMNH); Mt Sisa, Misima I. (AMNH); N slopes of Mt Misima, Misima I. (AMNH); N slope of Mt Dayman, Maneau Range (AMNH); Narian, Misima I. (AMNH); Waikaiuna, Normanby I. (AMNH); Wakaiuna, Sewa Bay, Normanby I. (BPBM); Woodlark I. (AMNH). **Morobe Province:** Busu R., E of Lae (BPBM); Finschhafen (CAS); *c.* 8 km WNW of Laboratory Laboratory, Umboi I. (BPBM); Lae (SAM); 55 km NW of Lae (as Lea), Highlands Hwy (MCZ); Lasanga I., eastern side (QM S31074); Mt Missim (as Mt Misim) (MCZ); Mt Rawlinson, north slopes, Huon Peninsula (AMNH); Mt Shungol (BPBM); Nadzaba (USNM); Tuwep, Salawaket Range (BPBM); Umboi I. (as Rook I.), Bismarck Archipelago (NMB 600.s, 600 March d, 600 February g); Uni R., camp 14, Markham Valley (AMNH); Wau Ecology Institute grounds (WAM T51621; USNM); Wau (BPBM, MCZ, RMNH 8254, 8256, SAM); Wau, Bishop Museum Field Station (CAS); Wau, Big Wau Ck (CAS). **New Britain Province:** New Britain (MNHN, MNZ). **New Ireland Province:** Fissoa (NMB 600.r); Gilingil Plantation (BPBM); New Ireland (AM KS17045, NMB 600.t, 600 February h, SAM); Tanga (AM KS33777). **Bougainville Province:** Gagan, Buka I. (BPBM); Bougainville (QM W1651); Bougainville I. (AMNH; NMB 600 February f); Buin (AM KS33811; BPBM); Buin, Kangu (BPBM). **Northern Province:** Baiawa, Moi Biri Bay, Collingwood Bay (AMNH); Biniguni Camp, Gwariu R., 1 mile S of Biniguni (AMNH); Mt Lamington District (AM KS33781, KS33786); Oro Bay (AMNH); Papa, Kokoda-Pitoki (BPBM); Peria Ck, Kwagila (as Kwagira) R. (AMNH). **Sandaun Province:** Feramin, NE of Telefomin (BPBM); Telefomin (BPBM). **Southern Highlands Province:** Bosavi (BPBM). **West New Britain Province:** Linga Linga Plantation, W of Willaumez Pon (BPBM); Silanga, Nakanai Mts (BPBM); Ti, Nakanai Mts (BPBM). **Western District Province:** Fly R., 5 miles below Palmer Junction (AMNH); Lake Davimbu, Middle Fly R. (AMNH); Mabaduan (AMNH); Matkomrae village, approx. 50 km N of Kiunga (AM KS44899); Tabubil Natl Park (AM KS45699); Tabubil (AM KS44900). **Western Highlands Province:** Jimi R., Cattle Co. Headquarters (AM KS8255); Kaironk R., Schrader Mts (RMNH 7280); Korn (AM KS33674, KS8243); Nondugl (SMNH); Yaramanda, N slopes of Mt Hagen (MNZ); Yaramanda, W. Baiyer Valley, Hagen Range (RMNH 7282). **Unlocated sites:** Koombangara (BPBM); Rouna (BPBM). **Samoa:** Upolu (RMNH 5369). **Solomon Islands: Florida Island:** Florida I. (AMNH). **Ganongga Island:** Ganongga I. (AMNH). **Guadalcanal Island:** Guadalcanal (AMNH; CAS; MNZ; NMB 600.p, 600 February c); Honiara (AMNH; AM KS35058); Nini Ck, 35 km SSE of Honiara (BPBM); Suta (BPBM); Tenaru R. (BPBM). **Kolombangara:** Iriri (BPBM). **Malaita:** Auiki (BPBM, MCZ); Dala (BPBM); Mbita'ama (as Bita'ama) (AM KS17533); Sinaranggo (= Sinalanggu), Ngarinaasoru (MCZ); 'along coast of North Malaita' (AM KS33595, KS33598, KS33601); 'I. Malaïta' (NMB 600 February e). **New Georgia:** Javae, near Seghe (QM S42954); Kundurumbangara, Vella Lavella (BPBM); Mt Javae, 300 m (QM S42979); Mt Arewana, Vella Lavella (BPBM); Munda (AMNH, BPBM, USNM); Pusisama, Vella Lavella (= Pusuraghi?) (BPBM); Rendova (MCZ); Ulo Crater, Vella Lavella (BPBM). **Russell Islands:** Bycee I., now Marulaon I. (AM KS33586, KS33602, KS33604); Cape Marsh, Karamula I. (AM KS33571–33573); Russell I. (AM KS33499, KS33588, KS33600; AMNH). **San Cristóbal:** Ugi (AM KS33592, KS49707, MCZ); Wai-ai (MCZ); Wainoni Bay (= Wanione Bay (MCZ). **Santa Cruz:** Carlisle Bay (AM KS33805); Vanikoro (AM KS33486–33487). **Santa Isabel:** Buala (BPBM); 'Govt Stn' (AM KS33577-KS33578); 'Ysabel I.' (= Santa Isabel) (AM KS33574, KS33676, KS33806, KS33677). **Savo Island**: Savo I. (MNZ, NMB 600 March d, 600 March e). **Shortland Island:** Fauro I. (AMNH); Maleai (SAM). **Unlocated site:** Howla (AM KS33490). **Vanuatu (New Hebrides): Aneityum:** Aneityum (AMNH); Anelgannat (now Anelghowhat) (BPBM). **Aoba:** Aoba I. (NMB 600.m). **Efate:** Port Vila (MNHN). **Espiritu Santo:** Espiritu Santo (AMNH, WAM T51518–51519);

'Santo', Big Bay (AM KS33794). **Pentecost:** Ile Pentecôte (MNHN, NMB 600.l). **Unlocated site:** Mae (NMB 600.k).

### Diagnosis

Females are easily recognised by the following combination of characters: carapaceal tubercles absent (Fig. 21), sternum uniformly black or very occasionally with large yellow spots and without tubercles (Fig. 20), tibia IV longer than carapace (Fig. 1), and the basal segments of pedipalp bright red (in life, Figs 1, 2) or yellow (in ethanol). Males differ from all other Australasian species by the very long and straight conductor that is about twice as long as bulb (Figs 25, 26).

### Description

#### Female (Australia: NT: Cahills Crossing, Kakadu Natl Park, WAM 97/2946)

*Carapace* (Figs 19, 21). Very dark brown, nearly black, postero-lateral corners with indistinct yellow markings; evenly covered with small, pale setae; fovea a broad depression; dorso-medial horns represented by extremely small rounded protuberances; antero-lateral margins with red-orange crenulated mound that opposes cheliceral boss; chilum present, medially divided.

*Chelicera*. Very dark brown; cheliceral boss covered with tuberculations; fang furrow with three large teeth on anterior furrow (central tooth largest), four large teeth on posterior furrow; cheliceral denticles present between tooth rows.

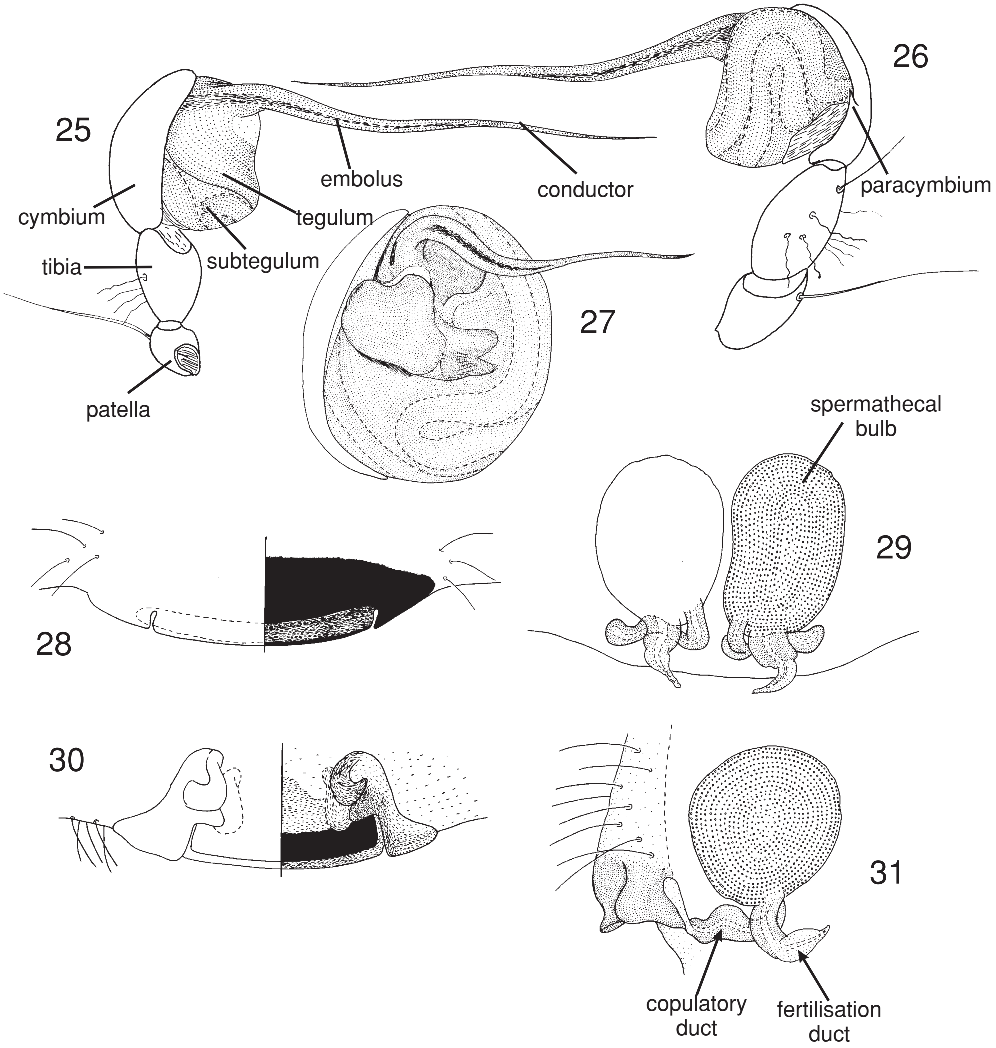
*Maxilla.* Dark brown.

*Labium*. Black; much longer than broad, anteriorly rounded.

*Pedipalp*. Trochanter, femur, patella and tibia yellow-brown (red in life, Figs 1, 2); tarsus dark brown.

*Sternum* (Fig. 20). Black; cordate, extending between coxae IV; smooth, except for small, glabrous protuberances adjacent to coxae I, II and III.

*Legs*. Coxae black mesally, dark brown on all other lateral margins, yellow-brown centrally; all other segments very dark



**Figs 25–31.** *Nephila pilipes* (Fabricius) from Cahills Crossing, Kakadu Natl Park, NT, Australia (WAM 97/2945–2946): *25–27*, male, left pedipalp: *25*, prolateral; *26*, retrolateral; *27*, ventral; *28–31*, female, epigyne: *28*, ventral; *29*, dorsal; *30*, posterior; *31*, lateral.

brown to black; intersegmental membranes bright yellow in life. Without tufts of setae.

*Abdomen* (Figs 22–24). Mostly dark yellow-brown, with conspicuous yellow stripe anteriorly; much longer than broad; dorsal surface with three pairs of sigillae; ventral surface with one unpaired sigilla posterior to epigastric furrow and three pairs of sigillae situated between unpaired sigilla and spinnerets; posterior portion of abdomen overhanging spinnerets; book lung covers red-brown and with conspicuous grooves.

*Epigyne* (Figs 28–31). Very wide and narrow, with paired lateral indentations and deep depression across posterior margin; internally with two ovoid spermathecae, and short copulatory and insemination ducts.

*Dimensions* (*mm*). Total length 37.50. Carapace length 11.05, width 8.15. Eyes: AME 0.29, ALE 0.32, PME 0.29, PLE 0.34, AME–AME 0.51, AME–ALE 1.81, PME–PME 0.58, PME–PLE 1.88, PLE–ALE 0.10, eye group width 5.04, MOQ front width 1.16, MOQ back width 1.11, MOQ length 1.10. Sternum length 4.78, width 4.47. Abdomen length 26.20, width 9.90. Pedipalp: femur 4.48, patella 1.72, tibia 2.95, tarsus 4.98, total 14.13. Leg I: femur 21.10, patella 3.98, tibia 18.03, metatarsus 16.38, tarsus 4.65, total 64.14. Leg IV: femur 20.15, patella 3.48, tibia 13.66, metatarsus 20.70, tarsus 3.50, total 61.49.

### Male (Australia: NT: Cahills Crossing, Kakadu Natl Park, WAM 97/2945)

*Carapace*. Yellow; with very few setae, these mostly situated around ocular region; fovea absent; dorso-medial horns absent; chilum absent.

*Chelicera.* Yellow; cheliceral boss covered with tuberculations; fang furrow with one sub-basal tooth on anterior margin, and three teeth on posterior margin; cheliceral denticles present between tooth rows.

*Labium.* Yellow, much longer than broad, anteriorly rounded.

*Pedipalp* (Figs 25–28). Yellow, except for the black conductor and embolus; patella and tibia each with one macroseta; tibia with three retrolateral and four dorsal trichobothria; paracymbium small and sharply pointed; conductor long and straight, orientated at 90° to the tegulum; embolus situated within conductor groove.

*Sternum.* Yellow; cordate, barely extending between coxae IV; without protuberances adjacent to coxae.

*Legs.* Uniformly yellow; without tufts of setae.

*Abdomen.* Mostly yellow, except posterior margin that has black-brown stripes; dorsal scute present; sigillae not evident; book-lung covers with 3–4 grooves.

*Dimensions* (*mm*). Total length 4.10. Carapace length 1.64, width 1.40. Eyes: AME 0.18, ALE 0.11, PME 0.11, PLE 0.06, AME–AME 0.13, AME–ALE 0.04, PME–PME 0.12, PME–PLE 0.20, PLE–ALE 0.00, eye group width 0.77, MOQ front width 0.40, MOQ back width 0.37, MOQ length 0.26. Sternum length 0.80, width 0.80. Abdomen length 3.02, width 1.40. Pedipalp: femur 0.73, patella 0.27, tibia 0.40, tarsus (cymbium only) 0.62, total 2.02. Leg I: femur 3.51, patella 0.75, tibia 3.21, metatarsus 4.93, tarsus 1.60, total 14.00. Leg IV: femur 3.17, patella 0.59, tibia 2.20, metatarsus 3.32, tarsus 1.26, total 10.54.

### Variation

The major colour forms apparent within our study area are as follows:

Abdomen with distinct dorsal yellow stripes: we have examined specimens with these stripes from north-western Australia (Western Australia and Northern Territory), Christmas I., most mainland Asian localities, and many regions of Indonesia (including West Papua), Palau, Philippines, New Guinea, and the Solomon Is.

Abdomen without dorsal yellow stripes or with indistinct yellow markings: this form occurs in eastern Australia, as well as parts of montane New Guinea (Robinson and Robinson 1973) and Vanuatu.

Abdomen with spots: some specimens from New Britain and New Ireland, Solomon Is and Samoa possess distinct abdominal spots.

Sternum with colour pattern, and carapace with paired dorsal projections: as mentioned below, this form includes the syntypes of *N. pictithorax*, and the specimens may possibly represent hybrids between *N. pilipes* and *N. antipodiana*. We have examined specimens with these features from West Papua (1 ♀, ‘Hollandia and L. Sentani’ (AMNH); 1 ♀, Waris (BPBM)), and Papua New Guinea (1 ♀, Busu R., E of Lae, Morobe Province (BPBM); 1 ♀, Fly R., 5 miles below Palmer Junction, Western District Province (AMNH); 2 ♀, ‘N.G.-1’ (AMNH); 1 ♀, May R. Station (BPBM)).

### Remarks

Dahl (1911, 1912), Bonnet (1958) and numerous other authors have incorrectly utilised the name *Nephila maculata* (Fabricius, 1793) for this species. Fabricius’ original binomen *Aranea maculata* is a junior primary homonym of *Aranea maculata* Olivier, 1789 and must be replaced by the next available name, *Aranea pilipes* Fabricius, 1793, as correctly undertaken by Roewer (1942), who mistakenly used ‘*N. pictipes’* on p. 930. In his belief that *N. maculata* was a valid name, Bonnet (1958) then mistakenly utilised *N. pilipes* (Lucas, 1858) for an African species that should be correctly known as *N. fenestrata* Thorell, 1859 (see Dahl 1911, 1912).

Numerous colour forms are apparent within *N. pilipes*, which Dahl retained as varieties of *N. maculata*: *annulipes*, *fuscipes*, *kuhli*, *lauterbachi*, *maculata*, *pecuniosa*, *pilipes*, *penicillum*, *procera* and *walckenaeri*. Close examination of many of these colour forms amongst the material available to us indicates that these colour patterns are usually not supported by any other morphological character states that would warrant the recognition of a separate species or subspecies. The sole exception is a series of specimens from Papua New Guinea and West Papua, including the syntypes of *N. pictithorax* from Moaif, West Papua, which differ from ‘typical’ *N. pilipes* only in the possession of a distinct sternal colour pattern and a pair of carapaceal projections. The presence of carapaceal projections is certainly unusual amongst specimens of *N. pilipes*, but we prefer to attribute the presence of these projections, as well as the sternal colour pattern to intraspecific variation. In all other respects, including the morphology of the female genitalia, the specimens are identical to typical *N. pilipes*. Dahl (1912) suggested that he had examined a hybrid between *N. pilipes* (as *N. maculata*) and *N. laurinae* (as *N. imperialis*) from West Papua, and the combination of character states observed in specimens of '*N. pictithorax*' may also suggest a hybrid origin for these specimens.

The status of the colour forms recognised by Dahl (1912) is difficult to assess solely on the basis of preserved material, but as an interim measure, we propose that the varietal names utilised by Dahl (1912) should be abandoned. The status of these populations may be best studied by the investigation of allozyme variation or DNA sequences, but we do not have access to adequately preserved material to conduct such a study at present. However, relevant to this issue is the finding that normal and melanic colour forms of *N. pilipes* found on Taiwan (Tso *et al*. 2002) are genetically very similar and experience high gene flow.

Our allozyme analysis demonstrates that *N. pilipes* is distinct at the 80% FD level from *N. edulis*, *N. plumipes* and *N. tetragnathoides* (Fig. 11). This divergence appears to be similarly reflected in some morphological and life history traits. The male pedipalp is unusual in possessing an extremely long, straight embolus and conductor (Figs 25, 26). It has a more complex premating behaviour that includes the male laying down a fine mat of silk on the dorsal side of the abdomen and pedicel of the female (Robinson and Robinson 1973, 1976). Also, matings are often in excess of 30 min, and are far less aggressive than other species (Robinson and Robinson 1973, 1976).

### New synonymies

*Epeira* (*Nephila*) *walckenaeri*, *E.* (*N.*) *hasseltii*, *N. maculata* var. *annulipes*, *N. maculata jalorensis*, *N. maculata* var. *novaeguineae*, *N. pictithorax*, *N. maculata* var. *flavornata*, *N. pictithorax*, *N. maculata* var. *flavornata*, *N. maculata piscatorum*, and *N.* (*N.*) *maculata* var. *lauterbachi* are proposed as new synonyms of *N. pilipes* as there is nothing that would serve to separate them from *N. pilipes*.

### Common name

Although named the 'giant wood-spider' by Robinson and Robinson (1973), we prefer the term 'giant golden orb-weaving spider' for this species as Australasian forests are not locally referred to as 'woods'.

### Distribution

*Nephila pilipes* has been recorded from much of South-East Asia as far north as China (Dahl 1911; Su *et al*. 2007, Fig. 1), and as far east as Vanuatu (Fig. 32). A record of *N. pilipes* from Samoa is presented here based upon a single female lodged in RMNH but the lack of any further specimens from this area suggests that it may be mislabelled. It is somewhat surprising that *N. pilipes* does not occur on New Caledonia or the Loyalty Is, given their close proximity to the southern islands of Vanuatu where the species is abundant (Fig. 32). Records from Africa and Madagascar (Karsch 1879; Strand 1906*a*, 1907) are based upon misidentifications (M. Kuntner, in litt.). The holotype of *N. submaculata* from Cameroon was unfortunately destroyed during World War II (Dr M. Geisthardt, in litt., 5.xi.1996), thus denying us the opportunity to confirm the synonymy of this species with *N. pilipes*.

In Australia, *N. pilipes* is known from closed forests in north-eastern NSW, eastern Qld, northern NT, northern WA as well as Christmas I. (Fig. 32). An adult female specimen from Bacchus Marsh, Vic., is undoubtedly mislabelled, as *N. pilipes* has not been otherwise recorded from Australia south of Bellingen, NSW (Fig. 32). The distribution map provided here (Fig. 32) also includes the localities given by Chrysanthus (1959, 1960, 1971) in his reviews of the New Guinean species of this genus.

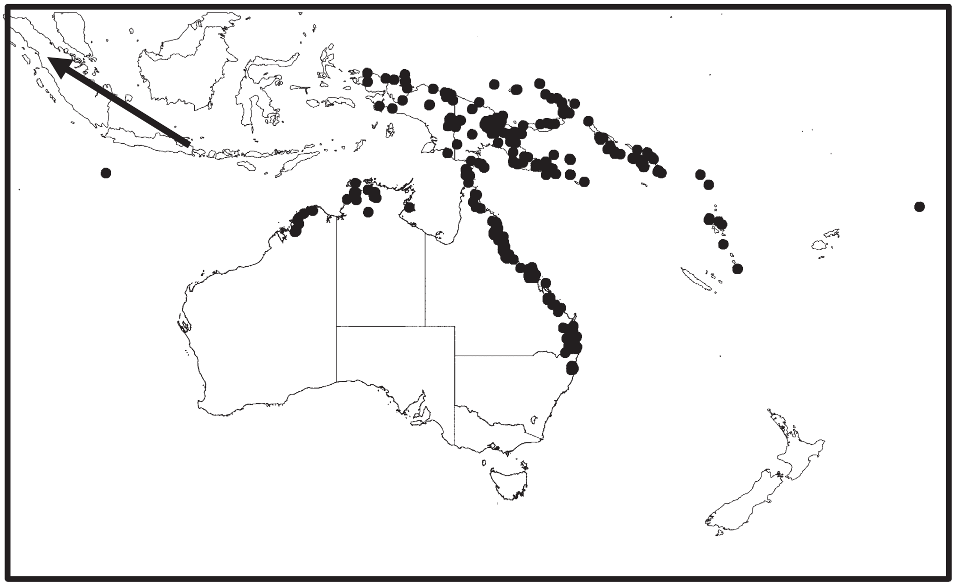


**Fig. 32.** Recorded distribution of *Nephila pilipes* (Fabricius) in the study area. The range of this species also extends to the north-west into Asia.

## ***Nephila plumipes*** (Latreille)

### Humped golden orb-weaving spider

(Figs 8, 9, 33–46)

*Aranea plumipes* Latreille, 1804: 275.

*Nephila cunninghamii* MacLeay, 1827: 468.

*Nephila venosa* L. Koch, 1867: 183–184.

*Nephila victorialis* L. Koch, 1872: 150–151, plate 12, figs 3, 3*a*–*b*.

*Nephila nigritarsis* L. Koch, 1872: 152–153, plate 12, figs 4, 4*a*–*b*.

*Nephila flagellans* L. Koch, 1872: 153–156, plate 12, figs 5, 5*a*–*b*, 6, 6*a* (in part; see *Nephila tetragnathoides*).

*Nephila labillardierii* Thorell, 1875: 130–132, figs 1–2.

*Nephila insularis* Keyserling, 1887: 215–216, plate 19, figs 5, 5*a*.

*Nephila fletcheri* Rainbow, 1895: 347–349, plate 22, figs 1, 1*a*.

*Nephila edwardsii* Rainbow, 1895: 349–351, plate 22, figs 2, 2*a*.

*Nephila ventricosa* Rainbow, 1895: 351–354, plate 23, figs 1, 1*a*, 2, 2*a*.

*Nephila ornata* Rainbow, 1896: 320–321, plate 18, figs 1, 1*a*–*b* (junior primary homonym of *Nephila ornata* Adams, 1847 and *Nephila ornata* Blackwall, 1864; junior secondary homonym of *Meta ornata* L. Koch, 1872).

## Type material

*Type*(*s*) *of Aranea plumipes*. Unknown number of specimens, South Sea Islands (as 'îles de la mer du Sud') (not found in MNHN, not examined).

*Type*(*s*) *of Nephila cunninghamii*. Unknown number of specimens, Australia and neighbouring regions (see route shown in King, 1827) (possibly unlabelled in MMS, not examined).

*Holotype of Nephila venosa*. ♀, Brisbane, Queensland, Australia (27°28′S, 153°01′E) (ZMH, Mus. Godeffroy No. 2251).

*Syntypes of Nephila victorialis*. 1 ♀, Rockhampton, Queensland, Australia (23°22′S, 150°32′E) (MNHN 111; possible syntype); 1 ♀, Port Mackay, Queensland, Australia (21°09′S, 149°11′E), 1869 (SMNH, Museum Godeffroy; possible syntype, see below).

*Syntypes of Nephila nigritarsis*. 2 ♀, without locality data (presumably from Rockhampton or Port Mackay, Queensland, Australia) (ZMH, Mus. Godeffroy No. 7664).

*Syntypes of Nephila flagellans* (*in part*). 1 pen. ♂, 2 juv. ♀, 1 juv., Port Mackay, Queensland, Australia (21°09′S, 149°11′E) (ZMH, Mus. Godeffroy No. 7655); 2 juv. ♀, Sydney, New South Wales, Australia (33°53′S, 151°13′E) (SMNS?, not examined).

*Syntypes of Nephila imperatrix*. 2 ♀, without locality data (MV K-3858, Mus. Godeffroy No. 7538) (see below).

*Syntypes of Nephila labillardierii*. 2 ♀, New Caledonia, Vinson (SMNH 137/724).

*Syntypes of Nephila insularis*. 9 ♀, 1 juv. ♀, Île Loyauté (Loyalty Islands), New Caledonia (ZMH).

*Holotype of Nephila fletcheri*. ♀, New England District, New South Wales, Australia, J. J. Fletcher (AM, lost, not examined).

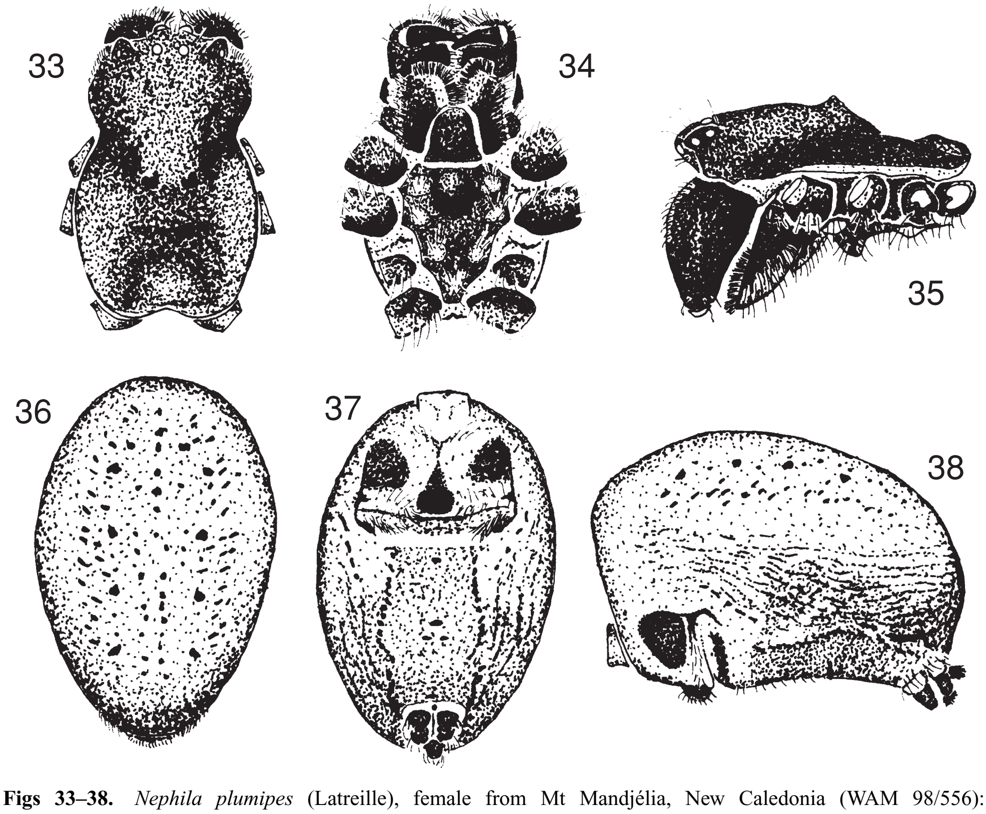
*Syntypes of Nephila edwardsii*. 2 ♀, Sydney, New South Wales, Australia (33°53′S, 151°13′E), C. A. Edwards (AM KS7828, see *Remarks* below).

*Syntypes of Nephila ventricosa*. 1 ♂, 1 ♀, Sydney, New South Wales, Australia (33°53′S, 151°13′E) (AM KS7827).

*Type*(*s*) *of Nephila ornata*. 1 or more ♀, Sydney, New South Wales, Australia (33°53′S, 151°13′E) (AM, lost, not examined).

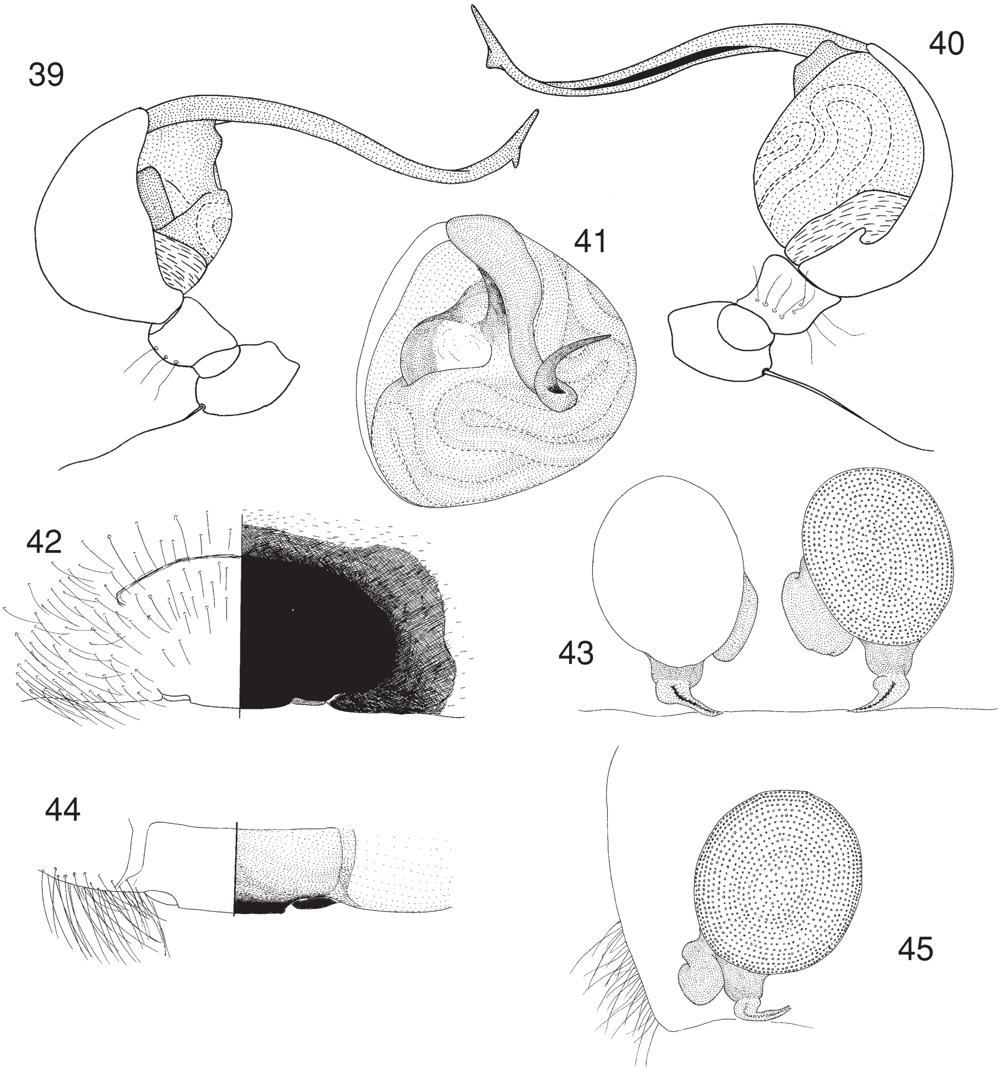
## Other material examined

**Australia: Lord Howe Island:** Lord Howe I. (AM KS33652; ANIC; MV K-3866; SAM N1981298-N1981301; WAM T52210–52215); lower road station (AM KS33657); lowlands (AM KS17530); Station 27



**Figs 33–38.** *Nephila plumipes* (Latreille), female from Mt Mandjélia, New Caledonia (WAM 98/556): *33*, cephalothorax, dorsal; *34*, cephalothorax, ventral; *35*, cephalothorax, lateral; *36*, abdomen, dorsal; *37*, abdomen, ventral; *38*, abdomen, lateral.

(AM KS33767); Station 28 (AM KS33659); Station 29 (AM KS33666, KS33688); Station 30a (AM KS33683); Station 31 (AM KS33668); Station 32 (AM KS33693); Station 34 (AM KS33697); Station 35 (AM KS33694); Station 36 (AM KS33698, KS33691); Station 36b (AM KS33646); Station 37 (AM KS33651, KS33654, KS33664, KS33665, KS33685, KS33647); Station 38 (AM KS33692); Station 40 (AM KS33663, AM KS33681); Station 42 (AM KS33689, KS33649, KS33660, AM KS33653); Station 44–47 (AM KS33658); Station 48 (AM KS33682); Neds Beach (TMAG J1593); Salmon Bay (AM KS33705). **New South Wales:** Banksia (AM KS33465); Beecroft (AM KS22696); Bellata (AM KS33187); Brighton-Le-Sands, Botany Bay (AM KS7829); Broken Bay (AM KS33629, AM KS33637); Camden (AM KS33302); Castle Hill (AM KS33768, AM KS33791); Cataract Glen, near Ballengarra (AM KS33627); Clifton Gardens (AM KS33809); Coasters Retreat (AM KS33636); Collins Ck, Kyogle (AM KS33797); Corna (AM KS33632); Currawong (AM KS33452, KS33699); Dangar Isles, Hawkesbury R. (AMNZ 5035–5036); Dawson R. bridge, 9 km N of Taree (AM KS9259); Engadine (AM KS33747); Epping (AM KS33623); Epping Strip (AM KS49908-KS49909); Euroka (AM KS33635); 6 km S of Forster (AM KS10202); Grafton (MV K-3861); Homebush (AM KS3081, KS33803); Hunters Hill (AM KS7830); Huskisson (AM KS33644); Ingleburn (AM KS33717); Kenthurst (AM KS21561); Kilcare, near The Entrance (AM KS23353); Kurnell (AM KS7831); La Perouse (MCZ); Linden (AM KS33737, KS33669); Longueville (AM KS33672); Manly (AM KS33608, MCZ); Milford Point, N of Menai (AM KS14385); Moree (AM KS32592); Mossman Bay (AM KS33614); Neutral Bay (AM KS33607, AM KS5154); Newcastle (MNHN 216–75); North Sydney (AM KS33615); Oatley (AM KS33609); Oxford Falls (AM KS7832); Patonga (AM KS5080); Pearl Beach (WAM T52203-T52209; WINC); Point Clare, Gosford (AMNH); Pymble (AM KS33801); Quakers Hill (AM KS 33457); Riverwood (AM KS33461); Royal Natl Park (AM KS33643); 'Scalloway', Willowvale, near Gerringong (AM KS18478); Scotts Head (WAM T52216); Seven Mile Beach, Gerroa (SAM); The Spit, Narriwi Park, Mosman (AM KS8844-KS8845); Spit Park, Mosman (AM KS8945); Sydney (AM KS33606, KS33621; MCZ; ZMH Mus. Godeffroy No. 2251); 3 km N of Taree (AM KS49113); Tumbulgum, Tweed R. (AM KS33625); Turners Dip, near Piggabeen (QM S33049); Warrawee (AM KS33772); Waverley (AM KS46055); Willoughby (AM KS7833); Wilton (ANIC); Windsor (AM KS33645); Wingham (AM KS7834); Woolooware



**Figs 39–45.** *Nephila plumipes* (Latreille): *39–40*, male from Mt Panié, New Caledonia (WAM T52250), left pedipalp: *39*, prolateral; *40*, retrolateral; *41*, ventral; *42–45*, female from Mt Mandjélia, New Caledonia (WAM 98/556), epigyne: *42*, ventral; *43*, dorsal; *44*, posterior; *45*, lateral.

Bay, Sydney (WAM T52217-T52228). **Norfolk Island:** Norfolk I. (AM KS49879). **Northern Territory:** Bat I., Liverpool R. (WINC); Ben Hole Billabong (AMNH); Casuarina Foreshore Reserve, Darwin (QM S33082); Darwin (AMNH); East Point, near Darwin (NTMAG); Groote Eyelandt (AM KS48936); Holmes Jungle (NTMAG); Maningrida (NTMAG); Nhulunbuy (NTMAG; WAM T52201). **Queensland:** Alderley, Brisbane (QM S33101); Alexandra Headland (QM S33009, S33011); Annerley, Brisbane (QM S3491); Aspley (QM S29727); Badu I. (QM S33001); Bahrs Scrub (QM S29712); Bardon, Brisbane (QM S20333); Brampton I. (QM S29708); Bribie I. (QM W1008); Brighton, Brisbane (QM S28925, S33028); Brisbane (QM S29697, S29717, S33014, S33029; MV K-3865; SAM; MNHN 199–67, Godeffroy collection); Brookfield, 85 Savages Rd (QM S24777); Brown (as Brown's) Ck, Pascoe R. (AMNH); Bulwer Swamp, Moreton I. (QM S29695); Bunya (QM S29718); Bushy I. (QM S33020); Cairns (AM KS33634); Camira (QM S2469, S33052); Canal 92 Rd Crossing, Cape York (QM S33022); Clayfield, Brisbane (QM S29692); Clifton Beach (QM S29710); Coconut I. (QM S33004); Cooktown (MV K-3868, K-3862, K-3871); Cooloola (QM S29795, S33382); Coolum (MV K-3870); Coorparoo (QM S20377); Corinda, Brisbane (QM W1074); Crows Nest (QM S33030); Currumbin Sanctuary, Gold Coast (SMNH); Denham I. (SAM); Double I. (QM S28963); Dunk I. (MCZ); Dutton Park (QM S20966–20968); Eidsvold (QM S29723); Enoggera, Army Lands (QM S22416, S22422); Farmer I., Great Barrier Reef (QM S29711, S28961); Flinders I. (QM S28980, S29693); Flinders Peak, near Ipswich (QM S29703); Friday I. (QM S33003); Gracemere (AM KS34303); Hamilton, Brisbane (MV K-3863); Heron I. (QM S29689, S29690, S29700, S29701, S29713, S33025; AM KS7835; MV K-3859; WINC); Horn I. (QM S33002, S33006, S33041); 19 km SSW of Indian Head, Fraser I. (ANIC); Indooroopilly (QM S28939); Indooroopilly I. (QM S29702); Ipswich (QM S29696); Isla Gorge (QM S29714); Jacksons Ck (QM S33018); Jardine R., Cape York (QM S33017); Jimna State Forest (QM S29719); Kroombit Tops, 1000 m (QM S29716); Laidley Ck (QM S29704); Lake Broadwater (QM S42953); Lindeman I. (AM KS33795, KS33798); Lizard I. (QM S42952; KS33616-KS33617); Merina Downs (QM S33084); Moreton I. (QM S33026); Morningside, Brisbane (QM S3492); Mt Coot-tha (QM S33031); Mt Cotton, Michaelsens Farm (QM S33047); Mt Elliott Natl Park, Bruce Hwy and Mt Cleveland Rd junction (WAM T41758); Mt Goonaneman (QM S29698); Mt Gravatt State School, Mt Gravatt, Brisbane (QM S21978); Mt Greville (QM S42951); Mt Molloy (QM S33015); Mt Mulligan (QM S33019); Mt Nebo (QM S29722); Mt Tamborine (QM S29726); Nangur State Forest (QM S31865); Nathan (QM S42935); near 'Trench', Moreton I. (QM S33013, S29709); Nelson, now Gordonvale (AM KS33620); Noosa Heads (QM W828); 5 km S of Noosa Heads (SAM); North Pine R., Deep Water Bend (QM S33010); North Stradbroke I. (QM S20278); North West I. (AM KS34065); Orchid Beach, Fraser I. (QM S31866, S41341, S41976, S31042); Oxley (QM S29724); Paddington (WAM 92/541–546, T52229-T52235); Percy Isles (QM S42941); Pialba (Hervey Bay) (SAM); Pinkenba (QM S46665); Port Stewart (QM S33079); Prince of Wales I. (QM S33005); road between Mt Tamborine and Canungra (CAS); Rochedale State Forest (QM S29720, S33046); Rockhampton (MNHN 347, 3471); Rockhampton District (SAM); Rocklea, Brisbane (QM S33024); Rundle Range (QM S42595); Sandgate (QM S29688, S33087); Serpentine Ck (QM S33027); Sherwood, Brisbane (QM W642); Somerset (SMNH 733); South Percy I., Lagoon area (QM S27572); St Johns Wood, Brisbane (QM S33008); Stradbroke I. (QM S29699, S33021; MV K-3864); Strathpine, Brisbane (QM S15560); Telegraph Crossing, Jardine R. (AMNH); Tewantin (QM W1584); Townsville (QM S28978); 'Trench', Moreton I. (QM S29691); Tyron I. (QM S28965); Ubobo Rd, Kroombit Tops (QM S33050); Upper Brookfield (QM S29706, S29715); West Burleigh (QM S33007); West End, Brisbane (QM S29721); Windsor, Brisbane (QM S29694); Wreck I. (AM KS33618); Wynnum (QM S42744, S33016); Yam I. (QM S12420); Yarrabah (SMNH); **Western Australia:** Bay of Rest, north side, North-West Cape (WAM T52200). **New Caledonia:** Baie de Magenta (as Magenta Bay), Noumea (MNZ); Col de Roussettes (WAM T51633); Hienghène (MNHN); Kwakwa, Iles des Pins (WAM T52247); Mt Koghi(s), Noumea (CAS); Mt Mandjélia (WAM 98/556); Mt Mou (WAM T52248); Mt Ouen Toro (SAM); Mt Panié (WAM T52249-T52251); N du Mt Mau (MNHN); Nouméa (MNHN); Nouméa (MNHN 3974); Noumea, Ouen-toro (QM S13815); Oua Tom Valley (AMNH); Ouen Toro (MNZ); Sarramea (BPBM); St Gabriel (AMNH); Tyto Cave, Gilles area (MNZ); Yaté (MNHN); *Île Loyauté* (*Loyalty Islands*): La Roche, Maré I. (BPBM); Lifu I. (AMNH); Maré I. (AMNH); Uvea I. (AMNH). **Papua New Guinea: New Ireland Province:** Toam I. (= Toau I.) (ANIC). **Solomon Islands: Santa Cruz:** Namumblo Valley, Reef I. (AM KS33796). **Vanuatu (New Hebrides): Anatom:** Anelgannat (now Anelghowhat) (MNHN). **Aneityum:** Aneityum (AMNH). **Aoba:** Aoba (MNHN). **Banks Island:** Banks I. (NMB 807.b); Sola, Vanua Lava (BPBM). **Efate:** (Port) Vila (BPBM); near Port Vila (MNHN); Vila Harbour (AMNH). **Emae Island:** Emae (as Mai) (AM KS33495); Erromango: no precise locality (MNHN). **Espiritu Santo:** Espiritu Santo (AMNH, MNZ, WAM T52202); hill E of Luganville (BPBM); Hog Harbour (AM KS33779); Surenda (= Sourunda) (MNHN). **Futuna:** Futuna I. (AMNH). **Maewo:** Kerepai (BPBM). **Malekula:** 'Mallicolo' (MNHN 15805); Malekula (MNHN). **Pentecost:** Pentecost (MNHN 165–94). **Tanna:** Tanna (AM KS33581); Whitesands area (AMNH).

### Diagnosis

Specimens of *N. plumipes* differ from all other Australasian species except *N. tetragnathoides* by the presence of pronounced tubercles on the sternum (females and larger juveniles) (Fig. 35), and the pedipalpal conductor with a subdistal triangular protuberance (males) (Figs 39–41). Females differ from those of *N. tetragnathoides* by the lack of a large pale patch on the ventral surface of the abdomen (Fig. 37). Males appear to be morphologically indistinguishable from those of *N. tetragnathoides*.

### Description

#### Female (New Caledonia: Mt Mandjélia, WAM 98/556)

*Carapace* (Fig. 33, 35). Very dark brown, posterior region slightly lighter; evenly covered with extremely fine, white setae; fovea a broad, shallow depression; dorso-medial horns present; antero-lateral margins with red-orange crenulated mound that opposes cheliceral boss; chilum present, medially divided.

*Chelicera.* Very dark brown; cheliceral boss covered with tuberculations; fang furrow with three large teeth on anterior margin (central tooth largest), three large teeth on posterior margin (uniformly sized); cheliceral denticles present between tooth rows.

*Maxilla* Dark brown with yellow anterior and mesal margins.

*Labium.* Dark brown, slightly paler anteriorly; much longer than broad, anteriorly rounded.

*Pedipalp.* All segments brown, tarsus darker in distal half.

*Sternum.* Mostly dark brown, with several yellow patches laterally and posteriorly; cordate, not extending very far between coxae IV; large protuberance situated behind labium, three pairs of smaller protuberances situated adjacent to coxae I, II and III, and single protuberance near posterior corner.

*Legs.* Coxae mostly brown, with some yellow patches centrally; all other segments brown, except for tarsus that is black distally; some of the longer segments appearing banded; without tufts of setae.

*Abdomen* (Figs 36–38). Beige, tending slightly darker posteriorly; ovoid; dorsal surface with three pairs of sigillae; ventral surface with one unpaired sigilla posterior to epigastric furrow and one pair of sigillae situated between unpaired sigilla and spinnerets; book lung covers fuscous and with conspicuous grooves.

*Epigyne* (Figs 42–45). Postero-medially slightly concave and smooth; posterior margin nearly straight but with thin upturned lip; lateral regions coarsely striated and with medially directed setae; copulatory duct opening laterally inserted at the end of groove; internally with one pair of large oval spermathecae; copulatory duct very short.

*Dimensions* (*mm*). Total length 20.10. Carapace length 8.75, width 6.40. Eyes: AME 0.30, ALE 0.20, PME 0.23, PLE 0.21, AME–AME 0.53, AME–ALE 1.25, PME–PME 0.53, PME–PLE 1.33, PLE–ALE 0.30, eye group width 0.40, MOQ front width 1.00, MOQ back width 1.00, MOQ length 0.61. Sternum length 4.20, width 3.69. Abdomen length 1.22, width 0.80. Pedipalp: femur 3.04, patella 1.33, tibia 1.68, tarsus 3.21, total 9.26. Leg I: femur 14.48, patella 3.46, tibia 11.90, metatarsus 16.92, tarsus 3.25, total 50.01. Leg IV: femur 12.34, patella 2.62, tibia 7.70, metatarsus 11.50, tarsus 2.34, total 36.50.

### Male (New Caledonia: Mt Panié, WAM T52250)

*Carapace*. Mostly yellow, with fuscous markings latero-medially; with very few setae, these mostly situated around ocular region; fovea absent; dorso-medial horns absent; chilum absent.

*Chelicera*. Yellow, slightly darker distally; cheliceral boss covered with tuberculations fang furrow with three teeth on anterior margin and three teeth on posterior furrow; cheliceral denticles present between tooth rows.

*Labium*. Grey-brown posteriorly, yellow-white medially; much longer than broad, anteriorly rounded.

*Pedipalp* (Figs 39–41). Yellow, except for bulb that is dark-brown; patella with one macroseta; tibia with six retrolateral and three dorsal trichobothria; paracymbium small and distally rounded; conductor long, slightly curved, orientated at 90° to the tegulum; embolus situated within conductor groove; conductor with subdistal triangular protuberance.

*Sternum*. Brown laterally, yellow medially; cordate, barely extending between coxae IV; without protuberances adjacent to coxae.

*Legs*. Without tufts of setae; most larger segments with indistinct bands of colour.

*Abdomen*. Mottled grey-brown, with white patches, scute yellow; dorsal scute present; sigillae not evident; book-lung covers with several grooves.

*Dimensions* (*mm*). Total length 5.00. Carapace length 2.12, width 1.58. Eyes: AME 0.13, ALE 0.11, PME 0.09, PLE 0.10, AME–AME 0.15, AME–ALE 0.15, PME–PME 0.13, PME–PLE 0.22, PLE–ALE 0.00, eye group width 0.80, MOQ front width 0.40, MOQ back width 0.34, MOQ length 0.31. Sternum length 1.11, width 0.92. Abdomen length 3.08, width 1.66. Pedipalp: femur 0.60, patella 0.33, tibia 0.28, tarsus (cymbium only) 0.61, total 1.82. Leg I: femur 4.06, patella 0.93, tibia 3.49, metatarsus 5.10, tarsus 1.75, total 15.33. Leg IV: femur 3.23, patella 0.69, tibia 2.07, metatarsus 3.24, tarsus 1.30, total 10.53.

### Variation

Some females from Vanuatu possess a white patch on the ventral surface of the abdomen, characteristic of *N. tetragnathoides* from Fiji, Tonga and surrounding areas. However, these specimens possess distinct carapaceal tubercles and are here considered to belong to *N. plumipes*. Female specimens from Lord Howe I. possess orange-brown leg segments, in contrast to the mainland Australian populations that are less orange and indistinctly banded.

### Remarks

Latreille (1804) described *Aranea plumipes* from 'îles de la mer du Sud' based on an unknown number of specimens that are either lost or unrecognisable amongst the MNHN collections.

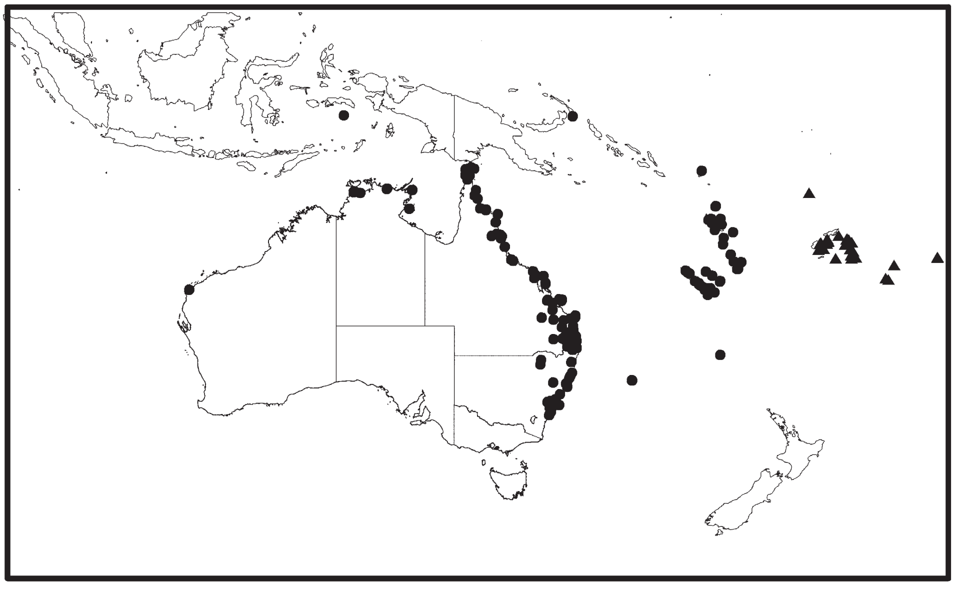


**Fig. 46.** Recorded distribution of *Nephila plumipes* (Latreille) (●) and *N. tetragnathoides* (Walckenaer) (▲).

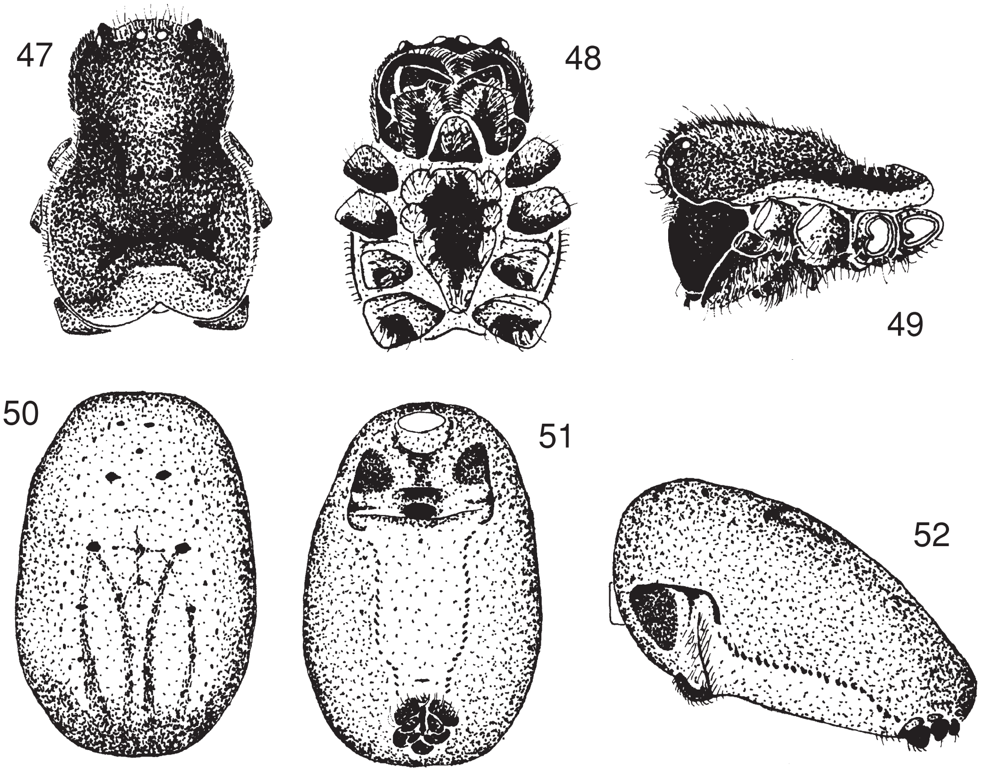
Therefore, the identity of this species is based upon the interpretations given by authors such as Dahl (1912) and Berland (1931), who recognised *N. plumipes* from New Caledonia and Australia. Unfortunately, Berland (1931) mismatched males and females of *N. plumipes* and *N. edulis* in his redescription of these species, which was noted and corrected by Chrysanthus (1971).

In his description of *Nephila venosa*, L. Koch (1867) listed a single juvenile female from 'Brinsbane' (a consistent lapsus throughout the entire publication for Brisbane), which is thus considered the holotype. This specimen is lodged in ZMH and is, in fact, an adult female. Rack (1961) listed additional specimens from Port Mackay and Sydney as paratypes, but these were not mentioned in the original paper and were presumably the specimens available to L. Koch (1872) in his later redescription of this species. As they were not mentioned by L. Koch (1867), these are not considered as part of the type series. A single female labelled in Koch's handwriting 'Nephila victorialis L. Koch n. sp. Port Mackay Mus. Godeffroy 1869' is only doubtfully considered part of the type series, as Koch (1872) only listed Rockhampton in the list of sites from which this species was collected.

Two poorly preserved specimens from the Godeffroy collection lodged in the MV appear to represent part of the syntype series of *N. imperatrix*, but they do not fit the description presented by Koch (1872) and their status is extremely doubtful. They clearly represent specimens of *N. plumipes* and may have inadvertently replaced some original specimens of *N. imperatrix*.

The description of *N. edwardsii* by Rainbow (1895) specifically mentions only a single specimen ('The specimen described above was obtained by Dr C. A. Edwards, ... and it affords me great pleasure in connecting his name with it.', p. 351), and the original label retained in the type vial reads 'Type'. Therefore, it is curious that there are now two specimens in the vial, and the possibility exists that another specimen may have been inadvertently added to the vial. Candidates may include the type of *N. fletcheri*, described in the same paper (Rainbow 1895), and now missing from the AM collections. However, it is impossible to determine from Rainbow's description which specimen may actually represent the true holotype of *N. edwardsii*, and, as there is no confusion regarding the identity of the two specimens, which are both confirmed as specimens of *N. plumipes*.

Despite the loss of the type material of *N. fletcheri* and *N. ornata*, there is sufficient evidence to maintain at least the former as a junior synonym of *N. plumipes* as proposed by Dahl (1912). Indeed, Rainbow (1895) clearly described the 'uneven' sternum characteristic of *N. plumipes*. However, in his description of *N. ornata* (Rainbow, 1896) he failed to mention any details of the sculpturing of the sternum, and there is a possibility that the sternum is in fact relatively flat. If this is the case then this species would be better placed as a synonym of *N. edulis*.



**Figs 47–52.** *Nephila tetragnathoides* (Walckenaer), female from Suva, Fiji (WAM 97/9): *47*, cephalothorax, dorsal; *48*, cephalothorax, ventral; *49*, cephalothorax, lateral; *50*, abdomen, dorsal; *51*, abdomen, ventral; *52*, abdomen, lateral.

*Nephila plumipes* is very similar to *N. tetragnathoides* (Dahl 1912), and although males are indistinguishable but female differ in a small number of morphological characters and in their allozyme profile where they differ at six loci (Table 2). The limited allozyme analysis conducted on some of the Australasian species of *Nephila* suggests that *Nephila plumipes* and *N. tetragnathoides* are very similar to each other and we suggest that the presence of a triangular protuberance on the male pedipalpal conductor (Figs 39–41, 53–55) further strengthens this claim. Indeed, we suggest that these species represent vicariant sister-taxa.

### Common name

The name 'humped golden orb-weaving spider' refers to the tuberculate sternum characteristic of this species and some of its close relatives.

### Distribution

*Nephila plumipes* is widespread in the Australasian region, and we have examined specimens from eastern, northern and western Australia, Lord Howe I., Norfolk I., New Caledonia, Vanuatu, eastern Solomon Is, New Ireland, the Banda Is, and one unlocalised specimen from New Guinea (Fig. 46). *Nephila plumipes* is particularly abundant in eastern Australia, ranging from northern Queensland to central-coastal New South Wales, where it prefers mangrove habitats, especially in the southern portion of its range.

The two juvenile females from the Indonesian island of Banda identified as *N. venosa* by Strand (1911b) have been examined and appear to represent *N. plumipes*. However, adult specimens are needed to confirm this record, which is somewhat disjunct from most other records of *N. plumipes*.

The records of this species from the Mascarene Is (Butler 1879) and the Seychelles (Blackwall 1877) are extremely doubtful, and probably represent misidentified specimens. Bonnet (1958) recorded *N. plumipes* from the Hawaiian region based upon Pocock's (1900) record of *N. nigritarsis insulicola* from Christmas I. However, Pocock's specimens were from the Christmas I. situated in the Indian Ocean (*c.* 10°30′S, 105°40′E) rather than that situated in the Pacific, now known as Kiritimati (2°00′N, 157°30′W), and that species has now been recognised as a synonym of *N. antipodiana* (see below).

## ***Nephila tetragnathoides*** (Walckenaer)
## Pacific golden orb-weaving spider

(Figs 46–59)

*Epeira tetragnatoides* (sic) Walckenaer, 1842: 100–101.
*Epeira durvilla* Walckenaer, 1842: 103.
*Nephila prolixa* L. Koch, 1872: 149–150, plate 12, figs 2, 2*a*.
*Nephila flagellans* L. Koch, 1872: 153–156, plate 12, figs 5, 5*a–b*, 6, 6*a* (in part; see *Nephila plumipes*).

### Type material

*Holotype of Epeira tetragnathoides*. ♀, Tongatapu (as Tongatabou) (*c.* 21°10′S, 175°10′W), Tonga (not found in MNHN, presumably lost).

*Syntypes of Epeira durvilla*. 1 ♀, Tongatapu (as Tongatabou) (*c.* 21°10′S, 175°10′W), Tonga, Quoy and Gaimard (MNHN); 1 juvenile ♀, same data (MNHN).

*Syntypes of Nephila prolixa*. 2 ♀, Viti Levu, Samoa or Tonga (ZMH, Mus. Godeffroy No. 1902); 1 juv. ♀, Tonga (ZMH, Mus. Godeffroy No. 1902); 1 juv. ♀, Tongatapu (as Tonga Tabu) (~21°10′S, 175°10′W) (ZMH, Mus. Godeffroy); 2 juv. ♀, Viti Levu, 1869 (SMNH, Mus. Godeffroy No. 1902); 1 ♀, 1 juv. ♀, no data, presumably from Tonga, Fiji or Samoa (ZMH, Mus. Godeffroy No. 1902); 1 ♀, no data, presumably from Tonga, Fiji or Samoa (MV K-3867, Mus. Godeffroy No. 1902).

*Syntypes of Nephila flagellans* (*in part*). 1 juv., Viti Levu, Fiji (ZMH, Mus. Godeffroy No. 7655); 1 juv., no data (MV, Mus. Godeffroy No. 7655).

### Other material examined

**Fiji: Makongai:** Makongai (BPBM); Mokogai (= Makongai I.) (BPBM). **Lau:** Lau (AMNH). **Lau (Eastern) Group:** Avea (AMNH); Fulanga (AMNH); Kanathea (AMNH); Katafanga (AMNH); Lakemba (AMNH); Mothe (AMNH); Naituamba (AMNH); Namuka (= Namuka-i-Lau) (AMNH); Namuka-i-Lau (AMNH); Oneata (AMNH); Thithia (AMNH); Tubutha (= Tuvutha) (MCZ); Vanua Ava (= Vanuava) (MCZ); Vanua Mbalavu (AMNH); Yangasa cluster (= Yangasa Levu) (AMNH). **Matuku:** Matuku I. (AMNH). **Ovalau:** Ovalau I. (ZMB 25213). **Vanua Levu:** Savusavu (AMNH). **Viti Levu:** Nasese, Suva (WAM 97/6–7); Nukulau I. (MCZ); Suva (AMNH, MCZ); Suva, University of the South Pacific (WAM 97/8–9); Taveuni (MNZ); Walu Bay (MCZ); no precise locality (ZMB 2812). **Niue:** Niue I. (MCZ); Tamakautoga (MNZ); Tuila power station (MNZ); Vaitafe (MNZ). **Tonga:** Ha'apai (AMNH); Homa Tonga (= Houma) (ZMB 25210); Tongatapu (Tongatabu I.) (MCZ); no further locality (AM KS33773, KS33793; MNHN; ZMB 25211).

### Diagnosis

Specimens of *N. tetragnathoides* differ from all other Australasian species except *N. plumipes* by the presence of tubercles on the sternum (females and larger juveniles) (Fig. 49), and the pedipalpal conductor with a subdistal triangular protuberance (males) (Figs 53–55). Females differ from those of *N. plumipes* by the presence of a large pale patch on the ventral surface of the abdomen (Fig. 51). Males appear to be indistinguishable from those of *N. plumipes*.

### Description

#### Female (Fiji: Suva, WAM 97/9)

*Carapace* (Figs 47, 49). Dark brown, lateral and posterior regions slightly lighter; evenly covered with extremely fine, white setae; fovea a broad, shallow depression; small dorso-medial horns present; antero-lateral margins with red-orange crenulated mound that opposes cheliceral boss; chilum present, medially divided.

*Chelicera.* Very dark brown; cheliceral boss covered with tuberculations; fang furrow with three large teeth on anterior margin (central tooth largest), three large teeth on posterior margin (uniformly sized); cheliceral denticles present between tooth rows.

*Maxilla.* Dark brown with yellow anterior and mesal margins.

*Labium.* Dark brown, paler anteriorly; much longer than broad, anteriorly rounded.

*Pedipalp.* All segments brown, tarsus darker in distal half.

*Sternum* (Fig. 48). Mostly dark brown, with several yellow patches laterally and posteriorly; cordate, not extending very far between coxae IV; large protuberance situated behind labium, three pairs of smaller protuberances situated adjacent to coxae I, II and III, and single protuberance near posterior corner.

*Legs.* Coxae mostly brown, with some yellow patches centrally; all other segments brown, except for tarsus and distal portion of metatarsus that are black distally; some of the longer segments appearing banded; tibia and metatarsus IV with tufts of setae.

*Abdomen* (Figs 50–52). Beige, tending slightly darker posteriorly; ovoid; dorsal surface with three pairs of sigillae; ventral surface with one unpaired sigilla posterior to epigastric furrow and one pair of sigillae situated between unpaired sigilla and spinnerets; book lung covers fuscous and with conspicuous grooves.

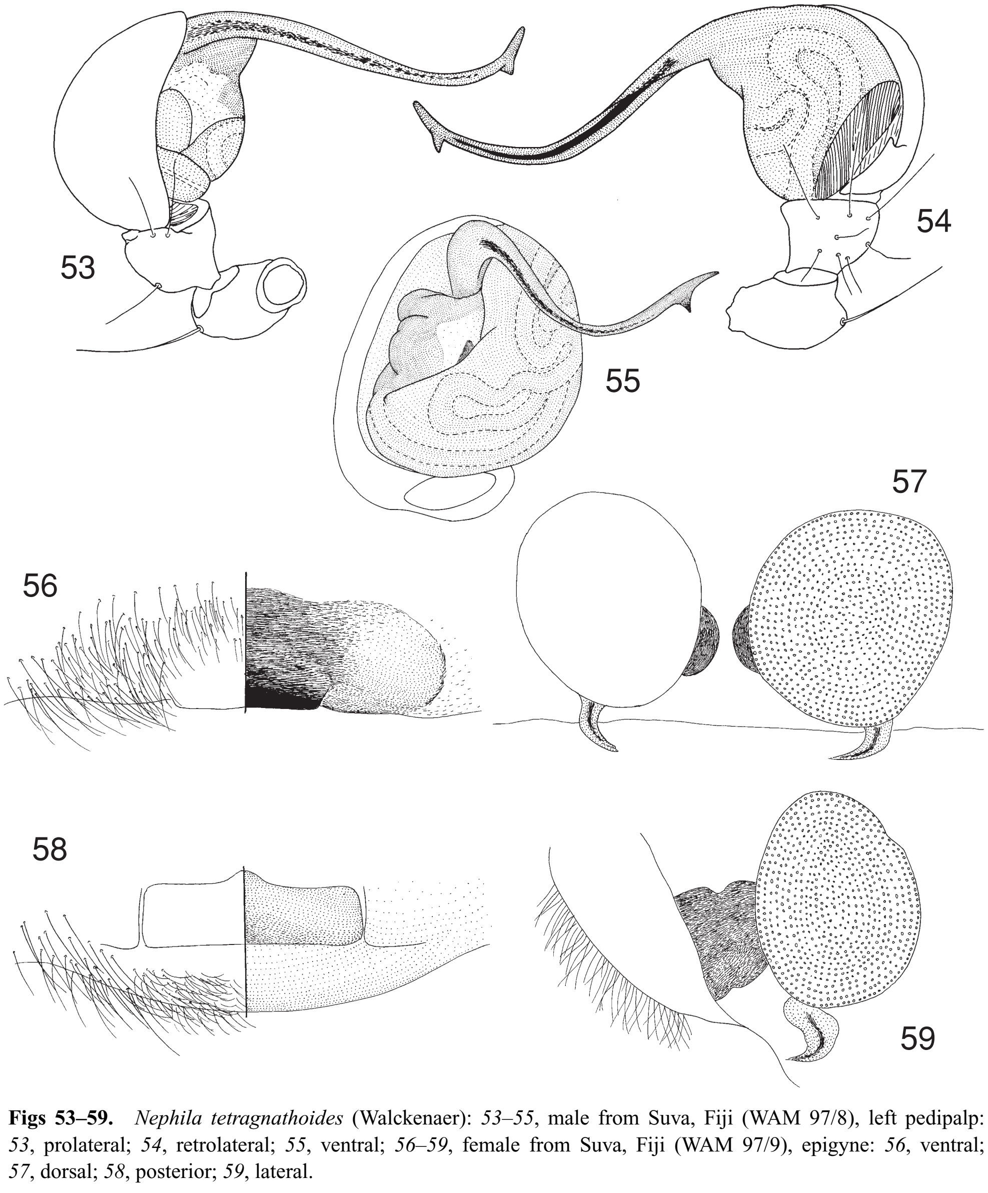
*Epigyne* (Figs 56–59). Postero-medially slightly concave and smooth; posterior margin nearly straight but with thin upturned lip; lateral regions coarsely striated and with medially directed setae; copulatory duct opening laterally inserted at the end of groove; internally with one pair of large oval spermathecae; copulatory duct short.

*Dimensions* (*mm*). Total length 23.15. Carapace length 12.20, width 7.44. Eyes: AME 0.28, ALE 0.20, PME 0.21, PLE 0.16, AME–AME 0.61, AME–ALE 1.25, PME–PME 0.67, PME–PLE 1.40, PLE–ALE 0.24, eye group width 4.22, MOQ front width 1.07, MOQ back width 1.13, MOQ length 0.45. Sternum length 5.00, width 3.80. Abdomen length 13.25, width 8.64. Pedipalp: femur 3.11, patella 1.51, tibia 2.20, tarsus 3.73, total 10.55. Leg I: absent. Leg IV: femur 12.30, patella 3.08, tibia 8.71, metatarsus 13.20, tarsus 2.90, total 40.19.

### Male (Fiji: Suva, WAM 97/8)

*Carapace.* Mostly yellow, with darker markings on pars thoracica; with very few setae, these mostly situated around ocular region; fovea present, longitudinal, poorly defined; dorso-medial horns absent; chilum present, medially divided.

*Chelicera.* Yellow, slightly darker distally; cheliceral boss covered with tuberculations; fang furrow with three teeth on



**Figs 53–59.** *Nephila tetragnathoides* (Walckenaer): *53–55*, male from Suva, Fiji (WAM 97/8), left pedipalp: *53*, prolateral; *54*, retrolateral; *55*, ventral; *56–59*, female from Suva, Fiji (WAM 97/9), epigyne: *56*, ventral; *57*, dorsal; *58*, posterior; *59*, lateral.

anterior margin and three teeth on posterior furrow; cheliceral denticles present between tooth rows.

*Labium.* Yellow-brown, with white central patch; much longer than broad, anterior margin forming obtuse point.

*Pedipalp* (Figs 53–55). Yellow, except for brown cymbium and palpal sclerites; patella with one macroseta; tibia with five retrolateral and four dorsal trichobothria; paracymbium small and sharply pointed, separated from cymbium by desclerotised area; conductor long, slightly curved, orientated at 90° to the tegulum; embolus situated within conductor groove; conductor with subdistal triangular protuberance.

*Sternum.* Dusky brown laterally, with broad medial yellow area and white sub-cuticular pigment; cordate, barely extending between coxae IV; without protuberances adjacent to coxae.

*Legs.* Most segments brown, femur and tibia with faint annulations; without tufts of setae.

*Abdomen.* Mostly yellow, except region surrounding spinnerets, which is black-brown; dorsal scute present; two pairs of sigillae; book-lung covers with several grooves.

*Dimensions* (*mm*). Total length 5.04. Carapace length 2.37, width 1.71. Eyes: AME 0.12, ALE 0.10, PME 0.12, PLE 0.12, AME–AME 0.15, AME–ALE 0.13, PME–PME 0.12, PME–PLE 0.20, PLE–ALE 0.02, eye group width 0.90, MOQ front width 0.41, MOQ back width 0.35, MOQ length 0.34. Sternum length 1.20, width 0.98. Abdomen length 3.00, width 1.53. Pedipalp: femur 0.69, patella 0.38, tibia 0.24, tarsus (cymbium only) 0.80, total 2.11. Leg I: femur 4.10, patella 0.94, tibia 3.27, metatarsus 5.08, tarsus 1.70, total 15.09. Leg IV: femur 3.12, patella 0.67, tibia 1.98, metatarsus 3.16, tarsus 1.19, total 10.12.

### Remarks

Despite the lack of type specimens of *Epeira tetragnathoides* (erroneously spelt *Epeira tetragnatoides* in the original description), the identity of this species is confirmed by the presence of only a single species of *Nephila* at the type locality, Tonga.

*Nephila tetragnathoides* is very similar to *N. plumipes*, but females can be distinguished by the presence of small carapaceal tubercles (large in *N. plumipes*) and the large white spot on the ventral surface of the abdomen. Males appear to be indistinguishable from those of *N. plumipes*, and both possess a triangular, subdistal protuberance on the conductor (Figs 39–41, 53–55). The allozyme data indicate that a Fijian population of *N. tetragnathoides* differs from Australian populations of *N. plumipes* at 15% FD. This comparison was conducted without samples from geographically intermediate areas (e.g. Solomon Is, New Caledonia) and inclusion of specimens from these areas will provide a clearer understanding of the relationships of the Pacific species of *Nephila*.

### Common name

The name ‘Pacific golden orb-weaving spider’ is used for this species, as it is restricted to islands in the southern Pacific Ocean.

### Distribution

Known only from Fiji, Tonga and Niue (Fig. 46) in the southern Pacific Ocean. We have found no specimens from Samoa and we discount Dahl’s (1911, 1912) record of this species from that island. The Samoan records appear to be solely based upon the locality data given for *N. prolixa* by Koch (1872), but as there is no unequivocal evidence that one or more of the specimens was collected in Samoa, we restrict the distribution of *N. tetragnathoides* to Fiji, Tonga and Niue.

## ***Nephila antipodiana*** (Walckenaer)
Asian golden orb-weaving spider

(Figs 60–73)

*Epeira antipodiana* Walckenaer, 1842: 93.

*Epeira* (*Nephila*) *imperialis* Doleschall, 1857: 413 (junior primary homonym of *Epeira? imperialis* Walckenaer, 1805). Synonymised by Kuntner (in litt.).

*Nephila ornata* Blackwall, 1864: 43 (junior primary homonym of *Nephila ornata* Adams, 1847).

*Nephila baeri* Simon, 1877: 82.

*Nephila holmerae* Thorell, 1881: 141.

*Nephila laurinae* Thorell, 1881: 142–145.

*Nephila nigritarsis insulicola* Pocock, 1900: 160. **New synonymy.**

*Nephila ambigua* Kulczyński, 1911: 464–469, figs 41–42. **New synonymy**.

*Nephila imperialis* var. *novae-mecklenburgiae* Strand, 1911*a*: 204. **New synonymy**.

*Nephila sarasinorum* Merian, 1911: 198, figs 10–11. **New synonymy.**

*Nephila celebesiana* Strand, 1915: 206, plate 13, figs 12, 13, plate 16, fig. 50. **New synonymy.**

### Type material

*Syntype of Epeira antipodiana:* 1 ♀, ‘Nouvelle Zealande’ (New Zealand), Quoy and Gaimard (MNHN).

*Syntype of Epeira* (*Nephila*) *imperialis*. 1 ♀, Ambon, Maluku, Indonesia (3°35′S, 128°20′E) (NHMW, not examined).

*Holotype of Nephila ornata*. Juv. ♀, ‘East-Indies’ (repository unknown, not examined).

*Syntypes of Nephila baeri*. 2 ♀, Manila, Philippines, M. Baer (MNHN).

*Holotype of Nephila holmerae*. ♀, Bangkok, Thailand (probably in MCG, not examined).

*Syntypes of Nephila laurinae*. 2 ♀, Ternate, Halmahera, Maluku, Indonesia (0°45′N, 127°25′E) (probably in MCG, not examined).

*Syntypes of Nephila nigritarsis insulicola*. 2 ♀ from type series, above Flying Fish Cove, Christmas Island, Australia (10°26′S, 105°40′E), 30.ix.–1.x. no year, J. J. Lister (BMNH 1888.96).

*Syntypes of Nephila ambigua*. ♀, ‘Sinum Humboldtii’ (= Teluk Humboldt), West Papua, Indonesia (2°30′S, 140°50′E) (not in MZPW, not examined); 4 ♂, 4 ♀, 6 juv., Segaisar, West Papua, Indonesia (3°05′S, 133°46′E), 21.v.1903 (MZPW); ♀, Pulau Mansinam (as Mansinam), West Papua, Indonesia (0°54′S, 134°06′E) (not in MZPW, not examined).

*Holotype of Nephila imperialis* var. *novaemecklenburgiae*. ♀, label reads ‘Käwieng’ (= Kavieng) but Strand states ‘Kamieng, Inseln bei Neu-Mecklenburg’, New Ireland, New Ireland Province (as New Mecklenburg), Papua New Guinea (2°36′S, 150°51′E), 5.ix.1909, E. Wolf (SMF 4995).

*Holotype of Nephila sarasinorum*: ♀, Mapane, Sulawesi, Indonesia (1°24′S, 120°40′E), Dec. (18)95 (NMB, 605).

*Syntypes of Nephila celebesiana*: 3 ♀, Boeton (now Baubau), Sulawesi, Indonesia (5°28′S, 122°38′E), 1909, J. Elbert (SMF, 4018).

### Other material examined

**Australia: Christmas Island:** 6 1/2 mile Road area (ANIC); The Dales (WAM 92/526–527); Murray Hill (ANIC); National Parks Office, Drumsite (WAM T64887); Ross Hill (ANIC; WAM 92/528–530); Ross Hill, Old Water Supply (WAM 92/533–534); Settlement (WAM 92/525); South Point

(WAM 92/535–536); no. 1 clearing, South Road (ANIC); western jungle area (WAM 92/531–532); in jungle (WAM 92/540). **Queensland:** Saibai I. (QM S33000). **Indonesia: West Papua (West Papua):** Doromena, near Jayapura (as Hollandia) (AMNH). **Papua New Guinea: New Britain Province:** New Britain (as Neu Pommern) (ZMB 24988). **New Ireland Province:** Kraewing (QM S28904); New Ireland (AM KS49701, ZMB 24990); ridge above 'Camp Bishop', 20 km up Kait R. (BPBM). **Northern Province:** Nineba, Mt Scratchley (QM S29725). **Solomon Islands: Kolombangara:** Sandfly Harbour (now Lotu Harbour) (BPBM). **New Georgia:** Munda (AMNH; USNM); Roviana (AM KS33597). **San Cristóbal:** Pamua (MCZ, WAM T52199); Pawa, Ugi (AMNZ 5037); Ugi (AM KS33489, KS49672); Wai-ai (MCZ). **Santa Cruz:** Vanikoro, now Vanikolo (AM KS49673, KS49671). **Santa Isabel:** 'Govt Stn' (AM KS49664). **Unlocated site:** Howla (AM KS49708).

## Diagnosis

Females of *N. antipodiana* differ from other Australasian species of *Nephila* by the combined presence of large protuberances on the sternum (Fig. 62) and an abdomen that is much longer than broad (Figs 63, 64). Males can be recognised by the slight curvature of the conductor and embolus, and the lack of a subdistal triangular process (Figs 66, 67).

## Description

### Female (Australia: Christmas I., WAM 92/532)

*Carapace* (Figs 60, 62). Very dark brown to black; evenly covered with numerous extremely fine, white setae; fovea a broad, shallow depression; dorso-medial horns present; antero-lateral margins with orange crenulated mound that opposes cheliceral boss; chilum present, medially divided.

*Chelicera.* Entirely black; cheliceral boss covered with tuberculations; fang furrow with three large, uniformly sized teeth on anterior margin, and three large, uniformly sized, teeth on posterior margin; cheliceral denticles present between tooth rows.

*Maxilla.* Dark brown with yellow anterior and mesal margins.

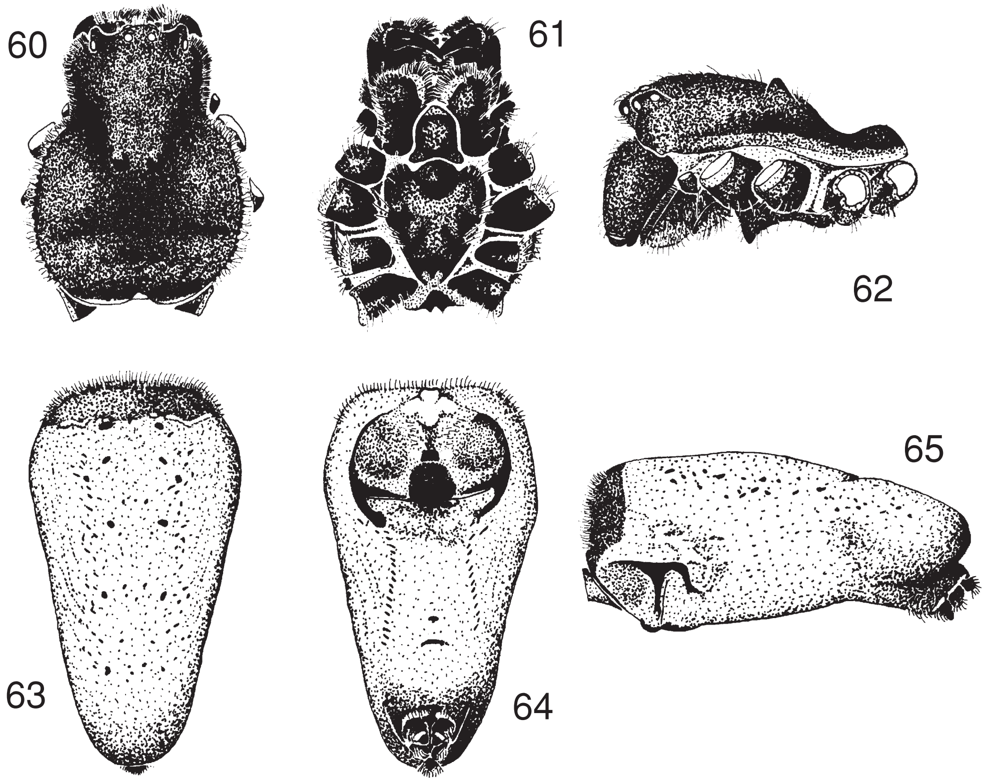
*Labium.* Dark brown, slightly paler anteriorly; much longer than broad, anteriorly rounded.

*Pedipalp.* All segments black.

*Sternum* (Figs 61, 62). Black, except for two small yellow-orange patches on posterior-lateral corners; cordate, not extending very far between coxae IV; large protuberance situated behind labium, four pairs of smaller protuberances situated adjacent to coxae.

*Legs.* Coxae mostly dark brown, with some yellow patches centrally; all other segments dark brown, except for tarsus that is black distally; some of the longer segments slightly lighter distally; without tufts of setae.

*Abdomen* (Figs 63–65). Pale yellow, with darker markings on anterior and posterior margins; much longer than broad; dorsal surface with four pairs of sigillae; ventral surface with one unpaired sigilla midway between epigastric furrow and spinnerets; book lung covers brown and with several conspicuous grooves; with large sclerotised patch anterior to epigyne.



**Figs 60–65.** *Nephila antipodiana* (Walckenaer), female from western jungle area, Christmas I. (WAM 92/532): *60*, cephalothorax, dorsal; *61*, cephalothorax, ventral; *62*, cephalothorax, lateral; *63*, abdomen, dorsal; *64*, abdomen, ventral; *65*, abdomen, lateral.

*Epigyne* (Figs 69–72). Dark brown to black with slightly crenulate posterior margin and evenly covered with short setae; copulatory duct opening laterally inserted at the end of groove; internally with pair of rounded spermathecae; copulatory duct short and strongly convoluted.

*Dimensions* (*mm*). Total length 27.3. Carapace length 10.95, width 8.30. Eyes: AME 0.29, ALE 0.22, PME 0.24, PLE 0.26, AME–AME 0.62, AME–ALE 0.31, PME–PME 0.70, PME–PLE 1.57, PLE–ALE 0.36, eye group width 4.56, MOQ front width 1.10, MOQ back width 1.19, MOQ length 0.60. Sternum length 4.81, width 3.93. Abdomen length 16.0, width 9.35. Pedipalp: femur 3.41, patella 1.65, tibia 2.02, tarsus 3.80, total 10.88. Leg I: femur 18.30, patella 3.96, tibia 15.55, metatarsus 21.95, tarsus 3.85, total 63.61. Leg IV: femur 16.40, patella 3.08, tibia 9.72, metatarsus 15.45, tarsus 2.94, total 47.59.

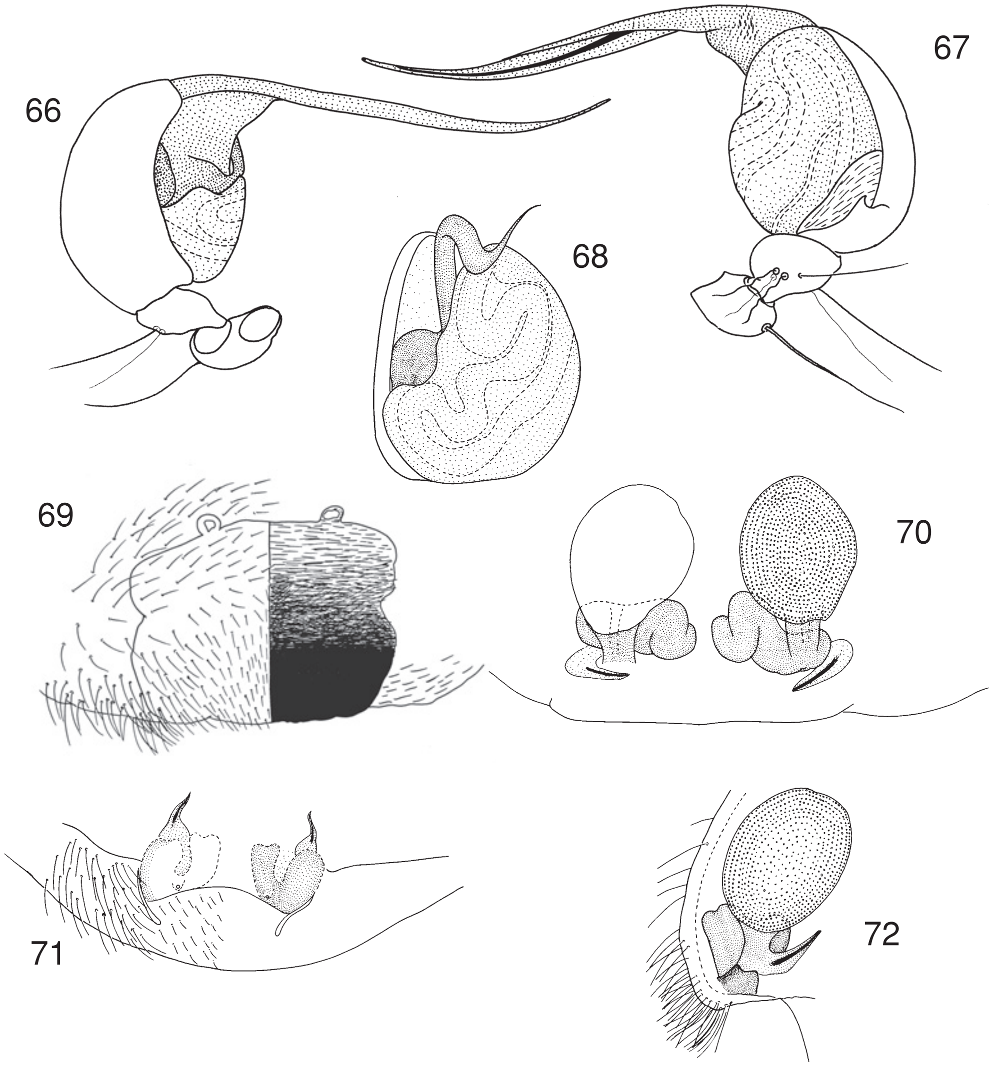
### Male (Australia: Christmas I., WAM 92/531)

*Carapace.* Mostly yellow, with darker lateral markings on pars thoracica; with very few setae, these mostly situated around ocular region; fovea absent; dorso-medial horns absent; chilum absent.

*Chelicera.* Yellow, fang dark brown; cheliceral boss covered with tuberculations; fang furrow with three teeth on anterior margin and three teeth on posterior furrow; cheliceral denticles present between tooth rows.

*Labium.* Yellow, much longer than broad, anterior margin forming obtuse point.

*Pedipalp* (Figs 66–68). Yellow, except for brown cymbium and palpal sclerites; patella and tibia each with one macroseta; tibia with three retrolateral and two dorsal trichobothria; paracymbium small and sharply pointed; conductor and embolus slightly curved; embolus situated within conductor groove.



**Figs 66–72.** *Nephila antipodiana* (Walckenaer) from Christmas I. (WAM 92/531–532): *66–68*, male, left pedipalp: *66*, prolateral; *67*, retrolateral; *68*, ventral; *69–72*, female, epigyne: *69*, ventral; *70*, dorsal; *71*, posterior; *72*, lateral.

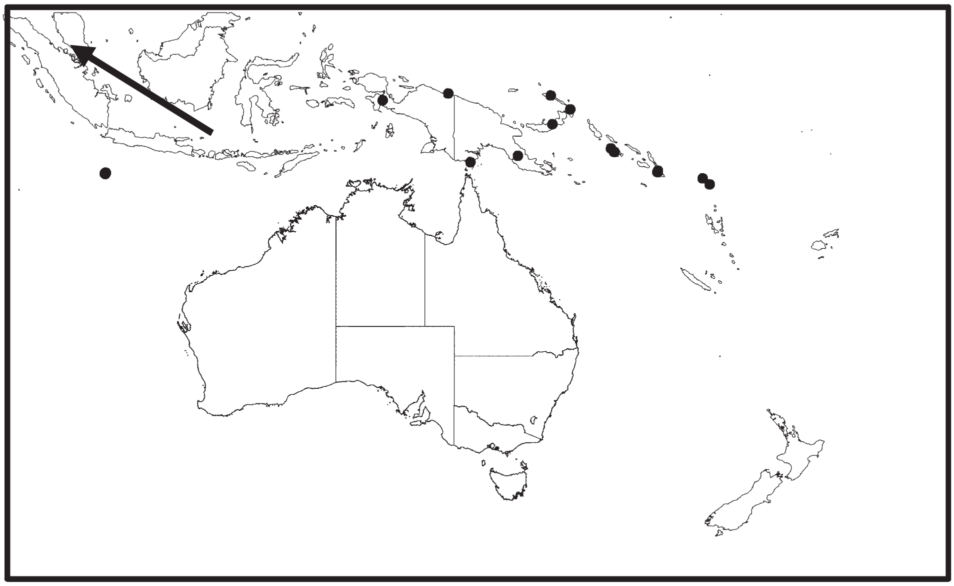


**Fig. 73.** Recorded distribution of *Nephila antipodiana* (Walckenaer) in the study area. The range of this species also extends to the north-west into Asia.

*Sternum*. Brown laterally, with broad medial yellow stripe; cordate, barely extending between coxae IV; without protuberances adjacent to coxae.

*Legs*. Most segments brown, femur and tibia with faint annulations; without tufts of setae.

*Abdomen*. Mostly yellow, except region surrounding spinnerets, which is black-brown; dorsal scute present; two pairs of sigillae; book-lung covers with 3–4 grooves.

*Dimensions* (*mm*). Total length 2.80. Carapace length 1.41, width 1.10. Eyes: AME 0.01, ALE 0.09, PME 0.09, PLE 0.08, AME–AME 0.13, AME–ALE 0.06, PME–PME 0.11, PME–PLE 0.12, PLE–ALE 0.01, eye group width 0.61, MOQ front width 0.35, MOQ back width 0.29, MOQ length 0.23. Sternum length 0.79, width 0.74. Abdomen length 1.80, width 1.07. Pedipalp: femur 0.34, patella 0.21, tibia 0.19, tarsus (cymbium only) 0.59, total 1.33. Leg I: femur 2.13, patella 0.59, tibia 1.60, metatarsus 2.30, tarsus 1.15, total 7.77. Leg IV: femur 1.51, patella 0.42, tibia 1.01, metatarsus 1.50, tarsus 0.81, total 5.25.

### Remarks

Originally described by Walckenaer (1842) from an unknown number of specimens collected from New Zealand, the distribution of this species was reduced to South-East Asia by Dahl (1912). A single adult female lodged in MNHN labelled 'Nephila imperialis Dols. Type de antipodiana Walck. E. Simon det. N$^{elle}$ Zèlande Quoy et Gaimard' is here considered to represent a syntype of that species. As no species even faintly resembling *N. antipodiana* has ever been collected from New Zealand we consider that the locality data provided with this specimen is in error, and therefore *N. antipodiana* can be excluded from the New Zealand fauna.

*Nephila celebesiana* was named from '1 ♀' from 'Boeton, Bau-Bau' (Strand 1915), but we have found three female syntypes with identical locality data in SMF (4018) that conforms to Strand's description. These three females are in a vial labelled 'Typus' and we therefore presume that the published details are in error, and that the three specimens are syntypes.

Some populations of this species have large yellow abdominal spots, as presented in the photograph by Koh (1989). All populations recorded in this study lack such spots.

### New synonymies

Our examination of the type material of *Nephila nigritarsis insulicola*, *N. ambigua*, *N. imperialis* var. *novaemecklenburgiae*, *N. sarasinorum* and *N. celebesiana* clearly demonstrates that all three names are synonyms of *N. antipodiana*. Kuntner (in litt.) has placed *N. laurinae* as a synonym of *N. antipodiana*, and we follow his usage.

### Common name

The name 'Asian golden orb-weaving spider' refers to the primary distribution of this large, forest dwelling species.

### Distribution

*Nephila antipodiana* is found over much of South-East Asia, including Indonesia, Singapore, Thailand, Burma, Philippines and China. Within the present study area, it has been recorded from Christmas I., West Papua, Papua New Guinea, northern Queensland in Torres Strait, and the Solomon Is. It is much less common in museum collections than other *Nephila* spp. in the study area.

## ***Nephila edulis*** (Labillardière)
## Australian golden orb-weaving spider

(Figs 7, 74–87)

*Aranea edulis* Labillardière, 1799: 240–241, plate 12, figs 4–6.
*Nephila imperatrix* L. Koch, 1872: 159–160, plate 13, figs 3, 3*a*–*c*.
*Nephila eremiana* Hogg, 1896: 318–320, fig. 3.

*Meta aerea* Hogg, 1896: 320–321, figs 4–5. **New synonymy.**
*Nephila picta* Rainbow, 1896: 321–322, plate 19, fig. 1. **New synonymy.**
*Nephila meridionalis* Hogg, 1910: 59–61, figs 1, 1*a–c*. **New synonymy.**
*Nephila adelaidensis* Hogg, 1910: 61–62, figs 2, 2*a–c*. **New synonymy.**
*Nephila meridionalis hermitis* Hogg, 1914: 72, plate 1, fig. 2. **New synonymy.**

## Type material

*Type*(*s*) *of Aranea edulis*. New Caledonia (not found in MNHN, lost, not examined).

*Syntypes of Nephila imperatrix*. 3 ♀, 1 juv. ♀, without locality data (presumably from Port Mackay, Rockhampton, or Bowen, Qld, Australia) (ZMH, Museum Godeffroy No. 7538); 1 specimen, 'Neuholland' (SMNS, not examined).

*Syntypes of Nephila eremiana*. 1 ♀, 'Goyder's River, Bagots Creek, camps 11 . 23 . 25, Oodnadatta, Henbury, Dalhousie' (Horn Expedition) (MV K-933); 1 ♀, Oodnadatta, South Australia, Australia (27°33′S, 135°27′E), Horn Expedition (BMNH 1897.1.18.1); 1 ♀, central Australia, B. Spencer (MNHN 124–97).

*Holotype of Meta aerea*. ♂, 'camp 05' and 'camp 25' (= Tempe Downs Station, NT, Australia, 24°23′S, 132°25′E), (Horn Expedition) (MV K-934).

*Holotype of Nephila picta*. ♀, Condobolin, NSW, Australia (33°05′S, 147°09′E), S. J. A. Roberts (AM KS7826).

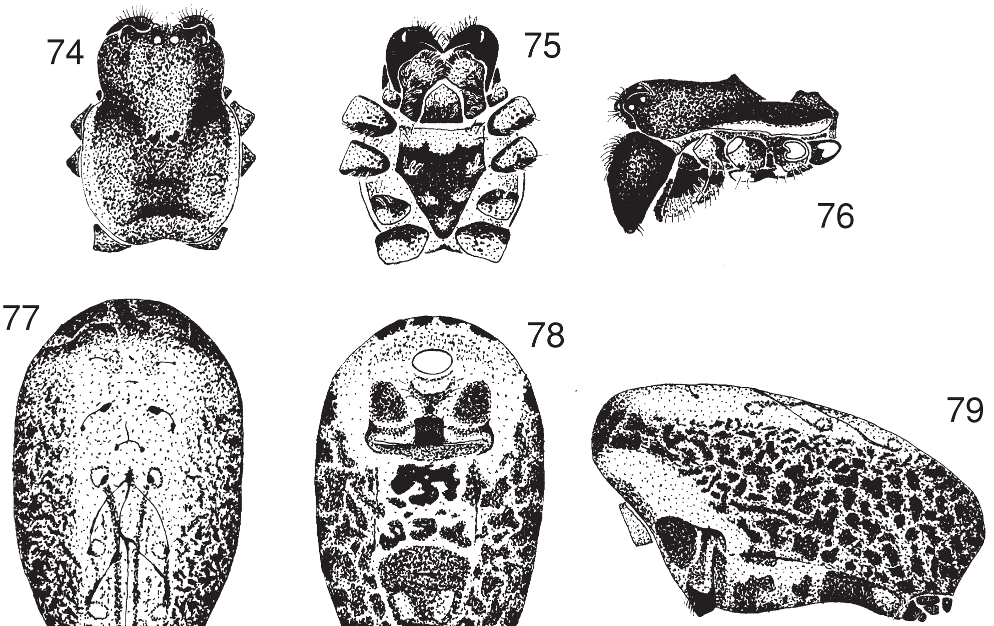
*Holotype of Nephila meridionalis*. ♀, Kangaroo Island, SA, Australia (~35°52′S, 137°14′E) (SAM N1985227).

*Syntype of Nephila adelaidensis*. 1 ♀, SA, Australia (SAM N1985228).

*Syntypes of Nephila meridionalis hermitis*. 1 ♀, Hermite I., Montebello Islands, WA, Australia (20°28′S, 115°31′E), 14.viii.1912, G. D. Montague (BMNH 1924.3.1.242); 1 ♀, same data except 1.vi.1912 (BMNH 1924.3.1.243).

## Other material examined

**Australia: Australian Capital Territory:** Belconnen (WAM T41879); Black Mt (ANIC); Botanic Gardens, Canberra (ANIC); Canberra (ANIC); Najor Orchard, Canberra (ANIC); Scullin (ANIC). **Cocos (Keeling) Islands:** no further locality data (AMNH; QM S42943); Pulo Klapa Satu (QM S42945); Trannies Beach (WAM T41865); West I. (QM S28946). **New South Wales:** 5 miles (= 8 km) E of Albury (MV K-3281); Armidale (AM KS33802); Ballimore (AM KS33459); *c.* 8 km WNW of Balranald (ANIC); Bargo (AM KS33453); Bellata (AM KS10416); Blackheath (MV K-3288, K-3363); Blacktown (AM KS733); Blayney (AM KS33631); Broken Hill (AM KS33471, KS33481, KS33738); 15 miles NW of Byrock (AM KS34063, KS33675); Caldwell (MV K-3353); Camden, Razorback (AM KS34060, KS33641); Chatswood (AM KS33483); Conoble (AM KS33454); Coolah Valley (AM KS33769); Cooranbong (AM KS33800); Deniliquin (AM KS33622); Dunedoo (MV K-3294); East Maitland (AM KS45731); Finley (AM KS8675); Fivedock (AM KS33460); Fort Grey Basin (QM S28878); Goolagong (AM KS33593); Guildford (MCZ); Guyra (AM KS33610); Ingleburn (AM KS33740); Kyogle (AM KS33458); Lake Cargelligo (AM KS 7836); Lake Cowal (ANIC); Mandurama (AM KS45732); Maroubra (AM KS7837); Mittagong (AM); Moombooldool (AM KS33788); Moree (AM KS33808, KS33810); Nabiac (AM KS7838); Narrabeen Lake (AM KS45726); near Murrurundi (AM KS33478); Newtown (AM KS7839); 85 km N of Nyngan (MV K-3328); Parkes (AM KS33775); E of Parkes (AM KS33670); Parklea, via Blacktown (AM KS33742); Queanbeyan (ANIC); Revesby (AM KS33470); Round Hill (AM KS33673); Rouse Hill (AM KS33474); Spring Ridge, via Quirindi (AM KS33466); 'Springerlee' gates S of Neville on Kentucky Rd (AM KS29824–5, KS29821); Sydney (MNHP 1911; MCZ); 6 km SE of Wagga Wagga (WAM T41875–6); 10 km S of Wagga Wagga, near Collorboralli Ck (WAM T41877–8); Walgett (AM KS17231); Waterfall (AM KS33464); Willow Tree, New England Hwy (QM S33687, S33689); Yancannia (MV K-3279); Yass (AM KS40649); S of Yathong Nat. Res. (MV K-3325); Young



**Figs 74–79.** *Nephila edulis* (Labillardière), female from Harvey, WA, Australia (WAM 98/659): *74*, cephalothorax, dorsal; *75*, cephalothorax, ventral; *76*, cephalothorax, lateral; *77*, abdomen, dorsal; *78*, abdomen, ventral; *79*, abdomen, lateral.

(ANIC). **Northern Territory:** Alexandria Station (AM KS33745); Alice Springs (AM KS33770, KS41034; CAS; MV K-3357); 39 km E of Alice Springs (ANIC); between Alice Springs and Halls Ck (MV K-3316, 3283, 3879); Uluru (Ayers Rock) (MV K-3276); Uluru (Ayers Rock), Uluru Natl Park (WAM T41866); Barkley Highway-Barracoola Road Junction, beside bore (QM S42946); 17 km S of Barrow Ck (NTMAG); Barry Cave, Barkley Hwy (AM KS33642, KS33792); Borroloola (MV K-3298); Borroloola Inn, Borroloola (SAM); Cattle Ck, AMG 770626E 8072248N (NTMAG); Cattle Ck, AMG 771996E 8052307N (NTMAG); Ellery Ck, Fincke Gorge Natl Park, 82 km W of Alice Springs (CAS); Ellery Ck, MacDonnell Ranges (SAM N1985221); Groote Eyelandt (AM KS73456); 16 miles (= 26 km) E of Hay R., near Qld border (AM KS33472); Idracowra Station, Finke R. (SAM); Jabiru Residency (WAM T41867); east of Lake Mackay from Sandy Bight Junction to Sandford Cliffs (ANIC); Lander R., Mala Paddock (NTMAG); Liebig Bore (WAM T41868); MacDonnell Ranges (SAM); Mt Cahill (ANIC); Mt Olga (ANIC); Narwietooma Homestead (SAM); Newcastle Waters Stn (NTMAG); Owen Springs (NTMAG); Palm Springs, No 2 Kimberleys (QM S28974); 23 miles (= 37 km) N of Renner Springs (CAS); Roper Ck crossing on Mataranka Homestead Rd (NTMAG); Roper R. region (MV K-3280); Tanami, Government Borehole (ANIC); 2 km S of Tennant Ck (NTMAG); 93.5 km W of Timber Ck (WAM T41869–70); Todd R. Block, *c.* 50 km SE of Alice Springs (MV K-3311); Trephina Gorge Natl Park (NTMAG); Undoolya (MV K-3305); Yirrkala (AM KS33799); Yulara Resort, via Uluru (WAM 94/1945–1956). **Queensland:** Albion Heights, Brisbane (QM S33086); Almaden (AM KS33463); Ambathala (QM S33109); Aratula (QM S33097); Berkina Bore, Cluny Station (QM S28881); Birdsville (AMNH); Birdsville Track to Mt Isa (MV K-3873); E branch of Blackfellas Ck (QM S28875); Brisbane (QM G305, S28874, S28915; MV K-3295); Buhooha, 26 miles (= 42 km) SE of Roma (MV K-3282); Bundaberg, Baldwin Swamp (QM S25351, S25353); Bunya (QM S66810); Cairns (QM S28937); Camp 19 (AM KS33479); Camp 21, Annandale Station (AM KS33475); Camp 23, 30 miles (= 48 km) NW of Birdsville (AM KS33480); Canal 92 Rd crossing, Cape York (QM S66811); Cania Gorge (WAM T41872); Carnarvon Range (QM S28910); Charleville (MV K-3875); Charters Towers, Thornborough College (QM S31081); Childers (QM S33067); Chillagoe (QM S28914, S28931); Chinchilla on Condamine R. (WAM 92/1968, T41873–4); 18 km ESE of Cloncurry (ANIC); Closeburn (QM S33069); Condamine (AM KS34061); Cooktown (MNHP 18113); Cooladdi (QM W1258); Cooloola (QM S33055); Cuddapan Station, near Windorah (QM S28923, S33064); Cunnamulla (AM KS33468, KS34064); Davies Ck (QM S28960); Dawson R. Gorge (QM S36404); Delta Station, near Blackall (SAM); Dryander (AM KS12837); Eidsvold (QM S33098); Emerald (QM S33077); 15 miles (= 24 km) W of Emerald (QM S28966); Fletchers Ck, 43 km N of Charters Towers (AM KS42351, KS43599); Gary Mt, near Toowoomba (QM S33066); Georgetown (MV K-3271); Gladstone (QM S46669); Goat Rock, Babbiloora Station (QM S28870); Great Basalt Wall (WAM 94/1839–1842); Hammond Downs, Coopers Ck (MV K-3286); Hermitage Research Station, Warwick (QM S28986); Hughenden (QM S28938); 3 km SW of Ipswich on Cunningham Hwy (WAM T52331); Isisford (QM W625); Jondaryan (QM S28912); Julia Ck (QM S31082, S33058); Kalbar (AM KS28617); Kaliduwarry Station, Coll. 620 (AM KS33484); Kaloola Station, 200–250 m (QM S21238); Karumba (MV K-3324); Kensington Downs (AM KS33613); Koongal (MV K-3274); Kroombit Tops (QM S28876); Kroombit Tops, Barracks (QM S28920); Kroombit Tops, Lower Kroombit Ck (QM S28879); Kroombit Tops, northern escarpment (QM S28882); Kumbarilla, via Dalby (QM S33682); Kuranda (MV K-3303, K-3362); Lake Moondarra (QM S25091); Lake Moondarra Lookout, Mt Isa (QM S30697); Lake Moondarra turnoff, Mt Isa, 300 m (QM S33761); Lake Nappanerica (QM S33059); Lake Nuga Nuga (QM S28872); Lethbridge Pocket, Mt Moffatt Station (QM S33072, S33105); Lindeman I. (AM KS48702); Malling, between Quinalow and MacLagen (QM S6306); Mareeba (MV K-3876); Marraba Copper Mine, Mt Isa (AM KS30271); Mayne (AM KS30424); Meelia Stn, via Capella (QM S26320); Merina Downs [Merino Downs) (QM S33102); 18 km NE of Middleton (ANIC); Moonie (QM S28924); Mt Bauple (SAM); Mt Cameron Station, Winton (QM S28936, S28977); Mt Colliery, Yangan (Field 3) (QM S28959); Mt Dryander, lower slopes (AM KS12836); Mt Elliott Natl Park, Bruce Hwy and Mt Cleveland Rd junction (WAM T44700); Mt Emlyn, via Milmerran (MV K-3287); Mt Garnet (QM S28964; AM KS6201); 46 km SW of Mt Garnett (AM KS42446); Mt Isa, E Leichhardt R., 1 km downstream dam wall (AM KS30263); Mt Moffatt Natl Park, Cathedral Rock, 1000 m (QM S33081); Mt Molloy (QM S28909, S66812); Mt Munro, Elderslie Station (QM S28877); Mt Pleasant, Dalby (QM W428); Mulgowie (QM S28913, S28922); Muncoonie Lakes (QM S28970, S33056, S33088, S33104); Murphys Ck (QM S28934); Musgrave Station, 22 miles N of (QM S33106); Musgrave Station, 7 miles (= 11 km) NE of (QM S28916); Musgrave, 29 miles S of (QM S33054, S33089); near Lake Moondarra, Mt Isa, 420 m (QM S41984); near The Tombs, Moffat Station (QM S28930); Nerimberah, via Rockhampton (QM S9928); Newmarket, Brisbane (QM S42648); 6 km S of Normanton (MV K-3270); 'North Qld (Gulf) and Roper Estuary' (MV K-3355); north half of Birdsville Track (MV K-3330–3331); northern Queensland (AMNH); Nundah, Brisbane (QM S28886); Old Annandale Homestead, Eyre Ck, Simpson Desert (QM S33065, S33073); Percy Isles (QM W574); Proa Stn, 20 miles S of Nelia (QM S33075); Rockhampton (QM W504, S28933); Rocky Knoll, 11 miles (= 17.7 km) N of Moombah Station (QM S28871); Rocky Scrub Ck, Junction View (QM S28919, S28921); 10 miles E of Rokeby Station (QM S33061); Rosella Plains (QM S28929); S of Mt Larcom (QM S28932); Sapphire (SAM); Stannery Hills (QM S28979); ? Station, 40 miles W of Westmar (QM S28880); Storm Dam, Broken R., 'Wandovale' (QM S42947); Tarragindi (QM S28885); Tennyson Power House, Tennyson (QM S28928); The Gap, Brisbane (QM S28884); Thylungra (MV K-3299); Tooloona (or Taloona?) Homestead, SCQ (QM S28911); Townsville (AM KS36941; SAM); Tranby Homestead, W of Winton (MV K-3307); Undara Lava Tunnels, 100 Mile Swamp (QM S24998); Upper Brookfield (QM S33085); Villeneuve, via Kilcoy (QM S28918); Warro Station (now Charnwood Station), via Lomead (QM S33074); 94 km ENE of Warwick on Cunningham Hwy (WAM 92/1965–1967); Wellers Hill, Brisbane (QM S28927); West Burleigh (QM S28873); Wilston Heights, Brisbane (QM S28917); Wolfgang Peak, Peak Downs (QM S28883); Wolfgang Peak, south slope (QM S28962); Wolfram (AM KS6203; QM S28908); Wyandra (QM S28926); Yandaburra, 125 km SW of Springsure (QM S28940); Yaramulla Station, near Mt Surprise (QM S28935); Yarronvale, 60 miles (= 97 km) W of Charleville (MV K-3313); Yeppoon (QM S33070). **South Australia:** Adelaide (SAM, WARI, ZMB 765); Aldinga Scrub Reserve (SAM); Algebuckina Waterhole, Neales R. (SAM); Antikoolirrinna Waterhole, between Hamilton and Eringa Stations (SAM); Arcoona Ck, Gammon Ranges (SAM); Arcoona Ck, Gammon Ranges, Sambot Waterhole to Base Camp (SAM); Baird Bay (WAM T41916); Balcanoona Homestead (WAM T41917); adjacent Beautiful Valley Caravan Park, near Wilmington (SAM); Belair, Mt Lofty Ranges (SAM); Beltana (SAM); between Yudnapinna and Carriewerloo (SAM); Blackiston (SAM); Bollard[s Lagoon] Station, S of Cameron Corner, on dog fence (MV K-3300); Bopeechee Railway Siding near Maree (SAM); Bordertown (SAM); Bowhill, R. Murray (SAM); Brighton, Adelaide (SAM); Bunyeroo Ck, ABC Range, Flinders Ranges Natl Park (SAM); bank of Bunyeroo Ck, Flinders Ranges (SAM); Barton Vale Home, Enfield (SAM); Bunyeroo Gorge (SAM); Burnside (SAM); Cadell (SAM); 13.2 km NE of Canegrass, along Radium Hill Powerline (SAM); Carappee Hill Cons. Park (SAM); Chambers Gorge, Flinders Ra. (WAM T41897–41906); Chowilla (SAM); Clarendon (AM KS32113); Cobdogla, near Barmera (SAM); Cooper Ck, 3 km upstream from Punt (SAM); 150 km N of Coober Pedy (AM KS22703); 21 km N of Cook (SAM); Copley-Birdsville Track (WAM T41918); Coward Springs (SAM); 20 miles (= 32 km) W of Cowarie [as Corowie] Station, Coll. 661 (AM KS33476); Dingley Dell Nat. Pleasure Resort (SAM); Dog Lake Rd, SE of Langhorne Ck (SAM); '407 miles E-W. line' (AM KS33784); 11 miles (= 18 km) S of Emu (WAM T41919); Eringa Waterhole (SAM); Finke R., Loc. 520 (AM KS33477); Flat Rockhole, Everard Range (SAM N1985166–7); Fowlers Bay (SAM); French Track, Simpson Desert (SAM); Glen Osmond

Road, Adelaide (SAM); Hambidge Conservation Park (SAM); Hammond (AM KS33462); 24 km N of Hughes (SAM); ICI Salt Fields, near Port Parham (SAM); Kangaroo I. (SAM); Kensington Gardens, Adelaide (SAM); 40 km E of Koonalda Station (SAM); *c.* 35 km E of Koonalda (ANIC); Krupp Hill, Granite Downs (SAM); Lake Callabonna (SAM); Lake Hamilton, 3 miles (= 5 km) from north end, Eyre Peninsula (SAM); Lake Hart (SAM); Langhorne Ck (SAM); Largs Bay, Adelaide (SAM); Lobethal, Mt Lofty Ranges (SAM); Loftia Recreation Park, Mt Lofty Ranges (SAM); Loxton (SAM); Marryatville, Adelaide (SAM); McLaren Vale (SAM); Meadows (SAM); W of Mimili (SAM); Modbury (SAM); Mt Barr Forest (AM KS28618); Mt Grainger (SAM); Mt Lofty (SAM); Mt Lyndhurst Station (WARI); waterhole 3 miles (= 5 km) N of Mt Sarah Station (SAM); 8 km NE of Mt Woodroffe (SAM); Muckera Rockhole (SAM); Murray Bridge (SAM); Musgrave Ranges (SAM N1985168; AM KS33467); Nalpa, Lake Alexandrina (SAM); Naracoorte (SAM); near East Well (AM KS33771); near mouth of Rocky R., Flinders Chase, Kangaroo I. (SAM); near Mungeranie bore drain (SAM); 'Oriantos', on road to Innamincka (MV K-3285); near Poeppel Corner, Simpson Desert (SAM); near Price, Yorke Peninsula (SAM); no further locality data (MV K-3284); North Middleback Ranges (SAM); 34 km W of Nullarbor Homestead (ANIC); Ooldea (MV K-3309; AM KS33807); Orroroo (SAM); Paralowie (SAM); Penola (SAM); Poole Ck, 42 km W of Marree (Alberrie Ck) (SAM); Port Augusta (SAM); Port Pirie (SAM); Punkah I. (SAM N1988439); Purple Downs, N of Pimba (SAM); Red Hill (WARI); Roonka Station, Blanchetown, alongside Cumbunga Ck (SAM); Rostrevor, Adelaide (SAM); Sandilands, via Ardrossan (SAM); Sedan (SAM); Sellick's-Aldinga Scrub (SAM); slopes of Scrubby Peak (SAM); south end of Lake Eyre North (SAM); South Gap Station, foot of Beda Hill (SAM); South Middleback Ranges (SAM); St Morris, Adelaide (SAM); Strathearn Homestead (SAM); Strzelecki Track, S of Lyndhurst (MV K-3304); Survey Locks Well, via Woomera (SAM); Tea Tree Gully, Adelaide (SAM); Unley Park, Adelaide (SAM); Vokes Hill Corner (SAM); 39 km SW of Vokes Hill corner (SAM); Waikerie, R. Murray (SAM); Weetootla Well, Gammon Ranges Natl Park (SAM); 2 km E of Weetootla Well, Balcanoona Ck, Gammon Ranges Natl Park (SAM); Wilpena Ck, Wilpena Pound (SAM); Wilpena Pound, Flinders Range Natl Park (WAM T41907–41915); Winbring (SAM); 5 km W of Wirrula, at road junction to Petina (SAM); Woodville, Adelaide (SAM); Yelpawaralinna Waterhole (SAM); Yunta Dam (SAM); Yurgo (SAM). **Tasmania:** 'Carinya', Sandford (TMAG J1592); East Risdon (TMAG J1647); Risdon Vale (TMAG J1590); Sorell (TMAG J953, J1595); South Hobart (TMAG J1594); Trevallyn (TMAG J1646). **Victoria:** near Albury (MCZ); Altona (MV K-3312); Avoca (MV K-3878); Balwyn (MV K-3360); Bendigo (MV K-3323); Bendigo, German Gully (MV K-3301); Broadmeadows (MV K-3317); Camberwell (MV K-3361); Canterbury (MV K-3315, K-3326); Cheltenham (MV K-3352); Condowie, Torrumbarry (MV K-3319); Dimboola (MV K-3314, 3881); Eaglehawk (AM KS33785; MV K-3322); Elaine (MV K-3349); Frankston (MV K-3320); Hampton (MV K-3877); Kew (MV K-3359); Koondrook (MV K-3308); Lilydale (MV K-3321); Melbourne (MV K-3292); Merbein (AM KS28665); Mooroopna (MV K-3297); Nilma (MV K-3291); North Melbourne (MV K-3874); Prairie (MV K-3310); 30 miles N of Rainbow, Wyperfeld Natl Park (MCZ); Seymour (SAM); Thornbury (MV K-3306); Thornton (AM KS32507); via Piangil (MV K-3327); Violet Town (WAM T41880–41895); Walwa (MV K-3296); Warrnambool (MV K-3289); Whipstick (MV K-3293); Wilkur (MV K-3329); Winnambool (MV K-3273); Wolgan Lookout (AM KS3433); Wyperfeld Natl Park (MV K-3354). **Western Australia:** 39 km E of Laverton (WAM T42046); 50 km towards Abydos Homestead from Woodstock Homestead (WAM T42276); 6 km SW of Gidgegannup (WAM T42039); 7 km S of Goongarrie (WAM T41963); 7–8 km WNW of Point Salvation (WAM T41853, T41928, T53598–9); 8 miles (12.8 km) N of Roy Hill (WAM T53925); 8 miles E of Warrarga (MCZ); 87 miles (= 140 km) before Warburton Mission on road from Cosmo Newberry (WAM T42420); Abrakurrie [Cave] (SAM); Airlie I., 30 km N of Onslow (WAM T42280); Albany Highway, just S of Arthur R. Crossing (WAM T57878); Albion Downs (WAM T42283); Alexander Spring (WAM T52259); Anjo Peninsula (AMNH); Applecross (WAM T52260); Bald I. (WAM 90/2001); Balladonia (AM KS33782); 21 miles (= 34 km) E of Balladonia Homestead (WAM T42284); 27 km S of Balladonia Motel (ANIC); Banganup Lake (WAM T52261); Barradale (WAM T42288); Barrow I. (WAM 92/547–557, T52263); Barrow I., Airport (WAM T41793); Barrow I., Mattress Point (WAM T41794); Barrow I., Shark Point (WAM T41795); Barrow I., Valley of the Giants (WAM 98/522, T41796–41804, T41996, T52262); Barrow I., WAPET Camp (WAM T41805); Beaufort R., Albany Highway, 2 km S of Beaufort R. Tavern (WAM T53922); Belmont, 219 Keyner Street (WAM T52264); Beta Ck, 3 km up from King George R. (WAM T41809, T41839); between 30–34 mile pegs, Great Northern Highway (WAM T53597); between Arrowsmith Lake and Naraling, sand plain (MCZ); Booanya (AM KS33776); Boolathana Station (WAM T42380, T46105); Boorabin (WAM T42029); Bowerbird Gorge, Cape Range Natl Park (WAM T41957); Broadwater (WAM T41810); Brooke I., Monte Bello I. (WAM T42278); Broome (WAM T41958; CAS; SAM); Broome, Reid Road (WAM T52265); Browse I. (WAM T41840); Bruce Rock (WAM 92/1969, T42010); Bullsbrook (WAM T42384); Bunbury (WAM T41921); Buningonia Spring area (WAM T42385); Buningonia Spring (WAM T42030); Burrup Peninsula, *c.* 2 km S of Withnell Bay (WAM T52347); Bushfire Rock (WAM T41841); Busselton (WAM T41973); Byford (WAM T41981); Cadjeput Gorge (WAM T42269, T42274); Calvert Range (WAM T41971, T57589); Canning Stock Route, Well no. 4 (WAM T41959, T42031, T52266–7); Canning Stock Route, Well no. 4B (WAM T41960); Canning Stock Route, Well nos 10–1 (MV K-3356); Canning Stock Route, Well no. 25 (WAM 92/1970); Canning Stock Route, Well no. 28 (WAM T42425); Canning Stock Route, Well no. 30 (SAM); Canning Stock Route, Well no. 31 (WAM T42426); Cape Preston (WAM T41552); Cape Preston (WAM T41553); Cape Range (WAM T52269); Cape Range [Natl Park), near Cape Range No. 2 [Oil) Well (WAM T52268); Cape Range Natl Park, Lakeside camp (WAM T41842); Cape Range, near cave C-139 (WAM 92/1971–3); Cape Range, near cave C-64 (WAM T44315); Cardabia Station, near Black Dam on Cardabia Ck (WAM 98/437); Cardup Nature Reserve (WAM T42011); Carnac I. (SMNH); Carnarvon (AMNH; SAM); Carrollgouda Well, 6 miles (= 10 km) E of Gee Gie (WAM T42386); 3 miles (= 4.8 km) NE of Carrollgouda Well (WAM T52270); Carson Escarpment (WAM T42012); Charlies Knob (WAM 92/1975); Cheritons Find (WAM 92/1976); City Beach (WAM T42286, T52271); 15 miles (= 24 km) before Cosmo Newberry on road from Warburton (WAM 92/1977); Culham (WAM T42034); Cunyu Station, 4 km N of Twenty One Well (beside State Barrier Fence) (WAM T44326); Dardanup (WAM T42035); Darlington (WAM 16/170, 92/1978); Dawerra Ck, S of Poonjurra Hill, Drysdale R. Station (WAM T41814); Denham (ZMB 24870); Denham/Monkey Mia (WAM T42013); Derby (AM KS33594); 2 km E of Drummond Cove (WAM T41961, T52273); Dryandra (WAM T42388); Drysdale R. Station (WAM T41962); Drysdale R. Station, Mt McCrann area (WAM T41812); Duketon region (WAM T52275); Dwellingup (WAM T42389); E of Anchorage Bay, Rosemary I., Dampier Archipelago (WAM T41924); East Chapman (WAM 32/2482); Edjudina Station (WAM T42036); Elashgin Nature Reserve, N side on Maitland Rd (WAM T41843); Ethel Ck Station (WAM T52242); Exmouth (WAM 92/559–566); Eyre Bird Observatory (WAM T57491); 'Fairfields', 13 km N of Bungulla (WAM T42381); Floreat Park (WAM T42390); Forrest R. Mission (MV K-3290, K-3350); Garden I. (WAM 92/1979, T42391, T52277); Gelorup (WAM T41844); Geraldton (WAM T41815, T42392, T52278; AM KS33744; ANIC; MCZ; MV K-3272); Gibson Desert Reserve, no. 2 trapline (WAM T42038); Gidgee Gold Mine (WAM T41922); Gidgegannup (WAM T42393); Giles (ANIC); Glen Cummings Gorge (WAM 92/1980–1981, T52279); Glen Forrest (WAM T42040); Glenayle camp, 0.5 km N of homestead (WAM T41823); Gleneagle Forest (WAM T42394); Goongarrie Station (WAM T41845–8); Grannys Soak (WAM T41849); Great Sandy Desert (WAM T52280); Great Sandy Desert, Eil Eil Spring (WAM T57648–9); Greenough (WAM T42041, T52274); Greenough Flats (WAM 92/1982); Greenshield Soak, Lake Magenta (WAM T42281); Gun I., Abrolhos I. (WAM T42383);

Hamilton Hill (WAM T42395); Hampton Tower, Roe Plains (WAM 95/1261–1270, T41975); Harvey (WAM 98/659, T42382; AM KS33605); Helena-Aurora Range (WAM T41983); Hermite I., Monte Bello I. (WAM T42279); Hillside Tin Mine (WAM 92/1986, T42277); Hope Downs (WAM T41811); Houtman Abrolhos, West Wallabi I., Pelican Point (WAM T41759); Hussah Bore, Gibson Desert (WAM T42037); Internal Gorge, Murchison R. (WAM T42410); Israelite Bay (WAM T42396); Jarrahdale (Alcoa) mine site (WAM T52328); Jarrahwood (WAM 23/174); Jubilee Downs Station, near Alexander I. (WAM T53923); junction of Midlands/Tabletop Roads, 17 km E of Dongara (WAM T52255); Jurien Bay (WAM T42397); Kalamunda (WAM T52281); Kalbarri (WAM T42398, T52284); 11 miles SE of Kalbarri (WAM T52343); Kalbarri Natl Park, 10 km on road to The Loop (WAM T52282); Kalbarri Natl Park, Murchison R., The Loop (WAM T42042, T52283); Kalgoorlie (WAM T42043–4); Karratha (WAM T41964, T42399); Kathleen Valley (WAM T42014, T42045); Kestrel Sinkhole (= Kestrel No. 1 Cavern, 6N-40?), 20 miles (= 32 km) N of Madura (SAM); Keysbrook (WAM T52285); Kimberley District (SMNH); King Edward R. Crossing (WAM T41813); Koolan I. (WAM 92/1987); Koongamia (WAM T41984); Kulin (WAM T42287, T42290); Kununurra (WAM T41923); Kurrawang [Nature] Reserve (WAM T52286); Kwelkan (WAM T42008); Laidlaw Range, Christmas Ck Station (WAM T42400); Lake Auld (WAM T52287); Lake Cronin (WAM T42401); Lake Culcurdoo (WAM T52272); Lake Dumbleyung, near Cooran Hill (WAM T52288); Lake Grace North (WAM 37/1745); Lake Kununurra, top of diversion dam wall (WAM T41986–41995); Lake Magenta, near Greenshield Soak (WAM T42402); 30 miles (= 48 km) W of Langi Crossing (CAS); Laverton (WAM 24/665); 1.3 km W of Learmonth (WAM T41965); Ledge Point (WAM T42047–8, T42285); Leeman Swamp (WAM T52289); *c.* 28 km NW of Leinster (WAM T51586–9); Lower Carawine Gorge, East Pilbara (WAM 92/1974, T42032, T52252, T52254); 12 km E of Madura (ANIC); Mandurah (WAM T52291); Maylands (WAM 98/438); Meenaar Industrial Park track (WAM T41850); Messenger Patch, 50 km SE of Yalgoo (WAM T42404); Middle I., Recherche Archipelago (WAM T52290); Miling (WAM T42049–50); 10 miles N of Miling (WAM T42405); Milly Milly Station (WAM 30/379–380); Minara Station, Mailman Hill, W of Murrin Murrin (WAM T53927); 10 km NW. by N of Mining Camp, Mitchell Plateau (ANIC); Mondrain I., Recherche Archipelago (WAM T41806); Monkey Mia (WAM T41925, T41966, T42210); Moonyoonooka (MV K-3358); Morley (WAM 90/1746); Mt Augustus (WAM 92/1983); Mt Brockman (WAM T41851); Mt Claremont (WAM T42016–42028); Mt Cooke (WAM T41977); Mt Hawthorn (WAM 36/1204); 10 miles (= 16 km) S of Mt Holland (WAM T42406); Mt Jackson (WAM 39/834, 92/1984, T52293–4); Mt Pierre (WAM T52295); Mt Pleasant (WAM T42407); Mt Ragged, Cape Arid Natl Park (WAM T41982); Mt Webb (WAM T52296); Mulga Downs Station, Bloodwood Bore (WAM T42206); Mullaloo (WAM T41926); Mullewa (MCZ); Mundaring Dam (WAM T42409); Mundaring Weir (WAM T42408, T52297); Murchison District (WAM 11/4271); Nambi Station, Kiar Paddock (WAM 90/570); Nambung R. (WAM T42411, T52298); Narembeen (WAM T52299); Narndee Station (WAM 37/2240–1); Narrogin (WAM T46106); near Kununoppin (WAM T41765); near Stirling Dam (WAM T42416); Neerabup, 62 Sublime Glade (WAM T41852); Nerren Nerren Station (WAM T52326); Nerren Nerren Station (WAM T41826); Newdegate (WAM 25/321); Norseman (MV K-3318); North Irwin R. (WAM T42412); North Subiaco (WAM 11/4297); Northam (AM KS33774, KS33789); Northampton (WAM 13/7227); Nullarbor (ANIC); Nullarbor Plain, SE of Reid (WAM T41974, T41985); Oakford (WAM T41807); old gravel pit on road between Fitzroy Crossing & Derby (WAM T52276); Old Homestead Cave, 6N-83 (WAM T41972); Pallottine Mission (WAM 90/619); Parkeston, near Kalgoorlie (WAM T41967, T52300); Parmelia (WAM 95/479); Pelican Point, West Wallabi I., Houtman Abrolhos (WAM T41808); Perth (AM KS33456); Rat I., Easter Group, Houtman Abrolhos (WAM T41968, T42282, T42291, T52301–2, T53928); Rawlinson Range (ANIC); Red Sands (WAM T52303); Riverton, 413 Riverton Drive East (WAM T42413); Roebourne (MV K-3278); Rosemary I., Dampier Archipelago (WAM T42414); Rottnest I. (WAM T52304–6); Rottnest I., Bathurst Point (WAM 30/629–630); Roy Hill Station, homestead area (WAM T42207); Rudall R. Natl Park (WAM T53356); Rudall R. Natl Park, Tjingkulatjatjarra Pool (WAM T53355); Rudall R., camp (WAM T52307); Rudall R., W. at campsite (WAM T52308); S of Glenayle Homestead (WAM T42509); S of Moore R. Natl Park (WAM T52292); S of Pinjarra (WAM T41970); S side of Greenough R., approx. 3 km upstream from mouth, S of Geraldton (WAM 95/460–478); Sabina R. (WAM T41978–80); Shark Bay (WAM T52309); Sorrento (WAM T42415); South Bunbury (WAM T52253); southern part of Hermite I., Monte Bello I. (ANIC); Spillway Creek road crossing (WAM T52310); St George Ranges (SMNH); Sten Park, Rottnest I. (WAM T41969); Surveyors Pool, Mitchell Plateau (MV K-3348); Swanbourne (WAM T52311); Theda Station (WAM T41927, T53600); Thornlie (WAM T52312); Tim Ealey Hill (WAM T42272–3); Trayning (WAM T42417); Upper Liveringa Pool (as Levarynga) (SMNH); Vlamingh Head, Cape Range (WAM T53601); Walcott Inlet (South) (WAM T41854); Walk Walkin (WAM 35/1438, 40/1084); Walkaway (WAM 33/381–382); Wanneroo (WAM T42418); Warburton Mission (WAM T42423); Warburton Range (WAM T42289, T42421–2, T52313; SAM); Warrawagine Station (WAM 34/1633); Weaber Range, *c.* 20 km NNEof Kununurra (WAM T53602); Weebubbie Cave and doline (6N-2) (WAM T42015); Weeli Wolli Ck, *c.* 47 km SW of Marillana (WAM T51578); Weld Spring (WAM T52314); Well no. 28, Canning Stock Route (WAM T42525); Wembley Beach (= Floreat Beach) (WAM T42424); Weowanie Rock (WAM T52315); West Wallabi I., Houtman Abrolhos (WAM T42432); Widgiemooltha (WAM T52316); Winduldarra Rockhole (WAM T41976); 100 km N of Windy Corner, Gary Junction Track (WAM T53603); Wingellina Hills (WAM T42419); Wittenoom (WAM 92/1985); Wittenoom Gorge (CAS); Wongan Hills area (WAM 94/1864–1865); Woodman Point (WAM T52317); Woodstock Station Homestead (WAM T42271); Woodstock Station (WAM T42270, T42275); Wooleen Station (WAM 32/1895); Wooroloo Brook, Red Hill (WAM T42427); Wubin (WAM T42428); Wyndham (MV K-3275); 22 miles (= 35 km) NE of Yuna (WAM T52318); Yundamindra (WAM T42429–30, T52319); Yunderup (WAM 90/1747, T53604). **New Caledonia:** Bouloulparis (WAM T41920); Gilles (MNZ); 7 miles (= 11 km) SE of La Foa (AMNH); Nouméa (MNHP); Tyto Cave, Gilles area (MNZ); no precise locality (MNHP including 1360–81; SMNH 133/716). **New Zealand: Auckland:** Glen Innes (NZAC); Mangere East (NZAC); Mt Roskill (NZAC); Papatoetoe (NZAC). **Papua New Guinea: Eastern Highlands Province:** Kiote (= Kiobe?) (ZMB 24875); **Milne Bay Province** Misima I. (MV K-3880). **Unlocated sites:** (AM KS33469, KS33485; ZMB 24872–4, 24876).

### Diagnosis

Females of *N. edulis* differ from all other Australasian species by the following combination of characters: sternum without tubercles or with very small tubercles (Fig. 76), and carapace approximately same length as or longer than tibia IV (Fig. 7). Males can be recognised by the lack of a subdistal triangular protuberance on the conductor and a slightly curved conductor (Fig. 80, 81).

### Description

#### Female (Australia: WA: Barrow I., WAM T41801)

*Carapace* (Figs 74, 76). Dark red-brown, with paler markings on the lateral and posterior edges; densely covered with white setae, especially on pars cephalica; deep broad fovea present; dorso-medial horns present; antero-lateral margins with red-orange crenulated mound that opposes cheliceral boss; chilum present, medially divided.

*Chelicera.* Black, posterior face red-yellow; cheliceral boss covered with tuberculations; fang furrow with three large teeth (medial largest) on anterior furrow, and four large teeth (sub-basal tooth the largest) on posterior furrow (Fig. 13); cheliceral denticles present between tooth rows (Figs 13, 14).

*Maxilla*. Dark brown laterally and posteriorly, red-brown medially and with yellow mesal margins.

*Labium*. Dark brown laterally and posteriorly, with yellow anterior and mesal regions; much longer than broad, anteriorly rounded.

*Pedipalp*. Femur and patella brown, tibia becoming black distally, tarsus black.

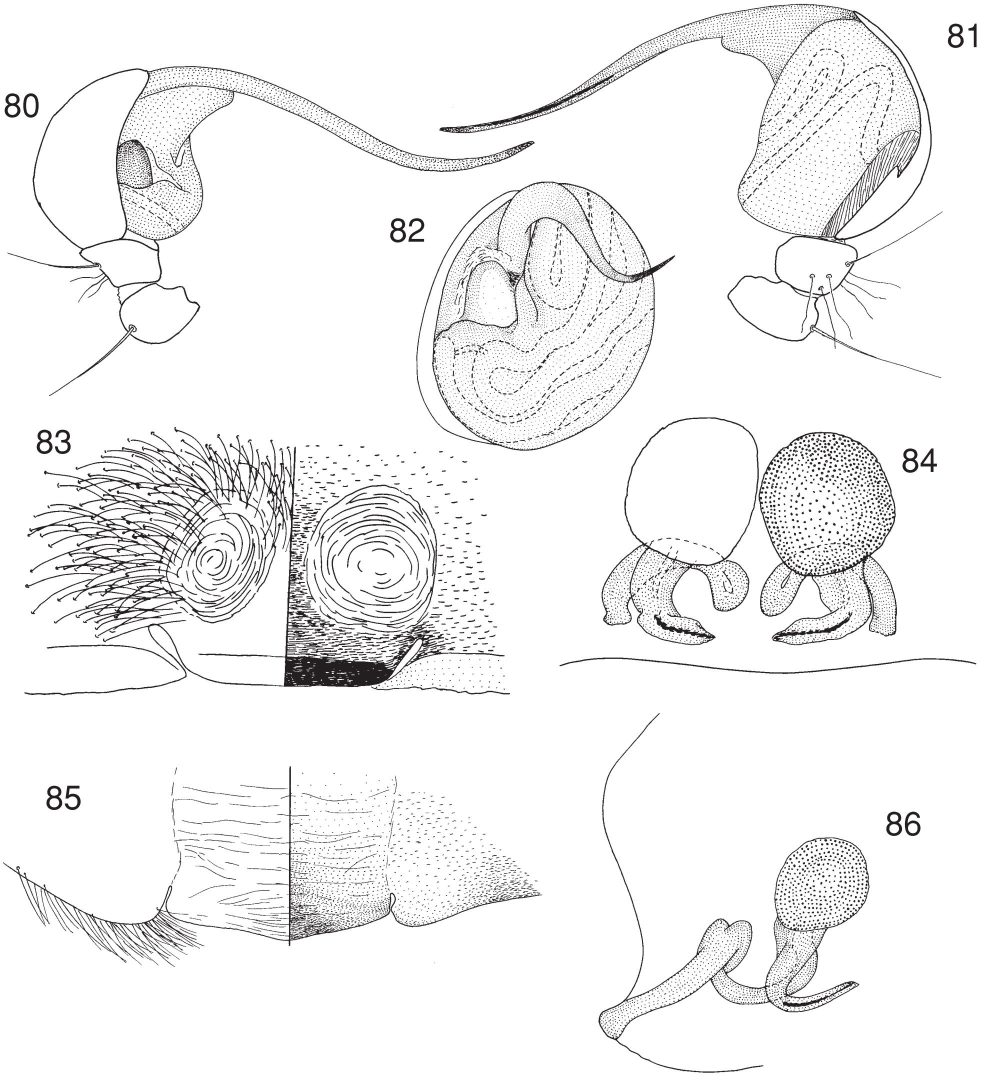
*Sternum* (Figs 12, 75, 76). Anterior third yellow, posterior two-thirds brown with two pairs of large yellow spots laterally and a single large yellow spot posteriorly; cordate, not extending very far between coxae IV; without any protuberances.

*Legs*. Coxae with dark brown anterior and posterior faces, medial regions yellow; other segments mostly dark brown, except for tarsus that is black; tibia and metatarsus IV with tufts of setae.

*Abdomen* (Figs 77–79). Pale yellow brown, with slightly darker markings on posterior margins; rounded, twice as long as broad; dorsal surface with two pairs of large sigillae; ventral surface with one pair of sigillae and one unpaired sigilla midway between epigastric furrow and spinnerets; book lung covers brown and with several conspicuous grooves; with large sclerotised patch anterior to epigyne.

*Epigyne* (Figs 83–86). Brown with two deep depressions separated by a median raised septum; lateral margins with long setae converging medially; copulatory duct opening laterally inserted at the end of groove; internally with one pair of large oval spermathecae; copulatory duct long and slightly convoluted.

*Dimensions* (*mm*). Total length 22.30. Carapace length 9.90, width 6.72. Eyes: AME 0.33, ALE 0.21, PME 0.22, PLE 0.17, AME–AME 0.38, AME–ALE 1.00, PME–PME 0.46, PME–PLE 1.19, PLE–ALE 0.31, eye group width 3.53, MOQ



**Figs 80–86.** *Nephila edulis* (Labillardière) from Barrow I., WA, Australia: *80–82*, male (WAM T41795), left pedipalp: *80*, prolateral; *81*, retrolateral; *82*, ventral; 83–86, female (WAM T41801), epigyne: *83*, ventral; *84*, dorsal; *85*, posterior; *86*, lateral.

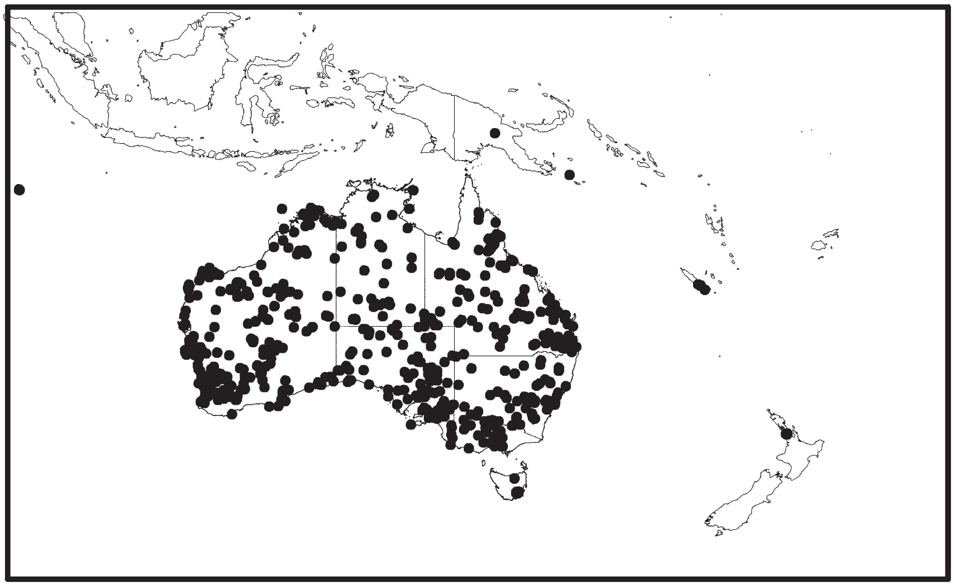


**Fig. 87.** Recorded distribution of *Nephila edulis* (Labillardière).

front width 1.03, MOQ back width 0.97, MOQ length 0.69. Sternum length 5.65, width 3.70. Abdomen length 11.50, width 6.45. Pedipalp: femur 3.07, patella 1.59, tibia 1.90, tarsus 3.45, total 10.01. Leg I: femur 14.22, patella 3.79, tibia 11.83, metatarsus 17.49, tarsus 2.86, total 50.19. Leg IV: femur 12.99, patella 3.03, tibia 7.59, metatarsus 12.37, tarsus 2.77, total 38.75.

### Male (Australia: WA: Barrow I., WAM T41795)

*Carapace.* Dark brown posteriorly and laterally, with broad median yellow section; covered with very fine white setae; fovea absent; dorso-medial horns absent; chilum absent.

*Chelicera.* Yellow, fang dark brown; cheliceral boss covered with tuberculations (Fig. 17); fang furrow with three teeth on anterior margin and three teeth on posterior furrow; cheliceral denticles present between tooth rows.

*Labium.* Brown laterally, yellow medially and anteriorly, much longer than broad, anterior margin forming obtuse point.

*Pedipalp* (Figs 18, 80–82). Yellow, except for brown cymbium and palpal sclerites; patella and tibia each with one macroseta; tibia with three retrolateral and three dorsal trichobothria; paracymbium small and distally rounded; conductor and embolus slightly curved; embolus situated within conductor groove.

*Sternum.* Brown laterally, with broad medial yellow stripe; cordate, barely extending between coxae IV; without protuberances adjacent to coxae.

*Legs.* Most segments brown, femur and tibia with faint annulations; without tufts of setae.

*Abdomen.* Dorsal surface mostly yellow with mottled brown patches medially and posteriorly, ventral surface mostly dark brown or black; dorsal scute present; two pairs of sigillae; book-lung covers without grooves.

*Dimensions* (*mm*). Total length 3.80. Carapace length 1.85, width 1.36. Eyes: AME 0.15, ALE 0.10, PME 0.82, PLE 0.70, AME–AME 0.12, AME–ALE 0.05, PME–PME 0.10, PME–PLE 0.13, PLE–ALE 0.75, eye group width 0.65, MOQ front width 0.36, MOQ back width 0.28, MOQ length 0.22. Sternum length 1.04, width 0.76. Abdomen length 2.50, width 1.50. Pedipalp: femur 0.37, patella 0.22, tibia 0.17, tarsus (cymbium only) 0.55, total 1.31. Leg I: femur 2.68, patella 0.70, tibia 1.94, metatarsus 2.94, tarsus 1.12, total 9.38. Leg IV: femur 1.81, patella 0.51, tibia 1.12, metatarsus 1.90, tarsus 0.80, total 6.14.

### Variation

There is very little colour pattern or morphological variation within *N. edulis*, apart from some very minor differences in epigynal shape. Males of this species vary significantly in size by almost an order of magnitude; this is not the case for *N. plumipes* (Elgar *et al.* 2003*b*).

### Remarks

Despite the lack of type material for *Aranea edulis*, there appears to be little doubt concerning the identity of this widespread and abundant species. Some variation has been found in the morphology of the epigyne in a few specimens, but the differences are very slight and are not supported by any concordance with geographic patterns or by the allozyme data (see above).

The original label associated with the syntype of *Nephila eremiana* lodged in MV bears more than one locality, and it is unclear from where the specimen was collected. Examination of the female holotype of *N. picta* from Condobolin, NSW, reveals that Dahl (1912) was incorrect in assigning this species as a junior synonym of *N. plumipes*. The specimen lacks the sternal tubercles characteristic of that species, and possesses an epigyne consistent with other females of *N. edulis*. Therefore, we treat *N. picta* as a synonym of *N. edulis*. As noted above under *N. plumipes*, Berland (1931) mismatched the males and females of *N. plumipes* and *N. edulis* in his redescription of these species, a mistake that was corrected by Chrysanthus (1971).

Some populations of *N. edulis* appear to be transient with individual specimens appearing and disappearing over relatively short periods of time. This is particularly true in New Zealand where they appear in the North I. 'every few years' (G. Hall, personal communication), and in Tasmania (Green 1981).

### Common name

The common name used here – 'Australian golden orb-weaving spider' – refers to the primary distribution of this species.

### Distribution

*Nephila edulis* occurs in Australia, Cocos (Keeling) Is, Papua New Guinea, New Caledonia and New Zealand. In Australia, it has been recorded from open forests and shrubland over much of the country, including Tasmania (Fig. 87). The few precise locality records from New Caledonia seem to indicate a preference for the south-western area (Fig. 87) where the climate is quite dry and the vegetation is relatively sparse. In New Zealand, it has been sporadically recorded from the Auckland region. Hirst (1909) reported this species (as *N. imperatrix*) from Cocos (Keeling) Is, Australia and Buitenzorg (now Bogor), Java. The latter record is very questionable but M. Kuntner (in litt.) has examined specimens of *N. edulis* from Java and Wetar I. suggesting that the species is more widely distributed in Indonesia.

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## Appendix 1. Index to species names

Valid names in italics, synonyms in Roman