



A molecular phylogeny of nephilid spiders: Evolutionary history of a model lineage

Matjaž Kuntner^{a,b,c,*}, Miquel A. Arnedo^d, Peter Trontelj^e, Tjaša Lokovšek^a, Ingi Agnarsson^{b,f}

^a Institute of Biology, Scientific Research Centre, Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia

^b Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

^c College of Life Sciences, Hubei University, Wuhan 430062, Hubei, China

^d Institut de Recerca de la Biodiversitat & Departament de Biologia Animal, Universitat de Barcelona, Spain

^e Department of Biology, Biotechnical Faculty, University of Ljubljana, Slovenia

^f Department of Biology, University of Vermont, Burlington, VT, USA

ARTICLE INFO

Article history:

Available online 27 June 2013

Keywords:

Sexual size dimorphism

Female gigantism

Coevolution

Biogeography

Sexual selection

Nephila

ABSTRACT

The pantropical orb web spider family Nephilidae is known for the most extreme sexual size dimorphism among terrestrial animals. Numerous studies have made Nephilidae, particularly *Nephila*, a model lineage in evolutionary research. However, a poorly understood phylogeny of this lineage, relying only on morphology, has prevented thorough evolutionary syntheses of nephilid biology. We here use three nuclear and five mitochondrial genes for 28 out of 40 nephilid species to provide a more robust nephilid phylogeny and infer clade ages in a fossil-calibrated Bayesian framework. We complement the molecular analyses with total evidence analysis including morphology. All analyses find strong support for nephilid monophyly and exclusivity and the monophyly of the genera *Herennia* and *Clitaetra*. The inferred phylogenetic structure within Nephilidae is novel and conflicts with morphological phylogeny and traditional taxonomy. *Nephilengys* species fall into two clades, one with Australasian species (true *Nephilengys*) as sister to *Herennia*, and another with Afrotropical species (*Nephilingis* Kuntner **new genus**) as sister to a clade containing *Clitaetra* plus most currently described *Nephila*. Surprisingly, *Nephila* is also diphyletic, with true *Nephila* containing *N. pilipes* + *N. constricta*, and the second clade with all other species sister to *Clitaetra*; this “*Nephila*” clade is further split into an Australasian clade that also contains the South American *N. sexpunctata* and the Eurasian *N. clavata*, and an African clade that also contains the Panamerican *N. clavipes*. An approximately unbiased test constraining the monophyly of *Nephilengys*, *Nephila*, and Nephilinae (*Nephila*, *Nephilengys*, *Herennia*), respectively, rejected *Nephilengys* monophyly, but not that of *Nephila* and Nephilinae. Further data are therefore necessary to robustly test these two new, but inconclusive findings, and also to further test the precise placement of Nephilidae within the Araneoidea. For divergence date estimation we set the minimum bound for the stems of Nephilidae at 40 Ma and of *Nephila* at 16 Ma to accommodate *Palaeonephila* from Baltic amber and Dominican *Nephila* species, respectively. We also calibrated and dated the phylogeny under three different interpretations of the enigmatic 165 Ma fossil *Nephila jurassica*, which we suspected based on morphology to be misplaced. We found that by treating *N. jurassica* as stem *Nephila* or nephilid the inferred clade ages were vastly older, and the mitochondrial substitution rates much slower than expected from other empirical spider data. This suggests that *N. jurassica* is not a *Nephila* nor a nephilid, but possibly a stem orbicularian. The estimated nephilid ancestral age (40–60 Ma) rejects a Gondwanan origin of the family as most of the southern continents were already split at that time. The origin of the family is equally likely to be African, Asian, or Australasian, with a global biogeographic history dominated by dispersal events. A reinterpretation of web architecture evolution suggests that a partially arboricolous, asymmetric orb web with a retreat, as exemplified by both groups of “*Nephilengys*”, is plesiomorphic in Nephilidae, that this architecture was modified into specialized arboricolous webs in *Herennia* and independently in *Clitaetra*, and that the web became aerial, gigantic, and golden independently in both “*Nephila*” groups. The new topology questions previously hypothesized gradual evolution of female size from small to large, and rather suggests a more mosaic evolutionary pattern with independent female size increases from medium to giant in both “*Nephila*” clades, and two reversals back to medium and small; combined with male size

* Corresponding author. Address: Scientific Research Centre, Slovenian Academy of Sciences and Arts, Novi trg 2, 1000 Ljubljana, Slovenia.

E-mail address: kuntner@gmail.com (M. Kuntner).

evolution, this pattern will help detect gross evolutionary events leading to extreme sexual size dimorphism, and its morphological and behavioral correlates.

© 2013 Elsevier Inc. All rights reserved.

1. Introduction

The golden orb weaver genus *Nephila* is one of the few groups of spiders that have a substantial appeal outside of the small specialist arachnological community. It is known for the most extreme cases of sexual size dimorphism among terrestrial animals (Fig. 1c)—females are on average 125 times, and up to 500 times, heavier than the small males (Kuntner et al., 2012b)—and this represents a unique case of evolutionary female gigantism because the females have increased in size whereas the males have not (Coddington et al., 1997; Hormiga et al., 2000; Kuntner and Coddington, 2009). Species of *Nephila* also produce gigantic aerial orb webs (Fig. 6a and c) sometimes reaching a meter and a half in diameter (Kuntner et al., 2010b), and these are characteristically composed of shiny golden silk (Craig et al., 1996) and are made of densely spun fibers capable of subduing even vertebrate prey (Sakai, 2007; Nyffeler and Knörnschild, 2013). The sheer size of these

webs attracts various kleptoparasitic spiders sometimes vastly outnumbering the host (Agnarsson, 2003, 2011; Higgins and Buskirk, 1998). *Nephila* is pantropical, and some species have ranges that are uncharacteristically extensive for invertebrates, e.g. *N. pilipes* (Fabricius, 1793) occupies mainland forests of south and southeast Asia and Australia, as well as islands as far east as Japan, the Solomons, and Vanuatu (Harvey et al., 2007; Su et al., 2007), while others are restricted to smaller parts of continents, e.g. *N. sexpunctata* Giebel, 1867 to a part of South America and *N. komaci* Kuntner and Coddington, 2009 to small pockets of southeast Africa (Kuntner and Coddington, 2009). These distributions raise interesting biogeographical and speciation hypotheses relating to the organisms' dispersal abilities (Agnarsson and Kuntner, 2012; Kuntner and Agnarsson, 2011a,b; Lee et al., 2004; Su et al., 2007, 2011), and may suggest that some species are habitat specialists at risk of extinction while others thrive in anthropogenically altered habitats.

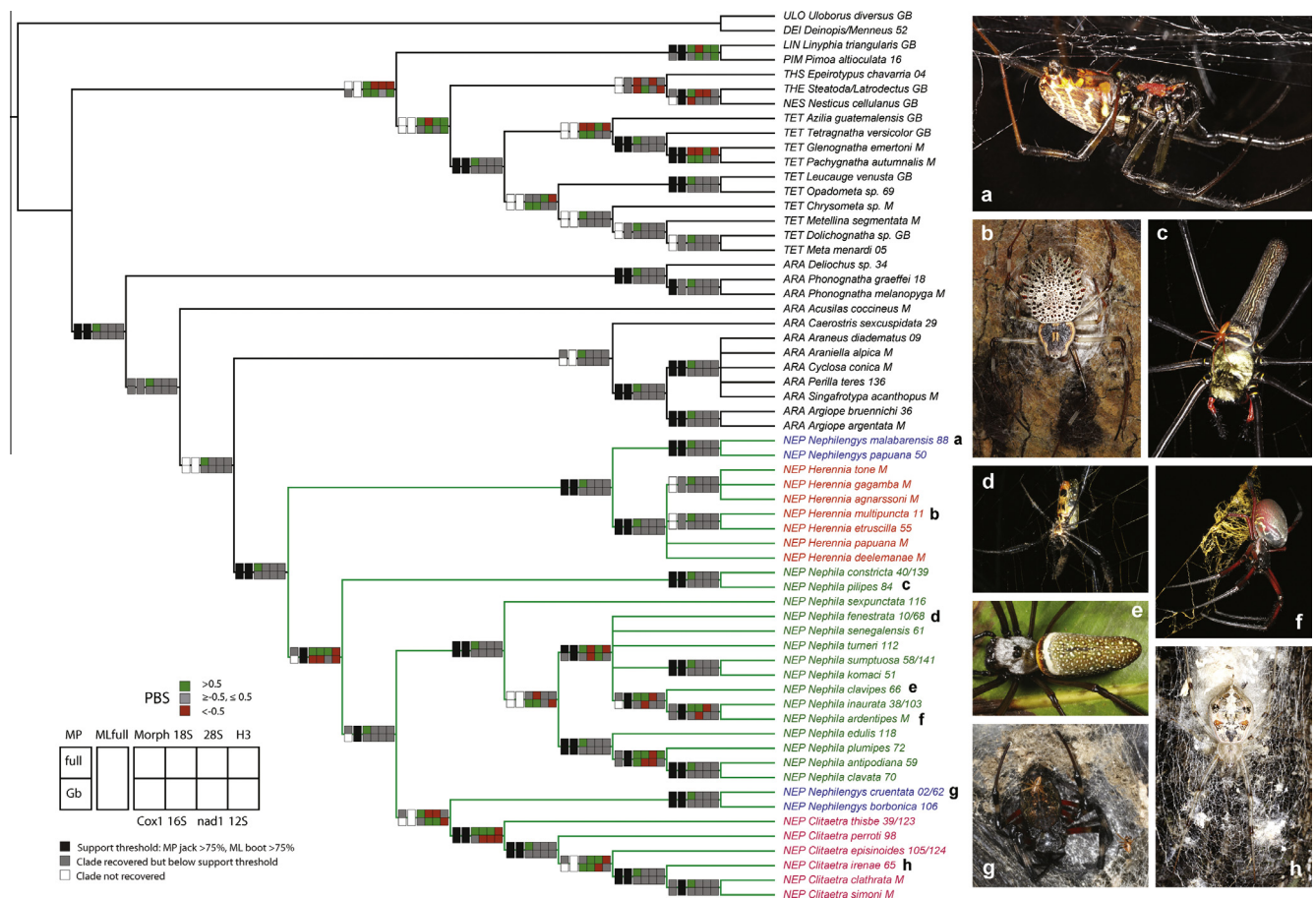


Fig. 1. A pictorial summary of nephilid phenotypic diversity (right, a–h), and a strict consensus of 36 trees resulting from parsimony analyses combining molecular markers (full matrix) with morphology (left). The three sets of squares on branches represent node supports from alternative analyses, as follows: the left set corresponds to the parsimony jackknife support for the full (above branch) and Gblocked (Gb, below) matrices, respectively. The middle bar shows maximum likelihood (ML) bootstrap support of the full matrix under the full codon partition scheme. The right set indicates the Bremer supports for the different partitions (PBS) on the reference tree: above branches, from left to right, values for morphology + behavior, followed by the Bremer support values for the nuclear genes and below branches for the mitochondrial genes. See legend for support thresholds. Terminals have the first three letters of current taxonomic familial placement (from bottom: NEP = Nephilidae, ARA = Araneidae, TET = Tetragnathidae, NES = Nesticidae, THE = Theridiidae, THS = Theridiosomatidae, PIM = Pimoidae, LIN = Linyphiidae, DEI = Deinopidae, ULO = Uloboridae). The ingroup, nephilid part of the tree is colored in green and the ingroup terminals are colored according to the accepted nomenclature prior to the classification changes in the current study. Terminals with original molecular data end with specimen codes (as in Table 1), those with data from GenBank end with GB, and those for which only morphological (and behavioral) data were used are labeled M.

Download English Version:

<https://daneshyari.com/en/article/5919723>

Download Persian Version:

<https://daneshyari.com/article/5919723>

[Daneshyari.com](https://daneshyari.com)